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Attributing seabirds at sea to appropriate breeding colonies and populations

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A Butler, M Carroll, K Searle, M Bolton, J Waggitt, P Evans, M Rehfisch, B Goddard, M Brewer, S Burthe and F Daunt

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Attributing Seabirds at Sea to Appropriate Breeding Colonies and Populations (CR/2015/18)

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This report presents the results of marine and freshwater scientific work carried out for Marine Scotland under external commission.

Table of Contents

Executive Summary 1

1. Introduction 4

2. Methods: Data 7
- 2.1 GPS data and explanatory variables 7
- 2.2 Colony count data 7
- 2.3 Spatial survey data 8
- 2.4 Foraging range 13

3. Statistical Methods 14
- 3.1 Overview 14
- 3.2 SNH apportioning tool 14
- 3.3 Novel tool for apportioning of breeding birds 15
  - 3.3.1 Previous development of a Poisson GLMM for GPS data 15
  - 3.3.2 Apportioning using the Poisson GLMM 15
- 3.4 Re-calculating apportioning with updated colony counts 19
- 3.5 Comparison of methods for apportioning breeding birds 20
- 3.6 Apportioning for both non-breeding and breeding birds 21
  - 3.6.1 Proposed BNB model for the distribution of non-breeders 19
  - 3.6.2 Constraining the parameters of the BNB model 26
  - 3.6.3 Estimating the parameters of the BNB model 28
  - 3.6.4 Estimating abundance from spatial survey data 29
- 3.7 Uncertainty in apportioning 30
- 3.8 Model performance 30

4. Results 31
- 4.1 Parameter estimation for the BNB model 31
  - 4.1.1 Ratio of non-breeders to breeders 32
  - 4.1.2 Spatial distribution of non-breeders and breeders 32
- 4.2 Local spatial distribution of birds 35
- 4.3 Colony counts 40
- 4.4 Global spatial distribution of birds 42
- 4.5 Apportioning percentages 47
  - 4.5.1 Apportioning R tool 47
  - 4.5.2 Example: results for a single target location 47

4.5.3 Example: spatial distribution of apportioning percentages 52
4.5.4 Overall comparison of apportioning percentages 58
4.5.5 Locations with low similarity between methods 60
4.6 Model performance. 61
5. Discussion 62
5.1 Key findings 62
5.2 Limitations and further work 64
5.3 Recommendations 69
6. Acknowledgements 71
7. References 72
Appendix A. Pre-processing of spatial survey data 77
Appendix B. Mathematical description of the model in Wakefield et al. 2017 78
Appendix C. Methodology for updating SMP colony counts 79
Appendix D. Translating changes from SMP sites into changes to Seabird 200 sites 81
Appendix E: Calculating the ratio of non-breeders to breeders 83
Annex A. Assessment of models to estimate distribution of breeding and non-breeding razorbills and guillemots in the waters around the Shiants islands, northwest Scotland. M. Carroll and M. Bolton 85

Executive Summary

- A key part of the consenting process for proposed marine offshore renewable developments is to establish the colonies of origin of birds that may be affected. The majority of data on seabird distributions are collected through observations from ships or planes, and the connectivity of the observed birds to colonies is unknown. In such cases, the current approach is a calculation that apportions effects such as collision mortality to different colonies based on the distance to each colony and the size of each colony.

- This approach assumes that foraging ranges of adjacent colonies overlap. However, segregation between colonies may occur if birds aim to forage close to the colony to minimise travel costs or avoid competition with individuals from other colonies. Thus, the current approach could result in a greater number of colonies apparently affected, whilst segregation could result in fewer colonies affected, but to a greater degree. A further limitation of the current approach is that it does not account for environmental heterogeneity. Furthermore, it assumes that the density of birds increases in relation to the inverse of the square of the distance from the colony (the “distance decay”), and this is pre-defined and identical for all species, not estimated empirically from data.

- The aim of this research project was to utilise existing information to produce a new tool to apportion birds observed in transect surveys (i.e. ship-based and aerial surveys) to individual colonies. To do so, we used GPS tracking data available for a sample of colonies and colony size data for three species (black-legged kittiwake, common guillemot and razorbill). We used predicted spatial distributions from a recently published paper (Wakefield et al. 2017) estimated from GPS tracking data from breeding birds of these species as a basis for apportioning birds to colonies.

- We implemented four different statistical methods for apportioning birds to breeding colonies. The four methods include the existing approach that is currently used in practice (the “SNH tool”) and three novel approaches based upon statistical modelling of GPS data.

- The first of these novel approaches (“WAKE”) derived the apportioning percentages associated with a statistical model (Wakefield et al., 2017) which

describes the utilisation distribution of birds from a particular colony in terms of variables relating to accessibility, competition and environmental effects, and which can be used to predict the utilisation distribution of birds originating from each breeding colony in the British Isles.

- Wakefield et al. (2017) used colony size data derived from the Seabird 2000 census. The second novel approach (“UCC”) is similar to the first, but revised the calculations to use more recent colony size data, where available (and to impute more recent colony sizes in situations where data were not available).

- Wakefield et al. (2017) only considered breeding birds. The third novel approach (“BNB”) extends this, by using spatial survey data (both at-sea and aerial) to estimate the distribution of non-breeding as well as breeding birds, and, thereby, to calculate the apportioning percentages associated with all birds (whether breeding or non-breeding).

- The BNB model for kittiwake and razorbill estimated the distribution of breeding and non-breeding birds to be identical. This may either suggest that the distributions are genuinely similar, or that the data are insufficiently informative to be able to detect differences between the distributions. Therefore, the WAKE and BNB approaches only provide different results for guillemot.

- We developed a simple tool, implemented within the free R statistical programming environment, to calculate apportioning percentages for a user-defined location using each of these four methods.

- We compared the results obtained using the four methods, across a randomly selected set of locations throughout the waters of the UK Economic Exclusion Zone. The results suggested broad agreement between all four methods, but with relatively substantial differences between the SNH method and the other three methods at some locations. Agreement between the WAKE and UCC methods was generally very high, and agreement between the WAKE and BNB methods was relatively high.

- We recommend that the WAKE method should be used in preference to the current (SNH) method for these three species, and for other species that have extensive GPS data. The UCC and BNB methods merit further investigation, but the BNB method requires further work and the UCC method yields very similar results to the WAKE method, so we do not recommend their use in practice at this time. We cannot reach any direct conclusions regarding species for which extensive GPS data are not available. However, our results suggest that the SNH tool can, in some situations, yield results that differ substantially from those obtained using more biologically plausible methods, suggesting that alternatives to the SNH tool should be considered for these species.

1. Introduction

Scotland is committed to achieving 100% of electricity demand from renewable sources by 2020 through a balanced portfolio of onshore and offshore technologies (Scottish Government 2011a). The Scottish Government has the duty to ensure that the development of the renewable sectors is achieved in a sustainable manner. The UK is also committed to put in place measures including Marine Protected Areas (MPAs) to attain Good Environmental Status (GES) in the Marine Strategy Framework Directive (MSFD) by 2020, and to designate Special Protection Areas (SPAs) and Special Areas of Conservation (SACs) in accordance with implementation of the Birds and Habitats Directives, respectively. Policy makers, therefore, have to follow a balancing process in which there is both achievement of sustainable development and growth of marine industries (e.g. marine renewables) and protection and enhancement of the marine environment (e.g. seabird populations). Accordingly, any licensed marine activity that has the potential to negatively impact on an SPA or SAC is subject to Habitat Regulation Appraisal (HRA) as well as Environmental Impact Assessment (EIA). This is relevant in this context, since renewable developments have the potential to impact on seabirds primarily through collisions, displacement from favoured habitats or because they may act as barriers to movements (Drewitt and Langston 2006; Larsen and Guillemette 2007; Masden et al. 2010; Grecian et al. 2010, Langton et al. 2011, Scottish Government 2011b; Furness et al. 2012; 2013).

The consenting process for developments which may interact with seabirds, such as marine offshore renewables developments, may involve assessing whether the development is likely to have an adverse effect on the integrity of SPAs. In order to assess potential impacts on SPAs designated for breeding seabirds, it is necessary to determine whether seabirds potentially impacted by proposed offshore marine renewables originate from SPAs. The predicted effects are generally quantified in terms of the number of individuals at the development site likely to be affected. Effects are then attributed to appropriate breeding colonies or populations in order to determine population-level (or SPA) impacts. This attributing or apportioning is of particular importance where SPAs are involved and an Appropriate Assessment is required, but is also relevant to Environmental Impact Assessment. The majority of data on seabird distributions are collected at sea from ships or planes, so the connectivity of observed birds to colonies is unknown. In such cases, the current approach is a simple calculation that apportions effects such as collision mortality to different colonies based on the distance to each colony and the size of each colony (Scottish Natural Heritage 2014).

This approach is based on an implicit assumption that foraging ranges of adjacent colonies overlap, with birds from adjacent colonies occurring in these overlap zones (Furness and Birkhead 1984). However, between-colony segregation is predicted to occur at a greater level than expected if birds aim to forage close to the colony to minimise travel costs or avoid competition with individuals from other colonies (Ashmole 1963; Cairns 1989; Wanless and Harris 1993; Grémillet et al. 2004; Louzao et al. 2011; Wakefield et al. 2011; 2013). This could be important, since current approaches (Scottish Natural Heritage 2014) could result in a greater number of SPAs considered to be affected, whilst segregation could result in fewer SPAs affected, but to a greater degree. Furthermore, environmental heterogeneity is not accounted for in the current approach, and it assumes a specific pre-defined form for the distance decay that is identical for all species, rather than estimating it empirically from data.

The aim of this research project was to utilise existing information to produce a tool capable of apportioning birds at sea to their appropriate breeding colony. We developed an analytical tool that apportions birds that have been observed in transect surveys (i.e. ship-based and aerial surveys) to individual colonies. In order to do so effectively, we made use of GPS tracking data available for a sample of breeding colony SPAs and colony size data (which are available for all colonies through the Seabird Monitoring Programme; Mitchell et al. 2004; JNCC 2016). We used predicted spatial distributions estimated by Wakefield et al. (2017) from GPS tracking data from breeding black-legged kittiwakes, common guillemots and razorbills as a basis for apportioning birds to colonies, and for quantifying the uncertainty associated with this apportioning. Apportioning was estimated in three ways:

a) predictive maps of the spatial distribution of birds based upon utilisation distributions that have been estimated from GPS data (collected over 2010-2014), and from colony size data derived from the Seabird 2000 census (Mitchell et al. 2004), following the analysis of Wakefield et al. (2017), which assumes that the spatial distribution of non-breeding birds is the same as the distribution of breeding birds;
b) a variant on (a) in which the colony size data have been updated to cover the same period (2010-2014; JNCC 2016) as that within which GPS data were collected;
c) a variant on (a) in which the distribution of non-breeding birds is assumed to differ from the distribution of breeding birds in terms of the magnitude of the effect of explanatory variables relating to accessibility and competition. The

magnitude of this effect for non-breeding is estimated by optimising the goodness-of-fit between the predictive distributions of breeding and non-breeding birds and the spatial distribution of birds that derived from observed aerial and vessel-based survey data.

We regard b) and c) as a form of sensitivity analysis of a) to address, respectively, the temporal mismatch between the colony count data (1998-2002) and the GPS data (2010-2014) used in creating them; and that the maps developed in Wakefield et al (2017) were designed to deal only with breeding birds, although at-sea survey data comprise a mixture of breeding and non-breeding birds and their relative proportion may vary between species and between periods in the breeding season. The results from c) needed to be interpreted carefully because of the temporal mismatch in the periods of data collection for GPS and transect survey data.

The project evaluated the performance of these three models using a data set comprising GPS and at-sea survey data collected simultaneously in the same spatial area (see Annex A). In June 2015, GPS tracking data were acquired from guillemots and razorbills breeding on the Shiant Islands. Boat-based surveys (funded by RSPB and the Sea Watch Foundation) were carried out throughout the Minch at the time that the birds were carrying the GPS loggers. This dataset, therefore, provided a unique resource allowing direct comparisons to be made between distributions derived from the two survey methods. As such, it provided a unique opportunity to test the relative distributions of breeding and non-breeding birds.

Finally, the results from the three approaches outlined above were compared with the existing apportioning tool (Scottish Natural Heritage 2014).

2. Methods: Data

2.1 GPS data and explanatory variables

We use the same GPS data as in Wakefield et al. (2017) and the data are analysed in the same way as in that paper. The data were collected during the period 2010-2014 as part of the FAME project. We conduct no new analyses of the GPS data within this project; as part of this project we have re-run the models that were fitted in Wakefield et al. (2017), in order to store elements of the model outputs that were not available from the original model runs, but the methods and results are identical to those obtained in the previous analysis.

We also consider the same explanatory variables as those used in Wakefield et al. (2017): distance to colony, area of available sea, sympatric competition, parapatric competition (i.e. competition from conspecifics originating from neighbouring colonies) and a suite of static and dynamic variables describing the habitat (depth, seabed slope, distance to coast, proportion of gravel, sand to mud ratio, proportion of time stratified, potential energy anomaly, sea surface temperature, thermal front gradient density and net primary production). We use the same data sources as in their analysis.

The spatial extent for each species is also the same as in the Wakefield et al. (2017), and reflects the spatial extent of the explanatory variables that were included within the final model. The models for razorbill and guillemot only include grid cells for which sediment type data are available, because variables relating to sediment type were included in the final models for these species, and so cover a narrower spatial extent than the models for kittiwake.

2.2 Colony count data

For most of the analyses considered in this project we use the same colony count data as in Wakefield et al. (2017). These data are derived from the Seabird 2000 census (Mitchell et al 2004), the last national census of seabirds in the UK, which comprises counts of colony size, collected during the period 1998-2002.

In order to maximise the spatial resolution of colony locations, Wakefield et al. (2017) modelled the data at the finest resolution available i.e. the “sub-site”-level within Seabird 2000, the finest spatial resolution at which abundance data are recorded. Seabird 2000 sites with lengths (distance from start grid reference to end grid reference) in excess of 1 km were sub-divided into units of length approximately 1 km, and, in the absence of any data on the distribution of birds within the colony, the count for the sub-site was split equally between these units); we follow Wakefield et al. (2017) in referring to these spatial units as “sites", but note that these differ from the units that are referred to as “sites” within Seabird 2000. The number of sites per species was 1122 for kittiwake, 1164 for guillemot and 1398 for razorbill, leading to a total of 3684 species-by-site combinations. The apportioning tool which accompanies this project allows the user to automatically aggregate results up from the “site” level to the “colony” level, if desired, but we make the results available at the finest spatial resolution because SPA boundaries do not always correspond to Seabird 2000 colonies.

There are 15 “sites” that are included in Seabird 2000, but which are not included in the modelling here. This is because they were not modelled by Wakefield et al. (2017) since explanatory variables relating to sympatric competition do not appear to have been available for these colonies. However, the underlying reasons for these variables being missing for these colonies are not clear, since we used the explanatory data files produced for Wakefield et al., 2017, rather than attempting to re-create these from scratch. The “sites” all relate solely to razorbill, and all lie within Wales. Thirteen of the “sites” relate to Seabird 2000 sub-sites in Gwynedd (NW Wales): Great Orme, Little Orme, Bwrdd Arthur to Fedw Fawr, Middle Mouse, Puffin Island, Abraham’s Bosom, Gogarth, South Stack and Penlas. The remaining two sites relate to a Seabird 2000 sub-site in West Glamorgan: Worm North. These 15 sites collectively represent 0.57% of the total British Isles population for razorbill, but most of these birds originate from a single “site” (South Stack and Penlas; 0.33% of the total population). The impacts of omitting these colonies on the overall, national-scale, results are likely to be minor, since they constitute such a small proportion of the overall population, but the impact upon apportioning percentages for locations that are within the foraging range of these colonies (particularly locations close to the NW Wales coast) could be fairly substantial.

2.3 Spatial survey data

We utilise survey data on the spatial distribution of birds at sea that were collated within the NERC Marine Ecosystems Research Programme. The data were collected as part of a range of different survey efforts and utilised a range of different survey platforms and methodologies. These data required pre-processing prior to analysis (Appendix A).

The pre-processed data are summarised in Table 1. The data consist of two main sources: vessel-based survey data, and aerial data (visual and digital). We include both sources here because the vessel-based data are often relatively old (with good coverage during the 1980s) but have more comprehensive spatial coverage, whereas the aerial data are typically much more recent (and therefore better aligned in time with the GPS data) but have patchy and more coastal spatial coverage (Figures 1 and 2). Detailed descriptions of the different survey methods can be found in Tasker et al. (1984), Camphuysen et al. (2004), Thaxter and Burton (2009), McLean et al. (2009), BirdLife International (2010), Rehfisch and Michel (2015), Ross et al. (2016) and Coppack et al. (2017).

Table 1

Summary of available spatial survey data for each species. Note that ‘Single platform aerial visual’ is where surveys are not using the double-platform method for checking detectability on the transect line (two sets of independent observers where each observation of one team becomes a trial for recapture by the other team; G. Bradbury pers. comm.).

Method	Year		Species	Number of (2x2 km) grid cells with survey data	Area surveyed (km^2)	Individuals
	First	Final				
ESAS vessel-based	1979	2012	Kittiwake	50586	241065	742289
			Guillemot	22457	120032	372623
			Razorbill	44222	233487	720718
ESAS aerial visual	1984	2012	Kittiwake	3201	2891	7405
			Guillemot	1488	1300	3486
			Razorbill	2941	2638	7356
Aerial Digital Stills	2011	2012	Kittiwake	1515	3709	1302
			Guillemot	754	1790	784
			Razorbill	1461	3482	1262
Single platform aerial visual	2002	2011	Kittiwake	1692	20896	12311
			Guillemot	699	8214	5405
			Razorbill	1388	17100	10573

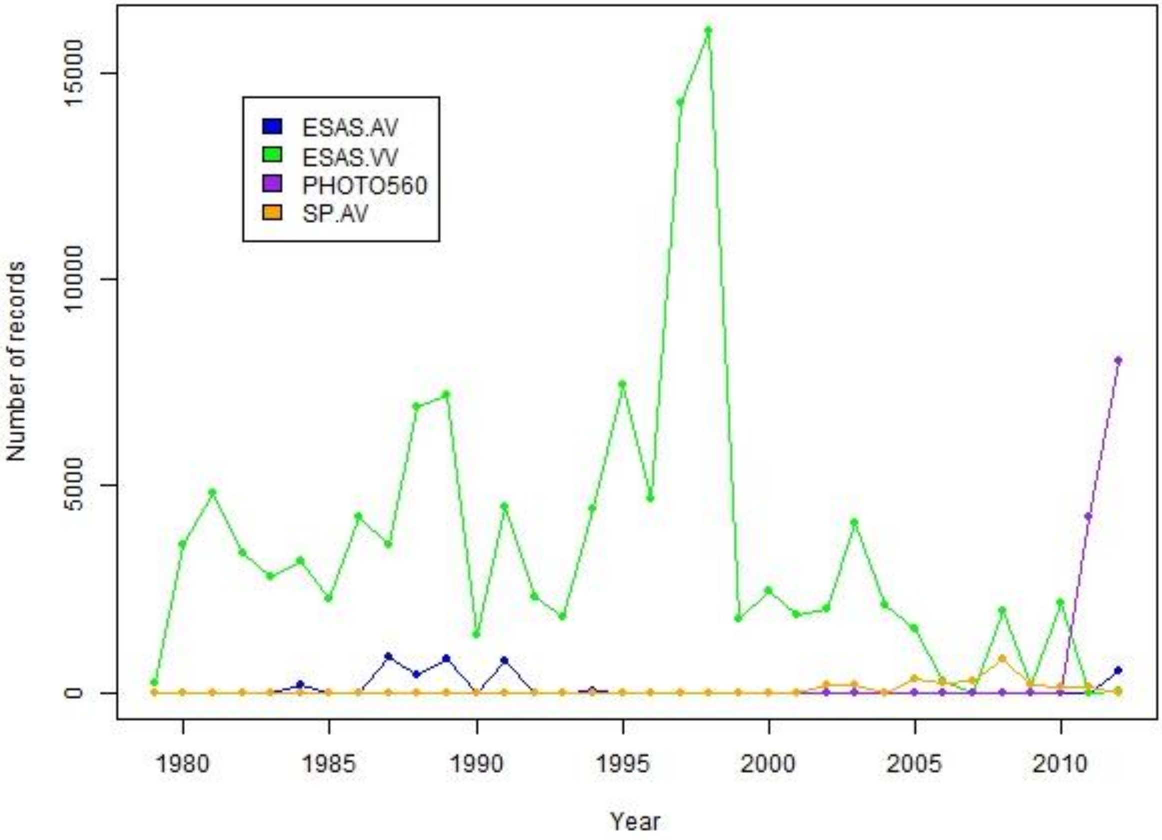

Figure 1: Annual coverage for each source of spatial survey data, in terms of number of survey records per year for each of the four platforms. ESAS.AV: ESAS aerial visual; ESAS.VV: ESAS vessel visual; PHOTO560: aerial digital stills; SP.AV: single platform aerial visual.

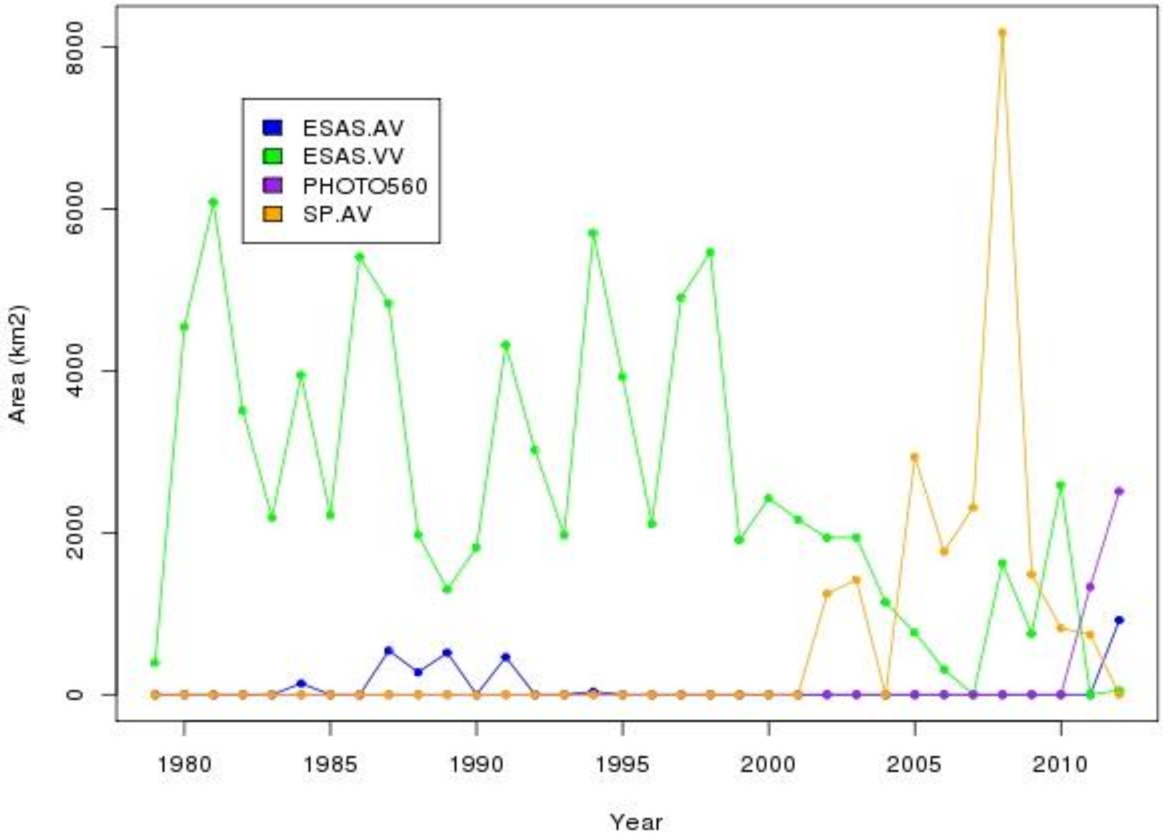

Figure 2: Annual coverage for each source of spatial survey data, in terms of number of area surveyed (km2), per year, for each of the platforms.

