Incorporating periodic variability in hidden Markov models for animal movement

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Abstract

Clustering time-series data into discrete groups can improve prediction as well as providing insight into the nature of underlying, unobservable states of the system. However, temporal variation in the probability that individuals occupy or move between groups can obscure such signals. We use finite mixture and hidden Markov models, two standard clustering techniques, to model high-resolution hourly movement data from Florida panthers (*Puma concolor coryi*). Allowing for temporal heterogeneity in transition probabilities, a straightforward but rarely explored model extension, resolves some shortcomings of current modeling frameworks and clarifies the behavioural patterns of panthers. More generally, incorporating previously neglected structure in statistical models can allow researchers to more accurately identify models of appropriate complexity.

Keywords: hidden Markov model, animal movement, temporal autocorrelation, temporal heterogeneity, Florida panther

1 Introduction

Given a sequence of animal movements observed directly or via telemetry, movement models aim to find a parsimonious description that can be used to understand past movements as well as predict future movements. Ecologists have long considered the effects of individual-level covariates (sex, age, nutritional status) and environmental covariates (habitat type, location of predators or prey) on movement (Patterson et al., 2008; McKenzie et al., 2009; Pal et al., 1998). More recently, modelers have developed hidden Markov models (HMMs) (Firle et al., 1998; Nathan et al., 2008; Langrock et al., 2012) — used in animal ecology under the rubric of the "multiphasic movement framework" (Fryxell et al., 2008) — that consider the effects of organisms' internal states; in particular, HMMs model animal movement as though individual animals' movement behaviour is determined by which of a discrete set of unobserved movement states (e.g. "foraging", "traveling", "resting") they currently occupy. Conditional on the state occupied by an individual, HMMs typically assume that animals follow a standard correlated walk model (Okubo, 1980; Turchin, 1998).

Ever-increasing capabilities of remote sensors are making movement data available over an ever-wider range of time scales, at both higher resolution (e.g. hourly data from GPS collars vs. daily or weekly fixes for radio or VHF collars) and longer extent (e.g. from a few days to significant fractions of a year, or longer). When analyzing such remote-sensing data, ecologists will more often have to account for temporal variability in movement behaviour at diurnal and seasonal scales that were previously not captured in the data.

HMMs have typically been used to model movements over short time scales, where the probability of transitioning between movement states is approximately constant. Changes in latent/hidden behavioural state/mode transition probabilities based on the local environment can be accounted for incorporating environmental covariates in the HMM (Patterson et al., 2009), or by more ad hoc comparisons between inferred states and environmental conditions (Fryxell et al., 2008). Schliehe-Diecks et al. (2012) consider temporal trends in behavioural transitions over the time scales of a six-hour observation period, but

in general ecologists have turned to other tools to describe behavioural changes over longer (diurnal, seasonal, or ontogenetic) time scales (Gurarie et al., 2009).

For movement behaviours that change on a fast time scale, such that movement behaviours recorded at successive observations are effectively independent, finite mixture models (FMM) — which can be considered a special case of HMMs where the probability of state occupancy is independent of the previous state — can adequately describe movement (Tracey et al., 2012). When movement varies over long time scales (relative to the time between observations) with little short-term persistence or correlation, movement could be well represented by FMMs where the occupancy probabilities change deterministically over time. Thus FMMs and HMMs, with or without temporal variation in the occupancy or transition probabilities, form a useful family of models for capturing changes in movement behaviour over a range of time scales.

Our primary goal in this paper is to introduce the use of HMMs with temporally varying transition probabilities – in particular, transition probabilities that follow a diurnal cycle – for modeling animal movement recorded over long time scales. In addition to simulation-based examples, we also re-analyze data from van de Kerk et al. (2015), who used temporally homogeneous hidden semi-Markov models (HSMMs: an extension of HMMs that allow flexible modelling of the distribution of *dwell times*, the lengths of consecutive occupancy of a behavioural state) to describe the movement and putative underlying behavioural states of Florida panthers (*Puma concolor coryi*).

van de Kerk et al. (2015) found that the best-fitting HSMMs incorporated a surprisingly large number of hidden behavioural states (as many as 6 for individuals with a large amount of available data); for practical reasons, they restricted their detailed analysis to models with only 3 underlying states. In contrast, most studies using HMM have chosen the number of underlying states

a priori, typically using either two (Schliehe-Diecks et al., 2012; McKellar et al., 2014; Langrock et al., 2012; Fryxell et al., 2008), or three states (Dean et al., 2012; Morales et al., 2004; Franke et al., 2006; van de Kerk et al., 2015). As van de Kerk et al. (2015) comment, and as we discuss further below, behavioural repertoires with more than three distinct states are difficult to interpret — one possible reason that other authors have not adopted van de Kerk et al.'s model-based approach to identifying the number of latent states.

