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

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

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Abstract

We present 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 independently 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. Common guillemots (*Uria aalge*) 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 adult telemetry data were collated for similar spatial and temporal extents. The locations and sizes of guillemot 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 the importance of benthic variables (bathymetry, sediment) but also surface cues (thermal fronts and energy anomalies). Strong differences between juveniles and adults were inferred in terms of their attachment to their colonies, but not so much in terms of their attachment to regions closer to the coast. We present results on the spatial distribution of usage by different colonies and ages and the output of an illustrative calculation of apportionment for an exemplar off-shore region, along with a software tool that can use parameterisations from our modelling to perform the same apportioning calculation for any proposed area of potential offshore development.



Figure 1: Common guillemots (*Uria aalge*). By Henrik Thorburn - Own work

Contents

1	Overview	4
1.1	Study objectives	4
1.2	Relevant facts about guillemot natural history	5
2	Environmental covariates	7
2.1	Derived covariates	7
2.2	Survey transects	7
2.3	Tracking data	7
3	Inference	11
3.1	Model selection on Joint model	11
3.2	Comparison with single-datatype models	13
4	Spatial prediction	14
4.1	Usage maps	14
4.2	Apportioning impact	14
5	Appendix I: JAGS implemetation of joint model for telemetry & survey data	18

6	Appendix II: Usage of R functions for the generation of apportioning predictions for a given marine boundary	23
	References	34

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 guillemots.
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 (i.e., telemetry-only and survey-only) with the results of the best joint model selected under Objective 2. A graphical view of selected colonies and both age stages is produced under Objective 3, using the best joint model only. In the case of guillemots, telemetry data were only available for adults. So, the modelling task is more challenging compared to cases (such as the northern gannet) 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 the purposes of impact assessment, 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 guillemot natural history

The guillemot (Figure 1) is a large auk that breeds on suitable cliff habitat on islands and mainland coasts around the UK. Suitable sites occur where nest sites are safe from terrestrial mammalian predators. Their diet is dominated by sandeels, sprats and juvenile herring, which they catch by diving from the water surface. Guillemots can dive to relatively deep water and are able to dig sandeels out of the substrate in the winter. Guillemots in Wales are less dependent on sandeels than birds breeding on the North Sea coast, and consequently have higher productivity (Riordan and Birkhead 2018). (Woodward et al. 2019) reported summary statistics for the foraging range of tracked guillemot from their breeding colonies across multiple studies. The mean foraging range ($\pm$ SD) was 23.9km ($\pm$ 21.1). However, the mean of the maximum foraging ranges across the studies was 55.5 km ($\pm$ 39.7), showing the birds can, and do, forage further than the mean value. Note that these foraging range metrics exclude data from Fair Isle, which were thought to be unusually high due to low prey availability in the years that birds were tracked.

In total, the analysis examined 73 colonies whose size ranged from 7 to 75493 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	133
Bigton to Maywick - Shetland	-1.33	59.99	68
Birsay - Brough of Birsay	-3.34	59.14	1429
Birsay Cliffs - Point of Buckquoy to Loop of Cruie	-3.31	59.14	78
Boddam to Collieston	-1.79	57.36	19667
Bressay	-1.06	60.1	142
Bressay - Shetland	-1.07	60.12	227
Burn of Daff	-2.14	57.04	25
Caithness - Dunbeath Bay	-3.42	58.23	13
Caithness - Duncansby Stacks SSSI/SPA	-3.04	58.6	24197
Caithness - North Eastern Cliffs SSSI/SPA	-3.08	58.24	53555
Caithness - South Eastern Cliffs SSSI	-3.43	58.14	52964
Caithness - Wick Bay to Freshwick Bay	-3.07	58.47	117
Calf of Eday - Orkney	-2.74	59.23	1714
Cape Wrath - Kyle of Durness	-4.87	58.6	27328
Catterline to Inverbervie	-2.22	56.85	1933
Copinsay	-2.66	58.89	13429
Costa Head - Orkney	-3.2	59.14	6452
Crawton - Stonehaven (Fowlsheugh)	-2.2	56.91	44951
Crawton to Catterline	-2.2	56.91	1342
Deerness	-2.71	58.93	1348
Droman to Geodha Ruadh na Fola	-5.11	58.48	1032
Duncansby Head to Smoo (includes Stroma) - Highland	-3.12	58.56	23788

Dunglass to Fast Castle	-2.27	55.92	407
East Yell	-1.01	60.5	139
Eday - Orkney	-2.75	59.22	33
Eyemouth to Burnmouth	-2.07	55.84	598
Fair Isle	-1.63	59.53	26302
Faraid Head/ Balnakeil	-4.77	58.59	1340
Fetlar - Shetland	-0.86	60.56	115
Findon Ness - Hare Ness	-2.09	57.07	282
Flotta & Calf of Flotta	-3.1	58.82	20
Forth Islands - Bass Rock to Haystack	-3.14	56.03	2799
Foula	-2.07	60.12	27762
Girdle Ness to Hare Ness	-2.06	57.11	50
Handa Island	-5.18	58.38	75493
Heylor to Stenness	-1.63	60.48	3103
Heylor to Stenness - Shetland	-1.6	60.47	225
Hoy and Southwalls	-3.39	58.78	14591
Isle of May	-2.56	56.19	18829
Kettlaness - Shetland	-1.37	60.05	17
Lunan Bay to Arbroath	-2.48	56.58	671
Marwick Head	-3.34	59.1	22585
Mousa - Shetland	-1.16	60	13
Muckle Skerry (Coastal)	-2.92	58.69	293
Mull Head	-2.71	58.97	1323
Newtonhill - Hall Bay	-2.15	57.02	41
No Ness to Levenwick and Boddam to Virkie	-1.21	59.9	2442
North Hill - Papa Westray	-2.87	59.37	1147
North Sutor to Shandwick	-3.97	57.69	1303
Noss NNR	-1.02	60.15	30671
Papa Stour - Shetland	-1.72	60.33	736
Point of Buckquoy to Latha Skerry to Marwick Head	-3.34	59.99	650
Ramna Stacks - Shetland	-1.3	60.65	1363
Ronas Hill to Uyea - Shetland	-1.42	60.62	232
Ronas Voe to the Ness - Shetland	-1.48	60.56	27
Roseheartly to Bay of Cullen	-2.41	57.67	32130
Rousay Coast	-3.07	59.16	4158
Sands of Forvie NNR (Cliff Nesters)	-1.94	57.33	7
Shapinsay (Coastal)	-2.82	59.02	18
South West Unst - Shetland	-0.97	60.7	28
St Abbs to Fast Castle	-2.13	55.9	28901
St. Ninian's Isle - Shetland	-1.35	59.97	28
Stoer Headland	-5.37	58.24	209
Sule Skerry	-4.4	59.08	6922
Sule Stack	-4.5	59.02	712
Sumburgh Head - Shetland	-1.28	59.86	10269

Sumburgh to Peerie Voe of Spiggie - Shetland	-1.36	59.89	698
Swona (Coastline)	-3.05	58.74	79
Vaila - Shetland	-1.59	60.19	250
West Westray Cliffs	-3.07	59.29	36660
Westray	-2.86	59.25	304
Yesnaby to Marwick (West Mainland)	-3.35	59.02	3953

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.

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).

