

Statistical Mechanics of Individual Animal Movement

Paulo Tilles* & Sergei Petrovskii#

*Universidade Estadual de Londrina, Londrina - Parana, Brazil

#Department of Mathematics, University of Leicester, U.K.

DSABNS 2016: Evora, February 2-5, 2016

Plan of the talk

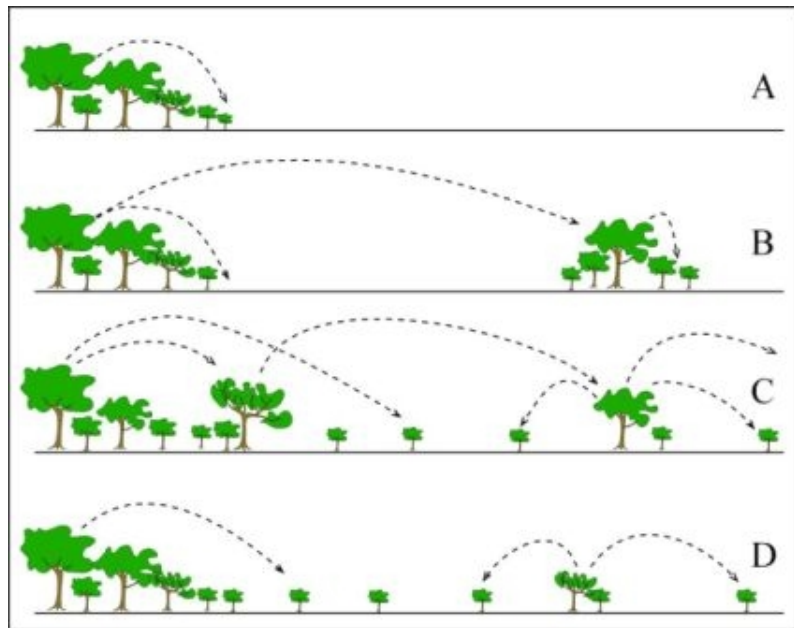
- Introduction: what it is all about
- Complexity of individual movement
- Why move? – behaviour and its implications
 - ▶ Scenario 1
 - ▶ Scenario 2
 - ▶ Scenario 3
- Discussion & conclusions

Dispersal in ecology

Dispersal is redistribution of a given population in space due to the **motion of its individuals**







Importance of dispersal

Dispersal is the factor that makes ecology essentially spatial.

- ◇ Biological invasions and spread of infectious diseases
- ◇ Synchronization of population dynamics in a fragmented habitat

Importance of dispersal

Dispersal is the factor that makes ecology essentially **spatial**.

- ◇ Biological invasions and spread of infectious diseases
- ◇ Synchronization of population dynamics in a fragmented habitat

The dynamics of **spatial** and **non-spatial** systems is often **qualitatively different**, hence the understanding of dispersal patterns is crucial for the understanding of ecological dynamics.

Importance of dispersal

Dispersal is the factor that makes ecology essentially **spatial**.

- ◇ Biological invasions and spread of infectious diseases
- ◇ Synchronization of population dynamics in a fragmented habitat

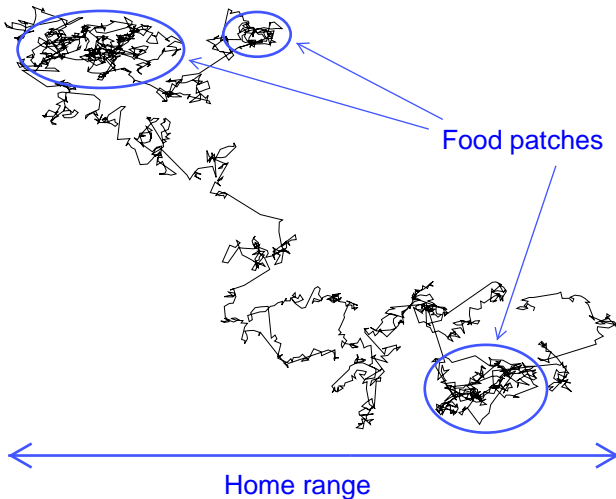
The dynamics of **spatial** and **non-spatial** systems is often **qualitatively different**, hence the understanding of dispersal patterns is crucial for the understanding of ecological dynamics.

