RESEARCH METHODS GUIDE

Modelling habitat selection using tracking data from central place foraging species: 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 foraging species, 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 stud-

ies. Newer, more sophisticated methods have emerged to address these issues, yet most have been developed and presented in isolation, leading to a fragmented and often confusing methodological landscape that is difficult to navigate, even for experienced practitioners.

3. Here, we provide an accessible guide to modelling habitat selection at regional scales from tracking data. We purposefully focus on building conceptual understanding rather than formal mathematical detail, with 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. We hope that this paper can help readers make sense of the ecological and statistical literature while offering a practical, hands on reference for analysing tracking data in habitat

selection studies.

KEYWORDS

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

1 | INTRODUCTION

Many animals forage by making repeated trips to and from a fixed home base such as a nest or den (Orians and Pearson, 1979), a behaviour known as *central place foraging* (CPF). 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 prey capture outweigh the energetic costs of commuting (Rueffler and Lehmann, 2024). Such constraints may leave CPF species 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 nesting site 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. While 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 funnelling prey remains and waste through a focal point, CPF species 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 in CPF species essential to both forecasting population responses to global change and informing ecosystem-based management (Allen and Singh, 2016).

Animal-borne global positioning system (GPS) and Argos tags have revolutionised the study of CPF by revealing where, when, and how animals select and use habitats within their environment (Hebblewhite and Haydon, 2010). With significant advances in microelectronics and satellite infrastructure, modern instruments now allow minute- or second-level monitoring of hundreds of CPF species over days to months (Whitney, 2022; Sequeira et al., 2025). Although animal-borne telemetry provides critical insights for decision-making (Hays et al., 2019), extracting ecological insights from movement paths requires linking location estimates to environmental covariates. This is a complex task as sensors often fail in harsh conditions, fixes vary in accuracy, and battery constraints force trade-offs between sampling frequency and deployment duration. In recent years, these issues have prompted the development of statistical modelling frameworks that can extract reliable ecological signals from noisy, incomplete, or irregular tracking data (Matthiopoulos et al., 2023; Northrup et al., 2022). However, applying these models to CPF species is particularly challenging for two main reasons. First, traditional modelling frameworks such as resource selection functions (RSFs) assume that each part of the landscape is equally accessible to animals (Paton and Matthiopoulos, 2016), which is not true for CPF. Ignoring this constraint can make uninformative covariates appear spuriously important, leading to apparent preferences that are artefacts of geometry rather than true ecological selection (Benhamou and Courbin, 2023; Rosenberg and McKelvey, 1999; Alston et al., 2023). Second, tracking data are virtually always temporally autocorrelated (Noonan et al., 2019; Fleming et al., 2015), as sequential fixes capture adjacent segments of the same continuous path (Boyce et al., 2010). As such, the location of an individual at time t reflects both its preference for the resources available there and the proximity of that site to its previous position at time $t - 1$. While 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).

Model-based approaches that explicitly account for autocorrelation without sacrificing information are therefore preferable for analysing tracking data (Alston et al., 2023; Eisaguirre et al., 2025). A rich statistical toolbox – largely grounded in point process theory – now exists for inferring habitat selection from observations of animals recorded across space and time (Matthiopoulos et al., 2023). Yet the rapid pace and technical nature of methodological development in this area create barriers for practitioners without specialised training (Northrup et al., 2022), and guidance on when and how to apply different models is 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). These issues are exacerbated in studies of central place foragers, as existing papers on habitat selection modelling rarely consider the unique spatial and ecological constraints imposed by CPF behaviour. The common practice of applying a single model to empirical data also makes it difficult to assess how alternative methods may perform and whether estimated model coefficients genuinely reflect true selection (DiRenzo et al., 2023).

