Reports

Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model

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Abstract. Like many species, movement patterns of southern elephant seals (*Mirounga leonina*) are being influenced by long-term environmental change. These seals migrate up to 4,000 km from their breeding colonies, foraging for months in a variety of Southern Ocean habitats. Understanding how movement patterns vary with environmental features and how these relationships differ among individuals employing different foraging strategies can provide insight into foraging performance at a population level. We apply new fast-estimation tools to fit mixed effects within a random walk movement model, rapidly inferring among-individual variability in southern elephant seal environment–movement relationships. We found that seals making foraging trips to the sea ice on or near the Antarctic continental shelf consistently reduced speed and directionality (move persistence) with increasing sea-ice coverage but had variable responses to chlorophyll *a* concentration, whereas seals foraging in the open ocean reduced move persistence in regions where circumpolar deep water shoaled. Given future climate scenarios, open-ocean foragers may encounter more productive habitat but sea-ice foragers may see reduced habitat availability. Our approach is scalable to large telemetry data sets and allows flexible combinations of mixed effects to be evaluated via model selection, thereby illuminating the ecological context of animal movements that underlie habitat usage.

Key words: correlated random walk; habitat; latent variable; random effects; southern elephant seals; spatial ecology; telemetry; template model builder.

Introduction

Long-term environmental change is influencing southern elephant seal (*Mirounga leonina*) populations, with their trajectories linked to the success of individuals' foraging migrations (Hindell et al. 2017). These seals migrate long distances from breeding colonies to forage, encountering a range of environmental conditions during many months at sea (Hindell et al. 2017). Foraging strategies vary among seals and are often associated with open

ocean or Antarctic continental shelf habitats, with individuals showing fidelity to these over several years (Authier et al. 2012). Understanding how seal movements vary with environmental conditions and how these relationships may differ among individuals can yield insight into population-level foraging performance and habitat usage. Yet, quantifying how individuals differently respond to their environment is a challenge due to a paucity of accessible analytical tools that can efficiently account for among-individual differences in movement patterns.

Spatial habitat modeling approaches often are used to infer habitat usage and preference from animal movement data (Aarts et al. 2008). Most of these approaches infer preference or selectivity from a combination of observed (presence) and simulated (pseudo-absence)

locations (Aarts et al. 2008) but are blind to the ecological mechanisms, such as density dependence (McLoughlin et al. 2010), movement, and individual behavior (Bestley et al. 2013, Auger-Méthé et al. 2017), underlying those preferences.

Although high individual variation is common in studies of animal movement, models that explicitly account for among-individual variability in inferred movement–environment relationships are rare (e.g., McClintock et al. 2013). These random effects or hierarchical models can be computationally demanding, inhibiting realistic analysis of ever-growing animal movement data sets. There is a need for efficient movement modeling approaches, accessible to ecologists, where responses to environmental, physiological, and/or social predictors can be inferred using flexible combinations of fixed and random terms (mixed effects) to account for variability among moderate to large numbers (tens to hundreds) of individuals.

We present a mixed-effects modeling approach for animal movement data that takes advantage of new fast-estimation tools. Our model estimates time-varying movement persistence (autocorrelation in speed and directionality) along animal movement trajectories. We focus here on showing how the approach can be used to infer relationships between animal movement patterns and the environmental features they encounter. The model can be fit rapidly and flexibly with single or multiple random effects, enabling inference across individuals and assessment of the extent to which relationships may differ among them. We apply our approach to infer how southern elephant seals employing different foraging strategies, ice-bound vs. open ocean (pelagic) trips, may respond differently to their environment. This represents a step towards bridging models of animal movement and habitat preference (e.g., Avgar et al. 2016), which in future may converge in a more complete framework.

METHODS

We build our modeling approach in three steps. First, we define a basic model that can be used to estimate changes in move persistence along an animal's observed trajectory. Second, we expand the model to infer how these changes may be related to environmental variables. Any combination of other extrinsic or intrinsic variables 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 movement–environment relationships may differ among individual animals.

