Territorial Pattern Formation Through Scent Marking

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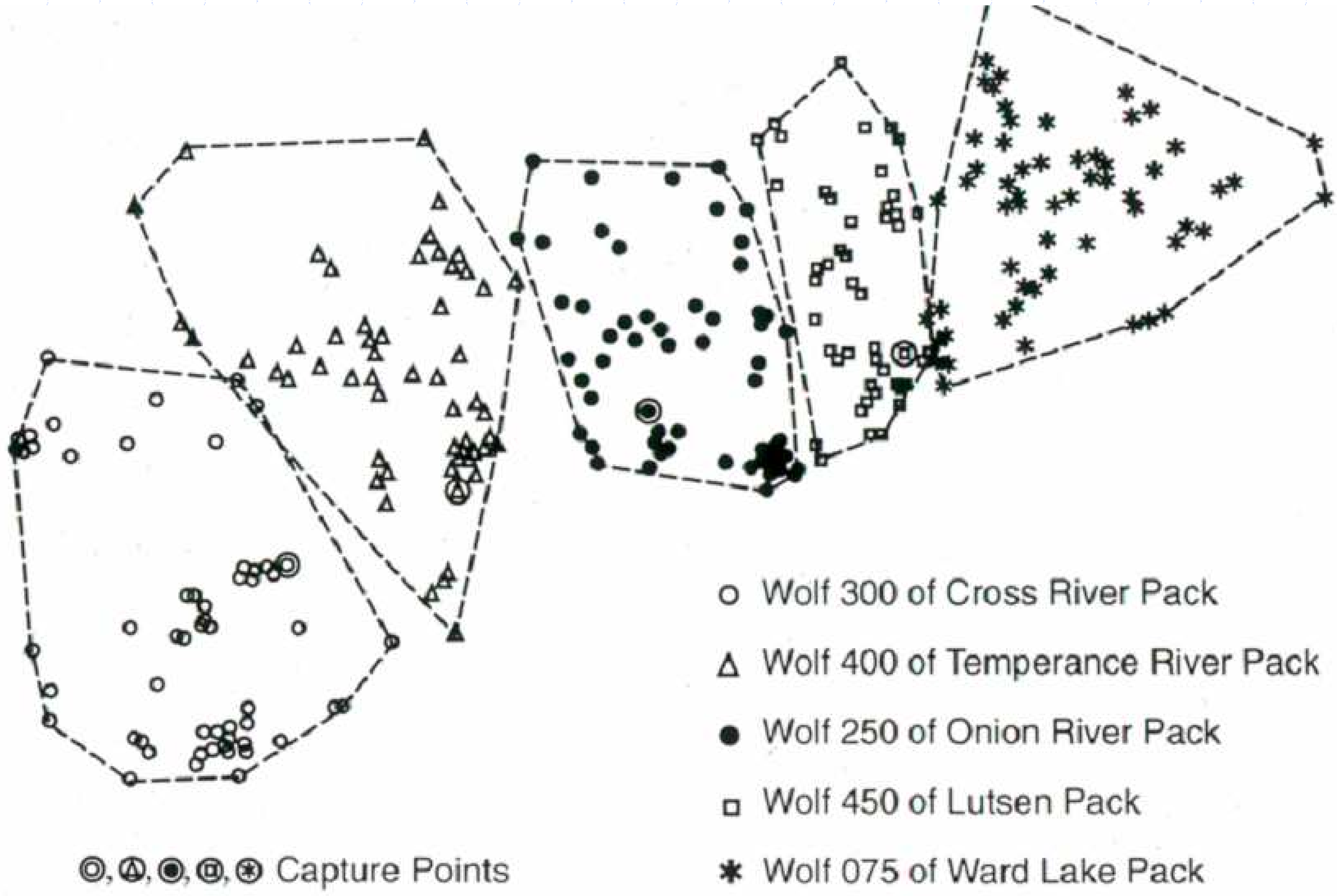
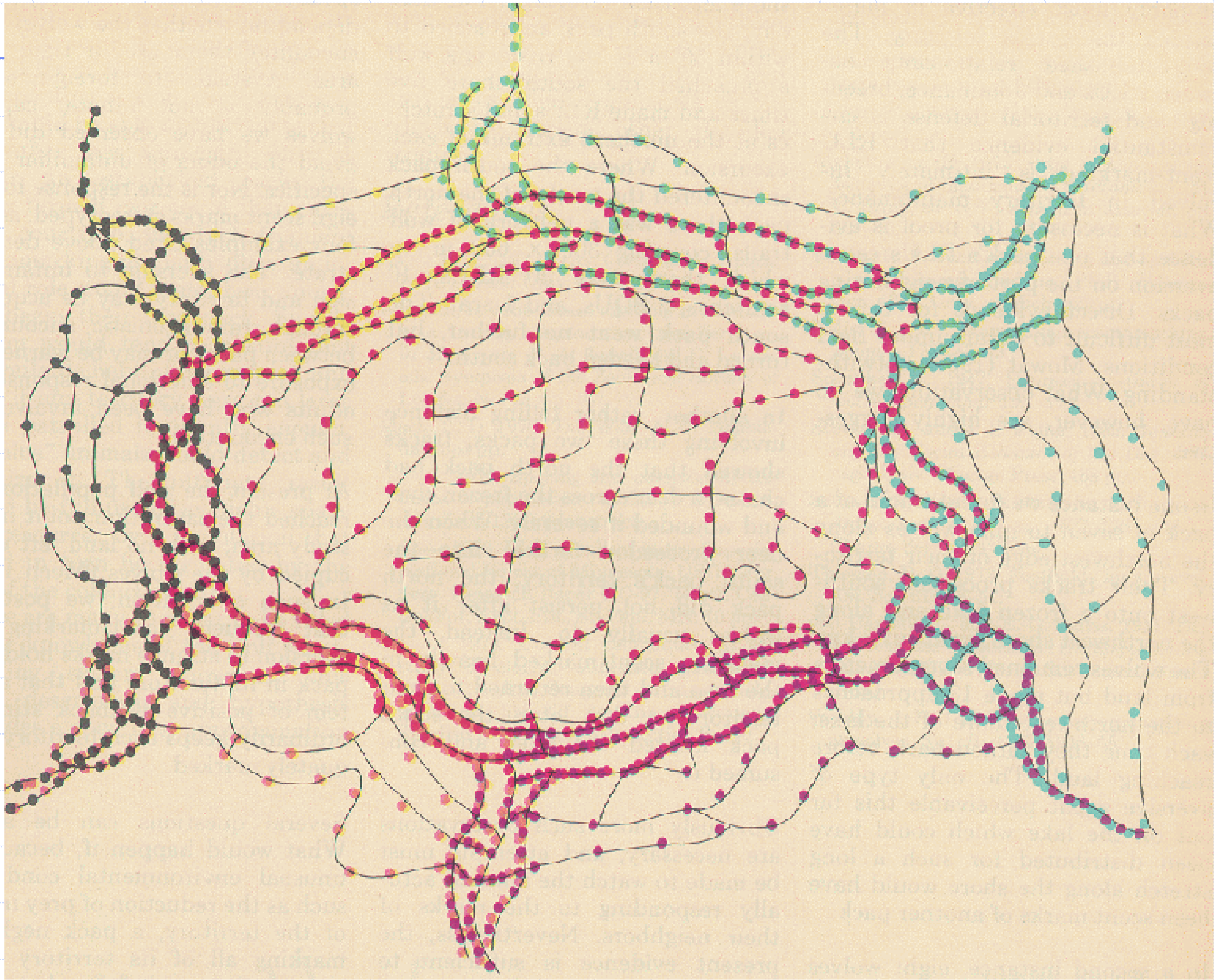
Social carnivores, such as wolves and coyotes, have distinct and well-defined home ranges.



Van Ballenberghe (1978)


Banff National Park

Scent marks provide important cues regarding the use of space by familiar and foreign packs.



