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Appendix 1. GPS tracking sample sizes, summary trip metrics & bathymetry data coverage

Table A1. Sample sizes of individuals, trips and tracking dates at all colonies and years.

Colony	Year	No. of individuals	No. of trips	Mean trips per individual	Unique tracking days	First tracking date	Last tracking date	Individuals with one trip	Individuals with 2-3 trips	Individuals with >4 trips
ALL	ALL	80	457	5.71	41	28/06/2010	09/07/2017	8	26	53
Puffin	ALL	49	341	6.96	33	28/06/2010	02/07/2016	2	12	39
Puffin	2010	14	133	9.50	11	28/06/2010	14/07/2010	0	0	14
Puffin	2011	20	116	5.80	15	27/06/2011	11/07/2011	1	4	15
Puffin	2015	9	41	4.56	3	10/07/2015	12/07/2015	0	4	5
Puffin	2016	10	51	5.10	4	28/06/2016	02/07/2016	1	4	5
Skomer	ALL	14	33	2.35	5	27/06/2016	29/06/2017	6	10	1
Skomer	2016	11	20	1.82	2	27/06/2016	28/06/2016	4	7	0
Skomer	2017	6	13	2.17	3	27/06/2017	29/06/2017	2	3	1
Rathlin	ALL	17	83	4.88	4	06/07/2017	09/07/2017	0	4	13
Rathlin	2017	17	83	4.88	4	06/07/2017	09/07/2017	0	4	13

Table A2. Summary trip characteristics

Colony	Year	Mean trip duration (hrs)	± SE	Trip duration range (h)	Mean total distance travelled (km)	± SE	Total distance travelled range (km)	Mean max distance to colony (km)	± SE	Max distance to colony range (km)
ALL	ALL	4.14	0.24	0.1 - 40.7	43.1	2.25	0.1 - 273.7	13.0	0.63	0.3 - 71.0
Puffin	ALL	3.77	0.27	0.1 - 40.7	39.4	2.45	0.1 - 245.2	11.9	0.73	0.3 - 71.0
Puffin	2010	2.58	0.22	0.2 - 12.8	29.1	2.70	0.7 - 182.1	9.1	0.95	0.3 - 71.0
Puffin	2011	5.00	0.44	0.2 - 23.6	58.2	4.58	0.7 - 245.2	17.8	1.25	0.3 - 61.6
Puffin	2015	5.48	1.50	0.2 - 40.7	40.2	9.60	0.5 - 219.4	10.6	2.71	0.4 - 68.3
Puffin	2016	2.69	0.49	0.1 - 13.2	22.5	5.00	0.1 - 169.0	7.3	1.73	0.3 - 53.7
Skomer	ALL	9.68	1.52	0.3 - 32.5	90.0	13.27	0.6 - 273.7	22.0	2.58	0.4 - 49.2
Skomer	2016	9.91	1.93	0.3 - 24.2	87.5	17.60	0.6 - 243.3	20.0	3.28	0.4 - 44.9
Skomer	2017	9.31	2.54	0.5 - 32.5	93.8	20.88	2.4 - 273.7	25.0	4.20	1.1 - 49.2
Rathlin	ALL	3.44	0.31	0.2 - 14.7	39.7	3.70	0.4 - 167.1	13.5	1.29	0.3 - 57.1

Rathlin	2017	3.44	0.31	0.2 - 14.7	39.7	3.70	0.4 - 167.1	13.5	1.29	0.3 - 57.1
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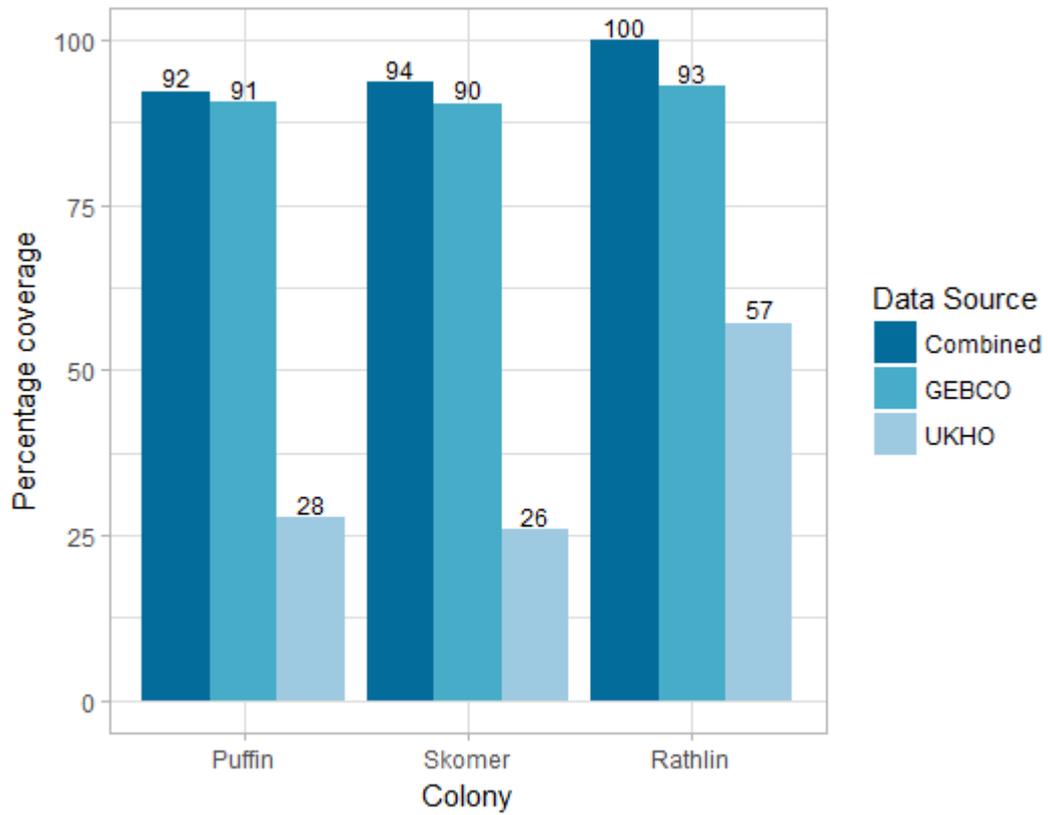


Figure A1.1. Percentage coverage of kittiwake GPS tracking points at each colony of combined, GEBCO and UKHO bathymetry data.