2.4 Foraging range

All of the methods that we consider require the specification of a foraging range; if the distance between a particular location and a particular colony exceeds the foraging range then the percentage of birds at that location arising from that colony is assumed to be exactly zero.

We use the same foraging ranges as in Wakefield et al. (2017), which were calculated to be (approximately) equal to 1.1 times the largest observed foraging range seen within the FAME GPS data. The values used by Wakefield et al. (2017), which we also use here, were 300 km for kittiwake, 305 km for razorbill and 340 km for guillemot. Note that Wakefield *et al.* (2017) deliberately select foraging range values that encompass all of the available GPS data, and which, through the addition of a 10% additional buffer, are designed to also try to encompass all unobserved trips taken by birds (i.e. to represent the maximum foraging range of any bird, from any colony). Within the models fitted by Wakefield *et al*. (2017) the sole role of the foraging range is to limit the spatial extent of the area within which predictions are generated – the foraging range is not directly used in the estimation of the utilisation distribution. It follows that bias may arise if the foraging range used is too low, but there should be no bias if the foraging range used is too high – the only cost in specifying the foraging range to be too high is computational (since increasing the foraging range increases the number of grid cells being considered, and therefore the time required for fitting models). We would ideally have considered the sensitivity of the results of our analysis to the choice of foraging range, by, for example, considering values equal to 1, 1.1, 1.2, 1.5 and 2 times the maximum observed range, but (a) this is computationally intensive, and was not feasible within the timescale of this project, and (b) data on explanatory variables (primarily sediment type) tend to become missing for a high proportion of grid cells when very high values are used for the foraging range.

3. Statistical Methods

3.1 Overview

This project was concerned with estimating, for any particular location, the percentage of the birds present at that location that come from each of the sites for each species. It was, therefore, concerned with calculating the *relative* number of birds that come from each of the different possible sites.

In mathematical terms, the project involved calculating the percentage of birds a_{ij} that arise from colony j for a particular location i: we, henceforth, refer to these as "apportioning percentages". In practice, the "locations" refer to the cells of a fine regular grid.

The analysis was performed for three species – black-legged kittiwake, common guillemot and razorbills – and covered breeding colonies within the British Isles (UK, Republic of Ireland, Isle of Man, and Channel Islands).

3.2 SNH apportioning tool

The current approach to apportioning percentages of birds observed at sea to candidate SPAs is a method developed by SNH (SNH 2014). The SNH tool assumes that the number of birds increases in proportion to:

a) the size of the colony;
b) the inverse of the square of the distance from the colony; and
c) the proportion of land within the area that lies within this distance of the colony.

The tool assumes that these relationships each have a fixed and known form (i.e. that the number of birds decays quadratically with distance from colony), and assumes that it is only these three variables that are important – the effects of competition and environmental heterogeneity are not accounted for. The tool uses a deterministic formula that contains no unknown parameters, so no quantification of the uncertainty associated with it is possible. The key advantage of the tool is that the calculations involved are straightforward. More importantly, the tool can be used for a wide range of species, including those with very limited amounts of data, since it only depends upon having (a) colony size data and (b) an estimate of the foraging range of the species; the other methods that we will consider in this project require GPS tracking data for multiple colonies, and such data will only be available for a subset of species. The key disadvantage of the tool is that it relies upon a number of assumptions which may not be biologically realistic: that the parametric form of the distance-decay function is inverse quadratic, that the density of birds is unaffected by competition, and that the density of birds is unaffected by environmental heterogeneity.

Note that the SNH tool assumes that, all else (i.e. colony size and proportion of land) being equal, the *total* abundance of birds at a distance d from the colony is proportional to d^{-1}, which represents an assumption of a relatively strong central place foraging effect. This follows from the fact that the abundance of birds at a particular location of distance d from the colony is assumed to be proportional to d^{-2}, and that the number of locations lying at this distance is proportional to the circumference of a circle of radius d, which is $2\pi d$; the total abundance of birds at distance d is therefore proportional to $d^{-2} 2\pi d$, and therefore to d^{-1}.

3.3 Novel tool for apportioning of breeding birds

The first stage of analysis for the current project involves using a habitat association model, fitted to GPS tracking data, as an alternative approach to quantifying the proportion of birds that can be attributed to each colony. This approach accounts for the fact that birds have environmental preferences for some habitats, and for the fact that the relationship with distance to colony may not follow the inverse quadratic rule that is assumed within the SNH apportioning tool. The approach also allows the uncertainty associated with the estimation of apportioning percentages to be explicitly quantified and mapped. This analysis relates solely to the distribution of breeding birds – or equivalently to the distribution of all birds under an assumption that the distributions of non-breeding birds are identical to those of breeding birds. In Section 3.6 we consider a version of the model where this assumption is relaxed such that the distribution of non-breeding birds is allowed to differ from that of breeding birds.

3.3.1 Previous development of a Poisson GLMM for GPS data

This approach utilises the results from statistical modelling work that was previously undertaken by Wakefield et al. (2017). This work involved fitting a habitat association model to GPS tracking data for breeding birds that were collected at a number of colonies around the British Isles during the period 2010-2014. Data were collected for four species – kittiwake, guillemot, razorbill and shag – during the breeding season (May to July) but only the first three of these are considered within the current project (since shag is out-with the remit of this project).

The habitat association model that Wakefield et al. (2017) applied to these data was a weighted Poisson generalized linear mixed model (GLMM), that is designed to provide a discrete approximation to a spatial point process model (Warton and Shepherd, 2010). This approach represents the state-of-the-art, in terms of the statistical analysis of presence-only data, and has a number of advantages over more standard approaches that involve simulating pseudo-absences (Aarts et al. 2012). The approach estimates a quantity that is proportional to the utilisation distribution (UD) for a bird – it can be converted into an estimate for the UD by normalising the predicted values from the model so that they add to one when summing them across all possible spatial locations (e.g. all cells on a fine grid that covers the study area). The Poisson GLMMs each contained a single random effect for "colony", to account for overall differences in the number of points between colonies; they also contained an offset for the log of the number of birds at the colony, to account for the fact that the number of tracked locations will be proportional to the number of tracked birds. The models were fitted to tracking data for a randomly selected 24-hour period for each individual, interpolated to one location every 100 seconds; individuals with less than 24 hours of GPS data were excluded from the analysis.

The model can be used to predict UDs for both monitored and unmonitored colonies (i.e. for those with and without local GPS data). We let $u_{ij}(\boldsymbol{\beta})$ denote the UD at location i of a bird from colony j that would be produced by putting parameter values $\boldsymbol{\beta}$ into the model of Wakefield et al. (2017); a full mathematical description of the model for the UD is given in Appendix B. The model was implemented within the **R** statistical programming environment (Gentleman and Ihaka, 1996) using the **lme4** package (Bates et al. 2015).

The parameters $\boldsymbol{\theta}$ describe the effect of explanatory variables upon the UD. Wakefield et al. (2017) considered a number of potential explanatory variables, including distance to colony, the area of available sea, variables relating to sympatric and parapatric competition, and a range of environmental variables. A forward selection procedure was used to identify the best model for each species. This procedure involved adding variables to the model sequentially (in an order that is justified based on the biology), and evaluating whether the inclusion of the variable leads to an improvement in the empirical performance of the model. The fixed effects that were included within the final model for each of the three species of interest here are shown in Table 2; note that “distance to colony” appeared in the final model for all three species, and that models containing distance to colony have, in all cases, substantially better empirical performance than those without this variable.

The UDs are multiplied by colony size, c_j, in order to calculate the expected number of (breeding) birds from colony j at location i:

$$n_{bij} = c_j * u_{ij}(\boldsymbol{\beta})$$

[**Equation 1**]

The total number of expected birds at this location, from all colonies, is then equal to:

$$N_{bi} = \mathrm{SUM}_{\{\text{all colonies } j\}}(n_{bij})$$

[**Equation 2**]

Table 2

The fixed effects contained within the final GLMM for each species. Terms within the model are denoted in green if captured by a single parameter, in blue if captured by two parameters (a linear and quadratic term), in yellow if captured by three parameters (variable + variable E1 + interaction of the two), and in orange if captured by four parameters (the parameters for yellow, plus a quadratic term). Numbers define numbers of parameters relating to each variable. For ease of presentation transformations of variables are not described.

Variable	**Kittiwake**	**Guillemot**	**Razorbill**
Block 1 - Colony distance			
Distance by sea from the colony	1	1	1
Block 2 – Cumulative area			
Cumulative area of sea	1	1	1
Block 3 – Sympatric competition			
Number of conspecific breeders	1	1	1
…interacted with cumulative area	1	1	1
Block 4 – Parapatric competition			
Density relative to other colonies	1	1	
Block 5 - Environmental variables			
Seabed slope	4		3
SST			3
Standardized SST	1		
Stratification	3		
Gravel		1	
Sand:mud ratio		4	2
Thermal front gradient density		1	
Distance to coast		3	
Summary			
Total number of parameters	**14**	**15**	**13**

3.3.2 Apportioning using the Poisson GLMM

It is possible to use the outputs from the Poisson GLMM to calculate the percentage of birds that can be attributed to each colony, j, for any particular location in space, i. In order to do this, we simply divide the number of birds from colony j that we would expect to see at location i by the total number of birds from all colonies that we would expect to see at location i, and then multiply by 100 to convert from a proportion to a percentage. In mathematical terms, this is equal to:

$$a_{bij} = 100 * \frac{n_{bij}}{N_{bi}}$$

[**Equation 3**]

Although the calculation is straightforward, it is fairly computationally intensive to implement because the number of locations (grid cells) and colonies are both very large. Within the current project, we have substantially re-written the R code from the analysis in Wakefield et al (2017) in order to reduce the computational time required for this calculation.

3.4 Re-calculating apportioning with updated colony counts

The calculations so far have all assumed that the colony sizes, c_j, are precisely known. This is probably a reasonable approximation for periods in which a complete census of the national population was undertaken: e.g. the period 1998-2002, during which the Seabird 2000 survey took place. The analyses in Section 3.3 used observed colony counts from Seabird 2000.

However, it is known that certain populations of some species have changed substantially since the period in which Seabird 2000 occurred, and the use of the Seabird 2000 counts is therefore likely to lead to some bias when estimating apportioning percentages.

We, therefore, attempt to update the colony counts to cover the period, 2010-2014, for which the GPS data that were used in fitting the Poisson GLMM are available. There is uncertainty associated with this updating, because not all colonies were surveyed during the 2010-2014 period, so we attempt to quantify this uncertainty within our analysis.

Specifically, we simulate the value of:

$$c_{jk}^{*} = c_j \exp\left(l_{jk}^{*}\right)$$

[**Equation 4**]

Where c_j denotes the abundance of colony j within Seabird 2000 and:

$$l_{jk}^{*} \sim \mathrm{N}(m_j, s_j)$$

[**Equation 5**]

denotes the simulated log-ratio of change between this period and the FAME period (2010-2014). The mean m_j and standard deviation s_j for the log-ratio of change are calculated by applying a multiple imputation procedure to SMP data (this procedure is a variant on the approach of Thomas, 1993, which was used in JNCC (2016), and is described in Appendix C). Simple rules are then used to convert the mean and standard deviation of this log-ratio from SMP to Seabird 2000 sites (see Appendix D for details).

3.5 Comparison of methods for apportioning breeding birds

We compare the results obtained using the novel approach (Section 3.3) against those obtained using the SNH apportioning approach (Section 3.2). Because the novel approach is effectively a generalisation of the SNH approach we would expect the empirical performance of the newer approach to be better – the key question is whether the improvement in empirical performance is sufficient to justify the increase in model complexity.

We map the apportioning percentages generated by the two approaches for each colony-species combination, to allow visual comparison of the percentages. A formal comparison of the apportioning percentages for all colonies at any particular location in space is also made using Bhattacharyya's affinity index (BA):

$$\mathrm{BA} = \left(\frac{1}{100}\right) * \mathrm{SUM}_{\text{all colonies}, j}\left\{\sqrt{a_{sij} a_{bij}}\right\}$$

[**Equation 6**]

The BA metric was used to compare utilisation distributions (UDs) within Wakefield et al. (2017), and has previously been used for this purpose within the ecological literature. The BA metric was originally designed for the purposes of comparing any two probability density functions or probability mass functions (their discrete analogue), and it is also used for this purpose in many applications outside ecology; UDs are just a special case of a probability mass function. In the current context we are using the same metric to compare apportioning percentages generated using different methods at a single location (since, after dividing by 100, the apportioning percentages associated with all colonies at a specific location also constitute a probability mass function). In practice, we calculate the BA scores separately for each of 100 locations that have been randomly selected from within the study region; we then present the mean of these values, but also, in order to represent spatial variations in performance, present the minimum, median and maximum values.

3.6 Apportioning for both non-breeders and breeders

The next stage of our analysis involves apportioning non-breeding, as well as breeding, birds to colonies. The approach outlined in Section 3.3 utilises distributions that have been derived from GPS data that relate to data for breeding birds. The resulting apportioning percentages therefore should be regarded as relating only to breeding birds – or, equivalently, should be regarded as having been calculated under the assumption that the distribution of breeding birds is identical to that of non-breeding birds. This assumption is, however, not biologically plausible, because although non-breeding birds may attend colonies extensively during certain periods of the breeding season in many species, they are not constrained in the same way as breeding birds that are tasked with delivery of food to the offspring or relief of the mate from offspring attendance duties such as incubation and brood guarding (Camphuysen et al. 2011).

In this section we therefore outline an extension to the approach of Section 3.3 in which the spatial distributions of non-breeding birds are allowed to differ from those of breeding birds. Note that we are concerned with modelling the distribution of non-breeding birds during the breeding season: not in modelling the distribution of birds (either breeders or non-breeders) outside the breeding season. This extension is based on the idea that spatial surveys of bird populations, whether collected using ship-based or aerial surveys, include a mixture of breeding and non-breeding birds, whereas the distributions that are derived from GPS data (e.g. using the Poisson GLMM of Section 3.3) relate to breeding birds. It should, therefore, be possible to, indirectly, quantify the number of non-breeding birds by calculating the discrepancy between the spatial distribution of birds that is estimated from spatial survey data and the distribution of breeding birds that is estimated rom GPS data. The substantial temporal mismatch between the timing of the survey data collection and the timing of the tracking data means that this quantification should be treated with considerable caution, but is unavoidable due to the relatively sparse spatial coverage (at a national level) of surveys in recent years. The indirect approach that we are using to quantify the distribution of non-breeding birds is necessary because (a) auks cannot be aged within spatial survey data (such as ESAS) and (b) not all non-breeding birds are juvenile.

The model that we develop in this section essentially involves predicting the number of breeding and non-breeding birds that we would expect to be present at each location, using the result from fitting the Poisson GLMM to GPS data. These predictions also depend upon additional unknown parameters, however, – the overall ratio of non-breeding and breeding birds within the population, and the differential effects of explanatory variables in determining the distribution of non-breeding birds relative to that of breeding birds. The value of the first of these parameters is specified based on published values in the existing literature. Note that this parameter relates to the overall ratio of non-breeders to breeders (at the whole population level), but that there may be spatial variations in the ratio of non-breeders to breeders resulting from the model allowing for differential effects of the explanatory variables on breeding and non-breeding birds. The remaining parameters are estimated by choosing the values that minimise the discrepancy (as quantified by the BA score) between the resulting predictions and the number of birds observed in spatial survey data.

The structure of the model is shown graphically in Figure 3, and, for comparison, the model of Section 3.3 is shown in Figure 4.

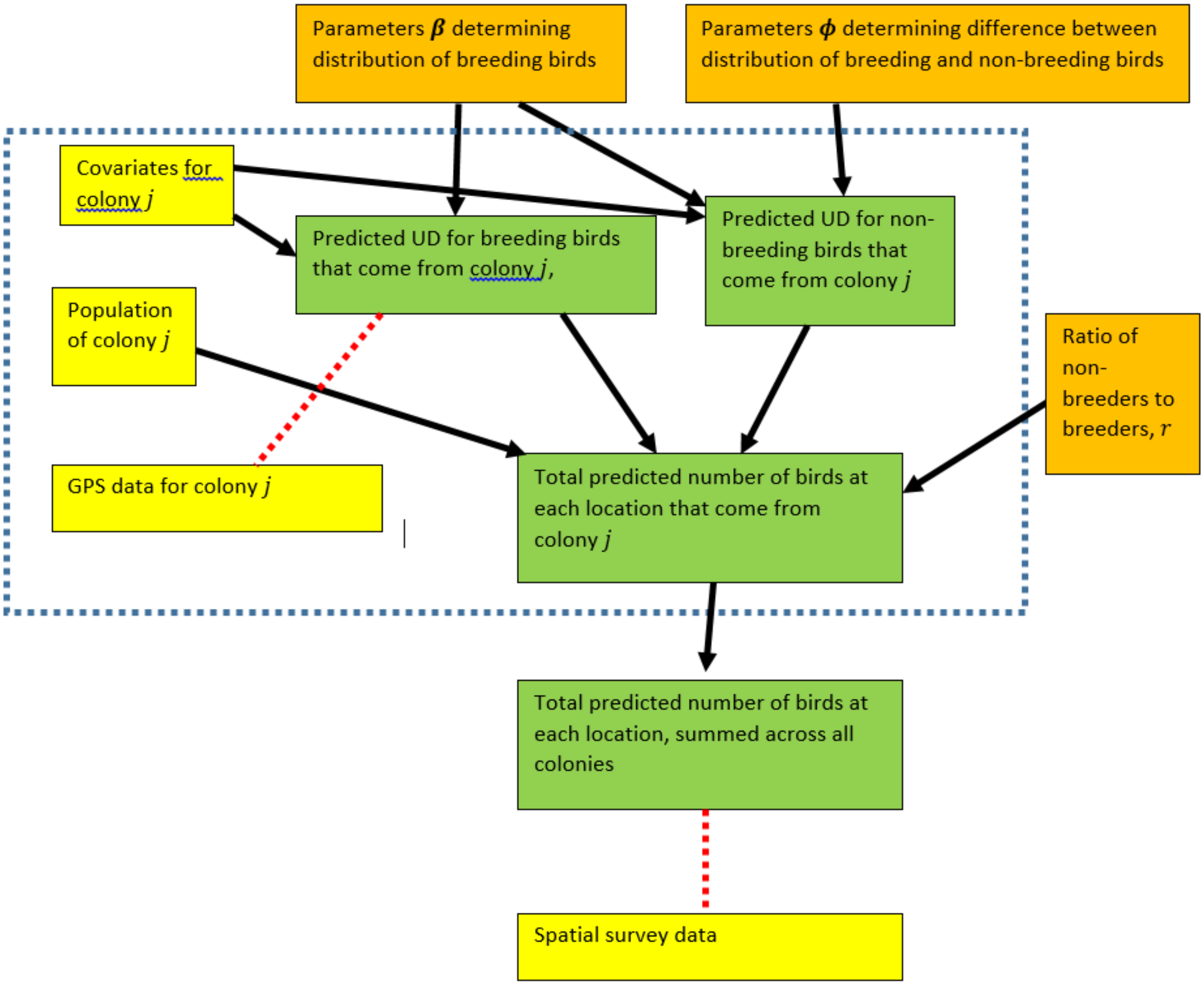

Figure 3: Graphical illustration of the BNB model described in Section 3.6. Yellow boxes show observed data, orange boxes show unknown parameters, and green boxes show derived quantities (that can be calculated deterministically from the values in other boxes). Red dotted lines show the quantities that are compared during the process of parameter estimation.

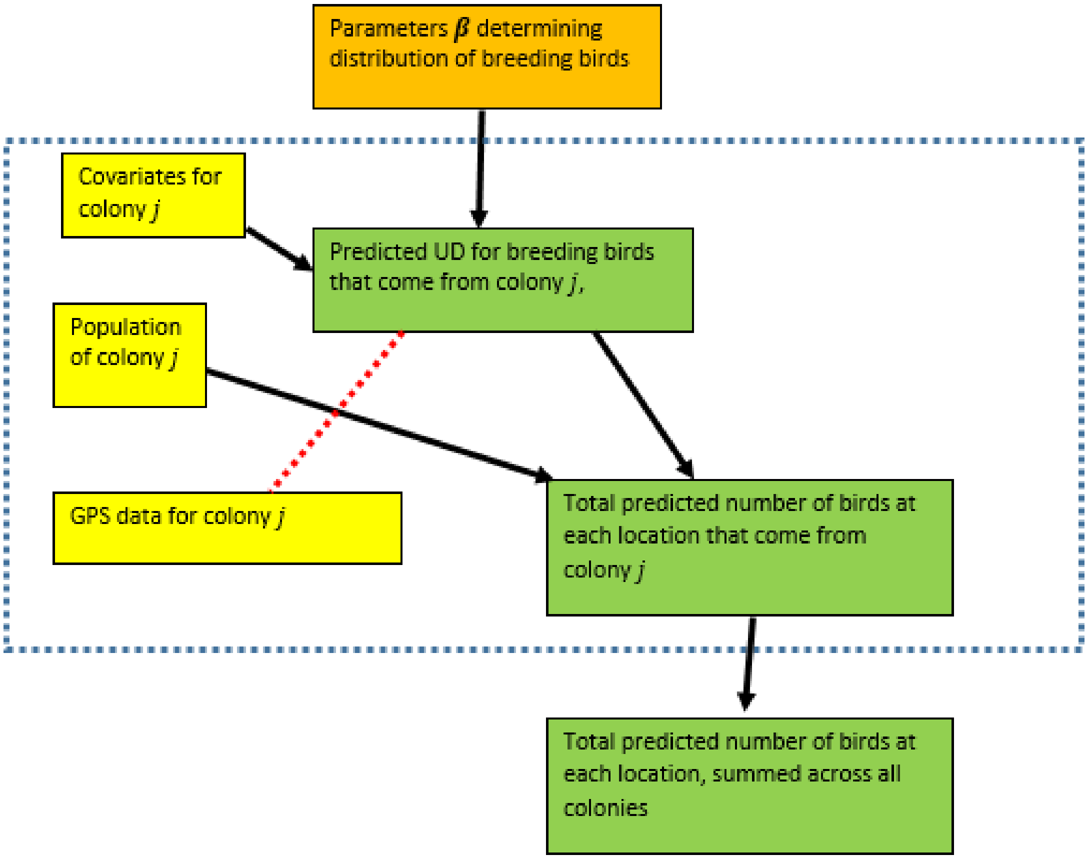

Figure 4: Graphical illustration of the Wakefield et al. (2017) model of Section 3.3, in the same format as Figure 3.

