momentuHMM: R package for analysis of telemetry data using generalized multivariate hidden Markov models of animal movement

Brett T. McClintock¹ and Théo Michelot²

¹Marine Mammal Laboratory Alaska Fisheries Science Center NOAA National Marine Fisheries Service Seattle, U.S.A.

 ${\it Email:} \ {\tt brett.mcclintock@noaa.gov}$

²School of Mathematics and Statistics University of St Andrews St Andrews, U.K.

RUNNING HEAD: R package momentuHMM

August 21, 2019

Summary

- 1. Discrete-time hidden Markov models (HMMs) have become an immensely popular tool for inferring latent animal behaviors from telemetry data, largely because they are relatively fast and easy to implement when data streams are observed without error and at regular time intervals. While movement HMMs typically rely solely on location data, auxiliary biotelemetry and environmental data are powerful and readily-available resources for incorporating much more behavioral realism and inferring ecological relationships that would otherwise be difficult or impossible to infer from location data alone. However, there is a paucity of generalized user-friendly software available for implementing (multivariate) HMMs of animal movement. Furthermore, location measurement error, temporal irregularity, and other forms of missing data are often pervasive in telemetry studies (particularly in marine systems).
- 2. Here we provide a guide to using an open-source R package, momentum wersion 1.5.0, that addresses many of the deficiencies in existing software. Features for multivariate HMMs in momentuHMM (pronounced "momentum") include: 1) tools for data pre-processing and visualization; 2) user-specified probability distributions for an unlimited number of data streams and latent behavior states, such as those based on location (e.g., step length, turning angle) and auxiliary biotelemetry data (e.g., from pressure, conductivity, heart rate, or motion sensors); 3) biased and correlated random walk movement models, including "activity centers" associated with attractive or repulsive forces; 4) user-specified design matrices and constraints for covariate modelling of initial distribution, state transition probability, and probability distribution parameters using linear model formulas familiar to most R users; 5) multiple imputation methods that account for observation error attributable to measurement error and temporally-irregular or missing data; 6) seamless integration of spatio-temporal covariate raster data; 7) cosinor and spline regression formulas for cyclical (e.g., daily, seasonal) and other complicated patterns; 8) discrete individual-level random effects on state transition probabilities; 9) hierarchical hidden Markov models for data streams and/or state switching at multiple time scales; 10) "recharge" models for an aggregated physiological process associated with state switching in heterogeneous environments; 11) model checking and selection; and 12) data simulation capabilities for study design, power analyses and assessing model performance, including simulation of location data subject to movement constraints (e.g. land for marine animals), temporal irregularity,

and/or measurement error.

- **3.** After providing a brief introduction to (multivariate) HMMs for telemetry data, we demonstrate some of the capabilities of momentuHMM using real-world examples. This brief tutorial includes workflows for data formatting, model specification, model fitting, and diagnostics.
- 4. While many of the features of momentuHMM were motivated by animal movement data, the package can be used for analyzing any type of data that is amenable to (multivariate) HMMs. Practitioners interested in additional features for momentuHMM are encouraged to contact the authors.

Key-words animal biotelemetry, biologging, crawl, moveHMM, state-space model, state-switching

Contents

1	Intr	roduction	4
2	moı	nentuHMM overview	8
	2.1	Data preparation and visualization	10
	2.2	HMM specification and fitting	14
	2.3	Circular-circular regression model for the angle mean	17
	2.4	Individual-level random effects	19
	2.5	Hierarchical hidden Markov models	20
	2.6	Random walk probability distributions	21
	2.7	Multiple imputation	21
	2.8	Model visualization and diagnostics	22
	2.9	Simulation	23
3	Exa	mples	2 4
	3.1	African elephant	24
	3.2	Northern fur seal	29
	3.3	Loggerhead turtle	34
	3.4	Grey seal	39
	3.5	·	41

Ļ	Disc	eussion	144
	3.11	Simulating constrained movement	141
		3.10.4 Horn shark	130
		3.10.3 Atlantic cod	124
		3.10.2 Garter snakes	110
		3.10.1 Harbor porpoise	91
	3.10	Hierarchical HMMs	90
	3.9	Pilot whales	72
	3.8	Northern fulmars	60
	3.7	Harbour seals	54
	3.6	Group dynamic animal movement	49

1 Introduction

Discrete-time hidden Markov models (HMMs) have become immensely popular for the analysis of animal telemetry data (e.g. Morales et al. 2004; Jonsen et al. 2005; Langrock et al. 2012; McClintock et al. 2012). In short, an HMM is a time series model composed of a (possibly multivariate) observation process $(\mathbf{Z}_1, \ldots, \mathbf{Z}_T)$, in which each data stream is generated by N state-dependent probability distributions, and where the unobservable (hidden) state sequence $(S_t \in \{1, \ldots, N\}, t = 1, \ldots, T)$ is assumed to be a Markov chain. The state sequence of the Markov chain is governed by (typically first-order) state transition probabilities, $\gamma_{ij}^{(t)} = \Pr(S_{t+1} = j \mid S_t = i)$ for $i, j = 1, \ldots, N$, and an initial distribution $\delta^{(0)}$. The likelihood of an HMM can be succinctly expressed using the forward algorithm:

$$\mathcal{L} = \boldsymbol{\delta}^{(0)} \boldsymbol{\Gamma}^{(1)} \mathbf{P}(\mathbf{z}_1) \boldsymbol{\Gamma}^{(2)} \mathbf{P}(\mathbf{z}_2) \boldsymbol{\Gamma}^{(3)} \cdots \boldsymbol{\Gamma}^{(T-1)} \mathbf{P}(\mathbf{z}_{T-1}) \boldsymbol{\Gamma}^{(T)} \mathbf{P}(\mathbf{z}_T) \mathbf{1}^N, \tag{1}$$

where $\mathbf{\Gamma}^{(t)} = \left(\gamma_{ij}^{(t)}\right)$ is the $N \times N$ transition probability matrix, $\mathbf{P}(\mathbf{z}_t) = \operatorname{diag}(p_1(\mathbf{z}_t), \dots, p_N(\mathbf{z}_t))$, $p_s(\mathbf{z}_t)$ is the conditional probability density of \mathbf{Z}_t given $S_t = s$, and $\mathbf{1}^N$ is a N-vector of ones (for a thorough introduction to HMMs see Zucchini *et al.* 2016).

One of the most common discrete-time animal movement HMMs for telemetry location data is composed of two data streams, step length and turning angle (or bearing), which are calculated for each of the T time steps from the temporally-regular obser-

vations of an animal's position, (x_t, y_t) , for t = 1, ..., T + 1 (e.g. Morales et al. 2004; Langrock et al. 2012; McClintock et al. 2012). Step length (l_t) is typically calculated as the Euclidean distance between the locations (x_t, y_t) and (x_{t+1}, y_{t+1}) , while turning angle (ϕ_t) is calculated as the change in bearing $(b_t = \text{atan2}(y_{t+1} - y_t, x_{t+1} - x_t))$ between the intervals [t-1,t] and [t,t+1] (e.g. $\phi_t = 0$ if $b_{t-1} = b_t$). For this HMM composed of 2 data streams, $\mathbf{z}_t = (l_t, \phi_t)$, and, conditional on the latent state S_t , independent probability distributions are typically assumed for each stream; that is, $p_s(\mathbf{z}_t) = p_s(l_t)p_s(\phi_t)$. Some common probability distributions for the step length data stream are the gamma or Weibull distributions, while the wrapped Cauchy or von Mises distributions are often employed for turning angle or bearing. For a fitted HMM, the Viterbi algorithm is used to compute the most likely sequence of underlying states (Zucchini et al. 2016). In movement HMMs, the states are often considered as proxies for animal behaviour.

While HMMs for animal movement based solely on location data are somewhat limited in the number and type of biologically-meaningful movement behavior states they are able to accurately identify, advances in biologging technology are now allowing the collection of valuable auxiliary biotelemetry data (e.g., dive activity, accelerometer, heart rate, stomach temperature), which, when combined with location data, allow for multivariate HMMs that can incorporate much more behavioral realism and facilitate inferences about complex ecological relationships that would otherwise be difficult or impossible to infer from location data alone (e.g. McClintock et al. 2013; DeRuiter et al. 2017; McClintock et al. 2017). Multivariate HMMs that utilize both location and auxiliary biotelemetry data can facilitate the identification of additional states that go beyond the N=2 state approaches that are most frequently used by practitioners. For example, the most widely used 2-state HMMs for animal movement include "encamped" (or "foraging") and "exploratory" (or "transit") states characterized by area-restrictedsearch-type movements (shorter step lengths with little to no directional persistence) and migratory-type movements (longer step lengths with high directional persistence), respectively (Morales et al. 2004; Jonsen et al. 2005). However, very different behaviors can exhibit similar horizontal trajectories. For example, for herbivores such as North American elk (Morales et al. 2004) or central-place foragers such as harbour seals (McClintock et al. 2013), the horizontal trajectories of "resting" and "foraging" movements can be very difficult to distinguish. Standard 2-state HMMs based solely on horizontal trajectory will tend to lump these behaviors together, and this could

have unintended consequences if, for example, one intends to use the estimated state sequences to identify foraging habitat. In order to tweeze apart distinct behaviors with similar horizontal trajectories, additional states can be informed by auxiliary information (such as mandible accelerometer or dive data), incorporated as additional data stream(s) in a multivariate HMM.

When data streams are observed without error and at regular time intervals, a major advantage of HMMs is the relatively fast and efficient maximization of the likelihood using the forward algorithm (Eq. 1). However, location measurement error is rarely non-existent in animal-borne telemetry studies and depends on both the device and the system under study. For example, GPS errors are typically less than 50m, but Argos errors can exceed 10km (e.g. Costa et al. 2010). An extreme case of missing data can arise when location data are obtained with little or no temporal regularity, as in many marine mammal telemetry studies (e.g. Jonsen et al. 2005), such that few (if any) observations align with the regular time steps required by discrete-time HMMs. When explicitly accounting for uncertainty attributable to location measurement error, temporally-irregular observations, or other forms of missing data, one must typically fit (multivariate) HMMs using computationally-intensive (and often time-consuming) model fitting techniques such as Markov chain Monte Carlo (Jonsen et al. 2005; McClintock et al. 2012). However, complex analyses requiring novel statistical methods and custom model-fitting algorithms are not practical for many practitioners.

While statisticians have been applying HMMs to telemetry data for decades, R (R Core Team 2017) packages such as bsam (Jonsen et al. 2005), moveHMM (Michelot et al. 2016), and swim (Whoriskey et al. 2017) have recently helped make these models of animal movement behavior more accessible to the practitioners that are actually conducting telemetry studies. These advances represent important steps toward making HMMs of animal movement more accessible, but the models that can currently be implemented using existing software remain limited in many key respects. For example, existing HMM software for animal movement is limited to two data streams based solely on location data (e.g. step length and turning angle), and while moveHMM allows for a user-specified number of latent behavioral states (bsam and swim are limited to N=2 states), it is typically difficult to identify >2 biologically-meaningful behavior states from only 2 data streams (e.g. Morales et al. 2004; Beyer et al. 2013; McClintock et al. 2014). Both moveHMM and swim are designed for temporally-regular

(or linearly-interpolated) location data with negligible measurement error, but the realities of animal-borne telemetry often yield temporally-irregular location data subject to error (particularly in aquatic environments). Other notable deficiencies of existing software include limited abilities to incorporate spatio-temporal environmental or individual covariates on parameters, biased (or directed) movements in response to attractive or repulsive forces (e.g. McClintock et al. 2012; Langrock et al. 2014), cyclical (e.g. daily, seasonal) and other more complicated behavioral patterns, or constraints on parameters.

To address these deficiencies in existing software, we developed a user-friendly R package, momentuHMM (Maximum likelihood analysis Of animal MovemENT behavior Using multivariate Hidden Markov Models), intended for practitioners wishing to implement more flexible and realistic (multivariate) HMM analyses of animal movement while accounting for common challenges associated with telemetry data (McClintock & Michelot 2018). Features for multivariate HMM analyses in momentuHMM include: 1) tools for data pre-processing and visualization; 2) user-specified probability distributions for an unlimited number of data streams and latent behavior states; 3) biased and correlated random walk movement models, including "activity centers" associated with attractive or repulsive forces (e.g. McClintock et al. 2012); 4) user-specified design matrices and constraints for covariate modelling of state transition probability and probability distribution parameters using linear model formulas familiar to most R users; 5) multiple imputation methods that account for observation error attributable to measurement error and temporally-irregular or missing data (Hooten et al. 2017; McClintock 2017); 6) seamless integration of spatio-temporal environmental covariate data (e.g., wind direction, forest cover, sea ice concentration) using the raster package (Hijmans 2016b); 7) cosinor (e.g. Cornelissen 2014) and spline regression formulas for cyclical and other complicated behavioral patterns; 8) discrete individual-level random effects on state transition probabilities (e.g. DeRuiter et al. 2017); 9) hierarchical hidden Markov models (e.g. Leos-Barajas et al. 2017; Adam et al. 2019) for data streams and/or state switching at multiple time scales; 10) "recharge" models for an aggregated physiological process associated with state switching in heterogeneous environments (Hooten et al. 2019); 11) model checking and selection; and 12) data simulation capabilities for study design, power analyses and assessing model performance, including simulation of location data subject to movement constraints (e.g. land for marine animals), temporal

irregularity, and/or measurement error.

In the following tutorial, we demonstrate some of the capabilities of momentuHMM using real-world examples, including an example of periodic cycles in African elephant movement, a 3-state ("resting", "foraging", "transit") northern fur seal example incorporating auxiliary dive activity data (McClintock et al. 2014), a loggerhead turtle example relating "foraging" and "transit" movements to ocean surface currents, a 5state grey seal example incorporating biased movements toward haul-out and foraging locations (McClintock et al. 2012), a 4-state ("outbound", "searching", "foraging", "inbound") southern elephant seal example with biased movements toward and away from a colony (Michelot et al. 2017), a 3-state ("resting", "foraging", "transit") harbour seal example using population-level constraints on movement parameters (McClintock et al. 2013), a 6-state northern fulmar example incorporating biased movements relative to both static (i.e. colony) and dynamic (i.e. fishing vessels) activity centers (Pirotta et al. 2018), a 4-state long-finned pilot whale example including individuallevel random effects on state transition probabilities (Isojunno et al. 2017), and hierarchical HMMs fitted to harbor porpoise, garter snake, Atlantic cod, and horn shark data (Leos-Barajas et al. 2017; Adam et al. 2019). Using simulated data, we also demonstrate how the group dynamic model of Langrock et al. (2014) can be implemented using momentuHMM. Finally, we demonstrate how to simulate movement subject to barriers or other constraints (e.g. land for marine animals) using potential functions (e.g. Brillinger et al. 2012). This brief tutorial includes workflows for data formatting, model specification, model fitting, and diagnostics. While many of the features of momentuHMM were motivated by animal movement data, the package can be used for analyzing any type of data that is amenable to (multivariate) HMMs. Additional information, including help files, data, examples, and package usage is available by downloading the momentuHMM package from CRAN (https://cran.r-project.org) or Github (https://github.com/bmcclintock/momentuHMM). This article describes momentuHMM version 1.5.0.

2 momentuHMM overview

Before delving into some of the finer details, we will first provide an overview of the main features and functions of momentuHMM (pronounced "momentum"). While space is

Table 1. Workhorse functions for the R package momentuHMM.

Function	Description
crawlMerge	Merge crawlWrap output with additional data streams or covariates
crawlWrap	Fit crawl models and predict temporally-regular locations
fitHMM	Fit a (multivariate) HMM to the data
MIfitHMM	Fit (multivariate) HMMs to multiple imputation data
MIpool	Pool momentuHMM model results across multiple imputations
plot.crwData	Plot crawlWrap output
plot.miSum	Plot summaries of multiple imputation momentuHMM models
plot.momentuHMM	Plot summaries of momentuHMM models
plot.momentuHMMData	Plot summaries of selected data streams and covariates
plotPR	Plot time series, qq-plots and sample ACFs of pseudo-residuals
plotSat	Plot locations on satellite image
${ t plotSpatialCov}$	Plot locations on raster image
plotStates	Plot the (Viterbi-)decoded states and state probabilities
${ t plotStationary}$	Plot stationary state probabilities
${ t prepData}$	Pre-process data streams and covariates
pseudoRes	Calculate pseudo-residuals for momentuHMM models
simData	Simulate data from a (multivariate) HMM
simHierData	Simulate data from a (multivariate) hierarchical HMM
stateProbs	State probabilities for each time step
viterbi	Most likely state sequence (using the Viterbi algorithm)

limited in this tutorial, further details on implementation can be found in the package's documentation and vignette. The workhorse functions of momentuHMM are listed in Table 1. Usage of several of these functions (e.g. fitHMM, prepData, simData) is deliberately very similar to equivalent functions in moveHMM (Michelot et al. 2016), but the momentuHMM arguments for these functions have been generalized and expanded to accommodate a more flexible framework for data pre-processing, model specification, parameterization, and simulation. R users already familiar with moveHMM will therefore likely find it easy to immediately begin using momentuHMM.

One of the key features of momentuHMM is the ability to include an unlimited number of HMM data streams (e.g. step length, turning angle, dive activity, heart rate) arising from a broad range of commonly used probability distributions (e.g. beta, categorical, gamma, normal, multivariate normal, Poisson, von Mises, Weibull), including (multivariate) normal random walks that can be particularly useful for modeling positions directly (instead of step lengths and turning angles). Any of the parameters of the

probability distributions used for the observed data can be modelled as a function of environmental and individual covariates using link functions (Tables 2 and 3). For any given "natural scale" (or "real scale") probability distribution parameter θ , all of the link functions (g) in momentuHMM are of the general form $g(\theta) = \mathbf{X}_{\theta} \boldsymbol{\beta}_{\theta}$, where \mathbf{X}_{θ} is the $T \times K$ design matrix (composed of K covariates) and $\boldsymbol{\beta}_{\theta}$ is the corresponding K-vector of "working scale" (or "beta scale") parameters for θ . For example, suppose step length is assumed to have a gamma distribution, $l_t \mid S_t = s \sim \text{gamma}(\mu_s, \sigma_s)$. In momentuHMM, the natural scale parameters for the gamma distribution are the (state-dependent) step length mean $(\mu_s > 0)$ and standard deviation $(\sigma_s > 0)$. Because both of these parameters must be positive, the log link function is a natural choice for modelling these parameters as a function of covariates, e.g., $\log(\boldsymbol{\mu}) = \mathbf{X}_{\mu} \boldsymbol{\beta}_{\mu}$ and $\log(\boldsymbol{\sigma}) = \mathbf{X}_{\sigma} \boldsymbol{\beta}_{\sigma}$.

The state transition probabilities ($\Gamma^{(t)}$) and initial distribution ($\delta^{(0)}$) can also be modelled as functions of covariates, using a multinomial logit link, as described e.g. by Michelot et al. (2016). Permissable R classes for covariates include numeric, integer, or factor. Factors can be particularly useful for specifying models with individual-or group-level (e.g. sex or age class) effects on state transition and probability distribution parameters. Spatio-temporal covariates can also be of classes rasterLayer, rasterStack, or rasterBrick (Hijmans 2016b), in which case momentuHMM automatically extracts the appropriate covariate values from the raster based on the time and location of each observation (see example in section 3.3).

2.1 Data preparation and visualization

For temporally-regular location data with negligible measurement error, the prepData function is used to create a momentuHMMData object that can be used for data visualization and further analysis. The arguments for prepData include:

- data A data frame with T+1 rows including optionally a field 'ID' (identifiers for different individuals), coordinates from which step length ('step') and turning angle ('angle') data streams are to be calculated, any additional data streams, and any covariates identified in the covNames and angleCovs arguments. Altervatively, data can be a crwData object returned by crawlWrap.
- type Coordinate type; 'UTM' if easting-northing or 'LL' if longitude-latitude.

Table 2. Univariate data stream (z) probability distributions, natural parameters, and default link functions for covariate modelling. Probability distributions with positive support can be zero-inflated (with additional zero-mass parameters), while the beta distribution can be zero- and/or one-inflated (with additional one-mass parameters). If user-specified bounds are provided, then custom link functions are used instead of the defaults (see package documentation for further details). If both zero- and one-inflation are included, then a multinomial logit (mlogit) link is used because these probabilities must sum to less than one (in this case, any user-specified bounds for the zero- and one-inflation parameters are ignored). If circular-circular regression is specified for the mean of angular distributions ("vm" and "wrpcauchy"), then a link function based on Rivest et al. (2016) is used. The von Mises consensus distribution ("vmConsensus") is a von Mises circular-circular regression model where the concentration parameter depends on the level of agreement among short-term directional persistence and angular covariates. Users seeking additional univariate probability distributions are encouraged to contact the authors.

Distribution	Support	Parameters	Link function ¹
Bernoulli ("bern")	$z_t \in \{0, 1\}$	$\mathtt{prob} \in (0,1)$	logit
Beta ("beta")	$z_t \in (0,1)$	shape1 > 0	log
		$\mathtt{shape2} > 0$	log
		$\texttt{zero-mass} \in (0,1)$	logit
		$\mathtt{one\text{-}mass} \in (0,1)$	logit
Categorical ("cat")	$z_t \in \{1, \ldots, k\}$	$\mathtt{prob}_1, \dots, \mathtt{prob}_{k-1} \in (0,1)$	mlogit
Exponential ("exp")	$z_t > 0$	$\mathtt{rate} > 0$	\log
		$\texttt{zero-mass} \in (0,1)$	logit
Gamma ("gamma")	$z_t > 0$	$\mathtt{mean} > 0$	\log
		$\mathtt{sd} > 0$	\log
		$\texttt{zero-mass} \in (0,1)$	logit
Log normal ("lnorm")	$z_t > 0$	$\texttt{location} \in {\rm I\!R}$	identity
		scale > 0	\log
		$\texttt{zero-mass} \in (0,1)$	logit
Normal ("norm")	$z_t \in \mathbb{R}$	$\mathtt{mean} \in {\rm I\!R}$	identity
		$\mathrm{sd}>0$	\log
Normal random walk ("rw_norm")	$z_t \in \mathbb{R}$	$\mathtt{mean} \in {\rm I\!R}$	identity
		$\mathrm{sd}>0$	\log
Poisson ("pois")	$z_t \in \{0, 1, \ldots\}$	$\mathtt{lambda} > 0$	\log
Von Mises ("vm")	$z_t \in (-\pi, \pi]$	$\mathtt{mean} \in (-\pi,\pi]$	$\tan(\mathtt{mean}/2)$
		${\tt concentration} > 0$	\log
Von Mises ("vmConsensus")	$z_t \in (-\pi, \pi]$	$\mathtt{mean} \in (-\pi,\pi]$	Rivest et al.
		$\mathtt{kappa} > 0$	\log
Weibull ("weibull")	$z_t > 0$	$\mathtt{shape} > 0$	\log
		$\mathtt{scale} > 0$	\log
		$\texttt{zero-mass} \in (0,1)$	logit
Wrapped Cauchy ("wrpcauchy")	$z_t \in (-\pi, \pi]$	$\mathtt{mean} \in (-\pi,\pi]$	$\tan(\mathtt{mean}/2)$
		${\tt concentration} \in (0,1)$	logit

¹Link functions (g) relate natural scale parameters (θ) to a $T \times K$ design matrix (\mathbf{X}) and K-vector of working scale parameters $(\boldsymbol{\beta} \in \mathbb{R}^K)$ such that $\boldsymbol{\beta}(\boldsymbol{\theta}) = \mathbf{X}\boldsymbol{\beta}$.

Table 3. Multivariate data stream (**z**) probability distributions, natural parameters, and default link functions for covariate modelling. If user-specified bounds are provided, then custom link functions are used instead of the defaults (see package documentation for further details). Users seeking additional multivariate probability distributions are encouraged to contact the authors.

Distribution	Support	Parameters	Link function ²
Bivariate normal ("mvnorm2")	$\mathbf{z}_t \in \mathrm{I\!R}^2$	$\texttt{mean.x} \in {\rm I\!R}$	identity
		$\mathtt{mean.y} \in {\rm I\!R}$	identity
		$\mathtt{sigma.x} > 0$	log
		$\mathtt{sigma.xy} \in \mathrm{I\!R}$	identity
		$\mathtt{sigma.y} > 0$	\log
Bivariate normal random walk ("rw_mvnorm2")	$\mathbf{z}_t \in \mathbb{R}^2$	$\mathtt{mean.x} \in {\rm I\!R}$	identity
		$\texttt{mean.y} \in {\rm I\!R}$	identity
		$\mathtt{sigma.x} > 0$	\log
		$\mathtt{sigma.xy} \in \mathrm{I\!R}$	identity
		$\mathtt{sigma.y} > 0$	\log
Trivariate normal ("mvnorm3")	$\mathbf{z}_t \in \mathbb{R}^3$	$\mathtt{mean.x} \in {\rm I\!R}$	identity
		$\texttt{mean.y} \in {\rm I\!R}$	identity
		$\mathtt{mean.z} \in {\rm I\!R}$	identity
		$\mathtt{sigma.x} > 0$	\log
		$\mathtt{sigma.xy} \in \mathrm{I\!R}$	identity
		$\mathtt{sigma.xz} \in \mathrm{I\!R}$	identity
		$\mathtt{sigma.y} > 0$	log
		$\texttt{sigma.yz} \in {\rm I\!R}$	identity
	_	$\mathtt{sigma.z} > 0$	log
Trivariate normal random walk ("rw_mvnorm3")	$\mathbf{z}_t \in \mathbb{R}^3$	$\mathtt{mean.x} \in {\rm I\!R}$	identity
		$\texttt{mean.y} \in {\rm I\!R}$	identity
		$\mathtt{mean.z} \in {\rm I\!R}$	identity
		$\mathtt{sigma.x} > 0$	\log
		$\mathtt{sigma.xy} \in \mathrm{I\!R}$	identity
		$\mathtt{sigma.xz} \in \mathrm{I\!R}$	identity
		$\mathtt{sigma.y} > 0$	log
		$\texttt{sigma.yz} \in \rm I\!R$	identity
		${\tt sigma.z} > 0$	log

Link functions (g) relate natural scale parameters (θ) to a $T \times K$ design matrix (\mathbf{X}) and K-vector of working scale parameters $(\boldsymbol{\beta} \in \mathbb{R}^K)$ such that $g(\boldsymbol{\theta}) = \mathbf{X}\boldsymbol{\beta}$.

- coordNames Names of the two coordinate columns in data. If coordNames=NULL then step lengths, turning angles, and any location-based covariates (i.e., those specified by spatialCovs, centers, centroids, and angleCovs) are not calculated.
- covNames Character vector indicating the names of any covariates in data. Any variables in data (other than "ID") that are not identified in covNames or angleCovs are assumed to be data streams.
- spatialCovs List of Raster-class objects (Hijmans 2016b) containing spatiotemporally referenced covariates. Covariates specified by spatialCovs are extracted from the raster layer(s) based on the location data. Raster stacks may also be included, in which case the appropriate z values (e.g. time, date) must also be included in data.
- centers 2-column matrix providing the coordinates for any activity centers (e.g., potential centers of attraction or repulsion) from which distance and angle covariates will be calculated based on the location data and returned in the momentuHMMData object.
- centroids List where each element is a data frame containing the x-coordinates ('x'), y-coordinates ('y'), and times for a centroid (i.e., a dynamic activity center for which the coordinates can change over time) from which distance and angle covariates will be calculated based on the location data and returned in the momentuHMMData object.
- angleCovs Character vector indicating the names of any circular-circular regression angular covariates in data or spatialCovs that need conversion from standard direction (in radians relative to the x-axis) to turning angle (relative to previous movement direction).

Summary plots of the momentuHMMData object returned by prepData can be created for any data stream or covariate using the generic plot function.

If location data are temporally-irregular or subject to measurement error, then they are not suitable for prepData. In this case, momentuHMM can be used to perform a 2-stage multiple imputation approach (McClintock 2017). We discuss this pragmatic

approach to incorporating uncertainty attributable to observation error and temporal irreglarity into multivariate HMM analyses in section 2.7.

2.2 HMM specification and fitting

Once a momentuHMMData object has been created using prepData, then the data are ready to be passed to the generalized multivariate HMM-fitting function fitHMM. There are many different options for specifying HMMs using fitHMM, so here we will only focus on several of the most important and useful features (further details of all fitHMM arguments are in the package documentation). The bare essentials of fitHMM include the arguments:

- data A momentuHMMData object
- nbStates Number of latent states (N)
- dist A named list indicating the probability distributions of the data streams.
- estAngleMean An optional named list indicating whether or not to estimate the angle mean for data streams with angular distributions (e.g. turning angle). If not estimated (the default), the angle mean is fixed to 0.
- formula Regression formula for the transition probability covariates
- stationary Logical indicating whether or not the initial distribution is considered equal to the stationary distribution (must be FALSE if formula includes covariates)
- Par0 A named list containing vectors of starting values for the state-dependent probability distribution parameters of each data stream

These seven arguments are all that are needed in order to fit the HMMs currently supported in moveHMM (Michelot et al. 2016). For example, here is how the analysis of 15 "wild haggis" tracks described in Michelot et al. (2016) would be implemented using momentuHMM:

```
library(momentuHMM)
### Load raw data
rawHaggis<-read.csv("rawHaggises.csv")</pre>
```

Note that many of the arguments in fitHMM are lists, with each element of the list corresponding to a data stream. The list names provided in dist, ParO, and estAngleMean (e.g. 'step' and 'angle') must therefore have a corresponding column in data with the same name. Additional data streams can be added to the model by simply adding the additional elements to these list arguments (see examples in sections 3.2, 3.8, and 3.9).

As seen above, the formula argument can include many of the functions and operators commonly used to construct terms in R linear model formulas (e.g. a*b, a:b, cos(a)). The formulaDelta argument can be similarly used to specify covariate models for the initial distribution. The formula argument can also be used to specify transition probability matrix models that incorporate cyclical patterns (using the cosinor special function; see example in section 3.1), splines for explaining other more complicated patterns (e.g., bs and ns functions in the R base package splines), and factor variables (e.g., formula=~ID for individual-level effects). By default the formula argument applies to all state transition probabilities, but the special functions state, toState, and betaCol allow for state- and parameter-specific formulas to be specified (see examples in sections 3.4 and 3.8). While betaCol allows a formula to be specified for a specific transition (e.g. state $3 \to 1$), state and toState allow a formula to be specified for all transitions from (e.g. $3 \to 1, 3 \to 2$) and to (e.g. state $1 \to 3, 2 \to 3$) specific states, respectively. The betaCons argument allows for equality constraints among any of the transition probability parameters (e.g. $\gamma_{12}^{(t)} = \gamma_{21}^{(t)}$; see example in section 3.8). Specific state transition probabilities can also be fixed to zero (or any other value) using the

fixPar argument, which can be useful for incorporating more behavioral realism. For example, fixPar can be used to prohibit or enforce switching from one particular state to another (possibly as a function of spatio-temporal covariates).

