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Incorporating Periodic Variability in Hidden Markov Models for Animal Movement

Michael Li[1]* and Benjamin M. Bolker[1,2]

Sample of title note

Correspondence:
m88@mcmaster.ca
Department of Biology,
McMaster University, 1280 Main
St. West, L8S 4K1, Hamilton,
Ontario, Canada
Full list of author information is
available at the end of the article
Equal contributor

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

Background

Given a sequence of animal movements, movement models aim to find a parsimonious description that can be used to understand past movements and 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 [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

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 [8, 9].

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 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 environmental 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

general ecologists have turned to other tools to describe behavioural changes over

longer (diurnal, seasonal, or ontogenetic) time scales [12].

For movement behaviours that change on a fast time scale, such that movement

behaviours recorded at successive observations are effectively independent, *finite*

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

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.

Methods

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.[14]. 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

89 decomposing contiguous sequences of hourly GPS coordinates into successive step

90 lengths (in meters) and turning angles (in radians) [9, 14].

91 van de Kerk et al.[14] used hidden semi-Markov models (HSMM), an extension of

92 HMM that permits explicit modelling of dwell times [6], considering both Poisson

93 and negative binomial distributions for dwell times. As shown by van de Kerk et

94 al.[14] (Figure S3b, top row, middle panel), the estimated shape parameter of the

95 negative binomial dwell time distribution was typically close to 1 ($\approx 0.4 - 1.6$;

96 confidence intervals were not given), implying that a geometric distribution (i.e.,

97 negative binomial with shape=1) might be adequate. In turn, this suggests that we

98 might not lose much accuracy by reverting to a simpler HMM framework, which

99 corresponds to making precisely this assumption.

100 van de Kerk et al.[14] considered time-homogeneous models with a variety of

101 candidate distributions — log-Normal, Gamma, and Weibull distributions for step

102 lengths and von Mises and wrapped Cauchy distributions for the turning angle

103 — concluding on the basis of the Akaike information criterion (AIC) that Weibull

104 step length and wrapped Cauchy turning angle distributions were best. Since our

105 analysis aims for simplicity and qualitative conclusions rather than for picking the

106 very best predictive model, we focus on models that treat each step as a univariate,

107 log-Normally distributed observation, glossing over both the differences in shape

108 between the three candidate step-length distributions and the effects of consider-

109 ing multivariate (i.e., step length plus turning angle) observations. However, we do

110 briefly compare log-Normal and Weibull step-length distributions, with and without

111 a von Mises-distributed turning angle included in the model (Figure 2). (Note that

112 most movement analyses, including van de Kerk et al. [14], are only partially multi-

113 variate, treating step length and turning angle at a particular time as multivariate

114 observations for the purpose of HMM analysis but neglecting possible correlations

115 between the two measures.)

116   van de Kerk et al.[14] used the Bayesian (Schwarz) information criterion (BIC)

117   to test the relative penalized goodness of fit for models ranging from 2 to 6 latent

118   states. In general, BIC values decreased as the number of states increased from

119   three to six states, suggesting that the six-state model was favoured statistically;

120   however, the authors used three-state models in most of their analyses for ease of

121   biological interpretation. We follow van de Kerk et al.[14] in using BIC-optimality

122   (i.e., minimum BIC across a family of models) as the criterion for identifying the

123   best model, because we are interested in explaining the data generation process by

124   identifying the "true" number of underlying movement states.

125   Using BIC also simplifies evaluation of model selection procedures; it is easier to

126   test whether our model selection procedure has selected the model used to simulate

127   the data, rather than testing whether it has selected the model with the minimal

128   Kullback-Leibler distance [20]. We recognize that ecologists will often be interested

129   in maximizing predictive accuracy rather than selecting a true model, and that as

130   usual in ecological systems the true model will be far more complicated than any

131   candidate model [21]; we believe that the qualitative conclusions stated here for

132   BIC-optimality will carry over to analyses using AIC instead.

133   Model description

134   In a HMM, the joint likelihood of *emissions* (i.e., direct observations) $\mathbf{Y} = \mathbf{y}_1, ..., \mathbf{y}_T$

135   and a hidden state sequence $\mathbf{Z}, z_t \in \{1, ..., n\}, t = 1, ..., T$, given model parameters

136    $\boldsymbol{\theta}$ and covariates $\mathbf{X}_{1:T} = \mathbf{x}_1, ..., \mathbf{x}_T$, can be written as:

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

137   The emissions $\mathbf{y}_i$ are boldfaced to denote that we may have a vector of observations

138   at each time point (e.g., step length and turning angle). The model contains three

139   distinct components:

140   **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

141           $t = 1$ where the covariate is $\mathbf{x_1}$, times the vector of observations $\mathbf{y_1}$ condi-

142   tioned on covariates $\mathbf{x_1}$ and state z_1.