3.6.1 Proposed BNB model for the distribution of non-breeders

The predicted number of breeding birds from colony j at location i, based on fitting the Poisson GLMM model to GPS data, is equal to:

$$n_{bij} = c_j * u_{ij}(\boldsymbol{\beta})$$

We assume here that the corresponding number of non-breeding birds is equal to

$$n_{oij} = c_j * r * u_{ij}(\boldsymbol{\phi} * \boldsymbol{\beta})$$

[**Equation 7**]

where r is an unknown parameter denoting the overall ratio of non-breeding to breeding birds, and where $\boldsymbol{\phi}$ are parameters that measure the (multiplicative) difference between the effects of the explanatory variables upon breeding birds and upon non-breeding birds. Note that the bold-face font on the values of $\boldsymbol{\phi}, \boldsymbol{\beta}$ indicates that these are vectors; this formula therefore implicitly allows each element of $\boldsymbol{\beta}$ to be associated with a different element of $\boldsymbol{\phi}$**.** The total number of birds from colony j that we would predict to be at location i based on this model is therefore equal to:

$$n_{tij} = n_{bij} + n_{oij} = c_j * \left\{u_{ij}(\boldsymbol{\beta}) + r * u_{ij}(\boldsymbol{\phi} * \boldsymbol{\beta})\right\}$$

[**Equation 8**]

Thus, the total number of non-breeding birds at this location (summed across all colonies) is equal to:

$$N_{oi} = \text{SUM}_{\{\text{all colonies } j\}}\left(n_{oij}\right)$$

[**Equation 9**]

and the total number of overall birds (both breeding and non-breeding) is equal to:

$$N_{ti} = \text{SUM}_{\{\text{all colonies } j\}}\left(n_{tij}\right)$$

[**Equation 10**]

This model for the number of non-breeders therefore (comparing Equation 7 to Equation 1) allows explanatory variables to have different effects for non-breeding and breeding birds, but, in order to make the model tractable (i.e. to ensure the parameters can actually be estimated from the available data) it makes two important simplifying assumptions:

Assumption A: the UD for non-breeders depends upon the same explanatory variables as the UD for breeding birds, and has the same parametric form (i.e. the model for the UD is of the same type);

Assumption B: the overall ratio of the number of non-breeding to breeding birds is the same for all colonies.

These assumptions are undoubtedly strong in a statistical sense, and their biological plausibility (especially that of Assumption B) may be questionable. They are nonetheless, however, still much weaker than the assumption that we made in Section 3.3 – in that section we assumed that the distribution of breeding and non-breeding birds is identical, and that is believed to be biologically implausible. The model that we are proposing here can essentially be regarded as a generalisation of the model developed in Wakefield et al. (2017): the model that was developed in that paper corresponds to the special case of the more general model in which $r = 0$ (there are no breeding birds). If $r > 0$ but $\boldsymbol{\phi} = \mathbf{1}$ the more general model is not strictly equivalent to the model in Wakefield et al. (2017), but it produces results that are directly proportional to those presented in that paper because $n_{tij} = n_{bij}(1 + r)$ (from Equation 8).

The apportioning percentages for non-breeding birds are calculated in exactly the same way for non-breeding birds as for breeding birds, so that:

$$a_{oij} = 100 * \frac{n_{oij}}{N_{oi}}$$

[**Equation 11**]

and the apportioning percentages for all birds (breeding and non-breeding) can also be calculated in the same way:

$$a_{tij} = 100 * \frac{n_{tij}}{N_{ti}}$$

[**Equation 12**]

3.6.2 Constraining the parameters of the BNB model

The model that we have outlined in Section 3.6.1 is very general, and it contains a relatively large number of unknown parameters. In particular, if no constraints are imposed upon the parameters $\boldsymbol{\phi}$ the model allows the distribution of non-breeding and breeding birds to be entirely unrelated. Available data are unlikely to be sufficient to estimate completely separate distributions for non-breeding birds, so the model is unlikely, in this completely general form, to be usable in practice. We, therefore, impose constraints upon the values of $\boldsymbol{\phi}$.

The key differences between breeding and non-breeding birds will relate to the degree to which birds are constrained to be central-place foragers - i.e. that the effects of distance to colony, cumulative area, and sympatric competition are likely to vary between non-breeders and breeding birds. Immature birds attend colonies during the breeding season; however, we might expect that there will be differences in the extent to which they forage to and from a central place compared with adult birds which return to the colony multiple times per day on average. Such differences may be exacerbated by immatures having larger foraging ranges to reduce intraspecific competition. We would expect the effects of these variables to have the same sign (positive/negative) for both breeding and non-breeding birds, but would expect the effects of these variables to be weaker for non-breeding than for breeding birds. We, therefore, constrain the parameters that relate to these variables, ϕ_k, to lie between zero and one – if $\phi_k = 0$ this implies that the variable has no effect for non-breeding birds, if $\phi_k = 1$ this implies that the magnitude of the variable for non-breeding birds is identical to that for breeding birds.

We assume that the remaining variables – which relate to parapatric (rather than sympatric) competition and environmental effects – have the same effect for both breeding and non-breeding birds (so that $\phi_k = 1$ for these variables).

In practice, these constraints mean that for each of the three species being considered the effects of four variables are allowed to vary between non-breeding and breeding birds: distance by sea from the colony, cumulative area of sea, number of conspecific breeders (colony size), and the interaction between cumulative area of sea and number of conspecific breeders. Note that the results would be identical if we included the number of conspecific non-breeders, rather than the number of breeders, in the model, since we are assuming that the ratio of non-breeders to breeders is the same for all colonies, so it does not matter which of these is used.

3.6.3 Estimating the parameters of the BNB model

The model that we have proposed here depends upon the parameters $\boldsymbol{\beta}$ of the original model of Wakefield et al. (2017), which can be estimated from GPS data. The model also, however, depends upon the values of additional parameters: r and $\boldsymbol{\phi}$. These parameters relate to the distribution of non-breeding birds, and so cannot be estimated from GPS data.

Initial explorations suggested that the value of r – the overall ratio of non-breeders to breeders within the population - is difficult to estimate empirically, so the value of this parameter is fixed based on expert biological knowledge. A simple age-structured population model is used to calculate the value of this ratio for each species (see Appendix E for details).

The parameters $\boldsymbol{\phi}$ are estimated empirically, using spatial survey data. Spatial survey data can be used to directly estimate the overall number of birds, N_{si}, for a subset of spatial locations – those for which data have been collected. We can calculate the empirical distribution (gridded but not smoothed) associated with these numbers, based solely on the subset of locations for which data are available, to be:

$$U_{si} = \frac{N_{si}}{\text{SUM}_{\{\text{locations with spatial survey data } i\}}(N_{si})}$$

[**Equation 13**]

For each value of the parameters $\boldsymbol{\phi}$ we can calculate the predicted distribution associated with the BNB model for this set of locations to be:

$$U_{ti} = \frac{N_{ti}}{\text{SUM}_{\{\text{locations with spatial survey data } i\}}(N_{ti})}$$

[**Equation 14**]

We compare these two distributions using the BA score:

$$\text{BA}(\boldsymbol{\phi}) = \text{SUM}_{\text{all locations},i}\left\{\sqrt{U_{ti}, U_{si}}\right\}$$

[**Equation 15**]

We do this for a range of different combinations of parameter values, and select the combination that gives the highest score (i.e. the best empirical performance).

In practice, we calculate the value of BA for a regular grid of parameter values: we consider values of 0, 0.25, 0.5, 0.75 and 1 for each of the four parameters that are allowed to differ between non-breeding and breeding birds. This would lead us to consider $5^4 = 625$ possible parameter combinations for each species, but we exclude combinations in which (a) the interaction between cumulative area and parapatric competition is non-zero but one or both of the corresponding main effects is zero, since this is standard statistical practice, (b) the effect of parapatric competition is non-zero but the interaction between parapatric competition and cumulative area is zero, since parapatric competition only affects the model outputs if the interaction is included. These restrictions lead us to consider 345 possible parameter combinations.

3.6.4 Estimating abundance from spatial survey data

The abundance of birds at each spatial location, N_{si}, is estimated from the spatial survey data described in Section 2.3. The methodology is:

a) for each survey (row in the "effort" dataset) calculate: the total number of birds of the species of interest seen within this survey, and the total area surveyed (i.e. transect length multiplied by transect width*survey time);
b) for each grid cell on the LAEA grid, identify all of the surveys for which the midpoint location lies within this grid cell, and sum the number of birds observed within these surveys, and the total area of sea (in km^2) covered by these surveys;
c) calculate the density of birds per km^2 to be (total number of birds / total area surveyed).

Within the current analysis we do not account for non-detection when calculating this density, which results from availability bias (birds undetected because they are underwater) and perception bias (birds available for detection but missed by the observer). These effects will differ with the different survey methodology (e.g. between aerial and boat-based survey data) and there is no straightforward way to do this, but in future work it would be useful to extend the analysis to account for this.

3.7 Uncertainty in apportioning

There are two different forms of uncertainty associated with apportioning:

1) the uncertainty associated with estimating the apportioning percentages themselves (e.g. the uncertainty associated with the values created via Equation 3);

2) the uncertainty associated with apportioning values from an actual sample of birds, of size s, given these percentages.

The latter can be quantified by simulating a large number of times from a multinomial distribution with sample size s and probabilities $(a_{bi1}, \ldots, a_{bin})/100$; the 95% confidence interval is then quantified by calculating the 2.5% and 97.5% quantile across the set of simulations for each colony.

We would ideally also quantify the uncertainty associated with the percentages themselves (the first form of uncertainty); in practice, however, this turned out not to be feasible in this context. The uncertainty arises from a) uncertainty in the colony sizes and b) uncertainty in the (local) UDs for each colony. Uncertainty in Seabird 2000 counts is not readily quantified. Uncertainty in the UDs could, in principle, be quantified in the context of the WAKE and BNB, but the standard errors associated with the WAKE predictive maps are likely to be under-estimated due to pseudo-replication: Wakefield et al. (2017) do not make use of these standard errors for this reason. Moreover, uncertainty in the SNH apportioning percentages does not appear to be quantifiable at all.

We therefore, focus solely on quantifying the second source of uncertainty within the context of this project.

3.8 Model performance

The performance of the model was tested using an independent data set comprising GPS tracking and at-sea survey data collected simultaneously in the region of the Shiant Islands in 2015. This work is described in detail in Annex A. In summary, the performance of the model described in Section 3.6 which incorporated the distribution of non-breeders was assessed by comparing the fit of predictions from the approaches described in Sections 3.3 and 3.6 to (i) tracking data and (ii) boat survey data for guillemots and razorbills. Since tracking data relate solely to breeding birds, and boat survey data relate to breeders and non-breeders combined, we predict that, if the model of breeding and non-breeding birds represents an improvement on the model of breeding birds in the prediction of densities of all birds at sea (regardless of breeding status), then: (i) the former model will provide a better fit than the latter model to the boat survey data; (ii) the latter model will provide a better fit than the former model to the tracking data. Since the former and latter models can be used to generate predicted distributions for a single colony or multiple colonies combined, we generated predictions for both models for birds from: (i) the Shiant Islands alone (the site of the tracking work, "local models"), and (ii) from all colonies within foraging range of the area around the Shiant islands ("global models").

4. Results

In this section we compare the results of the apportioning calculations, and of the preliminary calculations that lead up to these. We compare four methods, which we abbreviate as follows:

SNH: Simple distance-decay model ("SNH apportioning tool") with colony sizes based on Seabird 2000 data

WAKE: Spatial point process model ("WAKE model") fitted to GPS data for a sample of colonies, and then used to produce predictive UDs of breeding birds for all colonies, with colony sizes based on Seabird 2000 (Wakefield et al., 2017)

UCC (Updated Colony Count): Equivalent to "WAKE" but with colony counts based on SMP data, imputed (when missing) and summed over the period 2010-2014, rather than Seabird 2000 data.

BNB (Breeder Non Breeder): Variant of the spatial point process model that accounts for non-breeding birds ("BNB model"). Colony counts based on Seabird 2000 data.

4.1 Parameter estimation for the BNB model

4.1.1 Ratio of non-breeders to breeders

The values of the parameter (r) for each species are determined using a simple age-structured population model. The input parameters to this model are shown in Table 3, along with the resulting values of r. It can be seen that the ratios of non-breeders to breeders are very similar for both kittiwake and guillemot (between 0.28 and 0.30), but are much higher for razorbill (0.65).

The greater proportion of non-breeding birds for razorbill follows from the fact that this species has shown a fairly substantial population increase over the past 15 years – such an increase requires a substantial proportion of the population to be immature. The fact that the ratios for kittiwake and guillemot are similar arises even though these species have different population trajectories (strong decline in population for kittiwake, minimal overall change for guillemot). This appears to be because the effects of the differing population trajectories (which would, all else being equal, make the ratio of non-breeders to breeders higher for guillemot than kittiwake) are cancelled out by the fact that adult survival rates in guillemot are higher than in kittiwake (which would, all else being equal, make the ratio of non-breeders to breeders lower for guillemot than kittiwake).

Table 3

Values of ratio of non-breeders to breeders (r) that are used for each species, and the input parameter values for the age-structured population model that was used to calculate these (demographic parameters from Furness et al. 2013 – see references in footnote of their Table 5.2.1).

Parameter		Kittiwake	Guillemot	Razorbill
Input parameters				
Number of age classes		3	5	4
Immature annual survival rates (%)	Age 0 to 1	79	56	94
	Age 1 to 2	79	79	94
	Age 2 to 3	79	92	94
	Age 3 to 4		94	94
	Age 4 to 5		97	
Percentage of juveniles that are within UK waters	Age 0 to 1	50	100	100
	Age 1 to 2	50	100	100
	Age 2 to 3	100	100	100
	Age 3 to 4		100	100
	Age 4 to 5		100	
Adult annual survival rate (%)		88	97	90
Percentage of adults that are non-breeders		5	7	3
Percentage population change over last 15 years		-44	5	32
Derived quantities				
Ratio of non-breeders to breeders (r)		0.283	0.292	0.647

4.1.2 Spatial distribution of non-breeders and breeders

The parameters ϕ_k quantify the difference between the spatial distribution of non-breeding and breeding birds. The values of the parameters *phi* which optimise the empirical performance of the BNB model relative to spatial survey data are shown in Table 4. Note that only four parameters are allowed to vary between non-breeding and breeding birds – the values of ϕ_k for the remaining parameters (relating to parapatric competition and to environmental variables) are constrained to be equal to one, so that the effects for non-breeding and breeding birds are identical.

For guillemot we see that the optimal parameter estimates for all four variables are equal to zero, implying that the distribution of non-breeding birds is unrelated to any of these variables. This corresponds to the maximum possible difference between the distribution of breeding and non-breeding birds that is allowable within the BNB model.

For kittiwake and razorbill, in contrast, the optimal parameter estimates for “distance to colony” and “cumulative area” are both equal to one, implying that the effects of these variables are identical for non-breeding and breeding birds. The estimates for “colony size” and the colony size-by-cumulative area interaction are both zero, implying that these variables are unrelated to the distribution of non-breeding birds.

The BA scores for the optimal model for each species are shown in Table 5, along with BA scores for the two most extreme possible versions of the BNB model – that in which the parameters associated with accessibility variables are all fixed to be zero (so that the spatial distributions of non-breeders do not depend on these variables), and that in which the parameters associated with these variables are fixed to be equal to the parameters used in the WAKE predictive maps (so that the spatial distributions of breeding and non-breeding birds are assumed to be the same).

For kittiwake we see that the BA scores for all of these models are extremely similar, suggesting the spatial survey data have very little capability to distinguish between these different possibilities. For guillemot and razorbill, in contrast, the differences in BA score between the “best model” and “worst models” are modest but non-negligible: a difference of 0.014 in the case of guillemot and of 0.021 in the case of razorbill. For guillemot, the best model is equivalent to that with all parameters equal to zero (this follows directly from the parameter estimates above), and the model with all parameters equal to one has almost identical performance to that of the worst model, suggesting modest but consistent evidence for the distribution of non-breeding birds being substantially different from that of breeding birds. For razorbill, in contrast, the best model has similar performance to that of the model in which all parameters are equal to one, and the worst model is that in which all parameters are equal to zero – this could be interpreted as evidence for the distribution of non-breeding birds being the same as (or similar to) that of breeding birds. However, the survey data may not contain sufficient information to meaningfully estimate differences in the distribution of breeders and non-breeders.

Table 4

Parameter estimates for the values of ϕ_k for each species. These parameters control the difference between the effect of each variable upon the spatial distribution of non-breeders and that of breeders: a value of zero indicates that the variable has no impact on the distribution of non-breeders, and a value of one indicates that the impact of the variable on non-breeders is identical to that on breeding birds

Parameter	Kittiwake	Guillemot	Razorbill
Distance to colony	1	0	1
Cumulative area	1	0	1
Colony size	0	0	0
Colony size–by–cumulative area interaction	0	0	0

Table 5

Similarity scores (BA) for the comparison of the BNB model predictions against at-sea survey data. Values are shown for the model with optimum parameter values (Table 4), for the model with the lowest BA score, and for the two most extreme special cases of the BNB model – that in which the parameters ϕ_k are all equal to one, and that in which they are all equal to zero.

BA score	Kittiwake	Guillemot	Razorbill
Best model (model with highest BA score)	0.511	0.587	0.445
Accessibility parameters ϕ_k all equal to zero	0.510	0.587	0.424
Accessibility parameters ϕ_k all equal to values in WAKE model	0.510	0.574	0.440
Worst model (model with lowest BA score)	0.510	0.573	0.424

4.2 Local spatial distribution of birds

In Figures 5-7 we show the local density (UD) of birds of a single species (guillemot) originating from two focal colonies (Isle of May, top, and St. Abbs, bottom), where the UDs have been derived using two different methods: WAKE and BNB. For the latter approach (BNB) we show the UD for non-breeding birds only, as well the overall UD (for all birds), in order to illustrate the way in which this model operates. We do not show a UD for the SNH approach because this approach does not have an explicit UD model underpinning it.

The UDs for the WAKE approach are shown in Figure 5. These densities are strongly dependent upon distance from colony, but they also exhibit more subtle spatial variations, because they account for the effects of environmental heterogeneity and for inter-colony variation.

The UDs for the BNB approach – which includes both non-breeding and breeding birds – are shown in Figure 6. We see that the spatial distributions are similar to those of the WAKE approach, but with a weaker relationship to the colony – i.e. with lower densities close to the colony and higher densities far from the colony. This is the defining characteristic of the BNB model (or at least of the implementation of it that we have used here).

In Figure 7 we show the UD for the non-breeding birds only within the BNB model. These show an even weaker relationship to colony – Figure 6 is, effectively, a weighted average of the distribution of breeding birds (Figure 5) and non-breeding birds (Figure 7), and so the spatial distribution is intermediate between these.

We do not show a UD for the UCC method, because for a single colony this method is identical to the WAKE method – the difference between these methods only becomes important when combining distributions across colonies (Sections 4.3 and 4.4).

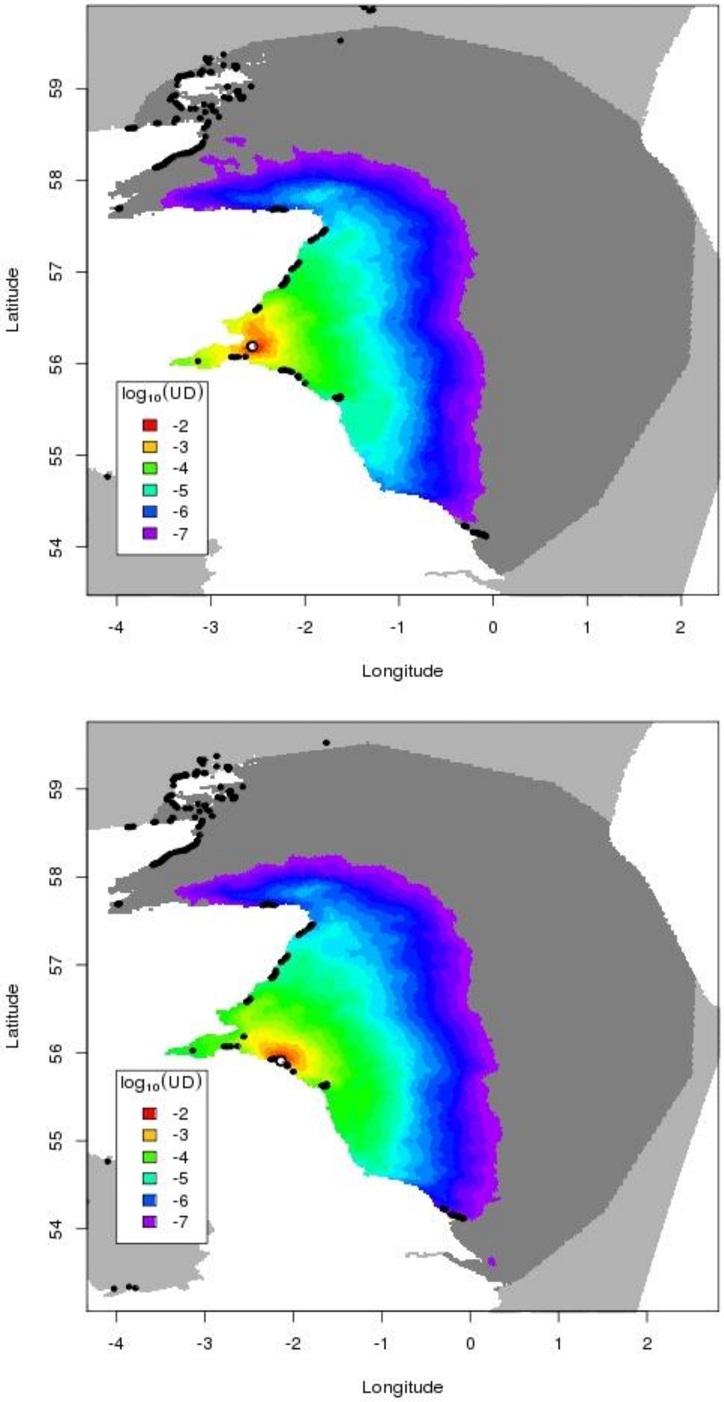

Figure 5: Predicted local utilisation distributions for guillemot from Isle of May (top) and St. Abbs (bottom) based on the WAKE method. Light grey denotes areas with a predicted UD of zero; dark grey denotes with a predicted UD of less than 10^{-7}

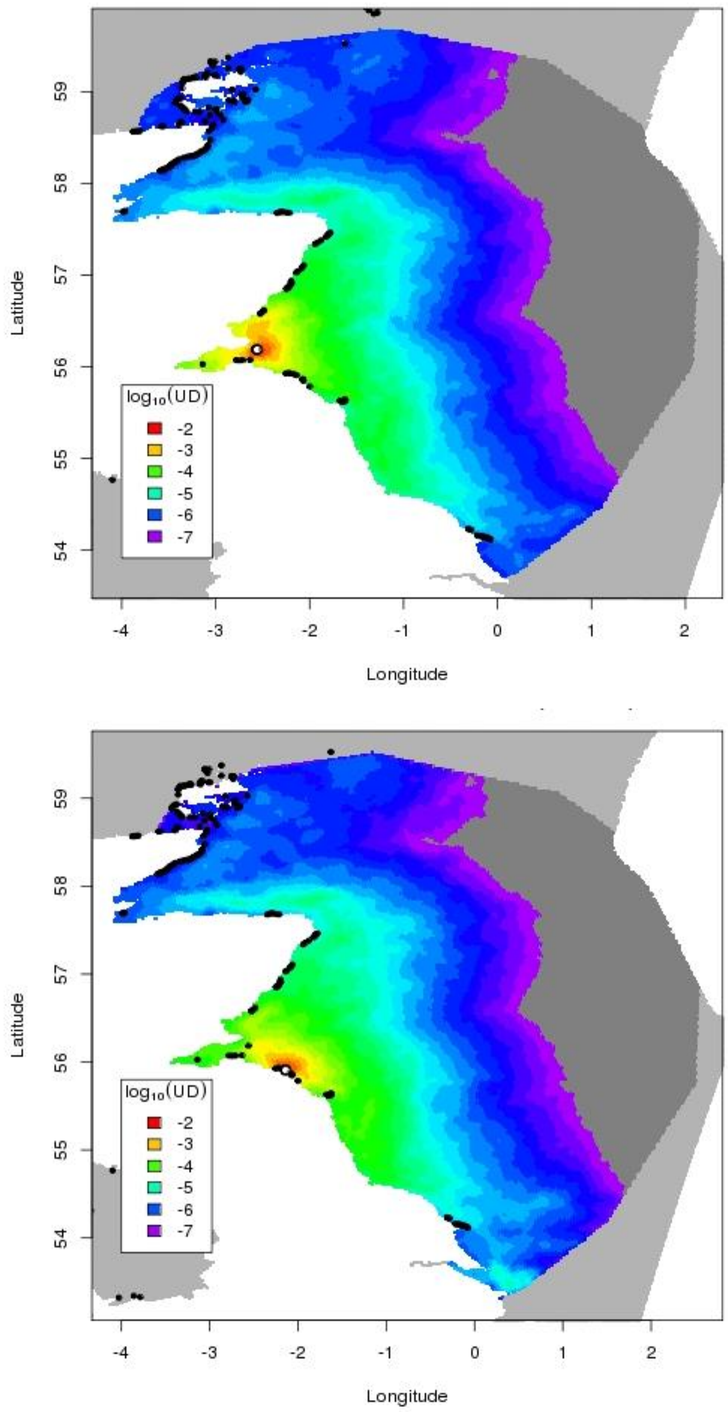

Figure 6: Predicted local utilisation distributions for guillemot from Isle of May (top) and St. Abbs (bottom) based on the BNB method. Light grey denotes areas with a predicted UD of zero; dark grey denotes with a predicted UD of less than 10^{-7}.

