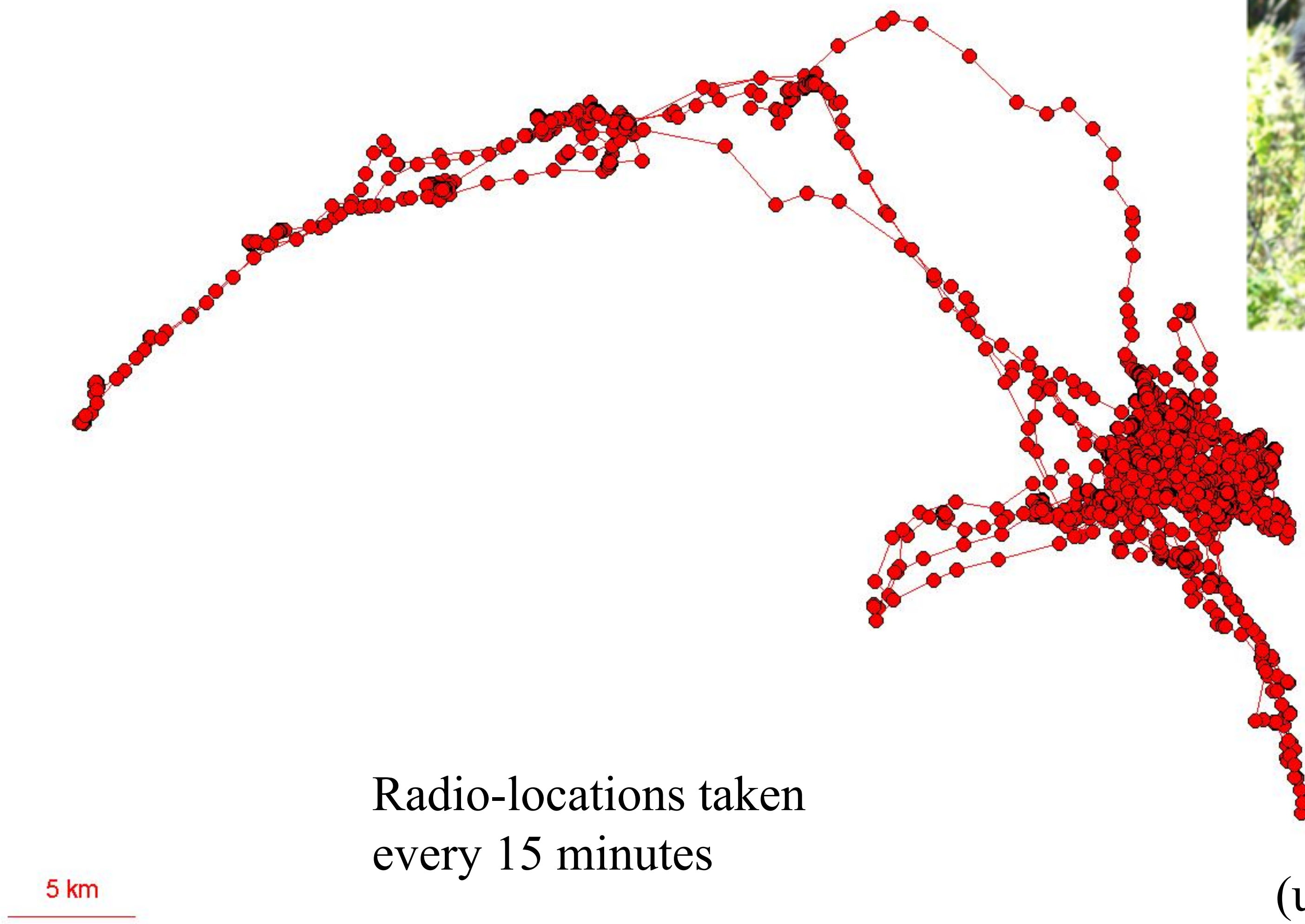
Towards a general theory for modelling animal movement patterns in ecology

Mark Lewis (Alberta)

Jonathan Potts (Sheffield)

Movement as a biased random walk: Wolf 77 from Ya Ha Tinda Ranch pack, Jan-Mar 2004

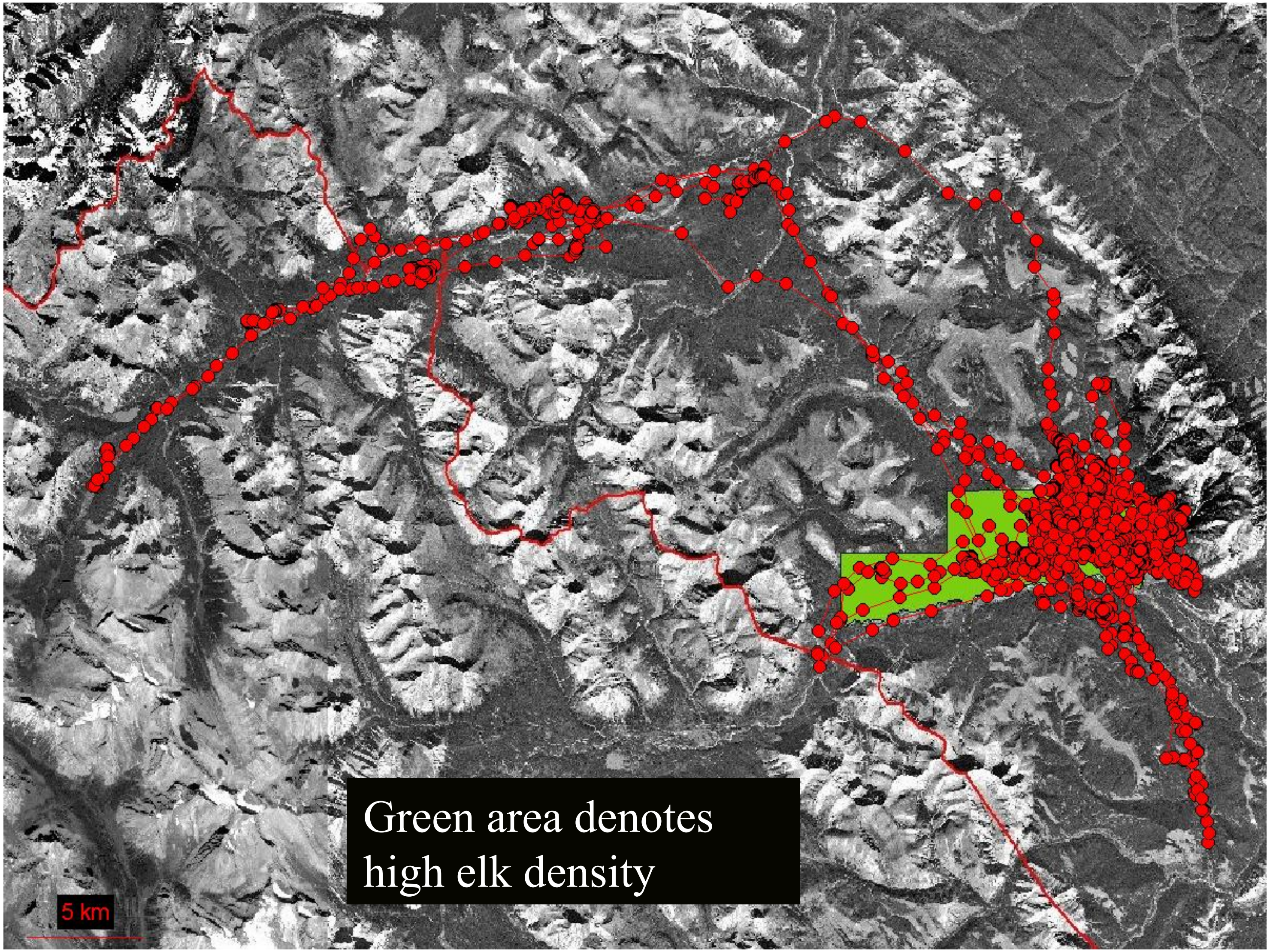


Radio-locations taken every 15 minutes

Photo: A. Bertrand

(unpublished)

Movement pattern with background terrain and prey included



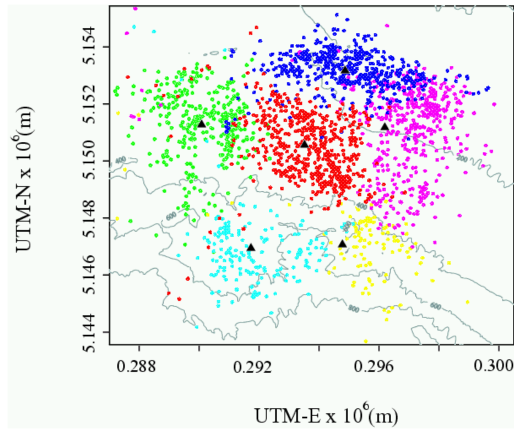
Phenomenological versus mechanistic models for patterns

- **Phenomenological models** describe patterns at the same level they are observed
- **Mechanistic models** posit rules for interactions at one level of organization, and then deduce the patterns that emerge at another level

Connecting movement models to data

Fit to macrodata

Phenomenological model for macroscale space use patterns

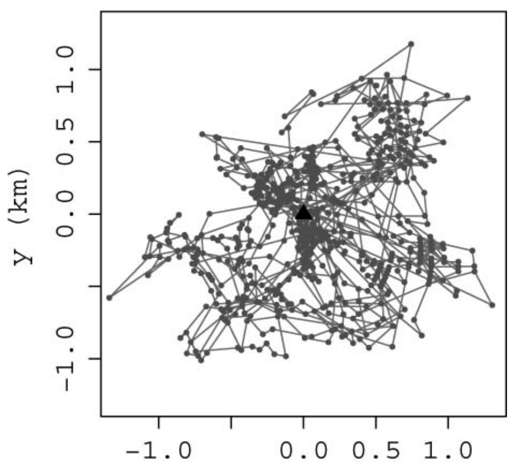


Mechanistic model (micro->macro) fitted to space use patterns

Single level model

Multilevel model

Phenomenological model for microscale movement patterns



Mechanistic model (micro->macro) fitted to microscale movement patterns

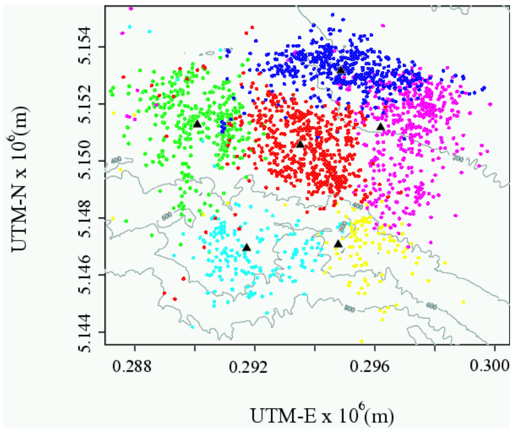
Fit to microdata

Talk Outline

- Mechanistic modelling of home range behaviour: two approaches to parameterizing the same model
- Using *advection-diffusion equations* to understand territorial structures (eg. coyotes, meerkats, gang activity)
- Using statistical *resource selection* and *step selection functions* to understand movement and space use
- Connecting resource selection with advection-diffusion
- Using *coupled step selection functions* to understand territorial and home range structures (e.g. Amazonian birds)
- Challenges for the future

Connecting movement models to data

Fit to macrodata

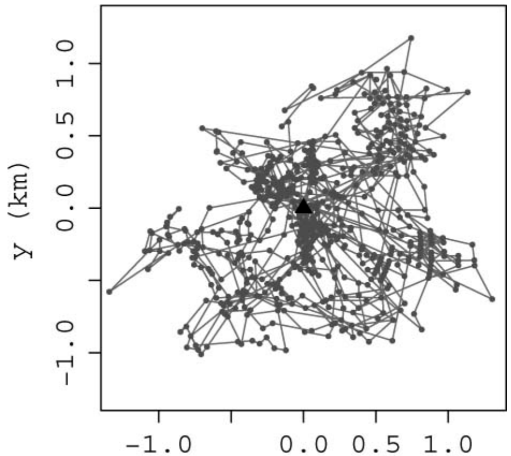


Phenomenological model for macroscale space use patterns

Mechanistic model (micro->macro) fitted to space use patterns

Single level model

Multilevel model



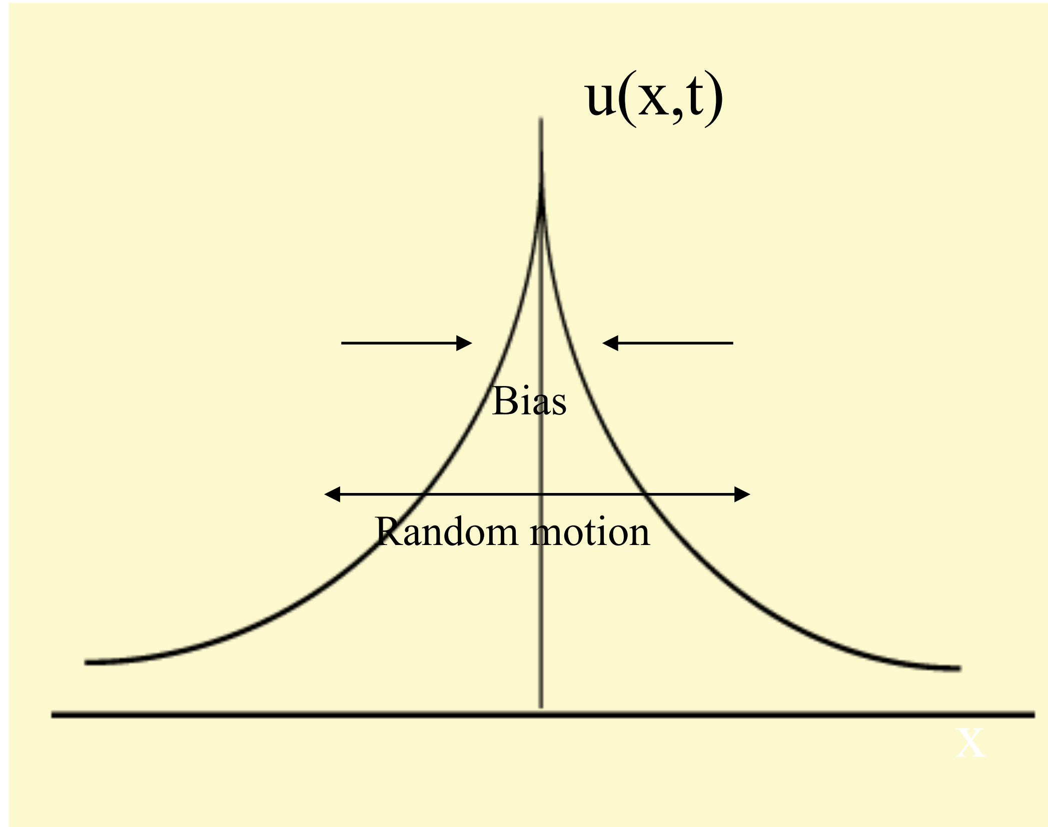
Phenomenological model for microscale movement patterns

Mechanistic model (micro->macro) fitted to microscale movement patterns

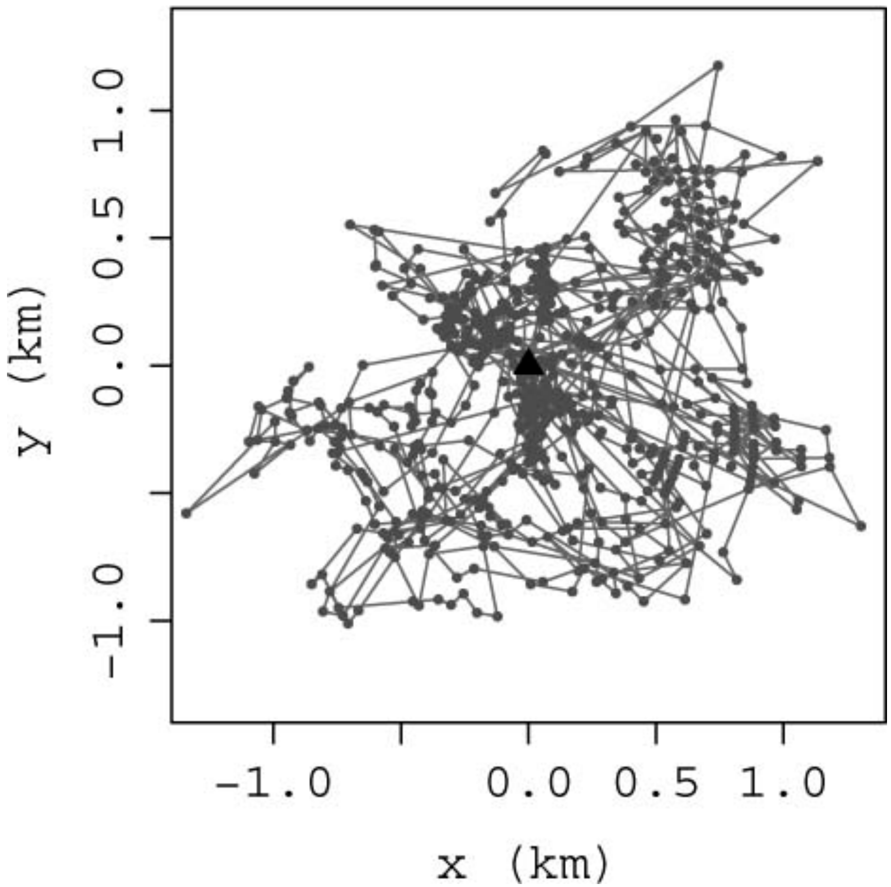
Fit to microdata

Mechanistic modelling of home range behaviour: two approaches to parameterizing the same model

- Home range model (Holgate, 1971): individuals move via random motion plus a constant bias towards a den site.
- Here $u(x,t)$ denotes the intensity of space use by an individual

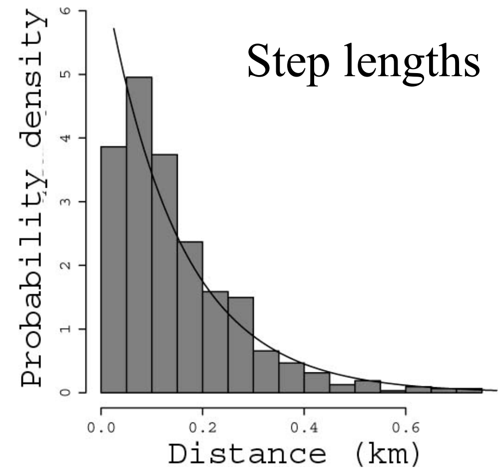


Biased random walk relative to a den site

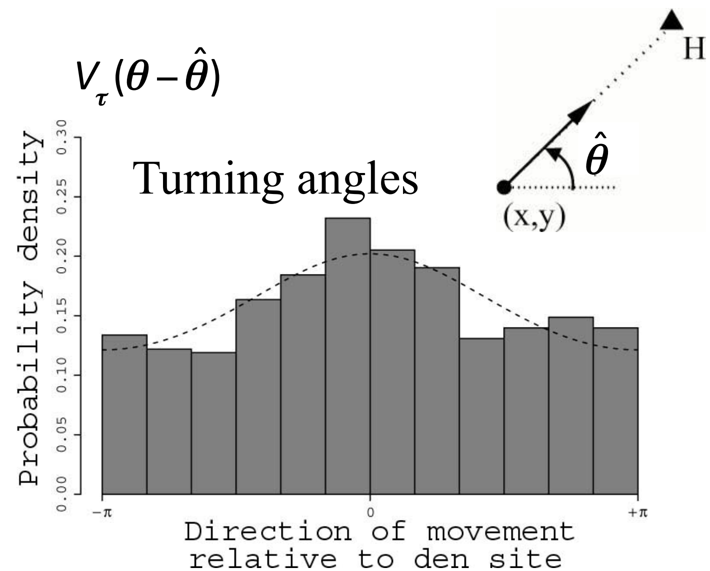


Red fox movement data (microdata, Siniff and Jessen, 1969)

$\rho_\tau(|x - x'|)$



$V_\tau(\theta - \hat{\theta})$



Equation for space use: advection-diffusion

eg, Okubo (1980)

Model 1

$$\underbrace{u(\boldsymbol{x},t+\boldsymbol{\tau})}_{\substack{\text{space use at}\\ \text{time } t+\tau}}=\int u\ \underbrace{(\boldsymbol{x}',t)}_{\substack{\text{space use at}\\ \text{time } t}}\ \underbrace{f_{\boldsymbol{\tau}}(\boldsymbol{x},\boldsymbol{x}',t)}_{\text{movement kernel}}\,d\boldsymbol{x}'$$

Master equation

Model 2

$$\underbrace{\frac{\partial u}{\partial t}}_{\substack{\text{rate of change}\\ \text{of local}\\ \text{space use}}}+\underbrace{\nabla\cdot\left[\boldsymbol{c}(\boldsymbol{x},t)u\right]}_{\substack{\text{change due to}\\ \text{biased motion}}}=\underbrace{\sum_{i,j=1}^{2}\frac{\partial^{2}}{\partial x_i x_j}\left[d_{ij}(\boldsymbol{x},t)u\right]}_{\substack{\text{change due to}\\ \text{random motion}}}$$

differential eq approximates the Master eq

$$\boldsymbol{c}(\boldsymbol{x},t)=\lim_{\boldsymbol{\tau}\to 0}\frac{1}{\boldsymbol{\tau}}\int(\boldsymbol{x}'-\boldsymbol{x})f_{\boldsymbol{\tau}}(\boldsymbol{x},\boldsymbol{x}',t)d\boldsymbol{x}'$$

Advection coefficient

$$d_{ij}(\boldsymbol{x},t)=\lim_{\boldsymbol{\tau}\to 0}\frac{1}{2\boldsymbol{\tau}}\int(x_i'-x_i)(x_j'-x_j)f_{\boldsymbol{\tau}}(\boldsymbol{x},\boldsymbol{x}',t)d\boldsymbol{x}'$$

Diffusion coefficient

$u(\boldsymbol{x},t)$ is density function for the location of individual at time t.

