

# A brief introduction to some **Movement Models**

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17. – 28. JUNE 2024 IN GERMANY



# 1. Discrete Movement Models

- Steps
- Turning angles
- USUALLY - assume **constant sampling**
- Dominant paradigm because **movement data** are a "discrete" sample



# 1D White Noise

$$X \sim \sigma W_t$$

where  $W_t \sim \mathcal{N}(0, 1)$  = white noise

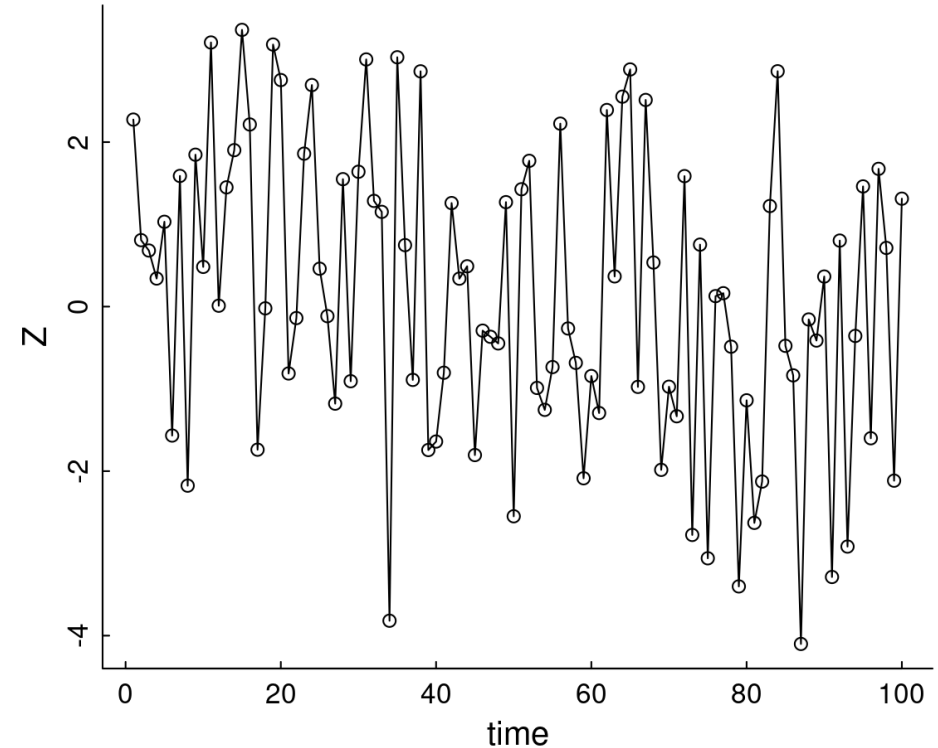
```
sigma = 2  
Z <- rnorm(100, sd = sigma)
```

## Properties

$$\mathbb{E}(Z_t) = 0$$

$$\text{Var}(Z_t) = \sigma^2$$

Goes nowhere, can't escape.



# 2D White Noise

$$\mathbf{Z} \sim \text{WN}_{2d}(\sigma)$$

(**boldfacing** means 2-d vector, but will drop going forward.)

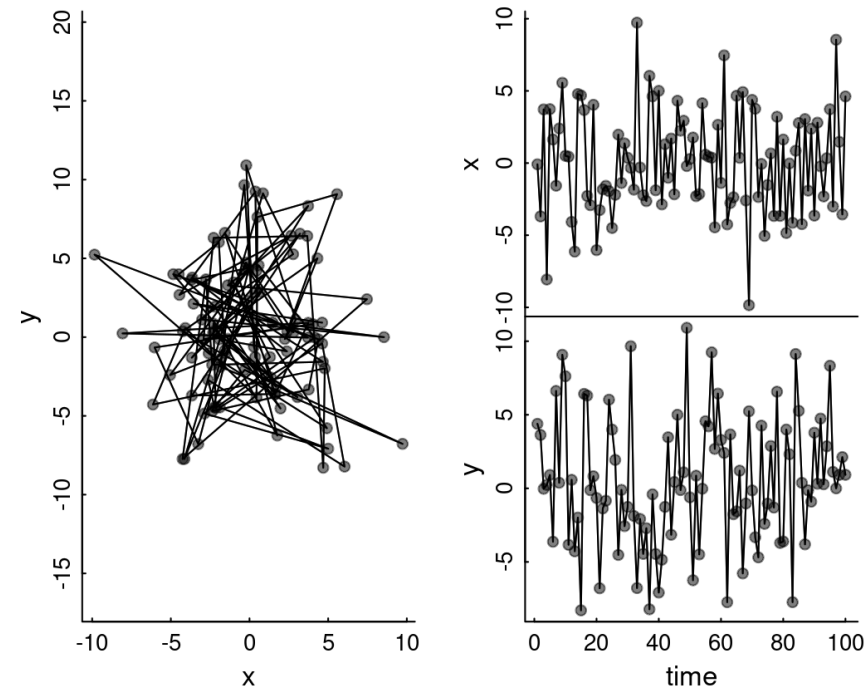
```
sigma <- 4  
n <- 100  
Z <- rnorm(n, sd = sigma) + 1i*rnorm(n, sd = sig
```

## Properties

$$\mathbb{E}(Z_t) = \{0, 0\}$$

$$\mathbb{E}(|Z_t|) = \sigma \sqrt{\frac{\pi}{2}}$$

- Goes nowhere
- Jiggles around like crazy



**Note:** the useful *scan-track*: X-Y. X-Time, Y-Time.

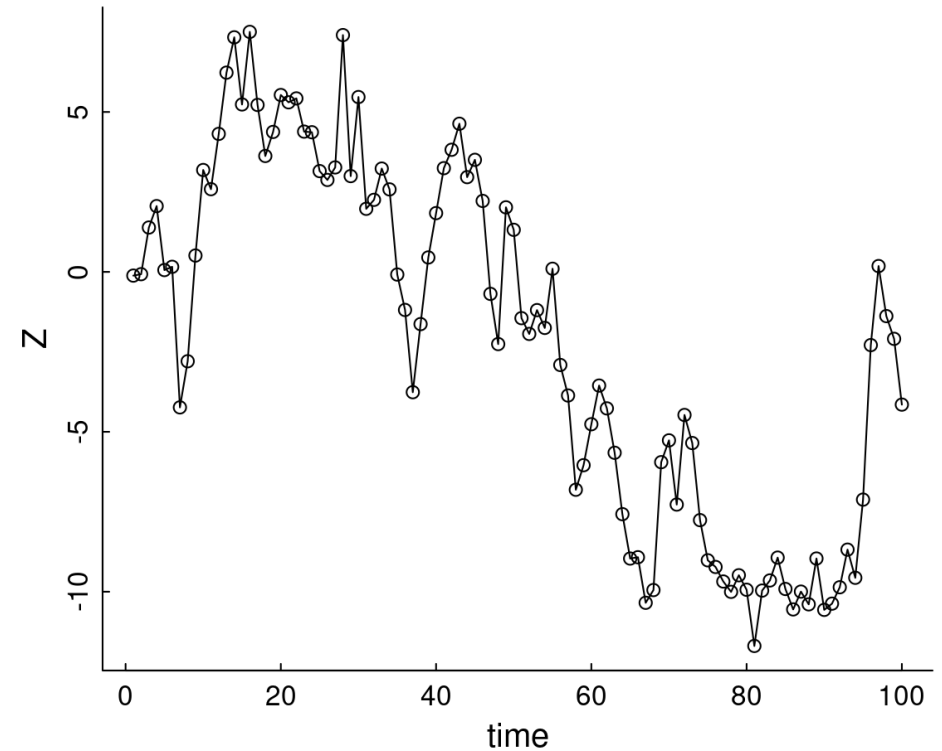
# 1D Random Walk

$$X \sim \text{RW}_{1d}(\sigma)$$

$$X_t = X_{t+1} + \sigma W_t$$

where  $W_t \sim \mathcal{N}(0, 1)$  = white noise

```
sigma = 2  
Z <- cumsum(rnorm(100, sd = sigma))
```



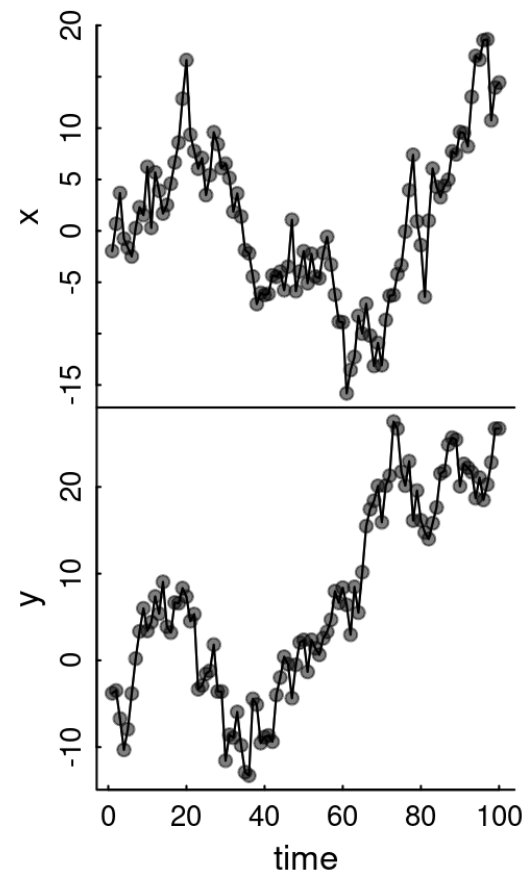
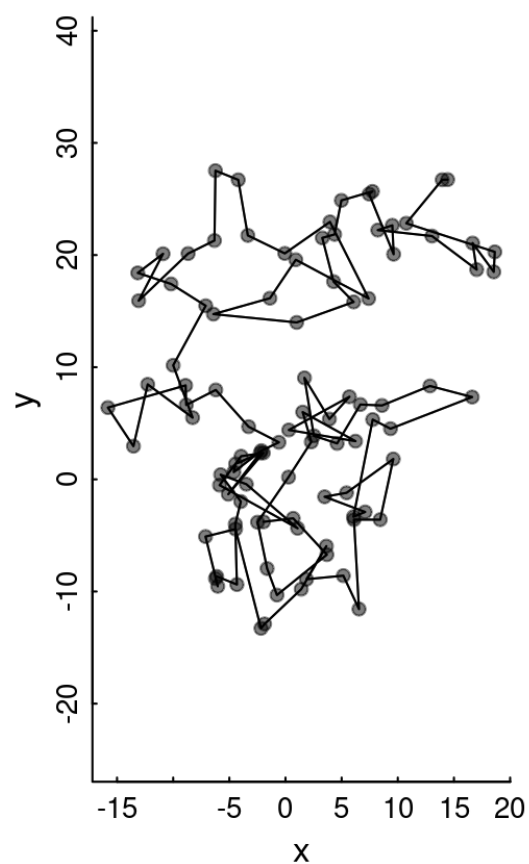
# 2D Random Walk

$$\mathbf{Z} \sim \text{RW}_{2d}(\sigma)$$

$$\mathbf{Z}_t = \mathbf{Z}_{t-1} + \sigma \mathbf{W}_t$$

boldfacing means 2-d vector, but will drop going forward.

```
sigma <- 3; n <- 100  
Z <- cumsum(rnorm(n, sd = sigma)) +  
  1i*cumsum(rnorm(n, sd = sigma))
```



## Properties

$$\mathbb{E}(\mathbf{Z}_t) = \{0, 0\}$$

$$\text{Var}(|\mathbf{Z}_t|) = 2\sigma^2 t$$

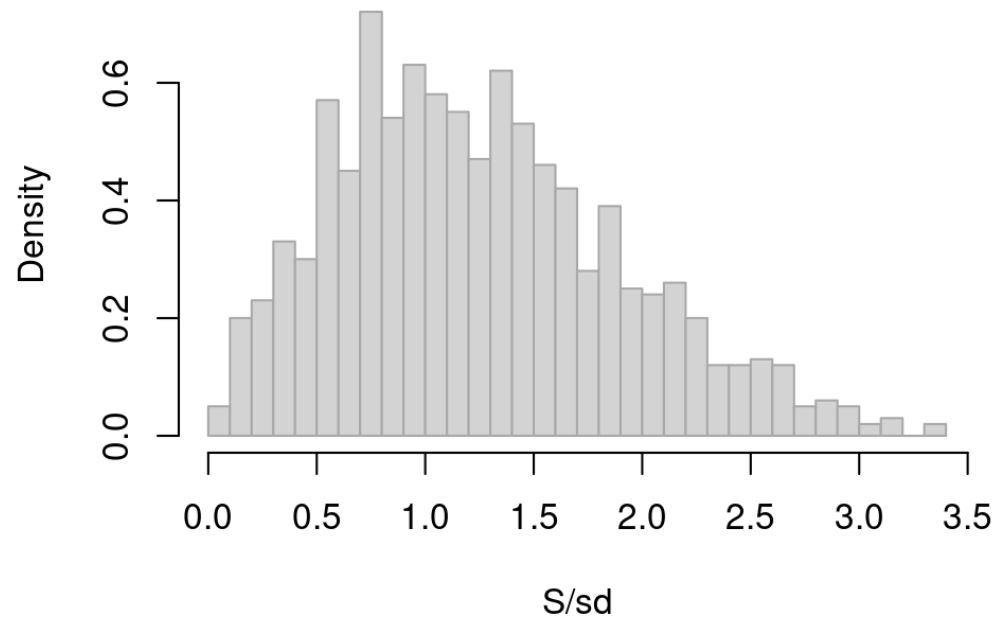
## Step & turning angles:

$$\theta \sim \text{Unif}(-\pi, \pi)$$

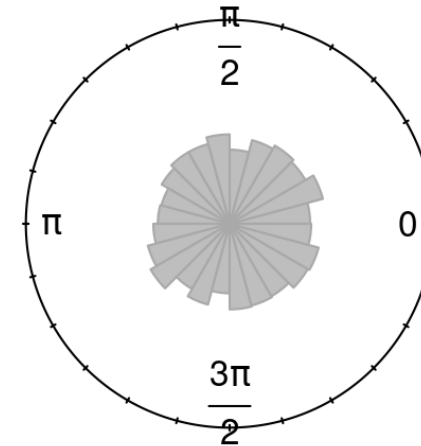
$$|\mathbf{S}|/\sigma \sim \text{Chi}(k=2); \quad \mathbb{E}(|\mathbf{S}|) = \sqrt{2}\sigma$$