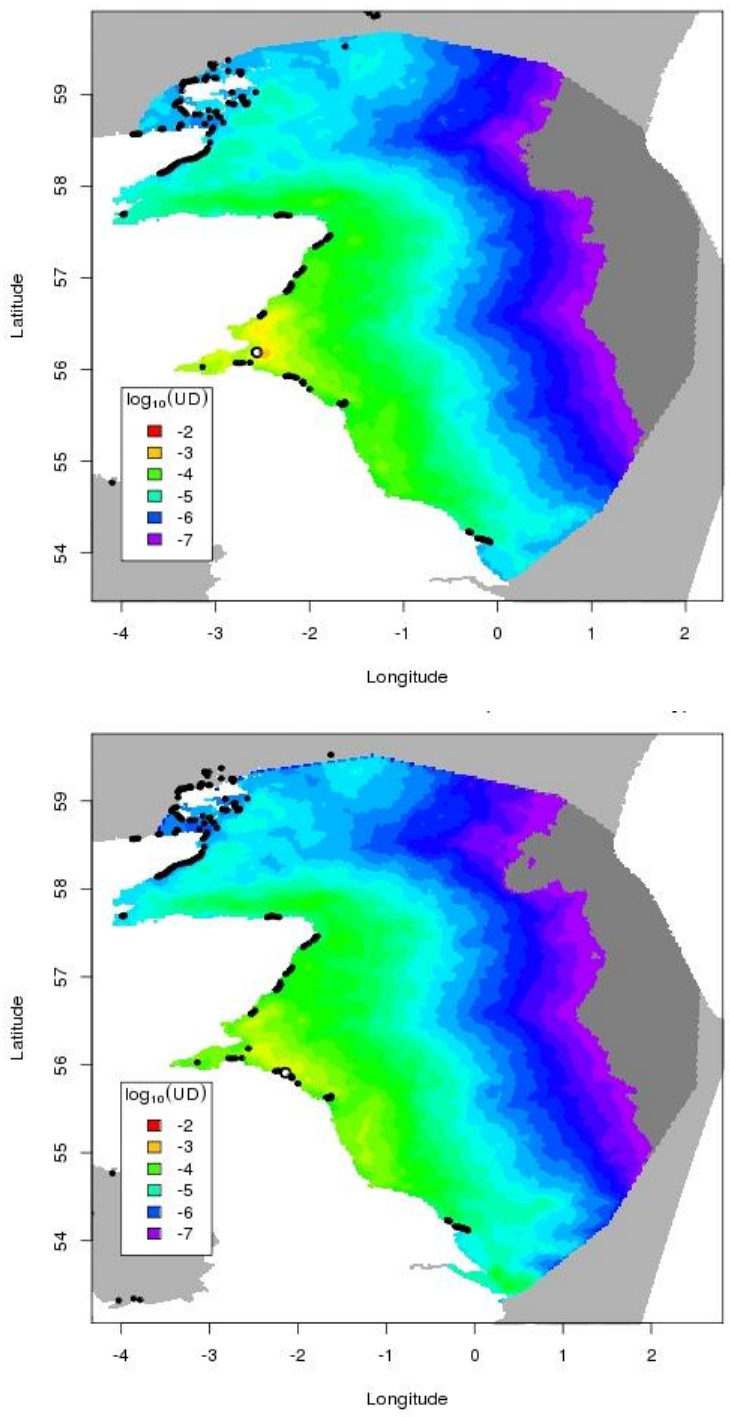

Figure 7: As Figure 6, but for non-breeding birds only.

4.3 Colony counts

As well as considering Seabird 2000 counts for each colony (which cover the period 1998-2002), we also, for the UCC method, consider colony counts that have been updated to use mean (observed or, where missing, imputed) counts for the period 2010-2014 (the period for which the GPS data used in the spatial modelling are available).

The relationships between the original (Seabird 2000) and updated counts for the SMP colonies are shown in Figure 8. It can be seen that there is a high correlation between the original and updated counts for all three species, but that for all species (but especially kittiwake) there is still a fair amount of variation between updated and original counts. The mean abundance for guillemot and razorbill (averaged across all colonies) is similar for the two periods, but the abundance of kittiwake has shown a fairly substantial reduction – this accords with long-term trends recorded by the SMP over this period (JNCC 2016). There are no obvious outliers in the graphs, but there are a set of six colonies for kittiwake that seem to behave rather differently to the remainder of sites: these sites are showing rapid increases in abundance between the two periods, but because these sites were all small these increases are not unusually large in absolute terms.

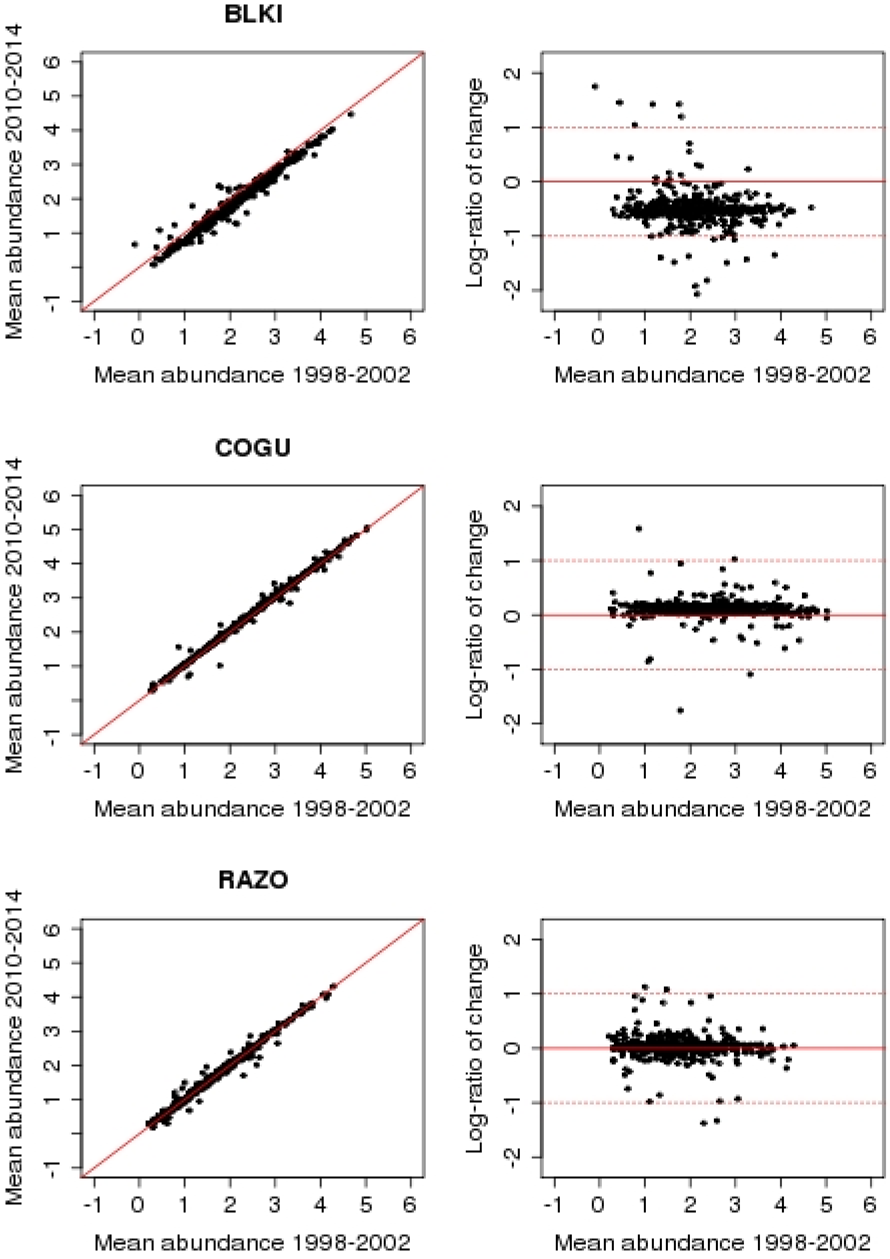

Figure 8: Log-ratios of change in colony size from the Seabird 2000 period (1998-2002) until the FAME period (2010-2014), graphed against mean abundance during the Seabird 2000 period. Each point refers to a single colony. Abundance, and change, are both shown on a logarithmic scale (base 10). Top panel: black-legged kittiwake, middle panel: common guillemot; lower panel: razorbill

4.4 Global spatial distribution of birds

The global UDs (i.e. spatial distributions obtained by summing the weighted UDs across colonies, where the weights are given by colony size) for guillemot for each method are shown in Figures 9-12.

The distribution based on the WAKE predictive maps (Figure 9) is to a large extent determined by distance to colony (and colony size) – other effects (e.g. environmental heterogeneity) are also captured by these maps, but it is clear that the accessibility is of central importance to the overall predictive maps.

The distribution based on the UCC method (Figure 10) is virtually identical to that for the WAKE method for this species.

The distribution based on the BNB method (Figure 11) shows a noticeable shallower relationship with distance to colony than the WAKE method, as we saw for the local UDs, leading to lower densities close to colonies and higher densities in areas far from the nearest colony.

If we focus solely on the non-breeding birds within the BNB method this effect is more extreme (Figure 12): the overall results for the BNB model (Figure 11) are effectively a weighted average of the results for the WAKE method which describe breeding birds (Figure 9) and the results for non-breeding birds (Figure 12). The weighted average is closer to the distribution of breeding birds than that of non-breeding birds because the value for the ratio of non-breeders to breeders r for this species is low (much less than one).

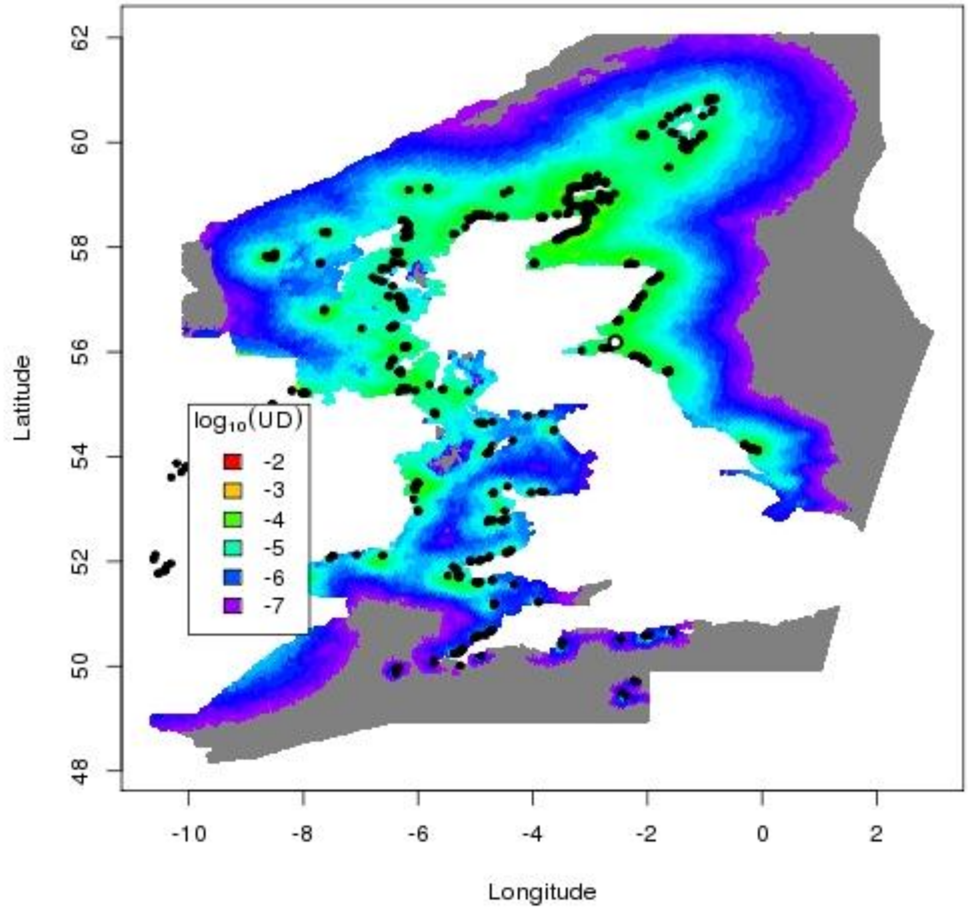

Figure 9: Predicted global utilisation distributions for guillemot, based on the WAKE method. Grey denotes areas with a predicted UD of less than 10^{-7}.

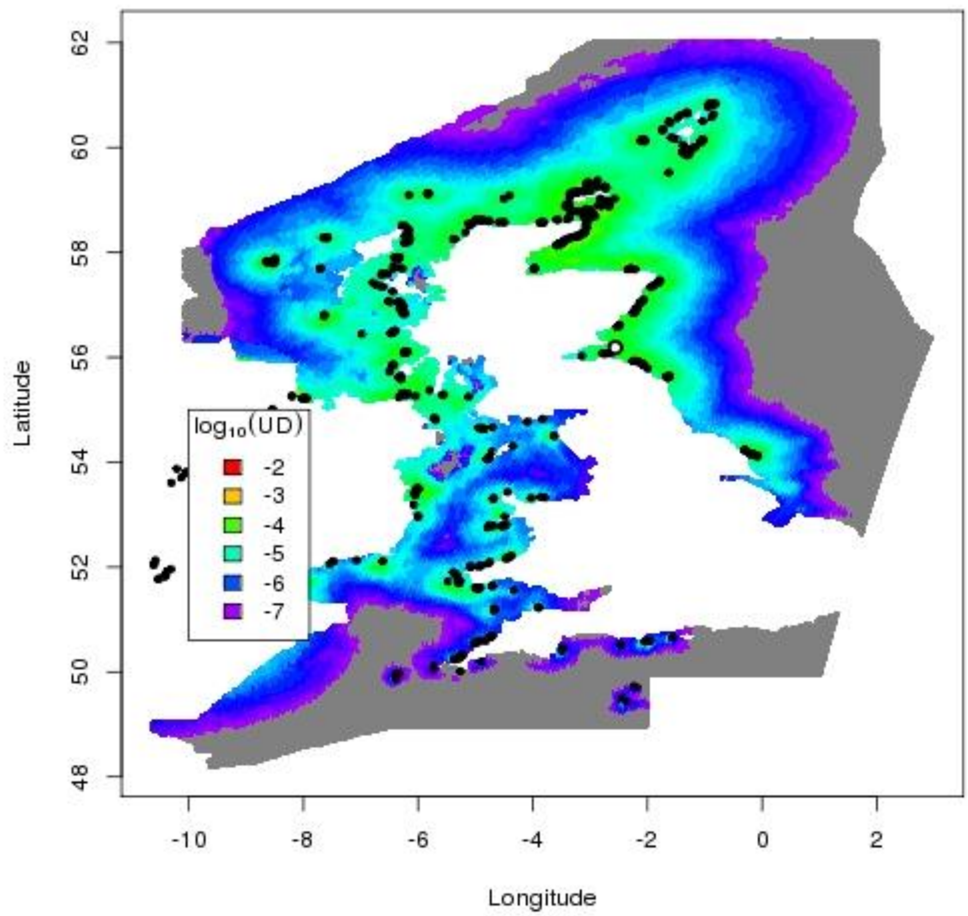

Figure 10: Predicted global utilisation distributions for guillemot, based on the UCC method. Grey denotes areas with a predicted UD of less than 10^{-7}

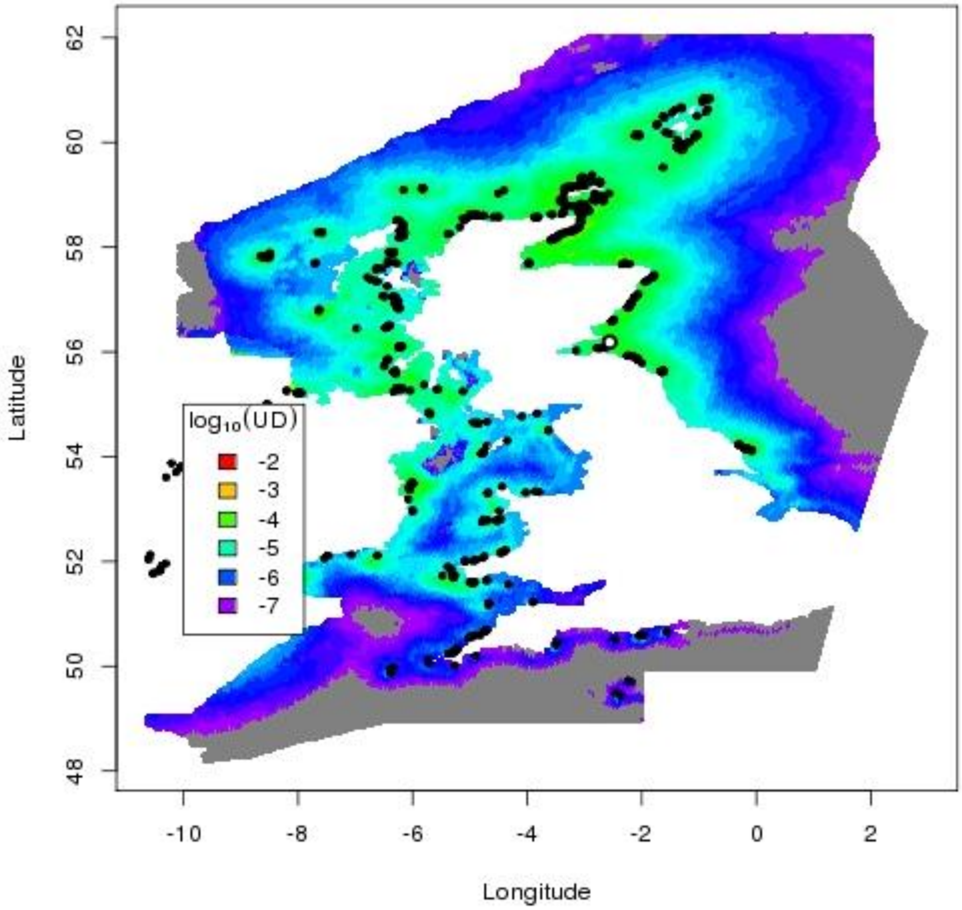

Figure 11: Predicted global utilisation distributions for guillemot, based on the BNB method. Grey denotes areas with a predicted UD of less than 10^{-7}.

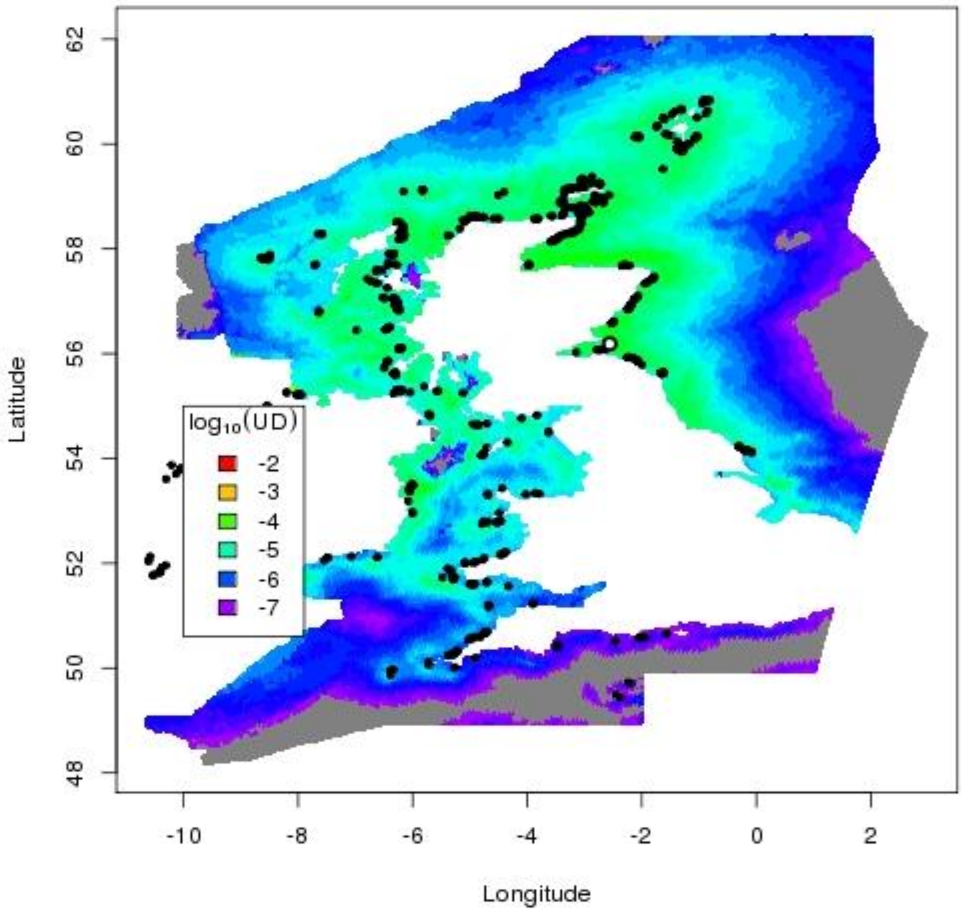

Figure 12: As Figure 11, but for non-breeding birds only.

4.5 Apportioning percentages

The key outputs from this project are the apportioning percentages.

4.5.1 Apportioning R tool

We present a limited set of apportioning results within this report, for illustrative purposes. The results files contain an enormous amount of information (approximately 20GB of data), because there are three species, in excess of 1000 colonies, and in excess of 100,000 grid cells within the study area. It is, therefore, only possible for us to present a tiny amount of that information within this report.

To accommodate these data we have, therefore, developed an R tool that can be used to access the relevant model output files, and to present these in a user-friendly format. The tool is designed to extract all of the apportioning percentages that relate to a particular species and target location (longitude and latitude), and to save these as a spreadsheet. The rows of the output file relate to the breeding colonies for the species, and the columns present apportioning percentages derived using different methods (the SNH Apportioning tool, the WAKE model for breeding birds, and the BNB model) along with relevant spatial information (colony name, administrative area, and distance to the colony from the target location).

The R tool consists of a) the model output files themselves and b) two R functions that provide the user interface to these outputs. The tool is freely available; it requires users to install R, and the “sp” add-on package for R. The use of the tool is described in more detail within the User Manual (Butler et al. 2017).

4.5.2 Example: results for a single target location

In Table 6 we present an example which illustrates the output from the Apportioning R tool for a single species (guillemot) at a single target location (with a longitude of 2°30’ W and a latitude of 56 °12’ N; this is a location close to the Isle of May, on the east coast of Scotland).

The output file for this example contains results for a total of 224 colonies – all colonies for which the target location lies within the foraging range for this species. We only show the results here for the 20 top colonies (ranked in terms of the SNH apportioning percentages); these 20 colonies account for a total of 98.86% of birds for the SNH tool, 98.72% of birds for the WAKE predictive maps and 96.71% of birds for the BNB predictive maps, so the apportioning percentages for the remaining 204 colonies are very low for all three methods.