2.2 Survey transects

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 guillemots 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 96 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

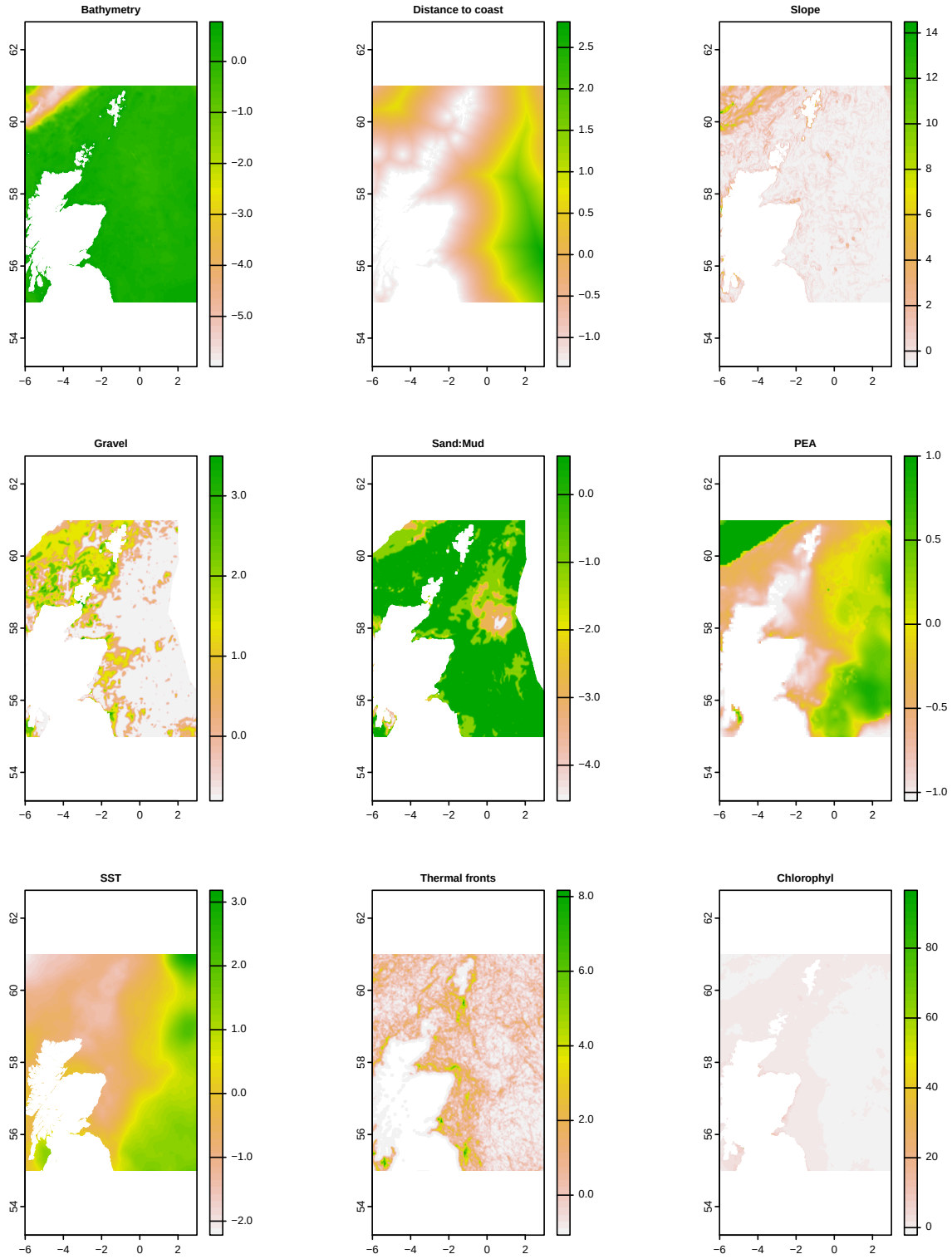


Figure 2: The candidate covariate layers considered in this analysis. All covariates are standardised to mean zero and $sd=1$.

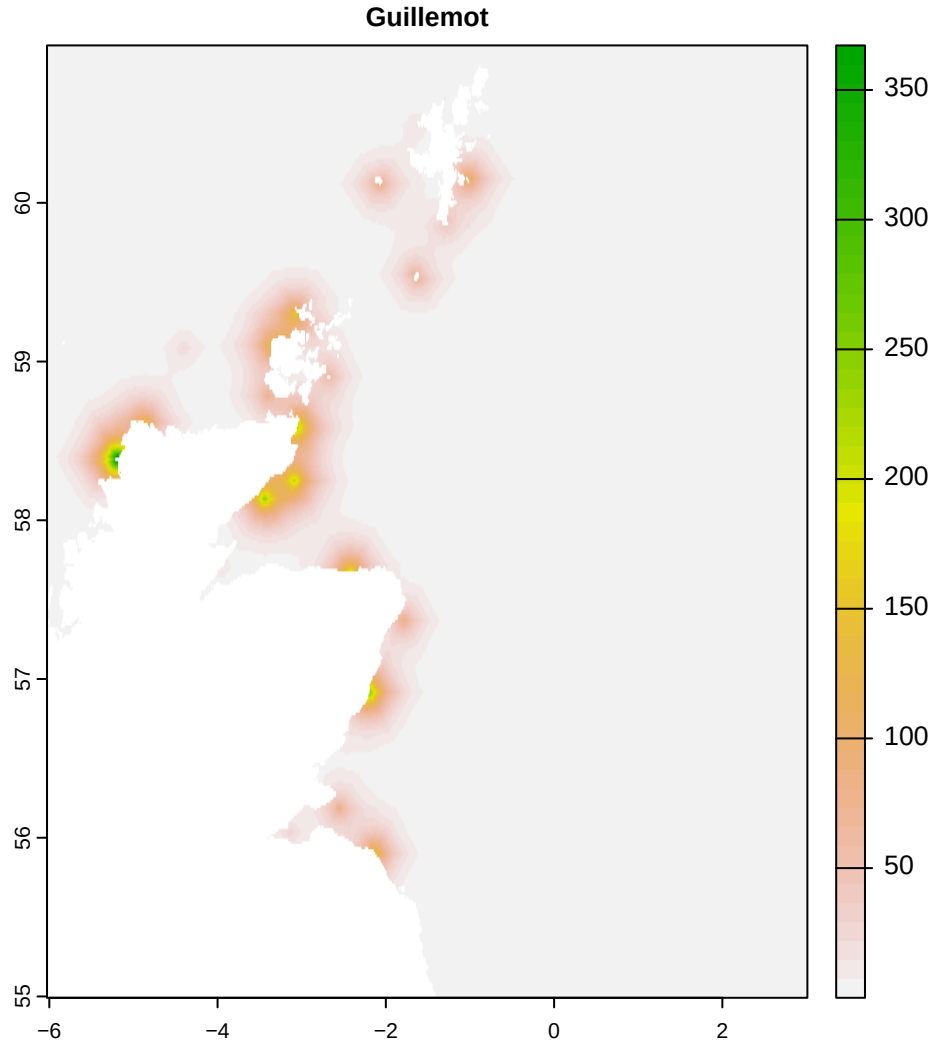


Figure 3: A visualisation of a possible accessibility surface for the guillemot metapopulation in the east coast of Scotland. Here, we used a negative exponential distance function for each colony and weighted the accessibility of each colony by its relative population size. The rate of decay with distance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

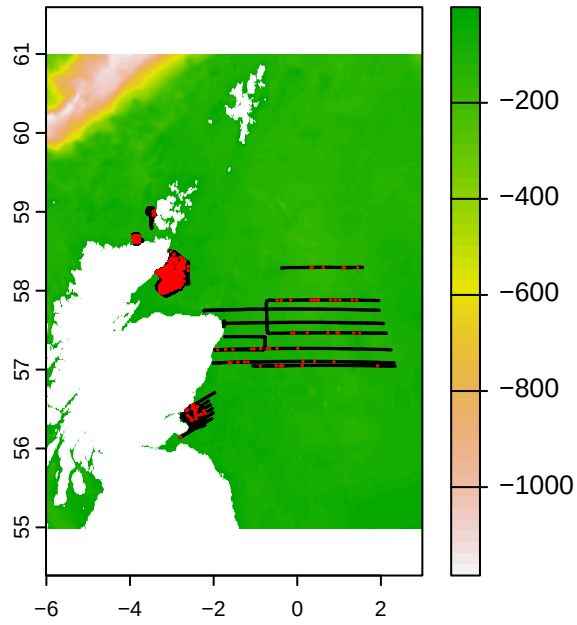


Figure 4: The survey transects considered in the analysis (black lines) and the detections of individuals from the study species (red dots).

