# L4. Animal movement

## OVERVIEW

. L1. Approaches to ecological modelling

. L2. Model parameterization and validation

. L3. Stochastic models of population dynamics (math)

. L4. Animal movement (math + stat)

. L5. Quantitative population genetics (math + stat)

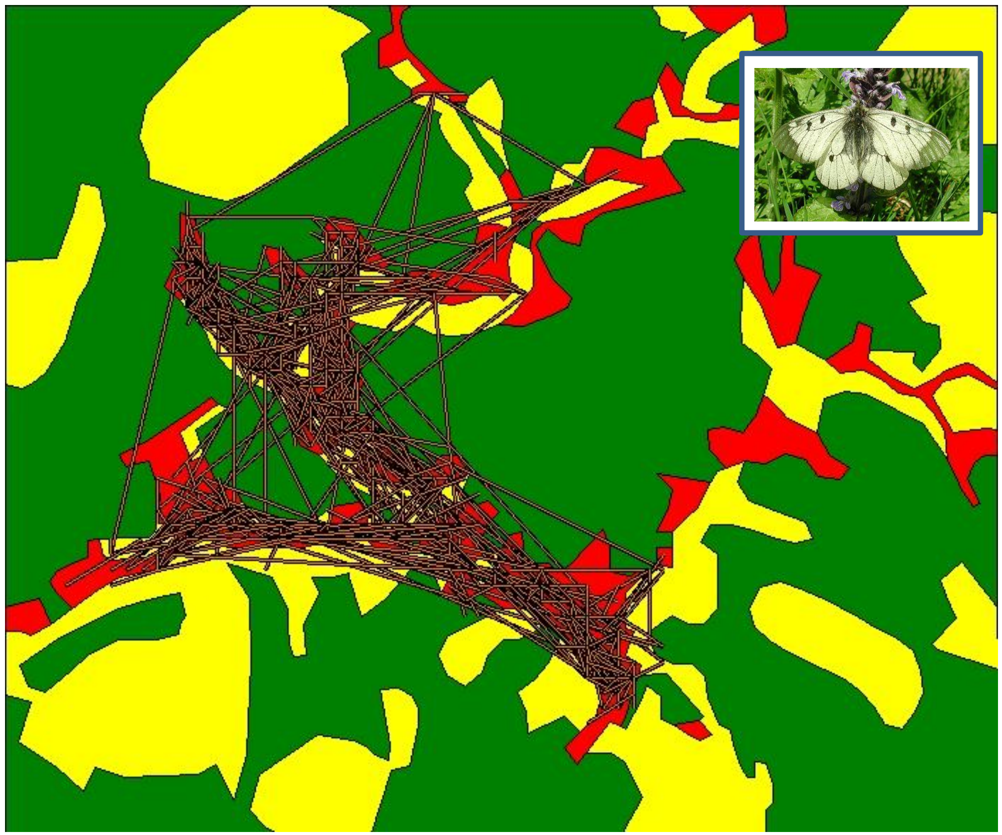
. L6. Community ecology (stat)

# Movement plays a central role in ecology

- All organisms move!
- Understanding movement is central to all questions in spatial ecology, because movement is the process which brings the spatial aspect to population dynamics.
- Applications, such as monitoring, managing, and conserving populations, often require an understanding of movement.
- Habitats are fragmenting – can the organisms move between the fragments?
- Climate is changing – can the organisms move to the areas where climate will be suitable in the future?

Examples of movement data (1/4):

# Mark-recapture data on butterfly movements



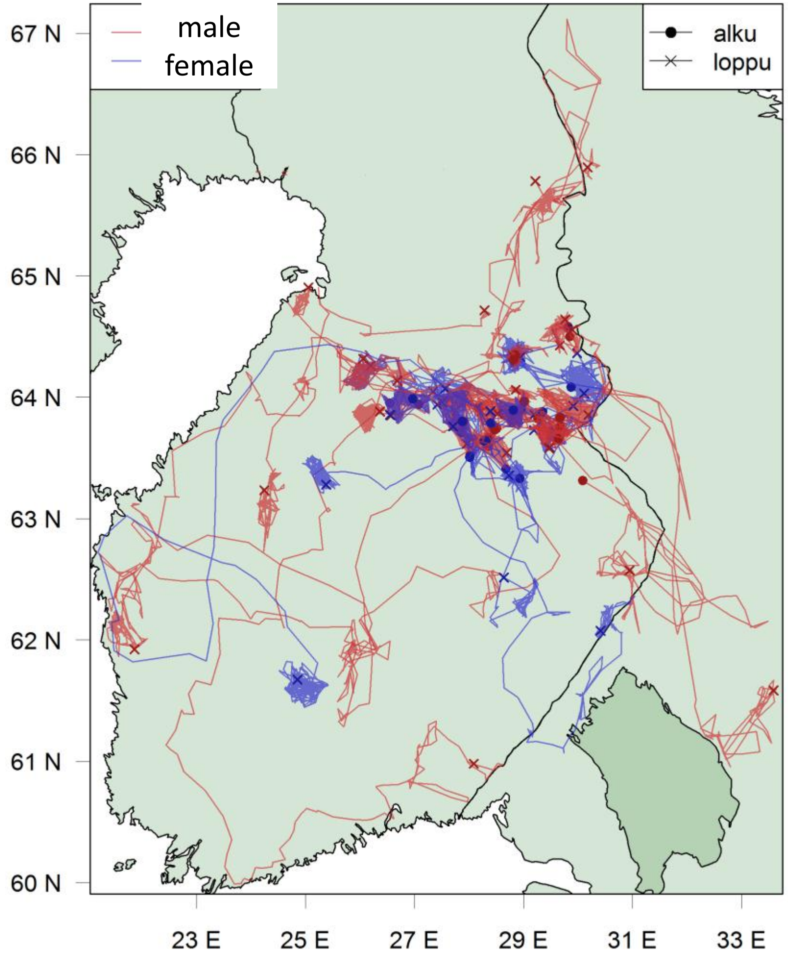

Ovaskainen, Luoto, Ikonen, Rekola, Meyke and Kuussaari 2008. An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *American Naturalist* **171,** 610-619.

Examples of movement data (2/4):

# GPS data on wolf, bear, lynx, moose, forest reindeer, ...



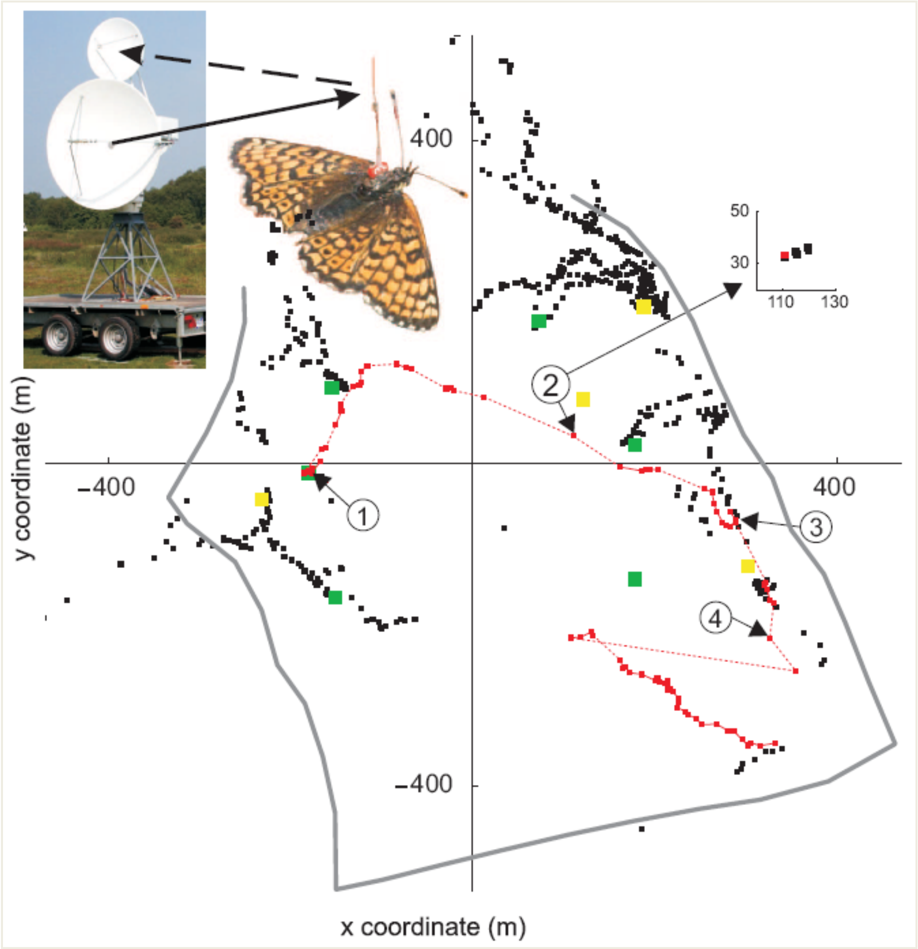
Movements by GPS collared wolves (2002-2008)




Gurarie, Suutarinen, Kojola and Ovaskainen. 2011. Summer movements, predation and habitat use of wolves in human modified boreal forests. *Oecologia* **165**, 891-903.

Examples of movement data (3/4):

# Harmonic radar data on butterfly movements

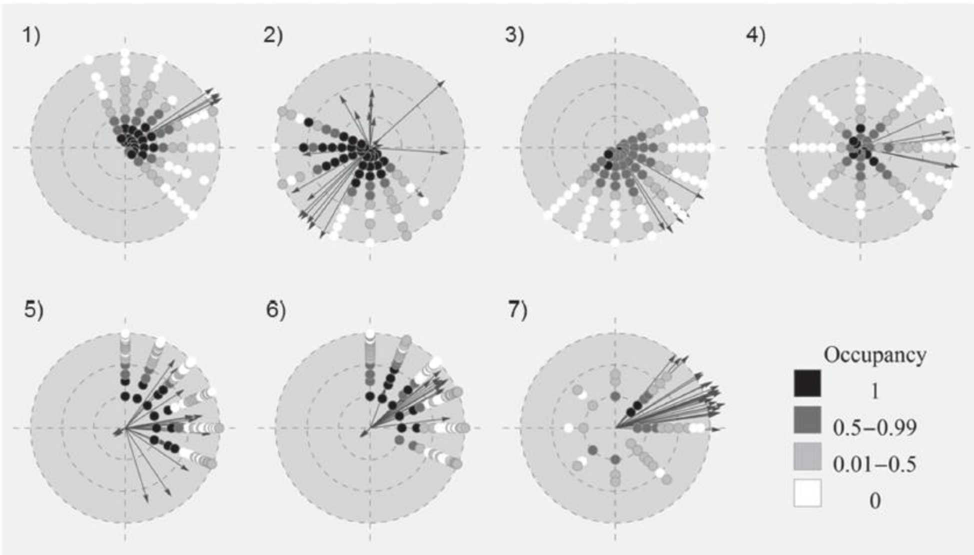



Ovaskainen, Smith, Osborne, Reynolds, Carreck, Martin, Niitepõld and Hanski 2008. Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. *PNAS* **105**, 19090-19095.

