State-space models and inference approaches for aquatic animal tracking with passive acoustic telemetry and biologging sensors

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Abstract

1. Passive acoustic telemetry systems are widely deployed to track animals in aquatic environments. However, investments in integrative methods of data analysis have remained comparatively limited, with current workflows typically considering individual movements separately from space use, home ranges and residency.
2. This review presents a unifying perspective that bridges this divide. We argue that the core of animal-tracking analyses lies in the estimation of individual locations based on probabilistic principles. We formalise a generic state-space model for individual movements and a set of targets for statistical inference, unifying existing literature in a common framework. We critically assess inference algorithms and connect model-based inference to downstream ecological analyses of individual centres of activity, occurrence, residency, home ranges, habitat selection and behaviour.
3. We provide guidance to practitioners on model formulation, algorithm choice and software suitability in different contexts and identify key avenues for future research.
4. This review provides a roadmap for integrative data analysis in passive acoustic telemetry systems that should support research into the ecology and conservation of many aquatic species.

Keywords

behaviour, biologging, biotelemetry, data integration, hidden Markov model, Markov chain, Monte Carlo, movement ecology

1. Introduction

Passive acoustic telemetry is one of the most widely used technologies for animal tracking in aquatic environments (Hussey et al., 2015; Matley et al., 2022). This technology uses receiver arrays to detect individual-specific acoustic transmissions from tagged animals. Receiver arrays have been deployed in freshwater, coastal and marine environments and expanded from local to continental scales (Abecasis et al., 2018; Iverson et al., 2018). The data accumulating in these systems contain information on the movements of a wide range of species (Lennox et al., 2024), but require the application of appropriate statistical methods for analysis (Whoriskey et al., 2019).

Two broad approaches have emerged for the analysis of passive acoustic telemetry data. One approach is to analyse discrete detection events directly (Whoriskey et al., 2019). This approach encompasses models of detection (‘residency’) metrics (such as detection counts) in relation to environmental variables (Lavender et al., 2021b), survival analyses (Martins et al., 2013), network analyses (Lédée et al., 2015) and mark-recapture studies (Moore et al., 2015). These analyses shed light on habitat use around receivers, event timing, connectivity and demographic processes.

The second approach considers ‘spatially continuous data’ (estimated positions) rather than discrete detection events (Whoriskey et al., 2019). This approach is broadly concerned with mapping space use. Heuristic methods that interpolate positions using tuning parameters, without uncertainty quantification, are typically used for this purpose (Kraft et al., 2023; Lavender et al., 2023). Examples include the mean-position algorithm, which estimates individual ‘centres of activity’ (COAs) as detection-location averages over sequential time intervals (Simpfendorfer et al., 2002), and the Refined Shortest Path (RSP) algorithm, which interpolates positions (and user-defined errors) along the shortest paths between receivers (Niella et al., 2020). Post-hoc smoothing (e.g. kernel density estimation) is used to map space use (Udyawer et al., 2018). These approaches are useful but have limitations. The central issue is that heuristic methods do not represent the movement or (imperfect) detection processes that generate observations. It is also difficult to integrate additional observations (such as depth measurements) alongside detections to refine analyses. This can lead to variable performance and maps of space use that lack a clear biological interpretation or uncertainty quantification (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a; Winton et al., 2018). It is therefore unsurprising that most reviews highlight the importance of further methodological development (Jacoby & Piper, 2023; Matley et al., 2022).

Recent studies have synthesised available methods in tables or decision trees to guide analyses (Jacoby & Piper, 2023; Kraft et al., 2023; Whoriskey et al., 2019). These structures link research questions to existing methodologies but draw distinctions between analyses of movements (e.g., network analysis), space use (e.g., kernel smoothing) and residency (e.g., residency metrics). Fundamentally, these analyses all examine aspects of an underlying animal movement process that is imperfectly observed.

This review presents a unifying perspective that bridges the divide between movement, space-use and residency analyses in passive acoustic telemetry systems. We consider an animal's underlying movement process and the observation processes that connect movements to observations (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a). In a passive acoustic telemetry system, observations principally comprise detections, when tagged animals move within receiver detection ranges, and non-detections (Kessel et al., 2014). Ancillary observations, such as depth measurements, may be also recorded by animal-borne sensors at regular or irregular intervals (Matley et al., 2023). These observations provide an imperfect ‘glimpse’ into the underlying behavioural/movement process that generates emergent ecological patterns.

State-space models (SSMs) provide a natural representation of such a system (Patterson et al., 2008). These models represent how the underlying (‘latent’) state (location) of a tagged individual evolves through time, conditional on the observations. The ‘state’ contains the individual’s location, but may also include other variables of interest, such as behaviour. The primary objective of model-based inference (or ‘model fitting’) is to use the observations to infer the latent states. We argue that probabilistic estimates of these states that correctly represent uncertainty should lie at the heart of animal-tracking analyses. These estimates will strengthen studies of movement patterns (Lavender et al., 2021b), space use (Udyawer et al., 2018), residency (Futia et al., 2024), habitat selection (Griffin et al., 2021) and behaviour (Niella et al., 2020).

SSMs are widely used for animal tracking (Auger-Méthé et al., 2021) but in passive acoustic telemetry systems their unifying role has been underappreciated and only a handful of studies have explored the approach (Alós et al., 2016; Hostetter & Royle, 2020; Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025; Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a; Pedersen & Weng, 2013). One reason for this is that inference of the latent states (and characteristics of the movement or observation processes) can be challenging (Auger-Méthé et al., 2016).

Model-based inference for passive acoustic telemetry and biologging sensors is the focus of this review. Our aspiration is to complement recent reviews of passive acoustic telemetry (Jacoby & Piper, 2023; Matley et al., 2022, 2023) and data analysis (Kraft et al., 2023; Whoriskey et al., 2019) with a reflective treatment of model-based inference that links to the wider animal-tracking literature where appropriate. We formalise a generic SSM for individual states (§2) and the inference problem (§3); assess inference algorithms, including those we have seen used and those in development that seem most promising (§4); connect model-based inference to downstream ecological analyses (§5); provide practical guidance (§6); and identify future research avenues (§7). For more generic SSM treatments, see Jonsen et al. (2013), Auger-Méthé et al. (2021) and Newman et al. (2023). For a broader list of available software (focusing on the `R` programming language), see Joo et al. (2020). In acoustic telemetry systems, we still see a role for analyses of detection metrics, network analysis and heuristic space-use analyses. These methods can be straightforward to apply and provide useful descriptive summaries of detection data when uncertainty quantification is not required (Kraft et al., 2023). Approaches such as survival analysis will also continue to play a role (Martins et al., 2013). But by presenting a unified statistical framework, we hope to encourage the adoption of SSMs and support the community to develop integrative data analyses. This review should support research in animal tracking across the globe.

2. State-space model

We begin by formalising a generic SSM that represents how the state ($\boldsymbol{s}$) of a tagged individual (typically its location) evolves through time (t) conditional on our observations ($\boldsymbol{y}$). If we think about the evolution of the state in discrete time (where $t = 1, 2, \dots, T$), we can represent the system with the joint probability distribution $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$ of all states ($\boldsymbol{s}_{1:T}$) and parameters

($\boldsymbol{\theta}$), given all observations ($\boldsymbol{y}_{1:T}$). (We focus on discrete-time models here, but for an entry into the continuous-time literature, see Auger-Méthé et al. (2021).) Applying Bayes Theorem allows us to represent the joint (posterior) distribution in terms of an underlying movement process $f(\boldsymbol{s}_{1:T} \mid \boldsymbol{\theta})$, an observation process (the likelihood) that links movements to observations $f(\boldsymbol{y}_{1:T} \mid \boldsymbol{s}_{1:T}, \boldsymbol{\theta})$, and our prior knowledge of the movement and observation model parameters $f(\boldsymbol{\theta})$:

$$f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T}) \propto f(\boldsymbol{s}_{1:T} \mid \boldsymbol{\theta})\, f(\boldsymbol{y}_{1:T} \mid \boldsymbol{s}_{1:T}, \boldsymbol{\theta})\, f(\boldsymbol{\theta}). \qquad \text{eqn 1}$$

The SSM can be applied to different species by tailoring the movement and observation processes (Fig. 1). Model formulation should be informed by available information, domain knowledge and literature.