You can use this result to estimate  $\sigma$  - take the mean step lengths and divide by  $\sqrt{2}$

**Histogram of S/sd**



**turning angle  $\theta$**



# 1D Autoregression Process

$$X_t = \phi X_{t+1} + \sigma W_t$$

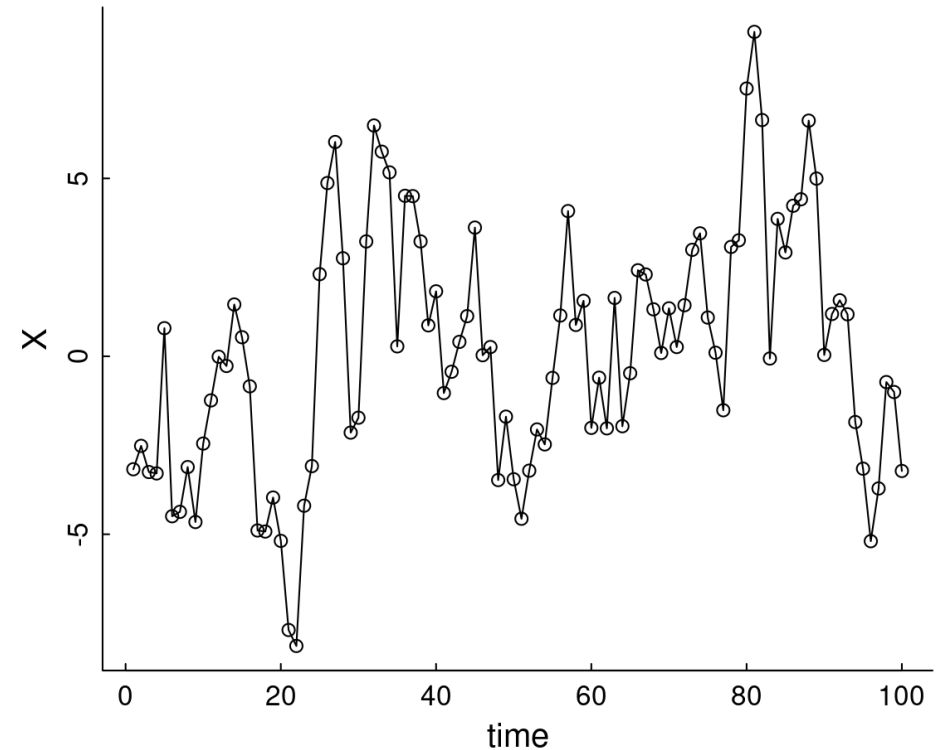
## Properties

$$\mathbb{E}(X_t) = 0$$

$$\text{Var}(X_t) = \frac{\sigma^2}{1 - \phi^2}$$

(Auto)-regresses to mean (easily rescaled to  $\mu \neq 0$ ).

Spatially constrained!

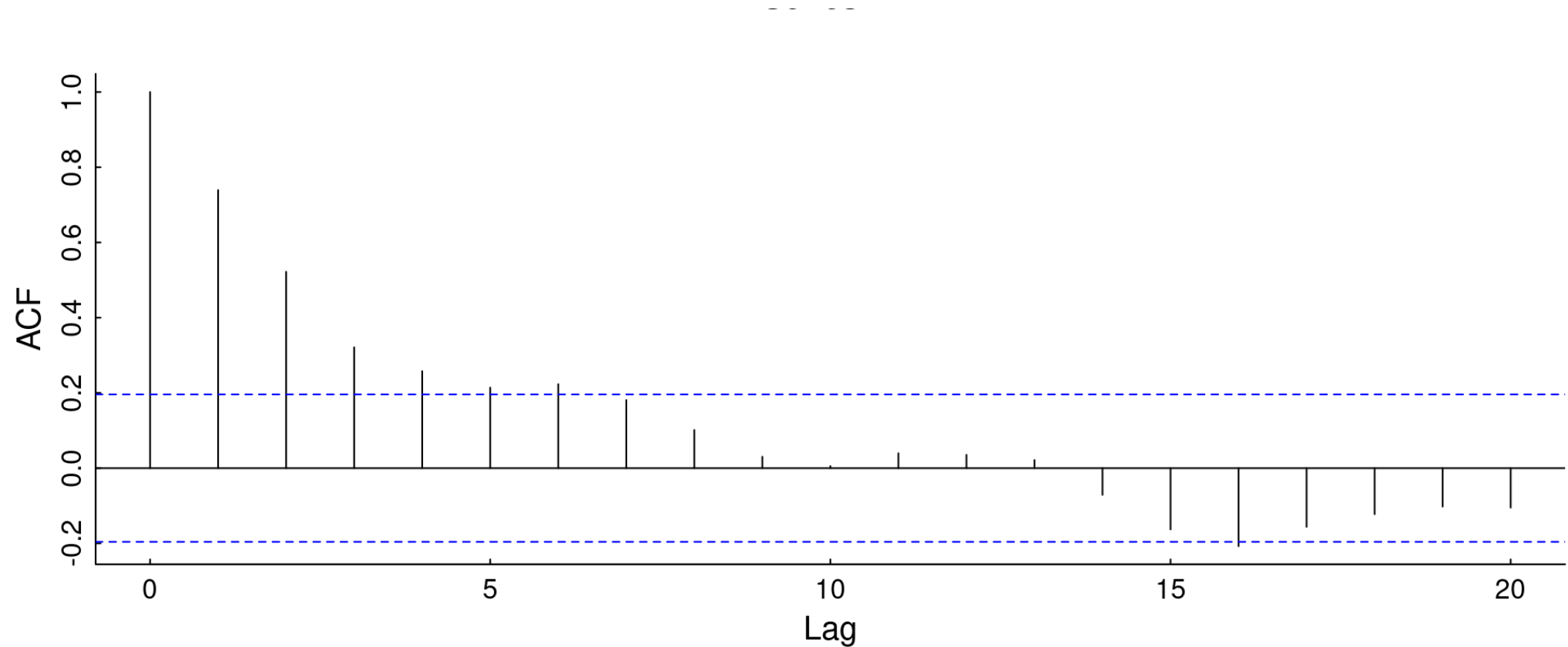




# the Autocorrelation function

This calculates whether subsection locations at a specific lag depend on prior locations.

```
acf(X)
```

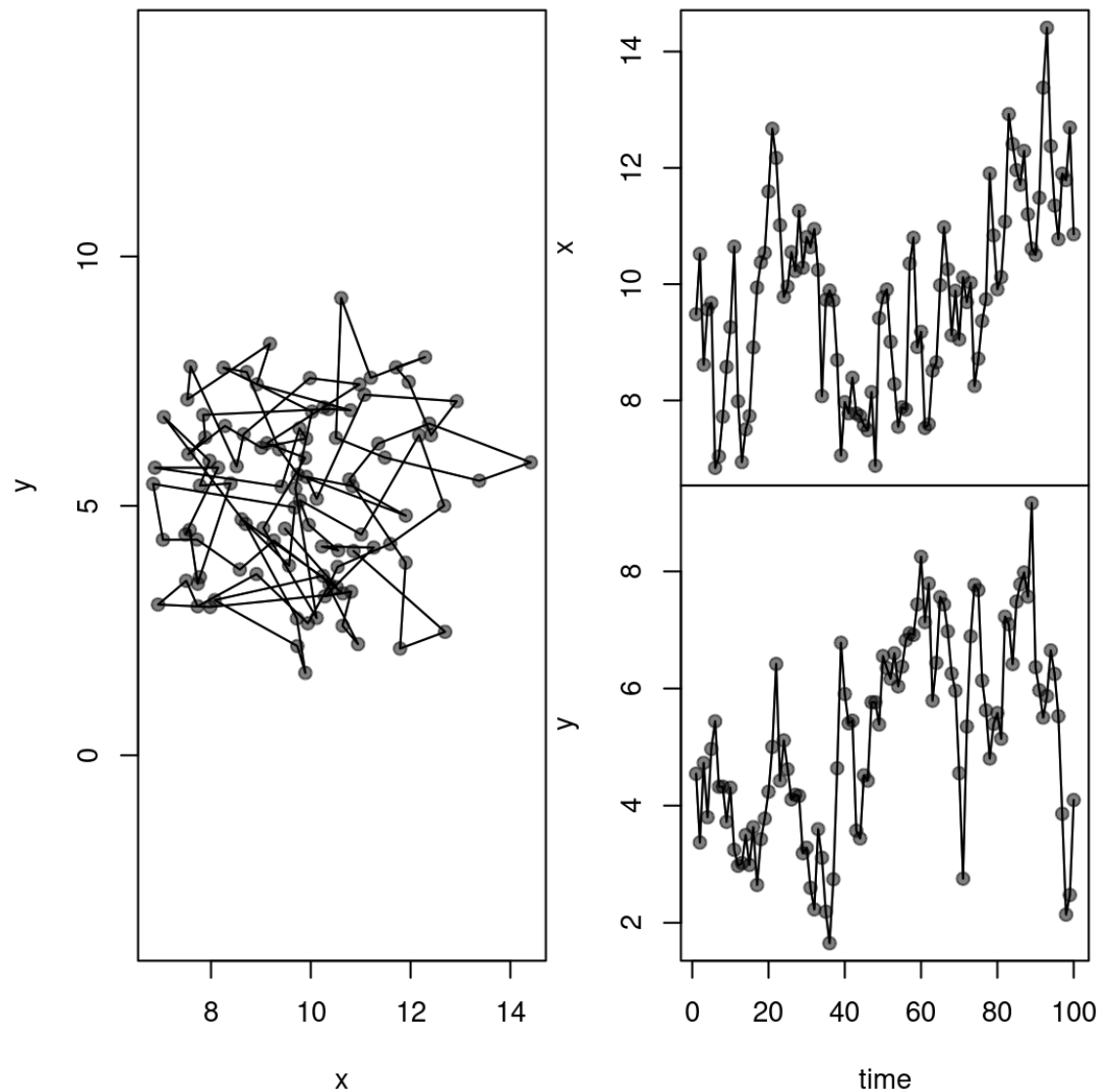


# 2D autoregressive walk

$$\mathbf{Z} \sim \text{AR}_{2d}(\phi, \sigma)$$

$$\mathbf{Z}_t = \phi \mathbf{Z}_{t-1} + \sigma \mathbf{W}_t$$

Where everything is 2D. And easily scaled to a different mean  $\mathbf{m}$



## 2D-AR walk: Properties

Spatially constrained in 2D!

Actually looks kind of like home ranging. In fact, the 95% home-ranging area is:

$$A \approx \frac{6\pi\sigma^2}{1 - \phi^2}$$

(Where  $6 \approx -2 \log(\alpha)$ ,  $\alpha = 5\%$ )

Rewrite in terms of "steps" (displacements):

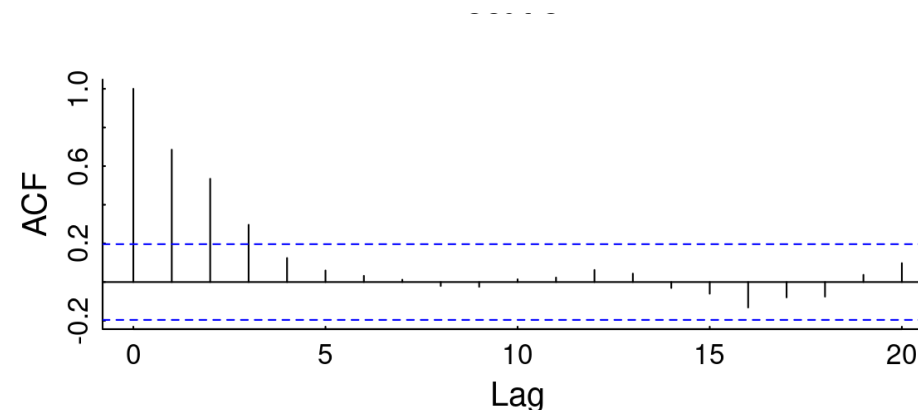
$$\mathbf{Z}_t = \mathbf{Z}_{t-1} - (1 - \phi)\mathbf{Z}_{t-1} + \sigma\mathbf{W}_t$$

$$\mathbf{S}_t = -(1 - \phi)\mathbf{Z}_{t-1} + \sigma\mathbf{W}_t$$

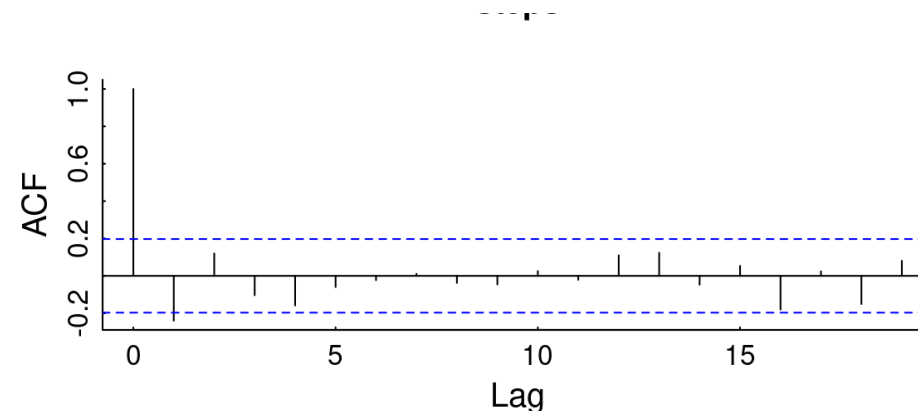
This means that the *step* process itself is NOT stationary / independent, but depends on **absolute location**.