Examples of movement data (4/4):

# Data on fungal spore dispersal

Dispersal data




Creating a point source

Sampling with a
cyclone sampler ->
DNA based molecular
species identification

Species-specific spore traps

*Norros et al. 2012, Oikos*
*Hussein et al. 2013,*
*J. Aerosol Science*
*Norros et al. 2014, Ecology*

# How do organisms move in a heterogeneous landscape?

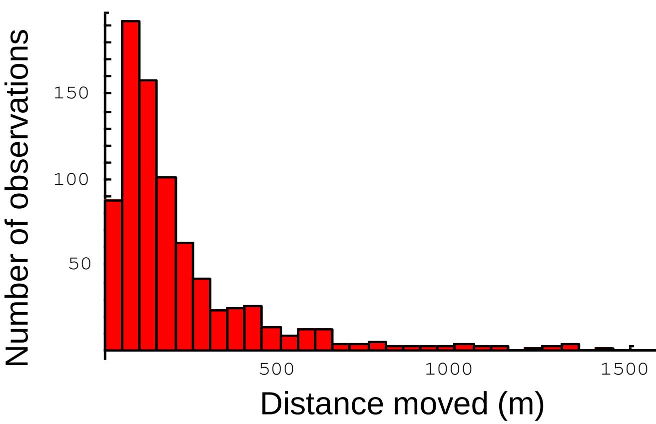
# What is the movement rate of a butterfy?

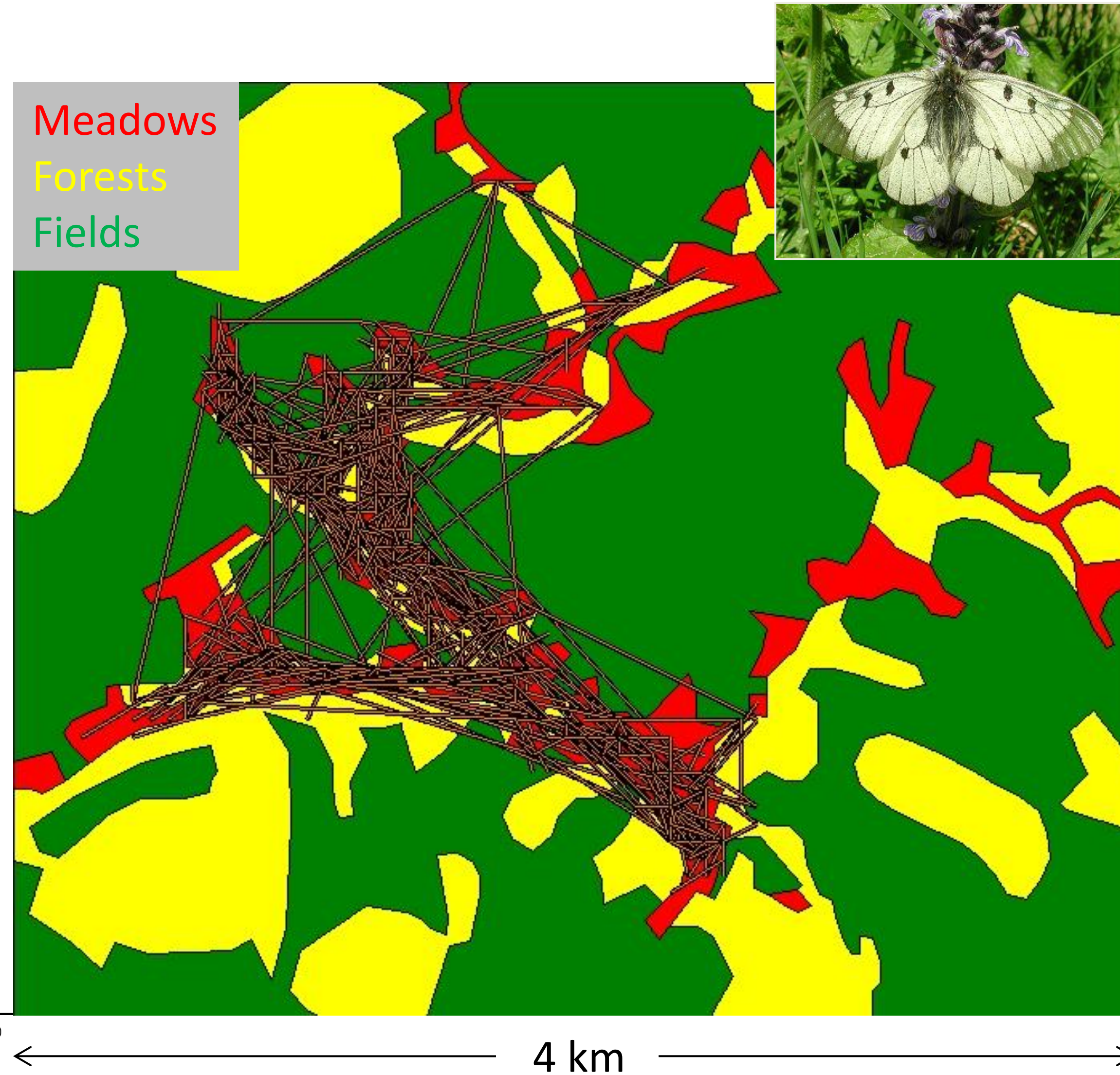
**Spatial mark-recapture data depend on**