Red fox space use

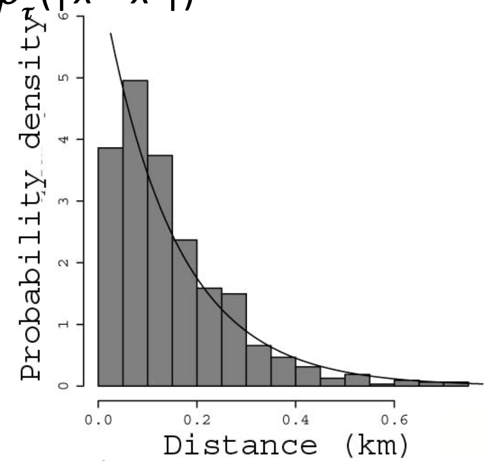
- $f_\tau(\boldsymbol{x},\boldsymbol{x}',t) = \rho_\tau(\boldsymbol{x}-\boldsymbol{x}')V_\tau(\theta-\hat{\theta})$ and the coefficients for the advection-diffusion equation can be calculated.

$$\underbrace{\frac{\partial u}{\partial t}}_{\text{rate of change of local space use}} + \underbrace{\nabla \cdot \left[c\,\frac{-\boldsymbol{x}}{\|\boldsymbol{x}\|}\,u \right]}_{\text{biased motion towards den}} = \underbrace{d\sum_{i,=1}^{2}\frac{\partial^2}{\partial x_i^2}[u]}_{\text{change due to random motion}}$$

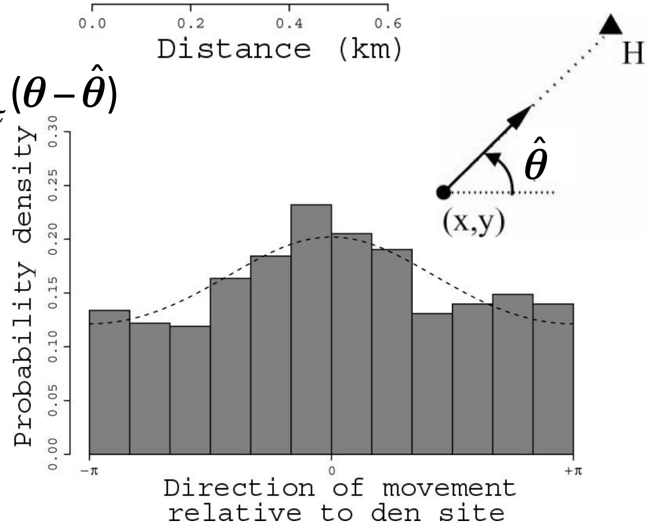
$$c(\boldsymbol{x},t) = \lim_{\tau\to 0}\frac{1}{\tau}\int(\boldsymbol{x}'-\boldsymbol{x})f_\tau(\boldsymbol{x},\boldsymbol{x}',t)\,d\boldsymbol{x}'$$

$$d_{ij}(\boldsymbol{x},t) = \lim_{\tau\to 0}\frac{1}{2\tau}\int(x_i'-x_i)(x_j'-x_j)f_\tau(\boldsymbol{x},\boldsymbol{x}',\tau,t)\,d\boldsymbol{x}'$$

$\rho_\tau(|x-x'|)$



$V_\tau(\theta-\hat{\theta})$



(Moorcroft and Lewis 2006)

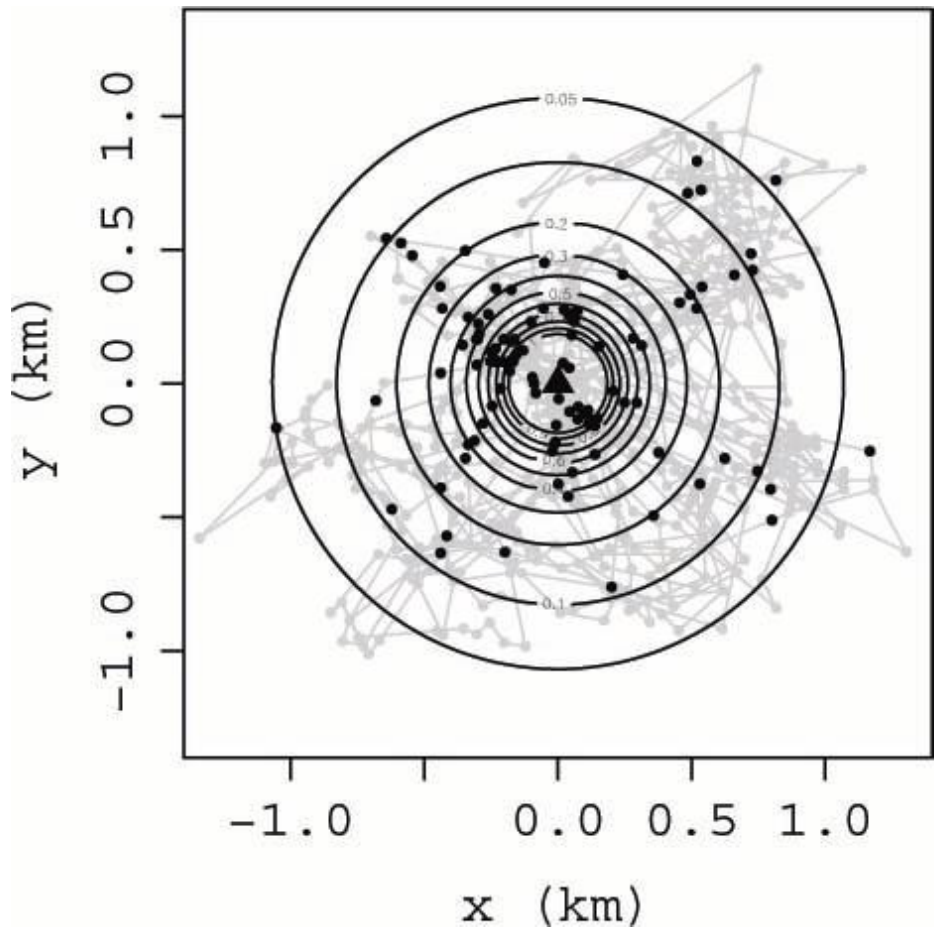
Red fox space use

- $k(\boldsymbol{x},\boldsymbol{x}'\tau,t) = f_\tau(\rho)K_\tau(\phi-\hat{\phi})$ and the coefficients for the advection-diffusion equation can be calculated.
- After a period of time the space use settles down to a steady state solution $(\partial u/\partial t = 0)$.
- Alternatively we could have first calculated the steady state solution to the advection diffusion equation,

$$u(r) = \frac{c}{d}\exp\left(-\frac{c}{d}r\right)$$

- and then fit the solution to "independent" relocation data (macrodata).

$$\underbrace{\frac{\partial u}{\partial t}}_{\text{rate of change of local space use}} + \underbrace{\nabla\cdot\left[c\,\frac{-\boldsymbol{x}}{\|\boldsymbol{x}\|}\,u\right]}_{\text{biased motion towards den}} = \underbrace{d\sum_{i,=1}^{2}\frac{\partial^2}{\partial x_i^2}[u]}_{\text{change due to random motion}}$$



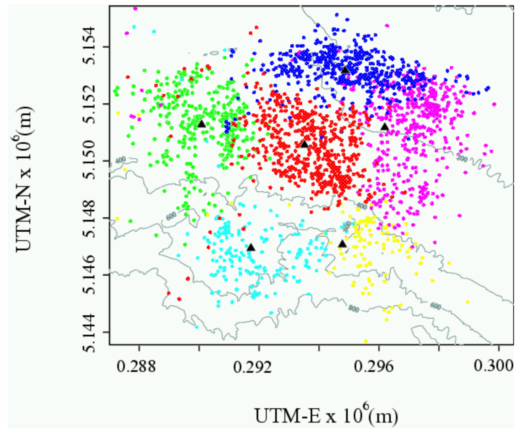
(Moorcroft and Lewis 2006)

Talk Outline

- Mechanistic modelling of home range behaviour: two approaches to parameterizing the same model
- Using *advection-diffusion equations* to understand territorial structures (eg. coyotes, meerkats, gang activity)
- Using statistical *resource selection* and *step selection functions* to understand movement and space use
- Connecting resource selection with advection-diffusion
- Using *coupled step selection functions* to understand territorial and home range structures (e.g. Amazonian birds)
- Challenges for the future

Connecting movement models to data

Fit to macrodata

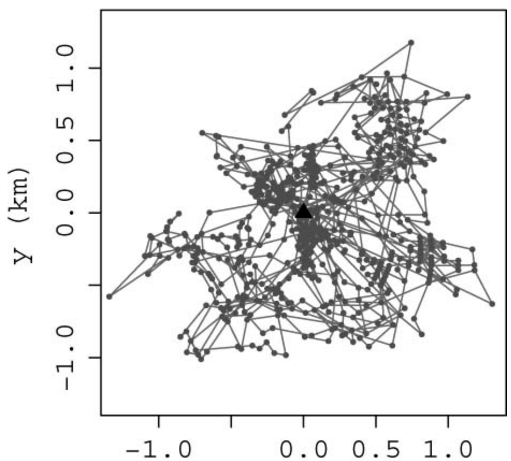


Phenomenological model for macroscale space use patterns

Mechanistic model (micro->macro) fitted to space use patterns

Single level model

Multilevel model



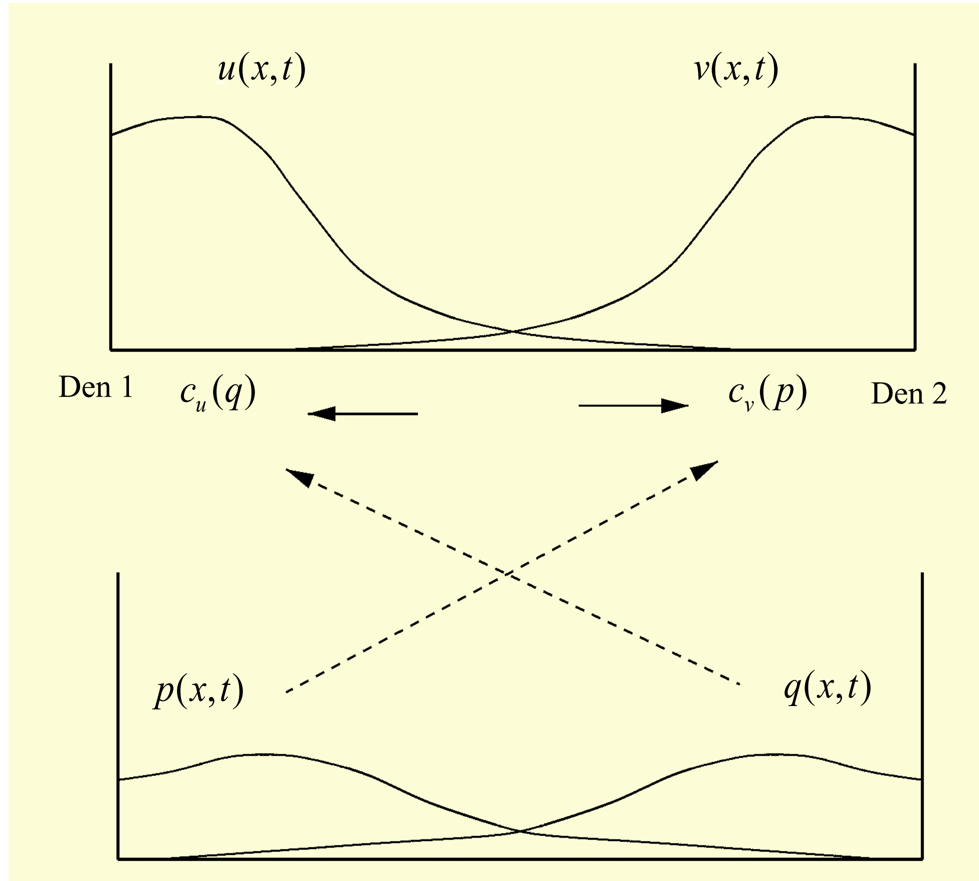
Phenomenological model for microscale movement patterns

Mechanistic model (micro->macro) fitted to microscale movement patterns

Fit to microdata

Mechanistic Home Range Model

- Individuals have random and biased components of motion.
- Biased component is directed towards den site/ rendezvous site
- Rate of biased movement is proportional to density of *foreign* scent marks
- Scent marks are deposited at an underlying rate that is increased in the presence of *foreign* scent marks



Lewis and Murray, *Nature* (1993)
Moorcroft (1997)

Mathematical description of model

Movement

$$\underbrace{\frac{\partial u}{\partial t}}_{\text{local density change}} - \underbrace{\frac{\partial}{\partial x}\big(c(q)u\big)}_{\text{directed motion to den on left}} = \underbrace{d\frac{\partial^2 u}{\partial x^2}}_{\text{random motion}}$$

Pack U density

$$\underbrace{\frac{\partial v}{\partial t}}_{\text{local density change}} + \underbrace{\frac{\partial}{\partial x}\big(c(p)v\big)}_{\text{directed motion to den on right}} = \underbrace{d\frac{\partial^2 v}{\partial x^2}}_{\text{random motion}}$$

Pack V density

Marking

$$\underbrace{\frac{\partial p}{\partial t}}_{\text{local density change}} = \underbrace{u(l+m(q))}_{\text{deposition by U individuals}} - \underbrace{\phi p}_{\text{decay}}$$

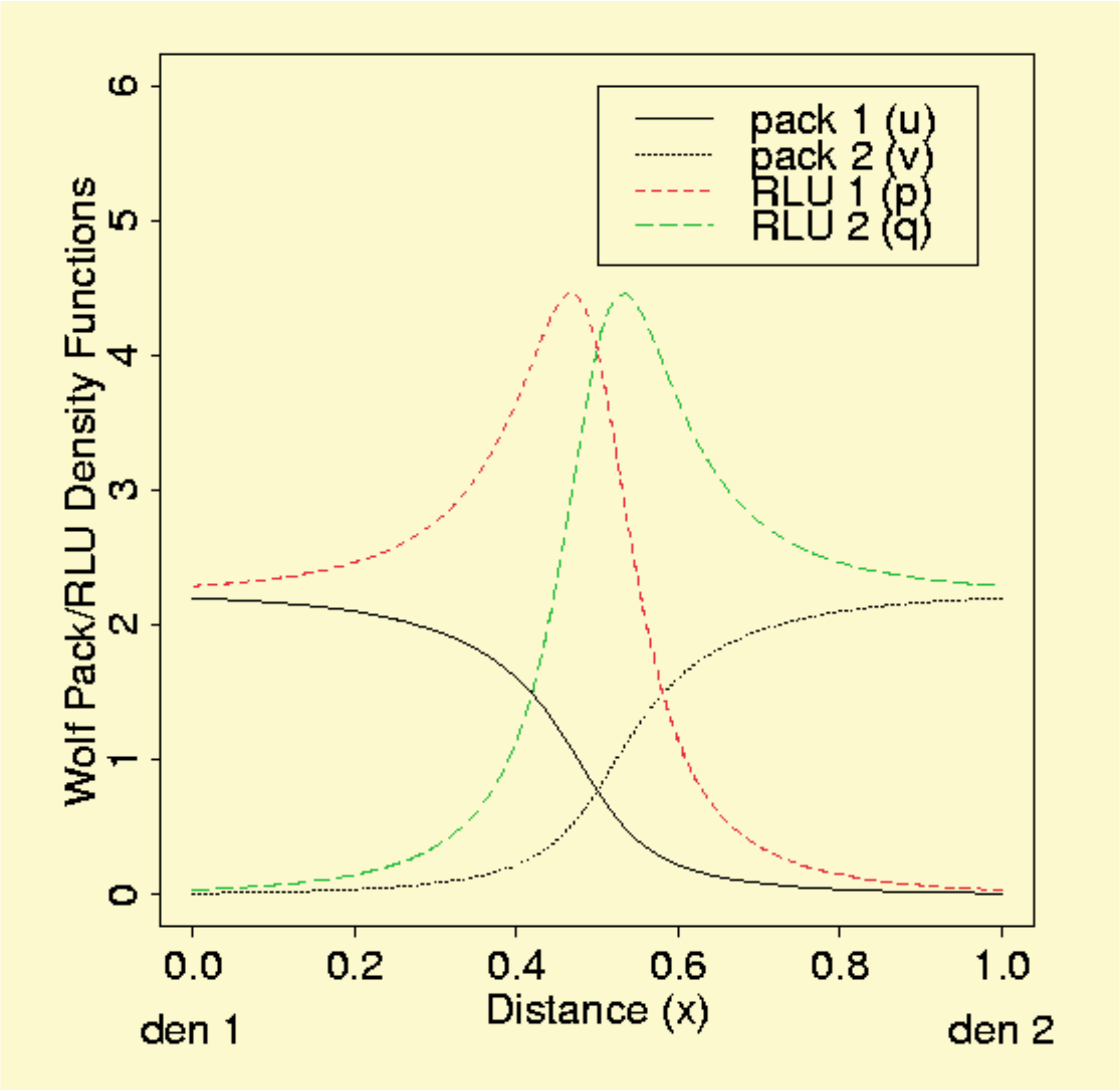
Pack U scent marks

$$\underbrace{\frac{\partial q}{\partial t}}_{\text{local density change}} = \underbrace{v(l+m(p))}_{\text{deposition by V individuals}} - \underbrace{\phi q}_{\text{decay}}$$