Specifically, the urge to "go home" is proportional to the distance from home.

There **is** auto-correlation in **locations**:



But **NOT** in the **steps**:

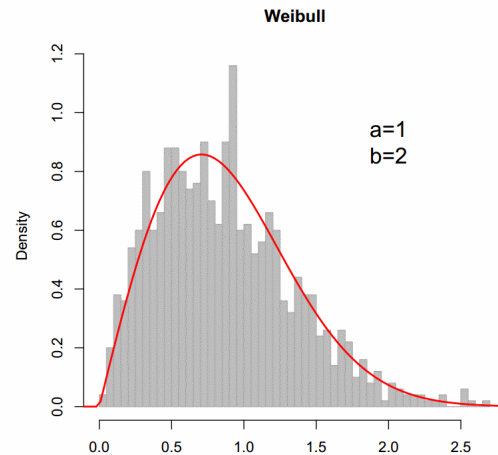
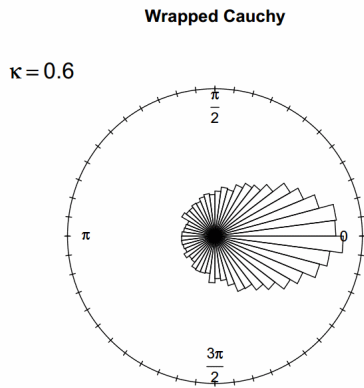


# Correlated Random Walk

Basically:

$$Z_t = Z_{t-1} + S_t$$

$\theta = \text{Arg}(S) \sim \text{some distribution}$   
 $|S| \sim \text{some distribution}$



## The famous one:

Oecologia (Berlin) (1983) 56:234-238

*Oecologia*  
© Springer-Verlag 1983

### Analyzing Insect Movement as a Correlated Random Walk

P.M. Kareiva<sup>1</sup> and N. Shigesada<sup>2</sup>

<sup>1</sup> Division of Biology, Brown University, Providence, RI 02912, USA

<sup>2</sup> Department of Biophysics, Kyoto University, Kyoto, 606 Japan

## The totally forgotten one:

BULLETIN OF  
MATHEMATICAL BIOPHYSICS  
VOLUME 15, 1953

### A MATHEMATICAL CONTRIBUTION TO THE STUDY OF ORIENTATION OF ORGANISMS

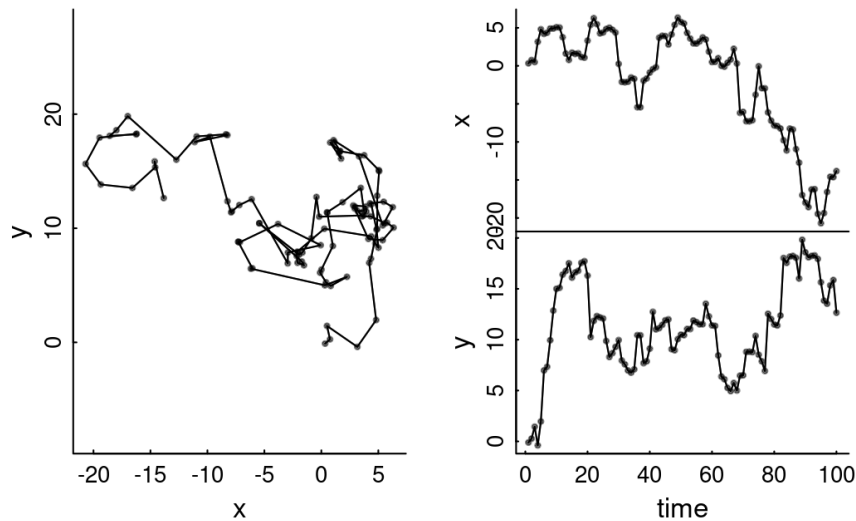
CLIFFORD S. PATLAK\*

COMMITTEE ON MATHEMATICAL BIOLOGY  
THE UNIVERSITY OF CHICAGO

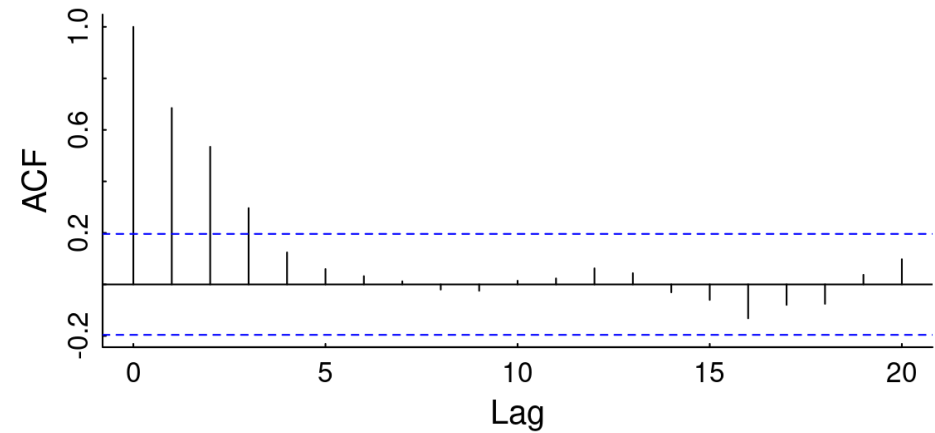
# Simulate in R

```
require(circular)
CRW <- function(n = 100, rho=0.8, alpha = 1, beta = 1) {
  theta <- rwrappedcauchy(n, rho)
  phi <- cumsum(theta)
  S <- complex(arg = phi, mod = rweibull(n, alpha = 1, beta = 1))
  cumsum(S)
}
```

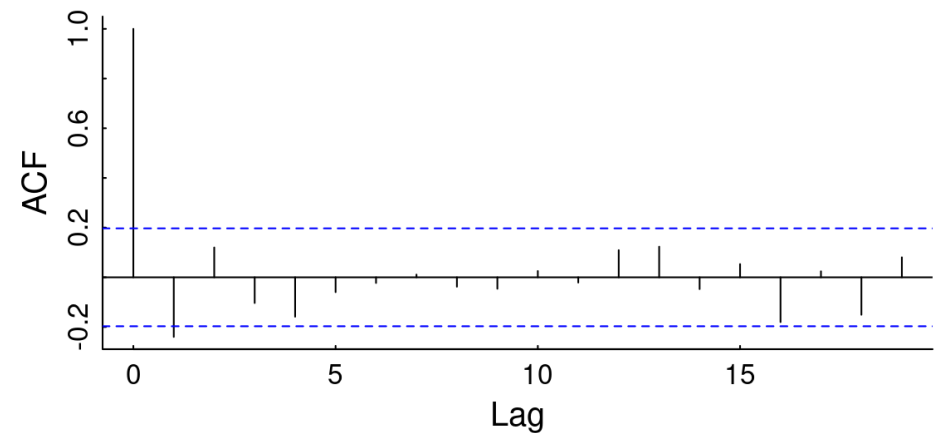
Also - flies off to infinity.



Also - autocorrelated in position:



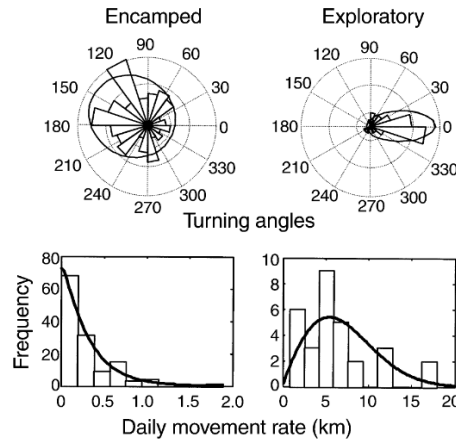
but not in steps!



# Multi-state Correlated Random Walk



*Ecology*, 85(9), 2004, pp. 2436–2445  
© 2004 by the Ecological Society of America



## EXTRACTING MORE OUT OF RELOCATION DATA: BUILDING MOVEMENT MODELS AS MIXTURES OF RANDOM WALKS

JUAN MANUEL MORALES,<sup>1,4</sup> DANIEL T. HAYDON,<sup>2</sup> JACQUI FRAIR,<sup>3</sup> KENT E. HOLSINGER,<sup>1</sup>  
AND JOHN M. FRYXELL<sup>2</sup>

Pretty self-explanatory!

**BUT ... what is the model of transitioning between these states?**

The general model structure can be formulated as a latent variable model where each observation  $y_t$  ( $t = 1, \dots, T$ ) is associated with an unobserved (latent) state-indicator variable  $I_t = i$ ,  $i \in \{1, \dots, M\}$  where  $M$  is the number of different movement states considered. In this way, every observation is assigned to only one of  $M$  movement states. Observations  $y_t = [r_t, \phi_t]$ , are pairs of daily average movement rates and turning angles. Conditioned on the  $i$ th movement state, each observation is assumed to be independently drawn from a Weibull distribution (for step length) with parameters  $a_i$  and  $b_i$  ( $i \in \{1, \dots, M\}$ ), and wrapped Cauchy distribution (for turning angles) with parameters  $\mu_i$  and  $\rho_i$ .

# Markov Chains

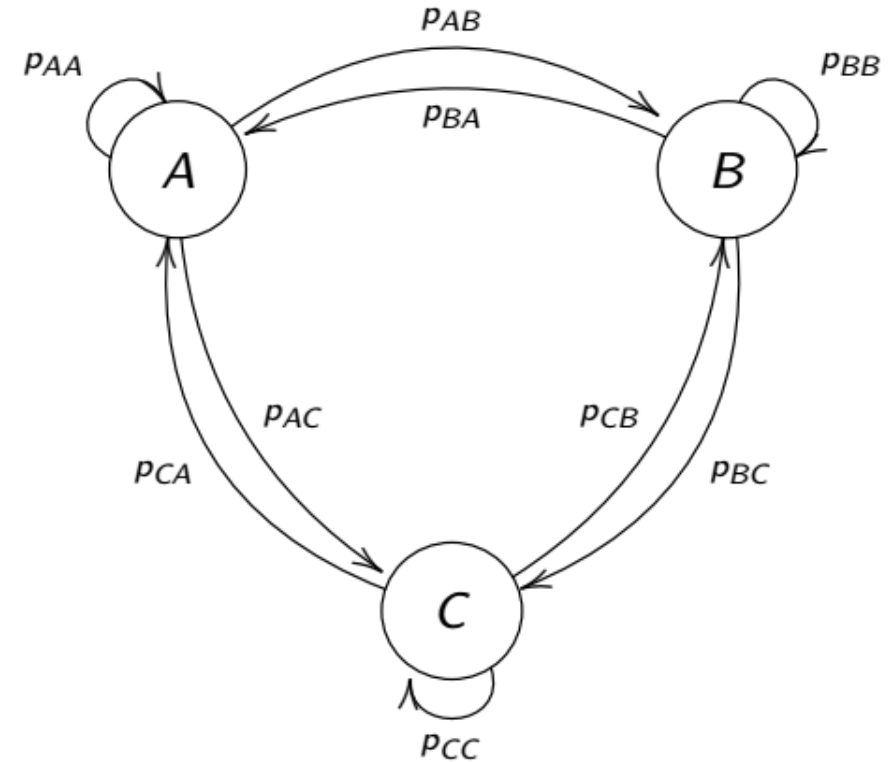
... model **state transitions**

Consider  $\mathbf{X} = \{X_1, X_2, X_3, \dots, X_n\}$  is in some discrete **state** (A, B or C) with fixed probabilities of transitioning from one state to another:

Sample sequence:

$\mathbf{X} = CCCBBCACCBABCBA \dots$

This is called a **Markov chain**.



# Probability transition matrix

We express this process in terms of a **Probability Transition** matrix:

from: \ to:		A	B	C
M =	A	$p_{AA}$	$p_{AB}$	$p_{AC}$
	B	$p_{BA}$	$p_{BB}$	$p_{BC}$
	C	$p_{CA}$	$p_{BC}$	$p_{CC}$

Such that:

$$M_{ij} = \Pr(X_{t+1} = j | X_t = i) = p_{ij}$$

Such that:

$$\Pr(X_{t+1} = j) = \sum_{i=1}^N M_{ij} \Pr(X_t = i)$$

Which can be conveniently rewritten in matrix notation as:

$$\pi_{t+1} = \mathbf{M} \times (\pi_t)^T$$

Where  $\pi_t$  is the distribution of the system over all states at time  $t$ .



