

WO9 - Random Walks

Howard Berg's book (RW in biology)

Nelson's "Physical models of living systems" ch 7

- Molecules subject to thermal fluctuations
- Organelles inside a cell
- Mosquitoes infesting a forest (Karl Pearson 1905)
- Dust particles in air (Einstein)
- Genetic drift
- Cell mutations
- Ecology (Animal telemetry)
- Bacteria swimming in lipid media

1D random walk (discrete space and time)

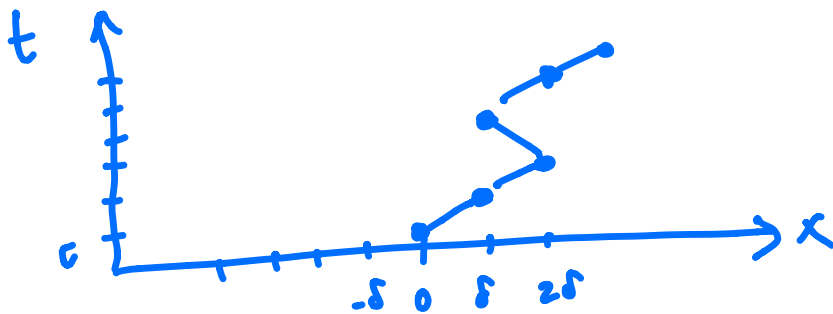
Random walk → Diffusion
discrete time continuous time
" space " space

1D Random Walks

How could a mosquito infest a forest (Pearson)

How dust moves in air (Einstein)

Start at $x=0$ $t=0$



i) each particle moves after a fixed time " τ "
a fixed step distance " δ " to the left or right.

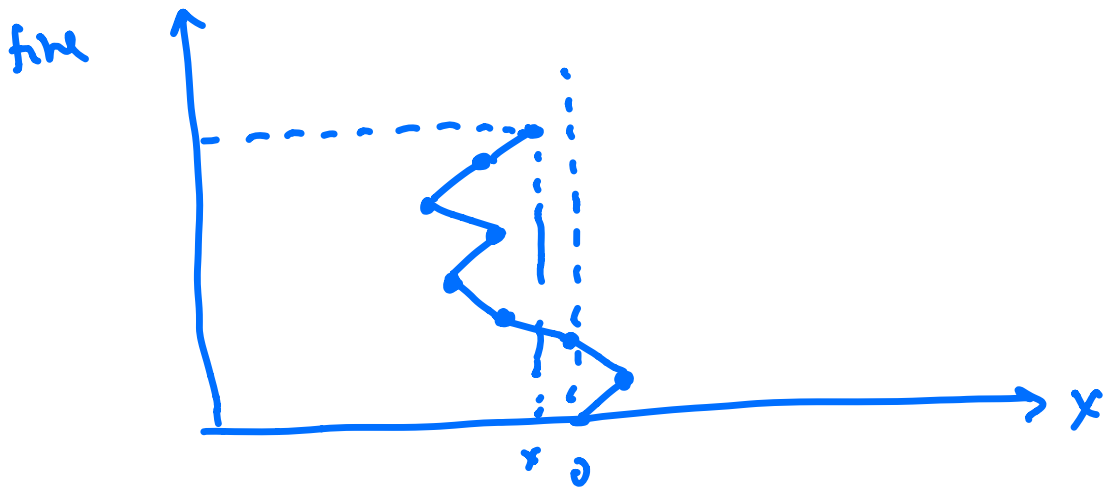
ii) each particle steps
left with probability P
or right " " " $q = 1 - P$

iii) particles move independently from each other

iv) particles don't interact:

- they don't get destroyed
- they don't get created from other particles

The RW probability distribution



$P(x|t)$ probability particle is at position x after time t

$$x = m \cdot \delta \quad m = \text{displacement in units of } \delta$$

$$t = N \cdot \tau \quad N = \text{time steps}$$

N steps, assume it takes l = steps left
 $N-l$ = steps right

$$P(l|N) = \binom{N}{l} p^l (1-p)^{N-l}$$

$$= \frac{N!}{l! (N-l)!} p^l (1-p)^{N-l}$$

Using the relationship

$$m = \text{displacement} = (N-l) - l = N - 2l$$

$$m = N - 2l$$

$$l = \frac{N-m}{2}$$

$$N-l = N - \frac{N-m}{2} = \frac{N+m}{2}$$

$$P(m|N) = \frac{N!}{\left(\frac{N-m}{2}\right)! \left(\frac{N+m}{2}\right)!} p^{\frac{N-m}{2}} (1-p)^{\frac{N+m}{2}}$$

