

# 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. 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 behavior 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.

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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.

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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.

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, 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 the HMM, 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.

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

## 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, 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 makes precisely this assumption.

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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.

Our analysis again 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 relatively subtle distinctions in shape between the three candidate step-length distributions and the effects of considering multivariate (step length plus turning angle) observations. (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.) However, we do briefly compare all three step-length distributions, with and without incorporating a von Mises-distributed turning angle in the model (Figure 1).

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)’s lead 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

not sure about terminology here (should be consistent about what we call the modes/latent states/whatever) ML: latent states

should decide on rules for numbers vs numerals (3 vs three) and be consistent. ML: numeric

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 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)  $\mathbf{Y} = \mathbf{y}_1, \dots, \mathbf{y}_T$  and a hidden state sequence  $\mathbf{Z}, z_t \in \{1, \dots, n\}, t = 1, \dots, T$ , given model parameters  $\boldsymbol{\theta}$  and covariates  $\mathbf{X}_{1:T} = \mathbf{x}_1, \dots, \mathbf{x}_T$ , can be written as:

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

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  $\mathbf{x}_1$ ; the vector of observation densities  $\mathbf{y}_1$  conditions 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 observation density  $\mathbf{y}_k$  condition on covariates  $\mathbf{x}_k$  at state  $z_k$  at time  $t = k$ .

The following description of the Viterbi algorithm is not coherent; need to give just a *brief* definition here (since we are going to use it) and criticize/ explain shortcomings later. ML: I moved the whole previous paragraph to the end where we actually talk about viterbi

Eq. 1 gives the likelihood of the observed sequence given (conditional on) a particular hidden sequence. In order to calculate the overall, unconditional (or marginal) likelihood of the observed sequence, we need to average over all possible hidden sequences. While naive approaches to this averaging process there are several more efficient algorithms for computing the marginal likelihood and numerically estimating parameters (Zucchini and MacDonald, 2009); we use the implementations 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  $\pi_{ij}$  of being in movement states  $j$  at time  $t + 1$  given that the individual is in state  $i$ . However, this matrix needs to respect the constraints that (1) all probabilities are between 0 and 1 and (2) transition probabilities out of a given state sum to 1. The FMM is a special case of HMM where; it can be modelled in the HMM framework by setting the transition probabilities:

$$\pi_{ij} = \pi_{i*j}, \forall i \quad (2)$$

Therefore, as is standard for HMMs with covariates (Visser and Speekenbrink, 2010), we define this multinomial logistic model in terms of a linear predictor  $\eta_{ij}$ , where  $\eta_{i1}$  is unnecessary (i.e. we have only  $n \times (n - 1)$  distinct parameters; we nevertheless index  $j$  from 2 to  $n$  for notational clarity):

$$\begin{aligned} \pi_{ij} &= \exp(\eta_{ij}(t)) / \left( 1 + \sum_{j=2}^n \exp(\eta_{ij}(t)) \right), \text{ for } j = 2, \dots, n \\ \pi_{i1} &= 1 - \sum_{j=2}^n \pi_{ij} \end{aligned} \quad (3)$$

where do we actually focus on these three states? Think this could probably be introduced in the Discussion, if we need it. ML: I took it out and gave a half a line in model evaluation subsection



We considered three different transitions models for diurnal variation in behaviour; extension of “Switch with covariates” by Morales et al. (2004) to account for temporal heterogeneity .

second clause isn't clear; expand? ML: okay now?

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

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

where  $a_{ijm}$  are parameters, and  $\delta_{m=t}$  is a Kronecker delta or indicator variable (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, with an additional diurnal continuity constraint that  $\eta_{ij}(0) = \eta_{ij}(24)$

am I right/do we actually impose this constraint? give a bit more detail ...

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

**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.

apparently true from eqs here, but not true if we constrain the quadratic model??

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

Model complexity and number of parameters increase as the number of latent states increase, FMM to HMM, and lastly, FMM and HMM incorporating temporal heterogeneity.

