An Introduction to Animal Movement Modeling with Hidden Markov Models using Stan for Bayesian Inference

Vianey Leos-Barajas¹ & Théo Michelot²

¹Iowa State University/Bielefeld University - vleosbarajas@wiwi.uni-bielefeld.de
²University of Sheffield - tmichelot1@sheffield.ac.uk

Introduction

Hidden Markov models (HMMs) are popular time series model in many fields including ecology, economics and genetics. HMMs can be defined over discrete or continuous time, though here we only cover the former. In the field of movement ecology in particular, HMMs have become a popular tool for the analysis of movement data because of their ability to connect observed movement data to an underlying latent process, generally interpreted as the animal’s unobserved behavior. Further, we model the tendency to persist in a given behavior over time.

Those already familiar with Michael Betancourt’s case study “Identifying Bayesian Mixture Models” will see a natural extension from the independent mixture models that are discussed therein to an HMM, which can also be referred to as a dependent mixture model. Notation presented here will generally follow the format of Zucchini et al. (2016) and cover HMMs applied in an unsupervised case to animal movement data, specifically positional data. We provide Stan code to analyze movement data of the wild haggis as presented first in Michelot et al. (2016). Implementing HMMs in Stan has also been covered by Luis Damiano here: https://github.com/luisdamiano/gsoc17-hhmm For a thorough overview of HMMs, see Zucchini et al. (2016).

Hidden Markov Models

An HMM is a doubly stochastic time series with an observed process \( (Y_t) \) that depends on an underlying state process \( (S_t) \). The observations \( \{Y_t\}_{t=1}^T \) are taken to be conditionally independent given the states \( \{S_t\}_{t=1}^T \) and are generated by so-called state-dependent distributions, \( \{f_n\}_{n=1}^N \). In this case we assume that \( S_t \) can take on a finite number \( N \geq 1 \) of states, such that we can also refer to this as an \( N \)-state HMM. The evolution of states over time is governed by a first-order Markov chain, i.e. \( \Pr(S_t|S_{t-1}, \ldots, S_1) = \Pr(S_t|S_{t-1}) \), with transition probability matrix \( \Gamma^{(t)} = \gamma_{i,j}^{(t)} \), where \( \gamma_{i,j}^{(t)} = \Pr(S_t = j|S_{t-1} = i) \) for \( i, j = 1, \ldots, N \). Assuming a time-homogeneous process, we have that \( \Gamma^{(t)} = \Gamma \). A consequence of this formulation is that the amount of time \( D_n \) spent in a given state \( n \) (before switching to another state) is a random variable that follows a geometric distribution with parameter \( 1 - \gamma_{n,n} \), formally \( D_n \sim Geom(1 - \gamma_{n,n}) \) with \( D_n \in \mathbb{N} \). Lastly, it is necessary to define the initial state distribution \( \delta^{(1)} \) for the state process at time \( t = 1 \) with entries \( \delta_n^{(1)} = \Pr(S_1 = n) \), for \( n = 1, \ldots, N \).

All together, an HMM is completely defined by specification of three components:

- State-dependent distributions, \( \{f_n\}_{n=1}^N \)
- Transition probability matrix, \( \Gamma^{(t)} = \gamma_{i,j}^{(t)} \) for \( i, j = 1, \ldots, N \)
- Initial state distribution, \( \delta^{(1)} \)
  - Stationary distribution, \( \delta = \delta \Gamma \)
  - Estimate the initial state distribution, e.g. \( \delta^{(1)} \sim \text{Dirichlet}(\nu) \)
For a time-homogeneous process we can use the stationary distribution as the initial state distribution, otherwise we can estimate the distribution.

Likelihood

There are two functions referred to as the “likelihood” in the HMM literature, the complete-data likelihood, i.e. the joint distribution of the observations and states, or the marginal likelihood, i.e. the joint distribution of the observations only. The complete-data likelihood is written as follows,

\[ f(y, s) = \mathcal{L}_c = \delta_{s_1} \prod_{t=2}^{T} \gamma_{s_{t-1}, s_t} \prod_{t=1}^{T} f_{s_t}(y_t) \]  

(1)

The simplicity of the complete-data likelihood formulation may be one reason why many conduct inference for parameters and states jointly, typically through a Gibbs sampler, alternating between estimation of states and parameters. In contrast, evaluation of the marginal likelihood requires summation over all possible state sequences,

\[ \mathcal{L}_m = \sum_{s_1=1}^{N} \cdots \sum_{s_T=1}^{N} \delta_{s_1} \prod_{t=2}^{T} \gamma_{s_{t-1}, s_t} \prod_{t=1}^{T} f_{s_t}(y_t) \]  

(2)

However, evaluation of the marginal likelihood is necessary for implementation in Stan as the states are discrete random variables. Zucchini et al. (2016) show that the marginal likelihood can be written explicitly as a matrix product,

\[ \mathcal{L}_m = \delta^{(1)} \mathbf{P}(y_1) \Gamma \mathbf{P}(y_2) \cdots \Gamma \mathbf{P}(y_T) \mathbf{1}^T \]  

(3)

for an \( N \times N \) matrix \( \mathbf{P}(y_t) = \text{diag}(f_1(y_t), \ldots, f_N(y_t)) \) and a vector of \( 1 \)s of length \( N \), \( \mathbf{1} = (1, \ldots, 1) \). For observations missing at random, we simply have \( \mathbf{P}(y_t) = \mathbf{I}_{N \times N} \). The marginal likelihood can be calculated efficiently with the forward algorithm, which calculates the likelihood recursively. We define the forward variables \( \alpha_t \), beginning at time \( t = 1 \), as follows

\[ \alpha_1 = \delta^{(1)} \mathbf{P}(y_1), \quad \alpha_t = \alpha_{t-1} \Gamma \mathbf{P}(y_t), \]  

(4)

Then, the marginal likelihood is obtained by summing over \( \alpha_T \),

\[ \mathcal{L}_m = f(y_1, \ldots, y_T) = \sum_{i=1}^{N} \alpha_T(i) = \alpha_T \mathbf{1}^T. \]  

(5)

Notably, the computational effort involved in evaluating \( \mathcal{L}_m \) is only linear in \( T \), the number of observations, for a given number of states, \( N \). Direct evaluation of the likelihood can result in numerical underflow. However, we can also use the forward algorithm to evaluate the log marginal likelihood, \( \log(\mathcal{L}_m) \), and avoid underflow when calculating each forward variable – as demonstrated in the implementation in Stan model given below.