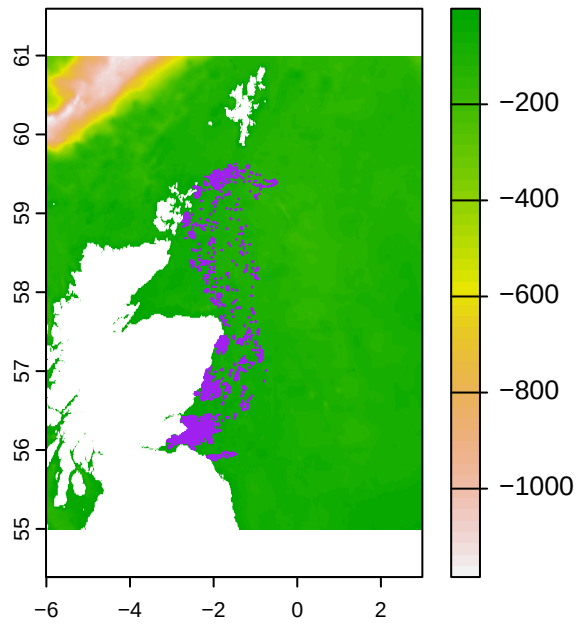


Figure 5: The telemetry data from adult individuals.

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.

Table 2: Telemetry locations by colony and breeding stage

Colony code	Adults
BNCC	10273
FAI	24937
FOW	14292
IOM	71846
ORK:COP	7972
SAB	3016

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 40 models were examined (Table 3) and the best model was 6.412568.

The selected model indicated that adults have a strong tie to their colony, unlike juveniles that appear to be considerably wider-roaming. The model also indicated an avoidance of very distant offshore areas for both adults and juveniles, but, within the limits of this, a preference for relatively deeper areas. In terms of sediment, there was avoidance of gravel and mud. Surface cues

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
39	6.412568			*	*	*	*	*	*		*	0
33	5.41256	*	*		*	*	*				*	150
35	5.41258	*	*		*	*			*		*	172
32	5.41253	*	*	*	*	*					*	214
27	4.4125	*	*		*	*					*	244
28	4.4126	*	*		*		*				*	246
36	5.41259	*	*		*	*				*	*	248
29	4.4127	*	*		*			*			*	253
31	4.4129	*	*		*					*	*	292
26	4.4123	*	*	*	*						*	321
19	3.412	*	*		*						*	342
24	3.418	*			*				*		*	374
22	3.416	*			*		*				*	428
23	3.417	*			*			*			*	428
21	3.415	*			*	*					*	472
25	3.419	*			*					*	*	502
11	2.41	*			*						*	556
12	2.42		*		*						*	667
17	2.48				*				*		*	1043
18	2.49				*					*	*	1055
14	2.45				*	*					*	1064
16	2.47				*			*			*	1138
15	2.46				*		*				*	1144
5	1.4				*						*	1230
10	1.9									*	*	2462
9	1.8								*		*	2525
6	1.5					*					*	2635
7	1.6						*				*	2778
1	0.0										*	NA
2	1.1	*									*	NA
3	1.2		*								*	NA
4	1.3			*							*	NA
8	1.7							*			*	NA
13	2.43			*	*						*	NA
20	3.413	*		*	*						*	NA
30	4.4128	*	*		*				*		*	NA
34	5.41257	*	*		*	*		*			*	NA
37	6.412563	*		*	*	*	*		*		*	NA
38	6.412567		*	*	*	*	*		*		*	NA
40	6.412569			*	*	*	*		*	*	*	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	-14.289895	-14.166418	-14.044829
Intercept Adults	-15.211158	-14.755517	-14.369138
Bathymetry Juveniles	0.516738	0.832362	1.190883
Bathymetry Adults	9.776342	10.701501	11.550108
Distance from Coast Juveniles	-0.182497	-0.124935	-0.07198
Distance from Coast Adults	-1.136048	-0.839009	-0.538542
Slope Juveniles	0	0	0
Slope Adults	0	0	0
Gravel Juveniles	-0.087517	-0.057896	-0.030597
Gravel Adults	-2.06239	-1.822509	-1.607567
Mud:Sand Juveniles	0.470591	0.591331	0.722161
Mud:Sand Adults	0.251014	0.384507	0.535167
PE Anomaly Juveniles	0.573348	0.699852	0.837947
PE Anomaly Adults	1.2429	1.774784	2.153379
SST Juveniles	0	0	0
SST Adults	0	0	0
Therm Fronts Juveniles	0.040902	0.063891	0.088557
Therm Fronts Adults	0.119989	0.166713	0.21184
Chlorophyl Juveniles	0	0	0
Chlorophyl Adults	0	0	0
Dist to colony Juveniles	0	3.9e-05	0.000166
Dist to colony Adults	0.16782	0.186906	0.206118

such as energy anomalies and thermal frontds appear to be attracting features. There was no evidence that other surface characteristics such as temperature and chlorophyl productivity shaped the distribution of guillemots. showed avoidance of gravel and mud (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 (6.412568). 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. There was no evidence that the joint model agreed more with the telemetry model or the survey model. Indeed, there were pronounced differences in most parameters. Notably, neither the survey nor the telemetry model converged.

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.

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.

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	1.4	(1.26 - 1.54)	0	(0 - 0)
Bigton to Maywick - Shetland	1.4	(1.26 - 1.53)	0	(0 - 0)
Birsay - Brough of Birsay	1.4	(1.26 - 1.54)	0	(0 - 0)
Birsay Cliffs - Point of Bu...	1.4	(1.26 - 1.54)	0	(0 - 0)
Boddam to Collieston	1.4	(1.27 - 1.55)	0.08	(0.04 - 0.18)
Bressay	1.39	(1.26 - 1.53)	0	(0 - 0)
Bressay - Shetland	1.39	(1.26 - 1.53)	0	(0 - 0)
Burn of Daff	1.41	(1.27 - 1.56)	3.22	(2.15 - 4.87)
Caithness - Dunbeath Bay	1.4	(1.26 - 1.54)	0	(0 - 0)
Caithness - Duncansby Stack...	1.4	(1.26 - 1.54)	0	(0 - 0)
Caithness - North Eastern C...	1.4	(1.26 - 1.54)	0	(0 - 0)
Caithness - South Eastern C...	1.4	(1.26 - 1.54)	0	(0 - 0)
Caithness - Wick Bay to Fre...	1.4	(1.26 - 1.54)	0	(0 - 0)
Calf of Eday - Orkney	1.4	(1.26 - 1.54)	0	(0 - 0)
Cape Wrath - Kyle of Durness	1.4	(1.26 - 1.54)	0	(0 - 0)
Catterline to Inverbervie	1.41	(1.27 - 1.56)	12.95	(10.79 - 15.75)

