

A brief introduction to some Movement Models

Elie Gurarie

June 18, 2024



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

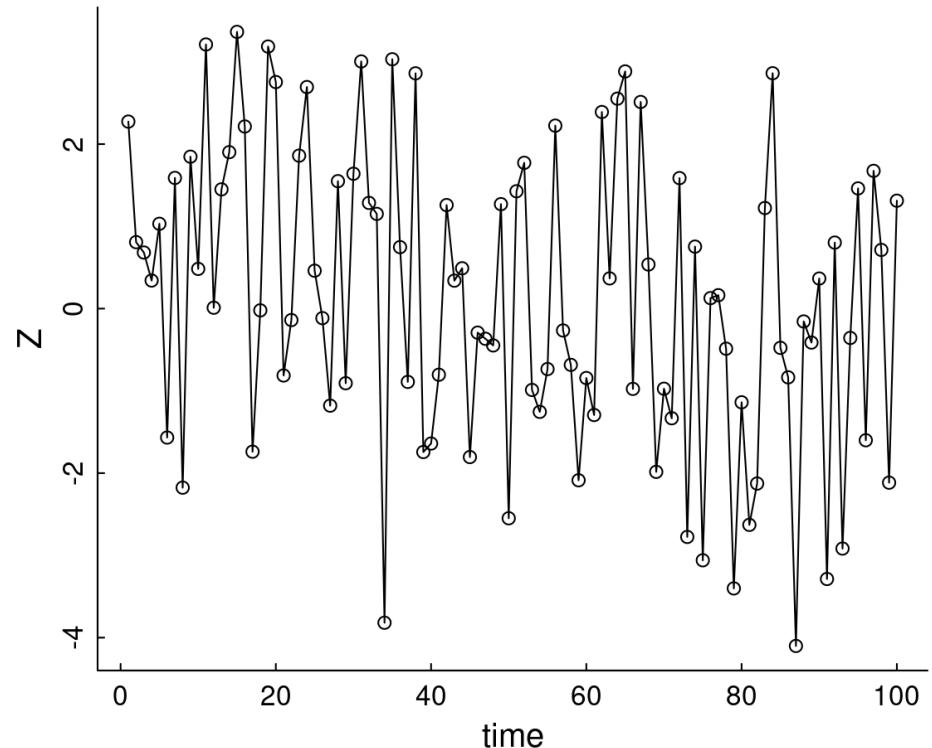
```
sigma = 2  
Z <- rnorm(100, sd = sigma)
```

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.)

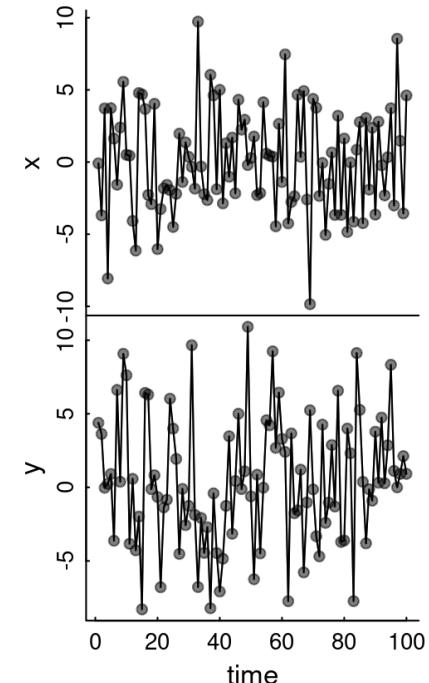
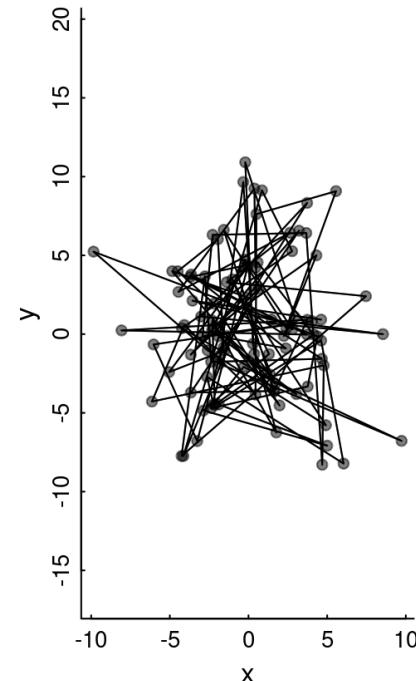
```
sigma <- 4
n <- 100
Z <- rnorm(n, sd = sigma) + 1i*rnorm(n, sd = sig
◀ ────────────────────────────────────────────────── ▶
```

Properties

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

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

- Goes nowhere
- Jiggles around like crazy



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

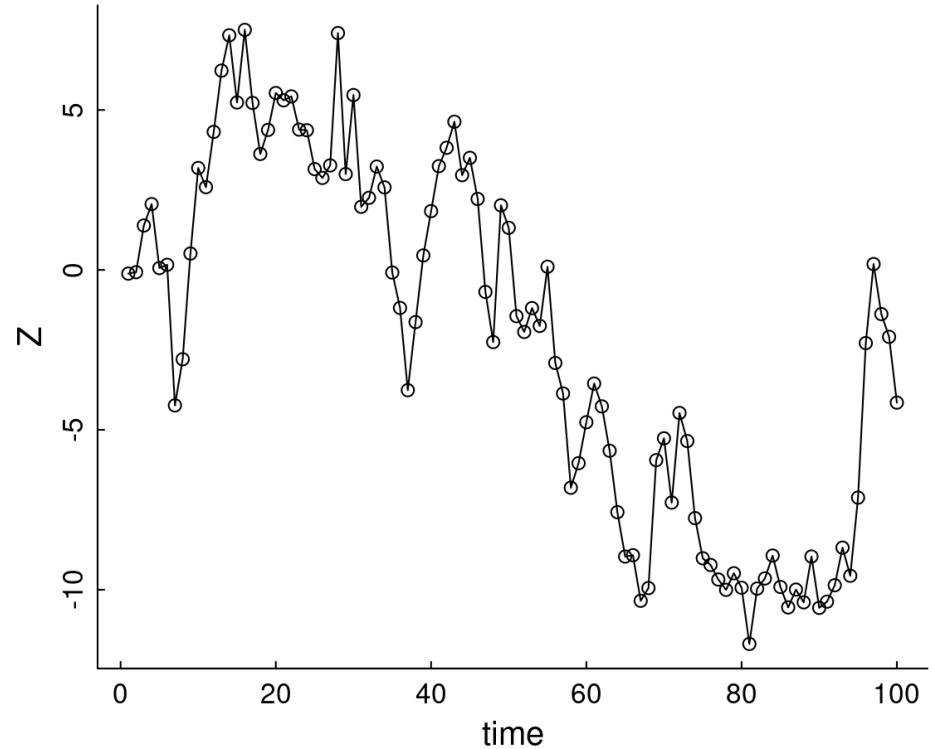
1D Random Walk

$$X \sim RW_{1d}(\sigma)$$

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

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

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



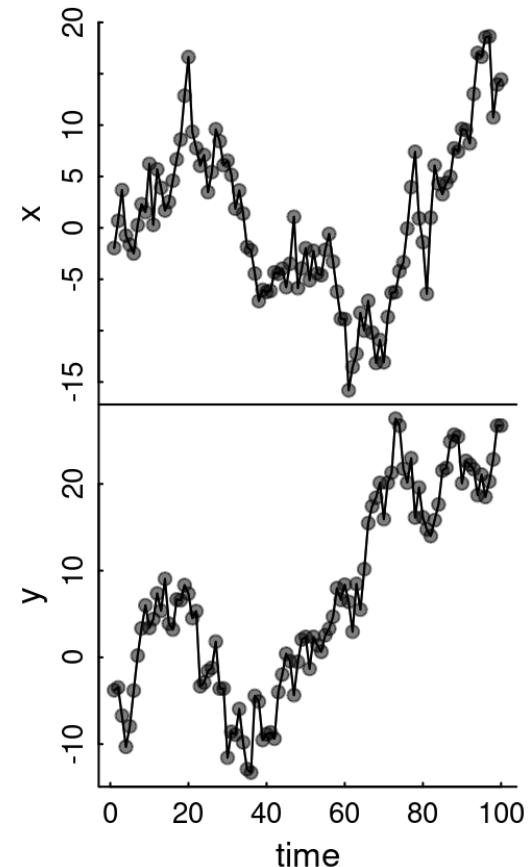
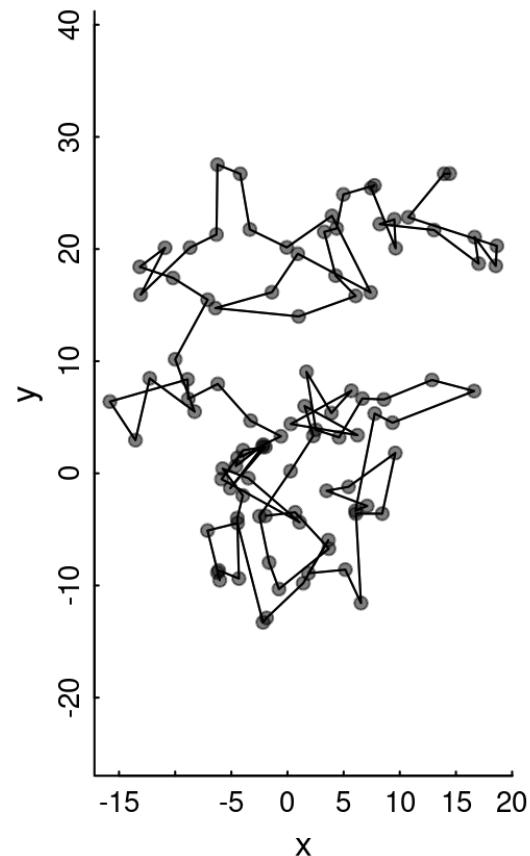
2D Random Walk

$$\mathbf{Z} \sim RW_{2d}(\sigma)$$

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

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

Step & turning angles:

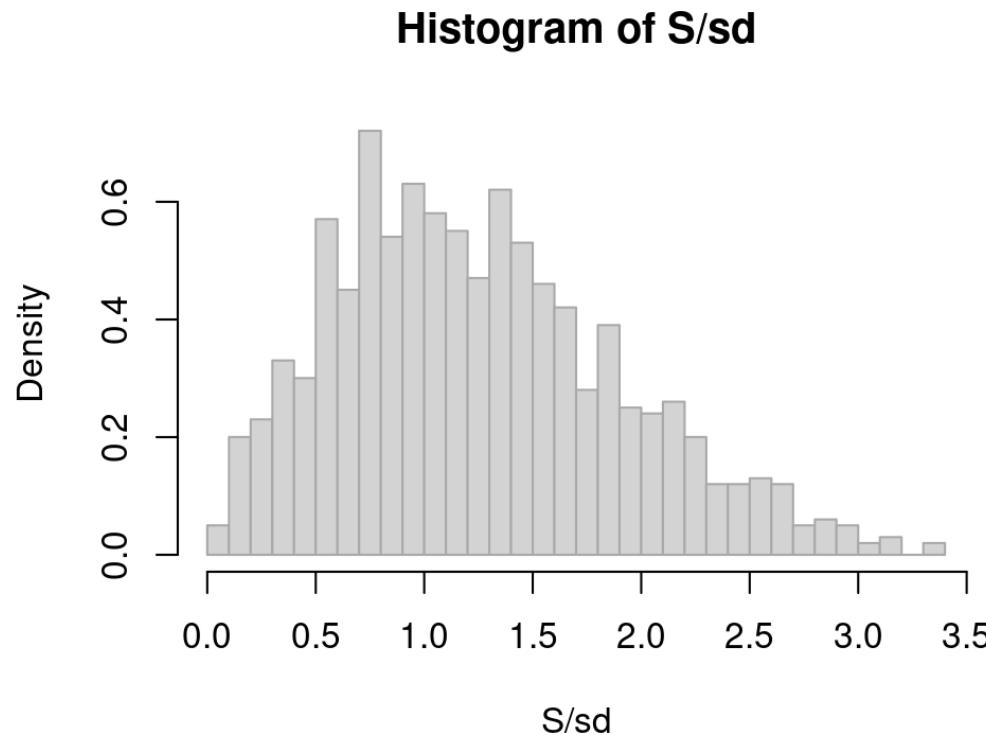
$$E(\mathbf{Z}_t) = \{0, 0\}$$

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

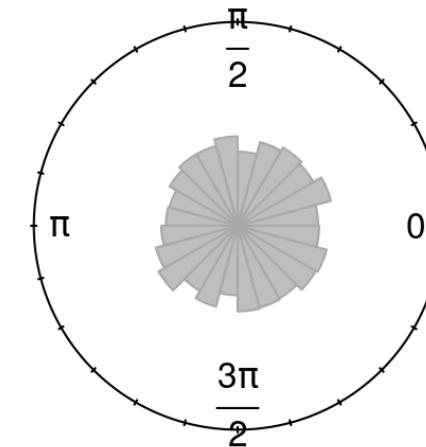
$$\text{Var}(|\mathbf{Z}_t|) = 2\sigma^2 t$$