143   **Transition probability** $P(z_k = j|z_{k-1} = i, \mathbf{x_k})$: the probability of a transition

144   from state i at time $t = k - 1$ to state j with covariate $\mathbf{x_k}$ at time $t = k$.

145   **Emission probability** $P(\mathbf{y_k}|z_k, \mathbf{x_k})$: a vector of observations $\mathbf{y_k}$ conditioned on

146   covariates $\mathbf{x_k}$ at state z_k at time $t = k$.

147   Eq. 1 gives the likelihood of the observed sequence given (conditional on) a partic-

148   ular hidden sequence. In order to calculate the overall, unconditional (or marginal)

149   likelihood of the observed sequence, we need to average over all possible hidden

150   sequences. There are several efficient algorithms for computing the marginal like-

151   lihood and numerically estimating parameters [22]; we used those implemented in

152   the `depmixS4` package for R [23, 24].

153   For any n-state HMM, we need to define a $n \times n$ matrix that specifies the

154   probabilities π_{ij} of being in movement states j at time $t+1$ given that the individual

155   is in state i. The FMM is a special case of HMM where the probabilities of *entering*

156   a given state are identical across all states — i.e., the probability of occupying a

157   state at the next time step is independent of the current state occupancy. It can be

158   modelled in the HMM framework by setting the transition probabilities $\pi_{ij} = \pi_{i*}$.

159   In any case, the transition matrix π_{ij} must respect the constraints that (1) all

160   probabilities are between 0 and 1 and (2) transition probabilities out of a given state

161   sum to 1. As is standard for HMMs with covariates [23], we define this multinomial

162   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 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 π_{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 ($\delta_{m=t} = 1$ 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.

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

177 **Sinusoidal transition model** A sinusoidal model with a period of 24 hours is

178 identical in complexity to the quadratic model, but automatically satisfies

179 the diurnal continuity constraint.

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

180 **Hourly model** Lastly, we extended the multi-block approach and assign a differ-

181 ent transition matrix for every hour of the day. This model is included for

182 comparative purposes due to the large number of parameters in the model

183 which makes it not really practical. We only fitted up to four states using the

184 hourly model.

185 Other periodic functions, such as Fourier series (the sinusoidal transition model

186 augmented by additional sinusoidal components at higher frequencies) or periodic

187 splines, could be useful directions for future exploration.

188 Model evaluation

189 We used the `depmixS4` package to fit covariate-dependent transition HMMs, simu-

190 late states and step lengths using the estimated parameters, and estimate the most

191 likely states with the Viterbi algorithm.

192 We used three approaches to assess the fit of both time-homogeneous and time-

193 inhomogeneous HMMs with 3 to 6 states to step-length data from the four of the

194 thirteen Florida panthers with the most data ($> \mathbf{9000}$ observations). (1) Comparing

195 BICs to the optimal-BIC model within each type of transition complexity ($\mathbf{\Delta}$BIC

196 $=$ BIC - min(BIC)) assesses the overall goodness of fit of each model type. (2)

197 Comparing average step-length by hour of day for the observed data and for data

198 simulated from the models shows how well a particular class of models can capture

199 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.

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:

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

As the number of states increases, the number of free parameters in time-

homogeneous FMMs and HMMs and FMMs with temporal heterogenity will in-

crease linearly, whereas HMMs with temporal heterogenity will increase quadrat-

ically (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 homoge-

neous 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

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-homogenous 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

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 from the observed data (Figure 4). As expected, temporally homogeneous models (whether FMM or 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 (changing the block definitions might help), and the (over-parameterized) hourly model does better than any other model at capturing the early-evening peak (but worse at capturing the mid-day trough). We also included average hourly step lengths from three-state temporally homogeneous HMM Viterbi 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

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 long-term 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 deviation of the step length in each state) between the time-homogeneous and time-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 14 and 15, the states with the longest or next-longest mean step lengths have similar means and standard deviations; for cats 1 and 2, three long-step states in the homogeneous HMM appear to divide two long-step states in the heterogeneous HMM. For short-step states, the heterogeneous HMM tends to identify a high-variance state, while the homogeneous HMM picks up states with very short step lengths (questionable in any case because we have not taken any special efforts to account for GPS error).

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

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

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.

Conclusion

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

Declarations

Author's contributions

Equally contributed.

Competing interests

The authors declare that they have no competing interests.

Author details

[1] Department of Biology, McMaster University, 1280 Main St. West, L8S 4K1, Hamilton, Ontario, Canada. [2] Department of Mathematics and Statistics, McMaster University, 1280 Main St. West, L8S 4K1, Hamilton, Ontario, Canada.

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