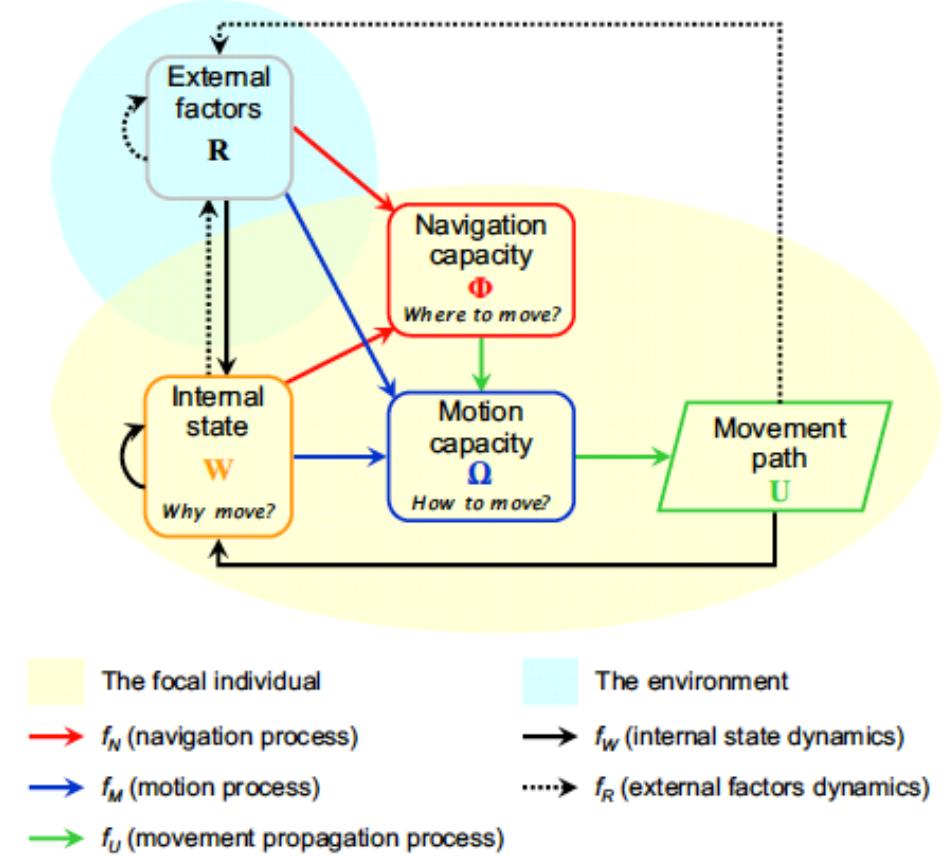


Characterizing Movement

Nov 16

Components of Movement Ecology

- **Why?** Internal state– energy, physiology, mental state or motivation to move (hungry, afraid)
- **How?** Motion capacity - machinery, wings of birds or seeds
- **When and where?** Navigation mechanisms– movement is not random in space and time, need some machinery to decide when and where to move
- External factors abiotic and biotic environment
- **Movement path** From these 4 and feeds back to internal state that feeds into the next path
- Applies to everything from seed dispersal to bird migration, common language



From Nathan et al. 2008

Movement Models

Parameter Estimation

statistical model of movement parameters such as speed or tortuosity
(many packages)

Home Range Estimation

want to know where an animal is spending time
(adehabitatHR, ctmm)

Behavior Segmentation

what behavioral state the animal was in at each time step
(moveHMM, momentuHMM)

Path Reconstruction

how to reconstruct a path from data that are noisy?
(crawl, foieGras)

Step Selection Analyses

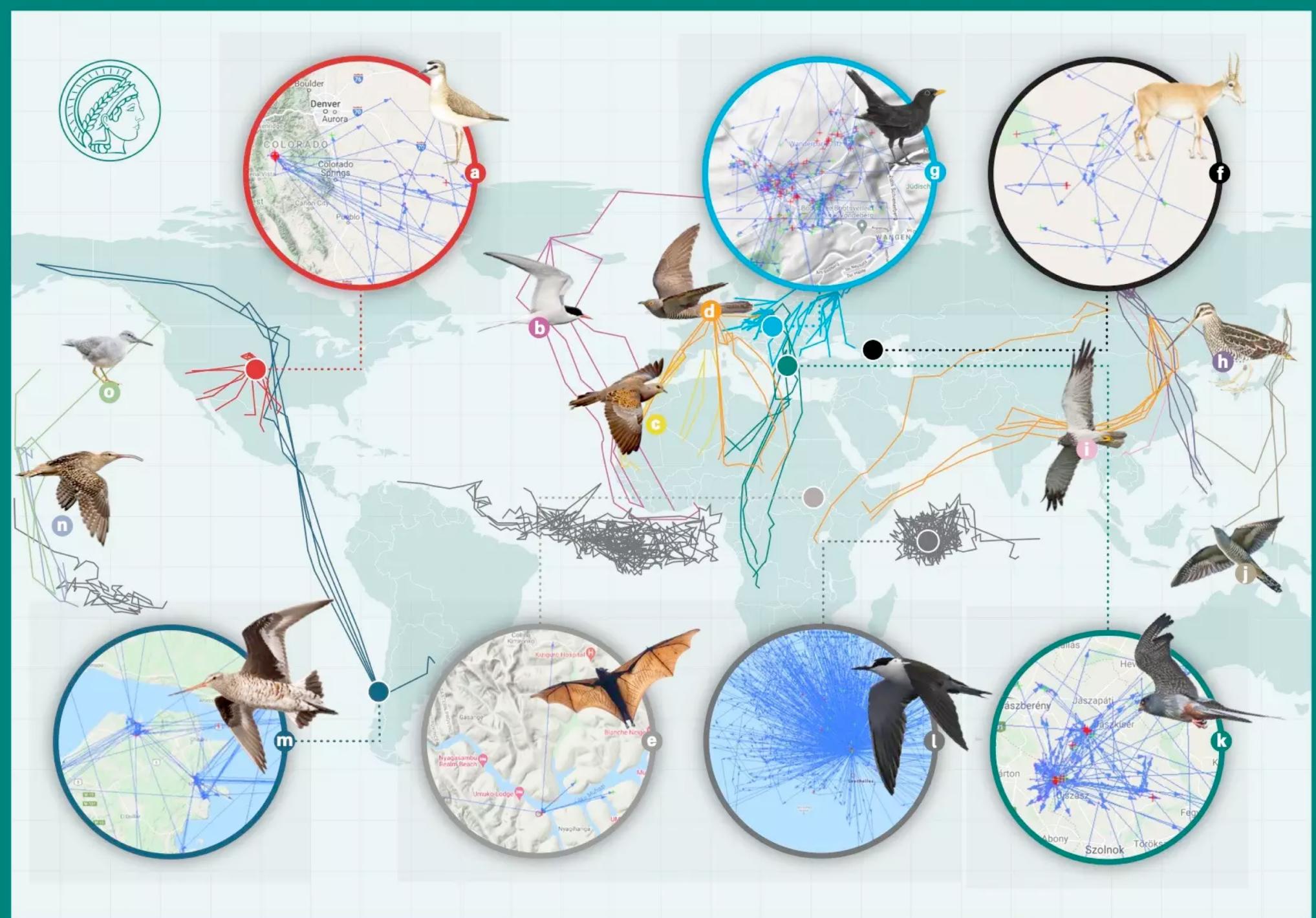
understand how animals make movement decisions based on the environment
(amt, adehabitatLT, others)

Icarus tracked in near-real time during migratory cycles, March - November 2021

GPS sensors weighing <5g record GPS and other data

Jetz et al., TREE 2022

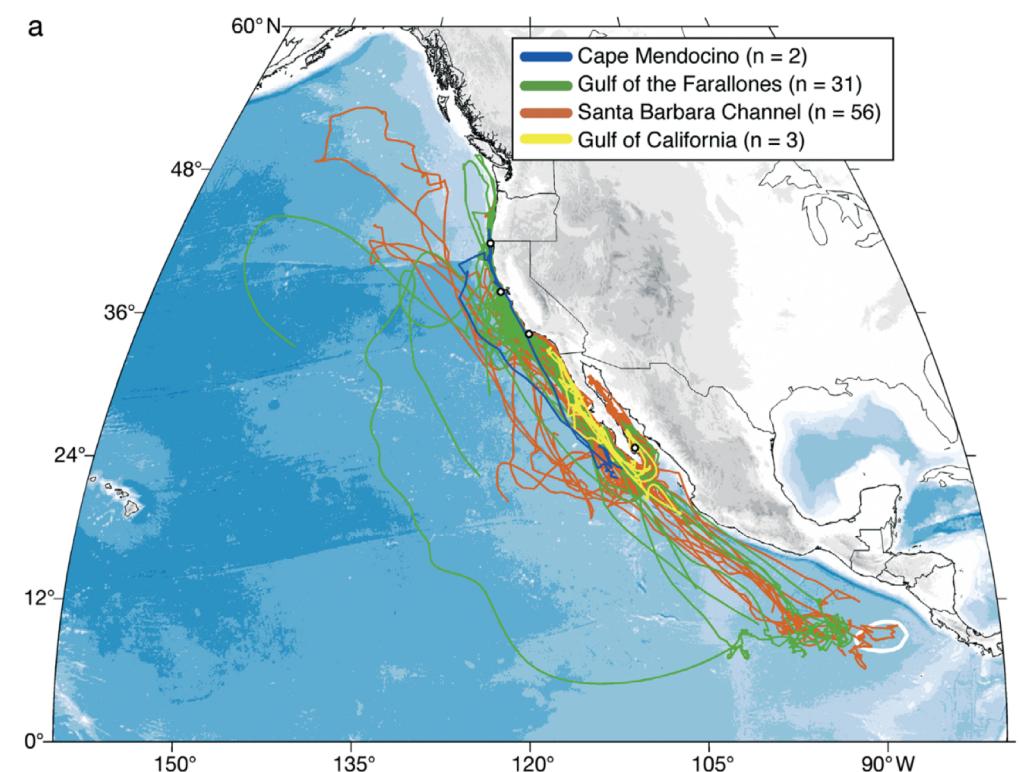
animals remotely sense the environment
(now shut down due to tracking on Russian satellite)



Movement parameter estimation

- See track of movement- the movement is not homogeneous through the time series different types of movement
- Sometimes it is fast and directed, sometimes it will slow down
- It may switch back and forth between behavioral states that will give rise to different movement patterns
- Foraging, resting, traveling
- Try to model movement patterns from different types of movement

