OFFSHORE RENEWABLES JOINT INDUSTRY PROGRAMME (ORJIP) FOR OFFSHORE WIND

CARBON TRUST

Integration of tracking and at-sea survey data: WP2. Analysis framework

Project report for the Carbon Trust´s Offshore Renewables Joint Industry Programme (ORJIP) for Offshore Wind Species Protection Plan

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ORJIP Offshore Wind

The Offshore Renewables Joint Industry Programme (ORJIP) for Offshore Wind is a collaborative initiative that aims to:

- Fund research to improve our understanding of the effects of offshore wind on the marine environment.
- Reduce the risk of not getting, or delaying consent for, offshore wind developments.
- Reduce the risk of getting consent with conditions that reduce viability of the project.

The programme pools resources from the private sector and public sector bodies to fund projects that provide empirical data to support consenting authorities in evaluating the environmental risk of offshore wind. Projects are prioritised and informed by the ORJIP Advisory Network which includes key stakeholders, including statutory nature conservation bodies, academics, non-governmental organisations and others.

The current stage is a collaboration between the Carbon Trust, EDF Energy Renewables Limited, Ocean Winds UK Limited, Equinor ASA, Ørsted Power (UK) Limited, RWE Offshore Wind GmbH, Shell Global Solutions International B.V., SSE Renewables Services (UK) Limited, TotalEnergies OneTech, Crown Estate Scotland, Scottish Government (acting through the Offshore Wind Directorate and the Marine Directorate) and The Crown Estate Commissioners.

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Who we are

Our mission is to accelerate the move to a decarbonised future.

We have been climate pioneers for more than 20 years, partnering with leading businesses, governments and financial institutions globally. From strategic planning and target setting to activation and communication - we are your expert guide to turn your climate ambition into impact. We are one global network of 400 experts with offices in the UK, the Netherlands, Germany, South Africa, Singapore and Mexico. To date, we have helped set 200+ science-based targets and guided 3,000+ organisations in 70 countries on their route to Net Zero.

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Abstract

This is the dedicated interim report concerning WP2 of this project, which deals with methodological review and development. The task of apportioning overlapping components of usage belonging to different colonies and breeding stages of seabirds is not possible from telemetry data alone (because generally only adults are tagged) and very difficult with survey data (because it is hard to tease apart overlapping surfaces with unknown characteristics). However, it should be possible if both data types are combined into a joint analysis. We review the challenges and current methodologies involved in data integration and usage apportioning in seabird species. The task presents two methodological challenges. First, the existing analysis frameworks for telemetry and surveys are not compatible (i.e., the interpretations of their estimates differ). We adopt recent contributions we have made to the statistical literature that bridge this gap. Second, there has been no software implementation of these theoretical advancements into a framework that can deal with multiple overlapping surfaces, corresponding to colonies and ages (adults v juveniles). We present the principles and illustrative examples of the R package TrackTrans, developed for this project. Throughout, we discuss the motivation, remit and methodology for jointly analysing telemetry and survey data and propose possible extensions. We find that the framework leads to inferential improvements compared to the survey-only, or telemetry-only analyses. We finally discuss and present illustrations of marine usage apportionment, based on this methodology.

Background

There is a wide variety of technologies and field protocols for collecting spatial data on the distribution of animals. However, the majority of the resulting spatial data fall into one of two broad classes (Matthiopoulos et al. 2020), either telemetry (radiotelemetry, satellite tracking, geolocators, archival tags – (Cagnacci et al. 2010)) or surveys (line transects, strip transects, point transects, grid counts - (Buckland et al. 2005)). There is a sharp distinction between the two main data types used for estimating the spatial distributions of wildlife. Surveys focus on particular regions of space and can (in principle) observe any individual population member that comes into detection range. Telemetry studies focus on particular individuals and can (in principle) observe any region in space visited by the tagged animals. Analytically, the two data types correspond to two different ways of thinking about spatial processes (Turchin 1998, Phillips et al. 2019) although both observation platforms are extracting data from the same underlying biological processes (habitat preferences and spatial abundance), that form the scientific focus of our statistical inference. Therefore, despite their fundamental differences in perspective, both telemetry and survey data have been used in the past to derive species distribution maps (e.g., compare (Matthiopoulos et al. 2004) and (Herr et al. 2009), using telemetry and surveys respectively to model the distribution of the same species) and model species-habitat associations (SHAs, e.g. telemetry: (Aarts et al. 2008), survey: (Hedley and Buckland 2004)). Nevertheless, full integration between telemetry and survey data has not yet been possible without severe information losses. Additional to the statistical reasons for mismatches between the predictions of analyses based on telemetry and tracking data is the fact that often, these data come from very different classes of individuals, locations and periods of time (Carroll et al. 2019). This project therefore aimed to construct an analysis approach that permitted the integration of telemetry and survey data, exploiting complementarities in their information content. The modelling framework needed to recognise that observed seabird distributions are made up of different species, colonies and breeding life stages. Aptly, by *aggregating* different data types, this project aimed to *disaggregate* the underlying components of seabird marine utilisation.

Objectives of WP2

- Existing approaches to data integration
- Data integration framework
- Presentation of results to the ORJIP SG and PEP

Existing approaches to data integration

When developing new data-integration frameworks, a necessary conceptual distinction is between process and observation models. Rather than integrating the results of several distinct analyses post-hoc (as in model-averaging approaches (Cade 2015)), an integrated analysis assumes that *the same* latent biological process (in this case, the spatial distribution of seabirds) is observed from multiple distinct platforms (in this case, surveys and tracking) that may not necessarily overlap in space and time. This allows information from multiple data types and corresponding observation models, to flow back into the parameters of the latent process model.