Our second goal, therefore, is to explore whether van de Kerk et al.'s results might be driven at least in part by structural problems with their statistical model, i.e. the assumption of temporally homogeneous behaviour. When large data sets are available, information-theoretic model selection methods will typically choose complex, highly parameterized models; when there is only one way in which models can become more complex (e.g. by increasing the number of latent states), complexity that is present in the data but not accounted for in the model (e.g. spatial or temporal heterogeneity) can be misidentified as other forms of complexity. We predict that increasing volumes of data will increasingly lead researchers who are accustomed to fitting small models to sparse data into such traps. We examine whether allowing for diurnal variation in the Florida panther data leads to selection of models with smaller numbers of latent states; we also fit models to simulated data with varying numbers of latent states and degrees of temporal heterogeneity to test our conjecture that heterogeneity can be misidentified as behavioural complexity.

2 Methods

2.1 Data and previous analyses

GPS collars were fitted to 18 Florida panthers in 2005-2012 by Florida Fish and Wildlife and Conservation Commission staff using trained hounds and houndsmen. Of these animals, 13 had sufficient data to be used by van de Kerk et al. (2015). Here we focus on the four cats with the most data (all with approximately 10,000-15,000 observations: see Table 1 in Supplementary Material), in part because our goal is to understand the issues that arise when simple models are fitted to large data sets, and in part because the general trend in telemetry studies is toward larger data sets. As is typical in studies of animal movement, we took first differences of the data by decomposing contiguous sequences of hourly GPS coordinates into successive step lengths (in meters) and turning angles (in radians) (Turchin, 1998; van de Kerk et al., 2015).

van de Kerk et al. (2015) used hidden semi-Markov models (HSMM), an extension of HMM that permits explicit modelling of dwell times (Langrock et al., 2012), considering both Poisson and negative binomial distributions for dwell times. As shown by van de Kerk et al. (2015) (Figure S3b, top row, middle panel), the estimated shape parameter of the negative binomial dwell time distribution was typically close to $1 \approx 0.4 - 1.6$; confidence intervals were not calculated), implying that a geometric distribution (i.e., negative binomial with shape=1) might be adequate. In turn, this suggests that we might not lose much accuracy by reverting to a simpler HMM framework, which corresponds to making precisely this assumption.

van de Kerk et al. (2015) considered time-homogeneous models with a variety of candidate distributions — log-Normal, Gamma, and Weibull distributions for step lengths and von Mises and wrapped Cauchy distributions for the turning angle — concluding on the basis of the Akaike information criterion (AIC) that

Weibull step length and wrapped Cauchy turning angle distributions were best. Since our analysis aims for simplicity and qualitative conclusions rather than for picking the very best predictive model, we focus on models that treat each step as a univariate, log-Normally distributed observation, glossing over both the differences in shape between the three candidate step-length distributions and the effects of considering multivariate (step length plus turning angle) observations. However, we do briefly compare log-Normal and Weibull step-length distributions, with and without a von Mises-distributed turning angle included in the model (Figure 1). (Note that most movement analyses, including van de Kerk et al. (2015), are only partially multivariate, treating step length and turning angle at a particular time as independent observations while neglecting possible correlations between them.)