Dispersal of a population takes place through movement of its individuals. Hence, a **good understanding of the individual (animal) movement is necessary**

Individual animal movement path is often quite complicated...



Individual animal movement path is often quite complicated...
because it normally arises as a result of interaction between
internal states of the animal and the landscape structure



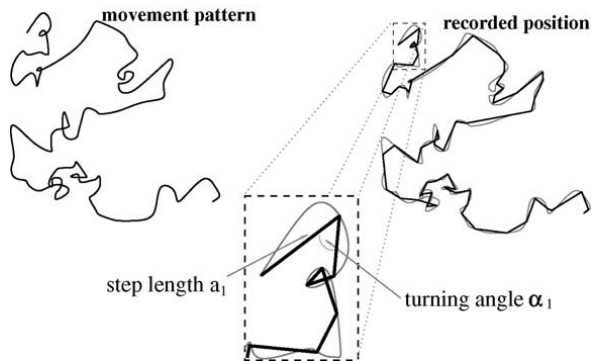
Complexity of individual movement

Individual animal movement has several movement modes involving **different spatial and temporal scales**.

We will focus on the **intermediate scale** of foraging in a homogeneous environment (e.g. between feeding grounds), ultimately reducing it to the 'microscale' of a single step or an **elementary movement decision**.

How the movement can be quantified?

We assume that a curvilinear path can be mapped into a broken line (e.g. due to discreteness of observations):



(from Jopp & Reuter, 2005)

How the movement can be quantified (contd.)

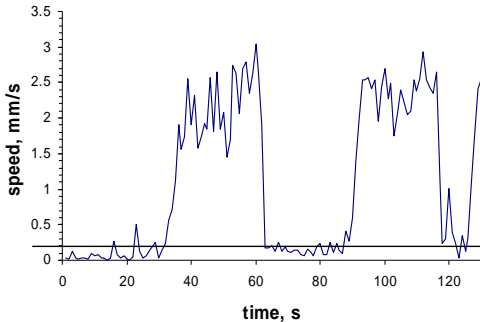
We assume that the individual movement is a **random process**.

The movement along a broken line can then be quantified by probability distribution of **steps** and turning **angles**.

For simplicity, we will focus on the **movement in 1D space**; hence we only consider distribution of step length, say $p(r)$.

How the movement can be quantified (contd.)

Movement is usually split into periods of motion (or fast displacement), aka **bouts**, and rest (or slow displacement):



The duration of uninterrupted movement is **exponentially distributed** (e.g. Petrovskii et al. 2011 *PNAS* **108**: 8704-8707)

How the movement can be quantified (contd.)

Depending on the context, there are two different ways to describe the movement:

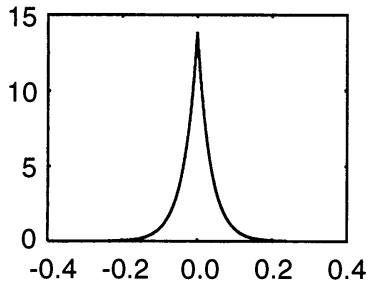
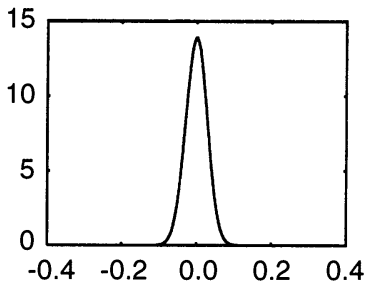
1. **Dispersal kernel** – the probability density to find the “next” position of the dispersing animal (after a given time)

This is useful when the focus is on the long-distance dispersal (i.e. long jumps).

Frequency of long distance dispersal events is given by the **large-distance asymptotics**. The two important alternatives are:

$$\begin{aligned} p(r) &\sim e^{-\alpha r} && \text{or faster,} \\ p(r) &\sim r^{-\mu} && \text{where } \mu > 1. \end{aligned}$$

Examples of dispersal kernels



Left: the Gaussian distribution, right: “back-to-back” exponential

The [rate of decay at the tail](#) of the kernel is important, cf. “thin tails” vs “fat tails” (exponentially bounded vs power law decay)

For long-distance dispersal, both **collecting data and their statistical analysis** are challenging, so the question “fat or thin” remains controversial; for instance:

- ▶ Dispersal of albatrosses (Viswanathan et al. 1996): **fat-tailed** with a power-law decay ($\mu = 1.7$)

