

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

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15 **Abstract**

- 16 1. Animal-borne sensor and tracking data are indispensable for understanding the ecology,
17 behaviour and physiology of mobile or cryptic species. Meaningful signals in these data
18 can be obscured by noise due to imperfect measurement technologies, requiring rigorous
19 quality control as part of any comprehensive analysis.
- 20 2. State-space models are powerful tools that can separate meaningful signals from noise.
21 These tools are ideal for quality control of error-prone location data and for inferring
22 where animals are and what they are doing when they record or transmit sensor
23 information. However, they are complex statistical models that can be challenging and
24 time-consuming to fit to diverse animal tracking data sets.
- 25 3. The R package **foieGras** eases the tasks of conducting quality control on and behavioural
26 inference from animal tracking data. This is achieved via: 1) a simple but extensible
27 workflow that accommodates both novice and experienced users; 2) automated processes
28 that alleviate complexity from data processing and model specification/fitting steps; 3)
29 simple movement models coupled with a powerful numerical optimization approach for
30 rapid and reliable model fitting.
- 31 4. We highlight **foieGras**' capabilities through three applications to real animal tracking
32 data. Full R code for these and additional applications are included as Supporting
33 Information so users can gain a deeper understanding of how to use **foieGras** for their
34 own analyses.

35 **Keywords:**

- 36 animal movement, biologging, bio-telemetry, movement behaviour, move persistence, random
37 walk, simulation, state-space model

38 1 | Introduction

39 The collection of animal-borne sensor data has become essential for understanding the
40 movements, behaviour, social interactions, foraging ecology, physiology, habitat use and
41 population dynamics of mobile and/or cryptic species (Kays *et al.*, 2015). In addition, the
42 sophistication and precision of current sensor technology now enables the use of tagged animals
43 to collect in situ environmental information that complements data collected from traditional
44 Earth observing platforms (McMahon *et al.*, 2021). However, in each of these applications,
45 common issues with tracking data such as irregularly timed measurements, sensor biases and
46 location measurement errors must be overcome. Underlying animal movement processes must
47 also be adequately characterised before robust inferences can be made about where animals
48 are and what they are doing when they record or transmit information.

49 State-space models (SSMs) are powerful tools for conducting quality control of and making
50 behavioural inference from animal tracking data (Patterson *et al.*, 2008). Within this
51 framework, an animal's true location and/or behaviour in the wild are unobserved states,
52 while measurements recorded by animal-borne sensors provide noisy observations. The SSM
53 comprises both a movement process model (e.g., a correlated random walk) and a measurement
54 model that are fit to animal tracks to estimate true location and behaviour states, thereby
55 separating ecologically-meaningful signals from the noise of sensor measurements.

56 Here we introduce **foieGras** (pronounced “*fwah grah*”), a package for fitting SSMs in R (R
57 Core Team, 2021). This package has two aims: (1) to be a simple and fast implementation of
58 SSMs to quality control error-prone animal location data (Jonsen *et al.*, 2020); and (2) for
59 inference of changes in behaviour along animal tracks (Jonsen *et al.*, 2019). Although several
60 implementations of SSMs for animal movement data exist, e.g. **bsam** (Jonsen *et al.*, 2005),
61 **crawl** (Johnson *et al.*, 2008), and **ctmm** (Calabrese *et al.*, 2016), their broad utility can be
62 hampered by their technical complexity. **foieGras** has a more user-friendly implementation
63 suitable for novices, yet users can exert control over many aspects of the package functions

64 via optional arguments, accommodating the needs of experienced users.

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

69 **2 | foieGras overview**

70 The workflow for **foieGras** is deliberately simple, with many of the usual track data processing
71 checks handled automatically. Here we outline the main aspects of the **foieGras** package.
72 The package's main functions with brief code examples are listed in Table 1, and a generalized
73 workflow with example code is depicted in Figure 1.

74 **2.1 | Data preparation**

75 Animal tracking data, consisting of a time-series of location coordinates, can be read into R
76 as a data frame using standard functions such as `read.csv`. Possible input data formats are
77 shown in Figure 1. More details on input data formats are provided in the Overview vignette
78 (<https://ianjonsen.github.io/foieGras/articles/Overview.html>).

79 **2.2 | State-space model fitting - fit_ssm**

80 State-space models are fit using the function `fit_ssm` (Fig. 1). The type of location data
81 is automatically detected from the location quality classes that are typical of Argos data
82 and that can be added by the user for other data types. Based on the location quality
83 classes and optional information on measurement errors contained in the data, an appropriate
84 measurement error model is selected for each observation (Jonsen *et al.*, 2020). Fits to single
85 versus multiple individuals are handled automatically, with sequential SSM fits occurring in
86 the latter case. No hierarchical or pooled estimation among individuals is currently available.

Table 1: Main **foieGras** functions with description and example code. In the code examples, ... denotes optional arguments. Details on these arguments can be found in the package help files for each function (e.g., `?fit_ssm`).