The overarching project objective required that results are produced for individual species, colonies and breeding states. Therefore, although the survey data can only discriminate between different species, the model results are in the form of distribution surfaces for each colony, distinguishing between breeders and non-breeders (Carneiro et al. 2020). This format for the results is compatible with the requirements of current and future apportionment algorithms (Bolton et al. 2019). Finer forms of disaggregation (e.g., into individual-level usage via agent-based models) are likely to be counterproductive for both computational speed and user-friendliness. We therefore review existing work in the areas of seabird distribution models, data integration and the application of these analyses to apportionment of effects.

Model of seabird distributions

The approaches taken to model seabird distributions face the challenges of every other SDM framework. These, briefly include issues of sampling such as false negatives, false positives, effort imbalances and location error (Miller et al. 2011, 2019, Hefley and Hooten 2016), partially (Camphuysen et al. 2004) or wholly (Barry and Elith 2006, Fieberg et al. 2018) missing covariates, dynamical environmental effects, spatial (Dormann et al. 2007, Beale et al. 2010) and temporal (Fieberg et al. 2010) autocorrelation in both survey and telemetry data, limitations in model transferability and predictive power (Matthiopoulos et al. 2011, Paton and Matthiopoulos 2018, Holbrook et al. 2019), the need for nonlinear features (Bachl et al. 2019) and high computational demands (Beaumont 2010, Csilléry et al. 2010, Martino and Chopin 2007, Rue et al. 2009, Lindgren 2015, Bachl et al. 2019). However, there are two biological features, central place foraging and density-dependent effects that, while not entirely unique to seabirds, must shape the necessary modelling approaches for colonial species.

For at least some parts of the year, species of seabirds are central place foragers. Their use of different marine locations is therefore likely to be affected by how accessible these locations are from the breeding colony. Accessibility constraints vary by species and season. They are dynamically determined by age,

breeding state (Sansom et al. 2018), the influence of the environment (Fauchald 2009) and their competitors (from the same or different colonies, and from the same or different species) (Lewis et al. 2001, Wakefield et al. 2013, Jovani et al. 2016). These features require nonlinear models that are not always well-suited to the mathematical form of classic statistical modelling. It is possible to build distributions up from individual-based simulation, but these are slow to fit to data and they suffer from high Monte Carlo error. The effects of accessibility on distribution have been anticipated theoretically (Matthiopoulos 2003a, 2003b) and found empirically in marine central place foragers such as seabirds (Lewis et al. 2001, Wakefield et al. 2011, Grecian et al. 2012, Thaxter et al. 2012, Waggitt et al. 2019) and pinnipeds (Matthiopoulos et al. 2004b, Aarts et al. 2008b, Jones et al. 2015a). In addition, the coloniality of seabirds leads to foraging aggregations and potential resource depletion in the regions surrounding the colonies (Lewis et al. 2001). Ultimately, the use of particular locations at sea will be determined by the trade-off between commuting costs (as shaped by accessibility) and foraging benefits (as shaped by environmental resources and depletion).

Both accessibility and depletion/interference may be thought of as functions of distance from the colony, but they are complex, highly non-linear processes for distinct reasons. Accessibility is mainly complicated by the fact that different colonies will be placed in locations that are variably affected by the coastline. Hence, colonies on a small island are likely to be unconstrained in every direction, colonies on a relatively straight coastline will only have a semicircle of marine directions available for departure, while colonies in an inlet may be limited to a single waterbody access route into the sea. To capture declines in accessibility with distance, it is possible, as a first approximation, to introduce a distance-decay function, parameterised identically for different colonies (Matthiopoulos et al. 2004b, Grecian et al. 2012, Matthiopoulos et al. 2022a). However, the fact that the available area of water around each colony will depend on coastal morphology, means that the resulting marine distribution from such a function would not allocate equal numbers of birds at units of area that are the same distance from different colonies. These behaviours will not be independent of age structure. Seabird populations include a high proportion of immatures that are less competitive than adults so may tend to distribute at sea in areas away from colonies (at least until they start to seek to recruit into a colony themselves).

Density dependence is complicated initially by resource competition between colony members (Lewis et al. 2001). As the size of the colony grows, individuals need to travel further to escape the density dependent effects of depletion or interference. At the same time, there is evidence that usage from neighbouring colonies can saturate space leading to the appearance of home ranging behaviour at the colony level (Wakefield et al. 2013). This implies that even without the constraints of commuting costs, a colony might not extend its foraging range (and, consequently, its population size) indefinitely. In addition to inter-colony competition with conspecifics, it is possible that individuals from a colony are experiencing competition from neighbouring colonies of other species. In this case, the resulting asymmetries in range will not only be due to relative colony sizes, but also due to trophic niche overlap and competitive dominance between species. All the above aspects of biology will interact with each other and with environmental productivity. For example, for a given colony size, colonies that are obscured by coastline formations may tend to have greater ranges than island colonies because density dependence is acting over smaller areas close to the obscured colonies.

Non-linearity in the relationship between abundance and its covariates is widely recognised in the statistical literature as well as in the seabird-related literature (Oedekoven et al. 2012). The sophistication that is used for modelling accessibility and density dependence will determine the computational feasibility of the approach. As was discussed in (Matthiopoulos et al. 2022a), a pragmatic approach would express accessibility as distance-decay function. These distances would need to be calculated as spatial

layers, specific to each colony. Any measure of distance can be used (e.g. Euclidean, travel-time, landscape resistance (Matthiopoulos 2003a, Zeller et al. 2012, 2017)), because these calculations are part of pre-processing, not model fitting.