Copinsay	1.4	(1.26 - 1.54)	0	(0 - 0)
Costa Head - Orkney	1.4	(1.26 - 1.54)	0	(0 - 0)
Crawton - Stonehaven (Fowls...	1.41	(1.27 - 1.56)	9.34	(7.44 - 11.88)
Crawton to Catterline	1.41	(1.27 - 1.56)	10.3	(8.33 - 12.91)
Deerness	1.4	(1.26 - 1.54)	0	(0 - 0)
Droman to Geodha Ruadh na Fola	1.4	(1.26 - 1.54)	0	(0 - 0)
Duncansby Head to Smoo (inc...	1.4	(1.26 - 1.54)	0	(0 - 0)
Dunglass to Fast Castle	1.41	(1.27 - 1.56)	68.65	(65.09 - 70.76)
East Yell	1.39	(1.26 - 1.53)	0	(0 - 0)
Eday - Orkney	1.4	(1.26 - 1.54)	0	(0 - 0)
Eyemouth to Burnmouth	1.41	(1.27 - 1.56)	33.02	(30.09 - 35.75)
Fair Isle	1.4	(1.26 - 1.54)	0	(0 - 0)
Faraid Head/ Balnakeil	1.4	(1.26 - 1.54)	0	(0 - 0)
Fetlar - Shetland	1.39	(1.26 - 1.53)	0	(0 - 0)
Findon Ness - Hare Ness	1.41	(1.27 - 1.56)	1.85	(1.16 - 2.97)
Flotta & Calf of Flotta	1.4	(1.26 - 1.54)	0	(0 - 0)
Forth Islands - Bass Rock t...	1.41	(1.27 - 1.56)	4.6	(2.98 - 7.34)
Foula	1.4	(1.26 - 1.53)	0	(0 - 0)
Girdle Ness to Hare Ness	1.41	(1.27 - 1.56)	1.25	(0.76 - 2.09)
Handa Island	1.4	(1.26 - 1.54)	0	(0 - 0)
Heylor to Stenness	1.39	(1.26 - 1.53)	0	(0 - 0)
Heylor to Stenness - Shetland	1.39	(1.26 - 1.53)	0	(0 - 0)
Hoy and Southwalls	1.4	(1.26 - 1.54)	0	(0 - 0)
Isle of May	1.41	(1.27 - 1.56)	55.69	(51.94 - 58.29)
Kettlaness - Shetland	1.4	(1.26 - 1.53)	0	(0 - 0)
Lunan Bay to Arbroath	1.41	(1.27 - 1.56)	40.04	(38.26 - 41.83)
Marwick Head	1.4	(1.26 - 1.54)	0	(0 - 0)
Mousa - Shetland	1.39	(1.26 - 1.53)	0	(0 - 0)
Muckle Skerry (Coastal)	1.4	(1.26 - 1.54)	0	(0 - 0)
Mull Head	1.4	(1.26 - 1.54)	0	(0 - 0)
Newtonhill - Hall Bay	1.41	(1.27 - 1.56)	3.38	(2.27 - 5.08)
No Ness to Levenwick and Bo...	1.4	(1.26 - 1.53)	0	(0 - 0)
North Hill - Papa Westray	1.4	(1.26 - 1.54)	0	(0 - 0)
North Sutor to Shandwick	1.4	(1.26 - 1.55)	0	(0 - 0)
Noss NNR	1.39	(1.26 - 1.53)	0	(0 - 0)
Papa Stour - Shetland	1.4	(1.26 - 1.53)	0	(0 - 0)
Point of Buckquoy to Latha ...	1.4	(1.26 - 1.54)	0	(0 - 0)
Ramna Stacks - Shetland	1.39	(1.26 - 1.53)	0	(0 - 0)
Ronas Hill to Uyea - Shetland	1.39	(1.26 - 1.53)	0	(0 - 0)
Ronas Voe to the Ness - She...	1.39	(1.26 - 1.53)	0	(0 - 0)
Rosehearty to Bay of Cullen	1.4	(1.26 - 1.55)	0	(0 - 0)
Rousay Coast	1.4	(1.26 - 1.54)	0	(0 - 0)
Sands of Forvie NNR (Cliff ...	1.4	(1.27 - 1.55)	0.13	(0.06 - 0.28)
Shapinsay (Coastal)	1.4	(1.26 - 1.54)	0	(0 - 0)

South West Unst - Shetland	1.39	(1.26 - 1.53)	0	(0 - 0)
St Abbs to Fast Castle	1.41	(1.27 - 1.56)	49.42	(46.85 - 51.36)
St. Ninian's Isle - Shetland	1.4	(1.26 - 1.53)	0	(0 - 0)
Stoer Headland	1.4	(1.26 - 1.54)	0	(0 - 0)
Sule Skerry	1.4	(1.26 - 1.54)	0	(0 - 0)
Sule Stack	1.4	(1.26 - 1.54)	0	(0 - 0)
Sumburgh Head - Shetland	1.4	(1.26 - 1.53)	0	(0 - 0)
Sumburgh to Peerie Voe of S...	1.4	(1.26 - 1.53)	0	(0 - 0)
Swona (Coastline)	1.4	(1.26 - 1.54)	0	(0 - 0)
Vaila - Shetland	1.4	(1.26 - 1.53)	0	(0 - 0)
West Westray Cliffs	1.4	(1.26 - 1.54)	0	(0 - 0)
Westray	1.4	(1.26 - 1.54)	0	(0 - 0)
Yesnaby to Marwick (West Ma...	1.4	(1.26 - 1.54)	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)
Birsay Cliffs - Point of Bu...	0	(0 - 0)	0	(0 - 0)
Boddam to Collieston	0.02	(0.02 - 0.02)	0	(0 - 0)
Bressay	0	(0 - 0)	0	(0 - 0)
Bressay - Shetland	0	(0 - 0)	0	(0 - 0)
Burn of Daff	0	(0 - 0)	0	(0 - 0)
Caithness - Dunbeath Bay	0	(0 - 0)	0	(0 - 0)
Caithness - Duncansby Stack...	0.03	(0.02 - 0.03)	0	(0 - 0)
Caithness - North Eastern C...	0.06	(0.05 - 0.06)	0	(0 - 0)
Caithness - South Eastern C...	0.06	(0.05 - 0.06)	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	0.03	(0.03 - 0.03)	0	(0 - 0)
Catterline to Inverbervie	0	(0 - 0)	0.02	(0.02 - 0.02)
Copinsay	0.01	(0.01 - 0.02)	0	(0 - 0)
Costa Head - Orkney	0.01	(0.01 - 0.01)	0	(0 - 0)
Crawton - Stonehaven (Fowls...	0.05	(0.04 - 0.05)	0.33	(0.26 - 0.42)
Crawton to Catterline	0	(0 - 0)	0.01	(0.01 - 0.01)
Deerness	0	(0 - 0)	0	(0 - 0)
Droman to Geodha Ruadh na Fola	0	(0 - 0)	0	(0 - 0)
Duncansby Head to Smoo (inc...	0.03	(0.02 - 0.03)	0	(0 - 0)

Dunglass to Fast Castle	0	(0 - 0)	0.02	(0.02 - 0.02)
East Yell	0	(0 - 0)	0	(0 - 0)
Eday - Orkney	0	(0 - 0)	0	(0 - 0)
Eyemouth to Burnmouth	0	(0 - 0)	0.02	(0.01 - 0.02)
Fair Isle	0.03	(0.03 - 0.03)	0	(0 - 0)
Faraid Head/ Balnakeil	0	(0 - 0)	0	(0 - 0)
Fetlar - Shetland	0	(0 - 0)	0	(0 - 0)
Findon Ness - Hare Ness	0	(0 - 0)	0	(0 - 0)
Flotta & Calf of Flotta	0	(0 - 0)	0	(0 - 0)
Forth Islands - Bass Rock t...	0	(0 - 0)	0.01	(0.01 - 0.02)
Foula	0.03	(0.03 - 0.03)	0	(0 - 0)
Girdle Ness to Hare Ness	0	(0 - 0)	0	(0 - 0)
Handa Island	0.08	(0.07 - 0.09)	0	(0 - 0)
Heylor to Stenness	0	(0 - 0)	0	(0 - 0)
Heylor to Stenness - Shetland	0	(0 - 0)	0	(0 - 0)
Hoy and Southwalls	0.02	(0.01 - 0.02)	0	(0 - 0)
Isle of May	0.02	(0.02 - 0.02)	0.82	(0.77 - 0.86)
Kettlaness - Shetland	0	(0 - 0)	0	(0 - 0)
Lunan Bay to Arbroath	0	(0 - 0)	0.02	(0.02 - 0.02)
Marwick Head	0.02	(0.02 - 0.03)	0	(0 - 0)
Mousa - Shetland	0	(0 - 0)	0	(0 - 0)
Muckle Skerry (Coastal)	0	(0 - 0)	0	(0 - 0)
Mull Head	0	(0 - 0)	0	(0 - 0)
Newtonhill - Hall Bay	0	(0 - 0)	0	(0 - 0)
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	0.03	(0.03 - 0.04)	0	(0 - 0)
Papa Stour - Shetland	0	(0 - 0)	0	(0 - 0)
Point of Buckquoy to Latha ...	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	0.04	(0.03 - 0.04)	0	(0 - 0)
Rousay Coast	0	(0 - 0.01)	0	(0 - 0)
Sands of Forvie NNR (Cliff ...	0	(0 - 0)	0	(0 - 0)
Shapinsay (Coastal)	0	(0 - 0)	0	(0 - 0)
South West Unst - Shetland	0	(0 - 0)	0	(0 - 0)
St Abbs to Fast Castle	0.03	(0.03 - 0.04)	1.12	(1.06 - 1.17)
St. Ninian's Isle - Shetland	0	(0 - 0)	0	(0 - 0)
Stoer Headland	0	(0 - 0)	0	(0 - 0)
Sule Skerry	0.01	(0.01 - 0.01)	0	(0 - 0)
Sule Stack	0	(0 - 0)	0	(0 - 0)
Sumburgh Head - Shetland	0.01	(0.01 - 0.01)	0	(0 - 0)