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

87 There are a large number of optional arguments that can be specified in `fit_ssm`, and these
88 are explained in the package documentation. We focus only the essential arguments here:

- 89 • `data` the input data structured as illustrated in Fig. 1
90 • `model` the process model to be used (one of `rw`, `crw`, or `mp`)
91 • `time.step` the prediction time interval (expressed in hours)

92 The function first invokes an automated data processing stage where the data type and
93 measurement error model(s) are determined, observation times are sorted and checked for
94 duplicates, and a speed filter identifies potential extreme locations to be ignored by the
95 SSM. The SSM is then fitted to the processed data, with the user-specified process model
96 and automatically selected measurement error model(s). The joint likelihood is optimized
97 numerically using either of the standard R optimizers, `optim` or `nlminb`. The R package TMB,
98 Template Model Builder (Kristensen *et al.*, 2016), is used to compute the gradient function in
99 C++. A fit object is returned as a nested data frame, listing the individual animal id(s), basic
100 convergence information and a list of model output including estimated parameters and states,
101 processed data, and diagnostic information. A simple data frame of SSM fitted (location
102 estimates corresponding to the observation times) or predicted values (locations predicted at
103 regular `time.step` intervals) can be extracted using the `grab` function. Parameter estimates,
104 AIC and other model fit information can be viewed using the `summary` function.

105 **2.3 | Behavioural estimation - `fit_ssm`, `fit_mpm`**

106 Move persistence, an index of movement behaviour, can be estimated as a continuous-valued
107 (0 - 1), time-varying latent variable that represents changes in movement pattern based
108 on autocorrelation in speed and direction (Jonsen *et al.*, 2019). There are two approaches
109 in `foieGras` for estimating move persistence. The first is to use `fit_ssm` with `model =`
110 '`mp`', which fits a continuous-time move persistence model in state-space form and thereby
111 simultaneously estimates true locations and move persistence from the error-prone telemetry
112 data (Fig. 1). This approach is most appropriate for fitting to irregularly-timed and error-

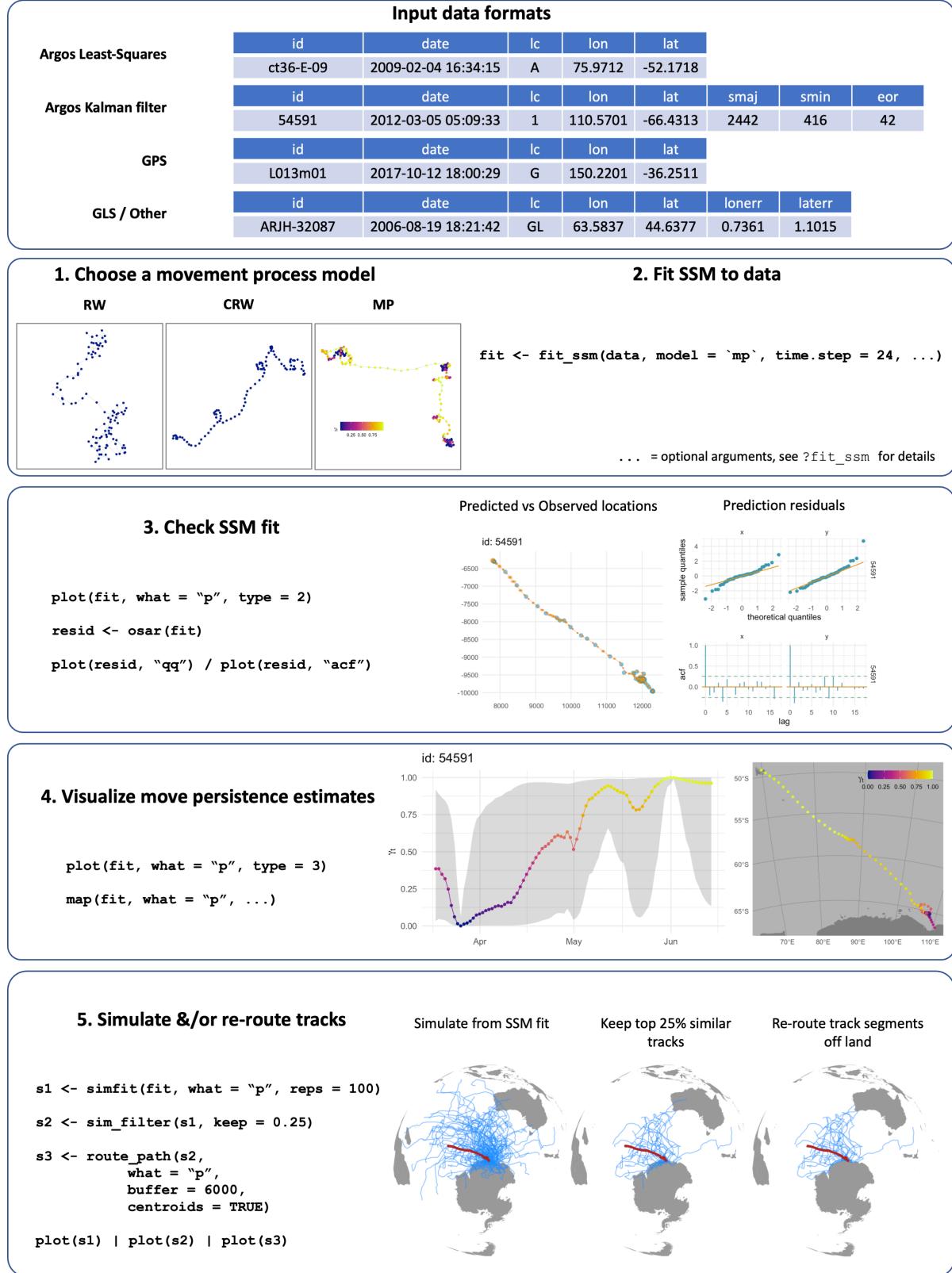


Figure 1: A generalized foieGras workflow showing required input data formats, model fitting, model checking/validation, visualisation of movement behaviour estimates, track simulation and re-routing around land. Example code is displayed for each stage.

