

RESEARCH ARTICLE

Towards biologically realistic estimates of home range and spatial exposure for colonial animals

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Funding information

UK Department for Energy Security and Net Zero DESNZ Offshore Energy Strategic Environmental Assessment OESEA programme

Handling Editor: Huijie Qiao

Abstract

1. Mobile colonial animals are particularly vulnerable to localised stressors around their colonies. Accurate home range (HR) estimation is therefore fundamental for spatial risk assessment. HRs are shaped by complex interactions between landscape permeability to movement and spatial resource competition between and within colonies, which are challenging to implement with density estimation methods (e.g. kernel smoothing) or species distribution models. We propose a new HR estimation method for colonial animals that accounts for such spatially complex interactions without computationally expensive individual-based modelling (IBM).
2. We present a model for colony space use following mechanistic rules of (1) heterogeneous landscape permeability, (2) between- and within-colony density-dependent competition, (3) flexible definitions of overlap between colonies, and (4) secondary space use due to commuting. Using the example of Northern gannets (*Morus bassanus*) foraging around the British Isles, we show how model parameters can be fitted to a small subset of tracking data from a colony network and how resulting estimated HRs can be used to derive colony-specific exposure to a spatial stressor (offshore wind farms).
3. Validation with simulated data showed a high level of overlap between true and estimated HRs and no significant difference between true and estimated colony-specific exposure to an example stressor. Estimated gannet HRs showed striking similarities to tracking data from 10 gannet colonies. Our model assigned 73% of tracking locations to their correct colonies, compared to 41% and 31% from HRs derived from two approaches commonly used for risk assessments. These methods also underestimated exposure compared to our model-derived HR.
4. In contrast to industry-standard approaches, our method relies neither on exhaustive tracking from all colonies nor on computer-intensive IBMs. Rather, it can predict HRs from colony size estimates and locations and can be flexibly tuned to different species' characteristics to investigate fundamental and applied questions on colonial space-use patterns.

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KEYWORDS

colonial animals, density-dependent competition, exposure to stressor, home range estimation, individual-based models (IBMs), offshore wind farm impact, projected distributions, species distribution models (SDMs)

1 | INTRODUCTION

Colonial animals must commute between foraging locations and a central breeding site and thus are particularly vulnerable to stressors within their home ranges (HRs; Burt, 1943; Sydesman et al., 2021). Determining such HRs can be challenging due to complex interactions between landscape permeability (Matthiopoulos, 2003; Matthiopoulos, Fieberg, Aarts, Barraquand, & Kendall, 2020) and time-varying competition within and between colonies (Ashmole, 1963; Furness & Birkhead, 1984). For example, changes in colony size induce changes in competition, influencing the size and shape of the colony network HR mosaic. With increasing policy and industry interest in the accurate and precise assessment of the exposure of colonial animals to anthropogenic stressors (ABPmer, 2020; O'Hanlon et al., 2023), it becomes essential that we integrate these complicating factors in biologically realistic HR estimation methods.

HR models for colonial animals (e.g. seabirds, pinnipeds, bats, social insects) need to include space-use constraints such as their periodic return to the colony for offspring provisioning (Briscoe et al., 2018; Stephens et al., 2007). Near-colony foraging creates competition for food (intra-colony competition). As colonies grow, interference competition increases and local resources deplete, forcing animals to travel further (Ashmole's Halo; Ashmole, 1963, demonstrated empirically by Weber et al., 2021). Competition and space use are expected to decline away from the colony due to radial spreading and increasing energetic and time expenditure with distance (Wakefield et al., 2013).

In a colony network, HRs of neighbouring colonies can overlap, leading to direct or indirect competition for resources (inter-colony competition; Furness & Birkhead, 1984). The type and degree of inter-colony competition are species-specific and range on a continuum of possible inter-colony HR overlap scenarios from no overlap (exclusive or segregated HRs) to unimpeded overlap (Bolton et al., 2019). Inter-colony HR overlap additionally depends on colony sizes and the distance between them (Ashmole, 1963; Bolton et al., 2019; Lewis et al., 2001; Patterson et al., 2022). Spatial segregation mechanisms may vary between species (e.g. individual memory in pinnipeds; Aarts et al., 2021, social information transfer in seabirds; Wakefield et al., 2013). However, a mathematical description of this overlap spectrum has not yet been formulated.

Finally, landscape features and permeability shape HRs by limiting accessibility (Matthiopoulos, 2003; Matthiopoulos, Fieberg, Aarts, Barraquand, & Kendall, 2020). For example, coastal morphology can decrease the accessibility of marine habitat such that coastally breeding seabirds travel further to forage than those breeding on offshore islands (Furness & Monaghan, 1986; Wakefield et al., 2017).

Traditional HR estimation is challenged by complex geomorphology and individual interactions. Eulerian approaches estimate space use from a population perspective using density estimation methods or species distribution models (SDM; Matthiopoulos, Fieberg, & Aarts, 2020), while Lagrangian approaches mechanistically model animal movement using individual-based models (IBMs; Grimm & Railsback, 2005). In Eulerian models, complex interactions arising from inter-colony competition and varying landscape permeability are difficult to account for (e.g. Ronconi et al., 2022; Waggitt et al., 2020; Wakefield et al., 2017). Further, density estimation methods require data for all colonies and times of interest, and SDMs, while less data demanding, may predict poorly outside the spatial and temporal data range (Conn et al., 2015). Lagrangian models often fail to capture large-scale usage patterns (Michelot et al., 2019), may have large Monte Carlo errors predicting for large maps and populations, and fitting them to large datasets can be computationally prohibitive (e.g. Chudzinska et al., 2021; Ollason et al., 2009; Warwick-Evans et al., 2018).

For systems with low data availability, more mechanistic models such as representative foraging ranges (Thaxter et al., 2012; Woodward et al., 2024) and foraging radius models (e.g. projected at-sea foraging distributions; Critchley et al., 2018, 2020; Grecian et al., 2012; Soanes et al., 2016) have been developed. These methods assume circular HRs around colonies (Bolton et al., 2019), ignore inter-colony competition and accessibility constraints due to impermeable landscape features, and some assume constant density across the HR, i.e. do not account for commuting or intra-colony competition (e.g. Soanes et al., 2016). In another mechanistic model, the '*hinterland model*' (Cairns, 1989), HRs are non-overlapping, bounded by lines of equidistance between colonies due to animal space-use dominance near the home colony. Empirical evidence for the postulated relationship between hinterland and colony size is lacking. The density-dependent hinterland (DDH) model (Wakefield et al., 2013) based on Ashmole's Halo and Cairn's hinterland model introduced inter-colony competition regulated by colony size and distance. However, this method may not be transferable between species and cannot easily be fitted to new data.