Time-varying move persistence

We focus on estimating the persistence (sensu Patlak 1953) of consecutive pairs of animal relocations (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), correlated (i.e., a correlated random walk), or somewhere in between. Allowing move persistence to vary along a trajectory means it can be used as an index of behavior (Breed et al. 2012), identifying segments of relatively low or high persistence

$$\mathbf{d}_t = \gamma_t \mathbf{d}_{t-1} + \mathbf{\eta}_t \qquad (1)$$

where displacements $\mathbf{d}_t = \mathbf{x}_t - \mathbf{x}_{t-1}$ and $\mathbf{d}_{t-1} = \mathbf{x}_{t-1} - \mathbf{x}_{t-2}$ are the changes in an animal's location $\mathbf{x}$ at times t and $t - 1$. The random variable $\mathbf{\eta}_t = N(\mathbf{0}, \mathbf{\Sigma})$, with variance–covariance matrix $\mathbf{\Sigma}$ specifying the magnitude of variability in the two-dimensional movements. γ_t is the time-varying move persistence between displacements $\mathbf{d}_t$ and $\mathbf{d}_{t-1}$. γ_t is continuous-valued between 0 (low move persistence; Appendix S1: Fig. S1a, c) and 1 (high move persistence; Appendix S1: Fig. S1b, c). To avoid potential parameter identifiability issues between γ_t and $\mathbf{\Sigma}$, we set the covariance term in $\mathbf{\Sigma}$ to 0 but this constraint could be relaxed to better account for correlation in movements in the east-west and north-south directions. We assume γ_t follows a simple random walk in logit space

$$\text{logit}(\gamma_t) = \text{logit}(\gamma_{t-1}) + \varepsilon_t \qquad (2)$$

where the random variable $\varepsilon_t = N(0, \sigma_\gamma)$ represents variability in move persistence along an animal's track.

This process model (Eqs. 1 and 2) can be fit (1) to location data with minimal error, (2) to state-space filtered location data, or (3) coupled with an observation model for error-prone data. We focus on the second case with locations occurring at regular time intervals, but this could be relaxed (e.g., Auger-Méthé et al. 2017).

The time-varying move persistence model can be used to objectively identify changes in movement pattern. Here γ_t forms the behavioral index but unlike switching models (e.g., Michelot et al. 2017), these changes occur along a continuum (0–1) rather than as switches between discrete states.

Move persistence in relation to environment

To make inferences about the factors associated with move persistence, we can model γ_t as a linear function of environmental predictors measured at each location or time. With this approach, we replace the random walk on $\text{logit}(\gamma_t)$ (Eq. 2) with a linear regression of covariates on $\text{logit}(\gamma_t)$

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

where $\beta_0, \beta_1, \ldots, \beta_n$ are the fixed intercept and regression coefficients, $m_{t,1}, \ldots, m_{t,n}$ are the predictor variables, and $\varepsilon_t = N(0, \sigma_\gamma)$ are the random errors. This model can be fit to a single animal track, or to multiple tracks 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 Eq. 3 to a mixed-effects regression of covariates on logit(γ_t), within the behavioral model

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

where k indexes individual animals, the β's are the fixed intercept and slope terms as in Eq. 3, $b_{0,k}$ is a random deviation for the intercept of the kth individual, $b_{1,k}, \ldots, b_{n,k}$ are random deviations for the slopes of the kth individual and $m_{t,1,k}, \ldots, m_{t,n,k}$ are the covariates measured along the kth individual's track. As in Eq. 3, the random variable ε_t is the fixed effects errors. We use an unstructured covariance matrix for the random effects.