In this example, it can be seen that the three methods all assign more than 66% of birds to a single colony (the Isle of May), but the exact percentages assigned to this colony vary between methods – they are highest for the SNH tool and lowest for the BNB predictive maps. The high percentages for this colony within the SNH tool probably arise from the fact that this location is very close to the colony (approximately 6 km away) and the distance-decay function used in the SNH tool assigns very high weight to points that are close to the colony. The fact that the BNB percentages are lower than the WAKE percentages follows from the fact that the BNB model includes non-breeding as well as breeding birds and these show a weaker (shallower) relationship with distance to colony.

Conversely, the SNH tool allocates only 3.29% of birds to the next most important colony (St. Abbs Head), whereas the WAKE predictive maps allocate 10.10% of birds and the BNB predictive maps allocate 11.00% of birds. This colony is relatively far from the target location (approx. 40 km), and this probably explains why the percentages for the methods have the opposite order from that found for the Isle of May (since the shallower relationship with distance to colony in the BNB model relative to the WAKE leads to assign more weight to colonies further from the target location, and, at least in this case, the same is true of the WAKE model in relation to the SNH tool).

More generally, it can be seen from Table 6 that the percentages for all three methods depend upon colony size as well as distance to colony. The ranking of colonies is generally similar in the three methods, but with some differences (e.g. Bass Rock is ranked 3rd for the SNH tool but 4th for the WAKE and BNB predictive maps).

The BA score can be used to compare the similarity of the apportioning percentages generated using the three different methods. For this example location we find extremely high similarity between the WAKE and BNB predictive maps (BA = 0.990), and slightly lower, but still very high, similarity between the WAKE maps and SNH tool (BA = 0.963) and between the BNB maps and SNH tool (0.952).

In Table 7 we present the uncertainty associated with apportioning birds from a sample of 30 based on these percentages. It can be seen that under all methods there is high confidence that the majority of birds can be allocated to the Isle of May (the lower limit of the confidence interval is always 15 or higher), but there is more uncertainty as to how many birds can be allocated to the remaining colonies.

Table 6

Output of the Apportioning R Tool for a single species (guillemot) at a single spatial location (2˚30’ W, 56˚12’ N). For clarity only the top 20 of 224 colonies within foraging distance of the spatial location, ranked according to SNH apportioning percentage, are shown, and the “country” column that is also output by the tool is excluded here. Note that the colony names are based upon those used in Seabird 2000, except the Isle of May, which is incorrectly labelled as “Whole island count” in the Seabird 2000 data set.

Colony name (Seabird 2000 classification)	Administrative area	Distance to colony		Colony size (pairs)	Apportioning percentages		
		Air	Sea		SNH	WAKE	BNB
Isle of May	North East Fife	6.32	6.47	56206	89.86	71.20	66.32
St Abb's Head NNR	Berwickshire	40.72	41.15	81447	3.29	10.10	11.00
Bass Rock	East Lothian	14.42	14.60	4844	1.53	3.35	3.30
The Lamb	East Lothian	21.26	21.44	7520	1.11	3.39	3.52
Fowlsheugh 3	Kincardine and Deeside	68.73	70.36	52632	0.58	2.96	3.21
Craigleith	East Lothian	19.80	19.80	3416	0.58	1.90	1.92
Fowlsheugh 4	Kincardine and Deeside	68.73	70.36	38888	0.43	2.13	2.33
Fowlsheugh 2	Kincardine and Deeside	68.73	70.36	29560	0.33	1.67	1.82
Staple	Northumberland	90.44	91.62	28996	0.24	0.35	0.60
Broadhaven to Moorburn Point	Berwickshire	38.95	39.24	4064	0.18	0.51	0.57
Troup Head	Banff and Buchan	142.60	181.74	61826	0.14	0.06	0.32
Fidra	East Lothian	22.80	23.09	752	0.10	0.27	0.29
Brownsman	Northumberland	90.44	91.62	11034	0.09	0.12	0.22
Fast Castle Head to unnamed Cleugh east of Green Stane	Berwickshire	33.94	33.94	1212	0.07	0.17	0.19
Inver Hill	Caithness	210.62	283.24	76374	0.07	0.02	0.24
Thornyhive Bay	Kincardine and Deeside	70.46	72.83	6486	0.07	0.30	0.35
Inner Farne	Northumberland	90.00	91.16	7968	0.07	0.07	0.14
Lion's Head	Banff and Buchan	141.43	179.98	21894	0.05	0.02	0.11
Cat's Bank to Hare Craig	Banff and Buchan	123.22	126.61	14202	0.04	0.04	0.12
Moorburn Point to Fast Castle	Berwickshire	36.44	36.59	772	0.04	0.10	0.11
Total (%)					98.86	98.72	96.71

Table 7

Uncertainty associated with apportioning of birds from a sample of size 30, using the apportioning percentages shown in Table 6 (i.e. for guillemots at 2˚30’ W, 56˚12’ N).

Colony name (Seabird 2000 classification)	SNH			WAKE			BNB		
	CI lower	Mean	CI upper	CI lower	Mean	CI upper	CI lower	Mean	CI upper
Whole Island count	23	26.98	30	16	21.38	26	15	19.92	25
St Abb's Head NNR	0	0.98	3	0	3.01	7	0	3.26	7
Bass Rock	0	0.45	2	0	1.01	3	0	1.01	3
The Lamb	0	0.33	2	0	1.02	3	0	1.05	3
Fowlsheugh 3	0	0.18	1	0	0.88	3	0	0.96	3
Craigleith	0	0.17	1	0	0.57	2	0	0.58	2
Fowlsheugh 4	0	0.13	1	0	0.64	3	0	0.70	3
Fowlsheugh 2	0	0.10	1	0	0.51	2	0	0.54	2
Staple	0	0.07	1	0	0.10	1	0	0.19	1
Broadhaven to Moorburn Point	0	0.06	1	0	0.15	1	0	0.17	1
Troup Head	0	0.04	1	0	0.02	0	0	0.10	1
Fidra	0	0.03	1	0	0.08	1	0	0.08	1
Brownsman	0	0.03	1	0	0.04	1	0	0.07	1
Fast Castle Head to unnamed Cleugh east of Green Stane	0	0.02	0	0	0.05	1	0	0.05	1
Inver Hill	0	0.02	0	0	0.00	0	0	0.07	1
Thornyhive Bay	0	0.02	0	0	0.09	1	0	0.11	1
Inner Farne	0	0.02	0	0	0.02	0	0	0.05	1
Lion's Head	0	0.01	0	0	0.01	0	0	0.03	1
Cat's Bank to Hare Craig	0	0.01	0	0	0.01	0	0	0.04	1
Moorburn Point to Fast Castle	0	0.01	0	0	0.03	1	0	0.04	1

4.5.3 Example: spatial distribution of apportioning percentages

In Figures 13-16 we show the apportioning percentages associated with two specific colonies – Isle of May and St. Abbs – at all locations within the foraging range of these colonies, for each of the four methods (SNH, WAKE, UCC, BNB).

The results largely reflect the estimated local UDs (Figures 5-7), but with three key differences:

1) the apportioning percentages are low in the vicinity of other sizeable colonies, even if the predicted UD from the focal colony is quite high in these areas. It is particularly noticeable that the apportioning percentages for St. Abbs are low in the vicinity of the Isle of May, even though the estimated UDs for birds from St. Abbs are fairly high in this area. It's important to note that this effect is *not* (at least in itself) evidence of competition between colonies: it is, rather, a mathematical inevitably that follows from the definition of apportioning percentages. Consider the following simple example in which there are only two colonies: assume that the predicted number of birds from Colony [1] is 10 at location [a] and 20 at location [b], and that the predicted number of birds from Colony [2] is 5 at location [a] and 40 at location [b]. Then the apportioning percentage for Colony [1] will be equal to 67% at location [a] and 33% at location [b]: i.e. the apportioning percentage for Colony [1] at location [b] is half that at location [a], even though the predicted number of birds from Colony [1] at location [b] is double that at location [a].

2) the apportioning percentages for a colony are much higher at locations that are far from the colony but also far from any other colonies than the corresponding UDs; this is because the apportioning percentages focus solely on the *relative* contribution of different colonies, so the apportioning percentage for a colony at a particular location may be very high even if the predicted number of birds from that colony is very low (if the predicted number of birds from other colonies is even lower);

3) there are edge effects (straight lines) close to the edge of the foraging range; these arise from the edge of the foraging range being reached for some colonies (so that those colonies suddenly disappear from the calculations). The effect of this on absolute predicted abundance is low (e.g. Figures 9-11), but in areas

where the predicted number of birds from all colonies is extremely low the impact on apportioning percentages can be high. The estimation of apportioning percentages is essentially quite unstable in areas with very low overall predicted densities of birds.

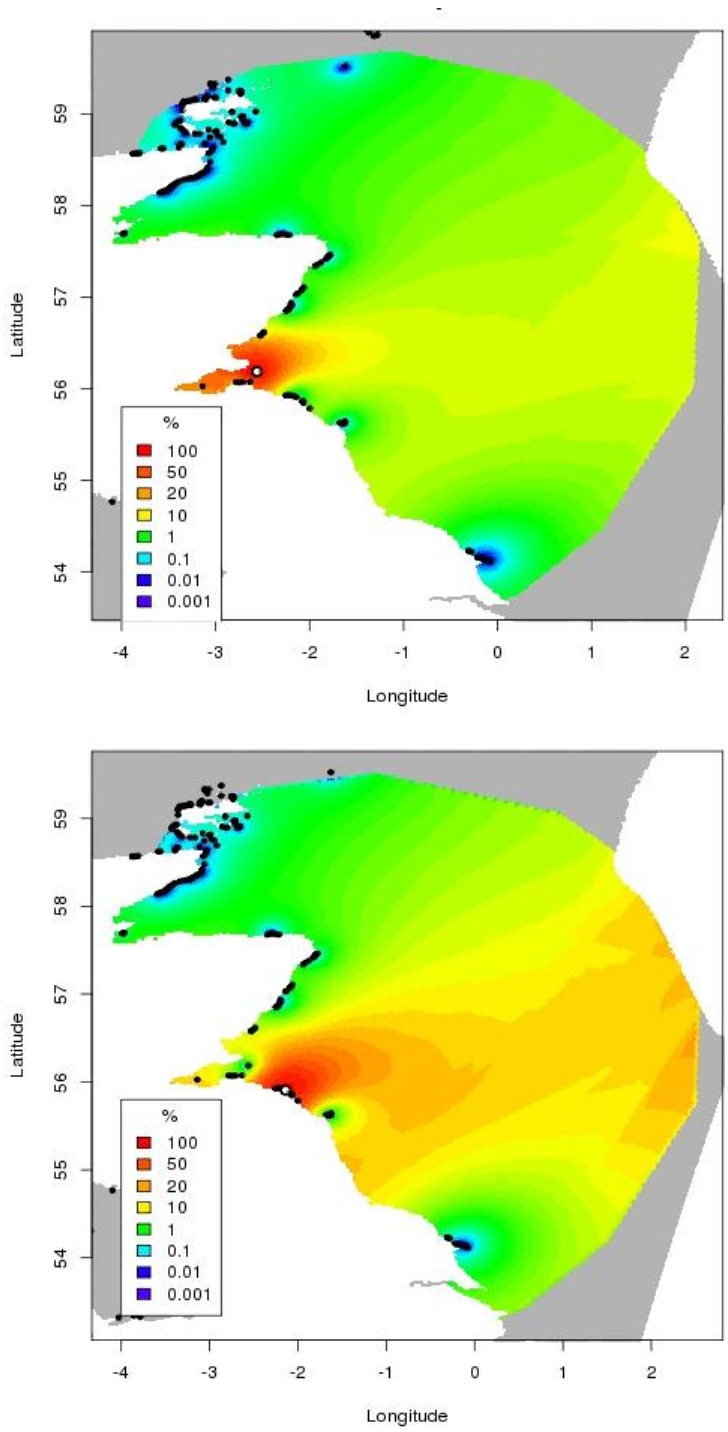

Figure 13: Spatial distribution of apportioning percentages for guillemots associated with the Isle of May (top) and St. Abbs (bottom) based on the SNH method. Grey denotes areas with an apportioning percentage of less than 0.001%.

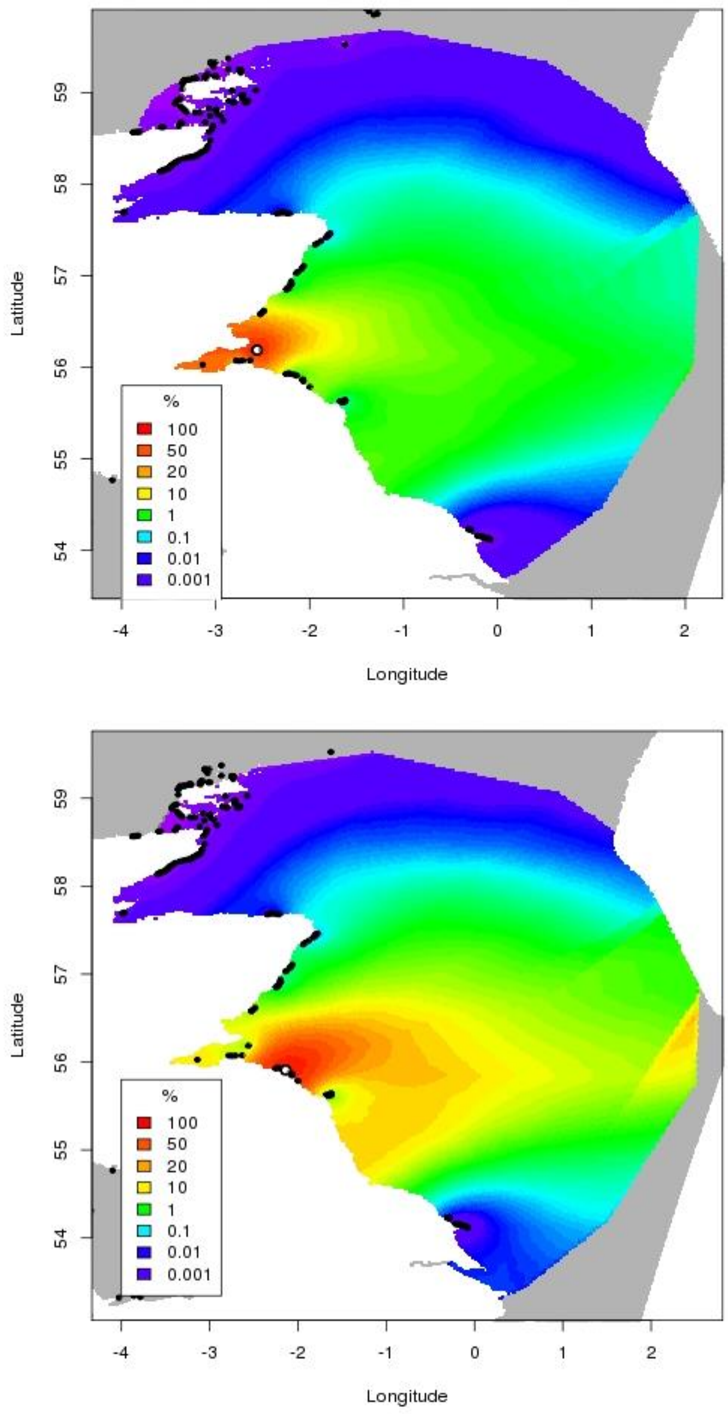

Figure 14: Spatial distribution of apportioning percentages for guillemots associated with the Isle of May (top) and St. Abbs (bottom) based on the WAKE method. Grey denotes areas with an apportioning percentage of less than 0.001%.

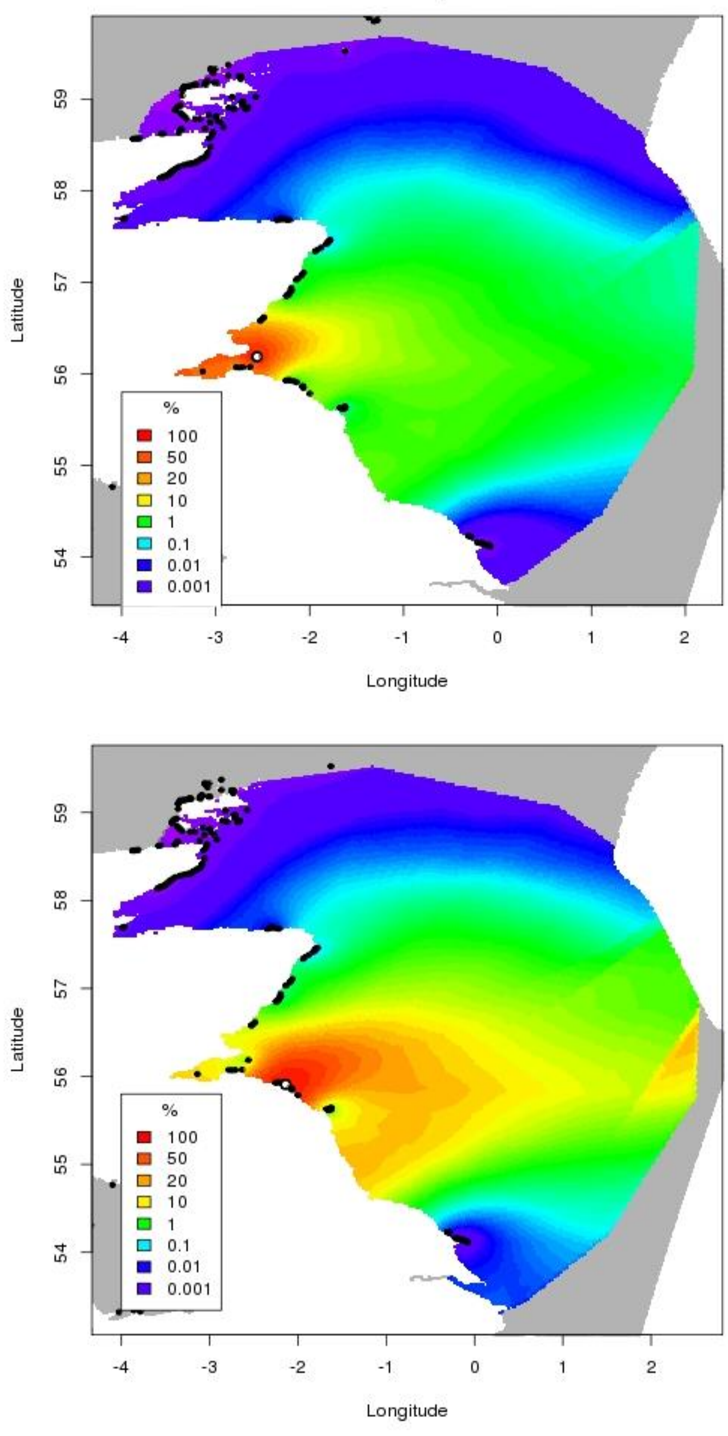

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Figure 15: Spatial distribution of apportioning percentages for guillemots associated with the Isle of May (top) and St. Abbs (bottom) based on the UCC method. Grey denotes areas with an apportioning percentage of less than 0.001%.

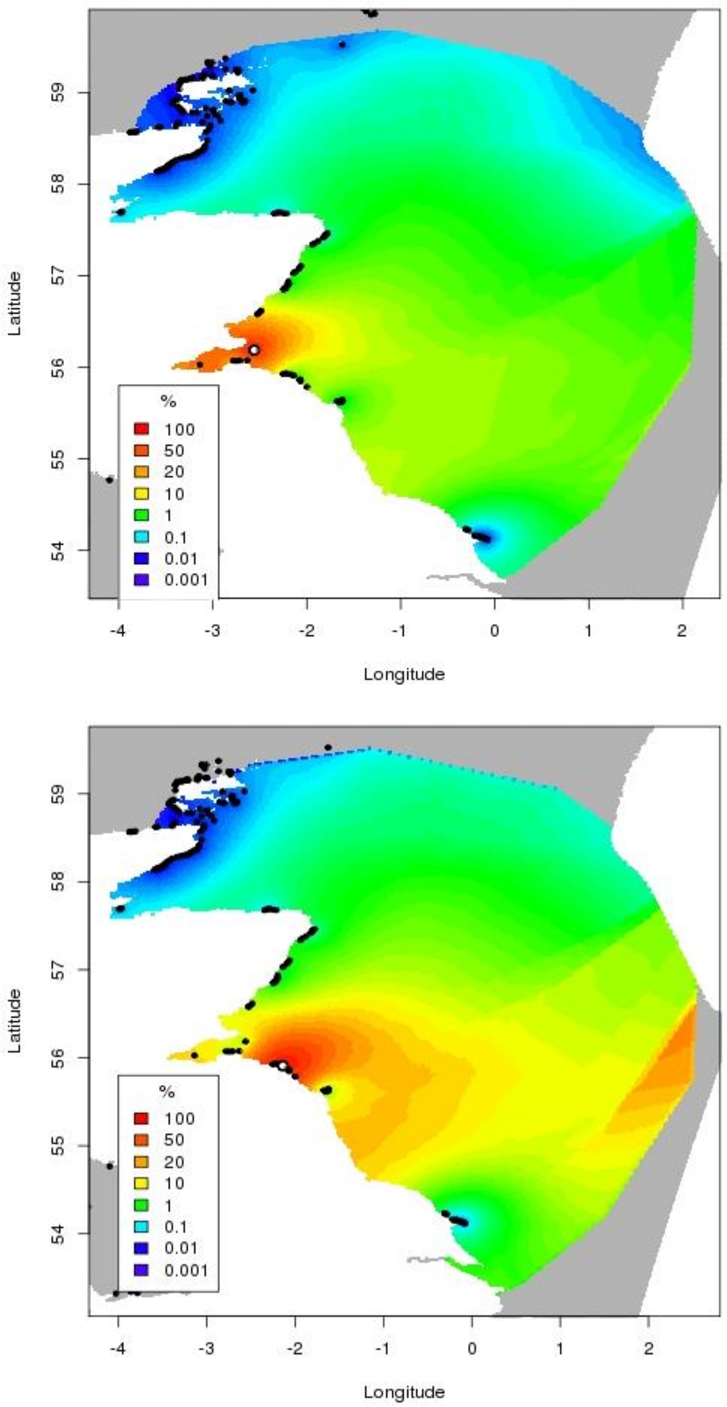

Figure 16: Spatial distribution of apportioning percentages for guillemots associated with the Isle of May (top) and St. Abbs (bottom) based on the BNB method. Grey denotes areas with an apportioning percentage of less than 0.001%.

4.5.4 Overall comparison of apportioning percentages

We compare the overall similarity of the apportioning percentages generated using the four methods for each of the three species. This is done by randomly selecting 100 locations (grid squares) from within the study region for each species; for each location we calculate the similarity (BA score) between apportioning percentages generated using pairs of methods, and we then summarise these similarity scores by looking at the mean, median, minimum and maximum values (across the 100 locations).

The results are shown in Table 8.

The apportioning percentages for WAKE and UCC approaches are always very similar to each other for guillemot and razorbill (BA > 0.98 for all simulated locations); the levels of similarity for kittiwake are lower (minimum BA of 0.94, mean BA of 0.95) but still very high in absolute terms. This suggests that altering the colony counts to cover the period 2010-2014 rather than 1998-2002 has a minimal effect upon apportioning results; there are two possible reasons for this:

1) if the population change during this period is common to all colonies, then, even if the overall change is large, it will not alter the apportioning percentages (which focus solely on relative levels of abundance);
2) the 2010-2014 abundance at many colonies is unobserved, and the imputation approach that we have used to infer these values – which necessarily smooths out spatial differences to some extent – is not likely to fully capture the true variations in population change between colonies. When the proportion of missing data is high, the under-estimation of variability in population changes between colonies is likely to be substantial, because the imputation method will lead population changes to default towards the overall (national) rate of change.

