

1 **foieGras** an R package for animal movement data:
2 rapid quality control, behavioural estimation and
3 simulation

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15 Abstract

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20 Keywords:

²¹ 1 | Introduction

²² The use of animal-borne electronic sensors has matured, with tracking data now virtually
²³ essential for understanding behaviour and social interactions, foraging ecology, physiology,
²⁴ habitat use and population dynamics of mobile and/or cryptic species. The sophistication of
²⁵ current technology also enables the use of animal-borne sensors as a cost-effective approach
²⁶ for observing our planet that complements more traditional observing platforms (Harcourt
²⁷ et al., 2019; Kays et al., 2015; McMahon et al., 2021). In all these applications, data from
²⁸ electronic tracking devices require rigorous quality control procedures to account for common,
²⁹ though not universally present, issues such as irregularly timed measurements, sensor biases
³⁰ and location measurement error. Some of these issues may be handled by a manufacturer's
³¹ on-board or post-processing algorithms and some must be addressed by researchers using the
³² data.

³³ State-space models (SSMs) and hidden Markov models (HMMs) are powerful tools for
³⁴ conducting quality control of and making behavioural inference from animal tracking data
³⁵ (Jonsen et al., 2013; Patterson et al., 2008). These are time-series models used across a
³⁶ wide range of research disciplines that estimate the state of an unobserved process from
³⁷ an observed data set. Here, we view an animal's true location and/or behaviour as the
³⁸ unobserved state(s), though many other types of states are possible (Hooten et al., 2019; e.g.,
³⁹ Schick et al., 2013), and measurements recorded by electronic devices provide the observations.
⁴⁰ In practical yet simplistic terms, SSMs are usually preferred when the goal is to quality
⁴¹ control error-prone location data and/or make inference directly from the parameters of
⁴² their underlying movement models. HMMs are usually preferred when measurements have
⁴³ negligible error and occur at regular time intervals (but see McClintock & Michelot, 2018), and
⁴⁴ when the goal is to infer behavioural states hidden within the data along with their potential
⁴⁵ external or internal drivers. Other more technical distinctions and reasons for preferring one
⁴⁶ of these methods exist (Jonsen et al., 2013; Patterson et al., 2017). Our primary focus here is

47 on SSMs as tools for quality control of error-prone location data and for making fast inference
48 of behavioural changes along animal tracks.

49 A number of R packages such as `moveHMM` (Michelot et al., 2016), `momentuHMM` (McClintock
50 & Michelot, 2018), and `swim` (Whoriskey et al., 2017) provide highly accessible and flexible
51 tools for fitting HMMs to animal tracking data, and facilitating general inference of animal
52 movement behaviour and its drivers. Similarly, R packages such as `bsam` (I. Jonsen et al., 2005),
53 `crawl` (Johnson et al., 2008), `argosTrack` (Albertsen et al., 2015), `ctmm` (Calabrese et al.,
54 2016), and `yaps` (Baktoft et al., 2017) all provide tools for fitting movement process models in
55 either discrete- or continuous-time, ranging from simple random walks to Ornstein-Uhlenbeck
56 processes, in state-space form to various types of tracking data.

57 Here, we introduce the package `foieGras`, pronounced “*fwah grah*”, developed for R (R
58 Core Team, 2021). This package was developed with two aims: (1) to be a simple and fast
59 implementation of SSMs for quality control of error-prone animal (re)location data (including
60 via Argos satellite, Service Argos (2016);Jonsen:2020); and (2) for inference of changes in
61 behaviour along animal movement tracks (Jonsen et al., 2019). The simplicity of use sets
62 `foieGras` apart from many of the related SSM R packages listed above, yet users can exert
63 control over many aspects of the package functions via optional arguments. This design
64 accommodates both novice and experienced users.

65 Here, we describe the main features of `foieGras` and illustrate its use through a set of
66 applications drawing on Argos and GPS tracking data. Full R code and data for each of
67 the applications is provided in the Supporting Information. Additional details on package
68 functions and their use can be found in their help files and in the package vignettes.

69 **2 | foieGras overview**

70 The workflow for `foieGras` is deliberately simple, with many of the usual track data processing
71 checks and formatting handled automatically. Here we outline the main aspects of the

Table 1: Main functions for the R package `foieGras`

Function	Description
<code>fit_ssm</code>	Fit a State-Space Model to location data
<code>fit_mpm</code>	Fit a Move Persistence Model to location data
<code>grab</code>	Extract fitted/predicted/observed locations from a foieGras model, with or without projection information
<code>osar</code>	Estimate One-Step-Ahead Residuals from a foieGras SSM
<code>map</code>	Map fitted/predicted locations with or without a defined projection
<code>sim</code>	Simulate individual animal tracks with Argos LS or KF errors
<code>simfit</code>	Simulate animal tracks from ‘ssm_df’ fit objects
<code>sim_filter</code>	Filter tracks simulated with ‘simfit’ according to similarity criteria
<code>route_path</code>	Reroute path so estimated locations are off land
<code>plot.ssm_df</code>	Plot the fit of a foieGras SSM to data
<code>plot.osar</code>	Plot One-Step-Ahead Residuals from a foieGras SSM

⁷² `foieGras` package. The packages’s main functions are listed in Table 1.