Intra-colony competition could be treated by expressing accessibility as a function of colony size, so that it is larger for smaller colonies and vice-versa. This means that as colony size increases, the decay of expected usage with distance from the colony slows down, hence extending the range of the colony to take account of intra-colony density dependence. The function may be allowed to be non-monotonic, so that total usage initially increases with distance, and then eventually starts to decay. More sophisticated approaches may take a spatially explicit view, including seabird density as an autocovariate (Augustin et al. 1996) in the model, effectively using the response variable *in the neighbourhood* of a point as an explanatory variable for the response variable *at the location* of the point. A related approach is to introduce an explicit autocorrelation term in the response, but this would need to be made colony-specific (and ideally, colony-size specific). Further suggestions for modelling more indirect effects such as inter-colony and inter-specific spatial competition are explored in (Matthiopoulos et al. 2022a).

Methods of data integration

Within the methodological literature, it is becoming recognised that combining telemetry and survey datasets in some quantitative way could increase the effective sample size of the resulting data (Largey et al. 2021), but may also capitalise on their complementary inferential value (González-Solís and Shaffer 2009). This recognition is happening within the broader move in applied ecology towards integrated analyses and adaptive resource management. Such ambitions (and, indeed, the terms “data integration” or “data pooling”) are motivated by the statistical community but are also expressed by more descriptive papers (e.g. (Perrow et al. 2015), indicating that there is an increasing dissatisfaction with piece-wise comparisons between different types of analyses. Momentum behind these ideas is encouraging the incorporation of different sources of spatial information onto a single, joint inference framework, greatly enhancing statistical power, even if the data themselves cannot be directly pooled because of their qualitative differences.

Early integrative work made the plausible assumption that the results obtained from analysing telemetry and survey data should agree (Sansom et al. 2018, Carroll et al. 2019). Therefore, some papers in this area (Ball et al. 2005, Pinto et al. 2016, Prichard et al. 2019) used one datatype as a means of validation for the results of the analysis of the other type. In some cases (Munson et al. 2010), the comparison has assumed the existence of a gold standard (i.e., a high-resolution, precise and accurate data set), which may not necessarily be available, particularly in the marine environment.

Comparisons from different (imperfect) data sets are carried out either visually (Bradbury et al. 2014, Perrow et al. 2015), or via some ad-hoc quantitative method (Sardà-Palomera et al. 2012, Sansom et al. 2018). For example, (Sansom et al. 2018) used four distinct analyses carried out on data (both survey and telemetry) from four UK seabird species. Using as their starting point the utilisation maps generated from each analysis, on each species, they performed all possible pairwise comparisons. They focused on overlap between each pair of maps measured both as the extent (area) and density (utilisation) shared by them at their core areas (defined using varying density contours). This allowed them to discuss patterns of similarity in these estimated snapshots of distribution. However, they were not able to draw combined inferences about parameter values relating the patterns of utilisation to their underlying covariates. Further, they were not in a position to share statistical power between surveys conducted on the same species, possibly at similar times or regions. Such ad-hoc comparisons are biologically valuable because

they inform intuition and motivate scientific hypotheses but they have limited statistical utility because they do not facilitate the flow of information between data sets.

Other studies have exploited the different information carried by survey and telemetry data for purposes of calibration, for example, by using survey data to constrain the utilisation distributions generated by telemetry analysis (Matthiopoulos et al. 2004, Jones et al. 2015), using telemetry to ground-truth the absolute detection probabilities of surveys (Bächler and Liechti 2007, Udevitz et al. 2008, Popescu et al. 2017, Willson et al. 2018, Boback et al. 2020, Glennie et al. 2020), using telemetry to generate foraging-specific distributions from survey data (Louzao et al. 2009, Camphuysen et al. 2012), or trying to understand the composition of survey maps in terms of population components observed by tracking (Yamamoto et al. 2015). These are sequential or post-hoc approaches that extract added value from different data sets but do not constitute true integration.

Note however, that the core idea of calibrating one data set based on another need not require that either data set is perfect. Indeed, the concept of imperfect observations "borrowing strength" from each other has been widely applied elsewhere in spatial survey design (Buckland et al. 2010). Integrated analyses aim to enhance statistical power by greatly increasing the effective sample size of the data set but, also, by using data from different methods, regions, times and spatial resolutions in a complementary way. Developing the fundamentally useful idea of calibration, into the more general concept of integration, several papers (Fletcher et al. 2016, Pacifici et al. 2017, Koshkina et al. 2017, Peel et al. 2019) showed that using presence-only (opportunistic) data in combination with the more informative presence-absence (survey) data improves the descriptive and predictive ability of species distribution models.

Data integration must be done in a way that does not aggravate problems of pseudoreplication (Miller et al. 2019) particularly for analyses of multiple data sets that may have overlapped in space or in time. Such overlaps offer unique corroborative opportunities, but only if they are explicitly modelled in the analysis. Equally important, is the propagation of statistical uncertainty to the final model predictions. Underestimating uncertainty can threaten the precautionary approach and have adverse implications for management and policy decisions. The current situation in the literature is far from ideal, given that most published marine SDM studies (94%) have failed to report the amount of uncertainty derived from data deficiencies and model parameters (Robinson et al. 2017).