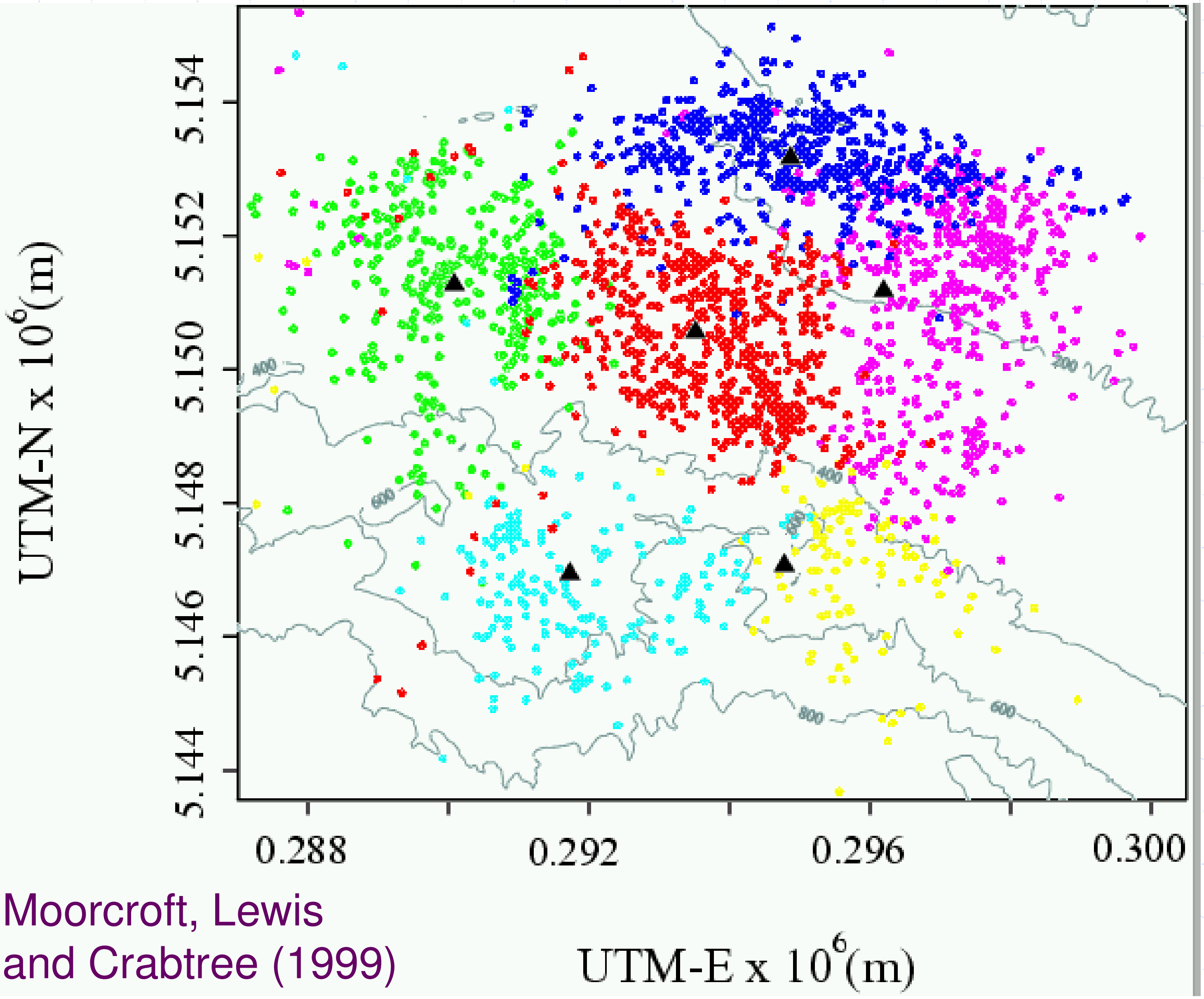
Peters and Mech (1975)


David Mech, photo

Territorial Interactions

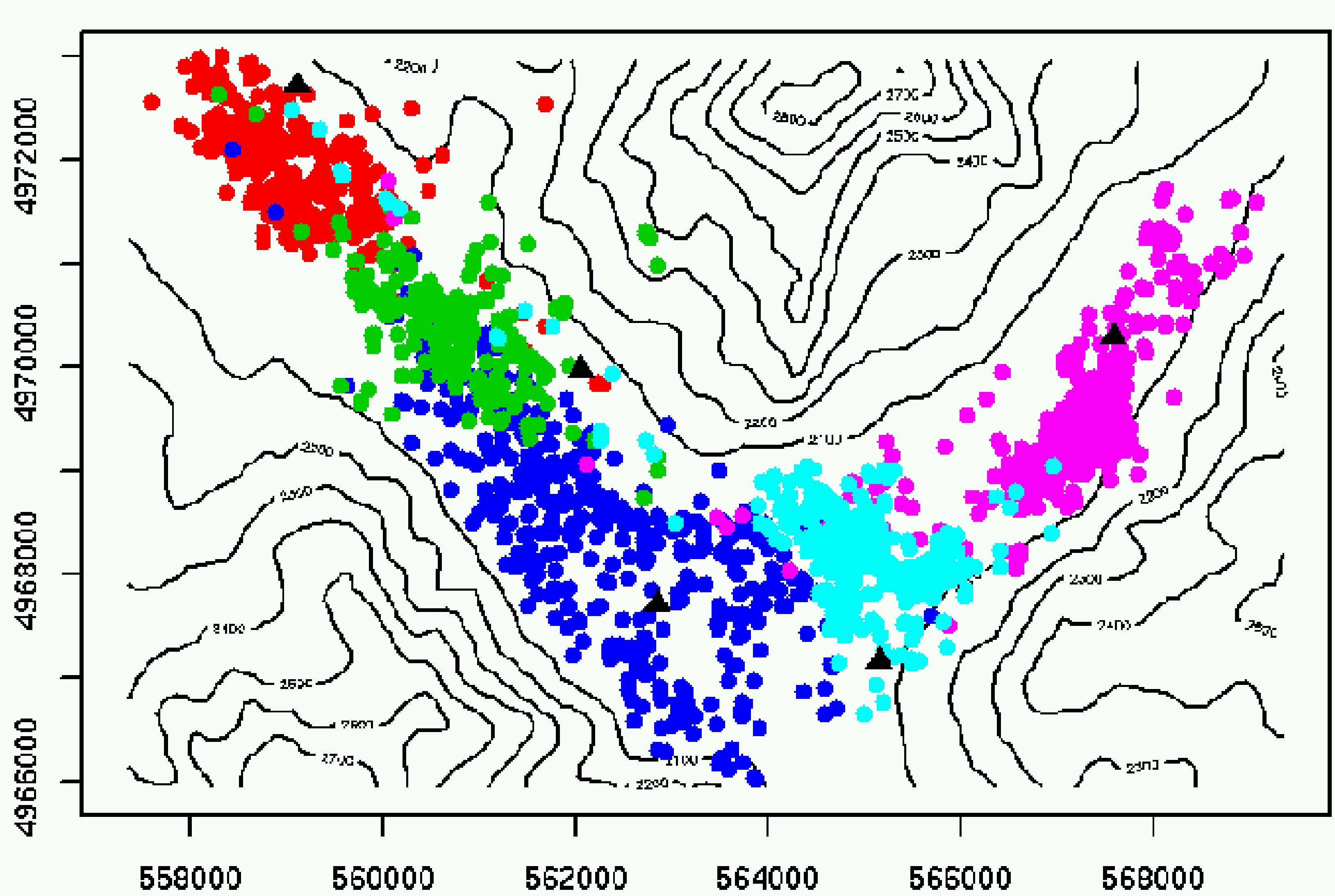
- Individuals forage by moving around their territory while searching for prey
- Scent-marking occurs throughout the territory
- “Bowl”-shaped pattern of scent marks
- Existing scent-marks (both foreign and familiar) elicit increased marking rates
- Movement patterns change in response to scent-marks
- In some wolf populations there are observed “buffer zones” between territories which are infrequently visited

