# **Theoretical Crawling**

A guide to the mathematics and statistics of animal movement

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## Outline

#### **Mathematics**

- 1 Discrete-time random walks
- 2 Correlated random walks
- 3 Brownian motion
- 4 Ornstein-Ulenbeck (OU) process
- Stochastic differential equations
- **6** Integrated SDEs
- 7 Continuous-time CRW

# Outline

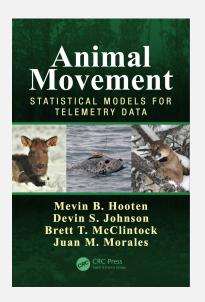
#### Mathematics

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- 6 Integrated SDEs
- 7 Continuous-time CRW

#### **Statistics**

- Maximum likelihood inference
- 2 Bayesian inference
- 3 State-space models
- Kalman filter/smoother (KFS)
- 5 Practical Bayesian inference
- 6 Process imputation

# For more information...



- Available from Amazon (\$86)
- Soon to be available at the MML library
- Borrow from me (maybe Brett)

Part I

movement

Mathematics of animal

# Discrete-time models

## Time series models

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- We want to know something about space use
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#### Notation (discrete time)

- $\mu_t = (\mu_{x,t}, \mu_{y,t})$  is the location of the animal at time t.
- $\mathbf{s}_t = (s_{x,t}, s_{y,t})$  is the observed location at time t.
- $d\mu_t = \mu_t \mu_{t-1}$  is movement!

## Random walk

$$egin{aligned} m{\mu}_t &= m{\mu}_{t-1} + m{\epsilon}_t \ & [m{\epsilon}_t] &= \mathcal{N}(0, m{\Sigma}) \end{aligned}$$

- ullet The movements,  $d\mu_t=\epsilon_t$  are all independent of each other.
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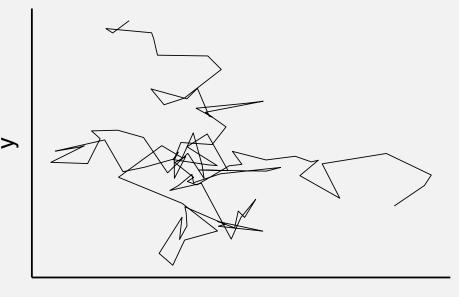
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#### An unconditional view

We can rewite the RW using the accumulation of movements:

$$egin{aligned} \mu_t &= \mu_{t-1} + \epsilon_t \ &= \mu_{t-2} + \epsilon_{t-1} + \epsilon_t \ &= \mu_0 + \sum_{i=1}^t \epsilon_i \end{aligned}$$

# random walk (n = 100)



# Vector autoregressive models (VAR)

Let's suppose that an animal would like to stay close to some focal point, say  $\bar{\mu}$ .

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#### VAR(1) model

$$egin{aligned} \mu_t &= ar{\mu} + \mathsf{M}(\mu_{t-1} - ar{\mu}) + \epsilon_t \ &= (\mathsf{I} - \mathsf{M})ar{\mu} + \mathsf{M}\mu_{t-1} + \epsilon_t \end{aligned}$$

- Weighted mean of last location and point of attraction
- If  $\mathbf{M} \equiv \gamma \mathbf{I}$  and  $|\gamma| < 1$  then as  $t \to \infty$

$$[oldsymbol{\mu}_t] = \mathcal{N}\left(ar{oldsymbol{\mu}}, rac{1}{1-\gamma^2}oldsymbol{\Sigma}
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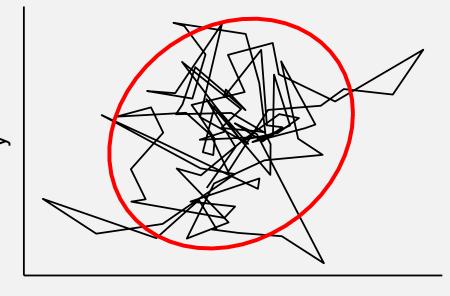
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• What happens if  $\gamma \to 1$ ?