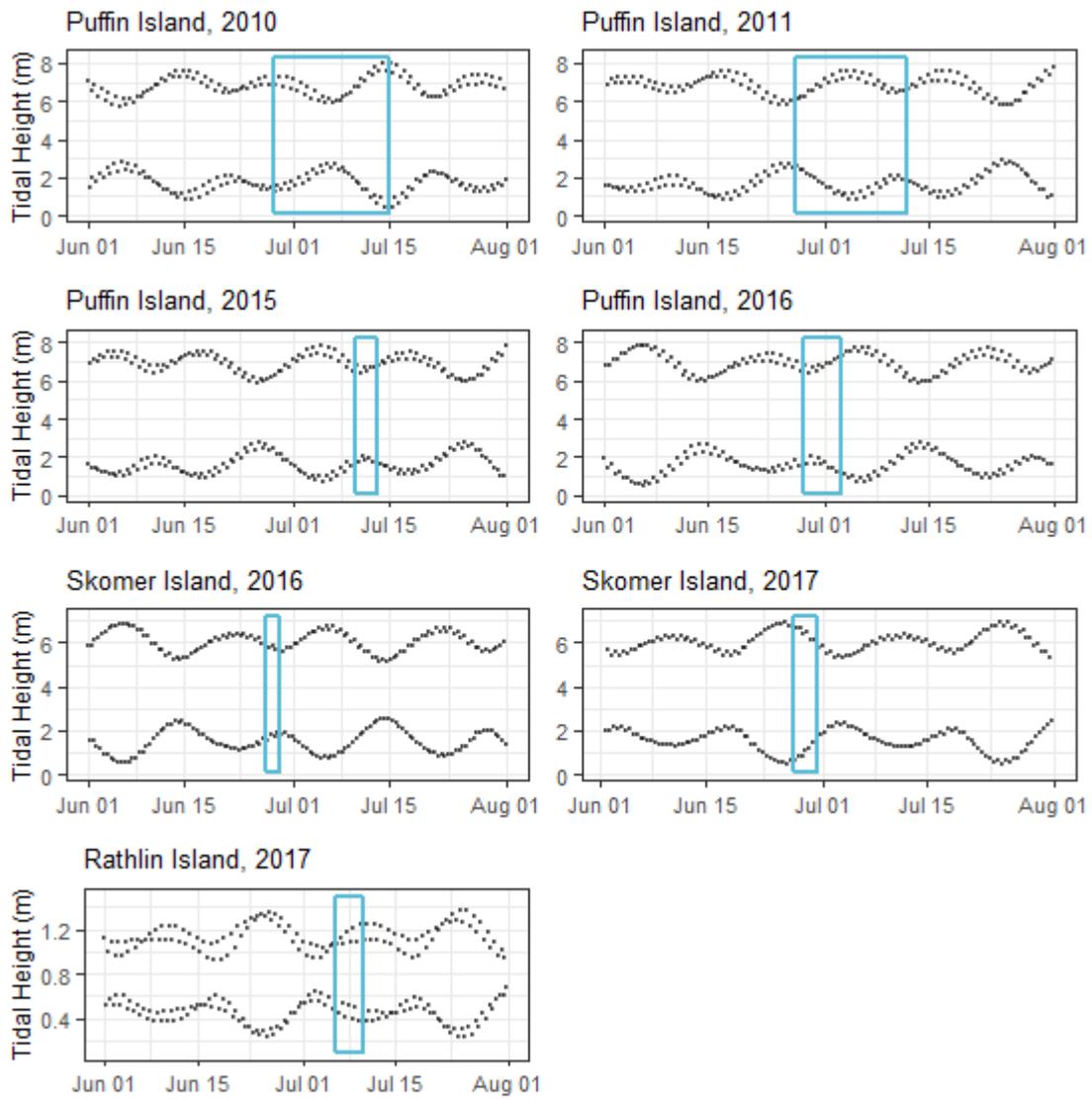


Figure A1.2. Heights of all high and low tides during June and July for each year of tracking at Puffin Island, Skomer Island and Rathlin Island. Boxes show periods of kittiwake GPS tracking.

Appendix 2

Assessing colony environmental heterogeneity

Methods

To understand the effect of the physical marine environment surrounding the breeding colony on kittiwake foraging behaviour, we characterised the proximal environment at each colony by comparing depth and tidal regime within the maximum foraging area of kittiwakes. In this case, maximum foraging area was determined from all years of kittiwake tracking data at each study site.

To characterise spatial heterogeneity in the physical environment, we studied the bathymetric landscape using UKHO bathymetry data, in combination with GEBCO data outside the gridded area of UKHO data (sources of data detailed in paper methods). We also characterised spatial differences in the depth scaled shear stress (τ) caused by tidal velocity as a proxy for the extent to which tidal flow alters the foraging environment over the tidal cycle. Tidal shear stress is a measure of force caused by the friction between tidal flow and the seafloor. High tidal stress values indicate high tide-driven turbulence at the maximum tidal velocities during the tidal cycle, which in turn indicates a bigger alteration to the physical foraging environment. Depth scaled tidal shear stress (in Newtons per m³) is given as:

$$\frac{\tau}{h} = \frac{\rho C_d U^2}{h}$$

Where τ is the shear stress driven by tidal velocity, ρ is water density (assumed constant, 1025 kg m⁻³), C_d is the drag coefficient, here taken as 0.0025 (Pérez-Ortiz et al. 2017). U is depth-averaged maximum tidal velocities from the 12.4 h tidal cycle (M2 tidal constituent). Tidal velocities were generated from a 3D hydrostatic simulation of the north west European shelf using the NEMO AMM60 configuration (Guihou et al. 2018). The simulation has 51 stretched layers in the vertical and a resolution of 1.8 km in the horizontal. A barotropic harmonic analysis was performed on the simulation and the M2 constituent is processed here (as the most energetic constituent). The M2 tidal speeds are defined as the amplitude of maximum barotropic M2 velocity, over the tidal cycle. Values of tidal speed range from 0.001 to 1.99 m s⁻¹. h is water depth, from bathymetry data described above. Between the three study colonies, we compared mean values of depth and tidal shear stress, standard deviation and range of values as an indication of heterogeneity. We conducted analyses of variance tests (ANOVA) with post hoc Tukey tests to determine whether the environment (depth or tidal shear stress data) differed between colonies. Both depth and tidal shear stress were square root transformed to approximate to Gaussian distributions (Fig. A1.1 and 2 respectively) in order to use parametric analyses of variance.

