PrePARED Report No. 012

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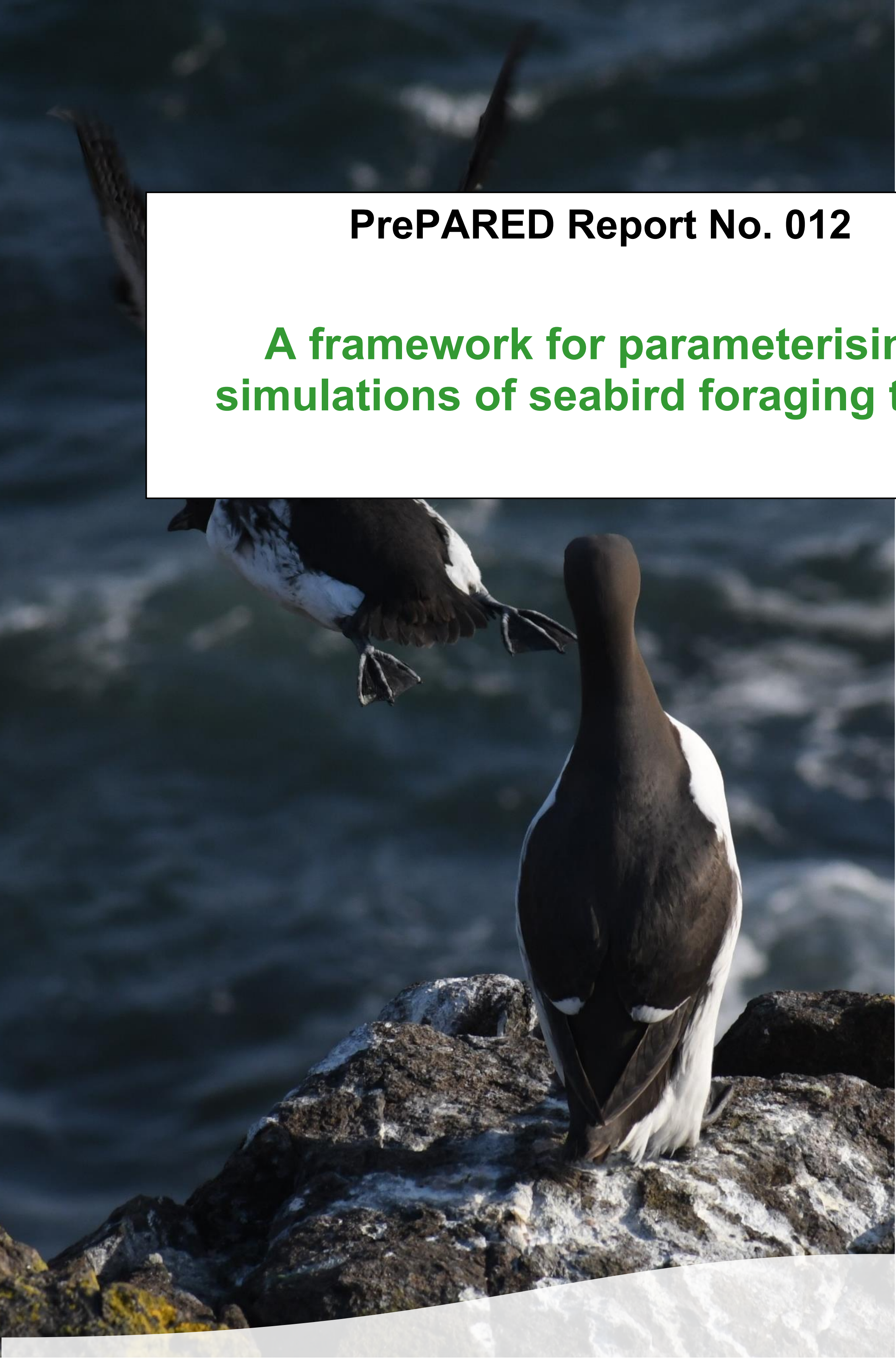

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Predators + Prey Around Renewable Energy Developments

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A framework for parameterising simulations of seabird foraging trips

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Summary

Breeding seabird populations are central place foragers, and their behaviour is shaped by energetic constraints, prey availability and the need to regularly return to the colony during chick-rearing. To predict potential long-term impacts of offshore wind farm development on population demographics, we have developed a tool that generates realistic simulations of seabird foraging trips, which can be used as inputs to Individual Based Models. Here, we present a framework for parameterising simulations of individuals' movement patterns so as to reflect biological processes observed in empirical GPS tracking data from the Isle of May, Firth of Forth.

To parameterise simulations, we (1) determined key parameters and relevant empirical data to use, (2) determined metrics to use from outputs of movement models (Hidden Markov Models; HMMs) to feed into the simulations, (3) where possible, assessed parameter estimates using literature values or visual assessment, and then calibrated the remaining values against empirical data using Approximate Bayesian Computation (ABC).

The simulation tool produces fine-scale foraging trips for four focal species (black-legged kittiwake, common guillemot, razorbill and Atlantic puffin) based on underlying mechanisms that capture outbound travel from colonies, switching between commuting, foraging and resting behaviours, responses to changes in prey density, land avoidance, and inbound travel to the colony to return to the chick based on energetic constraints. These mechanisms generate realistic trip trajectories that include commuting, central foraging bouts and opportunistic foraging during the

inbound part of the trip. Simulated trips varied by trajectory, duration and behaviours (activity budget), reflecting the variation found in empirical data.

