Improving Our Understanding of Seabird Behaviour at Sea

June 2022

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Published by Marine Scotland Science
ISBN: 978-1-80435-217-5 (web only)

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Report of work carried out by the British Trust for Ornithology
on behalf of Marine Scotland

July 2019

The British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU
Registered Charity No. 216652

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Summary

Offshore wind farms form a key part of the Scottish Government's strategy to mitigate the impacts of climate change by generating 100% of electricity using renewable energy. However, Scotland also hosts internationally important populations of seabirds during the breeding season and it is important to ensure any offshore wind farms do not adversely affect these populations. At present assessments of the likely impacts of offshore wind farms on seabirds are largely based on data collected using boat and/or digital aerial surveys. However, such surveys are constrained by light levels and weather conditions in when they can be carried out. This leads to concerns that the data used in assessments may be biased towards favourable conditions and may not accurately reflect the conditions experienced by birds. Furthermore, understanding the behaviour of seabirds at sea is key to understanding the potential exposure of seabirds to impacts such as displacement and barrier effects. However, the behavioural data that can be collected using standard survey approaches is extremely limited.

The widespread application of tracking technologies offers an opportunity to investigate the behaviour of seabirds at sea in more detail. We collate tracking data collected from five seabird species thought to be vulnerable to the impacts of offshore wind farms – Northern Gannet, Lesser Black-backed Gull, Black-legged Kittiwake, Common Guillemot and Razorbill – from colonies from across the UK. We analyse these data in relation to the diel cycle and weather conditions in order to understand how seabird distributions may vary between conditions in which traditional survey methods can and cannot be applied. We further analyse these data using Hidden Markov Models in order to classify these data into one of three

behavioural states – floating, commuting and foraging. We investigate the spatial patterns in these different behaviours and consider how they may be influenced by the diel cycle and weather conditions.

Our analyses highlight that, during the breeding season, the constraints related to traditional surveys are unlikely to mean data are biased towards particular conditions. However, our analyses also highlighted clear spatial patterns in seabird behaviour at sea. We discuss the implications of these spatial patterns for the assessment of the impacts associated with offshore wind farm.

1 Introduction

In order to mitigate the impacts of climate change, the Scottish Government aim to generate 100% of Scotland’s gross electricity consumption from renewable sources by 2020. Globally, Offshore wind farms are likely to play a key role in strategies to reduce our reliance on energy generated using fossil fuels (Toke 2011). In Scotland, operational projects at Robin Rigg and the Aberdeen Bay European Offshore Wind Deployment Centre (EOWDC) and the larger Round Three projects in the Moray Firth and the outer Forth and Tay estuaries which are either under construction or, have received planning consent, will play a key role in meeting the government’s ambitious targets for renewable energy. Further projects are likely as part of ScotWind (Crown Estate Scotland), the next offshore wind leasing round in Scotland and with the successful ongoing testing of floating wind turbines, there is the potential for these wind farms to be located further offshore.

However, there are also concerns about the potential for offshore wind farms to negatively impact the environment, with the risk to seabirds receiving particular attention (Furness *et al.* 2013). Scotland hosts internationally important populations of seabirds (Mitchell *et al*., 2004) and there are concerns about the potential for these populations to be affected through collisions with turbines, the loss of habitat as a result of displacement and barrier effects resulting in elevated energy expenditure costs. Consequently, potential impacts on seabird populations are a key focus of Environmental Impact Assessments (EIAs) carried out as part of the consenting process for proposed offshore wind farms.

Concern about the potential impacts of offshore wind farms on seabird population has led to the refusal of planning consent in relation to one offshore wind farm in England (Broadbent & Nixon, 2019) and legal challenges in relation to others (Scottish Courts and Tribunals, 2016; Scottish Courts and Tribunals, 2017). This can involve significant costs for all involved and may put the financial viability of projects in doubt. Furthermore, the delays such challenges cause to the consenting process can cause problems in relation to attracting the necessary financial support from government required for the project to proceed.

It is important that consenting decisions made in relation to offshore wind farms make use of the best available evidence. In relation to seabirds, this has traditionally involved making use of data collected using boat or digital aerial surveys (Buckland *et al*., 2012; Camphuysen *et al*., 2004; Thaxter & Burton, 2009). In addition to providing information on the distribution and numbers of birds at sea, they often include additional information such as species flight heights (Johnston & Cook, 2016;

Johnston *et al.* 2014). However, these surveys are limited to daylight hours and conditions of good visibility and sea states of four or less (Camphuysen *et al.* 2004). Consequently, there is concern that the data currently used during EIAs may be biased towards particular times and conditions, and not accurately reflect seabird use of the offshore environment at other times.

There is a growing recognition of the potential for tagging data to inform EIAs for offshore wind farms (Fijn & Gyimesi, 2018; Furness *et al.* 2018; Ross-Smith *et al.* 2016). There are an increasing number of tracking studies from a wide range of seabirds tagged at breeding colonies around the UK (and Europe), and comparison between transect-based survey data and tracking data collected during the breeding season has revealed a far greater degree of overlap in the location of high use areas at sea than would be expected by chance alone (Sansom *et al.* 2018). However, the extent of this overlap declines with increasing distance from colony. Area usage also appears to differ in relation to environmental conditions. This may have implications for the assessment of displacement. For example, if distributions differ between good and poor weather conditions, then the potential for displacement in different conditions may also differ.

In addition to understanding how distributions may vary between times when boat and digital aerial survey data can, or can't, be collected, it is important to understand how species behaviour may differ. This is particularly important in relation to assessing potential collision risk. Collision Risk Models (CRMs) such as the Band model (Band, 2012) require reliable estimates of behavioural parameters such as estimates of species-specific flight heights, flight speeds and levels of nocturnal activity (Masden & Cook, 2016). In assessing collision risk, estimates of species flight heights have typically been based on boat or digital aerial survey data (Johnston & Cook, 2016; Johnston *et al.* 2014). However, it has been demonstrated that Lesser Black-backed Gull flight heights may differ between day and night (Ross-Smith *et al*., 2016). This has implications for the assessment of collision risk in this species as it means birds are less likely to encounter turbine blades during the night than during the day. It seems likely that other aspects of bird flight behaviour may differ between day and night as well. Furthermore, estimates of parameters such as flight speed and levels of nocturnal activity have been drawn from studies with limited sample sizes or, based on reviews inferred from our understanding of the ecology of the species concerned (Alerstam *et al.* 2007; Garthe & Huppop, 2004). Recent analyses of tracking data have highlighted how these assumptions may be misleading, with potential consequences for the assessment of collision risk (Fijn & Gyimesi, 2018; Furness *et al.* 2018).

In order to assist the Scottish Government deliver its ambitious targets for renewable energy generation, we aim to use seabird tracking data to enable a better understanding of seabird behaviour at sea, by considering seabird data collected in different weather conditions and throughout the diel cycle. This will allow, for the first time, an assessment of the potential biases in EIAs based solely on transect-based survey and the potential implications this has in relation to assessing the potential impacts of offshore renewable energy developments on seabirds. We will also consider the potential for tracking data to improve the evidence base with which to assess the potential impacts of offshore wind farms on seabird populations. This will help mitigate conflict in the consenting process, reducing costs for all stakeholders and minimise the potential for delays by reducing uncertainty in relation to the data that are used in the assessment process (Masden *et al*., 2015).

2 Methods

The workflow within this project is summarised in a schematic (Figure 1), which highlights the acquisition and application of raw datasets included within the study, their preparation and manipulation, leading further through the stages of behavioural and spatial analyses. We highlight flows of information through each stage, with key final outputs and summaries of information also highlighted.

2.1 Data sourcing

2.1.1 Study species

We considered a total of nine species of UK seabird for potential inclusion within this project: Northern Gannet, hereafter 'Gannet' (*Morus bassanus*), European Shag (*Phalacrocorax aristotelis*), Lesser Black-backed Gull (*Larus fuscus*), Herring Gull (*Larus argentatus*), Great Black-backed Gull (*Larus marinus*), Black-legged Kittiwake, herafter 'Kittiwake' (*Rissa Trydactyla*), Common Guillemot, hereafter 'Guillemot' (*Uria aalge*), Razorbill (*Alca torda*) and Atlantic Puffin (*Fratercula arctica*). However, these species were reduced to a subset of six species (Gannet, Lesser Black-backed Gull, Herring Gull, Kittiwake, Guillemot and Razorbill, Table 1) that were identified as priority species based on perceived importance within impact assessments and policy relevance. Data for these six species were then acquired and for each species we selected key sites from a wider available tracking dataset to, where possible, represent a mix of colonies from north to south and east to west per species, as well as coastal and island colonies for gulls. For Herring Gull, however, the amount of data collected in the offshore environment was very small across datasets, and so was not modelled as part of this study, reducing the number of species presented to five (Table 1).

2.1.2 GPS data

GPS data were acquired from various data sources. Tracking data for guillemots, Razorbills, Kittiwakes and herring gulls were obtained from the RSPB and CEH through the FAME-STAR consortium (Wakefield *et al.* 2017). Gannet data for Bass Rock were obtained from the University of Leeds and for Alderney from the University of Liverpool (Warwick-Evans *et al.* 2016; Soanes *et al.* (2012). Tracking data for Lesser Black-backed Gulls and Herring gulls were obtained through the BTO.

Table 1 Breakdown of the species and sites covered in this project, with information on numbers of birds and years available for each site, east/west, north/south location of the site, whether and island of mainland colony and the colony size at each site for each species. LBBG = Lesser Black-backed Gull.

Species	**Colony**	**N Birds**	**N Years**	**East/ West**	**North/ South**	**Island/ Mainland**	**Colony size**
Gannet	Alderney	61	4	West	South	Island	5765
Gannet	Bass Rock	133	4	East	Central	Island	75259
LBBG	Orford Ness	25	3	East	South	Mainland	640
LBBG	Walney	54	4	West	Central	Mainland	4987
LBBG	Skokholm	25	2	West	South	Island	1486
Kittiwake	Isle of May	50	3	East	Central	Island	3433
Kittiwake	Orkney	86	5	Central	North	Mainland	~
Kittiwake	Colonsay	84	5	West	North	Island	~
Kittiwake	Bempton Cliffs	104	6	East	Central	Mainland	37617
Guillemot	Isle of May	48	3	East	Central	Island	21598
Guillemot	Colonsay	77	5	West	North	Island	~
Guillemot	Puffin Island	40	5	West	South	Island	3627
Guillemot	Fowlsheugh	11	1	East	North	Mainland	55507
Razorbill	Puffin Island	58	5	West	South	Island	592
Razorbill	Isle of May	28	3	East	Central	Island	4590
Razorbill	Colonsay	42	5	West	North	Island	~

2.1.3 TDR data

Time-Depth Recorders (TDRs) were attached to 29 Guillemots from Colonsay and seven Guillemot from Puffin Island and 26 Razorbills from Colonsay; these deployments were in addition to GPS tags attached to birds (dual deployment) to identify dive locations. TDR pressure recordings were taken at 1 second intervals and were used in this study to refine classification of foraging behaviour for guillemots and Razorbills.

2.1.4 Covariates: Wind speed, direction and time of day

To test whether behaviour and area use of birds differed under different times of the day and in different wind speeds, we specified additional covariates alongside the prepared GPS data ahead of further use-availability assessments and behavioural modelling. Hour of the day (UTC) and Julian date were extracted from the date-times of GPS fixes. The distance (Rhumb line loxodrome) of GPS points to the breeding colony for the species of interest were also specified for inclusion within behavioural analyses (see below). Wind speed and direction data were obtained through the European Centre for Medium Range Weather Forecasts (ECMWF) 'ERA5' reanalysis model, and the mean 10 m u and v wind components were extracted at hourly temporal resolution and *ca*. 30 km spatial grid resolution (ECMWF 2019). Grid squares were then matched to the GPS locations for each colony and species, ahead of further analyses.

2.1.5 Summary of wind speed and direction experienced by GPS tracked birds relative to that available over the period of GPS tracking per colony

The wind speeds that birds experience at sea may or may not be a reflection of the conditions available to them, for example if they avoid particular conditions such as times when wind speeds are high by either remaining at the colony or (for generalist species) foraging inland rather than offshore. Further, the period of tracking itself is often restricted to a phase during the breeding season, which may or may not reflect the general conditions in the area for the month of study.

For this assessment the mean and maximum wind speed and mean wind direction that individual birds encountered for each colony and year were summarized as an indication of the conditions birds actually experienced during their periods of tracking. To gain perspective how this 'use' of conditions compared to that 'available' in the area, we also extracted wind speed and direction information from each 30 km

Copernicus grid square (matched to the GPS data as above) that GPS tracks of birds overlapped with. This availability assessment was conducted for two temporal scales: (i) the entire months in which tracking at the colony and year had been conducted and (ii) the specific tracking durations of individual birds. This enabled a comparison of conditions birds could have experienced across the entire month (for example should tracking have been conducted across a wider period in the months of tracking), and across individual tracking durations of birds (if birds had used all areas equally, albeit with a caveat that more distant offshore areas naturally may be windier).

To present use-availability assessments in a meaningful way specific to the aims of this project, we quantified the proportional use of wind speeds above that deemed too windy for aerial and boat-based surveys to be carried out. We examined the proportion of grid cells per hour, per day that had mean wind speeds greater than 8 m/s and 10 m/s, representing an equivalency to wind speed thresholds above which planes are unlikely able to survey an area (being equivalent to ca. Beaufort Scale 5) and thus informed proportion of use and availability that may be outside of these survey windows for each species, colony and year. This was examined for (a) the grid cells that birds used on a given date and time, (b) those that could have been used at the two temporal scales described. A lower and upper threshold of this window were also specified – see below – to maximize the GPS data available when carrying out investigations of utilization distributions within high and low wind categories.

Proportional use-availability comparisons data were summarised as histograms and spatial plots, using code adapted from the R:rWind package (Fernández-López & Schliep 2018). We note, however, that this is not a full resource-selection approach and further statistical assessment would be needed to fully understand how birds interacted with particular conditions.

2.2 Data Manipulation

Wind speed and direction data were extracted from raster Copernicus layers and matched to GPS data using a simple overlap of GPS points over Copernicus grid squares and a point-in-polygon assessment. This manipulation step also informed the patterns of use of particular wind speeds in relation to that available as introduced above. This ensured that for further analyses, each GPS fix then had a geo-referenced wind speed and wind direction value appropriately assigned. Time of day was specified as a continuous (circular) covariate for behavioural modelling –

see below – which was automatically available for timestamped GPS data. Further data manipulation was also carried out below in an initial step prior to further behavioural modelling – see Section 2.3 below. Further divisions of data for wind speed and time of day were used for assessment of area use – see Section 2.4 below.

2.3 Behavioural modelling

2.3.1 Interpolation of GPS tracks to obtain regular sampling rates

GPS data, although collected under specified sampling rates in each study (five minutes for gulls), and 100-120 seconds for other species, suffer variations in precision delivering a GPS fix at precise rates, due to issues such as signal retention, time-to-fix, and many other variables. For subsequent behavioural analyses, a requirement is that data are "regular" in date and time, necessitating interpolation to translate GPS points to a regular interval so that step lengths and turning angles can be analysed without bias of time variation. To achieve this, we used R package:crawl to fit continuous-time correlated random walk (CTCRW) models (Johnson *et al*. 2008) to predict temporally-regular locations at the level of the original sampling rate. We specified interpolations at either 300 s (Lesser Black-backed Gulls), 120 s (Gannets and Kittiwakes) and 100 s (auks: Guillemot and Razorbill). CTRCW models were specified using a bivariate normal measurement error model; predictions along the track were then made avoiding gaps among strings of points that were more than 2.5 times the sampling rate to distinguish "gaps" in GPS records that we did not wish to interpolate over, avoiding introducing further error into the models. Although specifying a measurement error, and thus potential for drawing multiple imputations from the CTRCW models for each species and site, we instead extracted single 'consensus tracks' to fit models. This decision was made because of computational issues in the subsequent run-times for behavioural models, given the scope of the analysis across several species and sites. Covariates for 'regularised' data points were obtained through matching the nearest observed true GPS point to the predicted regularised point, to preserve biological realism for the environment that each individual species encountered. For each species the CTRCW model was run once per individual and site.

2.3.2 Hidden Markov Models

In this study we used multivariate discrete-time Hidden Markov Models (HMMs) to carry out behavioural analyses. HMMs are a popular and useful tool that permits classification of different behaviours from telemetry data, and further investigation into the drivers of movement in relation to covariates of interest. HMMs are a form of time-series model and use movement characteristics such as distances travelled (hereafter step lengths) and turning angles between successive positional coordinates recorded at a constant sampling unit, to reveal 'hidden' states through a Markov-chain modelling process; these states in turn may align with behaviours of ecological relevance for species.

For mobile species, these behavioural states may fall into general categories such as 'floating', 'commuting' and 'foraging', and such categories are frequently specified in such a 'three-state' model for animals of different species. For central place foragers, such as birds during the breeding season, commuting to and from a central place may be indicated by steps between GPS points at the upper end of the distribution (i.e. faster movement), with a high consistency of travel direction (i.e. perhaps being in a straight line). For a marine bird species, this state contrasts with when an individual may be floating on the sea surface, typified by much smaller step lengths between GPS fixes, but that also may be in a consistent alignment similar to commuting. A further third state captures the remaining residual behaviour that can be generally regarded as foraging or searching behaviours while marine birds are away from the colony out at sea, and may be typified by medium-length steps between fixes (i.e. medium speed) but with very different turning angles between points representing an individual moving back and forth over an area of interest. However, foraging/searching as a 'behaviour' is a broad category and may encompass many finer-scale activities – further, without ground-truthed observations of what birds were actually doing, there will always be some observational error in our interpretation of behaviour within each state. A further fourth category may also be determined for some cases, where very stationary activity, here termed 'perching', applicable for marine bird species that land on objects away from the colony, in particular species such as gulls, that may perch main-made structures, or coastal locations away from the colony. Such a further state, although introducing further modelling complexity, may be typified by very short step lengths and wide turning angle distributions, essentially representing either very small movements at a perching location or GPS signal 'noise' for a stationary individual (i.e. representing positional error in successive GPS locations).

The behaviour of seabird species may be greatly affected by time of day (Ross-Smith *et al*. 2016) and wind speed, hence at-sea surveys in particular discrete areas may therefore record species adopting different combinations of floating (or here more accurately termed 'floating'), commuting and foraging/searching behaviours. In this study, we use HMMs for three main purposes: (i) first to initially separate out these different behaviours for each species and colony; (ii) to investigate the effects that covariate of wind speed may have directly on step lengths and turning angles, and (iii) to investigate the probability of transition to and from different states under different environmental conditions. Thus, (i) can be used to descriptively determine where behaviours are concentrated, and parts (ii) and (iii) directly address the aims of this study to determine how behaviour is influenced by wind speed (and direction) and time of day.

2.3.3 Initial parameterisation of HMMs

We specified a three-state model for all species and colonies, with states numbered from 1-3, representing State 1 (floating on the sea), State 2 (commuting), and State 3 (foraging). We specified a gamma distribution for step length and a von Mises distribution for turning angles. The unobservable (hidden) time series state sequence was estimated by specifying initial starting parameters for each state. These were specified differently depending on the GPS sampling rate used at each site (Table 2). State 1 (floating) was therefore characterized as slow movement with consistent directions between points, State 2 (commuting) as fast movement with consistent direction, and State 3 (searching or foraging) as medium speed with variable direction, i.e. wider turning angles between successive GPS fixes.

Table 2 Specified regularized sampling rates from CTCRW models for species for: Gannet (GX), Lesser Black-backed Gull (LB), Kittiwake (KI), Guillemot (GU) and Razorbill (RA); data streams here refer to models including two (step length and turning angle) as done for all species and three (step length, turning angle and diving depth) as for auks for state refinement; State 1 = floating on sea (floating), state 2 = commuting, State 3 = foraging/searching.

N. states	N. streams	Species	Sampling rate (s)	State	Step mean (m)	SD	Angle mean	Concentration
3	2	LB	300	1	400	200	0	50
3	2	LB	300	2	3000	800	0	30
3	2	LB	300	3	800	500	0	1
4	2	LB	300	1	50	50	0	1
4	2	LB	300	2	150	80	0	50
4	2	LB	300	3	3000	1000	0	20
4	2	LB	300	4	500	400	0	1
3	2	GX, KI	120	1	100	50	0	50
3	2	GX, KI	120	2	1600	400	0	30
3	2	GX, KI	120	3	500	300	0	1
3	2	RA, GU	100	1	50	30	0	50
3	2	RA, GU	100	2	1000	500	0	30
3	2	RA, GU	100	3	200	100	0	1
3	3	RA, GU	100	1	20	10	0	50
3	3	RA, GU	100	2	1000	500	0	30
3	3	RA, GU	100	3	200	100	0	1
4	2	KI	120	1	20	10	0	1
4	2	KI	120	2	100	50	0	10
4	2	KI	120	3	1600	400	0	10
4	2	KI	120	4	200	100	0	1

As introduced above, we used HMMs to investigate patterns of movement in relation to covariates to address the main aims of this project. Models were conducted in two main stages representing the ‘core’ analysis (Section 2.3.4-2.3.5) including some additional further investigations (Section 2.3.6), and ‘state refinement’ analysis (Section 2.3.7), where improvements to existing state classifications were also investigated for some species – this work flow is shown in the schematic Figure 1 below. In addition to being used to (i) classify GPS points into different behavioural states, core analyses (represented by steps 1-4 in the schematic in Figure 1) also included the investigation of (ii) the direct effects of covariates on step lengths and turning angles as well as (iii) assessment of effects of covariates on transition and stationary state probabilities.

2.3.4 Core analyses: Direct effects of covariates on step length and turning angle

For all species, we initially investigated the effects of wind speed and direction on step lengths (Number 1 in schematic in Figure 1). These models specified an effect of wind speed on the mean step length parameter for all states, but for simplicity we did not fit any relationship for the variance of step length [i.e. step = list(mean=~ws, sd = ~1)]. For turning angles, we specified an effect of wind direction on the mean of angular distributions, but not for the von Mises concentration parameter [i.e. angle = list(mean=~wd, concentration = ~1)], and was undertaken using a circular-circular regression for the mean of angular distributions, using a specialised link function (see McClintock *et al*. 2018 for more information). To aid model convergence, wind speed was standardised prior to inclusion in models through the formula: $z = (x - \bar{x}) / \sigma$, where x is the existing variable, $\bar{x}$ is the mean, σ is the standard deviation and z is the new standardised variable.

2.3.5 Core analyses: effects of covariates on transition and stationary state probabilities

Also as part of ‘core’ analysis work (Figure 1), we then investigated the effects of covariates on transition probabilities between states. These models specified the full list of variables within this project, including of time of day and wind speed. However, further variables of distance to colony and Julian date were also included alongside time of day wind speed to investigate further patterns of transition between behavioral states. As above, wind speed and distance to colony were standardised prior to inclusion in the transition part of models. Consequently, trends in transition probabilities and stationary states are plotted at the mean of other covariates; see Appendix AD for translation of standardised lengths to real wind speed values. Thus, a fully saturated model was specified as: wind speed + hour of day + Julian date + distance to colony (Number 2 in schematic in Figure 1). Hour of day was specified as using the consinor function in R package: MomentuHMM (McClintock *et al*. 2018), which allowed this variable to take a circular form across the 24 hour cycle, and all other variables were initially fitted as splines (R packages:Splines) with degrees of freedom, specified as df = 4, to study potential non-linear patterns over each covariate. All models (15 in total) were allowed to compete, with best models selected through Akaike’s Information Criterion (AIC). These analyses were conducted for all species and sites.

Given the complexities of models, it was not possible to fully investigate annual patterns as part of this study. However, for Bass Rock a large volume of data has been collected, which prevented a single three-state model being used for testing effects of covariates on transition probabilities between states (due to computing constraints). Therefore, for Bass Rock only, we summarise models from individual years (2011-2015) thus providing a level of annual investigation for this colony.

2.3.6 Further analyses: wind speed, and travel alignment with wind direction

As above, wind speed may have a direct effect on movement parameters such as step length as well as how birds may transition to and from different states. However, wind direction may also play a key role in these relationships, such as the influence of birds moving in relation to headwinds, tailwinds and cross-winds of varying strength.

To better understand these interactions, we further investigated the direct influence of wind speed and direction on step lengths and turning angles. However, we restricted this analysis to the commuting state only (State 2), given that such movements to and from locations would likely yield the strongest relationships. We also restricted this analysis to three species where such patterns were perceived to be strongest: Lesser Black-backed Gulls, Kittiwake and Gannet (Number 3 in schematic in Figure 1). Following McClintock (2018), we specified an additional variable of "angular oscillation": angle_osc = $\cos(b^t - r^t)$, where b^t = bearing of travel between times t and r^t is wind speed (in radians in relation to the x-axis). This variable neatly encompassed the full range of movement direction in relation to wind direction in a circular fashion, ranging at opposite ends of the spectrum from tailwinds (angle_osc = -1) to headwinds (angle_osc = +1). By allowing interaction of this angle oscillation variable with wind speed, we were therefore able to investigate the effects on step length of birds commuting faster in tailwinds than headwinds, here hypothesizing that birds would show faster travel speeds with a direct tailwind. In addition, we further investigated whether any directional preference in relation to wind direction was observed between time steps for each state through a circular-circular regression link function (McClintock 2018).

A further hypothesis may be that as wind strength increases, but veers more to a head wind direction, then birds may find it increasingly harder to locate prey, and thus may have to switch between from floating and commuting states more often to allow more time for foraging. For the same subset of species (gulls and gannets), we then further investigated (4) the effect of movement direction alignment and wind speeds on transition probabilities between states, by specifying an interaction between wind speed and the angular oscillation parameter (ws*angle_osc) presented in model stage (3) above. This model, therefore, tested whether transition probabilities between different states was more or less likely with increasingly strong winds that were in turn increasingly more aligned with travel direction of the bird. For simplification, a linear effect was specified for wind speed for this analysis. To assess the significance of the interaction effect and the effect of including the angle_osc variable component models of ws and ws + angle_osc were fitted.

2.3.7 Refinements to state classifications

For gulls (Lesser Black-backed Gull and Kittiwake) we investigated a four-state HMM to ascertain a more likely classification of “in flight” foraging/searching state (State 4) separate from a likely “stationary resting” state (State 1), but retaining other states of floating on the sea (State 2) and commuting (State 3) (Number 5 in schematic in Figure 1); primarily this analysis was used to better approximate speeds of likely foraging/searching “in flight”, albeit still with caveats over trajectory speed as indicated in Section 2.3.4 above.

Further analysis (Number 6 in schematic in Figure 1) was also conducted for the two auk species (Guillemot and Razorbill) by incorporating a third data stream in existing three-state models, using dive depth, to give additional indication of “foraging” activity, thus refining States 1 and 3 in the original model. This was achieved by inclusion of pressure sensor data from TDRs that were attached to a subset of birds from some colonies. TDR pressure recordings were taken at one second intervals. After converting pressure readings into depth (m), each record was identified as being greater or less than 5 m deep. To align TDR data to GPS points, TDR recordings were grouped into two minute segments, and matched to the nearest two minutes corresponding to the GPS points. The proportion of TDR readings deeper than 5 m were calculated for each two minute segment. Dive proportion was then used as a third variable within HMMs along with step length and turning angle, to help split behaviours – foraging states were therefore defined as having a higher proportion of dives.

2.3.8 Summary information from HMMs and assigning behaviours to GPS data

Mean step lengths (from a gamma distribution) and angle parameters (mean and concentration from Von Mises) for each state were obtained from model outputs. The matrix of transition probabilities for each state were also derived from standard model outputs showing the overall probabilities of each species and colony remaining within a state, or switching to another in a 3x3 matrix (for the three-state models). HMM model summaries also provided an indication of the speeds of each state through mean and SD values of step lengths (over constant temporal sampling rate) estimated for each state. However, to gain further perspective into the full distribution of speeds for each state for each species and colony, we produced boxplots of speed distributions based on state classifications back on the positional data feeding into the HMM.

This was achieved through the viterbi algorithm in R package:momentuHMM (McClintock 2018) to derive the best-estimated state for each GPS fix. State-assignments were made using the best-fitting covariate model, i.e. including effects such as wind speed and time of day (Figure 1). These distributions were produced across all variables, such as varying conditions and were carried out for all species for three-state models (floating, commuting, foraging/searching), and also for four-state models for gulls (floating, commuting, foraging/searching, perching). In a similar way, we summarised the time spent per state for all individuals at each colony to give an indication of time budgets at each colony, again using the state-assigned categorisation of individual GPS fixes.

To visualise the direct effects of wind speed on step length and turning angle, we used the plot.momentuHMM function within the momentuHMM R package (McClintock *et al*. 2018) to present these relationships graphically for each state. We then used the same plotting function to visualise the effects of each covariate on transition probabilities; standard outputs here include 3x3 matrices of panel plots depicting how the probability changes over the covariate of interest for each state-switch (i.e. 1-2, 1-3, 2-1, 2-3, 3-1, 3-2) as well as for remaining in each state (i.e. 1-1, 2-2, 3-3). These plots are produced for each covariate retained in final minimum adequate models for each species and colony. Finally, visualisations are made for ‘stationary-state probabilities’, that combine the transitional probabilities information as above into a fixed probability of a point being classified in a particular state; these latter plots are useful to summarise how overall behaviours (and hence time budgets within such behaviours) change in relation to each covariate, such as time of day or over increasing wind speed. Equivalent graphical outputs are also presented for further analyses conducted using the interaction between wind speed and angle_osc.

2.3.9 Interpretation of states and a priori caution

HMMs offer a means of classifying positional information based on movements between successive fixes. This means that the summaries presented in this report are trajectory speeds, and are, therefore, influenced by the sampling rate available for birds, which varied between 100s and 300s. Individual animals may carry out many behaviours at much finer scales between the intervals recorded, and so it is likely that in these intervals, the classification will miss such complexities, and that would require much finer resolution or other ways of recording behaviour, such as through accelerometry. The behaviours from HMMs therefore serve as a coarser-grained measure of behaviour. This particularly applies to the state of foraging/searching as suggested can be identified as an HMM state through medium-distance step lengths and wide turning angles, representing an individual turning back and forth over an area and slower speeds than, for instance commuting. However, for all species in this project foraging/searching may also encompass periods on or below the sea surface associated with birds capturing prey and associated functional rest periods. Some data categorized as foraging/searching may be potentially area-restricted foraging (e.g. Weimerskirch *et al*. 2007), however, even in flight a bird may move to and from the same location where it may be foraging, but the interval of GPS suggests that the bird has not moved far and thus recording a slow trajectory speed. The movement between fixes may also be non-linear in speed. The combination of these factors means that for the state of foraging/searching, although likely associated with foraging activity, cannot be used to with certainty to indicate “in-flight” activity.

Further, for gulls (Lesser Black-backed Gull and Kittiwakes), birds may perch or rest on structures when away from the colony, either at sea or around coastlines. The models under analysis steps 1-4 (in Figure 1) using a three state model are considered appropriate for assessment of transition probabilities for the core aims of this project. However, where feasible, we conducted further refinements to HMMs to attempt to resolve “foraging/searching” behaviours more precisely, and attempt to separate out potential “perching” activity through a further behavioural state.

2.4 Utilisation distributions

Following the HMM behaviour classification all data had equal sampling rates. We, therefore, calculated utilisation distributions for each subset of behaviour, wind speed, and day period using fixed kernel density estimation (KDE; Worton 1989) with the R package:adhabitatHR (Calenge *et al*. 2006) pooled across all years and individuals. The 50%, 75% and 95% KDEs of the utilisation distribution, were taken to represent the core, middle, and total areas, respectively. For each species and colony combination a range of bandwidth values were plotted and an ad hoc selection was made for each based on visual assessment. Any individuals with fewer than five fixes in any given subset were excluded.

To investigate how the distributions of each species and colony for particular behaviours vary in relation to wind speed and time of day, we further subsetted the data for categorical splits representing these variables. To test whether distributions varied between day and night, we used the timing of dawn and dusk to delineate periods of 'day' and night' in the datasets. To assess whether distributions varied over wind speed, as a proxy for environmental conditions, KDEs were calculated separately for data subset for two levels of wind speed, high (>=8 m/s) and low (<8m/s). This threshold corresponds to Beaufort Scale 5+ and an approximate Douglas Sea Scale 4 for the high wind subset, representing conditions that at-sea surveys are less likely to occur. We also investigated a threshold of 10 m/s to assess more extreme conditions but sample sizes were too imbalanced between the groups, for all species fewer than 5% of the total number of GPS fixes were obtained in conditions > 10m/s, except for Gannet (7.6%). This provided a 4x4 panel for each state, for each species and colony. We subset the data at the individual fix level, i.e. partial trips may be included in either group, to better represent distribution under different conditions which may have changed over the duration of an individual trip away from the colony.

For a semi-quantitative assessment of sample sizes within each category split of the data, we use the following logic to show varying degrees of confidence that can be placed on interpretations, such as overlap analysis of distributions (see also Appendix AA for a summary of sample sizes).

(1) Lowest: Less than 100 fixes or five or fewer birds provided data per state and category split of the data (i.e. day-low, day-high, night-low, night-high).
(2) Low-medium: 101-250 or 6-10 birds.
(3) Medium: 251-1000 fixes or 11-15 birds.
(4) Medium-high: 1001-2500 fixes or 16-20 birds.
(5) Highest: More than 2500 fixes or 25+ birds.

In particular where there is the lowest amount of data and thus confidence in the distributions, this is highlighted, indicating that results should be treated with a high degree of caution. Maps of distributions that contained lowest confidence are also highlighted through a red border placed around the image. Further, we also highlight where the proportion of available data falls below 5% of the total available for the state identified in the HMM for the specific category split of the data. This additional assessment provided a further quantification useful for showing where perhaps sufficient sample sizes existed under the above confidence levels, but that would otherwise mask disparity in proportionality of data among each category.

The issues of sample size influencing utilisation distributions is well-known (e.g. Soanes *et al*. 2013), and here we also acknowledge this as a more general point of caution within this section of the analysis.

2.5 Overlap analyses

We further tested the overlap within and between utilisation distributions over varying conditions and times of the day by using Bhattacharyya's affinity (BA) index (estimated using the R package:adhabitatHR, overlap function). We carried out pair-wise comparison of the different splits in the data, i.e. 'conditions' of day-low, day-high, night-low and night-high, with the first of these, day-low, considered representative of data that may be obtained from aerial and boat-based surveys. Overlap indices were then generated for each pair of distributions for the total area use (95% KDE) and the core area use (50% KDE). We qualitatively assigned degrees of overlap to the BA indices (ranging from 0.0, no overlap to 1.0 total overlap), given as follows: very low 0-0.2, low 0.2-0.4, moderate 0.4-0.6, high, 0.6-0.8 and very high 0.8-1.0. These comparisons were also carried out for each state 1-3 from the main three-state HMMs.

Caution, however, is still required in interpretation of these results. Given the implications of increasing KDE size with increasing numbers of birds and spans of data (Soanes *et al*. 2013, Thaxter *et al*. 2017), we did not formally compare areas of KDEs among these differing conditions. However, overlaps may also be sensitive to comparing KDEs with differing sample sizes. We, therefore, highlight the smallest number of points behind splits in the data, here given as n = 50 or fewer, as being of 'low confidence'.

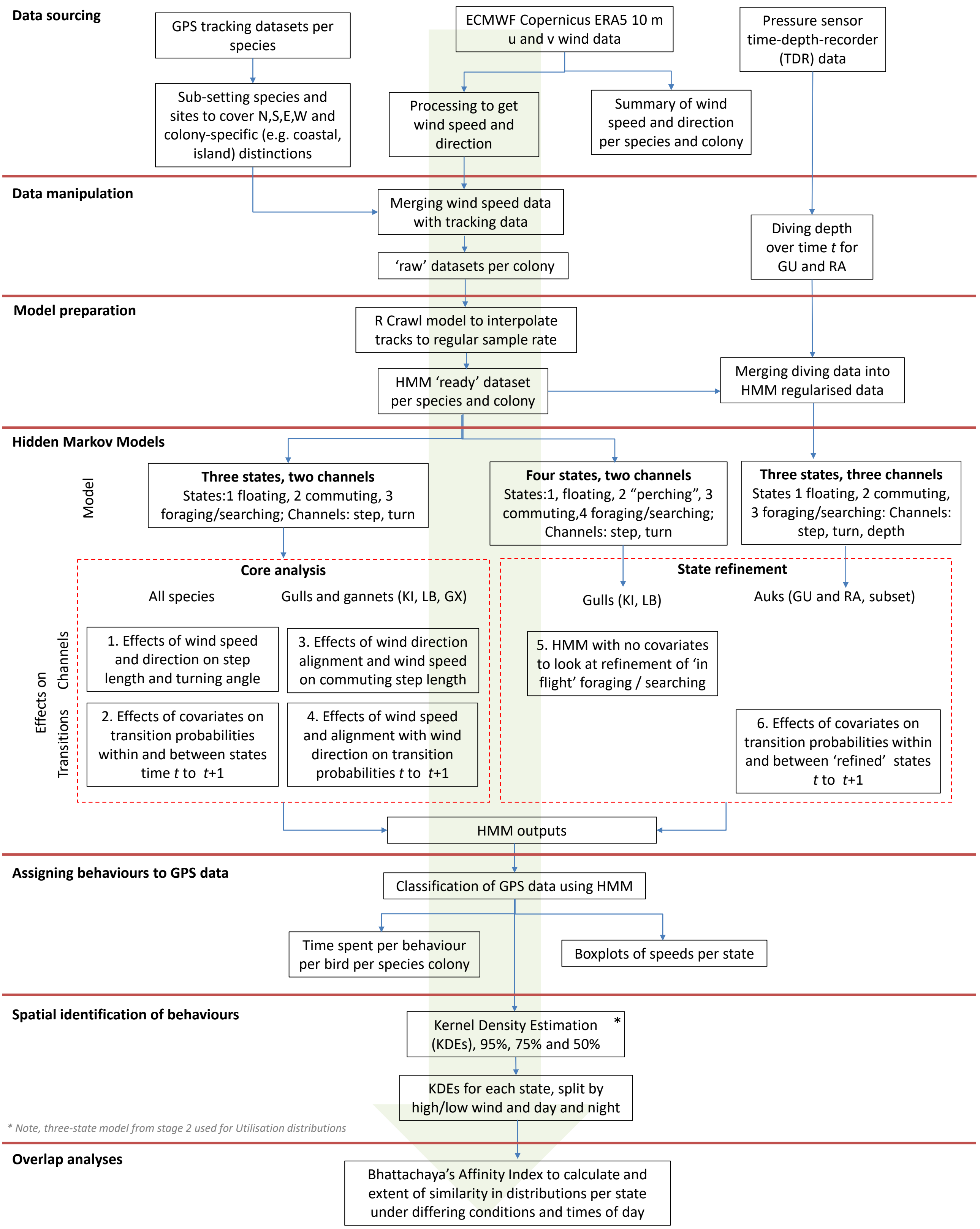


Figure 1 Schematic representing the work flow in this project.

3 Results

3.1 Northern Gannet

3.1.1 Comparison of wind speed use vs availability

Comparisons of wind speeds experienced and those available within the wider area were made for all colonies – see Table 3, Figure 2 and Appendix AB.

For Bass Rock, values of proportional use were slightly lower than available for Bass Rock for both 8 m/s and 10 m/s splits of the dataset, whereas at Alderney the reverse was true. It is not possible here to fully tease out these drivers, which would require further analysis, however, these differences may reflect colony variations in foraging activity.

Table 3 For Gannet, summary of the proportions of tracking data by wind speed thresholds of more than 10 m/s or more than 8 m/s, and further comparing wind speeds encountered by birds (‘used’) vs wind speeds ‘available’. Assessment is made both (i) within the full months that tracking was carried out and (ii) for the precise tracking date-times, for all Copernicus grid squares that birds overlapped with; proportions for ‘use’ data are calculated on the data modelled within HMMs, thus each data point is a GPS fix; for ‘available’ calculations, each data point is an hourly wind speed estimate for each Copernicus grid square.

		Used (%)		Available (tracking period, %)		Available (all months, %)	
Colony / State	**Tracking months and years**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**
Alderney	Jun 2011, 2013 – 2015	25.61	12.22	21.33	8.41	23.22	8.74
Bass Rock	Jul – Aug 2010, Jun – Aug 2011, Jul – Aug 2012, Jun – Aug 2015	19.01	6.53	26.42	10.4	28.56	12.04

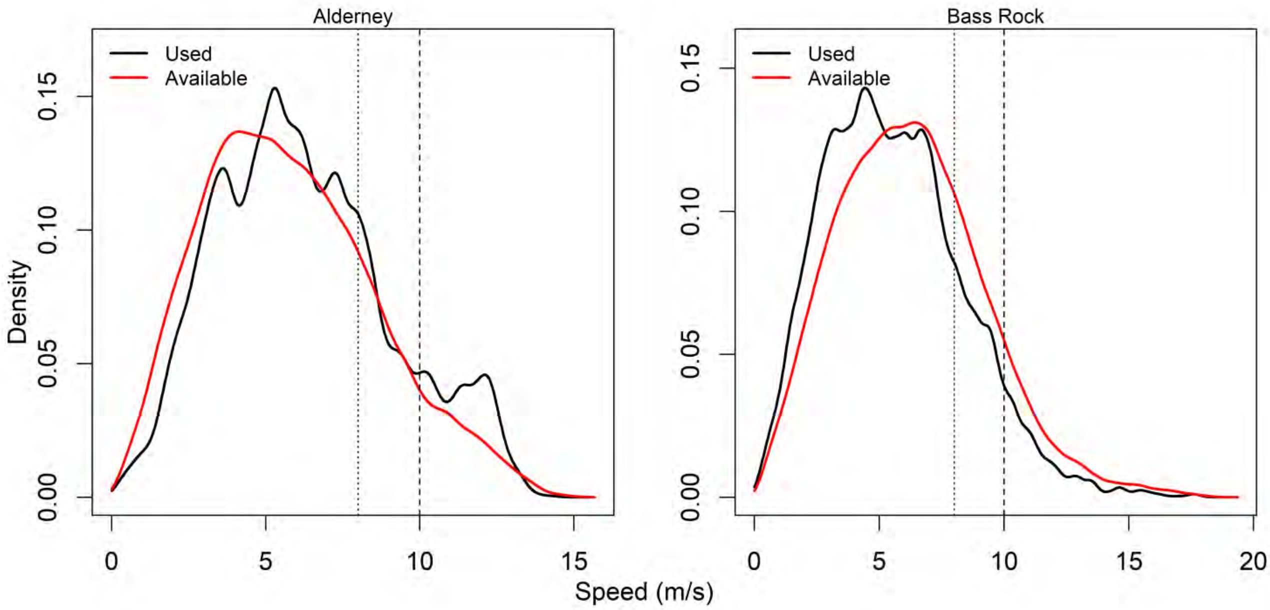


Figure 2 For Gannet, histograms of wind speed during the period of study at each site that was available for birds to experience, vs that actually experienced when on foraging trips (‘availability’ vs ‘used’); data here are pooled across each tracking period per bird in each year for each colony.

3.1.2 Model summary

For Alderney and Bass Rock mean step lengths (from gamma distribution) and angle parameters (mean and concentration from Von Mises) for each state are shown in Table 4 below. These indicated consistent direction for slower floating on the sea State 1 and faster commuting State 2, in contrast to State 3 with wider turning angles and a lower consistency in direction between fixes (Appendix AC).

Table 4 For Gannet, summary of mean ± SD step length and turning angles (mean, concentration) for each site.

	Step			**Turn**		
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/ search)**	**1 (floating)**	**2 (commuting)**	**3 (forage/ search)**
Alderney	96.35 ± 52.24	1645.48 ± 440.29	322.18 ± 397.34	0, 61.51	0, 18.98	0, 0.95
Bass Rock 2010	42.31 ± 22.36	1772.07 ± 410.64	360.39 ± 470.03	0, 14.38	0, 22.92	0, 0.55
Bass Rock 2011	46.53 ± 24.74	1636.53 ± 385.42	333.88 ± 431.06	0, 16.18	0, 19.11	0, 0.47
Bass Rock 2012	42.75 ± 21.63	1761.88 ± 435.62	409.61 ± 499.06	0, 13.22	0, 21.07	0, 0.49
Bass Rock 2015	35.85 ± 18.49	1737.19 ± 410.03	423.63 ± 535.22	0, 26.94	0, 49.08	0, 1.35

For Bass Rock, models were run separately for each year (see methods and Appendix AC). Mean step lengths and turning angles, however, were fairly consistent across the four year-specific models (2010 – 2012, 2015), hence we do not believe that this meaningfully changed the behavioural classifications between years for this colony as a result of using slightly different step and turning angle distributions per year for specifying behavioural classifications.

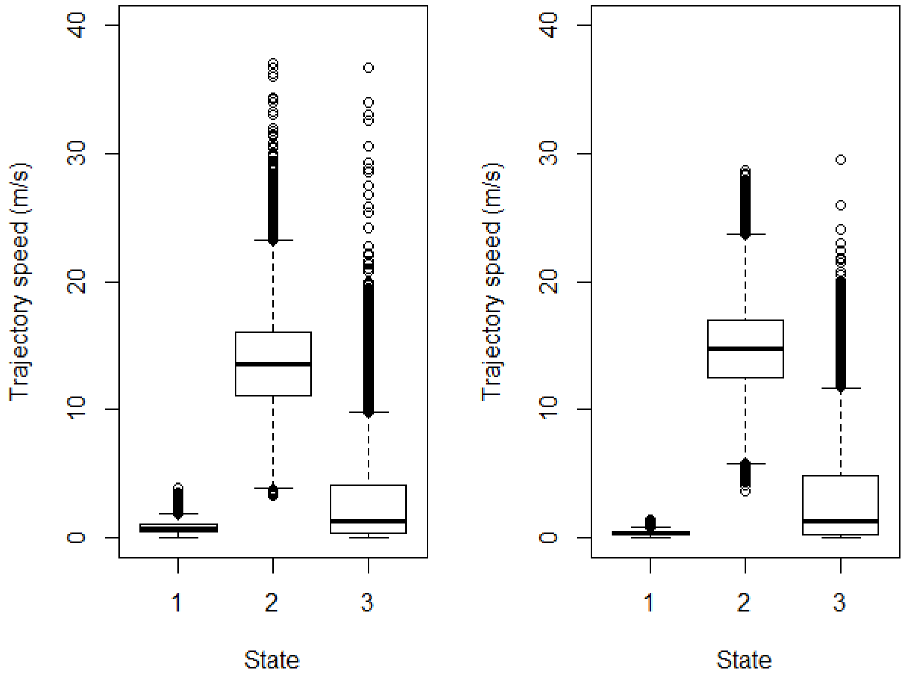
At all colonies, direct transitions to and from states 1 (floating) and 2 (commuting) were rarer in the datasets (see Dean *et al*. 2013). Most frequently, fixes following a particular state were most likely to be classified as the same state again. However, where switches did occur, typically floating on the sea was preceded and succeeded by locations classified as state 3, with further switches occurring between commuting and foraging (Appendix AC).

3.1.3 Travel speeds

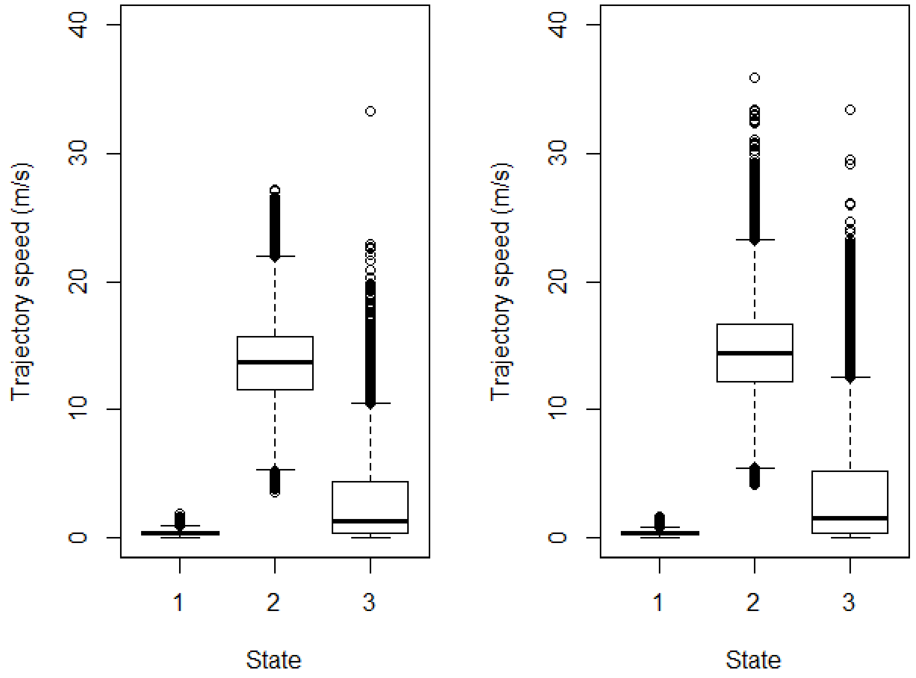
Models indicated that during commuting (using the mean parameter estimate above), on average (over other covariates), Gannets flew at a mean of 13.60 m/s and 14.37 m/s for Alderney and Bass Rock (Table 5, see also Figure 3); note for Bass Rock models from individual years were used, which are broken down further in Table 5. Note, these values were obtained across headwinds and tailwinds, and given slower travel in stronger headwinds, and faster travel in tailwinds (Appendix AD), represent the mean wind travel speed at mean wind speed with no directional bias during commuting. Foraging/searching speeds were low, and often lower than that speed expected to be needed to sustain powered flight, suggesting strongly much of the activity for State 3 included other behaviours associated with foraging, such as diving, and associated phases on the sea (see Section 2.3.9 for further anticipation of this bias).

Table 5 For Gannet, summary of speeds per state (m/s), as obtained through classification of tracking data using HMMs.

Colony / State	1 (floating)	2 (commuting)	3 (forage/search)
Alderney	0.72 (0.47 – 1.05)	13.60 (11.15 – 16.01)	1.25 (0.34 – 4.15)
Bass Rock 2010	0.32 (0.21 – 0.45)	14.78 (12.53 – 17.00)	1.28 (0.28 – 4.87)
Bass Rock 2011	0.35 (0.28 – 0.51)	13.70 (11.55 – 15.72)	1.27 (0.30 – 4.38)
Bass Rock 2012	0.35 (0.22 – 0.46)	14.53 (12.18 – 16.96)	1.77 (0.42 – 5.53)
Bass Rock 2015	0.27 (0.18 – 0.39)	14.33 (12.25 – 16.54)	2.15 (0.40 – 5.88)
Bass Rock (all yr)	0.31 (0.21 – 0.45)	14.37 (12.16 – 16.63)	1.58 (0.35 – 5.24)


(a) Alderney

(b) Bass Rock 2010


(c) Bass Rock 2011

(d) Bass Rock (all years)

Figure 3 For Gannet, boxplots of speed for States 1, 2 and 3 (floating, commuting and foraging/searching) at Alderney and Bass Rock respectively.

3.1.4 Effects of wind speed on step length (speed)

For Alderney, models specifying a simple effect of wind speed on step length showed a general (shallow) decreasing trend in step length over increasing wind speed for commuting (β = -0.056), corresponding to a *ca*. 500 m (per 2 min) reduction in step length (ca 4.2 m/s travel speed) over increasing wind speed (between 0.03 – 14.0 m/s, corresponding to standardised wind speeds (-2.21 – 3.02) (Appendix AE). Slight increases in step lengths were recorded for floating on the sea and foraging (β = 0.016, β = 0.006). Similarly, for Bass Rock (Appendix AE), individual year models also showed negative beta coefficients for wind speed and commuting (2010, β = -0.040; 2011, -0.053, 2012 -0.054, 2015 -0.033), and (mainly) increases for floating (β = 0.046, β = -0.010, β = 0.018, β = 0.032) and foraging (β = 0.020, β = 0.038, β = 0.054, β = 0.031). For commuting, such patterns with wind speed alone (without any directional component), are likely due to the negative effects of crosswinds and headwinds, outweighing the positive gains from headwinds, but also linked to complexities of colony location and route taken on outward and inward commutes during trips, and the prevailing wind speed and direction over the tracking period; for instance during 2011, winds were more northerly and north-westerly than westerly mean flows in 2010, which could have affected relationships compared to other years; however, patterns with head and tail winds reveal much clearer patterns with commuting (Appendix AE).

For Alderney, models for Gannets including effects of wind speed*angle_osc, showed a strong positive coefficient value for the interaction (wind speed:angle_osc *β* = 0.408), indicating faster commuting speeds in faster tailwinds (angular_osc -1 = headwind, +1 = tailwind), and the opposite in a headwind. There was little influence of birds aligning commuting with prevailing wind directions, i.e. turning with the wind during commuting (*β* = -0.012). Similarly, for Bass Rock, wind speed:angle_osc parameters were as follows: *β* = 0.407, 0.431, 0.387 and 0.358 for 2010 – 2012 and 2015, respectively, indicating the same general pattern (Appendix AE).

3.1.5 Transition effects between states in relation to covariates

The best-fitting model, as assessed by AIC, was the full model with all covariates, being best across all colonies (Appendix AF); transition and stationary state probability plots are given in Figure 4, Figure 5 and Appendix AD.

As with other species, there were clear patterns for each of the three colonies in distance from the colony at which transitions occurred from floating to commuting and commuting to foraging (see Appendix AG). Over Julian date patterns across the gannet datasets were varied and less clear given the shorter time span for this variable included in models (as compared to Lesser Black-backed Gulls where a wider period of time could be modelled).

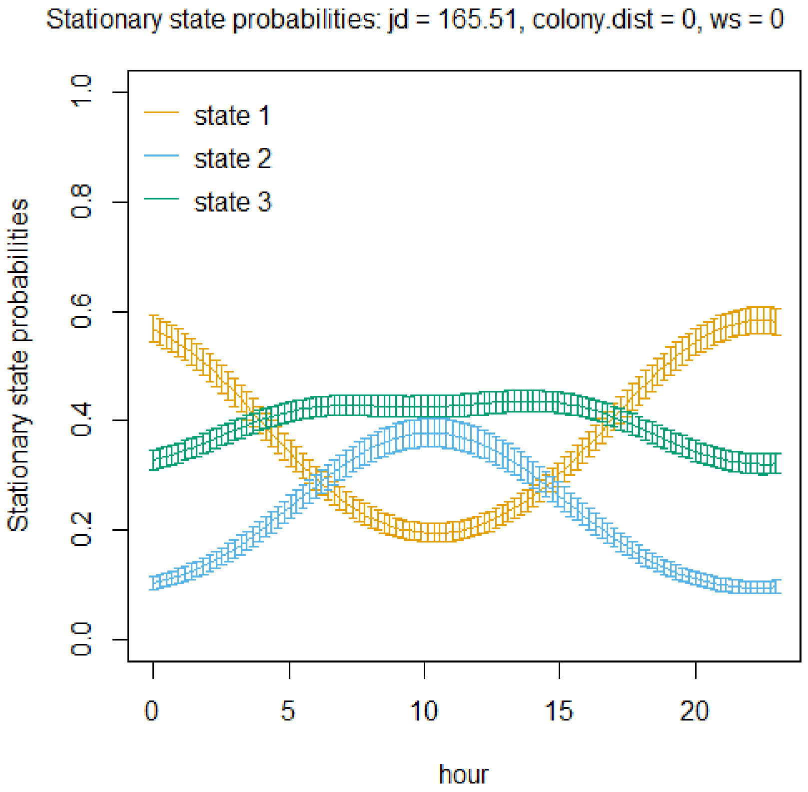
As with other species, the models showed very strong patterns over hour of the day. At both colonies, gannets were much more likely to be floating on the sea overnight and foraging and commuting in the day. For Bass Rock, patterns across years were also similar, and matched those of Alderney, with a small double peak in stationary state classifications seen for foraging/searching across the day, and similar timing of a peak in commuting behaviour, at the expense of reduced probability of remaining in State 1 (floating on the sea) between times t and t + 1.

Spline models for the wind speed variable indicated a complex pattern over increasing wind speed. Typically, the probability of a bird remaining in the state of floating decreased as wind speed increased, switching to foraging/searching, although for Bass Rock 2012 the spline was less strong. These patterns were clearer when investigated further as a simplified linear term in interaction with the variable angle_osc for alignment of travel with wind direction.

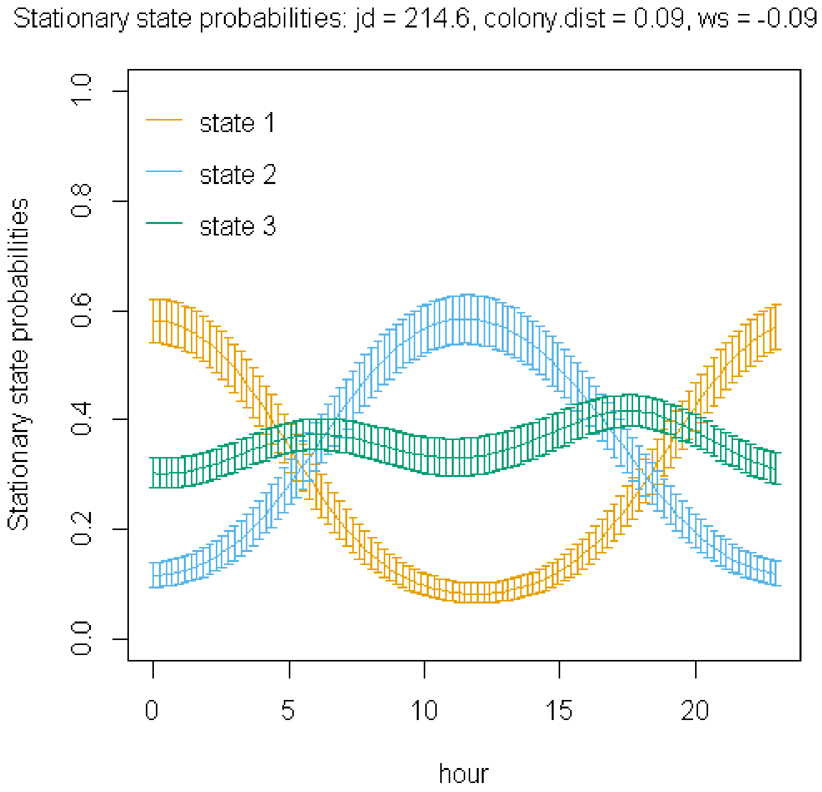
In headwinds the probability of remaining in the floating State 1 between time t to t+1 decreased over increasing wind speed. However, the probability of switching from floating to foraging from time t to t+1 in a headwind increased over increasing wind speed. This pattern was evident but less apparent for Alderney. However, at both Bass Rock and Alderney, the balance of remaining and switching between different states yielded a similar stationary state probability for floating on the sea, with, particularly at Bass Rock very strong patterns in birds being classified as floating as head-wind speed increased.

When viewed in terms of the varying tail- and headwind spectrum of values (+1 to -1) at the strongest wind speeds where patterns were most pronounced, the patterns observed were similar for gannets compared to other species in this study. As winds veered towards a headwind (-1), clear increases in commuting time and reductions in floating time were seen in stationary state probabilities with foraging/searching increasing markedly with increasing. For tailwinds, birds remained in the state of floating (t to t + 1) more often, and did not switch as often to foraging/searching, which for Bass Rock in particular, further resulted in reduced time spent foraging/searching in tailwinds, although for Alderney the pattern indicated relatively consistent foraging over the head-tail wind spectrum.

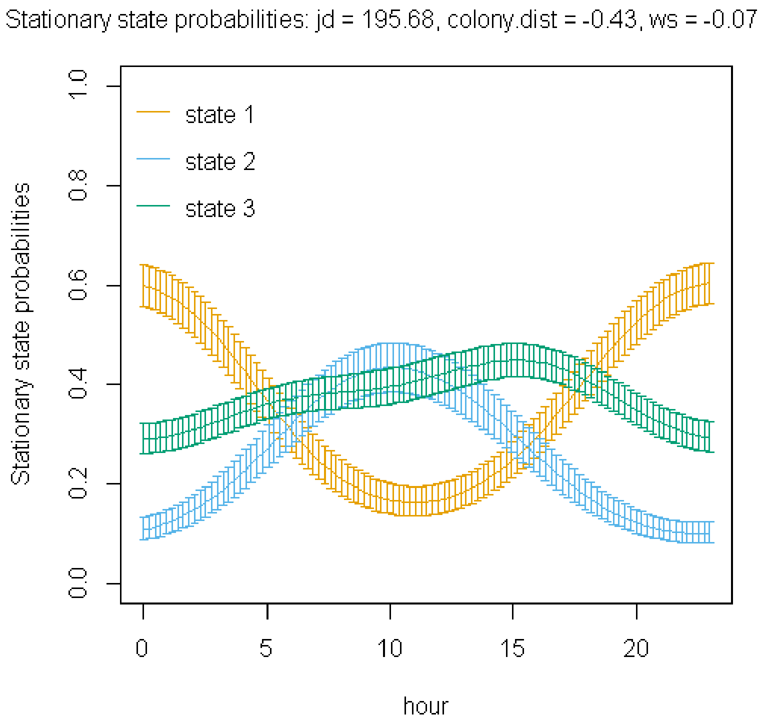
(a) Alderney all years



(b) Bass Rock 2010



(c) Bass Rock 2011



(d) Bass Rock 2012

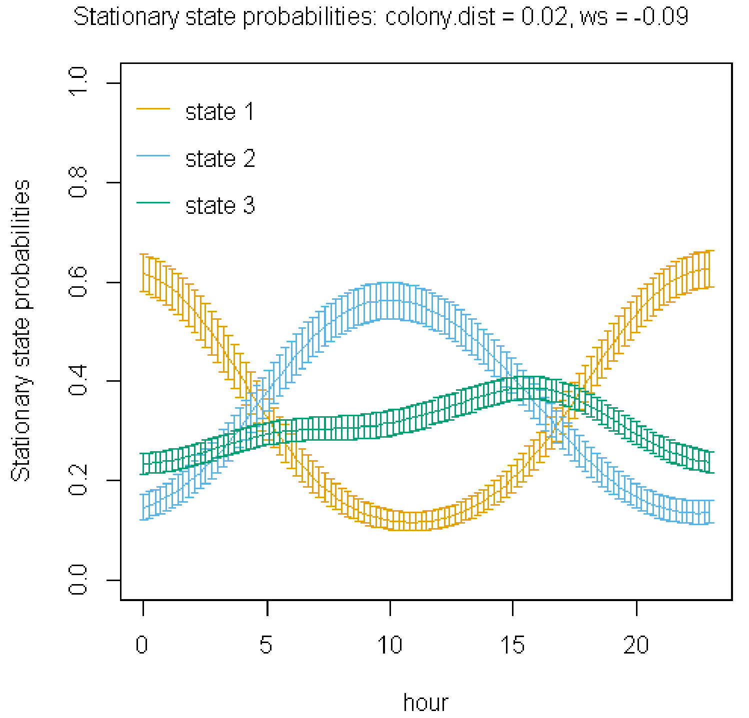
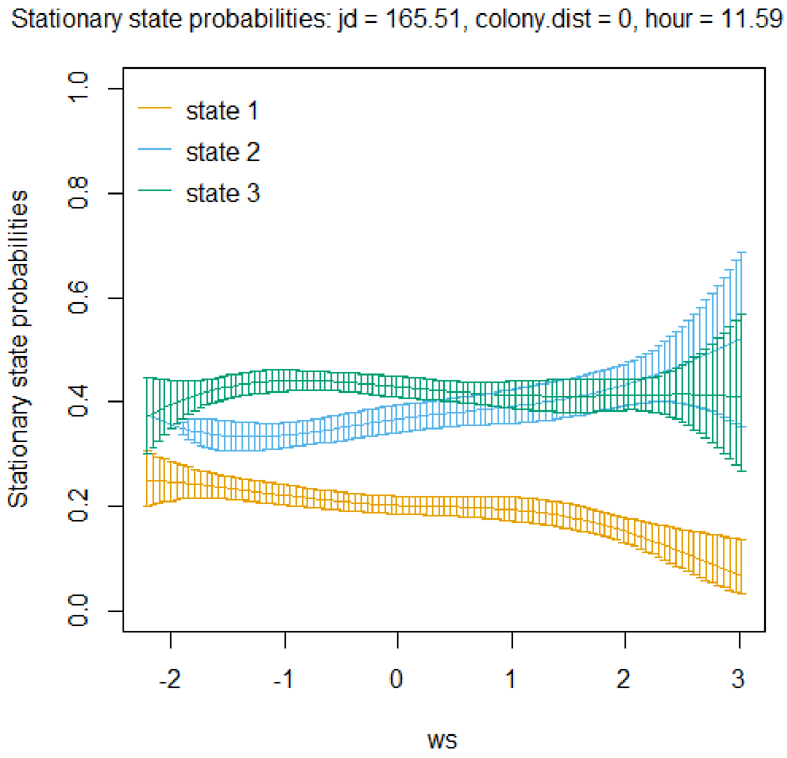
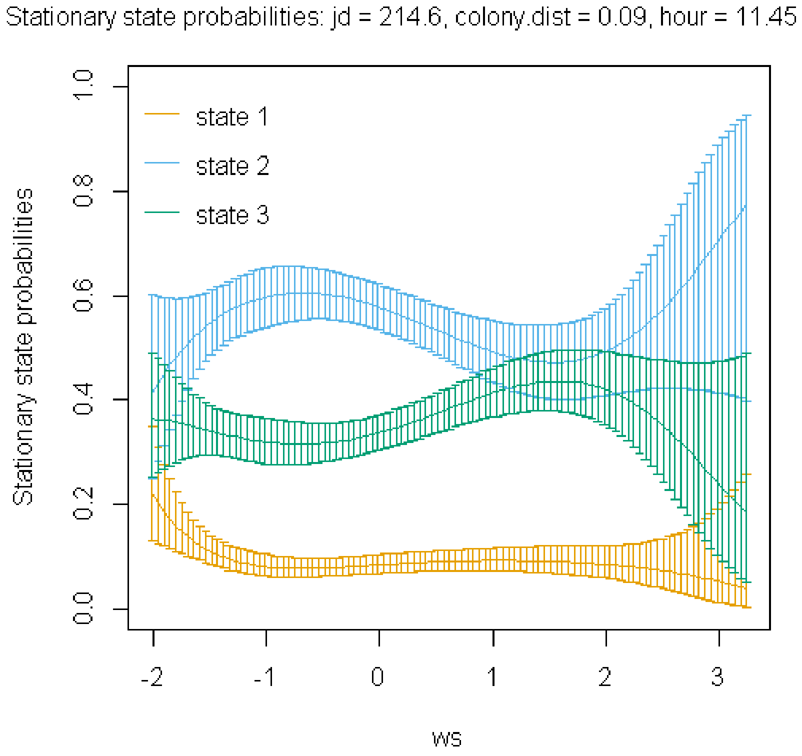


Figure 4 For Gannet, stationary state probabilities for the variable of cosinor(hour of day) for States 1, 2 and 3 (floating, commuting and foraging/searching). In all four graphs State 1 begins at the top, State 2 the bottom and State 3 the middle.

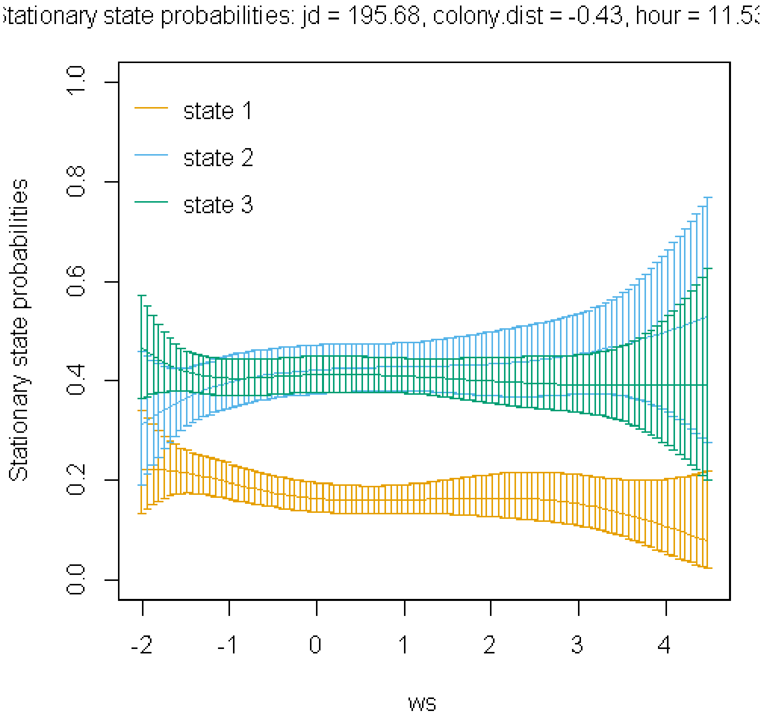
(a) Alderney



(b) Bass Rock 2010



(c) Bass Rock 2011



(d) Bass Rock 2012

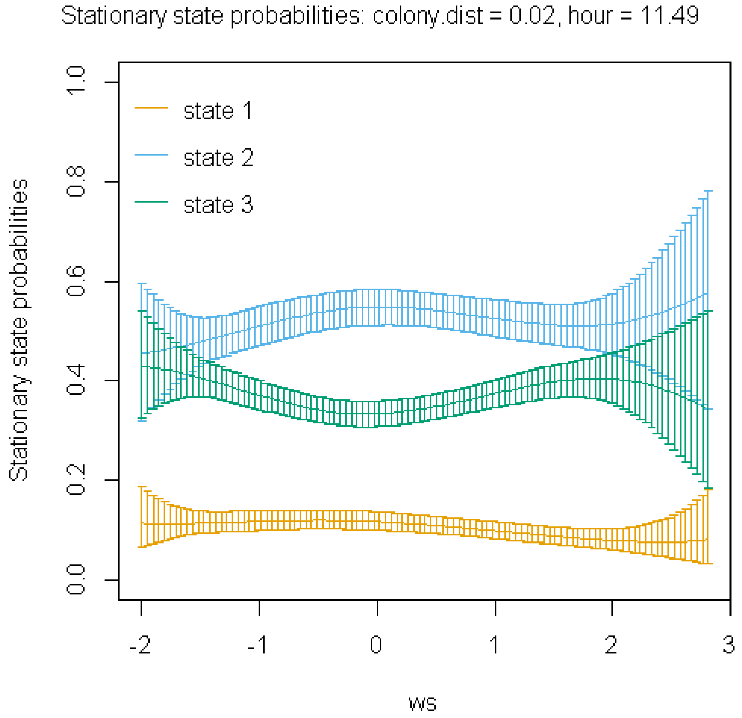


Figure 5 For Gannet, stationary state probabilities for the variable of bSpline(wind speed), fitted as a standardised variable for States 1, 2 and 3 (floating, commuting and foraging/searching).

3.1.6 Time in states

The range of duration of data per bird and the proportion of time spent in different states are shown in Table 6. As birds with fewer data had less time to demonstrate their overall time spent in different states, we used information from birds with more than ten hours of data, to exclude any very small tracking durations that could otherwise skew any patterns.

Table 6 For Gannet, estimated time spent in states for each colony for birds at each colony across years; note occasionally initial movement models could not be fitted due to a lack of data available for some individuals, hence the effective sample size feeding into assessments is provided in brackets.

			Duration of tracking			**Proportion time spent per state**		
Colony	**No. birds total (modelled)**	**Years**	**No. birds > 10 hrs tracking data**	**Duration (hrs) mean ± SD per bird**	**Tracking data range (hrs)**	**1 floating mean ± SD**	**2 commuting mean ± SD**	**3 foraging / searching mean ± SD**
Alderney	61 (61)	2011, 2013 – 2015	58	107.36 ± 62.43	5.1 – 234.1	0.36 ± 0.09	0.27 ± 0.07	0.37 ± 0.08
Bass Rock	133 (133)	2010 – 2012, 2015	130	101.13 ± 44.94	3.8 – 270.4	0.32 ± 0.08	0.35 ± 0.13	0.35 ± 0.10

3.1.7 Utilisation distributions

Figures depicting utilisation distributions for each colony are shown in Appendix AH – see also methods for further description. Depending on the colony, there was a smaller amount of data from the very highest wind speeds (greater than 8 m/s) – see also section above comparing use and availability for wind speed distributions.

Where sample sizes of number of fixes and birds used to compute utilisation distributions was low, here taken as less than 100 fixes and less than five birds for the lowest amounts of data (see Appendix AA and methods), then confidence in the overlap result is considered lowest, and is here indicated as requiring a high degree of caution in interpretation of results. Also highlighted is the proportion of fixes available per split of data, with proportions of less than 5% of the total for the state also flagged up as requiring caution.

For gannets, sample sizes are here considered sufficient for both Alderney and Bass Rock in different conditions based on these sample size criteria. However, we also caution the comparison between utilisation distributions with very different sample sizes, as this in itself a recognised issue (see methods). Further, night-high wind categories for both colonies for the state of commuting and the night-high foraging/searching category at Bass Rock represented less than 5% of the total data for each state per colony.

3.1.8 Overlap indices

Overlaps between states in different conditions and times of the day are visualized in Appendix AI, and summarised in Table 7.

For Alderney, most 95% KDEs, representing total area usage, showed moderate to very high levels of overlap (ca. 0.4+, see methods, one being a perfect match and zero being completely different) between the daytime low-wind conditions (taken here as representative of similar conditions that aerial surveys would encounter), and the other scenarios of day-high wind, night-low wind and night-high wind scenarios across different states; highest overlaps in distributions were seen for day-low vs day-high conditions for commuting (state 2, BA = 0.9) and least for day-low vs night-high for State 3 foraging (BA = 0.53). Core area use (represented by 50% KDEs) showed that there were lower overlaps that for 95%, being between 0.14 (very low overlap, day-low vs night-high foraging) and 0.73 (day-low vs day-high, for commuting). We also note that State 1 floating had consistently lower 95% and 50% KDE overlaps than other states.

For Bass Rock, similar to Alderney, State 1 resting showed lower overlaps for day-low vs other conditions, with the lowest overlap for total area use (95% KDE) for day-low and night-high (low degree of overlap, BA = 0.4), and equal lowest overlap of the core 50% KDE for the same pairwise comparison. Highest overlaps at Bass Rock for both the 95% and 50% KDEs were seen for the day-low vs day-high comparison of commuting (BA = 0.88, ‘very high’ overlap and 0.72, ‘high’).

For both colonies across states, overlaps for the night-high vs night-low comparison (min 95% KDE, BA = 0.44; min 50% KDE, BA = 0.17, Bass Rock floating state) were slightly lower than day-high vs day-low comparisons (min 95% KDE, BA = 0.52; min 50% KDE, BA = 0.19, Bass Rock floating state). However, for both colonies, there were bigger differences when comparing day-low and night-low, and day-high and night-high; BA indices were higher (for 95% and 50% KDEs) between day and night in low wind conditions, than comparing day and night in high wind conditions, which was true across all states (e.g. lowest 95% KDE BA indices across colonies and states for daytime low vs night low = 0.69 compared with day-high vs night-high, BA = 0.46, again for Bass Rock floating state). In generalising, this may indicate a stronger driver of wind speed than time of day for distributions.

Table 7 For Gannet, overlap indices (Bhattacharyya's Affinity Index) for pair-wise combinations of utilisation distribution assessing similarity in 95% KDEs (and 50%, brackets) for different levels of day and night, and high/low wind and States 1, 2 and 3 (floating, commuting and foraging/searching); bold highlights indicate comparisons of greatest interest, comparing the equivalent conditions when surveys are made (low wind daytime) to other conditions.

(a) Alderney

state		day.high	day.low	night.high
Floating (state 1)	day.low	**0.61 (0.34)**		
	night.high	0.54 (0.25)	**0.55 (0.21)**	
	night.low	0.53 (0.28)	**0.75 (0.58)**	0.53 (0.2)
Commuting (state 2)	day.low	**0.9 (0.73)**		
	night.high	0.62 (0.29)	**0.58 (0.26)**	
	night.low	0.65 (0.31)	**0.74 (0.39)**	0.51 (0.21)
Foraging/searching (state 3)	day.low	**0.75 (0.6)**		
	night.high	0.54 (0.21)	**0.5 (0.14)**	
	night.low	0.58 (0.39)	**0.78 (0.68)**	0.49 (0.15)

(b) Bass Rock

state		day.high	day.low	night.high
Floating (state 1)	day.low	**0.52 (0.19)**		
	night.high	0.46 (0.22)	**0.4 (0.15)**	
	night.low	0.44 (0.16)	**0.69 (0.49)**	0.44 (0.17)
Commuting (state 2)	day.low	**0.88 (0.72)**		
	night.high	0.62 (0.4)	**0.65 (0.38)**	
	night.low	0.79 (0.65)	**0.87 (0.8)**	0.62 (0.39)
Foraging/searching (state 3)	day.low	**0.68 (0.33)**		
	night.high	0.51 (0.24)	**0.46 (0.15)**	
	night.low	0.56 (0.25)	**0.74 (0.53)**	0.45 (0.16)

3.2 Lesser Black-backed Gull

3.2.1 Comparison of wind speed use vs availability

Comparisons of wind speeds experienced and those available within the wider area were made for all colonies – see Table 8, Figure 6 and Appendix AB.

For all Lesser Black-backed Gull colonies, the conditions that birds experienced revealed much lower percentages of use of wind speeds more than 8 m/s and 10 m/s, compared to that available over the tracking period and the full months in which tracking was carried out (Appendix AB). The tracking period availability also closely matched that available within the months of tracking, since the attachment method for gulls in this study was a harness, which lasted over long period, thus covering the majority of the months in which tracking was conducted.

The apparent lack of use of high winds was therefore pronounced for Lesser Black-backed Gulls. This is due to a couple of different reasons – the use of offshore areas for Lesser Black-backed Gulls is biased to particular times in the breeding season, typically the mid to -late chick rearing period ca. June-July (see e.g. Thaxter *et al*. 2015). At other times, area use is inshore and coastal and so has not been included in these assessments. Further, the data included for use-availability assessment includes a wide period of the year from March to August, when Lesser Black-backed Gulls were associated with their breeding colony. Given there is a lack of use of offshore areas at times of the year such as March and April (typically pre-breeding) when conditions are likely much windier offshore, and use of offshore areas in June – July being more likely to coincide with periods of calmer weather, this would explain the lack of use of high wind speeds for this species.

Table 8 For Lesser Black-backed Gull, summary of the proportions of tracking data by wind speed thresholds of more than 10 m/s and more than 8 m/s, and further comparing wind speeds encountered by birds ('used') vs wind speeds 'available'. Assessment is made both (i) within the full months that tracking was carried out and (ii) for the precise tracking date-times, for all Copernicus grid squares that birds overlapped with; proportions for 'use' data are calculated on the data modelled within HMMs, thus each data point is a GPS fix; for 'available' calculations, each data point is an hourly wind speed estimate for each Copernicus grid square.

		Used (%)		**Available (tracking period, %)**		**Available (all months, %)**	
Colony / State	**Tracking months and years**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**
Walney	May – Aug 2014, Mar – Aug 2015 – 2018	10.68	2.83	26.04	11.2	26.76	11.33
Skokholm	May – Aug 2014, Mar – Aug 2015 –2017	11.96	1.77	31.69	14.27	31.98	14.67
Orford Ness	Jun – Aug 2010, Mar – Aug 2011 –2015	13.3	3.31	28.68	12.25	27.79	11.62

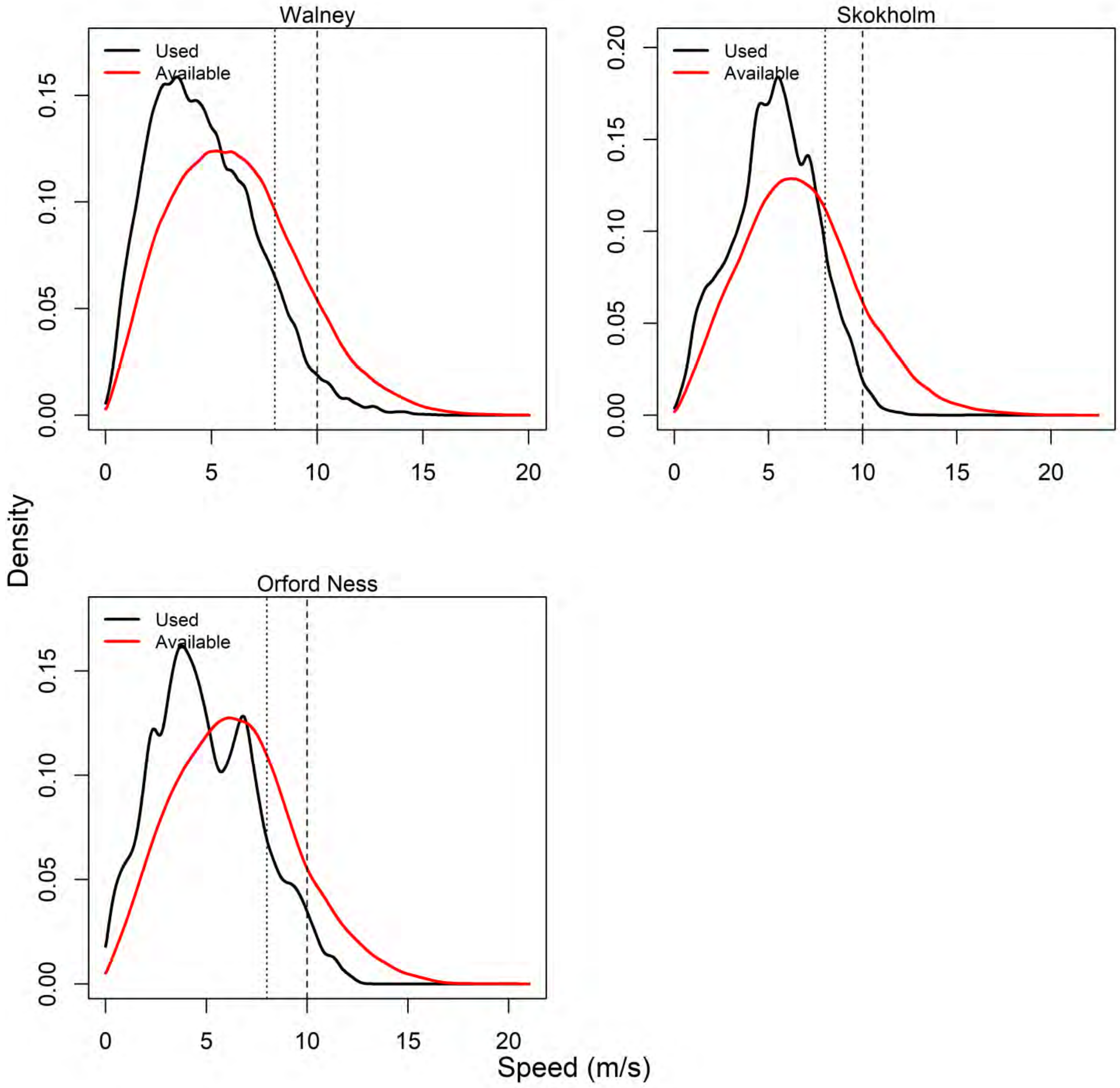


Figure 6 For Lesser Black-backed Gull, histograms of wind speed during the period of study at each site that was available for birds to experience, vs that actually experienced when on foraging trips (‘availability’ vs ‘used’); data here are pooled across each tracking period per bird in each year for each colony.

3.2.2 Model summary

Three-state offshore model

For each colony, mean step lengths (from gamma distribution) and angle parameters (mean and concentration from Von Mises) for each state are shown in Table 9 below. Together these models indicated more consistent direction for slower floating State 1 and faster commuting State 2, in contrast to State 3 with wider turning angles and a lower consistency in direction between fixes (Appendix AC).

Table 9 For Lesser Black-backed Gull, summary of mean ± SD step length and turning angles (mean, concentration) for each site.

	Step			**Turn**		
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/ search)**	**1 (floating)**	**2 (commuting)**	**3 (forage/ search)**
Walney	143.10 ± 70.84	2647.87 ± 913.43	553.26 ± 681.72	0, 59.44	0, 6.02	0, 0.31
Skokholm	267.23 ± 212.73	2953.14 ± 931.75	704.21 ± 814.41	0, 42.21	0, 12.99	0, 0.72
Orford Ness	228.99 ± 92.09	2995.43 ± 896.05	786.32 ± 834.20	0, 169.93	0, 10.30	0, 0.78

At all colonies, direct transitions to and from States 1 (floating) and 2 (commuting) were typically rarer in the datasets, as also found in some other studies (see Dean *et al*. 2013). Most frequently, fixes following a particular state were most likely to be classified as the same state again. However, where switches did occur, floating on the sea was typically preceded and succeeded by locations classified as State 3, switches relatively frequently occurred between commuting and foraging, generally being most consistent for commuting and foraging.

Four-state offshore model

Four-state models indicated that a further stationary state could be identified from the datasets, that may represent birds perching at sea or on land away from the breeding colony, or other behaviours such as preening or social interactions on the sea surface when not in flight. Comparing this model to the three state model, generally involved differing classifications of the “foraging/searching” and “floating on sea” states from the original three state model; note, commuting was more consistently classified between three and four state models. For example, for Walney, a four-state model gave mean step lengths for each state as 135.03 ± 137.54, 149.96 ± 76.34, 2846.75 ± 869.89 and 1216.65 ± 841.87 for “stationary”, “floating on the sea”, “commuting” and “foraging/searching respectively” (States 1-4 for the four-state approach), with concentration parameters for the von Mises angle distribution given as 0.21, 70.10, 10.52 and 0.79 for each state respectively. Thus as with the three-state model, commuting and floating on the sea had more consistent direction, differing by speed distinctions, and similarly, slow potential perching behaviour had similar wide turning angles between fixes, t and t+1, differing in speed delineations.

3.2.3 Travel speeds

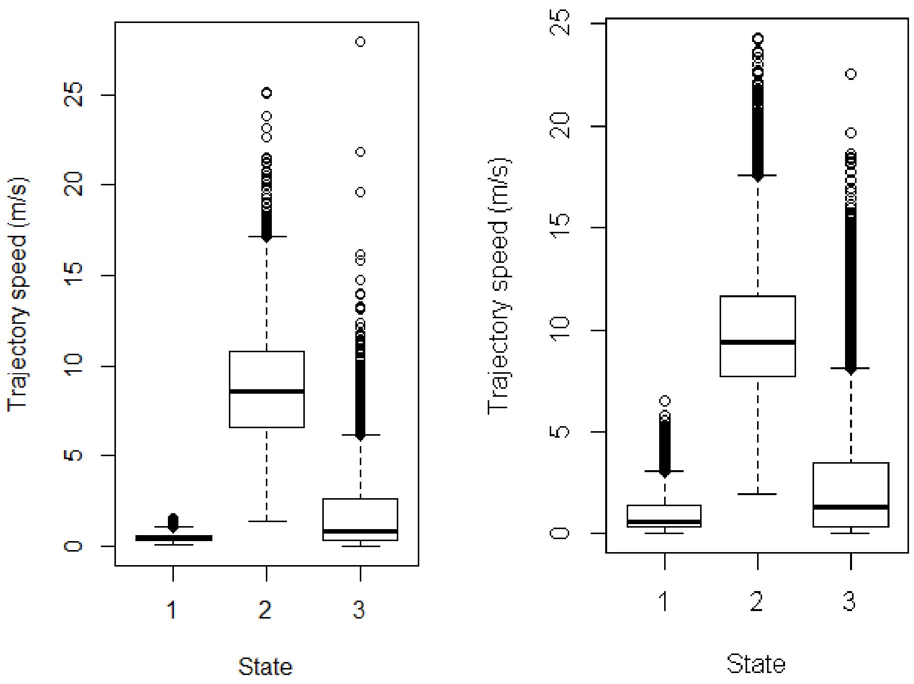
Three-state model

The Lesser Black-backed Gull models can be used to estimate travel speeds in each state. During commuting (using the mean parameter estimate above), on average (over other covariates), Lesser Black-backed Gulls travelled at a mean of 8.83 m/s, 9.84 m/s and 9.98 m/s for Walney, Skokholm and Orford Ness; these values were obtained across headwinds and tailwinds, and given slower travel in stronger headwinds, and faster travel in tailwinds (Appendix AE), represent the mean wind travel speed at zero wind speed with no directional bias during commuting.

Table 10 below shows the distributions of speeds from boxplot analysis (Figure 7) after assigning states back to the raw data. As with other species in this study, we note, however, that precise behaviours within this broad category of foraging/searching could also include non-flight activities. Further, for gulls in particular, “foraging/searching” could also encompass perching activity if birds rest on structures at sea away from the colony – see methods Section 2.3.9. A further four-state model was specified for this species – see below.

Table 10 Lesser Black-backed Gull, summary of speeds per state (m/s), as obtained through classification of tracking data using three-state HMMs.

Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**
Walney	0.49 (0.27 – 0.79)	8.59 (6.61 – 10.83)	0.84 (0.29 – 2.65)
Skokholm	0.58 (0.33 – 1.43)	9.41 (7.71 – 11.64)	1.35 (0.37 – 3.46)
Orford Ness	0.77 (0.55 – 0.96)	9.54 (7.80 – 11.71)	1.62 (0.61 – 3.73)


(a) Walney

(b) Skokholm

(c) Orford Ness

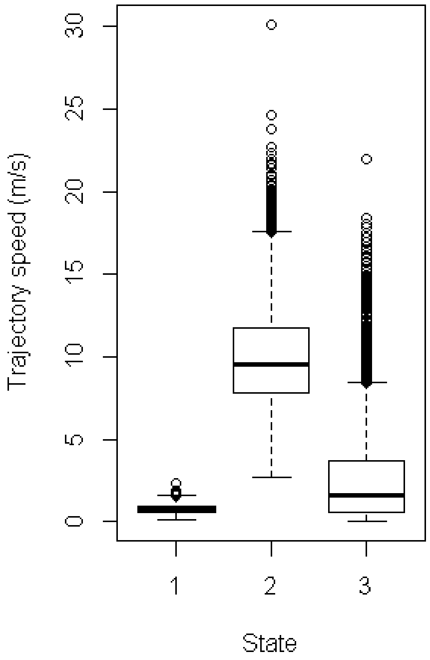


Figure 7 Lesser Black-backed Gull, boxplots of speed for states 1, 2 and 3 (floating, commuting and foraging/searching) at South Walney, Skokholm and Orford Ness respectively.

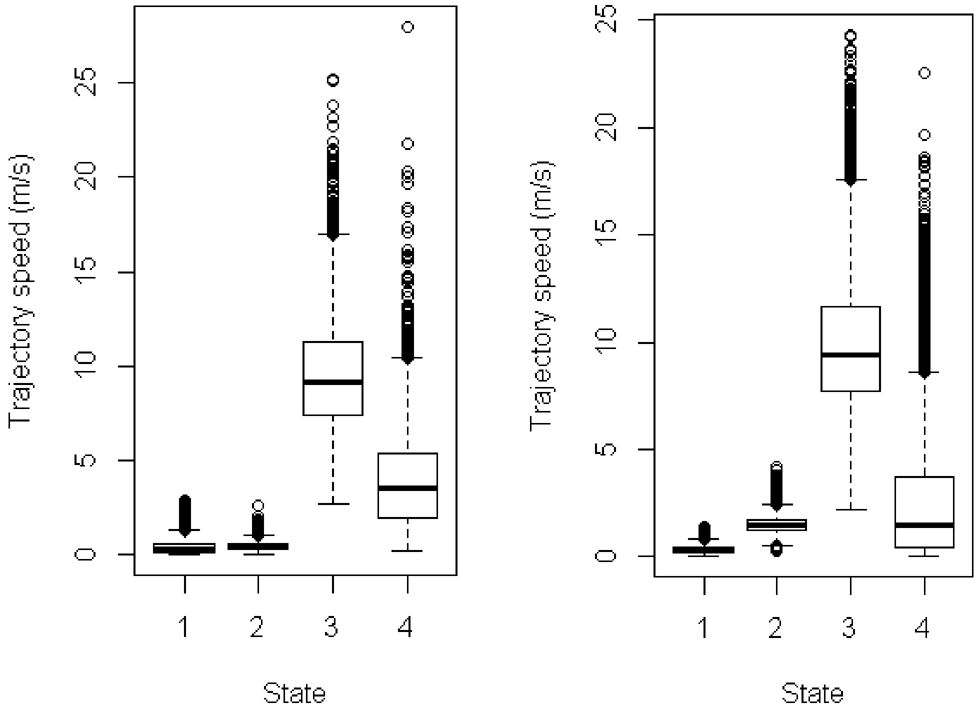
Four-state model

Four-state HMMs estimated a further state of “perching”, separate to the existing three states above, and generally involved differing classifications of the “foraging/searching” and “floating on sea” states from the three state model (Table 11); the state of commuting (here now given as State 3, from the four-state model) was more consistently classified between three- and four-state models. The perching state identified from the four-state model was identified at very slow speeds and thus the foraging/searching state was greater, and therefore was potentially representative of a greater proportion of in-flight activity compared to the three-state model.

Table 11 For Lesser Black-backed Gull, summary of speeds per state (m/s), as obtained through classification of tracking data using four-state HMMs.

Colony / State	**1 (perching)**	**2 (floating)**	**3 (commuting)**	**4 (forage/search)**
Walney	0.32 (0.13 – 0.59)	0.45 (0.31 – 0.62)	9.17 (7.42 – 11.26)	3.55 (1.99 – 5.39)
Skokholm	0.34 (0.22 – 0.46)	1.49 (1.23 – 1.71)	9.43 (7.72 – 11.67)	1.49 (0.44 – 3.70)
Orford Ness	0.26 (0.15 – 0.37)	0.81 (0.64 – 0.99)	9.65 (7.94 – 11.84)	2.41 (1.03 – 4.48)

It has been estimated that a minimum powered flight speed of 4 km/h, or ca. 1.1 m/s is a reasonable assumption for lesser black-blacked gulls (Shamoun-Baranes *et al*. 2011). For each of the colonies here, the four-state model gave median (boxplot) speed estimates greater than this value, although speeds were still on the low side, with values for the lower 25th percentile of the distribution dropping to 0.44 m/s for Skokholm. We note also, that the commuting flight speeds are considerably faster than “travel” speeds within the foraging/searching category. It is likely that many behaviours in this revised foraging/searching state may have been in flight, but given the caveats for these delineations from HMMs (Section 2.3.9) this is not fully certain.


(a) Walney

(b) Skokholm

(c) Orford Ness

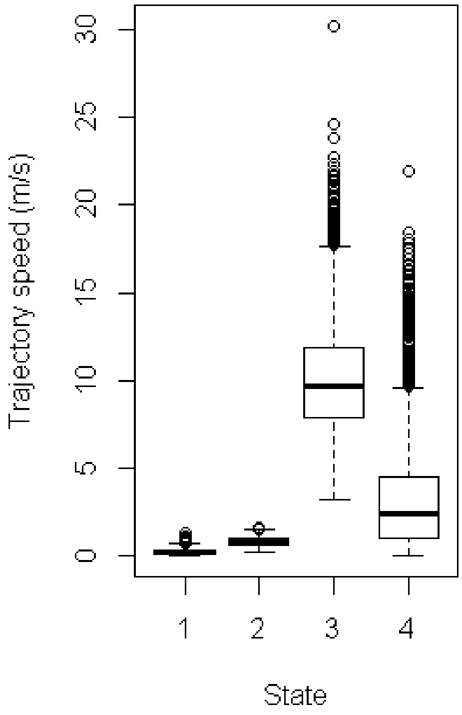


Figure 8 For Lesser Black-backed Gull, estimation of travel speed states 1, 2, 3 and 4 (perching, floating, commuting and foraging/searching) for each colony from a four-state model.

3.2.4 Effects of wind speed on step length (speed)

For all further analyses, the three-state model was used to investigate effects of covariates.

For Walney, models specifying a simple effect of wind speed on step length (Appendix AE) showed a general decreasing trend in step length over increasing wind speed for commuting (β = -0.117), corresponding to a *ca*. 1500 m/5 min reduction in step length (ca 5.0 m/s travel speed) over increasing wind speed (between 0.07-13.3 m/s, corresponding to standardised wind speeds (-1.85-3.47). Slight decreases in step lengths were recorded for States 1 and 3 (floating on the sea and foraging) (β = -0.024, β = -0.015). Similarly, for Skokholm and Orford Ness, models also showed negative beta coefficients for wind speed and commuting (β = -0.062, β = -0.051), and very shallow contrasting trends for floating state 1 (β = 0.033, β = -0.028) and foraging/searching state 3(β = -0.002, β = 0.054).

For commuting, such patterns with wind speed alone (without any directional component), are likely due to the negative effects of crosswinds and headwinds, outweighing the positive gains from headwinds, but also linked to complexities of colony location and route taken on outward and inward commutes during trips, and the prevailing wind speed and direction over the tracking period; however, patterns with head and tail winds reveal much clearer patterns with commuting (see below).

For the state of commuting, there was a distinct effect of wind speed in interaction with wind direction on travel speeds for all colonies (Appendix AE), with a positive value recorded for the specified wind speed:angle_osc coefficient (Walney, *β* = 0.554, Skokholm, 0.566, and Orford Ness, *β* = 0.523). Thus, faster commuting speeds were recorded in faster wind speeds that were aligned with the direction of travel of the bird (i.e. tailwinds) (angular_osc, -1 = headwind, +1 = tailwind). The coefficient for wind speed:angle_osc was also highly consistent across colonies. At all colonies, there was little influence of birds aligning turning angles during commuting with prevailing wind directions, i.e. turning with the wind (Walney, *β* = -0.085, Skokholm, -0.039, Orford Ness, *β* = -0.017), being perhaps unsurprising as birds make outward and return movements often against the wind.

3.2.5 Transition effects between states in relation to covariates

The best-fitting model, as assessed by AIC, was the full model with all covariates, being best across all colonies (Appendix AF). Transition and stationary state plots are show in Figure 8, Figure 9 and Appendix AD.

There were clear patterns over distance to colony for each of the three colonies modelled. These plots highlighted distances at which switches in behavioural states occurred from floating and foraging to commuting closer to colonies (as birds began travel to more distant feeding grounds), and then gradual switches to foraging/searching and floating away from commuting, presumably at foraging grounds (see Appendix AG). Over Julian date, there was also indication as the breeding season progressed that time spent floating at sea was reduced as birds transition to more searching and commuting activity – this may reflect birds having increasing breeding demands such as incubation and chick-rearing that required increasing amounts of foraging/searching activity and commuting to and from feeding locations (see Appendix AG).

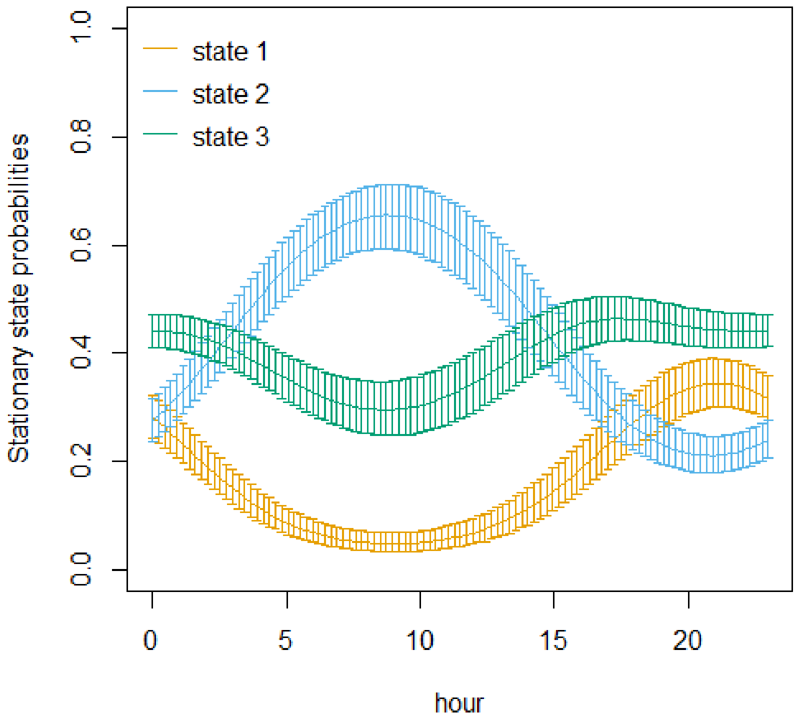
The models showed very strong patterns over hour of the day (Figure 9). At all colonies, Lesser Black-backed Gulls were more likely to be floating on the sea during hours of darkness; a peak in floating activity was observed after 20:00 but the level of resting activity began to decrease after midnight, when transitions occurred from floating to foraging/searching and greater likelihood of remaining commuting. This resulted in clear peaks in commuting activity at the expense of other behaviours as seen in stationary state probabilities; however, the exact timing of peaks and troughs in foraging behaviour differed across colonies.

Models also indicated a complex pattern of transition probabilities between and within states over increasing wind speed (Figure 10). Patterns using the spline trends from the most parsimonious model (Appendix AF), were varied across colonies; for example, as wind speed increased, birds at Orford Ness spent less time resting and showed a greater tendency to switch from resting to foraging but wind speed had less effect on time spent resting at the other colonies. Noticeably at Walney, the likelihood of a fixes being commuting increased as wind speed increased. The effect of wind speed, however, was very closely linked with wind direction and the alignment of travel; hence all best-fitting models were significantly improved with this additional component added (dAIC >2.0), albeit as a linear effect rather than a spline.

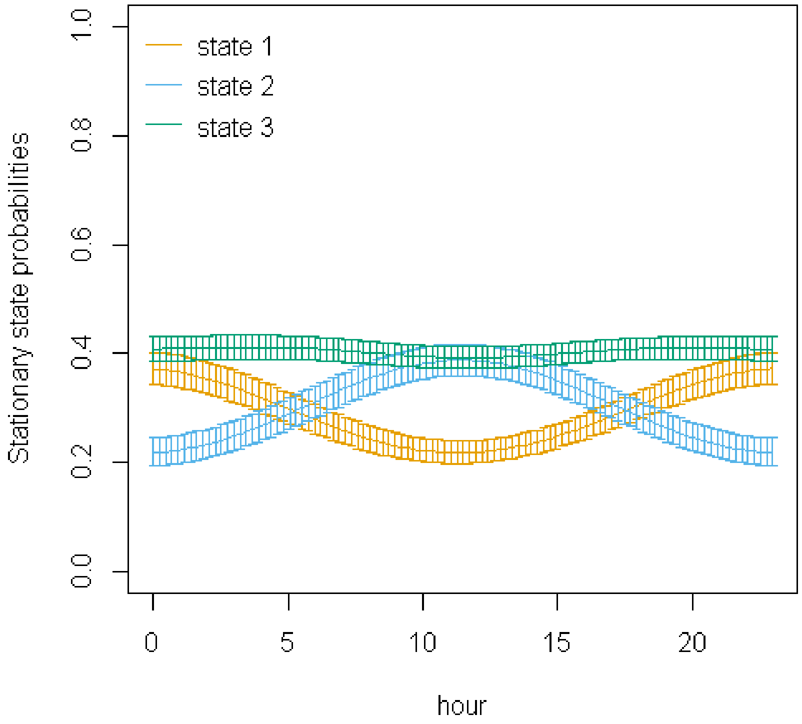
When encountering headwinds birds were less likely to remain in the resting state and were more likely to transition from resting to foraging at Walney and Orford Ness. This pattern was not so apparent at Skokholm. However, at all colonies, the balance of remaining within and switching between different states yielded a similar stationary state probability over increasing wind speed, with reduced likelihood of floating over increasing wind speed, and increased likelihood of commuting. In headwinds, there was also an increased likelihood of birds remaining commuting and a clear increase in the time spent commuting over increasing wind speed in a headwind.

When viewed in terms of the strongest winds over the varying tail- and headwind spectrum of values (+1 to -1) patterns were similar over colonies; for Walney and Orford Ness, strong patterns of remaining in State 1 (floating) with a tailwind, and switching to State 3 (foraging/searching) in a headwind were observed, and for all colonies birds were less likely to remain commuting (2-2) and switch to foraging/searching with increasing tailwinds (2-3), being most similar between Walney and Skokholm. Consequently, stationary state probabilities were generally similar over colonies, with patterns of decreasing time spent commuting, and increasing foraging and floating over extent of tailwind alignment. Note however, that switches to foraging/searching from floating in headwinds were somewhat overshadowed within stationary state plots by the increasingly greater probability of commuting behaviour and birds being more likely to remain commuting when in headwinds.

(a) Walney



(b) Skokholm



(c) Orford Ness

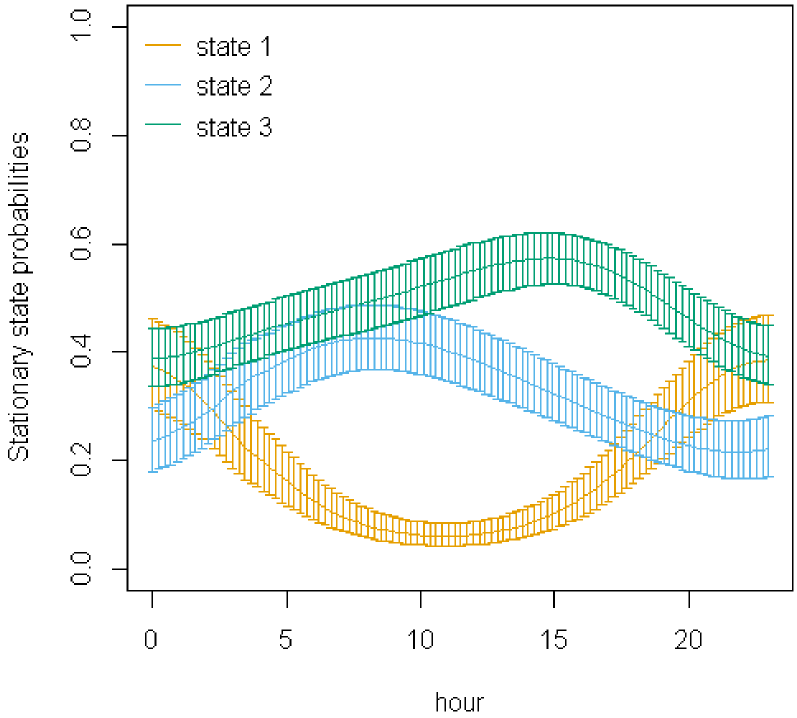
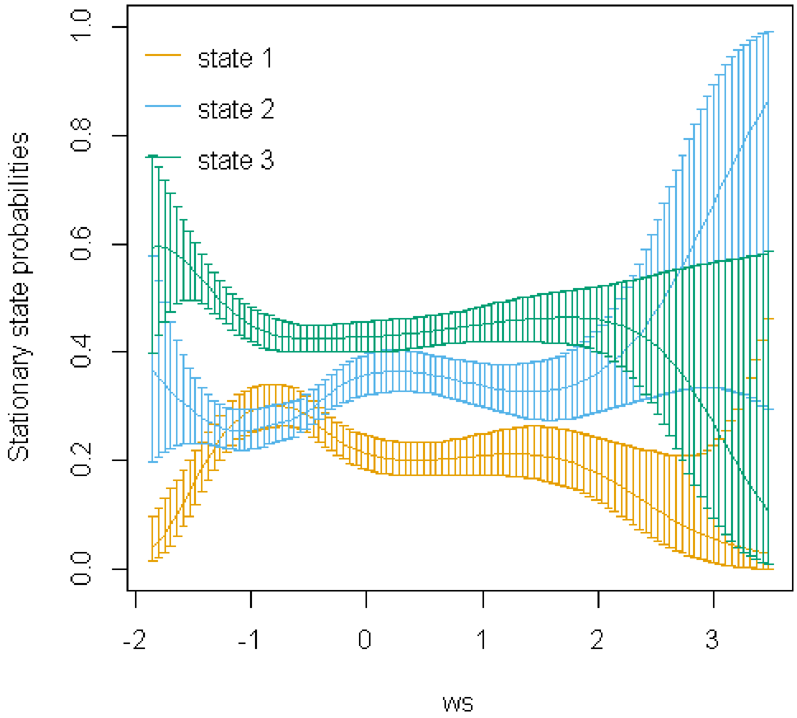
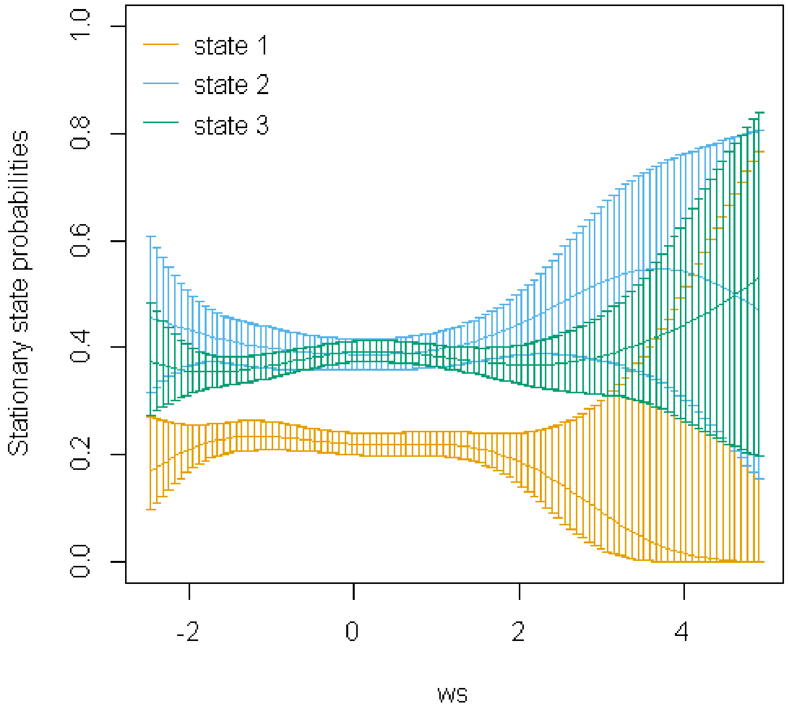


Figure 9	For Lesser Black-backed Gull, stationary state probabilities for the variable of cosinor(hour of day), for States 1, 2 and 3 (floating, commuting and foraging/searching).

(a) Walney



(b) Skokholm



(c) Orford Ness

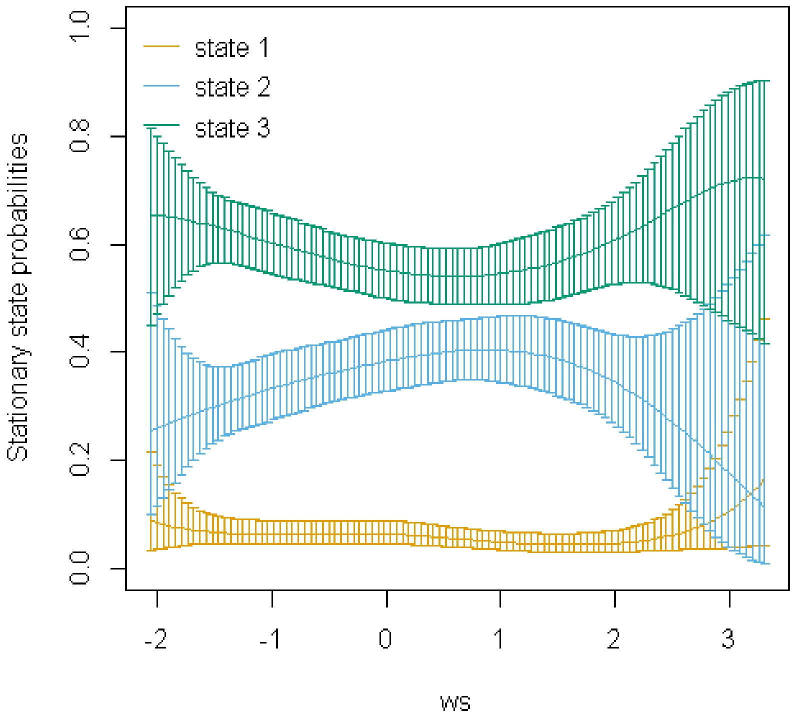


Figure 10 For Lesser Black-backed Gull, stationary state probabilities for the variable of bSpline(wind speed). fitted as a standardised variable, for States 1, 2 and 3 (floating, commuting and foraging/searching).

3.2.6 Time in states

The range of duration of data per bird and the proportion of time spent in different states are shown in Table 12.

Table 12 For Lesser Black-backed Gull, estimated time spent in states for each colony for birds at each colony across years; note occasionally initial movement models could not be fitted due to a lack of data available for some individuals, hence the effective sample size feeding into assessments is provided in brackets.

			Duration of tracking			**Proportion time spent per state**		
Colony	**No. birds total (modelled)**	**Years**	**No. birds > 10 hrs tracking data**	**Duration (hrs) mean ± SD per bird**	**Tracking data range (hrs)**	**1 floating mean ± SD**	**2 commuting mean ± SD**	**3 foraging / searching mean ± SD**
Walney	24 (22)	2014 to 2018	17	58.45 ± 120.11	1.67 – 497.42	0.20 ± 0.16	0.41 ± 0.22	0.39 ± 0.17
Skokholm	25 (25)	2014 to 2017	23	237.47 ± 183.88	3.8 – 270.4	0.32 ± 0.08	0.35 ± 0.13	0.35 ± 0.10
Orford Ness	24 (18)	2010 to 2015	17	90.80 ± 90.56	6.42 – 339.33	0.19 ± 0.15	0.39 ± 0.18	0.42 ± 0.08

3.2.7 Utilisation distributions

Figures depicting utilization distributions for each colony are shown in Appendix AH. Depending on the colony, there was a smaller amount of data from the very highest wind speeds (greater than 8 m/s) – see methods, and also section above comparing use and availability for wind speed distributions.

Low sample sizes were recorded for the day-high category for the floating state at Walney, with less than three birds and only 78 fixes providing data. For Orford Ness, low sample sizes of only two birds and 49 fixes were obtained for the day-high category for the same floating state, and further, only four birds provided data for the night-high floating state. These data should be treated with caution, and are highlighted in plots with red borders around utilisation distribution maps. We again also caution the comparison of utilisation distributions based on very disparate numbers of fixes. For Lesser Black-backed Gulls at all colonies, a number of high and low wind categories (day and night) represented less than 5% of the number of fixes available, and was found across all three states.

3.2.8 Overlap indices

Overlaps between states in different conditions and times of the day are visualized in Appendix AI, and summarised in Table 13.

For Lesser Black-backed Gulls across all colonies, the 95% KDEs, representing total area usage, generally showed a moderate (BA = 0.4-0.6) to very high (BA = 0.8+) level of overlap, between the daytime low-wind conditions (taken here as representative of similar conditions that aerial surveys would encounter), and the other scenarios of day-high wind, night-low wind and night-high wind scenarios across different states; the exception to this was the resting State 1 for Walney (BA = 0.37). At all colonies, the greatest overlaps were between day-low and day-high wind for the state of commuting (BA = 0.84, 0.90 and 0.90 for each colony, respectively), suggesting commuting zones used were not noticeably different during the day in different wind conditions. Overlaps between the core (50% KDE) day-low and other conditions were lower than the total 95% KDE for all states. Overlaps were generally lowest for the comparison of day-low vs night-high across colonies, and were again most pronounced for the State 1 floating, however, the smallest overlap index (BA = 0.06) was seen for day low vs day high floating at Walney.

We found that overlaps for the night-high vs night-low comparison were lower than day-high vs day-low comparisons across states (Table 13). There were also similar magnitudes of difference when comparing day-low and night-low and day-high and night-high; overlap indices were higher (for 95% and 50% KDEs) between day and night in low wind conditions, than comparing day and night in high wind conditions, which was true across all states. Birds at all colonies often rested just offshore (close to the colony) on the sea overnight, which was not done so during the day, however, during both day and night birds rested on the sea offshore during day and night periods. In generalising, these results may indicate similar magnitudes of drivers of wind speed than time of day for distributions for Lesser Black-backed Gulls but again overall overlaps in distributions are generally considered moderate to very high for this species.

Table 13 For Lesser Black-backed Gull, overlap indices (Bhattacharyya's Affinity Index) for pair-wise combinations of utilisation distribution assessing similarity in 95% KDEs (and 50%, brackets) for different levels of day and night, and high/low wind and states 1, 2 and 3 (floating, commuting and foraging/searching); bold highlights indicate comparisons of greatest interest, comparing the equivalent conditions when surveys are made (low wind daytime) to other conditions; red highlight shows where confidence in overlap assessment is lowest due to low sample sizes (see methods and Appendix AA).

(a) Walney

state		day.high	day.low	night.high
1	day.low	**0.37 (0.06)**		
1	night.high	0.17 (0)	**0.37 (0.08)**	
1	night.low	0.32 (0)	**0.59 (0.29)**	0.38 (0.08)
2	day.low	**0.84 (0.6)**		
2	night.high	0.68 (0.46)	**0.68 (0.42)**	
2	night.low	0.79 (0.5)	**0.88 (0.6)**	0.87 (0.68)
3	day.low	**0.72 (0.5)**		
3	night.high	0.58 (0.06)	**0.55 (0.12)**	
3	night.low	0.68 (0.27)	**0.82 (0.54)**	0.69 (0.27)

(b) Skokholm

state		day.high	day.low	night.high
1	day.low	**0.77 (0.46)**		
1	night.high	0.47 (0.19)	**0.56 (0.28)**	
1	night.low	0.53 (0.21)	**0.72 (0.39)**	0.48 (0.22)
2	day.low	**0.9 (0.85)**		
2	night.high	0.75 (0.66)	**0.81 (0.7)**	

2	night.low	0.84 (0.74)	**0.92 (0.84)**	0.8 (0.69)
3	day.low	**0.85 (0.56)**		
3	night.high	0.51 (0.09)	**0.57 (0.24)**	
3	night.low	0.67 (0.18)	**0.8 (0.35)**	0.62 (0.36)

(c) Orford Ness

state		day.high	day.low	night.high
1	day.low	**0.47 (0.45)**		
1	night.high	0.38 (0.17)	**0.4 (0.14)**	
1	night.low	0.39 (0.26)	**0.6 (0.37)**	0.43 (0.26)
2	day.low	**0.9 (0.84)**		
2	night.high	0.61 (0.32)	**0.63 (0.33)**	
2	night.low	0.87 (0.79)	**0.92 (0.9)**	0.64 (0.36)
3	day.low	**0.71 (0.59)**		
3	night.high	0.54 (0.39)	**0.5 (0.22)**	
3	night.low	0.64 (0.53)	**0.77 (0.43)**	0.47 (0.21)

3.3 Black-legged Kittiwake

3.3.1 Comparison of wind speed use vs availability

Comparisons of wind speeds experienced and those available within the grid cells of the Copernicus weather data that birds overlapped with offshore were made for all colonies – see Table 14, Figure 11 and Appendix AB.

For all colonies except Colonsay, precise periods where individual birds were tracked percentages were lower than that of the entire month. The use, however, as recorded through wind speeds experienced at GPS fixes, revealed lower proportions of 8 m/s and 10 m/s data compared to that available during the same period of tracking. Birds at Colonsay and Orkney also showed a higher proportion of high wind speed data than Isle of May and Bempton, being northerly and westerly in location.

Table 14 For Kittiwake, summary of the proportions of tracking data by wind speed thresholds of more than 10 m/s and more than 8 m/s, and further comparing wind speeds encountered by birds (‘used’) vs wind speeds ‘available’. Assessment is made both (i) within the full months that tracking was carried out and (ii) for the precise tracking date-times, for all Copernicus grid squares that birds overlapped with; proportions for ‘use’ data are calculated on the data modelled within HMMs, thus each data point is a GPS fix; for ‘available’ calculations, each data point is an hourly wind speed estimate for each Copernicus grid square.