113 prone Argos data as both aspects are taken into account explicitly. The second is to use
114 `fit_mpm`, which can take as input either location data or SSM-estimated locations from an
115 `fit_ssm` model fit object. This approach is generally more appropriate when the data have
116 minimal measurement error (e.g., GPS locations; see Application 3.2).

117 **2.4 | Model checking and visualization - osar, plot, map**

118 Before using fitted or predicted locations, a `fit_ssm` model fit should be checked and visualized
119 to confirm that the model adequately describes the data. There is no simple way to calculate
120 residuals for latent variable models that have non-finite state-spaces and that may be nonlinear,
121 but they can be computed based on iterative forecasts of the model (Thygesen *et al.*, 2017).
122 The `osar` function computes one-step-ahead (prediction) residuals via the `oneStepPredict`
123 function from the `TMB` R package (Kristensen *et al.*, 2016). A set of residuals are calculated
124 for the `x` and `y` values corresponding to the fitted values from the SSM. A generic `plot`
125 (`plot.osar`) method provides an easy way to visualize the prediction residuals as time-series
126 plots, quantile-quantile plots, or autocorrelation functions (Fig. 1).

127 State-space model fits to data can also be visualised by using the generic `plot` (`plot.ssm_df`)
128 function on a model fit object. Options exist to plot fitted or predicted values along with
129 observations as either paired, 1-D time-series (using the `type = 1` argument), or as 2-D tracks
130 (`type = 2`) with 95% confidence intervals or ellipses. These plots provide a rapid check on
131 SSM fits to data. Additionally, when the fitted SSM is the move persistence model (i.e.,
132 `model = 'mp'`), 1-D time-series (`type = 3`) or 2-D track plots (`type = 4`) of move persistence
133 estimates can be displayed (Fig. 1).

134 `fit_ssm` model fits can be mapped using the `map` function for single or multiple individuals.
135 By default, `map` uses the coastline data from the `rnaturrearth` R package (South, 2022)
136 at medium or high resolution (Fig. 1), but can also use tiled maps for finer-scale detail,
137 via the `rosm` (Dunnington, 2019) and `ggspatial` (Dunnington, 2021) R packages. Mapping
138 aesthetics (e.g., plot symbols, sizes, colours, fills) can be customized via the `aes` argument

139 and use of the `aes_1st` function. See code in SI for examples.

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

143 **2.5 | Simulation - `sim`, `simfit`, `sim_filter`**

144 Track simulation can be a helpful, yet informal, way of evaluating the degree to which
145 statistical movement models capture essential features of animal movement data (Michelot
146 *et al.*, 2017). The `sim` function can simulate a variety of movement process, including the `rw`,
147 `crw`, and `mp` process models, as well as simple multiple movement state switching processes.

148 Simulation is also used frequently in habitat usage modelling to provide a measure of habitat
149 availability (Aarts *et al.*, 2012) by generating a source of ‘background’ points representing a
150 null model of the distribution of foraging animals in the absence of external drivers (Raymond
151 *et al.*, 2015). The `simfit` function extracts movement parameters from an SSM fit object and
152 simulates random tracks of the same duration from these parameters. The argument `cpf`
153 = `TRUE` allows simulation of central place foragers by ensuring that tracks start and end at
154 approximately the same location. Movements can also be constrained to remain mostly in
155 water via a potential function (Preisler *et al.*, 2013), using included gradient rasters and the
156 `grad` and `beta` arguments. These are illustrated in the code for Application 3.3.

157 The choice of null points can impact the performance of habitat suitability models Phillips
158 *et al.* (2009), and so the `sim_filter` function provides a tool to filter the simulated tracks
159 based on their similarity to the original path. Filtering uses one of two metrics that capture the
160 difference in the net displacement and bearing between the two paths (see `?similarity_flag`
161 for more detail). These metrics are motivated by the ‘flag value’ described in Hazen *et al.*
162 (2017). The the quantile of flag values to be retain is specified via the `keep` argument; i.e. `keep`
163 = `0.25` (the default) will return a `simfit` object containing those simulated tracks with flag

164 values in the top 25% of values calculated for the input `simfit` object (Fig. 1).

165 **2.6 | Path rerouting - `route_path`**

166 As the SSMs implemented in `foieGras` have no information about potential barriers to animal
167 movement it is possible for locations to be estimated in implausible locations, such as on
168 land for marine species. To overcome this, `foieGras` makes use of the `pathroutr` R package
169 (London, 2020) to efficiently re-route locations from land back to water by using visibility
170 graphs (Jan *et al.*, 2014). The `route_path` function can be applied to either an SSM fit
171 object or the simulations generated by `simfit`. When the input is an SSM fit object the
172 re-routed path can be appended to the object for visualization and use in subsequent analyses.
173 When the input is a `simfit` object the locations within the simulation are replaced with the
174 re-routed paths (Fig. 1). We illustrate the latter in Application 3.3.

175 **3 | Applications**

176 We illustrate the main capabilities of `foieGras` through a set of applications that are for
177 demonstration purposes. Complete code for reproducing the applications and for gaining
178 a deeper understanding of `foieGras` functions are provided in the Supporting Information.
179 Data used in the application are available here.