As an illustration of this model formulation, consider the following example with simple assumptions. We illustrate a first-order Markovian random walk for the movement process,

$$f(\boldsymbol{s}_{1:T} \mid \boldsymbol{\theta}) = f(\boldsymbol{s}_{t=1} \mid \boldsymbol{\theta}) \prod_{t=2}^{T} f(\boldsymbol{s}_t \mid \boldsymbol{s}_{t-1}, \boldsymbol{\theta}), \qquad \text{eqn 2}$$

in which an individual's location is normally distributed around its previous location:

$$f(\boldsymbol{s}_t \mid \boldsymbol{s}_{t-1}, \sigma) = N(\boldsymbol{s}_t;\ \boldsymbol{s}_{t-1}, \sigma^2 \boldsymbol{I}). \qquad \text{eqn 3}$$

Assuming independence between observations, we formulate the observation process as

$$f(\boldsymbol{y}_{1:T} \mid \boldsymbol{s}_{1:T}, \boldsymbol{\theta}) = \prod_{t=1}^{T} f(\boldsymbol{y}_t \mid \boldsymbol{s}_t, \boldsymbol{\theta}). \qquad \text{eqn 4}$$

In a passive acoustic telemetry system, we model the likelihood $f(\boldsymbol{y}_t \mid \boldsymbol{s}_t, \boldsymbol{\theta})$ for acoustic observations $\left(\boldsymbol{y}_t^{(A)}\right)$, which comprise detections $\left(y_{t,k}^{(A)} = 1\right)$ or non-detections $\left(y_{t,k}^{(A)} = 0\right)$ at receivers (k), using a Bernoulli distribution. We then model the probability of a detection as some function (g) of the distance between the location of the individual ($\boldsymbol{s}_t$) and the receiver ($\boldsymbol{r}_k$); that is,

$$f\left(\boldsymbol{y}_t^{(A)} \mid \boldsymbol{s}_t, \boldsymbol{\theta}\right) = \prod_k f\left(y_{t,k}^{(A)} \mid \boldsymbol{s}_t, \boldsymbol{\theta}\right), \qquad \text{eqn 5}$$

where

$$f\left(y_{t,k}^{(A)} \mid \boldsymbol{s}_t, \boldsymbol{\theta}\right) = \text{Bernoulli}\left(p_{t,k}(\boldsymbol{s}_t, \boldsymbol{\theta})\right) \qquad \text{eqn 6}$$

and

$$p_{t,k}(\boldsymbol{s}_t, \boldsymbol{\theta}) = g(\text{distance}(\boldsymbol{s}_t, \boldsymbol{r}_k), \boldsymbol{\theta}). \qquad \text{eqn 7}$$

Other observations can be incorporated in a similar way via additional observation models. By performing inference for this model, we can estimate the latent states alongside properties of the movement and observation processes.

3. Inference targets

To perform model-based inference for eqn 1, we can consider a selection of possible target distributions, depending on our requirements, expertise and computational resources (Table 1). The main choice is whether to perform inference for the marginal or joint distributions of the individual's states (i.e., $\boldsymbol{s}_t$ or $\boldsymbol{s}_{1:T}$). Inference of the marginal distributions is the simpler option. These distributions provide a 'snapshot' (map) of the individual's possible states $\boldsymbol{s}_t$ at each time step, but do not encode how sequential snapshots are connected into trajectories (i.e., the most likely movements may not be those between sequential high probability regions, if those regions are far apart). Joint distributions of all states $\boldsymbol{s}_{1:T}$ represent plausible trajectories. In both cases, static parameters (in the movement or observation models) may be given or estimated (with increased computational cost). Different target distributions map loosely onto different inference algorithms (§4) and are suitable for different downstream ecological analyses (§5).

4. Inference algorithms

4.1. Filtering algorithms

4.1.1. Overview

Filtering algorithms are recursive methods that infer an individual's state ($\boldsymbol{s}_t$) at each time step (t) given the observations ($\boldsymbol{y}_{1:t}$) up to that time (Doucet & Johansen, 2009). That is, filtering algorithms generally consider the partial marginal distribution $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:t}, \boldsymbol{\theta})$ rather than the joint distribution $f(\boldsymbol{s}_{1:T} \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$. The general procedure involves a recursive representation of the partial marginal

$$f(\boldsymbol{s}_t | \boldsymbol{y}_{1:t}, \boldsymbol{\theta}) \propto \int f(\boldsymbol{s}_{t-1} | \boldsymbol{y}_{1:t-1}, \boldsymbol{\theta}) \, f(\boldsymbol{s}_t \mid \boldsymbol{s}_{t-1}, \boldsymbol{\theta}) \, d\boldsymbol{s}_{t-1} \, f(\boldsymbol{y}_t \mid \boldsymbol{s}_t, \boldsymbol{\theta}) \qquad \text{eqn 8}$$

in which the distribution for one time step $f(\boldsymbol{s}_{1:t-1} \mid \boldsymbol{y}_{1:t-1}, \boldsymbol{\theta})$ is projected forwards in time in line with a movement process $f(\boldsymbol{s}_t \mid \boldsymbol{s}_{t-1}, \boldsymbol{\theta})$ and then updated by the data $f(\boldsymbol{y}_t \mid \boldsymbol{s}_t, \boldsymbol{\theta})$. These two steps are sometimes termed the 'prediction' and 'update' steps (Thygesen et al., 2009). Inference focuses on the states, but by calculating the likelihood of the observations it is also possible to estimate $\boldsymbol{\theta}$ via maximum likelihood or Bayesian inference over multiple filter runs (Brockwell & Davis, 1987; Kantas et al., 2009). Subsequent smoothing algorithms can be used to infer the full marginal distribution $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$ of the individual's state ($\boldsymbol{s}_t$) given all observations ($\boldsymbol{y}_{1:T}$). Filtering and smoothing algorithms generate probabilistic maps (snapshots) of an individual's possible locations at sequential time points, but not trajectories. Sampling trajectories is also possible, but expensive (Doucet & Johansen, 2009).

4.1.2. Kalman filtering

The Kalman filter is an efficient filtering algorithm that is applicable to linear systems with Gaussian errors (Kalman, 1960). The vanilla Kalman filter requires a Gaussian movement model, in which the transition from one state to another is described by a linear function. The observations are assumed to follow a Gaussian distribution with a mean that depends linearly on the state. However, developments have been proposed that relax these assumptions (Fasano et al., 2021; Katzfuss et al., 2020).

In animal-tracking studies, the Kalman filter is typically applied in contexts in which the observations comprise noisy location measurements. Example applications include processing Argos satellite telemetry data (McClintock et al., 2015) and light-level geolocation (Sibert et al., 2003). The Kalman filter has also been tailored for applications in fine-scale positioning systems, via software such as `animalEKF` (Ackerman, 2018) and `kaltoa` (Campbell, 2024).

Kalman filtering has attracted limited attention in passive acoustic telemetry systems. The requirement for a Gaussian likelihood function is not directly compatible with binary (detection, non-detection) observations. A simple fix is to consider the receiver positions at which an individual was detected as our observations and ignore non-detections. Providing we assume a Gaussian movement model and Gaussian uncertainty in an individual's position around the receiver, the vanilla Kalman filter is a suitable choice for state inference. However, extensions that use binary observations directly are preferable (Fasano et al., 2021).

The Kalman filter trades computational efficiency for flexibility. The filter is efficient because the update equations can be solved analytically. However, the restrictions on the movement and observation models limit applications in some settings. Problematic cases include coastal environments, where animal distributions are truncated by land (Pedersen et al., 2011), as well as integrative modelling studies that combine acoustic and depth datasets in complex bathymetric landscapes to refine inferences (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a). These contexts require more flexible filtering algorithms.

4.1.3. Particle filtering

Particle filters are Bayesian sequential Monte Carlo algorithms that approximate $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:t}, \boldsymbol{\theta})$ with a set of 'particles' (Doucet & Johansen, 2009). These algorithms are a sensible initial choice for state inference in most real-world passive acoustic telemetry systems, given their flexibility and accessibility. The inference process involves a Monte Carlo simulation of N weighted particles, which represent candidate states for an individual. In a classic particle filter, a movement model simulates particle movement from one time step to the next and an observation model weights particles in line with their compatibility with the data. (Both models are customisable.) By periodically resampling particles in line with the weights, some particles are eliminated or duplicated such that the collection of particles at each time step approximate the partial marginal $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:t}, \boldsymbol{\theta})$. Smoothing and sampling routines then effectively re-weight particles to approximate the full marginal distribution $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$ or sample trajectories.