Discuss model complexity/parameter-number computations here, or with each model. Also discuss the “hourly” model here.

Table 2: Number of Parameters for each model type

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
HMM	HMM	3	18
HMM	HMM	4	28
HMM	HMM	5	40
HMM	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

## 2.3 Model evaluation

The `depmixS4` package was used for fitting covariate dependent transition HMM models, simulating states and step lengths using the estimated parameters, and for estimating states with the Viterbi algorithm.

Give more details about parameters, structure of simulations, etc.

We assessed the fit of 3 to 6 state, time homogeneous and inhomogeneous transition HMMs to four of the thirteen Florida panthers with the most data using three approaches. First, goodness of fit of different number of states by scaled BIC within each type of transition complexity ( $\Delta\text{BIC} = \text{BIC} - \min(\text{BIC})$ ). Secondly, the average distance by time of day comparison of observed and simulated data from each type of transition complexity. Lastly, autocorrelation comparison between the observed and simulated data. Increasing the number of latent states of HMM, and incorporating temporal transition heterogeneity of FMM and HMM, can both (independently) improve goodness of fit in their own ways, but it is unclear the tradeoff between the two methods and the combination of both is an underused model extension.

describe the Viterbi algorithm here, and the autocorrelation function computation - everything that appears in the results should be described explicitly here....ML: at the bottom

## 3 Results

Adding temporal heterogeneity in the transitions for 3 to 6 state HSMM was a challenge because the number of parameters and model complexity increase dramatically, thus creating overfitting problems. Model reduction was used to balance out the increase in parameters and see if there are evidence suggesting adding temporal heterogeneity complexity can reduce the number of states to a statistically and biologically interpretable level. Without loss of generality,

give at least a hint of why/what each of these three approaches ( $\Delta\text{BIC}$ , hourly averages, ACF) will show. ML: What do you think?