Results

Local bathymetry within the foraging range of GPS tracked kittiwakes significantly differed between the three different study colonies ($F_{(2,191831)} = 30469$, $p < 0.001$). A post hoc Tukey test showed that all three colonies were significantly different at pair-wise level (for all comparisons, $p < 0.001$). The area around Puffin Island was shallowest and least variable (based on standard deviation from the mean), although reached a maximum depth intermediate to Skomer Island and Rathlin Island (mean \pm SD = 35.9 m \pm 20.9, max = 167.4 m). Around Rathlin Island, the water column was deepest and most variable, and extended to the greatest maximum depths of the study colonies (mean \pm SD = 76.5 m \pm 42.4, max = 269.3 m). Around Skomer Island, average and variability in depth was intermediate to Puffin Island and Rathlin Island, and the maximum depth within the foraging range was the shallowest out of the three colonies (mean \pm SD = 65.3 m \pm 27.1, max = 135.8 m). Interestingly at Rathlin Island, the deepest waters, at over 200 m deep, were found within 10 km of the colony, whereas at both Skomer Island and Puffin Island deeper waters were found further away from the colony (Fig. A2.1). Variability in depth from different data sources (GEBCO/UKHO/Combined) supports the above results (Fig. A2.3).

Local tidal shear stress within the foraging range of GPS tracked kittiwakes significantly differed between the three different study colonies ($F_{(2,5573)} = 516.7$, $p < 0.001$). A post hoc Tukey test showed that all three colonies were significantly different at pair-wise level (for all comparisons, $p < 0.001$). Tidal shear stress was highest on average around Puffin Island (mean \pm SD = 44.5 mN m⁻³ \pm 29.1), however this may be because of an area of high tidal stress off the north-west tip of Anglesey. Maximum tidal shear stress was lowest out of the three study colonies at Puffin Island (401 mN m⁻³). Tidal shear stress was similar at Skomer Island (mean \pm SD = 25.9 mN m⁻³ \pm 24.1) and Rathlin Island (mean \pm SD = 26.4 mN m⁻³ \pm 35.5) although the maximum tidal shear stress at Skomer Island (448 mN m⁻³) was intermediate to Puffin Island and Rathlin Island, and was greatest out of the three study colonies at Rathlin Island (523 mN m⁻³). As with bathymetry, the proximity of areas of high tidal stress to the colony varied between the sites (Fig. A2.2). At both Rathlin Island and Skomer Island, there were areas of higher tidal stress adjacent to the colony, whereas at Puffin Island, the colony was surrounded by lower tidal stress.

Results from non-parametric analyses of variance on the original, un-transformed depth data concur with parametric tests on transformed depth data that there is a significant difference in water depth within the foraging range of kittiwakes at the three different study colonies (Kruskal–Wallis rank sum test, $\chi^2 = 51381$, $p < 0.001$). Pairwise comparisons showed that there is a significant difference between all three colonies (Wilcoxon rank sum test, in all cases $p < 0.001$). Likewise for tidal shear stress, results from non-parametric analyses of variance on the original, un-transformed data concur with parametric tests on transformed data that there is a significant difference in tidal

shear stress within the foraging range of kittiwakes at the three different study colonies (Kruskal–Wallis rank sum test, $\chi^2= 1247$, $p < 0.001$). Pairwise comparisons showed that there is a significant difference between all three colonies (Wilcoxon rank sum test, in all cases $p < 0.001$).

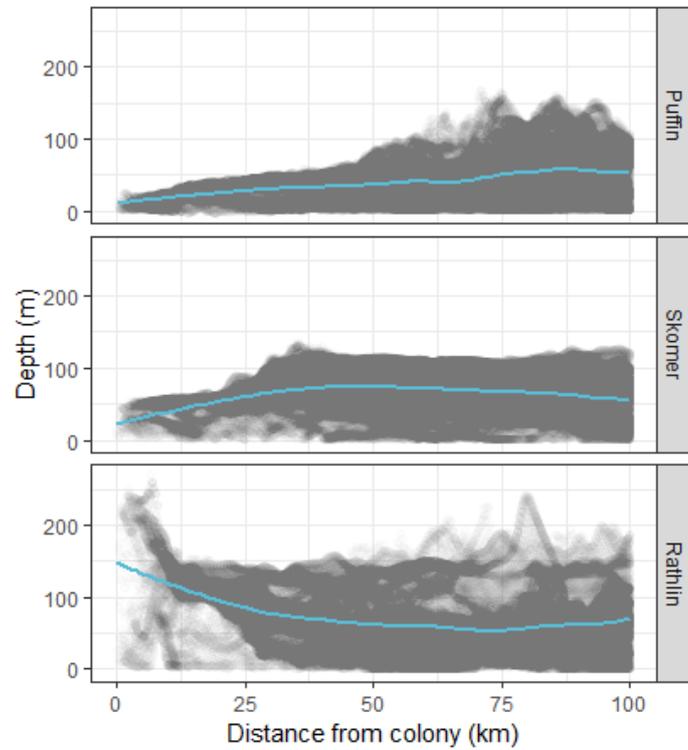


Figure A2.1. Differences in water depth with increasing distance to the colony at the three study sites, Puffin Island, Skomer Island and Rathlin Island, showing all points (grey) and GAM smoothing (blue).