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

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



turning angle θ



1D Autoregression Process

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

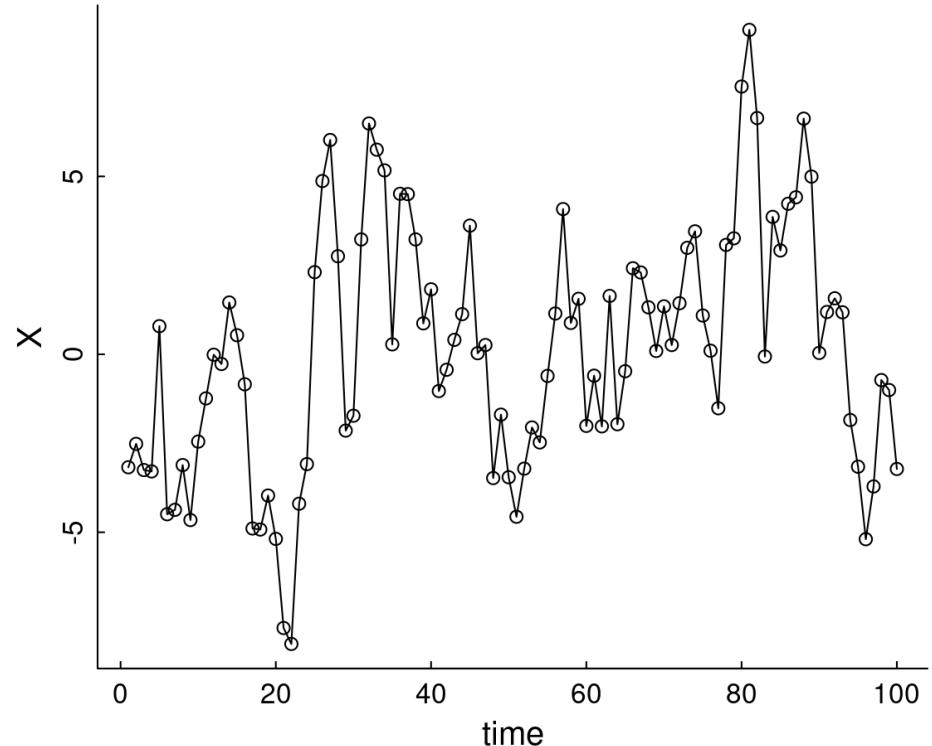
Properties

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

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

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

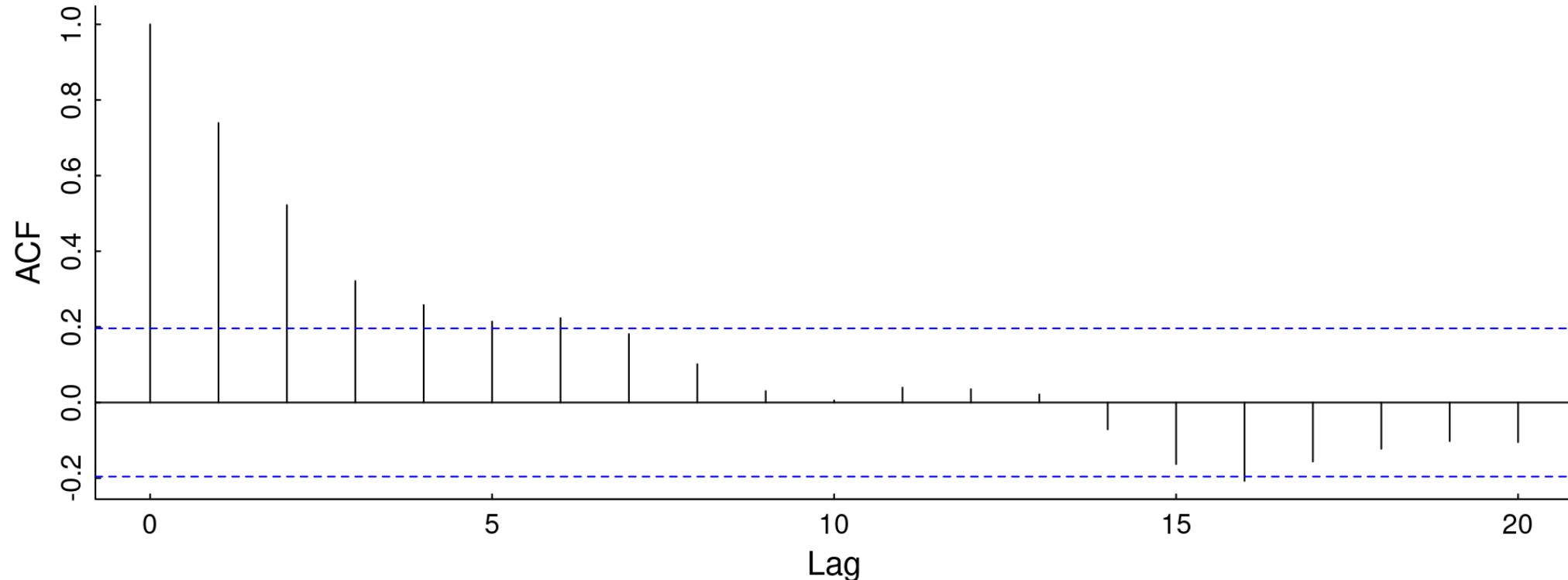
Spatially constrained!



the Autocorrelation function

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

`acf(X)`

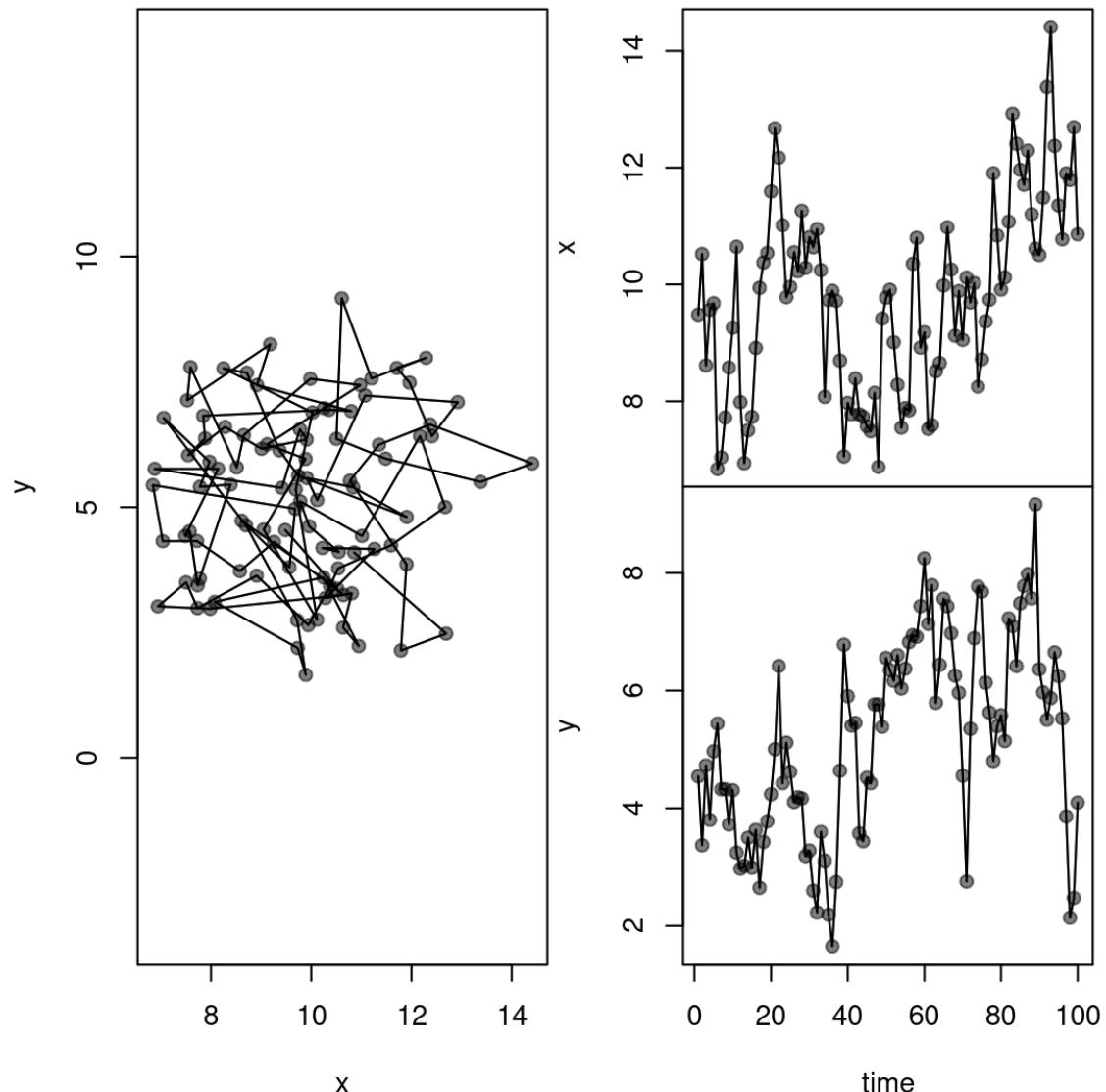


2D autoregressive walk

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

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

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):

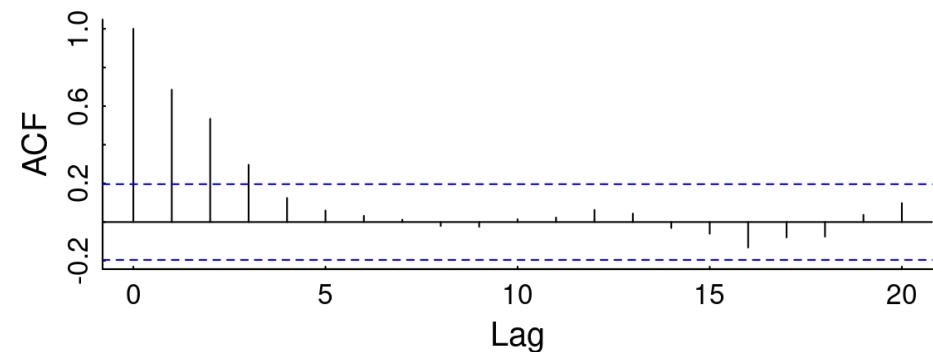
$$\mathbf{Z}_t = \mathbf{Z}_{t-1} - (1 - \phi)\mathbf{Z}_{t-1} + \sigma \mathbf{W}_t$$

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

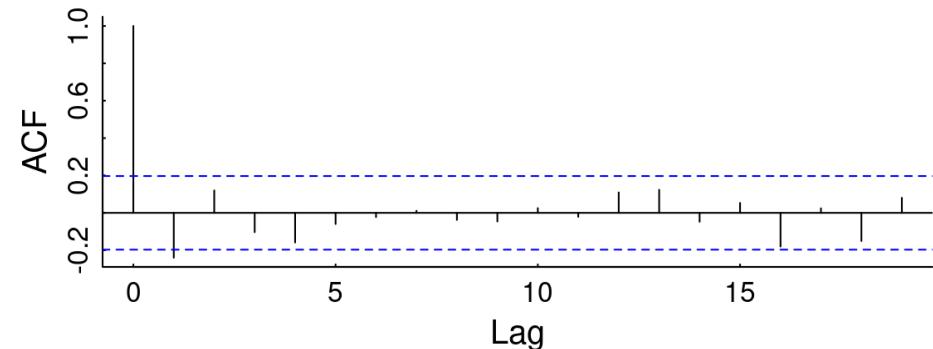
This means that the *step* process itself is NOT stationary / independent, but depends on **absolute location**.