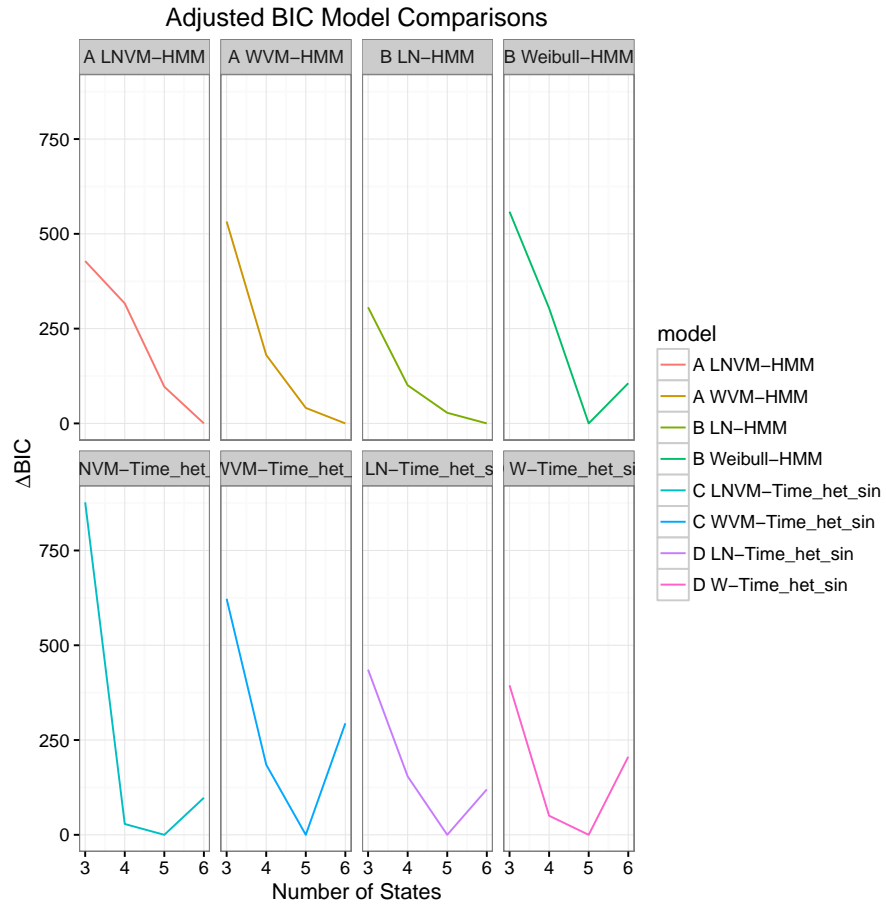


Figure 1: Model Reduction Process via Individual based Model Adjusted BIC

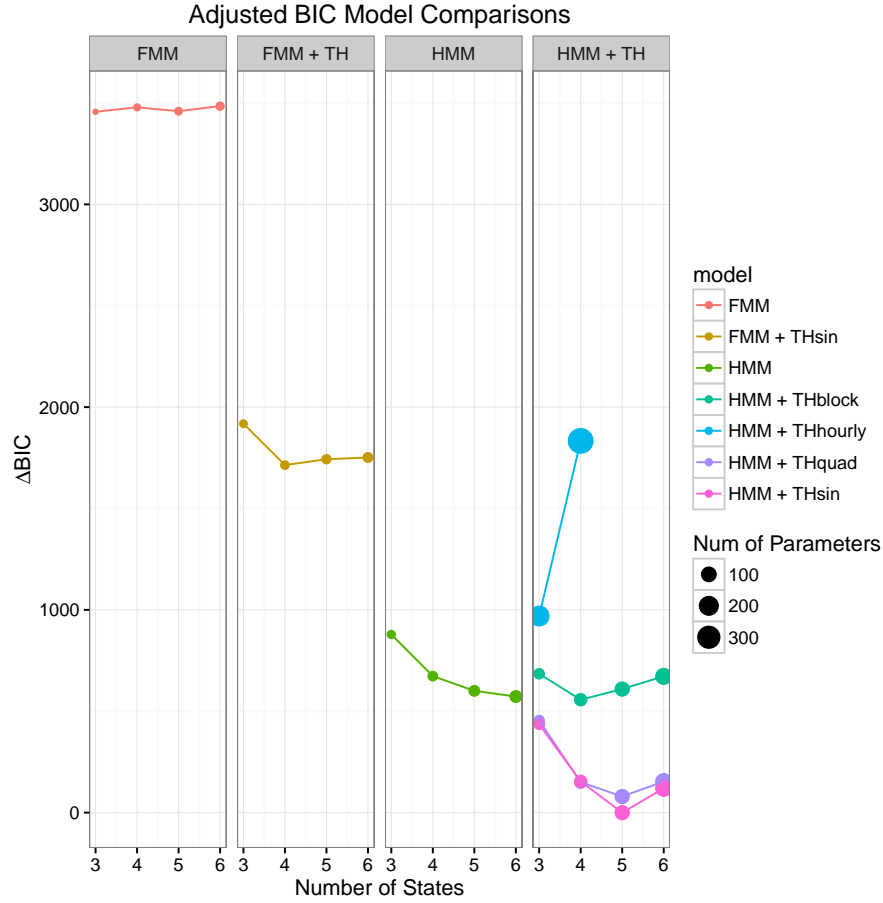


Figure 2: Overall Adjusted BIC Comparisons between different HMM models

we assessed time homogeneous transition HMM models instead of HSMM and made sure each model reduction does not change the BIC selection of number of states, which HMM heavily depends on. Goodness of fit will decrease, but the information on the number of states remains the same.

As a complement, we also added FMM, FMM with sinusoidal temporal heterogeneities, and HMM with hourly transitions to compare the temporal effects in goodness of fit. Looking at figure 2, time inhomogenous transition HMMs (vertically) and 5 states yield the lowest  $\Delta$  BIC. The time inhomogeneous tran-

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sition HMMs reduced the number of states from the HMM by 1 state consistently across all panthers via  $\Delta$  BIC. Two of the four panthers dropped to 4 states from 5 states after adding time inhomogeneity transition moving closer to a biologically and statistically interpretable level. Although adding the time inhomogeneous only reduce the number of states by 1, it does support that adding temporal heterogeneity reduce the number of states and at the same time, increase goodness of fit by BIC.