Here, we propose a new method that improves biological realism, accuracy and transferability of HR estimation in colonial species. The HR is modelled as a weighted combination of animal usage surfaces from *foraging* and *commuting*. The foraging surface is shaped by the effects of intra- and inter-colony density-dependent competition, landscape permeability, flexibly defined overlap between colonies and home colony constraints. The commuting surface is the usage arising from commuting between home colony and foraging locations, controlling for landscape permeability. The method

is predictive and only needs tracking data for a small subset of the colony network for model fitting and then only colony sizes and locations to estimate all HRs. To illustrate the utility of the method, we use it to calculate the exposure of three example Northern gannet (*Morus bassanus*, hereafter, gannet) colonies bounding the Irish Sea to planned offshore wind farms (hereafter, OWFs). We compare the estimated exposure to the foraging range method (Thaxter et al., 2022; Woodward et al., 2024) and projected distributions method (Critchley et al., 2018; Grecian et al., 2012).

2 | MATERIALS AND METHODS

To achieve a balance between the realism of IBMs that can account for complex interactions and the computational efficiency of SDMs that can be expediently fitted to data with negligible Monte Carlo error, we model the flux of animal usage (instead of the movement of individuals, as in an IBM) in a regular grid of cells in R (R Core Team, 2023). We formalise evidence-based space-use rules in colonial animals into an iterative allocation algorithm. By computing the flux of usage iteratively, we can capture complex interrelationships between landscape permeability and inter- and intra-colony competition. However, it requires less iterations than an IBM (iterating the movement of thousands of individuals) and they are more accurate. The model's parameters, relating to the carrying capacity of the landscape, density-dependent competition, home colony constraints, the extent of overlap between colonies, and the relative time spent foraging to commuting are estimated by fitting the model to tracking data. We illustrate the approach using real tracking and colony data.

2.1 | Usage allocation rules

We use a regular discretisation of space, referring to each square grid cell by its centre-point coordinates (i, j) . Each cell has a Moore neighbourhood (MN) comprising itself and its eight nearest neighbours. Our algorithm implements eight evidence-based rules:

1. Define the total amount of usage, based on colony size at a given time, to be distributed across space.
2. Define the intrinsic carrying capacity of each cell (maximum animal usage that the cell can support indefinitely by its productivity (Wakefield et al., 2013)).
3. Animal usage spreads only through permeable landscape cells.
4. Animal usage is only informed by local resource availability, i.e. it is absorbed by cells closest to the colony according to their carrying capacity regardless of whether richer cells with excess capacity exist at greater distances.
5. Surplus animal usage is redistributed preferentially as a balance between less saturated neighbouring cells (Ashmole, 1963; Wakefield et al., 2013) and cells closer to the colony to reduce transport costs (Stephens et al., 2007).
6. Inter-colony resource sharing within a cell can range from complete sharing to exclusive 'occupation' by a dominant colony (Bolton et al., 2019), to allow for a range of inter-colony overlap scenarios.
7. Commuting usage is efficiently directed to the connecting routes between foraging usage and the home colonies.
8. The proportion of time spent commuting and foraging is fixed over different distances. Therefore, if animals exploit resources further away from a colony, they will tend to spend more time foraging there before returning to their colony (Mullers et al., 2009; Thaxter et al., 2022). We do not consider the case that some provisioning animals may be prevented from doing this by constraints in the total time they can be away from their offspring or partner and their loading capacity, mainly because rule 4 ensures that remote locations are not prioritised, even if they are very rich.

We propose these rules as a minimally realistic set that captures the necessary large-scale features of HR expansion without surplus assumptions about individual-level behaviour, energetics, etc. used in IBMs.

2.2 | Foraging surface

The first part of the model determines foraging usage via an iterative, outward allocation of a fixed overall amount of total usage per colony (rule 1) until convergence (the iteration at which the dispersive drivers and home colony constraints equilibrate). To ensure usage is concentrated around the colony (rule 4), total usage is initially assigned to the colony centre and allowed to spread out through space by subsequent spillover into neighbouring cells according to distance from the colony and inter- and intra-colony competition (rule 5), as local carrying capacity is filled (rule 2). For speed, we only loop through and evaluate cells where usage is above the carrying capacity.

We specify the carrying capacity for each grid cell (rule 2). We assume for the remainder of this paper, without loss of generality, that all permeable cells have the same carrying capacity (γ , parameter 1, rule 2), while impermeable cells have near-zero carrying capacity. Our model can be readily extended to incorporate (and refine) spatially heterogeneous carrying capacity surfaces, obtained via SDMs.

For each iteration, k , and colony, l , from n total colonies, we model the foraging density of animals, $N_{i,j,k,l}$, via the net flux between the cell (i, j) and its MN (rule 4):

$$N_{i,j,k,l} = N_{i,j,k-1,l} - \underbrace{f(N_{i,j,k-1,l})}_{\text{outflux}} + \underbrace{\sum_{di=-1}^1 \sum_{dj=-1}^1 g(N_{i+di,j+dj,k-1,l})}_{\text{influx}}, \quad (1)$$

where the influx g into cell i, j is a function of the outfluxes of MN cells (including cell i, j), redistributed via h :

$$g(N_{i+di,j+dj,k-1,l}) = f(N_{i+di,j+dj,k-1,l}) \underbrace{\frac{h(N_{i+di,j+dj,k-1,l})}{H_{i+di,j+dj,k-1,l}}}_{\text{influx distribution ratio}}. \quad (2)$$

H is a normalising term for the influx distribution ratio to conserve total usage through the algorithm's iterations:

$$H_{i+di,j+dj,k-1,l} = \sum_{dx=-1}^1 \sum_{dy=-1}^1 \sum_{l=1}^n h(N_{i+di+dx,j+dj+dy,k-1,l}). \quad (3)$$

2.2.1 | Case with one colony in a cell (i.e. no inter-colony competition)