Pack V scent marks

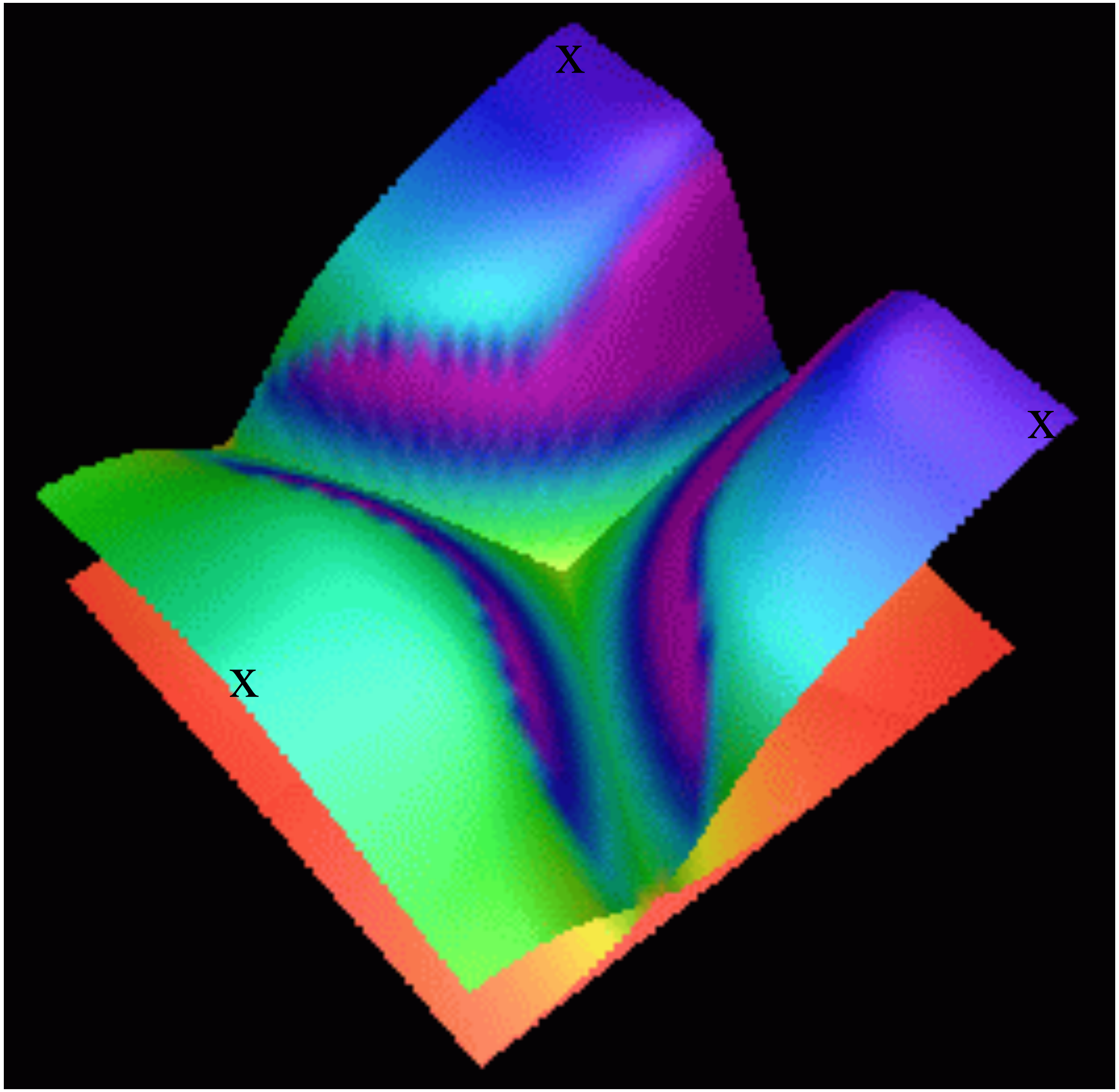
plus boundary and initial conditions

Steady state solutions give complex territorial patterns



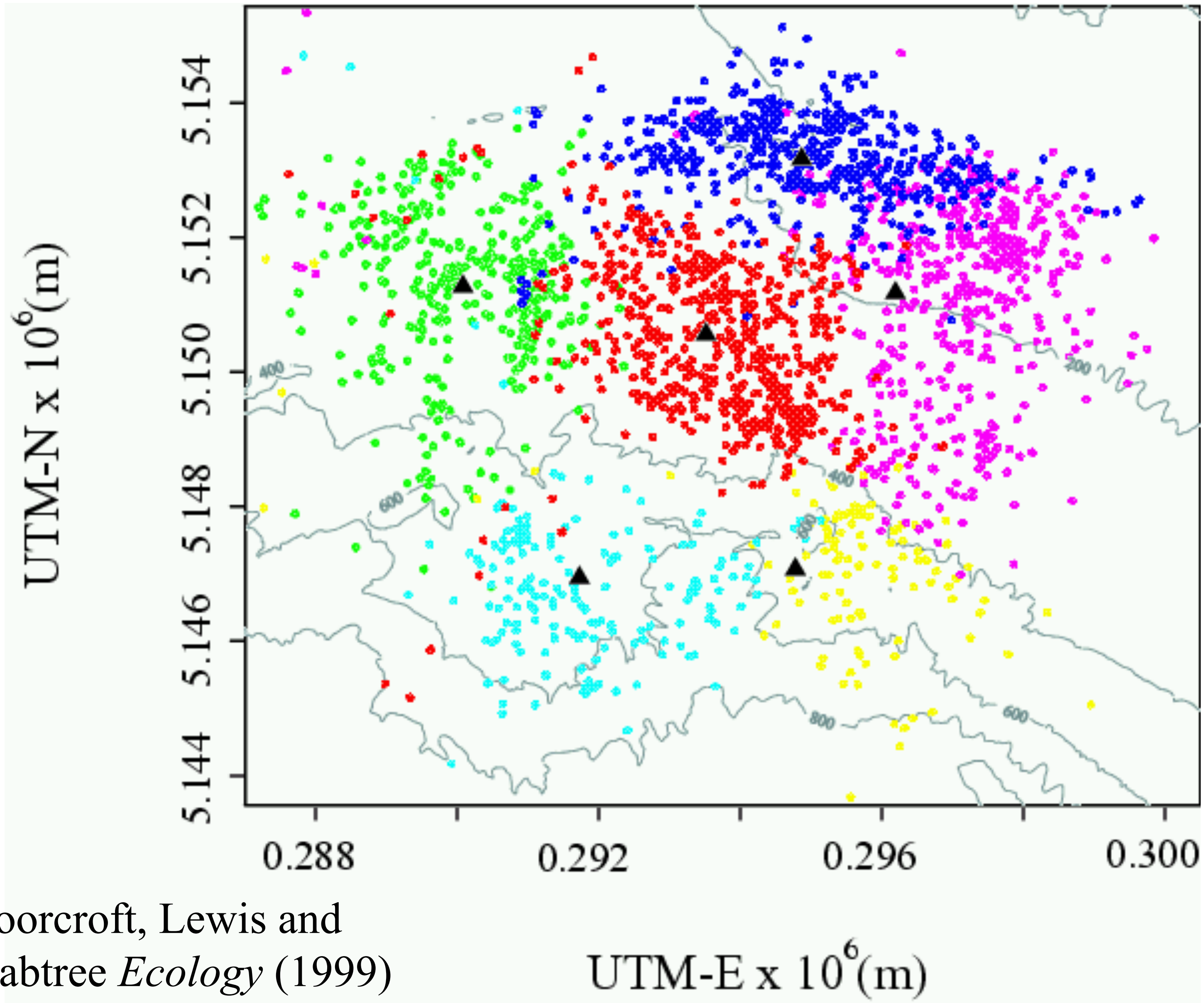
Positive feedback in scent-marking dynamics gives “bowl” shape scent-mark densities

Qualitative analysis in two dimensions



Lewis, White and Murray (1997)

Coyote locations from Hanford Arid Lands Ecosystem



Moorcroft, Lewis and Crabtree *Ecology* (1999)

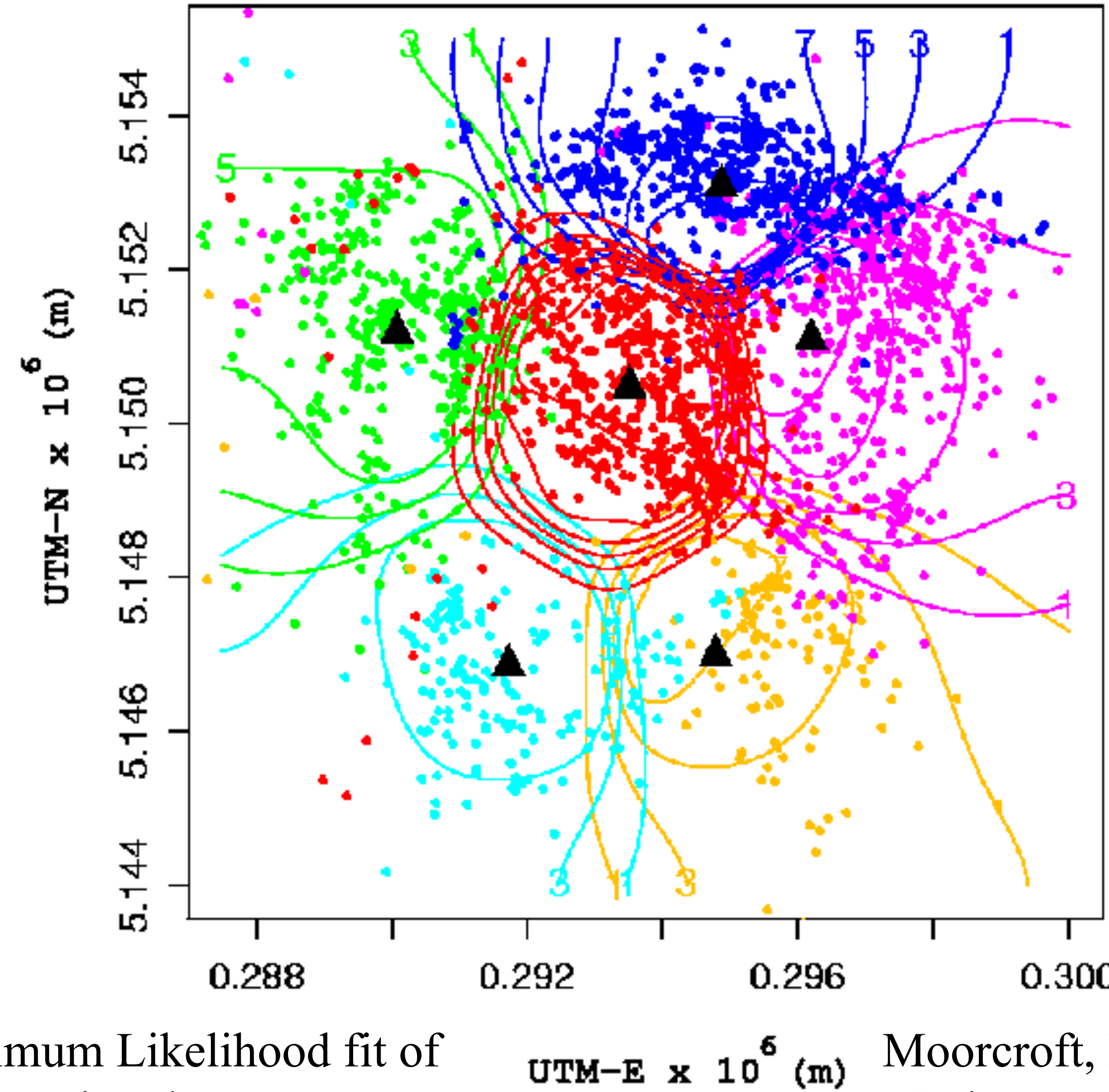
Applying Maximum Likelihood to the territoriality model

- For each parameter set, the model generates a probability density function for the locations of an individual in a territory $u(x, y)$
- Using radio tracking data locations (x_i, y_i) , which are independent observations of where the territorial individual is found, the likelihood that the data locations would come from this model is

$$L = u(x_1, y_1)u(x_2, y_2)...u(x_n, y_n)$$

- We choose the model parameters so as to give the maximum possible value for L

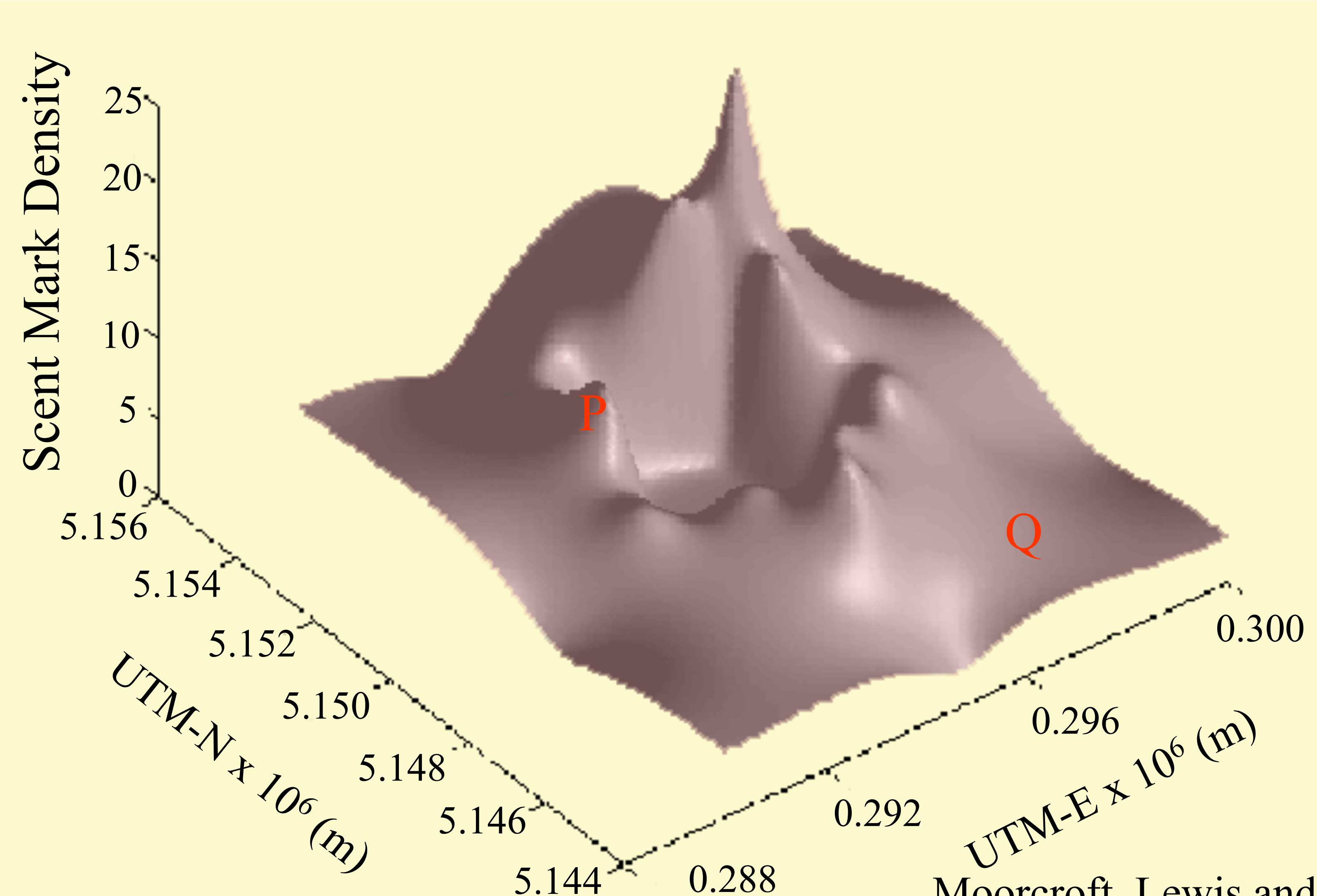
Fit of the mechanistic home range model



Numerical Maximum Likelihood fit of model to radio-location data

Moorcroft, Lewis and Crabtree *Ecology* (1999)

Inferred foreign scent mark levels

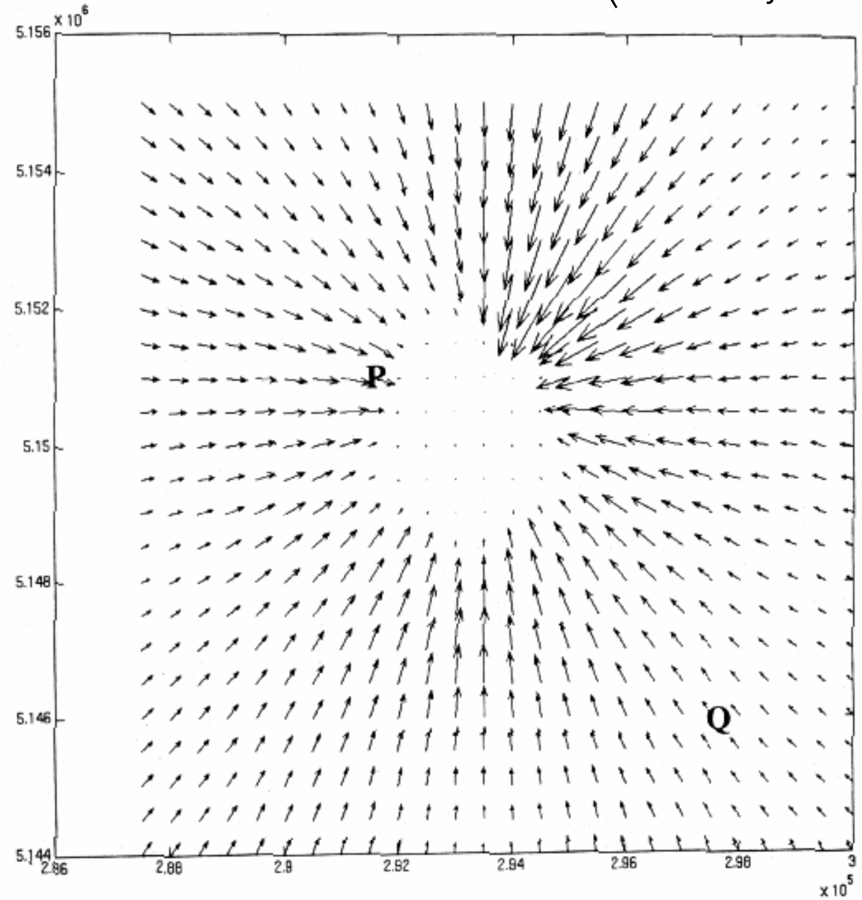


Moorcroft, Lewis and Crabtree *Ecology* (1999)

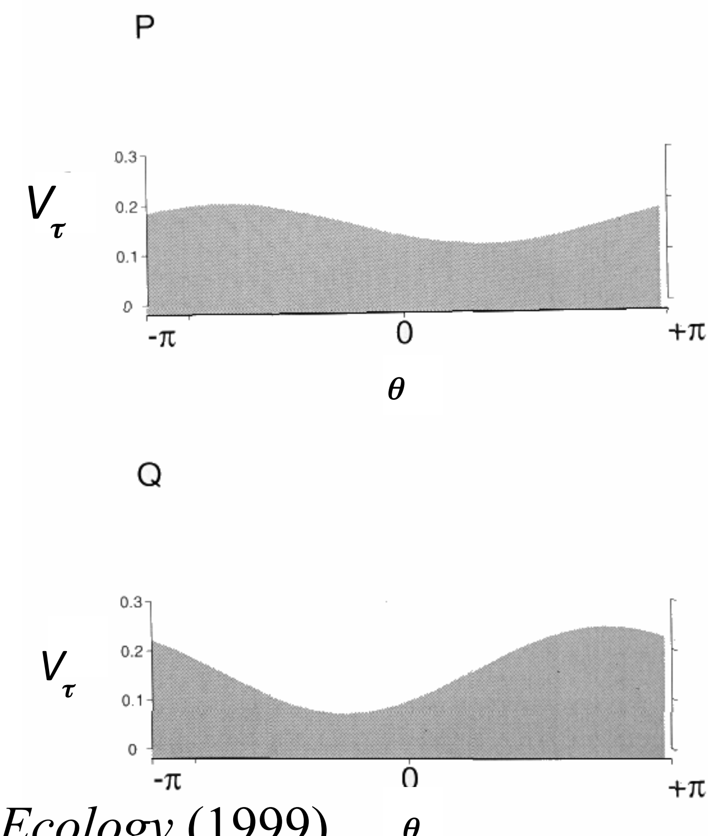
Relationship to a Random Walk Model

- The nonlinear PDE model for densities can be related to an underlying random walk model for individuals

$$f_{\tau i}(\boldsymbol{x},\boldsymbol{x}',t) = \rho_\tau(\boldsymbol{x}-\boldsymbol{x}')V_\tau\left(\theta-\hat{\theta},\sum_{j\neq i}p_j(x,t)\right)$$



Preferential movement direction



Moorcroft, Lewis and Crabtree *Ecology* (1999)