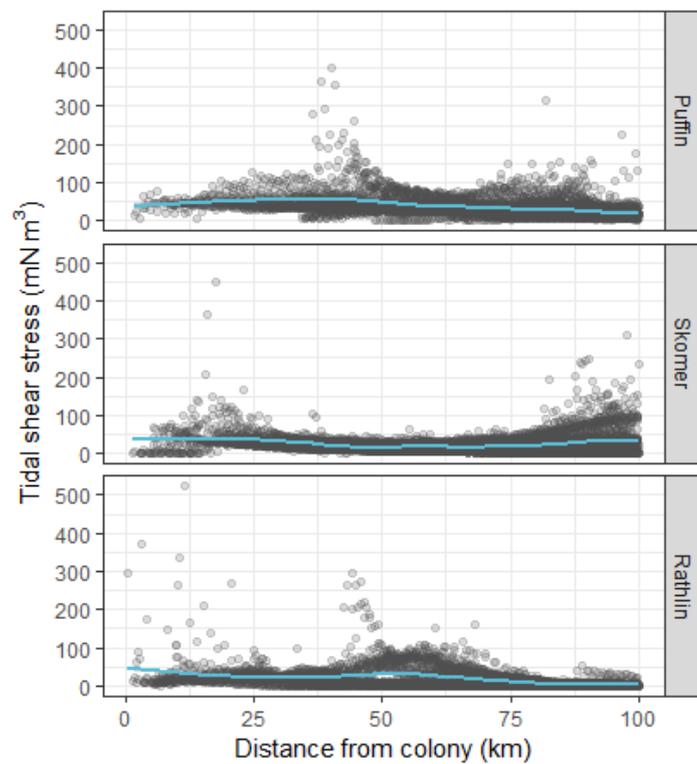


Figure A2.2. Differences in tidal stress with increasing distance to the colony at the three study sites, Puffin Island, Skomer Island and Rathlin Island, showing all points (grey) and GAM smoothing (blue).

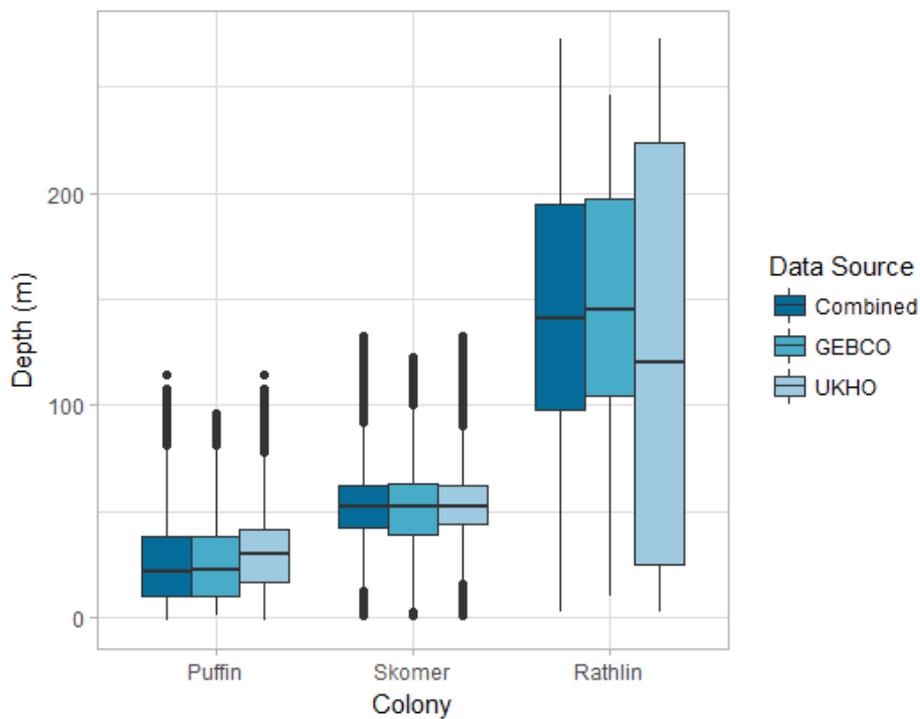


Figure A2.3. Water depth within the foraging radius at each colony from different bathymetry data (see paper methods for more details). Combined data, used in the paper analyses, takes UKHO data, and then GEBCO data where UKHO data is unavailable.

Appendix 3

Hidden Markov models for behavioural classification

The hidden Markov model successfully classified kittiwake tracks into three movement types, which we use as proxies of behaviour: 1) resting: short step lengths and narrow turning angles (step: 0.08 ± 0.05 km; turn: $\mu = 0$, $\kappa = 14$), 2) foraging: short-medium step lengths and wide turning angles (step: 0.27 ± 0.31 km; turn: $\mu = 0$, $\kappa = 0.4$) and 3) transiting: long step lengths and narrow turning angles (step: 1.00 ± 0.35 km; turn: $\mu = 0$, $\kappa = 6.8$). The model was robust to different priors, each time converging on the same parameters of step lengths and turning angles (Fig. A3.1). Using the Viterbi algorithm to determine the most likely sequence of behavioural states, 21.1% of GPS locations were classified as resting, 55.1% as foraging and 24% as transiting. Maps of foraging points only, by each state of the tidal cycle are given in Fig. A3.3.