Estimation

In principle, any combination of fixed and random effects can be specified within the movement model described in Eqs. 1 and 4. 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 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, which massively speeds calculation of the marginal likelihood. Comparing Bayesian and TMB versions of a location-filtering model, Auger-Méthé et al. (2017) found a 30-fold decrease in computation time for the TMB fit with no loss of accuracy. All code for fitting these models in R is *available online.*[7,8]

Data and analysis

We use Argos telemetry data collected from 24 adult female southern elephant seals. 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 molt. Animal handling and instrument attachment details can be found elsewhere (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 S2: Fig. S1a) and entirely pelagic foraging trips in sub-Antarctic waters (12 seals; Appendix S2: Fig. S1b). Prior to fitting the move persistence models, we used a TMB implementation of a state-space model (SSM; Auger-Méthé et al. 2017) to filter the observed locations, accounting for error in the Argos telemetry, and to regularize the filtered locations to a 12-h time interval (see Appendix S2 for details).

We fit the move persistence model (`mpm`; Eqs. 1 and 2) to the state-space filtered seal tracks. Fitting to filtered tracks accounts for some of the uncertainty inherent in telemetry data but potential effects of residual location uncertainty should be examined post-analysis. To ascertain whether γ_t adequately captures changes in the seals' movement patterns, we compare the γ_t-based behavioral index to discrete behavioral states estimated from a switching state-space model (Jonsen 2016) fitted using the `bsam` R package. Details on how we fit the `bsam` model are in Appendix S3. We then fit the move persistence mixed effects model (`mpmm`; Eqs. 1 and 4) to the same state-space filtered seal tracks to infer how the seals' movement behavior 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 three potential environmental correlates of elephant seal move persistence: sea ice cover (the proportion of time the ocean is covered by ≥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). These variables are known predictors of elephant seal habitat preference (Hindell et al. 2017) and foraging (C. R. McMahon et al., *unpublished data*). Data sources and processing details are provided in Appendix S3. The environmental data values were extracted at each state-space filtered location. As saldiff is only calculated in areas where the bathymetry is deeper than 600 m this covariate is only relevant to the pelagic foragers (Appendix S4: Fig. S1). Similarly, ice was excluded from the models fit to seals making pelagic foraging trips as they spent little time in regions with sea-ice cover (Appendix S3: Fig. S1; Appendix S4: Fig. S1). R code for the model selection is in Appendix S5.

RESULTS

Time-varying move persistence (`mpm`)