Bailey et al.: Blue whale movements in NE Pacific



Types of research questions

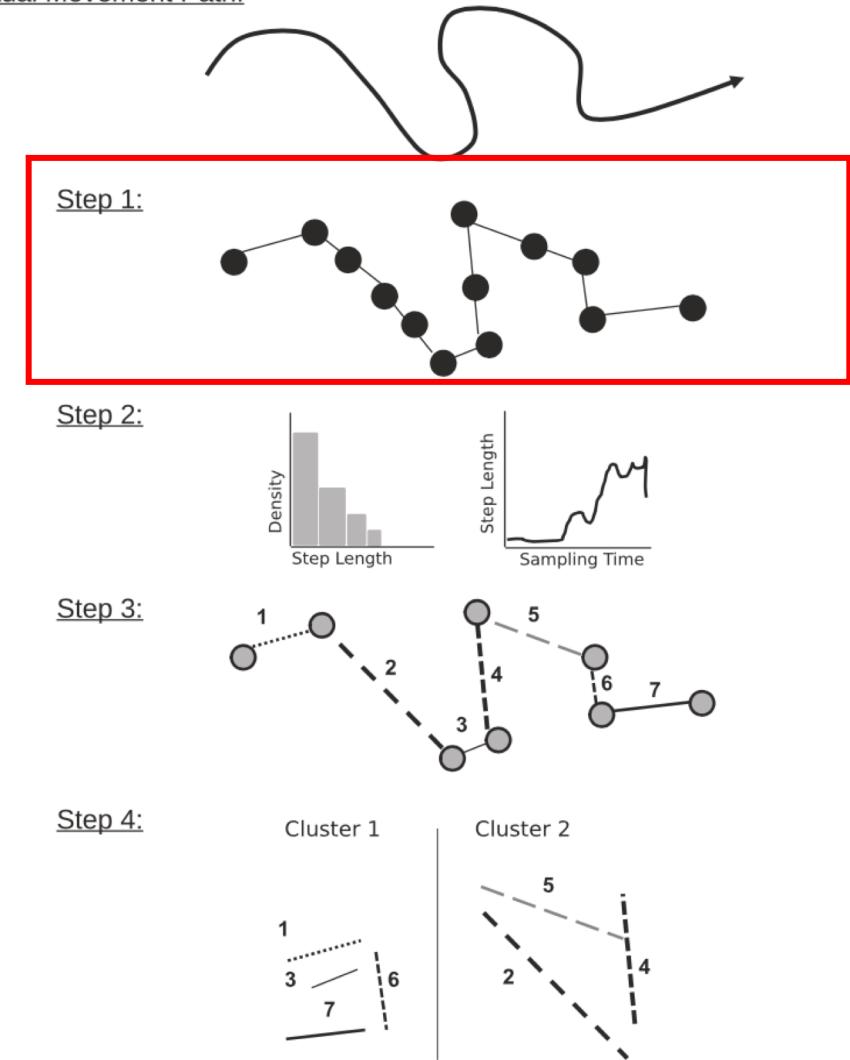
1. The quantitative description of movement patterns
2. The detection of significant change-points
3. The identification of underlying processes (“hidden states”)

Sampling Movement

1. The quantitative description of movement patterns

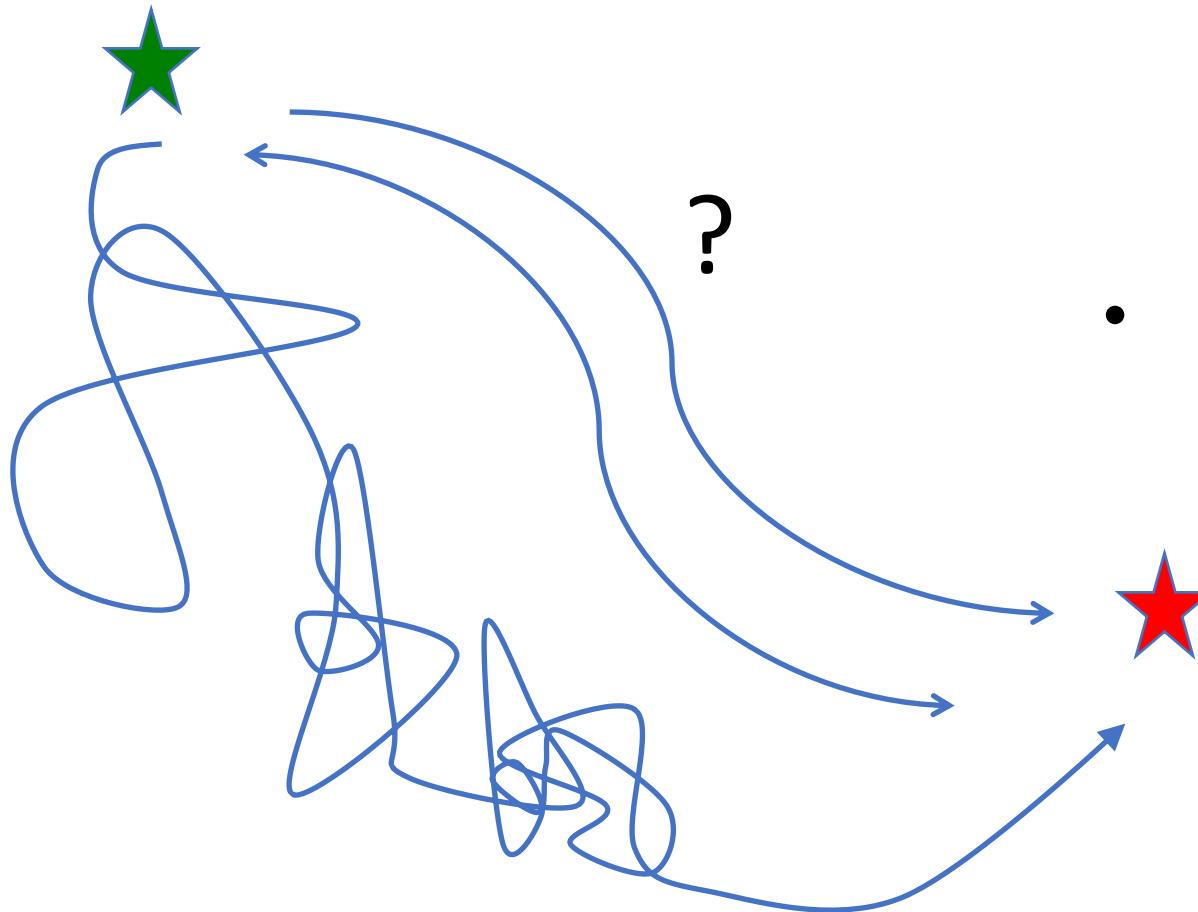
- We don't observe the complete, continuous movement
- Sample a set of discrete relocations to approximate the path (Step 1)
- Sequence of consecutive records -> movement track or trajectory
- Accuracy reflects sampling regime (spatial accuracy and frequency of relocations)

Actual Movement Path:



From Edelhoff et al. 2016

Accuracy reflects sampling regime



- Increasing uncertainty in movement pathway as time between locations increases.
- Device type also important

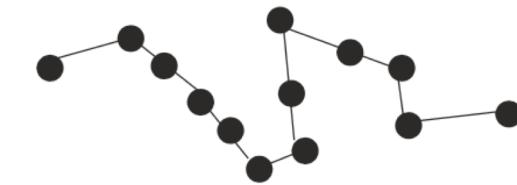
Path Characteristics

1. The quantitative description of movement patterns
 - Path characteristics that capture movement patterns
 - Derived from spatial position and time stamp
 - Calculated stepwise or across multiple steps

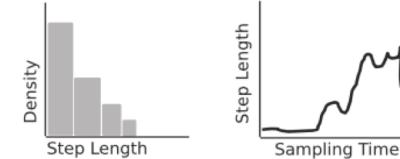
Actual Movement Path:



Step 1:



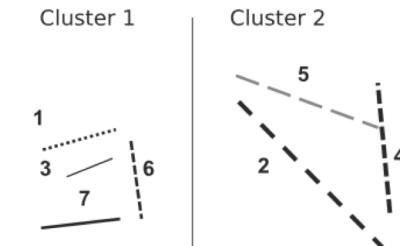
Step 2:



Step 3:



Step 4:



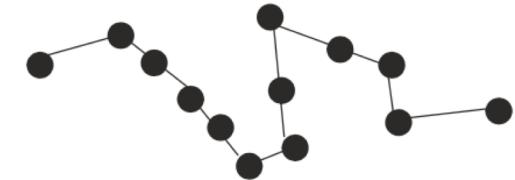
From Edelhoff et al. 2016

Characteristic	Description
Displacement	Increment of the X and Y values between two consecutive relocations, change in absolute spatial position
Time lag	Duration / increment in time between consecutive relocations (usually determined by sampling regime)
Turning angles / heading	Relative and absolute turning angles between consecutive relocations, change in direction
Step length	Euclidean distance between two consecutive relocations
Velocity / speed	Distance traveled in a given time interval between two relocations; less sensitive to missing data than step length
Persistence / turning velocity	Transformations of speed and turning angle: persistence velocity represents the tendency and degree of a movement to persist in a certain direction. Turning velocity shows the tendency of a movement to turn in a perpendicular/opposite direction
Net / mean squared displacement	Squared displacement between the first and current relocation of the trajectory; applied to characterize diffusion behavior or migration patterns
First passage time	Time required for crossing a predefined endpoint based on a circle (radius) around a starting relocation. Sums the times of all forward and backwards relocations within the radius; index of area-restricted search behavior

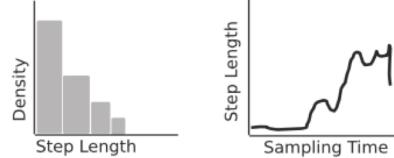
Actual Movement Path:



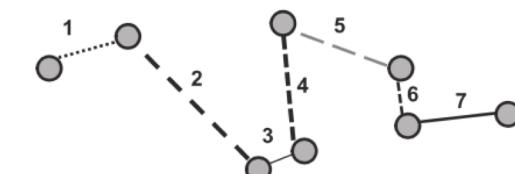
Step 1:



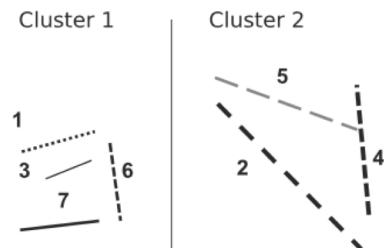
Step 2:



Step 3:



Step 4:



From Edelhoff et al. 2016

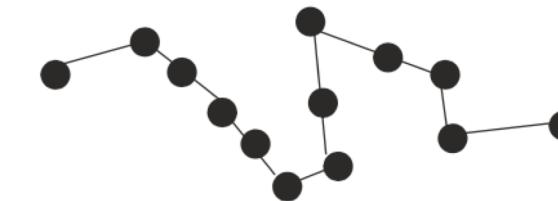
Path Characteristics

- Step length
- Turning angle
- Random walk models
- Speed
- Straightness index
- First-passage time
- State-space models