i) the properties of the species

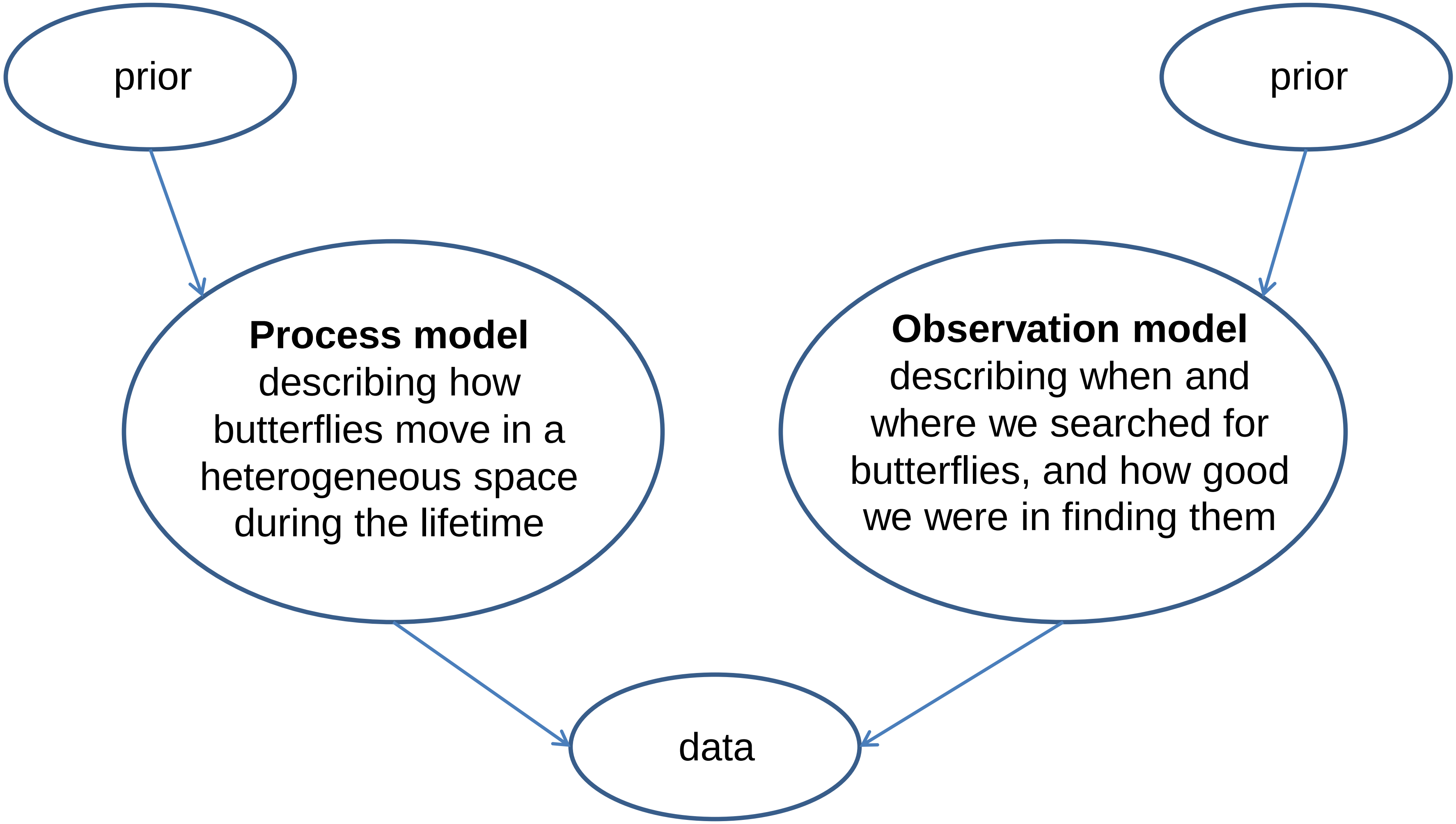
ii) the structure of the landscape

iii) the design of the study

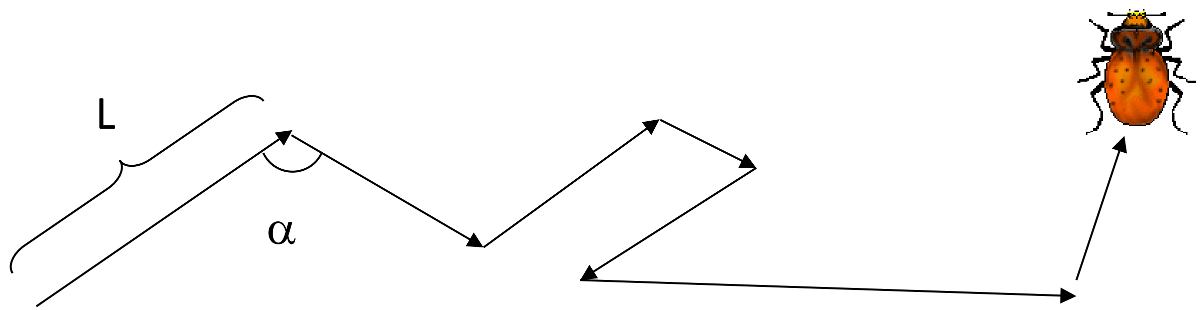


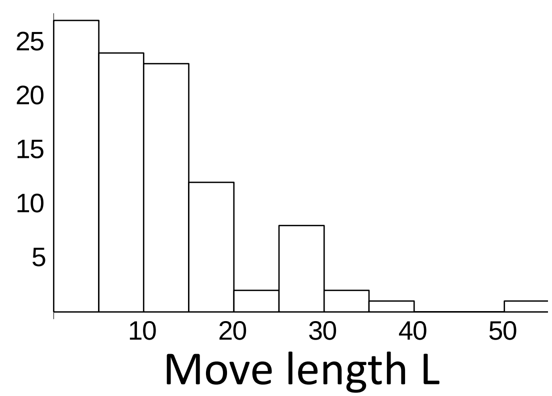



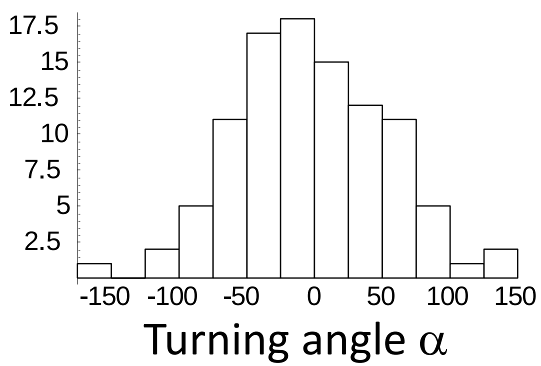
# Bayesian state-space approach



# Animal movements in homogeneous space: random walks and their diffusion approximations



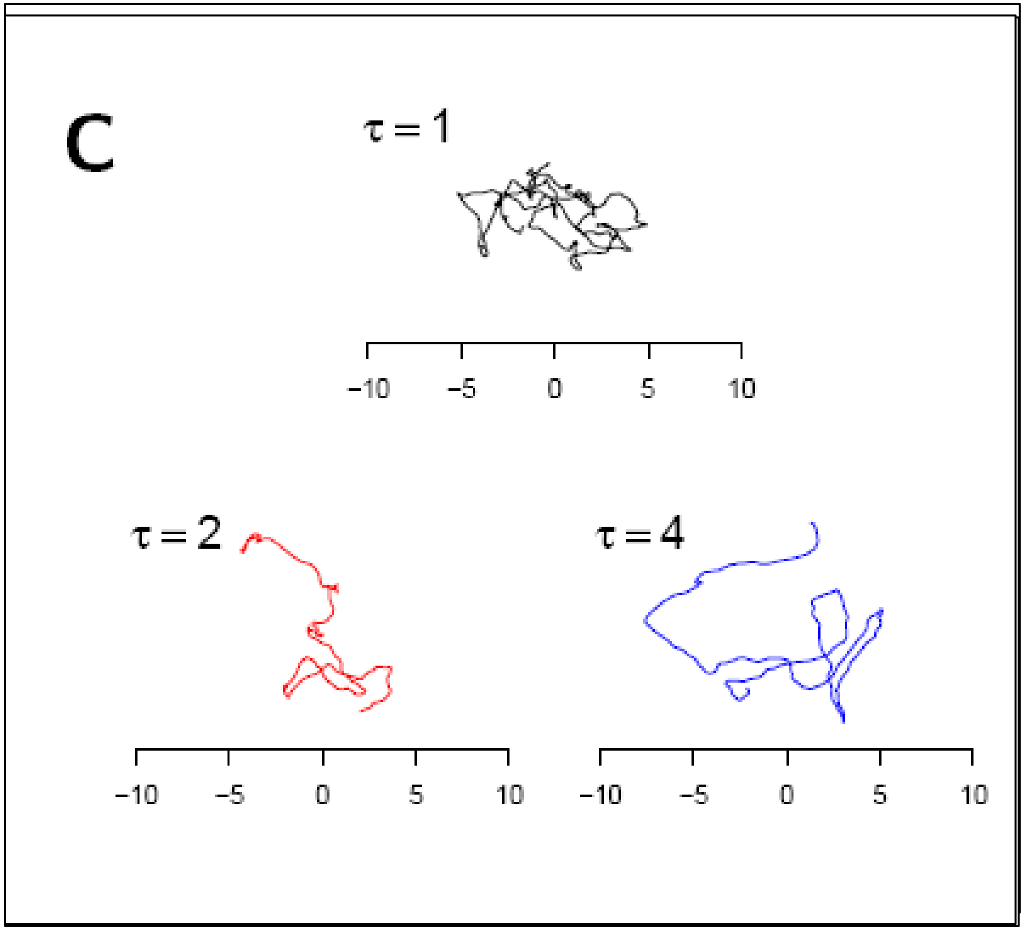
# What is the right movement model?

Diffusion, correlated random walk, stochastic differential equation models, Lévy flights, individual based simulation models...

**Model A:** Correlated random walk in discrete time

**Model B:** Correlated random walk in continuous time

**Model C:** The Ornstein-Uhlenbeck model for velocity



# How much do the model specific details matter?

**Often not very much!**

Gurarie, E. and Ovaskainen, O. 2011. Characteristic spatial and temporal scales unify models of animal movement. *American Naturalist* **178**, 113-123

Key parameters: $(\sigma, \tau)$

Spatial and temporal scales of movement

$$D = \frac{\sigma^2}{4\tau}$$

Diffusion coefficient

# Characteristic scales of movement determine model behavior at small and large time scales

At long time scales, a broad range of movement models lead to diffusion:

$$<|\mathbf{z}(t)-\mathbf{z}(0)|^2>=4Dt$$

At short time scales, movement behaviour can be characterized by the velocity autocorrelation function:

$$C_V(\Delta t)=\frac{<\mathbf{v}(t+\Delta t)\cdot\mathbf{v}(t)>}{<|\mathbf{v}(t)|^2>}\approx \exp(-\Delta t/\tau)$$

Characteristic spatial and temporal scales of movement $(\sigma,\tau)$ ,with $\sigma=2\sqrt{D\tau}$ , are sufficient for describing many essential aspects of movement, such as encounter rates.

Gurarie, E. and Ovaskainen, O. 2011. Characteristic spatial and temporal scales unify models of animal movement. *American Naturalist* **178**, 113-123

# Matching models in terms of the characteristic scales

Key parameters: $(\sigma, \tau)$

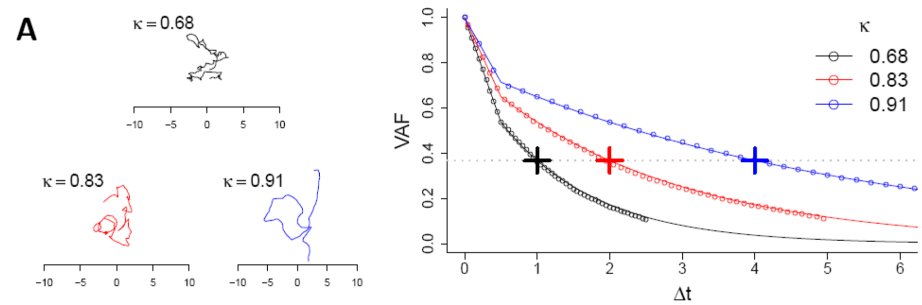
Spatial and temporal scales of movement

$$D = \frac{\sigma^2}{4\tau}$$

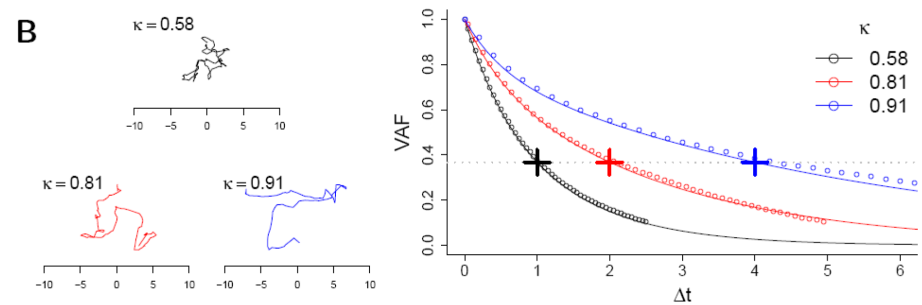
Diffusion coefficient

VAF = velocity autocorrelation function

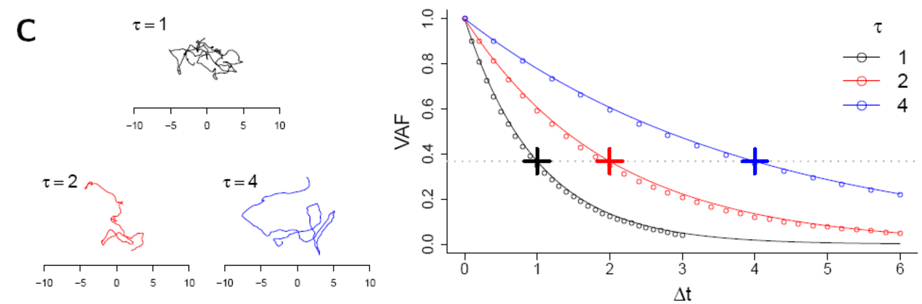
**Model A:** Correlated random walk in discrete time



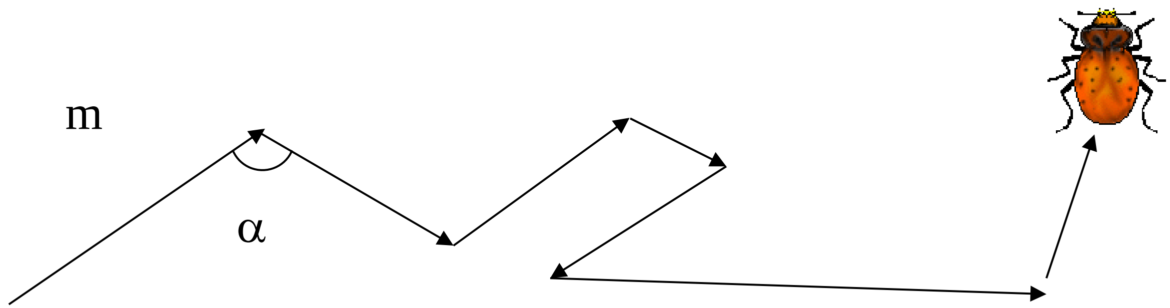

**Model B:** Correlated random walk in continuous time

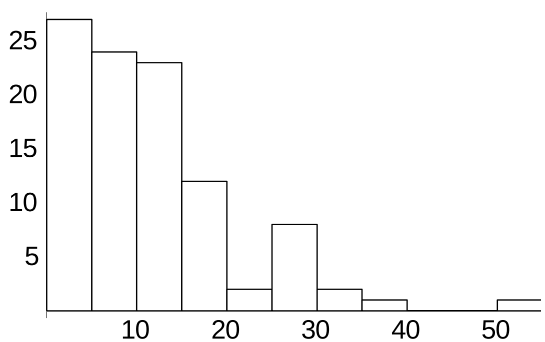



**Model C:** The Ornstein-Uhlenbeck model for velocity

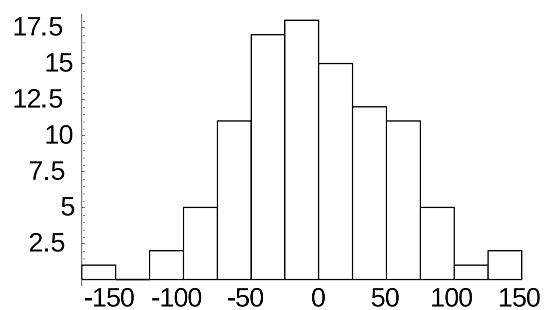


# From random walk to diffusion




Move length m




Turning angle α

Patlak 1953:

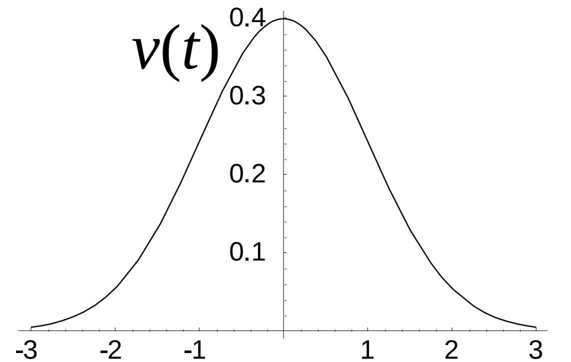
# At long time scales, correlated random walk can be approximated by diffusion

Let $v=v(x,y;t)$ be the probability that the individual is at location $(x,y)$ at time $t$. Then $v$ evolves as

$$\frac{\partial v}{\partial t} = D\Delta v - \mu v$$

Diffusion coefficient — mortality

(integrates the information on movement characteristics)

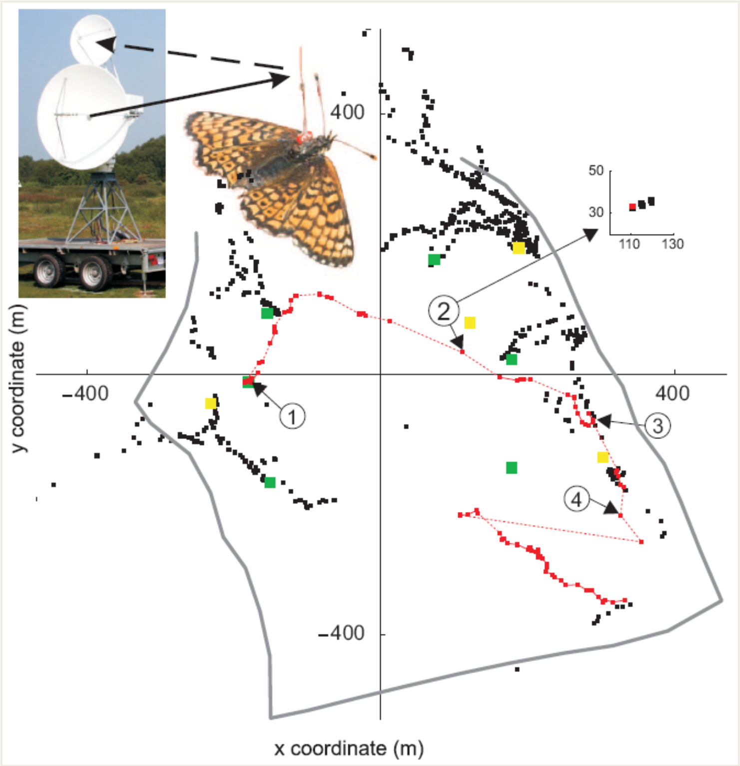


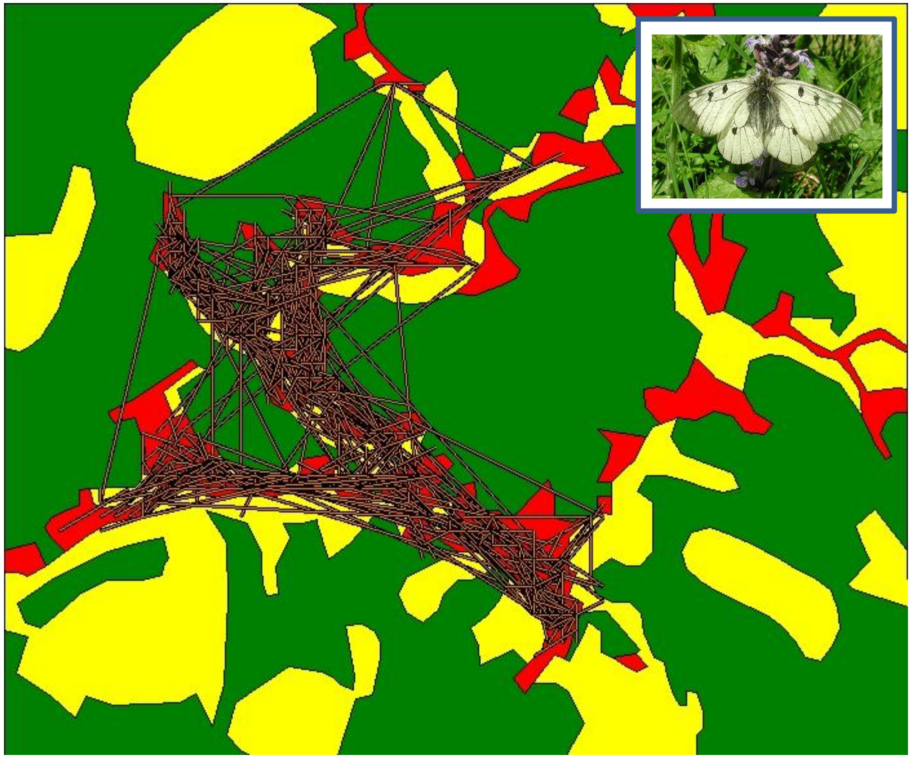

release point

# The choice of model complexity depends on the data and on the question

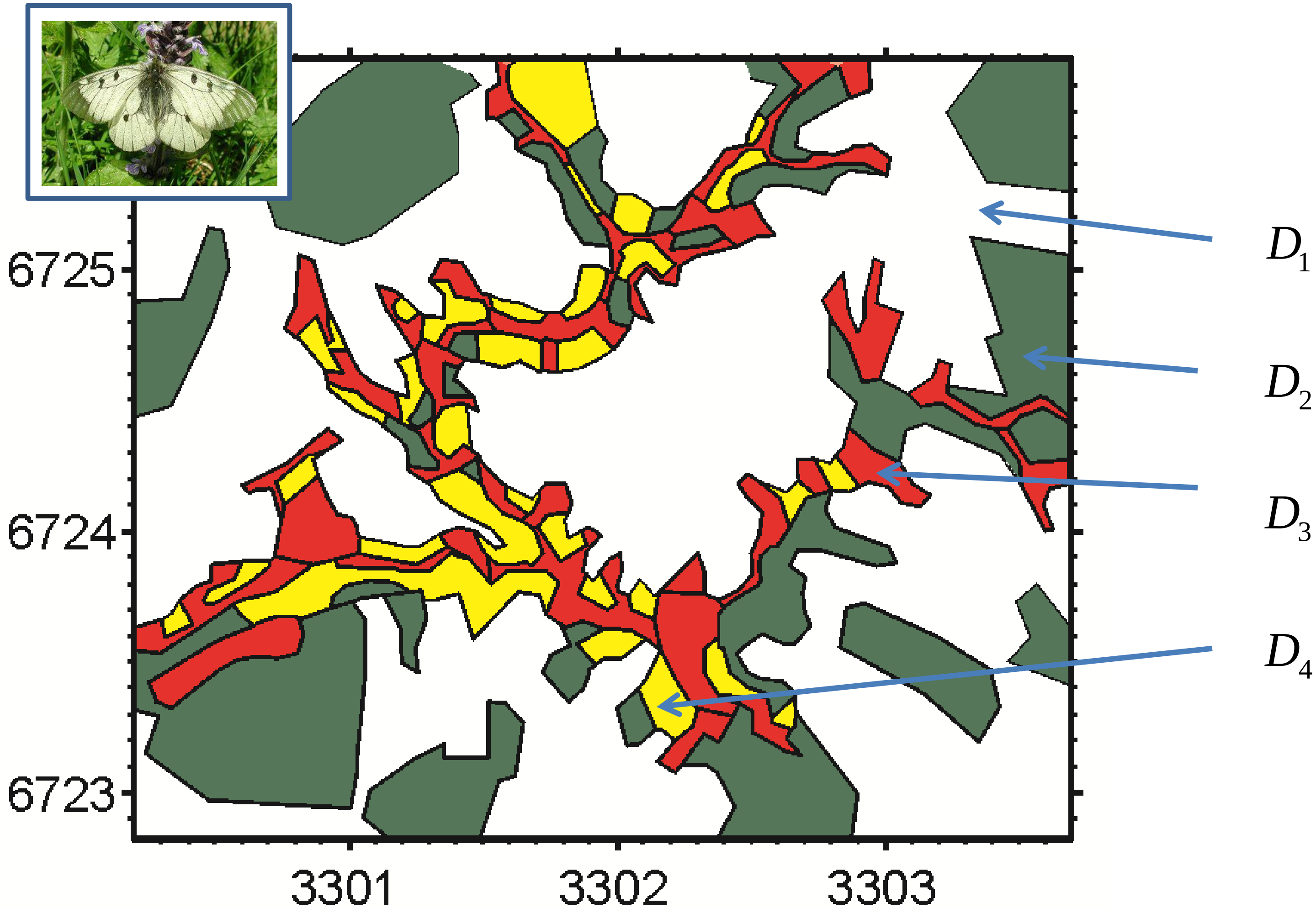
$$(\sigma, \tau)$$

$$D = \frac{\sigma^2}{4\tau}$$



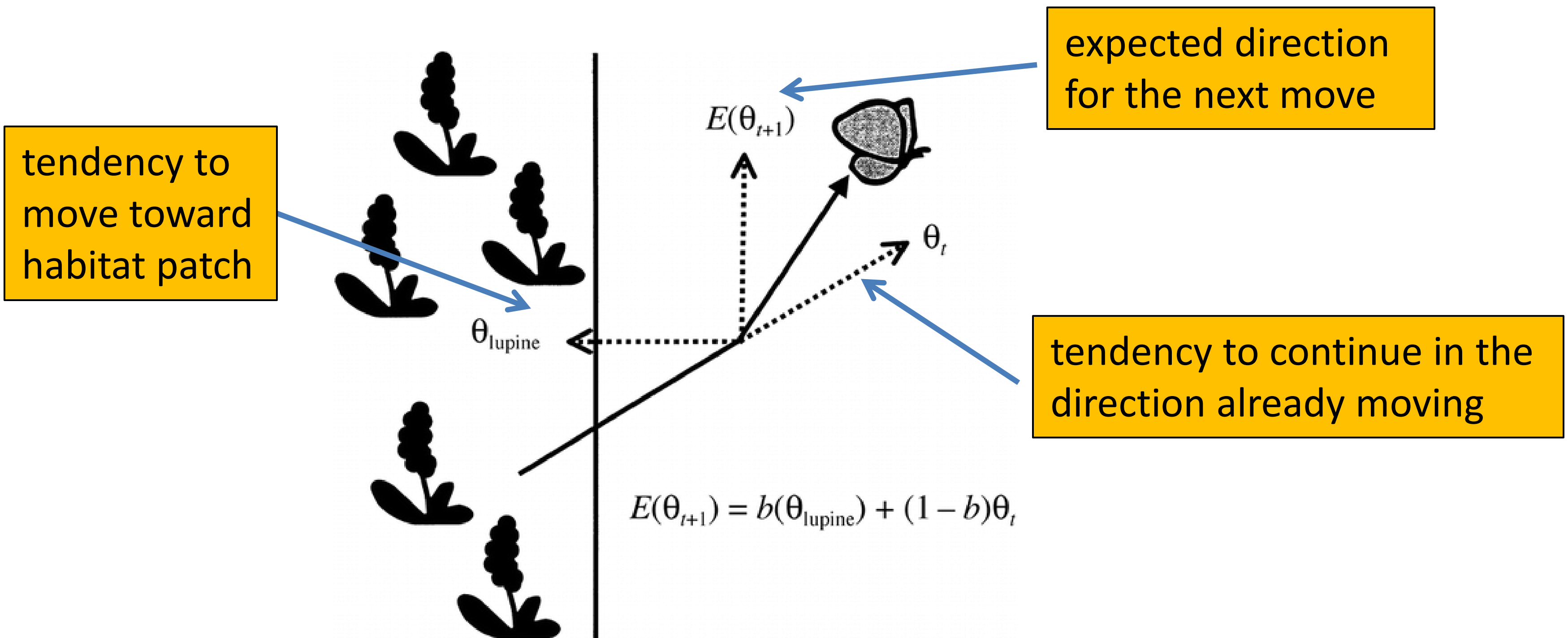



# Animal movement in heterogeneous space



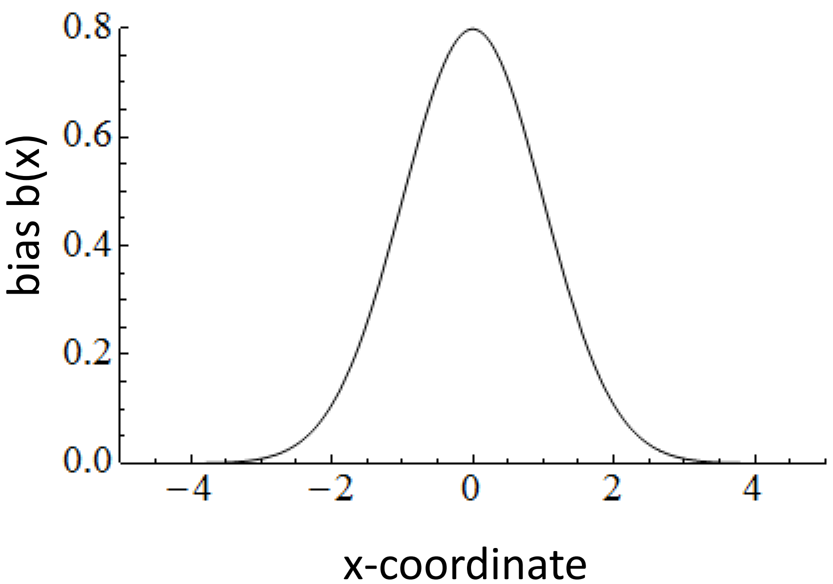

$$\frac{\partial v}{\partial t} = Lv, \qquad Lf(\mathbf{x}) = \sum_{i,j} \partial_{ij}[a_{ij}(\mathbf{x}) f(\mathbf{x})] + \sum_i \partial_i [b_i(\mathbf{x}) f(\mathbf{x})] - c(\mathbf{x}) f(\mathbf{x}).$$