⁷³ 2.1 | Data preparation

⁷⁴ Animal tracking data, consisting of a time-series of location coordinates, can be read into R
⁷⁵ as a data frame using standard functions such as `read.csv`. The canonical data format for
⁷⁶ Argos tracks consists of a data frame with 5 columns corresponding to the following named
⁷⁷ variables: `id` (individual id), `date` (date and time), `lc` (location class), `lon` (longitude), `lat`
⁷⁸ (latitude). Optionally, an additional 3 columns, `smaj` (semi-major axis), `smin` (semi-minor
⁷⁹ axis), `eor` (ellipse orientation), providing Argos error ellipse information may be included.
⁸⁰ Other types of location data can be accommodated, for example, by including the `lc` column
⁸¹ where all `lc = "G"` for GPS data. In this case, measurement error in the GPS locations is
⁸² assumed to have a standard deviation of 0.1 x Argos class 3 locations (approximately 30 m).
⁸³ If location standard errors exist, these can be added by appending the columns `lonerr` and

84 `laterr` to the data (see the Overview vignette for further details).

85 **2.2 | State-space model fitting - `fit_ssm`**

86 State-space models are fit using `fit_ssm`. When fitting a SSM to location data, the type of
87 data is automatically detected from the location quality class designations that are typical of
88 Argos data and that can be added to the data by the researcher for other types of location
89 data. Based on the location quality classes and optional information on measurement errors
90 contained in the data, an appropriate measurement error model is selected for each observation
91 (Jonsen et al., 2020). This capability can allow different tracking data types, such as Argos
92 and GPS, to be combined in a single input data frame and to be fit in a single state-space
93 model.

94 There are a large number of arguments that can be set in `fit_ssm`, and these are explained
95 in the documentation. We focus only the essential arguments here:

- 96 • `data` the input data structured as described in **2.1**
97 • `model` the process model to be used
98 • `time.step` the prediction time interval (h)

99 The function first invokes an automated data processing stage where the following occurs:
100 1) data type (Argos Least-Squares, Argos Kalman Filter/Smoother, GPS, or General (e.g.,
101 processed light-level geolocations, acoustic telemetry, coded VHF telemetry) is determined; 2)
102 date-times are converted to POSIXt format, chronological order is ensured, and duplicate
103 date-time records are removed; 3) observations occurring less than `min.dt` seconds after a
104 prior observation are removed (default: 60 s); 4) a speed filter [`sda` from the `trip` R package;
105 Sumner et al. (2009)] is used to identify potential extreme locations to be ignored by the
106 SSM; 5) locations are projected from spherical lon,lat coordinates to global Mercator x,y
107 coordinates in km.

108 The function then fits a state-space model to the processed data, where the process model

109 (one of `rw`, `crw`, or `mp`) is specified by the user via the `model` argument, and the measurement
110 model(s) are selected automatically. The model is fit by numerical optimization of the
111 likelihood using either of the standard R optimizers, `optim` or `nlminb`. The R package `TMB`,
112 Template Model Builder (Kristensen et al., 2016), is used to compute the gradient function
113 in C++ via reverse-mode auto-differentiation and the Laplace Approximation is used to
114 integrate out the latent states (random effects). Fits to a single versus multiple individuals are
115 handled automatically, with sequential SSM fits occurring in the latter case. No hierarchical
116 or pooled estimation among individuals is currently available.

117 `fit_ssm` returns a `ssm_df` fit object (a nested data frame with class `ssm_df`). The outer data
118 frame lists the individual id(s), basic convergence information and a list with class `ssm`. This
119 list contains dense information on the estimated parameters and states, predictions, processed
120 data, optimizer results, and other diagnostic and contextual information. Users can extract a
121 simple data frame of SSM fitted (location estimates corresponding to the observation times) or
122 predicted values (locations predicted at regular `time.step` intervals) using the `grab` function.
123 Parameter estimates, AIC and other model fit information can be viewed in tabular form
124 using the `summary` function.

125 **2.3 | Behavioural estimation - `fit_ssm`, `fit_mpm`**

126 Move persistence, an index of along-track movement behaviour, can be estimated as a
127 continuous-valued (0 - 1), time-varying latent variable that represents changes in movement
128 pattern based on autocorrelation in speed and direction Jonsen et al. (2019). There are
129 two approaches in `foieGras` for estimating move persistence. The first is to use `fit_ssm`
130 with `model = 'mp'`, which fits a continuous-time move persistence model in state-space
131 form and thereby simultaneously estimates true locations and move persistence from the
132 error-prone telemetry data. This approach is most appropriate for fitting to irregularly-timed
133 and error-prone Argos data as both aspects are taken into account explicitly. The second
134 is to use `fit_mpm`, which can take as input either location data or SSM-estimated locations

135 from an `ssm_df` fit object. This approach is generally more appropriate when the data have
136 minimal measurement error (e.g., GPS locations), or when time-regularization is desired. We
137 illustrate both approaches in Application 3.2.