# VAR(1) (n = 100)



# Modeling velocity

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What does that mean for our random walk models in discrete-time?

velocity 
$$=d\mu_t \ = \mu_t - \mu_{t-1}$$

# VAR(1) model for velocity

Instead of directly modeling location as a VAR(1), we can model movement (velocity) with a VAR(1)

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#### Why CRW?

- Step at time t,  $d\mu_t$ , tends to be similar to the previous step,  $d\mu_{t-1}$
- The correlation in steps produces a superdiffusive process for  $\mu_t$
- Why is it useful? Better model of movement in the short term (i.e.,  $t << \infty$ )

If we model  $d\mu_t = \mathbf{M} \ d\mu_{t-1} + \epsilon_t$ , what does this mean for  $\mu_t$ ?

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$$egin{aligned} \mu_t &= \mu_{t-1} + (\mu_t - \mu_{t-1}) \ &= \mu_{t-2} + (\mu_{t-1} - \mu_{t-2}) + (\mu_t - \mu_{t-1}) \ &dots \ &= \mu_0 + \sum_{i=1}^t (\mu_i - \mu_{i-1}) \ &= \mu_0 + \sum_{i=1}^t d\mu_i \end{aligned}$$

Notice that there was no distributional assumption for  $d\mu_t$ . It's a simple recursion.

The CRW can also be represented as a VAR(2) process

$$\begin{split} \boldsymbol{\mu}_t &= \boldsymbol{\mu}_{t-1} + \mathsf{M} d \boldsymbol{\mu}_{t-1} + \boldsymbol{\epsilon}_t \\ &= \boldsymbol{\mu}_{t-1} + \mathsf{M} (\boldsymbol{\mu}_{t-1} - \boldsymbol{\mu}_{t-2}) + \boldsymbol{\epsilon}_t \\ &= (\mathbf{I} + \mathbf{M}) \boldsymbol{\mu}_{t-1} - \mathsf{M} \boldsymbol{\mu}_{t-2} + \boldsymbol{\epsilon}_t \end{split}$$

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#### The **M** matrix

Turning angle specification

$$\mathbf{M} = \gamma \begin{bmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{bmatrix}$$

- $\theta$  represents mean turning angle (probably close to 0)
- $0 < \gamma < 1$  controls the correlation in velocity

Let's suppose  $\theta=$  0, so,

 $\mathbf{M}=\gamma\mathbf{I}$ 

Then  $\operatorname{corr}(d\mu_t,d\mu_s)=\gamma^{|t-s|}$ 

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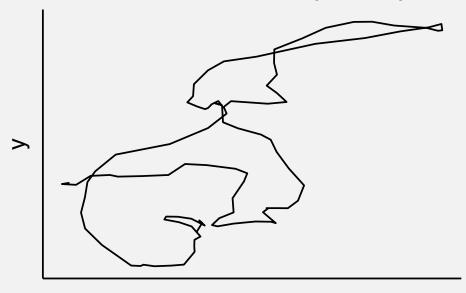
Then 
$$\operatorname{corr}(d\mu_t,d\mu_s)=\gamma^{|t-s|}$$

But let's reparameterize  $\gamma = e^{-\beta}$ , then

- $\gamma \approx 1 \implies \beta \approx 0$
- $\gamma \approx 0 \implies \beta$  very large (sort of)

So,  $\operatorname{corr}(d\mu_t,d\mu_s)=e^{-\beta|t-s|}$ 

# discrete time CRW (n = 100)



# Continuous-time models

Forms the basis of all continuous-time models

Forms the basis of all continuous-time models Random walk in continuous-time

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Random walk in continuous-time

So, let's start from the beginning...

$$\mathbf{b}_{t} = \mathbf{b}_{t-1} + \epsilon_{t}$$

$$= \mathbf{b}_{0} + \sum_{j=1}^{t} [\mathbf{b}_{j} - \mathbf{b}_{j-1}]$$

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Recall,  $[d\mathbf{b}_j] = N(\mathbf{0}, \sigma^2 \mathbf{I})$  and  $d\mathbf{b}_j$  is indep. of  $d\mathbf{b}_i$  (usually,  $\mathbf{b}_0 = \mathbf{0}$  and  $\sigma = 1$ )

