# Incorporating Periodic Variability in Hidden Markov Models for Animal Movement

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Sample of title note

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## **Abstract**

Background: Clustering time-series data into discrete groups can improve prediction and provide insight into the nature of underlying, unobservable states of the system. However, temporal variation in the rates at which individuals move between groups can obscure such signals. We use finite mixture and hidden Markov models (HMMs), 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 little-used extension of the standard HMM framework, resolves some shortcomings of current models and clarifies the behavioural patterns of panthers.

Results: Simulations and Florida panthers data showed model misspecification (omitting important sources of variation) can lead to overfitting and over-estimating number of behavioural states. Models incorporating temporal heterogeneity have lower number of states with slightly higher variation in short movement states, and able to make out of sample predictions that captures observed diurnal and autocorrelation patterns exhibited by Florida panthers.

**Conclusion:** Incorportating temporal heterogeneity reduce the selected number of behavioural states closer to a biologically interpretable level, improved goodness of fit and predictability. Our suggest that incorporating previously neglected structure in statistical models can allow more accurate assessment of appropriate model complexity.

**Keywords:** Hidden Markov Model; Animal Movement; Temporal Autocorrelation; Temporal Heterogeneity; Florida Panther

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# Background

- 5 Given a sequence of animal movements, movement models aim to find a parsimo-
- 6 nious description that can be used to understand past movements and predict future
- 7 movements. Ecologists have long considered the effects of individual-level covariates

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(sex, age, nutritional status) and environmental covariates (habitat type, location of predators or prey) on movement [1, 2, 3]. More recently, modelers have developed hidden Markov models (HMMs) [4, 5, 6] — used in animal ecology under the rubric of the "multiphasic movement framework" [7] — that consider the effects of organisms' internal states; in particular, HMMs model animal movement as though individual animals' movement behaviour at particular times is determined by which 13 of a discrete set of unobserved movement states (e.g. "foraging", "traveling", "resting") they currently occupy. Conditional on the state occupied by an individual, 15 HMMs typically assume that animals follow a standard correlated walk model [8, 9]. Ever-increasing capabilities of remote sensors are making movement data avail-17 able over an ever-wider range of time scales, at both higher resolution (e.g. hourly 18 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 20 analyzing such long-term 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 [10], or by more direct comparisons between inferred states and en-28 vironmental conditions [7]. Schliehe-Diecks et al. [11] consider temporal trends in behavioural transitions over the time scales of a six-hour observation period, but in 30 general ecologists have turned to other tools to describe behavioural changes over 31 longer (diurnal, seasonal, or ontogenetic) time scales [12]. 32 For movement behaviours that change on a fast time scale, such that movement

behaviours recorded at successive observations are effectively independent, finite

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mixture models (FMMs) — 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 [13]. 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.[14], 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.[14] found that the best-fitting HSMMs incorporated a surprisingly large number of hidden behavioural states (as many as six for individuals with
a large amount of available data); for reasons of computational practicality and biological interpretability, they restricted their detailed analysis to models with only
three underlying states. In contrast, most studies using HMM have chosen the number of underlying states a priori, typically using either two [11, 15, 6, 7], or three
states [16, 17, 18]. In contrast, [19] evaluated models with up to 10 states, but like
[14] they chose to consider only models with three states. As van de Kerk et al.
[14] comment, and as we discuss further below, behavioural repertoires with more

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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 on optimal model complexity might be driven at least in part by structural problems with their statistical model, i.e. the assumption of temporally homogeneous behaviour. For large data sets, 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.

## 79 Methods

- 80 Data and previous analyses
- GPS collars were fitted to 18 Florida panthers in 2005-2012 by Florida Fish and
- 82 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.[14]. Here
- we focus on the four cats with the most data (all with approximately 10,000-15,000
- 85 observations: see Table 1), 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
- $_{\it 87}$   $\,$  the general trend in telemetry studies is toward larger data sets. As is typical in
- 88 studies of animal movement, we took first differences of the data by decomposing

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contiguous sequences of hourly GPS coordinates into successive step lengths (in meters) and turning angles (in radians) [9, 14].

