

## APPLICATION

# patter: Particle algorithms for animal tracking in R and Julia

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**Abstract**

1. State-space models are a powerful modelling framework in movement ecology that represents individual movements and the processes connecting movements to observations. However, fitting state-space models to animal-tracking data can be difficult and computationally expensive.
2. Here, we introduce *patter*, a package that provides particle filtering and smoothing algorithms that fit Bayesian state-space models to tracking data, with a focus on data from aquatic animals in receiver arrays. *patter* is written in R, with a performant Julia backend. Package functionality supports data simulation, preparation, filtering, smoothing and mapping.
3. In two examples, we demonstrate how to implement *patter* to reconstruct the movements of a tagged animal in an acoustic telemetry system from acoustic detections and ancillary observations. With perfect information, the particle filter reconstructs the true (unobserved) movement path (Example One). More generally, particle algorithms represent an individual's possible location probabilistically as a weighted series of samples ('particles'). In our illustration, we resolve an individual's (unobserved) location every 2 min during 1 month and use particles to visualise movements, map space use and quantify residency (Example Two).
4. *patter* facilitates robust, flexible and efficient analyses of animal-tracking data. The methods are widely applicable and enable refined analyses of space use, home ranges and residency.

**KEYWORDS**

Bayesian inference, movement ecology, package, particle filter, passive acoustic telemetry, state-space model

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## 1 | INTRODUCTION

The field of movement ecology has expanded in recent decades (Nathan et al., 2008; Rafiq et al., 2021). Electronic tagging and tracking technologies are used to track animals across the globe, providing a 'panoramic window' into their lives (Hussey et al., 2015). In aquatic environments, satellite tracking has reconstructed the migrations of air-breathing animals (Hays & Hawkes, 2018), archival geolocation has revealed the transoceanic movements of pelagic fish (Block et al., 2005) and passive acoustic telemetry arrays have been established to track acoustically tagged animals from local to continental scales (Matley et al., 2022). This accumulation of animal-tracking data is outpacing the development of modelling methods and software packages for analysis (Rafiq et al., 2021).

State-space models (SSMs) have emerged as a powerful modelling framework for animal tracking (Patterson et al., 2008). An SSM is a hierarchical representation of a process-observer system in which the evolution of an unobserved ('latent') state ( $\mathbf{s}$ ) through time ( $t$ ) is imperfectly observed, generating 'noisy' observations ( $\mathbf{y}_t$ ). Discrete-time SSMs for animal-tracking data model the movement process  $f(\mathbf{s}_t | \mathbf{s}_{t-1})$  by which an animal's state (typically, location) evolves through time ( $t \in \{1, \dots, T\}$ ) and the observation processes  $f(\mathbf{y}_t | \mathbf{s}_t)$  connecting movements to observations. The SSM thus forms a formal statistical framework within which it is possible to estimate the unobserved states of an animal that are of interest, while accounting for movement properties (including speeds and barriers) and observation processes (such as detectability). However, fitting SSMs can be challenging and computationally expensive (Patterson et al., 2008).

Particle filters are flexible Monte Carlo algorithms used to fit state-space models (Doucet & Johansen, 2009). In an animal-tracking context, a particle filter approximates the distribution of possible locations of an individual with a set of weighted samples termed 'particles' (Lavender et al., 2025a). A movement model simulates possible locations of the individual (i.e.  $\mathbf{s}_t \sim f(\mathbf{s}_t | \mathbf{s}_{t-1})$ ) and observation model(s) weight particles in line with the probability of the observations (i.e.  $f(\mathbf{y}_t | \mathbf{s}_t)$ ). By resampling particles in line with the weights, we duplicate particles that are compatible with the data and eliminate incompatible particles. The result is an approximation of the distribution of the individual's location at each time step, given the preceding data (i.e. the partial marginal distribution,  $f(\mathbf{s}_t | \mathbf{y}_{1:t})$ ). Particle smoothers and samplers are extensions that approximate the full marginal ( $f(\mathbf{s}_t | \mathbf{y}_{1:T})$ ) and the joint ( $f(\mathbf{s}_{1:T} | \mathbf{y}_{1:T})$ ) distributions, respectively (Doucet & Johansen, 2009). Compared to alternative SSM-fitting methods for animal-tracking data, advantages of particle algorithms include their flexibility, scalability and the ease with which they can be intuitively understood. In the ecological literature, a handful of particle filtering routines have been developed, including for fish geolocation over coarse spatial scales (Liu et al., 2019). However, existing routines are relatively specialised, computationally intensive and require user expertise.