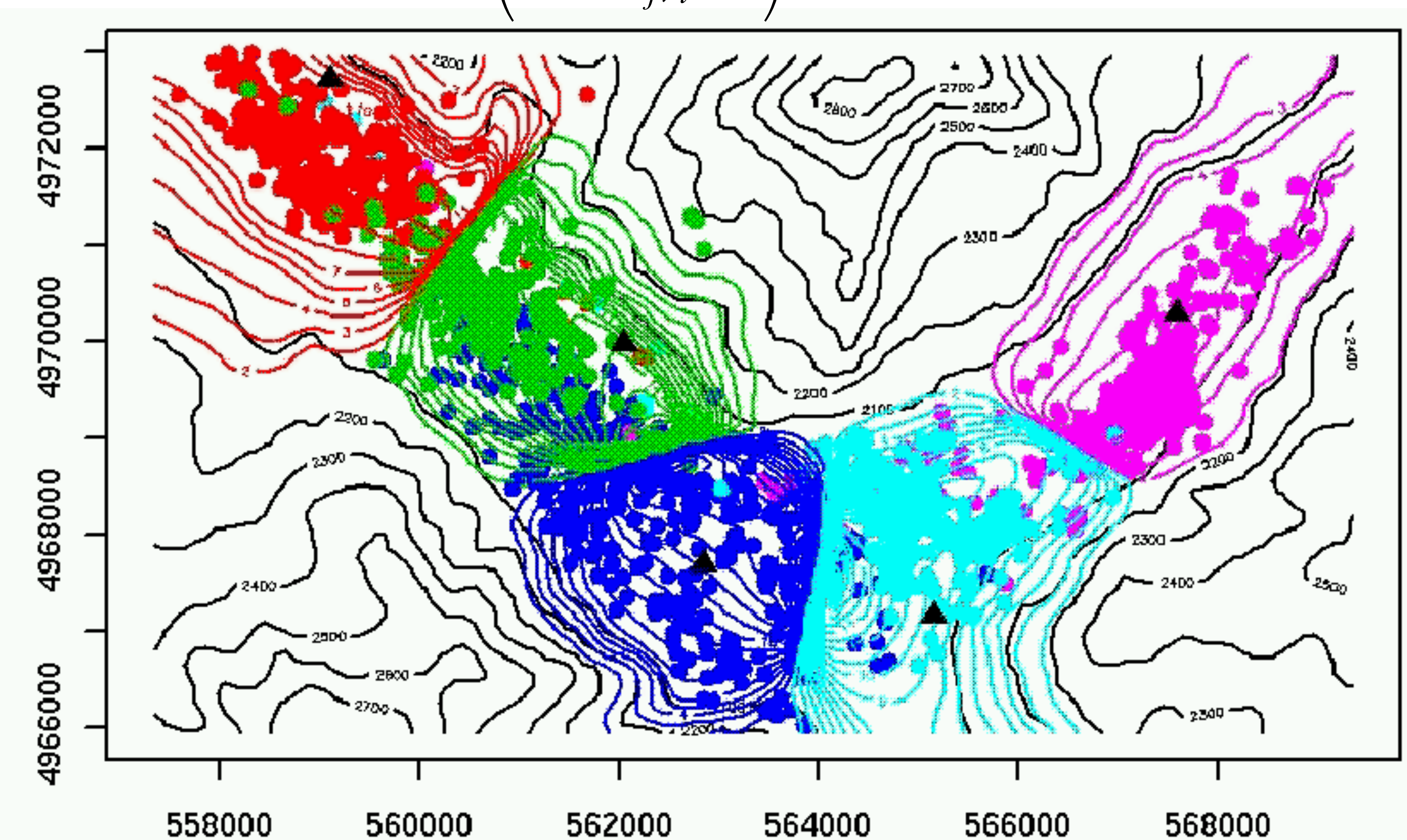
Hanford vs. Yellowstone

Moorcroft and Lewis (2006)

Scent avoidance model with added "terrain taxis"

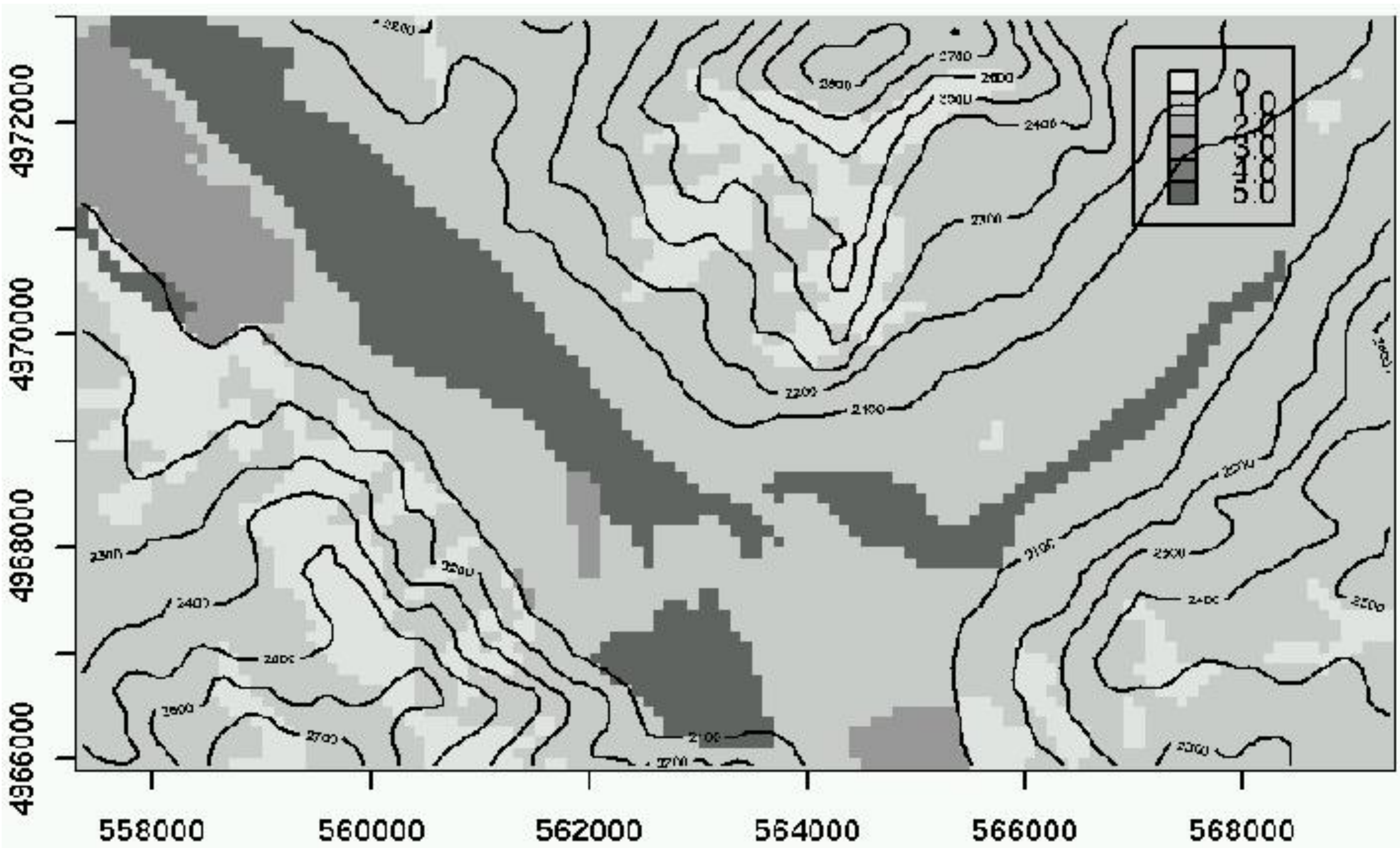
$$f_{\tau i}(\boldsymbol{x},\boldsymbol{x}',t)=\boldsymbol{\rho}_{\boldsymbol{\tau}}(\boldsymbol{x}-\boldsymbol{x}')V_{\boldsymbol{\tau}}\left(\theta-\hat{\theta},\sum_{j\neq i}p_j(x,t),\nabla z\right)$$

$$0=\Delta u_i-\nabla\cdot\left(\beta \boldsymbol{x}_i u_i\sum_{j\neq i}p_j\right)+\nabla\cdot\left(\alpha_z u_i\nabla z\right)$$



Moorcroft, Lewis and Crabtree *Proc Roy Soc. Lond B* (2006)

Prey density, as indicated by habitat type

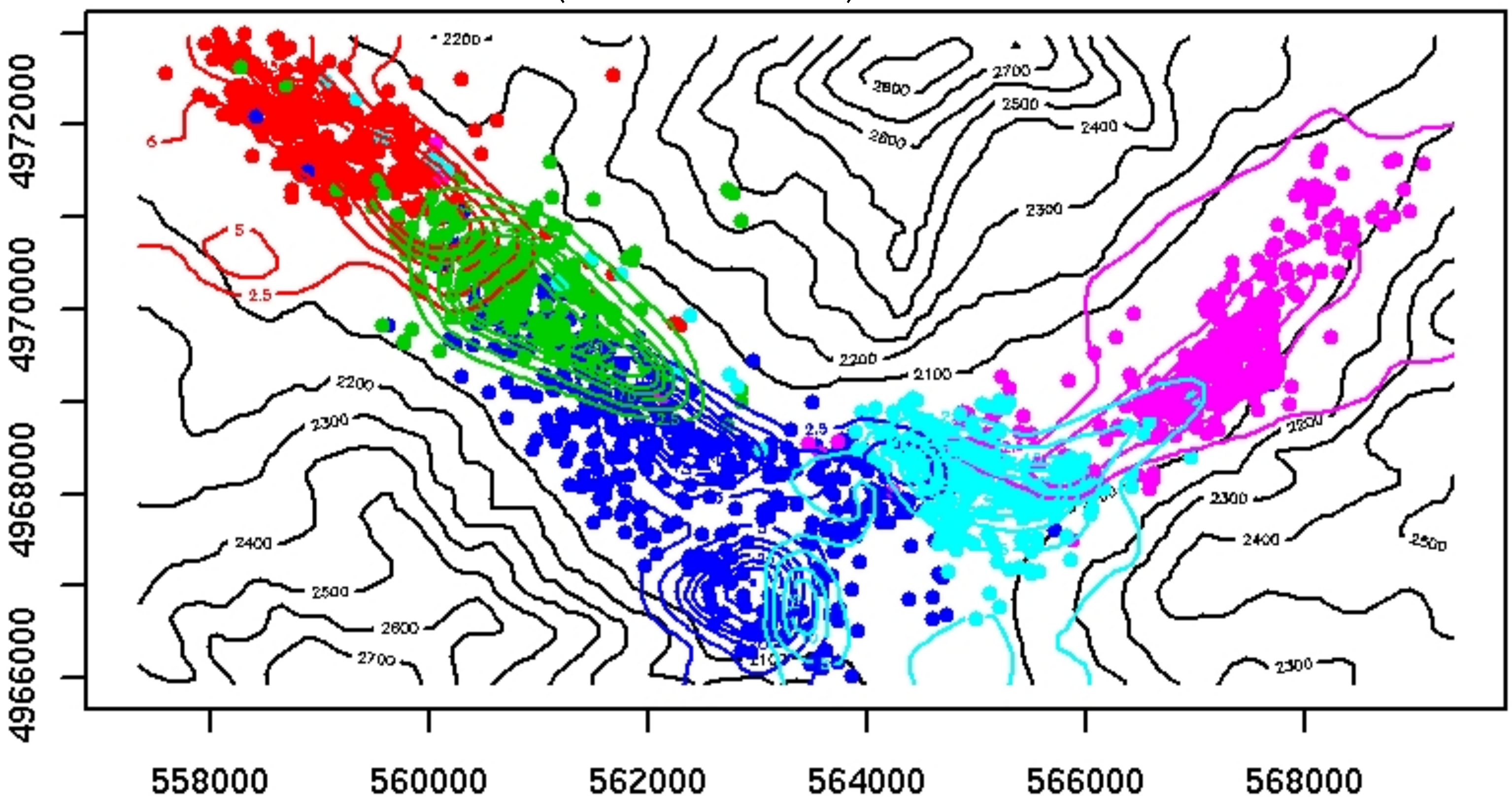


Moorcroft, Lewis and Crabtree *Proc Roy Soc. Lond B* (2006)

Model with added "prey-taxis"

$$f_{\tau i}(\boldsymbol{x},\boldsymbol{x}',t)=\rho_{\tau}(\boldsymbol{x}-\boldsymbol{x}',\boldsymbol{h})V_{\tau}\left(\theta-\hat{\theta},\sum_{j\neq i}p_j(x,t)\right)$$

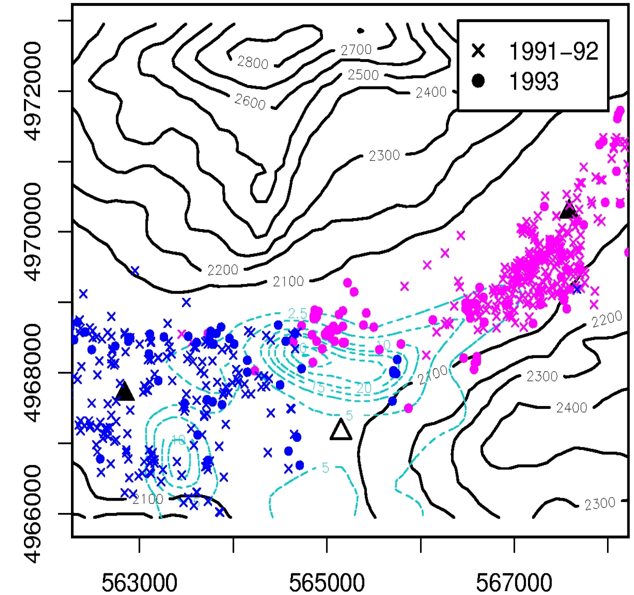
$$0=\Delta u_i-\nabla\cdot\left(\beta\boldsymbol{x}_i u_i\sum_{j\neq i}p_j\right)+\nabla\cdot\left(\alpha_h u_i\nabla h\right)$$



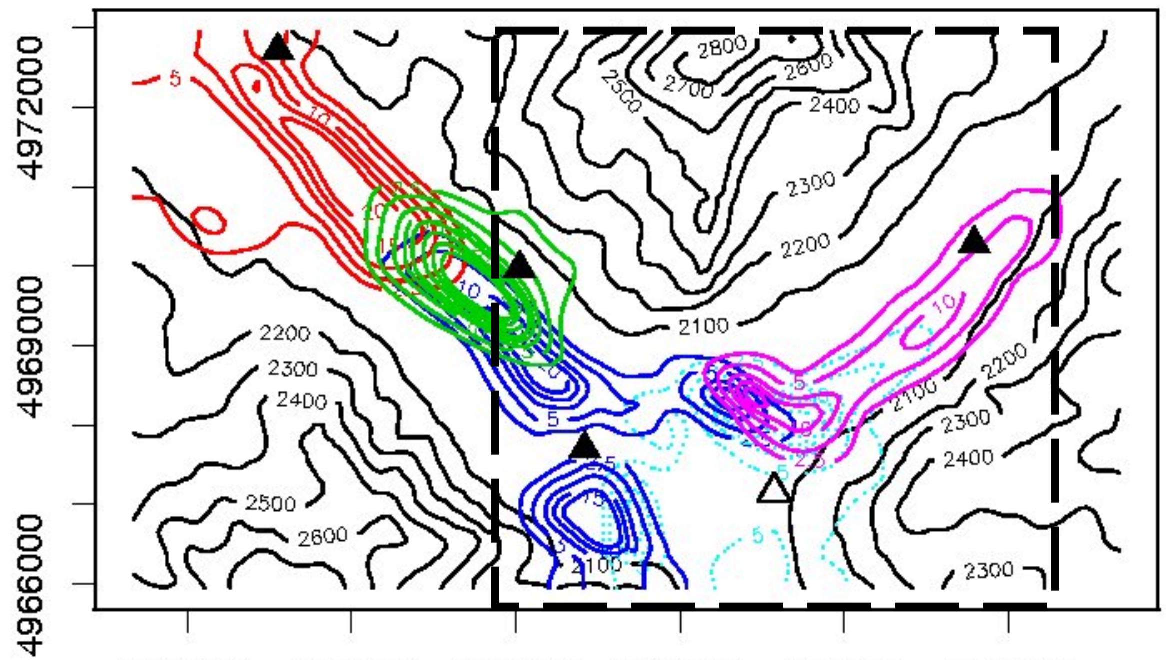
Moorcroft, Lewis and Crabtree *Proc Roy Soc. Lond B* (2006)

Observed and predicted shift in territories after loss of Norris Pack, 1993

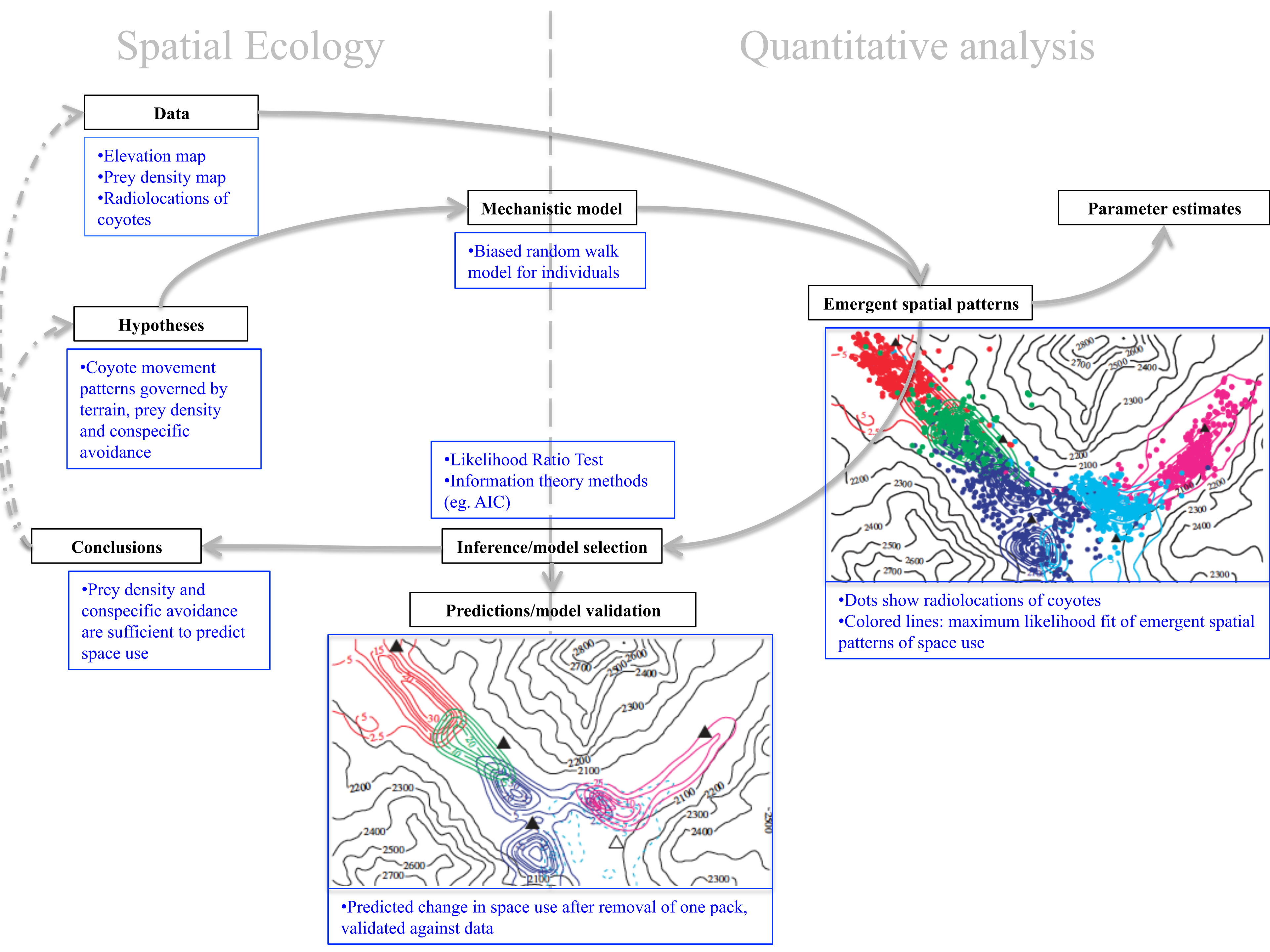
Observation



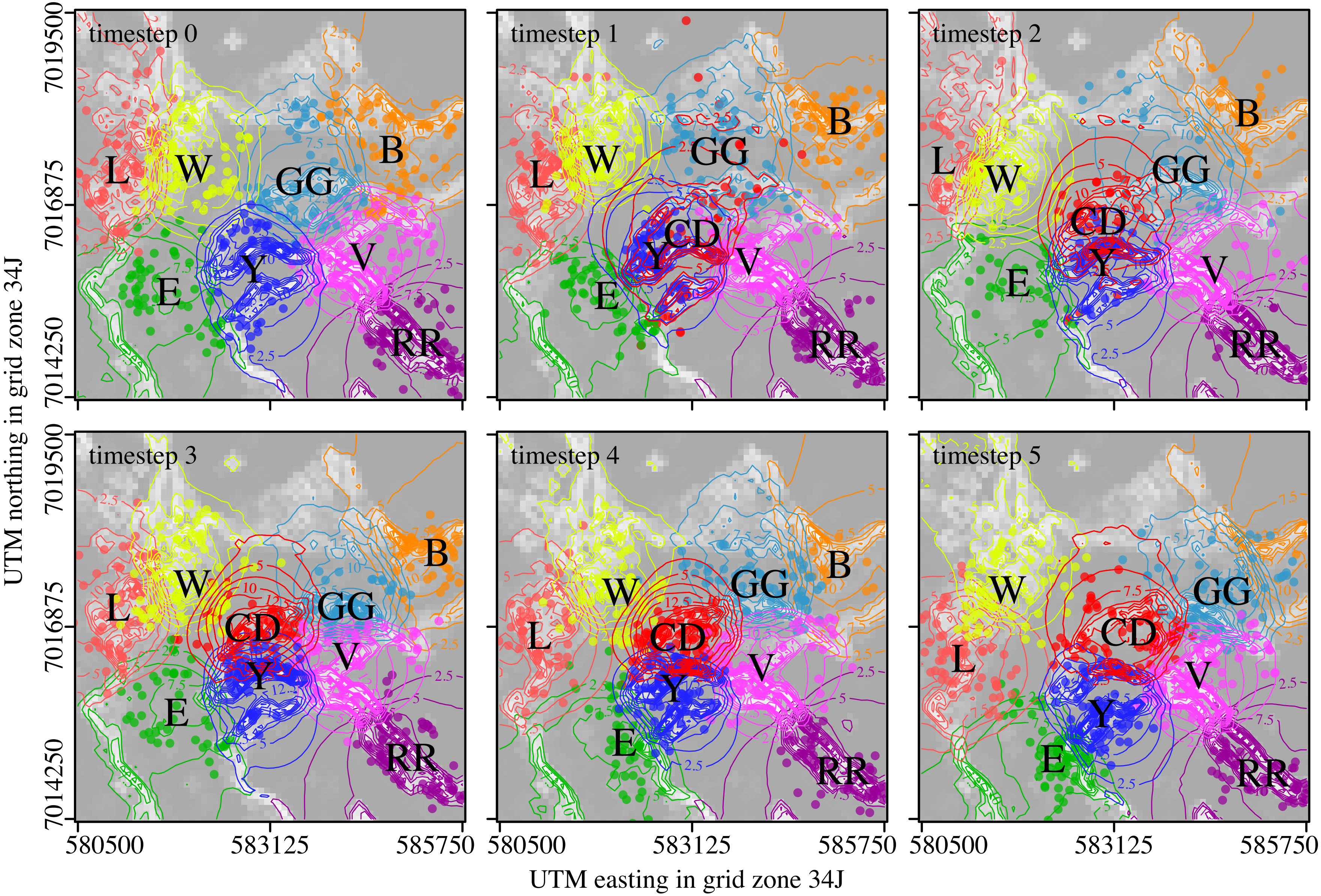
Prediction



Moorcroft, Lewis and Crabtree *Proc Roy Soc. Lond B* (2006)