A central theme in integrated SDMs is the idea of *complementarity* in achieving spatial breadth and depth. In most situations of data-collection, logistic and budgetary constraints mean that we need to settle on trade-offs between the resolution and the extent of surveys. For example, opportunistic data tend to have greater sample sizes but lower accuracy and precision, compared to formal survey data. Several authors (Pacifici et al. 2017, Nelli et al. 2019) have now pointed out that, by integrating different surveys and different data types into one analysis we do not merely achieve an increase in sample size, but a complementary use of the different spatial extents and resolutions that characterise these data. Complementarity means that detailed features of species distributions can be embedded in big-picture data, even where such details have not been directly observed.

The few studies (Louzao et al. 2009, Pikesley et al. 2018) that have attempted a joint analysis have tended to use purely graphical methods or telemetry censoring and abundance thresholding to convert the data into a similar form, amenable to treatment by the same likelihood function. A major obstacle to joint inference is the incongruence between frameworks used for these two data types. Telemetry data are most conveniently analysed via step selection functions (SSFs (Thurfjell et al. 2014)), while habitat selection functions (HSFs (Boyce and McDonald 1999)) are most appropriate for survey data. Rather disconcertingly, these approaches do not, by default, lead to the same results. Specifically, scaling up by

simulation the microscopic model obtained via SSFs does not yield the same steady-state utilisation distribution generated by an HSF (Barnett and Moorcroft 2008, Signer et al. 2017). An important development in this area is the convergence between the frameworks of habitat selection and step selection analyses (Michelot et al. 2019b). This work has established the conditions under which SSF and HSF frameworks agree, and has derived methods for joint inference (Michelot et al. 2019a). The extension and broader application of this work to real data, particularly for colonial species was a key aim of this project.

Apportionment of effects

The main application of this work is in the renewables impact apportionment for risk assessments (Bolton et al. 2019). Apportionment is motivated by the need to assess the impacts of offshore renewables on colonies found within special protection areas (SPAs). The environmental impact assessment process for offshore wind farms (OWFs) requires us to estimate the proportion of potentially affected birds that may originate from a given SPA.

In general, apportioning relies on being able to weight the spatial distribution of the birds from each colony, by that colony's size. Broadly, apportioning methods distinguish between effects within and outside the breeding season. Methods that focus on the breeding season either tend to hardwire assumptions about spatial accessibility or obtain usage directly from data. In the first category, are methods implemented by Nature Scotland (SNH 2016, 2018) which assume that for a given marine location, the proportion of birds originating from a colony scales linearly with the size of the colony (the breeding population) and inversely with the square of the distance from the colony. The distance metric was originally great-circle Euclidean but was later revised to account for land-shadowing effects, since most seabirds avoid travelling over land. Such approaches are computationally expedient, but they are not able to capture effects such as density dependence and they do not make use of data on distribution. For example, the inverse-square assumption has no biological basis and hence does not distinguish between different ranging strategies across species.

On the other hand, data-driven apportioning methods use the spatial outputs from species distribution models to identify the contributions of different colonies. The (Butler et al. 2017) approach uses telemetry-based spatial utilisation models and re-weights them according to colony size. This allows it to avoid some of the ad-hoc parameters used by the NatureScot frameworks (e.g., by estimating the strength of attraction to the colony for different species) and also permits the inclusion of observed hotspots in the distribution of birds due to associations with habitat. Although not based on an integrative approach, the principles of apportioning are likely to remain unaffected from further improvements, and the implementations of this approach into user-friendly software (Searle et al. 2019) have shown the route that management of marine wildlife will be taking in the immediate future.

Methods operating outside the breeding season (Furness, R.W 2015) follow a related approach, combining knowledge from a range of data sources such as ringing recovery data and GPS tracking to apportion birds to SPA populations based on the relative sizes of the populations wintering in UK waters and, the size of the population within each SPA. Additional data to support such approaches are currently being discussed, that would allow the use of light level geolocators (Lisovski et al. 2020) to extend our observation reach into the non-breeding season.

None of the available approaches currently distinguishes between adults and juveniles and there is minimal functionality for estimating and representing uncertainty in the results. These are therefore key areas of improvement that need to be offered by the present project.

Data integration framework

Motivation and requirements

The requisite level of disaggregation for the process model implies that usage will be modelled for the given species, colony and breeding state. Each combination of these three attributes must have its own distribution model - a habitat selection function or HSF (Boyce and Mcdonald 1999, Matthiopoulos et al. 2020) expressed in terms of relevant environmental covariates relating to habitat preferences or home range accessibility (Matthiopoulos 2003c). However, it is desirable for these components to share some parameters, at least within the same species and age class. Here, we have assumed that HSF parameters are common for animals of the same species and breeding state (i.e., the stationarity assumption, that similar animals from different colonies respond to the environment in a similar way). Of course, this assumption is not in general true (Arthur et al. 1996, Mysterud and Ims 1998) since animals behave differently in different environmental contexts. This can have impacts for model transferability (Yates et al. 2018). However, this is a feature that can be built into HSFs via functional response extensions (Gillies et al. 2006, Matthiopoulos et al. 2011). Parameter sharing is a useful way to increase the inferential value of the data, but also to help generate predictions for areas, times, or species that have very little or no data. Exploring other possibilities of parameter sharing may be valuable. For example, it may be argued that there are links between the parameters for adults and juveniles of the same species. These links may not imply identical parameters, but may nevertheless be helpful. For example, it is known that juveniles are less constrained in their movements than provisioning adults. This can be implemented in a model as a constraint, so that one of the two parameters is free (e.g., adult constraint) but the other is condition (e.g., juvenile constraint no stronger than the estimated adult equivalent). Further extensions may be possible by looking at the taxonomic and functional relatedness between different species. Benthic foragers of a similar size and flight mode will have similar adaptations and, perhaps will tend to relate to environmental variables (such as depth and sediment) in a related way, possibly very different to pelagic foragers.