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

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



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

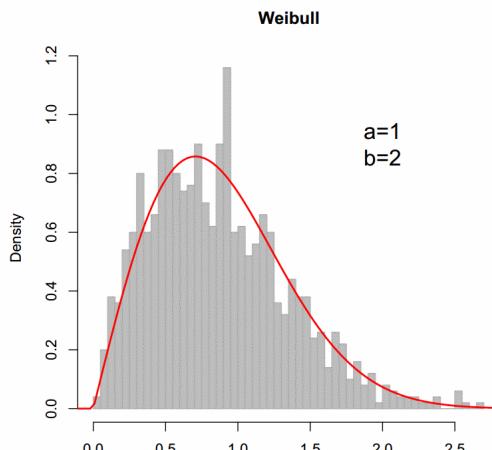
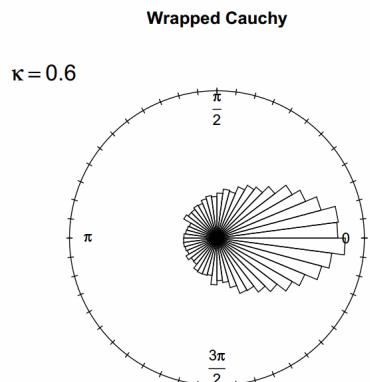


Correlated Random Walk

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. Kareiva¹ and N. Shigesada²

¹ Division of Biology, Brown University, Providence, RI 02912, USA

² 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

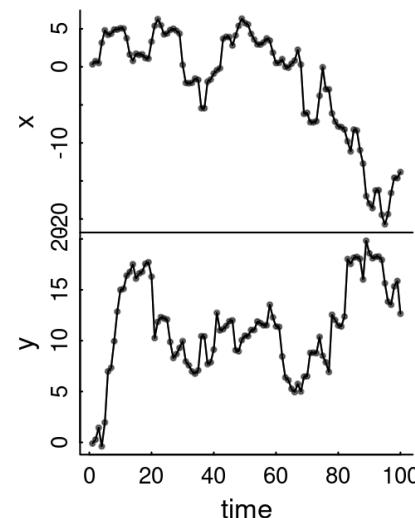
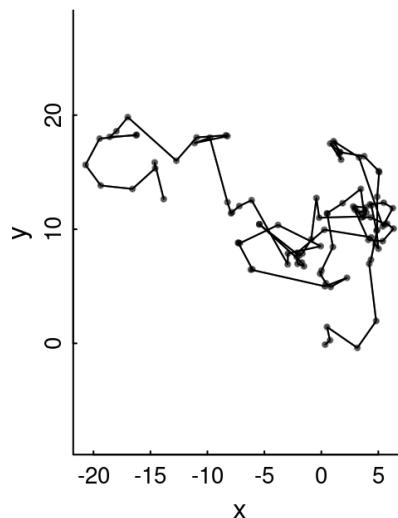
CLIFFORD S. PATLAK*

COMMITTEE ON MATHEMATICAL BIOLOGY
THE UNIVERSITY OF CHICAGO

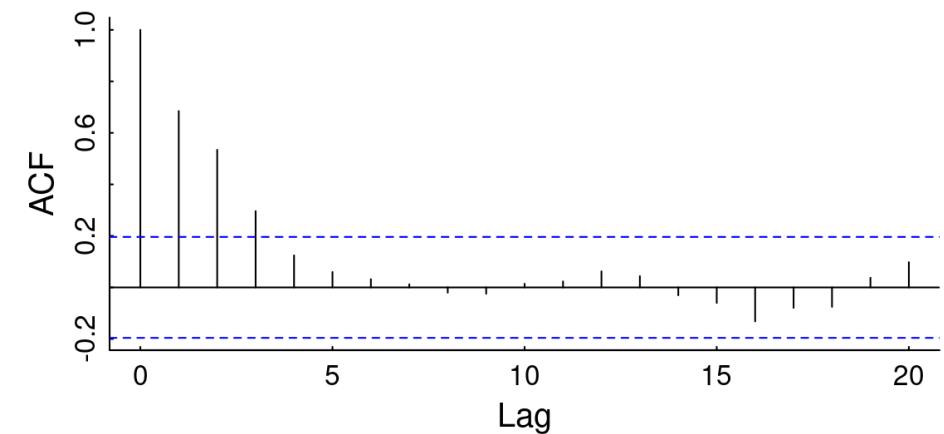
Simulate in R

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

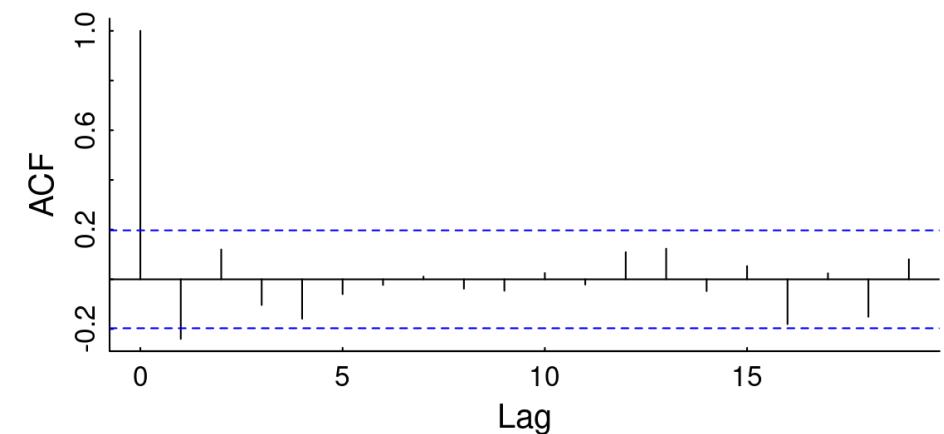
Also - flies off to infinity.



Also - autocorrelated in position:



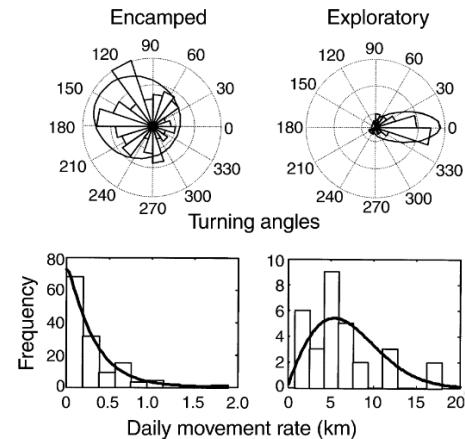
but not in steps!



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,^{1,4} DANIEL T. HAYDON,² JACQUI FRAIR,³ KENT E. HOLINGER,¹ AND JOHN M. FRYXELL²

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 μ_i and ρ_i .

Pretty self-explanatory!