To assess the simulation tool against empirical data, a parameterisation framework was developed in which simulations from the tool were compared against empirical GPS data. GPS data were cleaned, and both simulations and empirical data were regularised to a common temporal resolution before behavioural states (commuting, foraging, resting) were classified for each location of both simulated and empirical data using HMMs. A suite of summary statistics describing movement and behaviour within foraging trips were calculated for both simulated and empirical data using the HMM outputs. Parameters were calibrated by comparing the simulated and empirical data either visually (for parameters less influenced by behaviour, such as land avoidance) or by using Approximate Bayesian Computation (ABC) to select those parameter sets associated with summary statistics that best match those derived from the empirical data.

This framework produces biologically realistic simulations and within PrePARED will be applied to determine parameter values for the four seabird species. Once parameterised, the simulation tool will generate realistic foraging trips by species. The tool can generate movement predictions across varying environmental and prey landscapes to address specific research questions.

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1. Introduction

Within PrePARED, a key goal is to improve understanding of the interactions between seabirds, fish, and offshore wind farm development. The collection of new concurrent data of both seabirds and their prey is providing important insights into predator-prey interactions (PrePARED, 2024), feeding into evidence and assessment tools which can be used to predict the potential effects of offshore wind farm developments on these ecosystems. To achieve this, one task is to develop a simulation tool which is capable of generating realistic foraging tracks of seabirds during the breeding season. This simulation tool would allow multiple foraging trips to be generated, allowing hypotheses to be modelled and tested on how aspects such as foraging trip route, prey distribution, and individual energetic requirements interact with operational offshore wind farms (OWFs), and ultimately influence seabird population demographics such as breeding success and adult survival.

By capturing key mechanistic processes, simulations offer a versatile tool for testing ecological theories and predicting outcomes under novel conditions. To achieve the latter, it is necessary to produce a simulation tool in which the emergent behaviour of individuals sufficiently resembles the relevant processes inherent in the real system (Gallagher et al., 2021). In practice, animals make decisions based on their needs and on the opportunities or risks they perceive in their environment (Owen et al., 2017). As computing power has increased so too has our ability to simulate these complex processes with greater realism (DeAngelis and Grimm, 2014), allowing us to understand how the consequences of individual decisions scale to the population-level by characterising how they emerge from simulating complex interactions between individuals and their environments.

Specifically, more realistic simulations of foraging tracks will also provide an important input into the Individual Based Model (IBM) SeabORD (Searle et al., 2018, 2026; Pollock at al., 2026). SeabORD provides a framework for estimating effects on seabirds through individuals encountering OWFs in their environment, with a focus on displacement and barrier effects. However, the current versions of SeabORD (v1.0, v2.0) include relatively simple mechanisms for simulating the individual foraging trips themselves. Including the ability to incorporate more realistic foraging trips would be a substantial improvement, increasing the realism and complexity that can be considered within the model, giving rise to more accurate predictions of key parameters and ultimately improving predictions of population impacts arising from encounters with operational OWFs.

To develop realistic foraging trip simulations requires two components. First, a general simulation framework which captures the key biological and ecological mechanisms for generating trips with the correct overall properties. Second, appropriate parameterisation of that framework to adequately match the quantitative properties of the simulated tracks to empirical data for the species of interest. Here, we present a framework for how this was approached, i.e. how the simulation tracks are parameterised for each seabird species.

The aim of this work was to develop a framework for parameterising simulations of seabird foraging trips for use within IBMs designed to predict seabird demographic responses to offshore wind farms. This was approached by (1) examining common approaches to parameterisation used in the wider literature, (2) identifying key parameters and empirical data required for parameterisation, and (3) considering best approaches to translate the information obtained from movement modelling into the parameterisation process.

2. Simulating seabird foraging trips

Here, we considered how to approach parameterisation for a simulation tool that generates simulated foraging trips of seabirds. In this section, we summarise the development of the simulations leading up to the parameterisation stage.

Seabirds are central place foragers during the breeding season, faced with prey resources which can be heterogeneously distributed and variable in predictability (Weimerskirch, 2007). Most species breed in colonies where many conspecifics exploit overlapping resources, which may lead to competition for resources (Fayet et al., 2021; Lewis et al., 2001). Further to this, during the chick-rearing season, breeding seabirds must acquire enough prey to feed both themselves and their chick(s); a period during which parents often lose mass (Storey et al., 2017; Wanless et al., 2023), indicating the high constraints faced by birds during this period. While there is evidence that many seabirds have some knowledge of where to find food, built on previous experience and social cues (Jones et al., 2018; Regan et al., 2024; Thiebault et al., 2014), individuals will not have complete knowledge of their environment.

