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PROGRAMME (ORJIP) FOR OFFSHORE WIND



ORJIP InTAS project: Report on the distribution and habitat preferences of Kittiwakes on the east coast of Scotland

InTAS

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ORJIP InTaS project: Report on the distribution and habitat preferences of Kittiwakes on the east coast of Scotland

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Abstract

The results in this report represent the application of the modelling framework developed under WP2 of the InTaS project funded by the Carbon Trust as part of the broader ORJIP initiative. The framework combines, for the first time, the statistical inference methods traditionally used in isolation for survey and telemetry data. It aims to accurately and precisely apportion the exposure of particular seabird colonies and age stages, to anthropogenic offshore disturbance. Black-legged Kittiwakes (*Rissa tridactyla*) were identified as one of four priority species during the literature survey undertaken in WP1 of the same project. A large-scale proof of concept was agreed for the east coast of Scotland. Survey and telemetry data (from both adults and, where available, juveniles) were collated for similar spatial and temporal extents. The locations and sizes of gannet colonies were provided and used to guide the habitat modelling and apportionment algorithm. Model selection was carried out to explore combinations of nine environmental covariates that most parsimoniously explained the pooled telemetry and survey data sets. Using the best model, a comparison of survey-only, telemetry-only and joint survey-telemetry analyses confirmed the conclusions of simulation experiments from WP2 suggesting that the convergence and precision of joint analyses are superior to the single-data analyses. The covariates retained in the selected model indicated that kittiwakes of both breeding stages are strongly attached to the locations of colonies. Avoidance of gravelly substrates, was countered by attraction towards thermal fronts, areas of high primary production and relatively colder sea surfaces. We present results on the spatial distribution of usage by different colonies and size ages and present an illustrative calculation of apportionment for an exemplar off-shore region, along with a software tool that can use the results of our modelling for any area of interest for potential offshore development.



Figure 1: An adult black-legged kittiwake (*Rissa tridactyla*). By Yathin S Krishnappa - Own work, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=24551364>

Contents

1 Overview	4
1.1 Study objectives	4
1.2 Relevant facts about kittiwake natural history	5
2 Environmental covariates	7
2.1 Derived covariates	9
2.2 Survey transects	10
2.3 Tracking data	10
3 Inference	11
3.1 Model selection on Joint model	12
3.2 Comparison with single-datatype models	12
4 Spatial prediction	12
4.1 Usage maps	12
4.2 Apportioning impact	17
5 Appendix I: JAGS implemetation of joint model for telemetry & survey data	22

6	Appendix II: Usage of R functions for the generation of apportioning predictions for a given marine boundary	24
	References	36

1 Overview

Different types of data carry more or less information about particular aspects of a seabird species' distribution. If the interest is in broad scale maps of distribution representing the aggregate usage of particular regions of space by all birds of a given species, then survey data can be an effective source of information. These may provide estimates about the usage within a region of interest (if the surveys are targeted geographically), or they may provide wider comparisons between the region of interest and the rest of the distribution of the species. Integration of data from multiple surveys, particularly if combined with environmental covariates into habitat models (Jason Matthiopoulos, Fieberg, and Aarts 2020) can provide spatial breadth and the ability for such comparisons. Taking further steps along the path of data integration (J. Matthiopoulos et al. 2022) is essential if we wish to apportion usage by colony or breeding stage. This requires folding into the analysis individually-referenced data, the prime example of which are telemetry data on individual movement.

1.1 Study objectives

Here we aimed to:

1. Analyse patterns of spatial utilisation of the Scottish north sea by kittiwakes.
2. Deduce which environmental variables are primarily driving this distribution.
3. Generate reconstructions of spatial usage by different colonies and age classes.
4. Demonstrate apportionment results with associated credible intervals for a particular area of development.
5. Encode the above in reproducible code so that the data, covariates and areas of interest can be altered, allowing the analysis to be re-run expediently.

Objective 1 aims to generate the best possible description of distribution. To this end, we have used survey and telemetry data that combine breadth and resolution. Objective 2 uses model selection among an extensive array of candidate models, to decide which environmental variables are covariates of this species distribution. We visualise the spatial effect of all the variables retained in the final model. We also present a comparison of the results of fitting the two single data models with the results of the best joint model selected under Objective 2. A comprehensive graphical view of all colonies and both age stages is produced under Objective 3, using the best joint model only. In the case of kittiwakes, telemetry data were not available for juveniles. So, the modelling task is considerably harder compared to cases, such as gannets where both breeding stages have been tracked, because the utilisation parameters for juveniles need to be indirectly inferred from the combination of aggregate survey data and adult telemetry only. Under objective 4, using the best joint model only, we demonstrate how to apportion the spatial overlap of marine installations with the distribution of animals belonging to different ages and colonies. Specifically, we consider exposure of different breeding stages and colonies, by calculating the amount of spatial usage by each population component that is enclosed in an arbitrary boundary at sea. Crucially for management decisions, this apportionment of effects is accompanied by spatially explicit measures of uncertainty. The Bayesian framework employed here is ideal for this purpose because parametric bootstrapping of the spatial uncertainty can be performed directly by sampling from the posterior distribution of the fitted models. Finally, we provide instructions and appendices with code to facilitate running the apportionment functions from a given model object and within a given offshore area.

1.2 Relevant facts about kittiwake natural history

In the breeding season kittiwakes (Figure 1) are a central-place foraging species nesting in coastal cliff colonies. Their diet is dominated by small shoaling fish, particularly sandeels, sprats and juvenile herring. Adults forage from their nest site to areas at sea to capture prey for either self-maintenance or to bring back for dependent chicks. Woodward et al. (2019) reported summary statistics for the foraging range of tracked kittiwakes from their breeding colonies across multiple studies. The mean foraging range ($\pm$ SD) was 54.7 km ($\pm$ 50.4). However, the mean of the maximum foraging ranges across the studies was 156.1 km ($\pm$ 144.5), showing the birds can, and do, forage much further than the mean value.

There is some variation on the foraging range across the breeding season. Kittiwakes breeding on Coquet Island in northeast England foraged much further from the colony during the incubation phase than during the chick rearing phase (Robertson et al. 2014). The mean of the maximum foraging range during the incubation phase could be more than 5 times the distance during chick-rearing (9.03 ± 1.17 km during incubation, 50.95 ± 12.99 km during chick rearing). This reduction in foraging range during the early chick rearing phases was due to the requirement to feed chicks regularly and the shift from adults feeding themselves larger (1+ year group) sandeels during incubation to feeding chicks smaller (0 year group) sandeels.

There is also some interannual variation in the foraging behaviour of nesting kittiwakes. In years with high breeding success there was no difference in foraging range during chick-rearing and during incubation; both were relatively short. However, in years with low breeding success foraging ranges were longer but were very much longer during incubation and only slightly longer during chick-rearing (Osborne et al. 2020).

In total, the analysis examined 88 colonies whose size ranged from 1 to 34864 breeding pairs (Table 1). The data originate from the Seabird2000 surveys in order to align with the CEF, however, these analyses are now automated and spatial predictions can be readily updated with new population data.

Table 1: Characteristics of the colonies included in this analysis (Based on Seabird2000 survey data).

Colony	Longitude	Latitude	Breeding pairs
Auskerry	-2.58	59.03	19
Bigton to Maywick - Shetland	-1.33	59.99	175
Birsay - Brough of Birsay	-3.34	59.14	1298
Boddam to Collieston	-1.79	57.36	13922
Burn of Daff	-2.14	57.04	450
Caithness - Dunbeath Bay	-3.42	58.23	40
Caithness - Duncansby Stacks SSSI/SPA	-3.04	58.6	3140
Caithness - North Eastern Cliffs SSSI/SPA	-3.08	58.24	16023
Caithness - South Eastern Cliffs SSSI	-3.43	58.14	24387
Caithness - Wick Bay to Freshwick Bay	-3.07	58.47	249
Calf of Eday - Orkney	-2.74	59.23	765
Cape Wrath - Kyle of Durness	-4.87	58.6	10316
Catterline to Inverbervie	-2.22	56.85	3068

Copinsay	-2.66	58.89	4364
Costa Head - Orkney	-3.2	59.14	1256
Covesea Bay	-3.39	57.72	29
Crawton - Stonehaven (Fowlsheugh)	-2.2	56.91	24606
Crawton to Catterline	-2.2	56.91	4739
Deerness	-2.71	58.93	577
Droman to Geodha Ruadh na Fola	-5.11	58.48	188
Dunbar Coast	-2.53	56.01	1060
Dunbar Harbour	-2.52	56.01	131
Duncansby Head to Smoo (includes Stroma) - Highland	-3.12	58.56	7761
Dunglass to Fast Castle	-2.27	55.92	792
East Yell	-1.01	60.5	246
Eday - Orkney	-2.75	59.22	14
Eilean Nan Ron/Rabbit Islands/Neave Island	-4.35	58.55	69
Eyemouth to Burnmouth	-2.07	55.84	2516
Fair Isle	-1.63	59.53	8204
Faraid Head/ Balnakeil	-4.77	58.59	1810
Fethaland to North Roe - Shetland	-1.3	60.63	15
Fetlar - Shetland	-0.86	60.56	62
Findon Ness - Hare Ness	-2.09	57.07	1142
Forth Islands - Bass Rock to Haystack	-3.14	56.03	2283
Foula	-2.07	60.12	1934
Girdle Ness to Hare Ness	-2.06	57.11	1395
Handa Island	-5.18	58.38	7013
Heylor to Stenness	-1.63	60.48	103
Heylor to Stenness - Shetland	-1.6	60.47	4
Hopeman Bay	-3.41	57.71	355
Hoy and Southwalls	-3.39	58.78	795
Huxter to Brindister - Shetland	-1.5	60.31	14
Isle of May	-2.56	56.19	3639
Lunan Bay to Arbroath	-2.48	56.58	2542
Marwick Head	-3.34	59.1	5410
Montrose to Lunan Bay	-2.48	56.66	384
Muckle Roe - Shetland	-1.41	60.35	134
Muckle Skerry (Coastal)	-2.92	58.69	219
Mull Head	-2.71	58.97	559
Newton Hill	-2.16	57.01	8
Newtonhill - Hall Bay	-2.15	57.02	788
No Ness to Levenwick and Boddam to Virkie	-1.21	59.9	653
North Hill - Papa Westray	-2.87	59.37	602
North Sutor to Shandwick	-3.97	57.69	663
Noss NNR	-1.02	60.15	2395
NW Yell - Whale Firth to Gloup	-1.11	60.73	54
Papa Stour - Shetland	-1.72	60.33	324