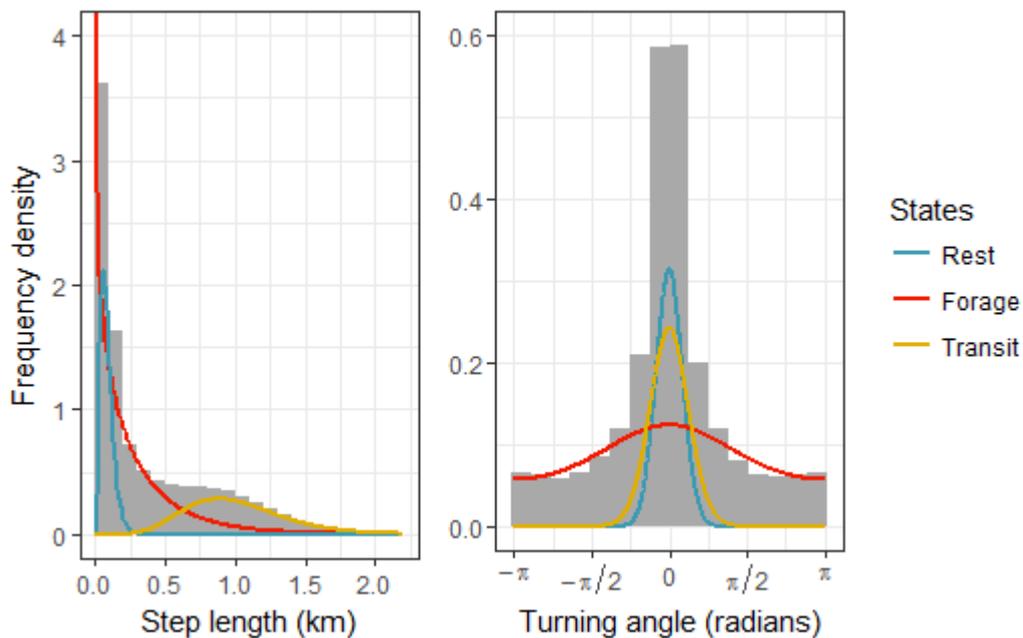


Figure A3.1. Histograms of observed step lengths (left) and turning angles (right) for GPS-tracked kittiwakes. Lines show fitted HMM state distributions for each behavioural state.

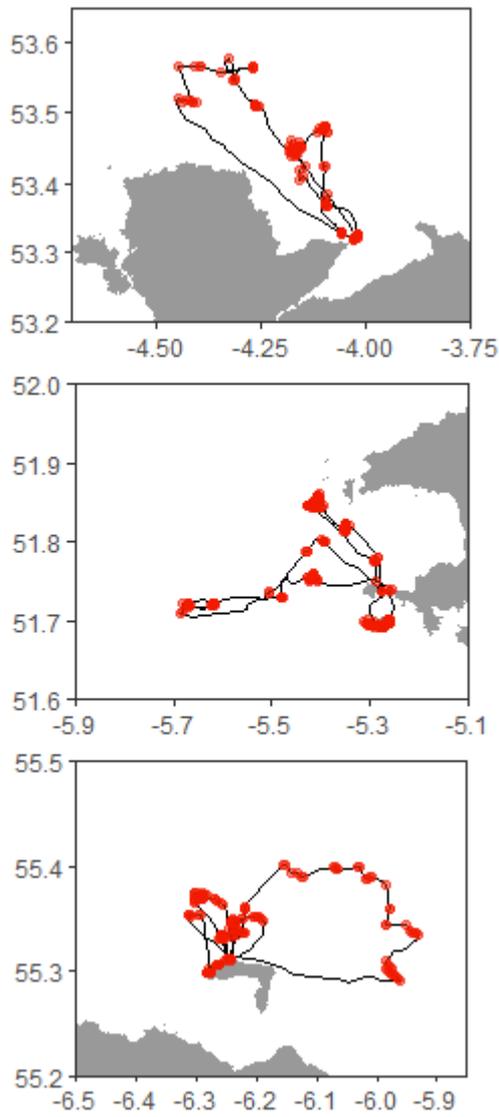


Figure A3.2. An example individual from each kittiwake colony (Puffin Island top, Skomer middle and Rathlin bottom) showing the total GPS track (black), and foraging points (red) as identified from the HMM model.