		Used (%)		**Available (tracking period, %)**		**Available (all months, %)**	
Colony / State	**Tracking months and years**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**
Isle of May	May – July, 2012 – 2014	6.72	1.71	13.94	3.11	18.57	6.2
Colonsay	June – July, 2010 – 2014	14.57	4.35	21.86	9.91	18.5	7.06
Bempton Cliffs	June – July, 2010 – 2015	12.24	2.93	16.29	3.66	21.65	7.29

Orkney	June – July, 2010 – 2014	13.88	3.07	20.37	6.02	23.77	7.91

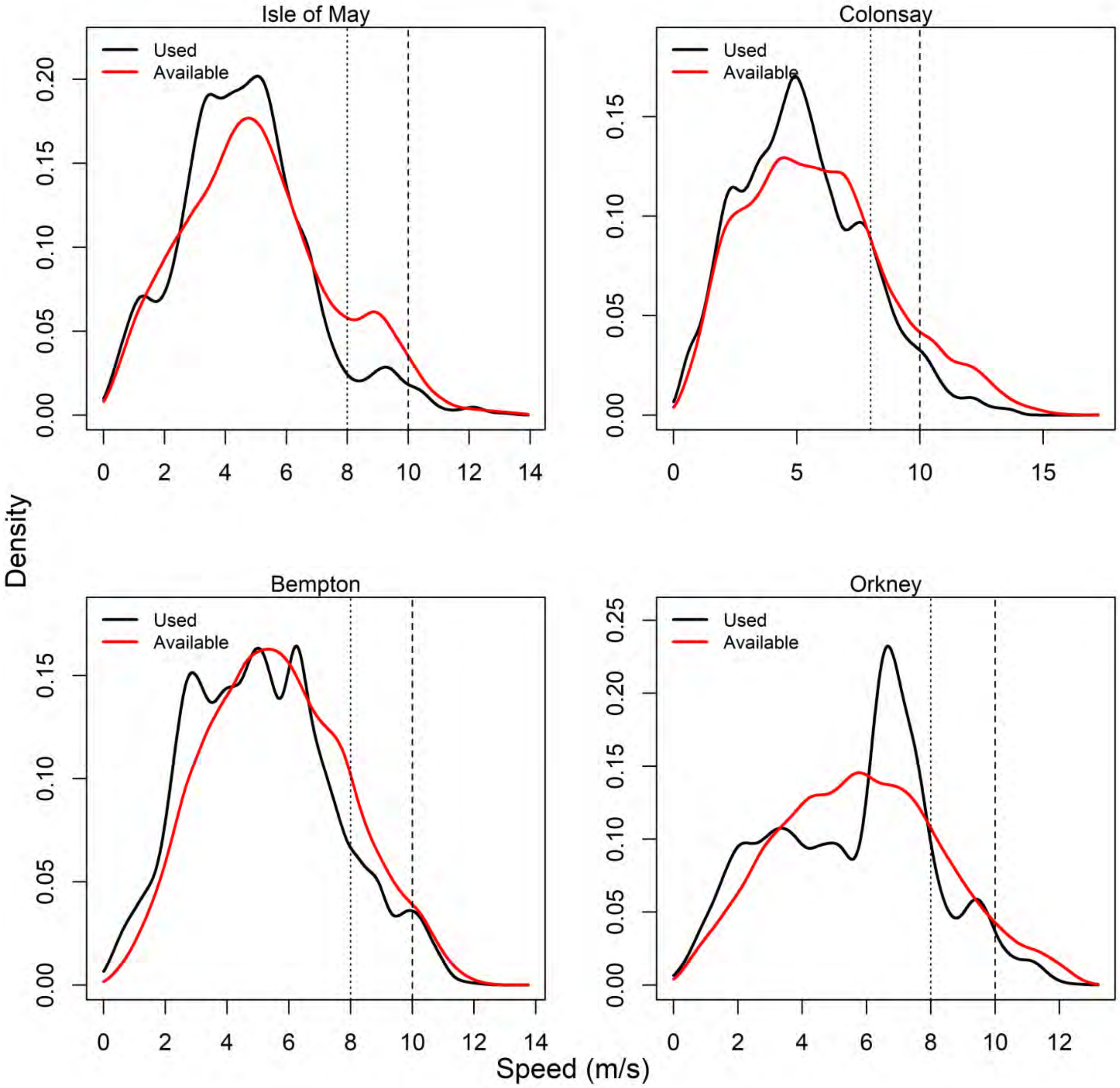


Figure 11 For Kittiwakes, histograms of wind speed during the period of study at each site that was available for birds to experience, vs that actually experienced when on foraging trips (‘availability’ vs ‘used’); data here are pooled across each tracking period per bird in each year for each colony.

3.3.2 Model summary

Three-state model

For each colony, mean step lengths (from gamma distribution) and angle parameters (mean and concentration from Von Mises) for each state are shown in Table 15 below. Together these models indicated more consistent direction for slower floating on the sea State 1 and faster commuting State 2, in contrast to State 3 with wider turning angles and a lower consistency in direction between fixes (Appendix AC).

Table 15 Summary of mean ± SD step length and turning angles (mean, concentration) for each site.

	Step			**Turn**		
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/ search)**	**1 (floating)**	**2 (commuting)**	**3(forage/ search)**
Isle of May	48.37 ± 20.39	1066.33 ± 355.12	176.51 ± 193.25	0, 8.65	0, 8.26	0, 0.41
Colonsay	56.95 ± 36.92	1087.81 ± 383.62	144.07 ± 186.63	0, 13.29	0, 8.26	0, 0.19
Bempton Cliffs	59.73 ± 28.41	1239.50 ± 317.34	262.19 ± 297.57	0, 21.70	0, 26.33	0, 0.70
Orkney	105.80 ± 88.67	1020.85 ± 437.68	98.62 ± 139.30	0, 12.72	0, 40.50	0, 0.28

At all colonies, direct transitions to and from States 1 (floating) and 2 (commuting) were typically rarer in the datasets, as also found in some other studies (see Dean *et al*. 2013). Most frequently, fixes following a particular state were most likely to be classified as the same state again. However, where switches did occur, typically floating on the sea was preceded and succeeded by locations classified as State 3, with further switches occurring between commuting and foraging (Appendix AC).

Four-state model

Four-state models indicated that a further stationary state could be identified from the datasets, that aimed to represent birds perching at sea or on land away from the breeding colony, or other behaviours such as preening or social interactions on the sea surface when not in flight. Comparing this model to the three state model, generally involved differing classifications of the “foraging/searching” and “floating on sea” states from the three state model; note, commuting was more consistently classified between three and four state models.

For example, for the Isle of May, a four-state model gave mean step lengths for each state as 61.69 ± 52.32, 49.20 ± 17.04, 1156.47 ± 318.38 and 433.15 ± 295.74 for “stationary floating”, “floating on the sea”, “commuting” and “foraging/searching respectively” (States 1-4 for the four-state approach), with concentration parameters for the von Mises angle distribution given as 0.55, 16.78, 14.58 and 0.89 for each state respectively. Thus as with the three-state model, commuting and floating on the sea had more consistent direction, differing by speed distinctions, and similarly, slow potential perching behaviour had similar wide turning angles between fixes, t and t + 1, differing in speed delineations.

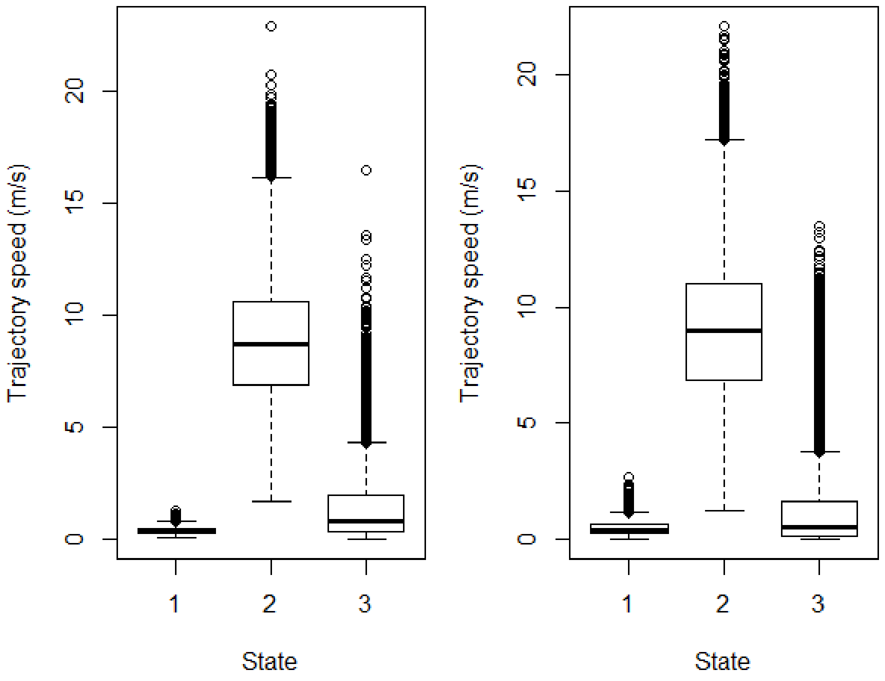
3.3.3 Travel speeds

Three-state model

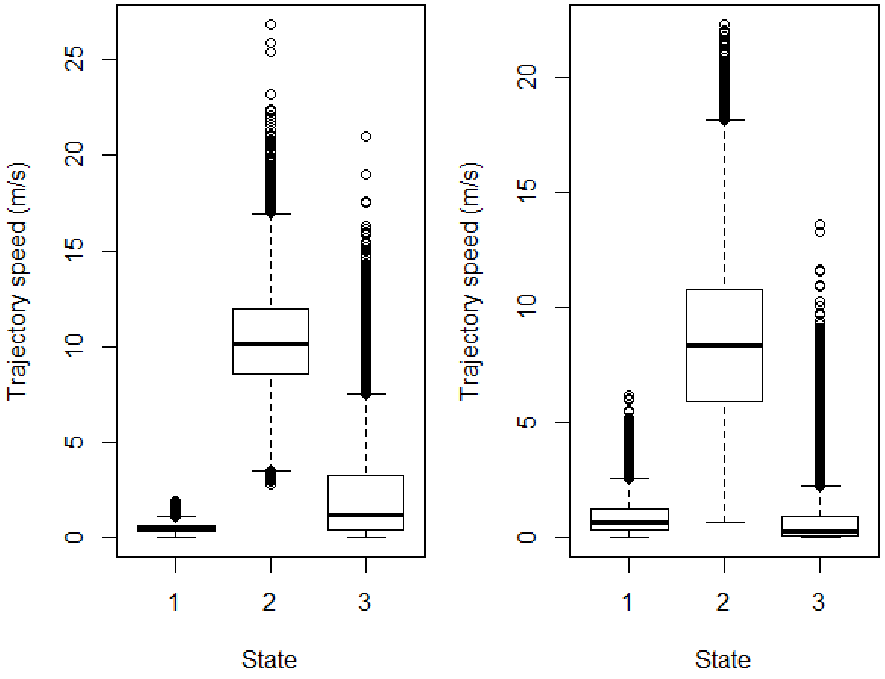
The HMMs can be used to estimate travel speeds in each state (Figure 12). Table 16 below shows the distributions of speeds from boxplot analysis after assigning states back to the raw data. The behaviour of “foraging/searching” identified from HMMs, although encompassing behaviours associated with foraging at or near the sea surface at very slow speeds including potentially not being in flight, could also encompass some stationary activity, for example if birds perch on structures at sea, or around coastlines when away from the colony. Four-state models were, therefore, also specified for investigation of potential behaviours that were slower and that had wide-turning angles, thus simulating possible floating in a single location or bathing activity on the sea surface – see below.

Table 16 For Kittiwake, summary of speeds per state (m/s), as obtained through classification of tracking data using three-state HMMs.

Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**
Isle of May	0.39 (0.29 – 0.49)	8.69 (6.91 – 10.61)	0.78 (0.31 – 1.92)
Colonsay	0.38 (0.25 – 0.62)	8.97 (6.87 – 11.00)	0.49 (0.13 – 1.60)
Bempton Cliffs	0.47 (0.33 – 0.63)	10.17 (8.54 – 11.92)	1.15 (0.40 – 3.24)
Orkney	0.64 (0.36 – 1.24)	8.35 (5.89 – 10.79)	0.26 (0.05 – 0.93)


(a) Isle of May

(b) Colonsay


(c) Bempton Cliffs

(d) Orkney

Figure 12 For Kittiwake, travel speed (m/s) at the Isle of May, Colonsay, Bempton Cliffs and Orkney for states 1, 2 and 3 (floating, commuting and foraging/searching), as assessed via assignment to raw data through the Viterbi algorithm of the three state model.

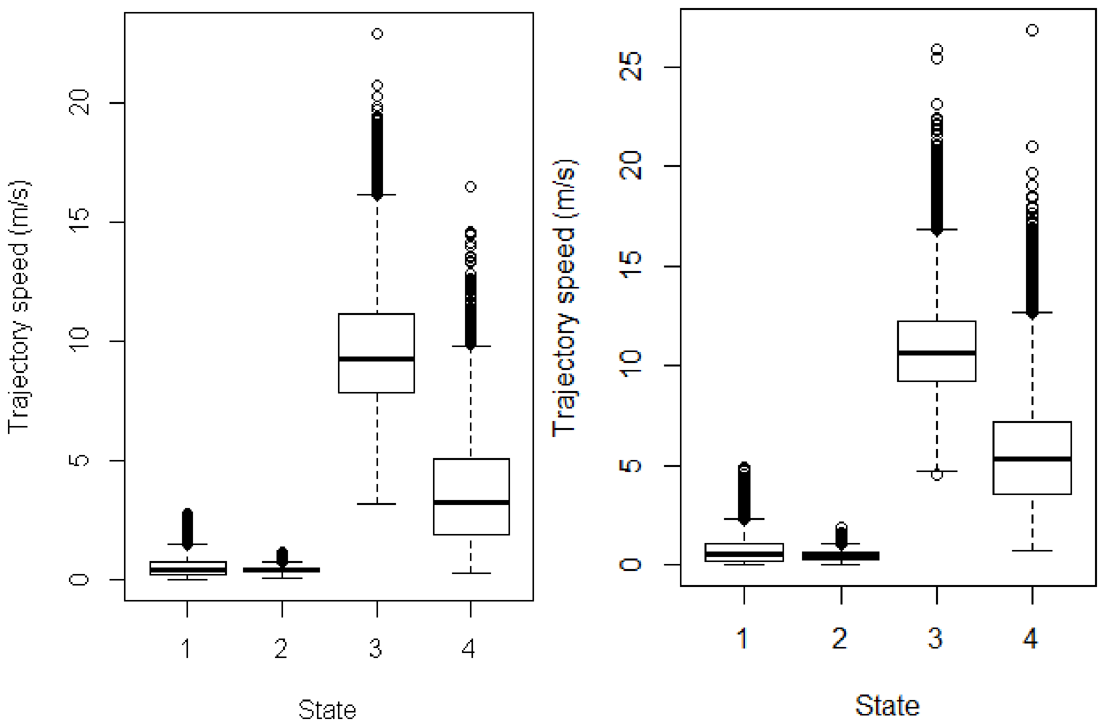
Four-state model

Four-state HMMs estimated that a further stationary state could be identified (Table 17), and generally involved differing classifications of the “foraging/searching” and “floating on sea” states from the three state model (see Table 16); note, commuting was more consistently classified between three and four state models.

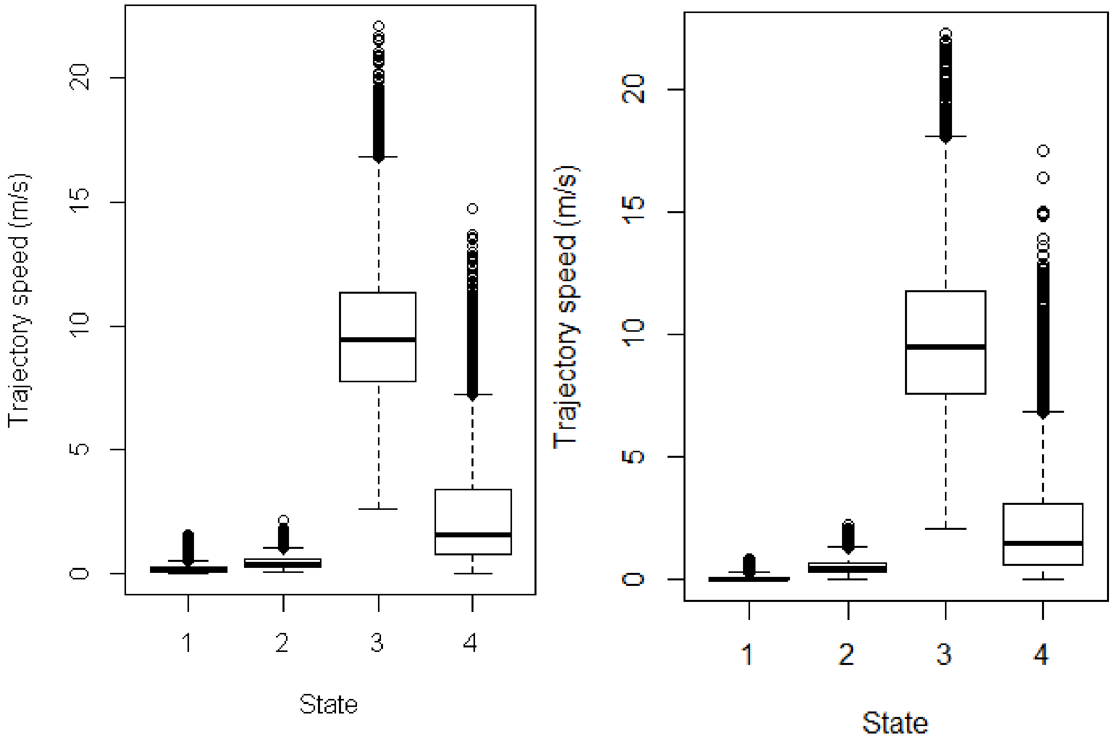
Table 17 For Kittiwake, estimated median (lower quartile – upper quartile trajectory speeds for each site, as obtained through classification of GPS fixes by HMM States (1-3).

Colony / State	1 (perching)	2 (floating)	3 (commuting)	4 (forage/search)
Isle of May	0.41	0.39	9.26	3.21
	(0.20 – 0.72)	(0.31 – 0.49)	(7.82 – 11.14)	(1.86 – 5.05)
Colonsay	0.12	0.40	9.45	1.56
	(0.05 – 2.47)	(0.28 – 0.60)	(7.76 – 11.37)	(0.78 – 3.36)
Bempton Cliffs	0.55	0.48	10.61	5.37
	(0.24 – 1.09)	(0.34 – 0.63)	(9.20 – 12.27)	(3.57 – 7.21)
Orkney	0.05	0.48	9.52	1.50
	(0.02 – 0.13)	(0.31 – 0.72)	(7.59 – 11.78)	(0.63 – 3.13)

This analysis revealed a greater speed for “foraging/searching” speed for each colony respectively than the three-state model for “foraging/searching” (see above); the four-state model also varied between colonies in the speed for this category (Figure 13). The four-state delineation for “foraging/searching” is likely more indicative of inflight behaviour, however, conversely it is not possible to rule out activity that is within the three-state model “foraging/searching” category that is also non-flight activity related to foraging, such as on-the-sea activity.


(a) Isle of May

(b) Colonsay


(c) Bempton

(d) Orkney

Figure 13 For Kittiwake, estimation of travel speed for states 1, 2, 3 and 4 (perching, floating, commuting and foraging/searching) for each colony from a four-state model.

3.3.4 Effects of wind speed on step length (speed)

For all further analyses, the three-state model was used to investigate effects of covariates.

For all colonies, there was a distinct effect of wind speed in on travel speeds for commuting that further varied by whether wind direction was aligned with travel direction of the bird (Appendix AE) - a positive value was recorded for the interaction effect of wind speed:angle_osc coefficient (Isle of May, β = 0.507, Colonsay 0.408, Bempton Cliffs, β = 0.490 m and Orkney β = 0.407). Thus, faster commuting speeds were recorded in faster wind speeds that were in turn aligned with the direction of travel of the bird (i.e. tailwinds), as given through the angular_osc covariate (-1 = headwind, +1 = tailwind). At all colonies, there was little influence of birds aligning turning angles during commuting with prevailing wind directions, i.e. turning with the wind (Isle of May, β = -0.021, Colonsay β =-0.022, Bempton Cliffs, β = -0.002, Orkney β = -0.058), being perhaps unsurprising as birds make outward and return movements often against the wind.

3.3.5 Transition effects between states in relation to covariates

Across all colonies, the best fitting models was the full model containing all covariates (Appendix AF). Transition and stationary state probability plots are presented in Figure 14, Figure 15 and Appendix AD.

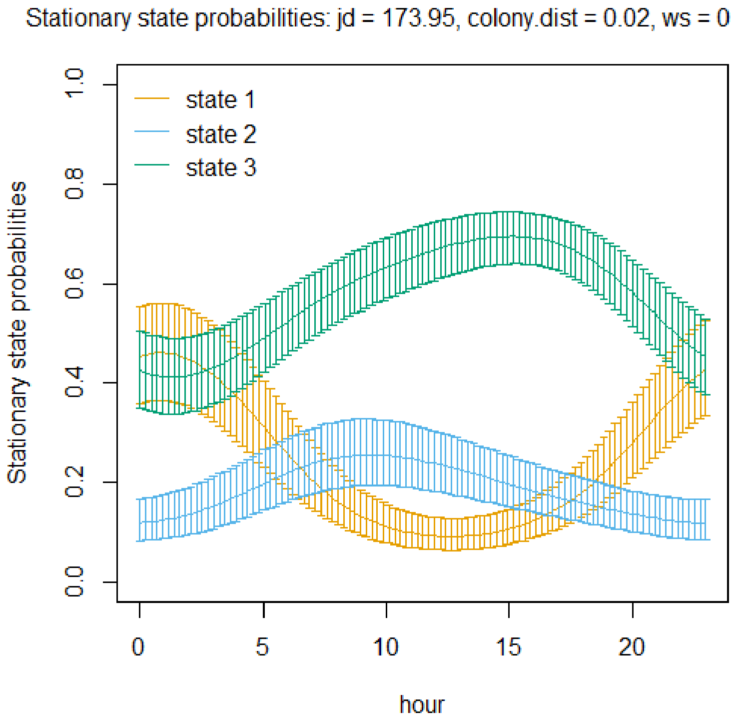
There were clear associations between behavioural state and distance from the colony (Appendix AD). For example, distances can be identified at which switches in behavioural states occurred from floating and foraging to commuting close to colonies (as birds began travel to more distant feeding grounds), and then gradual switches to foraging/searching and floating away from commuting, presumably at foraging grounds (see Appendix AG). The relationship between behavioural states and Julian date varied across colonies (see Appendix AG) and are difficult to reliably compare due to different periods of study for each colony and are also hard to appreciate without further scrutiny of egg and chicks stage analyses, thus here serving mainly as a control variable.

In terms of the aims of this project, the models for all colonies showed strong diurnal patterns in behaviour, but naturally also dependent on the amount of daylight across the season (Figure 14). At all colonies, Kittiwakes, were more likely to be floating on the sea during hours of darkness; the spline model (df = 4) indicated a gradual reduction of floating activity from ca. 00:00 – 03:00 until ca. 09:00 – 15:00 when floating was at its lowest and birds were most active in flight at sea. As noted above, transitions between States 1 and 2 were uncommon, and thus patterns of commuting were informed by likelihood of remaining commuting or transitioning to and from foraging/searching activity; switches between floating and foraging indicated birds at all colonies were more likely to transition to foraging/searching (State 3) later in the day (e.g. ca. 10:00 – 20:00), most apparently for Isle of May and Colonsay.

Models also indicated a complex pattern over increasing wind speed (Figure 15). At the Isle of May, Kittiwakes were more likely to transition from floating on the sea surface to searching/foraging as wind speed increased, although not at the very lightest or strongest winds, but with more error at this point in the curve. For Colonsay, likewise there were complexities in the spline relationship but overall there were decreases in probabilities for remaining floating over increasing wind speed, and swicthes to foraging, this time at the fastest wind speeds. For Bempton Cliffs, shapes of the splines for transitions 1-1 and 1-3 were similar to the Isle of May, albeit less pronounced. At all colonies, the probability of birds remaining in the commuting state increased as wind speed (was positively associated with wind speed), partly also reflected in stationary state probability plots.

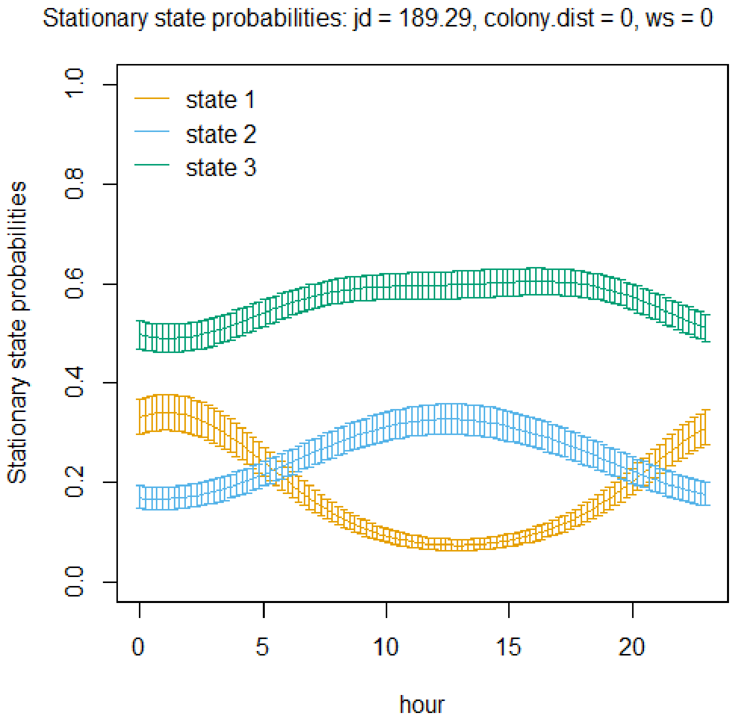
Examining wind speed patterns more closely through interaction with headwinds and tailwinds (wind speed x angle_osc parameter) and modelling wind speed as a linear term rather than a spline, revealed some clearer relationships. At the Isle of May, birds were less likely to remain in the resting state and more likely to switch from resting to foraging with increasing tailwind speeds. A similar, although shallower trends in relationships was shown for Bempton Cliffs, and even less so for Colonsay. At all colonies, birds were less likely to persist in the foraging state but more likely to persist in the commuting state as tailwind speed increased, reflected in the stationary state plots. Patterns of state likelihoods across colonies showed greater parity when viewed at the fastest wind speeds at each site, and examined across the spectrum of tail, cross and headwind (+1 to -1) spectrum for the angle_osc variable. At all colonies, birds were more likely to switch from floating to foraging as birds encountered headwinds rather than tailwinds, and vice versa. Further, birds were more likely to remain commuting in headwinds, and switch from commuting to foraging/searching over increasing tailwinds.

(a) Isle of May



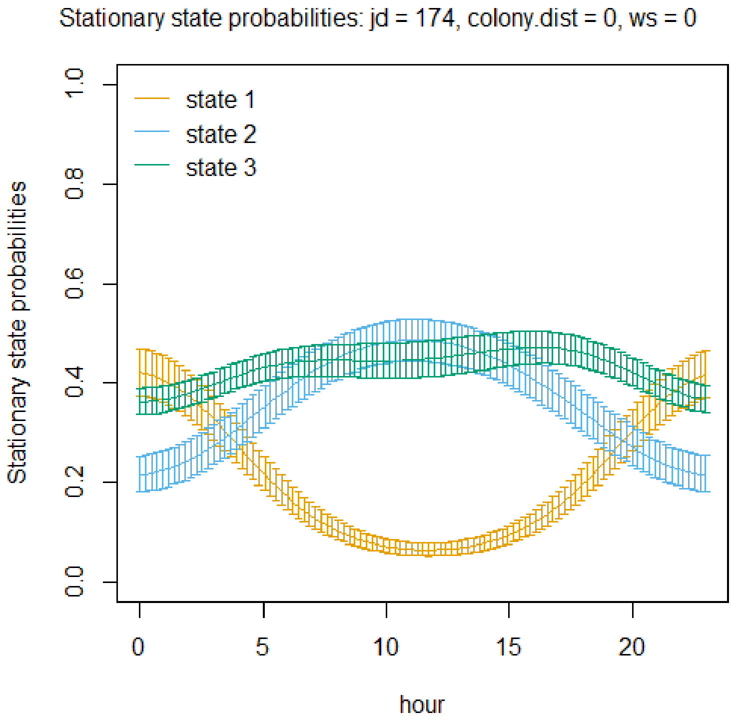
Stationary state probabilities: jd = 173.95, colony.dist = 0.02, ws = 0

(b) Colonsay



Stationary state probabilities: jd = 189.29, colony.dist = 0, ws = 0

(c) Bempton


Stationary state probabilities: jd = 174, colony.dist = 0, ws = 0

(d) Orkney

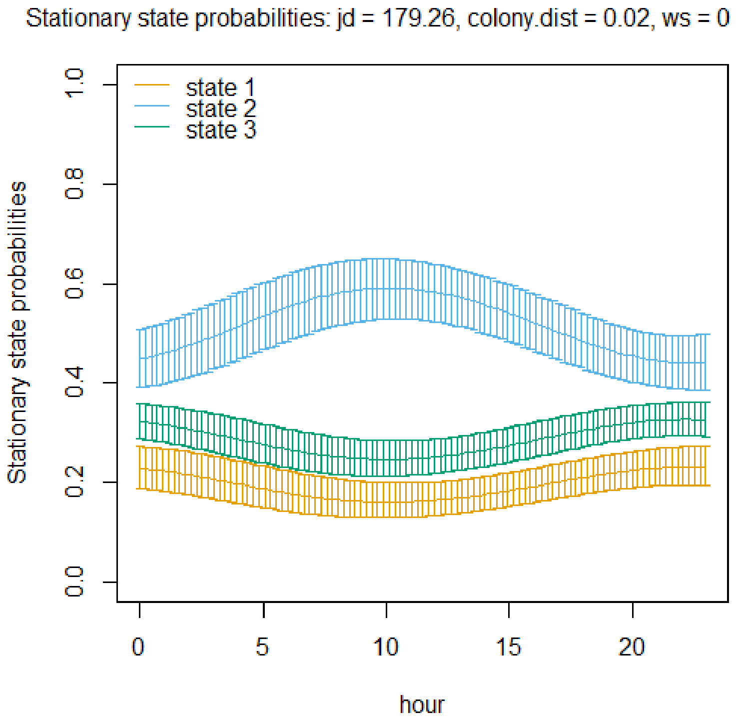
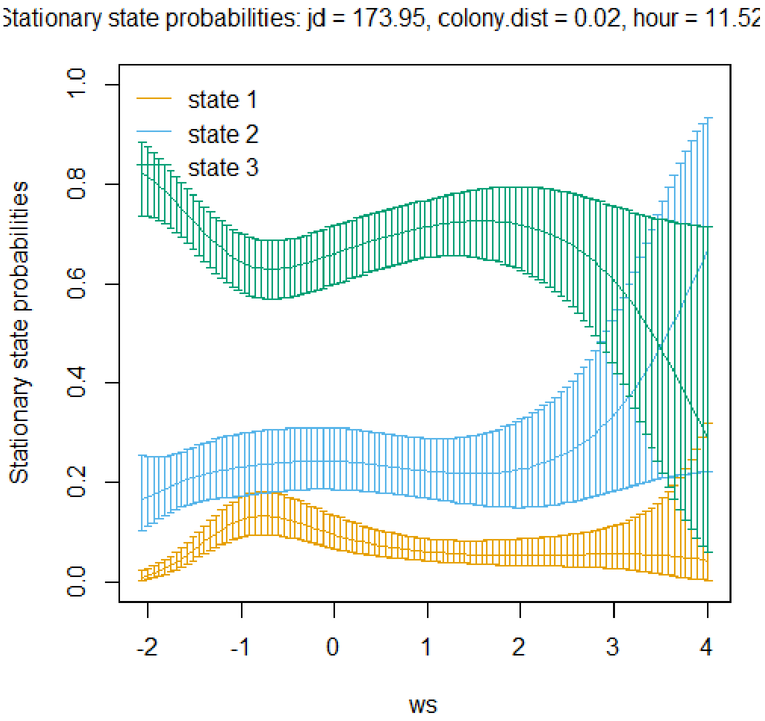
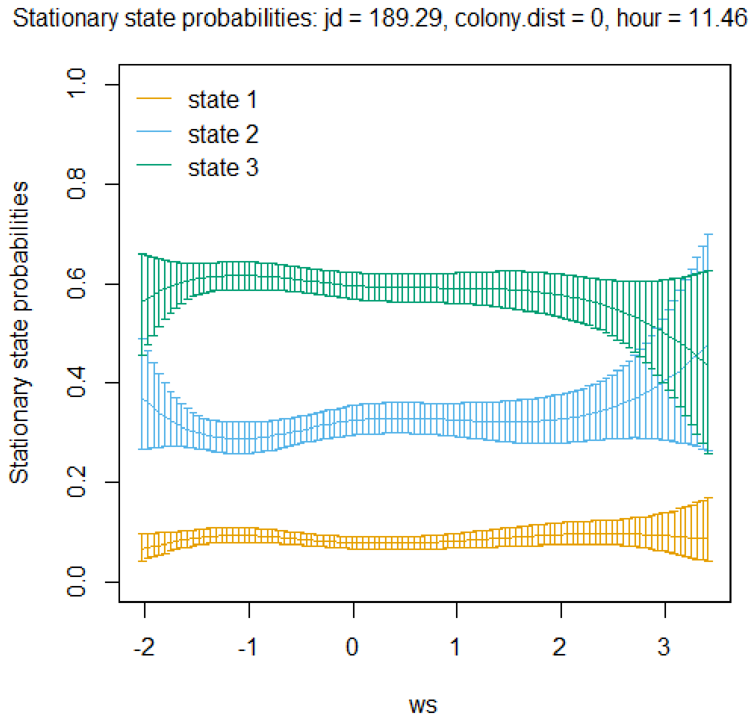

Stationary state probabilities: jd = 179.26, colony.dist = 0.02, ws = 0

Figure 14 For Kittiwake, stationary state probabilities for the variable of cosinor(hour of day), for states 1, 2 and 3 (floating, commuting and foraging/searching).

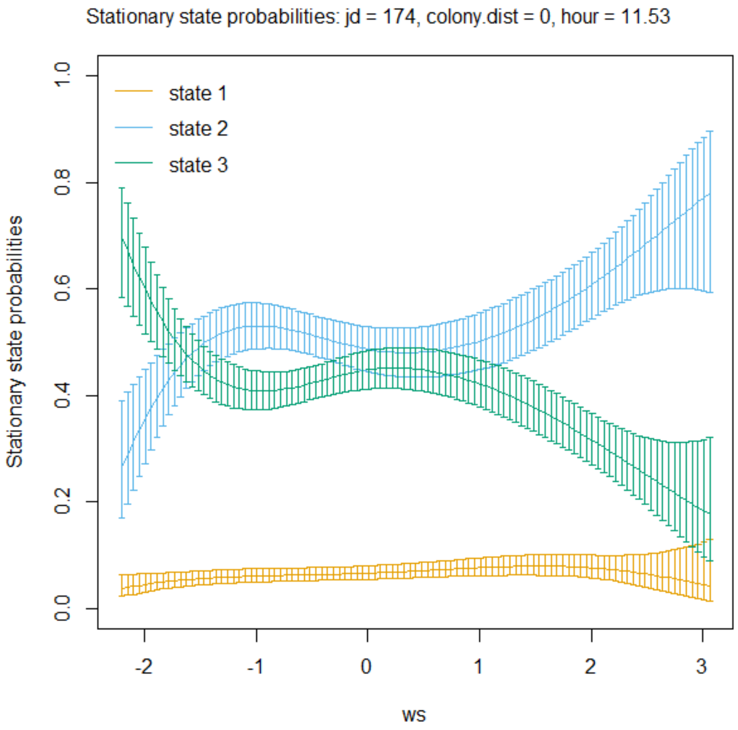
(a) Isle of May



(b) Colonsay



(c) Bempton



(d) Orkney

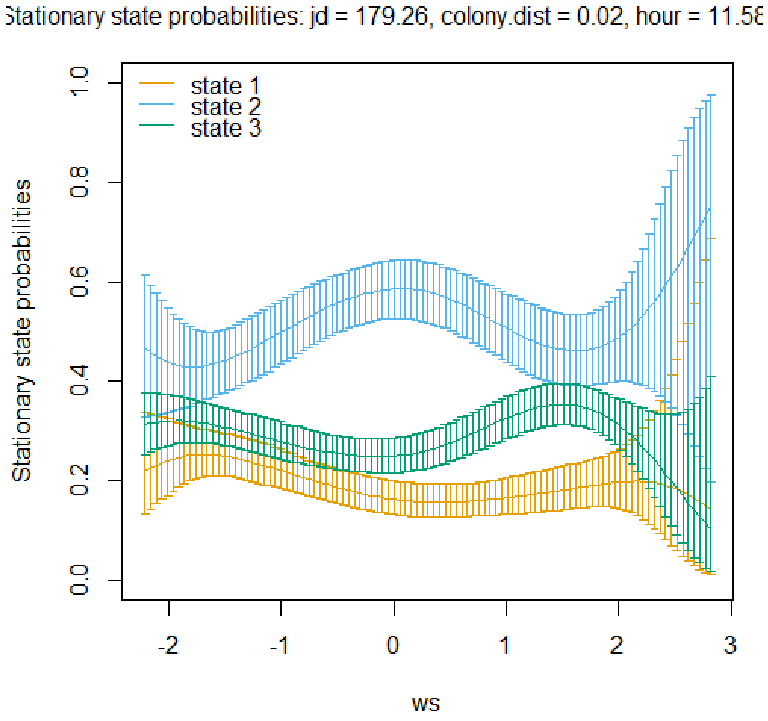


Figure 15 For Kittiwake, stationary state probabilities for the variable of bSpline(wind speed), fitted as a standardised variable, for states 1, 2 and 3 (floating, commuting and foraging/searching).

3.3.6 Time in states

The range of duration of data per bird and the proportion of time spent in different states are shown in Table 18. As birds with fewer data had less time to demonstrate their overall time spent in different states, we used information from birds with more than ten hours of data, to exclude any very small tracking durations that could otherwise skew patterns observed.

Table 18 For Kittiwake, estimated time spent in states for each colony for birds at each colony across years; note occasionally initial movement models could not be fitted due to a lack of data available for some individuals, hence the effective sample size feeding into assessments is provided in brackets.

			Duration of tracking			**Proportion time spent per state**		
Colony	**No. birds total (modelled)**	**Years**	**No. birds > 10 hrs tracking data**	**Duration (hrs) mean ± SD per bird**	**Tracking data range (hrs)**	**1 floating mean ± SD**	**2 commuting mean ± SD**	**3 foraging / searching mean ± SD**
Isle of May	50 (49)	2012 to 2014	33	21.92 ± 9.47	4.3 – 50	0.22 ± 0.09	0.25 ± 0.07	0.53 ± 0.10
Colonsay	84 (81)	2010 to 2014	81	32.58 ± 18.34	3.57 – 97.13	0.20 ± 0.10	0.26 ± 0.12	0.55 ± 0.12
Bempton Cliffs	104 (97)	2010 to 2015	81	28.97 ± 16.96	0.3 – 89.4	0.22 ± 0.10	0.30 ± 0.10	0.47 ± 0.11
Orkney*	86 (80)	2010 to 2014	64	21.91 ± 8.55	0.8 – 42.1	0.17 ± 0.09	0.28 ± 0.17	0.55 ± 0.18

* = data for Orkney from Copinsay and Muckle Skerry combined

3.3.7 Utilisation distributions

Figures depicting utilization distributions for each colony are shown in Appendix AH. Depending on the colony, there was a smaller amount of data from the very highest wind speeds (greater than 8 m/s) – see also section above comparing use and availability for wind speed distributions.

For Kittiwakes, low sample sizes were primarily an issue for the Isle of May and centered around the number of birds available under high wind conditions; the day-high floating state was based on only two birds (103 fixes); the night-high category had less than or equal to five birds providing data for all states, and the commuting state had only 45 fixes. These categories should thus be treated with a high degree of caution, with less confidence placed in the final overlap assessments based on these data. For other colonies, in each category and state, there were more than five birds and more than 100 fixes, however, night-high categorisations at all colonies for the states of commuting and foraging represented less than 5% of the total data available. We again also caution the comparison of utilisation distribution based on very different numbers of GPS fixes.

3.3.8 Overlap indices

Overlaps between states in different conditions and times of the day are visualized in Appendix AI, and summarised in Table 19.

For Kittiwakes at all colonies, the 95% KDEs, representing total area usage, showed generally moderate (BA = 0.4 – 0.6) to very high (BA = 0.8+) levels of overlap, between the daytime low-wind conditions (taken here as representative of similar conditions that aerial surveys would encounter), and the other scenarios of day-high wind, night-low wind and night-high wind scenarios across different states; the exception to this was for the Isle of May and Bempton Cliffs night-high floating State 1 pair-wise test (BA = 0.34 in both cases), and also the night-high comparison for Bempton Cliffs for the foraging/searching State 3 (BA = 0.34).

At all colonies, a high (BA = 0.6 – 0.8) degree of overlaps was seen across colonies between day-low and day-high wind for the state of commuting, suggesting (generally) commuting zones used were not noticeably different during the day in different wind conditions. This wasn’t fully the case however, with moderate overlaps with day-low and night-high for the Isle of May and Bempton commuting State 2 (BA = 0.43 and 0.51). Overlaps between the core (50% KDE) day-low and other conditions were lower than the total 95% KDE for all states, and generally reflected the same patterns above for total area use. Comparing day-low with the other three conditions, some notably very low overlaps in the core 50% KDEs were recorded for the day-low vs nigh high at three colonies, Colonsay, Bempton and Orkney, with low overlaps for Isle of May (BA = 0.28, 0.17, 0.15 and 0.07) – this comparison, therefore, represents the most extreme difference of the four-way paired tests, but note that sample sizes for night-high wind conditions was lowest of all categorisations of data.

On inspection, the overlaps for the night-high vs night-low comparison were lower than day-high vs day-low comparisons across states, and these difference in BA indices were similar in magnitude to comparisons of day-low and night-low and day-high and night-high (Table 19). There were therefore some clear differences in overlaps across times of day and conditions that in turn varied between different states, and further variation between colonies, making drawing general conclusions difficult. For example, there was an indication for Isle of May and Colonsay that some areas further offshore were not used for floating on the sea (floating) during higher wind conditions (but noting reduced high wind speed sample sizes). However, given that many BA indices were classed as ‘moderate’ and above for 95% and 50% KDE comparisons, a general conclusion may be that space use overall can be considered similar across day-night and high and low wind.

Table 19 For Kittiwake, overlap indices (Bhattacharyya's Affinity Index) for pair-wise combinations of utilisation distribution assessing similarity in 95% KDEs (and 50%, brackets) for different levels of day and night, and high/low wind and states 1, 2 and 3 (floating, commuting and foraging/searching); bold highlights indicate comparisons of greatest interest, comparing the equivalent conditions when surveys are made (low wind daytime) to other conditions; red highlight shows where confidence in overlap assessment is lowest due to low sample sizes (see methods and Appendix AA).

(a) Isle of May

state		day.high	day.low	night.high
1	day.low	**0.46 (0.21)**		
1	night.high	0.33 (0.05)	**0.34 (0.28)**	
1	night.low	0.28 (0.04)	**0.52 (0.29)**	0.31 (0.15)
2	day.low	**0.62 (0.56)**		
2	night.high	0.54 (0.37)	**0.43 (0.29)**	
2	night.low	0.59 (0.6)	**0.72 (0.65)**	0.53 (0.41)
3	day.low	**0.59 (0.48)**		
3	night.high	0.6 (0.41)	**0.48 (0.39)**	
3	night.low	0.48 (0.33)	**0.71 (0.58)**	0.52 (0.41)

(b) Colonsay

state		day.high	day.low	night.high
1	day.low	**0.61 (0.67)**		
1	night.high	0.59 (0.37)	**0.44 (0.17)**	
1	night.low	0.51 (0.51)	**0.66 (0.58)**	0.45 (0.19)
2	day.low	**0.73 (0.74)**		
2	night.high	0.68 (0.69)	**0.6 (0.63)**	

2	night.low	0.7 (0.67)	**0.83 (0.72)**	0.62 (0.62)
3	day.low	**0.72 (0.72)**		
3	night.high	0.7 (0.55)	**0.54 (0.4)**	
3	night.low	0.68 (0.72)	**0.81 (0.76)**	0.56 (0.46)

(c) Bempton Cliffs

state		day.high	day.low	night.high
1	day.low	**0.47 (0.28)**		
1	night.high	0.48 (0.38)	**0.34 (0.15)**	
1	night.low	0.49 (0.35)	**0.63 (0.45)**	0.36 (0.19)
2	day.low	**0.8 (0.58)**		
2	night.high	0.63 (0.38)	**0.51 (0.32)**	
2	night.low	0.77 (0.62)	**0.82 (0.79)**	0.56 (0.43)
3	day.low	**0.57 (0.37)**		
3	night.high	0.49 (0.35)	**0.32 (0.03)**	
3	night.low	0.51 (0.37)	**0.75 (0.68)**	0.39 (0.09)

(d) Orkney

state		day.high	day.low	night.high
1	day.low	**0.74 (0.77)**		
1	night.high	0.48 (0.06)	**0.47 (0.07)**	
1	night.low	0.36 (0.38)	**0.61 (0.45)**	0.38 (0.13)
2	day.low	**0.69 (0.7)**		
2	night.high	0.66 (0.33)	**0.56 (0.46)**	
2	night.low	0.53 (0.54)	**0.72 (0.68)**	0.57 (0.51)

3	day.low	**0.87 (0.9)**		
3	night.high	0.83 (0.92)	**0.82 (0.93)**	
3	night.low	0.75 (0.89)	**0.86 (0.97)**	0.79 (0.93)

3.4 Razorbill

3.4.1 Comparison of wind speed use vs availability

Comparisons of wind speeds experienced and those available within the wider area were made for all colonies – see Table 20 and Figure 16 and Appendix AB.

For Razorbills at Colonsay and Puffin Island, similar availability percentages were obtained when using data from the full months of tracking and the precise periods where individual birds were tracked within these months. For the Isle of May, windier conditions were experienced during tracking periods than across the months of tracking. Correspondingly, the use of wind speeds by birds at the Isle of May was disproportionally higher than that available across the month, but not in comparison to available within the tracking period, and all proportions over 10 m/s was lower for conditions birds actually experienced vs that available. The conditions that birds experienced at Colonsay, revealed slightly lower but similar percentages to availability percentages, however, for Puffin Island, lower ‘use’ percentages were recorded. In comparison to Colonsay, Puffin Island wind speeds over the squares utilised by birds were windier, yet similar proportions of ‘use’ wind speeds were found at both sites, providing potential indication that Razorbills may have not selected stronger winds at Puffin Island to the extent at which they were available Razorbill. These findings may be attributable to the shorter foraging ranges at Puffin Island, meaning that windier conditions offshore are not used, in turn making it harder to assess how birds at this colony respond to windier conditions. Such colony-specific variations are therefore apparent, and may be further complicated by some individuals at some colonies struggling to find enough prey for chicks and thus having to travel further (in turn experiencing windier conditions offshore).

Table 20 For Razorbill, summary of the proportions of tracking data by wind speed thresholds of more than 10 m/s and more than 8 m/s, further comparing wind speeds encountered by birds ('used') vs wind speeds 'available'. Assessment is made both (i) within the full months that tracking was carried out and (ii) for the precise tracking date-times, for all Copernicus grid squares that birds overlapped with; proportions for 'use' data are calculated on the data modelled within HMMs, thus each data point is a GPS fix; for 'available' calculations, each data point is an hourly wind speed estimate for each Copernicus grid square.

		Used (%)		**Available (tracking period, %)**		**Available (all months, %)**	
Colony / State	**Tracking months and years**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**
Isle of May	June – July 2012, June 2013, 2014	12.31	0.48	16.23	3.3	7.07	1.34
Colonsay	July 2010, June – July 2011 – 2014	14.9	3.99	15.83	4.96	15	4.69
Puffin Island	May – June, 2011; June 2013; May 2012, 2015	11.91	3.92	23.64	11.19	27.46	11.62

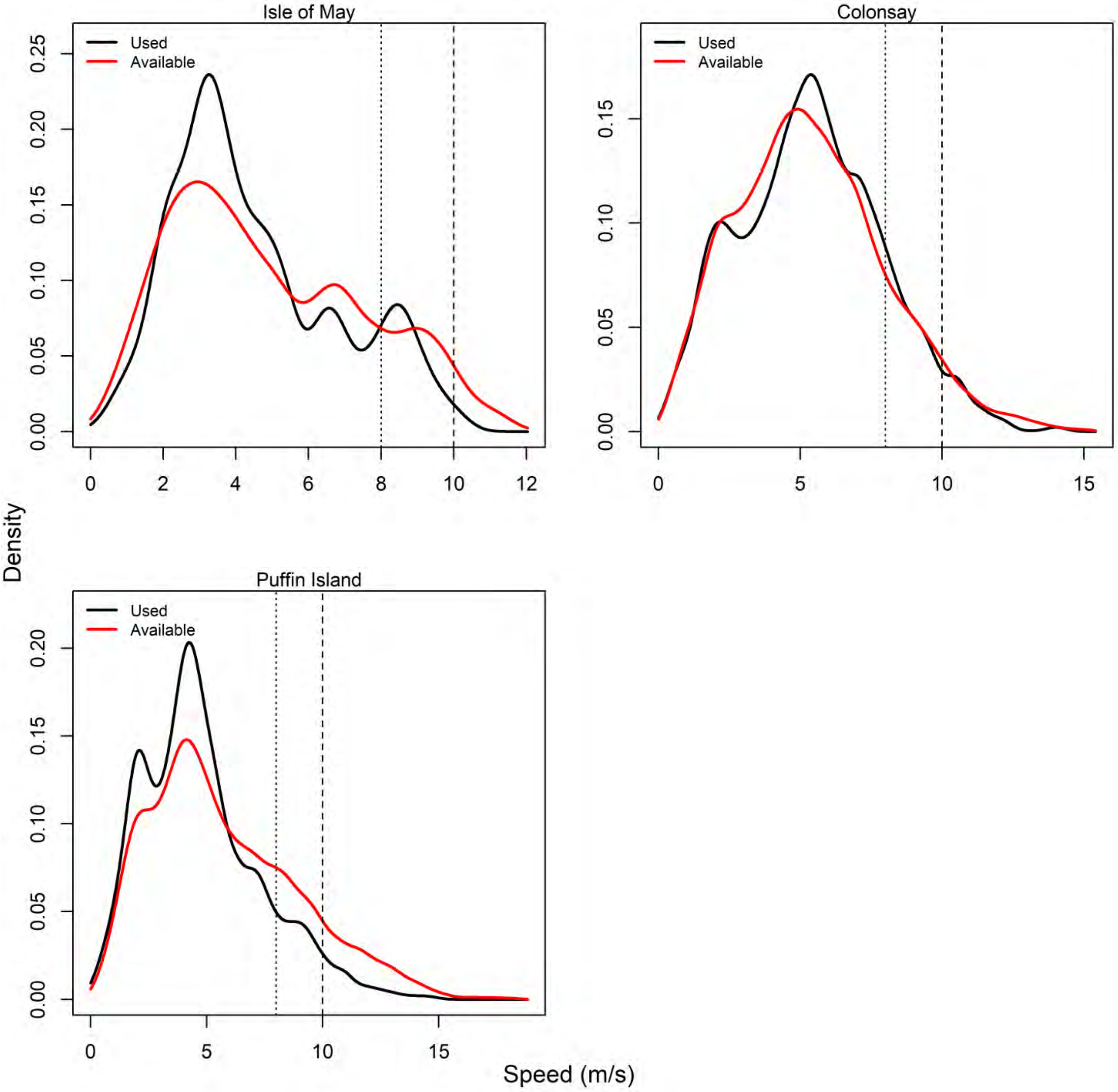


Figure 16 For Razorbill, density histograms of wind speed during the period of study at each site that was available for birds to experience within the grid cells they overlapped with, vs that actually experienced when on foraging trips (‘Used’ vs ‘Available’); data here are pooled across each tracking period per bird in each year for each colony.

3.4.2 Model summary

The best fitting models corresponding to Razorbills tagged on Colonsay, Puffin Island, and the Isle of May are presented in Appendix AF. Table 21 displays the step lengths and angle concentrations corresponding to the three behavioural states in relation to each study site. In general, State 1 (floating) and State 2 (commuting) contained obtuse turning angles, with step lengths being relatively short in State 1, and longer in State 2. State 3 (foraging) exhibited acute turning angles and the shortest relative step lengths (Appendix AC).

Table 21 For Razorbill, summary of mean ± SD step length and turning angles (mean, concentration) for each site.

	Step			**Turn**		
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/ search)**	**1 (floating)**	**2 (commuting)**	**3 (forage/ search)**
Colonsay	41.33 ± 21.64	806.16 ± 837.69	18.81 ± 17.00	0, 17.16	0, 2.01	0, 0.06
Puffin Island	79.87 ± 32.49	768.72 ± 816.18	21.67 ± 19.98	0, 107.09	0, 2.21	0, 0.82
Isle of May	39.88 ± 18.15	648.27 ± 843.31	11.42 ± 10.02	0, 7.46	0, 0.67	0, 0.01

Razorbills from Colonsay transitioned between floating (States 1) and commuting (State 2) less frequently than transitions between floating to foraging (State 3) (Appendix AC). In contrast, individuals from Puffin Island and the Isle of May transitioned proportionately more frequently from floating (State 1) to commuting (State 2) than floating to foraging (State 3). State changes from foraging to floating occurred more frequently than transitions from foraging directly to commuting at all three study sites. These relationships are proportionally less in Razorbills from Puffin Island than from Colonsay or the Isle of May, with no clear trends between state transitions (Appendix AC). Razorbills from all three colonies exhibited strong tendencies to remain within their previous states. With regards to Razorbills from

Colonsay, the tendency for birds to remain foraging was weaker than Colonsay or the Isle of May, this potentially contributed to a lack of discernible trends in state transitions on Puffin Island.

For Colonsay, the model incorporating an additional dive depth parameter displayed some differing transition probabilities in comparison to the model excluding diving (Appendix AC). Primarily, the proportional transition from float to commute was much more pronounced, with the probability of remaining floating reduced. The probability of a foraging state transitioning to floating or commuting remained similar, although the probability of remaining in a foraging state increased.

Time-depth recorder (TDR) data was available for sub-sample of concurrently GPS tracked individuals (n = 25, Colonsay). The proportion of dives > 5 m used as a third covariate alongside turning angle and step length within HMMs. Table 22 displays the step lengths and angle concentrations corresponding to the three behavioural states in relation to each study site, using the best-fitting model (Appendix AF).

Table 22 For Razorbills, summary of mean ± SD step length and turning angles (mean, concentration) for Colonsay based on HMMs using both GPS and TDR data.

	Step			**Turn**		
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**
Colonsay	35.8 ± 20.38	151.34 ± 254.66	201.66 ± 253.57	0, 13.05	0, 0.12	0, 1.59

The proportion of dives per GPS fix that were classified as belonging to different States (1-3) are given in Table 23 below. These comparisons acted as a post-hoc verification of the classifications using TDR data through the HMM model with the additional channel of dive depth; these results indicate that the foraging/searching state contained the most GPS fixes that were identified from the model as being both in the state “foraging/searching” and being beneath the water, i.e. dives indeed did fall within the foraging/searching category.

Table 23 For Razorbills, total number of GPS fixes for states 1, 2 and 3 (floating, commuting and foraging/searching) categorised by the proportion of time spent deeper than 5 m at Colonsay.

Dive proportion category	**State 1 (floating)**	**State 2 (commuting)**	**State 3 (foraging/searching)**
0	16427	32318	0
0 – 0.5	14	403	1341
0.5 – 1.0	12	1	94

We also investigated the corresponding classification of GPS points between the non-TDR (standard HMM with no dive depth channel included) and TDR HMMs (including the additional dive channel). This comparison was conducted on the subset of Razorbills at Colonsay that were included in both analyses, and for each GPS fix, assessing the state assignment between the two approaches. Table 24 below shows this comparison and indicated that although there was a good match for the floating State 1, there was considerably more discrepancy between commuting State 2 and the foraging/searching State 3. In particular, the standard HMM most often assigned a foraging state, which for the TDR models was classified mostly as commuting. These discrepancies are perhaps testimony to the difficulty of applying HMMs to these species, which requires further work to fully resolve. These discrepancies, however, were less apparent in spatial plots comparing the distribution of states (Appendix AC) Further, the HMMs also classified some points as resting on the sea for commuting (see the strings of red aligned points, i.e. at lower speed, to the bottom right of the images), with potential consequences for interpretation of commuting speed for this species.

Table 24 For Razorbill, total number of GPS fixes corresponding in behavioural states 1, 2 and 3 (floating, commuting and foraging/searching) between Non-TDR and TDR incorporating models for Colonsay.

		TDR		
	States	1	2	3
Non-TDR	1	12693	581	543
	2	87	5010	378
	3	3673	27131	514

3.4.3 Travel speeds

Table 25 below shows the distributions of speeds from boxplot analysis (Figure 17) after assigning states back to the raw data and birds modelled using the additional TDR dive variable (Figure 18). It is likely that the foraging state encompassed bouts of diving, in which birds will move only negligible distances between GPS fixes. The influence of diving on the outcome of the models was also investigated in Guillemots, where TDR data was available for a subsample of birds.

Table 25 For Razorbills, summary of speeds per state (m/s), as obtained through classification of tracking data using HMMs.

Colony / State	1 (floating)	2 (commuting)	3 (forage/search)
Standard model			
Colonsay	0.37 (0.26 – 0.53)	3.62 (1.34 – 14.44)	0.13 (0.06 – 0.25)
Puffin Island	0.77 (0.56 – 1.01)	4.75 (1.10 – 14.23)	0.15 (0.06 – 0.28)
Isle of May	0.36 (0.27 – 0.47)	1.50 (0.65 – 12.03)	0.07 (0.04 – 0.15)
TDR data included			
Colonsay	0.31 (0.21 – 0.47)	0.15 (0.06 – 0.41)	0.51 (0.28 – 0.88)

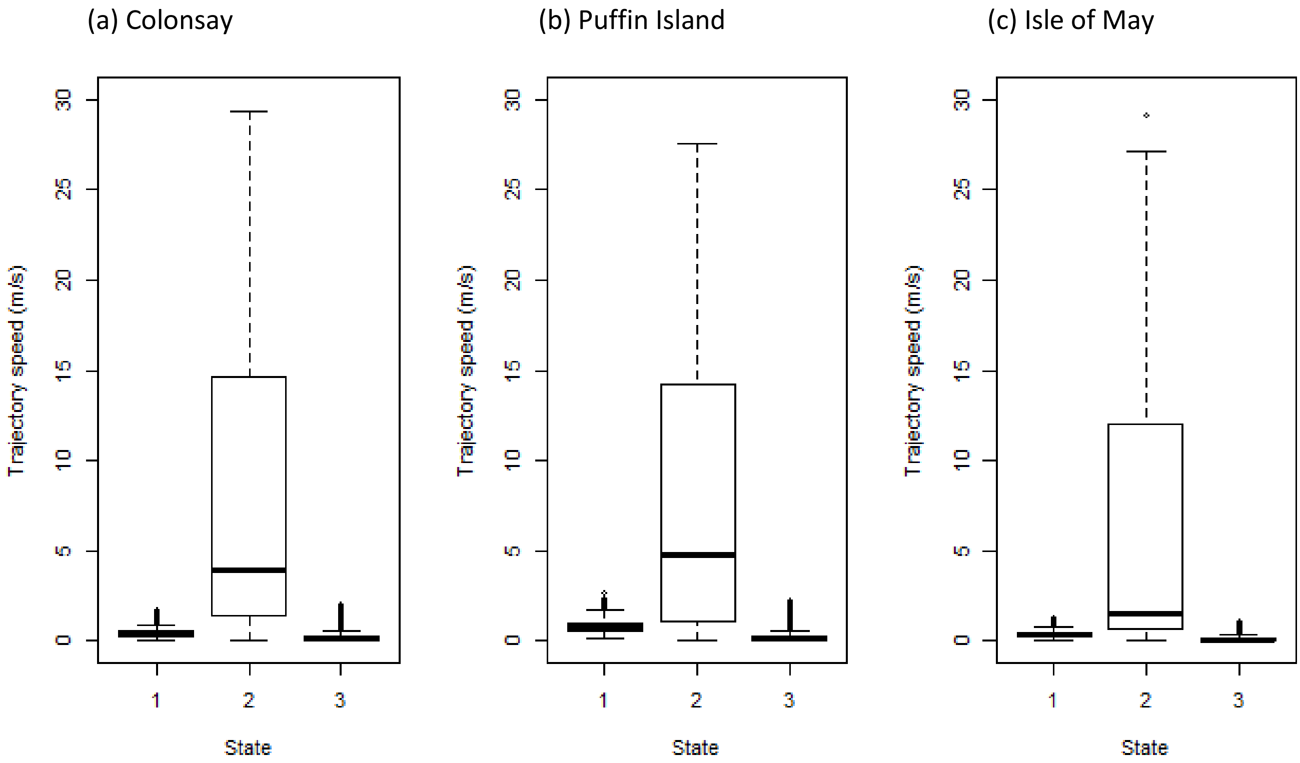


Figure 17 For Razorbills, travel speed (m/s) of at (a) Colonsay, (b) Puffin Island and (c) Isle of May, for each states 1, 2 and 3 (floating, commuting and foraging/searching) as assessed via assignment to raw data through the Viterbi algorithm of the three state model.

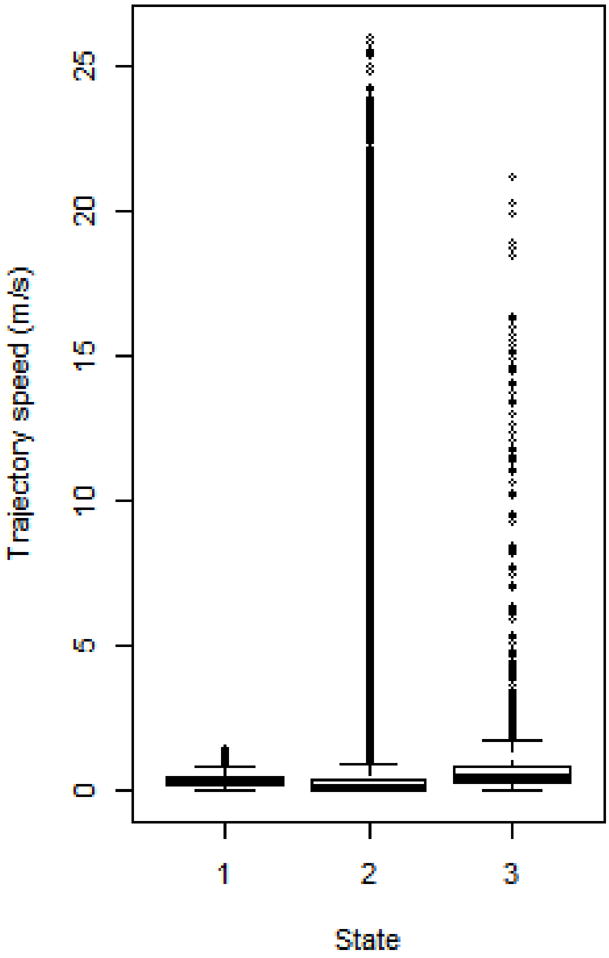


Figure 18 For Razorbills, travel speed (m/s) at Colonsay with TDR, for states 1, 2 and 3 (floating, commuting and foraging/searching) as assessed via assignment to raw data through the Viterbi algorithm of the three state model.

3.4.4 Effects of wind speed on step length (speed)

Step lengths relating to specific states were plotted over increasing wind speeds for Colonsay, Puffin Island and Isle of May (Appendice AD and AE). Colonsay Razorbills exhibited a decrease in floating (State 1) and foraging (State 3) step lengths in relation to increasing wind speeds (β = -0.048, β = -0.012). Conversely, step lengths in the commuting state (State 2) were positively associated with wind speed (β = 0.0069) at Colonsay. Wind speed maintained a positive relationship with increasing step lengths across all states at Puffin Island state 1 (β = 0.033), state 2 (β = 0.023), and state 3 (β = 0.055). With regards to the Isle of May Razorbills, step length exhibited a decreasing relationship with increasing wind speeds in in relation to State 1 (β = -0.027) and 2 (β = -0.014), but displayed a weak positive relationship in state 3 (β = 0.0017).

3.4.5 Transition effects between states in relation to covariates

AIC selection indicated the best-fitting model, for both Colonsay, Puffin Island, and the Isle of May contained all the covariates (hour + Julian date + colony distance + wind speed) (Appendix AF). The best-fitting model selected for Colonsay, when incorporating dive depth variable, retained only ‘hour’.

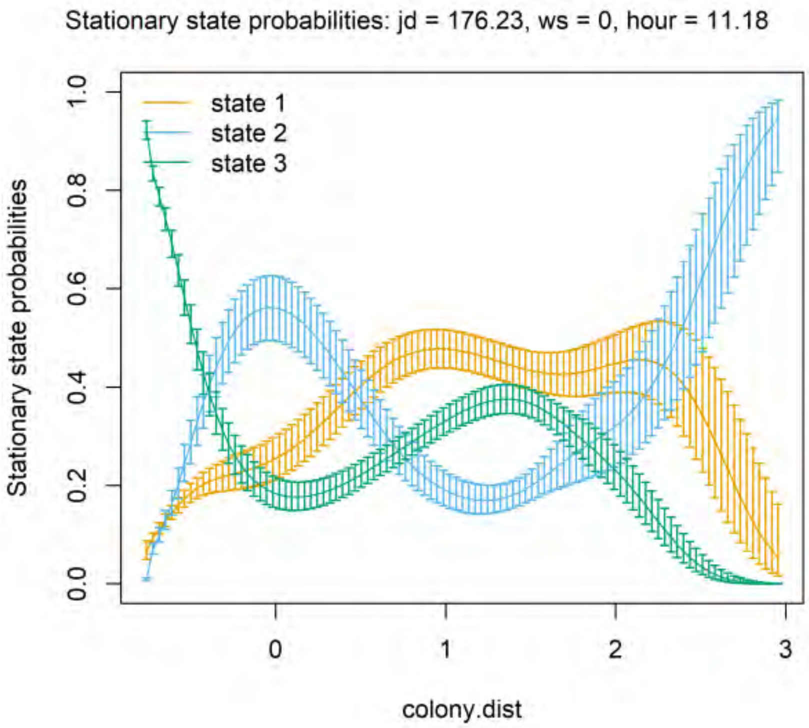
At each colony, behavioural states transitioned in variable manners with increasing colony distance (Figure 19 and Appendix AD). At all colonies, the probability (occurrence) of the being classified as foraging decreased close to the colony. At Colonsay, as distance from the colony increased birds were increasingly likely to be classified as commuting. In contrast, at Puffin Island as distance from the colony increased birds were more likely to be classified as foraging. At the Isle of May, commuting decreased slightly with increasing colony distance, but remained the primary state.

At the three colony colonies, Julian date did not influence the probability (likelihood) of switching between behavioural states (Figure 20 and Appendix AD). However, individuals were not tracked continuously across this period (max = 99.11 hours, Colonsay; max = 133.88 hours, Puffin Island; max = 118.71 hours, Isle of May). These confined individual tracking periods will potentially be further influenced by varying breeding stages/individualistic foraging behaviour.

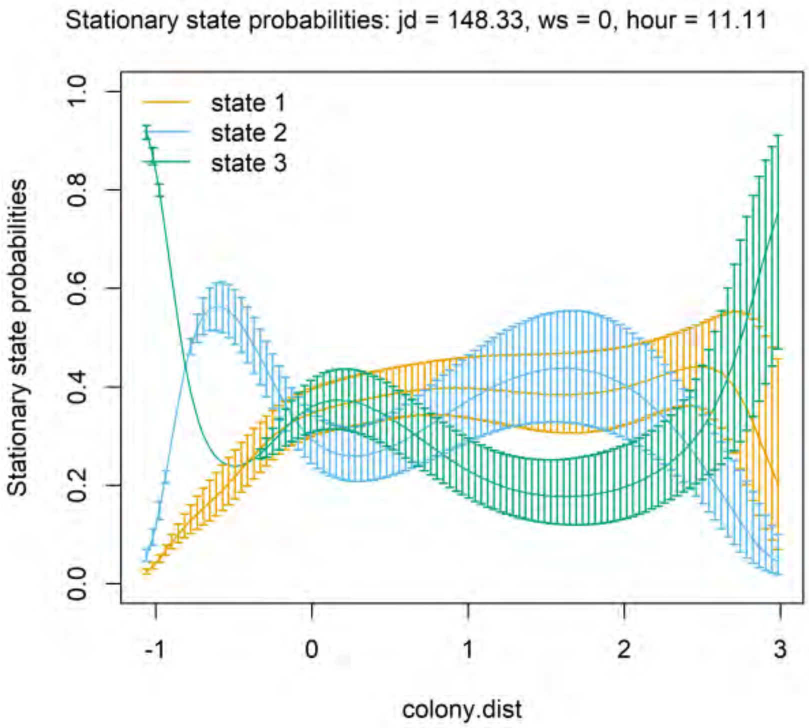
Similar patterns in behaviour are seen between Colonsay, Puffin Island, and the Isle of May in their relationship with hour of the day (Appendix AD). At both colonies, foraging (State 3) remained static throughout the day and night. Floating (State 1) and commuting (State 2) exhibited contrasting relationships with hour of day, with floating increasing, and commuting decreasing during night hours (20:00 – 05:00). The opposite relationship was exhibited during daylight hours (10:00 – 15:00) with decreased floating and an increased commuting. When incorporating a dive depth variable for Colonsay birds, the relationship with time of day followed the same pattern as displayed at other colonies, with increase in commuting (State 2) during daylight hours (06:00 – 20:00) coinciding with a decrease in floating (State 1), and foraging (State 3) remaining static.

Wind speed had a variable influence on behaviour between Colonsay, Puffin Island, and Isle of May colonies, with transition probabilities largely unaffected by wind speed. Stationary state probabilities show alternate trends with increasing wind speed with floating and foraging increasing at higher winds speeds (> 2 standardised variable) at Colonsay and the Isle of May. Conversely, commuting increases at greater wind speeds (> 2 standardised variable) on Puffin Island.

(a) Colonsay



(b) Puffin Island



(c) Isle of May

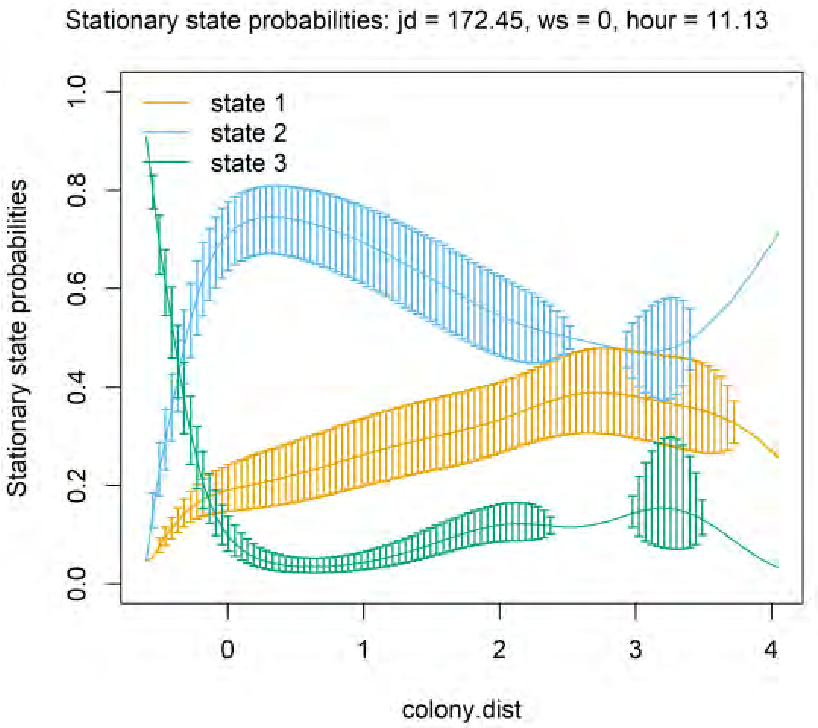
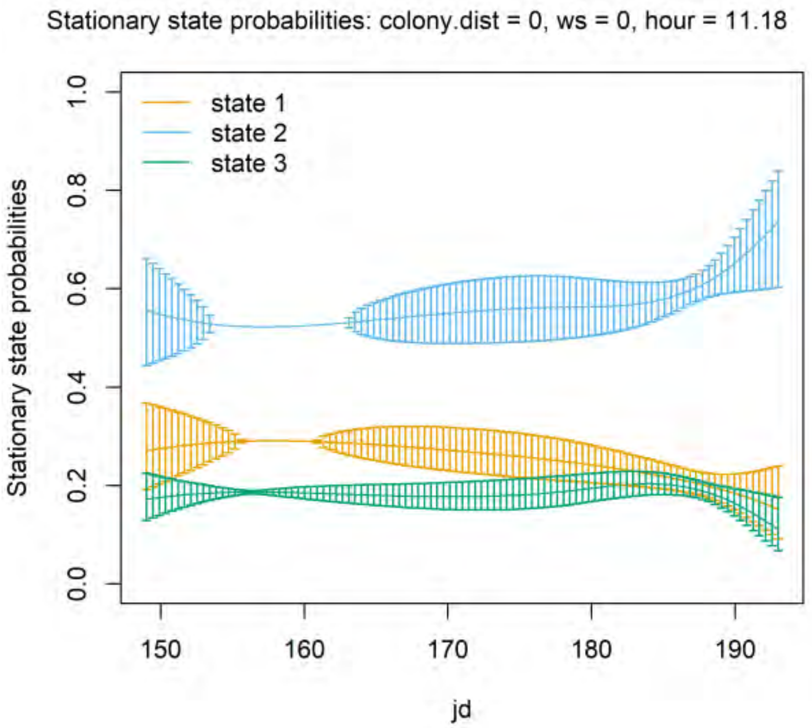
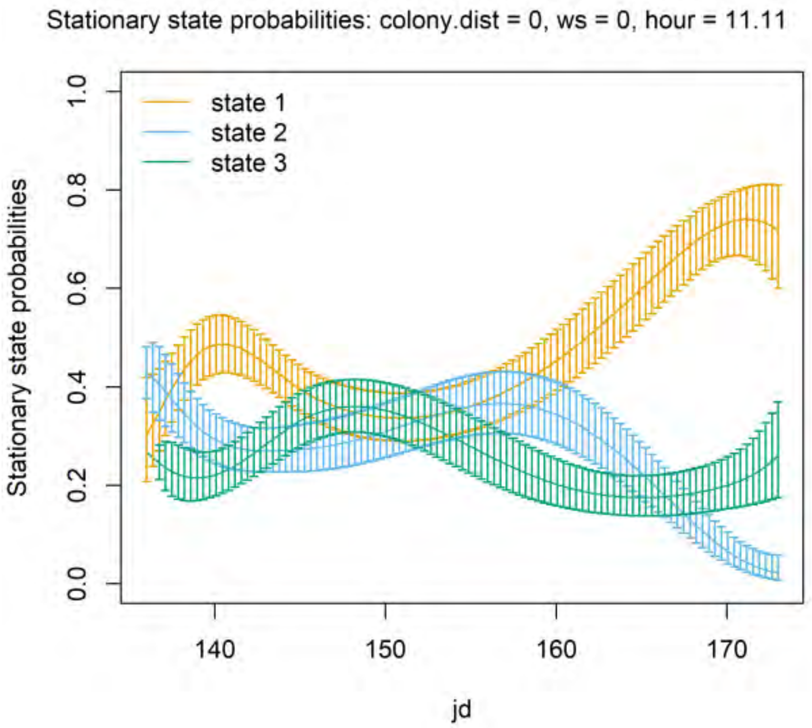


Figure 19 For Razorbill, stationary state probabilities for the variable of distance to colony, fitted as a standardised variable for states 1, 2 and 3 (floating, commuting and foraging/searching).

(a) Colonsay



(b) Puffin Island



(c) Isle of May

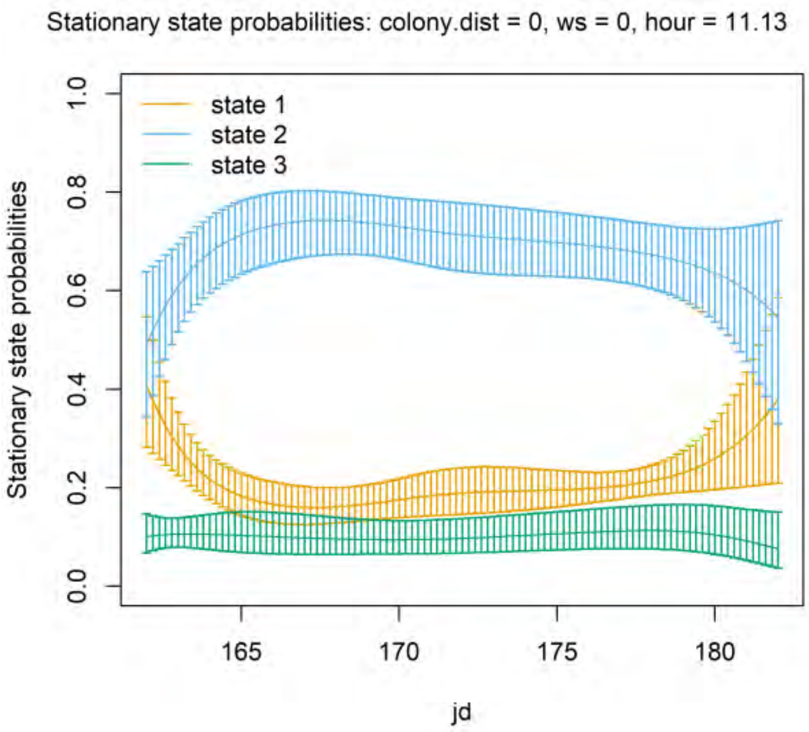


Figure 20 For Razorbill, stationary state probabilities for the variable of Julian date at (a) Colonsay, (b) Puffin Island and (c) Isle of May for states 1, 2 and 3 (floating, commuting and foraging/searching).

3.4.6 Time in states

The range of duration of data per bird and the proportion of time spent in different states are shown in Table 26. As birds with fewer data had less time to demonstrate their overall time spent in different states, we used information from birds with more than ten hours of data, to exclude any very small tracking durations that could otherwise skew patterns observed. At Colonsay and Puffin Island, the smallest mean proportion of time was attributed to State 2 (commuting), Colonsay and Isle of May Razorbills spent a greater proportion of time to foraging (Table 26), than Puffin Island individuals.

Table 26 For Razorbill, estimated time spent in states for each colony for birds at each colony across years; note occasionally initial movement models could not be fitted due to a lack of data available for some individuals, hence the effective sample size feeding into assessments is provided in brackets.

			Duration of tracking			Proportion time spent per state		
Colony	**No. birds total (modelled)**	**Years**	**No. birds > 10 hrs tracking data**	**Duration (hrs) mean ± SD per bird**	**Tracking data range (hrs)**	**1 floating mean ± SD**	**2 commuting mean ± SD**	**3 foraging / searching mean ± SD**
Colonsay	42 (42)	2010 to 2014	41	54.94 ± 22.05	1.64 – 99.11	0.25 ± 0.12	0.13 ± 0.06	0.63 ± 0.12
Puffin Island	58 (43)	2011 to 2013, 2015	42	45.05 ± 23.38	4.95 – 133.88	0.44 ± 0.12	0.14 ± 0.05	0.42 ± 0.13
Isle of May	28 (28)	2012 to 2014	28	40.06 ± 20.93	14.37 – 118.71	0.16 ± 0.08	0.21 ± 0.07	0.63 ± 0.09
+ TDR data								
Colonsay	26	2011 to 2014	26	56.35 ± 20.65	16.31 – 99.11	0.33 ± 0.11	0.63 ± 0.11	0.04 ± 0.02

3.4.7 Utilisation distributions

Figures depicting utilization distributions for each colony are shown in Appendix AH. Depending on the colony, there was a smaller amount of data from the very highest wind speeds (greater than 8 m/s) – see also section above comparing use and availability for wind speed distributions.

Where sample sizes of number of fixes and birds used to compute utilisation distributions is low, here taken as less than 100 fixes and less than five birds for the lowest amounts of data (see Appendix AA and methods), then confidence in the overlap result is considered low, and is here indicated as requiring a high degree of caution in interpretation of results. Also highlighted is the proportion of fixes available per split of data, with proportions of less than 5% of the total for the state also flagged up as requiring caution.

Low sample sizes were an issue for some Razorbill colonies and splits of the data. For the Isle of May, only five birds provided data for the night-high categorisation, across all states, albeit with a suitable number of GPS fixes. At Colonsay, sample sizes were considered sufficient, however, when using TDR data within HMMs thus reducing sample sizes in the analysis, no birds or fixes provided information for the night-high wind categorisation of the data.

3.4.8 Overlap indices

Overlaps between utilisation distributions based upon the different behavioural states identified by HMMs across each time of day (day vs. night) and wind speed (high vs. low) category are visualised in Appendix AI, and summarised in Table 27.

Regarding Colonsay, all 95% KDEs, representing total area usage, showed moderate to very high levels of overlap (ca. 0.4+, see methods) between all combinations of night/day and high/low wind conditions. Highest overlaps are seen between day-low and day-high conditions (BA > 0.7), with high to very high BA values sustained across all three states (state 1, BA = 0.77; state 2, BA = 0.91; State 3, BA = 0.96). Very high affinities were held between low wind, day and night conditions, this was apparent within each state (State 1, BA = 0.77; State 2, BA = 0.8; State 3, BA = 0.87). Relative to State 1 and 2, high affinities between all conditions (day-low, day-high, night-low and night-high) were maintained within State 3 for both 95% and 50% KDEs.

In comparison to Colonsay, Razorbills at Puffin Island exhibited lower overlap affinity indices were seen in all compared conditions. However, similar to Colonsay night-low and day-low conditions maintained relatively high affinities across all three states. The highest affinities were exhibited in State 2 and 3 between 95% KDEs of day low vs. high wind conditions (state 2, BA = 0.74; state 3, BA = 0.78). Comparable to Colonsay, the highest 50% KDE affinity was maintained within State 3 between day low vs high wind conditions (Colonsay, BA = 0.91; Puffin Island, BA = 0.87).

At the Isle of May, Razorbills showed a variable degree of overlap for total area use (95% KDE) – overlaps for day-low and day-high were highest (state 1, BA = 0.53; state 2, BA = 0.79; state 3, BA = 0.99), with almost a complete overlap for foraging/searching. However, overlaps were lowest within each state for day-low and night-high conditions (State 1, BA = 0.28; State 2, BA = 0.31; State 3, BA = 0.79).50% overlaps BA values were generally lower or identical , with a range of affinities ranging from zero (e.g. day-low, night-high) to 0.92 (day-low, night-low). At all colonies, the lowest affinity indices were seen for the state of floating (State 1) in all conditions.

Overlaps within behavioural states of 95% KDEs from models incorporating a dive depth parameter varied in certain distinct aspects from models not incorporating diving (Table 28). To a large extent within State 1 the overlap between conditions of night/day and high/low wind conditions remained similar between GPS + TDR and just GPS. State two displayed some reduction, when incorporating a dive variable, in overlaps the between day-low and night-high (BA = 0.67), night-high and night-low (BA = 0.61). State 3 underwent the greatest change in between GPS and GPS + TDR models, with a reduction in BA values across all conditions and no overlaps present during night-high conditions.

Table 27 For Razorbills, overlap indices for combinations of KDEs assessing similarity in 50% and 95% KDEs for different levels of day and night, and high/low wind and states 1, 2 and 3 (floating, commuting and foraging/searching); for example the top row takes the 95% KDEs for daytime low wind conditions for each State 1, 2 and 3, and computes Bhattacharyya's Affinity index for those three distributions, taking a mean and standard deviation, omitting the diagonal of the matrix that compares each the distribution to itself; note for the comparison of day and night (across wind conditions) for specific states, this results in a simple 2 x 2 matrix and thus, only one comparison value that cannot therefore have a standard deviation; red highlight shows where confidence in overlap assessment is lowest due to low sample sizes (see methods and Appendix AA).

(a) Colonsay

state		day.high	day.low	night.high
1	day.low	**0.77 (0.55)**		
1	night.high	0.64 (0.34)	**0.69 (0.58)**	
1	night.low	0.66 (0.37)	**0.77 (0.49)**	0.69 (0.52)
2	day.low	**0.91 (0.91)**		
2	night.high	0.66 (0.48)	**0.67 (0.5)**	
2	night.low	0.69 (0.51)	**0.8 (0.54)**	0.61 (0.61)

3	day.low	**0.96 (0.96)**		
3	night.high	0.86 (0.88)	**0.86 (0.85)**	
3	night.low	0.85 (0.84)	**0.87 (0.82)**	0.84 (0.95)

(b) Puffin Island

state		day.high	day.low	night.high
1	day.low	**0.48 (0.23)**		
1	night.high	0.39 (0.06)	**0.4 (0.15)**	
1	night.low	0.56 (0.33)	**0.78 (0.61)**	0.52 (0.23)
2	day.low	**0.74 (0.48)**		
2	night.high	0.32 (0.04)	**0.25 (0)**	
2	night.low	0.53 (0.27)	**0.57 (0.15)**	0.37 (0.19)
3	day.low	**0.78 (0.87)**		
3	night.high	0.14 (0)	**0.06 (0)**	
3	night.low	0.5 (0.6)	**0.63 (0.52)**	0.28 (0.03)

(c) Isle of May

state		day.high	day.low	night.high
1	day.low	**0.53 (0.58)**		
1	night.high	0.35 (0.08)	**0.28 (0.04)**	
1	night.low	0.4 (0.28)	**0.6 (0.4)**	0.23 (0.01)
2	day.low	**0.79 (0.97)**		
2	night.high	0.28 (0)	**0.31 (0)**	
2	night.low	0.61 (0.66)	**0.7 (0.69)**	0.33 (0.02)

3	day.low	**0.99 (0.98)**		
3	night.high	0.8 (0.77)	**0.79 (0.79)**	
3	night.low	0.93 (0.91)	**0.92 (0.92)**	0.81 (0.84)

Table 28 For Razorbills, overlap indices for combinations of KDEs at Colonsay, using a subset of birds with GPS + TDR data (from HMMs including the additional channel of dive for refined state assignment); for details of overlap tables see Table 27 above – note, no data were available for the night-high condition for this subset of data.

state		day.high	day.low	night.high
1	day.low	0.74 (0.78)		
1	night.high	0.6 (0.51)	0.64 (0.57)	
1	night.low	0.61 (0.37)	0.71 (0.44)	0.5 (0.34)
2	day.low	0.93 (0.94)		
2	night.high	0.9 (0.98)	0.89 (0.94)	
2	night.low	0.88 (0.86)	0.9 (0.9)	0.82 (0.86)
3	day.low	0.59 (0.3)		
3	night.high	----	----	
3	night.low	0.41 (0.11)	0.6 (0.36)	-----

3.5 Common Guillemot

3.5.1 Comparison of wind speed use vs availability

Comparisons of wind speeds experienced and those available within the wider area were made for all colonies – see Table 29, Figure 21 and Appendix AB.

For Guillemots at Colonsay and Fowlsheugh, similar percentages were obtained when using data from the full month of tracking and the precise periods where individual birds were tracked within these months. However, at Puffin Island, smaller percentages for the 10 m/s category were obtained when using or the precise periods where individual birds were tracked; for the Isle of May (as also seen for Razorbills), the tracking periods appeared to coincide with windier conditions than seen foe the rest of the months of tracking. Further, the proportion of tracking data more than 8 m/s at the Isle of May was disproportionally higher still than that available within the tracking period. For Colonsay, Fowlsheugh and Puffin Island, birds experienced lower wind speeds and thus proportions of data that were categorized above 8 m/s and 10 m/s, than that available to birds, which was particularly pronounced for Puffin Island (as also seen for Razorbills). These patterns may reflect the fact that birds foraged away from Puffin island in more ‘coastal’ regions to the northeast of the island, where wind speeds were lower than further offshore to the north and west (Appendix AB), but even so compared to other colonies, the wind speed here were less for Puffin Island.

Further the distribution for Isle of May and Puffin Island, and perhaps also the other colonies, appeared to show a tendency for bimodal “use” of wind speeds. Thus, there may be a spatial influence of area use on the distribution of wind speeds that birds experienced.

Table 29 For Guillemot, summary of the proportions of tracking data by wind speed thresholds of more than 10 m/s and more than 8 m/s, further comparing wind speeds encountered by birds ('used') vs wind speeds 'available'. Assessment is made both (i) within the full months that tracking was carried out and (ii) for the precise tracking date-times, for all Copernicus grid squares that birds overlapped with; proportions for 'use' data are calculated on the data modelled within HMMs, thus each data point is a GPS fix; for 'available' calculations, each data point is an hourly wind speed estimate for each Copernicus grid square.

		Used (%)		**Available (tracking period, %)**		**Available (all months, %)**	
Colony / State	**Tracking months and years**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**	**8 m/s**	**10 m/s**
Isle of May	June – July 2012, June 2013, 2014	18.86	3.53	16.65	4.17	9.45	2.14
Colonsay	July 2010, June – July 2011 – 2014	10.79	2.71	12.72	4.23	13.58	4.57
Fowlsheugh	June 2012	8.60	0.89	22.11	7.95	23.29	5.89
Puffin Island	June, 2012, 2013, 2015	2.42	0.00	15.22	1.41	17.62	6.66

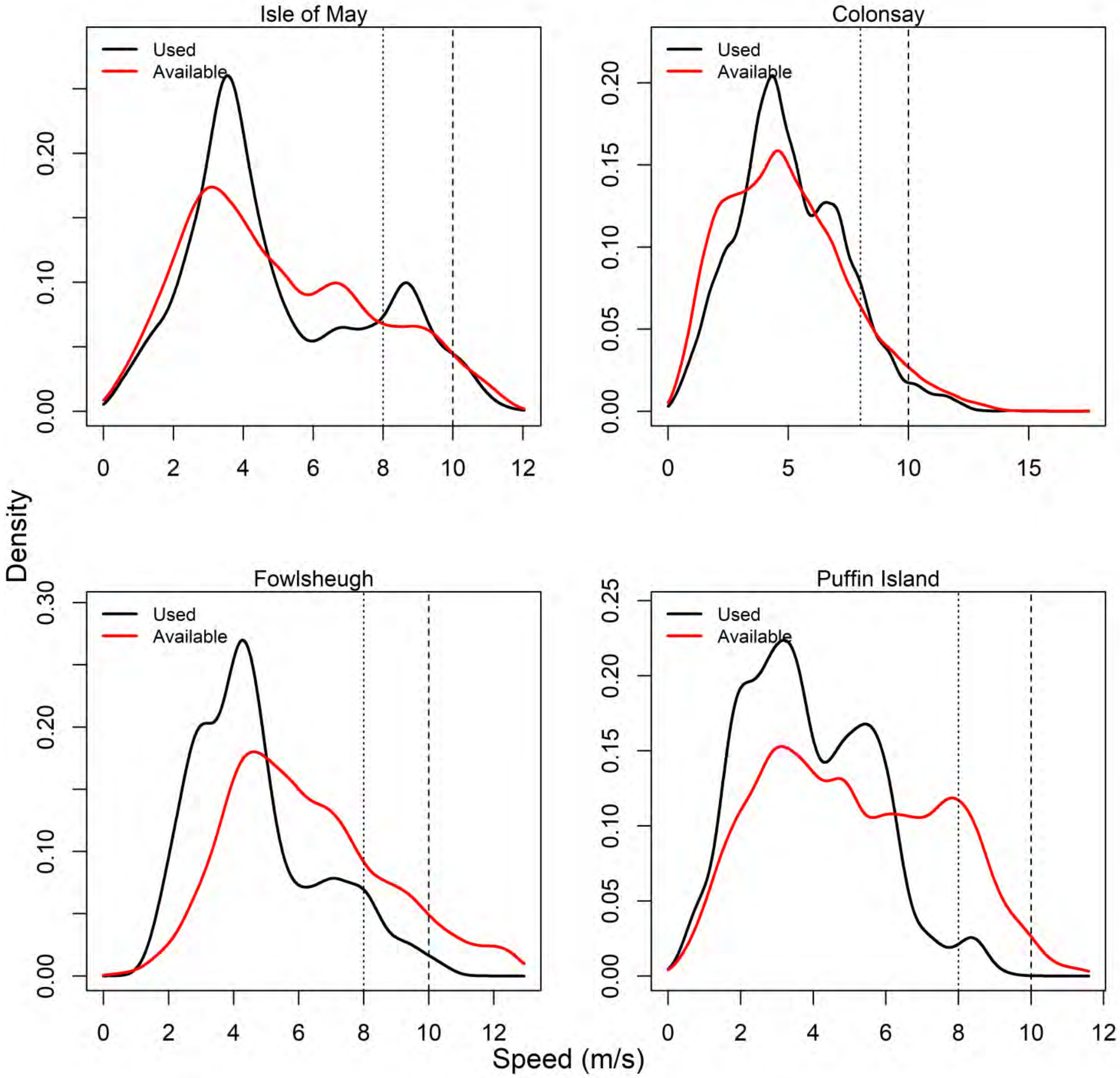


Figure 21 For Guillemots, density histograms of wind speed during the period of study at each site that was available for birds to experience within the grid cells they overlapped with, vs that actually experienced when on foraging trips (‘Used’ vs ‘Available’); data here are pooled across each tracking period per bird in each year for each colony.

3.5.2 Model summary

The best fitting models selected for Guillemot tagged on Colonsay, Puffin Island, Fowlsheugh, and the Isle of May are presented in Appendix AF. Table 30 displays the step lengths and angle concentrations corresponding to the three behavioural states in relation to each study site. In general, State 1 (floating) and State 2 (commuting) contained obtuse turning angles, with step lengths being relatively short in State 1, and longer in State 2. State 3 (foraging) exhibited acute turning angles and the shortest relative step lengths (Appendix AC).

Table 30 For Guillemots, summary of mean ± SD step length and turning angles (mean, concentration) for each site

	Step			**Turn**		
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**
Colonsay	39.79 ± 18.58	530.02 ± 679.80	13.05 ± 11.80	0, 15.72	0, 0.97	0, 0.18
Puffin Island	63.12 ± 28.39	364.49 ± 476.70	10.42 ± 10.24	0, 66.05	0, 1.10	0, 0.22
Fowlsheugh	59.28 ± 25.51	559.57 ± 730.86	11.99 ± 10.44	0, 14.12	0, 0.65	0, 0.04
Isle of May	42.35 ± 21.41	557.87 ± 733.69	11.96 ± 10.66	0, 9.91	0, 0.69	0, 0.01

Guillemots from all colonies transitioned from commuting (State 2) to floating/floating (State 1) more readily than commuting to foraging (State 3) (Appendix AC). Similarly switching from foraging to commuting was proportionally less than state changes from foraging to floating/floating. Therefore, state transitions generally occurred in the sequence: commute (State 2) -> float (State 1) -> foraging (State 3) -> float (state 1) -> commute (State 2).

Time-depth recorder (TDR) data was available for sub-sample of concurrently GPS tracked individuals (n = 29, Colonsay; n=7, Fowlsheugh). The proportion of dives > 5m used as a third covariate alongside turning angle and step length within HMMs. Table 31 displays the step lengths and angle concentrations corresponding to the three behavioural states in relation to each study site, using the best-fitting model (Appendix AF).

Table 31 For Guillemots, summary of mean ± SD step length and turning angles (mean, concentration) for each site based on HMMs using both GPS and TDR data.

	Step			**Turn**		
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**
Colonsay	38.55 ± 20.71	124.14 ± 218.49	141.39 ± 172.55	0, 15.99	0, 0.33	0, 1.43
Fowlsheugh	47.38 ± 32.23	430.19 ± 869.27	212.56 ± 231.16	0, 13.83	0, 0.001	0, 3.30

The proportion of dives per GPS fix that were classified as belonging to different States (1 – 3) are given in Table 32. These comparisons acted as a post-hoc verification of the classifications using TDR data through the HMM model with the additional channel of dive depth; these results indicate that the foraging/searching state contained the most GPS fixes that were identified from the model as being both in the state "foraging/searching" and being beneath the water, i.e. dives indeed did fall within the foraging/searching category.

Table 32 For Guillemots, total number of GPS fixes per state categorised by the proportion of time spent deeper than 5 m for (a) Colonsay and (b) Fowlsheugh.

(a)

Dive proportion category	**State 1 (floating)**	**State 2 (commuting)**	**State 3 (foraging/searching)**
0	16409	33156	0
0 – 0.5	26	0	1449
0.5 – 1.0	0	0	955

(b)

Dive proportion category	**State 1 (floating)**	**State 2 (commuting)**	**State 3 (foraging/searching)**
0	2568	4990	0
0 – 0.5	9	76	162
0.5 – 1.0	0	10	71

As with Razorbills, for guillemots we also investigated the corresponding classification of GPS points between the non-TDR (standard HMM with no dive depth channel included) and TDR HMMs (including the additional dive channel). This comparison was conducted on the subset of guillemots at Colonsay and Fowlsheugh that were included in both analyses, and for each GPS fix, assessing the state assignment between the two approaches. Table 33 below shows this comparison and indicated that although there was a good match for the floating State 1, there was considerably more discrepancy between commuting State 2 and the foraging/searching State 3. These discrepancies require further work to fully resolve, but were less apparent in spatial plots comparing the distribution of states (Appendix AC). Further, the proportional relationships between state changes indicated that the sequence of transitions- of commuting to floating to foraging then returning to floating before commuting- remains similar in models incorporating diving, to those which did not. However, in contrast to models which did not incorporate dive data, TDR models had smaller proportions relating to successive foraging. This indicated that states more readily transitioned to and from foraging when a diving parameter was used within the model. Proportional relationships between the state transitions remained broadly similar between colonies.

Table 33 For Guillemots, total number of GPS fixes corresponding in behavioural state between Non-TDR and TDR incorporating models for (a) Colonsay and (b) Fowlsheugh.

(a)

		TDR		
	States	**State 1 (floating)**	**State 2 (commuting)**	**State 3 (foraging/searching)**
Non-TDR	1	2222	228	185
	2	55	1103	37
	3	300	3745	11

(b)

		TDR		
	States	**State 1 (floating)**	**State 2 (commuting)**	**State 3 (foraging/searching)**
Non-TDR	1	14222	855	1014
	2	167	5910	545
	3	2046	26391	845

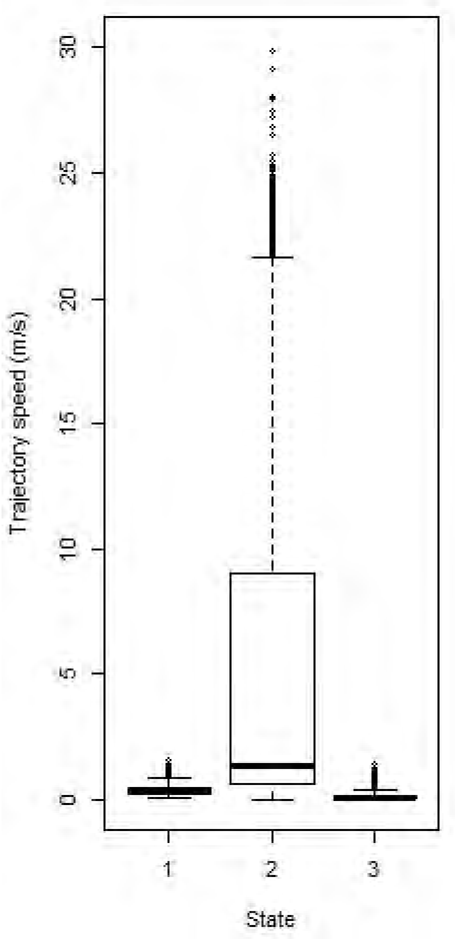
3.5.3 Travel speeds

Table 34 below shows the distributions of speeds from boxplot analysis after assigning states back to the raw data (Figure 22) and birds modelled using the additional TDR dive variable (Figure 23).

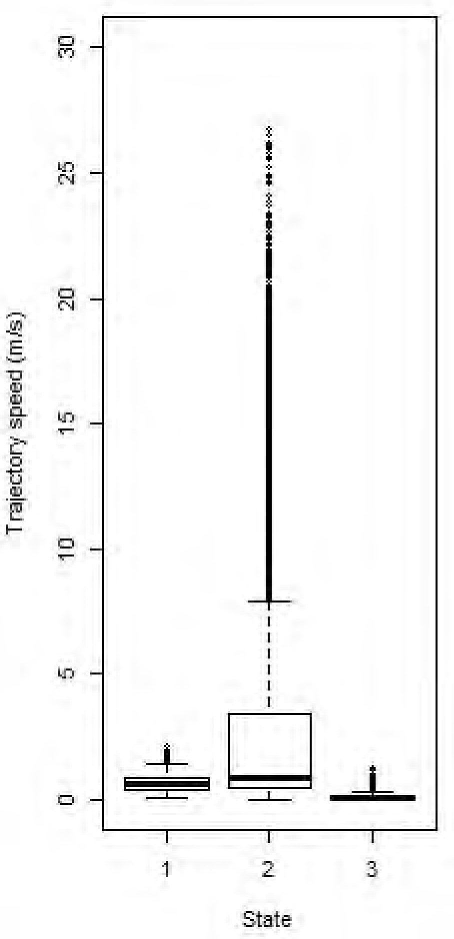
Table 34 For Guillemots, summary of speeds per state (m/s), as obtained through classification of tracking data using HMMs.

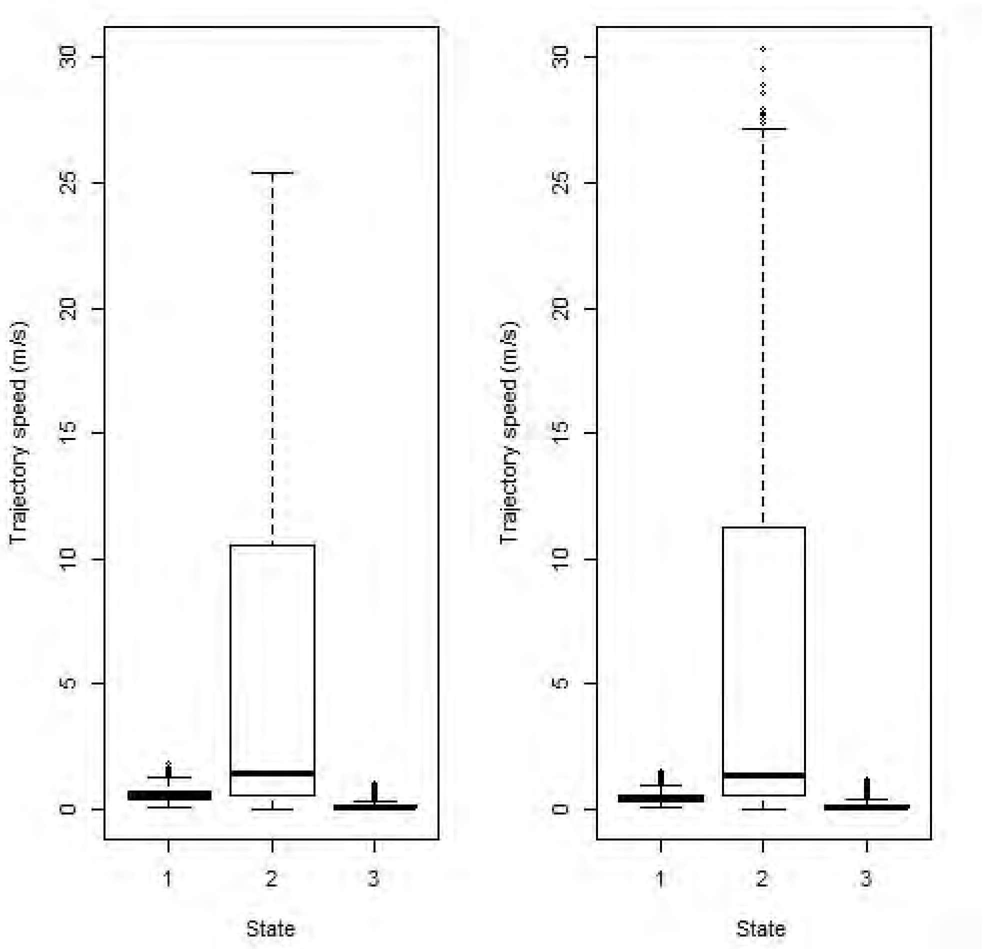
Colony / State	**1 (floating)**	**2 (commuting)**	**3 (forage/search)**
Standard model			
Colonsay	0.36 (0.26 - 0.50)	1.34 (0.59 – 9.02)	0.09 (0.04 – 0.18)
Puffin Island	0.62 (0.42 - 0.83)	0.86 (0.86 – 3.41)	0.07 (0.02 – 0.15)
Fowlsheugh	0.56 (0.40 - 0.74)	1.40 (0.50 – 10.50)	0.08 (0.04 – 0.16)
Isle of May	0.38 (0.27 - 0.54)	1.30 (0.58 – 11.28)	0.09 (0.04 – 0.17)
TDR data included			
Colonsay	0.35 (0.23 - 0.50)	0.11 (0.05 – 0.31)	0.39 (0.23 – 0.61)
Fowlsheugh	0.49 (0.34 - 0.66)	0.12 (0.05 – 0.46)	0.85 (0.55 – 2.46)

(a) Colonsay



(b) Puffin Island





(c) Fowlsheugh

(d) Isle of May

Figure 22 For Guillemots, travel speed (m/s) at (a) Colonsay, (b) Puffin Island, (c) Fowlsheugh, and (d) Isle of May for states 1, 2 and 3 (floating, commuting and foraging/searching), as assessed via assignment to raw data through the Viterbi algorithm of the three state model.

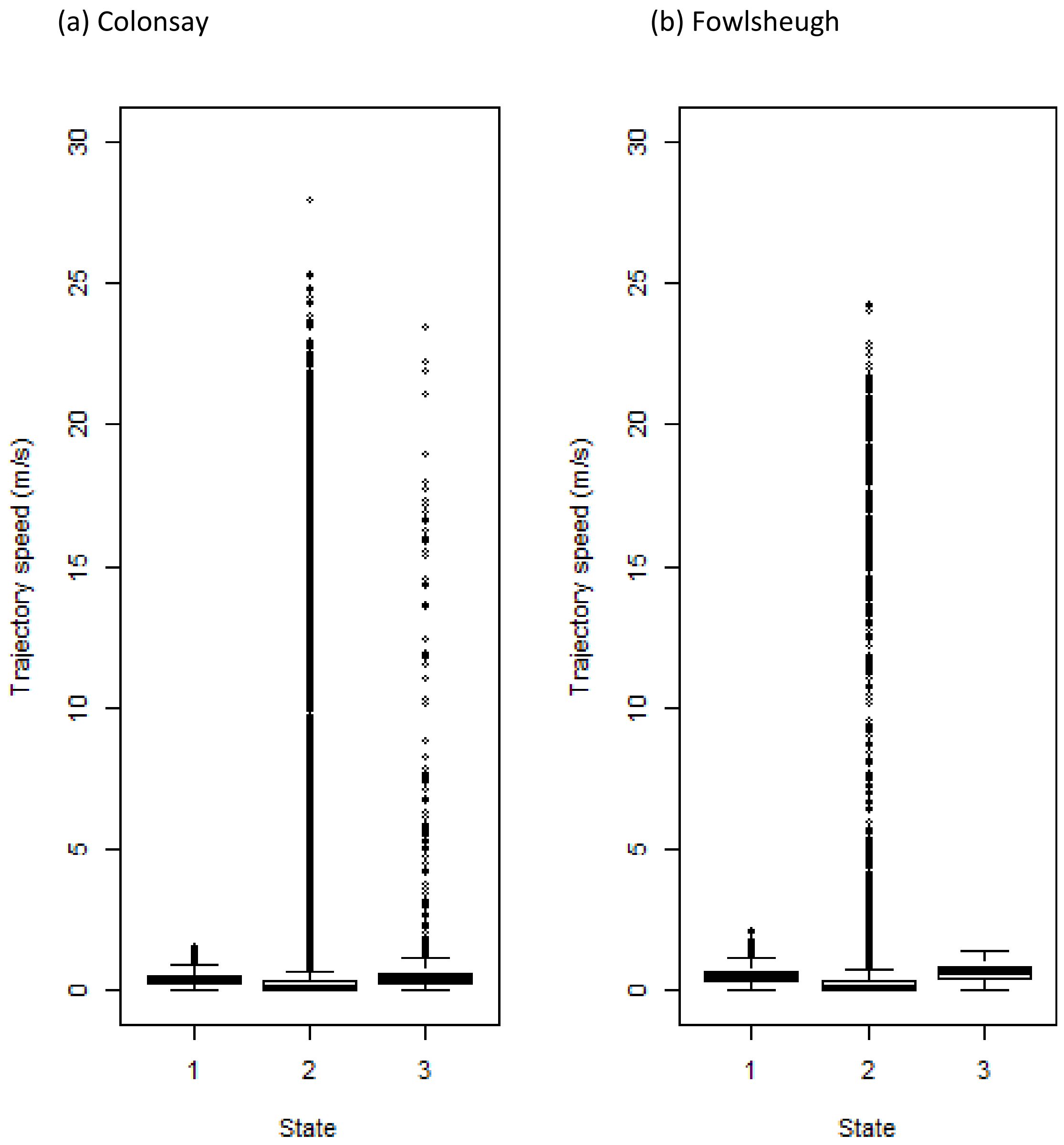


Figure 23 For Guillemot, travel speed (m/s) with TDR data at (a) Colonsay, and (b) Fowlsheugh, for states 1, 2 and 3 (floating, commuting and foraging/searching) as assessed via assignment to raw data through the Viterbi algorithm of the three state model.

3.5.4 Effects of wind speed on step length (speed)

Wind speed was included in the best-fitting model for Puffin Island, the Isle of May, and Colonsay incorporating TDR dive data (Appendices AD and AE). Step lengths specific to behavioural state (State 1 floating, State 2 transit/commute, State 3 foraging) were plotted in relation to wind speed for models without TDR data and models including TDR. From the Puffin Island model, increasing step lengths are observable in relation to wind speed state 1 (β = 0.029), contrasting a marked decrease in relation to State 3 (β = -0.095) (e.g. Figure 3.127). Puffin Island commuting (State 2) step lengths increased only slightly in relation to wind speed(β = 0.002). For all three states derived from the Isle of May model, step length increased with wind speed, State 1 (β = 0.004), State 2 (β = 0.011), and State 3 (β = 0.013).

In relation to the Colonsay model which incorporated TDR dive data, step lengths decreased with increasing wind speed across State 1 (β = -0.014), and State 3 (β = -0.001), and increased in State 2 (β = 0.001).

3.5.5 Transition effects between states in relation to covariates

AIC selection indicated the best-fitting model for Colonsay contained the covariates (hour + colony distance), Puffin Island and the Isle of May contained all the covariates (hour+ Julian date+ colony distance + wind speed), the model corresponding to Fowlsheugh contained (hour + colony distance) (Appendix AF). Model selection indicated the best-fitting model incorporating TDR dive data for Colonsay contained wind speed as the sole covariate, the best-fitting model corresponding to Fowlsheugh included (hour + colony distance) (Appendix AF), thus being more similar than Colonsay to the standard HMM model for Fowsheugh. Differences between standard HMMs and those further models including TDR data are hard to compare reliably given differences in sample size, but may indicate model sensitivity at Colonsay, individual variation in responses to covariates, and findings could be expected to be more similar for Fowlsheugh than Colonsay given the subset of data is based on one year, thus removing any potential annual biases in representivity.

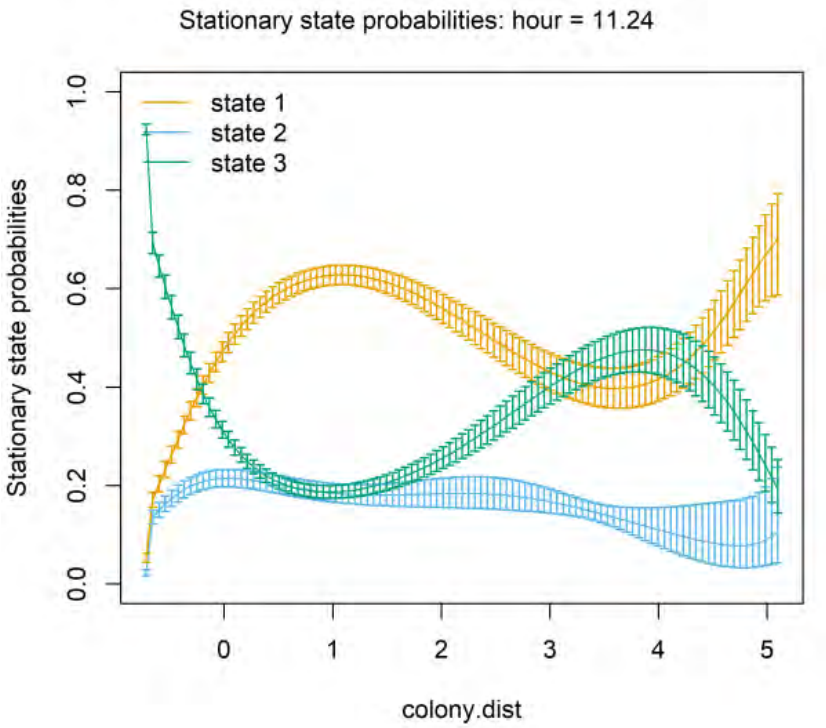
Birds from Colonsay and the Isle of May exhibited clear relationships with colony distance and transitions between states (Figure 24; Appendix AD), potentially related to distinct foraging locations where birds will consistently transition to a foraging state. However, no definitive relationship was present in relation to Puffin Island, and only a weak relationship was shown for birds from Fowlsheugh. Models incorporating TDR dive data, displayed that birds from Fowlsheugh that decreased commuting and increased floating at greater distances from the colony (Appendix AD).

Julian date appears to influence the extent of commuting and floating at Puffin Island over the course of the tracking period with a peak in floating exhibited at Julian day 170 (Figure 25; Appendix AD). While this may be due environmental effects on behaviour related to season, it should be noted that individuals were not tracked continuously across this period (max = 77.93 hours, Puffin Island max = 79.85 hours, Fowlsheugh). These relatively short tracking periods are potentially subject to breeding stage and individualistic foraging behaviour. Compared with Puffin Island, Fowlsheugh and the Isle of May showed no discernible pattern of influence between Julian date and stationary state probabilities.

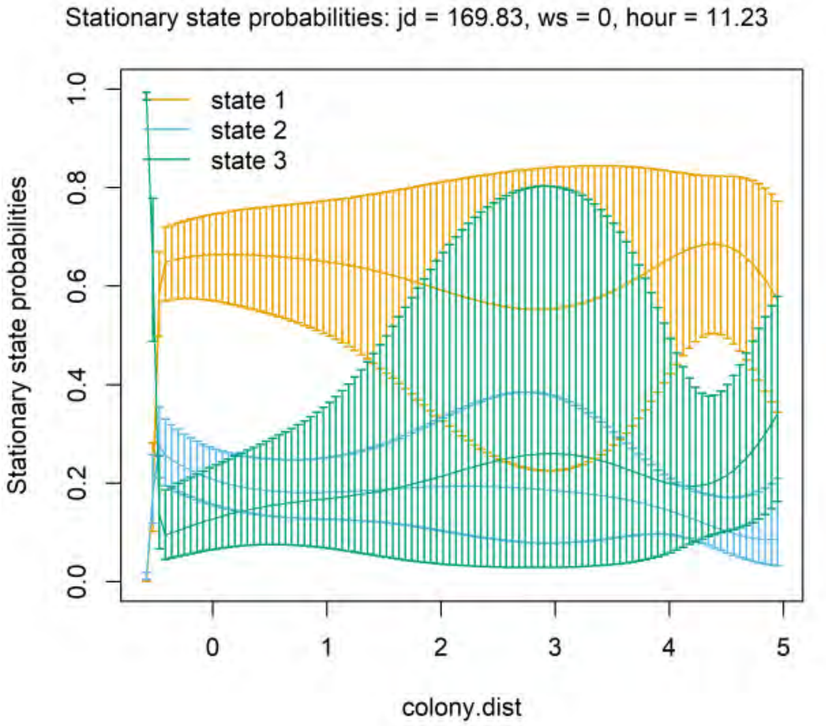
Hour of the day produces less defined relationships between behavioural state transitions in Guillemot (Appendix AD) than exhibited by Razorbills. Though, a degree of reduced floating coinciding with increased commuting and foraging is discernible during daylight hours (09:00-15:00) at all colonies. When TDR dive data is incorporated within the model, the relationship of behavioural state with time of day still exhibits a similar pattern (Appendix AD).

Wind speed remained a covariate in the best-fitting model for Puffin Island and the Isle of May (Appendix AF). However, the transition probabilities and stationary state probabilities are unaffected by wind speed at both colonies (Appendix AD). Foraging was largely unaffected by increasing wind speeds, however, floating increased and commuting decreased at standardised values > 2.

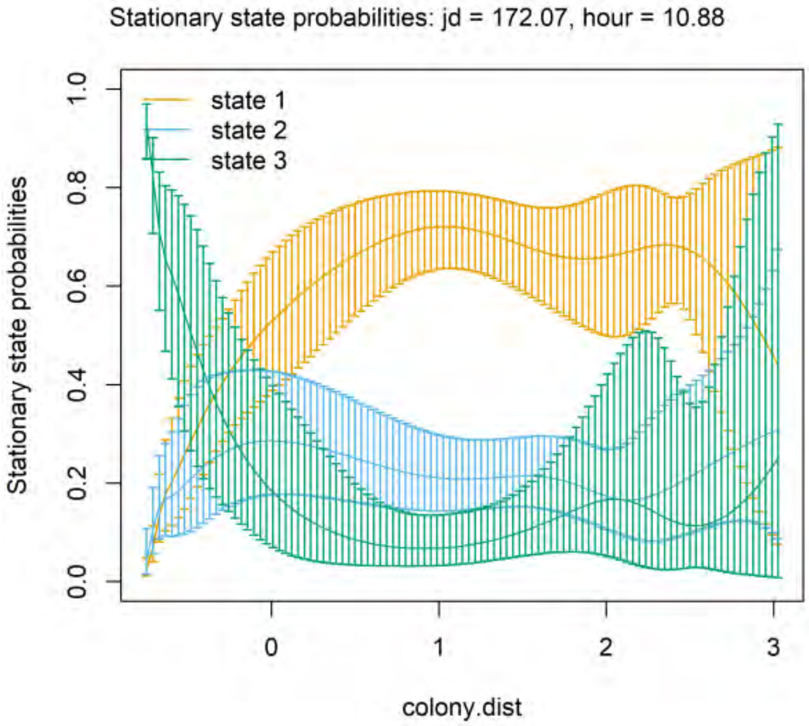
(a) Colonsay



(b) Puffin Island

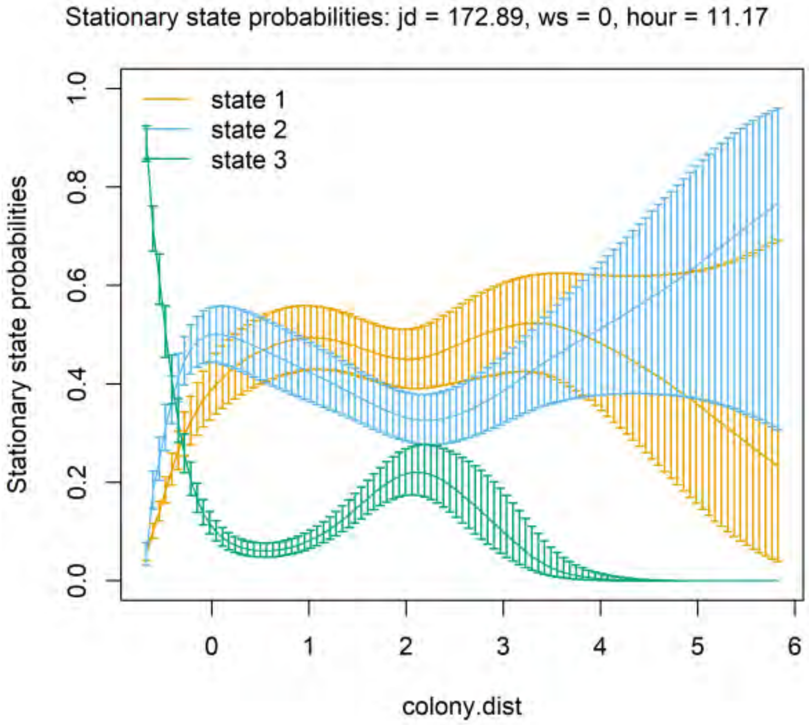


(a) Fowlsheugh



Stationary state probabilities: jd = 172.07, hour = 10.88

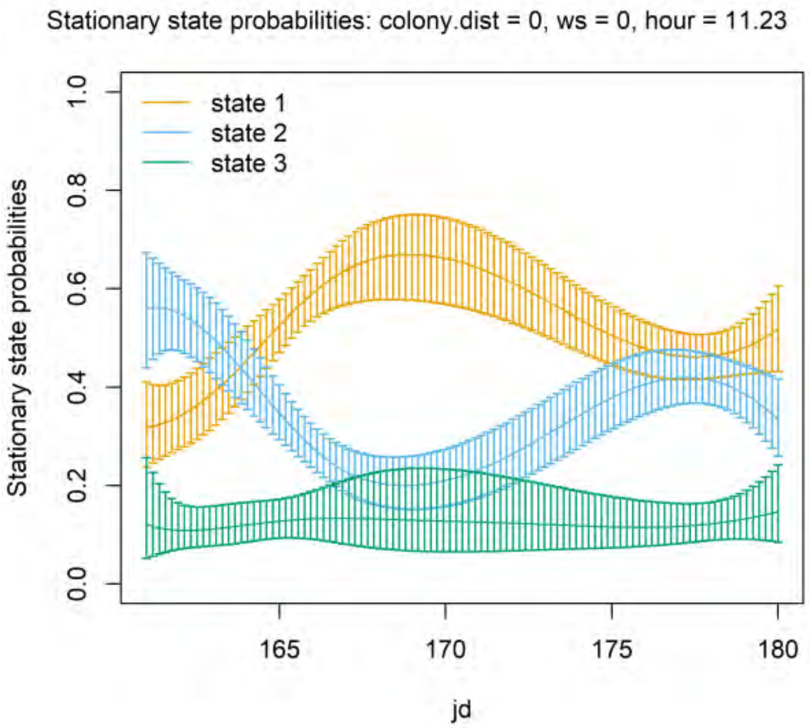
(d) Isle of May



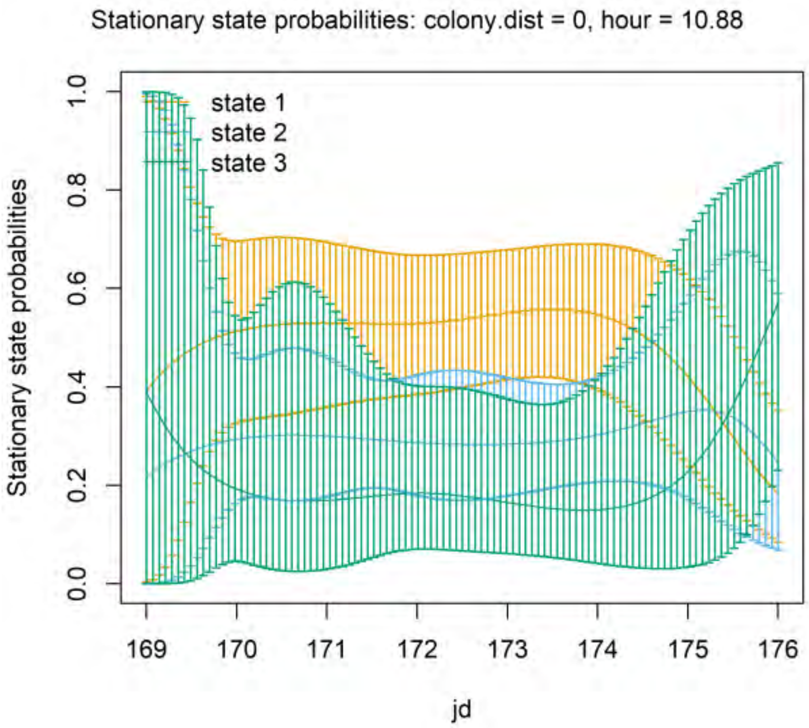
Stationary state probabilities: jd = 172.89, ws = 0, hour = 11.17

Figure 24 For Guillemots, stationary state probabilities for the variable of distance to colony for states 1, 2 and 3 (floating, commuting and foraging/searching), fitted as a standardised variable.