For the HMM details we provide here, we assume the following:

- The state-dependent distributions are distinct, \( f_1 \neq \cdots \neq f_N \);
- The t.p.m. \( \Gamma \) has full rank and is ergodic

These two points are sufficient for an HMM to be identifiable. The first point is important when applying an HMM to animal movement data because the states are assumed to reflect different behaviors. The second point indicates we would like for the animal to be able to transition between behaviors across time.
Priors

An HMM has two main sets of parameters that require specification of prior distributions, the parameters corresponding to the i) state-dependent distributions and ii) transition probabilities, with a possible third set if estimating the initial distribution as well.

However, because an HMM lies within the class of mixture models, the lack of identifiability due to label-switching (i.e. a reordering of indices can lead to same joint distribution) should be taken into account.

State-dependent distributions

As in the independent mixture models discussed in Betancourt (2017), identification and inferences of the state-dependent distributions of an HMM can be problematic. Issues related to label-switching can make it difficult for the MCMC chains to efficiently explore the parameter space. In practice, HMMs are also notorious for their multi-modality. As such, some additional restrictions and information, such as ordering of a subset of the parameters of interest and/or informative priors can aid inference. For example, we can impose an ordering on the means, \( \mu_1 < \mu_2 < \cdots < \mu_N \), of the state-dependent distributions (if possible), which is easily done in Stan:

```stan
parameters {
  positive_ordered[N] mu;
}
```

Other parametrizations can also be used to order the means. For example, given \( \mu_1 \in \mathbb{R} \) and a vector of length \( N - 1 \), \( \eta \in \mathbb{R}^+ \), \( \mu_n = \mu_{n-1} + \eta_{n-1} \), for \( n \in 2, \ldots, N \).

```stan
parameters {
  real mu;
  vector<lower=0> etas[N-1];
}
transformed parameters{
  vector[N] ord_mus;
  ord_mus[1] = mu;
  for(n in 2:N)
    ord_mus[n] = ord_mus[n-1] + etas[n-1];
}
```

As the state-dependent distributions reflect characteristics of the observed data, priors for the parameters of interest should not place the bulk of the probability on values that are unrealistic. Also, note that because of potential label-switching, some type of ordering will likely be needed so that the priors correspond to the appropriate distributions (if not exchangeable). See Betancourt (2017) for similar issues in mixture models.

Transition Probability Matrix

It is typically easier to form some type of intuition of the parameters of the state-dependent distributions than entries of the t.p.m. However, in animal movement data there is generally persistence in the estimated states that we would like to capture (hence the reason for using HMMs). For the model, this behavior corresponds to large diagonal entries, \( \gamma_{n,n} \) for \( n \in \{1, \ldots, N\} \), typically \( >0.8 \) in our own experience, though this could of course vary depending on the temporal resolution of the data and question of interest.
Capturing Important Features of the Data and Model Evaluation

There are two features of the movement data that we aim to capture, a) the marginal distribution of \( Y_t \) and b) the temporal dependence of the observed data (e.g. autocorrelation).

Marginal Distribution of \( Y_t \) and Temporal Dependence

The marginal distribution of \( y_t \) of an HMM is the distribution a given observation at time \( t \) unconditional on the states, \( f(y_t|\theta) \), with \( \theta \) reflecting the state-dependent parameters requiring estimation. For a time-homogeneous process with stationary distribution, \( \delta \), the marginal distribution is derived as a mixture of the state-dependent densities weighted by entries of \( \delta \),

\[
f(y_t|\theta) = \delta_1 \cdot f_1(y_t) + \cdots + \delta_N \cdot f_N(y_t)
\]

In the analysis of animal movement data, the stationary distribution can give the ecologist an estimate of the proportion of time that the animal exhibits the states (and related behaviors) overall. However, it is important to not only report this result of the HMM because there are infinitely many HMM formulations that lead to the same marginal distribution for \( y_t \). For example,

\begin{align*}
\text{HMM1} & : f_1 \sim N(0, 4); f_1 \sim N(5, 5) \\
\text{HMM2} & : f_2 \sim N(0, 4); f_2 \sim N(5, 5)
\end{align*}

This result is a key difference between independent mixture models and HMMs. An HMM is identifiable, even given the above result, because there is dependence over time that we take into account via the transition probability matrix, \( \Gamma \). The marginal distribution does not completely relay all of the information about the manner in which the data were generated. In particular, taking into account the temporal dependence, as an HMM does, allows for identification of state-dependent distributions that may significantly overlap and other flexible forms, see Alexandrovich et al. (2016) and Langrock et al. (2015).

Aside from capturing the marginal distribution of \( y_t \), we also aim to capture the temporal dependence present in the data. In particular, the autocorrelation structure of data produced by the fitted HMM should be comparable to the data itself. As a result, this can be a key characteristics with which to do posterior predictive checking (Morales et al., 2004).

Assessing Model Adequacy Using Forecast (Pseudo-)Residuals and Posterior Predictive Checks

Forecast (Pseudo-)Residuals

One manner in which the fitted HMM can be assessed is through evaluation of the (pseudo-)residuals. The pseudo-residuals are computed in two steps. First, for continuous observations, the uniform pseudo-residuals \( u_t \) are defined as

\[
u_t = \Pr(Y_t \leq y_t | Y^{(t-1)} = y^{(t-1)}), \quad t \in \{1, \ldots, T\}.
\]

Then, the normal pseudo-residuals are obtained as

\[r_t = \Phi^{-1}(u_t), \quad t \in \{1, \ldots, T\},\]
where $\Phi$ is the cumulative distribution function of the standard normal distribution. If the fitted HMM is the true data-generating process, the $r_t$ have a standard normal distribution. In practice, a qq-plot can be used to compare the distribution of pseudo-residuals to the standard normal, and assess the fit. Further, the (pseudo-)residuals of a fitted HMM should not be autocorrelated, indicating that the dependence is adequately captured.

**Posterior Predictive Checks**

Posterior predictive checks allow one to assess the adequacy of the fitted model by generating $M$ replicate data sets from the distribution $f(y^*|y) = f(y^*|\theta)f(\theta|y)$. In particular here, we use these checks to assess the fitted model’s ability to be interpreted as the data generating mechanism. The main idea is that the model should be able to produce data that is similar to the one observed in the key features defined a priori.