During the chick-rearing period, seabird at-sea movements are typically divided into discrete foraging trips. A trip begins when a bird departs the colony, and generally consists of: (i) a period of travel outbound from the colony, (ii) a period (or periods) of foraging at-sea, and (iii) a period of travel inbound as the bird returns to the colony (Figure 1). Seabird foraging movements are complex, with multiple drivers and constraints determining the foraging route taken on each trip away from the colony. For example, they can exhibit sinuous and relatively slow-moving foraging periods, likely a response to higher prey density, which are linked by faster, more linear movements between these foraging bouts and when travelling to and from the colony (Figure 1). The ubiquitous requirement to obtain prey, coupled with the need to regularly return to the colony, results in common characteristics of foraging trips between different seabird species at the broad scale. Nonetheless, these trips are highly variable, not only between individuals of the same species, but also at the individual-level. For example, foraging trips can range in distance, duration, overall shape, and in activity budgets of different behaviours (e.g., time spent foraging vs. commuting). This study uses data from the Isle of May, for which GPS tracking data for several seabird species have been collected over multiple years (see Supplementary Material Table S1 for specific data and funders of data included here). From these data we can extract a wide range of foraging trips for different species, and use these to construct respective sets of summary statistics that we can use to parameterise our simulation tool for each species of interest.

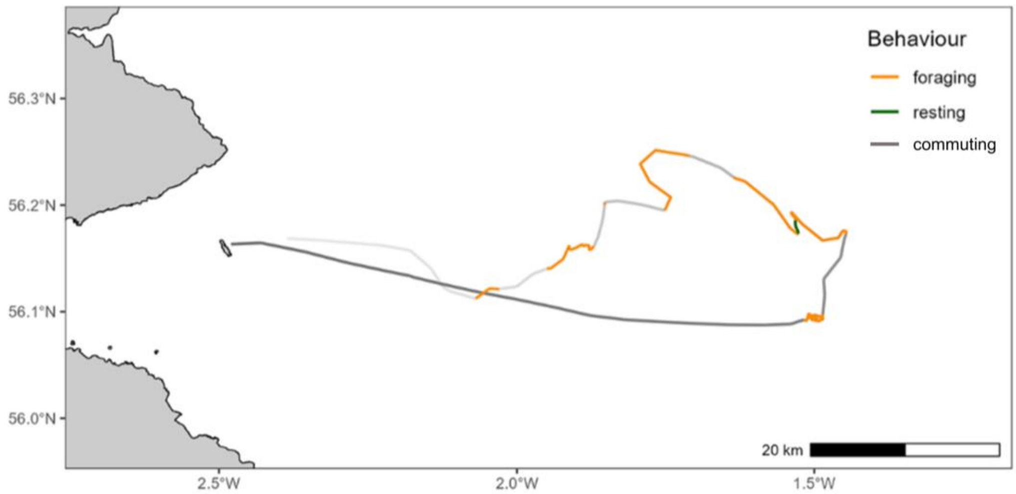

Figure 1: Example of a single kittiwake (black-legged kittiwake; Rissa tridactyla) foraging trip from GPS data of a bird tagged on the Isle of May, east Scotland, UK. The movement path is coloured by the behavioural mode of the individual, as estimated from a Hidden Markov model (HMM): foraging (orange), resting (green), commuting (grey). The portion of the track which is in commuting behaviour (grey) transitions from light to dark as the trip progresses, to illustrate the order of the foraging route taken. See Supplementary Material Table S1 for details of data collection and acknowledgements of relevant funders.

Simulation models need a well-defined scope. Finding the right balance between including as few underlying mechanisms as possible and achieving the ecological realism necessary to meet the model's purpose is essential. The purpose of our model was to produce fine-scale central place foraging trips of four different species (kittiwake, common guillemot (*Uria aalge)*, razorbill (*Alca torda)*, and Atlantic puffin (*Fratercula arctica*)) during the chick-rearing season at the Isle of May National Nature Reserve (NNR). Our first aim was to design a general simulation framework that emulates key aspects of decision-making at the individual level. This aim would be achieved when the simulation produced fine-scale foraging trips that were visually similar to empirical observations, while incorporating mechanisms that allow for the emergence of species-specific foraging behaviours and movement patterns across the four target species.

Single foraging trips were considered to be independent, i.e. the simulation tool considered a trip as the unit to be developed, simulated and parameterised. As such, sequences of trips from an individual were not simulated, nor were associated behaviours, such as memory for previously profitable foraging areas (Collet et al., 2025; Regan et al., 2024). Memory is only (partially) implied in one modelled mechanism - when a bird leaves the colony, it picks a direction of travel based on the distribution of empirical departure headings. This mechanism is an obvious candidate for testing memory in future model iterations, by having individuals recall successful foraging locations from previous experience, for example.

Some key aspects of the model include discrete 10-second time steps, individuals can switch behavioural movement modes (travelling/foraging/resting at-sea), and movement calculations are based upon a biased correlated random walk (bCRW) algorithm (Chudzinska et al., 2021). We chose this as it results in a persistence of turning angles from which realistic looking trip trajectories emerge (i.e. individuals navigate towards areas of interest such as potential foraging patches or their colony). The model approximates an energetic requirement by imposing a threshold of time spent in foraging behaviour as a proxy for successful foraging. Upon reaching this threshold, the bird travels directly back to the colony with no further foraging taking place. If the threshold for time spent foraging is not achieved, another time limit is imposed, which directs movement back towards the colony, but the individual can still uptake foraging opportunities during the inbound leg of the trip.

To detail all the mechanisms included in the foraging trip simulation tool is beyond the scope of this report, and will be set out in an upcoming peer-reviewed manuscript. The simulation protocol to generate a typical trip can be seen in Figure 2, where each annotated number highlights a key mechanism or component of the trip with some brief expansion on each in the panel on the right.