Among the different types of time inhomogeneous transition HMMs, sinusoidal time dependent transition HMMs yields the lowest BIC. The multiple block transitions was a good fit for the male panthers, using a combination of three transition matrix ( $b_1$  for  $t = 1 - 6, 21 - 24$ ,  $b_2$  for  $t = 7 - 16$ , and  $b_3$  for  $t = 17 - 20$ ) and it reduced the number of states by 1 but had no effect on the females. The quadratic and sinusoidal time covariate transitions was motivated by the multiple block transition pattern attempting to capture the cyclic diurnal cycle and same complex level in terms of number of parameters. We concluded that sinusoidal time dependent transition HMM was suitable for modeling these panthers.

Next, we used the fitted models and simulate the same number of observations as the observed movement data and compare the average distance by time with the observed data. Models that assume temporal homogeneity (FMM and HMM) fail to capture the diurnal activity cycle. Models incorporating temporal heterogeneity can capture the observed patterns in the hourly average step.

Lastly, the observed data has strong 24 hour lag autocorrelation (correlation with itself) which suggest temporal heterogeneity. FMM has no autocorrelation at all. HMM without temporal heterogeneity can capture the first few lags of the ACF but is unable to capture lags beyond 7. FMM with temporal heterogeneity can capture lags beyond 12, but not short-term correlation. HMM with temporal