Given $M$ posterior draws $\theta_1^*,\ldots,\theta_M^*$, we generate $M$ data sets from the distribution $f(y^*|\theta^*)$. We then compare key features of the replicate data sets to observed features. See Betancourt (2018) for more details.

We demonstrate a few graphical posterior predictive checks in the HMM examples.

**State Estimation**

In animal movement modeling (the focus presented here), estimation of the underlying state sequence is not the primary focus of the analysis but rather a convenient byproduct of the HMM framework. It is most important that the estimated state-dependent distributions can be connected to biologically meaningful processes, though state estimation can help one visualize the results of the fitted models.

There are two approaches to state estimation:

- Local State Decoding: $Pr(S_t|y_1,\ldots,y_T,\theta)$ OR
- Global State Decoding: $Pr(S_1,\ldots,S_T|y_1,\ldots,y_T,\theta)$

The first considers the distribution of the state at time $t$, $S_t$, given the observations and estimated parameters $\theta$. These distributions can be obtained through implementation of the forward-backward algorithm.

The aim of the second approach is to obtain the most likely state sequence given all of the observations. For this, we use the Viterbi algorithm which returns the most likely state sequence given the observations and estimated parameters. Both approaches are already covered by Luis Damiano: [https://github.com/luisdamiano/gsoc17-hhmm](https://github.com/luisdamiano/gsoc17-hhmm). In general, both will return similar (if not equal) results when it comes to state decoding (assigning an observation to one of $N$ states).

Going beyond assignment of observations to states and obtaining the state probabilities at each point in time can also be highly informative. In particular, two models may result in similar state decodings yet correspond to different estimates of the parameters of interest. While this is not a problem *per se*, it can be difficult to connect the estimated states to key biological processes when the observations have large probabilities of being associated with more than one state.

**Example: Fitting a 2-state HMM**

```r
# Initialisation
library(rstan)
library(bayesplot)
library(ggplot2)
library(coda)
library(circular)
```
Before getting into details about how HMMs are applied to animal movement data, we present how to fit a basic HMM in Stan (Stan 2018). We consider a 2-state HMM with Gaussian state-dependent distributions for the observation process $X_t$. That is, at each time step $t = 1, 2, \ldots$, we have

$$Y_t | S_t = j \sim N(\mu_j, \sigma^2),$$

for $j \in \{1, 2\}$.

The following code simulates from the model. Note that here we take the initial state distribution to be the stationary distribution.

```r
# Number of states
N <- 2

# transition probabilities
Gamma <- matrix(c(0.9, 0.1, 0.1, 0.9), 2, 2)

# initial distribution set to the stationary distribution
delta <- solve(t(diag(N) - Gamma + 1), rep(1, N))

# state-dependent Gaussian means
mu <- c(1, 5)

nobs <- 1000
S <- rep(NA, nobs)
y <- rep(NA, nobs)

# initialise state and observation
S[1] <- sample(1:N, size=1, prob=delta)
y[1] <- rnorm(1, mu[S[1]], 2)

# simulate state and observation processes forward
for(t in 2:nobs) {
  S[t] <- sample(1:N, size=1, prob=Gamma[S[t-1],])
y[t] <- rnorm(1, mu[S[t]], 2)
}

plot(y, col=pal[S], type="h")
```

The likelihood of the model can be written with the forward algorithm, given in Equation 4 with

$$P(x_t) = 
\begin{pmatrix}
\phi(x_t | \mu_1, \sigma^2) & 0 \\
0 & \phi(x_t | \mu_2, \sigma^2)
\end{pmatrix},$$

where $\phi$ is the Gaussian pdf.

The following code provides the complete implementation of the $N$-state HMM with Gaussian state-dependent distributions in Stan, based on the forward algorithm.

First, we define the known quantities in the data block:
data {
    int<lower=0> N; // number of states
    int<lower=1> T; // length of data set
    real y[T]; // observations
}

There are two sets of parameters that requires estimation, $\Gamma$ and $\mu$, which we define in the parameter block:

parameters {
    simplex[N] theta[N]; // N x N tpm
    ordered[N] mu; // state-dependent parameters
}

We assume stationarity of the underlying Markov chain and initialize the process with the stationary distribution, $\delta$. As $\delta$ is a function of $\Gamma$, we compute it in the transformed parameters block:

transformed parameters{

    matrix[N, N] ta; //
    simplex[N] statdist; // stationary distribution

    for(j in 1:N){
        for(i in 1:N){
            ta[i,j]= theta[i,j];
        }
    }

    statdist = to_vector((to_row_vector(rep_vector(1.0, N))/
                            (diag_matrix(rep_vector(1.0, N)) - ta + rep_matrix(1, N, N)))) ;
}

Given the information in the data block, and having defined all parameters of interest, we now define the rest of the model in the model block:
model {

  vector[N] log_theta_tr[N];
  vector[N] lp;
  vector[N] lp_p1;

  // prior for mu
  mu ~ student_t(3, 0, 1);

  // transpose the tpm and take natural log of entries
  for (n_from in 1:N)
    for (n in 1:N)
      log_theta_tr[n, n_from] = log(theta[n_from, n]);

  // forward algorithm implementation

  for (n in 1:N) // first observation
    lp[n] = log(statdist[n]) + normal_lpdf(y[1] | mu[n], 2);

  for (t in 2:T) { // looping over observations
    for (n in 1:N) // looping over states
      lp_p1[n] = log_sum_exp(log_theta_tr[n] + lp) +
                  normal_lpdf(y[t] | mu[n], 2);

    lp = lp_p1;
  }

  target += log_sum_exp(lp);
}

We first run 2000 iterations for each of the 4 chains, with the first 1000 draws drawn during the warm-up phase, and verify that the posterior draws capture the true parameters.

```
stan.data <- list(y=y, T=nobs, N=2)
fit <- stan(file="HMM1.stan", data=stan.data, refresh=2000)

mus <- extract(fit, pars=c("mu"))

hist(mus[[1]][,1],main="",xlab=expression(mu[1]))
abline(v=1, col=pal[1], lwd=2)
hist(mus[[1]][,2],main="",xlab=expression(mu[2]))
abline(v=5, col=pal[2], lwd=2)
```