Together, the combination of these mechanisms and their parameters result in the emergence of foraging trips that possess many of the characteristics seen in our study species, with considerable variation akin to that seen across empirical observations, thus paving the way for our more formalised parameterisation process.

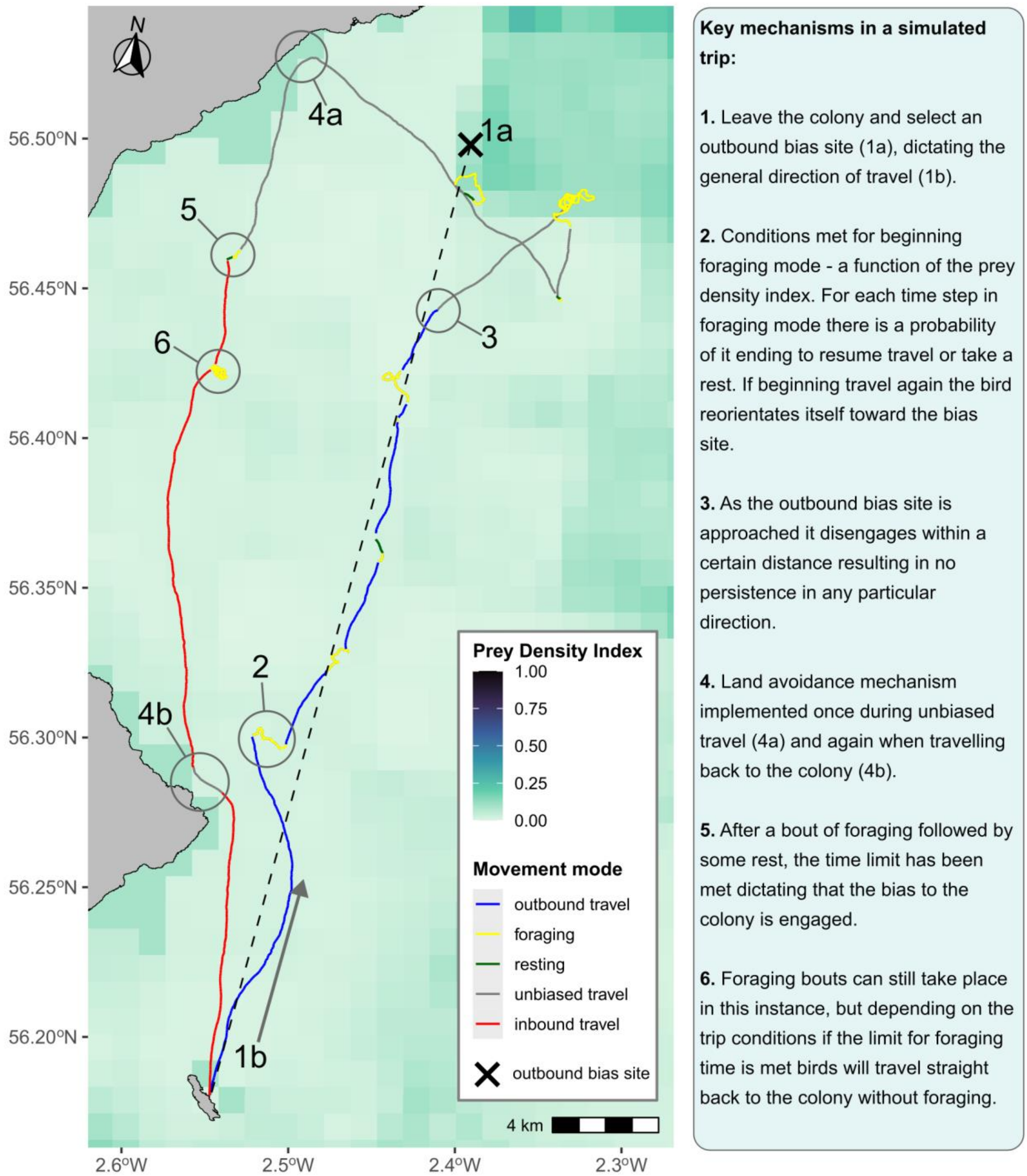

Figure 2: Example of a simulated seabird foraging trip from the Isle of May. The simulated bird travels towards an outbound bias site, switches between different movement modes, and then returns to the colony. Simulated birds interact with a map of prey density from empirical data-see Supplementary Material Table S1 for data details and acknowledgements. Note that the movement modes (i) outbound, (ii) unbiased and (iii) inbound are all sub-types of travel (a.k.a. commuting) behaviour, where each movement mode has a different bias, or lack thereof, in movement direction. Annotated numbers are used to illustrate key mechanisms or stages of the trip with explanations in the panel on the right.

3. Designing a framework for parameterisation

3.1 Identifying appropriate empirical data

Tracking data from tagged individuals are the most applicable empirical data for parameterisation here as they match most closely with the simulations they are trying to emulate. Within PrePARED, GPS tracking data are available across different seabird species in the study region (see Supplementary Material Table S1 for details of data and funders of data collection). Whilst GPS tracking data will likely be the most relevant, additional data sources such as prey and environmental maps, broadscale seabird distribution maps and seabird diet information are likely to be valuable for further refinement of particular parameters or for providing independent validation.