van de Kerk et al. (2015) used the Bayesian (Schwarz) information criterion (BIC) to test the relative penalized goodness of fit for models ranging from 2 to 6 latent states. In general, BIC values decreased as the number of states increased from 3 to 6 states, suggesting that the 6-state model was favoured statistically; however, the authors used 3-state models in most of their analyses for ease of biological interpretation. We follow van de Kerk et al. (2015) in using BIC-optimality (i.e., minimum BIC across a family of models) as the criterion for identifying the best model, because we are interested in explaining the data generation process by identifying the "true" number of underlying movement states. Using BIC also simplifies evaluation of model selection procedures; it is easier to test whether our model selection procedure has selected the model used to simulate the data, rather than testing whether it has selected the model with the minimal Kullback-Leibler distance (Richards, 2005). We recognize that ecologists will often be interested in maximizing predictive accuracy rather than selecting a true model, and that as usual in ecological systems the true

it occurs to me that we haven't really included any information about simulation testing in this version! We should probably add a short section if don't, then we should delete following sentence model will be far more complicated than any candidate model (Burnham and Anderson, 1998); we suspect that the qualitative conclusions stated here for BIC-optimality will carry over to analyses using AIC instead.

2.2 Model description

In a HMM, the joint likelihood of *emissions* (i.e., direct observations) $\mathbf{Y} = \mathbf{y}_1, ..., \mathbf{y}_T$ and a hidden state sequence $\mathbf{Z}, z_t \in \{1, ..., n\}, t = 1, ..., T$, given model parameters $\boldsymbol{\theta}$ and covariates $\mathbf{X}_{1:T} = \mathbf{x}_1, ..., \mathbf{x}_T$, can be written as:

$$P(\mathbf{Y}_{1:T}, \mathbf{Z}_{1:T} | \boldsymbol{\theta}, \mathbf{X}_{1:T}) = P(z_1 | \mathbf{x}_1) P(\mathbf{y}_1 | z_1, \mathbf{x}_1) \cdot \prod_{k=2}^{T} P(z_k | z_{k-1}, \mathbf{x}_k) P(\mathbf{y}_k | z_k, \mathbf{x}_k)$$

$$(1)$$

The emissions \mathbf{y}_i are boldfaced to denote that we may have a vector of observations at each time point (e.g., step length and turning angle). The model contains three distinct components:

Initial probability $P(z_1 = i|\mathbf{x}_1)P(\mathbf{y}_1|z_1, \mathbf{x}_1)$: the probability of state i at time t = 1 where the covariate is \mathbf{x}_1 , times the vector of observations \mathbf{y}_1 conditioned on covariates \mathbf{x}_1 and state z_1 .

Transition probability $P(z_k = j | z_{k-1} = i, \mathbf{x}_k)$: the probability of a transition from state i at time t = k - 1 to state j with covariate \mathbf{x}_k at time t = k.

Emission probability $P(\mathbf{y}_k|z_k, \mathbf{x}_k)$: a vector of observations \mathbf{y}_k conditioned on covariates \mathbf{x}_k at state z_k at time t = k.

Eq. 1 gives the likelihood of the observed sequence given (conditional on) a particular hidden sequence. In order to calculate the overall, unconditional

maybe give the for mula for number o parameters (constrained) for each model type here? (or marginal) likelihood of the observed sequence, we need to average over all possible hidden sequences. There are several efficient algorithms for computing the marginal likelihood and numerically estimating parameters (Zucchini and MacDonald, 2009); we use those implemented in the depmixS4 package for R (Visser and Speekenbrink, 2010; R Core Team, 2015).

For any n-state HMM, we need to define a $n \times n$ matrix that specifies the probabilities π_{ij} of being in movement states j at time t+1 given that the individual is in state i. The FMM is a special case of HMM where the probabilities of entering a given state are identical across all states — i.e., the probability of occupying a state at the next time step is independent of the current state occupancy. It can be modelled in the HMM framework by setting the transition probabilities $\pi_{ij} = \pi_{i*}$.

In any case, the transition matrix π_{ij} must respect the constraints that (1) all probabilities are between 0 and 1 and (2) transition probabilities out of a given state sum to 1. As is standard for HMMs with covariates (Visser and Speekenbrink, 2010), we define this multinomial logistic model in terms of a linear predictor η_{ij} , where η_{i1} is set to 1 without loss of generality (i.e. we have only $n \times (n-1)$ distinct parameters; we nevertheless index j from 2 to n for notational clarity):

$$\pi_{ij} = \exp(\eta_{ij}(t)) / \left(1 + \sum_{j=2}^{n} \exp(\eta_{ij}(t)) \right), \text{ for } j = 2, ..., n$$

$$\pi_{i1} = 1 - \sum_{j=2}^{n} \pi_{ij}$$
(2)

We considered four different transition models for diurnal variation in behaviour, incorporating hour-of-day as a covariate following the general approach of Morales et al. (2004) of incorporating covariate dependence in the transition matrix.