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

Markov Chains

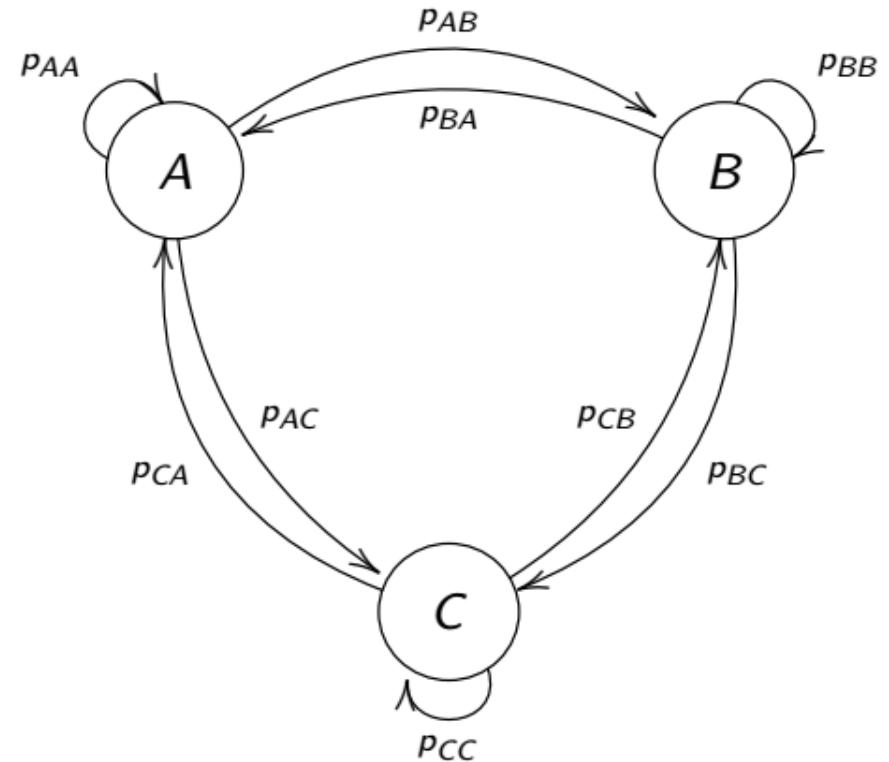
... model **state transitions**

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
		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 π_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
```

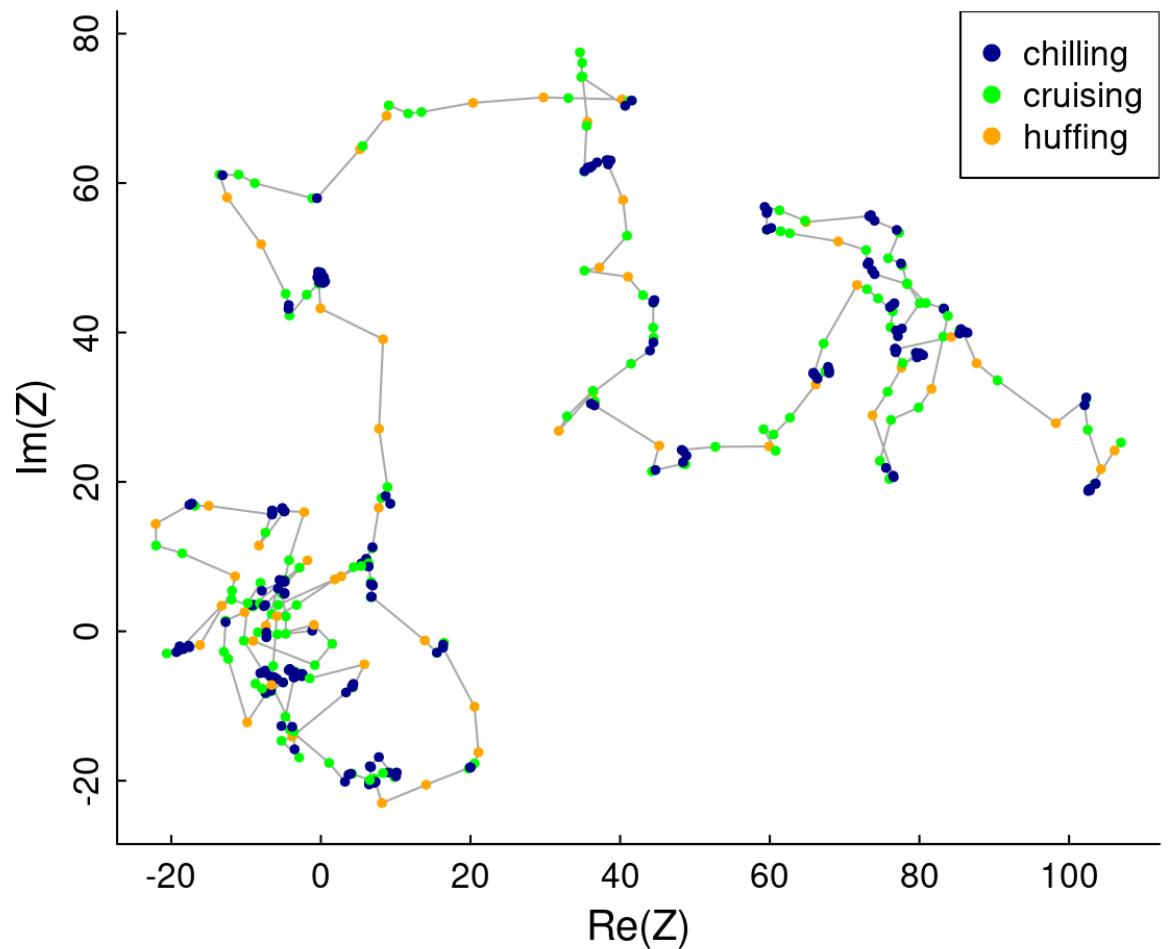
```
##          chilling  cruising  huffing
## chilling      0.7       0.2      0.1
## cruising      0.4       0.4      0.2
## huffing       0.0       0.8      0.2
```

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 2 3 2 1 1 2 2 1 1 1 1 2 1 2 2 1 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 1 2 1 2 1 1 1 1 2 1 2 2 1 1 1 1
## [75] 2 2 2 1 2 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 β .

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

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, bu 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 do 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.