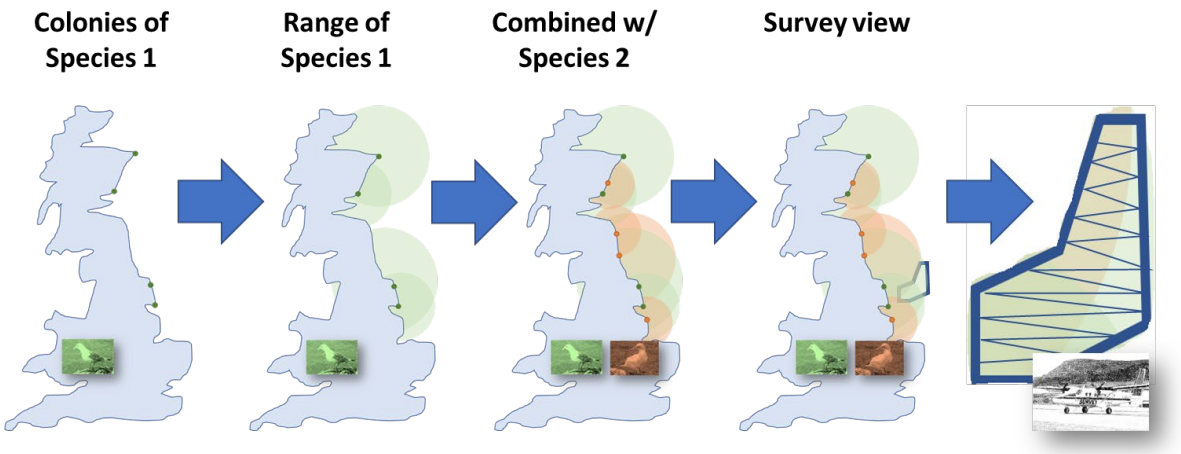


Figure 1. A schematic of the relationship between the underlying ecological process and the observations collected via survey methodologies. The marine polygon surveyed by a particular platform (far right) is a complex superposition of utilisation layers originating from different colonies of different species. An unknown number of these individuals are non-breeders who relate to the environment in different ways compared to provisioning individuals.

The underlying utilisation surface for each species/colony/age combination can be thought of as an Inhomogeneous Poisson Process (Warton and Shepherd 2010, Aarts et al. 2012). The overall usage of a marine region by seabirds can be thought of as a compound surface. Realisations from this process are the observations of bird detections made by survey platforms at-sea. The problem faced by apportioning analyses of survey data (Fig. 1) is that the compound intensity surface within any polygon at sea, may be a complex superposition of intensity surfaces from multiple species, colonies or breeding states.

The proposed modelling framework needed to overcome four distinct challenges:

1. **Formulate biologically acceptable representations for the ranging behaviour of breeders from each colony (i.e., the accessibility covariates) (Thaxter et al. 2012).** For this, we will mainly follow the phenomenological models proposed in (Matthiopoulos et al. 2022). These are sufficiently linear for the HSF and even some of their moderately non-linear versions may be parameterised by expert opinion before incorporation into HSF.
2. **Derive a pragmatic calculation of the number of juvenile birds that are associated with each colony.** This can be derived from species-specific observations and life-history calculations (Furness, R.W 2015).
3. **Formulate biologically acceptable representations for the ranging behaviour of non-breeders from each colony.** Non-breeders differ in two ways from breeders. To the extent that they are less experienced and have the facility to explore and prospect, their usage is likely to be broader-ranging and less targeted than the usage of breeders. The accessibility and HSF components must therefore be specific to non-breeders. The parameters of the accessibility model will be partly provided, but the majority of habitat preference and ranging parameters will be fitted from the combination of data simultaneously with those of breeders.
4. **Integrate between telemetry and survey data.** The key challenge of this project is to exploit recent developments in statistical inference leading to the convergence between the frameworks used to analyse telemetry and survey data (Michelot et al. 2019a, 2019a, 2019c).

Telemetry and survey data integration

The methodology comprises a joint likelihood function of the same underlying process, rigorously scaled to account for the difference between the individual (tracking) and population (survey) perspectives on animal movement. This scaling operation relies on a particular movement model, called Langevin diffusion. The motivation for the approach adopted by (Michelot et al. 2019c) originates from computational methods for statistical inference, and in particular, the broad class of Markov Chain Monte Carlo algorithms (Hastings 1970). Computational inference methods often involve a procedure in which a search particle moves through parameter space, responding to density gradients (density is usually either the posterior probability density in Bayesian approaches, or the normalised likelihood in frequentist approaches, but might also cover other quantities such as entropy in machine learning algorithms (Phillips et al. 2006) or fitness in genetic algorithms (Barricelli 1957). Unlike the category of maximum likelihood algorithms, which come under the heading of optimisation, MCMC does not prioritise searching for the point of peak density (the mode, or maximum likelihood point), but, rather, it tries to faithfully approximate

the density landscape around the peak. It achieves this by adopting a pattern of search that is guaranteed to visit different locations in parameter space in proportion to their underlying density. Counting the frequency of visits of each point in parameter space thus gives an approximation of the underlying density landscape. Therefore, the derivation of MCMC algorithms prizes the property that individual (microscopic) particles describe with their movement an underlying steady-state (macroscopic) distribution. Borrowing the properties of these algorithms for specifying the rules of movement for step selection functions, is therefore guaranteed to give us steady-state distributions, the surfaces of population space-use (utilisation) described by habitat selection functions (Michelot et al. 2019a, 2019b). Imposing this requirement on the two inferential frameworks of SSF and HSF leads to a tractable mathematical relationship (dependence) between their selection coefficients. Such a relationship can allow us to conduct joint inference of telemetry and survey data because they are essentially being used to estimate only one set of coefficients. A key challenge of this approach therefore is to formulate movement models for use by the SSF framework that maintain the essential MCMC scaling properties, while at the same time being realistic models for animal movement. It transpires that this class of models is sufficiently broad to cover many of the commonly used movement models used in the ecological literature.