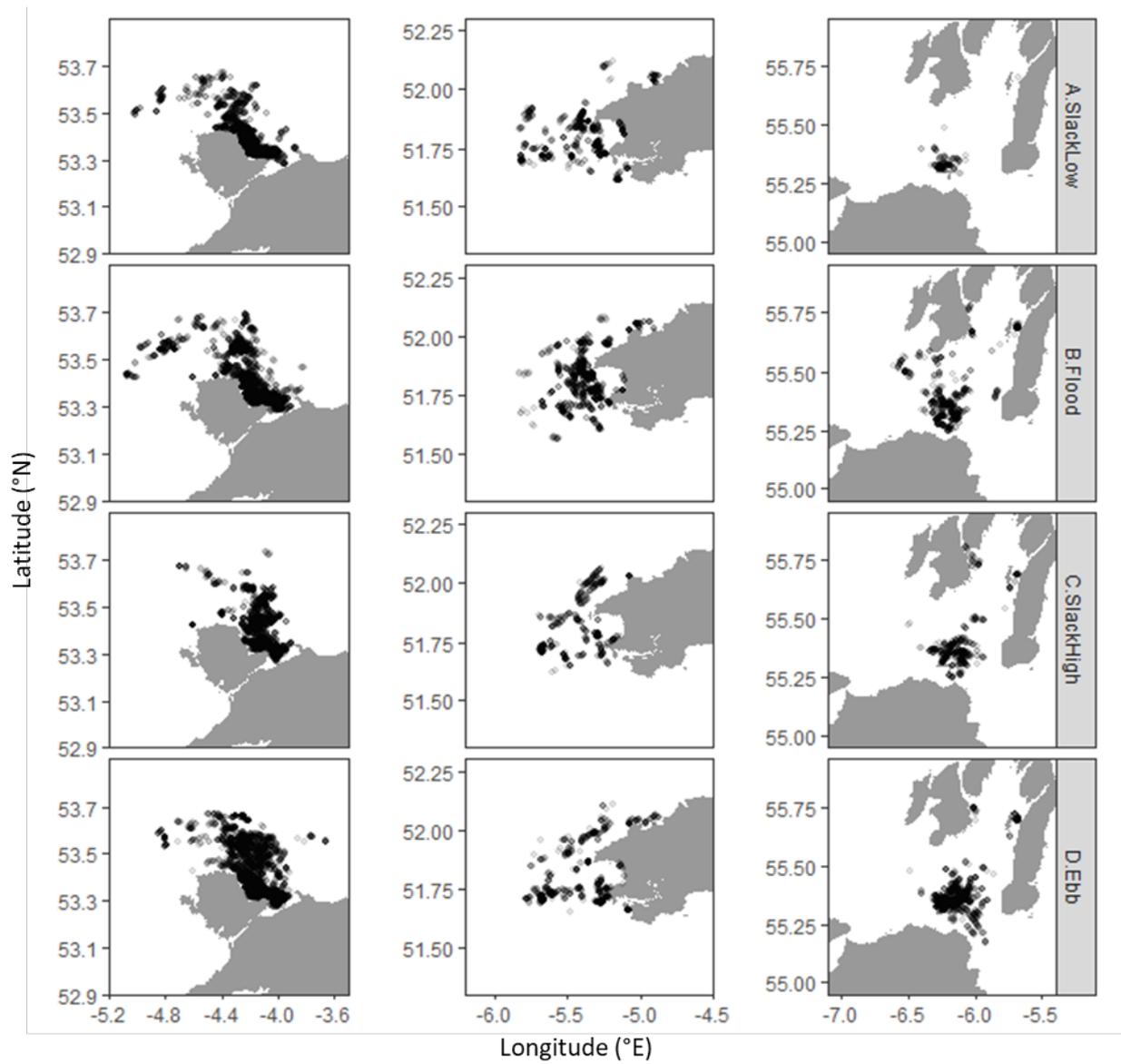


Figure A3.3. Kittiwake GPS locations classed as foraging at Puffin Island (left), Skomer Island (middle) and Rathlin Island (right) by tidal state. Tidal states are defined as slack low: >5 h either side of high water; flood: 1–5 h before high water; slack high: 1 h either side of high water; and ebb: 1–5 h after high water.

Appendix 4

Model selection

Table A4.1. Generalised linear mixed effects models testing for habitat use in relation to distance to the colony, with different fixed effects structures for model selection. In all cases, models include Year (specific to colony), Bird ID and Trip ID as random effects, and are run with a logit link.

Model	Coefficients	Marginal R ² (%)	Difference compared to most parsimonious model	
			AIC	Marginal R ² (%)
Full model	ColonyDist:Tidal.state:Colony + ColonyDist:Colony + Colony:Tidal.state + ColonyDist:Tidal.state + ColonyDist + Colony + Tidal.state	64.8	0	0
Without 3-way interaction	ColonyDist:Colony + Colony:Tidal.state + ColonyDist:Tidal.flag + ColonyDist + Colony + Tidal.state	63.5	2146.6	-1.33
Without Colony:Tidal.state	ColonyDist:Colony + ColonyDist:Tidal.state + ColonyDist + Colony + Tidal.state	63.1	2589.9	-1.70
Without ColonyDist:Tidal.state	ColonyDist:Colony + Colony:Tidal.state + ColonyDist + Colony + Tidal.state	62.7	3350.9	-2.13
Without ColonyDist:Colony	Colony:Tidal.state + ColonyDist:Tidal.state + ColonyDist + Colony + Tidal.state	60.6	4638.4	-4.24

Table A4.2. Generalised linear mixed effects models testing for habitat use in relation to water depth, with different fixed effects structures for model selection. In all cases, models include Year (specific to colony), Bird ID and Trip ID as random effects, and are run with a logit link.

Model	Coefficients	Marginal R ² (%)	Difference compared to most parsimonious model	
			AIC	Marginal R ² (%)
Full model	Depth:Tidal.state:Colony + Depth:Colony + Colony:Tidal.state + Depth:Tidal.state + Depth + Colony + Tidal.state	19.8	0	0
Without 3-way	Depth:Colony + Colony:Tidal.state + Depth:Tidal.state +	19.5	811.3	-0.30

interaction	Depth + Colony + Tidal.state			
Without Colony:Tidal.state	Depth:Colony + Depth:Tidal.state + Depth + Colony + Tidal.state	19.1	1453.6	-0.68
Without Depth:Tidal.state	Depth:Colony + Colony:Tidal.state + Depth + Colony + Tidal.state	18.8	2549.6	-0.99
Without Depth:Colony	Colony:Tidal.flag + Depth:Tidal.state + Depth + Colony + Tidal.state	2.1	69534.0	-17.7

Table A4.3. Model scores from receiving operator characteristic curves of full models presented in Table A4.1 and A4.2.

Model	Correct classification (%)	Positive Predictive Power (%)	Negative Predictive Power	Sensitivity	Specificity	Area under curve
Colony distance	83.3	34.1	98.8	0.90	0.83	0.86
Depth	64.6	16.4	95.6	0.71	0.64	0.67

Table A4.4. Generalised linear mixed effects models testing for foraging habitat use in relation to distance to the colony for each colony separately, with different fixed effects structures for model selection. In all cases, models include Bird ID and Trip ID as random effects, and are run with a logit link.

Colony	Model	Coefficients	Difference in AIC compared to most parsimonious model
Puffin	Full model	ColonyDist:Tidal.state + ColonyDist + Tidal.state	0
	Without interaction	ColonyDist + Tidal.state	1696.3
Skomer	Full model	ColonyDist:Tidal.state + ColonyDist + Tidal.state	0
	Without interaction	ColonyDist + Tidal.state	664.2
Rathlin	Full model	ColonyDist:Tidal.state + ColonyDist + Tidal.state	0
	Without interaction	ColonyDist + Tidal.state	978.3

Table A4.5. Generalised linear mixed effects models testing for foraging habitat use in relation to water depth for each colony separately, with different fixed effects structures for model selection. In all cases, models include Bird ID and Trip ID as random effects, and are run with a logit link.

Colony	Model	Coefficients	Difference in AIC compared to most parsimonious model
Puffin	Full model	Depth:Tidal.state + Depth + Tidal.state	0
	Without interaction	Depth + Tidal.state	495.6
Skomer	Full model	Depth:Tidal.state + Depth + Tidal.state	0
	Without interaction	Depth + Tidal.state	419.4
Rathlin	Full model	Depth:Tidal.state + Depth + Tidal.state	0
	Without interaction	Depth + Tidal.state	1655.6

Appendix 5

Sensitivity analysis of resource selection model to available habitat selection

To determine habitat preference of kittiwakes, we compared habitat for foraging only GPS points to a set of random points as a proxy of available habitat. Resource selection methods can be sensitive to available habitat selection, and therefore sensitivity analyses are advisable (Northrup et al. 2013). Here, we consider the sensitivity of our model to varying available habitat selection in light of the ecology of our species, the black-legged kittiwake.

