Movement behaviour responses to environment: fast inference of individual variation with a mixed effects model

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Abstract

Telemetry data provide a rich source of information on animals use of space, habitat preferences and movement behaviour. Yet habitat models fit to these data are blind to the underlying behavioural context. Conversely, behavioural models accounting for individual variability are too slow for meaningful analysis of large telemetry datasets. Applying new fast-estimation tools, we show how a model incorporating mixed effects within a flexible random walk movement process rapidly infers among-individual variability in environment-movement behaviour relationships. We demonstrate our approach using southern elephant seal (*Mirounga leonina*) telemetry data. Seals consistently reduced speed and directionality (move persistence) with increasing sea ice coverage, had variable responses to chlorophyll concentration and consistently reduced move persistence in regions where circumpolar deep water shoaled. Our new modelling framework is extensible and substantively advances analysis of telemetry data by allowing fast and flexible mixed effects estimation of potential drivers of movement behaviour processes.

Key Words: correlated random walk; habitat; individual movement; latent variable; telemetry; Template Model Builder; random effects; southern elephant seal; habitat model

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Introduction

Understanding animals' use of geographical and environmental space (i.e., where animals are and why they are there) is one of the central aims of ecology (Rosenzweig, 1981). Movement is the key process that defines space-use at spatial and temporal scales relevant to individual animals and telemetry is the predominant approach to observe this process (Kays *et al.*, 2015; Hussey *et al.*, 2015). Inferences about the behavioural context of animal movements, such as foraging, resting or predator avoidance, are often made by relating movement behaviour to physical habitat features (e.g., Breed *et al.*, 2017).

Various spatial habitat modelling approaches are used to infer animals' space-use and habitat preferences, through combining telemetry and environmental information, e.g., from remotely sensed data (Aarts *et al.*, 2008; Thurfjell *et al.*, 2014; Raymond *et al.*, 2015). Most habitat models infer animals' habitat preference or selectivity from a combination of observed (presence) and simulated (pseudo-absence) tracking locations (Aarts *et al.*, 2008) but are generally blind to the behavioural context (e.g., whether animals are migrating, foraging or resting) underlying those inferred preferences. Hidden Markov models (HMMs) and state-space models (SSMs) can provide this context by inferring (unobserved) behavioural states, and relating state-switching probabilities to environmental features (Morales *et al.*, 2004; Patterson *et al.*, 2009; Bestley *et al.*, 2013; Michelot *et al.*, 2016).

Both HMMs and SSMs offer great flexibility in modelling movement behaviour as a function of extrinsic and/or intrinsic drivers (Bestley *et al.*, 2015; Michelot *et al.*, 2017). Although high individual variation is a commonly reported feature in telemetry analyses, methods to account for individual variability in movement-environment relationships (e.g., using random effects, Pinheiro & Bates, 2000; Bolker *et al.*, 2009) have been implemented in a limited way to date (Langrock *et al.*, 2012; Bestley *et al.*, 2015). A fully flexible approach where any sensible combination of fixed and random terms can be considered, that allows different environmental responses across individuals, has yet to be implemented.

This is mainly because complex mixed effects models (Thorson & Minto, 2015) applied to large time-series can be computationally demanding.

Here we present a modelling approach that takes advantage of fast, powerful estimation tools provided by the relatively new R package Template Model Builder (TMB, Kristensen *et al.*, 2016). We illustrate a mixed effects modelling approach for animal tracking data that takes advantage of TMB's fast estimation (Albertsen *et al.*, 2015; Auger-Méthé *et al.*, 2017) to parametrize movement behaviour using a time-varying term for movement persistence. Our primary aim is to show how the approach can be used to infer relationships between animals' movement behaviour and the environmental features they encounter. These models can be fit flexibly with single or multiple random effects, enabling inference across multiple individuals and assessment of the extent to which relationships differ among individuals. We illustrate our approach using southern elephant seal (*Mirounga leonina*) telemetry data, with cases demonstrating both sea-ice and oceanic foraging trips, to show how seals engaging in different foraging tactics may respond differently to their environment.

Materials and methods

Here we describe our mixed effects modelling approach for inference of covariate relationships with movement behaviour. We divide the description of our approach into three sections. First, we focus on a basic move persistence model that can be used to estimate behavioural change along an animal's observed movement trajectory. Second, we show how this basic model can be expanded to infer how these behavioural changes may be related to environmental features. We focus on relationships with environmental covariates but any combination of extrinsic or intrinsic covariates could be modelled provided they are measured at locations and/or times consistent with the telemetry data. Third, we add random effects to the model to enable inference about how these behaviour - environmental relationships may differ among individual animals.