Similar to the formula argument for state transition probability modelling, it is through the DM argument of fitHMM that models are specified for the state-dependent probability distribution parameters for each data stream. DM is a list argument containing an element for each data stream, but each element itself is also a list specifying the design matrix formulas for each parameter. For example, the following fits the exact same wild haggis model as above, but employs a user-specified (intercept-only) design matrix for the step length data stream:

Note that when DM is specified for a data stream, the initial parameter values (Par0) for that data stream now correspond to columns of the resulting design matrix and must be on the working scale instead of the natural scale. In this case, because the log link is used for the natural parameters of the gamma distribution, Par0\$step was specified on the log scale. The functions getPar, getPar0, checkPar0, and getParDM are designed to assist users in the specification of design matrices and corresponding initial values on the working scale for any given model (see package documentation for further details). DM formulas are just as flexible as the formula argument and, in addition to common linear model formula functions and operators, can also include cyclical cosinor models (see section 3.1), splines, factor variables, and state-specific probability distribution parameter formulas (see examples in sections 3.3 and 3.4). As with the state transition probabilities, working parameters for probability distributions can also be fixed to user-specified values using the fixPar argument.

Specification of design matrices using DM is not limited to formulas. Alternatively, "pseudo-design" matrices can be specified, using an R matrix with rows corresponding

to the natural parameters and columns corresponding to the working parameters. The elements in the matrix may be numeric or character strings containing model formula terms (see examples in sections 3.4, 3.7, and 3.8). Using a pseudo-design matrix for step length, the following is yet another way to implement the exact same wild haggis model:

(note that column and row names for pseudo-design matrices are not required but can be useful). Pseudo-design matrices allow for the sharing of common working parameters (such as intercept terms) among natural scale parameters, and this can be used to constrain natural scale parameters (e.g., $\mu_1 \leq \mu_2$) when used in tandem with the workBounds argument (see sections 3.2, 3.7, and 3.8). This is particularly useful for preventing state label switching when repeatedly fitting the same HMM using multiple imputation methods (see section 2.7).

2.3 Circular-circular regression model for the angle mean

Another noteworthy fitHMM argument, circularAngleMean, is a list argument that enables users to specify circular-circular regression models for the mean (μ) parameter of angular distributions, such as the wrapped Cauchy and von Mises, instead of circular-linear models based on the tangent link function (Table 2). When circularAngleMean is specified as TRUE for any given angular data stream (e.g. turning angle), then a

special link function based on Rivest et al. (2016) is used:

$$\boldsymbol{\mu} = \operatorname{atan2}(\sin(\mathbf{X}_{\mu})\boldsymbol{\beta}_{\mu}, 1 + \cos(\mathbf{X}_{\mu})\boldsymbol{\beta}_{\mu}), \tag{2}$$

where \mathbf{X}_{μ} is a $T \times K$ matrix composed of the turning angles between K angular covariates (e.g., wind direction, sea surface current direction) and the bearing of movement during the previous time step; that is, each element

$$x_{t,k} = \operatorname{atan2}(\sin(r_{t,k} - b_{t-1}), \cos(r_{t,k} - b_{t-1}))$$
(3)

for angular covariate $r_{t,k}$ and $k=1,\ldots,K$ (note that prepData and MIfitHMM calculate X_{μ} based on the angleCovs, centers, or centroids arguments so users need not bother). Because this link function is designed for turning angles, a turning angle of 0 is provided as the reference angle (hence the "1+" preceding the cosine term in Eq. 2). Thus as a trade-off between biased and correlated movements, the working parameters (β_{μ}) for the expected turning angle at time t weight the attractive (or repulsive) strengths of the angular covariates relative to directional persistence. When all $\beta_{\mu} = 0$, the model reduces to a correlated random walk, but an increasingly biased random walk results as β_{μ} gets larger (or smaller). Alternatively, circular Angle Mean can be specified as a numeric scalar, where the value specifies the coefficient for the reference angle (i.e., directional persistence) term in Eq. 2. For example, setting circularAngleMean to 0 specifies a circular-circular regression model with no directional persistence term (thus specifying a biased random walk instead of a biased correlated random walk; see examples in sections 3.4, 3.5.2, and 3.6). Setting circular Angle Mean to 1 is equivalent to setting it to TRUE, i.e., a circular-circular regression model with a coefficient of 1 for the directional persistence reference angle. Many interesting hypotheses about animal movmement can be addressed using circular-circular regression on movement direction, including the effects of wind, sea surface currents (see example in section 3.3), centers of attraction or repulsion (see examples in sections 3.4, 3.5, and 3.8), group dynamic models (see example in section 3.6), and dynamic activity centers (see example in section 3.8.

The special function angleFormula can be included in DM formulas or pseudo-design matrices in order to model the circular-circular regression angle mean as a function of

the relative strength (or importance) of angular covariates (Rivest et al. 2016):

$$\boldsymbol{\mu} = \operatorname{atan2}((\mathbf{Z}_{\mu} \circ \sin(\mathbf{X}_{\mu}))\boldsymbol{\beta}_{\mu}, 1 + (\mathbf{Z}_{\mu} \circ \cos(\mathbf{X}_{\mu}))\boldsymbol{\beta}_{\mu}), \tag{4}$$

where \mathbf{Z}_{μ} is a $T \times K$ matrix of positive real covariates (e.g. wind speed, sea surface current speed) and \circ is the Hadamard (i.e. element-wise) product. The special function angleFormula can also be used to specify group- or individual-level effects on the circular-circular regression angle mean coefficients $(\boldsymbol{\beta}_{\mu})$.

Also based on Rivest *et al.* (2016), the von Mises consensus distribution is a special von Mises circular-circular regression model where the concentration parameter (ρ) depends on the level of agreement among short-term directional persistence (i.e. moving forward) and the angular covariates:

$$\boldsymbol{\rho} = \kappa \sqrt{\left[(\mathbf{Z}_{\mu} \circ \sin(\mathbf{X}_{\mu})) \boldsymbol{\beta}_{\mu} \right]^{2} + \left[1 + (\mathbf{Z}_{\mu} \circ \cos(\mathbf{X}_{\mu})) \boldsymbol{\beta}_{\mu} \right]^{2}}.$$
 (5)

Note that the von Mises consensus distribution is parameterized in terms of μ and κ (see Table 2), but momentuHMM returns and plots real parameter estimates in terms of μ and ρ . When all β_{μ} are non-negative, then the minimum and maximum values for ρ are $\kappa|1-\min(\mathbf{Z}_{\mu}\boldsymbol{\beta}_{\mu})|$ and $\kappa\left[1+\max(\mathbf{Z}_{\mu}\boldsymbol{\beta}_{\mu})\right]$, respectively. In the consensus model, κ can be interpreted as the concentration towards a turning angle of zero (i.e. moving forward) when the angular covariate components perfectly cancel out. See section 3.3 for example code using angleFormula and the von Mises consensus ("vmConsensus") distribution.

2.4 Individual-level random effects

HMM applications often assume the initial distribution and state transition probability matrix is the same for all individuals (i.e. "complete pooling" of the individuals' time series). But in reality, individuals often do not exhibit the same state-switching dynamics and there is individual-level variation. Individual heterogeneity can often be well explained by covariates (e.g., sex, age class) and included in formula, but it is not always possible to identify (and/or measure) all of the important covariates that drive this variation. One option is to include separate state-switching dynamics for each individual (i.e. "no pooling") by specifying formulaDelta = "ID and formula = "ID, but this "fixed" effect approach can result in many additional parameters to estimate (it

also doesn't explain very much about potential factors driving individual heterogeneity). Alternatively, generic individual heterogeneity in state-switching dynamics can be modeled as a "random" effect. While continuous-valued individual-level random effects can be computationally demanding, discrete-valued random effects are more computationally feasible and can be effective in "mopping up" individual heterogeneity in the initial distribution and state transition probabilities that is not explained by measurable covariates. Discrete-valued random effects have recently been used in HHMs of animal movement (e.g. McKellar et al. 2014; Towner et al. 2016; DeRuiter et al. 2017; Isojunno et al. 2017), and these "mixed" HMMs can be fitted with fitHMM (or MIfitHMM) through the mixtures and formulaPi arguments. The mixtures argument specifies the number of mixtures (K) in the model, where each mixture represents a possible initial distribution and transition probability matrix, and each individual time series is assumed to be driven by exactly one of these mixtures. For K mixtures, the mixture weight $(\pi_k; k = 1, \ldots, K)$ is the probability that the kth mixture underlies the state-switching dynamics for a given individual, and a model formula for π can be specified using the formulaPi argument. For example, Towner et al. (2016) found support for K=3mixtures and a sex covariate on π in their HMM for white shark movement, indicating that each of the three possible state-switching dynamics were exhibited differently for males and females; the random effects component of their model would be specified in fitHMM (or MIfitHMM) by simply setting mixtures = 3 and formulaPi = "sex. Note that because $\sum_{k=1}^{K} \pi_k = 1$, momentuHMM uses a multinomial logit link function for π when covariates are included in formulaPi. We demonstrate how to fit discrete-valued individual-level random effects on the initial distribution and state transition probabilities using the long-finned pilot whale example from Isojunno et al. (2017) in section 3.9.

2.5 Hierarchical hidden Markov models

Hierarchical hidden Markov models (HHMMs; see Leos-Barajas et al. 2017; Adam et al. 2019) can also be fitted in momentuHMM. HMMs with hierarchical structures allow for data streams and/or state transitions to occur at multiple regular time scales. For example, biotelemetry data are often collected at different time scales (e.g. 1-hr intervals for one data stream and 1-min intervals for another data stream) or state transitions can be governed by both larger- and finer-scale behavioral processes. HHMMs are inte-

grated into the workhorse functions of momentuHMM and are specified via hierarchically-structured arguments for the data stream probability distributions (hierDist), behavioral states (hierStates), state transition probabilities (hierFormula, hierBeta), and initial distributions (hierFormulaDelta, hierDelta) using the data.tree package (Glur 2018). We demonstrate how the harbor porpoise and garter snake examples from Leos-Barajas et al. (2017) and the Atlantic cod and horn examples from Adam et al. (2019) can be fitted using momentuHMM in section 3.10.

2.6 Random walk probability distributions

momentuHMM includes several normal random walk probability distributions that can be specified in the dist argument (see Tables 2 and 3), including univariate (e.g. for modeling depths), bivariate (e.g. for modeling 2-D positions), and trivariate (e.g. for modeling 3-D positions) normal random walks. These can be particularly useful for modeling movement on positions directly instead of steps and turns. A random walk model assumes position at time t is a function of the position at time t-1; in its simplest form without any covariates, we have $x_t \sim N(x_{t-1}, \sigma^2)$ for the univariate case. We demonstrate use of the bivariate normal random walk model for loggerhead turtle movements relative to ocean surface currents in section 3.3. We also demonstrate how to simulate movement subject to barriers or other constraints (e.g. land for marine animals) using a bivariate normal random walk in section 3.11.

2.7 Multiple imputation

When location data are temporally-irregular or subject to measurement error, then they are not suitable for standard maximum-likelihood HMM analyses based on the forward algorithm (Eq. 1). In this case, momentuHMM can be used to perform the 2-stage multiple imputation approach of McClintock (2017). The basic concept is to first employ a single-state (i.e., N=1) movement model that is relatively easy to fit but can accommodate location measurement error and temporally-irregular or missing observations (e.g. Johnson et al. 2008). The second stage involves repeatedly fitting the desired HMM to m temporally-regular realizations of the position process drawn from the model output of the first stage. Data streams or covariates that are dependent on location (e.g., step length, turning angle, habitat type, snow depth, sea surface

temperature) will of course vary among the m realizations of the position process, and the pooled inferences across the HMM analyses therefore reflect location uncertainty.

There are three primary functions (MIfitHMM, MIpool, and crawlWrap) for performing multiple imputation HMM analyses in momentuHMM, and all rely on parallel processing to speed up computations. crawlWrap is a wrapper function for fitting the continuous-time correlated random walk (CTCRW) model of Johnson et al. (2008) to one or more tracks (subject to location measurement error and/or temporal irregularity) and then predicting temporally-regular tracks of the user's choosing (e.g. 15 min, hourly, daily) based on the CTCRW model output. crawlWrap returns a crwData object that can be used to draw m realization of the position process within the MIfitHMM function. MIfitHMM is essentially a wrapper function for fitHMM that repeatedly fits the same user-specified HMM to m imputed data sets and stores the output from each of the m model fits. If a crwData object is provided, then MIfitHMM will first draw m imputations based on the crwData output and then fit the specified HMM to each imputed data set. If users wish to use a movement model other than the CTCRW to account for measurement error and temporal irregularity (e.g. Calabrese et al. 2016; Gurarie et al. 2017), or if other observation error processes (e.g. missing data) are to be accounted for in the imputation step, MIfitHMM can also be used for analysis of a list of m momentuHMMData objects that were imputed by the user. Based on the m model fits, the MIpool function calculates pooled estimates, standard errors, and confidence intervals for the working scale parameters, natural scale parameters (based on transformations of the pooled working parameters and mean or user-specified values for any covariates), state sequences, state probabilities, and activity budgets (i.e. the proportion of the T times step assigned to each state) using standard multiple imputation formulae (Rubin & Schenker 1986; McClintock 2017). MIpool can be called separately or within MIfitHMM (using the poolEstimates argument), and the function returns a miSum object containing the pooled output across all imputations. See sections 3.2, 3.3, 3.4, and 3.7 for example HMM analyses that use multiple imputation to account for location measurement error and temporally irregularity.

2.8 Model visualization and diagnostics

The generic plot functions for momentuHMM models (plot.momentuHMM and plot.miSum) plot the data stream histograms along with their corresponding estimated probability

distributions, the estimated natural parameters and state transition probabilities as a function of any covariates included in the model, and the tracks of all individuals (color-coded by the most likely state sequence). By default, the probability distributions are plotted based on the means of any covariate values, but user-specified covariate values for the plots can be provided using the covs argument. When the argument plotCI=TRUE, then confidence intervals for the natural parameters and state transition probabilities are also plotted. Confidence intervals are calculated from the working parameter estimates based on the delta method and finite-difference approximations of the first derivative for the transformation using the numDeriv::grad function (Gilbert & Varadhan 2016). For multiple imputation analyses (plot.miSum), all plots are based on the pooled parameter estimates and the means of any covariates (if not provided by the covs argument) across each imputation. Using the argument errorEllipse, plot.miSum will include estimated location error ellipses in the plots of individual tracks. The functions plotSat, plotSpatialCov, and plotStates (Table 1) provide further methods for visualizing model results.

Diagnostic tools include the calculation and plotting of pseudo-residuals (Zucchini et al. 2016) using the pseudoRes and plotPR functions, respectively. For discrete distributions (e.g. Bernoulli, Poisson), a continuity adjustment is used for calculating pseudo-residuals. Akaike's Information Criterion can be calculated for one or more models using the AIC.momentuHMM function.

2.9 Simulation

The functions simData (and simHierData) can be used to simulate multivariate HMM (or HHMM) data from scratch or based on the estimated parameters of existing momentuHMM or miSum models. The simData and simHierData arguments are very similar to those used for model specification in fitHMM (e.g., dist, hierDist, DM) and data preparation in prepData (e.g., spatialCovs, centers), but they include additional arguments, lambda and errorEllipse, for simulating location data subject to temporal irregularity and measurement error, respectively. The spatialCovs argument allows for rasters of spatio-temporal covariate values to be utilized in simulation models, while the centers argument allows activity centers to be incorporated. Thus simData and simHierData can be used to simulate more ecologically-realistic tracks (potentially subject to observation error) that can be useful for study design, power analyses, and assessing model

performance. Goodness-of-fit can also be investigated by drawing simulated data sets from a fitted model and comparing them to observed properties of the data (Morales et al. 2004). While simData and simHierData can be used for simulating tracks from fitted models, we note that it assumes the location data are Cartesian coordinates; the simData and simHierData functions are therefore not appropriate for simulating tracks from models that were fitted to unprojected (latitude and longitude) data.

3 Examples

We will now demonstrate some of the capabilities of momentuHMM using real telemetry data. These examples are intended for demonstration purposes only, and we do not claim these example analyses represent improvements relative to previous or alternative analyses for these data sets. While only some of the key workflow elements are included here, complete R code and further details for these analyses are available in the "vignettes" source directory.

3.1 African elephant

As our first example, we use an African elephant (*Loxodonta africana*) bull track described in Wall *et al.* (2014) and publicly available from the movebank.org data repository.

We can load the data from the URL (this requires an Internet connection):

The data set contains two tracks; for this analysis, we only consider the first one. In addition to hourly locations, the tag also collected external temperature data. We subset the data frame to keep only the relevant rows and columns:

```
# select and rename relevant columns
rawData <- rawData[,c(11,3,4,5,6)]
colnames(rawData) <- c("ID","time","lat","temp")</pre>
```

```
# only keep first track
rawData <- subset(rawData, ID==unique(ID)[1])</pre>
```

The data now has the following columns:

```
head(rawData)
##
              ID
                                     time
                                                lon
                                                         lat temp
## 1 Salif Keita 2008-03-22 17:00:00.000 -2.160167 15.65350
## 2 Salif Keita 2008-03-22 18:00:00.000 -2.160075 15.65452
                                                               35
## 3 Salif Keita 2008-03-22 19:00:00.000 -2.159902 15.65451
                                                               32
## 4 Salif Keita 2008-03-22 20:00:00.000 -2.159435 15.65489
                                                               30
## 5 Salif Keita 2008-03-22 21:00:00.000 -2.158113 15.65512
                                                               29
## 6 Salif Keita 2008-03-22 22:00:00.000 -2.157848 15.65461
                                                               28
```

Location measurement error is negligible for these terrestrial GPS data, although about 1% of the hourly observations collected between 22 March 2008 and 30 September 2010 are missing. Instead of simply ignoring these missing data, we can employ crawlWrap to predict the missing locations based on the CTCRW model of Johnson et al. (2008) prior to conducting our HMM analysis.

To use crawlWrap, we convert times from factors to POSIX, and project the observed locations to UTM coordinates:

Then, we call crawlWrap to fit a CTCRW model and predict hourly locations:

Here the desired time step is specified by the timeStep argument, and theta and fixPar arguments are the same as for crawl::crwMLE (Johnson 2017). For the choice of initial parameters in crawlWrap, we refer the reader to the documentation of the package crawl, in particular crawl::crwMLE and crawl::crwPredict. We now have a complete set of temporally-regular location data.

Autocorrelation function (ACF) estimates suggest there are 24-hour cycles in the step length data, and this presents an opportunity to demonstrate the use of the cosinor function for incorporating cyclical behavior in model parameters using momentuHMM. We create a momentuHMMData object, and the 24-hour cosinor model covariate:

```
# create momentuHMMData object from crwData object
elephantData <- prepData(data=crwOut, covNames="temp")

# add cosinor covariate based on hour of day
elephantData$hour <- as.integer(strftime(elephantData$time, format = "%H", tz="GMT"))</pre>
```

As seen here, the function prepData can also be used for pre-processing the best predicted track data from crawlWrap output. The 24-hour cosinor covariate ("hour") is simply a set of integers (0, 1, ..., 23) indicating the hour of day for each observation. The ACF plot of the step lengths, shown in Figure 1, was obtained with:

```
acf(elephantData$step[!is.na(elephantData$step)],lag.max=300)
```

Our aim is to fit a 2-state HMM to the elephant track that includes temperature effects on the turning angle concentration parameters and cycling temperature effects (with a 24-hour periodicity) on the step length and state transition probability parameters. Complex models such as this can require many parameters, and it can be challenging to choose good starting parameter values for the optimization. Here, we take an incremental approach, starting from a simpler model with no covariates. In momentuhm, the function getParO extracts initial parameters from a fitted (nested) HMM, given arguments for the more complex model.

For the covariate-free 2-state model, six initial parameters need to be chosen: for each state, the mean and standard deviation of the gamma distribution of step lengths, and the concentration of the wrapped Cauchy distribution of turning angles. Looking at the histograms of the step lengths and the turning angles (e.g. output by plot(elephantData)) is often useful to choose good starting parameter values.

```
# label states
stateNames <- c("encamped","exploratory")
# distributions for observation processes
dist = list(step = "gamma", angle = "wrpcauchy")
# initial parameters
ParO_m1 <- list(step=c(100,500,100,200),angle=c(0.3,0.7))
# fit model
m1 <- fitHMM(data = elephantData, nbStates = 2, dist = dist, ParO = ParO_m1, estAngleMean = list(angle=FALSE), stateNames = stateNames)</pre>
```

To ensure convergence, we could also use the argument retryFits to specify the number of attempts to minimize the negative log-likelihood based on random perturbations of the parameter estimates at the current minimum.

We can build on complexity, by including the temperature and time of day as covariates in the state transition probabilities. We use the function getPar0 to extract the new starting parameter values.

The special function cosinor(hour, period = 24) internally creates the cosinor model covariates, $\cos(2\pi \times hour/period)$ and $\sin(2\pi \times hour/period)$, and includes both

terms (plus interactions with "temp") in the fitted model.

Finally, we can fit the more complex model, including the effect of temperature and time of day on the parameters of the state-dependent distributions of steps and angles.

The above model m3 identifed a state of slow undirected movement ("encamped"), and a state of faster and more directed movement ("exploratory") (Figure 1). For a fitted model, the function viterbi computes the most likely state sequence:

```
# decode most likely state sequence
states <- viterbi(m3)
# derive percentage of time spent in each state
table(states)/nrow(elephantData)</pre>
```

Here, about 74% of the steps were attributed to the "encamped" state, and 26% were attributed to the "exploratory" state.

We can use AIC(m1,m2,m3) to compare the three fitted models in terms of AIC; here, m3 is overwhelmingly supported by the AIC when compared to alternative models with fewer covariates.

The model can be visualized with the generic function plot, which was used for the plots shown in Figure 2, and the decoded track in Figure 1.

```
plot(m3, plotCI = TRUE, covs = data.frame(hour=12))
```

Interestingly, this model suggests step lengths and directional persistence for the "encamped" state decreased as temperature increased, step lengths for both states

tended to decrease in the late evening and early morning, and transition probabilities from the "encamped" to "exploratory" state decreased as temperature increased (Figure 2).

Model fit can be assessed using the pseudo-residuals, with the functions pseudoRes and plotPR. The residual ACF plot shown in Figure 1 was produced by:

```
# compute pseudo-residuals for the steps and the angles
pr <- pseudoRes(m3)

# plot the ACF of step pseudo-residuals
acf(pr$stepRes[!is.na(pr$stepRes)],lag.max = 300)</pre>
```

Autocorrelation function plots of the pseudo-residuals indicate this model explained much of the periodicity in step length, although there does still appear to be some room for improvement.

3.2 Northern fur seal

In our second example, we use the northern fur seal (Callorhinus ursinus) example from McClintock et al. (2014) to demonstrate the use of additional data streams for distinguishing behaviors with similar horizontal trajectories in a multivariate HMM. The data consist of 241 temporally-irregular Fastloc GPS locations obtained during a foraging trip of a nursing female near the Pribilof Islands of Alaska, USA, from 10-17 October 2007. The tag included time-depth recording capabilities, and the dive activity data were summarized as the number of foraging dives over T=228 temporally-regular 1 hr time steps. To fit the N=3 state (1="resting", 2="foraging", 3="transit") of McClintock et al. (2014) using momentuHMM, we first used crawlWrap to predict temporally-regular locations at 1 hr time steps assuming a bivariate normal measurement error model and merged the results with the foraging dive data using the crawlMerge function. Then multiple imputation was used to account for location measurement error by repeatedly fitting the HMM to nSims realizations of the position process using MIfitHMM:

```
nbStates <- 3
stateNames <- c("resting", "foraging", "transit")
dist <- list(step = "gamma", angle = "wrpcauchy", dive = "pois")
Par0 <- getParDM(nbStates = nbStates, dist = dist,</pre>
```



Figure 1. Plot of the elephant track produced using the 'plotSat' function (top-left panel), autocorrelation function (ACF) plot of the corresponding step length data (top-right panel), plot of the Viterbi-decoded state sequence for the 2-state ("encamped" and "exploratory") model generated using the generic 'plot' function (bottom-left panel), and the step length pseudo-residual ACF plot for this model using the 'plotPR' function (bottom-right panel).

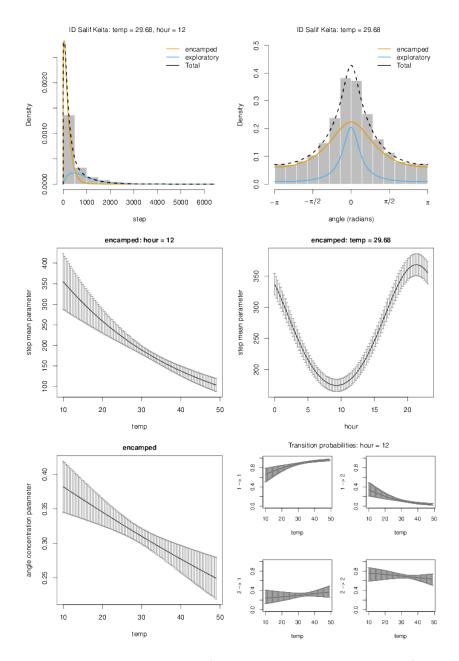


Figure 2. Selected plots for the 2-state ("encamped" and "exploratory") African elephant example generated using the generic 'plot' function. Top panels present histograms of the step length (top-left) and turning angle (top-right) data along with the estimated state-dependent probability distributions based on the mean temperature (temp = 29.7 degrees celsius) at 12:00 GMT (hour = 12). Middle panels present estimates (and 95% confidence intervals) for the step length mean parameter of the "encamped" state as a function of temperature and hour of day. Bottom-left panel presents estimates for the turning angle concentration parameter of the "encamped" state as a function of temperature. Bottom-right panel presents estimated state transition probabilities (1 = "encamped", 2 = "exploratory") as a function of temperature at 12:00 GMT.

Here we specified a gamma distribution for step length ('step'), wrapped Cauchy distribution for turning angle ('angle'), and Poisson distribution for the number of foraging dives ('dive'). The function getParDM was used to organize the starting values for the data stream working parameters (ParO) in the correct format based on DM, workBounds, and estimates of the natural parameters (Par) from McClintock et al. (2014). The DM and workBounds arguments were specified to avoid label switching among the nSims imputed data model fits and enforce similar state-dependent probability distribution constraints as McClintock et al. (2014); for example, constraining the Poisson rate parameters such that the "foraging" state tends to have higher numbers of foraging dives than the "transit" state ($\lambda_2 > \lambda_3$; see Eq. 11 in section 3.7 for more details on parameter constraints using DM in conjunction with the userBounds and workBounds arguments). To prohibit foraging dives for the "resting" state, we used the fixPar argument to effectively fix the Poisson rate parameter to zero on the natural scale (i.e. $\lambda_1 \approx 0$). To help deal with the problem of convergence to local maxima, the retryFits argument allows users to specify the number of times to attempt to re-fit each model using random perturbations of the parameter estimates as the starting values for optimization.

The results are very similar to those of the discrete-time model of McClintock *et al.* (2014), with periods of foraging often followed by resting (Figure 3). The "activity budgets" (i.e. the proportion of time steps allocated to each state) calculated by MIpool based on the estimated state sequences for each imputation were 0.31 (95% CI: 0.25-0.37) for "resting", 0.28 (95% CI: 0.23-0.35) for "foraging", and 0.41 (95% CI: 0.33-0.5) for "transit".

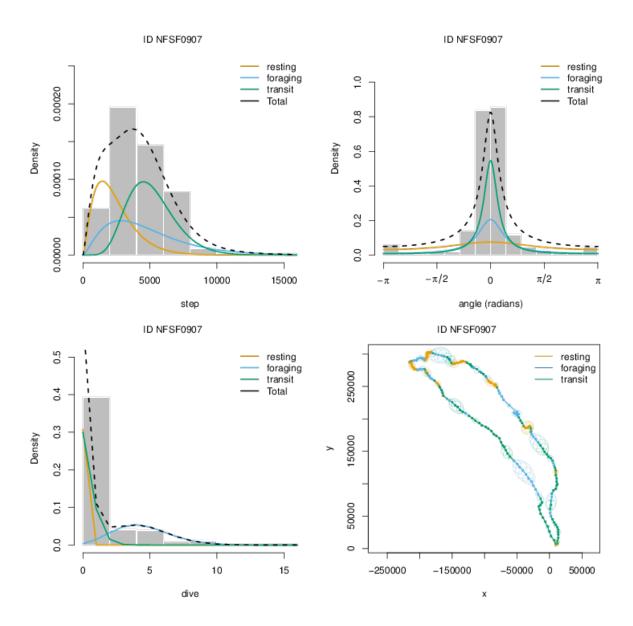


Figure 3. Plots of the northern fur seal example results generated using the generic 'plot' function. The estimated probability distributions for step length (top-left panel), turning angle (top-right panel), and number of foraging dives (bottom-left panel) for the 3-state ("resting", "foraging", and "transit") model are plotted along with histograms of these data streams. The temporally-regular predicted locations (and 95% ellipsoidal confidence bands) and estimated states are plotted in the bottom-right panel. All estimates are pooled across multiple imputations of the position process and thus reflect uncertainty attributable to location measurement error and temporally-irregular observations.