From the fitted model, we extract the parameters of interest and generate 4000 data sets in order to perform a few graphical posterior predictive checks.

```
## extract posterior draws
psam <- extract(fit, pars=c("theta", "mu"))

## generate new data sets

n.sims <- dim(psam[[1]])[1]
n <- length(y)

# state sequences
First, we check that the densities of the replicated data sets are similar to the observed data set. For this we use the R package \texttt{bayesplot}.

\begin{verbatim}
ppstates <- matrix(NA, nrow = n.sims, ncol = n)
# observations
ppobs <- matrix(NA, nrow = n.sims, ncol = n)
for (j in 1:n.sims) {
  theta <- psam[[1]][j, , ]
  statdist <- solve(t(diag(N) - theta + 1), rep(1, N))
  ppstates[j, 1] <- sample(1:N, size = 1, prob = statdist)
  ppobs[j, 1] <- rnorm(1, mean = psam[[2]][j, ppstates[j, 1]], sd = 2)
  for (i in 2:length(y)) {
    ppstates[j, i] <- sample(1:N, size = 1, prob = theta[ppstates[j, i - 1], ])
    ppobs[j, i] <- rnorm(1, mean = psam[[2]][j, ppstates[j, i]], sd = 2)
  }
}
\end{verbatim}

First, we check that the densities of the replicated data sets are similar to the observed data set. For this we use the R package \texttt{bayesplot}.

\begin{verbatim}
ppc_dens_overlay(y, ppobs[1:100,])
\end{verbatim}
We also plot the autocorrelation function of the observed data and compare to 90% credible intervals for the 
ACF of the replicated data sets.

```r
nlags <- 61
oac = acf(y[2:(n - 1)], lag.max = (nlags - 1), plot = FALSE)$acf  # observed acf

ppac = matrix(NA, n.sims, nlags)
for (i in 1:n.sims) {
  ppac[i, ] = acf(ppobs[i, ], lag.max = (nlags - 1), plot = FALSE)$acf
}

hpd.acf <- HPDinterval(as.mcmc(ppac), prob = 0.95)
dat <- data.frame(x = 1:61, acf = as.numeric(oac), lb = hpd.acf[, 1], ub = hpd.acf[, 2])

ggplot(dat, aes(x, acf)) + geom_ribbon(aes(x = x, ymin = lb, ymax = ub), fill = "grey70", 
  alpha = 0.5) + geom_point(col = "purple", size = 1) + geom_line() + coord_cartesian(xlim = c(2, 
  60), ylim = c(-0.1, 0.5)) + xlab("Lag") + ylab("ACF") + ggtitle("Observed Autocorrelation 
  Function with 90% CI for ACF of Predicted Quantities")
```
Finally, we use the posterior expected values of the variables of interest to construct the forecast (pseudo-)residuals.

```r
### R code for Forecast (Pseudo-)Residuals

## Calculating forward variables
HMM.lalpha <- function(allprobs, gamma, delta, n, N, mu) {
  la <- matrix(NA, N, n)
  foo <- 0
  la[, 1] <- log(allprobs[1, ])
  sumfoo <- sum(foo)
  for (i in 2:n) {
    foo <- foo %*% gamma * allprobs[i, ]
    sumfoo <- sum(foo)
    la[, i] <- log(foo) + scale
  }
  la
}

## Calculating forecast (pseudo-)residuals
HMM.psres <- function(x, allprobs, gamma, n, N, mu) {
  delta <- solve(t(diag(N) - gamma + 1), rep(1, N))
  la <- HMM.lalpha(allprobs, gamma, delta, n, N, mu)
  pstepmat <- matrix(NA, n, N)
  fres <- rep(NA, n)
```
ind.step <- which(!is.na(x))

for (j in 1:length(ind.step)) {
  pstepmat[ind.step[j], 1] <- pnorm(x[ind.step[j]], mean = mu[1], sd = 2)
  pstepmat[ind.step[j], 2] <- pnorm(x[ind.step[j]], mean = mu[2], sd = 2)
}

if (!is.na(x[1]))
  fres[1] <- qnorm(rbind(c(1, 0)) %*% pstepmat[1, ])
for (i in 2:n) {
  c <- max(la[, i - 1])
  a <- exp(la[, i - 1] - c)
  if (!is.na(x[i]))
    fres[i] <- qnorm(t(a) %*% (gamma/sum(a)) %*% pstepmat[i, ])
}
return(list(fres = fres))

means <- colMeans(mus[[1]])

allprobs <- matrix(1, nrow = n, ncol = N)
for (j in 1:N) allprobs[which(!is.na(y)), j] <- dnorm(y, mean = means[j], sd = 2)

gamma <- matrix(c(mean(psam[[1]][, , 1]), 1 - mean(psam[[1]][, , 1]), 1 - mean(psam[[1]][, , 2]), mean(psam[[1]][, , 2])), nrow = 2, byrow = T)

fres <- HMM.psres(x = y, allprobs = allprobs, gamma = gamma, n = n, N = N, mu = means)

Plotting the residuals in a Q-Q plot:

ggplot(data=data.frame(x=fres$fres), aes(sample = x)) + stat_qq() +
  stat_qq_line(color="purple", size=1) +
  ggtitle("Q-Q Plot") + theme_classic()
Note that it is also possible to construct the distribution of forecast residuals at each time $t$.

**Covariates**

In HMMs applied to animal movement, covariates are typically incorporated at the level of the hidden states. For the general case of time-varying covariates, we define the corresponding time-dependent transition probability matrix $\Gamma^{(t)} = (\gamma_{ij}^{(t)})$, where $\gamma_{ij}^{(t)} = \Pr(S_{t+1} = j | S_t = i)$. The transition probabilities at time $t$, $\gamma_{ij}^{(t)}$, can then be related to a vector of environmental (or other) covariates, $(\omega_1^{(t)}, \ldots, \omega_p^{(t)})$, via the multinomial logit link:

$$
\gamma_{ij}^{(t)} = \frac{\exp(\eta_{ij})}{\sum_{k=1}^{N} \exp(\eta_{ik})},
$$

where

$$
\eta_{ij} = \begin{cases} 
\beta_0^{(ij)} + \sum_{l=1}^{p} \beta_l^{(ij)} \omega_l^{(t)} & \text{if } i \neq j; \\
0 & \text{otherwise}. 
\end{cases}
$$

Essentially there is one multinomial logit link specification for each row of the matrix $\Gamma^{(t)}$, and the entries on the diagonal of the matrix serve as reference categories.

**Modeling Animal Movement with HMMs**

**Motivation**

We consider the application of HMMs to the analysis of animal movement tracks. Movement data typically consist of a bivariate time series of longitude-latitude positions, collected at regular time intervals over the study period (e.g. hourly locations). HMMs are widely used in movement ecology to describe such data as arising from several distinct movement patterns, modelled by the underlying Markov chain $S_t$. In particular, these movement patterns serve as proxies for general behaviors of interest. At each time step, we consider that an animal is in one of $N$ (behavioural) states (e.g. “exploratory”, “foraging”...), on which depend some metrics of movement. Note that there is generally no 1-1 mapping from state to behavior of interest, but more on this later.
In this context, the most common HMM formulation is based on the step lengths and turning angles, which can be derived from the location data. The step length $L_t$ is the distance between the two successive locations $X_t$ and $X_{t+1}$, and the turning angle $\phi_t$ is the angle between the two successive directions $(X_{t-1}, X_t)$ and $(X_t, X_{t+1})$.

**Wild Haggis**

We present a simulation study based on the (simulated) wild haggis tracking data from Michelot et al. (2016). The data set comprises 15 tracks, with slope and temperature covariates.

![Wild Haggis Image](image)

**Figure 3:** Andrea Langrock’s impression of the elusive wild haggis

We use the function `prepData` in the package moveHMM to derive step lengths and turning angles from the location data.