For long-distance dispersal, both **collecting data and their statistical analysis** are challenging, so the question “fat or thin” remains controversial; for instance:

- ▶ Dispersal of albatrosses (Viswanathan et al. 1996): **fat-tailed** with a power-law decay ($\mu = 1.7$)
- ▶ ...was later **re-analyzed** by Edwards et al. (2007) to reveal a thin (exponential) tail

For long-distance dispersal, both **collecting data and their statistical analysis** are challenging, so the question “fat or thin” remains controversial; for instance:

- ▶ Dispersal of albatrosses (Viswanathan et al. 1996):
fat-tailed with a power-law decay ($\mu = 1.7$)
- ▶ ...was later **re-analyzed** by Edwards et al. (2007) to reveal a thin (exponential) tail
- ▶ Dispersal of mussels on the sea bed (de Jager et al. 2011):
fat-tailed with $\mu = 2$

For long-distance dispersal, both **collecting data and their statistical analysis** are challenging, so the question “fat or thin” remains controversial; for instance:

- ▶ Dispersal of albatrosses (Viswanathan et al. 1996):
fat-tailed with a power-law decay ($\mu = 1.7$)
- ▶ ...was later **re-analyzed** by Edwards et al. (2007) to reveal a thin (exponential) tail
- ▶ Dispersal of mussels on the sea bed (de Jager et al. 2011):
fat-tailed with $\mu = 2$
- ▶ ...was later proved to be **better described** by a composite-exponential kernel (Jansen et al. 2012)

How the movement can be quantified (contd.)

2. Alternatively, one can think about the **rate of dispersal**, e.g. dependence of the **mean squared displacement (MSD)** on time.

Typically,

$$\langle (x(t) - x_0)^2 \rangle \sim t^H$$

where $H = \frac{1}{2}$ for the standard diffusion (Brownian motion),
 $H > \frac{1}{2}$ for the “superdiffusion”.

The two approaches (dispersal kernel vs MSD) are thought to be related; in general, **the dispersal rate is higher for a fatter tail**.

We will show that it is not necessarily so.

Why move? - there must be a reason...

Reducing the movement pattern to the properties of the kernel is far too formal: What are the **processes** 'behind the kernel'?

The answer is likely to be scale-dependent.

Consider the '**microscale**' of a single step:

Assumption 1: the animal only change its velocity when there is a **reason** for this (looking for food, avoiding predators etc.)

Assumption 2: the animal change its speed as a **response** to external (environmental) clues or signals

Generic model

We describe the movement as a sequence of bouts (steps). A bout ends (and the next bout starts) when the animal receives a signal from the environment.

Let the signals are distributed in time homogeneously. This results in the Poisson distribution: the probability that an animal receives at least one cue during the time t is

$$P_t(\omega) = 1 - e^{-\omega t},$$

where ω is the mean number of cues per unit time.

The probability density of bout duration:

$$\psi(t) = \omega e^{-\omega t}.$$

Hence, $\omega = 1 / \langle t \rangle$ where $\langle t \rangle$ is the mean time between the subsequent signals.

Upon receiving a signal, the animal reacts by exerting a force. The corresponding acceleration changes the movement velocity.

Scenario 1:

Upon receiving a signal, the animal changes its movement by **choosing a new value of the velocity** v , which we consider to be a random variable described by a certain pdf $\phi(v)$.

We consider velocity and bout duration to be statistically independent.

Let t_k is the **duration** of the k th bout, v_k is the **velocity** along the k th bout, and y_k the animal's **position at the end** of the k th bout. Then,

$$y_k = y_{k-1} + v_k t_k \quad (k = 1, 2, \dots) \quad \text{so that} \quad y_k = \sum_{n=1}^k v_n t_n .$$

For an **arbitrary** t (i.e. between the signals):

$$\sum_{n=1}^{k-1} t_n < t < \sum_{n=1}^k t_n,$$

we obtain

$$x_k(t) = y_{k-1} + v_k \tilde{t}_k = \sum_{n=1}^{k-1} v_n t_n + v_k \left(t - \sum_{n=1}^{k-1} t_n \right),$$

where $x_k(t)$ is the position of the animal **during** the k th bout.

Scenario 1 (contd.)

For an arbitrary $\phi(v)$, calculations are not possible.