(a) Puffin Island



(b) Fowlsheugh



(c) Isle of May

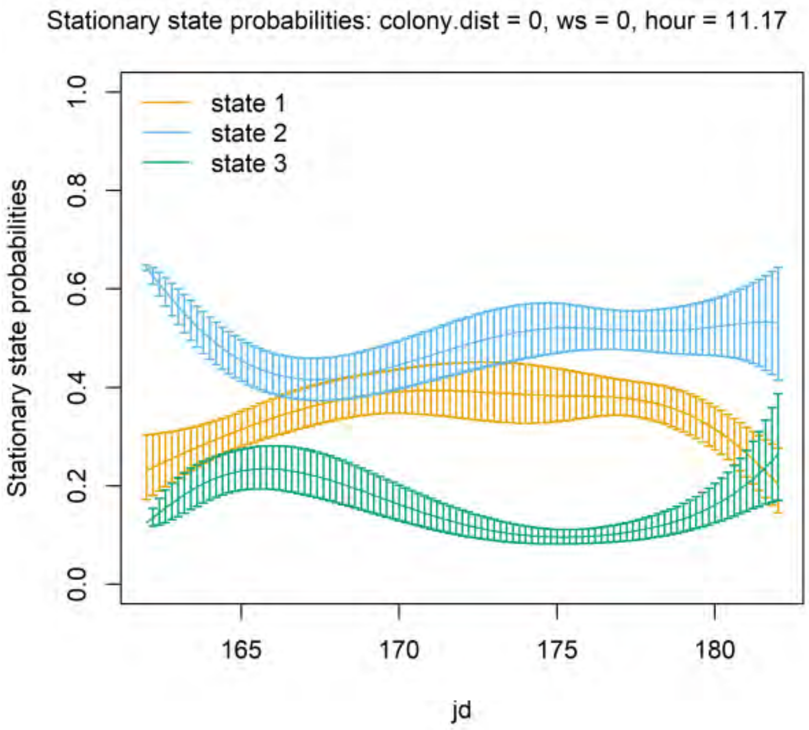


Figure 25 For Guillemot, stationary state probabilities for the variable of Julian date for states 1, 2 and 3 (floating, commuting and foraging/searching).

3.5.6 Time in states

The range of duration of data per bird and the proportion of time spent in different states are shown in Table 35. As birds with fewer data had less time to demonstrate their overall time spent in different states, we used information from birds with more than ten hours of data, to exclude any very small tracking durations that could otherwise skew patterns observed. Across all the colonies State 3 (foraging) held the greatest proportion of time, followed by State 1 (floating). State 2 (transit/commuting) held the lowest proportion of time, potentially related to the energetic demands of remaining within that state.

In comparison to non-TDR models, the mean proportion of a State 3 (foraging) is reduced in the models incorporating diving data (Table 35). State 2 (commuting) increases in proportion compared to non-TDR models, potentially as it is encompassing GPS fixes previously regarded as foraging.

Table 35 For Guillemots, estimated time spent in states for each colony for birds at each colony across years; note occasionally initial movement models could not be fitted due to a lack of data available for some individuals, hence the effective sample size feeding into assessments is provided in brackets

			Duration of tracking			**Proportion time spent per state**		
Colony	**No. birds total (modelled)**	**Year**	**No. birds > 10 hrs tracking data**	**Duration (hrs) mean ± SD per bird**	**Tracking data range (hrs)**	**1 floating mean ± SD**	**2 commuting mean ± SD**	**3 foraging / searching mean ± SD**
Colonsay	77 (77)	2010 to 2014	76	52.99 ± 23.93	6.20 – 133.29	0.30 ± 0.12	0.17 ± 0.07	0.53 ± 0.13
Puffin Island	40 (27)	2012 to 2013, 2015	25	51.36 ± 13.78	5.76 – 77.93	0.39 ± 0.14	0.16 ± 0.05	0.45 ± 0.14
Fowlsheugh	11 (11)	2012	11	36.07 ± 17.15	17.75 – 79.85	0.32 ± 0.09	0.14 ± 0.04	0.53 ± 0.11
Isle of May	51 (51)	2012 – 2014	51	35.86 ± 16.03	14.37 – 118.71	0.24 ± 0.11	0.14 ± 0.06	0.61 ± 0.13
+ TDR data								
Colonsay	29	2011 – 2014	28	51.46 ± 17.61	6.2 – 88.53	0.31 ± 0.12	0.64 ± 0.12	0.05 ± 0.03
Fowlsheugh	7	2012	7	31.35 ± 8.25	21.40 – 42.94	0.32 ± 0.09	0.65 ± 0.09	0.03 ± 0.01

3.5.7 Utilisation distributions

Figures depicting utilization distributions for each colony are shown in Appendix AH. Depending on the colony, there was a smaller amount of data from the very highest wind speeds (greater than 8 m/s) – see also section above comparing use and availability for wind speed distributions.

Where sample sizes of number of fixes and birds used to compute utilisation distributions is low, here taken as less than 100 fixes and less than five birds for the lowest amounts of data (see Appendix AA and methods), then confidence in the overlap result is considered low, and is here indicated as requiring a high degree of caution in interpretation of results. Also highlighted is the proportion of fixes available per split of data, with proportions of less than 5% of the total for the state also flagged up as requiring caution.

Low sample sizes were an issue for guillemots at some colonies. Fowlsheugh in particular did not have enough data for reliable comparisons across many categorisations of the data, in particular for the night-high wind data split, with only one bird providing data, and in once case giving only 13 fixes (for the foraging/searching state) thus being too low for use. For the day-high category at Fowsheugh, likewise only three birds provided data often with less than 100 fixes. For Puffin Island too, for guillemots the nigh-high category for commuting and foraging was based on only one bird with a very small number of fixes. For all colonies except the Isle of May, the number of fixes in the night-high category were less than 5% of the total data available. The Isle of May had higher sample sizes of birds and fixes in each category thus being sufficient for comparison of distribution overlaps.

3.5.8 Overlap indices

Overlaps between states in different wind conditions and times of the day are visualized in Appendix AI, and summarised in Table 36 and Table 37

For Colonsay, Guillemot overlaps between 95% KDEs (representing total area use) were all moderate to very high (BA ≥ 0.4). The highest affinities consistently exhibited across states 1, 2, and 3 were between day high and low wind speed conditions. Day-low vs night high display a degree of moderate affinity (> 0.4) across all states, though affinity is weakest in State 1, further reflected in a low BA index for core area use, as given by the 50% KDE (BA = 0.37). State 3 affinities are consistently high between all conditions. The high affinities between conditions, within all states, is reflective is of the exhibited by Colonsay Razorbills, this is potentially attributed to foraging sympatry.

Puffin Island affinities were consistently high (BA > 0.8) between both day/night low wind conditions across all three states. High vs low wind speeds during the day display affinities > 0.5 between State 2 and 3, with comparatively lower values than

Colonsay. However, similar to Colonsay, the overlap affinity between night and day low wind speeds for State 3 is the highest for Puffin Island. As with Colonsay and Puffin Island, day/night low wind speeds are consistently moderate to high in affinity across all three states for Fowlsheugh. Similar to Colonsay, Fowlsheugh produces very high affinities (BA > 0.8) within State 3 between comparisons of conditions. For the Isle of May, BA indices were generally moderate to very high for 95% KDEs, but for 50% KDE overlaps were highly variable across states spanning all ranges of BA indices (very low to very high). Very high overlaps in both 95% and 50% KDEs were seen for State 3 (foraging/searching) across all conditions.

Some overlaps for guillemots showed BA indices of zero, indicating no overlaps – this was apparent for the 50% KDE for Puffin Island and was evident for all states for the comparison of day-low versus night-high conditions, and was also true for the 95% KDE for the same pair-wise comparison for the state of foraging/searching, with further very low overlaps for the other states. Although we caution sample sizes were low in these tests with fewest data available for night-high categorization of the data, this nonetheless indicates differences in area use for Puffin island in particular. However, these patterns were not ubiquitous across other colones – at the Isle of May, for example, 50% KDE overlaps between day-low and night-high were classed as high or very high, being over 0.6 for the states of commuting and foraging/searching.

Overlaps between 95% KDEs for TDR incorporating models for Colonsay and Fowlsheugh, as with the non-TDR models, produce high affinities between day/night low wind speed conditions for State 1, 2. However, in contrast TDR and non-TDR models, day/night low wind speed affinities in relation to State 3 are greatly reduced (Colonsay, BA = 0.51; Fowlsheugh, BA = 0.16). Both TDR incorporating models for Colonsay and Fowlsheugh produce much lower overlap affinities within State 3 than their TDR incorporating counterparts. This may be due in part dive data providing a stringent parameter to the allocation State 3. The highest affinities (BA > 8) are, therefore, displayed in State 2 of TDR models for Colonsay and Fowlsheugh.

Table 36 For Guillemots, overlap indices for combinations of KDEs assessing similarity in 50% and 95% KDEs for different levels of day and night, and high/low wind and states 1, 2 and 3 (floating, commuting and foraging/searching); for example the top row takes the 95% KDEs for daytime low wind conditions for each State 1, 2 and 3, and computes Bhattacharyya's Affinity index for those three distributions, taking a mean and standard deviation, omitting the diagonal of the matrix that compares each the distribution to itself; note for the comparison of day and night (across wind conditions) for specific states, this results in a simple 2 x 2 matrix and thus, only one comparison value that cannot therefore have a standard deviation; red highlight shows where confidence in overlap assessment is lowest due to low sample sizes (see methods and Appendix AA).

(a) Colonsay

state		day.high	day.low	night.high
1	day.low	**0.54 (0.4)**		
1	night.high	0.41 (0.25)	**0.42 (0.37)**	
1	night.low	0.52 (0.34)	**0.75 (0.53)**	0.4 (0.31)
2	day.low	**0.78 (0.72)**		
2	night.high	0.58 (0.61)	**0.57 (0.62)**	
2	night.low	0.72 (0.66)	**0.81 (0.7)**	0.48 (0.53)
3	day.low	**0.91 (0.97)**		
3	night.high	0.89 (0.93)	**0.88 (0.95)**	
3	night.low	0.87 (0.97)	**0.91 (0.95)**	0.84 (0.94)

(b) Puffin Island

state		day.high	day.low	night.high
1	day.low	**0.33 (0)**		
1	night.high	0.59 (0.16)	**0.3 (0)**	
1	night.low	0.24 (0)	**0.81 (0.6)**	0.25 (0)
2	day.low	**0.55 (0.48)**		
2	night.high	0.18 (0)	**0.15 (0)**	
2	night.low	0.43 (0.37)	**0.84 (0.75)**	0.26 (0.22)
3	day.low	**0.87 (0.9)**		
3	night.high	0.02 (0)	**0 (0)**	
3	night.low	0.75 (0.95)	**0.88 (0.86)**	0.06 (0)

(c) Fowlsheugh

state		day.high	day.low	night.high
1	day.low	**0.25 (0.1)**		
1	night.high	0.14 (0)	**0.25 (0.13)**	
1	night.low	0.24 (0.09)	**0.52 (0.45)**	0.15 (0)
2	day.low	**0.47 (0.33)**		
2	night.high	0.15 (0.02)	**0.36 (0.07)**	
2	night.low	0.31 (0.23)	**0.68 (0.81)**	0.29 (0.08)
3	day.low	**0.82 (0.81)**		
3	night.high	0.85 (0.86)	**0.91 (0.84)**	
3	night.low	0.84 (0.83)	**0.96 (0.96)**	0.94 (0.86)

(d) Isle of May

state		day.high	day.low	night.high
1	day.low	**0.46 (0.32)**		
1	night.high	0.52 (0.36)	**0.42 (0.26)**	
1	night.low	0.32 (0.17)	**0.62 (0.46)**	0.32 (0.17)
2	day.low	**0.71 (0.66)**		
2	night.high	0.6 (0.63)	**0.61 (0.75)**	
2	night.low	0.55 (0.57)	**0.72 (0.73)**	0.57 (0.69)
3	day.low	**0.94 (0.91)**		
3	night.high	0.91 (0.95)	**0.9 (0.86)**	
3	night.low	0.88 (0.87)	**0.92 (0.91)**	0.84 (0.86)

Table 37 For Guillemots, overlap indices for combinations of KDEs, using a subset of birds with GPS+TDR data (from HMMs including the additional channel of dive for refined state assignment); for details of overlap tables see Table 36 above.

(a) Colonsay

state		day.high	day.low	night.high
1	day.low	**0.47 (0.4)**		
1	night.high	0.42 (0.21)	**0.29 (0.27)**	
1	night.low	0.39 (0.24)	**0.61 (0.41)**	0.22 (0.21)
2	day.low	**0.84 (0.92)**		
2	night.high	0.8 (0.85)	**0.82 (0.91)**	
2	night.low	0.8 (0.96)	**0.89 (0.95)**	0.79 (0.88)
3	day.low	**0.36 (0.16)**		
3	night.high	0.38 (0.3)	**0.16 (0.06)**	

3	night.low	0.29 (0.08)	**0.51 (0.21)**	0.05 (0)

(b) Fowlsheugh

state		day.high	day.low	night.high
1	day.low	**0.08 (0)**		
1	night.high	0.1 (0)	**0.23 (0.17)**	
1	night.low	0.02 (0)	**0.51 (0.46)**	0.1 (0)
2	day.low	**0.04 (0)**		
2	night.high	0.08 (0)	**0.1 (0)**	
2	night.low	0 (0)	**0.9 (0.91)**	0.01 (0)
3	day.low	**0.07 (0)**		
3	night.high	0.15 (0)	**0.13 (0)**	
3	night.low	0 (0)	**0.16 (0.06)**	0 (0)

3.6 Species summary

All species for the State 1 behaviour (floating) had a generally very-low or low-moderate overlap of day-low conditions of 50% KDEs with the night-high wind conditions; overlaps with this opposing condition for floating were lowest in all the three pair-wise comparisons that included day-low conditions and across all states. The greatest general overlap across species was seen for the day-low versus day-high comparison for commuting and foraging/searching, with frequent affinities across species being typically high or very high. Greatest general disparity was between day-low and night-high conditions, although note, that in many cases, sample size was an issue for these comparisons.

Between species, the auks (and also Kittiwakes) showed generally lower overlaps than Lesser Black-backed Gulls and Gannets commuting, although patterns were quite varied. Conversely, the auks (using non-TDR data) showed greater overlaps for the foraging/searching state, particularly for the day-low vs night-high comparison, than other species, although again with variation – note Puffin Island was an exception to this pattern.

Overall, although there was much variation, the average BA index (see: 2.5 Overlap analyses) across all pair-wise comparisons in Table 38 (GPS + TDR in Table 39) below, was 0.65 ± 0.20 for the 95% KDE and 0.51 ± 0.28 for the 50% KDE, indicating a highly generalised 'high' degree of spatial overlap in distributions across conditions, states, species and colonies, and a moderate overlap for the 50% KDE.

Table 38 Comparison of Bhattacharrya’s Affinity indices between day-low wind scenarios, representative of suitable survey conditions, with other conditions (day-high, night-low and night-high), split by behavioural state, arranged by species and colony, coloured by BA index values very low – very high five-tier categorisation (see section 2.5); cells highlighted with asterisk indicates lowest confidence in overlaps due to lowest sample sizes (see methods and Appendix AA). LBBG = Lesser Black-baked Gull.

			95% KDE			**50% KDE**		
State	**Species**	**Colony**	**day-high**	**night-high**	**night-low**	**day-high**	**night-high**	**night-low**
1	Gannet	Alderney	0.61	0.55	0.75	0.34	0.21	0.58
		Bass Rock	0.52	0.40	0.69	0.19	0.15	0.49
	LBBG	Orford Ness	**0.47***	**0.40***	0.60	**0.45***	**0.14***	0.37
		Skokholm	0.77	0.56	0.72	0.46	0.28	0.39
		Walney	**0.37***	0.37	0.59	**0.06***	0.08	0.29
	Kittiwake	Bempton	0.47	0.34	0.63	0.28	0.15	0.45
		Colonsay	0.61	0.44	0.66	0.67	0.17	0.58
		Isle of May	**0.46***	**0.34***	0.52	**0.21***	**0.28***	0.29
		Orkney	0.74	0.47	0.61	0.77	0.07	0.45
	Razorbill	Colonsay	0.77	0.69	0.77	0.55	0.58	0.49
		Isle of May	0.53	**0.28***	0.60	0.58	**0.04***	0.40
		Puffin Island	0.48	0.40	0.78	0.23	0.15	0.61

	Guillemot	Colonsay	0.54	0.42	0.75		0.40	0.37	0.53
		Fowlsheugh	**0.25***	**0.25***	0.52		**0.10***	**0.13***	0.45
		Isle of May	0.46	0.42	0.62		0.32	0.26	0.46
		Puffin Island	0.33	0.30	0.81		0.00	0.00	0.60
2	Gannet	Alderney	0.90	0.58	0.74		0.73	0.26	0.39
		Bass Rock	0.88	0.65	0.87		0.72	0.38	0.80
	LBBG	Orford Ness	0.90	0.63	0.92		0.84	0.33	0.90
		Skokholm	0.90	0.81	0.92		0.85	0.70	0.84
		Walney	0.84	0.68	0.88		0.60	0.42	0.60
	Kittiwake	Bempton	0.80	0.51	0.82		0.58	0.32	0.79
		Colonsay	0.73	0.60	0.83		0.74	0.63	0.72
		Isle of May	0.62	**0.43***	0.72		0.56	**0.29***	0.65
		Orkney	0.69	0.56	0.72		0.70	0.46	0.68
	Razorbill	Colonsay	0.91	0.67	0.80		0.91	0.50	0.54
		Isle of May	0.79	**0.31***	0.70		0.97	**0.00***	0.69
		Puffin Island	0.74	0.25	0.57		0.48	0.00	0.15
	Guillemot	Colonsay	0.78	0.57	0.81		0.72	0.62	0.70
		Fowlsheugh	**0.47***	**0.36***	0.68		**0.33***	**0.07***	0.81

		Isle of May	0.71	0.61	0.72		0.66	0.75	0.73
		Puffin Island	0.55	**0.15***	0.84		0.48	**0.00***	0.75
3	Gannet	Alderney	0.75	0.50	0.78		0.60	0.14	0.68
		Bass Rock	0.68	0.46	0.74		0.33	0.15	0.53
	LBBG	Orford Ness	0.71	0.50	0.77		0.59	0.22	0.43
		Skokholm	0.85	0.57	0.80		0.56	0.24	0.35
		Walney	0.72	0.55	0.82		0.50	0.12	0.54
	Kittiwake	Bempton	0.57	0.32	0.75		0.37	0.03	0.68
		Colonsay	0.72	0.54	0.81		0.72	0.40	0.76
		Isle of May	0.59	**0.48***	0.71		0.48	**0.39***	0.58
		Orkney	0.87	0.82	0.86		0.90	0.93	0.97
	Razorbill	Colonsay	0.96	0.86	0.87		0.96	0.85	0.82
		Isle of May	0.99	**0.79***	0.92		0.98	**0.79***	0.92
		Puffin Island	0.78	**0.06***	0.63		0.87	**0.00***	0.52
	Guillemot	Colonsay	0.91	0.88	0.91		0.97	0.95	0.95
		Fowlsheugh	**0.82***	**0.91***	**0.96***		**0.81***	**0.84***	**0.96***
		Isle of May	0.94	0.90	0.92		0.91	0.86	0.91
		Puffin Island	0.87	0.00	0.88		0.90	0.00	0.86

Table 39 Additional overlap summary of the auks using GPS+TDR HMM classifications, to supplement Table 38; comparison of Bhattacharrya's Affinity indeces between day-low wind scenarios, representative of suitable survey conditions, with other conditions (day-high, night-low and night-high), split by behavioural state, arranged by species and colony, coloured by BA index values very low – very high five-tier categorisation (see section 2.5 in methods)

			95% KDE			**50% KDE**		
State	**Species**	**Colony**	**day-high**	**night-high**	**night-low**	**day-high**	**night-high**	**night-low**
1	Razorbill	Colonsay						
	Guillemot	Colonsay	0.47	0.29	0.61	0.4	0.27	0.41
		Fowlsheugh	0.08	0.23	0.51	0	0.17	0.46
2	Razorbill	Colonsay						
	Guillemot	Colonsay	0.84	0.82	0.89	0.92	0.91	0.95
		Fowlsheugh	0.04	0.1	0.9	0	0	0.91
3	Razorbill	Colonsay						
	Guillemot	Colonsay	0.36	**0.16***	0.51	0.16	**0.06***	0.21
		Fowlsheugh	**0.07***	**0.13***	**0.16***	**0***	**0***	**0***

4 Discussion

This study aimed to investigate how weather and diurnal patterns influenced the behaviour and distribution of seabirds at sea during the breeding season. A particular focus for these analyses was the extent to which data collected during boat and/or digital aerial surveys may be biased as a consequence of the constraints imposed in relation to when such surveys can be carried out (e.g. during the day and sea-state 4 or lower). By using seabird tracking data, we were able to consider how the behaviour and distribution of five key species (Kittiwake, Lesser Black-backed Gull, Gannet, Guillemot and Razorbill) varied over the course of the day and in relation to wind speed and direction. By considering this in relation to the constraints imposed by boat and digital aerial surveys, we are able to better understand the implications of relying on survey data in the assessment of the impacts from offshore wind farms, in particular, the implications for the assessment of collision, displacement and barrier effects.

As an initial finding, the use of high wind speeds (based on cut offs of > 8m/s and > 10m/s) appeared to be generally lower than the wind speeds “available” to individual birds when at sea. This indicates that birds away from the colony were actively avoiding areas with high wind speeds. This was more pronounced for Lesser Black-backed Gull and to a lesser extent, Kittiwake. Lesser Black-backed Gull, however, has a relative bias towards offshore use during the chick-rearing period in June and July when wind speeds tend to be lower compared to earlier in the breeding season. There was a notable exception to this pattern, with gannets breeding on Alderney appearing to actively select areas with higher winds that are associated with lower flight costs in this species (Amélineau *et al*. 2014). These general findings, however, should still be considered indicative; a full habitat resource-selection analysis would be needed to verify these patterns statistically.

4.1 Model parameters

Across the five study species, behaviour was classified based on a combination of step length and turning angle. Our analyses identified three core behaviours for each species – resting on the sea surface, commuting and foraging. For Gannet, Lesser Black-backed Gull and Kittiwake the floating state was characterised by short step lengths and relatively acute turning angles implying birds were moving over relatively short distances in a consistent direction. Commuting behaviour was also characterised by birds moving in a consistent direction, but over longer distances. Foraging behaviour was characterised by wider turning angles and shorter step lengths than those observed during commuting. Patterns in behaviour such as this are consistent with area-restricted search whereby birds travel directly towards areas with predictable resources before using slower, less directed flight when looking for foraging opportunities within those areas, with such flights potentially being intermittent in nature punctuated by attempts to capture and handle prey (Hamer *et al*. 2009; Votier *et al*. 2013; Sommerfeld *et al*. 2016). For Lesser Black-backed Gull and Kittiwake we also identified a fourth behavioural classification which was characterised by short step lengths and wide turning angles and we believe is likely to reflect birds perching on objects at sea, for example buoys and other structures, confirmed for example with Lesser Black-backed Gulls in the Irish Sea.

In contrast to the gulls and Gannet, for Guillemot and Razorbill foraging behaviour was associated with shorter step lengths and more acute turning angles. This is likely to reflect birds foraging by diving from the sea surface rather than searching for prey from the air. For a subset of data we were able to validate predicted foraging areas using TDR data to confirm where diving behaviour took place.

4.2 Impact of covariates on behavioural state

All species exhibited a strong effect of the time of day on the likelihood of different states occurring, with floating on the sea being much more frequent at night and less common during the day (Table 40). Some species such as Lesser Black-backed Gulls have previously been found to differ diurnally in other key behavioural parameters important to collision risk, including flight heights outside of wind farms (Ross-Smith *et al*. 2016), and time within wind farms (Thaxter *et al*. 2018). However, to our knowledge, this is the first study to fully test how behaviours such as commuting, floating on the sea and foraging varies across a wider suite of species.

Wind speed had a marked effect on the probability of individuals of species transitioning between states or remaining within their existing state (Table 40). Wind speed was found to have variable influence on state transitioning in Razorbills and Guillemots, although commuting step lengths maintained a positive relationship with increasing wind speeds (assuming they had tailwinds) as birds were able to fly faster. Across species, a key finding was that Gannets and Lesser Black-backed gulls were more likely to transition from floating on the sea to foraging/searching for prey in greater wind speeds and with headwinds, with strongest effects in strongest headwinds – this suggests birds may be able to take advantage of strong wind conditions, for example for Gannets use of high wind speeds resulted in lower flight costs (Amélineau *et al*. 2014), and birds may adjust foraging time in relation to wind speed, maximising foraging time and reducing transition to resting. Spatially, the interactions with wind speed and direction may translate into a limitation of foraging range for some species particularly those that do not use dynamic soaring as a flight method, as has been suggested (e.g. Allerstam *et al* 2019). Further, the energetic costs of taking off from the water (e.g. following plunge diving for prey) are very high (Nudds and Bryant 2000) but, are reduced during stronger wind conditions when birds take off into the wind (Furness and Bryant 1996; Mullers *et al*. 2009).

Table 40 Summary of main HMM outputs from each species and colony, with ‘*’ denoting a significant effect of covariates on transition probabilities between behavioural states.

		Core analysis				**Further wind models**		
Species	**Colony**	**cosinor(hour)**	**s(wind speed)**	**s(colony distance)**	**s(Julian date)**	**Wind speed**	**angle _osc**	**wind speed* angle_ osc**
Gannet	Alderney	*	*	*	*	*	*	*
	Bass Rock 2010	*	*	*	*	*	*	*
	Bass Rock 2011	*	*	*	*	*	*	*
	Bass Rock 2012	*		*	*	*	*	*
Lesser Black-backed Gull	Walney	*	*	*	*	*	*	*
	Skokholm	*	*	*	*	*	*	*
	Orford Ness	*	*	*	*	*	*	*
Kittiwake	Isle of May	*	*	*	*	*	*	*
	Colonsay	*	*	*	*	*	*	*
	Bempton Cliffs	*	*	*	*	*	*	*
	Orkney	*		*	*	*	*	*
Razorbill	Colonsay	*	*	*	*			
	Puffin Island	*	*	*	*			
	Isle of May	*	*	*	*			
+TDR	Colonsay	*						
Guillemot	Colonsay	*		*				
	Puffin Island	*	*	*	*			
	Fowlsheugh	*		*	*			

+TDR	Isle of May	*	*	*	*			
	Colonsay		*					
	Fowlsheugh	*		*				

4.3 Species behavioural characteristics

For each species, the proportions of time spent floating, commuting and foraging were broadly consistent across different colonies (Table 41). However, there were clear differences in the proportion of time spent in each activity between species. The analyses suggest that Gannets spend a greater proportion of their time floating on the sea surface than either Lesser Black-backed Gull or Kittiwake. However, the four state model for the two gulls split the foraging behaviour from the three state model into a foraging and perching behaviour, indicating that the three species may have spent similar proportions of their time resting. In contrast, the auks spent a far lower proportion of their time commuting. This is likely linked to a higher wing loading of these species associated with a higher cost of flight, in turn a product of adaptation of wing-propelled foraging strategies below water (Thaxter *et al*. 2010).

Table 41 Proportion of time spent in different behavioural states based on 3-state Hidden Markov Models.

Species	Colony	Floating	Commuting	Foraging
Gannet	Alderney	0.36 ± 0.09	0.27 ± 0.07	0.37 ± 0.08
	Bass Rock	0.32 ± 0.08	0.35 ± 0.13	0.35 ± 0.10
Lesser Black-backed Gull	Walney	0.20 ± 0.16	0.41 ± 0.22	0.39 ± 0.17
	Skokholm	0.27 ± 0.10	0.35 ± 0.13	0.38 ± 0.06
	Orford Ness	0.19 ± 0.15	0.39 ± 0.18	0.42 ± 0.08
Kittiwake	Isle of May	0.22 ± 0.09	0.25 ± 0.07	0.53 ± 0.10
	Colonsay	0.20 ± 0.10	0.26 ± 0.12	0.55 ± 0.12
	Bempton	0.22 ± 0.10	0.30 ± 0.10	0.47 ± 0.11
	Orkney	0.17 ± 0.09	0.28 ± 0.17	0.55 ± 0.18
Razorbill	Colonsay	0.25 ± 0.12	0.13 ± 0.06	0.63 ± 0.12
	Puffin Island	0.44 ± 0.12	0.14 ± 0.05	0.42 ± 0.13

	Isle of May	0.16 ± 0.08	0.21 ± 0.07	0.63 ± 0.09
Guillemot	Colonsay	0.30 ± 0.12	0.17 ± 0.07	0.53 ± 0.13
	Puffin Island	0.39 ± 0.14	0.16 ± 0.05	0.45 ± 0.14
	Fowlsheugh	0.32 ± 0.09	0.14 ± 0.04	0.53 ± 0.11
	Isle of May	0.24 ± 0.11	0.14 ± 0.06	0.61 ± 0.13

4.4 Species distributions

Our analyses highlighted clear spatial patterns in the areas used for resting, commuting and foraging across all species. Generally, the differences in the areas used for each activity were greatest between day and night, rather than in relation to different wind conditions (Table 38). However, the robustness of these conclusions may be limited by the lack of data from stronger wind conditions. Such limited data may mean that KDEs are patchier and, whilst similar areas are being used, the extent of any overlap may be reduced. Where there were differences in area use, these were generally most pronounced for resting behaviour. For example, there were suggestions from the analyses the Kittiwakes may be less likely to rest in areas further offshore during periods with high wind conditions.

4.5 Flight speed

At present, estimates of seabird flight speeds typically used in assessment for collision risk modelling have been derived using Ornithodolites or radar systems (Pennycuik 1987, 1997; Alerstam *et al.* 2007). However, it is unclear how representative these values are and there are concerns that some estimates are based on extremely limited data. For example, the estimate flight speed for Kittiwake from Alerstam *et al.* (2007) is based on just two tracks over a period of 660 seconds. Our analyses highlighted that for gulls and Gannet, wind speed and direction could influence bird flight speed (ground speed), thus matching previous findings in Gannet and Kittiwake (Lane *et al.* 2019, Collins *et al.* 2020). This emphasizes the importance of collecting measurements of flight speed from a range of conditions, rather than relying on data collected over a short time period which may not be representative of the conditions to which birds are exposed.

Our measures of flight speed were calculated by dividing the step length (the distance between two adjacent GPS fixes) and the intervening time elapsed between these points. Birds in flight may not travel straight between two such consecutive points. For example many seabirds use dynamic soaring, i.e. increasing wind speed over height, and slope soaring over waves, i.e. updrafts of wind over wave crests (Pennycuick 1982) to deploy an energy saving non-flapping flight and results in a characteristic small scale flight manoeuvres (Sachs *et al*. 2013). Hence any new flight speeds estimates presented here are likely to be a minimum value and further dependent on the time interval used (see Safi *et al*. 2013). The HMMs were used to differentiate what is classified here as commuting and foraging flight based on step lengths and the turning angles. The latter type of behaviour however, may also include other types of behaviour which lasted shorter than the sampling period covered. For diving species such as auks and to a lesser extent the Gannet, the particularly slow speeds recorded during apparent foraging flight (Table 42) will include time on the water between dives. The same is likely to be true for surface feeders such as Kittiwakes, and other gull species in open water, which are likely to spend time on the water between foraging bouts. Therefore, although we would urge caution in the interpretation and application of the flight speeds associated with foraging, this study highlights the need to distinguish between different types of flight behaviour and how this relates to flight speed. For Gannets the commuting flight speeds, estimated from Alderney and the Bass Rock, were broadly consistent with previous published estimates (Table 42 ; Pennycuik 1987). Whilst commuting flight speeds for Kittiwakes and Lesser Black-backed Gulls were slower than those used as part of current guidance (e.g. Alerstam *et al*. 2007), they were broadly consistent with the speeds estimated using laser rangefinders as part of the ORJIP Bird Collision Avoidance study (Skov *et al.* 2018). However, for both Razorbill and Guillemot, commuting flight speeds were considerably slower than those that have been estimated previously and, although these species are typically not considered vulnerable to collision (e.g. Furness *et al*. 2013), these estimates must nonetheless be treated with caution. However, for Gannet, Kittiwake and Lesser Black-backed Gull, commuting flight speeds were broadly consistent between colonies, suggesting that these values may be more widely applicable, for example, in relation to collision risk modelling.

Table 42 Comparison of recommended flight speeds that are widely used within the Band (2012) model, and those obtained under different states in this study, noting that speeds presented from this study are ground speeds under all wind conditions. LBBG = Lesser Black-backed Gull.

Species	Recommended Flight Speed (m/s)	Commuting Flight Speed (m/s)	Foraging Flight Speed (m/s)*
Gannet			
Alderney	14.9^1	13.6 (11.2 – 16.0)	1.25 (0.3 – 4.1)
Bass Rock		14.4 (12.16 – 16.63)	1.58 (0.3 – 5.2)
Kittiwake			
Isle of May	13.1^2	9.26 (7.82 – 11.14)	3.21 (1.86 – 5.05)
Colonsay		9.45 (7.76 – 11.37)	1.56 (0.78 – 3.36)
Orkney		9.52 (7.59 – 11.78)	1.50 (0.63 - 3.13)
Bempton Cliffs		10.61 (9.20 – 12.27)	5.37 (3.57 – 7.21)
LBBG			
Walney	13.1^2	9.17 (7.42 – 11.26)	3.5 (1.99 – 5.4)
Skokholm		9.43 (7.72 – 11.67)	1.49 (0.44 – 3.70)
Orford Ness		9.65 (7.94 – 11.84)	2.41 (1.03 – 4.48)
Guillemot			
Colonsay	19.1^3	1.34 (0.59 – 9.02)	0.09 (0.04 – 0.18)
Puffin Island		0.86 (0.40 – 3.41)	0.07 (0.02 – 0.15)
Fowlsheugh		1.40 (0.50 – 10.50)	0.08 (0.04 – 0.16)
Isle of May		1.30 (0.58 – 11.28)	0.09 (0.04 – 0.17)
Razorbill			
Colonsay	16.0^3	3.62 (1.34 – 14.44)	0.13 (0.06 – 0.25)
Puffin Island		4.75 (1.10 – 14.23)	0.15 (0.06 – 0.28)
Isle of May		1.50 (0.65 – 12.03)	0.07 (0.04 – 0.15)

[1] Pennycuik 1987 [2] Alerstam *et al*. 2007 [3] Pennycuik 1997.

*see text for caveats regarding this data.

4.6 Implications for the assessment of collision risk

Flight speed is a key parameter in the Band Collision Risk Model (Band 2012). Firstly, it is used to estimate the total number of birds which may pass through a wind farm over any given time period, otherwise known as the flux rate. This is done calculating the length of time an individual bird may take to pass through the wind farm and scaling this up based on the density of birds within the wind farm at any given time. Secondly, it is used to estimate the probability of a bird passing through the rotor swept area of a turbine being hit by a turbine blade, based on the probability of the blade and the birds occupying the same space at the same time (Masden & Cook 2016). Consequently, estimates of collision risk are highly sensitive to assumptions about bird flight speed (Masden 2015).

As a consequence of the assumptions made by the Band Collision Risk Model (Band 2012), higher flight speeds results in a higher estimated collision rate. Hence using the previously published estimates of flight speed is likely to result in a higher collision rate than those derived as part of this study. This study also confirms the importance of accounting for different types of behaviour when assessing collision risk. Our analyses suggest that birds are likely to spend roughly equal proportions of time engaged in foraging and commuting flight which are likely to have differing flight speeds. Whilst the foraging flight speeds we estimated above should be treated with caution, we believe they highlight the importance of collecting estimates of flight speed that can be linked to behaviour. This can be achieved using existing GPS tags, which are capable of providing an instantaneous estimate of bird flight speed using the Doppler-shift principle for radio signals received from multiple satellites (Safi *et al*. 2013). Given the influence of wind speed and direction on bird flight speed accounting for these when estimating collision risk may have a significant effect on predicted collision rates. In particular, consideration should be given to incorporating different flight speeds in relation to upwind and downwind movements when estimating collision risk. For gulls and Gannet, there was a greater tendency for birds to be classified as commuting or foraging, as opposed to resting, during periods of stronger winds. This raises the possibility that by relying on survey data we may be underestimating the proportion of birds in flight during strong wind conditions. However, as data suggest that birds may avoid leaving their colonies during strong wind conditions, it is unclear what overall impact this may have on the total number of birds estimated to be at risk of collision.

There are also different levels of risk associated with different types of behaviour e.g. birds when foraging may be at greater risk if their attention is focussed on the sea surface, as opposed to when commuting flight, when they are more likely to be looking ahead (e.g. Martin 2011). Further work using cameras on birds (e.g. Votier at al. 2013 study on Gannet) would be extremely informative in testing this assertion. It is important to note however, that whilst we strive to understand how birds behave within wind farms and the likely risk of collision, the modelling framework does not currently allow us to easily include variation in flight speeds.

4.7 Implications for the assessment of displacement and barrier effects

Displacement and barrier effects are both likely to be manifested in a reduction in the density of birds within a wind farm. Whilst barrier effects are likely to result in an increased energetic cost as birds have to fly round a wind farm (Masden *et al.* 2010), displacement may reflect the loss of key foraging areas (Furness *et al*. 2013; Dierschke *et al*. 2016). The consequences of these two effects may be very different depending on the level of additional flight costs imposed by barrier effects and the relative importance of any lost foraging areas (Masden *et al*. 2010; Dierschke *et al*. 2016). Despite this, distinguishing between areas where birds may be vulnerable to barrier effects and those where they may be vulnerable to displacement using survey data can be extremely challenging, particularly in relation to species like Gannet which dive whilst in flight.

Our analysis highlights how tagging data can be used to link spatial information describing the distribution of birds at sea to their behaviour and differentiate between areas used for foraging, commuting and resting behaviours. When used in a pre-construction context, such information would enable us to assess both the likelihood and magnitude of any displacement and barrier effects more formally. For example, by comparing a wind farm footprint to areas used for commuting, it may be possible to infer the additional energetic cost associated with avoiding a wind farm. However, this would need to be considered in the context of prevailing wind conditions which may exacerbate or, ameliorate any additional costs. Similarly, in relation to displacement, it may be possible to assess the relative importance of any wind farm footprint to birds foraging from a given colony by adapting the approach in Wakefield *et al*. (2017) to estimate the total number of birds foraging within a particular area.

4.8 Transferability of results across colonies

Through our analyses we were able to identify the spatial and temporal distribution of seabird behaviours at different colonies. However, such data may not be available in relation to all colonies at which species may be impacted by offshore wind farms.

Consequently, it is important to consider how transferable our conclusions may to other locations.

Our analyses suggested that the proportion of time that birds are engaged in different behaviours may be relatively consistent between colonies. However, there were clear differences in the locations and extents of areas used for different behaviours. Previous studies have shown that foraging areas may differ between colonies in relatively close proximity (Wakefield *et al*. 2013; Wischnewski *et al*. 2017). These effects may be influenced by intra-specific competition between birds from different colonies. However, colony-specific ecological and oceanographic conditions are also likely to play a key role in determining foraging areas and space use amongst seabirds. The geographic situation of a colony (e.g. mainland vs island, sheltered vs open coast) may play a key role linked to favourable hydrodynamic conditions and predictable resources such as upwelling zones, and shelf-sea fronts (Waggitt *et al*. 2016; Christensen-Dalsgaard *et al*. 2018; Grecian *et al*. 2012). Within colonies, there may be further partitioning in at sea space-use which may influence interactions with wind farms. While within-colony intra-specific variation is not investigated here, strong interspecific variation in movement direction can be seen at Puffin Island between Razorbills, flying northwest, and Guillemots, flying northeast (Appendix AD).

4.9 Analytical limitations

Although robust in the testing of the main aims of this project, the study has a number of limitations that need to be considered when drawing conclusions. First, as a result of the use-availability bias for some species in this study, there were limited sample sizes when making comparisons between low and high wind scenarios. Utilisation distributions are notably influenced by sample size in area (Soanes *et al*. 2013, Thaxter *et al*. 2017), which, therefore, hampers comparisons among KDEs. As such, for these reasons, the sizes of areas used under different scenarios are not presented and overlap indices should also be treated with some caution. Second, following from this, we also used an initial movement model to regularise the GPS data to precise equivalent specific time steps and HMMs can be used to explore the error in such interpolations and assumptions of movement between fixes through multiple permutations of the modelled tracks. However, given the volume of data across species and colonies analysed, such exploration of model error could not be carried out. Third, the amount of data itself was a limitation in this study – analyses were carried out at the colony level across years, being identified as a sensible compromise between model run-time and interest in the level of variation for the hypotheses tested. Note, however, for Bass Rock, the amount of data was large and as single model could not be reliably produced, instead individual year models were produced, which in turn provided opportunity to examine the variation across years for this case. Similarly, the amount of data collected for Lesser Black-backed Gulls spanned multiple months and years for individual birds, however, data for Lesser Black-backed Gulls were subset for investigation of offshore movements separate from terrestrial movements to meet the aims of the project. Fourth, within models, further aspects could be considered that were not investigated for the sake of simplicity – interactions for instance between time of day and wind speed were not tested, nor were the effects over distance to colony fitted in interactions to test if birds remained or transitioned between states further from the colony. Lastly, the study was focused on tracking data of known breeding individuals, yet at-sea surveys pick up other demographic components, such as non-breeders and immatures. The tracking datasets likely also contained failed breeders, particularly for Lesser Black-backed Gulls where nest monitoring prevents certain assessment of breeding status later in the season. Further, the stage of breeding was not tested in this study but could reveal further patterns. As such, the representativeness of the tracking dataset alongside birds that may be recorded in offshore surveys is here highlighted.

4.10 Recommendations for future work

Data collection

- The use of TDR devices in combination with positional telemetry technology such as GPS for diving species are recommended where possible. This would indicate key areas used for foraging.
- Further use of accelerometry incorporated with positional information collected by tags, or direct visual observations in wind farms would help further in refining behavioural states recorded at sea (Bouten *et al*. 2013).
- Additional weather covariates could also be explored to test correlations or biases in movement under different weather conditions, such as rainfall and visibility.
- Relating contemporaneous oceanographic variables e.g. state of tides or oceanographic fronts to positional telemetry data collected from tags
- Improved monitoring data at colonies which would allow differentiation between the different breeding stages of the bird as well as picking out birds that have failed that breeding attempt for the year.

- Determining the sex of the individual birds may also provide insight into their behaviour e.g. Sex mediated segregation of foraging area is well established in even monomorphic species e.g. Lewis *et al*. 2002.
- Deployment of tags pre-and post -construction of wind farms to provide greater understanding over how behaviour modified by the presence of artificial structures in the sea. This could arise through the provision of roosting or foraging sites for birds. There may also be changes in flight behaviour (e.g. height and speed) as birds actively avoid the turbine blades or even respond to changes in wind energy as consequence of the turbines rotating.

Analyses and modelling

- Further work examining the spatial distributions, for example in continuous time movement models (e.g. Wilson *et al*. 2018) could be beneficial for investigating spatial patterns in more detail.
- Incorporation of environmental covariates (see above under Data Collection) into predictive modelling frameworks. This would provide key insight into understanding the spatial and temporal patterns in birds’ distribution and abundance at sea as well as their behaviour.
- It has already been shown that the flight height of gannets when foraging can put birds at a higher risk of collision with turbines compared to when commuting between sites (Cleasby *et al* 2015). Although flight heights were not part of this study, we would recommend that spatial patterns in flight heights for other species be further explored in future work.
- Revisions and/or updates to Collision Risk Models to better reflect spatial patterns in behaviour e.g. variation in key parameters such as flight height and speed.

4.11 Conclusions

Our analyses suggest that, in general, the at-sea distribution of birds during the breeding season was not strongly affected by wind speed or time of day. Consequently, when assessing the spatial overlap with offshore wind farms, data collected using boat or digital aerial surveys during the breeding season are unlikely to be biased relative to these variables. However, it is important to note that these results are limited to the breeding season when there were relatively few periods during which strong winds were likely to constrain at sea surveys. More data are needed in order to understand how strong winds outside the breeding season, when birds are not constrained by the need to remain close to their breeding colonies, may influence at sea distributions and the implications for survey data collected during these times.

Whilst survey data collected during the breeding season are likely to be representative of species distributions for breeding birds at this time, there are clear spatial patterns in behaviour which are more challenging to capture using at sea surveys. This is important as species behaviour may influence their vulnerability to the different impacts associated with offshore wind farms. For example, commuting birds may be vulnerable to barrier effects whilst foraging birds may be vulnerable to displacement. In order to better understand how offshore wind farms are likely to affect seabird populations and reduce uncertainty in the consenting process, a better understanding of seabird behaviour is required.

5 Acknowledgements

This project was funded by the Scottish Government’s The Rural and Environmental Science and Analytical Services Division (RESAS) Contract Research Fund. We wish to that Marine Scotland and the project steering group for support and guidance throughout this project..

The project would not have been possible without the collaboration of others who supplied data. We thank the RSPB, and particularly Ian Cleasby for help and advice, for supplying data collected as part of the FAME and STAR projects. Francis Daunt (CEH) supplied data for Kittiwakes, Guillemots and Razorbills from the Isle of May. Keith Hamer (University of Leeds) supplied data for Gannets from the Bass Rock and Jon Green (University of Liverpool) supplied Gannet data collected from Alderney in collaboration with the Alderney Wildlife Trust and its’ Track A Gannet programme and additional data from Puffin Island.

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7 Appendices

7.1 Appendix AA. Sample sizes for utilisation distributions under day/night and high/low wind conditions

As noted in the methods, we used a classification of sample sizes of to highlight degrees of confidence that can be placed on interpretations of the data, such as overlap analysis of distributions. Sample sizes are presented on all utilisation maps for each species, however, these are also summarised here:

(1) Lowest (red filled cells): Less than 100 fixes or five or fewer birds provided data per state and category split of the data (i.e. day-low, day-high, night-low, night-high).
(2) Low-medium (orange): 101 – 250 or 6 – 10 birds.
(3) Medium (yellow): 251 – 1000 fixes or 11 – 15 birds.
(4) Medium-high (light green): 1001 – 2500 fixes or 16 – 20 birds.
(5) Highest (green): More than 2500 fixes or 25 + birds.

Further, we also highlight where the proportion of available data falls below 5% (cells with asterisk) of the total available for the state identified in the HMM for the specific category split of the data. This additional assessment provided a further quantification useful for showing where perhaps sufficient sample sizes existed under the above confidence levels, but that would otherwise mask disparity in proportionality of data among each category.

Table A 1	Sample sizes for utilisation distributions under day/night and high/low wind conditions, LBBG = Lesser Black-backed Gull

			All		Floating		Commuting		Foraging/searching	
Species	**Colony**	**Level**	**Birds**	**fixes**	**Birds**	**fixes**	**Birds**	**fixes**	**Birds**	**Fixes**
Gannet	Alderney	Day-low	59	98978	58	25673	59	33493	59	39812
		Day-high	58	28006	46	5671	57	11134	57	11492
		Night-low	57	46142	56	30031	50	2791	56	13314
		Night-high	46	13331	43	8651	39	1073*	42	3600
Gannet	Bass Rock	Day-low	131	216505	130	40069	131	97323	131	79113
		Day-high	119	51722	92	7931	118	21117	113	22660
		Night-low	128	98001	127	6341	123	8964	128	25369
		Night-high	95	22728	91	15668	56	1548*	84	5475*
LBBG	Walney	Day-low	33	7443	15	878	29	3411	29	3154
		Day-high	19	590*	3	78*	19	274*	10	238*
		Night-low	32	10644	26	3284	27	2434	32	4926
		Night-high	12	1229	6	355	12	302*	10	572
	Skokholm	Day-low	23	37476	22	10331	23	12648	23	14494
		Day-high	20	4647	17	1158	19	1625	20	1860
		Night-low	23	16786	22	6819	23	3524	23	6441
		Night-high	18	2336*	14	855*	13	552*	16	921*
	Orford Ness	Day-low	18	9161	10	991	18	3723	18	4440

		Day-high	12	1416	2	49*	11	740	9	618
		Night-low	16	4764	14	2283	13	1021	14	1449
		Night-high	9	638*	4	193	8	181*	7	258*
Kittiwake	Isle of May	Day-low	48	16190	38	1693	47	5038	48	9444
		Day-high	7	1133*	5	103*	7	317	7	707
		Night-low	42	6807	34	3194	33	769	41	2823
		Night-high	5	525	4	242	4	45*	4	234*
	Colonsay	Day-low	81	44473	76	4906	80	13288	81	26262
		Day-high	40	7306	27	855	35	2581	37	3848
		Night-low	78	18134	71	7084	66	2669	77	8355
		Night-high	34	3352*	23	1553	20	424*	29	1347*
	Bempton	Day-low	97	44197	82	5188	95	16205	96	22776
		Day-high	28	6813	23	975	26	3008	26	2819
		Night-low	88	19387	75	9228	67	2581	84	7523
		Night-high	14	2110*	13	1115	10	310*	14	681*
	Orkney	Day-low	78	28836	71	4038	72	9079	78	15695
		Day-high	30	4542	24	648	25	1149	30	2735
		Night-low	73	9081	44	2209	48	1638	73	5166
		Night-high	22	1737*	9	436	8	165*	21	1095*

Razorbill	Colonsay	Day-low	41	18456	39	7248	41	6012	41	5193
		Day-high	27	3079	20	1062	23	1173	21	818
		Night-low	37	14412	36	9519	28	734	37	4152
		Night-high	21	2424	19	1470	11	115*	17	826
	Colonsay TDR	Day-low	25	11816	25	5216	25	5508	25	1092
		Day-high	16	1429	12	677*	16	568	8	178
		Night-low	23	9763	23	7354	23	2239	11	153
		Night-high	11	872*	8	618*	9	240*	0*	0*
	Puffin Island	Day-low	43	24707	43	9842	43	6288	43	8573
		Day-high	20	3084	18	1599	18	969	12	500*
		Night-low	41	19614	42	14772	29	571	41	4129
		Night-high	16	3993	15	3008	8	159*	12	818
	Isle of May	Day-low	28	7135	28	2067	28	4065	26	1000
		Day-high	8	695*	6	165*	8	401	7	125
		Night-low	25	4750	20	3155	21	710	24	868
		Night-high	5	1389	5	757	5	264*	5	368
Guillemot	Colonsay	Day-low	77	43526	76	23252	75	9459	74	10801
		Day-high	44	5478	36	2703	36	1323	28	1421
		Night-low	73	21437	72	13827	65	2695	68	4891

		Night-high	16	1949*	11	1178*	12	267*	10	581*
	Puffin Island	Day-low	29	16818	29	9122	29	5235	28	2459
		Day-high	15	565*	12	340*	10	134*	4	71*
		Night-low	28	11679	27	8557	24	1151	26	1961
		Night-high	6	421*	6	385*	1	12*	1	24*
	Fowlsheugh	Day-low	10	3539	10	2146	10	995	8	398
		Day-high	3	469	3	326	3	91	3	52
		Night-low	9	1563	7	1190	8	273	6	91
		Night-high	1	149*	1	102*	1	34*	1	13*
	Isle of May	Day-low	50	13569	49	6375	50	4566	47	2619
		Day-high	24	3700	21	1852	24	1347	15	553
		Night-low	45	7365	37	4285	39	1027	39	2027
		Night-high	18	2481	14	1397	17	519	17	519
	Colonsay TDR	Day-low							27	1351
		Day-high							6	146
		Night-low							20	316
		Night-high							2	27
	Fowlsheugh TDR	Day-low							7	113
		Day-high							1	5

		Night-low							3	18
		Night-high							0	0

7.2 Appendix AB. Comparison of wind speed use vs availability

7.2.1 Northern Gannet

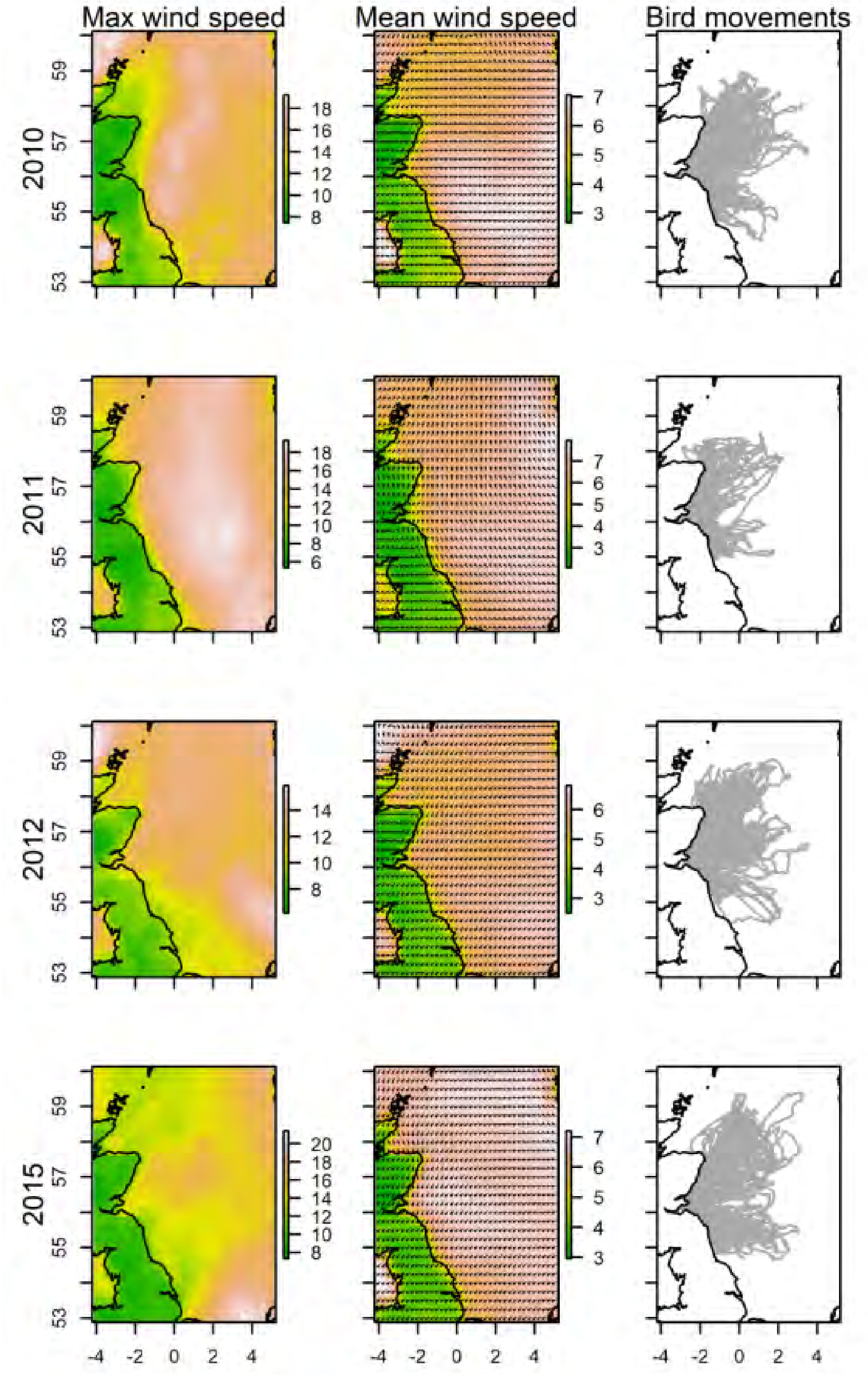


Figure A1 For Gannet, Bass Rock wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

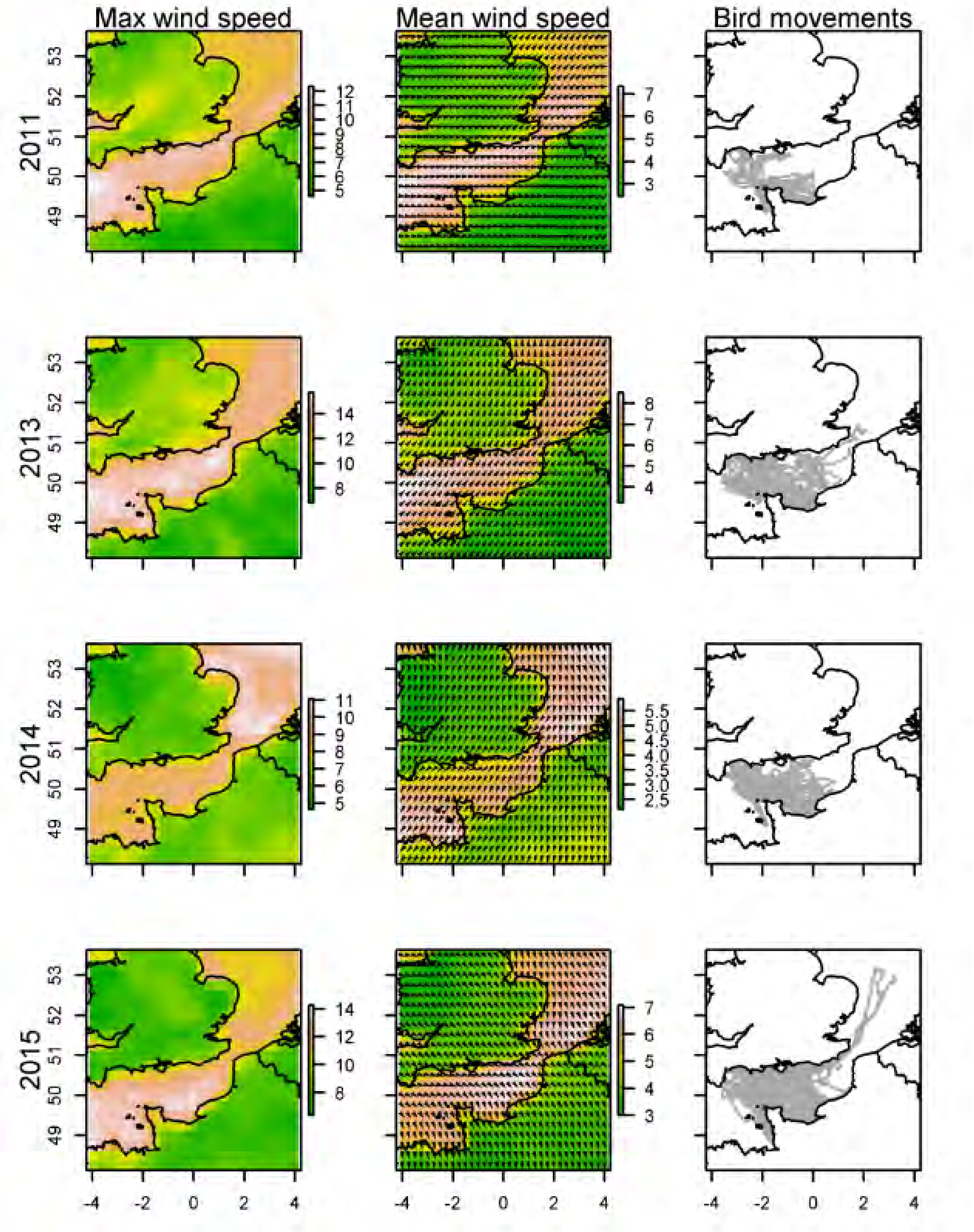


Figure A2 For Gannet, Alderney wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

7.2.2 Lesser Black-backed Gull

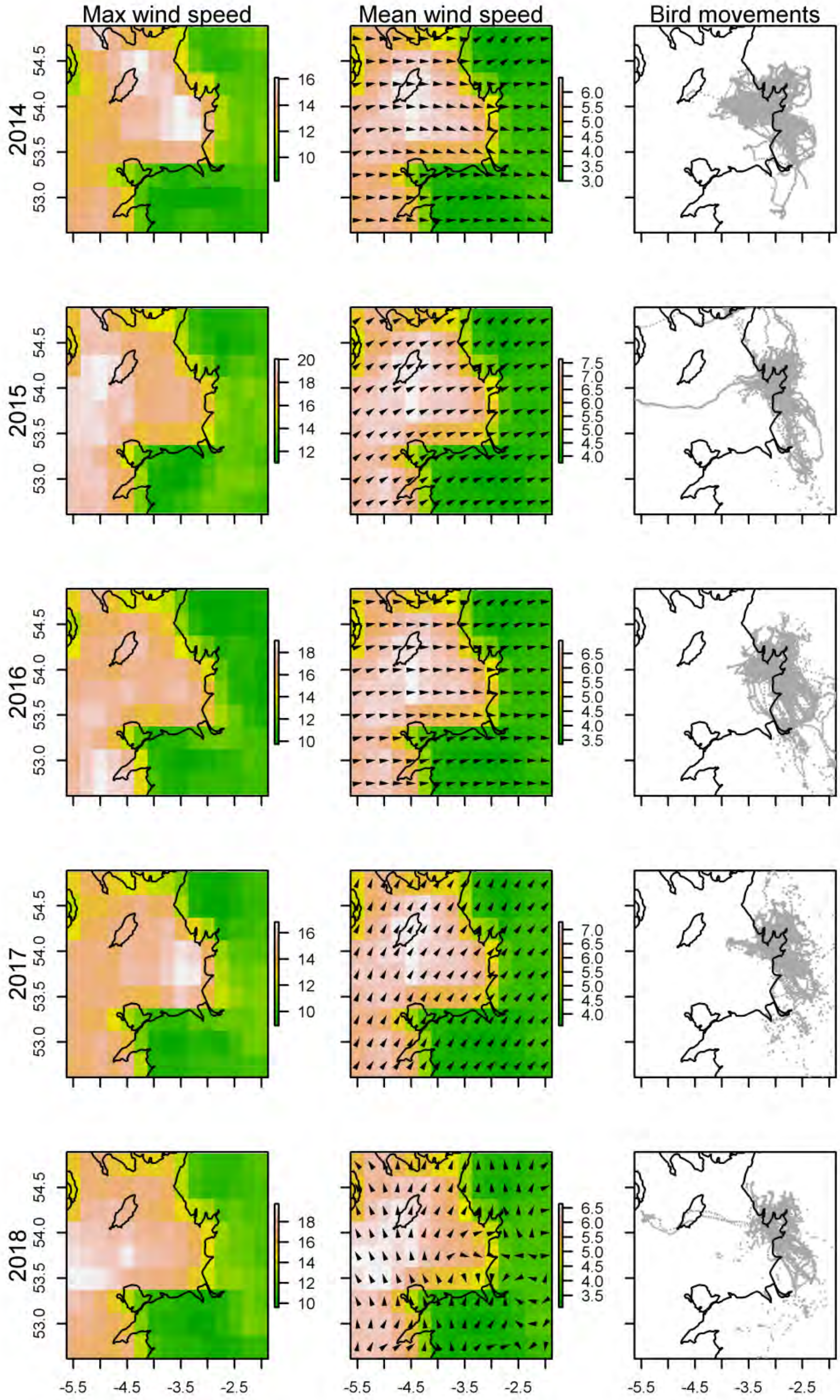


Figure A3 For Lesser Black-backed Gull, Walney wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

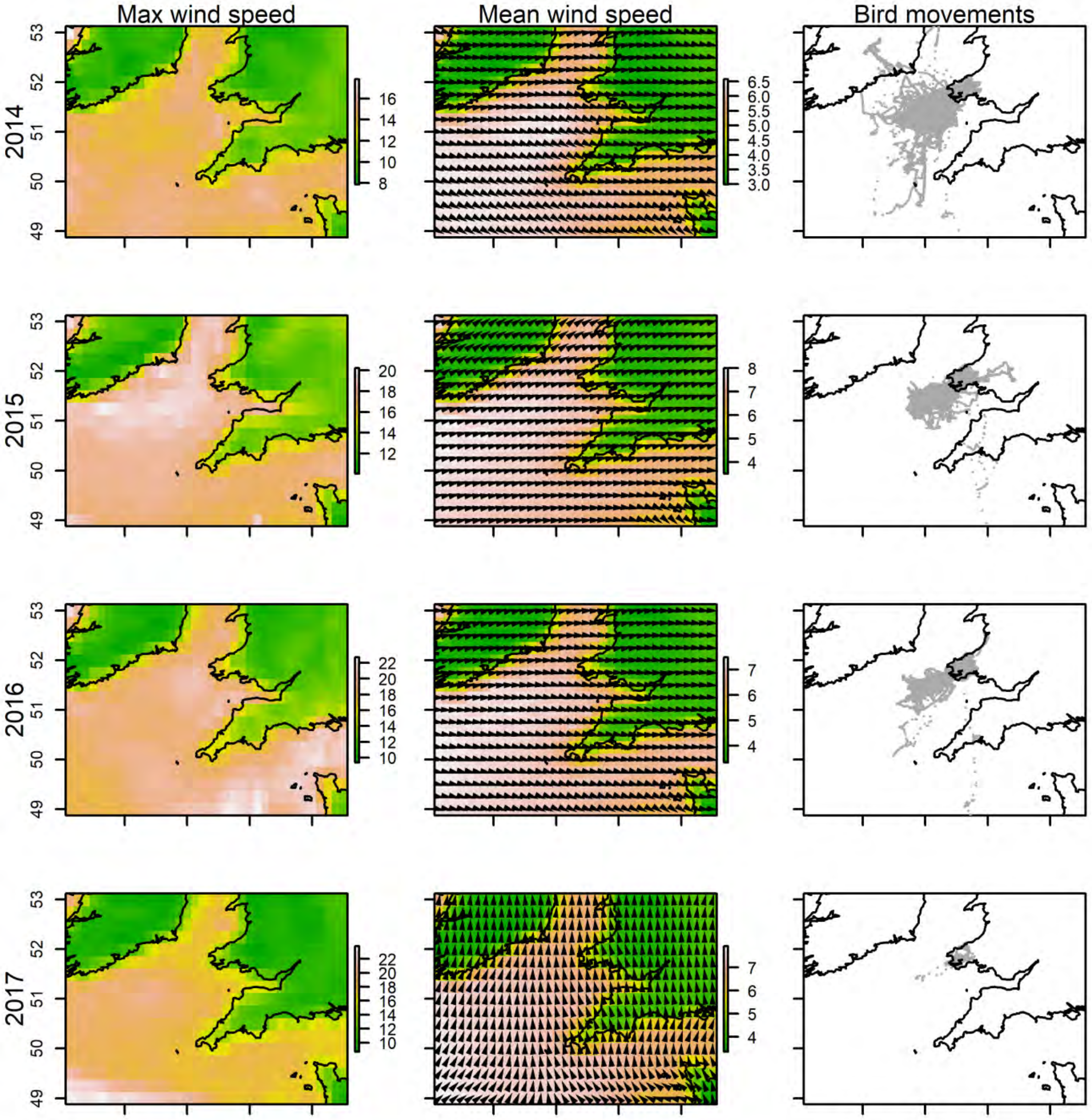


Figure A4 For Lesser Black-backed Gull, Skokholm wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

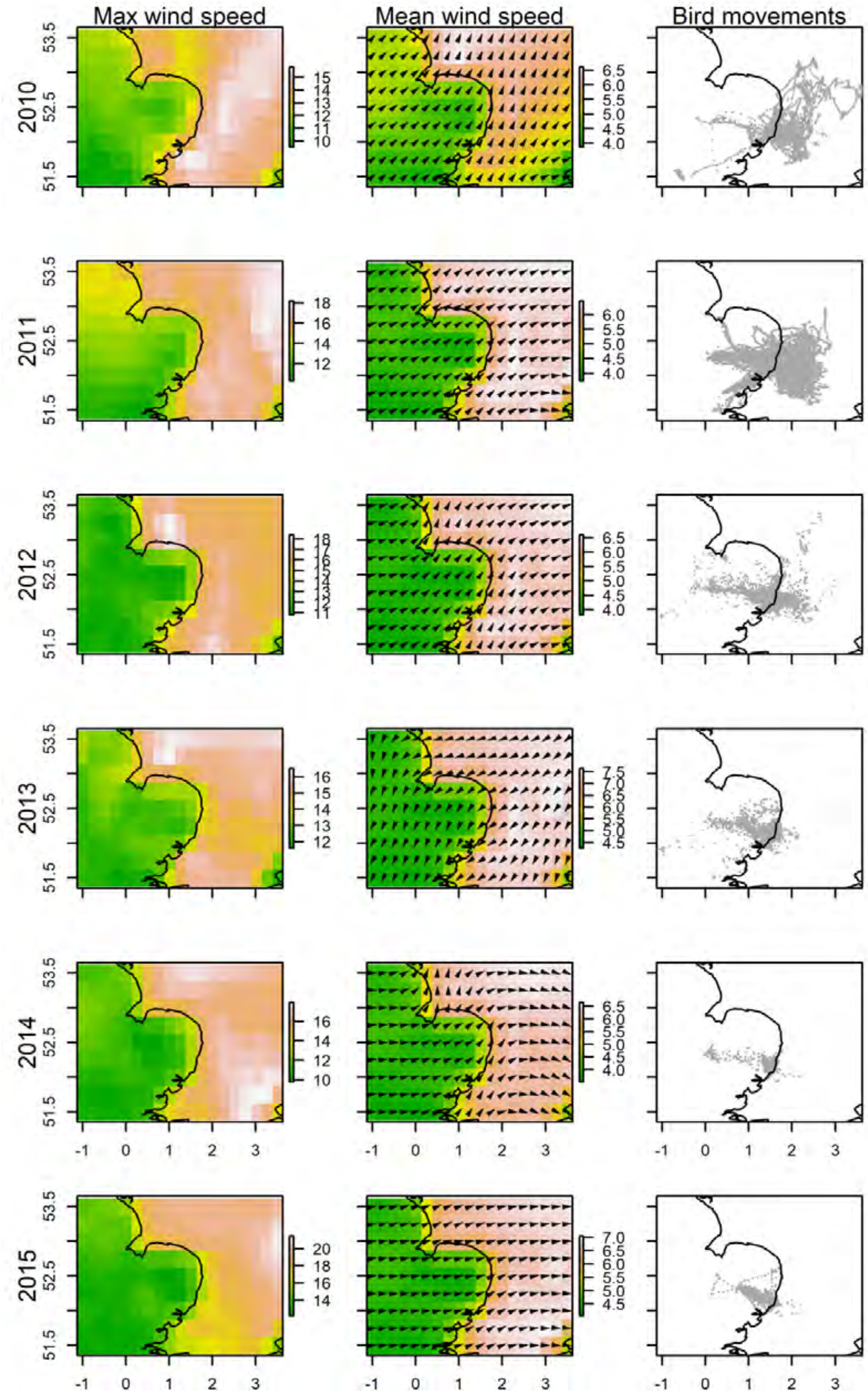


Figure A5 For Lesser Black-backed Gull, Orford Ness wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

7.2.3 Black-legged Kittiwake

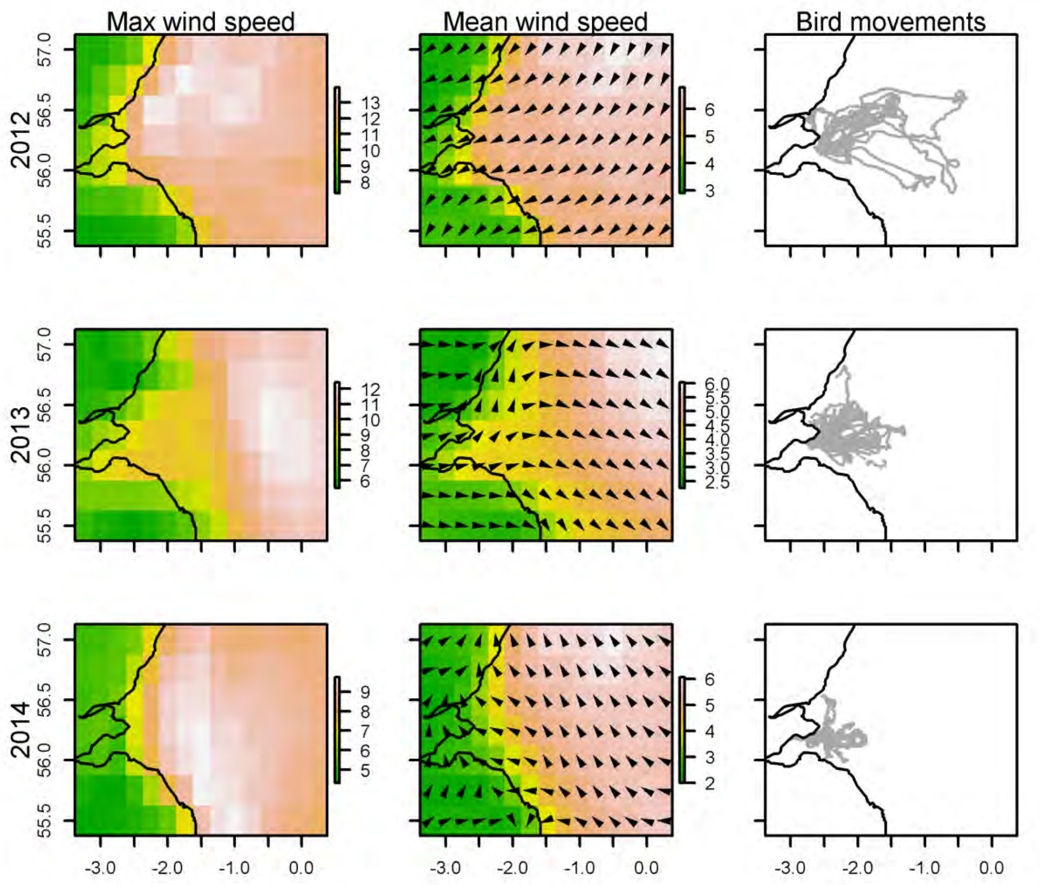


Figure A6 For Kittiwake, Isle of May wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

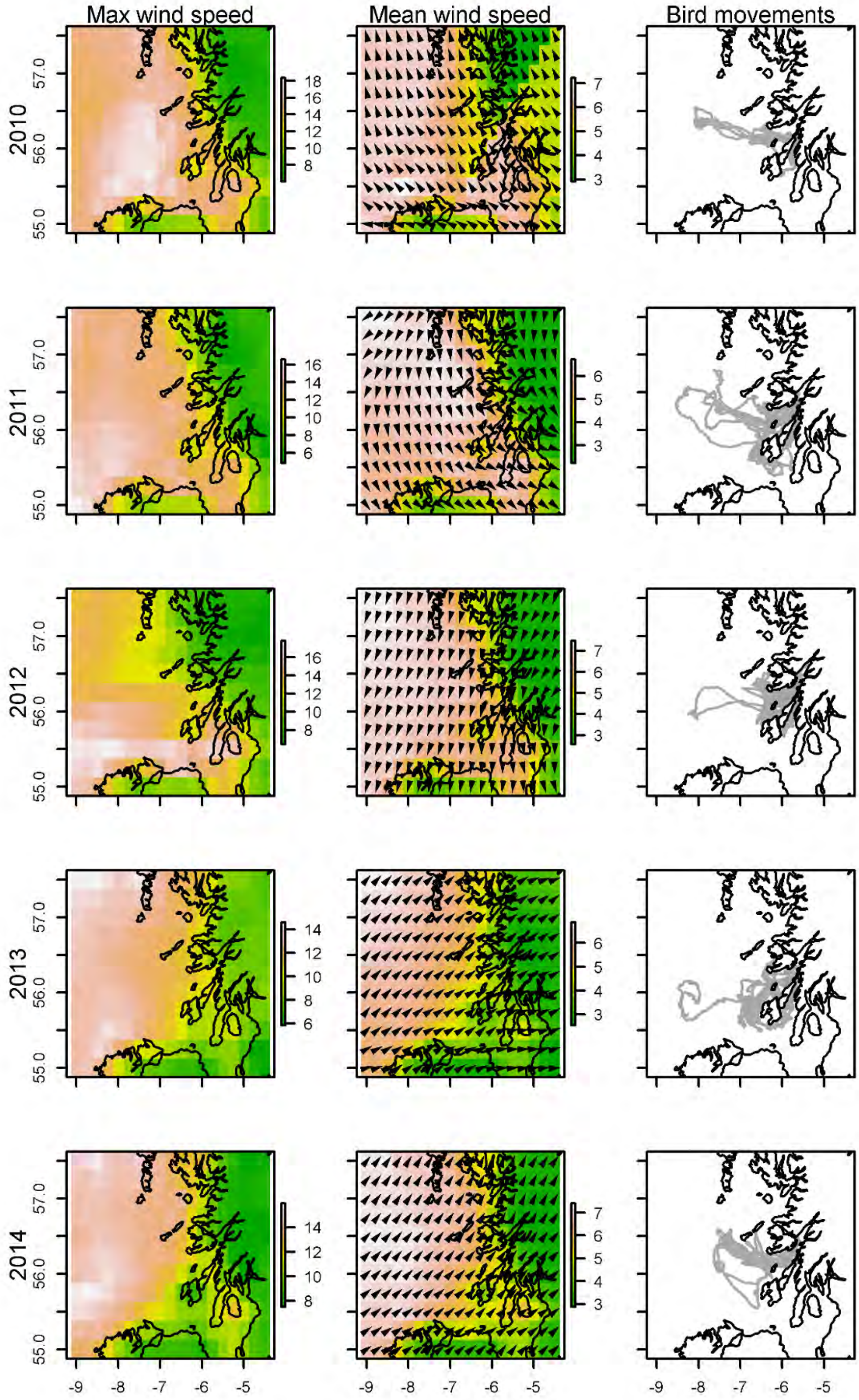


Figure A7 For Kittiwake, Colonsay wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

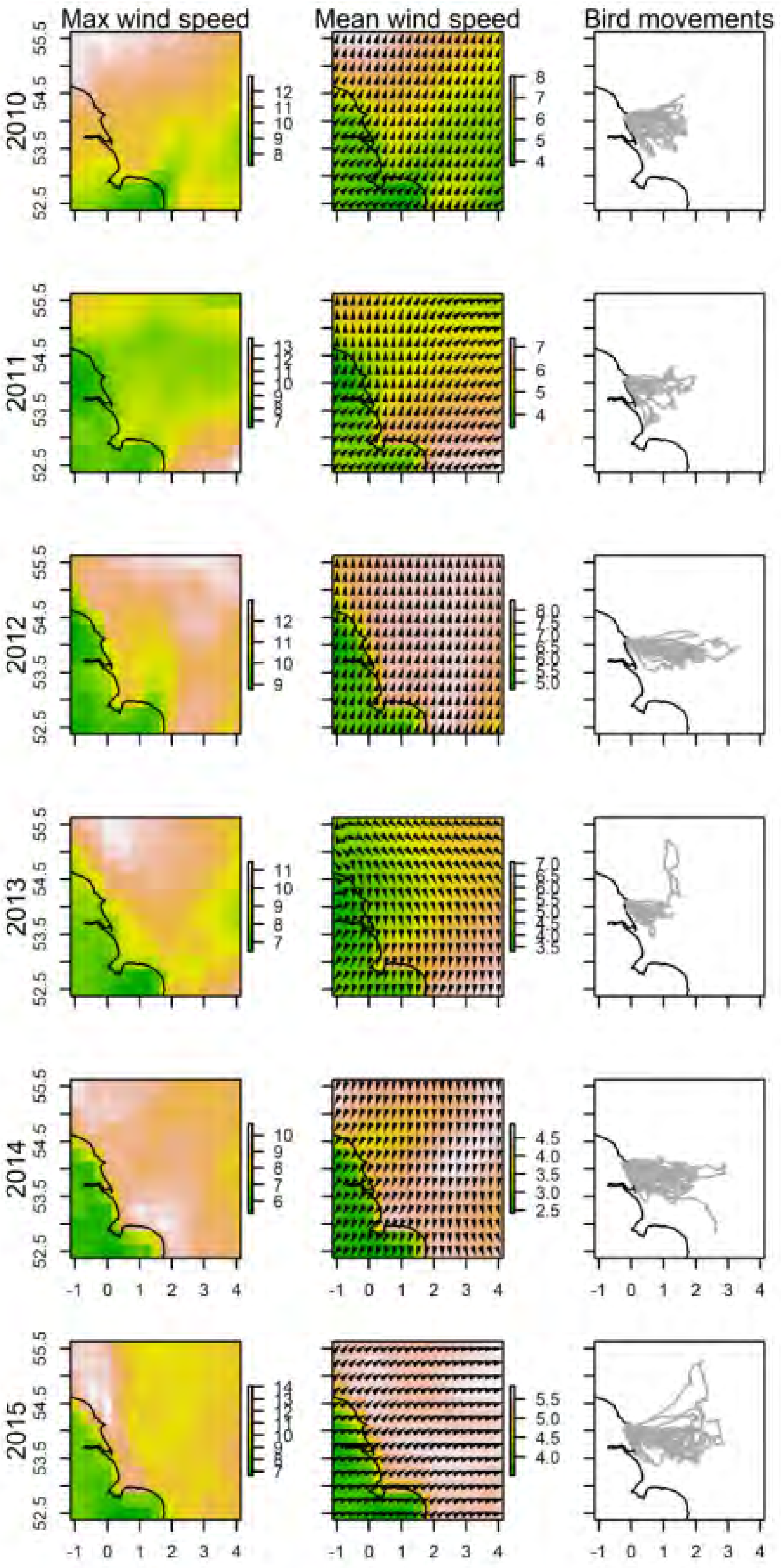


Figure A8 For Kittiwake, Bempton Cliffs wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

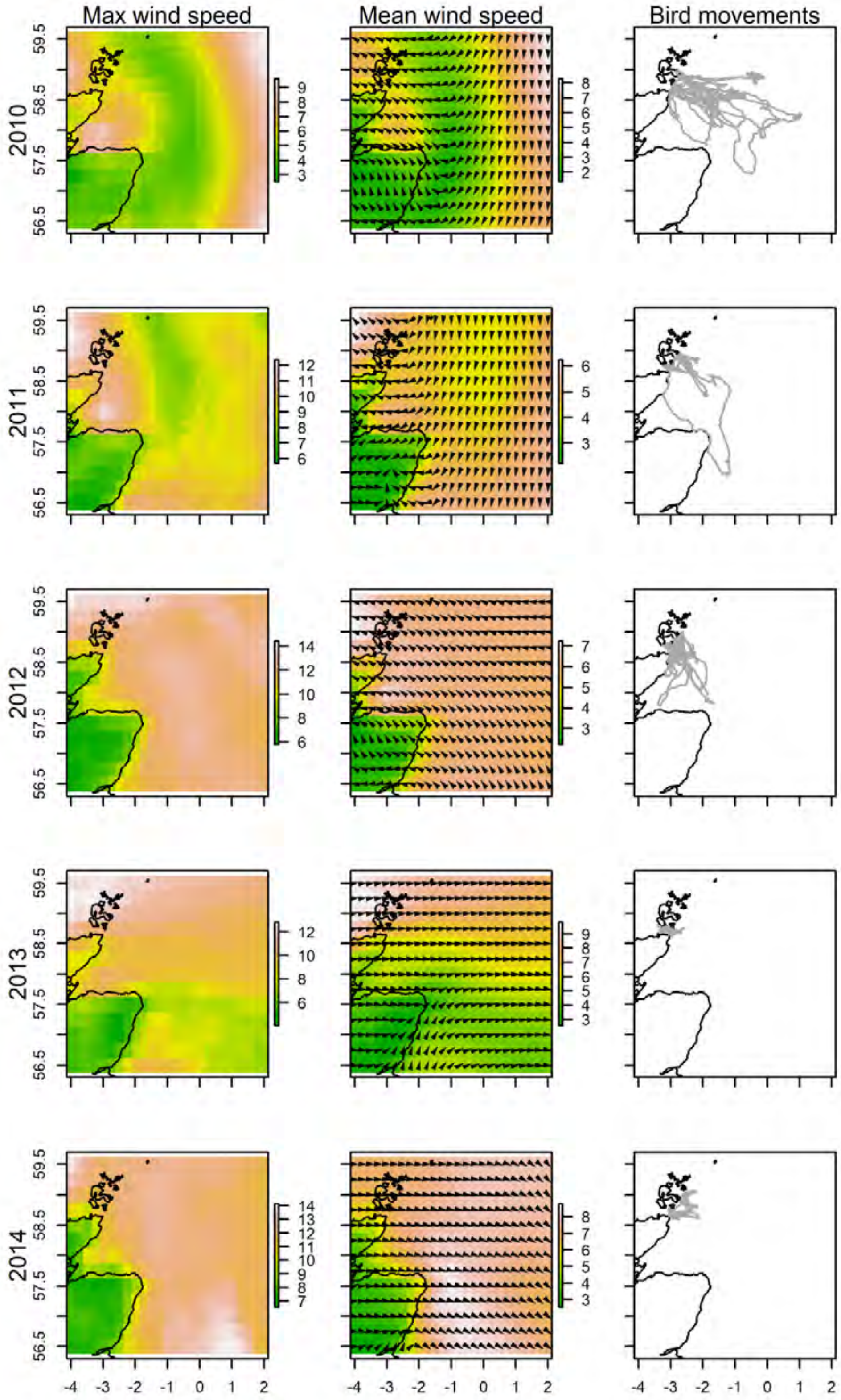


Figure A9 For Kittiwake, Orkney wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

7.2.4 Razorbill

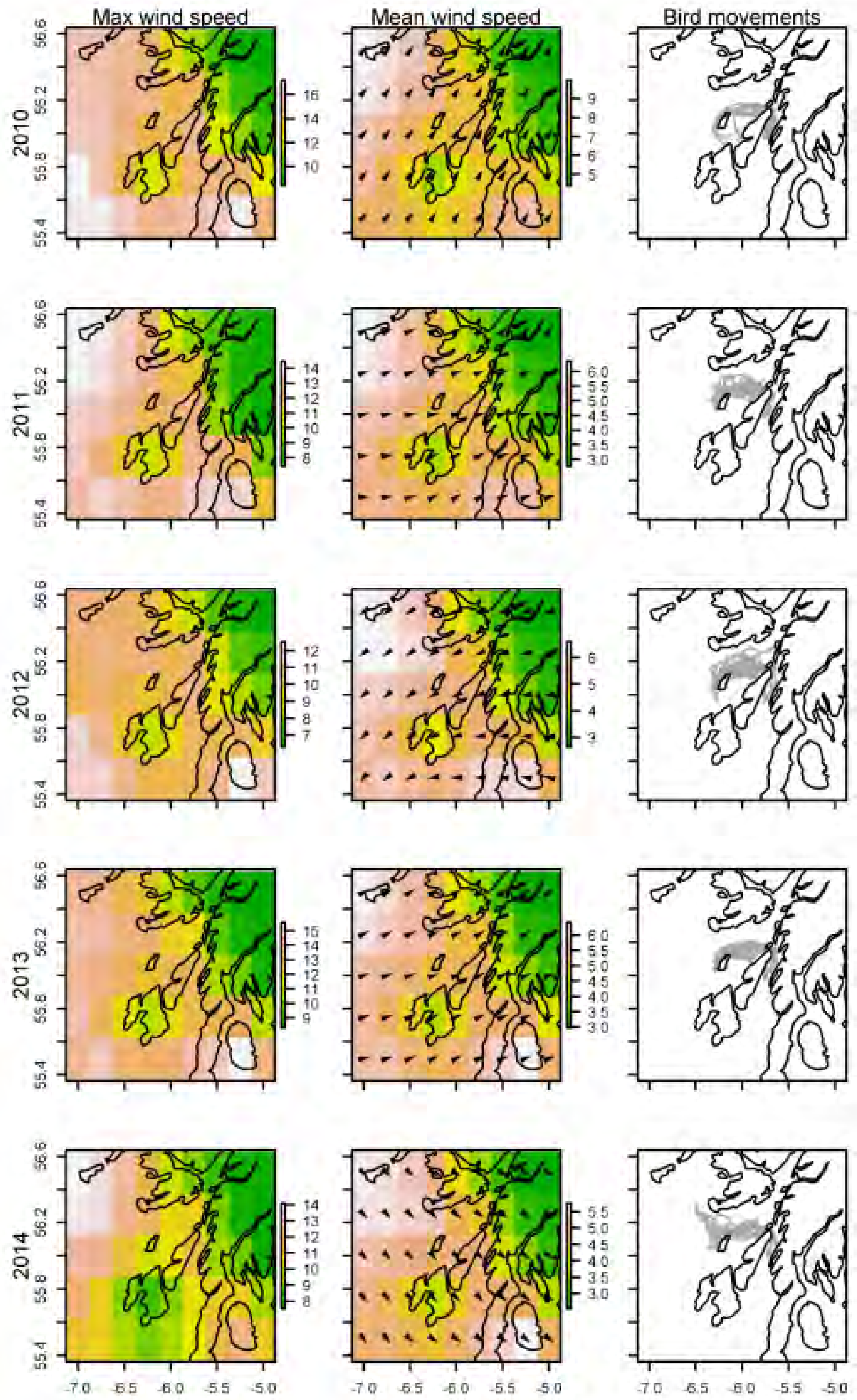


Figure A10 For Razorbill, Colonsay wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

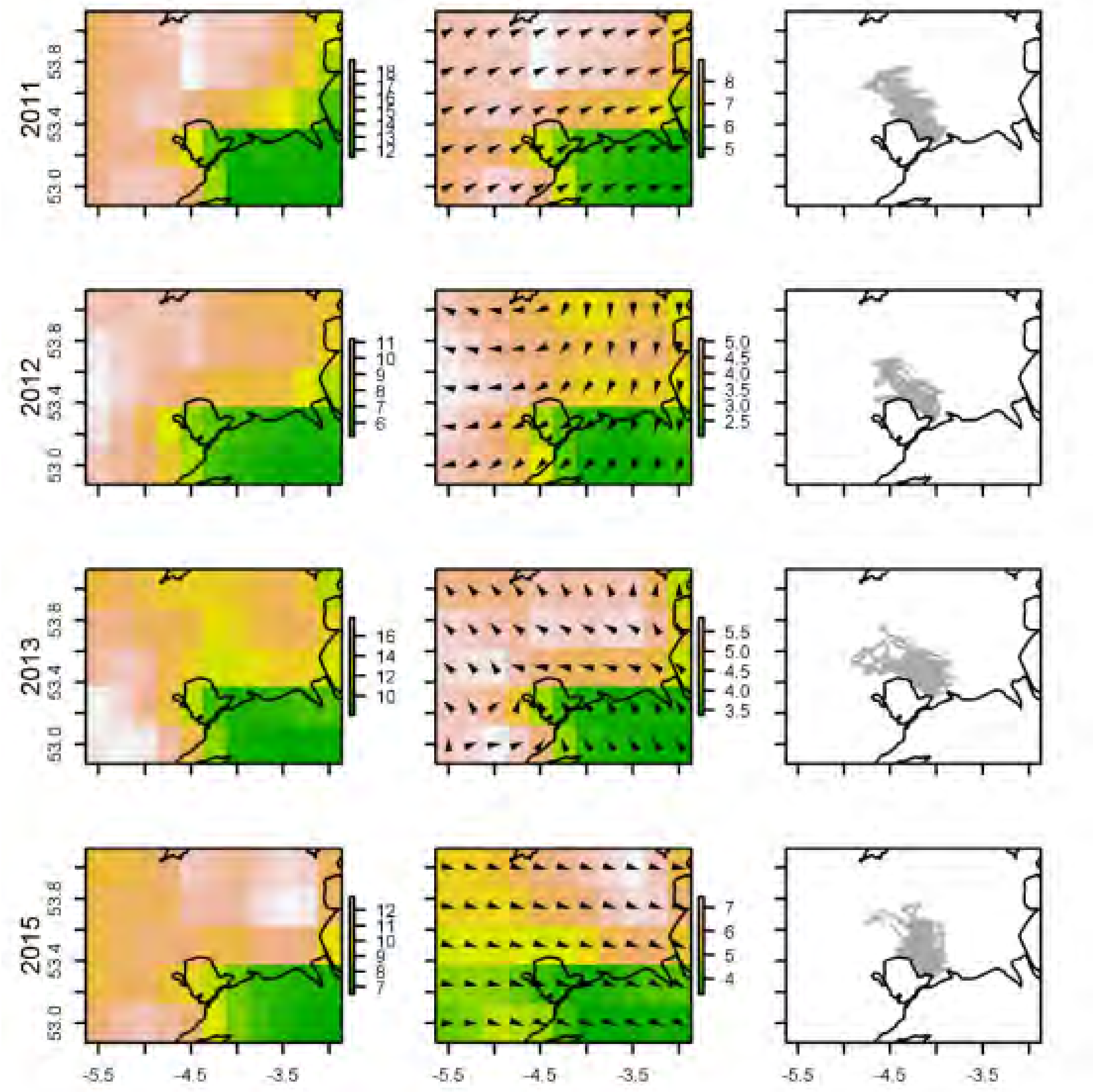


Figure A11 For Razorbill, Puffin Island wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

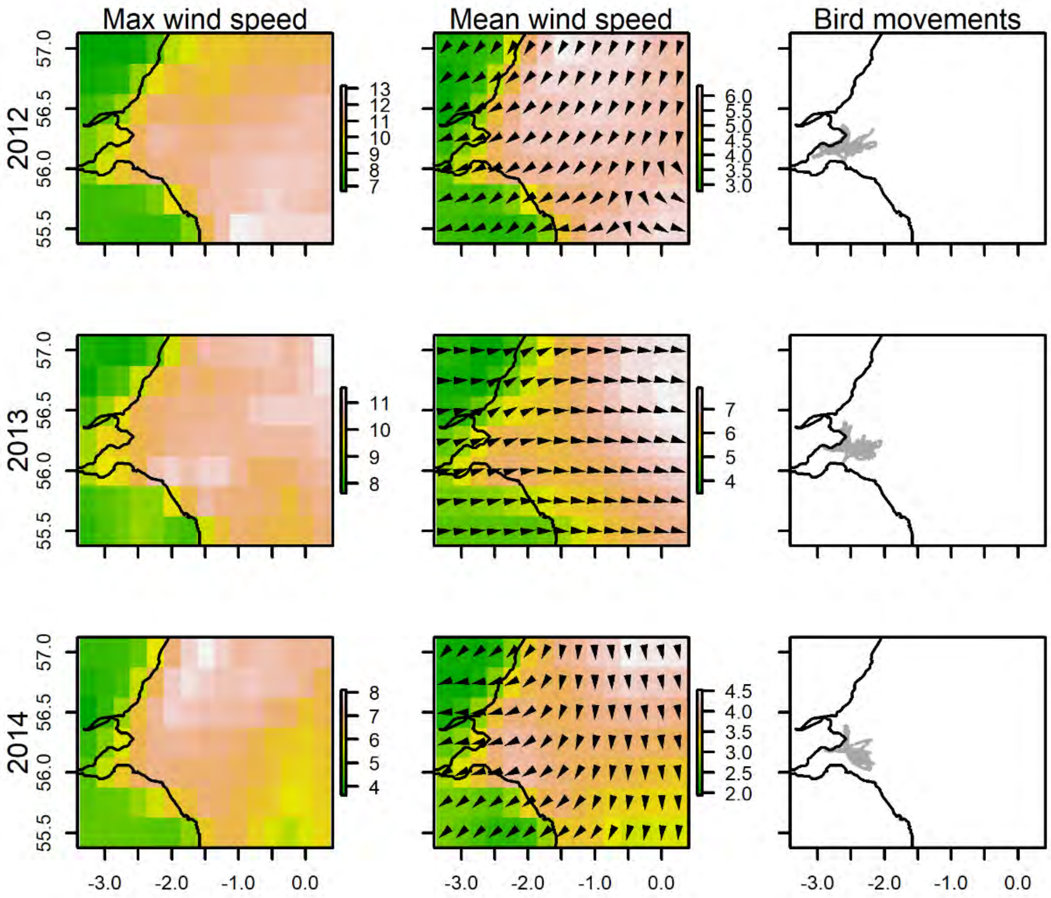


Figure A12 For Razorbill, Isle of May wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

7.2.5 Common Guillemot

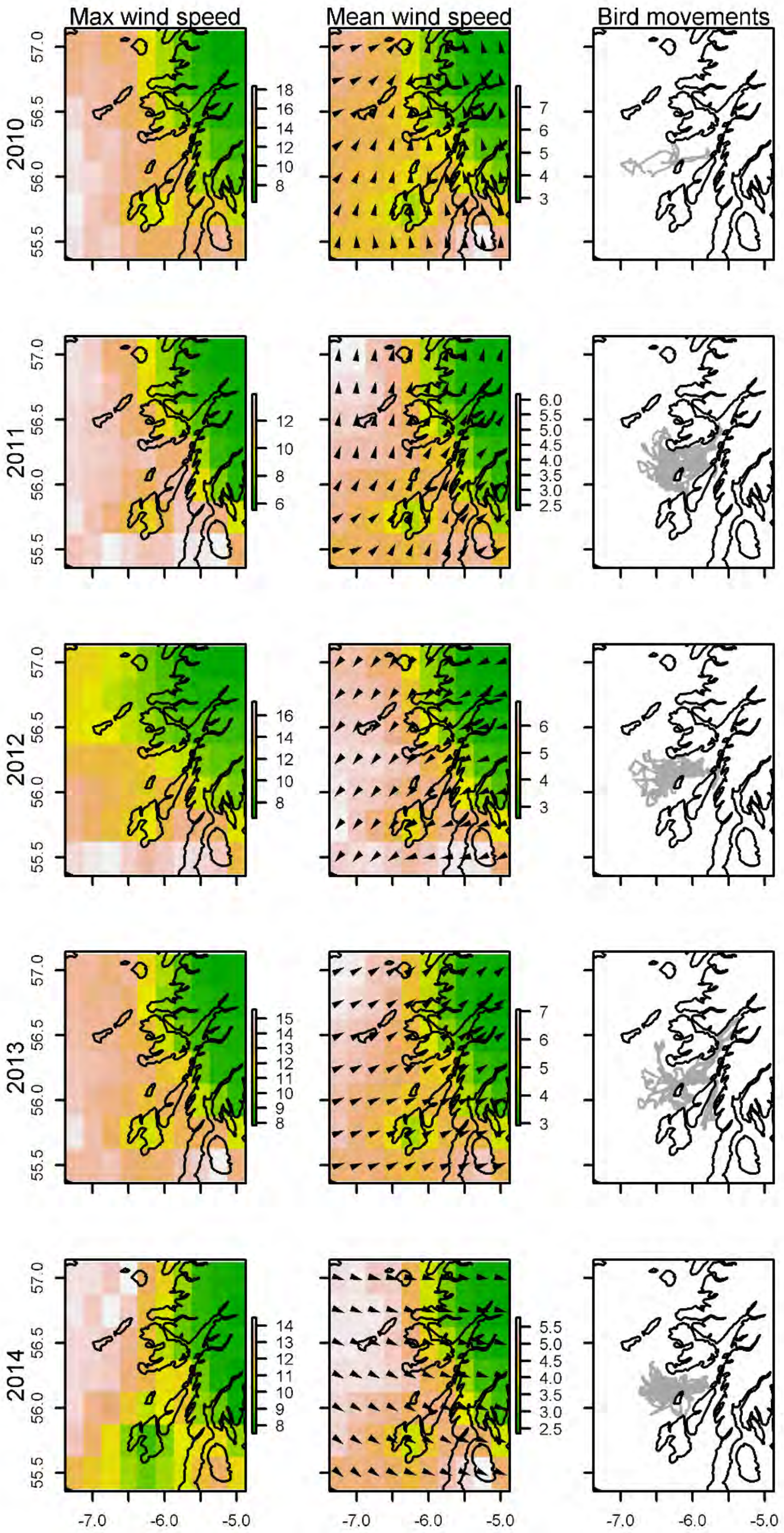


Figure A13 For Guillemot, Colonsay wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

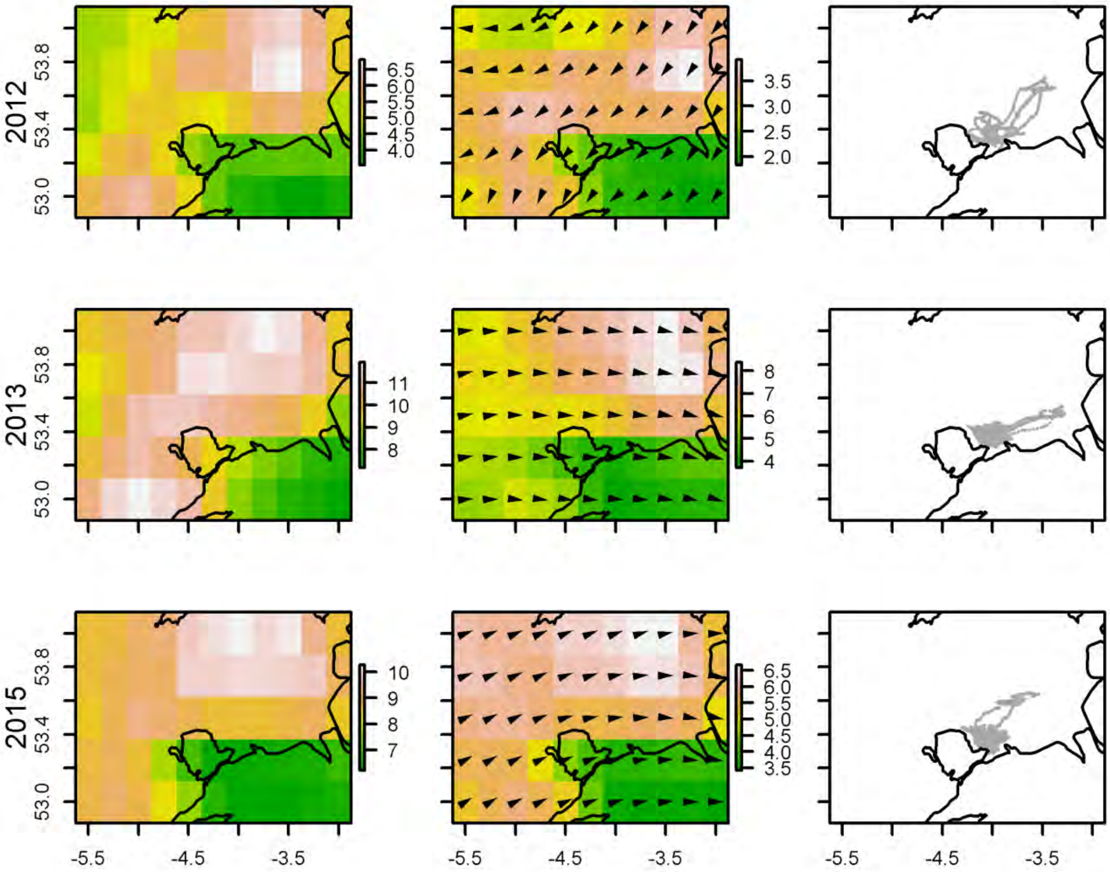


Figure A14 For Guillemot, Puffin Island wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

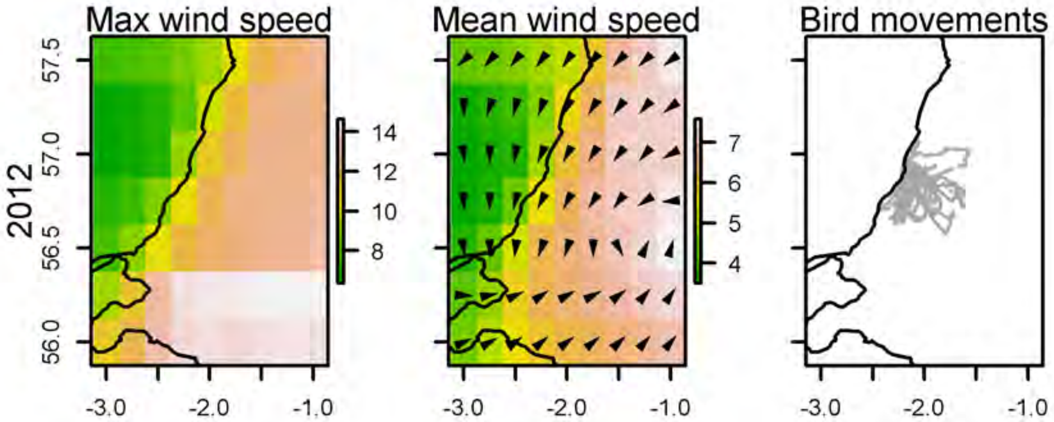


Figure A15 For Guillemot, Fowlsheugh wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

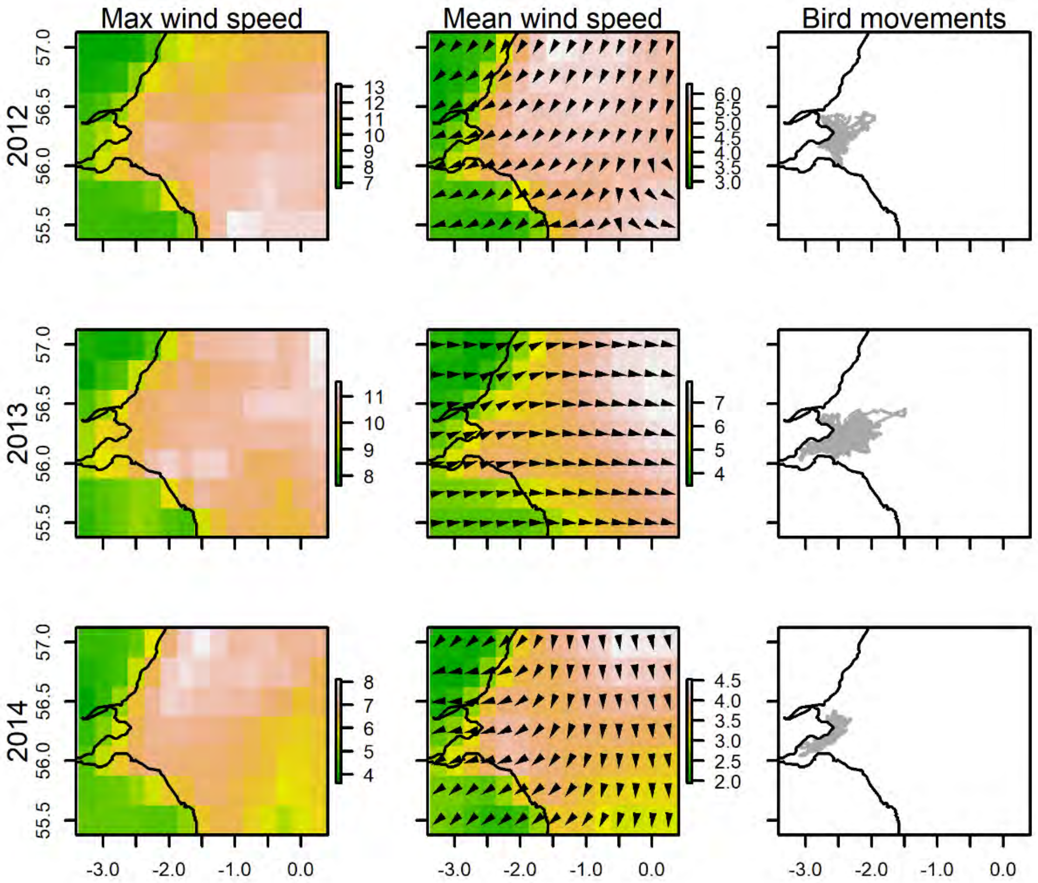
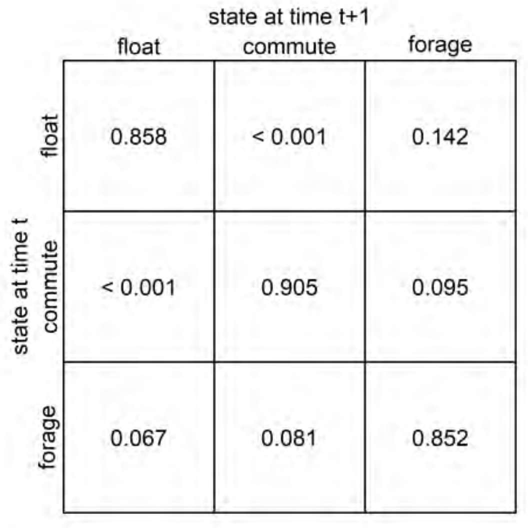


Figure A16 For Guillemot, Isle of May wind speed plots showing the maximum wind speed, the mean wind speed over the tracking duration for each bird per year, and the tracks of birds in each year.

7.3 Appendix AC. Model summaries

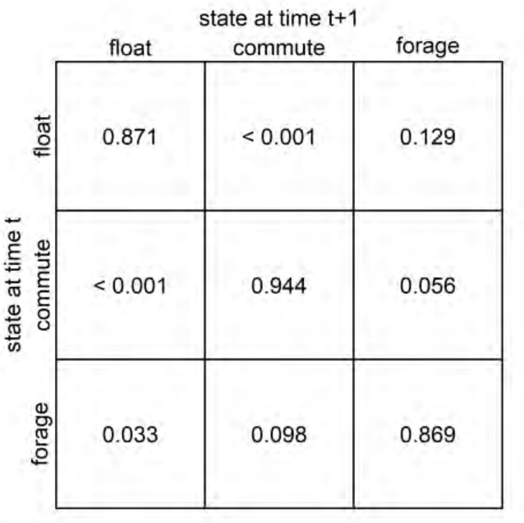
7.3.1 Northern Gannet

(a) Alderney



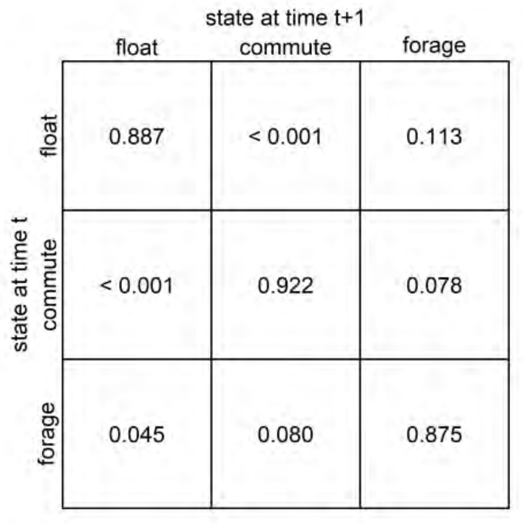
		state at time t+1		
		float	commute	forage
state at time t	float	0.858	< 0.001	0.142
	commute	< 0.001	0.905	0.095
	forage	0.067	0.081	0.852

(b) Bass Rock 2010



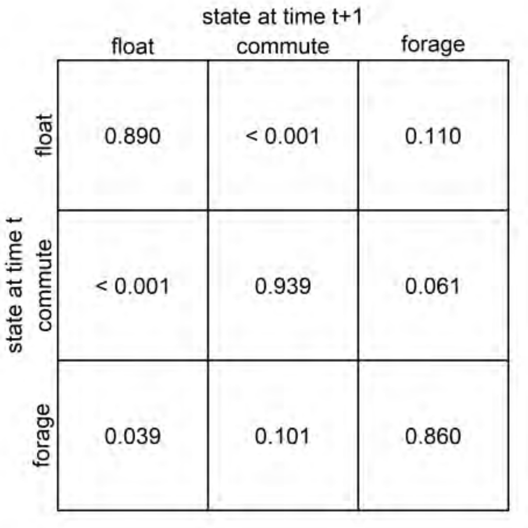
		state at time t+1		
		float	commute	forage
state at time t	float	0.871	< 0.001	0.129
	commute	< 0.001	0.944	0.056
	forage	0.033	0.098	0.869

(c) Bass Rock 2011



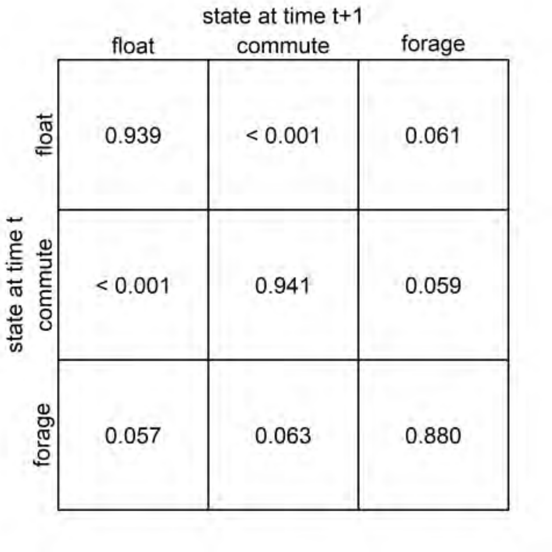
		state at time t+1		
		float	commute	forage
state at time t	float	0.887	< 0.001	0.113
	commute	< 0.001	0.922	0.078
	forage	0.045	0.080	0.875

(d) Bass Rock 2012



		state at time t+1		
		float	commute	forage
state at time t	float	0.890	< 0.001	0.110
	commute	< 0.001	0.939	0.061
	forage	0.039	0.101	0.860

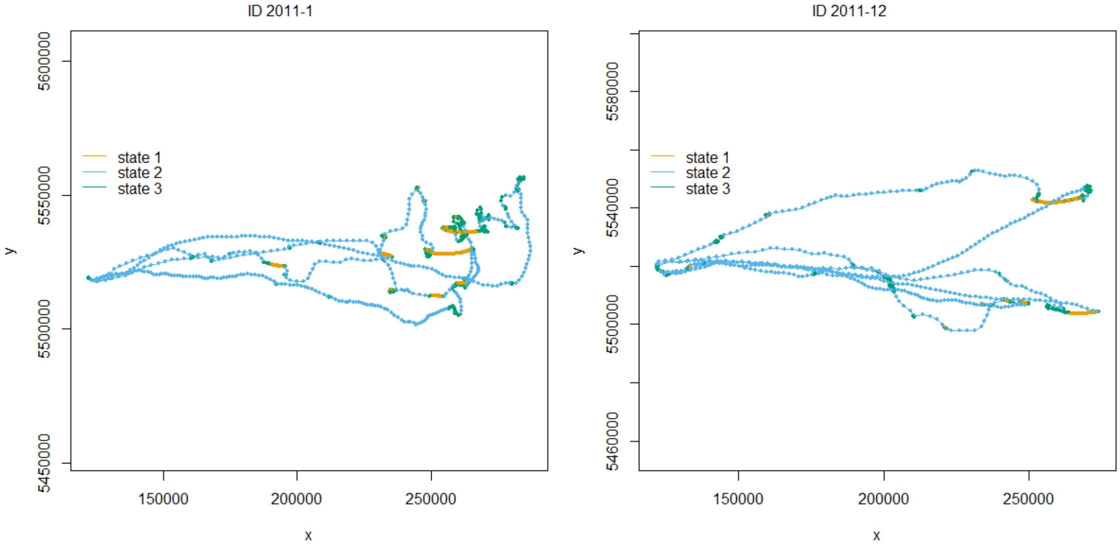
(e) Bass Rock 2015



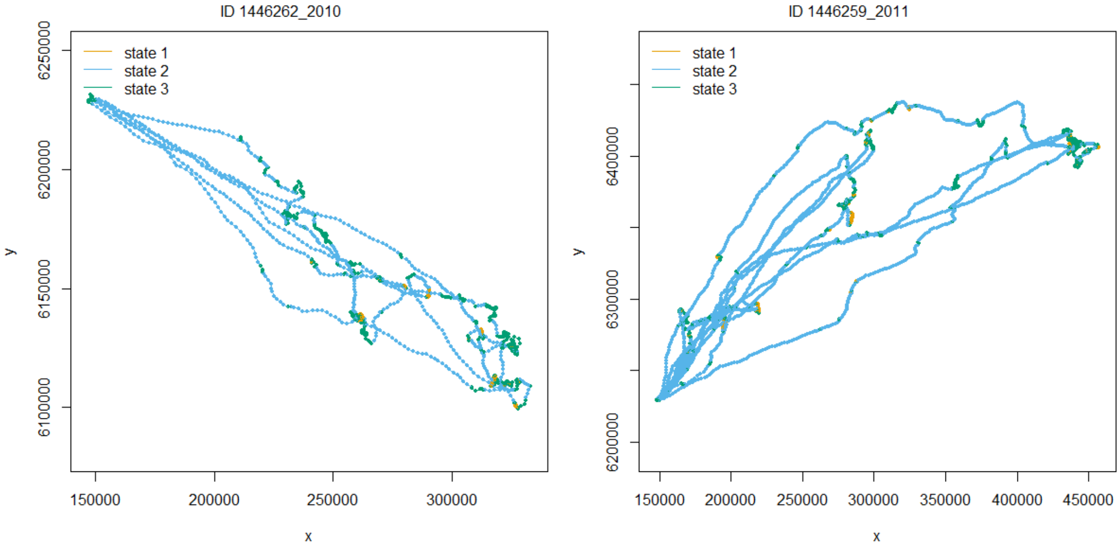
state at time t \ state at time t+1	float	commute	forage
float	0.939	< 0.001	0.061
commute	< 0.001	0.941	0.059
forage	0.057	0.063	0.880

Figure A17 For Gannet, HMM transition probabilities.

