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Preface

The Dutch KEC (Kader Ecologie en Cumulatie; Framework for Assessing Ecological and Cumulative Effects (Rijkswaterstaat 2019)) used the Band model (Band 2012) to estimate the number of bird victims caused by collisions with offshore wind turbines. However, both the Band model and its stochastic variant (Marine Scotland 2018) are quite sensitive to various parameters, including flux (intensity of bird movements), flight height and the level of avoidance. The margin of uncertainty in the number of predicted victims is therefore very large. In addition, recent research in the UK has shown that a number of assumptions in the Band model regarding bird flight behaviour do not correspond to how birds actually behave.

An additional or alternative method is therefore needed that considers the actual flight behaviour of birds in response to wind turbines, reducing sensitivities and uncertainties relating to the predicted number of victims. Individual- or Agent-Based Models (IBMs) can be used for this purpose. IBMs are widely used as an instrument for predicting the consequences of changes in species' habitats. It is also possible to estimate the cumulative consequences of several changes in the habitat.

Rijkswaterstaat (RWS) has commissioned Bureau Waardenburg (BuWa) to develop an Individual-Based Model (IBM) for lesser black-backed gulls in the Netherlands and to determine the international desirability and feasibility of an IBM for three additional (priority) seabird species. The project is carried out by a team of researchers and statistical modellers from Bureau Waardenburg (BuWa: Rob van Bemmelen, Astrid Potiek, Abel Gyimesi), Wageningen Marine Research (WMR: Floor Soudijn, Daniel Benden, Tobias van Kooten, Niels Hintzen en Tony Wilkes) and Research Institute Nature and Forest (INBO: Nicolas Vanermen). From Rijkswaterstaat, Jos de Visser has coordinated the project together with Dagmar van Nieuwpoort (technical manager Wozep) and Maarten Platteeuw (bird ecology expert). We thank them for the fruitful cooperation. We also acknowledge the useful critical comments of Kate Searle from the UK Centre for Ecology & Hydrology. We are also grateful for Judy Shamoun-Baranes from the University of Amsterdam for providing feedback and organizing fruitful meetings with her department to discuss developments.

In this report, we present the methods of model development and various outputs produced by the model. Furthermore, this report also describes knowledge gaps for further research and a feasibility study on the three additional species that were identified by researchers, nature protection policy makers and other stakeholders as of priority interest during an international interview carried out in the course of the project. The original version of the report was published in December 2021. Later, an error in the model scripts was discovered and repaired at the end of 2022. This report is a revision of the original document, including the adjusted results based on the script modification.

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1 Introduction

In Environmental Impact Assessments and Appropriate Assessments seabird mortality due to wind turbines is currently calculated based on collision rate models, of which the SOSS Band model (Band 2012; hereafter 'Band model') is the most commonly applied model for offshore situations in the Netherlands. Although this is considered to be the best model currently available to estimate seabird collision casualty rates (Masden & Cook 2016), the model relies on static parameter inputs, despite Band (2012) stressing himself the importance of identifying uncertainties. Recently, Marine Scotland published a Stochastic Collision Risk Model (sCRM; Marine Scotland 2018), in which variation in input parameters results in an uncertainty range around the estimated number of victims.

Nevertheless, these collision rate models are relatively simple and work in a theoretical way. The models work with a static number of birds entering a wind farm, resulting in a static number of casualties. Even if a variance around fixed means is introduced, the problem remains that the model deals with bird fluxes as a large number of individuals entering the wind farm at one specific moment of which a certain number of birds die. In summary, the aggregation of model input in terms of time and conditions results in general collision rates and do not allow a detailed assessment of the effects of short-term and individual-level effects.

An alternative approach to model collision risks of seabirds is to develop individual-based models (IBMs). IBMs are models that simulate individuals as discrete and autonomous entities (Grimm *et al.* 2006; DeAngelis & Grimm 2014; Wood *et al.* 2015; Brown & Stillman 2021). IBMs have been used as a tool to estimate collision mortality for several bird species, such as the northern gannet (Warwick-Evans *et al.* 2018) and red kite (Eichhorn *et al.* 2012). These models can take individual differences in behaviour into account, which can change over space and time. Furthermore, they can deal with the typical energetics of individuals of a certain species and the additional energetic costs resulting from the presence of wind farms (Kaiser *et al.* 2002; Searle *et al.* 2019; Van Kooten *et al.* 2019). Hence, IBMs could potentially integrate collision risk and displacement effects into one model, while accounting for habituation to offshore wind farms and adaptive behaviour to rotating turbines in the future. Finally, IBMs may produce more realistic mortality rates with associated uncertainty intervals that can be fed into population models. In that way, IBMs could be a valuable step forward in the assessment of cumulative effects of offshore wind farm developments, among others, on birds, while the models could also be improved step by step as new information becomes available.

A disadvantage of IBMs is that they require a lot of specific data on the behaviour of individuals from the different bird species. Therefore, to start the development of IBMs a specific species in a specific geographical area was chosen. For such purposes, the lesser black-backed gull was the perfect starting point for the Netherlands, being the best locally studied seabird species in terms of life history parameters, offshore distribution and flight behaviour, following comprehensive colony and tracking studies.

The first priority of the current project was to develop a spatially explicit individual-based model that can be used at the species level, based on the lesser black-backed gull on the Dutch Continental Shelf as a case study. For these purposes, RWS acquired GPS tracking data from 2008 – 2015 of lesser black backed gulls breeding on Texel from the University of Amsterdam. To this, we have added data collected by the INBO in Belgian coastal colonies (funded for LifeWatch by the Hercules Foundation and maintained in collaboration with UvA-BiTS and the Flanders Marine Institute (VLIZ)) and own data collected in the Dutch Delta (financed by Rijkswaterstaat), and by that creating a dataset containing data from five different colonies instead of one, and four times more individuals than only relying on the Texel data.

The model aimed to estimate the number of individuals that enter a certain offshore wind farm each day of the year, and then the number of birds that collide with wind turbines once they are in the wind farm, based on wind farm specific collision risks. The modelling of the distribution of birds also included the effects of fishing activities being a presumed important food source for lesser black-backed gull. In addition, also stochasticity was introduced in the model based on GPS tagging data. This included e.g. variation in bird distribution based on initial flight directions from the colony and trip duration and distance, but also parameters in flight behaviour (e.g. flight speed and -height). The baseline model was produced for the examination of two future wind farm scenarios delivered by RWS. The sensitivity analysis was carried out by examining the effect of varying different parameters, while the validation of the model was partly based on comparing the model output on bird distribution with spatially explicit bird densities calculated according to the ESAS database.

Our report at hand first of all describes the model, the input data and their sources and the choices made during the model development. Subsequently we provide the results of the simulations of the various wind farm scenarios. In our report we also give an overview of the main knowledge gaps, which could be filled to reduce uncertainties in the outcome of future model developments.

Ultimately, IBMs could be developed for more bird species that are vulnerable to the impacts of offshore wind farms (OWFs). As mentioned above, IBMs are “data hungry”, and hence we will also investigate whether there are adequate data and knowledge available to develop IBMs that estimate collision mortality and/or displacement due to the presence of offshore wind farms for other species. The outcome of this is reported in a chapter on the feasibility for the development of an IBM for three seabird species in addition to the lesser black-backed gull. The selection of the three most relevant species for this feasibility study relied on an international questionnaire sent out to European scientists and stakeholders.

2 Statistical analysis of GPS tracking data

2.1 GPS tracking

Adult lesser-blacked gulls *Larus fuscus* were captured on the nest during the second half of the incubation period and fitted with GPS-loggers at five colonies along the Belgian and Dutch North Sea coasts: Oostende (BEL), Zeebrugge (BEL), Vlissingen (NL), Neeltje Jans (NL) and Texel (NL) (Figure 2-1). Tracking data from Texel have been collected by and are owned by Judy Shamoun-Baranes (UvA), Willem Bouten (UvA) and Kees Camphuysen (NIOZ). Data from Zeebrugge, Oostende and Vlissingen have been collected by and is owned by Eric Stienen and colleagues (INBO). Data from Neeltje Jans have been collected by BuWa and INBO and are owned by Rijkswaterstaat (RWS).

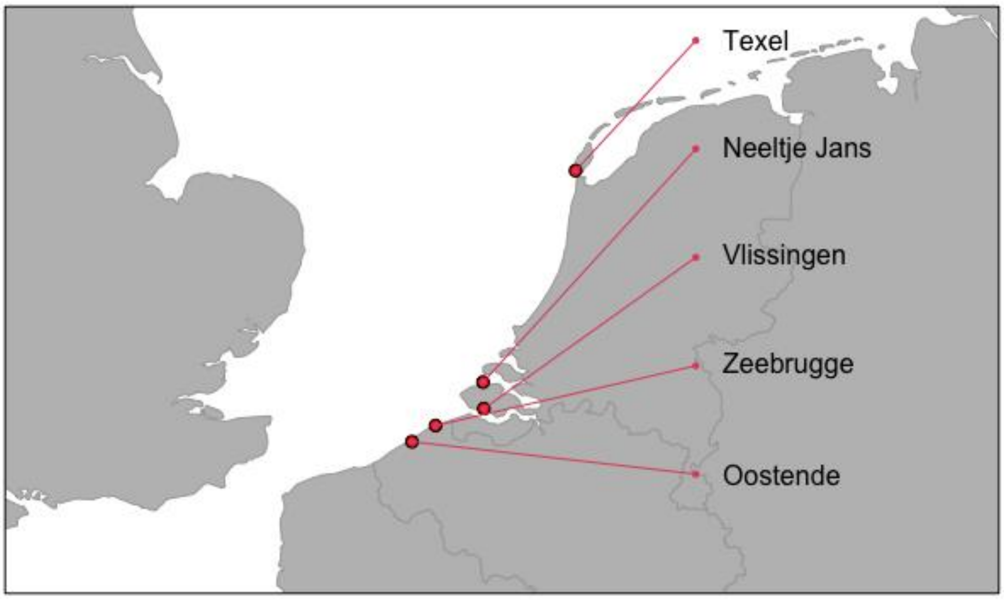

Figure 2-1 Distribution of colonies with GPS-tracking data of lesser black-backed gulls.

Tracking data sets were combined and contained the following variables: colony, bird ID, date/time, longitude, latitude, altitude and 2d speed. For the data from Zeebrugge, Vlissingen and Oostende, relocations that were manually labelled as outliers, based on visual inspection of the tracks, were excluded. In addition, individuals with 3 or fewer positions were excluded.

Loggers were set to collect positions at fixed time intervals, and these settings varied between logger types, projects and seasons depending on the specific goals of each project. Irregularities in time intervals between GPS fixes may arise when the logger is not able to take a position (which can happen for various reasons). Resulting time intervals between fixes were mostly 5 minutes during May-July, and 20 minutes in other months. The Hidden Markov Models (HMMs) that were used to classify behavioural states from the tracking data (see below), require positions taken at equal time intervals. Therefore, the raw tracking data needed to be resampled at a rate that ensured sufficient detail to infer behavioural states, while retaining most of the data and ensuring that analyses of different sets of the data permit direct comparison. Therefore, the original data were resampled at time intervals of 20 minutes.

For each position in the resulting dataset, the following covariates were derived: whether the position was on land or at sea, distance from the colony, distance to the coast, the time since colony departure, wind direction and wind force (derived from the RNCEP project; Kemp *et al.* 2012), proximity to the nearest active fishing vessel (see below for details), distance to the nearest offshore wind farm. Distance of each bird GPS observation to the nearest bottom trawling fishing vessel (beam trawl, otter trawl, dredge, flyshoot and shrimp trawl) was calculated making use of VMS data of Dutch and Belgian vessels. VMS pings were processed as described in Hintzen (2012) and checked for erroneous entries. Fishing activity was defined based on the method described by Poos (2013) who developed a statistical model based on vessel speed to filter out non-fishing behaviour. Nearest distance calculation was limited to active fishing behaviour. To match the temporal resolution of bird observations (every 20min) with the fishing vessel movements (every 2h), trawl tracks were reconstructed for the VMS data through an interpolation routine (Hintzen 2010) that generated an intermediate GPS location and time-stamp equally spaced 5 minutes apart. Finally, for each bird observation, the GPS position that was closest to any fishing vessel GPS location within 60 km, in a time-window of 10 minutes prior to 2 minutes after the bird observation, was selected as the distance indicator.

Foraging trips were defined as tracks that started and ended at a colony; not necessarily the colony of origin (considering the data also included non- or failed breeders that may have visited other colonies). This was done for both breeding and non-breeding data; resulting in occasionally very long trips for non-breeders. Data were split into separate trips whenever a time step to the next relocation was more than 35 minutes.

The start and end of a breeding attempt, during which birds are central-place foragers, was inferred from the time between colony visits. We assumed the breeding period is the longest period whenever a bird never ventured away from the colony for more than 48 hr. The remaining data, except the first and last 24h, were used for the non-breeder analyses. The non-breeder data thus reflected individuals that were not behaving as central place foragers. Exclusion of the first and last 24h aimed to exclude migratory periods.

Tracking data were analysed to provide parameter estimates for the Individual Based Model (IBM). Whereas the HMM provides parameters on the movement (speed, turning angles) and behavioural states, it does not provide all information required in the IBM to simulate realistic tracks. Therefore, in separate analyses of the tracking data, we estimated the probability for mostly terrestrial or marine trips, the initial departure direction from the colony, the time spent in the colony between trips and the flight altitude close to OWFs.

In our data, behaviour may vary at two main levels: individuals and colonies. Individual LBBGs may differ in behaviour as a function of intrinsic factors such as food specialization or experience (Camphuysen 2013). Individuals may also differ as a function of the colony where they breed in or originate from. For example, the distribution of breeding birds will be determined by the proximity and quality of foraging areas, as well as the proximity and foraging distributions of adjacent colonies. Whereas movement parameters (step size, turning angles) are likely similar between individuals during specific behaviours (e.g., transit, foraging), their spatial and temporal behaviour may differ. Therefore, we used the same HMM results for step size and turning angle across all individuals, but (attempted to) estimate transition probabilities and parameters not obtained from the HMM separately for individuals and colonies.

2.2 Hidden Markov Models for behavioural states

Hidden Markov Models (HMMs) model the time series of observations that are driven by underlying, ‘hidden’, serially correlated states. HMMs, as implemented in the package ‘momentuHMM’ (McClintock & Michelot 2018), were used here to characterize behavioural states from the regularized tracking data of lesser black-backed gulls. Step size (distance between subsequent positions, in km), turning angles (the difference in bearing to the previous and next position, in radians) were used as input variables.

The output of HMMs consists of two parts: 1) distribution parameters of step size and turning angle per behavioural state and 2) transition probabilities between the behavioural states. HMMs can include covariates on both parts, thus: 1) covariates can affect the distribution of step size and turning angle or 2) the transition probabilities. Here, covariates were added stepwise (see below for details) and resulting model fit is evaluated using the Akaike Information Criterion (AIC).

In HMMs, the number of potential states needs to be provided a priori. While a large number of potential states may seem to be biologically more realistic, adding states will increase the overlap between states, and reduce the interpretability of the output. Basic behavioural states characteristics for foraging trips of seabirds, are:

- Stationary: very small step lengths, no directionality
- Transit flights: large step lengths, strong directionality
- Foraging: short step lengths, weak directionality

A simple 3-state HMM was fitted to obtain starting values for more complex models.

Typical seabird trips consist of a sequence of states, starting with an outbound transit state, a part in which it is foraging, stationary and/or makes longer flights to other foraging areas, and finally an inbound transit flight to the colony. We largely followed the example of Michelot *et al.* (2017) to obtain step size, turning angle distributions and transition probabilities of such a stereotyped sequence of states. This approach should also result in realistic trajectories in the simulations of the IBM. As the example of Michelot *et al.* (2017) deals with single trips for each individual (whereas we have multiple trips per individual), and as lesser black-backed gulls may transit between two or more foraging areas within a single trip, we extended the number of states with the following three states:

- In colony: movements within 2 km from the colony centre, with very small step lengths and no directionality.
- Outbound transit flight: movements away from the colony, with large step lengths and strong directionality.
- Inbound transit flight: movement towards the colony, with large step lengths and strong directionality.

This resulted in a 6-state HMM.

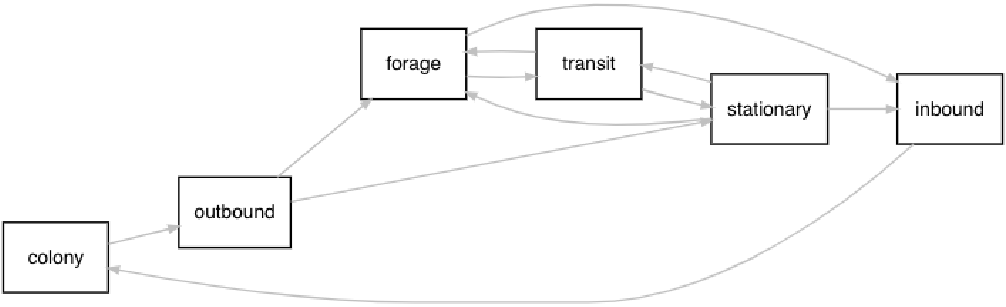

Figure 2-2 Diagram showing the possible transitions between behavioural states.

Part of the transition probabilities between states were fixed at zero, effectively making these transitions impossible, so that the remaining transitions are as shown in Figure 2-2. In addition, we added the following covariates affecting certain transition probabilities at the start and end of outbound and inbound states:

- Distance from the colony. Affecting only the transition from outbound flights to foraging or stationary states.
- Time since colony departure. Affecting only the transitions to inbound flights.
- In range. When the bird is in (or near) the colony. Affecting only the transition from inbound to the in-colony state and from the 'in colony' state to the outbound state.

With this 6-state model as a basis with the above three covariates acting on the transition probabilities of the inbound and outbound states, we added four more covariates acting on the transition probabilities:

- On land. Whether positions were on land or at sea.
- Distance to the coast
- Proximity to OWFs. Binary variable indicating whether birds were within 3 km of the perimeter of an OWF. The 3 km threshold was chosen, as this is the distance at which potentially macro-avoidance is expected (Skov *et al.* 2018).
- Proximity to an active fishing vessel. Binary variable indicating whether birds were within 6 km of an actively fishing vessel. The 6 km threshold was selected based on exploratory analysis indicating a sudden increase at 6 km distance from an active fishing vessel in foraging versus transit flights.

As we were only interested in movements at sea, we used only 'marine' trips (see below under 'Probability for terrestrial or marine trips') in the HMMs. Fitting these HMMs on the entire dataset took many hours or even more than a day. Therefore, we reduced the sample size on a subset of the data, selecting 30 trips at random from each individual.

2.3 Probability of terrestrial versus marine trips

For each trip, the proportion of positions on land and at sea was calculated. The proportion of terrestrial positions in trips showed a strong bimodal distribution, with many trips either having <5% positions on land or <5% at sea. Trips with >60% positions on land were classified as ‘terrestrial’ trips. This threshold was selected to balance the discarded number of positions at sea and the retained number of positions on land. Although lesser black-backed gulls are known to show high individuality in site preference, all individuals showed a mix between terrestrial and marine trips, with some variation between colonies. We modelled the proportion of terrestrial trips in a Generalized Linear Mixed Model (GLMM) as a function of colony, with random intercepts for individuals.

2.4 Initial departure direction from the colony

If the direction of departure from the colony would be selected at random, birds would disperse in all directions around the colony. This is not realistic, as lesser black-backed gulls show clear preference for certain directions and foraging areas, with marked differences between colonies. Therefore, the initial departure direction was obtained for each marine trip, using the colony centre as the point of departure, and the mean direction to the first three positions after departure as the direction. All colonies except Vlissingen showed a unimodal distribution of initial departure direction. Lesser black-backed gulls from Vlissingen departed either in a southern or western direction. Trips in southern direction typically headed inland but were still often classified as ‘marine trips’ because they lingered in the Westerschelde. They also regularly first flew southwards, and then changed direction westwards to the North Sea. The setup of our model is not able to capture such behaviour, given that outbound flights were strongly directional and therefore highly dependent on the initial departure direction. Therefore, to ‘force’ marine trips from Vlissingen to go to the North Sea we filtered trips from Vlissingen that had departure directions above 200°. Subsequently, we estimated the mean and concentration parameters of Von Mises distributions, describing the initial departure direction per individual (with at least 10 trips) and per colony. A Von Mises distribution has two parameters that together describe the unimodal distribution of circular data. The mean represents the mean angle; the concentration describes how strong the values are concentrated around the mean. A concentration parameter of 0 indicates a uniform distribution around the circle.

To estimate the initial departure direction from the colony for colonies without tracking data, we correlated a rough measure of the orientation of the coastline to the mean initial departure direction and used the resulting relation to predict this initial departure direction.

2.5 Time spent in the colony between trips and duration of terrestrial trips

The duration of intervals between foraging trips was calculated. Shape and rate parameters of the gamma distribution were estimated for the time in the colony between trips for each individual (with at least 10 trips) and colony.

Similarly, the duration of terrestrial foraging trips was first calculated from the tracking data as the time between departure from the colony and arrival at the colony. Subsequently, shape and rate parameters of gamma distributions were estimated per individual (with at least 10 trips) and per colony.

2.6 Flight altitude near offshore wind farms

Ideally, altitude would have been a third input variable in the HMMs, given its clear relevance to the study of bird collisions with wind turbines. Although altitude was available for most of the tracking data, altitude data were missing for a substantial proportion of the data, which is not allowed in HMMs. Altitude data also included many unlikely values: (large) negative or extremely large positive values. Therefore, altitude could not be included as an input variable in the HMMs. To include altitude in the IBM, altitude parameters were estimated from the data, for positions within 3 km of OWFs. As altitude data contained a lower proportion of negative or extremely high values when sampled at shorter time intervals and at higher speeds, altitude data were selected with time intervals of <60 s and when the instantaneous speed was >5 km h^{-1} to calculate the mean and standard deviation.

3 IBM structure

Here, we give a description of the IBM following the overview, design and details (ODD) protocol (Grimm *et al.* 2006; Grimm *et al.* 2010). The IBM is based on the analysis of GPS tracking data, providing the number and definition of behavioural states, as well as the dependence of the movement on the environment. The tracking data analysis also defines the environmental variables that are included in the maps underlying the IBM. For a definition of non-breeding and breeding individuals based on the tracking data, see section 2.1.

3.1 Purpose

The IBM is developed to quantify the mortality of lesser black-backed gulls from collisions with offshore wind farms on the Dutch Continental Shelf (DCS).

3.2 Entities, state variables and scales

The IBM consists of the entities: agents (individual lesser black-backed gulls), fishing vessels, colonies, Offshore Wind Farms (OWFs) and the environment. For each agent, the state variables *position* and *behavioural type* are defined at each time step (Table 3.1). Agents also possess state variables that define their bearing, step size, altitude, and being alive or not (Table 3.1). The initial bearing for each marine trip during the outbound state is also a state variable. Time since the start of the simulation is a dynamic state variable of each agent. Other time dependent state variables include the time of departure from the colony (when on a marine trip), or the maximum duration of a trip (when on a terrestrial trip); as well as the time since arrival at the colony and the maximum time in the colony (when in the colony). Agents also possess constant state variables that describe their home colony, life stage, body length and avoidance probabilities (Table 3.2).

OWFs, colonies and fishing vessels are non-moving entities that are present on the map. The fishing vessel presence is a partly stochastic process in time that relies on underlying maps with probabilities of active fishing presence. Fishing vessel presence thus changes through time to mimic vessel movement. The locations of colonies and OWFs are predefined at the start of the simulation based on external data. OWF characteristics may vary in the constant state variables: rotor radius, rotor height, turbine density, activity percentage, angular velocity, number of blades per rotor, blade width, pitch angle of the blades, local mean water depth (Table 3.3).

The environment is defined by grid cells and the maps underlying the environmental values may differ in their grid resolution (Table 3.4). The state variables of each grid cell are *location*, *environment type*, and *environmental values* (Table 3.3). The model has time steps of 20 minutes (following the HMM) and is run for a period of 6479 time steps (covering a period of 90 days – the length of the breeding period of lesser black-backed gulls). To allow comparisons, the same time steps and total period were used for non-breeders.

Table 3-1 The dynamic state variables of the agents.

State	*Description/value*	*Process*
Position	Set of real numbers indicating the position on the grid in latitude and longitude	Emerges from behaviour
Alive	True or false	Emerges from behaviour
Behavioural type	Marine trip (outbound flight, foraging, inbound flight, transit flight, stationary), in colony, terrestrial trip	Stochastic, chosen based on environment-dependent transition probabilities at each time step in a marine trip. In colony follows always after inbound flight. After colony waiting time has ended, binomial distribution for probability of a land or marine trip.
Bearing	Direction that indicates their bearing	Stochastic, generated from a behavioural type, dependent on Von Mises distribution at each time step in a marine trip.
Step size	Step size in current time step	Stochastic, drawn from a behavioural state-dependent gamma distribution at each time step in a marine trip.
Altitude	Altitude in current time step	Stochastic, drawn from a general normal distribution for each marine trip. Only calculated when within 3km from an OWF.
Initial direction	Direction that indicates bearing during first step of outbound state	Stochastic, drawn from a colony/individual-level Von Mises distribution.
Time	Time since start of simulation	
Time of departure	Time of departure from the colony for the current land or marine trip	Emerges from behaviour
Time of arrival	Time of arrival at the colony when resting in the colony	Emerges from behaviour
Duration of colony time		Stochastic, drawn from a colony/individual level gamma distribution at start of the colony state
Duration of terrestrial trip		Stochastic, drawn from a colony/individual level gamma distribution at start of the terrestrial trip

Table 3-2 The constant state variables of the agents.

Variable	*Value(s)*	*Symbol*	*units*	*Description*	Source
Colony				Position of the individuals' home colony.	
Life stage	Breeding or non-breeding			Life stage that determines the set of values for the movement parameters	
Body length	0.58	L	m		http://www.oiseaux-birds.com/card-lesser-black-backed-gull.html
Bird flapping constant	1	F			
Macro avoidance probability	0.64				(Skov *et al.* 2018)
Meso avoidance probability (P_{meso})	0.89				(Skov *et al.* 2018)
Micro avoidance probability (P_{micro})	0.96				(Skov *et al.* 2018)

Table 3-3 The state variables of the grid cells in the environment.

State	*Description/values*
Position	Set of real values indicating the position on the map as latitude and longitude, in WGS84 format.
Environment type	Sea, land, colony, OWF
OWF characteristics	Rotor radius, rotor height, turbine density, activity percentage, angular velocity, number of blades per rotor, blade width, pitch angle of the blades, local mean water depth.
Environmental variables	Water depth, probability of active fishing vessel, distance to colony, colony angle, distance to OWF, distance to coast.
Fishing vessel presence	Fishing vessel presence is stochastic, a new map is generated each 4 hours based on the probabilities of an active fishing vessel

3.3 Process overview and scheduling

3.3.1 Agents

When agents are in the colony, they are waiting for an allotted period. From the colony they can either go on a terrestrial trip or a marine trip. Terrestrial trips are not modelled explicitly but result in an allotted waiting time of the agents. When on a marine trip, agents move around on the map with different types of behaviour. At each time step, a step size, a turning angle and a behavioural state transition probability were drawn. Movement is thus stochastic, driven by the effects of the environment on the behavioural state transition probabilities. The parameter set and the movement patterns depend on the life stage of the agents. Whenever birds encounter an OWF, there is a possibility for avoidance of or collision with the wind turbines.

Time is modelled as a discrete process. All changes in the state variables are stored asynchronously. Each agent has the possibility to collect and store state variables at the end of each time step.

There are no interactions between agents in the model. At each time step, the state of an agent is updated by calculating a new position. For output purposes we collect the state of a part of or all agents at each time step. This process is described below in pseudocode:

```
for each agent
    if agent is alive
      if agent is on a marine trip
          calculate agent new position
          if agent is at edge of map
             switch to inbound state
          if agent  away from colony for > 48 hours
             switch to inbound state
        if   inside windfarm
          if macro-avoidance
             pass
          else
             if a collision[1]
                agent alive state set to false
      collect agent state
```

---

[1] Meso and micro avoidance are incorporated into the collision probability calculation.

3.3.2 Fishing vessels

Each 4 hours (12 time steps), fishing vessels are generated in each water grid cell.

3.4 Design concepts

3.4.1 Basic principles

The IBM describes the behaviour of the lesser black-backed gulls on the DCS and the adjacent land areas. The rules of movement are largely based on the analysis of GPS-track data analysis (chapter 2), largely following the approach described by Michelot *et al.* (2017). The movement behaviour of lesser black-backed gulls is analysed using Hidden Markov Models (HMMs), providing distributions of step sizes and turning angles for different behavioural states (outbound, foraging, transit, stationary, inbound), which are subsequently used to simulate step sizes and turning angles of the birds during marine trips in the IBM. In addition, the HMM predicts transition probabilities between different behavioural states and the effect of environmental variables on these transitions. In the IBM, maps with different environmental variables are incorporated and the transition probabilities simulated in the model depend on the values in these environmental maps. Some components of the movement, such as the initial departure directions, the waiting times in the colony, the flight altitudes and the duration and proportion of terrestrial trips were derived from separate tracking data analyses, as explained in chapter 2. The set of parameters used depends on the life stage of the agents, the GPS track analyses were performed for both breeders and non-breeders.