Here, we present a practical roadmap for modelling habitat selection in CPF species, with an emphasis on regional-scale methods most relevant to conservation and management decisions (Sofaer et al., 2019). We use the term *regional scale* to describe the level at which selection is modelled rather than the geographic extent of the study area. In this sense, regional-scale selection points to approaches that capture broad spatial patterns of behaviour without necessarily modelling the mechanics of step-by-step movement explicitly. Using seabirds as a motivating example, we evaluate how several classes of models recover known habitat selection patterns from simulated tracks, and we contrast these with non-central place foraging species. 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 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* to what is available to them (Figure 1). Just as a diner's restaurant choice depends on which venues are open and within commuting distance, an animal's habitat preference can only be inferred when multiple habitats are available but some are used more frequently than others (Manly et al., 2002). As a result, habitat selection is often conceptualised as a simple ratio:

$$\text{Selection} = \frac{\text{Use}}{\text{Availability}} \tag{1}$$

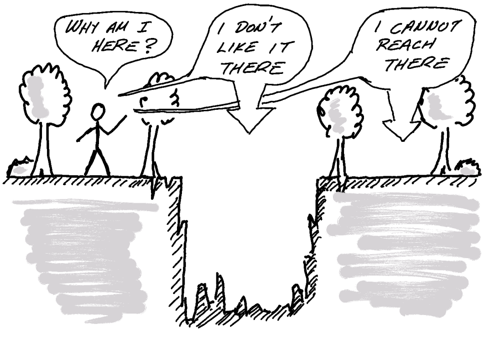

FIGURE 1 Selection can only be defined relative to availability. For example, consistent observations of animals at high elevations may suggest an influence of altitude on space use, yet this conclusion is only valid if lower elevations are also available but used less frequently. If animals never encounter these environments, 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).

where the numerator ("use") reflects locations where animals were recorded and the denominator ("availability") denotes the parts of the landscape accessible to individuals. Availability is rarely known and must therefore be approximated statistically. Early work relied on resource selection functions (RSFs), which contrast the conditions at used sites ("cases") with those at randomly sampled locations ("controls", "pseudo-absences", "quadrature", or "background points") representing available habitat (Boyce et al., 2002). Because the number of controls is chosen arbitrarily, the overall level of use cannot be determined 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:

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

Here, $w(\mathbf{x})$ quantifies the relative use of locations with habitat values $\mathbf{x}$, where $x_1, x_2, \ldots, x_k$ are each of k covariates (e.g., elevation, prey density, etc.) and $\beta_1, \beta_2, \ldots, \beta_k$ 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:

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

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

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

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:

$$\begin{aligned} y &\sim \text{Bernoulli}(p) \\ \text{logit}(p) &= \ln\left(\frac{p}{1-p}\right) = \beta_0 + \mathbf{x}^\top \boldsymbol{\beta} \end{aligned} \tag{5}$$

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 β. 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:

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

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 $\lambda_{\text{IPP}}(s)$. 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:

$$\begin{aligned} \mu_i &= \int_{A_i} \lambda_{\text{IPP}}(s) \\ \Leftrightarrow \mu_i &\approx a_i \times \lambda_{\text{IPP}}(s_i) \end{aligned} \tag{7}$$

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:

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

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

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

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,

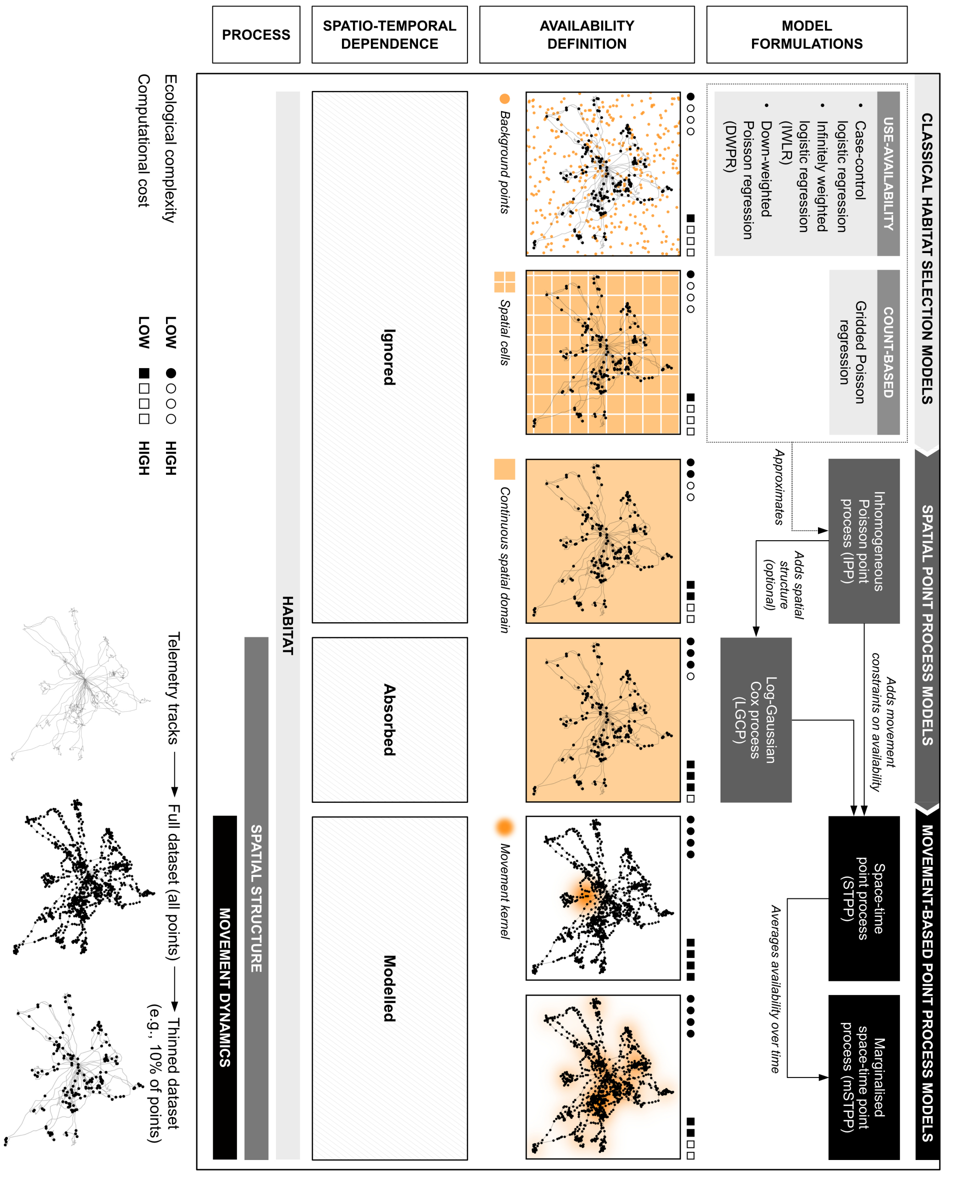

FIGURE 2 Conceptual relationships between models used to estimate habitat selection from tracking data. All models can be viewed as extensions or approximations of the inhomogeneous Poisson point process (IPP) (Table 1). Orange shading indicates how each model represents availability (Table 1) relative to the data used for model fitting; earlier models rely on data thinning to reduce autocorrelation, whereas movement-based models utilise the full tracking record.

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 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 (Moller and Waagepetersen, 2003):

$$\lambda(s) = \lambda_{\mathrm{IPP}}(s) \times \exp u(s) \tag{10}$$

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

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

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), whereby distant habitats appear underused simply because they were never reachable (i.e., false avoidance) and those near the animal's path 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., 2021), which creates a circularity in which movement shapes exposure to habitats, yet habitat preferences also influence movement. *Space-time point process* models (STPPs) attempt to address this by defining 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

TABLE 1 Comparison of modelling frameworks used to estimate habitat selection from animal location data.

Model	Data type	Likelihood	Model output (interpretation)	Availability representation	Key assumptions	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	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 very 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	Warton and Shepherd (2010), Renner et al. (2015)
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 and random field	Illian and Burslem (2017)
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	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	Eisaguirre et al. (2025)

interval itself (i.e., length, start and end positions) and the animal's movement behaviour. As such, STPPs extend the IPP to vary over both space *and* time (Johnson et al., 2013). For tracking data, the STPP intensity can be expressed as the product of a habitat selection term and a movement-based availability function:

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

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 $G(s \mid s_{t-1}, \Delta_t; \boldsymbol{\theta})$ describes the set of locations that were accessible at time t, given the time interval Δ_t elapsed since the last observation, the animal's previous location s_{t-1}, and its movements ($\boldsymbol{\theta}$). In other words, the function G (known as the movement "kernel", Figure 2) indicates where an animal could plausibly be given how much time it had to travel and how it moves. On the log scale:

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

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 movement models can be used to derive G, including Brownian motion (e.g., Johnson et al., 2013), ecological diffusion (e.g., Michelot et al., 2019) and Ornstein–Uhlenbeck (OU) models (e.g., Johnson et al., 2008; Eisaguirre et al., 2025). 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 the 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). Irrespective of the model used, the STPP framework links each location to the environmental conditions prevailing at the time of observation, enabling fine-scale analyses of space use in dynamic systems. However, these benefits come with substantial computational costs because G must be evaluated at every time step, which is particularly onerous with large datasets. Additionally, inference from an STPP is restricted to the subset of environmental conditions encountered during tracking, which may limit transferability to new areas or time periods (Eisaguirre et al., 2025).

One way to overcome these limitations is to average habitat selection over time so that inference reflects all the locations an animal could have used rather than only those tied to specific observation times. *Marginalised space-time point process models* (mSTPPs) implement this idea by integrating the movement process across the entire tracking record to produce a single availability surface describing where an animal could plausibly have been during the study period. This surface underpins spatial predictions of habitat use that account for movement constraints (Eisaguirre et al., 2025), and is constructed by summing the time-specific movement kernels in Eq. 13 across all time intervals:

$$\begin{aligned} \lambda &= \lambda_{\mathrm{IPP}} \times G^*(s;\boldsymbol{\theta}) \\ \Leftrightarrow \log \lambda(s) &= \beta_0 + \mathbf{x}(s)^\top \boldsymbol{\beta} + \log G^*(s;\boldsymbol{\theta}) \end{aligned} \tag{14}$$

where

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

Marginalising over time 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.

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 & 8 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 each model to simulated tracking data generated under controlled conditions. Our aim is to compare how different representations of availability and movement influence estimates of habitat selection. By contrasting CPF and non-central place foraging (NCPF) scenarios, we show how model structure interacts with movement constraints to shape ecological inference. Models that treat availability independently of movement produce selection estimates that consistently diverge from those obtained under a full point process formulation. 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. The simulation domain was a 2,500 km^2 area (50 × 50 km) discretized at 100 m resolution. Habitat suitability followed a binary chequerboard of alternating 2.5 km squares (Figure 3), ensuring equal availability of suitable and unsuitable habitat and avoiding directional or distance-related bias. CPF simulations reflected the spatial ecology of colonial breeding seabirds, which commute repeatedly between nests on land and foraging grounds at sea. Following Michelot et al. (2017), each CPF track comprised four behavioural states: (1) outbound travel, (2) search, (3) foraging, and (4) inbound travel (Figure 3). Parameters were chosen to align with published reports of black-legged kittiwake (*Rissa tridactyla*) movement behaviour (O'Hanlon et al., 2024). 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 removed the inbound state; this allowed trajectories to evolve without a fixed destination, analogous to seabirds dispersing outside the breeding season. In this scenario, each individual completed a single 360-minute track.