We consider two special cases, that is

$$\phi_G(v) = \frac{e^{-\frac{v^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}} \quad \text{and} \quad \phi_L(v) = \frac{e^{-\frac{|v|}{2\alpha}}}{2\alpha}.$$

Then it appears possible to **calculate the moments** $\langle x^{2n} \rangle$ of the dispersal kernel

(Tilles & Petrovskii 2016, *J. Math. Biol.*, in press)

$$\rho_k(x, t | \mathbf{k}_{k-1}) = \frac{\exp\left[-\frac{x^2}{2\sigma^2 \Delta_k^2(t, \mathbf{k}_{k-1})}\right]}{\sqrt{2\pi\sigma^2 \Delta_k^2(t, \mathbf{k}_{k-1})}} \quad (10)$$

where $\mathbf{k}_k = (t_1, \dots, t_k)$, and the function $\Delta_k^2(t, \mathbf{k}_{k-1})$, associated to the variance, is obtained directly from (8) as

$$\Delta_k^2(t, \mathbf{k}_{k-1}) = \sum_{n=1}^{k-1} t_n^2 + \left(t - \sum_{n=1}^{k-1} t_n\right)^2 \quad (11)$$

(note that we have dropped the k index from the variable x_k to put it on the probability function ρ_k). In order to obtain the unconditioned contribution $\rho_k(x, t)$, we need to sum Eq. (10) over all possible bout durations. The sum of all periods up to t_{k-1} is constrained on the interval $(0, t)$, and the summation over all possible configurations is obtained from the multidimensional integral

$$\int \mathcal{D}t_{k-1} = \int_0^t dt_1 \int_0^{t-t_1} dt_2 \dots \int_0^{t-\sum_{n=1}^{k-2} t_n} dt_{k-1}. \quad (12)$$

For the last bout period t_k we should set the integration limits in order to make it superi-ori unbounded and to assure that the observational time t lies inside the domain. Since the conditional probability (10) does not depend on the last bout duration t_k , we may compute its contribution (integrate) directly, and when we consider the probabilities from all duration we may write

$$\prod_{j=1}^{k-1} \Psi(t_j) \int_{t-\sum_{n=1}^{k-1} t_n}^{\infty} dt_k \psi(t_k) = \omega^{k-1} e^{-\omega t}, \quad (13)$$

which leads to the unconditioned probability density

$$\rho_k(x, t) = \omega^{k-1} e^{-\omega t} \int \mathcal{D}t_{k-1} \rho_k(x, t | \mathbf{k}_{k-1}). \quad (14)$$

Equation (14) is not analytically solvable, but we may extract all statistical information from this system through the moments of the distribution, which are obtained via

$$\langle x^{2n}(t) \rangle = \sum_{k=1}^{\infty} \int_{-\infty}^{\infty} x^{2n} \rho_k(x, t) dx = \frac{(2n)!}{2^n n!} \sigma^{2n} e^{-\omega t} \sum_{k=1}^{\infty} \omega^{k-1} \mathcal{H}_{n,k}(t), \quad (15)$$

where we use the following notation:

$$\mathcal{H}_{n,k}(t) = \int \mathcal{D}t_{k-1} \Delta_k^{2n}(t, \mathbf{k}_{k-1}) = \int \mathcal{D}t_{k-1} \left[\sum_{m=1}^{k-1} t_m^2 + \left(t - \sum_{m=1}^{k-1} t_m\right)^2 \right]^n \quad (16)$$

where $\mathcal{P}_n(k)$ are polynomials of order $n - 1$. A general expression for these polynomials is not available, but the first few ones can be readily calculated:

$$\mathcal{P}_1(k) = 1, \quad (23a)$$

$$\mathcal{P}_2(k) = 5 + k, \quad (23b)$$

$$\mathcal{P}_3(k) = 74 + 15k + k^2, \quad (23c)$$

$$\mathcal{P}_4(k) = 2118 + 371k + 30k^2 + k^3, \quad (23d)$$

$$\mathcal{P}_5(k) = 97944 + 14290k + 1115k^2 + 50k^3 + k^4. \quad (23e)$$

Now the summations in Eq. (15) are easily doable, and the exact expressions for the moments of the system may be written as

$$\langle x^{2n}(t) \rangle = \frac{(2n)!}{2^n n!} \left(\frac{\sigma}{\omega}\right)^{2n} \left[\mathcal{Q}_{1,n}(\omega t) + e^{-\omega t} \mathcal{Q}_{2,n}(\omega t) \right], \quad (24)$$