Sumburgh to Peerie Voe of S...	0	(0 - 0)	0	(0 - 0)
Swona (Coastline)	0	(0 - 0)	0	(0 - 0)
Vaila - Shetland	0	(0 - 0)	0	(0 - 0)
West Westray Cliffs	0.04	(0.04 - 0.04)	0	(0 - 0)
Westray	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 0 in (Table 5) indicates that adults from Copinsay spend 0% 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 in (Table 6) indicates that 0% the total usage of the population is attributable to adults from Copinsay 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]+
```

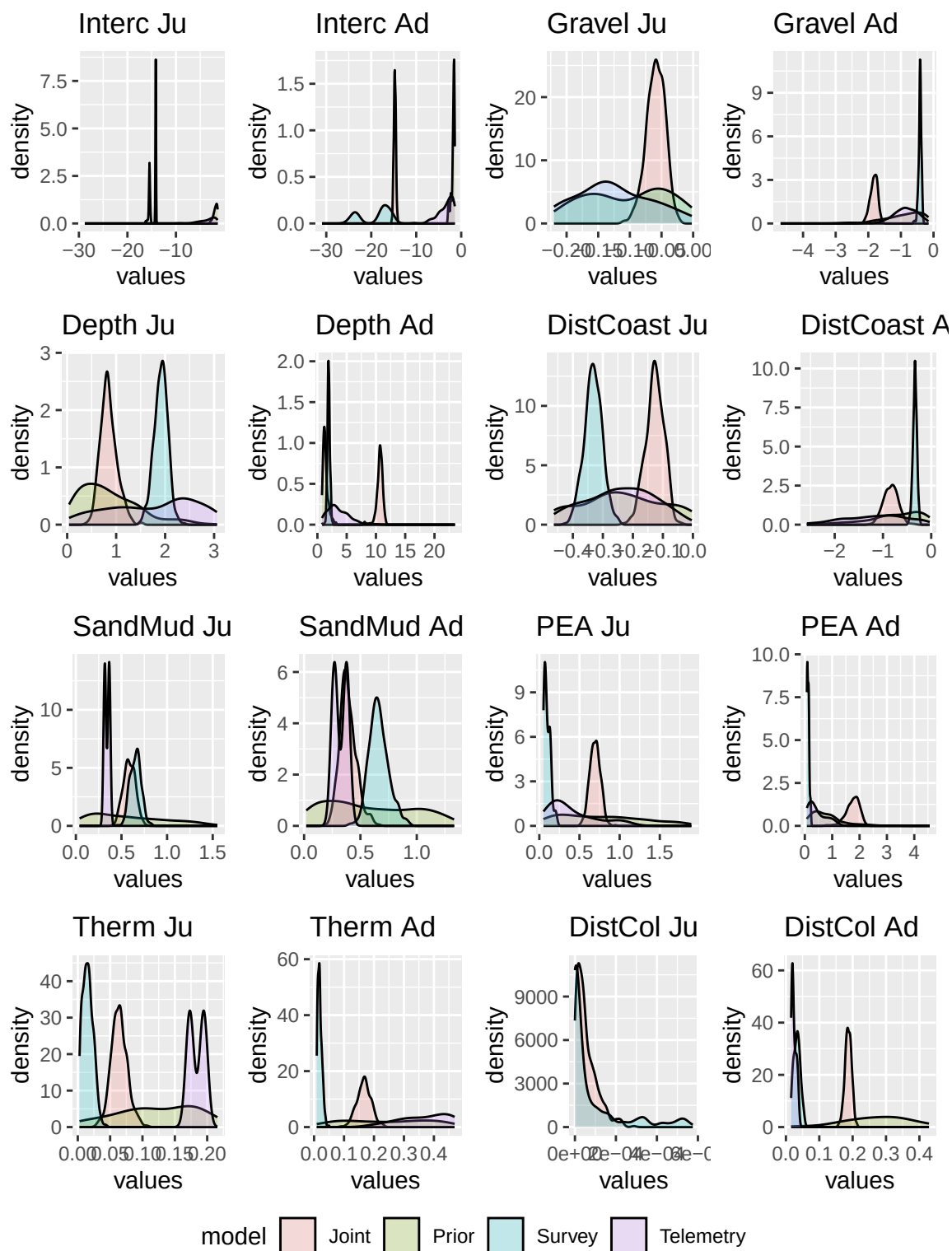


Figure 6: Comparison of the Prior distributions for each parameter, with the posteriors generated from two single-datatype models (Survey and Telemetry) and the Joint model. Posteriors from any non-converging models are also shown for comparison

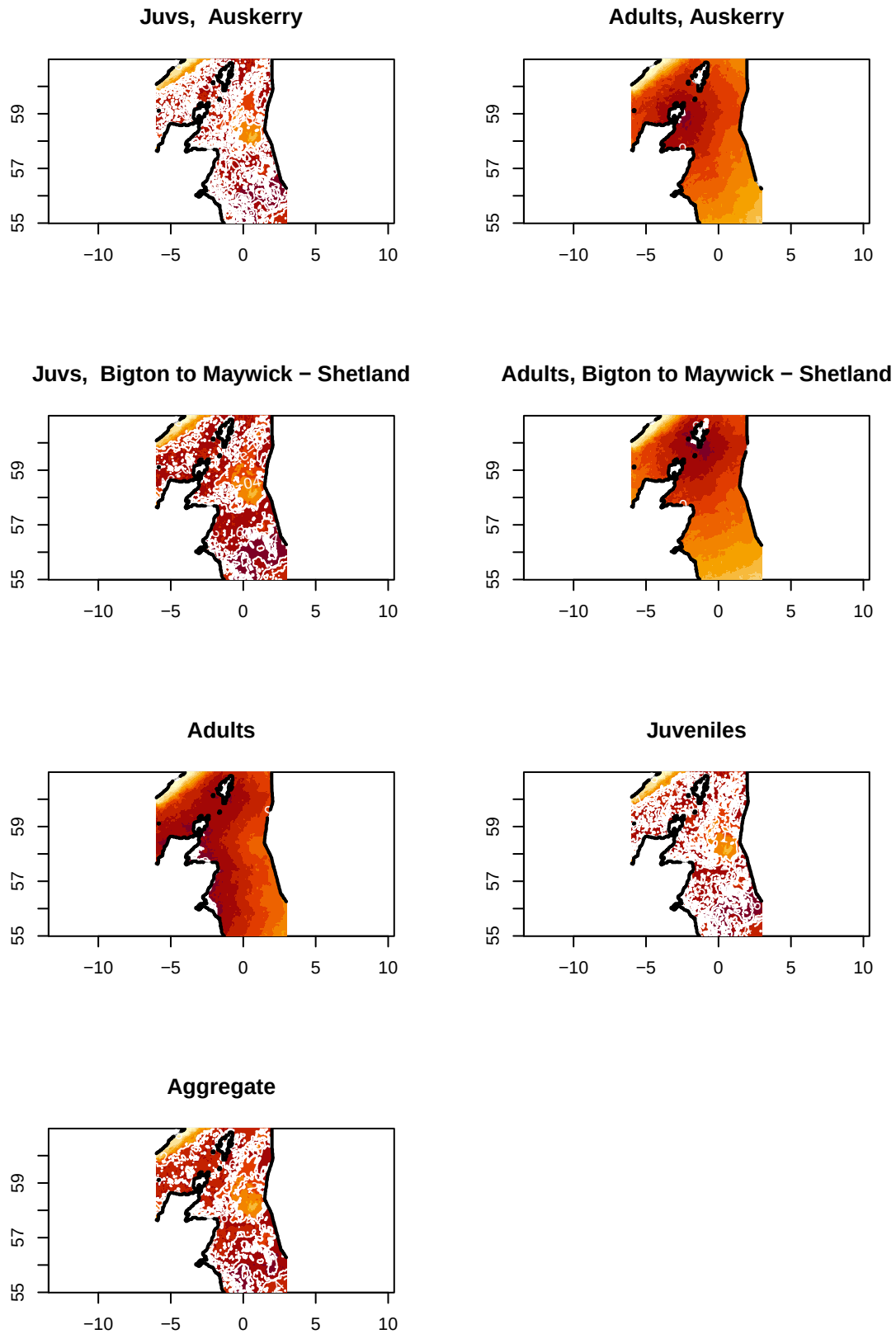


Figure 7: Predictions of spatial usage from the joint model. We show juvenile and adult maps for two colonies, total juvenile and adult usage maps²⁰, and the aggregate map from all colonies and both breeding stages. To facilitate visualisation, colours are in logarithmic scale. White contours indicate the hotspots of expected usage in linear scale. These are especially pronounced for juveniles given their loose attachment to their colonies.

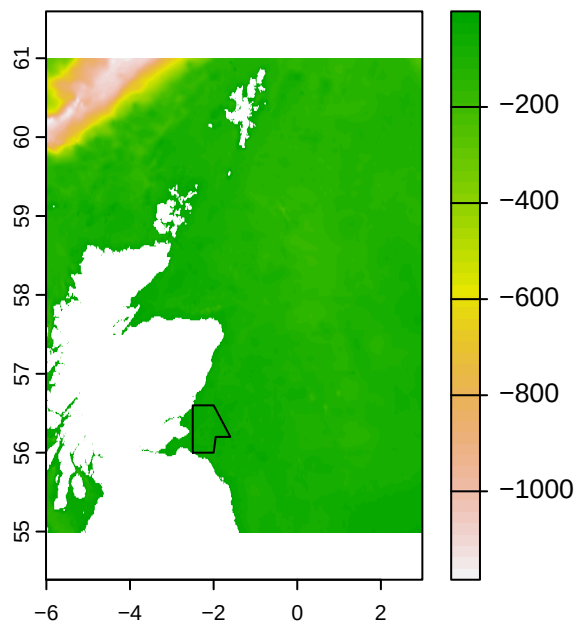


Figure 8: An example of a marine region that might be used to interrogate the model about apportioning usage.