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

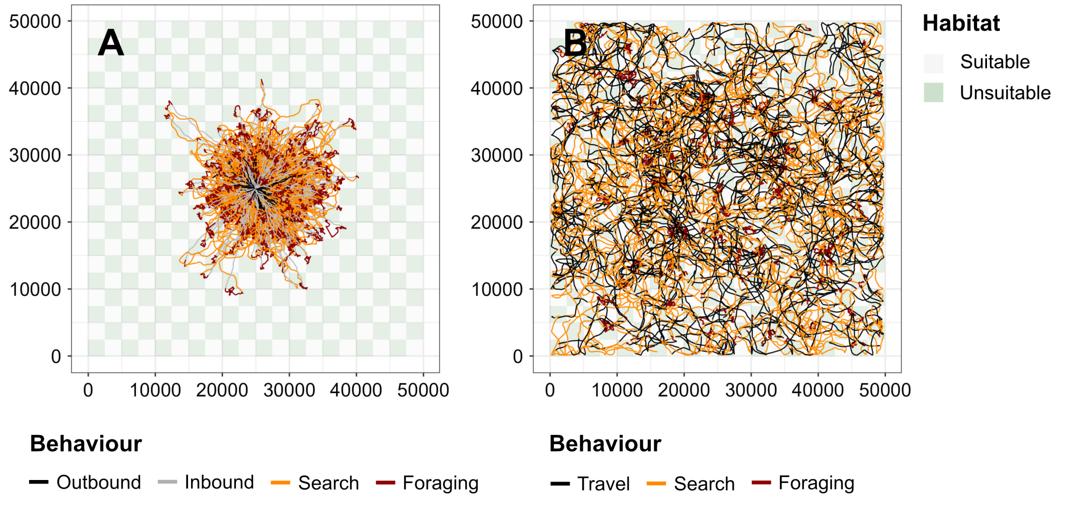

FIGURE 3 Examples of simulated movement tracks. CPF animals **(A)** make outward trips to foraging grounds but consistently navigate back to their colony. By contrast, NCPF animals **(B)** explore the landscape freely and exhibit no tendency to return to a fixed site. Behavioural states for each movement type are represented using distinct colours.

selection) to 1.5 in 0.25 increments. An empirical measure of habitat preference was then obtained by calculating the log-ratio $\hat{\Delta}$ 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). 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 $\hat{\beta} \pm 1.96 \times \mathrm{SE}(\hat{\beta})$ assuming asymptotic normality.

3.2 | Results

In the CPF scenario, $\hat{\Delta}$ was consistently higher than the simulated habitat selection coefficient (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 true 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 marginal STPP (mSTPP) models also improved estimation by incorporating movement into a spatial availability surface. By including the kernel as an offset, 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 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.

3.3 | Limitations

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

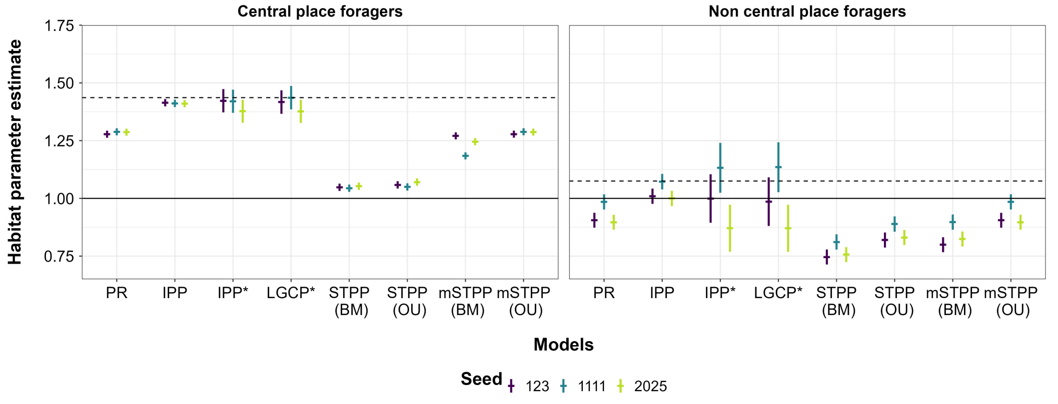

FIGURE 4 Estimates of habitat selection coefficients (horizontal bars) with 95% intervals (vertical bars) for central place and non-central place foragers. The dashed line marks the observed relative selection following Lauret et al. (2025) ($\hat{\Delta} = 1.42$ and $\hat{\Delta} = 1.02$ respectively), and the solid line shows the habitat selection parameter $\beta = 1$ used in the simulations (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.

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 it is not accounted for. Fifth, the simulated movement process did not include interactions with dynamic attractors such as fishing vessels (Pirotta 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 (Pirotta et al., 2018). We expect that incorporating this additional complexity 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 and the spatial grain of the habitat field. 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 way 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