```r
rawhaggis <- read.csv("data/haggis.csv")
# derive step lengths and turning angles from locations
data <- prepData(rawhaggis, type="UTM")

hist(data$step, main="", xlab="Step length")
hist(data$angle, breaks=seq(-pi,pi,length=15), main="", xlab="Turning angle")
```

Following Michelot et al. (2016), we consider a 2-state HMM with gamma and von Mises state-dependent distributions. That is, for $j \in \{1, 2\}$

![Histograms of step lengths and turning angles](image)

**Figure 4:** Histograms of the step lengths (left) and turning angles (right) in the wild haggis data.
\[ L_t | S_t = j \sim \text{gamma}(\alpha_j, \beta_j) \]
\[ \varphi_t | S_t = j \sim \text{von Mises}(\mu_j, \kappa_j), \]

where \( \alpha_j \) is the shape and \( \beta_j \) the rate of the gamma distribution, and \( \mu_j \) is the mean and \( \kappa_j \) the concentration of the von Mises distribution. The larger the concentration, the smaller the variance of the turning angles around their mean.

We find it more convenient to parametrise the gamma distribution in terms of its mean and standard deviation, rather than its scale and rate parameters (default in R and Stan). We use the following transformation to obtain one set of parameters from the other:

\[
\text{shape} = \frac{\text{mean}^2}{\text{SD}^2}, \quad \text{rate} = \frac{\text{mean}}{\text{SD}^2}.
\]

The mean parameter of the von Mises distribution is constrained between \(-\pi\) and \(\pi\). This can cause estimation issues, if the sampler gets stuck around either bound. To address this problem, we consider the alternative parametrisation: for each state \( j \),

\[
\begin{align*}
x_j^\varphi &= \kappa_j \cos(\mu_j) \\
y_j^\varphi &= \kappa_j \sin(\mu_j)
\end{align*}
\]

(6)

The point \((x_j^\varphi, y_j^\varphi)\) is unconstrained in \(\mathbb{R}^2\).

The following code implements a \(N\)-state HMM with gamma and von Mises state-dependent distributions, with the possibility to include covariates in the state process. We describe each block separately.

```plaintext
data {
    int<lower=0> T; // length of the time series
    int ID[T]; // track identifier
    vector[T] steps; // step lengths
    vector[T] angles; // turning angles
    int<lower=1> N; // number of states
    int nCovs; // number of covariates
    matrix[T,nCovs+1] covs; // covariates
}
```

In the ‘data’ block, we include the vector of step lengths, the vector of turning angles, and the (design) matrix of covariate values. The design matrix has one column of 1s, corresponding to the intercept, and one column for each covariate. We also need to specify the length of the time series (i.e. number of locations), the number of states (two in the analysis), and the number of covariates (three in the analysis: temperature, slope, and slope^2).

```plaintext
parameters {
    positive_ordered[N] mu; // mean of gamma - ordered
    vector<lower=0>[N] sigma; // SD of gamma
    // unconstrained angle parameters
    vector[N] xangle;
    vector[N] yangle;
    // regression coefficients for transition probabilities
    matrix[N*(N-1),nCovs+1] beta;
}
```

We define the state-dependent movement parameters: the mean and standard deviation of the gamma distribution (step lengths), and the transformed unconstrained parameters of the turning angle distribution...
defined in Equation 6. The vector of mean step lengths is defined to be ordered, to avoid label switching. We also introduce the matrix of regression coefficients for the transition probabilities, with one row for each non-diagonal entry of the transition probability matrix, and one column for each covariable (plus one for the intercept).

**transformed parameters**

```c++
vector<lower=0>[N] shape;
vector<lower=0>[N] rate;
vector<lower=-pi(),upper=pi()>[N] loc;
vector<lower=0>[N] kappa;
```

// derive turning angle mean and concentration
for(n in 1:N) {
    loc[n] = atan2(yangle[n], xangle[n]);
    kappa[n] = sqrt(xangle[n]*xangle[n] + yangle[n]*yangle[n]);
}

// transform mean and SD to shape and rate
for(n in 1:N)
    shape[n] = mu[n]*mu[n]/(sigma[n]*sigma[n]);
for(n in 1:N)
    rate[n] = mu[n]/(sigma[n]*sigma[n]);
```

In the ‘transformed parameters’, we calculate the parameters expected by the state-dependent pdfs, i.e. the shape and rate of the gamma distribution, and the location (mean) and concentration of the von Mises distribution.

**model**

```c++
vector[N] logp;
vector[N] logptemp;
matrix[N,N] gamma[T];
matrix[N,N] log_gamma[T];
matrix[N,N] log_gamma_tr[T];

// priors
mu ~ normal(0, 5);
sigma ~ student_t(3, 0, 1);
xangle[1] ~ normal(-0.5, 1); // equiv to concentration when yangle = 0
xangle[2] ~ normal(2, 2);
yangle ~ normal(0, 0.5); // zero if mean angle is 0 or pi

// derive array of (log-)transition probabilities
for(t in 1:T) {
    int betarow = 1;
    for(i in 1:N) {
        for(j in 1:N) {
            if(i==j) {
                gamma[t,i,j] = 1;
            } else {
                gamma[t,i,j] = exp(betarow * to_vector(covs[t]));
                betarow = betarow + 1;
            }
        }
    }
}
```

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We derive the transition probability matrix $\Gamma^{(t)}$, at each time point, from the regression coefficients and the covariates values provided. We store the log transition probabilities, which we use in the forward algorithm, in the array $\text{log\_gamma\_tr}$. Note that each matrix (each layer of the array) is transposed, so that each row corresponds to the probabilities of transitioning into a state, rather than out of a state.