Hourly model

Multiple block transition Here we assume piecewise-constant transition probabilities. The transition probability π_{ij} is a function of time (hour of day), where it is assigned to one of M different time blocks:

describe hourly model. Explain that it's included for comparative purposes, i.e. not really practical. Explain that we only fitted up to 4 states (because too many parameters)

$$\eta_{ij}(t) = \sum_{m=1}^{M} a_{ijm} \delta_{m=t}$$

where a_{ijm} are parameters, and $\delta_{m=t}$ is a Kronecker delta ($\delta_{m=t} = 1$ for the time block at the corresponding time t, and 0 otherwise).

Quadratic transition model We assume the elements of the linear predictor are quadratic functions of hour. The quadratic model is not diurnally continuous, i.e. there is no constraint that forces $\eta_{ij}(0) = \eta_{ij}(24)$; imposing a diurnal continuity constraint would collapse the model to a constant.

$$\eta_{ij}(t) = b_{ij1} + b_{ij2} \left(\frac{t}{24}\right) + b_{ij3} \left(\frac{t}{24}\right)^2$$

Sinusoidal transition model A sinusoidal model with a period of 24 hours is identical in complexity to the quadratic model, but automatically satisfies the diurnal continuity constraint.

$$\eta_{ij}(t) = b_{ij1} + b_{ij2} \cos\left(\frac{2\pi t}{24}\right) + b_{ij3} \sin\left(\frac{2\pi t}{24}\right)$$

Other periodic functions, such as Fourier series (the sinusoidal transition model augmented by additional sinusoidal components at higher frequencies) or periodic splines, could be useful directions for future exploration.

citation?

Model complexity and the number of parameters increase as the number of latent states increase, FMM to HMM, and lastly, FMM and HMM incorporating temporal heterogeneity (Supplementary material, Table 1).

2.3 Model evaluation

We used the depmixS4 package to fit covariate-dependent transition HMMs, simulate states and step lengths using the estimated parameters, and estimate the most likely states with the Viterbi algorithm.

We used three approaches to assess the fit of both time-homogeneous and time-inhomogeneous HMMs with 3 to 6 states to step-length data from the four of the thirteen Florida panthers with the most data (> observations). (1) Comparing BICs to the optimal-BIC model within each type of transition complexity (ΔBIC = BIC - min(BIC)) assesses the overall goodness of fit of each model type. (2) Comparing average step-length by hour of day for the observed data and for data simulated from the models shows how well a particular class of models can capture the diurnal variation in behaviour. (3) Comparing temporal autocorrelations for the observed data and for data simulated from the models shows how well a particular class of models captures serial correlation at both short and long scales. We used simulations to predict hourly step length and ACF because, while the computation is reasonably straightforward for FMMs, and manageable for homogeneous HMMs, the interaction between the geometric dwell time within each state and the temporally varying interaction probabilities makes it unreasonably complex.

3 Results

Figure 1 shows the BIC-optimal number of states for time homogenous models is consistent with van de Kerk et al.'s results. Furthermore, BIC-optimal number of states does not depend on the model for both time-homogenous and time-inhomogenous within their respective framework, but time-inhomogenous

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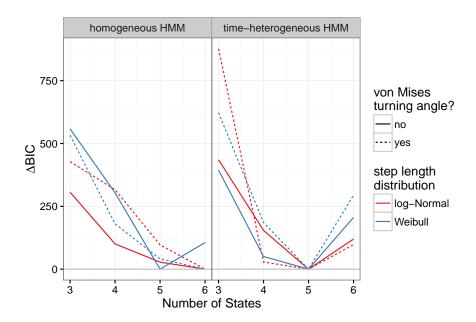


Figure 1: Change in BIC across models, cat #1. Δ BIC is scaled individually per model, so that Δ BIC = 0 represents the BIC-optimal number of states for a particular model.