(a) Alderney



(b) Bass Rock



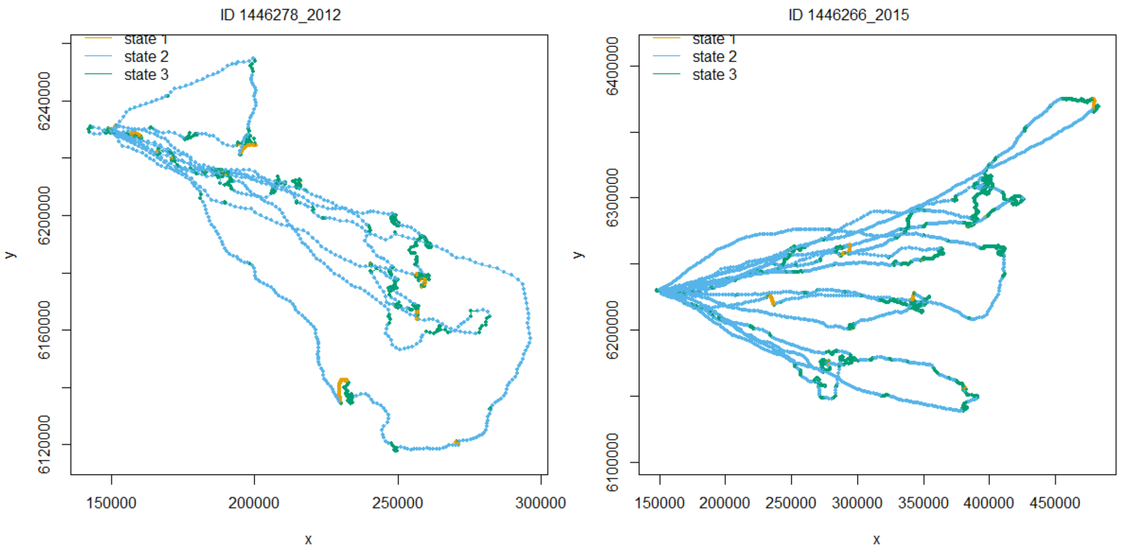
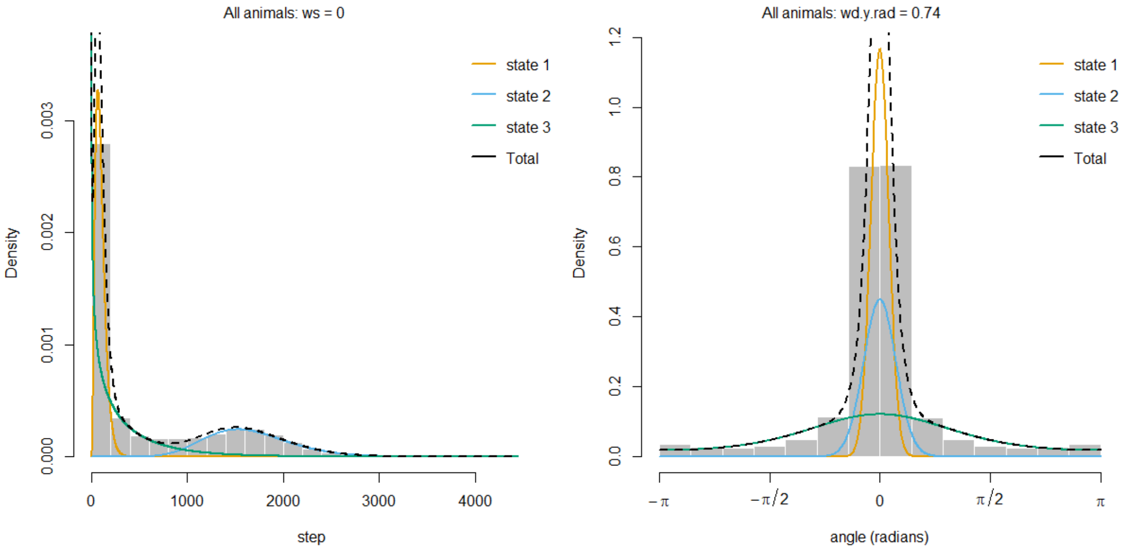
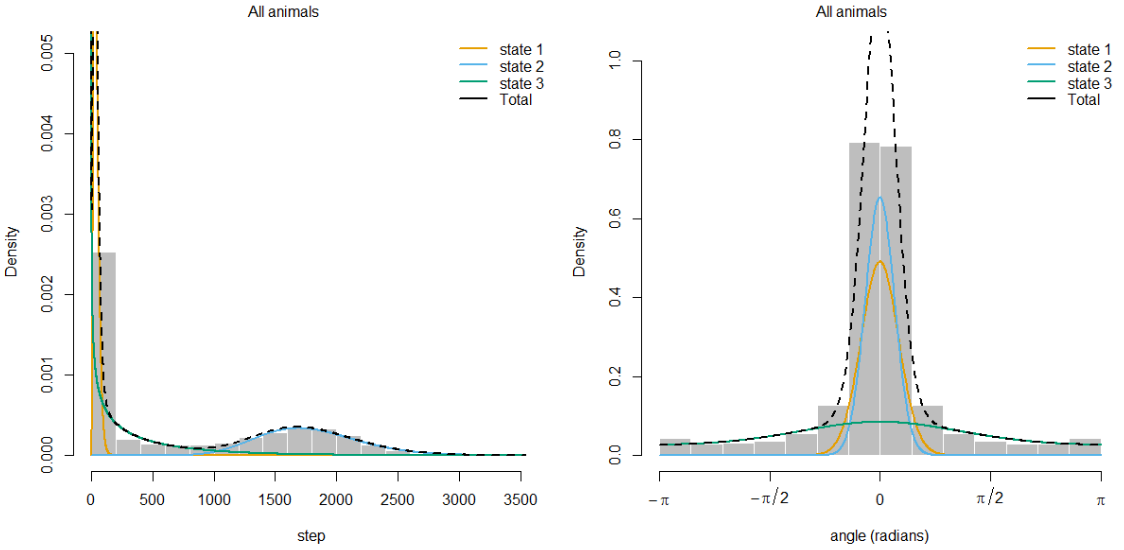


Figure A18 For Gannet, examples of states 1, 2 and 3 (floating, commuting and foraging/searching) identified for individuals at both colonies.

(a) Alderney (all years)



(b) Bass Rock 2010



(c) Bass Rock 2011

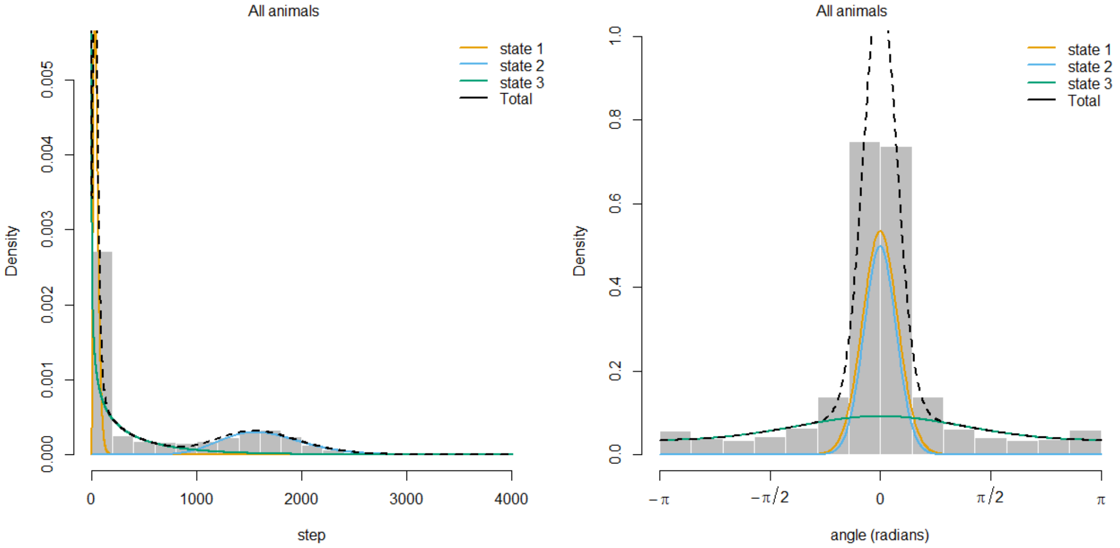
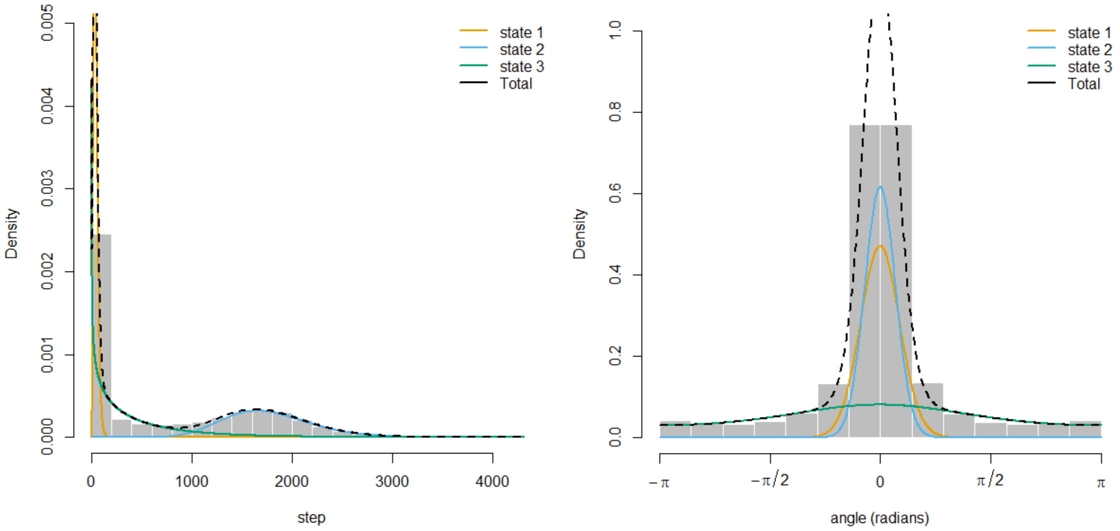


Figure A19 For Gannets, distributions of step length and turning angle at two sites: Alderney and Bass Rock for states 1, 2 and 3 (floating, commuting and foraging/searching); note due to quantity of information causing computational issues, models for Bass Rock were split annually – here we present the first two years of data (2010 and 2011), with information for the latter two (2012, 2015) provided in appendices.

(a) 2012



(b) 2015

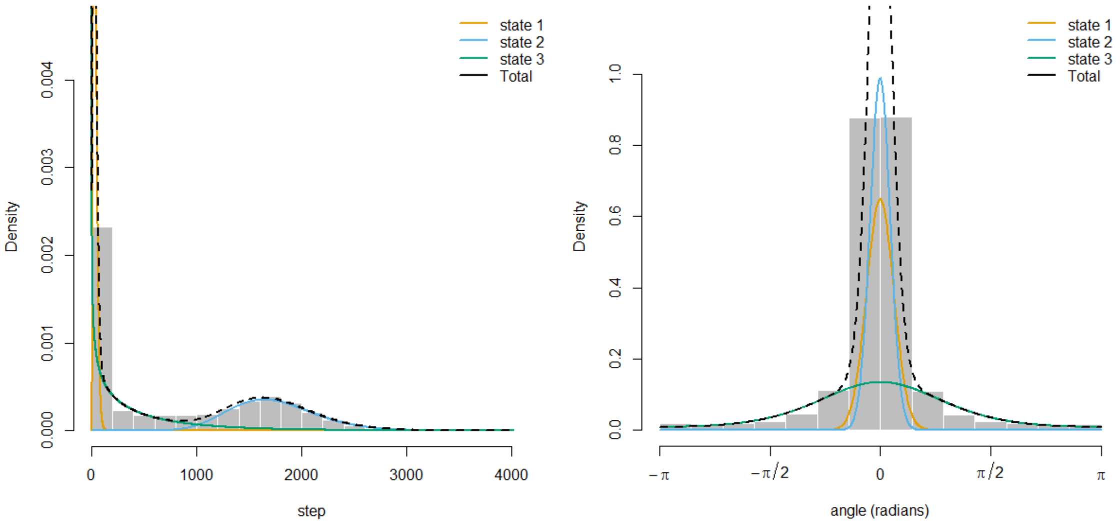
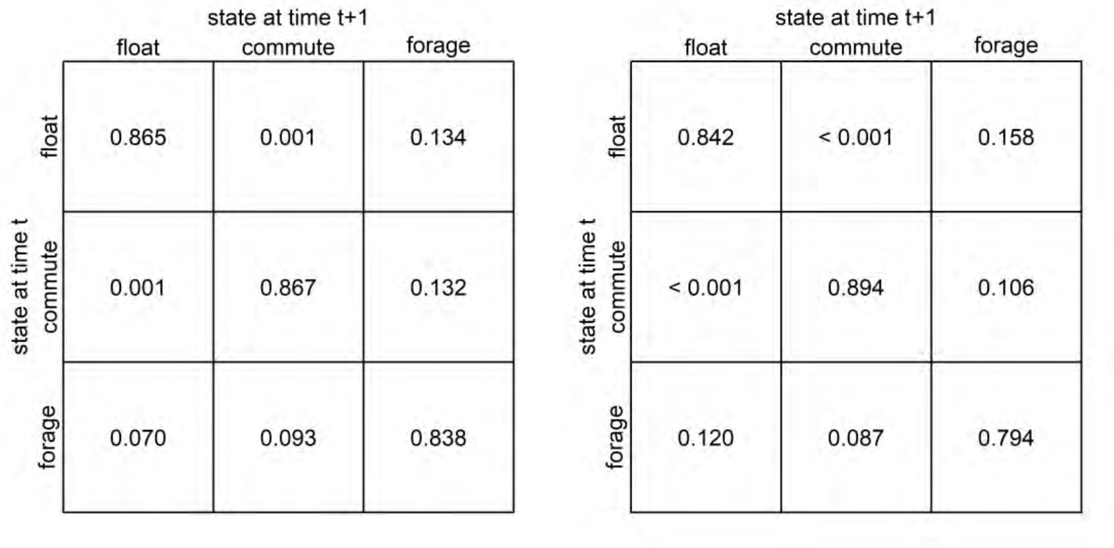


Figure A20 For Gannets, distributions of step length and turning angle at two sites: Alderney and Bass Rock for states 1, 2 and 3 (floating, commuting and foraging/searching); note due to quantity of information causing computational issues, models for Bass Rock were split annually – here we present the other two years of data (2012 and 2015).

7.3.2 Lesser Black-backed Gull



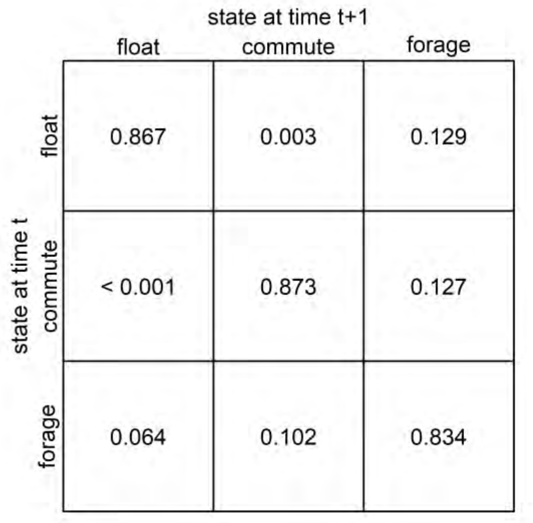
(a) Walney

state at time t \ state at time t+1	float	commute	forage
float	0.865	0.001	0.134
commute	0.001	0.867	0.132
forage	0.070	0.093	0.838

(b) Skokholm

state at time t \ state at time t+1	float	commute	forage
float	0.842	< 0.001	0.158
commute	< 0.001	0.894	0.106
forage	0.120	0.087	0.794

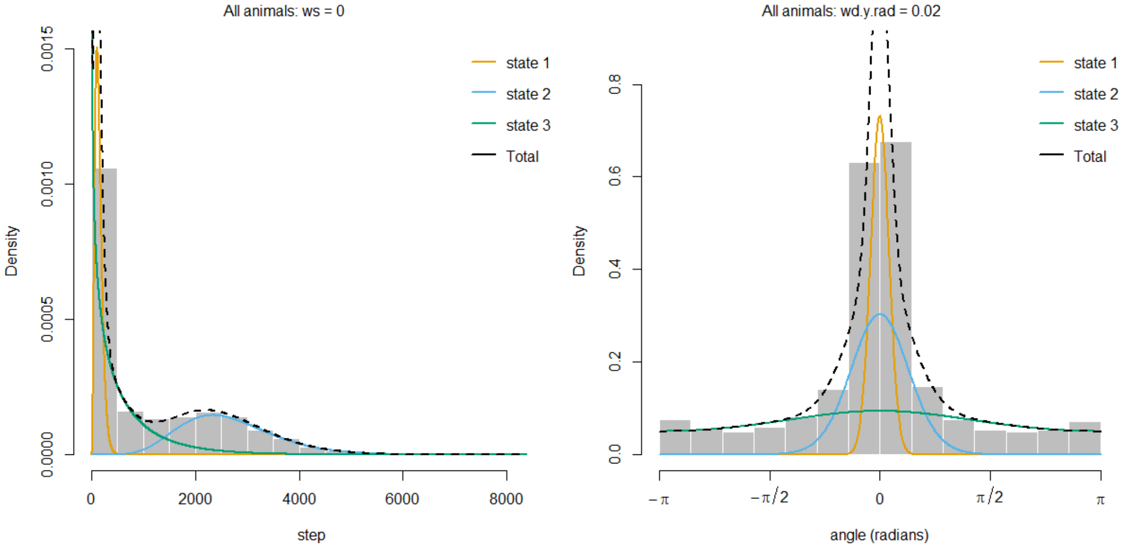
(c) Orford Ness



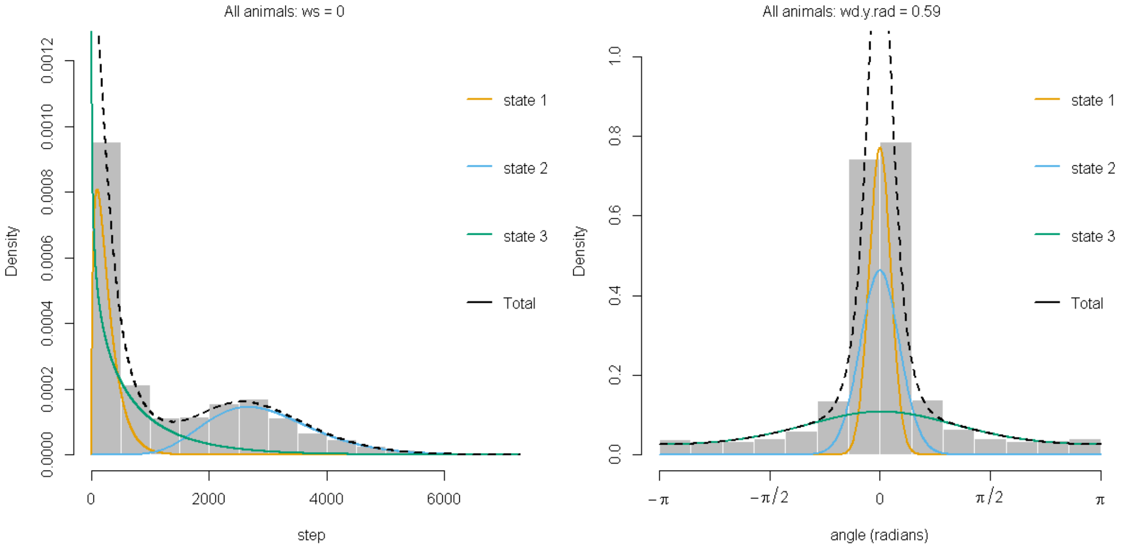
state at time t \ state at time t+1	float	commute	forage
float	0.867	0.003	0.129
commute	< 0.001	0.873	0.127
forage	0.064	0.102	0.834

Figure A21 For Lesser Black-backed Gulls, plot of transitions between states from a three-state model.

(a) Walney



(b) Skokholm



(c) Orford Ness

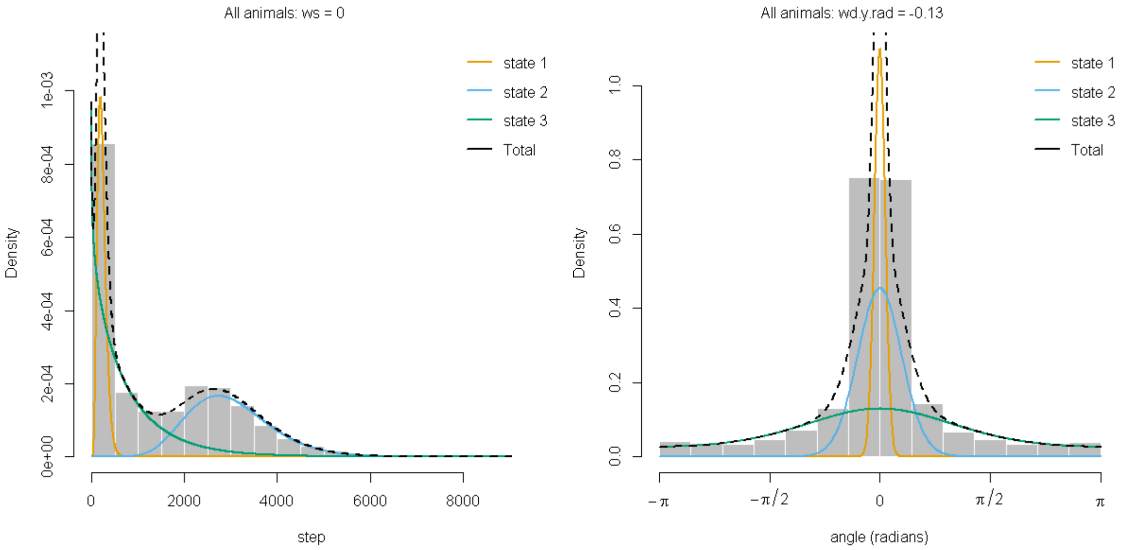


Figure A22 For Lesser Black-backed Gulls, distributions of step length and turning angles for each colony modelled and states 1, 2 and 3 (floating, commuting and foraging/searching).

7.3.3 Black-legged Kittiwake

(a) Isle of May

	state at time t+1		
state at time t	float	commute	forage
float	0.704	< 0.001	0.296
commute	< 0.001	0.809	0.191
forage	0.043	0.071	0.886

(b) Colonsay

	state at time t+1		
state at time t	float	commute	forage
float	0.742	< 0.001	0.258
commute	< 0.001	0.862	0.138
forage	0.035	0.075	0.890

(c) Bempton

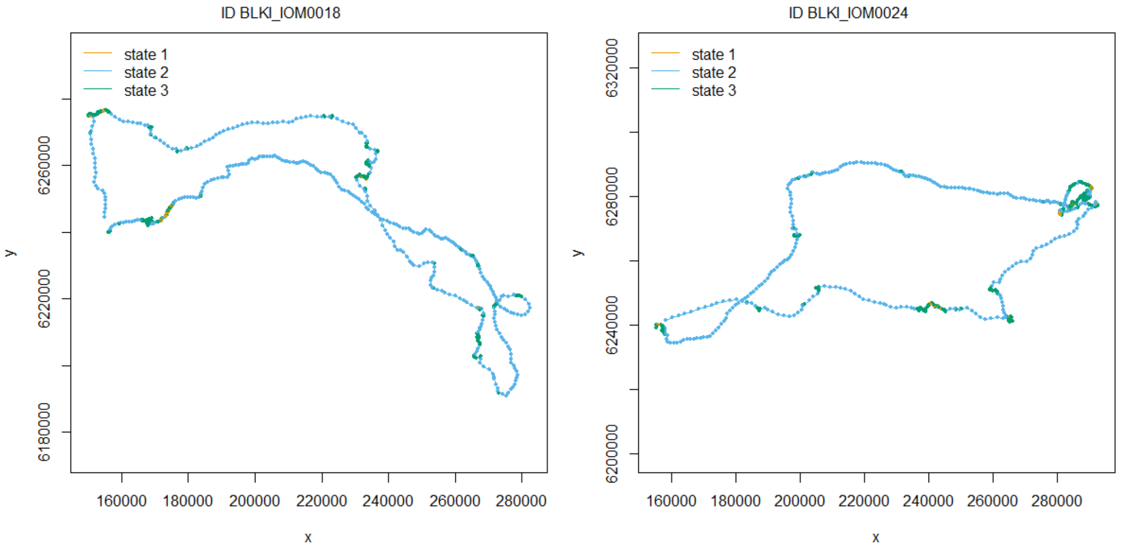
	state at time t+1		
state at time t	float	commute	forage
float	0.780	< 0.001	0.220
commute	< 0.001	0.911	0.089
forage	0.032	0.096	0.871

(d) Orkney

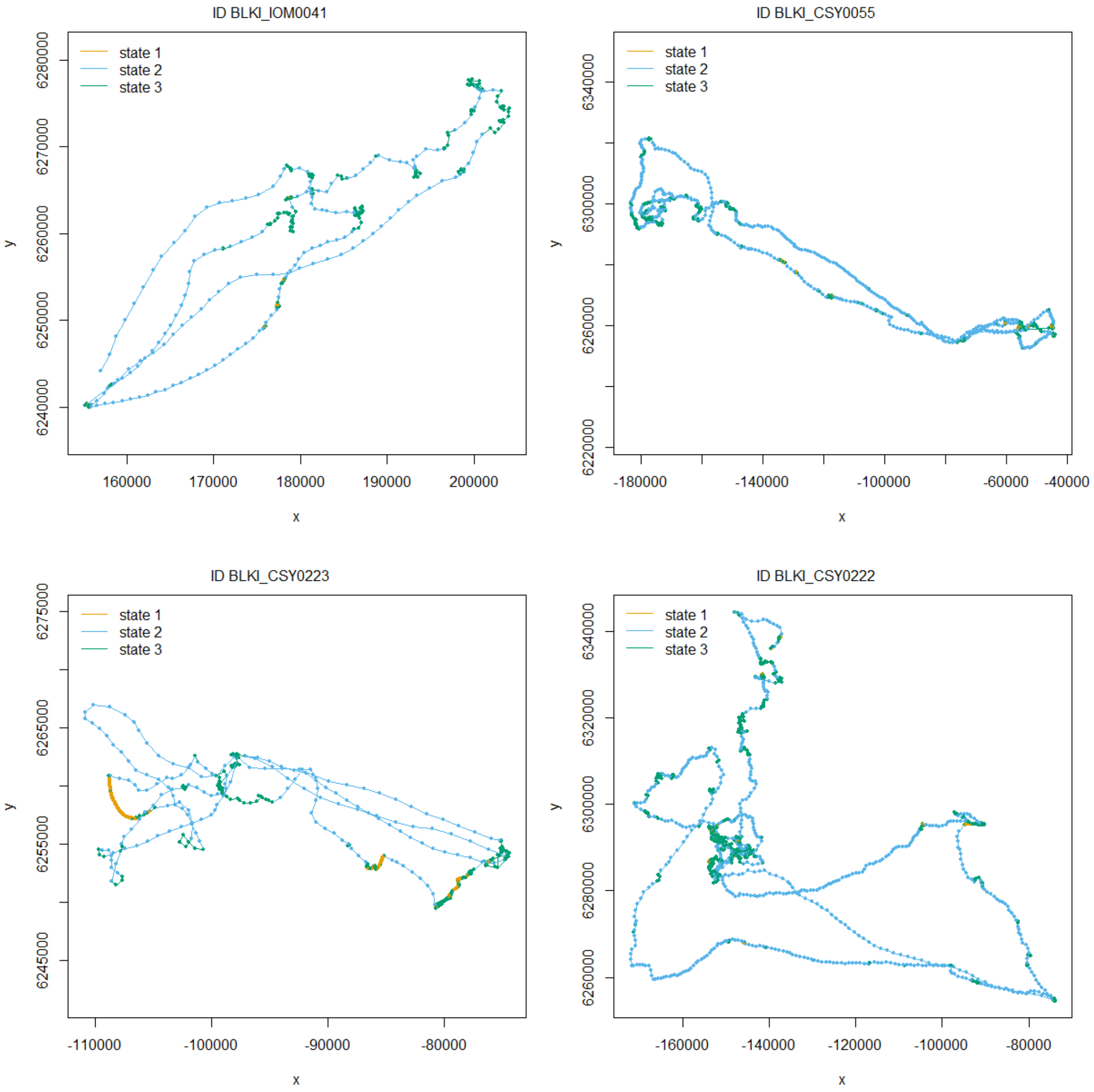
	state at time t+1		
state at time t	float	commute	forage
float	0.715	0.018	0.267
commute	0.018	0.891	0.091
forage	0.082	0.056	0.863

Figure A23 For Kittiwake, plot of transitions between states.

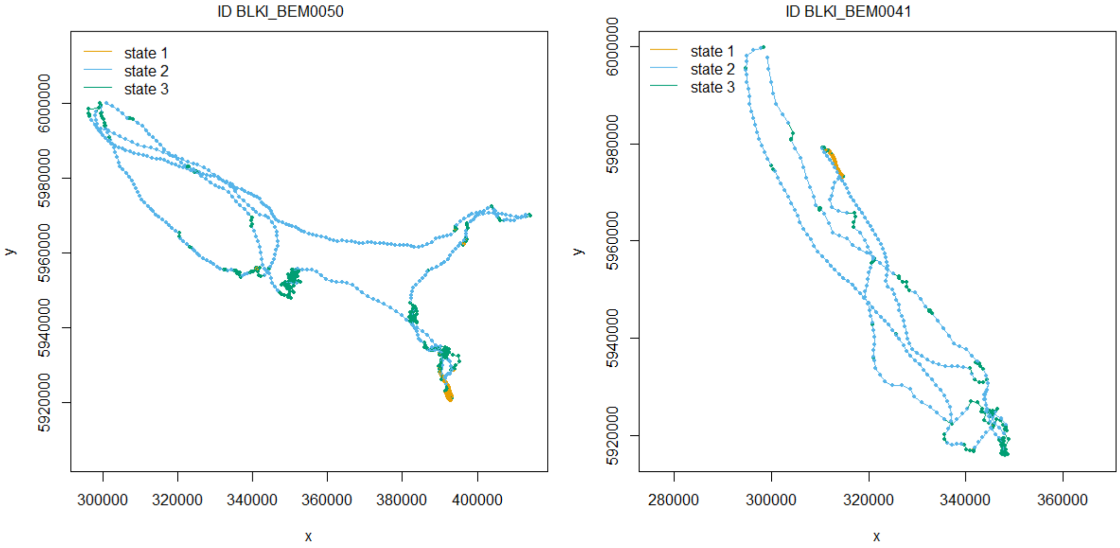
(a) Isle of May

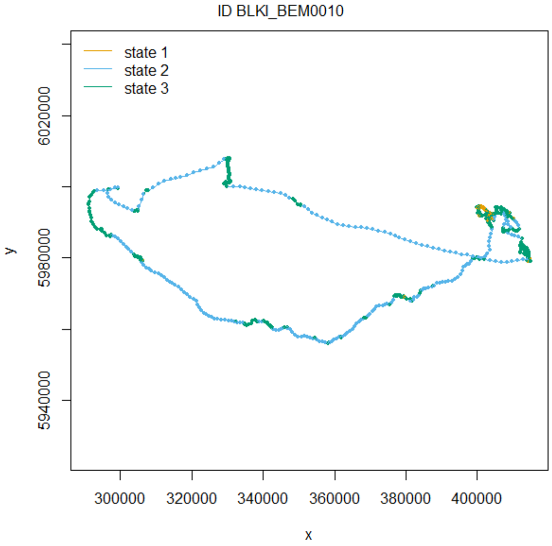


(b) Colonsay

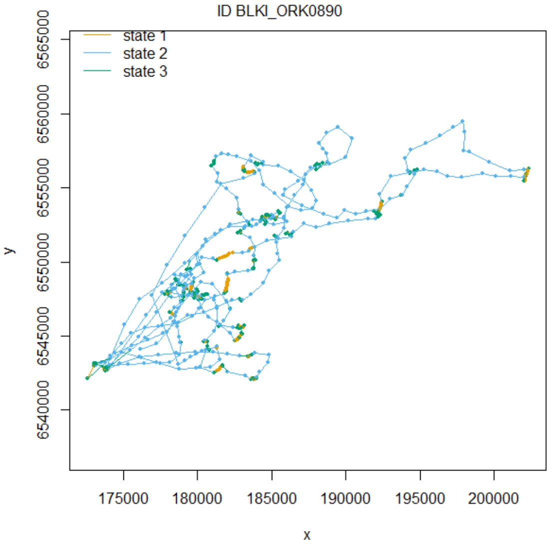


(c) Bempton





(d) Orkney



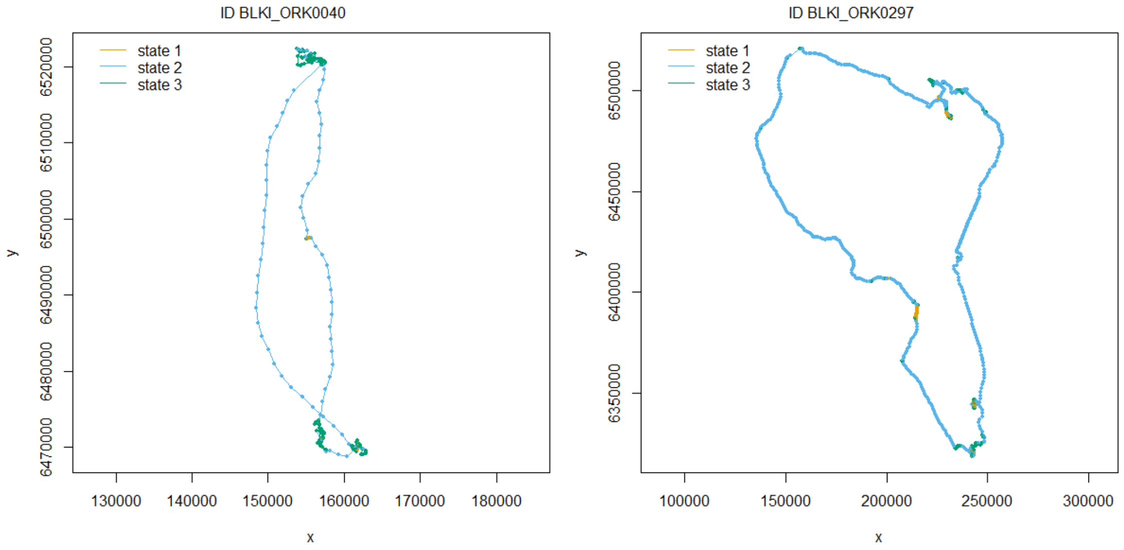
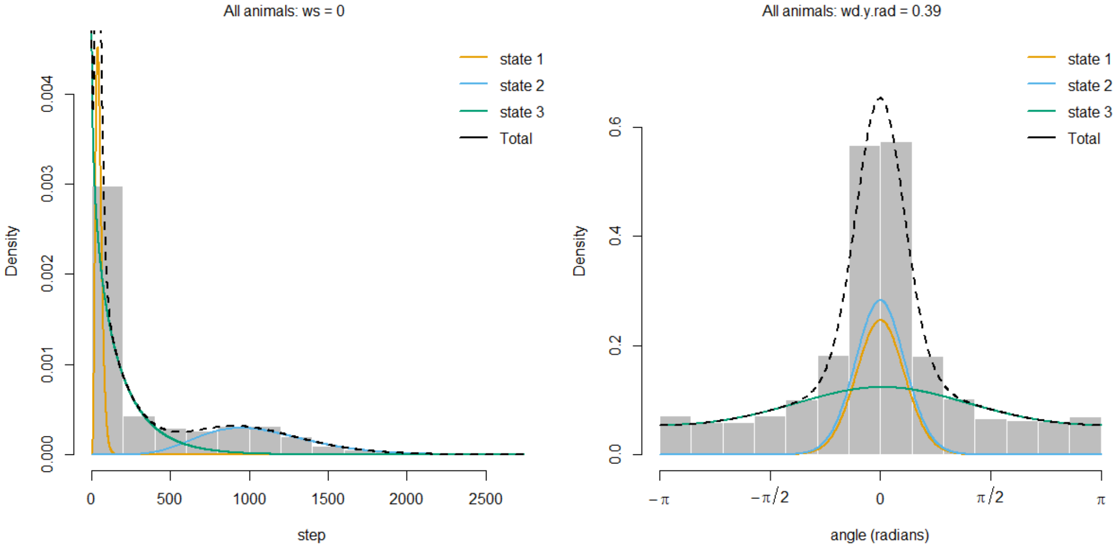
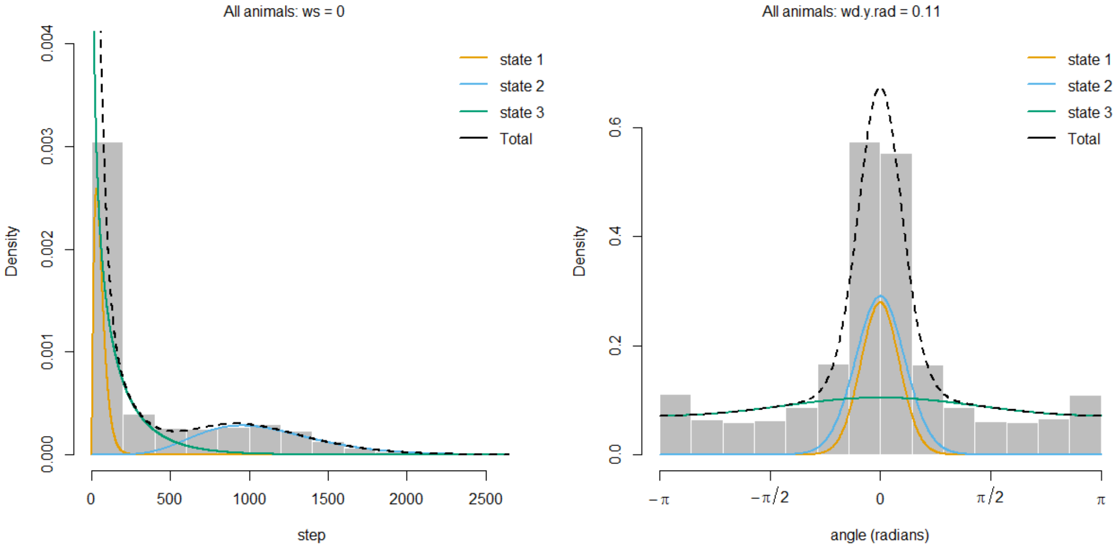


Figure A24 For Kittiwake, states 1, 2 and 3 (floating, commuting and foraging/searching) identified for example birds at each colony.

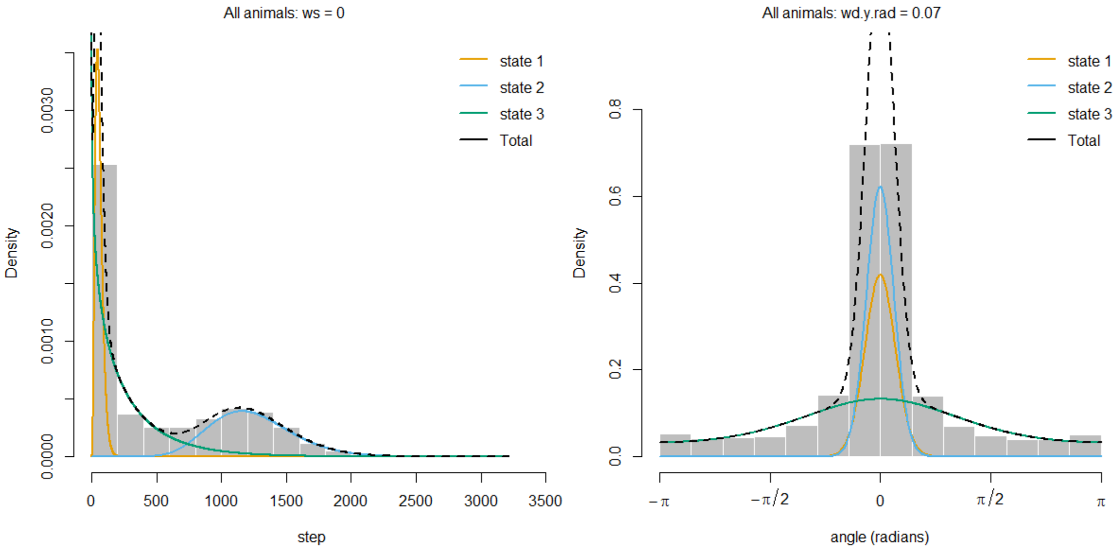
(a) Isle of May



(b) Colonsay



(c) Bempton



(d) Orkney

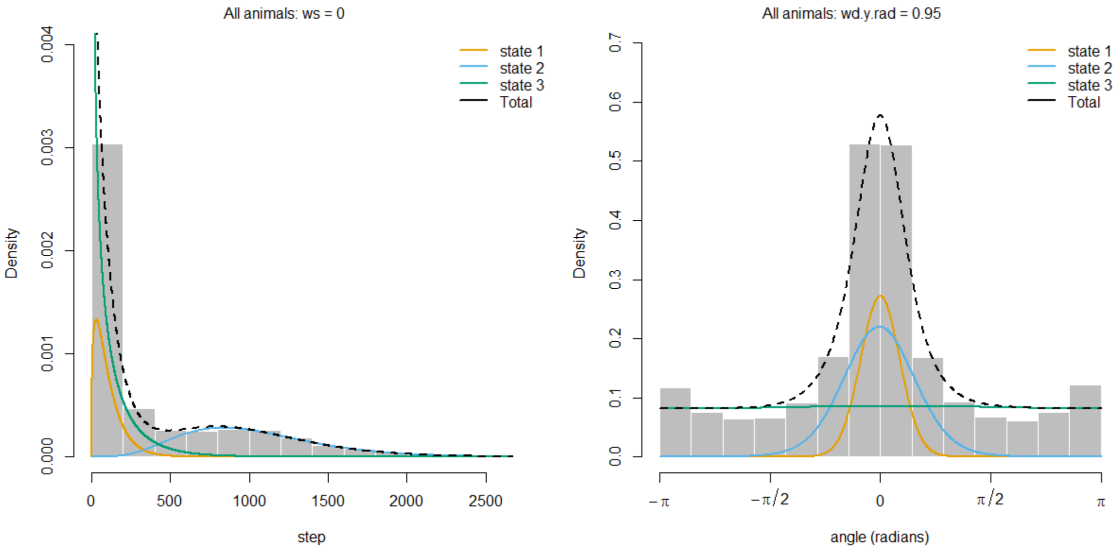
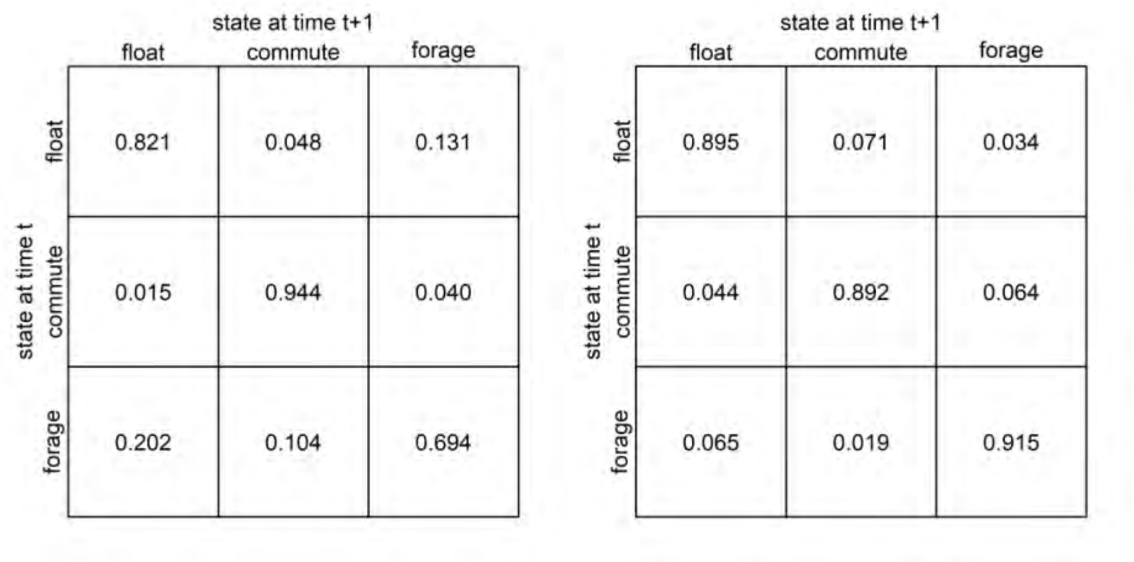


Figure A25 For Kittiwake, step length and turning angle distributions for states 1, 2 and 3 (floating, commuting and foraging/searching) specified at (a) Isle of May, Colonsay, (c) Bempton Cliffs and (d) Orkney.

7.3.4 Razorbill

(a) Colonsay

(b) Puffin Island



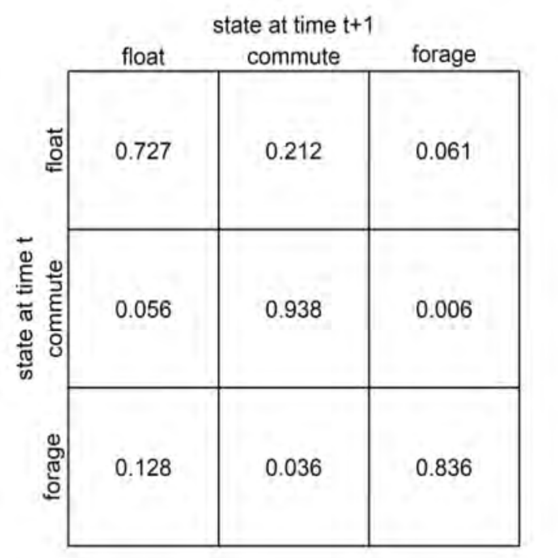
(a) Colonsay

state at time t	float	commute	forage
float	0.821	0.048	0.131
commute	0.015	0.944	0.040
forage	0.202	0.104	0.694

(b) Puffin Island

state at time t	float	commute	forage
float	0.895	0.071	0.034
commute	0.044	0.892	0.064
forage	0.065	0.019	0.915

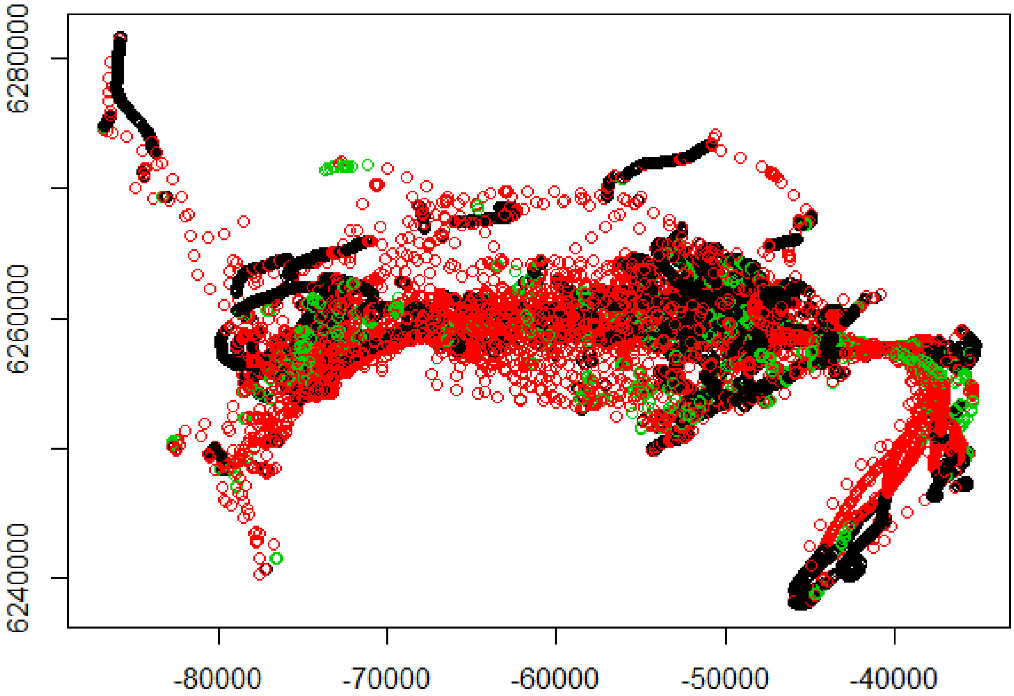
(c) Isle of May



state at time t	float	commute	forage
float	0.727	0.212	0.061
commute	0.056	0.938	0.006
forage	0.128	0.036	0.836

Figure A 26 For Razorbill, plot of transitions between states in relation to (a) Colonsay, (b) Puffin Island and (c) Isle of May.

(a) non-TDR HMM



(b) TDR HMM

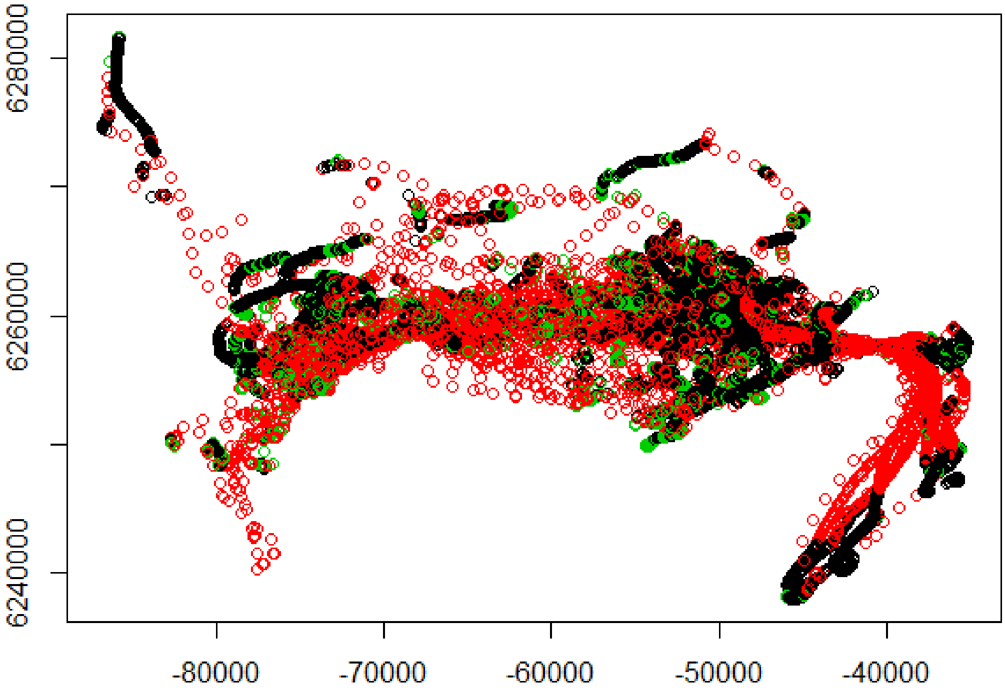
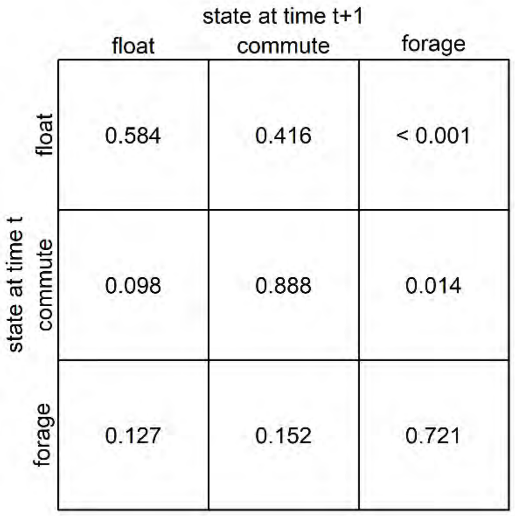


Figure A27 For Razorbills, comparison of non-TDR and TDR HMMs for Razorbills at Colonsay (black = state 1, floating, red = state 2, commuting, green = state 3, foraging/searching).

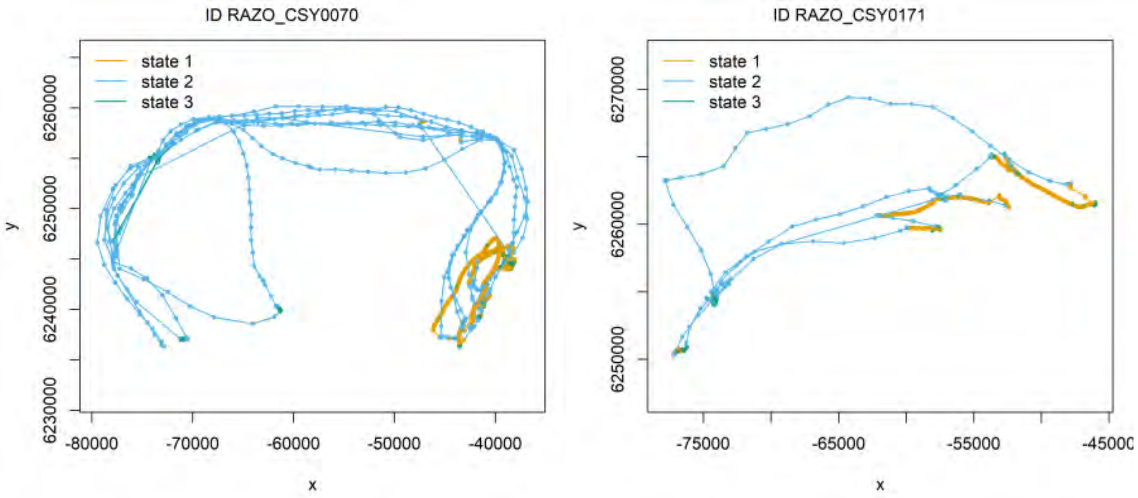
(a) Colonsay inc. diving



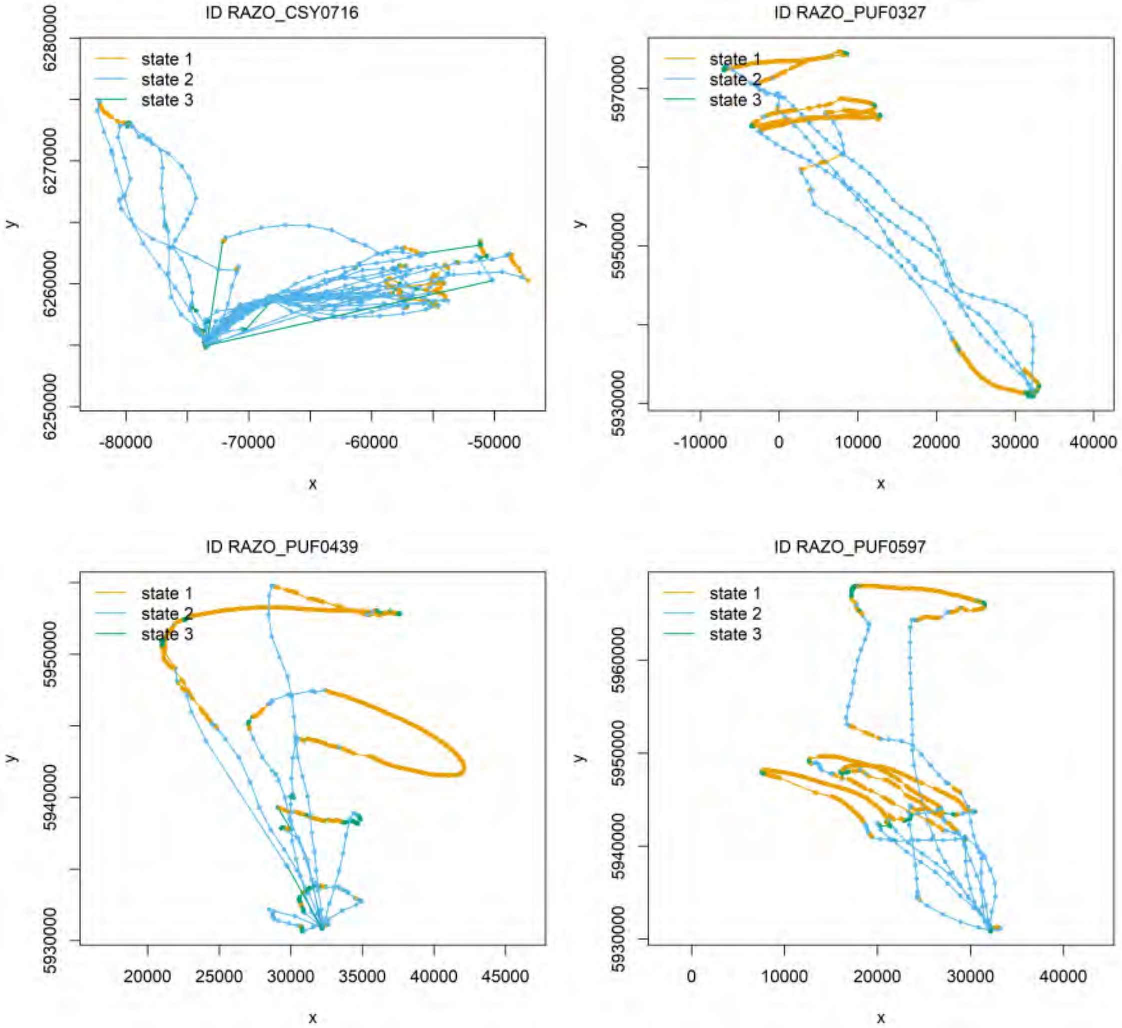
state at time t	state at time t+1 float	commute	forage
float	0.584	0.416	< 0.001
commute	0.098	0.888	0.014
forage	0.127	0.152	0.721

Figure A28 For Razorbill, plot of transitions between states of models incorporating TDR dive data.

(a) Colonsay



(b) Puffin Island



(c) Isle of May

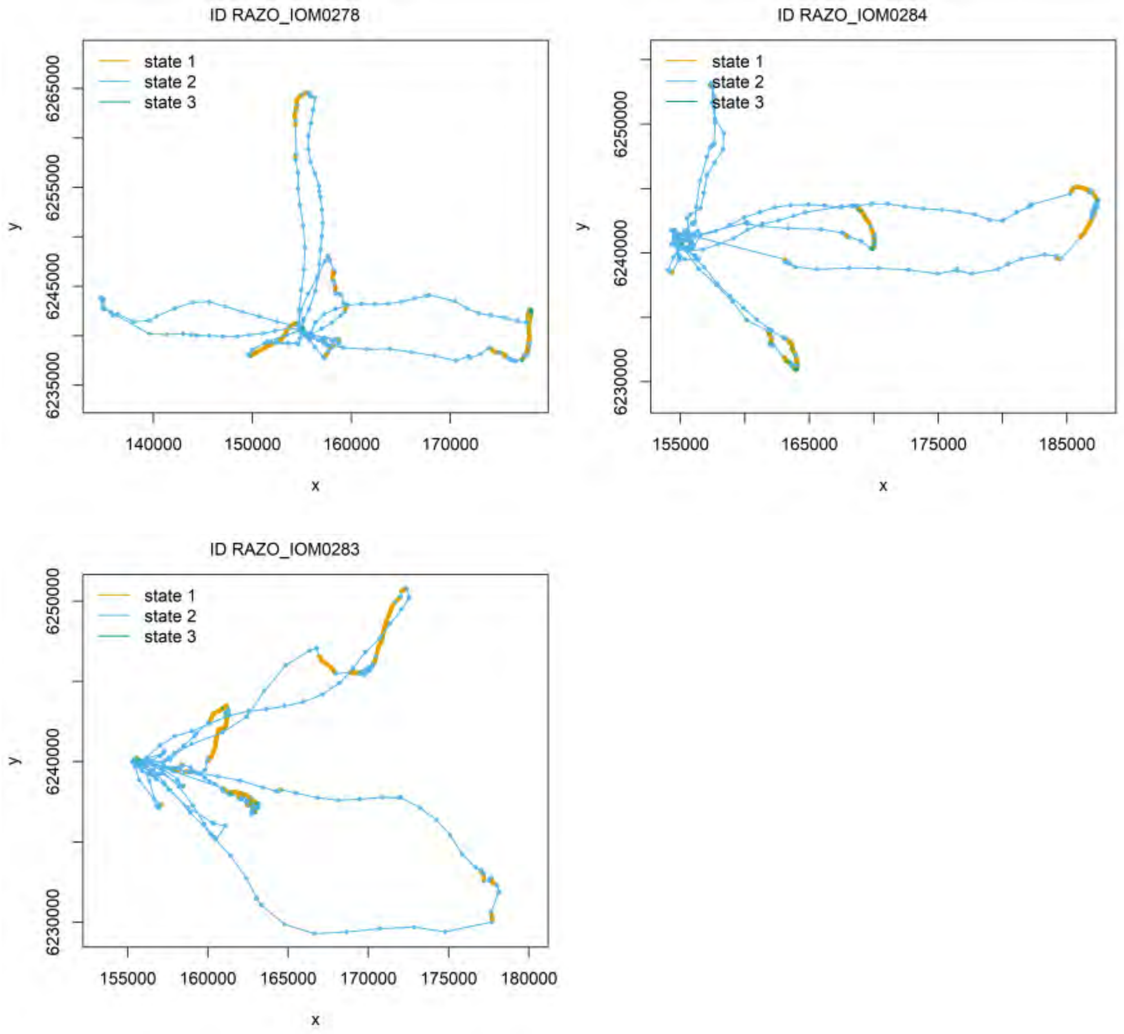


Figure A29 For Razorbill, states 1, 2 and 3 (floating, commuting and foraging/searching) identified for example birds at (a) Colonsay, (b) Puffin Island and (c) Isle of May.

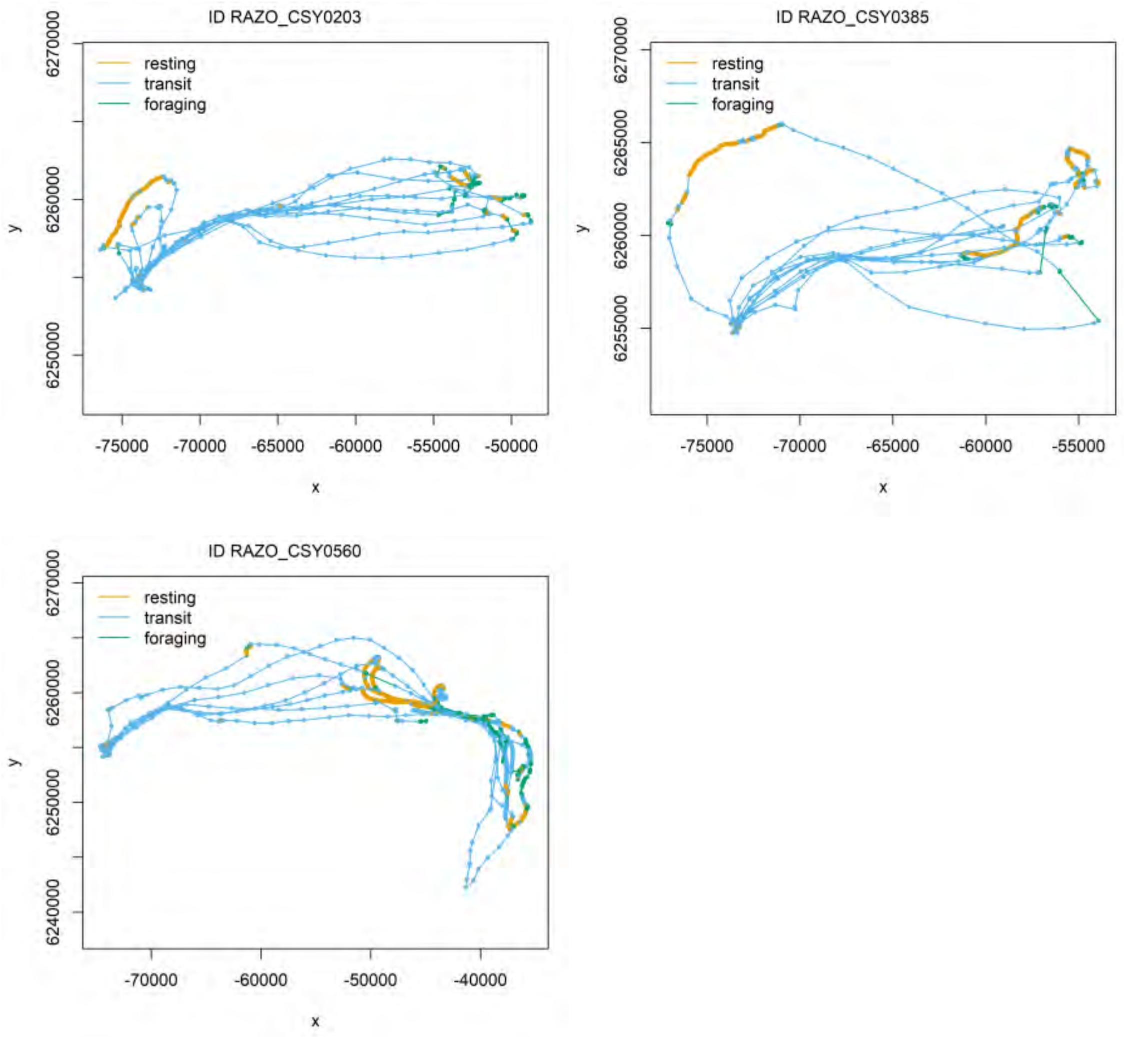
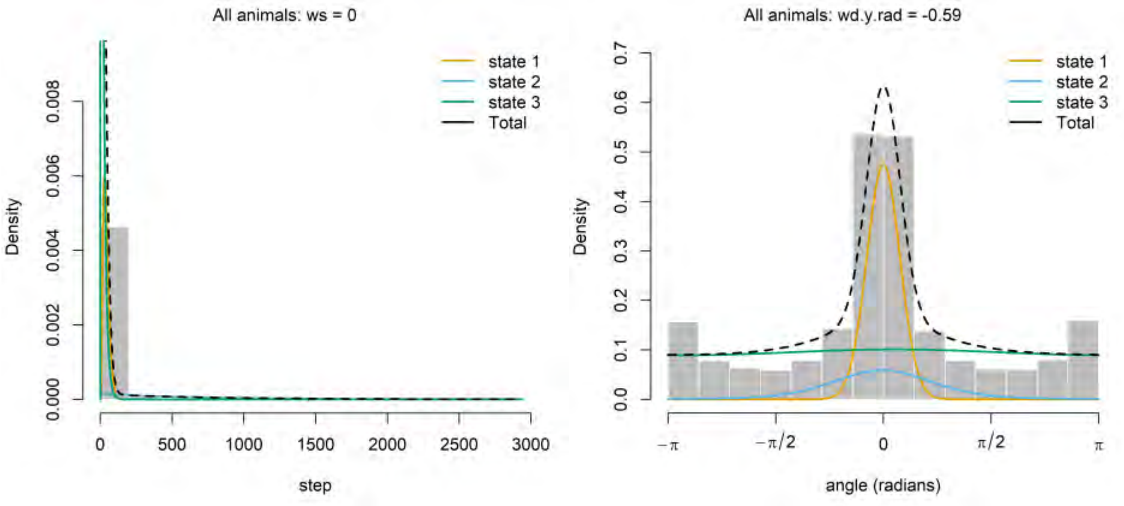
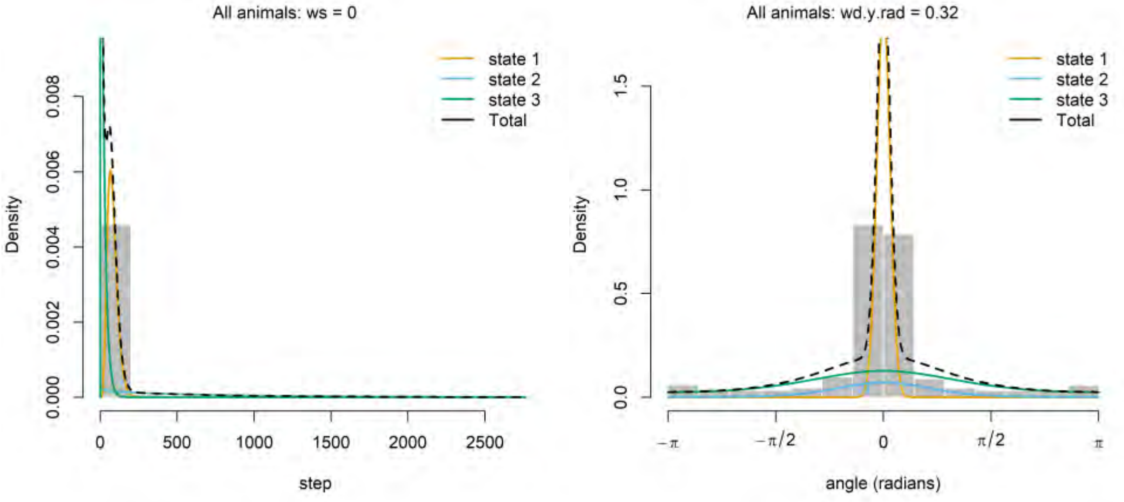


Figure A30 For Razorbill, states 1, 2 and 3 (floating, commuting and foraging/searching) modelled with TDR data for example birds at Colonsay.

(a) Colonsay



(b) Puffin Island



(c) Isle of May

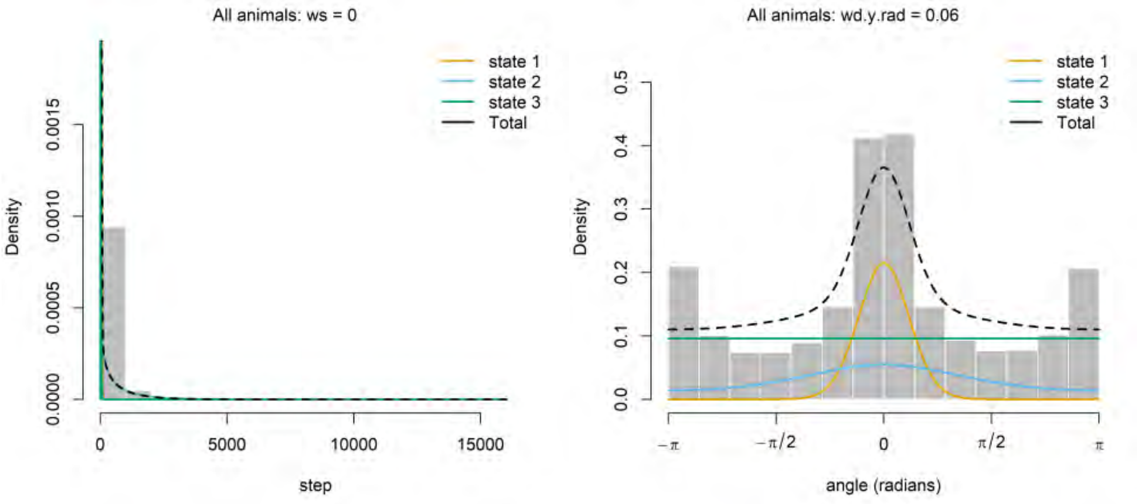


Figure A31 For Razorbill, step length and turning angle distributions for states 1, 2 and 3 (floating, commuting and foraging/searching) specified at (a) Colonsay, (b) Puffin Island and (c) Isle of May.

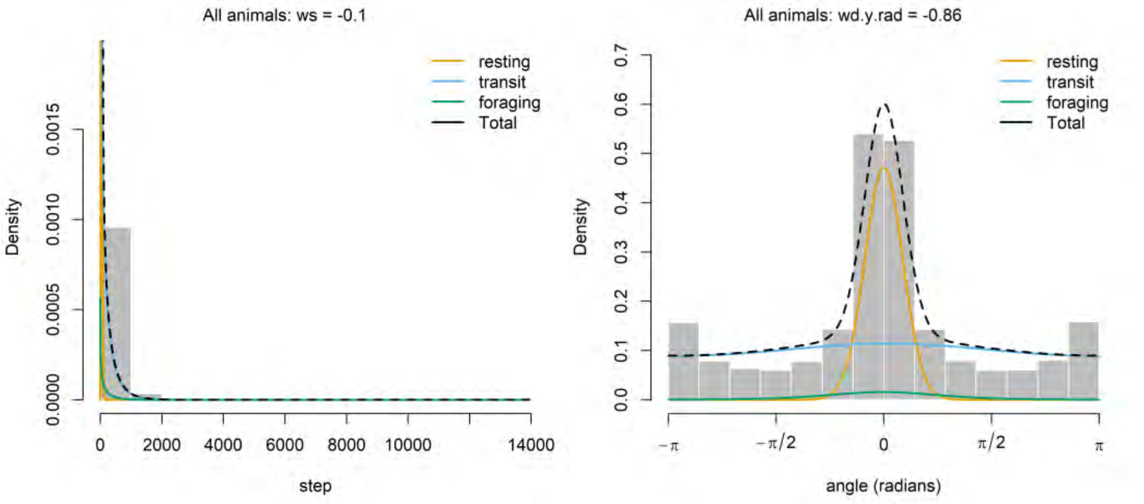


Figure A32 For Razorbills, step length and turning angle distributions for states 1, 2 and 3 (floating, commuting and foraging/searching) modelled with TDR dive data at Colonsay.

7.3.5 Common Guillemot

(a) Colonsay

state at time t \ state at time t+1	float	commute	forage
float	0.897	0.040	0.063
commute	0.088	0.870	0.043
forage	0.099	0.029	0.872

(b) Puffin Island

state at time t \ state at time t+1	float	commute	forage
float	0.947	0.042	0.010
commute	0.139	0.853	0.008
forage	0.047	0.019	0.934

(c) Fowlsheugh

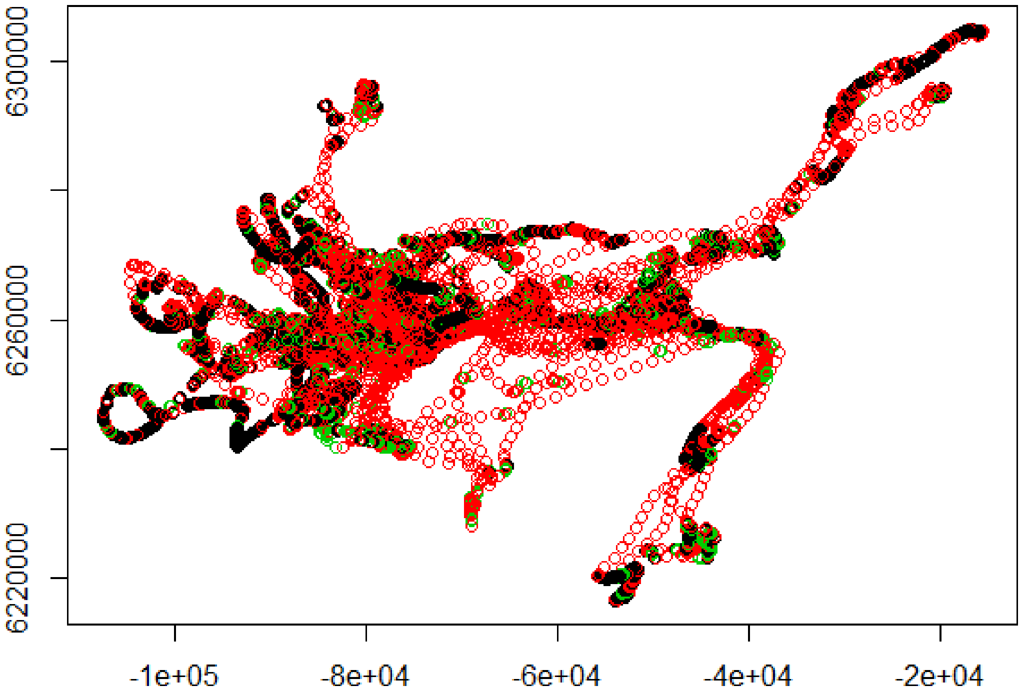
state at time t \ state at time t+1	float	commute	forage
float	0.939	0.048	0.014
commute	0.101	0.893	0.006
forage	0.047	0.006	0.948

(d) Isle of May

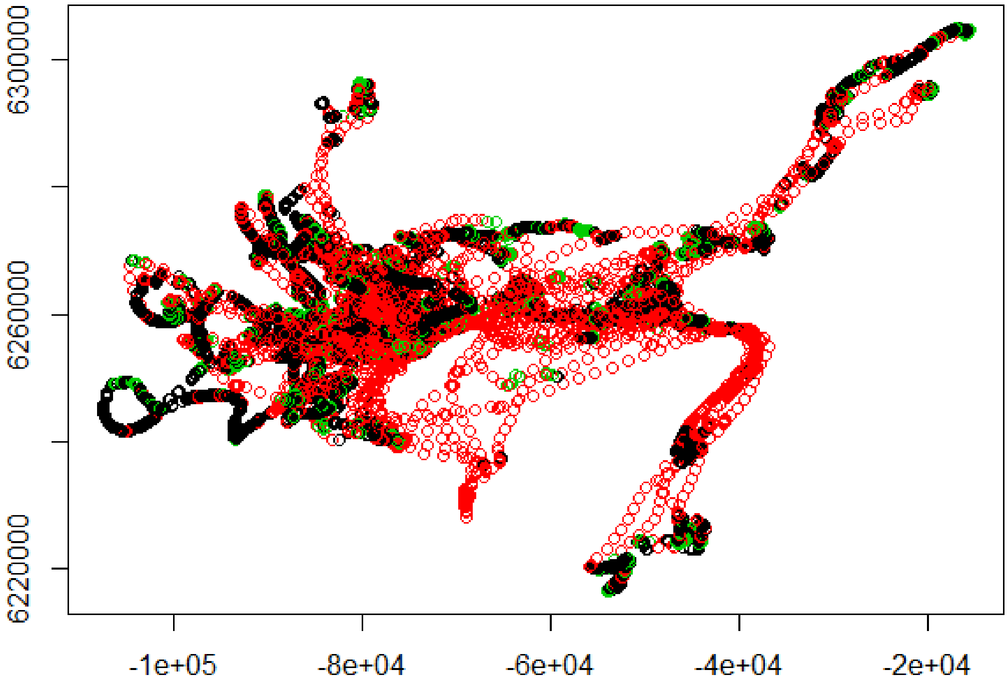
state at time t \ state at time t+1	float	commute	forage
float	0.855	0.122	0.022
commute	0.091	0.891	0.019
forage	0.101	0.063	0.835

Figure A33 For Guillemot, plot of transitions between states.

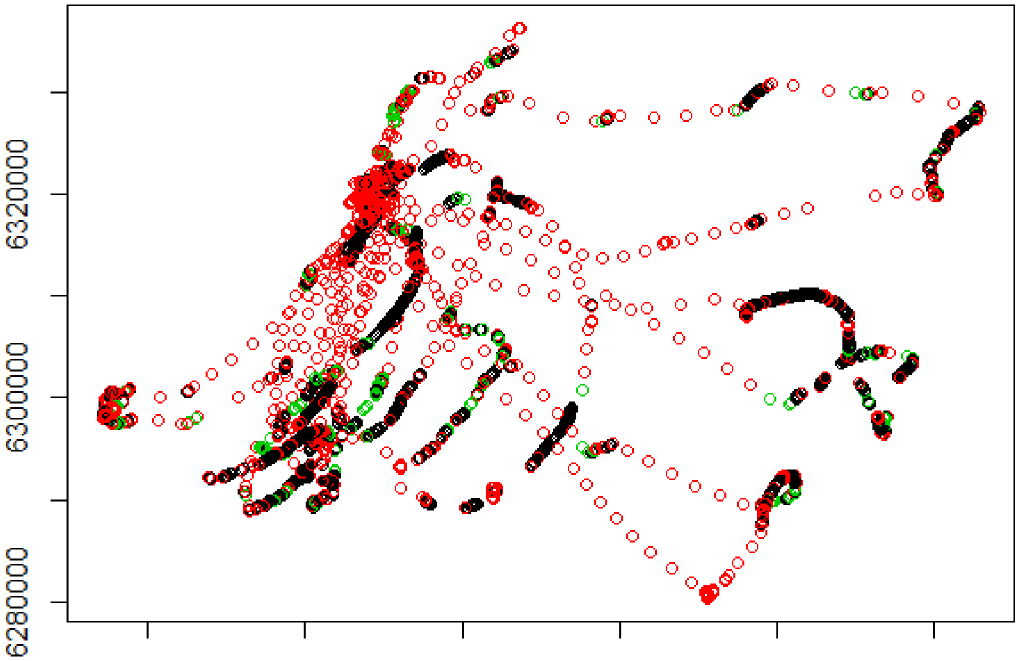
(a) Colonsay non-TDR HMM



(b) Colonsay TDR HMM



(c) Fowlsheugh non-TDR HMM



(d) Fowlsheugh TDR HMM

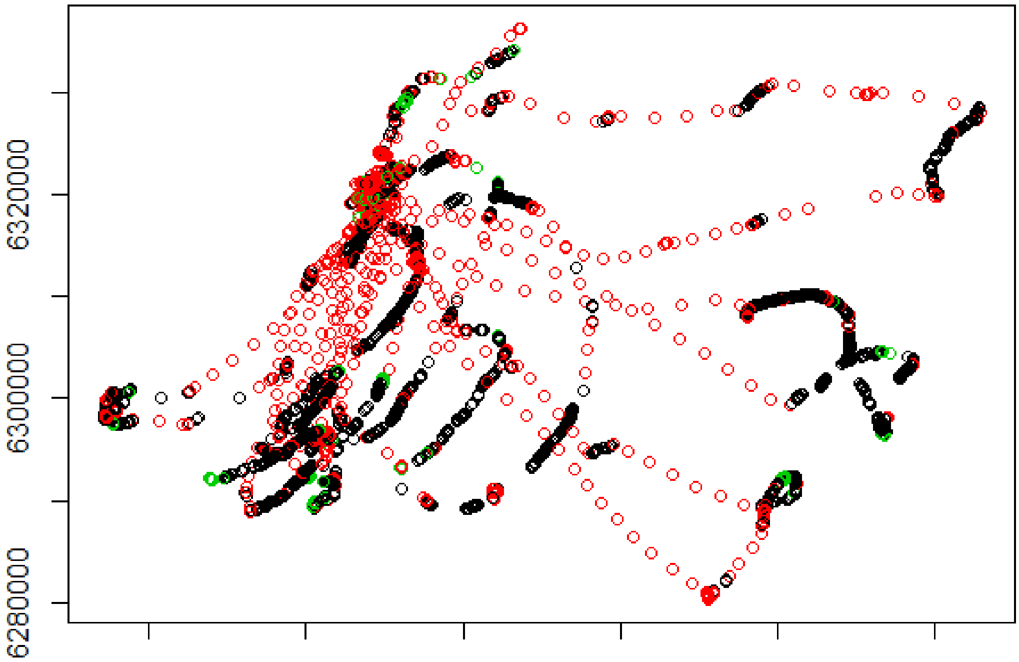
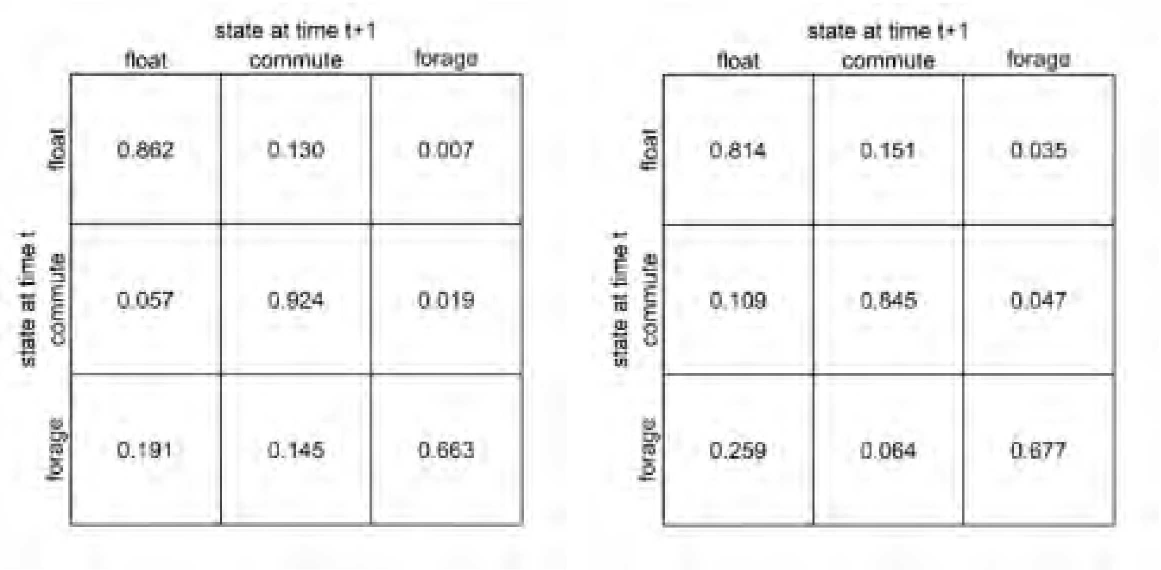


Figure A34 For Guillemot, comparison of non-TDR and TDR HMMs at Colonsay (black = State 1, floating, red = State 2, commuting, green = State 3, foraging/searching).



(a) Colonsay inc. diving

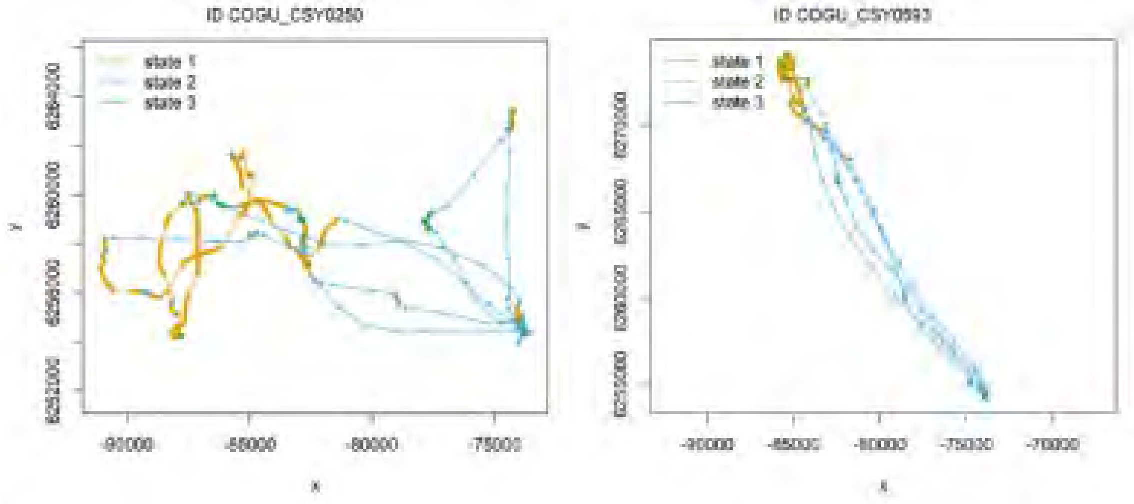
	state at time t+1		
state at time t	float	commute	forage
float	0.862	0.130	0.007
commute	0.057	0.924	0.019
forage	0.191	0.145	0.663

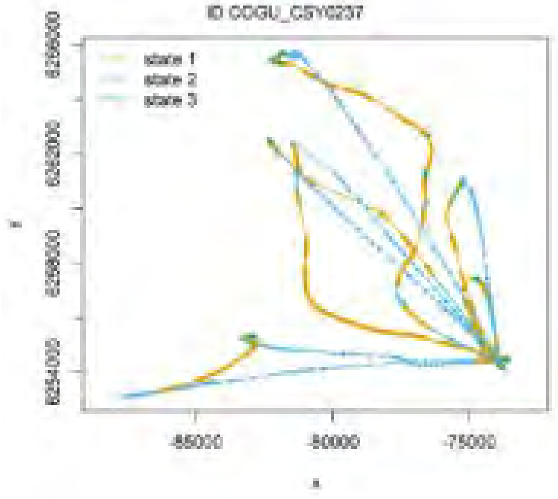
(b) Fowlsheugh inc. diving

	state at time t+1		
state at time t	float	commute	forage
float	0.814	0.151	0.035
commute	0.109	0.845	0.047
forage	0.259	0.064	0.677

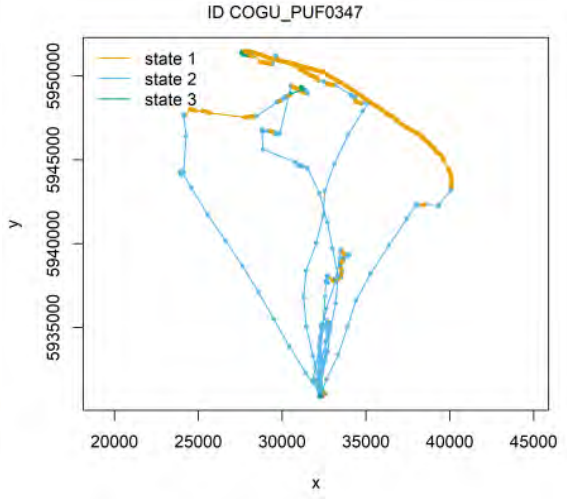
Figure A35 For Guillemot, plot of transitions between states of models incorporating TDR dive data.

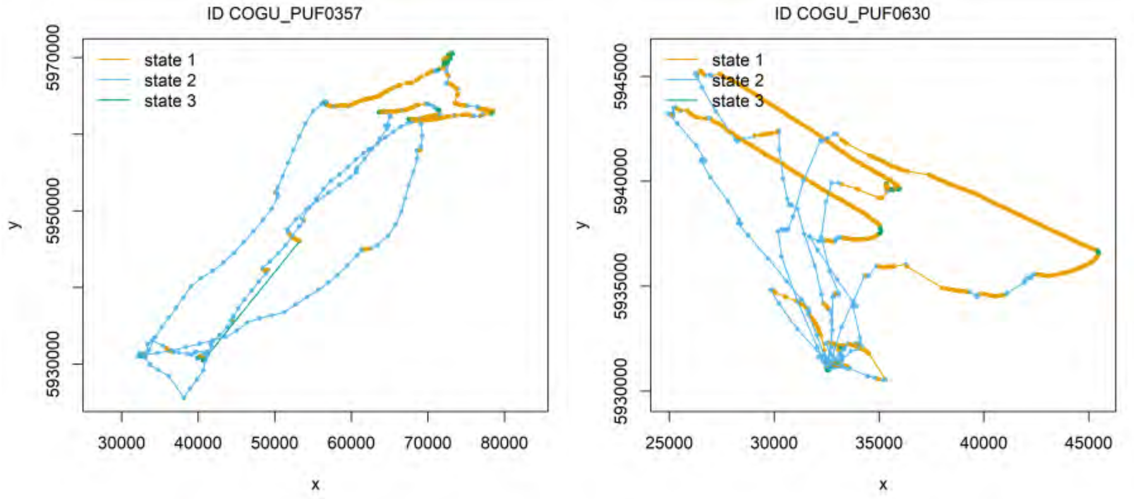
(a) Colonsay



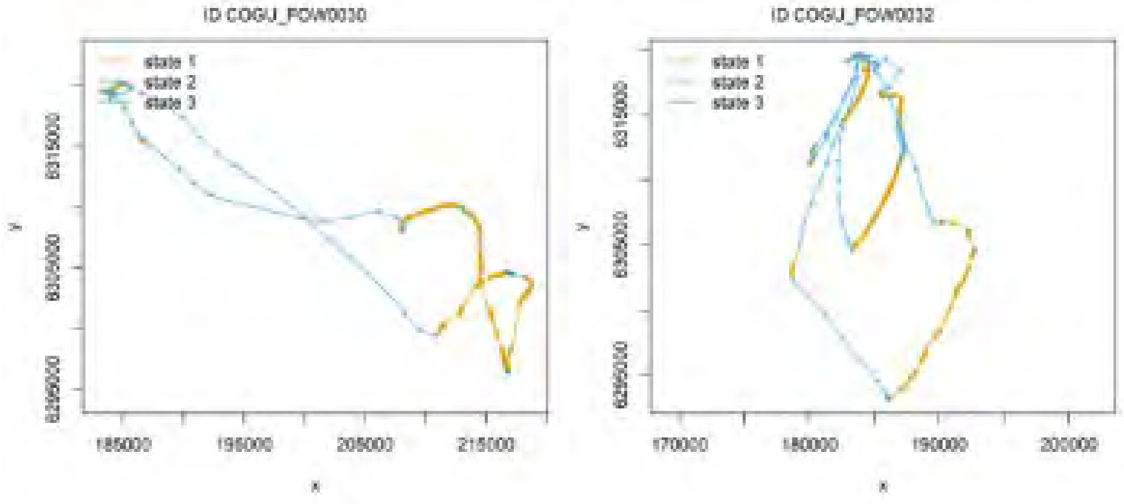


(b) Puffin Island





(c) Fowlsheugh



(d) Isle of May

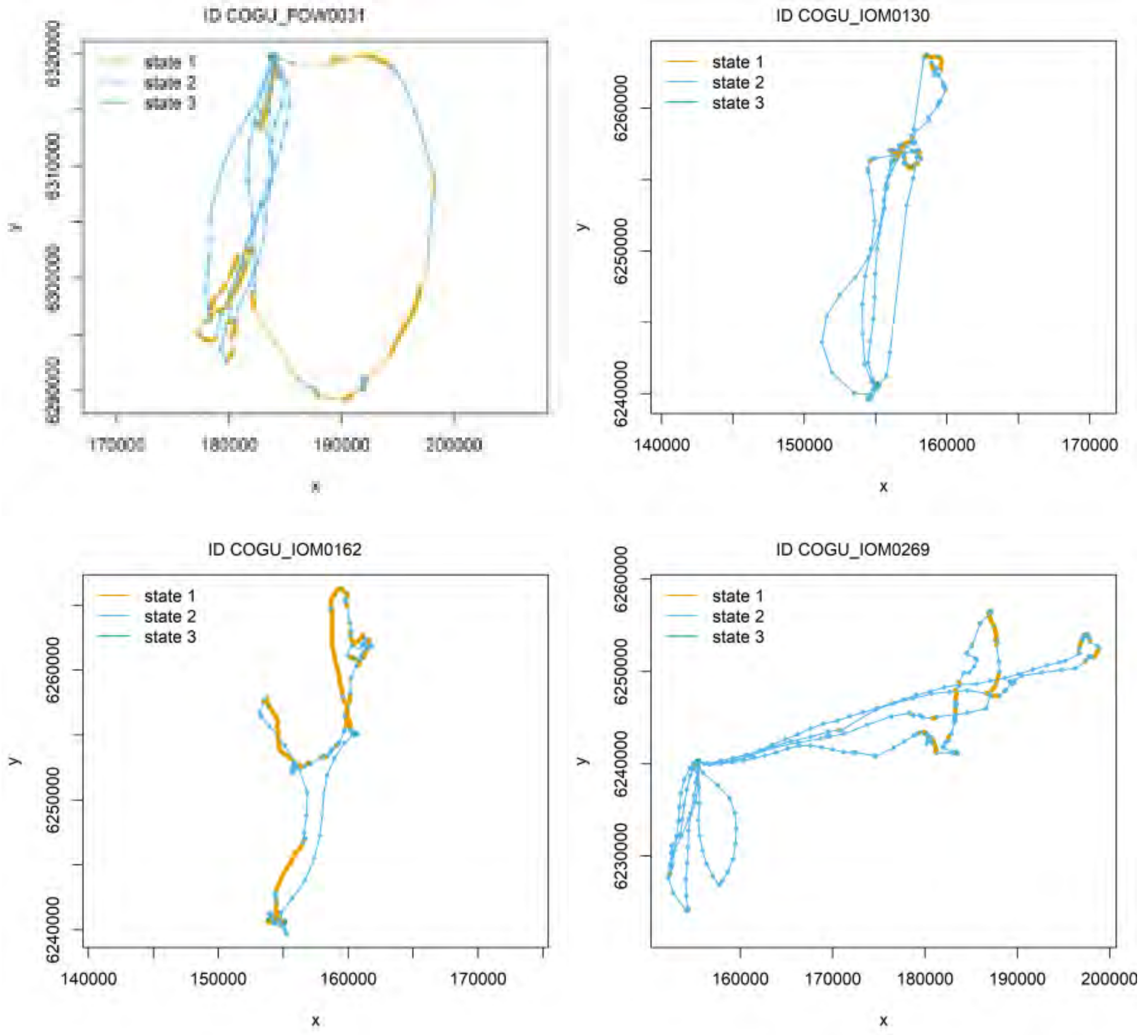
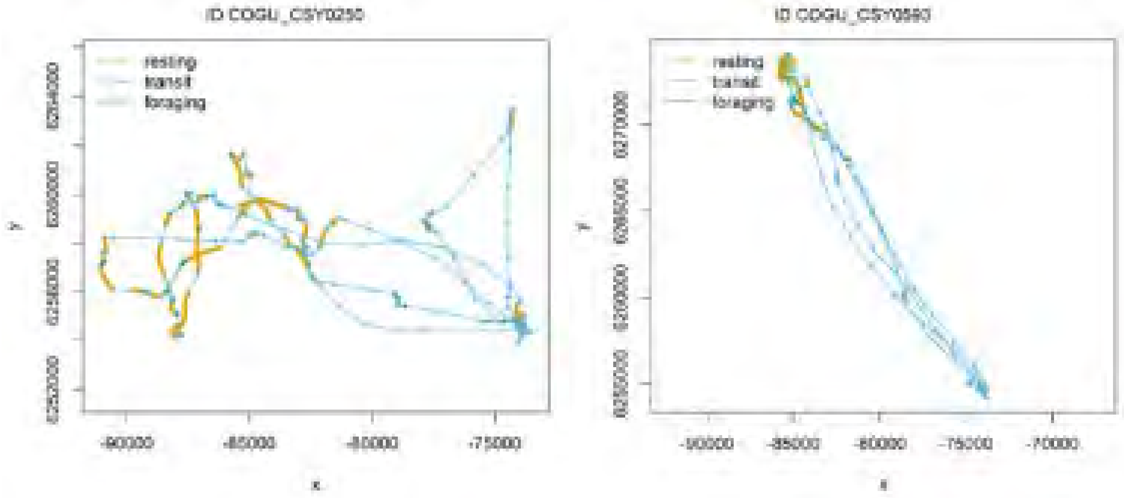


Figure A36 For Guillemot, states 1, 2 and 3 (floating, commuting and foraging/searching) identified for example birds at each colony.

(a) Colonsay inc. diving



(c) Fowlsheugh inc. diving

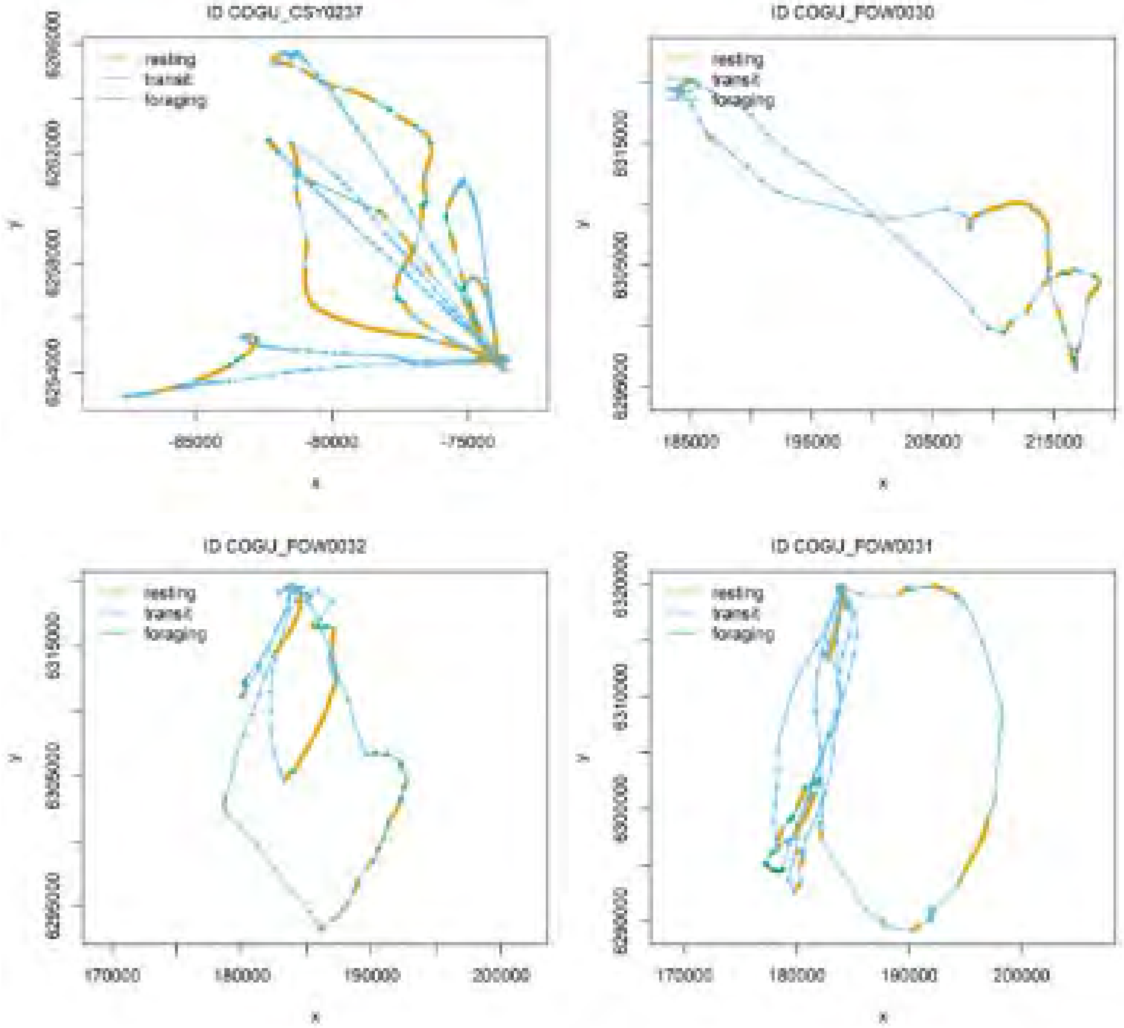
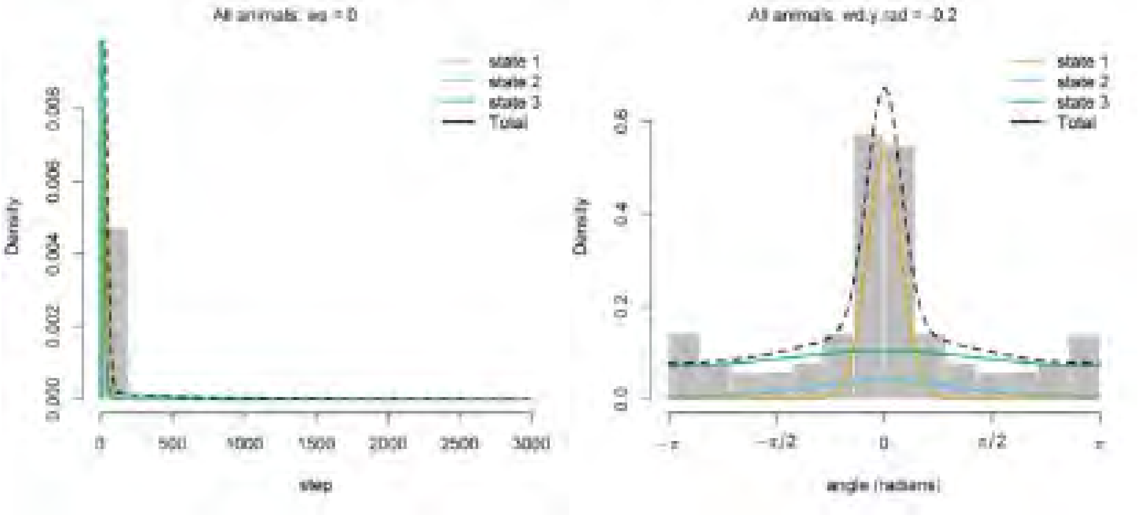
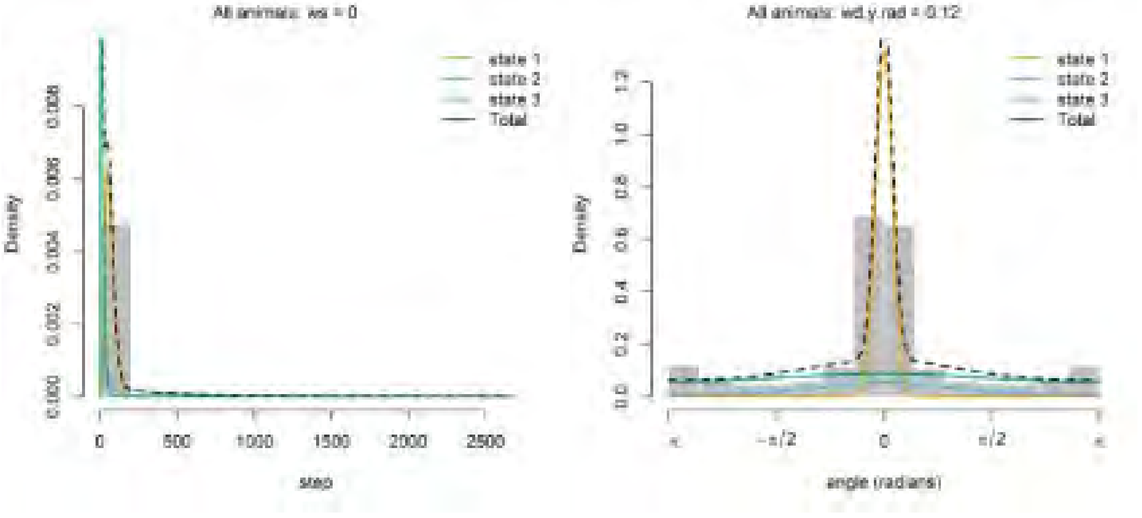


Figure A37 For Guillemots, states 1, 2 and 3 (floating, commuting and foraging/searching) modelled with TDR data for corresponding example birds at each colony.

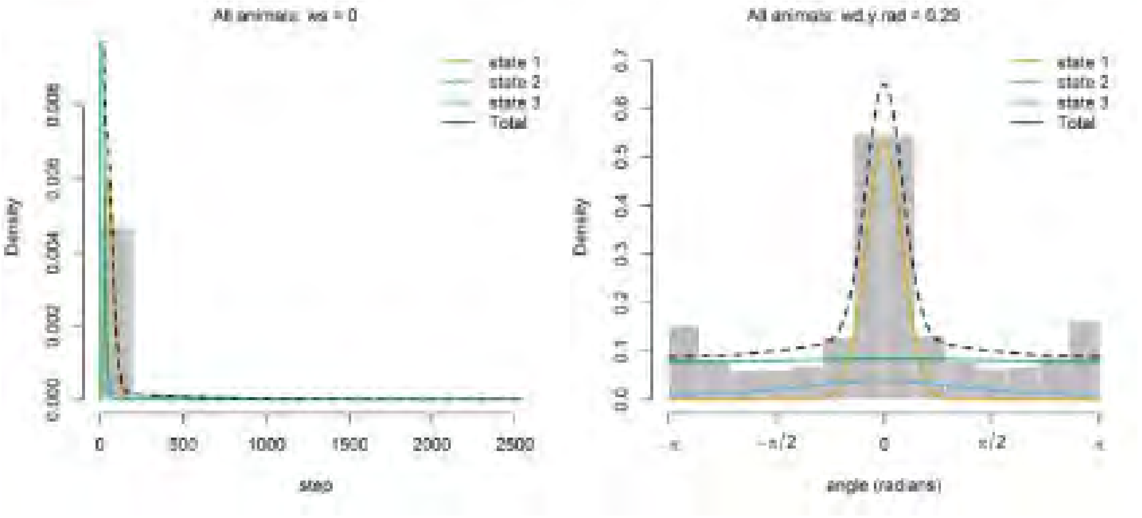
(a) Colonsay



(b) Puffin Island



(c) Fowlsheugh



(d) Isle of May

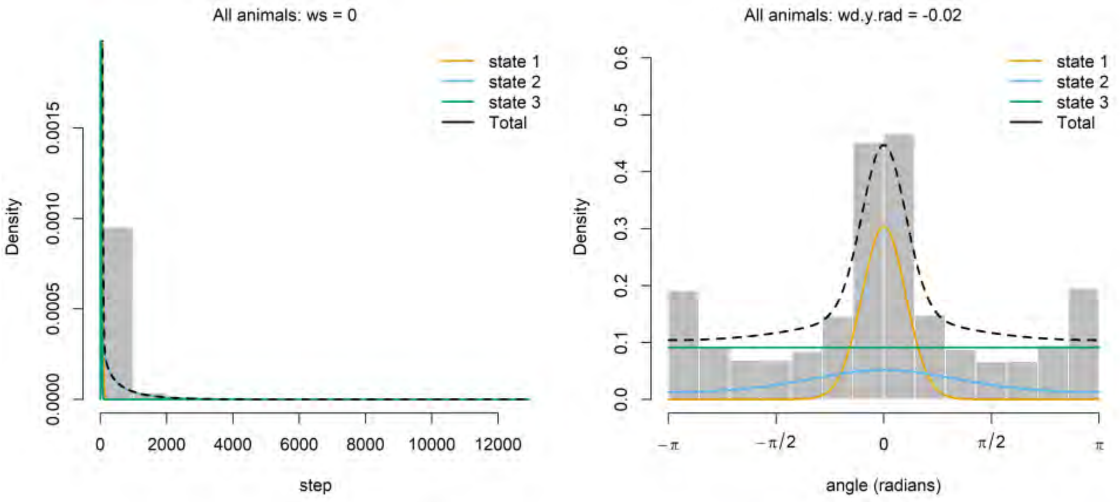
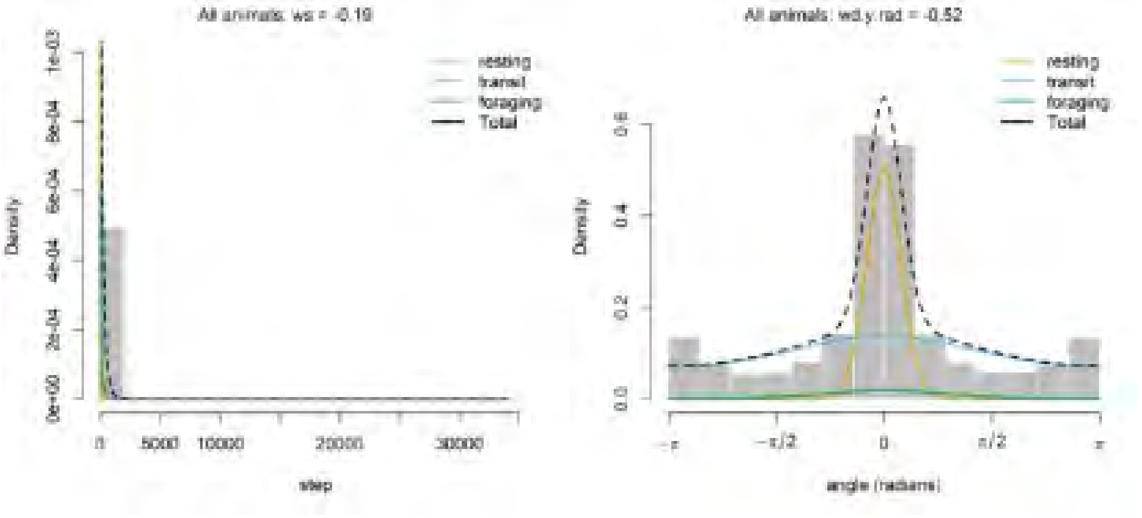


Figure A38 For Guillemot, step length and turning angle distributions for states 1, 2 and 3 (floating, commuting and foraging/searching) at (a) Colonsay (b) Puffin Island, (c) Fowlsheugh, and (d) Isle of May.

(a) Colonsay inc. diving



(b) Fowlsheugh inc. diving

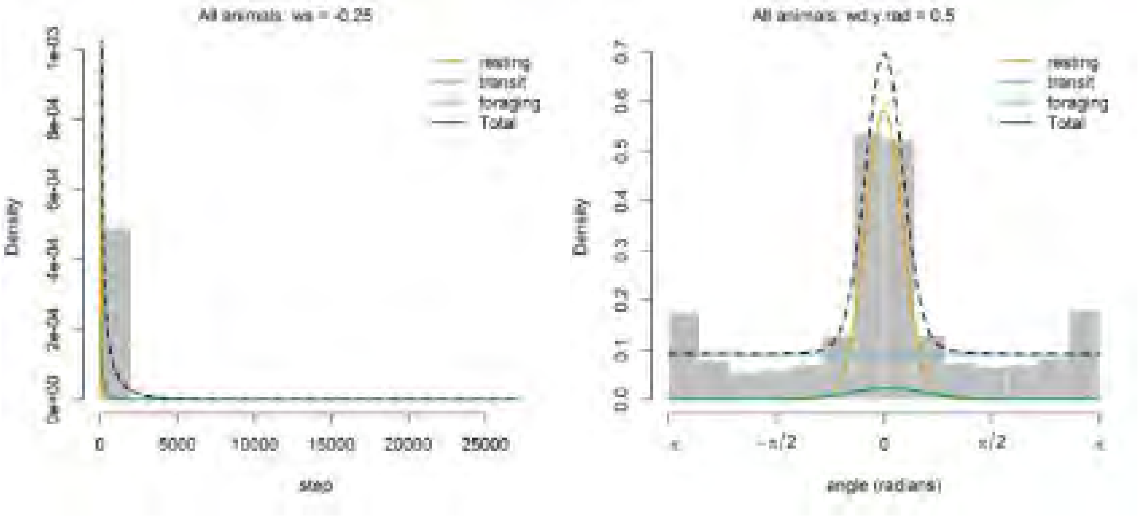


Figure A39 For Guillemot, step length and turning angle distributions for the states 1, 2 and 3 (floating, commuting and foraging/searching) specified modelled with TDR dive data at (a) Colonsay and (b) Fowlsheugh.

7.4 Appendix AD. Transition effects between states in relation to covariates

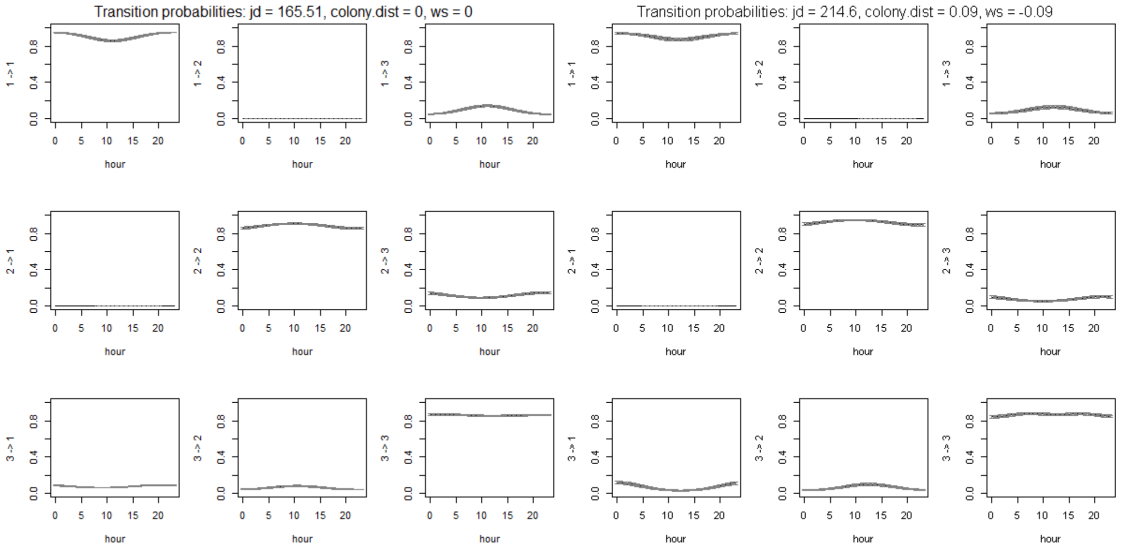
Plots are generated for specific covariates at the means of other covariates in the model. The range of wind speeds, as with other covariates, within plots are presented as standardised values. The following corresponding range of real wind speed values is given as follows to aid interpretation:

- Gannet: Alderney, 0.03 – 14.45 (6.26 ± 2.83) m/s; Bass Rock, 0.03 – 18.02 (5.59 ± 2.76) m/s;
- Lesser Black-backed Gulls (offshore): Walney, 0.07 m/s – 13.34 (4.69 ± 2.49) m/s; Skokholm, 0.04 m/s – 16.67 (5.31 ± 2.22) m/s; Orford Ness 0.04 m/s – 12.46 (4.99 ± 2.56) m/s;,
- Kittiwake: Isle of May, 0.18 m/s – 13.19 (4.60 ± 2.14) m/s; Colonsay, 0.07 – 13.94 (5.24 ± 2.55) m/s; Bempton Cliffs, 0.03 – 12.26 (5.15 ± 2.32) m/s; Orkney, 0.05 – 12.63 (5.58 ± 2.50) m/s;
- Razorbill: Colonsay, 0.03 – 14.26 m/s; Puffin Island, 0.05 – 14.81 m/s (4.77 ± 2.77); Isle of May, 0.17 – 10.29 (4.53 ± 2.51) m/s;
- Guillemot: Puffin Island, 0.25 m/s – 9.36 (3.86 ± 2.11) m/s, Isle of May, 0.20 – 11.8 (4.96 ± 2.08) m/s, Colonsay, 0.06 m/s – 11.26 (4.68 ± 2.42) m/s; Fowlseugh 0.60 m/s – 12.91 (5.30 ± 2.29) m/s.

7.4.1 Northern Gannet

(a) Alderney all years

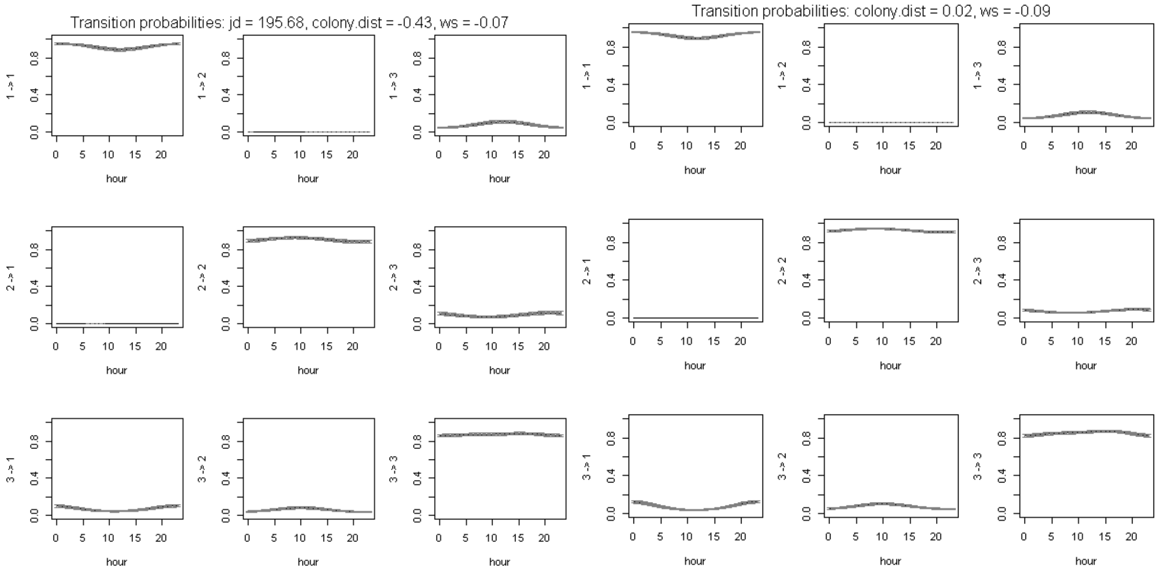
(b) Bass Rock 2010


Transition probabilities: jd = 165.51, colony.dist = 0, ws = 0

Transition probabilities: jd = 214.6, colony.dist = 0.09, ws = -0.09

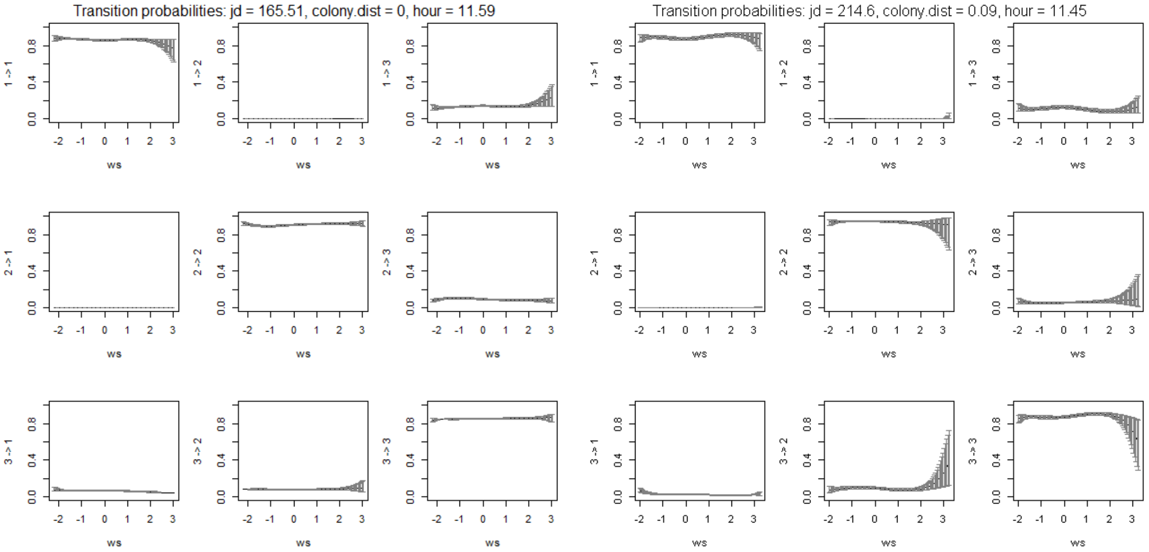
(c) Bass Rock 2011

(d) Bass Rock 2012


Transition probabilities: jd = 195.68, colony.dist = -0.43, ws = -0.07

Transition probabilities: colony.dist = 0.02, ws = -0.09

Figure A40 For Gannet, transition probabilities and stationary state probabilities for the variable of cosinor(hour of day).