Time-varying move persistence

Our modelling approach focuses on estimation of the persistence (sensu Patlak, 1953) of consecutive pairs of animal relocations (move steps) along an entire movement trajectory. Move persistence, which captures autocorrelation in both speed and direction, has been modelled as an average across entire movement trajectories (Jonsen, 2016), indicating whether that trajectory is, on average, uncorrelated (i.e., a simple random walk or Brownian motion), correlated (i.e., a correlated random walk), or somewhere in between (Codling *et al.*, 2008). Allowing move persistence to vary along a trajectory means it can be used as an index of behaviour, identifying segments of relatively low or high persistence. This model can be written as:

$$\boldsymbol{d}_t = \gamma_t \boldsymbol{d}_{t-1} + \mathrm{N}(0, \boldsymbol{\Sigma}) \tag{1}$$

where $\boldsymbol{d}_t$ and $\boldsymbol{d}_{t-1}$ are the changes in an animal's location at times t and $t-1$. $\boldsymbol{\Sigma}$ is a variance-covariance matrix specifying the magnitude of randomness in the 2-dimensional movements. γ_t is the time-varying move persistence (autocorrelation) between displacements $\boldsymbol{d}_t$ and $\boldsymbol{d}_{t-1}$. γ_t is continuous-valued between 0 (low move persistence, Fig. 1a,c) and 1 (high move persistence, Fig. 1b,c). To avoid potential parameter identifiability issues between γ_t and Σ, we set the covariance term in Σ to 0 but note this constraint could be relaxed. We assume γ_t follows a simple random walk in logit space (to keep γ_t bounded between 0 and 1):

$$\mathrm{logit}(\gamma_t) = \mathrm{logit}(\gamma_{t-1}) + \mathrm{N}(0, \sigma_\gamma) \tag{2}$$

where σ_γ is a scale parameter describing how much move persistence varies along an animal's observed movement track.

This process model (Eqn's 1 and 2) can be fit either directly to location data with minimal error, such as GPS data, fit to SSM-filtered locations, or coupled with an observation model to fit to error-prone data, such as Argos or light-based geolocation data. We assume the locations occur at regular time intervals, but other implementations can accommodate irregularly observed location data (Auger-Méthé *et al.*, 2017).

The time-varying move persistence model can be used to objectively identify changes in movement pattern. The γ_t's are the behavioural index but unlike switching state-space models (e.g., Jonsen *et al.*, 2005) or hidden Markov models (e.g., Langrock *et al.*, 2012) of animal movement behaviour, these changes are modelled along a continuum (0 - 1) rather than as switches between a pre-specified number of discrete states.

Move persistence in relation to environment

To make inferences about the factors associated with these behaviours, we can model γ_t as a linear function of environmental predictors like proportion of ice cover, or other extrinsic or intrinsic covariates measured at each location. With this approach, we replace the random walk on logit(γ_t) (Eqn 2) with a linear regression of covariates on logit(γ_t):

$$\text{logit}(\gamma_t) = \beta_0 + \beta_1 m_{t,1} + \cdots + \beta_n m_{t,n} \tag{3}$$

where β_0, $\beta_1 \cdots \beta_n$ are the fixed intercept and regression coefficients and $m_{t,1} \cdots m_{t,n}$ are the predictor variables. This model can be fit to a single animal track, or multiple tracks could be pooled together. Typically, we wish to make inference across multiple individual tracks and assess the extent to which relationships may differ among individuals.

Incorporating individual variability

To account for variation among individual responses to environment, we can expand Eqn 3 to a mixed-effects regression of covariates on logit(γ_t), embedded directly in the behavioural model:

$$\text{logit}(\gamma_t) = (\beta_0 - b_{0,k}) + (\beta_1 - b_{1,k}) m_{t,1,k} + \cdots + (\beta_n - b_{n,k}) m_{t,n,k} \tag{4}$$

where the β's are the fixed-effect intercept and slope terms as in Eqn 3, $b_{0,k}$ is a random deviation for the intercept of the k-th individual, $b_{1,k}$ through $b_{n,k}$ are random deviations for the slopes of the k-th individual and $m_{t,1,k}$ through $m_{t,n,k}$ are the covariates measured along the k-th individual's track.

Estimation

In principle, any combination of fixed and random effects can be specified within the movement model described in equations 1 and 4. However, estimation of multiple random effects can be extremely computationally demanding and this has limited the use of such models for animal telemetry data. Here we use TMB to fit the move persistence models (Auger-Méthé *et al.*, 2017). The TMB package allows complex latent variable mixed effects models, such as SSMs (Albertsen *et al.*, 2015), to be specified in C++ and fit efficiently via maximum likelihood using reverse-mode auto-differentiation and the Laplace approximation (Kristensen *et al.*, 2016). The Laplace approximation avoids the need for high-dimensional integration by using a second-order Taylor expansion that massively speeds the calculation of the marginal likelihood (e.g., Albertsen *et al.*, 2015). Comparing Bayesian and TMB versions of the same location-filtering model fit to individual Argos location datasets, Auger-Méthé *et al.* (2017) found a 30-fold decrease in computation time for the TMB fit with no apparent loss of accuracy.