Whenever birds encounter an OWF, there is a possibility for avoidance of the wind turbines. The avoidance occurs at multiple levels. The details of the collision model are described in section 3.7.3. When the turbines are not avoided, there is a probability of collision of the bird with the turbines. The collision probability is calculated based on an adapted version of the Band model (Band 2012).

3.4.2 Emergence

The movement behaviour on a large scale is an emergent property of the model. The collision mortality also emerges from the model dynamics. In addition, the positions of birds on the map, the time of arrival at the colony and the time of departure on a sea or terrestrial trip all emerge from the model dynamics.

3.4.3 Sensing

Agents know the exact location of their home colony. In addition, agents know the values of the environmental variables that affect their transition probabilities (distance to coast, distance to colony, presence of a fishing vessel, distance to OWF, water depth, being on land and being in the colony).

3.4.4 Stochasticity

The chosen step sizes, initial directions during the first step of the outbound flight and changes in the bearing during trips at sea are all determined based on probability distributions and thereby partly stochastic. The same goes for the transitions between different behavioural states. In addition, the duration of a terrestrial trip, altitude when on a marine trip and the resting time in the colony, the avoidance and collision mortality and the presence of fishing vessels at the map are all partly stochastic.

3.4.5 Collectives

Agents are classified based on a life stage, which in turn, determines the set of parameters that are used for the movements of the agents. Each agent belongs to a specific home colony, which affects some of the parameters, such as the initial bearing during an outbound flight, the probability of a terrestrial trip, duration of terrestrial trips and the time spent in the colony between trips. Of these parameters, the initial bearing during an outbound flight and the time spent at the colony between trips can either be appointed based on individual level observations or colony level observations. For the simulations for which these were appointed based on individual level observations, each agent belongs to a colony as well as an ‘individual’ group.

3.4.6 Observation

For testing, the state variables of each agent are collected at each time step during the simulation and processed after the simulation.

3.5 Initialization

Each simulation shown in the results section was initialized with 250 agents. All agents were initialized with a starting position in their colony, a time duration of the colony stay, a life stage and with the status of being alive. The initial behavioural state is ‘in colony’ and the time duration of the first colony stay is drawn from the relevant gamma distribution at initialization (see section 3.7.1.5). All other dynamic state variables of the agents are set to “NULL”.

3.5.1 Model performance

For the performance test we initialized 300 simulations per colony with 250 breeding agents. The estimates slowly stabilize with more iterations. The patterns look similar for different numbers of birds (results not shown). The performance tests were run for the colonies Texel, Neeltje Jans, Oostende, Vlissingen and Zeebrugge. The change in the mean and SE of the percentage mortality differs between the colonies (Figure 3-1, Figure 3-2, Figure 3-3, Figure 3-4 and Figure 3-5). For each of the colonies, 300 simulations in combination with 250 birds, give a satisfactory SE as well as a manageable running time of the simulations. For the BA (Bhattacharyya’s Affinity) results, 50 simulations were run with 250 birds, these results require no precision of the mortality estimate and give a good representation of the spatial distributions of the agents (Figure 5-16). For the sensitivity analysis, 201 iterations with 250 birds were performed per parameter set. The number of parameter combinations was so extensive that the total running time prevented us from using more iterations per parameter set.

3.5.2 Sensitivity analysis

We tested the sensitivity of the model outcomes to changes in the model parameters for the breeder parameter set for a single colony (Texel). A sensitivity simulation was run for 1200 time steps to keep the running time manageable. Each of the sensitivity simulations was initialized with 250 birds, with slightly different parameter values (section 3.7.6). Per set of parameter values, 201 iterations were performed.

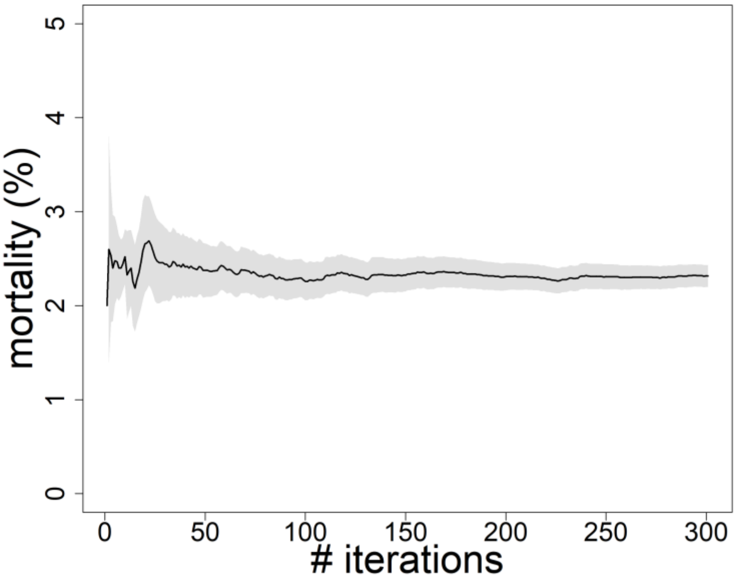

Figure 3-1 Performance test for Texel based on breeder, colony level parameter values and 2030 OWF scenario. Simulation with 250 birds. Mean percentage mortality (black line) +/- the SE (grey area) for each iteration including the previous iterations.

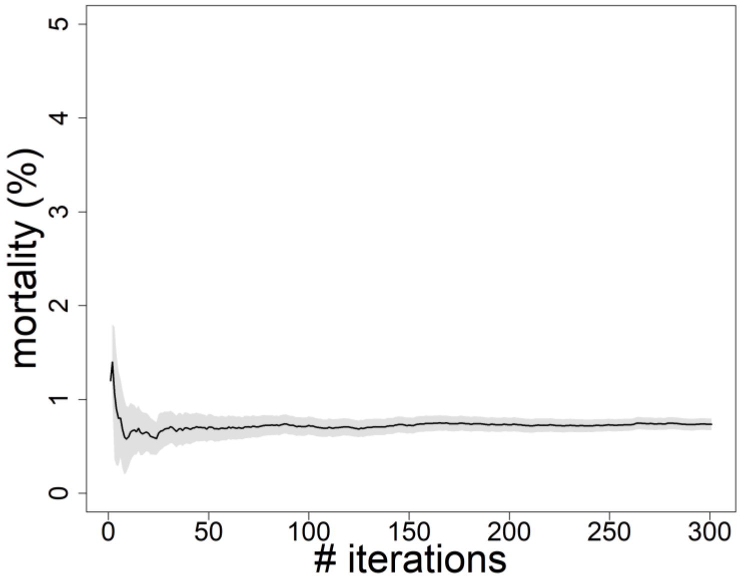

Figure 3-2 Performance tests for Neeltje Jans, based on breeder, colony level parameter values and 2030 OWF scenario. Simulation with 250 birds. Mean percentage mortality (black line) +/- the SE (grey area) for each iteration including the previous iterations.

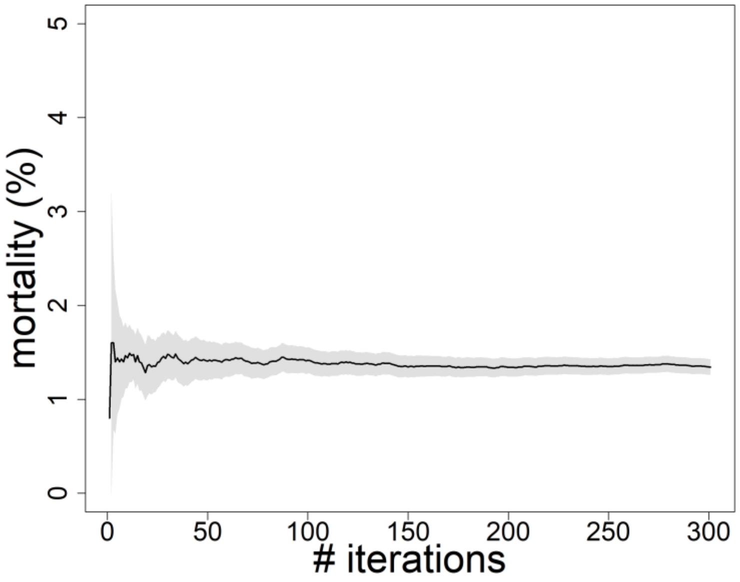

Figure 3-3 Performance tests Zeebrugge, based on breeder, colony level parameter values and 2030 OWF scenario. Simulation with 250 birds. Mean percentage mortality (black line) +/- the SE (grey area) for each iteration including the previous iterations.

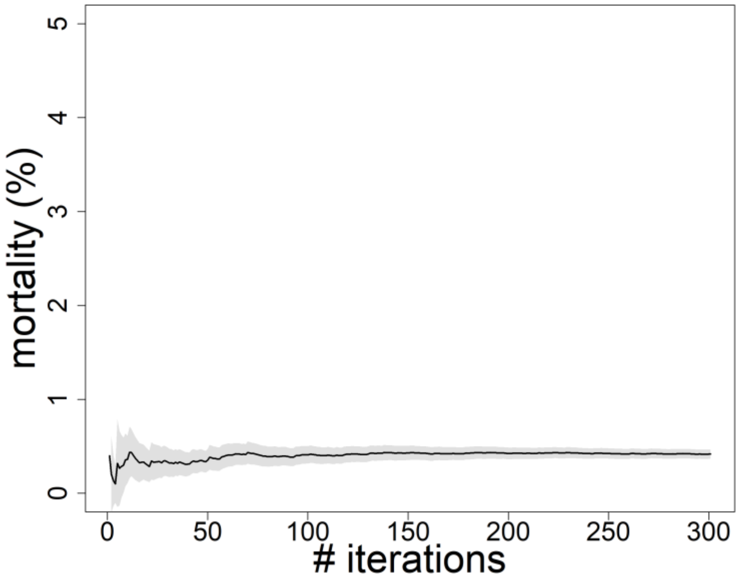

Figure 3-4 Performance tests Vlissingen, based on breeder, colony level parameter values and 2030 OWF scenario. Simulation with 250 birds. Mean percentage mortality (black line) +/- the SE (grey area) for each iteration including the previous iterations.

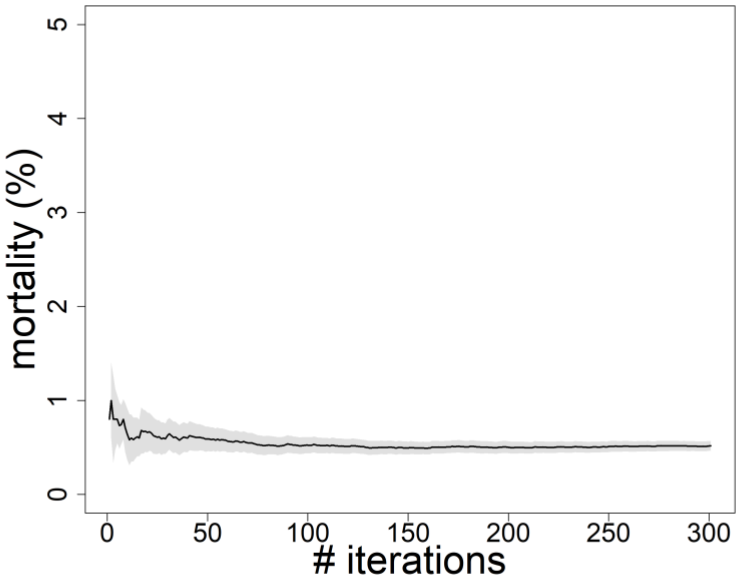

Figure 3-5 Performance tests Oostende, based on breeder, colony level parameter values and 2030 OWF scenario. Simulation with 250 birds. Mean percentage mortality (black line) +/- the SE (grey area) for each iteration including the previous iterations.

3.6 Input data

The environmental grid includes the colony locations and maps for water/land, OWFs, water depth, distance to coast, distance to colony, distance to the nearest OWF and the probability of fishing vessel presence. These maps are all read from external csv files. A complete list of the data maps used, and the resolution of these maps can be found in Table 3.4. The study area was limited to 1-8 degrees longitude and 51-56 degrees latitude. The study area was chosen such that the trips with the maximum distance to the colony found in the GPS data fitted into the study area.

A 2030 and 2040 scenario were used for the OWF map. These maps include current and future wind farms. For each OWF, a list of characteristics, which are informing the collision risk calculations (section 3.7.4), was used based on the information provided by Rijkswaterstaat. Both scenarios are hypothetical and still under discussion within the Dutch government. They were chosen as a realistic possibility for future OWF sizes and locations. For the chord widths of the turbines, or the widths of the turbine blades, a different set of values was used of previously measured coupled values for the distance of a point to the rotor centre r and chord width c, $[r_i, c_i]$.

Table 3-4 Complete list of input data.

Description	Contents	Filename	resolution
Colony information	Colony names and locations	colonies.csv	Per colony
Environmental variables	Longitude, latitude, On land, distance to coast, depth	ibm_grid.csv	0.01 x 0.01 grid
OWF scenario 2030	Longitude, latitude, is OWF, distance to OWF	owf_map_2030.csv	0.01 x 0.01 grid
OWF scenario 2040	Longitude, latitude, is OWF, distance to OWF	owf_map_2040.csv	0.01 x 0.01 grid
OWF characteristics	Name, country, power, estimated turbine number, surface, water depth, activity percentage, upwind probability	owf.csv	per OWF
Turbine characteristics	Power, number of blades, rpm, rotor diameter, rotor height, blade width, pitch	turbines.csv	Per turbine type
Rotor blade chord width values	Distances of a point to the rotor centre r and chord widths c, $[r_i, c_i]$.	rotorblade.csv	
Fishing vessel presence probability per month for 2015 and 2018	Longitude, latitude, probability vessel presence	Vessel_max_2015.5.csv Vessel_max_2015.6.csv Vessel_max_2015.7.csv Vessel_max_2018.5.csv Vessel_max_2018.6.csv Vessel_max_2018.7.csv	0.05 x 0.05 grid

3.6.1 Colonies

Simulations were run for all colonies for which GPS-track data were available. In addition, simulations were run for the largest lesser black backed gull colonies in the Netherlands. Results in the main section are shown for Ameland, Maasvlakte, IJmuiden, Rottumeroog, Rottumerplaat and Schiermonnikoog. Parameters for these colonies were based on the main HMM analysis, and for the colony specific parameters, Texel parameters were used for the Wadden Sea colonies, while for IJmuiden and the Maasvlakte parameters from Zeebrugge were used. A location specific adjustment was made to the mean departure direction (see section 2.4).

3.6.2 Probability fishing vessel presence

The probabilities of fishing vessel presence were based on data regarding spatio-temporal fishing vessel activity. The study period was limited to the months of May, June and July from 2009 to 2018. Analyses were performed on a grid with cell sizes of 0.05 in both longitudinal and latitudinal directions as fisheries data were only available at this resolution.

Fisheries data were obtained from two sources: an international dataset covering effort (in fishing hours) of all bottom trawl fisheries in the North Sea as collated by ICES, aggregated at a monthly basis, identifying 13 different fleet segments, ‘benthis metiers’ as described by Eigaard *et al.* (2016). The second set contained Dutch VMS and logbook data in an unaggregated form and was analysed to derive the indicators listed below.

The effort measurements as available in the ICES dataset were converted to an estimate of total numbers of fishing vessels per grid cell per month (of any countries’ origin). To achieve this, two indicators were prepared: 1. the number of unique vessels in a grid cell and 2. the consecutive fishing time per single vessel in one trip in a grid cell. Informed predictions were made for both indicators with a statistical model based on the variables: season, and distance to coast, and surface area per grid cell. The distance to the nearest coastline was calculated for each mid-point of the grid cells using GIS software. The water surface for each grid cell was calculated by subtracting the surface area of land, as available in high-resolution maps of Northern Europe, from the total surface area of the grid cell.

3.6.2.1 Predicting the number of Unique Vessels

For each benthis metier (see also Eigaard *et al.* 2016), the relationship between fishing hours and active vessels was modelled as:

$$N_{\text{vessels}} = a \times t^b + \exp(X\beta) + \epsilon,$$

where t and N_{vessels} refer respectively to fishing hours and number of unique vessels per grid cell. The model matrix X contains information on grid cell location, distance to coast, season, and grid cell surface area. β refers to the vector of coefficients corresponding to the columns of the model matrix X. The model was fitted using non-linear least-squares (and thus assumes $\epsilon \sim \text{Norm}(0, \sigma_\epsilon)$).

For some benthis metiers, not enough observations were available or model fitting did not result in appropriate fits. Therefore, generic models for gear groups otter-trawl (OT), beam-trawl (TB), dredge (DR) and flyshoot (SC) were fitted. Another generic model was created based on the entire dataset to allow predictions of numbers of vessels when the fleet segment was unknown. This model only had fishing hours as the sole covariate, i.e.: $N_{\text{vessels}} = a \times t^b + \epsilon$

Model diagnostics were examined and considered appropriate. The models were applied to cover fishing hours as available in the ICES dataset to predicted number of unique vessels per grid cell.

3.6.2.2 Calculating and imputing the consecutive fishing hours per trip

A relationship was established between total fishing hours in a grid cell and the consecutive number of hours a boat from a certain benthis metiers is, on average, expected to spend during a single trip in one grid cell for a certain month. The Dutch VMS and logbook data were used for this purpose. Fishing hours were summed by fleet segment, trip ID, vessel ID, grid cell, year and month. Hereafter, the dataset was averaged dropping trip ID, vessel ID and year to retrieve an indicator of fishing hours per benthis metiers, grid cell and month. The consecutive fishing hours were then matched to the ICES data when a match was not available. For the fleet segments present in the ICES data but not in the Dutch data, fishing hours per trip were imputed. The mean fishing hours per trip for all combinations of month and grid cell were calculated, ignoring fleet segment. These mean values were then distributed over the area, using the observed total fishing hours as a scalar for the spatial distribution of the fishing hours per trip.

This relationship allowed estimation of the number of vessels, simultaneously fishing in a grid cell.

3.6.2.3 *Maximum and minimum probability of fishing vessel activity*

Based on the assumption of minimum overlap between vessels in their presence in a c-square, the maximum probabilities of fishing vessel activity can be calculated. The hours per month that fishing may occur f_m are equal to 0 hours for weekend days, 12 hours for each Friday, plus 24 hours for the other weekdays. The total hours of fishing activity f_h were calculated by summing across benthis metiers per c-square. The probability of the presence of an active fishing vessel in a c-square P_f is then formulated as:

$$P_f = \begin{cases} \dfrac{f_h}{f_m}, & if\ \dfrac{f_h}{f_m} < 1 \\ 1, & if\ \dfrac{f_h}{f_m} \geq 1 \end{cases}.$$

3.7 Submodels

3.7.1 Movement

Each agent starts in the colony. The time duration of a colony stay is set at initialization and every time an agent arrives back at the colony. The waiting time at the colony is chosen from a colony-level or individual-level gamma distribution. When the colony waiting time ends, the bird may commence a land-directed or a sea-directed trip. The likelihood of leaving for a terrestrial trip is based on a colony-specific binomial distribution. The choice of a terrestrial vs a marine trip is implemented as a stochastic process.

The terrestrial trips are not modelled explicitly, and the duration of the trip is another waiting period in the model. The length of a terrestrial trip is implemented as a stochastic process and is pulled from a colony-specific gamma distribution.

At each iteration in a marine trip, the agent may change to a different type of movement. The transition probabilities depend on the local environmental variables (Table 3-6), but are partly hard-coded, with some transitions not being possible. If an agent commences a marine trip, it will start off with the outbound state, which ends depending on the distance from the colony, which in turn affects the transition probabilities from outbound to other states. From the outbound state, birds can switch to foraging or stationary behavioural states. From these states, they can move back and forth between transit flights, foraging and stationary. Finally, from foraging and stationary they can switch to an inbound state back to the colony, which is driven by the time since colony departure. When an agent has a trip duration of more than 48 hours, the state is set to the inbound state.

In addition, when on a marine trip, values are chosen at each iteration for step sizes from a gamma distribution and turning angles from a Von Mises distribution; these distributions depend on the behavioural states. The new bearing for the states foraging, stationary and transit is the bearing of the previous time step plus the chosen turning angle. The new bearing for the outbound state is the angle between the agent and the colony that leads away from the colony plus the chosen turning angle. On the other hand, the bearing for the inbound state is set at the angle that leads straight to the colony plus the chosen turning angle. Thus, the bearing for the outbound and inbound states depends on the position of the agent relative to the colony at that moment. The initial bearing for the first step of the outbound state, or the departure directions, are derived from a separate tracking data analysis, which is explained in section 2.4 and can be appointed, based on individual level or colony level observations. Altitudes during marine trips are appointed, based on a normal distribution, one value per time step.

The values of all movement parameters depend on the life stage of the agents. An analysis of the GPS track data for breeding and non-breeding agents were performed (section 2).

3.7.1.1 State switches

The transitions to new states are drawn from a weighted list of possible states. This list always contains the current state and one or more other states. The current state determines the possible new states (Table 3-5).

When in the colony state c, the probability of staying in the colony is 1 for a period with length τ_c:

$$P_{c\to c} = \begin{cases} 1, & if\ \tau_c > t - t_a \\ 0, & if\ \ \tau_c \leq t - t_a \end{cases},$$

where t is the current time and t_a the time of arrival at the colony.

At the end of the colony waiting time, the probability of switching to a terrestrial trip state l is equal to l_k , which is dependent on the colony k that the agent belongs to. The definition of the probability of switching from the colony state to the terrestrial trip state is thus defined as:

$$P_{c\to l} = \begin{cases} 0, & if\ P_{c\to c} = 1 \\ l_k, & if\ P_{c\to c} = 0 \end{cases}, \qquad (1)$$

A marine trip always starts with the outbound state. The probability of switching to a marine trip at the end of the colony waiting time, or switching to the outbound state o instead of a terrestrial trip, is equal to $1 - l_k$. The probability of switching from the colony state to the outbound state is thus defined as:

$$P_{c\to o} = \begin{cases} 0, & if\ P_{c\to c} = 1 \\ 1 - l_k, & if\ P_{c\to c} = 0 \end{cases}, \qquad (2)$$

When in the terrestrial trip state, the probability of being on a terrestrial trip is 1 for a period of length τ_l:

$$P_{l\to l} = \begin{cases} 1, & if\ \tau_l > t - t_s \\ 0, & if\ \tau_l \leq t - t_s \end{cases},$$

where t is the current time and t_s the time the terrestrial trip started.

When the terrestrial trip ends, the agents always switch to the colony state. The definition of the probability of switching from the terrestrial trip state to the colony state is thus defined as:

$$P_{l \to c} = \begin{cases} 0, & if\ \tau_l > t - t_s \\ 1, & if\ \tau_l \leq t - t_s \end{cases}.$$

When an agent switches to the outbound state, a marine trip begins and the bird starts following the movement rules as defined by the HMM (section 2.2). The probability to switch from state i to state j during a marine trip is given by:

$$P_{i \to j}(\vec{X}) = \frac{e^{\vec{a_j}\vec{X} + b_j}}{1 + \sum_{k=1}^{N} e^{\vec{a_k}\vec{X} + b_k}}\ if\ i\ \neq j, \qquad (3)$$

and the probability to not change state is defined as:

$$P_{i \to i}(\vec{X}) = \frac{1}{1 + \sum_{k=1}^{N} e^{a_k X_k + b_k}}, \qquad (4)$$

where $\vec{a_i}$ is a vector with the regression coëfficients of state i, $\vec{X}$ a vector with the corresponding environmental covariates and b_i the intercept of state i.

Table 3-6 shows the covariates that make up the vectors $\vec{a_i}$ and $\vec{X}$.

When an agent has a trip duration of more than 48 hours, the state is forced into the inbound state. In addition, when an agent reaches the edge of the map, the state is set to the inbound state.

Table 3-5 Possible state switches at each time step for sea-bound trips of breeding and non-breeding agents, values for $P_{i \to i}(\vec{X})$ and $P_{i \to j}(\vec{X})$ are defined by equations 1 and 2.

FROM ↓

	Outbound	Transit	Foraging	Stationary	Inbound	Colony	Terrestrial trip
Outbound	$P_{i \to i}(\vec{X})$					$P_{c \to o}$	
Transit		$P_{i \to i}(\vec{X})$	$P_{i \to j}(\vec{X})$	$P_{i \to j}(\vec{X})$			
Foraging	$P_{i \to j}(\vec{X})$	$P_{i \to j}(\vec{X})$	$P_{i \to i}(\vec{X})$	$P_{i \to j}(\vec{X})$			
Stationary	$P_{i \to j}(\vec{X})$	$P_{i \to j}(\vec{X})$	$P_{i \to j}(\vec{X})$	$P_{i \to i}(\vec{X})$			
Inbound		$P_{i \to j}(\vec{X})$	$P_{i \to j}(\vec{X})$	$P_{i \to j}(\vec{X})$	$P_{i \to i}(\vec{X})$		
Colony					$P_{i \to j}(\vec{X})$	$P_{c \to c}$	$P_{l \to c}$
Landtrip						$P_{c \to l}$	$P_{l \to l}$

Table 3-6 Environmental covariates for transitions between behavioural states during marine trips (HMM covariates).

Environmental covariates	*Description*
Distance to colony	Distance between the current position of the bird and the centre of the colony.
Distance to OWF	Shortest distance between the agent and the closest offshore windfarm.
In colony	An agent is considered in the colony when the current position is within a 2 km range of the colony.
On land	Current position is on land or not on land.
Vessel present	Current position is in a cell with or without fishing vessel.
Water depth	Depth of the water at the current position of the bird.
Distance to coast	Distance between the current position of the bird and the closest coastline.

3.7.1.2 Step sizes

During marine trips the behaviour is explicitly modelled. At each time step, the IBM draws a step size from a state-specific gamma distribution (Figure 4-5, Figure 4-6).

3.7.1.3 Bearing

During marine trips, agents change their bearing each time step. Changes in bearing (turning angles) are drawn from state-specific Von Mises distributions at each time step (Figure 4-5, Figure 4-6). In the transit, foraging and stationary states, the turning angles are added to the current bearing of the agents. For the inbound state, the turning angle is added as a derivation from the colony bearing, which is calculated based on angle of the direction to the home colony of the agent. For the outbound state, the turning angle is added as a derivation from the angle between the agents' colony and the current position. When an agent leaves the colony, the initial direction is drawn from a Von Mises distribution at the start of the outbound state.

Initial bearing in outbound state

The initial direction of a marine trip is drawn from a colony-specific or individual-specific Von Mises distribution (sections 2.4 and 4.4). For the individual level distributions, kappa values >17 were excluded. For the colonies with no GPS track data, the mean departure direction was based on the angle of the coastline, while the deviation was based on a similar colony (Texel for the Wadden Sea colonies and Zeebrugge for the colonies along the mainland coast).

3.7.1.4 Probability of terrestrial trip or marine trip

The probability for making a terrestrial trip (l_k in equations 1 and 2) is taken from a colony-specific generalized linear mixed-effect model of the GPS track data (sections 2.3 and 4.3, Figure 4-7, Figure 4-8). The probability of taking a marine trip is $1 - l_k$.

3.7.1.5 Time in the colony

The duration of the colony waiting time is drawn from a colony-level (Figure 4-12, Figure 4-13) or individual-level gamma distribution. The gamma distributions for time in the colony are determined from a GPS-track analysis (section 4.1).

3.7.1.6 Duration of terrestrial trips

The duration of the terrestrial trips is drawn from colony-level (Figure 4-14, Figure 4-15) or individual-level gamma distributions. The gamma distributions for the durations of terrestrial trips are determined from the tracking data analysis (section 4.1).

3.7.1.7 Altitudes

For each marine trip at each time step, an altitude is drawn for the agent from a normal distribution (Figure 4-16). The normal distribution for the altitudes is based on GPS-track analysis (section 4.1).

3.7.2 Fishing vessels

The presence of a fishing vessel was drawn from a binomial distribution based on a map with probabilities of the presence of a fishing vessel. These maps were recreated every 4 hours (12 timesteps). The observed lengths of fishing trips per benthis metiers commonly range between 2-4 hours (Figure 3-6 Consecutive).