# Back to Multi-state CRW ...

To simulate a multi-state CRW, first create a transition matrix:

```
M <- rbind(c(0.7,0.2,.1), c(.4,.4,.2), c(0,0.8,0.2))
row.names(M) <- colnames(M) <- c("chilling", "cruising", "huffing")
M
```

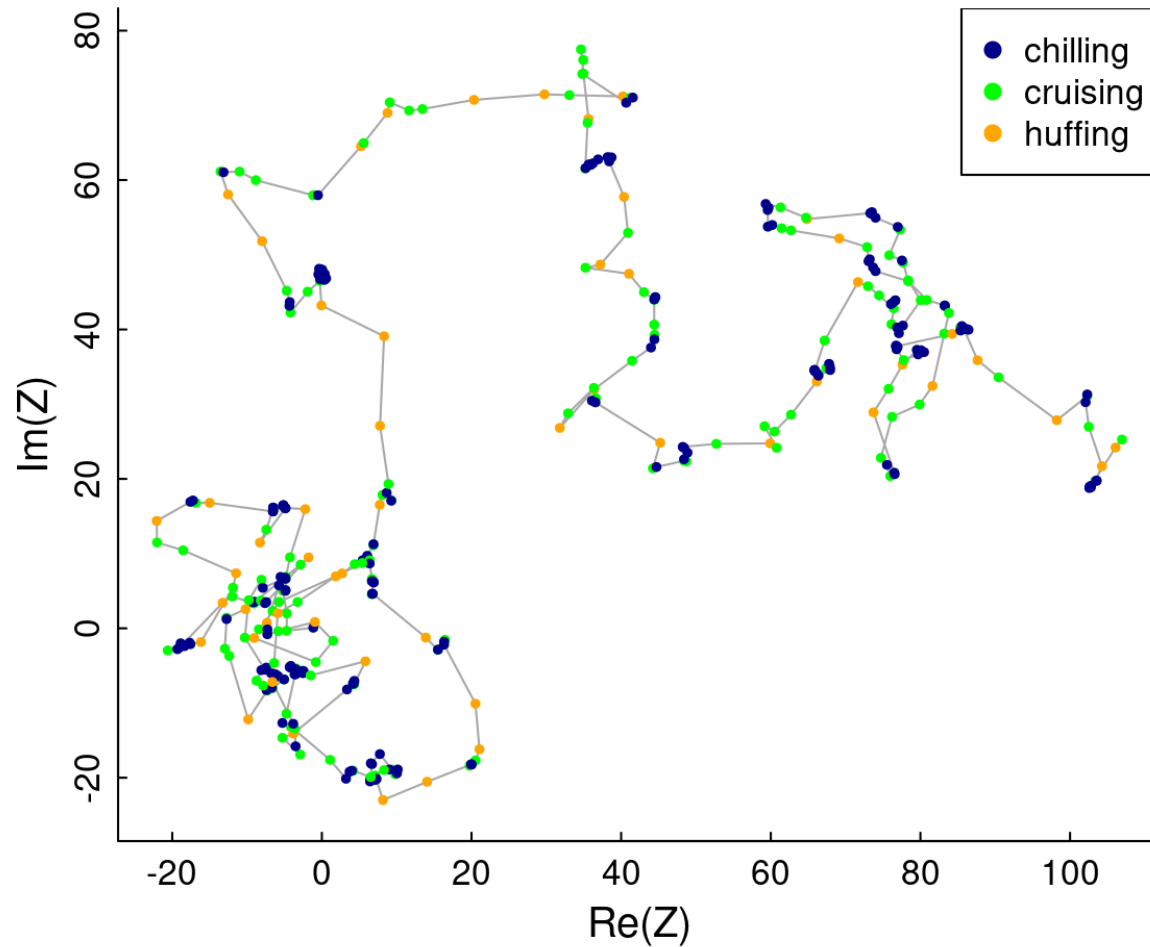
```
##           chilling cruising huffing
## chilling      0.7      0.2      0.1
## cruising      0.4      0.4      0.2
## huffing        0.0      0.8      0.2
```

Create a vector of simulated states:

```
n <- 400
states <- 1:nrow(M)
State <- c(1, rep(NA, n=1))
for(i in 2:n) State[i] <- sample(states, 1, prob=M[State[i-1],])
State[1:100]
```

```
##   [1] 1 2 2 2 1 1 2 2 3 2 1 1 1 1 1 3 2 2 1 1 1 1 3 2 1 1 3 2 2 3 2 3 2 1 1 1
##  [38] 1 2 1 1 1 3 2 2 1 1 2 1 1 3 2 3 2 1 2 2 3 2 1 1 1 1 2 1 2 1 2 2 1 1 1 1
##  [75] 2 2 2 1 2 1 1 1 1 3 2 1 1 2 3 2 2 3 2 2 3 2 2 1 1 1
```

# Simulated MRW



Stationary state proportions:

```
## chilling cruising huffing
## 0.4848485 0.3636364 0.1515152
```

Simulated proportions:

```
table(State) |> prop.table()
```

```
## State
##      1      2      3
## 0.51 0.35 0.14
```

# Habitat dependent Multi-state random walk

The actual Morales MRW was more interesting than just transitions ... each transition was modeled as **depending on covariates** (  $\mathbf{X}$  ) according to coefficients  $\beta$ .

$$p_{12} = \frac{e^{\beta\mathbf{X}}}{1 + e^{\beta\mathbf{X}}}$$

and  $p_{11} = 1 - p_{12}$ . This sounds crazy complicated, but  
- with recent technology is - in fact - quite easy to do!

Before, we had to struggle a lot with writing Bayesian Markov Chain Monte Carlo simulators, but now this is (relatively) easy to do with the `momentuhmm` package.

# Continuous Time Movement Models

## Advantages

- Models of locations at **all times** (not just measured times)
- Naturally robust to irregular data (*all data!*)
- Parameters and estimates to not depend on sampling scale
- Processes can be parameterized in terms of biologically meaningful measures (like *speeds*, *ranging areas*, *time scales*)

## Disadvantages

- Unfamiliar math (*stochastic partial differential equations*)
- Hard to estimate
- Difficult to add structure (e.g. behavioral changes)
- **Contains strong assumptions that are not sufficiently questioned**



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# White Noise

**White Noise** is uncorrelated random independent locations.

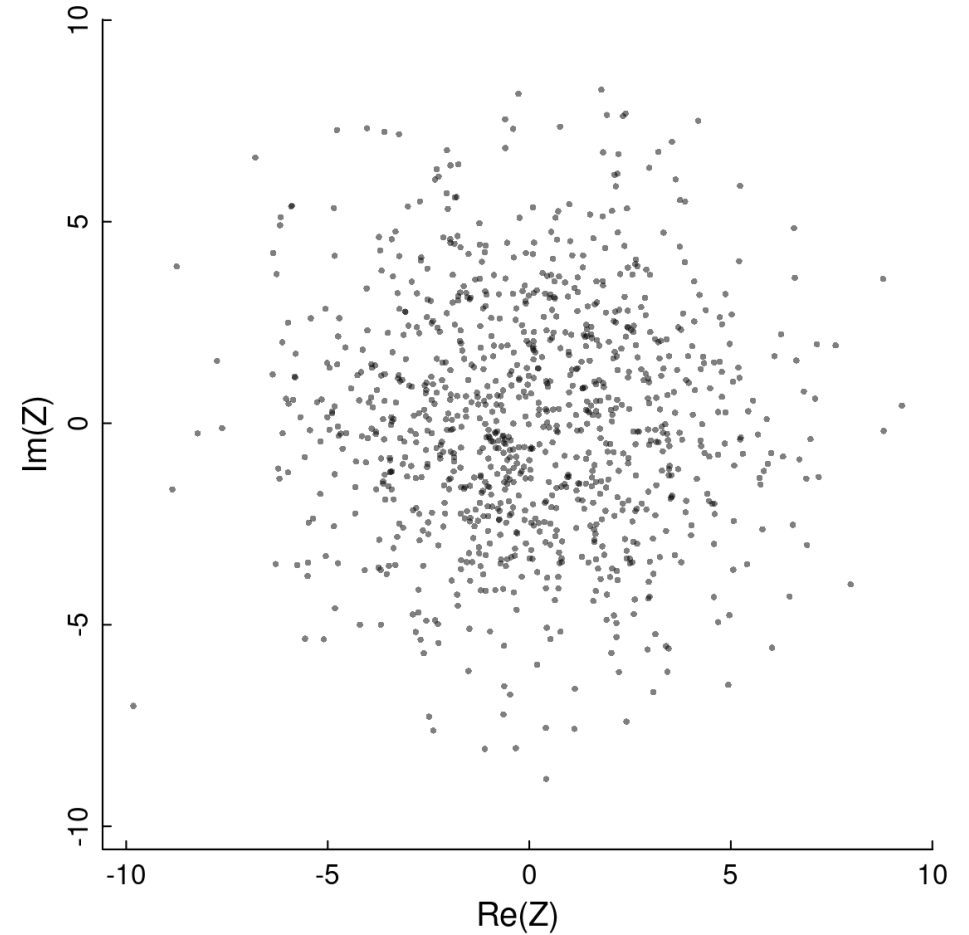
$$Z(t) = \sigma W_t$$

where:

- $W_t$  - is **white noise**, i.e. independent Gaussian process in  $X$  and  $Y \mathcal{N}(0, 1)$ .
- $\sigma$  - is **spatial scale of randomness**

**Equivalent to the discrete time WN**

- no matter how frequently you sample, you will get the same (statistical) process.



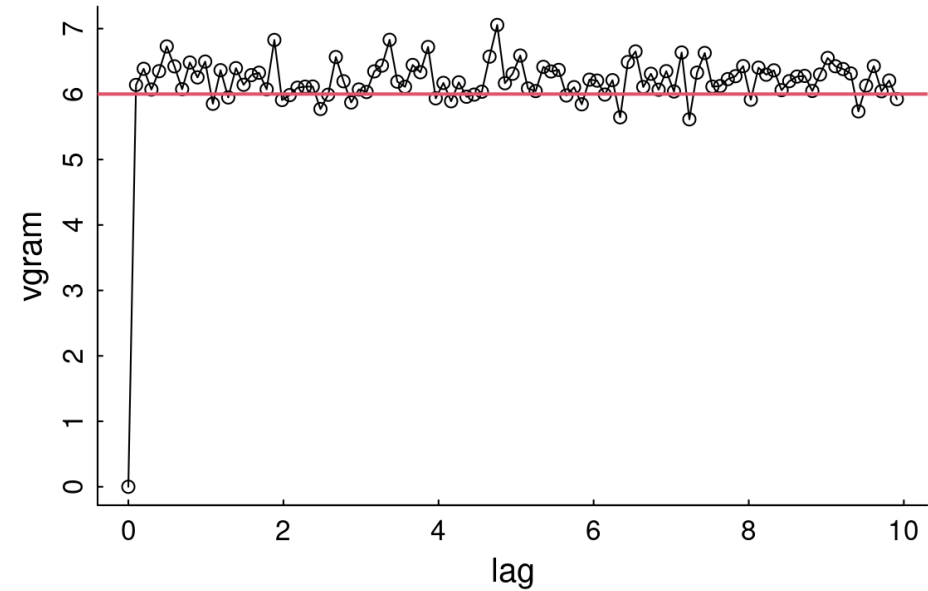
**Obviously: no animal does this!!** This is a model for *data* not *behavior*

# Semi-variogram

This is the **Variance** of the difference between all **pairs of locations** across given **lags**:

$$v(lag) = \frac{1}{2} (\text{Var}(X_{i+lag} - X_i) + \text{Var}(Y_{i+lag} - Y_i))$$

For white noise it is 0 at lag 0 (all  $v(0) = 0$ ), and then is immediately equal to  $2\sigma$ :



# Brownian Motion

Position is the integral of the **velocities** - which are **White Noise**.

Brownian motion has **zero autocorrelation** and **no spatial constraints**

$$Z(t) = Z(0) + \int_0^t V(t)dt$$

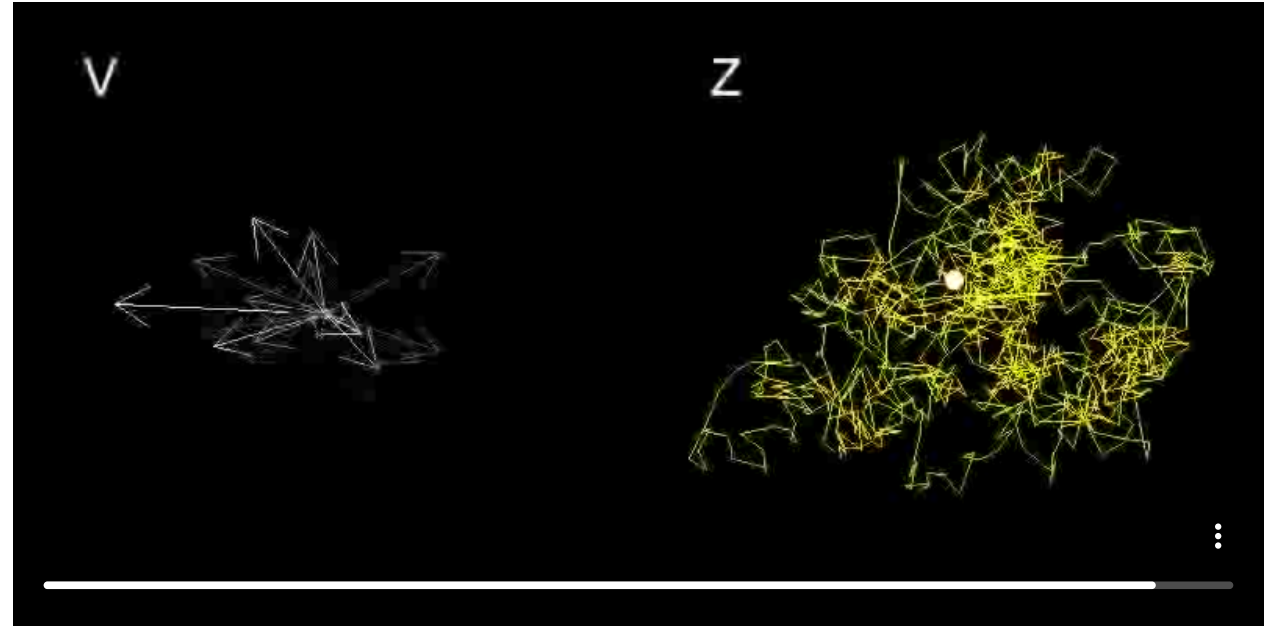
where

$$V(t) = \beta dW_t$$

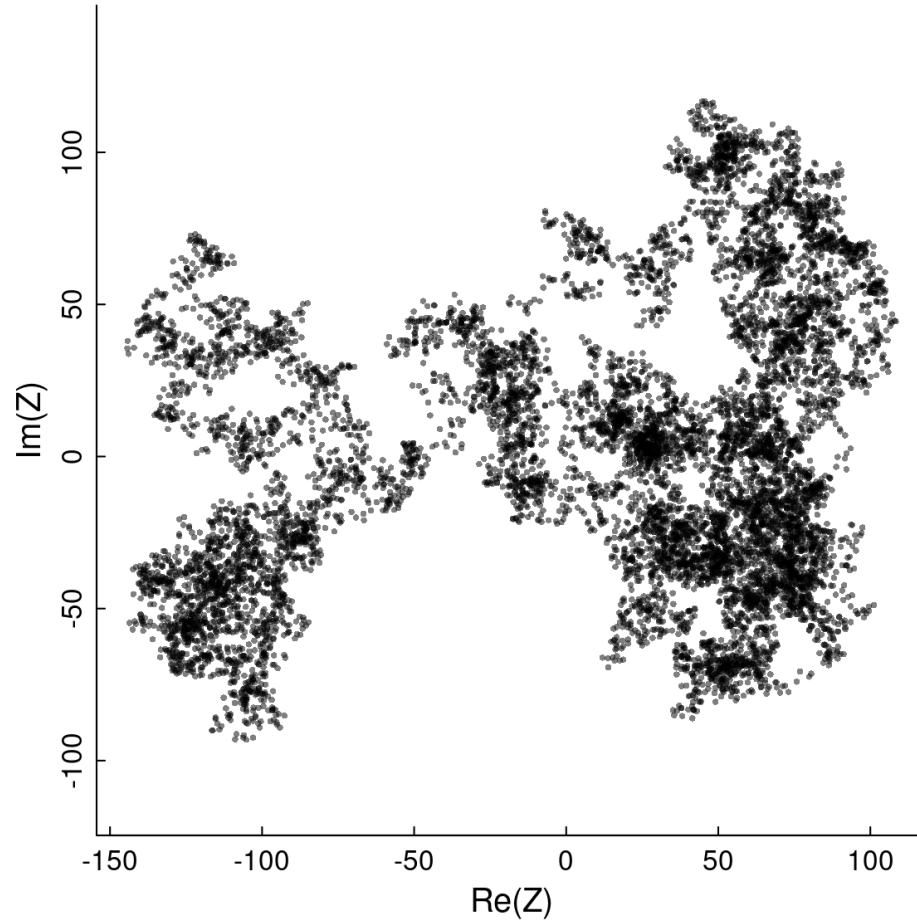
where:

$W_t$  - is **white noise**, i.e. independent Gaussian process in  $x$  and  $y$ .

$\beta$  - is **magnitude of randomness**

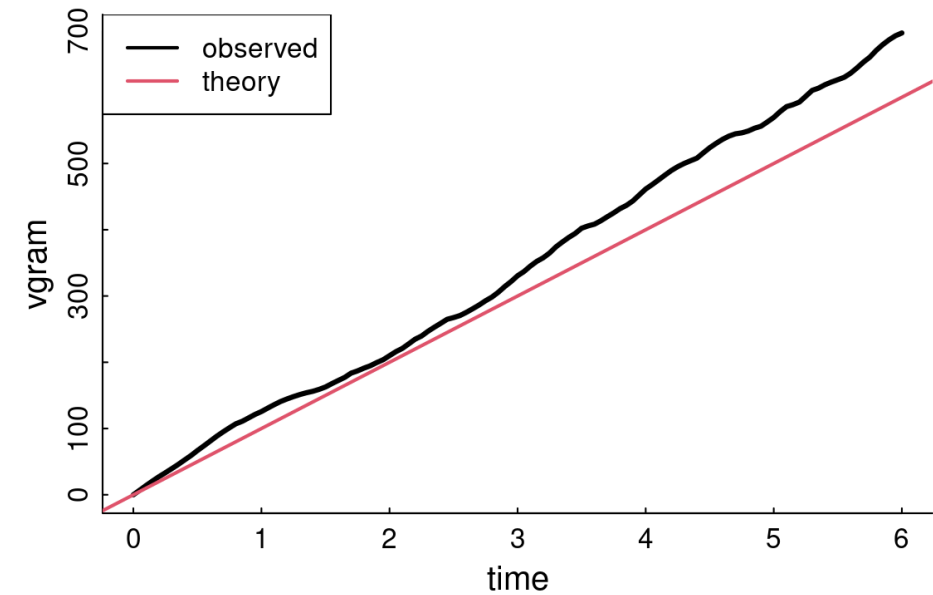


# Brownian Motion



# Semi-variogram

For **White Noise**, the variance grows *linearly* with time, i.e. the trajectory always moves further and further and away from origin.



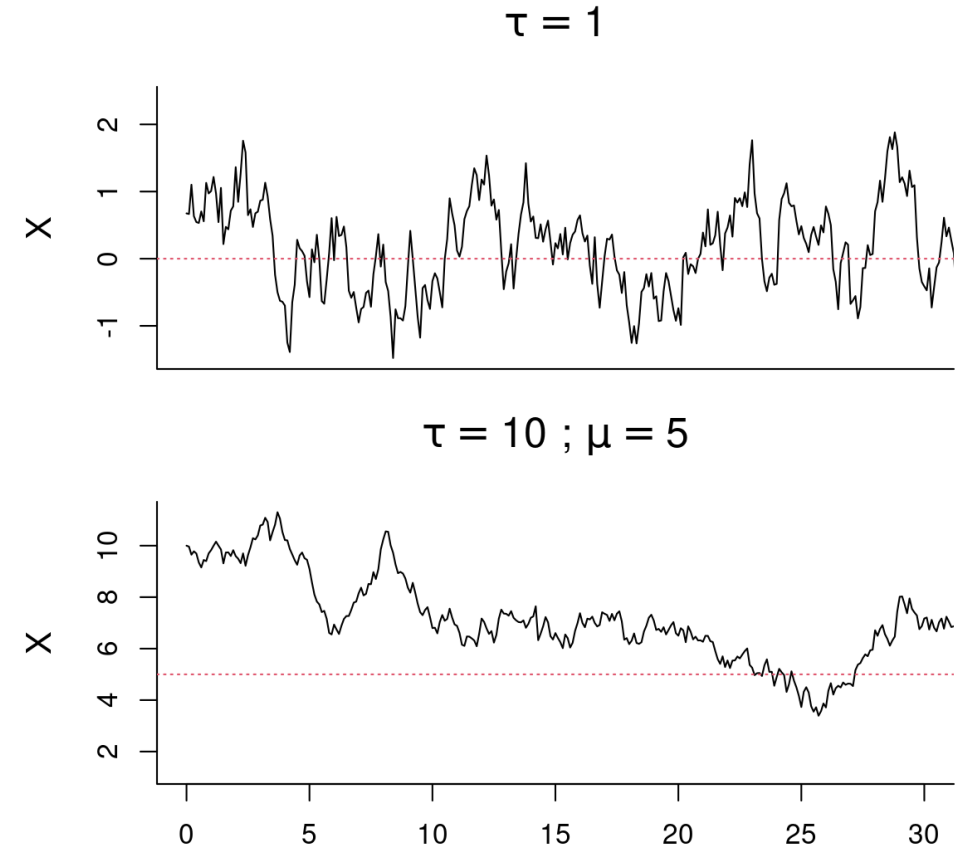


# OU-Position (OUP) in 1 dimension

The Ornstein-Uhlenbeck process is expressed in terms of a *stochastic differential equation*:

$$\frac{dX}{dt} = -\frac{1}{\tau_p}(X - \mu) + \alpha W_t$$

Equivalent of **discrete auto-regression** (AR1)



This is sometimes called a **Mean reversion** process.

# OUP: in 2D

A 2-D OUP models the  $x$  and the  $y$  components of movement as independent OU processes.

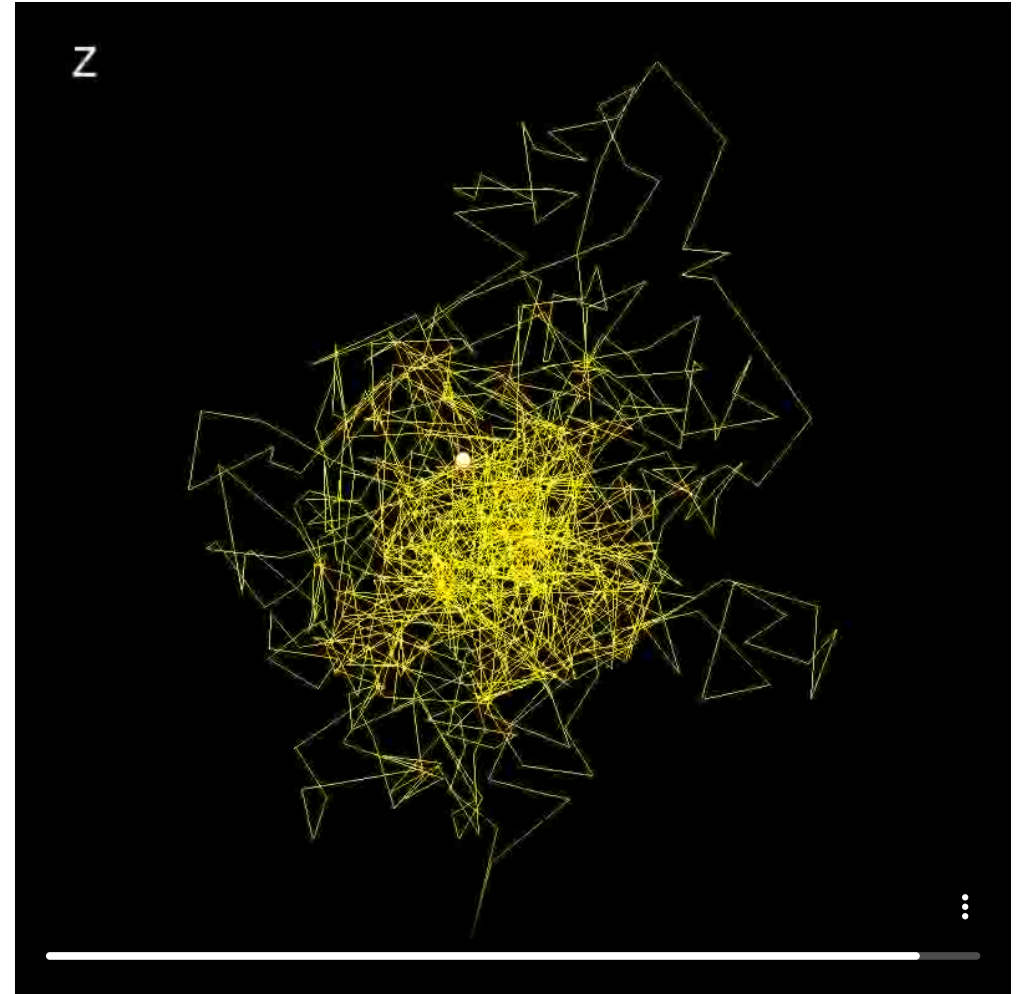
$$\frac{dZ}{dt} = -\frac{1}{\tau_p}(Z - \mu) + \alpha W_t$$

Can be written in terms of Area!

$$OUP(\tau_p, A)$$

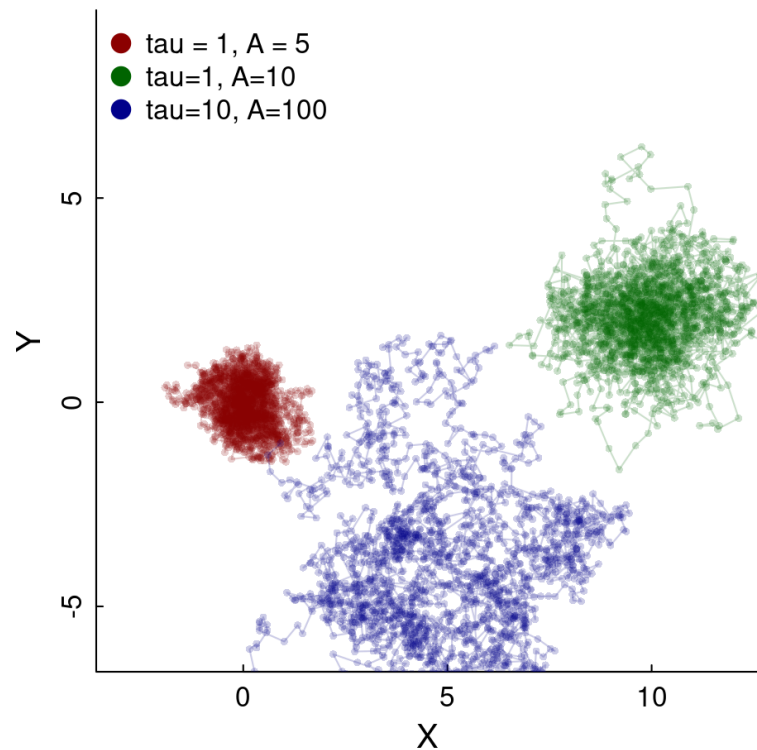
)

Constrained in Space!



## OUP: Sample Tracks

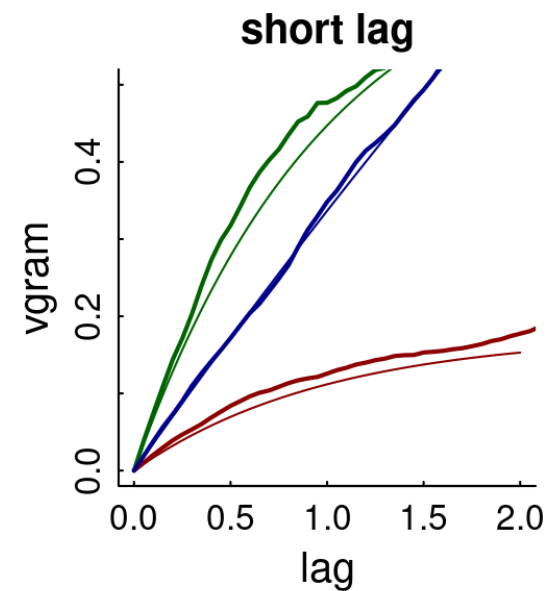
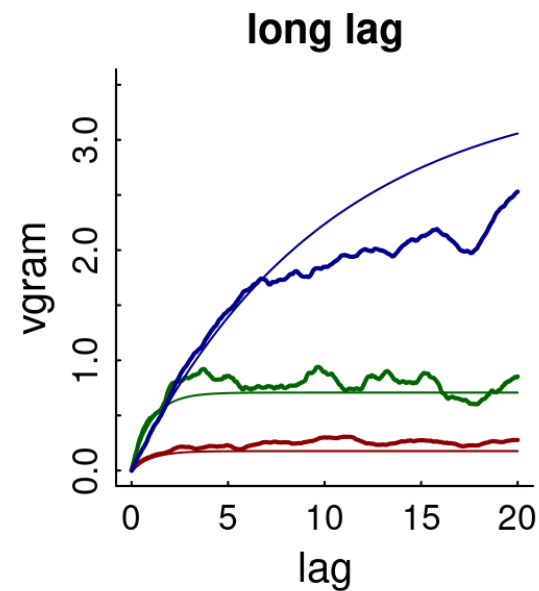
$$OU(\tau_p, A)$$



## OUP: Semivariogram

Theory:

$$\hat{V}(t) \approx \frac{A}{6\pi} \left(1 - e^{-t/\tau}\right)$$



# Correlated Velocity Model

Also known as "*Ornstein Uhlenbeck Velocity*" Model.