3.3 Loggerhead turtle

For our third example, we demonstrate how to model movement direction and step length as a function of angular covariates using hitherto unpublished loggerhead turtle (Caretta caretta) data for a captive-raised juvenile released in 2012 on the coast of North Carolina, USA. The data consist of 165 temporally-irregular Argos locations subject to measurement error and rasters of daily ocean surface currents collected between 20 November and 19 December 2012. Assuming a gamma distribution for step length (l_t) and a wrapped Cauchy distribution for turning angle (ϕ_t), we model the mean step length parameter (μ_t^l) as a function of ocean surface current speed (w_t) and direction (r_t) relative to the bearing of movement (b_t):

$$\mu_t^l = \exp(\beta_0^l + \beta_1^l w_t \cos(b_t - r_t)), \tag{6}$$

and the turning angle mean parameter (μ_t^{ϕ}) as a trade-off between short-term directional persistence and bias in the direction of ocean surface currents using the circular-circular regression link function:

$$\mu_t^{\phi} = \operatorname{atan2}(\sin(d_t)\beta^{\phi}, 1 + \cos(d_t)\beta^{\phi}), \tag{7}$$

where $d_t = \text{atan2}(\sin(r_t - b_{t-1}), \cos(r_t - b_{t-1})).$

We wish to fit a 2-state HMM to the turtle data, with a "foraging" state unaffected by currents and a "transit" state potentially influenced by ocean surface currents as in Eqs. 6 and 7. We used crawlWrap to predict T=350 temporally-regular locations at 2 hr time steps assuming a bivariate normal measurement error model that accounts for the Argos location quality class (i.e. 3,2,1,0,A,B) of each observation. We then again used multiple imputation to account for location uncertainty by repeatedly fitting the HMM to nSims realizations of the position process using MIfitHMM. We first draw nSims realizations of the position process and extract the corresponding spatial covariates from the raster bricks for ocean surface current speed ("speedBrick") and direction ("dirBrick") using MIfitHMM with fit=FALSE:

When the fit argument is FALSE, MIfitHMM returns a list of length nSims composed of momentuHMMData objects (miData). For convenience and ease of interpretation, we manually added an additional covariate ($angle_osc = cos(b_t - r_t)$) to each of the imputed data sets and fitted the 2-state HMM using Eqs. 6 and 7 for state 2 ("transit"):

Note that the state2 special function in DM indicates the covariate formulas are specific to state 2 ("transit") and the circularAngleMean argument indicates that circular-circular regression link function is to be used on the mean turning angle parameter as in Eq. 7.

For the "transit" state, pooled parameter estimates indicated step lengths increased with ocean surface current speed and as the bearing of movement aligned with ocean surface current direction ($\beta_1^l = 0.4,95\%$ CI: 0.09 - 0.7; Figure 4). The estimated wrapped Cauchy distribution for turning angle had mean angles (μ_t^{ϕ}) biased towards the direction of ocean surface currents for each time step ($\beta^{\phi} = 0.26,95\%$ CI: 0.04 - 0.48), with concentration parameter $\rho_2^{\phi} = 0.86$ (95% CI: 0.82 - 0.9) indicating turning angles were concentrated at μ_t^{ϕ} . Thus movement during the "transit" state appears to strongly follow ocean surface currents (mean $angle_osc = 0.88$, SD = 0.22), while movement during the "foraging" state exhibited shorter step lengths ($\mu_1^l = 3001$ m, 95% CI: 2439 - 3563) perpendicular to ocean surface currents (mean $angle_osc = 0.07$, SD = 0.27), with some directional persistence ($\rho_1^{\phi} = 0.49,95\%$ CI: 0.37 - 0.61). The turtle spent 0.56 (95% CI: 0.46 - 0.66) of the 2 hr time steps in the "foraging" state and 0.44 (95% CI: 0.34 - 0.54) of time steps in the "transit" state as it travelled northeast along a predominant current until it (presumably) found an attractive foraging patch (Figure 4).

It may often make more sense to weight angular covariates (such as ocean surface current direction) by their relative strength or importance. For example, weak

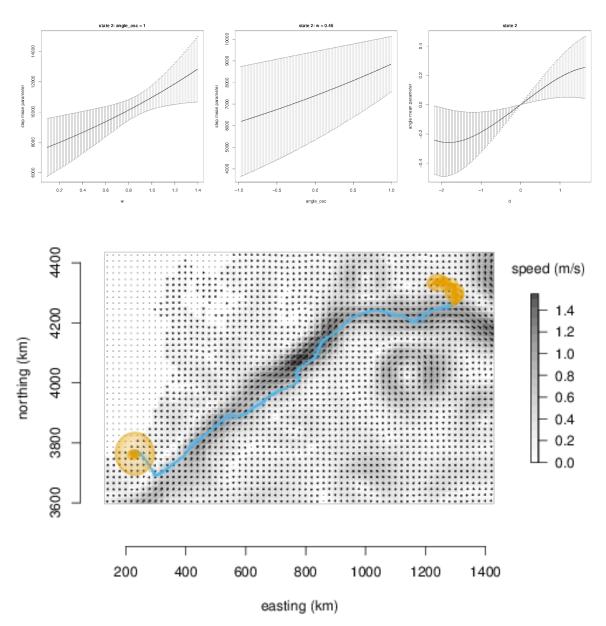


Figure 4. Selected results from the loggerhead turtle example. Top panels include estimates and 95% confidence intervals for the mean step length parameter as a function of ocean surface current speed (w) when ocean surface current direction (r_t) is the same as the bearing (b_t) of movement (i.e. $angle_osc = cos(b_t - r_t) = 1$; top-left panel), mean step length parameter as a function of $angle_osc$ at the mean ocean surface current speed (w = 0.46 m/s; top-middle panel), and mean turning angle parameter as a function of $d_t = atan2(\sin(r_t - b_{t-1}), \cos(r_t - b_{t-1}))$ (top-right panel). Bottom panel plots the pooled track, 95% error ellipse confidence bands, and state (orange = "foraging", blue = "transit") estimates based on multiple imputations of the position process relative to ocean surface current speed (m/s) and direction on 2 December 2012.

ocean surface currents may be less likely to influence movement direction than strong ocean surface currents. This could easily be included in our turtle model using the angleFormula(cov, strength, by) special function in DM, where cov is an angle covariate (e.g. wind direction), strength is an optional positive real covariate (e.g. wind speed), and by is an optional factor variable for individual- or group-level effects (e.g. ID, sex):

which would yield the following model for the "transit" state mean angle parameter:

$$\mu_t^{\phi} = \operatorname{atan2}(w_t \sin(d_t)\beta^{\phi}, 1 + w_t \cos(d_t)\beta^{\phi}). \tag{8}$$

Still another option would be to use the von Mises consensus model, where the concentration parameter would now depend on the level of agreement between short-term directional persistence (i.e. going forward) and ocean surface currents:

which would yield the following model for the "transit" state concentration parameter:

$$\rho_t^{\phi} = \kappa \sqrt{[w_t \sin(d_t)\beta^{\phi}]^2 + [1 + w_t \cos(d_t)\beta^{\phi}]^2}.$$
 (9)

If there were multiple turtles in this dataset, then individual-level effects could be included on μ^{ϕ} by simply specifying angleFormula(d, strength = w, by = ID) or angleFormula(d, by = ID) (with no strength effects).

One disadvantage of modeling steps and turns as above is that the fitted model cannot be properly simulated using simData. This is because simData is unable to calculate new realizations of the constructed covariate ($angle_osc = cos(b_t - r_t)$). However, we can implement a very similar model on the positions directly using a bivariate normal random walk. While arguably more intuitive, modeling the positions directly also has the added benefit that the fitted model can be properly simulated using simData. Similar to the continuous-time potential function approach of Brillinger et al. (2012) and

Hooten et al. (2019), we can model the current position (x_t, y_t) as a bivariate normal random walk where the position at time t is a function of the position at time t-1 and the ocean surface current velocity vectors u_{t-1} (easting) and v_{t-1} (northing):

$$(x_t, y_t) \sim N\left((\mu_{x,t}, \mu_{y,t}), \Sigma\right)$$

where

$$\mu_{x,t} = x_{t-1} + (x_{t-1} - x_{t-2})\beta_1 + u_{t-1}\beta_2,$$

$$\mu_{y,t} = y_{t-1} + (y_{t-1} - y_{t-2})\beta_1 + v_{t-1}\beta_2,$$
(10)

and

$$\Sigma = \begin{bmatrix} \sigma_x^2 & 0\\ 0 & \sigma_y^2 \end{bmatrix}$$

This is analogous to state 2 in our model for steps and turns, where the terms $(x_{t-1} - x_{t-2})$ and $(y_{t-1} - y_{t-2})$ account for persistence in velocity. For state 1 we would simply remove the terms related to ocean surface current velocities $(u_t \text{ and } v_t)$.

Multivariate normal distributions require some additional book-keeping when preparing the data; the altCoordNames argument in prepData and MIfitHMM and the mvnCoords argument in fitHMM and MIfitHMM are designed to help properly format and identify multivariate coordinate data streams. For example, if a bivariate normal data stream name is "loc" (e.g. dist=list(loc="mvnorm2")), then the data must include columns "loc.x" and "loc.y" for the x- and y- coordinates, respectively. When using a multivariate normal random walk distribution, the previous position can be referenced in DM formulas or pseudo-design matrices. For example, for a bivariate normal random walk data stream named "mu" (e.g. dist=list(mu="rw_mvnorm2")), the previous position can be refered in DM as "mu.x_tm1" and "mu.y_tm1". This allows for persistence in velocity to be included as in Eq. 10 via the special formula function crw(x_tm1,lag), where argument x_tm1 is the previous position (e.g. "mu.x_tm1" or "mu.y_tm1") and argument lag specifies the time lag for the persistence (lag=1 in this example, but higher order lags could also be included). A complete demonstration of how to implement this bivariate normal random walk model can be found in the "turtleExample_rw_mvnorm2.R" script in the momentuHMM "vignettes" source directory

(or at https://github.com/bmcclintock/momentuHMM).

3.4 Grey seal

For our next example, we perform a similar analysis of a grey seal (Halichoerus grypus) track that was originally conducted by McClintock et al. (2012) using Bayesian methods and (computationally-intensive) Markov chain Monte Carlo. The data consist of 1045 temporally-irregular Fastloc GPS locations collected in the North Sea between 9 April and 11 August 2008. Because the seal repeatedly visited the same haul-out and foraging locations, it provides a nice example for demonstrating how to implement biased movements relative to activity centers using momentuHMM. McClintock et al. (2012) fitted a 5-state model to these data that included three center of attraction states, with movement biased towards two haul-out sites ("Abertay" and "Farne Islands") and a foraging area ("Dogger Bank"), and two "exploratory" states ("low speed", "high speed") that were unassociated with an activity center. After using crawlWrap to predict T=1515temporally-regular locations at 2 hr time steps including a bivariate normal measurement error model, we can perform a very similar analysis to McClintock et al. (2012) in momentume by using the centers argument and state-specific functions for the probability distribution parameters. A cluster analysis on the observed locations using the R package dtwclust (Sarda-Espinosa 2017) identified three centroids with coordinates that were nearly identical to the three activity centers ("Abertay", "Farne Islands", and "Dogger Bank") identified by McClintock et al. (2012). We use these coordinates to derive covariates relative to the activity centers when drawing nSims realizations of the position process:

Specifying the **centers** argument results in the calculation of two covariates for each activity center: the distance (with '.dist' suffix) and angle (with '.angle' suffix) from each location at time t. These covariates can then be used to model parameters as a function of the distance and angle to activity centers for each time step:

Similar to McClintock et al. (2012), we assume a Weibull distribution for step length where both the shape and scale parameter depend on the distance from the location at time t to each activity center. For the activity centers on land ("Abertay" and "Farne"), we allow the (state-dependent) step length parameters to change when the seal is beyond 2500m of the haulout. For the "Dogger" activity center, we allow the parameters to change when the seal is beyond 15000m of this (presumably) foraging area. We thus allow the movement behavior to change within these activity center states upon entering or leaving the vicinity of these sites. We assume a wrapped Cauchy distribution for turning angle with (state-dependent) mean angle derived from the direction to each activity center at time t, and the concentration parameter is modeled similarly to the step length parameters. For the two "exploratory" states, we assumed they are simple random walks unaffected by proximity to activity centers. To complete our model specification, we use the knownStates argument to assign the seal to the corresponding activity center state whenever it was within the 2500m (haul-out area) or 15000m (foraging area) thresholds for each imputed data set:

As with the step length and turning angle concentration parameters, the state transition probabilities are also allowed to change as a function of distance to activity centers (as specified by the formula argument). The starting values (Par0 and beta0) for each

imputation were extracted from a single HMM fitted to the best predicted locations from crawlWrap, and circularAngleMean=list(angle=0) was used to remove short-term directional persistence (and thus formulate the model as a mixture of biased and simple random walks).

Estimated activity budgets for the 5 states of this multiple imputation HMM were 0.28~(0.27-0.3) for the "Abertay" haul-out state, 0.12~(0.11-0.13) for the "Farne Islands" haul-out state, 0.37~(0.35-0.38) for the "Dogger Bank" foraging state, 0.11~(0.05-0.2) for a low-speed "exploratory" state, and 0.12~(0.07-0.21) for a high-speed "exploratory" state. All three activity center states exhibited shorter step lengths and less biased movements when within the vicinity of these targets (Figure 5). Results from this analysis were thus very similar to those of McClintock *et al.* (2012), but this implementation required far less computation time and no custom model-fitting algorithms.

The simData function can be used to simulate tracks from a fitted model:

A simulated track is presented along with the fitted track in Figure 6. While potentially useful for study design, power analysis, and prediction, the simData function can also be helpful in assessing goodness of fit by repeatedly drawing simulated data sets from a fitted model and comparing them to observed properties of the data (e.g. Morales *et al.* 2004).

3.5 Southern elephant seals

Here, we analyse the southern elephant seal (*Mirounga leonina*) data from Michelot et al. (2017) using momentuHMM. The data set consists of 15 tracks, each encompassing (at most) one foraging trip, starting from Kerguelen Island. We want to fit the model described by Michelot et al. (2017), with the four following states:

- 1. outbound trip from the colony to the ice;
- 2. searching;
- 3. foraging;

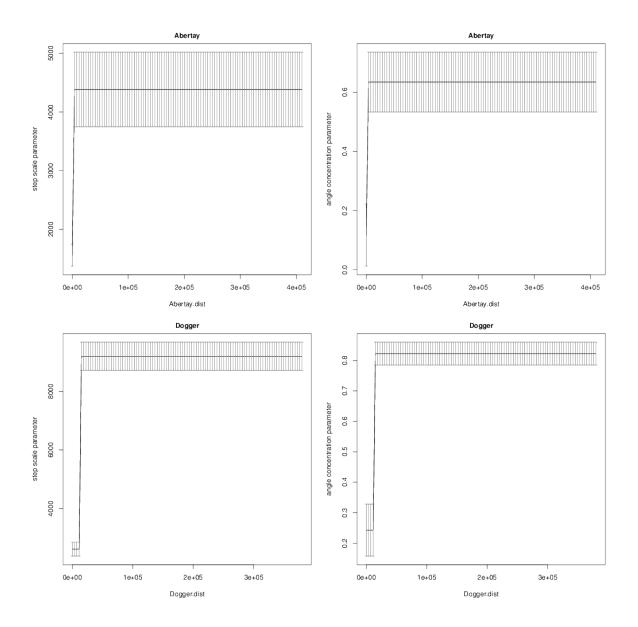
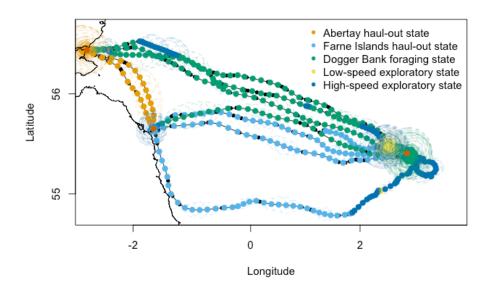


Figure 5. Selected results from the grey seal example. Panels include estimates and 95% confidence intervals for the "Abertay" haul-out state step length scale parameter as a function of distance in meters ('Abertay.dist'; top-left panel), "Abertay" haul-out state turning angle concentration parameter as a function of distance (top-right panel), "Dogger Bank" foraging state step length scale parameter as a function of distance ('Dogger.dist'; bottom-left panel), and the "Dogger Bank" foraging state turning angle concentration parameter as a function of distance (bottom-right panel).



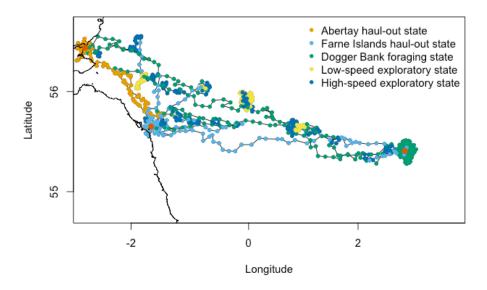


Figure 6. Fitted and simulated tracks from the grey seal example. This seal tended to move in a clockwise fashion between two haul-out locations ("Abertay" and "Farne Islands") and a foraging area ("Dogger Bank") in the North Sea. Top panel plots the pooled track, 95% error ellipse confidence bands, and state estimates based on the 5-state HMM fitted to multiple imputations of the position process. Red points indicate the locations of the three activity centers. Black points indicate the (temporally-irregular) observed locations. Bottom panel presents the locations and states for a track simulated from the fitted model using the 'simData' function.

4. inbound trip from the ice to the colony.

The data set has three columns: "ID" (track ID), "x" (longitude), and "y" (latitude):

From the locations, we use prepData to derive the step lengths and turning angles, as well as the distance and bearing (relative to previous movement direction as in Eq. 3) to the Kerguelen Island colony (with coordinates 70° longitude and -49° latitude):

```
center <- matrix(c(70,-49),nrow=1,dimnames=list("colony"))
data <- prepData(data=tracks, type="LL", centers=center)</pre>
```

Note that distances are in kilometers and angles are based on initial bearings (using geosphere::bearing; Hijmans 2016a) when calculated from longitude and latitude coordinates.

3.5.1 Model 1: no covariates

We start by fitting a covariate-free 4-state correlated random walk model, which we will use to extract starting parameter values for more complex models. We use the argument fixPar to fix some transition probabilities to zero, following Michelot et al. (2017). We set to NA the columns of unconstrained transition probabilities, and we fix the intercept of the other columns to a large negative number (here -100) to set the corresponding transition probabilities to be virtually zero (i.e. impossible transition). As in Michelot et al. (2017), we set transition probabilities from outbound to forage, outbound to inbound, search to outbound, forage to outbound, forage to be effectively zero.

3.5.2 Model 2

This model mimics the formulation of Michelot *et al.* (2017). We model the effect of the distance to colony on the transition probability from outbound to search, and of the time since departure on the transition probability from search to inbound.

```
# time spent since left colony
time <- NULL
for(id in unique(data$ID)) {
    nbSubObs <- length(which(data$ID==id))

    # approximately in months for interval = 9.6h
    time <- c(time, (1:nbSubObs)/75)
}
data$time <- time

# compute time since departure and include in formula below
formula <- ~ colony.dist + time</pre>
```

As before, we constrain the transition probability matrix to prevent some of the transitions (e.g. from forage to inbound, etc.). We define a 3×12 matrix for the beta parameters, in which each column corresponds to a transition $(1 \to 2, 1 \to 3, 1 \to 4, 2 \to 1, \ldots)$, and each row corresponds to a covariate (intercept, distance to center, time since departure). We set to NA the columns of unconstrained transition probabilities, and we

again fix the intercept of the other columns to a large negative number (here -100) to set the corresponding transition probabilities to be virtually zero (i.e. impossible transition).

Biased random walks are used to model the movement in states 1 and 4, with repulsion away from the colony in the outbound trip, and attraction towards the colony in the inbound trip. For that purpose, we include 'colony.angle' as a covariate on the angle mean of the von Mises distributions for turning angles in states 1 and 4.

```
angleFormula <- ~ state1(colony.angle) + state4(colony.angle)</pre>
```

To specify the direction of the bias (away from or towards the colony), we fix the parameters linking the mean turning angle to the direction of the colony. Because we will remove the correlated random walk component of Eq. 2 for states 1 and 4 (by setting circularAngleMean=list(angle=0); see section 2.3), we fix the coefficient to -1 for state 1 (so that the mean direction is away from the colony), and we fix the coefficient to +1 for state 4 (so that the mean direction is towards the colony). Note that with only a single angular covariate, the magnitude of these fixed coefficients is not important; only the sign is important (i.e. positive for attraction, negative for repulsion). The four other parameters correspond to the angle concentrations and should be estimated (NAs in fixPar).

```
fixPar <- list(angle=c(-1,1,NA,NA,NA,NA),beta=fixbeta)</pre>
```

Because no covariates are specified for the mean angle of state 2 (searching) and state 3 (foraging), these states are reduced to correlated random walks with a mean turning angle of zero (i.e. atan2(0,0) = 0; see Eq. 2).

We can now fit the second model with starting parameter values extracted from the simpler model using getPar0. In fitHMM, we use the arguments estAngleMean and circularAngleMean to indicate that the angle mean is to be estimated using circular-circular regression (with short-term directional persistence removed for states 1 and 4).

Instead of relying entirely on fixPar for parameter constraints, an equivalent model for the transition probabilities could be specified using the special function betaCol in formula:

Here betaCol1(colony.dist) specifies an effect of distance to colony only on the transition from state 1 to state 2 (which corresponds to the first column of the beta matrix) and betaCol6(time) specifies an effect of time since departure only on the transition from state 2 to state 4 (which corresponds to the sixth column of the beta matrix). When the special function betaCol is used, then fitHMM automatically fixes the appropriate elements in the second ('colony.dist') and third ('time') rows of the beta matrix to zero (without the user needing to do so manually using fixPar). However, note that the first row (corresponding to the intercept terms) must still be manually fixed to achieve the desired constraints on the transition probability matrix.

3.5.3 Model 3

In addition to the covariates included in model 2, we add the effect of distance to colony on the step length and turning angle concentration parameters for states 1 and 4. We specify the following formulas:

```
distFormula <- ~ state1(colony.dist) + state4(colony.dist)
stepDM <- list(mean=distFormula, sd=distFormula)
angleDM <- list(mean=angleFormula, concentration=distFormula)</pre>
```

The initial parameters are extracted from model 2, again using the function getPar0. Instead of fixing the mean direction of movement like in model 2, we estimate it here as a trade-off between short-term directional persistence and bias toward (or away) from the colony (i.e. a biased correlated random walk as in Eq. 2).

```
# remove fixed angle parameters
fixPar <- list(beta=fixbeta)</pre>
# get starting parameters from m2
Par0 <- getPar0(model=m2, nbStates=4,
                DM = list(step=stepDM, angle=angleDM),
                estAngleMean=list(angle=TRUE),
                circularAngleMean=list(angle=TRUE),
                formula=formula)
# the bias is estimated rather than fixed
Par0$Par$angle[c("mean_1:(colony.angle)", "mean_4:(colony.angle)")] <- 0</pre>
m3 <- fitHMM(data=data, nbStates=4, dist=list(step="gamma",angle="vm"),
             Par0=list(step=Par0$Par$step, angle=Par0$Par$angle),
             beta0=Par0$beta, fixPar=fixPar, formula=formula,
             DM = list(step=stepDM, angle=angleDM),
             estAngleMean=list(angle=TRUE),
             circularAngleMean=list(angle=TRUE),
             stateNames = stateNames)
```

The three fitted model can be compared with AIC(m1,m2,m3), which overwhelmingly supports model 3. The most likely state sequence is obtained with viterbi(m3). Figure 7 shows a map of the state-decoded track. The estimated circular-circular regression coefficients for the angle means of state 1 (outbound) and state 4 (inbound) were -0.66 (95% CI: -0.82 - -0.5) and 0.4 (95% CI: 0.32 - 0.49), respectively, thus indicating biased correlated random walks with repulsion away from the colony during outbound movements and attraction towards the colony during inbound movements.

The estimated regression coefficients for the step length mean and turning angle concentration parameters for states 1 and 4 suggest that step lengths decreased and turning angles became more concentrated at the mean angle as distance to colony increased (Figure 8)

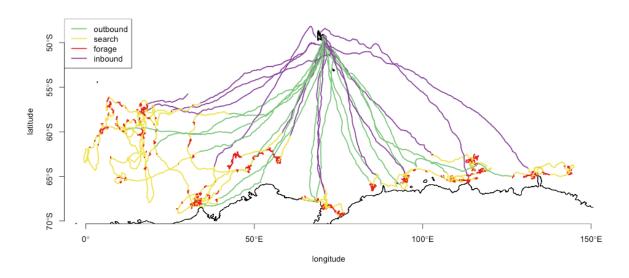


Figure 7. The 15 elephant seal tracks, colored by the most likely state sequence.

3.6 Group dynamic animal movement

Here we demonstrate how momentuHMM can be used to simulate and fit the group dynamic animal movement model of Langrock et al. (2014). In group dynamic models, groups (e.g., herds, packs, schools) are allowed to influence the movement of social individuals. One way to accomplish this is to model individual movements as being attracted to a group "centroid". Depending on the system, the centroid could simply be the location of the group center (e.g., the mathematical centroid of the group) or group leader (e.g., alpha wolf) at times t = 1, ..., T. In this sense, the centroid can be considered a dynamic activity center that changes position over time, and these models are not necessarily limited to groups. For example, the centroid could instead refer to predators, competitors, or human activity (in which case the centroid might be repulsive rather than attractive!).

Dynamic activity centers can be simulated in simData using the centroids argument. Following simulation scenario A of Langrock et al. (2014), we first simulate a

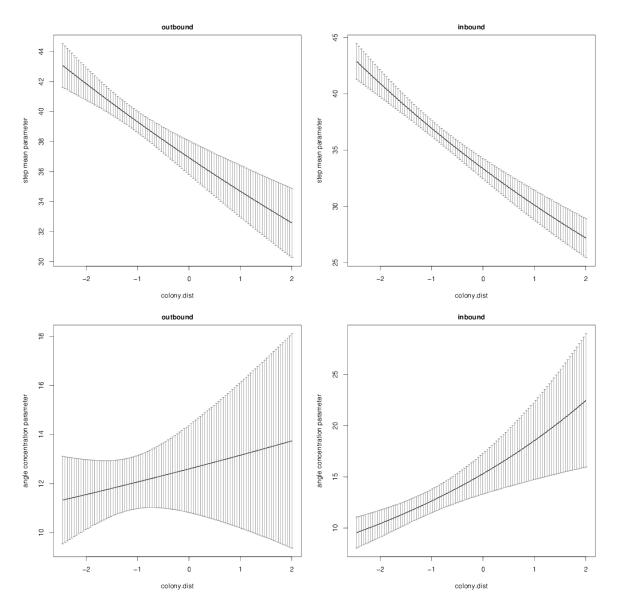


Figure 8. Selected results from the elephant seal example. Panels include estimates and 95% confidence intervals for the "outbound" mean step length parameter (top-left panel), "inbound" mean step length parameter (top-right panel), "outbound" turning angle concentration parameter (bottom-left panel), and "inbound" turning angle concentration parameter (bottom-right panel) as a function of distance to colony ('colony.dist'). Distance to colony has been standardized based on a mean of 2539 km (SD = 1021.3).

group centroid as a single-state (i.e. N=1) biased correlated random walk relative to the origin:

Now we can use the simulated centroid track (Fig. 9) as a dynamic activity center and simulate the movement of a group of 20 individuals as a 2-state mixture of a biased random walk (relative to the centroid) and a correlated random walk (independent of the centroid):

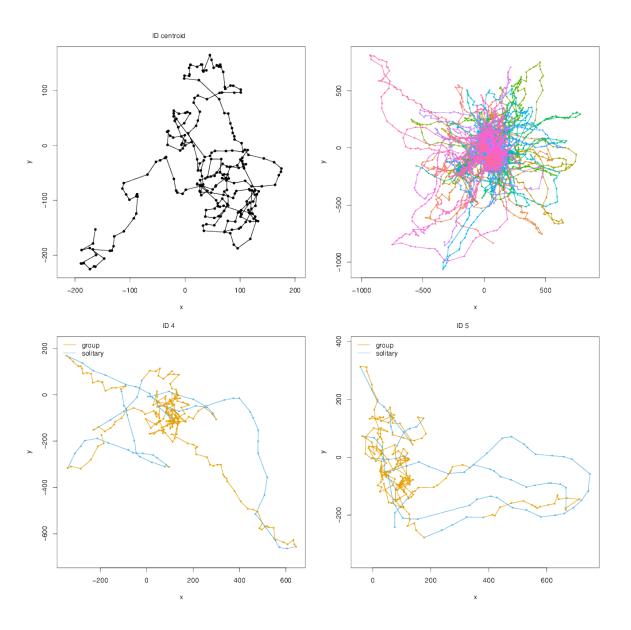


Figure 9. Selected results from the group dynamic animal movement example. Panels include the simulated centroid path (top-left panel), the simulated paths of 20 individuals where state 1 ("group") includes biased movements towards the centroid and state 2 ("solitary") is a correlated random walk independent of the group centroid (top-right panel), and two fitted tracks that are colored by the most likely state sequence (bottom panels).

Here state 1 ("group") has biased movements toward the centroid and state 2 ("solitary") is simply a correlated random walk independent of the group centroid (Fig. 9). Note that despite this being a 2-state HMM, the working scale parameters for turning angle (Par\$angle) only includes 3 parameters (1 for the angle mean and 2 for the concentration parameters). This is because under the circular-circular regression model, no working parameter is specified³ for the reference turning angle of zero (i.e., the component for short-term directional persistence; see Eq. 2) and no angular covariates were specified in the model for state 2 ("solitary"). Thus the first parameter corresponds to the working scale parameter of the centroid.angle covariate for state 1 ("group"), while the second and third parameters are the working scale parameters for the concentration parameters for states 1 and 2, respectively. In this case, we remove the correlated random walk component for state 1 by setting circularAngleMean = list(angle = 0), and the angle mean parameter for state 1 was set at a positive value (+1) to enforce a biased random walk with attraction towards the group centriod. As there is only a single angular covariate here, the magnitude of this value is not important; only the sign matters (i.e. positive for attraction, negative for repulsion).

Finally, we can fit the group dynamic model using fitHMM:

³More accurately, the working parameter for the reference angle is automatically fixed to $\beta_0 = 1$ (or whatever scalar is provided by the circularAngleMean argument).

3.7 Harbour seals

Here we demonstrate how more complicated parameter constraints can be implemented using the userBounds and workBounds arguments in fitHMM and MIfitHMM. This example is based on the harbour seal analysis of McClintock et al. (2013). Using individual-level random effects on probability distribution parameters, McClintock et al. (2013) performed a Bayesian analysis of population-level activity budgets for 3-states ("resting", "foraging", and "transit"). While momentuHMM cannot be used to replicate this analysis exactly, we can perform a similar analysis in the absence of individual-level random effects. Here we will focus on several specific parameter constraints, but the full example code can be found in the "vignettes" source directory.