For the available habitat in the final model, we chose 10 random points from within the foraging radius of each colony during the given tracking year. For GPS tracking studies such as ours, sampling more individuals increases the measured foraging area of the sampled population (Soanes et al. 2013). We therefore chose to use foraging radius specific to each tracking year at each colony to allow for differences in the number of tracking years at each colony and maintain potential inference from results.

Reduced area for available habitat selection

To test sensitivity of results to the area of available habitat, we restricted the available habitat to within 90% and 75% of the maximum foraging range in a given tracking year for each colony and ran habitat selection models of water depth, and a test of the three-way interaction between depth, colony and tidal state. Results concur with those presented in the main paper, that when available habitat was selected from 90% of the maximum foraging range, the most parsimonious model retained the three-way interaction between environment (distance to colony or depth), colony and tidal state for both habitat selection by distance to the colony (model without 3-way interaction: $\Delta\text{AIC} = +3645.0$, $\Delta\text{R}^2\text{m} = -2.0\%$) and water depth (model without 3-way interaction: $\Delta\text{AIC} = +771.7$, $\Delta\text{R}^2\text{m} = -0.3\%$). When available habitat was selected from 75% of the maximum foraging range, the most parsimonious model retained the three-way interaction between environment (distance to colony or depth), colony and tidal state for both habitat selection by distance to the colony (model without 3-way interaction: $\Delta\text{AIC} = +2508.3$, $\Delta\text{R}^2\text{m} = -1.7\%$) and water depth (model without 3-way interaction: $\Delta\text{AIC} = +733.1$, $\Delta\text{R}^2\text{m} = -0.3\%$).

Full data set

To test sensitivity of results to restriction to foraging only data points, we ran identical models to the full data set, i.e. all GPS points, each with 10 random ‘available’ points. The most parsimonious model retained the three-way interaction between environment (distance to colony or depth), colony and tidal state for both habitat selection by distance to the colony (model without 3-way interaction: $\Delta\text{AIC} = +3230.35$, $\Delta\text{R}^2\text{m} = -1.0\%$) and water depth (model without 3-way interaction: $\Delta\text{AIC} = +530.87$, $\Delta\text{R}^2\text{m} = -0.2\%$). Parameter estimates are plotted in Figure D1. Models for each colony separately also support results in the main paper. In all cases model selection retained the two-way interaction between environment (distance to colony or depth) and tide by AIC values. As in the main results, the interaction between tide and the environmental variable (distance to colony or depth) explained more additional variation in the model at Rathlin Island, where environmental heterogeneity was greatest (7.5% for colony distance, and 2.1% for depth; Table 3), and least variation at Puffin Island, where environmental heterogeneity was lowest (1.5% for colony distance, and 0.6% for depth; Table 3).

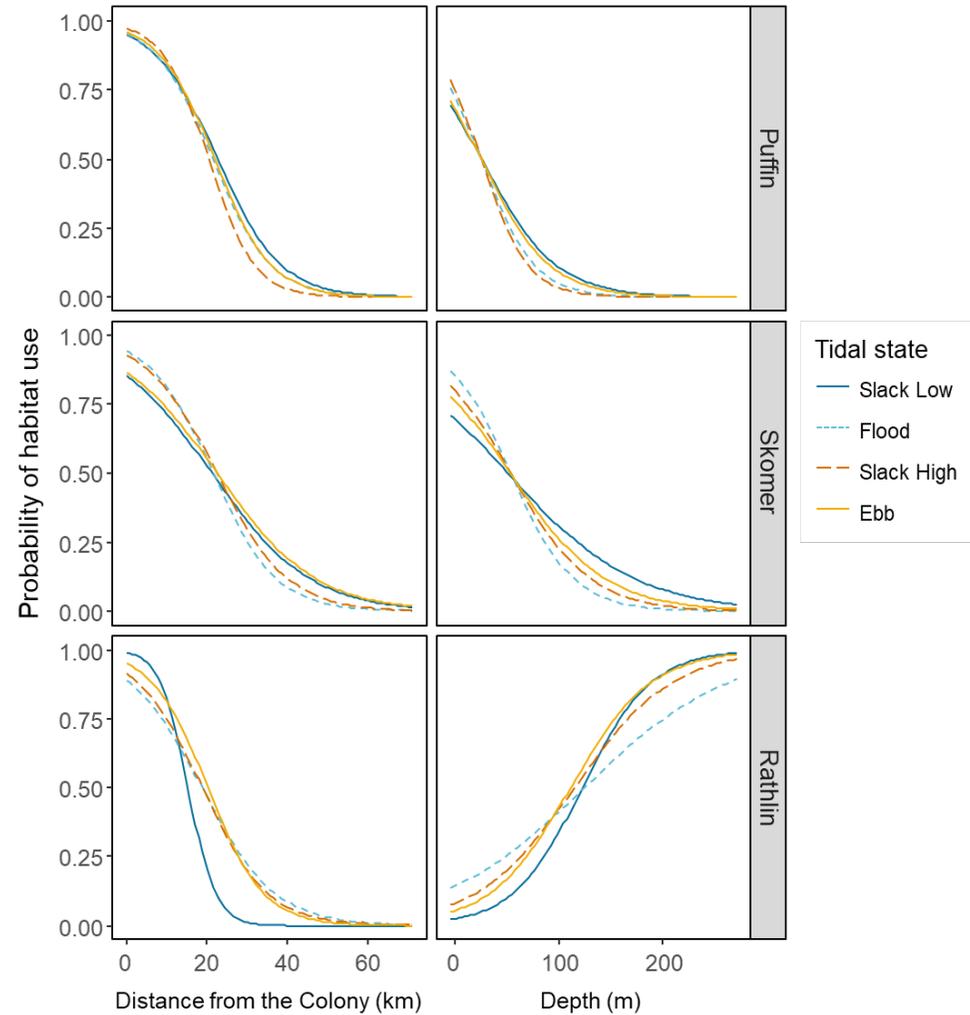


Figure A5.1. Probability of habitat use at different distances to the colony (left) and at varying water depths (right) for GPS tracked kittiwakes during different tidal states at three different colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom). Results are from models with all GPS points, and are concurrent with findings of foraging only models presented in the main paper.