Point of Buckquoy to Latha Skerry to Marwick Head	-3.34	59.99	163
Portknockie	-2.84	57.7	104
Portsoy to Cullen	-2.79	57.68	523
Ramna Stacks - Shetland	-1.3	60.65	32
Ronas Hill to Uyea - Shetland	-1.42	60.62	165
Ronas Voe to the Ness - Shetland	-1.48	60.56	71
Roseheartly to Bay of Cullen	-2.41	57.67	19294
Rousay Coast	-3.07	59.16	2713
Rubha Reidh Peninsula	-5.81	57.82	195
Saltness to Skeld - Shetland	-1.4	60.18	34
Sanday	-2.63	59.25	134
Sands of Forvie NNR (Cliff Nesters)	-1.94	57.33	420
Shapinsay (Coastal)	-2.82	59.02	46
South Sutor	-4	57.68	86
South West Unst - Shetland	-0.97	60.7	1
St Abbs to Eyemouth	-2.13	55.9	1
St Abbs to Fast Castle	-2.13	55.9	15430
St. Ninian's Isle - Shetland	-1.35	59.97	54
Stoer Headland	-5.37	58.24	299
Sule Skerry	-4.4	59.08	1275
Sule Stack	-4.5	59.02	51
Sumburgh Head - Shetland	-1.28	59.86	722
Sumburgh to Peerie Voe of Spiggie - Shetland	-1.36	59.89	204
Swona (Coastline)	-3.05	58.74	49
Ulsta to Whalefirth (Yell) - Shetland	-1.2	60.58	18
Vaila - Shetland	-1.59	60.19	78
West Burra - Shetland	-1.34	60.06	173
West Westray Cliffs	-3.07	59.29	34864
Westray	-2.86	59.25	379
Whalsay - Shetland	-0.99	60.33	48
Yesnaby to Marwick (West Mainland)	-3.35	59.02	1565

2 Environmental covariates

A total of nine environmental covariates were considered for this analysis (Figure 2). Their derivation and interpretation is described in detail in the Data report generated for this project under WP1. Briefly, the variables were: (1) depth, (2) minimum distance to coast, (3) seabed slope, (4) proportion of gravel, (5) sand:mud ratio, (6) potential energy anomaly (PEA), (7) sea surface temperature, (8) thermal front gradient density (TFGD), and (9) net primary production (alpha-chlorophyll - NPP). To facilitate comparisons between the magnitude of influence and to help with model convergence, all covariates were standardized to mean zero and standard deviation one.

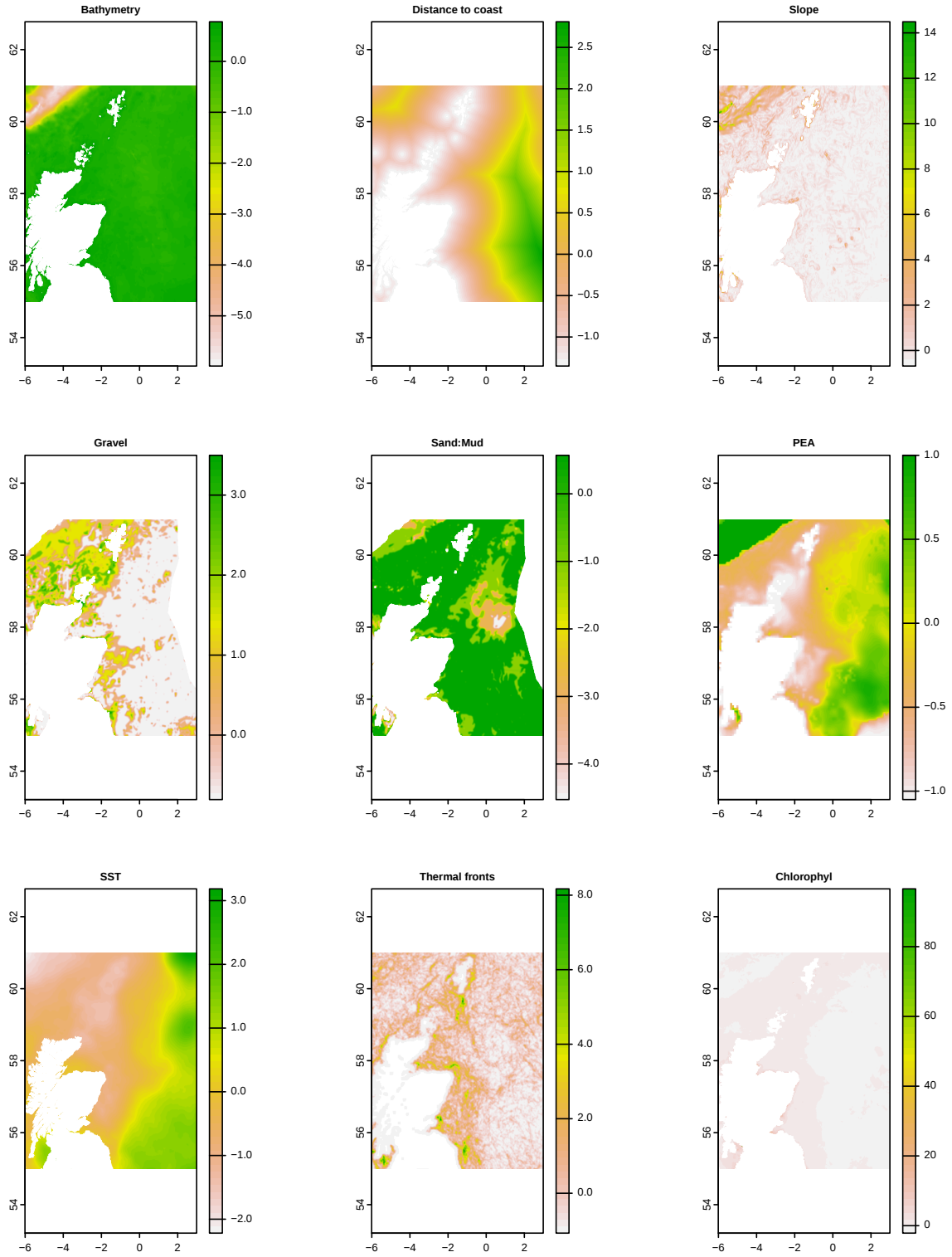


Figure 2: The candidate covariate layers considered in this analysis. All covariates are standardised to mean zero and $sd=1$.

2.1 Derived covariates

The main derived covariates required for models of central-place foragers are the maps of distance-to-colony. A stack of rasters is required, one raster for every colony to be included in the modelling. The nominal positions of the colonies are approximate, and recorded in (Table 1). This is a requirement regardless of whether a particular colony is associated with tagging data or not. The distances were calculated but not standardised. A synoptic view of the accessibility of different points at sea can be obtained by weighting the accessibility of each colony by its relative population size (Figure 3). Note that this accessibility model is for illustrative purposes only, but it is numerically based on the parameter value retrieved for adults in the final model selected in this analysis (Table 4).

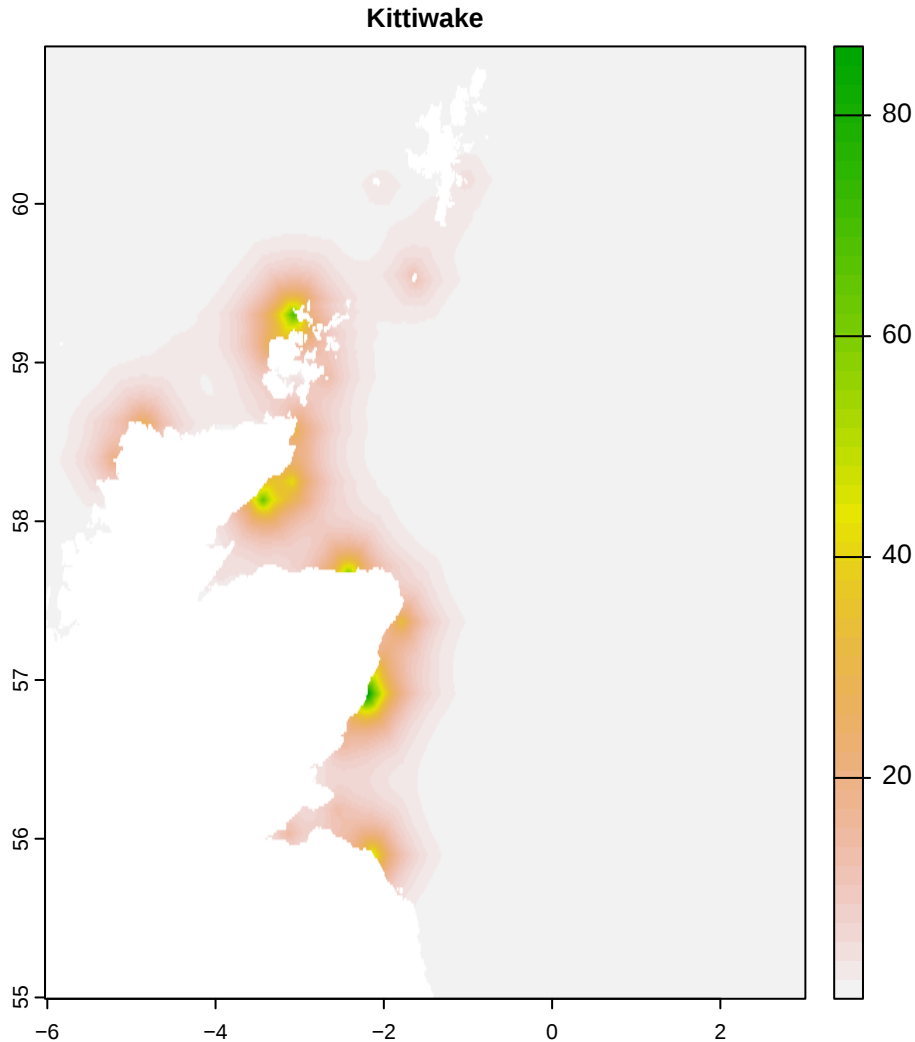


Figure 3: A visualisation of a possible accessibility surface for the kittiwake metapopulation in the east coast of Scotland. Here, we used a negative exponential distance function for each colony and weighted the accessibility of each colony by its relative population size. The rate of decay with distance is the corresponding parameter retrieved for adults in the final model (see below).