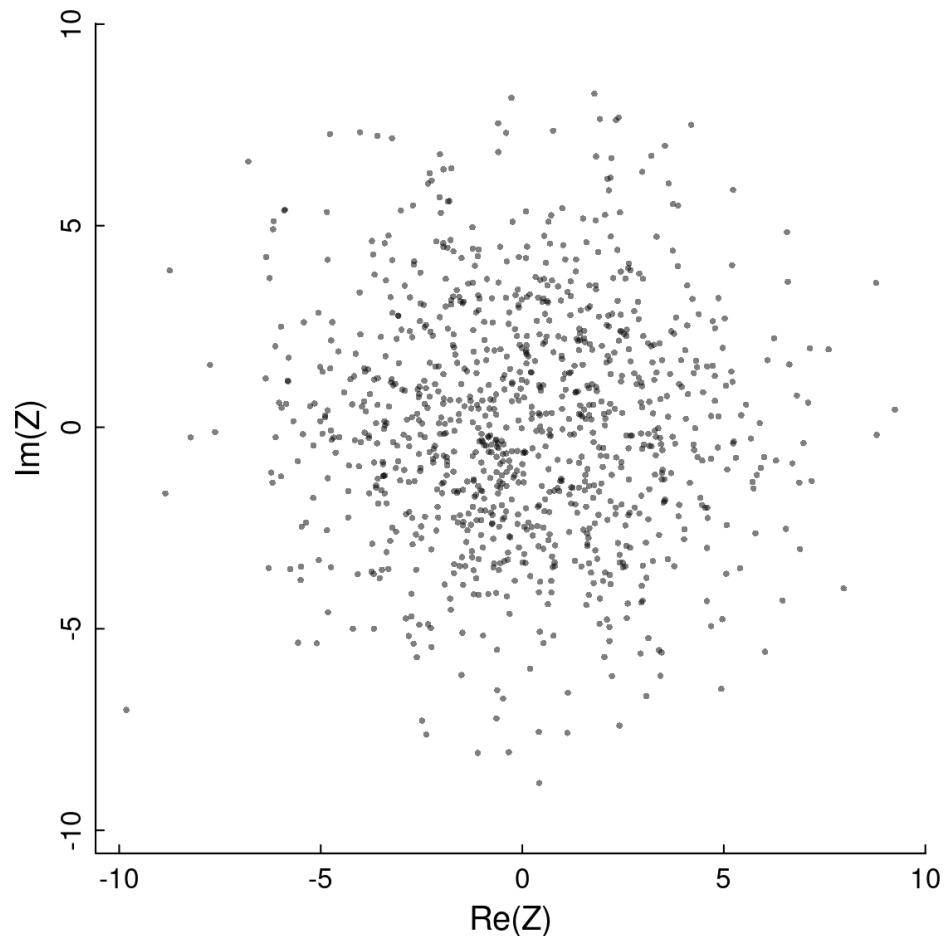
$$Z(t) = \sigma W_t$$

where:

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

Equivalent to the discrete time WN

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



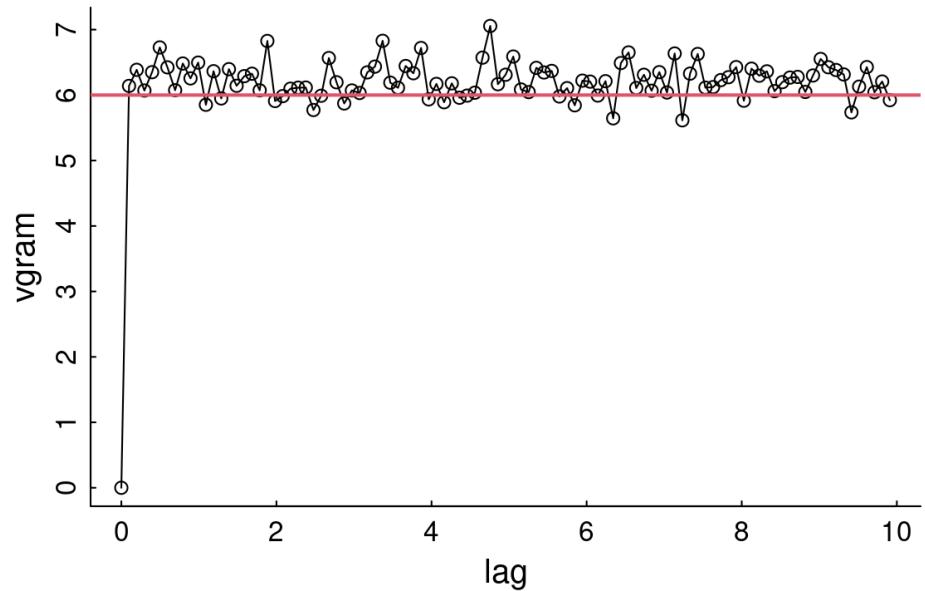
Obviously: no animal does this!! This is a model for *data* not *behavior*

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 2σ :



Brownian Motion

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

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

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

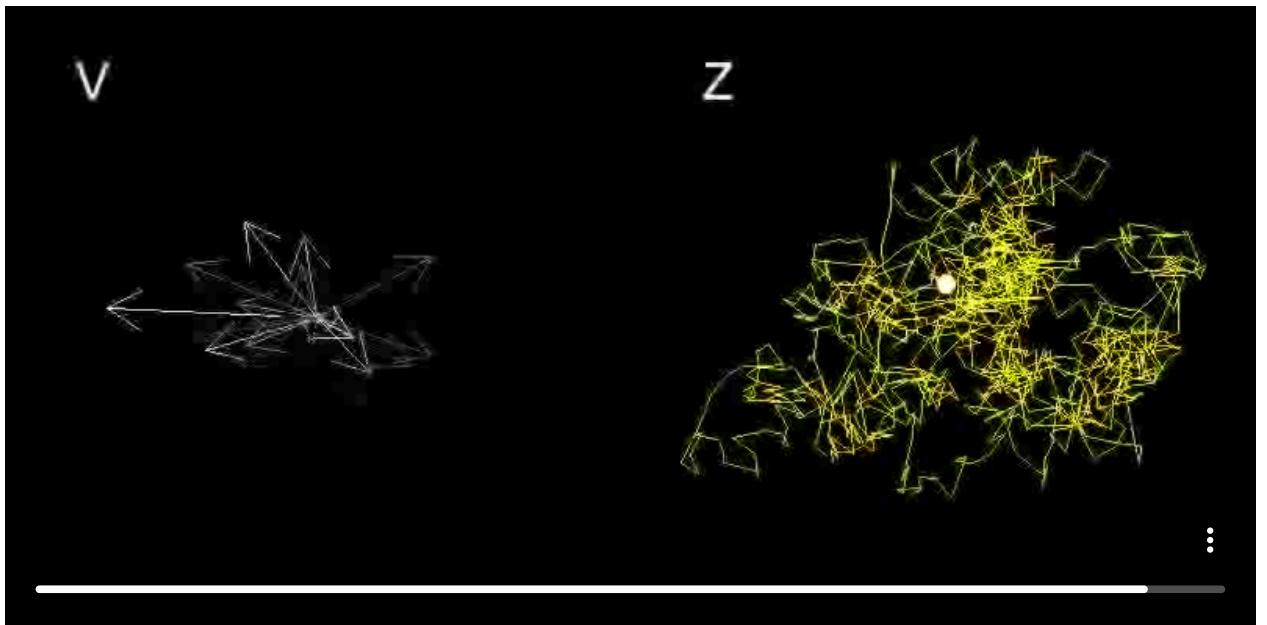
where

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

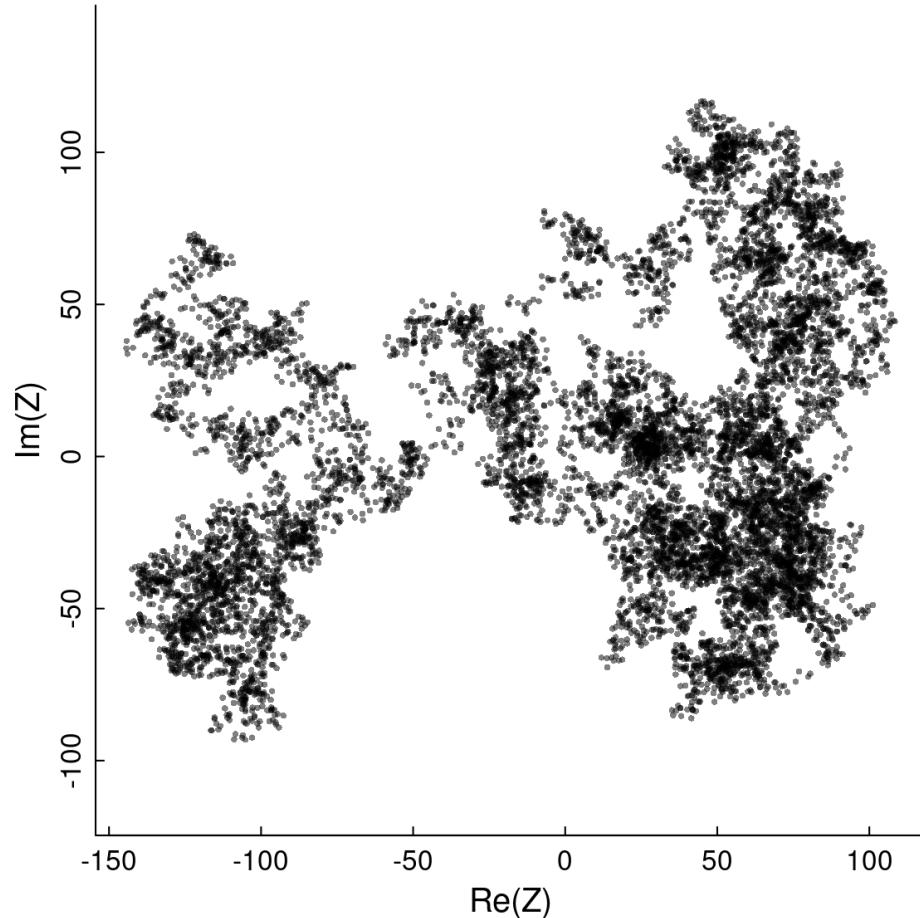
where:

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

β - is **magnitude of randomness**

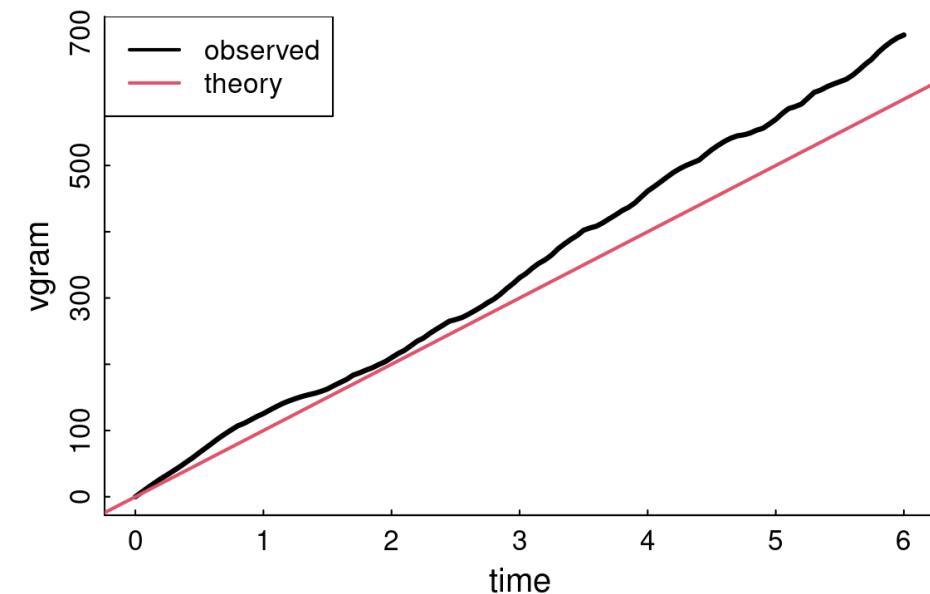


Brownian Motion



Semi-variogram

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