We choose priors on the movement parameters based on previous biological knowledge of the movements of the wild haggis.

The loop over the observations corresponds to the forward algorithm, on the log-scale to obtain the log-likelihood and circumvent numerical problems. At time $t$, the $j$-th element of the log forward variable can be written as

$$
\log(\alpha_{t,j}) = \log \left( \sum_{i=1}^{N} \gamma_{ij} \alpha_{t-1,i} \right)
$$

$$
= \log \left( \sum_{i=1}^{N} \exp(\log(\gamma_{ij}) + \log(\alpha_{t-1,i})) \right)
$$

where the $\{\log(\gamma_{ij})\}_{i=1}^{N}$ are given by the $j$-th row of the (transposed) matrix of log transition probabilities.
\( \log_{\text{gamma}} \) tr, and the \( \log(\alpha_{t-1,i}) \) are obtained iteratively.

We fit the model to the haggis data.

```r
# set NAs to out-of-range values
data$step[is.na(data$step)] <- -10
data$angle[is.na(data$angle)] <- -10
data$ID <- as.numeric(data$ID)

stan.data <- list(T=nrow(data), ID=data$ID, steps=data$step, angles=data$angle, N=2, nCovs=3, 
covs=cbind(1, scale(data$temp), scale(data$slope), scale(data$slope)^2))

inits <- list(list(mu=c(1,5), sigma=c(1,5), xangle=c(-1,3), 
yangle=c(0,0), beta=matrix(c(-2,-2,0,0,0,0,0,0),nrow=2)),
list(mu=c(1,5), sigma=c(1,5), xangle=c(-1,3),
yangle=c(0,0), beta=matrix(c(-2,-2,0,0,0,0,0,0),nrow=2)))

fit <- stan(file="HMMmovement.stan", data=stan.data, iter=1000, init=inits, 
control=list(adapt_delta=0.9), chains=2)
```

We can obtain summaries and diagnostics from the fitted model object:

```r
get_elapsed_time(fit)

## warmup sample
## chain:1 963.890 2480.15
## chain:2 945.301 2494.70

summary(fit, pars = c("shape", "rate", "loc", "kappa"), probs = c(0.05, 0.95))
```

```
## mean se_mean sd 5% 95% 
## shape[1] 4.118301 0.003746 0.118450 3.927876 4.3177401 
## shape[2] 2.785982 0.002068 0.065397 2.680773 2.8941504 
## rate[1] 4.143358 0.004079 0.128977 3.930484 4.3526516 
## rate[2] 0.557604 0.000436 0.013802 0.534991 0.5814677 
## loc[1] -2.485117 0.059702 1.851187 -3.134587 3.1300015 
## loc[2] -0.309105 0.000192 0.006072 -0.319176 -0.2989181 
## kappa[1] 1.011625 0.001156 0.036555 0.952281 1.0730602 
## kappa[2] 8.007154 0.006321 0.013000 7.699328 8.3305498 
## 
## n_eff Rhat 
## shape[1] 1000.000 1.002919 
## shape[2] 1000.000 0.9989344 
## rate[1] 1000.000 1.0029198 
## rate[2] 1000.000 0.9991912 
## loc[1] 961.7489 0.9984171 
## loc[2] 1000.000 0.9989916 
## kappa[1] 1000.000 0.9988296 
## kappa[2] 1000.000 0.9988326 

We plot the estimated step length and turning angle densities for each state.

```r
# restore NAs
data$step[data$step < 0] <- NA
data$angle[data$angle < (-pi)] <- NA

# unpack posterior draws
shape <- extract(fit, pars = "shape")$shape
rate <- extract(fit, pars = "rate")$rate
```

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Figure 5: Histograms of the observed step lengths (left) and turning angles (right), with the estimated state-dependent densities weighted by the stationary distributions.

```
loc <- extract(fit, pars = "loc")$loc
kappa <- extract(fit, pars = "kappa")$kappa

# indices of posterior draws to plot (thinned for visualisation purposes)
ind <- seq(1, nrow(shape), by = 5)

# plot step length densities
stepgrid <- seq(min(data$step, na.rm = TRUE), max(data$step, na.rm = TRUE), length = 100)
plot(NA, xlim = c(0, 20), ylim = c(0, 1.1), xlab = "step length", ylab = "density")
for (i in ind) {
  # plot density for each state
  points(stepgrid, dgamma(stepgrid, shape = shape[i, 1], rate = rate[i, 1]),
         type = "l", lwd = 0.2, col = adjustcolor(pal[1], alpha.f = 0.1))
  points(stepgrid, dgamma(stepgrid, shape = shape[i, 2], rate = rate[i, 2]),
         type = "l", lwd = 0.2, col = adjustcolor(pal[2], alpha.f = 0.1))
}