We first define the outflux function f (Equation 1) and redistribution function h (Equation 2). f is a pre-defined proportion p of animal usage above the cell's carrying capacity, γ_{ij} :

$$f_{i,j,k-1,l} = \begin{cases} p(N_{i,j,k-1,l} - \gamma_{ij}), & N_{i,j,k-1,l} > \gamma_{ij} \\ 0, & \text{otherwise} \end{cases}. \quad (4)$$

The redistribution function h (Equation 2) needs to be a monotonically decreasing function (e.g. an exponential decay), so more outgoing usage is directed to neighbouring cells that are less saturated (rule 5, parameter 2, $b_2 < 0$) and closer to the colony (rule 5, parameter 3, $b_3 < 0$), where Δ is the colony distance avoiding impermeable cells (see Section 2.3 for more details):

$$h(N_{i+di,j+dj,k-1,l}) = \exp\left(b_2 \frac{\sum_{l=1}^n N_{i+di,j+dj,k-1,l}}{\gamma_{i+di,j+dj}} + b_3 \Delta_{i+di,j+dj,l}\right). \quad (5)$$

Other forms of relationship with $\frac{N_{i+di,j+dj,k-1,l}}{\gamma_{i+di,j+dj}}$ and $\Delta_{i+di,j+dj,l}$ are possible as future extensions.

2.2.2 | Case with multiple colonies in a cell (i.e. with inter-colony competition)

The outflux function, f , is defined by the overlap spectrum (rule 6). This represents the level of colony overlap within a neighbourhood and, as far as we know, is the first mathematical description of inter-colony overlap not based off an underlying biological mechanism, thus making it transferable between species. The level of inter-colony resource sharing is controlled by the overlap spectrum parameter m (rule 6, parameter 4), which allows for a continuum of colony interactions within a cell, from complete resource sharing ($m = 0$, complete overlap) to exclusive 'occupation' by one dominant colony ($m \gg 1$, no overlap). For $0 < m < 1$, colonies with a lower proportion of usage in MN cells have the advantage, while for $m > 1$, colonies with even small dominance in usage have the advantage (Figure S1).

$$f(N_{i,j,k-1,l}) = \begin{cases} pN_{i,j,k-1,l} - p\gamma_{ij} \underbrace{q(N_{i,j,k-1,l}, m)}_{\text{overlap spectrum}}, & \sum_{l=1}^n N_{i,j,k-1,l} > \gamma_{ij} \text{ and } N_{i,j,k-1,l} > q(N_{i,j,k-1,l}, m) \\ 0, & \text{otherwise} \end{cases} \quad (6)$$

$$q(N_{i,j,k-1,l}, m) = \frac{\left(\sum_{di=-1}^1 \sum_{dj=-1}^1 N_{i+di,j+dj,k-1,l}\right)^m}{\sum_{l=1}^n \left(\sum_{di=-1}^1 \sum_{dj=-1}^1 N_{i+di,j+dj,k-1,l}\right)^m}. \quad (7)$$

For successive iterations k , the foraging usage (Equation 1) is determined for each cell in space and updates the overall foraging usage surface. Convergence is reached when the gradient of the last 50 summed squared residuals, r , between consecutive surfaces no longer differs significantly from zero. We test this using a linear model between the timesteps (t from 1 to 50) and the residuals, $t \sim r$ using the lm function (R Core Team, 2023). Our final foraging surface is the mean of all foraging surfaces in the last 50 timesteps, where there was no more change in residuals.

2.3 | Commuting surface

The second part of the model determines commuting usage. From the final foraging surface, we iteratively 'rewind' animal usage back towards the colony, recording the cumulative flux of usage through all cells. First, we calculate the distance from each cell to the colony, avoiding impermeable cells (rule 3) using the *gridDist* function from the *terra* package (Hijmans, 2024). Then, we iterate through each grid cell, redistributing the colony usage, $N_{i,j,k,b}$ between all neighbouring cells closer to the colony centre (rule 7), recording the cumulative flux of usage through all cells until the difference in summed residuals between successive iterated surfaces becomes negligible (less than 10^{-8}), i.e. the usage has been returned to the colony centre. The distances from *gridDist* are calculated by summing local distances to the MN, resulting in shorter distance paths along the cardinal directions and more commuting usage directed on these paths. This can create artefacts in the commuting surface and HR (Figure 3).

2.4 | Home ranges

The third part of the model combines the foraging and commuting surfaces (U_F and U_C respectively) to obtain the HR, U , defined by an underlying utilisation distribution (Fieberg & Kochanny, 2005), from which different HR isopleths can be calculated (e.g. 95% HR). We normalise the foraging and commuting surfaces to unit sum and then combine them via a weighting proportion, w (rule 8, parameter 5):

$$U = wU_F + (1 - w)U_C. \quad (8)$$

2.5 | Model fitting

Model parameters γ , (rule 2), b_2 , (rule 5), b_3 , (rule 5), m (rule 6) and w (rule 8) can be fitted to telemetry data. Instead of requiring comprehensive tracking data from all colonies in a network, our method requires GPS tracking data from as few as two proximate (likely

interacting) colonies of different sizes and in complex landscape geomorphology. Tracking data should be sampled with low temporal autocorrelation (to allow for independence assumption in the likelihood). Tracking points within a certain radius of the colony centre should be removed if animals tend to raft or rest close to the colony rather than forage or commute there (Carter et al., 2016).

Our model's HRs were viewed as the intensity surface of an Inhomogeneous Poisson Point Process (IPP; Matthiopoulos, Fieberg, & Aarts, 2020), hence generating the log likelihood (LL) function

TABLE 1 Parameter upper and lower bounds used in model fitting (γ =carrying capacity, b_2 =density-dependent competition, b_3 =energetic constraint, m =overlap spectrum parameter, w =relative time spent foraging to commuting).

Parameter	Lower bound	Upper bound
γ	0.01	30
b_2	-1	-0.82
b_3	-0.1	0
m	0	10
w	0	1

TABLE 2 Locations, names, name abbreviations, colonisation and extinction years of the network of Northern gannet colonies around the British Isles.