Generic packages that implement particle algorithms in `R` include `pomp` (King et al., 2016) and `nimble` (de Valpine et al., 2017). The packages `patter` (for `R`) and `Patter.jl` (for `Julia`) provide filtering and smoothing routines for animal-tracking datasets (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025b). These packages support customisable movement and observation models and automatic truncation of individual movements to account for barriers. Particles can be summarised to compute maps of space use and residency over desired time intervals. In a simulation study, Lavender et al. (2025a) showed that particle algorithms produced improved maps of space use compared to heuristic methods and coupling filtering with smoothing was beneficial, especially in sparse arrays. For a real-world analysis, see Lavender et al. (2025c), who analysed acoustic and archival (depth) data collected from flapper skate (*D. intermedius*) over a period of 14 months. That study inferred individual states using a behavioural switching correlated random walk model and observational models derived from prior research (Lavender et al., 2021b, 2021a). `Python` routines for particle filtering have also been developed for animal tracking (Liu et al., 2019).

Particle algorithms have strengths and weaknesses. The key strength is the flexibility with which we can tailor the movement and observation models, leveraging prior information, domain expertise and literature (Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025; Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a). Particle filtering algorithms can also be relatively fast, although smoothing is generally more expensive (Doucet & Johansen, 2009). In illustrative examples using `patter`, Lavender et al. (2025b) report filtering and smoothing times of 5–32 minutes for one month of acoustic and depth time series (21,960 two-minute time steps). In a real-world analysis involving hundreds of thousands of particles, we recorded computation times under two hours for comparable time series (Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025).

There are two main disadvantages. The first is that joint estimation of the latent states alongside static parameters can be expensive. The `patter` package therefore encourages users to parameterise movement and observation models *a priori*, drawing on available datasets, domain expertise and literature, before performing inference for the latent states (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025b). In principle it is possible with `patter` to estimate static parameters (by tracking the log-likelihood of the observations given the parameters from each filter run), but multiple filters runs with different parameterisations are required to do so.

The second disadvantage is particle degeneracy (Doucet & Johansen, 2009). This occurs when a minority of particles acquire the majority of the weight, due to inadequacies in the sub-models and resampling a finite number of particles. This can lead to poor approximations or convergence failures (when all particles are incompatible with the data). Mitigating strategies include containerisation, where particle samples are restricted within ‘containers’ around relevant receivers (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a), as well as larger numbers of particles and low-variance adaptive resampling. These strategies are implemented by `patter`. Nevertheless, challenges have been reported when integrating sparse detections with depth measurements for understudied, highly mobile benthic species in labyrinthine bathymetric environments (where particles are easily killed by the depth observation model) (Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025). Inference in these situations is a hard task for sampling methods, though extensions such as gradient-based filtering may help (Maken et al., 2022).

4.1.4. Grid-based filtering

Grid-based filters discretise the study area, and compute probabilities for each grid cell directly, avoiding the degeneracy issues that affect particle filters (Pedersen et al., 2008; Thygesen et al., 2009). SSMs with discrete states are often called hidden Markov models (HMMs). Ecologists are familiar with HMMs that represent movement time series (such as individual trajectories from satellite tracking) as outcomes of a ‘hidden’ sequence of discrete behavioural states (Glennie et al., 2023; McClintock & Michelot, 2018). The idea is similar here, but the discrete states are locations on a grid. At each time step, we approximate $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:t}, \boldsymbol{\theta})$ with the probability $P_{ij,t}(\boldsymbol{y}_{1:t})$ of the individual being in each grid cell $\boldsymbol{s}_{i,j}$, with coordinates (i, j), at time t, conditional on the data $\boldsymbol{y}_{1:t}$. This is a three-step process: given an initial probability distribution for the location of the animal (initialisation), we iteratively diffuse the distribution, in line with the animal's movement behaviour (the prediction step), before weighting the resulting probabilities in each cell in line with their compatibility with the data (the update step). For certain kinds of movement models, the diffusion step can be efficiently implemented as a two-dimensional convolution process (see below). Flexibility over the observation model is maintained. As for other filtering routines, smoothing and sampling algorithms are required to approximate full marginal and joint distributions, respectively (Thygesen et al., 2009). Static parameters can be estimated via maximum likelihood or Bayesian inference.

Grid-based filtering was developed for demersal fish tracking using archival depth tags by Pedersen et al. (2008) and Thygesen et al. (2009). Those studies related tidal patterns in depth time series (observed when fish rest on the seafloor) to geographic tidal variation to estimate individual positions though time. The MatLab HMM Geolocation Toolbox was developed for this purpose (Pedersen et al., 2008). This toolbox estimates states and movement parameters. The approach has been extended for pop-up satellite archival transmitters that record day lengths (and other measurements) for light-level geolocation. The `HMMoce` `R` package was developed for this purpose (Braun et al., 2018). Few studies have leveraged the approach for passive acoustic telemetry data though (Gonse et al., 2024; Pedersen & Weng, 2013; Strøm et al., 2017). For an example, see Pedersen & Weng (2013). They used an Ornstein-Uhlenbeck process to model home range behaviour in humphead wrasse (*C. undulatus*) and estimated smoothed probability distributions and movement parameters using acoustic detections. We hope that routines in development in `Python` (Woillez, 2024) and `Julia` (Scheidegger, 2025) will encourage adoption of the approach. The `Julia` package `Wahoo.jl` implements filtering, smoothing and sampling of trajectories. As in the `patter` package, movement and observation model parameters are specified by the user, but the log-likelihood of the observations given the parameters is tracked, which enables users to estimate static parameters over multiple filter runs.

Grid-based filtering has advantages and disadvantages. An exciting advantage is the potential to leverage modern graphical processing unit (GPU) technology. Since the approach was conceptualised, there have been massive improvements in GPU technology and efficient convolution algorithms have been developed that exploit these improvements (e.g. Innes, 2018). The `Wahoo.jl` package leverages these routines to reduce computation time (Scheidegger, 2025). (There are also particle filtering routines that exploit GPU parallelisation (Liu et al., 2019), but these involve repeated data-transfers to/from the GPU, reducing efficiency.) Furthermore, as probabilities are computed directly, approximation with particles and related convergence issues are avoided, even in complex landscapes. Computational efficiency also appears to be predictable since the same computations are repeated over all pixels (unlike particle algorithms where computation time depends more on the complexity of the inference problem, which can be difficult to predict). We therefore believe this is a powerful and reliable approach for modelling studies that integrate multiple data types, especially in complicated landscapes where probability distributions are multimodal.

There are also disadvantages. As for other filters, it is possible to estimate static parameters alongside locations, but this can be expensive (Thygesen et al., 2009). There are also some requirements for the design of the movement model to allow efficient implementations via convolution, as the probability density of a movement between two states must only depend on the spatial distance between sequential states (as in a Gaussian random walk, for example). In any case, there remains a speed cost to computing probabilities in every grid cell. In 'simple' environments, we expect particle algorithms to outpace convolution algorithms; but as the number of particles required to achieve convergence increases, convolution algorithms should gain the edge. With GPU-acceleration, the tipping point may be reached sooner rather than later. However, memory and disk-space requirements remain constraints that limit grid resolution and the time resolution at which probability distributions can be recorded.

The above filtering approaches can be extended to estimate parameters and obtain samples from the joint distribution $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$ with increased computational cost. Other approaches, such as Laplace approximation and Markov Chain Monte Carlo (MCMC) algorithms, can directly target the joint distribution. These approaches make different trade-offs that we now consider.

4.2.Laplace approximation

The Laplace approximation is an efficient option for joint inference of trajectories and static parameters (Kristensen et al., 2016). This approach considers the marginal likelihood

$$f(\boldsymbol{y}_{1:T} \mid \boldsymbol{\theta}) = \int f(\boldsymbol{s}_{1:T}, \boldsymbol{y}_{1:T} \mid \boldsymbol{\theta})\, d\boldsymbol{s}_{1:T}. \qquad \text{eqn 9}$$

We assume that the integrand $f(\boldsymbol{s}_{1:T}, \boldsymbol{y}_{1:T} \mid \boldsymbol{\theta})$ can be approximated by an (un-normalised) multivariate Gaussian distribution around the most likely (maximum a posteriori) trajectory ($\hat{\boldsymbol{s}}_{1:T}$) conditional on $\boldsymbol{\theta}$:

$$f(\boldsymbol{s}_{1:T}, \boldsymbol{y}_{1:T} \mid \boldsymbol{\theta}) \approx f(\hat{\boldsymbol{s}}_{1:T}, \boldsymbol{y}_{1:T} \mid \boldsymbol{\theta}) \times \qquad \text{eqn 10}$$

$$\exp\left[-\tfrac{1}{2}\left(\boldsymbol{s}_{1:T} - \hat{\boldsymbol{s}}_{1:T}(\boldsymbol{y}_{1:T}, \boldsymbol{\theta})\right)^{T} H(\boldsymbol{y}_{1:T}, \boldsymbol{\theta})\left(\boldsymbol{s}_{1:T} - \hat{\boldsymbol{s}}_{1:T}(\boldsymbol{y}_{1:T}, \boldsymbol{\theta})\right)\right].$$

This approximation renders the integration numerically cheap: given a set of $\boldsymbol{\theta}$ values, we maximise $f(\boldsymbol{s}_{1:T}, \boldsymbol{y}_{1:T} \mid \boldsymbol{\theta})$ to find $\hat{\boldsymbol{s}}_{1:T}$ and obtain the Hessian matrix (H) around $\hat{\boldsymbol{s}}_{1:T}$, which defines the uncertainty envelope. We can then run a second optimisation over possible $\boldsymbol{\theta}$ values to find the optimum of $f(\boldsymbol{y}_{1:T} \mid \boldsymbol{\theta})$, which gives the most likely $\boldsymbol{\theta}$ (and associated $\hat{\boldsymbol{s}}_{1:T}$).