The harbour seal data consist of 17 individuals (10 male, 7 female) and, as in the northern fur example in section 3.2, both location and dive activity data. The location data were obtained at temporally-irregular intervals, while the dive activity data were obtained at regular 2-hour time steps. We therefore first used crawlWrap to fit and predict locations for all 17 tracks at 2-hour time steps and then used crawlMerge to merge the predicted locations with the dive activity data. We then fitted several different models assuming: 1) no individual- or sex-level effects on all parameters (i.e., the "null" model); 2) sex-level effects on all parameters; and 3) individual-level effects on all parameters. Based on fitHMM fits for the best predicted tracks, AIC overwhelmingly supported the model including individual-level effects on all parameters, but for simplicity we will use the model including no individual- or sex-level effects to demonstrate how the constraints of McClintock et al. (2013) can be implemented in momentuHMM. In addition to the lack of individual-level random effects in our example, we also depart

from McClintock *et al.* (2013) in our use of zero-inflation parameters to account for steps of length zero (i.e., $l_t = 0$) and time steps with no dive activity (i.e., $\omega_t = 0$). Unlike McClintock *et al.* (2013), note that our model 3 also includes individual-level fixed effects on the state transition probabilities.

McClintock et al. (2013) fit their 3-state model using more complicated constraints on the probability distribution parameters than any of our previous vignette examples. In addition to relational constraints among the "resting", "foraging", and "transit" states similar to those used in the northern fur seal example (section 3.2), these constraints included upper bounds for the shape and scale parameters of the Weibull distribution for step length, a minimum value for the "transit" concentration parameter of the wrapped Cauchy distribution for turning angle, and bounds on the shape parameters of the beta distribution for dive activity specifically chosen to prevent any "bathtub" shaped distributions for the proportion of each time step spent diving below 1.5m.

Before we demonstrate how to implement these constraints, we should first provide more detail on exactly how the DM, userBounds, and workBounds arguments work together in fitHMM (and MIfitHMM). While the DM argument should now be familiar, we have thus far spent little time discussing the latter two arguments. The userBounds argument specifies the lower and upper bounds for the natural scale parameters as a 2-column matrix. By default all working scale parameters (β_{θ}) are bounded on the real line, but the workBounds argument can be used to specify the lower and upper bounds for the working scale parameters as a 2-column matrix. Specifically, momentuHMM calculates natural scale parameters with finite bounds as

$$\boldsymbol{\theta} = (\mathbf{U}_{\theta} - \mathbf{L}_{\theta}) g^{-1} (\mathbf{X}_{\theta} \boldsymbol{\beta}_{\theta}^{*}) + \mathbf{L}_{\theta},$$

where \mathbf{L}_{θ} is the lower bound on the natural scale and \mathbf{U}_{θ} is the upper bound on the natural scale. Note that $\boldsymbol{\beta}_{\theta}^* = \boldsymbol{\beta}_{\theta}$ under the default values for workBounds. For natural scale parameters with finite lower bounds and infinite upper bounds, we have

$$\boldsymbol{\theta} = g^{-1} \left(\mathbf{X}_{\theta} \boldsymbol{\beta}_{\theta}^{*} \right) + \mathbf{L}_{\theta}.$$

When workBounds is specified, then additional link functions are used on the working scale parameters. For example, for working scale parameters with finite bounds, we

have

$$oldsymbol{eta_{ heta}^*} = (\mathbf{U}_{eta_{ heta}} - \mathbf{L}_{eta_{ heta}}) \operatorname{logit}^{-1} (oldsymbol{eta}_{ heta}) + \mathbf{L}_{eta_{ heta}},$$

where $\mathbf{L}_{\beta_{\theta}}$ is the lower bound on the working scale and $\mathbf{U}_{\beta_{\theta}}$ is the upper bound on the working scale. When constraining working parameters with finite lower bounds (e.g. zero) and infinite upper bounds, we have

$$\boldsymbol{\beta}_{\theta}^{*} = \exp{(\boldsymbol{\beta}_{\theta})} + \mathbf{L}_{\beta_{\theta}}.$$

When constraining working parameters with infinite lower bounds and finite upper bounds (e.g. zero), we have

$$\boldsymbol{\beta}_{\theta}^{*} = -\left(\exp\left(-\boldsymbol{\beta}_{\theta}\right) - \mathbf{U}_{\beta_{\theta}}\right).$$

Although optimization within fitHMM and MIfitHMM is always performed on β_{θ} , note that β_{θ}^{*} (and a delta method approximation for the variance of this transformation) is returned by CIbeta, MIpool, and print function calls.

For the Weibull distribution parameters for step length, McClintock et al. (2013) constrained the shape parameter $a_s < 5$ (to prevent too "peaked" distributions) and the scale parameter less than the maximum distance a harbour seal could travel in 2 hours at 2 m/s (i.e., $b_s < 14400$ m) for $s \in \{1 = \text{``resting''}, 2 = \text{``foraging''}, 3 = \text{``transit''}\}$. They also constrained $b_3 \ge b_2 \ge b_1$. This is easily accomplished in momentuHMM using the DM, userBounds, and workBounds arguments:

```
paste0("scale_",1:nbStates),
                        paste0("zeromass_",1:nbStates)),
                       c(paste0("shape_",1:nbStates,":(Intercept)"),
                         "scale: (Intercept)", "scale_2", "scale_3",
                        paste0("zeromass_",1:nbStates,":(Intercept)"))))
stepworkBounds<-matrix(c(rep(-Inf,4),0,0,rep(-Inf,3),
                   rep(Inf,ncol(stepDM))),ncol(stepDM),2,
                   dimnames=list(colnames(stepDM),c("lower","upper")))
stepBounds<-matrix(c(0,5,
                     0,5,
                     0,5,
                     0,14400,
                     0,14400,
                     0,14400,
                     0,1,
                     0,1,
                     0,1),nrow=3*nbStates,byrow=TRUE,
                    dimnames=list(rownames(stepDM),c("lower","upper")))
```

When included in workBounds and userBounds for the step length data stream, 'stepworkBounds' and 'stepBounds' above constrain the parameters $\beta_{l,5}^* > 0$ and $\beta_{l,6}^* > 0$ such that $14400 \ge b_3 \ge b_2 \ge b_1 \ge 0$:

```
b_1 = (14400 - 0) \operatorname{logit}^{-1}(\beta_{l,4}) + 0
b_2 = (14400 - 0) \operatorname{logit}^{-1}(\beta_{l,4} + \exp(\beta_{l,5}) + 0) + 0
b_3 = (14400 - 0) \operatorname{logit}^{-1}(\beta_{l,4} + \exp(\beta_{l,5}) + 0 + \exp(\beta_{l,6}) + 0) + 0.
```

In order to force the "transit" state to have strong directional persistence, McClintock et al. (2013) constrained the concentration parameter $\rho_3 > 0.75$. In the absence of relational constraints, userBounds could be used to constrain $\rho_3 > 0.75$. However, because we also wish to constrain $\rho_2 \leq \rho_3$, we must make use of the workBounds argument. We can constrain $\rho_3 \geq 0.75$, $\rho_2 \leq \rho_3$, and $\rho_s \leq 0.95$ ($s \in \{1, 2, 3\}$) using the following combination of DM, userBounds, and workBounds arguments:

When 'angleworkBounds' and 'angleBounds' are respectively included in workBounds and userBounds for the turning angle data stream, this yields

$$\rho_1 = (0.95 - 0) \operatorname{logit}^{-1}(\beta_{\phi,1}) + 0$$

$$\rho_2 = (0.95 - 0) \operatorname{logit}^{-1}(\exp(\beta_{\phi,2}) + 1.32 - (\exp(-\beta_{\phi,3}) - 0)) + 0$$

$$\rho_3 = (0.95 - 0) \operatorname{logit}^{-1}(\exp(\beta_{\phi,2}) + 1.32) + 0.$$

Here we constrained $\rho_s \leq 0.95$ to avoid numerical convergence issues that can arise with sparse data sets as $\rho_s \to 1$. Also note that when using workBounds to enforce a specific constraint on the natural scale, userBounds should not also include the corresponding natural parameter constraint(s). For example, because we are constraining $\rho_3 \geq 0.75$ with the workBounds argument, we did not also include a 0.75 lower bound for ρ_3 in 'angleBounds' above.

For the beta distribution of the dive activity data, McClintock *et al.* (2013) constrained the shape1 (v_s) and shape2 (δ_s) parameters as follows:

$$1 \le v_1 \le \delta_1 \le 10$$
$$1 < \delta_2 < v_2 < 10$$

where $v_2 = v_3$ and $\delta_2 = \delta_3$. These constraints can be imposed using the following combination of DM, userBounds, and workBounds arguments:

```
1,1,0,0,0,0,
                     0,0,1,0,0,0,
                     0,0,1,0,0,0,
                     0,0,0,0,1,0,
                     0,0,0,0,0,1,
                     0,0,0,0,0,1),nrow=nbStates*3,byrow=TRUE,
                dimnames=list(c(paste0("shape1_",1:nbStates),
                                 paste0("shape2_",1:nbStates),
                                 paste0("zeromass_",1:nbStates)),
                               c("shape_1:(Intercept)","shape2_1",
                                 "shape_2:(Intercept)", "shape1_2",
                                 "zeromass_1:(Intercept)",
                                 "zeromass_23:(Intercept)")))
omegaworkBounds <- matrix(c(-Inf,0,-Inf,0,-Inf,-Inf,</pre>
                             rep(Inf,ncol(omegaDM))),ncol(omegaDM),2,
                           dimnames=list(colnames(omegaDM),c("lower","upper")))
omegaBounds <- matrix(c(1,10,
                         1,10,
                         1,10,
                         1,10,
                         1,10,
                         1,10,
                         0,1,
                         0,1,
                         0,1),nrow=nbStates*3,byrow=TRUE,
                       dimnames=list(rownames(omegaDM),c("lower","upper")))
```

Lastly, we wish to impose some biologically-meaningful constraints on the zero-inflation parameters using the fixPar argument. Because we would never expect a harbour seal in the "transit" state to exhibit a step length of zero, it makes sense to constrain the zero-mass step length parameter for the "transit" state to (effectively) zero. Similarly, we would not expect a harbour seal in the "foraging" or "transit" states to exhibit no dive activity, and it therefore also makes sense to constrain the zero-mass dive activity parameters for these states to zero. We can accomplish this using the following fixPar argument:

Putting it all together, we can fit our constrained model assuming no individual- or sex-level effects using MIfitHMM:

As was mentioned earlier, we found overwhelming AIC support for the individual-level effects model relative to the sex-level effects models and the null model above. While our best supported momentuHMM model included individual-level fixed effects, the estimated tracks (Fig. 10) and inferences about population-level activity budgets were similar to the individual-level random effects model of McClintock et al. (2013). Estimated activity budgets for the males were 0.36 (95% CI: 0.35-0.37) for "resting", 0.53 (95% CI: 0.52-0.55) for "foraging", and 0.11 (95% CI: 0.1-0.12) for "transit". Activity budgets for females were 0.3 (95% CI: 0.29-0.3) for "resting", 0.61 (95% CI: 0.6-0.62) for "foraging", and 0.09 (95% CI: 0.09-0.1) for "transit". We found considerable individual variation in the state transition probabilities (Fig. 11), and when comparing the estimated activity budgets of our analysis with those of McClintock et al. (2013), we suspect the more noticeable differences between the time spent in the "resting" and "foraging" states for males is attributable to our having included individual-level effects on the state transition probabilities.

3.8 Northern fulmars

Using Bayesian analysis methods, Pirotta et al. (2018) fit a 6-state biased random walk model to northern fulmar (Fulmarus glacialis) tracks in northern Scotland, UK. These states included biased movements relative to a colony in Eynhallow (59.12° N, 3.1° W) and fishing vessels that frequently work in the area. Pirotta et al. (2018) framed their



Figure 10. Two harbour seal tracks, colored by the most likely state sequence.

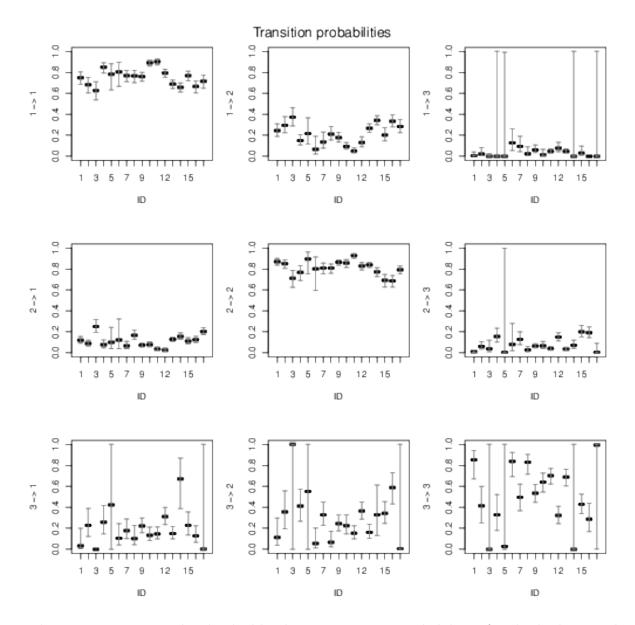


Figure 11. Estimated individual-level state transition probabilities for the harbour seal example.

model as having two latent state process. Under the first state process, the direction of movement could be biased away from the colony ("sea"), towards the nearest fishing vessel ("boat"), or towards the colony ("colony"). Under the second state process, the movement mode could either be fast and directionally-persistent ("transit") or area-restricted search ("ARS"). Thus the six states are "sea ARS", "sea transit", "boat ARS", "boat transit", "colony ARS" and "colony transit". Pirotta et al. (2018) also allowed the distance to the nearest fishing vessel and time since leaving the colony to affect state transitions to the "boat" and "colony" states. Here we demonstrate how a very similar (but not identical) model can be implemented in momentuHMM.

The data are provided in a Dryad repository, but these will require some additional formatting and preparation. We first load the raw data, create the required "ID" column based on individual trips, convert time stamps to class POSIXct, and project the northern fulmar ("Longitude", "Latitude") and nearest fishing vessel ("Boat_Longitude", "Boat_Latitude") locations using the sp package:

```
library(sp)
# load data provided by Pirotta et al
fulmarURL <- "https://datadryad.org/bitstream/handle/10255/dryad.174482/"</pre>
fileName <- "Fulmar_trackingData.csv?sequence=1"</pre>
raw_data <- read.csv(url(paste0(fulmarURL,fileName)),</pre>
                       stringsAsFactors = FALSE)
raw_data$ID <- raw_data$tripID</pre>
raw_data$Date <- as.POSIXct(raw_data$Date,tz="UTC",</pre>
                               format="%d/%m/%Y %H:%M")
# project data
oldProj <- CRS("+proj=longlat +datum=WGS84")</pre>
newProj <- CRS("+init=epsg:27700")</pre>
coordinates(raw_data) <- c("Longitude","Latitude")</pre>
proj4string(raw_data) <- oldProj</pre>
raw_data <- as.data.frame(spTransform(raw_data, newProj))</pre>
coordinates(raw_data) <- c("Boat_Longitude", "Boat_Latitude")</pre>
proj4string(raw_data) <- oldProj</pre>
raw_data <- as.data.frame(spTransform(raw_data, newProj))</pre>
```

For movements away from the colony ("sea ARS" and "sea transit"), Pirotta et al.

(2018) included bias in the direction of the farthest location from the colony for a given trip. We can use the centers argument of prepData to identify these locations ("max_dist") and then calculate the expected angle for the "sea" states ("sea.angle") using momentuHMM:::distAngle:

```
# use prepData to calculate colony distance covariate ('sea.angle')
colony \leftarrow data.frame(x = -3.1, y = 59.12)
coordinates(colony) <- c("x", "y")</pre>
proj4string(colony) <- oldProj</pre>
colony <- as.matrix(as.data.frame(spTransform(colony, newProj)))</pre>
rownames(colony) <- "colony"</pre>
colony_dist <- prepData(raw_data, coordNames = c("Longitude", "Latitude"),</pre>
                          centers = colony)
# calculate "sea" mean angle covariate
sea.angle <- NULL
for(id in unique(colony_dist$ID)) {
  idat <- subset(colony_dist,ID==id)</pre>
  nbSubObs <- length(which(colony_dist$ID==id))</pre>
  max_dist <- as.numeric(idat[which.max(idat$colony.dist),c("x","y")])</pre>
  max_angle <- momentuHMM:::distAngle(colony,colony,max_dist)[2]</pre>
  sea.angle <- c(sea.angle, rep(max_angle,nbSubObs))</pre>
raw_data$sea.angle <- sea.angle
```

Next we calculate the time since leaving colony covariate ("time"):

```
# calculate time since left colony covariate ('time')
time <- aInd <- NULL
for(id in unique(raw_data$ID)) {
  idInd <- which(raw_data$ID==id)
  aInd <- c(aInd,idInd[1])
  nbSubObs <- length(idInd)
  time <- c(time, (1:nbSubObs)/nbSubObs)
}
raw_data$time <- time</pre>
```

To complete our data preparation, we convert the nearest fishing vessel data to the centriods argument format and use prepData to calculate step lengths, turn angles, and our "sea", "boat", and "colony" covariates:

Note that we use the **centers** argument for the colony (because its location is static) and the **centroids** argument for the nearest fishing vessel (because its location is dynamic).

Now that we've formatted the data, we're ready to specify the 6-state HMM. Using 10 min time steps, Pirotta *et al.* (2018) included three data streams in their model: step length ("step"), turn angle ("angle"), and distance to nearest boat ("d"). These were respectively modelled using Weibull, wrapped Cauchy, and log-normal distributions:

Similar to the harbour seal example (section 3.7), Pirotta et al. (2018) used relational parameter constraints that can be specified in momentuHMM using pseudo-design matrices:

```
# specify data stream probability distribution parameter constraints
stepDM \leftarrow matrix(c(1,0,0,0,
                    0,1,0,0,
                    1,0,0,0,
                    0,1,0,0,
                    1,0,0,0,
                    0,1,0,0,
                    0,0,1,0,
                    0,0,1,1,
                    0,0,1,0,
                    0,0,1,1,
                    0,0,1,0,
                    0,0,1,1),2*nbStates,4,byrow=TRUE,
                  dimnames=list(c(paste0("shape_",1:nbStates),
                                  paste0("scale_",1:nbStates)),
                                c("shape:ARS","shape:Tr",
                                  "scale:(Intercept)", "scale:Tr")))
# constrain scale parameters such that Tr > ARS
stepworkBounds <- matrix(c(-Inf,Inf,</pre>
                            -Inf, Inf,
                            -Inf, Inf,
                            0,Inf),ncol(stepDM),2,byrow=TRUE,
                          dimnames=list(colnames(stepDM),c("lower","upper")))
# include trip-level effects on angle mean concentration parameter
nbTrips <- length(unique(fulmar_data$ID))</pre>
angleDM <- matrix(c("sea.angle",0,0,0,0,rep(0,2*nbTrips),</pre>
                     "sea.angle",0,0,0,0,rep(0,2*nbTrips),
                     0,"boat.angle",0,0,0,rep(0,2*nbTrips),
                     0, "boat.angle", 0, 0, 0, rep(0, 2*nbTrips),
                     0,0,"colony.angle",0,0,rep(0,2*nbTrips),
                     0,0,"colony.angle",0,0,rep(0,2*nbTrips),
                     0,0,0,1,0,paste0("ID",1:nbTrips),rep(0,nbTrips),
                     0,0,0,1,1,paste0("ID",1:nbTrips),paste0("ID",1:nbTrips),
                     0,0,0,1,0,rep(0,2*nbTrips),
                     0,0,0,1,1,rep(0,2*nbTrips),
                     0,0,0,1,0,rep(0,2*nbTrips),
                     0,0,0,1,1,rep(0,2*nbTrips)),2*nbStates,3+2+2*nbTrips,byrow=TRUE,
                   dimnames=list(c(paste0("mean_",1:nbStates),
                                   paste0("concentration_",1:nbStates)),
                                 c("mean:sea", "mean:boat", "mean:colony",
```

```
"concentration:(Intercept)","concentration:Tr",
                                    paste0("concentration:ID",1:nbTrips,":(Intercept)"),
                                    paste0("concentration:ID",1:nbTrips,":Tr"))))
\# constrain concentration parameters such that Tr > ARS
angleworkBounds <- matrix(c(-Inf,Inf,</pre>
                              -Inf, Inf,
                              -Inf, Inf,
                              -Inf, Inf,
                              0, Inf,
                              rep(c(-Inf,Inf),nbTrips),
                              rep(c(0,Inf),nbTrips)),ncol(angleDM),2,byrow=TRUE,
                          dimnames=list(colnames(angleDM),c("lower","upper")))
dDM \leftarrow matrix(c(1,1,0,0,
                 1,1,0,0,
                 1,0,0,0,
                 1,0,0,0,
                 1,1,0,0,
                 1,1,0,0,
                 0,0,1,1,
                 0,0,1,1,
                 0,0,1,0,
                 0,0,1,0,
                 0,0,1,1,
                 0,0,1,1),2*nbStates,4,byrow=TRUE,
               dimnames=list(c(paste0("location_",1:nbStates),
                                paste0("scale_",1:nbStates)),
                              c("location:(Intercept)","location:noboat",
                                "scale:(Intercept)", "scale:noboat")))
# constrain location and scale parameters such that sea and colony > boat
dworkBounds <- matrix(c(-Inf,Inf,</pre>
                         0, Inf,
                         -Inf, Inf,
                         0,Inf),ncol(dDM),2,byrow=TRUE,
                       dimnames=list(colnames(dDM),c("lower","upper")))
DM <- list(step = stepDM, angle = angleDM, d = dDM)</pre>
workBounds <- list(step = stepworkBounds,</pre>
                    angle = angleworkBounds,
```

d = dworkBounds)

To complete our model specification, we use the toState special function to model transitions to the "boat" and "colony" states as a function of distance to nearest fishing vessel ("boat.dist") and time since leaving colony ("time"), respectively. Following Pirotta et al. (2018), we will use the knownStates argument to fix the initial state to "sea transit". We will also use the fixPar argument to fix the initial state probabilities (because we are assuming these are known) and, as in section 3.6, constrain the model to a biased random walk by fixing the mean angle working scale parameters to a large positive value:

Lastly, we used the betaCons argument to impose similar constraints as Pirotta et al. (2018) for the transition probability parameters. We accomplish this by using betaCons to set the transition probability working parameter intercept terms equal among the three "ARS" states and the three "transit" states. We also use betaCons to constrain the effects of 'boat.dist' and 'time' to be identical for each of the two movement modes ("ARS" and "transit") within each of the three biased movement states ("sea", "boat", and "colony"). betaCons must be a matrix of the same dimension as beta0 and be composed of integers, where each beta working parameter is sequentially indexed in a column-wise fashion. Equality constraints can then be incorporated by having parameters share the same index. In this example we have:

```
betaCons
##
                 1 -> 2 1 -> 3 1 -> 4 1 -> 5 1 -> 6 2 -> 1 2 -> 3 2 -> 4 2 -> 5
                      1
                              4
                                      1
                                              4
                                                      1
                                                             16
                                                                     16
                                                                             22
                                                                                     16
##
   (Intercept)
                      2
                              5
                                                                              5
## boat.dist
                                      5
                                             11
                                                     14
                                                             17
                                                                      5
                                                                                     26
## time
                      3
                              6
                                      9
                                             12
                                                     12
                                                             18
                                                                     21
                                                                             24
                                                                                     12
                2 -> 6 3 -> 1
                                3 -> 2 3 -> 4 3 -> 5 3 -> 6 4 -> 1 4 -> 2 4 -> 3
##
                     22
                              4
                                              1
                                                                     16
                                                                             22
##
  (Intercept)
                                      1
                                                      4
                                                              1
                                                                                     16
                             32
## boat.dist
                     29
                                     35
                                             38
                                                     41
                                                             44
                                                                     47
                                                                             50
                                                                                     38
## time
                     12
                             33
                                     36
                                             39
                                                     42
                                                             42
                                                                     48
                                                                             51
                                                                                     54
##
                 4 -> 5 4 -> 6 5 -> 1 5 -> 2 5 -> 3 5 -> 4 5 -> 6 6 -> 1 6 -> 2
## (Intercept)
                     16
                             22
                                      4
                                              1
                                                      4
                                                              1
                                                                      1
                                                                             16
                                                                                     22
                             59
                                     62
                                                                     74
                                                                             77
## boat.dist
                     56
                                             65
                                                     68
                                                             68
                                                                                     80
## time
                     42
                             42
                                     63
                                             66
                                                     69
                                                             72
                                                                     75
                                                                             78
                                                                                     81
                 6 -> 3 6 -> 4 6 -> 5
##
                             22
                     16
## (Intercept)
                                     16
                     68
                             68
## boat.dist
                                     89
## time
                     84
                             87
                                     75
```

Again, betaCons constrains any of the transition probability matrix working parameters with the same index to be equal to one another. For example, all of the intercept terms indexed by a '1' $(1 \rightarrow 2, 1 \rightarrow 4, 1 \rightarrow 6, 3 \rightarrow 2, 3 \rightarrow 4, 3 \rightarrow 6, 5 \rightarrow 2, 5 \rightarrow 4,$ and $5 \rightarrow 6)$ are equal, and these terms correspond to the transitions from the "ARS" movement mode (states 1, 3, and 5) to the "transit" movement mode (states 2, 4, and 6). Similarly, all of the intercept terms indexed by a '16' are equal and correspond to the transitions from the "transit" movement mode to the "ARS" movement mode. For further details on the betaCons argument, see the fitHMM help file and the northern fulmar example code in the "vignettes" source directory.

Now we are ready to fit our 6-state HMM:

With decent starting values, this model required about 2 min to fit on a standard desktop computer (macOS El Capitan, 2.8 GHz Intel Core i7, 16 GB RAM). For com-

parison, Pirotta *et al.* (2018) required about 18 hr to fit their Bayesian model using MCMC (2.9 GHz Intel Core i7, 16 GB RAM).

We can compare the estimated activity budgets with those of Pirotta *et al.* (2018) using the timeInStates function:

```
timeInStates(m2)
```

```
## seaARS seaTr boatARS boatTr colonyARS colonyTr
## 1 0.2582469 0.1687088 0.1705938 0.06503299 0.1677663 0.1696513
```

Pirotta et al. (2018) estimated 0.28 ("seaARS"), 0.20 ("seaTr"), 0.18 ("boatARS"), 0.06 ("boatTr"), 0.12 ("colonyARS"), and 0.16 ("colonyTr"). While these are very similar, there a handful of state assignments that differ between the analyses. These differences could be attributable to several factors, including: 1) the use of informative priors in the Bayesian analysis of Pirotta et al. (2018); 2) our use of fixed trip-level effects on the "sea" state turn angle concentration parameters; and 3) Pirotta et al. (2018) assumed the state transition probability covariates ("boat.dist" and "time") only affected the movement direction states ("sea", "boat", "colony"), but in our momentuHMM implementation the covariates can affect state transitions for both the movement direction ("sea", "boat", "colony") and the movement mode ("ARS", "transit").

We can also examine activity budgets by individual bird (which are indexed in the raw data "birdID" column), where it is clear that the first 3 individuals tended to spend a larger proportion of their foraging trips in the "boat" states:

```
timeInStates(m2, by = "birdID")
```

```
##
     birdID
                seaARS
                             seaTr
                                       boatARS
                                                   boatTr colonyARS
## 1
          1 0.35564854 0.117154812 0.22594142 0.11297071 0.09623431
          2 0.14102564 0.134615385 0.28205128 0.10256410 0.25641026
## 2
          3 0.08333333 0.269607843 0.35294118 0.06862745 0.04411765
## 3
          4 0.49019608 0.196078431 0.00000000 0.04575163 0.05882353
## 4
## 5
          5 0.61475410 0.008196721 0.00000000 0.00000000 0.30327869
## 6
          6 0.00000000 0.235294118 0.05882353 0.02673797 0.32085561
##
       colonyTr
## 1 0.09205021
```

```
## 2 0.08333333

## 3 0.18137255

## 4 0.20915033

## 5 0.07377049

## 6 0.35828877
```

Finally, we can create a plot similar to Pirotta et al. (2018) using the plotSat function (Figure 12):

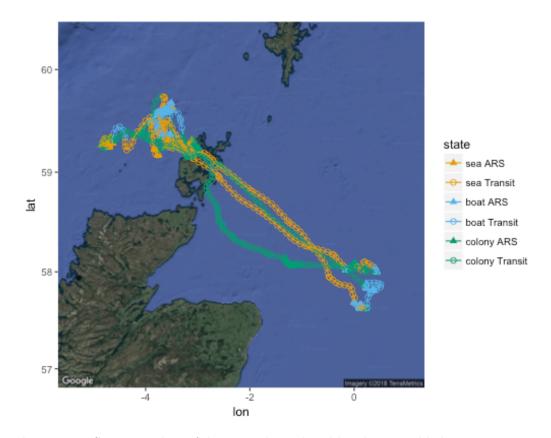


Figure 12. Seven northern fulmar tracks, colored by the most likely state sequence.