The ice-bound seals exhibited similar movement patterns (Fig. 1a), with high move persistence on their outbound migrations and lower move persistence near the Antarctic continent in areas of higher sea-ice coverage.
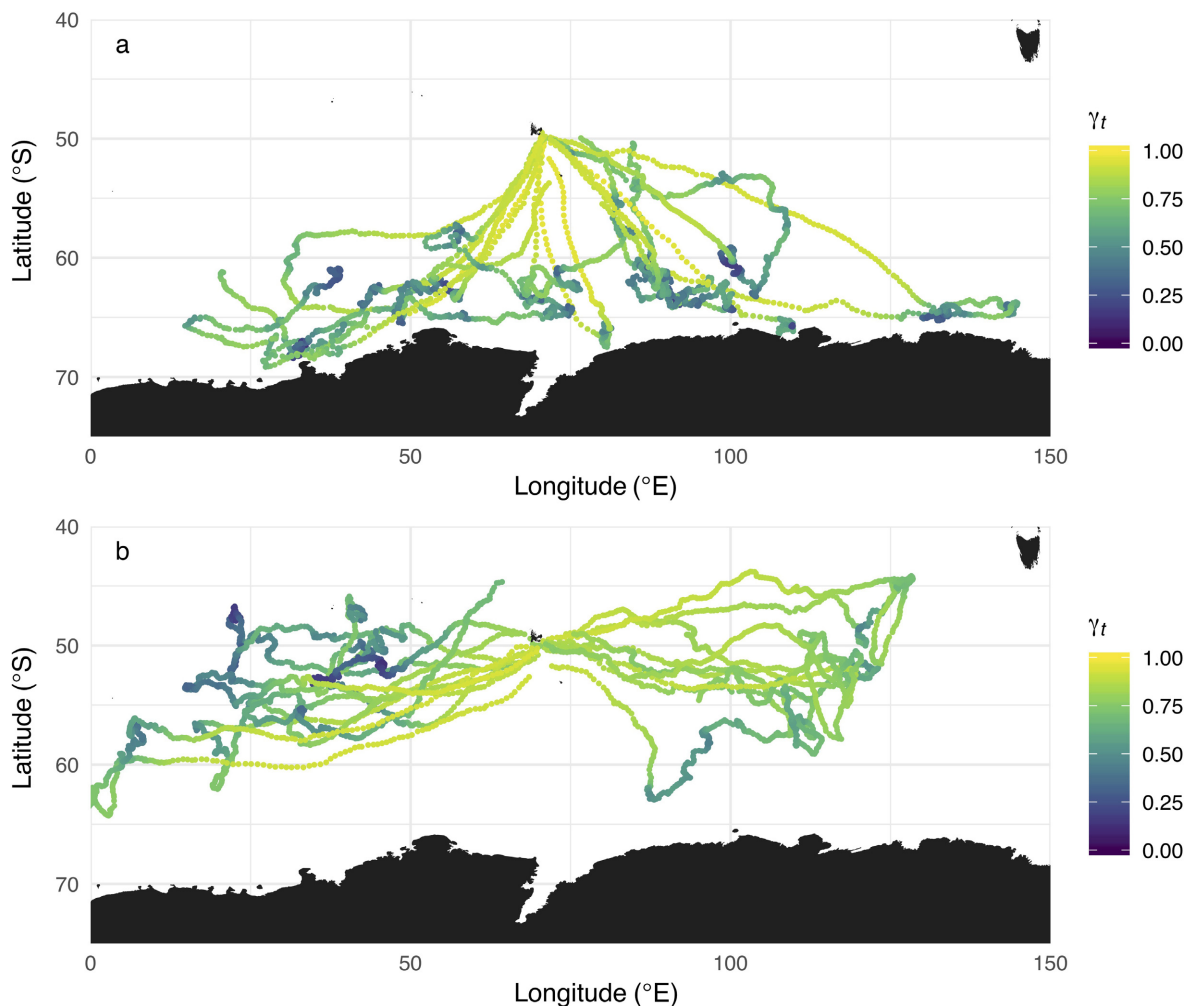
Reports

Fig. 1. Maps of SSM-filtered southern elephant seal tracks originating from Iles Kerguelen. (a) Ice-bound foraging trips were predominantly directed to locations south of 60° S, whereas (b) pelagic foraging trips are predominantly north of 60° S. Each location is colored according to its associated move persistence (γ_t) estimated from the move persistence model.

Return migrations to Iles Kerguelen were more variable, with some individuals moving persistently and others meandering, possibly foraging en route. Pelagic foraging seals (Fig. 1b) migrated approximately 2,000 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. 1b).

The γ_t-derived behavioral index is comparable but not identical to the discrete behavioral states estimated from the bsam switching state-space model (SSSM) (Appendix S3: Fig. S1). The γ_t index captured the same changes in movement pattern 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 S3: Table S1).

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

Sea-ice strategy.—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. 2a, b). Among individuals, the relationship with ice was consistently negative but the degree to which move persistence declined differed markedly (Fig. 2a), whereas the relationship with chl was highly variable with four individuals having strong negative relationships and the rest weak to moderately positive relationships (Fig. 2b; $Z = -1.04$, $P = 0.3$). Using the fixed effects from the best model, the prediction of γ_t over the spatial domain implies that seal move persistence changes, suggestive of search and foraging

TABLE 1. Model rankings by the change in the Akaike information criterion (ΔAIC) and likelihood ratios (LR) for the move persistence mixed effects model's (mpmm) fit to the 12 sea-ice and 12 pelagic foraging seals.