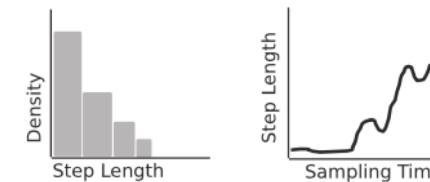
Actual Movement Path:



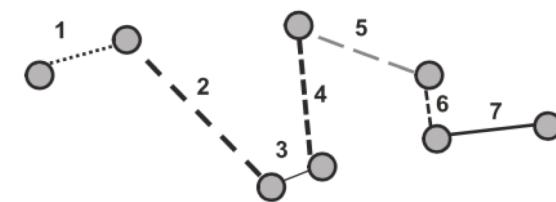
Step 1:



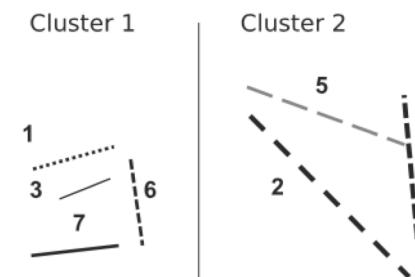
Step 2:



Step 3:



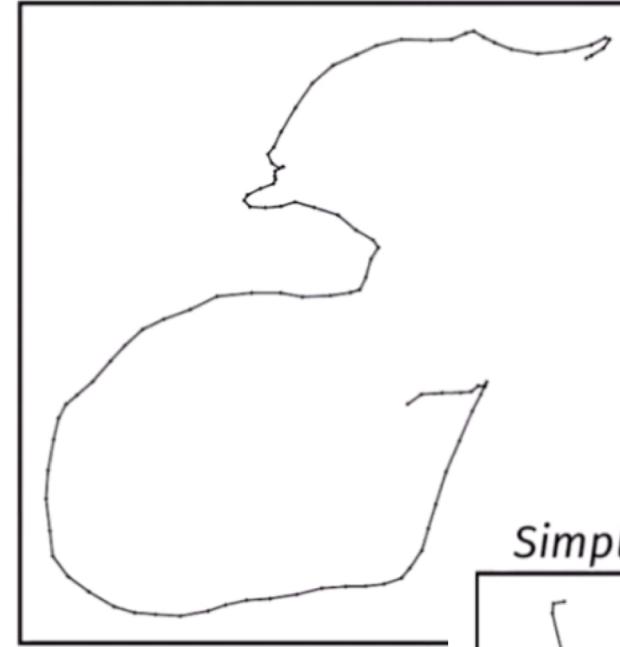
Step 4:



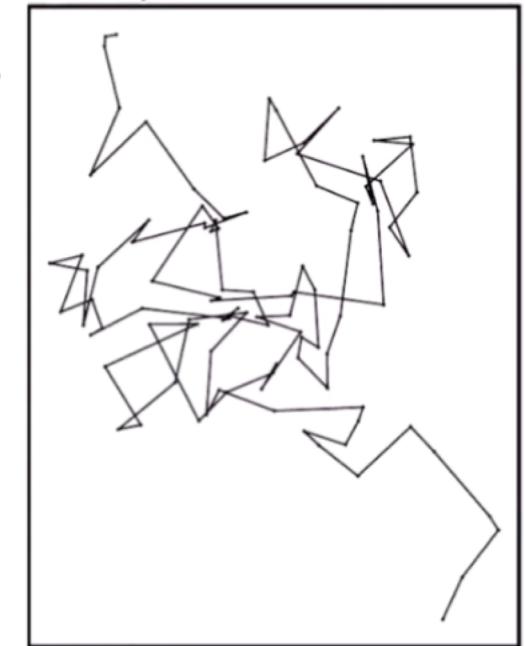
Random Walk

- Simple statistical model of behavior
- Building block for behavioral models
- Within each behavior, animal follows a correlated random walk model
- **Persistence in movement direction** captured in the model
- Persistence is defined by the degree of correlation between successive step directions

Correlated random walk

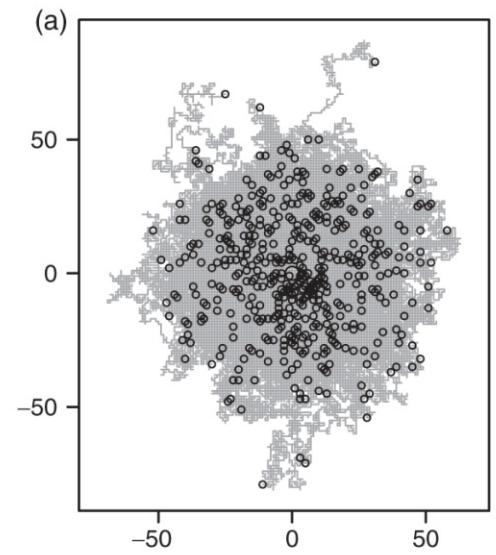


Simple random walk



Random Walk

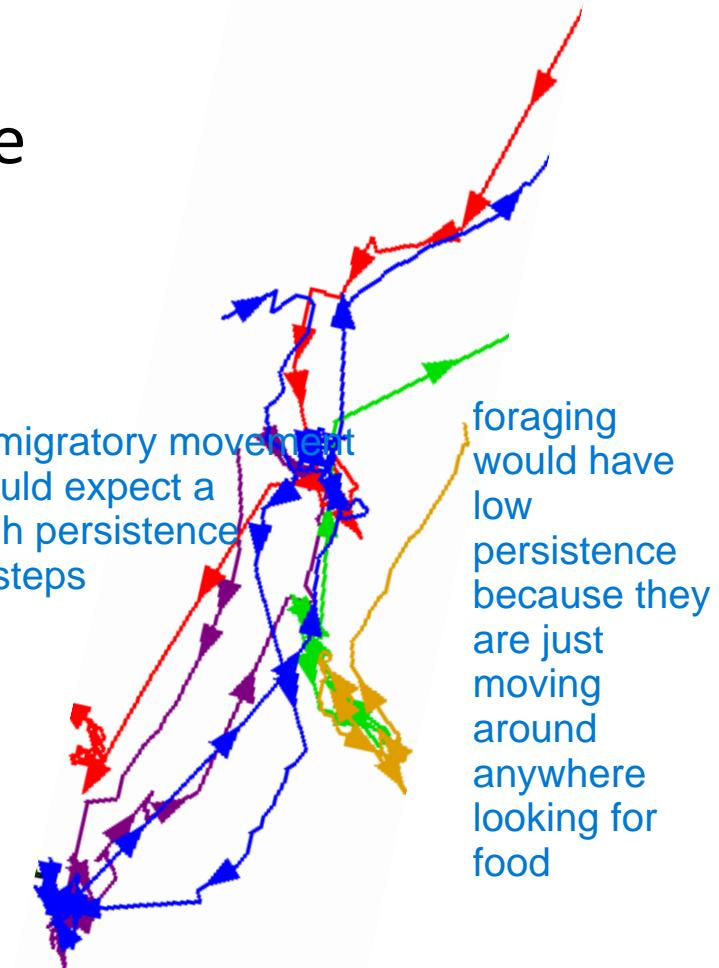
- In reality, true randomness is unexpected
- Null model for comparison
- Choice of movement direction each time step is completely random
- No bias and no relationship between the direction of the previous and current step
- Predict density distribution shows little displacement
- Tortuous path, retraces steps



End points of 500 random walks of 1K steps
Spatial Simulation textbook

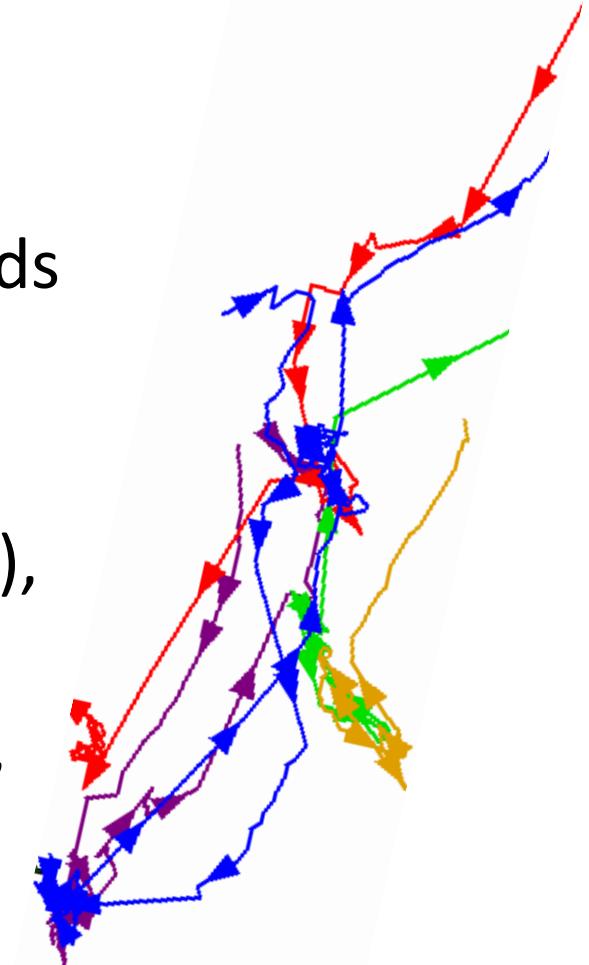
Random Walk

- Simple Random Walk -> individual step direction in the walk are strictly independent of one another, step length is fixed or step length drawn from a probability distribution
- Correlated Walks - later steps influenced by earlier ones or by the environment, directional persistence
- These models describe one phase but to incorporate multiple phases combine with models of behavioral switching (foraging mode, dispersal mode)



Correlated Random Walk

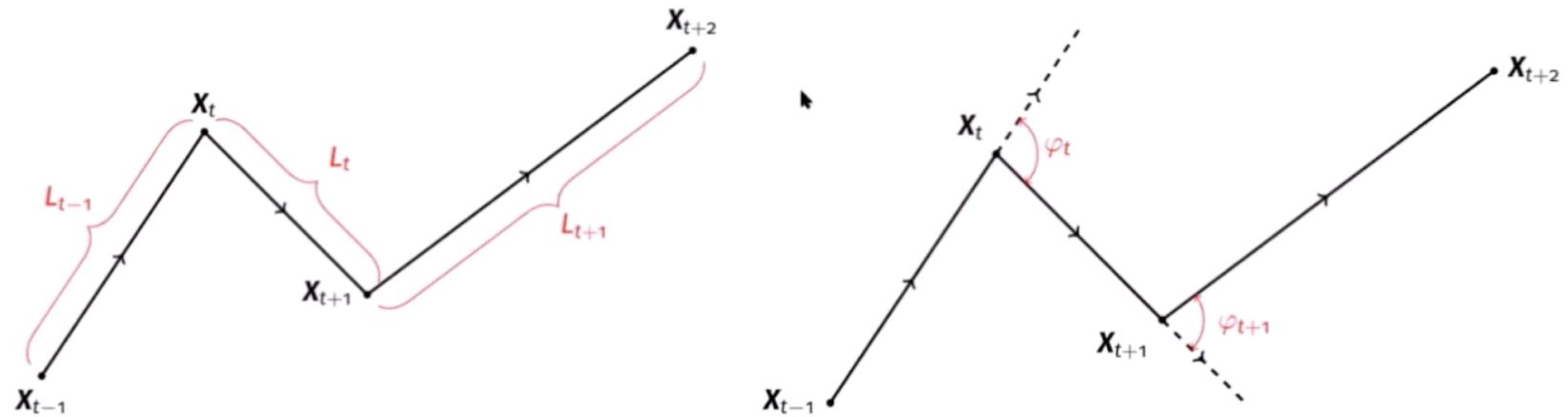
- bit more realistic
- Animals tend to move in the direction of their heads
- Direction of the next step chosen by selecting a turning angle relative to the previous step
- If the turning angles are small (more concentrated), then walks become straighter
- If the turning angles are larger (less concentrated), then walks become more tortuous or clumped