3.9 Pilot whales

Here we demonstrate how to include individual heterogeneity in state-switching dynamics via discrete-valued random effects by fitting the 4-state ("exploratory", "foraging", "crowded", "directed") mixed HHM for long-finned pilot whales described in Isojunno et al. (2017). The pilot whale data consist of 11 data streams collected from 15 individuals, and, as usual, we must first prepare the data for fitHMM using prepData. Let's summarize our prepared data using the summary function:

```
summary(pilotData, dataNames=names(pilotData)[-1])
## HMM data for 15 individuals:
##
## gm08_150c -- 156 observations
## gm08_154d -- 142 observations
## gm08_159a -- 192 observations
## gm09_137b -- 152 observations
## gm09_138a -- 223 observations
## gm09_156b -- 254 observations
## gm10_000a -- 119 observations
## gm10_143a -- 146 observations
## gm10_152b -- 50 observations
## gm10_157b -- 130 observations
## gm10_158d -- 148 observations
## gm13_137a -- 144 observations
## gm13_149a -- 88 observations
  gm13_169a -- 190 observations
   gm14_180a -- 180 observations
##
##
##
##
  Data summaries:
##
##
       dive.dur
                       dive.depth
                                         GR.speed2
                                                        dive.pitchvar2
           : 0.14
##
    Min.
                            :
                               0.86
                                              :0.025
                                                        Min.
                                                               :0.010
                    Min.
                                       Min.
    1st Qu.: 0.64
                     1st Qu.:
                               5.36
                                       1st Qu.:0.838
##
                                                        1st Qu.:0.042
                    Median :
##
    Median: 0.81
                               7.08
                                       Median :1.272
                                                       Median : 0.070
                    Mean
##
    Mean
           : 1.40
                            : 26.36
                                       Mean
                                              :1.367
                                                        Mean
                                                               :0.100
##
    3rd Qu.: 1.41
                    3rd Qu.: 11.73
                                       3rd Qu.:1.732
                                                        3rd Qu.:0.121
           :13.75
                            :617.37
                                              :8.824
                                                       Max.
                                                               :0.673
##
    Max.
                    Max.
                                       Max.
##
                                       NA's
                                                        NA's
                                                               :142
                                              :892
##
    breath.headchange
                           GR.size
                                          GR.tight
                                                        dive.CS.pres
```

```
Min. :-3.12587
                        Min. : 0
                                       Min. :0.00
                                                       Min. :0.0
##
    1st Qu.:-0.19089
                        1st Qu.: 6
                                       1st Qu.:1.00
                                                       1st Qu.:0.0
##
    Median: 0.00066
                        Median: 9
                                       Median:1.00
                                                       Median:1.0
           :-0.00407
##
    Mean
                        Mean
                               :11
                                       Mean
                                               :0.82
                                                       Mean
                                                               :0.6
    3rd Qu.: 0.18903
##
                        3rd Qu.:13
                                       3rd Qu.:1.00
                                                       3rd Qu.:1.0
##
           : 3.05424
    Max.
                        Max.
                                :79
                                       Max.
                                               :1.00
                                                       Max.
                                                               :1.0
    NA's
           :261
                        NA's
                                :665
                                       NA's
                                              :1128
                                                       NA's
                                                               :905
##
##
     dive.SS.pres
                       presurf
                                       postsurf
##
    Min.
           :0.00
                           :0.00
                                    Min.
                                           :0.00
##
    1st Qu.:0.00
                    1st Qu.:0.00
                                    1st Qu.:0.00
    Median :1.00
                    Median :1.00
##
                                    Median:1.00
##
   Mean
           :0.56
                   Mean
                           :0.74
                                    Mean
                                           :0.74
    3rd Qu.:1.00
##
                    3rd Qu.:1.00
                                    3rd Qu.:1.00
           :1.00
##
   Max.
                    Max.
                           :1.00
                                    Max.
                                            :1.00
##
   NA's
                    NA's
                           :15
                                    NA's
                                           :15
           :905
```

After specifying the data stream probability distributions and starting values for the parameters (based on those reported by Isojunno *et al.* 2017), let's first fit the null model with no discrete-valued individual-level random effects on the state-switching dynamics:

```
## 11 data streams
dist <- list(dive.dur = "weibull",</pre>
             dive.depth = "gamma",
             GR.speed2 = "gamma",
             dive.pitchvar2 = "beta",
             breath.headchange = "vm",
             GR.size = "pois",
             GR.tight = "bern",
             dive.CS.pres = "bern",
             dive.SS.pres = "bern",
             presurf = "bern",
             postsurf = "bern")
## initial values
Par0 \leftarrow list(dive.dur = c(1.9, 2.72, 1.64, 4.21,
                           1.3, 8.14, 1.53, 0.79),
             dive.depth = c(10.23, 315.91, 10.74, 5.51,
                              4.93, 233.12, 6.32, 1.91),
             GR.speed2 = c(1.15, 1.32, 1.36, 1.57,
                            0.66, 0.51, 0.77, 0.76),
```

Isojunno *et al.* (2017) found that model selection criteria favored models that assume the initial distribution is the stationary distribution, so we'll set **stationary=TRUE**:

```
## fit model with single mixture on TPM
fitmix1 <- fitHMM(pilotData, nbStates=4, dist=dist,</pre>
                  Par0=Par0, beta0=beta0,
                  stationary=TRUE,
                  stateNames=stateNames,
                  nlmPar=list(hessian=FALSE))
fitmix1
## Value of the maximum log-likelihood: -18510.4
##
##
## dive.dur parameters:
##
        exploratory foraging crowded directed
## shape
           1.895587 2.719570 1.640040 4.2099390
            1.301088 8.142114 1.529318 0.7911992
## scale
##
## dive.depth parameters:
       exploratory foraging crowded directed
##
## mean 10.221159 315.7408 10.752753 5.507151
## sd
          4.920867 233.2394 6.325075 1.908221
```

```
##
## GR.speed2 parameters:
## -----
## exploratory foraging crowded directed
## mean 1.1469499 1.3170625 1.36225 1.5706933
       0.6602282 0.5121064 0.77157 0.7628831
## sd
##
## dive.pitchvar2 parameters:
## -----
## exploratory foraging crowded directed
## shape1 2.205733 2.876755 1.823291 3.186465
## shape2 17.948930 6.036487 16.067474 55.491769
##
## breath.headchange parameters:
             exploratory foraging crowded directed
                0.000000 0.000000 0.000000 0.00000
## concentration 3.068759 5.653926 2.644184 18.04806
##
## GR.size parameters:
## -----
  exploratory foraging crowded directed
## lambda 5.996763 7.392536 20.38838 9.522725
##
## GR.tight parameters:
## -----
     exploratory foraging crowded directed
## prob 0.8885557 0.6629627 0.7609689 0.8072405
##
## dive.CS.pres parameters:
## -----
## exploratory foraging crowded directed
## prob 0.7630851 0.9892991 0.4077435 0.4703789
##
## dive.SS.pres parameters:
## exploratory foraging crowded directed
## prob 0.7167555 0.9789121 0.3955766 0.4115657
## presurf parameters:
## -----
## exploratory foraging crowded directed
```

```
0.76011 0.9924097 0.70787 0.7068425
##
## postsurf parameters:
## -----
       exploratory foraging crowded directed
         0.8081057 0.9619604 0.7164094 0.6568226
## prob
##
## Regression coeffs for the transition probabilities:
                        1 -> 3 1 -> 4 2 -> 1
##
               1 -> 2
                                                      2 -> 3
  (Intercept) -2.3725 -3.871793 -1.230078 0.2005482 -1.623498 -0.4895434
##
                 3 -> 1
                           3 \rightarrow 2 3 \rightarrow 4 4 \rightarrow 1 4 \rightarrow 2 4 \rightarrow 3
##
  (Intercept) -3.543939 -4.120499 -2.272679 -1.163733 -3.035013 -2.539986
##
##
## Transition probability matrix:
##
              exploratory foraging crowded
## exploratory 0.71106663 0.06630503 0.01480512 0.20782321
## foraging 0.40303342 0.32979502 0.06503813 0.20213342
## crowded
              0.02516983 0.01414110 0.87095004 0.08973904
               0.21699916 0.03340193 0.05479726 0.69480165
## directed
##
## Initial distribution:
## -----
## exploratory foraging crowded
                                        directed
## 0.36640726 0.05854032 0.22161529 0.35343713
```

(note that we've set the nlmPar option hessian=FALSE simply to speed up the compile time for this vignette).

Now we'll fit a model with K = 2 mixtures of discrete-valued individual-level random effects by setting mixtures=2, but first we'll set some starting values based on the null model (using getPar0) and check our model specification (using checkPar0):

```
-1.76, -2.14, -1.38)
ParO_mix2$beta$pi <- c(0.73, 0.27)
```

Note that because mixtures is > 1, the starting values for beta0 must now be specified as a list with elements named beta (containing the starting values for the t.p.m. parameters) and/or pi (containing the starting values for the mixture probability parameters).

```
# check model specification
checkPar0(pilotData, nbStates=4, dist=dist,
         Par0=Par0_mix2$Par, beta0=Par0_mix2$beta,
          stationary=TRUE,
         mixtures=2,
          stateNames=stateNames)
##
## dive.dur parameters:
##
        exploratory foraging crowded directed
          1.895587 2.719570 1.640040 4.2099390
## shape
## scale
           1.301088 8.142114 1.529318 0.7911992
##
## dive.depth parameters:
       exploratory foraging crowded directed
        10.221159 315.7408 10.752753 5.507151
## mean
          4.920867 233.2394 6.325075 1.908221
## sd
##
## GR.speed2 parameters:
##
       exploratory foraging crowded directed
##
## mean 1.1469499 1.3170625 1.36225 1.5706933
## sd
         0.6602282 0.5121064 0.77157 0.7628831
##
## dive.pitchvar2 parameters:
         exploratory foraging crowded directed
##
           2.205733 2.876755 1.823291 3.186465
## shape1
          17.948930 6.036487 16.067474 55.491769
## shape2
##
## breath.headchange parameters:
```

```
exploratory foraging crowded directed
## concentration 3.068759 5.653926 2.644184 18.04806
##
## GR.size parameters:
      exploratory foraging crowded directed
## lambda 5.996763 7.392536 20.38838 9.522725
##
## GR.tight parameters:
## -----
## exploratory foraging crowded directed
## prob 0.8885557 0.6629627 0.7609689 0.8072405
##
## dive.CS.pres parameters:
## -----
## exploratory foraging crowded directed
## prob 0.7630851 0.9892991 0.4077435 0.4703789
##
## dive.SS.pres parameters:
## -----
     exploratory foraging crowded directed
## prob 0.7167555 0.9789121 0.3955766 0.4115657
##
## presurf parameters:
## -----
     exploratory foraging crowded directed
## prob 0.76011 0.9924097 0.70787 0.7068425
##
## postsurf parameters:
## -----
## exploratory foraging crowded directed
## prob 0.8081057 0.9619604 0.7164094 0.6568226
##
## Mixture probabilities (pi):
## mix1 mix2
## 0.73 0.27
## Regression coeffs for the transition probabilities (beta):
                     ._____
                 1 -> 2 1 -> 3 1 -> 4 2 -> 1 2 -> 3 2 -> 4 3 -> 1 3 -> 2
```

```
## (Intercept)_mix1 -2.26 -3.93 -0.58 0.03 -2.25 -0.26 -3.38 -4.79
## (Intercept)_mix2 -2.51 -3.32 -2.63 0.03 -1.26 -0.12 -96.80 -3.62
## 3 -> 4 4 -> 1 4 -> 2 4 -> 3
## (Intercept)_mix1 -2.82 -1.06 -3.30 -3.43
## (Intercept)_mix2 -1.75 -1.76 -2.14 -1.38
```

We can see above that by setting mixtures=2 we now have K=2 sets of state transition probability matrix parameters, each suffixed by a mixture label (_mix1 or _mix2). We also now have K=2 mixture probability parameters (π), where the first (π 1) corresponds to parameters suffixed with _mix1 and the second (π 2) corresponds to parameters suffixed with _mix2. Now let's fit the K=2 mixture model from Isojunno et al. (2017):

```
fitmix2 <- fitHMM(pilotData, nbStates=4, dist=dist,</pre>
                  Par0=Par0_mix2$Par, beta0=Par0_mix2$beta,
                  stationary=TRUE,
                  mixtures=2,
                  stateNames=stateNames, nlmPar=list(hessian=FALSE))
## Fitting HMM with 4 states and 11 data streams
    dive.dur ~ weibull(shape=~1, scale=~1)
##
    dive.depth ~ gamma(mean=~1, sd=~1)
##
##
    GR.speed2 \sim qamma(mean=1, sd=1)
##
    dive.pitchvar2 ~ beta(shape1=~1, shape2=~1)
##
    breath.headchange ~ vm(concentration=~1)
##
    GR.size ~ pois(lambda=~1)
##
    GR.tight ~ bern(prob=~1)
    dive.CS.pres ~ bern(prob=~1)
##
##
    dive.SS.pres ~ bern(prob=~1)
##
    presurf ~ bern(prob=~1)
    postsurf ~ bern(prob=~1)
##
##
##
    Transition probability matrix formula:
```

```
##
##
   Initial distribution formula: ~1
##
##
  Number of mixtures:
  Mixture probability formula:
## -----
## DONE
fitmix2
## Value of the maximum log-likelihood: -18481.29
##
##
## dive.dur parameters:
## -----
     exploratory foraging crowded directed
## shape 1.936296 2.765043 1.648316 4.0151432
## scale 1.372185 8.194463 1.525709 0.7855839
##
## dive.depth parameters:
## -----
##
  exploratory foraging crowded directed
## mean 10.65323 319.2099 10.708474 5.650962
         5.19198 230.5566 6.319645 1.960661
## sd
##
## GR.speed2 parameters:
## -----
      exploratory foraging crowded directed
## mean 1.1379085 1.3188728 1.379888 1.5330244
       0.6637213 0.5154339 0.774373 0.7589017
## sd
##
## dive.pitchvar2 parameters:
## -----
       exploratory foraging crowded directed
## shape1 2.156273 2.954203 1.788241 2.791914
          17.462342 6.134090 15.932112 44.398296
## shape2
##
## breath.headchange parameters:
             exploratory foraging crowded directed
                  0.00000 0.000000 0.000000 0.0000
## mean
```

```
## concentration 2.86254 5.650729 2.636543 17.5883
##
## GR.size parameters:
## -----
       exploratory foraging crowded directed
## lambda 5.893962 7.428444 20.5167 9.348098
##
## GR.tight parameters:
## -----
## exploratory foraging crowded directed
## prob 0.9054784 0.6575736 0.7645632 0.7937692
##
## dive.CS.pres parameters:
## -----
## exploratory foraging crowded directed
## prob 0.7570289 0.9892898 0.3978535 0.5077637
##
## dive.SS.pres parameters:
## -----
## exploratory foraging crowded directed
## prob 0.7246258 0.9795692 0.3849078 0.440141
##
## presurf parameters:
## -----
## exploratory foraging crowded directed
## prob 0.7519146 0.9923487 0.7113906 0.7172221
##
## postsurf parameters:
## -----
     exploratory foraging crowded directed
##
## prob 0.8176395 0.9621881 0.7139607 0.6647271
##
## Regression coeffs for the transition probabilities:
## -----
                    1 -> 2
                            1 -> 3
                                     1 -> 4 2 -> 1
## (Intercept)_mix1 -2.255164 -3.921555 -0.5878246 0.03912368 -2.230029
## (Intercept)_mix2 -2.474720 -3.374581 -2.6435725 0.03630417 -1.202661
                     2 -> 4 3 -> 1 3 -> 2
                                                3 -> 4 4 -> 1
##
## (Intercept)_mix1 -0.2580981 -3.390892 -4.797065 -2.838810 -1.053870
## (Intercept)_mix2 -0.0930870 -96.800000 -3.526245 -1.723148 -1.730594
                   4 -> 2 4 -> 3
## (Intercept)_mix1 -3.310025 -3.418480
```

```
## (Intercept)_mix2 -2.081930 -1.406935
##
## Mixture probabilities:
## -----
##
      mix1
                mix2
## 0.7334777 0.2665223
##
## Transition probability matrix:
## -----
##
                   exploratory
                                  foraging
                                             crowded
## exploratory_mix1 5.951668e-01 0.062407036 0.01179041 0.33063572
## foraging_mix1 3.561367e-01 0.342472347 0.03682443 0.26456654
## crowded_mix1
                  3.060502e-02 0.007500662 0.90873748 0.05315684
## directed_mix1
                  2.458530e-01 0.025753712 0.02310673 0.70528657
## exploratory_mix2 8.406711e-01 0.070773201 0.02877825 0.05977742
## foraging_mix2 3.192174e-01 0.307836357 0.09247212 0.28047408
## crowded_mix2
                  7.555383e-43 0.024351947 0.82787036 0.14777769
## directed_mix2
                  1.145485e-01 0.080613179 0.15832611 0.64651221
##
## Initial distribution:
  -----
##
       exploratory foraging crowded directed
         0.3283189 0.05061176 0.1756211 0.4454483
## mix1
## mix2
         0.3359432 0.07584579 0.3323006 0.2559104
```

Based on our fitted model, we can calculate the probability of each individual being in a particular mixture using the mixtureProbs function and the t.p.m. for each mixture using the getTrProbs function:

```
## calculate mixture probabilities for each individual

round(mixtureProbs(fitmix2),4)

## mix1 mix2

## ID:gm08_150c 1.0000 0.0000

## ID:gm08_154d 1.0000 0.0000

## ID:gm08_159a 1.0000 0.0000

## ID:gm09_137b 1.0000 0.0000

## ID:gm09_138a 0.0004 0.9996

## ID:gm09_156b 0.9969 0.0031

## ID:gm10_000a 0.0000 1.0000

## ID:gm10_143a 1.0000 0.0000

## ID:gm10_152b 0.9999 0.0001
```

```
## ID:gm10_157b 0.0000 1.0000
## ID:gm10_158d 1.0000 0.0000
## ID:gm13_137a 1.0000 0.0000
## ID:gm13_149a 1.0000 0.0000
## ID:gm13_169a 0.0038 0.9962
## ID:gm14_180a 1.0000 0.0000
## calculate state transition probabilities for each mixture
trProbs2 <- getTrProbs(fitmix2, covIndex=1)</pre>
# mixture 1
round(trProbs2[[1]][,,1],2)
##
               exploratory foraging crowded directed
## exploratory
                       0.60
                                0.06
                                         0.01
                                                  0.33
## foraging
                       0.36
                                0.34
                                         0.04
                                                  0.26
## crowded
                      0.03
                                0.01
                                         0.91
                                                  0.05
## directed
                      0.25
                                0.03
                                         0.02
                                                  0.71
# mixture 2
round(trProbs2[[2]][,,1],2)
##
               exploratory foraging crowded directed
## exploratory
                       0.84
                                0.07
                                         0.03
                                                  0.06
## foraging
                       0.32
                                0.31
                                         0.09
                                                  0.28
## crowded
                       0.00
                                0.02
                                         0.83
                                                  0.15
## directed
                       0.11
                                0.08
                                         0.16
                                                  0.65
```

Now let's fit a model with K=3 mixtures by setting some starting values with the help of getPar0:

```
-96.8, -2.98, -1.53,
-2.29, -2.07, -1.55)
Par0_mix3$beta$pi <- c(0.4, 0.4, 0.2)
```

and then calling fitHMM with mixtures=3:

```
fitmix3 <- fitHMM(pilotData, nbStates=4, dist=dist,</pre>
                Par0=Par0_mix3$Par, beta0=Par0_mix3$beta,
                stationary=TRUE,
                mixtures=3,
                stateNames=stateNames,
                nlmPar=list(hessian=FALSE))
## -----
## Fitting HMM with 4 states and 11 data streams
   dive.dur ~ weibull(shape=~1, scale=~1)
##
   dive.depth ~ gamma(mean=~1, sd=~1)
##
  GR.speed2 \sim gamma(mean=1, sd=1)
##
##
   dive.pitchvar2 ~ beta(shape1=~1, shape2=~1)
   breath.headchange ~ vm(concentration=~1)
##
   GR.size ~ pois(lambda=~1)
##
  GR. tight ~ bern(prob=~1)
##
## dive.CS.pres ~ bern(prob=~1)
## dive.SS.pres ~ bern(prob=~1)
   presurf ~ bern(prob=~1)
##
   postsurf ~ bern(prob=~1)
##
##
   Transition probability matrix formula: ~1
##
##
   Initial distribution formula:
##
##
## Number of mixtures:
  Mixture probability formula:
## DONE
```

```
fitmix3
## Value of the maximum log-likelihood: -18445.14
##
##
## dive.dur parameters:
## -----
## exploratory foraging crowded directed
## shape 1.975978 2.813776 1.648341 3.8522580
## scale 1.422555 8.246565 1.520763 0.7864722
##
## dive.depth parameters:
## -----
## exploratory foraging crowded directed
## mean 10.977415 322.5798 10.638125 5.769243
## sd
       5.427491 228.1005 6.314569 2.013745
##
## GR.speed2 parameters:
## -----
## exploratory foraging crowded directed
## mean 1.1385507 1.3201513 1.3861439 1.5065078
       0.6663534 0.5203517 0.7776481 0.7581291
## sd
##
## dive.pitchvar2 parameters:
## -----
       exploratory foraging crowded directed
## shape1 2.15122 3.028038 1.764795 2.524053
           17.62926 6.225084 15.844942 37.637633
## shape2
##
## breath.headchange parameters:
## -----
##
             exploratory foraging crowded directed
               0.000000 0.000000 0.000000 0.00000
## mean
## concentration 2.768482 5.696489 2.629183 17.09466
##
## GR.size parameters:
## -----
       exploratory foraging crowded directed
## lambda 5.672187 7.460572 20.48158 9.345636
##
## GR.tight parameters:
## -----
## exploratory foraging crowded directed
```

```
## prob 0.9098293 0.6533947 0.7686185 0.7903651
##
## dive.CS.pres parameters:
## -----
      exploratory foraging crowded directed
## prob 0.7618571 0.9892938 0.3923022 0.5248959
##
## dive.SS.pres parameters:
## -----
## exploratory foraging crowded directed
## prob 0.7364702 0.9804547 0.3799649 0.4544787
##
## presurf parameters:
## -----
## exploratory foraging crowded directed
## prob 0.748499 0.9922603 0.7107198 0.7227432
##
## postsurf parameters:
## -----
## exploratory foraging crowded directed
## prob 0.8213494 0.9624941 0.7156723 0.6705817
##
## Regression coeffs for the transition probabilities:
## -----
##
                     1 \rightarrow 2 1 \rightarrow 3 1 \rightarrow 4 2 \rightarrow 1 2 \rightarrow 3
## (Intercept)_mix1 -2.152085 -4.306731 -1.0867497 0.2791947 -1.880898
## (Intercept)_mix2 -2.498738 -2.469649 0.6277231 -17.2200002 -13.180019
## (Intercept)_mix3 -2.714484 -3.475361 -3.0076135 -0.3548059 -1.124543
##
                       2 -> 4 3 -> 1
                                           3 -> 2
                                                    3 -> 4
## (Intercept)_mix1 -0.29671906 -3.501065 -4.714406 -3.111360 -0.6813091
## (Intercept)_mix2 0.58694161 -3.926036 -13.960064 -2.270529 -1.2524123
## (Intercept)_mix3 -0.09724842 -96.800000 -2.975692 -1.531841 -2.2900315
##
                     4 -> 2
                             4 -> 3
## (Intercept)_mix1 -2.488782 -2.599644
## (Intercept)_mix2 -3.567966 -3.753564
## (Intercept)_mix3 -2.073131 -1.549459
##
## Mixture probabilities:
## -----
    mix1 mix2 mix3
##
## 0.4018629 0.3980198 0.2001172
##
```

```
## Transition probability matrix:
## -----
##
                     exploratory
                                     foraging
                                                   crowded
                                                             directed
## exploratory_mix1 6.816492e-01 7.923599e-02 9.186948e-03 0.22992783
## foraging_mix1
                  4.108636e-01 3.107742e-01 4.737849e-02 0.23098376
## crowded_mix1
                    2.783618e-02 8.272980e-03 9.227895e-01 0.04110136
## directed_mix1
                    3.041933e-01 4.990848e-02 4.467117e-02 0.60122702
## exploratory_mix2 3.289318e-01 2.703446e-02 2.783241e-02 0.61620128
## foraging_mix2
                  1.187207e-08 3.573367e-01 6.746335e-07 0.64266266
## crowded_mix2
                    1.756192e-02 7.706355e-07 8.904877e-01 0.09194960
## directed_mix2
                    2.136992e-01 2.109457e-02 1.752130e-02 0.74768494
## exploratory_mix3 8.721443e-01 5.777009e-02 2.699344e-02 0.04309217
                   2.390740e-01 3.408966e-01 1.107235e-01 0.30930588
## foraging_mix3
                   7.202219e-43 4.025737e-02 7.891729e-01 0.17056974
## crowded_mix3
## directed_mix3
                   7.035018e-02 8.739041e-02 1.475339e-01 0.69472552
##
## Initial distribution:
##
##
       exploratory foraging
                                 crowded directed
        0.3870062 0.06849400 0.2553623 0.2891375
## mix2 0.2012576 0.02880544 0.1502894 0.6196476
## mix3
         0.3234760 0.08566424 0.2940851 0.2967747
## calculate mixture probabilities for each individual
round(mixtureProbs(fitmix3),4)
##
                 mix1
                        mix2 mix3
## ID:gm08_150c 0.0000 1.0000 0e+00
## ID:gm08_154d 0.0000 1.0000 0e+00
## ID:gm08_159a 0.0000 1.0000 0e+00
## ID:gm09_137b 1.0000 0.0000 0e+00
## ID:gm09_138a 0.0000 0.0000 1e+00
## ID:gm09_156b 1.0000 0.0000 0e+00
## ID:gm10_000a 0.0000 0.0000 1e+00
## ID:gm10_143a 1.0000 0.0000 0e+00
## ID:gm10_152b 0.0276 0.9724 0e+00
## ID:gm10_157b 0.0000 0.0000 1e+00
## ID:gm10_158d 0.0006 0.9994 0e+00
## ID:gm13_137a 1.0000 0.0000 0e+00
## ID:gm13_149a 1.0000 0.0000 0e+00
## ID:gm13_169a 0.9991 0.0000 9e-04
## ID:gm14_180a 0.0000 1.0000 0e+00
## calculate state transition probabilities for each mixture
```

```
trProbs3 <- getTrProbs(fitmix3, covIndex=1)</pre>
# mixture 1
round(trProbs3[[1]][,,1],2)
##
                exploratory foraging crowded directed
## exploratory
                       0.68
                                0.08
                                         0.01
                                                   0.23
## foraging
                       0.41
                                0.31
                                         0.05
                                                  0.23
## crowded
                       0.03
                                0.01
                                         0.92
                                                  0.04
                       0.30
## directed
                                0.05
                                         0.04
                                                  0.60
# mixture 2
round(trProbs3[[2]][,,1],2)
##
                exploratory foraging crowded directed
## exploratory
                       0.33
                                0.03
                                         0.03
                                                   0.62
                       0.00
                                0.36
                                         0.00
                                                  0.64
## foraging
## crowded
                       0.02
                                0.00
                                         0.89
                                                  0.09
## directed
                       0.21
                                0.02
                                         0.02
                                                  0.75
# mixture 3
round(trProbs3[[3]][,,1],2)
##
                exploratory foraging crowded directed
## exploratory
                       0.87
                                0.06
                                         0.03
                                                   0.04
## foraging
                       0.24
                                0.34
                                         0.11
                                                   0.31
## crowded
                       0.00
                                0.04
                                         0.79
                                                   0.17
## directed
                       0.07
                                0.09
                                                  0.69
                                         0.15
```

And let's do the same with K=4:

For comparison to the null and random effects models, let's also fit a model including individual-level fixed effects:

```
Par0_fix <- getPar0(fitmix1, formula= "ID, formulaDelta= "ID)</pre>
ParO_fix$delta[1,] <- log(fitmix1$mle$delta[1,-1]/fitmix1$mle$delta[1,1])
fitfix <- fitHMM(pilotData, nbStates=4, dist=dist,</pre>
                  formula = "ID, formulaDelta = "ID,
                  Par0=Par0_fix$Par, beta0=Par0_fix$beta,
                  delta0=Par0_fix$delta,
                  stateNames=stateNames,
                  nlmPar=list(hessian=FALSE))
## Fitting HMM with 4 states and 11 data streams
    dive.dur ~ weibull(shape=~1, scale=~1)
##
    dive.depth ~ gamma(mean=~1, sd=~1)
##
   GR.speed2 \sim gamma(mean=1, sd=1)
##
    dive.pitchvar2 ~ beta(shape1=~1, shape2=~1)
##
    breath.headchange ~ vm(concentration=~1)
##
    GR.size ~ pois(lambda=~1)
##
    GR.tight ~ bern(prob=~1)
##
##
   dive.CS.pres ~ bern(prob=~1)
## dive.SS.pres ~ bern(prob=~1)
   presurf ~ bern(prob=~1)
##
    postsurf ~ bern(prob=~1)
##
    Transition probability matrix formula:
##
##
##
    Initial distribution formula: "ID
## DONE
```

Based on AIC, we find overwhelming support for the discrete-valued individual-level random effects model with K=3 mixtures:

```
AIC(fitmix1,fitmix2,fitmix3,fitmix4,fitfix)
##
       Model
                  AIC
## 1 fitmix3 37086.29
## 2 fitmix4 37098.24
## 3 fitmix2 37132.58
## 4 fitmix1 37164.80
     fitfix 37190.99
AICweights(fitmix1,fitmix2,fitmix3,fitmix4,fitfix)
##
       Model
                   weight
## 1 fitmix3 9.974679e-01
## 2 fitmix4 2.532142e-03
## 3 fitmix2 8.825442e-11
## 4 fitmix1 8.904782e-18
## 5 fitfix 1.828650e-23
```

3.10 Hierarchical HMMs

As we already noted in section 2.5, HMMs with hierarchical structures allow for data streams and/or state transitions to occur at multiple regular time scales. Leos-Barajas et al. (2017) provide two examples where state transitions are allowed to occur at both "coarse" and "fine" time scales, while Adam et al. (2019) provide two examples where both data streams and state transitions occur at both "coarse" and "fine" time scales. Here we demonstrate all four of these examples can be fitted in momentuHMM. The key to fitting (and simulating) hierarchical hidden Markov models (HHMMs) in momentuHMM is specifying certain fitHMM (and simHierData) arguments hierarchically using the data.tree package (Glur 2018). For HHMMs, instead of simply specifying the number of states (nbStates), distributions (dist), and a single t.p.m. (formula) or initial distribution (formulaDelta) formula, the hierStates argument specifies the hierarchical nature of the states, the hierDist argument specifies the hierarchical nature of the data streams, and the hierFormula or hierFormulaDelta arguments specify a t.p.m. or initial distribution formula for each level of the hierarchy. All are specified as Node objects from the data.tree package. In the examples below, we focus on how to implement these HHMMs in momentuHMM and refer readers to Leos-Barajas et al. (2017) and Adam et al. (2019) for specific details about the data sets and the particular models

being fitted.

3.10.1 Harbor porpoise

In order to replicate the harbor porpoise HHMM example from Leos-Barajas et al. (2017) in momentuHMM, we must first use prepData to prepare our hierarchical data. This requires an additional field named level to be included in data that identifies the level of the hierarchy for each observation. These levels must be ordered from the coarsest to finest time scales, and must also indicate the initial observations at each level of the hierarchy (except for the coarsest level). For example, if there are M=3 time scales in the hierarchy (e.g. "coarse", "medium", and "fine" scales), then the level field must include 2M-1=5 ordered factors: "1" (corresponding to coarse-scale observations), "2i" (initial medium-scale observations), "2" (medium-scale observations), "3i" (initial fine-scale observations), and "3" (fine-scale observations). Regardless of the number of levels in the hierarchy, note that for each individual the level field for the first observation must always be "1", the second obervation must always be "2i", the third observation must always be "2", and the last observation must always be from level M. Also note that every "1" observation must be followed by "2i", every "2i" must be followed by one or more "2", every "3i" must be preceded by "2" and followed by one or more "3", and, after the first observation, every "1" must be preceded by an observation from level M.