The apportioning percentages for WAKE and BNB approaches are very similar to each other for razorbill (resulting directly from the fact that the BNB model assumes that the distribution of non-breeding birds for razorbill is similar to that for breeding birds). The differences for guillemot and kittiwake are larger, but overall levels of similarity are still high (mean BA = 0.95 for both species). For guillemot there are some specific locations with fairly low levels of similarity, however (minimum BA = 0.69).

The apportioning percentages for SNH and WAKE show moderately high levels of similarity on average (mean BA between 0.81 and 0.87 depending on species), but the levels of similarity are substantially lower than for the previous two comparisons (WAKE and UCC; WAKE and BNB). In addition, for guillemot and razorbill there are some locations for which the similarity between the percentages generated by these methods is very low: the minimum BA for guillemot is 0.25 and that for razorbill is 0.34.

The remaining comparisons largely follow from these three comparisons: the comparisons of UCC with SNH and BNB models are very similar to the comparisons of WAKE with SNH and BNB (because UCC and WAKE methods are themselves so similar).

Table 8

Comparison of apportioning percentages generated by the four different methods (SNH, WAKE, UCC, BNB). Similarity between the percentages is calculating by a) finding apportioning percentages for each method for all colonies at 100 randomly selected locations within the study region, b) calculating the BA score for each pair of methods for each of these locations, and c) calculating summaries (mean, min, median, max) across the 100 locations.

		Similarity (BA) scores					
		SNH vs WAKE	SNH vs UCC	SNH vs BNB	WAKE vs UCC	WAKE vs BNB	UCC vs BNB
Kittiwake	Mean	0.858	0.844	0.894	0.946	0.950	0.937
	Min	0.718	0.703	0.768	0.940	0.941	0.929
	Median	0.907	0.887	0.938	0.988	0.993	0.980
	Max	0.998	0.993	0.999	1.000	1.000	1.000
Guillemot	Mean	0.813	0.812	0.894	0.998	0.945	0.944
	Min	0.246	0.243	0.340	0.985	0.694	0.678
	Median	0.894	0.890	0.954	0.999	0.956	0.955
	Max	0.991	0.990	1.000	1.000	0.996	0.996
Razorbill	Mean	0.866	0.863	0.872	0.996	0.996	0.993
	Min	0.343	0.346	0.343	0.987	0.954	0.950
	Median	0.930	0.928	0.942	0.997	0.997	0.994
	Max	0.992	0.987	0.995	1.000	1.000	1.000

4.5.5 Locations with low similarity between methods

We investigate the instances of low similarity in rather more detail in Tables 9 and 10. These show the simulated locations that have the lowest level of similarity between WAKE and BNB models and between WAKE and SNH models, respectively. The immediate thing to note about both of these locations is that:

a) they are relatively far from any colony; and
b) the nearest colony, geographically, to each location is fairly small, whereas all large colonies are at a considerable distance from the target locations.

The differences between the methods relate largely to the extent to which they assign weight to colonies that are large but very far from the target location (close to the edge of the foraging range).

Table 9

Output of the Apportioning R Tool for a single species (guillemot) at a single spatial location (7˚30’ W, 50˚30’ N). For clarity only the top ten colonies, ranked according to SNH apportioning percentage, are shown.

Colony name (Seabird 2000 classification)	Administrative area	Distance to colony		Colony size (pairs)	Apportioning percentages		
		Air	Sea		SNH	WAKE	BNB
Great Saltee Island	Wexford	167.63	171.22	42872	24.75	0.59	2.58
Skomer	Dyfed	206.81	209.42	27704	11.79	0.04	0.46
Lambay Coastal 5	Dublin	306.89	317.61	36528	8.53	0.00	0.13
Lambay Coastal 2	Dublin	306.32	318.08	33478	7.81	0.00	0.11
Green Bridge of Wales to Flimston Bay	Dyfed	220.55	222.50	13634	5.00	0.00	0.14
Lambay Coastal 3	Dublin	306.89	317.61	21124	4.94	0.00	0.07
Carreg y Llam	Gwynedd	321.93	326.66	15960	3.76	0.00	0.01
Old Head of Kinsale 4	Cork	141.87	143.26	6954	3.47	10.04	12.98
Lambay Coastal 1	Dublin	306.32	318.08	12990	3.03	0.00	0.04
Ramsey W	Dyfed	208.47	210.41	6540	2.81	0.00	0.08

Table 10

Output of the Apportioning R Tool for a single species (guillemot) at a single spatial location (4˚40’ W, 48˚48’ N). For clarity only the top ten colonies, ranked according to SNH apportioning percentage, are shown.

Colony name (Seabird 2000 classification)	Administrative area	Distance to colony		Colony size (pairs)	Apportioning percentages		
		Air	Sea		SNH	WAKE	BNB
Skomer	Dyfed	202.04	263.44	27704	22.15	4.38	21.25
Great Saltee Island	Wexford	285.52	313.38	42872	15.30	2.19	21.32
Green Bridge of Wales to Flimston Bay	Dyfed	180.50	255.58	13634	13.40	1.16	9.51
Ramsey W	Dyfed	213.55	272.03	6540	4.80	0.20	2.90
Berry Head 1	Devon	105.39	107.60	1422	4.28	7.90	7.23
Gull Rock	Cornwall	44.94	45.45	296	3.61	76.35	11.09
Lundy F	Devon	135.20	229.43	1636	2.64	0.13	1.69
Saddle Point to Griffth Lorts Hole	Dyfed	179.00	257.00	2172	2.18	0.07	1.27
Grassholm	Dyfed	205.77	258.14	2692	2.04	0.06	1.53
Lundy E	Devon	135.20	229.43	1198	1.93	0.10	1.24

4.6 Model performance.

Full results of the test of the performance of the model, using the independent data set comprising GPS tracking and at-sea survey data collected simultaneously in the region of the Shiant Islands in 2015, can be found in Annex A. In brief, both the BNB and WAKE models made rather similar predictions about the distribution of guillemots and razorbills in the waters around the Shiants islands, and both sets of models generally performed well in predicting the distribution of these species assessed both by tracking of breeders from the Shiants and boat surveys. However, there was little support, for either species, for the hypothesis that the BNB model performed better than the WAKE model in predicting boat survey distributions. For guillemots, most (6/7) similarity scores indicated the WAKE global model performed slightly better than the BNB global model, whilst for razorbill, model performance was more evenly balanced, with 4/7 scores indicating the WAKE model provided slightly more reliable prediction of boat survey distributions. For both species local BNB models performed as well as, or generally better than, global BNB models.

In contrast, there was very good support for guillemots for the second hypothesis, that the observed distribution of birds tracked from the Shiants would be predicted more reliably by the local WAKE model than by either the local BNB or global WAKE model. Almost all comparison metrics indicated this was indeed the case. However, there was little support for this hypothesis for razorbills, with both the WAKE and BNB models performing similarly well.

5. Discussion

5.1 Key findings

This project has been concerned with the development and implementation of novel methods for calculating apportioning percentages for birds seen at sea to the appropriate breeding colony. The key development has been the use of predictive maps developed by Wakefield et al. (2017) as the basis for this apportioning, and the comparison of this method against the existing approach (Scottish Natural Heritage 2014).

The predictive maps developed by Wakefield et al. (2017) provide a more defensible basis for apportioning than the SNH tool because (a) they allow the effects of accessibility (e.g. distance to colony) to be estimated empirically rather than fixed *a priori* and (b) they account for variables that potentially affect at-sea distribution of birds other than accessibility, in particular sympatric and parapatric competition and environmental heterogeneity. Incorporating these variables is necessary because of a strong theoretical framework and growing empirical support for the importance of intrinsic and extrinsic factors in determining distribution (e.g. Ashmole 1963; Cairns 1989; Wanless and Harris 1993; Hunt et al. 1999; Grémillet et al. 2004; Louzao et al. 2011; Wakefield et al. 2011; 2013; 2017; Scales et al. 2014; Carroll et al. 2015).

Our results show that the apportioning percentages obtained using the SNH and Wakefield et al. (2017) approaches are reasonably similar, on average (across a set of 100 randomly selected locations), but far from identical. There are also specific locations at which the differences between the approaches can be very large – it appears from initial investigation that these are often locations that are a long way from any large colony and a moderate distance from one or more smaller colonies. The apportioning estimates from all methods are likely to be very uncertain in these instances.

Within this project, we also developed and implemented two extensions to the Wakefield et al. (2017) approach, and calculated the apportioning percentages associated with these. We regard the consideration of these alternatives as a form of sensitivity analysis, to assess the sensitivity of the Wakefield et al. (2017) predictive maps to (a) the temporal mismatch between the colony count data (1998-2002) and the GPS data (2010-2014) used in creating them and (b) their design to only consider breeding birds, yet spatial survey data (boat-based or aerial) will contain a mixture of breeding and non-breeding birds.

The first extension involved using updated colony counts (mean counts for the period 2010-2014) rather than Seabird 2000 counts used in the Wakefield et al. (2017) method (which cover the period 1998-2002). This extension required statistical modelling (a multiple imputation approach) because not all colonies were counted during the period 2010-2014. The results suggested that for kittiwakes, the use of the updated counts had a modest impact on the apportioning percentages, but that the impact for guillemot and razorbill was very small – with the apportioning percentages very similar to those obtained using Seabird 2000. This is likely due to the marked declines in kittiwake numbers that have occurred over the last 15 years, in contrast to guillemots and razorbills (JNCC 2016).

The second extension involved developing a refinement of the Wakefield et al. (2017) model that included non-breeding as well as breeding birds. It is important to note that this extension involves modelling the distribution of non-breeding birds *during the breeding season* (as defined in Wakefield et al. 2017) – not the distribution of birds outside the breeding season. The results from this model were very similar to those from the maps in Wakefield et al. (2017) for razorbill. For kittiwake and guillemot, the results were moderately similar, but with noticeable differences - the distribution with non-breeding birds included was flatter - less closely linked to distance to colony – than the distribution based on breeding birds alone. This suggests that immature age classes in these two species are less strongly associated with the breeding colony than adults, in keeping with predictions (Camphuysen et al. 2011). In contrast, models suggested that immature razorbills may be associated with colonies to a similar extent as adults, potentially suggesting that the colony may act as a central place for these age classes on a daily basis throughout the breeding season, in the same way as adults, though we are not aware of any independent information to verify this. However, the lack of evidence for a difference may also arise from the temporal mismatch between GPS and at-sea survey data, and from the fact that it is inherently difficult to estimate the distribution of non-breeding birds from the datasets that we have used (which record the overall distribution of all birds, and the distribution of breeding birds from specific colonies, but never directly record the spatial locations of non-breeding birds) and further work is needed to better understand these processes.

Application of the WAKE and BNB models to independent datasets collected on the Shiant islands indicated that both models had high power to predict the distributions of guillemots and razorbills observed from GPS-tracking and boat survey transects. For guillemots, as predicted, the WAKE model performed slightly better than the BNB model in predicting the distribution of GPS tracked breeders. However, this was not the case for razorbills, where both models tended to perform similarly well. This is likely due to the very high similarity between predicted distributions from both BNB and WAKE models for this species. When compared to boat transect data, the BNB model (incorporating the modelled distribution of non-breeders) did not perform better than the WAKE model for either species, probably due to the preponderance of breeding adults in the population, and, as noted above particularly for razorbill, the similarity in modelled distribution of non-breeders and breeders. We conclude, therefore, that while the incorporation of information on the modelled distribution of non-breeders does not improve the fit of models applied to an independent boat transect dataset, the predictions of models based on breeders alone reliably indicate general patterns of distribution of these species.

5.2 Limitations and further work

It is important to consider the limitations that are associated with the modelling undertaken in this project. A common limitation associated with all four approaches that we have considered lies in the fact that it is currently not possible to accurately quantify the uncertainty associated with the apportioning percentages generated using them. In the context of the SNH tool, it is not obvious how such uncertainty would ever be calculated. It would be possible, in principle, to quantify uncertainty for the remaining methods as part of the estimation process, and it is already possible to do this (for the WAKE and UCC methods, and, to some extent, for the BNB method) – the issue, however, lies in the fact that these assessments of uncertainty are likely to be unreliable, because of the presence of residual spatial autocorrelation which is unaccounted for within the models, and are therefore not of practical use.

All four approaches rely upon the specification of a foraging range, and assume that the density suddenly reduces to zero when we cross this range. We have used the values calculated by Wakefield et al. (2017), which are relatively large (300 km or more for all of the species considered here); since all four methods either assume or estimate a strong effect of distance to colony upon predicted bird density, all of the methods would allocate low predicted densities to locations that lie beyond this range. We, therefore, anticipate that the results should be relatively insensitive to the exact specification of this foraging range, except for locations that are close to the maximum foraging range for *all* breeding colonies (which, since the overall density of birds at such locations will be very low, are unlikely to be of practical interest). Uncertainty in foraging range could, in principle, be incorporated into the calculation of the apportioning percentages (e.g. via simulation), but we suggest that as this is likely to be a relatively small source of uncertainty for most locations and a higher priority would be the quantification of other sources of uncertainty (e.g. full quantification of the uncertainty associated with parameter estimation). A key point to note about the choice of foraging range is that, at least within the WAKE, UCC and BNB methods, bias will only result from specifying the foraging range to be too *low* – specifying the value to be too *high* will not lead to bias, but will merely increase the computational time required to fit the models – it is, therefore, sensible to be very conservative in specifying the foraging range within the context of these models (i.e. it may well be sensible to consider foraging ranges higher than the values used by Wakefield *et al*., 2017, but there would be no defensible reason to consider lower foraging ranges than these).

WAKE approach

The limitations of this approach essentially reflect those of the analysis in Wakefield et al. (2017), and are discussed in more detail in that paper. Key limitations to be aware of include the following:

1. the models are estimated using the relatively small proportion of colonies for which GPS data are available, but are then assumed to be valid for all colonies;
2. the UDs are assumed to be constant over time (both within year and between years);
3. locations with missing explanatory variables are excluded from analysis, and this may potentially lead the UD values at locations with available (non-missing) explanatory variable data to be over-estimated (since the UD for each colony will be assumed to sum to one across the set of locations for which explanatory

variables are available, but birds may also spend time in locations for which explanatory variables are missing);

BNB method

The limitations of this approach include all of the limitations of the WAKE method, except, crucially, 5). This method allows the spatial distribution of breeding and non-breeding birds to differ, but there are a number of limitations to be aware of in the way this was done:

I. We have estimated the spatial distribution of non-breeding birds by comparing the distributions that are estimated from GPS data against those estimated from spatial survey data, but these data were collected during different periods, with a substantial majority of the spatial survey data having been collected prior to the GPS data collection period (2010-2014). This temporal mismatch not only introduces noise into the comparison, but may also introduce systematic bias into the comparison of the spatial distributions given the marked population size changes over the full period from which at-sea survey data were available (1980s to the present), especially in kittiwakes (JNCC 2016).

II. The coverage of survey data is spatially patchy – this could potentially lead either to bias in the estimation of the density for non-breeders, or to low precision in the estimation of this relationship.

III. We have essentially used the raw spatial survey data, but these data are likely to contain considerable variations in the probability of detection. A key avenue of future would involve accounting more fully for heterogeneity in sampling effort within the spatial survey data.

IV. The calculation of the ratio of non-breeders to breeders makes a number of simplifying assumptions about the population structure, and relies on the accuracy of the parameter values that are used as inputs to the simple population model which generates it.

V. We have assumed that the ratio of non-breeding to breeding birds is the same for all colonies, but this assumption is unlikely to be biologically plausible because it will very much depend on population demography and trajectories which are known to vary markedly across the British Isles for all three species. It would be valuable to try to extend the model to allow this parameter to vary between colonies: e.g. by treating it as a colony-specific random effect with an unknown variance, or by allowing the parameter to have a separate value within each of a pre-specified set of geographical regions.

VI. We have assumed here that only variables related to accessibility (e.g. distance to colony, colony size, cumulative area of sea) vary between breeding and non-breeding birds. It is possible that the effects of environmental variables are also different for these two groups, and that future work could, in principle, be extended to allow for this.

VII. We have assumed here that only variables that are important for breeding birds are important for non-breeders; however non-breeders may, in reality, respond to other variables than those most influential on breeders due to being removed from breeding constraints. It would be possible to re-run the model selection of Wakefield et al. (2017) using the BNB model.

VIII. We have assumed here that the status of birds observed in spatial survey data is entirely unknown – i.e. that we do not know whether any particular bird is a breeding bird or non-breeder. Survey data do sometimes record data that are informative regarding the status of birds, however, – most notably their age, which could be used to identify non-breeding individuals. Age could be determined by looking at the proportion of birds identified to be in immature plumage from surveys (e.g. for kittiwake). One could exploit these “partial data” within the analysis in species for which this is possible (e.g., gannets, gulls), and if the data on non-breeding are extensive then this could substantially increase the power of the BNB model to detect differences between the spatial distributions of breeding and non-breeding birds.

IX. Further work could explore differential effects of distance to colony depending upon the age of non-breeders, with younger immatures potentially being less affected by distance to colony than older immatures.

X. We have constrained the signs of effects to be the same for non-breeders as breeders, but this assumption could be relaxed; e.g. to allow for the possibility that the density of non-breeders could be positively related to distance to colony (e.g. if the requirement to avoid intraspecific competition is strong).

UCC method

The limitations of this approach include all of the limitations of the WAKE method, except 6). This method makes a number of assumptions about the missing counts, for colonies that lack SMP data for the period of interest (2010-2014). These assumptions, which are summarized in Thomas (1993), essentially assume that the inter-annual changes in abundance for colonies with missing data match overall inter-annual population-level changes (across all colonies with available data). This means that the approach will only capture differential changes in abundance at different colonies if there are sufficient non-missing data to be able to detect this. When the amount of missing data is very high, the approach will tend to assume that changes in abundance are largely common to all colonies (and so may fail to capture the effects of population change upon apportioning percentages, since apportioning percentages will only differ from those obtained using Seabird 2000 as a result of differential changes in population at different colonies). If all colonies exhibit identical changes, the apportioning percentages using current abundance will be identical to those obtained using Seabird 2000.

An alternative approach to imputation would involve grouping colonies into regions, estimating change ratios for each region, and then applying those ratios to unmonitored colonies within each region. If the regions can be defined in a biologically defensible way (such that colonies within each region show relatively synchronous trends (Cook & Robinson 2010) then this may give more accurate estimates of change than the current UCC method.

Apportioning percentages for the SNH, WAKE and BNB methods could be updated to include new census data, if and when these become available. If this happened, the updated results for the WAKE method would replace the results from the current UCC method (since census data provides a more defensible basis for determining colony sizes than the sample data and imputation procedure which underpin the UCC method). The updating for the WAKE and BNB methods would be relatively straightforward if the parameter estimates were assumed to be unchanged. The parameters for both models, depend, however, on colony size, so it would be more defensible to re-estimate the parameters of the models using the revised colony counts, and that would be time and resource intensive.

5.3 Recommendations

It is our view that the spatial point process models (WAKE model) which utilises the results from statistical modelling work that was previously undertaken by Wakefield et al. (2017) offer substantial improvements over the SNH tool. These improvements arise because the models allow for aggregation-segregation effects, environmental heterogeneity and for the magnitude of the relationship with distance to colony to be estimated empirically. The two models differ quite substantially in practice which further strengthens our view that the WAKE model should be preferred.

The UCC models, which are equivalent to WAKE but with colony counts based on SMP data imputed (when missing) and summed over the period 2010-2014, rather than Seabird 2000 data, give results that are very similar to the WAKE models. Since the WAKE models utilise actual colony counts, we think these should be used in preference to the UCC models, but the close similarity between the two gives some confidence that changes in colony size between 1998-2002 and 2010-2014 will not substantially alter the apportioning percentages.

The BNB models, which are variants of the spatial point process model that accounts for non-breeding birds, give results that are quite similar to the WAKE models. It may ultimately be preferable to replace the WAKE models with results from a model that includes non-breeders, but since it requires some additional work that we could not achieve in the timescale of the project to make the distributions of non-breeders fully defensible (in particular, to allow for non-detection in the spatial survey data), we think the WAKE maps should be used at this stage. The similarity between the two gives some confidence that the results would not be substantially changed by the inclusion of non-breeders, but this result should not be over-interpreted. It is relatively difficult and data intensive to estimate the distribution of non-breeders in the way that we are doing within the BNB model (since the distribution of non-breeders is not directly observed, but only inferred indirectly), and the temporal mismatch between the timings of the GPS data collection and the spatial survey data collection make this especially hard, so it is possible that there are differences between the spatial distributions of breeding and non-breeding birds that we have not been able to detect. In future, it would be useful to compare these distributions with ongoing analyses of at-sea survey data (e.g. Waggitt et al. in prep, NERC Marine Ecosystems Research Programme; www.marine-ecosystems.org.uk/).

We have produced estimates of uncertainty, but these should be regarded as providing lower limits on the true amount of uncertainty, since there are key sources of uncertainty (including parameter estimation uncertainty for the BNB model, which is likely to be large) that we did not currently quantify.

Apportioning percentages based on the Wakefield et al. (2017) method are currently only available for the three species considered here. It would also be possible to apply the same methodology to data for two additional species: GPS data for European shag were modelled by Wakefield et al. (2017), and GPS data for northern gannet are currently being modelled by CEH and BioSS as part of another project (Searle et al. in prep, NERC Marine Ecosystems Research Programme; www.marine-ecosystems.org.uk/). For most remaining species, however, there are insufficient GPS data to allow the Wakefield et al. (2017) method to be applied. For these species, we suggest that there are potentially two alternatives to the use of the SNH tool:

a) using a simple extension of the SNH tool in which the rate of distance decay (e.g. the exponent of the power law function) is estimated empirically, rather than being fixed *a priori*. This rate parameter could either be estimated from GPS data (if they exist for the species), or else derived from published foraging ranges (e.g. by assuming that the foraging range corresponds to a specific extreme quantile of the distance-decay function, and deriving the rate parameter value associated with this);

b) using the statistical model developed by Wakefield et al. (2017), but estimating the parameters of this model from spatial survey data (at-sea survey data and/or aerial survey data) rather than GPS data. There are technical challenges in doing this (the model is no longer a GLMM, so parameter estimation cannot use standard software), but the approach is conceptually straightforward. This approach allows the rate of distance decay to be estimated empirically, as in alternative approach a), but also allows the effects of other variables (sympatric competition, parapatric competition, and environmental variables) to be estimated and accounted for.

The key qualitative differences between the process approaches are highlighted in Table 11. We cannot meaningfully speculate on the likely scale of the quantitative differences between the results obtained using these approaches for other species.

Table 11

Summary of the possible methods available for estimating apportioning in species that lack GPS data.

Method	Biological realism	Ability to apply this model to data
Point process model of Wakefield et al. (2017)	High – allows the effects of distance to colony, competition and environmental effects to all be estimated empirically	High for species with GPS data Intermediate for spatial survey data (at-sea and/or aerial): the model parameters could, in principle, be estimated, from such data but in practice spatial survey data may not be able to reliably estimate parameters relating to some colony-specific effects (since data represent aggregate effects across colonies)
Distance decay model (i.e. SNH tool, but with power law parameter estimated empirically)	Intermediate – allows the relationship with distance to colony to be estimated empirically	High for species with GPS data Intermediate for species without GPS data: the required inputs are a foraging range, and an assumption regarding the extreme quantile of the distance-decay distribution that this range corresponds to
SNH tool	Low – assumes a very specific model, with no free parameters	Very high – only a foraging range is required

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Appendix A

Pre-processing of spatial survey data

Raw data

The raw data consist of two files – a file (“effort”) that records the date and sampling path (start location and end location) for each survey, and the meta-data associated with each survey (distance travelled, speed, exact details of the survey methodology, sea state).

Pre-processing steps

The raw data were pre-processed, so as to:

1. link the “effort” and “sightings” data using a unique identifier (which consisted of the combination of survey start and end locations, date and survey name), allowing each row in the “sightings” data to be linked to a unique row within the “effort” data;
2. remove duplicate records from the “effort” data;
3. convert coordinates from the UTM-30 to the LAEA projection, which was the projection used by RSPB when modelling the spatial distribution of GPS data;
4. standardise units (to hours, km, and km/hour);
5. simplify and rationalise the classification of survey methodologies;
6. remove records corresponding to locations that are out-with the extent of the WAKE maps for any of the three species of interest.