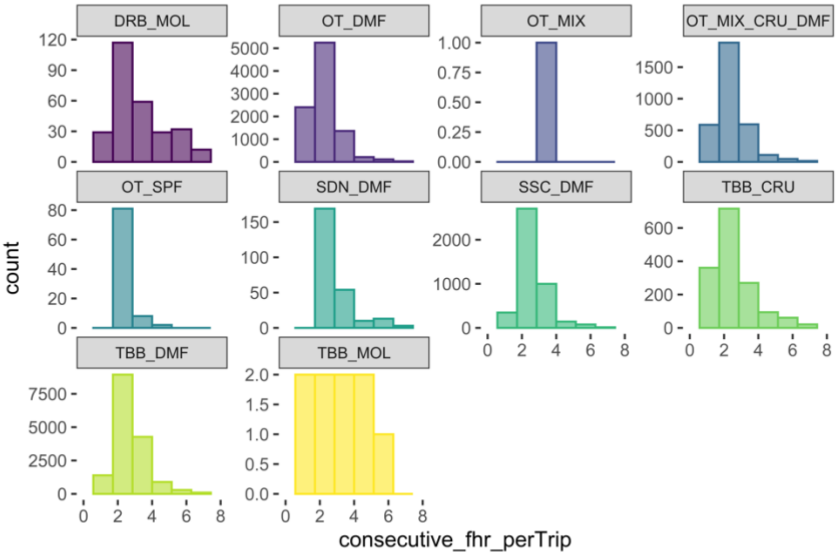

Figure 3-6 Consecutive fishing hours per trip per c-square for the benthis metiers included in the fishing vessel dataset. For the definition of the benthis metiers (DRB_MOL, OT_DMF, OT_MIX, OT_MIX_CRU_DMF, OT_SPF, SDN_DMF, SCC_DMF, TBB_CRU, TBB_DMF and TBB_MOL) see Eigaard et al. (2016).

3.7.3 Avoidance

Avoidance of the wind turbines occurs at three different levels. At the moment a bird first enters a cell with a wind farm, macro-avoidance can occur. When macro-avoidance occurs, the birds do not encounter any turbines while flying through OWF grid cells. The probability of macro-avoidance is a constant state variable that is equal for all agents (Table 3-2). Macro-avoidance occurs based on a draw from a binomial distribution. When it does, macro-avoidance will continue to occur for all consecutive wind farms cells the agent passes, until a cell without OWF is encountered. Once the agent encounters a cell with no wind turbines, the avoidance stops and will be activated again when an OWF is encountered anew. When no macro-avoidance occurs, the agent enters the wind farm. If the agent moves at an altitude that falls in the range of the rotor, the probability of collision will be estimated by the IBM (section 3.7.4) and the meso- and micro-avoidance are taken into account during that process. The meso- and micro- avoidance together lead to avoidance probability P_a by:

$$P_a = 1 - (1 - P_{meso})(1 - P_{micro}),$$

where P_{meso} is the probability of meso-avoidance and P_{micro} that of micro avoidance probability. Later the collision probability is multiplied with the probability an agent does not avoid the turbine $1 - P_a$, see section 3.7.4.

3.7.4 Collisions

Each time a bird flies over a cell with wind turbines and no macro-avoidance occurs, the probability of a collision is evaluated. The collision depends on a range of factors, such as the wind turbine density, the turbine characteristics, the bird characteristics and the flight height and speed of the bird at the current moment.

For the collision probability, we adapted the Band model (Band 2012) in such a way that it predicts the collision probability of a single individual. Following Band (2012), the probability of collision at a single point is defined as:

$$P_c(r) = \min\left(1, \frac{b*60*f(r)}{\Omega v}\right),$$

which depends on the number of blades b, the angular velocity Ω, the distance of the agent to the rotor centre r and the velocity of the agent v, and where the function $f(r)$ is defined as:

$$f(r) = |Cc(r)\sin\gamma + C\alpha\cos\gamma| + \begin{cases} L\ if\ L > \alpha \\ LF\alpha\ otherwise \end{cases},$$

with $\alpha = \frac{60v}{2\pi r\Omega}$. The function depends on the chord width at the distance of the agent to the rotor centre $c(r)$, the maximum chord width C, the pitch angle of the blades γ, the length of the agent L and bird flapping constant F. The chord width at the distance of the agent to the rotor centre is defined as:

$$c(r) = \begin{cases} inter(r, [r_i, c_i]), & g(r) \leq 1 \\ 0, & g(r) \geq 1 \end{cases},$$

with function $g(r) = \frac{|r|}{R}$, which depends on the rotor radius R (Band 2012). The calculation of the chord width is based on linear interpolation, which is indicated by $inter(r, [r_i, c_i])$ and depends on previously measured coupled values for r and c, $[r_i, c_i]$.

Since we do not normally know the exact point of passage of the agent through the rotor swept area, we calculate the collision probability for a certain height of passage through the rotor swept area instead and integrate the probability over the width of the rotor disk at that height of passage. The collision probability for an agent that passes a wind turbine at a height h within the rotor range is then defined as:

$$P_{hc}(Y) = (1 - P_a)\frac{\int_{-\sqrt{R^2-Y^2}}^{\sqrt{R^2-Y^2}} P_c(\sqrt{x^2 + Y^2})\,dx}{2\sqrt{R^2 - Y^2}},$$

which depends on the height of passage within the rotor height Y, and the rotor radius R, and $Y = h - H_r$, with rotor height H_r (Band 2012). The parameter values of these equations are described in Table 3-7.

In addition to the collision probability for an agent passing through the rotor, we need to estimate the probability of the encounter with a wind turbine. This probability is not included in the Band model (Band 2012). We therefore newly derive this probability here.

When an agent moves through a grid cell C in an OWF, the agent can encounter one or more wind turbines or none at all. Since we cannot determine the exact number of wind turbine encounters of the agent we estimate the encounters based on the turbine density in the wind farm. Let ρ be the density of wind turbines per km^2 and A the area of grid cell C. Then, the number of wind turbines N in C is equal to ρA. To allow for an estimate of the number of encountered turbines we assume the wind turbines are evenly spaced and that each grid cell can be considered as a square with the same surface area as cell C. Based on this assumption, N can be expressed as $N = (\sqrt{\rho A})^2$.

In addition, we assume that the agents' flight direction is perpendicular to the rotor area and thus, that the chance of encounter with the rotors in a single row is equal to:

$$P_e = \frac{2R\sqrt{\rho A}}{L_e},$$

where R is the rotor radius and L_e the edge length of the (square) grid cell. Depending on the length of the agents' flight trajectory L_t, the agent encounters a certain number of rows of wind turbines per cell. Let L_d be the length of the diagonal of the grid cell C, then the number of rows of wind turbines an agent encounters is defined as $r_w = \frac{L_t}{L_d}\sqrt{\rho A}$. Since r_w for this definition does not always result in integers, whether a partial row was actually encountered, was determined based on a draw from a binomial distribution.

Table 3-7 Collision model parameters

Symbol	*Description*	*unit*	*Source*
b	Number of blades		Depends on wind turbine type, see section 3.6
Ω	Angular velocity		Depends on wind turbine type
C	Maximum chord width		Depends on wind turbine type
$[r_i, c_i]$	Measured coupled values for the distance of the agent to the rotor centre r and chord width c.		See section 3.6
γ	pitch angle of blade		Depends on wind turbine type, see section 3.6
R	Rotor radius		Depends on wind turbine type, see section 3.6
H_r	Rotor height		Depends on wind turbine type and location, see section 3.6
L	Length of bird		See Table 3-2
F	Bird flapping constant		See Table 3-2
v	Bird flying velocity		$1/\delta_s$
δ_s	Bird step size		See section 1.7.1.2
h	Bird altitude		
P_a	Avoidance probability		See section 3.7.3

The number of encountered wind turbines E_w can then be calculated based on random draws from a binomial distribution with r_w trials and probability of an encounter P_e. Subsequently, the probability of a single collision is calculated as:

$$P_{sc}(Y) = \sum_{i=1}^{L} P_{hc}(Y) \times (1 - P_{hc}(Y))\hat{}(E_w - i)$$

And, whether a collision occurs, depends on a single random draw from a binomial distribution with the chance of collision $P_{sc}(Y)$.

Table 3-8 Turbine encounter parameters

Symbol	*Description*	*unit*	*Source*
ρ	density wind turbines	km^{-2}	Depends on OWF location
A	Area of grid cell	C^{-1}	Depends on OWF location
L_e	Length of edge of grid cell	km	Depends on OWF location
L_d	Length of diagonal of grid cell	km	Depends on OWF location

3.7.5 Bhattacharyya's Affinity (BA) overlap spatial distributions

To test the overlap between the spatial distributions of the model tracks and the GPS tracks, we calculated the Bhattacharyya's Affinity (BA) overlap index (Bhattacharyya 1943) of two Utilization Density (UD) kernels (Calenge 2006). Smoothing factor for the UD kernels was estimated using the 'href' method for each colony, and subsequently fixed at the median across colonies: 3100m. As UD kernel shape may also be affected by the number of positions, a sample size equal to the number of positions per colony in the data was randomly selected from the simulation results for UD kernel estimation. Finally, BA indices were calculated, which range from 0 (no overlap) to 1 (identical kernels).

3.7.6 Sensitivity analysis

We tested the sensitivity of the breeder model to changes in the parameters for the colony Texel. The sensitivity analysis is based on the elementary effect method proposed by Morris (1991). This is a method that allows changing multiple parameters simultaneously and testing the effect of changes in multiple parameters at the same time. The method generates many trajectories through the multidimensional parameter space that are simulated point by point with the IBM. The collision mortality is then calculated for each point in each trajectory and the effect of the changes in parameters on the collisions can be determined. The average and standard deviations of the collision mortalities function as indicators, which allow the calculation of the level of influence of the parameters and linear and non-linear influences to be distinguished.

The IBM contains a total of 170 parameters, of which 121 parameters were included in the sensitivity analysis (SA). We excluded parameters related to the collisions and wind turbine encounters (Table *3-7* and Table 3-8) because the sensitivity of the Band model to these parameters is extensively tested in other studies (Masden *et al*. 2015, 2021). We did include the macro avoidance and the OWF activity percentage, because these were parameters used outside the collision model. The sensitivity analysis included only colony-level parameters and no individual-level parameters and was run for the breeding model and the colony Texel only. Even with this limitation, the computational time for the SA is about two weeks. The SA was conducted based on the assumption that the parameters are uncorrelated and that the value of each parameter can be varied independently from other parameters.

The k-dimensional parameter space was discretized into a k-by-p grid with p-levels per parameter. A maximum and minimum realistic value was determined for each parameter based on +/- twice the standard deviations or standard errors found in the GPS-track data analysis. For the OWF activity percentage, a maximum of 100% and a minimum of 50% were considered realistic. For the macro avoidance, we considered a range from 0.52-0.76 realistic (Skov *et al*. 2018, mean +/- 2*SD). For the estimated turbine densities, we considered a range of +/- 10% around the estimate. The ranges between the minima and maxima were discretized into $p = 4$ levels. The step size (delta) was taken as $p/(2 * (p - 1))$, which is a recommended delta value for good symmetry and coverage. A trajectory in the parameter space starts with a randomly chosen point in the k-dimensional space, while each two adjacent points on the trajectory allow one randomly chosen parameter to change for a given step size. As a result, a trajectory contains $k + 1$ points and each parameter has changed once in this trajectory. We performed the sensitivity analysis with 100 trajectories.

The averages (μ_j^*) and standard deviations (σ_j) of the elementary elements ($EE_{i,j}$) were, calculated as (Campolongo *et al.* 2000, 2007):

$$\mu_j^* = \frac{1}{r}\sum_{i=1}^{r}\left|EE_{i,j}\right|$$

$$\sigma_j = \sqrt{\frac{1}{r}\sum_{i=1}^{r}\left(EE_{i,j} - \frac{1}{r}\sum_{i=1}^{r}\left(EE_{i,j}\right)\right)^2}$$

Values of μ_j^* and sigma are used to interpret, sort and classify the influential parameters. The higher μ_j^* value indicates a stronger main effect. Additionally, a higher σ_j implies stronger nonlinear effects or interactions with other parameters.

4 Results of tracking data analysis

4.1 Sample size and spatial distribution of data

After regularization of the tracking data, 305082 positions of 155 individuals from 5 colonies were left that fitted our selection criteria for data reflecting the breeding period (Table 4.1). Data were unequally distributed among individuals, with, for example, 14 individuals with less than 100 positions, 116 individuals with over 5000 positions and a maximum of 10134 positions for a single individual. Also between colonies, sample sizes differed substantially both for breeders and non-breeders (Table 4.1). Less data were available for non-breeders, with 157837 positions of 56 individuals from 5 colonies. There were no individuals with less than 100 positions, 52 with over 5000 positions, and the maximum number of positions was 8437 (Table 4-2).

The spatial distribution of all data (Figure 4-1 and Figure 4-3) and Utilization Density (UD) kernels only for marine foraging trips (Figure 4-2 and Figure 4-4) show substantial overlap in the south (Belgium - Zeeland) for both breeders and non-breeders, with many trips venturing far inland, and a distribution of birds from Texel that is directed to the southwest. The UD kernels show less overlap between kernels closer to the colonies.

Table 4-1 Sample size per colony for breeders.

colony	n individuals	n positions	n years	range years
Zeebrugge	59	133,168	6	2013 - 2018
Vlissingen	39	91,204	4	2015 - 2018
Texel	38	64,902	8	2008 - 2015
Neeltje Jans	14	10,831	1	2020 - 2020
Oostende	5	4,977	3	2016 - 2018

Table 4-2 Sample size per colony for non-breeders.

colony	n individuals	n positions	n years	range years
Zeebrugge	20	58,963	6	2013 - 2018
Vlissingen	14	39,471	6	2008 - 2014
Texel	12	29,464	4	2008 - 2015
Neeltje Jans	9	25,438	1	2020 - 2020
Oostende	1	4,501	1	2016

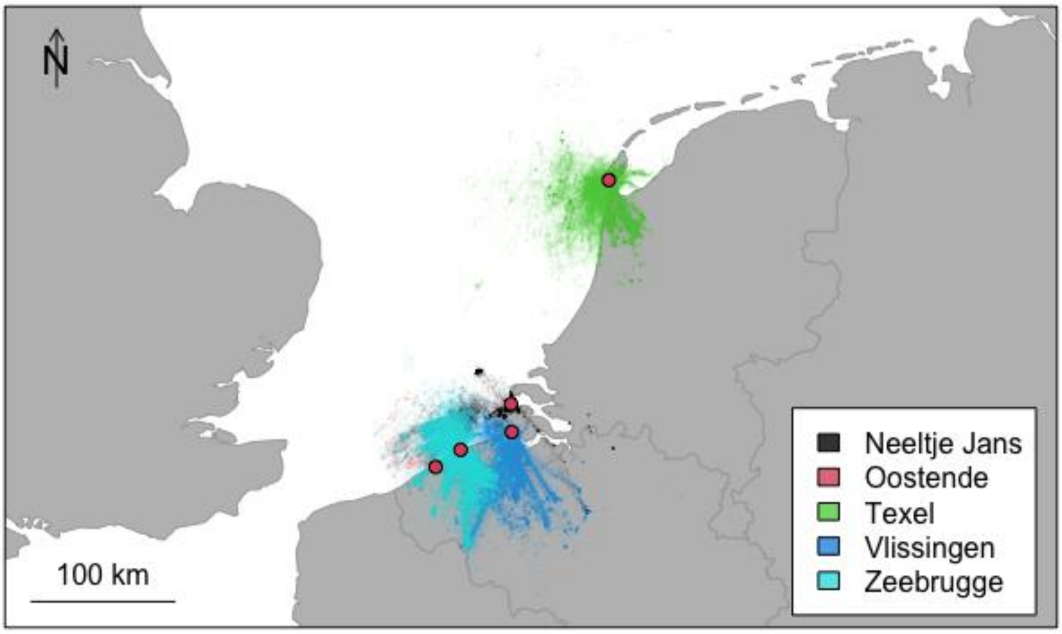

Figure 4-1 All tracking data for breeders. Red dots show colony locations.

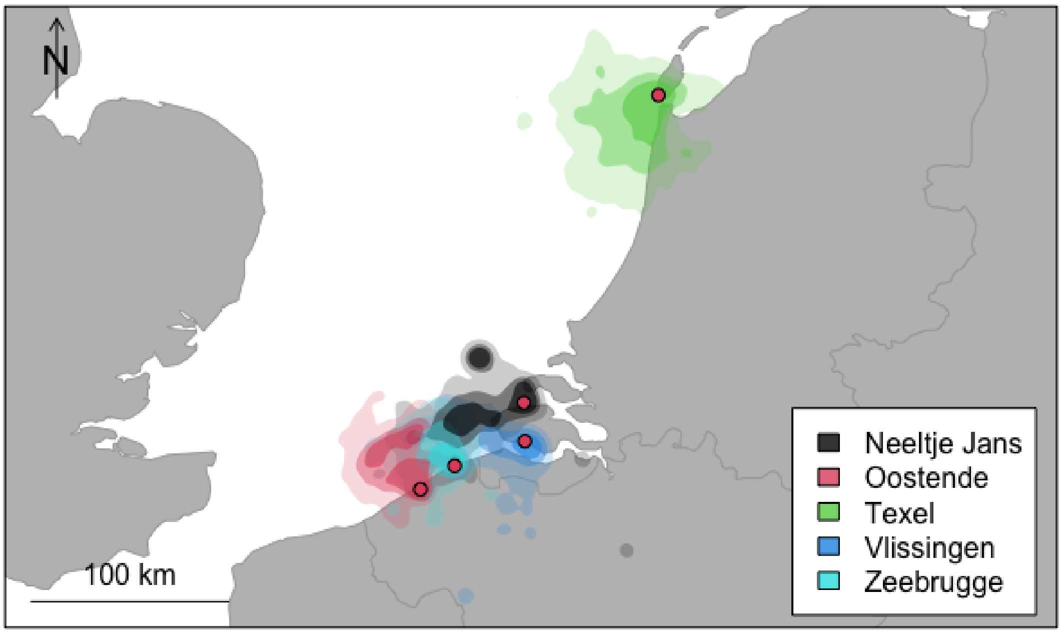

Figure 4-2 Utilization density kernels for breeders per colony, showing 50%, 75% and 95% of usage during foraging trips with at least 40% of the positions on land. Note that birds departing from Vlissingen often lingered in the Westerschelde before venturing inland in southern direction.

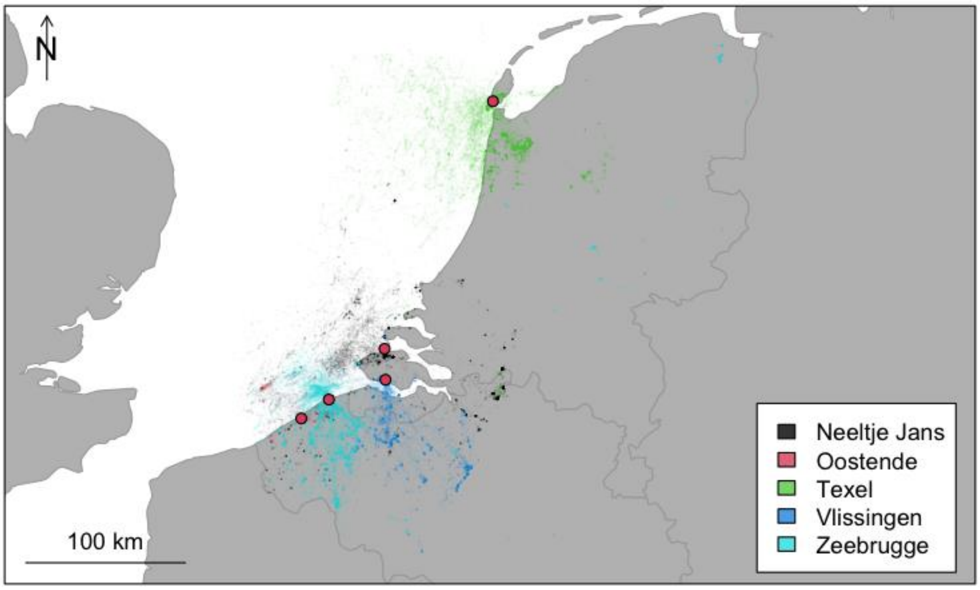

Figure 4-3 All tracking data for non-breeders. Red dots show colony locations.

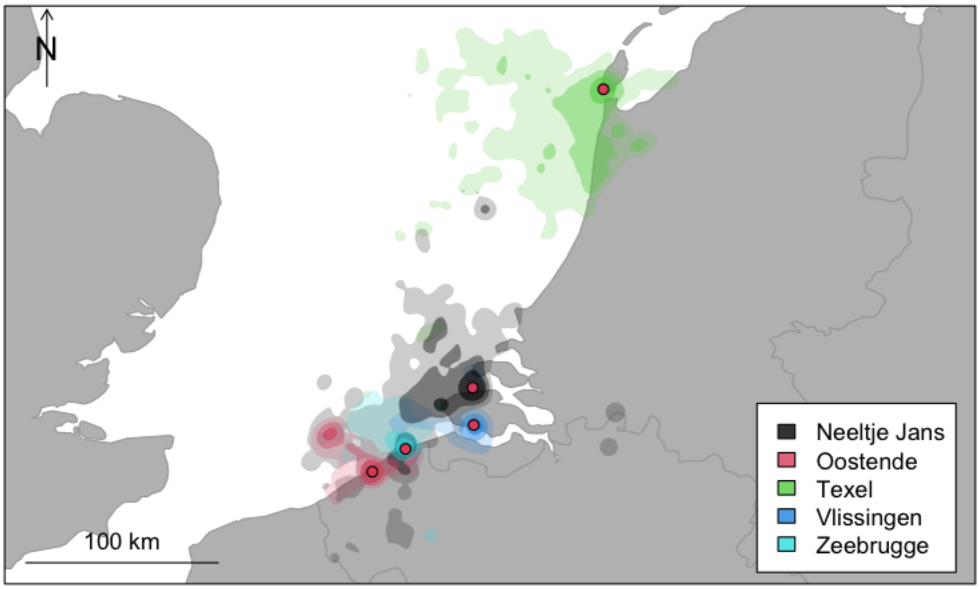

Figure 4-4 Utilization density kernels for non-breeders per colony, showing 50%, 75% and 95% of usage during foraging trips with at least 40% of the positions on land. Note that birds departing from Vlissingen often lingered in the Westerschelde before venturing inland in southern direction.

4.2 Hidden Markov Models for behavioural states

Models including mixtures to account for colony-level or individual-level variation failed to converge. In comparison to the model with no covariates on the data stream parameters, a model with wind speed and wind direction affecting the step length and turning angles did not result in a better fit to the data (ΔAIC = -1609). Therefore, wind effects were not included.

Following the constraints of the transition matrix, the colony and stationary states were both characterized by very small step sizes and no directionality, whereas the three transit states combined large step sizes and strong directionality (either away from, towards, or indifferent to the colony). Finally, the foraging state included intermediate step sizes and weak directionality (breeders: Figure 4-5, Table 4-3, non-breeders: Table 4-4 and Figure 4-6). The transition probabilities of the final model containing all covariates are presented in Table 4-5 for breeders and in Table 4-6 for non-breeders.

Table 4-3 Mean and standard deviation of the step size parameters (in km) and concentration parameter of the turning angle for breeders.

	outbound	forage	stationary	inbound	colony	transit
mean	7.25	2.06	0.07	7.51	0.06	8.15
sd	4.17	1.97	0.10	4.48	0.06	2.94
concentration	1.91	-0.16	-24.50	3.71	-24.50	1.82

Table 4-4 Mean and standard deviation of the step size parameters (in km) and concentration parameter of the turning angle for non-breeders.

	outbound	forage	stationary	inbound	colony	transit
mean	6,80	1,82	0,08	7,8	0,07	7,03
sd	4,03	1,65	0,11	4,36	0,07	2,96
concentration	1,48	-0,19	-21,97	3,56	-21,95	0,85

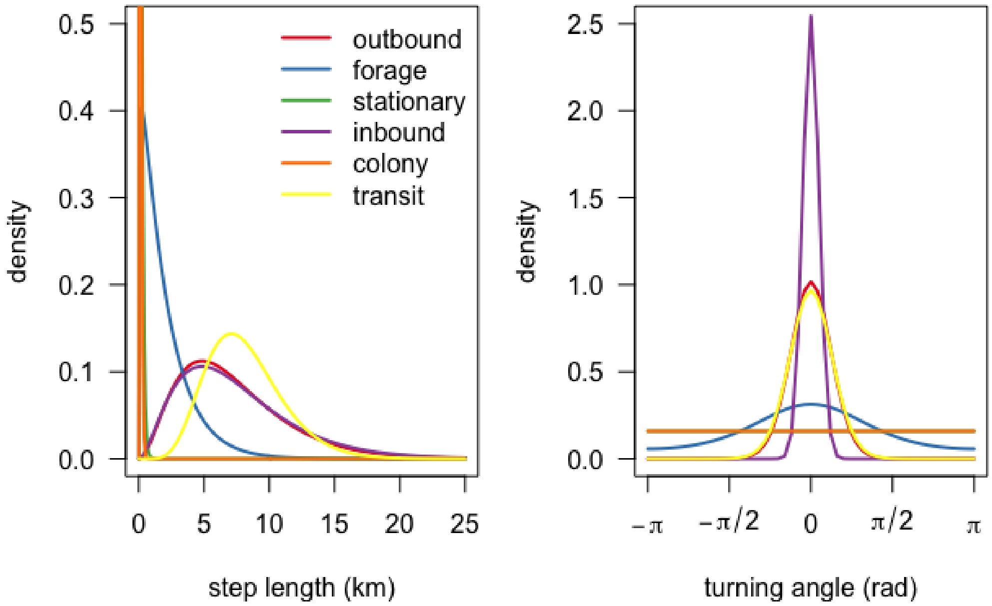

Figure 4-5 Distributions of step length (left) and turning angles (right) per behavioural state as estimated in the HMM for breeders.

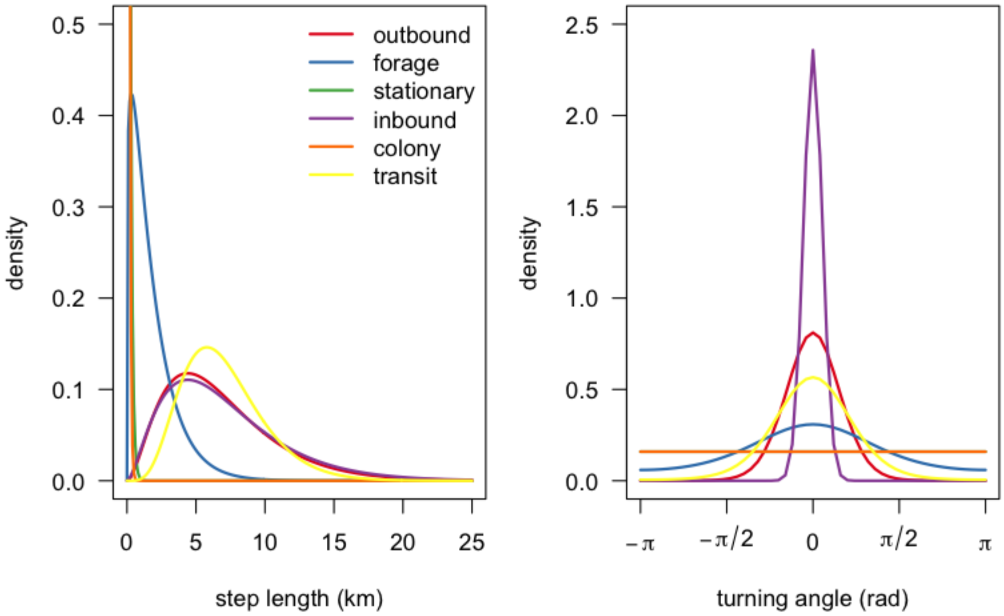

Figure 4-6 Distributions of step length (left) and turning angles (right) per behavioural state as estimated in the HMM for non-breeders.