Here, we introduce *patter*, a package that provides particle filtering and smoothing algorithms for animal-tracking data, motivated

by our research in acoustic telemetry systems. *patter* is written in R (Lavender, 2024a) and integrates a Julia backend, *Patter.jl* (Lavender, 2024b). Julia is a programming language that combines the ease of use of an interpreted language like R with the speed of a compiled language like C++ (Bezanson et al., 2017). *patter* includes routines for simulation, data preparation, particle filtering, smoothing and mapping. These routines extend the acoustic telemetry and animal-tracking package ecosystems (Joo et al., 2020; Kraft et al., 2023). In the context of passive acoustic telemetry, *patter* is unique in the provision of routines that reconstruct individual movements and patterns of space use within a coherent probabilistic framework. The routines enable refined analyses of space use, home ranges and residency.

## 2 | METHODOLOGY

### 2.1 | Model formulation

The statistical methodology is described in Lavender et al. (2025a). This section provides a summary.

#### 2.1.1 | Posterior

We consider a Bayesian state-space model for the state of a tagged animal; that is, the joint distribution  $f(\mathbf{s}_{1:T} | \mathbf{y}_{1:T})$ , where  $\mathbf{s}_t = (s_x, s_y)$  denotes the state (a two-dimensional location in our examples),  $\mathbf{y}_t$  denotes observations and  $t \in \{1, 2, \dots, T\}$  indexes time steps. The joint distribution is proportional to the product of a prior (the movement process) and the likelihood (the observation process), that is,  $f(\mathbf{s}_{1:T} | \mathbf{y}_{1:T}) \propto f(\mathbf{s}_{t=1}) f(\mathbf{y}_{t=1} | \mathbf{s}_{t=1}) \prod_{t=2}^T f(\mathbf{s}_t | \mathbf{s}_{t-1}) f(\mathbf{y}_t | \mathbf{s}_t)$ .

#### 2.1.2 | Prior

The prior comprises a probability density distribution of the animal's initial location ( $f(\mathbf{s}_{t=1})$ ) and a movement model ( $f(\mathbf{s}_t | \mathbf{s}_{t-1})$ ). A simple model for  $f(\mathbf{s}_t | \mathbf{s}_{t-1})$  in the two-dimensional case is a discrete-time random walk, where  $\mathbf{s}_t = (s_{x,t-1} + d_t \cos \phi_t, s_{y,t-1} + d_t \sin \phi_t)$  and  $d$  (step length) and  $\phi$  (heading) are independently distributed random variables, restricted by boundary conditions (e.g. land).

#### 2.1.3 | Likelihood

The likelihood measures the probability of the observations given the latent states ( $\mathbf{s}_t$ ). In an acoustic telemetry system, observations may include acoustic measurements at each of  $M$  receivers (an  $M \times T$  matrix,  $\mathbf{y}^{(A)}$ ) and ancillary measurements, such as depths (a row vector,  $\mathbf{y}^{(D)}$ ). By way of example, here we consider a combined dataset  $\mathbf{y} = \{\mathbf{y}^{(A)}, \mathbf{y}^{(D)}\}$  and the likelihood  $f(\mathbf{y}_t | \mathbf{s}_t) = f(\mathbf{y}_t^{(A)} | \mathbf{s}_t) f(\mathbf{y}_t^{(D)} | \mathbf{s}_t)$ .