Coyote locations from Hanford Arid Lands Ecosystem



Moorcroft, Lewis
and Crabtree (1999)

Coyote locations from Lamar valley, Yellowstone



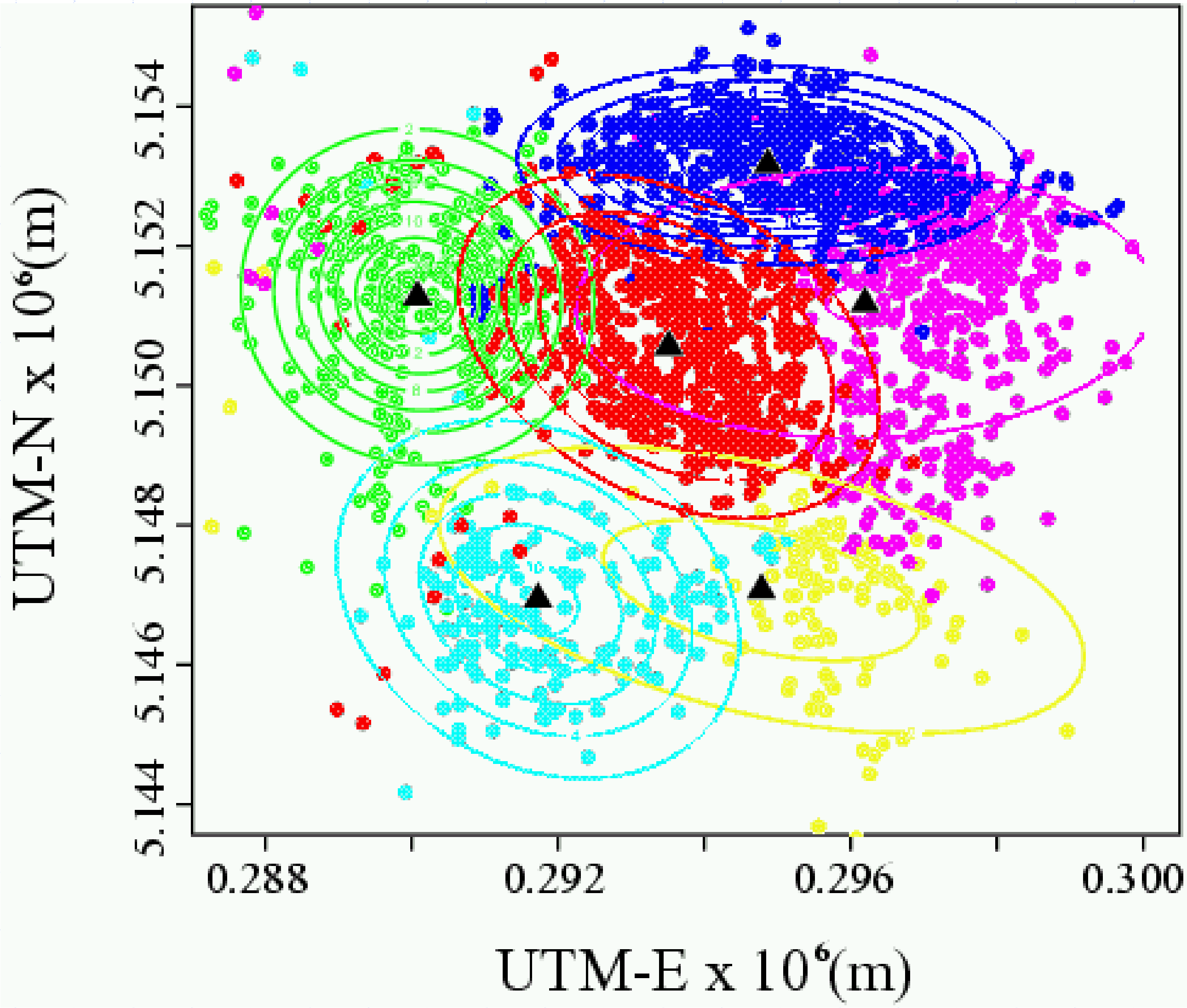
Moorcroft and Lewis (2004), based on Crabtree (unpublished)

Terrain

Hanford Arid Lands Ecosystem

Lamar Valley, Yellowstone

Fitting probability density functions: Bivariate Gaussian



Objective

- Formulate a mechanistic model for territorial pattern formation and maintenance based on behaviour rules for individuals, and test this model against radio-tracking data.

Outline

- Model with no den site
  - Formulation from random walk
  - Analysis and 'energy method'
  - Patterns
  - Conclusions
- Models based on den site
  - Territorial interactions
  - Evolutionarily stable strategies
  - Complex scent marking
  - Fit to radiotracking data
  - Other territorial patterns
  - Conclusions
- Discussion

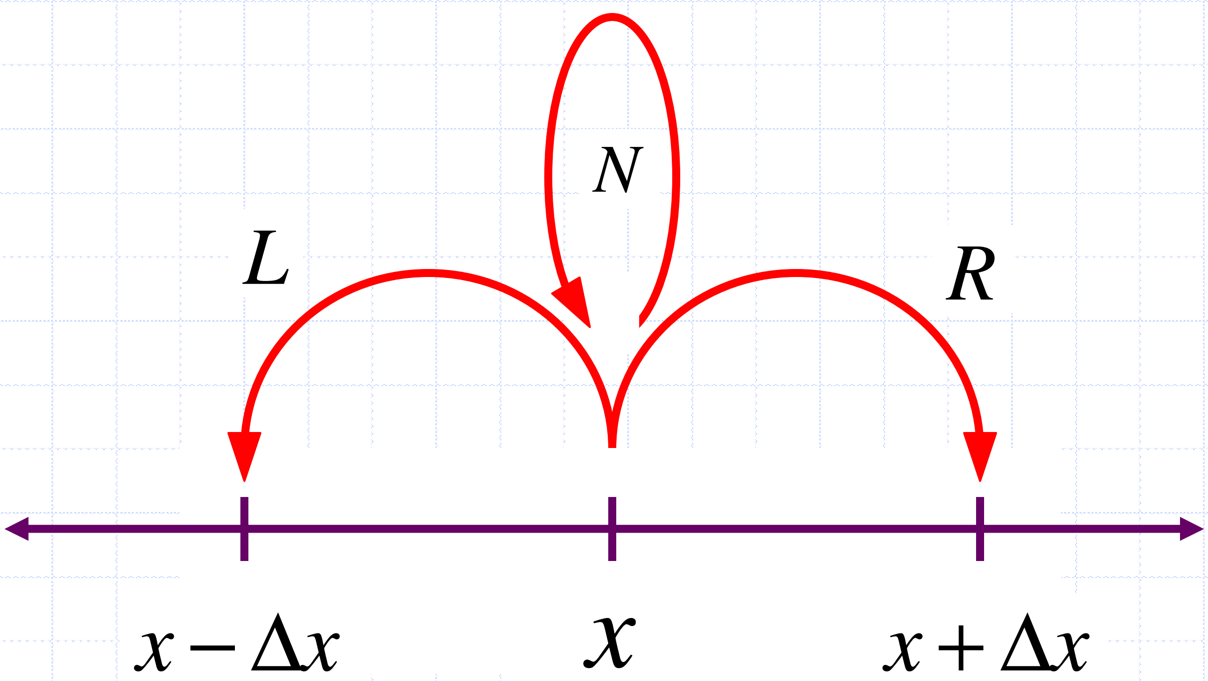
Home Range Model With No Den Site

- Well-defined wolf home-ranges can form in the absence of a den site (Rothman and Mech, 1979), and even in the absence of surrounding packs (Mech, 1991)
- Can we propose a mechanistic model involving interaction between scent-marking and movement behaviour that yield home range pattern formation?
- Model assumes (1) positive feedback in scent-marking dynamics (2) movement rate is a decreasing function of local scent-mark density