Movement Metrics

In a correlated random walk, we use steps on a trajectory to model two distributions:

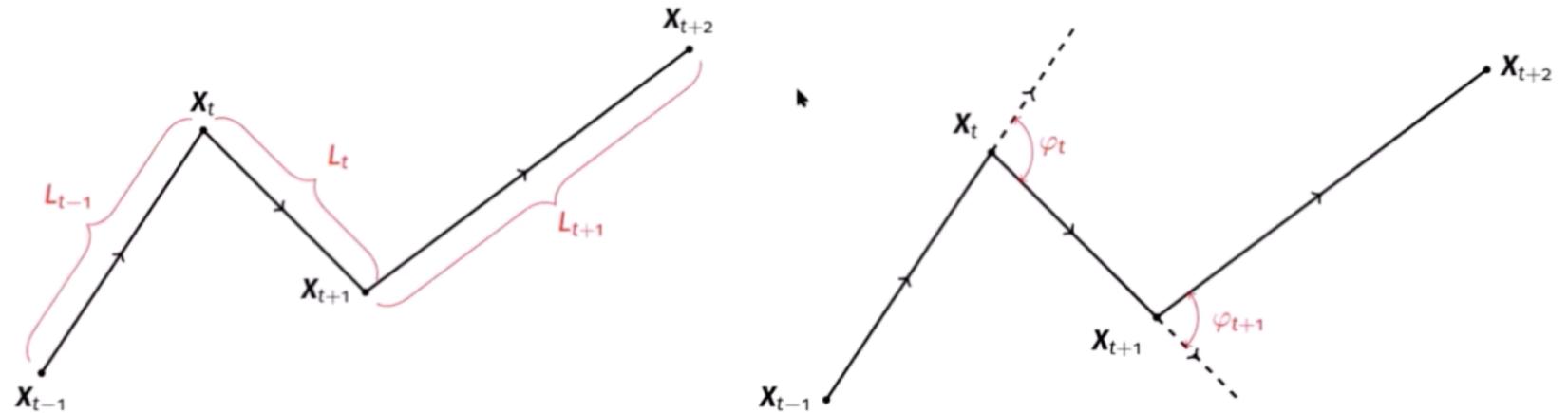
- Step lengths
- Turning angles



Movement Metrics

Turning angle:

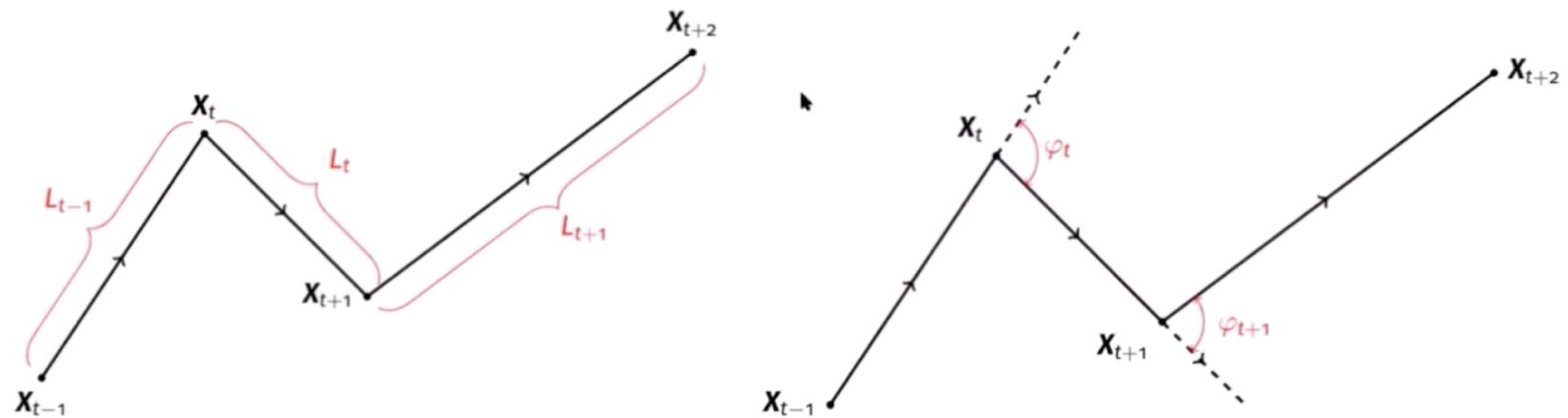
- Changes in direction, how persistent is the movement?
- Wrapped normal distribution
- Concentration parameter low= uncorrelated/clustered, high= straight



Movement Metrics

Step length:

- distances between steps
- given constant time interval, longer step faster

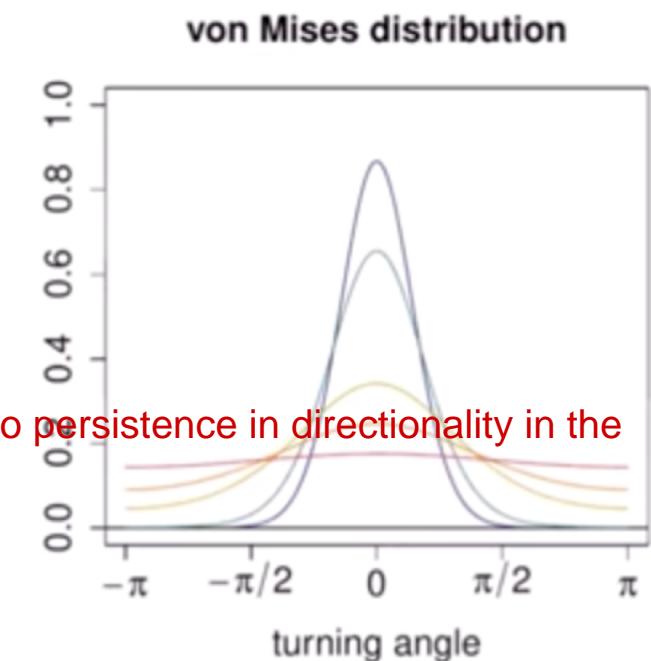
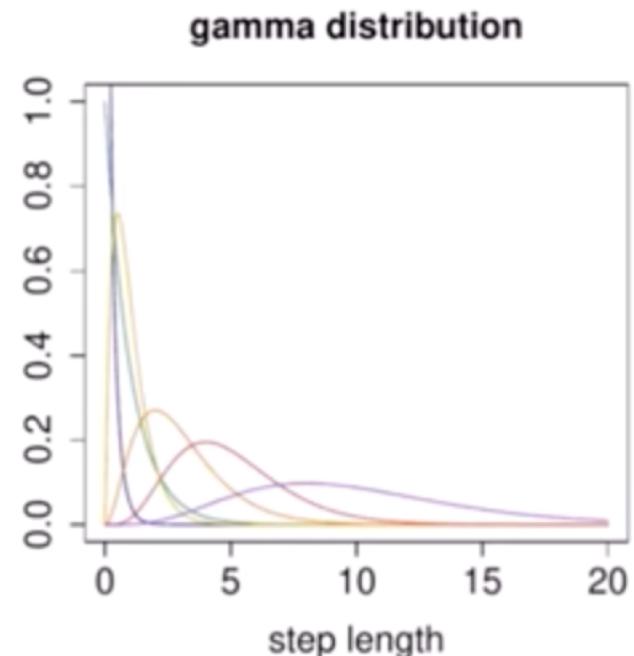


[show R simm.crw](#)

Movement Metrics

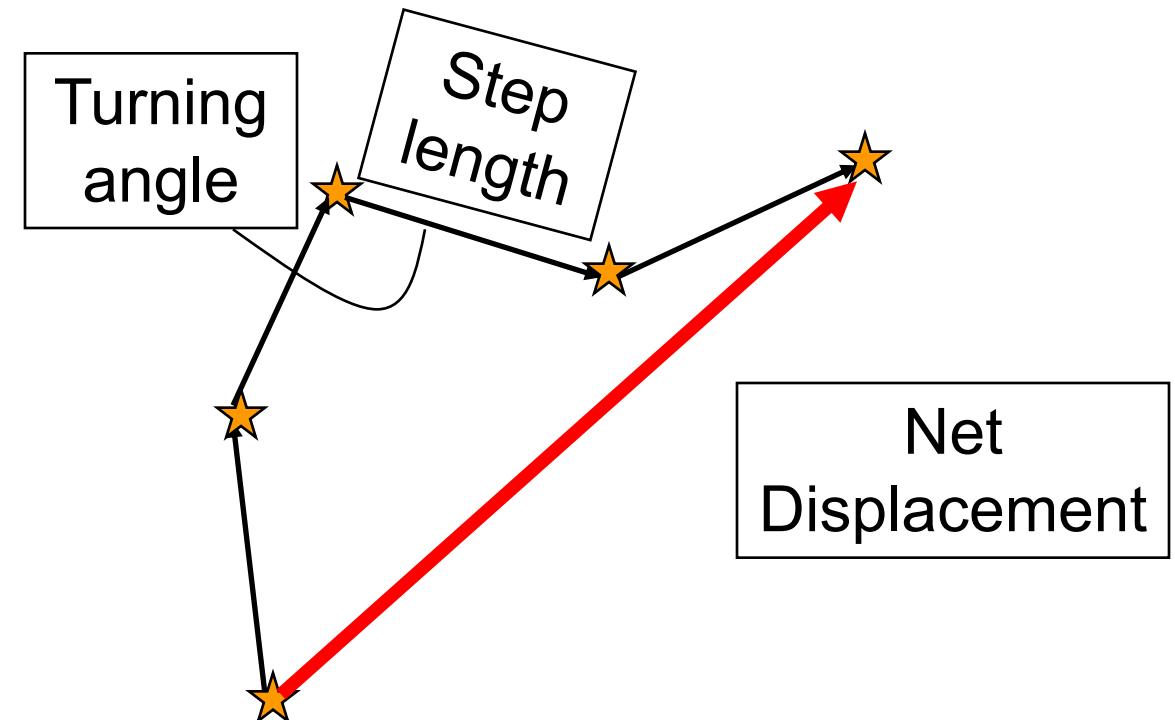
- Step length: Gamma distribution because non-negative densities (also Weibull)
- Capture different speeds of movement, purple 5-15km, yellow 0-3km
- Concentration of turning angle: circular distribution (also wrapped)
- Captures how directed or persistent the movement, dark blue quite directed, red is flat so no persistence

red R=0 random path and no persistence in directionality in the movement



Net squared displacement

- Straight-line squared distance from a starting location
- Squared so that it avoids negative quantities with changes in direction
- How far the walk goes as a function of the number of steps