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#### Definition

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#### Brownian motion

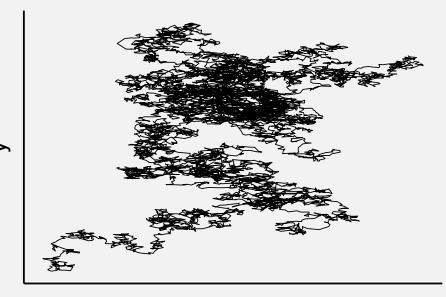
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#### **Definition**

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- db<sub>τ</sub> is infinitely rough
- $oldsymbol{b}_{ au}$  is a continuous function of time with no classical derivative
- Trivia fact for the bar: Here '∫' represents an Ito integral

# **Brownian motion**



#### Brownian motion

#### **Properties**

- Mean $[\mathbf{b}_{ au}] = \mathbf{0}$
- $Var[\mathbf{b}_{\tau}] = \tau \mathbf{I}$
- Independent increments ...

 $\mathbf{b}_{\tau_2} - \mathbf{b}_{\tau_1}$  is independent of  $\mathbf{b}_{\tau_4} - \mathbf{b}_{\tau_3}$  if  $[\tau_1, \tau_2]$  does not overlap  $[\tau_3, \tau_4]$ .

(1) 
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$$\mu_t = \mu_0 + \sum_{j=1}^t [\mu_j - \mu_{j-1}]$$
  
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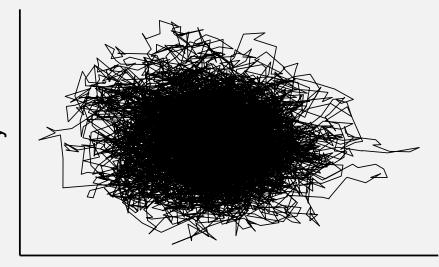
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which implies  $(\beta = 1 - \gamma)$ 

$$d\boldsymbol{\mu}_\tau = -\beta(\boldsymbol{\mu}_\tau - \bar{\boldsymbol{\mu}})d\tau + \sigma d\mathbf{b}_\tau$$

# **Ornstein-Uhlenbeck motion**

corr = 0.95



# Stochastic differential equations

General form

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For OU model

$$m{\mu}_{ au} = e^{-eta t} m{\mu}_0 + (1 - e^{-eta au}) ar{m{\mu}} + m{\zeta}_{ au}$$

where 
$$[oldsymbol{\zeta}_{ au}] = \mathcal{N}\left(oldsymbol{0}, rac{\sigma^2(1-\mathrm{e}^{-2eta au})}{2eta}oldsymbol{I}
ight)$$

# Integrated SDEs (Velocity modeling)

#### New notation:

- $\nu_{\tau} =$  velocity at time  $\tau$
- $H(\mu_{ au}) = ext{potential function to control movement}$
- $\nabla H(\cdot) = \text{spatial gradient of } H$

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#### **CTCRW**

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u}_{ au} &= \mathsf{OU}(eta, \sigma) \ oldsymbol{\mu}_{ au} &= oldsymbol{\mu}_{0} + \int_{0}^{ au} oldsymbol{
u}_{u} du \end{aligned}$$

- $u_{ au}$  is an Ornstein-Uhlenbeck (continuous-time AR(1)) process
- H ≡ 0
- $m{\cdot}$   $m{\mu}_{ au}$  accumulates instantaneous changes in location

#### Some useful properties:

• 
$$\boldsymbol{\nu}_{\tau+\delta} = \boldsymbol{\nu}_{\tau} e^{-\beta \delta} + \boldsymbol{\zeta}_{\tau+\delta}$$
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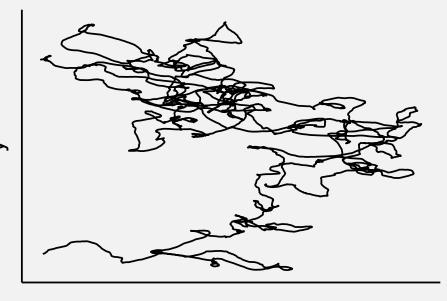
•  $\epsilon_{\tau+\delta} = (\zeta_{\tau+\delta}, \xi_{\tau+\delta})$  are zero mean independent (through time) normal errors that depend only on  $\delta$ ,  $\beta$ , and  $\sigma$  (**Not**  $\tau$ !)