van de Kerk et al.[14] used hidden semi-Markov models (HSMM), an extension of HMM that permits explicit modelling of dwell times [6], considering both Poisson and negative binomial distributions for dwell times. As shown by van de Kerk et al.[14] (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 given), 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. [14] considered time-homogeneous models with a variety of 100 candidate distributions — log-Normal, Gamma, and Weibull distributions for step 101 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 105 very best predictive model, we focus on models that treat each step as a univariate, 106 log-Normally distributed observation, glossing over both the differences in shape 107 between the three candidate step-length distributions and the effects of consider-108 ing multivariate (i.e., step length plus turning angle) observations. However, we do 109 briefly compare log-Normal and Weibull step-length distributions, with and without 110 a von Mises-distributed turning angle included in the model (Figure 2). (Note that 111 most movement analyses, including van de Kerk et al. [14], are only partially multi-112 variate, treating step length and turning angle at a particular time as multivariate 113 observations for the purpose of HMM analysis but neglecting possible correlations 114 between the two measures.)

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van de Kerk et al.[14] used the Bayesian (Schwarz) information criterion (BIC) 116 to test the relative penalized goodness of fit for models ranging from 2 to 6 latent 117 states. In general, BIC values decreased as the number of states increased from 118 three to six states, suggesting that the six-state model was favoured statistically; 119 however, the authors used three-state models in most of their analyses for ease of 120 biological interpretation. We follow van de Kerk et al. [14] in using BIC-optimality 121 (i.e., minimum BIC across a family of models) as the criterion for identifying the 122 best model, because we are interested in explaining the data generation process by 123 identifying the "true" number of underlying movement states. 124

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 [20]. 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 [21]; we believe that the qualitative conclusions stated here for BIC-optimality will carry over to analyses using AIC instead.

## 133 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:

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

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The emissions 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
138
    distinct components:
139
    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 x_1, times the vector of observations y_1 condi-
141
          tioned on covariates x_1 and state z_1.
142
    Transition probability P(z_k = j | z_{k-1} = i, 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(y_k|z_k, x_k): a vector of observations y_k conditioned on
          covariates \mathbf{x}_k at state \mathbf{z}_k at time t = k.
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      Eq. 1 gives the likelihood of the observed sequence given (conditional on) a partic-
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    ular hidden sequence. In order to calculate the overall, unconditional (or marginal)
    likelihood of the observed sequence, we need to average over all possible hidden
149
    sequences. There are several efficient algorithms for computing the marginal like-
    lihood and numerically estimating parameters [22]; we used those implemented in
    the depmixS4 package for R [23, 24].
152
      For any n-state HMM, we need to define a n \times n matrix that specifies the
153
    probabilities \pi_{ij} of being in movement states j at time t+1 given that the individual
154
    is in state i. The FMM is a special case of HMM where the probabilities of entering
155
    a given state are identical across all states — i.e., the probability of occupying a
156
    state at the next time step is independent of the current state occupancy. It can be
157
    modelled in the HMM framework by setting the transition probabilities \pi_{ij} = \pi_{i*}.
158
      In any case, the transition matrix \pi_{ij} must respect the constraints that (1) all
159
    probabilities are between 0 and 1 and (2) transition probabilities out of a given state
160
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sum to 1. As is standard for HMMs with covariates [23], we define this multinomial

logistic model in terms of a linear predictor  $\eta_{ij}$ , where  $\eta_{i1}$  is set to 1 without loss

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of generality (i.e. we have only  $n \times (n-1)$  distinct parameters; we 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.[17] of incorporating covariate dependence in the transition matrix.

Multiple block transition Here we assume piecewise-constant transition probabilities. The transition probability  $\pi_{ij}$  is a function of time (hour of day), 169 where it is assigned to one of M different time blocks: 170

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

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 173 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. 176

171

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

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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.

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

Hourly model Lastly, we extended the multi-block approach and assign a different transition matrix for every hour of the day. This model is included for
comparative purposes due to the large number of parameters in the model
which makes it not really practical. We only fitted up to four states using the
hourly model.

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.

## 188 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 timeinhomogeneous HMMs with 3 to 6 states to step-length data from the four of the
thirteen Florida panthers with the most data (> 9000 observations). (1) Comparing
BICs to the optimal-BIC model within each type of transition complexity ( $\Delta$ BIC
= 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

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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.