All code for fitting these models in R is available at `https://github.com/ianjonsen`. This code draws on the `lme4` (Bates *et al.*, 2015) and `glmmTMB` (Brooks *et al.*, 2017) R packages to specify the mixed effects models in a general and flexible manner.

Data application

We demonstrate our move persistence models with 24 adult female southern elephant seal tracks. The seals were captured at Iles Kerguelen (49.35° S, 70.22° E) between late January and mid-March in 2009 and 2013-2015, at the end of their annual moult. Animal handling and instrument attachment details can be found elsewhere (McMahon *et al.*, 2000; Field *et al.*, 2012; McMahon *et al.*, 2008). These data were sourced from the Australian Integrated Marine Observing System (IMOS) deployments at Iles Kerguelen and are publicly available (`http://imos.aodn.org.au`). The tracks comprise a mixture of sea ice foraging trips on or near the Antarctic continental shelf (12 seals; Appendix S1.1a) and entirely pelagic foraging trips in sub-Antarctic waters (12 seals; Appendix S1.1b). Prior to fitting the move persistence models, we used a TMB implementation of a state-space model (Jonsen *et al.*, 2005; Auger-Méthé *et al.*, 2017) to filter the observed locations, accounting for error in the Argos telemetry, and to regularize the filtered locations a 12-h time interval (see Appendix S1 for details).

We fit the move persistence model (`mpm`; Eqn's 1 and 2) to the SSM-filtered seal tracks. To ascertain whether γ_t adequately captures changes in the seals' movement patterns, we compare the γ_t-based behavioural index from the `mpm` to discrete behavioural states estimated from a behavioural switching state-space model (SSSM; Jonsen, 2016) fitted using the `bsam` R package. Details on how we fit the `bsam` model are in Appendix S2. We then fit the move persistence mixed effects model (`mpmm`; Eqn's 1 and 4) to the same SSM-filtered seal tracks to infer how the seals' movement behaviour may be influenced by environmental features encountered during their months-long foraging trips. In both analyses, we fitted separate models to the ice and pelagic foraging trips. For the `mpmm`'s, we specified mixed effects models with random intercept and slopes to account for variability among individual seals. We fit all possible combinations of fixed and random effects and use AIC and likelihood ratios to find the best supported model for each set of tracks.

We examined 3 potential environmental correlates of elephant seal movement behaviour: sea ice cover (the proportion of time the ocean is covered by $\geq 85\%$ ice; `ice`), chlorophyll *a* concentration (near-surface summer climatology in mg m^{-3}; `chl`) and the salinity difference between 600 and 200 m depths (based on winter climatology averaged over 1955-2012 in psu, `saldiff`). Sea ice and chl *a* data were obtained from the Australian Antarctic

Data Centre (Raymond, 2014). Salinity data were obtained from the World Ocean Atlas (Zweng *et al.*, 2013). All three covariates were spatially interpolated to the same 0.1 x 0.1 degree grid covering the spatial domain of the 24 elephant seal tracks (Appendix S3.1). The environmental data values were then extracted at each seal location from the SSM-filtered track data. As `saldiff` could not be calculated in areas where the bathymetry was shallower than 600 m, we did not include this variable in the models fit to the seals making ice-bound foraging trips as several of them spent considerable time in waters shallower than 600 m (Appendix S2.2). Similarly, `ice` was excluded from the models fit to seals making pelagic foraging trips as they spent relatively little time in regions with sea-ice cover.

R code for the model selection exercise is in Appendix S4.

Results

Time-varying move persistence (`mpm`)

The ice-bound seals all exhibited similar movement patterns (Fig. 2a), with high move persistence on their outbound migrations and lower move persistence near the Antarctic continent in areas of higher sea-ice coverage. Return migrations to Iles Kerguelen were more variable, with some individuals travelling back in a persistent fashion and others taking meandering routes, possibly to forage en route. Pelagic foraging seals (Fig. 2b) migrated approximately 2000 km either east or west of Iles Kerguelen in relatively persistent fashion. Less persistent movements occurred at the distal ends of these migrations, although seals travelling to the west of Iles Kerguelen had markedly less persistent and slower movements, suggestive of more intense search and foraging, compared to those travelling to the east (Fig. 2b).

The γ_t-derived behavioural index is comparable but not identical to the discrete behavioural states estimated from the `bsam` SSSM (Fig. S2.1). The γ_t index captured the same changes in movement behaviour but the magnitudes of those changes generally were smaller. Fitting the move persistence model, including the SSM filtering step, was almost 500 times faster than fitting the `bsam` SSSM (Appendix S2.1).