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- $\epsilon_{\tau+\delta} = (\zeta_{\tau+\delta}, \xi_{\tau+\delta})$  are zero mean independent (through time) normal errors that depend only on  $\delta$ ,  $\beta$ , and  $\sigma$  (**Not**  $\tau$ !)
- Can we write μ<sub>τ+δ</sub> just as a function of μ<sub>τ</sub>?
   No. Distribution of μ<sub>τ</sub> is a function of the whole μ<sub>u</sub>, u < τ.</li>



#### Some more properties:

```
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- $\mu_{ au} o$  Brownian motion as eta becomes large  $\mu_{ au}$  becomes very smooth as eta becomes small
- $u_{\tau+\delta}$  roughly indep. of  $u_{\tau}$  at time gap  $\delta=3/\beta$ , so, ...  $\mu_{\tau}, \ \mu_{\tau+3/\beta}, \ \mu_{\tau+6/\beta}, \ldots$  not really distinguishable from Brownian motion

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#### Numerical solution to general ISDE model

for small  $\delta$ 

$$u_{\tau+\delta} \approx -\beta (\nu_{\tau} - \nabla H(\mu_{\tau}))\delta + \epsilon_{\tau+\delta}; \qquad [\epsilon_{\tau}] = N(\mathbf{0}, \sigma^2 \delta \mathbf{I})$$

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Resulting approximation:

$$\boldsymbol{\mu}_{\tau+2\delta} = (2 - \beta \delta) \boldsymbol{\mu}_{\tau+\delta} - (1 - \beta \delta) \boldsymbol{\mu}_{\tau} + \beta \delta^2 \nabla H(\boldsymbol{\mu}_{\tau}) + \boldsymbol{\epsilon}_{\tau+\delta}$$

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Notice that  $\nu_{\tau}$  process disappears and there is a spatial component,  $\nabla H(\mu_{\tau})!$  Something missing from the standard CTCRW model.

# Part II Statistics of animal movement

# Inference refresher

### Maximum likelihood estimation

#### Notation

- $\mathbf{d} = (d_1, \dots, d_n) = \text{vector general data}$
- $oldsymbol{ heta}$  general set a parameters
- $[d_i|\theta] =$  probability model that generates data
- $L(\theta|\mathbf{d}) = \text{likelihood function}$ typically  $L(\theta|\mathbf{d}) = [\mathbf{d}|\theta] = \prod_i [d_i|\theta]$

MLE is very straightforward (in theory) ...

$$\hat{\boldsymbol{\theta}} = \max_{\boldsymbol{\theta}} \{ \log L(\boldsymbol{\theta}|\mathbf{d}) \}$$

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boom!

#### Large sample theory

If  $\mathbf{d} = (d_1 \dots d_n)$  is 'large' then

$$\hat{oldsymbol{ heta}} \sim \mathcal{N}(oldsymbol{ heta}, -\mathbf{H}_{oldsymbol{ heta}}^{-1}),$$

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#### Dependent data

If the data are dependent, then  $[\mathbf{d}|\boldsymbol{\theta}] \neq \prod_i [d_i|\boldsymbol{\theta}].$ 

$$[\mathbf{d}|\boldsymbol{\theta}] = [d_1|\boldsymbol{\theta}] \times [d_2|d_1,\boldsymbol{\theta}] \times [d_3|d_1,d_2,\boldsymbol{\theta}] \times \cdots \times [d_n|d_1,\ldots,d_{n-1},\boldsymbol{\theta}]$$

If we're lucky, our data are Markov

$$[\mathbf{d}|\boldsymbol{\theta}] = [d_1|\boldsymbol{\theta}] \times [d_2|d_1,\boldsymbol{\theta}] \times [d_3|d_2,\boldsymbol{\theta}] \times \cdots \times [d_n|d_{n-1},\boldsymbol{\theta}]$$