The mathematical framework underpinning the integration is detailed in a separate manuscript, currently in submission (Blackwell and Matthiopoulos, in prep).

Framework implementation

The TrackTrans R package, developed for this project has functions for simulation and inference. The simulation functionality is included for the purposes of validation, method performance comparisons and intuition-building. Inference functionality is aimed at performing analyses with real data, but can be applied equally easily to the output of the simulations.

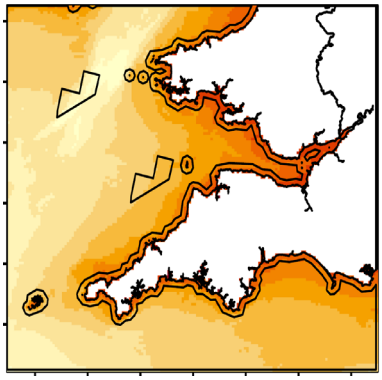
The simulation components come with exemplar coastline and environmental data sets (both continuous and factor variables) that can be used for realistic simulation at high spatial resolutions. In selecting these examples we aimed for 1) a sufficiently large spatial extent, compared to the grid resolution used, 2) a level of complexity in the coastline, so that usage would present “shadowing” effects due to movement obstacles and 3) use of continuous as well as categorical covariates (factors) to demonstrate how each of these can be handled. Shadowing effects of land on calculating distance from a colony are particularly important for movement because they may also be applied on other types of obstacles (such as marine renewable installations) that may need to be circumnavigated, hence shaping the marine distribution of seabirds. TrackTrans offers the capability to generate complex at-sea distributions of seabirds from individual movement models. Classic step selection function models are implemented as well as the more scalable Langevin diffusion used by the inferential part of the package. In designing the simulation we wanted the capability to 1) place multiple colonies of different sizes arranged along the coastline, 2) generate population usage from individual movement, to enable us to collect tracking data, 3) have different movement rules for different breeding stages, 4) the option for individuals to return to the colony periodically and 5) a distinction in the strength of the colony’s attraction between provisioning adults and juveniles. These facilities provides user-control in generating scenarios of underlying biological “truths” that can have an unlimited number of colonies and environmental covariates. Simulated processes can then be sampled realistically, to generate synthetic survey and telemetry data. A real set of transects is used but the user is allowed to regulate the frequency of sampling along the length of the transects and the detection probability. Collection of telemetry data follows a similar ark, where users can determine the frequency of uplinks and the number of individuals tagged from each colony. Tagging is unbalanced

in the sense that only adults are tagged and the number of tagged adults from each colony can be disproportionate, compared to the population sizes of the colonies.

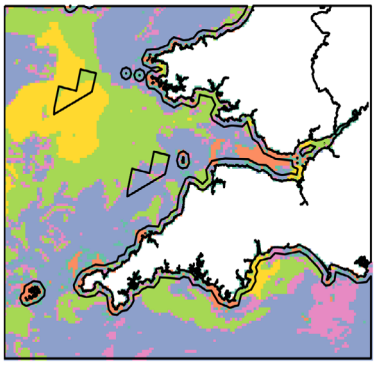
The inference components offer several tools for data manipulation (pre-processing) and several modalities for analysis. Telemetry data can be analysed on their own, using i) a frequentist conditional logistic regression framework (the standard framework used to implement step selection), ii) a Bayesian implementation of the same, iii) a Bayesian implementation of the Langevin diffusion model. Survey data can be analysed as point processes under iv) a frequentist point process model of aggregate usage, v) a Bayesian version of the same and vi) a Bayesian implementation of a disaggregated point process model allowing for the separate estimation of usage from different colonies and ages. Of the above six approaches, the only one that could be used effectively as the engine in an apportioning tool is (vi). Finally, the combined telemetry and survey data can be analysed via vii) a Bayesian implementation of the joint Langevin likelihood.

The TrackTrans R package comes with dedicated plotting functions for the aggregate (as well as the disaggregated) components of spatial usage. The package also has parametric bootstrapping functionality for estimating medians and credible intervals for the contribution of each colony/age combination to the utilisation of a given area or set of areas in the marine environment.

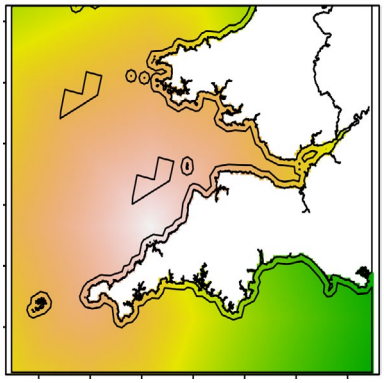
The functions and examples included in the package are described in the associated R-manual and a possible workflow through a joint analysis is detailed in the accompanying vignette (ORJIP InTaS project: Modelling framework for the joint analysis of survey and telemetry data in seabirds, using the R-package TrackTrans).