Table 4-5 Estimates of intercepts of and covariate effects on transition probabilities in the 6-state HMM for breeders. In part of the transitions, the intercept is fixed at an extremely small value by fixing it to -100, rendering the transition virtually impossible. For these and other transitions, effects of covariates are fixed to zero. States are numbered as follows: 1 = outbound, 2 = forage, 3 = stationary, 4 = inbound, 5 = in colony, 6 = transit

transition	intercept	distance to colony	time since colony departure	in colony	on land	near fishing vessel	near OWF	distance to coast	water depth
1 -> 2	-1.08	0.015	0	0	0	0.684	-0.013	0.033	0.01
1 -> 3	-1.637	-0.022	0	0	0	-0.068	0	-0.037	-0.765
1 -> 4	-100	0	0	0	0	0	0	0	0
1 -> 5	-100	0	0	0	0	0	0	0	0
1 -> 6	-100	0	0	0	0	0	0	0	0
2 -> 1	-100	0	0	0	0	0	0	0	0
2 -> 3	-0.893	0	0	0	0	-1.293	0.172	0.003	-0.249
2 -> 4	-1.312	0	-0.001	0	0	0.343	-1.53	0.013	-0.064
2 -> 5	-100	0	0	0	0	0	0	0	0
2 -> 6	-2.537	0	0	0	0.49	-0.608	-0.016	0.006	-0.034
3 -> 1	-100	0	0	0	0	0	0	0	0
3 -> 2	-1.684	0	0	0	0	-0.343	0.22	-0.014	-0.001
3 -> 4	-2.079	0	-0.001	0	0	0.43	-0.014	0.011	-0.073
3 -> 5	-100	0	0	0	0	0	0	0	0
3 -> 6	-8.747	0	0	0	-2.385	-0.123	0	-0.08	-2.879
4 -> 1	-100	0	0	0	0	0	0	0	0
4 -> 2	-100	0	0	0	0	0	0	0	0
4 -> 3	-100	0	0	0	0	0	0	0	0
4 -> 5	-0.872	0	0	0	0	0	0	0	0
4 -> 6	-100	0	0	0	0	0	0	0	0

transition	intercept	distance to colony	time since colony departure	in colony	on land	near fishing vessel	near OWF	distance to coast	water depth
5 -> 1	-1.716	0	0	0	0	0	0	0	0
5 -> 2	-100	0	0	0	0	0	0	0	0
5 -> 3	-100	0	0	0	0	0	0	0	0
5 -> 4	-100	0	0	0	0	0	0	0	0
5 -> 6	-100	0	0	0	0	0	0	0	0
6 -> 1	-100	0	0	0	0	0	0	0	0
6 -> 2	0.405	0	0	0	-0.911	0.636	0.943	0.011	-0.056
6 -> 3	-0.826	0	0	0	-1.455	-0.032	-0.001	0.033	-0.942
6 -> 4	-100	0	0	0	0	0	0	0	0
6 -> 5	-100	0	0	0	0	0	0	0	0

Table 4-6 Estimates of intercepts of and covariate effects on transition probabilities in the 6-state HMM for non-breeders. In part of the transitions, the intercept is fixed at an extremely small value by fixing it to -100, rendering the transition virtually impossible. For these and other transitions, effects of covariates are fixed to zero. States are numbered as follows: 1 = outbound, 2 = forage, 3 = stationary, 4 = inbound, 5 = in colony, 6 = transit

transition	intercept	distance to colony	time since colony departure	in colony	on land	near fishing vessel	near OWF	distance to coast	water depth
1 -> 2	-1.413	0.042	0	0	0	0.85	-1.255	0.003	0.01
1 -> 3	-1.543	-0.03	0	0	0	0.909	0	-0.087	-0.963
1 -> 4	-100	0	0	0	0	0	0	0	0
1 -> 5	-100	0	0	0	0	0	0	0	0
1 -> 6	-100	0	0	0	0	0	0	0	0
2 -> 1	-100	0	0	0	0	0	0	0	0
2 -> 3	-0.768	0	0	0	0	-0.73	2.286	-0.005	-0.208

transition	intercept	distance to colony	time since colony departure	in colony	on land	near fishing vessel	near OWF	distance to coast	water depth
2 -> 4	-1.214	0		0	0	0.161	-0.546	0.002	-0.044
2 -> 5	-100	0	0	0	0	0	0	0	0
2 -> 6	-2.405	0	0	0	0.321	-0.516	0.813	-0.003	-0.003
3 -> 1	-100	0	0	0	0	0	0	0	0
3 -> 2	-1.955	0	0	0	0	-0.057	2.057	-0.025	0.021
3 -> 4	-1.696	0	-0.001	0	0	-0.286	-0.093	0.027	-0.09
3 -> 5	-100	0	0	0	0	0	0	0	0
3 -> 6	-5.968	0	0	0	2.169	-1.627	-0.001	0.139	-2.43
4 -> 1	-100	0	0	0	0	0	0	0	0
4 -> 2	-100	0	0	0	0	0	0	0	0
4 -> 3	-100	0	0	0	0	0	0	0	0
4 -> 5	-0.714	0	0	0	0	0	0	0	0
4 -> 6	-100	0	0	0	0	0	0	0	0
5 -> 1	-1.724	0	0	0	0	0	0	0	0
5 -> 2	-100	0	0	0	0	0	0	0	0
5 -> 3	-100	0	0	0	0	0	0	0	0
5 -> 4	-100	0	0	0	0	0	0	0	0
5 -> 6	-100	0	0	0	0	0	0	0	0
6 -> 1	-100	0	0	0	0	0	0	0	0
6 -> 2	-0.826	0	0	0	0.282	0.605	-0.075	-0.029	0.021
6 -> 3	0.413	0	0	0	-2.293	0.221	0	-0.001	-1.147
6 -> 4	-100	0	0	0	0	0	0	0	0
6 -> 5	-100	0	0	0	0	0	0	0	0

4.3 Probability of terrestrial versus marine trips

The proportion of terrestrial (as opposed to marine) trips varied between colonies, with roughly 10% of the trips from Vlissingen and Zeebrugge, and *ca.* 1% from Texel and Neeltje Jans. Note that after data selection, no terrestrial trips were left for Oostende. Substantial variation in the proportion of terrestrial trips is expressed by the individual-level random intercepts, which vary between 0 and *ca.* 60% for breeders (Figure 4-7). For non-breeders, colonies showed the same pattern, probabilities for terrestrial trips were higher for Vlissingen and Zeebrugge and confidence intervals were much wider due to lower sample sizes (Figure 4-8).

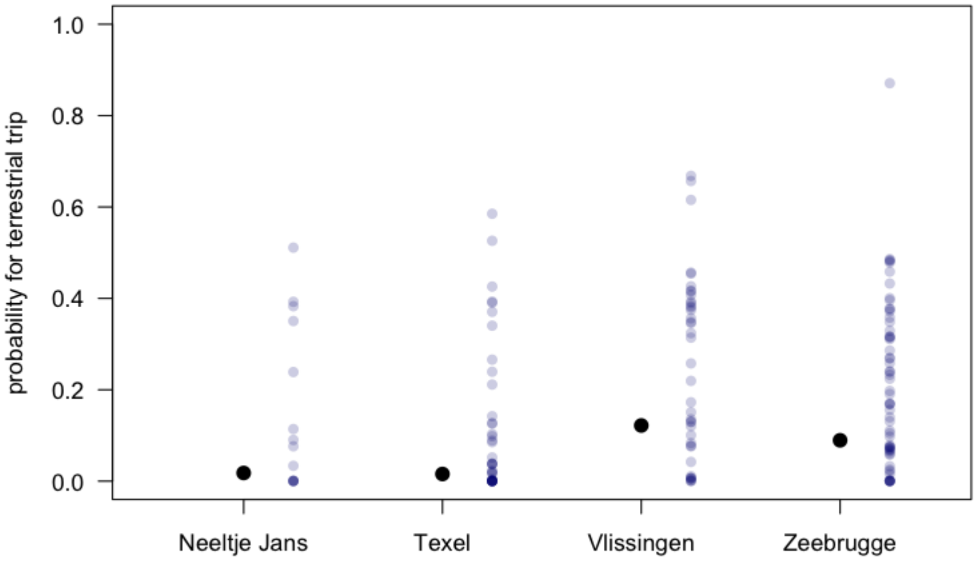

Figure 4-7 Probability of terrestrial as opposed to marine trips for each colony for breeders, as estimated by a GLMM (black dots), showing individual-level random effects (blue transparent dots). Note that Oostende is missing here as no terrestrial trips were left after data selection.

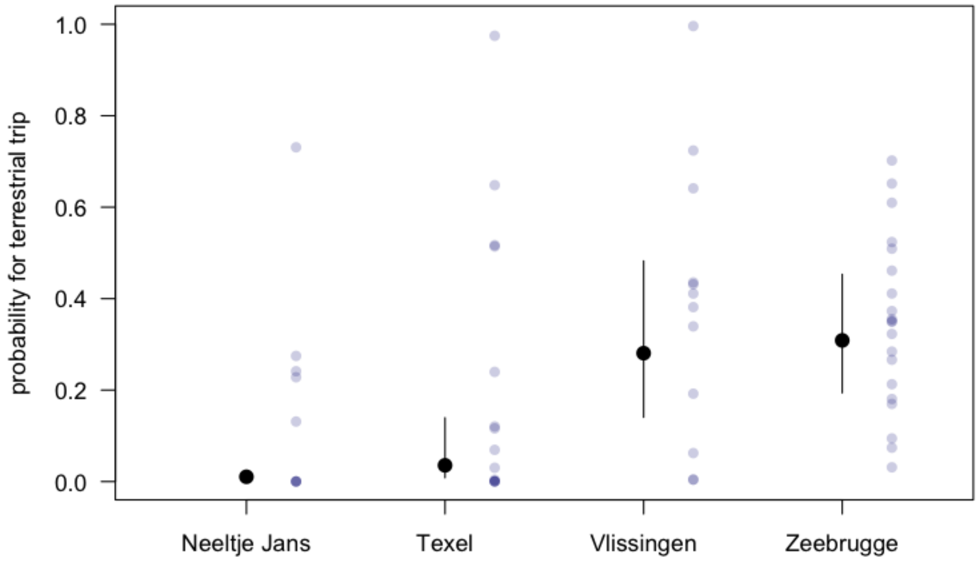

Figure 4-8 Probability of terrestrial as opposed to marine trips for each colony for non-breeders, as estimated by a GLMM (black dots), showing individual-level random effects (blue transparent dots). Note that Oostende is missing here as no terrestrial trips were left after data selection.

4.4 Initial departure direction from the colony

Initial departure directions of marine trips from the colony were strongly colony-specific for both breeders and non-breeders (Table 4-7, Figure 4-9, Table 4-8 and Figure 4-10). Distributions were not always unimodal. Bimodal distributions were observed for Neeltje Jans and Texel, which led to low concentration (kappa) parameters for these colonies. In Vlissingen, the strongly bimodal distribution was caused by individuals that stayed for some time in the Westerschelde, before either venturing inland into Belgium or to sea. However, as outbound flights are strongly directional, southward departures would lead always inland. We solved this ad-hoc by excluding directions below 200 degrees.

The general orientation of the coastline correlated with the mean direction of marine trips, with an intercept of 3.89 and a slope of 1.63 (R^2=0.81, Figure 4-11). However, the concentration parameter of the departure direction did not correlate with the orientation of the coastline. The same relation was used for both breeders and non-breeders.

Table 4-7 Estimates of the mean and concentration of departure direction for each colony for breeders.

site	mean	sd	kappa	sd
Neeltje Jans	5.14	0.06	1.19	0.10
Oostende	5.60	0.03	3.31	0.40
Texel	3.99	0.02	1.52	0.05
Vlissingen	4.56	0.01	7.52	0.47
Zeebrugge	5.57	0.01	3.58	0.08

Table 4-8 Estimates of the mean and concentration of departure direction for each colony for non-breeders.

site	mean	sd	kappa	sd
Neeltje Jans	4,44	0,07	1,02	0,09
Oostende	5,48	0,08	3,16	1,75
Texel	3,84	0,04	1,03	0,08
Vlissingen	4,34	0,05	2,75	0,33
Zeebrugge	4,85	0,07	0,54	0,05

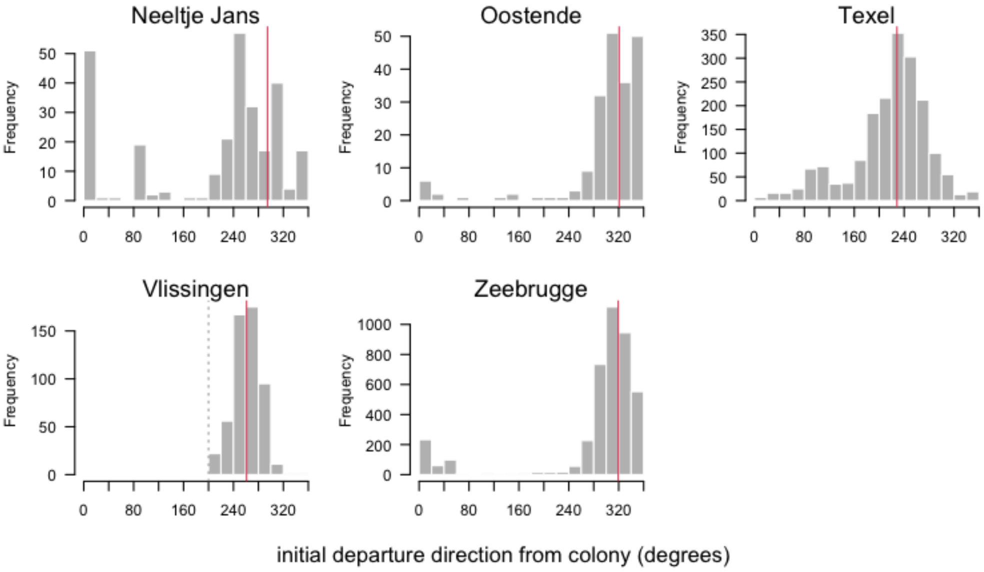

Figure 4-9 Initial departure directions for each colony for breeders. North is at 0 and 360. Note that for Vlissingen, directions below 200 degrees have been excluded (see main text).

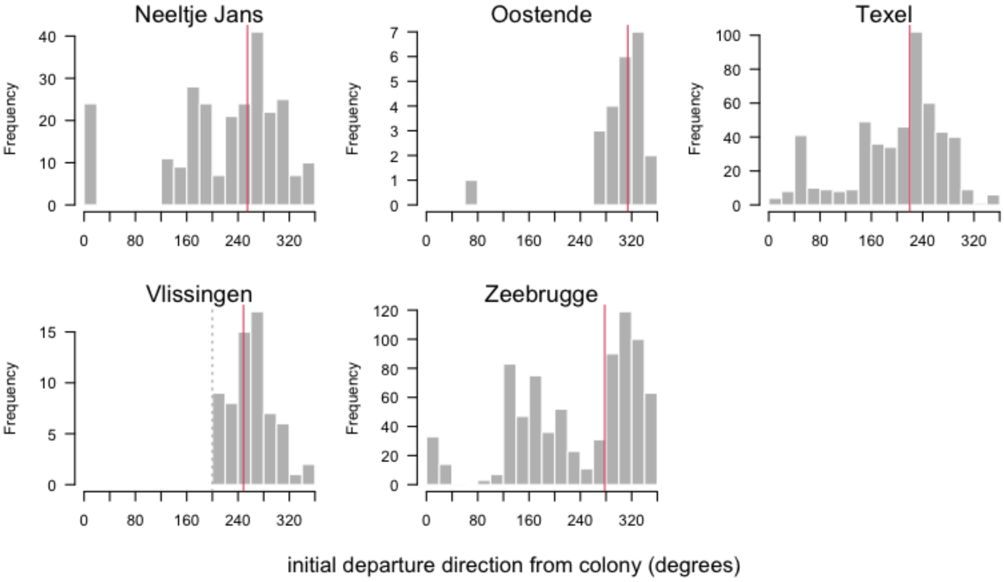

Figure 4-10 Initial departure directions for each colony for non-breeders. North is at 0 and 360. Note that for Vlissingen, directions below 200 degrees (marked by a dashed grey line) have been excluded (see main text).

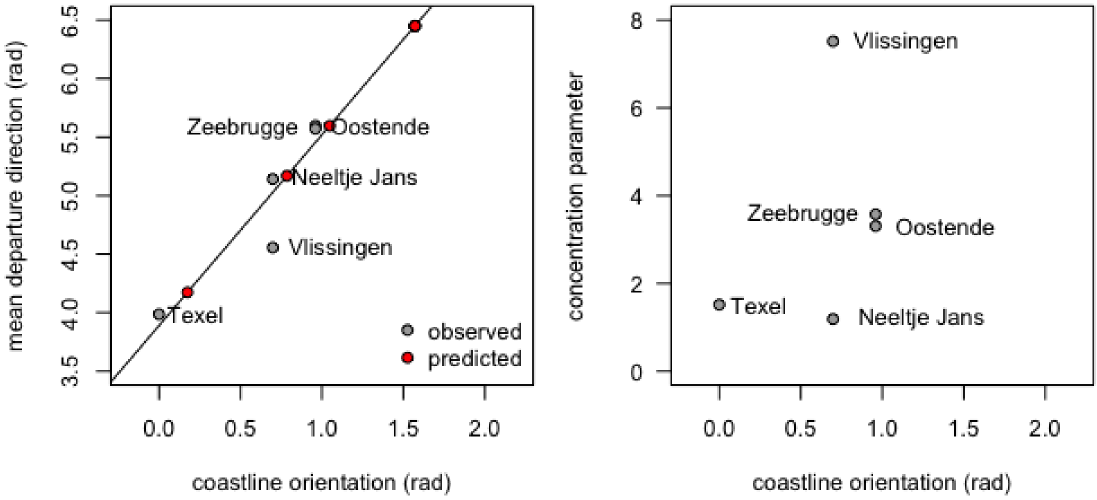

Figure 4-11 Mean departure direction (left) and the concentration parameter of departures (right) as a function of the orientation of the coastline.

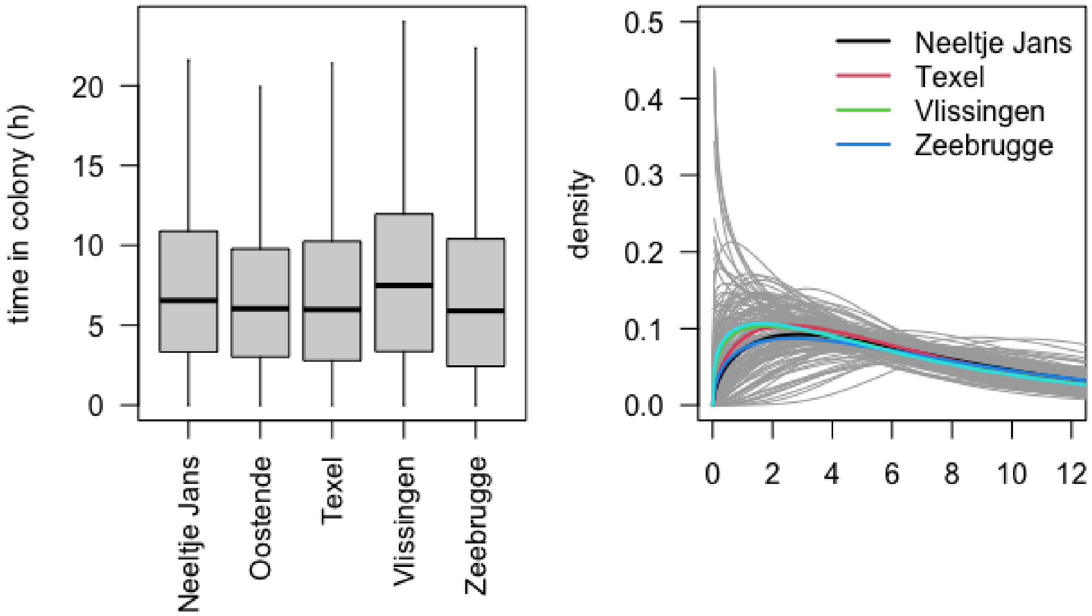

Figure 4-12 Time spent in the colony between foraging trips for breeders. Left: Variation in time bouts spent in the colony between trips, per colony. Whiskers extend to data extremes. Right: Gamma distributions of the time in the colony estimated at the individual level (grey lines) and for colonies (coloured lines).

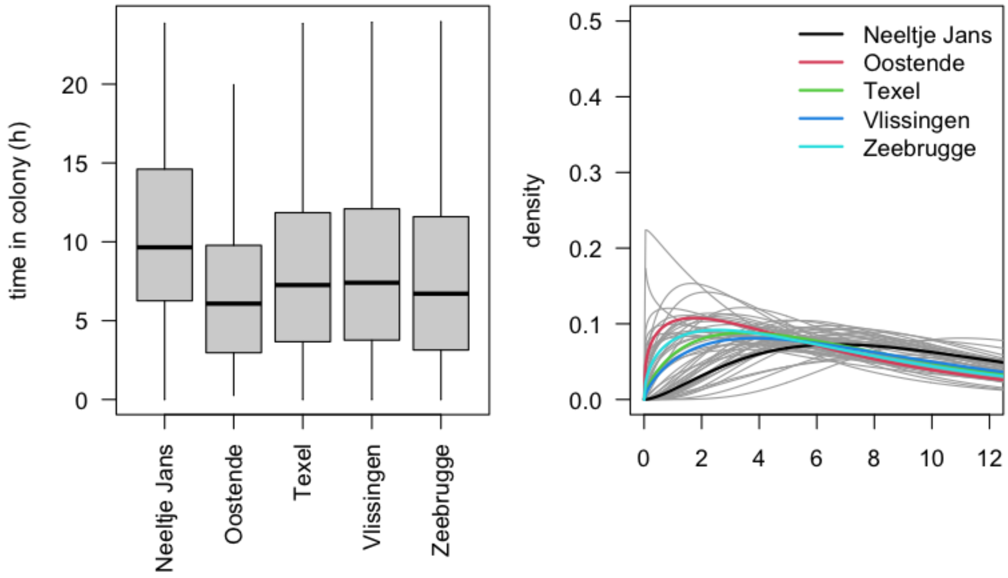

Figure 4-13 Time spent in the colony between foraging trips for non-breeders. Left: Variation in time bouts spent in the colony between trips, per colony. Whiskers extend to data extremes. Right: Gamma distributions of the time in the colony estimated at the individual level (grey lines) and for colonies (coloured lines)

4.5 Time spent in the colony between trips

The time spent in the colony between trips showed a left-skewed distribution, which was similar among colonies. However, individuals varied substantially in the time between trips (Figure 4-12 and Figure 4-13). For non-breeders, Neeltje Jans generally showed longer bouts in the colony (Figure 4-13).

4.6 Duration of terrestrial trips

The duration of terrestrial trips followed heavily left-skewed distributions for both breeders and non-breeders, which were approximated by gamma distributions (Figure 4-14 and Figure 4-15).

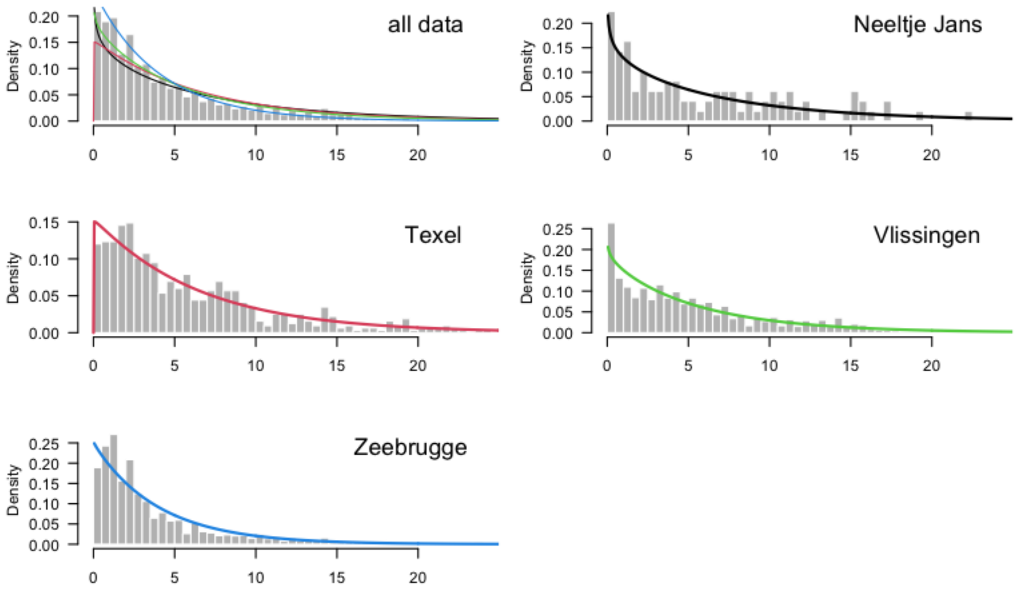

Figure 4-14 Distribution of the duration of terrestrial trips for breeders, for all data (upper left) and per colony. Note that the x-axis has been zoomed in to 0-24h (instead of the original 0-48h) to allow more detail.

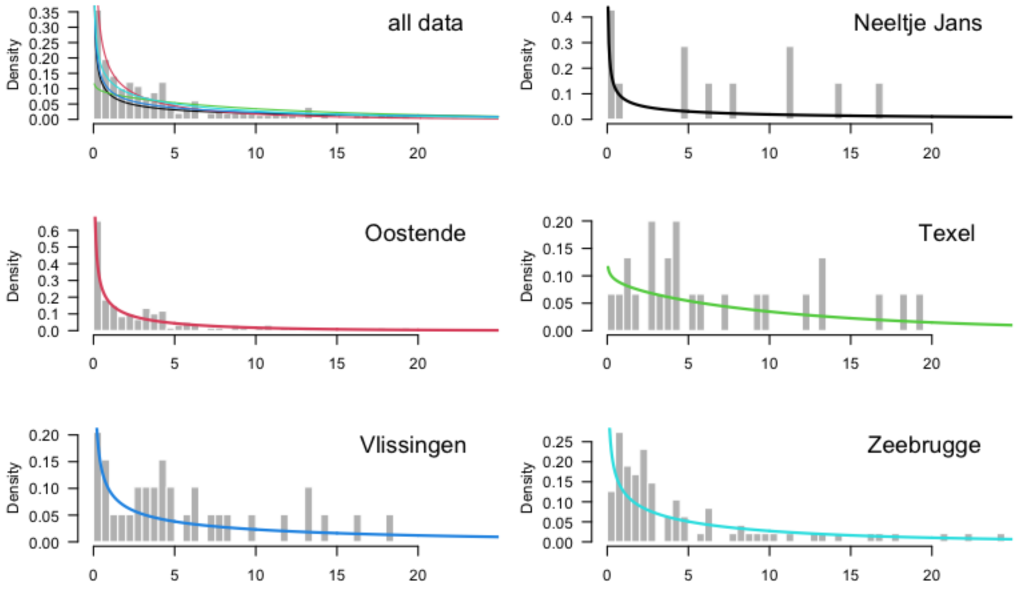

Figure 4-15 Distribution of the duration of terrestrial trips for non-breeders, for all data (upper left) and per colony. Note that the x-axis has been zoomed in to 0-24h (instead of the original 0-48h) to allow more detail.

4.7 Flight altitude near OWFs

Selected flight altitudes showed a broad distribution (Figure 4-16) around a mean of 44.2 m (SD = 0.6) and with a standard deviation of 36.4 m (SD = 0.4; N = 3398 positions). Despite selection for data containing less negative and extremely high positive values, selected altitude data contained values between -232 and 326 m.

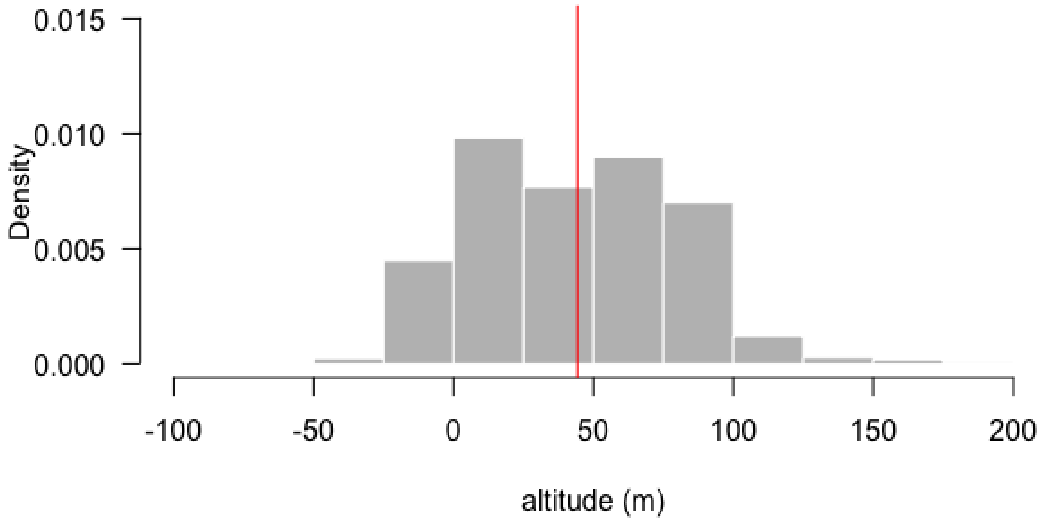

Figure 4-16 Flight altitude within 3 km of an OWF, across all individuals. The red line shows the mean flight altitude.

5 IBM results

5.1 Trip durations and time per state compared between IBM and tracking data

Example tracks show typical patterns in behavioural states during marine trips as defined in the HMM: colony, outbound, forage/stationary/transit, inbound and again the colony state (Figure 5-1). Not all tracks contain all states, but inbound, outbound and at least one other state always occur. This is in accordance with the tracking data, in which short trips also consist of an outbound, foraging/stationary and inbound segment.

The marine trip durations resulting from the IBM and the tracking data are similar for the breeders (Figure 5-2) and non-breeders (Figure 5-3). The match between model and data is better for the breeders than for the non-breeders. Trip duration is not hard-coded in the IBM directly, but emerges through the covariates on the transition probability of switching to an inbound trip. In addition, there is no colony-specific relationship for the effect of the trip durations on the state switches implemented. Therefore, such a good correspondence between model and data is remarkable.