where $\mathcal{Q}_{1,n}(\omega t)$ and $\mathcal{Q}_{2,n}(\omega t)$ are polynomials in ωt , defined by

$$\mathcal{Q}_{1,1}(y) = 2(y - 1), \quad (25a)$$

$$\mathcal{Q}_{1,2}(y) = 4(y^2 - 6), \quad (25b)$$

$$\mathcal{Q}_{1,3}(y) = 8(y^3 + 3(y^2 - 40)), \quad (25c)$$

$$\mathcal{Q}_{1,4}(y) = 16(y^4 + 8(y^3 + 6y^2 - 567)), \quad (25d)$$

$$\mathcal{Q}_{1,5}(y) = 32(y^5 + 15(y^4 + 12y^3 + 108y^2 - 17856)), \quad (25e)$$

and

$$\mathcal{Q}_{2,1}(y) = 2, \quad (26a)$$

$$\mathcal{Q}_{2,2}(y) = 8(y^2 + 3y + 3), \quad (26b)$$

$$\mathcal{Q}_{2,3}(y) = 4(5y^4 + 32y^3 + 114y^2 + 240y + 240), \quad (26c)$$

$$\mathcal{Q}_{2,4}(y) = \frac{16}{15} \left[37y^6 + 12(31y^5 + 195y^4 + 875y^3 + 2775y^2 + 5670y + 5670) \right], \quad (26d)$$

$$\mathcal{Q}_{2,5}(y) = \frac{4}{21} \left[353y^8 + 24(204y^7 + 7(266y^6 + 1856y^5 + 10155y^4 + 42840y^3 + 132300y^2 + 267840y + 267840)) \right]. \quad (26e)$$

Figure 2 shows the perfect match between these analytical expressions and the results obtained from Monte Carlo simulations of the original system. To compare these results with the ones obtained from the Goldstein-Kac (GK) telegraph process,

contributions of different number of bouts, as in Eq. (3), we can write the characteristic function of each of these contributions as the product of the characteristic functions from each variable α_n, t_n present in Eq. (8). This approach will work as long as the original velocity distribution admits a characteristic function representation, and as for the Laplace distribution we have $1/(1 + \alpha^2 z^2)$, the characteristic function for this Laplace composed case may be written as

$$\begin{aligned} \Phi_L(z, t) &= e^{-\alpha t} \sum_{m=0}^{\infty} \alpha^{k-1} \int \mathcal{D}t_{k-1} \prod_{i=1}^{k^*} \frac{1}{1 + \alpha^2 z_i^2 t_i^2} \\ &= e^{-\alpha t} \sum_{m=0}^{\infty} (-1)^m (\alpha z)^{2m} \sum_{k=1}^{\infty} \alpha^{k-1} \int \mathcal{D}t_{k-1} \Theta_{m,k}(t, \mathbf{t}_{k-1}). \end{aligned} \quad (45)$$

On the first part, the upper bound index k^* is just a short notation to remind that the summations should go up to the value k and followed by imposing the constraint $t_k \rightarrow t - \sum_{m=1}^{k-1} t_m$, as previously discussed. Once we expand this expression around $z = 0$, we obtain the functions $\Theta_{m,k}(t, \mathbf{t}_{k-1})$ shown on the second part, which are just polynomials in the bout durations t_n . Just as in the Gaussian case, we are not going to compute all the terms, but just focus on the first three ones:

$$\Theta_{1,k}(t, \mathbf{t}_{k-1}) = \sum_{i=1}^{k^*} t_i^2, \quad (46a)$$

$$\Theta_{2,k}(t, \mathbf{t}_{k-1}) = \sum_{i=1}^{k^*} t_i^4 + \sum_{i=1}^{k^*} \sum_{j=i+1}^{k^*} t_i^2 t_j^2, \quad (46b)$$

$$\Theta_{3,k}(t, \mathbf{t}_{k-1}) = \sum_{i=1}^{k^*} t_i^6 + \sum_{i=1}^{k^*} \sum_{j=i+1}^{k^*} t_i^2 t_j^4 + \sum_{i=1}^{k^*} \sum_{j=i+1}^{k^*} \sum_{l=j+1}^{k^*} t_i^2 t_j^2 t_l^2. \quad (46c)$$