Colony	Abbreviation	Colonisation year	Extinction year	Latitude	Longitude
Rouzie	Rz	1938	NA	-3.43639	48.78261
Ortac	Or	1940	NA	-2.29056	49.61508
Les Etacs	LE	1945	NA	-2.23981	49.70459
Lundy	Ln	1274	1905	-4.66875	51.17681
Bull Rock	BIR	1856	NA	-10.3003	51.50864
Grassholm	Gr	1820	NA	-5.47948	51.73127
Little Skellig	LS	1700	NA	-10.5084	51.78175
Great Saltee	GS	1929	NA	-6.62005	52.11043
Ireland's Eye	IE	1989	NA	-6.05896	53.40764
Lambay	Lm	2007	NA	-6.01623	53.49098
Clare Island	CI	1978	NA	-9.9939	53.80428
Bempton Cliff	BC	1924	NA	-0.16889	54.14609
Scar Rocks	SR	1939	NA	-4.70099	54.66414
Ailsa Craig	AC	1526	NA	-5.11666	55.25257
Bass Rock	BsR	1448	NA	-2.64038	56.07735
Barra Head	BH	2007	NA	-7.63634	56.78446
Troup Head	TH	1987	NA	-2.30018	57.68806
St Kilda	SK	1600	NA	-8.58466	57.81756
Flannan Isles	FII	1969	NA	-7.58955	58.28723
Sule Stack	SISSt	1710	NA	-4.50691	59.02401
Sule Skerry	SISk	2003	NA	-4.40809	59.08405
Sula Sgeir	SISg	1549	NA	-6.15779	59.09457
Westray	Ws	2003	NA	-3.06992	59.3329
Fair Isle	Frl	1975	NA	-1.63954	59.54849
Foula	FI	1980	NA	-2.1	60.13
Noss	Ns	1914	NA	-1.0039	60.139
Hermaness	Hr	1917	NA	-0.90669	60.82321

against which the gridded telemetry data ($D_t, \sum_{i=1}^{N_i} \sum_{j=1}^{N_j} D_{t\,ij} = P_t$, the total number of telemetry points) were evaluated (in grid, dimensions N_i, N_j) assuming observations are approximately temporally independent (Aarts et al., 2012):

$$LL = \sum_{i=1}^{N_i} \sum_{j=1}^{N_j} -P_t U_{ij} + D_{t\,ij} \ln(P_t U_{ij}) - \ln(D_{t\,ij}!). \quad (9)$$

The nonlinear features of the model resulted in erratic localised behaviour of the likelihood in parameter space, challenging optimisation procedures with fixed step sizes (e.g. the L-BFGS-B method from the *optimParallel* package (Gerber & Furrer, 2019)). Instead, we used an adaptive optimisation routine, *optim ARS* (Foracchia et al., 2004; Nyberg et al., 2012) and provided biologically plausible parameter constraints (Table 1). However, this method in R does not estimate confidence intervals (CIs).

Computation time for parameter estimation depends on the grid size and resolution, and the number of inter-colony interactions in the network; however, it only needs to be completed once for a species and uses a subset of the metapopulation for computational speed.

3 | METHOD VALIDATION AND CASE STUDY

We applied the model to the Northwest Atlantic network of gannet breeding colonies concentrated around the British Isles (Table 2; Figure S2). Gannets are pelagic seabirds that usually avoid travelling over land (Furness et al., 2018), so we considered land cells impermeable. Colony sizes range from 10s to 10,000s of apparently occupied sites (AOS) and gannets can forage at distances of 100s km (Hamer et al., 2007). Between 1900 and 2016, the British Isles breeding population increased from $\approx 18,000$ to $\approx 360,000$ AOS, and 18 new colonies were founded (Table 2; Figure S2) (Jeglinski et al., 2023). Gannet HRs scale with colony size (Lewis et al., 2001) and are partially segregated (Wakefield et al., 2013), but the effect of colony growth on segregation is unknown. Predicting biologically realistic HRs is important as gannets are vulnerable to OWFs due to collision risk (Lane et al., 2020), strong avoidance behaviour (Dierschke et al., 2016), and the proximity of current and planned developments to their largest breeding colonies (Warwick-Evans et al., 2018).

Colony sizes were obtained from Jeglinski et al. (2023). We ran our model on a 5×5 km grid.

3.1 | Validation with simulated data

We first performed validation with simulated data to test the ability of our model to retrieve the correct parameters, assuming the model is not mis-specified. Pseudo-data were generated for two colony locations—Grassholm and Great Saltee (Table 2; Figure S2). We chose parameter values for γ , b_2 , b_3 , m , w (hereafter *true* parameter values, Table 3) such that the HRs of the two colonies interacted. We then projected *true* HRs using the method described above. From these *true* HRs (U_1 , U_2), with total animal usages P_1 , P_2 , we generated pseudo count data (U_{s1} , U_{s2}) using a count process that matches the likelihood used (a Poisson) for all cells i, j :

$$U_{s1\ ij} \sim \text{Pois}(P_1 U_{1\ ij}). \quad (10)$$

$$U_{s2\ ij} \sim \text{Pois}(P_2 U_{2\ ij}). \quad (11)$$

TABLE 3 True and estimated parameter values of model validation with simulated data (γ =carrying capacity, b_2 =density-dependent competition, b_3 =energetic constraint, m =overlap spectrum parameter, w =relative time spent foraging to commuting).

Parameter	True value	Starting value	Estimated value
γ	15	10	11.5
b_2	-0.9	-0.85	-0.83
b_3	-0.02	-0.015	-0.028
m	1	0.4	3.48
w	0.6	0.4	0.51

We then fitted our model to U_{s1} , U_{s2} to estimate γ , b_2 , b_3 , m , w (hereafter, *estimated* parameters). From the endpoint of the model fitting, we tried different methods of confidence interval (CI) estimation: the L-BFGS-B method (Gerber & Furrer, 2019) and direct hessian estimation (*numDeriv* package; Gilbert & Varadhan, 2019). However, we could not obtain CIs due to the erratic likelihood surface. We therefore validated the method by producing HRs for all gannet colonies around the UK and Ireland (Table 2; Figure S2) using the true and estimated parameters. We compared the true and estimated HRs (U_{true} and U_{est} , respectively) using Bhattacharya's affinity (BA; Bhattacharyya, 1946) and $\text{PHR}_{\text{est, true}}$, $\text{PHR}_{\text{true, est}}$, the probability of finding one HR within another (Fieberg & Kochanny, 2005):

$$\text{PHR}_{\text{est, true}} = \iint_{A_{\text{est}}} U_{\text{true}}(x, y) dx dy. \quad (12)$$

$$\text{PHR}_{\text{true, est}} = \iint_{A_{\text{true}}} U_{\text{est}}(x, y) dx dy. \quad (13)$$

As a second validation test, we calculated the true and estimated exposure of all colonies to planned OWFs (*EMODNet*, *Human Activities*, *Energy*, *Wind Farms*, 2014). All OWF polygons were converted to rasters (*st_rasterize*, *stars* package; Pebesma, 2021), where OWF presence (α) was indicated by the value 1, and 0 otherwise. We defined true and estimated exposure (E_{true} , E_{est}) to OWFs as the aggregate overlap between OWFs and HRs:

$$E_{\text{true}} = \sum_{i=1}^{N_i} \sum_{j=1}^{N_j} \alpha_{ij} U_{\text{true}\ ij}, \quad (14)$$

$$E_{\text{est}} = \sum_{i=1}^{N_i} \sum_{j=1}^{N_j} \alpha_{ij} U_{\text{est}\ ij}, \quad (15)$$

We tested the similarity of the true and estimated OWF exposure for all colonies by fitting a linear model of true exposure against estimated exposure, $E_{\text{true}} \sim E_{\text{est}}$, using the *lm* function (R Core Team, 2023).