## 2.1.4 | Acoustic measurements

The likelihood of the acoustic measurements at time  $t$  ( $y_t^{(A)}$ ), which comprise detections (1) or non-detections (0) at each operational receiver (i.e.  $y_{k,t}^{(A)} \in \{0, 1\}$ ), can be modelled using the Bernoulli probability mass function,  $f(y_t^{(A)} | s_t) = \prod_k p_{k,t}(s_t)^{y_{k,t}^{(A)}} (1 - p_{k,t}(s_t))^{1 - y_{k,t}^{(A)}}$  (assuming independence). We typically model detection probability,  $p$ , as a function of the distance between the receiver (at location  $r_k$ ) and transmitter (at  $s$ ), such as  $p_{k,t}(s_t) = \begin{cases} (1 + e^{-(\alpha - \beta |s_t - r_k|)})^{-1} & \text{if } |s_t - r_k| < \gamma \\ 0 & \text{otherwise} \end{cases}$ , where  $\alpha$  and  $\beta$  are parameters and  $\gamma$  is the detection range.

## 2.1.5 | Depth measurements

A simple model for the likelihood of a depth observation is:

$$f(y_t^{(D)} | s_t) = \begin{cases} z_t & \text{if } b(s_t) - \epsilon_{\text{shallow}}(s_t) \leq y_t^{(D)} \leq b(s_t) + \epsilon_{\text{deep}}(s_t) \\ 0 & \text{otherwise} \end{cases},$$

where  $z_t = (\epsilon_{\text{deep}}(s_t) + \epsilon_{\text{shallow}}(s_t))^{-1}$ . This requires  $y_t^{(D)}$  to be within a window around the bathymetric depth  $b(s_t)$ . The window's width is defined by the shallow and deep depth-adjustment functions,  $\epsilon_{\text{shallow}}(s_t)$ ,  $\epsilon_{\text{deep}}(s_t) \leq b(s_t)$ . These functions capture observational uncertainty (i.e. tag accuracy and the accuracy of the bathymetric measurement) and can be tailored for different species (depending on how much time they spend near the seabed). For benthic species, small errors ( $\epsilon_{\text{shallow}}(s_t)$ ,  $\epsilon_{\text{deep}}(s_t) \ll b(s_t)$ ) only permit observations close to the seabed; for pelagic species, larger  $\epsilon_{\text{shallow}}(s_t)$  values permit observations in the water column.

## 2.2 | Inference

### 2.2.1 | Filter

For inference, we begin with the partial marginal distribution,  $f(s_t | y_{1:t})$ . Particle filters approximate  $f(s_t | y_{1:t})$  as a sum of  $N$  weighted particles, that is,  $f(s_t | y_{1:t}) \approx \sum_{i=1}^N \delta(s_t - s_{i,t}) w_i$ , where  $\delta$  is the Dirac delta function,  $w$  denotes normalised weights and  $i$  indexes particles. We perform inference for the latent states, assuming static parameters (in the movement and observation models) can be specified using supporting datasets, domain expertise and literature. Starting with an initial set of particles sampled from the prior (i.e.  $s_{i,1} \sim f(s_1)$ ), the filter iteratively simulates particles via the movement model (i.e.  $s_{i,t} \sim f(s_{i,t} | s_{i,t-1})$ ), weights particles in line with the likelihood (via  $w_{i,t} \propto w_{i,t-1} f(y_t | s_{i,t})$ ) and resamples particles accordingly.

### 2.2.2 | Smoother

Particle smoothers re-weight filtered particles to approximate the full marginal,  $f(s_t | y_{1:T})$ . The two-filter smoother uses  $N$

particles ( $s_{i,t}$ ) from a forward filter (with weights  $w_{i,t}$ ) and  $N$  particles ( $\tilde{s}_{j,t}$ ) from a backward filter (with weights  $\tilde{w}_{j,t}$ ). The distribution  $f(s_t | y_{1:T})$  is approximated as a sum of re-weighted particles via  $f(s_t | y_{1:T}) \approx \sum_{j=1}^N \delta(s_t - \tilde{s}_{j,t}) \tilde{w}_{j,t|T}$ , where the smoothed weights for each particle  $\tilde{s}_{j,t}$  represent a summation over all possible movements from preceding particles on the forward filter, that is,  $\tilde{w}_{j,t|T} \approx \tilde{w}_{j,t} \sum_{i=1}^N f(\tilde{s}_{j,t} | s_{i,t-1}) w_{i,t-1}$ . We use samples from  $f(s_t | y_{1:T})$  to map utilisation distributions (Lavender et al., 2025a). Sampling from the joint distribution,  $f(s_{1:T} | y_{1:T})$ , is more expensive and beyond the scope of this contribution.