138 **2.4 | Model checking and visualization - `osar`, `plot`, `map`**

139 Before using fitted or predicted locations, a `fit_ssm` model fit should be checked and visualized
140 to confirm that the model adequately describes the data. There is no simple way to calculate
141 residuals for latent variable models that have non-finite state-spaces and that may be nonlinear,
142 but they can be computed based on iterative forecasts of the model (Thygesen et al., 2017).

143 The `osar` function computes one-step-ahead (prediction) residuals via the `oneStepPredict`
144 function from the `TMB` R package to make this as efficient as possible. A set of residuals
145 are calculated for the `x` and `y` values corresponding to the fitted values from the SSM and
146 returned as an `osar` object. A generic `plot` (`plot.osar`) method provides an easy way to
147 visualize the `osar` residuals as time-series plots, quantile-quantile plots, or autocorrelation
148 functions.

149 State-space model fits to data can also be visualised by using the generic `plot` (`plot.ssm_df`)
150 function on an `ssm_df` fit object. Options exist to plot fitted or predicted values along with
151 observations as either paired, 1-D time-series, as 2-D tracks with 95% confidence intervals or
152 ellipses, by using the argument `type = 1` and `type = 2`, respectively. These plots provide a
153 rapid check on SSM fits to data. Additionally, when the fitted SSM is the move persistence
154 model (i.e., `model = 'mp'`), 1-D time-series (`type = 3`) or 2-D track plots (`type = 4`) of
155 move persistence can be viewed.

156 Additionally, a `fit_ssm` model fit can be mapped using the `map` function for single or multiple
157 individuals. By default, `map` uses the coastline data from the `rnaturrearth` R package
158 (South, 2022a) at medium or high resolution, if the `rnaturrearthhires` (South, 2022b) R
159 package is installed, but can also use tiled maps for finer-scale detail, if the `rosm` (Dunnington,
160 2019) and `ggspatial` (Dunnington, 2021) R packages are installed. Mapping aesthetics (e.g.,

161 plot symbols, sizes, colours, fills) can be customized via the `aes` argument and use of the
162 `aes_lst` function. See code in SI for examples.

163 All `foieGras` visualizations draw on the `ggplot2` R package (Wickham, 2016), with multi-
164 panel plots also using the `patchwork` R package (Pedersen, 2020), and generally can be
165 modified through additive calls in the usual `ggplot2` manner. See code in SI for examples.

166 **2.5 | Simulation - `sim`, `simfit`, `sim_filter`**

167 Track simulation can be a helpful, yet informal, way of evaluating the degree to which
168 statistical movement models capture essential features of animal movement data (Michelot et
169 al., 2017). The `sim` function can simulate a variety of movement process, including the `rw`,
170 `crw`, and `mp` process models, as well as simple multiple movement state switching processes.
171 Simulations from different process models can be used to evaluate the robustness of SSM
172 location and move persistence estimates to model misspecification. An example is provided in
173 the SI.

174 Simulation is also used frequently in habitat usage modelling to provide a measure of habitat
175 availability (Aarts et al., 2012) by generating a source of ‘background’ points representing a
176 null model of the distribution of foraging animals in the absence of external drivers (Hindell
177 et al., 2020; S. J. Phillips et al., 2009; Raymond et al., 2015). The `simfit` function extracts
178 movement parameters from a `ssm_df` fit object and simulates a user defined number of random
179 tracks of the same duration from these parameters. The argument `cpf = TRUE` allows the
180 user to simulate central place foragers by ensuring that the simulated tracks start and end at
181 approximately the same location. It is also possible to constrain movements to remain mostly
182 in water via a potential function (Preisler et al., 2013), using included gradient rasters and
183 the `grad` and `beta` arguments. These are illustrated in the code for Application 3.3.

184 The choice of null points can have a large impact on the performance of habitat suitability
185 models (Lobo et al., 2010; S. J. Phillips et al., 2009), and so the `sim_filter` function provides

186 a tool to filter the simulated tracks based on their similarity to the original path. The filtering
187 is based on one of two metrics that capture the difference in the net displacement and bearing
188 between the two paths (see `similarity_flag` for more detail). This metric is motivated by
189 the ‘flag value’ described in Hazen et al. (2017). The user can also specify the quantile of flag
190 values to retain; i.e. `keep = 0.25` (the default) will return a `simfit` object containing those
191 simulated tracks with flag values in the top 25% of values calculated for the input `simfit`
192 object.

193 **2.6 | Path rerouting - `route_path`**

194 As the SSMS implemented in `foieGras` have no information about potential barriers to animal
195 movement it is possible for locations to be estimated in implausible locations, such as on
196 land for marine species. To overcome this, `foieGras` makes use of the `pathroutr` R package
197 (London, 2020) to efficiently re-route locations from land back to water by using visibility
198 graphs (Jan et al., 2014). The `route_path` function can be applied to either a `fit_ssm` model
199 fit (`ssm_df` object) or the simulations generated by `simfit`. When the input is an `ssm_df`
200 object the re-routed path can be appended to the object for visualisation and use in subsequent
201 analyses. When the input is a `simfit` object the locations within the simulation are replaced
202 with the re-routed paths. We illustrate how the latter can be achieved in Application 3.3.