Briscoe, Lewis and Parrish (2001)

Model With No Den Site

$$R(x,t) = L(x,t) = (1 - N(x,t))/2$$



Animal movement modelled by random walk on a lattice

Take "diffusion" limit as space and time steps approach zero

Formulation From Random Walk

Forward Kolmogorov equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}\left[D(x,t)u(x,t)\right]$$

Motility

$$D(x,t) = D_0(1 - N(x,t))$$

Individuals remain at areas with high scent levels

$$N(x,t) = \frac{p(x,t)}{\alpha + p(x,t)}$$

Thus motility decreases with local scent levels

$$D(x,t) = \frac{D_0}{1 + p(x,t)/\alpha}$$

Model with scent marking

Movement equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}\left(\frac{u}{1+p}\right)$$

Scent-marking equation with feedback

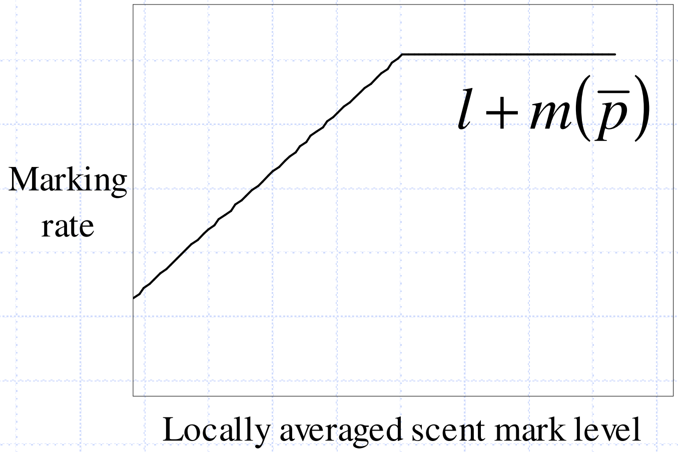
$$\varepsilon \frac{\partial p}{\partial t} = u\left(l + m(\bar{p})\right) - fp$$

Zero flux boundary conditions

$$0 = \frac{\partial}{\partial x}\left(\frac{u}{1+p}\right) \quad \text{at} \quad x = 0,1$$

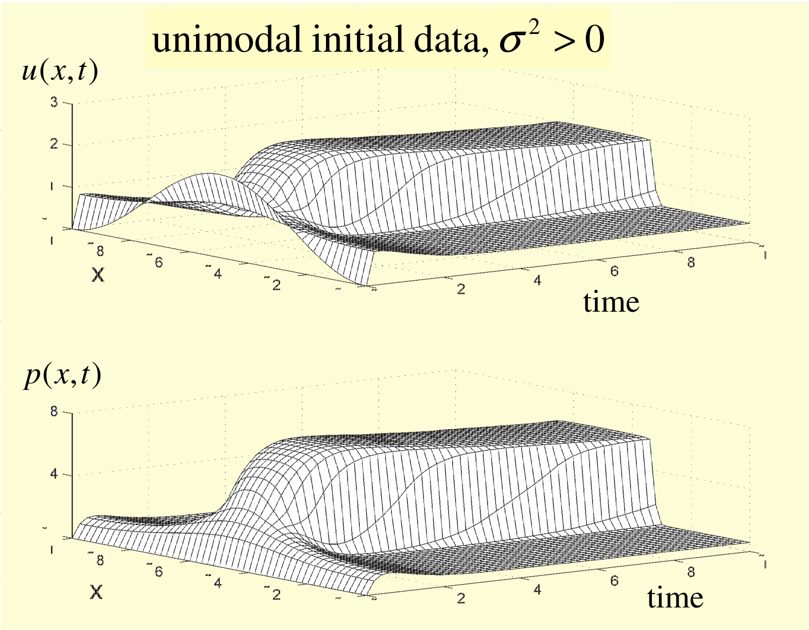
Local averaging of scent mark in positive feedback response m

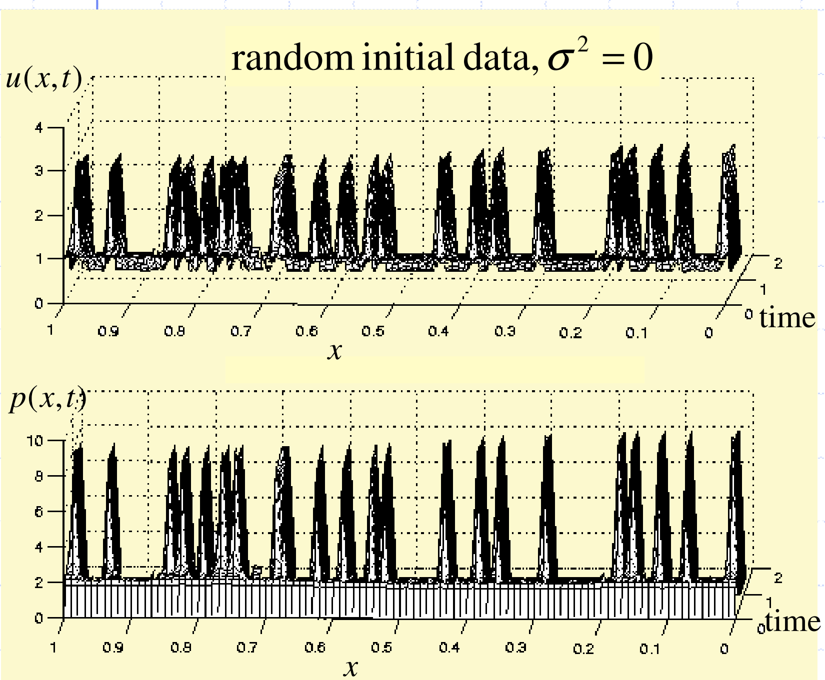
$$\bar{p}(x,t) = p(x,t) + \frac{\sigma^2}{2}\frac{\partial^2}{\partial x^2} p(x,t)$$

