

Modelling wildlife habitat selection from tracking data: A practical guide for ecologists

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Abstract

1. The study of habitat selection has long been at the heart of ecological research and is critical to deciphering the mechanisms that govern species' responses to global change. This is particularly important for central place foragers, whose ability to adapt to shifting environmental conditions and anthropogenic disturbance is limited by persistent attachment to a fixed site.
2. Recent advances in remote sensing have led to the widespread use of animal-borne telemetry to parameterise habitat selection models. However, many early model formulations rely on assumptions of temporal independence and unconstrained movement that are typically violated in modern tracking studies. Newer, more sophisticated methods have emerged to address these issues, yet most have been developed and

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presented in isolation, leading to a fragmented and often
confusing methodological landscape that is difficult to navigate,
even for experienced practitioners.

3. Here, we present an accessible guide to modelling habitat
selection from tracking data. We purposefully focus on building
conceptual understanding rather than formal mathematical
detail, with a particular emphasis on reconciling how different
models define and approximate availability – a pervasive source
of confusion for quantitative ecologists. In doing so, we clarify
how all existing approaches can be understood through the
lens of point process theory and articulate connections that
are often difficult to discern from the literature.

4. Using a realistic simulation of colonially-breeding seabirds, we
provide a worked example with reproducible code demonstrating
how models can be fitted in the R software using syntax familiar
to many ecologists. Our case study shows that explicitly
accounting for how movement dictates the range of locations
accessible to individuals yields more robust estimates of habitat
effects. We also highlight how the spatial constraints imposed
by central place foraging can inflate the apparent importance
of habitats that are simply encountered due to the mechanics
of central place commuting rather than genuine preference.

5. With this paper, we aim to help readers make sense of the
ecological and statistical literature and provide a practical
reference to analysing tracking data for habitat selection
studies.

KEYWORDS

space use, resource selection, telemetry, point process,
spatio-temporal models, use-availability

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1 | INTRODUCTION

The advent of animal-borne remote sensors such as global positioning system (GPS) or Argos tags has revolutionised studies of wildlife behaviour in recent decades (Hebblewhite and Haydon, 2010), offering unprecedented insights into where, when, and how individuals select and use habitats within their environment. With continued innovations in microelectronics, satellite infrastructure, and battery technology, the experimental radio transmitters first deployed in the 1950s (LeMunyan et al., 1959) rapidly gave way to lightweight, high-performance instruments that shrank in size and became capable of near-continuous tracking over continental and ocean-basin scales (Whitney, 2022; Rafiq et al., 2021). At the same time, improvements in manufacturing and scalability have reduced overall costs, allowing recorders to be deployed more widely across individuals and species. Today, animal-borne telemetry yields millions of behavioural observations across the globe, enabling the monitoring of hundreds of marine and terrestrial species – from the smallest swift (e.g., Bloch et al., 2025) to the largest seal (e.g., Rodríguez et al., 2017) – at minute-by-minute resolution over periods spanning days to months (Sequeira et al., 2025).

Although telemetry can provide critical information to support decision-making (Hays et al., 2019), modelling habitat selection from tracking data remains challenging, both practically and statistically. In practice, deriving ecological understanding from movement paths requires linking estimated coordinates to environmental covariates, a task complicated by sensor failures (e.g., in harsh conditions), variable positional accuracy, and battery constraints that force unavoidable trade-offs between sampling frequency and deployment duration. Statistically, the locations recorded by animal-borne tags cannot be treated as independent observations as successive fixes sample adjacent segments of the same continuous movement path (Boyce et al., 2010), meaning that the location of an individual at time t depends both on the resources available there and on where the individual was at time $t - 1$. Tracking data are therefore almost always temporally autocorrelated (Noonan et al., 2019; Fleming et al., 2015), and models

that ignore this dependence risk confounding habitat preference with movement capacity. Although data thinning (i.e., sub-sampling data to retain only locations sufficiently far apart to be considered statistically independent) has long been used to mitigate autocorrelation (Swihart and Slade, 1985), it is an inefficient approach that discards valuable information and undermines the financial costs of data collection as well as the ethical responsibility to maximise knowledge from instrumented animals (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016). Moreover, thinning relies on arbitrary criteria that risk either retaining problematic autocorrelation or removing biologically meaningful structure (De Solla et al., 1999; Alston et al., 2023). Approaches that explicitly account for movement-based autocorrelation without sacrificing information are thus preferable for analysing tracking data (Alston et al., 2023; Eisaguirre et al., 2025).

Behavioural constraints on movement can further complicate the interpretation of habitat selection relationships. One particularly important case is that of central place foraging (hereafter "CPF"), a behavioural strategy in which individuals forage by making repeated trips to and from a fixed home base such as a burrow, a haul out, or a rookery (Orians and Pearson, 1979; Bell, 1990). CPF manifests across a wide range of taxa (from insects to birds, reptiles, and mammals) and spatial scales (from a few metres to thousands of kilometres) and can arise in a variety of ecological contexts. For example, many species with established home ranges can be regarded as central place foragers (Bell, 1990). Well-known examples of this include beavers (e.g., Værøyvik and Madden, 2025) or squirrels (e.g., Hefley et al., 2017), whose territories are centred around food caches or shelters. In other species, CPF may only emerge during particular life-history stages or seasonally important activities such as reproduction, when individuals are temporarily constrained to a breeding site while provisioning or caring for dependent young. For instance, guillemots (*Uria aalge*) return to the same cliff site to feed their chicks (e.g., Burke and Montevvecchi, 2009), and grey wolves (*Canis lupus*) regularly travel back to the den during pup rearing (e.g., Ylitalo et al., 2021). While central places offer protection against predators and parasites, cover from inclement weather, and physiological buffering from climatic extremes (Ord and Blazek, 2025), attachment to a fixed site also curtails mobility to a limited neighbourhood around the central place where the energetic gains from resource acquisition or prey capture outweigh the energetic costs of commuting (Rueffler and Lehmann, 2024). Such constraints may leave species displaying CPF behaviour unable to respond to shifting resources or deteriorating conditions, increasing their vulnerability to habitat loss, environmental variability,

and anthropogenic disturbance (Matthiopoulos et al., 2005). For instance, Pichegru et al. (2010) showed that nest fidelity restricted the foraging range of Cape gannets (*Morus capensis*) during an oceanic regime shift, preventing birds from tracking the re-distribution of their prey and causing dramatic declines in breeding success. Although early work on CPF concentrated on theories behind the decision-making of individual foragers (Orians and Pearson, 1979), recent years have also seen growing recognition of CPF as a key driver of ecosystem structure and function. By funneling prey remains and waste through a focal point, central place foragers redistribute organic matter and nutrients across otherwise isolated habitats (e.g., Appoo et al., 2024; Mari et al., 2009; Hentati-Sundberg et al., 2020; Strickland et al., 2013). In this context, a shift in foraging patterns can cascade into losses of key ecosystem functions (Strickland et al., 2013), making our understanding of habitat selection as it relates to CPF essential to both forecasting population responses to global change and informing ecosystem-based management (Allen and Singh, 2016). From a statistical perspective, however, CPF poses additional challenges because repeated returns to a fixed location fundamentally constrain the range of habitats that an individual can realistically access. Classical habitat selection models such as resource selection functions (RSFs) typically assume that all parts of the study domain are equally accessible (Manly et al., 2002), yet this assumption is rarely appropriate in the context of CPF, particularly where physical barriers (e.g., land mass) and variable energetic costs of travel mediate accessibility from the central place such that some areas within the nominal home range remain effectively unreachable or disproportionately costly to visit (Paton and Matthiopoulos, 2016). Ignoring central place constraints can thus make uninformative covariates appear spuriously important, producing apparent habitat preferences that are artefacts of geometry rather than genuine ecological selection (Benhamou and Courbin, 2023; Rosenberg and McKelvey, 1999; Alston et al., 2023).

Together, these challenges have prompted the development of increasingly sophisticated statistical modelling frameworks – many grounded in point process theory – capable of extracting reliable ecological signals from noisy, incomplete, or irregular tracking data (Matthiopoulos et al., 2023; Northrup et al., 2022). However, the rapid pace and technical nature of methodological development in this area have created barriers for practitioners without specialised training (Northrup et al., 2022), with guidance on when and how to apply different models scattered across the literature. Consequently, key analytical decisions such as model choice and parameter interpretation remain unintuitive and the implications of those decisions are often poorly understood (Northrup et al., 2022;

[Gerber et al., 2025](#)). This is particularly problematic in studies of central place foragers because existing frameworks are typically developed for unconstrained movement and rarely account for the unique spatial and behavioural constraints imposed by CPF. Furthermore, empirical studies lack knowledge of the true underlying habitat selection process and usually only consider a single model in isolation, making it difficult to assess how alternative models may perform or whether estimated coefficients recover unbiased habitat selection effects ([DiRenzo et al., 2023](#)). Here, we present a practical roadmap for modelling habitat selection in support of conservation and management decisions ([Sofaer et al., 2019](#)), with a particular emphasis on central place foragers. Using seabirds as a motivating example, we evaluate how several classes of models recover known habitat selection patterns from simulated tracks, and we contrast model performance across both CPF and non-CPF scenarios. Our goal is to demystify the application of point process models to animal-borne telemetry by providing a digestible synthesis of how commonly used model formulations relate to one another, how they differ in their treatment of autocorrelation, and how their parameters and outputs should be interpreted. We do not attempt a comprehensive technical review; instead, we pair essential mathematical notation with intuitive explanations accessible to readers with basic statistical knowledge. To increase transparency, we also provide reproducible code demonstrating how models can be fitted in the open-source R programming language. By drawing explicit connections between modelling frameworks and demonstrating them using visuals and empirical examples, our review expands on recent conceptual efforts to bridge statistical theory with ecological practice (e.g., [Gerber et al., 2025](#)) and offers a hands-on reference for working with tracking data in habitat selection studies.