Appendix B

Mathematical description of the model in Wakefield et al. 2017

Let $\boldsymbol{x_{ij}}$ denotes the vector of explanatory variables colony j at location i, and let t_j denote the number of birds tracked at colony j. The expected number of birds from this colony at this location is assumed to be equal to:

$$\log(\mu_{ij}) = \log(t_{ij}) + \boldsymbol{\beta}^T \boldsymbol{x}_{ij} + \delta_j$$

or, equivalently:

$$\log(\mu_{ij}/t_{ij}) = \boldsymbol{\beta}^T \boldsymbol{x}_{ij} + \delta_j$$

where $\boldsymbol{\beta}$ denote unknown parameters regarding the effect of the explanatory variables, and where:

$$\delta_j \sim N(0, \sigma_\delta^2)$$

denotes the colony-specific random effect. The predicted UD, based on this model, is then equal to:

$$u_{ij}(\boldsymbol{\beta}) = \frac{\exp(\boldsymbol{\beta}^T \boldsymbol{x}_{ij})}{\sum_{k \in D} \exp(\boldsymbol{\beta}^T \boldsymbol{x}_{kj})}$$

where D denotes the entire spatial region of interest (i.e. the set of all possible locations that are being considered within the modelling).

Appendix C

Methodology for updating SMP colony counts

C1. Notation

SMP colony count data consist of annual counts, c_{ij}, of breeding birds for colony i in year j. We assume here that these data consist of a complete census of the colony, and that birds are counted without error. The need for an analysis arises because counts are only collected for a subset of colonies in each year; this means that some values of y_{ij} are observed, but many are unobserved (missing). Let O_{yi} denote the set of years for which observations are available for site i and let O_{si} denote the set of sites for which observations are available for year j.

C2. Algorithm

We use the approach of Thomas (1993) to calculate the best estimate for an unobserved count to be:

$$c_{ij}^{*} = \begin{cases} c_{ij} & \text{if} \quad j \in O_i \\ \displaystyle\sum_{l \in O_{yi}} c_{il} r_{jl} & \text{if} \quad j \notin O_i \end{cases}$$

Where:

$$r_{jl} = \frac{\sum_{m \in \{O_{sj} \cap O_{sl}\}} c_{mj}}{\sum_{m \in \{O_{sj} \cap O_{sl}\}} c_{ml}}$$

denotes the overall ratio of change between years l and j (calculated across all colonies). This is a generalisation of the “simple chaining” approach, which makes more efficient use of the available data by utilising the ratios of change r_{jl} for all pairs of years (whereas simple chaining only utilises the ratios that are calculated for consecutive pairs of years).

C3. Quantification of uncertainty

Uncertainty is calculated by bootstrapping across sites – i.e. randomly selecting a set of colonies with replacement from the set of colonies within the population – as in Thomas

(1993). In Thomas (1993), however, interest lies solely in calculating the overall year-to-year change across all colonies, whereas interest here lies in calculating the change separately for each colony. We do this by calculating the quantity of interest (ratio of mean abundance from the Seabird 2000 period [1998-2002] until the FAME period [2010-2014]) directly from the imputed counts for that colony, as obtained by applying the Thomas algorithm to the bootstrapped dataset. If the colony was not included in the bootstrap sample then the quantity is regarded as missing from this bootstrap sample. The ratios of change is then log-transformed, to achieve approximate normality, and the mean and standard deviation are calculated across bootstrap samples.

Appendix D

Translating changes from SMP sites into changes to Seabird 2000 sites

D1. Methodology

The analysis in A1 relates to colonies within the SMP dataset, but colony definitions within the SMP and Seabird 2000 data are not always consistent.

We adopt the following approach in order to identify the SMP colony, or colonies, that are associated with each Seabird 2000 colony:

a) fix a distance threshold, u; we consider three options for this – 2 km, 5 km and 10 km;
b) if there is an SMP colony that has the same name as the Seabird 2000 colony, and lies within a distance u, of it, then we assume that the log-ratio of change for the Seabird 2000 colony (both mean and SD) is the same as that for this SMP colony;
c) if there is no SMP colony whatsoever within a distance u of the Seabird 2000 colony then we assume that the SMP data cannot be used to tell us anything about change at the Seabird 2000 colony. We, therefore, in the absence of any other information, use the Seabird 2000 count for this colony (i.e. assume a log-ratio of zero);
d) if there are one or more SMP colonies that lie within a distance u of the Seabird 2000 colony, but none of these has the same name as the Seabird 2000 colony, then we assign the log-ratio for the Seabird 2000 colony to be the weighted mean of the log-ratios from these SMP colonies.

The calculations in the final case are based on simulation: we use the mean and SD of the log-ratios for each SMP site, together with the mean abundance for that site in the Seabird 2000 period, to simulate the mean abundance for the FAME period. We sum simulated counts for both periods across the relevant SMP sites, and calculate the log-ratio between these. We then take the mean and SD of these log-ratios, across simulations, and use these as the mean and SD log-ratio for the corresponding Seabird 2000 colony.

D2. Results of matching

For the species in question there are a total of 1080 colonies within the Seabird 2000 dataset, and 928 colonies within the SMP dataset. We attempt to match each of the Seabird 2000 colonies against one or more SMP colonies; the results are shown in Table D1. We see that the vast majority of colonies can be matched uniquely to an SMP colony, regardless of which threshold is used, but that the number of unique matches decreases as the threshold increases (78% of colonies for a threshold of 2 km, 76% for a threshold of 5 km and 70% for a threshold of 10 k). The number of Seabird 2000 colonies that cannot be matched to any SMP colony is fairly substantial (10%) for a threshold of 2 km, but becomes very low (2%, and <1%) for thresholds of 5 km or 10 km.

Overall, we see that 758 of the 1080 Seabird 2000 colonies can be matched unambiguously against a unique SMP colony (regardless of which spatial threshold is used), and that a further four colonies cannot be matched at all (even when a threshold of 10 km is used). For the remaining 318 colonies there is some ambiguity associated with the matching: the Seabird 2000 colony does not have the same name as an SMP colony, and, at least at some thresholds, there are multiple colonies that it could potentially be matched with.

Table D1

Number of Seabird 2000 colonies that can be matched against one or more SMP colonies using the approach outlined in Appendix D, with a range of different threshold values (2 km, 5 km, 10 km).

	Number of Seabird 2000 colonies that match to an SMP colony		
	Uniquely match to a single SMP colony	Match to multiple SMP colonies	No match
Threshold = 2km	840	134	106
Threshold = 5km	816	239	25
Threshold = 10km	758	318	4

Appendix E

Calculating the ratio of non-breeders to breeders

The BNB model (Section 3.6) depends upon knowing the ratio of non-breeders to breeders.

We determine this ratio using an age-structured population model whose parameters are based upon a combination of published values and expert opinion.

E1. The model

The population model depends upon knowing the values of the parameters given in Table E1.

Given these parameters, the number of birds fledged in year 1 is equal to $n_{I11} = b * n_{A1}$. In each subsequent year, $t = 1, \ldots, T$, it is then straightforward to calculate:

1. the number of adult birds, $n_{At} = s_A * (n_{A,t-1} + n_{Im})$;
2. the number of immature birds in the i-th age class, $n_{Iit} = s_{I,i-1} * n_{Ii,t-1}$; and
3. the number of fledged chicks, $n_{I1t} = b * n_{At}$

The ratio of non-breeders to breeders in year t is then given by:

$$\delta_t = \frac{q n_{At} + SUM_{\{k=1,\ldots,m\}} n_{Ikt}}{(1-q) n_{At}}$$

E2. Parameter estimation

The values of the parameters relating to adult survival (s_A), number of immature age classes (m), immature survival (s_{Ii}) and the proportion of adult birds that are non-breeders (q) are fixed based upon expert opinion and existing literature for each species. The initial conditions (n_{A1}, n_{Ii1}) are unknown, but it is easily shown that the results after sufficient time t are independent of these conditions (and that their values are consequently unimportant, and can be fixed arbitrarily).

The overall (national) population trajectory of each species is relatively well-estimated by empirical data, so we choose the value of the productivity rate (b) such that the model simulates levels of population change that are as close to possible to those seen in empirical data.

The percentage change between years $t-1$ and t within the population model is equal to:

$$p_{t.\text{mod}}(b) = 100 * \left(\frac{n_{it} - n_{i,t-1}}{n_{i,t-1}}\right)$$

We choose the value of b which minimises:

$$(p_{T.\text{mod}}(b) - p_{\text{obs}})^2$$

where p_{obs} denotes an empirical estimate the annual population change in the overall population.

Table E1

Input parameters to the population model that is used to estimate the ratio of non-breeders to breeders.

s_A	Adult annual survival rate (proportion)
m	Number of immature age classes
s_{Ii}	Annual survival rate for i-th immature age class, where $i = 1, \ldots, m$
q	Proportion of adult birds that are non-breeders
n_{A1}	Number of adults in Year 1
n_{Ii1}	Number of immatures in the i-th age class in Year 1
b	Productivity (fledged chicks per adult per year)

ANNEX A

Assessment of models to estimate distribution of breeding and non-breeding razorbills and guillemots in the waters around the Shiants islands, northwest Scotland

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Background

One of the strictest approaches to testing the generality of models is to compare predictions to an independent dataset (i.e. one that has not been used in model building). Such testing can indicate how generally applicable the model is; if it predicts independent datasets poorly, the model may have limited wider applicability. The WAKE model utilised in this project was fitted using out-of-sample cross validation across multiple seabird colonies to quantify parameter estimates, thus it should be generally applicable. However, the resultant model has not been tested against a completely independent dataset. Moreover, the non-breeding component, which is incorporated into the BNB model has not undergone out-of-sample validation, but rather, is based on the assumption that non-breeders and breeders are influenced by the same environmental variables, but to varying extents. Hence, to increase confidence in the apportioning results, it is necessary to validate the underlying modelled distributions, for both the breeder and non-breeder components, against independent datasets.

An opportunity for such out-of-sample testing is provided by datasets collected in the Minch in June 2015. The RSPB carried out GPS tracking of guillemots and razorbills from the Shiant Islands, and carried out contemporary boat-based surveys throughout the region, beyond the maximum foraging range of birds from the colony at which tracking occurred. The study aimed to minimise temporal differences between the datasets, thus ensuring that observed differences reflect genuine differences in distributions derived from the two survey methods. The resulting datasets provide an opportunity to independently validate the estimated distributions of (i) breeders and (ii) all-individuals generated for this project.

GPS tracking was carried out only on breeding birds from the Shiants, whereas boat surveys sampled both breeders and non-breeders, as well as birds from other colonies. Hence, GPS data can be used to test the breeding bird component (WAKE) model, whilst the boat survey data can be used to test the overall distribution (i.e. breeders and non-breeders, BNB model). Further, although it is not possible to meaningfully estimate non-breeder distributions from the survey datasets, both can be compared to modelled non-breeder distributions (NB model) to examine which provides a better match. Given the temporal matching of the datasets, they provide a unique opportunity to evaluate model performance without the confounding effects of temporal mismatch.

Methods

Data collection

Boat surveys

Surveys were carried out in the Minch on 9th, 12th, 14th, 15th, 20th, 21st, 23rd and 24th June 2015. Birds were observed over ~970 km of transects sailed by boat (Figure X1a). Observations followed standard boat survey methodology (Camphuysen et al. 2004); all birds on the water or in flight within 300 m of the boat were recorded, with observations of birds on the water binned into one of four distance bands (see below). In total, 3,814 1-minute observation periods were recorded; each was assigned to the boat's location at the interval midpoint. 2,338 guillemots (859 in flight, 1,479 on water) and 776 razorbills (453 in flight, 323 on water) were recorded across approximately 291 km^2 surveyed. Information was recorded on sea state, wind, rain and visibility, but surveys could not be carried out under particularly poor conditions.

GPS tracking

GPS tags were deployed on 20 guillemots and 39 razorbills breeding on the Shiant Islands (57.90 N, 6.36 W; Figure 1b) from 7th to 23rd June 2015. Birds were caught on the nest by wire noose or by hand, and Mataki tags (http://mataki.org) were attached to back feathers with waterproof tape. Mataki tags are open-source GPS tags with wireless data download, meaning that recapture is not necessary to recover data. Tags weighed 19 g (<3.2% body weight of razorbills, <2.3% body weight of guillemots). Recording frequencies of 100 seconds, 200 seconds and 600 seconds were trialled to allow for uncertain battery performance, meaning that tags were active for varying durations; mean duration was 105 hours (± 61 SD) for guillemots and 78 hours (± 42 SD) for razorbills, and final data were recorded on 27th June for both species. Data were retrieved from 18 guillemots and 33 razorbills.

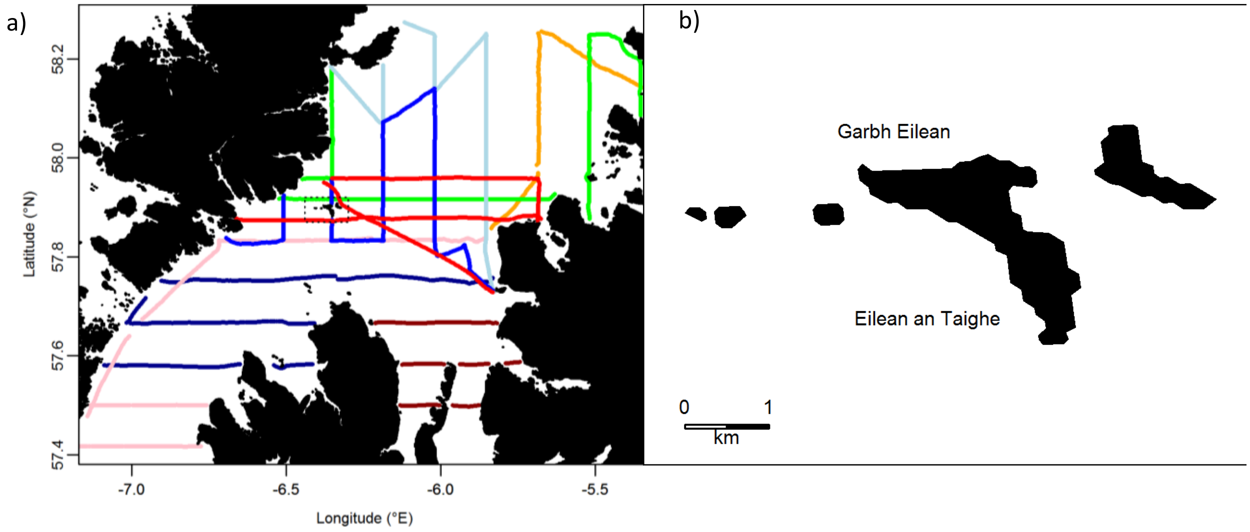

Figure 1: Maps indicating location of study within the Minch. Part a) shows transects carried out in boat surveys; different colours refer to different days; dotted black box in centre of map indicates Shiant Islands. Part b) shows detailed plot of Shiants, indicating locations of main islands where GPS tracking took place.

Data processing

Boat surveys

Field data represented on-water and in-flight abundances for each species at each observation location. A correction was applied to on-water abundance to account for reduced detectability in outer distance bands (Camphuysen et al. 2004). Following previous studies (Pollock et al. 2000, Kober et al. 2010), a simple correction factor was calculated using Equation 1:

$$\frac{(nA+nB)\times 3}{(nA+nB+nC+nD)} \qquad \text{(Equation 1).}$$

Here, nA, nB, etc., are abundances in each distance band: A = 0–50 m, B = 50–100 m, C = 100–200 m, D = 200–300 m. It is assumed that detection is perfect up to 100 m, so the numerator is multiplied by the ratio of the total transect width (300 m) to the width of perfect detection. To account for differing detectability under different conditions, separate corrections were calculated for sea states 0 and 1-3 (Kober et al. 2010); no observations occurred at sea states ≥4. Estimated corrections were: Guillemot, sea state 0 = 1.646, sea state 1-3 = 1.991; Razorbill, sea state 0 = 2.017, sea state 1-3 = 2.132. On-water abundance was multiplied by the appropriate correction and added to in-flight abundance to produce a single abundance for each observation location.

Generalised additive mixed models (GAMMs) were used to convert these corrected observations to abundance estimates across the whole survey region. GAMMs were fitted with the ‘mgcv’ R package (Wood 2003, 2006, 2011), and described abundance as a function of latitude and longitude (projected in Lambert Azimuthal Equal Area projection to match model outputs), fitted as a 2-dimensional thin-plate regression spline. Models were fitted with negative binomial error distribution (fractional abundances from the correction process were rounded to the nearest integer) and log link function. ‘Transect’ and ‘hour-within-transect’ random effects accounted for spatial and temporal clustering of observations (Zuur et al. 2014). A $\log_e$(section area) offset accounted for varying travel distances associated with each observation (Miller et al. 2013). Spline complexity (maximum basis dimension, k) was set by examining change in Akaike Information Criterion (AIC) over a range of values; there was limited improvement in AIC beyond k = 150, so k was set to 150 for both species. Model residuals showed evidence of spatial autocorrelation, but models fitted with exponential spatial correlation structure either did not converge or showed little difference in predicted values, so spatial autocorrelation was not considered further. Models (excluding random effects) were used to predict abundance on a 2 km x 2 km grid covering the survey area, and land cells were removed.

GPS data

Visual checks of GPS data led to removal of data from one guillemot that did not leave the nest, and removal of data from two razorbills, one of which did not leave the nest and one of which produced very few records, indicating likely tag failure. This left data for 17 guillemots and 31 razorbills.

Due to the varying reporting intervals (see above), different tags contributed different amounts of data over the same time period. Further, when tags did not have a clear view of the sky (such as when the bird was in a burrow or diving), gaps in records occurred. Consequently, all tracks were rediscretised to 600 second intervals using the ‘adehabitatLT’ R package (Calenge 2006). 600 s corresponded to the lowest-frequency reporting interval, so standardising tracks to this interval reduced interpolated points, thus reducing the risk of introducing bias. Interpolations were allowed to proceed across gaps in records; few gaps were associated with substantial spatial displacement, so introduced bias should be minimal. Locations within 500 m of the nest or on land were removed, leaving 5,246 locations for guillemots and 5,769 for razorbills. The method of Lascelles et al. (2016) indicated that tracking sample sizes were sufficiently representative (i.e. representativeness > 70%; Figure X2), with razorbills achieving slightly higher representativeness than guillemots.

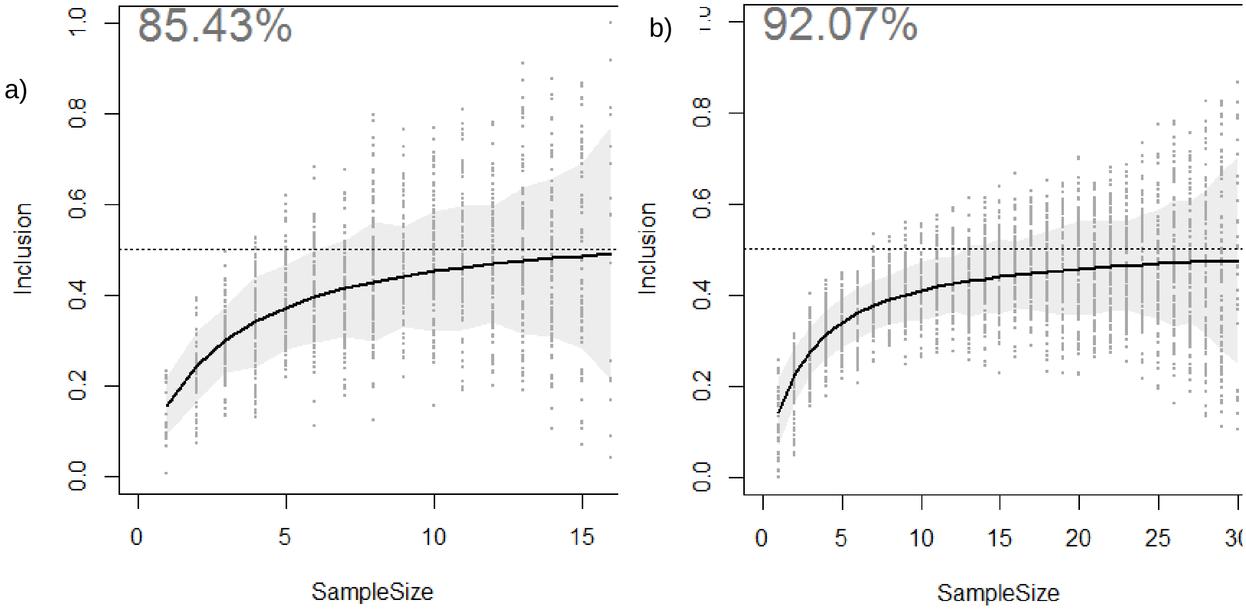

Figure 2: Representativeness of GPS tracking data for a) guillemots and b) tazorbills following methods of Lascelles et al. (2016). The scale parameter was set to 2 km, the scale at which comparisons were to be carried out in analyses; 100 bootstrap iterations were carried out.

Tracking data were projected in the same Lambert Azimuthal Equal Area projection as used for other datasets, and kernel density estimates (KDEs) were produced using the ‘adehabitatHR’ R package (Calenge 2006). KDEs were based on a bivariate Gaussian kernel, and were evaluated on 2 km x 2 km grids. Smoothing parameters were estimated using the *ad hoc* ‘href’ method: Guillemots, h = 2202.617; Razorbills, h = 2701.432. Estimates falling on land were removed.

Model data

Distribution data were extracted from model outputs, for all colonies (hereafter, ‘global’ predictions) and just for sub-colonies on the Shiant Islands. As birds observed in surveys could have originated from any of the sub-colonies on the Shiants defined by

Seabird 2000, data from all such colonies were extracted. These were Eilean an Tighe 1 and 2, Eilean Mhuire 1-4, Galta Beag Group, Galta Mor Group, and Garbh Eilean 1-6. For these colonies, modelled abundances were summed to produce an overall distribution for Shiants birds (hereafter, ‘local’ predictions).

Model predictions described either breeding birds only (WAKE model), or breeding birds and non-breeding birds together (BNB model). However, as the distribution of non-breeding birds could differ from that of breeding birds, a ‘non-breeders only’ surface was calculated by subtracting breeding birds from the overall distribution (NB model). Hence, model predictions were available for breeding birds only, non-breeding birds only, and all birds together; each was available as global (i.e. all colonies) and local (i.e. Shiants only) distributions, resulting in six possible combinations. Equivalent ‘non-breeder’ surfaces could not be estimated from GPS and boat survey data: GPS data referred to usage density by breeding bids from the Shiants, and boat survey data referred to abundances of all birds observed on surveys, which could relate to breeders and non-breeders from multiple colonies in the region, so the discrepancy between the two would not be meaningful.

Comparisons

The focal area for comparisons was defined as a 50 km radius circle centred on the Shiant Islands; the maximum observed distance in GPS tracking for both species was ~ 45 km, so this represented ~1.1x maximum distance. This region should, therefore, exclude breeding birds from other colonies, which all lay > 100 km from the Shiants. Extending the area beyond this boundary to encompass the entire area covered by boat survey produced very similar results (not shown) did not alter the conclusions.

All distributions were cropped to the focal area and values were divided by their sums, such that each data source summed to 1. Hereafter, these are termed utilisation distributions (UDs). UDs were compared using several of the metrics explored by Fieberg and Kochanny (2005).

95% and 50% home ranges (HRs) were first calculated for each UD; these are the areas which contain 95% and 50% of the probability, and can be seen as the home range and core usage area respectively (Soanes et al. 2013). The overlap between data sources for each of these areas was used as a simple comparison metric. HR overlap is presented as two values: overlap area as a percentage of UD_1 and as a percentage of UD_2. Plots were produced to indicate the location of overlaps.