```

        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])
}
}
# labda
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("GuillemotPostData.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,] 0.01401483 9.098836e-12
## [2,] 0.01399244 5.768859e-14
## [3,] 0.01401165 6.939244e-13
## [4,] 0.01401051 6.377213e-13
## [5,] 0.01407892 1.230067e-04
## [6,] 0.01399003 4.701100e-15
## [7,] 0.01398998 4.214324e-15
## [8,] 0.01409532 4.458856e-04
## [9,] 0.01403748 2.415770e-11
## [10,] 0.01402897 1.664220e-10
## [11,] 0.01403771 1.281032e-10
## [12,] 0.01403976 1.908702e-11
## [13,] 0.01403221 1.850216e-10
## [14,] 0.01400942 4.750485e-12
## [15,] 0.01401783 3.209128e-14
## [16,] 0.01410135 5.984663e-04
## [17,] 0.01401950 2.521179e-11
## [18,] 0.01400901 9.735430e-13
```

[19,] 0.01409888 6.201273e-04
[20,] 0.01409953 6.409811e-04
[21,] 0.01401873 2.248687e-11
[22,] 0.01401714 1.641144e-15
[23,] 0.01402971 1.779198e-10
[24,] 0.01412352 1.869648e-03
[25,] 0.01398598 1.688023e-16
[26,] 0.01401050 5.791610e-12
[27,] 0.01412505 3.860170e-03
[28,] 0.01399961 3.557880e-12
[29,] 0.01401816 5.258884e-14
[30,] 0.01398488 8.906471e-17
[31,] 0.01409353 3.832951e-04
[32,] 0.01402576 5.577709e-11
[33,] 0.01411907 3.869765e-05
[34,] 0.01398923 3.599591e-15
[35,] 0.01409211 3.502146e-04
[36,] 0.01401704 4.971646e-16
[37,] 0.01398544 7.773707e-17
[38,] 0.01398567 9.868842e-17
[39,] 0.01402326 1.394458e-11
[40,] 0.01412022 3.461128e-04
[41,] 0.01399193 3.160980e-14
[42,] 0.01410980 1.440148e-04
[43,] 0.01401428 8.948086e-13
[44,] 0.01399155 1.272737e-14
[45,] 0.01402745 1.195151e-10
[46,] 0.01401765 1.823241e-11
[47,] 0.01409536 4.430515e-04
[48,] 0.01399281 4.891638e-14
[49,] 0.01400617 1.953216e-12
[50,] 0.01404942 5.329752e-12
[51,] 0.01398935 2.837274e-15
[52,] 0.01398716 6.370126e-16
[53,] 0.01399513 5.394485e-15
[54,] 0.01398316 3.636077e-17
[55,] 0.01398185 1.876712e-17
[56,] 0.01398337 2.511305e-17
[57,] 0.01405783 1.026995e-07
[58,] 0.01400933 1.357203e-12
[59,] 0.01408185 1.034744e-04
[60,] 0.01401604 1.435034e-11
[61,] 0.01398355 5.469484e-17
[62,] 0.01412443 3.028145e-03
[63,] 0.01399250 6.349461e-14
[64,] 0.01401687 9.159597e-17
[65,] 0.01401211 1.906295e-14
[66,] 0.01401301 2.017866e-14

```

## [67,] 0.01399329 8.345665e-14
## [68,] 0.01399310 9.953505e-14
## [69,] 0.01402624 8.111768e-11
## [70,] 0.01398956 5.094724e-15
## [71,] 0.01400850 1.800563e-12
## [72,] 0.01400998 4.512799e-12
## [73,] 0.01401627 1.329633e-12
##
## $'Lower Unweighted'
##           [,1]           [,2]
## [1,] 0.01327534 3.164206e-13
## [2,] 0.01324686 5.354775e-16
## [3,] 0.01327114 1.228855e-14
## [4,] 0.01326971 1.067380e-14
## [5,] 0.01335585 4.356467e-05
## [6,] 0.01324384 2.440677e-17
## [7,] 0.01324378 2.111113e-17
## [8,] 0.01337628 2.016687e-04
## [9,] 0.01330397 1.393151e-12
## [10,] 0.01329317 1.068093e-11
## [11,] 0.01330425 8.693169e-12
## [12,] 0.01330684 1.065612e-12
## [13,] 0.01329729 1.282224e-11
## [14,] 0.01326843 1.114525e-13
## [15,] 0.01327891 2.247294e-16
## [16,] 0.01338381 2.933459e-04
## [17,] 0.01328124 1.122989e-12
## [18,] 0.01326785 1.476835e-14
## [19,] 0.01338073 3.051912e-04
## [20,] 0.01338154 3.166920e-04
## [21,] 0.01328025 9.740979e-13
## [22,] 0.01327804 7.730997e-18
## [23,] 0.01329412 1.181458e-11
## [24,] 0.01341151 1.128716e-03
## [25,] 0.01323861 3.873843e-19
## [26,] 0.01326980 1.547076e-13
## [27,] 0.01341342 2.489650e-03
## [28,] 0.01325606 6.919933e-14
## [29,] 0.01327935 4.120161e-16
## [30,] 0.01323724 1.880695e-19
## [31,] 0.01337406 1.690922e-04
## [32,] 0.01328909 2.150279e-12
## [33,] 0.01340593 1.396574e-05
## [34,] 0.01324275 1.943004e-17
## [35,] 0.01337228 1.529857e-04
## [36,] 0.01327791 1.966382e-18
## [37,] 0.01323790 1.701157e-19
## [38,] 0.01323819 2.281432e-19