Individual variability in move persistence - environment relationships (`mpmm`)

Sea-ice foragers. The best supported model for elephant seals foraging in the sea-ice zone included fixed and random coefficients for both the proportion of ice cover and chlorophyll *a* concentration (Table 1). On average, seals had movements that became less persistent or directed as sea-ice cover and chlorophyll *a* concentration increased (Fig. 3a,b). Among individuals, the relationship with `ice` was consistently negative but the degree to which move persistence declined differed markedly (Fig. 3a), whereas the relationship with `chl` was highly variable with 4 individuals having strong negative relationships and the rest weak to moderately positive relationships (Fig. 3b). Unsurprisingly, the `chl` fixed-effect was not significant (Z-value = -1.04, p = 0.3). Using the fixed-effects from the best supported model, the spatial prediction of γ_t over the entire spatial domain implies that the best foraging habitat generally lies south of 65° S (south of the black contour line, Fig. 3d).

Pelagic foragers. The best supported model for elephant seals foraging pelagically included fixed and random coefficients for the salinity difference between 600 and 200 m depths (`saldiff`, Table 2). On average, seals had movements that became strongly less persistent as the salinity difference decreased (Fig. 3c). Among individuals, this relationship was moderately variable with two individuals exhibiting relatively small changes in move persistence over the full range of `saldiff` (Fig. 3c). The spatial prediction of γ_t over the entire spatial domain implies that animals generally adopt a movement behaviour indicative of search or forage south of 65° S (south of the black contour line, Fig. 3e) or north in the vicinity of the Subantarctic Front (north of the black contour line, Fig. 3e).

Discussion

Animal telemetry data obtained at the level of individual animals poses a challenge to scale from individual to population ecology. While correlative statistical analyses using mixed effects models have been widely applied to behavioural datasets (e.g., marine animal diving and bird migration ecology analyses, Hassrick *et al.*, 2010; Mandel *et al.*, 2008), individual variability currently is incorporated into process-based models of movement behaviour in a relatively limited way. This is partly due to the extra complexity required for building random effects into a process-oriented approach (i.e., the temporal nature of the data are taken into account explicitly) though primarily due to the significant computational overhead entailed. Our method uses TMB estimation for a process model describing animal movement behaviour in direct relation to environmental features. Our results show this enables multiple fixed and random effects in movement-environment relationships to be fit simply and efficiently. Taking advantage of TMB's speed and power, this approach provides a feasible solution to analysing increasingly large and detailed telemetry datasets, and for harnessing individual-to-population level information on animal movement responses to environment.

Environmental responses

Our analyses revealed relatively consistent responses by individual animals to environmental variables we tested, however substantial individual variability was also a persistent feature of the telemetry data. Comparisons of model structures allowed these individual-level effects to be directly evaluated. Those animals whose forage migrations went towards the Antarctic continent showed low move persistence once in areas of higher sea ice coverage. Some individuals also showed positive responses to elevated chlorophyll a concentrations, targeting productive coastal polynya areas (Malpress *et al.*, 2017; Labrousse *et al.*, 2018); however this was not a persistent response with many others foraging farther offshore in the marginal ice zone (Labrousse *et al.*, 2015) where chlorophyll a concentrations are lower

(Appendix S3.1). For the pelagic foraging animals, our results indicated seals moved persistently away from the region in which salty Circumpolar Deep Water was confined to depths (i.e., where the salinity difference was highly positive). The majority then adopted a lower move persistence in areas where the CDW shoaled (salinity difference closer to zero, southern areas) with four animals targeting the vicinity of the Subantarctic Front (salinity difference negative) where cold fresh Antarctic Intermediate Water subducts under saline Subantarctic surface waters (northwestern areas, Appendix S3.1).

Substantial variability among individuals is a persistent feature reported from animal telemetry data (e.g., Block *et al.*, 2011). Understanding this variability is essential for scaling from data collected on individuals up to inferences of population-level processes (Morales *et al.*, 2010) and for predicting future responses to a changing environment. For example, within the Southern Ocean climatic changes are impacting the sea-ice extent and duration, the location of major oceanic frontal features, and potentially the meridional overturning circulation (whereby water masses sink and rise as governed by density gradients) with large-scale consequences for marine ecosystem structure, function and productivity (Constable *et al.*, 2014).

We used environmental climatologies to demonstrate our data application, however for many analyses relevant covariates may be extracted from time-varying environmental fields. Many automated options for this exist via websites such as ZoaTrack (`http://www.zoatrack.org/`) managed by the Atlas of Living Australia or Xtractomatic (`http://coastwatch.pfel.noaa.gov/xtracto/`) managed by the US National Oceanic and Atmospheric Administration. We also note here the need to incorporate location uncertainty when sampling environmental covariates from spatially gridded remote-sensing data. This can be done using multiple imputation methods as implemented in momentuHMM R package (McClintock & Michelot, 2018), i.e., drawing realizations of the locations from the uncertainty of the location-filtering SSM estimates.