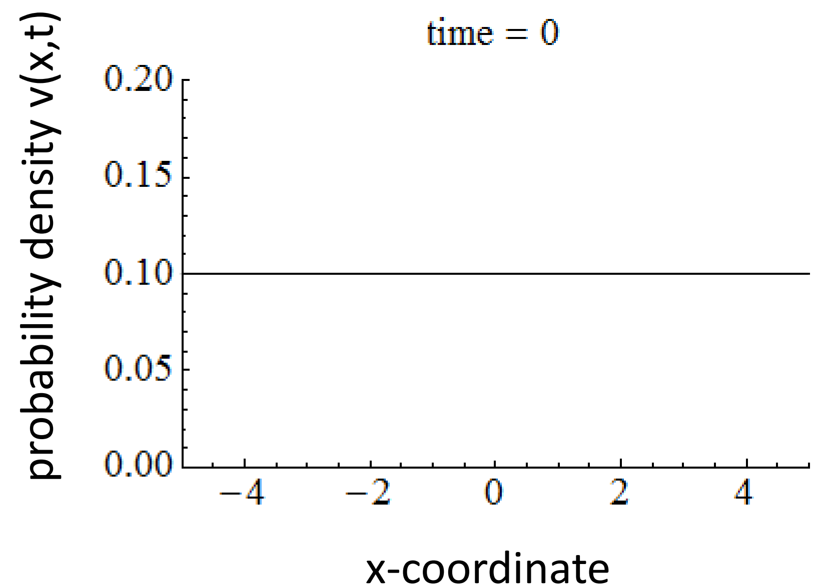
# Edge-mediated behavior (habitat selection at edges)




Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* **82**, 1879-1892.

# Edge-mediated behaviour pushes the individual towards the preferred habitat




← EDGE → 

PATCH MATRIX

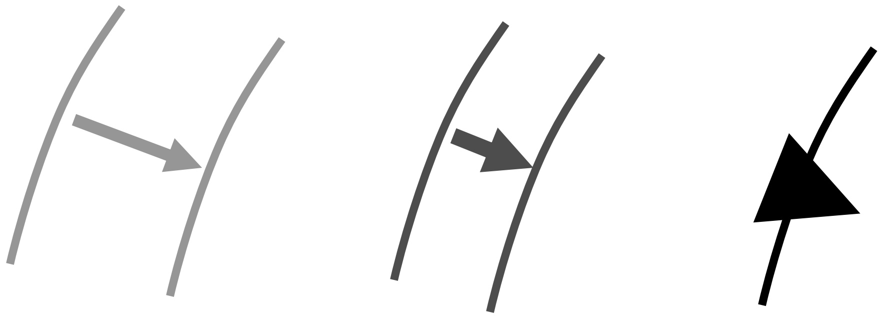
← EDGE →

PATCH MATRIX

Ovaskainen, O. and Cornell, S. J. 2003. Biased movement at a boundary and conditional occupancy times for diffusion processes. *Journal of Applied Probability* **40**, 557-580.

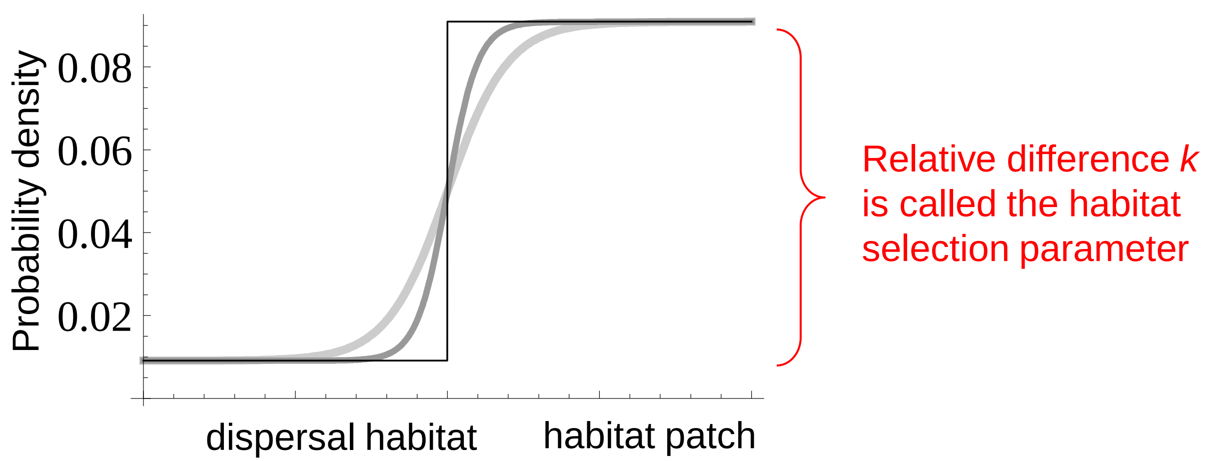
# Model simplification by a scaling limit

*1-dimensional approximation of the 2-dimensional model*



Matching condition: discontinuous probability density, continuous flux

(Ovaskainen & Cornell, Journal of Applied Probability 2003)