## 3 | PACKAGE

patter supports data input, algorithms and mapping (Figure 1).

For data input, patter provides `sim_*`() functions for de novo simulation or accepts real-world datasets.

Particle algorithms are implemented by `pf_*`() functions. Filtering and smoothing are implemented via `pf_filter()` and `pf_smoother_two_filter()`. We provide movement models and methods that evaluate the likelihood of acoustic and depth observations, but algorithm components can be customised as required. The main output is a `data.table` of particles. The core routines use Patter.jl. JuliaCall implements the coupling between the patter and Patter.jl packages (Li, 2019). Movement and observation models are multithreaded and designed for numerical stability. We anticipate that most users will prefer the R front end, but Patter.jl can also be used directly.

Mapping functions (`map_*`()) facilitate subsequent analysis, including the reconstruction of utilisation distributions (Lavender et al., 2025a). Routines include `map_pou()`, which maps probability-of-use across a grid; `map_dens()`, which incorporates kernel smoothing; and `map_hr_*`() functions, which compute home ranges.

## 4 | EXAMPLES

### 4.1 | Overview

We provide two examples using simulated data. Both examples consider the movements of a benthic animal in a hypothetical acoustic array spanning a marine protected area (MPA) in Scotland (Figure 2). The study area is defined by a 100 × 100m resolution bathymetry grid. We base the grid on real-world data (Howe et al., 2014) but, for the purposes of our first example, add some random noise such that each cell's depth is unique. Within this region, we tag an animal with an acoustic transmitter and an archival depth tag. We imagine that both tags operate at a resolution of 2min and simulate a discrete-time random walk at this resolution over a 1-month period (Figure 2b,c). We simulate acoustic and depth observations arising from the simulated path and apply our algorithms to these data to reconstruct movements and patterns of space use. In the first example,