In evaluating whether empirical data are appropriate for the parameterisation of a simulation tool, there are several aspects that are important to consider (Table 1). Principally, this should include an assessment of whether the empirical data have properties that are likely to be comparable to the system or species that is being simulated, e.g., that they relate to a similar ecosystem and are of a comparable spatiotemporal scale (Table 1). Additionally, to avoid unexpected issues of mismatch between real and simulated data, empirical data should be carefully cleaned of errors and consideration should be given to whether simulated and empirical data both arise from the same (assumed) ecological process (Table 1), e.g., seabird tracking data may need to be limited to a particular part of the breeding season to match the assumptions in the simulation tool. See Table 1 for a summary of key prompts as recommendations for this stage of analysis.

For example, for the simulation of seabird foraging tracks here, we use tracking data from four species from the Isle of May colony: kittiwake, razorbill, guillemot, puffin (i.e. the colony and species considered directly in the simulations). The GPS tracking data cover a similar spatial scale to the simulation framework (the Forth and Tay coastal area) but are on a coarser time resolution (typically 5-10 minutes vs. 10 seconds) which requires some adjustment to make direct comparisons. The GPS tracking data need to be cleaned to remove probable erroneous locations (e.g., as identified by unrealistic speeds, low number of satellites used). As the simulations aim to generate foraging trips, the empirical data also need to be divided into distinct and completely observed return trips (i.e. partial trips are discarded), and the criteria used for this will ultimately determine some of the characteristics of the simulations (e.g., minimum trip length). Here, we use only tracking data from the chick-rearing period during the summer breeding season, as this is the time period on which the simulation framework is focussed.

Table 1: Checklist of considerations to review when determining appropriate empirical data for parameterisation of simulation tools and Individual Based Models (IBMs).

Aspect of empirical data	Prompts and alternative adaptations to consider
Similar ecological system and/or study species	Do data on the exact species and ecological system exist? If not, do data on a similar species/system exist, and which parameters are likely to still be common or similar? If limited data exist, can parameter values be sourced from elsewhere (e.g., literature, expert elicitation)?
Comparable spatial and temporal scales	Are the empirical data of a similar spatial and temporal scale to the simulated data (or relevant part of the simulated data)? If not, can either data source be reasonably adjusted to allow direct comparisons (e.g., downsampling, interpolation)?
Data cleaning and errors	Are the empirical data cleaned and free of measurement or observation errors that could cause unexpected mismatches with the simulated data?
Measurements of the same process	Is it expected that both the empirical and the simulated data are measurements (or measure components of) of the same ecological process? Are there either (i) any aspects of the empirical data that are not likely to be considered in the simulation, or (ii) any aspects of the simulation that are not likely to be represented in the empirical data? If so, do empirical data need to be edited to provide better matching (e.g. cropping), or do they need to be supplemented with another data source?

3.2 Identifying key parameters and options for parameterisation

Simulation tools often require many different parameters to fully characterise the ecological system of interest. Therefore, consideration needs to be given to how each parameter value will be chosen and whether the choice of some parameters may be more important than others. Parameter values will interact with one another, and so sensitivity analyses can be used to identify parameters that may be more influential and therefore require more careful refinement. A combination of quantitative understanding of the simulation framework itself, and ecological knowledge of the importance of drivers in the real-life system being modelled should be used to determine the choice of approach for refining each parameter value. Parameter values can be refined using comparisons with relevant empirical data but can also be determined from the wider literature or expert elicitation (Martin et al., 2012) particularly where empirical data may be limited.

For the simulations here, each parameter was considered separately to decide the best approach for parameterisation. As an illustration, a selection of example parameters and the reasoning for the parameterisation approach taken is presented in Table 2.

Table 2: Example parameters from the seabird foraging track simulation and justification for different parameterisation approaches used to determine appropriate values.

Parameter name and description	Parameterisation approach proposed	Justification
Land avoidance parameters (used to ensure simulated bird tracks do not cross over land)	Visual assessment (simulated tracks compared visually to empirical tracks)	A relatively simple mechanism is needed to emulate this part of animal behaviour, which is mostly independent from other parameters. Outputs are easy to directly visualise and interpret.
Foraging behaviour switching parameters (used to determine behaviour switching rates)	Empirical data analysis exercise (independent data analysis of empirical seabird tracking and prey data)	These parameters are thought to be very influential in determining interaction with prey maps, as well as final tracks and activity budgets. Choosing a value is challenging and interpreting how they influence the simulated tracks is not straightforward.
Movement step and turn parameters (used to determine overall movement characteristics)	Approximate Bayesian Computation (formal iterative comparison using summary statistics)	These parameters will have a strong influence on how the simulations move throughout space and time, and will therefore interact with many other parameters. The translation in temporal scale between the real and empirical data is challenging to interpret manually.

3.3 Integrating information from movement modelling of empirical data

Movement modelling encapsulates a wide range of methodological approaches (Patterson et al., 2017), with common aims of using animal tracking data to: (i) quantify how animals move through space and interact with their environment, (ii) characterise how animals spend their time across different behaviours or movement modes, and/or (iii) identify drivers of movement and/or behaviour. One common approach is the use of Hidden Markov models (HMMs) to divide animal tracking data into discrete, estimated behaviours (Langrock et al., 2012; McClintock et al., 2020). These models use characteristics of the animal's observed movement path (e.g., step lengths, turn angles between locations) to estimate the underlying behavioural state which was most likely to generate those movement characteristics. For example, some movement characteristics will be more indicative of potential commuting behaviour (e.g., fast, directed movement), and others will be more indicative of potential foraging behaviour (e.g., slower, more meandering movements). The models do not provide the ecological function of each inferred state grouping (i.e. the data are divided into unlabelled groups), but ecological knowledge can be used to interpret the identified groupings and infer the likely behavioural function associated with each grouping (Pohle et al., 2017).