To compute the bout durations integrals in Eq. (45) we may resort to the same approach used before, in which for a given m we use the result from the first integrals to infer the general behavior as a function of k . As the first multidimensional integral of $\Theta_{1,k}$ is exactly the same as $\mathcal{H}_{1,L}$ shown in Eq. (16), we only need to compute the next two:

$$\int \mathcal{D}t_{k-1} \Theta_{2,k}(t, \mathbf{t}_{k-1}) = \frac{2k(k+1)}{(k+3)!} t^{k+3}, \quad (47)$$

$$\int \mathcal{D}t_{k-1} \Theta_{3,k}(t, \mathbf{t}_{k-1}) = \frac{4k(k^2 + 33k + 506)}{3(k+5)!} t^{k+5}. \quad (48)$$

Now it is just a matter of rewriting the summation into known functions to obtain the series expansion of the characteristic function, and when we compare it to the general relation

$$\Phi_L(z, t) = \sum_{m=0}^{\infty} \frac{(-1)^m (t^{2m} (t))! z^{2m}}{(2m)!} z^{2m}, \quad (49)$$

it becomes easy to determine the statistical moments of the system as

$$\langle x^2(t) \rangle_L = 4 \left(\frac{\alpha}{\omega} \right)^2 (\omega t - 1 + e^{-\omega t}), \quad (50a)$$

$$\langle x^4(t) \rangle_L = 48 \left(\frac{\alpha}{\omega} \right)^4 \left[\omega^2 t^2 + 6\omega t - 24 + e^{-\omega t} (5\omega^2 t^2 + 18\omega t + 24) \right], \quad (50b)$$

$$\begin{aligned} \langle x^6(t) \rangle_L &= 240 \left(\frac{\alpha}{\omega} \right)^6 \left[4(\omega^3 t^3 + 21\omega^2 t^2 + 270\omega t - 1830) \right. \\ &\quad \left. + e^{-\omega t} (79\omega^4 t^4 + 592\omega^3 t^3 + 2496\omega^2 t^2 + 6240\omega t + 7320) \right]. \end{aligned} \quad (50c)$$

If, in order to make the Laplace and Gaussian distributions comparable, we consider the relation between the distribution parameters as $\alpha = \sigma/\sqrt{2}$ (to ensure that both distribution have the same variance), then $\langle x^2 \rangle_L$ obviously shows the dependence on time exactly the same as in the previous case of the normal distribution; see Eq. (18). However, it is readily seen that all the higher moments are different from the previous case given by Eqs. (24–26).

As Fig. 5 (left) shows the perfect agreement of these equations to the MC results, we may proceed to compute the asymptotic values of the cumulants,

$$\kappa_{L,2}(t) \simeq 4 \left(\frac{\alpha}{\omega} \right)^2 (\omega t - 1),$$

$$\kappa_{L,4}(t) \simeq 48 \left(\frac{\alpha}{\omega} \right)^4 (8\omega t - 25),$$

$$\kappa_{L,6}(t) \simeq 1920 \left(\frac{\alpha}{\omega} \right)^6 (183\omega t - 952), \quad (51)$$

which allows us to obtain an approximate expression for the dispersal function simply as the inverse Fourier transform,

$$\rho_L(x, t) \approx \frac{1}{2\pi} \int_{-\infty}^{\infty} \cos(xz) \exp \left[-\frac{\kappa_{L,2}(t)}{2!} z^2 + \frac{\kappa_{L,4}(t)}{4!} z^4 - \frac{\kappa_{L,6}(t)}{6!} z^6 \right] dz. \quad (52)$$

Also in this case the cumulants are linear functions of time t , so we already know that the probability distribution may be asymptotically approximated by a Gaussian diffusion

$$\rho_L(x, t) \simeq \sqrt{\frac{m}{8\pi\alpha^2 t}} e^{-\frac{x^2}{4\omega t}}, \quad (53)$$

where the diffusion coefficient is connected to the model parameters via the relation

$$D_L(\alpha, \omega) = \frac{4\alpha^2}{\omega}. \quad (54)$$

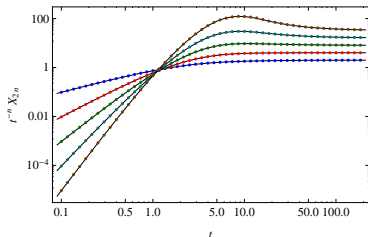
Finally, we obtain

$$\langle x^2(t) \rangle_G = \frac{2\sigma^2}{\omega^2} (\omega t - 1 + e^{-\omega t}),$$