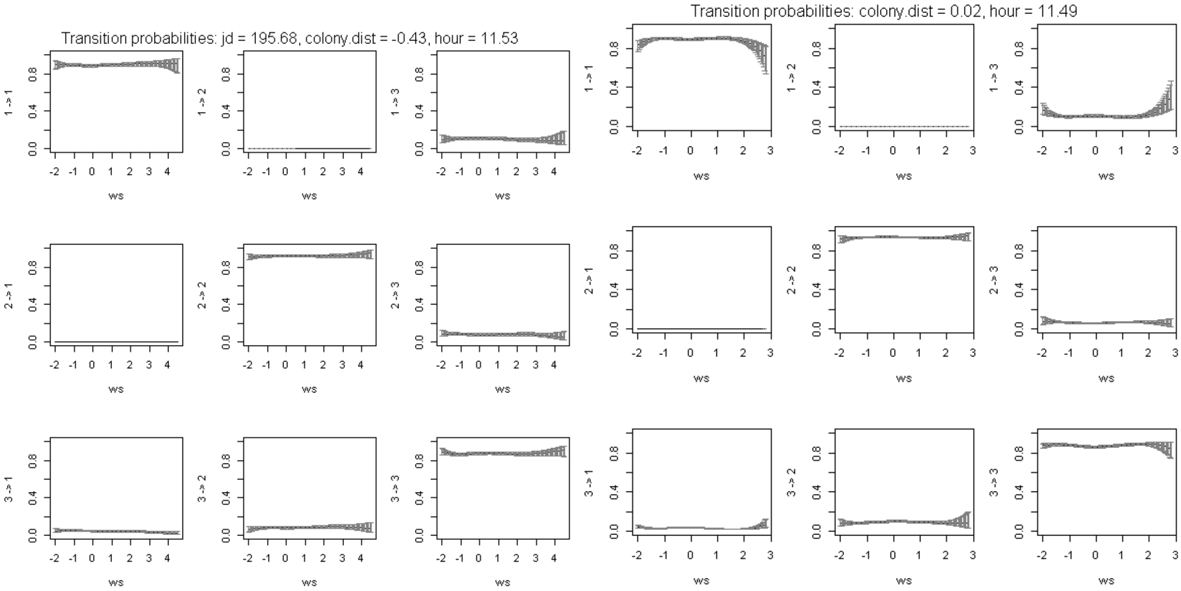


(a) Alderney

Transition probabilities: jd = 165.51, colony.dist = 0, hour = 11.59

(b) Bass Rock 2010

Transition probabilities: jd = 214.6, colony.dist = 0.09, hour = 11.45



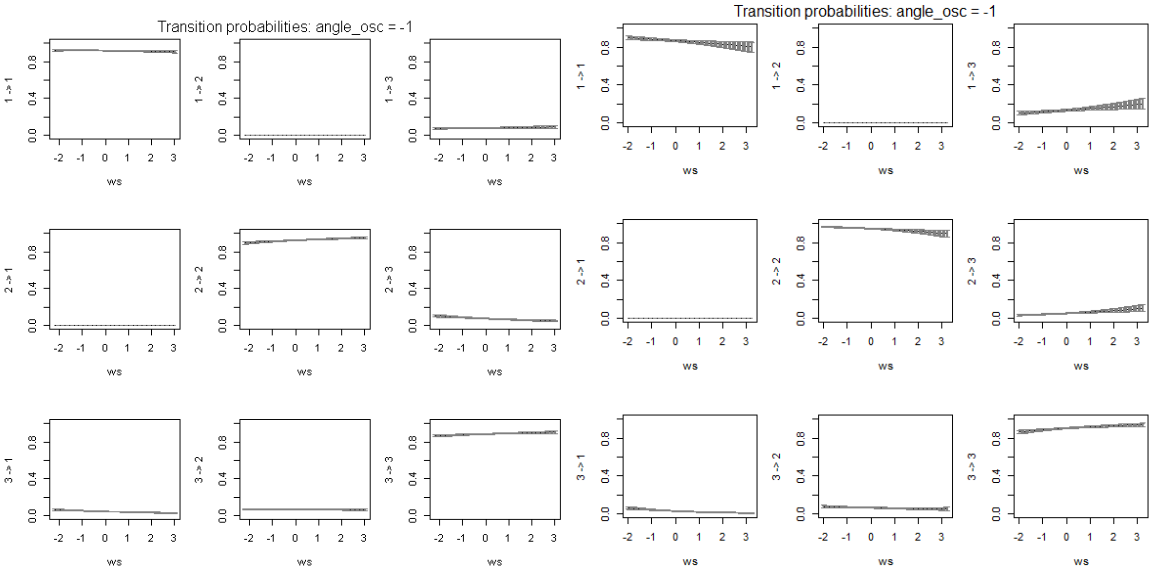
(c) Bass Rock 2011

Transition probabilities: jd = 195.68, colony.dist = -0.43, hour = 11.53

(d) Bass Rock 2012

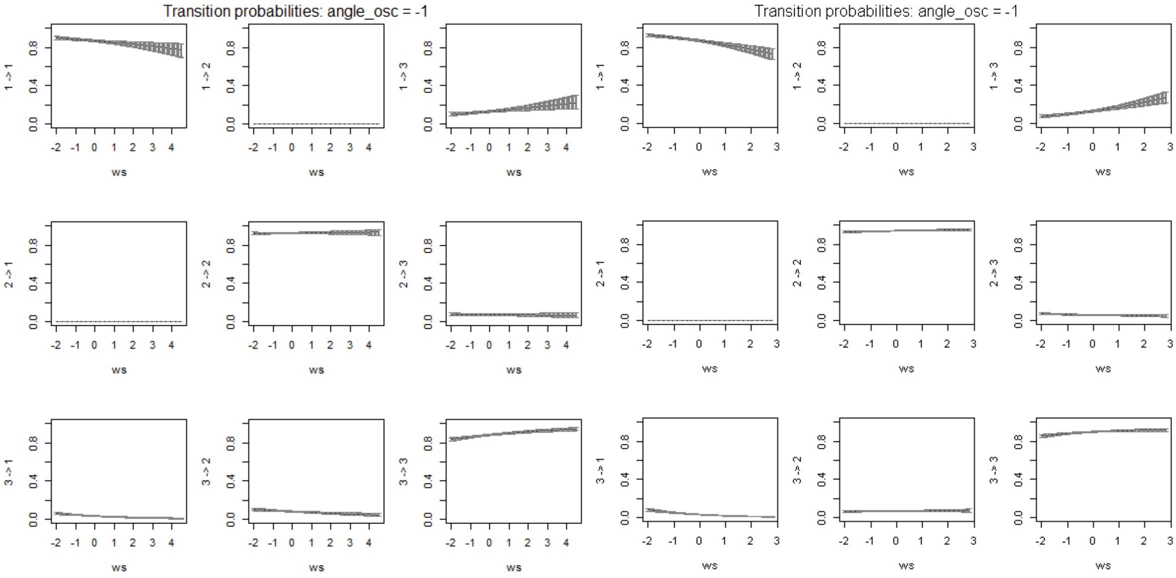
Transition probabilities: colony.dist = 0.02, hour = 11.49

Figure A41 For Gannet, transition probabilities for the variable of bSpline(wind speed), fitted as a standardised variable.



(a) Alderney all years

(b) Bass Rock 2010



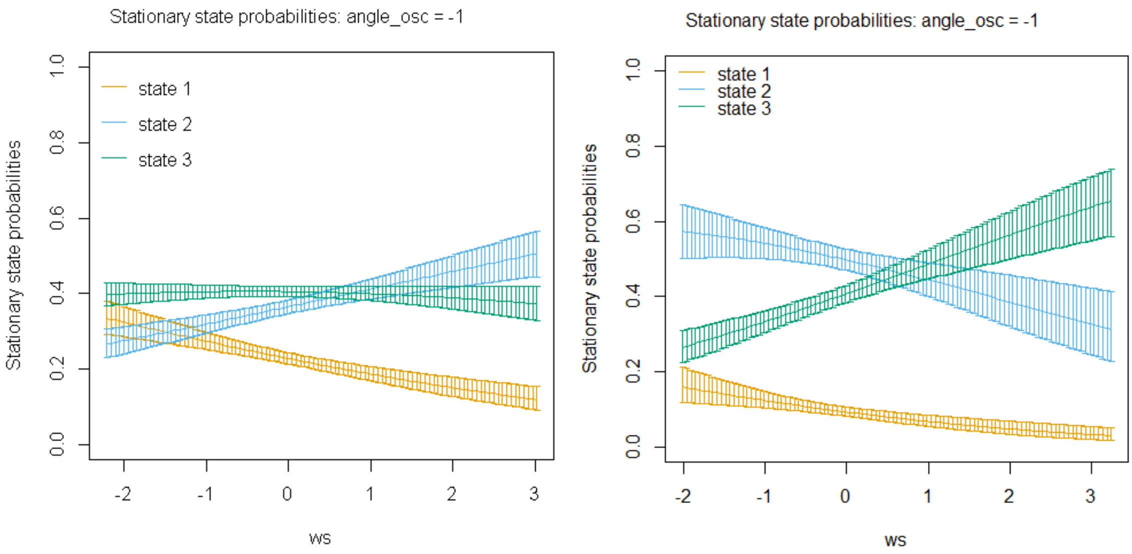
(c) Bass Rock 2011

(d) Bass Rock 2012

Figure A42 For Gannet, transition plots for wind speed in interation with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a full headwind (-1) over varying wind speed, showing effects on transition between states.

(a) Alderney all years

(b) Bass Rock 2010



(c) Bass Rock 2011

(d) Bass Rock 2012

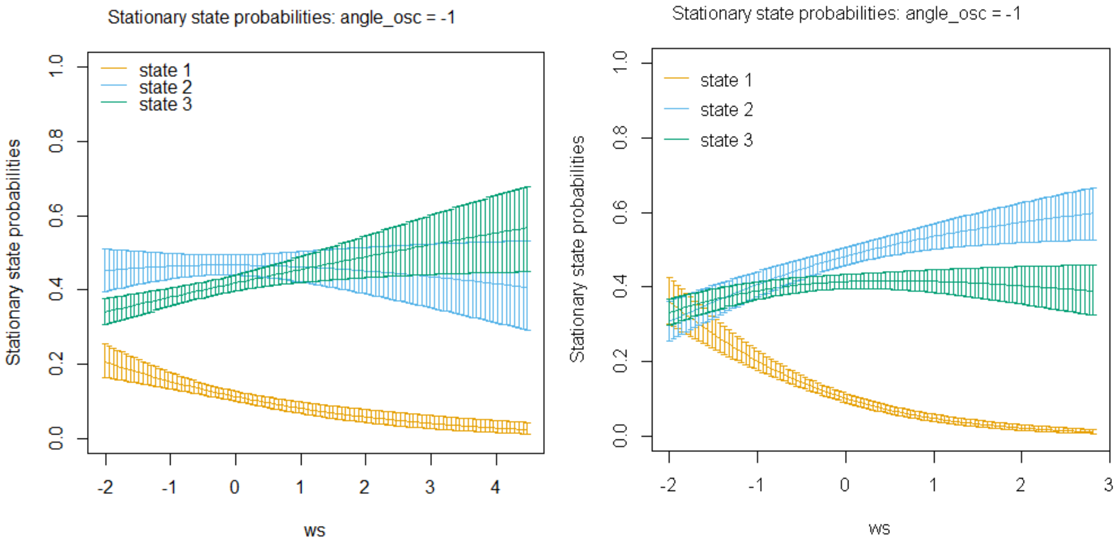
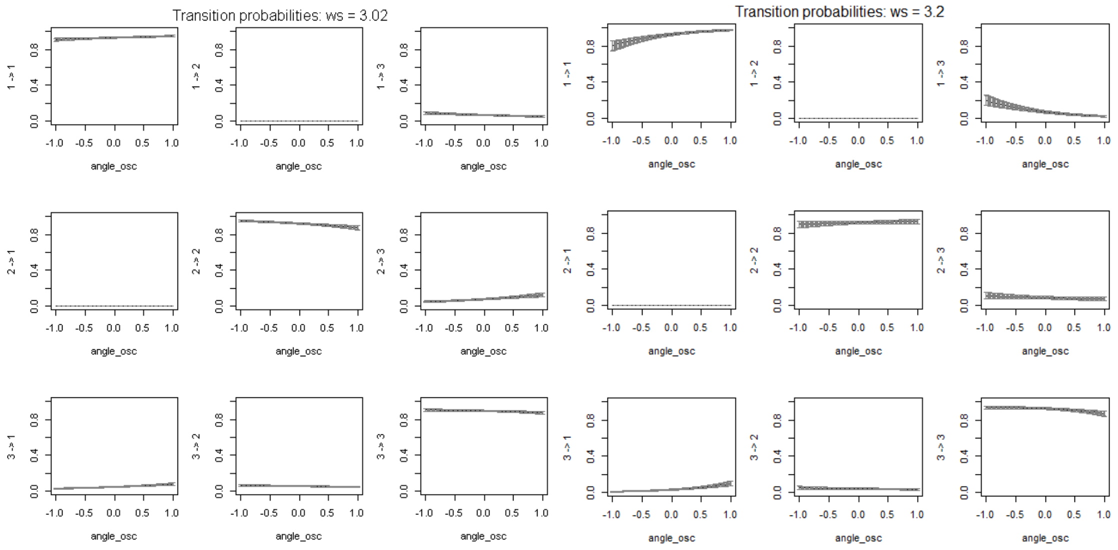
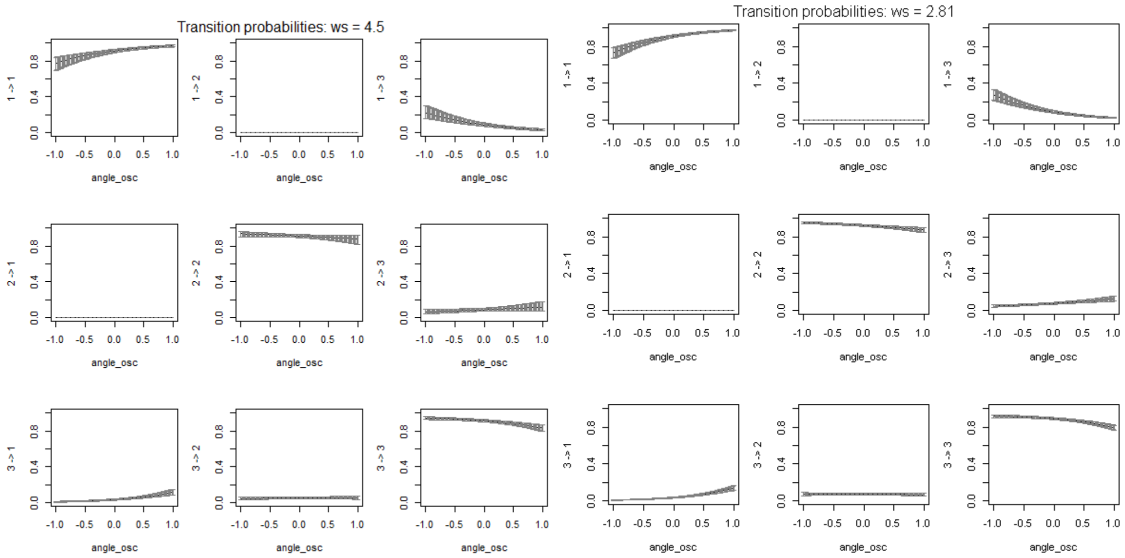


Figure A43 For Gannet, stationary state probability plots for wind speed in interation with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a full headwind (-1) over varying wind speed, for states 1, 2 and 3 (floating, commuting and foraging/searching).


(a) Alderney all years

(b) Bass Rock 2010

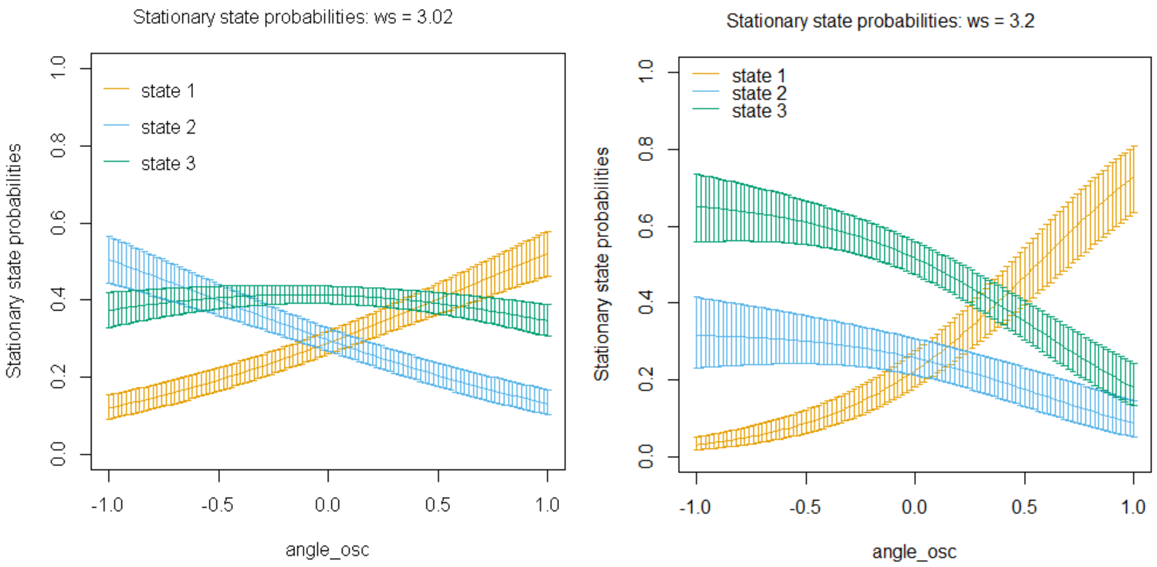

(c) Bass Rock 2011

(d) Bass Rock 2012

Figure A44 For Gannet, transition plots for wind speed in interation with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), plotted for a varying values of angular_osc for strongest wind speeds.

(a) Alderney all years

(b) Bass Rock 2010



(c) Bass Rock 2011

(d) Bass Rock 2012

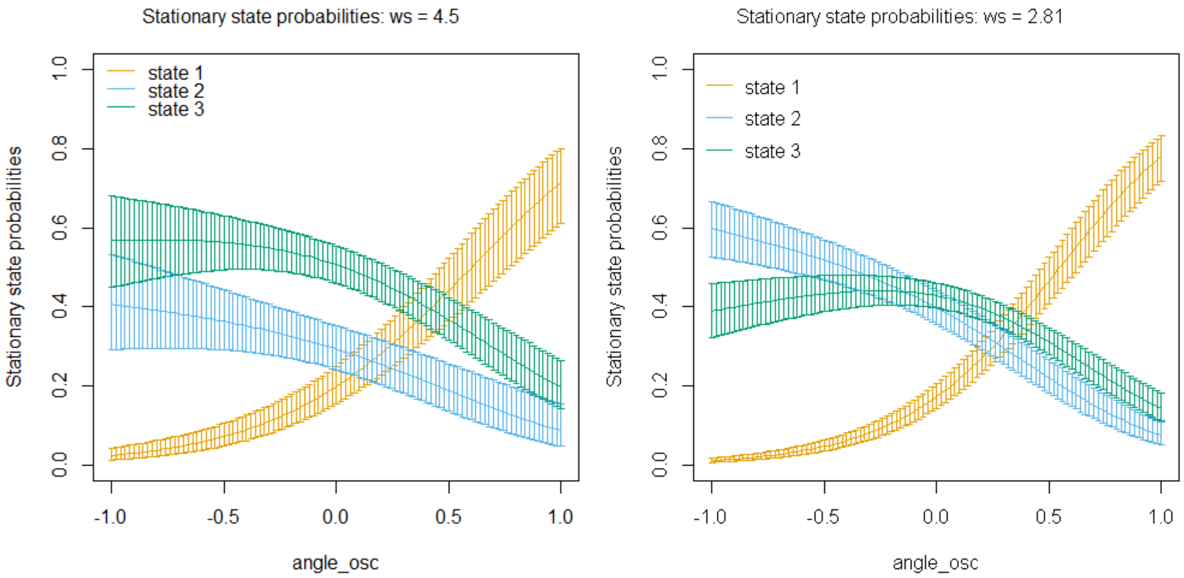
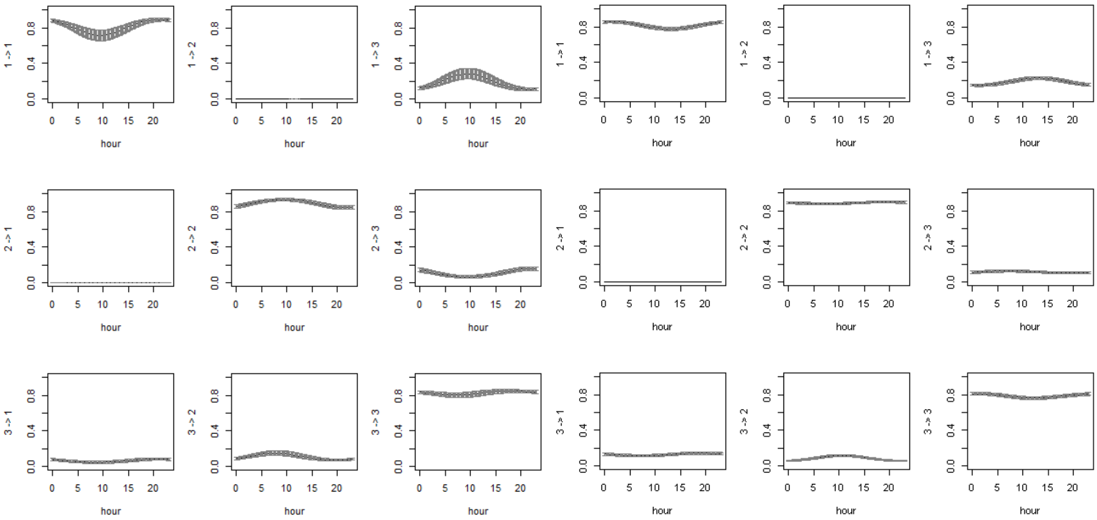


Figure A45 Stationary state probability plots for wind speed in interation with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), plotted for a varying values of angular_osc for strongest wind speeds per colony for states 1, 2 and 3 (floating, commuting and foraging/searching).

7.4.2 Lesser Black-backed Gull


(a) Walney

(b) Skokholm

(c) Orford Ness

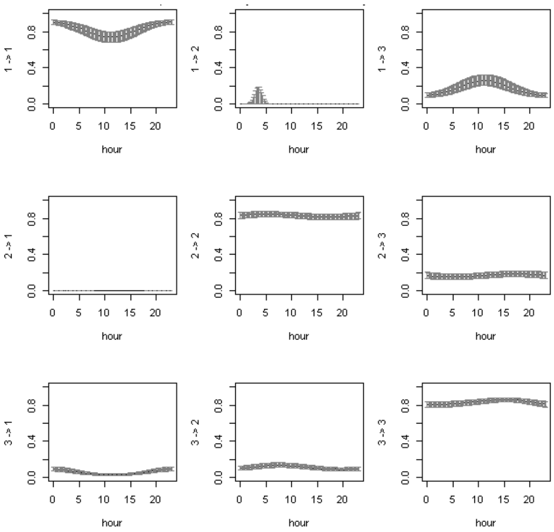
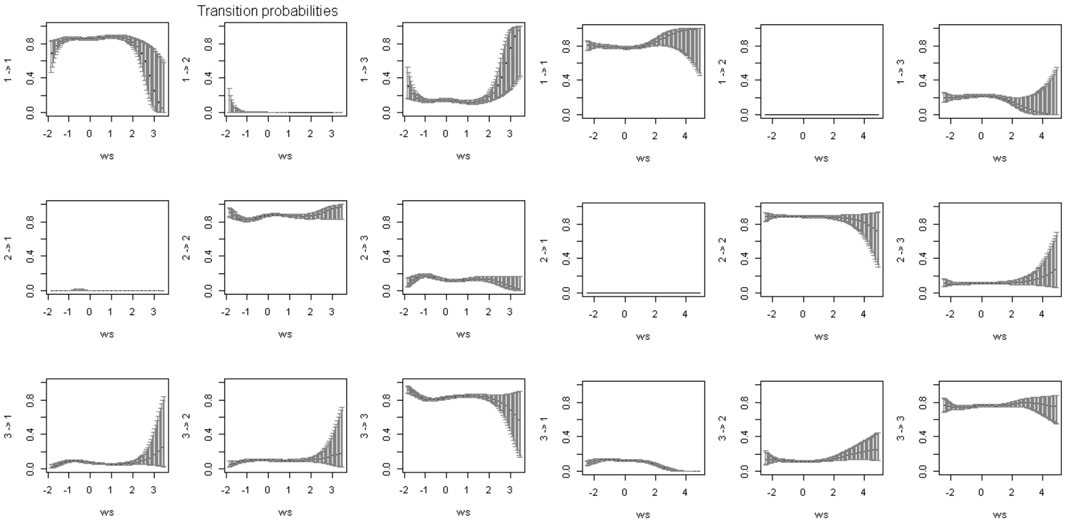


Figure A46 For Lesser Black-backed Gull, transition probabilities for the variable of cosinor(hour of day)..


(a) Walney

(b) Skokholm

(c) Orford Ness

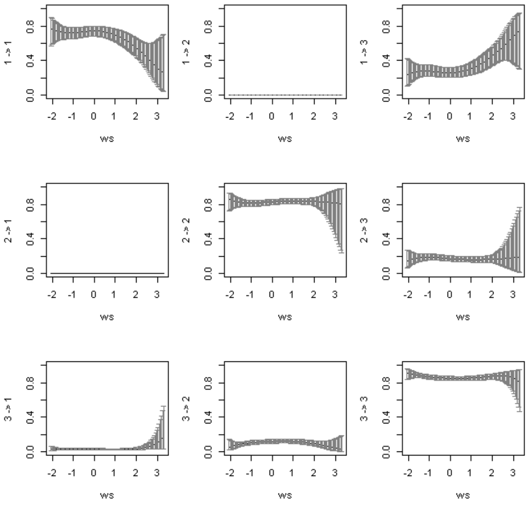
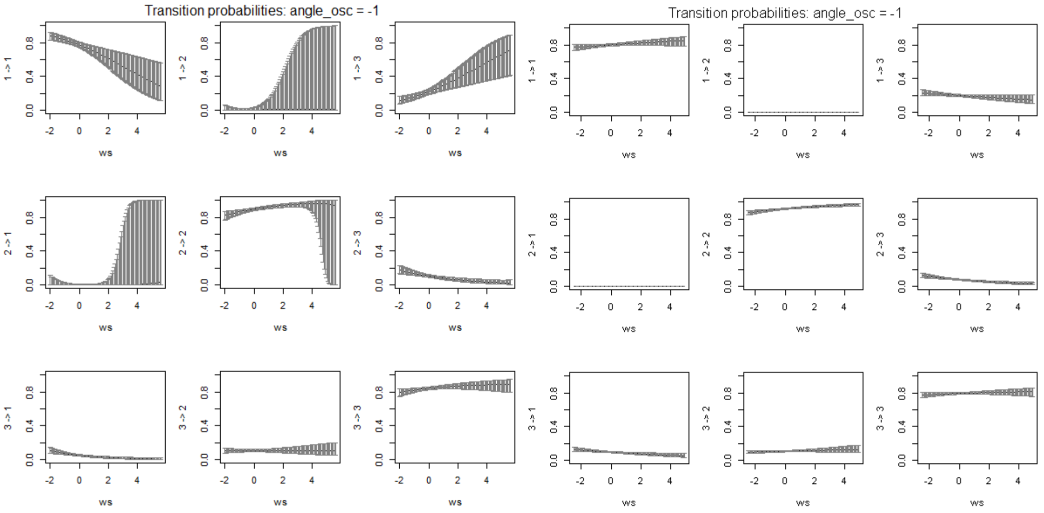


Figure A47 For Lesser Black-backed Gull, transition probabilities for the variable of bSpline(wind speed), fitted as a standardised variable.

(a) Walney (b) Skokholm



(a) Orford Ness

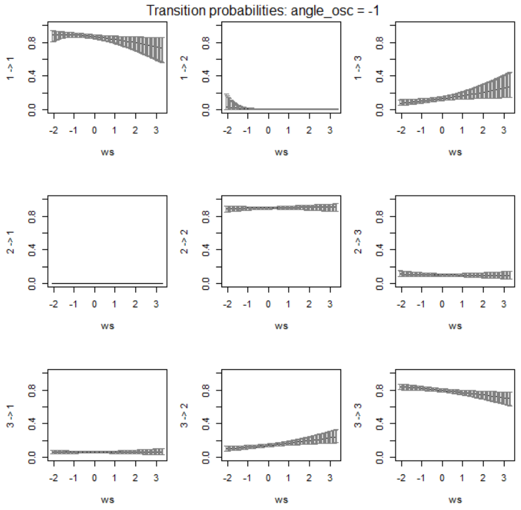
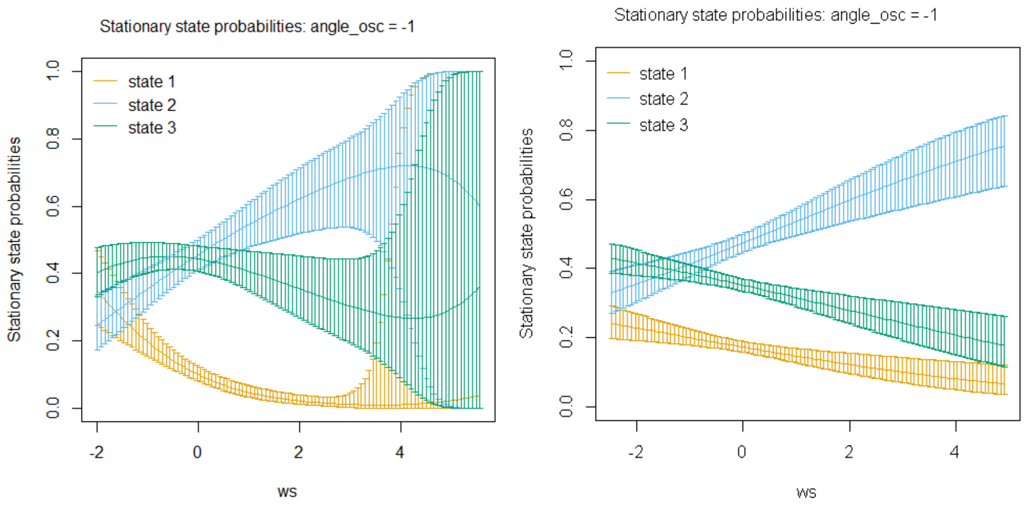


Figure A48 For Lesser Black-backed Gull, transition probabilities over time t and t+1 depicting the interaction of wind speed with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for varying wind speeds (standardised variable range per colony), for headwinds (angular_osc = -1).


(a) Walney

(b) Skokholm

(a) Orford Ness

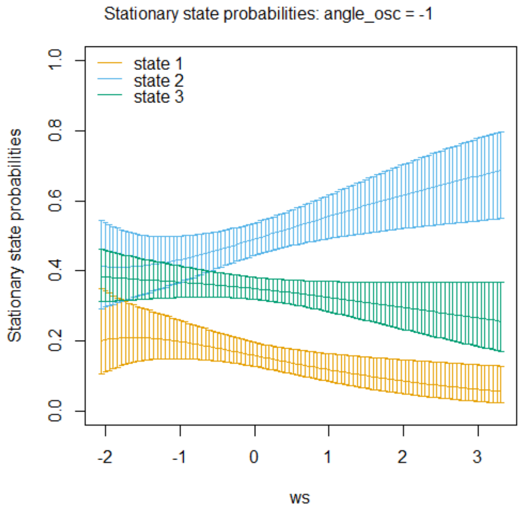
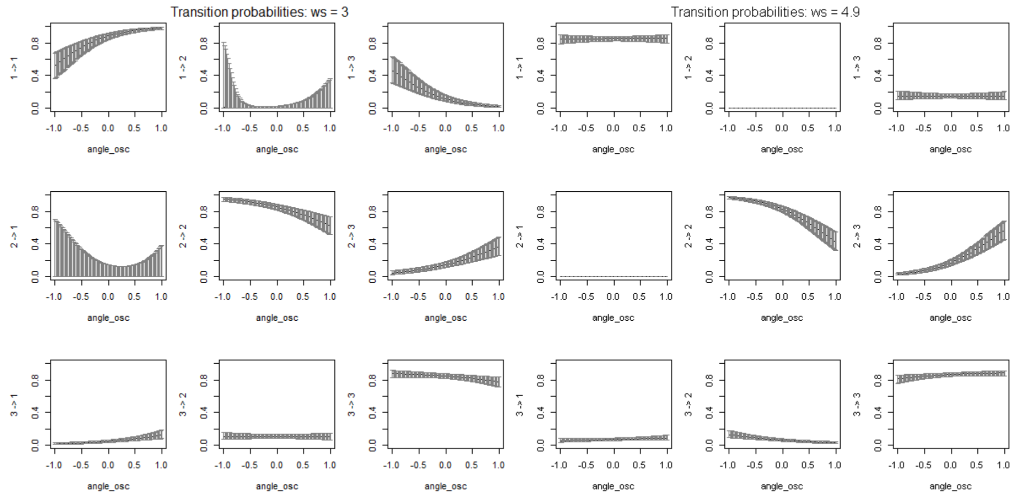


Figure A49 For Lesser Black-backed Gull, stationary state probabilities (i.e. likelihood of point being classified as a particular state) depicting wind speed in interation with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a full headwind (-1) over varying wind speed, showing effects on transition between states; see above for details on the standardised variable of wind speed and it’s equivalent true valules of wind speed for each colony.


(a) Walney

(b) Skokholm

(a) Orford Ness

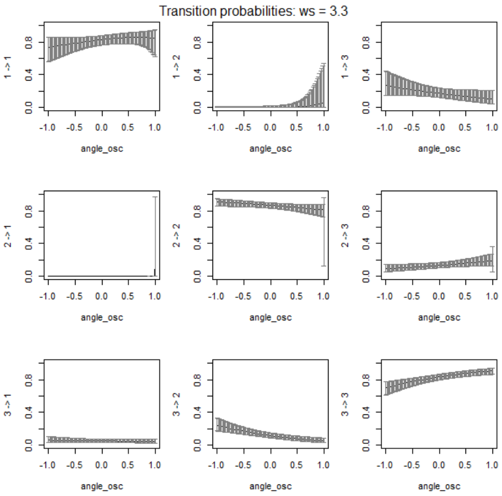
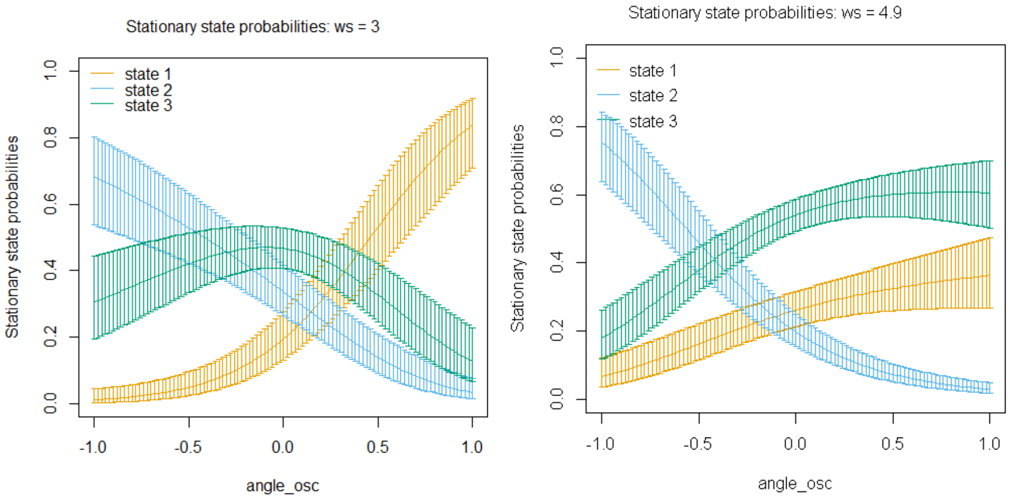


Figure A50 For Lesser Black-backed Gull, transition probabilities between states over time t and t+1 depicting the interaction of wind speed with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a varying values of angular_osc for strongest wind speeds per colony (3.0, 4.9 and 3.3 for Walney, Skokholm and Orford Ness, respectively), equating to ca. 11.4 m/s, 16.0 m/s and 12.9 m/s for Walney, Skokholm and Orford Ness; note large errors at the tail end of the Walney model up to max wind (17.4 m/s) produced the same patterns but with low confidence in the trends.


(a) Walney

(b) Skokholm

(a) Orford Ness

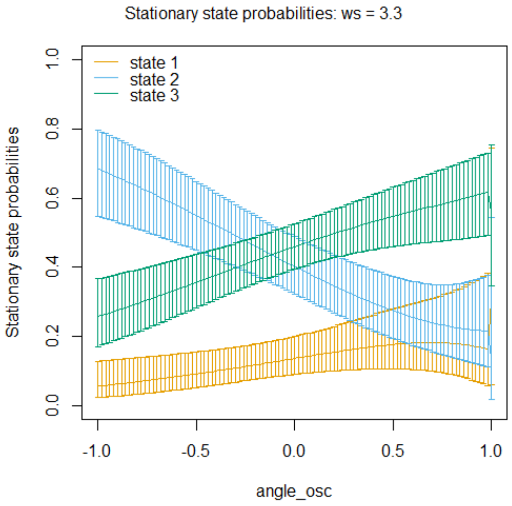
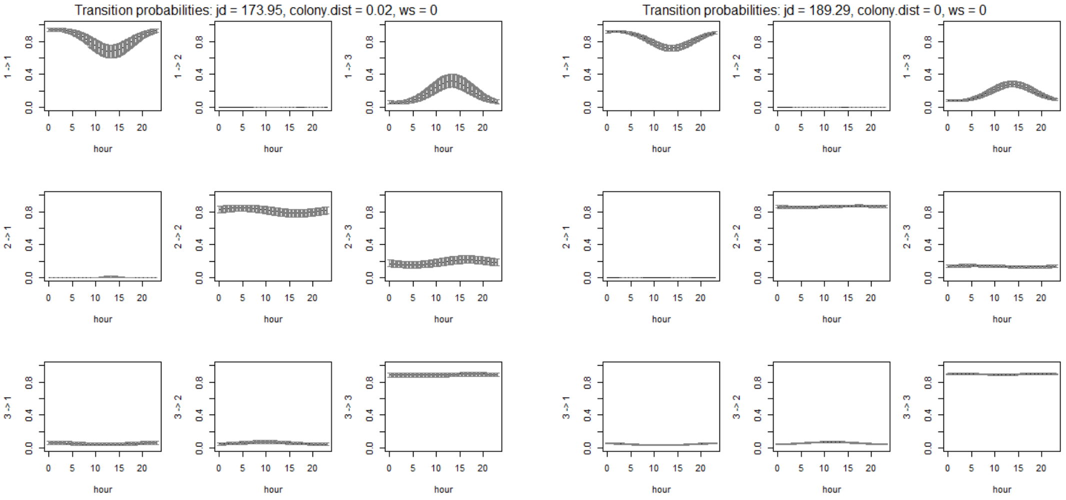


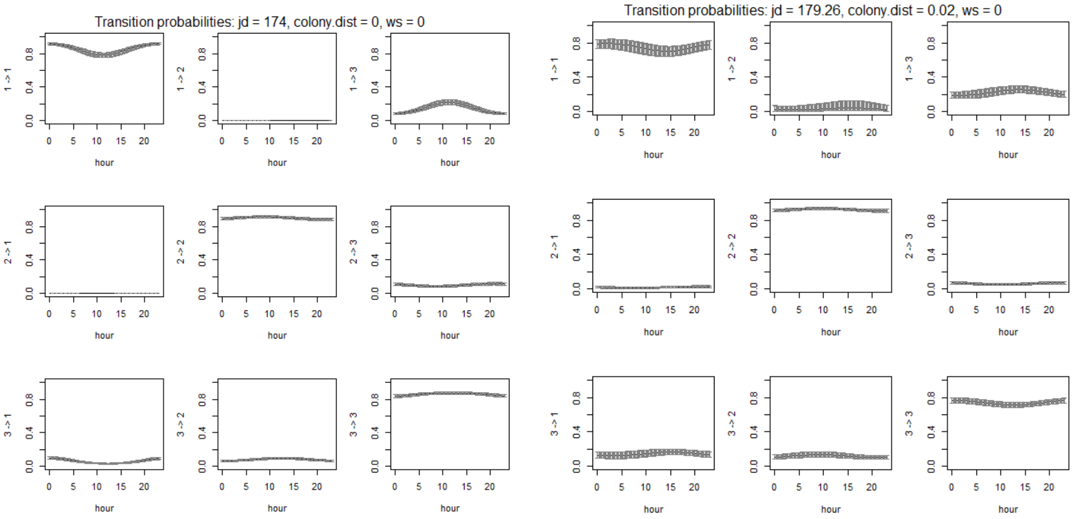
Figure A51 For Lesser Black-backed Gull, stationary state probabilities depicting the interaction of wind speed with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a varying values of angular_osc for strongest wind speeds per colony (3.0, 4.9 and 3.3 for Walney, Skokholm and Orford Ness, respectively), equating to ca. 11.4 m/s, 16.0 m/s and 12.9 m/s for Walney, Skokholm and Orford Ness; note large errors at the tail end of the Walney model up to max wind (17.4 m/s) produced the same patterns but with low confidence in the trends.

7.4.3 Black-legged Kittiwake



(a) Isle of May

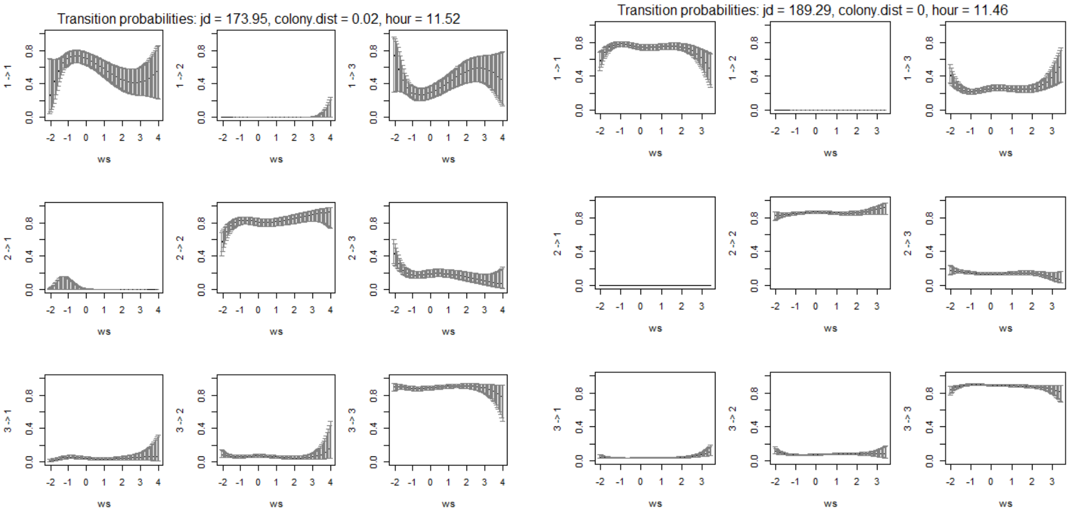
(b) Colonsay



(c) Bempton

(d) Orkney

Figure A52 For Kittiwake, transition probabilities for the variable of cosinor (hour of day).

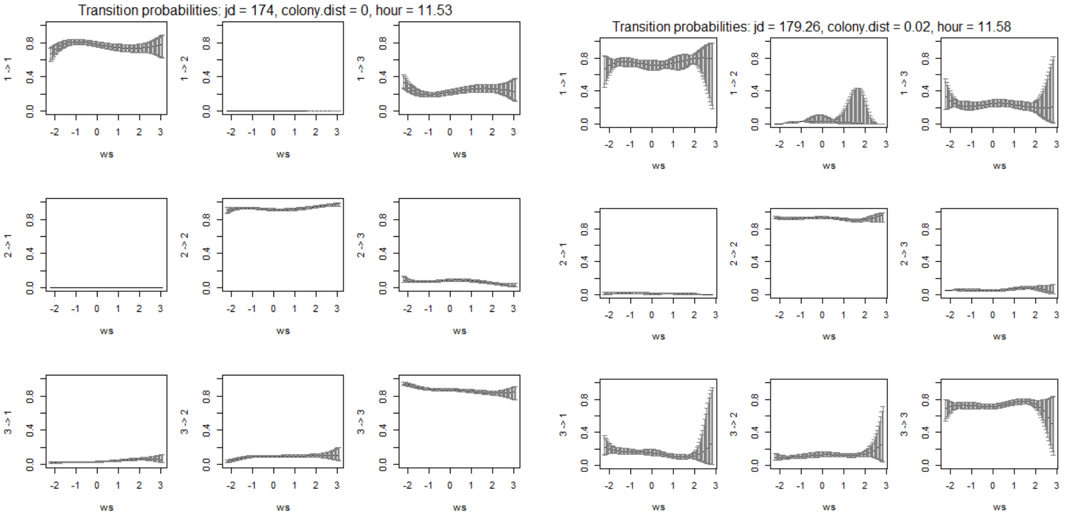


(a) Isle of May

Transition probabilities: jd = 173.95, colony.dist = 0.02, hour = 11.52

(b) Colonsay

Transition probabilities: jd = 189.29, colony.dist = 0, hour = 11.46



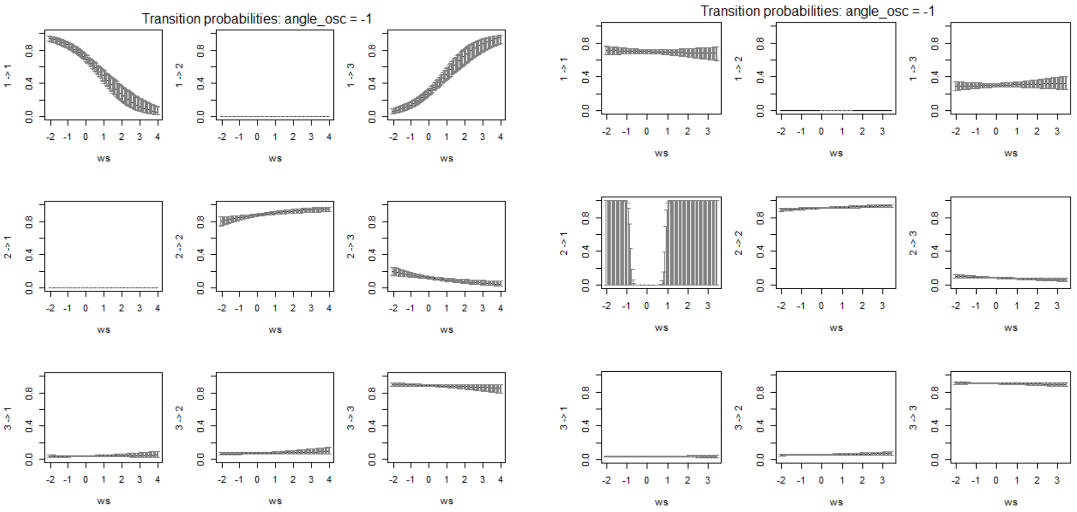
(c) Bempton

Transition probabilities: jd = 174, colony.dist = 0, hour = 11.53

(d) Orkney

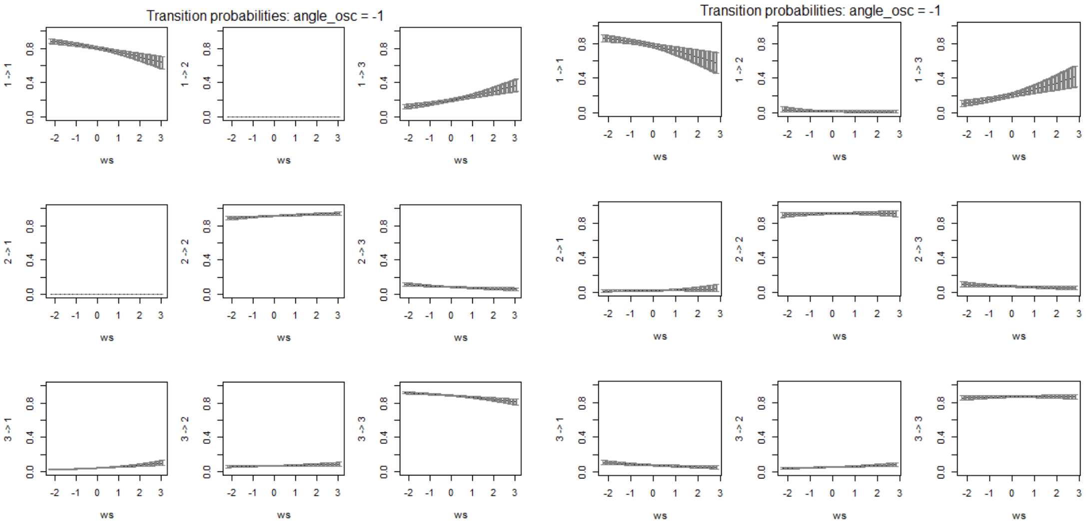
Transition probabilities: jd = 179.26, colony.dist = 0.02, hour = 11.58

Figure A53 For Kittiwake, transition probabilities for the variable of bSpline(wind speed), fitted as a standardised variable.



(a) Isle of May

(b) Colonsay



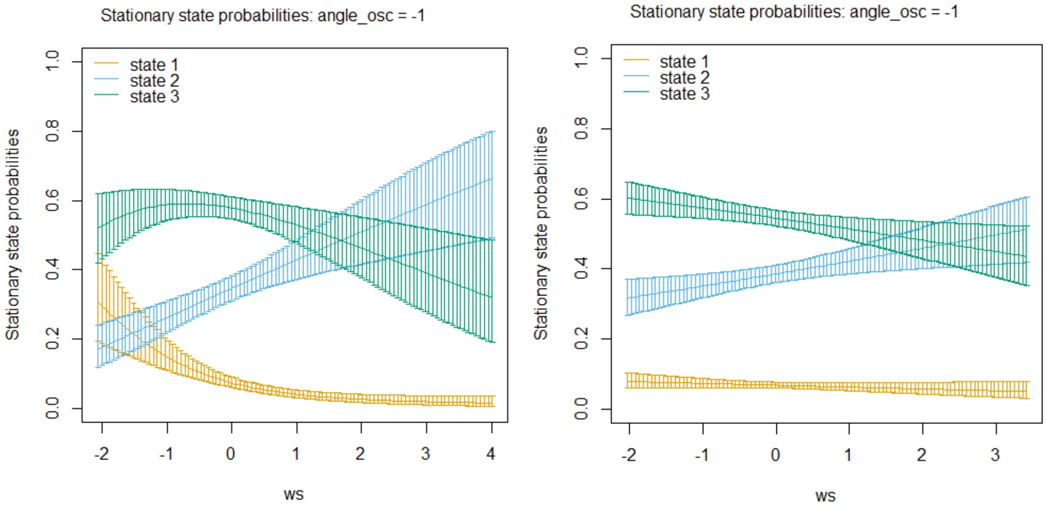
(a) Bempton

(b) Orkney

Figure A54 For Kittiwake, transition probabilities between states over time t and t+1 depicting the interaction of wind speed with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for varying wind speeds (standardised variable range per colony), for headwinds (angular_osc = -1).

(a) Isle of May

(b) Colonsay



(a) Bempton

(b) Orkney

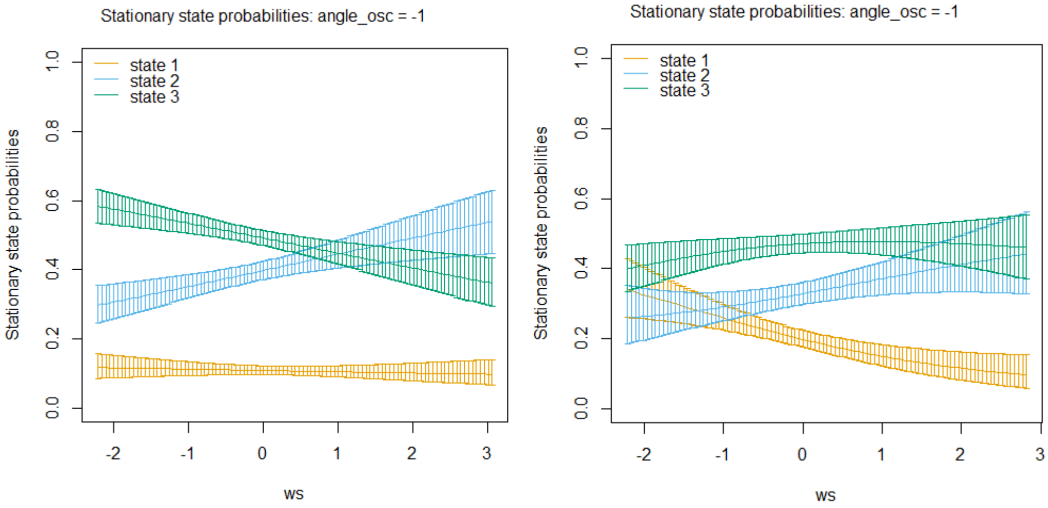
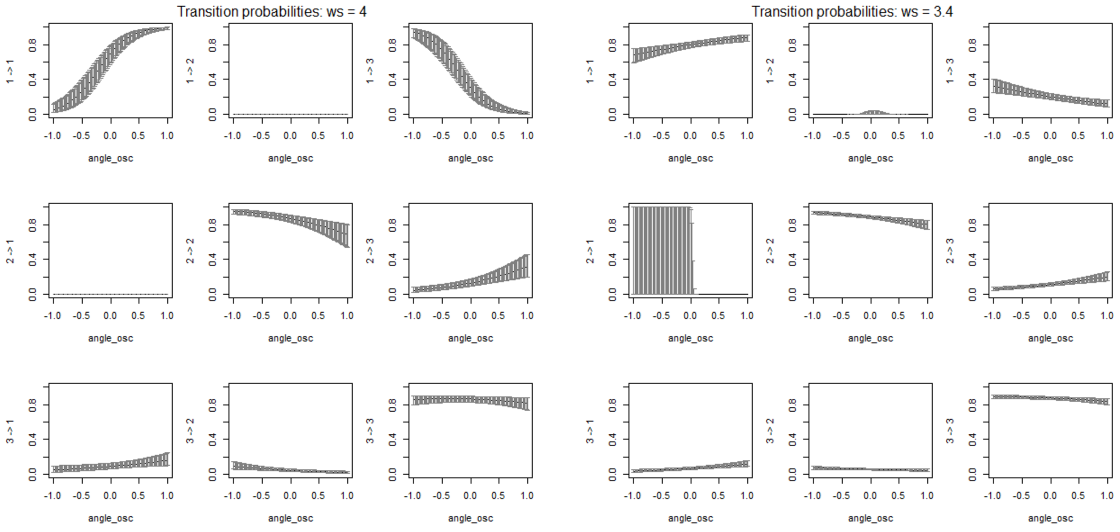
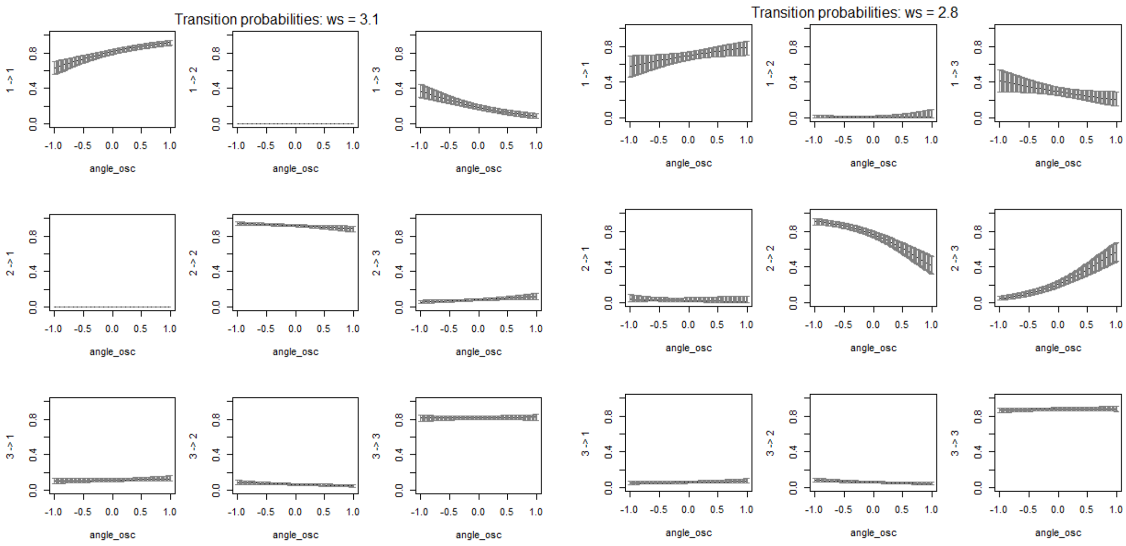


Figure A55 For Kittiwake, stationary state probabilities (i.e. likelihood of point being classified as a particular state) depicting the interaction of wind speed with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a varying values of wind speed for for tailwinds (angle_osc = +1).

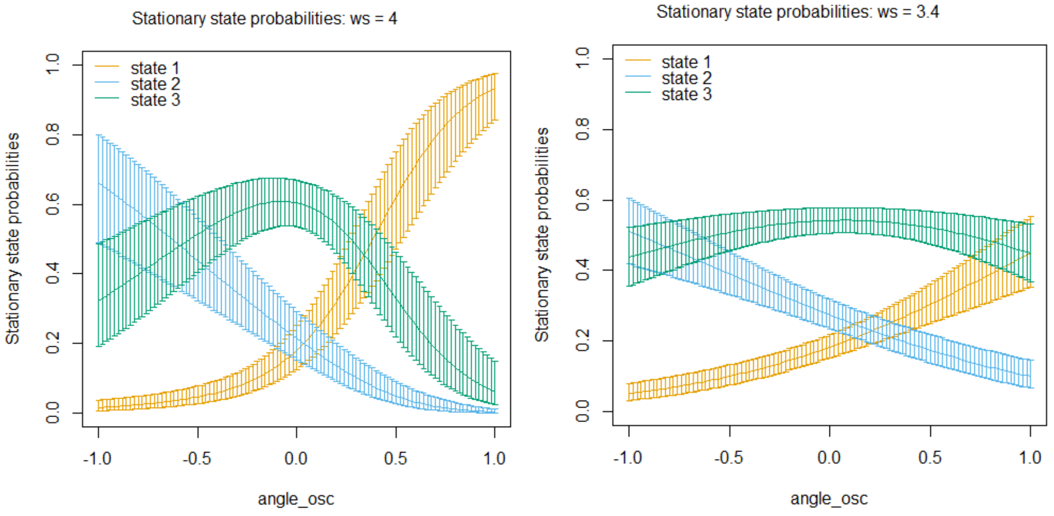

(a) Isle of May

(b) Colonsay


(a) Bempton

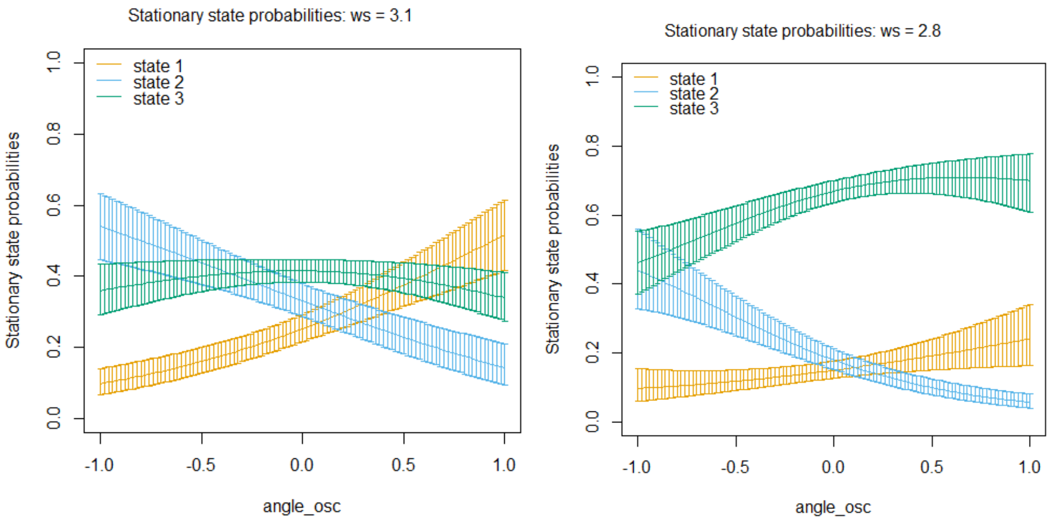
(b) Orkney

Figure A56 For Kittiwake, transition probabilities between states over time t and t+1 depicting the interaction of wind speed with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a varying values of angular_osc for strongest wind speeds per colony.



(a) Isle of May

(b) Colonsay

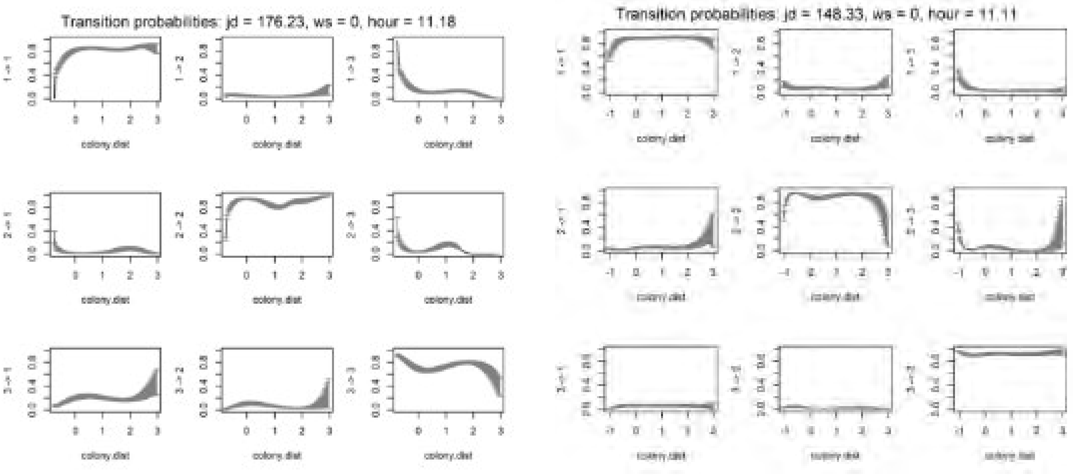


(a) Bempton

(b) Orkney

Figure A57 For Kittiwake, stationary state probabilities depicting the interaction of wind speed with angular_osc (travel direction alignment to wind direction, -1 = direct headwind, +1 = direct tailwind), here plotted for a varying values of angular_osc for strongest wind speeds per colony.

7.4.4 Razorbill


(a) Colonsay

(b) Puffin Island

(c) Isle of May

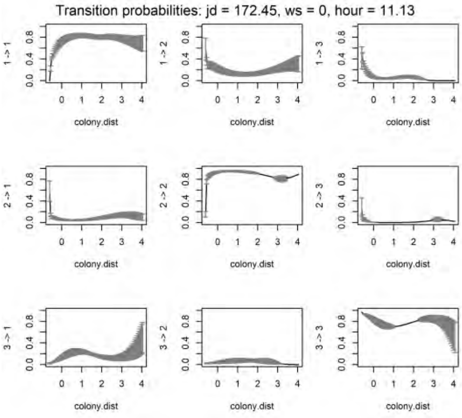
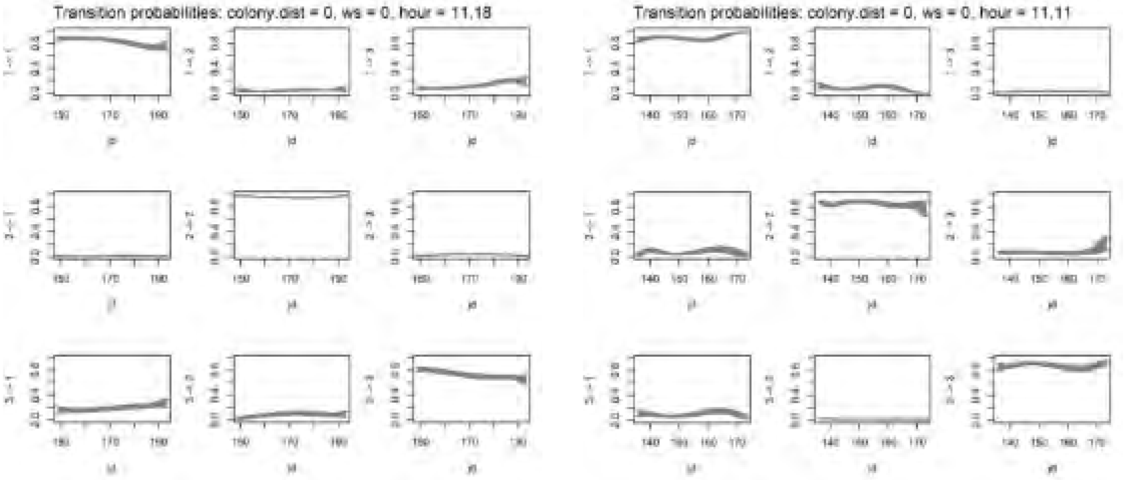


Figure A58 For Razorbill, transition probabilities for the variable of distance to colony, fitted as a standardised variable.



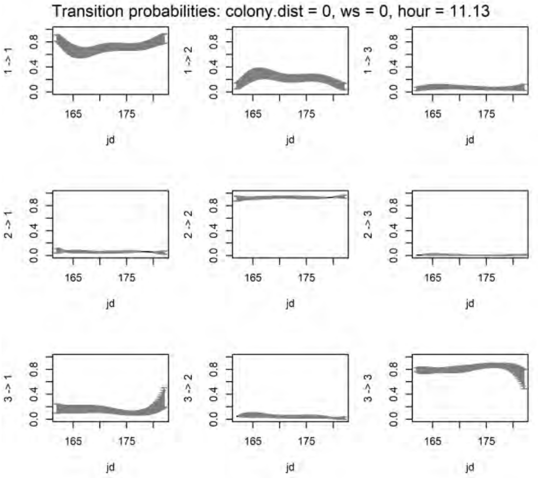
(a) Colonsay

Transition probabilities: colony.dist = 0, ws = 0, hour = 11.18

(b) Puffin Island

Transition probabilities: colony.dist = 0, ws = 0, hour = 11.11

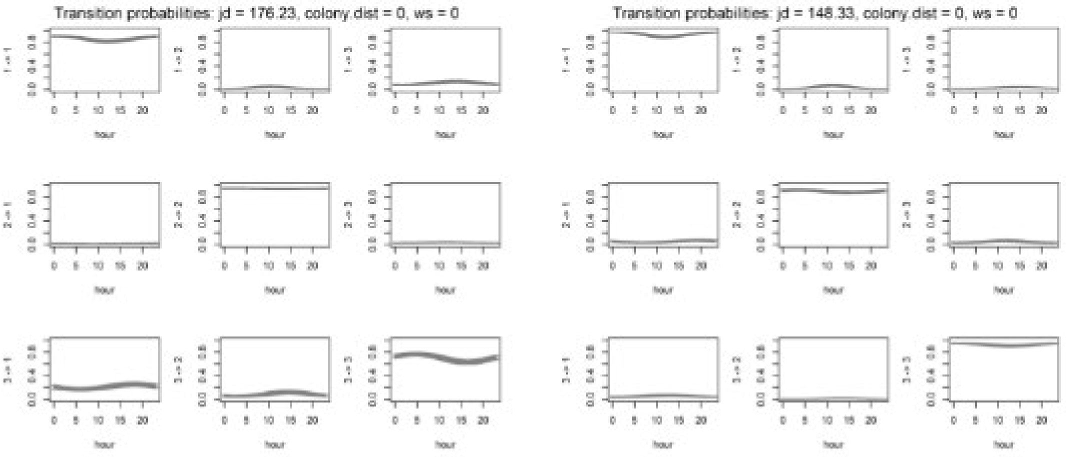
(c) Isle of May



Transition probabilities: colony.dist = 0, ws = 0, hour = 11.13

Figure A59 For Razorbill, transition probabilities for the variable of Julian date at (a) Colonsay,(b) Puffin Island and (c) Isle of May.

(a) Colonsay (b) Puffin Island



(c) Isle of May (d) Colonsay inc. diving

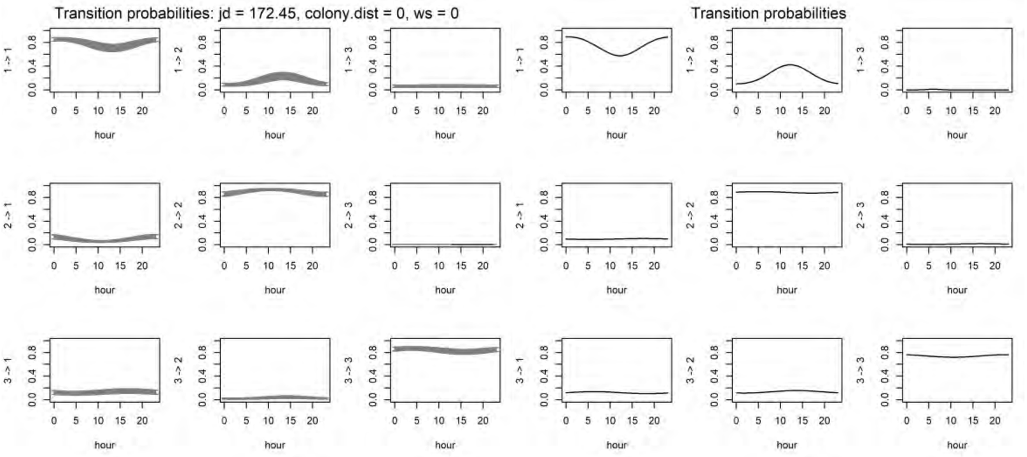
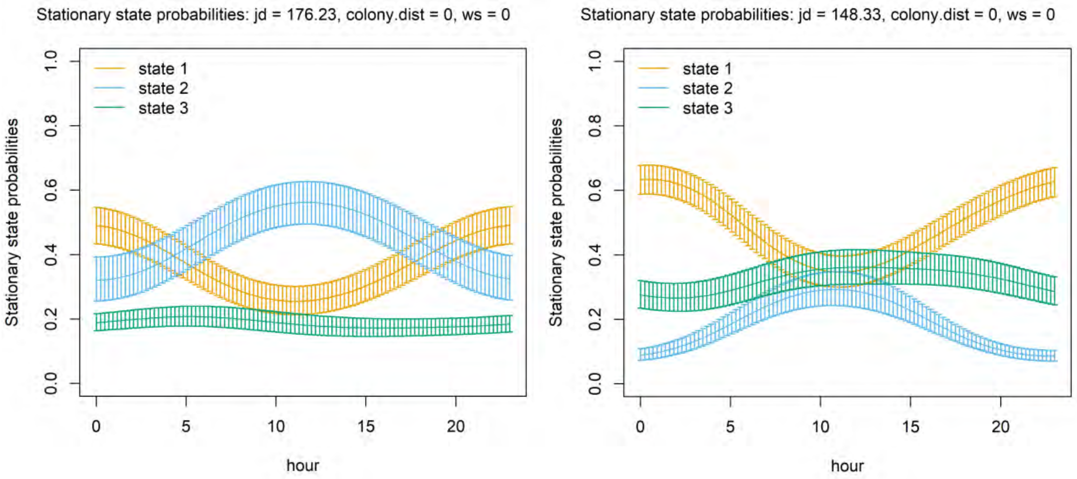
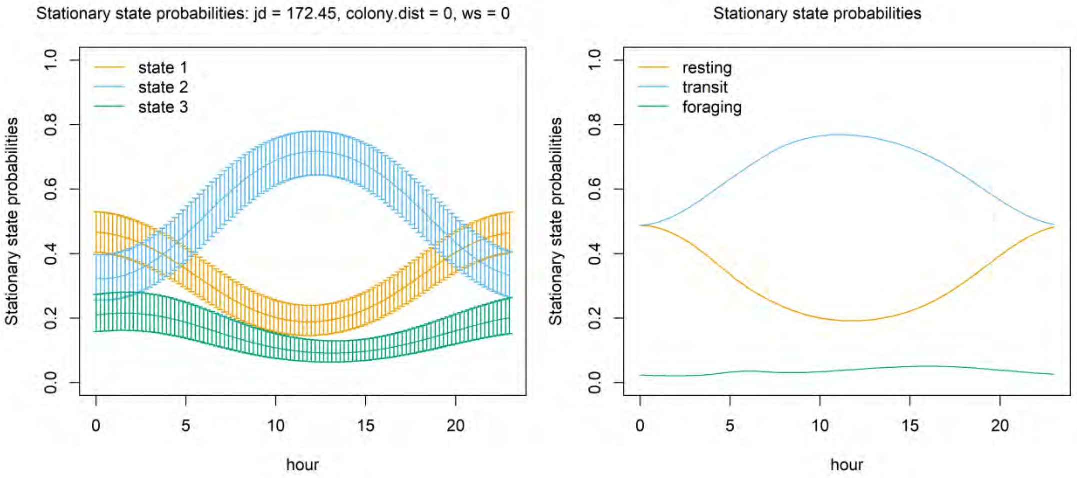


Figure A60 For Razorbill, transition probabilities for the variable of cosinor(hour of day) at (a) Colonsay,(b) Puffin Island and (c) Isle of May (d) Colonsay + TDR.


(a) Colonsay

(b) Puffin Island

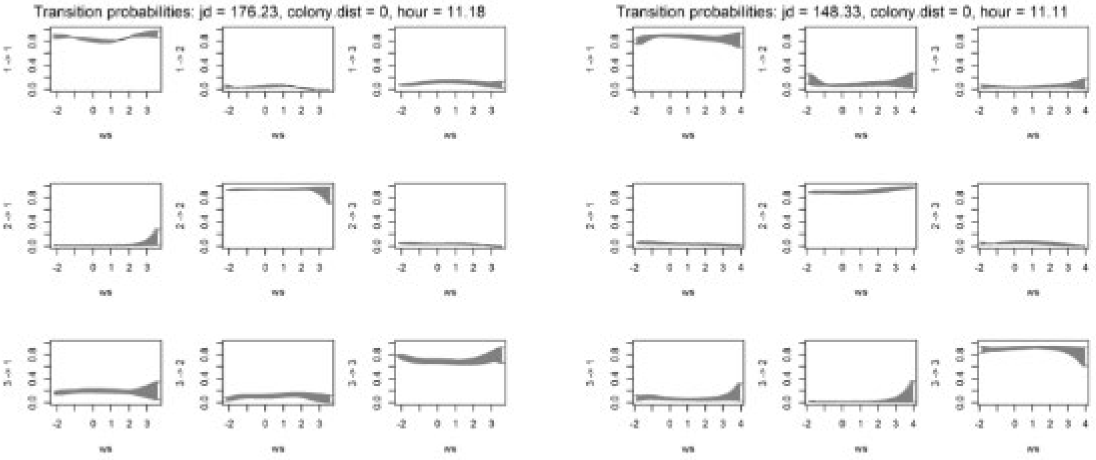

(c) Isle of May

(d) Colonsay inc. diving

Figure A61 For Razorbill, stationary state probabilities for the variable of cosinor(hour of day) at (a) Colonsay, (b) Puffin Island, and (c) the Isle of May,(d) Colonsay + TDR.

(a) Colonsay

(b) Puffin Island



(c) Isle of May

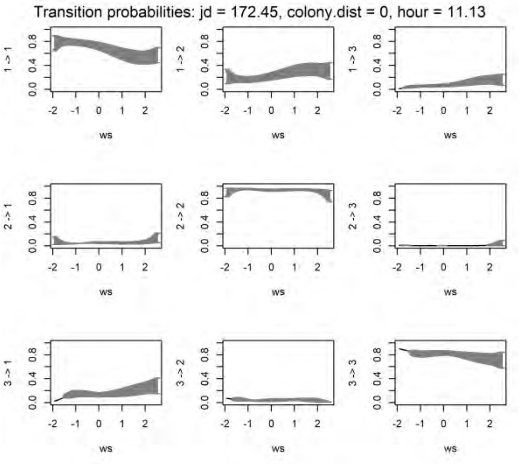
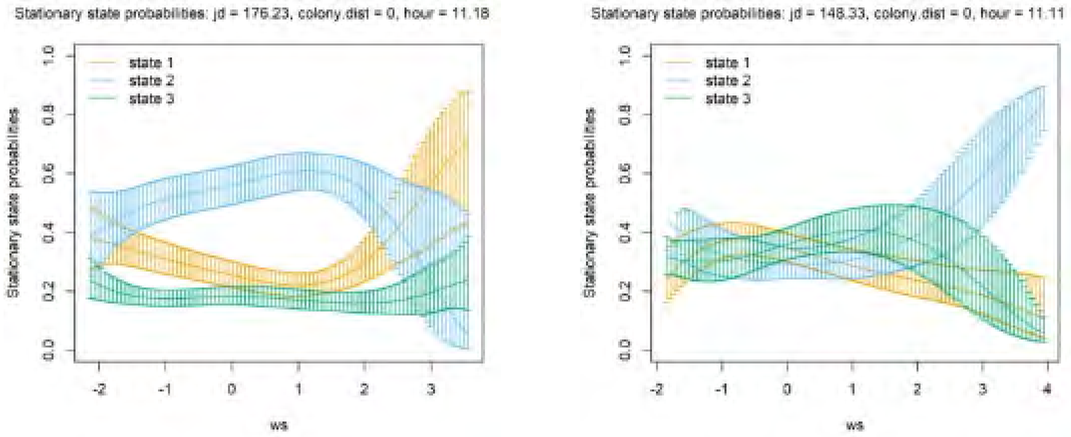


Figure A62 For Razorbill, transition probabilities for the variable of bSpline(wind speed), fitted as a standardised variable



(a) Colonsay

(b) Puffin Island

(c) Isle of May

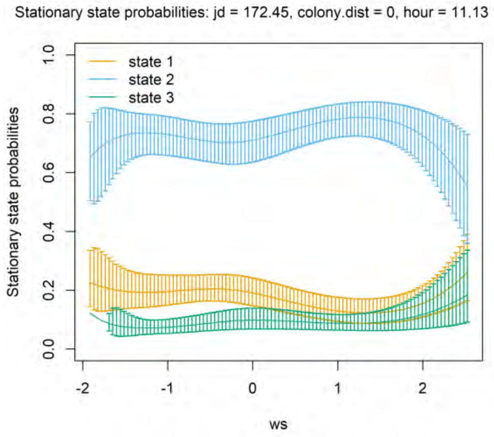
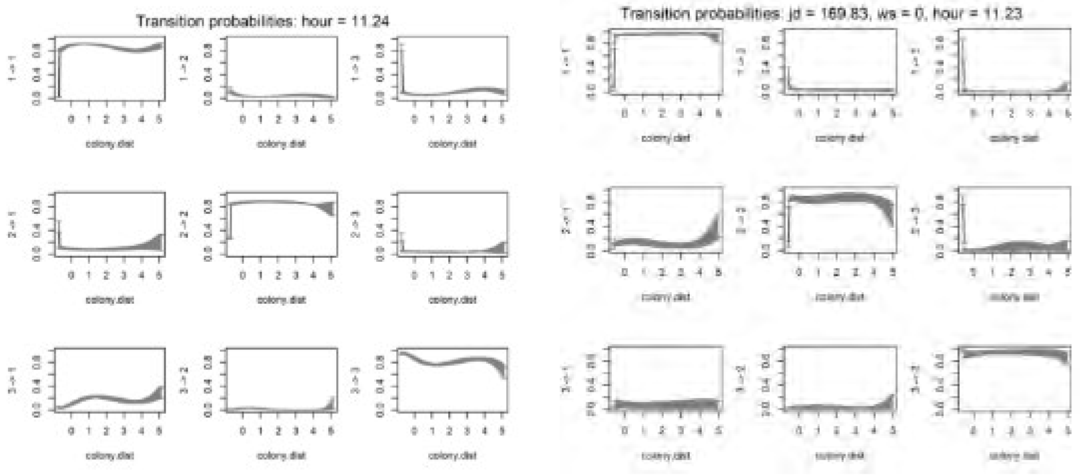


Figure A63 For Razorbill, stationary state probabilities for the variable of bSpline(wind speed), fitted as a standardised variable.

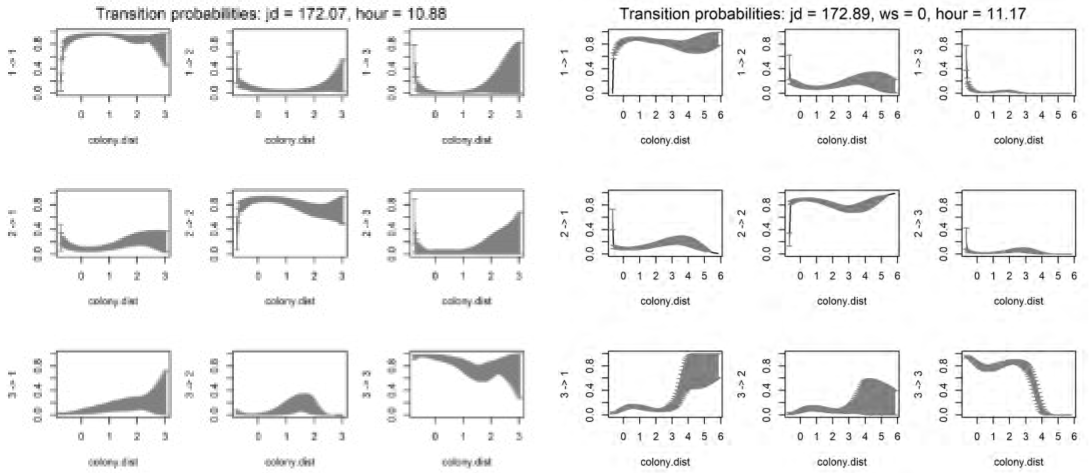
7.4.5 Common Guillemot

(a) Colonsay (b) Puffin Island


Transition probabilities: hour = 11.24

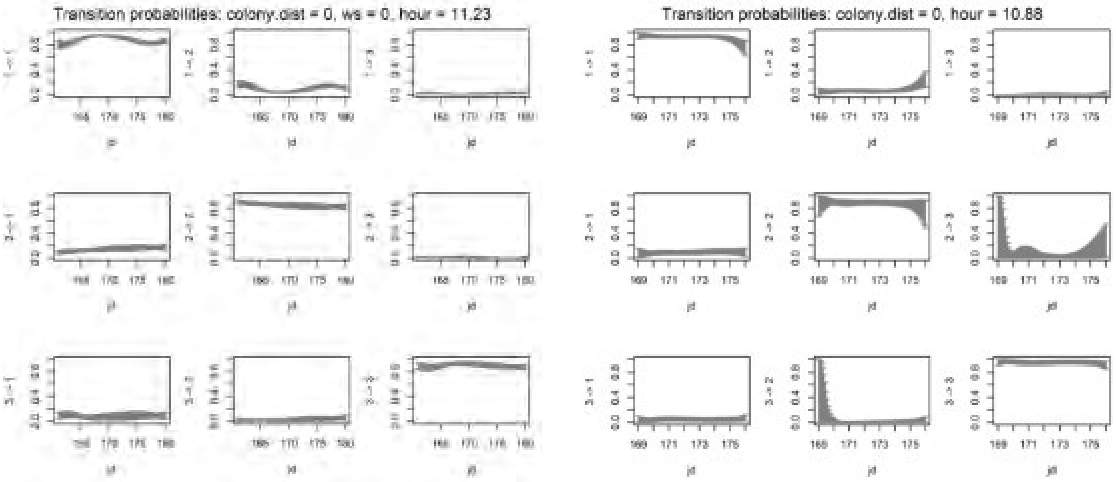
Transition probabilities: jd = 169.83, ws = 0, hour = 11.23

(c) Fowlsheugh (d) Isle of May


Transition probabilities: jd = 172.07, hour = 10.88

Transition probabilities: jd = 172.89, ws = 0, hour = 11.17

Figure A64 For Guillemot, transition probabilities for the variable of distance to colony, fitted as a standardised variable.


(a) Puffin Island

Transition probabilities: colony.dist = 0, ws = 0, hour = 11.23

(b) Fowlsheugh

Transition probabilities: colony.dist = 0, hour = 10.88

(c) Isle of May

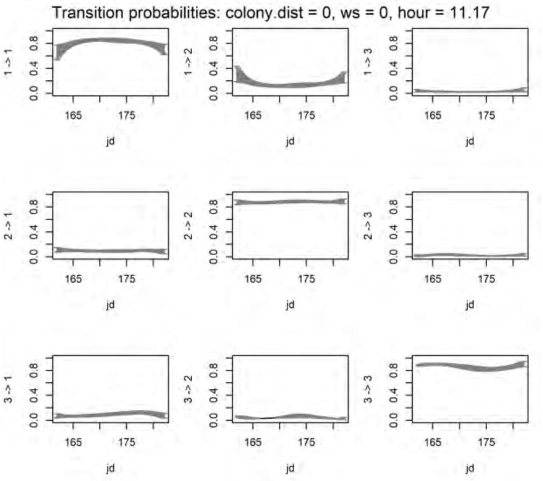
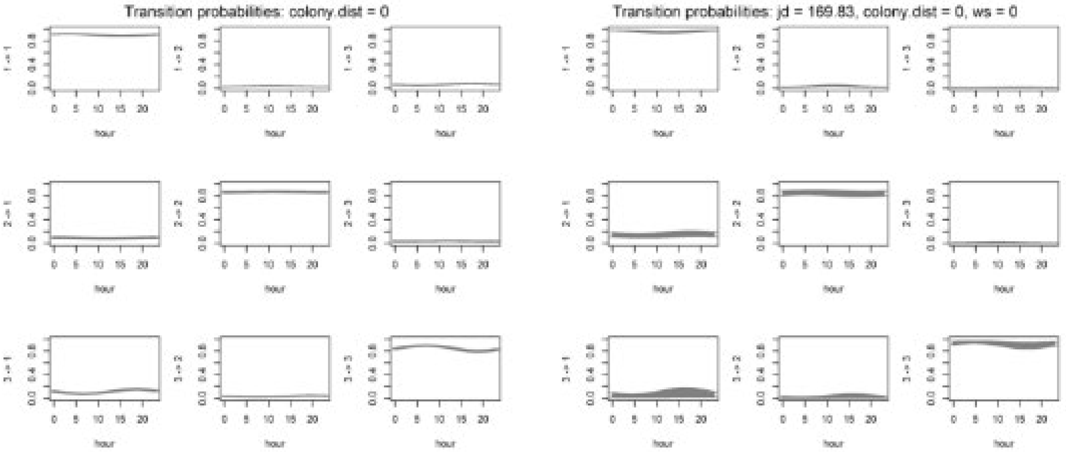

Transition probabilities: colony.dist = 0, ws = 0, hour = 11.17

Figure A65 For Guillemot, transition probabilities for the variable of Julian date.

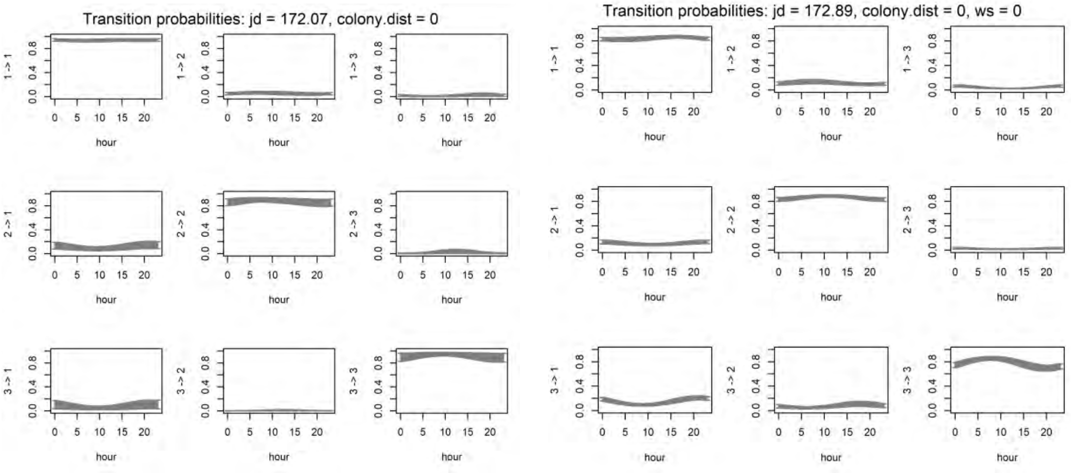
(a) Colonsay (b) Puffin Island



Transition probabilities: colony.dist = 0

Transition probabilities: jd = 169.83, colony.dist = 0, ws = 0

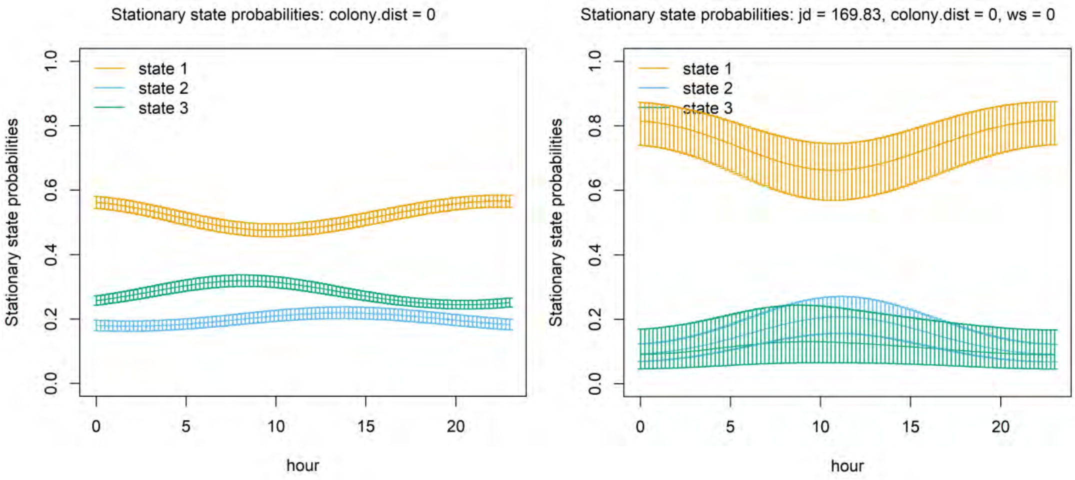
(c) Fowlsheugh (d) Isle of May



Transition probabilities: jd = 172.07, colony.dist = 0

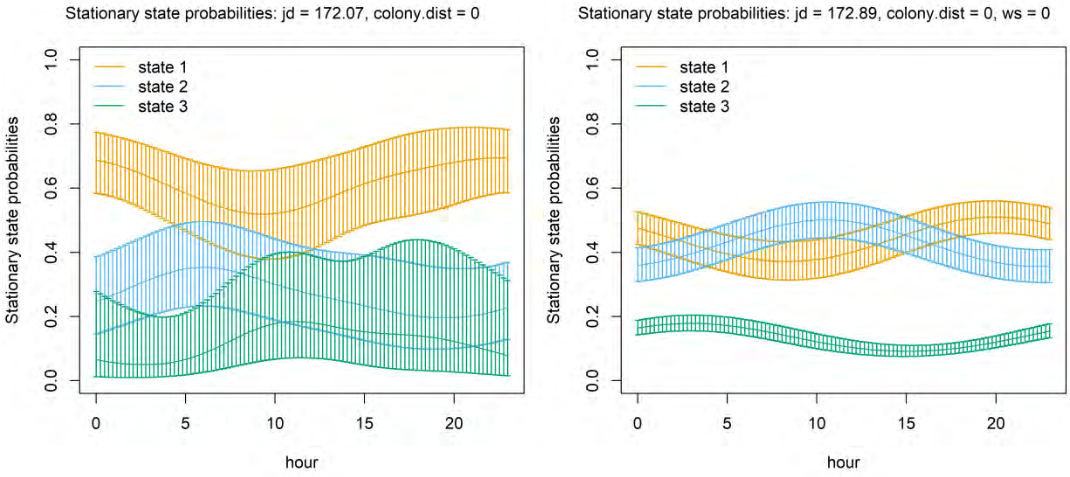
Transition probabilities: jd = 172.89, colony.dist = 0, ws = 0

Figure A66 For Guillemot, transition probabilities for the variable of cosinor(hour of day).



(a) Colonsay

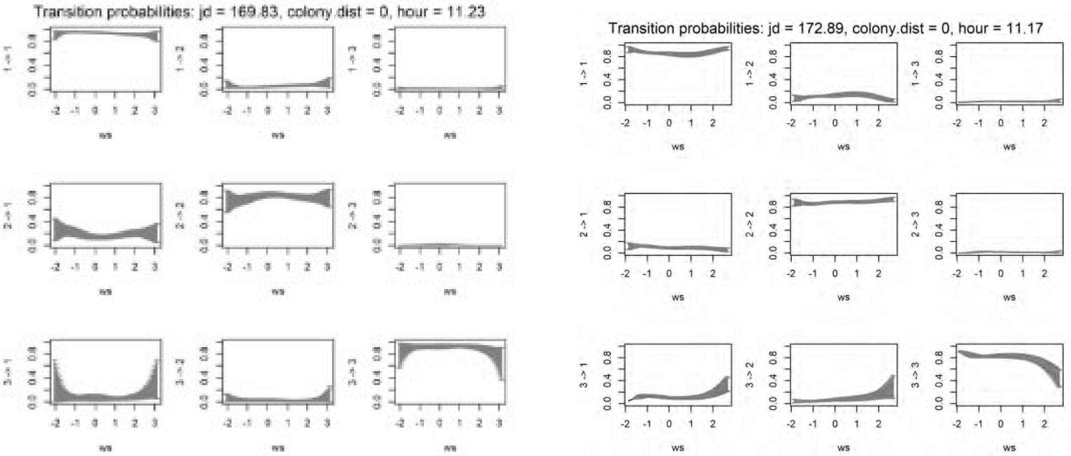
(b) Puffin Island



(c) Fowlsheugh

(d) Isle of May

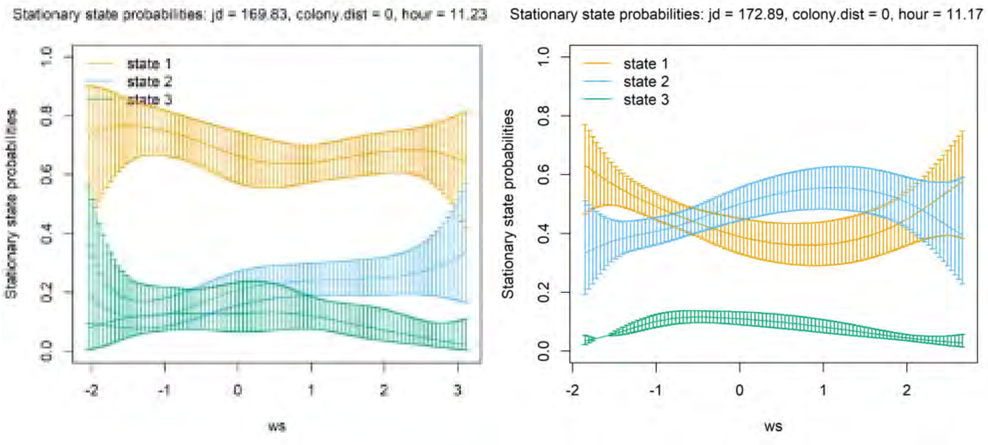
Figure A67 For Guillemot, stationary state probabilities for the variable of cosinor(hour of day).



(a)Puffin Island

(b) Isle of May

Figure A68 For Guillemot, transition probabilities for the variable of bSpline(wind speed), fitted as a standardised variable.

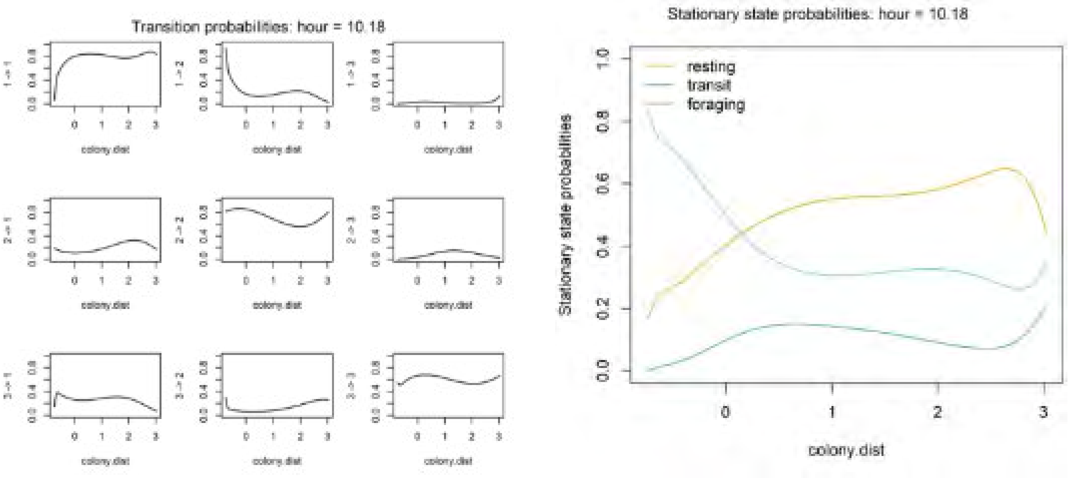


(a)Puffin Island

(b) Isle of May

Figure A69 For Guillemot, stationary state probabilities for the variable of bSpline(wind speed), fitted as a standardised variable

(a) distance to colony



(b) hour of day

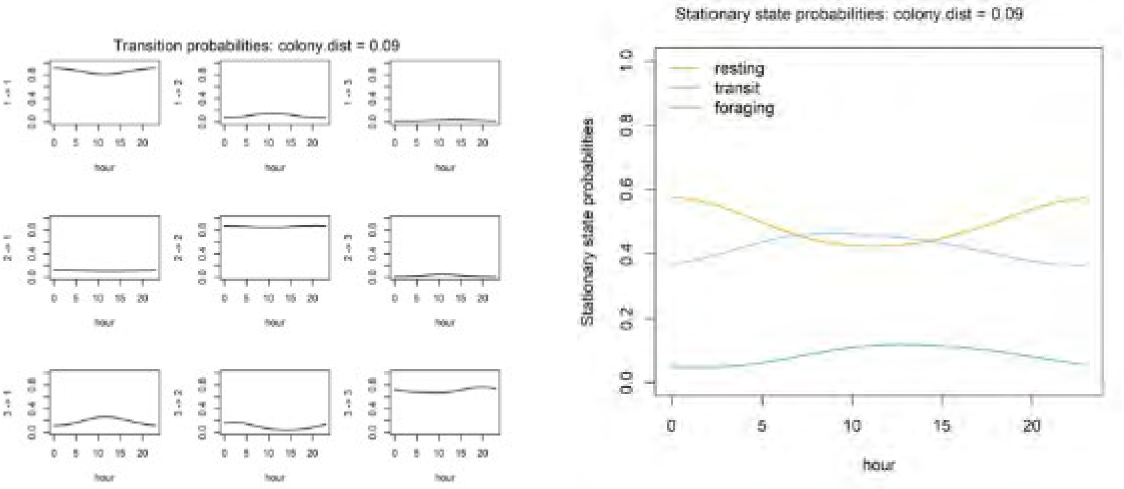


Figure A70 For Guillemot, transition and stationary state probabilities at Fowlsheugh from models incorporating TDR dive data for the variables of distance to colony and cosinor(hour of day).

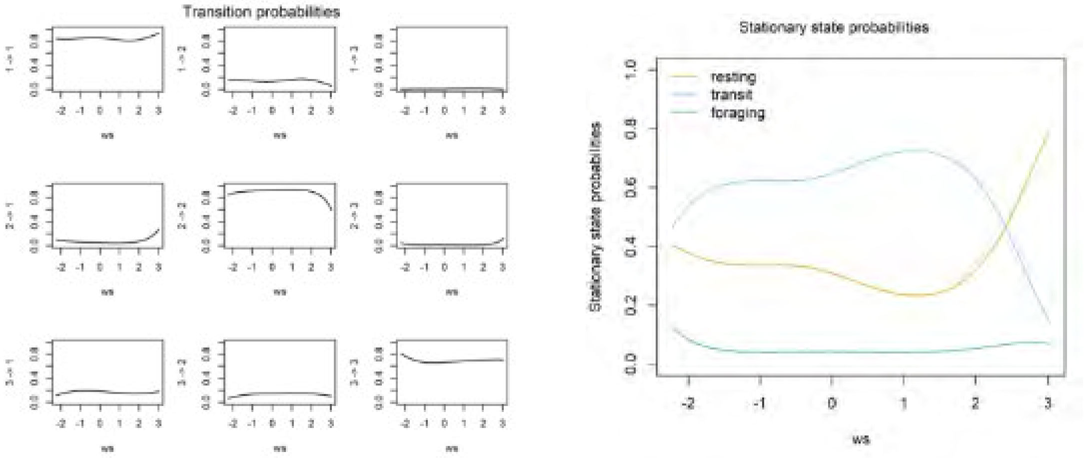
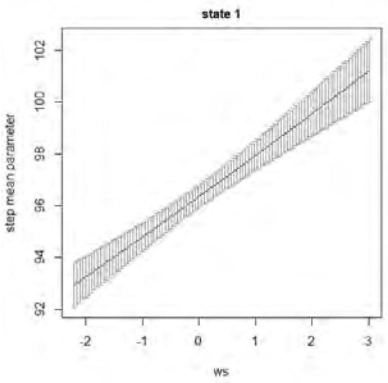


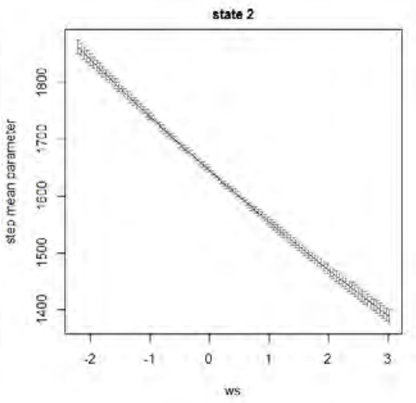
Figure A71 For Guillemot, transition and stationary state probabilities at Colonsay from models incorporating TDR dive data for the variable of bSpline(wind speed), fitted as a standardised variable.

7.5 Appendix AE. Effects of wind speed on step length (speed)

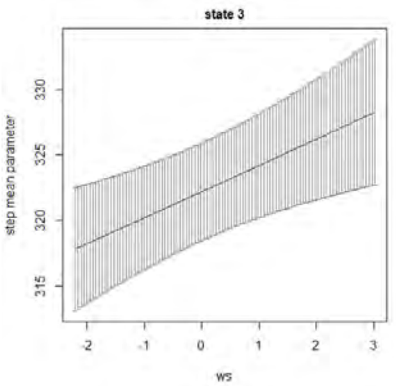
7.5.1 Northern Gannet

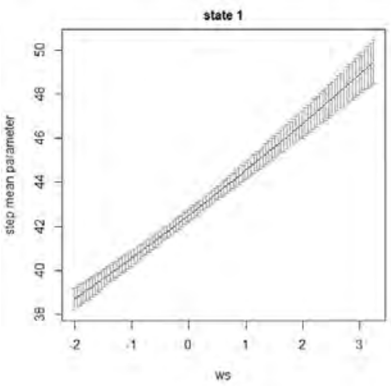
(a) Alderney

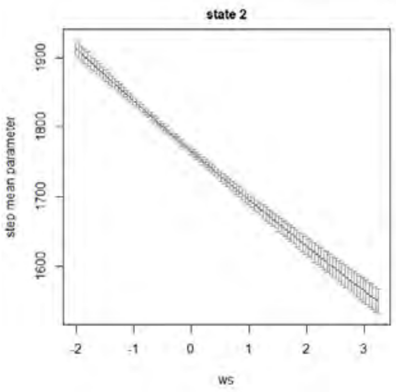


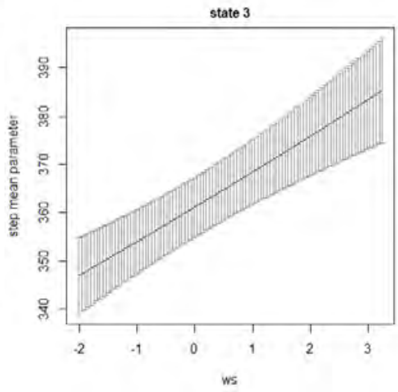


(b) Bass Rock 2010









(c) Bass Rock 2011

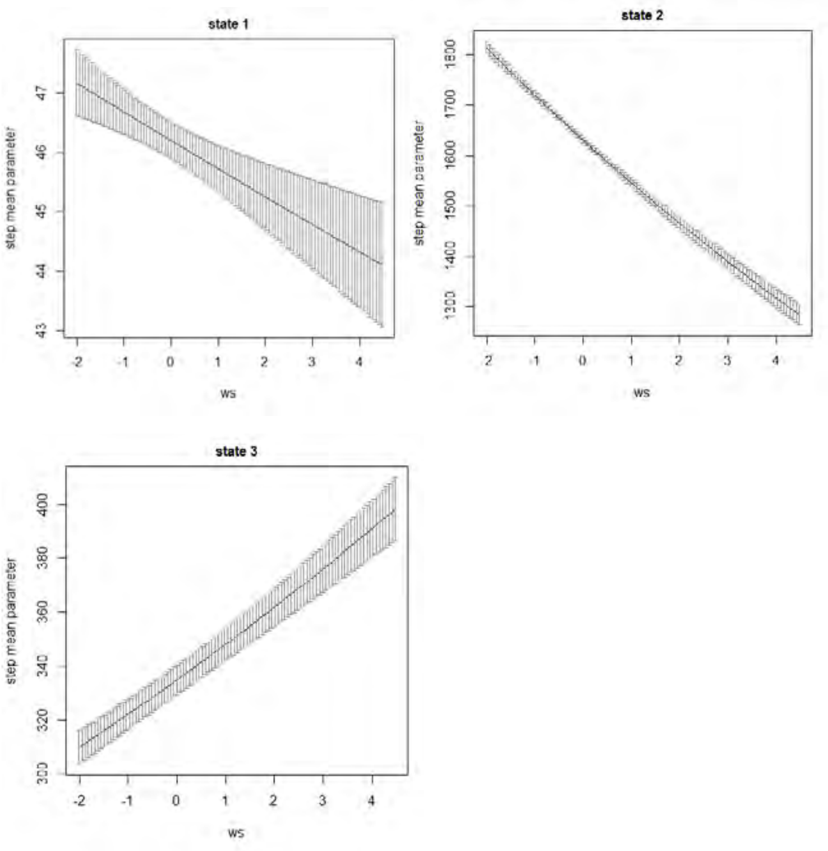


Figure A72 For Gannet, simple relationships of wind speed and step length for states 1, 2 and 3 (floating, commuting and foraging/searching); wind speeds are standardised (see methods) for each colony.

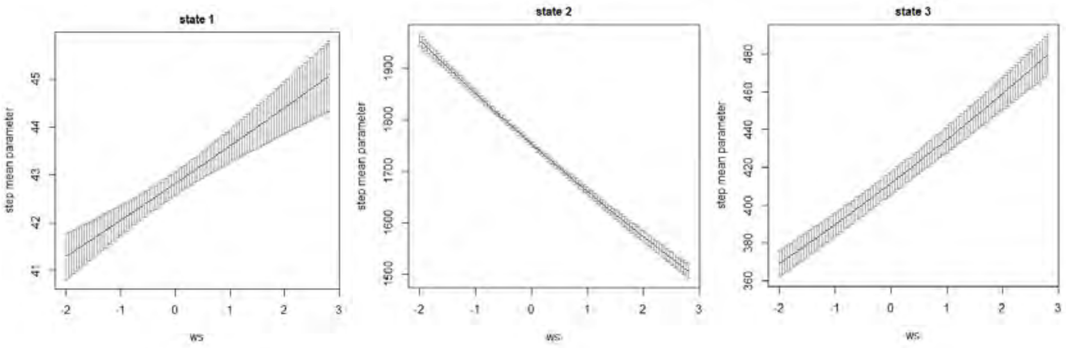
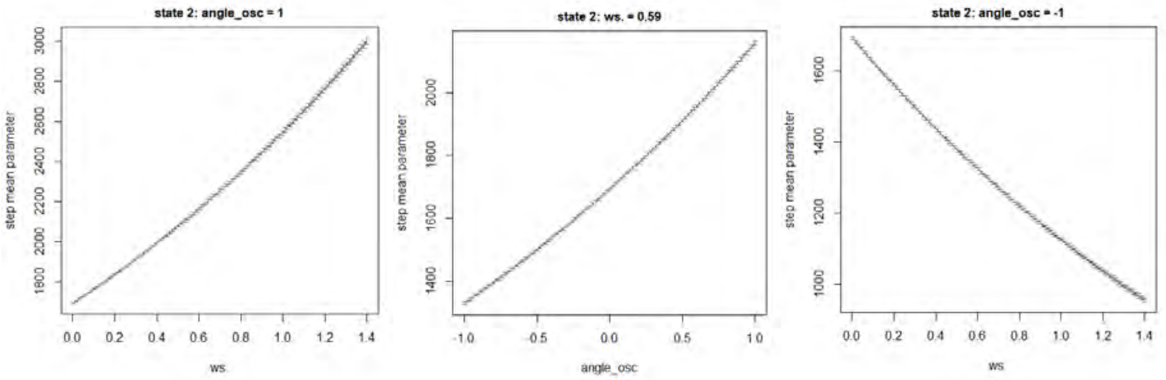
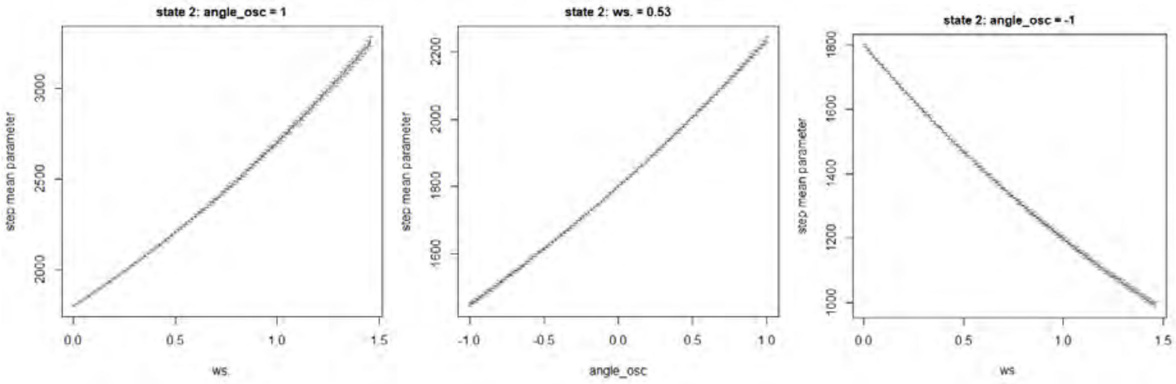


Figure A73 For Gannet, simple relationships of wind speed and step length for states 1, 2 and 3 (floating, commuting and foraging/searching) for the Bass Rock model in 2012.

(a) Alderney all years



(b) Bass Rock 2010



(c) Bass Rock 2011

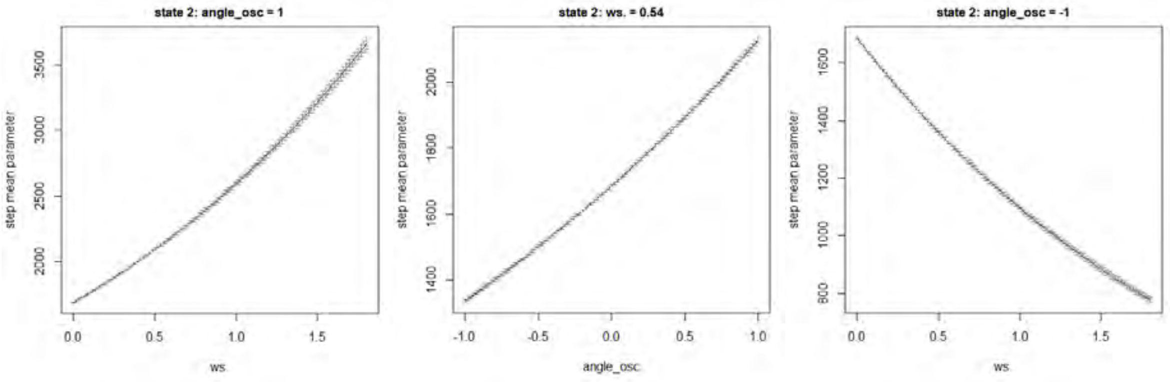
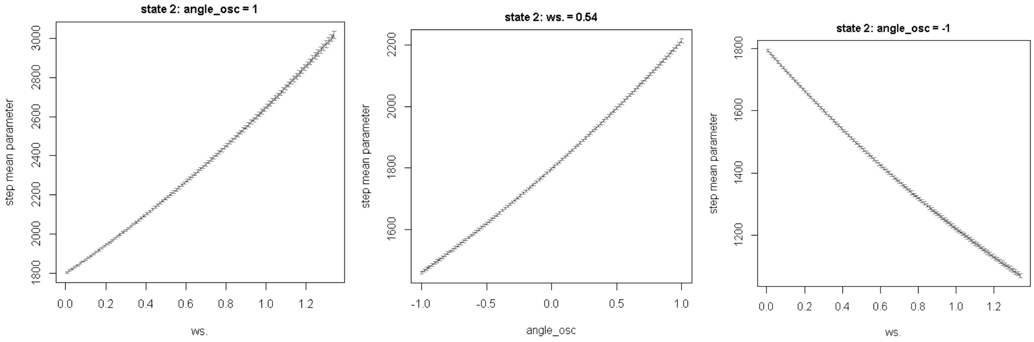


Figure A74 For Gannet, effects of wind speed and direction of travel alignment to wind direction (angular_osc) on commuting step length, showing patterns of step length over increasing (a) wind speed and (b) angular_osc; note wind speed is here adjusted to be ws/10 to allow model convergence and also include a wind strength effect on angular covariates – see methods); thus a mean 'ws' for this site as 0.59 is 5.9 m/s.

(a) Bass Rock 2012



(d) Bass Rock 2015

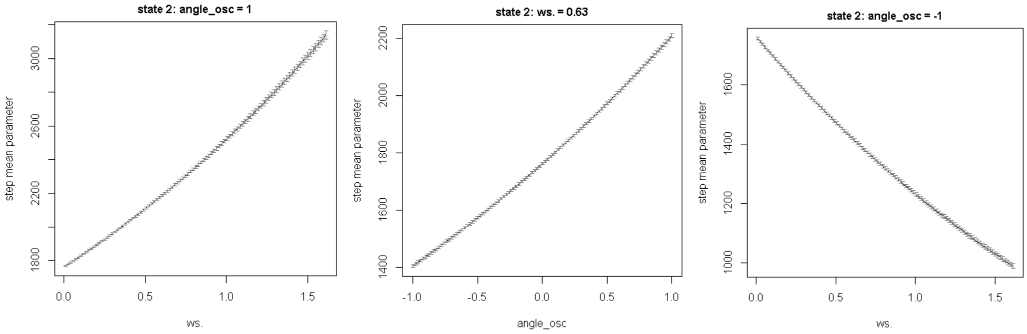
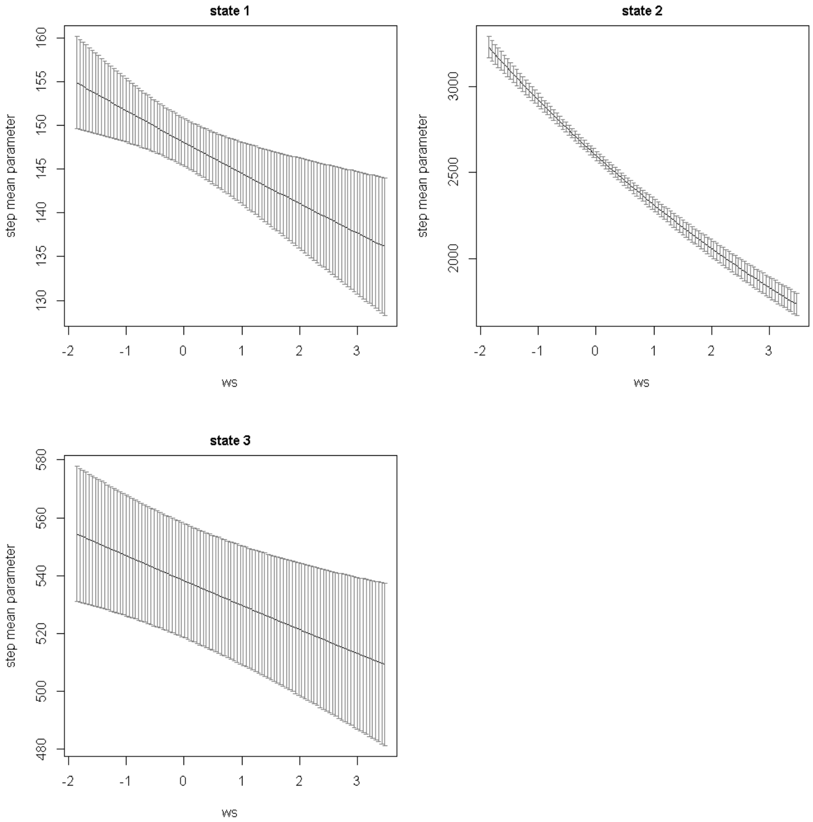


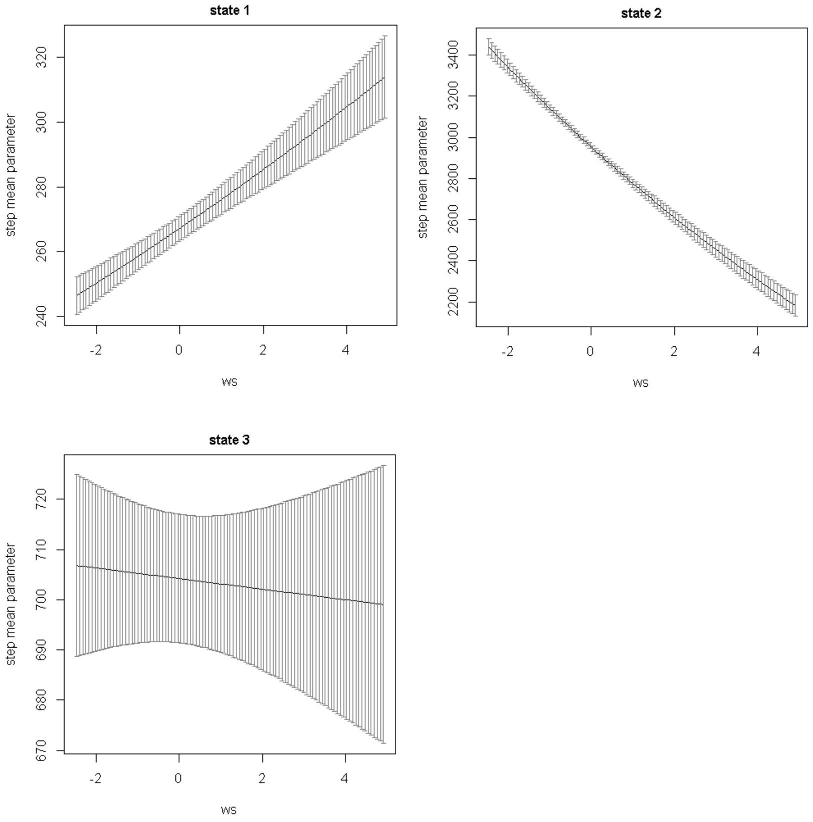
Figure A75 For Gannet, effects of wind speed and direction of travel alignment to wind direction (angular_osc) on commuting step length, showing patterns of step length over increasing (a) wind speed and (b) angular_osc; note wind speed is here adjusted to be ws/10 to allow model convergence and also include a wind strength effect on angular covariates – see methods); thus a mean ‘ws’ for this site as 0.63 is 6.3 m/s.

7.5.2 Lesser Black-backed Gull

(a) Walney



(b) Skokholm



(c) Orford Ness

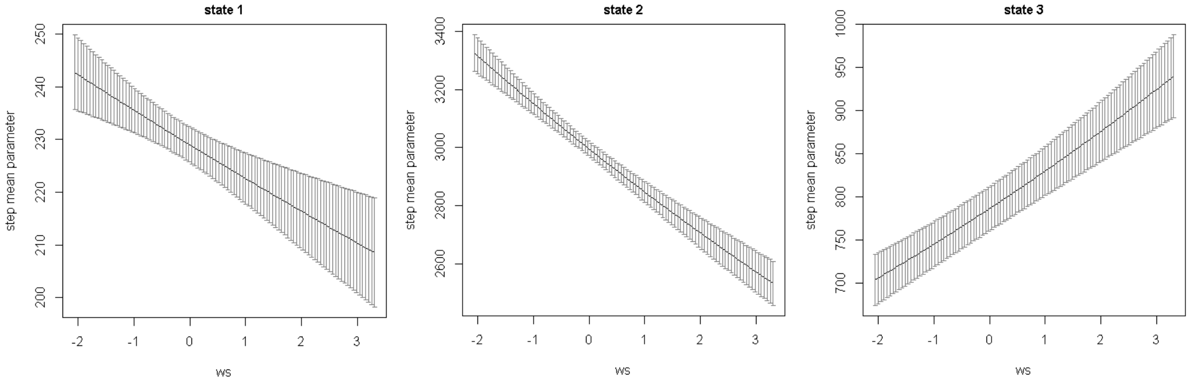
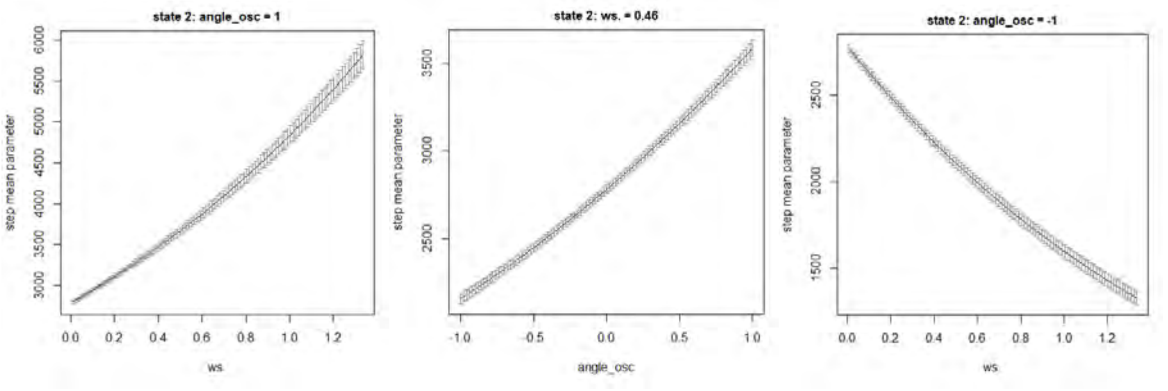
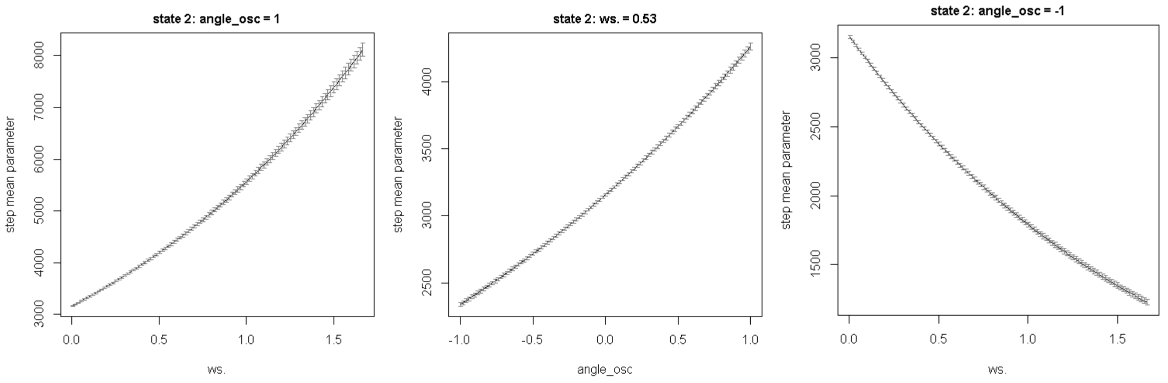


Figure A76 For Lesser Black-backed Gull, simple relationships of wind speed and step length for states 1, 2 and 3 (floating, commuting and foraging/searching).