2.2 Survey transects

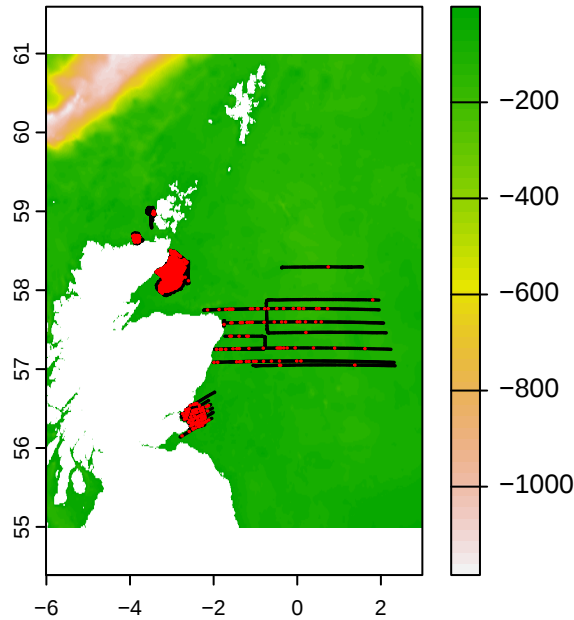


Figure 4: The survey transects considered in the analysis (black lines) and the detections of individuals from the study species (red dots).

A total of 8 survey projects were combined into the pooled data set, comprising 45 surveys from 2012 to 2017. These were slightly different from the surveys described in the data report of WP1. Despite there being more surveys close to the east coast of mainland Scotland, these had specifically excluded seabird records. In contrast, additional survey transects were acquired for a large offshore area east of Aberdeenshire (Figure 4). The detections of kittiwakes were made at the level of individual birds, so it was possible to get accurate counts for particular transect locations. The resulting span and resolution of the survey data provided both contrast and detail for the models to work on.

2.3 Tracking data

The telemetry dataset comprised locations from 202 tagged individuals, and the distribution of data by colony and breeding stage is shown in (Table 2). Importantly, not all colonies will be associated with tagged individuals and the number of individuals tagged in each colony will not be proportional to that colony's size (as reported in (Table 1)). Similarly, the tags were deployed on a sample of individuals that is not representative of population structure (males/females, adults/juveniles). These imbalances in sampling effort are accounted for in the modelling and prediction stage so that spatial apportioning results are unbiased, but of course, colonies and breeding stages with more data will be characterised with more precision in these results.

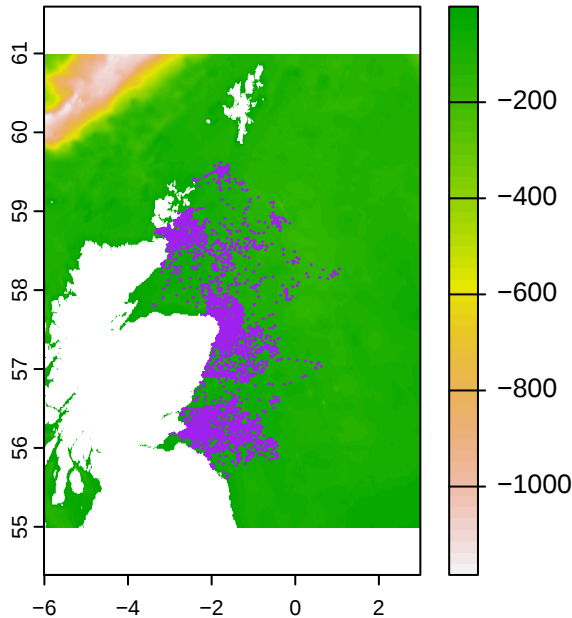


Figure 5: The telemetry data from adult individuals.

Table 2: Telemetry locations by colony and breeding stage

Colony	Adults
BNCC	41913
FAI	7661
FOW	20214
IOM	50417
ORK:COP	29631
ORK:MKS	61797
SAB	27572

3 Inference

The telemetry and survey data were modelled under a joint likelihood in the Bayesian framework described and validated in the report from WP2 of this project. The objective of the joint model was to better reconcile the aggregate usage (as observed via survey data) with the colony and age-specific data (as observed via the tagging data). The JAGS code for the model (see Appendix I for code) is a direct extension of the basic model outlined in WP2, using more than two candidate covariates and more than two colonies. We have additionally made the assumption that both juveniles and adults respond in the same direction to different covariates (i.e., they prefer or avoid them), although the strength of those preferences can be very different for the two breeding stages.

3.1 Model selection on Joint model

Unlike the proof-of-concept analyses presented in the WP2 report, with real data, we cannot know a-priori which of the candidate covariates are relevant for the seabirds. We therefore followed a forward addition model selection approach using the Deviance Information Criterion to balance goodness of fit with parsimony. Each model was given a unique code indicating how many and which covariates were included. For example, 3.568 indicates a model with the three covariates **SandMud**, **PEA** and **Thermal** included in that order. All models had an intercept and distance from the colony was retained by default, since it is known (at least for provisioning adults) that they will have an association with their colony. This association is likely to be weaker for juveniles, so that was encoded in the prior for the juvenile parameter for distance to colony (see priors for parameters **aD[1]** and **aD[2]** in Appendix I).

A total of 43 models were examined (Table 3) and the best model was 5.91478.

The selected model showed avoidance of gravelly substrates and areas with warmer sea surface. Both adults and juveniles showed strong attachment to the locations of colonies, but no additional attachment to near-coast areas. Regions with thermal fronts and high primary production were attractive to kittiwakes. Juveniles, in particular were deduced to show strong preferences for relatively deeper waters (Table 4).

3.2 Comparison with single-datatype models

Since the main methodological contribution of this project is the combination of survey and telemetry data, we examined the two single-datatype models corresponding to the best joint model (5.91478). We were interested in examining first, whether these models would converge, second, whether they would arrive at similar parameter estimates and third, if these estimates would be characterised by similar precision as those delivered by the joint model. In the present area of application, a model that does not converge indicates overparameterisation, i.e. data insufficiency, for the number of variables included. We decided to plot posteriors for parameters, even if the single-datatype models did not converge. These information-rich comparisons are illustrated in (Figure 6). In addition to parameters for the three models examined, we also plot the priors provided to the model as way of examining relative increases in parameter precision in the final results. Compared to the prior distributions, all three models resulted in posteriors with higher precision but different median estimates. The joint model and the survey model were predominantly in agreement, although they presented some differences for variables such as PEA, and importantly, unlike the joint model, the survey model had poor convergence.

4 Spatial prediction

4.1 Usage maps

The joint model can be used to generate spatial predictions for the marine usage of individuals (both breeders and non-breeders) from all colonies individually, or together. Since the model also estimates the relative proportion of adults and juveniles across the sea, the results can be weighted and aggregated in different ways. Any such visualisations are possible, but in (Figure 7) we show individual plots for only two colonies, aggregate plots for Adults and Juveniles and combined plots for the whole population.

Table 3: The different models compared in the study. For each model, asterisks indicate the participating covariates. Models are sorted by increasing delta-DIC value (the best model is at the top). Wherever an NA value is cited in place of a delta-DIC, the model failed to converge.

	Mod	Dpth	DCst	Slp	Grvl	SndMd	PEA	SST	Thrml	NPP	DCol	DDIC
36	5.91478	*			*			*	*	*	*	0
40	6.914786	*			*		*	*	*	*	*	5
33	5.91473	*		*	*			*		*	*	27
30	4.9147	*			*			*		*	*	50
34	5.91475	*			*	*		*		*	*	54
26	4.9142	*	*		*					*	*	58
27	4.9143	*		*	*					*	*	68
21	3.914	*			*					*	*	72
29	4.9146	*			*		*			*	*	76
20	3.913	*		*						*	*	82
22	3.915	*				*				*	*	84
11	2.91	*								*	*	86
19	3.912	*	*							*	*	93
31	4.9148	*			*				*	*	*	95
38	6.914783	*		*	*			*	*	*	*	108
25	3.918	*							*	*	*	168
24	3.917	*						*		*	*	204
18	2.98								*	*	*	455
12	2.92		*							*	*	468
16	2.96						*			*	*	492
13	2.93			*						*	*	516
10	1.9									*	*	525
17	2.97							*		*	*	526
7	1.6						*				*	878
4	1.3			*							*	914
3	1.2		*								*	994
5	1.4				*						*	1011
6	1.5					*					*	1028
1	0.0										*	NA
2	1.1	*									*	NA
8	1.7							*			*	NA
9	1.8								*		*	NA
14	2.94				*					*	*	NA
15	2.95					*				*	*	NA
23	3.916	*					*			*	*	NA
28	4.9145	*			*	*				*	*	NA
32	5.91472	*	*		*			*		*	*	NA
35	5.91476	*			*		*	*		*	*	NA
37	6.914782	*	*		*			*	*	*	*	NA
39	6.914785	*			*	*		*	*	*	*	NA
41	7.9147862	*	*		*	13	*	*	*	*	*	NA
42	7.9147863	*		*	*		*	*	*	*	*	NA
43	7.9147865	*			*		*	*	*	*	*	NA

Table 4: Parameter median estimates from the posteriors of the joint model, accompanied by their 95% credible intervals.

Description	2.5%	Median	97.5%
Intercept Juveniles	-19.348178	-18.674449	-17.846943
Intercept Adults	-11.836515	-11.720264	-11.624557
Bathymetry Juveniles	11.780074	13.189805	14.444449
Bathymetry Adults	1.08777	1.177831	1.389478
Distance from Coast Juveniles	0	0	0
Distance from Coast Adults	0	0	0
Slope Juveniles	0	0	0
Slope Adults	0	0	0
Gravel Juveniles	-0.076643	-0.046521	-0.019671
Gravel Adults	-0.136696	-0.092015	-0.049881
Mud:Sand Juveniles	0	0	0
Mud:Sand Adults	0	0	0
PE Anomaly Juveniles	0	0	0
PE Anomaly Adults	0	0	0
SST Juveniles	-0.258089	-0.154598	-0.063439
SST Adults	-0.343645	-0.239726	-0.132137
Therm Fronts Juveniles	0.036009	0.071001	0.10833
Therm Fronts Adults	0.047548	0.072037	0.094891
Chlorophyl Juveniles	0.01615	0.035857	0.060518
Chlorophyl Adults	0.233414	0.262397	0.291373
Dist to colony Juveniles	0.117473	0.129304	0.140137
Dist to colony Adults	0.122368	0.132397	0.143403