#### Missing 'data' likelihoods

$$L(\theta|\mathbf{d}_{obs}) = [\mathbf{d}_{obs}|\theta] = \int [\mathbf{d}_{obs}|\mathbf{d}_{mis},\theta] \ [\mathbf{d}_{mis}|\theta] d\mathbf{d}_{mis}$$

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#### Penalized likelihood

Sometimes the likelihood is hard to maximize or parameters are not full identifiable. So, a penalty term is added

$$\log L_p(\boldsymbol{\theta}|\mathbf{d}) = \log L(\boldsymbol{\theta}|\mathbf{d}) + \kappa J(\boldsymbol{\theta})$$

We'll see some examples laster. But this is how spline regressions are fit (e.g., see mgcv package).

# Bayesian inference

Instead of a fixed quantity,  $\theta$ , is treated like a random variable itself. Before any data is collected, we might model our uncertainty about the value of  $\theta$  with the probability distribution  $[\theta]$ . This is the 'prior' distribution.

# Bayesian inference

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We already have the data model  $[\mathbf{d}|m{ heta}] = L(m{ heta}|\mathbf{d})$ 

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#### Bayes rule and posterior distribution

$$[\boldsymbol{ heta}|\mathbf{d}] = rac{L(oldsymbol{ heta}|\mathbf{d})~[oldsymbol{ heta}]}{\int [\mathbf{d}|oldsymbol{ heta}']~[oldsymbol{ heta}']doldsymbol{ heta}'}$$

Or, we can look at it on the log scale

$$\log[\theta|\mathbf{d}] = \log L(\theta|\mathbf{d}) + \log[\theta] - const.$$

# Bayes inference details

#### How do we work with a posterior distribution?

- $\hat{\theta} = \text{mean}$ , median or mode
- SE of  $\hat{\boldsymbol{\theta}} = SD$  of  $[\boldsymbol{\theta}|\mathbf{d}]$
- Interval estimates  $=(\hat{\theta}_I,\hat{\theta}_u)$  such that  $Pr(\hat{\theta}_I < \theta | \mathbf{d} < \hat{\theta}_u) = 0.95$ . These are called 'credible intervals'

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## How do we find these for general posteriors?

- Approximate with a sample  $\theta_1, \ldots, \theta_m$  from  $[\theta|\mathbf{d}]$  and use sample versions
- Numerically (including Monte Carlo) approximate integrals necessary
- Approximate with known distribution that is similar

# Telemetry analysis

# State-space models

#### **Notation**

- $\mathbf{s}_1, \dots, \mathbf{s}_n$  are observed locations
- $\tau_1, \ldots, \tau_n$  are the observation times
- $\mu_{ au}$  is the continuous path of the animal at time au
- $m{\cdot}$   $m{
  u}_{ au}$  is the velocity at time au
- $\bullet \ \alpha_{\tau} = (\mu_{\tau,\mathsf{x}}, \nu_{\tau,\mathsf{x}}, \mu_{\tau,\mathsf{y}}, \nu_{\tau,\mathsf{y}}),$

# State-space models

### CTCRW model

$$\mathbf{s}_i = \mathbf{z}' oldsymbol{lpha}_{ au_i} + oldsymbol{\epsilon}_i \ oldsymbol{lpha}_{ au_{i+1}} = \mathbf{T}_i oldsymbol{lpha}_{ au_i} + oldsymbol{\eta}_i$$

- $[\epsilon_i] = N(\mathbf{0}, \mathbf{V}_i)$ ;  $\mathbf{V}_i$  is the location error variance.
- z = (1, 0, 1, 0)