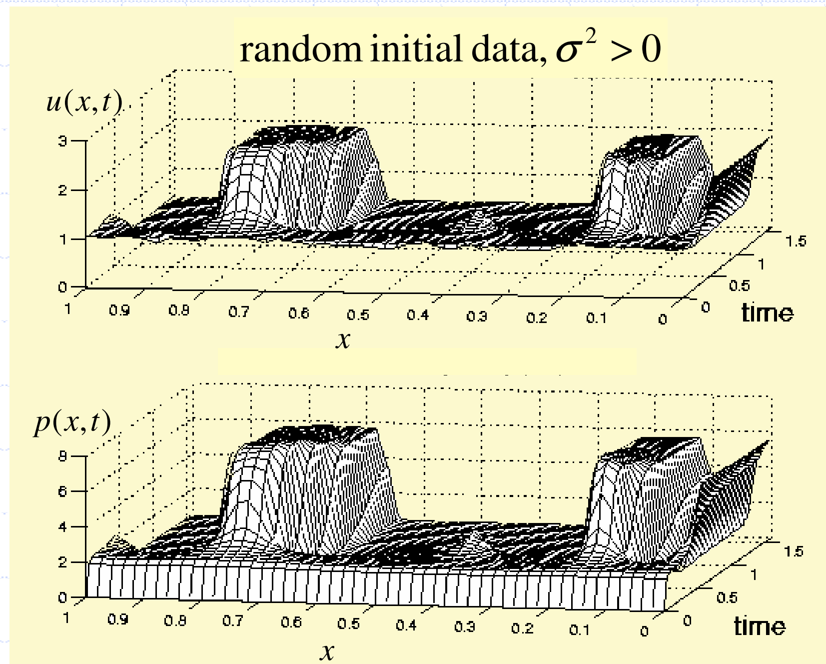


As ε, σ approach zero Turchin's (1989) aggregation model is regained

Numerical Solution – Home Range Patterns







Steady State Analysis

Scent-marking equation

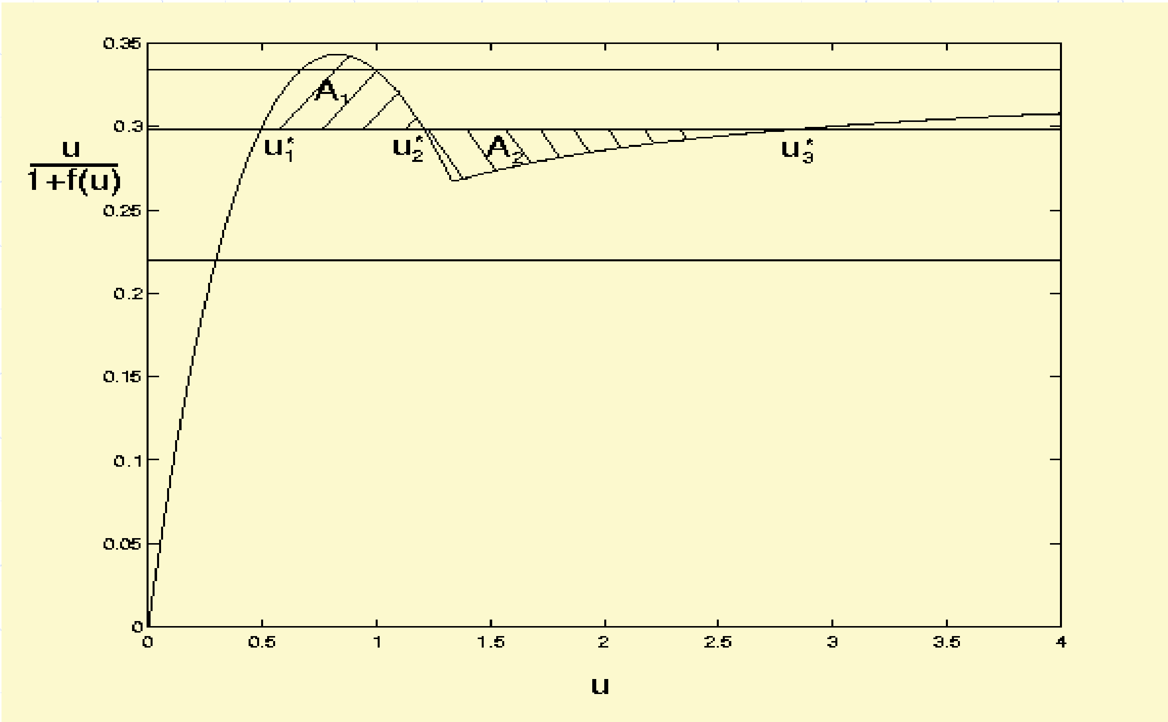
$$u(1+m(p))-\phi p=0 \rightarrow p=f(u)$$

p is scent-mark level

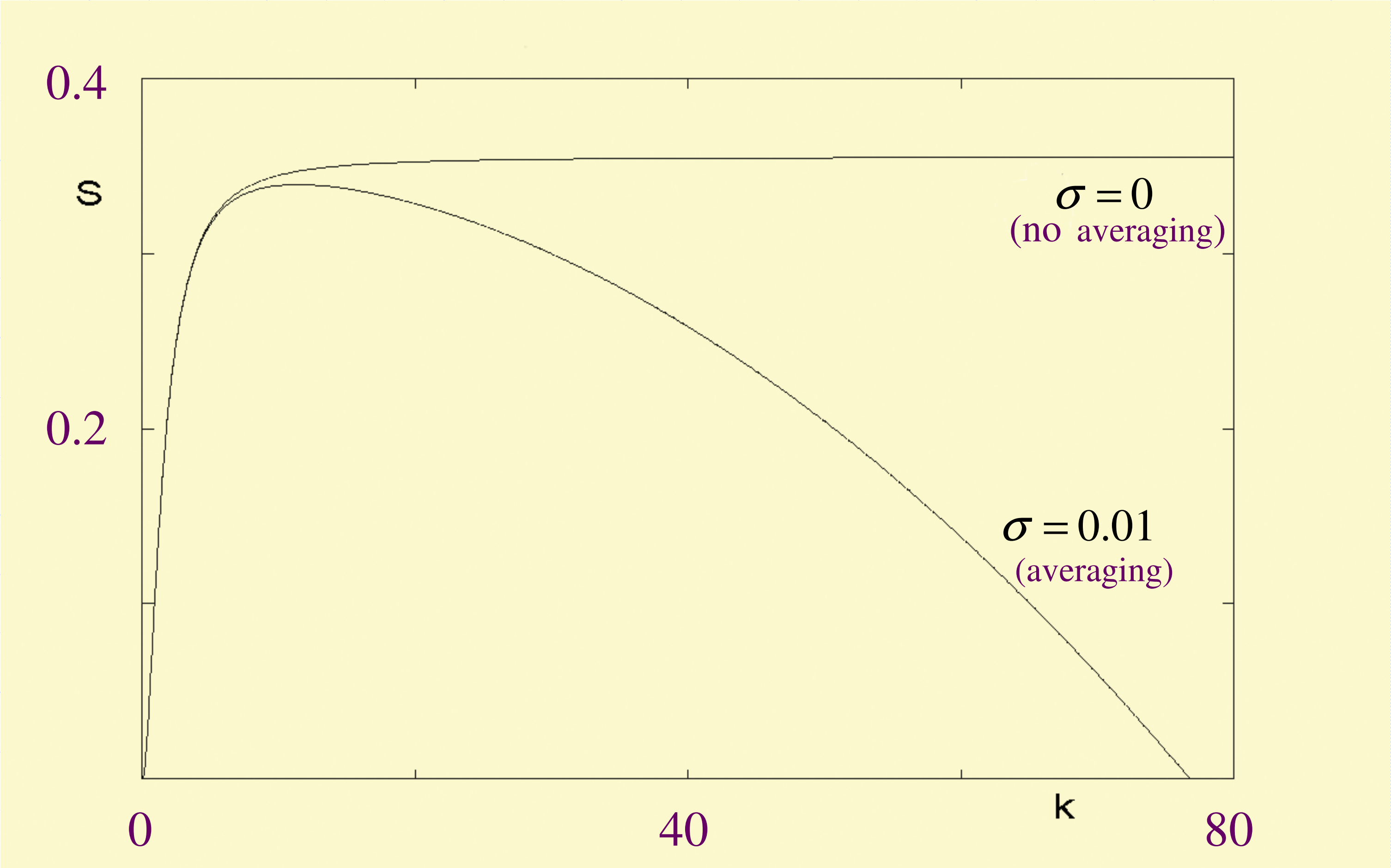
Movement equation

$$\frac{\partial^2}{\partial x^2}\left(\frac{u}{1+f(u)}\right)=0 \rightarrow \frac{u}{1+f(u)}=\text{const}$$