2 | EXPLANATION OF THE METHOD

In this section, we review habitat selection modelling methods with minimal statistical notation. Readers seeking a plain-language summary can also consult Appendix 1.

Any discussion of habitat selection modelling ought to begin with a simple but important clarification: habitat selection is not concerned with where animals occur in *absolute* terms, but rather with how they use their environment *relative*

141 to what is available to them (Figure 1). Just as a diner's restaurant choice depends on which venues are open and
 142 within walking or driving distance, an animal's habitat preference can only be inferred when multiple habitats are
 143 available but some are used more frequently than others (Manly et al., 2002). As a result, habitat selection is often
 144 conceptualised as a simple ratio:

$$\text{Selection} = \frac{\text{Use}}{\text{Availability}} \quad (1)$$

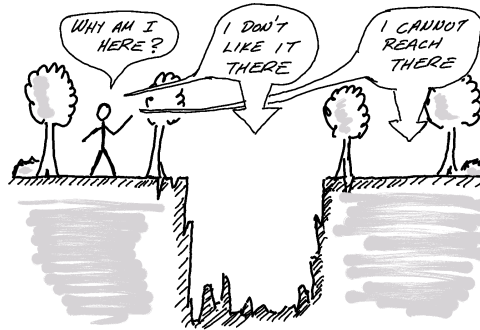


FIGURE 1 Selection ("why am I here?") can only be defined relative to availability, as an individual may occur in a location either because alternative habitat is less preferred ("I don't like it there"), or because otherwise suitable habitat is unavailable and/or cannot be reached ("I cannot reach there"). For example, consistent observations of animals at high elevations may suggest an influence of altitude on space use, yet this conclusion is only valid if lower elevations are also available but used less frequently. If animals never encounter these environments because they are either too rare or inaccessible, preference cannot be separated from lack of opportunity. Image reproduced from Matthiopoulos et al. (2023) under a Creative Commons Attribution 4.0 International License (CC BY 4.0).

145 where the numerator ("use") reflects locations where animals were recorded and the denominator ("availability")
 146 denotes the parts of the landscape accessible to individuals. Availability is rarely known and must therefore be
 147 approximated statistically. To do this, early work relied on resource selection functions (RSFs), which contrast
 148 the conditions at used sites ("cases") with those at randomly sampled locations ("controls", "pseudo-absences",
 149 "quadrature", or "background points") representing available habitat (Boyce et al., 2002). Because the number of
 150 controls is specified by the analyst (i.e., usually increased until parameter estimates stabilise) and therefore determined
 151 by the sampling design rather than the underlying ecological process, the overall level of use cannot be determined
 152 and RSFs only describe *relative* selection (Manly et al., 2002). The ratio in Eq. 1 is then modelled as an exponential

function of covariates that assigns higher weights to more favourable habitats:

$$w(\mathbf{x}) \propto \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k) \quad (2)$$

Here, $w(\mathbf{x})$ quantifies the relative use of locations with habitat values $\mathbf{x}$, where $x_1, x_2, \dots, x_k$ are each of k covariates (e.g., elevation, prey density, etc.) and $\beta_1, \beta_2, \dots, \beta_k$ their selection coefficients. Many habitat selection models share a common log-linear structure, which becomes clear when the RSF is re-expressed on the log scale:

$$\log w(\mathbf{x}) \propto \underbrace{\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k}_{\text{linear predictor}} \quad (3)$$

In many statistical texts (e.g., [Hastie et al., 2009](#)), the same expression is however often written more compactly using vector notation:

$$\log w(\mathbf{x}) \propto \mathbf{x}^\top \boldsymbol{\beta} \quad (4)$$

where $\mathbf{x}^\top \boldsymbol{\beta}$ is the dot product of habitat coefficients $\boldsymbol{\beta}$ and covariates $\mathbf{x}$ and the transpose $^\top$ is simply shorthand for arranging $\mathbf{x}$ in the correct orientation for matrix multiplication. [Eq. 4](#) is algebraically equivalent to [Eq. 2](#) and [Eq. 3](#). Note that an intercept (β_0) is omitted here because it only rescales the RSF (by a constant term e^{β_0}) and therefore does not change the relative ranking of habitats (i.e., which habitats are predicted to be used more or less often). RSFs are commonly fitted using case-control logistic regression ([Manly et al., 2002](#)), where each used/available outcome is modelled as:

$$y \sim \text{Bernoulli}(p) \quad (5)$$

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \mathbf{x}^\top \boldsymbol{\beta}$$

Here, observed locations are coded as 1, control points as 0, and p is the probability of a point being observed. Although written on the log-odds scale, [Eq. 5](#) is interpreted as estimating the coefficients of the RSF in [Eq. 4](#). The intercept (β_0) in [Eq. 5](#) is included as a necessary component of model fitting but has no direct biological relevance as it depends on the ratio of used to control points, which is subjective. We show it here only for completeness, but inference is based solely on the estimates of $\boldsymbol{\beta}$. Logistic regression thus serves as a convenient estimator of relative selection coefficients rather than as a definition of the RSF itself ([Boyce et al., 2002](#)).

To avoid arbitrary sampling choices (i.e., number and placement of control points), alternative frameworks model availability directly in continuous space (Warton and Shepherd, 2010). The simplest is the *inhomogeneous Poisson point process* (IPP), which treats locations as a realisation of a spatial (or spatio-temporal) point process with an *intensity function* $\lambda(s)$ describing the expected density of points at a given location s (Renner et al., 2015). Habitat selection is formalised by allowing this intensity to vary with habitat covariates. A common specification is:

$$\log \lambda(s) = \beta_0 + \mathbf{x}(s)^\top \boldsymbol{\beta} \quad (6)$$

where $\mathbf{x}(s)$ is the covariate vector at location s and other coefficients are as before. To emphasise how subsequent models extend this basic form, we refer to $\lambda(s)$ as $\lambda_{\text{IPP}}(s)$ from here. Unlike logistic regression (Eq. 5), the IPP intercept has a meaningful interpretation: $\exp(\beta_0)$ gives the baseline density of observations per unit area in the absence of habitat effects (or under average habitat conditions for mean-centred covariates). While $\lambda(s)$ is not a probability, higher intensities correspond to locations more likely to contain observations. Because the IPP is defined in continuous space, availability is implicit across the spatial domain (Warton and Shepherd, 2010). Evaluating its likelihood therefore requires integrating $\lambda(s)$ over infinitely many locations, which is infeasible. A practical solution is to discretise the study region into a spatial grid (Aarts et al., 2012) and model cell counts as $y \sim \text{Poisson}(\mu)$, with μ approximated by multiplying the cell area by the intensity at a representative point (e.g., the cell centroid), when cells are sufficiently small relative to the spatial scale of variation:

$$\mu_i = \int_{A_i} \lambda_{\text{IPP}}(s) \quad (7)$$

$$\Leftrightarrow \mu_i \approx a_i \times \lambda_{\text{IPP}}(s_i)$$

Here, s_i is the location of grid cell i , A_i the spatial domain of that cell, and a_i its surface area. The integral $\int_{A_i}$ sums the intensity across all infinitesimally small regions within cell i to obtain the expected number of points in that cell.