- $\mathbf{T}_i$  is a function of  $\beta$  and  $\delta_i = \tau_{i+1} \tau_i$
- $[\boldsymbol{\eta}_i] = N(\mathbf{0}, \mathbf{Q}_i)$
- $\mathbf{Q}_i$  depends only on  $\beta$ ,  $\delta_i$ , and  $\sigma$

# Temporally dynamic CTCRW

The parameters do not have to remain constant over time!

- $au_1^*, \dots, au_m^*$  are known times where eta and  $\sigma$  can change
- Define model as before based on merged observation and changepoint times,  $\tau_1, \ldots, \tau_{n+m}$

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## Temporally dynamic movement model

$$\mathbf{s}_i = \left\{ egin{array}{ll} \mathbf{z}' oldsymbol{lpha}_{ au_i} + oldsymbol{\epsilon}_i & ext{for } au_i ext{ an observed time} \ \mathrm{NA} & ext{for } au_i ext{ in } au_1^*, \dots, au_m^* \ oldsymbol{lpha}_{ au_{i+1}} = \mathbf{T}_i oldsymbol{lpha}_{ au_i} + oldsymbol{\eta}_i \end{array} 
ight.$$

Movement model is still continuous in time!

## Kalman filter

Method to calculate likelihood, NOT a model!

## Likelihood for state-space models

$$\begin{split} L(\boldsymbol{\theta}|\mathbf{s}_{1:n}) &= \prod_{i} [\mathbf{s}_{i+1}|\mathbf{s}_{1:i}, \boldsymbol{\theta}] \\ &= \int [\mathbf{s}_{1}|\boldsymbol{\alpha}_{\tau_{1}}, \boldsymbol{\theta}] \; [\boldsymbol{\alpha}_{\tau_{1}}|\boldsymbol{\theta}] \dots [\boldsymbol{\alpha}_{\tau_{i}}|\boldsymbol{\alpha}_{\tau_{i-1}}, \boldsymbol{\theta}] \times \dots \\ &\times [\mathbf{s}_{n}|\boldsymbol{\alpha}_{\tau_{n+m}}, \boldsymbol{\theta}] \; [\boldsymbol{\alpha}_{\tau_{n+m}}|\boldsymbol{\alpha}_{\tau_{n+m-1}}, \boldsymbol{\theta}] d\boldsymbol{\alpha}_{1:n+m} \end{split}$$

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Kalman filter is a numerical algorithm that allows calculation of  $L(\theta|\mathbf{s}_1,\ldots,\mathbf{s}_n)$  in an efficient manner.

- moves forward through the complete likelihood integrating on the way
- requires linear form and normal errors

## Kalman smoother

Obtain predictions from model fit

- optimal predictor  $\hat{\alpha}_i = E[\alpha_i | \mathbf{s}_{1:n}, \boldsymbol{\theta}]$
- prediction errors  $\widehat{\mathsf{var}}(\hat{lpha}_i) = \mathit{Var}[lpha_i | \mathbf{s}_{1:n}, oldsymbol{ heta}]$

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Kalman smoother is an algorithm to calculate mean and variance of  $[\alpha_i|\mathbf{s}_{1:n},\theta]$ 

- uses output from Kalman filter to go backwards through the model/data to calculate these quantities
- $\alpha_i | \mathbf{s}_{1:n}, \boldsymbol{\theta}$  is normally distributed.

# Practical Bayesian inference

Posterior

$$egin{aligned} [ heta, lpha | \mathbf{s}] &\propto [\mathbf{s} | lpha, heta] \; [lpha | eta] \; [eta] \ &\propto [lpha | \mathbf{s}, eta] \; [eta | \mathbf{s}] \end{aligned}$$

# Practical Bayesian inference

#### Posterior

$$egin{aligned} [ heta, lpha | extsf{s}] &\propto [ extsf{s} | lpha, heta] \ [lpha | extsf{s}, heta] \ [ heta | extsf{s}] \end{aligned} \ egin{aligned} &\propto [lpha | extsf{s}, heta] \ [ heta | extsf{s}] \end{aligned}$$