3.2 | Application with tracking data

We fitted our model to gannet GPS data to validate its ability to predict realistic HRs. We used data on adult gannets from the year 2011 from the Seabird Tracking Database (BirdLife International, 2023, see data availability statement) for two neighbouring colonies: Great Saltee and Grassholm of estimated sizes 3985 and 31,979 AOS (Jeglinski et al., 2023). We removed locations within 1km of the colonies (Scales et al., 2014) and sub-sampled the tracking data to 1 location per 40min. Using these, we estimated parameters and HRs for the whole colony network in 2011 (Table 2; Figure S2) and calculated 95% HRs (*hr_isopleth*, *amt* package; Signer et al., 2019) for easy visual comparison to all available gannet GPS tracking data from

2011 (including an additional 8 colonies): Ailsa Craig, Bull Rock, Bass Rock, Great Saltee, Grassholm, Les Etacs, Lambay, Île Rouzic, Sule Skerry, and Little Skellig (BirdLife International, 2023) (see Wakefield et al., 2013). To estimate the HRs of two interacting colonies using our method, in a 5 km grid, with 154 × 152 cells, using the estimated parameters, the runtime on a 3.79 GHz computer was 0.83 hours.

As an additional validation, we assigned each tracking location from the 8 out-of-sample colonies to a colony probabilistically based on the proportion of usage (p_{ijl}) of each colony, l , in each cell:

$$p_{u\ ijl} = \frac{P_l U_{ijl}}{\sum_{l=1}^{n_{ij}} P_l U_{ijl}} \quad (16)$$

and calculated the number of locations correctly assigned using our method and two other methods for comparison: a method assuming equal usage within the defined foraging range (foraging range method) and a method incorporating distance decay of usage (projected foraging distributions; Critchley et al., 2018). For the foraging range method, the outer edges of the buffers (st_buffer , *sf* package; Pebesma, 2018; Pebesma & Bivand, 2023) were based on the relationship that foraging range (f_r) scales with the square root of 50% of the colony size, P_s (AOS) (Lewis et al., 2001), from Grecian et al. (2012):

$$f_r = 0.344\sqrt{P_s} + 40.062. \quad (17)$$

Next, usage was distributed evenly across the buffer area, with land cells cropped out.

To investigate how HRs may change over time, we predicted HRs using the estimated parameters and corresponding seed median colony sizes (Jeglinski et al., 2023) for four different years: 1900, 1940, 1980 and 2020, and in accordance with Wakefield et al. (2013), calculated 75% HRs to visualise spatial segregation between colonies.

We estimated the exposure in 2020 of the three largest gannet colonies in the Irish Sea (Ailsa Craig, Grassholm and Great Saltee) to planned OWFs in their proximity (EMODNet, Human Activities, Energy, Wind Farms, 2014) using model HRs, foraging ranges and projected distributions, to assess how exposure estimates differed across models with varying biological realism.

4 | RESULTS

Under validation against simulated data, we obtained high similarity values between the true and estimated HRs in both similarity measures: Bhattacharyya's Affinity, BA; median = 0.965 (95% CI: 0.878, 0.996) and $PHR_{est,true}$; median = 0.987 (95% CI: 0.887, 1.000), $PHR_{true,est}$; median = 1.000 (95% CI: 1.000, 1.000). We found no significant difference between true exposure (E_{true}) and estimated exposure (E_{est}) to OWFs. The gradient and the intercept of the linear model ($E_{true} \sim E_{est}$) showed no significant difference from 1 and 0, respectively: gradient; 0.963 (95% CI: 0.871, 1.055), intercept; 0.0008 (95% CI: -0.0066, 0.0082).

We fitted the model to tracking data from two gannet colonies (Great Saltee and Grassholm) (Table 4). Producing HRs (95% HRs)

TABLE 4 Estimated parameter values from the model fitted to tracking data from two Northern gannet colonies (Grassholm and Great Saltee) (γ = carrying capacity, b_2 = density-dependent competition, b_3 = energetic constraint, m = overlap spectrum parameter, w = relative time spent foraging to commuting).

Parameter	Estimated value
γ	1.25
b_2	-0.920
b_3	-0.0354
m	1.87
w	0.500

from these parameter estimates for all gannet colonies around the British Isles in 2011 (Table 2; Figure S2), HRs show striking visual similarities to validation tracking data (Figure 1) and 73% of tracking locations were correctly assigned to their origin colonies, compared to 31% using projected distributions and 41% using foraging ranges. Most gannet colony 75% HRs increased in size and interacted more as colony size increased over time, and new colonies were founded (Figure 2). However, they were mostly exclusive, with overlap occurring at the fringe of neighbouring colonies and in places of higher colony density (e.g. Little Skellig and Bull Rock, Lambay and Ireland's Eye). Both the foraging range method and projected distributions method predicted lower exposure of gannets to OWFs overall (our method: 3.43%, projected distributions: 2.66%, foraging range: 2.41% of birds at sea at a given time exposed to OWFs, for simplicity assuming 50% of all birds are at sea, i.e. one of each breeding pair (e.g. during incubation and chick-rearing; Critchley et al., 2018), Figure 3). We make the 50% assumption for all methods so that the percentages are comparable. However, it is possible that more than 50% of birds at a colony are at sea at a given time, especially towards the end of the breeding season, which may increase exposure.