180 **3.1 | SSM validation with prediction residuals**

181 We used a sub-adult male southern elephant seal (*Mirounga leonina*) track included as example
182 data in `foieGras` (`sese2`, id: ct36-E-09), sourced from from the Australian Integrated Marine
183 Observing System (IMOS; data publicly available via imos.aodn.org.au) deployments at Iles
184 Kerguelen in collaboration with the French IPEV and SNO-MEMO programmes. The data
185 are temporally irregular Argos Least-Squares locations. We fitted both the `rw` and `crw` models
186 using `fit_ssm()` with a speed filter threshold (`vmax`) of 4 ms⁻¹ and a 12-h time step. We
187 calculated prediction residuals using `osar()`, and then used the generic `plot` method for `osar`

188 residuals to assess and compare the model fits (Fig. 2). R code is available in Appendix S1
189 (Supporting Information).

190 Plots of predicted states on top of the observations suggest both models yield similar global
191 fits (Fig. 2a; blue versus red lines), but discrepancies are visible at a local scale (Fig. 2a,
192 inset). Predicted locations from the two models differ by a median 6.62 km (range: 0.02,
193 53.02 km), and there are marked trends in the residuals for the `rw` model fit (Fig. 2b) with
194 significantly positive autocorrelation in both the x and y directions (Fig. 2d). The `crw`
195 prediction residuals show no trend through time and have little autocorrelation (Fig. 2c,e),
196 implying the `crw` process model is a better fit to the data.

197 3.2 | Inferring move persistence

198 To illustrate how move persistence (γ_t) can be estimated from GPS data, we use four little
199 penguin (*Eudyptula minor*) tracks of daily foraging trips during the chick-rearing period from
200 Montague Island, NSW, Australia (described in Phillips *et al.*, 2022). The data are temporally
201 irregular GPS locations, with high frequency sampling (mean 15 s) intermittently disrupted
202 by the birds' diving behaviour, and are assumed to have minimal measurement error. We
203 fitted the `crw` SSM to the GPS data to predict temporally regular locations at 5-min intervals,
204 and assumed consistently small bivariate normal location measurement errors (ie. ± 30 m
205 sd). We then used `fit_mpm()` to estimate γ_t from these regularized locations. Finally, we
206 visually compared γ_t estimates with prey capture events inferred from accelerometry data
207 (see Carroll *et al.*, 2014, for details) to ascertain whether reduced γ_t is indicative of active
208 foraging by these penguins.

209 R code is available in Appendix S2 (Supporting Information). We provide an extra application
210 to illustrate how move persistence can be inferred from Argos data using `fit_ssm()` (Appendix
211 S3).