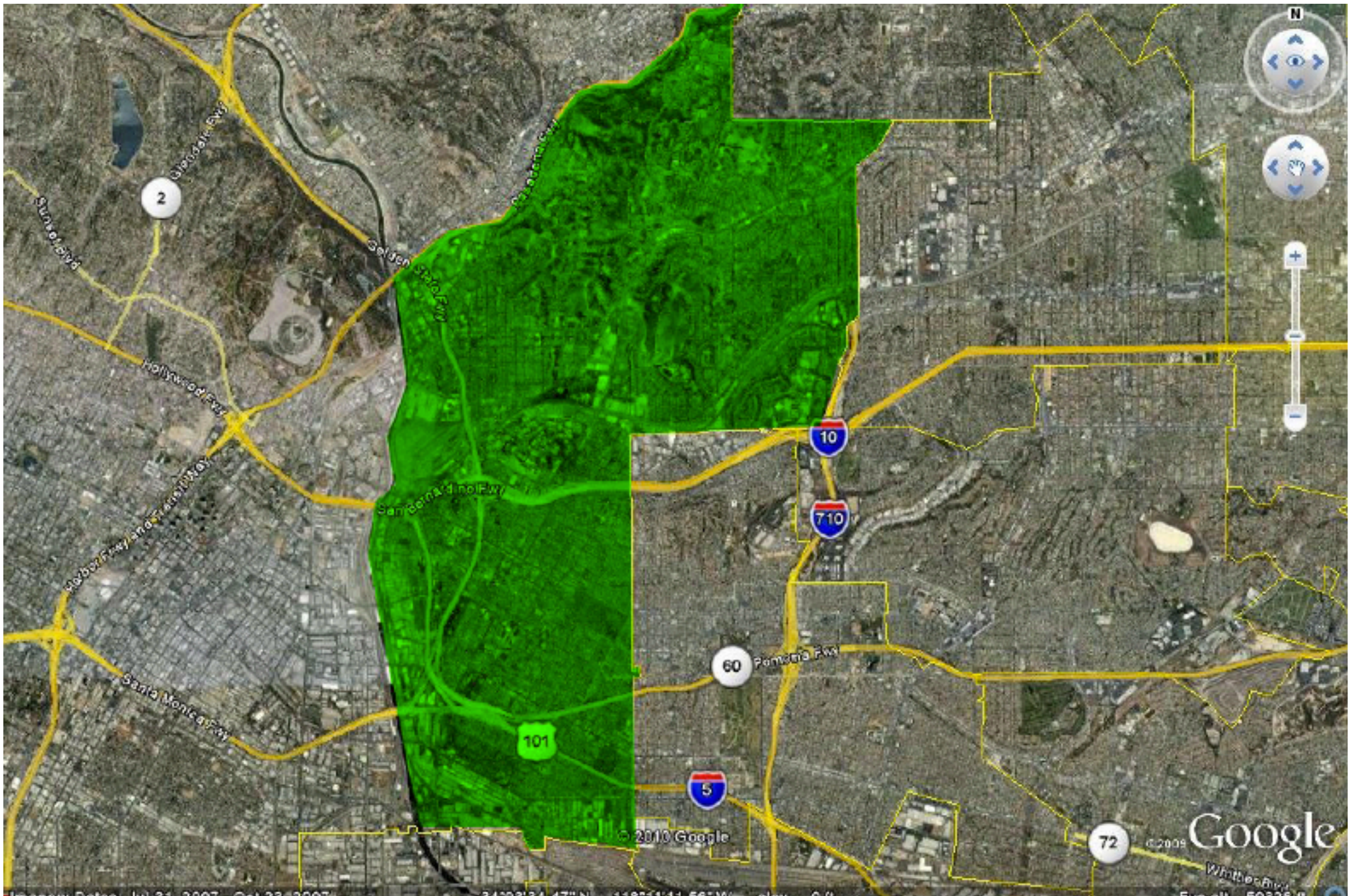

Spatial Ecology
Quantitative analysis
Data
•Elevation map
•Prey density map
•Radiolocations of coyotes
Mechanistic model
•Biased random walk model for individuals
Parameter estimates
Hypotheses
•Coyote movement patterns governed by terrain, prey density and conspecific avoidance
Emergent spatial patterns
•Dots show radiolocations of coyotes
•Colored lines: maximum likelihood fit of emergent spatial patterns of space use
•Likelihood Ratio Test
•Information theory methods (eg. AIC)
Conclusions
Inference/model selection
•Prey density and conspecific avoidance are sufficient to predict space use
Predictions/model validation
•Predicted change in space use after removal of one pack, validated against data

Emerging Meerkat Territories in the Kalahari



Bateman *et al* (2014) *Journal of Applied Ecology*

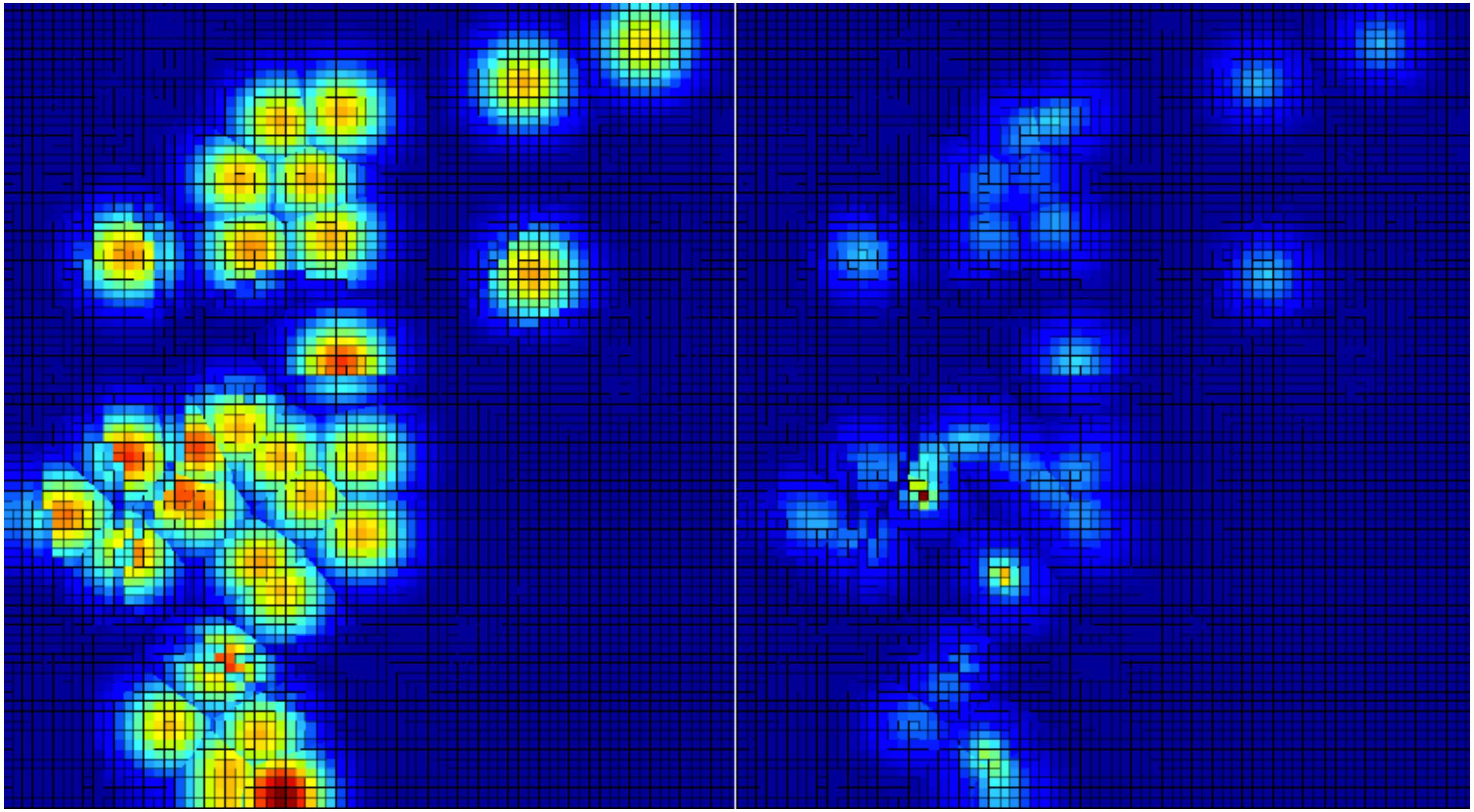
Gang Territories in Hollenbeck Los Angeles County



Observed Gang Network

- 29 active gangs in Hollenbeck.
- 69 Rivalries among gangs.
- A "set space" is a gang's centre of activity where gang members spend a large quantity of their time.
- Gang set spaces studied mathematically using a version of the "terrain-taxis coyote territory" model (Laura Smith, Andrea Bertozzi and coworkers at UCLA).
- Here "terrain" involves geographical landmarks that could inhibit movement (rivers, freeways, major roads).

Resulting set spaces and marking densities



- These were compared police records for locations of gang members and to locations of gang-related violence.

Smith et al (2012)

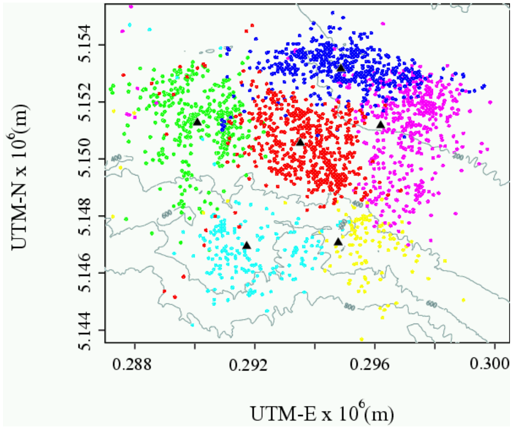
Talk Outline

- Mechanistic modelling of home range behaviour: two approaches to parameterizing the same model
- Using *advection-diffusion equations* to understand territorial structures (eg. coyotes, meerkats, gang activity)
- Using statistical *resource selection* and *step selection functions* to understand movement and space use
- Connecting resource selection with advection-diffusion
- Using *coupled step selection functions* to understand territorial and home range structures (e.g. Amazonian birds)
- Challenges for the future

Connecting movement models to data

Fit to macrodata

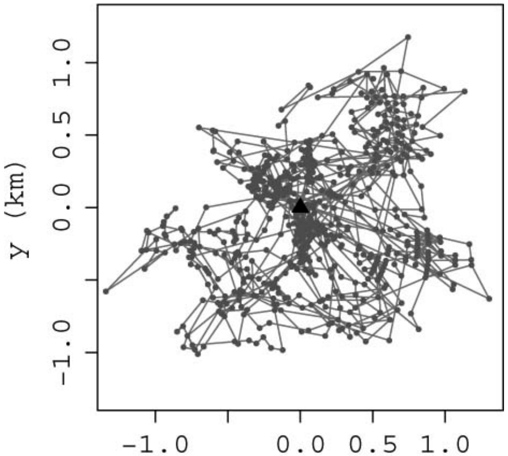
Phenomenological model for macroscale space use patterns



Mechanistic model (micro->macro) fitted to space use patterns

Single level model

Multilevel model

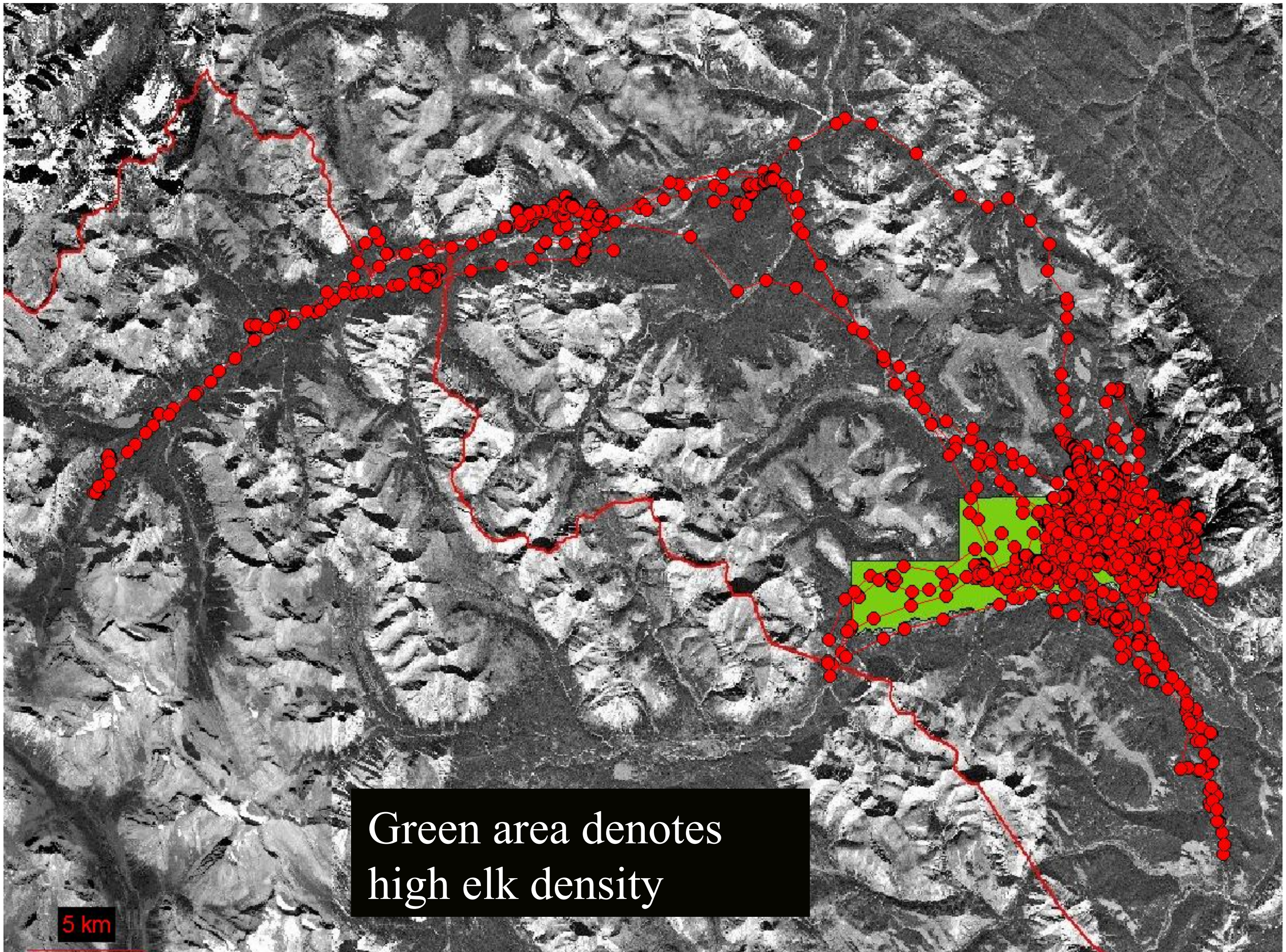


Phenomenological model for microscale movement patterns

Mechanistic model (micro->macro) fitted to microscale movement patterns

Fit to microdata

Where are animals found?
<u>Resource</u> Selection Functions



Where are animals found?
Resource Selection Functions

Each location in space x has attributes

E_1 = slope

E_2 = vegetation density

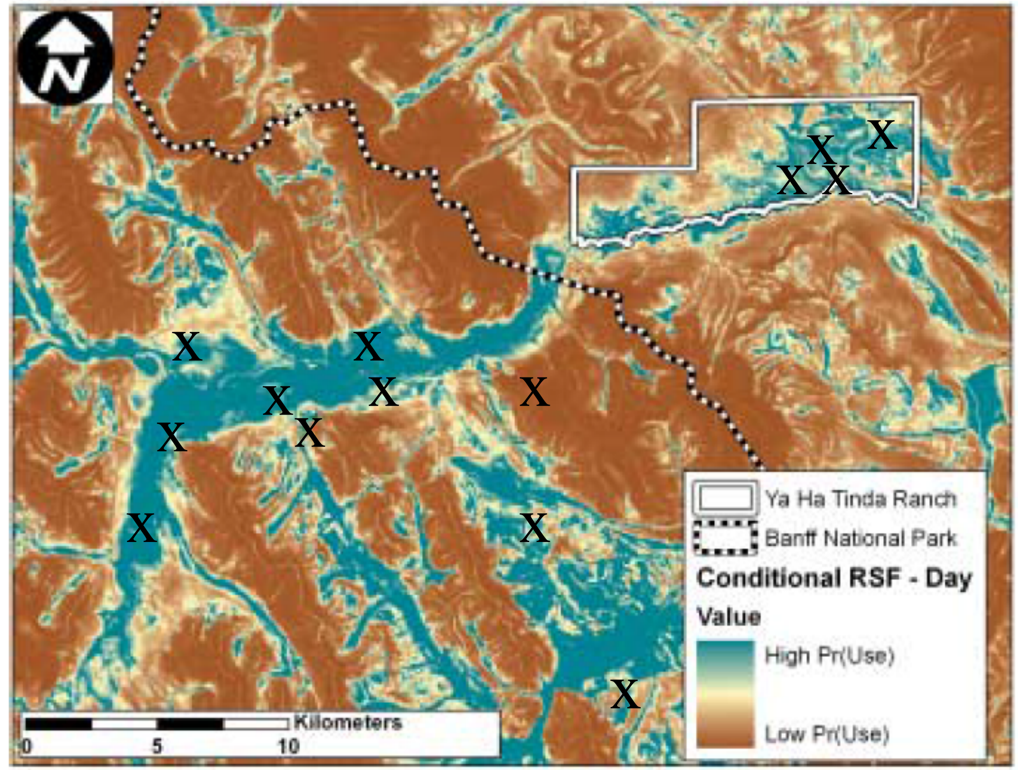
E_3 = estimated prey density

etc

Habitat use has probability density function

$$u(x) = \frac{\exp\left(\beta_0 + \sum_i \beta_i E_i(x)\right)}{\int_\Omega \exp\left(\beta_0 + \sum_i \beta_i E_i(x')\right) dx'}$$

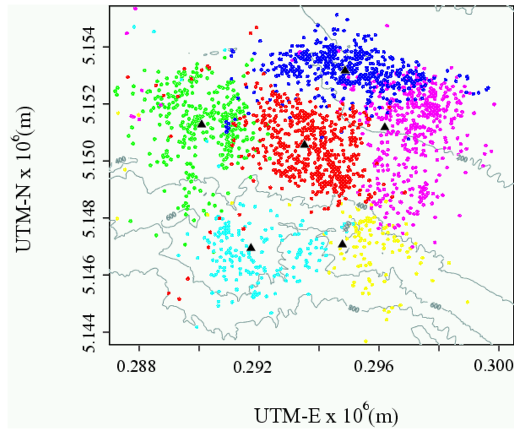
The model is fit to spatial observations of individuals in different habitats via a Generalized Linear Model (GLM)



Hebblewhite, M., & Merrill, E. (2008). Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, *45*(3), 834-844.)