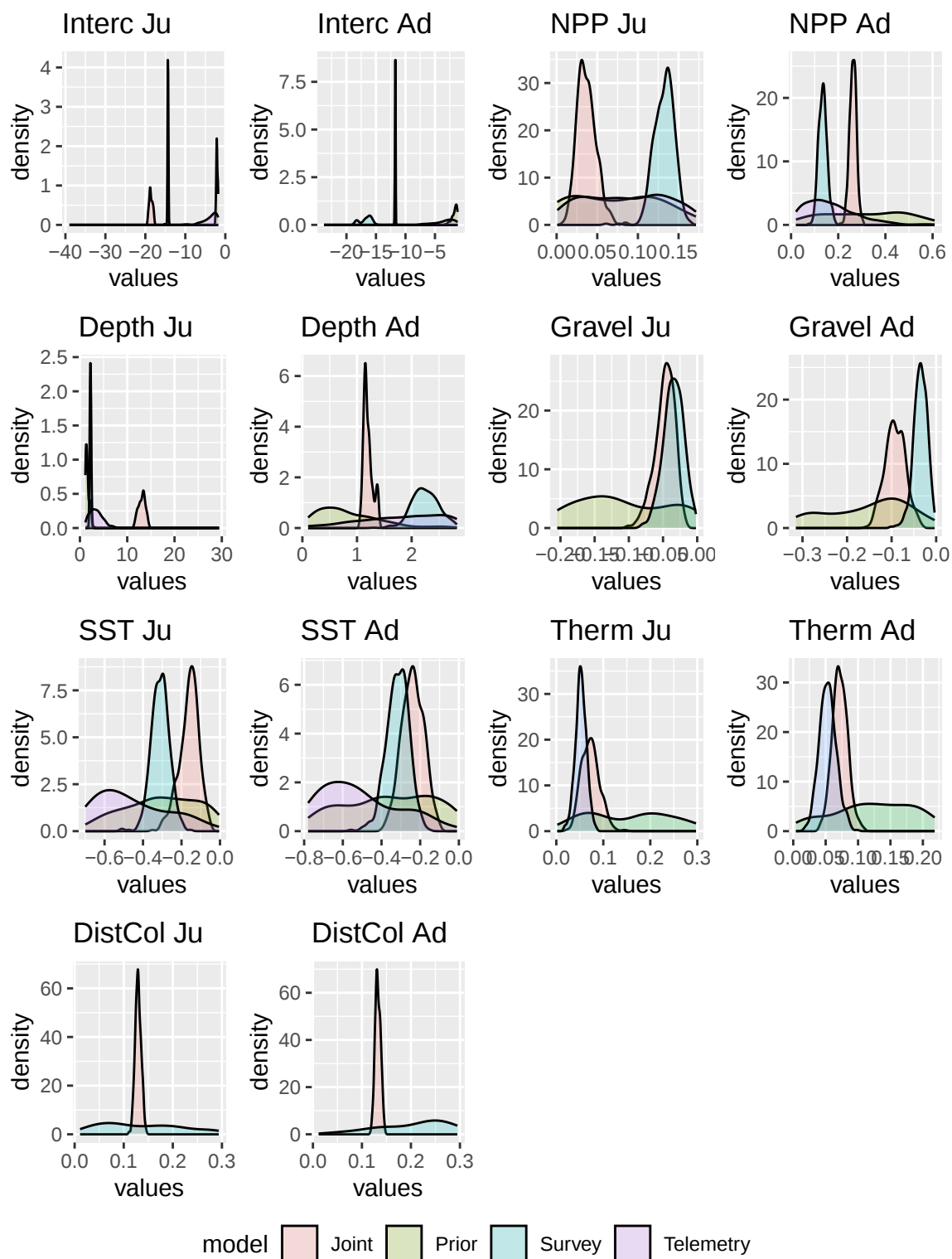


Figure 6: Comparison of the Prior distributions for each parameter, with the posteriors generated from two single-datatype models (Survey and Telemetry) and the Joint model. Posteriors from any non-converging models are also shown for comparison

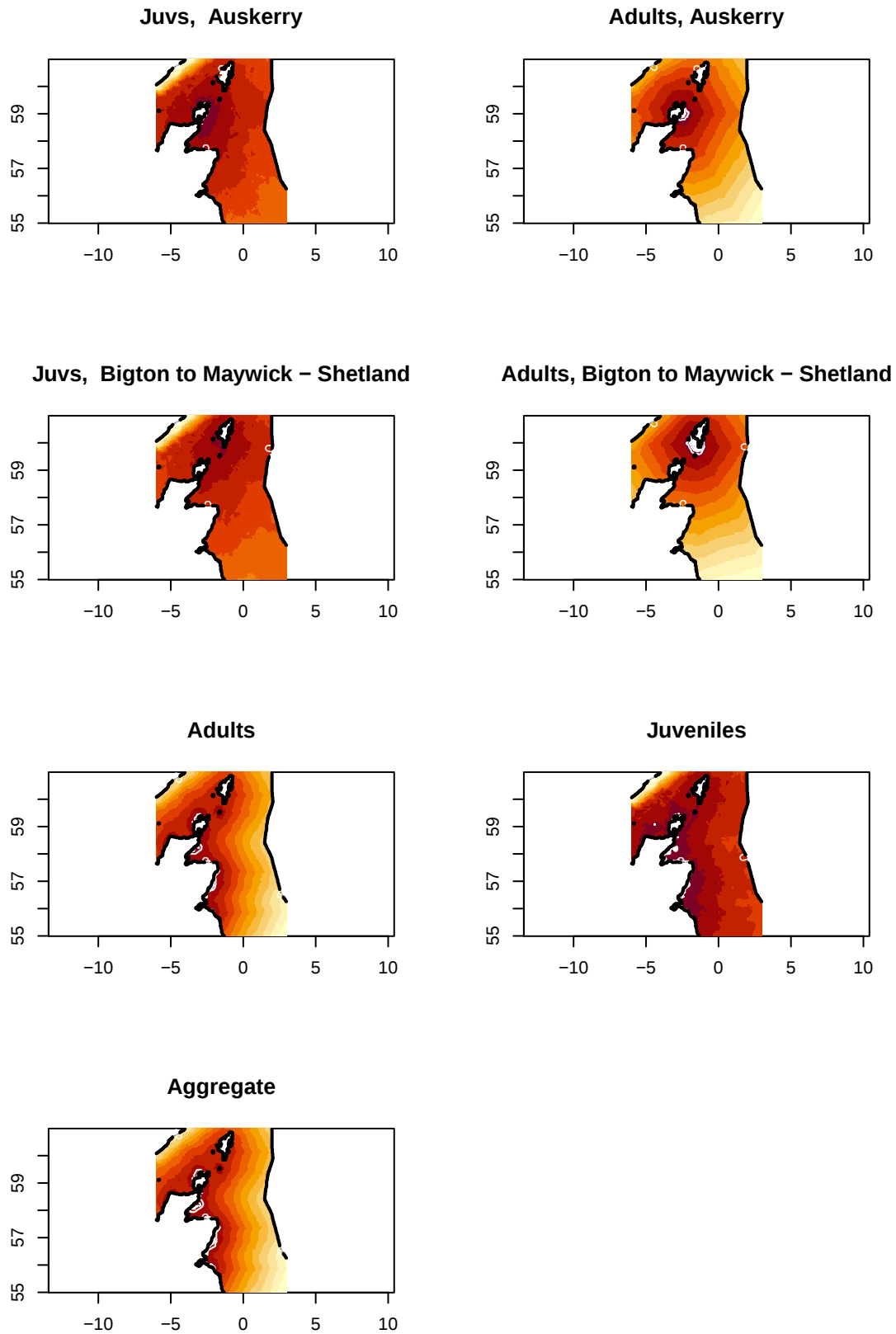


Figure 7: Predictions of spatial usage from the joint model. We show juvenile and adult maps for two colonies, total juvenile and adult usage maps, and the aggregate map from all colonies and both breeding stages. To facilitate visualisation, colours are in logarithmic scale. White contours indicate the hotspots of expected usage in linear scale.

4.2 Apportioning impact

The final step in producing the necessary results is to estimate the usage of a given region in space, by colony and population component. For the purposes of illustration, we introduce an arbitrary (and large) region (Figure 8). The use of functionality in the **TrackTrans** package for generating apportioning estimates is straightforward, and explained in Appendix II.

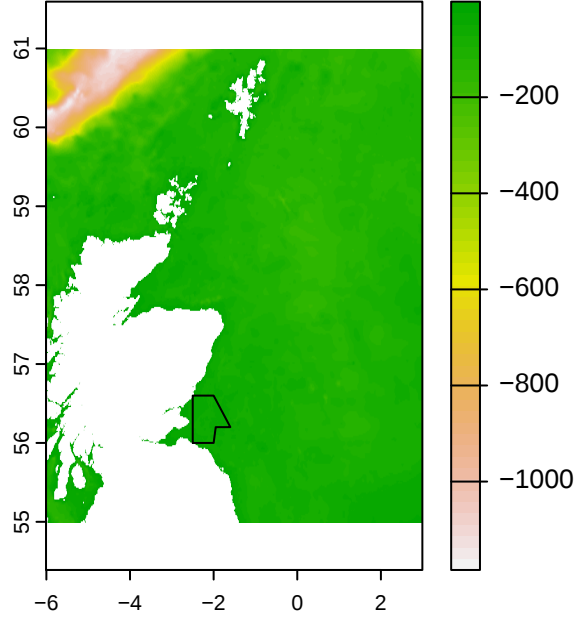


Figure 8: An example of a marine region that might be used to interrogate the model about apportioning usage.

Table 5: Exposure to development area by colony and age stage. This is unweighted exposure, representing the percentage of usage by this particular age class from the given colony.

Colony	MedJuv%	95% CI	MedAd%	95% CI
Auskerry	0	(0 - 0)	0	(0 - 0)
Bigton to Maywick - Shetland	0	(0 - 0)	0	(0 - 0)
Birsay - Brough of Birsay	0	(0 - 0)	0	(0 - 0)
Boddam to Collieston	0.69	(0.47 - 0.98)	0.21	(0.15 - 0.3)
Burn of Daff	7.36	(6.28 - 8.61)	3.82	(3.3 - 4.57)
Caithness - Dunbeath Bay	0	(0 - 0)	0	(0 - 0)
Caithness - Duncansby Stack...	0	(0 - 0)	0	(0 - 0)
Caithness - North Eastern C...	0	(0 - 0)	0	(0 - 0)
Caithness - South Eastern C...	0	(0 - 0)	0	(0 - 0)