212 The little penguin GPS tracks did not exhibit strong contrast in move persistence, with γ_t

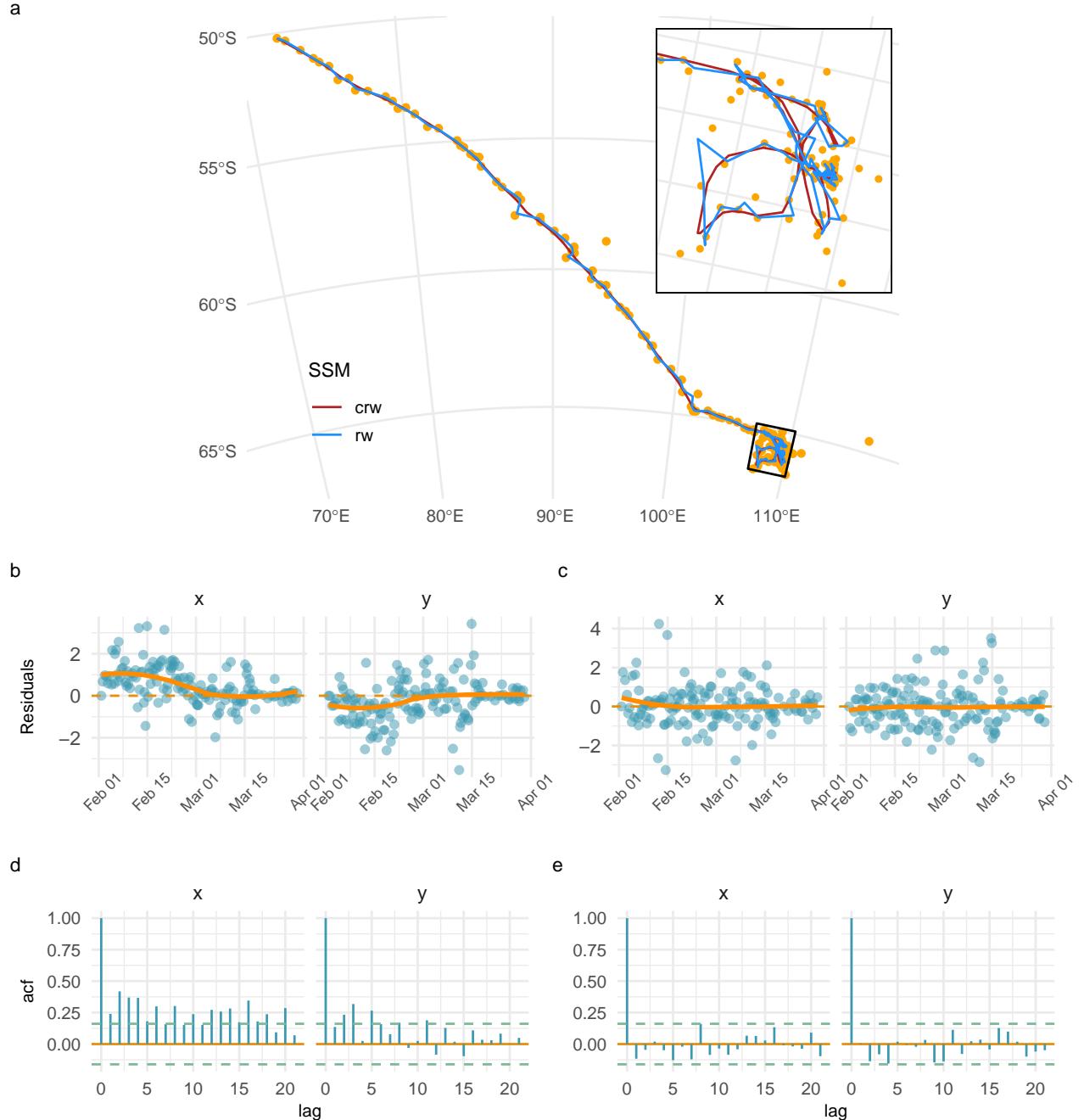


Figure 2: State-space model fits to a southern elephant seal track with finer scale detail inset (a), and diagnostic plots for assessing goodness-of-fit of the **rw** (b - prediction residual time-series; d - prediction residual autocorrelation) and **crw** (c,e) state-space models. All residual plots generated using the `plot.osar` function.

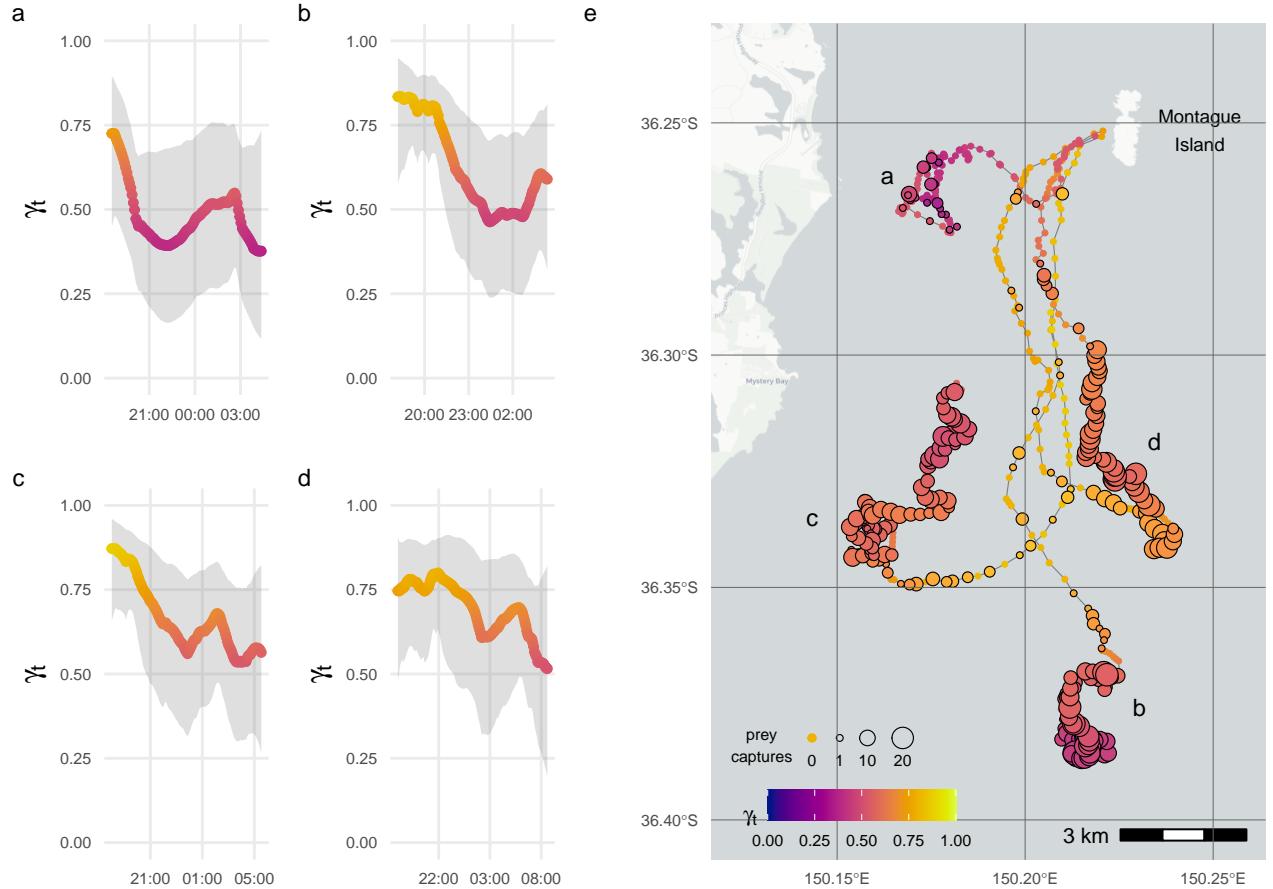


Figure 3: Inferred move persistence, γ_t , 1-D time-series (a-d; grey envelopes are 95 % CI's) and along SSM-predicted little penguin tracks (e). Location symbol sizes are proportional to the number of prey capture events, inferred from accelerometry data, at 5-min intervals corresponding to the SSM predicted location times.