Individual variation

Although the ultimate source of observed individual differences in behaviour - environment relationships is often unclear, two non-exclusive explanations seem likely. First, we often use relatively few predictors and these may represent the proximate influences which predators are actually responding to (i.e., prey density and/or distribution) indirectly or imperfectly. This may inflate apparent individual differences in predator movement behaviour. Modelling more direct indices of prey availability, and/or reducing error within covariates by accounting for location uncertainty as discussed above, may help to reduce apparent variation among individuals.

Second, individual variation is likely a real feature of foraging ecology (Magurran, 1993), where individual quality and personality (Dall *et al.*, 2004; Stamps, 2007) may confer real differences in foraging behaviour with relatively little difference in fitness (Mangel & Stamps, 2001). For example, consistent boldness in foraging can generate important ecological trade-offs, effecting increases in both growth and mortality rates (Stamps, 2007; Bergvall *et al.*, 2011; Chapman *et al.*, 2011). Research into behavioural syndromes along axes, such as boldness-shyness or proactiveness-reactiveness (Sih *et al.*, 2004), may provide insight into the functional connection between individual behavioural traits and physiological consequences (e.g. via metabolic rates, reproductive success or mortality rates), and hence the evolutionary significance for ecological patterns and processes. Individual differences likely represent yet another characteristic contributing to survival and resilience in a complex and variable environment.

Modelling approach and extensions

Our model is composed of a linear mixed effects regression embedded within a correlated random walk process model for animal movement behaviour. While the linear mixed effects approach allows flexible combinations of fixed and random effects, there is scope for further enhancement. In many cases parametric, linear fixed effects may not adequately capture the complexity of movement behaviour - environment relationships and a nonparametric approach using penalised splines may yield improved inference (Langrock *et al.*, 2017). Our random effects currently use an unstructured covariance matrix that may be less appropriate given the serial dependence structure typical of telemetry data. A first-order autoregressive covariance structure may better account for this dependence (Pinheiro & Bates, 2000). Finally, diagnosing lack of fit in latent variable models can be problematic as there is no "observed response" variable. One-step-ahead prediction residuals provide a useful model validation tool and can be estimated when fitting the model (Thygesen *et al.*, 2017).

This work addresses a key improvement in the quantitative integration of animal movement behaviour and environment. Habitat models are presently the dominant method for inference of environmental drivers of species' habitat preferences and space-use but largely ignore the behavioural context underlying observed animal locations. By modelling animal movement behaviours as a mixed effects function of environmental variables, we gain deeper insight into how individuals and populations actually use habitat. Additional effort is required to converge movement behaviour and habitat modelling approaches. For example, our behavioural models do not account for availability/accessibility of habitat in any way but this clearly must be considered when inferring habitat preferences (Wakefield *et al.*, 2011). A reasonable approach for this might be to use the movement process parameters to simulate animal tracks and examine implications of including/excluding environmental covariates. These pseudo-absence tracks may be used as the basis for developing a habitat accessibility surface and generating spatial predictions of animal behaviour conditional on this (e.g., Raymond *et al.*, 2015).

Our results show that TMB facilitates the fast estimation of multiple random effects by using the Laplace approximation to calculate the marginal likelihood of a movement behaviour process model. The model selection we conducted on the 24 southern elephant seal tracks took a total of 8 minutes to complete. This includes the time required to SSM filter the original Argos tracks and to fit the `mpmm`'s and is approximately 1500 times faster than a more limited hierarchical Bayesian model selection exercise, using Markov chain Monte Carlo simulation (Bestley *et al.*, 2013). The dramatically faster computation times achieved by our TMB-enabled approach means that similar analyses of movement behaviour - environmental relationships can be scaled up to very large telemetry datasets. This computation speed also opens up possibilities for far more realistic models of animal movement, incorporating the third dimension for diving or flying animals and/or high-volume accelerometry data.

The process model used here differs markedly from SSM used by Bestley *et al.* (2013). They used discrete behavioural state Markov-switching (Patterson *et al.*, 2009; Langrock *et al.*, 2012) embedded in a correlated random walk process model (Jonsen, 2016). Here, we used a time-varying move persistence parameter γ_t as a behavioural index that varied continuously between 0 and 1. This continuous behavioural index provides another tool for characterising animal movement patterns and for making inferences about the possible environmental drivers of animal movement behaviour. In some cases, a continuous index may offer more nuanced insight into variable behavioural sequences (Gurarie *et al.*, 2009; Breed *et al.*, 2012), whereas a discrete state approach may offer more flexibility in capturing the known structure of animal movement patterns (e.g., Michelot *et al.*, 2017).

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Table 1: Model rankings by ΔAIC and likelihood ratios (LR) for the MPMM's fit to the 12 ice foraging seals. Absolute AIC and deviance values for the best ranked model are displayed on the first row, under the ΔAIC and LR headings. All other ΔAIC and LR values are relative to the best ranked model. Computation time to convergence is also reported. Random effects are included in parentheses in the model formulas, following the `lme4` convention (Bates *et al.*, 2015).