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## [39,] 0.01328587 5.018539e-13
## [40,] 0.01340734 1.733836e-04
## [41,] 0.01324619 2.580856e-16
## [42,] 0.01339434 6.515162e-05
## [43,] 0.01327442 1.767824e-14
## [44,] 0.01324578 7.189323e-17
## [45,] 0.01329124 6.623244e-12
## [46,] 0.01327888 7.560178e-13
## [47,] 0.01337633 2.005437e-04
## [48,] 0.01324737 4.216961e-16
## [49,] 0.01326426 2.665206e-14
## [50,] 0.01331897 2.082020e-13
## [51,] 0.01324298 1.322315e-17
## [52,] 0.01324010 2.525213e-18
## [53,] 0.01325002 1.824064e-17
## [54,] 0.01323498 5.874993e-20
## [55,] 0.01323335 2.724665e-20
## [56,] 0.01323527 3.958976e-20
## [57,] 0.01332953 1.600646e-08
## [58,] 0.01326827 2.130934e-14
## [59,] 0.01335949 3.653399e-05
## [60,] 0.01327682 5.613840e-13
## [61,] 0.01323549 1.081817e-19
## [62,] 0.01341265 1.923338e-03
## [63,] 0.01324694 5.979452e-16
## [64,] 0.01327771 2.708747e-19
## [65,] 0.01327159 1.661892e-16
## [66,] 0.01327273 1.703513e-16
## [67,] 0.01324797 8.229254e-16
## [68,] 0.01324772 1.023646e-15
## [69,] 0.01328971 3.976386e-12
## [70,] 0.01324317 2.906684e-17
## [71,] 0.01326717 2.565154e-14
## [72,] 0.01326910 9.193918e-14
## [73,] 0.01327696 3.051142e-14
##
## $'Upper Unweighted'
##           [,1]           [,2]
## [1,] 0.01470689 5.027379e-11
## [2,] 0.01466460 4.131967e-13
## [3,] 0.01470168 4.552344e-12
## [4,] 0.01469945 4.264463e-12
## [5,] 0.01479171 3.040301e-04
## [6,] 0.01465989 3.704078e-14
## [7,] 0.01465981 3.347006e-14
## [8,] 0.01482978 9.302518e-04
## [9,] 0.01474936 1.314731e-10
## [10,] 0.01473366 9.122104e-10

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## [11,] 0.01474980 6.989886e-10
## [12,] 0.01475359 1.038169e-10
## [13,] 0.01473964 1.004965e-09
## [14,] 0.01469696 3.084197e-11
## [15,] 0.01471342 2.588416e-13
## [16,] 0.01484587 1.154935e-03
## [17,] 0.01471570 1.363750e-10
## [18,] 0.01469645 6.931079e-12
## [19,] 0.01483928 1.212376e-03
## [20,] 0.01484101 1.241820e-03
## [21,] 0.01471431 1.223782e-10
## [22,] 0.01471217 1.281300e-14
## [23,] 0.01473503 9.702766e-10
## [24,] 0.01490429 2.984369e-03
## [25,] 0.01465252 1.395414e-15
## [26,] 0.01469895 3.584159e-11
## [27,] 0.01490805 5.889970e-03
## [28,] 0.01467786 2.395173e-11
## [29,] 0.01471403 4.151419e-13
## [30,] 0.01465039 7.219105e-16
## [31,] 0.01482501 8.198619e-04
## [32,] 0.01472779 3.487478e-10
## [33,] 0.01489289 1.041617e-04
## [34,] 0.01465896 2.620951e-14
## [35,] 0.01482119 7.556863e-04
## [36,] 0.01471197 3.862609e-15
## [37,] 0.01465190 6.091583e-16
## [38,] 0.01465231 7.732714e-16
## [39,] 0.01472325 8.237061e-11
## [40,] 0.01489619 6.576566e-04
## [41,] 0.01466368 2.237863e-13
## [42,] 0.01486846 2.941245e-04
## [43,] 0.01470677 5.676387e-12
## [44,] 0.01466275 1.011665e-13
## [45,] 0.01473086 6.570248e-10
## [46,] 0.01471229 9.935074e-11
## [47,] 0.01482989 9.231182e-04
## [48,] 0.01466514 3.644713e-13
## [49,] 0.01469103 1.504981e-11
## [50,] 0.01477162 2.710343e-11
## [51,] 0.01465863 2.259215e-14
## [52,] 0.01465502 4.765211e-15
## [53,] 0.01467100 3.907246e-14
## [54,] 0.01464752 2.972172e-16
## [55,] 0.01464503 1.515931e-16
## [56,] 0.01464800 2.009734e-16
## [57,] 0.01478119 4.123333e-07
## [58,] 0.01469705 9.755412e-12

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## [59,] 0.01479365 2.573622e-04
## [60,] 0.01470935 7.893384e-11
## [61,] 0.01464809 4.473453e-16
## [62,] 0.01490656 4.653638e-03
## [63,] 0.01466470 4.569478e-13
## [64,] 0.01471166 7.332368e-16
## [65,] 0.01470298 1.380305e-13
## [66,] 0.01470462 1.491945e-13
## [67,] 0.01466606 6.131867e-13
## [68,] 0.01466576 7.255190e-13
## [69,] 0.01472865 4.804041e-10
## [70,] 0.01465938 3.723815e-14
## [71,] 0.01469555 1.391315e-11
## [72,] 0.01469816 3.146422e-11
## [73,] 0.01471045 8.074720e-12
##
## $'Median Weighted'
##           [,1]           [,2]
## [1,] 1.463408e-06 9.500873e-16
## [2,] 7.470133e-07 3.079817e-18
## [3,] 1.571982e-05 7.785211e-16
## [4,] 8.579747e-07 3.905274e-17
## [5,] 2.173870e-04 1.899298e-06
## [6,] 1.559671e-06 5.240996e-19
## [7,] 2.493268e-06 7.510689e-19
## [8,] 2.766565e-07 8.751641e-09
## [9,] 1.432711e-07 2.465614e-16
## [10,] 2.665099e-04 3.161537e-12
## [11,] 5.902314e-04 5.386244e-12
## [12,] 5.838034e-04 7.936790e-13
## [13,] 1.288956e-06 1.699551e-14
## [14,] 1.885198e-05 6.392560e-15
## [15,] 3.007562e-04 6.885270e-16
## [16,] 2.140024e-05 9.082336e-07
## [17,] 1.478094e-04 2.658112e-13
## [18,] 7.096231e-05 4.931460e-15
## [19,] 4.975651e-04 2.188498e-05
## [20,] 1.485536e-05 6.753420e-07
## [21,] 1.483627e-05 2.379824e-14
## [22,] 1.135704e-05 1.329696e-18
## [23,] 2.620189e-04 3.322830e-12
## [24,] 4.512981e-06 5.974206e-07
## [25,] 1.526278e-06 1.842126e-20
## [26,] 3.629890e-07 1.500511e-16
## [27,] 6.631581e-06 1.812315e-06
## [28,] 2.890884e-04 7.346933e-14
## [29,] 1.474762e-05 5.532538e-17
## [30,] 1.262649e-06 8.041361e-21

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## [31,] 3.120291e-06 8.486105e-08
## [32,] 2.202331e-07 8.758140e-16
## [33,] 3.102666e-05 8.503810e-08
## [34,] 3.049093e-04 7.845668e-17
## [35,] 5.531871e-07 1.374771e-08
## [36,] 8.307855e-04 2.946680e-17
## [37,] 3.407093e-05 1.893808e-19
## [38,] 2.470539e-06 1.743311e-20
## [39,] 1.606423e-04 1.597411e-13
## [40,] 2.087348e-04 5.116476e-06
## [41,] 1.867465e-07 4.218875e-19
## [42,] 7.433092e-06 7.586748e-08
## [43,] 2.484945e-04 1.586632e-14
## [44,] 1.428023e-07 1.298997e-19
## [45,] 3.226803e-06 2.749264e-14
## [46,] 1.455999e-05 1.893782e-14
## [47,] 4.537179e-07 1.426146e-08
## [48,] 2.682728e-05 9.378340e-17
## [49,] 1.261272e-05 1.758894e-15
## [50,] 1.437239e-05 5.452271e-15
## [51,] 3.368616e-04 6.832115e-17
## [52,] 8.082271e-06 3.680882e-19
## [53,] 7.141944e-06 2.752893e-18
## [54,] 1.496330e-05 3.890944e-20
## [55,] 2.546704e-06 3.418312e-21
## [56,] 2.964160e-07 5.323403e-22
## [57,] 3.546134e-04 2.590628e-09
## [58,] 4.573282e-05 4.430527e-15
## [59,] 7.738981e-08 5.686658e-10
## [60,] 1.980724e-07 2.027967e-16
## [61,] 3.073982e-07 1.202349e-21
## [62,] 3.204866e-04 6.870931e-05
## [63,] 3.075950e-07 1.395793e-18
## [64,] 2.299977e-06 1.502964e-20
## [65,] 7.614849e-05 1.035971e-16
## [66,] 7.833167e-06 1.127972e-17
## [67,] 1.128168e-04 6.728452e-16
## [68,] 7.668234e-06 5.454532e-17
## [69,] 8.699505e-07 5.031166e-15
## [70,] 2.745808e-06 9.999694e-19
## [71,] 4.031902e-04 5.182350e-14
## [72,] 3.343775e-06 1.077074e-15
## [73,] 4.349962e-05 4.126527e-15
##
## $'Lower Weighted'
##           [,1]           [,2]
## [1,] 1.386192e-06 3.304018e-17
## [2,] 7.072091e-07 2.858750e-20