→ class code

Properties

$$\langle m \rangle = \sum_m m P(m|N) = \sum_l (N-2l) P(l|N)$$

$$= N \sum_l P(l|N) - 2 \sum_l l \cdot P(l|N)$$

$$= N - 2 \cdot Np = N(1-2p) = N(q-p)$$

Mean displacement

$$\langle m \rangle = N(q - p)$$

if $p = q$ (Unbiased RW) $\langle m \rangle = 0$

- mean is proportional to # steps N
- mean is proportional to drift

$$q - p$$

Variance

$$\text{Var}(m) = \text{Var}(N - 2\ell) = 4 \text{Var}(\ell)$$

$$= 4 \cdot Npq$$

$$\tilde{\sigma} = \sqrt{\text{Var}(m)} = 2 \sqrt{Npq}$$

Grows with \sqrt{N}

- In the limit
 - $N \rightarrow \infty$
 - $Np \rightarrow \infty$
 } p is finite and γ takes a very large # of steps

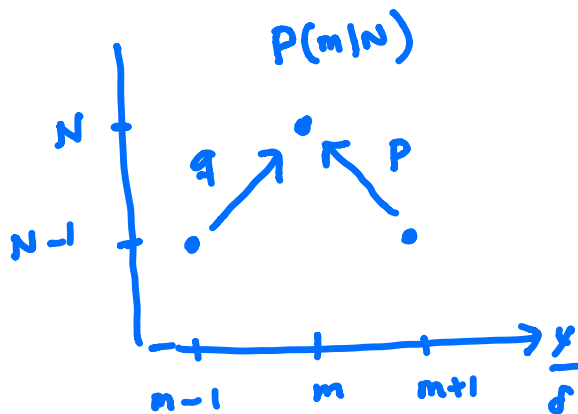
$$P(\ell|N) \longrightarrow \text{Normal Distribution}$$

$$\mu = \langle m \rangle = N(q-p)$$

$$\sigma = 2\sqrt{Npq}$$

$$P(m|N) \longrightarrow P(m|\mu, \sigma) dm = \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(m-\mu)^2}{2\sigma^2}} \cdot dm$$

- RW has no memory - A Markov process



$$P(m|N) = q P(m-1|N-1) + p P(m+1|N-1)$$

Master equation of a diffusion stochastic process

Random walks w/ drunken pauses

$$p + q < 1$$

$$1 = p + q + z$$

$$P(m|N) = q P(m-1|N-1) + p P(m+1|N-1) + z P(m|N-1)$$

$l = \#$ move left

$n = \#$ no move

$N - l - n = \#$ move right

$$m = \# \text{ right} - \# \text{ left}$$

$$= N - l - n - l = N - 2l - n$$

$$\langle m \rangle = N - 2Np - Nz =$$

$$= N(1 - 2p - z)$$

$$= N(1 - p - p - z)$$

$$= N(q + z - p - z) = \underline{N(q - p)}$$

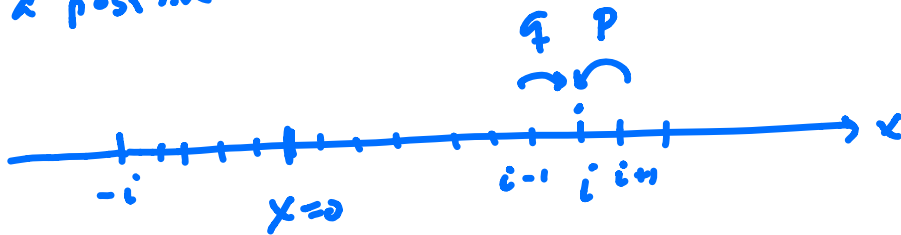
$$\text{Var}(m) = 4\text{Var}(z) + \text{Var}(u)$$

$$= 4Np(1-p) + Nz(1-z)$$

$$= 4Np(q+z) + Nz(p+q)$$

Probability of Capture

A random walk starts at $x=0$, what is the probability that it reaches a position i



$$P(\text{reaches } i | 0)$$

- No risk of reaching the edges

$$P(+\infty | 0) = 0$$

$$P(-\infty | 0) = 0$$

- $$P(i | 0) = p P(i+1 | 0) + q P(i-1 | 0)$$

$$P(i | 0) = P(i-1 | 0) \cdot q + P(i+1 | 0) \cdot p$$

Solving for $P(0|0)$

$$\text{Ansatz: } P(i|0) = A\beta^i + C$$

$$P(+\infty|0) = 0 \Rightarrow 0 < \beta < 1$$

$$P(-\infty|0) = 0 \quad C = 0$$

$$P(i|0) = A\beta^i$$

$$P(i=0|0) = 1 = A$$

$$P(i|0) = \beta^i$$

$$\beta^i = \beta^{i-1} q + \beta^{i+1} p$$

$$1 = \frac{q}{\beta} + \beta p$$

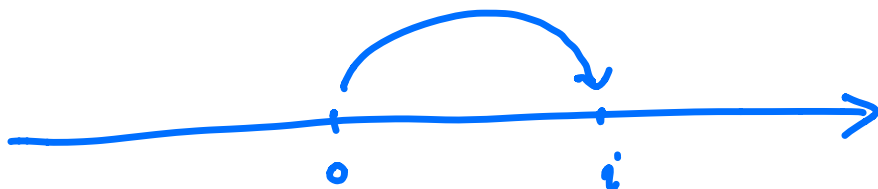
$$\beta = q + \beta^2 p \quad || \quad \beta^2 p - \beta + q = 0$$