Model formula	df	ΔAIC	LR	Time (s)
$\sim$ ice + chl + (ice + chl | id)	12	-9954.21	-9978.21	4.76
$\sim$ ice + chl + (chl | id)	9	0.78	6.78	3.61
$\sim$ ice + chl + (1 | id)	7	21.06	31.06	4.17
$\sim$ ice + (1 | id)	6	21.08	33.08	2.63
$\sim$ ice + chl + (ice | id)	9	23.59	29.59	5.76
$\sim$ ice + (ice | id)	8	24.14	32.14	4.55
$\sim$ chl + (chl | id)	8	219.74	227.74	4.09
$\sim$ chl + (1 | id)	6	245.16	257.16	3.48
$\sim$ 1 + (1 | id)	5	339.28	353.28	2.79

Table 2: Model rankings by ΔAIC and likelihood ratios (LR) for the MPMM's fit to the 12 ice foraging seals. Absolute AIC and deviance values for the best ranked model are displayed on the first row, under the ΔAIC and LR headings. All other ΔAIC and LR values are relative to the best ranked model. Computation time to convergence is also reported. Random effects are included in parentheses in the model formulas, following the `lme4` convention (Bates *et al.*, 2015).

Model formula	df	ΔAIC	LR	Time (s)
∼ saldiff + (saldiff | id)	8	-13897.26	-13913.26	3.87
∼ saldiff + chl + (saldiff | id)	9	1.68	-0.32	4.96
∼ saldiff + chl + (chl | id)	9	3.25	1.25	3.97
∼ saldiff + chl + (1 | id)	7	29.81	31.81	4.04
∼ saldiff + (1 | id)	6	36.35	40.35	3.21
∼ chl + (chl | id)	8	51.37	51.37	4.54
∼ chl + (1 | id)	6	107.41	111.41	4.19
∼ 1 + (1 | id)	5	129.93	135.93	2.34
∼ saldiff + chl + (saldiff + chl | id)	12	NA*	NA*	6.02