203 **3 | Applications**

204 We illustrate the main capabilities of `foieGras` through a set of applications that are for
205 demonstration purposes and not intended as a comprehensive guide for conducting analyses
206 with `foieGras`. Complete code and data for reproducing the applications and for gaining a
207 deeper understanding of `foieGras` functions are provided in the Supplementary Information.

208 **3.1 | SSM validation with prediction residuals**

209 We use a sub-adult male southern elephant seal (*Mirounga leonina*) track included as example
210 data in `foieGras` (`sese2`, id: ct36-E-09), sourced from the Australian Integrated Marine
211 Observing System (IMOS; data publicly available via imos.aodn.org.au) deployments at Iles
212 Kerguelen in collaboration with the French IPEV and SNO-MEMO programmes. The data
213 are temporally irregular Argos Least-Squares based locations, 74 % of which are in the poorest
214 location quality classes: A and B. We fit both the `rw` and `crw` models using `fit_ssm` with a
215 speed filter threshold (`vmax`) of 4 ms⁻¹ and a 12-h time step. We calculate prediction residuals
216 using `osar`, and then use the generic `plot` method for `osar` residuals to assess and compare
217 the model fits (Fig. 1).

218 The plots of predicted states on top of the observations suggest both models yield similar
219 fits (Fig. 1a; orange vs red lines). However, corresponding predicted locations from the two
220 models differ by a median 6.62 km (range: 0.02, 53.02 km), and there are marked trends in the
221 time-series of residuals for the `rw` model fit (Fig. 1b) with significantly positive autocorrelation
222 in both the x and y directions (Fig. 1d). The `crw` prediction residuals show little trend
223 through time and have relatively little autocorrelation (Fig. 1c,e), implying that the `crw`
224 process model provides a better fit to the data.

225 **3.2 | Inferring move persistence from Argos and GPS data**

226 ***Argos data - southern elephant seals***

227 Drawing on additional IMOS tracking data from Iles Kerguelen, we infer move persistence, γ_t ,
228 along four southern elephant seal tracks. We fitted the `mp` SSM with a 12-h prediction interval
229 with `fit_ssm`, using the Argos Kalman filter-derived error ellipse information provided with
230 each observation (Jonsen et al., 2020). The `mp` SSM simultaneously estimates locations and
231 γ_t , and their uncertainties. We then assess how γ_t changes along the seals' tracks to infer
232 regions where the seals spend disproportionately more or less time during their foraging trips.