A first consideration is the *scale of inference*. In this guide, we focus on models that estimate patterns of space use at a broader behavioural scale, which we refer to as *regional-scale* selection. These approaches describe how animals use space across larger spatial domains (i.e., often corresponding to second-order selection at the home-range level), and are well suited to inform conservation decision-making (Sofaer et al., 2019). However, habitat selection can also be examined at finer spatial and temporal resolutions, where inference is explicitly conditioned on local behaviour (i.e., third- or fourth-order selection); this is the realm of step-selection functions (SSFs), which model the choices animals make between successive locations (Florko et al., 2025). In brief, SSFs quantify how animals choose where to go next by comparing observed steps to a set of potential alternatives. In this sense, they define availability at each time step in a similar way as STPPs do, but the two approaches differ fundamentally in how this availability is constructed. In SSFs, availability is approximated by generating candidate steps from empirical distributions of step lengths and turning angles, which are typically estimated from the data. These represent locations that could be plausibly reached from the previous position, and inference is based on comparing observed steps to this finite set only. By contrast, STPPs define availability through a continuous movement kernel derived from an explicit movement model (e.g., a Brownian motion or an Ornstein–Uhlenbeck process; Appendices 3 and 5). This kernel specifies a probability density over all locations that could be reached within a given time interval, rather than a finite number of alternatives. As a result, STPPs treat availability as a continuous surface that can be evaluated across the entire spatial domain (therefore supporting regional-scale inference), with the movement kernel determining how strongly different locations contribute to availability at each time step. In practice, the STPP kernel rapidly down-weights distant locations and is therefore approximated locally for computational reasons (*via* local quadrature; see Appendices 3 and 5). However, the intensity surface is still defined over the full spatial domain and not restricted to a discrete set of points. For this reason, increasing the number of available points in an SSF only improves the numerical approximation of its likelihood, but does not cause the SSF to converge to an STPP. While outside the scope of this paper, SSFs play an important role in ecology and conservation (Thurfjell et al., 2014), and are the subject of a substantial body of literature. We direct interested readers to Forester et al. (2009), (Fieberg et al., 2021), Signer et al. (2017), Florko et al. (2025), or (Michelot et al., 2024) for further details.

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 well suited to understanding how animals respond to their immediate environment, but typically restrict inference to a narrower range of conditions encountered along movement paths. This need not be viewed as a strict trade-off; for example, it may be possible to carry forward the habitat relationships estimated from an STPP into an mSTPP to support spatial prediction, although further work is needed to formalise how this can 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.

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. 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 to produce spatially explicit predictions. 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 that of 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 lead to confounding and a degree of circularity that is difficult to eliminate and should be acknowledged. In practice, movement-based models that make availability explicit risk attributing a large share of the variation in space use to the movement component, thereby masking weaker habitat relationships. This is especially likely when movement kernels are included as parametric or smooth model terms (e.g., Eisaguirre et al., 2025) as they can dominate the likelihood and absorb structure that might otherwise reflect the influence of habitat. Treating the movement kernel as an offset is often preferable as it fixes availability as a known component of the model and helps separate it from selection. However, this does not fully resolve the issue as availability is itself derived from the same movement data, meaning that some degree of confounding between preference and constraint is unavoidable. Similar challenges arise when using other flexible modelling frameworks such as LGCPs, in which spatial random fields can absorb residual structure that might otherwise be attributed to environmental covariates, thereby raising concerns about identifiability and ecological interpretability. These issues highlight the importance of careful model checking and, wherever possible, comparison across alternative model formulations.