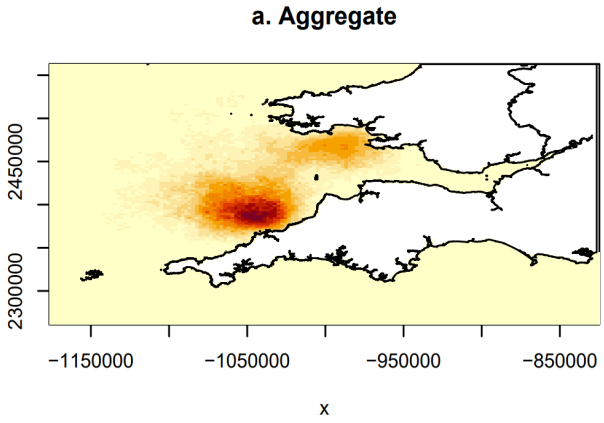
Bathymetry

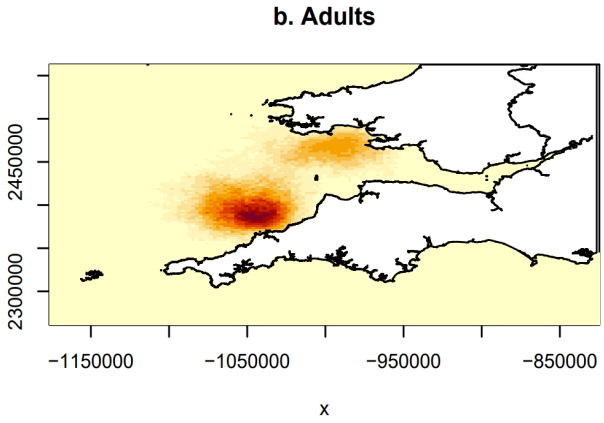


Sediment



Distance from colony





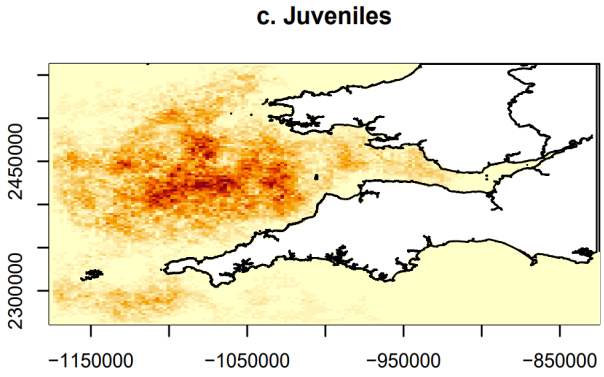


Figure 2. Examples of model covariates (sea depth, sediment type, distance from one of the colonies), and the resulting simulated distribution emanating from both adults and juveniles associated with two fictitious colonies. The assumed proportion of adults in the population is 70% and the southernmost colony is twice as large as the northern one.

Illustration with simulated data

We used the included covariate layers and two arbitrary colony locations and sizes to create a sufficiently challenging simulated system in which usage from both colonies and breeding stages overlapped in the marine environment (Fig. 2). These underlying processes were sampled according to partial tagging of the population (Fig. 3a) and partial coverage of the marine environment by surveys (Fig. 3b).

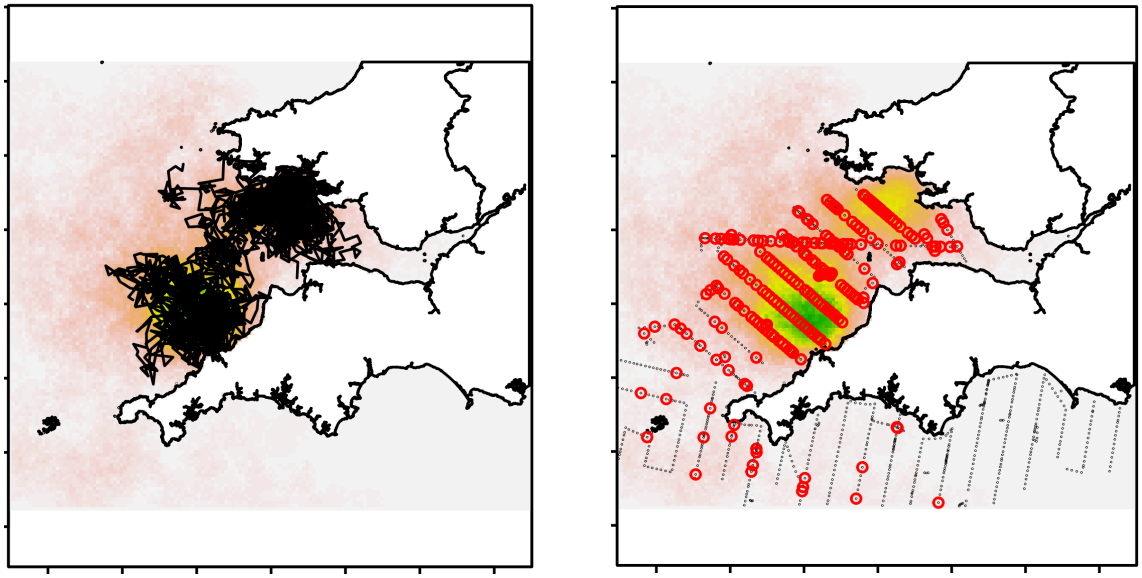


Figure 3. Illustration of the data collection processes in the simulation part of the TrackTrans package.