(a) Walney



(b) Skokholm



(c) Orford Ness

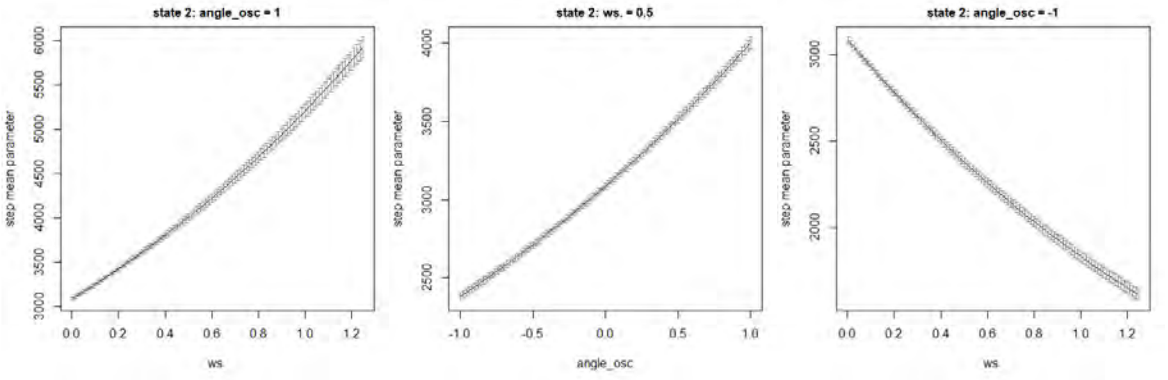
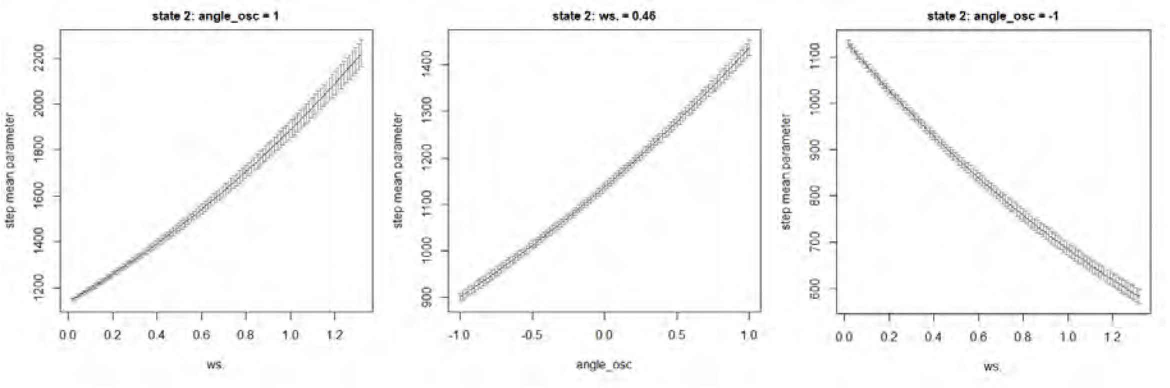


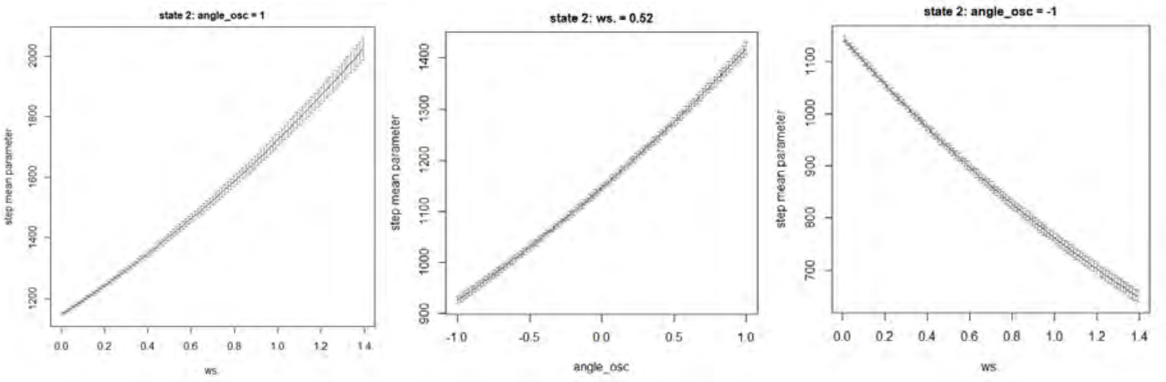
Figure A77 For Lesser Black-backed Gull, effects of wind speed and direction of travel alignment to wind direction (angular_osc) on commuting step length, showing patterns of step length over increasing wind speed and angular_osc; note wind speed is here adjusted to be ws/10 to allow model convergence and also include a wind strength effect on angular covariates – see methods); thus a mean ‘ws’ as 0.46 is 4.6 m/s.

7.5.3 Black-legged Kittiwake

(a) Isle of May



(b) Colonsay



(c) Bempton Cliffs

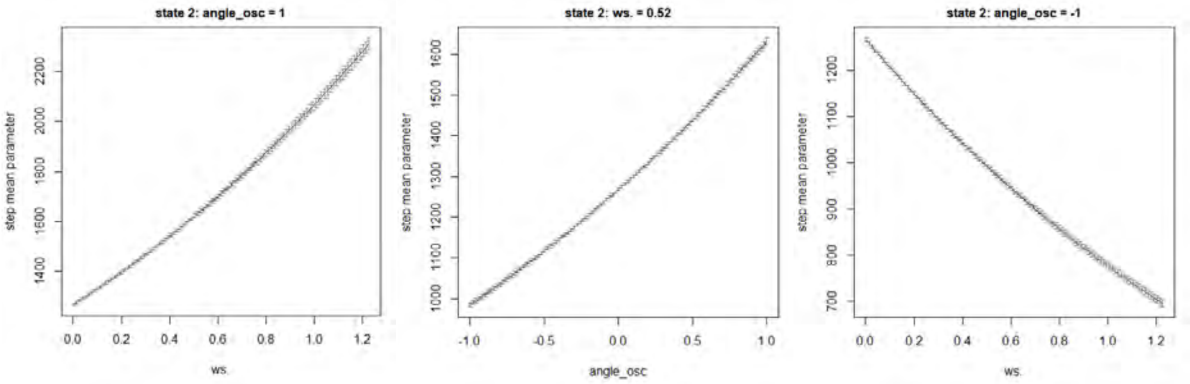


Figure A78 For Kittiwake, effects of wind speed and direction of travel alignment to wind direction (angular_osc) on commuting step length, showing patterns of step length over increasing wind speed and angular_osc; note wind speed is here adjusted to be ws/10 to allow model convergence and also include a wind strength effect on angular covariates – see methods); thus a mean ‘ws’ as 0.46 is 4.6 m/s.

(d) Orkney

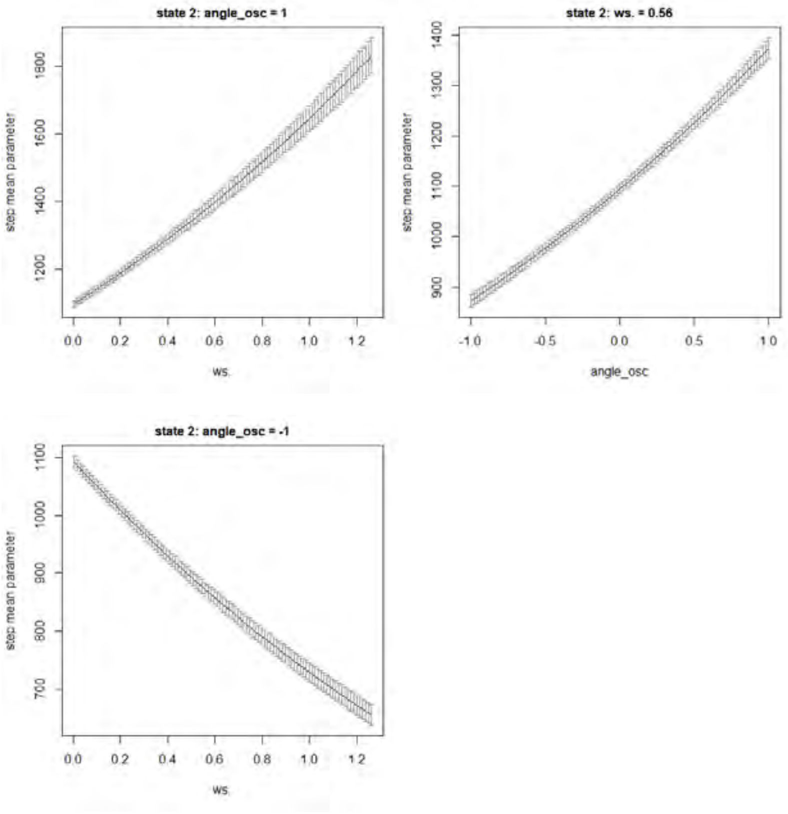
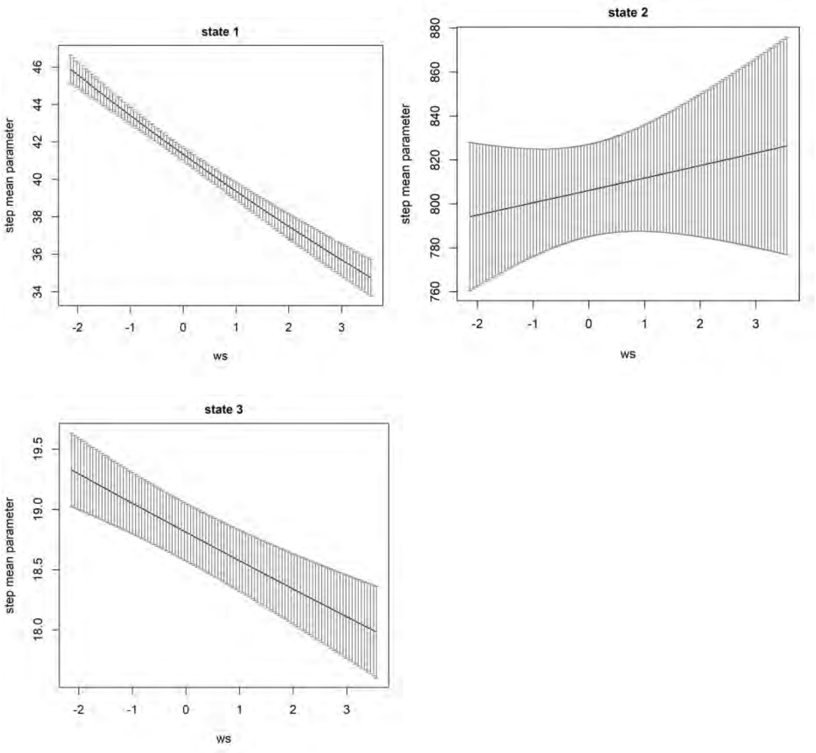


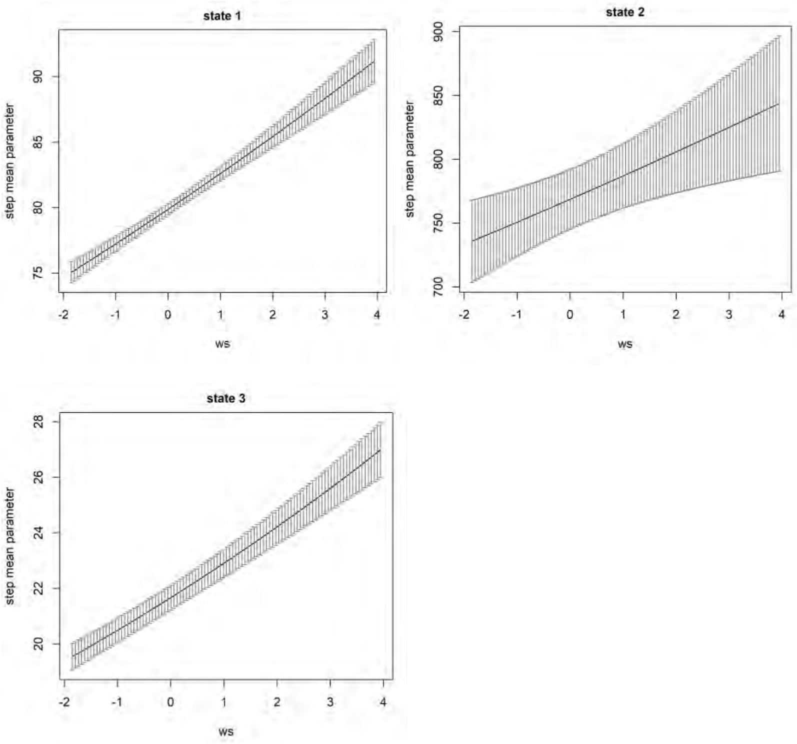
Figure continued.

7.5.4 Razorbill

(a) Colonsay



(b) Puffin Island



(c) Isle of May

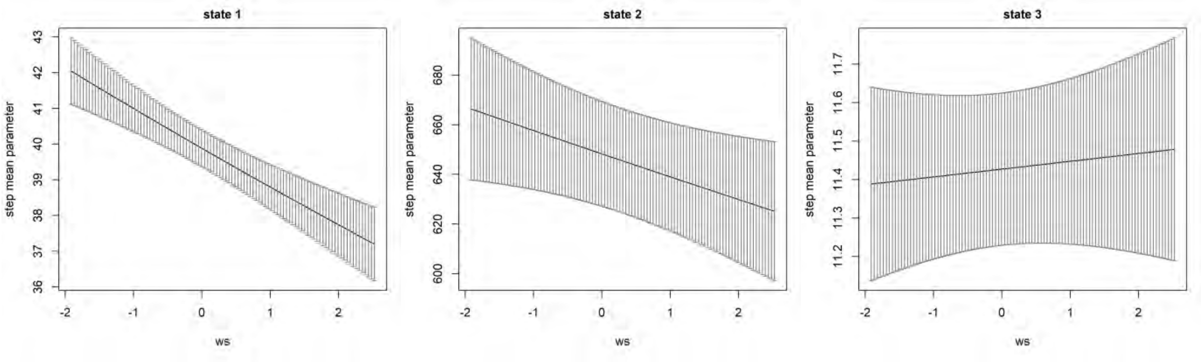
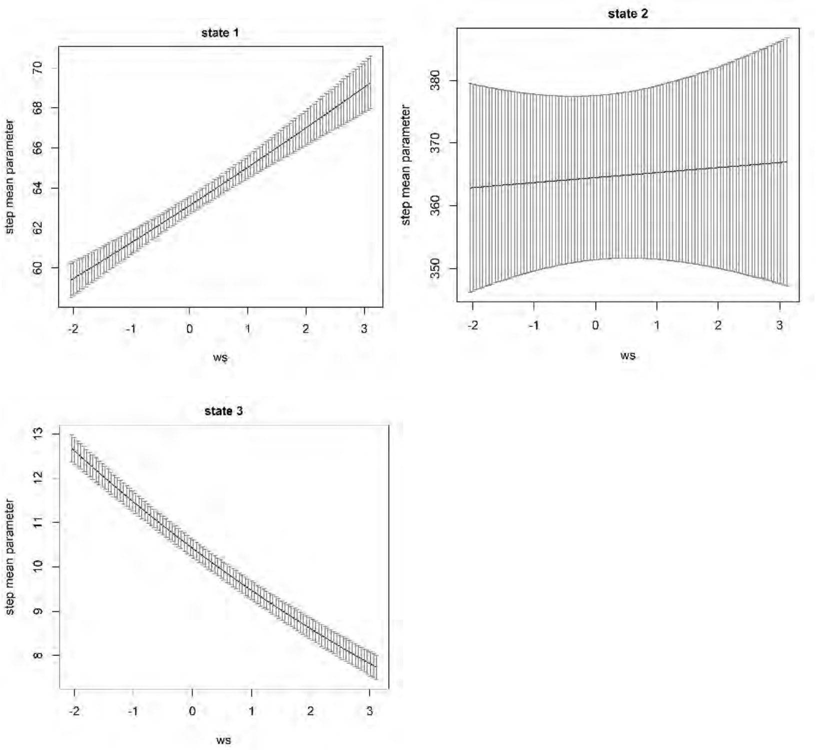


Figure A79 For Razorbill, simple relationships of wind speed and step length for states 1, 2 and 3 (floating, commuting and foraging/searching). Wind speed is fitted as a standardised variable.

7.5.5 Common Guillemot

(a) Puffin Island



(b) Isle of May

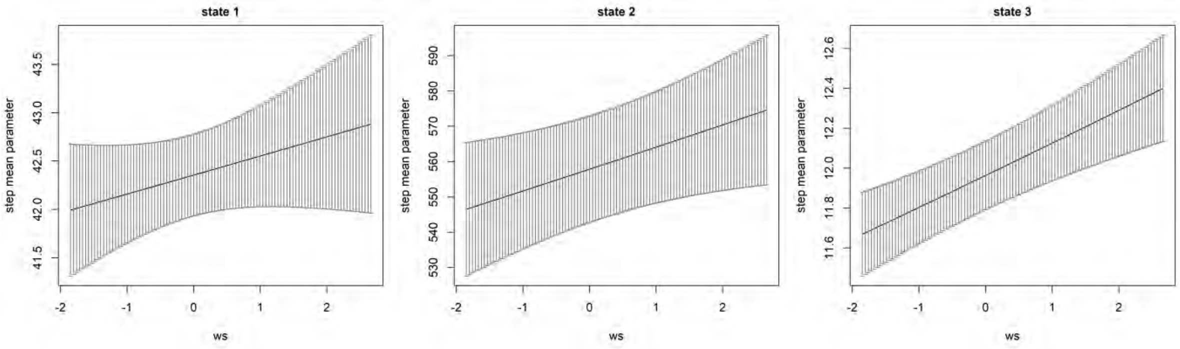


Figure A80 For Guillemot, simple relationships of wind speed and step length for states 1, 2 and 3 (floating, commuting and foraging/searching) for (a) Puffin Island and (b) Isle of May.

(a) Colonsay inc. diving

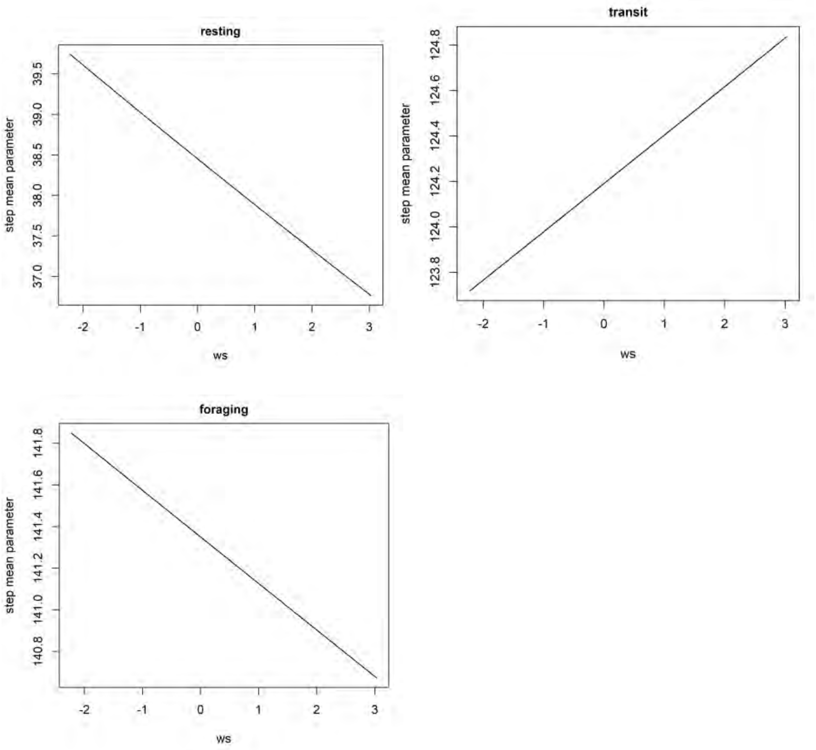


Figure A81 For Guillemot, simple relationships of wind speed and step length for states 1, 2 and 3 (floating, commuting and foraging/searching) in relation to (a) Colonsay inc. diving. Wind speed is fitted as a standardised variable.

7.6 Appendix AF. AIC tables for individual species

7.6.1 Northern Gannet

Table A2 For Gannet, competing model list for comparing inclusion of covariates on transition probability between and within states at each colony; 'hour' represents the circular consinor(hour) variable, 'ws' spline(ws), 'jd' Julian date, and 'cdist' distance from the colony; stepturn is a model with only wind speed and direction included for effects on step length and turning angle; NULL is a model with no covariates included at all. * = model not converged.

(a) Alderney

Rank	Model	AIC	dAIC
1	hour.jd.cdist.ws	2615401.84	0.00
2	hour.jd.cdist	2615411.00	9.16
3	hour.cdist.w	2615448.81	46.97
1	hour.cdist	2615453.09	51.26
2	hour.jd.ws	2616347.04	945.20
3	hour.jd	2616364.46	962.62
4	hour.ws	2616382.19	980.35
5	hour	2616409.21	1007.37
6	jd.cdist.ws	2616420.73	1018.89
7	jd.cdist	2616422.98	1021.14
8	cdist	2616455.74	1053.90
9	cdist.ws	2616461.14	1059.31
10	jd.ws.	2617558.10	2156.26
11	jd	2617582.27	2180.44
12	ws	2617585.60	2183.76
13	NULL.wswd.stan	2617614.00	2212.16
14	NULL	2619618.00	4216.16

(b) Bass Rock 2010

Rank	Model	AIC	dAIC
1	hour.jd.cdist.ws	1357071.00	0.00
2	hour.jd.cdist	1357114.00	43.00
3	hour.cdist.ws	1357129.00	58.00
4	hour.cdist	1357194.00	123.00
5	hour.ws	1357505.00	434.00
6	hour.jd	1357514.00	443.00
7	hour	1357587.00	516.00
8	jd.cdist	1357832.00	761.00
9	cdist.ws	1357840.00	769.00
10	cdist	1357913.00	842.00
11	jd.ws	1358272.00	1201.00
12	ws	1358315.00	1244.00
13	jd	1358334.00	1263.00
14	NULL.wswd.stan	1358388.00	1317.00
15	NULL	1359337.00	2266.00
16	hour.jd.ws*	-	-
17	jd.cdist.ws*	-	-

(c) Bass Rock 2011

Rank	Model	AIC	dAIC
1	hour.jd.cdist.ws	1249432.00	0.00
2	hour.jd.cdist	1249452.00	20.00
3	hour.cdist	1249492.00	60.00
4	hour.cdist.ws	1249507.00	75.00
5	hour.jd	1249609.00	177.00
6	hour.jd.ws	1249630.00	198.00
7	hour.ws	1249681.00	249.00
8	jd.cdist	1249978.00	546.00
9	jd.cdist.ws	1249989.00	557.00
10	cdist	1250034.00	602.00
11	cdist.ws	1250039.00	607.00
12	jd	1250193.00	761.00
13	jd.ws	1250215.00	783.00
14	NULL.wswd.stan	1250238.00	806.00

15	ws	1250257.00	825.00
16	NULL	1251612.00	-
17	hour	-	-

(d) Bass Rock 2012

Rank	**Model**	**AIC**	**dAIC**
1	hour.jd.cdist	1604325.00	0.00
2	hour.cdist.ws	1604392.00	67.00
3	hour.cdist	1604430.00	105.00
4	hour.jd.ws	1604698.00	373.00
5	hour.jd	1604723.00	398.00
6	hour.ws	1604782.00	457.00
7	hour	1604824.00	499.00
8	jd.cdist	1605132.00	807.00
9	cdist.ws	1605194.00	869.00
10	cdist	1605241.00	916.00
11	jd	1605626.00	1301.00
12	NULL.wswd.stan	1605674.00	1349.00
13	ws	1605689.00	1364.00
14	NULL	1606253.00	1928.00
15	hour.jd.cdist.ws	-	-
16	jd.cdist.ws	-	-
17	jd.ws	-	-

7.6.2 Lesser Black-backed Gull

Table A3 For Lesser Black-backed Gull, competing model list for comparing inclusion of covariates on transition probability between and within states at each colony; ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘cdist’ distance from the colony; stepturn is a model with only wind speed and direction included for effects on step length and turning angle; NULL is a model with no covariates included at all.; * = model not converged

(a) Walney

Rank	Model	AIC	dAIC
1	hour.jd.cdist.ws	352532.8	0
2	hour.jd.cdist	352582.1	49.3
3	hour.cdist.ws	352700.8	168
4	hour.cdist	352760.7	227.9
1	hour.jd.ws	352877.6	344.8
2	jd.cdist.ws	352893.9	361.1
3	jd.cdist	352904.7	371.9
4	hour.jd	352924.9	392.1
5	cdist.ws	353037.5	504.7
6	hour.ws	353096.1	563.3
7	hour	353154	621.2
8	jd.ws	353177	644.2
9	jd	353190	657.2
10	ws	353373.6	840.8
11	NULL.wswd.stan	353399.2	866.4
16	NULL	353814.2	NA
17	cdist	NA	NA

(b) Skokholm

Rank	**Model**	**AIC**	**dAIC**
1	hour.jd.cdist.ws	1064114.93	0.00
2	hour.jd.cdist	1064119.89	4.96
3	hour.cdist.ws	1064203.80	88.86

1	hour.cdist	1064213.93	99.00
2	jd.cdist.ws	1064314.90	199.97
3	jd.cdist	1064315.14	200.21
4	cdist.ws	1064393.71	278.78
5	cdist	1064409.55	294.62
6	hour.jd.ws	1064996.42	881.49
7	hour.jd	1065006.75	891.82
8	hour.ws	1065030.72	915.79
9	hour	1065040.22	925.28
10	jd.ws	1065141.04	1026.11
11	jd	1065151.53	1036.60
12	ws	1065181.42	1066.49
13	NULL.wswd	1065401.00	1286.07
14	NULL	1066117.00	2002.07

(c) Orford Ness

Rank	Model	AIC	dAIC
1	hour.jd.cdist.ws	283046.69	0.00
2	hour.cdist.ws	283066.72	20.03
3	hour.cdist	283082.40	35.71
4	jd.cdist	283252.55	205.86
5	jd.cdist.ws	283265.30	218.61
6	cdist	283296.15	249.46
7	cdist.ws	283304.93	258.24
8	hour	283323.60	276.91
9	hour.ws	283328.61	281.91
10	hour.jd	283330.83	284.14
11	jd	283491.16	444.46
12	jd.ws	283510.22	463.53
13	ws	283521.85	475.16
14	NULL.wswd	283690.20	643.51
15	NULL	283877.70	831.01
16	hour.jd.cdist	NA	NA
17	hour.jd.ws	NA	NA

7.6.3 Black-legged Kittiwake

Table A4 For Kittiwake, competing model list for comparing inclusion of covariates on transition probability between and within states at each colony; ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘cdist’ distance from the colony; stepturn is a model with only wind speed and direction included for effects on step length and turning angle; NULL is a model with no covariates included at all. * = model not converged

Colony	Rank	Model	AIC	dAIC
Isle of May	1	hour.jd.cdist.ws	371412.0	0.0
	2	ws	371930.8	518.8
	3	hour.jd.cdist	371955.2	543.2
	4	hour.cdist	371968.9	556.9
	5	hour.jd.ws	372100.4	688.4
	6	hour.ws	372128.9	716.9
	7	hour.jd	372160.6	748.6
	8	hour	372170.3	758.3
	9	cdist.ws	372220.8	808.8
	10	jd.cdist	372244.7	832.7
	11	cdist	372273.6	861.6
	12	jd.ws	372405.4	993.4
	13	jd	372465.7	1053.7
	14	stepturn	372481.7	1069.7
	15	NULL	372730.7	1318.7
Colonsay	1	hour.jd.cdist.ws	1099819.0	0.0
	2	hour.jd.cdist	1099823.0	4.0
	3	hour.cdist.ws	1100016.0	197.0
	4	hour.cdist	1100052.0	233.0
	5	jd.cdist.ws	1100368.0	549.0
	6	jd.cdist	1100373.0	554.0
	7	cdist.ws	1100606.0	787.0
	8	cdist	1100639.0	820.0
	9	hour.jd.ws	1101258.0	1439.0
	10	hour.jd	1101289.0	1470.0

	11	hour.ws	1101455.0	1636.0
	12	hour	1101515.0	1696.0
	13	jd.ws	1101886.0	2067.0
	14	ws	1102097.0	2278.0
	15	stepturn	1102148.0	2329.0
	16	NULL	1102663.0	2844.0
Bempton	1	hour.jd.cdist.ws	1064550.0	0.0
	2	hour.jd.cdist	1064657.0	107.0
	3	hour.cdist.ws	1064668.0	118.0
	4	hour.cdist	1064798.0	248.0
	5	hour.jd.ws	1064923.0	373.0
	6	hour.ws	1065034.0	484.0
	7	hour.jd	1065040.0	490.0
	8	hour	1065150.0	600.0
	9	jd.cdist.ws	1065165.0	615.0
	10	cdist.ws	1065252.0	702.0
	11	jd.cdist	1065268.0	718.0
	12	cdist	1065392.0	842.0
	13	jd.ws	1065552.0	1002.0
	14	ws	1065633.0	1083.0
	15	jd	1065655.0	1105.0
	16	stepturn	1065742.0	1192.0
	17	NULL	1065898.0	1348.0
Orkney	1	hour.jd.cdist	687026.7	0
	2	hour.jd.cdist.ws	687031.5	4.8
	3	hour.cdist	687049	22.3
	4	jd.cdist.ws	687069.4	42.7
	5	cdist.ws	687089.6	62.9
	6	jd.cdist	687096.4	69.7
	7	cdist	687100.3	73.6
	8	hour.jd.ws	688982.5	1955.8
	9	hour.jd	689066.2	2039.5
	10	jd.ws	689084.5	2057.8
	11	NULL_4state**	689084.5	2057.8
	12	hour.ws	689098.1	2071.4
	13	hour	689173.1	2146.4

	14	jd	689183.2	2156.5
	15	ws	689199	2172.3
	16	stepturn	689288.2	2261.5
	17	NULL_3state**	690191.7	3165

** Orkney note NULL four state model included, specifying a better fit to the data than a three state;

7.6.4 Razorbill

Table A5 For Razorbill, competing models comparing inclusion of covariates for effects on transition probability between and within states at each colony; ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘cdist’ distance from the colony; stepturn is a model with only wind speed and direction included for effects on step length and turning angle; NULL is a model with no covariates included at all.; ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘colony.dist’ distance from the colony.

Colony	Rank	Model	AIC	dAIC
Colonsay	1	hour.jd.colony.dist.ws	936966.10	0.00
	2	hour.jd.colony.dist	937012.20	46.10
	3	jd.colony.dist.ws	937221.67	255.57
	4	hour.colony.dist.ws	937229.74	263.64
	5	jd.colony.dist	937278.09	311.99
	6	hour.colony.dist	937299.35	333.24
	7	colony.dist.ws	937467.75	501.65
	8	colony.dist	937541.50	575.40
	9	hour.jd.ws	941621.90	4655.80
	10	hour.jd	941697.15	4731.05
	11	hour.ws	941882.16	4916.06
	12	hour	941963.98	4997.88
	13	jd.ws	942306.69	5340.59
	14	jd	942389.76	5423.66
	15	ws	942470.48	5504.38
Puffin Island	1	hour.jd.colony.dist.ws	703759.62	0.00
	2	hour.jd.colony.dist	703775.52	15.90
	3	hour.colony.dist.ws	704003.66	244.04
	4	hour.colony.dist	704027.67	268.05
	5	jd.colony.dist.ws	704174.25	414.63
	6	jd.colony.dist	704196.87	437.26
	7	colony.dist.ws	704346.18	586.56
	8	colony.dist	704378.73	619.11
	9	hour.jd.ws	705083.41	1323.79
	10	hour.jd	705131.17	1371.55
	11	hour.ws	705395.51	1635.89

	12	hour	705431.92	1672.30
	13	jd.ws	706086.68	2327.06
	14	jd	706156.30	2396.68
	15	ws	706296.72	2537.10
Isle of May	1	hour.jd.colony.dist.ws	482572.97	0.00
	2	hour.jd.colony.dist	482613.33	40.36
	3	hour.colony.dist.ws	482621.68	48.71
	4	hour.colony.dist	482685.98	113.01
	5	jd.colony.dist.ws	482746.35	173.38
	6	colony.dist.ws	482813.30	240.33
	7	jd.colony.dist	482814.87	241.90
	8	colony.dist	482912.49	339.52
	9	hour.jd.ws	484692.72	2119.75
	10	hour	484692.72	2119.75
	11	hour.ws	484742.77	2169.80
	12	hour.jd	484762.57	2189.60
	13	jd.ws	485108.87	2535.90
	14	ws	485218.02	2645.05
	15	jd	485243.32	2670.35

Table A6 Competing models, incorporating TDR data, comparing inclusion of covariates for effects on transition probability between and within states for each colony for Razorbills; ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘colony.dist’ distance from the colony.

Colony	Rank	Model	AIC	dAIC
Colonsay	1	hour	672997.4	0
	2	ws	673574.6	577.2223
	3	hour.colony.dist	721837.9	48840.51
	4	colony.dist	721949.3	48951.89
	5	hour.jd.colony.dist	722085.9	49088.53
	6	hour.colony.dist.ws	722119.4	49122.02
	7	jd.colony.dist	722164.1	49166.79
	8	colony.dist.ws	722186.2	49188.86
	9	hour.jd.colony.dist.ws	722366.9	49369.54
	10	jd.colony.dist.ws	722434.8	49437.43
	11	jd.RData	722656.8	49659.45
	12	hour.jd	722743.3	49745.94
	13	hour.ws	722779.8	49782.4
	14	jd.ws	722934.3	49936.92
	15	hour.jd.ws	723007.6	50010.22

7.6.5 Common Guillemot

Table A7 For Guillemot, competing models comparing inclusion of covariates for effects on transition probability between and within states at each colony; ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘cdist’ distance from the colony; stepturn is a model with only wind speed and direction included for effects on step length and turning angle; NULL is a model with no covariates included at all. ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘colony.dist’ distance from the colony.

Colony	Rank	Model	AIC	dAIC
Colonsay	1	hour.colony.dist	1567512.16	0.00
	2	hour.jd	1574766.43	7254.26
	3	hour.ws	1574801.31	7289.15
	4	hour	1574845.12	7332.95
	5	jd	1575044.13	7531.97
	6	ws	1575065.17	7553.00
	7	hour.jd.colony.dist.ws	1692599.56	125087.40
	8	hour.jd.colony.dist	1692612.85	125100.69
	9	hour.colony.dist.ws	1692778.75	125266.59
	10	jd.colony.dist.ws	1692950.00	125437.84
	11	jd.colony.dist	1692962.35	125450.19
	12	colony.dist.ws	1693108.83	125596.66
	13	colony.dist	1693122.04	125609.88
	14	hour.jd.ws	1699357.19	131845.03
	15	jd.ws	1699719.78	132207.61
Puffin Island	1	hour.jd.colony.dist.ws	509073.18	0.00
	2	hour.jd.colony.dist	509133.07	59.89
	3	jd.colony.dist.ws	509205.67	132.49
	4	hour.colony.dist.ws	509332.86	259.68
	5	jd.colony.dist	509340.91	267.73
	6	hour.colony.dist	509366.56	293.38
	7	colony.dist.ws	509502.95	429.76
	8	colony.dist	509564.27	491.09
	9	hour.jd.ws	510939.71	1866.52

	10	hour.jd	511036.59	1963.40
	11	jd.ws	511226.38	2153.20
	12	hour.ws	511246.46	2173.27
	13	hour	511358.75	2285.56
	14	jd	511400.52	2327.33
	15	ws	511551.97	2478.78
Fowlsheugh	1	hour.jd.colony.dist	143685.31	0.00
	2	hour.colony.dist.ws	143714.09	28.78
	3	hour.colony.dist	143720.85	35.53
	4	jd.colony.dist.ws	143723.79	38.48
	5	colony.dist.ws	143724.66	39.35
	6	jd.colony.dist	143724.82	39.51
	7	colony.dist	143740.12	54.81
	8	hour.jd.ws	144269.51	584.20
	9	jd.ws	144291.12	605.81
	10	hour.ws	144322.32	637.00
	11	ws	144323.64	638.33
	12	hour.jd	144350.50	665.19
	13	hour	144352.61	667.30
	14	jd	144359.44	674.13
	15	hour.jd.colony.dist.ws	157438.20	13752.89
Isle of May	1	hour.jd.colony.dist.ws	804590.45	0.00
	2	hour.jd.colony.dist	804712.55	122.10
	3	hour.colony.dist.ws	804749.56	159.12
	4	jd.colony.dist.ws	804819.43	228.99
	5	hour.colony.dist	804864.58	274.14
	6	colony.dist.ws	804977.75	387.30
	7	colony.dist	805104.91	514.46
	8	hour.jd.ws	807936.28	3345.84
	9	hour.ws	808027.03	3436.58
	10	hour.jd	808128.69	3538.24
	11	jd.ws	808132.87	3542.43
	12	hour	808232.64	3642.20
	13	ws	808239.87	3649.42
	14	jd	808336.16	3745.72

Table A8 Competing models, incorporating TDR data, comparing inclusion of covariates for effects on transition probability between and within states for each colony for Guillemots; ‘hour’ represents the circular consinor(hour) variable, ‘ws’ spline(ws), ‘jd’ Julian date, and ‘colony.dist’ distance from the colony.

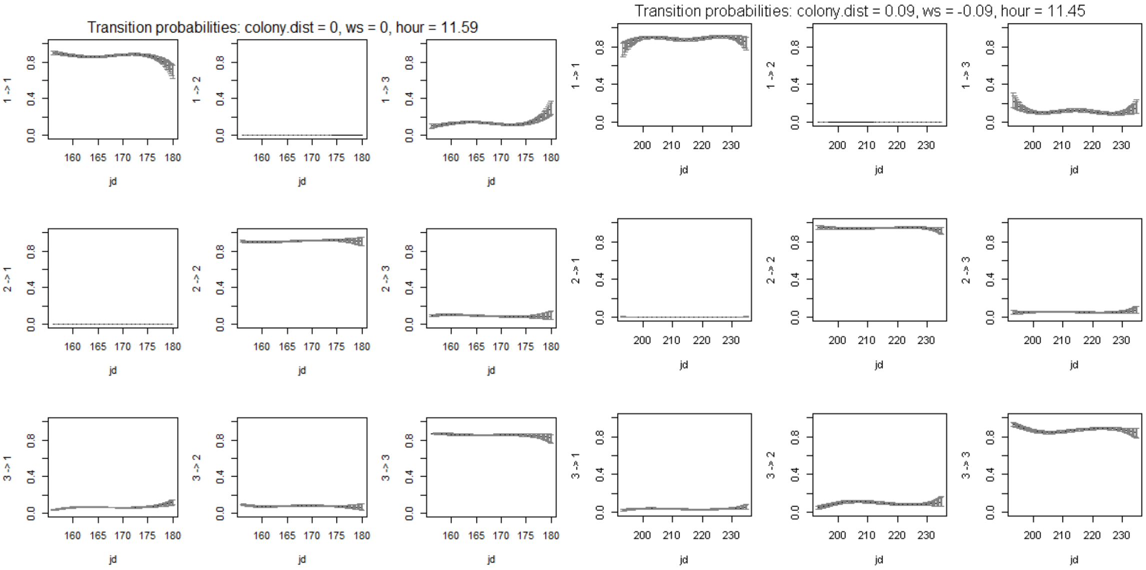
		Model	AIC	dAIC
Colonsay	1	ws	669906.04	0.00
	2	hour	670167.05	261.00
	3	colony.dist	719205.60	49299.56
	4	hour.colony.dist	719543.19	49637.15
	5	jd.colony.dist	719561.05	49655.01
	6	hour.jd.colony.dist	719675.81	49769.76
	7	colony.dist.ws	719716.35	49810.30
	8	hour.colony.dist.ws	719786.89	49880.84
	9	jd.colony.dist.ws	719803.55	49897.50
	10	hour.jd.colony.dist.ws	720038.67	50132.63
	11	jd	720487.47	50581.42
	12	hour.jd.RData	720573.10	50667.05
	13	hour.ws	720635.33	50729.29
	14	jd.ws	720710.69	50804.65
	15	hour.jd.ws	720819.45	50913.41
Fowlsheugh	1	hour.colony.dist	110156.08	0.00
	2	hour	110653.30	497.21
	3	hour.jd	110883.24	727.16
	4	hour.ws	110931.61	775.53
	5	jd.colony.dist	112349.66	2193.58
	6	colony.dist.ws	112871.52	2715.43
	7	colony.dist	120581.60	10425.52
	8	ws	120648.79	10492.71
	9	jd	120656.08	10499.99
	10	jd.ws	120915.81	10759.72
	11	hour.jd.colony.dist	120973.96	10817.87
	12	hour.colony.dist.ws	120998.44	10842.36
	13	hour.jd.ws	121028.70	10872.62
	14	jd.colony.dist.ws	121127.20	10971.11
	15	hour.jd.colony.dist.ws	121268.20	11112.12

7.7 Appendix AG Relationships between transition probability and additional variables of colony distance and Julian date

7.7.1 Northern Gannet

(a) Alderney

(b) Bass Rock 2010



(c) Bass Rock 2011

(d) Bass Rock 2012

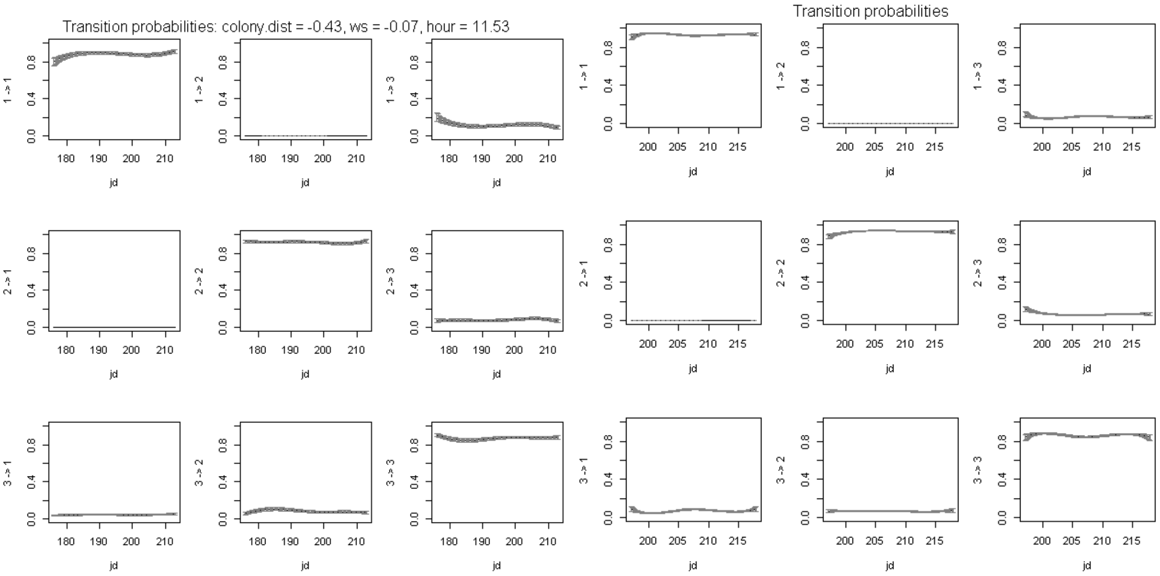
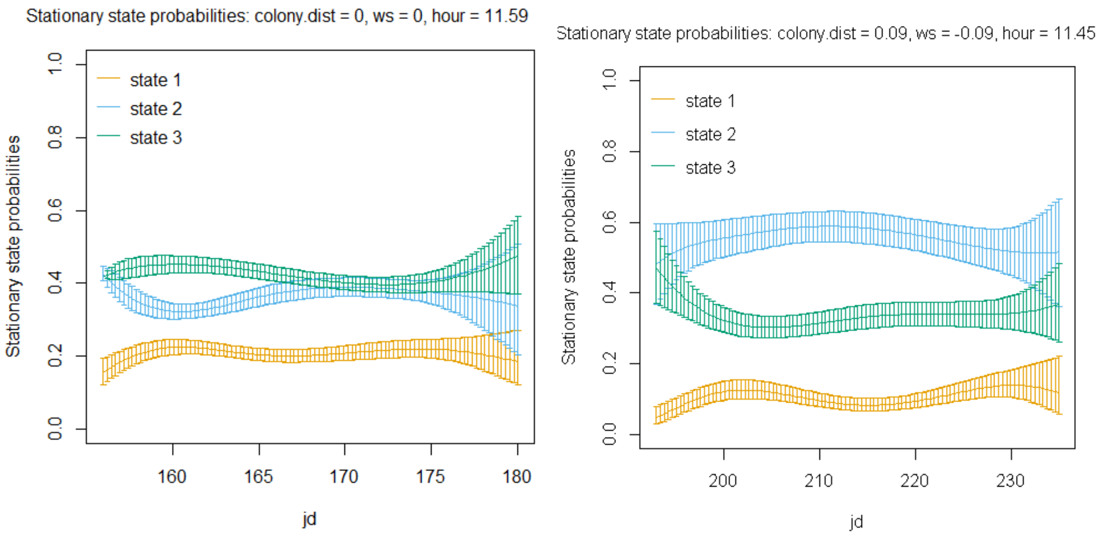
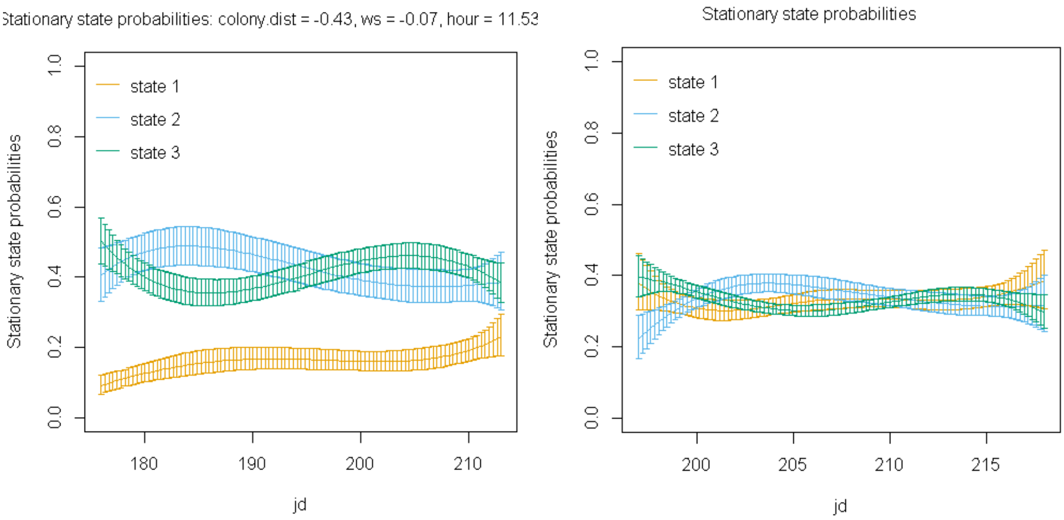


Figure A82 For Gannet, transition probabilities and stationary state probabilities for the variable of Julian date. Note, trends are plotted at the mean of other covariates. States: 1. floating, 2. commuting, 3. foraging/searching



(a) Alderney

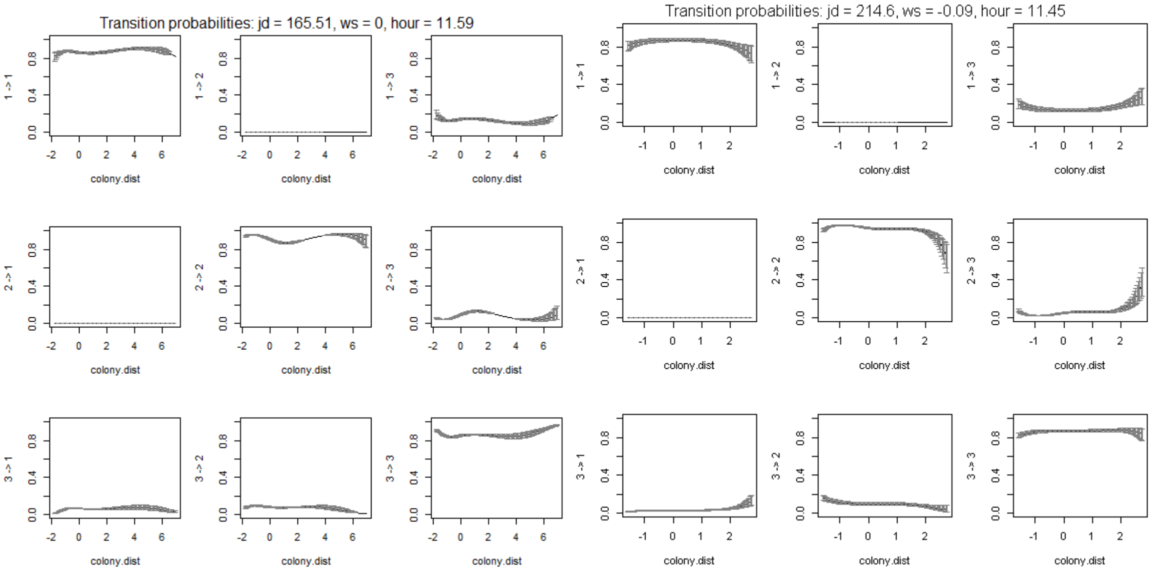
(b) Bass Rock 2010



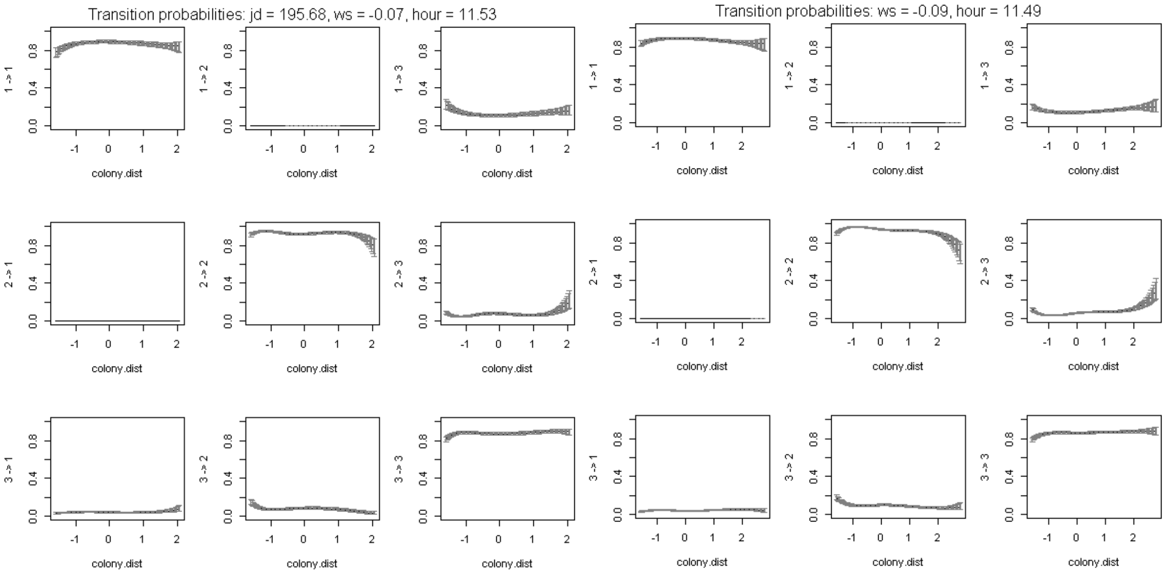
(c) Bass Rock 2011

(d) Bass Rock 2012

Figure A83 For Gannet, stationary state probabilities for the variable of Julian date for states 1, 2 and 3 (floating, commuting and foraging/searching). Note, trends are plotted at the mean of other covariates.

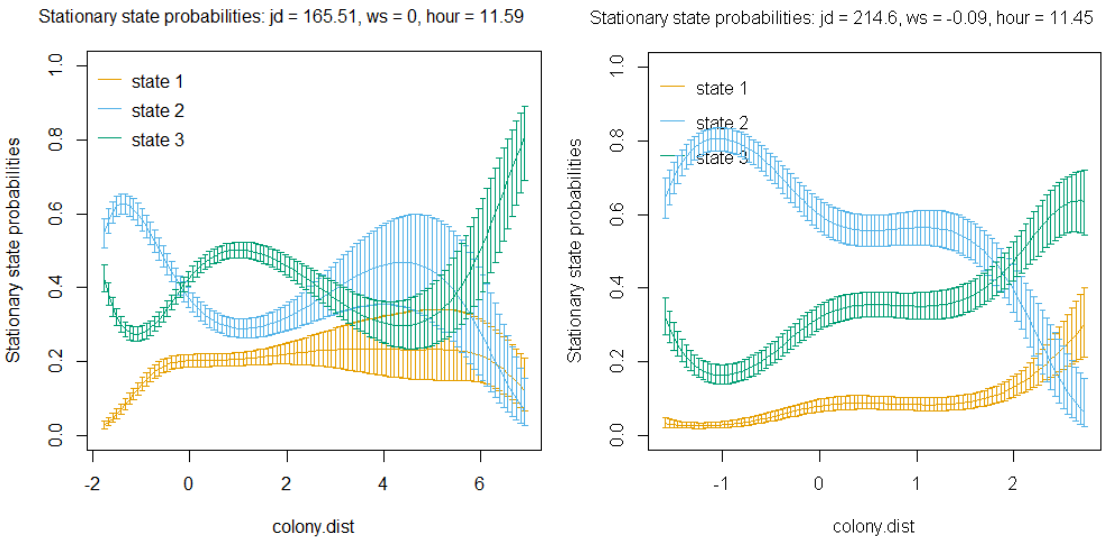


(a) Alderney (b) Bass Rock 2010



(c) Bass Rock 2011 (d) Bass Rock 2012

Figure A84 For Gannet, transition probabilities and stationary state probabilities for the variable of colony distance. Note, trends are plotted at the mean of other covariates. States: 1. floating, 2. commuting, 3. foraging/searching.



(a) Alderney

(b) Bass Rock 2010

(c) Bass Rock 2011

(d) Bass Rock 2012

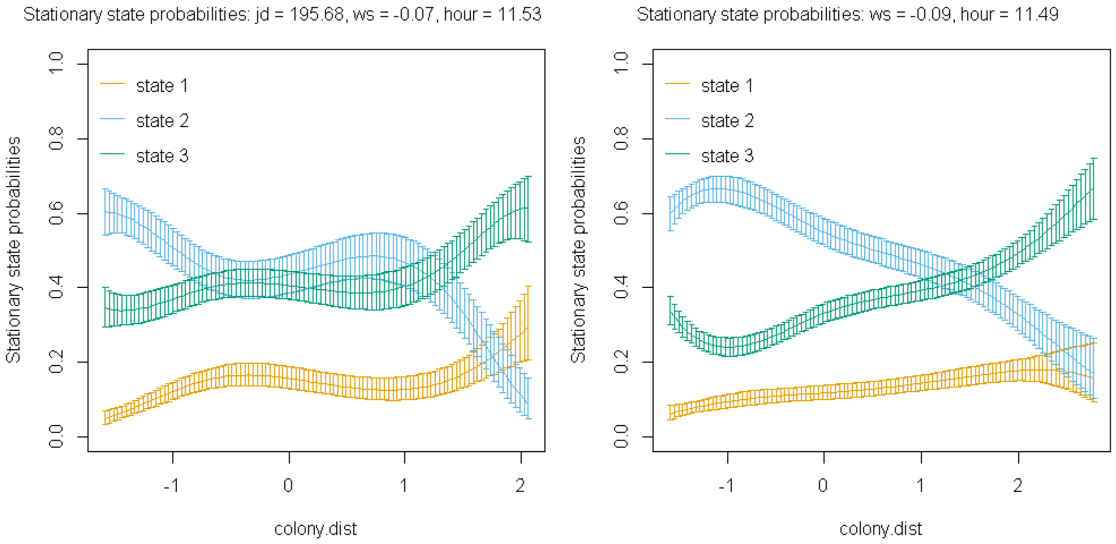
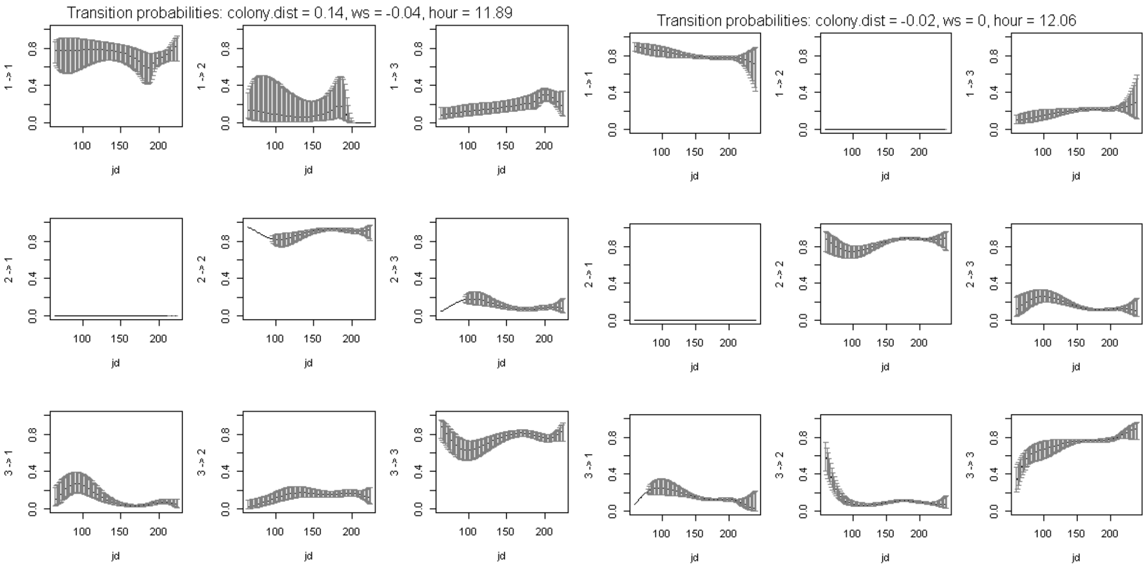


Figure A85 For Gannet, stationary state probabilities and stationary state probabilities for the variable of colony distance for states 1, 2 and 3 (floating, commuting and foraging/searching). Note, trends are plotted at the mean of other covariates.

7.7.2 Lesser Black-backed Gull



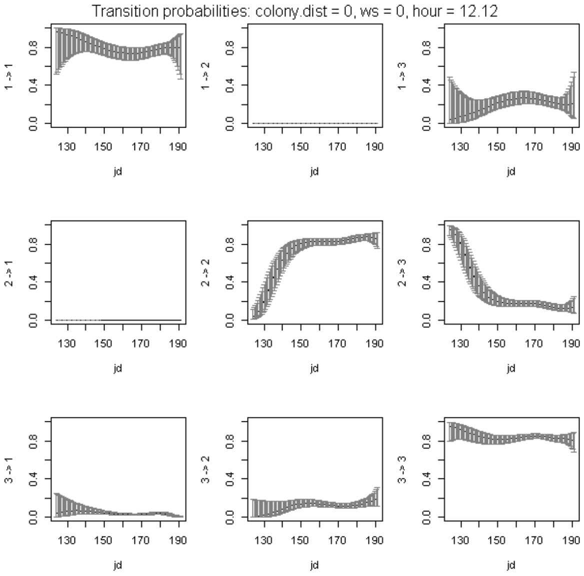
(a) Walney

Transition probabilities: colony.dist = 0.14, ws = -0.04, hour = 11.89

(b) Skokholm

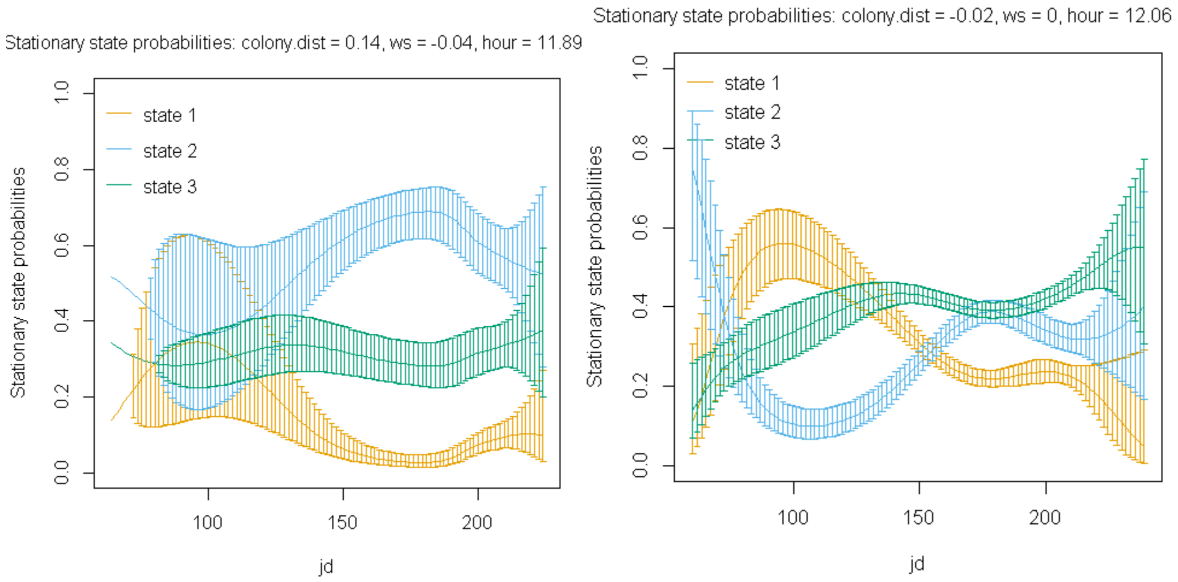
Transition probabilities: colony.dist = -0.02, ws = 0, hour = 12.06

(c) Orford Ness



Transition probabilities: colony.dist = 0, ws = 0, hour = 12.12

Figure A86 For Lesser Black-backed Gull, transition probabilities and stationary state probabilities for the variable of Julian date. Note, trends are plotted at the mean of other covariates. States: 1. floating, 2. commuting, 3. foraging/searching.


(a) Walney

(b) Skokholm

(c) Orford Ness

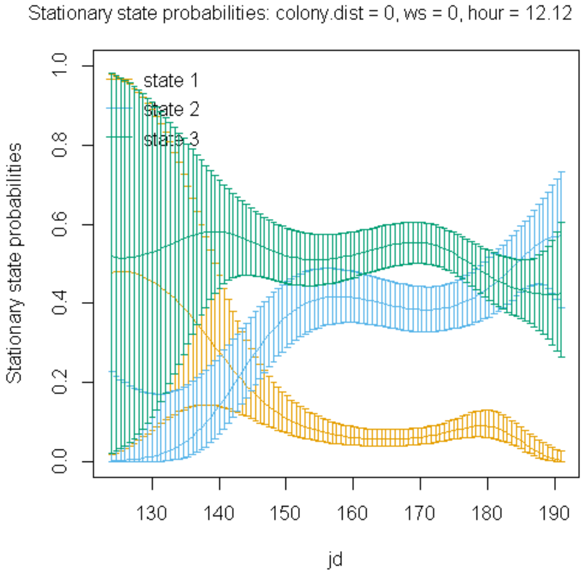
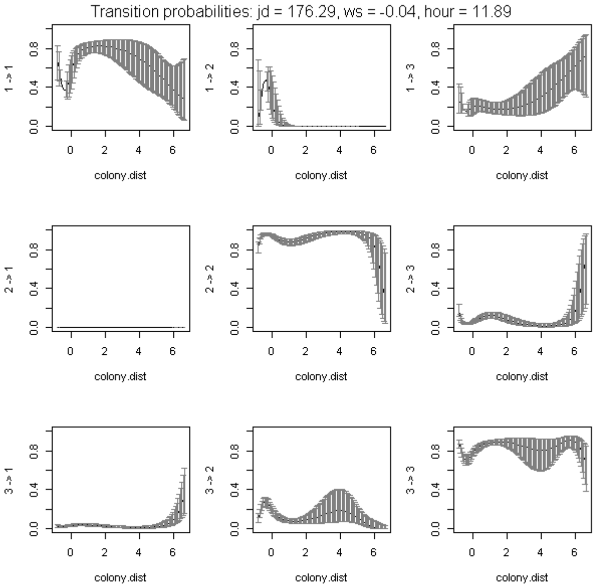
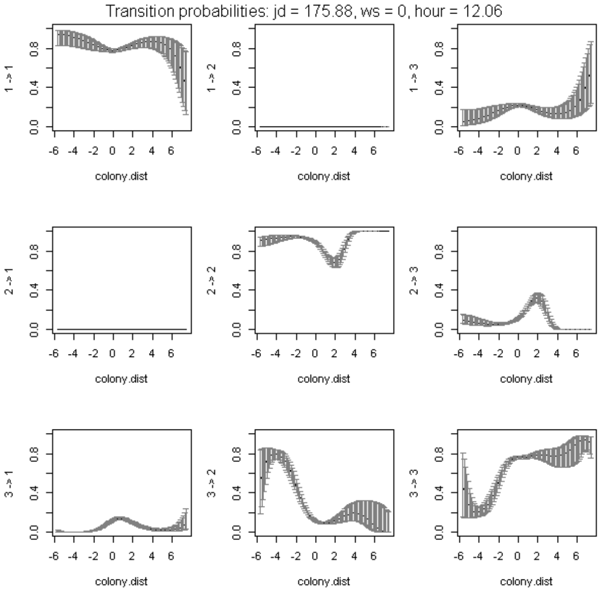


Figure A87 For Lesser Black-backed Gull, stationary state probabilities for the variable of Julian date for states 1, 2 and 3 (floating, commuting and foraging/searching). Note, trends are plotted at the mean of other covariates.

(a) Walney



(b) Skokholm



(c) Orford Ness

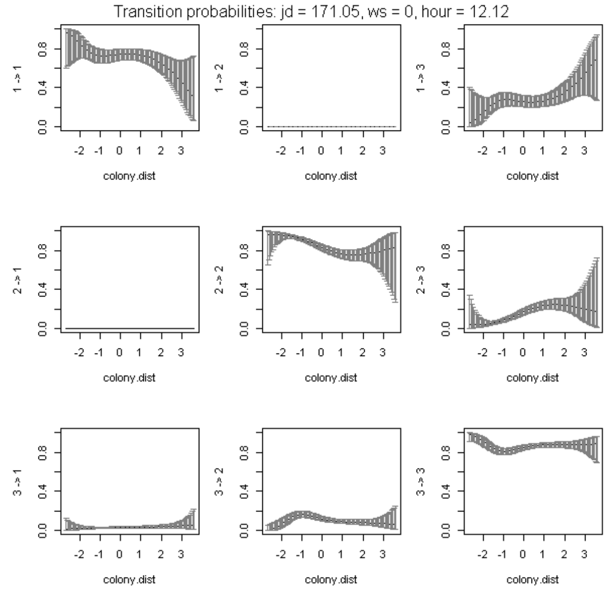
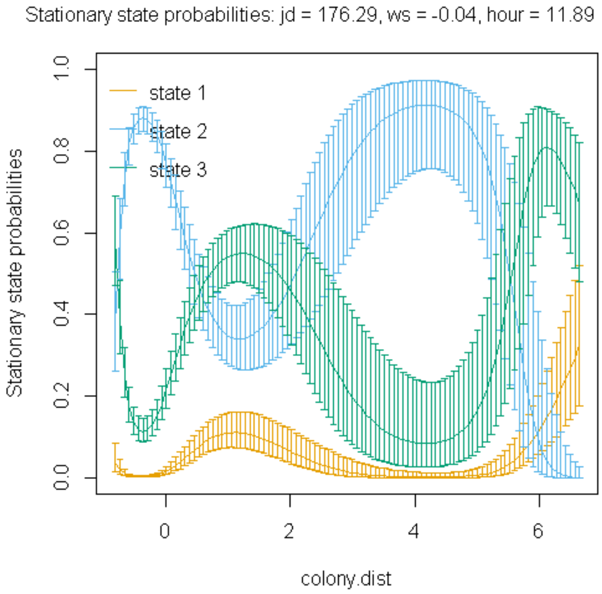


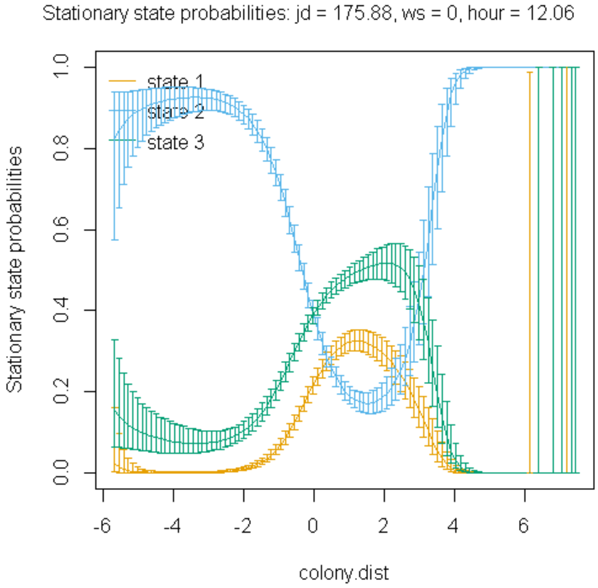
Figure A88 For Lesser Black-backed Gull, transition probabilities for the variable of distance to colony, fitted as a standardised variable. Note, trends are plotted at the mean of other covariates.

(a) Walney



Stationary state probabilities: jd = 176.29, ws = -0.04, hour = 11.89

(b) Skokholm



Stationary state probabilities: jd = 175.88, ws = 0, hour = 12.06

(c) Orford Ness

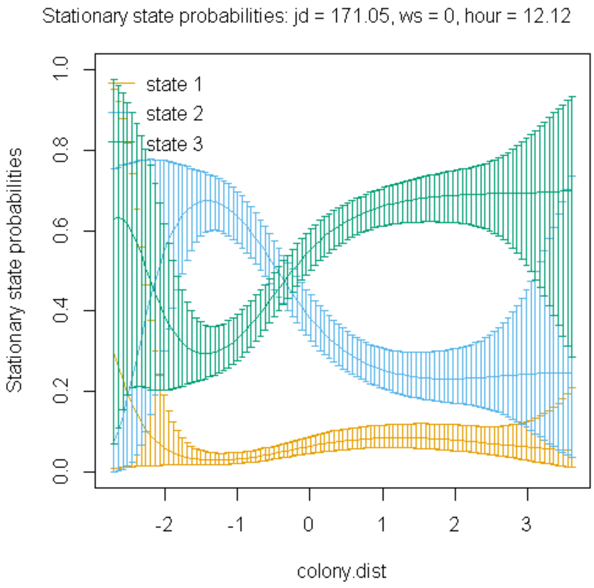
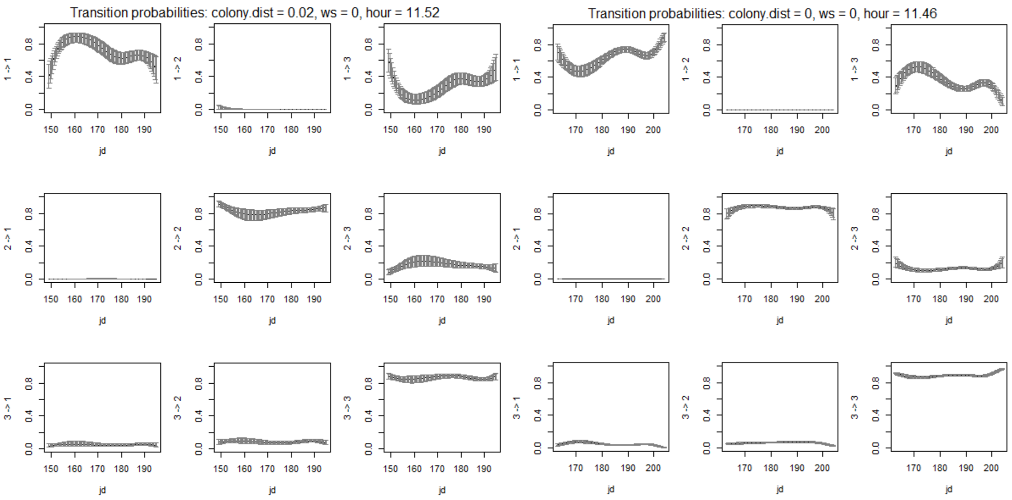
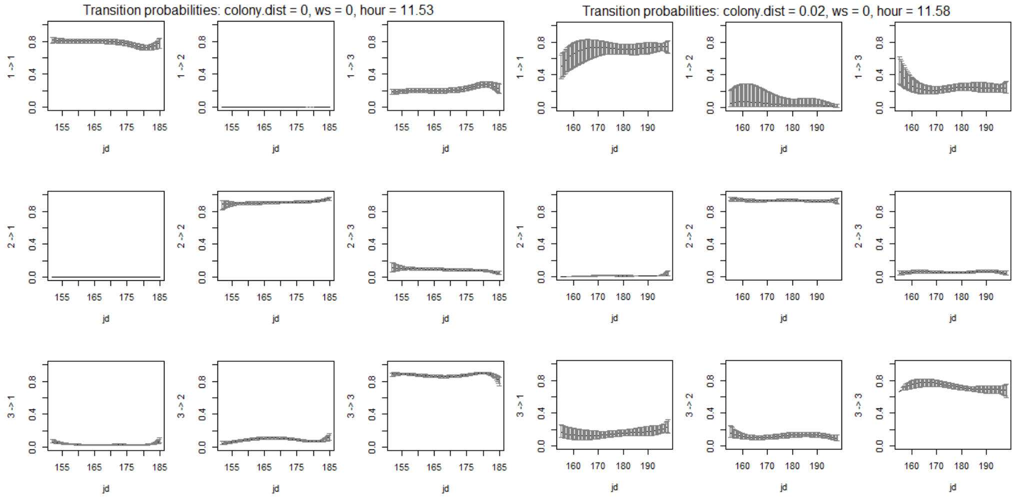


Figure A89 For Lesser Black-backed Gull, stationary state probabilities for the variable of distance to colony, fitted as a standardised variable for states 1, 2 and 3 (floating, commuting and foraging/searching)

7.7.3 Black-legged Kittiwake

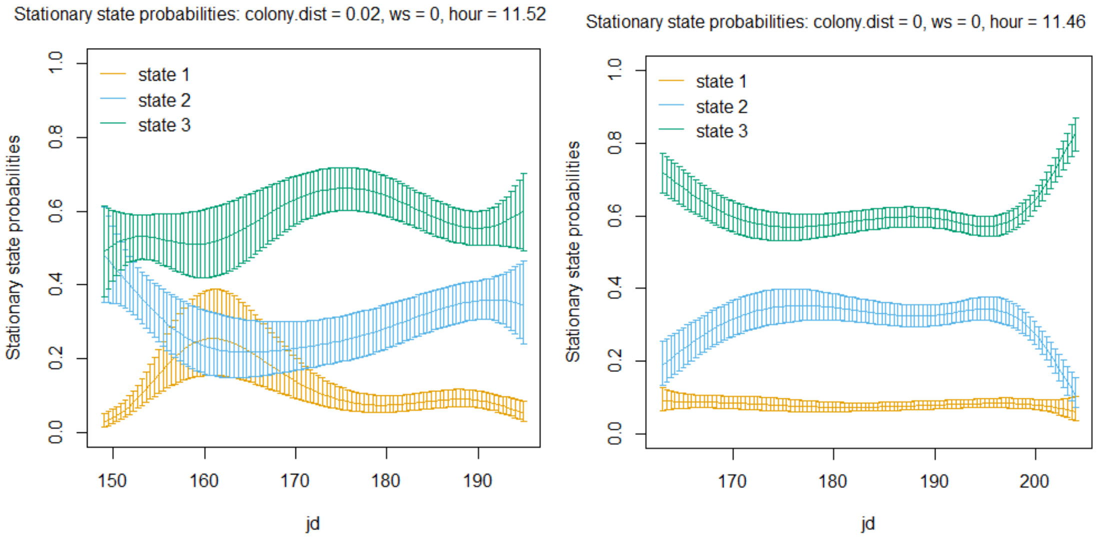

(a) Isle of May

(b) Colonsay


(c) Bempton

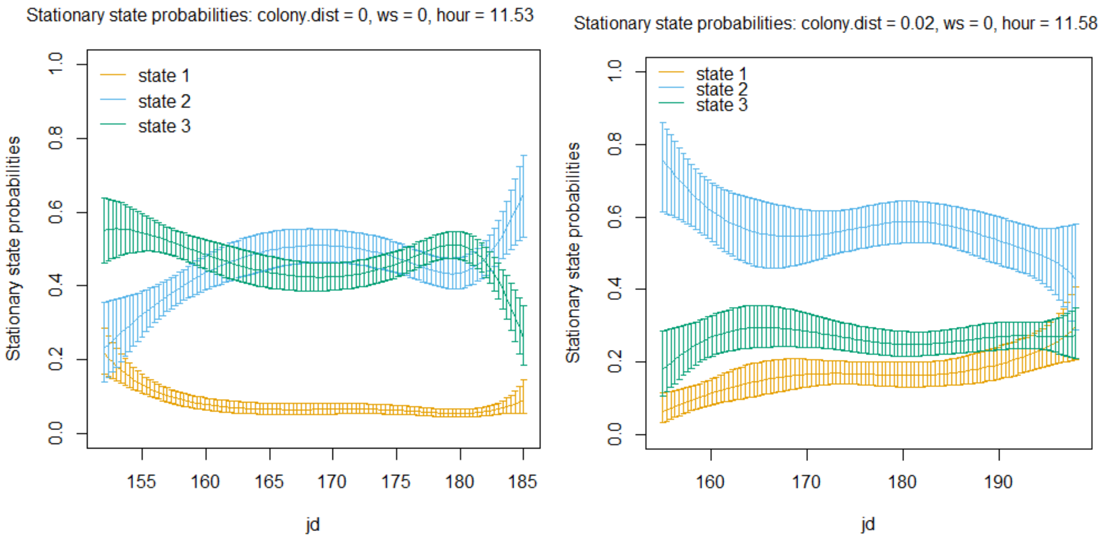
(d) Orkney

Figure A90 For kittiwake, transition probabilities and stationary state probabilities for the variable of Julian date. Note, trends are plotted at the mean of other covariates. States: 1. floating, 2. commuting, 3. foraging/searching.



(a) Isle of May

(b) Colonsay

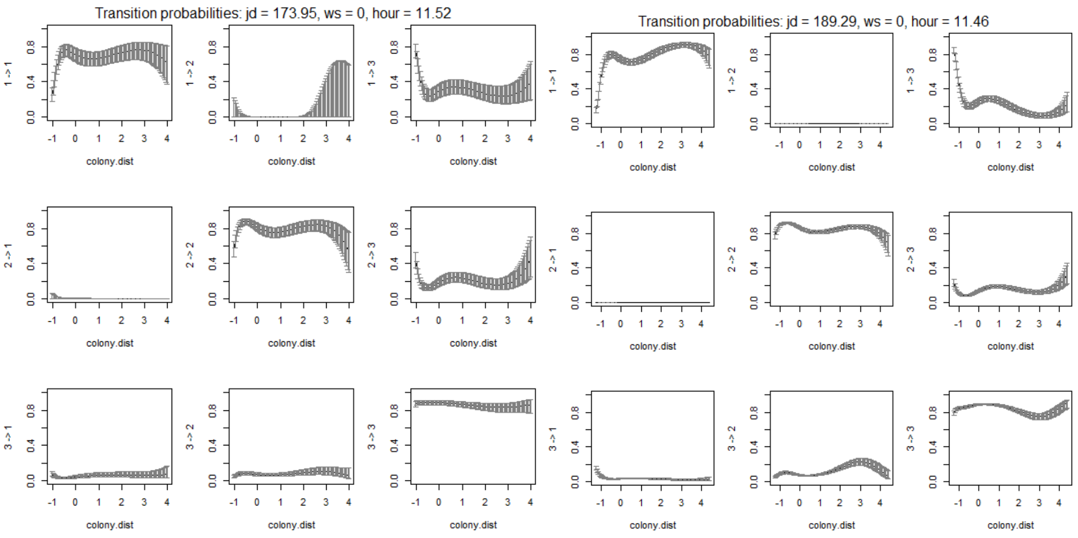


(c) Bempton

(d) Orkney

Figure A91 For Kittiwake, stationary state probabilities for the variable of Julian date for states 1, 2 and 3 (floating, commuting and foraging/searching). Note, trends are plotted at the mean of other covariates.

(a) Isle of May (b) Colonsay



(c) Bempton (d) Orkney

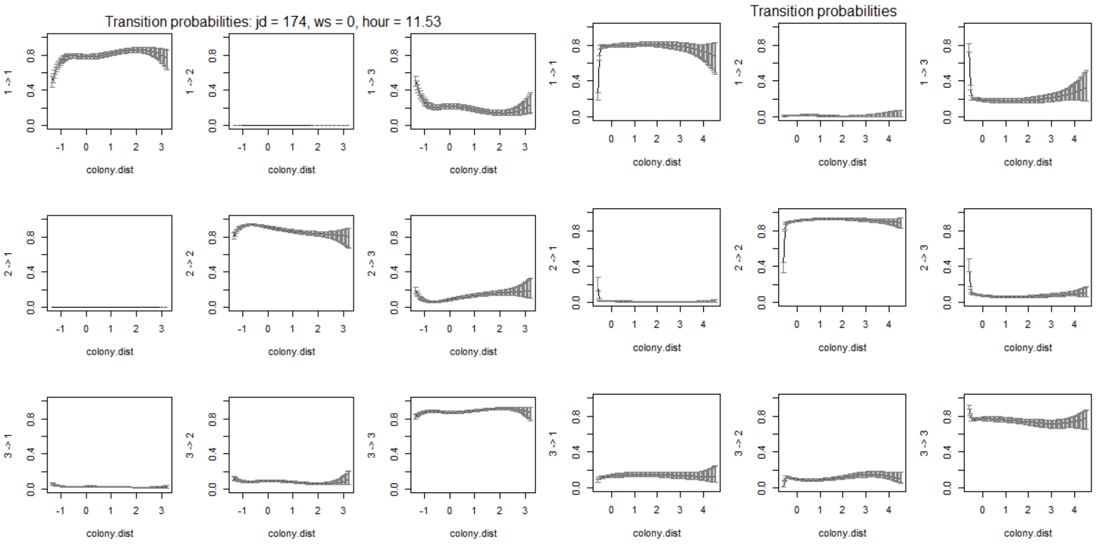
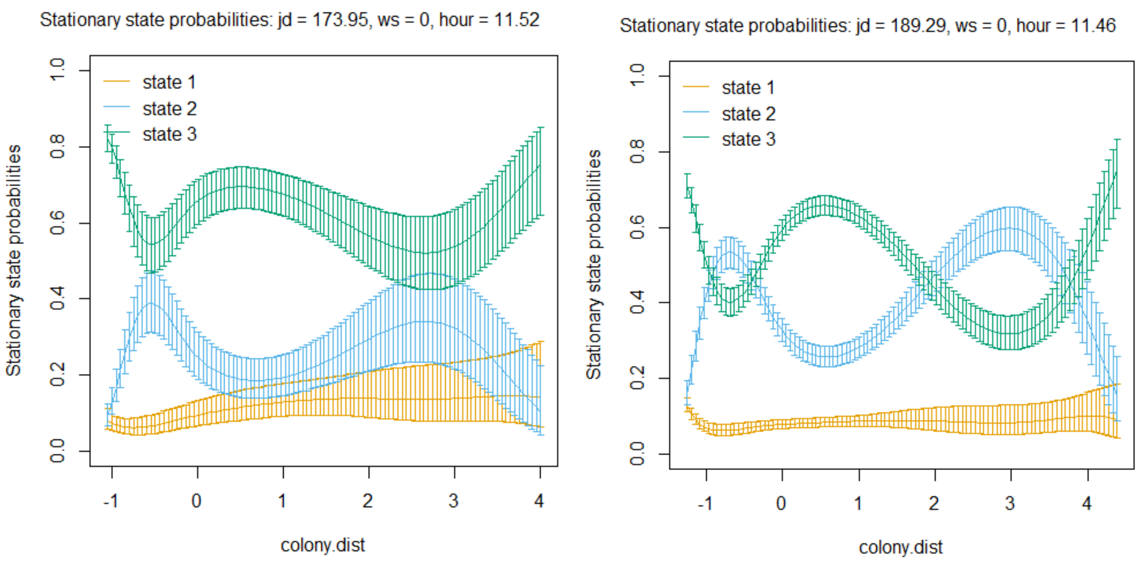
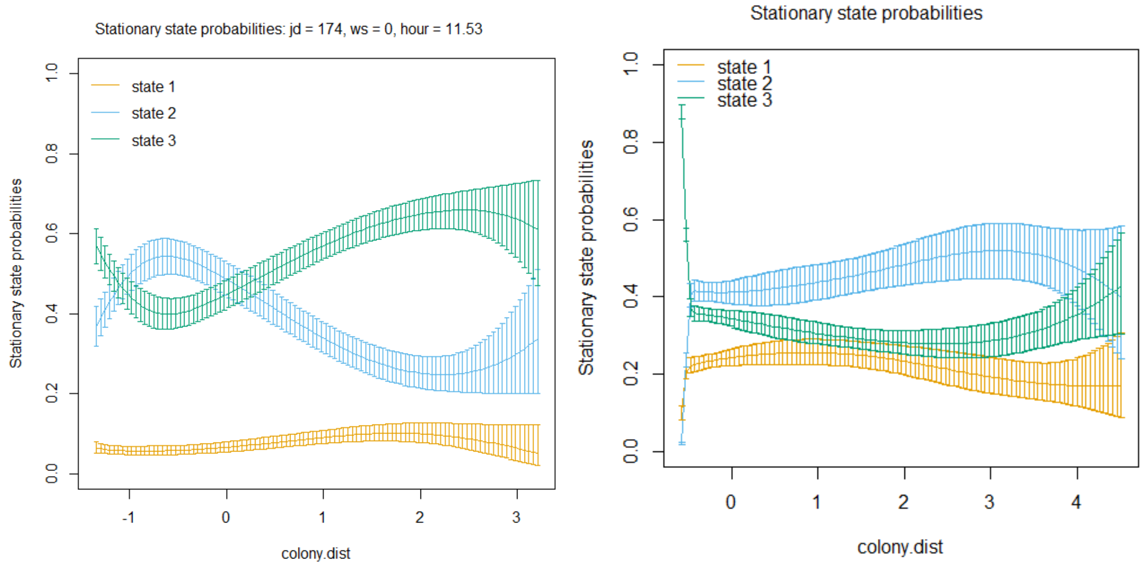


Figure A92 For Kittiwake, transition probabilities for the variable of distance to colony, fitted as a standardised variable. Note, trends are plotted at the mean of other covariates.



(a) Isle of May

(b) Colonsay



(c) Bempton

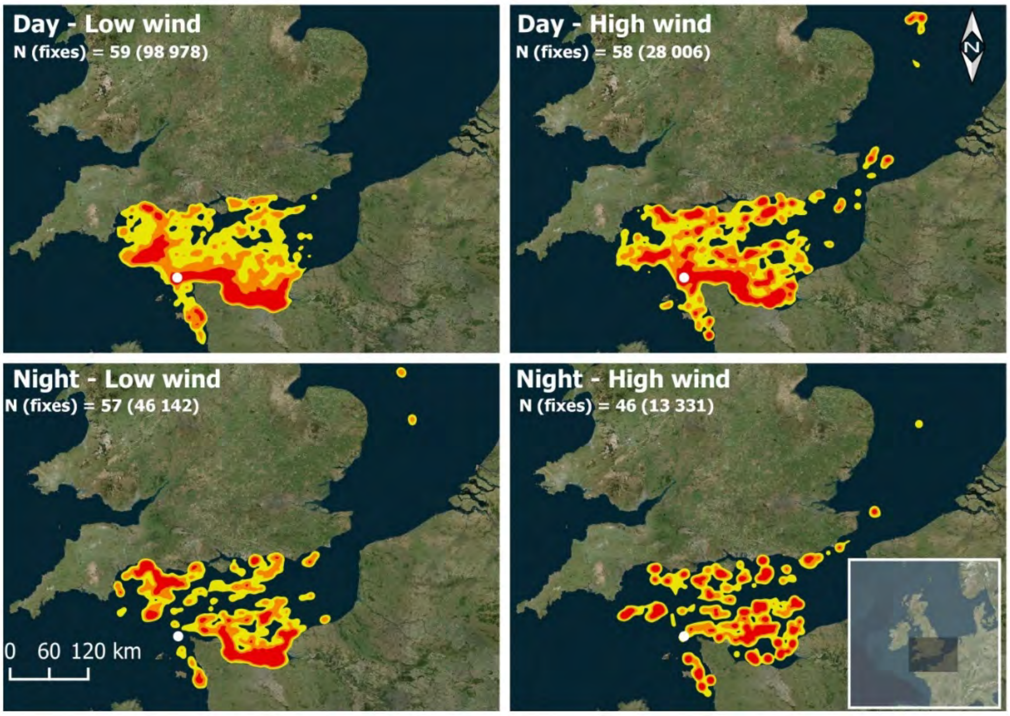
(d) Orkney

Figure A93 For Kittiwake, stationary state probabilities for the variable of distance to colony, fitted as a standardised variable for states 1, 2 and 3 (floating, commuting and foraging/searching) Note, trends are plotted at the mean of other covariates.

7.8 Appendix AH. Utilisation distributions

7.8.1 Northern Gannet

(a) All states



(b) Floating

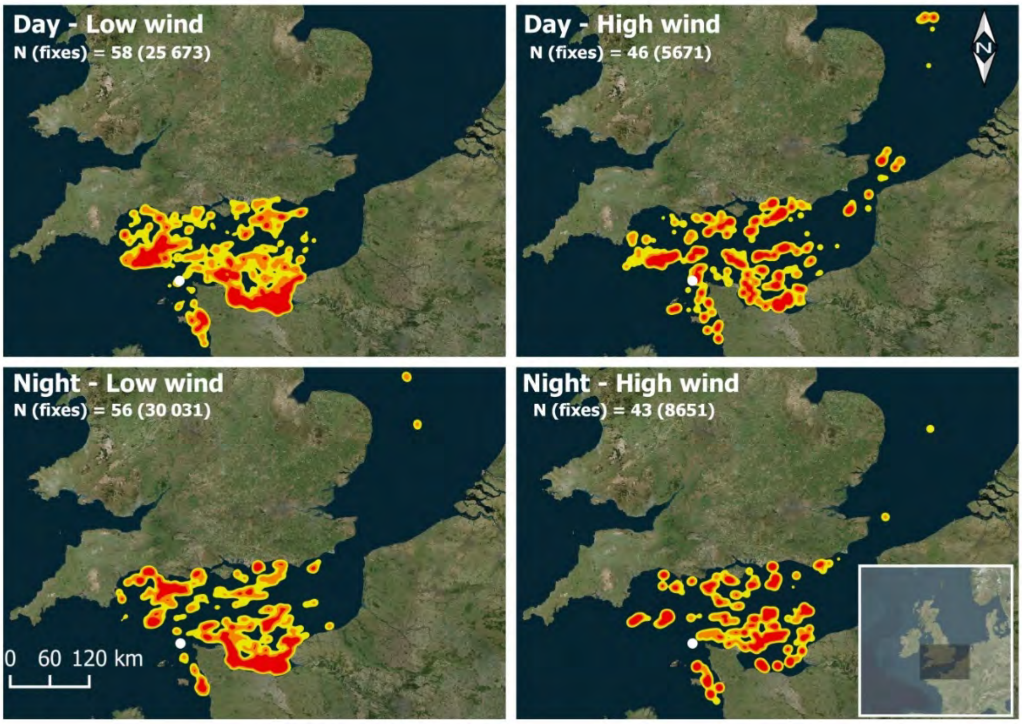
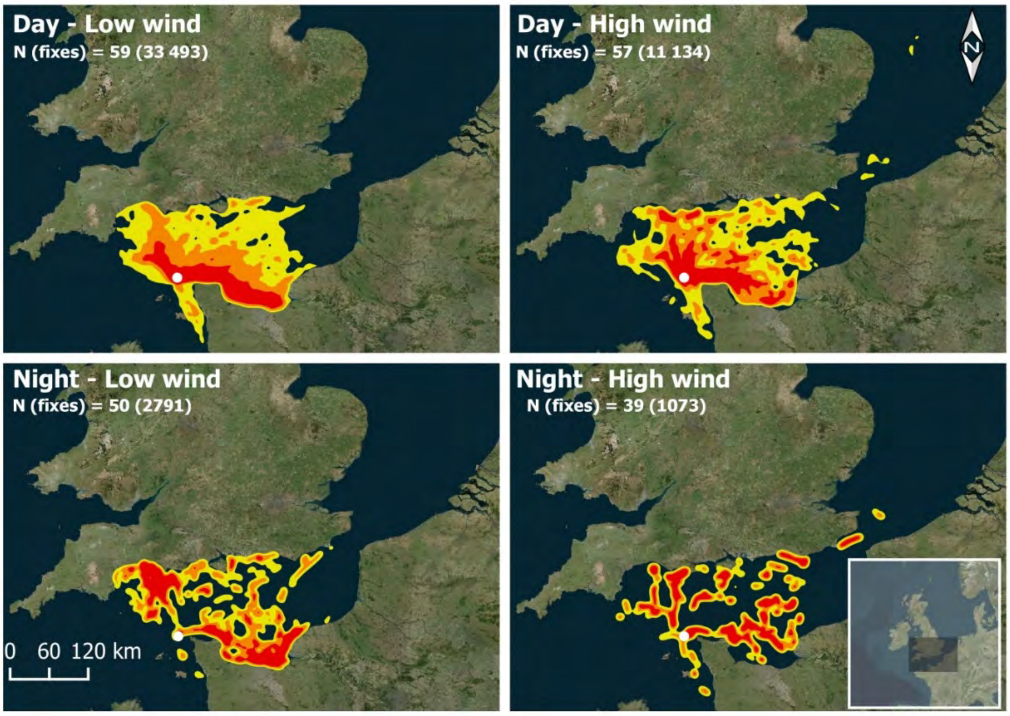


Figure A94 For Gannet, utilisation distributions at Alderney (across each state) showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and

95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging/searching)

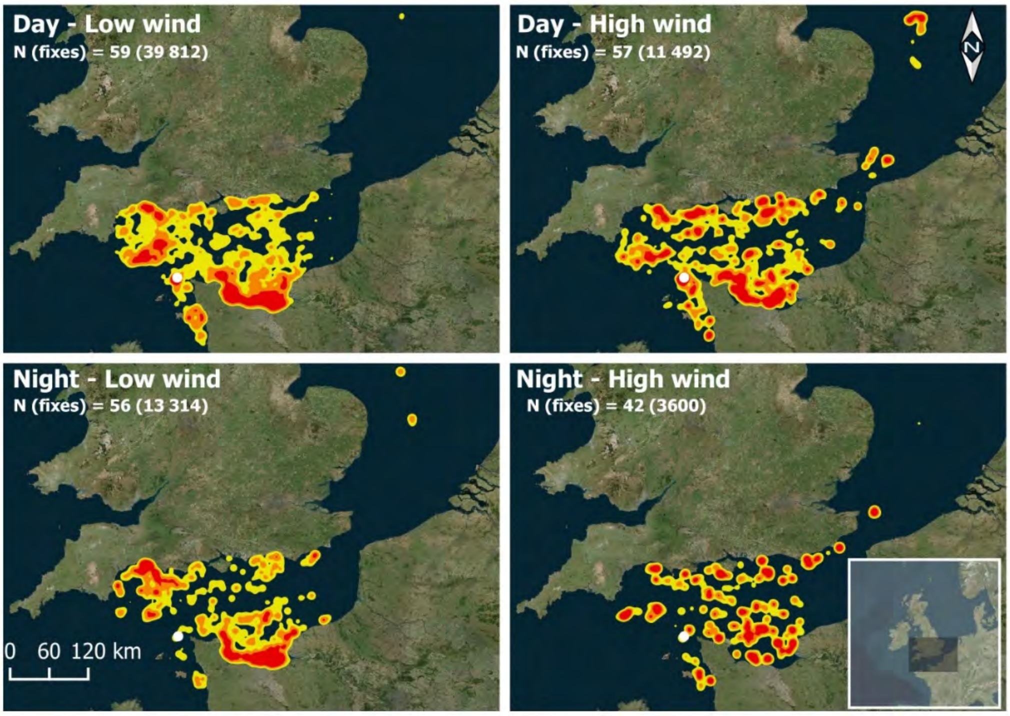
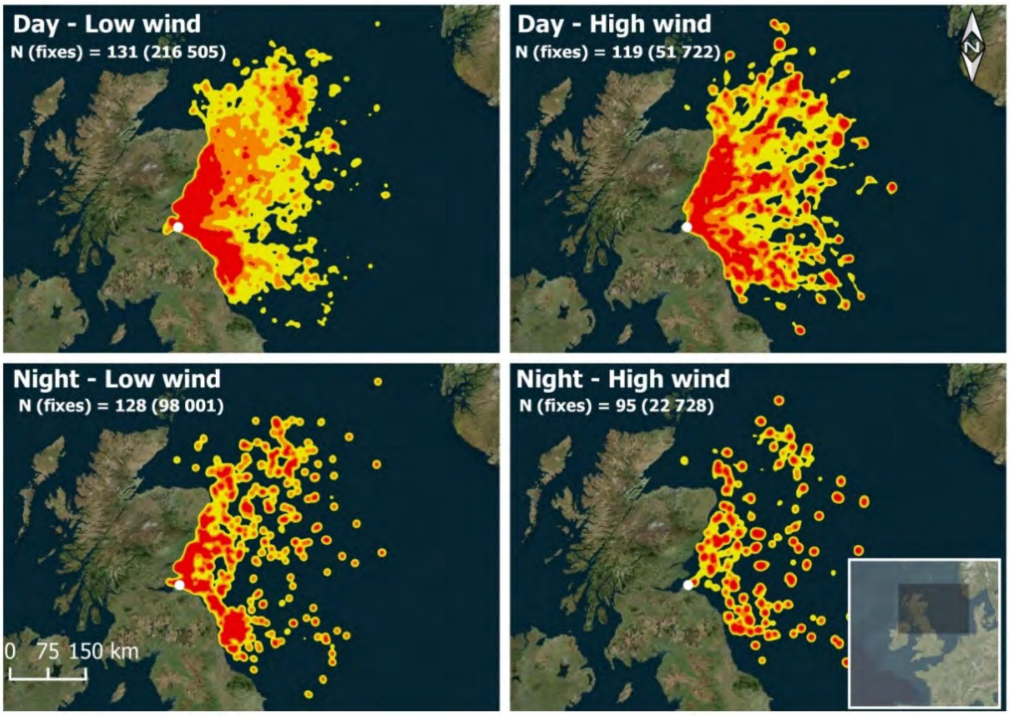


Figure continued.

(a) All states



(b) Floating

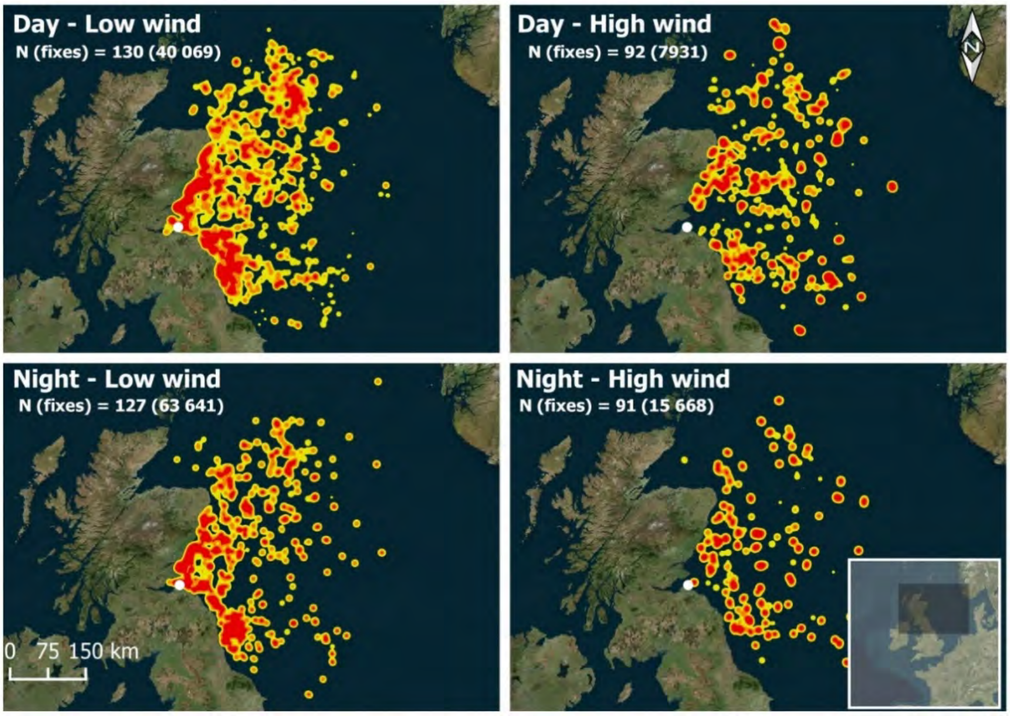
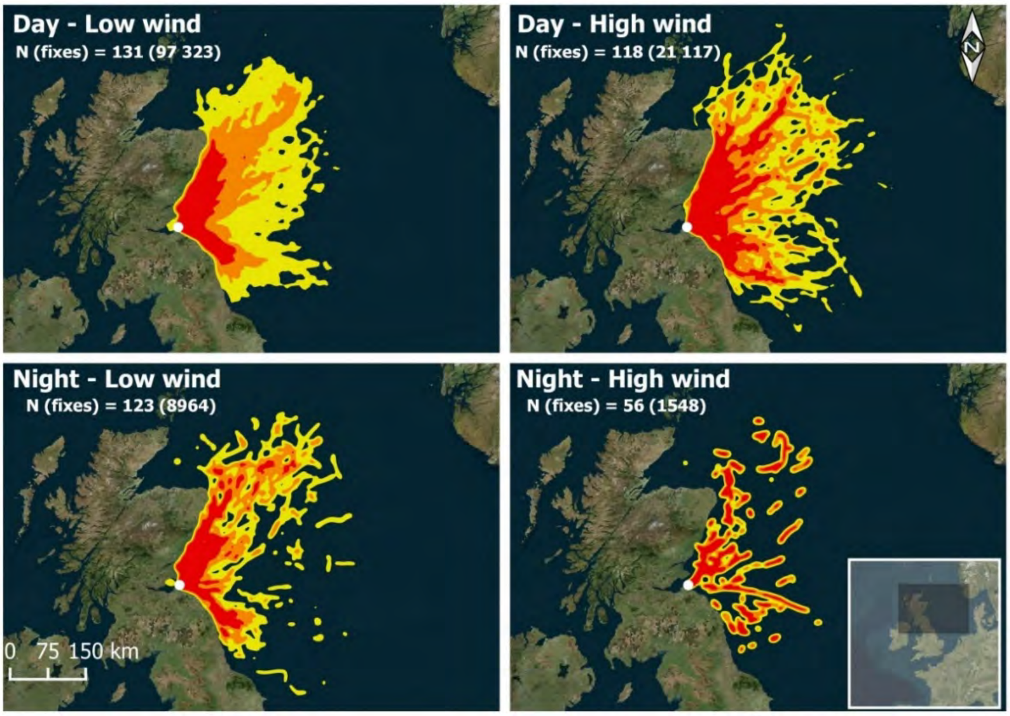


Figure A95 For Gannet, utilisation distributions at Bass Rock (across each state) showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level);

map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class

(c) Commuting



(d) Foraging/searching

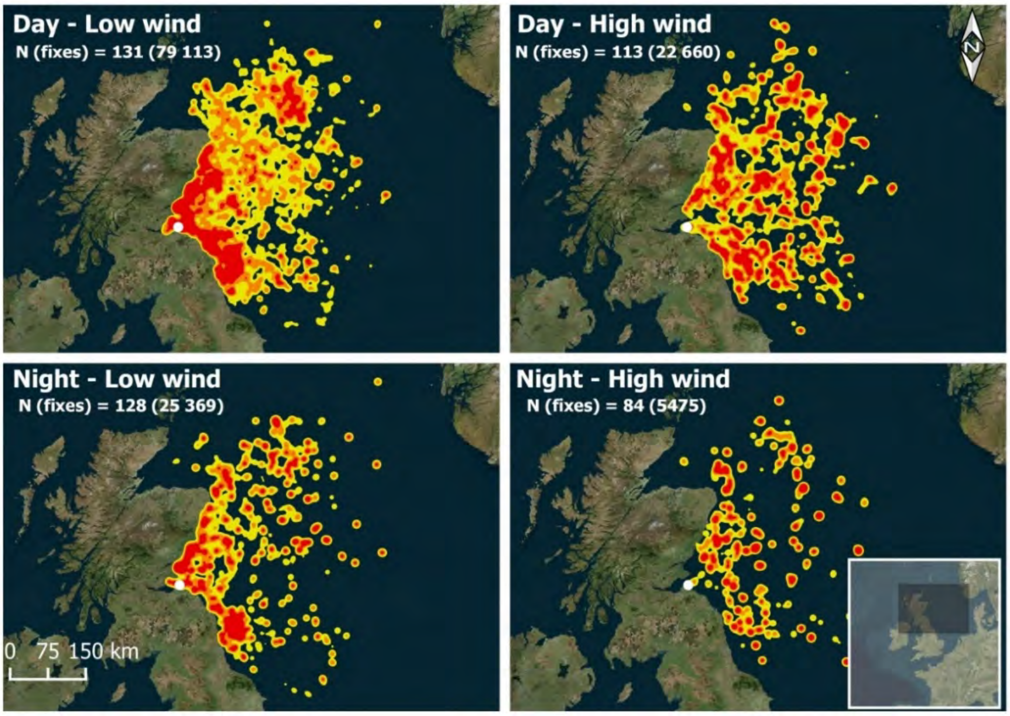
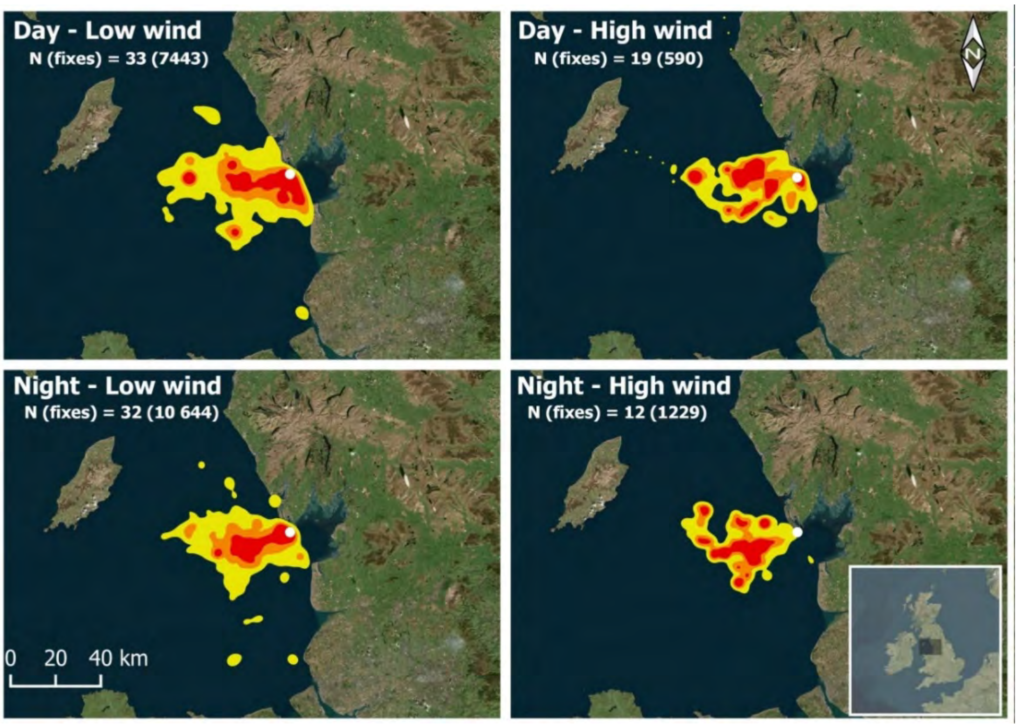


Figure continued.

7.8.2 Lesser Black-backed Gull

(a) All states



(b) Floating on sea

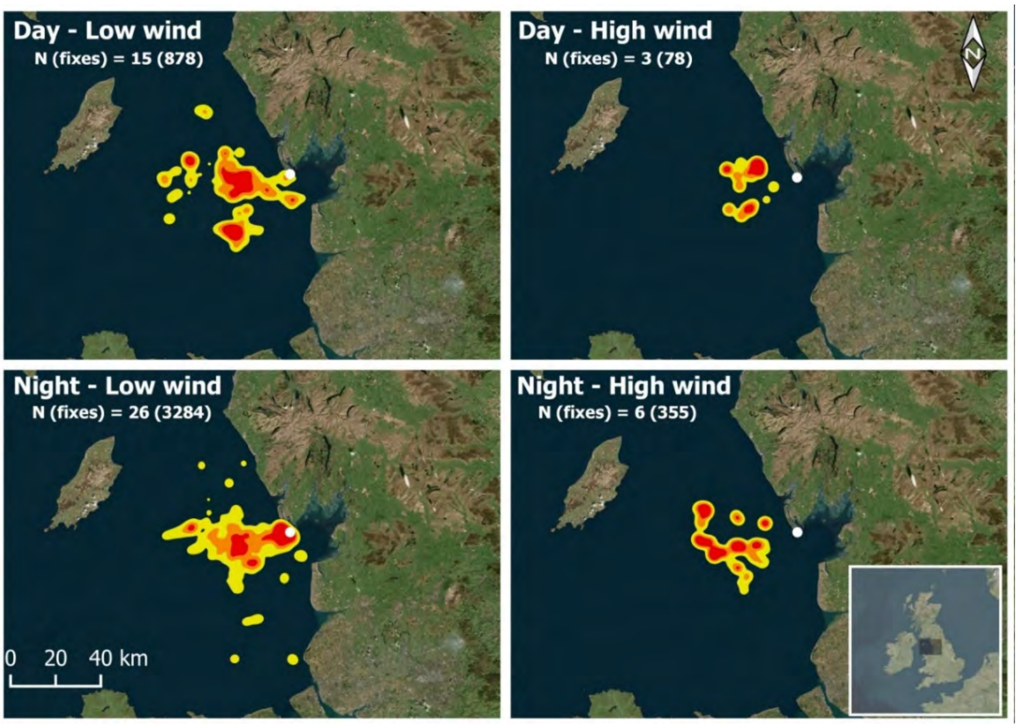
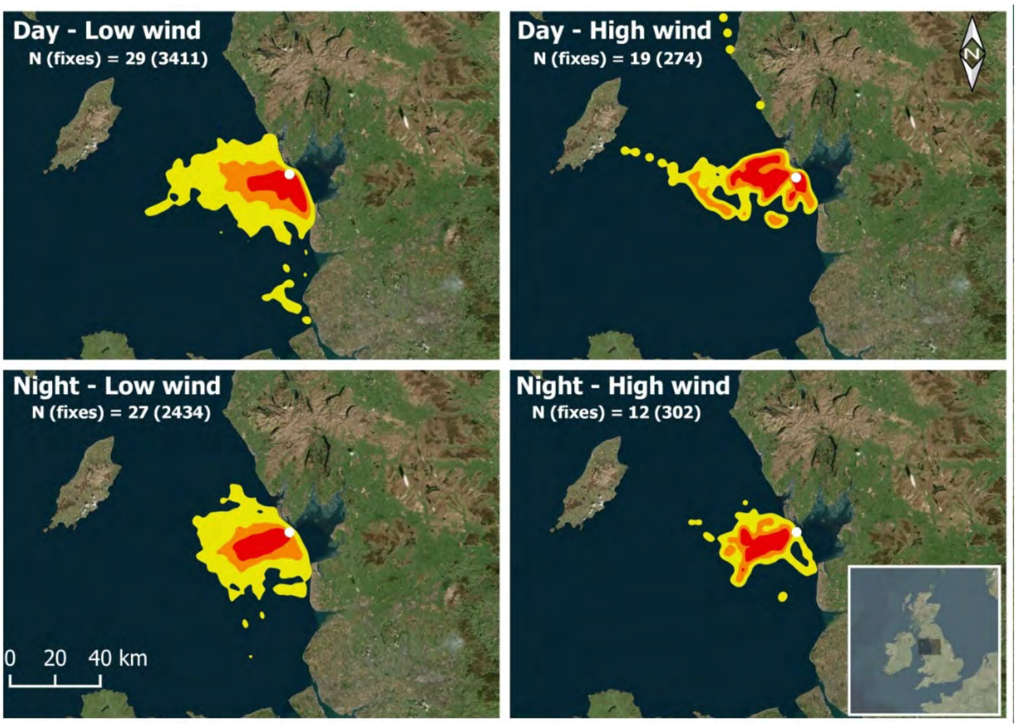


Figure A96 For Lesser Black-backed Gull, utilisation distributions at Walney showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class

(c) Commuting



(d) Foraging/searching)

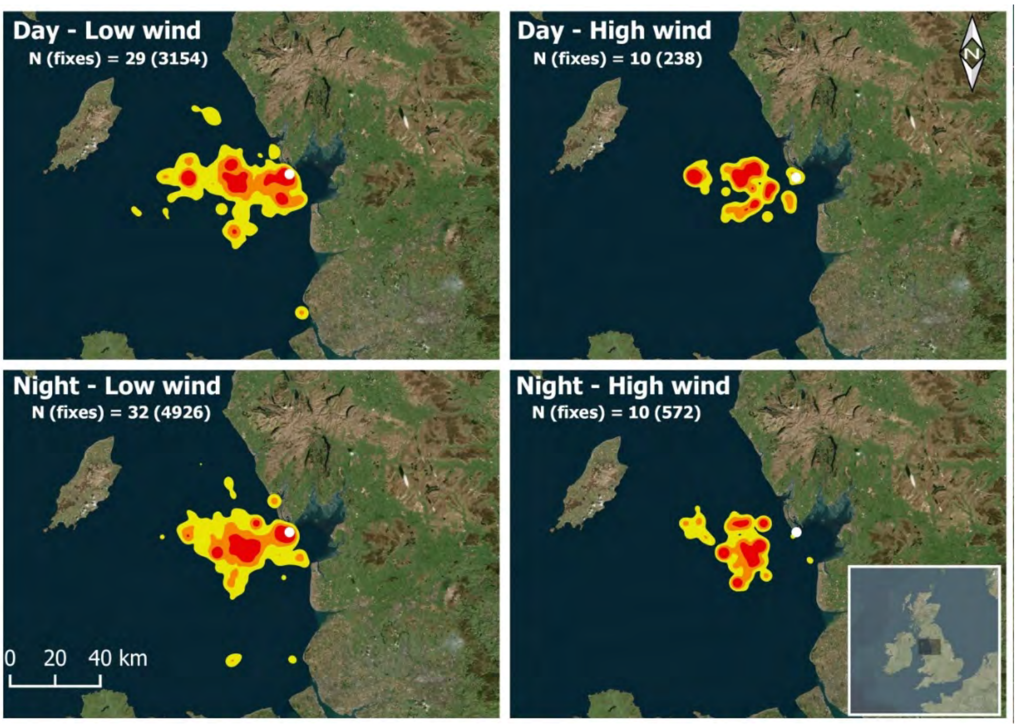
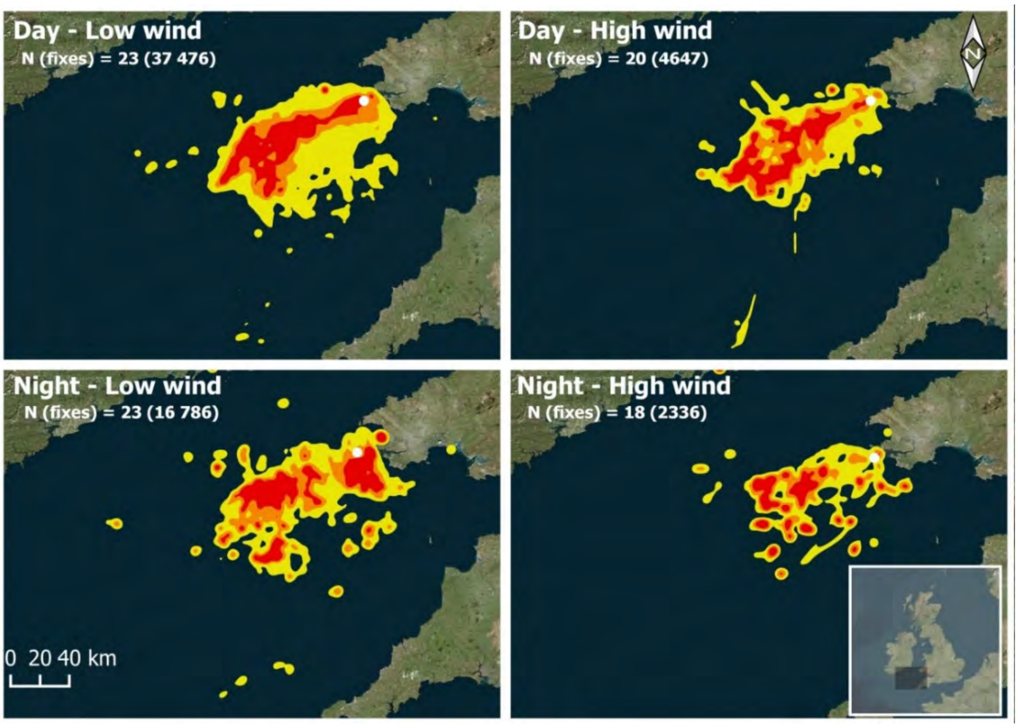


Figure continued.