Connecting movement models to data

Fit to macrodata

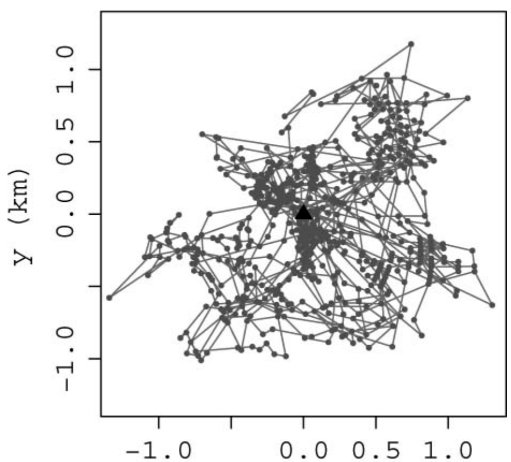


Phenomenological model for macroscale space use patterns

Mechanistic model (micro->macro) fitted to space use patterns

Single level model

Multilevel model

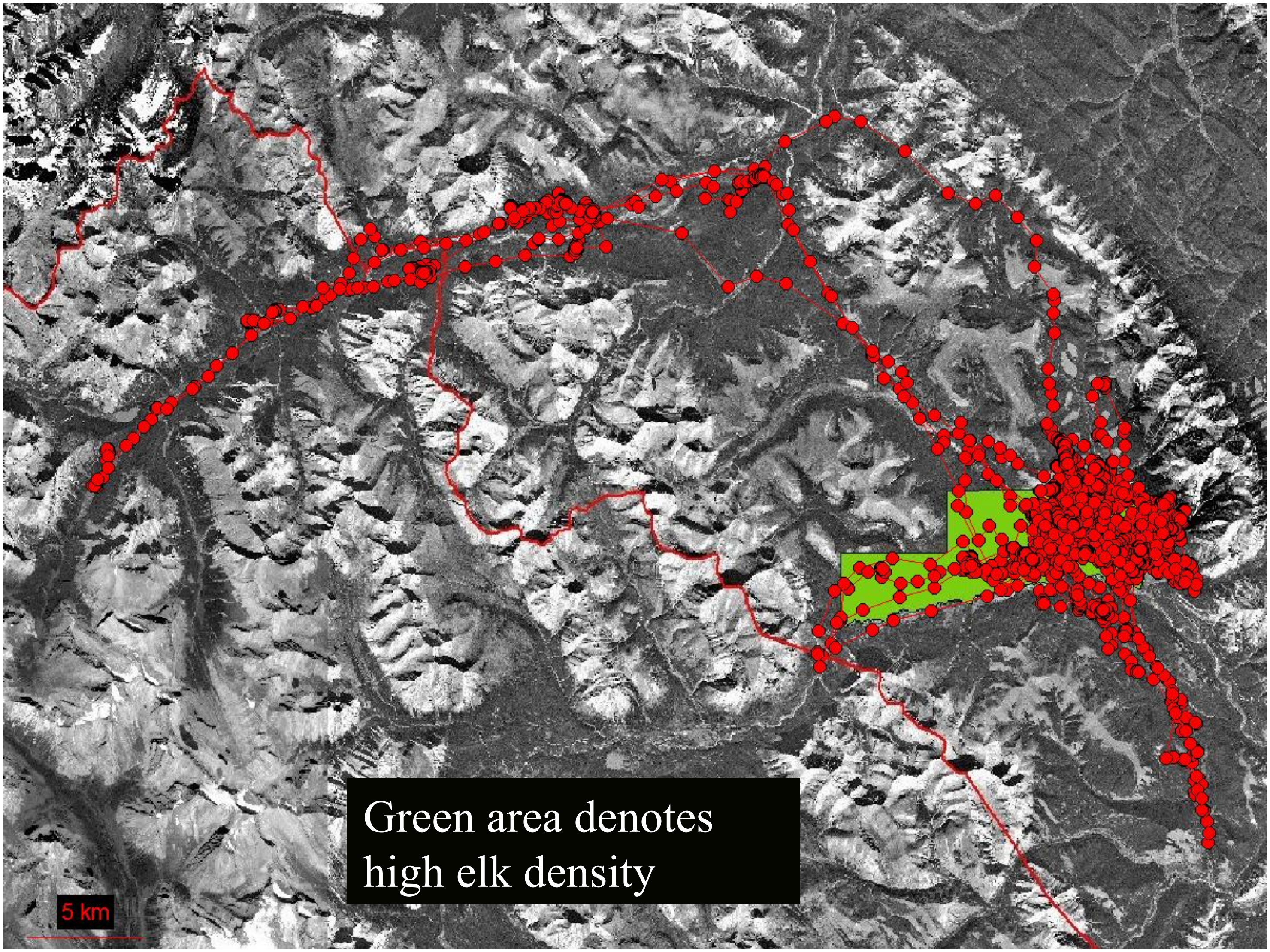


Phenomenological model for microscale movement patterns

Mechanistic model (micro->macro) fitted to microscale movement patterns

Fit to microdata

How do animals make movement decisions? Step Selection Functions

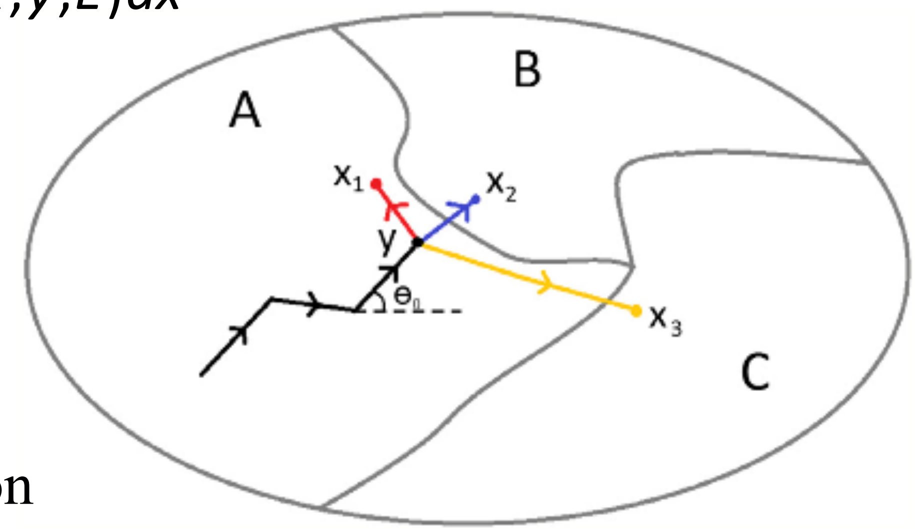


How do animals make movement decisions? Step Selection Functions

Models a step from y to x, given that the animal arrived at y with bearing θ_0, with probability density function

$$f(x|y,\theta_0) = \frac{\rho(|x-y|)\, V(x,y,\theta_0)\, W(x,y,E)}{\int_{\Omega} \rho(|x'-y|)\, V(x',y,\theta_0)\, W(x,y,E)dx'}$$

where



$\rho(|x-y|)$ is the step length distribution

$V(x,y,\theta_0)$ is the turning angle distribution

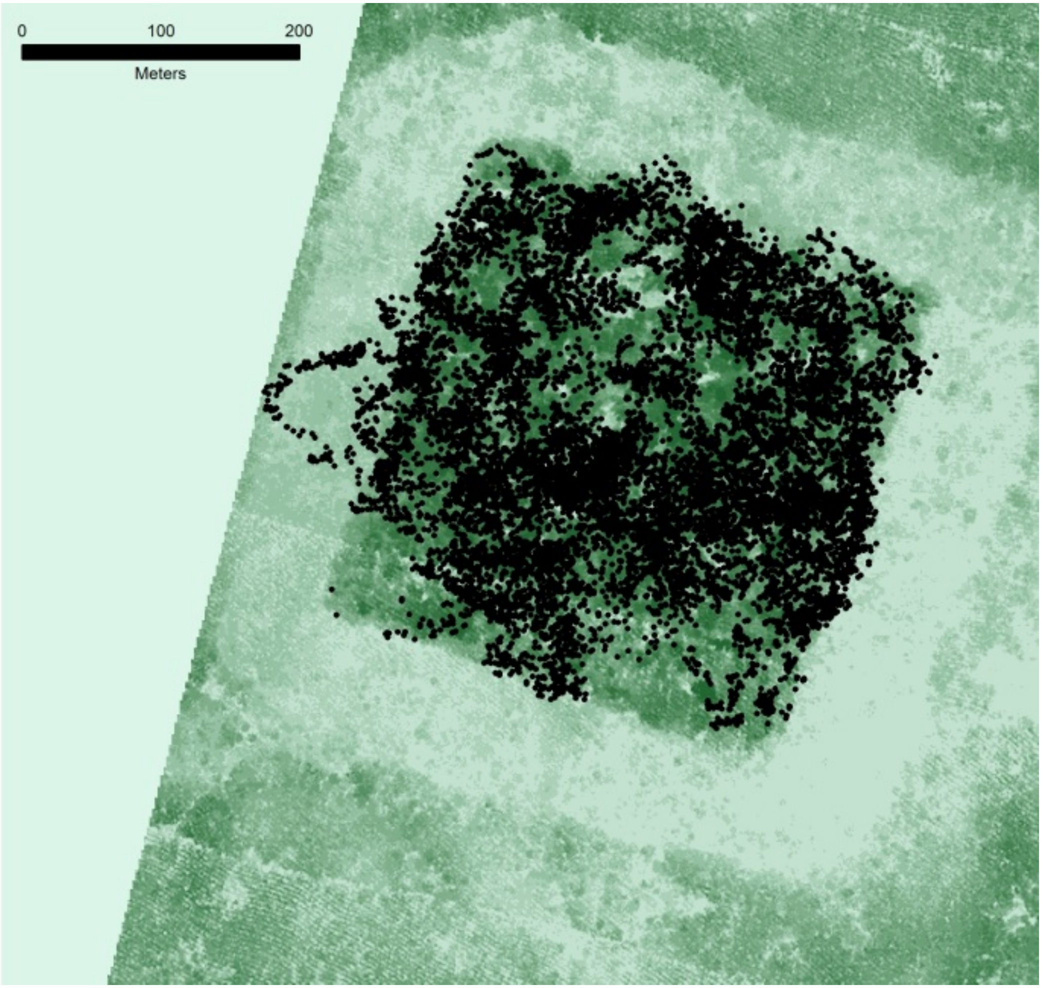
$W(x,y,E)$ is the weighting function

E differs in different habitat type: A, B, C, ...

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320-1330.

$$f(\boldsymbol{x}|\boldsymbol{y},\theta_0) \propto \rho(|\boldsymbol{x}-\boldsymbol{y}|)V(\boldsymbol{x},\boldsymbol{y},\theta_0)W(\boldsymbol{x},\boldsymbol{y},E)$$

Example : Amazonian bird flocks



Potts, J.R., Mokross, K., Stouffer, P.C., Lewis, M.A. (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4(24): 4578-4588

$$f(\boldsymbol{x}|\boldsymbol{y},\theta_0) \propto \rho(|\boldsymbol{x}-\boldsymbol{y}|)V(\boldsymbol{x},\boldsymbol{y},\theta_0)W(\boldsymbol{x},\boldsymbol{y},E)$$

Hypotheses

1. Birds are more likely to move to higher canopies:

$$W_1(\boldsymbol{x},\boldsymbol{y},E) = (\text{canopy height at } \mathbf{x})^{\boldsymbol{\alpha}}$$

Potts, J.R., Mokross, K., Stouffer, P.C., Lewis, M.A. (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4(24): 4578-4588

Maximum likelihood technique

1. Find the α that maximises:

$$\prod_{n=1}^{N} f_1(\boldsymbol{x}_n | \boldsymbol{x}_{n-1}, \theta_{n-1}, \alpha)$$

where $\boldsymbol{x}_0, \ldots, \boldsymbol{x}_N$ and $\theta_0, \ldots, \theta_N$ are, respectively, the sequence of positions and trajectories from the data, and

$$f_1(\boldsymbol{x}|\boldsymbol{y}, \theta_0) \propto \rho(|\boldsymbol{x} - \boldsymbol{y}|) V(\boldsymbol{x}, \boldsymbol{y}, \theta_0) W_1(\boldsymbol{x}, \boldsymbol{y}, E)$$

Avgar, T., Potts, J.R., Lewis, M.A, Boyce, M.S. (2016) Integrated step selection analysis: Bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*. doi: 10.1111/2041-210X.12528

$$f(\boldsymbol{x}|\boldsymbol{y},\theta_0) \propto \rho(|\boldsymbol{x}-\boldsymbol{y}|)V(\boldsymbol{x},\boldsymbol{y},\theta_0)W(\boldsymbol{x},\boldsymbol{y},E)$$

Hypotheses

1. Birds are more likely to move to higher canopies:

$$W_1(\boldsymbol{x},\boldsymbol{y},E) = (\text{canopy height at } \mathbf{x})^{\boldsymbol{\alpha}}$$

2. In addition, birds are more likely to move to lower ground:

$$W_2(\boldsymbol{x},\boldsymbol{y},E) = (\text{canopy height at } \mathbf{x})^{\boldsymbol{\alpha}}(\text{ground height at } \mathbf{x})^{-\boldsymbol{\beta}}$$

Potts, J.R., Mokross, K., Stouffer, P.C., Lewis, M.A. (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4(24): 4578-4588

Resulting model

$$f(\boldsymbol{x}|\boldsymbol{y},\theta_0) \propto \rho(|\boldsymbol{x}-\boldsymbol{y}|)V(\boldsymbol{x},\boldsymbol{y},\theta_0)C(\boldsymbol{x})^{\alpha}T(\boldsymbol{x})^{-\beta}$$

Step length distribution

Canopy height at end of step

Turning angle distribution

Topographical height at end of step

$$\alpha = 0.227, \beta = 1.697$$

Potts, J.R., Mokross, K., Stouffer, P.C., Lewis, M.A. (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4(24): 4578-4588

How does this movement pattern relate to a distribution pattern arising from habitat use?

Consider simple case:

(i) turning angle is uniform,
(ii) step selection depends only on destination $\boldsymbol{x}$ so $w(\boldsymbol{x})$ and
(iii) small step length τ

$$f_\tau(x|y) = \frac{\rho_\tau(|x-y|)\, w(x)}{\int_\Omega \rho_\tau(|x'-y|)\;\; w(x')dx'}$$

Moorcroft and Barnett (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* 89(4), 1112–1119

Talk Outline

- Mechanistic modelling of home range behaviour: two approaches to parameterizing the same model
- Using *advection-diffusion equations* to understand territorial structures (eg. coyotes, meerkats, gang activity)
- Using statistical *resource selection* and *step selection functions* to understand movement and space use
- Connecting resource selection with advection-diffusion
- Using *coupled step selection functions* to understand territorial and home range structures (e.g. Amazonian birds)
- Challenges for the future

From movement patterns to distribution patterns

Model 1

$$\underbrace{u(\boldsymbol{x},t+\boldsymbol{\tau})}_{\substack{\text{space use at} \\ \text{time } t+\boldsymbol{\tau}}} = \int_\Omega \underbrace{u(\boldsymbol{y},t)}_{\substack{\text{space use at} \\ \text{time } t}} \quad \underbrace{f_{\boldsymbol{\tau}}(\boldsymbol{x}\,|\,\boldsymbol{y})}_{\text{movement kernel}} \quad d\,\boldsymbol{y}$$

Master equation

Model 2

$$\underbrace{\frac{\partial u}{\partial t}}_{\substack{\text{rate of change} \\ \text{of local} \\ \text{space use}}} + \underbrace{\nabla\cdot\left[\boldsymbol{c}(\boldsymbol{x})u\right]}_{\substack{\text{change due to} \\ \text{biased motion}}} = \underbrace{\sum_{i,j=1}^{2}\frac{\partial^2}{\partial x_i x_j}\left[d_{ij}(\boldsymbol{x})u\right]}_{\substack{\text{change due to} \\ \text{random motion}}}$$

differential eq approximates the Master eq

$$\boldsymbol{c}(\boldsymbol{x}) = \lim_{\boldsymbol{\tau}\to 0}\frac{1}{\boldsymbol{\tau}}\int_\Omega (\boldsymbol{y}-\boldsymbol{x}) f_{\boldsymbol{\tau}}(\boldsymbol{x}\,|\,\boldsymbol{y})\,d\,\boldsymbol{y}$$

Advection coefficient

$$d_{ij}(\boldsymbol{x}) = \lim_{\boldsymbol{\tau}\to 0}\frac{1}{2\boldsymbol{\tau}}\int_\Omega (y_i - x_i)(y_j - x_j) f_{\boldsymbol{\tau}}(\boldsymbol{x}\,|\,\boldsymbol{y})\,d\,\boldsymbol{y}$$

Diffusion coefficient

$u(\boldsymbol{x},t)$ is density function for the location of individual at time t.

eg, Okubo (1980)

From movement patterns to distribution patterns

The simplified step selection function

$$f_\tau(x \mid y) = \frac{\rho_\tau(|x-y|)\; w(x)}{\int_\Omega \rho_\tau(|x'-y|)\;\; w(x')dx'}$$

diffusion and advection coefficients

$$d = \lim_{\tau \to 0} \frac{M_2(\boldsymbol{\tau})}{2\boldsymbol{\tau}} \text{ where } M_2(\boldsymbol{\tau}) = \int_\Omega r^2 \rho_\tau(r) dr$$

$$\boldsymbol{c}(\boldsymbol{x}) = \lim_{\tau \to 0} \frac{M_2(\boldsymbol{\tau})}{\boldsymbol{\tau}} \frac{\nabla w}{w} = 2d \frac{\nabla w}{w}$$

Moorcroft and Barnett (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* 89(4), 1112–1119

Distribution pattern as an equilibrium solution

The equilibrium solution to the advection diffusion equation is

$$\underbrace{\nabla \cdot \left[\boldsymbol{c}(\boldsymbol{x}) u \right]}_{\text{biased motion}} = \underbrace{\nabla^2 \left[d u \right]}_{\text{random motion}} \qquad \text{where } \boldsymbol{c}(\boldsymbol{x}) = 2d \frac{\nabla w}{w}$$

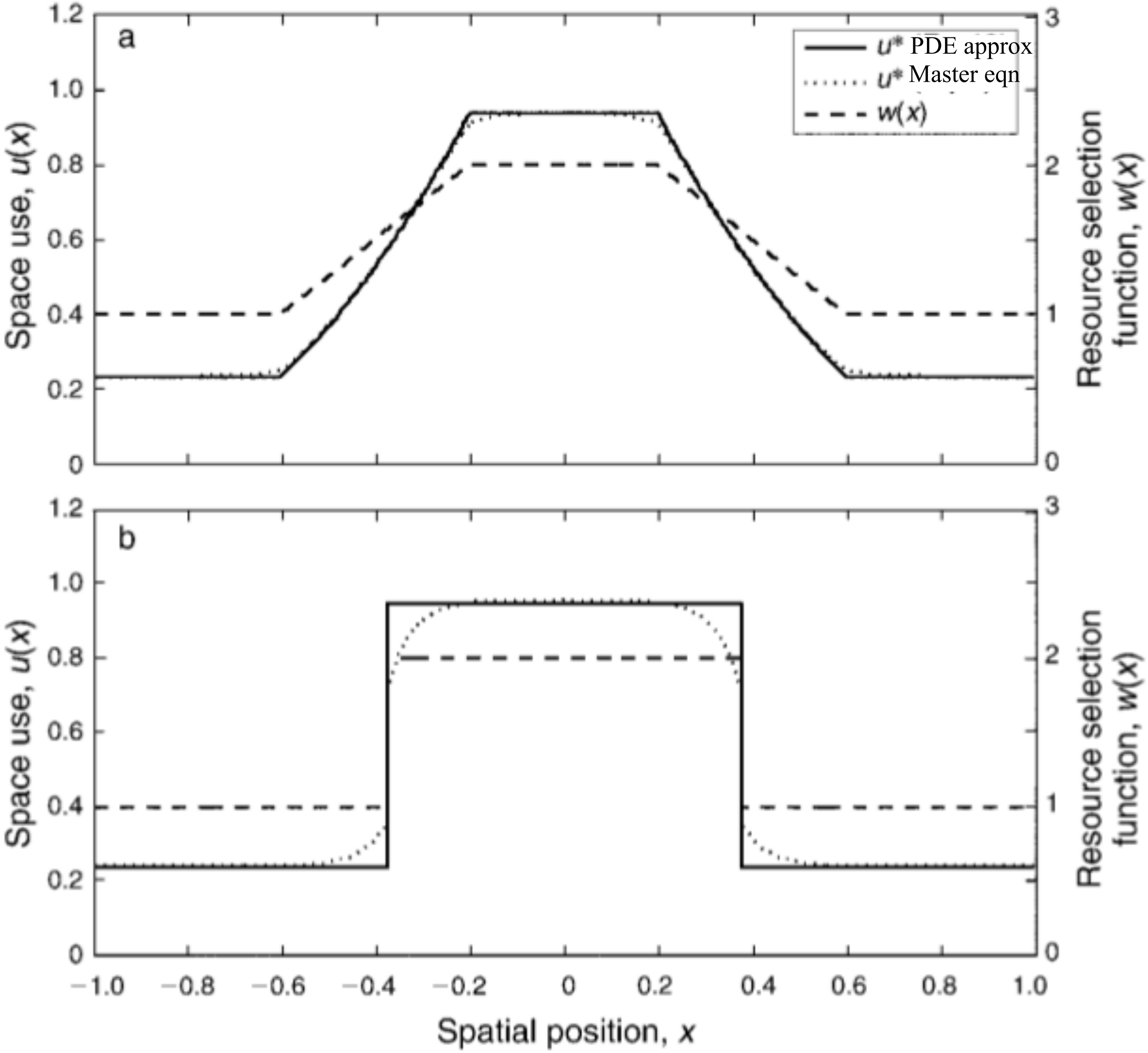
Integration and application of zero-flux boundary conditions gives

$$u_*(\boldsymbol{x}) = \frac{1}{W_0} w^2(\boldsymbol{x}) \qquad \text{where } W_0 = \int_\Omega w^2(\boldsymbol{x})\, dx$$

The equilibrium solution is proportional to the step selection function squared!