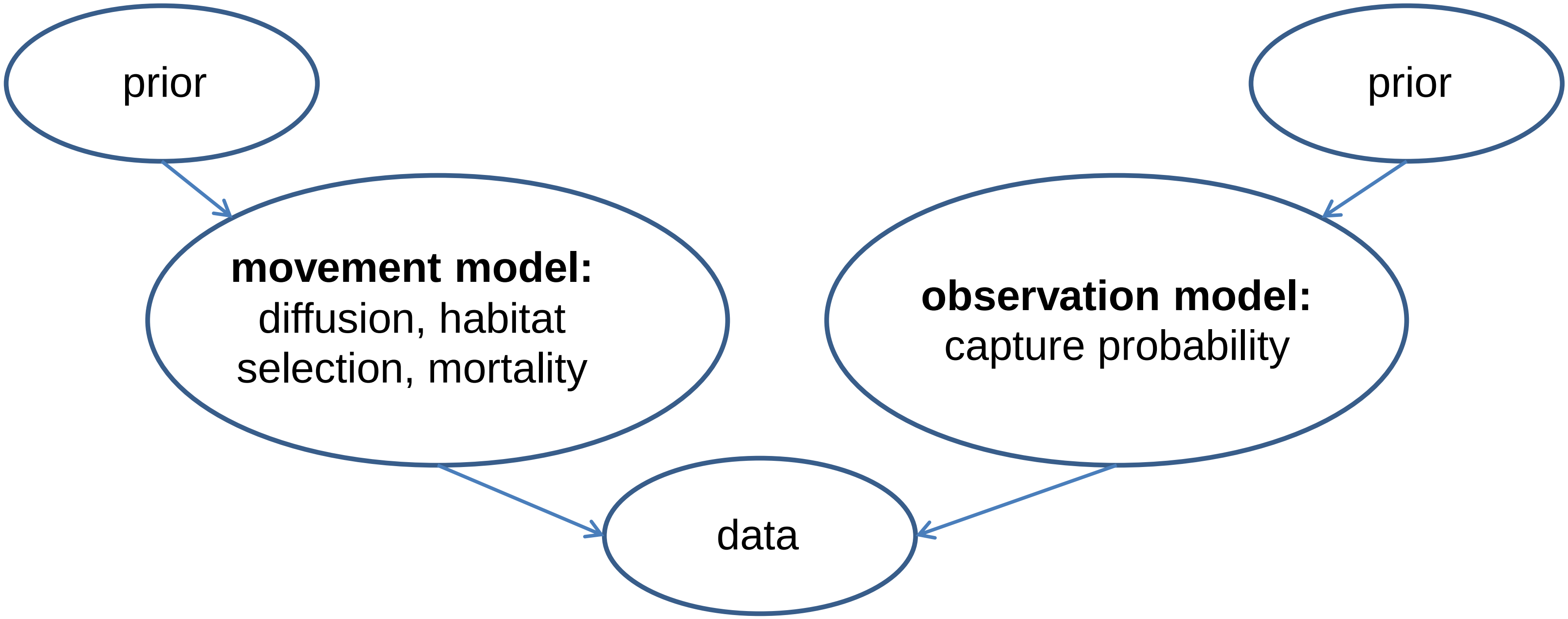
# Observation model: also searching but not finding gives information

The capture probability *p* is the probability of observing an individual given that it actually is at the site

| | site | somewhere else |
|---|---|---|
| Probability that an individual is in a site before the search | $\boldsymbol{x}$ | $1-x$ |
| Probability that an individual is in the site after the site is searched for (without finding the individual) | $\boldsymbol{\frac{x(1-p)}{1-px}}$ | $\frac{1-x}{1-px}$ |

Ovaskainen, O. 2004. Habitat-specific movement parameters estimated using mark–recapture data and a diffusion model. *Ecology* **85**, 242-257.

# Model fitting with Bayesian inference



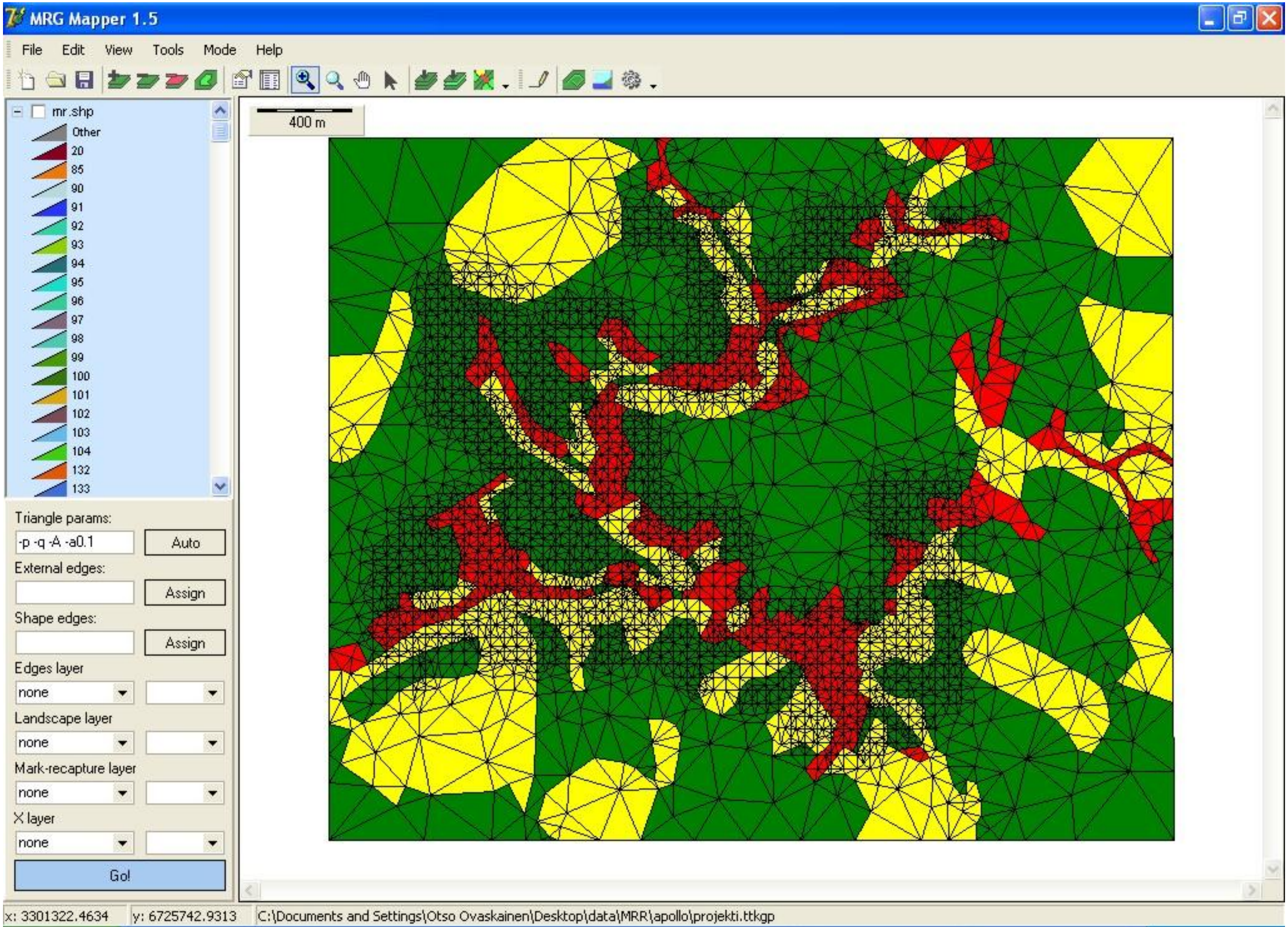

**Technical details on computation of likelihood and MCMC sampling:**

Ovaskainen, O. 2004. Habitat-specific movement parameters estimated using mark–recapture data and a diffusion model. *Ecology* **85**, 242-257.

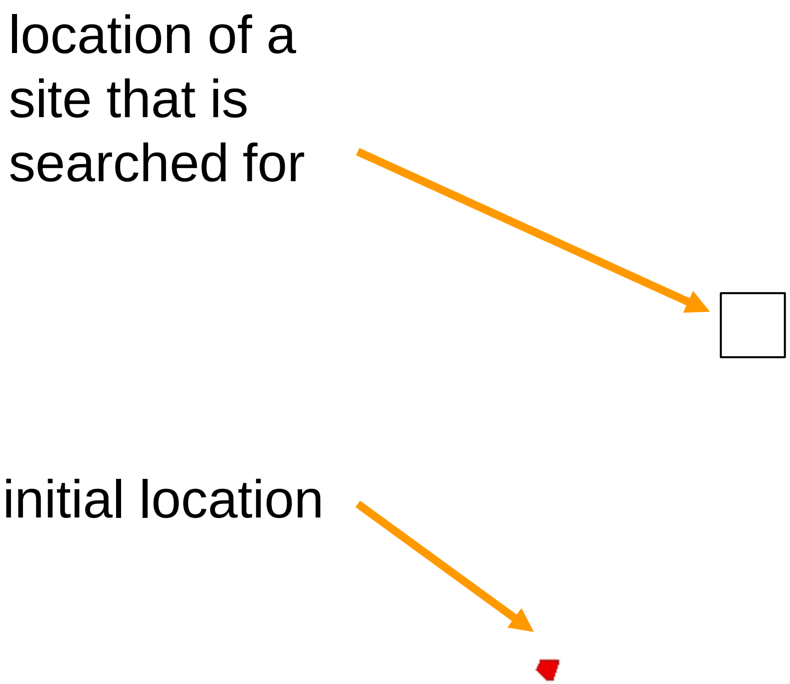
Ovaskainen, O., Rekola, H., Meyke, E. and Arjas, E 2008. Bayesian methods for analyzing movements in heterogeneous landscapes from mark-recapture data. *Ecology* **89**, 542-554.

Ovaskainen, O.  2008. Analytical and numerical tools for diffusion based movement models. *Theoretical Population Biology* **73**, 198-211.