u is density



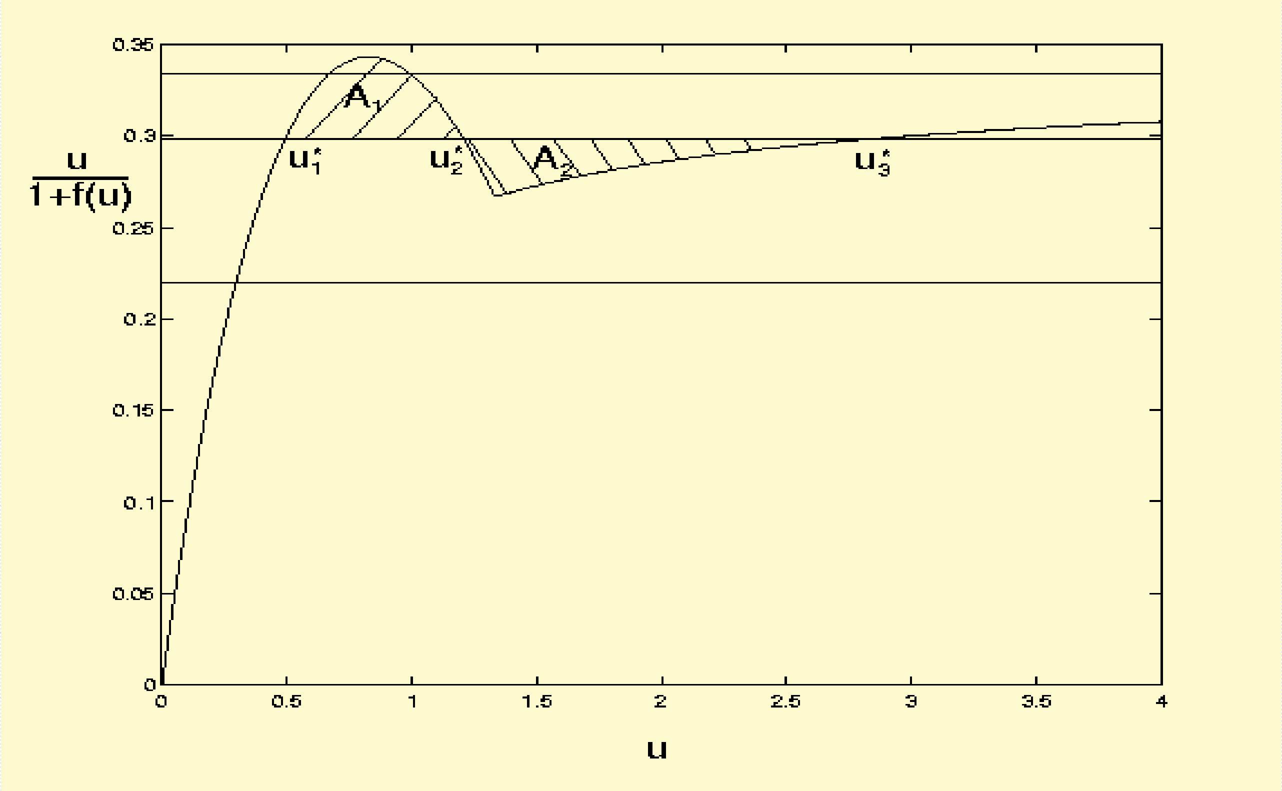
Linear analysis about the homogeneous solution $(u_2^*, f(u_2^*))$ yields a dispersion relation between the wave number k and the growth rate s



$\sigma^2 > 0$ regularizes the system

Equal Area Rule

- Energy methods can be used to prove that, as $\varepsilon, \sigma \to 0$, densities approach piecewise constant values asymptotically in time.
- The lowest energy solution is associated with piecewise constant solutions with values u_1^* and u_3^*.
- Transition layers joining u_1^* and u_3^* are of order σ.



Similar to "Maxwell condition" for phase-transition models

Energy method

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}\left(\frac{u}{1+p}\right) \qquad \varepsilon\frac{\partial p}{\partial t} = u\left(l + m\left(\overline{p}\right)\right) - \phi p$$

$$0 = \frac{\partial}{\partial x}\left(\frac{u}{1+p}\right) \quad \text{at} \quad x = 0,1$$

Consider case with no local averaging ($\sigma = 0$), so $\overline{p} = p$. As $\varepsilon \to 0$ we have a quasi-steady state for the scent marking equation ($p = f(u)$) and

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}(\psi(u)), \quad \psi(u) = \frac{u}{1+f(u)}$$

Define $E(u) = \int_0^1 F(u(x,t))dx$ where $F'(u) = \psi(u)$

$$\dot{E}(u) = \int_0^1 F'(u)\frac{\partial u}{\partial t}(x)dx = \int_0^1 F'(u)[\psi(u)]_{xx}dx$$

$$= -\int_0^1 \frac{\partial}{\partial x}(F'(u))\frac{\partial}{\partial x}[\psi(u)]dx = -\int_0^1 \left(\frac{\partial}{\partial x}[\psi(u)]\right)^2 dx \le 0$$

$E(u)$ is bounded below and decreasing until $\phi(u) = \lambda$

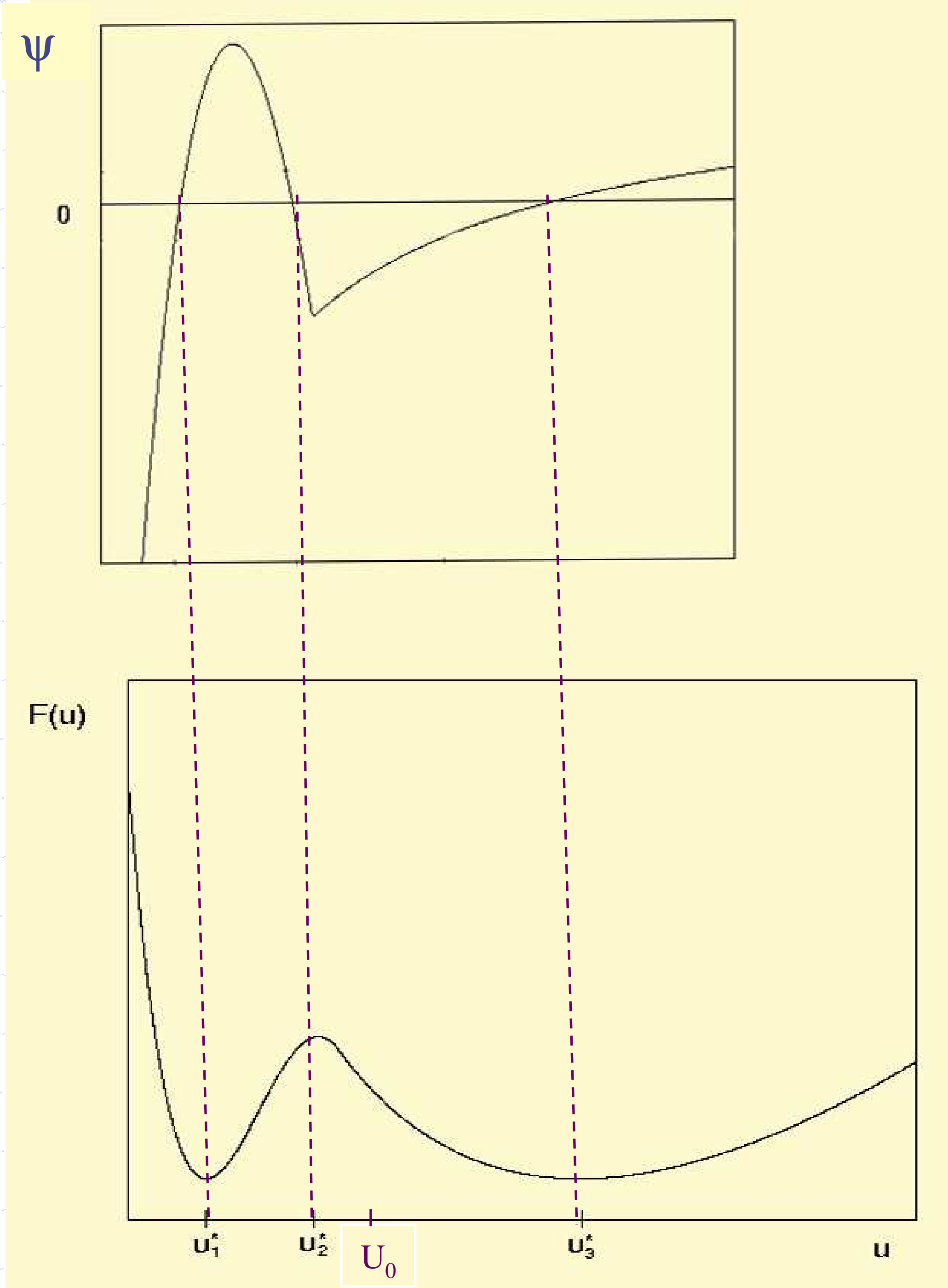
What λ gives the lowest energy solution?