Caithness - Wick Bay to Fre...	0	(0 - 0)	0	(0 - 0)
Calf of Eday - Orkney	0	(0 - 0)	0	(0 - 0)
Cape Wrath - Kyle of Durness	0	(0 - 0)	0	(0 - 0)
Catterline to Inverbervie	14.12	(12.83 - 15.43)	10.15	(9.34 - 11.38)
Copinsay	0	(0 - 0)	0	(0 - 0)
Costa Head - Orkney	0	(0 - 0)	0	(0 - 0)
Covesea Bay	0	(0 - 0)	0	(0 - 0)
Crawton - Stonehaven (Fowls...	11.25	(10 - 12.54)	7.26	(6.55 - 8.33)
Crawton to Catterline	11.83	(10.56 - 13.11)	7.83	(7.1 - 8.94)
Deerness	0	(0 - 0)	0	(0 - 0)
Droman to Geodha Ruadh na Fola	0	(0 - 0)	0	(0 - 0)
Dunbar Coast	28.04	(25.55 - 30.97)	42.35	(40.07 - 43.89)
Dunbar Harbour	29.53	(27 - 32.52)	43.91	(41.52 - 45.43)
Duncansby Head to Smoo (inc...	0	(0 - 0)	0	(0 - 0)
Dunglass to Fast Castle	36.69	(34.64 - 39.44)	45.71	(43.87 - 46.91)
East Yell	0	(0 - 0)	0	(0 - 0)
Eday - Orkney	0	(0 - 0)	0	(0 - 0)
Eilean Nan Ron/Rabbit Islan...	0	(0 - 0)	0	(0 - 0)
Eyemouth to Burnmouth	22.2	(20.68 - 23.79)	25.58	(24.38 - 26.56)
Fair Isle	0	(0 - 0)	0	(0 - 0)
Faraid Head/ Balnakeil	0	(0 - 0)	0	(0 - 0)
Fethaland to North Roe - Sh...	0	(0 - 0)	0	(0 - 0)
Fetlar - Shetland	0	(0 - 0)	0	(0 - 0)
Findon Ness - Hare Ness	5.71	(4.74 - 6.87)	2.65	(2.24 - 3.26)
Forth Islands - Bass Rock t...	2.04	(1.43 - 2.72)	3.43	(2.4 - 4.59)
Foula	0	(0 - 0)	0	(0 - 0)
Girdle Ness to Hare Ness	4.62	(3.76 - 5.69)	2.01	(1.66 - 2.52)
Handa Island	0	(0 - 0)	0	(0 - 0)
Heylor to Stenness	0	(0 - 0)	0	(0 - 0)
Heylor to Stenness - Shetland	0	(0 - 0)	0	(0 - 0)
Hopeman Bay	0	(0 - 0)	0	(0 - 0)
Hoy and Southwalls	0	(0 - 0)	0	(0 - 0)
Huxter to Brindister - Shet...	0	(0 - 0)	0	(0 - 0)
Isle of May	28.24	(25.87 - 31.21)	42.62	(40.05 - 44.32)
Lunan Bay to Arbroath	35.54	(33.73 - 37.41)	35.97	(33.75 - 37.21)
Marwick Head	0	(0 - 0)	0	(0 - 0)
Montrose to Lunan Bay	29.52	(27.87 - 31)	28.22	(26.97 - 29.21)
Muckle Roe - Shetland	0	(0 - 0)	0	(0 - 0)
Muckle Skerry (Coastal)	0	(0 - 0)	0	(0 - 0)
Mull Head	0	(0 - 0)	0	(0 - 0)
Newton Hill	7.65	(6.56 - 8.91)	4.06	(3.53 - 4.84)
Newtonhill - Hall Bay	7.5	(6.41 - 8.76)	3.94	(3.41 - 4.7)
No Ness to Levenwick and Bo...	0	(0 - 0)	0	(0 - 0)
North Hill - Papa Westray	0	(0 - 0)	0	(0 - 0)

North Sutor to Shandwick	0	(0 - 0)	0	(0 - 0)
Noss NNR	0	(0 - 0)	0	(0 - 0)
NW Yell - Whale Firth to Gloup	0	(0 - 0)	0	(0 - 0)
Papa Stour - Shetland	0	(0 - 0)	0	(0 - 0)
Point of Buckquoy to Latha ...	0	(0 - 0)	0	(0 - 0)
Portknockie	0	(0 - 0)	0	(0 - 0)
Portsoy to Cullen	0	(0 - 0)	0	(0 - 0)
Ramna Stacks - Shetland	0	(0 - 0)	0	(0 - 0)
Ronas Hill to Uyea - Shetland	0	(0 - 0)	0	(0 - 0)
Ronas Voe to the Ness - She...	0	(0 - 0)	0	(0 - 0)
Roseheartly to Bay of Cullen	0	(0 - 0.01)	0	(0 - 0)
Rousay Coast	0	(0 - 0)	0	(0 - 0)
Rubha Reidh Peninsula	0	(0 - 0)	0	(0 - 0)
Saltness to Skeld - Shetland	0	(0 - 0)	0	(0 - 0)
Sanday	0	(0 - 0)	0	(0 - 0)
Sands of Forvie NNR (Cliff ...	1.11	(0.78 - 1.54)	0.41	(0.3 - 0.57)
Shapinsay (Coastal)	0	(0 - 0)	0	(0 - 0)
South Sutor	0	(0 - 0)	0	(0 - 0)
South West Unst - Shetland	0	(0 - 0)	0	(0 - 0)
St Abbs to Eyemouth	30.55	(29.12 - 32.43)	35.04	(34.26 - 36.03)
St Abbs to Fast Castle	30.55	(29.12 - 32.43)	35.04	(34.26 - 36.03)
St. Ninian's Isle - Shetland	0	(0 - 0)	0	(0 - 0)
Stoer Headland	0	(0 - 0)	0	(0 - 0)
Sule Skerry	0	(0 - 0)	0	(0 - 0)
Sule Stack	0	(0 - 0)	0	(0 - 0)
Sumburgh Head - Shetland	0	(0 - 0)	0	(0 - 0)
Sumburgh to Peerie Voe of S...	0	(0 - 0)	0	(0 - 0)
Swona (Coastline)	0	(0 - 0)	0	(0 - 0)
Ulsta to Whalefirth (Yell) ...	0	(0 - 0)	0	(0 - 0)
Vaila - Shetland	0	(0 - 0)	0	(0 - 0)
West Burra - Shetland	0	(0 - 0)	0	(0 - 0)
West Westray Cliffs	0	(0 - 0)	0	(0 - 0)
Westray	0	(0 - 0)	0	(0 - 0)
Whalsay - Shetland	0	(0 - 0)	0	(0 - 0)
Yesnaby to Marwick (West Ma...	0	(0 - 0)	0	(0 - 0)

Table 6: Exposure to development area by colony and age stage. This is weighted exposure, representing the usage of the area inside boundary of interest by this particular age class from the given colony as a percentage of total population usage.

Colony	MedJuv%	95% CI	MedAd%	95% CI
--------	---------	--------	--------	--------

Auskerry	0	(0 - 0)	0	(0 - 0)
Bigton to Maywick - Shetland	0	(0 - 0)	0	(0 - 0)
Birsay - Brough of Birsay	0	(0 - 0)	0	(0 - 0)
Boddam to Collieston	0.02	(0.01 - 0.03)	0.01	(0 - 0.01)
Burn of Daff	0.01	(0.01 - 0.01)	0	(0 - 0)
Caithness - Dunbeath Bay	0	(0 - 0)	0	(0 - 0)
Caithness - Duncansby Stack...	0	(0 - 0)	0	(0 - 0)
Caithness - North Eastern C...	0	(0 - 0)	0	(0 - 0)
Caithness - South Eastern C...	0	(0 - 0)	0	(0 - 0)
Caithness - Wick Bay to Fre...	0	(0 - 0)	0	(0 - 0)
Calf of Eday - Orkney	0	(0 - 0)	0	(0 - 0)
Cape Wrath - Kyle of Durness	0	(0 - 0)	0	(0 - 0)
Catterline to Inverbervie	0.09	(0.08 - 0.1)	0.06	(0.06 - 0.07)
Copinsay	0	(0 - 0)	0	(0 - 0)
Costa Head - Orkney	0	(0 - 0)	0	(0 - 0)
Covesea Bay	0	(0 - 0)	0	(0 - 0)
Crawton - Stonehaven (Fowls...	0.57	(0.5 - 0.63)	0.36	(0.33 - 0.42)
Crawton to Catterline	0.11	(0.1 - 0.13)	0.08	(0.07 - 0.09)
Deerness	0	(0 - 0)	0	(0 - 0)
Droman to Geodha Ruadh na Fola	0	(0 - 0)	0	(0 - 0)
Dunbar Coast	0.06	(0.06 - 0.07)	0.09	(0.09 - 0.09)
Dunbar Harbour	0.01	(0.01 - 0.01)	0.01	(0.01 - 0.01)
Duncansby Head to Smoo (inc...	0	(0 - 0)	0	(0 - 0)
Dunglass to Fast Castle	0.06	(0.06 - 0.06)	0.07	(0.07 - 0.08)
East Yell	0	(0 - 0)	0	(0 - 0)
Eday - Orkney	0	(0 - 0)	0	(0 - 0)
Eilean Nan Ron/Rabbit Islan...	0	(0 - 0)	0	(0 - 0)
Eyemouth to Burnmouth	0.11	(0.11 - 0.12)	0.13	(0.13 - 0.14)
Fair Isle	0	(0 - 0)	0	(0 - 0)
Faraid Head/ Balnakeil	0	(0 - 0)	0	(0 - 0)
Fethaland to North Roe - Sh...	0	(0 - 0)	0	(0 - 0)
Fetlar - Shetland	0	(0 - 0)	0	(0 - 0)
Findon Ness - Hare Ness	0.01	(0.01 - 0.02)	0.01	(0.01 - 0.01)
Forth Islands - Bass Rock t...	0.01	(0.01 - 0.01)	0.02	(0.01 - 0.02)
Foula	0	(0 - 0)	0	(0 - 0)
Girdle Ness to Hare Ness	0.01	(0.01 - 0.02)	0.01	(0 - 0.01)
Handa Island	0	(0 - 0)	0	(0 - 0)
Heylor to Stenness	0	(0 - 0)	0	(0 - 0)
Heylor to Stenness - Shetland	0	(0 - 0)	0	(0 - 0)
Hopeman Bay	0	(0 - 0)	0	(0 - 0)
Hoy and Southwalls	0	(0 - 0)	0	(0 - 0)
Huxter to Brindister - Shet...	0	(0 - 0)	0	(0 - 0)
Isle of May	0.21	(0.19 - 0.23)	0.32	(0.3 - 0.33)
Lunan Bay to Arbroath	0.18	(0.18 - 0.19)	0.19	(0.18 - 0.19)