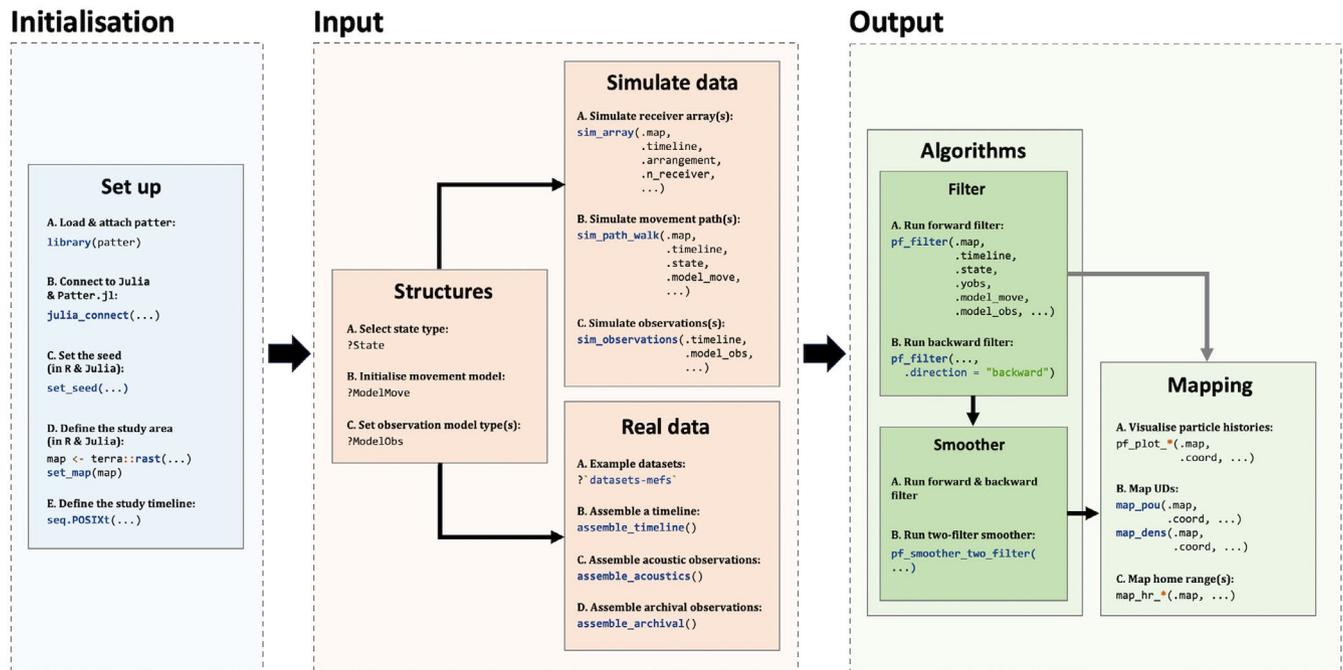
**patter workflow**

FIGURE 1 Package overview.

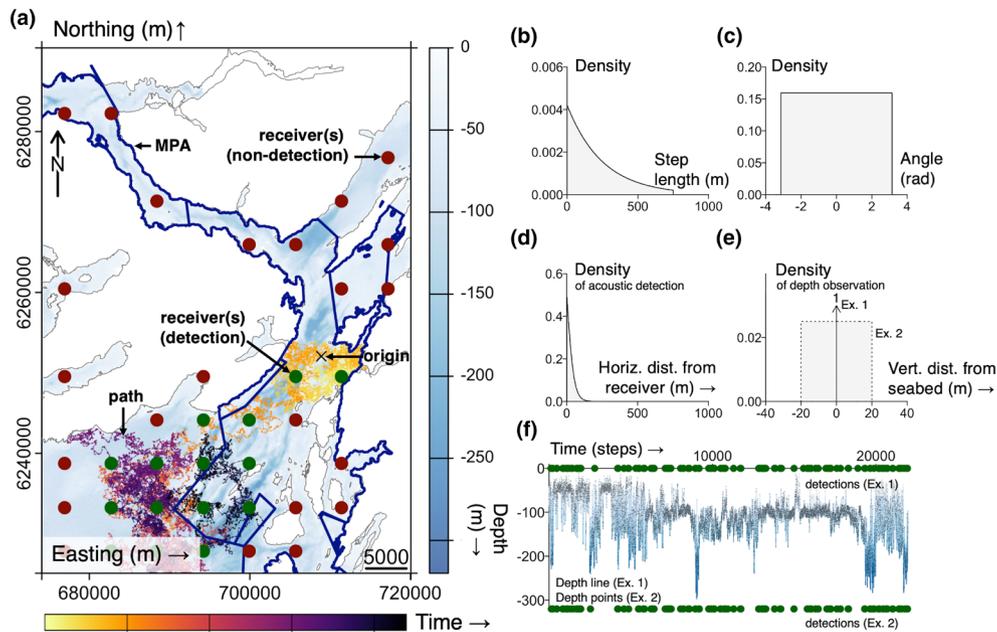


FIGURE 2 A state-space model for animal-tracking data. (a) A study area, including a simulated movement path (coloured by time) and acoustic receivers (sized by detection range and coloured by detection(s)/non-detection). (b, c) The components of the random walk used to simulate and model movements. (d, e) The observation models used to simulate and model acoustic and depth observations arising from the simulated path in the two worked examples; the acoustic observation model is constant, but the depth model differs (see Section 4.1). (f) The simulated time series for each example.

we simulate observations in such a way that the depth observation exactly defines the location of the individual (which is situated on the seafloor) (Figure 2d–f). This example will demonstrate that, in the absence of uncertainty, the particle filter reconstructs the true movement path. In the second example, we simulate observations

probabilistically and demonstrate the representation of uncertainty in particle algorithms and maps of space use (Figure 2d–f). The following sections showcase key functions and arguments (Figure 1). Additional arguments are denoted by ellipses. Complete code is available online (Lavender et al., 2025b).