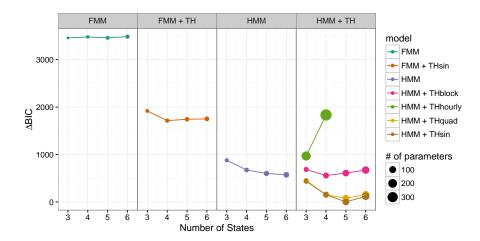


Figure 2: Overall adjusted BIC comparisons among models

models have the BIC-optimal number of states overall.

As a complement, we also fitted FMM; FMM with sinusoidal variation in state occupancy probabilities; and HMM with hourly transitions (24-hour multiple block transition model) to compare the temporal effects in goodness of fit. Figure 2 shows that models with temporal heterogenity are better (lower BIC) than homogeneous models in both FMM and HMM frameworks, but timehomogenous HMM models are better than FMM with sinusoidal temporal heterogeneity. Turning to the temporally heterogeneous HMMs (right panel), we see that the model with different transition probabilities for each hour of the day (HMM + THhourly) is overparameterized; it underperforms homogeneous HMM with even 3 states, and gets much worse with 4 states. The multipleblock model approximately matches the homogeneous HMM, although it gives the BIC-optimal number of states as 4, in contrast to 6 for the homogeneous HMM. Finally, the quadratic and sinusoidal models are considerably better than any other models tested; they both give the BIC-optimal number of states as 5, and they have similar goodness of fit. However, this similarity is somewhat overstated due to the very large variation in BIC (over thousands of units)

do we need to run some models with 7 states to show that ΔBIC eventually

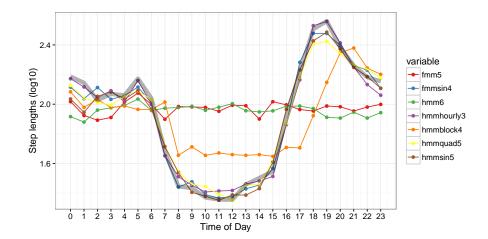


Figure 3: Average step length by time of day. todo: leave out hmm quad for clarity? fix factor labels; make y axis log-scale rather than showing log-step-length; make colours consistent with prev fig (may need scalecolourmanual [need underscores] with RColor-Brewer::brewer.pal(10,'Dark2') or some such. Maybe set obs as a wide, pointless, semitransparent line?)

across the full range of models; there is a difference of approximately 80 BIC units, which would normally be interpreted as an enormous difference in goodness of fit, between the sinusoidal and quadratic models (both of which have 90 parameters).

Figure 3 shows a clear diurnal pattern from the average hourly step lengths from the observed data. As expected, temporally homogeneous models (FMM and HMM) predict the same mean step length regardless of time of day, failing to capture the diurnal activity cycle. All of the models incorporating temporal heterogeneity, including the temporally heterogeneous FMM, can capture the observed patterns. However, the block model does markedly worse than the other temporal models, and the (overparameterized) hourly model does better than any other model at capturing the early-evening peak (but worse at capturing the mid-day trough).

The observed data has strong 24 hour lag autocorrelation (correlation with

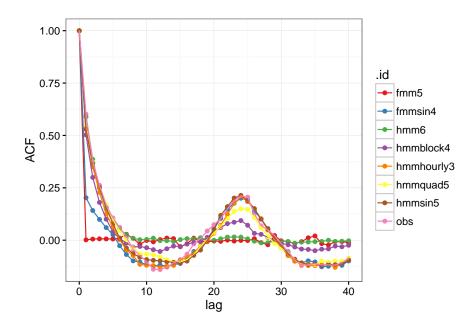


Figure 4: ACF fix similarly to Fig 3

itself) which suggest temporal heterogeneity (Figure 4). HMM without temporal heterogeneity can capture short-term autocorrelation (without Viterbi algorithm) but is unable to capture lags beyond 7. FMM with temporal heterogeneity can capture lags beyond 12, but not short-term autocorrelations. HMM with temporal heterogeneity can fully capture the autocorrelation pattern of the observed data whereas the FMM completely missed the autocorrelations.

TODO: add ellipses?