The proportion of time spent in each state corresponded well between the selected tracking data used to fit the HMM and the output of a single run of the IBM for the breeders (Figure 5-4) and non- breeders (Figure 5-5), generally with some minor differences. However, for the non-breeders, the time spent stationary is lower than expected based on the data (Figure 5-5). Note that generic HMM parameters (step size, turning angle and transition probabilities) were used for all colonies, but that behaviour differed among colonies nonetheless (compare, e.g., Oostende and Texel), due to different environmental conditions around colonies, which the IBM was able to reproduce.

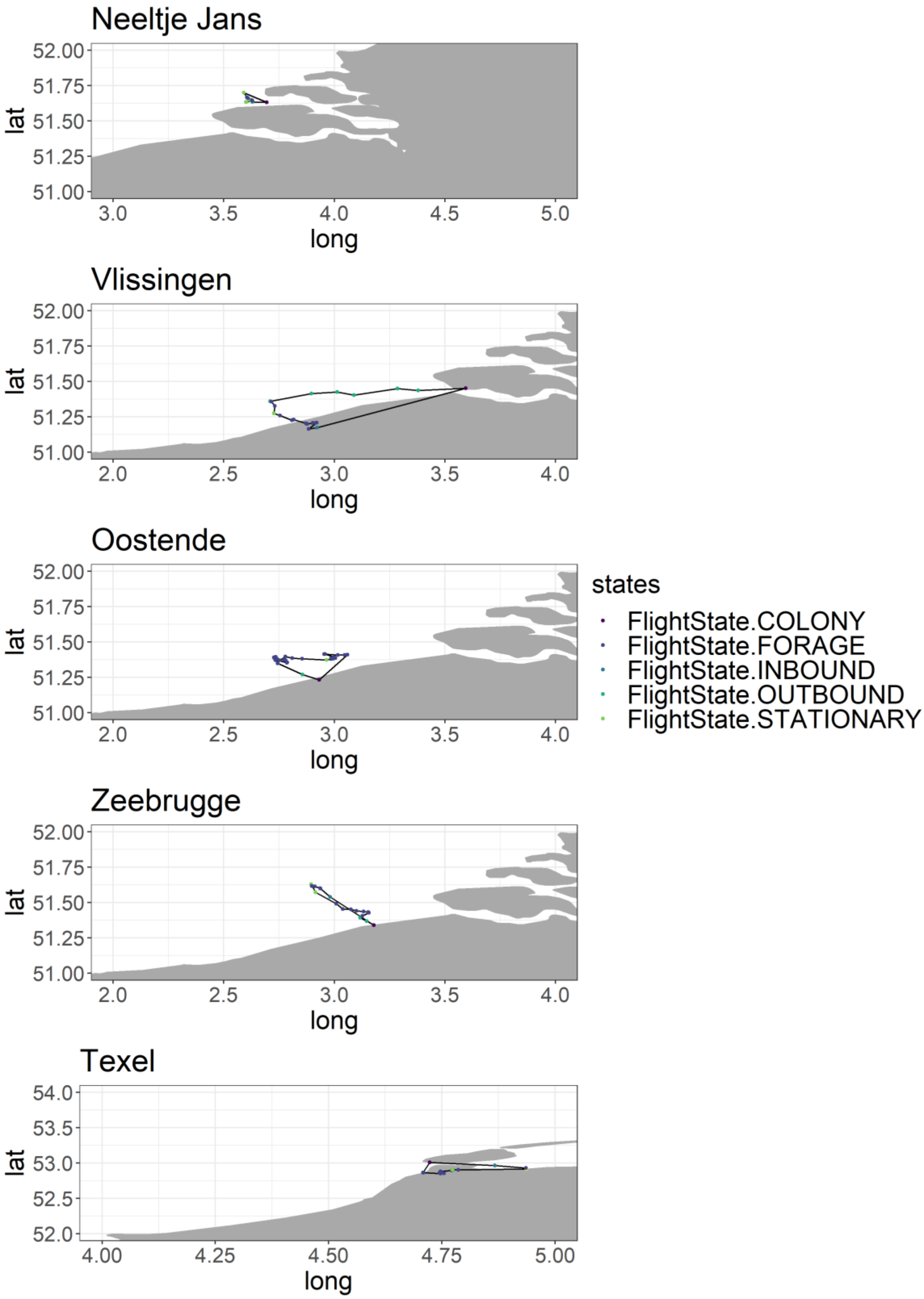

Figure 5-1 Examples of tracks per colony as simulated by the IBM

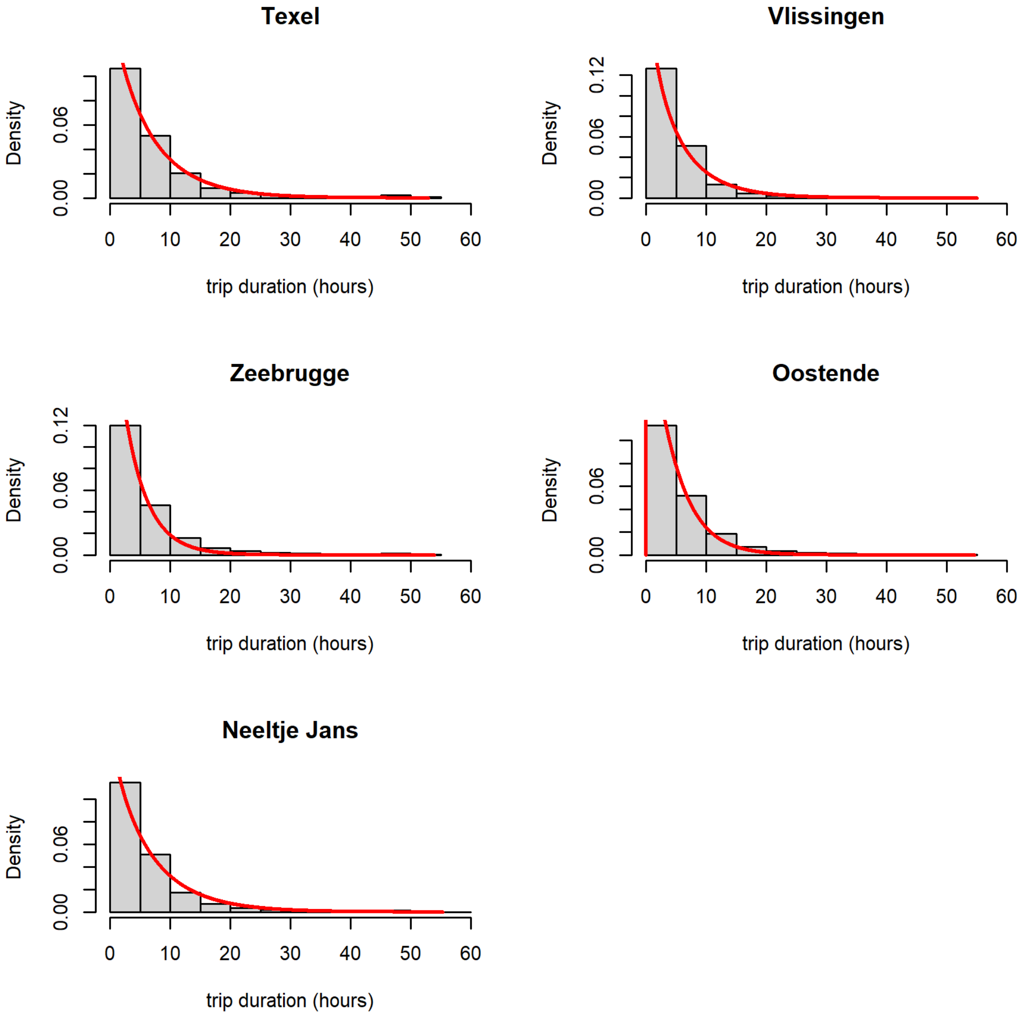

Figure 5-2 Duration of marine trips in the breeding model (grey bars; single simulation, 100 agents per colony, colony level parameters) and the tracking data (fitted gamma distribution; red lines).

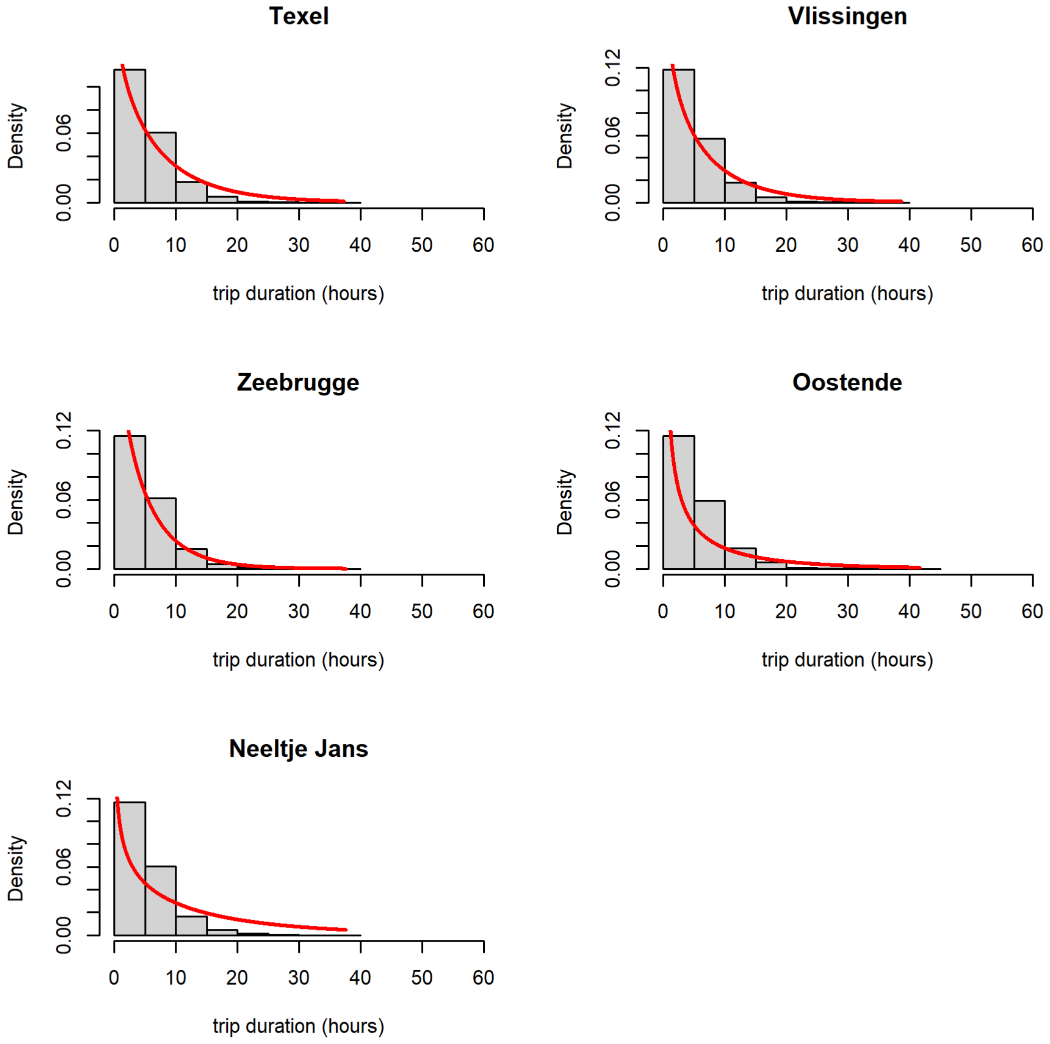

Figure 5-3 Duration of marine trips in the non-breeding model (grey bars; single simulation, 100 agents per colony, colony level parameters) and the tracking data (fitted gamma distribution; red lines).

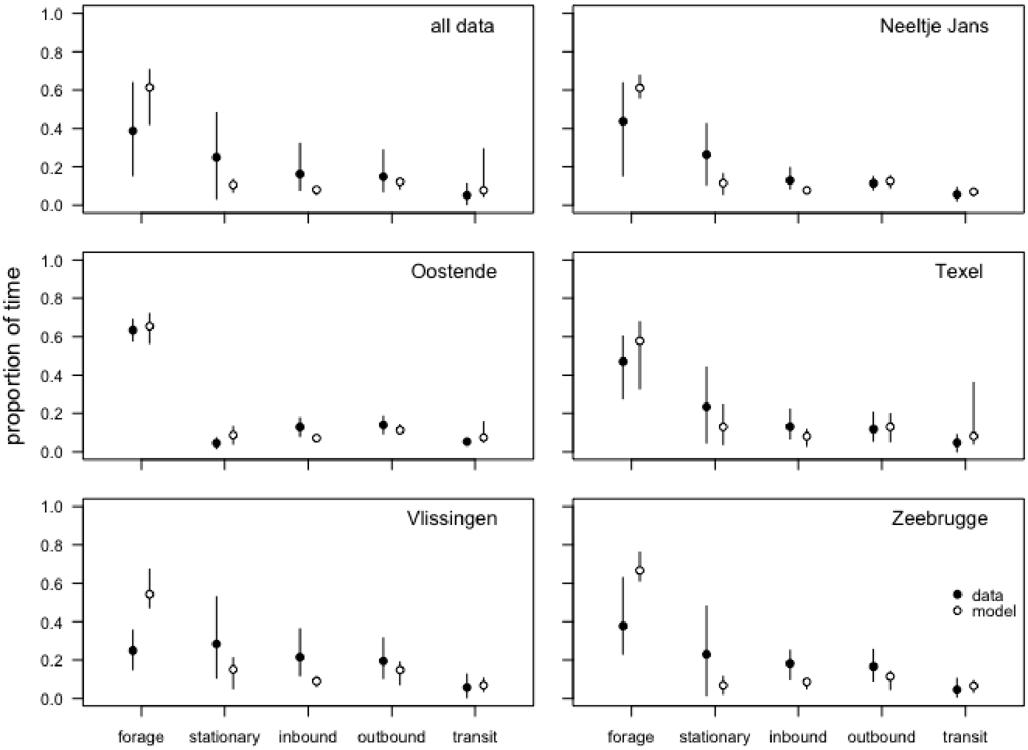

Figure 5-4 Time per state per colony for breeders for the IBM model (single simulation, 100 agents per colony, colony level parameters) and GPS-tracking data.

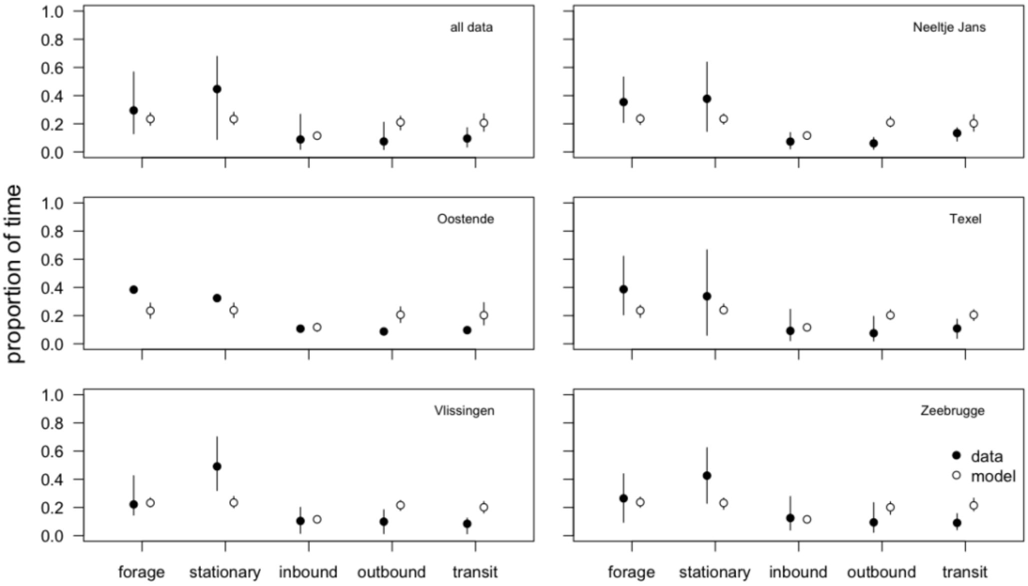

Figure 5-5 Time per state per colony for non-breeders for the IBM model (single simulation, 100 agents per colony, colony level parameters) and GPS-tracking data.

5.2 Similarity of Utilization Density kernels between data and IBM

The 95% Utilization Density (UD) kernels are generally wider for the model tracks than for the data tracks for all colonies and life stages that were considered (Figure 5-6 - Figure 5-15). For the spatial distributions of 50% and 75% of all locations, this difference is less pronounced. For Texel, Zeebrugge and Neeltje Jans, the 75% UDs show much more overlap with the OWF areas near the colonies for the model than for the data. In most cases, the model-based UD kernels based on the individual-level parameters and colony-level parameters show similar overlap with the data-based kernels. For the non-breeding individuals, the UD kernels based on the data are situated slightly more westwards than the UD kernels based on the model. As such, the data-based kernels show more overlap with the planned OWF areas than the model-based kernels do.

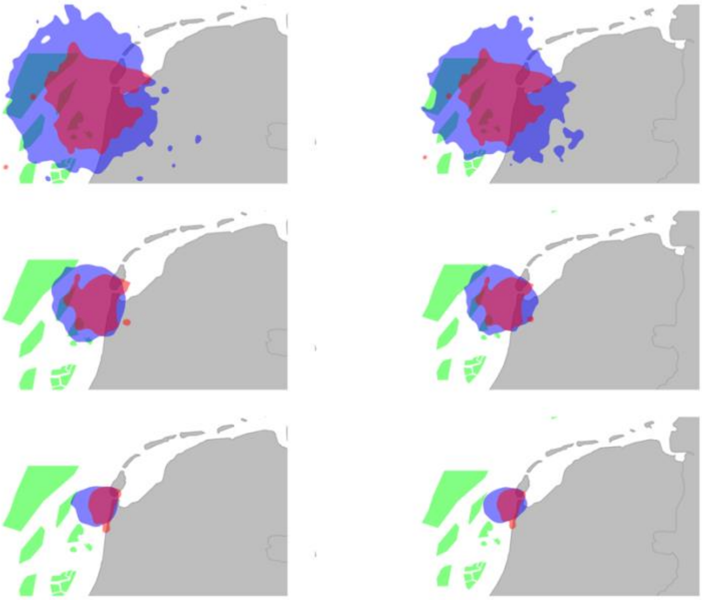

Figure 5-6 Texel, breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

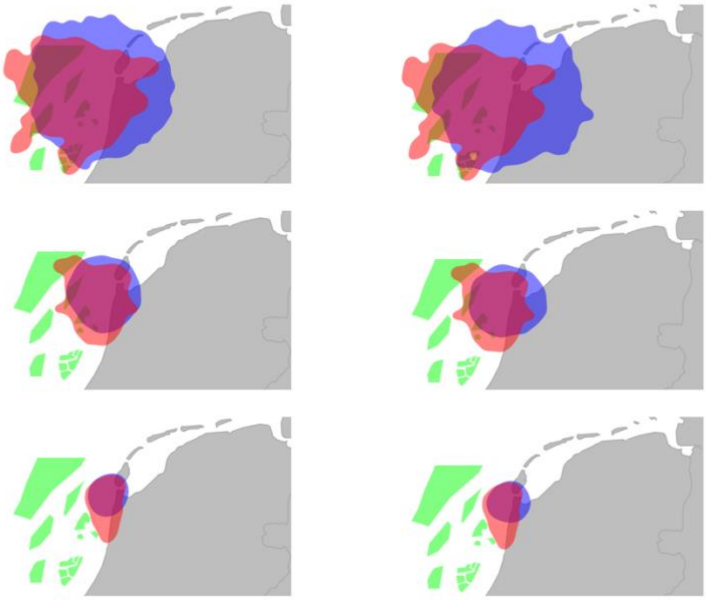

Figure 5-7 Texel, non-breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

Figure 5-8 Neeltje Jans, breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

Figure 5-9 Neeltje Jans, non-breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

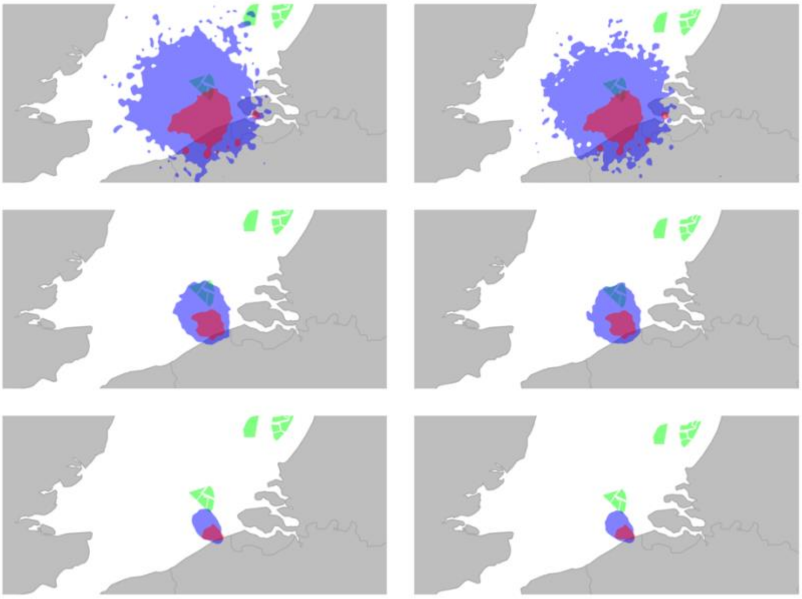

Figure 5-10 Zeebrugge, breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

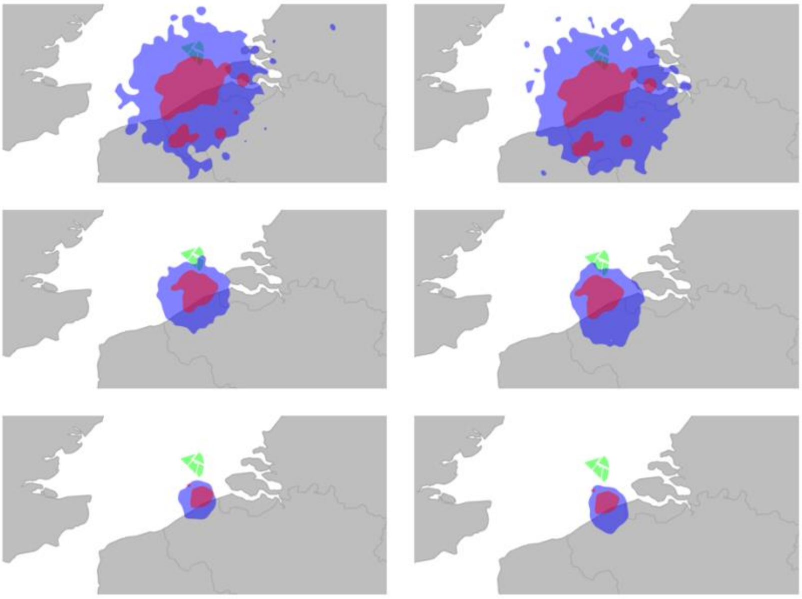

Figure 5-11 Zeebrugge, non-breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

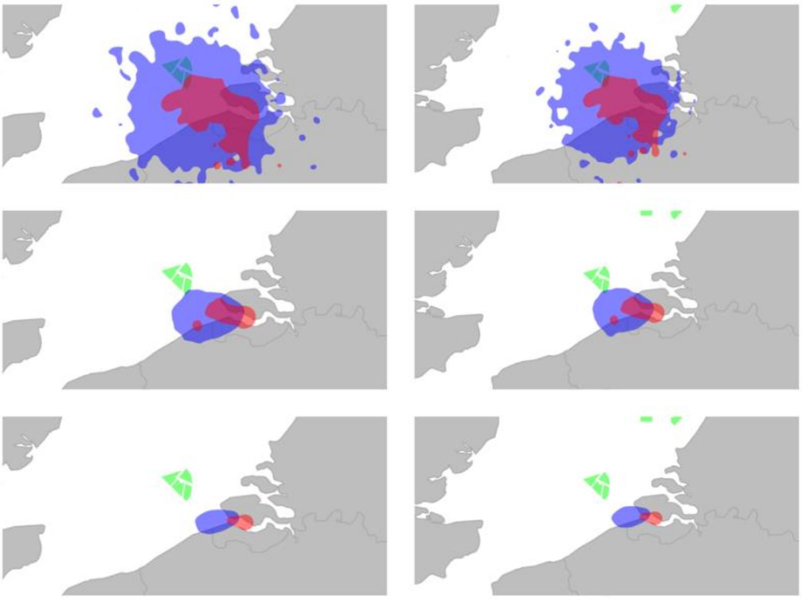

Figure 5-12 Vlissingen, breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

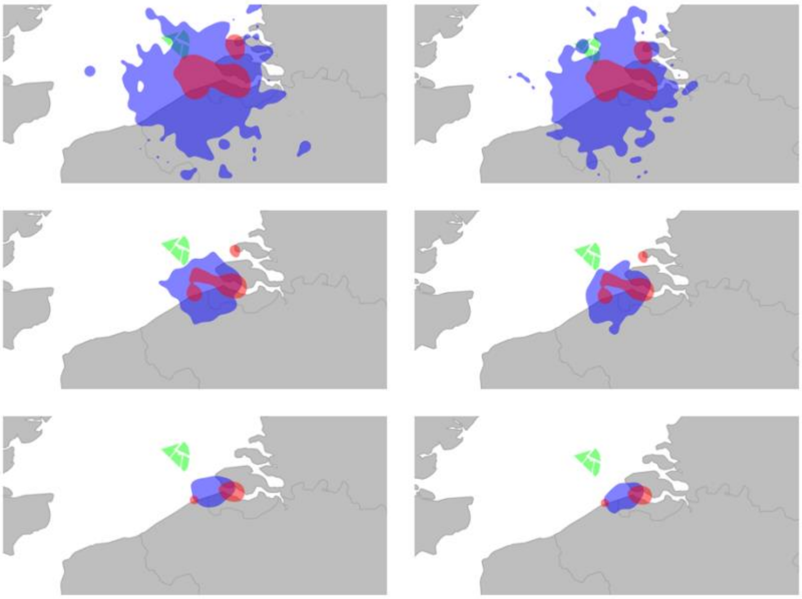

Figure 5-13 Vlissingen, non-breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

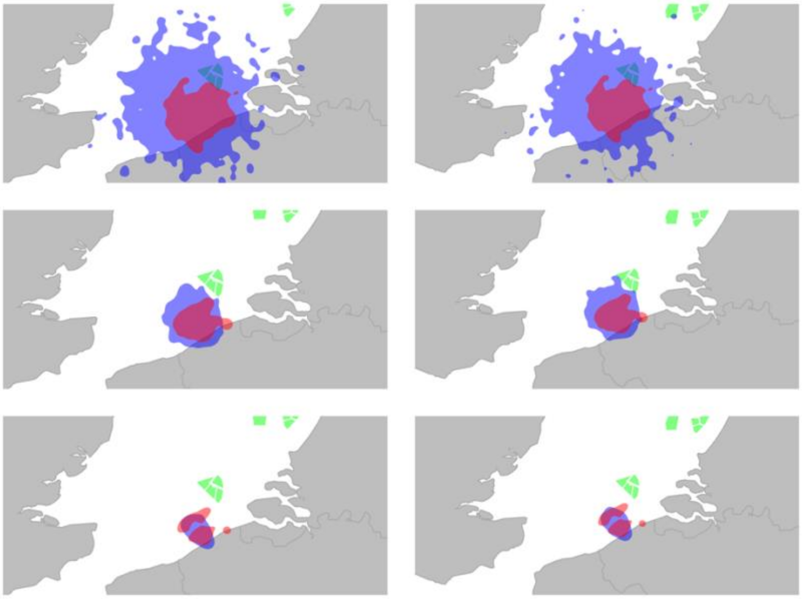

Figure 5-14 Oostende, breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

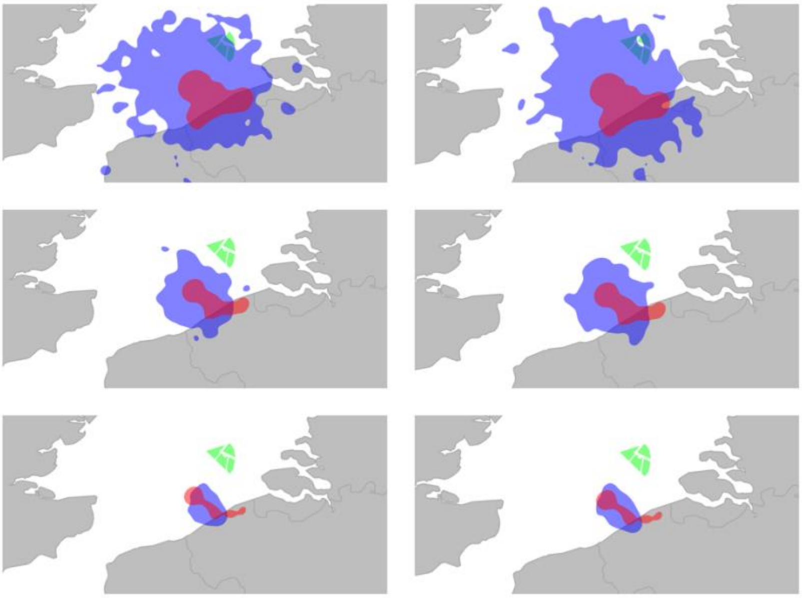

Figure 5-15 Oostende, non-breeding individuals: 50% (bottom), 75% (middle) and 95% (top) UD kernels for the tracking data (red) and an example model simulation (blue) for colony level (left) and individual level (right) parameters. OWFs are indicated in green.