The CVM model integrates a 2D-OU process for **velocity** to obtain positions. Thus:

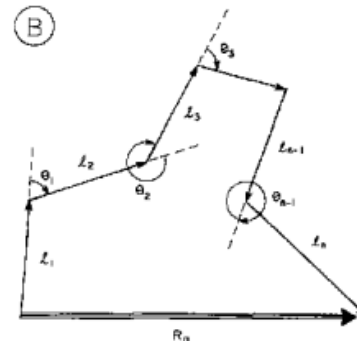
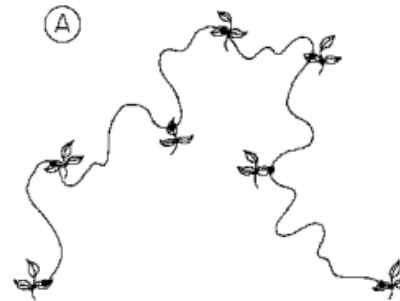
$$Z(t) = Z(0) + \int_0^t V(t)dt$$

$$\frac{dV(t)}{dt} = -\frac{1}{\tau}V + \frac{2\nu}{\sqrt{\pi\tau}}W_t.$$

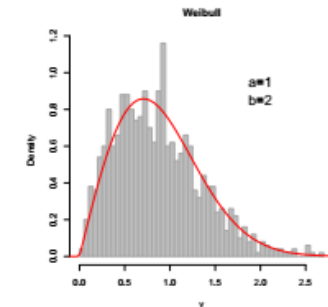
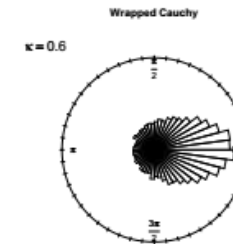
and  $v(0) = v_0$

- $\tau_v$  - characteristic time scale of *speed*
- $\nu$  - mean speed

Discrete analogue to **Correlated Random Walk (CRW)**



- $\theta_t \sim$  Some Circular Distribution
- $V \sim$  Unimodal Positive Distribution.

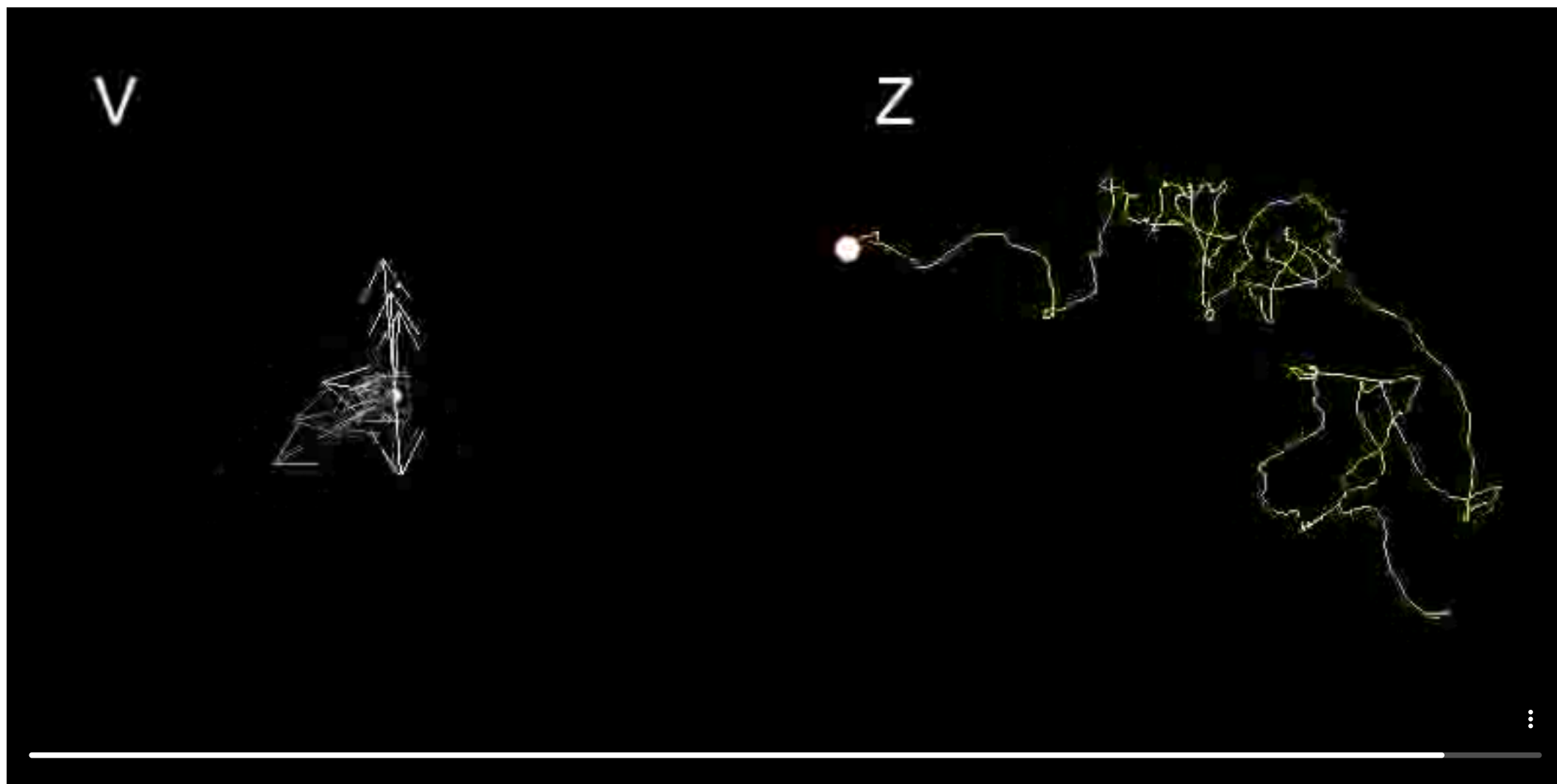


Analyzing Insect Movement  
as a Correlated Random Walk

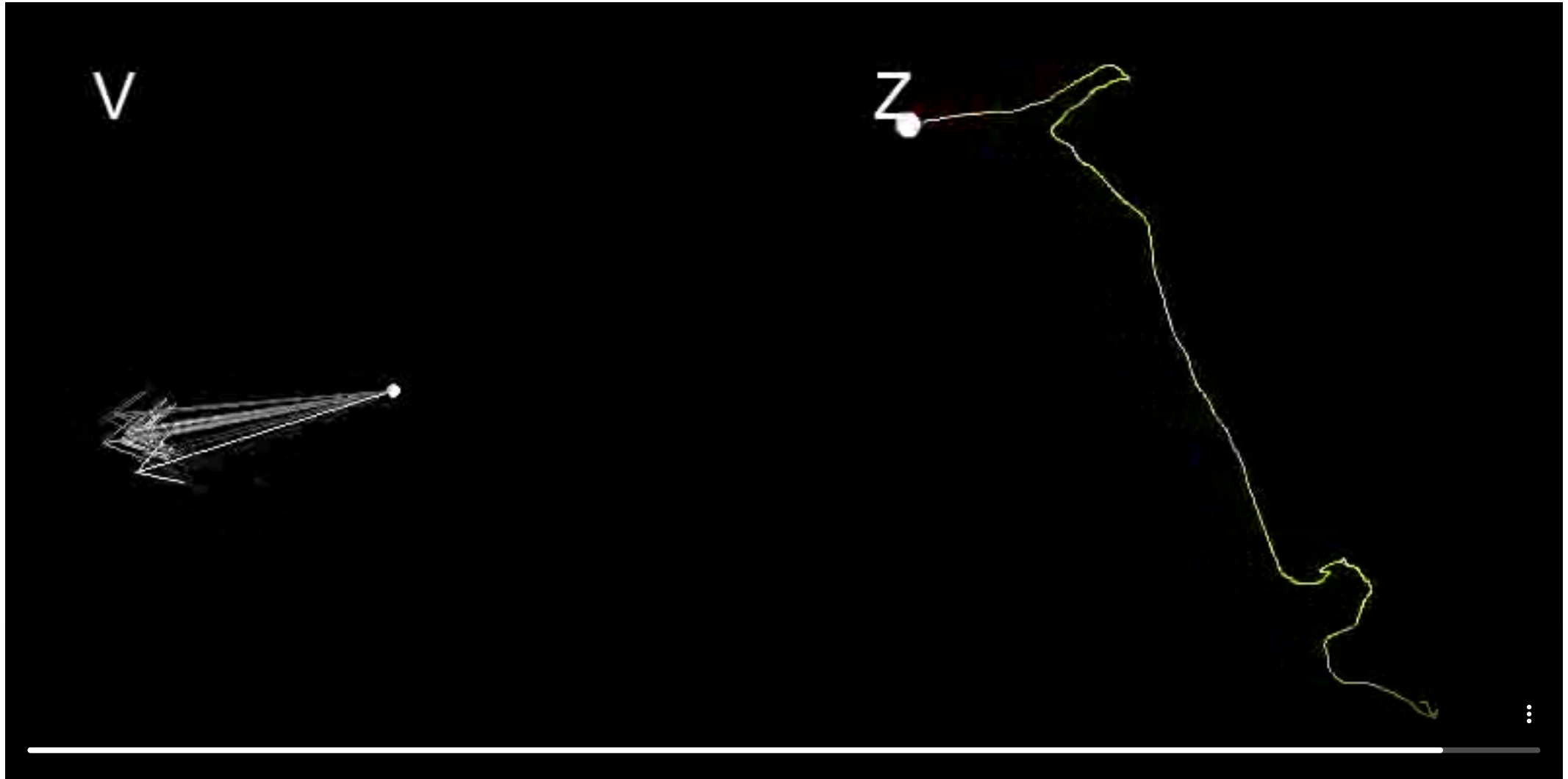
*Oecologia*  
© Springer-Verlag 1993

P.M. Kareiva<sup>1</sup> and N. Shigesada<sup>2</sup>  
<sup>1</sup> Division of Biology, Brown University, Providence, RI 02912, USA  
<sup>2</sup> Department of Biophysics, Kyoto University, Kyoto, 606 Japan