Appendix 6

Habitat selection models for colonies separately

To understand differences in results between colonies, we ran habitat selection models for distance to colony and depth at each colony separately, and looked at the difference in variance explained by the interaction of tide with the environmental variable in question. Parameter estimates and figures for each colony are given here for both colony distance and bathymetry.

Table A6.1. Parameter estimates, \pm standard error, for the slope of the interaction between the environment variable (distance to colony or depth) and tide, derived from models ran separately at each colony. A positive parameter estimate indicates a positive relationship between kittiwake habitat use and locations further away from the colony, or greater water depths.

Model	Colony	Parameter estimates for different tidal states			
		Slack low	Flood	Slack high	Ebb
Distance to colony	Puffin	-2.51 \pm 0.02	-2.50 \pm 0.01	-3.34 \pm 0.02	-2.83 \pm 0.01
	Skomer	-1.53 \pm 0.02	-2.37 \pm 0.03	-1.93 \pm 0.04	-1.69 \pm 0.03
	Rathlin	-5.80 \pm 0.24	-1.71 \pm 0.02	-2.10 \pm 0.03	-2.32 \pm 0.02
Bathymetry	Puffin	-1.30 \pm 0.01	-1.44 \pm 0.01	-1.71 \pm 0.02	-1.32 \pm 0.01
	Skomer	-0.70 \pm 0.02	-1.22 \pm 0.02	-0.86 \pm 0.03	-0.89 \pm 0.02
	Rathlin	0.74 \pm 0.02	0.29 \pm 0.01	0.65 \pm 0.01	0.78 \pm 0.01

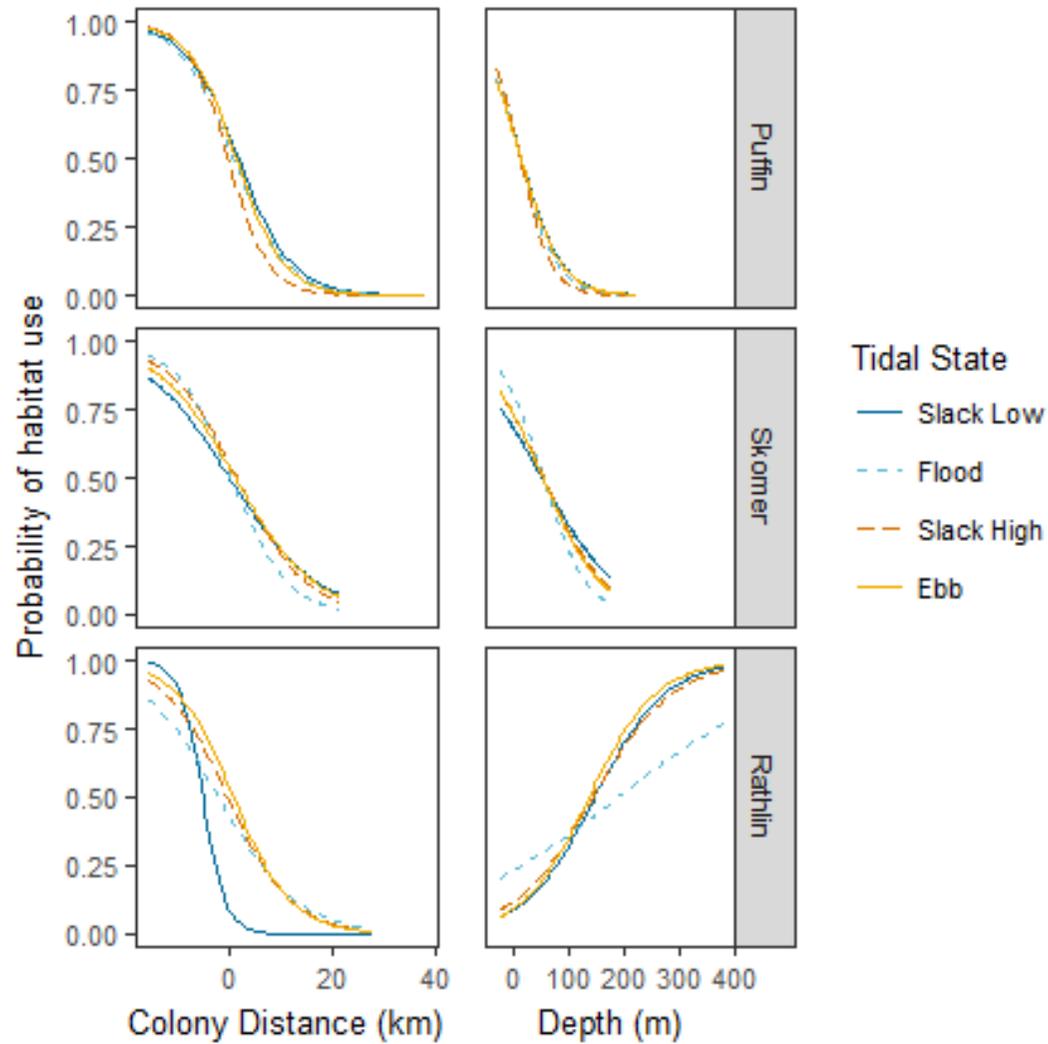


Figure A6.1. Probability of habitat use (from models of each colony separately) whilst foraging at different distances to the colony (left) and at varying water depths (right) for GPS tracked kittiwakes during different tidal states at three different colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom).

References

- Guihou, K. et al. 2018. Kilometric scale modeling of the north west European shelf seas: exploring the spatial and temporal variability of internal tides. – *J. Geophys. Res. Oceans* 123: 688–707.
- Northrup, J. M. et al. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. – *Ecology*, 94: 1456–1463.
- Pérez-Ortiz, A. et al. 2017. Characterization of the tidal resource in Rathlin Sound. – *Renewable Energy* 114: 229–243.
- Soanes, L. M. et al. 2013. How many seabirds do we need to track to define home-range area? – *J. Appl. Ecol.* 50: 671–679.