The Spearman rank correlation coefficient (ρ) was also calculated. ρ may be of limited utility in identifying UD overlap (Fieberg and Kochanny 2005), but it can indicate overall agreement, with $\rho = 1$ indicating perfect agreement, $\rho = 0$ indicating no relationship, and $\rho = -1$ indicating perfect disagreement. Due to non-independence of data points, *P*-values were not calculated.

Bhattacharyya's affinity (BA) was calculated. This is a good metric to indicate overall similarity of UDs and was calculated following Equation 2 (Fieberg and Kochanny 2005):

$$\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\sqrt{UD_1(x,y)}\ \times\sqrt{UD_2(x,y)}\,dx\,dy \qquad \text{(Equation 2).}$$

Here, $UD_1(x,y)$ indicates the value of UD_1 at location (x,y). BA = 0 for entirely non-overlapping UDs; BA = 1 for identical UDs.

Finally, the utilisation distribution overlap index (UDOI) was calculated, which indicates co-occurrence of high probabilities. The UDOI was calculated following Equation 3 (Fieberg and Kochanny 2005):

$$A_{1,2}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}UD_1(x,y)\ \times UD_2(x,y)\,dx\,dy \qquad \text{(Equation 3).}$$

$A_{1,2}$ indicates the area of overlap between UD_1 and UD_2; $UD_1(x,y)$ again indicates the value of UD_1 at location (x,y). UDOI = 0 indicates non-overlapping UDs; UDOI = 1 indicates perfectly overlapping UDs with uniform probabilities distributions; UDOI > 1 indicates overlapping UDs with non-uniform, co-occurring probabilities.

All metrics indicate elements of similarity between the different data sources. However, BA and UDOI should be seen as the main metrics on which performance is judged, as overall similarity and co-occurrence of high densities are key here.

If observation data provided the ‘true’ distribution, then models could be compared to this for an absolute measure of model performance. However, the ‘true’ distribution remains unknown, so performance can only be indicated by reference to absolute metric scores (e.g., whether a correlation is positive or negative, strong or weak) and relative similarity to the different observation datasets. Hence, given the comparisons and metrics available, model performance was assessed by reference to two key hypotheses:

1) Boat survey data were for all birds from all colonies, so similarity should be higher with (i) all-individuals (BNB model) predictions than breeder-only (WAKE model) distributions, and (ii) global rather than local distributions.
2) GPS data were obtained only for breeding birds from the Shiants, so similarity should be higher with (i) breeder-only (WAKE model) not all-individuals (BNB model) distributions and (ii) local, rather than (not global) distributions.

Results

Predicted distributions of guillemots

The WAKE model predicted the highest guillemot densities to occur around the Shiant Islands; this was true for both global (Figure 3a) and local (Figure 3d) distributions. The modelled distribution of all birds (BNB model, Figures 3b, 3e) strongly reflected that of breeding birds, which is perhaps surprising given that, unlike breeders, the distribution of non-breeding birds is not influenced by distance to colony, cumulative marine area or colony size (main report, Table 4). The similarity in distributions of breeding birds and all birds presumably reflects the predominance of breeders in the population. The boat survey distribution was much smoother, and showed higher densities around the Shiants, but also indicated high densities to the north of the region (Figure 3c). The distribution of GPS tracked birds (Figure 3f) indicated a radius of usage around the Shiants, with the highest density occurring to the north, between the Shiants and the coast of Lewis and Harris.

We did not find conclusive support for the first key hypothesis that guillemot distribution assessed from boat survey would be better predicted by the BNB model, which incorporated the estimated distribution of non-breeders, than by the WAKE model based on breeders alone (Table 1). Whilst the high values for the BA and UDOI similarity scores indicates there was generally very close agreement between predicted and observed distributions, five of seven similarity scores indicated that for predictions based on global models (i.e. those based on all colonies in the region) the WAKE model showed very slightly better performance than the BNB model, contrary to the predictions of this hypothesis. Considering model predictions based on birds from the Shiants colony alone (local models), the similarity scores again indicated very similar performance of the two models, with four similarity measures indicating the BNB model performed better, and three similarity measures indicating the WAKE model performed better. Further, there was no clear evidence that boat survey distribution was better predicted by the global, rather than local BNB model. Four similarity scores indicated better performance of the BNB global model and three indicated better performance of the BNB local model.

There was good support for the second key hypothesis, that the distribution of GPS tracked birds from the Shiants would be better predicted by the WAKE than BNB model. Table 1 shows that six of the seven similarity scores indicated better fit of predictions from the WAKE local model than the BNB local model, and, as predicted, all seven similar scores indicated that the distribution of guillemots tracked by GPS from the Shiants was better predicted by the WAKE local model, based on predictions from the Shiants colony alone, than by the WAKE global model, incorporating the distribution of breeders from other colonies in the region.

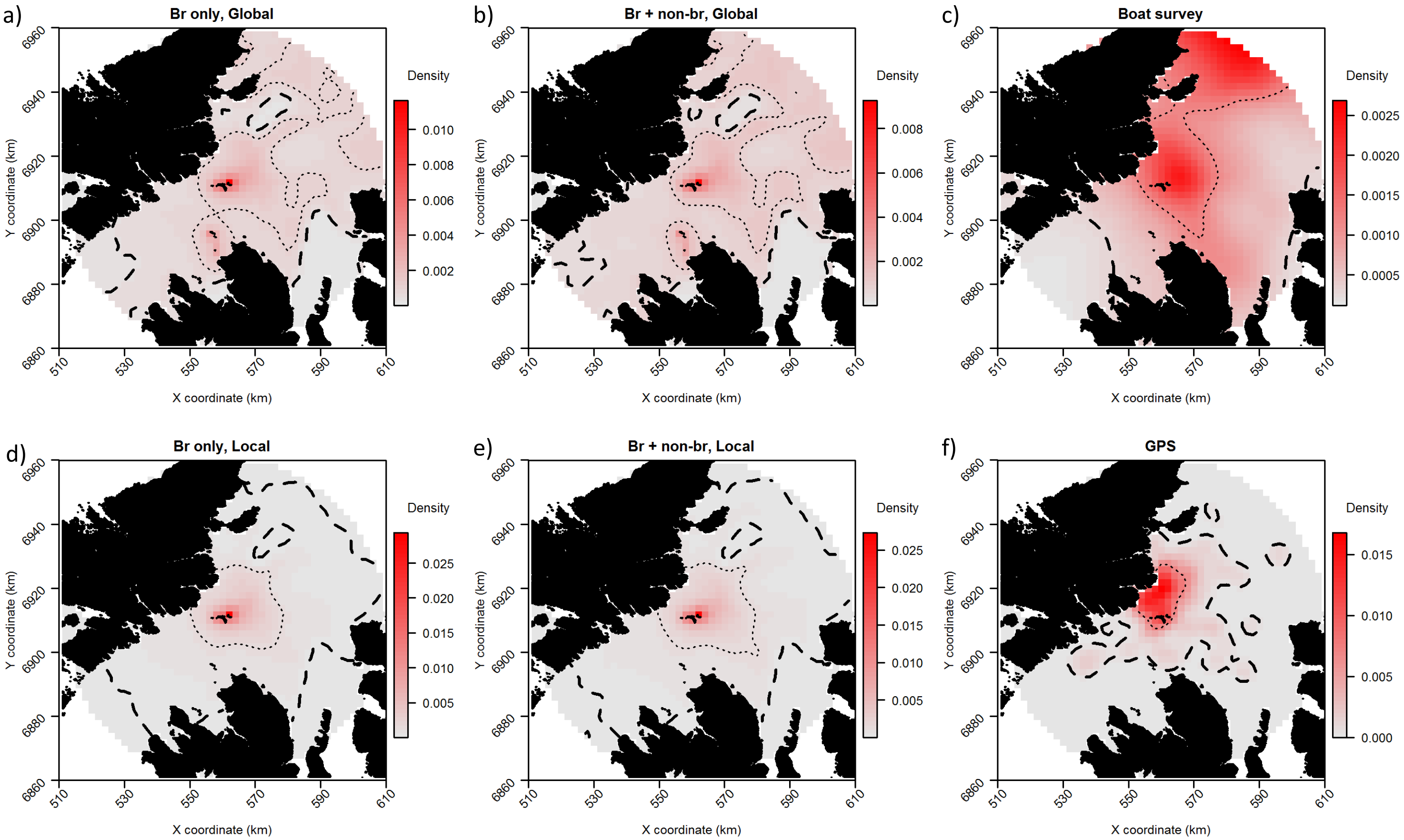

Figure 3: Guillemot UDs within 50 km radius around the Shiant Islands for: a) breeding birds (WAKE), global model; b) breeders and non-breeders (BNB, global model; c) boat survey; d) breeding birds (WAKE), local model; e) breeders and non-breeders (BNB, local model; f) GPS tracking. In all plots, darker reds indicate higher densities, but note that each plot's density scale differs, so the same shade of red indicates different densities in different panels; plots, therefore, show relative, rather than absolute, distribution patterns. Thick, dashed lines indicate extent of 95% home range; thin, dotted lines indicate extend of 50% home range. Black indicates land; white indicates areas outside of the focal area.

Table 1

Guillemot similarity scores from comparisons within 50 km buffer around the Shiant Islands.

	95% HR overlap	50% HR overlap	Spearman's ρ	BA	UDOI
UD_1 = BNB, global	$HR_{1,2} = 0.846$	$HR_{1,2} = 0.508$	0.538	0.941	1.226
UD_2 = Boat survey	$HR_{2,1} = 0.845$	$HR_{2,1} = 0.613$			
UD_1 = BNB, global	$HR_{1,2} = 0.319$	$HR_{1,2} = 0.099$	0.385	0.636	1.260
UD_2 = GPS	$HR_{2,1} = 0.927$	$HR_{2,1} = 0.783$			
UD_1 = BNB, local	$HR_{1,2} = 0.878$	$HR_{1,2} = 0.776$	0.452	0.890	1.486
UD_2 = Boat survey	$HR_{2,1} = 0.806$	$HR_{2,1} = 0.403$			
UD_1 = BNB, local	$HR_{1,2} = 0.357$	$HR_{1,2} = 0.295$	0.779	0.797	2.732
UD_2 = GPS	$HR_{2,1} = 0.955$	$HR_{2,1} = 1.000$			
UD_1 = WAKE, global	$HR_{1,2} = 0.866$	$HR_{1,2} = 0.531$	0.569	0.939	1.265
UD_2 = Boat survey	$HR_{2,1} = 0.852$	$HR_{2,1} = 0.603$			
UD_1 = WAKE, global	$HR_{1,2} = 0.327$	$HR_{1,2} = 0.126$	0.452	0.659	1.440
UD_2 = GPS	$HR_{2,1} = 0.937$	$HR_{2,1} = 0.935$			
UD_1 = WAKE, local	$HR_{1,2} = 0.885$	$HR_{1,2} = 0.855$	0.449	0.880	1.517
UD_2 = Boat survey	$HR_{2,1} = 0.791$	$HR_{2,1} = 0.393$			
UD_1 = WAKE, local	$HR_{1,2} = 0.367$	$HR_{1,2} = 0.326$	0.787	0.808	2.880
UD_2 = GPS	$HR_{2,1} = 0.955$	$HR_{2,1} = 0.978$			

Predicted distributions of razorbills

All razorbill distributions were concentrated around the Shiants (Figure. 4) and like guillemots, the predicted distributions of the WAKE and BNB models were extremely similar. The boat survey distribution (Figure 4c) differed somewhat, showing a high density area extending south east, to the coast of Skye, and showing the 95% HR to extend throughout the southeast part of the focal area. The distribution of GPS tracked birds (Figure 4f) was concentrated around the Shiants, but unlike modelled distributions, was not symmetric: the 50% HR extended north to the coast of Lewis and Harris, whilst the 95% HR showed a southern bias.

As for guillemots, there was no clear support for the hypothesis that the distribution of razorbills assessed from boat surveys was better predicted by the BNB model than by the WAKE model. Four of the seven similarity scores indicated that predictions based on global models (i.e. predicting for all colonies in the region) the WAKE models performed slightly better than the BNB model, whereas, for local forms of the models, four scores indicated better performance of the BNB model. Clearly there is very little difference in the performance of the two models in predicting distribution of breeders and non-breeders combined.

Contrary to expectation, six of seven similarity scores (including BA and UDOI) indicated that the distribution of razorbills assessed from boat surveys was better predicted by the local BNB model, considering just birds from the Shiants, than the global BNB model, incorporating birds from other colonies in the region (Table 2).

There was little support for the hypothesis that distribution of tracked razorbills would be predicted better by the WAKE than BNB model. Although models based on birds from the Shiants performed better than those including birds from neighbouring colonies, none of the seven similarity scores indicated better performance of the WAKE local model than the BNB local model (Table 2). However, it should be noted that all of the similarity scores indicate relatively good performance, with broad agreement between predicted and observed distributions.

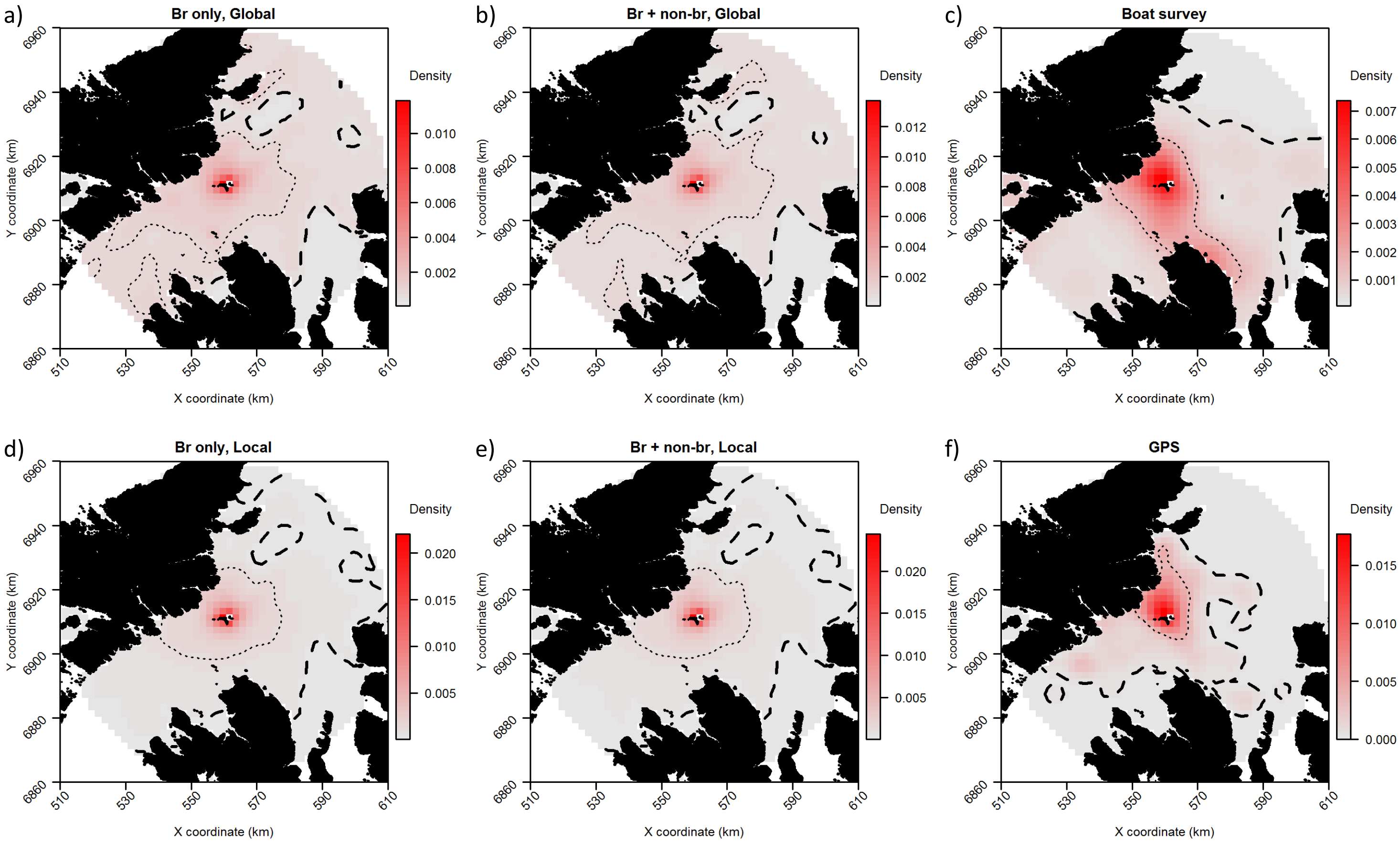

Figure 4: Razorbill UDs within 50 km radius around the Shiant Islands for: a) breeding birds only, WAKE global model; b) breeders and non-breeders, BNB global model; d) boat survey; e) breeding birds only, WAKE local model; g) breeders and non-breeders, BNB local model; h) GPS tracking. In all plots, darker reds indicate higher densities, but note that each plot's density scale differs, so the same shade of red indicates different densities in different panels; plots, therefore, show relative, rather than absolute, distribution patterns. Thick, dashed lines indicate extent of 95% home range; thin, dotted lines indicate extend of 50% home range. Black indicates land; white indicates areas outside of the focal area.

Table 2

Razorbill similarity scores from comparisons within 50 km buffer around the Shiant Islands.

	95% HR overlap	50% HR overlap	Spearman's ρ	BA	UDOI
UD_1 = BNB, global	$HR_{1,2} = 0.768$	$HR_{1,2} = 0.398$	0.369	0.925	1.874
UD_2 = Boat survey	$HR_{2,1} = 0.820$	$HR_{2,1} = 0.757$			
UD_1 = BNB, global	$HR_{1,2} = 0.413$	$HR_{1,2} = 0.193$	0.512	0.772	2.201
UD_2 = GPS	$HR_{2,1} = 0.929$	$HR_{2,1} = 0.939$			
UD_1 = BNB, local	$HR_{1,2} = 0.812$	$HR_{1,2} = 0.687$	0.518	0.938	2.602
UD_2 = Boat survey	$HR_{2,1} = 0.826$	$HR_{2,1} = 0.675$			
UD_1 = BNB, local	$HR_{1,2} = 0.445$	$HR_{1,2} = 0.367$	0.721	0.856	3.365
UD_2 = GPS	$HR_{2,1} = 0.953$	$HR_{2,1} = 0.924$			
UD_1 = WAKE, global	$HR_{1,2} = 0.774$	$HR_{1,2} = 0.396$	0.407	0.927	1.830
UD_2 = Boat survey	$HR_{2,1} = 0.828$	$HR_{2,1} = 0.757$			
UD_1 = WAKE, global	$HR_{1,2} = 0.415$	$HR_{1,2} = 0.189$	0.540	0.770	2.102
UD_2 = GPS	$HR_{2,1} = 0.936$	$HR_{2,1} = 0.924$			
UD_1 = WAKE, local	$HR_{1,2} = 0.809$	$HR_{1,2} = 0.651$	0.516	0.939	2.552
UD_2 = Boat survey	$HR_{2,1} = 0.828$	$HR_{2,1} = 0.675$			
UD_1 = WAKE local	$HR_{1,2} = 0.442$	$HR_{1,2} = 0.349$	0.718	0.852	3.263
UD_2 = GPS	$HR_{2,1} = 0.953$	$HR_{2,1} = 0.924$			

Discussion

Comparisons between modelled and observed distributions

Comparisons of modelled guillemot and razorbill distributions with observations from boat surveys and GPS tracking indicated that both the WAKE and BNB models predicted the observed distributions well. Performance of the WAKE model was particularly good: similarity metrics produced high values for comparisons of GPS tracking data and modelled local breeding birds, with high UDOI scores and moderate-to-strong correlations reflecting the co-occurrence of high densities around the Shiants. Indeed, all comparison metrics indicated good performance. However, not all patterns in GPS data were replicated by models: the extension of high razorbill densities to the Skye coast and northward biases in 50% HRs were not found. This reflects a key point of interpretation: models predict broad distributions, thus may not replicate fine-scale elements of distributions or areas used only some years. Overall, however, comparisons with independent GPS tracking data provided good support for breeding bird models.

There was little support, for either species, for the hypothesis that the distribution assessed by boat survey would be predicted better by the global BNB than the global WAKE or local BNB models. For guillemots most (6/7) similarity scores indicated the WAKE global model performed slightly better than the BNB global model, whilst for razorbill, model performance was more evenly balanced, with 4/7 scores indicating the WAKE model provided slightly more reliable prediction of boat survey distributions. For both species local BNB models performed as well as, or generally better than, global BNB models.

The was very good support for guillemots for the second hypothesis, that the observed distribution of birds tracked from the Shiants would be predicted more reliably by the local WAKE model than by either the local BNB or global WAKE model. Almost all comparison metrics indicated this was indeed the case. However, there was little support for this hypothesis for razorbills, with both the WAKE and BNB models performing similarly well. This is likely due to the high similarity between modelled distributions of all birds (BNB model)

Causes of differences between predicted and observed distributions

It is important to consider why modelled distributions may differ from observations. Firstly, models of the distribution of breeding bird may be inaccurate. As noted above, breeding bird models indicate only broad distributions, missing fine-scale and short-term patterns, so there will inevitably be discrepancies when compared to observations. From tests presented here, it is not possible to say whether discrepancies are systematic (which would reduce validity) or specific to the testing dataset. Systematic discrepancies could arise if, for example, model predictors were not at a sufficiently fine scale to describe processes, or if a key driver of distributions was missed. However, relatively good performance of WAKE models, combined with the out-of-sample cross validation used in their original derivation (Wakefield et al 2017), perhaps suggests that strong systematic bias is unlikely.

Alternatively, the modelling of the distribution of non-breeders may be responsible for discrepancies. Models of non-breeder distribution were fitted by relaxing the strong proximity-to-colony effect, but continuing to use the same relationships with environmental predictors. If non-breeders were influenced by different variables, which could arise if they foraged on different prey species, such models would therefore be less able to predict non-breeder distributions accurately. Further, the proportion of non-breeders in the population is important, with breeding birds strongly determining overall distributions. Hence, key assumptions in the non-breeder models may be responsible for some elements of the discrepancy with observations.

Finally, discrepancies could be linked to the differences in time-scales underpinning the observations themselves. Both boat survey and GPS data effectively provide snapshots, representing samples of distribution of individuals over differing time periods. Typically GPS tracking represent a few days, and the WAKE model was built from observed distributions of individuals over a 24 hour period, whereas boat transect data reflect the instantaneous distribution of individuals at a single point in time, and data are collected only during hours of daylight, when sea conditions are benign, and only birds visible on the sea surface or in flight are recorded. Hence, discrepancies may arise from the fact that telemetry and boat transect data are collected using very different sampling regimes.

Conclusions

Overall, similarity scores were high, supporting the general predictive capacity of both the WAKE and BNB models. For both species, there was particularly good support for the WAKE model, with high BA and UDOI scores, and with reasonably good replication of home range locations. For guillemots, there was evidence that the WAKE model provided more reliable predictions than the BNB model, when applied to birds tracked by GPS from the Shiant islands. However, there was no evidence that the BNB model performed better than the WAKE model in predicting the distribution of guillemots observed from boat survey transects. For razorbills, predicted distributions of WAKE and BNB models were very similar, rendering comparisons with boat survey data less informative – the BNB model provided no improvement on the predictions made by the WAKE model. Nevertheless, similarity scores were sufficiently high to suggest that even without fine-scale patterns predicted, overall performance of both models was good. There are various possible sources of error that could explain discrepancies between data sources, from the breeding bird models, to the non-breeder model assumptions, to the observation datasets themselves. Given the complexity of these possible causes and the limitations of the datasets, the exact causes cannot be examined in detail here. However, we conclude that the distributions predicted by both models are representative of observed distributions in an independent dataset.

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