Net squared displacement

$$R_n^2 = nm_2 + 2m_1^2 \left(\frac{c}{1-c} \right) \left(n - \frac{1-c^n}{1-c} \right)$$

R_n^2 is the net squared displacement

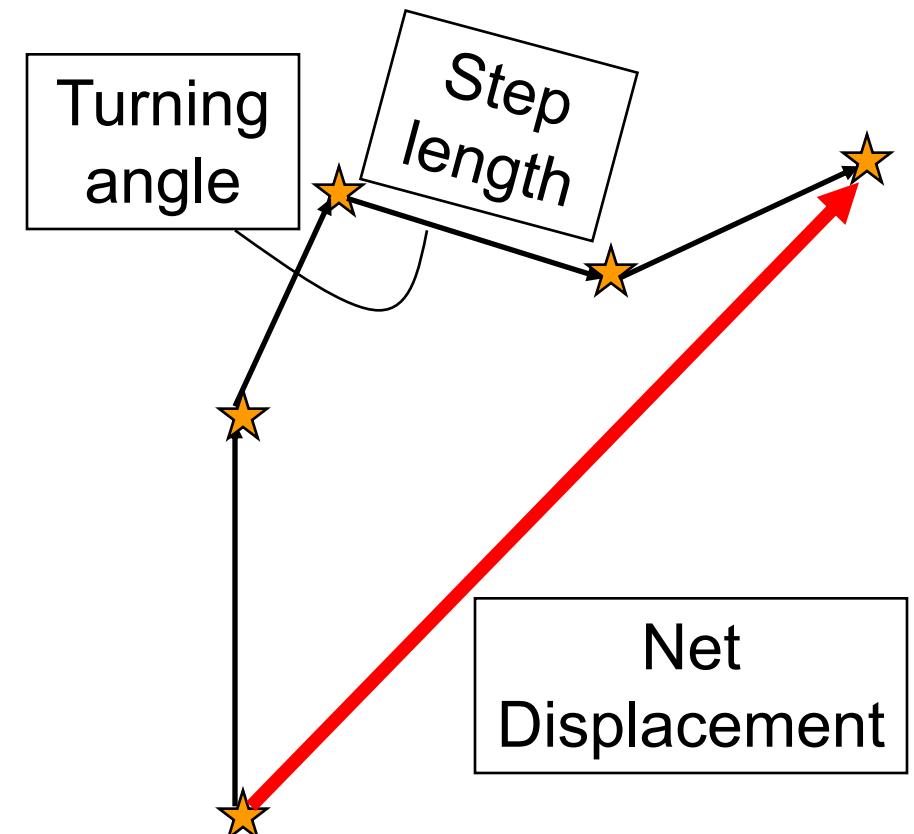
n is the number of moves from the first location

m_1 is the mean step length

m_2 is the mean squared step length

c is the mean of the cosines of the turning angles

- displacement grows as a square root of elapsed time
- dx/\sqrt{dt}



Net squared displacement

- Correlated Random Walk
- Exploration sphere is the range over which a typical random walk can extend over time t
- Density of visited sites inside exploration sphere
- Number of visited sites/volume of exploration sphere

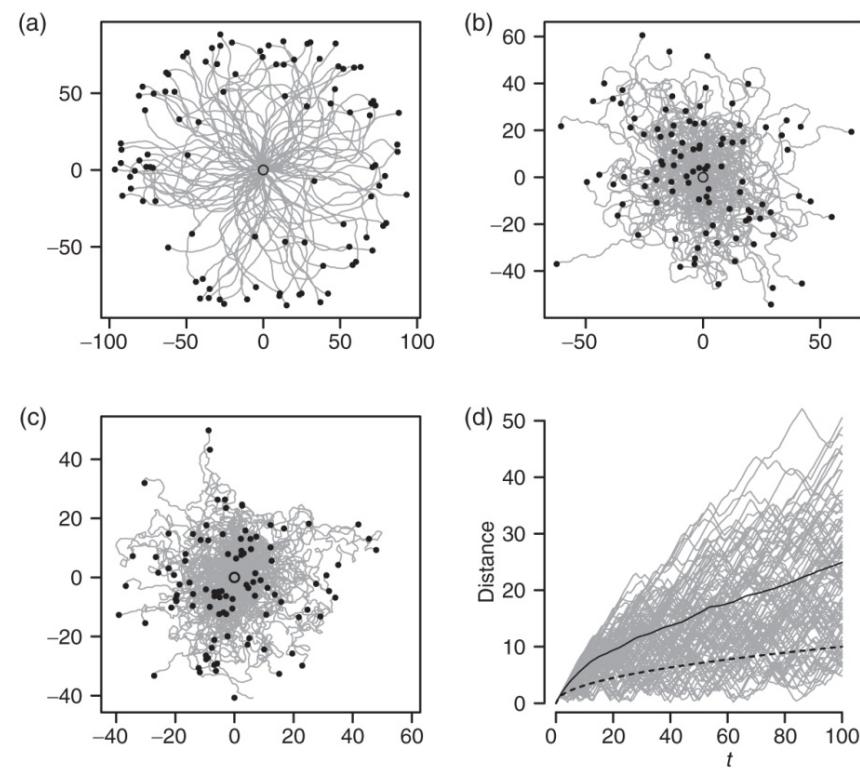


Figure 4.6 (a)–(c) 100-step random walks with turn angles chosen from a normal distribution, $\mu = 0^\circ$ and $\sigma = 10^\circ$, 30° and 50° , respectively. Note the different scale of each plot. (d) The distance from the origin of such walks still has the characteristic \sqrt{t} growth rate, shown here for the $\sigma = 50^\circ$ case. The dashed line shows the expected (slower) rate of progress for a simple random walk.

Correlated Random Walk

- Upper line – more linear,
Lower line – more diffusive
- Between lines- as expected
for random movement
- (a) root mean squared
distance increases linearly
with time
- (b,c) roll-off from linear to
diffusive behavior for the
correlated walks

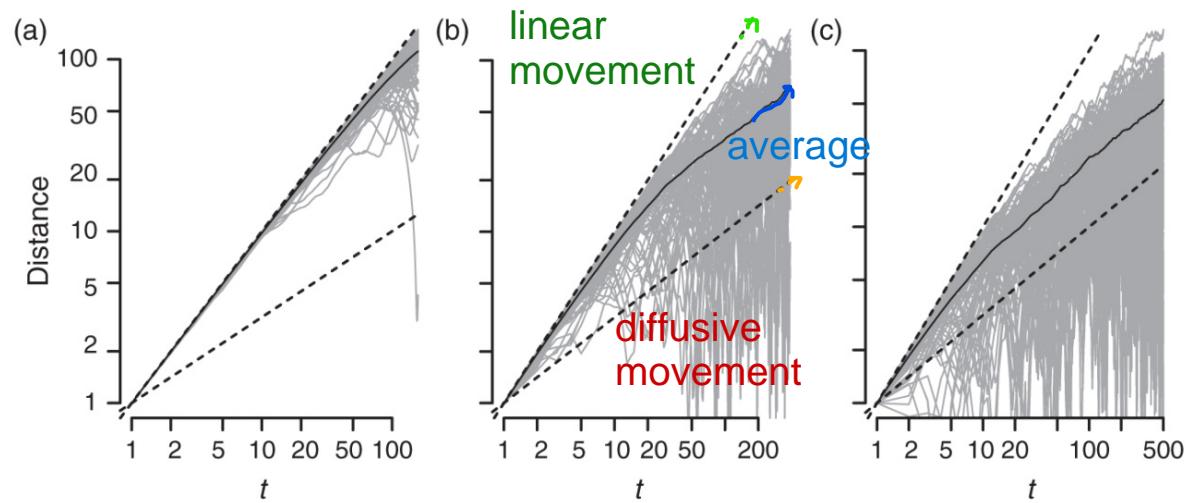
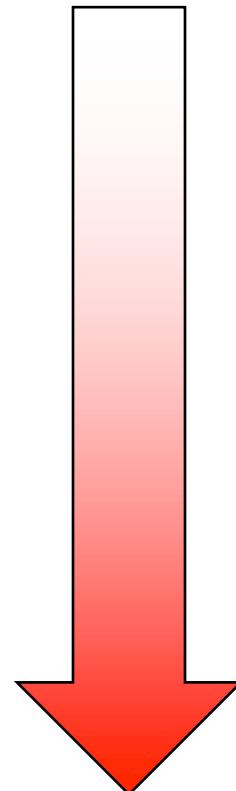


Figure 4.8 Expected distance of correlated random walks with turn angles chosen from a normal distribution, $\mu = 0^\circ$, and (a) $\sigma = 10^\circ$, (b) 30° and (c) 50° . Note the logarithmic time and distance scales.