In the harbor porpoise example from Leos-Barajas *et al.* (2017), there are only M=2 levels in the hierarchy so the 2M-1=3 ordered level factors are "1" (coarse level), "2i" (initial fine level), and "2" (fine level). After downloading the data, we can manually add the level field to our data frame as follows:

```
coarseInd <- data.frame(date_time=as.POSIXct(format(data[[i]]$date_time[1],</pre>
                                                          format="%Y-%m-%d %H:%M"),
                                                  tz="UTC"),
                            level=c("1","2i"),
                            dive_duration=NA,
                            maximum_depth=NA,
                            dive_wiggliness=NA)
  tmp <- rbind(coarseInd,data.frame(data[[i]],level="2"))</pre>
  porpoiseData <- rbind(porpoiseData,tmp)</pre>
head(porpoiseData)
##
                date_time level dive_duration maximum_depth dive_wiggliness
## 1 2015-11-02 14:43:00
                               1
                                             NA
                                                            NA
                                                                             NA
## 2 2015-11-02 14:43:00
                              2i
                                             NA
                                                            NA
                                                                             NA
## 3 2015-11-02 14:43:11
                               2
                                             28
                                                          8.19
                                                                           5.50
                               2
                                                          8.19
## 4 2015-11-02 14:44:08
                                                                           3.00
                                             18
## 5 2015-11-02 14:44:35
                               2
                                             14
                                                          6.19
                                                                           5.25
## 6 2015-11-02 14:44:58
                               2
                                                          7.44
                                             17
                                                                           2.50
```

By including the level field, we will be able to specify when the coarse-scale state switching can occur (i.e., a coarse scale t.p.m. will be used when level=1), the start of each fine-scale interval (i.e. a fine-scale initial distribution will be used when level=2i), and when the fine-scale state switching can occur (i.e. a fine scale t.p.m. will be used when level=2).

Now that we have labeled each observation in our data with a level factor, we can prepare our HHMM data using prepData:

```
##
## Data summaries:
##
##
     date_time
                                 level
                                           dive_duration maximum_depth
                                 1:275
                                                              : 2.2
##
   Min.
          :2015-11-02 14:43:00
                                           Min.
                                                 : 1
                                                         Min.
   1st Qu.:2015-11-06 02:01:24
                                 2i: 275
                                           1st Qu.: 15
                                                         1st Qu.: 7.2
##
   Median :2015-11-08 14:14:28
                                                         Median: 16.2
                                 2:7585
                                           Median: 43
##
##
   Mean
          :2015-11-08 11:59:48
                                           Mean: 58
                                                         Mean
                                                              : 22.2
                                                         3rd Qu.: 30.2
##
   3rd Qu.:2015-11-11 04:43:07
                                           3rd Qu.: 90
##
   Max.
         :2015-11-14 00:58:50
                                           Max.
                                                  :248
                                                         Max.
                                                                 :169.4
##
                                           NA's
                                                         NA's
                                                  :550
                                                                :550
##
   dive_wiggliness
          : 0.0
##
   Min.
   1st Qu.: 3.8
##
##
   Median: 15.0
##
   Mean : 23.4
   3rd Qu.: 36.0
##
##
   Max.
          :253.5
##
   NA's :562
```

For HHMMs, we must use the hierLevels argument to identify the ordered factor levels that prepData can expect to find in the level field. When hierLevels is specified, prepData assumes the data are intended for a HHMM analysis and assigns the classes hierarchical and momentuHierHMMData to the returned object (and corresponding methods for these classes will hereafter be used when calling functions such as fitHMM). Because prepData assumes the level field is a factor with levels ordered according to hierLevels, an error is returned if the order of hierLevels is not consistent with the level field (or vice versa):

Note that because there are no location data in this example, we have set coordNames

to NULL. Also note that in this example there are no data streams observed at the coarse time scale (level=1), but these could be easily included (if available; see sections 3.10.3 and 3.10.4). By definition there are no data streams observed at the initial fine scale (level=2i), but covariates (if available) could be included here for modeling the fine-scale initial distributions or state transition probabilities.

Now that our hierarchical data are prepared, we are ready to specify the HHMM. We will start with the hierarchical nature of the states, which is specified using the hierStates argument in fitHMM:

```
library(data.tree)

### define hierarchical HMM

### states 1-3 = coarse state 1 (nonforaging)

### states 4-6 = coarse state 2 (foraging)

hierStates <- data.tree::Node$new("harbor porpoise HHMM states")

hierStates$AddChild(name="nonforaging")

hierStates$nonforaging$AddChild(name="nf1", state=1)

hierStates$nonforaging$AddChild(name="nf2", state=2)

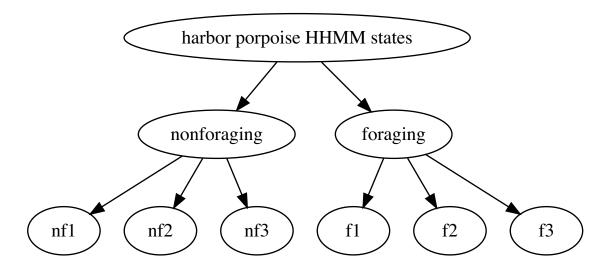
hierStates$nonforaging$AddChild(name="nf3", state=3)

hierStates$foraging$AddChild(name="f1", state=4)

hierStates$foraging$AddChild(name="f2", state=5)

hierStates$foraging$AddChild(name="f3", state=6)

plot(hierStates)</pre>
```



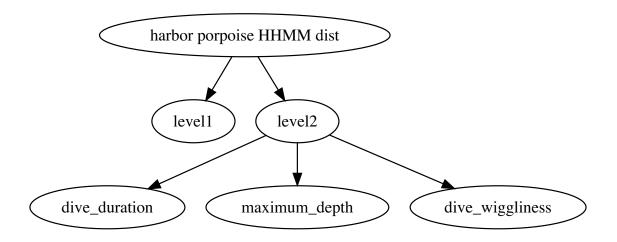
Here we can see that the coarse-scale "nonforaging" and "foraging" states are both composed of three fine-scale states. Note that the Node attribute state is required in hierStates and determines the index for each state in our HHMM. Alternatively, we could specify the exact same Node as:

The name for any of the "children" added to a node are user-specified and are akin to the stateNames argument in fitHMM for a standard HMM. While these names are arbitrary, the name and state attributes must be unique.

Next we will specify the hierarchical nature of the data streams for the hierDist argument in fitHMM:

```
# data stream distributions
# level 1 = coarse scale (no data streams)
# level 2 = fine scale (dive_duration, maximum_depth, dive_wiggliness)
```

```
hierDist <- data.tree::Node$new("harbor porpoise HHMM dist")
hierDist$AddChild(name="level1")
hierDist$AddChild(name="level2")
hierDist$level2$AddChild(name="dive_duration", dist="gamma")
hierDist$level2$AddChild(name="maximum_depth", dist="gamma")
hierDist$level2$AddChild(name="dive_wiggliness", dist="gamma")
plot(hierDist)
```



The Node attribute dist is required in hierDist and specifies the probability distribution for each data stream at each level of the hierarchy. In this case, level1 (corresponding to coarse-scale observations with level=1) has no data streams, and each of the data streams for level2 (corresponding to fine-scale observations with level=2) is assigned a gamma distribution. The first level of the hierDist Node must include a child for each level of the hierarchy, and the name for each child must be of the form paste0("level",i) for $i \in 1, 2, ..., M$, where M is the number of levels in the hierarchy; in this case, M = 2 and the names for each of the children at the first level of the hierDist Node must be level1 and level2. The children of these levels must be "leaves" (i.e. they have no children), where the name attribute indicates the data stream and the dist attribute indicates the probability distribution.

Leos-Barajas et al. (2017) did not include any covariates on the t.p.m. or initial

distribution for either level of the hierarchy, but, for demonstration purposes, here is how we would use the hierFormula and hierFormulaDelta arguments to specify the t.p.m. and initial distribution formula for each level of the hierarchy in fitHMM:

```
# define hierarchical t.p.m. formula(s)
hierFormula <- data.tree::Node$new("harbor porpoise HHMM formula")
hierFormula$AddChild(name="level1", formula=~1)
hierFormula$AddChild(name="level2", formula=~1)

# define hierarchical initial distribution formula(s)
hierFormulaDelta <- data.tree::Node$new("harbor porpoise HHMM formulaDelta")
hierFormulaDelta$AddChild(name="level1", formulaDelta=~1)</pre>
```

hierFormulaDelta\$AddChild(name="level2", formulaDelta=~1)

The Node attribute formula (or formulaDelta) is required in hierFormula (or hierFormulaDelta) and specifies the t.p.m. (or initial distribution) formula for each level of the hierarchy. Each child in hierFormula or hierFormulaDelta must be a leaf with a name of the form pasteO("level",i) for $i \in 1, 2, ..., M$, where M is the number of levels in the hierarchy.

Leos-Barajas *et al.* (2017) assume the data stream probability distributions do not depend on the coarse-scale state, so we can constrain the state-dependent parameters for states 1 ("nf1") and 4 ("f1"), states 2 ("nf2") and 5 ("f2"), and states 3 ("nf3") and 6 ("f3") to be equal using the DM argument:

```
# constrain fine-scale data stream distributions to be same
dw_DM \leftarrow matrix(cbind(kronecker(c(1,1,0,0,0,0),diag(3)),
                       kronecker(c(0,0,1,1,0,0),diag(3)),
                       kronecker(c(0,0,0,0,1,1),diag(3))),
                nrow=nbStates*3,
                ncol=9.
                  dimnames=list(c(paste0("mean_",1:nbStates),
                                   paste0("sd_",1:nbStates),
                                   paste0("zeromass_",1:nbStates)),
                                 paste0(rep(c("mean", "sd", "zeromass"), each=3),
                                         c("_14:(Intercept)",
                                           "_25:(Intercept)",
                                           "_36:(Intercept)"))))
DM <- list(dive_duration=dw_DM[1:(2*nbStates),1:6],</pre>
           maximum_depth=dw_DM[1:(2*nbStates),1:6],
           dive_wiggliness=dw_DM)
# get initial parameter values for data stream probability distributions
Par <- getParDM(porpoiseData, hierStates=hierStates, hierDist=hierDist,
                Par=Par0,DM=DM)
```

The (optional) last step for fitting this HHMM is specifying starting values for the t.p.m. and initial distribution parameters for each level of the hierarchy. In this case, we set them to "nudge" coarse state 1 (i.e., fine-scale states 1-3) to "nonforaging" and coarse state 2 (i.e., fine-scale states 4-6) to "foraging":

```
# initial values ('beta') for t.p.m. at each level of hierarchy
hierBeta <- data.tree::Node$new("harbor porpoise beta")
hierBeta$AddChild(name="level1",beta=matrix(c(-1, -1),1))
hierBeta$AddChild(name="level2")
hierBeta$level2$AddChild(name="nonforaging",beta=matrix(c(0,-1,1,0,1,1),1))
hierBeta$level2$AddChild(name="foraging",beta=matrix(c(-1,1,1,2,0,3),1))

# initial values ('delta') for initial distribution at each level of hierarchy
hierDelta <- data.tree::Node$new("harbor porpoise delta")
hierDelta$AddChild(name="level1",delta=matrix(0,1))
hierDelta$AddChild(name="level2")
hierDelta$level2$AddChild(name="nonforaging",delta=matrix(c(30, 30),1))
hierDelta$level2$AddChild(name="foraging",delta=matrix(c(-6, 2),1))</pre>
```

The Node attribute beta (or delta) is required in hierBeta (or hierDelta) and specifies the starting values for the t.p.m. (or initial distribution) at each level of the hierarchy. For each level of the hierarchy, these values are specified just as in beta0 (or delta0) for a standard HMM fitted with fitHMM. However, for HHMMs the starting values in hierDelta must always be provided as a matrix on the working scale (even if no covariates are included in hierFormulaDelta). Any additional arguments pertaining to t.p.m. or initial distribution parameters (such as workBounds\$beta, betaCons, fixPar\$beta, workBounds\$delta, deltaCons, and fixPar\$delta) must also be specified as data.tree Nodes (with Node attributes workBounds, betaCons, fixPar, workBounds, deltaCons, and fixPar, respectively).

Before fitting the HHMM, let's first check that everything is in order using the checkParO function:

```
# check hierarchical model specification and parameters
checkPar0(porpoiseData, hierStates=hierStates, hierDist=hierDist, Par0=Par,
          hierFormula=hierFormula, hierFormulaDelta=hierFormulaDelta,
          DM=DM, hierBeta=hierBeta, hierDelta=hierDelta)
##
## Regression coeffs for dive_duration parameters:
##
       mean_14:(Intercept) mean_25:(Intercept) mean_36:(Intercept)
##
                   1.609438
                                       3.401197
   [1,]
                                                             4.60517
       sd_14:(Intercept) sd_25:(Intercept) sd_36:(Intercept)
                 1.609438
                                    2.70805
                                                      3.688879
##
   [1,]
##
## Regression coeffs for maximum_depth parameters:
       mean_14:(Intercept) mean_25:(Intercept) mean_36:(Intercept)
##
## [1,]
                   1.609438
                                        2.70805
                                                            3.688879
       sd_14:(Intercept) sd_25:(Intercept) sd_36:(Intercept)
##
   [1,]
                0.6931472
                                   1.609438
                                                      2.995732
##
## Regression coeffs for dive_wiggliness parameters:
       mean_14:(Intercept) mean_25:(Intercept) mean_36:(Intercept)
##
                                       2.302585
##
                  0.6931472
                                                            3.688879
##
       sd_14:(Intercept) sd_25:(Intercept) sd_36:(Intercept)
## [1.]
                0.6931472
                                   2.302585
                                                      2.995732
       zeromass_14:(Intercept) zeromass_25:(Intercept)
```

```
##
  [1,]
                 -1.386294
                                      -4.59512
      zeromass_36:(Intercept)
  [1,]
                  -4.59512
##
##
##
##
## Regression coeffs for the transition probabilities (beta):
  ----- level1 -----
                    1 -> 4 4 -> 1
##
  I((level == "1") * 1) -1 -1
##
  ----- level2 ------
##
##
                    1 -> 2 1 -> 3 2 -> 2 2 -> 3 3 -> 2 3 -> 3
## I((level == "2") * 1) 0 -1 1
                                     0 1
##
##
                    4 -> 5 4 -> 6 5 -> 5 5 -> 6 6 -> 5 6 -> 6
## I((level == "2") * 1) -1
                              1
                                   1
                                         2
##
##
##
##
## Regression coeffs for the initial distribution (delta):
  ----- level1 ------
            state 4
##
  (Intercept)
##
##
##
  ------ level2 -----
##
                    state 2 state 3
## I((level == "2i") * 1)
                         30
                               30
##
##
                     state 5 state 6
## I((level == "2i") * 1)
                        -6
##
```

Note that for HHMMs, the reference states for the t.p.m. are determined by the lowest index for each state at the coarsest level in the hierarchy; in this case, the reference states are state 1 for "nonforaging" and state 4 for "foraging". This differs from standard HMMs fitted with fitHMM (where the reference states can be user-specified with the

betaRef argument).

Since everything looks good, we're now ready to fit our HHMM:

```
# fit hierarchical HMM
hhmm <- fitHMM(data=porpoiseData,hierStates=hierStates,hierDist=hierDist,</pre>
            hierFormula=hierFormula, hierFormulaDelta=hierFormulaDelta,
            ParO=Par, hierBeta=hierBeta, hierDelta=hierDelta,
            DM=DM,nlmPar=list(hessian=FALSE))
## Fitting hierarchical HMM with 6 states and 3 data streams
##
   dive_duration ~ gamma(mean: custom, sd: custom)
   maximum_depth ~ gamma(mean: custom, sd: custom)
##
   dive_wiggliness ~ gamma(mean: custom, sd: custom, zeromass:
##
                                                       custom)
##
   ##
I((level == "2i") * 1) + I((level == "2") * 1)
##
   Initial distribution formula:
## DONE
```

Before examining the output for our fitted HHMM, it's worth noting here that when data is a momentuHierHMMData object, fitHMM "shoehorns" the HHMM into a standard HMM by constraining the t.p.m. and initial distribution according to the hierarchical structure defined by hierStates. This is why the printed t.p.m. formula above may look a little strange at first. The initial distribution formula printed above pertains only to the initial distribution at the coarsest level of the hierarchy, and the initial distributions for all other levels are imbedded in the t.p.m. Let's look a little deeper:

```
## I((level == "2") * 1) NA NA -1e+10 -1e+10 NA NA
##
                       2 -> 4 2 -> 5 2 -> 6 3 -> 2 3 -> 3 3 -> 4 3 -> 5
## I((level == "1") * 1) NA -1e+10 -1e+10 -1e+10 NA -1e+10
## I((level == "2i") * 1) -1e+10 -1e+10 -1e+10 -1e+10 -1e+10 -1e+10 -1e+10
## I((level == "2") * 1) -1e+10 -1e+10 NA NA -1e+10 -1e+10
                       3 -> 6 4 -> 1 4 -> 2 4 -> 3 4 -> 5 4 -> 6 5 -> 1
##
## I((level == "1") * 1) -1e+10 NA -1e+10 -1e+10 -1e+10
## I((level == "2i") * 1) -1e+10 -1e+10 -1e+10 -1e+10
                                                  NA
                                                         NA -1e+10
## I((level == "2") * 1) -1e+10 -1e+10 -1e+10 NA NA -1e+10
                       5 -> 2 5 -> 3 5 -> 5 5 -> 6 6 -> 1 6 -> 2 6 -> 3
## I((level == "1") * 1) -1e+10 -1e+10 -1e+10 NA -1e+10 -1e+10
## I((level == "2i") * 1) -1e+10 -1e+10 -1e+10 -1e+10 -1e+10 -1e+10
## I((level == "2") * 1) -1e+10 -1e+10 NA NA -1e+10 -1e+10 -1e+10
                       6 -> 5 6 -> 6
##
## I((level == "1") * 1) -1e+10 -1e+10
## I((level == "2i") * 1) -1e+10 -1e+10
## I((level == "2") * 1) NA NA
hhmm$conditions$betaCons
##
                      1 -> 2 1 -> 3 1 -> 4 1 -> 5 1 -> 6 2 -> 2 2 -> 3
## I((level == "1") * 1) 1
                                  1
                                        7
                                               1
                                                     1
                                                           1
## I((level == "2i") * 1)
                          2
                                 5
                                        1
                                              1
                                                     1
                                                           1
                                                                  1
## I((level == "2") * 1)
                          3
                                  6
                                        1
                                               1
                                                     1
                                                          18
                                                                 21
                      2 -> 4 2 -> 5 2 -> 6 3 -> 2 3 -> 3 3 -> 4 3 -> 5
## I((level == "1") * 1)
                           7
                                 1
                                        1
                                              1
                                                           7
                                                     1
## I((level == "2i") * 1)
                                              1
                           1
                                 1
                                        1
                                                     1
                                                           1
                                                                  1
## I((level == "2") * 1)
                           1
                                 1
                                        1
                                              33
                                                    36
                                                           1
##
                       3 -> 6 4 -> 1 4 -> 2 4 -> 3 4 -> 5 4 -> 6 5 -> 1
## I((level == "1") * 1)
                          1 46
                                       1
                                             1
                                                    1
                                                           1
                                                                 46
## I((level == "2i") * 1)
                           1
                                 1
                                        1
                                              1
                                                    56
                                                          59
                                                                  1
## I((level == "2") * 1)
                           1
                                 1
                                        1
                                              1
                                                    57
                                                          60
                      5 -> 2 5 -> 3 5 -> 5 5 -> 6 6 -> 1 6 -> 2 6 -> 3
## I((level == "1") * 1)
                           1
                                        1
                                             1
                                                    46
                                 1
                                                           1
                                                                  1
## I((level == "2i") * 1)
                           1
                                  1
                                        1
                                             1
                                                    1
                                                           1
                                                                  1
## I((level == "2") * 1)
                                 1
                                      72
                                            75
                                                    1
                                                          1
                                                                  1
                           1
                      6 -> 5 6 -> 6
## I((level == "1") * 1)
                           1
                                  1
## I((level == "2i") * 1)
                           1
                                 1
## I((level == "2") * 1) 87
                                 90
hhmm$conditions$fixPar$delta
```

```
## state 2 state 3 state 4 state 5 state 6
## (Intercept) -1e+10 -1e+10 NA -1e+10 -1e+10

hhmm$conditions$deltaCons

## state 2 state 3 state 4 state 5 state 6
## (Intercept) 1 1 3 1 1
```

We can see that even though we did not explicitly specify fixPar\$beta, betaCons, fixPar\$delta, or deltaCons, the working parameters for the t.p.m. and initial distribution for each level of the hierarchy are constrained accordingly by making certain state transition and initial distribution probabilities equal and/or effectively zero. For example, these constraints do not allow fine-scale state switches between "nonforaging" (states 1-3) and "foraging" (states 4-6) when level=2. Similar to how the t.p.m. reference states are defined, higher-level (i.e. "parent") states are indexed based on the lowest state index of their "children". For example, "nonforaging" is indexed by state 1 and "foraging" is indexed by state 4, and only transitions to states 1 or 4 are permitted when level=1. Likewise, because delta corresponds to the initial distribution at the coarsest-scale, the initial distribution probabilities are effectively zero for all states except states 1 and 4.

Let's now examine our fitted HHMM:

```
hhmm
## Value of the maximum log-likelihood: -88242.08
##
##
## dive_duration parameters:
##
             nf1
                       nf2
                                 nf3
                                            f1
                                                     f2
## mean 5.637624 32.18047 106.82948 5.637624 32.18047 106.82948
##
        4.372832 15.13961 38.41245 4.372832 15.13961
##
## maximum_depth parameters:
##
##
             nf1
                        nf2
                                 nf3
                                            f1
                                                      f2
                                                               f3
## mean 3.740051 13.193085 39.61714 3.740051 13.193085 39.61714
##
                  5.288809 18.11188 1.426271 5.288809 18.11188
##
```

```
## dive_wiggliness parameters:
##
              nf1
                        nf2
                                  nf3
                                            f1
## mean 1.4566105 11.297304400 4.582790e+01 1.4566105 11.297304400
        1.2051899 7.683421367 2.437341e+01 1.2051899 7.683421367
## zeromass 0.3089819 0.007866278 2.885413e-04 0.3089819 0.007866278
                 f3
##
        4.582790e+01
## mean
## sd
        2.437341e+01
## zeromass 2.885413e-04
##
##
## -----
## Regression coeffs for the transition probabilities:
## ------ level1 ------
                     1 -> 4 4 -> 1
##
## I((level == "1") * 1) -1.29882 -1.285164
##
## ----- level2 ------
                       1 -> 2 1 -> 3 2 -> 2 2 -> 3 3 -> 2
## I((level == "2") * 1) 0.07465917 -1.014811 0.90907 -0.424281 0.6198106
##
                      3 -> 3
## I((level == "2") * 1) 0.7823011
##
                       4 -> 5 4 -> 6 5 -> 5 5 -> 6 6 -> 5
##
## I((level == "2") * 1) -0.5797742 0.7135748 0.7070142 1.621093 0.4255634
                      6 -> 6
## I((level == "2") * 1) 2.701054
##
## --
##
## -----
## Transition probability matrix (based on mean covariate values):
## -----
## ------ level1 ------
##
           nonforaging foraging
## nonforaging 0.7856364 0.2143636
## foraging 0.2166725 0.7833275
##
## ------ level2 ------
    nf1 nf2 nf3
```

```
## nf1 0.4098381 0.4416074 0.1485545
## nf2 0.2417647 0.6000632 0.1581721
## nf3 0.1982132 0.3683942 0.4333926
##
             f2 f3
         f1
##
## f1 0.27767750 0.15550628 0.5668162
## f2 0.12366226 0.25077807 0.6255597
## f3 0.05738593 0.08782643 0.8547876
##
## --
##
## -----
## Regression coeffs for the initial distribution:
## ------ level1 ------
            state 4
## (Intercept) -6.718877
##
## ------ level2 -----
                   state 2 state 3
## I((level == "2i") * 1) 30.34116 29.65686
##
##
                    state 5 state 6
## I((level == "2i") * 1) -6.010936 1.7169
##
## -----
##
## -----
## Initial distribution:
## -----
## ------ level1 ------
          nonforaging foraging
## ID:Animal1 0.9987936 0.001206437
##
## ------ level2 ------
                nf1
                     nf2
## nonforaging 4.42208e-14 0.6646966 0.3353034
##
##
              f1
## foraging 0.1522141 0.0003731974 0.8474127
##
## -----
```

These estimates are nearly identical to those reported by Leos-Barajas et al. (2017). The very slight differences are attributable to Leos-Barajas et al. (2017) assuming that the initial distribution for each level of the hierarchy is equal to the stationary distribution. However, because it constrains the t.p.m. based on level, this stationarity assumption is not possible when fitting HHMMs in momentuHMM.

As in a standard HMM, we can decode the most likely state sequence using the viterbi function:

```
states <- viterbi(hhmm)
length(states)

## [1] 8135
head(states)

## [1] 1 2 2 2 2 2</pre>
```

but we can also obtain the most likely state sequences at each level of the hierarchy by setting the argument hierarchical=TRUE

```
hStates <- viterbi(hhmm, hierarchical=TRUE)
lapply(hStates,length)

## $level1

## [1] 275

##

## $level2

## [1] 7860

head(hStates$level1)

## [1] "nonforaging" "nonforaging" "foraging" "foraging"

## [6] "foraging"

head(hStates$level2)

## [1] "nf2" "nf2" "nf2" "nf2" "nf2" "nf2"
```

We can plot the estimated state probabilities for each level of the hierarchy (Figures 13 and 14) using the plotStates function:

```
plotStates(hhmm)
```

We can also calculate the stationary probabilities of each state for each level of the hierarchy:

```
# stationary distributions
stats <- stationary(hhmm)</pre>
# coarse scale
stats[[1]]$level1[1,]
## nonforaging
                foraging
     0.5026783
                 0.4973217
# fine scale
lapply(stats[[1]]$level2,function(x) x[1,])
## $nonforaging
##
         nf1
                   nf2
                              nf3
## 0.2793776 0.5060948 0.2145275
##
## $foraging
##
                       f2
                                  f3
## 0.08308895 0.11164215 0.80526890
```

Finally, we can simulate from our fitted HHMM using the simHierData function. This requires that we specify the number of observations for each level of the hierarchy as a data.tree Node (with attribute obs) using the obsPerLevel argument:

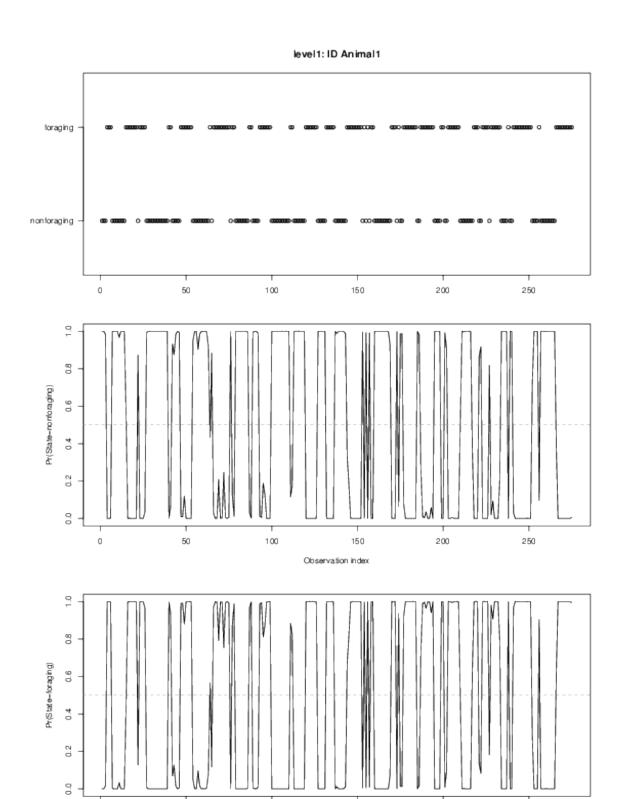


Figure 13. Coarse-scale state probabilities for the harbor porpoise example.