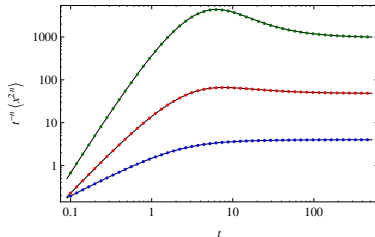
so that

$$\langle x^2(t) \rangle_G \sim t^2 \text{ for } t \ll \frac{1}{\omega} \quad \text{and} \quad \langle x^2(t) \rangle_G \sim t \text{ for } t \gg \frac{1}{\omega}.$$

For the higher moments:



Gaussian kernel

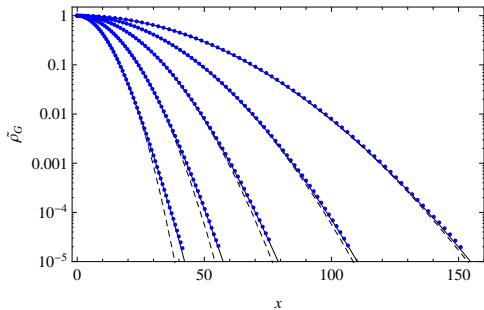


Laplace kernel

In the **large-time limit**, the pdf of animal location (dispersal kernel) becomes

$$\rho_G(x, t) \simeq \sqrt{\frac{\omega}{4\pi\sigma^2 t}} e^{-\frac{\omega x^2}{4\sigma^2 t}}$$

although at any finite time it has a somewhat **fatter tail**:



Scenario 2:

Upon receiving a signal, the animal changes its movement by choosing an **increment to the velocity**, that is

$$v \rightarrow v + \xi,$$

where ξ is a random variable described by a certain pdf $\phi(\xi)$.

In this case, we obtain

$$\langle x^2(t) \rangle_{G_c} = \frac{\sigma^2 t^2}{3} (3 + \omega t)$$

so that

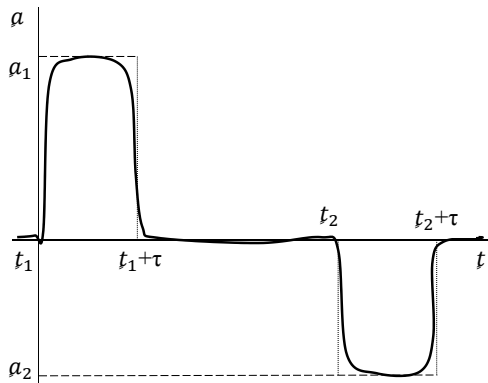
$$\langle x^2(t) \rangle_{G_c} \sim t^2 \text{ for } t \ll \frac{1}{\omega} \quad \text{and} \quad \langle x^2(t) \rangle_{G_c} \sim t^3 \text{ for } t \gg \frac{1}{\omega},$$

hence **super-ballistic spread**.

Velocity changes due to the acceleration...

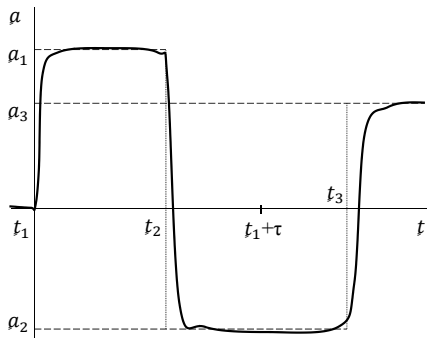
Let τ be the “reaction time”, i.e. time over which the animal is exerting force.

Scenarios 1 and 2 correspond to the case $\tau \ll \frac{1}{\omega}$:



Scenario 3: $\frac{1}{\omega} \ll \tau$

The animal reacts to a signal by **moving with a constant acceleration until the next signal** is received.



The **acceleration** is a random variable described by a pdf $\phi(a)$.