Summary of random walk models

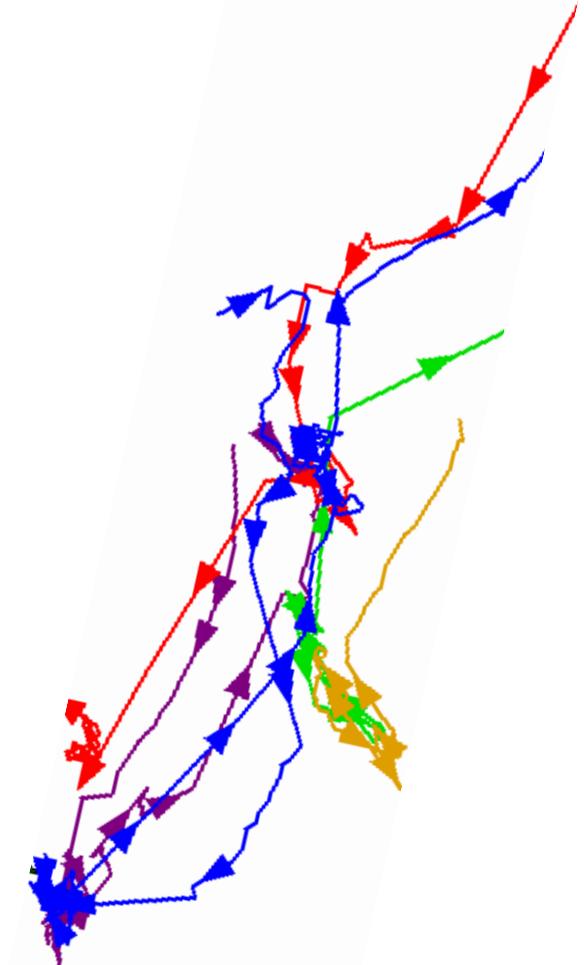
Model	Assumptions
Simple random walk	No directional bias
Correlated random walk (CRW)	Directional persistence, correlated movement from one step to another
Biased random walk (BRW)	Persistent bias in movement compass direction ie towards a resource or migration direction
Lévy flight	Short periods of localized steps interspersed with long-range jumps

Increasing distance traveled over time



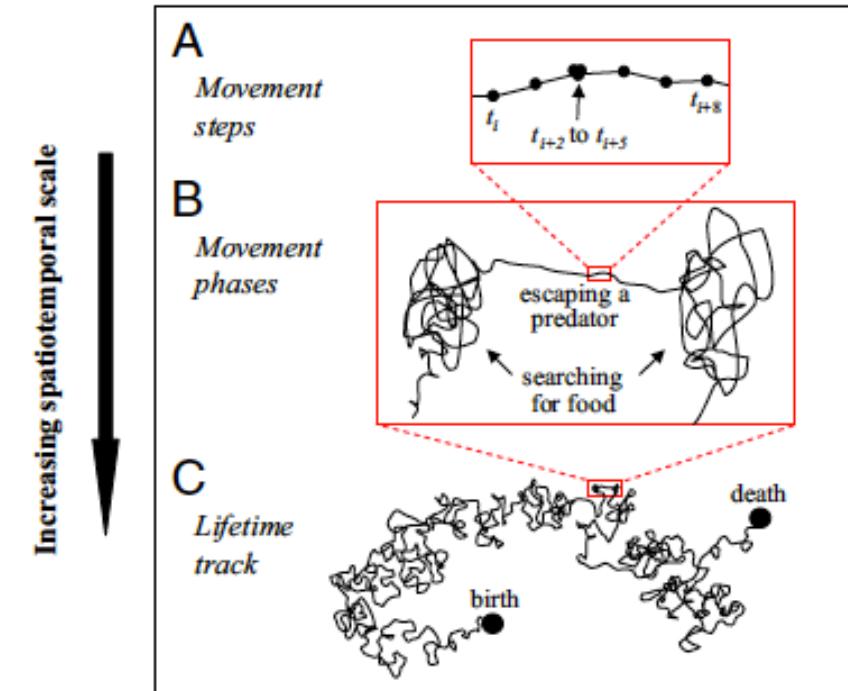
Biased Random Walk

- The direction is influenced by an absolute compass direction
- In a CRW, it is influenced only by the previous move direction
- Select direction of each step with respect to a fixed compass direction
- This can arise when animals respond to environmental gradients, are migrating to a destination or memory of preferred locations.



Lévy Flights

- Paul Pierra Levy (1885-1971) French Mathematician observed random walks in nature followed a power law rather than a normal distribution
- Travel small distances most of the time with longer “bursts” or long-range jumps
- Broad distribution of step lengths but each step is in a random direction
- Displacement after many steps dominated by the longest single step of the walk
- Cover ground more quickly than the other kinds of walk considered and is termed super-diffusive behavior.



From Nathan et al. 2008
PNAS 105: 19052-19059

Lévy Flights

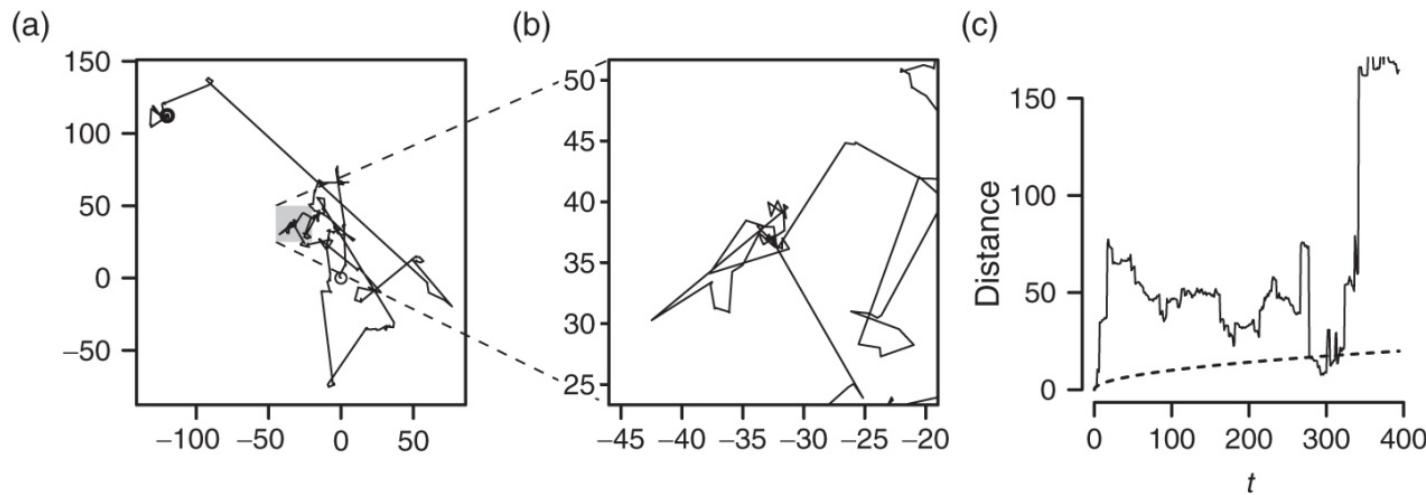


Figure 4.9 A walk of 281 steps, where each step is in a direction drawn from a uniform random distribution and step lengths are drawn from the Cauchy distribution with location parameter $x_0 = 0$ and scale $\lambda = 1.0$. (a) The full walk, (b) a zoomed-in region (grey area in (a)) and (c) the distance from the origin of the walk compared to a \sqrt{t} expectation.

Lévy Flights

- net squared displacement greater than predicted by the CRW model
- moved much further than expected by random movement

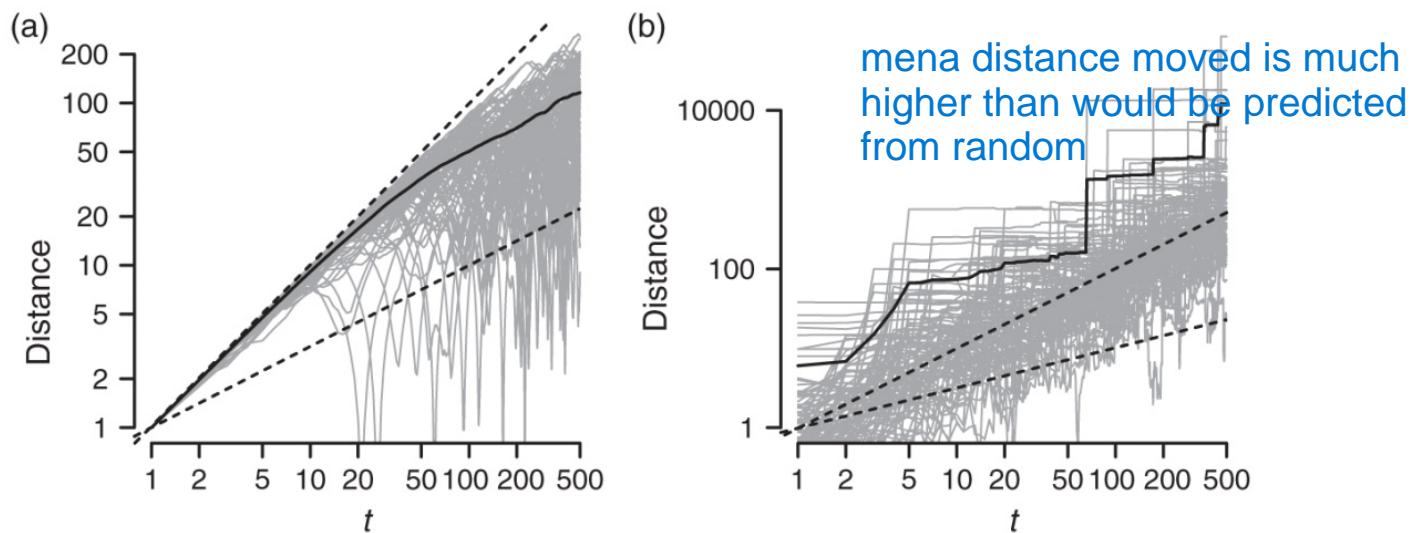
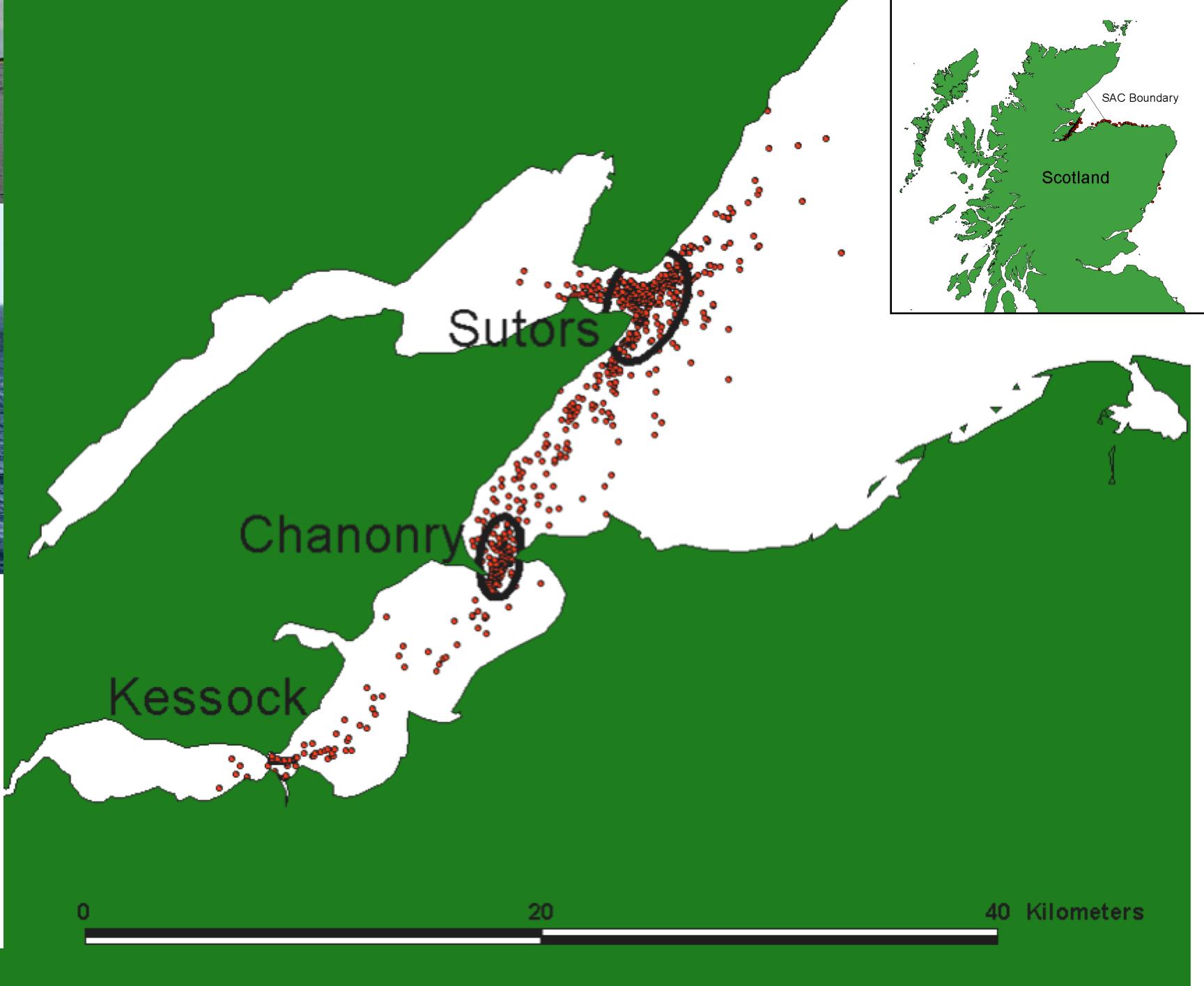