# Solving the diffusion model numerically

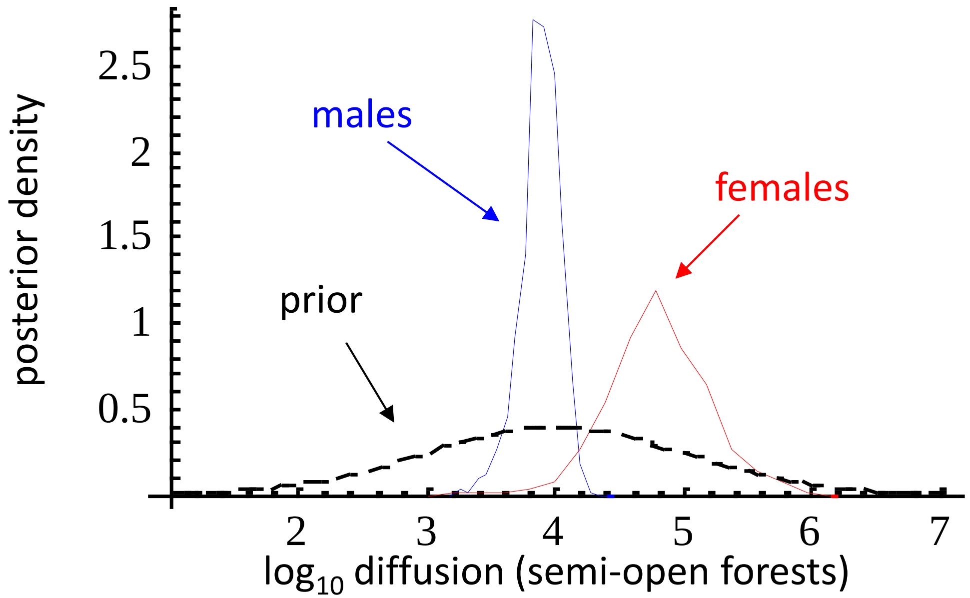


# Simulating the time-evolution of the probability density



# Example of biological inference

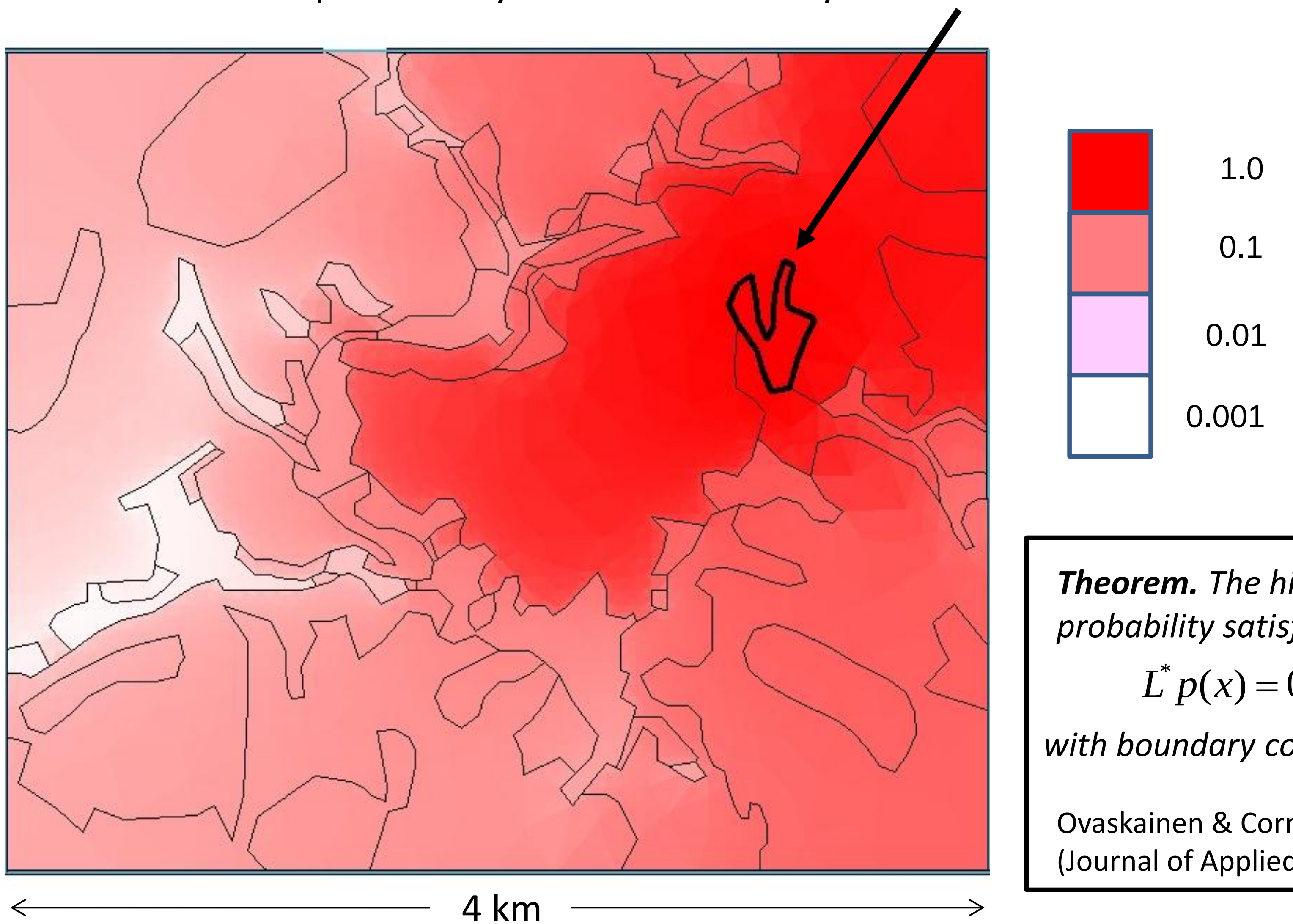
Females move faster than males outside the breeding habitat




Ovaskainen, O. et al. 2008. An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *American Naturalist* **171,** 610-619.

# Example of model prediction

What is the probability that the butterfly ever visits this meadow?




***Theorem.*** *The hitting probability satisfies*

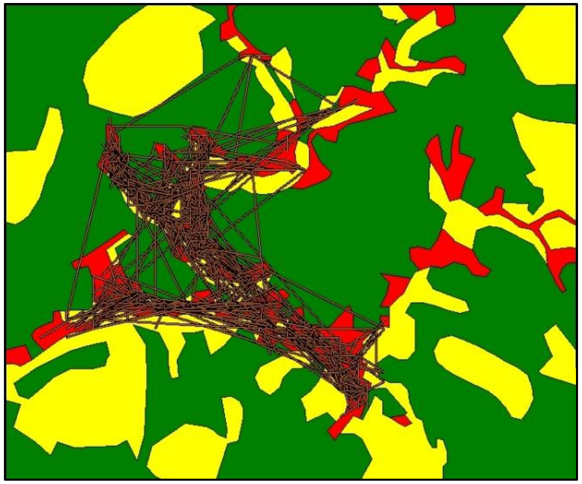
$$L^* p(x) = 0$$

*with boundary condition* $B^{C_{1*}}$

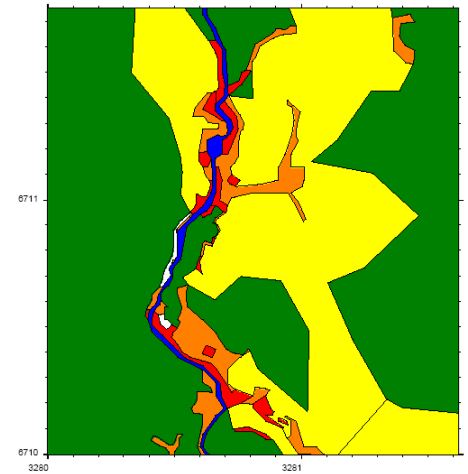
Ovaskainen & Cornell 2003
(Journal of Applied Probability)