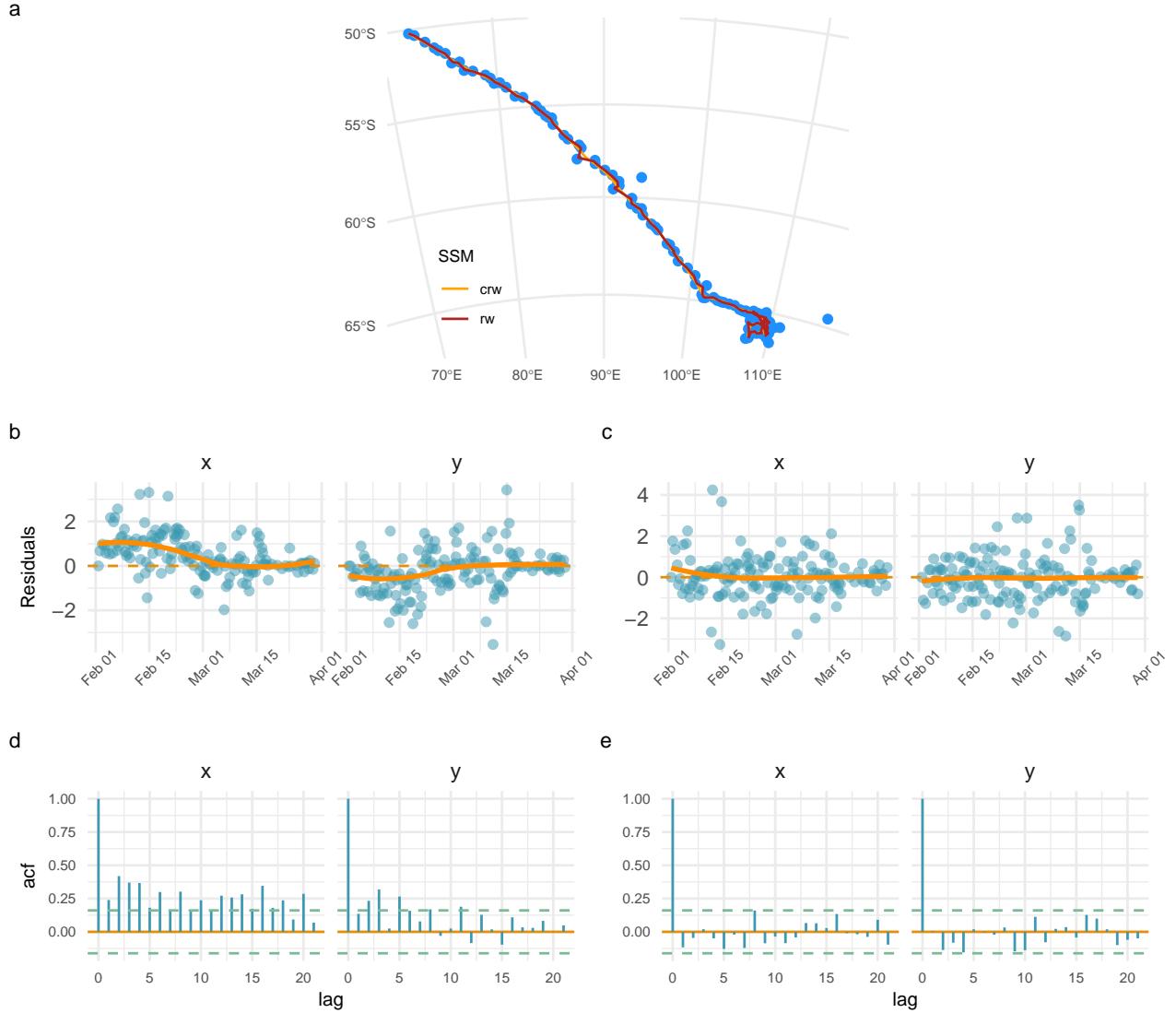


Figure 1: State-space model fits to a southern elephant seal track (a), and diagnostic plots for assessing goodness-of-fit of the **rw** (b - prediction residual time-series; d - prediction residual autocorrelation) and **crw** (c,e) state-space models. All residual plots generated using the `plot.osar` function.

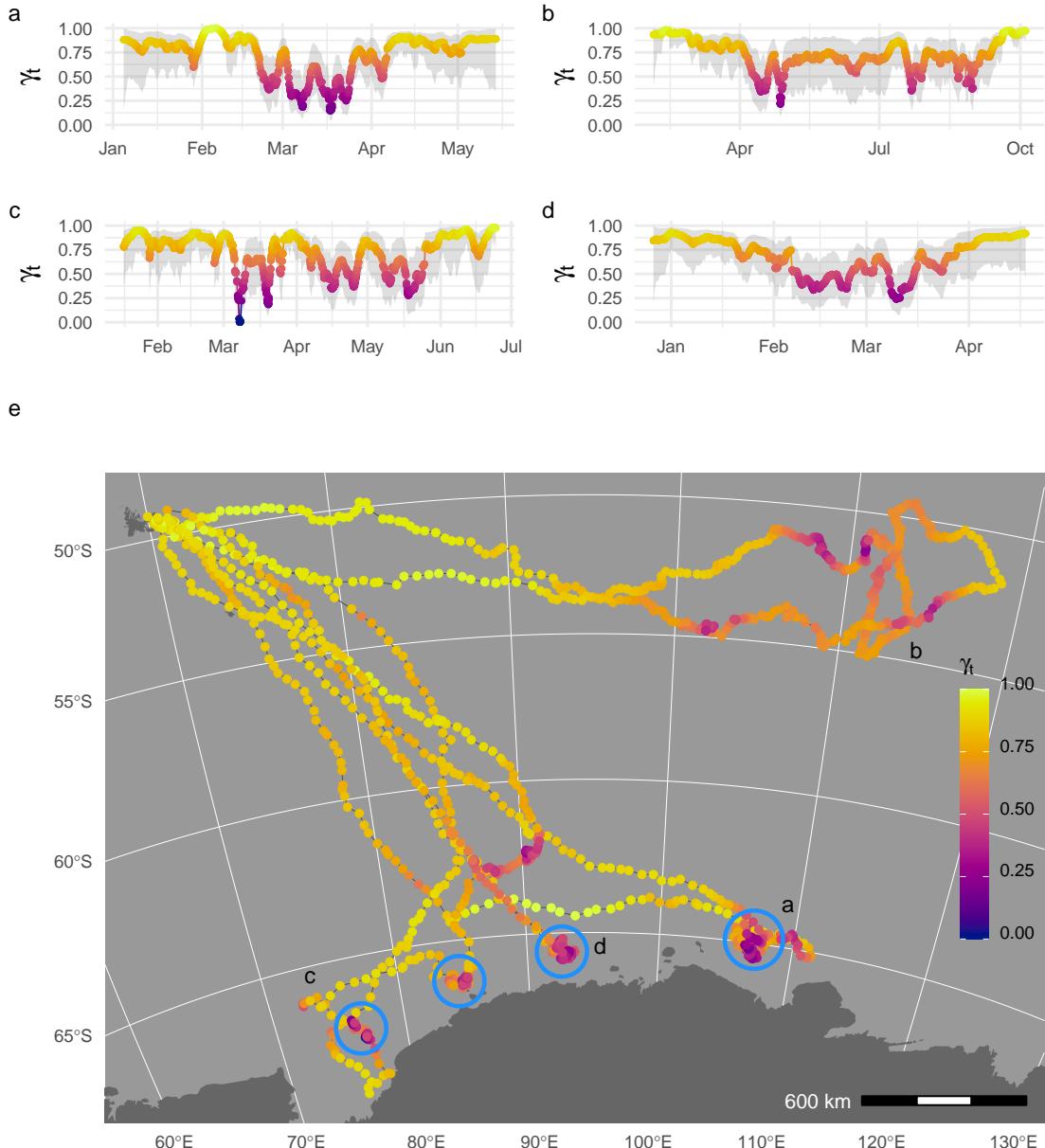


Figure 2: Inferred move persistence, γ_t , time-series for four southern elephant seals (a-d; grey envelopes are 95 % CI's, note differing date ranges on the x axes), and along their 2-D tracks (e; track labels, a-d, correspond to the time-series plots). Locations associated with low γ_t (purple) are indicative of slow, undirected movements, whereas high γ_t (yellow) is indicative of faster, directed movements. Blue circles highlight bouts of spatially constrained low γ_t .