The popular software Template Model Builder (`TMB`) implements the Laplace approximation (Kristensen et al., 2016). TMB is used by `yaps`, which fits SSMs to time-of-arrival signals in fine-scale acoustic positioning systems (Baktoft et al., 2017), and `aniMotum`, which fits continuous-time SSMs to positional data from satellite transmitters and related technologies (Jonsen et al., 2023). `INLA` may be another option (Rue et al., 2009). However, we haven't seen applications of these routines in passive acoustic telemetry systems.

The Laplace approximation is subject to the same underlying assumptions as in the Kalman filter (see §4.1.1). The key advantage of the Laplace approximation is that we automatically get the maximum a posteriori trajectory (and parameter estimates). The disadvantage is increased computational expense (Campbell, 2024). Both approaches are limited by non-Gaussianity (e.g., in coastal environments). In some situations, post-hoc corrections may be acceptable: `aniMotum`, for example, supports re-routing estimated paths for aquatic animals around land (Jonsen et al., 2023). In other situations, MCMC algorithms that sample from the joint distribution $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$ are required.

4.3. Markov chain Monte Carlo (MCMC)

4.3.1. Gradient-free methods

MCMC algorithms sample latent states and/or parameters from the joint distribution $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$ in such a way that the frequency distribution of values approximates their probability (Dorazio, 2016). That is, states and parameter values that are more likely are sampled more frequently than those that are unlikely. Gradient-free algorithms only require evaluations of a function that is proportional to the joint density $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$, and not its gradients, for sampling, which provides great flexibility in model formulation.

Traditional gradient-free algorithms include the Metropolis (Metropolis et al., 1953), Metropolis-Hastings (Hastings, 1970) and Gibbs sampling (Geman & Geman, 1984) algorithms. The former two algorithms randomly ‘walk’ around the posterior distribution; trajectories and parameters are iteratively sampled from a proposal distribution, given the current selection, and accepted or rejected depending on the joint posterior probability density $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$. Gibbs sampling is another approach that samples individual model components from their respective conditional distributions. That is, instead of sampling entire trajectories alongside parameters, we iterate between sampling individual states, given neighbouring states

$$\boldsymbol{s}_t \sim f(\boldsymbol{s}_t \mid \boldsymbol{s}_{t-1}, \boldsymbol{s}_{t+1}, \boldsymbol{\theta}, \boldsymbol{y}_t) \qquad \text{eqn 11}$$

and parameters, given a trajectory

$$\theta_i \sim f(\theta_i \mid \boldsymbol{\theta}_{-i}, \boldsymbol{s}_{1:T}, \boldsymbol{y}_{1:T}). \qquad \text{eqn 12}$$

In theory, this eliminates the need for a rejection step (since each sample is consistent with the full joint distribution). In practice, however, sampling from conditional distributions without closed form solutions (i.e., sampling parameters given trajectories) requires rejection steps (Metropolis-Hastings within Gibbs).

MCMC became popular in ecology following the development of `WinBUGS/OpenBUGS` (Lunn et al., 2000) and `JAGS` (Plummer, 2003), alongside accessible wrapper packages, such as `rjags` (Plummer, 2024) and `R2jags` (Su & Yajima, 2024). Generic inference packages such as `nimble` (de Valpine et al., 2017), `pyMC` (Abril-Pla et al., 2023), and `Turing.jl` (Ge et al., 2018) also support MCMC.

In passive acoustic telemetry systems, a small number of studies have used `JAGS` for model-based inference (Alós et al., 2016; Hostetter & Royle, 2020). Alós et al. (2016) used `R2jags` to fit a SSM to short (20-day) acoustic datasets collected from pearly razorfish (*X. novacula*) in Mallorca. They used an Ornstein-Uhlenbeck movement model and a logistic, distance-decaying detection probability model. They estimated individual trajectories and movement parameters, but fixed observation model parameters using independent analyses. Hostetter & Royle (2020) developed a similar methodology, coupling a random walk movement model with a half-normal detection probability function for simulated data. Using `JAGS`, they estimated individual trajectories plus movement and observation-model parameters. (They also developed a custom `R` code algorithm to account for random acoustic-transmission intervals.) Drawing the analogy between acoustic localisation and spatial capture-recapture (SCR), they termed the method ‘SCR movement-assisted localisation’.

There are several advantages of MCMC sampling. One is that it is relatively familiar to ecologists (Kéry, 2010; Schaub & Kéry, 2021). Another is that we can sample trajectories and parameters simultaneously in a fully Bayesian framework. Probabilistic programming languages like `JAGS` also provide a natural framework for thinking hierarchically about how group-level patterns emerge from the movements of multiple individuals analysed simultaneously (Jonsen, 2016). This is an exciting area of development.

However, there are disadvantages. An initial optimisation step may be required for effective initialisation of the algorithm with valid state and parameter samples (which are not extremely unlikely). Rejection sampling and iterative updates of individual model components (each $\boldsymbol{s}_t$ and θ_i), conditional on the other components, can be inefficient when the parameter space is high-dimensional (e.g., for long time series). Local state updates (i.e., $\boldsymbol{s}_t$ conditional on $\boldsymbol{s}_{t-1}$ and $\boldsymbol{s}_{t+1}$) can also limit exploration of the parameter space, leading to poor characterisation of multimodal distributions. Collectively, these conditions can lead to prolonged computation times that scale poorly with the size of the dataset, hampering real-world applications. Alós et al. (2016) report model fitting times of approximately three hours per individual (approximately 2,000 15-minute time steps over 20 days of tracking data). Similarly, we found Hostetter & Royle's (2020) code took 15 hours on a standard computer to run (150 time steps). Where trajectories and static parameter samples are required, gradient-based methods may be preferable.

4.3.2. Gradient-based methods

Gradient-based samplers leverage gradients for efficient sampling of high-dimensional distributions (Betancourt, 2017). Hamiltonian Monte Carlo is the most popular example. It conceptualises the (negative log) posterior as an energy landscape, with troughs that correspond to regions of high probability density and peaks that correspond to regions of low probability density. The algorithm iteratively simulates trajectories of a hypothetical particle over this landscape (following the rules of Hamiltonian dynamics). Each trajectory depends on the particle's position and the local gradient (which encourages the particle to 'roll' into high-density regions), plus its momentum (which facilitates exploration). At the start of each iteration, trajectories are initialised with a random momentum and then propagated, over L steps, using a numerical method (Leapfrog integration) that approximates Hamiltonian dynamics. At the end of each iteration, there is an accept/reject step for the proposed state. The No U-Turn Sampler is an extension that automates the choice of the trajectory length using the No U-Turn stopping criterion, improving performance (Stan Development Team, 2017). These dynamics enable more informed exploration of the posterior than in gradient-free methods. HMC has therefore become one of the most powerful inference algorithms available.

HMC is gaining popularity in ecology (Monnahan et al., 2017). `Stan` is a probabilistic programming language that implements HMC and automatic differentiation (Stan Development Team, 2017) and `Stan` interfaces, such as `cmdstanr`, have been developed for different scientific programming languages (Gabry et al., 2024). In `R`, the package `tmbstan` links `TMB` model objects to `Stan` (Monnahan & Kristensen, 2018). Generic packages, including `nimble` (de Valpine et al., 2017), `pyMC` (Abril-Pla et al., 2023), and `Turing.jl` (Ge et al., 2018), also support HMC.

In the acoustic telemetry literature, HMC has been used to analyse detection events (Lara-Lizardi et al., 2022) and infer COAs (Winton et al., 2018). For example, Winton et al. (2018) fitted a point-process model that estimates individual COAs from acoustic detections using `Stan` (via their `TelemetrySpace` package). Their model can be considered as a SSM with an unrestricted (‘teleportation’) movement process between sequential COAs and a binomial observation process that connects the latent COAs to detection counts at receivers (via a detection probability function). This is an efficient modelling choice for acoustic detections in high-coverage, regularly arranged receiver arrays, but subject to the limitations of COAs (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a; Winton et al., 2018). In the wider tracking literature, other applications of HMC include analyses of multinomial count data from radio telemetry (Wang, 2021) and behavioural state classification (Ruiz-Suarez et al., 2022). However, few studies have leveraged HMC for trajectory inference (Hance et al., 2021).