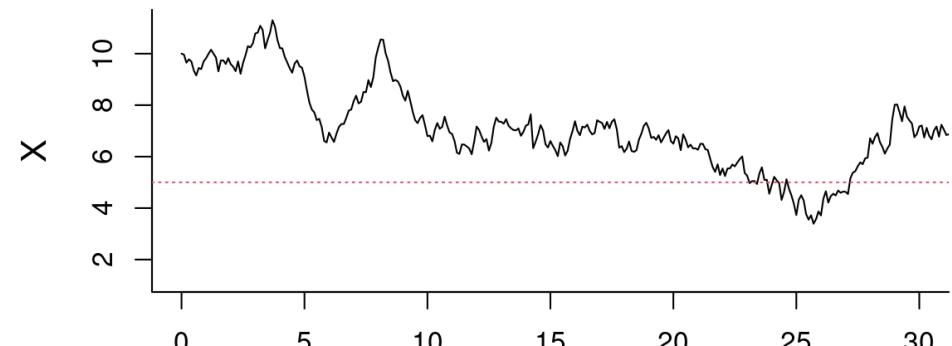
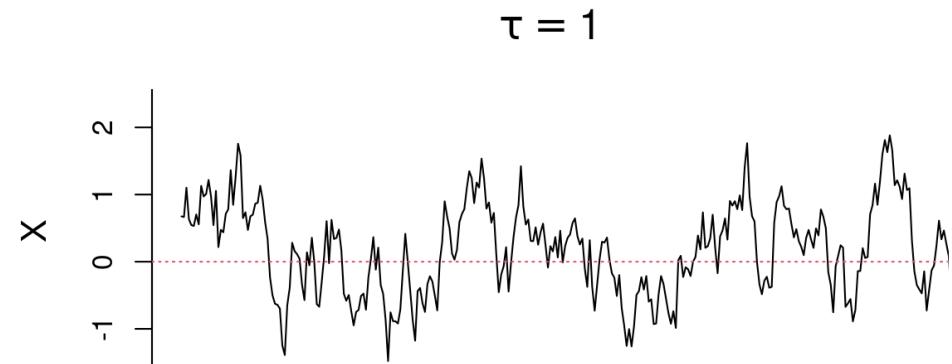


OU-Position (OUP) in 1 dimension

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.

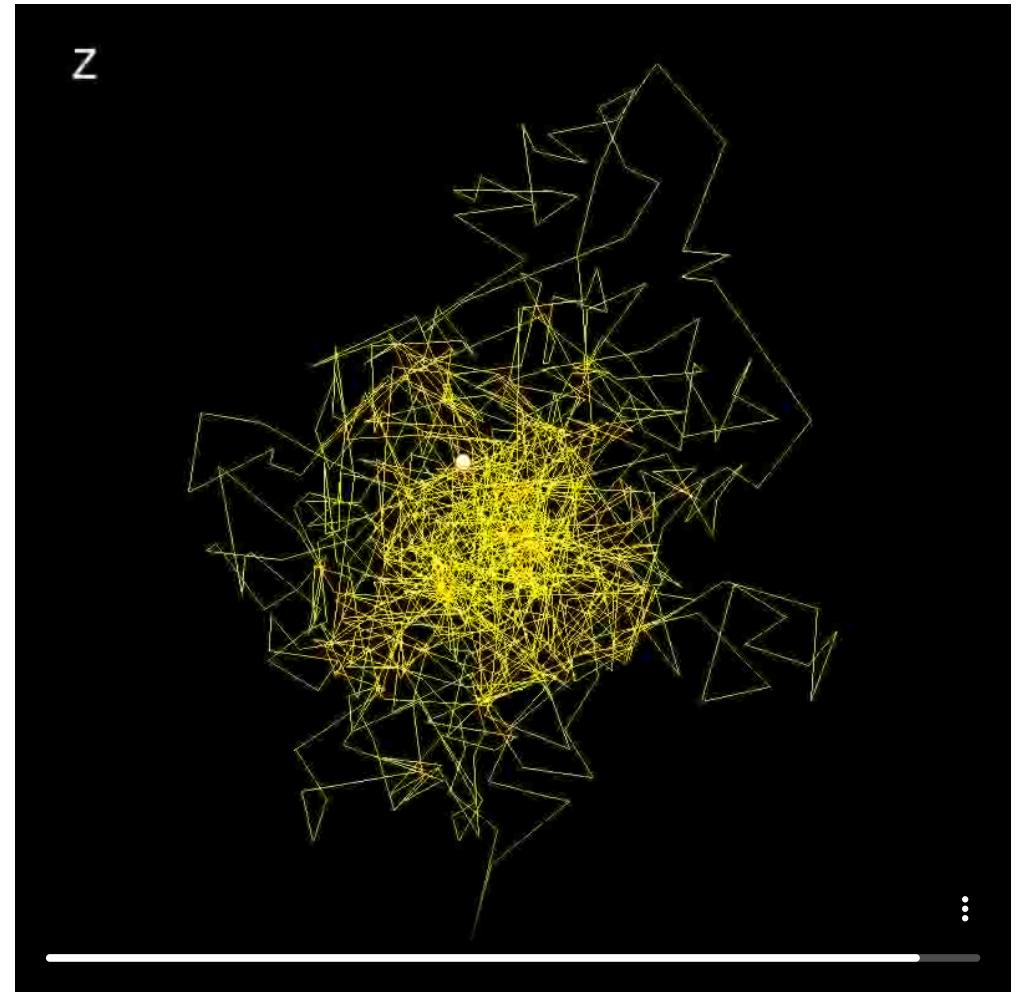
$$\frac{dZ}{dt} = -\frac{1}{\tau_p}(Z - \mu) + \alpha W_t$$

Can be written in terms of Area!

$$OUP(\tau_p, A)$$

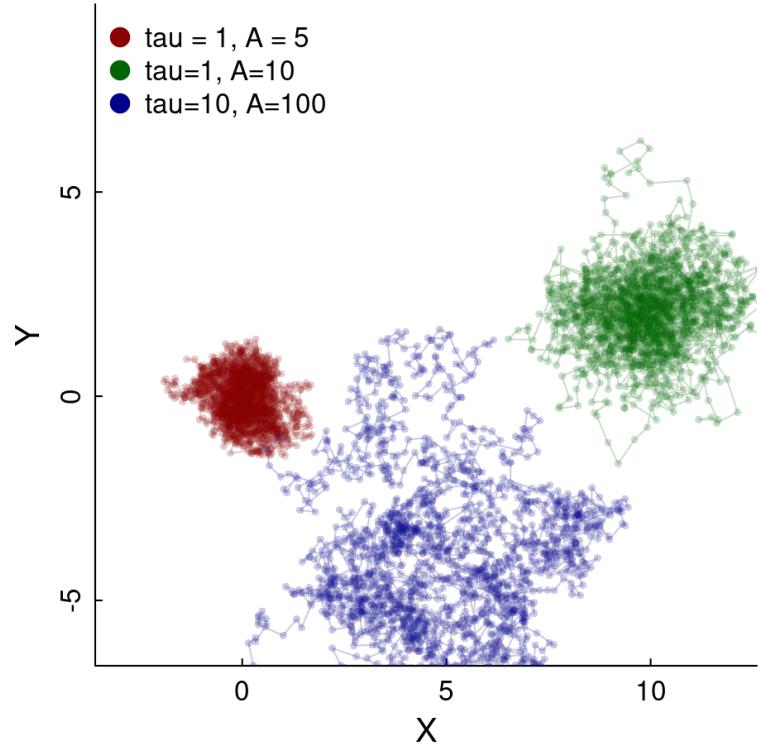
)

Constrained in Space!



OUP: Sample Tracks

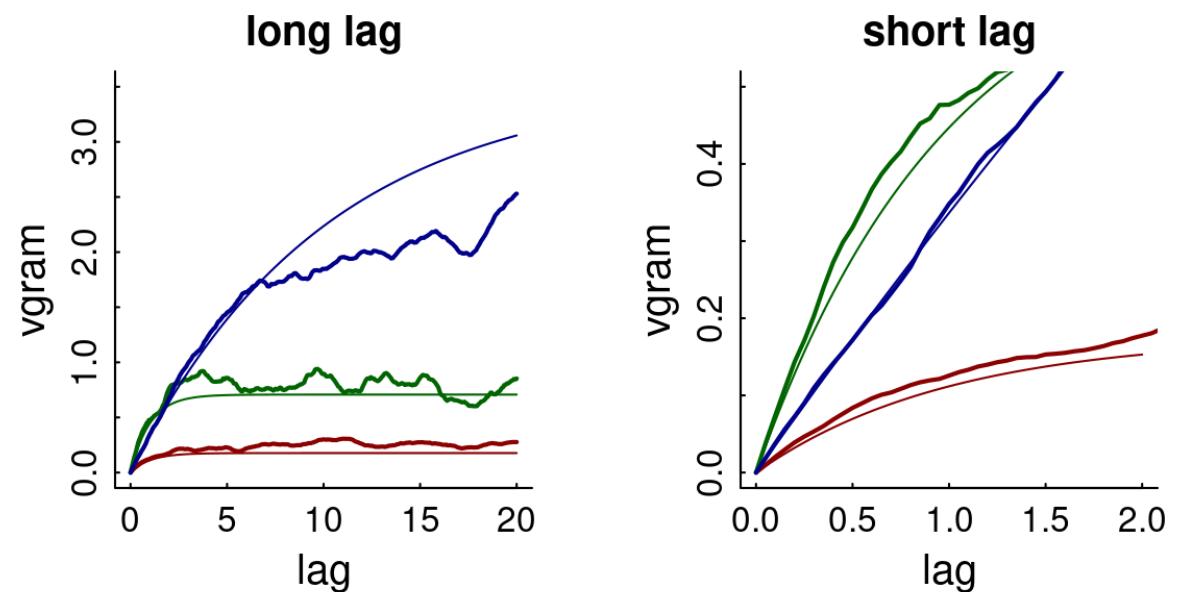
$$OU(\tau_p, A)$$



OUP: Semivariogram

Theory:

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



Correlated Velocity Model

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

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

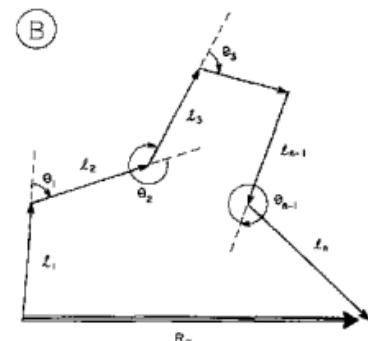
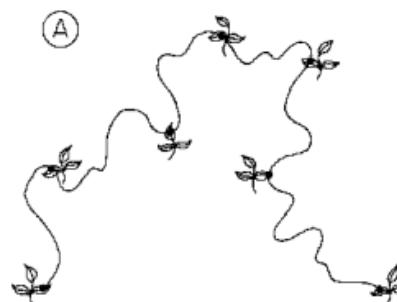
$$Z(t) = Z(0) + \int_0^t V(t)dt$$

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

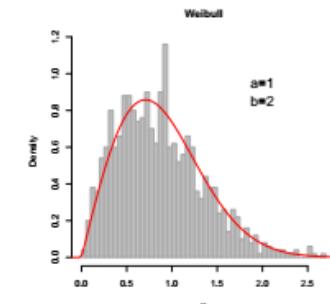
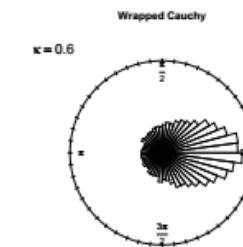