The biggest issue with multiple states is identifying them biologically. We really do not know if there Florida panthers really moves according to hidden states, and even if they do, we don't know the true number nor able to observe them. Three distinct movement states seems biologically interpretable for Florida panthers according van de Kerk et al. (2015): Short step length suggests resting states, intermediate step length might suggest foraging state and long step length might suggest traveling state. Long step lengths are easy to capture

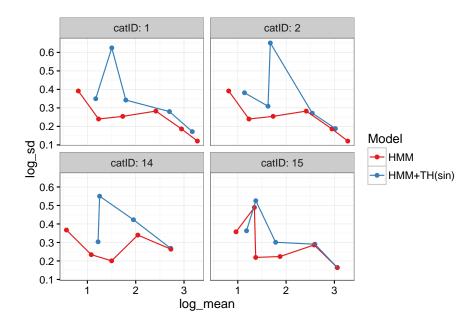


Figure 5: Step-length parameters

in all models, where as short step lengths are hard to capture given the GPS errors and unstable movements patterns suggesting multiple states associate with short step lengths. Thus, lower number of short step length states with higher variance can be equivalent or more realistic than multiple distinguishable short step length states with low variance.

4 Discussion

Identifying behavioural states based on some set of observations is a common methodological problem in behavioural ecology; finding solutions that are both biologically and statistically interpretable and defensible is challenging. Models that suggest a higher number of states fit the data well but are hard to interpret biologically; models that are biologically interpretable are not statistically supported. While the HMM framework has been applied in many research areas,

very few studies have considered modeling with more than 3 states. HMM is a simple straight forward framework, but HMM extensions of adding a small amount of complexity can complicate the model greatly and reveal deeper understanding. For example, van de Kerk et al. (2015) used 2 to 6 movement states HSMM to model Florida panthers, Morales et al. (2004) used habitat distance dependent transition HMM to model elk, and outside of ecology, Raffa and Dubin (2015) used mixed effect transition and emission HMM in a smoking study.

We have presented a relatively simple concept yet little-studied extension by covariate dependent HMM can overfit the number of true states in covariate dependent HMM (in our case, time-dependent transitions). HMM with more than three states are not biologically interpretable and often discarded, but we cannot ignore that increasing complexity (number of states) states can increase goodness of fit statistically. Our analyses revealed modeling temporal heterogeneity in HMM transition can reduce the number of states estimated in time homogeneous transitions HMM movement of Florida panthers and reduce the overall model complexity.

For some kinds of model predictions, the time homogeneous transition model can perform as good as the time inhomogeneous transition models in terms of predicting the states by the Viterbi algorithm (the tradition state prediction method) and can easily overlook more complicated models. The Viterbi algorithm solves/predicts for the most likely/probable sequence of movement states based on the observations (Zucchini and MacDonald, 2009; Langrock et al., 2012). This approach allows the time homogeneous transition model's prediction to capture the temporal heterogeneity from the observations. It is useful to predict missing data in the observation sequence, but because it is conditional on the observed values, it cannot predict future movements beyond the observation

sequence. In general, the time homogeneous transition model gives the broader scope of movement pattern where as the time inhomogeneous transitions models gives a more realistic movement structure and future predictions.

Although the time inhomogeneous transitions offer an objective approach to (1) reduce the number of states to a biologically interpretable level, (2) captures the observational autocorrelation and temporal pattern, (3) reduce the overall complexity as illustrated by our study, several challenges must be overcome in order to maximize its potential. The current model is based on the reduced univariate step length response emission without fitting turning angles. Although turning angles are strongly correlated with step length, it does not effect the overall prediction on number of states. But movement trajectories predictions, and spatial models still require both step length and turning angles. Furthermore, modelling temporal heterogeneity only reduce the number of predicted states by 1 resulting in 4/5 states might suggest (1) other factors such as spatial components that might also contribute to over predicting number of states, or (2) there really are 1 or 2 more different movement characteristics that are biologically unknown. Despite the challenges, our study provides an important extension in HMM modeling that is not in the seen before and a real life application that it exist and applicable in animal movement ecology.

Table 1: Cat-ID					
(van de Kerk 2015)	(IR@UF)	Number of Observations			
130	1	10286			
131	2	9458			
48	14	14645			
94	15	10250			

	homogeneous HMM	time-heterogeneous HMM				
300 200 4 100	3 4 5 6	3 4 5 6	von Mises turning angle? no voyes step length distribution log-Normal Weibull			
Number of States						

Figure 6: Change in BIC across models, cat #2. Δ BIC is scaled individually per model, so that Δ BIC = 0 represents the BIC-optimal number of states for a particular model.