For animal tracking, we foresee two use cases for HMC. The first is when joint inference of latent locations and static parameters is required (Albert et al., 2015). The second is when comprehensive sampling of trajectories is desired. Both tasks can be expensive within a filtering paradigm. Gradient-free methods are an option, but leveraging gradients can improve efficiency (Albert et al., 2015).

HMC also has limitations. Unlike gradient-free methods, HMC is not suitable for posterior distributions with discontinuities (Stan Development Team, 2017). In animal tracking, this poses potential hurdles for (i) movement barriers, (ii) raster datasets and (iii) landscape ruggedness. Hard movement barriers (such as land) where the likelihood becomes zero are a fundamental challenge. Such barriers require smoothing to be compatible with HMC. If raster datasets (such as bathymetric data) are used, users also need to decide how to interpolate them and how to derive gradients. Rugged rasters (e.g., complex bathymetries) may pose an additional challenge for HMC efficiency by reducing the information in local gradients and necessitating smaller step sizes for posterior exploration. However, in situations in which additional (e.g., depth) information substantially constrains trajectories, these challenges may be mitigated by optimisation prior to sampling.

Parallel tempering is one technique that can help to alleviate the challenges of sampling multimodal distributions (Gupta et al., 2018). This involves running multiple MCMC chains in parallel with different temperature schemes. Higher temperature schemes flatten the energy landscape, facilitating exploration, while periodic particle swaps between chains facilitate overall convergence. Extensions to packages such as `nimble` (Pleydell, 2025) and `Turing.jl` (TuringLang, 2023) support this, and there are select examples of the approach in the movement literature (Karin & Alon, 2021; Sacchi & Swallow, 2021), but it remains to be seen whether tempered HMC can handle multimodality in real-world tracking datasets as effectively as grid-based filtering. A more general challenge with HMC and other MCMC algorithms is that they can require tuning and expertise to run efficiently.

5. Downstream ecological analyses

Probabilistic estimates of a model's states ($\boldsymbol{s}$) provide a robust foundation for downstream ecological analyses (Table 2), which have hitherto largely been based on heuristic methods (Kraft et al., 2023). The term 'downstream ecological analyses' refers to analyses of properties of the distribution of states and how these are shaped by ecological processes. Examples include analyses of individual centres of activity, occurrence, residency, home ranges, habitat selection and individual behaviour (Jacoby & Piper, 2023).

Centres of activity (COAs) are an important summary statistic in many studies. In an SSM context, the COA ($\boldsymbol{c}_{[t_1,t_2]}$) is defined as the mean of the states $\boldsymbol{s}_t$ over some time interval $[t_1, t_2]$; i.e.,

$$\boldsymbol{c}_{[t_1,t_2]} = \sum_{\tau=t_1}^{t_2} \boldsymbol{s}_\tau \, f(\boldsymbol{s}_\tau \mid y_{1:T}). \qquad \text{eqn 13}$$

If we have N samples $\boldsymbol{s}_{t,i}$ from $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T})$, the COA is simply the mean location of the samples.

The occurrence distribution is the probability distribution for an individual's location over a study period (Fleming et al., 2015). If we discretise a study area on a grid, we can compute the occurrence distribution as a two-dimensional histogram. Mathematically, we compute the occurrence probability P in each grid cell A from the marginal distribution $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T})$ as the time-averaged probability mass in that cell:

$$P(A) = \frac{1}{T}\sum_{t=1}^{T}\int_A f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T})\, d\boldsymbol{s}_t. \qquad \text{eqn 14}$$

This two-dimensional histogram approach is computationally straightforward but can be sensitive to grid resolution. An alternative option is to obtain a smooth spatial density via kernel density estimation. For particle algorithms, both approaches are implemented by `patter` and produce more accurate maps than heuristic methods (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a, 2025b).

Using the occurrence distribution, we can also compute the expected fraction of time an animal spends in any region of interest, by cumulating the occurrence probabilities in that region. This may be termed the 'residence time'. To quantify the uncertainty in this fraction, samples of trajectories are required.

The home range distribution is defined as the 'long-run' probability distribution for the location of an individual (Fleming et al., 2015). Under certain assumptions, home range distributions can also be estimated from state samples ($\boldsymbol{s}_t$ or $\boldsymbol{s}_{1:T}$) via home range estimators (Fleming et al., 2015; Silva et al., 2022).

For analyses of habitat selection, samples from marginal ($\boldsymbol{s}_t$) and joint ($\boldsymbol{s}_{1:T}$) distributions can be used. The probabilistic representation of an individual's state $\boldsymbol{s}_t$ at every time step should refine resource-selection analyses (Griffin et al., 2021). Step-selection analyses leverage additional information in movement trajectories (Klappstein et al., 2024). While in theory it is possible (indeed preferable) to model individual movements and habitat selection jointly in a Bayesian framework, this would be computationally expensive. We suggest that coupling Bayesian inference for trajectories with step selection functions should enable habitat selection analyses that correctly represent uncertainty and leverage the strengths of existing software (Klappstein et al., 2024).

For analyses of behaviour, trajectories are required. Trajectories uniquely encode information on the mode of movement (e.g., smooth versus erratic movements). We foresee opportunities to analyse the properties of trajectories (such as step lengths and turning angles) to learn about the spatial distribution of movement behaviours via hidden Markov modelling (Hance et al., 2021).

Many other downstream ecological analyses of individual movements should benefit from model-based inference approaches that correctly represent uncertainty in individual states or trajectories. Examples include analyses of individual responses to disturbance (Lavender, Aleynik, Dodd, Illian, James, Wright, et al., 2022), co-occurrence patterns (Jacoby & Piper, 2023) and oceanographic studies (Lavender, Aleynik, Dodd, Illian, James, Smout, et al., 2022).

Leveraging model-based inference in downstream analyses is important but requires care. There is an important distinction between the true state of an individual and our knowledge of the individual’s state. The latter is shaped by both the movement process and the quality of our observations, which has important consequences for downstream analyses. For example, in an acoustic telemetry system, an absence of detections produces pitted maps with depressions around receivers (where we know the individual was unlikely to be located), rather than uniform maps. Similarly, both high mobility and information sparsity can produce diffuse maps of space use. In downstream analyses, it is therefore important to consider the limits of the observations while deriving conclusions about an individual's movements. Simple statistics, such as the average area spanned by 95 % of the probability mass of the latent states at each time step (over all time steps), shed light on how well an individual has been localised and should support interpretation of downstream analyses. Further research in this area will be beneficial.

6. Guidance for practitioners

We encourage the adoption of SSMs and model-based inference (Fig. 2). The initial challenge is to formulate a SSM, leveraging available datasets, domain knowledge and literature (Fig. 1). Biological objectives, computational cost, expertise and implementation options then shape how we should proceed with inference (Fig. 2). Inference of models that only incorporate acoustic observations may be relatively straightforward. Models that incorporate both acoustic and ancillary (e.g., depth) observations pose a harder inference problem (especially in complex coastal or rugged landscapes), but can provide refined insights if implemented successfully.

Filtering/smoothing algorithms are well-suited to sampling states $\boldsymbol{s}_t$ for analyses of space use, home range and residency (Fig. 2). Kalman filtering is an efficient option that may be appropriate for some applications. Particle filtering is a more general (non-linear, non-Gaussian) approach. At the time of writing, we believe the `patter` package is the most accessible and generally applicable option for direct use by practitioners. The package navigates the trade-offs between accessibility, speed and flexibility with comprehensive documentation and a performant `Julia` backend that supports a library of built-in models as well as user-defined structures. The price is that static parameters ($\boldsymbol{\theta}$) are expensive to estimate, convergence can be challenging and current routines only sample from the marginal distributions of states $\boldsymbol{s}_t$. In many situations, these are favourable trade-offs: models can be parameterised from external (e.g., accelerometery) datasets that contain more detailed information on movement and observation parameters, domain knowledge and literature; and sensitivity analyses can be used to evaluate epistemic uncertainty. However, with bespoke routines it is possible to relax these limitations (Doucet & Johansen, 2009; Kattwinkel & Reichert, 2017; Liu et al., 2019).