Strategy	Model formula	df	ΔAIC	LR	Time (s)
Sea ice	~ ice + chl + (ice + chl | id)	12	−9,954.21	−9,978.21	4.76
	~ ice + chl + (chl | id)	9	0.78	6.78	3.61
	~ ice + chl + (1 | id)	7	21.06	31.06	4.17
	~ ice + (1 | id)	6	21.08	33.08	2.63
	~ ice + chl + (ice | id)	9	23.59	29.59	5.76
	~ ice + (ice | id)	8	24.14	32.14	4.55
	~ chl + (chl | id)	8	219.74	227.74	4.09
	~ chl + (1 | id)	6	245.16	257.16	3.48
	~ 1 + (1 | id)	5	339.28	353.28	2.79
Pelagic	~ saldiff + (saldiff | id)	8	−13,897.26	−13,913.26	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

Notes: Absolute AIC and deviance for the best ranked model are on the first rows. All other ΔAIC and LR values are relative to these values. Time is the computation time to convergence. Random effects are in parentheses. chl, *a* concentration; ice, The predictor variables fit are sea ice cover; id, individual animal identifier; NA, model failed to converge; saldiff, salinity difference between 600 and 200 m.

behaviors, south of 65° S (south of the black contour line, Fig. 2d).

Pelagic strategy.— The best supported model for elephant seals foraging in the open ocean included fixed and random coefficients for the salinity difference between 600 and 200 m depths (saldiff, Table 1). On average, seals had movements that became strongly less persistent as the salinity difference decreased (Fig. 2c). Among individuals, this relationship was moderately variable with two individuals exhibiting relatively small changes in move persistence over the full range of saldiff (Fig. 2c). The spatial prediction of γ_t implies that animals generally adopt a movement pattern suggestive of search or forage once beyond the mid-latitudes near Kerguelen Island where saldiff is largest (i.e., south of the black contour line, in oceanic waters, or north in the vicinity of the Subantarctic Front; Fig. 2e).

DISCUSSION

Southern elephant seals employing specific foraging strategies respond to different environmental factors. Our modeling approach clearly identifies these responses, including strong decreases in move persistence associated with increasing ice coverage (sea-ice foragers) and decreasing salinity difference (pelagic foragers). Move persistence responses were relatively consistent among seals adopting either a sea-ice or a pelagic foraging strategy, but substantial individual variability in foraging location was evident.

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 (Labrousse et al. 2018); however this was not a consistent response with many others foraging farther offshore in the marginal sea-ice zone where chlorophyll *a* concentrations are lower (Appendix S4: Fig. S1). This pattern might be suggestive of density-dependent habitat selection, whereby seals distribute themselves so that foraging success is consistent across habitats of differing value (Morris 2011).

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 Circumpolar Deep Water 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 saline Subantarctic surface waters (northwestern areas, Appendix S4: Fig. S1).