The Bhattacharyya's Affinity (BA), an index of kernel overlap, ranged from 0.71 (Vlissingen) to 0.94 (Texel) between colonies (Figure 5-16) and life stages (Figure 5-17), indicating kernels were overall similar between model and data. For some colonies, the BA overlap indices are a bit higher for the breeding than for the non-breeding model (Oostende, Texel), for some they are similar (Vlissingen, Zeebrugge) and for Neeltje Jans, the breeders have a lower BA than the non-breeders. Compared to the colony-level parameters, individual-level parameters led to a higher variability in the BA score. For the non-breeders, the mean BA scores were also a bit lower for individual-level parameters than for colony-level parameters. This suggests that, for the non-breeders, colony level parameters lead to a better representation of the spatial distribution of the birds. For the breeders, the mean BA scores for colony-level parameters and individual-level parameters are similar.

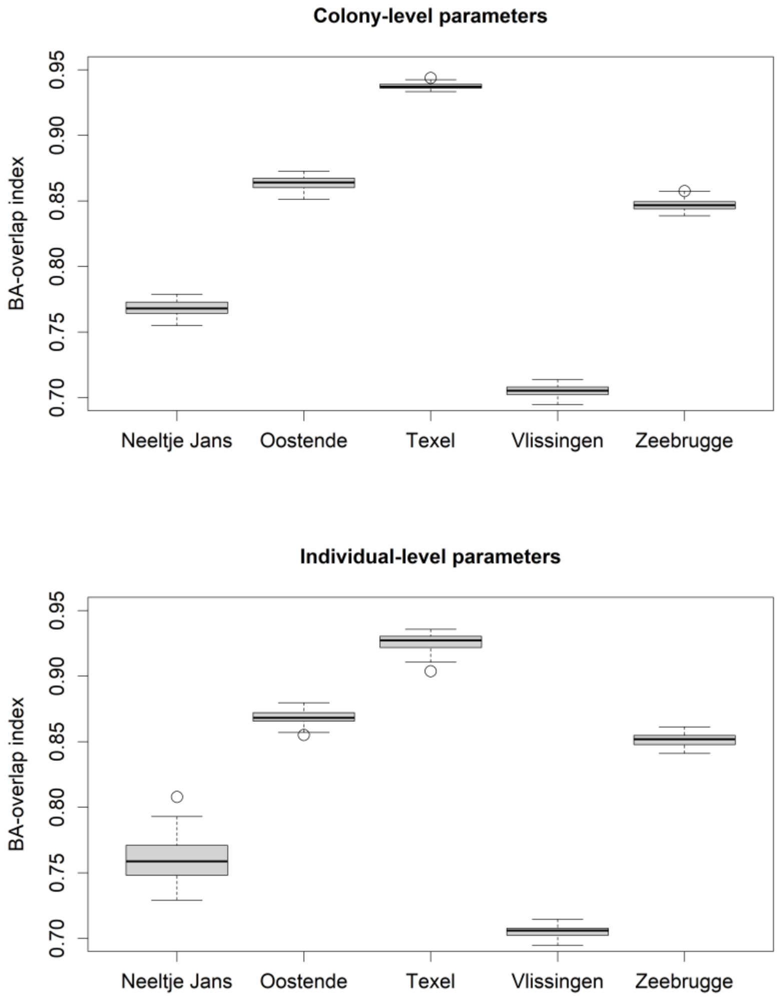

Figure 5-16 Overlap between model and data UD kernels for the breeders, for colony-level (top) and individual-level (bottom) parameters, as quantified by BA (Bhattacharyya's Affinity). Boxes and whiskers show the variation among 50 model simulations.

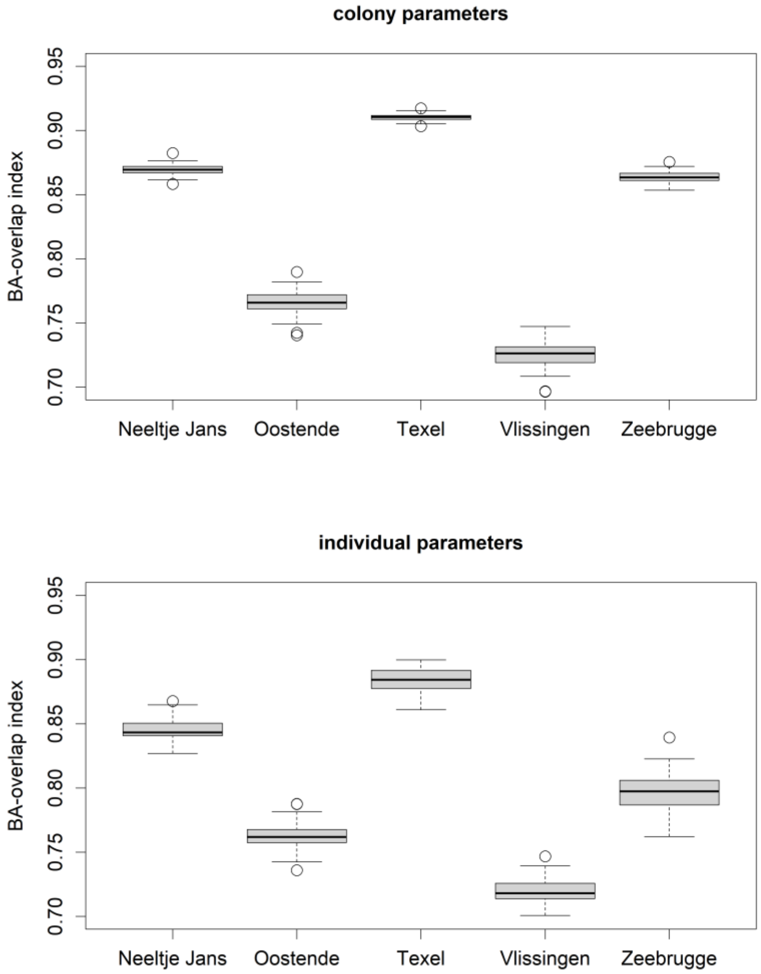

Figure 5-17 Overlap between model and data UD kernels for the non-breeders, for colony-level (top) and individual-level (bottom) parameters, as quantified by BA (Bhattacharyya's Affinity). Boxes and whiskers show the variation among 50 model simulations.

5.3 Collision mortality estimates

The collision mortality estimates differ strongly between colonies (Figure *5-18*- Figure 5-21 Total mortality). The mortality percentages are defined as the percentage of birds per colony that have died due to a collision at the end of the simulation period (a single breeding season of three months).

For the colonies with GPS track data (Table 5-2 and Table 5-3), Texel is the colony with most predicted collisions (~2% mortality). For Oostende, Neeltje Jans and Vlissingen the estimated mortality rates are lower (~1%, or lower), while for Zeebrugge the mortality rate is estimated at about 1.4%. The non-breeder model (Figure 5-20, Table 5-3) shows a similar pattern among the colonies as the breeder model (Figure *5-18*, Table 5-2), but the estimated mortalities are overall a bit lower, between 0.1-2.2% for the non-breeders versus 0.4-2.7% for the breeders.

The highest number of collisions for the southern colonies occurs in the Borssele wind farms (BSA; for the location of the wind farms see Figure 5-22, Table 5-2). For Texel, wind farm zone 2, Hollandse Kust South and Hollandse Kust NW claim most victims (Table 5-2). Table 5-1 shows the OWF names that correspond to the OWF abbreviations used in Table 5-2-Table 5-5.

For the colonies with no GPS tracking data (Table 5-4 and Table 5-5), IJmuiden is the colony with most predicted collisions (~7% mortality), followed by ~4% for the Maasvlakte. For the Wadden Island colonies the estimated mortality rates are <0.2%, except for Vlieland, for which ~0.8% mortality was predicted. The non-breeder model (Figure 5-20, Table 5-5) shows a similar pattern among the colonies as the breeder model (Figure *5-18*, Table 5-4) but the estimated mortalities are again overall lower, between 0.11-3.7% for the non-breeders instead of the 0.12-6.8% estimated for the breeders. Especially for the Maasvlakte and IJmuiden, the model predicts quite different mortality rates for breeders and non-breeders.

The difference between the OWF 2030 and 2040 scenarios is small for both breeders and non-breeders. Wind farm zones 4 and 7, which are added for the 2040 scenario relative to the 2030 scenario, claim only few victims. The differences between the 2030 and 2040 scenarios lie outside the standard error ranges only for some of the Wadden Island colonies without GPS track data (Ameland, Rottumeroog, Rottumerplaat, Terschelling and Schiermonnikoog). For these colonies, the 2040 scenario claims more victims, which leads to up to ~0.2% mortality, while for the 2030 scenario this is maximally ~0.09% mortality.

Generally, the model estimates similar mortality rates for the individual-level parameters (Figure 5-19, Figure 5-21) as for the colony-level parameters. For Neeltje Jans and Texel, however, the individual-level parameter values result in quite different estimates in the breeder model; the mortality rates with the individual-level parameters are about a quarter lower than with the colony-level parameter values (Table 5-2). For the non-breeders no such effect was observed (Table 5-3).

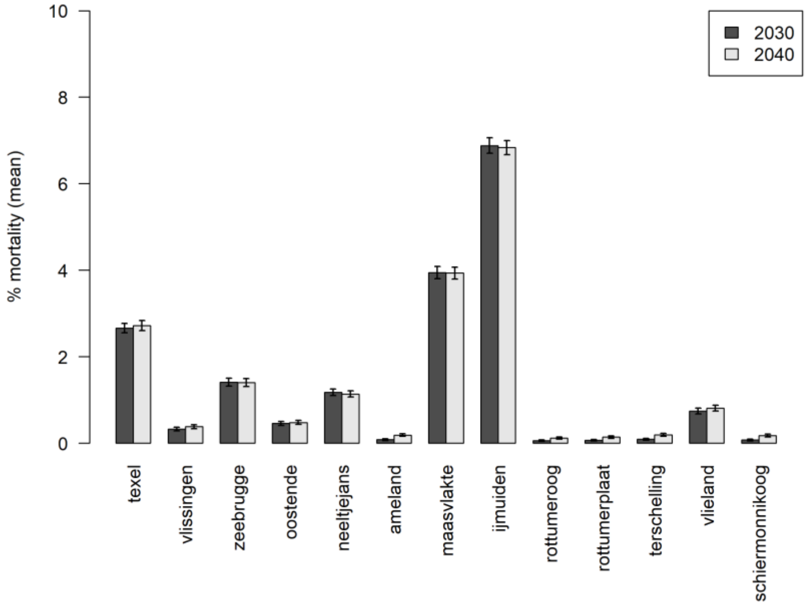

Figure 5-18 Total mortality estimates per colony from the breeding model, colony-level parameters, for the 2030 (black) and 2040 (grey) scenarios based on simulations with 250 agents per colony, 300 iterations, and colony level parameters. Whiskers indicate the standard error of the mean. Mortality percentage per colony is defined as the percentage of birds that died due to a collision at the end of the simulation period.

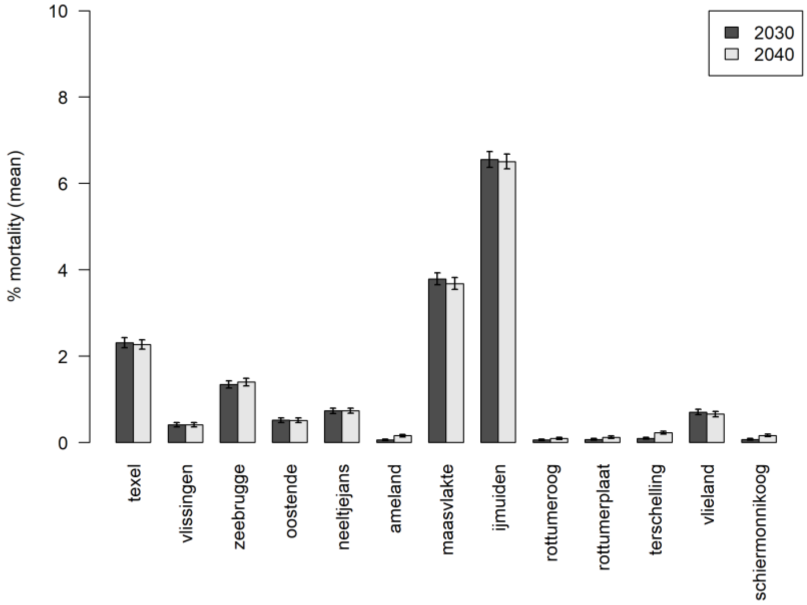

Figure 5-19 Total mortality estimates per colony from the breeding model, individual-level parameters, for the 2030 (black) and 2040 (grey) scenarios based on simulations with 250 agents per colony, 300 iterations, and colony level parameters. Whiskers indicate the standard error of the mean. Mortality percentage per colony is defined as the percentage of birds that died due to a collision at the end of the simulation period.

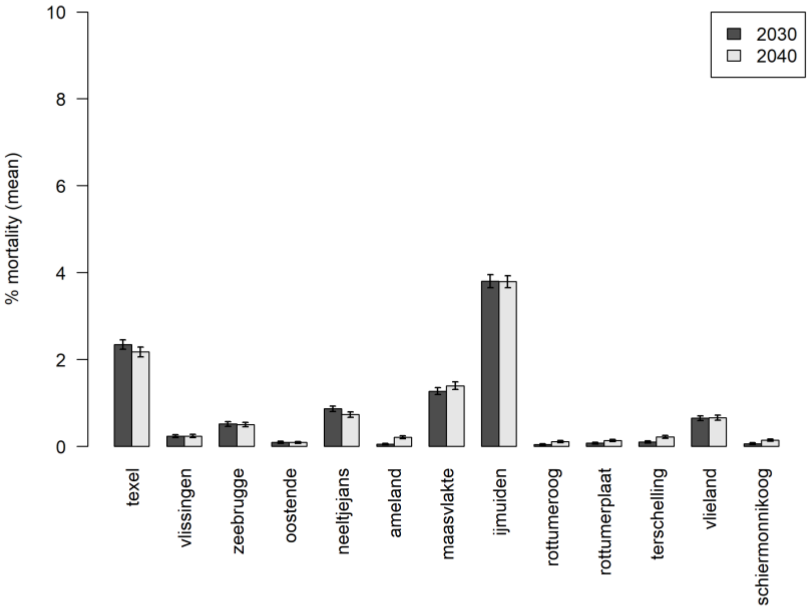

Figure 5-20 Total mortality estimates per colony from the non-breeding model, colony-level parameters, for the 2030 (black) and 2040 (grey) scenarios based on simulations with 250 agents per colony, 300 iterations, and colony level parameters. Whiskers indicate the standard error of the mean. Mortality percentage per colony is defined as the percentage of birds that died due to a collision at the end of the simulation period.

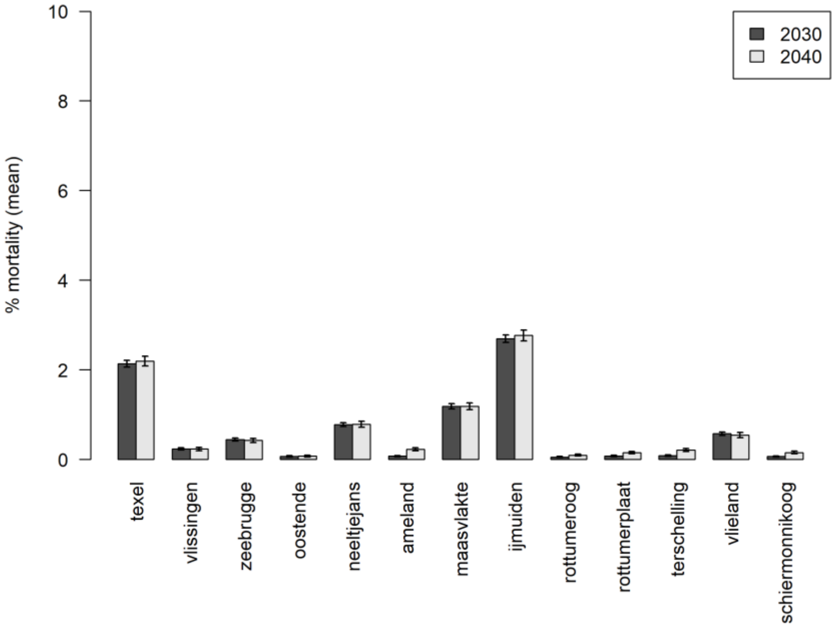

Figure 5-21 Total mortality estimates per colony from the non-breeding model, individual-level parameters, for the 2030 (black) and 2040 (grey) scenarios based on simulations with 250 agents per colony, 300 iterations, and colony level parameters. Whiskers indicate the standard error of the mean. Mortality percentage per colony is defined as the percentage of birds that has died due to a collision at the end of the simulation period.

Table 5-1 OWF abbreviations used and OWF name

OWF abbreviations	OWF name
2	Wind farm zone 2
5	Wind farm zone 5 (East)
BSA I-V	Borssele
Gem	Gemini
HKW I-II	Hollandse Kust West
HKN	Hollandse Kust North
HKZ I-IV	Hollandse Kust South
IJVer I-II	IJmuiden ver
OWEZ	Offshore Wind Farm Egmond aan Zee
PAWP	Princess Amalia Wind Farm
TNW	Ten Noorden van de Waddeneilanden
LUD	Luchterduinen
HKZW	Hollandse Kust SW
HKNW	Hollandse Kust NW
4	Wind farm zone 4
7	Wind farm zone 7

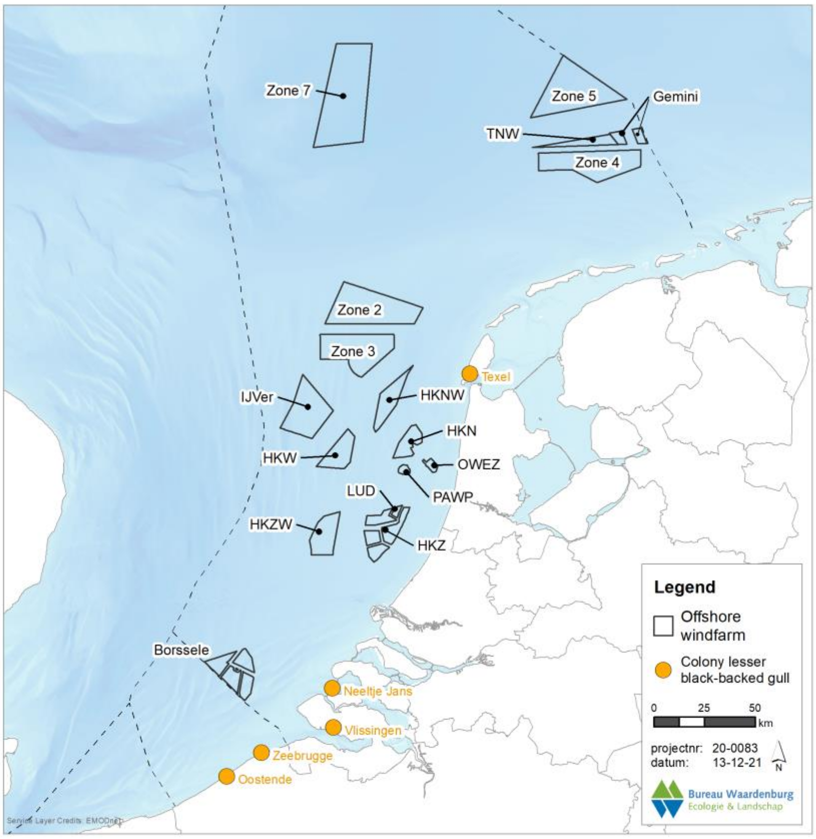

Figure 5-22 Location of lesser black-backed gull colonies with GPS data relative to the offshore wind farms used in the IBM.

Table 5-2 For the colonies with GPS-data, breeder mortality percentage estimates per colony and per windfarm for the 2040 OWF scenario, based on colony and individual level parameters. Mean values over 300 iterations with 250 birds per colony. OWFs with no predicted collisions are not shown.

Breeders, 2040 OWF scenario, colonies with GPS data										
OWF	Texel		Vlissingen		Zeebrugge		Oostende		Neeltje Jans	
	Col.	Indv.	Col.	Indv.	Col.	Indv.	Col.	Indv.	Col.	Indv.
2	0.3761	0.3415	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013
5	0.0000	0.0013	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA I	0.0000	0.0000	0.0757	0.0784	0.2286	0.2684	0.0904	0.0997	0.3522	0.1940
BSA II	0.0000	0.0000	0.1661	0.1834	0.5595	0.5409	0.1382	0.1542	0.3256	0.2299
BSA III	0.0000	0.0000	0.0731	0.0797	0.3468	0.3495	0.1289	0.1223	0.1528	0.0850
BSA IV	0.0000	0.0013	0.0492	0.0412	0.2100	0.1874	0.1076	0.1156	0.1103	0.0545
BSA V	0.0000	0.0000	0.0080	0.0093	0.0186	0.0279	0.0066	0.0106	0.0080	0.0093
Gem I	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HKW IN	0.0691	0.0585	0.0000	0.0013	0.0013	0.0027	0.0013	0.0000	0.0013	0.0013
HKW IZ	0.0186	0.0199	0.0027	0.0000	0.0027	0.0013	0.0000	0.0013	0.0133	0.0040
HKN	0.5953	0.5010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0066	0.0027
HKZ I	0.0532	0.0412	0.0000	0.0040	0.0013	0.0027	0.0000	0.0013	0.0146	0.0199
HKZ II	0.0266	0.0266	0.0000	0.0013	0.0080	0.0080	0.0000	0.0013	0.0332	0.0159
HKZ III	0.0213	0.0106	0.0013	0.0040	0.0120	0.0053	0.0027	0.0013	0.0385	0.0359
HKZ IV	0.0452	0.0425	0.0013	0.0000	0.0053	0.0000	0.0000	0.0000	0.0093	0.0173
IJVer I	0.0864	0.0625	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013
IJVer II	0.0983	0.0784	0.0000	0.0013	0.0027	0.0027	0.0000	0.0013	0.0040	0.0066
OWEZ	0.1262	0.1037	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0000
PAWP	0.1196	0.0917	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0000
TNW	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
LUD	0.0239	0.0385	0.0013	0.0000	0.0013	0.0000	0.0013	0.0000	0.0013	0.0040
Gem II	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HKZW	0.0066	0.0186	0.0053	0.0066	0.0053	0.0066	0.0053	0.0053	0.0664	0.0518
HKNW	1.0445	0.8239	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0040
4	0.0013	0.0027	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
7	0.0066	0.0053	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
total	2.7189	2.2698	0.3841	0.4106	1.4033	1.4033	0.4824	0.5143	1.1415	0.7389

Table 5-3 For the colonies with GPS-data, non-breeder mortality percentage estimates per colony and per windfarm for the 2040 OWF scenario, based on colony and individual level parameters. Mean values over 300 iterations with 250 birds per colony. OWFs with no predicted collisions are not shown.

Non-Breeders, 2040 OWF scenario, colonies with GPS data										
OWF	Texel		Vlissingen		Zeebrugge		Oostende		Neeltje Jans	
	Col.	Indv.	Col.	Indv.	Col.	Indv.	Col.	Indv.	Col.	Indv.
2	0.3096	0.3455	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0000
5	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA I	0.0000	0.0000	0.0478	0.0571	0.0850	0.0718	0.0120	0.0053	0.2086	0.2312
BSA II	0.0000	0.0000	0.1223	0.1063	0.2100	0.1927	0.0279	0.0372	0.3043	0.2884
BSA III	0.0000	0.0000	0.0425	0.0359	0.1169	0.0997	0.0266	0.0173	0.0957	0.1090
BSA IV	0.0000	0.0000	0.0213	0.0239	0.0797	0.0532	0.0279	0.0159	0.0651	0.0757
BSA V	0.0000	0.0000	0.0000	0.0053	0.0066	0.0093	0.0000	0.0013	0.0066	0.0066
Gem I	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HKW IN	0.0478	0.0399	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0000
HKW IZ	0.0252	0.0199	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0027
HKN	0.4970	0.5276	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HKZ I	0.0372	0.0372	0.0000	0.0027	0.0000	0.0000	0.0000	0.0000	0.0040	0.0080
HKZ II	0.0292	0.0279	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0093	0.0133
HKZ III	0.0133	0.0133	0.0027	0.0013	0.0027	0.0000	0.0000	0.0000	0.0120	0.0173
HKZ IV	0.0346	0.0492	0.0013	0.0000	0.0013	0.0013	0.0000	0.0000	0.0040	0.0066
IJVer I	0.0545	0.0664	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
IJVer II	0.0917	0.0797	0.0013	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0013
OWEZ	0.1116	0.0957	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
PAWP	0.1037	0.1037	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013
TNW	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
LUD	0.0252	0.0252	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0013	0.0013
Gem II	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HKZW	0.0093	0.0186	0.0013	0.0013	0.0000	0.0000	0.0000	0.0013	0.0186	0.0279
HKNW	0.7827	0.7389	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
4	0.0013	0.0027	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
7	0.0013	0.0027	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
total	2.1754	2.1940	0.2405	0.2339	0.5023	0.4279	0.0944	0.0784	0.7349	0.7907

Table 5-4 For the colonies with no GPS-data, breeder mortality percentage estimates per colony and per windfarm for the 2040 OWF scenario, based on colony level parameters. Mean values over 300 iterations with 250 birds per colony. OWFs with no predicted collisions are not shown.

Breeders, 2040 OWF scenario, colonies with no GPS data								
OWF	Ameland	Maasvlakte	IJmuiden	Rottumeroog	Rottumerplaat	Terschelling	Vlieland	Schiermonikoog
2	0.0040	0.0053	0.0811	0.0013	0.0013	0.0080	0.3017	0.0000
5	0.0266	0.0000	0.0000	0.0159	0.0106	0.0239	0.0066	0.0199
BSA I	0.0000	0.0213	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA II	0.0000	0.0133	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA III	0.0000	0.0093	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA IV	0.0000	0.0093	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA V	0.0000	0.0013	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gem I	0.0226	0.0000	0.0000	0.0213	0.0239	0.0080	0.0013	0.0266
HKW IN	0.0000	0.0279	0.1422	0.0000	0.0000	0.0000	0.0186	0.0000
HKW IZ	0.0000	0.0837	0.0917	0.0000	0.0000	0.0000	0.0040	0.0000
HKN	0.0000	0.0319	1.6850	0.0000	0.0000	0.0080	0.0771	0.0000
HKZ I	0.0000	0.4146	0.3442	0.0000	0.0000	0.0000	0.0040	0.0000
HKZ II	0.0000	0.7641	0.1555	0.0000	0.0000	0.0000	0.0027	0.0000
HKZ III	0.0000	1.3103	0.1076	0.0000	0.0000	0.0000	0.0040	0.0000
HKZ IV	0.0000	0.3601	0.3110	0.0000	0.0000	0.0013	0.0080	0.0000
IJVer I	0.0000	0.0027	0.0372	0.0000	0.0000	0.0013	0.0279	0.0000
IJVer II	0.0000	0.0452	0.1076	0.0000	0.0000	0.0000	0.0346	0.0000
OWEZ	0.0000	0.0066	1.7887	0.0000	0.0000	0.0000	0.0106	0.0000
PAWP	0.0000	0.0279	1.1269	0.0000	0.0000	0.0000	0.0146	0.0000
TNW	0.0279	0.0000	0.0000	0.0120	0.0173	0.0213	0.0040	0.0226
LUD	0.0000	0.1010	0.2432	0.0000	0.0000	0.0000	0.0013	0.0000
Gem II	0.0146	0.0000	0.0000	0.0213	0.0213	0.0146	0.0000	0.0186
HKZW	0.0000	0.6857	0.1063	0.0000	0.0000	0.0000	0.0040	0.0000
HKNW	0.0027	0.0146	0.5076	0.0000	0.0000	0.0133	0.2538	0.0013
4	0.0904	0.0000	0.0000	0.0492	0.0691	0.0890	0.0186	0.0877
7	0.0013	0.0000	0.0000	0.0000	0.0013	0.0066	0.0133	0.0013
total	0.1900	3.9362	6.8359	0.1209	0.1449	0.1953	0.8106	0.1781

Table 5-5 For the colonies with no GPS-data, non-breeder mortality percentage estimates per colony and per windfarm for the 2040 OWF scenario, based on colony level parameters. Mean values over 300 iterations with 250 birds per colony. OWFs with no predicted collisions are not shown.