233 The three southern elephant seals on foraging trips to the Antarctic shelf region all engaged in
234 spatially constrained bouts of low move persistence while in the shelf region (Fig. 2 a,c,d; blue
235 circles in e). Without additional data it is unclear exactly what these bouts of low horizontal
236 move persistence represent. They could result from area-restricted search and foraging within
237 dense prey aggregations, physical constraints of dense ice on horizontal movements, haulout
238 (resting) on sea-ice, or some combination of these. Conversely, the seal on a pelagic foraging
239 trip engaged in slower, more meandering movements with less spatially constrained bouts of
240 lower move persistence (Fig. 2 b, e). This general movement pattern may be consistent with
241 searching for suitable foraging resources within the highly variable eddy fields between the
242 Subantarctic and Polar Fronts (Jonsen et al., 2019).

243 ***GPS data - little penguins***

244 To illustrate how move persistence can be estimated from other types of animal tracking data,
245 we use four little penguin (*Eudyptula minor*) GPS tracks from daily foraging trips during the
246 chick-rearing period from Montague Island, NSW, Australia, and described in L. Phillips et
247 al. (2021). The data are temporally irregular GPS locations, with high frequency sampling
248 (15 s on average) intermittently disrupted by the birds' diving behaviour, and are assumed
249 to have minimal measurement error. We fitted the `crw` SSM to the GPS data to predict
250 temporally regular locations at 5-min intervals, and assumed consistently small bivariate
251 normal location measurement errors (ie. ± 10 m sd). We then used `fit_mpm` to estimate γ_t
252 from these regularised locations.

253 The little penguin GPS tracks did not exhibit strong contrast in move persistence, with γ_t
254 declining below 0.5 for only two of the birds (Fig. 3a-d). Nonetheless, the move persistence
255 estimates highlight change in movement pattern over the course of the penguins' daily foraging
256 trips (Fig. 3e). The penguins departed Montague Is. with relatively fast movements, three
257 directed southward (Fig. 3 tracks b-d in e) and one less directed and remaining close to the
258 island (track a), before slowing down and engaging in meandering movements (orange - red

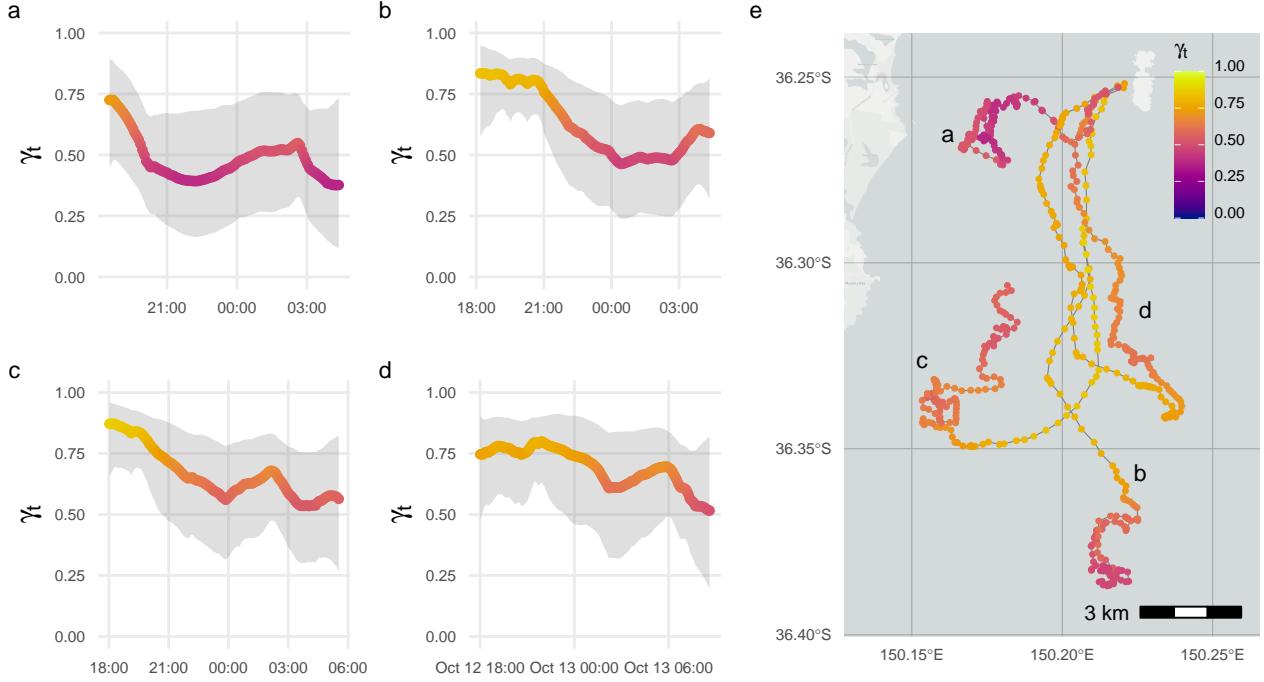


Figure 3: Inferred move persistence, γ_t , 1-D time-series (a-d; grey envelopes are 95 % CI's) and along little penguin GPS tracks (e).