Future climate scenarios project stronger westerly winds, leading to intensified ocean overturning circulation (Gao et al. 2018). With increased upwelling of nutrient-rich Circumpolar Deep Water, we might expect enhanced near-surface ocean productivity to benefit pelagically foraging southern elephant seals in future. Expectations for sea-ice foraging seals are highly uncertain due to complex physical processes occurring over the Antarctic
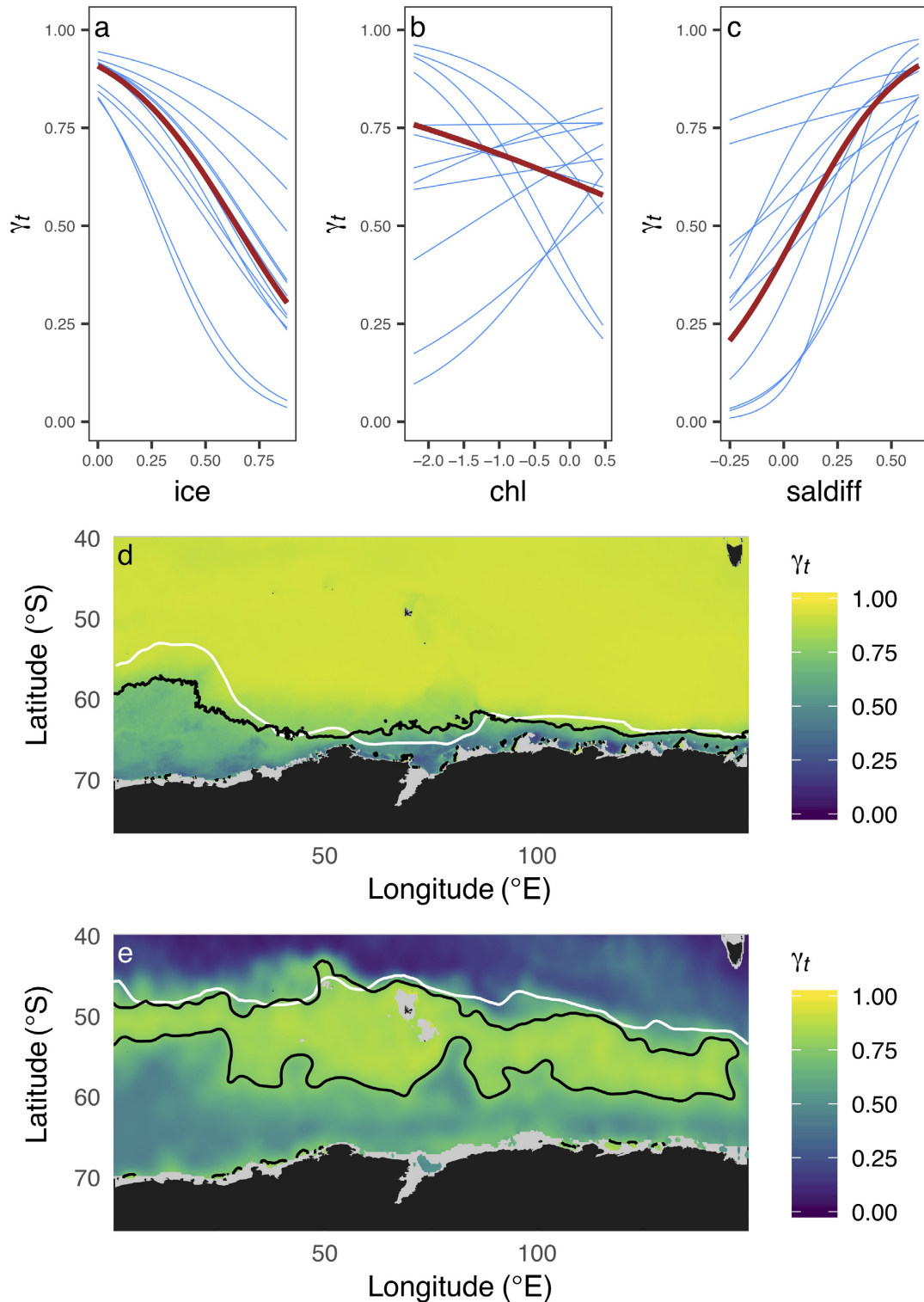
Reports

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Fig. 2. Fixed (red) and random (blue) effects relationships between move persistence γ_t and (a) the proportion of ice cover (ice) and (b) chlorophyll *a* concentration (chl) for ice-foraging seals and (c) between γ_t and the salinity difference (saldiff) between 600 and 200 m for pelagic foraging seals. All three panels display both random intercept and slopes, as per the best ranked models in Table 1. Spatial predictions of γ_t based on the fixed effect coefficients for the best fitting models for ice foraging seals for (d) ice-foraging seals and (e) pelagic-foraging seals. 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 boundaries of the Antarctic Circumpolar Current (d) and the Subantarctic Front (e) are displayed for reference (white lines).

continental shelf. However, projections of reduced sea-ice extent and duration may lead to reduced availability of foraging and/or resting habitat.