5 Supplementary material

Table 2: Number of Parameters for each model type. todo: add general formula for each model type, e.g. FMM = S (occupancies) + 2S (emissions: mean and std dev for each state); HMM = $S(S-1)+2S=S^2+S$. Be clear about whether we're talking about restricted (constrained) or unconstrained.

(constrained) or unconstrained.					
Type	Model	Number of States	Number of Parameters		
FMM	FMM	3	9		
FMM	FMM	4	12		
FMM	FMM	5	15		
FMM	FMM	6	18		
FMM + TH	FMM + TH (Sin)	3	15		
FMM + TH	FMM + TH (Sin)	4	20		
FMM + TH	FMM + TH (Sin)	5	25		
FMM + TH	FMM + TH (Sin)	6	30		
$_{\mathrm{HMM}}$	$_{ m HMM}$	3	18		
$_{\mathrm{HMM}}$	$_{ m HMM}$	4	28		
$_{\mathrm{HMM}}$	$_{ m HMM}$	5	40		
$_{\mathrm{HMM}}$	$_{ m HMM}$	6	54		
HMM + TH	HMM + TH (Block)	3	36		
HMM + TH	HMM + TH (Block)	4	60		
HMM + TH	HMM + TH (Block)	5	90		
HMM + TH	HMM + TH (Block)	6	126		
HMM + TH	HMM + TH (Quad)	3	36		
HMM + TH	HMM + TH (Quad)	4	60		
HMM + TH	HMM + TH (Quad)	5	90		
HMM + TH	HMM + TH (Quad)	6	126		
HMM + TH	HMM + TH(Sin)	3	36		
HMM + TH	HMM + TH (Sin)	4	60		
HMM + TH	HMM + TH(Sin)	5	90		
HMM + TH	HMM + TH (Sin)	6	126		
HMM + TH	HMM + TH (Hourly)	3	225		
HMM + TH	HMM + TH (Hourly)	4	396		

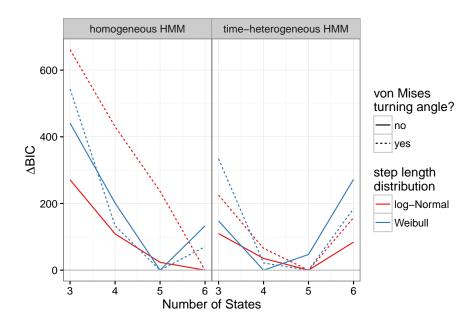


Figure 7: Change in BIC across models, cat #15. Δ BIC is scaled individually per model, so that Δ BIC = 0 represents the BIC-optimal number of states for a particular model.

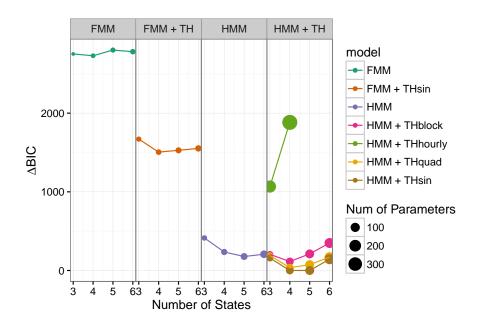
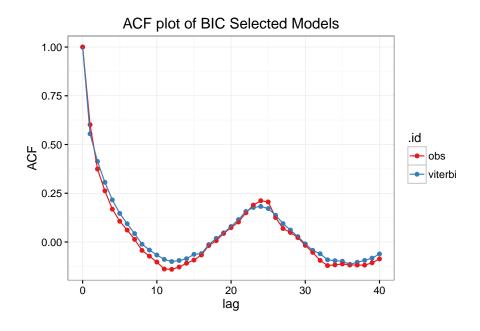