In log form:

$$\log \mu_i \approx \log a_i + \beta_0 + \mathbf{x}(s_i)^\top \boldsymbol{\beta} \quad (8)$$

Summing μ_i across cells approximates the integral of the intensity over the study region S :

$$\sum_i \mu_i \approx \int_S \lambda_{\text{IPP}}(s) ds \quad (9)$$

This *gridded Poisson* model is fitted via Poisson regression with $\log(a_i)$ as an offset and converges to the continuous-space IPP model as grid resolution increases (Baddeley et al., 2010; Aarts et al., 2012). Confusingly, alternative approximations to the integral of the IPP exist that do not discretise space but instead use the same control points defined in logistic regression (Fithian and Hastie, 2013). In *down-weighted Poisson regression*, each control point is treated as a small portion of the landscape and assigned a weight proportional to the area it represents (typically the total area divided by the number of control points). This formulation is directly analogous to the grid-based scheme described above, differing only in how the landscape is partitioned for numerical integration. Conversely, *infinitely weighted logistic regression* assigns very large weights to control points so that their contribution dominates the likelihood. This is a mathematical trick that forces the model to correctly account for the total amount of available space across the study region, ensuring that the expected number of points predicted by the intensity surface matches the number of observations. As the weights increase, the resulting likelihood converges to that of the continuous IPP, making the two formulations equivalent (Matthiopoulos et al., 2023). Similarly, recent work has shown that even logistic regression approximates the IPP likelihood when a sufficiently large number of control points are sampled (Warton and Shepherd, 2010; Renner et al., 2015). Understanding these connections helps demystify how many familiar yet seemingly unrelated classes of habitat selection models are in fact computational approximations of the same underlying ecological process shaping where animals occur in space and time (Northrup et al., 2022). Viewing these methods through the lens of point process theory therefore provides a coherent framework for linking different formulations and contrasting how each treats availability in the model likelihood (Figure 2, Table 1).

Under the IPP, observations are conditionally independent given $\lambda(s)$, meaning that points should appear randomly distributed once habitat effects are accounted for (Warton and Shepherd, 2010; Baddeley et al., 2015). In reality, ecological data often show additional clustering because animals reuse the same sites or because the conditions to which they respond vary across the landscape in spatially structured ways (e.g., prey occur in patches, temperature varies along gradients) (Illian et al., 2008). When these processes are not fully captured by the covariates, the resulting

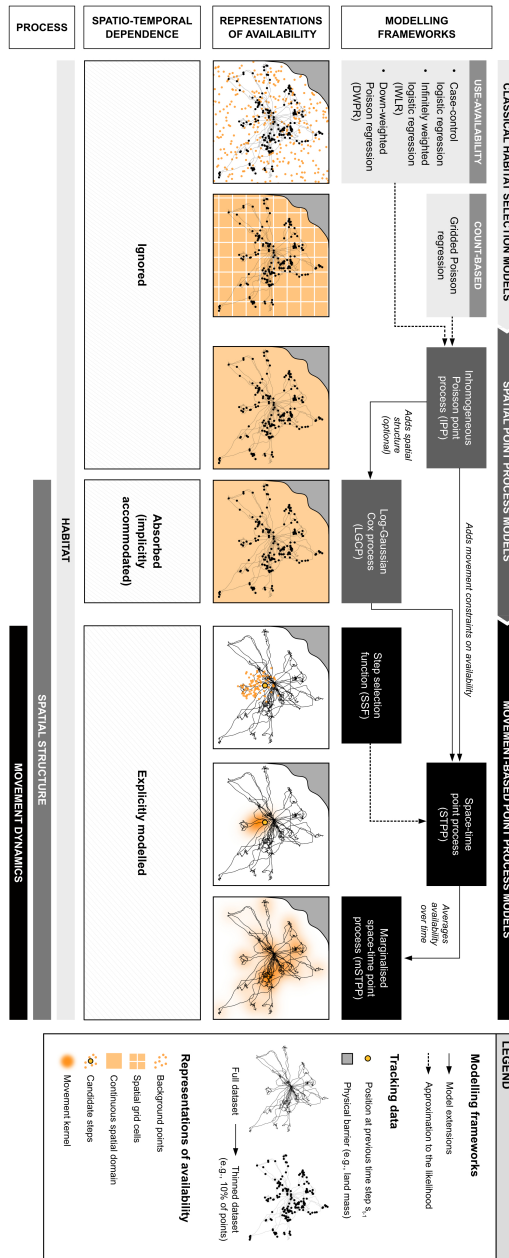


FIGURE 2 Conceptual relationships between models used to estimate habitat selection from tracking data. All models can be viewed as extensions (solid arrows) or approximations (dotted arrows) of the inhomogeneous Poisson point process (IPP), which differ in the way they represent availability (orange symbology) relative to the data used for model fitting (see also Table 1). Many of the earlier model formulations (left) rely on data thinning to reduce autocorrelation, whereas more recent movement-informed models (right) explicitly account for temporal dependence and can utilise the full tracking record. The depicted example shows hypothetical tracks from breeding seabirds returning to an offshore island off the mainland (grey); however, the models are equally applicable to any type of tracking data. Habitat covariates are defined over the relevant study domain (i.e., here, the ocean area enclosed within the black boundary).

spatial structure violates the assumption of independence implied by the IPP. Models that accommodate this residual structure are therefore appealing in many ecological contexts. One such model is the *log-Gaussian Cox process* (LGCP), which adds a spatial random effect into the IPP intensity of [Eq. 6 \(Møller and Waagepetersen, 2003\)](#):

$$\lambda(s) = \lambda_{\text{IPP}}(s) \times \exp u(s) \quad (10)$$

where $u(s)$ is a Gaussian random field, i.e., a smooth spatial surface representing unexplained variation.

This is the same as:

$$\begin{aligned} \log \lambda(s) &= \log \lambda_{\text{IPP}}(s) + u(s) \\ &= \beta_0 + \mathbf{x}(s)^\top \boldsymbol{\beta} + u(s) \end{aligned} \quad (11)$$

An LGCP can thus be viewed as an IPP whose intensity surface is adjusted locally by a spatially structured process. Because nearby locations share similar values of $u(s)$, the model distinguishes spatial patterns arising from species-habitat associations from residual spatial clustering arising from unmeasured environmental variation or behavioural processes such as site fidelity, social interactions, or aggregation.

The models above apply broadly to occurrence data collected at fixed sites (e.g., camera-traps, acoustic sensors, opportunistic sightings). However, tracking data consist of repeated snapshots of moving individuals whose successive locations are strongly autocorrelated ([Fieberg et al., 2010](#)). Ignoring the way in which animals move can cause movement-driven clustering to be mistaken for habitat selection ([Aarts et al., 2012](#); [Forester et al., 2009](#)): distant habitats may appear underused simply because they were unreachable (i.e., false avoidance) whereas habitats near an animal's path may appear disproportionately selected because they dominate the space accessible to that individual at that time (i.e., false preference). In this context, availability is *dynamic* rather than static ([Hooten et al., 2017](#)), creating a circularity whereby movement shapes exposure to habitats while habitat preferences themselves also influence movement.

TABLE 1 Comparison of modelling frameworks used to estimate habitat selection from animal location data. Each modelling framework is qualitatively ranked on Likert scales of increasing ecological complexity, computational cost, and transferability (i.e., the ability to apply inferred habitat selection relationships to new systems, time periods, or contexts). ≡ means 'same as above'.

Model	Data type	Likelihood	Model output (interpretation)	Availability representation	Key assumptions	Ecological complexity	Computational cost	Model transferability	References
Case-control logistic regression	Binary used–available (1/0)	Binomial	Relative selection strength / suitability	Sampled background points (user-specified)	Availability is adequately represented by sampled background points; observations are independent	Low – static habitat associations relative to availability	Low – standard regression framework	Moderate – conditional on availability sample; coefficients may change when the accessible domain varies	Manly et al. (2002) , Boyce et al. (2002)
Gridded Poisson regression (PR)	Counts per spatial unit (grid cell)	Poisson	Expected number of points per spatial unit (discretised intensity)	Discrete spatial units (grid cells)	Counts within spatial units are independent; intensity is constant within each unit	≡	≡	≡	Aarts et al. (2012)
Down-weighted Poisson regression (DWPR)	Binary used–available (1/0) with small weights on 0s	Weighted Poisson	Relative intensity / selection strength (IPP approximation)	Background points with small weights	Background sampling approximates continuous availability via weighting	≡	≡	≡	Fithian and Hastie (2013)
Infinitely weighted logistic regression (IWLR)	Binary used–available (1/0) with large weights on 0s	Binomial	Spatial intensity (IPP-equivalent in the limit)	Background points with very large weights	Infinite weighting yields equivalence to IPP likelihood	≡	≡	≡	Fithian and Hastie (2013)
Inhomogeneous Poisson process (IPP)	Point locations	Poisson point process	Spatial intensity	Continuous spatial domain	Observations arise from a spatial Poisson process; all locations in the domain are available; points are conditionally independent given intensity	Moderate – explicit spatial intensity of habitat use	Moderate – requires integration over the study domain	High – strong predictive capacity, provided relevant covariates are available and relationships remain stable across systems	Warton and Shepherd (2010) , Renner et al. (2015)