Marwick Head	0	(0 - 0)	0	(0 - 0)
Montrose to Lunan Bay	0.02	(0.02 - 0.02)	0.02	(0.02 - 0.02)
Muckle Roe - Shetland	0	(0 - 0)	0	(0 - 0)
Muckle Skerry (Coastal)	0	(0 - 0)	0	(0 - 0)
Mull Head	0	(0 - 0)	0	(0 - 0)
Newton Hill	0	(0 - 0)	0	(0 - 0)
Newtonhill - Hall Bay	0.01	(0.01 - 0.01)	0.01	(0.01 - 0.01)
No Ness to Levenwick and Bo...	0	(0 - 0)	0	(0 - 0)
North Hill - Papa Westray	0	(0 - 0)	0	(0 - 0)
North Sutor to Shandwick	0	(0 - 0)	0	(0 - 0)
Noss NNR	0	(0 - 0)	0	(0 - 0)
NW Yell - Whale Firth to Gloup	0	(0 - 0)	0	(0 - 0)
Papa Stour - Shetland	0	(0 - 0)	0	(0 - 0)
Point of Buckquoy to Latha ...	0	(0 - 0)	0	(0 - 0)
Portknockie	0	(0 - 0)	0	(0 - 0)
Portsoy to Cullen	0	(0 - 0)	0	(0 - 0)
Ramna Stacks - Shetland	0	(0 - 0)	0	(0 - 0)
Ronas Hill to Uyea - Shetland	0	(0 - 0)	0	(0 - 0)
Ronas Voe to the Ness - She...	0	(0 - 0)	0	(0 - 0)
Rosehearty to Bay of Cullen	0	(0 - 0)	0	(0 - 0)
Rousay Coast	0	(0 - 0)	0	(0 - 0)
Rubha Reidh Peninsula	0	(0 - 0)	0	(0 - 0)
Saltness to Skeld - Shetland	0	(0 - 0)	0	(0 - 0)
Sanday	0	(0 - 0)	0	(0 - 0)
Sands of Forvie NNR (Cliff ...	0	(0 - 0)	0	(0 - 0)
Shapinsay (Coastal)	0	(0 - 0)	0	(0 - 0)
South Sutor	0	(0 - 0)	0	(0 - 0)
South West Unst - Shetland	0	(0 - 0)	0	(0 - 0)
St Abbs to Eyemouth	0	(0 - 0)	0	(0 - 0)
St Abbs to Fast Castle	0.96	(0.92 - 1.02)	1.1	(1.08 - 1.14)
St. Ninian's Isle - Shetland	0	(0 - 0)	0	(0 - 0)
Stoer Headland	0	(0 - 0)	0	(0 - 0)
Sule Skerry	0	(0 - 0)	0	(0 - 0)
Sule Stack	0	(0 - 0)	0	(0 - 0)
Sumburgh Head - Shetland	0	(0 - 0)	0	(0 - 0)
Sumburgh to Peerie Voe of S...	0	(0 - 0)	0	(0 - 0)
Swona (Coastline)	0	(0 - 0)	0	(0 - 0)
Ulsta to Whalefirth (Yell) ...	0	(0 - 0)	0	(0 - 0)
Vaila - Shetland	0	(0 - 0)	0	(0 - 0)
West Burra - Shetland	0	(0 - 0)	0	(0 - 0)
West Westray Cliffs	0	(0 - 0)	0	(0 - 0)
Westray	0	(0 - 0)	0	(0 - 0)
Whalsay - Shetland	0	(0 - 0)	0	(0 - 0)
Yesnaby to Marwick (West Ma...	0	(0 - 0)	0	(0 - 0)

The package uses parametric bootstrapping from the posterior of the joint model to generate median and 95% CIs for the usage of the candidate area by different individuals from different colonies. These can be formulated as two types of exposure. First, we can extract the **unweighted exposure** (Table 5), representing the percentage of the usage of adults/juveniles from a given colony found inside the boundary. So, for example, the value 42.35 in (Table 5) indicates that adults from Dunbar Coast spend 42.35% of their marine foraging usage inside the area of interest.

Second, we can extract the **weighted exposure** (Table 6), representing the percentage of the usage of adults/juveniles from a given colony found inside the boundary. So, for example, the value 0.09 in (Table 6) indicates that 0.09% the total usage of the population is attributable to adults from Dunbar Coast spending their time inside the area of interest.

Note that the accompanying 95% credible intervals in the above tables need to be recalculated by bootstrapping every time the boundaries of the region are changed since, due to spatial autocorrelation, the individual CIs that may be generated for any given two cells in the map are not independent, and therefore not additive (in the way that median predictions are). Given a file with the post processing data from a fitted model object, the necessary code for recalculating exposure for any given boundary is given in Appendix II. The necessary data files for running this code will be provided along with the outputs of this project for use by other agencies such as CEH and BIOS.

5 Appendix I: JAGS implemetation of joint model for telemetry & survey data

```
jointJAGS <- "model{

### MAIN LOOP ###

# Survey data part
for(i in 1:nn) # Data row loop
{
  for(s in 1:2) # Age-stage loop
  {
    lambLoc[i,s]<-exp(a0[s]+
                      a1[s]*DepthTr[i]+
                      a2[s]*SlopeTr[i]+
                      a3[s]*DistCoastTr[i]+
                      a4[s]*GravelTr[i]+
                      a5[s]*SandMudTr[i]+
                      a6[s]*PEATr[i]+
                      a7[s]*SSTTr[i]+
                      a8[s]*ThermalTr[i]+
                      a9[s]*NPPTTr[i])

    for(c in 1:nC) # Colony loop
    {
      diLa[i,s,c]<-popS[c]*exp(-aD[s]*DistTr[i,c])
    }
  }
}
```

```

    }
  }
  # lambda
  lambda[i] <- lambLoc[i,2]*sum(diLa[i,2,1:nC])+lambLoc[i,1]*sum(diLa[i,1,1:nC])
  Count[i] ~ dpois(lambda[i])
}

# Telemetry data part
for(j in 1:pts)
{
  btilde[j,1] <- a1[St[j]]*Depth.x[j]+
    a2[St[j]]*Slope.x[j]+
    a3[St[j]]*DistCoast.x[j]+
    a4[St[j]]*Gravel.x[j]+
    a5[St[j]]*SandMud.x[j]+
    a6[St[j]]*PEA.x[j]+
    a7[St[j]]*SST.x[j]+
    a8[St[j]]*Thermal.x[j]+
    a9[St[j]]*NPP.x[j]-
    aD[St[j]]*ColonyDist.x[j]
  btilde[j,2] <- a1[St[j]]*Depth.y[j]+
    a2[St[j]]*Slope.y[j]+
    a3[St[j]]*DistCoast.y[j]+
    a4[St[j]]*Gravel.y[j]+
    a5[St[j]]*SandMud.y[j]+
    a6[St[j]]*PEA.y[j]+
    a7[St[j]]*SST.y[j]+
    a8[St[j]]*Thermal.y[j]+
    a9[St[j]]*NPP.y[j]-
    aD[St[j]]*ColonyDist.y[j]
  mu[j,1] <- xy0[j,1] + (thinTg)*Ga^2/2*btilde[j,1]
  mu[j,2] <- xy0[j,2] + (thinTg)*Ga^2/2*btilde[j,2]

  xy1[j,1] ~ dnorm(mu[j,1], 1/(thinTg*Ga^2))
  xy1[j,2] ~ dnorm(mu[j,2], 1/(thinTg*Ga^2))
}

# Priors

a0[2] ~ dnorm(0, 0.1)
a1[2] ~ dnorm(0, 0.1)
a2[2] ~ dnorm(0, 0.1)
a3[2] ~ dnorm(0, 0.1)
a4[2] ~ dnorm(0, 0.1)
a5[2] ~ dnorm(0, 0.1)
a6[2] ~ dnorm(0, 0.1)
a7[2] ~ dnorm(0, 0.1)

```

```

a8[2]~dnorm(0,0.1)
a9[2]~dnorm(0,0.1)

for(i in 1:10) {sc[i]~dgamma(10,10)}

a0[1]<-sc[1]*a0[2]
a1[1]<-sc[2]*a1[2]
a2[1]<-sc[3]*a2[2]
a3[1]<-sc[4]*a3[2]
a4[1]<-sc[5]*a4[2]
a5[1]<-sc[6]*a5[2]
a6[1]<-sc[7]*a6[2]
a7[1]<-sc[8]*a7[2]
a8[1]<-sc[9]*a8[2]
a9[1]<-sc[10]*a9[2]

aD[1]~dgamma(1,1) # Distance coefficient for juvs
aDdummy~dgamma(1,1)
aD[2]<-aD[1]+aDdummy # Distance coefficient for adults

Ga~dgamma(10,0.007)

#data# nn,nC, popS,Count,DepthTr,SandMudTr,SlopeTr,DistCoastTr,GravelTr,
#data# DistTr, PEATr, SSTTr, ThermalTr, NPPTr
#data# pts, xy0, xy1, Depth.x, Depth.y, SandMud.x, SandMud.y, DistCoast.x,DistCoast.y
#data# Gravel.x,Gravel.y,Slope.x,Slope.y,ColonyDist.x,ColonyDist.y
#data# PEA.x, PEA.y, SST.x, SST.y, Thermal.x, Thermal.y, NPP.x, NPP.y
#data# thinTg, St

#monitor# a0,a1,a2, a3, a4, a5, a6, a7, a8, a9, aD, Ga, dic
}"

```

6 Appendix II: Usage of R functions for the generation of apportioning predictions for a given marine boundary

The key function for going this is `TrackTrans::rApportion()` which uses parametric bootstrapping from the model's posterior to generate an arbitrary number of realisations of usage. The number of bootstraps is specified by the parameter `dr`. The necessary samples from the posterior, and environmental covariates are stored on the file `SpeciesPostData.rda`. The boundary of the area of interest also needs to be specified and, in the example of the main text we use an arbitrary boundary (Figure 8). The results comprise weighted and unweighted proportions of usage (median and lower/upper credible intervals) for each of the colonies and each of the two breeding stages.

```

# Import and unpack the post-processing data files for the species
load("KittiwakePostData.rda")
covariates<-list()
for(i in 1:length(postData$wrappedCovs))
  {covariates[[i]]<-rast(postData$wrappedCovs[[i]])}
dis<-list()
for(i in 1:length(postData$wrappedDis))
  {dis[[i]]<-rast(postData$wrappedDis[[i]])}

# Define or import polygon of interest
pollong<-c(-1.5,-1,-0.95,-0.6,-1,-1.5,-1.5)
pollat<-c(56,56,56.2,56.2,56.6,56.6,56)
polCRS<-crs(bath)
pollonglat<-cbind(pollong,pollat)
pol<-vect(pollonglat, type="polygons",crs=polCRS)

# Call apportioning function and look at results
app<-rApportion(dr=postData$dr, pars=postData$pars, covariates=covariates, dis=dis,
               pop=postData$pop, boundary=pol)

app

```

```

## $'Median Unweighted'
##           [,1]           [,2]
## [1,] 4.309227e-09 4.560593e-09
## [2,] 6.424856e-11 2.212809e-11
## [3,] 4.446938e-10 3.574461e-10
## [4,] 9.438994e-04 1.149002e-03
## [5,] 2.386957e-03 4.507922e-03
## [6,] 1.294027e-08 4.320869e-08
## [7,] 1.793434e-08 3.490092e-08
## [8,] 4.061600e-08 9.055176e-08
## [9,] 1.231383e-08 4.706273e-08
## [10,] 2.882934e-08 5.392044e-08
## [11,] 7.909974e-10 1.202679e-09
## [12,] 2.747460e-11 2.470165e-11
## [13,] 2.142282e-03 5.468287e-03
## [14,] 8.383103e-09 9.823792e-09
## [15,] 3.761488e-10 3.833571e-10
## [16,] 4.765600e-08 2.904682e-07
## [17,] 2.202821e-03 5.082195e-03
## [18,] 2.211010e-03 5.227209e-03
## [19,] 6.827869e-09 8.616565e-09
## [20,] 7.191483e-12 5.159221e-12
## [21,] 1.863459e-03 6.309975e-03
## [22,] 2.005168e-03 6.687741e-03
## [23,] 2.023296e-08 3.871843e-08