and $v(0) = v_0$

- τ_v - characteristic time scale of *speed*
- ν - mean speed

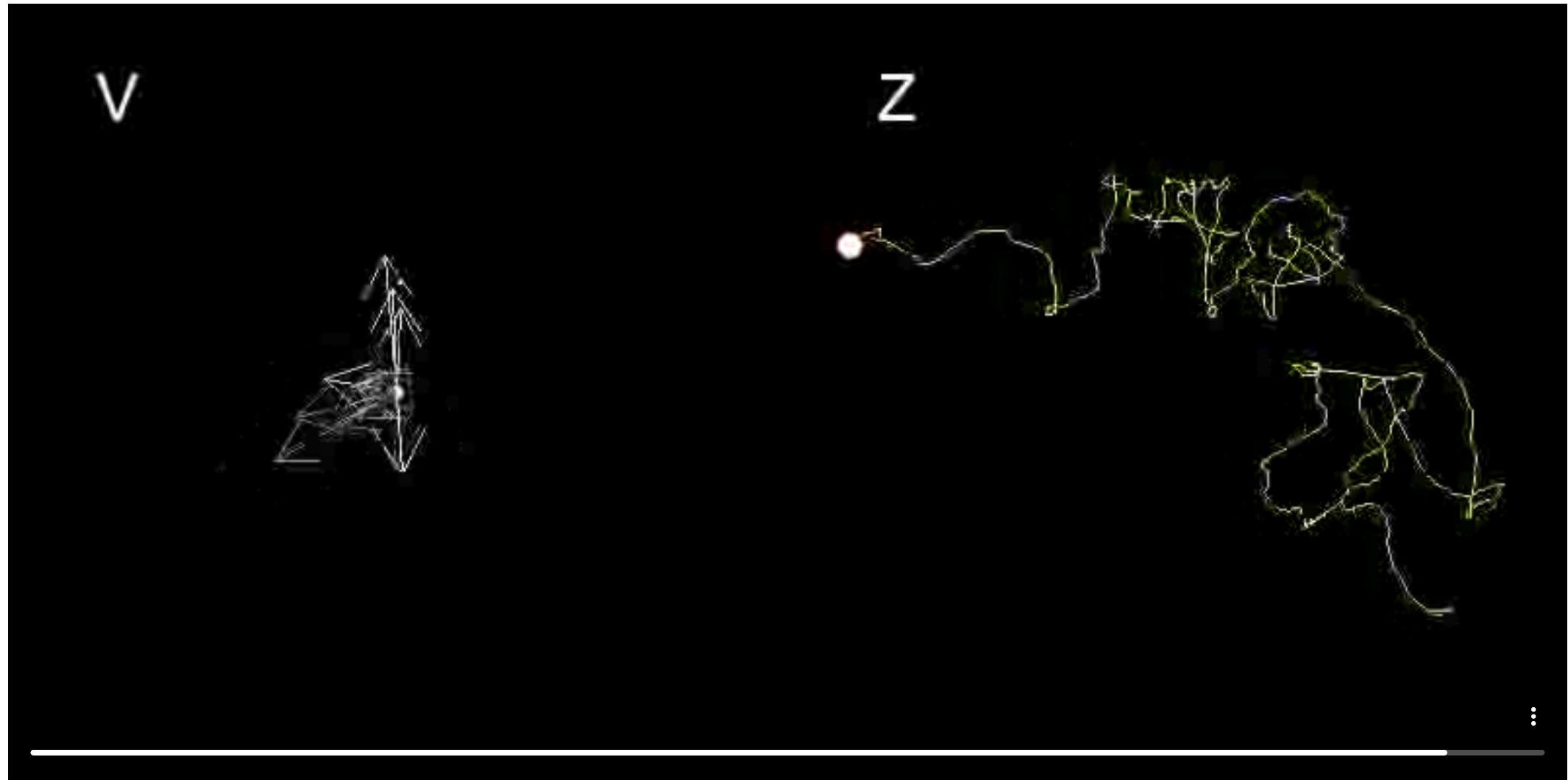
Discrete analogue to **Correlated Random Walk (CRW)**



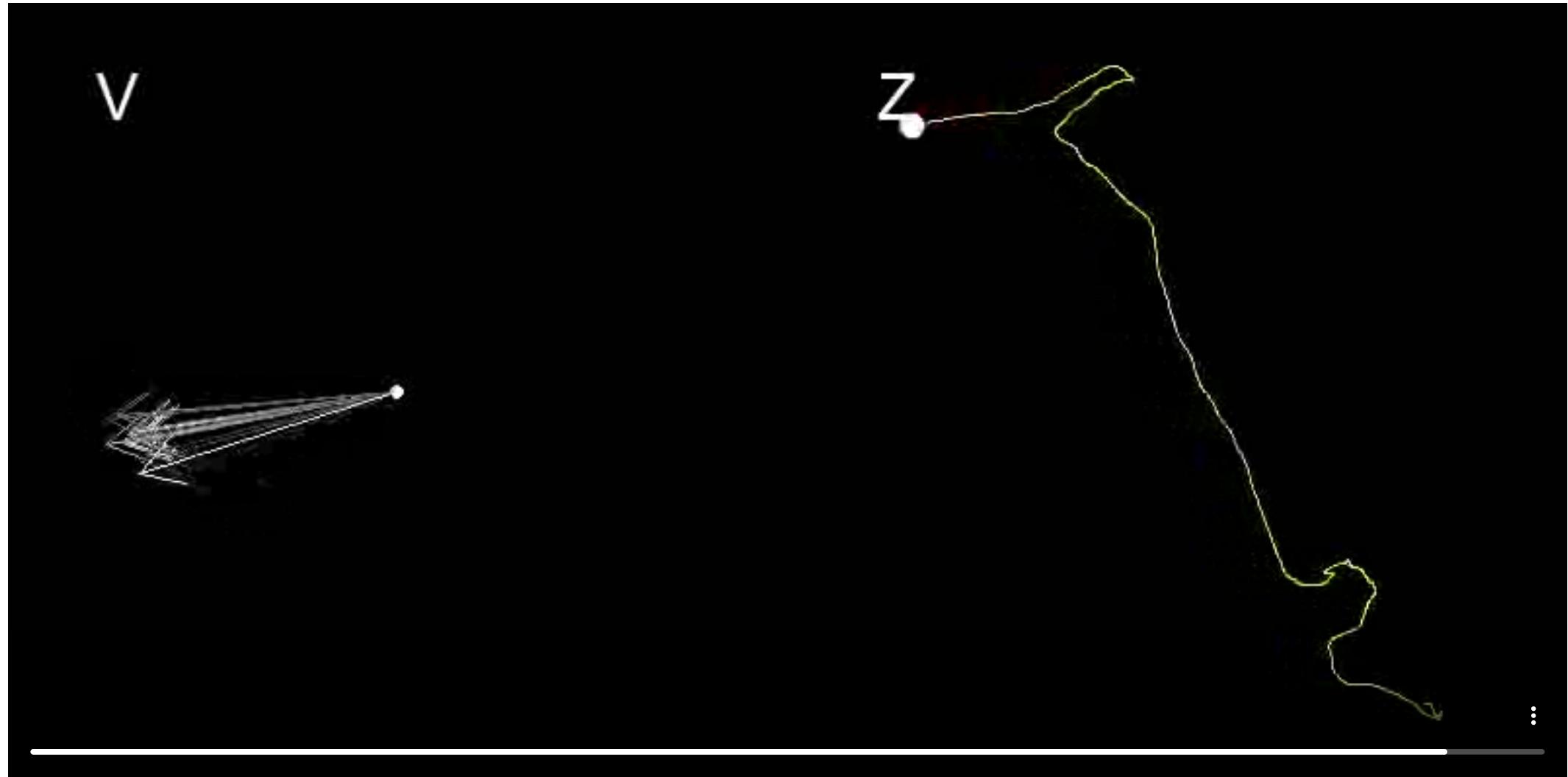
- $\theta_t \sim \text{Some Circular Distribution}$
- $V \sim \text{Unimodal Positive Distribution}$.



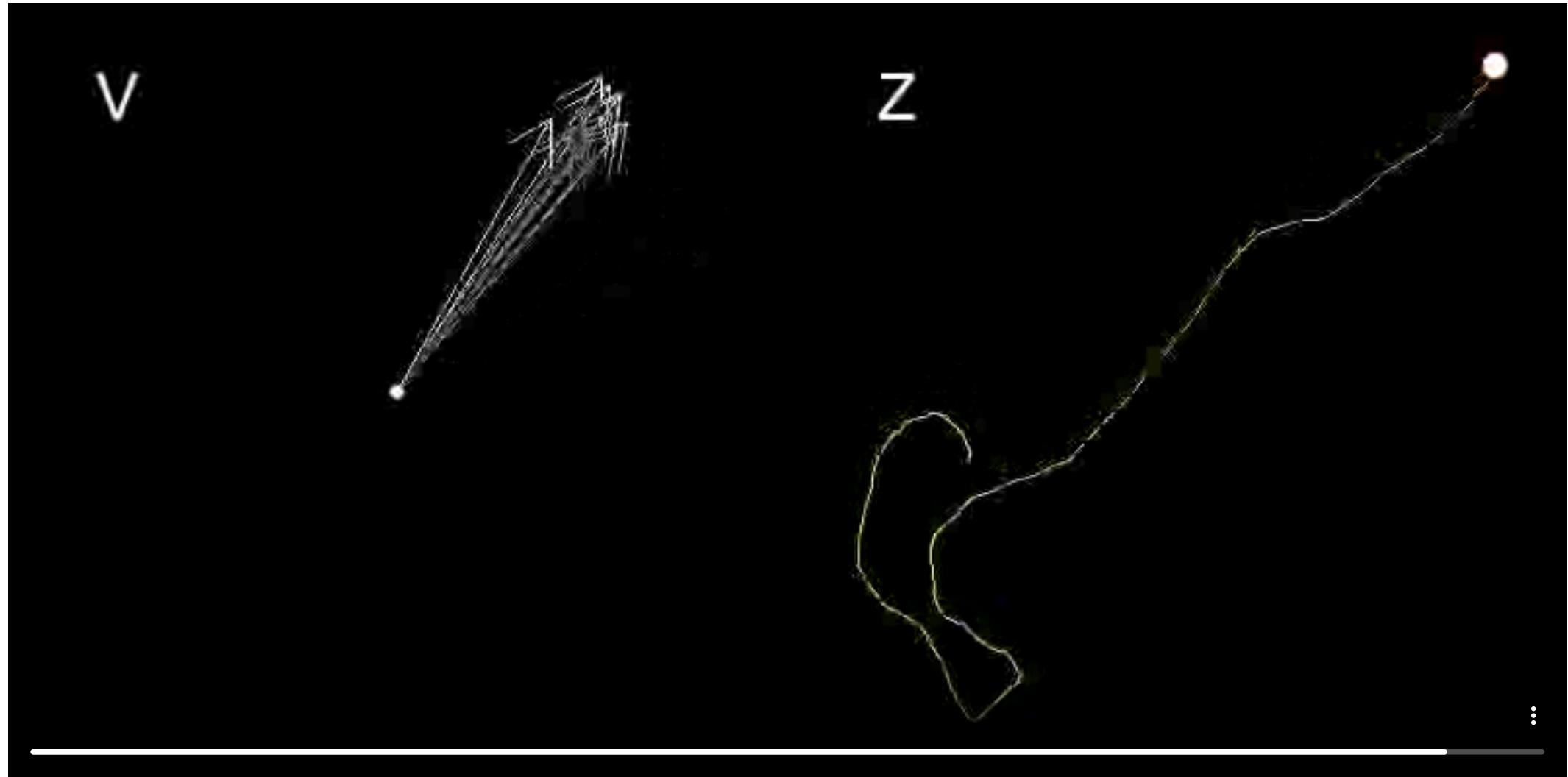
CVM: Compare time scales $\tau = 1$



CVM: Compare time scales $\tau = 10$



CVM: Compare time scales $\tau = 100$



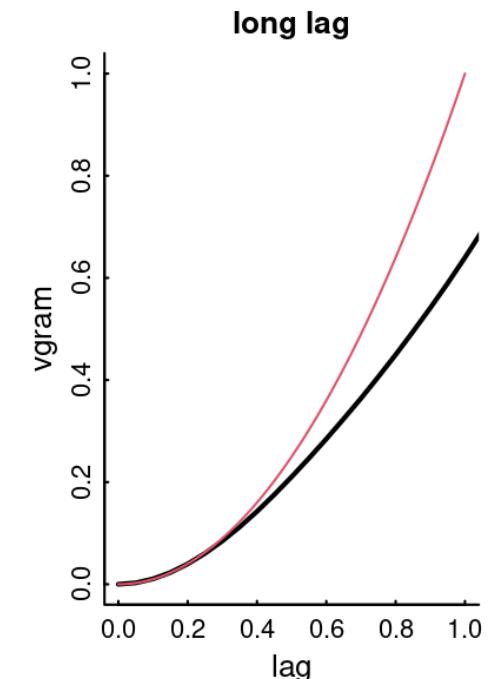
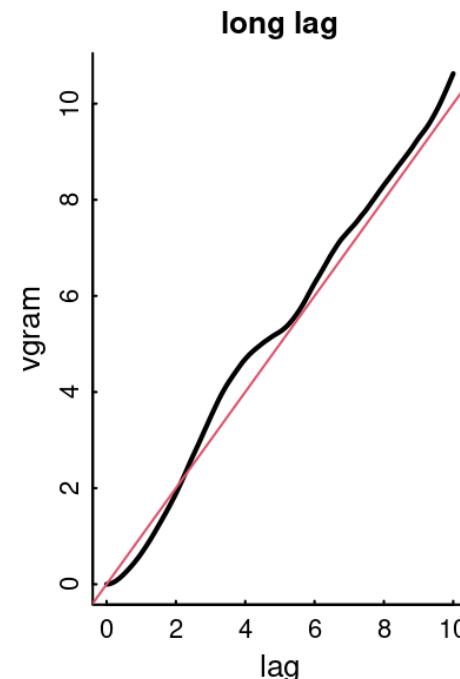
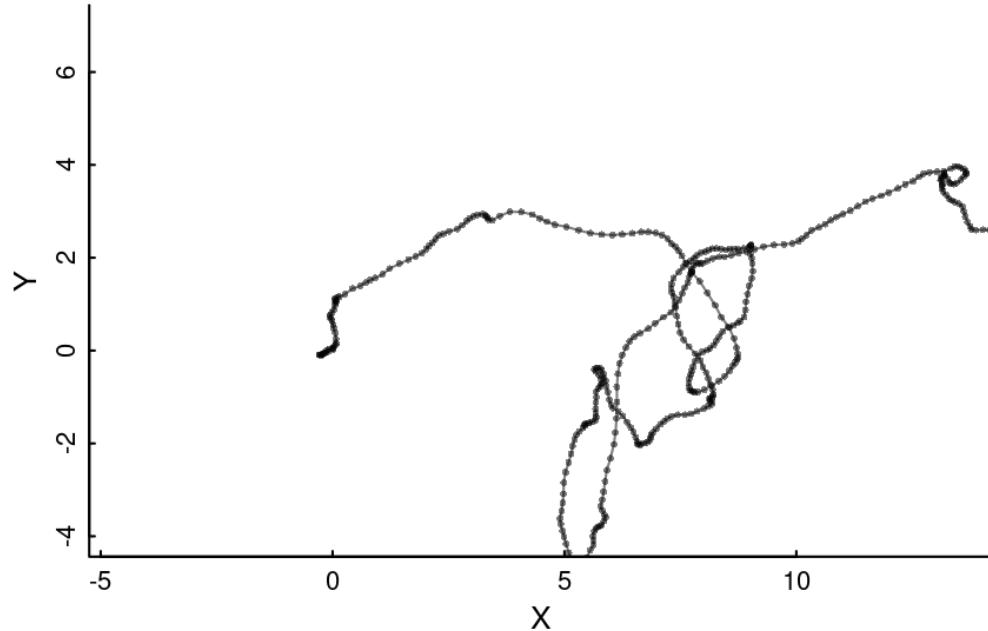
CVM (or OUV) variogram

Long time scale:

$$\text{linear} \propto t$$

Short time scale:

$$\text{parabola} \propto t^2$$



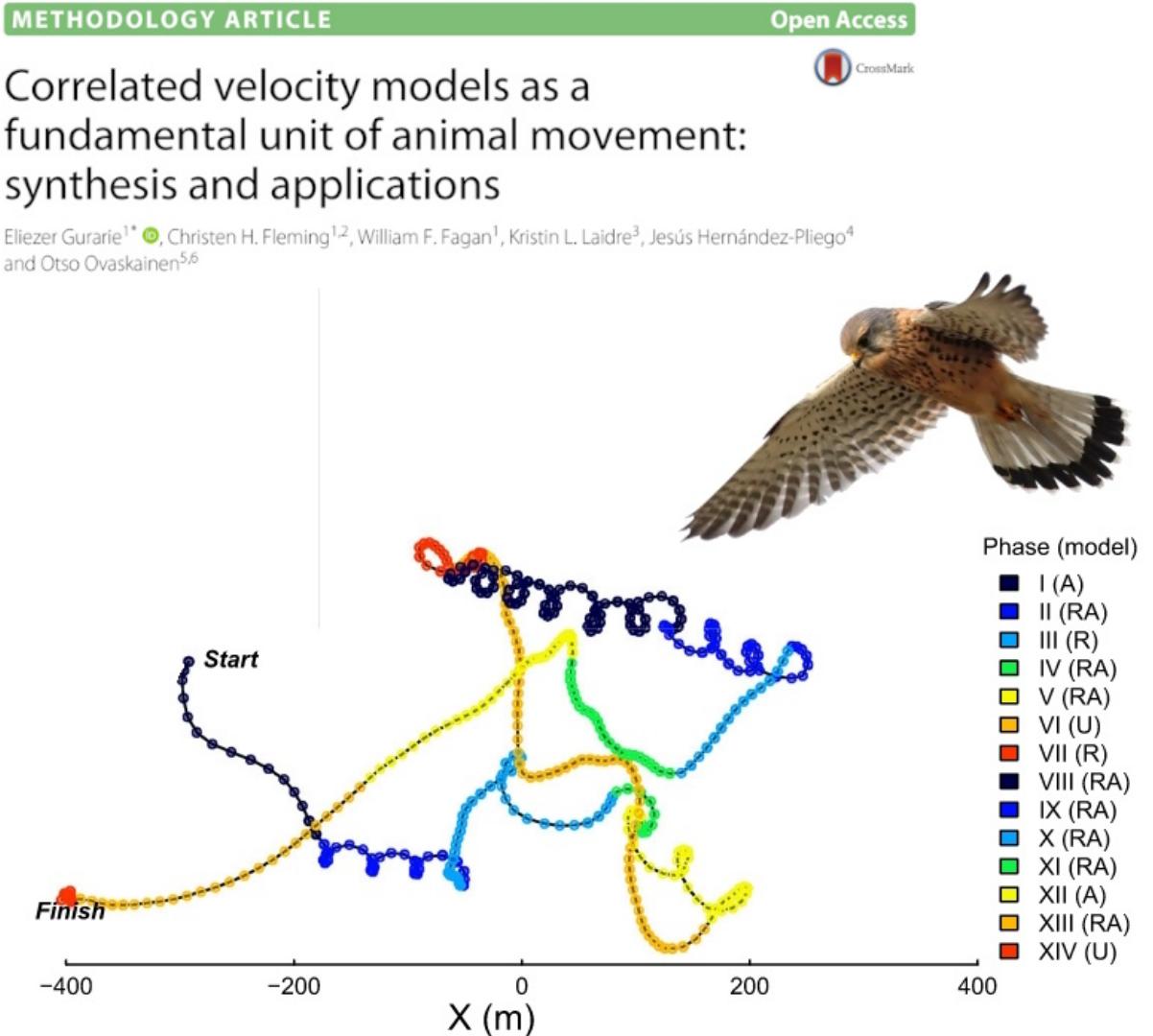
Variations on CVM

Gurarie et al. *Movement Ecology* (2017) 5:13
DOI 10.1186/s40462-017-0103-3

Movement Ecology

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