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Model	Data type	Likelihood	Model output (interpretation)	Availability representation	Key assumptions	Ecological complexity	Computational cost	Model transferability	References
Log-Gaussian Cox process (LGCP)	Point locations	Poisson point process with latent spatial field	Spatial intensity (with spatial structure)	Continuous spatial domain	Residual spatial autocorrelation is captured by a latent Gaussian field; conditional independence given intensity & random field	High – accounts for unmeasured drivers of habitat use	High – requires estimation of latent processes	Moderate – spatial random effects typically improve in-sample performance but are often difficult to transfer to new systems	Illian and Burslem (2017)
Step selection function (SSF)	Time-stamped point locations	Conditional multinomial	Relative selection strength conditional on movement	Movement-constrained locations (finite sample from empirical or fitted step-length & turning-angle distributions)	Available locations are drawn from a realistic movement kernel; selection is estimated conditional on movement; matched strata (used-available sets) are independent	High – accounts for movement-constrained habitat selection	Moderate – repeated comparison of used and available steps	Moderate – depends on the extent to which movement and selection processes remain consistent across systems	Fortin et al. (2005) , Forester et al. (2009)
Space-time point process (STPP)	Time-stamped point locations	Space-time Poisson point process	Time-varying spatial intensity	Movement-constrained locations (time-specific)	Movement constrains availability at each time step; observations depend on previous locations via movement kernel	Very high – jointly model of habitat selection and movement through space and time	Very high – repeated evaluation of time-varying, movement-informed availability	Moderate – predictions depend on the validity of the movement model in the new system	Johnson et al. (2013) , Eisaguirre et al. (2021)
Marginalised space-time point process (mSTPP)	Time-stamped point locations	Poisson point process with movement-derived availability	Time-averaged spatial intensity weighted by availability	Movement-constrained locations (time-averaged)	Movement-constrained availability can be approximated by averaging over time; temporal dependence is integrated out	Very high – broad-scale habitat selection accounting for movement constraints	High – requires estimation and aggregation of movement-informed availability	Moderate to high – supports broad-scale prediction, provided movement processes can be specified for the target system	Eisaguirre et al. (2025)

By modelling the choices that animals make between successive locations, *step selection functions* (SSFs) provide one approach to account for dynamic availability. SSFs have played an important role in ecology and conservation and are the subject of a substantial body of literature (Thurfjell et al., 2014). We direct interested readers to Fortin et al. (2005), Forester et al. (2009), Florko et al. (2025), Fieberg et al. (2021), Michelot et al. (2024), Avgar et al. (2016), and Eisaguirre et al. (2024) (among others) for full descriptions of their mechanics, theoretical foundations, and recent extensions. Briefly, SSFs quantify where animals choose to move next by comparing each observed movement step with a set of plausible alternatives. The latter are typically generated from empirical distributions describing how far (step lengths) and in which direction (turning angles) the animal could have travelled during the corresponding time interval, such that availability reflects the animal's movement capacity at each moment. In this way, availability is defined locally and updated at each successive step rather than remaining fixed across the study domain (Thurfjell et al., 2014). Habitat selection is then estimated by comparing covariates at observed and potential endpoints, most commonly *via* conditional logistic regression. Importantly, the set of alternative steps can be viewed as a discrete sample from a broader, continuous distribution of possible next locations that are accessible given the animal's movement constraints.

A closely-related class of models known as *space-time point process* models (STPPs), represent this surface directly and can therefore be viewed as extensions of the IPP over both space *and* time (Johnson et al., 2013). STPPs define availability as the set of locations an animal could realistically reach during each time interval (Johnson et al., 2013), given the characteristics of both the interval itself (i.e., length, start and end positions) and the animal's movement behaviour. For tracking data, the STPP intensity can be expressed as the product of a habitat selection term and a movement-based availability function:

$$\lambda(s, t) = \underbrace{\lambda_{\text{IPP}}(s, t)}_{\text{Habitat selection}} \times \underbrace{G(s \mid s_{t-1}, \Delta_t; \theta)}_{\text{Movement-aware availability}} \quad (12)$$

where $\lambda(s, t)$ represents the density of points at location s and time t , $\lambda_{\text{IPP}}(s, t)$ is a time-indexed habitat selection component equivalent in form to that of the IPP, and $G(s \mid s_{t-1}, \Delta_t; \theta)$ describes the relative accessibility of location s at time t , given the time interval Δ_t elapsed since the last observation, the animal's previous location s_{t-1} , and its

movement parameters (θ). Put simply, the function G (known as the movement *kernel*, Figure 2) indicates where an animal could plausibly be, and with what relative probability, given how much time it had to travel and the way in which it moves (e.g., travel speed, directionality, etc.). On the log scale:

$$\log \lambda(s, t) = \beta_0 + \mathbf{x}(s, t)^\top \beta + \log G(s \mid s_{t-1}, \Delta t; \theta) \quad (13)$$

This formulation preserves the familiar IPP structure but replaces the assumption of global availability with a time-specific availability surface, G , determined by the movement process. Doing so separates where animals *prefer* to be from where they *can* go at each moment. Various continuous movement models can be used to derive G , including Brownian motion (e.g., Johnson et al., 2013), Langevin or ecological diffusion (e.g., Michelot et al., 2019; Eisaguirre et al., 2024, 2025; Hooten et al., 2020), and Ornstein–Uhlenbeck (OU) models (e.g., Johnson et al., 2008; Eisaguirre et al., 2021). Brownian motion represents random, memoryless, and undirected movement (Codling et al., 2008), whereas diffusion models allow movement rates to vary with habitat quality (Ovaskainen, 2008; Hefley et al., 2017) and OU models add attraction to a central place, yielding tracks that wander stochastically but remain centred around a fixed point (Uhlenbeck and Ornstein, 1930). Another variant, the Ornstein–Uhlenbeck foraging (OUF) model, also considers velocity as an autocorrelated process to allow for short-term directional persistence (Fleming et al., 2014, 2015).

In practice, G rarely has a closed-form solution and must be approximated numerically. This is typically achieved by evaluating it over a large set of representative locations spread throughout the accessible area – a procedure known as *quadrature* (Appendices 3 & 5). At first glance, this can make the separation between STPPs and SSFs difficult to appreciate, as both approaches ultimately evaluate habitat selection at a finite set of locations (Michelot et al., 2024). However, those locations play fundamentally different roles in each framework. In an SSF, alternative steps define availability directly; they capture where the animal could have moved, and the observed step is compared against them. By contrast, in an STPP, availability is already represented by the continuous movement kernel. Quadrature locations do not determine available choices at all; they are simply a numerical trick used to make the model computationally tractable by avoiding calculations at every possible point in space. Importantly, under analogous formulations, the results of an SSF converge to those of the corresponding time-specific STPP as the number of

alternative steps in the SSF increases (Michelot et al., 2024). The main distinction between the two therefore lies in how movement-constrained availability is operationalised and how the models are fitted, rather than in fundamentally different views of availability itself.

One practical limitation of STPPs is that quadrature approximations must be repeated for every observation interval, which can make model fitting computationally onerous – particularly for large tracking datasets. Additionally, inference about habitat associations in an STPP is restricted to the subset of environmental conditions encountered during tracking, which may limit transferability to new areas or time periods. Despite this, STPPs offer both conceptual and analytical advantages that motivate their use over SSFs. One practical benefit is that they naturally accommodate irregular observations because the movement kernel reflects the length of time elapsed between successive locations. This can be particularly useful when the timing of fixes is affected by animal behaviour, such as for studies of marine mammals that are detected only at the surface (Johnson et al., 2013). Traditional SSFs have generally required that observations be made at constant intervals, although recent developments allow step selection analyses to accommodate variable step durations (Eisaguirre et al., 2024). Furthermore, because STPPs are formulated within a continuous-time point process framework, they establish a formal bridge between fine-scale movement and conventional point process models of resource selection (Johnson et al., 2013). Specifically, by linking each location along the track to the environmental conditions prevailing at that time, STPPs provide a direct probabilistic description of where an animal is expected to occur at any given time. This formulation makes STPPs particularly well suited to answering questions about fine-scale patterns of use in changing environments and, crucially, creates a natural pathway for scaling up local movement decisions to broader spatial distributions. The ability to connect inference across scales was an important motivation for the original development of STPPs (Johnson et al., 2013).