Let us consider

$$\phi_{G_a}(a) = \frac{e^{-\frac{a^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}}.$$

In this case, we obtain

$$\langle x^2(t) \rangle_{G_a} = \frac{\sigma^2}{3\omega^4} \left[6 - \omega^2 t^2 (3 - 2\omega t) \right] - \frac{2\sigma^2}{\omega^4} e^{-\omega t} (1 + \omega t),$$

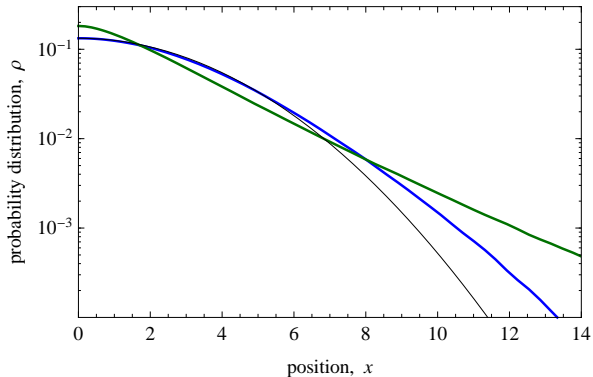
so that

$$\langle x^2(t) \rangle_{G_a} \sim t^4 \text{ for } t \ll \frac{1}{\omega} \quad \text{and} \quad \langle x^2(t) \rangle_{G_a} \sim t^3 \text{ for } t \gg \frac{1}{\omega},$$

hence the animal is moving **super-ballistically**

(Tilles & Petrovskii 2015, *Ecol. Compl.* **22**: 86-92.)

...but the dispersal kernel is clearly **thin-tailed**:



(Dispersal kernel at a given time obtained by Monte Carlo simulations for different acceleration distributions: blue for the **Gaussian**, green for the **Laplace** distribution)

Limitations and extensions

Scenarios 2 and 3 predict that the movement speed increases with time, apparently to some unrealistically high value.

In particular, in Scenario 2 we have

$$v_k = \sum_{n=1}^k \xi_n,$$

so that

$$\langle v^2 \rangle (T) \sim T,$$

where T is the period of uninterrupted movement

However, here we recall that the **time of uninterrupted movement is exponentially distributed**.

Therefore $\overline{\langle v^2 \rangle}$ has a well-defined, finite value.

A glance at (some) available data

We are interested in the rate of dispersal as given by

$$\langle x^2 \rangle (t) \sim t^H$$

where $H = 1$ corresponds to the standard diffusion.

- ▶ Albatrosses (Viswanathan et al. 1996): $H \approx 1.7$
- ▶ Spider monkeys (Ramos-Fernandez et al. 2004): $H \approx 1.7$
- ▶ Magellanic penguin (Sims et al. 2008): $H \approx 2.3$
- ▶ Leatherback turtle (Sims et al. 2008): $H \approx 2.5$.

Our model predicts that $2 \leq H \leq 3$.

Discussion and conclusions

- Superdiffusion can be a consequence of the animal's behavioral response to environmental clues or signals – effectively, to the environmental stochasticity
- Behaviorally induced superdiffusion does not require a fat-tailed dispersal kernel

Discussion and conclusions

- **Superdiffusion** can be a consequence of the animal's behavioral **response** to environmental clues or **signals** – effectively, to the environmental stochasticity
- Behaviorally induced **superdiffusion does not require a fat-tailed** dispersal kernel
- **Fat-tailed dispersal kernel** can appear as a result of variation in individual movement traits in a **population of diffusively moving individuals** (Petrovskii & Morozov 2009; Petrovskii et al. 2011)

References

- Tilles, PFC & Petrovskii, SV (2016) How animals move along? Exactly solvable model of superdiffusive spread resulting from animals decision making. *J. Math. Biol.*, in press.
- Tilles, PFC & Petrovskii, SV (2015) Statistical mechanics of animal movement: animals's decision-making can result in superdiffusive spread. *Ecol. Compl.* **22**, 86-92.
- Petrovskii, SV, Mashanova, A & Jansen, VAA (2011) Variation in individual walking behavior creates the impression of a Lévy flight. *PNAS* **108**, 8704-8707.
- Jansen, VAA, Mashanova, A & Petrovskii, SV (2012) Model selection and animal movement: Comment on "Levy walks evolve through interaction between movement and environmental complexity." *Science* **335**, 918.
- Petrovskii, SV & Morozov, AY (2009) Dispersal in a statistically structured population: Fat tails revisited. *American Naturalist* **173**, 278-289.

Thank you!