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. The number of free parameters in an HMM can be generalized by summing up the number of free parameters of the three distinct components. Let n be the number of hidden states and  $k_i, k_t, k_e$  be the number of parameters describing the covariate-dependence of the prior distribution, transition function and emission distributions; that is, for a homogeneous model, k = 1, while a single numeric covariate or a categorical predictor with two levels would give k = 2. Then the number of free parameters of an HMM is:

Number of Free Parameter = 
$$\underbrace{k_i \cdot (n-1)}_{\text{Initial}} + \underbrace{k_t \cdot n \cdot (n-1)}_{\text{Transition}} + \underbrace{k_e \cdot n}_{\text{Emission}}$$
 (3)

As the number of states increases, the number of free parameters in timehomogeneous FMMs and HMMs and FMMs with temporal heterogenity will increase linearly, whereas HMMs with temporal heterogenity will increase quadratically (Eq. 3). When comparing BICs, it is important to account for the tradeoff
between log-likelihood and number of states, but also log-likelihood and number of
free parameters.

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.
We used this approach to validate our models and comparing these models with the
observed movements instead of the standard Viterbi predictions by the Viterbi

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algorithm because Viterbi predictions, which use the most probable sequence of
movement states based on the observations [22, 6], double-count the observed data.

It is useful to predict missing data in the observation sequence, but because it is
conditional on the observed values, it can not reliably evaluate goodness of fit for
the different structural complexities of HMM models.

## Results

We simulated a two-state HMM with sinusoidal temporal transitions 100 times and fitted it with two to five state HMMs and without temporal transition. Heterogeneous transition models can always predict the correct number of states, whereas, can overestimate the number of states via BIC-optimal approach (Figure 1).

The BIC-optimal number of states for time homogenous models is consistent with van de Kerk et al.'s [14] results (Weibull wrapped-Cauchy to Weibull von Mises, and Weibull von Mises to log Normal without turning angles; Figure 2)

As a complement, we also fitted FMM and FMM with sinusoidal variation in state occupancy probabilities to compare the temporal effects in goodness of fit (dashed lines). As a reminder, FMMs assume that the latent state in each time step is *independent* of the latent state at the previous time step; time-varying FMMs can accurately describe movement when behaviour can change on a short time scale, but the average propensity for different behaviours changes over time.

Models with temporal heterogenity are better (lower BIC) than homogeneous models in both FMM and HMM frameworks, but time-homogeneous HMMs are better than FMMs with sinusoidal temporal heterogeneity (Figure 3). 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 multiple-block model approximately matches the homogeneous HMM, although it gives the BIC-optimal number of states as 4, in contrast

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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) 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).

The panthers exhibits a clear diurnal pattern from the average hourly step lengths 258 from the observed data (Figure 4). As expected, temporally homogeneous models 259 (whether FMM or HMM) predict the same mean step length regardless of time of 260 day, failing to capture the diurnal activity cycle. All of the models incorporating 261 temporal heterogeneity, including the temporally heterogeneous FMM, can capture 262 the observed patterns. However, the block model does markedly worse than the 263 other temporal models (changing the block definitions might help), and the (over-264 parameterized) hourly model does better than any other model at capturing the 265 early-evening peak (but worse at capturing the mid-day trough). We also included 266 average hourly step lengths from three-state temporally homogeneous HMM Viterbi 267 prediction (v points).

Like the diurnal pattern (Figure 4), the strong autocorrelation of the observed step lengths at a 24-hour lag (Figure 5) shows the need to incorporate temporal heterogeneity in the model — we could have reached this conclusion even without developing any of the temporal-heterogeneity machinery. Because there are a huge number of potential complexities that can be added to movement models (e.g. spatial/temporal/among-individual heterogeneity; effects of conspecific attraction or avoidance; memory or cognitive effects), each with associated costs in researcher and computational effort, such diagnostic plots are invaluable. In contrast to the

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hourly averages, the autocorrelation (ACF) captures both short- and long-term temporal effects. HMM without temporal heterogeneity captures the short-term autocorrelation, but misses the long-term autocorrelation beyond a 7-hour lag. Temporally homogeneous FMM, by definition, produces neither short- nor longterm autocorrelation. FMM without temporal heterogeneity, although it captures the diurnal pattern well, underpredicts the degree of short-term autocorrelation.

The hardest problem with multiple latent states is interpreting them biologically.

We have no way of knowing what panthers are actually thinking (it is certainly more

complex than being in one of a small number of discrete latent states); we don't

know the "true" number of latent states, nor are we able to observe them directly,

although incorporating additional direct observations of behaviour (if available)

can at least partially address this problem [7]. Three distinct movement states seem

biologically interpretable for Florida panthers according to van de Kerk et al.[14]:

Short step length suggests resting states, intermediate step length a foraging state,

and long step length a traveling state.