Figure 8: Overall adjusted BIC comparisons between different HMM models



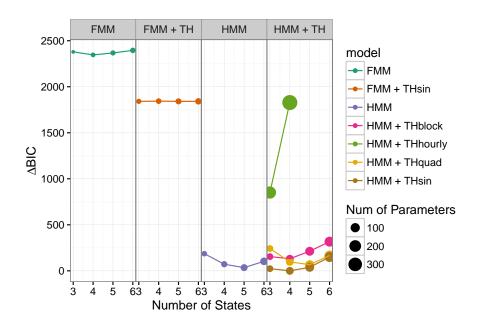


Figure 9: Overall Adjusted BIC Comparisons between different HMM models

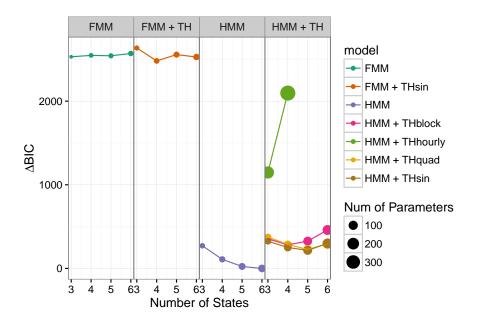


Figure 10: Overall Adjusted BIC Comparisons between different HMM models

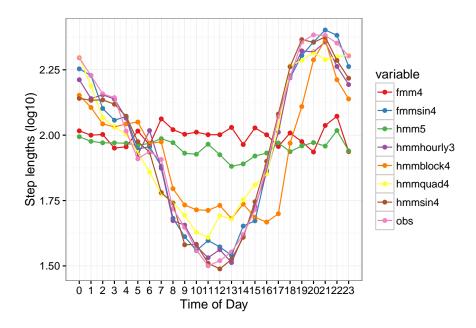


Figure 11: Average step length by time of day

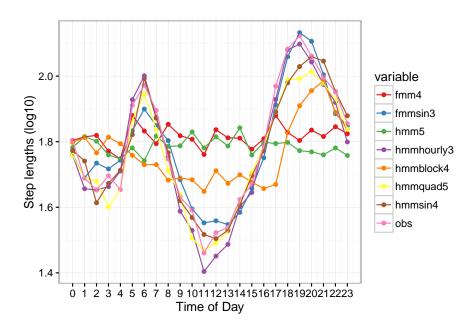


Figure 12: Average step length by time of day

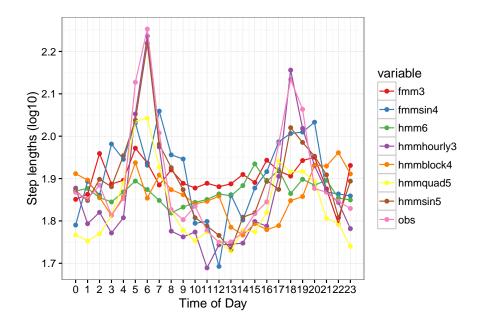


Figure 13: Average step length by time of day

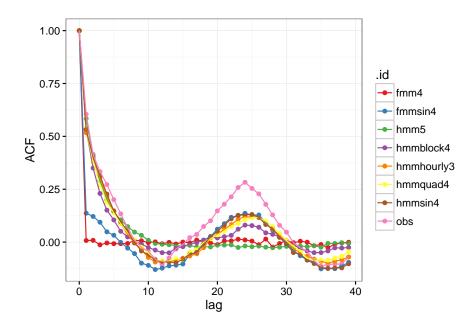


Figure 14: ACF

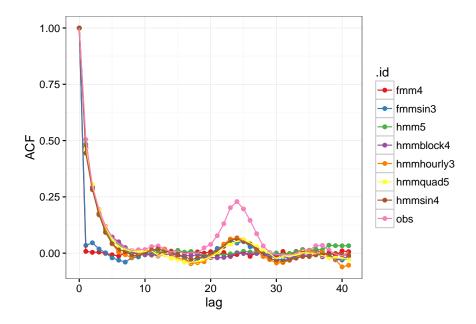


Figure 15: ACF

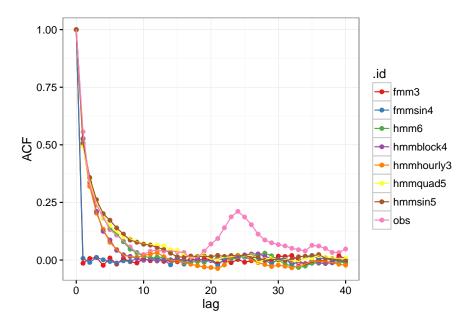


Figure 16: ACF

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