# Example of model validation

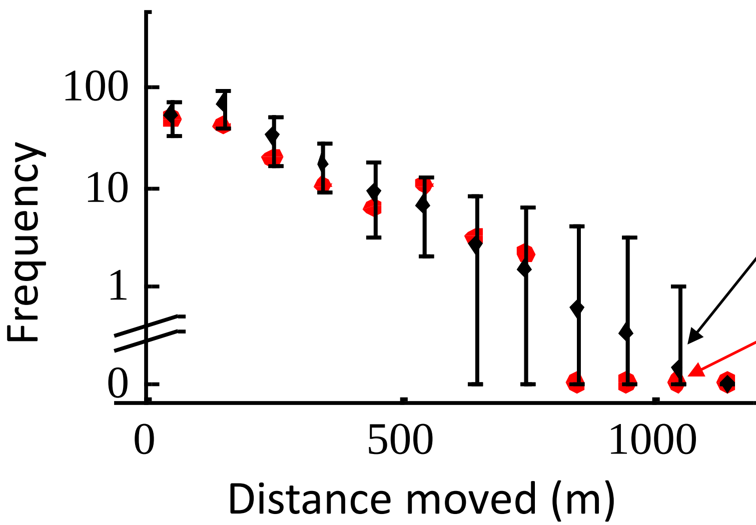
Landscape A



prediction



Landscape B



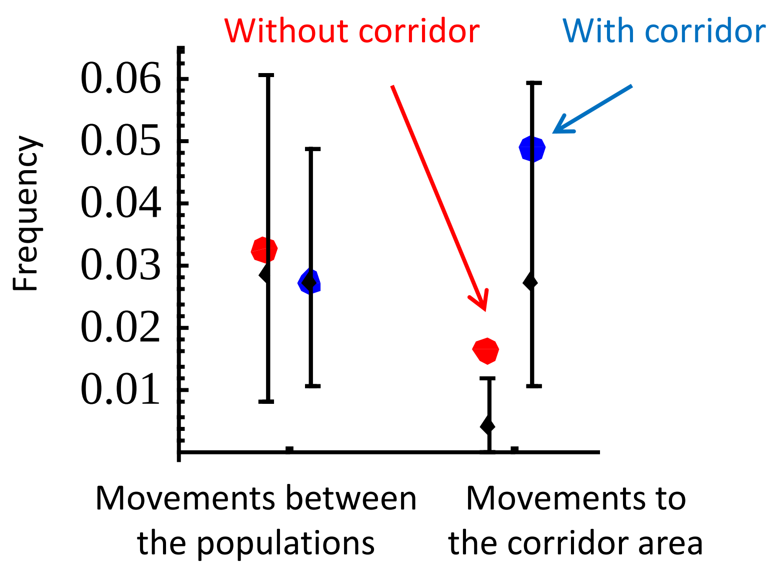

Model parameterized with data from Landscape A, prediction for Landscape B

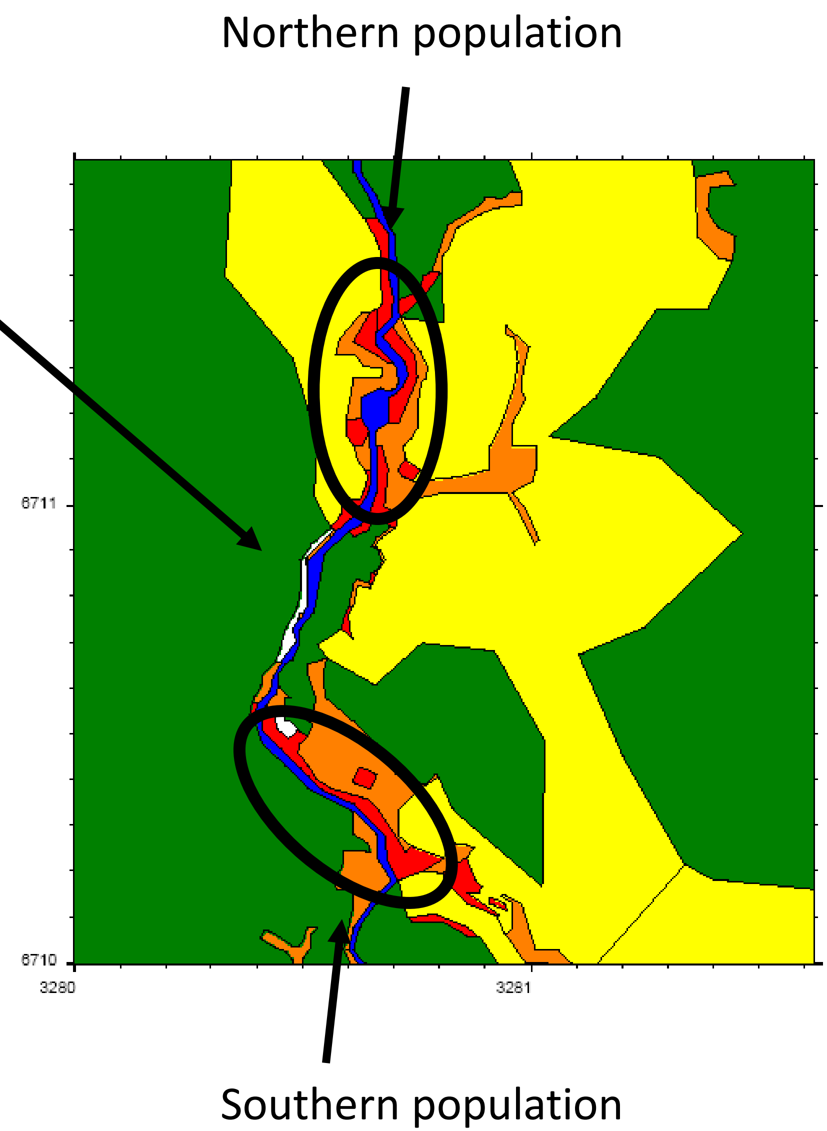
Empirical data on Landscape B

Ovaskainen, O., Luoto, M., Ikonen, I., Rekola, H., Meyke, E. and Kuussaari, M. 2008. An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *American Naturalist* **171,** 610-619.

# The effect of a movement corridor

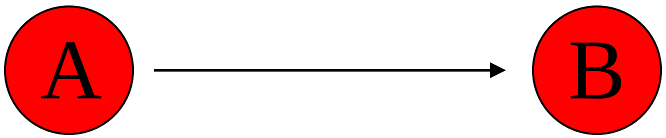
A movement corridor was cut through the forest



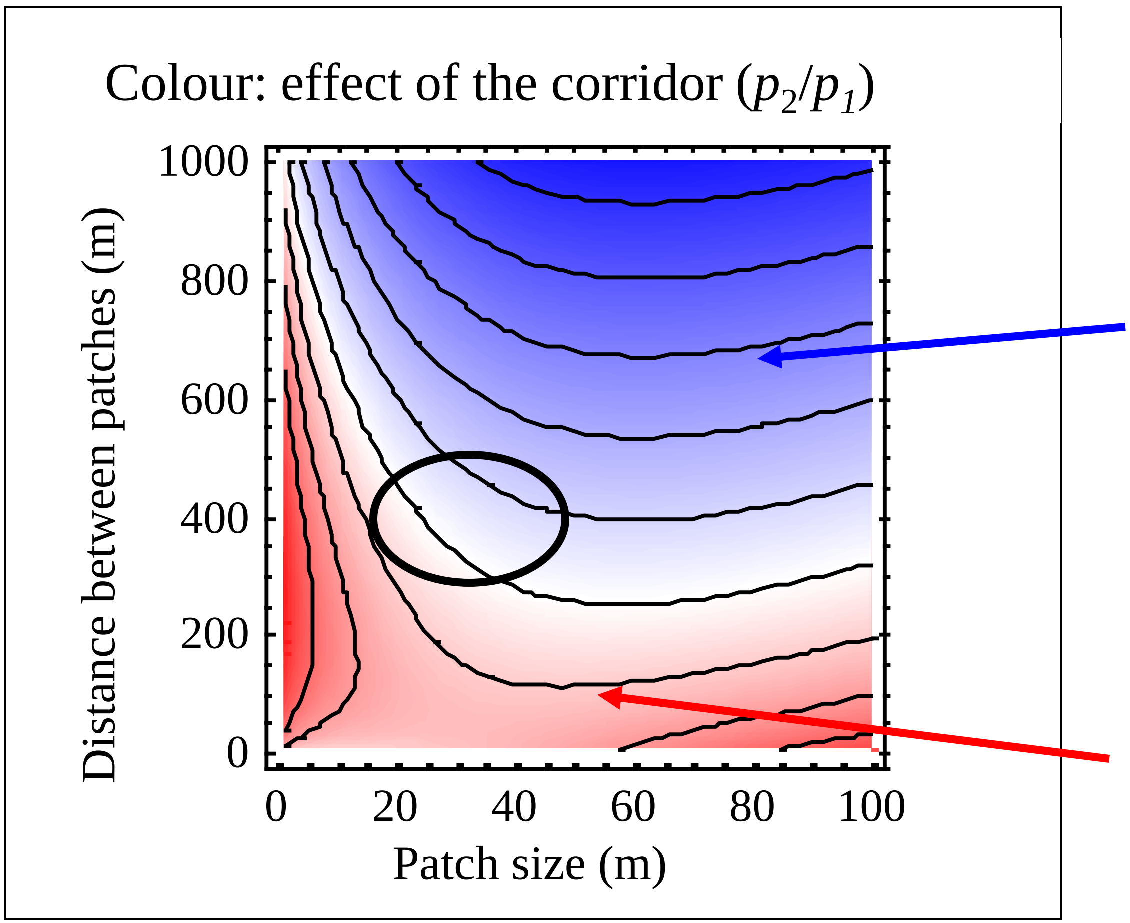



# What kind of a corridor would increase movements?

Movement probability $p_1$




Movement probability $p_2$


Corridor decreases movements ($p_2<p_1$)

Corridor increases movements ($p_2>p_1$)

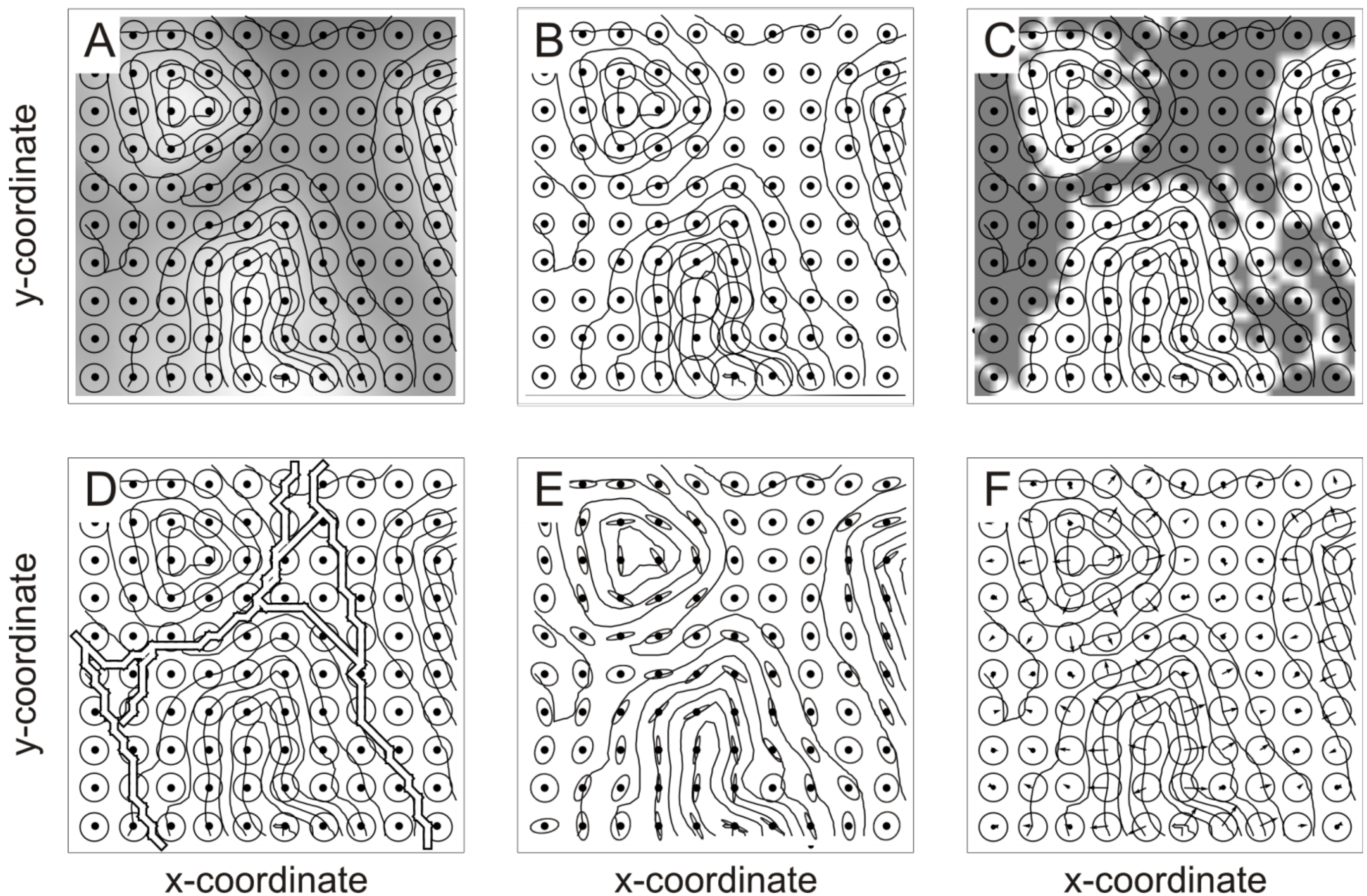
# Building biological assumptions in diffusion models: hypothetical movements in a mountainous landscape

Colour: habitat preference (the darker the better)

Ellipse: diffusion

Arrow: advection

Preference depends on altitude | Diffusion depends on altitude | Preference for forest over rocks




Roads as corridors | Anisotropy depends on slope | Advection downhill

Ovaskainen and Crone 2010. Modeling animal movement with diffusion. In "*Spatial Ecology*" (S. Cantrell, C. Cosner, S. Ruan, eds). Chapman and Hall/CRC Mathematical & Computational Biology)

# L4: take home messages

- Advances in tracking technology have lead to a massive increase in the amount and quality of movement data.
- Much of the movement data acquired for small organisms are still indirect in the sense that they do not include entire tracks. With such data, it is important to account for the observation method when parameterizing movement models.
- Diffusion-advection-reaction models provide a simple but flexible family of movement models. They can be adjusted to account e.g. for environmental heterogeneity (in space or time), edge-mediated behavior, home-range behavior, or many other biologically relevant features.
- Movement models can be integrated into models of demographic, genetic and evolutionary dynamics. Bringing different kinds of information together can help to get a more full picture.