*model failed to converge

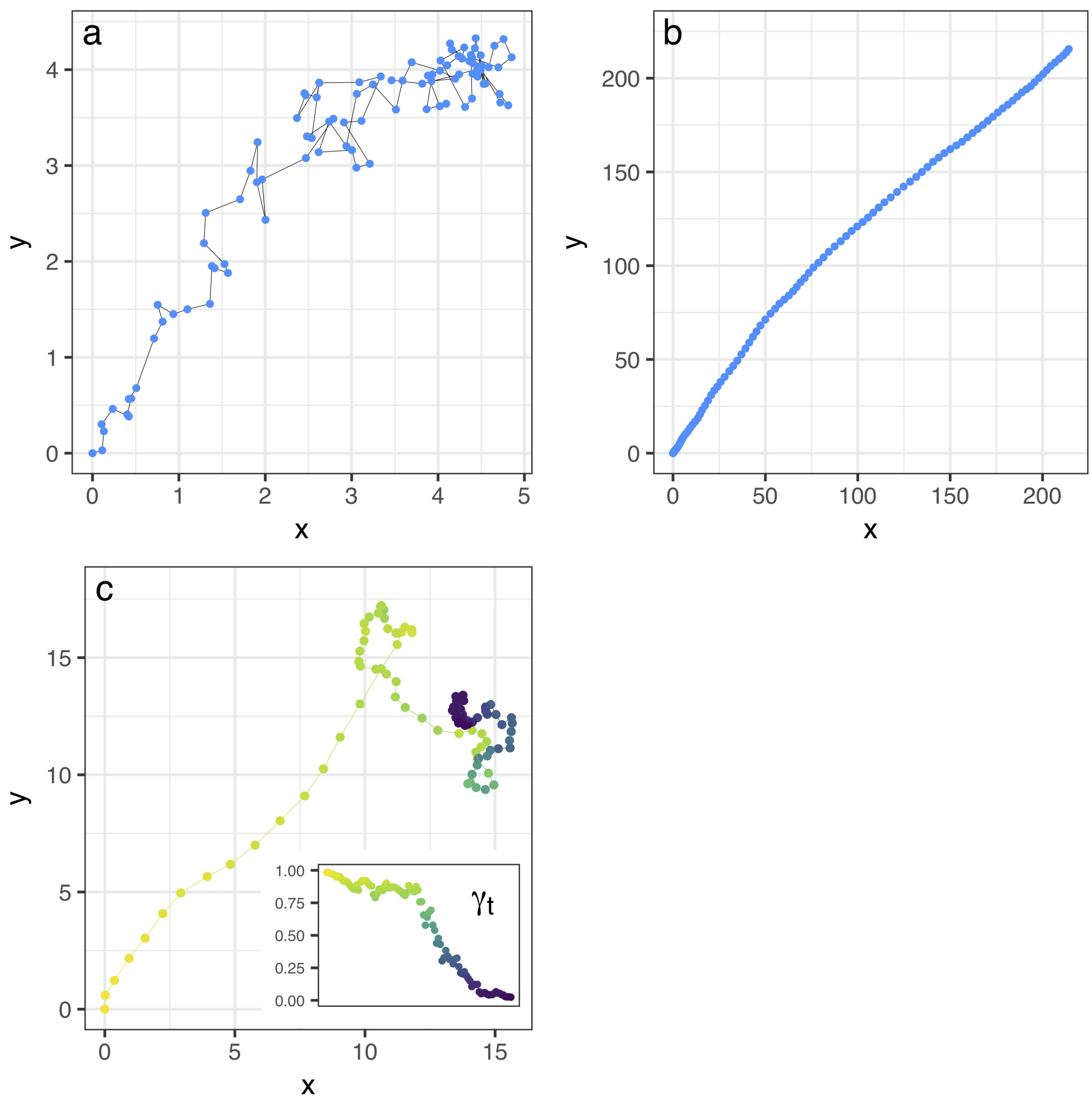

Figure 1: Example tracks simulated from the move persistence model with γ_t set to a constant 0.01 (low persistence) (a), γ_t set to a constant 0.99 (high persistence) and a time-varying γ_t (c). Locations in c are coloured by γ_t values with the random walk time-evolution of γ_t displayed inset in c. Note the substantially different scales of movement across panels a - c, despite sharing the same process covariance matrix (Σ). See Appendix S1 for simulation code.

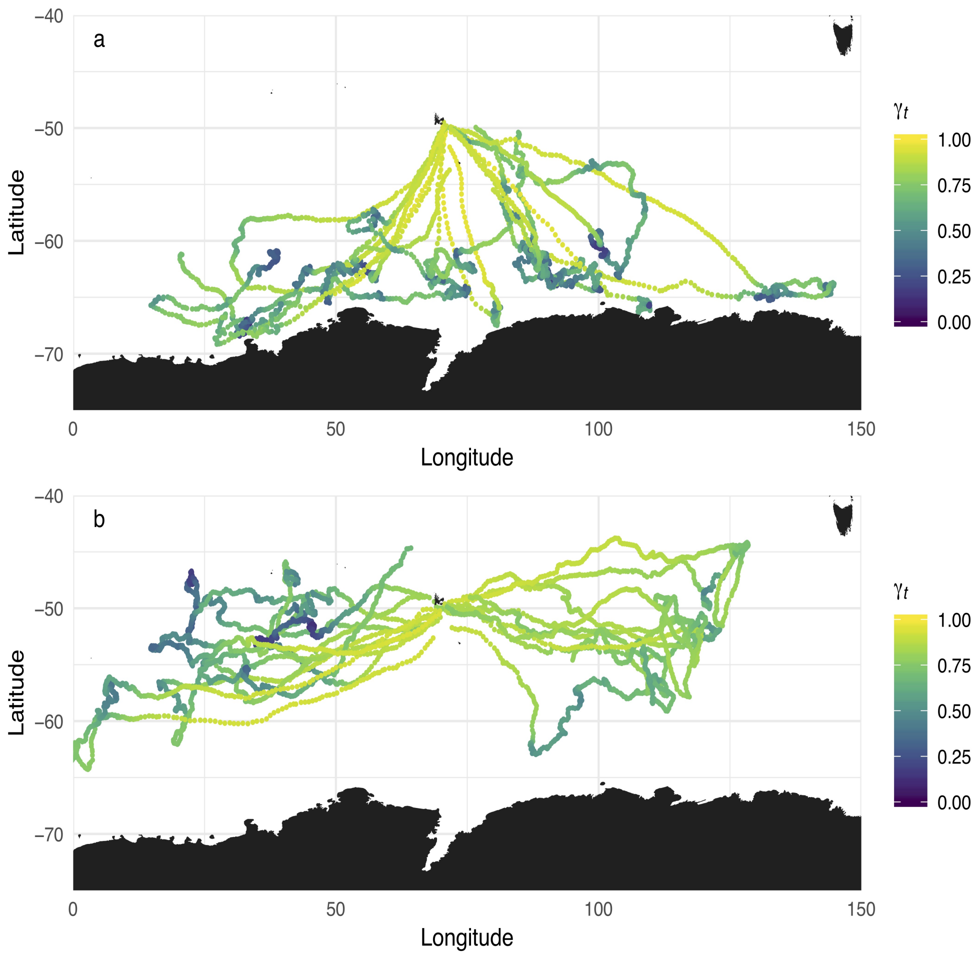

Figure 2: Maps of SSM-filtered southern elephant seal tracks originating from Iles Kerguelen. Ice-bound foraging trips (a) were predominantly directed to locations south of 60°S, whereas pelagic foraging trips (b) are predominantly north of 60°S. Each location is coloured according to its associated move persistence (see γ_t scale bar) estimated from the move persistence model.