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



Ornstein-Uhlenbeck-F...

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

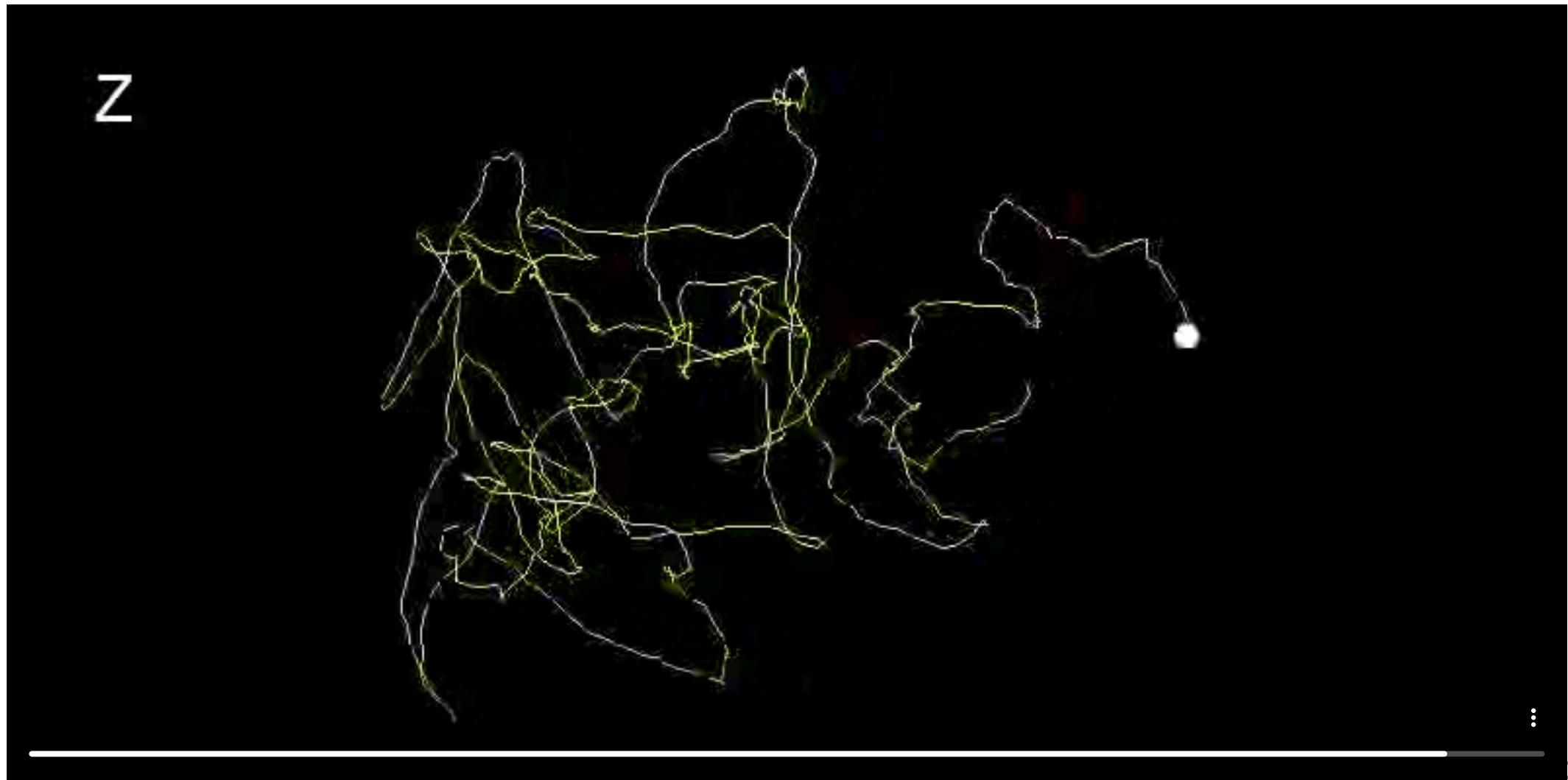
$$\frac{d}{dt} z(t) = -\frac{1}{\tau_z} (z(t) - \mu_z) + u(t)$$

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

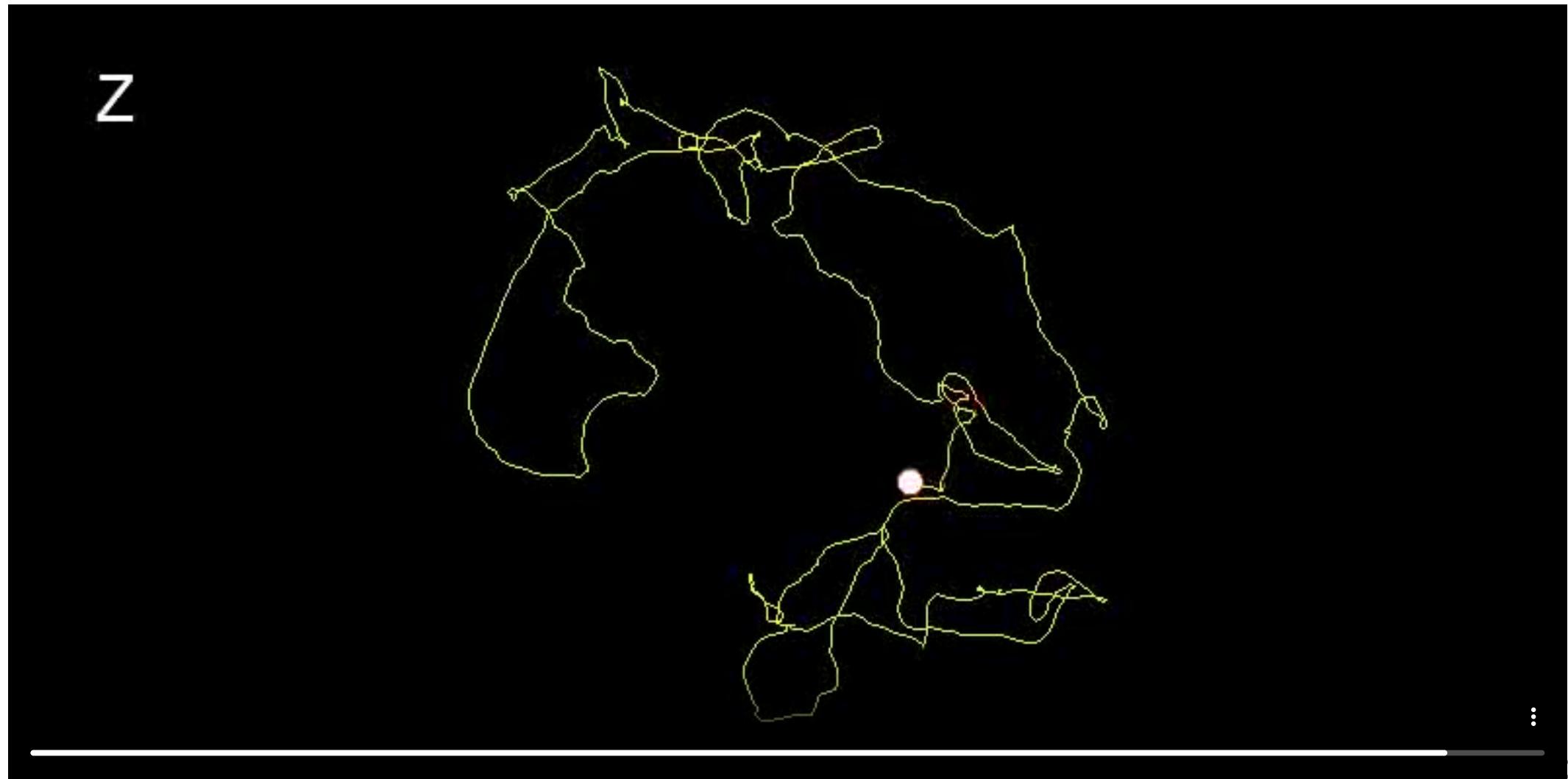
- τ_v is time scale of "pseudo-velocity" process
- τ_p is time scale of coverage of constrained area ("home range")

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

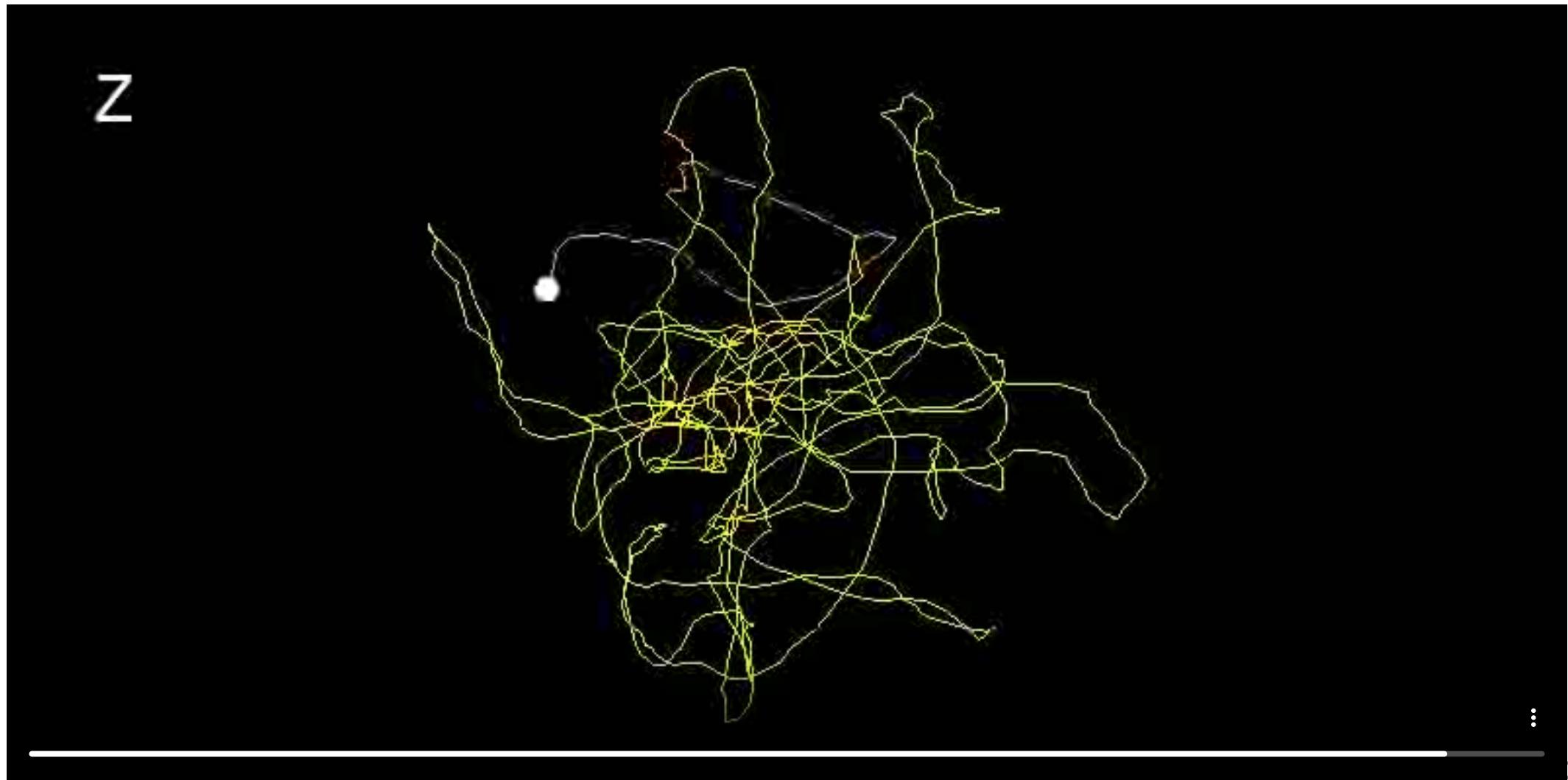
OUF: Animation 1 $\tau_p = 10$; $\tau_v = 1$



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

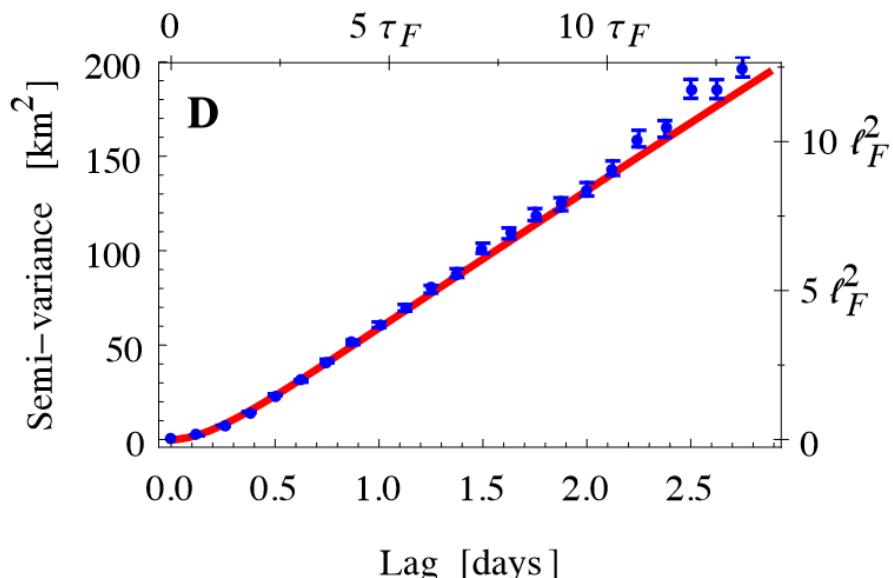


OUF: Animation 3 $\tau_p = 1.1$; $\tau_v = 1$

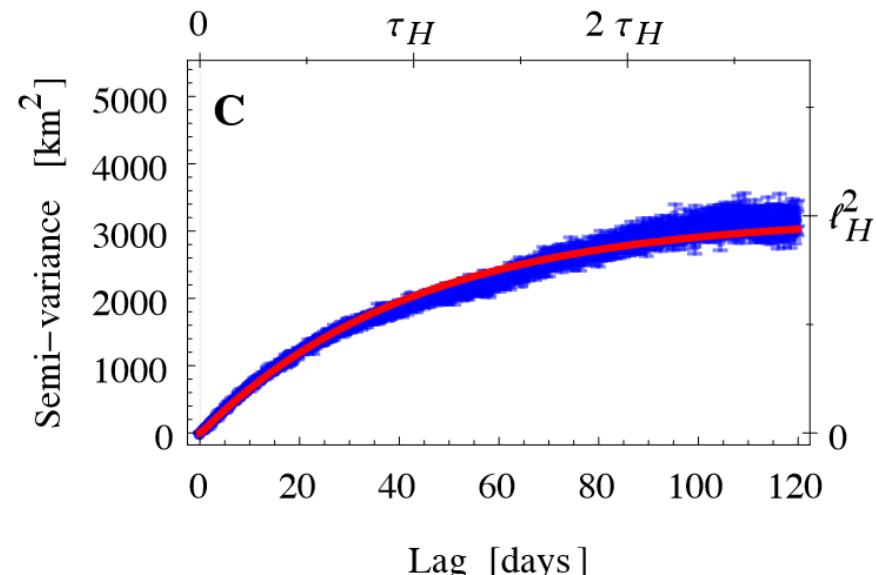


OUF semi-variogram

At small scales: looks like CVM

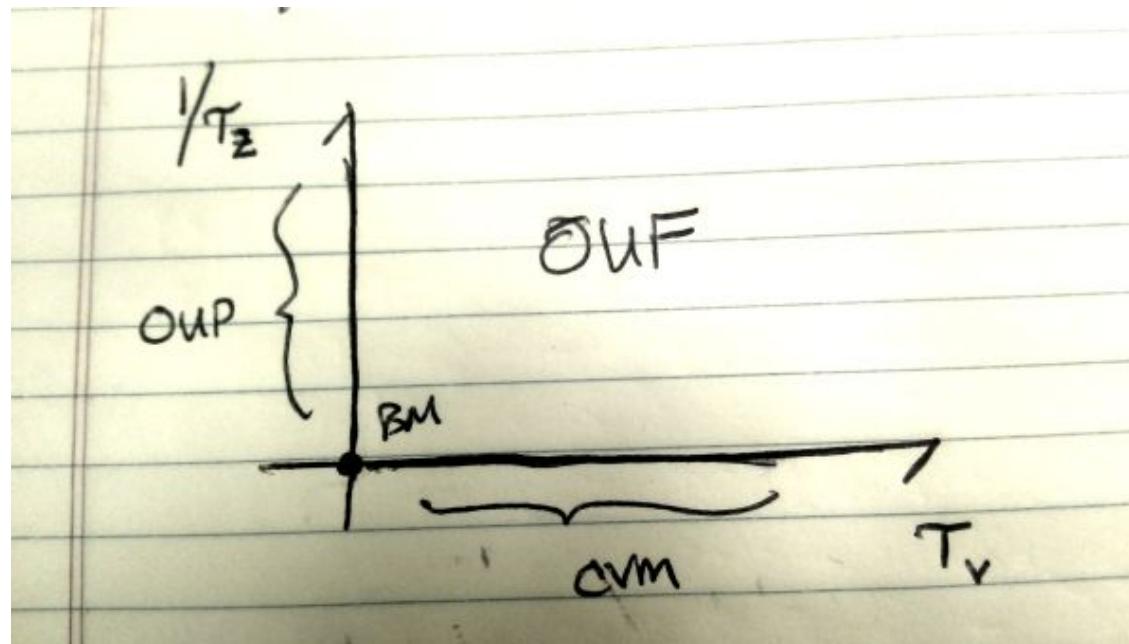


At large scales: looks like OUP



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