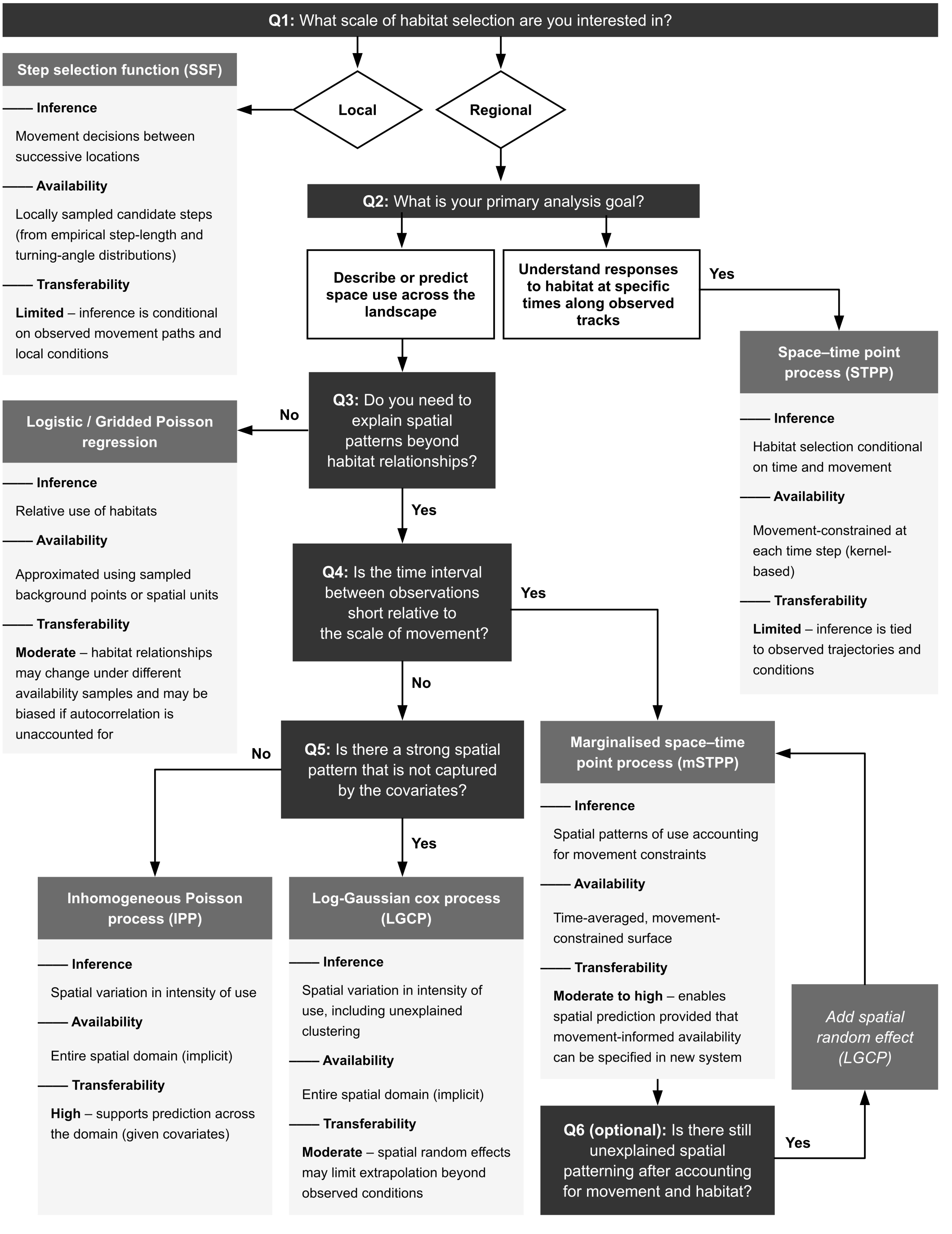

FIGURE 5 Decision tree for selecting a habitat selection model to apply to tracking data. The flowchart is structured around key questions that respectively address (Q1) the spatial scale of inference (i.e., local movement decisions vs. regional patterns of space use), (Q2) the temporal scale of inference (i.e., time-specific vs. time-aggregated), (Q3) the scope of inference beyond habitat effects, (Q4) movement constraints on availability (Q4), and residual spatial structure (Q5).

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. More generally, estimated quantities such as the intensity or the relative probability of use are 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. As a result, 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 5). 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* package (Wood, 2017), which provides a flexible and popular framework for model fitting in ecological research, with a user-friendly syntax that will be familiar to most readers. This choice is not prescriptive; analysts seeking full Bayesian inference may prefer integrated nested Laplace approximation (INLA; Rue et al., 2009) 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. By re-framing existing methods as a family of related models that differ primarily in their representation of availability and can all be understood as alternative expressions or approximations of an IPP, we can turn what has long been a confusing and disparate field into a unified perspective on space use as a point process problem. Viewing habitat selection models through the IPP lens helps to clarify underlying assumptions and reveal connections among algorithms, providing ecologists with a coherent guide to model choice, fitting, and interpretation. Importantly, we have shown 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 foraging species. Habitat selection modelling remains a rapidly evolving field, with new methodologies and software packages emerging at an accelerating 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 species, 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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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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