```

```

## [24,] 5.862869e-03 1.588274e-02
## [25,] 1.049271e-12 6.409419e-13
## [26,] 1.094728e-09 1.634305e-09
## [27,] 1.983845e-10 1.643495e-10
## [28,] 1.060170e-02 2.647798e-02
## [29,] 7.149070e-10 2.415669e-10
## [30,] 4.123519e-11 3.786433e-11
## [31,] 6.564185e-13 2.235934e-13
## [32,] 7.282704e-13 3.283110e-13
## [33,] 2.413848e-03 4.153710e-03
## [34,] 1.042182e-04 4.137890e-04
## [35,] 5.750887e-12 2.832025e-12
## [36,] 2.368912e-03 3.853832e-03
## [37,] 4.734427e-12 2.761014e-12
## [38,] 1.280354e-12 4.098485e-13
## [39,] 1.429275e-12 4.715450e-13
## [40,] 3.923095e-08 2.475242e-07
## [41,] 3.993431e-09 4.768364e-09
## [42,] 1.910941e-12 8.705179e-13
## [43,] 1.328370e-03 5.051805e-03
## [44,] 1.116417e-03 4.275493e-03
## [45,] 6.422274e-10 5.023173e-10
## [46,] 1.094868e-03 3.922205e-03
## [47,] 1.875946e-12 8.470474e-13
## [48,] 1.620714e-08 3.122744e-08
## [49,] 5.875278e-09 7.284025e-09
## [50,] 2.292244e-03 4.400543e-03
## [51,] 2.339487e-03 4.454112e-03
## [52,] 1.218011e-10 3.388889e-11
## [53,] 2.533550e-10 3.306191e-10
## [54,] 4.262495e-09 4.262146e-08
## [55,] 1.213520e-11 6.363390e-12
## [56,] 3.879982e-13 9.299720e-14
## [57,] 2.439466e-12 1.264972e-12
## [58,] 1.039316e-11 2.425060e-12
## [59,] 6.080371e-07 2.798138e-06
## [60,] 9.616605e-07 3.876086e-06
## [61,] 5.813108e-13 1.882369e-13
## [62,] 4.068884e-13 1.233242e-13
## [63,] 6.232152e-13 1.885084e-13
## [64,] 6.055998e-06 1.512199e-05
## [65,] 4.360710e-10 4.809605e-10
## [66,] 9.212330e-14 3.699533e-14
## [67,] 2.111657e-11 9.067975e-12
## [68,] 6.948139e-10 1.047874e-09
## [69,] 1.036071e-03 1.509533e-03
## [70,] 4.303832e-09 5.542646e-09
## [71,] 3.941529e-09 3.990310e-08

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## [72,] 5.723029e-13 1.724047e-13
## [73,] 9.372942e-03 2.307957e-02
## [74,] 9.372942e-03 2.307957e-02
## [75,] 6.746427e-11 2.320965e-11
## [76,] 2.310498e-12 8.963286e-13
## [77,] 2.116603e-11 2.065980e-11
## [78,] 2.082019e-11 1.957264e-11
## [79,] 1.365600e-10 3.909881e-11
## [80,] 1.052610e-10 3.367280e-11
## [81,] 9.270737e-09 2.130707e-08
## [82,] 1.034451e-12 4.349837e-13
## [83,] 9.620355e-12 4.532339e-12
## [84,] 4.698823e-11 1.692233e-11
## [85,] 3.797150e-10 4.067290e-10
## [86,] 7.354336e-10 1.066100e-09
## [87,] 2.266099e-12 1.870859e-12
## [88,] 1.089922e-09 8.602274e-10
##
## $'Lower Unweighted'
##           [,1]           [,2]
## [1,] 8.230599e-10 1.061232e-09
## [2,] 6.283233e-12 2.828214e-12
## [3,] 6.210890e-11 6.250619e-11
## [4,] 6.049563e-04 7.847946e-04
## [5,] 1.702011e-03 3.395486e-03
## [6,] 2.958208e-09 1.226358e-08
## [7,] 4.081439e-09 9.773725e-09
## [8,] 1.050016e-08 2.785637e-08
## [9,] 2.799570e-09 1.341790e-08
## [10,] 7.174428e-09 1.579785e-08
## [11,] 1.204575e-10 2.476476e-10
## [12,] 2.555840e-12 3.117078e-12
## [13,] 1.528458e-03 4.146544e-03
## [14,] 1.713962e-09 2.436972e-09
## [15,] 5.087613e-11 6.788713e-11
## [16,] 1.242243e-08 9.738947e-08
## [17,] 1.571040e-03 3.846151e-03
## [18,] 1.578818e-03 3.960895e-03
## [19,] 1.364217e-09 2.120757e-09
## [20,] 5.353543e-13 5.299555e-13
## [21,] 1.347229e-03 4.855743e-03
## [22,] 1.460130e-03 5.174144e-03
## [23,] 4.716759e-09 1.095453e-08
## [24,] 4.646077e-03 1.310535e-02
## [25,] 5.638300e-14 5.201656e-14
## [26,] 1.745265e-10 3.486057e-10
## [27,] 2.432043e-11 2.540352e-11
## [28,] 8.611701e-03 2.271148e-02

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## [29,] 9.544558e-11 4.076790e-11
## [30,] 4.068255e-12 5.006938e-12
## [31,] 3.491871e-14 1.597640e-14
## [32,] 3.720019e-14 2.437631e-14
## [33,] 1.723071e-03 3.113642e-03
## [34,] 5.316072e-05 2.180342e-04
## [35,] 4.034015e-13 2.861618e-13
## [36,] 1.686079e-03 2.872716e-03
## [37,] 3.263791e-13 2.599450e-13
## [38,] 7.539833e-14 3.177187e-14
## [39,] 8.551385e-14 3.721607e-14
## [40,] 1.000273e-08 8.143581e-08
## [41,] 7.399454e-10 1.074215e-09
## [42,] 1.167910e-13 7.448324e-14
## [43,] 9.303463e-04 3.805015e-03
## [44,] 7.589190e-04 3.195312e-03
## [45,] 9.458825e-11 9.113011e-11
## [46,] 7.479196e-04 2.941165e-03
## [47,] 1.146430e-13 7.230455e-14
## [48,] 3.548822e-09 8.635402e-09
## [49,] 1.158072e-09 1.773211e-09
## [50,] 1.627842e-03 3.306729e-03
## [51,] 1.664748e-03 3.350894e-03
## [52,] 1.312631e-11 4.602097e-12
## [53,] 3.277156e-11 5.766202e-11
## [54,] 8.048309e-10 1.101117e-08
## [55,] 9.102793e-13 6.807091e-13
## [56,] 1.924472e-14 5.863185e-15
## [57,] 1.524026e-13 1.141687e-13
## [58,] 8.114665e-13 2.390708e-13
## [59,] 1.991319e-07 1.165544e-06
## [60,] 3.303652e-07 1.664748e-06
## [61,] 3.028625e-14 1.309589e-14
## [62,] 1.993271e-14 8.122376e-15
## [63,] 3.302822e-14 1.323697e-14
## [64,] 2.469686e-06 7.344766e-06
## [65,] 6.002457e-11 8.759832e-11
## [66,] 3.143805e-15 1.787880e-15
## [67,] 1.816099e-12 1.031015e-12
## [68,] 1.032839e-10 2.117820e-10
## [69,] 6.625497e-04 1.045226e-03
## [70,] 8.286473e-10 1.335700e-09
## [71,] 7.323649e-10 1.016602e-08
## [72,] 2.979521e-14 1.202265e-14
## [73,] 7.663087e-03 1.965353e-02
## [74,] 7.663087e-03 1.965353e-02
## [75,] 6.607544e-12 2.986440e-12
## [76,] 1.395103e-13 7.255983e-14

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## [77,] 1.846677e-12 2.646524e-12
## [78,] 1.861070e-12 2.486330e-12
## [79,] 1.493016e-11 5.405331e-12
## [80,] 1.088892e-11 4.559187e-12
## [81,] 1.852431e-09 5.694383e-09
## [82,] 5.897177e-14 3.437769e-14
## [83,] 7.412850e-13 4.752501e-13
## [84,] 4.481399e-12 2.084293e-12
## [85,] 5.159466e-11 7.250166e-11
## [86,] 1.104670e-10 2.161522e-10
## [87,] 1.339429e-13 1.712172e-13
## [88,] 1.736710e-10 1.652238e-10
##
## $'Upper Unweighted'
##           [,1]      [,2]
## [1,] 9.673636e-09 1.278157e-08
## [2,] 1.651098e-10 7.383562e-11
## [3,] 1.076502e-09 1.089991e-09
## [4,] 1.291968e-03 1.693719e-03
## [5,] 3.137093e-03 6.067432e-03
## [6,] 2.551351e-08 1.062681e-07
## [7,] 3.614986e-08 9.036826e-08
## [8,] 7.824207e-08 2.179916e-07
## [9,] 2.442193e-08 1.151625e-07
## [10,] 5.751298e-08 1.356207e-07
## [11,] 1.834622e-09 3.577704e-09
## [12,] 7.139300e-11 7.925484e-11
## [13,] 2.844752e-03 7.315385e-03
## [14,] 1.827021e-08 2.674236e-08
## [15,] 9.088947e-10 1.170937e-09
## [16,] 9.387116e-08 6.676095e-07
## [17,] 2.927753e-03 6.820631e-03
## [18,] 2.936208e-03 7.006943e-03
## [19,] 1.484868e-08 2.357285e-08
## [20,] 1.953680e-11 1.687668e-11
## [21,] 2.432470e-03 8.327388e-03
## [22,] 2.605789e-03 8.781995e-03
## [23,] 4.076867e-08 9.959854e-08
## [24,] 7.082747e-03 1.936622e-02
## [25,] 2.742530e-12 2.345389e-12
## [26,] 2.513489e-09 4.809059e-09
## [27,] 5.002941e-10 5.134375e-10
## [28,] 1.258086e-02 3.106055e-02
## [29,] 1.769868e-09 7.461222e-10
## [30,] 1.064677e-10 1.209712e-10
## [31,] 1.808751e-12 8.468959e-13
## [32,] 1.939388e-12 1.218671e-12
## [33,] 3.160699e-03 5.615073e-03

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## [34,] 1.662916e-04 7.218809e-04