While the ultimate source of observed individual differences in movement–environment relationships is often unclear, three non-exclusive explanations seem likely. First, we often use relatively few predictors and these may indirectly or imperfectly represent the proximate influences to which predators are actually responding (i.e., prey density and/or distribution). This may inflate apparent individual differences in predator movement. Modeling more direct indices of prey, and/or reducing error within covariates by accounting for location uncertainty, 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 may confer real differences in foraging behavior with relatively little difference in fitness (Stamps 2007). For example, consistent boldness in foraging can generate important ecological trade-offs, effecting increases in growth and/or mortality rates (Stamps 2007).

Third, the inclusion of multiple random effects raises the possibility of over-fitting, especially when the number of individual tracks is low. Artificial variability, propagating from uncertainty in the locations and/or environmental covariates, could lead to spurious inference of strong individual differences in foraging behavior. A study design with repeat tagging of the same individuals would help resolve the issue. Ultimately, researchers must take care to address potential sources of error in their data and to use prior knowledge of their study species to guide model selection and interpretation.

Interpreting among-individual variability in movement–environment responses can be aided by considering established ecological theory. For example, density-dependent habitat selection and functional responses to prey availability likely underpin inferred relationships (Mason and Fortin 2017). Accounting for such effects when fitting and interpreting resource selection functions and habitat preference models can clarify understanding and thereby assist forecasting of species' distributions (McLoughlin et al. 2010).

Modeling approach and extensions

Our model is composed of a linear mixed effects regression embedded within a correlated random walk process model for animal movement behavior. 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–environment relationships and a nonparametric approach using penalized splines may improve inference (Langrock et al. 2017). Given the serial dependence structure of telemetry data, the unstructured covariance matrix we used for the random effects could be replaced with a first-order autoregressive covariance structure

(Brooks et al. 2017). 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 validation tool and can be estimated when fitting the model (Thygesen et al. 2017). Finally, there is a 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 and Michelot 2018), i.e., random draws of the environmental variables from the uncertainty of the state-space filtered location estimates.

Recent advances in habitat modeling methods (e.g., Avgar et al. 2016) hold promise for capturing the currently missing behavioral context in species' habitat preferences and space use. Here we model animal movement as a mixed effects function of environmental variables to gain deeper insight into how individuals and populations may actually use habitat. Our approach does not account for availability/accessibility of habitat in any way but this clearly must be considered when inferring habitat preferences. A reasonable approach for this might be to simulate animal tracks from our movement process model, examining implications of including/excluding environmental covariates. Pseudo-absence tracks can be combined into a habitat accessibility surface to condition spatial prediction of animal behavior from our process model (e.g., Raymond et al. 2015).

Our results show that TMB allows fast estimation of multiple fixed and random effects in an animal movement process model. Dramatically faster computation times allow analyses of movement–environment relationships in large telemetry data sets (hundreds of animals). This computation speed also opens up possibilities for more realistic models of animal movement, where warranted, perhaps by incorporating the third dimension for diving or flying animals and/or high-volume accelerometry data.

The process model used here differs markedly from the state-space model used by Bestley et al. (2013). Bestley et al. (2013) used discrete behavioral state Markov-switching embedded in a correlated random walk process model (Jonsen 2016). Here, we used time-varying move persistence γ_t as a behavioral index that varied continuously between 0 and 1. This continuous index provides another tool for characterising animal movement patterns and for making inferences about their environmental drivers. In some cases, a continuous index may offer more nuanced insight into variable but unknown behavioral sequences (Breed et al. 2012), whereas discrete states may offer more flexibility in capturing the known structure of animal movement patterns (Michelot et al. 2017).

Telemetry data obtained at the level of individuals poses a challenge to scale up to populations (Morales et al. 2010). Our approach enables multiple fixed (population) and random (individual) effects in movement–environment relationships to be fit simply and quickly. This provides a feasible solution to analysing increasingly large and detailed data sets, and for harnessing

Reports

Reports

individual-to-population level information on animal movement responses to environment.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2566/suppinfo