Moorcroft and Barnett (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* 89(4), 1112–1119

Distribution pattern as an equilibrium solution



PDE approx:

$$u_*(x) \approx \frac{1}{W_0} w^2(x)$$

Master eqn:

$$u_*(x) = \int_\Omega u_*(y)\rho_\tau(|x-y|)w(x)\,dy$$

Moorcroft and Barnett (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* 89(4), 1112–1119

Steady-state solution

$$u_*(\boldsymbol{x}) = \lim_{t\to\infty} u(\boldsymbol{x},t) \approx \frac{1}{W_0} w(\boldsymbol{x})^2,$$

where $W_0 = \int w(\boldsymbol{x})^2 d\boldsymbol{x}$.

Step weighting function based on resources

For the Amazonian birds, ignoring correlations in movement:

$$u_*(\boldsymbol{x}) \propto C(\boldsymbol{x})^{0.45} T(\boldsymbol{x})^{-3.40}$$

Potts, J.R., Mokross, K., Stouffer, P.C., Lewis, M.A. (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4(24): 4578-4588

Steady-state solution

$$u_*(\boldsymbol{x}) = \lim_{t\to\infty} u(\boldsymbol{x},t) \approx \frac{1}{W_0} w(\boldsymbol{x})^2,$$

where $W_0 = \int w(\boldsymbol{x})^2 d\boldsymbol{x}$.

Step weighting function
based on resources

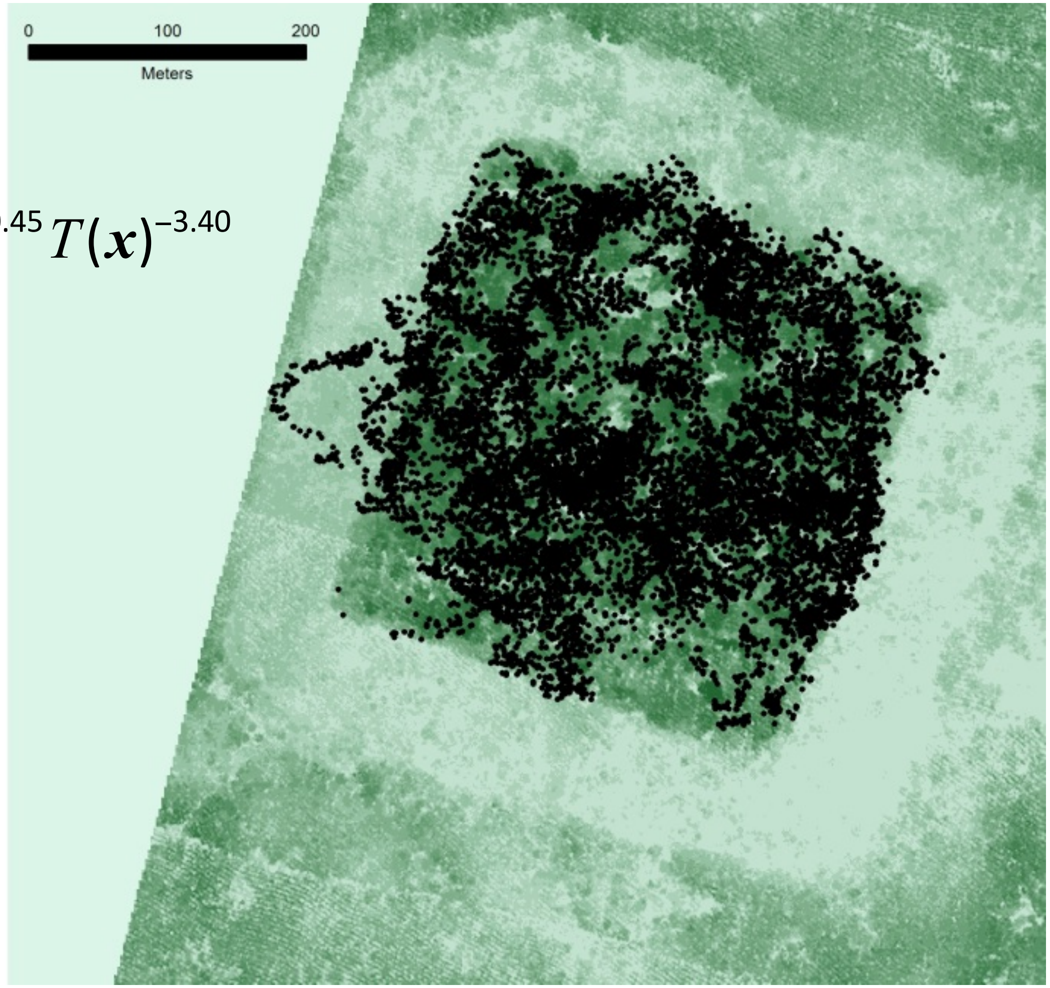
For the Amazonian birds, ignoring correlations in movement:

$$\underbrace{u_*(\boldsymbol{x}) \propto C(\boldsymbol{x})^{0.45} T(\boldsymbol{x})^{-3.40}}$$

Resource selection function

Potts, J.R., Mokross, K., Stouffer, P.C., Lewis, M.A. (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4(24): 4578-4588

Amazonian bird flocks



$$u_*(\boldsymbol{x}) \propto C(\boldsymbol{x})^{0.45}\, T(\boldsymbol{x})^{-3.40}$$

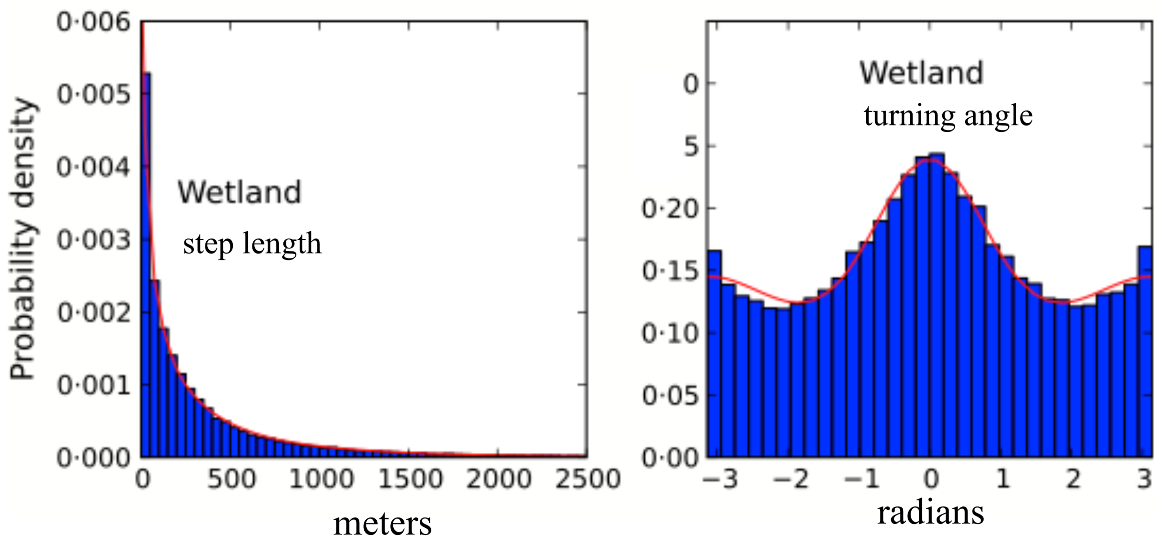
Potts, J.R., Mokross, K., Stouffer, P.C., Lewis, M.A. (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4(24): 4578-4588

How well does the approximation hold up?

Consider a more realistic situation:

(i) turning angle is not uniform,
(ii) step selection depends on start and destination points so $w(\boldsymbol{x},\boldsymbol{y})$ and
(iii) longer step length τ
(iv) step length and turning angles vary as a function of space

Eg. Barren land caribou



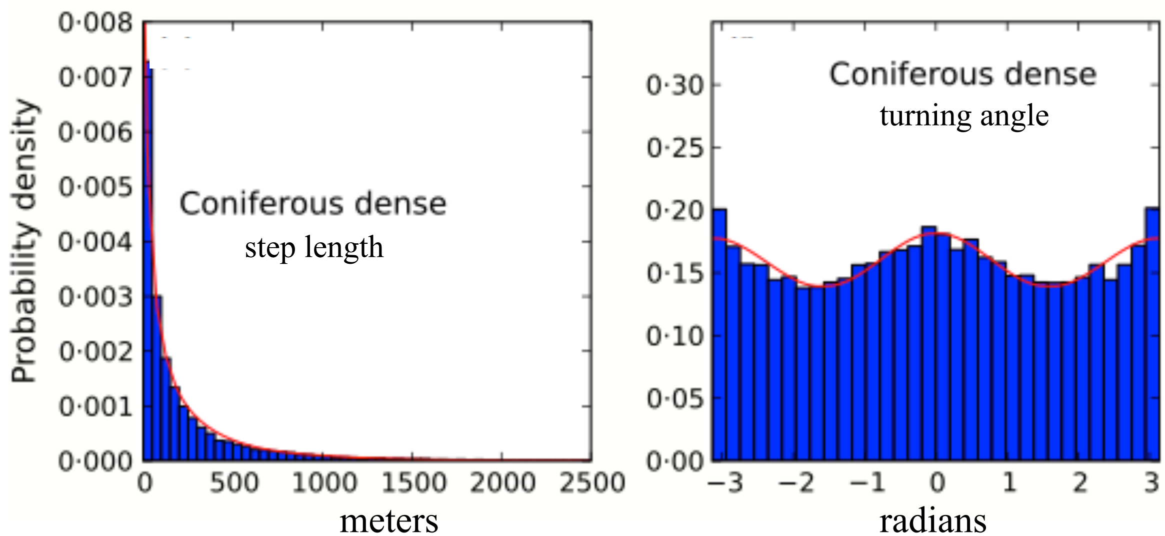
Potts, J.R., Bastille-Rousseau, G., Murray, D., Schaefer, J., Lewis, M.A. (2014) Predicting local and nonlocal effects of resources on animal space use using a mechanistic step-selection function. *Methods in Ecology and Evolution*. 5(3): 253-262.

How well does the approximation hold up?

Consider a more realistic situation:

(i) turning angle is not uniform,
(ii) step selection depends on start and destination points so $w(\boldsymbol{x},\boldsymbol{y})$ and
(iii) longer step length τ
(iv) step length and turning angles vary as a function of location

Eg. Barren land caribou

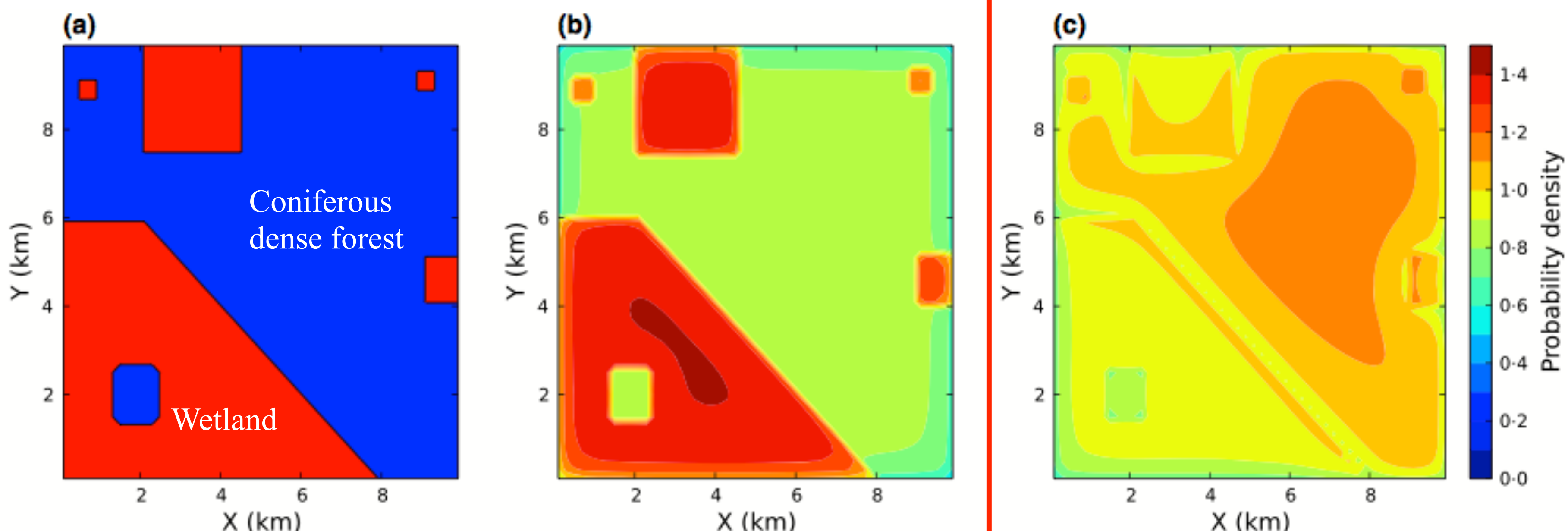


Potts, J.R., Bastille-Rousseau, G., Murray, D., Schaefer, J., Lewis, M.A. (2014) Predicting local and nonlocal effects of resources on animal space use using a mechanistic step-selection function. *Methods in Ecology and Evolution*. 5(3): 253-262.

Approximation breaks down when step length and turning angle are functions of location

Items (i)-(iii) included

Items (i)-(iv) included



Habitat type

Steady state

Steady state

Step length and turning angle are the same for both habitat types

Step length and turning angle differ for different habitat types

Potts, J.R., Bastille-Rousseau, G., Murray, D., Schaefer, J., Lewis, M.A. (2014) Predicting local and nonlocal effects of resources on animal space use using a mechanistic step-selection function. *Methods in Ecology and Evolution*. 5(3): 253-262.

Summary: Resource and Step Selection models

- **Resource Selection Models** correlate space use with available habitat type.
- **Step Selection Models** correlate movement decisions over fixed (specified) time steps with available habitat type, and also include step length and turning angles.
- Both types of models allow the inclusion of detailed habitat features based on geographical information systems.
- Step Selection Models can be approximated with PDEs and this allows for simple analytical approximations for resource selection.
- However, the approximations can break down, especially when step length and turning angle differ in different habitat types.

Talk Outline

- Mechanistic modelling of home range behaviour: two approaches to parameterizing the same model
- Using *advection-diffusion equations* to understand territorial structures (eg. coyotes, meerkats, gang activity)
- Using statistical *resource selection* and *step selection functions* to understand movement and space use
- Connecting resource selection with advection-diffusion
- Using *coupled step selection functions* to understand territorial and home range structures (e.g. Amazonian birds)
- Challenges for the future

Including behavioral interactions

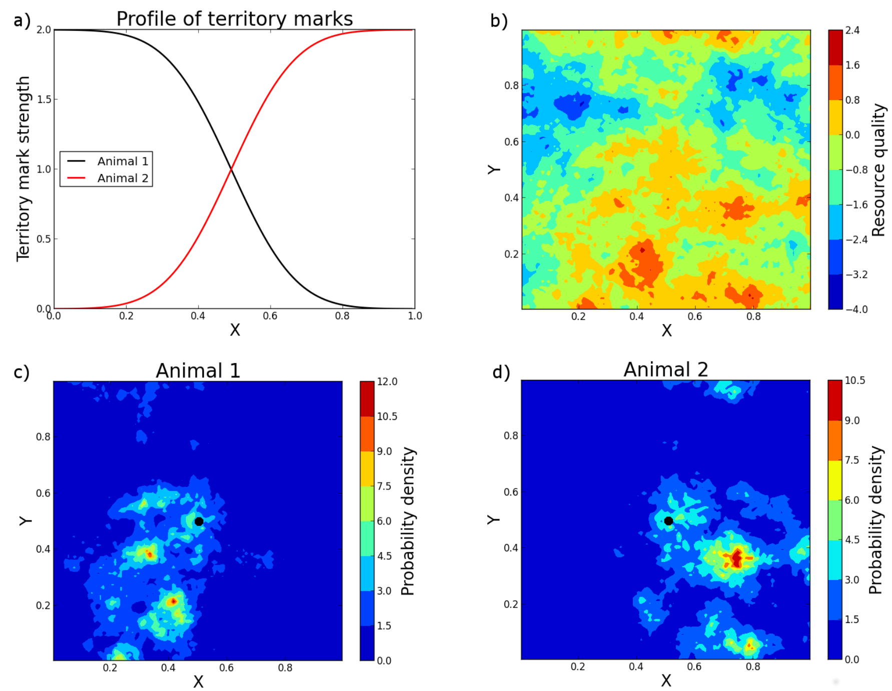
- Individuals interact and may be territorial. The same holds true for groups of individuals such as packs.
- As we have seen earlier in the lecture, there is a history of mechanistic home range models, which use PDEs to model interactions.
- One can undertake the same kind of extension to include interactions with **Coupled** Step Selection Functions

Coupled step selection functions

One step selection function for each agent and include an interaction term $C_i(\boldsymbol{x}, \boldsymbol{y}, P_{i,t})$:

$$f_{i,t}(\boldsymbol{x}|\boldsymbol{y}, \theta_0) \propto \rho_i(|\boldsymbol{x} - \boldsymbol{y}|)V_i(\boldsymbol{x}, \boldsymbol{y}, \theta_0)W_i(\boldsymbol{x}, \boldsymbol{y}, E)C_i(\boldsymbol{x}, \boldsymbol{y}, P_{i,t})$$

where $P_{i,t}$ represents both the population positions and any traces of their past positions left either in the environment or in the memory of agent i.



Potts, J.R., Mokross, K., Lewis, M.A. (2014) A unifying framework for quantifying the nature of animal interactions. *Journal of the Royal Society Interface*. 11(96): 20140333.

Detecting the territorial mechanism: the example of Amazonian birds

Territorial marking (vocalisations):

$P_{i,t}(\boldsymbol{x}) = T$ if any flock $j \neq i$ is at position $\boldsymbol{x}$ at time t

$\hat{P}_{i,t}(\boldsymbol{x}) = \min\{P_{i,t-\tau}(\boldsymbol{x}) - \tau, 0\}$ otherwise.

Hypothesis 1 (tendency not to go into another's territory):

Hypothesis 2 (tendency to retreat after visiting another's territory):

Potts, J.R., Mokross, K., Lewis, M.A. (2014) A unifying framework for quantifying the nature of animal interactions. *Journal of the Royal Society Interface*. 11(96): 20140333.