In particular, where the objective of the analysis shifts to describing broader patterns of space use, the time-specific availability surfaces from an STPP can be averaged (or *marginalised*, in statistical parlance) across the tracking record to characterise use over the full study period (e.g., to estimate a utilisation distribution) (Johnson et al., 2013; Hooten et al., 2017, Section 4.7). This idea is formalised by *marginalised space-time point process models* (mSTPPs; Eisaguirre et al., 2025), which combine successive movement kernels into a single spatial surface reflecting where the animal could plausibly have occurred over the course of the study. In doing so, mSTPPs transform instantaneous predictions

of occurrence into a cumulative representation of long-term space use that preserves movement constraints. Comparable predictions can be obtained from an SSF, often through simulation of stochastic trajectories from the fitted step selection model and aggregation of the resulting space use patterns (Signer et al., 2017, 2024) (though see Ellison-Neary et al. (2026) for an alternative approach based on matrix operations). However, this can be computationally demanding and sensitive to modelling choices such as boundary conditions, burn-in periods, and simulation duration, with large numbers of paths potentially needed to characterise the resulting distribution and its uncertainty reliably. In contrast, mSTPPs yield analogous estimates directly from the fitted point process:

$$\lambda = \lambda_{\text{IPP}} \times G^*(s; \theta) \quad (14)$$

$$\Leftrightarrow \log \lambda(s) = \beta_0 + \mathbf{x}(s)^\top \boldsymbol{\beta} + \log G^*(s; \theta)$$

where $G^*(s; \theta)$ represent the movement-informed availability aggregated across the full tracking record:

$$G^*(s; \theta) = \sum_{t=2}^T G(s \mid s_{t-1}, \Delta_t; \theta) \quad (15)$$

and each term in the sum denotes the movement kernel for a single observation interval. Summing kernels across all $T - 1$ intervals therefore gives greater weight to locations that were repeatedly accessible over the course of each track. $G^*(s; \theta)$ then enters the model in the same way as the time-specific movement kernel $G(s \mid s_{t-1}, \Delta_t; \theta)$ in the STPP (Eq. 13), but with the time dimension removed. Marginalising over time thus reduces computational burden by removing the need to evaluate a likelihood for each observation. Just as importantly, it broadens the range of environmental conditions represented in the data, allowing mSTPPs to generalise more readily to new contexts while still accounting for autocorrelation (Wilson et al., 2026).

The progression of models reviewed herein does not reflect a shift in how habitat selection is conceptualised but a gradual relaxation of simplifying assumptions about how individuals move through and interact with their environment. Early work (models 1–6 in Table 1) treated space as freely accessible, whereas later developments (models 7–9 in Table 1) acknowledged that animals experience their environment progressively through time (i.e. step by step along their paths), making availability dynamic and contingent on an individual's recent movement history. Reconciling these different perspectives clarifies the assumptions underlying each approach and highlights key considerations for

analysis, including how selection is defined across scales, how coefficients should be interpreted, and what kinds of predictions each model can support (Table 1). Rather than being interchangeable, the above methods form a continuum of increasing ecological complexity, from purely spatial models to formulations that explicitly incorporate movement and spatio-temporal structure (Figure 2).

3 | WORKED EXAMPLE

In this section, we fit habitat selection models to simulated tracking data generated under controlled conditions to benchmark model performance against a known habitat selection process. Our aim is to demonstrate the importance of accounting for autocorrelation and movement constraints when analysing tracking data, and to examine how different representations of availability influence estimates of habitat selection. To do so, we contrast scenarios *with* and *without* persistent attraction to a fixed location and show how model structure interacts with movement constraints to shape ecological inference. Critically, simulations of both central place foragers and non-central place foragers (NCPF) use the same bounded study domain representing the landscape potentially available to individuals, such that any differences in the realised spatial extent of simulated tracks arise solely from the underlying movement process rather than from differences in study design. We show that models that treat availability independently of movement produce selection estimates that consistently diverge from those obtained under a full point process formulation. This highlights a fundamental challenge in habitat selection analyses: many conventional frameworks define availability over the entire study region even though accessibility may vary markedly within that domain, particularly for central place foragers. Note that while the example shown is analogous to a seabird breeding on a truly offshore island, this is intended purely as a convenient setup rather than a modelling requirement. Neither the simulation framework nor the habitat selection models necessitate radial symmetry around the central place and more complex landscapes (e.g., coastlines, land barriers, etc.) can be accommodated by redefining the study domain and available locations accordingly. The statistical principles presented here therefore apply broadly to central place foragers across terrestrial, marine, and aerial systems. Complete code for the worked example and a full description

of the methodology are provided in Appendices 2–5.

3.1 | Simulation overview

We adapted the approach of [Klappstein et al. \(2023\)](#) to build a state-switching step selection function (SSF) in which movement trajectories are simulated by coupling behaviourally informed movement decisions with dynamic responses to habitat structure. We defined the simulation domain over which habitat selection is evaluated and spatial predictions may be generated as a 2,500 km² area (50 × 50 km, discretized at 100 m resolution) in which habitat suitability follows a binary chequerboard of alternating 2.5 km squares ([Figure 3](#)). This pattern was chosen to avoid directional or distance-related bias relative to the central place and to ensure equal availability of both suitable and unsuitable habitat, allowing model performance to be evaluated without confounding effects of landscape geometry. Note that the choice of habitat patch size is only illustrative, and equivalent simulations at larger spatial scales would lead to the same conceptual conclusions. CPF simulations reflected the spatial ecology of colonial breeding seabirds, which commute repeatedly between nests on land and foraging grounds at sea ([Pirodda et al., 2018](#)). During each foraging trip, behavioural state is treated as an unobserved process that changes over time, allowing individuals to switch probabilistically between different phases of movement ([Klappstein et al., 2023](#)). Following [Michelot et al. \(2017\)](#), each CPF track comprised a sequence of four behavioural states, namely: (1) outbound travel (fast, highly directed flight away from the central place), (2) search (moderately fast travel with some degree of directional persistence), (3) active foraging (slower, non-directed, and more sinuous movement), and (4) inbound travel (fast, directed flight toward the central place) ([Figure 3](#)). Directional travel was represented as a biased correlated random walk with repulsion from the colony during outbound movement and attraction during inbound movement. Remaining behaviours were captured by correlated random walks, which provide a standard null model of directionally persistent movement often used in ecology ([Michelot et al., 2017](#)). Model parameters were chosen to align with published reports on black-legged kittiwake (*Rissa tridactyla*) movement behaviour ([O'Hanlon et al., 2024](#)). In both scenarios, candidate movement steps were drawn at each iteration from gamma and von Mises distributions (for step lengths and turning angles, respectively), and the next step was selected with probabilities weighted by

habitat covariates. Transitions between states were allowed to depend on distance to colony, time since departure from the nest, and habitat suitability, and the model was purposely parameterised so as to increase the probability of switching from outbound travel (state 1) or search (state 2) to active foraging (state 3) in suitable habitat and increase the probability of inbound travel (state 4) as time since departure grows, thereby capturing key features of CPF behaviour (Michelot et al., 2017). The parameters of the movement kernels (i.e., step length and turning angle distributions), however, remained fixed *a priori* (Appendices 2 & 4). We simulated 1,000 individuals, each with 25 complete trips ending when birds entered an inbound state and were within 1 km of the colony. To represent NCPF behaviour, we implemented a reduced model in which the inbound state was removed; this allowed trajectories to evolve without a fixed destination (i.e., with no need to return to a nest), broadly analogous to seabirds dispersing outside the breeding season. Although the formulae and parameter values governing state transitions necessarily differed in the NCPF case to accommodate the reduced state space, habitat dependence was incorporated into the behavioural transitions in both scenarios using the same underlying principles. NCPF individuals each completed a single 360-minute track. All individuals were initialised at the colony at time $t = 0$.

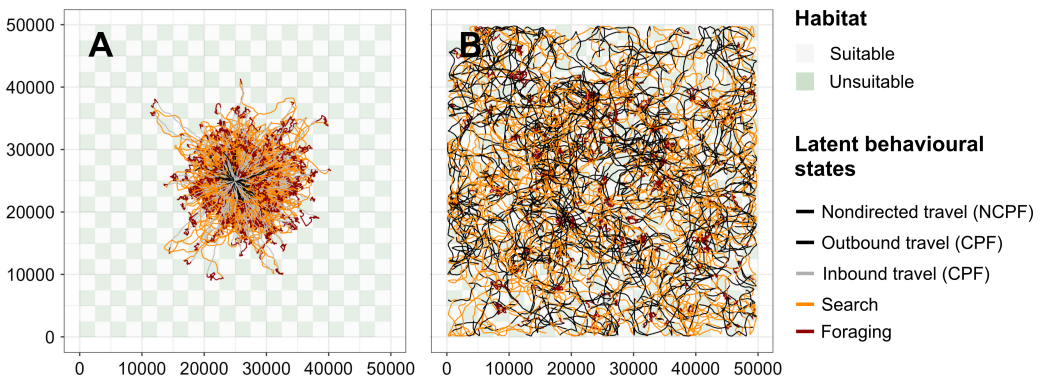


FIGURE 3 Examples of simulated movement tracks of a hypothetical species displaying either **(A)** central place foraging (CPF) behaviour (e.g., during the breeding season), and **(B)** non-central place foraging (NCPF) behaviour (e.g., outside the breeding season). In the CPF case, animals make outward trips to foraging patches but consistently navigate back to their colony at the centre of the domain ($x = 25,000$, $y = 25,000$). By contrast, NCPF animals explore their range freely with no tendency to return to a fixed site. Behavioural states for each movement type are represented using distinct colours, as indicated in the legend. Coordinates are expressed in metres (m).