The synthetic data collected in this way were prepared and analysed in several different informative ways. The telemetry data were analysed on their own first, using frequentist and Bayesian versions of the currently mainstream conditional logistic regression analysis (Duchesne et al. 2010, Prima et al. 2017), then using a version of the newly-introduced Langevin model (Michelot et al. 2019c). Similarly, the survey data were analysed on their own, either ignoring or acknowledging the population's subdivision into colonies and breeding stages. The data were then analysed jointly, and the findings are compared with the earlier single-method approaches. Comparisons were performed both at the level of parameter inference, but also spatial reconstruction of the underlying distributions.

As part of this validation process, we were interested in ensuring that the estimates derived from tracking data alone would scale correctly to the population level, which was the case. A further key comparison was between the performance of model vi (disaggregated modelling of survey data alone) and model vii (joint Langevin model for both survey and tracking data. For the particular example used in this illustration we found that survey data alone could be used for apportioning, but the task was made easier and more precise with the simultaneous use of telemetry data (all these results can be found in the accompanying vignette). Apportioning results were reliable (Fig. 4) and so were the parameters estimated by the model.

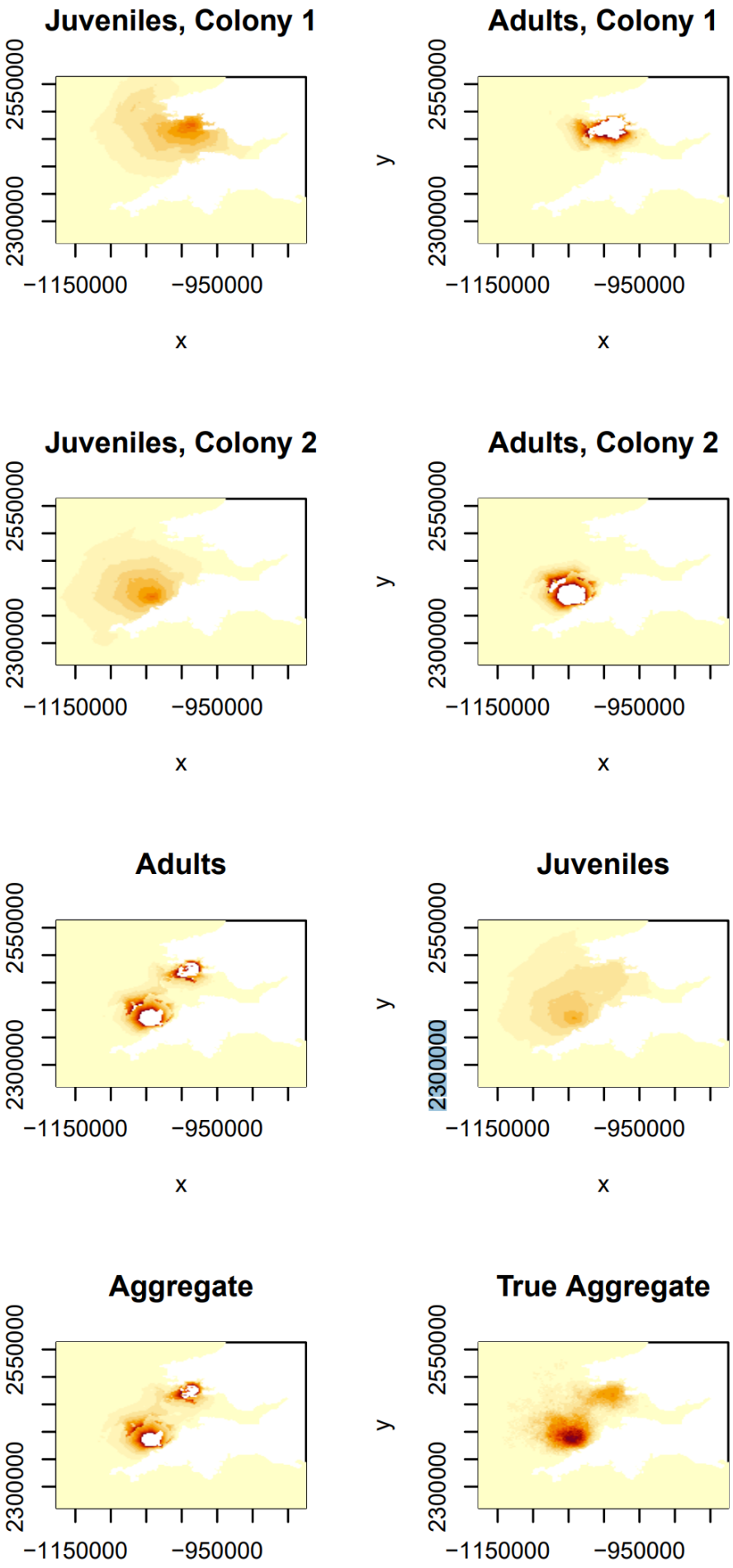


Figure 4. Different partitions of usage by colony and age stage, followed by population weighted aggregates, the total estimated aggregate and (for comparison) the true aggregate usage.

Finally, using the joint model only, we demonstrated how to apportion the effects of marine installations to different colonies and age-stages. Specifically, we considered exposure of different breeding stages and colonies, by calculating the amount of spatial usage by each population component that is enclosed in an arbitrary boundary at sea. Crucially for management decisions, this apportionment of effects is accompanied by spatially explicit measures of uncertainty. The Bayesian framework employed here is ideal for this purpose because parametric bootstrapping of the spatial uncertainty can be performed directly by sampling from the posterior distribution of the fitted models.

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