213 declining below 0.5 for only two of the birds (Fig. 3a-d). Nonetheless, the move persistence
214 estimates highlight change in movement pattern over the course of the penguins' daily foraging
215 trips (Fig. 3e). The penguins departed Montague Is. with relatively fast movements, three
216 directed southward (Fig. 3 tracks b-d in e) and one less directed and remaining close to the
217 island (track a), before slowing down and engaging in meandering movements (orange - red in
218 Fig. 3e). Lower γ_t was associated with consistently higher and more frequent prey captures,
219 implying that low move persistence is indicative of foraging activity by these penguins (Fig.
220 3e). The spatially diffuse bouts of lower move persistence may reflect the fine-scale patchiness
221 of the penguins' forage-fish prey with search and prey-capture occurring both within and
222 among discrete neighbouring prey aggregations (Carroll *et al.*, 2017).

223 **3.3 | Simulating tracks from foieGras model fits**

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

229 We simulate 50 animal movement paths from the **crw** process model using **simfit**, and apply
230 a potential function using the **grad** and **beta** arguments to constrain the simulated paths
231 to largely remain in water. These tracks are then filtered based on their similarity to the
232 original path using **sim_filter** and the top 10% retained (**keep = 0.1**) (Fig. 4a,b). As the
233 potential function does not guarantee all locations remain off land, we re-route any remaining
234 simulated locations from land back to water using **route_path** (Fig. 4c). In combination,
235 these functions provide a pragmatic, non-statistical method to generate and objectively filter
236 pseudo-tracks for use in movement or habitat modelling applications. R code is available in
237 Appendix S4 (Supporting Information).

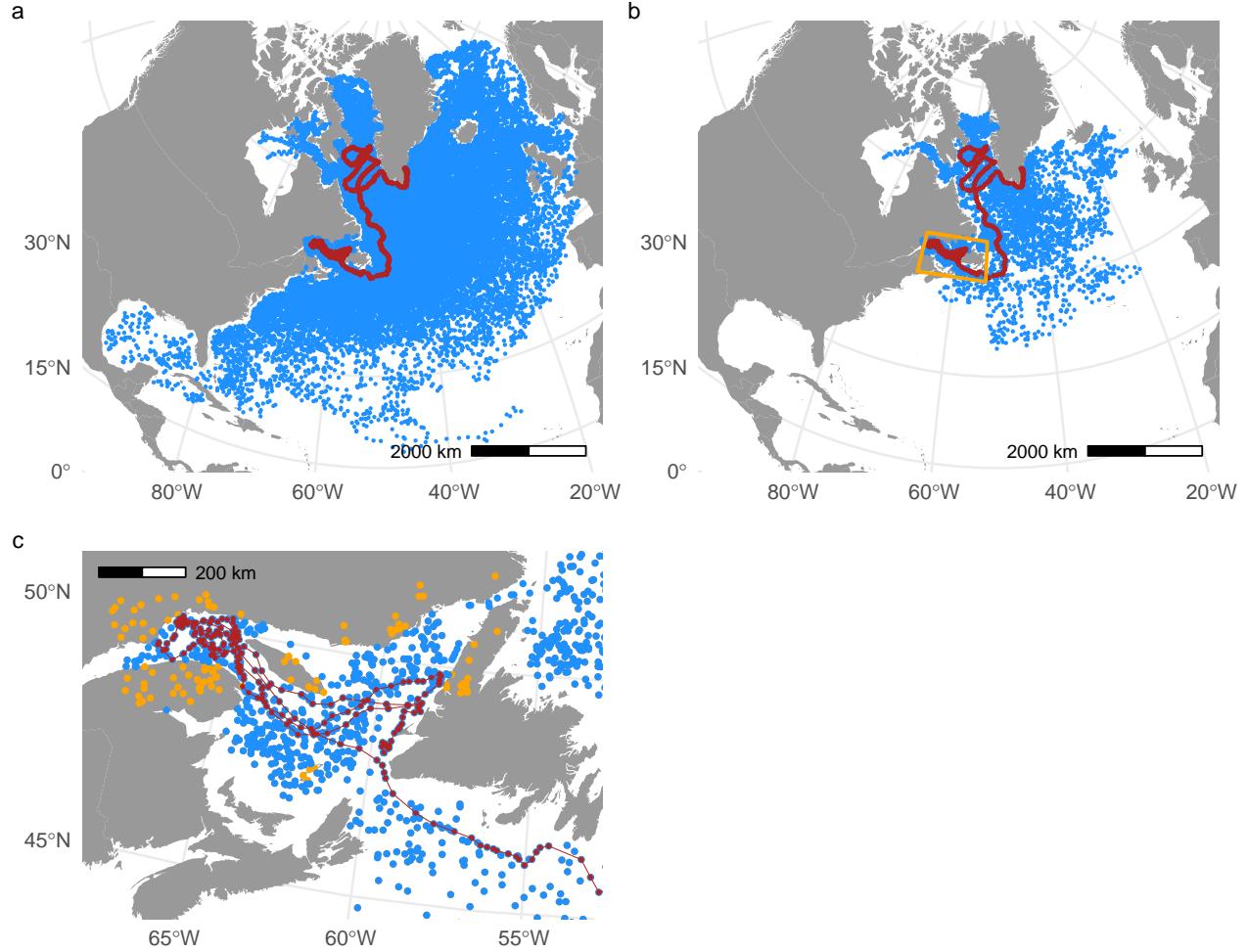


Figure 4: Simulating (a) 100 movement paths from a correlated random walk process model; (b) filtering those tracks to select the top 10% based on their similarity to the original SSM-predicted track (red); and (c) re-routing simulated locations on land (orange) back to ocean (blue). The orange box in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