To evaluate model performance across a range of scenarios, we varied the selection coefficient β from 0 (no habitat

selection) to 1.5 in 0.25 increments. An empirical measure of habitat preference (the 'observed relative selection', $\hat{\Delta}$) was then obtained by calculating the log-ratio of steps terminating in suitable *versus* unsuitable habitat (from the full population), following [Lauret et al. \(2025\)](#). Because both habitat types were equally available by design, this log-ratio provides a direct estimate of their relative intensity of use. Importantly, we randomly selected 50 individuals from the full population to mimic the limited sample sizes common in GPS tracking studies ([Hebblewhite and Haydon, 2010](#)) and to ensure that model performance could be evaluated under realistic data availability constraints. We repeated this subsampling three times using different random seeds to generate three independent datasets per simulation. We fitted the following models separately to each replicate to assess sensitivity to sampling variability: gridded Poisson regression, IPP, LGCP, STPP and mSTPP (with BM and OU movement kernels). All CPF models included distance to the colony as a covariate to account for variation in use associated with central place constraints. The only exception was the STPP (OU) model, in which attraction to the central place is already represented explicitly through the movement kernel. Note that the latent behavioural states only informed the simulation of movement; the fitted models did not condition on these states and treated all simulated locations as arising from a single underlying process. Consequently, model coefficients reflect overall patterns of space use pooled across multiple behaviours. Where relevant, we tested models on either the complete dataset (50 individuals) or a thinned dataset in which 10% of tracking locations were retained. Parameter estimates and their standard errors were extracted from model summaries, and 95% confidence intervals were calculated as $\hat{\beta} \pm 1.96 \times \text{SE}(\hat{\beta})$ assuming asymptotic normality.

3.2 | Results

In the CPF scenario, $\hat{\Delta}$ was consistently higher than the simulated habitat selection coefficient across all β values ([Figure 4](#), Appendix 6) because the habitat layer influenced both behavioural state transitions and habitat preference, meaning that $\hat{\Delta}$ reflects the combined effects of behaviour and selection rather than the selection component alone. Models that ignore movement constraints (e.g., IPP and LGCP) similarly conflate preference with movement-driven clustering, recovering only relative use rather than the underlying selection specified in the simulation. In our example, their estimates deviated systematically from the simulated parameter and aligned more closely with $\hat{\Delta}$. By contrast,

models that incorporate a movement kernel (e.g., STPP, mSTPP) are designed to separate movement behaviour from habitat preference and when the kernel approximated the movement process well, estimates were much closer to the chosen selection. Fitting the IPP and LGCP to thinned data produced nearly identical results, although with more realistic confidence intervals than the full-data IPP. This similarity likely reflects our choice of habitat pattern, with abrupt and discontinuous boundaries that are difficult for smooth Gaussian random fields to represent, unless forced to be extremely flexible. The LGCP therefore offers little advantage over the IPP in this setting. The full STPP models explicitly incorporated movement processes by conditioning on the previous location. Both BM and OU formulations produced estimates closer to the chosen parameter, demonstrating the importance of accounting for movement constraints. While the BM kernel included distance to the colony as a covariate and encouraged proximity to the central place, the OU kernel explicitly modelled colony attraction, capturing the return behaviour built into the simulated tracks. Although the STPP models yielded relatively narrow confidence intervals, this is consistent with their use of the full dataset and their explicit treatment of temporal dependence, which together support statistically efficient inference. By contrast, the narrow confidence intervals obtained from the IPP and LGCP arise from unmodelled serial dependence and therefore underestimate uncertainty. The mSTPP models also improved estimation by incorporating movement into a spatial availability surface. By including the kernel as an offset (see [Section 5](#)), these models separate habitat selection from movement-driven clustering. In these simulations, the mSTPP produced similar estimates to the gridded Poisson model, as the gridded model and the mSTPP BM model include distance to colony as a covariate and the stationary OU kernel defines a smooth spatial utilisation surface centred on the colony. As a result, both approaches capture movement-driven variation in availability in comparable ways. This equivalence reflects the simplicity of the movement structure; in more complex systems—such as those with anisotropic movement, multiple centres, or irregular space-use patterns—the mSTPP provides a more flexible and mechanistic representation of availability.

In the NCPF scenario ([Figure 4](#)), habitat selection estimates showed much smaller deviations from the simulated selection parameter. Because animals were no longer constrained to return to a central place, movement-driven clustering was weaker and $\hat{\Delta}$ reflected habitat preference more than behavioural artefacts. Although some residual difference remained, the magnitude of differences varied with the value of the habitat selection coefficient ([Appendix](#)

6), indicating that even non-central place movement can generate spatial structure that inflates empirical selection ratios. Across both types of movement behaviour, variation between random seeds arose because each seed drew a different sample of 50 individuals from the population of 1,000 simulated animals. Because individuals varied in their movement patterns, state switching, and realised habitat use (even under identical generative parameters) the subset of animals included in the fitted models influenced $\hat{\Delta}$ and the resulting estimates. Some samples contained individuals whose paths produced stronger apparent clustering or habitat use, leading to small shifts across seeds.

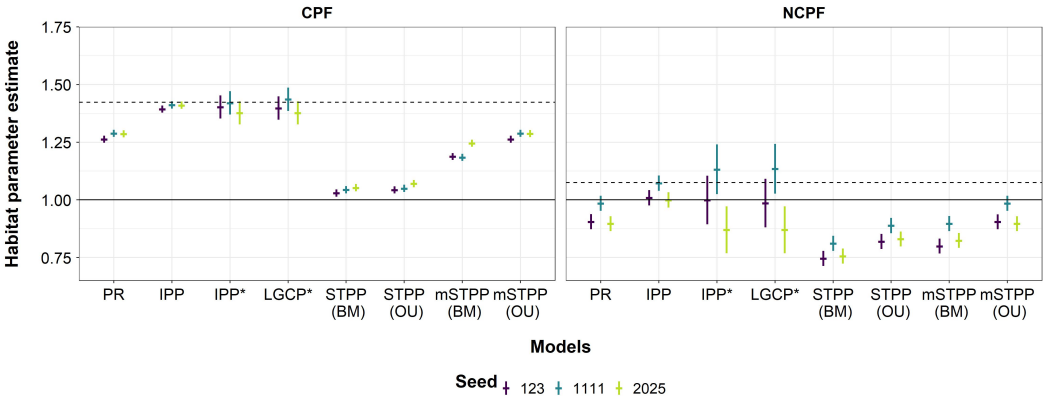


FIGURE 4 Estimates of habitat selection coefficients (horizontal bars) with associated 95% intervals (vertical bars) for both central place foragers (CPF) and non-central place foragers (NCPF). The dashed line marks the observed relative selection calculated as per [Lauret et al. \(2025\)](#) ($\hat{\Delta} = 1.42$ for CPF and $\hat{\Delta} = 1.02$ for NCPF, respectively) and the solid line shows the reference value of the underlying habitat selection coefficient (β) used to simulate the data. For illustration purposes, results are only shown for the representative case of $\beta = 1$ (but see Appendix 6 for other β values). Models fitted to thinned datasets are indicated with an asterisk. Colours denote different random seeds, each representing a distinct sample of 50 individuals drawn from the 1,000 simulated tracks. Two space–time point process variants were tested: one assuming Brownian motion (BM) and another using an Ornstein–Uhlenbeck (OU) process. See Appendices 3 and 5 for full parameterisation details and [Table 1](#) for model acronyms.

3.3 | Limitations

Our simulations provide a useful benchmark of model performance but are based on an idealised depiction of animal movement and habitat selection. As such, they rely on simplifying assumptions that should be considered when

interpreting the results. First, we simulated a static binary habitat layer (arranged as a chequerboard) with abrupt transitions between habitat types. This highly regular structure is unrepresentative of natural systems, where habitats are typically continuous, and heterogeneous. Comparisons of model performance under more realistic conditions (e.g., resource patchiness, environmental gradients, or temporal dynamics) may therefore be less clear than in our worked example. Second, the movement process used to generate tracks was deliberately simplified; the imposed behavioural states, transition rules, and movement kernels likely produce trajectories with more regular and more clearly separated movement phases than would be expected in real data, and do not explicitly capture additional drivers of seabird behaviour such as wind forcing (Thorne et al., 2023), memory (Collet et al., 2025), site/route fidelity (Regan et al., 2024), social cues (Monier, 2024), sex (Militão et al., 2023), body condition (Rishworth et al., 2014), or prey availability (Fayet et al., 2021; Legard et al., 2025). If animals exhibit weaker central place attraction or more gradual switching between behavioural states, differences among models may become less apparent. Third, we assumed that movement and selection processes were correctly specified and stationary, such that all individuals behave identically under equivalent conditions. In reality, patterns of movement and space use can vary substantially among individual seabirds, as well as between foraging trips, breeding stages, environmental conditions, and times of day (Phillips et al., 2017; O'Hanlon et al., 2024). Such variability could be accommodated by including random effects for individuals or trips in the models (e.g., Trevail et al., 2021). Initial movement directions were also generated independently of habitat, whereas in practice the bearing followed upon leaving the colony may already reflect prior knowledge, environmental cues, or habitat preferences, which could influence subsequent patterns of space use and selection. Fourth, we treated all locations as being measured without error (in line with simulation assumptions). However, in real studies, positional uncertainty can be non-negligible and may bias parameter estimates if not accounted for. Fifth, the simulated movement process did not include interactions with dynamic attractors such as fishing vessels (Pirodda et al., 2018) or conspecifics. In natural systems, animals may respond to transient features that vary in space and time, and may not follow a fixed or predictable sequence of behavioural states. We expect that incorporating this additional complexity would further blur the distinction between movement behaviour and habitat preference, making differences among models likely less pronounced. Sixth, our conclusions may depend on the temporal resolution of the tracks. Because serial dependence is particularly strong in high-resolution tracking

data, differences among models may be more or less pronounced at different sampling intervals. In this context, our simulations are best viewed as a controlled experiment that allows us to compare how models behave under plausible ecological scenarios (and imperfect modelling of behavioural processes), rather than as a full reconstruction of real-world ecological complexity.