### **Approach**

- **1** Approximate  $[\theta|\mathbf{s}]$  with something easy to sample from, say  $[\theta|\mathbf{s}]^*$
- 2 Draw  $\theta^{(i)} \sim [\theta | \mathbf{s}]^*$  then draw  $\alpha^{(i)} \sim [\alpha | \theta^{(i)}, \mathbf{s}]$   $([\alpha | \theta^{(i)}, \mathbf{s}]$  easy to sample from using KFS algorithms)
- $(\theta^{(1)}, \alpha^{(1)}), \dots, (\theta^{(K)}, \alpha^{(K)})$  is a posterior sample
- **4**  $m_i = f(\theta^{(i)}, \alpha^{(i)})$  will be a sample from  $[m|\mathbf{s}]$

# Approximating $[\theta|\mathbf{s}]$

- Normal approximation
  - **1** maximize  $\log[\mathbf{s}|\boldsymbol{\theta}] + \log[\boldsymbol{\theta}] = L_p(\boldsymbol{\theta}|\mathbf{s})$  (penalized likelihood)
  - 2  $[m{ heta}|\mathbf{s}]^* = N\left(\hat{m{ heta}}, -\mathbf{H}_{\hat{m{ heta}}}^{-1}
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- Importance sampling (exact sample)
  - $oldsymbol{0}$  sample  $ilde{ heta}^{(k)} \sim q( heta)$  (maybe normal from last item)
  - 2 form weights  $w_k = [\tilde{\boldsymbol{\theta}}^{(k)}|\mathbf{s}]/q(\tilde{\boldsymbol{\theta}}^{(k)})$
  - **3** sample  $\boldsymbol{\theta}^{(i)}$  from  $\tilde{\boldsymbol{\theta}}^{(1)},\ldots,\tilde{\boldsymbol{\theta}}^{(K)}$  with prob.  $\propto w_1,\ldots,w_K$

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- Deterministic sample (INLA)
  - $oldsymbol{0}$  sample  $ilde{ heta}^{(k)}$  from deterministic grid
  - **2** form weights  $w_k = [\tilde{\boldsymbol{\theta}}^{(k)}|\mathbf{s}]$
  - 3 sample  $\boldsymbol{\theta}^{(i)}$  from  $\tilde{\boldsymbol{\theta}}^{(1)},\ldots,\tilde{\boldsymbol{\theta}}^{(K)}$  with prob.  $\propto w_1,\ldots,w_K$

## Process imputation

- Allows us to account for location uncertainty in other analysis of movement data
- ullet Assume we know  $\mu_{ au}$  on a sufficiently fine time scale
- Response variable of interest  $\mathbf{y} = \mathbf{f}(\boldsymbol{\mu})$ , e.g.,
  - Distance traveled,
  - Utilization distribution, or
  - locations of dives
- Model of interest  $[\mathbf{y}|\psi]$ , e.g.,
  - ANOVA,
  - Spatial regression model, or
  - Point process model
- ullet But,... we don't observe  $oldsymbol{\mu}_{ au}$

## Process imputation

Solution Average over unknown 'true' paths

$$[\psi|\mathsf{s}] = \int [\mathsf{y}_{oldsymbol{\mu}}|\psi] \ [\psi] \ [\mu|\mathsf{s}] doldsymbol{\mu}$$

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#### Method

- **1** Simulate  $oldsymbol{\mu}^{(i)} \sim [oldsymbol{\mu} | \mathbf{s}] 
  ightarrow \mathsf{Calculate} \ \mathbf{y}^{(i)}$
- **2** Calculate summaries of  $[\psi^{(i)}|\mathbf{y}^{(i)}]$ 
  - posterior mean
  - posterior predictions
  - UDs
  - MCMC sample
- 3 Summarize over  $\mu^{(i)}$  realizations
  - $E[\psi|\mathbf{s}] = mean(E[\psi|\mathbf{s}])$
  - $\ \textit{Var}[\boldsymbol{\psi}|\mathbf{s}] = \textit{Var}(\textit{E}[\boldsymbol{\psi}|\mathbf{s}]) + \textit{mean}(\textit{Var}[\boldsymbol{\psi}|\mathbf{y}])$