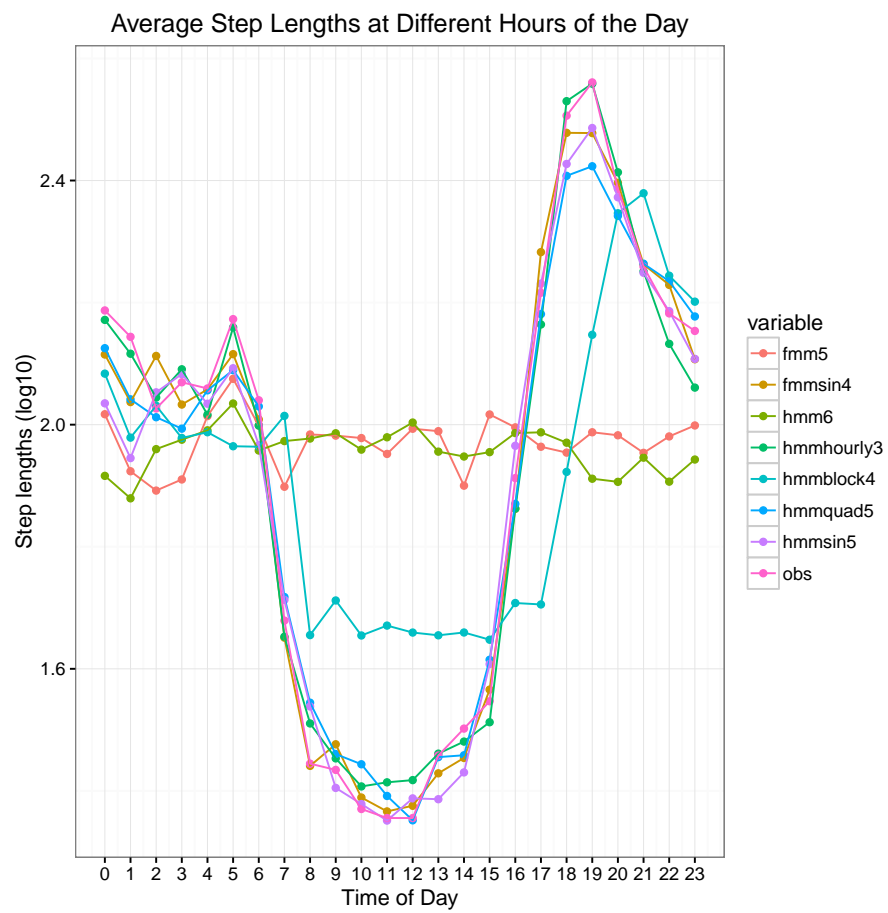


Figure 3: Average step length by time of day

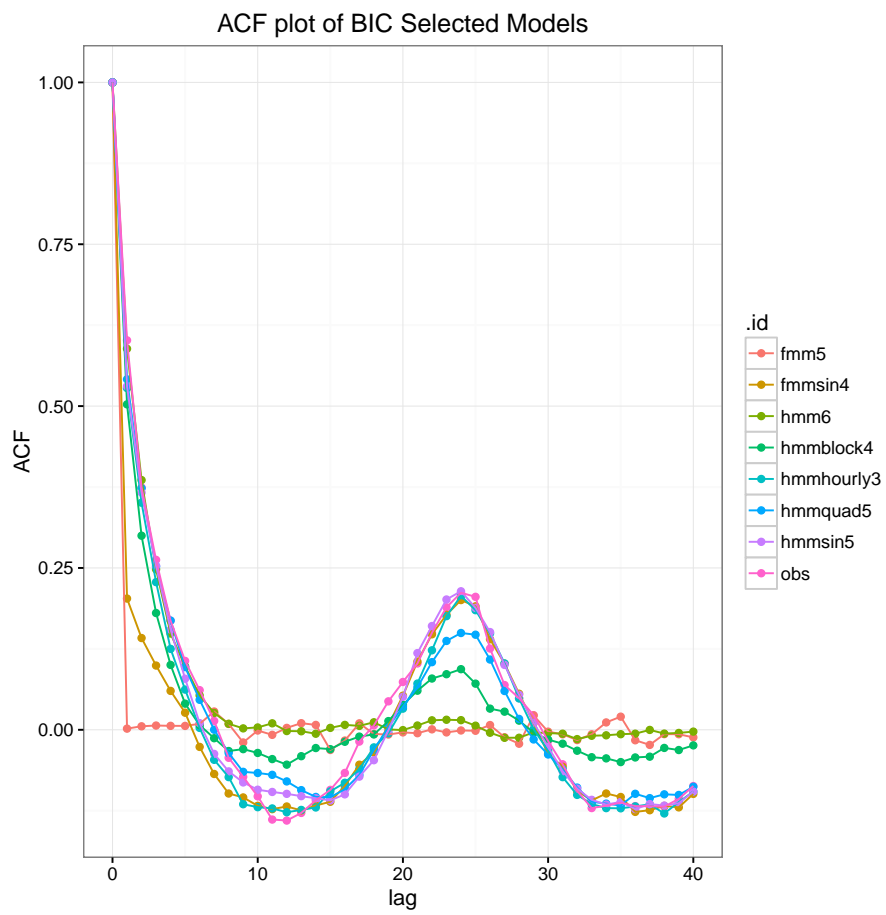


Figure 4: ACF



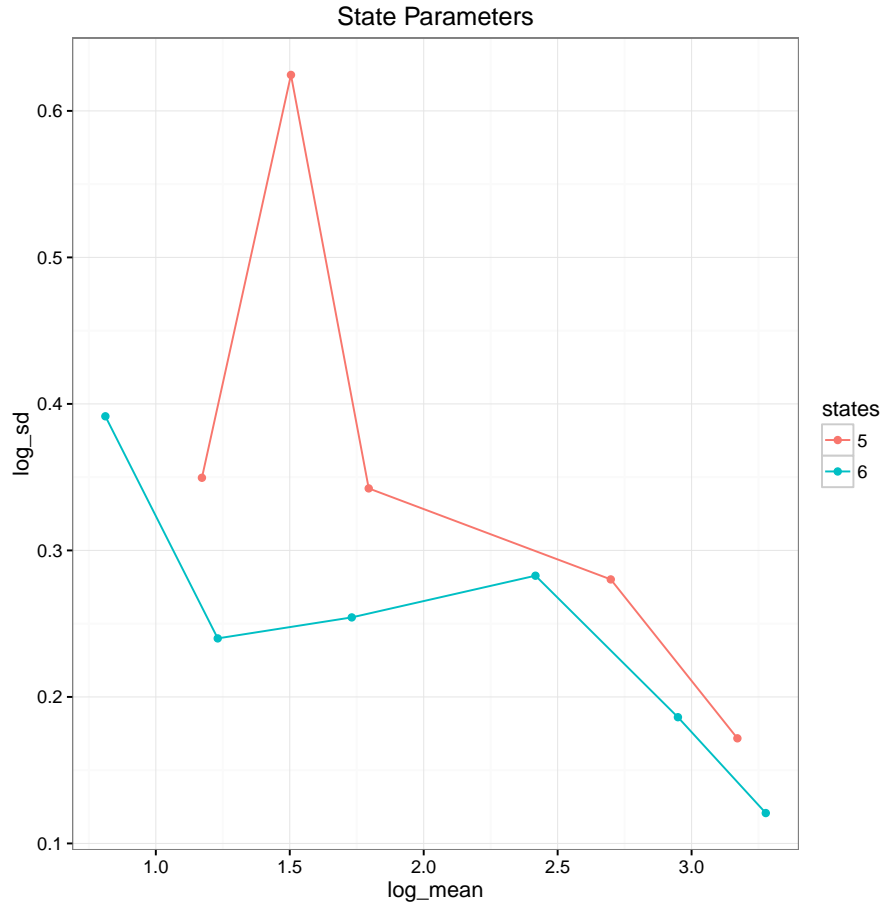


Figure 5: States

heterogeneity can fully capture the autocorrelation pattern of the observed data.

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: 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 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.

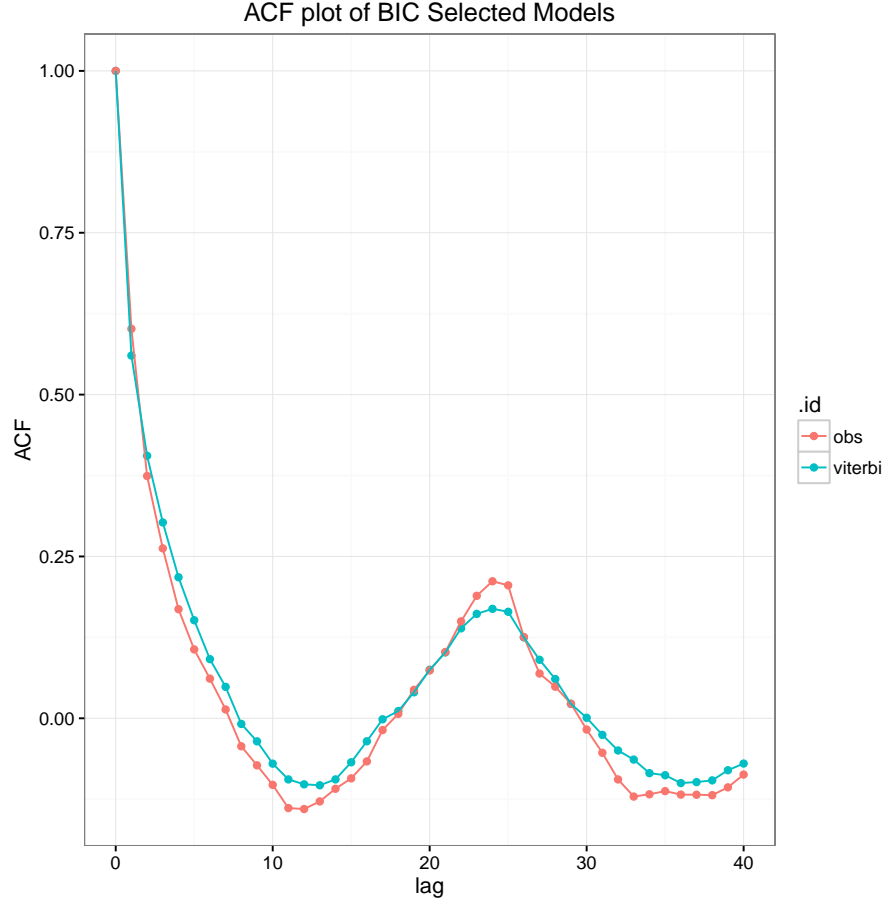
## 4 Discussion

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 hetero-

geneity 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 homogenous transition model's prediction to capture the temporal heterogeneity from the observations. It is useful to predict missing data in the observation sequence but fail to future movements beyond the observations 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 transition 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.