# plot turning angle densities
anglegrid <- seq(-pi, pi, length = 100)
plot(NA, xlim = c(-pi, pi), ylim = c(0, 1.2), xlab = "turning angle", ylab = "density")
for (i in ind[-1]) {
  # plot density for each state
  points(anglegrid, dvm(anglegrid, mu = loc[i, 1], kappa = kappa[i, 1]), type = "l",
         lwd = 0.2, col = adjustcolor(pal[1], alpha.f = 0.1))
  points(anglegrid, dvm(anglegrid, mu = loc[i, 2], kappa = kappa[i, 2]), type = "l",
         lwd = 0.2, col = adjustcolor(pal[2], alpha.f = 0.1))
}
```

We can also plot the transition probabilities as functions of the covariates. For example, we use the following code to visualise the effect of the slope on the transition probabilities when temperature is equal to 10.
# extract parameters of the t.p.m
samp <- as.matrix(fit)
beta <- samp[, grep("beta", colnames(samp))]

# build a design matrix
gridslope <- seq(min(data$slope), max(data$slope), length = 100)
gridslopesc <- seq(min(scale(data$slope)), max(scale(data$slope)), length = 100)
fixedtemp <- 10
DM <- cbind(1, fixedtemp, gridslopesc, gridslopesc^2)

# indices of posterior draws to plot (thinned for visualisation purposes)
ind <- seq(1, nrow(samp), by = 5)

# plot the transition probabilities
par(mfrow = c(2, 2))
for (i in 1:2) {
  for (j in 1:2) {
    tpm <- moveHMM:::trMatrix_rcpp(nbStates = 2, beta = t(matrix(beta[ind[1], ], ncol = ncol(DM))), covs = DM)
    plot(gridslope, tpm[i, j, ], type = "l", ylim = c(0, 1), col = rgb(1, 0, 0, 0.3), lwd = 0.5, xlab = "slope", ylab = paste0("Pr(", i, " -> ", j, ")")
    for (k in ind[-1]) {
      tpm <- moveHMM:::trMatrix_rcpp(nbStates = 2, beta = t(matrix(beta[k, ], ncol = ncol(DM))), covs = DM)
      points(gridslope, tpm[i, j, ], type = "l", col = rgb(0, 0, 0, 0.2), lwd = 0.5)
    }
  }
}

par(mfrow = c(1, 1))

We perform the same graphical posterior predictive checks from before. First, we simulate data using draws from the posterior distribution of the parameters:

## generate new data sets
n.sims <- dim(kappa)[1]
n <- length(data$step)

# state sequences
ppstates <- matrix(NA, nrow = n.sims, ncol = n)
# observations
ppsteps <- matrix(NA, nrow = n.sims, ncol = n)
ppangs <- matrix(NA, nrow = n.sims, ncol = n)

DM <- cbind(1, scale(data$temp), scale(data$slope), scale(data$slope)^2)
for (j in 1:n.sims) {
  tpm <- moveHMM:::trMatrix_rcpp(nbStates = 2, beta = t(matrix(beta[j, ], ncol = ncol(DM))), covs = DM)
  initdist <- rep(1/N, N)
  ppstates[j, 1] <- sample(1:N, size = 1, prob = initdist)
Figure 6: Posterior transition probabilities as functions of the slope covariate.
ppsteps[j, 1] <- rgamma(1, shape = shape[j, ppstates[j, 1]], rate = rate[j, ppstates[j, 1]])
ppangs[j, 1] <- rvm(1, mean = loc[j, ppstates[j, 1]], k = kappa[j, ppstates[j, 1]])

for (i in 2:n) {
  ppstates[j, i] <- sample(1:N, size = 1, prob = tpm[ppstates[j, i - 1], , i])
  ppsteps[j, i] <- rgamma(1, shape = shape[j, ppstates[j, i]], rate = rate[j, ppstates[j, i]])
  ppangs[j, i] <- rvm(1, mean = loc[j, ppstates[j, i]], k = kappa[j, ppstates[j, i]])
}

for (j in 1:n.sims) ppangs[j, ] <- as.numeric(minusPiPlusPi(ppangs[j, ]))

We check that the densities of the replicated data sets are similar to the observed data set, for both step lengths and turning angles.

ppc_dens_overlay(data$step[which(!is.na(data$step))],
  ppsteps[1:100, which(!is.na(data$step))])

We compare the observed autocorrelation with the autocorrelation of the simulated data sets.

ppc_dens_overlay(data$angle[which(!is.na(data$angle))],
  ppangs[1:100, which(!is.na(data$angle))])
nlags <- 61  
# observed acf
oac = acf(data$step[2:(n - 1)], lag.max = (nlags - 1), plot = FALSE, na.action = na.pass)$acf
ppac = matrix(NA, n.sims, nlags)
for (i in 1:n.sims) {
    ppac[i, ] = acf(ppsteps[i, ], lag.max = (nlags - 1), plot = FALSE)$acf
}

hpd.acf <- HPDinterval(as.mcmc(ppac), prob = 0.95)
dat <- data.frame(y = 1:61, acf = as.numeric(oac), lb = hpd.acf[, 1], ub = hpd.acf[, 2])

ggplot(dat, aes(y, acf)) + geom_ribbon(aes(x = y, ymin = lb, ymax = ub), fill = "grey70", alpha = 0.5) + geom_point(col = "purple", size = 1) + geom_line() + coord_cartesian(xlim = c(2, 60), ylim = c(-0.1, 0.5)) + xlab("Lag") + ylab("ACF") + ggtitle("Observed Autocorrelation Function with 90% CI for ACF of Predicted Quantities")

We also compute the forecast (pseudo-)residuals for the step lengths. We make an adjustment to the previous code because the t.p.m. is no longer stationary.

###### R code for Forecast (Pseudo-)Residuals

## Calculating forward variables
HMM.lalpha <- function(allprobs, gamma, delta, n, N) {
lalpha <- matrix(NA, N, n)
    lscale <- 0
    foo <- delta * allprobs[1, ]
    lscale <- 0
    lalpha[, 1] <- log(foo) + lscale
    sumfoo <- sum(foo)
    for (i in 2:n) {
        foo <- foo * gamma[, , i] * allprobs[i, ]
        # scaling
        sumfoo <- sum(foo)
lscale <- lscale + log(sumfoo)
foo <- foo/sumfoo
lalpha[, i] <- log(foo) + lscale
}
alphas

## Calculating forecast (pseudo-)residuals
HMM.psres <- function(x, allprobs, gamma, n, N, shape, rate) {

delta <- rep(1/N, N)

la <- HMM.lalpha(allprobs, gamma, delta, n, N)
pstepmat <- matrix(NA, n, N)
fres <- rep(NA, n)
ind.step <- which(!is.na(x))

for (j in 1:length(ind.step)) {
pstepmat[ind.step[j], 1] <- pgamma(x[ind.step[j]], shape = shape[1],
rate = rate[1])
pstepmat[ind.step[j], 2] <- pgamma(x[ind.step[j]], shape = shape[2],
rate = rate[2])
}

if (!is.na(x[1]))
  fres[1] <- qnorm(rbind(c(1, 0)) %*% pstepmat[1, ])
for (i in 2:n) {
  c <- max(la[, i - 1])
a <- exp(la[, i - 1] - c)
  if (!is.na(x[i]))
    fres[i] <- qnorm(t(a) %*% (gamma[, , i]/sum(a)) %*% pstepmat[i, ])
}
return(list(fres = fres))
}

shape.est <- colMeans(shape)
rate.est <- colMeans(rate)
beta.est <- colMeans(beta)

allprobs <- matrix(1, nrow = n, ncol = N)
for (j in 1:N) allprobs[which(!is.na(data$step)), j] <- dgamma(data[which(!is.na(data$step)),
"step"], shape = shape.est, rate = rate.est)

gamma <- moveHMM:::trMatrix_rcpp(nbStates = 2, beta = t(matrix(beta.est, ncol = ncol(DM))),
covs = DM)

fres <- HMM.psres(x = data$step, allprobs = allprobs, gamma = gamma, n = n,
N = N, shape = shape.est, rate = rate.est)
Plotting the residuals in a Q-Q plot:

```r
ggplot(data=data.frame(x=fres$fres), aes(sample = x)) + stat_qq() +
  stat_qq_line(color="purple", size=1) +
  ggtitle("Q-Q Plot") + theme_classic()
```

**Interpreting the results - Proceed with caution**

The application of an HMM to positional data is meant to serve as the data generating mechanism. Ideally, the estimated states serve as proxies for biologically meaningful behaviors, but...

---

**Important Lesson:**

The adequacy of the HMM is in no way validated by how well the states correspond to general behaviors of interest.

---

Keeping this in mind, is an HMM useful? Yes, of course! The usefulness lies in combining biological expertise with a modeling framework that is intuitive (from a biological standpoint) to use as the data generating mechanism for the observed movement data. But an HMM is not magic, nor will any other unsupervised technique magically identify general behaviors of interest without some understanding of the biological mechanism.

For various animals, the movement patterns that manifest themselves in positional data do tend to follow a general pattern: directed movements tend to correlate with large step lengths and larger turning angles are generally associated with shorter step lengths. In terrestrial animals, this can broadly serve as proxies for areas in which the animal will forage or travel through. In marine animals, like sharks, we have interpreted the states to correspond to area-restricted search and traveling behavior. Nonetheless, the HMM is useful for clustering movement patterns into these general behavioral states. From there, we can incorporate covariates to understand what may drive an animal to remain in a certain area (chum in the water, habitat quality, etc.).
En fin, an HMM can be quite a useful tool for the analysis of animal movement data, blending important ecological knowledge with sophisticated modeling techniques. And importantly, inferences can be made in the Stan programming language.

Acknowledgements

We thank Juan M. Morales and Roland Langrock for feedback on an earlier version.

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Extras

State decoding

We can obtain inferences into the hidden state process, using either global decoding' (Viterbi algorithm) or local decoding' (forward-backward algorithm). For a set of estimated parameters, the Viterbi algorithm computes the sequence of states most likely to have given rise to the observed data. The forward-backward algorithm is used to derive state probabilities, i.e. probabilities of being in each state at each time step.

In Stan, we can obtain the most likely state sequence (and/or state probabilities) for each posterior draw. We include the Viterbi and forward-backward algorithms in the 'generated quantities' block, as shown below.

generated quantities {
  int<lower=1,upper=N> viterbi[T];
  real stateProbs[T,N];
  vector[N] lp;
  vector[N] lp_p1;

  // Viterbi algorithm (most likely state sequence)
  { real max_logp;
    int back_ptr[T, N];
    real best_logp[T, N];
    
    for (t in 1:T) {
      if(t==1 || ID[t]!=ID[t-1]) {
        for(n in 1:N)
          best_logp[t, n] = gamma_lpdf(steps[t] | shape[n], rate[n]);
      } else {
        for (n in 1:N) {
          best_logp[t, n] = negative_infinity();
          for (j in 1:N) {
            real logp;
            logp = best_logp[t-1, j] + log_theta[t,j,n];
            if(steps[t]>0)
              logp = logp + gamma_lpdf(steps[t] | shape[n], rate[n]);
            if(angles[t]>(-pi()))
              logp = logp + von_mises_lpdf(angles[t] | loc[n], kappa[n]);
          
            if (logp > best_logp[t, n]) {
              back_ptr[t, n] = j;
              best_logp[t, n] = logp;
            }
          }
        }
      }
    }

    for(t0 in 1:T) {
      int t = T - t0 + 1;
      if(t==T || ID[t+1]!=ID[t]) {
        max_logp = max(best_logp[t]);
      }
    }
  }
}
for (n in 1:N)
    if (best_logp[t, n] == max_logp)
        viterbi[t] = n;
} else {
    viterbi[t] = back_ptr[t+1, viterbi[t+1]];
}

// forward-backward algorithm (state probabilities)
{
    real logalpha[T,N];
    real logbeta[T,N];
    real llk;

    // log alpha probabilities
    for(t in 1:T) {
        if(t==1 || ID[t]!=ID[t-1]) {
            for(n in 1:N)
                lp[n] = -log(N);
        }
        for (n in 1:N) {
            lp_p1[n] = log_sum_exp(to_vector(log_theta_tr[t,n]) + lp);
            if(steps[t]>0)
                lp_p1[n] = lp_p1[n] + gamma_lpdf(steps[t] | shape[n], rate[n]);
            if(angles[t] >= (-pi()))
                lp_p1[n] = lp_p1[n] + von_mises_lpdf(angles[t] | loc[n], kappa[n]);
            logalpha[t,n] = lp_p1[n];
        }
        lp = lp_p1;
    }

    // log beta probabilities
    for(t0 in 1:T) {
        int t = T - t0 + 1;
        if(t==T || ID[t+1]!=ID[t]) {
            for(n in 1:N)
                lp_p1[n] = 0;
        } else {
            for(n in 1:N) {
                lp_p1[n] = log_sum_exp(to_vector(log_theta_tr[t+1,n]) + lp);
                if(steps[t+1]>0)
                    lp_p1[n] = lp_p1[n] + gamma_lpdf(steps[t+1] | shape[n], rate[n]);
                if(angles[t+1] >= (-pi()))
                    lp_p1[n] = lp_p1[n] + von_mises_lpdf(angles[t+1] | loc[n], kappa[n]);
            }
            lp = lp_p1;
            for(n in 1:N)
                logbeta[t,n] = lp[n];
        }
    }
}
// state probabilities
for(t0 in 1:T) {
    int t = T - t0 + 1;
    if(t==T || ID[t+1]!=ID[t])
        llk = log_sum_exp(logalpha[t]);
    for(n in 1:N)
        stateProbs[t,n] = exp(logalpha[t,n] + logbeta[t,n] - llk);
}
}