(a) All states



(b) Floating on sea

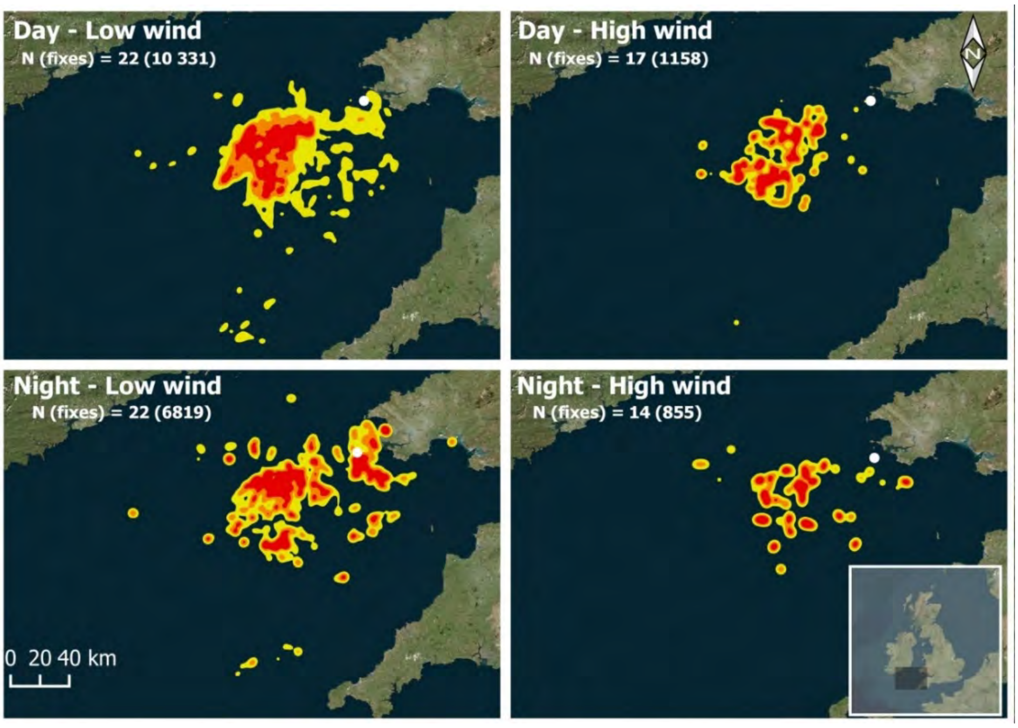
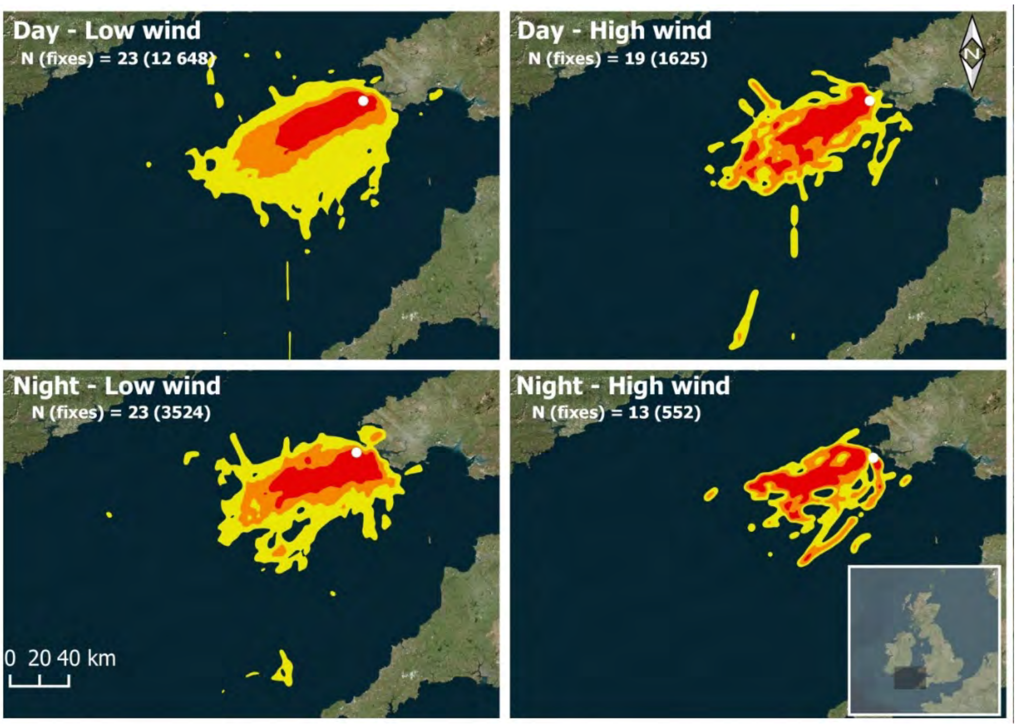


Figure A97 For Lesser Black-backed Gull, utilisation distributions at Skokholm showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level);

map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging/searching

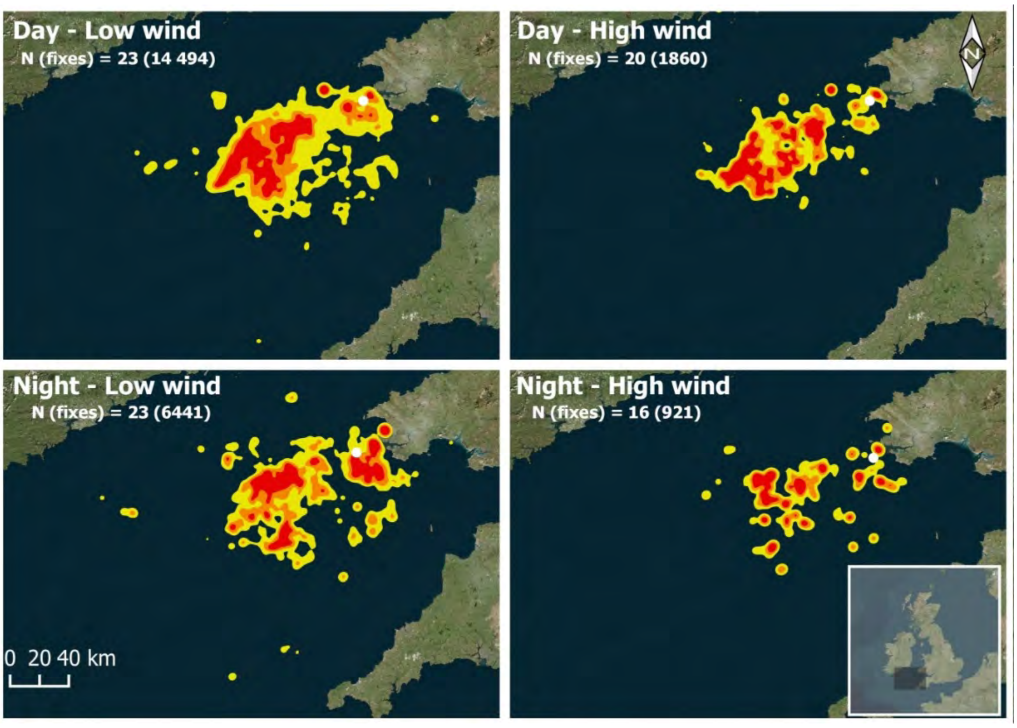
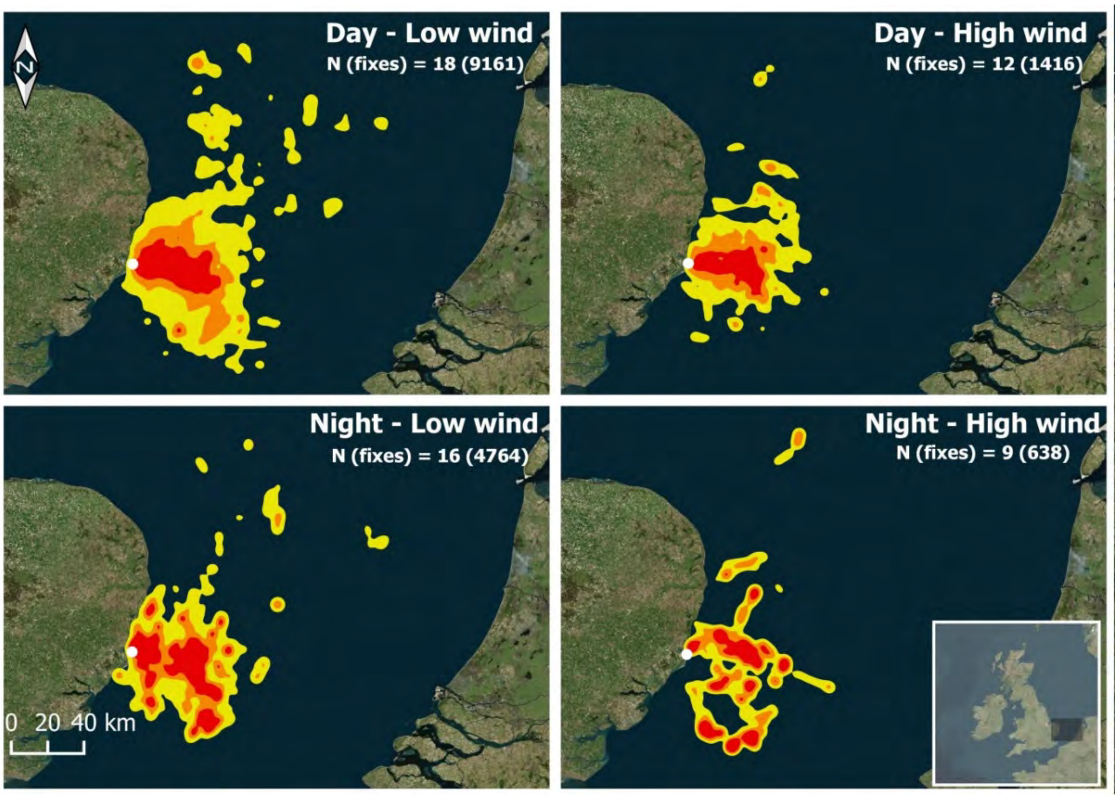


Figure continued.

(a) All states



(b) Floating on sea

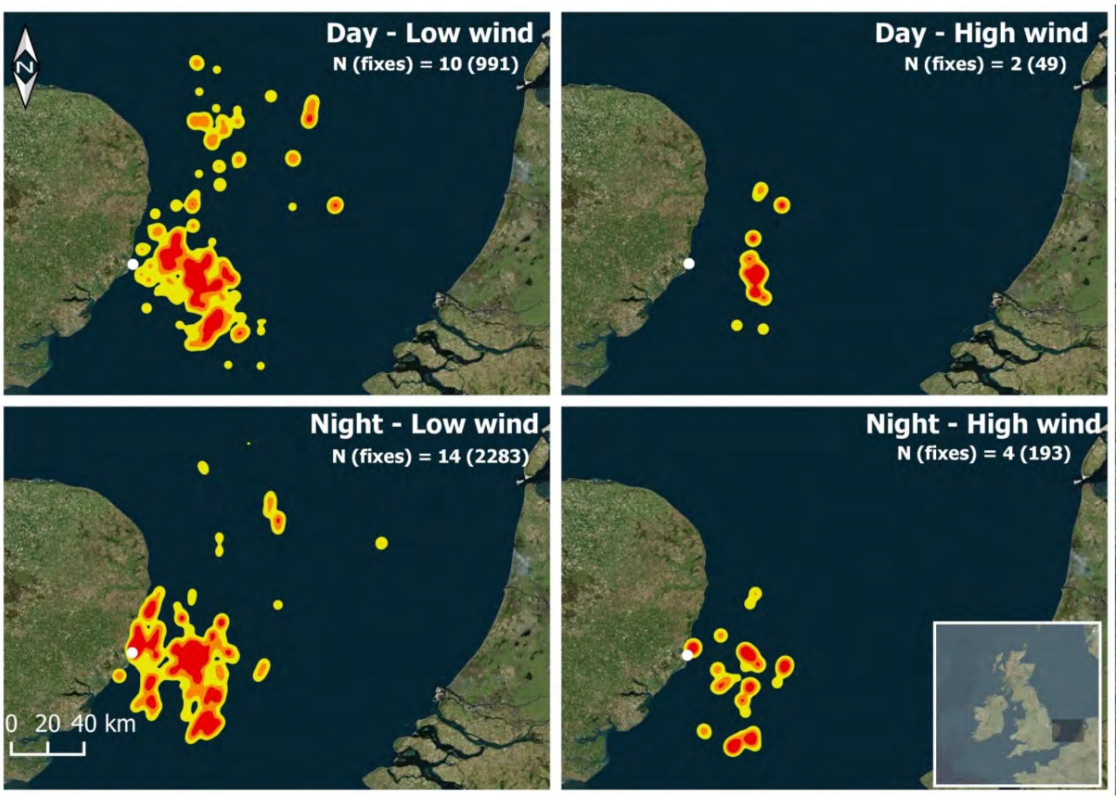
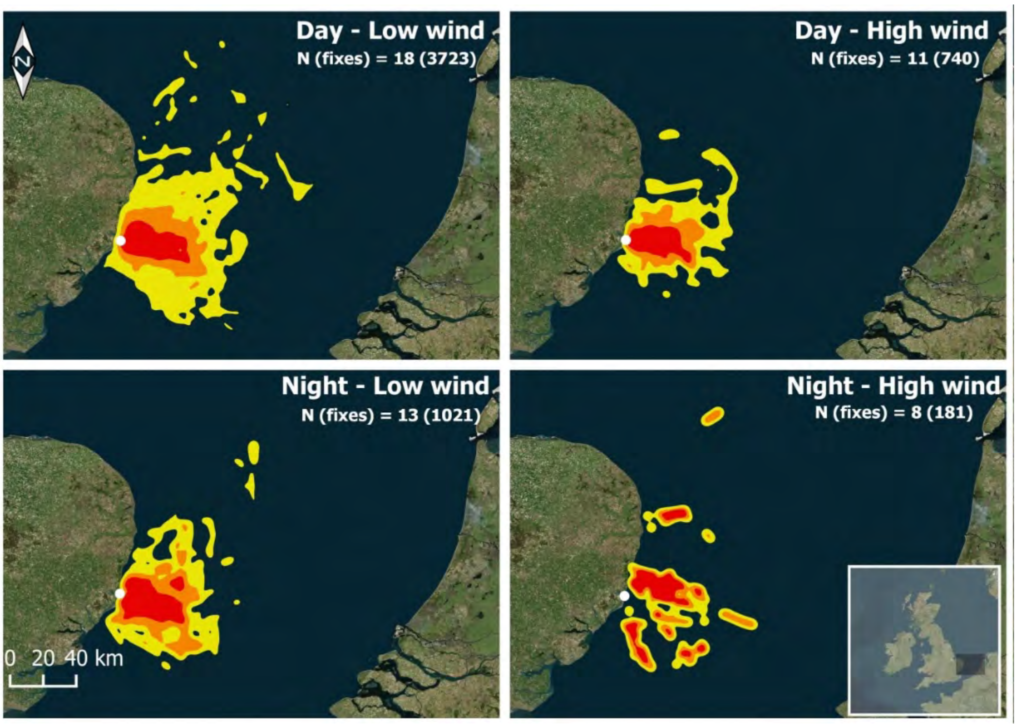


Figure A98 For Lesser Black-backed Gull, utilisation distributions at Orford Ness showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and

95% KDE (yellow, 'total') distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class.

(c) Commuting



(d) Foraging/searching

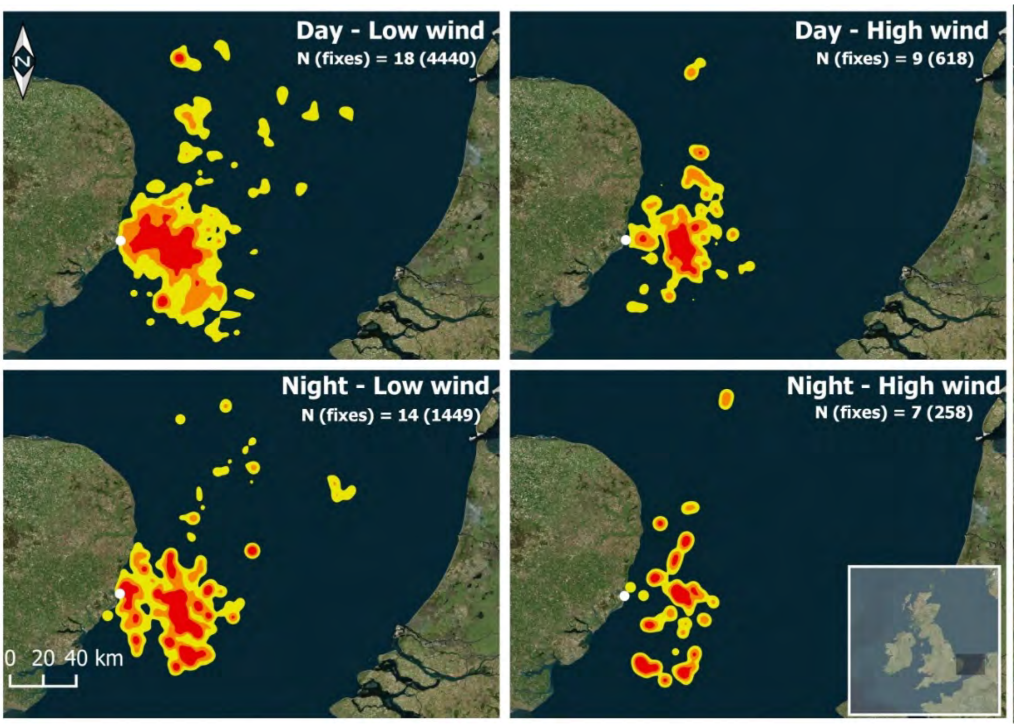
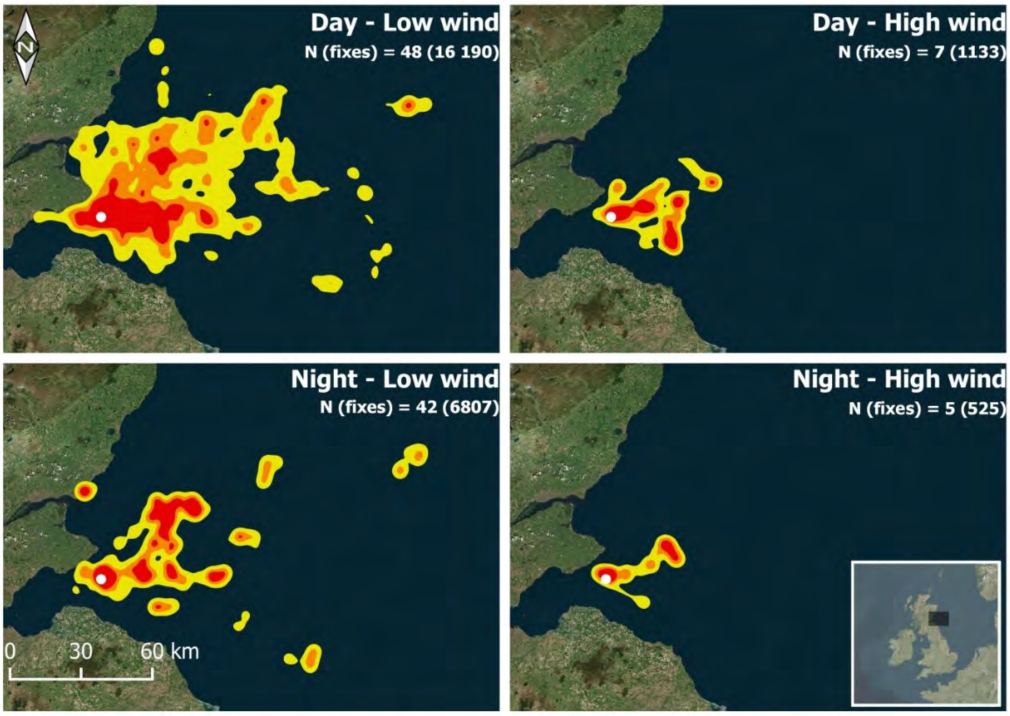


Figure continued.

7.8.3 Black-legged Kittiwake

(a) All states



(b) Floating on sea

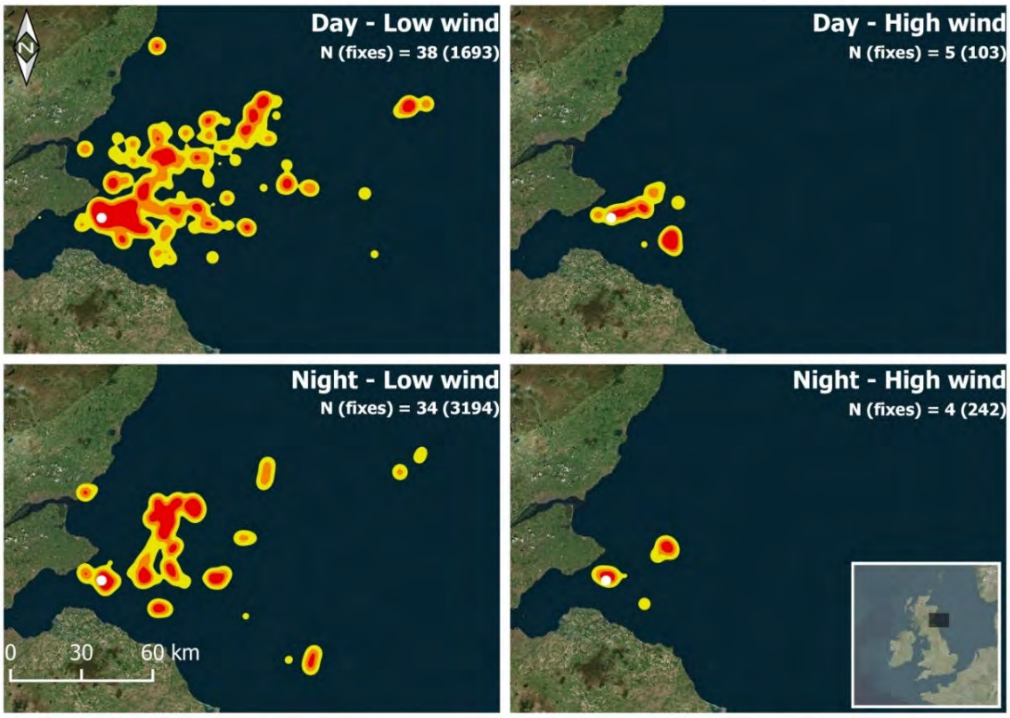
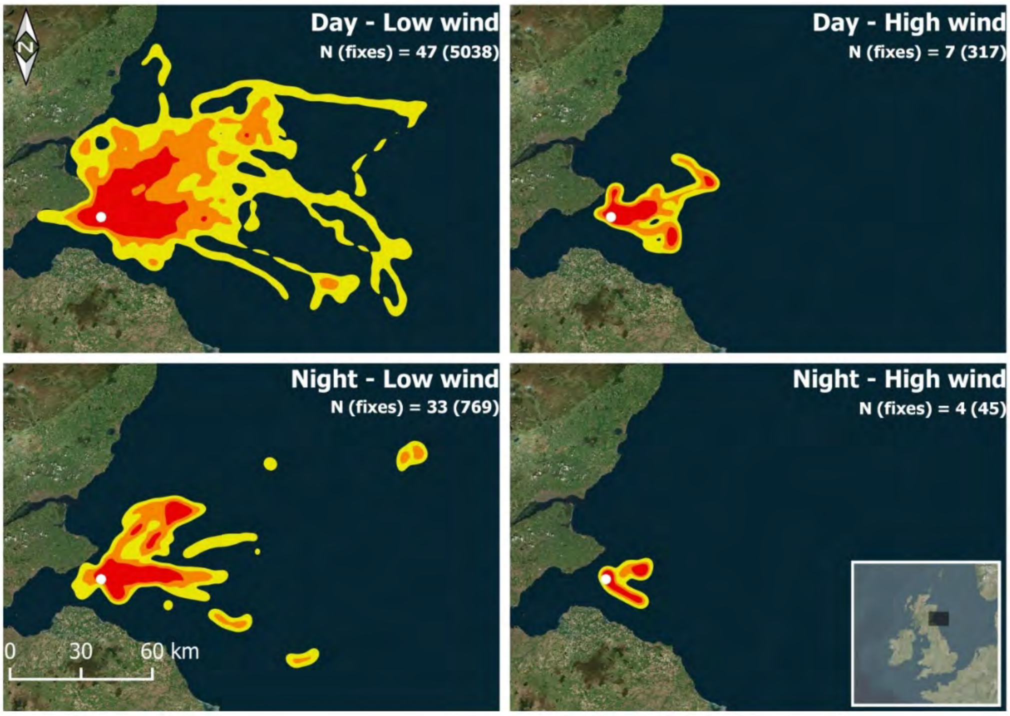


Figure A99 For Kittiwake, utilisation distributions at the Isle of May showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high

and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class.

(c) Commuting



(d) Foraging/searching)

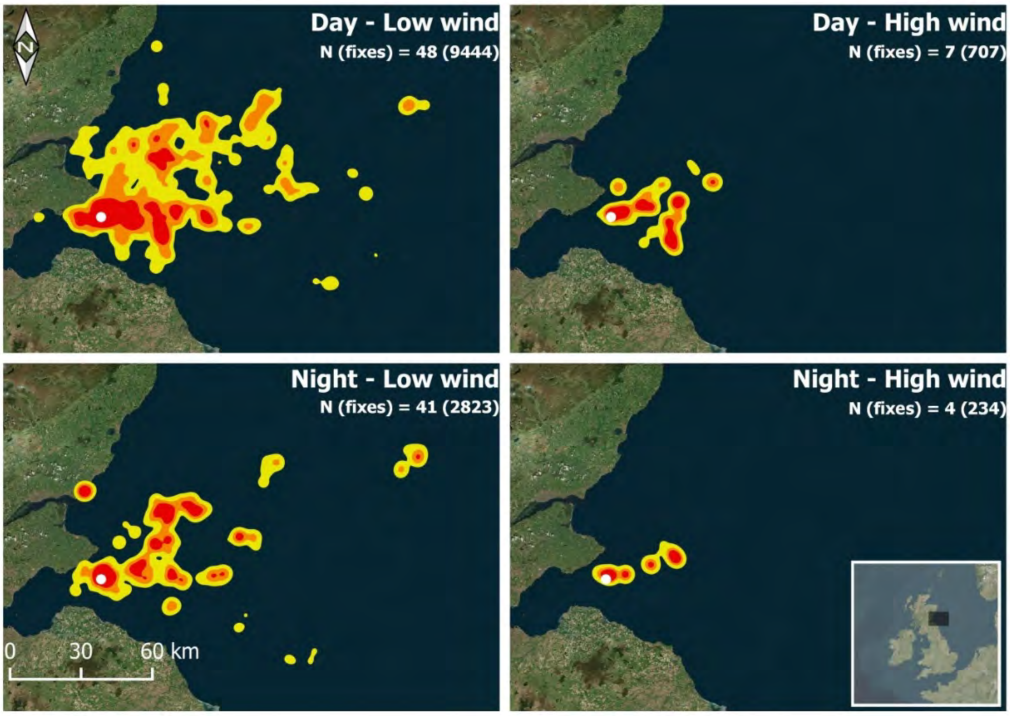
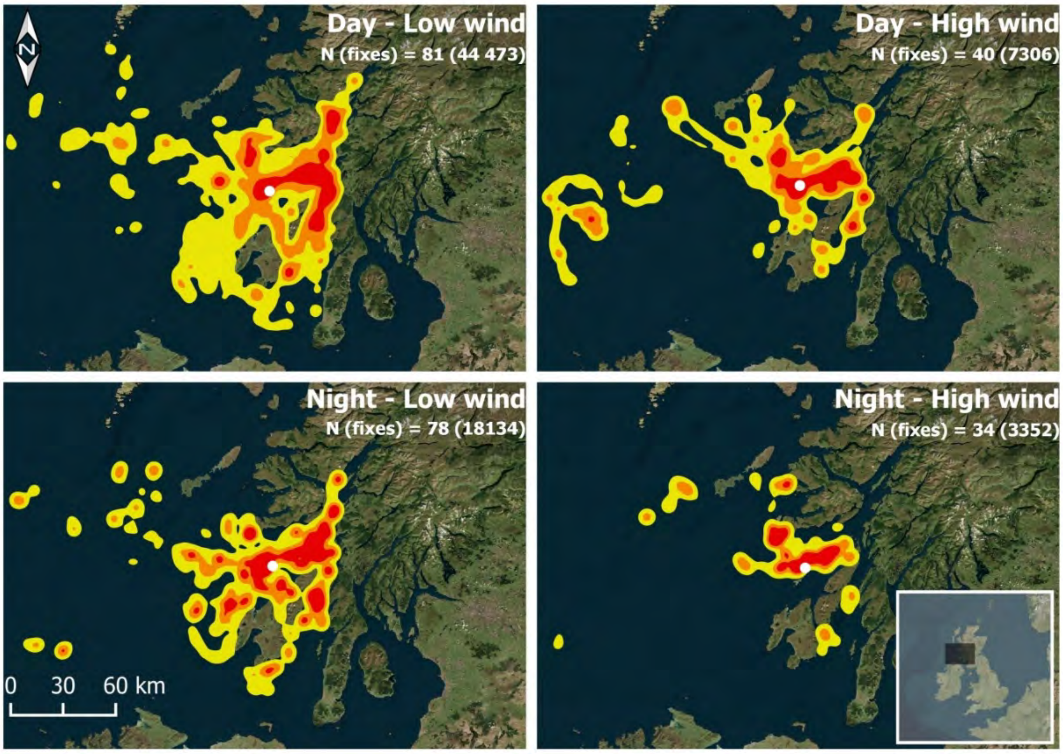


Figure continued.

(a) All states



(b) Floating on sea

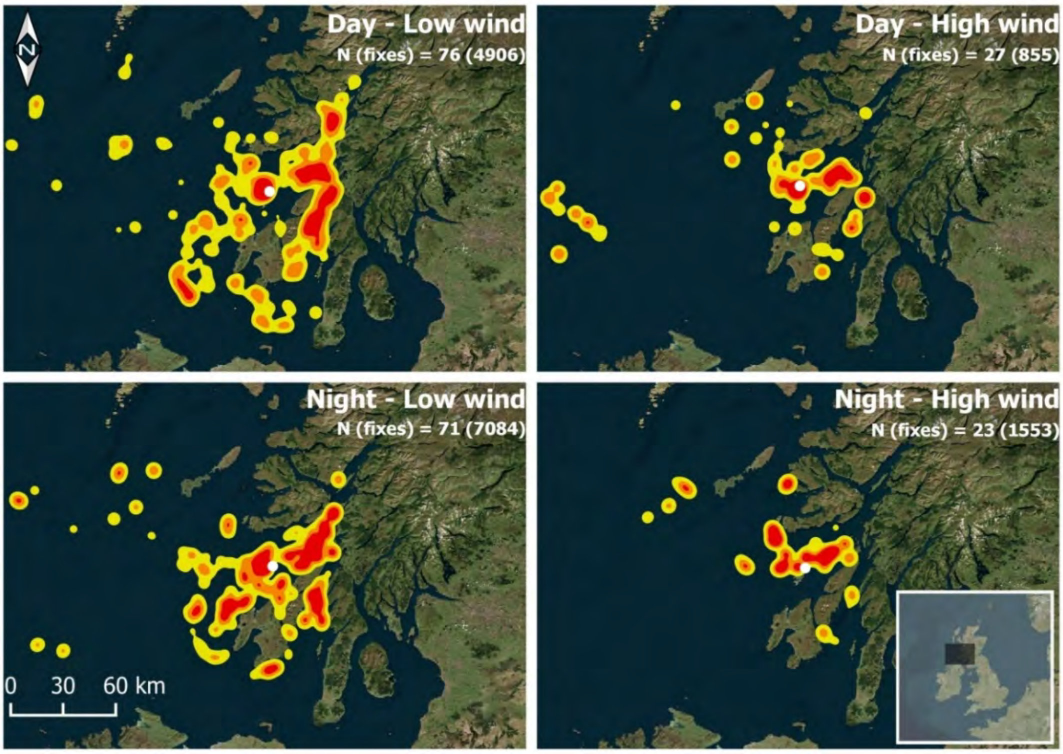
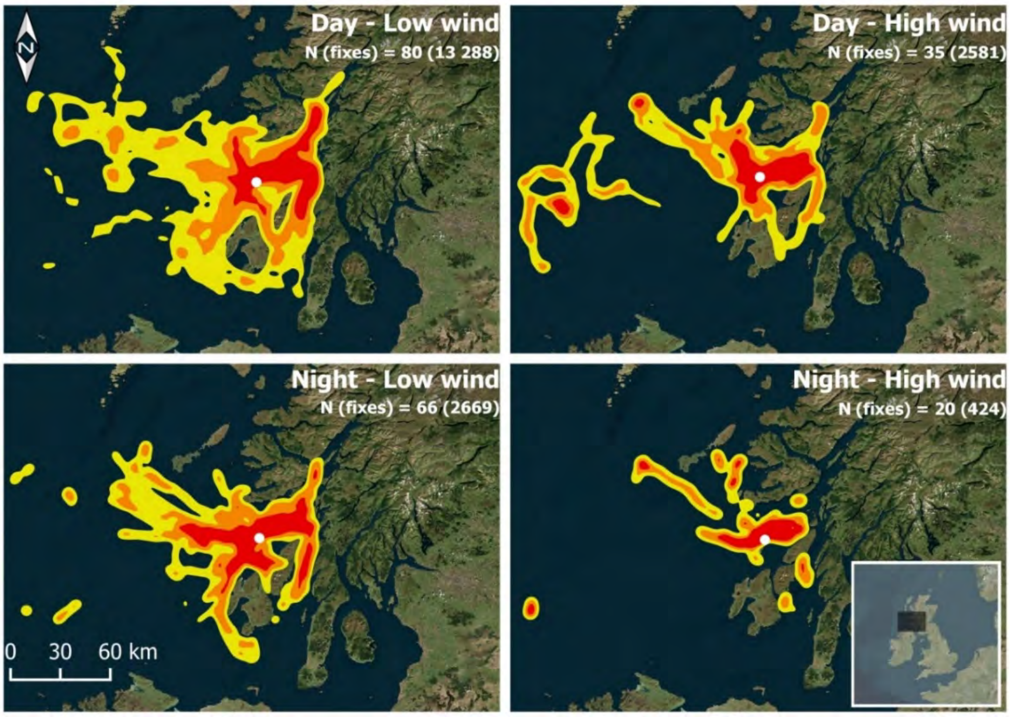


Figure A100 For Kittiwake, utilisation distributions at Colonsay (across each state) showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging/searching

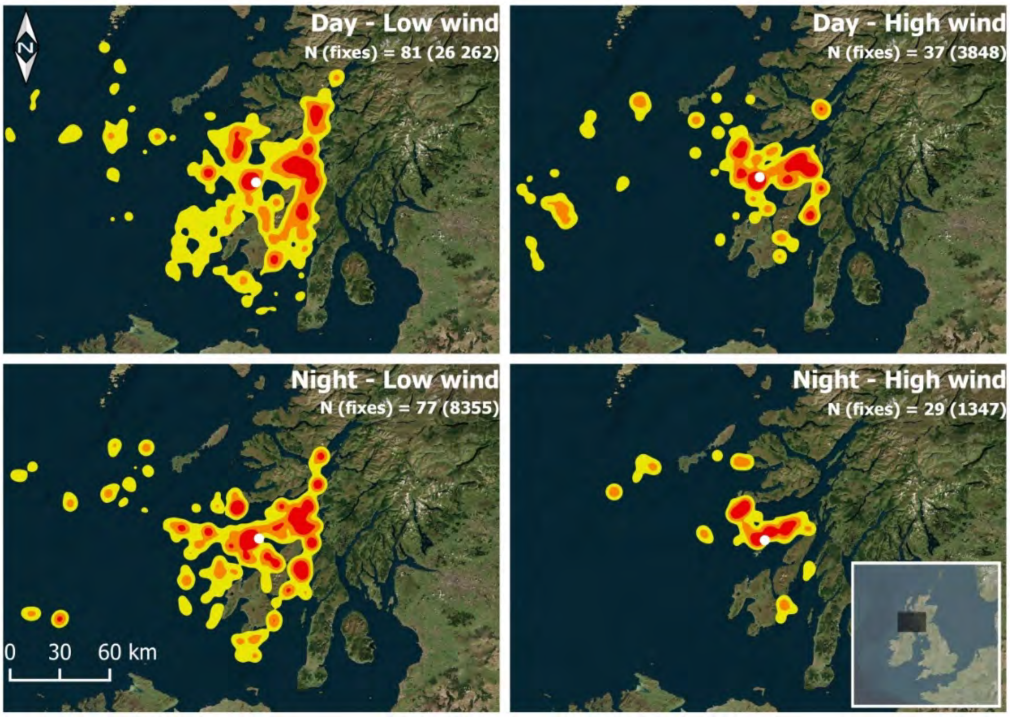
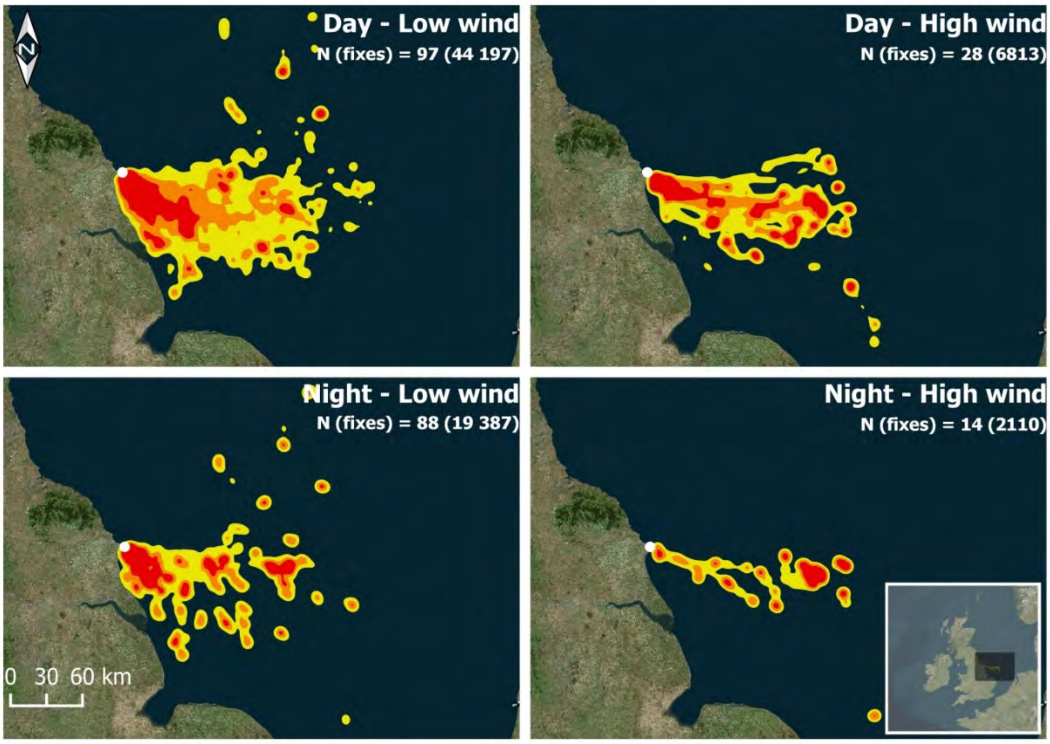


Figure continued.

(a) All states



(b) Floating on sea

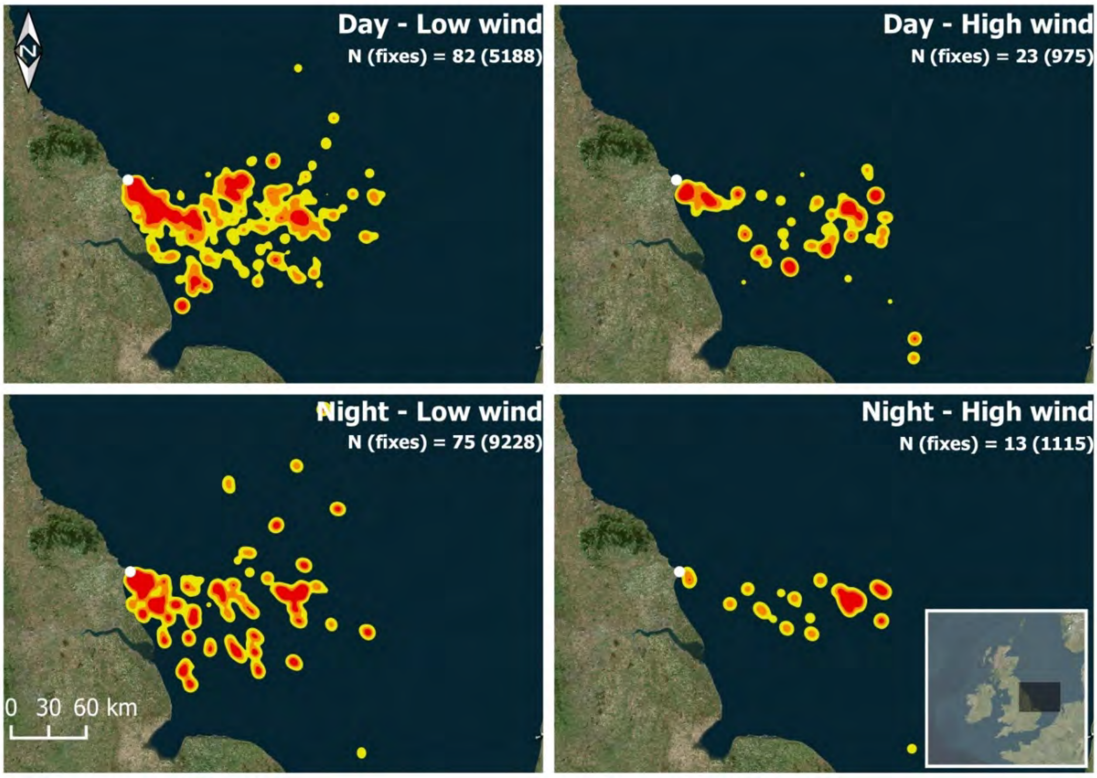
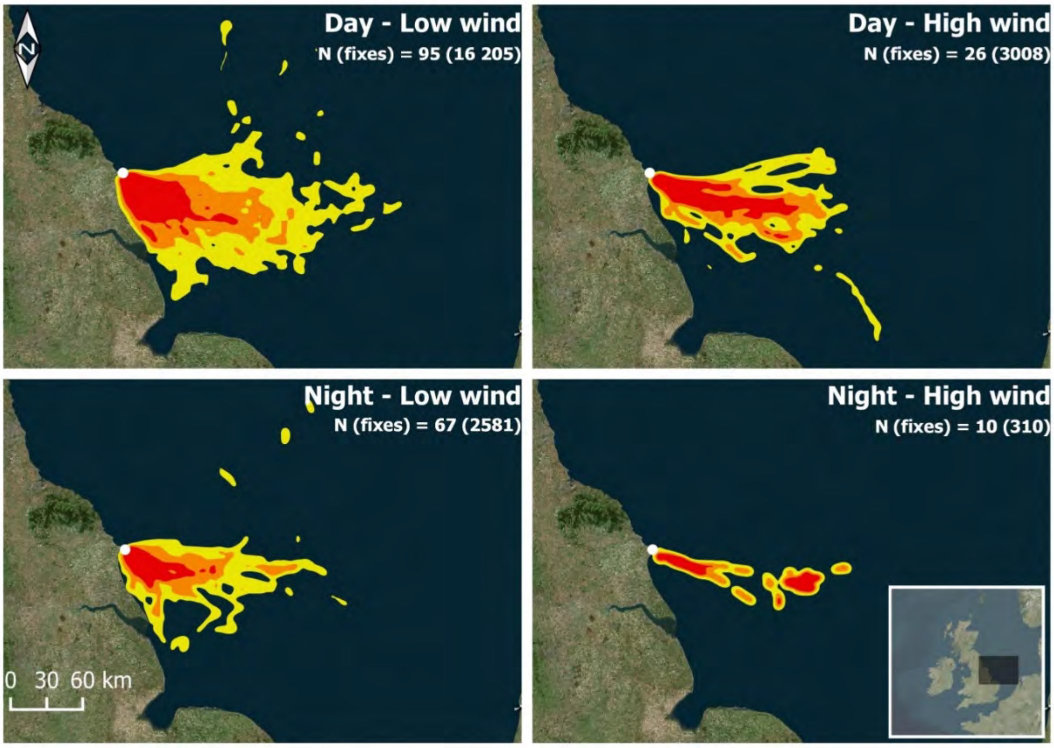


Figure A101 For Kittiwakes, utilisation distributions at Bempton Clilffs showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high

and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class.

(c) Commuting



(d) Foraging/searching

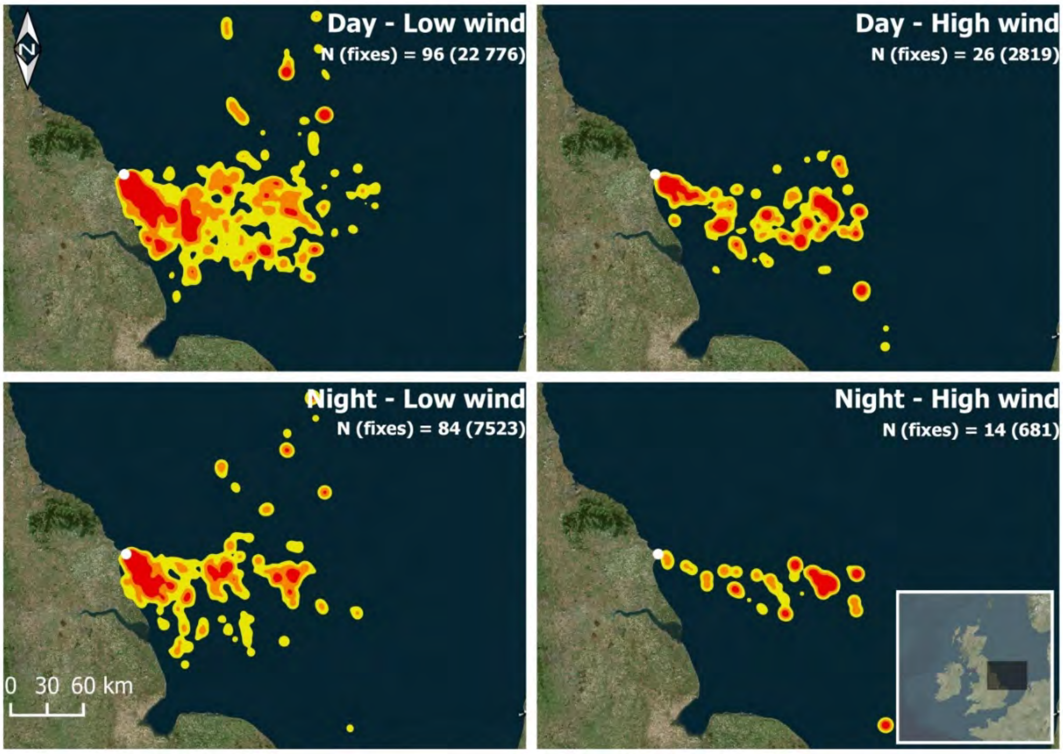
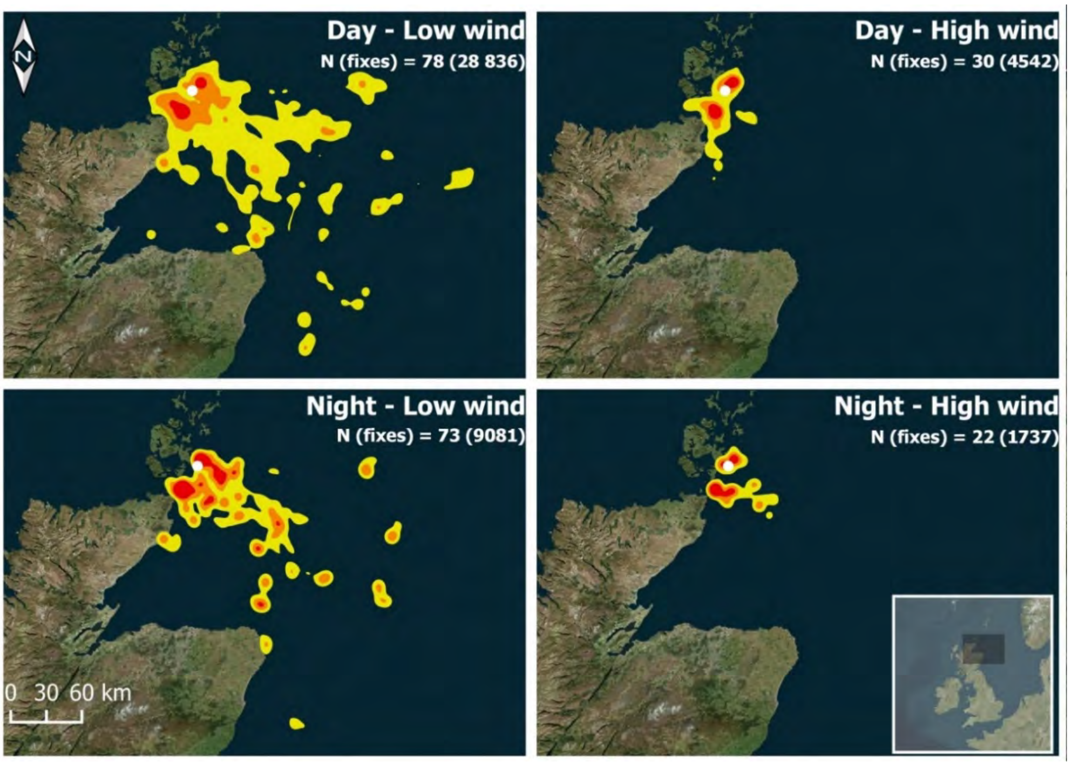


Figure continued.

(a) All states



(b) Floating on sea

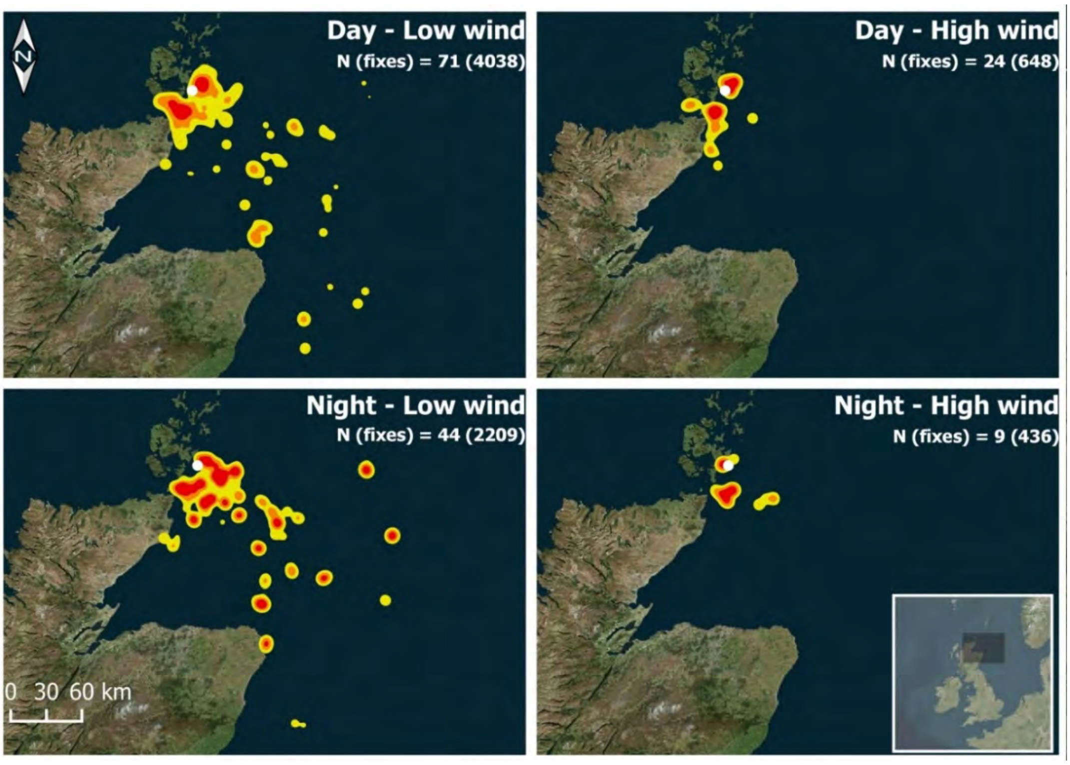
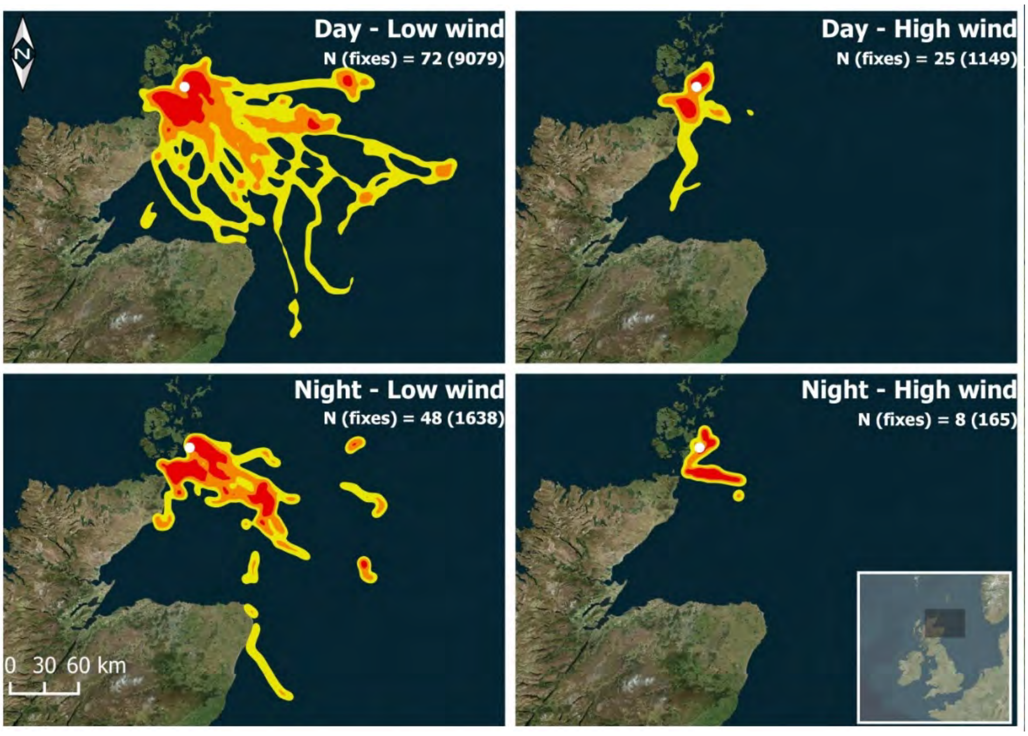


Figure A102 For Kittiwake, utilisation distributions at Orkney (across each state) showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level);

map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging/searching

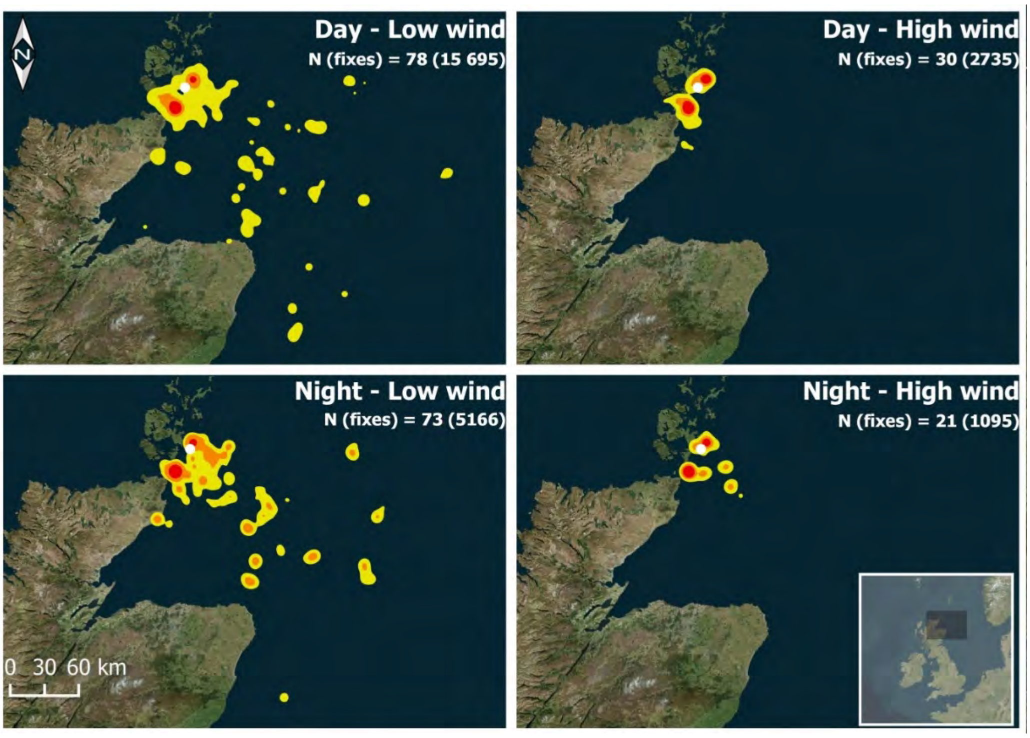
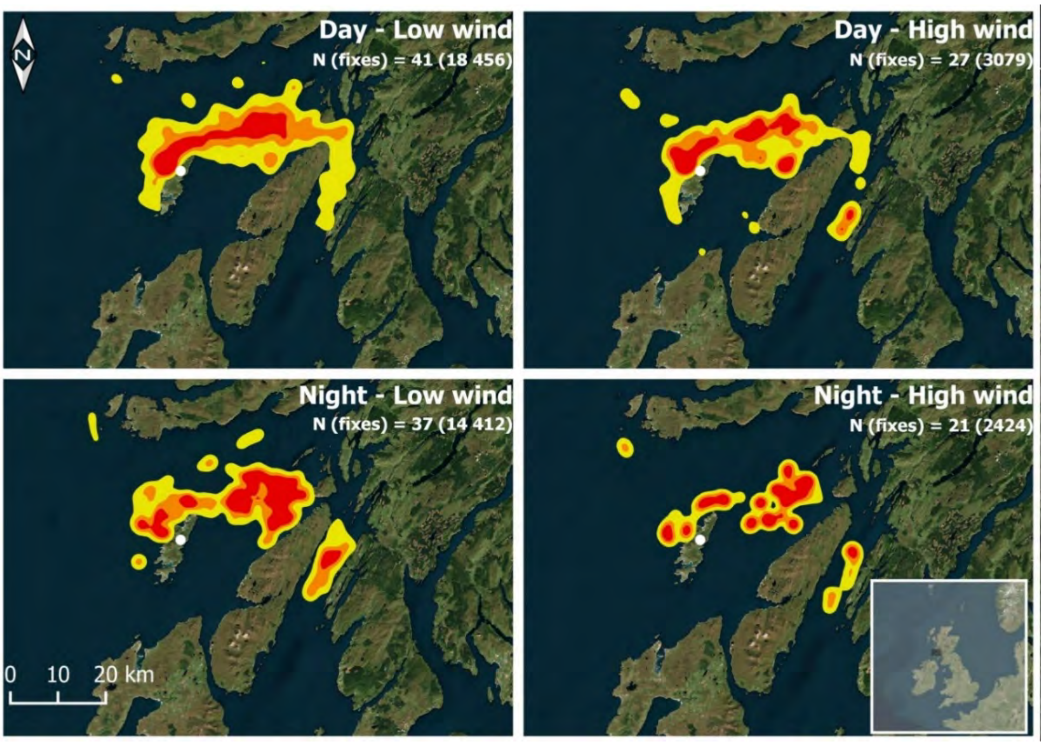


Figure continued.

7.8.4 Razorbill

(a) All states



(b) Floating on sea

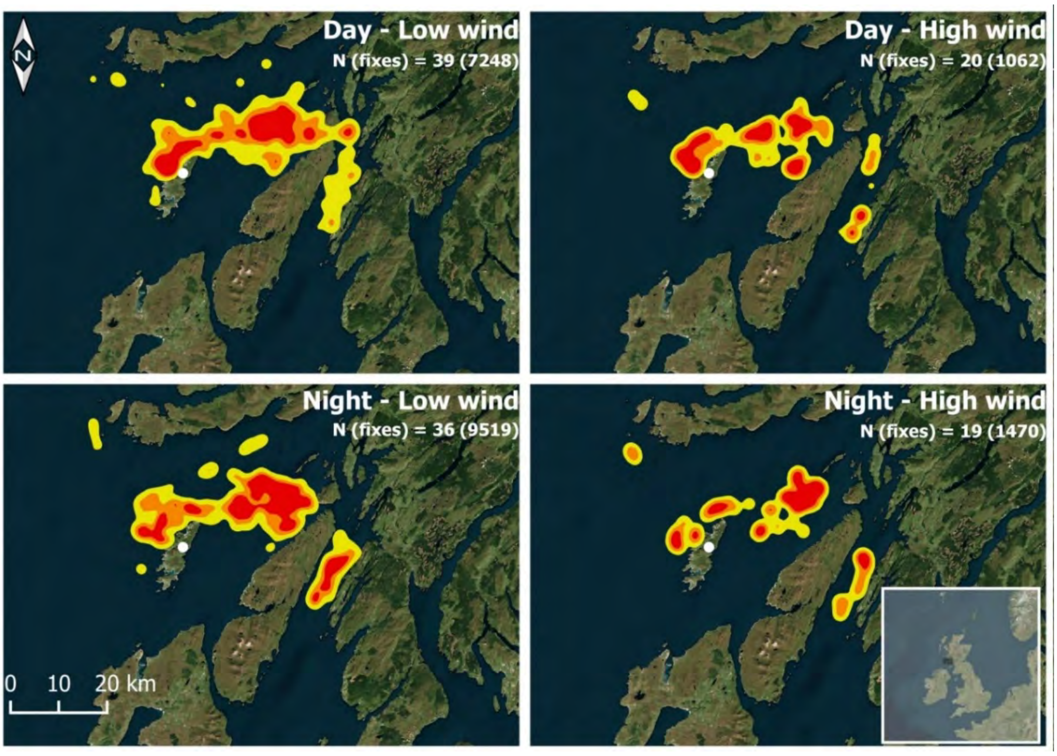
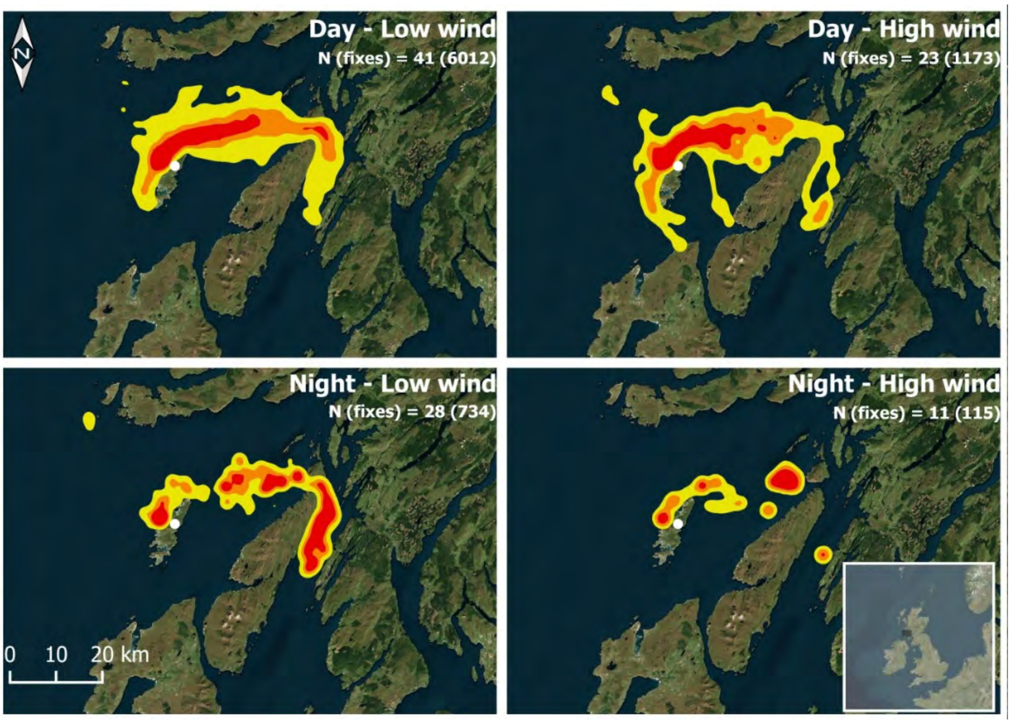


Figure A103 For Razorbill, utilisation distributions at Colonsay showing the 50% kernel density estimate (KDE, red, 'core'), 75% KDE (orange), and 95% KDE (yellow, 'total') distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging /searching

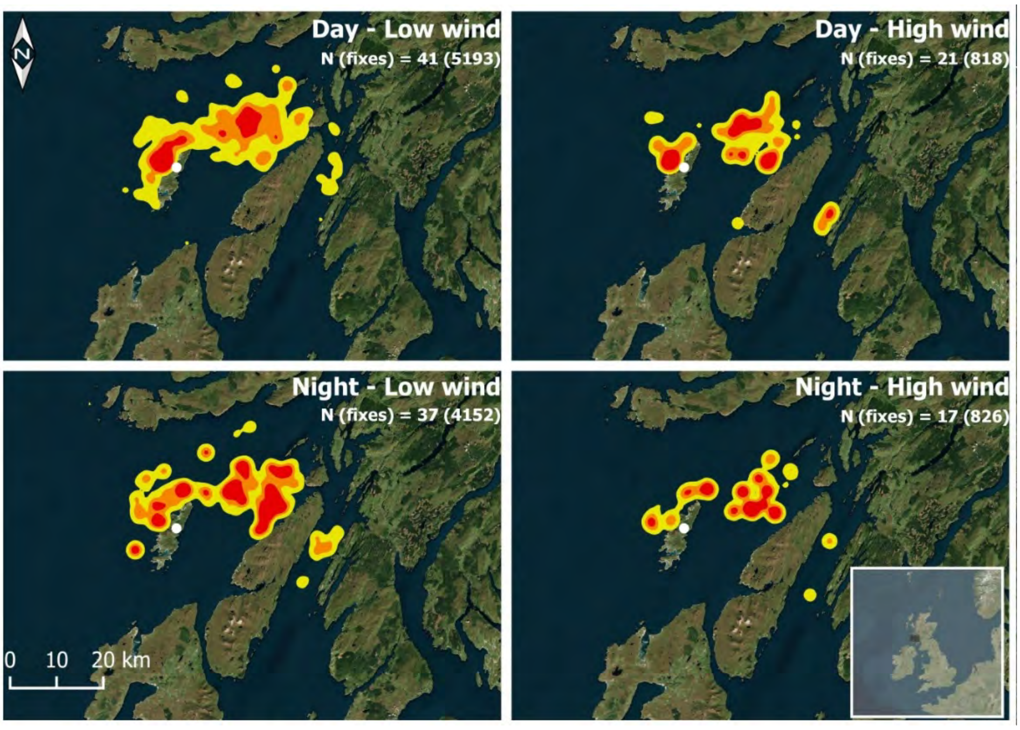
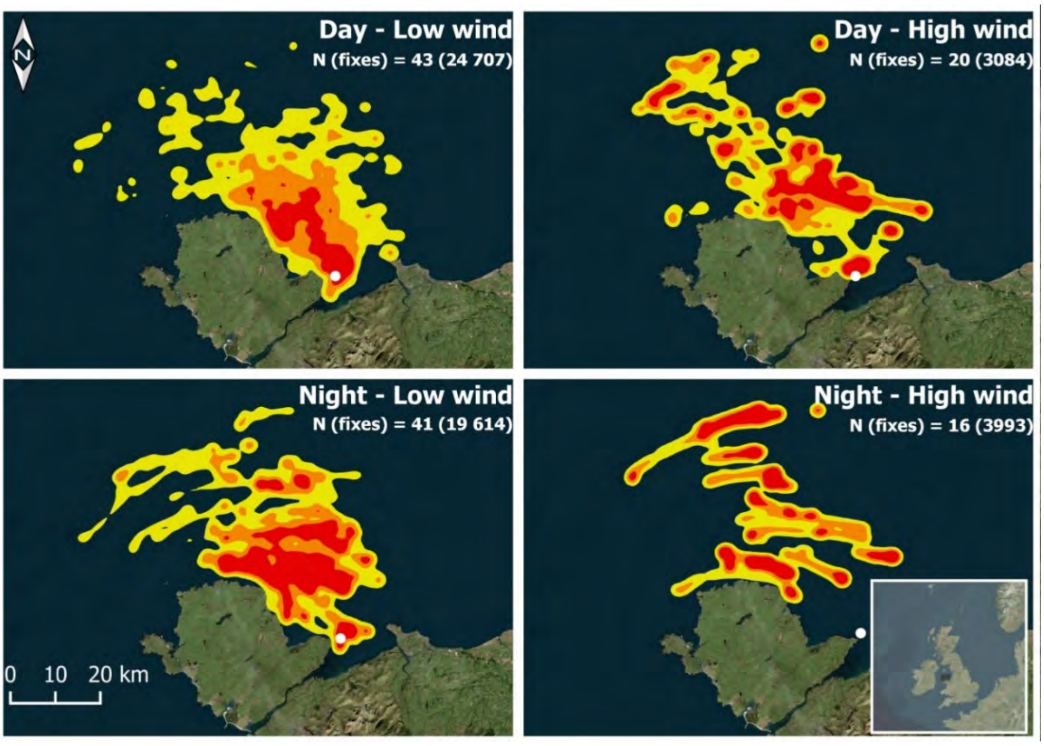


Figure continued.

(a) All states



(b) Floating on sea

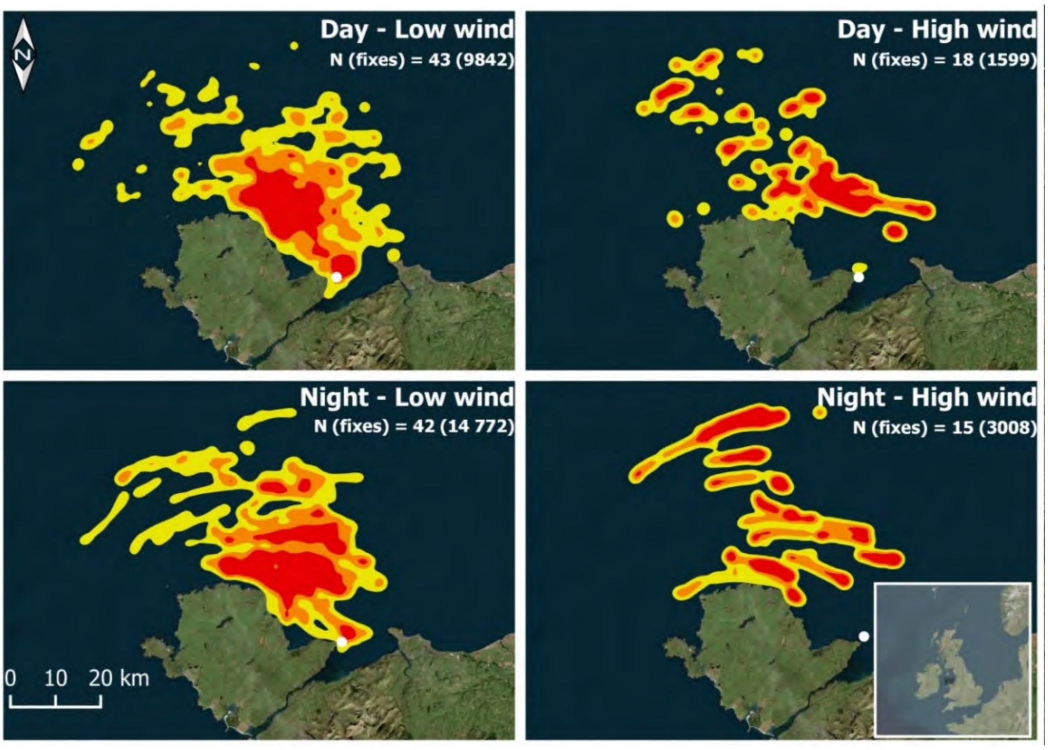
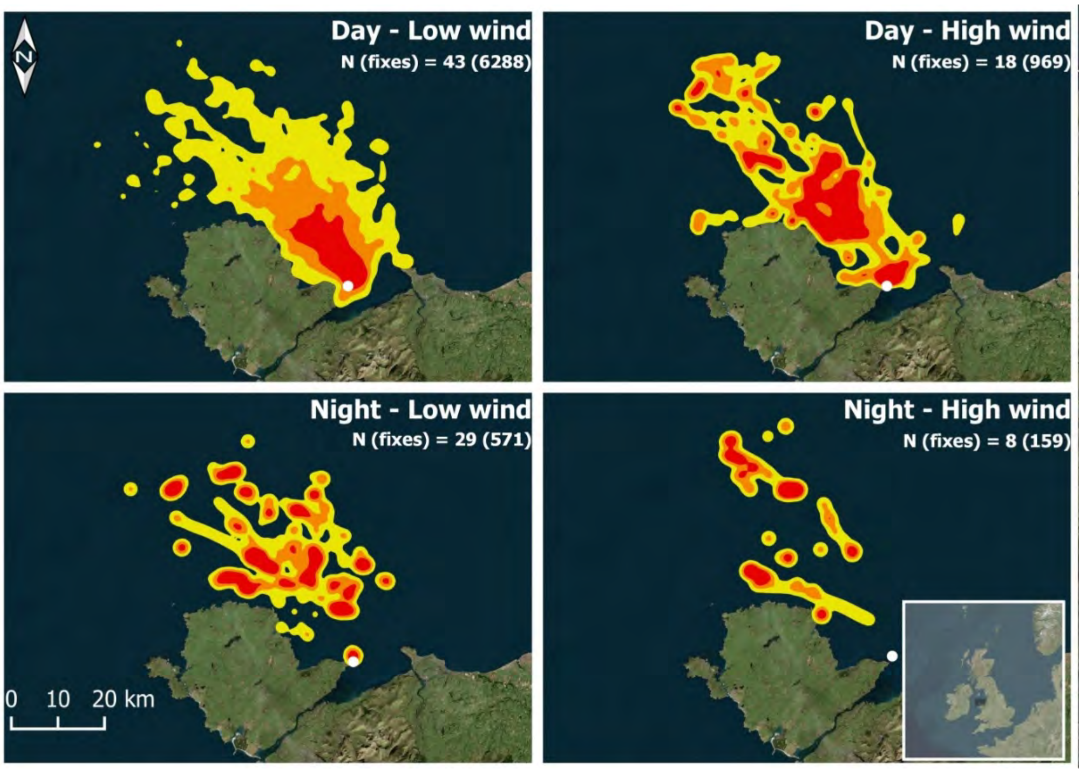


Figure A104 For Razorbill, utilisation distributions at Puffin Island showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class

(c) Commuting



(d) Foraging

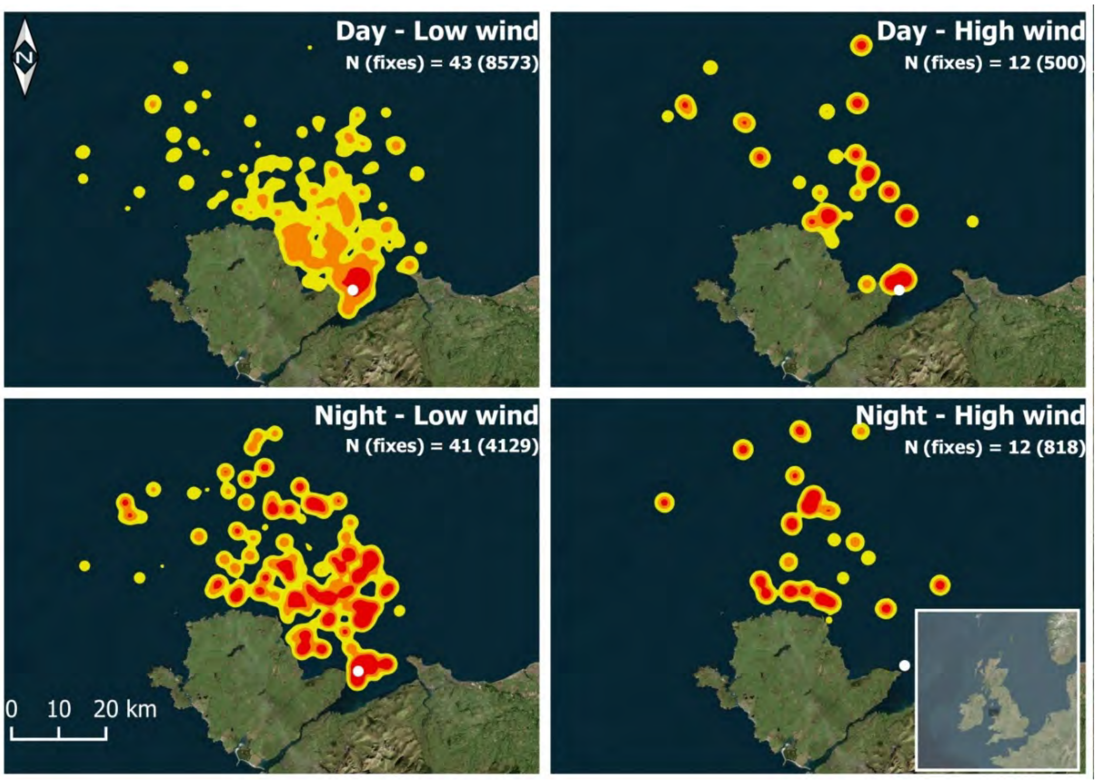
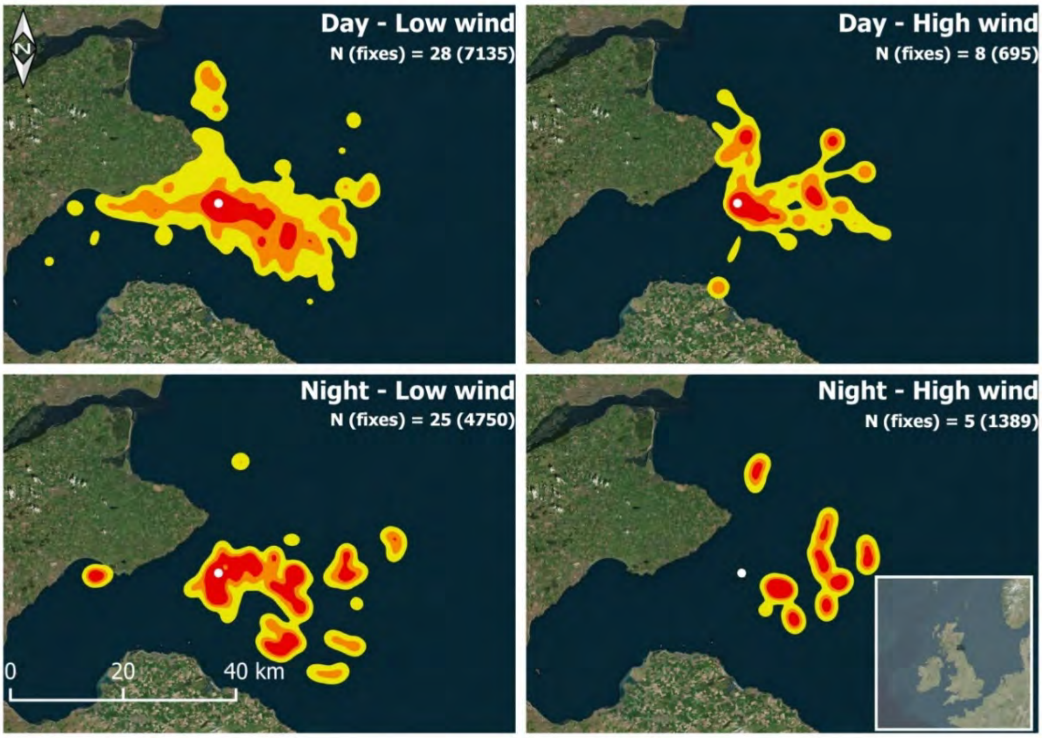


Figure continued.

(a) All states



(b) Floating on sea

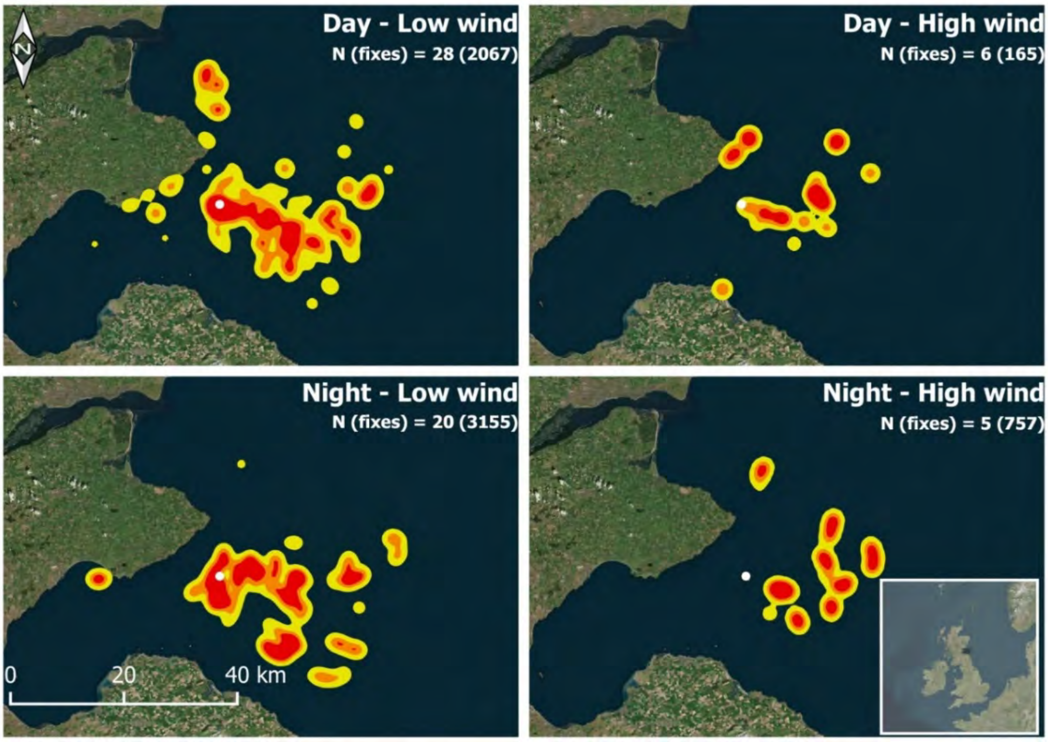
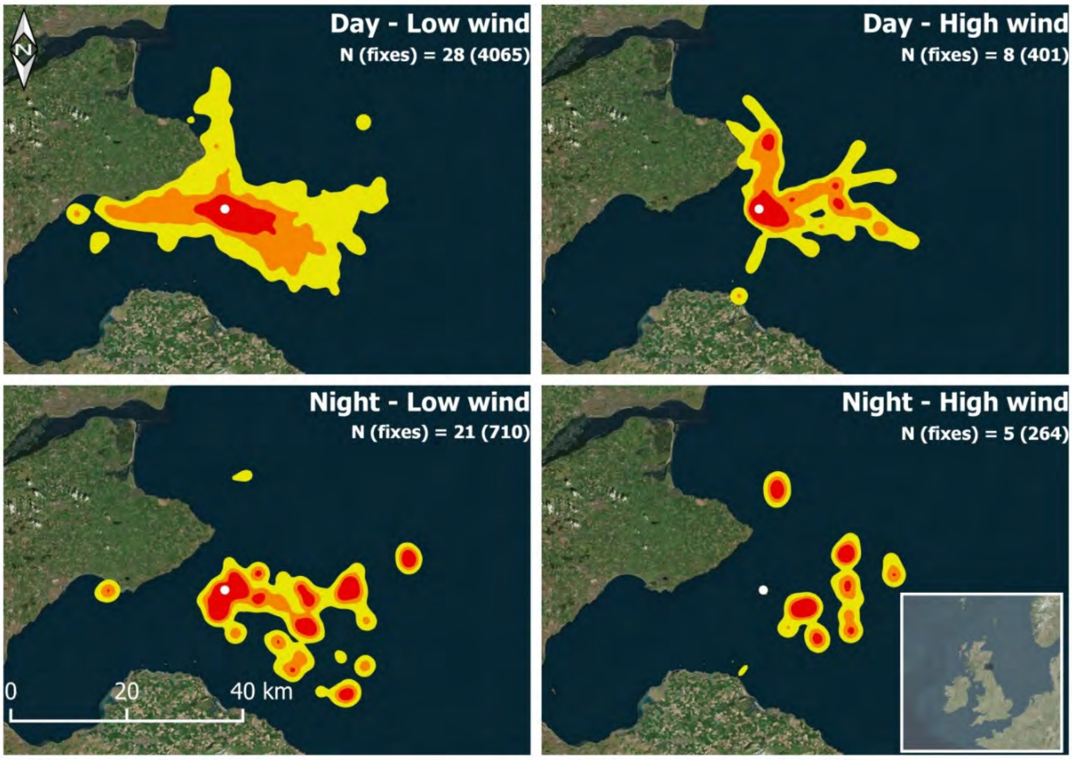


Figure A105 For Razorbill, utilisation distributions at the Isle of May showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class

(c) Commuting



(d) Foraging

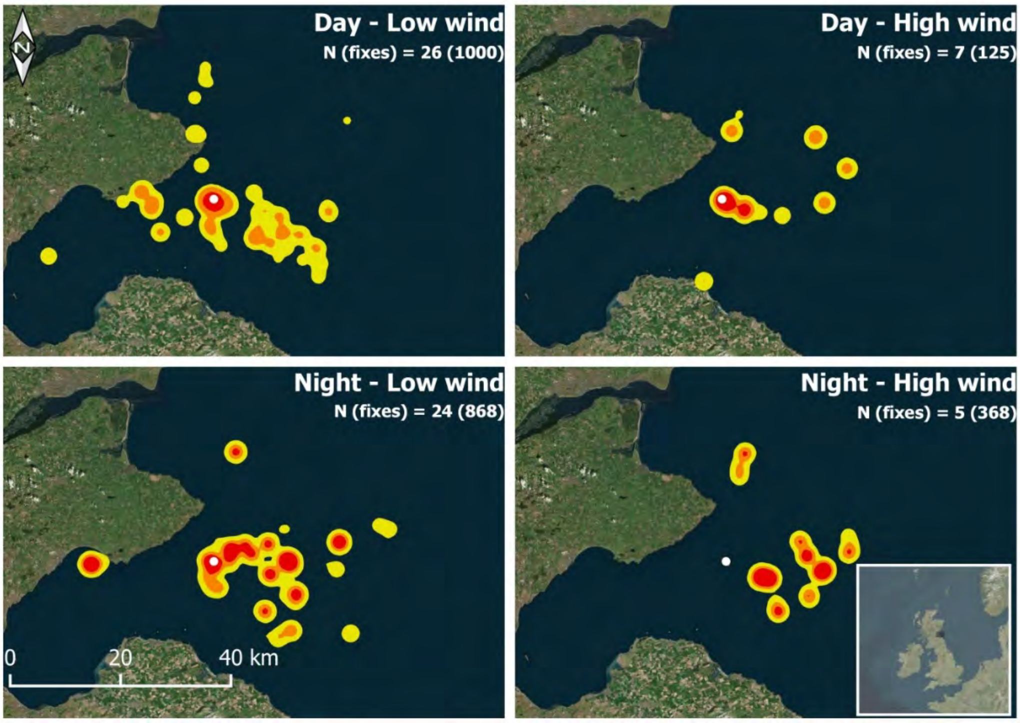
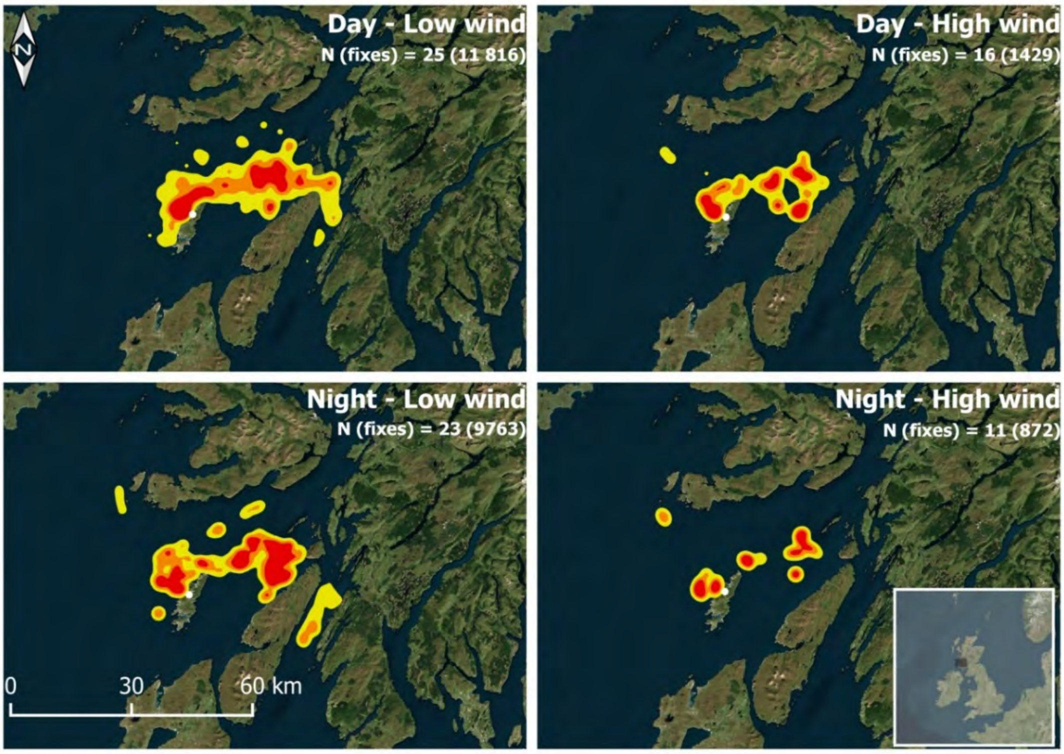


Figure continued.

(a) All states



(b) Floating on sea

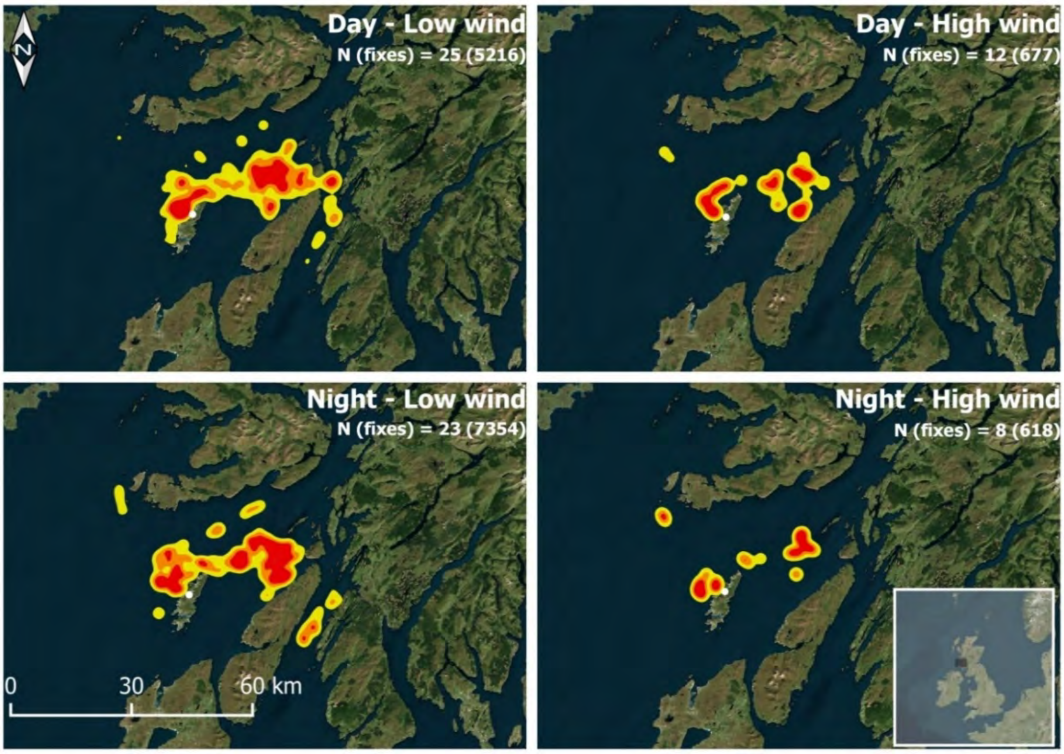
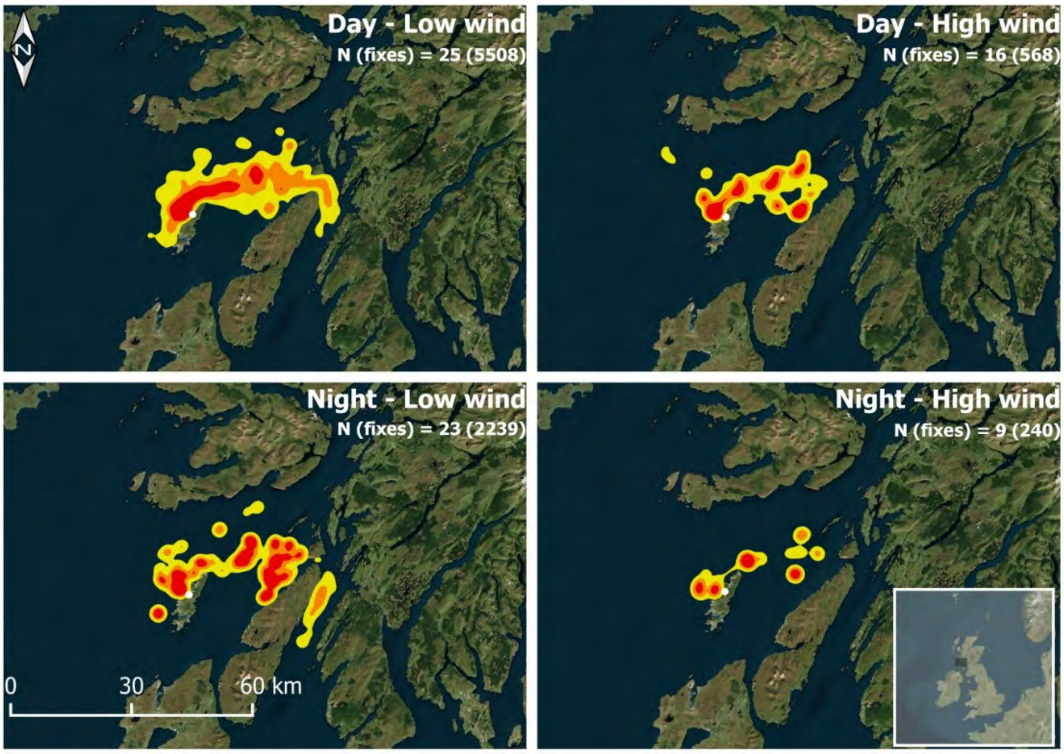


Figure A106 For Razorbill, utilisation distributions at Colonsay (based on HMMs using TDR data) showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class.

(c) Commuting



(d) Foraging

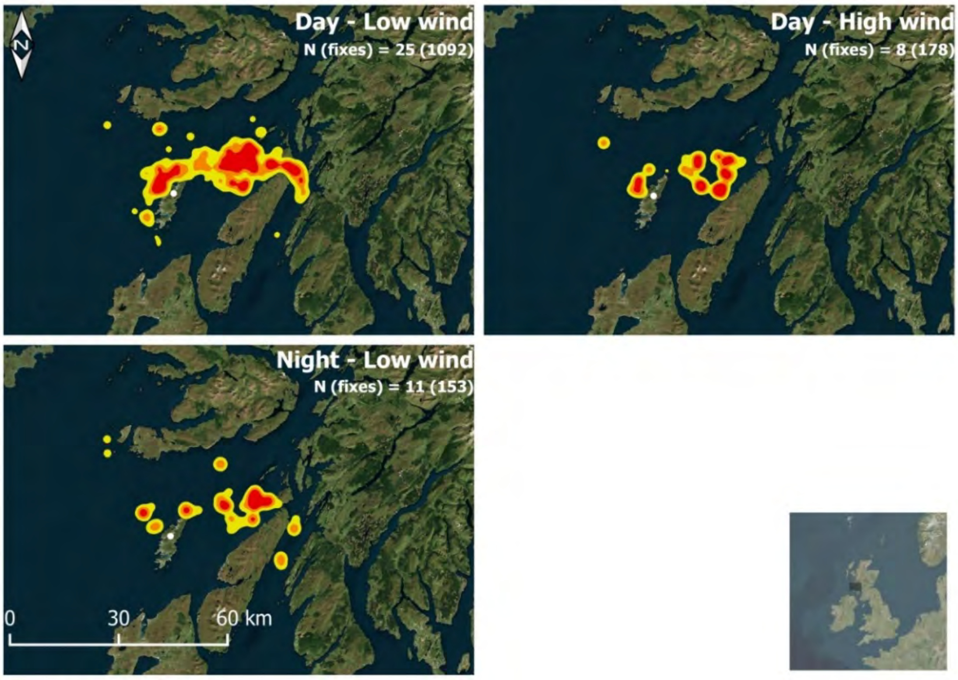
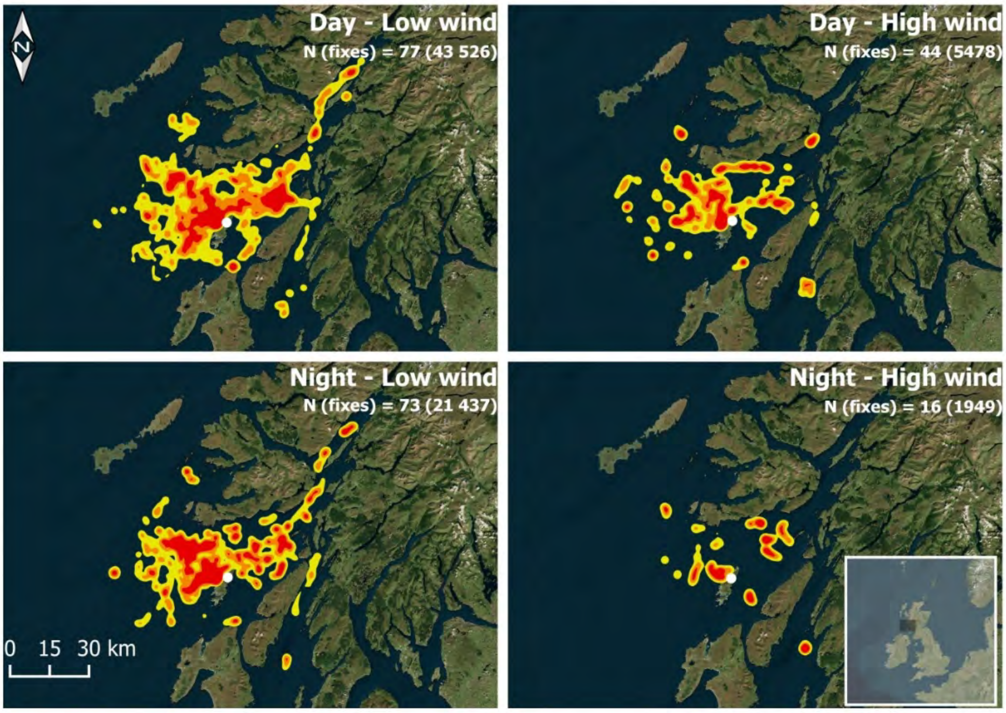


Figure continued.

7.8.5 Common Guillemot

(a) All states



(b) Floating on sea

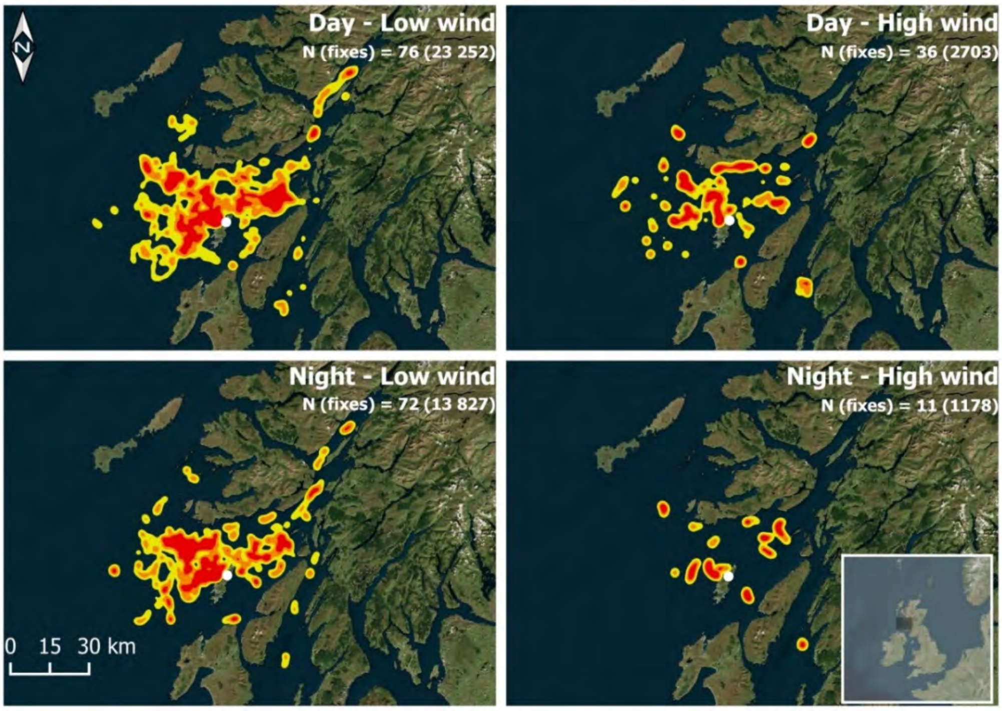
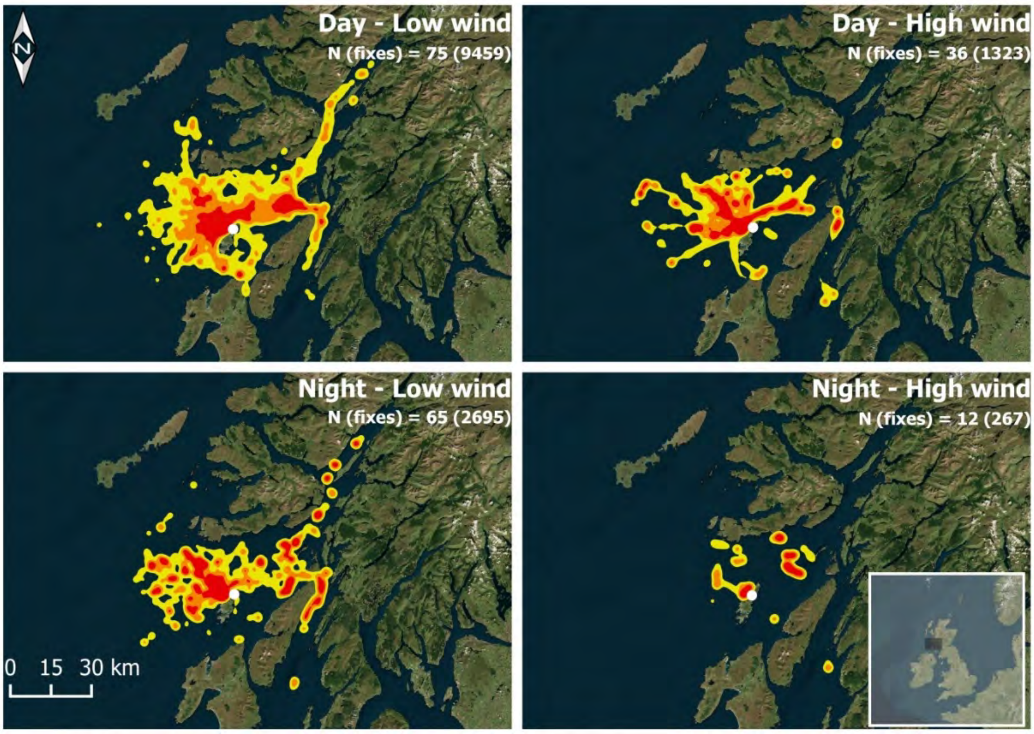


Figure A107 For Guillemot, utilisation distributions at the Colonsay (across each state) showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging

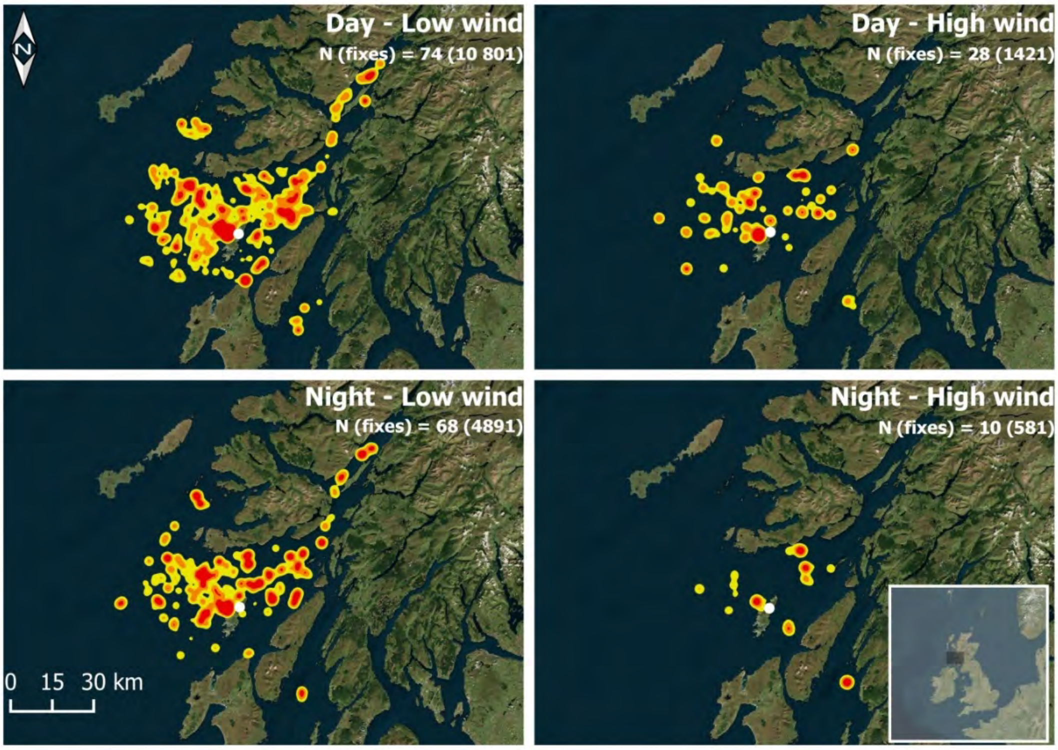
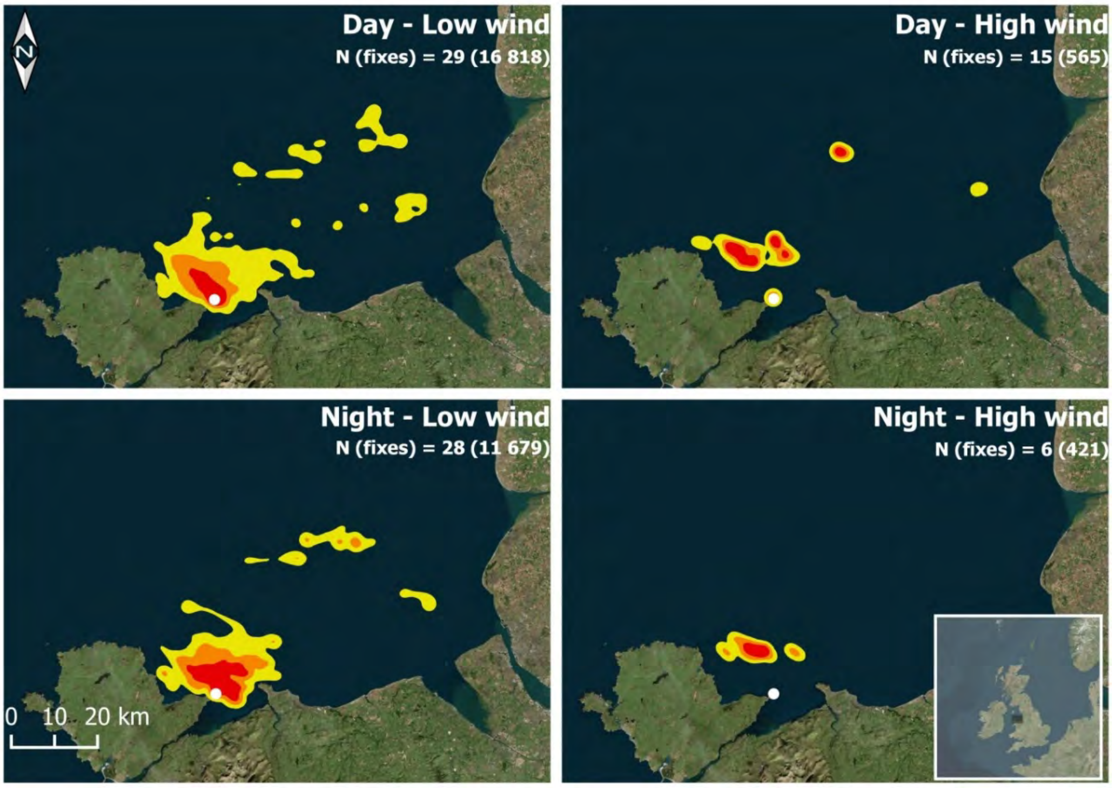


Figure continued.

(a) All states



(b) Floating on sea

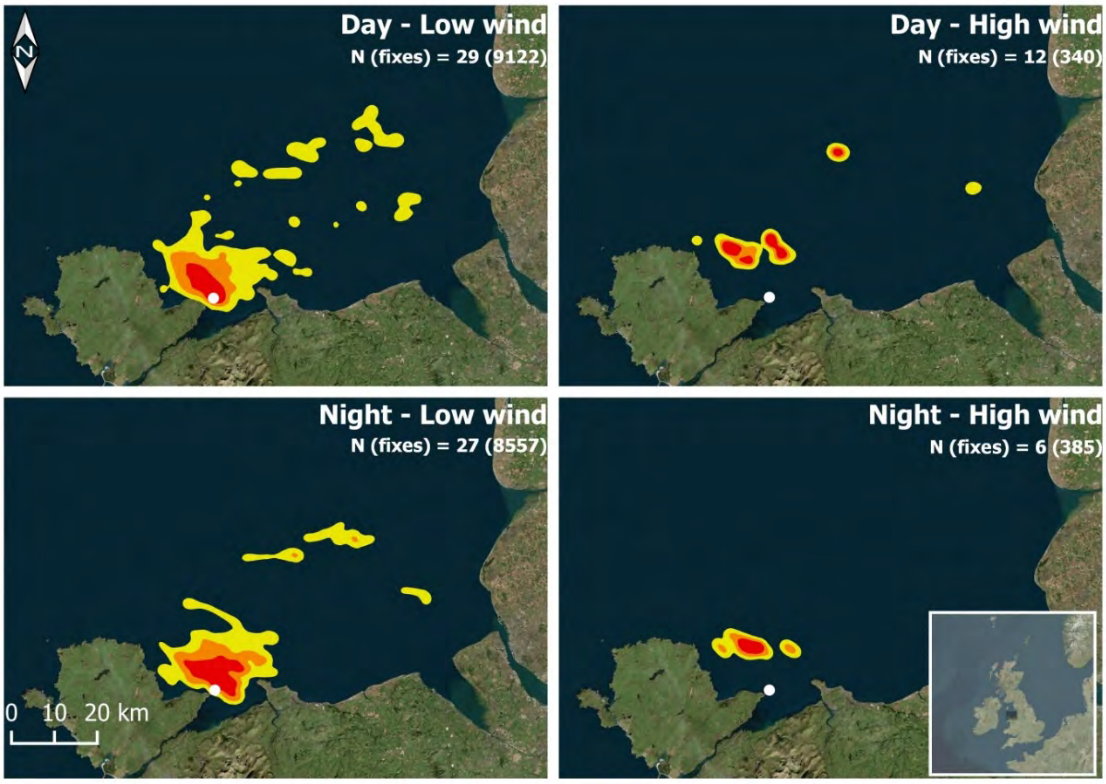
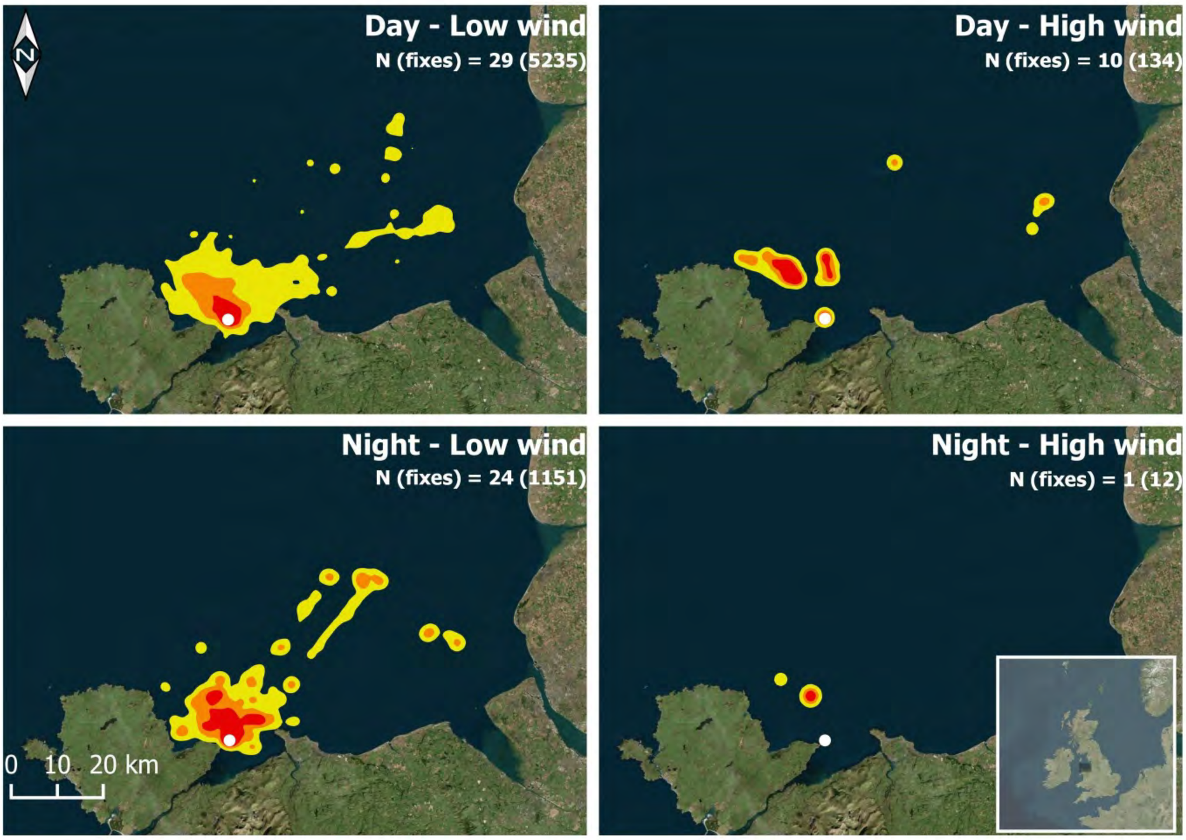


Figure A108 For Guillemot, utilisation distributions for at Puffin Island showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging

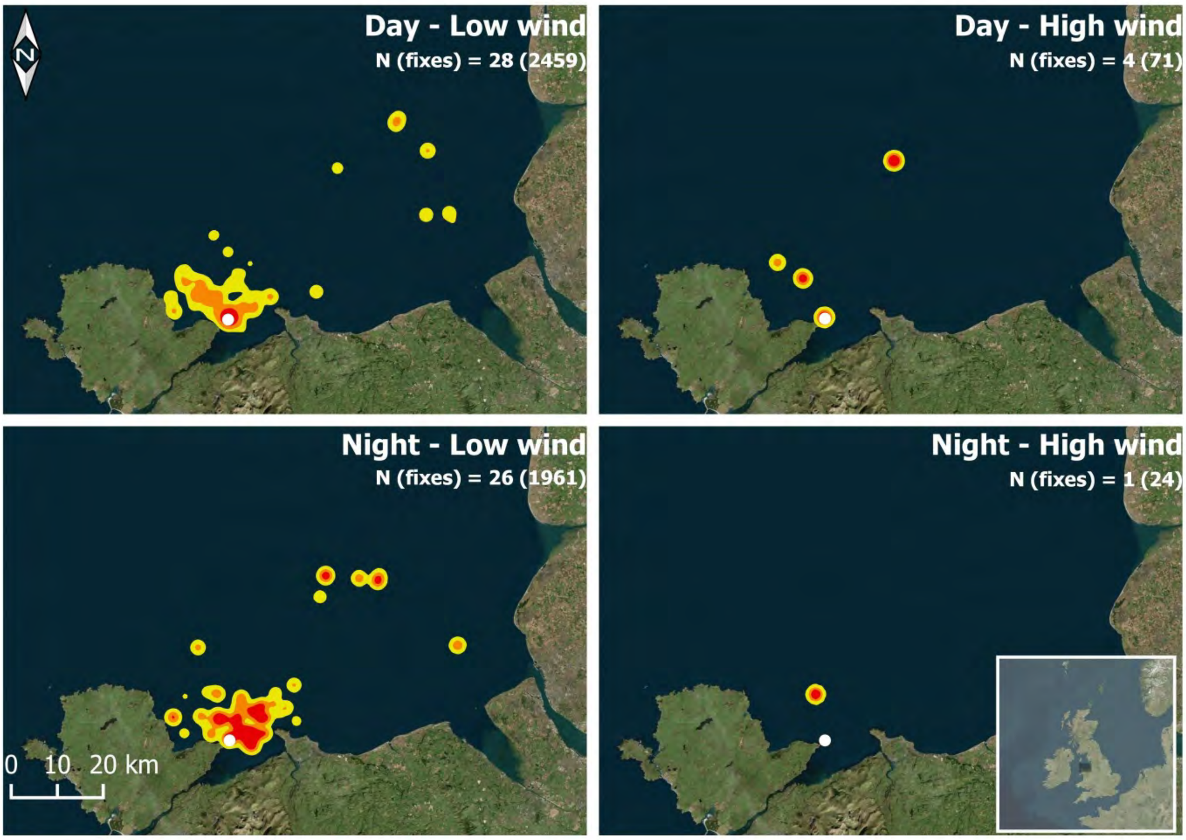
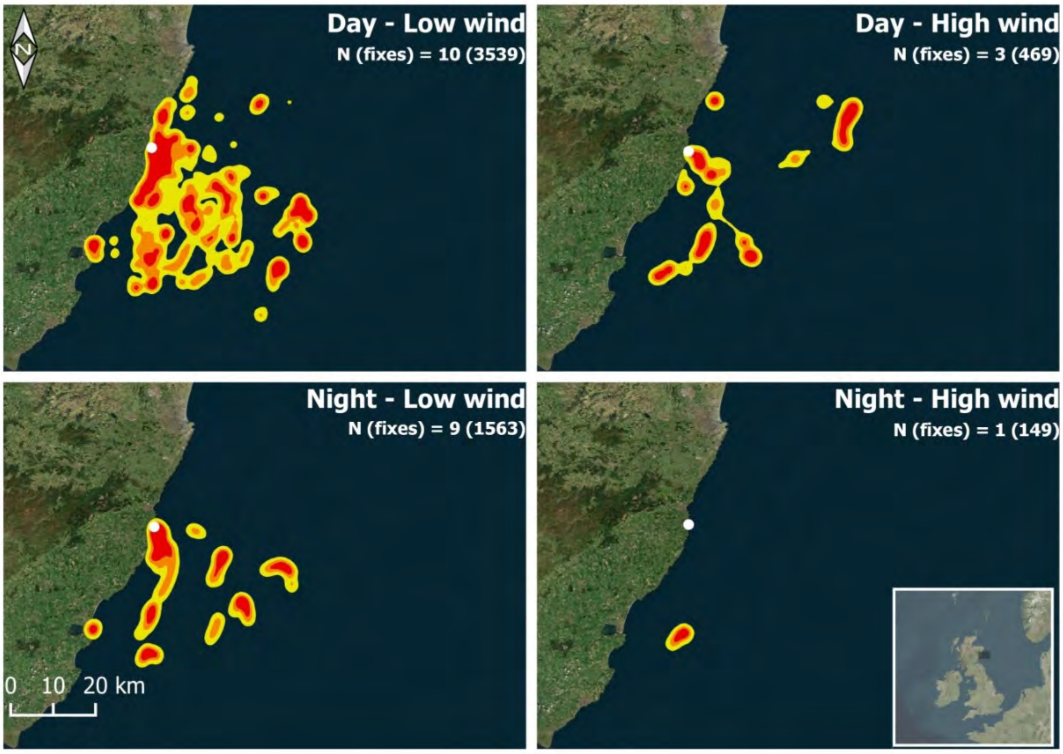


Figure continued.