Non-breeders, 2040 OWF scenario, colonies with no GPS data								
OWF	Ameland	Maasvlakte	IJmuiden	Rottumeroog	Rottumerplaat	Terschelling	Vlieland	Schiermonikoog
2	0.0053	0.0013	0.0252	0.0000	0.0000	0.0279	0.2711	0.0013
5	0.0146	0.0000	0.0000	0.0159	0.0093	0.0186	0.0013	0.0093
BSA I	0.0000	0.0292	0.0027	0.0000	0.0000	0.0000	0.0000	0.0000
BSA II	0.0000	0.0213	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA III	0.0000	0.0133	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
BSA IV	0.0000	0.0120	0.0013	0.0000	0.0000	0.0000	0.0000	0.0000
BSA V	0.0000	0.0013	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Gem I	0.0133	0.0000	0.0000	0.0173	0.0226	0.0053	0.0000	0.0093
HKW IN	0.0000	0.0066	0.1103	0.0000	0.0000	0.0013	0.0120	0.0000
HKW IZ	0.0000	0.0239	0.0957	0.0000	0.0000	0.0013	0.0053	0.0000
HKN	0.0027	0.0066	0.4651	0.0013	0.0000	0.0093	0.0651	0.0013
HKZ I	0.0000	0.1382	0.4598	0.0000	0.0000	0.0013	0.0133	0.0000
HKZ II	0.0000	0.2419	0.2405	0.0000	0.0000	0.0000	0.0027	0.0000
HKZ III	0.0000	0.4266	0.1993	0.0000	0.0000	0.0000	0.0013	0.0000
HKZ IV	0.0013	0.1648	0.6910	0.0000	0.0000	0.0013	0.0080	0.0000
IJVer I	0.0000	0.0013	0.0266	0.0013	0.0000	0.0000	0.0266	0.0000
IJVer II	0.0000	0.0173	0.0571	0.0000	0.0000	0.0013	0.0292	0.0013
OWEZ	0.0000	0.0093	0.4106	0.0000	0.0000	0.0027	0.0159	0.0000
PAWP	0.0000	0.0040	0.4000	0.0000	0.0013	0.0013	0.0080	0.0000
TNW	0.0120	0.0000	0.0000	0.0066	0.0159	0.0133	0.0000	0.0146
LUD	0.0000	0.0372	0.3415	0.0000	0.0000	0.0000	0.0027	0.0000
Gem II	0.0133	0.0000	0.0000	0.0120	0.0133	0.0066	0.0000	0.0106
HKZW	0.0013	0.2405	0.1183	0.0000	0.0000	0.0000	0.0013	0.0000
HKNW	0.0027	0.0027	0.1475	0.0013	0.0000	0.0133	0.1834	0.0000
4	0.1449	0.0000	0.0000	0.0598	0.0744	0.1169	0.0146	0.0983
7	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
total	0.2113	1.3993	3.7927	0.1156	0.1369	0.2219	0.6618	0.1462

5.4 Sensitivity analysis

The sensitivity analysis of survival estimates for the Texel colony was conducted for all model parameters using the breeder parameter set. Macro-avoidance and OWF activity percentage were found to have the strongest effect on the survival means and variances (Table 5-6 and Table 5-7). Intermediate effects were found for several parameters related to the transition probabilities between foraging and other behavioural states, such as transit-, inbound- and outbound-flight. For example, multiple parameters relating water depth to transition probabilities to and from the foraging behavioural state were found to be influential for the survival means and variances. Finally, the shape parameter of the distribution of step sizes in the foraging state was also among the ten parameters with the highest sensitivity for the survival means and variances.

Table 5-6 Sensitivity scores for the 10 highest ranking parameters for the mean survival, based on 201 iterations with 250 breeding birds for the colony Texel. Parameters entitled "Transitions" relate to transition probabilities between different behavioural states (in capital letters), in some cases in combination with an environmental parameter, such as water depth (depth) and distance to coast (dist.coast).

Parameter name	*Sensitivity score*
Macro avoidance	0.00144
OWF activity percentage	0.00106
Transitions FORAGE-TRANSIT.depth	0.00041
Transitions FORAGE-INBOUND.depth	0.00039
Transitions TRANSIT-FORAGE.depth	0.00032
Transitions FORAGE-INBOUND.dist.coast	0.00032
Transitions FORAGE-TRANSIT.intercept	0.00032
Transitions OUTBOUND-FORAGE.depth	0.00031
Shape for step sizes of FORAGE	0.000301
Transitions. OUTBOUND.-FORAGE.intercept	0.00029

Table 5-7 Sensitivity scores for the 10 highest ranking parameters for the variance in the survival, based on 201 iterations with 250 breeding birds for the colony Texel. Parameters entitled "Transitions" relate to transition probabilities between different behavioural states (in capital letters), in some cases in combination with an environmental parameter, such as water depth (depth), distance to coast (dist.coast) or distance to an OWF (OWF.dist).

Parameter name	*Sensitivity score*
Macro avoidance	0.00155
OWF activity percentage	0.00117
Transitions FORAGE-TRANSIT.depth	0.00050
Transitions FORAGE-INBOUND.depth	0.00048
Transitions FORAGE-TRANSIT.intercept	0.00041
Transitions FORAGE-INBOUND.dist.coast	0.00041
Transitions TRANSIT-FORAGE.depth	0.00040
Transitions OUTBOUND-FORAGE.intercept	0.00040
Shape for step sizes of FORAGE	0.00040
Transitions OUTBOUND-FORAGE.depth	0.00038

6 Discussion and knowledge gaps

6.1 Discussion

We developed an Individual Based Model (IBM) to estimate collision rates of lesser black-backed gulls *Larus fuscus* with offshore wind farms (OWFs) on the Dutch Continental Shelf (DCS). The IBM provides colony-specific and OWF-specific collision rates for lesser black-backed gulls breeding along the Belgian and Dutch North Sea coast. Being the first of its kind for OWFs and seabirds, the development of this model involved difficulties related to, e.g., data availability, obtaining parameters to describe movement patterns, assumptions and interpreting unforeseen results. Below, we discuss the first, preliminary version of our IBM.

6.1.1 High mortality rates

The IBM predicts relatively high collision mortalities. Between 0.1-2.7% mortality was estimated per colony for the colonies with GPS data during a single breeding period. For the colonies with no GPS data, this estimate was higher, between 0.1-6.8% per colony during the breeding season depending on the colony – partly because these colonies are closer to OWFs. Although the model generates exclusively relative mortality levels, these values can be translated into actual collision numbers based on the estimated size of the colonies. Considering for example the reported colony sizes in 2018 (Boele *et al.* 2020), our mortality percentages would lead to a total number of collisions of nearly 3,000 breeding lesser black-backed gulls of the studied Dutch colonies. In contrast, the latest assessment on the cumulative number of collision victims of all lesser black-backed gulls in the most extensive future wind farm scenario in the Netherlands predicted 153 casualties (Potiek *et al.* 2022).

In absence of actual measurements on collision rates of lesser black-backed gulls with offshore wind turbines, it is impossible to properly validate these mortality predictions. However, we suspect that the actual collision mortality is lower than our model predicts. For the IJmuiden colony, the breeding model predicts 1.7% mortality from OWEZ and 1.1% from PAWP, both of these being windfarms that are already present. The annual decline of the Dutch LBBG populations is less than 5% per annum (which in itself will probably only partly be attributable to collision mortality with OWFs). It must be noted that IJmuiden is one of the colonies for which we did not have tracking data available, which could lead to inaccuracies in the prediction. Furthermore, the difference in spatial use between the model and the data for the colonies with tracking data (Figure 5-6 – 5-15) indicates that some behaviour may be missing or is not properly captured by the IBM. The model predicts a wider spatial distribution for the birds, and thus perhaps also more overlap with the offshore windfarms than will occur in reality (see 6.1.3). Below we discuss several potential issues in the model that could affect the outcomes.

6.1.2 Missing behaviour component

For the colonies with no GPS data, the predictions of the IBM are highly uncertain. Due to the lack of UD kernels based on GPS data we have no reliable idea of the performance of the IBM for these colonies. Each colony has unique geographical characteristics such as their orientation of foraging trips relative to the coast and the spread in departure directions. The colony specific estimates for the initial directions, probability and duration of a terrestrial trip should thus really be determined at the colony level but are not available when GPS data are lacking. In order to improve the predictions for colonies with no data, there are two possibilities. First, obtain tracking data from the main colonies of interest (e.g. the largest colonies or those that are closest to OWFs) to provide better estimates for those specific colonies. Second, obtain tracking data from more colonies (not necessarily the colonies of main interest) to enable a statistical approach to relate colony-level behaviour to colony characteristics. Statistical models can then be used to better predict colony-level parameters. With the currently used data of only five colonies, robustly estimating colony-level parameters was not possible.

6.1.3 Overestimation simulated bird densities in OWFs

A major determinant of collision rates is the number of birds encountering the OWF. As none of the (planned) OWFs is close to lesser black-backed gull colonies with tracking data, none of the 50% Utilization Density (UD) kernels are overlapping with OWFs, while the 75% and 95% UDs do. Therefore, the lower densities at the periphery of the usual range are most relevant for predicting collision rates. However, the UD kernels of the IBM show a larger spatial range than the tracking data do, implying that simulated bird densities in OWFs will be overestimated. Better representation of the spatial distributions of the birds may be achieved through a more detailed analysis of preferred foraging areas. At this moment, the movement of the birds is not based on an explicit definition of foraging areas, while birds may, in reality, have preferred foraging areas that they direct their movements towards. Doing so, they may venture less far away from the colony than is now produced by the IBM based on the relation between the distance from the colony and the transition from outbound flight to foraging or stationary states, as well as the geometry of the foraging movements. If directed movements towards specific foraging sites could somehow be added to the model, these could strongly affect the UD kernels predicted by the model. However, this is difficult for several reasons. First, the location of targeted foraging areas may vary between colonies, individuals, breeding phase, time of day, season, tidal cycles and possibly other factors, and may even change in the future due to e.g. climate change, the realisation of offshore wind farms and changes in fishery activities. This variation will require to understand the spatio-temporal distribution of targeted foraging areas in great detail, and a method to generate a preferred foraging area to target for each foraging trip, individual, colony, etc. Second, foraging areas at sea are likely to be large habitats rather than specific sites. Third, directed flights towards foraging areas will require an additional behavioural state in the model. Fourth, modelling directed flights to foraging areas will require identification of these foraging areas before running HMMs. Alternatively, prediction of movements could be improved by adding covariates to the HMM that better capture the transition probabilities between behavioural states than our current set of covariates. This is also difficult, given the broad diet of lesser black-backed gulls and the difficulty of accurately capturing prey distributions with environmental proxies.

6.1.4 Avoidance of OWF areas

The HMMs included an effect of OWF on the transition probabilities between behavioural states, but this effect was weak. In other words, we did not find a strong effect of OWF presence on bird behaviour, but the HMM does not model movement directions directly. A potential response in distribution by the tracked individuals to operational OWFs was thus not explicitly included in the HMMs. Alternative approaches are needed to directly estimate macro-avoidance of OWFs by lesser black-backed gulls based on GPS-tracking data. One reason for the small effect of OWFs on behaviour in our HMM could be that currently a limited amount of GPS data is available from lesser black-backed gull colonies close to operational offshore wind farms. In most cases, these wind farms seem to lay at the edge of the foraging range of the studied birds and hence clear effects of wind farm avoidance are difficult to disentangle from other distance-related effects. Moreover, birds may avoid OWF areas at larger distances than previously assumed, resulting in small sample sizes near OWFs and without obvious changes in flight directions. In practice, the correction factor for avoidance used in the Band model does encompass this behaviour, as it is used to correct pre-construction densities to post-construction densities. In our IBM we mainly relied on GPS data from the post-construction period, which thus cannot tell us whether birds considerably changed their distribution and flight behaviour in the presence of the wind farms. In fact, the only proper way to estimate macro-avoidance that can be used in modelling exercises is to elaborately study bird habitat use in the pre-construction period of wind farms and compare that with data from the post-construction period. For example, the study currently running in the colony at Neeltje Jans promises to deliver such data, although the distance between the colony and the wind farm remains an important concern.

In addition to a better understanding of avoidance of wind farm areas, collision mortality estimates are known to be sensitive to meso- and micro-avoidance estimates (Masden *et al.* 2015). The IBM currently assumes that the encounter probability with wind turbines is proportional to the space the turbines occupy and turbines are assumed to be evenly distributed through space. The meso- and micro-avoidance are applied once an actual encounter with a turbine could occur. Yet, birds can in reality display sophisticated avoidance behaviour, such as a preference for flyways in between turbines, that are not caught in these assumptions. Also, birds, in particular highly manoeuvrable species like the lesser black-backed gull, may display several different flight types, such as flapping, soaring, gliding and circling. All these flight types may come with a different level of collision risk, while for instance soaring birds may also encounter a rotor swept area of the same turbine repeatedly within a very short time interval. Although the model of Band provides the possibility to calculate collision risk separately for flapping and gliding flight (Band 2012), the detailed flight behaviour of lesser black-backed gulls around wind turbines and the intraspecific variation in this is not yet studied well enough to be able to model this appropriately. In fact, our current level of understanding of general macro-, meso- and micro-avoidance rates remains limited (Cook *et al*. 2018, Dierschke *et al.* 2016). The best way to study micro- and meso-avoidance behaviour in OWF areas would be through the analysis of GPS track data collected at high temporal resolution (at the level of seconds of logging intervals). Whether sufficient GPS-positions are within OWFs to allow this analysis, should be the focus of a separate, detailed analysis of lesser black-backed gull behaviour around the turbines.

Once enough pre-construction and post-construction GPS data become available to study macro-avoidance behaviour and highly detailed GPS data to study meso- and micro-avoidance behaviour, the IBM could be updated with this information. With such data avoidance could eventually also become an emerging property of the IBM and hence further help in understanding the overall effects of offshore wind farms on the species.

6.1.5 Relative differences between wind farm areas

Regardless of the absolute outcomes of the model, the relative differences give an indication of the wind farm areas that are likely to claim more victims per colony, which result from higher encounter rates with wind farm areas. In addition, the IBM predicts higher collision mortalities for breeders than for non-breeders. The similarity in UD kernels between breeders and non-breeders suggest that not distribution, but other parameters such as perhaps connected to the time they spend at sea may cause the differences. For example, non-breeders can make longer foraging trips than breeders, because they are relieved from parental duties and therefore have no ‘obligation’ to regularly return to the colony. It is yet to be determined how such differences in behaviour affect the time spend near OWF areas. Further analysis could provide more insight in the differences in spatial use between these two groups in our model.

6.1.6 Model improvements

Several aspects of the model could be refined. In some instances, ad-hoc solutions for issues were implemented. One of these is the forcing of birds to return to the colony after 48 h. This mechanism was implemented because some trips were initially lasting much longer than can considered realistic; trips with a duration of 72 hours were observed. Such long trips were enabled by the negative effect of the time since colony departure on the transition probability to initiate inbound flights. In other words, the longer a trip lasts, the less likely it becomes that birds return to the colony. In reality, the probability to initiate the inbound flight should at some point increase with the time since colony departure. The negative relationship predicted by the HMM may be a result of the linear relation that is imposed in the HMM, whereas the relation in reality may be non-linear. One potential solution is to include b-spline smoothers of the time since colony departure in the HMM. Another potential improvement of the model is to let the behaviour of breeding individuals depend on the behaviour of their partner, such that their nest or chicks are always guarded by at least one parent.

In absence of field observations, the breeding status of tracked individuals had to be inferred from the tracking data. We selected a maximum time away from the colony of 48h. Part of the non-breeders, however, also still regularly return to the colony even after breeding failure, or during the pre-breeding period. Therefore, we cannot exclude that some non-breeders are included in the dataset used to model behaviour of breeding individuals and *vice versa*. However, the most important aspect of the data selected for the breeding period is that individuals returned to the colony regularly, thereby restricting the potential flight range of individuals.

Intuitively, including individual-level and colony-level parameter estimates is expected to result in more realistic model outcomes, especially since lesser black-backed gulls are known for their large inter-individual variation in diet, behaviour and preferred sites (Camphuysen 2013). Conceivably, not the data stream parameters, but the transition probabilities differ between individuals or colonies. However, including individual- or colony-level covariates in the HMM (as random intercepts in Generalized Linear Mixed Models) directly is not possible. In HMMs, individual- or colony-level effects can be included via mixtures, in which several sets of transition probabilities ('mixtures') are estimated, in addition to the probability that each individual or colony belongs to one of these 'mixtures' (McClintock & Michelot 2018). Unfortunately, our HMMs did not converge, potentially due to the starting values provided. Therefore, further attempts to starting values that result in converging models and stable results (possibly with a smaller set of covariates affecting the transition probabilities) may be advisable. However, it should be noted that implementing such mixtures in the IBM will result in additional assumptions and choices to be made, such as how the individual- or colony-level mixture probabilities should be generated for individuals and colonies with no tracking data. In addition, it would be interesting to consider variation between individuals in macro-avoidance. Some birds may be more likely to show risk averse behaviour than others. Such studies investigating such differences in avoidance of wind farms between individuals of the lesser black backed gull are largely lacking (Thaxter *et al.* 2018, 2019).

Transition probabilities were now modelled as a function of mostly static environmental covariates, such as water depth and distance to the coast. Although such covariates may capture the static distribution of foraging areas, they are unlikely to capture ephemeral phenomena such as schooling pelagic fish. This is a notorious difficulty in modelling at-sea distribution and behaviour of seabirds, which is not easily solvable, in particular in a generalist species such as the lesser black-backed gull with individual specialist foraging preferences, which forages on a wide array of prey species (Camphuysen 2013; Tyson *et al.* 2015).

Flight altitude of birds is an important factor in the risk of collision with wind turbines. Unfortunately, we were unable to include flight altitude in the HMM due to the large number of missing and/or unreliable values. If reliable altitudinal data would have been available, the HMM would probably have been able to distinguish more behavioural states, such as swimming (Shamoun-Baranes *et al.* 2011). More importantly, differences in altitude due to behavioural state changes would be available for the IBM. Altitude is one of the main components that determine collision risks for birds (Band 2012).

The sensitivity analysis (SA) that we applied to the model can be considered intermediate between a local and a global SA. It is a well-suited method when the number of parameters is high and/or the model is expensive to compute (Bracis *et al.* 2019). The advantage of varying multiple parameters simultaneously over a one-by-one parameter SA is that correlations between effects of different parameters are also considered. The SA indicated that the OWF activity percentage and the macro avoidance have the strongest effect on the collision mortality estimates. The OWF activity percentage is typically set to 100% as a precautionary approach, but finding more realistic values for this parameter could thus have strong effects on the mortality estimates. The role of macro avoidance was extensively discussed above. Surprisingly, we also found a relatively strong influence of the parameters related to state transitions between the foraging and other behavioural states. Apparently, the probability of simulated tracks to end up in OWFs strongly depends on the exact relation between environmental covariates (depth, distance to the coast) and the transitions from and to foraging flights. Some additional work is needed to tease out how all these factors are related. The strong dependence does not necessarily mean the current effects of environmental covariates on transition probabilities are biased, but indicate that it would be valuable to investigate whether adding additional covariates or non-linearity in the HMMs would improve the match between the distribution of GPS-tracking data and simulated tracks.

6.2 Knowledge gaps

Simulations of seabird movements need to be informed by high quality tracking data to obtain the right movement characteristics and transition probabilities. Unfortunately, tracking data are lacking for many groups other than breeding birds. For example, no tracking data were available for first-year juveniles, nor for immatures (between their first year and first breeding attempt). In addition, no distinction was made between birds that skipped breeding and those that failed breeding, although whether this distinction could be made can be further explored. Strong assumptions are therefore needed to estimate collision rates for these groups.

The avoidance behaviour of OWFs by lesser black-backed gulls is not understood in detail. The Utilization Density kernels of the tracking data around the colonies show remarkably little overlap with the closest OWF areas. For the model UDs, this is clearly different. This may be due to colony-specific movement patterns near OWFs, which do not necessarily reflect avoidance behaviour, but can also reflect habitat selection. Potential solutions include adding distance to OWF as a continuous covariate, rather than a binary variable as is used now, or include repulsion of OWFs in HMMs, but this would require additional behavioural states. Furthermore, parameters of avoidance were obtained from other studies and may therefore not reflect behaviour of the specific colonies, individuals and OWFs in our study. It would be advisable to estimate avoidance rates specific for the Dutch situation by modelling the GPS-tracking data from this study using integrated Step-selection Models (Peschko *et al.* 2020).

In addition, tracking data were lacking for some of the largest colonies along the Dutch coast, of which the colony at the Maasvlakte and adjacent areas of the port of Rotterdam (more than 25 000 pairs in 2013; Sovon 2019) is the largest. Having tracks from multiple (adjacent) colonies is important to estimate colony-level differences in behaviour as well as bird distribution. For example, northern gannets from adjacent colonies were shown to use non-overlapping spatial ranges (Wakefield *et al.* 2013). Although the data on lesser black-backed gulls used in our study do not appear to indicate such extensive segregation, it is remarkable that birds from Neeltje Jans predominantly move in south-westerly directions, which may be due to exclusion from areas to the west and northwest of Neeltje Jans by large numbers of birds from the Maasvlakte. Also, the Maasvlakte and IJmuiden colonies are situated closest to OWFs and GPS-tracks could be used to study behaviour of the birds in and outside of the wind farm areas.

Unfortunately, there were many missing and/or unlikely values in the altitude records in the GPS-tracking data. As a consequence, it was not possible to include altitude as a behavioural factor in the HMM, as HMMs require continuous data without missing values. Yet, it is likely that flight height varies with behavioural state, considering, for example, that during foraging birds will often be at low altitudes (Klaassen *et al.* 2011). Such differences in altitude with behavioural state could affect the estimations of collisions by the IBM; one of the main input parameters in the Band model is altitude. There is probably also clear spatial structuring in the behavioural states of the agents, if the states that are usually displayed further from the coast are states with lower altitude this would decrease the estimated collision mortalities and vice versa.

Collision rates may differ between day and night. In the current version of our IBM, these differences between day and night were not included. Although the analysis of tracking data would permit this, distinguishing this in the IBM would also require other parameters to be separately available for day and night, for example for avoidance behaviour. This was, however, not the case for all parameters. It is possible that birds are less or more able to signal turbines during the day and/or the night, or during inclement weather conditions.

The main difficulty encountered in developing the current IBM is the simulation of realistic foraging trips and we have proposed several ways in which the simulations could be improved. However, in future projects, exploring the possibility of circumventing the need to simulate individual trips would be an attractive alternative. This could perhaps be done by developing a statistical method based on the GPS-track data to predict the frequency of encounters between individuals and OWF. Such analysis would replace the bird density flux in the full Band model, which is currently used in most OWF assessments, with a more sophisticated estimate of the bird encounters with OWF.

7 Feasibility for the development of an IBM for three additional species

Based on a discussion of the output from the questionnaire with RWS, northern gannet *Morus bassanus*, black-legged kittiwake *Rissa tridactyla* and great black-backed gull *Larus marinus* were selected for the feasibility study. This chapter describes the data requirements and data availability for these species, and whether this is sufficient for the construction of an IBM. The inventory for the feasibility is based on literature research and expert knowledge.

7.1 Data required for individual-based model

A general description of the individual-based model (IBM) for lesser black-backed gull can be found in chapter 3. Data requirements for other species are largely comparable, although data on other environmental factors may be required. In this chapter, we describe the data requirements for the construction of an IBM. In chapter 7.2 and 7.3, we describe the availability of these data for northern gannet, black-legged kittiwake and great black-backed gull.

7.1.1 General individual-based model, without wind farms

The first step is to create a species-specific IBM to simulate movement behaviour in the area of interest. In case of lesser black-backed gull, this is the Dutch Continental Shelf. Within this inventory, we also look at data availability for the Dutch Continental Shelf.

Species-specific decisions

Types of individuals *Required:* tracking *data, ecological knowledge*

Movement behaviour may differ between individuals, depending on, e.g., age and breeding status. For each species of interest, the degree of variation needs to be explored and different types of individuals need to be specified. For example, in our IBM for lesser-black-backed gulls, **breeding** and **non-breeding** individuals were distinguished. We suggest the use of the same categories for these species. However, depending on data availability, additional distinctions can be made. For example, also first-year and immature stages could be distinguished, and non-breeding individuals could be split up in those that skip breeding in a given year (but that have been breeding previously) and those in which a breeding attempt failed. Within the breeders, distinctions can be made between different phases of the breeding cycle; for example: pre-breeding, incubation, chick-rearing and the post-fledging periods. To what extent these distinctions should and can be made, should be assessed per species.

Behavioural states *Required:* tracking *data, ecological knowledge*

Depending on the species, different behavioural states can be defined. In case of breeding lesser black-backed gull, the following behavioural states were distinguished for sea trips: **foraging**, **transit**, **stationary, outbound** and **inbound flight** (back to the colony). For the three species in this feasibility study, the definition of behavioural states is expected to be similar.

The categorization of these behavioural states is based on tracking data. Behavioural states differ in step length and turning angle, which can be categorized in an HMM, including the transition probabilities between states (see chapter 3). However, the number of states needs to be assigned a priori and should be informed by prior knowledge of the species, as well as an exploration of the tracking data.

(Breeding) locations and numbers of individuals *Required: (colony) locations and population sizes*

Depending on the research question, one or several colonies can be modelled within the IBM. For each colony, the number of individuals entering the individual-based model needs to be specified, as well as the location. This can be done based on colony counts, combined with expert knowledge and, if available, estimates of non-breeders and subadult individuals. Within the IBM for lesser black-backed gull, breeding adults are modelled to start in the colony. Non-breeding individuals can also be modelled from the colony of origin, but also elsewhere. For example, if the main interest is to show the potential effect of OWFs on numbers of birds in Natura2000 sites, simulations could also start within Natura2000 sites.

Variation among colonies *Required:* tracking *data of several colonies*

In addition to variation between individuals, movement behaviour may also differ among colonies. For example, the departure direction from the colony can vary, for example due to the distribution of foraging areas. Ideally, tracking data would be available for all colonies, but this is generally not realistic. In the absence of tracking data for part of the colonies, movement behaviour needs to be extrapolated from colonies with tracking data to colonies without tracking data. This is only possible if the differences in behaviour can be related to environmental factors, such as water depth gradients. Therefore, the variation in movement behaviour between colonies first needs to be assessed.

Factors affecting movement behaviour *Required:* tracking *data; data on environmental factors*

The transition probabilities between behavioural states can depend on external factors. For example, in case of lesser black-backed gull, the transition probability to foraging behaviour increased within 6 km from a fishing vessel. Prior knowledge of factors affecting movement behaviour helps to decide which variables to take into account. Factors which are known to play a correlate with movement behaviour in many seabirds are water depth, distance to coast, and for numerous species the distance to nearest fishing vessel. In addition, movement behaviour (e.g. flight altitude) may be different within a wind farm. If this is the case, this should be taken into account. See §3.7.3 for more details on modelling collision rates based on behaviour inside wind farms.

Within §7.2, we report which factors are likely to play an important role in determining movement behaviour of northern gannet, black-legged kittiwake and great black-backed gull. If data on these factors are available, the effect of these factors should be taken into account when fitting an HMM and constructing an IBM for these species.

Validation of general species-specific IBM

Validation IBM based on observed distribution *Required: survey data*

An important aspect of model construction is the validation, which shows whether the model predictions are plausible. Validation of the distribution of modelled birds can be done by comparing the modelled outcome with surveys of the area of interest. For the North Sea, this can be done, based on ESAS/MWTL survey data. Note that in at-sea surveys, no information is available on the breeding colony. A mismatch may therefore be caused by individuals from other breeding colonies and by immature individuals. Modelled movement behaviour can also be validated by comparing the model outcome with the tracking data.

Collision rate model

Time spent inside wind farm per individual *Required: locations of (planned) wind farms*

Based on the locations of (planned) wind farms, the IBM can produce information about the time spent inside wind farms per individual. In addition, the modelled movement behaviour and flight altitude of individuals within (planned) wind farms are based on tracking data of individuals flying through existing wind farms. Based on this number of individuals and the behaviour inside wind farms, the daily probability of collision can be modelled for each individual.

The collision rate model used for the lesser black-backed gull is based on Band (2012). Input parameters for this collision rate model include species-specific, turbine-specific and wind farm-specific parameters.

Species-specific data *Required: species characteristics*

The collision risk depends on the following species-specific characteristics: flapping versus gliding/soaring, body length, wingspan and avoidance within the wind farm.

Turbine-specific input data *Required: locations of wind farms, turbine and wind farm specifications*

The wind farm scenario should be defined based on the research question. In addition to current wind farms, this can include a road map with planned wind farms. Moreover, the collision rate model requires the following turbine-specific input data: rotor height, number of blades, angular velocity, blade width, pitch angle, rotor radius, percentage of activity and locations (and thereby spacing) of wind turbines.