The estimated parameter values for several cats (mean and standard devia-292 tion of the step length in each state) between the time-homogeneous and time-293 heterogeneous models are similar across all cats (Figure 7). In general, the states with longer mean step lengths are relatively similar between model classes. For cats 295 14 and 15, the states with the longest or next-longest mean step lengths have similar 296 means and standard deviations; for cats 1 and 2, three long-step states in the ho-297 mogeneous HMM appear to divide two long-step states in the heterogeneous HMM. 298 For short-step states, the heterogeneous HMM tends to identify a high-variance 299 state, while the homogeneous HMM picks up states with very short step lengths 300 (questionable in any case because we have not taken any special efforts to account for GPS error).

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## 303 Discussion

HMMs are a widely used and flexible tool for modeling animal movement behaviour; we need to work harder to make sure they are both appropriately complex and biologically interpretable. With the increasing volumes of movement data
available, ecologists who naively use traditional homogeneous HMMs and standard
information-theoretic criteria to estimate the number of behavioural states will generally overfit their data, in the sense of "discovering" large number of states that
are difficult to interpret biologically.

On a broad spectrum, it really depends on what kind of question that is being 311 answered. On one side of the spectrum, if the goal is to identify states, it might 312 be sufficient to use a simple/traditional HMM model and pre-specify the number 313 of states and, post hoc, match Viterbi-based states estimates with environmental 314 variation [7]. On the other side of the spectrum, if the goal of interest is to make 315 predictions (out of sample), it might be better to fit a covariate-dependent model so 316 that we can explicitly model the switching process. In that case, fitting a covariatedependent model is better for out of sample prediction because Viterbi can only estimate state occupancy if observed movements are available (within sample pred-319 itions). Finally, if we want to estimate the number of states, BIC is not necessarily 320 good for estimation of number of states [25], but it can be useful as an approximate 321 upper limit estimate. 322

Incorporating temporal heterogenity in animal movement is one step in the right
direction, but much remains to be done. Our model neglects other predictors, such
as habitat type or location with respect to environmental features such as roads,
that can potentially improve goodness of fit and predictions and further reduce the
estimated number of states. While adding more covariates is in principle straightforward using existing frameworks, including all possible biological complexities in
a HMM with state-dependent transitions may rapidly become intractable in terms

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of both computational time and complexity of choosing among possible reduced models and numbers of states. Better diagnostic procedures and tests are needed: these can both test overall goodness-of-fit [26] and, more importantly, localize fitting problems to particular aspects of the data so that models can be constructed without needing to include all possible features of interest.

## 335 Conclusion

We have presented a relatively simple but little-used extension (time-dependent 336 transitions) that partly resolves the problem. Time-dependent transitions appear to 337 offer a simple way to (1) reduce the selected number of states closer to a biologically 338 interpretable level; (2) capture observed diurnal and autocorrelation patterns in a 339 predictive model; (3) improve overall model fit (i.e., lower BIC) and reduce the level 340 of complexity (number of parameters) of the most parsimonious models. Simple 341 simulations where the true number of states is known, and transitions among states 342 vary over time, confirm that using BIC with homogeneous HMMs overestimates the number of behavioural states, while time-dependent HMMs correctly estimate the number.

# 6 Declarations

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# 351 1 Data accessibility

352 Hourly step lengths and turning angles of male and female Florida panthers available at:

353 http://ufdc.ufl.edu//IR00004241/00001.

## 54 Author's contributions

355 Equally contributed

#### 356 Competing interest

The authors declare that they have no competing interests.

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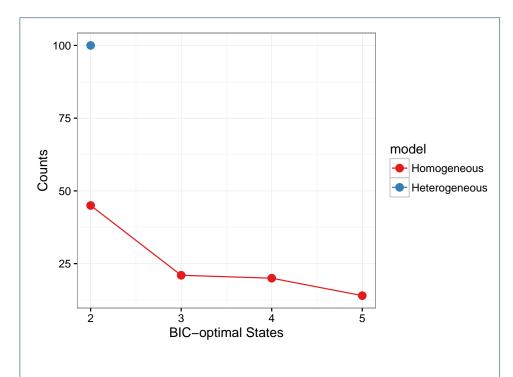
## 427 Figures