5 | DISCUSSION

Our new predictive method advances the biological realism of HR estimation without relying on computer-intensive IBMs. Our improvements are important for environmental risk assessment because, as shown here, industry-standard HR estimation methods less accurately predict colony HRs, leading to biased OWF exposure estimates (Figure 3).

A key advantage of our method is its ease of deployment: Once fitted to modest animal tracking datasets, it can predict HRs in both space and time (Figures 1 and 2) based solely on colony locations and sizes and is thus particularly useful when tracking data are missing for part of a colony network. Compared to foraging radius models (Critchley et al., 2020) and foraging ranges (Thaxter et al., 2012; Woodward et al., 2024) that often assume uniform usage within a nominal foraging radius (e.g. Soanes et al., 2016), our method more

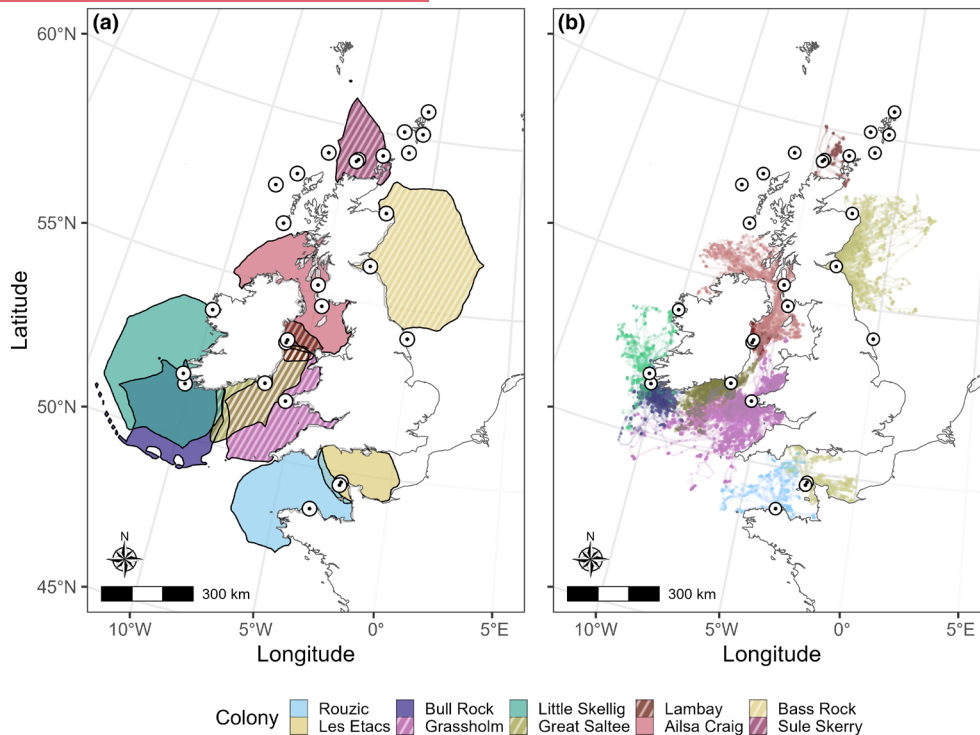


FIGURE 1 (a) Predicted 95% HRs for Northern Gannet colonies in 2011 surrounding the UK, Ireland and France. (b) Tracking data both used in model fitting (Grassholm; pink, Great Saltee; pale green) and not used in model fitting. Legend ordered by colony location from south to north.

realistically captures gradients in usage caused by accessibility, inter and intra-colony competition and carrying capacity constraints. Therefore, it can be used predictively, estimating exposure to potential future stressors using future HRs if population forecasts are available, and to estimate contact rates between colonies from their overlap, relevant to assessing inter-colony disease transmission risk (Lane et al., 2023) and inter-colony competition - potential additional stressors alongside environmental and resource change (Dias et al., 2019).

Despite difficulties obtaining CIs from model fitting, validation with simulated data produced high levels of overlap between true and estimated HRs and no significant difference in the calculated exposure of the true and estimated surfaces, giving confidence in the model fitting method. Validation with tracking data demonstrated the model's predictive power, with approximately double the amount of tracking locations correctly assigned to colonies (73%) compared to foraging radius models (31%) and foraging ranges (41%). This is of conservation importance, as our method could be used to more accurately apportion impacts to origin colonies and assign birds detected in at-sea surveys to their colonies during the breeding season, essential for environmental risk assessments. Although computationally demanding, model fitting in our method only needs to be completed once for a subset of a colony network and can then be used to predict HRs for other colonies and years. Future work may capture our mechanistic rules as advection-diffusion processes (Moorcroft & Lewis, 2006), considerably gaining in computational efficiency.

Our method could be extended to capture individual variation in HRs (Cleasby et al., 2023). For example, the model parameters could be fitted to animal tracking data stratified by sex or life history stage. In our current illustration, parameters were shared between colonies, assuming all inter-colony variation is captured by the processes formalised in the model (i.e. differences in colony size, location etc.). While inter-colony variation from other sources is currently not captured, our model has the advantage of predicting realistic HRs for colonies without tracking data (e.g. due to inaccessibility), assuming they have a similar colony composition to those sampled. We used data from adult gannets from a single year from two colonies to inform our parameters, assuming it is representative of this age class, year and of unsampled colonies. Crucially, our approach does not require tracking data from all/most colonies and is therefore less affected by potential cross-colony biases in tracking data (e.g. due to sample size differences) than other methods such as kernel smoothing. There is also emerging evidence of intra-colony foraging area segregation (Morinay et al., 2023) (but not in gannets; Waggitt et al., 2014), which may lead to within-colony differences in stressor exposure. As our understanding of inter- and intra-colony variation advances, more elaborate biological mechanisms can be incorporated into the model. For example, social information transfer and individual memory may modulate HRs and enhance spatial segregation between colonies (Aarts et al., 2021; Bolton et al., 2019; Wakefield et al., 2013).