238 **4 | Conclusions**

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

245 The **foieGras** package is an intermediate analysis toolbox where location quality control
246 typically occurs after some initial data processing but prior to any comprehensive, final
247 analysis. In this vein, the move persistence model tools provide a rapid approach for
248 objectively identifying changes in movement behaviour along animal tracks without any
249 required *a priori* knowledge or decisions about the kind or number of behavioural states
250 potentially hidden within the data. Subsequent analysis could entail use of a hidden Markov
251 model to infer potential drivers of observed movements (e.g., Michelot *et al.*, 2016; McClintock
252 & Michelot, 2018). Alternatively, move persistence - covariate relationships among multiple
253 individuals can be inferred rapidly in a mixed-effects model framework using the **mpmm** package
254 (Jonsen *et al.*, 2019, <https://github.com/ianjonsen/mpmm>).

255 The **foieGras** package will undergo further development, expanding the range of available
256 SSM's via new movement process models and/or enhanced measurement models for other
257 electronic tracking data types. Additionally, we will seek to enhance integration with other
258 R packages for processing and analysis of animal movement data, where feasible. Feedback
259 from users is invaluable and encouraged. Users may submit bug reports and enhancement
260 suggestions via the foieGras GitHub issues page ([https://github.com/ianjonsen/foieGras/is
sues/new/choose](https://github.com/ianjonsen/foieGras/issues/new/choose)). More general feedback is always welcome by contacting the lead author
262 directly.

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²⁸⁴ (little penguins), and University of St Andrews (harp seals).

²⁸⁵ **Author's Contributions**

²⁸⁶ IDJ developed the R package; WJG contributed harp seal data and to the R package; LP,
²⁸⁷ GC, and RGH contributed little penguin data; CRM, RGH and MAH contributed Southern

288 elephant seal data; IDJ and TAP developed the state-space models; IDJ wrote an initial
289 draft of the manuscript with contributions from WJG; all authors contributed to the final
290 manuscript.

291 **Data Accessibility**

292 All code used here is provided in the `foieGras` package for R or in the Supporting Information.
293 Data are publicly available here. The latest stable and cross-platform tested version of the
294 package (currently, 1.0-7) is available via ROpenSci's R-universe, at <https://ianjonsen.r-univ-erse.dev/ui#package:foieGras>. The latest partially tested stable and development versions are
295 available on the GitHub repository: <https://github.com/ianjonsen/foieGras>. An older version
296 of `foieGras` (0.7-6) remains on CRAN at <https://CRAN.R-project.org/package=foieGras>,
297 however, we recommend users upgrade to the latest R-universe version for full access to the
298 functionality presented here.
299

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309 **References**

- 310 Aarts, G., Fieberg, J. & Matthiopoulos, J. (2012) Comparative interpretation of count,
311 presence-absence and point methods for species distribution models. *Methods in Ecology
and Evolution*, **3**, 177–187.
- 313 Calabrese, J.M., Fleming, C.H. & Gurarie, E. (2016) ctmm: an R package for analyzing
314 animal relocation data as a continuous-time stochastic process. *Methods in Ecology and
315 Evolution*, **7**, 1124–1132.
- 316 Carroll, G., Cox, M., Harcourt, R., Pitcher, B., Slip, D. & Jonsen, I. (2017) Hierarchical
317 influences of prey distribution on patterns of prey capture by a marine predator. *Functional
Ecology*, **31**, 1750–1760.
- 319 Carroll, G., Slip, D., Jonsen, I. & Harcourt, R. (2014) Supervised accelerometry analysis can
320 identify prey capture by penguins at sea. *Journal of Experimental Biology*, **217**, 4295–4302.
- 321 Dunnington, D. (2019) *rosm: Plot Raster Map Tiles from Open Street Map and Other Sources*.
322 R package version 0.2.5.
- 323 Dunnington, D. (2021) *ggspatial: Spatial Data Framework for ggplot2*. R package version
324 1.1.5.
- 325 Grecian, W.J., Stenson, G.B., Biuw, M., Boehme, L., Folkow, L.P., Goulet, P.J., Jonsen, I.D.,
326 Malde, A., Nordøy, E.S., Rosing-Asvid, A. & Smout, S. (2022) Environmental drivers of
327 population-level variation in the migratory and diving ontogeny of an arctic top predator.
328 *Royal Society Open Science*, **9**.
- 329 Hazen, E.L., Palacios, D.M., Forney, K.A., Howell, E.A., Becker, E., Hoover, A.L., Irvine,
330 L., DeAngelis, M., Bograd, S.J., Mate, B.R. & Bailey, H. (2017) WhaleWatch: a dynamic
331 management tool for predicting blue whale density in the California Current. *Journal of
332 Applied Ecology*, **54**, 1415–1428.