Traditionally, movement modelling of empirical data is often considered as a separate set of analysis tools to simulation-based approaches of animal movement (including IBMs); however, there are opportunities to combine the strengths of both approaches to achieve improved inference. In particular, movement models can produce a range of outputs which are directly applicable to the parameterisation of simulation tools. They also provide an approach for bridging differences between different time resolutions of simulation tools and empirical data. For example, behavioural classifications produced from movement models can be used to provide activity budgets for simulation tools which include different behavioural modes (assuming the movement models were fitted to the same number of target behaviours), ensuring simulated tracks spend the correct proportions of time in each behaviour. The characteristics of these behaviours (e.g, step lengths, turn angles) can also be used to provide parameters describing the appearance of simulation tracks across the different behaviour modes being generated. Furthermore, although not considered directly here, movement models which look at drivers of movement will produce relationships between covariates (e.g., environmental, prey, or human activity covariates) and movement direction/behaviour. These relationships provide key information that can be incorporated into simulation tools to increase the realism of how simulated animals interact with their environment.

3.4 Overall framework outline

The considerations and decisions outlined above were integrated to produce a proposed framework (Figure 3) for parameterising the simulations of seabird foraging tracks described (see Section 2). This provides a workflow for using appropriate methods, such as Approximate Bayesian Computation (ABC; Beaumont, 2010; Hartig et al., 2011), to parameterise the simulations and to apply this across the different seabird species being simulated. A limited number of parameters are being determined by other approaches (e.g., literature values, visual assessment); these parameters should be determined first and then are fixed during calibration, which we are implementing via an ABC protocol. A brief description of each stage of the framework is described below.

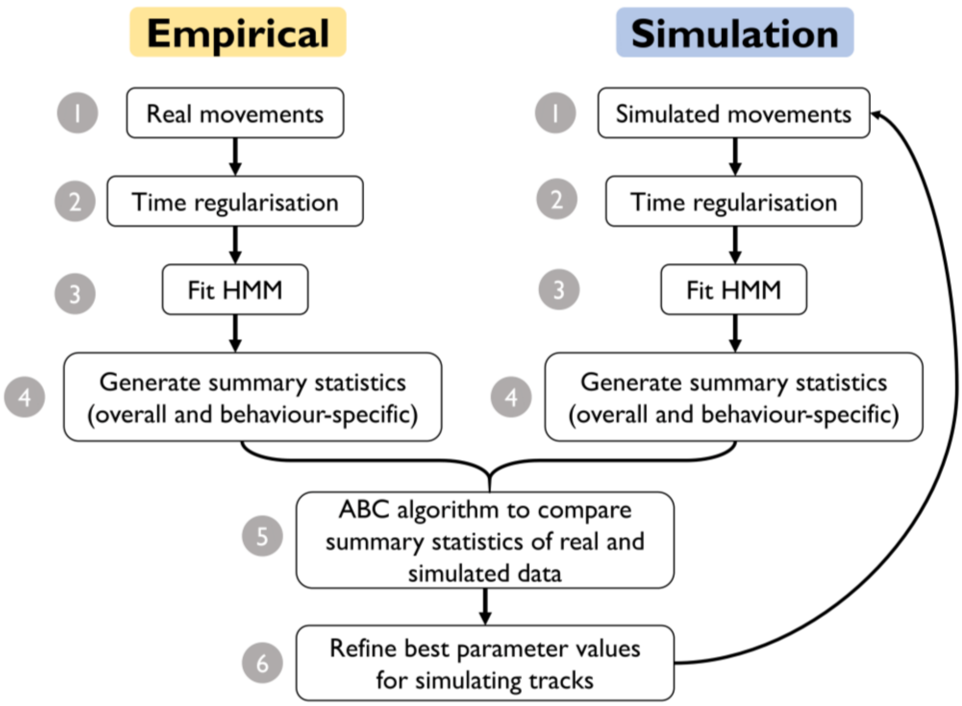

Figure 3: Summary of the six-step framework proposed for parameterisation of seabird foraging track simulations. The framework requires the collection of empirical data and the generation of simulated data (step 1). Steps 2-4 are then applied to both the empirical and simulated data separately, before integrating them in steps 5 and 6. The details of each step are described in the main text.