4 | THINGS TO CONSIDER BEFORE USING THESE METHODS

Model choice should be guided by the ecological question being asked rather than statistical convenience and potential users should consider several key points before selecting a habitat selection model that is fit for their data (Figure 5).

A first consideration is the *scale of inference*. Several of the models presented in this guide (e.g., IPP, LGCP, mSTPP) lend themselves to questions about animal space use across relatively broad spatial domains, for example by describing patterns of habitat use within or across home ranges, and can generate spatial predictions that are useful for conservation decision-making (Sofaer et al., 2019). However, habitat selection can also be examined at much finer spatial and temporal resolutions, where inference is explicitly conditioned on local movement. This is the realm of SSFs and STPPs, which characterise habitat selection at the scale of successive movements by accounting for the locations that an animal could have reached from its previous position (Florko et al., 2025; Johnson et al., 2013).

Second is the *inferential goal*. Clarifying whether the objective of the analysis lies in process understanding or prediction can help determine which formulation is most appropriate. Models such as IPPs, LGCPs, or mSTPPs operate on a single spatial domain and provide a time-averaged description of space use, which is often more appropriate for spatial prediction and facilitates extrapolation of habitat relationships across a broader range of environmental conditions. In principle, these models can learn from the full range of covariates present in the study region. By contrast, STPPs retain an explicit link to the timing and sequence of observations, making them appropriate for understanding how animals respond to their immediate environment, but typically restricting inference to a narrower range of conditions encountered along movement paths. Although habitat relationships estimated at fine and broad scales may reflect different ecological processes and yield different estimates, particularly in dynamic

environments where conditions change over short timescales, the two perspectives need not be treated as mutually exclusive. For example, it may be possible to carry forward habitat relationships estimated from an STPP into an mSTPP to support broader-scale spatial prediction, although further work is needed to formalise how this could be achieved. In our experience analysing real-world tracking data from seabirds, where both inference and prediction are of primary interest, such a complementary approach could be particularly valuable. More generally, determining when and how relationships can be transferred across models, when temporal marginalisation is sufficient, when predictions can reliably be extended beyond observed movement paths, and when multi-scale hierarchical models are instead required to link individual movement decisions to broader distribution patterns remains an important area for future research (Blackwell, 2026). Controlled simulation experiments, in which the true movement and selection processes are known, could provide a useful framework for identifying these conditions.

Closely related to this is *how availability is represented*. Because habitat selection is defined relative to availability (Eq. 1), different models can yield ostensibly similar results while answering subtly different ecological questions. In practice, availability may be approximated through sampled background points (e.g., as in logistic regression), spatial discretisation (e.g., as in gridded Poisson regression), implicit domain-wide definitions (e.g., as in IPPs or LGCPs), or movement-based constraints (e.g., as in STPPs or mSTPPs) (Figure 2). Each of these formulations alters the meaning of estimated effects and the scale at which inference applies (Fieberg et al., 2021). In logistic and gridded Poisson regression, coefficients describe relative use with respect to the background sample or the gridded map of the landscape. In IPPs and LGCPs, they quantify how the intensity of use changes across continuous space and can be interpreted as effects on the expected density of locations per unit area. In STPPs and mSTPPs, coefficients describe selection conditional on movement, reflecting how habitat influences space use once accessibility constraints have been taken into account (Table 1). Critically, models based on sampled or discretised availability are not inherently inferior to point processes but instead represent a simpler way of addressing the same ecological question. In many cases, inference based on relative use is in fact sufficient, particularly when the goal is to rank habitats or estimate covariate effects rather than predict intensity of use (Avgar et al., 2017). However, as demonstrated in our worked example, choosing simplicity carries the risk of understating uncertainty and producing estimates that diverge from those obtained under a full point process formulation.

A further consideration is how different models *handle dependence in the data* (Figure 2). Traditional RSFs commonly ignore autocorrelation or attempt to reduce it by thinning the data, whereas LGCPs absorb spatial dependence via latent random fields and STPPs incorporate mechanistic dependence through an underlying movement model. These approaches are not interchangeable, and each encodes a different ecological assumption about why observations are clustered in space and time. Choosing among them requires deciding whether clustering is best understood as a property of the environment, the movement process, or both.

Finally, practical considerations such as *data volume, computational cost, and software implementation* should not be overlooked. Movement-based models can be computationally demanding, particularly when kernels must be evaluated at each time step (e.g., in an STPP), while spatial models such as LGCPs require careful specification of spatial smooths and associated parameters (e.g., basis dimension, spline type). However, many of the approaches described here can be implemented within a common modelling framework such as *mgcv* (Appendices 3 and 5), allowing users to move between formulations without adopting entirely new software.

5 | CAVEATS AND PITFALLS

Inference from habitat selection models requires careful attention to their underlying assumptions and to the ecological context in which they are applied (Fieberg et al., 2021), as no single method can fully disentangle the various processes that shape space use. A central challenge is separating selection (i.e., true preference) from availability or accessibility (i.e., constraint), because environmental conditions influence not only where animals occur but also how they move. In particular, estimating both movement and habitat effects from the same data (e.g., as in an STPP or mSTPP) can introduce confounding that is difficult to eliminate and should be acknowledged (Johnson et al., 2013; Eisaguirre et al., 2025). In practice, movement-based models that make availability explicit risk attributing a large share of the variation in space use to the movement kernel G , thereby masking, or complicating the interpretation of, habitat relationships. In our experience, this is especially likely when movement kernels are included as parametric or smooth model terms (e.g., Eisaguirre et al., 2025), as they can then dominate the likelihood