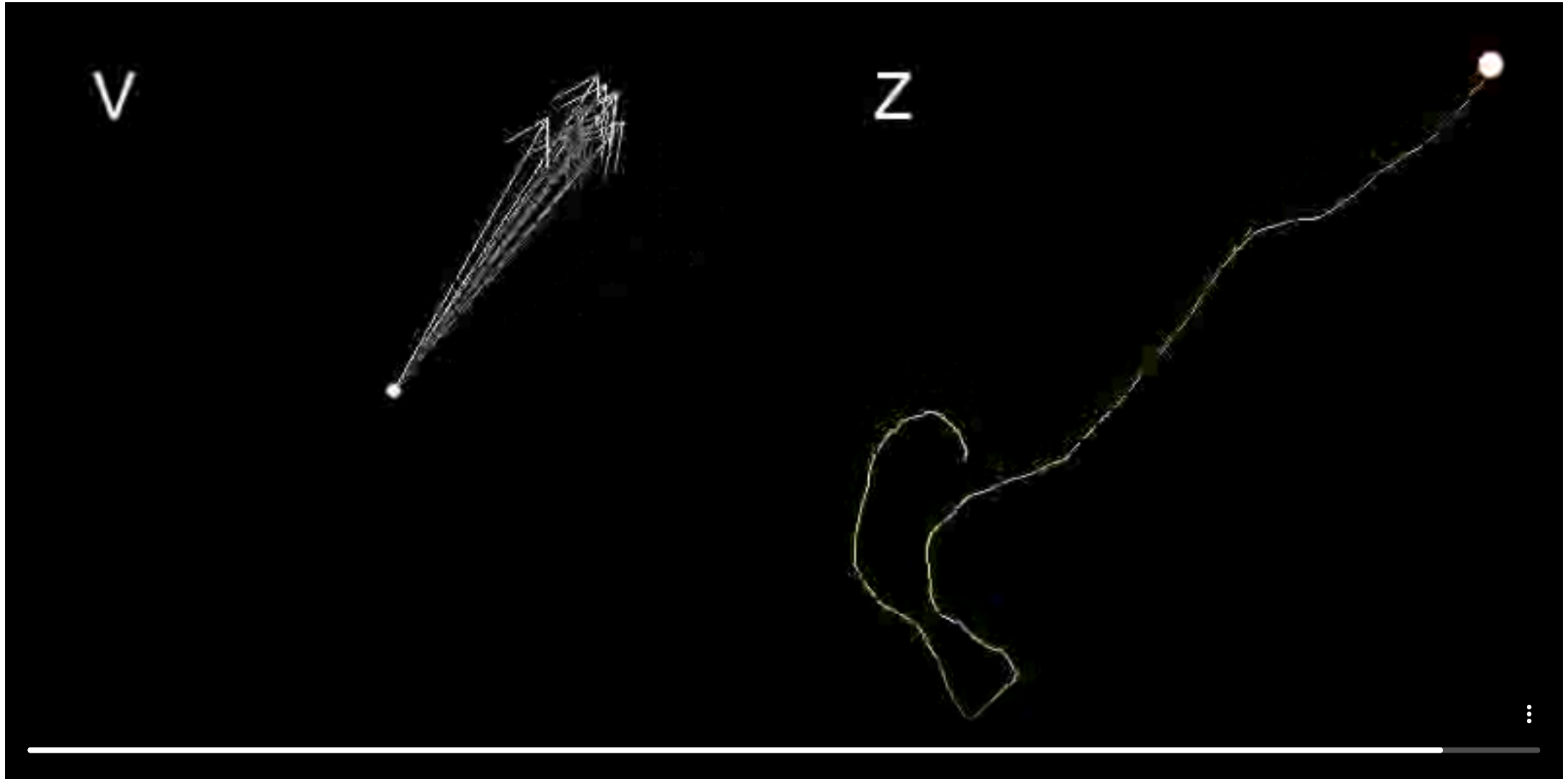
CVM: Compare time scales  $\tau = 1$



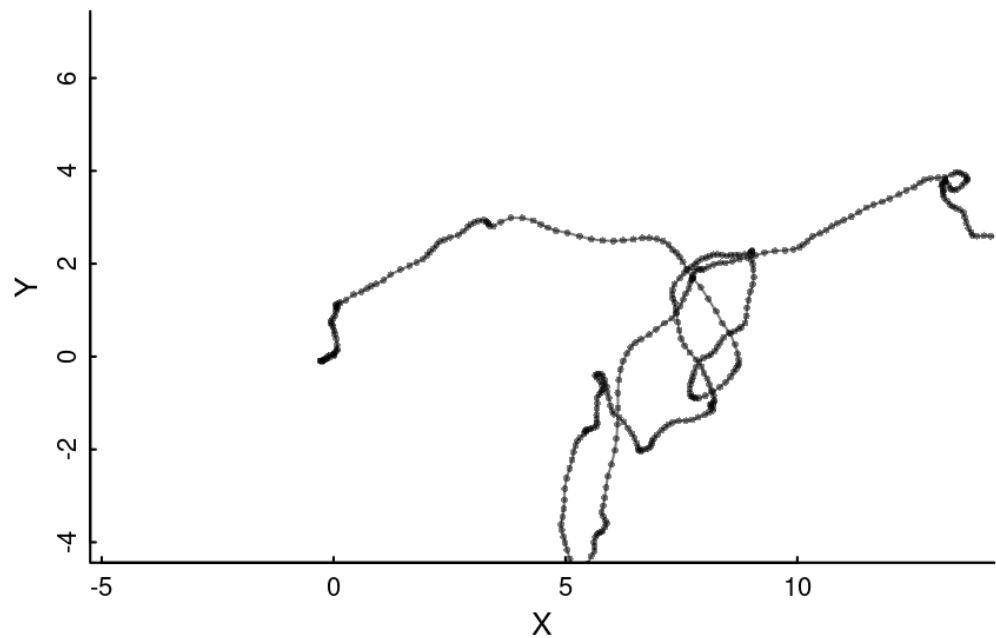
CVM: Compare time scales  $\tau = 10$



CVM: Compare time scales  $\tau = 100$

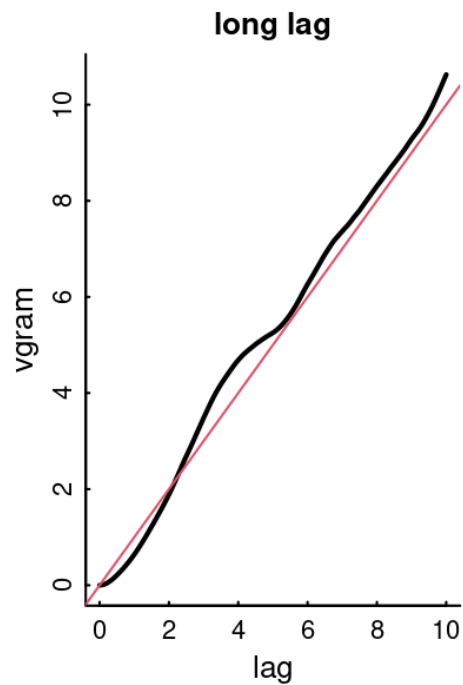


# CVM (or OUV) variogram



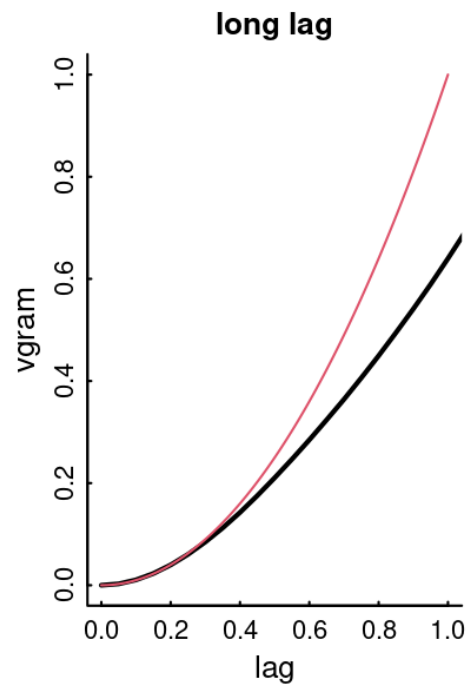
Long time scale:

**linear**  $\propto t$



Short time scale:

**parabola**  $\propto t^2$





# Variations on CVM

- Unbiased CVM
- Advective CVM
- Rotational CVM
- Rotational-Advective CVM

Good as **fundamental unit** of animal movement.

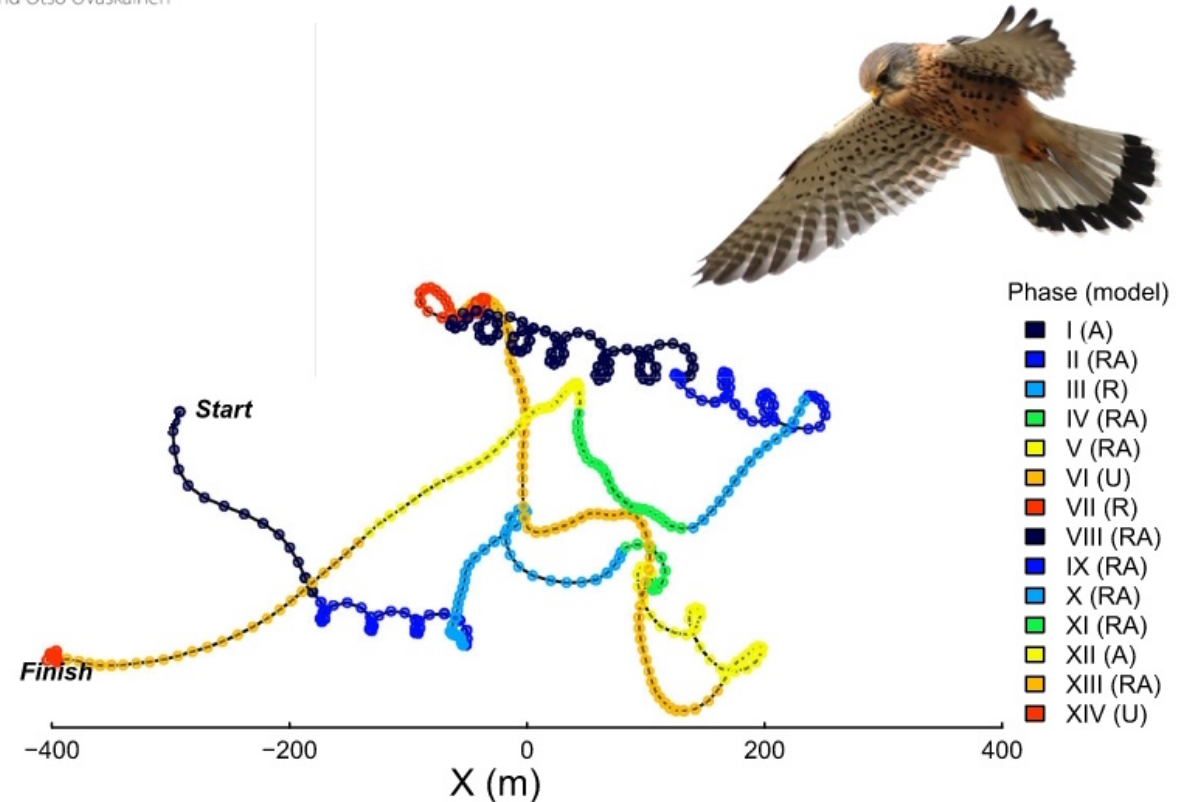
METHODOLOGY ARTICLE

Open Access



## Correlated velocity models as a fundamental unit of animal movement: synthesis and applications

Eliezer Gurarie<sup>1\*</sup>, Christen H. Fleming<sup>1,2</sup>, William F. Fagan<sup>1</sup>, Kristin L. Laidre<sup>3</sup>, Jesús Hernández-Pliego<sup>4</sup> and Otso Ovaskainen<sup>5,6</sup>



# Ornstein-Uhlenbeck-F...

The **Ornstein-Uhlenbeck Foraging** (or Fleming?) model is hybridized the OU-Position and CVM models:

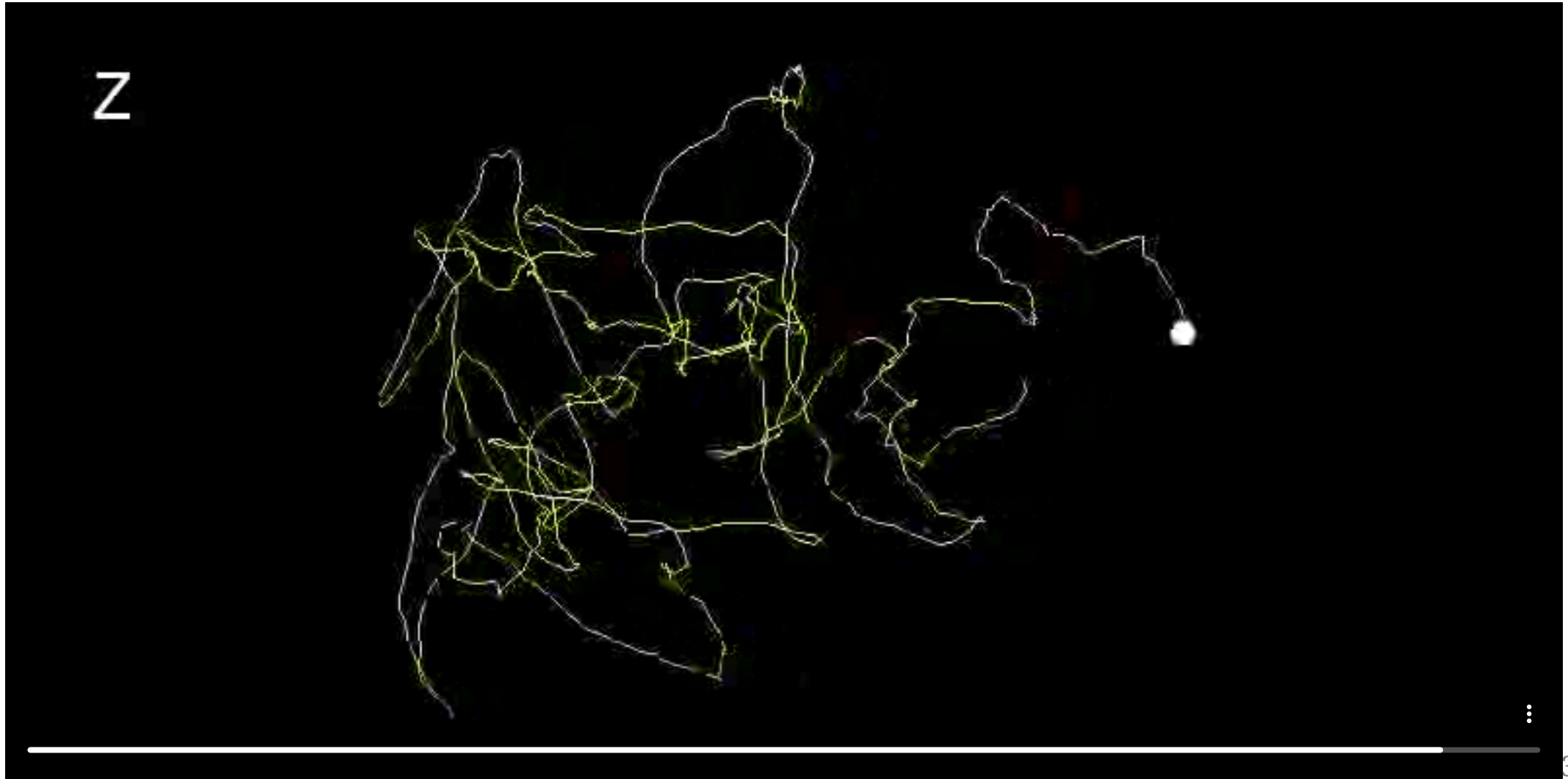
$$\frac{d}{dt}z(t) = -\frac{1}{\tau_z}(z(t) - \mu_z) + u(t)$$