In complex environments where coastline or rugged landscapes are represented in models, the posterior distribution from which we need to sample is much more complex and can be highly multimodal. In these situations, grid-based filtering is the most reliable option at the time of writing (Fig. 2). We have observed that convolution algorithms are particularly well-suited to modelling acoustic and archival data for benthic species in complex bathymetric landscapes (Lavender et al., in prep). Efficient GPU routines should make convolution algorithms an attractive option, even where other approaches perform well (especially if knowledge of the movement process is limited). User-friendly implementations of fast convolution algorithms have been lacking, but this is now changing (Scheidegger, 2025; Woillez, 2024).

When joint estimation of trajectories $\boldsymbol{s}_{1:T}$ and static parameters is required, Laplace approximation and MCMC are options (Fig. 2). Where appropriate, the Laplace approximation may be the more efficient choice and is associated with an animal-tracking code base that could be leveraged to support applications in passive acoustic telemetry systems (Baktoft et al., 2017; Jonsen et al., 2023). Otherwise, we recommend exploration of HMC if possible, especially in studies focused solely on acoustic observations. In general, we expect well-tuned HMC algorithms to outperform Gibbs samplers implemented by software such as `JAGS`, but it remains unclear how additional complexities (such as land barriers or depth observations) affect performance. In studies of multiple individuals, the other attractive feature of Bayesian MCMC algorithms is that they provide a natural hierarchical framework in which multiple individuals can be modelled simultaneously (Jonsen, 2016). These algorithms can be difficult for practitioners to use but statisticians can support this process.

For the estimation of static parameters, it remains uncertain in general how informative sparse detection data are and we encourage practitioners to leverage biological expertise to formulate and parameterise models, regardless of the choice of inference method. For parameter estimation, informative priors should help and existing studies suggest this approach is worth exploration (Alós et al., 2016; Hostetter & Royle, 2020). Comparison of prior and posterior distributions should inform our understanding of how much we can learn about movement and observation processes, alongside individual states, in acoustic telemetry systems.

7. Future research avenues

We encourage research into methods that have yet to be widely applied in passive acoustic telemetry systems. It is important to understand how well available approaches perform under different conditions and communicate their strengths and weaknesses (Ponisio et al., 2020).

Statistical research should be coupled with the development of software that supports real-world applications by practitioners. In software packages, we recognise potential trade-offs between accessibility, speed and flexibility and encourage plurality in the package ecosystem. In terms of accessibility, there are advantages in specialised packages (such as `patter`) that can provide bespoke routines, examples and guidance to selected user groups, but this can constrain flexibility (Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025b). In terms of speed, high-level language (e.g., pure `Python` or `R`) packages (such as `HMMoce`) can be easier to install, use and maintain, but pay a performance price (Braun et al., 2018). For animal tracking, we believe specialised backends written in compiled languages (with native GPU support) are generally advantageous. Computation time is also linked the complexity of the interface problem, algorithm choice, tuning parameters and other conditions. Benchmarking studies are required to inform our understanding of both algorithmic complexity and implementation trade-offs in different contexts. The availability of standard, open-access datasets should support this process.

For flexibility, we see advantages in generic inference packages (such as `Turing.jl`) that are fully embedded in scientific programming languages because they can leverage a wider language ecosystem. This can facilitate the incorporation of complex data types, such as raster data, in models. For animal tracking, this is important: truncated movement models (that account for barriers) and likelihood functions for many data types (such as depth measurements) require lookup routines that extract values (such as land/water or the bathymetric depth) from spatial datasets in the locations defined by the latent states. We believe this can be difficult in stand-alone languages, such as `Stan`. In `nimble`, `R` routines can be included, but `C++` code is required to maintain performance. In `patter`, this is one of the reasons we use `Julia` as a backend (this provides a high-level user experience while maintaining the performance of a compiled programming language). We expect that pure `Julia` packages, such as `Turing.jl`, may become increasingly important in ecology for these reasons (Ge et al., 2018). More broadly, we see advantages in flexible packages that link standard model syntax to different inference algorithms, either via probabilistic programming or an encoding of the joint distribution that can be passed to different sampling routines. These developments provide a basis to strengthen our understanding of the trade-offs of different inference algorithms in different contexts (Ponisio et al., 2020).

8. Conclusions

This review presents a unifying perspective of animal tracking in aquatic ecosystems (Fig. 3). We put state-space modelling and model-based inference at the core of animal-tracking analyses. This approach leverages our biological knowledge, and disparate datasets, as part of analyses and enables us to resolve individual movements, space use and residency within a formal framework, with uncertainty quantification and improved accuracy compared to heuristic methods (Alós et al., 2016; Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025; Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a). Improved estimates of individual locations through time, alongside correct estimates of uncertainty, also provide a robust foundation for analyses of habitat selection, behaviour and management measures (Alós et al., 2022; Jacoby & Piper, 2023).

Model-based inference is challenging, but there are multiple options available. Inference may focus on individual states (including location) or both states and static parameters. In sparse receiver arrays, the information available is limited and it may be sensible to parameterise the movement and observation sub-models *a priori*, drawing on available datasets, domain knowledge and literature, before inferring individual states (Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025; Lavender, Scheidegger, Albert, Biber, Illian, et al., 2025a). In other settings, data-driven parameter estimation via maximum likelihood or Bayesian inference may be desirable (Albert et al., 2015). Further research is needed to investigate the trade-offs between methods in different settings and how we can embed probabilistic estimates of individual locations in downstream ecological analyses. We see considerable potential for formal inference methods to strengthen these analyses, but caution that even these methods depend on well-designed studies that collect sufficient data. By highlighting the current state-of-the-art, we hope this review inspires further research into the development and application of statistical inference for underwater biotelemetry.

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Figures

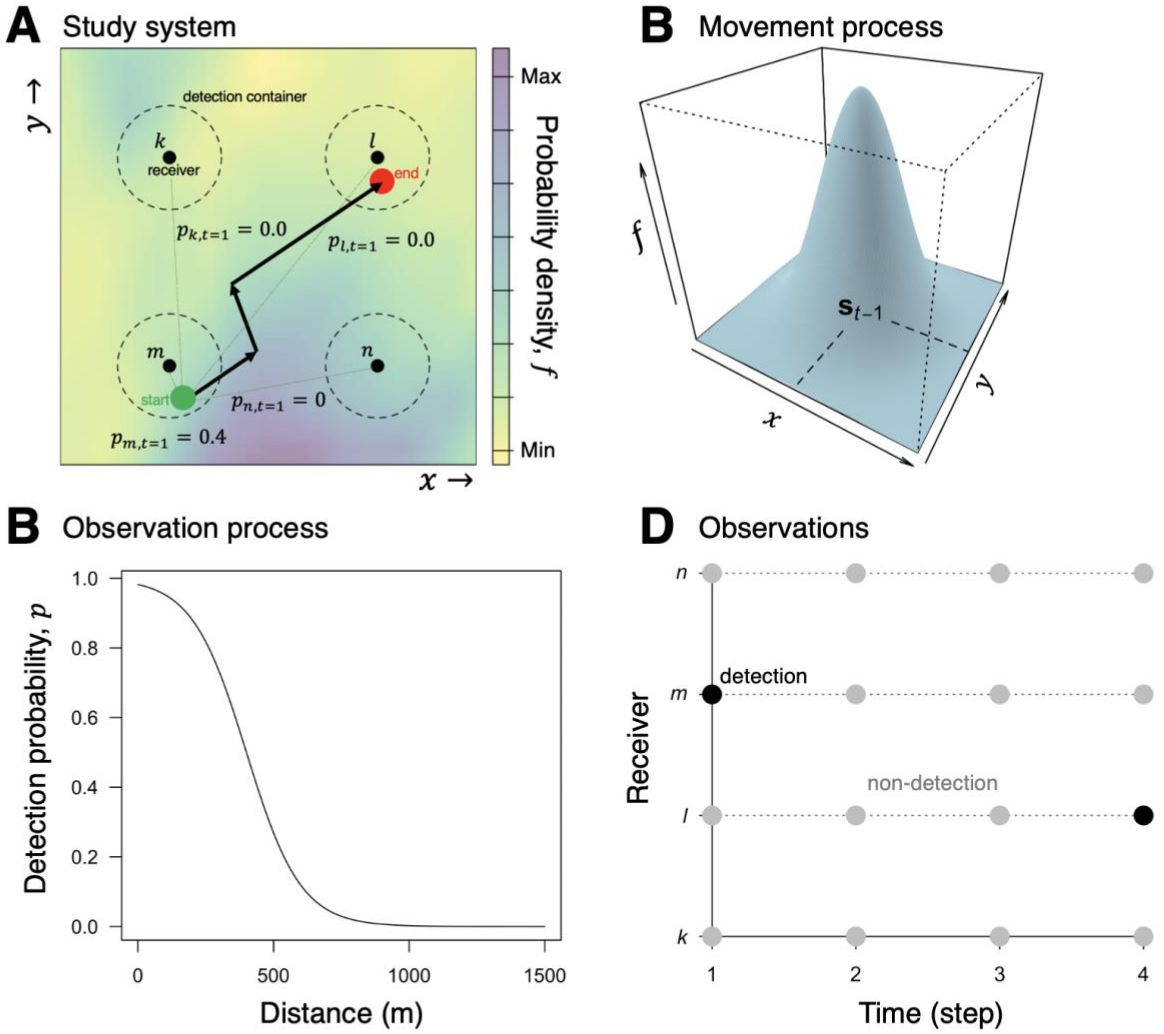
A
Study system
$y \rightarrow$
detection container
k
receiver
l
end
$p_{k,t=1} = 0.0$
$p_{l,t=1} = 0.0$
m
n
start
$p_{n,t=1} = 0$
$p_{m,t=1} = 0.4$
$x \rightarrow$
Max
Probability density, f
Min
B
Movement process
f
$\mathbf{s}_{t-1}$
x
y
B
Observation process
Detection probability, p
1.0
0.8
0.6
0.4
0.2
0.0
0
500
1000
1500
Distance (m)
D
Observations
Receiver
n
m
detection
non-detection
l
k
1
2
3
4
Time (step)