Our method's flexibility means it can incorporate obstacles that may alter colonies' HRs. Structures in the environment such

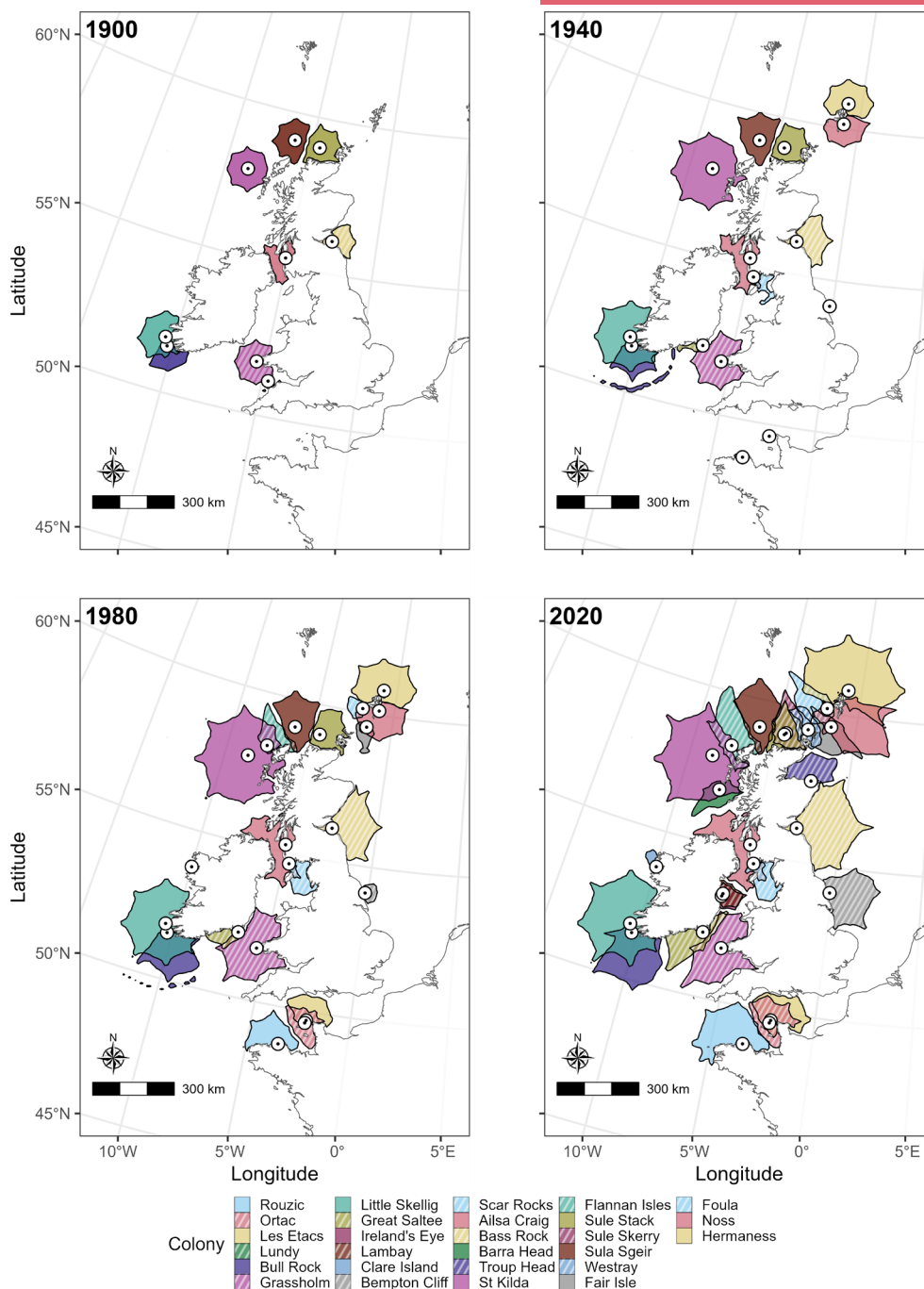


FIGURE 2 Estimated Northern Gannet colony model-derived 75% HRs by year (1900, 1940, 1980, 2020). Legend ordered by colony location from south to north. Spiky artefacts are due to grid distance calculation through 8 neighbouring cells. See Section 2.3 for more details.

as motorways and fences on land, or OWFs at sea, can cause displacement and increased energetic costs during commuting or prevent animals from foraging there (Berthinussen & Altringham, 2011; Dierschke et al., 2016). Once fitted, our model could be rerun to explore changes in HR and exposure under future obstacle scenarios, for example planned OWFs which seabirds may avoid (Dierschke et al., 2016). For such complex and semi-permeable landscapes, least cost path algorithms may represent improved distance calculation accuracy but come with a higher computational cost. A further extension is to use SDMs to initialise our model with a heterogeneous

carrying capacity surface as a function of covariates to capture elevated usage and competition at environmental 'hotspots' (Wakefield et al., 2009) and investigate how HRs change in a changing environment, e.g. due to anthropogenic climate change.

We have proposed fundamental improvements in HR model biological realism and predictive ability, and the robustness of exposure estimation. In addition, the relative computational expedience of our approach (compared to IBMs) and its modest data requirements (compared to density estimation) make it a valuable alternative to current approaches in a setting of multiple stressors, e.g. climate