Energy Method

$$E(u) = \sum_{i-1}^{N} L_i F(u_i)$$

$$\sum_{i-1}^{N} L_i = 1$$

$$U = \sum_{i-1}^{N} L_i u_i = U_0$$



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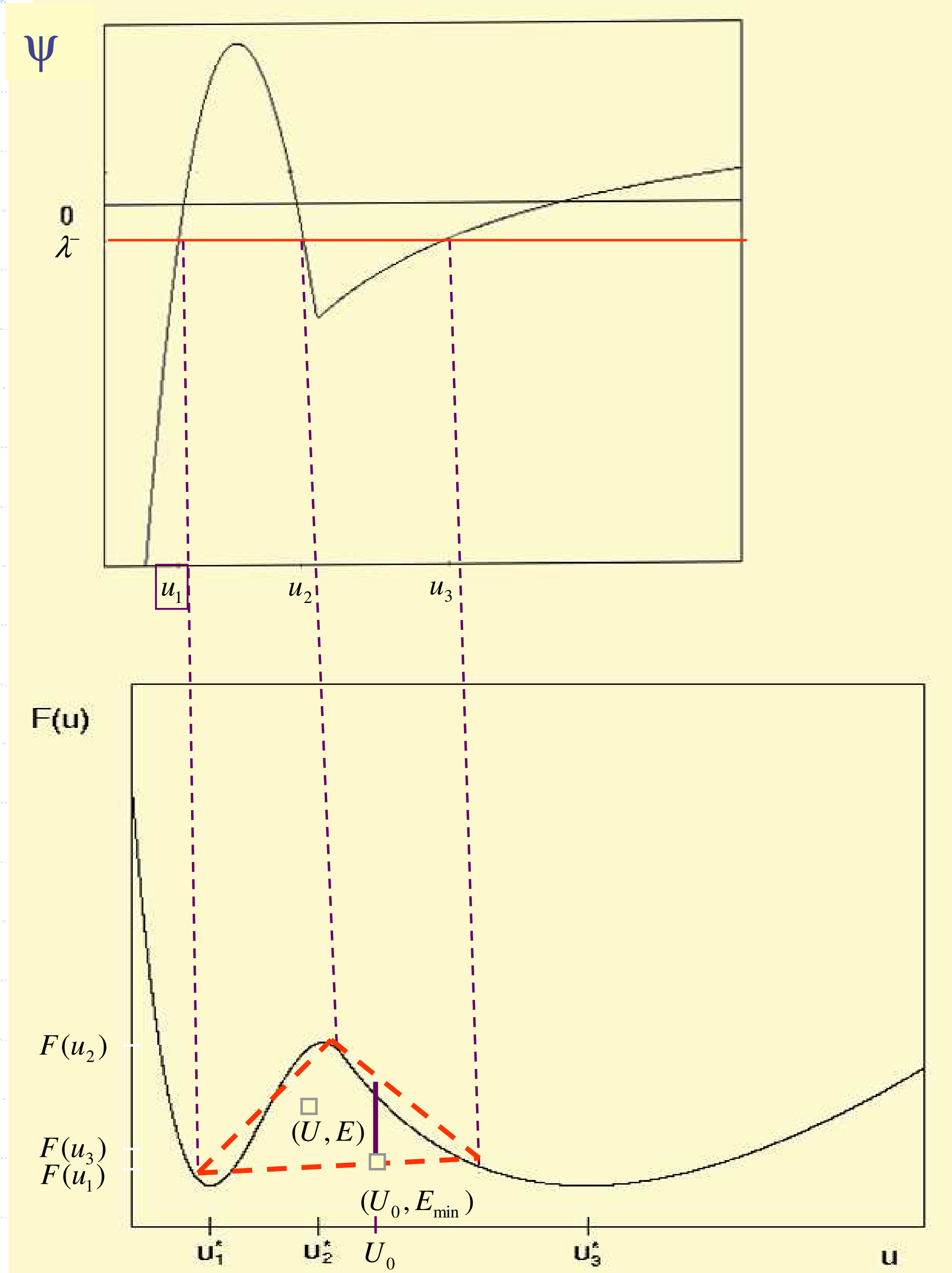

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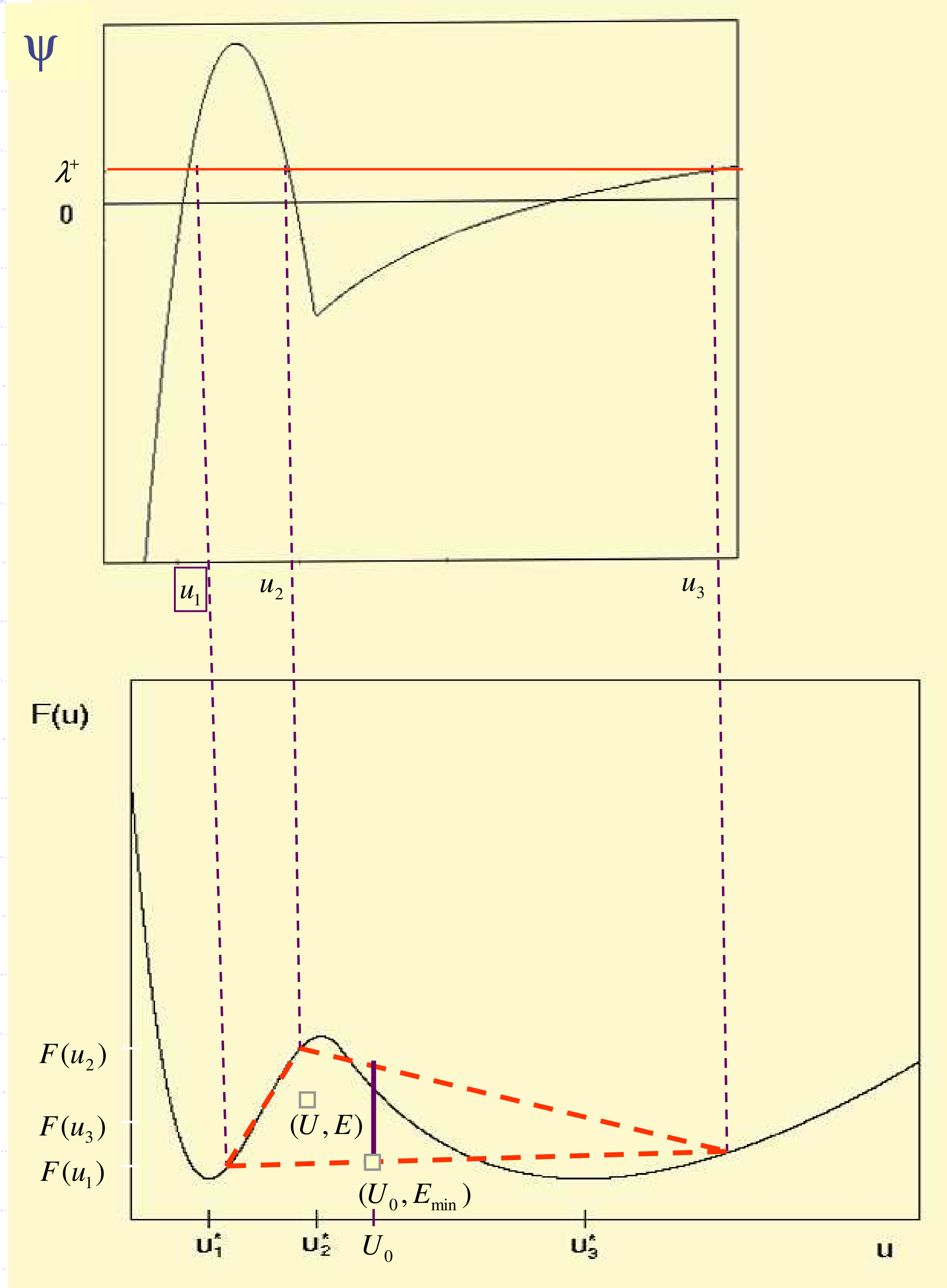