## References

- Burnham, K. P. and D. R. Anderson (1998). *Model Selection and Inference: A Practical Information-Theoretic Approach*. New York: Springer.
- Dean, B., R. Freeman, H. Kirk, K. Leonard, R. A. Phillips, C. M. Perrins, and T. Guilford (2012). Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of The Royal Society Interface*, rsif20120570.
- Firle, S., R. Bommarco, B. Ekbom, and M. Natiello (1998, September). The influence of movement and resting behavior on the range of three carabid beetles. *Ecology* 79(6), 2113–2122.
- Franke, A., T. Caelli, G. Kuzyk, and R. J. Hudson (2006, August). Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. *Ecological Modelling* 197(1–2), 237–246.
- Fryxell, J. M., M. Hazell, L. Börger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte (2008, December). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences* 105(49), 19114–19119.
- Langrock, R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J. M.

- Morales (2012, June). Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology* 93(11), 2336–2342.
- McKellar, A. E., R. Langrock, J. R. Walters, and D. C. Kesler (2014, September). Using mixed hidden Markov models to examine behavioral states in a cooperatively breeding bird. *Behavioral Ecology*, aru171.
- McKenzie, H. W., M. A. Lewis, and E. H. Merrill (2009). First passage time analysis of animal movement and insights into the functional response. *Bulletin of Mathematical Biology* 71(1), 107–129.
- Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85(9), 2436–2445.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse (2008, December). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* 105(49), 19052–19059.
- Okubo, A. (1980). Diffusion and Ecological Problems: Mathematical Models.
- Pal, S., B. Ghosh, and S. Roy (1998). Dispersal behaviour of free-ranging dogs (*Canis familiaris*) in relation to age, sex, season and dispersal distance. *Applied Animal Behaviour Science* 61(2), 123–132.
- Patterson, T. A., M. Basson, M. V. Bravington, and J. S. Gunn (2009, November). Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology* 78(6), 1113–1123.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos (2008). State-space models of individual animal movement. *Trends in ecology & evolution* 23(2), 87–94.

- R Core Team (2015). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raffa, J. D. and J. A. Dubin (2015, March). Multivariate longitudinal data analysis with mixed effects hidden Markov models. *Biometrics*, n/a–n/a.
- Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86(10), 2805–2814.
- Schliehe-Diecks, S., P. M. Kappeler, and R. Langrock (2012, April). On the application of mixed hidden Markov models to multiple behavioural time series. *Interface Focus* 2(2), 180–189.
- Tracey, J. A., J. Zhu, E. Boydston, L. Lyren, R. N. Fisher, and K. R. Crooks (2012, October). Mapping behavioral landscapes for animal movement: a finite mixture modeling approach. *Ecological Applications* 23(3), 654–669.
- Turchin, P. (1998). *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*, Volume 1. Sinauer Associates Sunderland.
- van de Kerk, M., D. P. Onorato, M. A. Criffield, B. M. Bolker, B. C. Augustine, S. A. McKinley, and M. K. Oli (2015). Hidden semi-Markov models reveal multiphasic movement of the endangered Florida panther. *Journal of Animal Ecology* 84(2), 576–585.
- Visser, I. and M. Speekenbrink (2010). `depmixS4`: An R package for hidden Markov models. *Journal of Statistical Software* 36(7), 1–21.
- Zucchini, W. and I. L. MacDonald (2009, April). *Hidden Markov Models for Time Series: An Introduction Using R*. CRC Press.