- 333 Jan, G.E., Sun, C.C., Tsai, W.C. & Lin, T.H. (2014) An $O(n \log n)$ shortest path algorithm
334 based on delaunay triangulation. *IEEE/ASME Transactions on Mechatronics*, **19**, 660–666.
- 335 Johnson, D.S., London, J.M., Lea, M. & Durban, J.W. (2008) Continuous-time correlated
336 random walk model for animal telemetry data. *Ecology*, **89**, 1208–1215.
- 337 Jonsen, I.D., Patterson, T.A., Costa, D.P., Doherty, P.D., Godley, B.J., Grecian, W.J., Guinet,
338 C., Hoennner, X., Kienle, S.S., Robinson, P.W., Votier, S.C., Whiting, S., Witt, M.J., Hindell,
339 M.A., Harcourt, R.G. & McMahon, C.R. (2020) A continuous-time state-space model for
340 rapid quality control of Argos locations from animal-borne tags. *Movement Ecology*, **8**, 31.
- 341 Jonsen, I.D., McMahon, C.R., Patterson, T.A., Auger-Méthé, M., Harcourt, R., Hindell, M.A.
342 & Bestley, S. (2019) Movement responses to environment: fast inference of variation among
343 southern elephant seals with a mixed effects model. *Ecology*, **100**, e02566.
- 344 Jonsen, I., Flemming, J. & Myers, R. (2005) Robust state-space modeling of animal movement
345 data. *Ecology*, **86**, 2874–2880.
- 346 Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an
347 eye on life and planet. *Science*, **348**, aaa2478.
- 348 Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H. & Bell, B.M. (2016) TMB: Automatic
349 differentiation and Laplace approximation. *Journal of Statistical Software*, **70**, 1–21.
- 350 London, J.M. (2020) *pathroutr: An R Package for (Re-)Routing Paths Around Barriers*.
- 351 McClintock, B.T. & Michelot, T. (2018) momentuHMM: R package for generalized hidden
352 Markov models of animal movement. *Methods in Ecology and Evolution*, **9**, 1518–1530.
- 353 McMahon, C.R., Roquet, F., Baudel, S., Belbeoch, M., Bestley, S., Blight, C., Boehme, L.,
354 Carse, F., Costa, D.P., Fedak, M.A., Guinet, C., Harcourt, R., Heslop, E., Hindell, M.A.,
355 Hoennner, X., Holland, K., Holland, M., Jaine, F.R.A., Jeanniard du Dot, T., Jonsen, I.,
356 Keates, T.R., Kovacs, K.M., Labrousse, S., Lovell, P., Lydersen, C., March, D., Mazloff,

- 357 M., McKinzie, M.K., Muelbert, M.M.C., O'Brien, K., Phillips, L., Portela, E., Pye, J.,
358 Rintoul, S., Sato, K., Sequeira, A.M.M., Simmons, S.E., Tsontos, V.M., Turpin, V., van
359 Wijk, E., Vo, D., Wege, M., Whoriskey, F.G., Wilson, K. & Woodward, B. (2021) Animal
360 borne ocean sensors – anibos – an essential component of the global ocean observing system.
361 *Frontiers in Marine Science*, **8**, 751840.
- 362 Michelot, T., Langrock, R. & Patterson, T.A. (2016) moveHMM: an R package for the
363 statistical modelling of animal movement data using hidden Markov models. *Methods in
364 Ecology and Evolution*, **7**, 1308–1315.
- 365 Michelot, T., Langrock, R., Bestley, S., Jonsen, I.D., Photopoulou, T. & Patterson, T.A.
366 (2017) Estimation and simulation of foraging trips in land-based marine predators. *Ecology*,
367 **98**, 1932–1944.
- 368 Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008) State-
369 space models of individual animal movement. *Trends in Ecology and Evolution*, **23**, 87–94.
- 370 Pedersen, T.L. (2020) *patchwork: The Composer of Plots*. R package version 1.1.1.
- 371 Phillips, L., Carroll, G., Jonsen, I., Harcourt, R., Brierley, A., Wilkins, A. & Cox, M. (2022)
372 Variability in prey field structure drives inter-annual differences in prey encounter by a
373 marine predator, the little penguin. *Royal Society Open Science*, Accepted, **26 Aug 2022**.
- 374 Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier,
375 S. (2009) Sample selection bias and presence-only distribution models: implications for
376 background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.
- 377 Preisler, H.K., Ager, A.A. & Wisdom, M.J. (2013) Analyzing animal movement patterns
378 using potential functions. *Ecosphere*, **4**, 1–13.
- 379 R Core Team (2021) *R: A Language and Environment for Statistical Computing*. R Foundation
380 for Statistical Computing, Vienna, Austria.

- 381 Raymond, B., Lea, M.A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.B.,
382 Cottin, M., Emmerson, L., Gales, N., Gales, R., Goldsworthy, S.D., Harcourt, R., Kato, A.,
383 Kirkwood, R., Lawton, K., Ropert-Coudert, Y., Southwell, C., van den Hoff, J., Wienecke,
384 B., Woehler, E.J., Wotherspoon, S. & Hindell, M.A. (2015) Important marine habitat off
385 east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, **38**,
386 121–129.
- 387 South, A. (2022) *rnatnuralearth: World Map Data from Natural Earth*. R package version
388 0.3.0.
- 389 Thygesen, U.H., Albertsen, C.M., Berg, C.W., Kristensen, K. & Nielsen, A. (2017) Validation
390 of ecological state space models using the Laplace approximation. *Environmental and*
391 *Ecological Statistics*.
- 392 Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.