7.1.2 Conclusion required data

As described in this chapter, the following data are required for the construction of an IBM using the same approach as used for the lesser black-backed gull in this project:

- Tracking data, ideally GPS data, from as many individuals and colonies as possible
- Ecological knowledge on, e.g., habitat preferences and behaviour
- Colony locations and number of breeding pairs (or numbers of birds in a given area, such as Natura2000 areas)

- Data on environmental factors which may affect movement behaviour
- Survey data for model validation

For the parameterization of the collision rate model, the following additional data are required:

- Species characteristics:
    - Flapping versus gliding/soaring flight
    - Body length
    - Wing span
    - Avoidance behaviour of wind farm and individual wind turbines
- Turbine characteristics
    - Rotor height
    - Number of blades
    - Angular velocity
    - Blade width
    - Pitch angle
    - Rotor radius
    - Percentage of activity

7.2 Inventory data availability for northern gannet, black-legged kittiwake and great black-backed gull

For each of these species of interest, we review the data availability for the construction of an IBM. This includes a review of the availability of tracking data, the existing knowledge on factors influencing movement behaviour and availability of data on these factors, and suitable data for validation.

7.2.1 Northern gannet

Data availability

Tracking data, ideally of several colonies

Tracking studies of northern gannets have been carried out in several breeding colonies, and results have been published for both the breeding season and migration (Table 7-1). More data are available on breeding adults than on immatures. Adults were breeding in the year of attachment of data loggers. If individuals were tracked for several years, skipped breeding during the following year can be inferred from the tracking data. If this is the case, these data can be used for analysing the movement behaviour of non-breeding adults that skip an entire breeding attempt. However, it is unclear whether these data are available. Two studies collected tracking data of immatures. These data likely give an impression of the movement behaviour of immatures, although it gives limited insight in variation among colonies.

Table 7-1 Tracking studies of northern gannet, relevant for modelling movement behaviour on and around the southern North Sea.

Location	Years	Season	Sample size	Reference
Bass Rock, UK	2015	Breeding season	34 adults, 15 immatures	Grecian *et al.* (2018)
Bass Rock, UK	2010-12	Breeding season	107 adults	Cleasby *et al.* (2015a); Cleasby *et al.* (2015b)
Bass Rock, UK				Lane *et al.* (2020)
Iceland	2010-11	Migration, wintering	15 adults	Garthe *et al.* (2016)
Helgoland, GE	2015-16	Breeding season	28 adults	Peschko *et al.* (2020)
Ailsa Craig, UK		Breeding season	adults	Hamer *et al.* (in prep.)
Wales, UK	2009	Breeding season	31 immatures	Votier *et al.* (2011)
Wales, UK	2006	Breeding season	25 adults	Votier *et al.* (2010)

Ecological knowledge

Northern gannets are present year-round on the Dutch Continental Shelf, with highest numbers in summer and autumn (Fijn *et al.* 2020). Gannets are strong flyers that range far from their breeding colonies. Therefore, also birds breeding north of the study area, particularly from Bass Rock, may visit the southern North Sea (Hamer *et al*. 2000; Wakefield *et al.* 2013), while many migrants from colonies further north migrate through the North Sea in autumn and spring, or winter here.

Other relevant ecological knowledge has been incorporated into the relevant sections.

Colony locations and number of breeding pairs

The main breeding locations around the Dutch Continental Shelf are reported in Table 7-2. Breeding locations closest to the Netherlands are Bempton Cliffs (NE England) and Helgoland (Germany). About half of the world population is breeding in Scotland, with Bass Rock as the largest breeding colony. Individuals from Bass Rock are known to make use of the Dutch Continental Shelf (Kubetzki *et al.* 2009).

Although individuals from Iceland may use the southern North Sea during winter, most individuals are found west of the British Isles, and off West Africa and southern Europe (Garthe *et al.* 2016).

Table 7-2 Breeding colonies nearby the Dutch Continental Shelf and number of breeding pairs of northern gannets.

Colony	Number of breeding pairs	Reference
Bass Rock (UK)	75,000	Grecian *et al.* (2018)
Shetland Isles (UK)	39,500	Mitchell *et al.* (2004)
NW France (FR)	14,900	Mitchell *et al.* (2004)
Bempton Cliffs (UK)	11,000	Mitchell *et al.* (2004)
Norway (NO)	4,500	Mitchell *et al.* (2004)
Helgoland (GE)	2,000	Mitchell *et al.* (2004)

Data on environmental factors which may affect movement behaviour

Peschko *et al.* (2020) studied how proximity to wind farms affected the flight behaviour of northern gannets breeding in Helgoland during the breeding season, showing that individuals were flying at significantly higher altitudes inside compared with outside the offshore wind farms. In addition, they found variation between individuals, with some individuals being ‘attracted’ to wind farms, and others ‘predominantly avoiding’ wind farms. Interestingly, the effect of inside versus outside a wind farm on flight height was not significant for individuals avoiding wind farms, but it was for individuals which were attracted to wind farms. However, the study found no significant change of the flight height with distance to the turbines.

Pettex *et al.* (2019) analysed habitat preferences of northern gannets during winter versus summer based on aerial surveys. In winter, water depth was the most important explaining variable, with a preference for shallow waters. In summer, distance to the closest colony was the most important variable, together with variables describing average and variation in sea surface temperature.

Votier *et al.* (2010) found effects of sea surface temperature on movement behaviour of adult northern gannets during the breeding season as well. In addition, they found effects of VMS-derived fishing vessel locations on flight path tortuosity. In absence of data on prey availability, they used chlorophyll *a* concentration and copepod abundance as proxy. These proxies also affected movement behaviour.

Data on the most important of these factors (locations of (planned) wind turbines, water depth, sea surface temperature and fishing vessel locations (VMS data)) are generally available or can be made available.

Survey data for model validation

For the Dutch Continental Shelf, data from MWTL/ESAS surveys can be used for model validation. If an IBM is constructed for an area outside the range of these surveys, alternative survey data should be acquired.

General decisions

Types of individuals

For northern gannet, we suggest an IBM with a structure comparable to the IBM for lesser black-backed gull. During the breeding season, we suggest distinguishing between breeding birds and non-breeding birds.

During the wintering season, some birds migrate to Africa while others move around in (N)W Europe (Garthe *et al.* 2016). As wintering (local) and migratory individuals have different types of movement behaviour, these types of individuals should be distinguished in the IBM. Searle *et al.* (2020) report that gannets in Scotland are associated with the colony between March and September. Note that the age distribution differs between the seasons, with a higher proportion of adults during winter due to immatures wintering in more southern areas (Camphuysen & Leopold 1994).

Foraging ranges of breeding adults are known to be much narrower than for immature birds (Grecian *et al.* 2018). Further analysis of tracking data can give insight into movement behaviour of non-breeding adults. Based on the current inventory, it is not feasible to conclude whether these data on non-breeding adults are available. If data availability is sufficient, non-breeding adults as well as immatures should either form a combined category, or form separate categories, depending on the variation in movement behaviour between those groups of individuals.

As described in the previous paragraph, individual differences in behaviour were found, with some individuals being ‘attracted’ to wind farms, and others ‘predominantly avoiding’ wind farms (Peschko *et al.* 2020).

Habitat use of northern gannets seems to be sex-specific (Phillips *et al.* 2017; Clark *et al.* 2021), with males preferably foraging in mixed, shallow waters, and females in stratified, deeper offshore waters. This may result in variation in collision risk between sexes. If data availability is sufficient, and if one is interested in differences in collision risk between the sexes, it would be interesting to differentiate between sexes in the IBM.

Behavioural states

Peschko *et al.* (2020) analysed movement behaviour using the following behavioural states: resting, transit and foraging. These are ecologically relevant states but are insufficient to also model the regular movements to and from the colony. In order to model central place foraging from the colony, additional states for outbound and inbound flights should be added, as well as a colony-state. This results in the six behavioural states as defined for lesser black-backed gull. The definition of these behavioural states is based on the step length and step size as obtained from temporally regularized tracking data.

Breeding locations and numbers of individuals

See Table 7-2 and the relevant paragraph of the data availability section.

Variation between colonies
Tracking data are available for several colonies. Using these data, variation in behaviour among colonies can be analysed.

Hamer *et al.* (in prep.) compared movement behaviour of adults breeding at Ailsa Craig and Bass Rock, and found that individuals from these colonies made trips of similar duration and travelled similar distances at sea, despite a large difference in colony size. Wakefield *et al.* (2013) found evidence for spatial segregation between colonies. This indicates that the foraging areas used differ between breeding colonies.

Factors affecting movement behaviour
The effect of external factors on movement behaviour needs to be analysed based on tracking data and external factors. We suggest that at least the effect of water depth, distance to coast, distance to wind farm, and distance to nearest fishing vessel should be analysed. Data on water depth should be available and distances to coast and nearest wind farm can easily be calculated. In order to assess the effect of the distance to the nearest fishing vessel, VMS data can be used. These data are not publicly available, but can be used if permission is acquired.

In addition, sea surface temperature was found to affect movement behaviour, as well as two proxies for prey availability (chlorophyll *a* concentration and copepod abundance) (Votier *et al.* 2010). If these data are available, these factors should be tested as well.

Other decisions to be made based on tracking data and assumptions
- Total trip duration of breeding and non-breeding individuals
- Initial departure direction of breeding and non-breeding individuals
- Length of breeding season
- Departure location of non-breeding individuals
- When is a breeding attempt assumed to be aborted

Required input for collision rate modelling
Collision rates were modelled for northern gannet in Rijkswaterstaat (2015) using the Band model (Band 2012). All input parameters were available or could be estimated. This analysis is currently being updated by Bureau Waardenburg within KEC4.0.

7.2.2 Black-legged kittiwake

Black-legged kittiwakes is an exclusively coastal and marine species. The species is breeding from Canada through Greenland and into Russia, and winters off the coasts of USA and West Africa as well as in the Pacific (Wernham *et al.* 2002; Mitchell *et al.* 2004). Black-legged kittiwakes also breed in the North Sea on platforms (Camphuysen & Leopold 2007), but numbers, trends and exact locations are unknown. Aerial surveys during the breeding season would improve the understanding of the Dutch breeding population.

Data availability

Tracking data, ideally of several colonies

Most of the available tracking data are collected during the breeding season (Table 7-3). However, Swindells (2019) reports foraging behaviour for the wintering season.

The types of individuals tracked are mostly breeding adults. In most cases, breeding failure is not analysed. However, Ponchon *et al.* (2014) did look at the effect of breeding failure on foraging behaviour.

In conclusion, data on breeding adults and non-breeding adults are available for the breeding season. For the non-breeding season, data on adults are available as well. Data on immatures and juveniles are lacking.

Table 7-3 Tracking studies of black-legged kittiwake, relevant for modelling movement behaviour on and around the southern North Sea.

Location	Years	Season	Sample size	Reference
NE England, North Sea; two colonies, one on the Farne Islands, and one inland	2010-12	Breeding season	19 in offshore colony, 5 in inland colony, loggers only attached for approx. 24 hours	Redfern and Bevan (2014)
Britain and Ireland	2010-14	Breeding season	464 breeding adults; recapture after approx.. 24 hours	Wakefield *et al.* (2017)
Norway, two colonies (Sør-Gjæslingan and Anda)	2011-14	Breeding season	294 breeding adults	Christensen-Dalsgaard *et al.* (2018)
Quebec, two colonies	2019	Breeding season	6 breeding adults	Petalas *et al.* (2021)
Forth-Tay region, UK, three colonies	2010-18	Breeding season	In total 147 breeding adults: 35 in Fowlsheugh, 87 in Isle of May, 25 in St. Abbs Head	Searle *et al.* (2020)
Lowestoft, urban colony in east UK	2012-19	Winter and breeding season	15 adults, data for up to four years	Swindells (2019)
Hornøya, southern Barents Sea	2011	Breeding season	9 adults, three of which failed breeding	Ponchon *et al.* (2014)

Ecological knowledge

The black-legged kittiwake is an exclusively coastal and marine species, seldom being found inland. The distribution is concentrated around the breeding colonies during the breeding season, while the species remains at open sea outside the breeding season. Kittiwakes are known to breed on the Dutch Continental Shelf on platforms (Camphuysen & Leopold 2007), but numbers, trends and exact locations are unknown. The species is year-round present in the North Sea, with higher numbers during winter. Kittiwakes migrating through the southern North Sea include not only birds from North Sea colonies, but also birds from Norwegian Sea and Barents Sea colonies. The majority of the birds in the southern North Sea in winter are expected to stem from these northern populations (Furness & Trinder 2016). Other relevant ecological knowledge has been incorporated into the relevant sections.

Based on a GPS analysis of kittiwakes breeding in Quebec, the average duration of a foraging trip of kittiwake was 8.6 ± 1.6 hours, covering a relatively large area (Petalas *et al.* 2021). The average of colony-specific maximum foraging ranges for kittiwake is 60.0 km (Thaxter *et al.* 2012). Kittiwakes tend to forage at specific locations, presumably with high prey densities (Petalas *et al.* 2021).

Movement behaviour clearly differs between the breeding season and the non-breeding season. Although data on foraging behaviour during the non-breeding season are limited, Swindells (2019) analysed this period for individuals from Lowestoft, an urban colony in the east of UK. The 15 individuals tracked from this colony dispersed over 6,000 km from the colony, covering almost the entire wintering area covered by birds from other colonies studied in Frederiksen *et al.* (2012), reaching the east coast of the USA in the west, Spain in the south, and Germany in the east of their range (Swindells 2019).

Ponchon *et al.* (2014) showed that upon breeding failure, the foraging patterns of individuals drastically change. These individuals which initiated breeding, travelled further north after breeding failure. Individuals which failed breeding performed long trips, with a maximal distance of 853 km in mid-July.

Colony locations and number of breeding pairs

The majority of kittiwakes in the southern North Sea in winter are expected to stem from Norwegian Sea and Barents Sea colonies (Furness & Trinder 2016). All relevant breeding colonies and the number of breeding pairs are reported in Table 7-4. Note that there is no recent data on the numbers of kittiwakes breeding on platforms in the (Dutch) North Sea.

Table 7-4 Breeding colonies nearby the Dutch Continental Shelf and number of breeding pairs of black-legged kittiwakes.

Colony	**Number of breeding pairs**	**Reference**
Norway (NO)	500,000	Mitchell *et al.* (2004)
Eastern Scotland (UK)	99,500	Mitchell *et al.* (2004)
Shetland and Orkney (UK)	75,000	Mitchell *et al.* (2004)
Eastern England (UK)	70,000	Mitchell *et al.* (2004)
Northeast Scotland (UK)	50,000	Mitchell *et al.* (2004)
Helgoland (DE)	6,500	Mitchell *et al.* (2004)
Denmark (DK)	1,600	Mitchell *et al.* (2004)
Netherlands (NL)	unknown	Camphuysen and Leopold (2007)

Data on environmental factors which may affect movement behaviour

Kittiwakes tend to forage at specific locations, presumably with high prey densities (Petalas *et al.* 2021). Although Watson (1981) found associations between kittiwakes and fishing boats in the Irish Sea, this was not found in the North Sea around the Shetland Islands (Hudson & Furness 1989).

Redfern & Bevan (2014) showed that the majority of foraging took place on sea areas with a water depth below 80 meters. The pattern of foraging trips consisted of direct flights to specific foraging areas, interrupted by short foraging bouts, before continuing in the same direction. This may indicate an association with fishing vessels, but this has not been analysed within this study.

In addition, Redfern & Bevan (2014) showed that foraging trips started throughout day and night, with most trips starting in the early morning, during the afternoon or late evening. The authors found no significant difference in trip duration between trips started in the day or in the period 1900–0200 hour.

Christensen-Dalsgaard *et al.* (2018) analysed movement behaviour of kittiwakes from two different colonies and showed that on one of these colonies the relative amount of time spent resting was lower for individuals using oceanic foraging areas compared to individuals using coastal areas. For the other colony, type of foraging area did not affect the time spent in each behaviour state. The decision of foraging area (coastal versus offshore) depends on departure time and wind speed in one colony, and on body condition in the other colony. The authors found that during daytime fewer birds were foraging in oceanic habitats compared to during night-time. In addition, during strong winds more birds foraged in coastal habitat instead of offshore. Moreover, individuals adjusted foraging behaviour according to time of the day, weather conditions, body condition, and the age of the chicks.

Prey availability is assumed to affect foraging behaviour (Woodward *et al.* 2019), with shorter foraging ranges in years with more abundant prey (Chivers *et al.* 2012; Robertson *et al.* 2014).

Survey data for model validation

For the Dutch Continental Shelf, data from MWTL/ESAS surveys can be used for model validation. If an IBM is constructed for an area outside the range of these surveys, alternative survey data should be acquired.

General decisions

Types of individuals

For black-legged kittiwake, we suggest an IBM with a structure comparable to the IBM for lesser black-backed gull. We suggest distinguishing between adults and immatures, and if sufficient data are available, juveniles. In addition, for the breeding season we suggest distinguishing between breeding adults and non-breeding adults.

Ring recoveries suggest that adults and subadults differ in their spatial distribution. Subadults, including juveniles, move into shallow continental shelf waters, generally away from the breeding colonies (Coulson 2011). Birds tend to return towards breeding colonies in their third summer, although some individuals of that age remain in the West Atlantic.

Behavioural states

For the analysis of tracking data, Redfern & Bevan (2014) distinguished three states: 'direct flight', 'foraging behaviour' and 'non-foraging behaviour'. Direct flight is characterized by minimal angular deviation between successive locations. The second and third state are distinguished by slow flight speed and/or frequent changes of direction. Foraging behaviour is characterized by meandering paths with frequent changes of direction. Non-foraging behaviour consists of periods of inactivity, resting on the surface and drifting with wind and currents.

Christensen-Dalsgaard *et al.* (2018) identified the states 'resting', 'commuting' and 'foraging'. In comparison to the states defined by Redfern and Bevan (2014), direct flight is comparable to commuting and non-foraging behaviour is similar to non-foraging behaviour.

To model movement behaviour within the breeding season, an additional state for inbound flights should be added, which ensures that individuals return to the colony. The definition of these behavioural states is based on the step length and step size. These parameters are based on tracking data.

Breeding locations and numbers of individuals

See Table 7-4 and the relevant paragraph of the data availability section.

Variation between colonies

A comparison between a coastal and an inland colony showed similar characteristics of foraging trips, with trips lasting up to 17.6 hours and covering distances of 6.2–370.6 km (Redfern & Bevan 2014).

Searle *et al.* (2020) report that kittiwakes in Scotland are associated with the colony between April and August. However, Furness & Trinder (2016) report that the timing of departure from breeding colonies varies with a longitudinal gradient, which seems related to prey availability. According to this source, departure in northern UK is around late July, early August, while adults breeding in southern UK leave their colonies later (Furness & Trinder 2016). The timing of returning to breeding colonies varies as well. While the first adults return to their breeding colonies in mid-February in the UK, adults breeding in the Arctic only return in April (Coulson 2011).

As referred to above, Christensen-Dalsgaard *et al.* (2018) analysed movement behaviour of kittiwakes from two different colonies and showed lower amounts of time spent resting for individuals using oceanic foraging areas compared to individuals using coastal areas.

Woodward *et al.* (2019) conclude based on a meta-analysis that foraging ranges strongly vary between colonies. Moreover, the authors report that foraging ranges may vary at different stages of the breeding cycle, but this may not be consistent: Robertson *et al.* (2014) recorded longer foraging distances during incubation, whereas Ponchon *et al.* (2014) recorded longer distances during chick-rearing.

Factors affecting movement behaviour

The effect of external factors on movement behaviour needs to be analysed based on tracking data and external factors. We suggest that at least the effect of water depth, wind speed, distance to coast, distance to wind farm, and distance to nearest fishing vessel should be analysed. Data on water depth and wind speed are available, and distances to coast and nearest wind farm can easily be calculated. To assess the effect of the distance to the nearest fishing vessel, VMS data can be used. These data are not publicly available but can be used if permission is acquired. If possible, the effect of the age of the chicks should be included, as this was found to affect the foraging behaviour of the parents. If these data are not available, day of year could be used as a proxy for progress of the breeding season, assuming synchronicity in laying and hatching dates between breeding pairs. In addition, if data on prey availability are available, these should be analysed as well.

Other parameters that need to be extracted from the tracking data or from literature

- Initial departure direction of breeding and non-breeding individuals
- Time spent in the colony between foraging trips
- Length of breeding season
- Departure location of non-breeding individuals
- Start and end of a breeding attempt

Required input for collision rate modelling

Collision rates were modelled for black-legged kittiwake in Rijkswaterstaat (2015) using the Band model (Band 2012). All input parameters were available or could be estimated. This analysis is currently being updated by Bureau Waardenburg within KEC4.0. The level of avoidance is uncertain (Furness & Trinder 2016).

7.2.3 Great black-backed gull

The species has a large range throughout the much of the North Atlantic rim south to the Caribbean and southern Europe (Wernham *et al.* 2002; Mitchell *et al.* 2004).

Data availability

Tracking data, ideally of several colonies

For great black-backed gull, only two tracking studies are available, of which only one study is relevant for the southern North Sea (Table 7-5). The number of tracked individuals is very limited, and only breeding adults were tracked during the breeding season.

Table 7-5 *Tracking studies of great black-backed gull. Only the German study is relevant for modelling movement behaviour on and around the southern North Sea.*

Location	Years	Season	Sample size	Reference
Foehr, Germany	2016	Breeding season	7 breeding adults	Borrmann *et al.* (2019)
Nova Scotia, Canada	2016	Breeding season	3 breeding adults	Maynard & Ronconi (2018)

Ecological knowledge

Great black-backed gulls are year-round present in the North Sea, with highest numbers during autumn and winter (Fijn *et al.* 2020). The North Sea is important for this species for migration and as wintering area (Skov *et al.* 2007). Other relevant ecological knowledge has been incorporated into the relevant sections.

Great black-backed gulls forage relatively close to the colony, with a mean foraging range of 9.9 +- 4.6 km based on a German tracking study (Borrmann *et al.* 2019). The authors also showed that there is spatial segregation between individuals, and individual-specific highly consistent departure directions occur. Critchley *et al.* (2018) report a mean maximum foraging range of 60 km (average of individual-based maximum foraging ranges).

Colony locations and number of breeding pairs

Relevant breeding colonies around the southern North Sea are reported in Table 7-6.

Table 7-6 *Breeding colonies nearby the Dutch Continental Shelf and number of breeding pairs of great black-backed gulls.*

Colony	Number of breeding pairs	Reference
Norway (NO)	40,000	Mitchell *et al.* (2004)
Sweden (S)	15,000	Mitchell *et al.* (2004)
Shetland and Orkney (UK)	8,500	Mitchell *et al.* (2004)
Eastern Scotland (UK)	2,000	Mitchell *et al.* (2004)
Denmark (DK)	1,600	Mitchell *et al.* (2004)
Germany	25-30	Borrmann *et al.* (2019)
Netherlands (NL)	78-80	Sovon.nl

Data on environmental factors which may affect movement behaviour

Most foraging flights from a German colony were recorded during the day (80%; Borrmann *et al.* 2019). In addition, most foraging positions occurred around low tide (on average 69%, with individual variation between 57 and 83%; Borrmann *et al.* 2019).

The stage of the breeding season also affects movement behaviour. Borrmann *et al.* (2019) showed that the average foraging range, trip duration and cumulative distance travelled were greater during chick-rearing than during incubation.

Survey data for model validation

For the Dutch Continental Shelf, data from MWTL/ESAS surveys can be used for model validation. If an IBM is constructed for an area outside the range of these surveys, alternative survey data should be acquired.

General decisions

Types of individuals

For great black-backed gull, we suggest an IBM with a structure comparable to the IBM for lesser black-backed gull. We suggest distinguishing between adults and immatures, and if sufficient data are available, juveniles. In addition, for the breeding season we suggest distinguishing between breeding adults and non-breeding adults.

Foraging behaviour is likely to differ between the breeding season and the non-breeding season. Based on a stable isotope analysis, great black-backed gulls feed on a higher trophic level during the breeding season compared to the non-breeding season (Steenweg *et al.* 2011). This difference in prey may indicate differences in foraging behaviour.

Note that within our data review, we only found tracking data for breeding adults during the breeding season. Based on these data, only this type of individuals can potentially be modelled, and only for the breeding season. Moreover, the number of tracked individuals is very limited, which results in uncertainty of the resulting IBM, especially if variation between individuals is large.

Behavioural states

If an IBM can be constructed (note that more tracking data are necessary than the data reported in Table 7-5), we suggest including the same behavioural states as for sea trips of lesser black-backed gull. These are: foraging, transit, stationary, outbound and inbound flight (back to the colony). We found no literature on behavioural models for this species.

Breeding locations and numbers of individuals

See Table 7-6 and the relevant paragraph of the data availability section.

Variation among colonies

Tracking data are available for only two colonies, one of which is less relevant for the southern North Sea. If foraging behaviour varies among colonies, this results in uncertainty of the IBM.

Variation in foraging behaviour among colonies may be the result of variation in diet. Large gulls breeding at lower proximity to anthropogenic food resources often make more use of these resources within their diet. This has been found for herring gull (Spaans 1971; Hanlon *et al.* 2017), and may apply to great black-backed gull as well.

Factors affecting movement behaviour

The effect of external factors on movement behaviour needs to be analysed based on tracking data and external factors. We suggest that at least the effect of water depth, distance to coast, distance to wind farm, and distance to nearest fishing vessel should be analysed. Data on water depth should be available and distances to coast and nearest wind farm can easily be calculated. In order to assess the effect of the distance to the nearest fishing vessel, VMS data can be used. These data are not publicly available, but can be used if permission is acquired.

In addition, the effects day versus night should be analysed using tracking data, as these factors were found to affect foraging behaviour (Borrmann *et al.* 2019).

Movement behaviour seems to strongly vary among individuals. Individual variation in mean trip duration based on tracking data from Germany ranged from 1.6 hours to 6 hours, and the average daily number of trips varies between 1.6 and 4.3 (Borrmann *et al.* 2019). In addition, individuals vary in habitat use. Of the three individuals tracked by Maynard & Ronconi (2018) in Canada, one individual specialized on coastal environments (81% of its foraging trips), while a second individual visited urban areas during 71% of its foraging trips. The third individual did not display any preference for habitat type. Niche width of chicks raised inshore was broader than of chicks raised offshore, which suggests that adult foraging behaviour differs between inshore and offshore feeding grounds.

Other decisions to be made based on tracking data and assumptions

- Initial departure direction of breeding and non-breeding individuals
- Time spent in the colony between foraging trips
- Length of breeding season
- Departure location of non-breeding individuals
- Start and end of a breeding attempt
- Terrestrial versus marine foraging trips: variation in time and between individuals and colonies

Required input for collision rate modelling

Collision rates were modelled for great black-backed gull in Rijkswaterstaat (2015) using the Band model (Band 2012). All input parameters were available or could be estimated. This analysis is currently being updated by Bureau Waardenburg within KEC4.0.

7.3 Conclusions and discussion

The main criterion for the construction of an IBM is the availability of tracking data, as this provides most of the input parameters for an IBM. Data on colony distribution and sizes, environmental conditions and OWF characteristics are also critical to the implementation of an IBM but are generally widely available.

Data availability for northern gannet is relatively high. Tracking studies have been carried out in several breeding colonies, both during the breeding and non-breeding seasons. Besides data on breeding adults, there is also some tracking data on immatures, which is rare among tracking studies of seabirds. Availability of tracking data on non-breeding adults during the breeding season is unclear but may be available if data were collected over several years. Tracking data of immatures are available, although the small number of studies (2 colonies) gives limited insight in variation between colonies. Hence, for the breeding season an IBM can be constructed for breeding adults and immatures. It is unclear whether data are available for non-breeding individuals during the breeding season. For the non-breeding season, data are only available for adults.

For black-legged kittiwake, tracking data are lacking for immatures and juveniles. An IBM could be constructed for breeding adults during the breeding season and for adults during the non-breeding season. Data are available for three non-breeding adults during the breeding season, which is likely insufficient to obtain parameter estimates that can be generalized across other individuals and colonies. In the Dutch North Sea, black-legged kittiwakes breed in only small numbers at offshore platforms (e.g. Geelhoed *et al.* 2011) but winter in substantial numbers (Fijn *et al.* 2020). No tracking data are available for individuals breeding at offshore platforms. In addition, the available tracking data for individuals wintering in the Dutch North Sea are very limited (few individuals in Swindells (2019)).

For great black-backed gull, tracking data are very limited. Tracking data are available for only one relevant colony for the southern North Sea, with a limited number of individuals. As a result, knowledge of variation in movement behaviour between individuals is very limited, and variation in movement behaviour between colonies in Europe is entirely unknown. However, as great black-backed gull is mainly a migratory and wintering species on the Dutch continental shelf (Fijn *et al.* 2020), tracking data collected from individuals wintering at sea in one of the SPAs that are assigned for the high number of individuals of this species (e.g. the Brown Ridge) would be most relevant.

Hence, to allow the development of IBMs for other species than the lesser black-backed gull with the aim to model collision rates at Dutch OWFs, future studies should aim to collect tracking data that is most relevant considering the development of offshore wind farms in the Dutch North Sea.

8 Literature

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