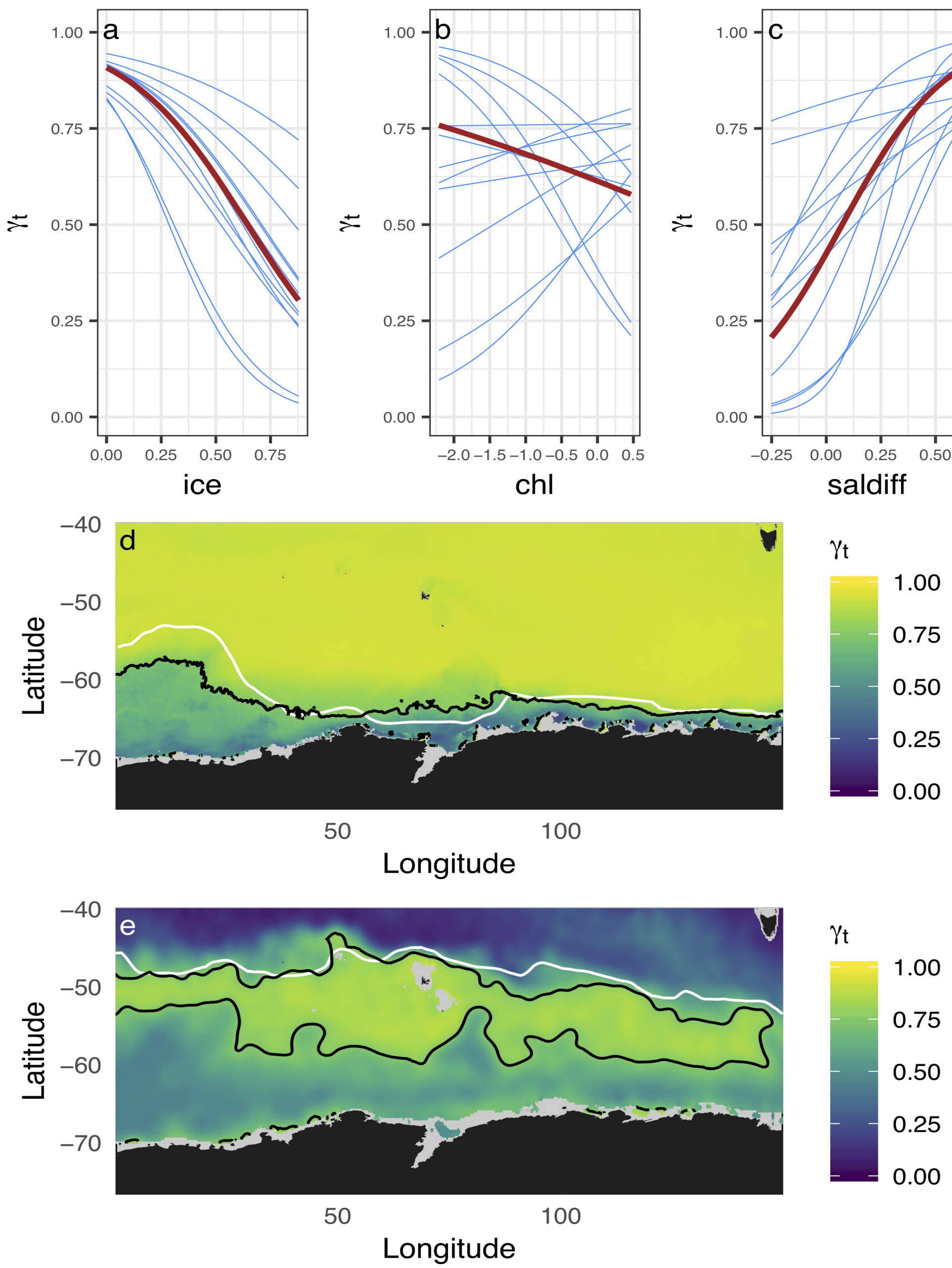

Figure 3: Fixed (red) and random (blue) effects relationships between move persistence γ_t and the proportion of ice cover (a) and chlorophyll a concentration (b) for ice foraging seals, and between γ_t and the salinity difference between 600 and 200m (c) for pelagic foraging seals. All three panels display both random intercept and slopes, as per the best ranked models in Tables 1 and 2. Spatial predictions of γ_t based on the fixed effect coefficients for the best fitting models for ice foraging seals (d) and pelagic foraging seals (e). The $\gamma_t = 0.75$ contour (black line) is displayed to aid delineation of predicted high move persistence ($\gamma_t > 0.75$; green - yellow) and low move persistence regions ($\gamma_t \leq 0.75$; green - blue). The southern boundary of the Antarctic Circumpolar Current (d) and the Subantarctic Front (e) are displayed for reference (white lines).