Observation index

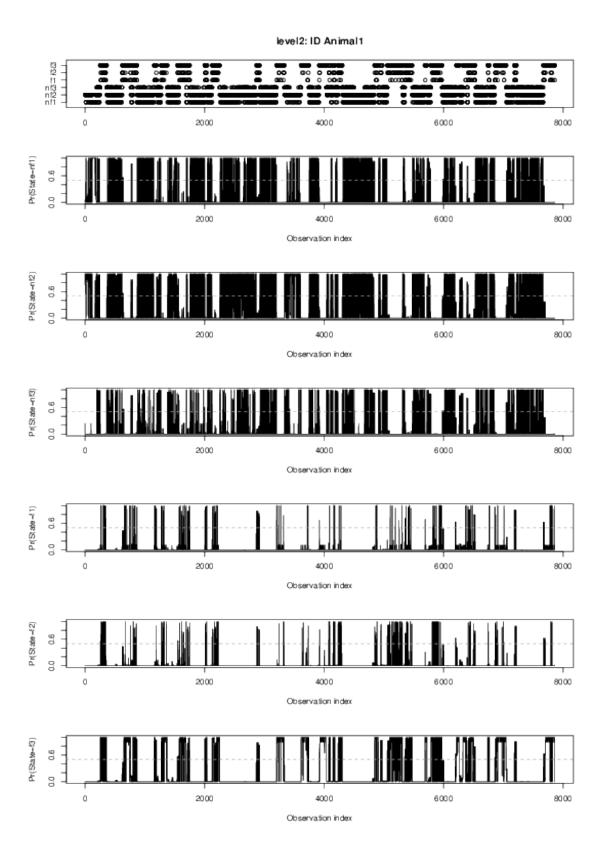


Figure 14. Fine-scale state probabilities for the harbor porpoise example.

```
## Simulating hierarchical HMM with 6 states and 3 data streams
    dive_duration ~ gamma(mean: custom, sd: custom)
##
##
    maximum_depth ~ gamma(mean: custom, sd: custom)
    dive_wiggliness ~ gamma(mean: custom, sd: custom, zeromass:
##
                                                                   custom)
##
    Transition probability matrix formula: ^{\circ}O + I((level == "1") * 1) +
##
I((level == "2i") * 1) + I((level == "2") * 1)
##
    Initial distribution formula:
##
## DONE
head(simHHMM)
     ID level dive_duration maximum_depth dive_wiggliness states
## 1 1
           1
                        NA
                                      NA
                                                      NA
                                                              1
          2i
                                                              2
## 2
    1
                        NA
                                      NA
                                                      NA
                                                              2
## 3 1
          2
                  50.75401
                              19.444787
                                              11.0461151
           2
                                                              2
## 4 1
                  16.89706
                              16.166635
                                              32.4377175
           2
## 5 1
                  11.40743
                               4.024188
                                               0.6959951
                                                              1
                  85.22059
                           35.200063
                                                              3
## 6 1
                                              60.0786026
```

3.10.2 Garter snakes

Next we'll quickly demonstrate how to perform the HHMM analysis for the garter snake movement data in Leos-Barajas et al. (2017) using momentuHMM. This is also a 2-level HHMM, but now we include three coarse-scale states each composed of three fine-scale states (for a total of N=9 states). As before, we must first add the level field to our data to indicate the level of the hierarchy for each observation and then create a momentuHierHMMData object with prepData:

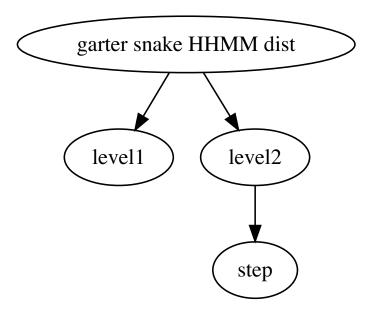
```
W <- dim(dataAr)[3] # number of individuals
M <- dim(dataAr)[2] # number of time series per individual
### add 2 extra rows for each time step where coarse scale behavior switches occur
# level=1 indicates when coarse-scale behavior switching can occur
# level=2i indicates start of each fine-scale interval
# level=2 indicates when fine-scale behavior switching can occur
snakeData <- NULL</pre>
for(w in 1:W){
  coarseInd <- data.frame(ID=w,level=c("1","2i"),step=NA)</pre>
  for (m in 1:M)
    tmp <- rbind(coarseInd,data.frame(ID=w,level="2",step=sqrt(dataAr[,m,w])))</pre>
    snakeData <- rbind(snakeData,tmp)</pre>
# prepare hierarchical data
snakeData <- prepData(snakeData,coordNames=NULL,hierLevels=c("1","2i","2"))</pre>
# summarize prepared data
summary(snakeData)
## Hierarchical HMM data for 19 individuals:
##
## 1 -- 606 observations
## 2 -- 606 observations
## 3 -- 606 observations
## 4 -- 606 observations
## 5 -- 606 observations
## 6 -- 606 observations
## 7 -- 606 observations
## 8 -- 606 observations
## 9 -- 606 observations
## 10 -- 606 observations
## 11 -- 606 observations
## 12 -- 606 observations
## 13 -- 606 observations
## 14 -- 606 observations
## 15 -- 606 observations
## 16 -- 606 observations
## 17 -- 606 observations
## 18 -- 606 observations
## 19 -- 606 observations
```

```
##
##
## Data summaries:
##
##
       step
                 level
##
   Min. :0.011 1: 114
   1st Qu.:0.334
##
                  2i: 114
##
   Median :0.700
                  2:11286
   Mean :0.790
   3rd Qu.:1.149
##
##
  Max.
         :3.130
##
   NA's :1496
```

The sole data stream for this example is step length at the fine-scale level, and no coordinates are provided (hence coordNames=NULL). As in section 3.10.1, this example has no data streams observed at the coarse-scale level, but these could be easily included (if available; see sections 3.10.3 and 3.10.4). Let's now specify the probability distribution for the fine-scale step length data stream via the hierDist data tree Node:

```
### data stream distributions:
### level 1 = coarse level (no data streams)
### level 2 = fine level (step="gamma")
hierDist <- data.tree::Node$new("garter snake HHMM dist")
hierDist$AddChild(name="level1")
hierDist$AddChild(name="level2")
hierDist$level2$AddChild(name="step", dist="gamma")

plot(hierDist)</pre>
```

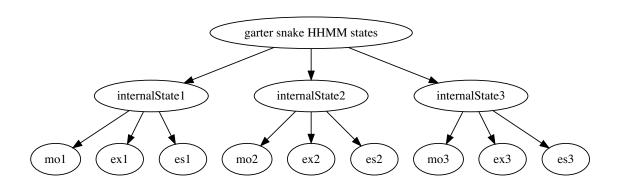


Next we define our HHMM structure via the hierStates data tree Node:

```
### define hierarchical HMM: states 1-3 = coarse state 1
###
                             states 4-6 = coarse state 2
###
                             states 7-9 = coarse state 3
hierStates <- data.tree::Node$new("garter snake HHMM states")
hierStates$AddChild(name="internalState1")
hierStates$internalState1$AddChild(name="mo1", state=1) # motionless
hierStates$internalState1$AddChild(name="ex1", state=2) # slow exploratory
hierStates$internalState1$AddChild(name="es1", state=3) # rapid escape
hierStates$AddChild(name="internalState2")
hierStates$internalState2$AddChild(name="mo2", state=4) # motionless
hierStates$internalState2$AddChild(name="ex2", state=5) # slow exploratory
hierStates$internalState2$AddChild(name="es2", state=6) # rapid escape
hierStates$AddChild(name="internalState3")
hierStates$internalState3$AddChild(name="mo3", state=7) # motionless
hierStates$internalState3$AddChild(name="ex3", state=8) # slow exploratory
hierStates$internalState3$AddChild(name="es3", state=9) # rapid escape
```

Or, equivalently:

```
hierStates <- data.tree::as.Node(list(name="garter snake HHMM states",
internalState1=list(mo1=list(state=1),
ex1=list(state=2),
```



As in the harbor porpoise example (section 3.10.1), we follow Leos-Barajas *et al.* (2017) and assume the fine-scale data stream probability distribution does not depend on coarse-scale state:

We do not include any covariates in hierFormula or hierFormulaDelta, so all that's left before fitting the model is the (optional) step of specifying starting values for the t.p.m. and initial distribution at each level of the hierarchy (based on values reported by Leos-Barajas et al. 2017):

```
hierBeta <- data.tree::Node$new("garter snake beta")
hierBeta$AddChild(name="level1")
hierBeta$AddChild(name="level2")
hierBeta$level2$AddChild(name="internalState1")
hierBeta$level2$AddChild(name="internalState2")
hierBeta$level2$AddChild(name="internalState3")
hierDelta <- data.tree::Clone(hierBeta)</pre>
hierDelta$name <- "garter snake delta"
# reference states for level1
level1states <- hierStates$Get(function(x) data.tree::Aggregate(x, "state", min),</pre>
                                filterFun=function(x) x$level==2)
hierBeta$level1$beta \leftarrow matrix(c(1.24, 0.44, 1.1, -0.87, -1.40, -1.11),
                                nrow=1,
                                ncol=hierStates$count*(hierStates$count-1),
                                 byrow=TRUE,
                                 dimnames=list("(Intercept)",
                                          c(sapply(level1states,function(x)
                                            paste(
                                             rep(x,each=hierStates$count-1),
                                             ^{11}->^{11}.
```

```
level1states[-which(level1states==x)])))))
hierDelta$level1$delta <- matrix(rep(c(-2.5,-3.5),hierStates$count-1),
                                nrow=1,
                                ncol=(hierStates$count-1),
                                byrow=TRUE,
                                dimnames=list("(Intercept)",
                                              paste("state",level1states[-1])))
beta0_level2 <- delta0_level2 <- list()</pre>
beta0_level2$internalState2 <- c(-1.72, -2.78, 3.54, 2.83, 34.72, 36.21)
beta0_level2$internalState3 <- c(-5.10, -17.69, 5.76, -11.34, 33.39, 37.37)
delta0_level2$internalState1 <- c(-1.39, 0.16)
delta0_level2$internalState2 <- c(-1.27, 2.33)
delta0_level2$internalState3 <- c(0.34, -0.26)
for(jj in 1:hierStates$count){
  j <- names(hierStates$children)[jj]</pre>
  # reference states for internalState j
  ref <- hierStates[[j]]$Get(function(x))</pre>
                             data.tree::Aggregate(x, "state", min),
                            filterFun=function(x) x$level==2)
  # states for internalState j
  states <- hierStates[[j]]$Get("state",filterFun = isLeaf)</pre>
  dimNames <- list("(Intercept)",</pre>
                  paste0(rep(states,each=hierStates[[j]]$count-1),
                         " -> ",
                         states[-which(states==ref)]))
  hierBeta$level2[[j]]$beta <- matrix(beta0_level2[[j]],
                                     ncol=hierStates[[j]]$count*
                                          (hierStates[[j]]$count-1),
                                     byrow=TRUE,
                                     dimnames=dimNames)
  hierDelta$level2[[j]]$delta <- matrix(delta0_level2[[j]],
```

Let's check our model specification:

```
checkParO(snakeData, hierStates=hierStates, hierDist=hierDist,
        Par0=Par, DM=DM,
        hierBeta=hierBeta, hierDelta=hierDelta)
##
## Regression coeffs for step parameters:
  _____
      mean_147:(Intercept) mean_258:(Intercept) mean_369:(Intercept)
##
## [1,]
               -2.111965
                               -0.388608
##
     sd_147:(Intercept) sd_258:(Intercept) sd_369:(Intercept)
## [1,]
            -2.813411 -1.136314 -0.718465
##
##
## Regression coeffs for the transition probabilities (beta):
  ______
## ------ level1 ------
                    1 -> 4 1 -> 7 4 -> 1 4 -> 7 7 -> 4
## I((level == "1") * 1) 1.24 0.44 1.1 -0.87 -1.4 -1.11
##
## ------ level2 -----
                   1 -> 2 1 -> 3 2 -> 2 2 -> 3 3 -> 2 3 -> 3
## I((level == "2") * 1) -2.99 -5.06 3.93 1.25 34.84 35.97
##
                    4 -> 5 4 -> 6 5 -> 5 5 -> 6 6 -> 5 6 -> 6
##
## I((level == "2") * 1) -1.72 -2.78 3.54 2.83 34.72 36.21
##
                    7 -> 8 7 -> 9 8 -> 8 8 -> 9 9 -> 8 9 -> 9
##
## I((level == "2") * 1) -5.1 -17.69 5.76 -11.34 33.39 37.37
##
##
##
```

```
## Regression coeffs for the initial distribution (delta):
  ------ level1 ------
##
            state 4 state 7
##
  (Intercept)
               -2.5 -3.5
##
##
       ----- level2
##
                      state 2 state 3
## I((level == "2i") * 1)
                       -1.39
                                0.16
##
                      state 5 state 6
## I((level == "2i") * 1)
                       -1.27
                                2.33
##
##
                      state 8 state 9
## I((level == "2i") * 1)
                       0.34
##
```

Again note that higher-level (i.e. "parent") states are indexed based on the lowest state index of their "children". For example, "internalState1" is indexed by state 1, "internalState2" is indexed by state 4, and "internalState3" is indexed by state 7. We can also examine the starting values for the t.p.m. on the real scale ("gamma") at each level of the hierarchy using the getTrProbs function:

```
iTrProbs <- getTrProbs(snakeData,hierStates=hierStates,</pre>
                       hierBeta=hierBeta, hierDist=hierDist)
# t.p.m. at first time step for level1
iTrProbs$level1$gamma[,,1]
##
                  internalState1 internalState2 internalState3
                                                      0.25842616
## internalState1
                       0.1664359
                                       0.5751380
## internalState2
                       0.6791965
                                       0.2260849
                                                      0.09471861
## internalState3
                       0.1564547
                                       0.2090903
                                                      0.63445500
# t.p.m. at first time step for level2
lapply(iTrProbs$level2,function(x) x$gamma[,,1])
## $internalState1
##
                mo1
                            ex1
                                        es1
## mo1 9.464024e-01 0.04759215 0.006005453
```

```
## ex1 1.805141e-02 0.91894296 0.063005628
## es1 1.806578e-16 0.24416110 0.755838899
## $internalState2
              mo2 ex2
                                   es2
## mo2 8.057338e-01 0.1442797 0.04998652
## ex2 1.907946e-02 0.6576103 0.32331027
## es2 1.534365e-16 0.1839217 0.81607827
##
## $internalState3
      mo3
##
                         ex3
                                       es3
## mo3 9.939402e-01 0.006059801 2.063911e-08
## ex3 3.141213e-03 0.996858749 3.734204e-08
## es3 5.785955e-17 0.018342891 9.816571e-01
```

Now let's fit our garter snake HHMM:

```
# fit hierarchical HMM
hhmm <- fitHMM(snakeData, hierStates=hierStates, hierDist=hierDist,</pre>
            ParO=Par, DM=DM, hierBeta=hierBeta, hierDelta=hierDelta,
            nlmPar=list(hessian=FALSE))
## -----
## Fitting hierarchical HMM with 9 states and 1 data stream
##
   step ~ gamma(mean: custom, sd: custom)
##
  Transition probability matrix formula: 0 + I((level == "1") * 1) + I((level == "1") * 1)
##
I((level == "2i") * 1) + I((level == "2") * 1)
##
## Initial distribution formula:
## -----
## DONE
hhmm
```

```
hhmm
## Value of the maximum log-likelihood: -2060.361
##
```

```
##
## step parameters:
           mo1 ex1 es1 mo2 ex2
##
## mean 0.12148244 0.6778589 1.3749453 0.12148244 0.6778589 1.3749453
## sd 0.05906919 0.3217373 0.4876126 0.05906919 0.3217373 0.4876126
##
                   ex3
## mean 0.12148244 0.6778589 1.3749453
## sd 0.05906919 0.3217373 0.4876126
##
##
## -----
## Regression coeffs for the transition probabilities:
## -----
## -----
           ------ level1 ------
                     1 -> 4 1 -> 7 4 -> 1
                                            4 -> 7
## I((level == "1") * 1) 1.245638 0.4309528 1.102461 -0.870203 -1.397521
## I((level == "1") * 1) -1.114278
## ------ level2 ------
                     1 -> 2 1 -> 3
                                     2 -> 2 2 -> 3
## I((level == "2") * 1) -2.993152 -5.064987 3.927787 1.246237 34.83412
                     3 -> 3
## I((level == "2") * 1) 35.96589
##
                     4 -> 5 4 -> 6 5 -> 5 5 -> 6 6 -> 5
##
## I((level == "2") * 1) -1.721131 -2.775771 3.540737 2.834405 34.7087
                     6 -> 6
## I((level == "2") * 1) 36.19201
##
                      7 -> 8 7 -> 9 8 -> 8 8 -> 9
## I((level == "2") * 1) -5.098125 -17.69051 5.761101 -11.34101 33.38974
                     9 -> 9
##
## I((level == "2") * 1) 37.36932
##
##
##
## Transition probability matrix (based on mean covariate values):
## -----
## ------ level1 ------
```

```
## internalState1 internalState2 internalState3
## internalState1 0.1662821 0.5778557 0.25586212
               0.6797456
## internalState2
                           0.2257114
                                      0.09454295
##
## ------ level2 ------
           mo1 ex1 es1
##
## mo1 9.465724e-01 0.04745091 0.005976649
## ex1 1.809245e-02 0.91899585 0.062911698
## es1 1.814804e-16 0.24383417 0.756165834
##
          mo2 ex2 es2
##
## mo2 8.056946e-01 0.1441095 0.05019591
## ex2 1.904305e-02 0.6568391 0.32411785
## es2 1.560287e-16 0.1849270 0.81507302
##
          mo3 ex3 es3
##
## mo3 9.939289e-01 0.006071107 2.062827e-08
## ex3 3.137768e-03 0.996862195 3.726331e-08
## es3 5.789852e-17 0.018350461 9.816495e-01
##
## -----
##
## -----
## Regression coeffs for the initial distribution:
## -----
## ------ level1 ------
           state 4 state 7
## (Intercept) -2.536649 -3.509269
##
## ----- level2 ------
                    state 2 state 3
## I((level == "2i") * 1) -1.387284 0.1582614
##
                    state 5 state 6
## I((level == "2i") * 1) -1.274323 2.327475
##
                    state 8 state 9
## I((level == "2i") * 1) 0.3387744 -0.2607024
## --
##
```

```
## Initial distribution:
         ----- level1 ------
         internalState1 internalState2 internalState3
## ID:1
                            0.07135036
              0.9016727
                                            0.02697695
## ID:2
              0.9016727
                            0.07135036
                                            0.02697695
## ID:3
              0.9016727
                            0.07135036
                                            0.02697695
## ID:4
              0.9016727
                            0.07135036
                                            0.02697695
## ID:5
              0.9016727
                            0.07135036
                                            0.02697695
## ID:6
              0.9016727
                            0.07135036
                                            0.02697695
## ID:7
              0.9016727
                            0.07135036
                                            0.02697695
## ID:8
              0.9016727
                            0.07135036
                                            0.02697695
## ID:9
                            0.07135036
                                            0.02697695
              0.9016727
## ID:10
                            0.07135036
                                            0.02697695
              0.9016727
## ID:11
              0.9016727
                            0.07135036
                                            0.02697695
## ID:12
              0.9016727
                            0.07135036
                                            0.02697695
## ID:13
              0.9016727
                            0.07135036
                                            0.02697695
## ID:14
                            0.07135036
                                            0.02697695
              0.9016727
## ID:15
              0.9016727
                            0.07135036
                                            0.02697695
## ID:16
             0.9016727
                            0.07135036
                                            0.02697695
## ID:17
              0.9016727
                            0.07135036
                                            0.02697695
## ID:18
              0.9016727
                            0.07135036
                                            0.02697695
## ID:19
              0.9016727
                            0.07135036
                                            0.02697695
##
                        level2
##
                        mo1
                                  ex1
                                             es1
  internalState1 0.4130141 0.1031514 0.4838346
##
##
                        mo2
                                   ex2
                                             es2
## internalState2 0.0867179 0.02424808 0.889034
##
##
                       mo3
                                 ex3
## internalState3 0.315086 0.4421371 0.242777
##
```

These estimates are virtually identical to Leos-Barajas *et al.* (2017); the only (very slight) difference is in the estimates for the coarse-scale initial distribution ($\boldsymbol{\delta}^{(0)}$) because, unlike in Leos-Barajas *et al.* (2017), the forward algorithm in momentuHMM (Eq. 1) includes a state transition between time steps t = 0 and t = 1.

As usual, we can check pseudo-residuals using plotPR (Figure 15):

plotPR(hhmm)

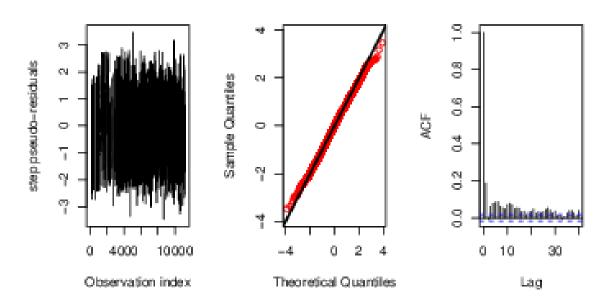


Figure 15. Pseudo-residual plot for the HHMM garter snake example.

and simulate from our fitted HHMM using simHierData:

```
##
    Transition probability matrix formula: ~0 + I((level == "1") * 1) +
##
I((level == "2i") * 1) + I((level == "2") * 1)
##
##
    Initial distribution formula:
## DONE
head(simHHMM)
##
     ID level
                step
                            x y states
## 1
     1
          1
                   NA
                            NA NA
     1
          2i
## 2
                   NA
                            NA NA
                                       6
     1
          2 1.992639 0.000000 0
                                       6
## 3
           2 1.182153 1.992639 0
                                       5
## 4 1
## 5
     1
          2 1.045767 3.174792 0
                                       5
        2 1.285761 4.220559 0
                                       6
## 6
```

3.10.3 Atlantic cod

Now we will demonstrate how HHMMs with data streams observed at multiple time scales can be fitted using momentuHMM. In their Atlantic cod example, Adam et al. (2019) fit a 9-state HHMM to coarse-scale horizontal (i.e., step length and turn angle) and fine-scale vertical movement data. The coarse-scale states were "resting/foraging" (hereafter "resForage"), "mobile/foraging" (hereafter "mobForage"), and "travelling/migrating" (hereafter "transit"), each of which was composed of three fine-scale states. To begin our analysis, we must first load and prepare the data (available for download from Adam et al. 2019):

```
# load the data from Adam et al
load("Atlantic_cod_data_set.RData")
```

```
time=0)
### add extra rows for fine-scale data
# level=1 indicates when coarse-scale behavior switching can occur
# level=2i indicates start of each fine-scale interval
# level=2 indicates when fine-scale behavior switching can occur
codData <- NULL
timeSeq <- seq(from=0,to=23+5/6,length=144) # time of day covariate
for(i in 1:nrow(data)){
  fineInd <- data.frame(level="2",
                        step=NA,
                        angle=NA,
                        vertical=verticals[[i]],
                        time=timeSeq)
  tmp <- rbind(data[i,,drop=FALSE],</pre>
               data.frame(level="2i",
                          step=NA,
                          angle=NA,
                          vertical=NA,
                          time=0),
               fineInd)
  codData <- rbind(codData,tmp)</pre>
# prepare hierarchical data
codData <- prepData(codData, coordNames=NULL,</pre>
                    covNames="time",
                    hierLevels=c("1","2i","2"))
head(codData)
##
                       step angle vertical
                                                time
                 1 5.236266
                               NA
                                        NA 0.000000
## 1 Animal1
## 2 Animal1
                2i
                        NA
                               NA
                                        NA 0.000000
## 3 Animal1
               2
                       NA NA 0.1285 0.0000000
## 4 Animal1
                2
                       NA
                            NA 0.0499 0.1666667
## 5 Animal1
                 2
                       NA
                            NA 0.1417 0.3333333
## 6 Animal1
                            NA 0.1713 0.5000000
                       NA
# data summary
summary(codData,dataNames=names(codData)[-1])
## Hierarchical HMM data for 1 individual:
##
```

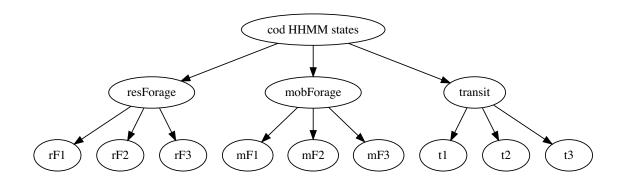
```
## Animal1 -- 42486 observations
##
##
## Data summaries:
##
   level
##
                    step
                                  angle
                                                 vertical
   1 : 291
                    : 0.21
                               Min. :-3.12
                                                    : 0.000
##
              Min.
                                               Min.
   2i:
        291 1st Qu.: 2.86
                               1st Qu.:-0.36
                                               1st Qu.: 0.083
##
   2:41904
              Median : 5.49
                               Median: 0.01
                                               Median : 0.182
##
              Mean
                    : 8.24
                               Mean
                                    :-0.03
                                               Mean
                                                    : 0.418
              3rd Qu.:11.89
                               3rd Qu.: 0.34
##
                                               3rd Qu.: 0.440
                     :31.49
                              Max. : 3.12
##
              Max.
                                               Max.
                                                     :18.223
              NA's
                    :42196
                              NA's :42197
                                               NA's
                                                     :582
##
        time
##
   Min. : 0.0
##
##
   1st Qu.: 5.7
   Median:11.8
##
##
   Mean
          :11.8
##
   3rd Qu.:17.8
##
   Max.
          :23.8
##
```

From sections 3.10.1 and 3.10.2, we should now be familiar with how to specify HHMMs with state transitions at multiple time scales. We will therefore focus on how to accommodate data streams that are observed at multiple time scales here, but complete details and code for fitting this model can be found in the "codExample.R" script in the momentuHMM "vignettes" source directory (or at https://github.com/bmcclintock/momentuHMM). First we specify the hierarchical nature of the states as a data.tree Node:

```
### define hierarchical HMM
# states 1-3 = coarse state 1 (resident/foraging)
# states 4-6 = coarse state 2 (mobile/foraging)
# states 7-9 = coarse state 3 (travelling/migrating)
hierStates <- data.tree::Node$new("cod HHMM states")
hierStates$AddChild("resForage") # resident/foraging
hierStates$resForage$AddChild("rF1", state=1)
hierStates$resForage$AddChild("rF2", state=2)
hierStates$resForage$AddChild("rF3", state=3)
hierStates$AddChild("mobForage") # mobile/foraging</pre>
```

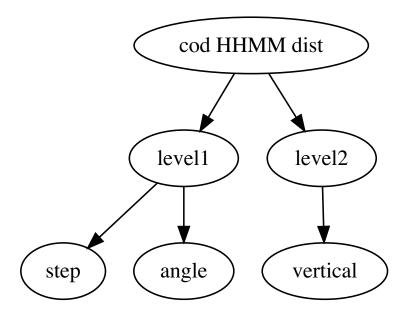
```
hierStates$mobForage$AddChild("mF1", state=4)
hierStates$mobForage$AddChild("mF2", state=5)
hierStates$mobForage$AddChild("mF3", state=6)
hierStates$AddChild("transit") # travelling/migrating
hierStates$transit$AddChild("t1", state=7)
hierStates$transit$AddChild("t2", state=8)
hierStates$transit$AddChild("t3", state=9)

plot(hierStates)
```



Next we specify the hierarchical nature of the data streams as a data.tree Node:

```
# data stream distributions
# level 1 = coarse level (step="gamma", angle="vm")
# level 2 = fine level (vertical="gamma")
hierDist <- data.tree::Node$new("cod HHMM dist")
hierDist$AddChild("level1")
hierDist$level1$AddChild("step", dist="gamma")
hierDist$level1$AddChild("angle", dist="vm")
hierDist$AddChild("level2")
hierDist$level2$AddChild("vertical", dist="gamma")</pre>
```



We then constrain the fine-scale states within each coarse-scale state to have the same parameters for the "step" and "angle" distributions using the DM argument:

```
nbStates <- length(hierStates$Get("state",filterFun=data.tree::isLeaf))</pre>
# constrain coarse-scale parameters for fine-scale states
DM <- list(step=matrix(kronecker(diag(6),c(1,1,1)),</pre>
                        nrow=2*nbStates,
                        ncol=6,
                        dimnames=list(paste0(rep(c("mean_","sd_"),each=nbStates)
                                              ,1:nbStates),
                                       c(paste0(rep(c("mean_", "sd_"), each=3),
                                                1:length(hierStates$children),
                                                ":(Intercept)")))))
DM$angle <- DM$step
dimnames(DM$angle) <- list(paste0(rep(c("mean_","concentration_"),each=nbStates)</pre>
                                    ,1:nbStates),
                            c(paste0(rep(c("mean_","concentration_"),each=3),
                                      1:length(hierStates$children),
                                      ":(Intercept)")))
```

and obtain starting values on the working scale using getParDM:

```
### defining start values based on those reported by Adam et al
hm.mu0 \leftarrow c(5.482, 6.786, 14.914)
hm.sigma0 \leftarrow c(4.27, 4.714, 11.242)
ha.mu0 \leftarrow c(0.011, -0.299, 0.044)
ha.kappa0 \leftarrow c(1.571, 1.426, 2.15)
vm.mu0 <- vm.sigma0 <- vm.pi0 <- list()</pre>
vm.mu0[[1]] \leftarrow c(0.116, 0.303, 0.691)
vm.mu0[[2]] \leftarrow c(0.109, 0.056, 0.351)
vm.mu0[[3]] \leftarrow c(0.125, 0.514, 1.987)
vm.sigma0[[1]] \leftarrow c(0.096, 0.261, 0.636)
vm.sigma0[[2]] \leftarrow c(0.043, 0.047, 0.342)
vm.sigma0[[3]] \leftarrow c(0.109, 0.462, 1.878)
vm.pi0[[1]] \leftarrow c(0.014, 0.003, 1.050e-06)
vm.pi0[[2]] \leftarrow c(1.791e-08, 0.035, 0.002)
vm.pi0[[3]] \leftarrow c(0.012, 2.933e-04, 3.462e-09)
Par0 <- list(step=c(rep(hm.mu0,each=3),rep(hm.sigma0,each=3)),
               angle=c(rep(ha.mu0,each=3),rep(ha.kappa0,each=3)),
               vertical=c(unlist(vm.mu0),unlist(vm.sigma0),unlist(vm.pi0)))
# starting values for data stream parameters on the working scale
Par <- getParDM(codData,</pre>
                  hierStates=hierStates,
                  hierDist=hierDist,
                  Par=Par0,
                  DM=DM,
                  estAngleMean = list(angle=TRUE))
```

Adam et al. (2019) included a periodic time-of-day covariate on the fine-scale state transition probabilities, and we specify this via the hierFormula argument:

```
# define hierarchical t.p.m. formula(s)
hierFormula <- data.tree::Node$new("cod HHMM formula")
hierFormula$AddChild("level1", formula=~1)
hierFormula$AddChild("level2", formula=~cosinor(time, period=24))</pre>
```

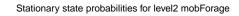
All that remains is (optionally) specifying starting values for the initial distribution (hierDelta) and t.p.m. (hierBeta) parameters, and we are now ready to fit the HHMM:

The resulting estimates are virtually identical to Adam et al. (2019); the slight differences are attributable to: 1) the forward algorithm in momentuHMM (Eq. 1) includes a state transition between time steps t = 0 and t = 1; and 2) momentuHMM uses the lowest fine-scale state index for each coarse-scale state as the mlogit-link reference state for the initial distribution and t.p.m.Nevertheless, we can see that the estimated stationary probabilities as a function of time of day are very similar (Figure 16).

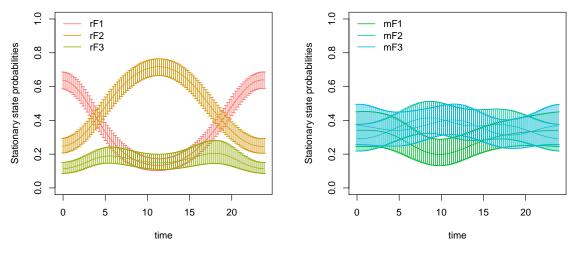
3.10.4 Horn shark

For our final HHMM example, we'll quickly demonstrate how the horn shark example from Adam et al. (2019) can be fitted in momentuHMM. The data streams in this example consist of coarse-scale categorical step lengths (stepCat) based on estimated geopositions at 2 second intervals over 194 distinct segments and, within each 2 second interval, fine-scale accelerometer data that were summarized as 50 sequential values of overall dynamic body acceleration (odba). The analysis included 8 categories for step length to construct a so-called histogram distribution of step lengths, where category 1 indicates zero step lengths and categories 2 – 8 were defined by increasing cutoffs at 0.00075, 0.00125, 0.00175, 0.00225, 0.00275, 0.00325, and 0.00375 m, respectively. The 9-state HHMM included three coarse-scale states ("activity", "resting", and "transit"), each composed of three fine-scale states.