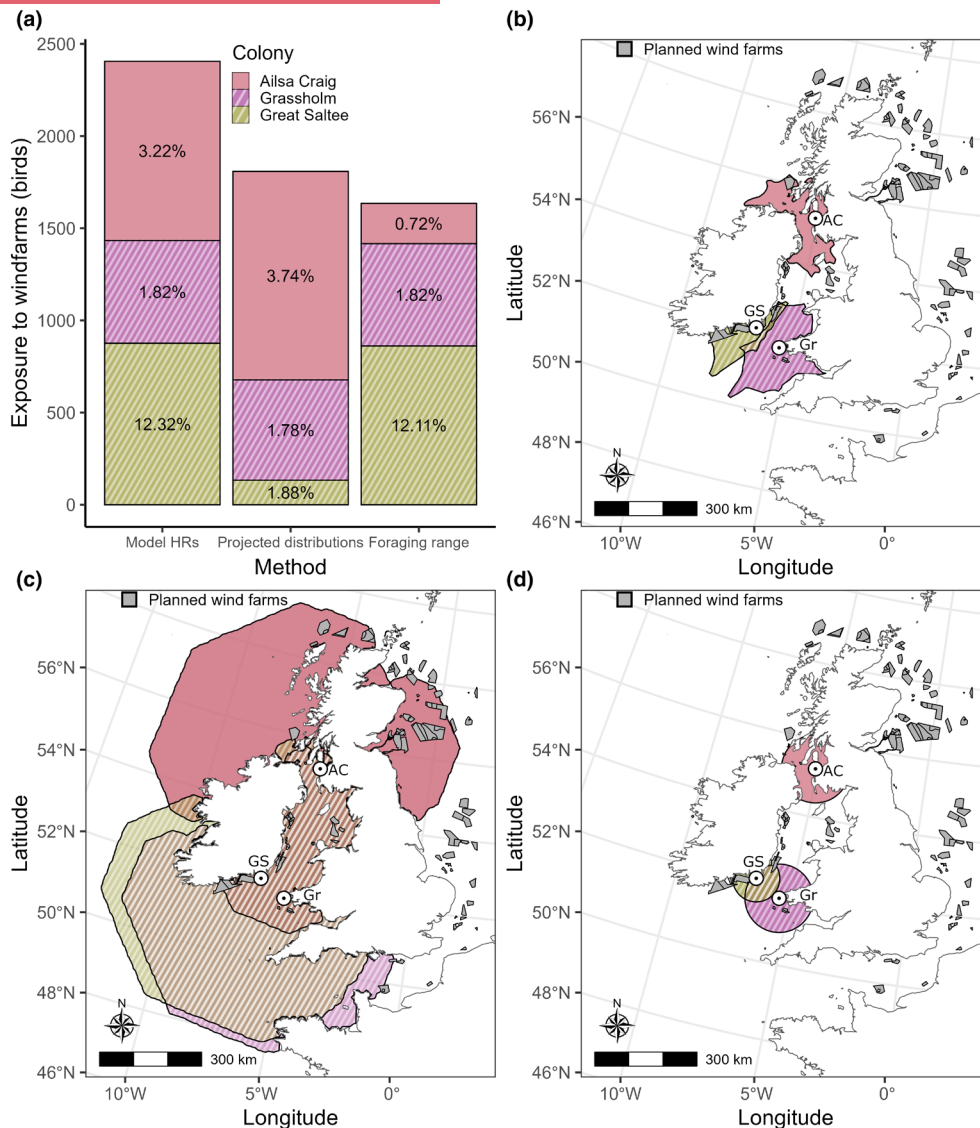


FIGURE 3 (a) Estimated exposure (number of birds at sea at a given time exposed to wind farms, assuming 50% of birds at sea) of the three largest Northern Gannet colonies in and around the Irish Sea in 2020 to planned offshore wind farms for three different exposure calculation methods. %'s in bars show the colony-specific percentage of birds at sea exposed. (b) Model-derived 75% HRs (c) 75% HRs of projected distributions. (d) Foraging range buffers.

change, disease, fisheries interactions, OWFs and habitat loss (Dias et al., 2019; Mickleburgh et al., 2002; Williams & Osborne, 2009).

AUTHOR CONTRIBUTIONS

Holly I. Niven, Jana W. E. Jeglinski, and Jason Matthiopoulos conceived the ideas and designed the methodology; Holly I. Niven led the analysis and software creation with support from Jana W. E. Jeglinski and Jason Matthiopoulos; Holly I. Niven led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Northern gannet tracking data were kindly contributed by: K. Hamer (Ailsa Craig), K. Hamer, R. Davies (Bass Rock), K. Hamer, J. Blackburn (Sule Skerry), S. Bearhop, T. Bodey (Bull Rock, Great Saltee, Lambay,

Little Skellig), S. Votier, G. Morgan, L. Morgan (Grassholm), L. Soanes, J. Green (Les Etacs), D. Grémillet (Ile Rouzic). We thank EMODnet—Human Activities and primary sources for providing wind farm data: The Wind Power, OSPAR Commission (ODIM OSPAR data and information Management System), HELCOM—Baltic Marine Environment Protection Commission—Helsinki Commission, Wind Europe, Royal Belgian Institute of Natural Sciences, Danish Maritime Authority (Secretariat for maritime spatial planning), Ministry of Finance (Planning Department) (Rahandusministerium), Ministry of The Environment and Regional Councils (Uusimaa, Kymenlaakso, Southwest Finland, Satakunta, Ostrobothnia, Central Ostrobothnia, North Ostrobothnia and Lapland), Åland Provincial Government, Cerema, Ministère de la Transition Écologique (GéoLittoral), Bundesamt für Seeschifffahrt und Hydrographie (BSH), Northland Deutsche Bucht GmbH, Marine Institute, Ministry

of Environmental Protection and Regional Development of The Republic of Latvia, EPSOG, Ministry of Energy of the Republic of Lithuania, Lithuanian Energy Agency, Ministry of Infrastructure and the Environment (Noordzeeloket), Rijkswaterstaat—Ministry of Infrastructure and Water Management, Ministry of Maritime Economy and Inland Navigation, Maritime offices of Gdynia, Słupsk and Szczecin, Direção-Geral de Recursos Naturais, Segurança e Serviços Marítimos (DGRM), The Crown Estate UK, Crown Estate Scotland, Government of Spain—Ministry for Ecological Transition and the Demographic Challenge, Swedish Agency for Marine and Water Management. This work was funded by the UK Department for Energy Security and Net Zero DESNZ Offshore Energy Strategic Environment Assessment OESEA programme.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.70019>.

DATA AVAILABILITY STATEMENT

All code associated with this contribution and wind farm data from (EMODNet, Human Activities, Energy, Wind Farms, 2014), accessed on 2023-11-24, available via <https://doi.org/10.5281/zenodo.14237231> and <https://doi.org/10.5281/zenodo.14918040> respectively (Niven, 2025; Niven et al., 2025). Northern gannet tracking data are available via Seabird Tracking Database (BirdLife International, 2023): Great Saltee (Dataset ID: 723) and Grassholm (IDs: 731, 732), Ailsa Craig (ID: 716), Bull Rock (ID: 720), Bass Rock (ID: 718), Les Etacs (ID: 733), Lambay (ID: 724), Ile Rouzic (ID: 734), Sule Skerry (ID: 719) and Little Skellig (ID: 721). Code to generate projected distributions is available via (Critchley et al., 2018). Northern gannet colony data are available via <https://doi.org/10.5281/zenodo.12513978> (Jeglinski et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: The overlap spectrum for two colonies with a dominant or non-dominant initial proportion of usage in a cell of interest (1000 vs. 100).

Figure S2: Map showing all gannet colony locations surrounding the British Isles with abbreviated names.

How to cite this article: Niven, H. I., Jeglinski, J. W. E., Aarts, G., Wakefield, E. D., & Matthiopoulos, J. (2025). Towards biologically realistic estimates of home range and spatial exposure for colonial animals. *Methods in Ecology and Evolution*, 00, 1–13. <https://doi.org/10.1111/2041-210X.70019>