in Fig. 3e). The spatially diffuse bouts of low move persistence within the penguin tracks may reflect the fine-scale patchiness of their forage-fish prey with search and prey-capture occurring both within and among discrete neighbouring prey aggregations (Carroll et al., 2017). **Lach/Gemma could we overlay SVM-inferred prey captures for these birds?**
(G123f02, G124m10, G126m05, L013m01)

3.3 | Simulating tracks from foieGras model fits

To illustrate how to simulate tracks from **foieGras** model fits we use a juvenile harp seal (*Pagophilus groenlandicus*) tracked from the Gulf of St Lawrence, Canada, and described in Grecian et al. (2022). The data are temporally irregular Argos locations including error ellipse information. We fit the **crw** model using **fit_ssm** with a 4 ms^{-1} speed filter threshold (**vmax**) and a 12-h prediction interval (**time.step**).

We simulate 50 animal movement paths from the **crw** process model using **simfit**, and apply

271 a potential function using the `grad` and `beta` arguments to constrain the simulated paths
 272 to largely remain in water. These tracks are then filtered based on their similarity to the
 273 original path using `sim_filter` and the top 10% retained (`keep = 0.1`) (Fig. 4a,b). As the
 274 potential function does not guarantee all locations remain off land, we re-route any remaining
 275 simulated locations from land back to water using `route_path` (Fig. 4c). In combination,
 276 these functions provide a pragmatic, non-statistical method to generate and objectively filter
 277 pseudo-tracks for use in movement or habitat modelling applications.