$$\begin{aligned} \beta &= \frac{1 \pm \sqrt{1 - 4pq}}{2p} = \frac{1 \pm \sqrt{(p-q)^2}}{2p} \\ &= \frac{1 \pm (p-q)}{2p} \end{aligned}$$

$$\beta = \frac{1 \pm (p-q)}{2p} \quad \begin{cases} \rightarrow \frac{1+p-q}{2p} = \frac{2p}{2p} = 1 \\ \hookrightarrow \frac{1-p+q}{2p} = \frac{q}{p} \end{cases}$$

$$P(i|0) = \begin{cases} 1 & \text{if } q > p \\ \frac{q}{p} & \text{if } q < p \end{cases}$$

$$\begin{matrix} p & q \\ \leftarrow & \rightarrow \end{matrix}$$



- i) $q > p$ always reaches $P(i|0) = 1$ if $q > p$
 ii) if $q < p$ still there is a probability of reaching!

$$P(i|0) = \left(\frac{q}{p}\right)^i \quad \text{if } q < p$$

- iii) $q = p$ $P(i|0) = 1$ always reached (eventually)

Applications to ecology

a small population in which

$$q = \text{pb of birth}$$

$$p = 1 - q = \text{pb of death}$$

Even if $q < p$, there is a $\neq 0$ pb of
reaching any population size i

$$O\left(\frac{q}{p}\right)^i$$

+ A gambler, no capital,

$$q = \text{pb of winning } (q < p)$$

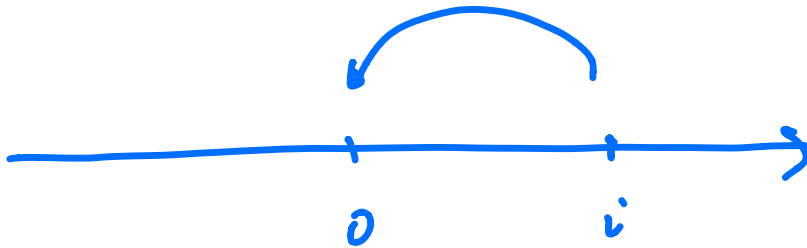
still can reach any gains i w/ probab

$$\left(\frac{q}{p}\right)^i$$

Reciprocally

$$\underline{P(0|i)} = \begin{cases} (P/q)^i & P < q \\ 1 & P > q \end{cases}$$

$q \leftarrow i \rightarrow P$



Time to Capture (Hitting time)

How long it will take to reach a certain population size (or position)?

Introduce $h(j|i)$ as the expected time for a random walk to go from i to j

Using the Markov recursion

$$h(i|0) = 1 + h(i+1|0) \cdot p + h(i-1|0) \cdot q$$

$$\text{Ansatz: } h(i|0) = A^i$$

$$A^i = 1 + A^{(i+1)}p + A^{(i-1)}q$$

$$A^i = 1 + A^i(p+q) + A^p - A^q$$

$$A^i = 1 + A^i + A^p - A^q$$

$$0 = 1 - A(q-p)$$

$$A = \frac{1}{q-p}$$

$$h(i|0) = \begin{cases} \frac{1}{q-p} & i > 0 \\ \frac{1}{p-q} & \text{if } i < 0 \end{cases}$$

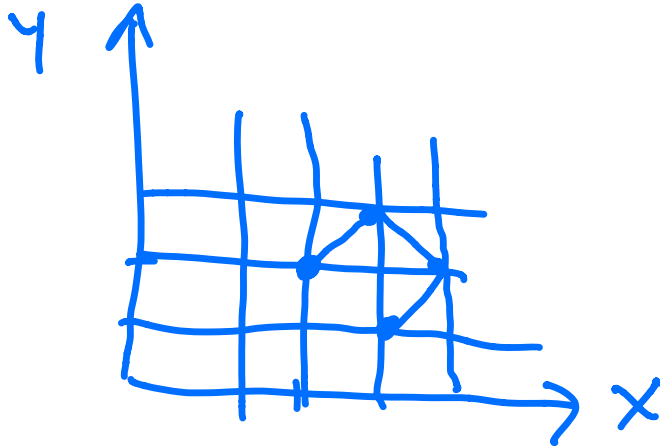
Notes

i) in general hitting times are not symmetric

ii) if $p=q$ $h(i|0) = +\infty$

iii) proportional to i

2D random walks



P_x = prob of moving left in X
 P_y = prob of " down in Y

$$\begin{aligned} P(x, y | t) = & P_x P_y P(x+1, y+1 | t) \\ & + P_x q_y P(x+1, y-1 | t) \\ & + q_x P_y P(x-1, y+1 | t) \\ & + q_x q_y P(x-1, y-1 | t) \end{aligned}$$

- Particles tend to explore close regions
- There is no knowledge of what has not been explored yet.