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## [3,] 1.488903e-05 1.378665e-17
## [4,] 8.126100e-07 6.536415e-19
## [5,] 2.062224e-04 6.726645e-07
## [6,] 1.476483e-06 2.720975e-21
## [7,] 2.360281e-06 3.762386e-21
## [8,] 2.625436e-07 3.958262e-09
## [9,] 1.357846e-07 1.421896e-17
## [10,] 2.525319e-04 2.029068e-13
## [11,] 5.593921e-04 3.655142e-13
## [12,] 5.533270e-04 4.431042e-14
## [13,] 1.221448e-06 1.177811e-15
## [14,] 1.785486e-05 1.499777e-16
## [15,] 2.849026e-04 4.821629e-18
## [16,] 2.031130e-05 4.451823e-07
## [17,] 1.400259e-04 1.183983e-14
## [18,] 6.720802e-05 7.480877e-17
## [19,] 4.722208e-04 1.077054e-05
## [20,] 1.409888e-05 3.336688e-07
## [21,] 1.405472e-05 1.030905e-15
## [22,] 1.075820e-05 6.263848e-21
## [23,] 2.482810e-04 2.206491e-13
## [24,] 4.285467e-06 3.606659e-07
## [25,] 1.444719e-06 4.227492e-23
## [26,] 3.437987e-07 4.008220e-18
## [27,] 6.297481e-06 1.168868e-06
## [28,] 2.737343e-04 1.428949e-15
## [29,] 1.397036e-05 4.334560e-19
## [30,] 1.195147e-06 1.698018e-23
## [31,] 2.960999e-06 3.743679e-08
## [32,] 2.086658e-07 3.376377e-17
## [33,] 2.945954e-05 3.068972e-08
## [34,] 2.886389e-04 4.234970e-19
## [35,] 5.249301e-07 6.005467e-09
## [36,] 7.869776e-04 1.165468e-19
## [37,] 3.224978e-05 4.144311e-22
## [38,] 2.338498e-06 4.030103e-23
## [39,] 1.521953e-04 5.748949e-15
## [40,] 1.981965e-04 2.563076e-06
## [41,] 1.767934e-07 3.444600e-21
## [42,] 7.056185e-06 3.432209e-08
## [43,] 2.353758e-04 3.134622e-16
## [44,] 1.351907e-07 7.337657e-22
## [45,] 3.057449e-06 1.523577e-15
## [46,] 1.379263e-05 7.852679e-16
## [47,] 4.305731e-07 6.455336e-09
## [48,] 2.539810e-05 8.084838e-19
## [49,] 1.194462e-05 2.400049e-17
## [50,] 1.362514e-05 2.129881e-16

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## [51,] 3.188890e-04 3.184115e-19
## [52,] 7.650591e-06 1.459157e-21
## [53,] 6.761698e-06 9.308495e-21
## [54,] 1.416267e-05 6.286794e-23
## [55,] 2.410370e-06 4.962804e-24
## [56,] 2.805580e-07 8.392139e-25
## [57,] 3.362416e-04 4.037683e-10
## [58,] 4.331364e-05 6.956337e-17
## [59,] 7.341995e-08 2.007803e-10
## [60,] 1.876258e-07 7.933385e-18
## [61,] 2.909538e-07 2.378141e-24
## [62,] 3.043361e-04 4.364098e-05
## [63,] 2.912055e-07 1.314454e-20
## [64,] 2.178690e-06 4.444683e-23
## [65,] 7.212415e-05 9.031514e-19
## [66,] 7.419360e-06 9.522511e-20
## [67,] 1.068079e-04 6.634599e-18
## [68,] 7.259766e-06 5.609591e-19
## [69,] 8.242684e-07 2.466276e-16
## [70,] 2.599309e-06 5.705108e-21
## [71,] 3.818535e-04 7.382983e-16
## [72,] 3.166949e-06 2.194322e-17
## [73,] 4.120516e-05 9.469242e-17
##
## $'Upper Weighted'
##           [,1]           [,2]
## [1,] 1.535672e-06 5.249517e-15
## [2,] 7.828978e-07 2.205930e-17
## [3,] 1.649397e-05 5.107323e-15
## [4,] 9.001641e-07 2.611470e-16
## [5,] 2.283928e-04 4.694407e-06
## [6,] 1.634351e-06 4.129472e-18
## [7,] 2.612644e-06 5.964972e-18
## [8,] 2.910722e-07 1.825856e-08
## [9,] 1.505367e-07 1.341857e-15
## [10,] 2.798970e-04 1.732936e-11
## [11,] 6.201719e-04 2.938977e-11
## [12,] 6.134858e-04 4.316927e-12
## [13,] 1.353938e-06 9.231300e-14
## [14,] 1.977718e-05 4.150296e-14
## [15,] 3.156804e-04 5.553514e-15
## [16,] 2.253012e-05 1.752731e-06
## [17,] 1.551495e-04 1.437820e-12
## [18,] 7.444453e-05 3.510922e-14
## [19,] 5.236948e-04 4.278609e-05
## [20,] 1.563659e-05 1.308390e-06
## [21,] 1.557241e-05 1.295150e-13
## [22,] 1.192017e-05 1.038141e-17

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## [23,] 2.751914e-04 1.812089e-11
## [24,] 4.762465e-06 9.536148e-07
## [25,] 1.599018e-06 1.522803e-19
## [26,] 3.808258e-07 9.285969e-16
## [27,] 6.999196e-06 2.765288e-06
## [28,] 3.030941e-04 4.945973e-13
## [29,] 1.547969e-05 4.367444e-16
## [30,] 1.322736e-06 6.517893e-20
## [31,] 3.282238e-06 1.815164e-07
## [32,] 2.312563e-07 5.476051e-15
## [33,] 3.272712e-05 2.288954e-07
## [34,] 3.195066e-04 5.712625e-16
## [35,] 5.818072e-07 2.966454e-08
## [36,] 8.719737e-04 2.289357e-16
## [37,] 3.569453e-05 1.484014e-18
## [38,] 2.588299e-06 1.365968e-19
## [39,] 1.686610e-04 9.435901e-13
## [40,] 2.202057e-04 9.721930e-06
## [41,] 1.957123e-07 2.986816e-18
## [42,] 7.832755e-06 1.549458e-07
## [43,] 2.607735e-04 1.006510e-13
## [44,] 1.496527e-07 1.032538e-18
## [45,] 3.388612e-06 1.511386e-13
## [46,] 1.528151e-05 1.031946e-13
## [47,] 4.773619e-07 2.971441e-08
## [48,] 2.811627e-05 6.987712e-16
## [49,] 1.322945e-05 1.355253e-14
## [50,] 1.511119e-05 2.772647e-14
## [51,] 3.529777e-04 5.440158e-16
## [52,] 8.468182e-06 2.753506e-18
## [53,] 7.486849e-06 1.993931e-17
## [54,] 1.567422e-05 3.180503e-19
## [55,] 2.667499e-06 2.761173e-20
## [56,] 3.105046e-07 4.260185e-21
## [57,] 3.728603e-04 1.040124e-08
## [58,] 4.797785e-05 3.184609e-14
## [59,] 8.130166e-08 1.414389e-09
## [60,] 2.078701e-07 1.115480e-15
## [61,] 3.220068e-07 9.833926e-21
## [62,] 3.382332e-04 1.055921e-04
## [63,] 3.223719e-07 1.004502e-17
## [64,] 2.413982e-06 1.203141e-19
## [65,] 7.990300e-05 7.501236e-16
## [66,] 8.219774e-06 8.339862e-17
## [67,] 1.182408e-04 4.943641e-15
## [68,] 8.036853e-06 3.975852e-16
## [69,] 9.135158e-07 2.979613e-14
## [70,] 2.877277e-06 7.308936e-18

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[71,] 4.229650e-04 4.004459e-13
[72,] 3.508025e-06 7.509597e-15
[73,] 4.565401e-05 2.505996e-14

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