First we load and prepare the data (available for download from Adam et al. 2019):







Stationary state probabilities for level2 transit

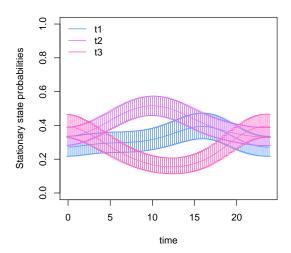


Figure 16. Stationary distributions of the fine-scale state processes for an Atlantic cod as a function of time of day for the coarse-scale states corresponding to "resting/foraging" (top-left panel), "mobile/foraging" (top-right panel), and "travelling/migrating" (bottom panel).

```
load("horn_shark_data_set.RData")
# coarse-scale data
data <- data.frame(ID=unlist(mapply(function(x) rep(paste0("seg",x),</pre>
                                                       nrow(steps[[x]])-1),
                                      1:length(steps))),
                    level="1".
                    steps=unlist(lapply(steps,function(x) x$steps[-nrow(x)])),
                    stepCat=unlist(lapply(steps,function(x) x$cats[-nrow(x)])),
                    odbas=NA)
data$stepCat[which(is.na(data$steps))] <- NA</pre>
### add extra rows for fine-scale data
# level=1 indicates when coarse-scale behavior switching can occur
# level=2i indicates start of each fine-scale interval
# level=2 indicates when fine-scale behavior switching can occur
odbas <- unlist(odbas)</pre>
sharkData <- NULL
for(i in 1:nrow(data)){
  fineInd <- data.frame(ID=data$ID[i],</pre>
                         level="2",
                         steps=NA,
                         stepCat=NA,
                         odbas=odbas[(i-1)*50+1:50])
  tmp <- rbind(data[i,,drop=FALSE],</pre>
                data.frame(ID=data$ID[i],
                           level="2i",
                           steps=NA,
                           stepCat=NA,
                           odbas=NA),
                fineInd)
  sharkData <- rbind(sharkData,tmp)</pre>
# prepare hierarchical data
sharkData <- prepData(sharkData,coordNames=NULL,</pre>
                       hierLevels=c("1","2i","2"))
head(sharkData)
       ID level
                       steps stepCat
                                           odbas
## 1 seg1 1 0.001447295
                                              NA
```

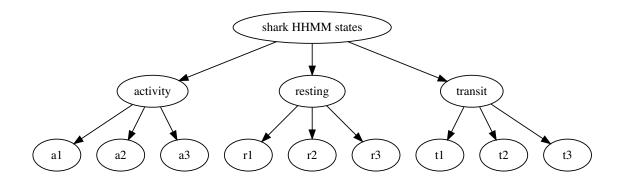
load the data from Adam et al

```
## 2 seg1
              2i
                           NA
                                    NA
## 3 seg1
               2
                           NA
                                    NA 0.07733020
               2
## 4 seg1
                           NA
                                    NA 0.07424251
## 5 seg1
               2
                                    NA 0.07866384
                           NΑ
               2
## 6 seg1
                                    NA 0.07899367
                           NA
```

Note that because the 194 segments were observed irregularly in bouts of time over the coarse of one night, Adam et al. (2019) essentially treated each segment as a different track whereby the HHMM "resets" at the beginning of each segment; this can be accomplished in momentuHMM by simply assigning each segment its own ID as was done above.

Next we define the hierarchical nature of the states and data streams:

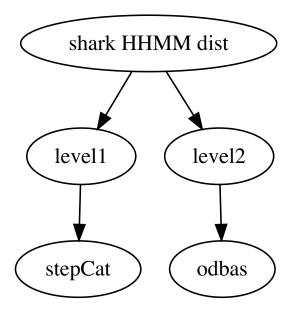
```
### define hierarchical HMM
# states 1-3 = coarse state 1 (high activity)
# states 4-6 = coarse state 2 (resting)
# states 7-9 = coarse state 3 (travelling)
hierStates <- data.tree::Node$new("shark HHMM states")
hierStates$AddChild("activity") # zero distance travelled, high activity
hierStates$activity$AddChild("a1", state=1)
hierStates$activity$AddChild("a2", state=2)
hierStates$activity$AddChild("a3", state=3)
hierStates$AddChild("resting") # zero distance travelled, low activity
hierStates$resting$AddChild("r1", state=4)
hierStates$resting$AddChild("r2", state=5)
hierStates$resting$AddChild("r3", state=6)
hierStates$AddChild("transit") # travelling
hierStates$transit$AddChild("t1", state=7)
hierStates$transit$AddChild("t2", state=8)
hierStates$transit$AddChild("t3", state=9)
plot(hierStates)
```



```
nbStates <- length(hierStates$Get("state",filterFun=data.tree::isLeaf))
nCat <- 8 # number of stepCat categories

# data stream distributions
# level 1 = coarse level (stepCat="cat8")
# level 2 = fine level (odbas="gamma")
hierDist <- data.tree::Node$new("shark HHMM dist")
hierDist$AddChild("level1")
hierDist$level1$AddChild("stepCat", dist=pasteO("cat",nCat))
hierDist$AddChild("level2")
hierDist$level2$AddChild("odbas", dist="gamma")

plot(hierDist)</pre>
```



This is the first example in the vignette that uses a categorical data stream probability distribution, so it is perhaps worth describing this in a little more detail. When specifying categorical distributions, the number of categories must be indicated. In this case, there are 8 stepCat categories, so we specify this as cat8. Generally, categorical distributions are specified as pasteO("cat",nCat), where nCat is an integer greater than 2 (note that a categorical distribution with only 2 categories is simply a Bernoulli distribution). The categorical distribution parameters are nCat probabilities that sum to 1, so the mlogit link is used and only nCat -1 working parameters are estimated in order to obtain the nCat categorical probabilities on the real scale.

Both the "activity" and "resting" coarse-scale states were assumed to have zero distance travelled (i.e., stepCat = 1), while the "transit" state was assumed to have > 0 distance travelled (i.e., $stepCat \in 2, ..., 8$). We therefore need to constrain the categorical step length probabilities for each fine-scale state within each coarse-scale state accordingly:

```
### starting values based on Adam et al mu0 <- c(0.191, 0.323, 0.721, 0.084, 0.15, 0.228, 0.094, 0.191, 0.39) sd0 <- c(0.047, 0.051, 0.248, 0.021, 0.025, 0.033, 0.026, 0.039, 0.159) probs0 <- c(1e+10, -1e+10, 0.958, 5.064, 3.261, 4.021, 0.473, 2.568)
```

```
# constrain coarse-scale parameters for fine-scale states
DM <- list(stepCat=matrix(cbind(c(rep(c(1,1,1),2),</pre>
                                     rep(0,(nCat-1)*nbStates-6)),
                                   kronecker(diag(nCat-1),
                                              c(0,0,0,0,0,0,1,1,1))),
                         nrow=(nCat-1)*nbStates,
                         ncol=8,
                         dimnames=list(paste0(rep(paste0("prob",
                                                            1: (nCat-1),
                                                            "_"),
                                                    each=nbStates),
                                                1:nbStates),
                                        c(paste0(c("prob1_12",
                                                    paste0("prob",
                                                            1: (nCat-1),
                                                            "_3")),
                                                  ":(Intercept)")))))
head(DM$stepCat,9)
            prob1_12:(Intercept) prob1_3:(Intercept) prob2_3:(Intercept)
##
## prob1_1
                                                      0
                                                                            0
                                                      0
                                                                            0
## prob1_2
                                1
                                1
                                                      0
                                                                            0
## prob1_3
## prob1_4
                                1
                                                      0
                                                                            0
## prob1_5
                                1
                                                      0
                                                                            0
## prob1_6
                                1
                                                      0
                                                                            0
## prob1_7
                                0
                                                      1
                                                                            0
## prob1_8
                                0
                                                      1
                                                                            ()
                                0
                                                      1
                                                                            0
## prob1_9
##
           prob3_3:(Intercept) prob4_3:(Intercept) prob5_3:(Intercept)
                                                     0
## prob1_1
                               0
                                                                           0
                                                     0
                                                                           0
## prob1_2
                               0
                               0
                                                     0
                                                                           0
## prob1_3
                                                     0
                                                                           0
## prob1_4
                               0
## prob1_5
                               0
                                                     0
                                                                           0
## prob1_6
                               0
                                                     0
                                                                           0
## prob1_7
                               0
                                                     0
                                                                           0
## prob1_8
                               0
                                                     0
                                                                           0
## prob1_9
                               0
                                                     0
                                                                           0
            prob6_3:(Intercept) prob7_3:(Intercept)
## prob1_1
                               0
                                                     0
                               0
                                                     0
## prob1_2
## prob1_3
                               ()
                                                     0
```

```
## prob1_4
                                 0
                                                       0
## prob1_5
                                 0
                                                       0
                                                        0
## prob1_6
                                 0
                                 ()
                                                       0
## prob1_7
                                 0
                                                       0
## prob1_8
                                 0
                                                        0
## prob1_9
Par0 <- list(stepCat = probs0,
              odbas = c(mu0, sd0))
fixPar \leftarrow list(stepCat=c(1.e+10,-1.e+10,rep(NA,6)))
```

By fixing the working parameter corresponding to the probability of observing step length category 1 (prob1) for coarse-scale state 1 (fine-scale states 1-3) and coarse-scale state 2 (fine-scale states 4-6) to a very large positive number, we have effectively fixed prob1 = 1 for these states. Likewise, by fixing the working parameter corresponding to prob1 for coarse-scale state 3 (fine-scale states 7-9) to a very large negative number, we have effectively fixed prob1 = 0 for this state.

All that remains is (optionally) specifying starting values for the initial distribution (hierDelta) and t.p.m. (hierBeta) parameters, and let's check our model specification before fitting using checkPar0:

```
### t.p.m. starting values based on Adam et al
hierBeta <- data.tree::Node$new("shark beta")
hierBeta$AddChild("level1",
   beta=matrix(c(-0.651, -0.169, -1.884, -0.369, -1.596, -0.737),
               ncol=length(hierStates$children)
                    *(length(hierStates$children)-1)))
hierBeta$AddChild("level2")
hierBeta$level2$AddChild("activity",
   beta=matrix(c(-2.902, -14.032, 3.059, -1.37, 8.098, 11.66),
               ncol=length(hierStates$activity$children)
                    *(length(hierStates$activity$children)-1)))
hierBeta$level2$AddChild("resting",
   beta=matrix(c(-3.264, -14.279, 3.107, 0.252, 13.861, 16.468),
               ncol=length(hierStates$resting$children)
                    *(length(hierStates$resting$children)-1)))
hierBeta$level2$AddChild("transit",
   beta=matrix(c(-3.21, -21.32, 3.463, -0.598, 14.636, 17.811),
               ncol=length(hierStates$transit$children)
```

```
*(length(hierStates$transit$children)-1)))
### initial distribution starting values based on Adam et al
hierDelta <- data.tree::Node$new("shark delta")
hierDelta$AddChild("level1",
   delta=matrix(c(0.582, 2.894),
               ncol=length(hierStates$children)-1))
hierDelta$AddChild("level2")
hierDelta$level2$AddChild("activity",
   delta=matrix(c(-0.001, -1.1),
               ncol=length(hierStates$activity$children)-1))
hierDelta$level2$AddChild("resting",
   delta=matrix(c(-0.103, -0.105),
               ncol=length(hierStates$resting$children)-1))
hierDelta$level2$AddChild("transit",
   delta=matrix(c(0.24, -0.777),
               ncol=length(hierStates$transit$children)-1))
# check hierarchical model specification and parameters
checkPar0(sharkData,
         hierStates=hierStates,
         hierDist=hierDist,
         Par0=Par0,
         DM=DM,
         hierBeta=hierBeta,
         hierDelta=hierDelta.
         fixPar=fixPar)
##
## Regression coeffs for stepCat parameters:
      prob1_12:(Intercept) prob1_3:(Intercept) prob2_3:(Intercept)
                                         -1e+10
                                                              0.958
                      1e+10
## [1,]
      prob3_3:(Intercept) prob4_3:(Intercept) prob5_3:(Intercept)
##
## [1,]
                     5.064
                                         3.261
                                                            4.021
      prob6_3:(Intercept) prob7_3:(Intercept)
## [1,]
                    0.473
                                         2.568
##
## odbas parameters:
## -----
          a1 a2 a3 r1 r2 r3 t1 t2
## mean 0.191 0.323 0.721 0.084 0.150 0.228 0.094 0.191 0.390
## sd 0.047 0.051 0.248 0.021 0.025 0.033 0.026 0.039 0.159
```

```
##
##
##
## Regression coeffs for the transition probabilities (beta):
  ______
 ----- level1 ------
                   1 -> 4 1 -> 7 4 -> 1 4 -> 7 7 -> 4
##
## I((level == "1") * 1) -0.651 -0.169 -1.884 -0.369 -1.596 -0.737
##
## ------ level2 ------
                   1 -> 2 1 -> 3 2 -> 2 2 -> 3 3 -> 2 3 -> 3
##
## I((level == "2") * 1) -2.902 -14.032 3.059 -1.37 8.098 11.66
##
                   4 -> 5 4 -> 6 5 -> 5 5 -> 6 6 -> 5 6 -> 6
##
## I((level == "2") * 1) -3.264 -14.279 3.107 0.252 13.861 16.468
##
                   7 -> 8 7 -> 9 8 -> 8 8 -> 9 9 -> 8 9 -> 9
##
## I((level == "2") * 1) -3.21 -21.32 3.463 -0.598 14.636 17.811
##
##
##
##
## Regression coeffs for the initial distribution (delta):
  _____
## ------ level1 ------
##
           state 4 state 7
## (Intercept) 0.582 2.894
##
## ----- level2 ------
##
                    state 2 state 3
## I((level == "2i") * 1) -0.001 -1.1
##
##
                    state 5 state 6
## I((level == "2i") * 1) -0.103 -0.105
##
##
                    state 8 state 9
## I((level == "2i") * 1) 0.24 -0.777
##
```

Everything checks out, so let's now fit the horn shark HHMM:

The resulting estimates are again very similar to Adam et al. (2019), with the slight differences attributable to: 1) the forward algorithm in momentuHMM (Eq. 1) includes a state transition between time steps t=0 and t=1; and 2) Adam et al. (2019) assume the initial distributions for each level of the hierarchy are equal to the stationary distributions. Nevertheless, we can see that the estimated t.p.m. and stationary distributions are very similar:

```
# t.p.m.
round(trProbs12$level1$gamma[,,1],3)
##
        activity resting transit
## activity
          0.423
               0.221
                     0.357
          0.082
## resting
               0.543
                     0.375
## transit
          0.121
               0.285
                     0.594
# stationary distribution
round(stats12[[1]]$level1[1,],3)
## activity resting transit
##
    0.153
          0.371
                0.477
# t.p.m.
lapply(trProbs12$level2,function(x) round(x$gamma[,,1],3))
```

```
## $activity
         a1
               a2
                     a3
## a1 0.948 0.052 0.000
## a2 0.044 0.944 0.011
  a3 0.000 0.028 0.972
##
## $resting
               r2
                     r3
##
         r1
## r1 0.963 0.037 0.000
## r2 0.041 0.907 0.052
## r3 0.000 0.069 0.931
##
## $transit
##
               t2
                     t3
         t1
## t1 0.961 0.039 0.000
## t2 0.030 0.954 0.016
## t3 0.000 0.040 0.960
# stationary distribution
lapply(stats12[[1]]$level2,function(x) round(x[1,],3))
## $activity
      a1
            a2
                  a3
## 0.377 0.443 0.181
##
## $resting
##
      r1
            r2
                  r3
## 0.385 0.349 0.265
##
## $transit
            t2
##
      t1
                  t3
## 0.353 0.459 0.188
************************************
```

3.11 Simulating constrained movement

In section 3.3 we briefly demonstrated how potential functions can be used within a bivariate normal random walk to model loggerhead turtle movements relative to ocean surface currents. Here we'll show how this approach can be used in simData to simulate movement data subject to barriers or other constraints (e.g. land for marine animals).

To accomplish this, we'll rely on the forest raster that is automatically loaded with momentuHMM. We'll start by pretending that forest cells with values > 0 are "land" and all others are "water". Then we'll create a new raster named boundary containing the shortest distance from land to water using raster::distance:

```
boundary <- forest
boundary[boundary>0] <- NA
boundary <- raster::distance(boundary)
names(boundary) <- "boundary"</pre>
```

Next we'll calculate the gradients in the x- and y-directions for inclusion as covariates in our potential function using ctmcmove::rast.grad:

```
# boundary needs to have a CRS for ctmcmove::rast.grad
proj4string(boundary) <- sp::CRS("+init=epsg:4326")

# compute gradients in x- and y- directions
grad <- ctmcmove::rast.grad(boundary)
grad.x <- grad$rast.grad.x
grad.y <- grad$rast.grad.y</pre>
```

Now we're ready to simulate our bivariate normal random walk model including these gradients in the potential function:

```
mvnCoords="mu", initialPosition=c(25000,75000))
plot(simBound,dataNames=c("mu.x","mu.y"),ask=FALSE)
plot(boundary$boundary)
points(simBound$mu.x,simBound$mu.y,type="l")
```

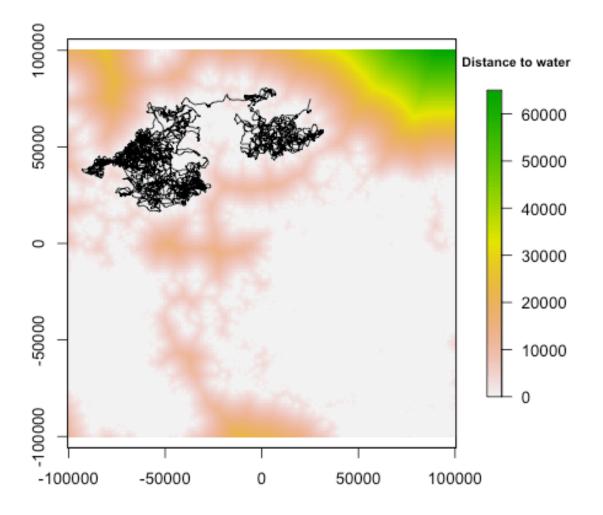


Figure 17. Simulated track from a bivariate normal random walk model with movements repulsed from "land" using a potential function.

The model specified in DM is identical to Eq. 10, except we have replaced the ocean surface current velocities with the gradients for shortest distance to water in the x- and

y-directions (grad.x and grad.y, respectively). As we can see in Figure 17, the track is repelled from "land" and tends to stay in the "water". This strong attraction to water owes to the large negative values for the coefficients corresponding to grad.x and grad.y.

4 Discussion

Here we have introduced version 1.5.0 of the R package momentuHMM and demonstrated some of its capabilities for conducting multivariate HMM analyses with animal location, auxiliary biotelemetry, and environmental data. The package allows for fitting (and simulating from) a suite of biased and correlated random walk movement process models (e.g. McClintock et al. 2012), can be used for an unlimited number of data streams and latent behavior states, includes multiple imputation methods to account for measurement error, temporal irregularity, and other forms of missing data that would otherwise be prohibitive to maximum likelihood analysis, and integrates seamlessly with rasters to facilitate spatio-temporal covariate modelling. Because the package incorporates biased random walks, it can also be used to implement group dynamic models (e.g. Langrock et al. 2014). The package therefore greatly expands on available software and facilitates the incorporation of more ecological and behavioral realism for hypothesis-driven analyses of animal movement that account for many of the challenges commonly associated with telemetry data. While many of the features of momentuHMM were motivated by animal movement data, we note that the package is not limited to location data and can be used for analyzing any type of data that is amenable to (multivariate) HMMs.

Model fitting in momentuHMM is relatively fast because the forward algorithm (Eq. 1) is coded in C++. Because multiple imputations are completely parallelizable, with sufficient processing power computation times for analyses that account for measurement error, temporal irregularity, or other forms of missing data need not be longer than that required to fit a single HMM. However, computation times will necessarily be longer as the number of states and/or parameters increase. For example, momentuHMM required about 1 hr to fit a single HMM with N=6 states, seven data streams, and T=7414 time steps (McClintock 2017).

As in any maximum likelihood analysis based on numerical optimization, compu-

tation times will also depend on the starting values (ParO and betaO). Specifying "good" starting values is arguably the most challenging aspect of model fitting in momentuHMM, particularly for the working scale coefficients when using covariates. The getPar, getParO, getParDM, and checkParO functions are designed to help with the specification of starting values, and the retryFits argument in crawlWrap, fitHMM, and MIfitHMM will re-optimize based on random perturbations of the parameters to help explore the likelihood surface and diagnose convergence to local maxima. Optimization for the circular-linear regression link function (tan(mean/2); see Table 2) in particular can be prone to local minima, so users are encouraged to explore a range of starting values when fitting these models.

While momentuHMM includes functions for drawing realizations of the position process based on the CTCRW model of Johnson et al. (2008), this is but one of many methods for performing the first stage of multiple imputation. Realizations of the position process from any movement model that accounts for measurement error and/or temporal irregularity (e.g. Calabrese et al. 2016; Gurarie et al. 2017) could be passed to MIfitHMM for HMM-type analyses in the second stage. Multiple imputation methods also need not be limited to these telemetry error scenarios. For example, conventional missing data could also be imputed using standard techniques (Rubin & Schenker 1986), thereby allowing the investigation of non-random mechanisms for missingness that can be problematic if left unaccounted for in HMMs.

There remain many potential avenues for refining and extending the capabilities of momentuHMM. Computation times could likely be improved by further optimizing the R and C++ code for speed. Notable extensions include hidden semi-Markov models and random effects on data stream probability distribution parameters (Zucchini et al. 2016). We would also like to incorporate additional parameters for change-point thresholds and the locations of activity centers instead of requiring that they be pre-specified (and potentially compared using AIC or other model selection criteria) as in grey seal example. Lastly, it is relatively straightforward to add additional probability distributions, and we are pleased to do so upon request. Practitioners interested in additional features for momentuHMM are encouraged to contact the authors.

Acknowledgments

We are grateful to R. Scott, B. Godley, M. Godfrey, J. Sudre, and North Carolina Aquariums for providing the data used in our turtle example. We are also grateful to the many authors who made their data publicly available for use in our examples (Wall et al. 2014; Pirotta et al. 2018; Isojunno et al. 2017; Leos-Barajas et al. 2017; Adam et al. 2019). The findings and conclusions in this vignette are those of the author(s) and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Any use of trade, product, or firm names does not imply an endorsement by the US Government.

References

- Adam, T., Griffiths, C.A., Leos-Barajas, V., Meese, E.N., Lowe, C.G., Blackwell, P.G., Righton, D. & Langrock, R. (2019) Joint modelling of multi-scale animal movement data using hierarchical hidden markov models. *Methods in Ecology and Evolution*.
- Beyer, H.L., Morales, J.M., Murray, D. & Fortin, M.J. (2013) The effectiveness of Bayesian state-space models for estimating behavioural states from movement paths. *Methods in Ecology and Evolution*, 4, 433–441.
- Brillinger, D.R., Preisler, H.K., Ager, A.A. & Kie, J. (2012) The use of potential functions in modelling animal movement. *Selected Works of David Brillinger*, pp. 385–409. Springer.
- Calabrese, J.M., Fleming, C.H. & Gurarie, E. (2016) ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, 7, 1124–1132.
- Cornelissen, G. (2014) Cosinor-based rhythmometry. Theoretical Biology and Medical Modelling, 11, 16.
- Costa, D.P., Robinson, P.W., Arnould, J.P., Harrison, A.L., Simmons, S.E., Hassrick, J.L., Hoskins, A.J., Kirkman, S.P., Oosthuizen, H., Villegas-Amtmann, S. et al. (2010) Accuracy of argos locations of pinnipeds at-sea estimated using fastloc gps. *PloS one*, **5**, e8677.

- DeRuiter, S.L., Langrock, R., Skirbutas, T., Goldbogen, J.A., Calambokidis, J., Friedlaender, A.S. & Southall, B.L. (2017) A multivariate mixed hidden Markov model to analyze blue whale diving behaviour during controlled sound exposures. *The Annals of Applied Statistics*, 11, 362–392.
- Gilbert, P. & Varadhan, R. (2016) numDeriv: Accurate Numerical Derivatives. R package version 2016.8-1.
- Glur, C. (2018) data.tree: General Purpose Hierarchical Data Structure. R package version 0.7.8.
- Gurarie, E., Fleming, C.H., Fagan, W.F., Laidre, K.L., Hernández-Pliego, J. & Ovaskainen, O. (2017) Correlated velocity models as a fundamental unit of animal movement: synthesis and applications. *Movement Ecology*, 5, 13.
- Hijmans, R.J. (2016a) geosphere: Spherical Trigonometry. R package version 1.5-5.
- Hijmans, R.J. (2016b) raster: Geographic Data Analysis and Modeling. R package version 2.5-8.
- Hooten, M.B., Johnson, D.S., McClintock, B.T. & Morales, J.M. (2017) Animal Movement: Statistical Models for Telemetry Data. CRC Press.
- Hooten, M.B., Scharf, H.R. & Morales, J.M. (2019) Running on empty: recharge dynamics from animal movement data. *Ecology letters*, **22**, 377–389.
- Isojunno, S., Sadykova, D., DeRuiter, S., Curé, C., Visser, F., Thomas, L., Miller, P.J.O. & Harris, C.M. (2017) Individual, ecological, and anthropogenic influences on activity budgets of long-finned pilot whales. *Ecosphere*, **8**, e02044.
- Johnson, D.S. (2017) crawl: Fit Continuous-Time Correlated Random Walk Models to Animal Movement Data. R package version 2.1.1.
- Johnson, D.S., London, J.M., Lea, M.A. & Durban, J.W. (2008) Continuous-time correlated random walk model for animal telemetry data. *Ecology*, **89**, 1208–1215.
- Jonsen, I.D., Flemming, J.M. & Myers, R.A. (2005) Robust state–space modeling of animal movement data. *Ecology*, **86**, 2874–2880.

- Langrock, R., Hopcraft, G., Blackwell, P., Goodall, V., King, R., Niu, M., Patterson, T., Pedersen, M., Skarin, A. & Schick, R. (2014) Modelling group dynamic animal movement. *Methods in Ecology and Evolution*, 5, 190–199.
- Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D. & Morales, J.M. (2012) Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology*, **93**, 2336–2342.
- Leos-Barajas, V., Gangloff, E.J., Adam, T., Langrock, R., Van Beest, F.M., Nabe-Nielsen, J. & Morales, J.M. (2017) Multi-scale modeling of animal movement and general behavior data using hidden markov models with hierarchical structures. *Journal of Agricultural, Biological and Environmental Statistics*, **22**, 232–248.
- McClintock, B.T. (2017) Incorporating telemetry error into hidden markov models of animal movement using multiple imputation. *Journal of Agricultural, Biological, and Environmental Statistics*, **22**, 249–269.
- McClintock, B.T., Johnson, D.S., Hooten, M.B., Ver Hoef, J.M. & Morales, J.M. (2014) When to be discrete: the importance of time formulation in understanding animal movement. *Movement Ecology*, **2**, 21.
- McClintock, B.T., King, R., Thomas, L., Matthiopoulos, J., McConnell, B.J. & Morales, J.M. (2012) A general discrete-time modeling framework for animal movement using multistate random walks. *Ecological Monographs*, **82**, 335–349.
- McClintock, B.T., London, J.M., Cameron, M.F. & Boveng, P.L. (2017) Bridging the gaps in animal movement: hidden behaviors and ecological relationships revealed by integrated data streams. *Ecosphere*, **8**, e01751.
- McClintock, B.T. & Michelot, T. (2018) momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*, **9**, 1518–1530.
- McClintock, B.T., Russell, D.J., Matthiopoulos, J. & King, R. (2013) Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. *Ecology*, **94**, 838–849.

- McKellar, A.E., Langrock, R., Walters, J.R. & Kesler, D.C. (2014) Using mixed hidden Markov models to examine behavioral states in a cooperatively breeding bird. *Behavioral Ecology*, **26**, 148–157.
- Michelot, T., Langrock, R., Bestley, S., Jonsen, I.D., Photopoulou, T. & Patterson, T.A. (2017) Estimation and simulation of foraging trips in land-based marine predators. *Ecology*, 98, 1932–1944.
- Michelot, T., Langrock, R. & Patterson, T.A. (2016) moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, 7, 1308–1315.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445.
- Pirotta, E., Edwards, E.W.J., New, L. & Thompson, P.M. (2018) Central place foragers and moving stimuli: A hidden-state model to discriminate the processes affecting movement. *Journal of Animal Ecology*, 87, 1116–1125.
- R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rivest, L.P., Duchesne, T., Nicosia, A. & Fortin, D. (2016) A general angular regression model for the analysis of data on animal movement in ecology. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, **65**, 445–463.
- Rubin, D.B. & Schenker, N. (1986) Multiple imputation for interval estimation from simple random samples with ignorable nonresponse. *Journal of the American Statistical Association*, **81**, 366–374.
- Sarda-Espinosa, A. (2017) dtwclust: Time Series Clustering Along with Optimizations for the Dynamic Time Warping Distance. R package version 3.1.2.
- Towner, A.V., Leos-Barajas, V., Langrock, R., Schick, R.S., Smale, M.J., Kaschke, T., Jewell, O.J.D. & Papastamatiou, Y.P. (2016) Sex-specific and individual preferences for hunting strategies in white sharks. *Functional Ecology*, **30**, 1397–1407.

- Wall, J., Wittemyer, G., LeMay, V., Douglas-Hamilton, I. & Klinkenberg, B. (2014) Elliptical time-density model to estimate wildlife utilization distributions. *Methods in Ecology and Evolution*, 5, 780–790.
- Whoriskey, K., Auger-Méthé, M., Albertsen, C.M., Whoriskey, F.G., Binder, T.R., Krueger, C.C. & Mills Flemming, J. (2017) A hidden markov movement model for rapidly identifying behavioral states from animal tracks. *Ecology and Evolution*, 7, 2112–2121.
- Zucchini, W., MacDonald, I.L. & Langrock, R. (2016) Hidden Markov Models for Time Series: An Introduction Using R. CRC Press.