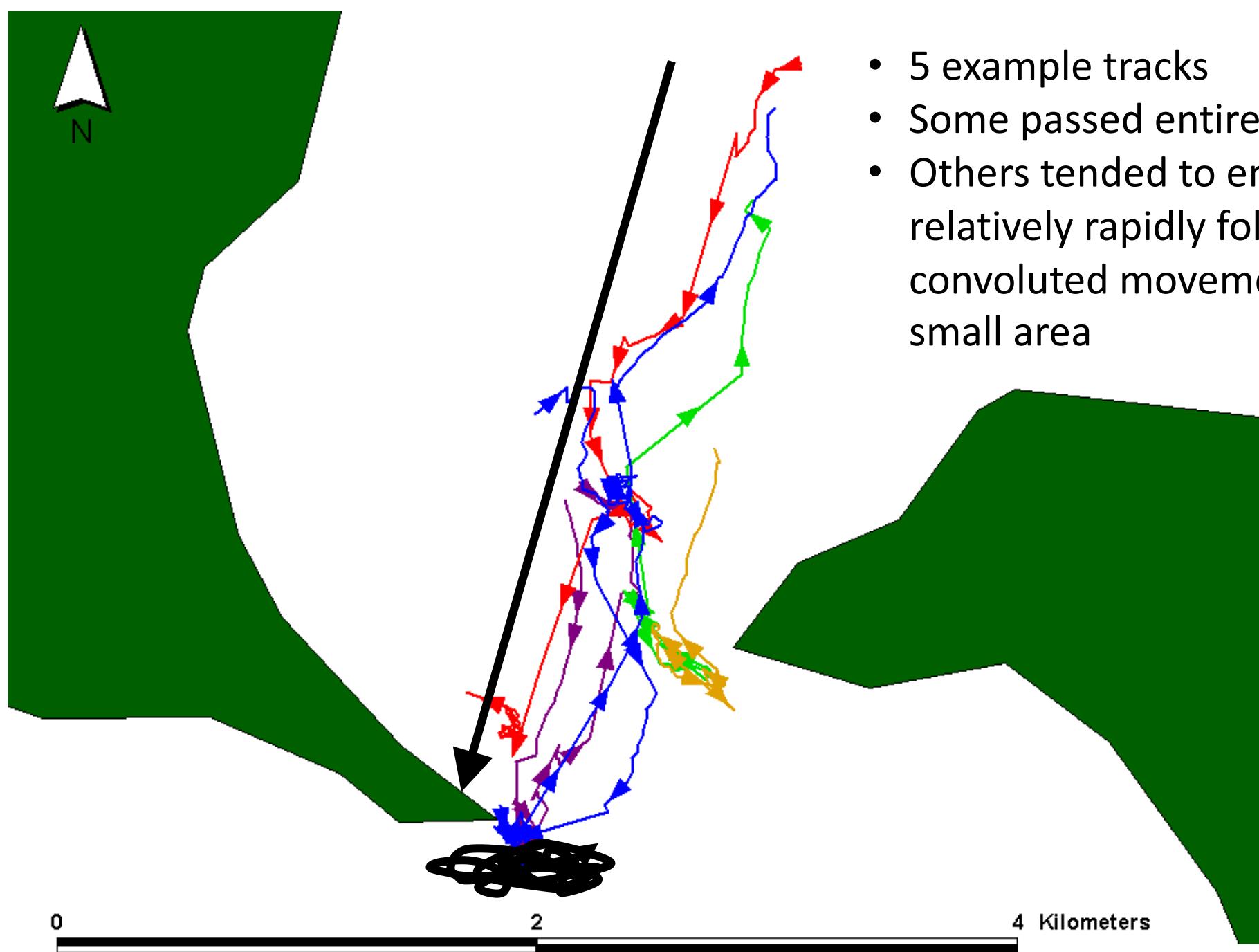
Figure 4.10 Comparison of the progress made by (a) 100 correlated random walks with exponential step lengths and (b) 100 Lévy flights with Cauchy distributed step lengths. Note the change in scales on the vertical axis and that both axes are logarithmic. The roll-off to diffusive behaviour already noted (see Figure 4.8) is clear for the correlated walks but does not occur for Lévy flights.

From Spatial Simulation textbook, p. 110

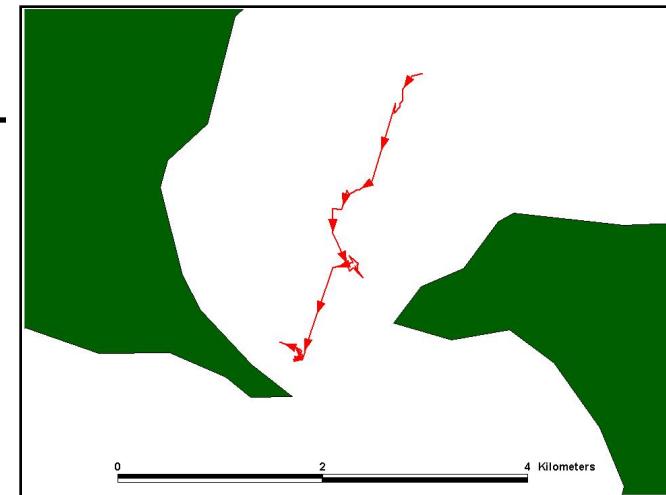
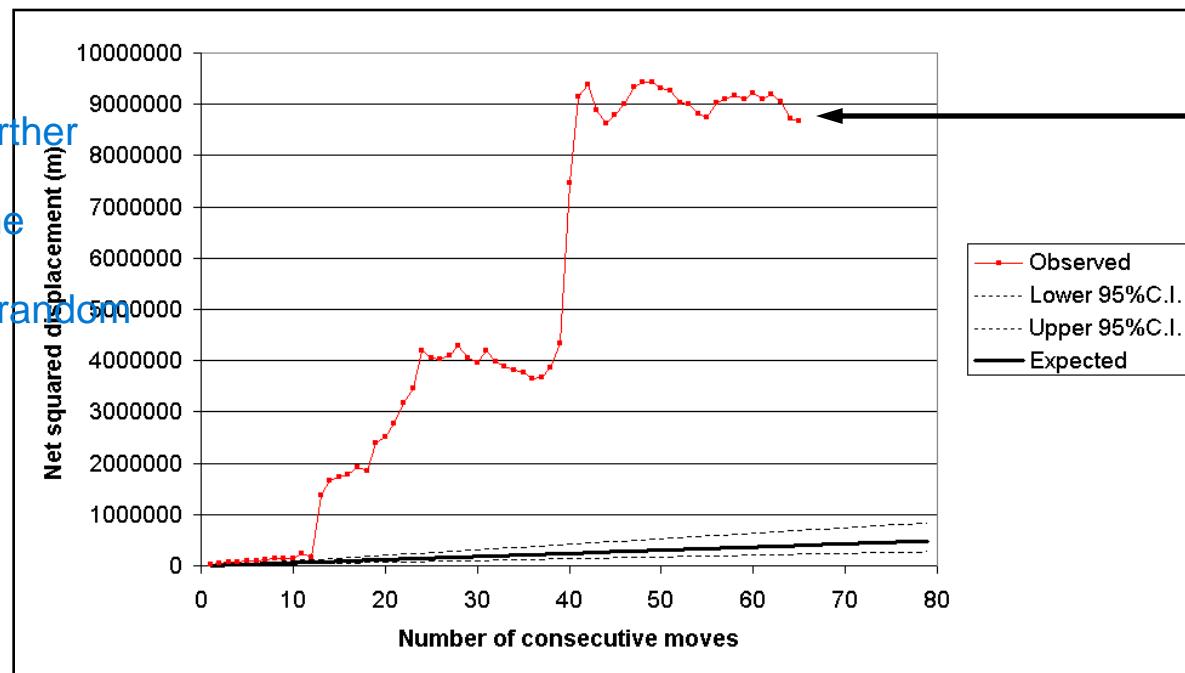


Is the Chanonry area
important for
bottlenose dolphins or
is it just part of a
route?