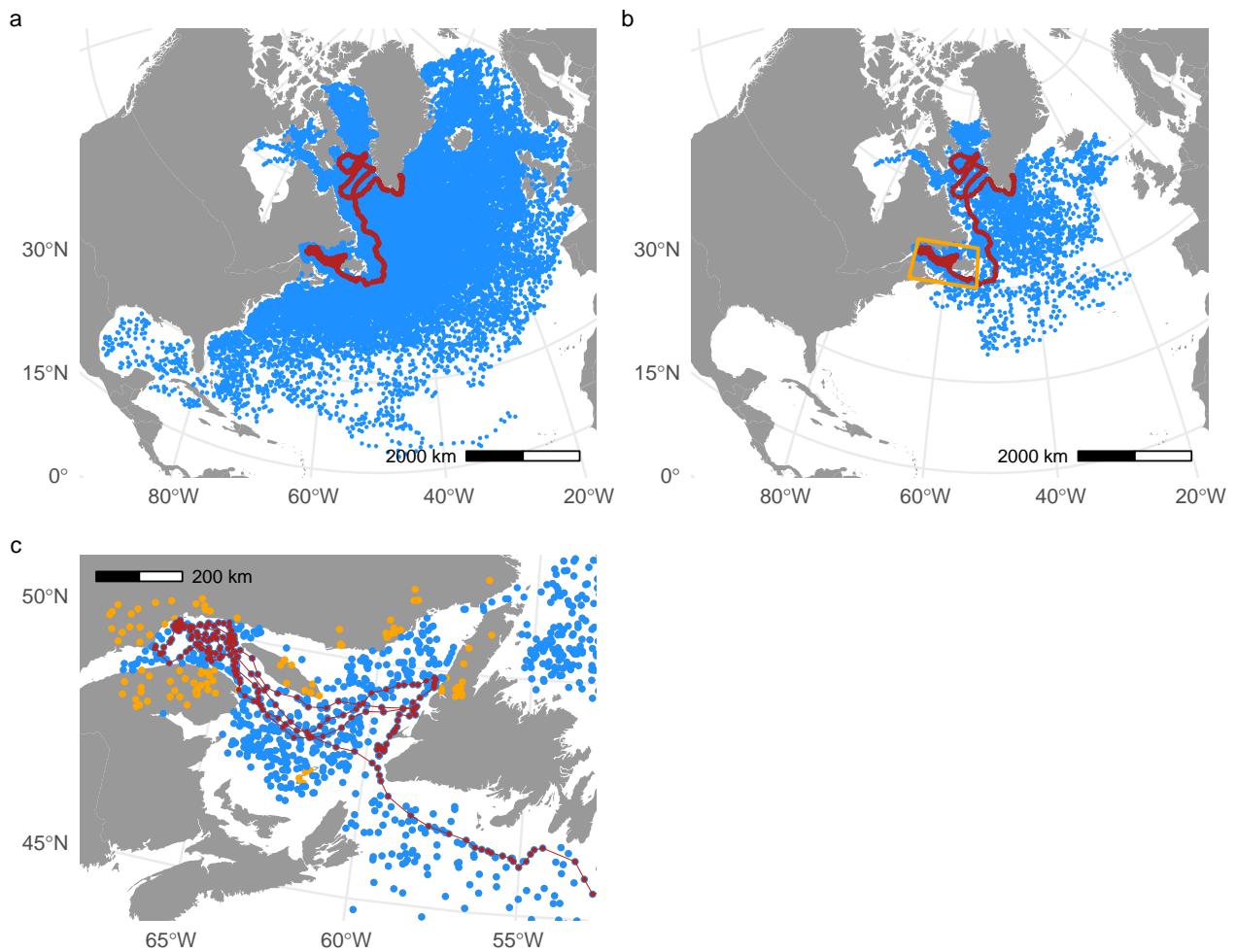


Figure 4: Simulating (a) 100 movement paths from a correlated random walk process model; (b) filtering those tracks to select the top 10% based on their similarity to the original SSM-predicted track (red); and (c) re-routing simulated locations on land (orange) back to ocean (blue). The orange box in (b) indicates region magnified in (c). SSM-predicted track (red) overlaid in all panels for context.

278 **4 | Conclusions**

279 The **foieGras** package was developed to ease fitting state-space models for quality control
280 of animal location data and for inference of behavioural change along animal tracks. We
281 achieve these primarily through a simple yet extensible workflow, model parsimony, and
282 computational speed. Combined, these traits accommodate both novice or occasional and
283 advanced users, and facilitate use in automated, operational quality-assurance/quality-control
284 processes for animal-borne ocean observations (Jonsen et al., 2020; McMahon et al., 2021).

285 The **foieGras** package is an intermediate analysis toolbox where location quality control
286 typically occurs after some initial data processing but prior to any comprehensive, final analysis.
287 In this vein, the move persistence model tools provide a simple, rapid approach for objectively
288 identifying changes in movement behaviour along animal tracks without any required *a priori*
289 knowledge or decisions about the kind or number of behavioural states hidden within the
290 data. Subsequent analysis could entail use of a hidden Markov model to infer relationships
291 between behaviour and environmental or individual covariates (McClintock & Michelot, 2018;
292 e.g., Michelot et al., 2016). Alternatively, move persistence - covariate relationships among
293 multiple individuals can be inferred rapidly in a mixed-effect model framework using the **mpmm**
294 package [Jonsen et al. (2019); <https://github.com/ianjonsen/mpmm>].

295 The package will undergo further development, expanding the range of available SSM's via
296 new movement process models and/or enhanced measurement models for other electronic
297 tracking data types. Additionally, we will seek to enhance integration with other R packages
298 for processing and analysis of animal movement data, where this makes sense. Feedback from
299 users is invaluable and highly encouraged. Users may submit bug reports and enhancement
300 suggestions via the foieGras GitHub issues page ([https://github.com/ianjonsen/foieGras/is
301 sues/new/choose](https://github.com/ianjonsen/foieGras/issues/new/choose)). More general feedback is always welcome by contacting the lead author
302 directly.

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310 Observing System (IMOS) supported seal fieldwork. IMOS is a national collaborative research
311 infrastructure, supported by the Australian Government and operated by a consortium of
312 institutions as an unincorporated joint venture, with the University of Tasmania as Lead
313 Agent. Field work at Illes Kerguelen was conducted as part of the IPEV programme N°
314 109 (PI H. WEIMERSKIRCH) and of the SNO-MEMO programme (PI C. GUINET) in
315 collaboration with IMOS. CTD tags were partly funded by CNES-TOSCA and IMOS. Little
316 penguin fieldwork was supported by an Australian Research Council Linkage grant to IDJ,
317 GC and RGH (LP160100162). All animal tagging procedures approved and executed under
318 the Animal Ethics Committee guidelines of the University of Tasmania (elephant seals),
319 Macquarie University (little penguins), and ... **University (harp seals) - JAMES, need**
320 **input here.**

321 **Author's Contributions**

322 IDJ developed the R package; WJG contributed harp seal data and to the R package; LP,
323 GC, and RGH contributed little penguin data; CRM and RGH contributed Southern elephant
324 seal data; IDJ and TAP developed the state-space models; IDJ wrote an initial draft of the
325 manuscript with contributions from WJG; all authors edited the manuscript.

326 **Data Accessibility**

327 All code and data used here are provided in the `foieGras` package for R or in the Supplemen-
328 tary Information. The latest stable and cross-platform tested version of the package (currently,
329 1.0-7) is available via ROpenSci’s R-universe, at <https://ianjonsen.r-universe.dev/ui#package:foieGras>. The latest partially tested stable and development versions are available on the
330 GitHub repository: <https://github.com/ianjonsen/foieGras>. An older version of `foieGras`
331 (0.7-6) remains on CRAN at <https://CRAN.R-project.org/package=foieGras>, however, we
332 recommend users upgrade to the latest R-universe version for full access to the functionality
333 presented here.

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