In step (1), relevant empirical data (i.e. seabird GPS tracks) on the study system are collected, cleaned and prepared for analysis. In parallel, simulated data (i.e. simulated seabird tracks) are generated from the simulation tool. To complete the parameterisation process, multiple versions of simulated tracks should be generated using a range of different possible parameter values. This will allow different parameter values and their combinations to be compared. In step (2), both empirical and simulated data should be regularised to a common time frequency (if they are not originally on the same time resolution). This is an important step because measures of animal movement and behaviour are scale-dependent (Laube and Purves, 2011; Michelot and Storey, 2025), and so regularisation is required to ensure direct and meaningful comparisons can be made across datasets (and so between simulations and empirical data). In general, data should be downsampled to the lowest observed time resolution, as significant uncertainty is introduced when upsampling data to a higher resolution than it was originally recorded at. In step (3), both empirical and simulated data are grouped into estimated behavioural states by fitting the same structure of HMM to both sets of data. This involves estimating the most-likely behaviour for each timestep in the tracking data. Animal movement and decision-making will depend on behaviour, and so this step allows behaviour-specific metrics and measures to be calculated. The true behaviours captured in the empirical data are unknown and so need to be estimated. Applying the same approach to the simulated data ensures that behaviours are considered in a comparable manner between empirical and simulated datasets. In step (4), key summary statistics are calculated for both datasets, including some metrics that are behaviour-specific. The summary statistics should include measures of mean and variance for metrics that describe key aspects of movement and behaviour within the foraging trip, and measures that we would expect to be the same if the simulations were fully representative of the real system. In step (5), an ABC algorithm is applied to directly compare summary statistics from both the empirical and simulated data. The ABC algorithm compares the overall difference between summary statistics of the empirical and simulated datasets, and uses this to select simulations that produce the most similar summary statistics to the empirical data (i.e. have the smallest difference). Simulations that produce very different summary statistics (by a predefined rejection threshold- e.g., rejecting those below the top 1%) are rejected. In step (6), the simulations that are retained are used to summarise the parameter values that produced these simulations. These new distributions of parameter values (i.e. the posteriors) are those that should then be used in the simulation tool to generate realistic tracks.

We will apply this framework to parameterise the general simulation framework to each species separately. We describe here how this framework applies to kittiwakes, but the same basic approach is used for the other species. Empirical GPS data on kittiwakes at the Isle of May are available across nine years of tag deployments (see Table S1 for details), resulting in an empirical dataset of ~3,500 foraging trips (post-data cleaning- see Section 3.1). Simulated data can be generated using a range of possible parameter values to produce a simulated dataset for each parameter combination. For each parameter combination being tested, we simulate a dataset with approximately the same number of foraging trips as the empirical data, to ensure that the summary statistics for each group of trips are directly comparable. Empirical data are available at ~5 minute time resolution (with some irregularity due to data recording), and so both empirical and simulated data can be regularised to a common five-minute frequency. HMMs can be fitted to all datasets (empirical and simulated), using key characteristics of movement (e.g., step lengths, turn angles) to estimate the occurrence of three broad behavioural activities (commuting, foraging, resting). A standardised list of summary statistics can be calculated across all datasets, and then the ABC algorithm can be applied to determine which parameter values produced summary statistics that best match those observed in the empirical data.

4. Conclusions and next steps

We have developed a quantitative framework for parameterising simulations of seabird foraging trips. This framework consists of several key steps including gathering and preparing appropriate empirical data, applying behavioural classification models to identify behavioural modes, identifying and calculating key summary statistics, and applying an ABC algorithm to directly compare empirical and simulated tracks, with the results ultimately being used to refine the simulation parameters (see Figure 3). Within PrePARED, this framework will be applied to each seabird species separately to determine appropriate parameter values for kittiwakes, razorbills, guillemots, and puffins. Once parameterised, the simulation tool (Section 2) will have the ability to generate biologically realistic foraging trips for each species, with key properties and characteristics of each trip that closely match those observed in empirical data. The tool can then be applied to generate simulations of movement in different environments and answer specific research questions, e.g. to predict responses to different prey landscapes. Within the offshore wind sector, increased realism in seabird foraging trip simulations also contributes to improved predictions of potential interactions and impacts of offshore wind developments, feeding into impact assessments and understanding of cumulative effects. Although the parameterisation framework was developed for this specific application to seabirds, the approach outlined here and the recommendations provided are generally applicable across a range of different simulation and IBM contexts in ecology.

5. References

Beaumont, M.A., 2010. Approximate Bayesian computation in evolution and ecology. *Annual Review of Ecology, Evolution, and Systematics,* 41, 379–406.

Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P. and McConnell, B., 2021. AgentSeal: Agent-based model describing movement of marine central-place foragers. *Ecological Modelling*, 440, 109397.

Collet, J., Thiebault, A., Bonnet-Lebrun, A.S., Tremblay, Y., Carpenter-Kling, T., Keys, D. and Pistorius, P., 2025. A marine predator relies on both social cues and frequently updated memory to search for prey. *Proceedings of the Royal Society B: Biological Sciences*, 292(2041).

DeAngelis, D.L. and Grimm, V., 2014. Individual-based models in ecology after four decades. *F1000prime reports*, 6, 39.

Fayet, A.L., Clucas, G.V., Anker-Nilssen, T., Syposz, M. and Hansen, E.S., 2021. Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *Journal of Animal Ecology*, 90(5), 1152-1164.

Gallagher, C.A., Chudzinska, M., Larsen-Gray, A., Pollock, C.J., Sells, S.N., White, P.J. and Berger, U., 2021. From theory to practice in pattern-oriented modelling: Identifying and using empirical patterns in predictive models. *Biological Reviews*, 96(5), 1868-1888.

Hartig, F., J. M. Calabrese, B. Reineking, T. Wiegand, and Huth, A., 2011. Statistical inference for stochastic simulation models— theory and application. *Ecology Letters* 14:816–827.

Jones, T.B., Patrick, S.C., Arnould, J.P., Rodríguez-Malagón, M.A., Wells, M.R. and Green, J.A., 2018. Evidence of sociality in the timing and location of foraging in a colonial seabird. *Biology letters*, 14(7).