(a) All states



(b) Floating on sea

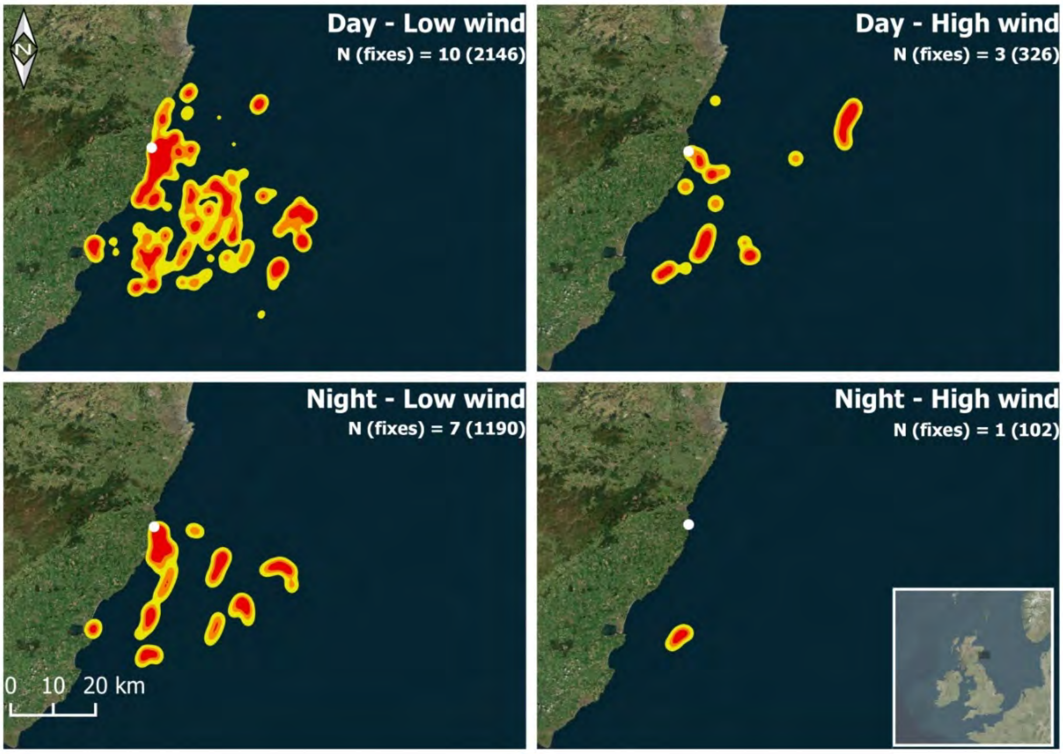
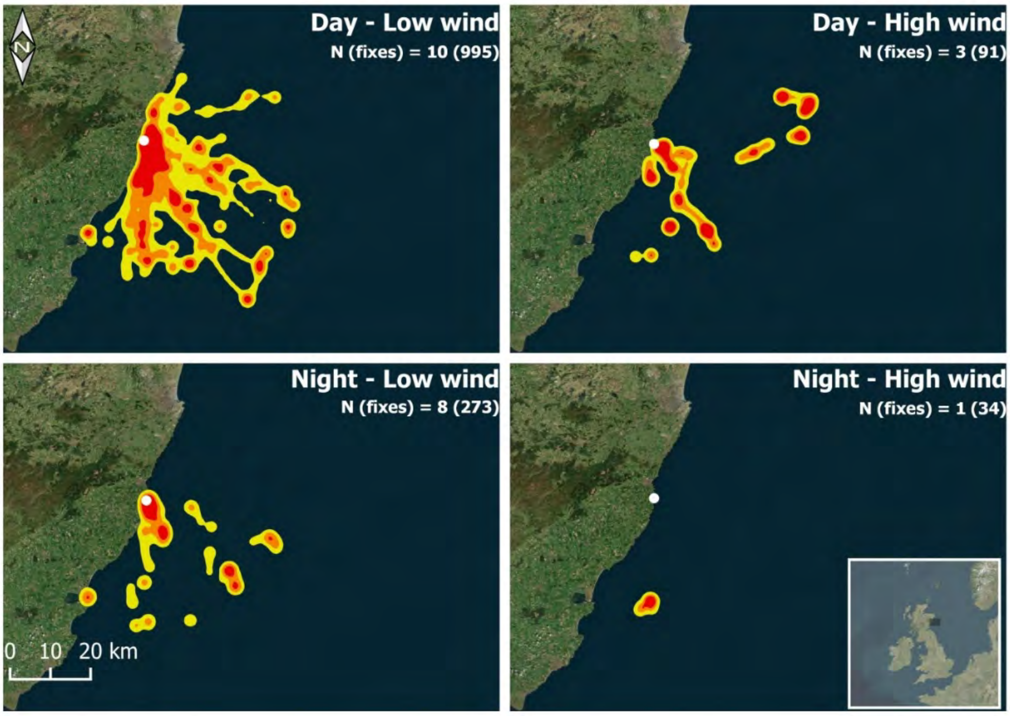


Figure A109 For Guillemot, utilisation distributions at Fowlsheugh showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; ‘N’ = number of birds and ‘fixes’ = no GPS points in each class.

(c) Commuting



(d) Foraging

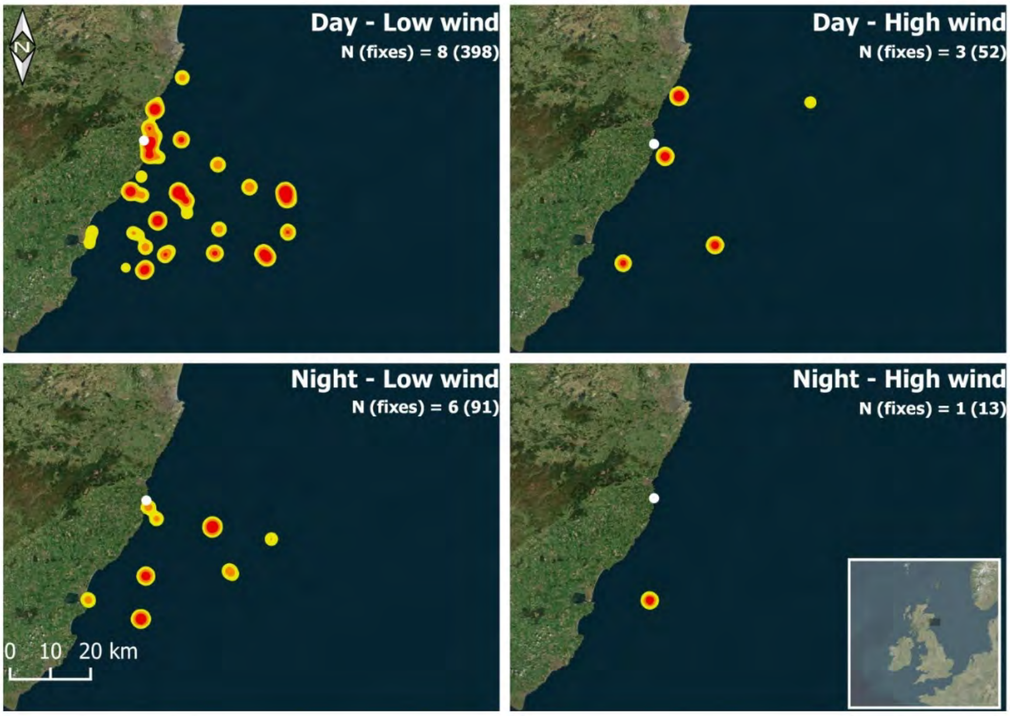
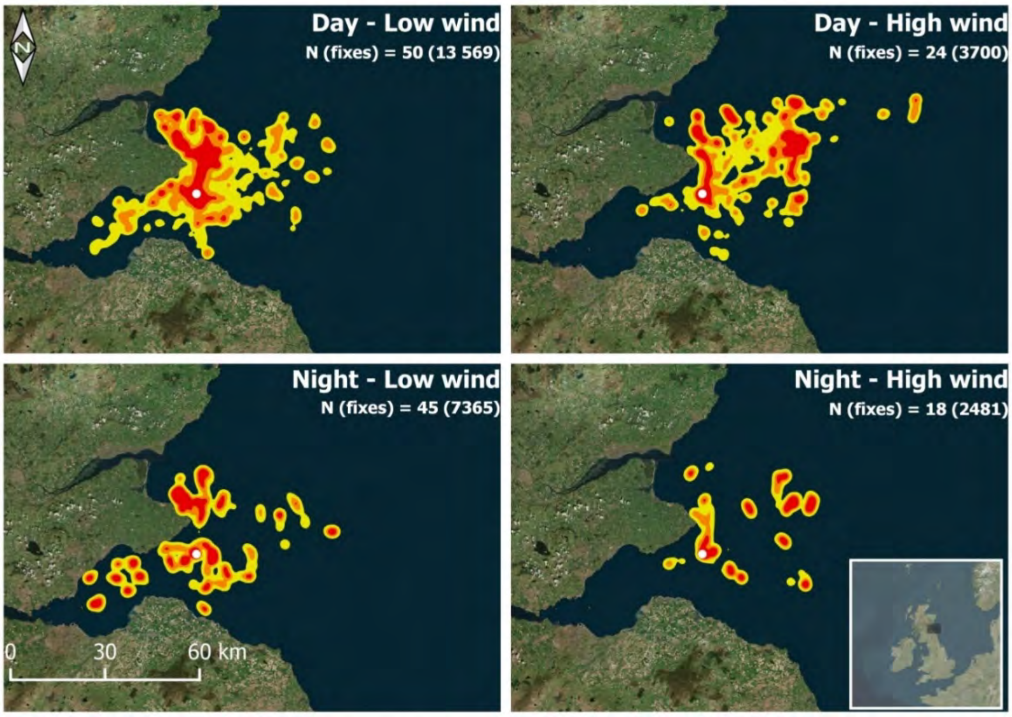


Figure continued.

(a) All states



(b) Floating on sea

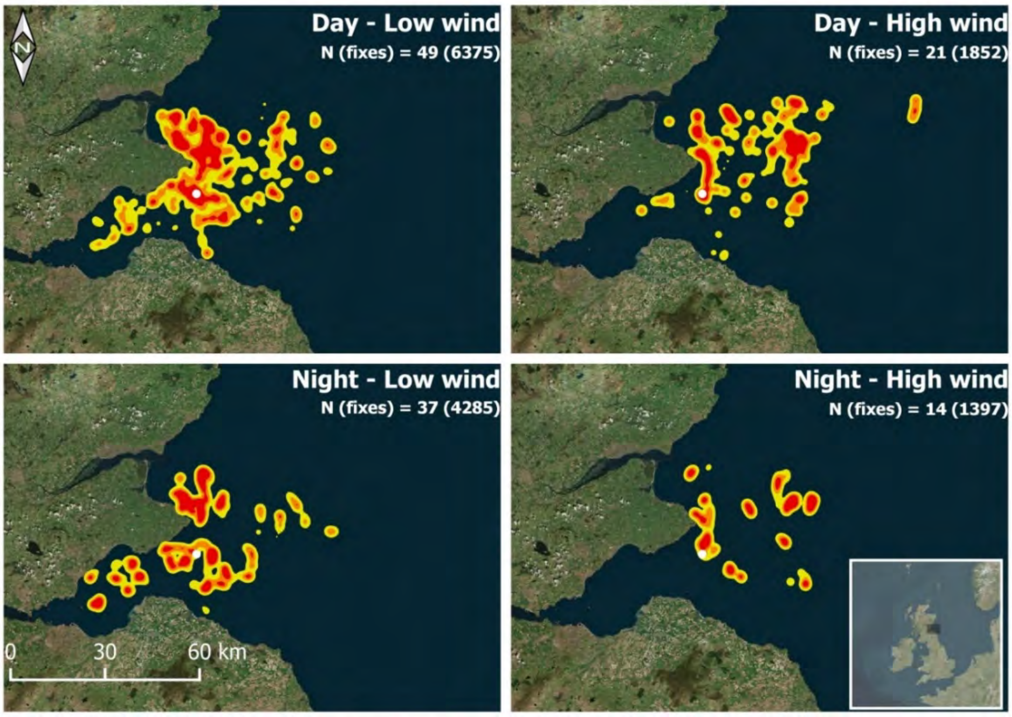
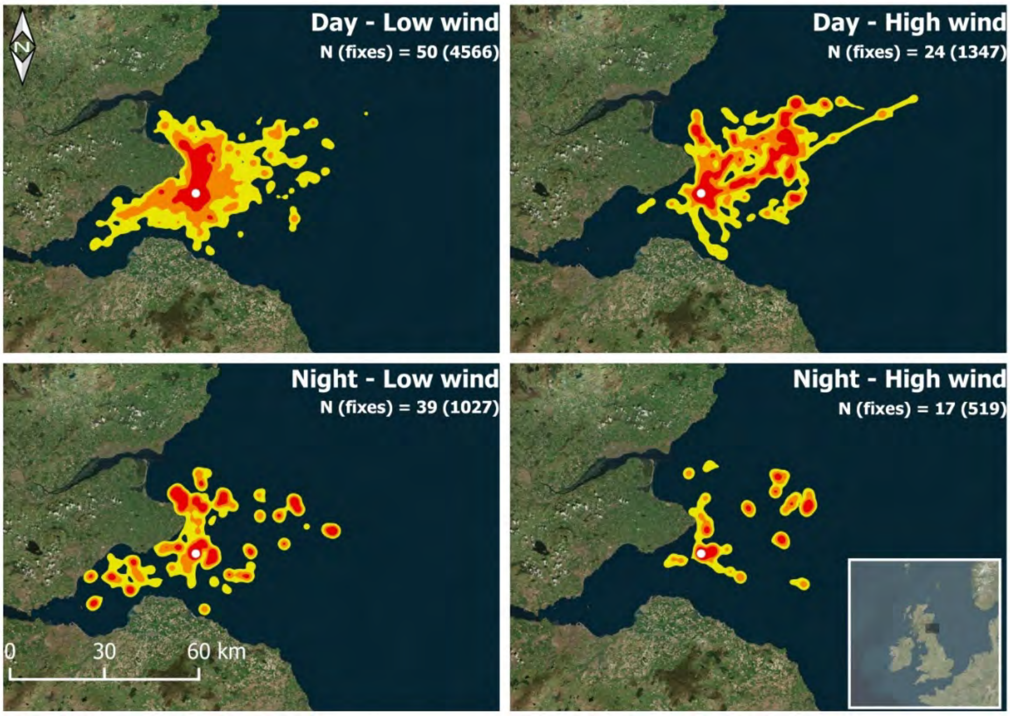


Figure A110 For Guillemot, utilisation distributions at the Isle of May showing the 50% kernel density estimate (KDE, red, ‘core’), 75% KDE (orange), and 95% KDE (yellow, ‘total’) distribution split by day and night (local sunrise and sunset) and high

and low wind conditions (split by a threshold of 8 m/s at the GPS fix level); map inset shows location; 'N' = number of birds and 'fixes' = no GPS points in each class.

(c) Commuting



(d) Foraging

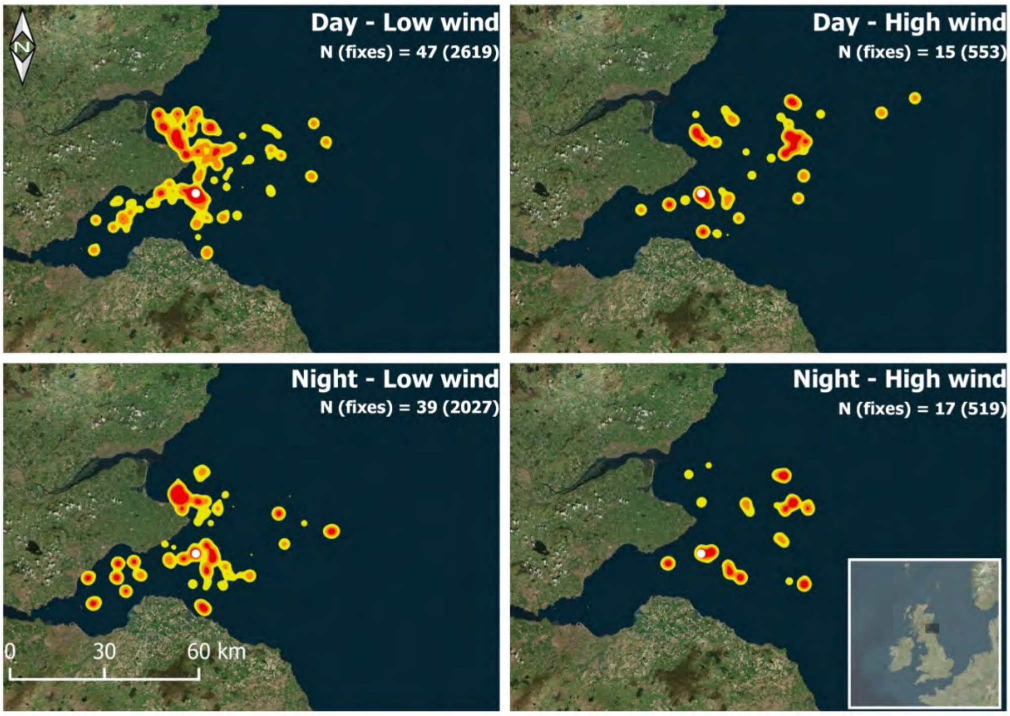


Figure continued.

7.9 Appendix AI. Overlap Indices

7.9.1 Northern Gannet

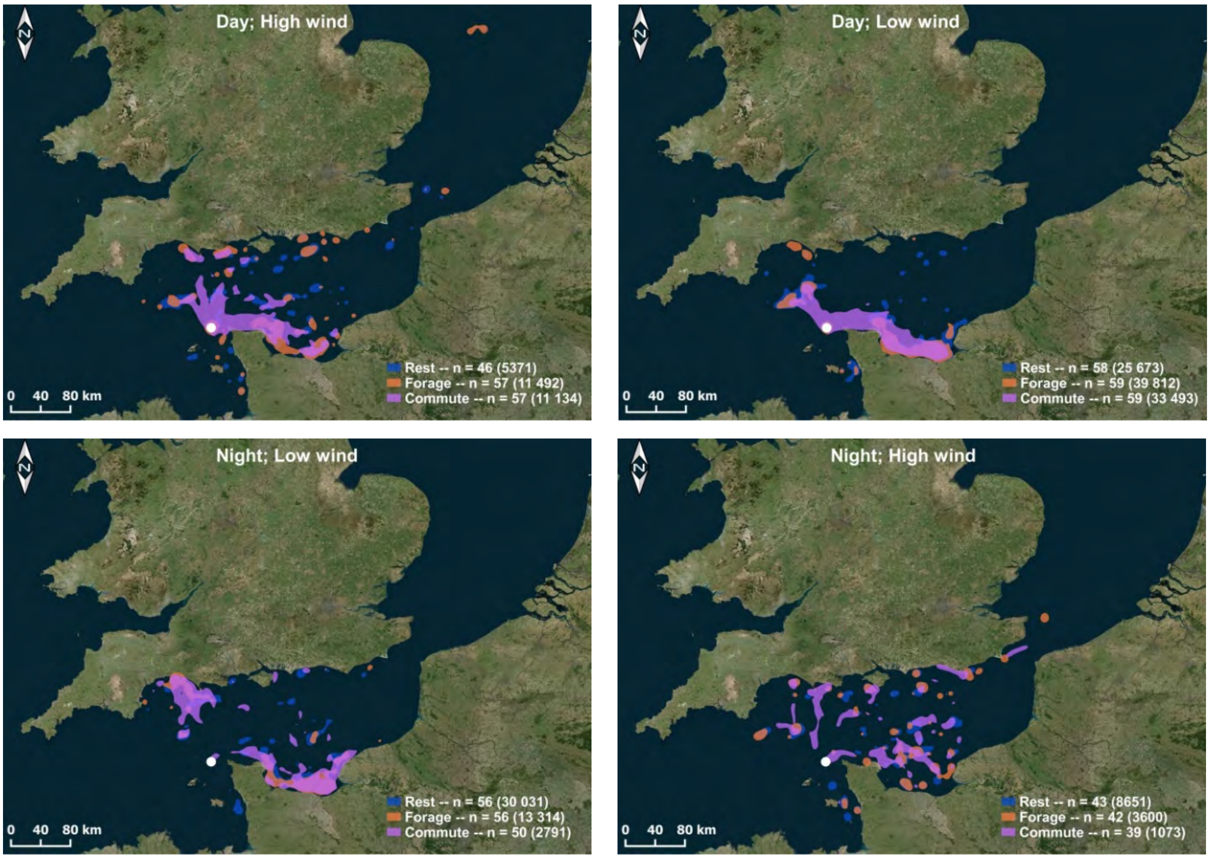


Figure A111 For Gannet, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Alderney.

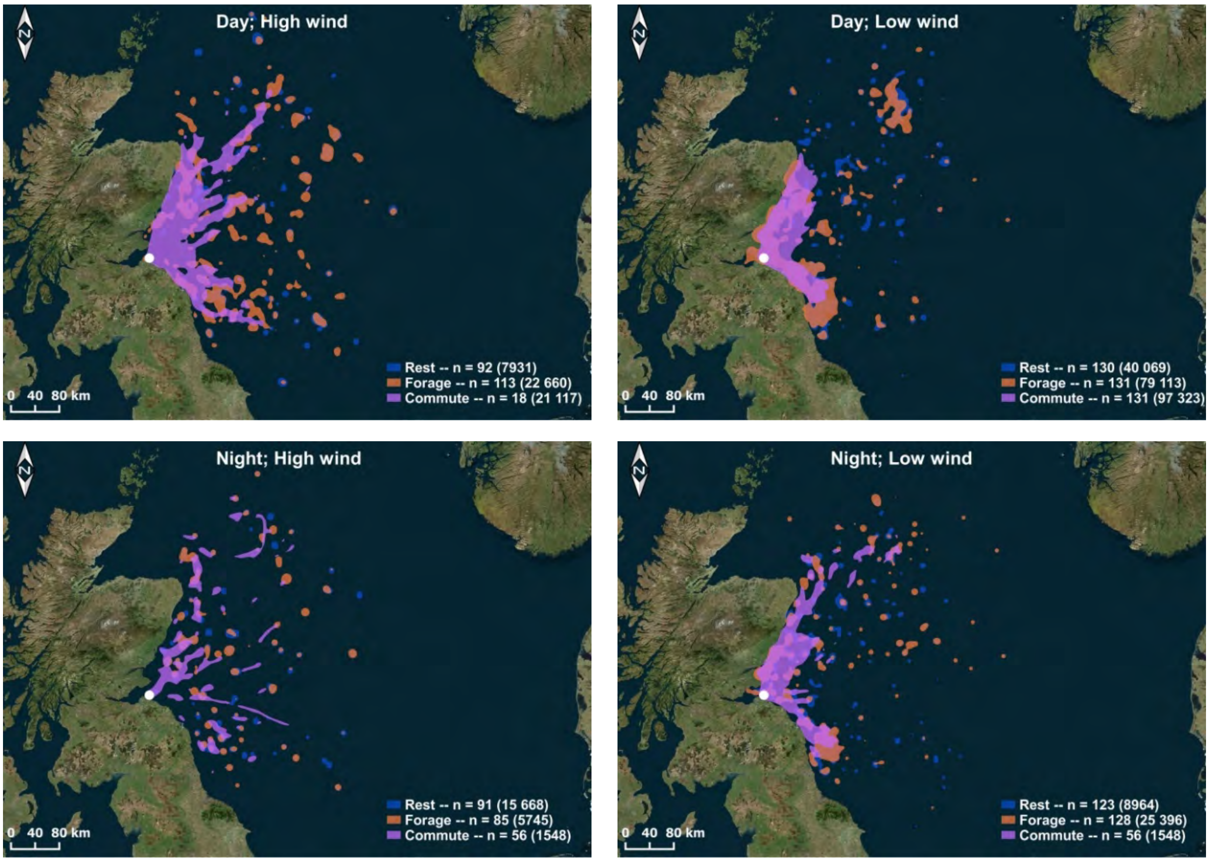


Figure A112 For Gannet, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Bass Rock.

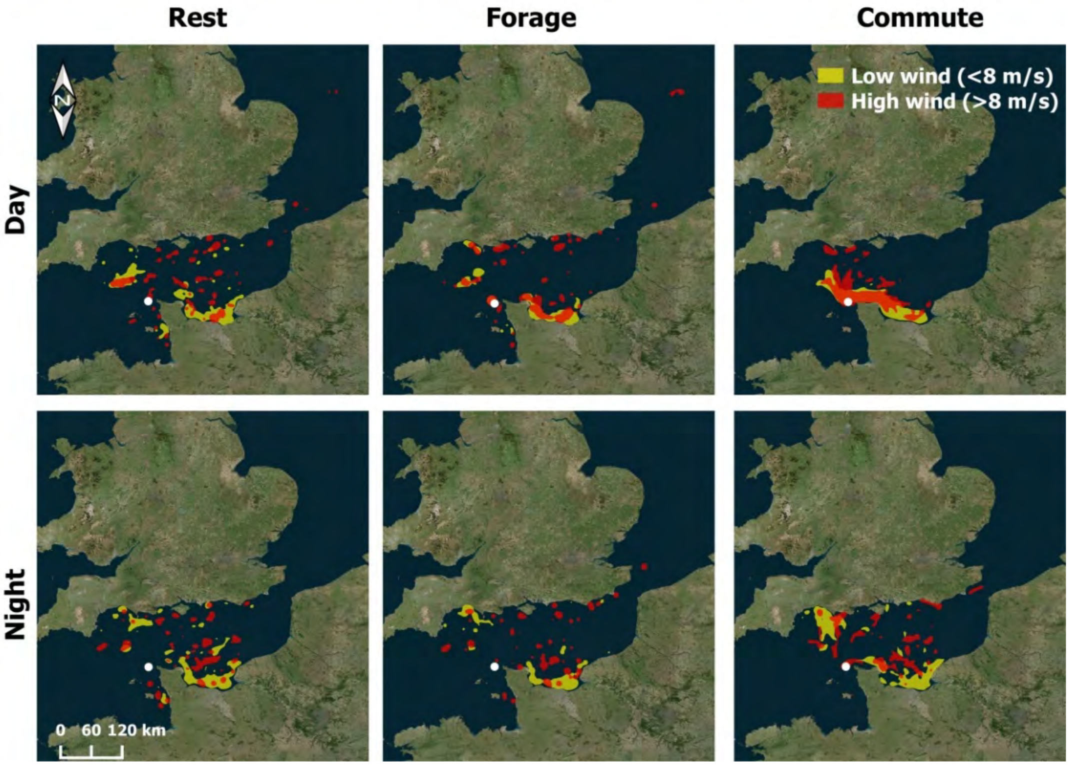


Figure A113 For Gannet, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Alderney.

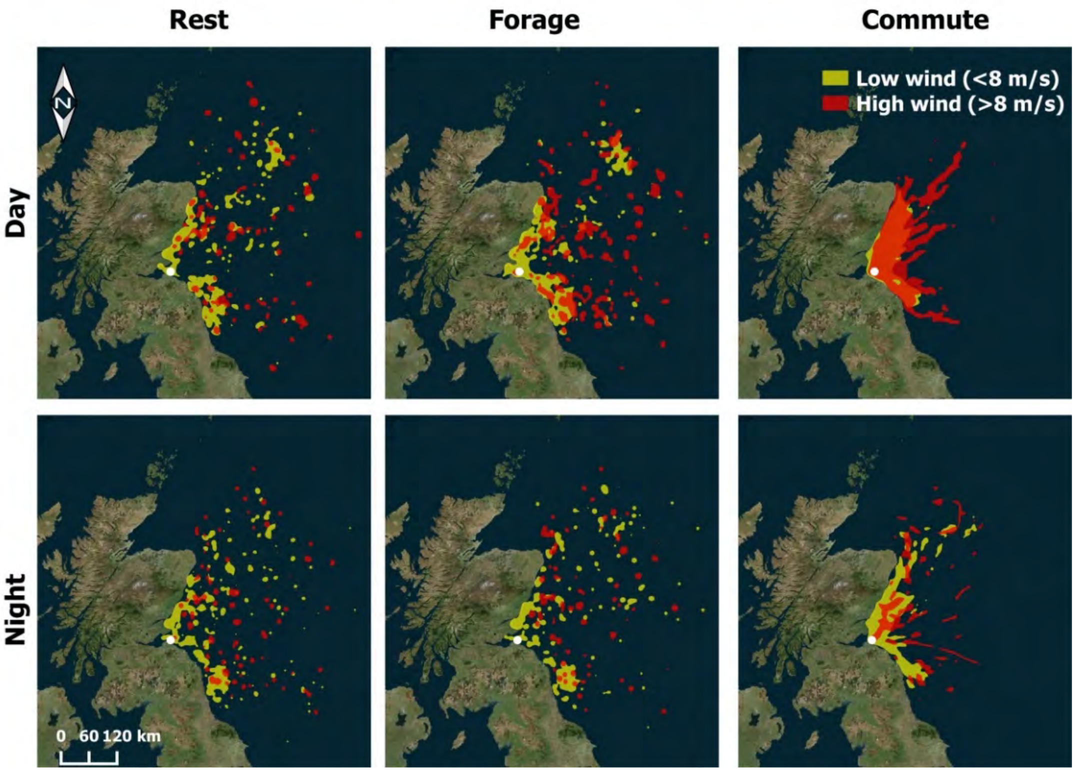


Figure A114 For Gannet, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Bass Rock.

7.9.2 Lesser Black-backed Gull

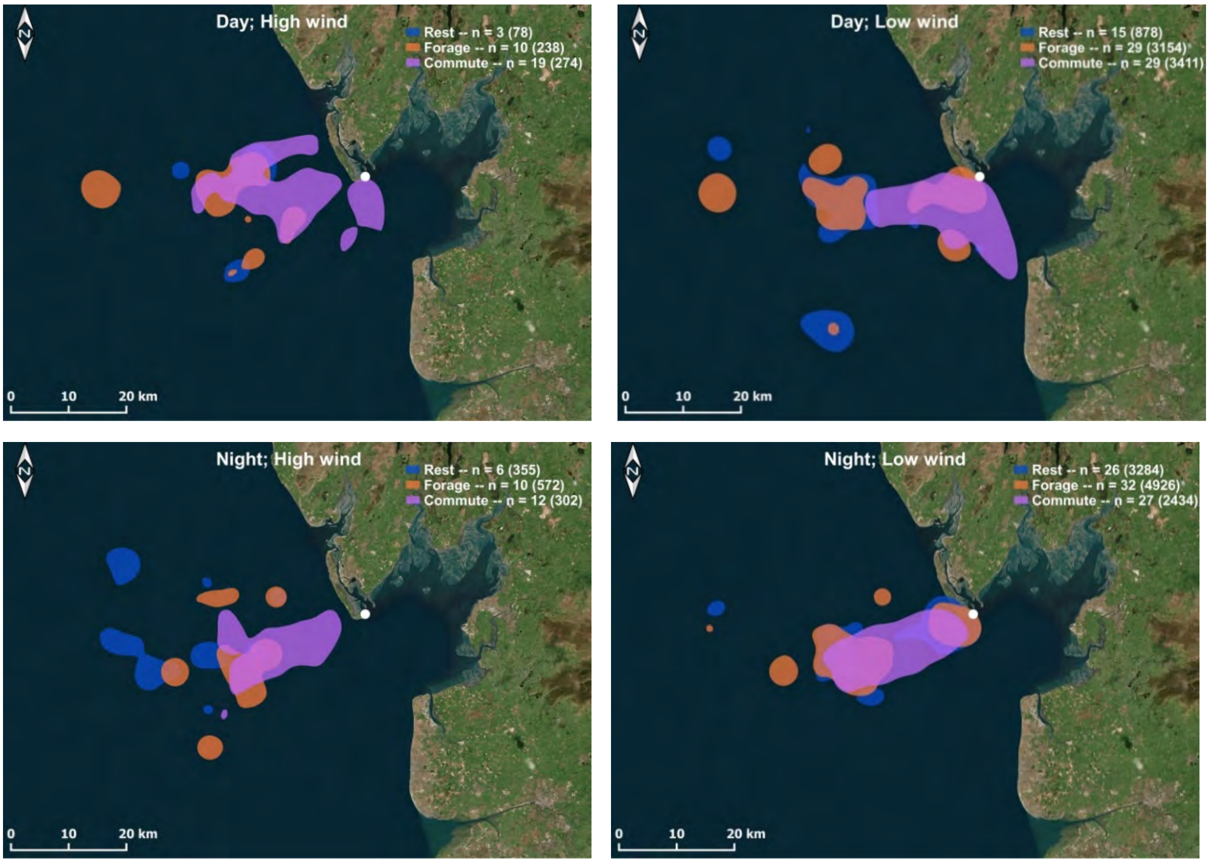


Figure A115 For Lesser Black-backed Gull, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Walney.

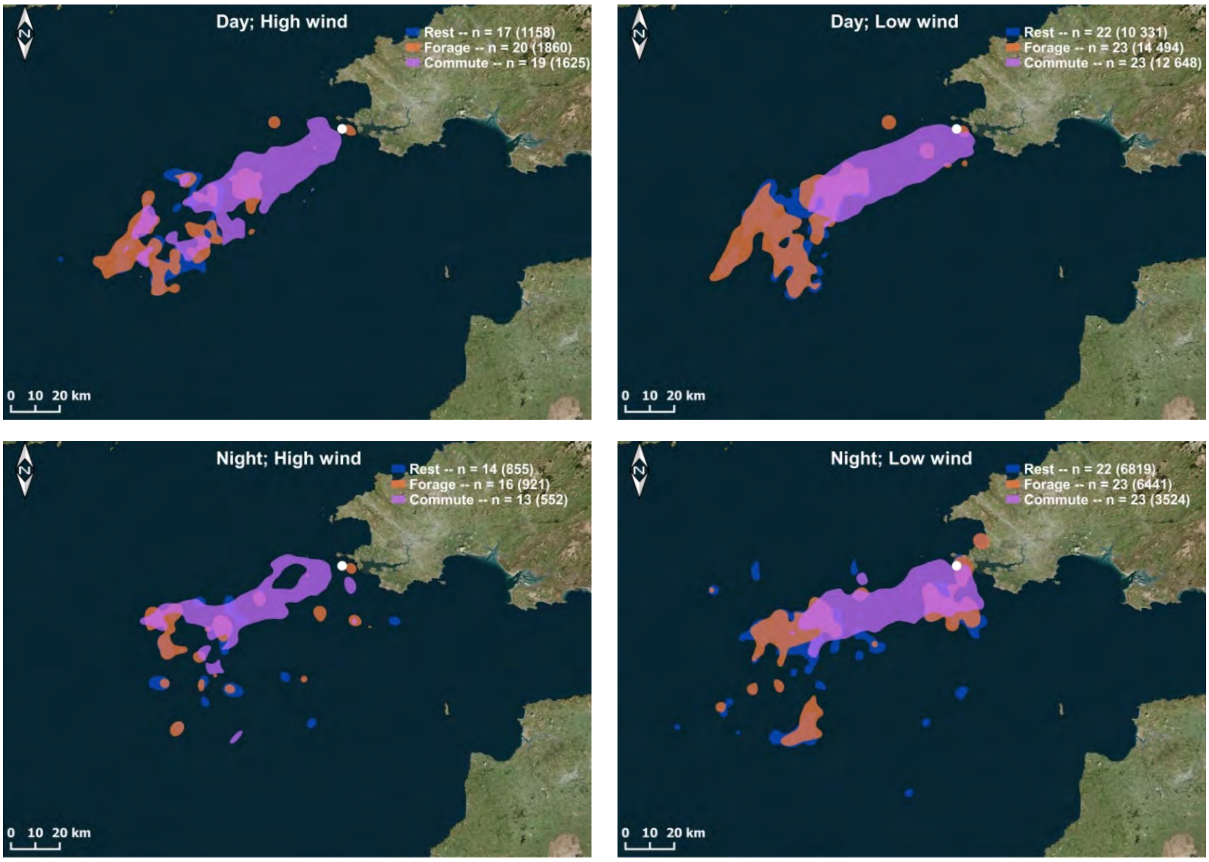


Figure A116 For Lesser Black-backed Gull, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Skokholm.

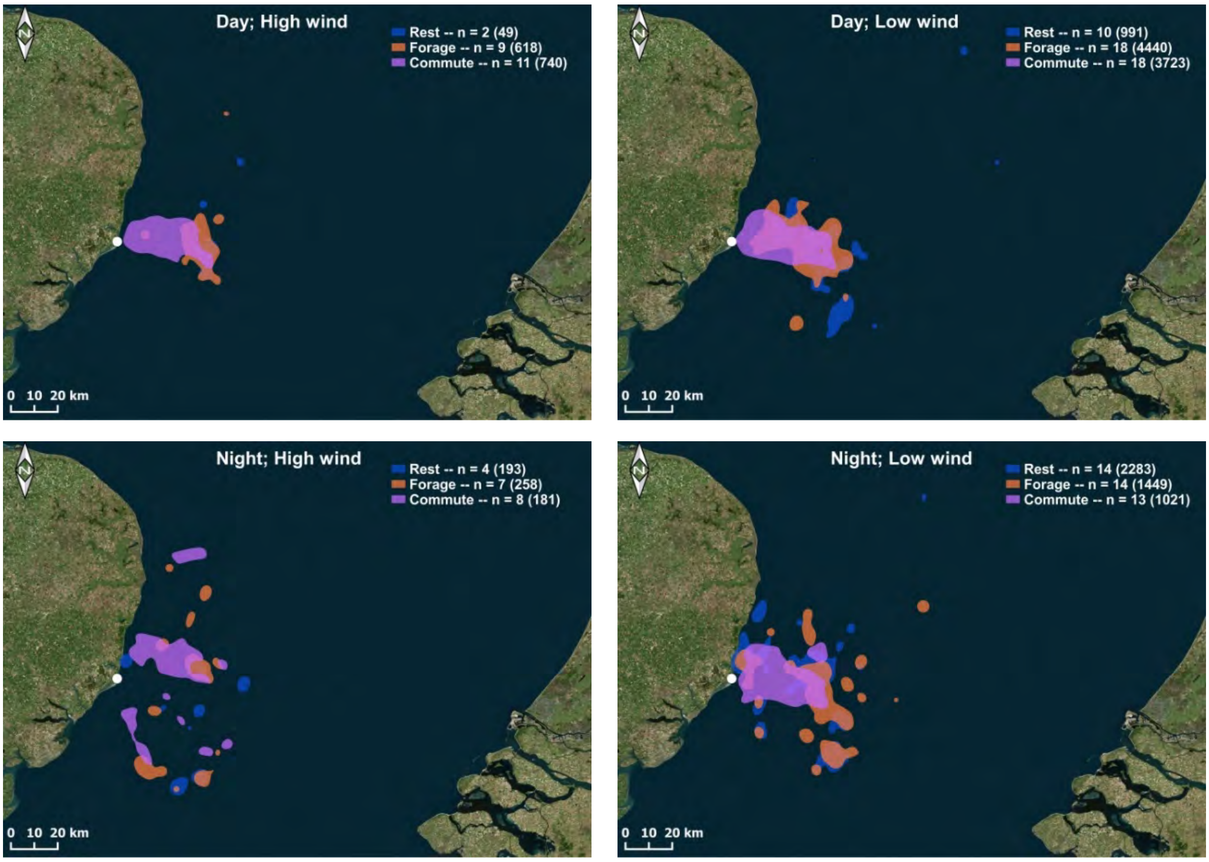


Figure A117 For Lesser Black-backed Gull, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Orford Ness note for the floating state for daytime high wind, less than 50 fixes were obtained, from only two birds, hence confidence in distribution comparisons is considered low.

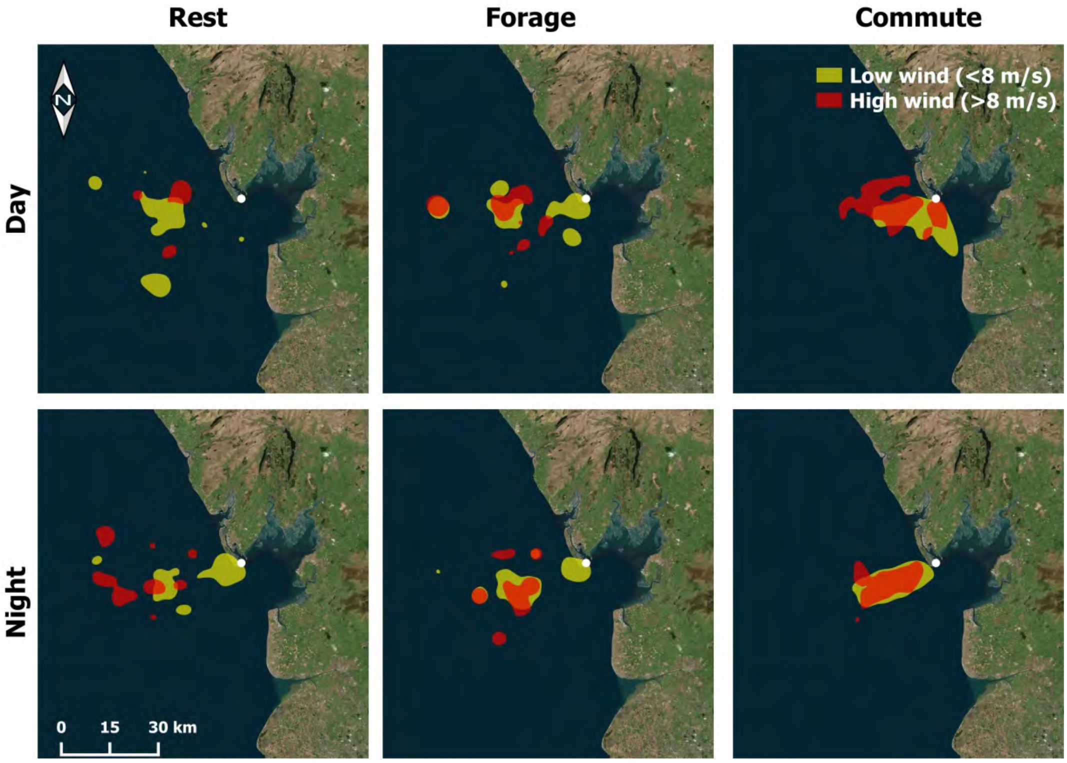


Figure A118 For Lesser Black-backed Gull, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Walney.

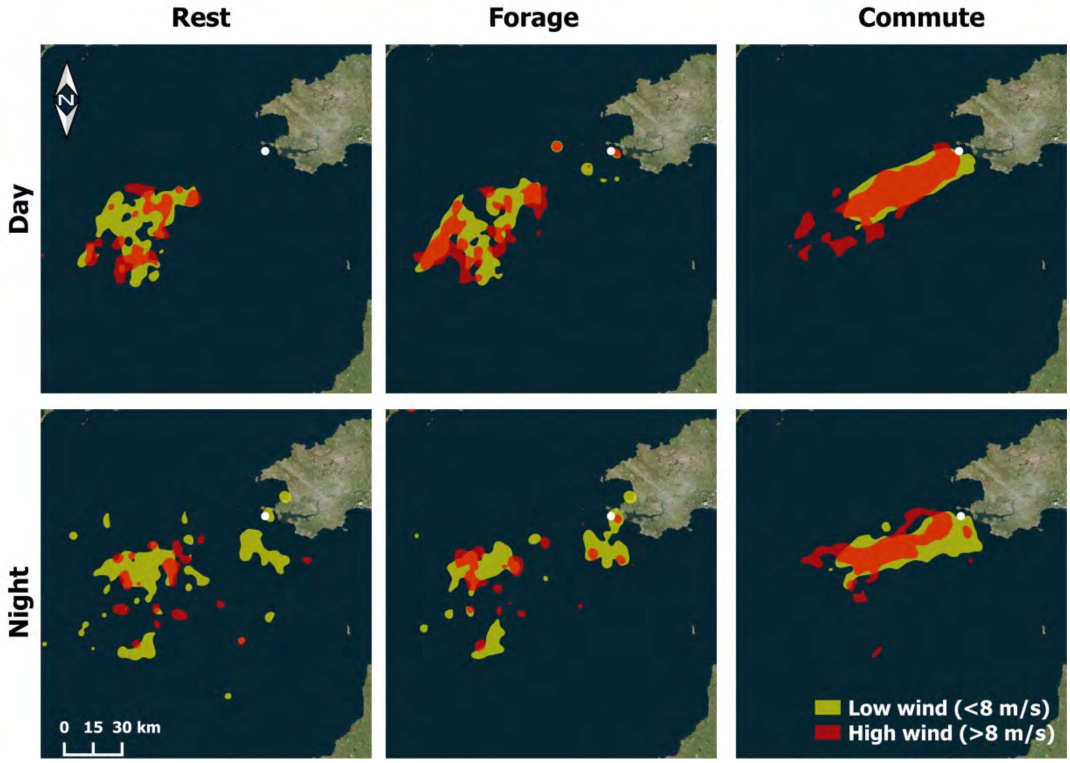


Figure A119 For Lesser Black-backed Gull, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Skokholm.

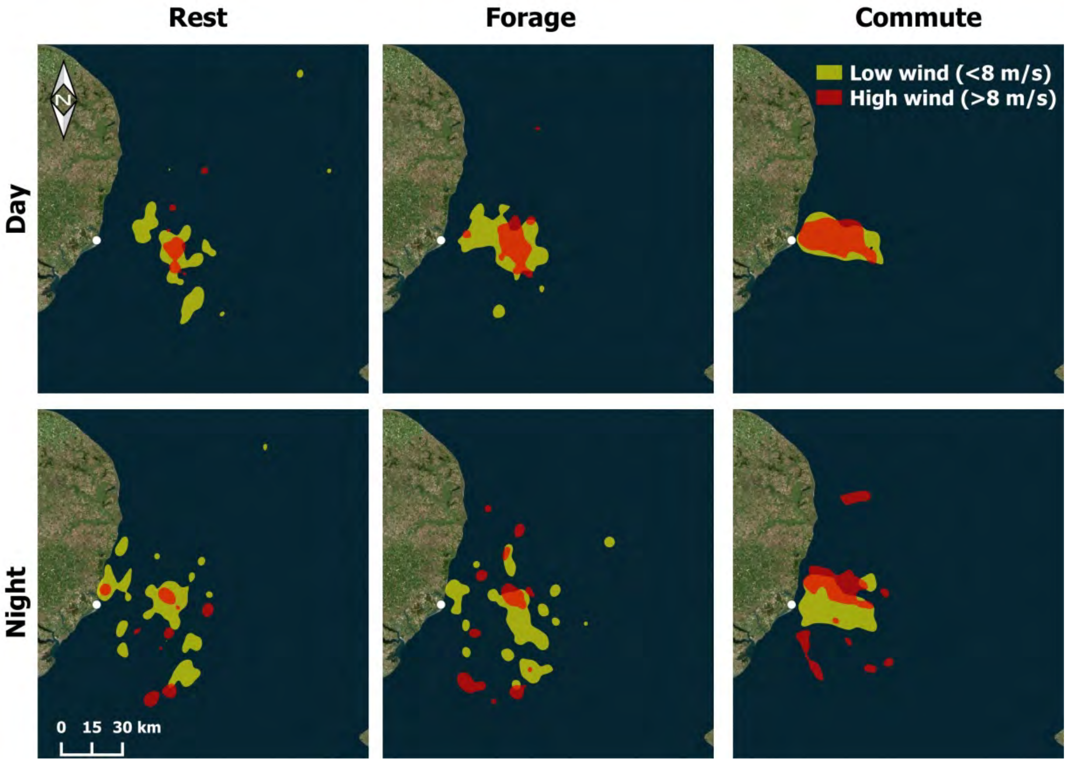


Figure A120 For Lesser Black-backed Gull, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Orford Ness.

7.9.3 Black-legged Kittiwake

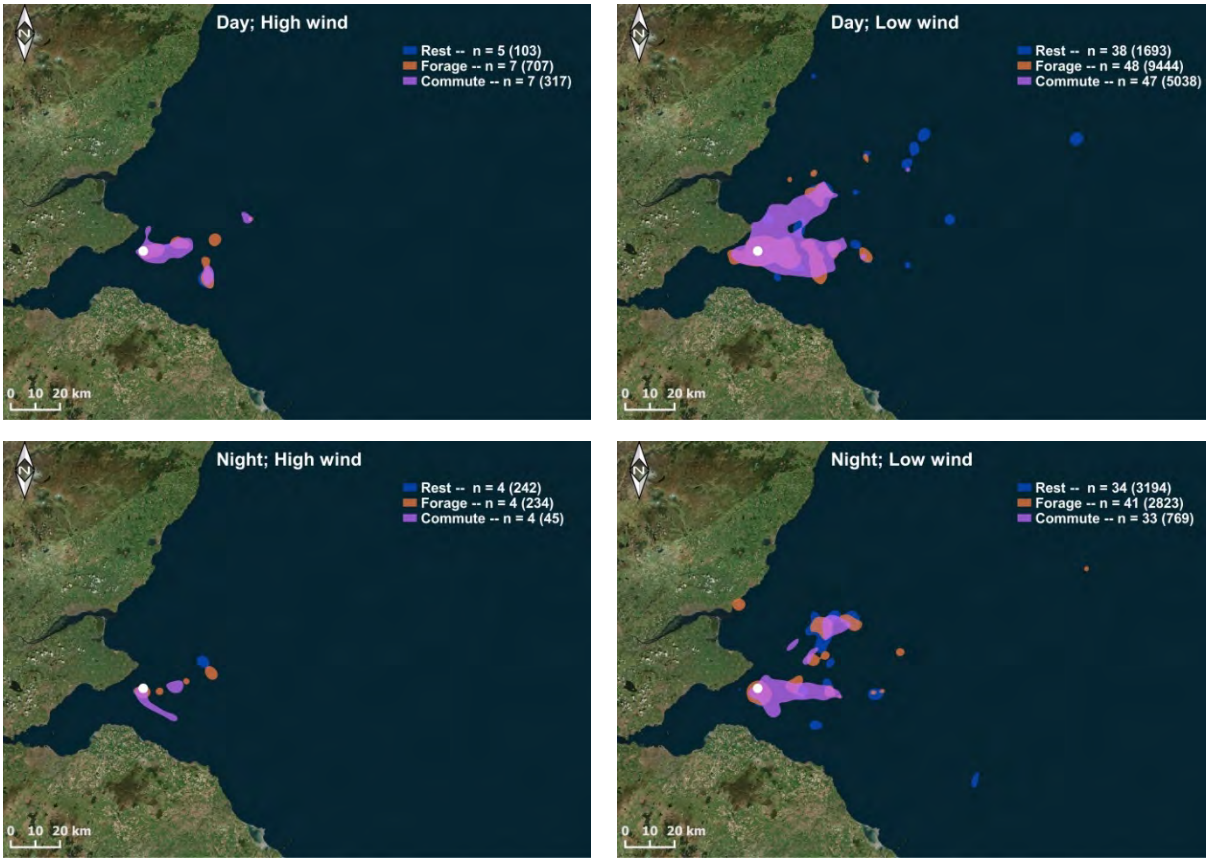


Figure A121 For Kittiwake, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at the Isle of May.

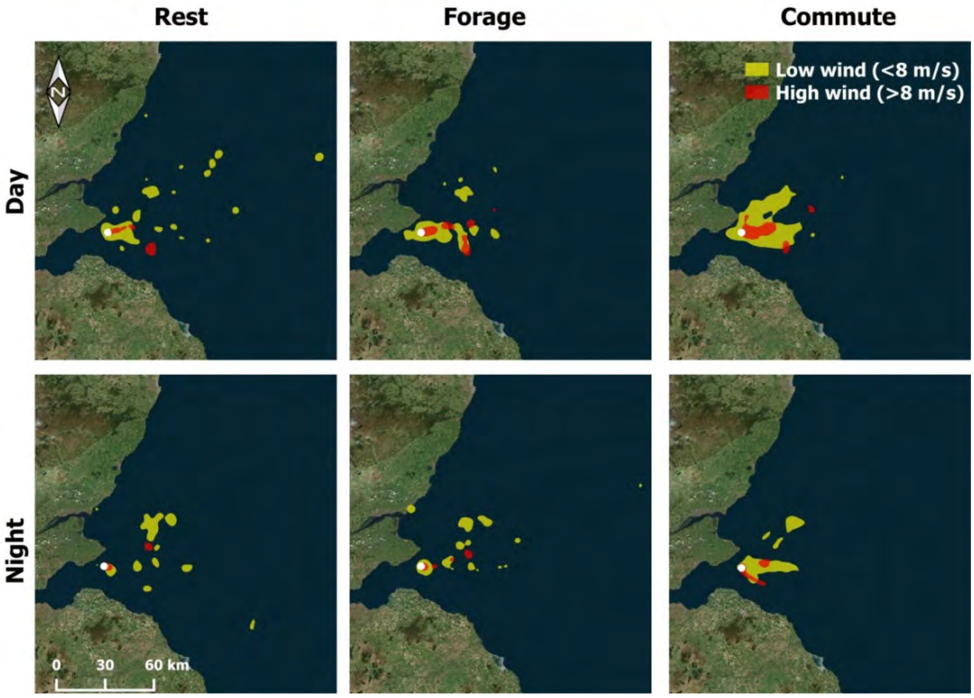


Figure A122 For Kittiwake, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at the Isle of May.

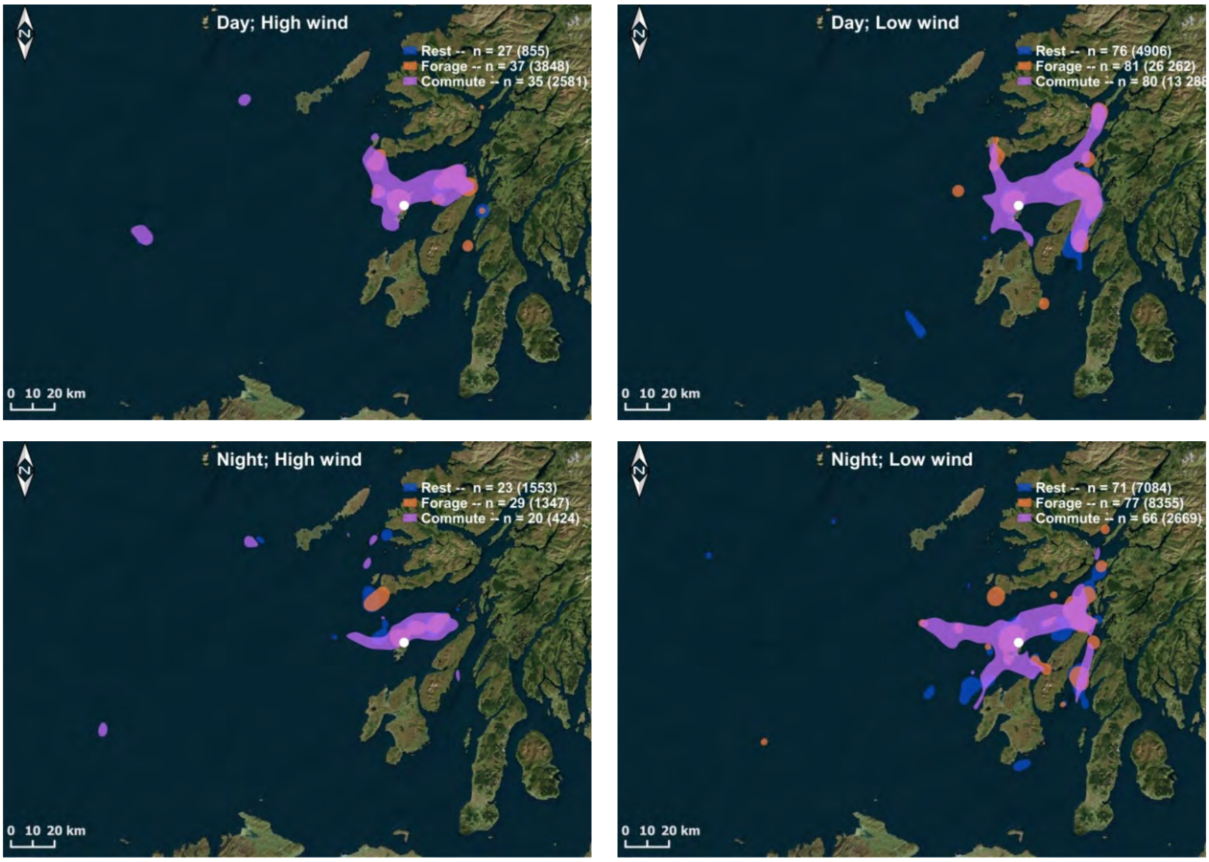


Figure A123 For Kittiwake, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Colonsay.

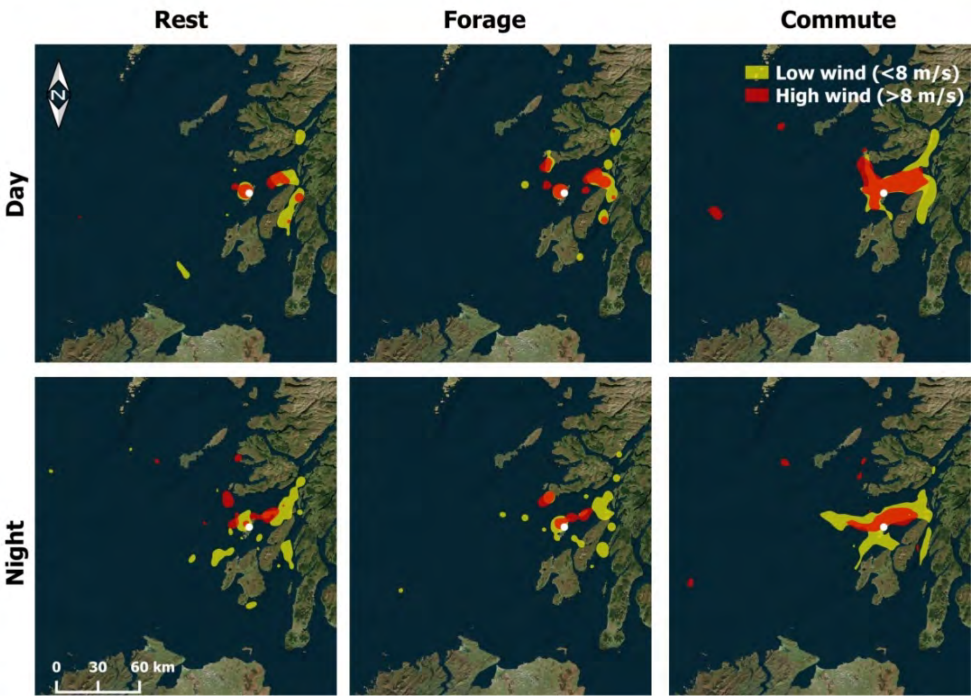


Figure A124 For Kittiwake, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Colonsay.

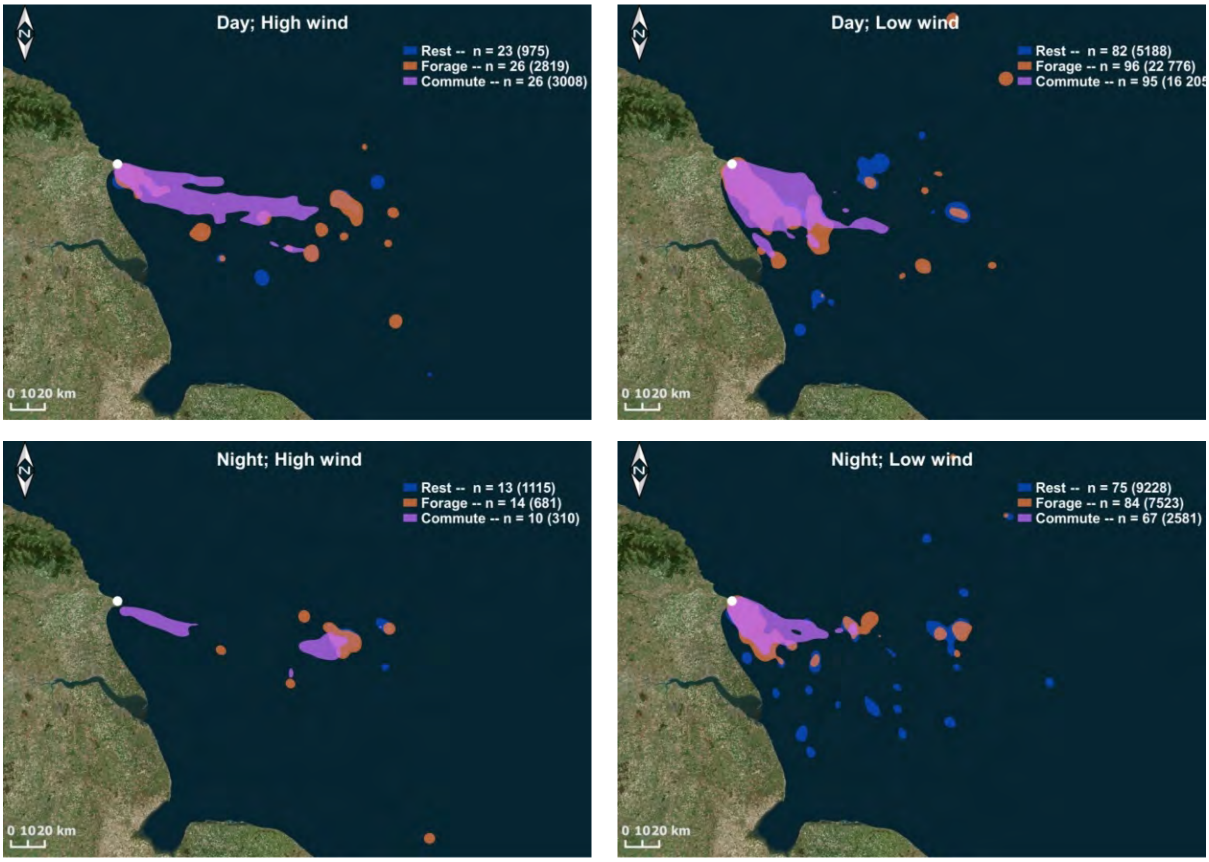


Figure A125 For Kittiwake, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Bempton Clilffs.

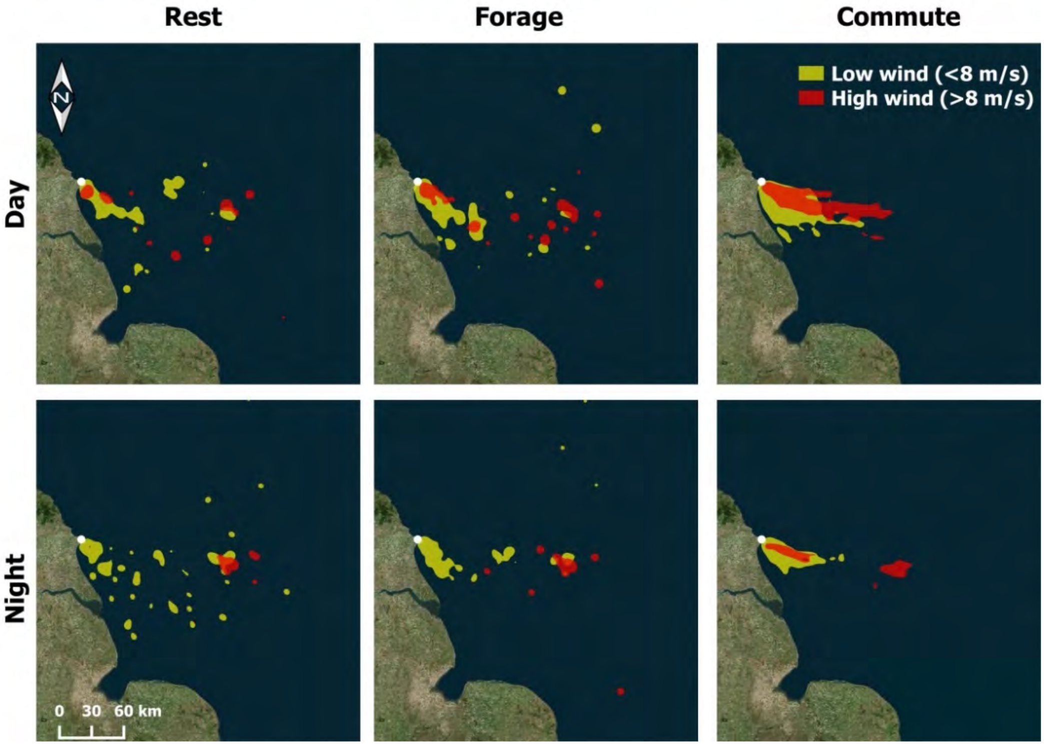


Figure A126 For Kittiwake, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at the Bempton Clilffs.

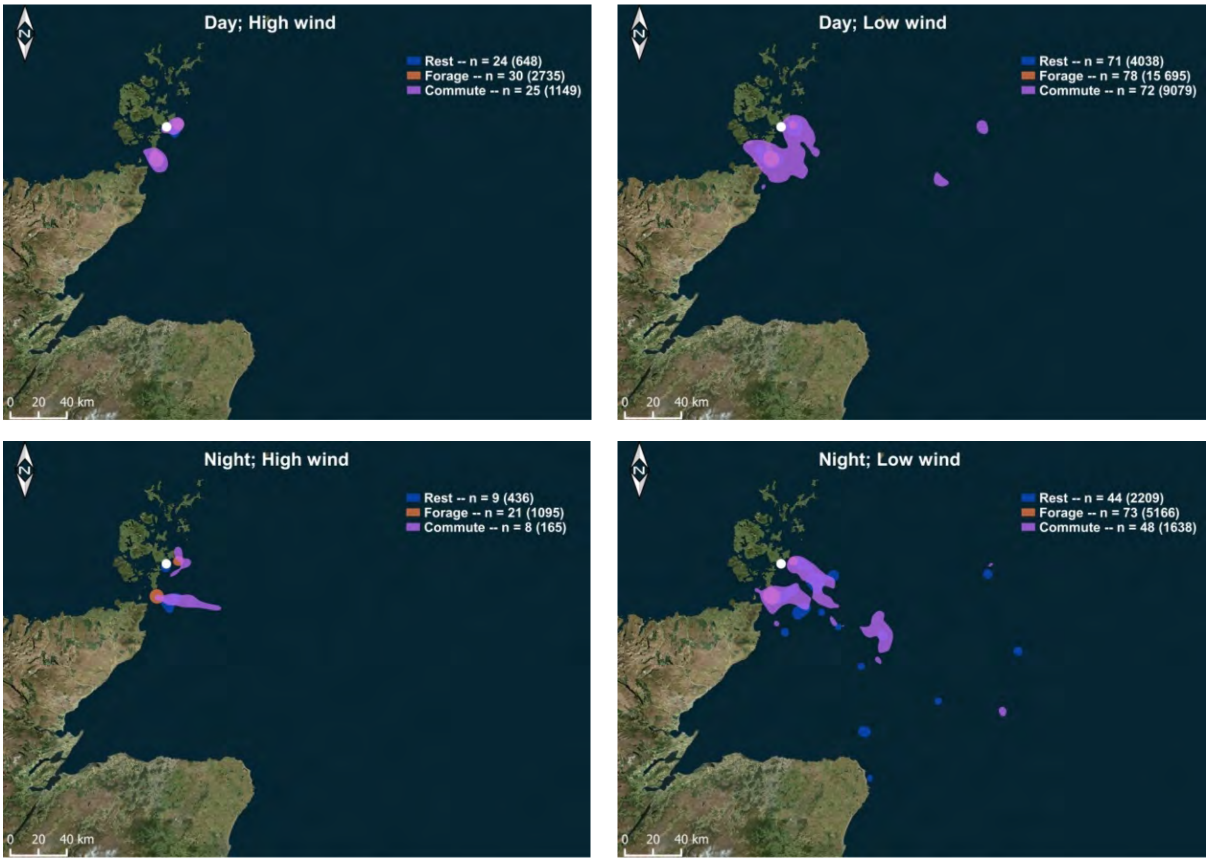


Figure A127 For Kittiwake, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Orkney.

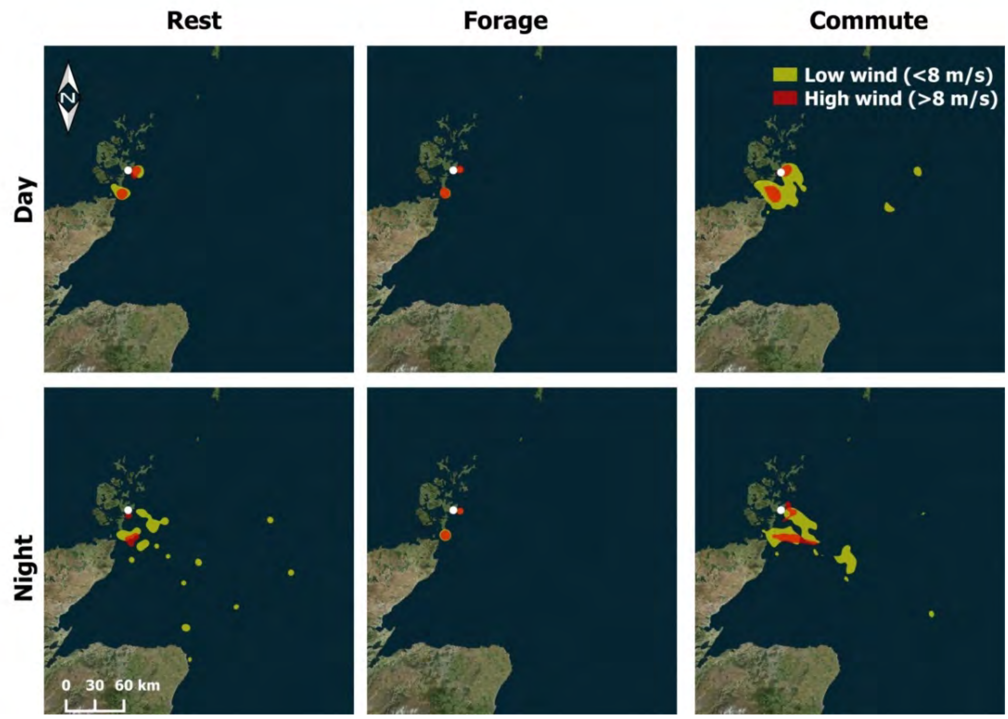


Figure A128 For Kittiwake, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Orkney.

7.9.4 Razorbill

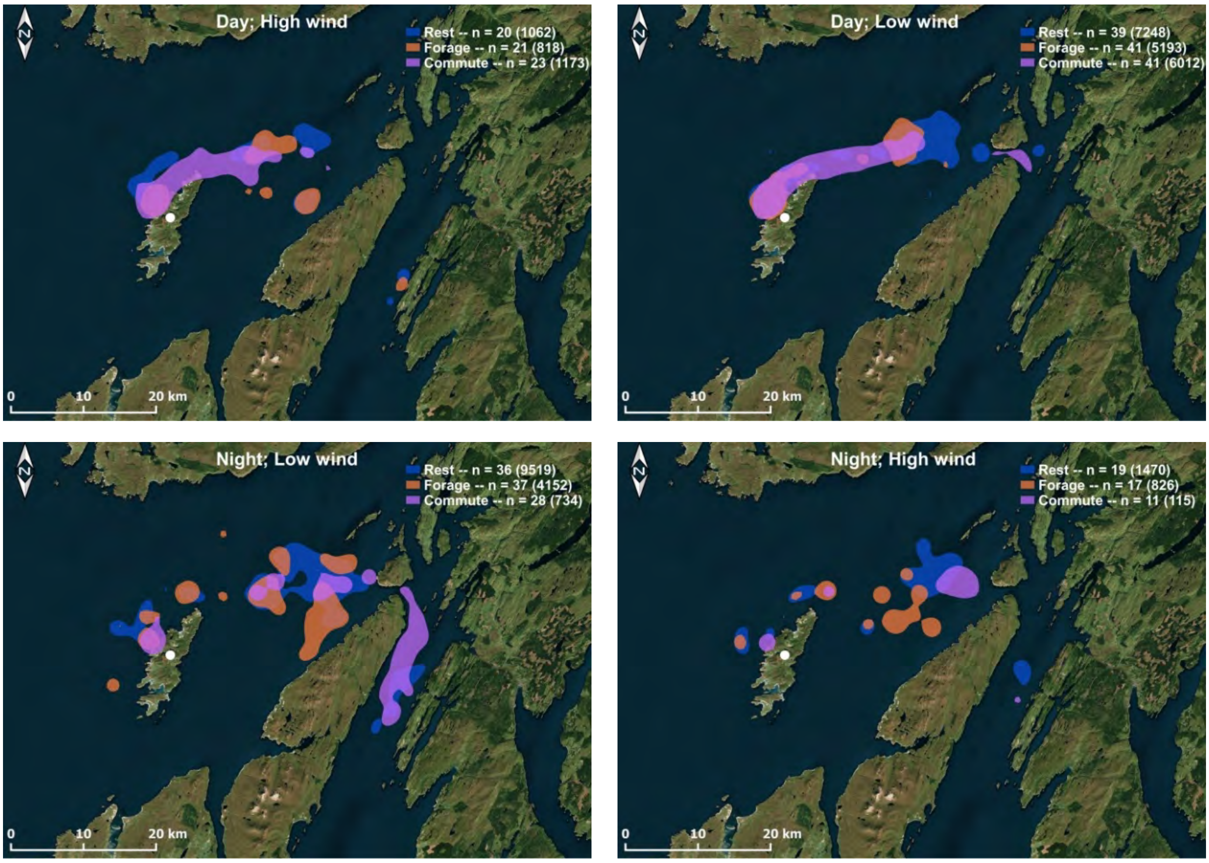


Figure A129 For Razorbill, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Colonsay.

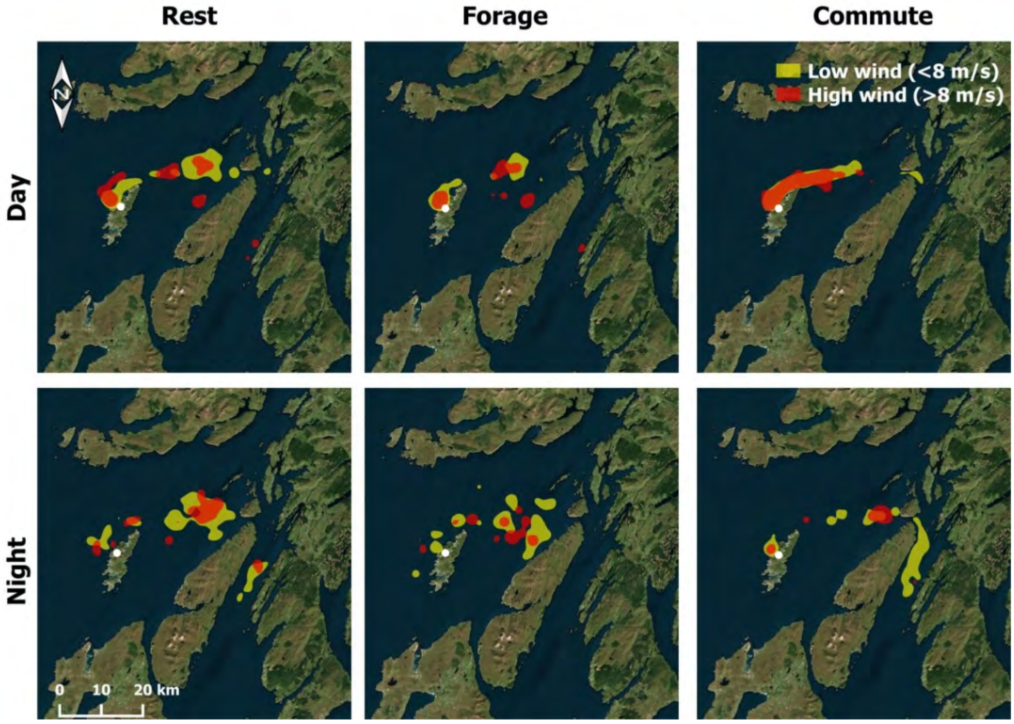


Figure A130 For Razorbill, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Colonsay.

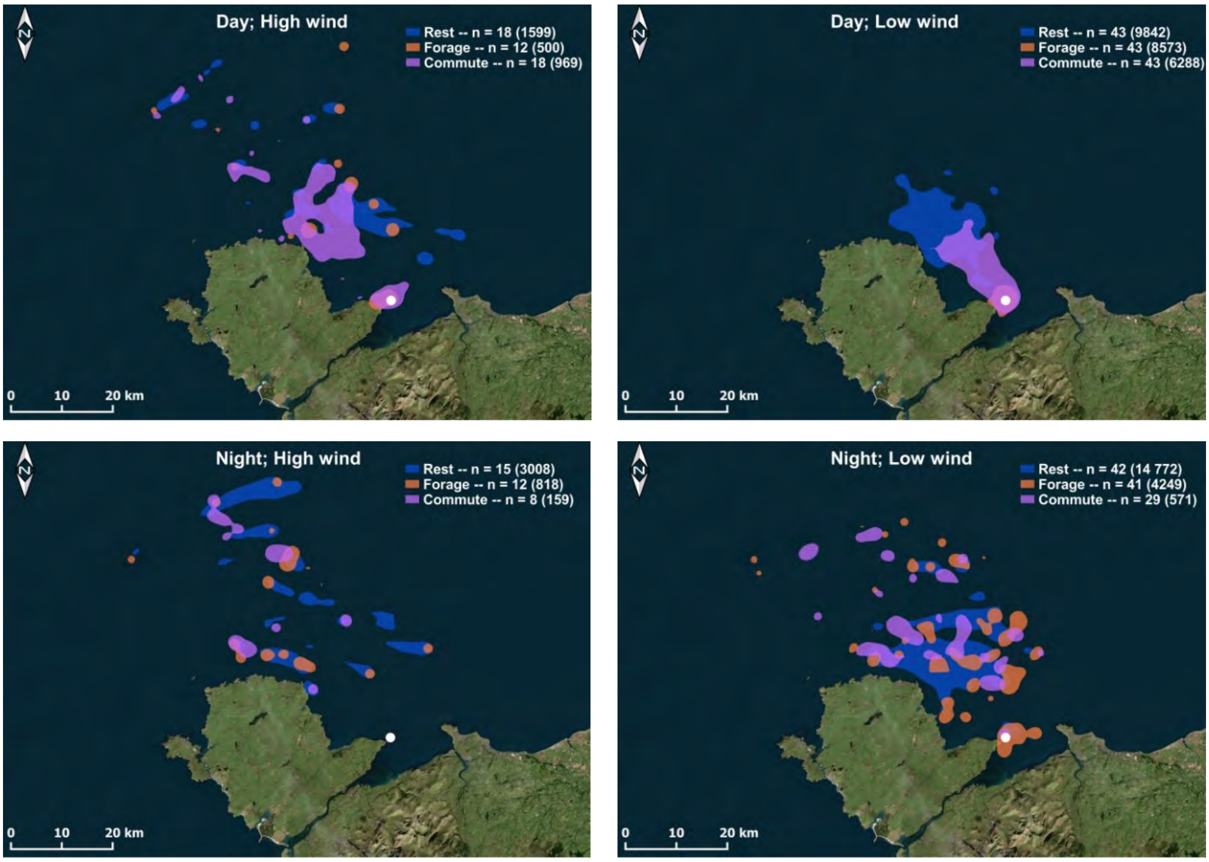


Figure A131 For Razorbill, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Puffin Island.

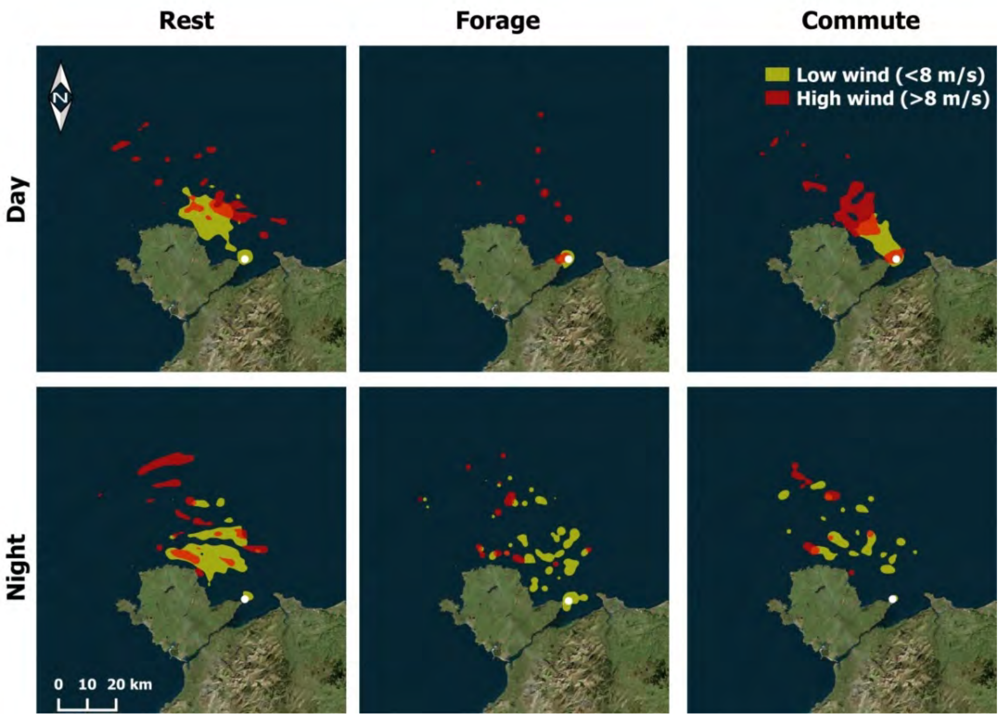


Figure A132 For Razorbill, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Puffin Island.

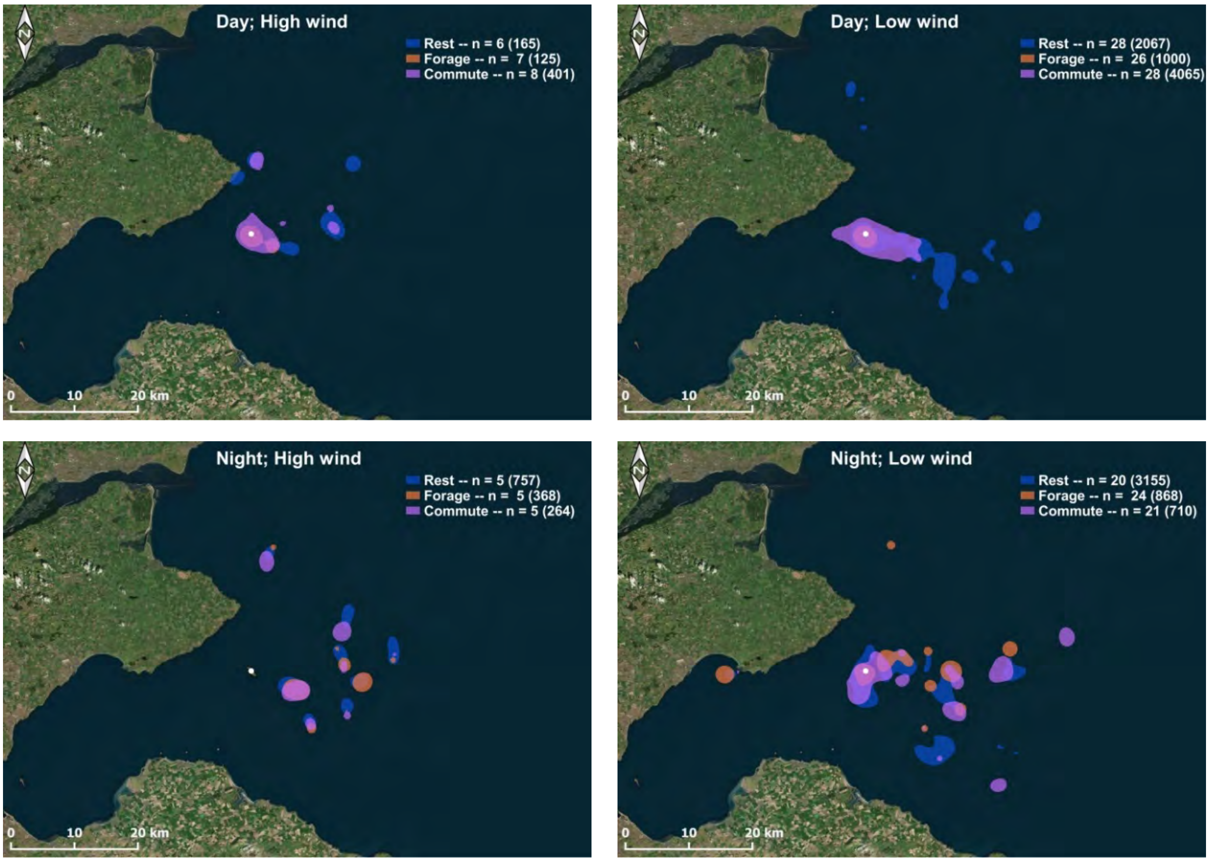


Figure A133 For Razorbill, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Isle of May.

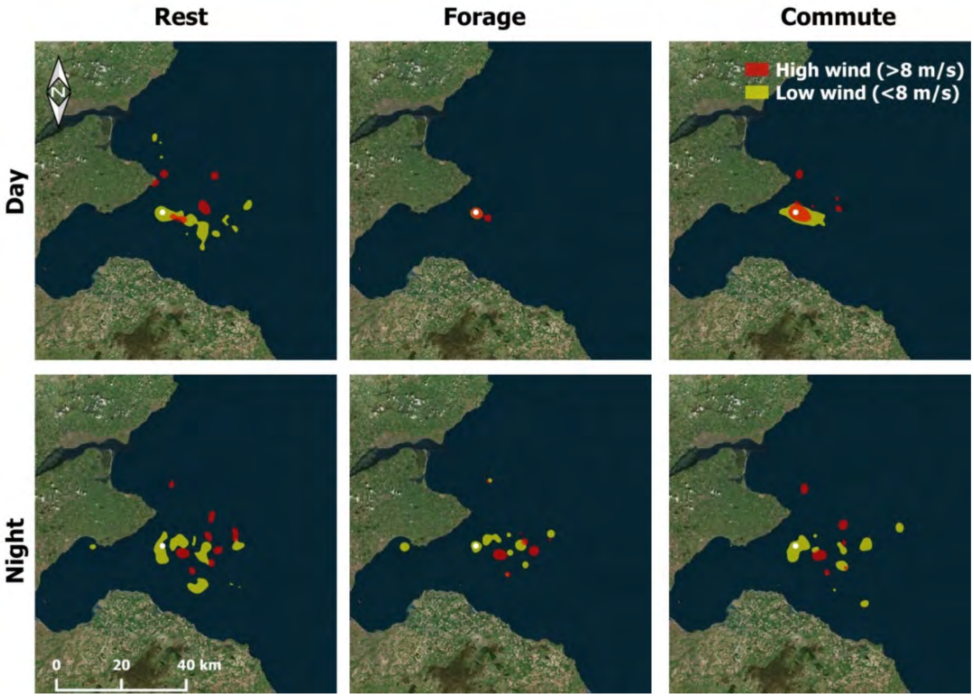


Figure A134 For Razorbill, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Isle of May.

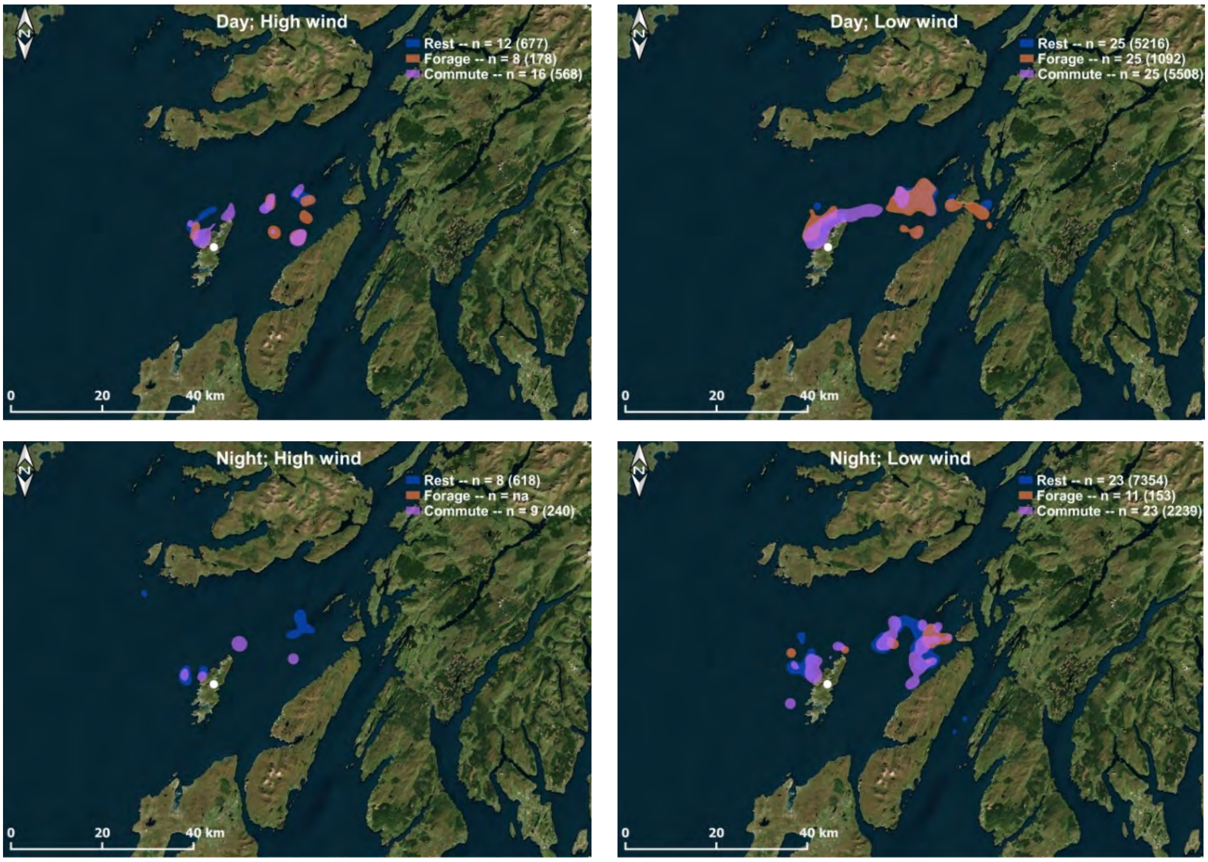


Figure A135 For Razorbill, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Colonsay, based on HMMs using TDR data.

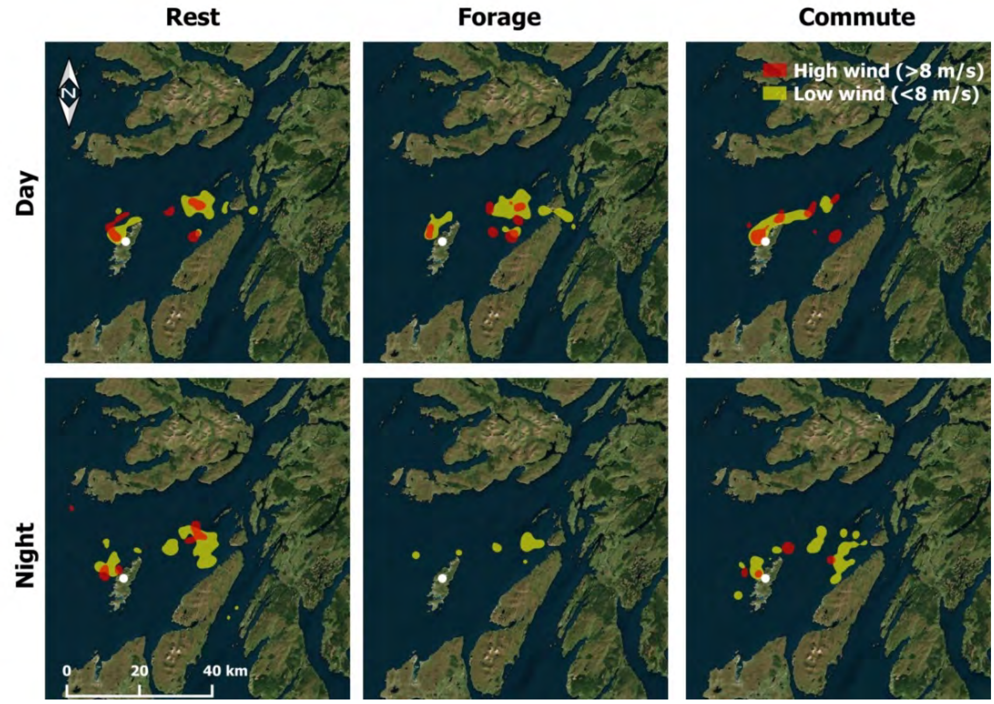


Figure A136 For Razorbill, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Colonsay, based on HMMs using TDR data.

7.9.5 Common Guillemot

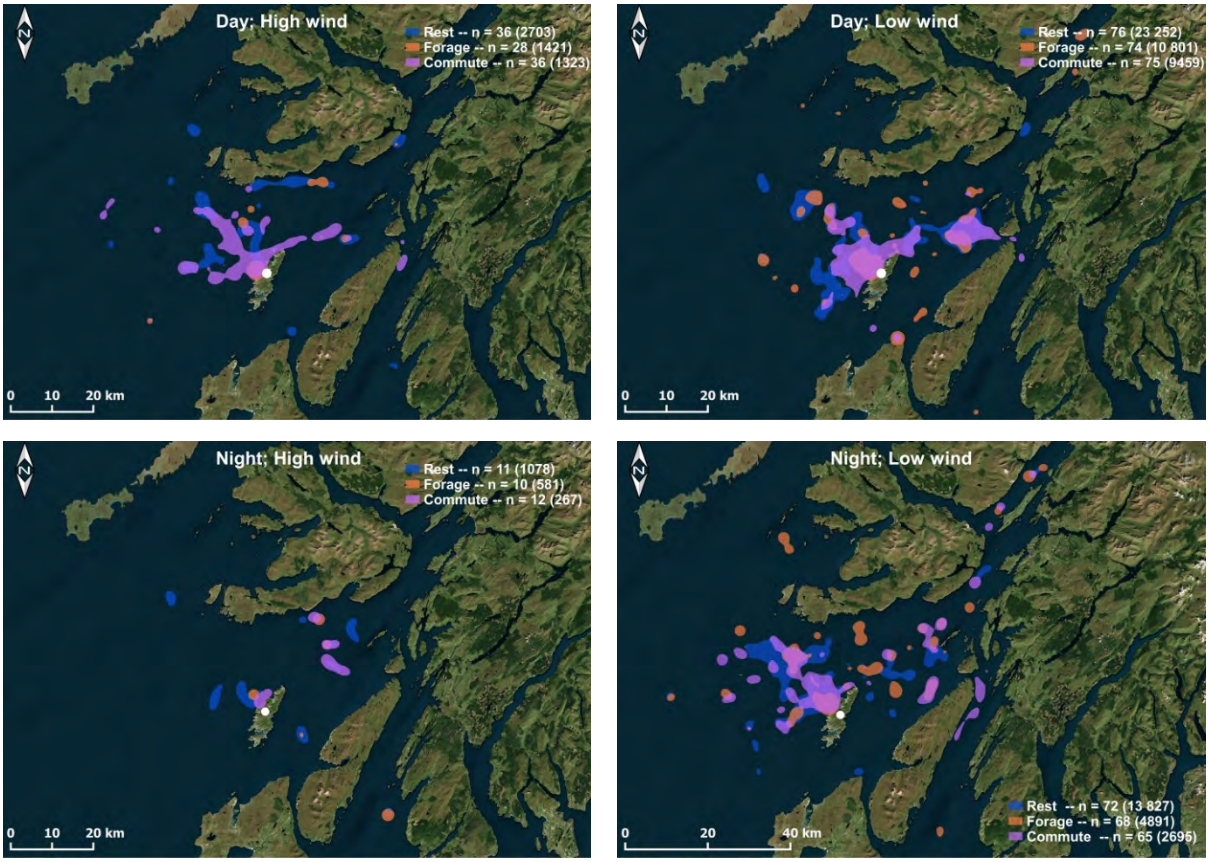


Figure A137 For Guillemot, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at the Colonsay.

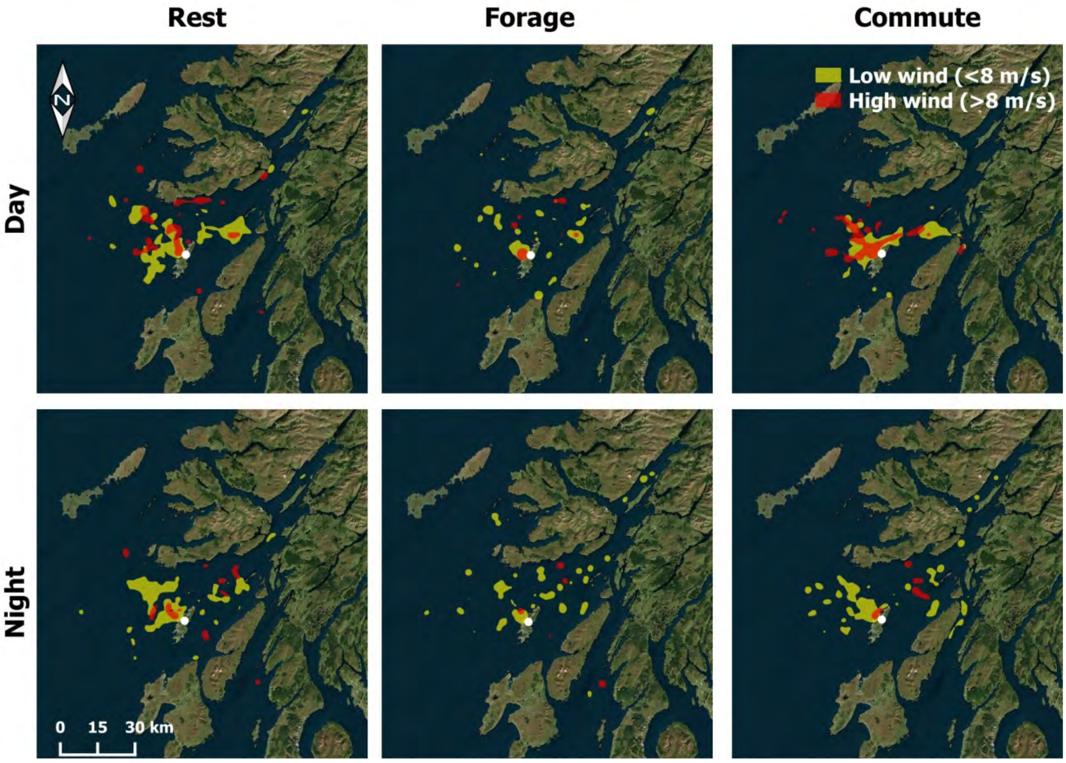


Figure A138 For Guillemot, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at the Colonsay.

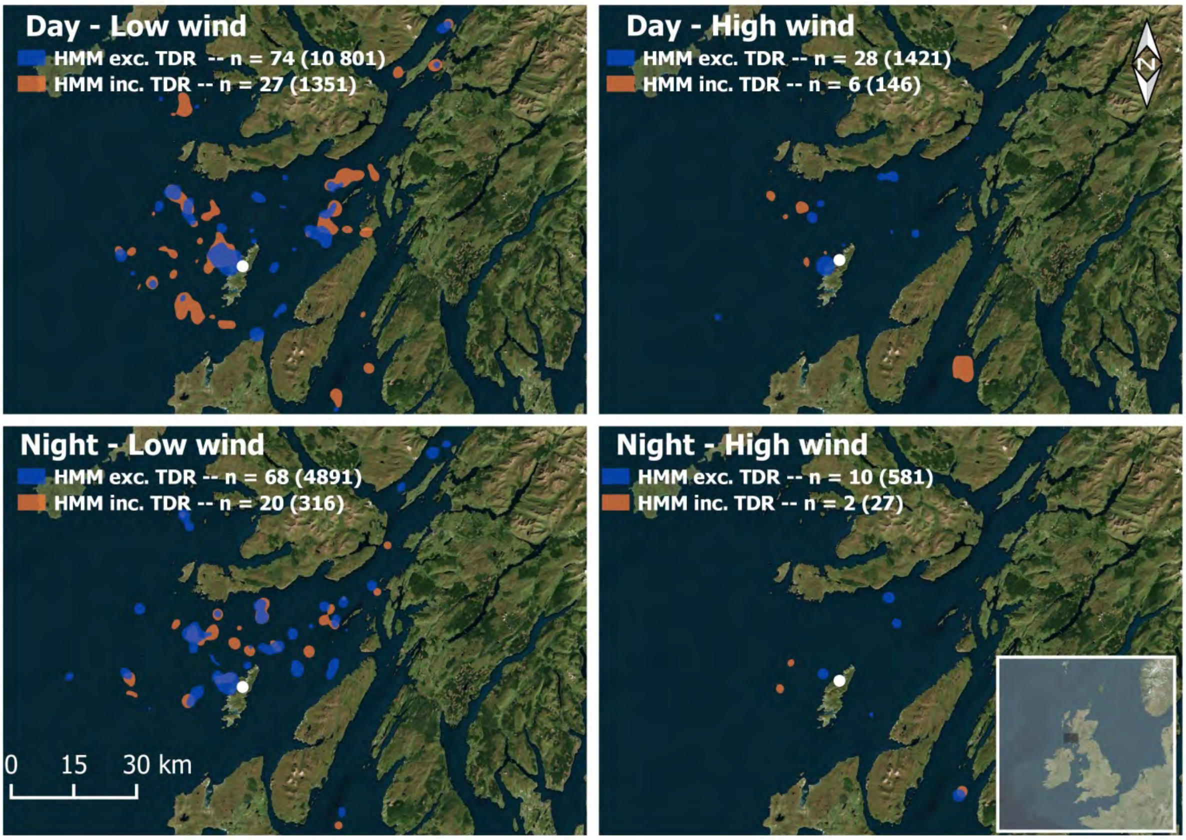


Figure A139 For Guillemot, visualisations of overlaps of 50% KDEs between models incorporating TDR and excluding TDR data, delineated by day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for the state of foraging/searching (State 3) at Colonsay.

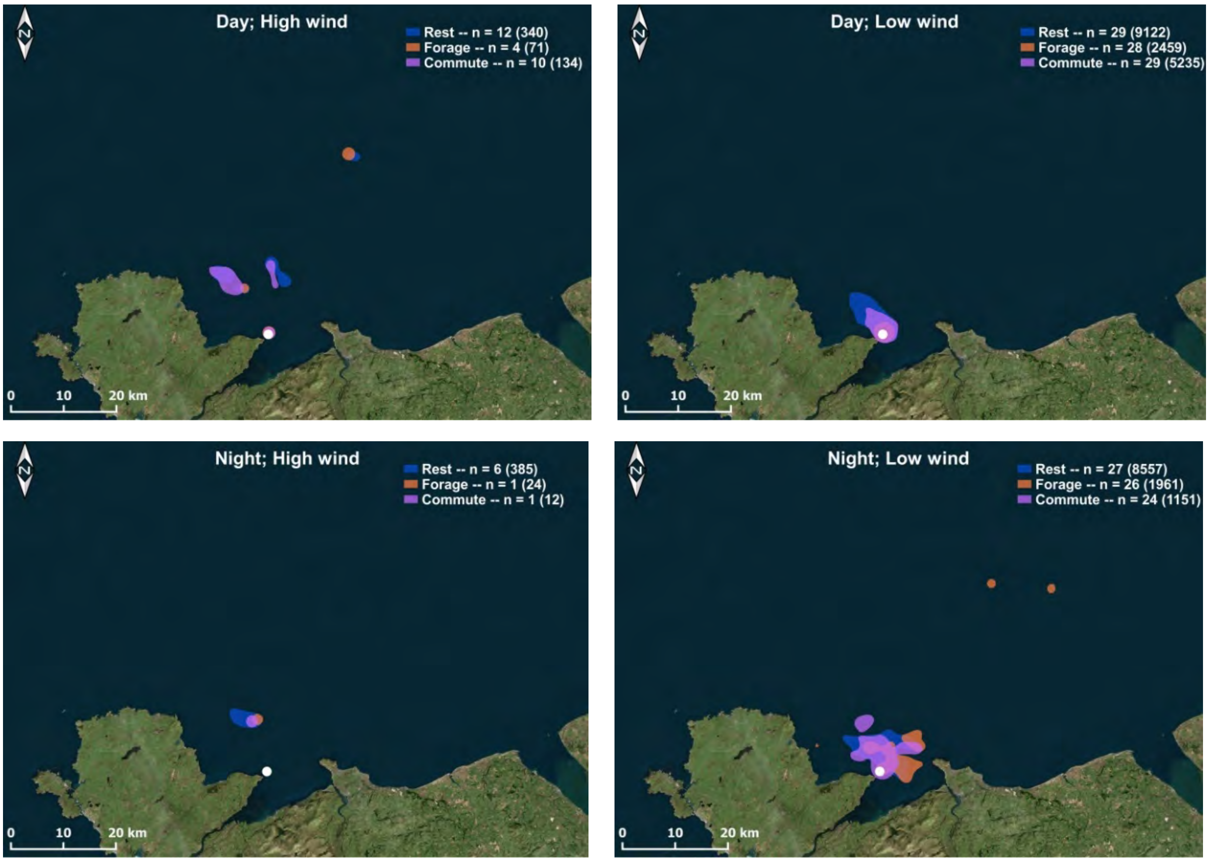


Figure A140 For Guillemot, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Puffin Island.

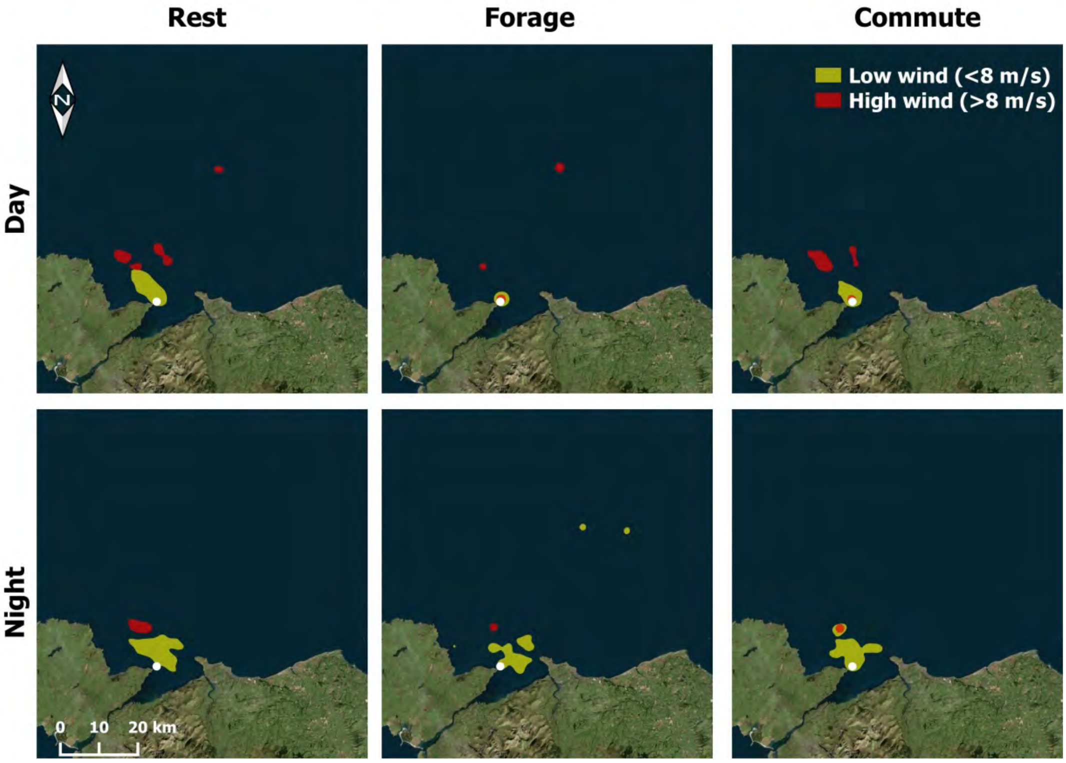


Figure A141 For Guillemot, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at Puffin Island.

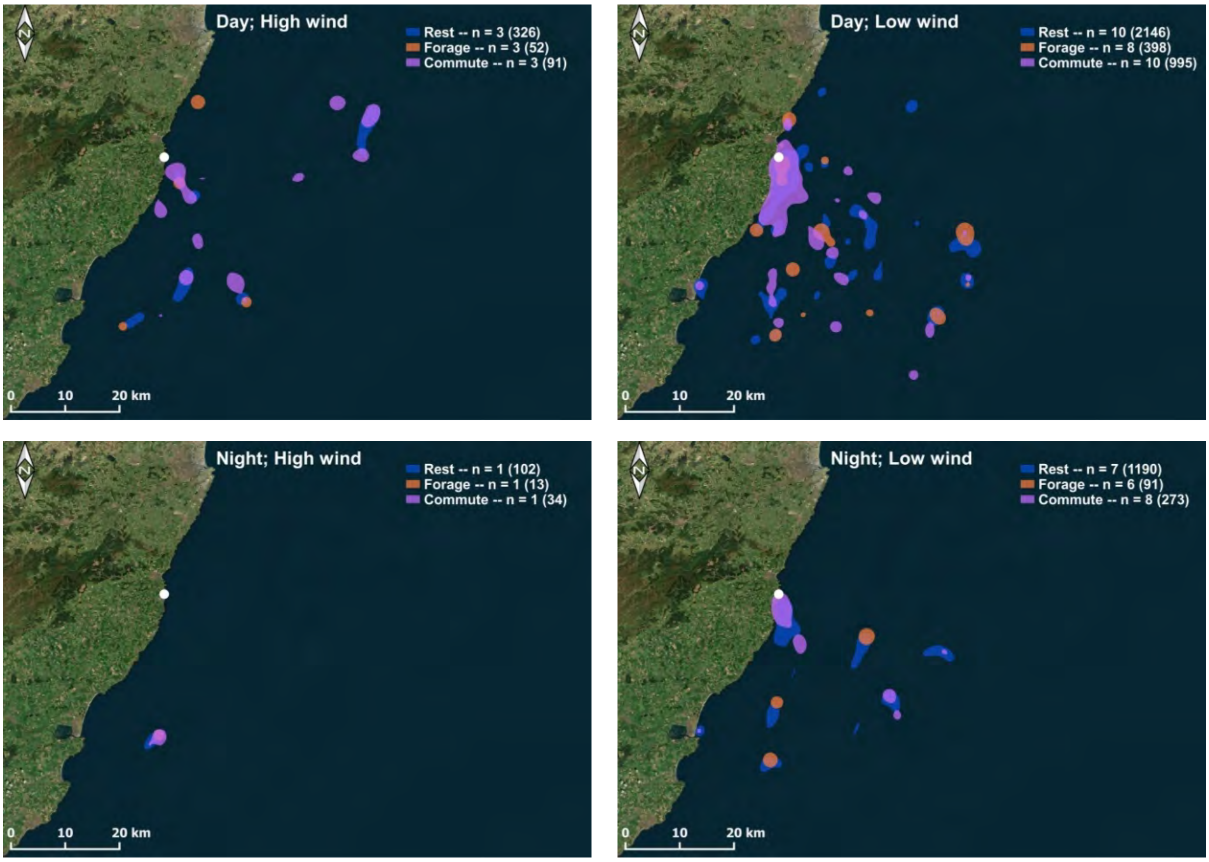


Figure A142 For Guillemot, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Fowlsheugh.

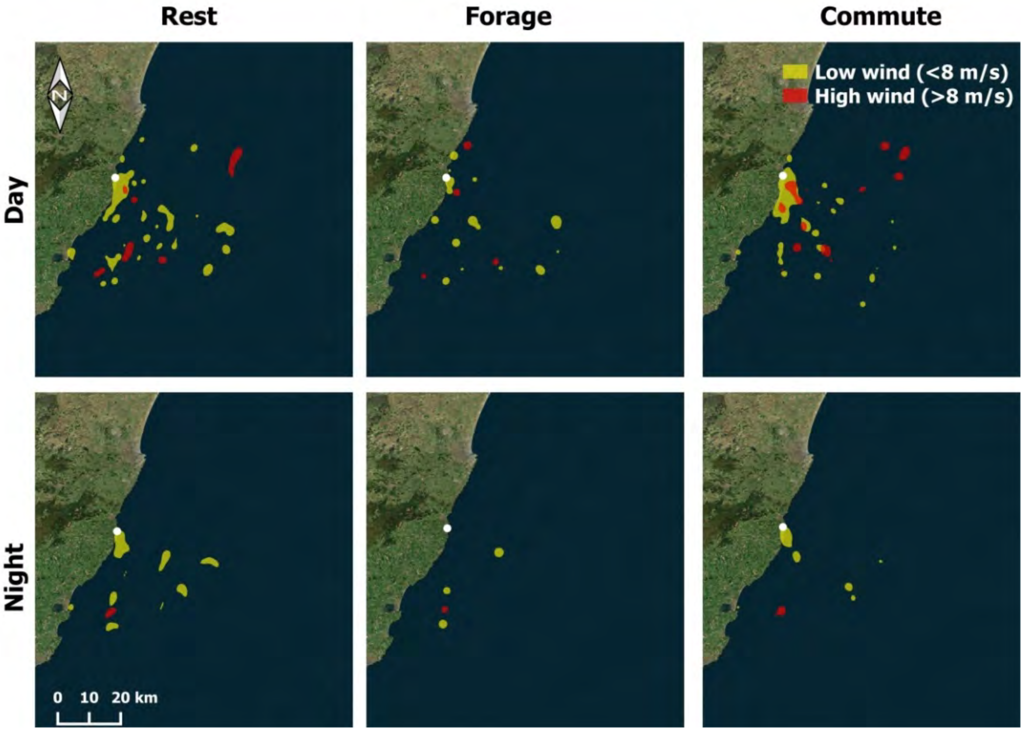


Figure A143 For Guillemot, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at the Fowlsheugh.

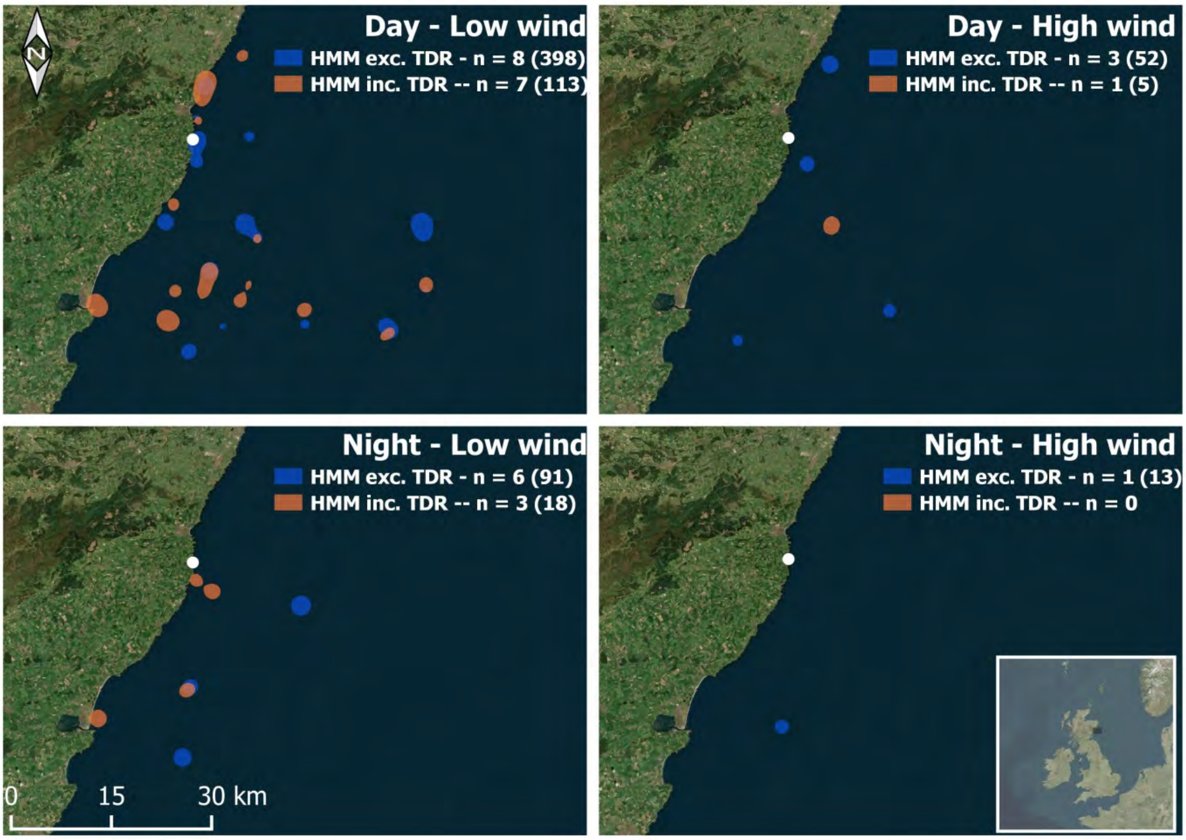


Figure A144 For Guillemot, visualisations of overlaps of 50% KDEs between models incorporating TDR and excluding TDR data, delineated by day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for the state of foraging/searching (State 3) at Fowlsheugh.

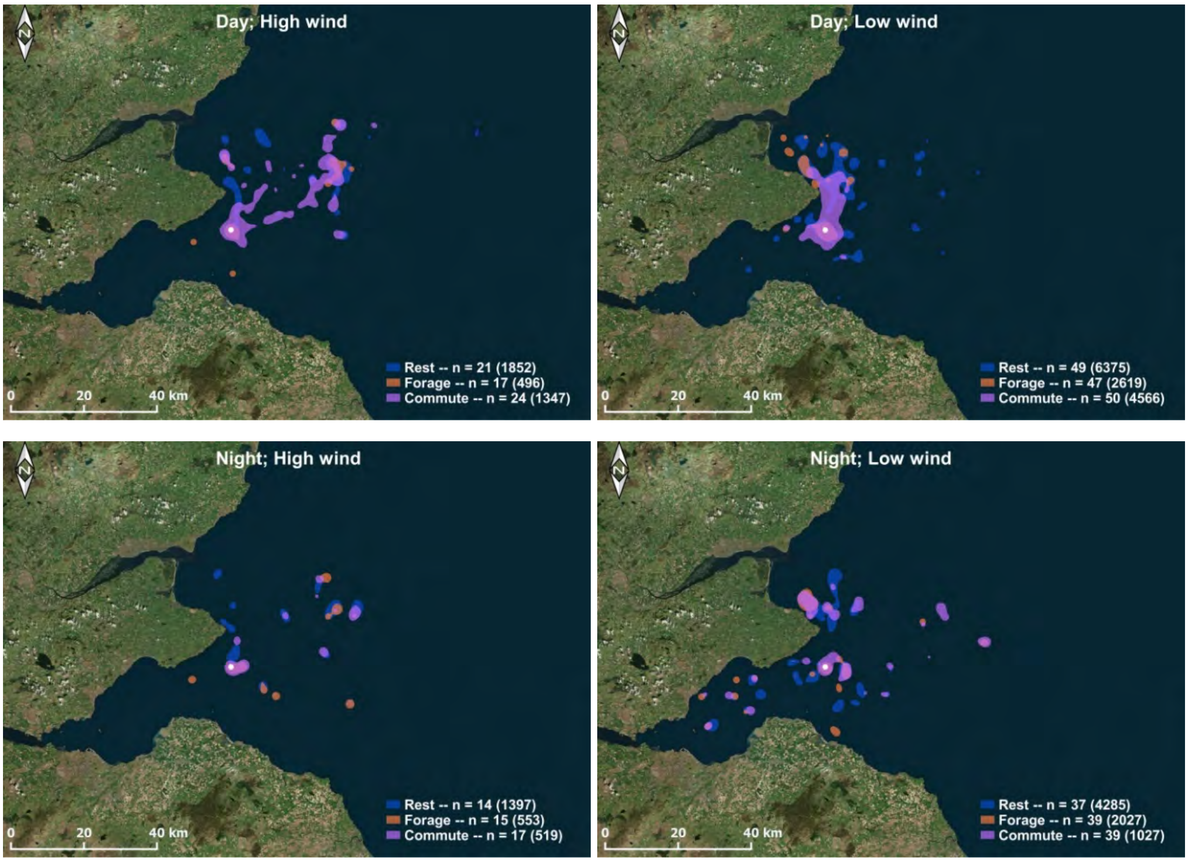


Figure A145 For Guillemot, visualisations of overlaps of 50% KDEs between states for across delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) at Isle of May.

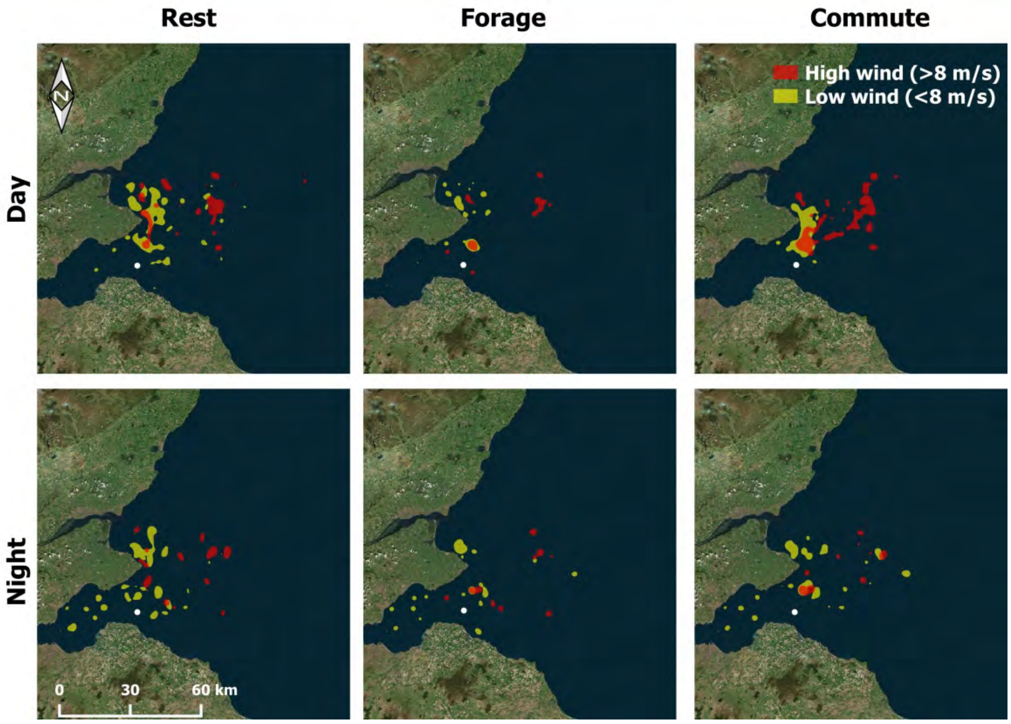


Figure A146 For Guillemot, visualisations of overlaps of 50% KDEs between delineations of day and night (sunrise and sunset) and wind speed (threshold of 8 m/s) for different individual states at the Isle of May.

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Any enquiries regarding this publication should be sent to us at

The Scottish Government
St Andrew’s House
Edinburgh
EH1 3DG

ISBN: 978-1-80435-217-5 (web only)

Published by The Scottish Government, June 2022

Produced for The Scottish Government by APS Group Scotland, 21 Tennant Street, Edinburgh EH6 5NA
PPDAS1035110 (06/22)