## 4.2 | Implementation

### 4.2.1 | Simulation

We begin with essential initiation:

```
library(patter)
library(data.table)
julia_connect()
```

Next, we define the study system:

```
# Define study period
timeline <- seq(as.POSIXct("2023-01-01 12:00:00", tz = "UTC"),
               as.POSIXct("2023-01-31 23:58:00", tz = "UTC"),
               by = "2 mins")

# Define study site (map: SpatRaster)
set_map(map)
```

We simulate an acoustic array (i.e. data.table of receivers). We include three receiver columns that represent observation model (detection probability) parameters:

```
moorings <- sim_array(map,
                     timeline,
                     .n_receiver = 100L,
                     .arrangement = "regular",
                     .receiver_alpha = 4,
                     .receiver_beta = -0.01,
                     .receiver_gamma = 750)
```

We then simulate a two-dimensional random walk in this area:

```
# Define state type for 2D walk
# (s_t = (s_x, t), s_y, t)), truncated by boundaries
state <- "StateXY"

# Define movement model that updates s_t
# d_t ~ TruncatedGamma(k, theta, 0, mobility)
# phi_t ~ Uniform(a, b)
model_move <-
  move_xy(dbn_length = "truncated(Gamma(1.0, 250.0), upper =
  750.0)",
          dbn_angle = "Uniform(-pi, pi)")

# Simulate 2D path (data.table of states)
# s_t = (s_x, t-1) + d_t * cos(phi_t), s_y, t-1) + d_t * sin(phi_t),
# subject to boundary conditions
path <- sim_path_walk(map,
                     timeline,
                     state,
                     model_move, ...)
```

Next, we simulate acoustic and depth observations. This requires defining a vector of observation model (ModelObs) structures (which hold model parameters) and a corresponding list of data.tables (with those parameters). For both examples, we simulate acoustic observations from a truncated logistic model (for which we provide the ModelObsAcousticLogisTrunc structure and the essential parameters are defined in moorings). To simulate depths, we consider a simple version of the uniform model described previously, as implemented by the ModelObsDepthUniform structure, where  $\epsilon_{\text{shallow}}(s_t)$  and  $\epsilon_{\text{deep}}(s_t)$  are the constants depth\_shallow\_eps and depth\_deep\_eps.

In the first example, we imagine an animal found exclusively on the seabed, the depth of which is known exactly, giving parameters:

```
data.table(sensor_id = 1L,
           depth_shallow_eps = 0,
           depth_deep_eps = 0)
```

In the second example, we incorporate uncertainty:

```
data.table(sensor_id = 1L,
           depth_shallow_eps = 20,
           depth_deep_eps = 20)
```

For each example, sim\_observations() simulates a list of observations:

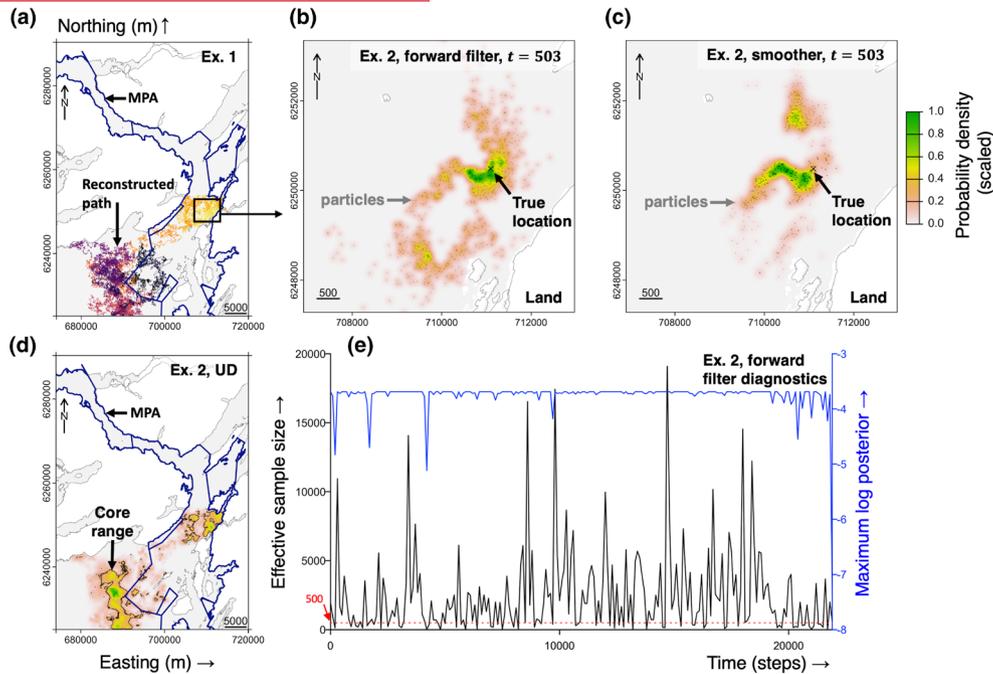
```
model_obs <- c("ModelObsAcousticLogisTrunc", "ModelObsDepthUniform")
obs <- sim_observations(timeline,
                      model_obs,
                      .model_obs_pars = list(...))
```

where list(...) denotes the parameter data.tables for the relevant example.

### 4.2.2 | Particle filter

The particle filter is implemented via:

```
pf_filter(
  map,
  timeline,
  state,
  xinit,
  .yobs = list(...),
  .model_obs = model_obs,
  .model_move = model_move,
  .n_particle = 1e5L,
  .direction = "forward", ...
)
```



**FIGURE 3** Outputs for the first (a) and second (b–e) worked examples. (a) is the movement path reconstructed by the particle filter for the first example. The simulated path is recovered perfectly (at grid resolution) because the observations exactly define the individual's location. (b, c) show particles and scaled probability densities from the forward filter and two-filter smoother, respectively, at a selected time step. (d) maps the pattern of space use over the entire time series using smoothed particles. Core ranges contain 50% of the probability mass volume. Estimated residency in the MPA is 37.0% (the true value is 36.3%). (e) shows diagnostics from the forward filter. The minimum value of each statistic is shown for every 100 time steps.

where `.xinit` (optional) is the simulated tagging location and `.jobs` is the list of datasets for the relevant example. This returns a `pf_particles`-class object that includes a `data.table` of particles and diagnostic statistics. In the first example, the filter reconstructs the true (unobserved) path. In the second example, we generate a 'cloud' of particles at each time step, for which we examine particle diagnostics and proceed to smoothing.

#### 4.2.3 | Particle smoother

Particle smoothing is implemented using outputs from a forward and backward filter via

```
pf_smoother_two_filter(...)
```

For illustration, we reconstruct the utilisation distribution and home range from smoothed particles via `map_dens()` and `map_hr()`. We also compare time spent in the MPA, estimated from the proportion of particles inside the MPA, to the truth.

This workflow is highly customisable. `patter` provides customisable, built-in structures for selected movement models (such as random walks) and observation types (such as acoustic observations). User-defined structures, for complete customisation, are also supported. See the package documentation for details.

### 4.3 | Results

In our first example, the particle filter reconstructs the simulated movement path perfectly (Figure 3a). In the second example, in which observations were simulated with error, the particle filter represents the individual's possible locations at each time step with a series of weighted particles that approximate  $f(s_t | y_{1:t})$  (Figure 3b). The particle smoother re-weights filtered particles, approximating  $f(s_t | y_{1:T})$  (Figure 3c). Smoothed particles can be used to map patterns of space use, estimate home ranges and quantify residency (Figure 3d). The quality of the smoothing depends on the filter. In this case, filter diagnostics are adequate (Figure 3e). Total computation time ranged from 5 to 32 min for examples 1–2 on a 2023 MacBook Pro (Apple M2 Pro, 32GB RAM, 12 CPUs).