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D. and Morales, J.M., 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology*, 93(11), 2336-2342.

Laube, P. and Purves, R.S., 2011. How fast is a cow? Cross-scale analysis of movement data. *Transactions in GIS*, 15(3), 401-418.

Lewis, S., Sherratt, T.N., Hamer, K.C. and Wanless, S., 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, 412(6849), 816-819.

Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S.A.M.A.N.T.H.A., McBride, M. and Mengersen, K., 2012. Eliciting expert knowledge in conservation science. *Conservation Biology*, 26(1), 29-38.

McClintock, B.T., Langrock, R., Gimenez, O., Cam, E., Borchers, D.L., Glennie, R. and Patterson, T.A., 2020. Uncovering ecological state dynamics with hidden Markov models. *Ecology letters*, 23(12), 1878-1903.

Michelot, T. and Storey, E., 2025. Scale dependence in hidden Markov models for animal movement. *arXiv preprint arXiv:2510.03958*.

Owen, M.A., Swaisgood, R.R. and Blumstein, D.T., 2017. Contextual influences on animal decision-making: significance for behavior-based wildlife conservation and management. *Integrative Zoology*, 12(1), 32-48.

Patterson, T.A., Parton, A., Langrock, R., Blackwell, P.G., Thomas, L. and King, R., 2017. Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. *AStA Advances in Statistical Analysis*, 101(4), 399-438.

Pohle, J., Langrock, R., Van Beest, F.M. and Schmidt, N.M., 2017. Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. *Journal of Agricultural, Biological and Environmental Statistics*, 22(3), 270-293.

Pollock, C.J., Butler, A., Mobbs, D.C., Daunt, F. and Searle, K.R., 2026. Predicting demographic impacts from sublethal cumulative effects of offshore renewable developments on breeding seabirds. *EcoEvoRxiv preprint*: https://doi.org/10.32942/X2V36P.

PrePARED, 2024. PrePARED – The First Two Years. Report from the PrePARED Annual Knowledge Exchange Meeting 2024 (AKEM24). *PrePARED Report No. 3*, April 2024.

Regan, C.E., Bogdanova, M.I., Newell, M., Gunn, C., Wanless, S., Harris, M.P., Lopez, S.L., Benninghaus, E., Bolton, M., Daunt, F. and Searle, K.R., 2024. Seabirds show foraging site and route fidelity but demonstrate flexibility in response to local information. *Movement Ecology*, 12(1), 46.

Searle, K.R., Mobbs, D.C, Butler, A., Furness, R.W., Trinder, M.N. and Daunt, F., 2018. Finding out the Fate of Displaced Birds. *Scottish Marine and Freshwater Science*, 9(8). DOI: 10.7489/12118-1.

Searle, K.R., Pollock, C.J., Tigli, M., Daunt, F., Butler, A. and Mobbs., D.C., 2026. SeabORD v2.0: An Individual-Based Model for estimating demographic impacts for breeding seabirds arising from offshore wind farm sub-lethal effects. *PrePARED Report, No. 011*. March 2026.

Storey, A.E., Ryan, M.G., Fitzsimmons, M.G., Kouwenberg, A.L., Takahashi, L.S., Robertson, G.J., Wilhelm, S.I., McKay, D.W., Herzberg, G.R., Mowbray, F.K. and MacMillan, L., 2017. Balancing personal maintenance with parental investment in a chick-rearing seabird: physiological indicators change with foraging conditions. *Conservation Physiology*, 5(1), cox055.

Thiebault, A., Mullers, R., Pistorius, P., Meza-Torres, M.A., Dubroca, L., Green, D. and Tremblay, Y., 2014. From colony to first patch: processes of prey searching and social information in Cape gannets. *The Auk: Ornithological Advances*, 131(4), 595-609.

Wanless, S., Albon, S.D., Daunt, F., Sarzo, B., Newell, M.A., Gunn, C., Speakman, J.R. and Harris, M.P., 2023. Increased parental effort fails to buffer the cascading effects of warmer seas on common guillemot demographic rates. *Journal of Animal Ecology*, 92(8), 1622-1638.

Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources?. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(3-4), 211-223.

Supplementary Material

Data acknowledgements

The following data products and data sources have been used in the preparation of this report.

Table S1: Summary of data products and data sources.

Name	Description	Acknowledgements
Seabird tracking data 2018-2024	GPS tracking data* from kittiwakes, razorbills, guillemots and puffins tagged on the Isle of May. * TDR data from guillemots and razorbills (2020-2024) also used.	Data collection funded by Neart na Gaoithe Offshore Wind Farm Limited (NnGOWL), Seagreen Wind Energy Limited (SWEL) and Berwick Bank Wind Farm Ltd (BBWFL). Data collection conducted by UK Centre for Ecology & Hydrology.
Seabird tracking data 2012-2014	GPS tracking data from kittiwakes, razorbills and guillemots tagged on the Isle of May.	Data collection funded by RSPB FAME/STAR projects and NERC National Capability. Data collection conducted by UK Centre for Ecology & Hydrology.
Prey maps	Predicted maps of fish distribution in the Forth and Tay.	Data collection funded by The Crown Estate (OWEC) as part of the PrePARED project. Data collection conducted by Scottish Government Marine Directorate. Data analysis conducted by Charlie Cooper and Thomas Regnier, Scottish Government Marine Directorate.