## [35,] 1.509293e-11 1.006379e-11
## [36,] 3.101365e-03 5.239058e-03
## [37,] 1.307874e-11 9.150744e-12
## [38,] 3.558372e-12 1.525644e-12
## [39,] 3.961024e-12 1.750970e-12
## [40,] 7.777807e-08 5.746105e-07
## [41,] 8.475907e-09 1.344696e-08
## [42,] 5.209756e-12 3.188707e-12
## [43,] 1.787242e-03 6.846499e-03
## [44,] 1.524887e-03 5.846183e-03
## [45,] 1.535224e-09 1.513447e-09
## [46,] 1.497646e-03 5.358340e-03
## [47,] 5.116667e-12 3.104750e-12
## [48,] 3.257523e-08 8.129345e-08
## [49,] 1.286878e-08 2.003450e-08
## [50,] 3.021055e-03 5.937087e-03
## [51,] 3.079015e-03 6.002306e-03
## [52,] 3.096157e-10 1.093773e-10
## [53,] 6.156339e-10 1.032272e-09
## [54,] 9.234839e-09 1.107543e-07
## [55,] 3.092315e-11 2.173193e-11
## [56,] 1.100639e-12 3.560603e-13
## [57,] 6.601357e-12 4.583965e-12
## [58,] 3.020125e-11 8.569620e-12
## [59,] 1.143999e-06 5.669851e-06
## [60,] 1.774603e-06 7.710162e-06
## [61,] 1.612049e-12 7.159638e-13
## [62,] 1.142587e-12 4.722173e-13
## [63,] 1.750354e-12 7.132976e-13
## [64,] 1.042796e-05 2.781234e-05
## [65,] 1.046394e-09 1.459294e-09
## [66,] 2.665288e-13 1.340695e-13
## [67,] 5.520355e-11 3.141484e-11
## [68,] 1.619303e-09 3.146573e-09
## [69,] 1.431041e-03 2.201236e-03
## [70,] 9.472012e-09 1.536838e-08
## [71,] 8.576336e-09 1.042827e-07
## [72,] 1.580141e-12 6.489879e-13
## [73,] 1.103951e-02 2.721827e-02
## [74,] 1.103951e-02 2.721827e-02
## [75,] 1.732303e-10 7.723770e-11
## [76,] 6.527838e-12 3.045050e-12
## [77,] 5.245516e-11 6.717321e-11
## [78,] 5.232135e-11 6.367038e-11
## [79,] 3.475377e-10 1.257966e-10
## [80,] 2.689030e-10 1.096150e-10
## [81,] 1.934234e-08 5.654731e-08

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## [82,] 2.776237e-12 1.616765e-12
## [83,] 2.550197e-11 1.599833e-11
## [84,] 1.213294e-10 5.723556e-11
## [85,] 9.196691e-10 1.246810e-09
## [86,] 1.713664e-09 3.166086e-09
## [87,] 5.829292e-12 6.643630e-12
## [88,] 2.548635e-09 2.545580e-09
##
## $'Median Weighted'
##           [,1]           [,2]
## [1,] 1.671648e-13 1.769159e-13
## [2,] 2.295585e-14 7.906310e-15
## [3,] 1.178495e-12 9.472774e-13
## [4,] 2.682991e-05 3.265985e-05
## [5,] 2.193052e-06 4.141721e-06
## [6,] 1.056806e-12 3.528766e-12
## [7,] 1.149759e-10 2.237476e-10
## [8,] 1.328718e-09 2.962324e-09
## [9,] 6.131170e-10 2.343297e-09
## [10,] 1.465635e-11 2.741225e-11
## [11,] 1.235459e-12 1.878465e-12
## [12,] 5.786748e-13 5.202705e-13
## [13,] 1.341911e-05 3.425299e-05
## [14,] 7.469325e-11 8.752977e-11
## [15,] 9.645864e-13 9.830712e-13
## [16,] 2.821678e-12 1.719842e-11
## [17,] 1.106654e-04 2.553196e-04
## [18,] 2.139288e-05 5.057646e-05
## [19,] 8.043644e-12 1.015084e-11
## [20,] 2.760375e-15 1.980313e-15
## [21,] 4.032901e-06 1.365606e-05
## [22,] 5.363076e-07 1.788721e-06
## [23,] 3.206040e-10 6.135180e-10
## [24,] 9.480412e-06 2.568281e-05
## [25,] 5.270049e-16 3.219183e-16
## [26,] 3.129149e-14 4.671463e-14
## [27,] 2.794787e-14 2.315311e-14
## [28,] 5.446005e-05 1.360152e-04
## [29,] 1.197477e-11 4.046271e-12
## [30,] 1.523837e-13 1.399267e-13
## [31,] 2.010314e-17 6.847659e-18
## [32,] 9.218838e-17 4.155938e-17
## [33,] 5.628179e-06 9.684877e-06
## [34,] 4.857817e-07 1.928753e-06
## [35,] 2.270822e-14 1.118267e-14
## [36,] 6.747066e-06 1.097637e-05
## [37,] 6.778961e-14 3.953342e-14
## [38,] 2.692522e-16 8.618912e-17

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## [39,] 1.167260e-17 3.851013e-18
## [40,] 2.843473e-11 1.794064e-10
## [41,] 6.481942e-12 7.739776e-12
## [42,] 5.462196e-17 2.488271e-17
## [43,] 9.869451e-06 3.753362e-05
## [44,] 5.794203e-06 2.218981e-05
## [45,] 7.093784e-12 5.548394e-12
## [46,] 8.583904e-07 3.075059e-06
## [47,] 5.132359e-16 2.317418e-16
## [48,] 7.246734e-12 1.396280e-11
## [49,] 6.705514e-12 8.313332e-12
## [50,] 3.744060e-08 7.187669e-08
## [51,] 3.763906e-06 7.166039e-06
## [52,] 1.623889e-13 4.518168e-14
## [53,] 3.113994e-13 4.063650e-13
## [54,] 5.769913e-12 5.769441e-11
## [55,] 5.933957e-14 3.111616e-14
## [56,] 4.277749e-17 1.025311e-17
## [57,] 1.613733e-15 8.367924e-16
## [58,] 3.458812e-15 8.070530e-16
## [59,] 1.291086e-10 5.941476e-10
## [60,] 1.026870e-09 4.138920e-09
## [61,] 3.797959e-17 1.229834e-17
## [62,] 1.370727e-16 4.154550e-17
## [63,] 9.034170e-17 2.732631e-17
## [64,] 2.385612e-07 5.956938e-07
## [65,] 2.415454e-12 2.664104e-12
## [66,] 3.667718e-17 1.472901e-17
## [67,] 1.465866e-15 6.294788e-16
## [68,] 1.900926e-13 2.866855e-13
## [69,] 8.884451e-07 1.294446e-06
## [70,] 4.042081e-13 5.205552e-13
## [71,] 6.920779e-13 7.006432e-12
## [72,] 1.168471e-18 3.519986e-19
## [73,] 1.913673e-08 4.712154e-08
## [74,] 2.952798e-04 7.270854e-04
## [75,] 7.438056e-15 2.558906e-15
## [76,] 1.410486e-15 5.471801e-16
## [77,] 5.509872e-14 5.378091e-14
## [78,] 2.167937e-15 2.038034e-15
## [79,] 2.013041e-13 5.763583e-14
## [80,] 4.384192e-14 1.402495e-14
## [81,] 9.274749e-13 2.131630e-12
## [82,] 3.801668e-17 1.598591e-17
## [83,] 1.532066e-15 7.217867e-16
## [84,] 1.659690e-14 5.977206e-15
## [85,] 2.702880e-11 2.895171e-11
## [86,] 5.690816e-13 8.249528e-13

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## [87,] 2.220813e-16 1.833472e-16
## [88,] 3.482583e-12 2.748650e-12
##
## $'Lower Weighted'
##           [,1]           [,2]
## [1,] 3.192838e-14 4.116763e-14
## [2,] 2.244983e-15 1.010514e-15
## [3,] 1.645964e-13 1.656493e-13
## [4,] 1.719561e-05 2.230743e-05
## [5,] 1.563748e-06 3.119653e-06
## [6,] 2.415909e-13 1.001542e-12
## [7,] 2.616585e-11 6.265873e-11
## [8,] 3.435039e-10 9.112977e-10
## [9,] 1.393932e-10 6.680898e-10
## [10,] 3.647359e-12 8.031360e-12
## [11,] 1.881426e-13 3.868008e-13
## [12,] 5.383154e-14 6.565243e-14
## [13,] 9.574163e-06 2.597368e-05
## [14,] 1.527136e-11 2.171337e-11
## [15,] 1.304655e-13 1.740880e-13
## [16,] 7.355233e-13 5.766361e-12
## [17,] 7.892600e-05 1.932232e-04
## [18,] 1.527603e-05 3.832410e-05
## [19,] 1.607131e-12 2.498381e-12
## [20,] 2.054902e-16 2.034179e-16
## [21,] 2.915676e-06 1.050881e-05
## [22,] 3.905302e-07 1.383890e-06
## [23,] 7.474002e-11 1.735815e-10
## [24,] 7.512828e-06 2.119170e-05
## [25,] 2.831882e-17 2.612574e-17
## [26,] 4.988629e-15 9.964473e-15
## [27,] 3.426196e-15 3.578779e-15
## [28,] 4.423759e-05 1.166670e-04
## [29,] 1.598723e-12 6.828666e-13
## [30,] 1.503414e-14 1.850302e-14
## [31,] 1.069403e-18 4.892853e-19
## [32,] 4.709000e-18 3.085685e-18
## [33,] 4.017549e-06 7.259834e-06
## [34,] 2.477928e-07 1.016301e-06
## [35,] 1.592890e-15 1.129952e-15
## [36,] 4.802242e-06 8.181987e-06
## [37,] 4.673240e-15 3.722007e-15
## [38,] 1.585590e-17 6.681467e-18
## [39,] 6.983744e-19 3.039362e-19
## [40,] 7.250012e-12 5.902495e-11
## [41,] 1.201043e-12 1.743613e-12
## [42,] 3.338329e-18 2.129014e-18
## [43,] 6.912236e-06 2.827029e-05

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## [44,] 3.938790e-06 1.658367e-05
## [45,] 1.044784e-12 1.006586e-12
## [46,] 5.863785e-07 2.305911e-06
## [47,] 3.136493e-17 1.978164e-17
## [48,] 1.586793e-12 3.861167e-12
## [49,] 1.321720e-12 2.023784e-12
## [50,] 2.658852e-08 5.401078e-08
## [51,] 2.678345e-06 5.391117e-06
## [52,] 1.750039e-14 6.135653e-15
## [53,] 4.027963e-14 7.087257e-14
## [54,] 1.089457e-12 1.490524e-11
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