## 5 | DISCUSSION

`patter` provides a robust, fast and accessible implementation of particle algorithms for animal tracking, especially with passive acoustic telemetry (Lavender et al., 2025a). These algorithms represent the movement and observation processes that generate observations, including movement capacity, barriers to movement and detection probability, within a biologically and statistically sound framework. The movement and observation models are fully customisable, making the routines applicable in many real-world settings. However,

understanding the settings in which different methods are more or less useful remains an important research area (Lavender et al., 2025a).

The patter workflow involves formulating a state-space model for the state of a tagged animal and performing inference via particle filtering and smoothing. A biological challenge during this process is the formulation of the movement and observation submodels. Currently, patter requires users to parameterise submodels a priori. This is a trade-off between inferential flexibility and computational efficiency. We consider the primary purpose of positional animal-tracking (e.g. acoustic telemetry) studies to learn about patterns of space use, rather than locomotory capacity or observational processes (such as detection probability). Other approaches, such as accelerometry studies and drift tests of detection probability, can provide more detailed information on the latter (especially in sparse acoustic arrays). We encourage users to leverage these data, alongside domain knowledge and literature, to parameterise models (Lavender et al., 2025a). That being said, we recognise that joint inference may be desirable in situations where data are sufficient and this is a possible future development. Joint inference is expensive, but there are routines, such as Hamiltonian Monte Carlo, that offer potential in this regard (Albert et al., 2015).

A key feature of patter is speed. We achieve competitive speeds by focusing inference on individual states, targeting marginal (rather than joint) distributions and via a performant Julia backend. While formal benchmarks are lacking, simple comparisons are instructive. Run times for a Python particle filtering application estimating daily posterior distributions for demersal fish over a 1-year period are approximately 1 h (Liu et al., 2019). Other geolocation routines that fit hidden Markov models via likelihood approximation typically require hours or days to derive daily geolocation estimates over the same timeframe (Pedersen et al., 2008). Inference using Markov Chain Monte Carlo algorithms (which directly sample static parameters and trajectories) is also often expensive. For example, we observed that Hostetter and Royle (2020)'s state-space model for acoustic detections ( $T = 150$ ) requires  $\approx 15$  h to fit with their JAGS code on a standard computer. With our particle filtering-smoothing algorithm, the estimation of latent locations in this situation is soluble in seconds. While run times are not directly comparable, it is encouraging to see patter achieving speeds sufficient to make particle algorithms serious candidates for real-world analyses.

For applied studies, we suggest the use of simulations to guide method implementation and interpretation. Particle filters can be sensitive to model parameters and tuning settings (such as particle number) and system-specific simulations can inform input arguments and quantify sensitivity (Lavender et al., 2025a). For an example real-world analysis, we direct the reader to Lavender, Scheidegger, Albert, Biber, Aleynik, et al. (2025), who analysed acoustic and archival data from a Critically Endangered elasmobranch to quantify patterns of space use and site affinity in a Scottish Marine Protected Area. There is much to be learnt from applications in other settings, and we welcome community feedback as these developments are exploited.

## AUTHOR CONTRIBUTIONS

Edward Lavender conceived the study and developed the methodology with Andreas Scheidegger, Carlo Albert and Helen Moor (Principal Investigator). This was motivated by work on the Movement Ecology of Flapper Skate project established by James Thorburn and an earlier modelling study led principally by Edward Lavender, Stanisław Biber, Janine Illian and Sophie Smout (Principal Investigator). In the current study, Edward Lavender and Andreas Scheidegger wrote the code. Edward Lavender analysed the data and led the writing of the manuscript. All authors contributed to drafts and gave approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.70029>.

## DATA AVAILABILITY STATEMENT

The patter and Patter.jl packages are available on GitHub (Lavender, 2024a, 2024b). Code is available via <https://doi.org/10.5281/zenodo.12771850> (Lavender et al., 2025b).

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