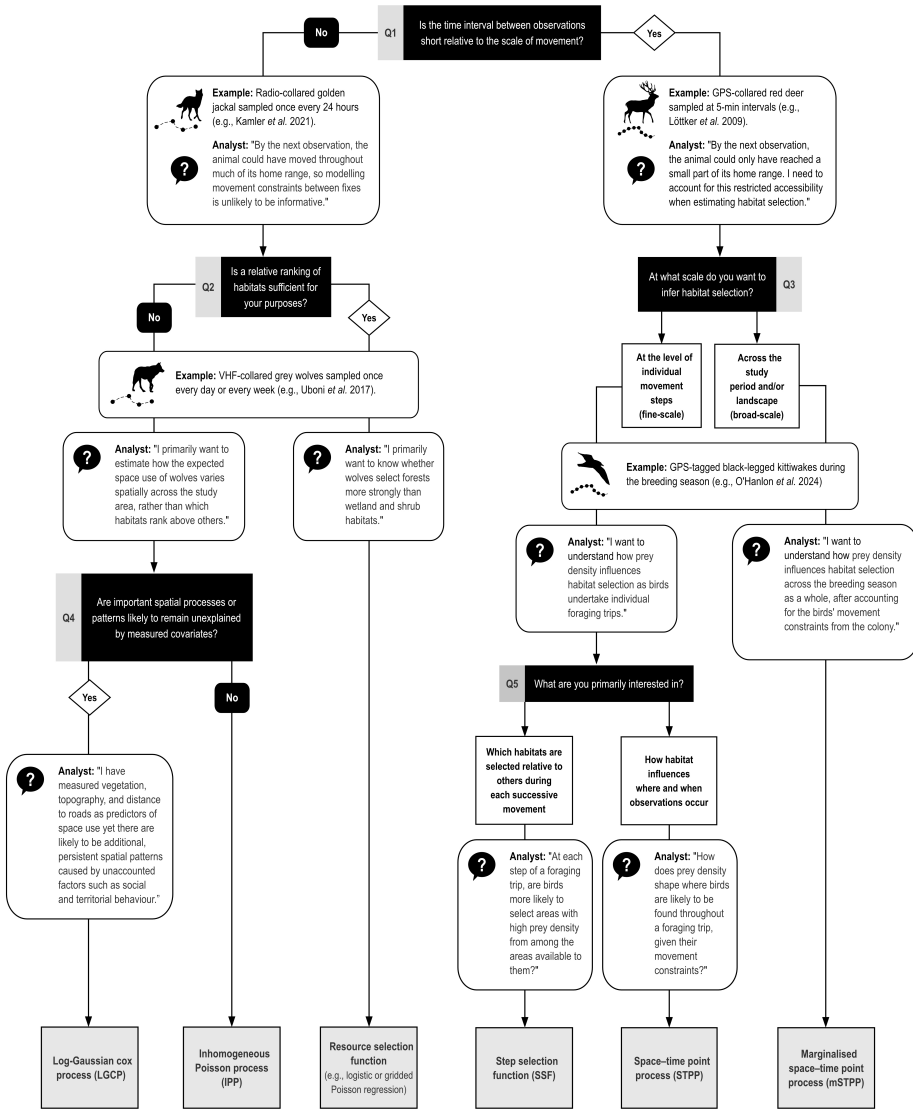


FIGURE 5 Decision framework for selecting a habitat selection model to apply to tracking data. The framework is structured around questions that relate to the temporal resolution of the data (Q1), the scale of inference (Q3), the quantity of interest (Q2 & Q5), and the need to account for unexplained spatial patterns (Q4). Branches indicate situations in which each model may be most appropriate but should not be interpreted as strict requirements for model use. Q1 asks whether animals can realistically reach most of the study area between successive observations. If observations are far apart in time, most locations may effectively be accessible and modelling movement-constrained availability may provide limited additional information. Q2 asks whether the goal of the analysis is simply to identify which habitats are preferred over others, or to predict how space use varies across the study area. Q3-Q5 distinguish between habitat selection during individual movement steps and selection at broader spatial and temporal scales, and whether the primary interest is in movement choices or patterns of space use. Q4 asks whether important drivers of space use are likely to be missing from the model, motivating the inclusion of a spatial random effect. Illustrative examples inspired by published literature (Kamler et al., 2021; Uboni et al., 2017; O'Hanlon et al., 2024; Lötter et al., 2009) are included to demonstrate the reasoning that an analyst might use when selecting among modelling approaches based on the characteristics of their tracking data, study species, and ecological questions of interest.

and absorb structure that would otherwise reflect the influence of habitat. One way to improve this separation is to treat G as an offset, fixing availability as a known component of the model rather than estimating it jointly with movement from the same locations. An alternative is to regress the kernel against the covariates and include the residuals in its place, as recommended by [Johnson et al. \(2013\)](#) and [Eisaguirre et al. \(2025\)](#). This is not a panacea, however, as availability is itself still derived from the movement data, so some degree of confounding between preference and constraint remains unavoidable. Similar challenges arise with other flexible frameworks such as LGCPs, in which spatial random fields can likewise absorb residual structure that might otherwise be attributed to environmental covariates, raising concerns about ecological interpretability. The same caution applies to using distance to the central place as a covariate to capture CPF constraints. If habitat covariates vary with distance, then a misspecification of the functional relationship between use and distance may result in biased estimates of habitat effects. In our simulations, habitat was deliberately balanced with respect to distance from the colony site, such that habitat selection estimates proved insensitive to whether that distance was represented linearly, non-linearly (e.g., as a spline), or omitted from the LGCP altogether (data not shown). However, such robustness largely reflects our choice of experimental design and should not be universally assumed in empirical applications. For instance, if suitable habitat becomes progressively more common further from the central place, habitat and distance effects may be confounded, making it important to assess whether the assumed functional form of the distance effect adequately represents the data. These issues highlight the importance of careful model checking and, wherever possible, comparison across alternative model formulations.

Model interpretation is also sensitive to the observation process. Tracking data reflect both animal behaviour and sampling design, such that the fix rate on the tag, temporal irregularity, and measurement errors can all influence the definition of availability and the strength and direction of estimated habitat relationships. In movement-based models (e.g., STPP or mSTPP), the time interval between observations directly determines the movement kernel and thus the set of locations that are considered accessible at any moment. By contrast, in discretised approximations to point processes (i.e., gridded Poisson regression), the assumption that there is negligible variation in intensity within each spatial unit may break down at coarser resolutions. In practice, the grid resolution should be sufficiently fine that parameter estimates have converged, as is standard practice when fitting discretised point process models. Once this

numerical approximation is adequate, it remains important to recognise that quantities such as intensity or the relative probability of use are inherently scale-dependent and will vary with the spatial and temporal resolution of the analysis. For example, the expected number of observations in a grid cell will increase with the size of the cell, the sampling frequency of the tag, and the duration of the study, even if the underlying ecological process giving rise to these observations remains unchanged. Critically, none of the models considered here explicitly account for non-random fix failure. If the probability of obtaining a location varies with habitat (e.g., because fixes are less likely under dense canopy), the observed pattern of space use is filtered through the detection process. The resulting estimates of habitat relationships may be biased unless that process is explicitly accounted for. Taken together, these issues mean that comparisons across studies or scales must be made with care.

A further limitation is that most habitat selection models implicitly average across different modes of behaviour, particularly when fitted to pooled location data or when availability is defined over broad spatio-temporal scales. Consequently, estimated relationships may represent a composite of multiple behavioural processes rather than a single, interpretable form of selection, which can obscure meaningful differences in habitat use across behavioural contexts (Cisneros-Araujo et al., 2025). While extensions such as behaviour-dependent models can address this (e.g., Klappstein et al., 2023), they are more complex and challenging to implement and generally require additional assumptions about behavioural states and their transitions, as well as sufficient data to estimate state-specific relationships. Estimates of selection coefficients should therefore be interpreted as aggregate responses across behavioural contexts, unless explicitly structured otherwise.

Finally, the extent to which model results generalise beyond observed conditions largely depends on how availability is defined (Figure 2). Models formulated over a fixed spatial domain (e.g., IPPs, LGCPs, or mSTPPs) can, in principle, support broader spatial prediction, whereas movement-based models that condition availability on realised paths tend to be more tightly linked to the range of conditions experienced by the animal. Predictions – especially those involving extrapolation to new environments, times, or behavioural contexts – should therefore be considered with appropriate caution.

6 | TOOLS

All models reviewed herein can be implemented using standard statistical software, most commonly within the R programming environment. In our worked example (Appendices 2–5), we rely exclusively on the *mgcv* R package (Wood, 2017) as it provides a flexible and popular framework for model fitting in ecological research, with a user-friendly syntax that will be familiar to most readers. However, this choice is not prescriptive and in practice, any software capable of fitting models with Poisson regression or point process-type likelihoods (or equivalent likelihood approximations) can be used, including machine learning algorithms (e.g., MaxEnt, boosted regression trees) (Renner and Warton, 2013; Renner et al., 2015). Analysts seeking full Bayesian inference may also prefer integrated nested Laplace approximation (INLA; *inlabru* Rue et al., 2009; Bachl et al., 2019) or *brms*, which interfaces with *via* Stan (Bürkner, 2017). A further option is *ctmm* (Calabrese et al., 2016), which provides a dedicated framework for continuous-time movement models but can be computationally intensive for large datasets.

7 | CONCLUSION

Habitat selection modelling presents a wealth of opportunities to understand where, when, and how animals interact with their environment. Viewing existing habitat selection models as a family of related methods that differ primarily in their representation of availability—and can all be understood as alternative expressions or approximations of an IPP—provides a unified perspective on space use as a point process problem. Our aim was to synthesise these connections to help readers navigate a broad and technical body of literature and equip practitioners with a coherent guide to model choice, fitting, and interpretation in habitat selection studies. Importantly, we showed how the movement constraints imposed by repeated returns to a fixed location can create strong spatial structure that may obscure or complicate habitat relationships. Approaches that explicitly account for movement dynamics such as marginalised or full STPPs offer a principled way to capture these constraints and strengthen inference for central place foragers. Habitat selection modelling remains a rapidly evolving field, with new methodologies and software packages

emerging at an accelerated pace. Most models are developed and tested using NCPF data and, as our simulations demonstrate, many perform reasonably well in those settings. A key challenge is that the same methods can yield markedly different results when applied to CPF systems. We therefore recommend that new tools be developed for, or at least explicitly validated on, CPF data, and that existing methods be applied with appropriate caution. Future efforts to (i) link movement-based inference with spatial prediction through integrated modelling, (ii) develop improved strategies for transferring results across spatial and temporal scales, and (iii) advance computational methods will undoubtedly expand the scope and scale of questions that can be addressed using tracking data. Ensuring that these developments explicitly accommodate the unique structure of CPF movement will be essential for producing reliable ecological insight.

8 | SUPPLEMENTARY INFORMATION

All appendices accompanying this article are available at <https://peer-review-anonymous.github.io/HabitatSelection/>.

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10 | CONFLICT OF INTEREST

The authors have no conflict of interest to declare that are relevant to the content of this article.

11 | AUTHOR CONTRIBUTIONS

AC and PJB conceived the study with direct support from ELJ, KFW, and TC. AC and PJB co-wrote the initial draft and developed R code for both the simulation and model fitting, with input from TC. All authors contributed to the manuscript and gave final approval for publication.

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