Fig. 1. State-space models for passive acoustic telemetry. A shows an individual's (unobserved) movement trajectory. The trajectory is represented in discrete time with four steps. The start (🟢) and end (🔴) of the trajectory are shown, alongside receivers k, l, m and n (●) and receiver detection containers (◌), beyond which detection probability is nominally zero. Individual movements over longer time periods generate emergent patterns of space use (i.e., the background map). We model these dynamics using state-space models. **B** shows an example random-walk model for the movement process in which the individual's state at time t ($\boldsymbol{s}_t$) is modelled with a Gaussian distribution centred on the previous location (defined by $\boldsymbol{s}_{t-1}$). **C** shows a model for the observation (detection) process. We assume acoustic observations (detections, non-detections) are outcomes of a Bernoulli ('coin toss') process in which the probability p of a detection ('head') declines with distance from a receiver (at shown in **A** for $t = 1$). **D** shows our acoustic observations. Our primary goal in model-based inference is to use the observations to infer the underlying (latent) movement trajectory and emergent ecological patterns.

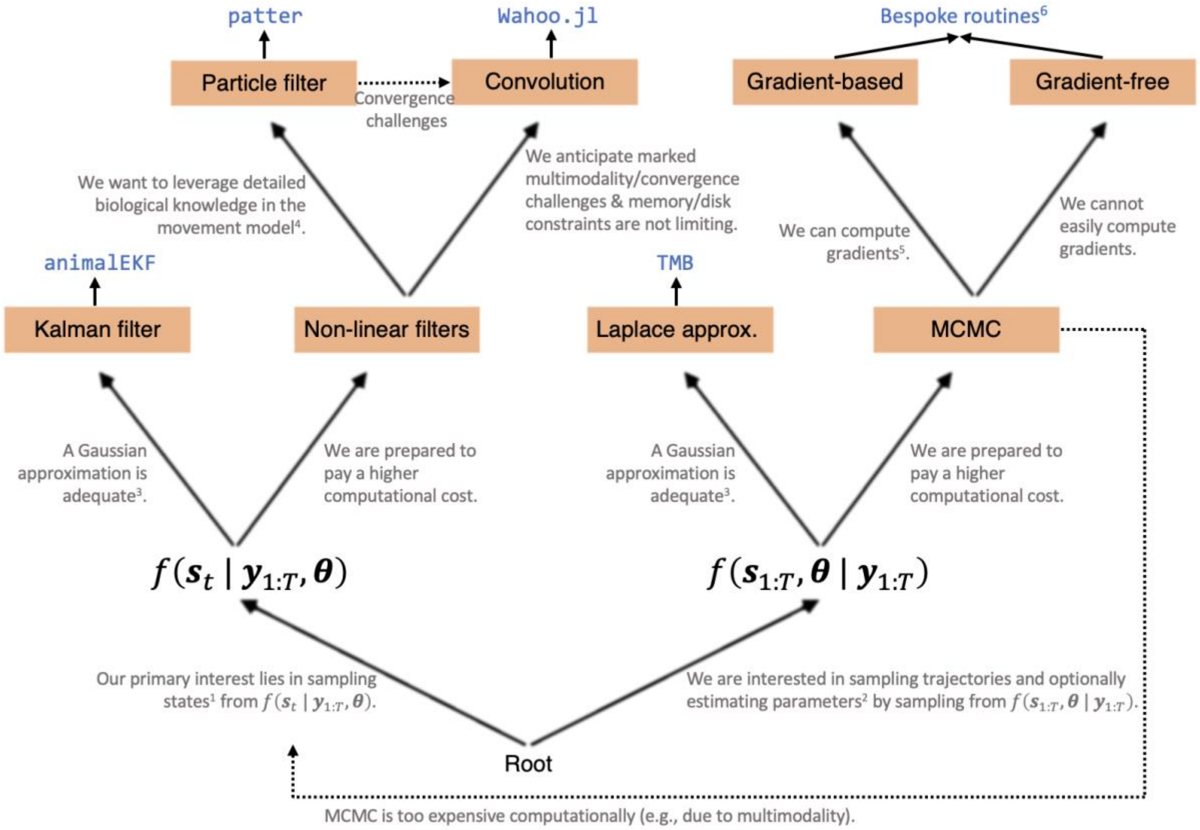
patter
Wahoo.jl
Bespoke routines[6]
Particle filter
Convergence challenges
Convolution
Gradient-based
Gradient-free
We want to leverage detailed biological knowledge in the movement model[4].
We anticipate marked multimodality/convergence challenges & memory/disk constraints are not limiting.
We can compute gradients[5].
We cannot easily compute gradients.
animalEKF
TMB
Kalman filter
Non-linear filters
Laplace approx.
MCMC
A Gaussian approximation is adequate[3].
We are prepared to pay a higher computational cost.
A Gaussian approximation is adequate[3].
We are prepared to pay a higher computational cost.
$f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$
$f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$
Our primary interest lies in sampling states[1] from $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$.
We are interested in sampling trajectories and optionally estimating parameters[2] by sampling from $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$.
Root
MCMC is too expensive computationally (e.g., due to multimodality).

Fig. 2. A simplified decision tree supporting model-based inference for passive acoustic telemetry. Start at the root and follow the branches. Arrows indicate possible decision pathways and relevant example software packages for inference are listed in blue. Note that differences between branches and inference algorithms are not black and white and composite inference of states and parameters, using multiple approaches, is possible. Illustrated pathways are subject to the following numbered qualifications. [1]That is, we are primarily interested in 'snapshots' of the individual's state (e.g., for mapping space use or estimating residency), using existing knowledge of the movement and observation processes. We can extend routines on this side of the tree to sample parameters (from $f(\boldsymbol{s}_t, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$) or a few trajectories (from $f(\boldsymbol{s}_{1:T} \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$ or $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$) with increased computational cost, though bespoke routines may be required. For more comprehensive sampling of parameters and trajectories, MCMC algorithms may be the better choice. [2]We should be prepared to rely on approximations and/or pay a higher computational price to sample from $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$ compared to $f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$. An initial optimisation step may be required for efficient sampling. [3]A Gaussian approximation may be appropriate if, for example, we assume a Gaussian random walk, a Gaussian acoustic observation model and our study system is far from movement/observation barriers (such as coastline). [4]Currently, particle algorithms may be most appropriate option for practitioners, given the `patter` package and a compilation of relevant examples. [5]We expect gradient-based algorithms to be more efficient, but this is not guaranteed. [6]Use a probabilistic programming language, such as `TuringLang`, or pass the joint density to a sampling package (such as `DynamicHMC.jl`).