# 428 Tables

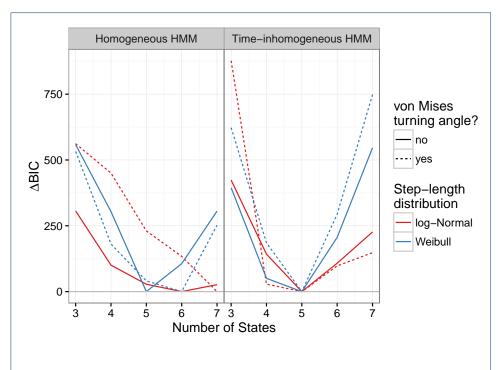
Table 1 Cat ID

van de Kerk 2015	IR@UF	Number of Observations
130	1	10286
131	2	9458
48	14	14645
94	15	10250

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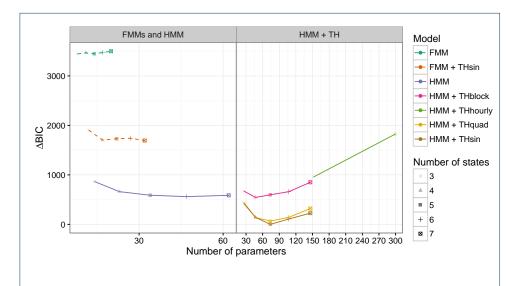


**Figure 1 Simulation Results** BIC-optimal state frequency for 2-6 state HMMs with and without covariate transition on 100 two-state hidden Markov models with covariate transitioning simulations.

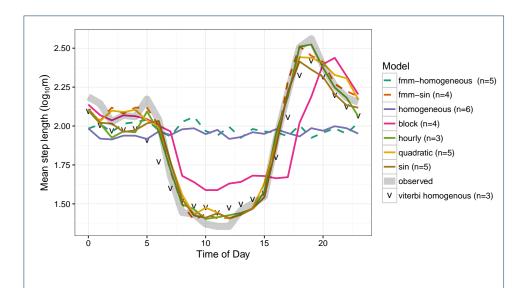


**Figure 2 Adjusted BIC Emission Distribution Comparison** Adjusted Bayesian information criterion values for 3-7 state HMMs with different step-length distributions, with and without temporal transitions and turning angles.

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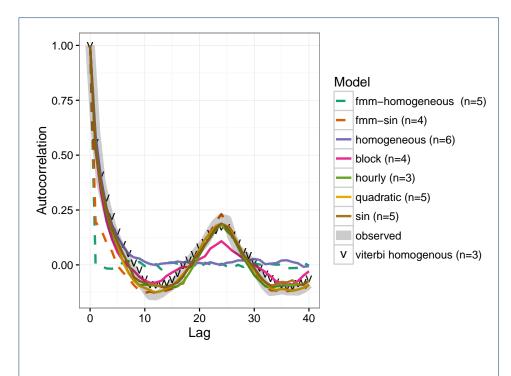


**Figure 3 Adjusted BIC Transition Comparison** Adjusted BIC by number of free parameters for HMM model types. The left panel shows FMM, FMM with a sin prior and HMM. The right panel shows HMMs with different temporal transitions.

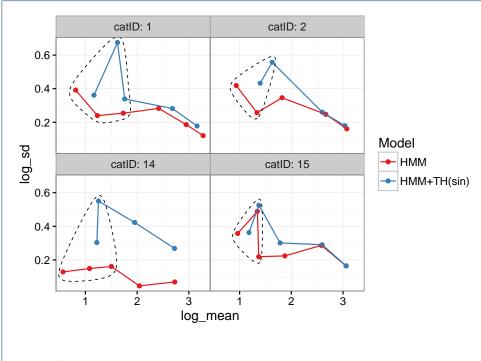


**Figure 4 Diurnal Step Lengths Plot** Average step length by time of day observed (gray highlight), three-state HMM Viterbi predictions (V points), and all transitions type HMMs predictions (out of sample) with their respective BIC-optimal states.

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**Figure 5 Autocorrelation Plot** Autocorrelation of observed (gray highlight), three-state HMM Viterbi predictions (V points), and all transitions type HMMs predictions (out of sample) with their respective BIC-optimal states.



**Figure 6 State Identification Plot** Log mean and standard deviation of BIC-optimal HMM and HMM with sinusoidal transition.