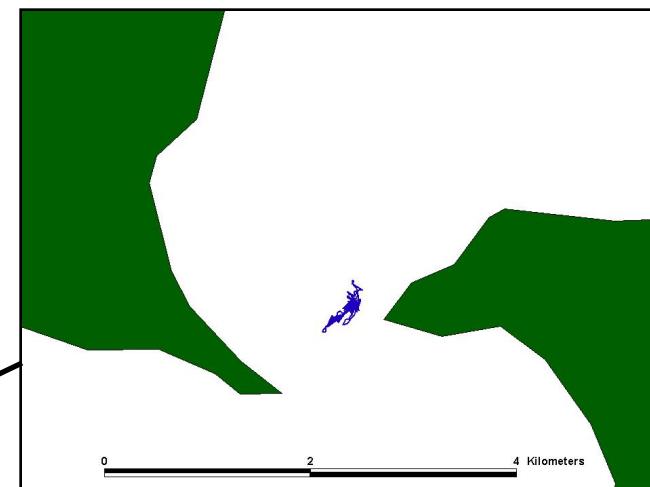
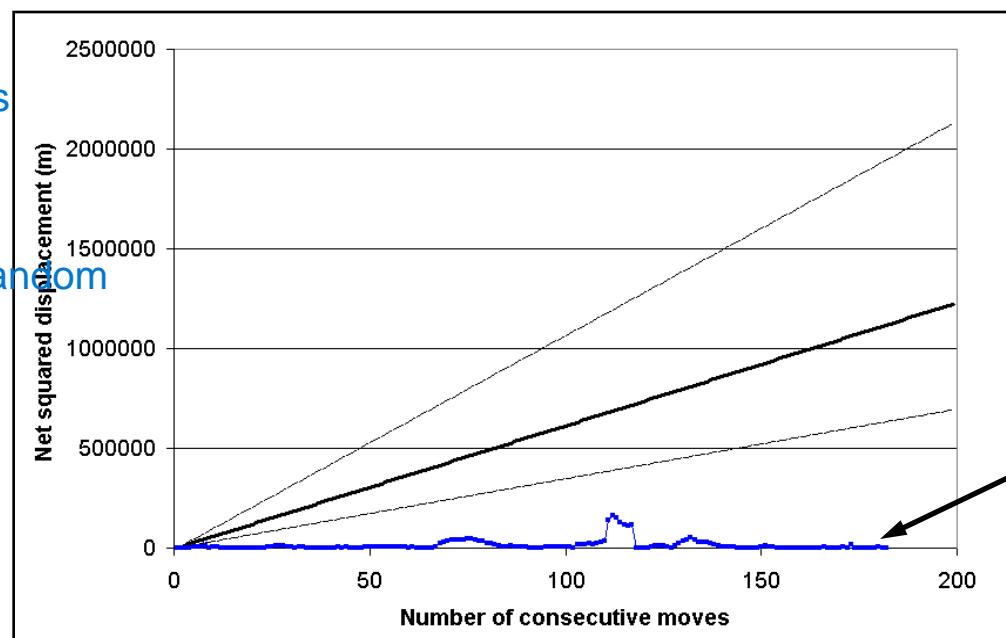


moving way farther
than expected
according to the
expectation by
the correlated random
walk model



Greater displacement
than predicted by CRW

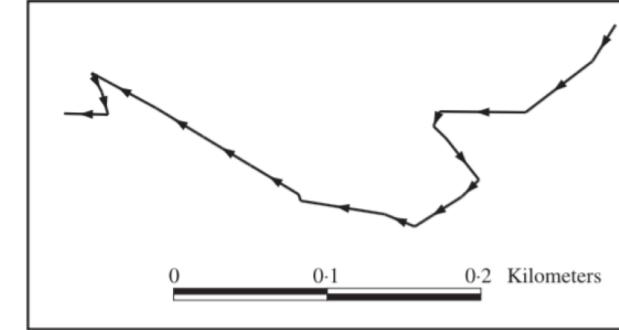
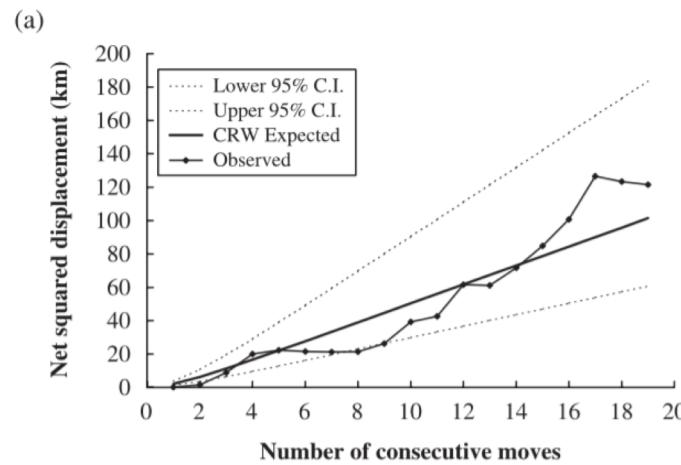
moving way less
than expected
according to the
expectation by
the correlated random
walk model



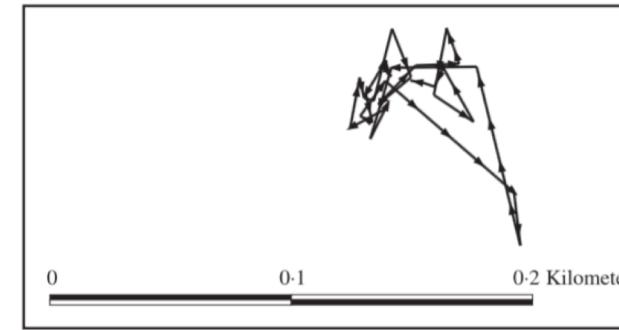
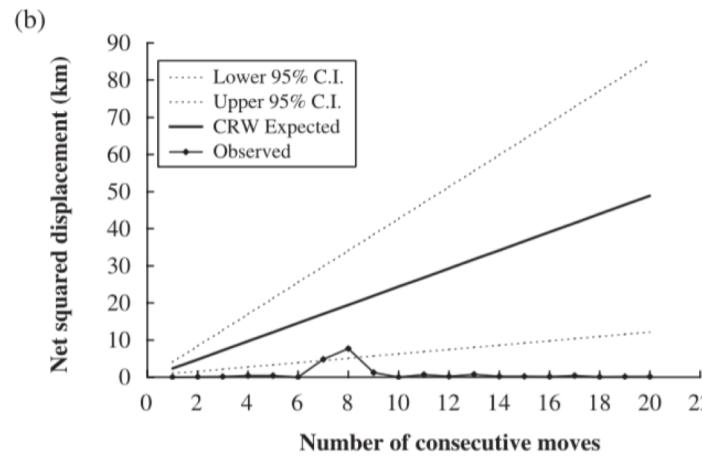
Lower displacement
than predicted by CRW

From Bailey & Thompson 2006

Fits a correlated random walk

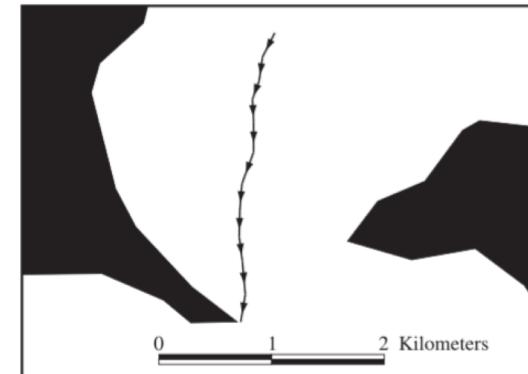
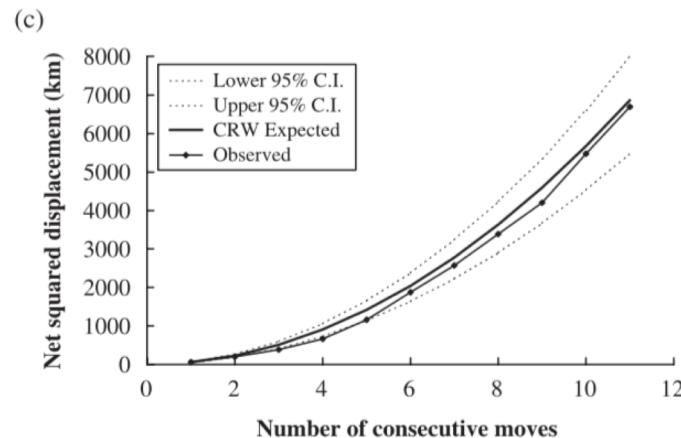


Displacement is lower than expected for a CRW



Fits a biased random walk model

Bailey and Thompson 2006



What is driving these changes in behavior?

Very few of the tracks actually followed a CRW indicating the animals were not moving randomly and were either deliberately remaining in an area or travelling away.



Net squared displacement

$$R_n^2 = nm_2 + 2m_1^2 \left(\frac{c}{1-c} \right) \left(n - \frac{1-c^n}{1-c} \right)$$

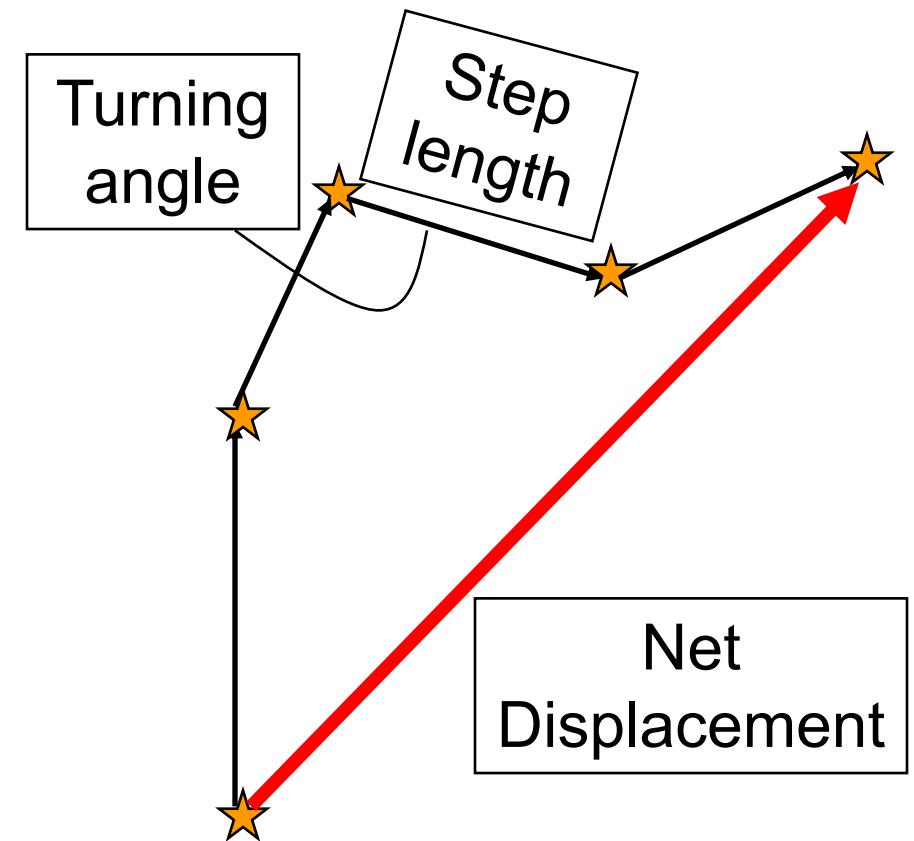
R_n^2 is the net squared displacement

n is the number of moves from the first location

m_1 is the mean step length

m_2 is the mean squared step length

c is the mean of the cosines of the turning angles



BRW Equation

- **Expected net squared displacement for a biased random walk (BRW):**

$$R_n^2 = nm_2 + n(n-1)m_1^2\theta^2$$

R_n^2 is the net squared displacement
n is the number of moves from the first location
 m_1 is the mean step length
 m_2 is the mean squared step length
 θ is the mean cosine of absolute move direction

Lévy Flight Model

$$N(x) \sim x^{-\mu}$$

$N(x)$ is the distribution of step lengths
 x is the step length between positions
 μ is the power law exponent (Levy flights
 $1 < \mu < 3$)