$$\frac{d}{dt}u(t) = -\frac{1}{\tau_u}u + \beta W_t.$$

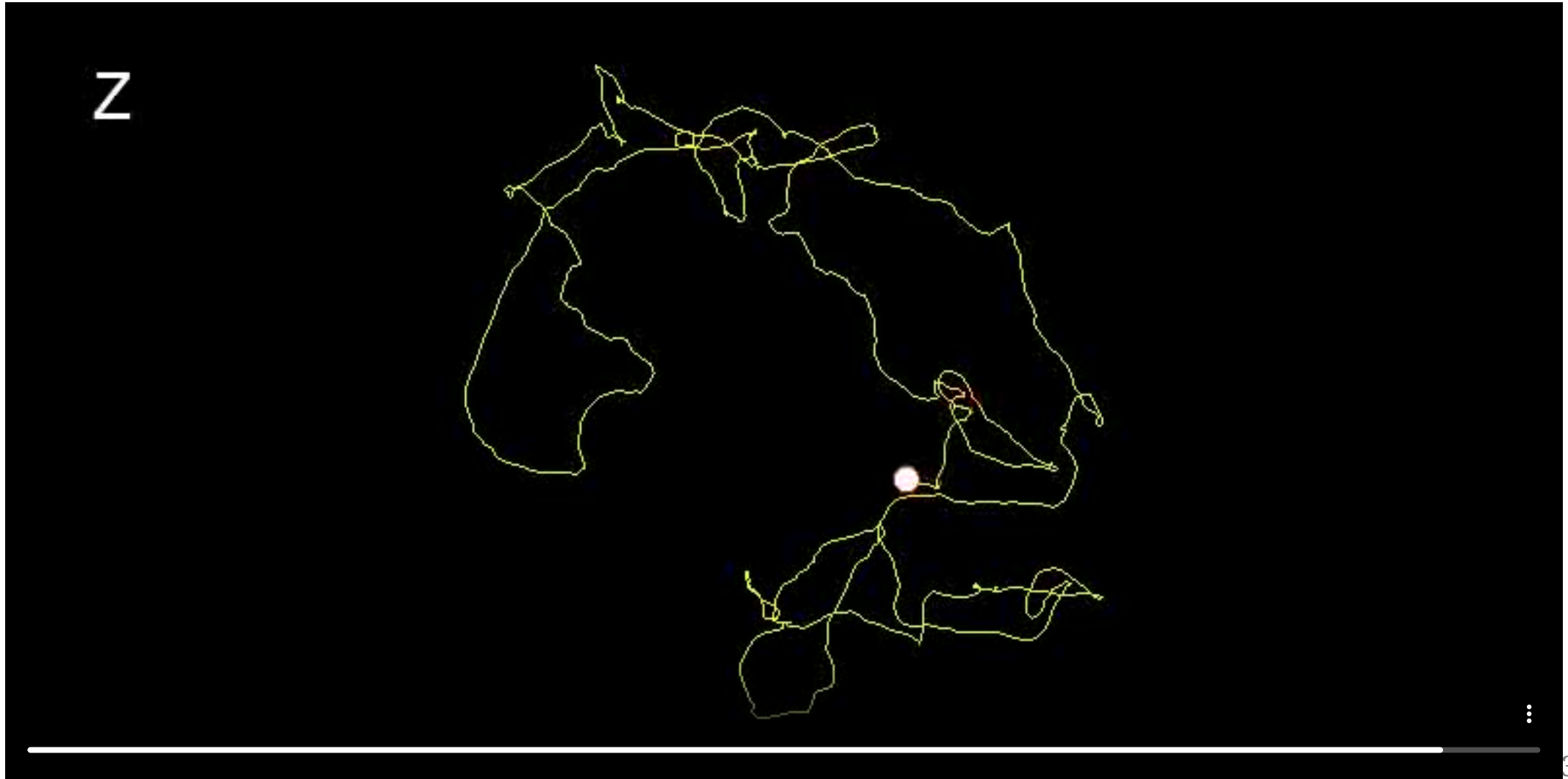
- $\tau_v$  is time scale of "pseudo-velocity" process
- $\tau_p$  is time scale of coverage of constrained area ("home range")

The position is a stochastic process that "relaxes" to the mean location  $\mu_z$  at rate  $\tau_z$  with a "stochastic kick" that is given by an additional velocity component that is identical to the CVM.

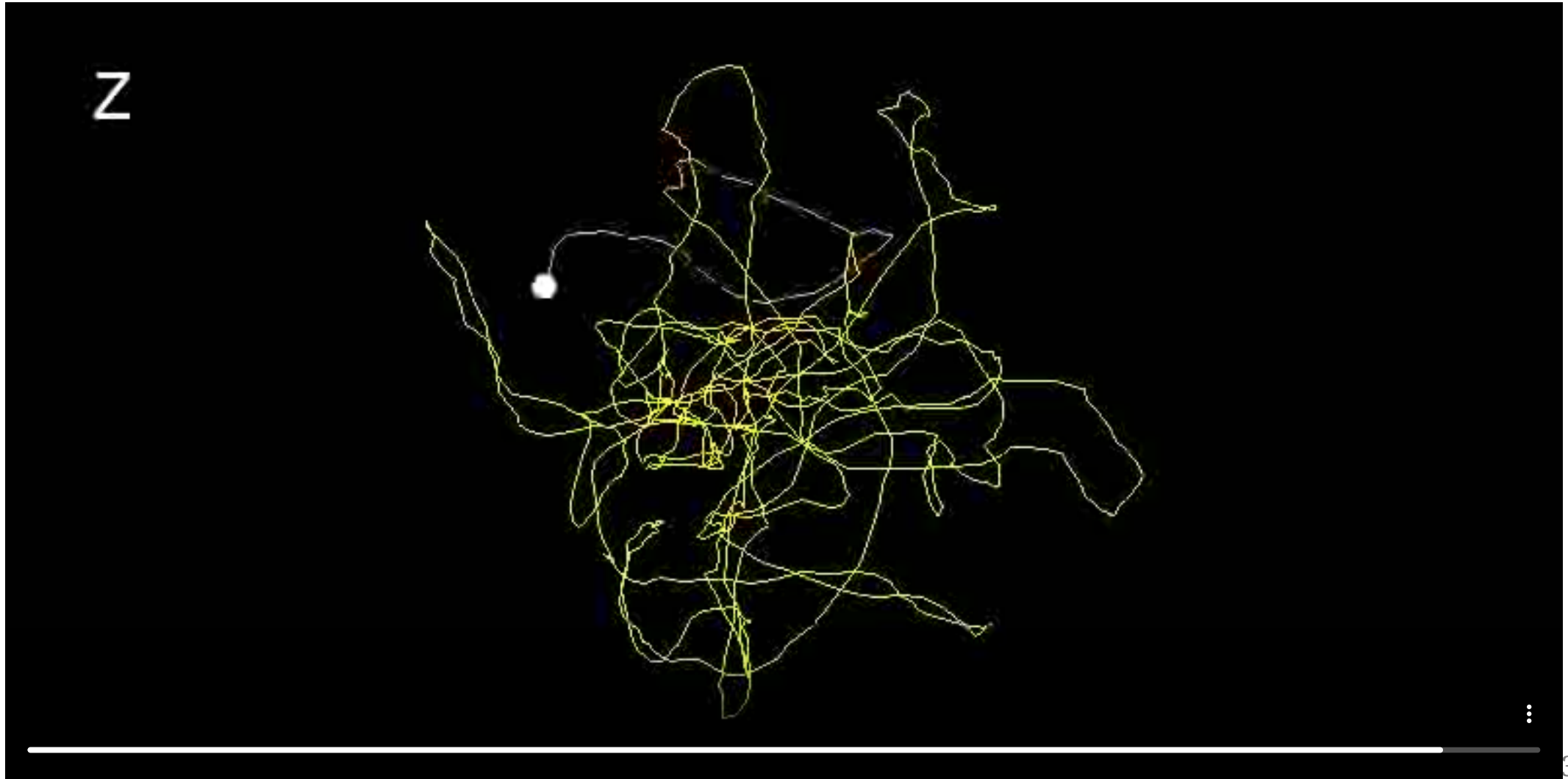
OUF: Animation 1  $\tau_p = 10; \tau_v = 1$



OUF: Animation 2  $\tau_p = 100; \tau_v = 1$

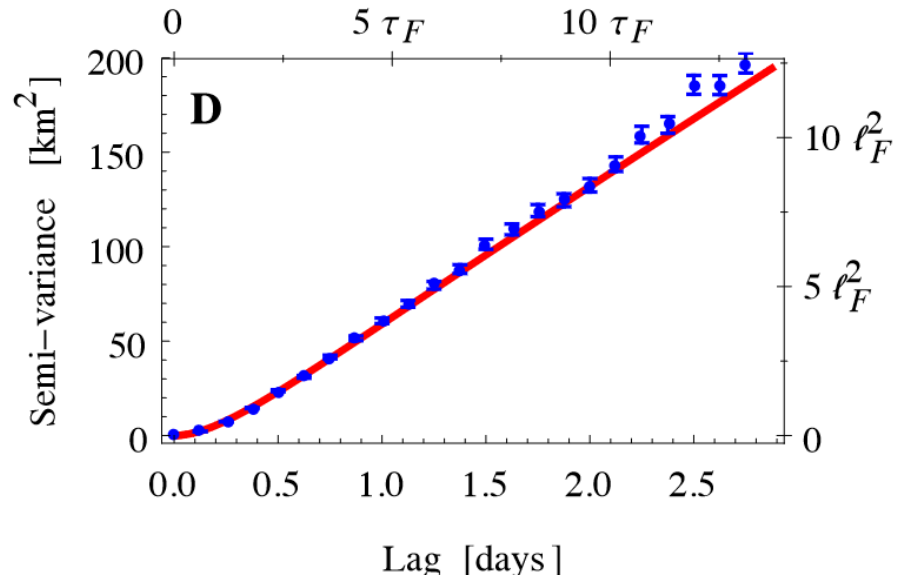


OUF: Animation 3  $\tau_p = 1.1; \tau_v = 1$

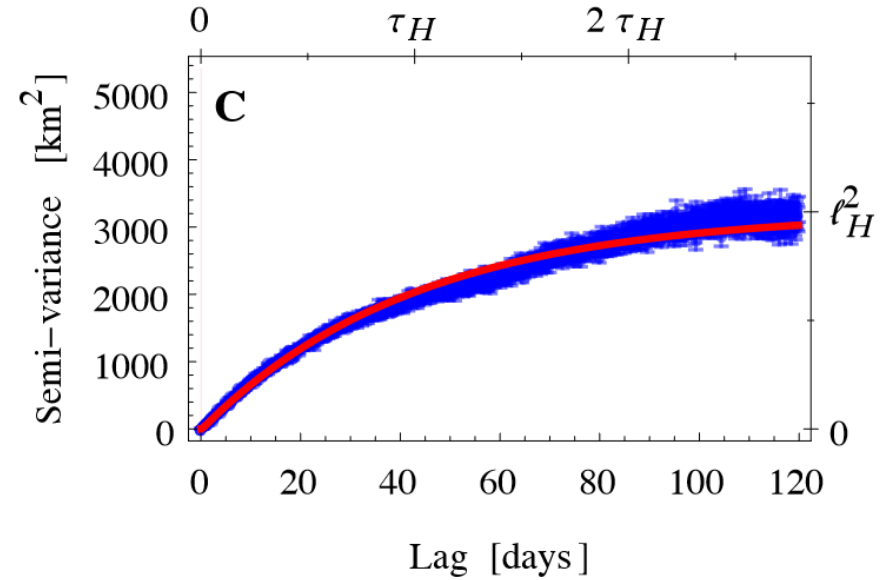


# OUF semi-variogram

At small scales: looks like CVM

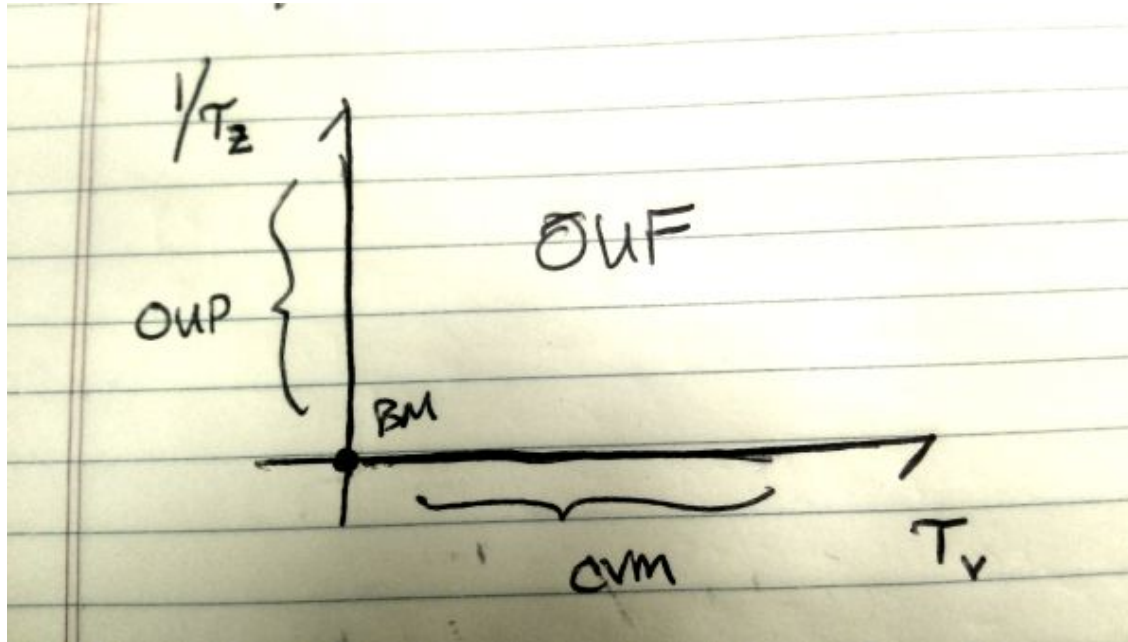


At large scales: looks like OUP



# BM-OU-CVM-OUF special Cases

These models are all special cases of the OUF.



- at  $\tau_p \rightarrow \infty$ , OUF is CVM,
- at  $\tau_v \rightarrow 0$ , OUF is OUP,
- at  $\tau_p \rightarrow \infty$  AND  $\tau_v \rightarrow 0$ , OUF is BM