Detecting the territorial mechanism: the example of Amazonian birds

Territorial marking (vocalisations):

$P_{i,t}(\boldsymbol{x}) = T$ if any flock $j \neq i$ is at position $\boldsymbol{x}$ at time t

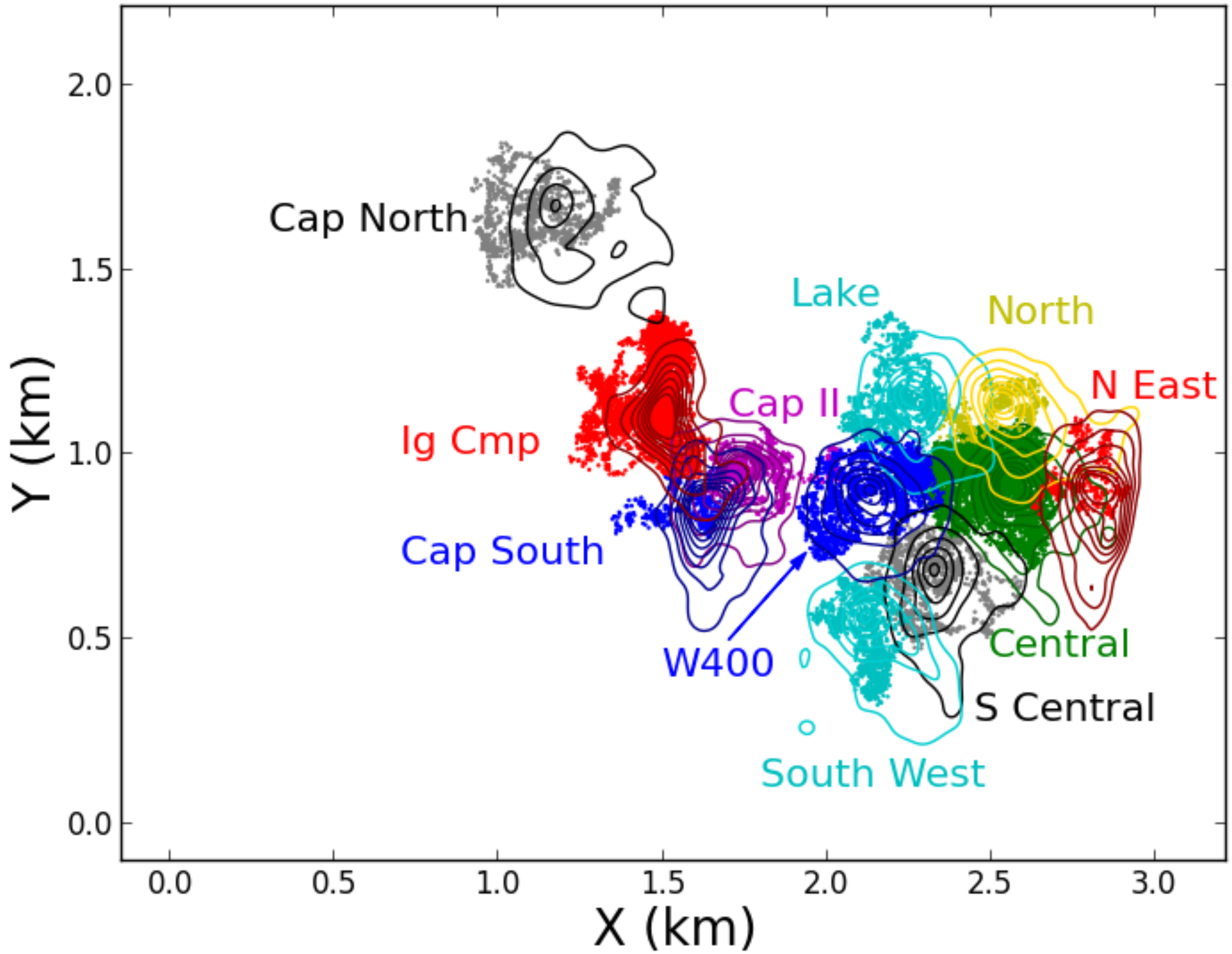
$\hat{P}_{i,t}(\boldsymbol{x}) = \min\{P_{i,t-\tau}(\boldsymbol{x}) - \tau, 0\}$ otherwise.

Hypothesis 1 (tendency not to go into another's territory): ✗

Hypothesis 2 (tendency to retreat after visiting another's territory): ✓

Potts, J.R., Mokross, K., Lewis, M.A. (2014) A unifying framework for quantifying the nature of animal interactions. *Journal of the Royal Society Interface*. 11(96): 20140333.

Amazonian birds: territorial space use patterns



Potts, J.R., Mokross, K., Lewis, M.A. (2014) A unifying framework for quantifying the nature of animal interactions. *Journal of the Royal Society Interface*. 11(96): 20140333.

Spatial Ecology

Quantitative analysis

Data

- Elevation map
- Canopy map
- Radiolocations of birds

Hypotheses

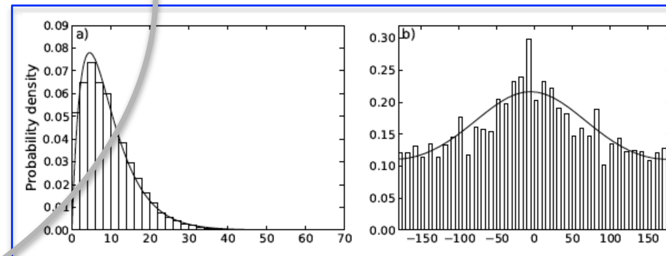
- Bird movement patterns governed by topography, canopy height and a conspecific avoidance mechanism

Mechanistic model

- Biased random walk model for individuals

Parameter estimates

Microscale movement patterns



- Data show step lengths and turning angle distributions for birds
- These vary, depending on elevation, canopy etc.

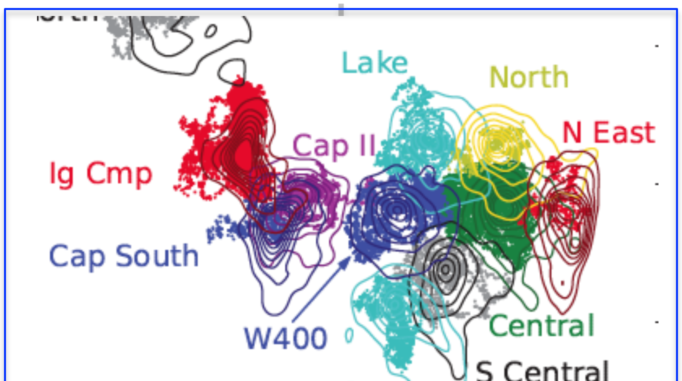
Inference/model selection

- Likelihood Ratio Test
- Information theory methods (eg. AIC)

Conclusions

- Topography, canopy height and conspecific avoidance go some way to explaining space use patterns
- But there are clearly missing aspects

Emergent patterns/validation



- Dots show radiolocations of bird flocks
- Colored lines: emergent patterns, with no fitting

Unifying collective behaviour and resource selection

Types of interaction: (E) Environmental, (BD) between-animal direct interactions, (BM) between-animal mediated; (AA) alignment-attraction models, (CA) conspecific avoidance models

Model	Reference	Interaction type
Resource selection	Boyce *et al.* (2002) *Ecol Model*	E
Step selection	Fortin *et al.* (2005) *Ecology*	E
Individual-based collective behavior	Couzin *et al.* (2002) *J Theor Biol*	BD, AA
Differential equation collective behavior	Eftimie *et al.* (2007) *PNAS*	BD, AA
Army ant foraging	Deneubourg *et al.* (1988) *J Insect Behav*	BM, AA
Individual-based territory formation	Potts *et al.* (2013) *Am Nat*	BM, CA
Differential equation territory formation	Moorcroft & Lewis (2006), PUP	BM, CA




Potts, J.R., Mokross, K., Lewis, M.A. (2014) A unifying framework for quantifying the nature of animal interactions. *Journal of the Royal Society Interface*. 11(96): 20140333.

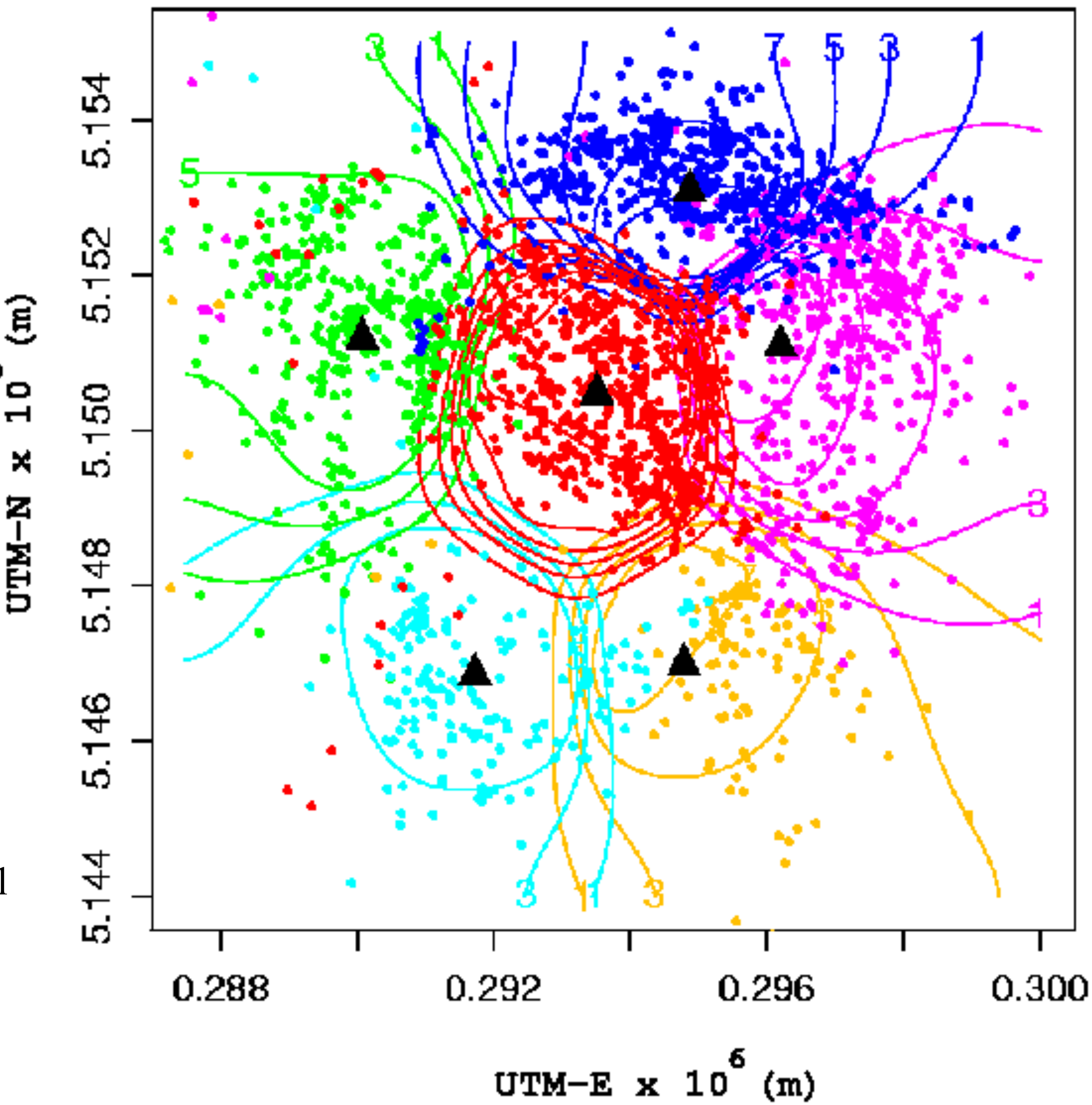
Acknowledgements

- Marie Auger-Méthé (Alberta)
- Mark Boyce (Alberta)
- Bob Crabtree (YERC)
- Luca Giuggioli (Bristol)
- Steve Harris (Bristol)
- The Lewis Lab (Alberta)
- Evelyn Merrill (Alberta)
- Karl Mokross (Louisiana State)
- Paul Moorcroft (Harvard)
- Jim Murray (Princeton)
- Phil Stouffer (Louisiana State)
- Jane White (Bath)

NSERC CRSNG

UNIVERSITY OF ALBERTA

Mechanistic home range model for coyote territories



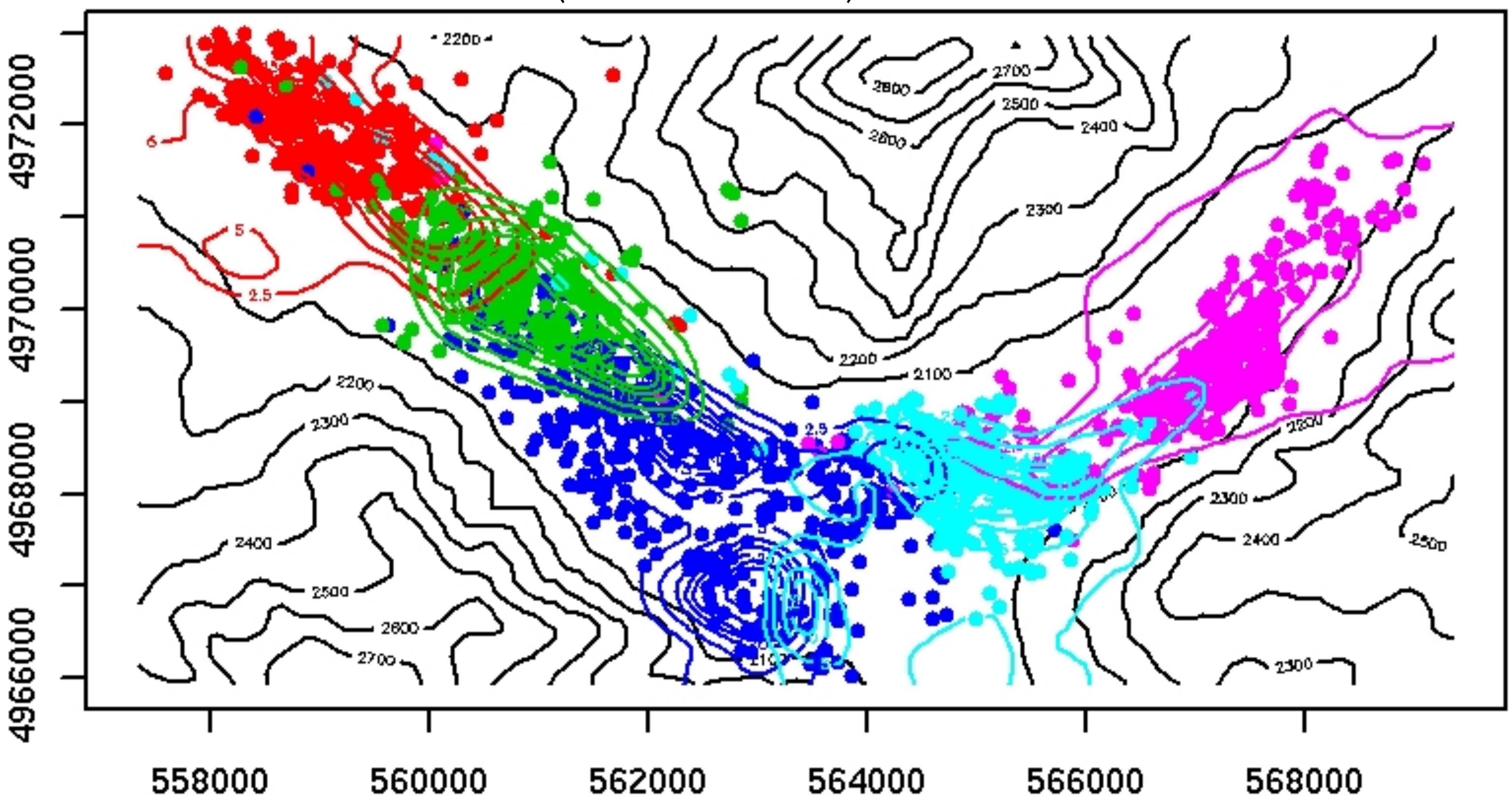
Numerical Maximum Likelihood fit of model to radio-location data

.Moorcroft, P.R., Lewis, M.A., Crabtree R. (1999). Home range analysis using a mechanistic home range model. *Ecology* 80:1656-1665.

Model fit to Yellowstone with added "prey-taxis"

$$k_i(\boldsymbol{x}, \boldsymbol{x}'\boldsymbol{\tau}, t) = f_\tau(\rho(h))K_\tau\left(\phi - \hat{\phi}, \sum_{j \neq i} p_j(x,t)\right)$$

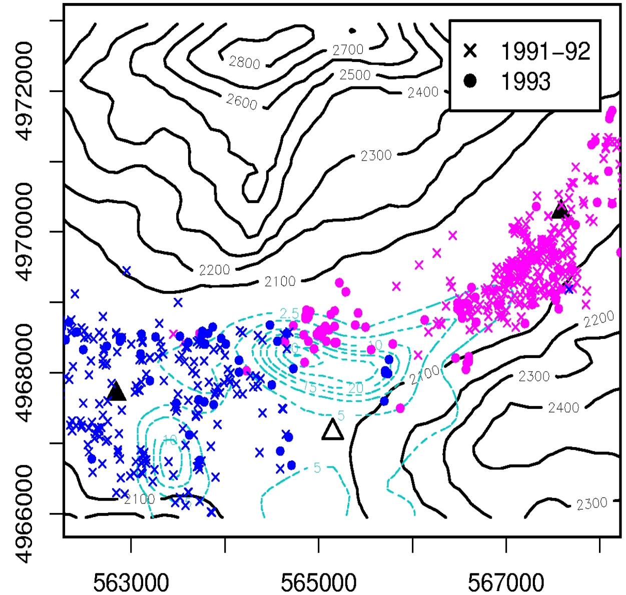
$$0 = \Delta u_i - \nabla \cdot \left(\beta \boldsymbol{x}_i u_i \sum_{j \neq i} p_j\right) + \nabla \cdot \left(\alpha_h u_i \nabla h\right)$$



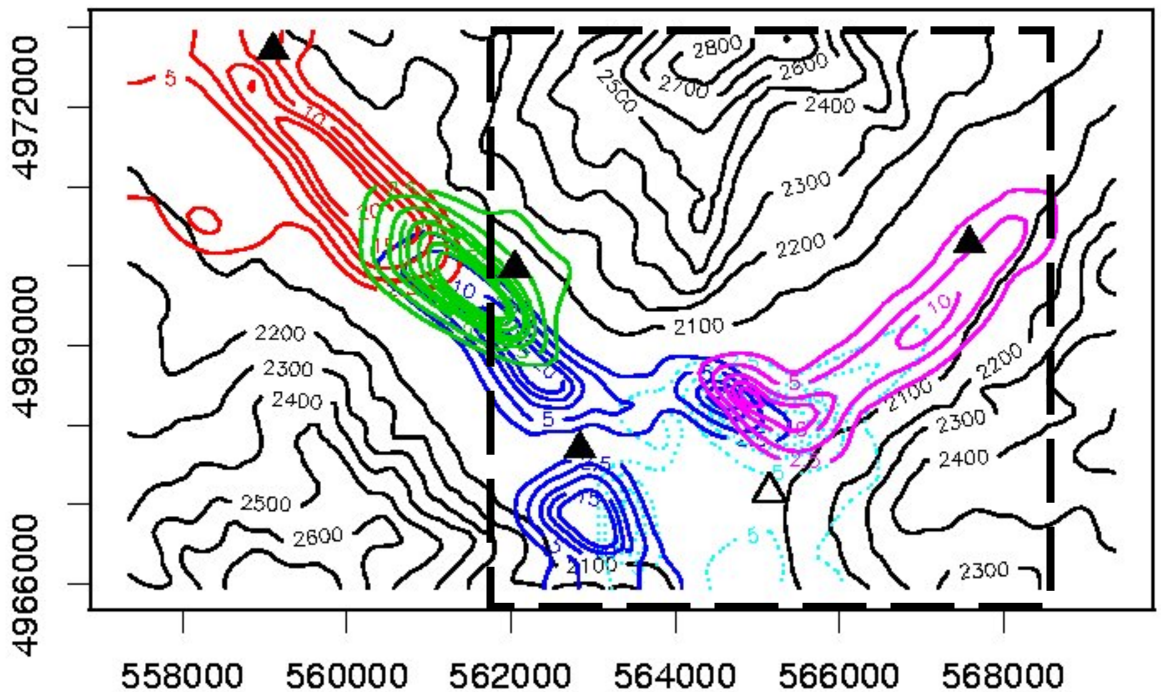
Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society of London B*, 273:1651-1659.

Shift in territories after loss of Norris Pack, 1993

Observation



Prediction



Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society of London B*, 273:1651-1659.