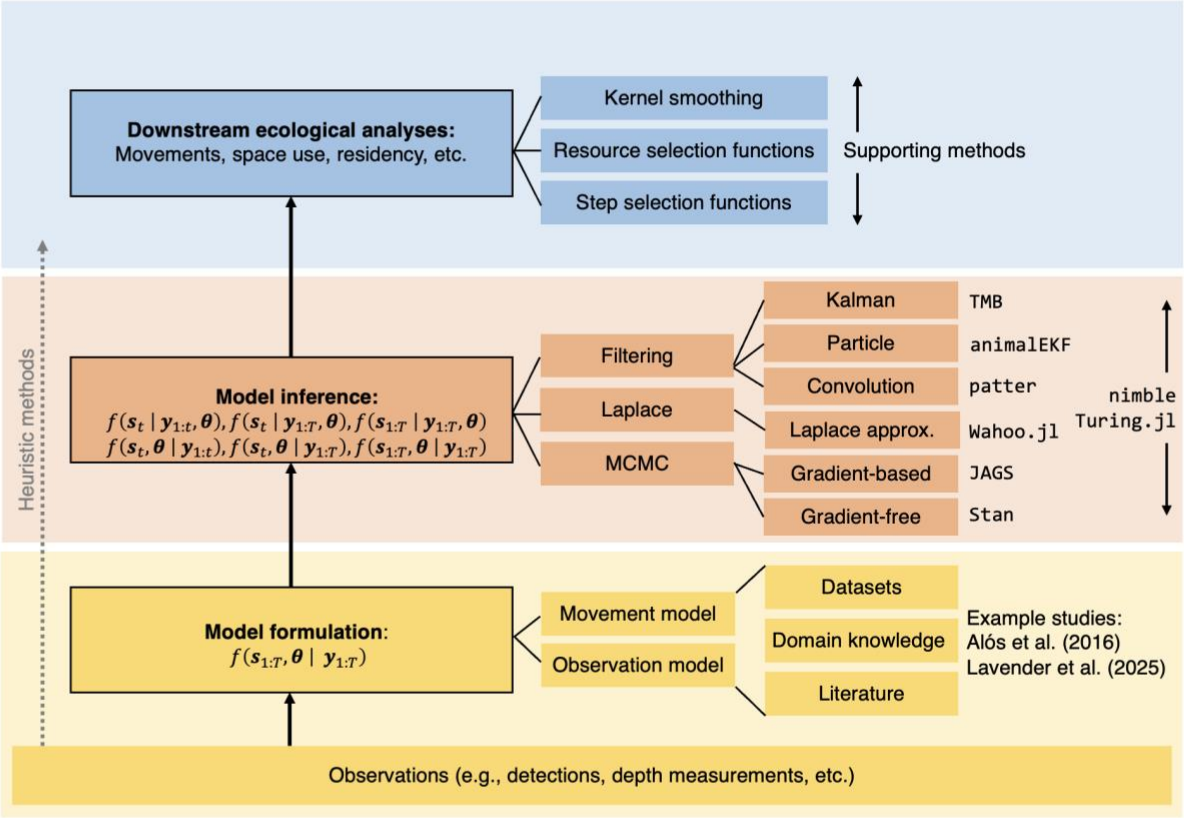
Downstream ecological analyses:
Movements, space use, residency, etc.
Kernel smoothing
Resource selection functions
Step selection functions
Supporting methods
Heuristic methods
Model inference:
$f(s_t \mid y_{1:t}, \theta), f(s_t \mid y_{1:T}, \theta), f(s_{1:T} \mid y_{1:T}, \theta)$
$f(s_t, \theta \mid y_{1:t}), f(s_t, \theta \mid y_{1:T}), f(s_{1:T}, \theta \mid y_{1:T})$
Filtering
Laplace
MCMC
Kalman
Particle
Convolution
Laplace approx.
Gradient-based
Gradient-free
TMB
animalEKF
patter
Wahoo.jl
JAGS
Stan
nimble
Turing.jl
Model formulation:
$f(s_{1:T}, \theta \mid y_{1:T})$
Movement model
Observation model
Datasets
Domain knowledge
Literature
Example studies:
Alós et al. (2016)
Lavender et al. (2025)
Observations (e.g., detections, depth measurements, etc.)

Fig. 3. **A state-space modelling framework for passive acoustic telemetry.** This comprises three stages. Step one is to formulate a state-space model for the joint distribution $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$ of the individual's states and parameters, given all data. The state-space model comprises a movement model and observation model(s), informed by available datasets, domain knowledge and literature. Model-based inference is the next step. We may perform inference for marginal or joint distributions. Static parameters $\boldsymbol{\theta}$ may be fixed or estimated. Example inference software is listed. Robust estimates of individual states, and associated measures of uncertainty, support downstream ecological analyses of individual movements, space use, residency, habitat selection and so on. Techniques such as kernel smoothing can be leveraged in these analyses. Heuristic methods can also support downstream ecological analyses.

Tables

Table 1. Inference targets. We can perform inference for marginal or joint distributions of individual states ($\boldsymbol{s}_t$ or $\boldsymbol{s}_{1:T}$), given the data ($\boldsymbol{y}$). Static parameters in the movement or observation models ($\boldsymbol{\theta}$) may be given or estimated. For a mapping of inference targets to downstream ecological analyses, see Table 2.

Statistical target		**Definition**	**Example applications**
State inference	**State & parameter inference**		
$f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:t}, \boldsymbol{\theta})$	$f(\boldsymbol{s}_t, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:t})$	A 'partial' marginal distribution of the individual's state at a given time, given all the data up to and including that time. This is often approximated by filtering algorithms (see §4.1). Static parameters can be estimated via maximum likelihood estimation or Bayesian inference.	• Lavender et al. (2025a) illustrate a particle filtering algorithm that samples states, given movement and observation models are specified (see §4.1.3).

Statistical target		**Definition**	**Example applications**
State inference	**State & parameter inference**		
$f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$	$f(\boldsymbol{s}_t, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$	The marginal distribution of the individual's state at a given time, given all data (before and after that time). This is often approximated by coupling filtering and smoothing algorithms (see §4.1).	• Lavender et al. (2025a) explored the behaviour of a particle filtering–smoothing algorithm using simulations. They found smoothing improves maps of space use, especially in sparse receiver arrays (see §4.1.3). • Lavender et al. (2025c) used the same filtering–smoothing algorithm to map space use and estimate residency of flapper skate (*Dipturus intermedius*) in a Marine Protected Area (see §4.1.3). • Pedersen & Weng (2013) used grid-based

Statistical target		**Definition**	**Example applications**
State inference	**State & parameter inference**		
			filtering to map patterns of space use in humphead wrasse (*Cheilinus undulatus*). Their algorithm estimates states and movement parameters, assuming detection probability parameters can be derived *a priori* (see §4.1.4).
$f(\boldsymbol{s}_{1:T} \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$	$f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$	The joint distribution of the individual’s trajectories and all data. Suitable approaches for inference include the Laplace approximation (see §4.2) and Markov Chain Monte Carlo (see §4.3).	• Thygesen et al. (2009) show how grid-based filtering algorithms can be extended to sample trajectories in geolocation studies. • Alós et al. (2016) sample trajectories and movement parameters for pearly razorfish

Statistical target		**Definition**	**Example applications**
State inference	**State & parameter inference**		
			(*Xyrichtys novacula*) using `JAGS` (see §4.3.1). • Hostetter & Royal sample trajectories and estimating states and both movement and detection-probability parameters, using `JAGS` and a bespoke algorithm (see §4.3.1).

Table 2. Mapping statistical inference to downstream ecological analyses. Statistical targets (i.e., a marginal or joint distribution) for model-based inference are linked to example use cases. Ticks or references indicate example applications. Samples from marginal distributions provide 'snapshots' of an individual's distribution through time and are sufficient for many analyses. Samples from joint distributions are generally more expensive, but necessary for analyses of movement trajectories.

Use case		**Statistical target**	
		Marginal distributions	**Joint distributions**
		$f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$, $f(\boldsymbol{s}_t, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$	$f(\boldsymbol{s}_{1:T}, \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$, $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$
Estimate COAs		✓	✓
Map occurrence or home range		(Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025; Pedersen & Weng, 2013)	(Alós et al., 2016; Hostetter & Royle, 2020)
Estimate residence time	Estimate the expected residence time	(Lavender, Scheidegger, Albert, Biber, Aleynik, et al., 2025)	✓
	Quantify the distribution of residence times	-	✓
	Analyse resource selection	✓	✓

Use case		**Statistical target**	
		Marginal distributions	**Joint distributions**
		$f(\boldsymbol{s}_t \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$, $f(\boldsymbol{s}_t, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$	$f(\boldsymbol{s}_{1:T}, \mid \boldsymbol{y}_{1:T}, \boldsymbol{\theta})$, $f(\boldsymbol{s}_{1:T}, \boldsymbol{\theta} \mid \boldsymbol{y}_{1:T})$
Examine habitat selection	Analyse step selection	-	✓
Examine behaviour		-	✓
Other movement analyses	Examine responses to disturbance	✓	✓
	Co-occurrence analyses	✓	✓
	Position animal oceanographers	✓	✓

Author contributions

Edward Lavender conceived and drafted the manuscript, during discussions with Andreas Scheidegger, Helen Moor Carlo Albert. All authors shared expertise, provided inputs and approved publication.

Data availability statement

Not applicable

Conflict of interest

The authors declare no conflicts of interest.

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