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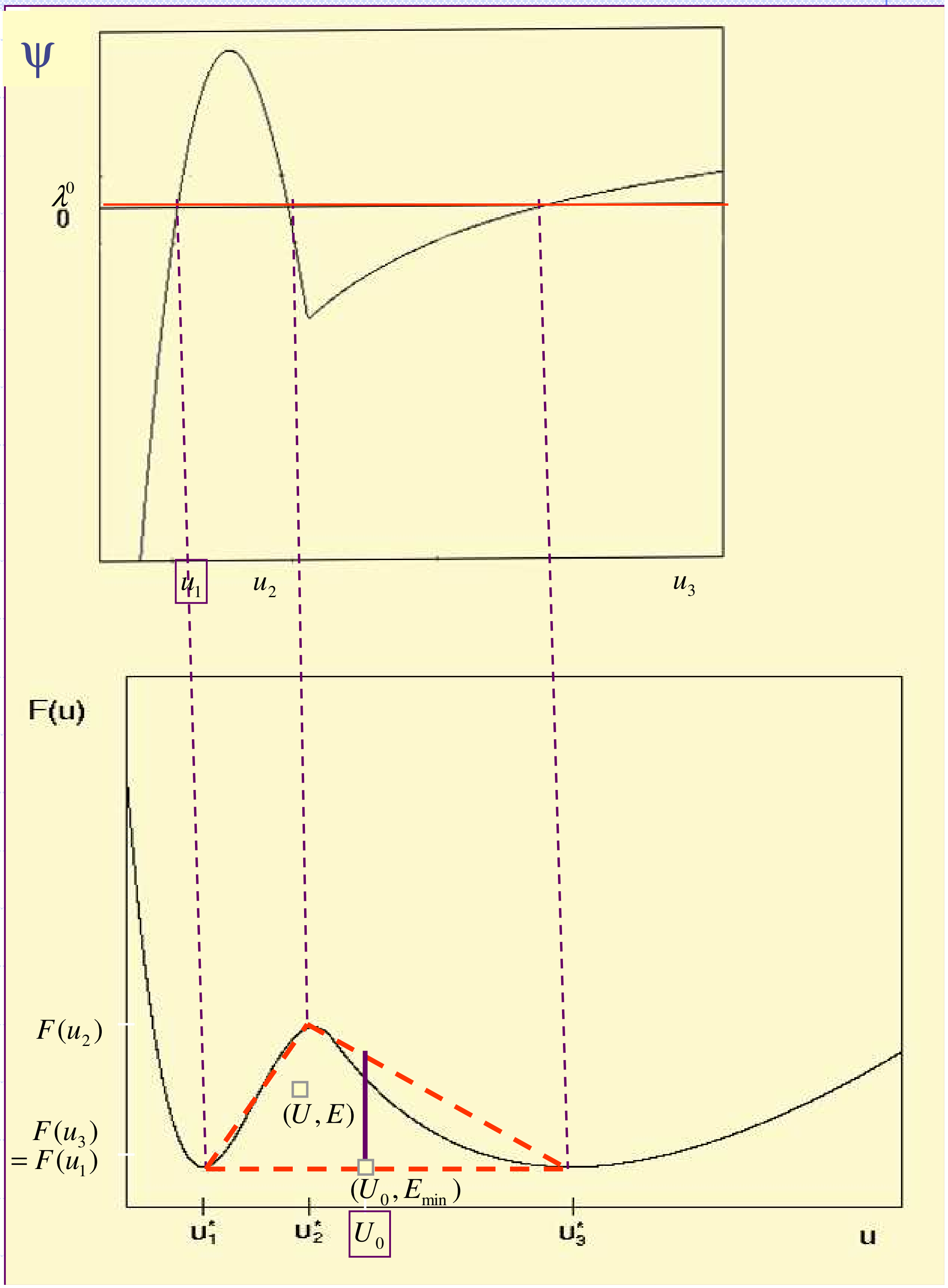
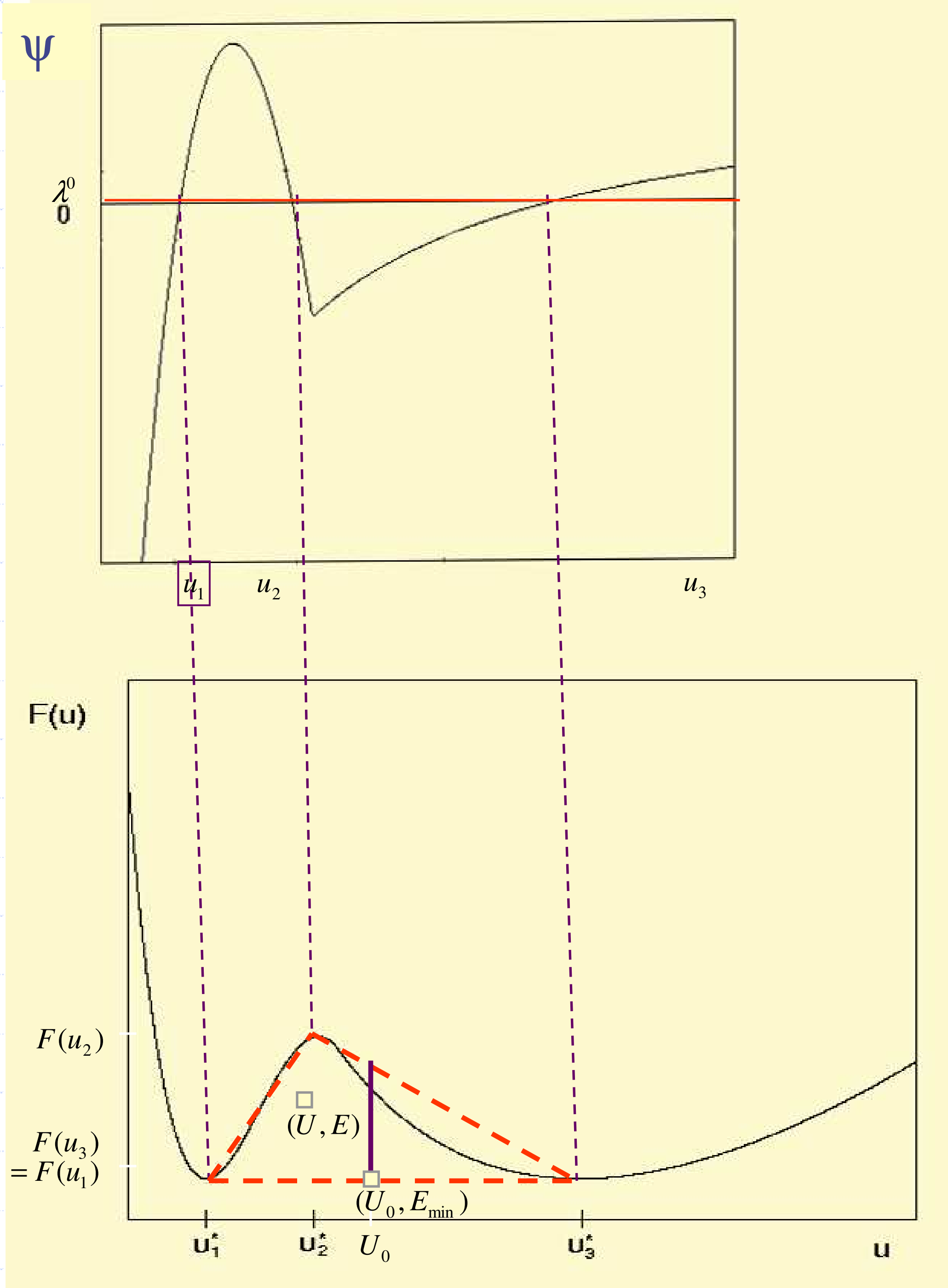


$$E(u) = \sum_{i-1}^{N} L_i F(u_i)$$

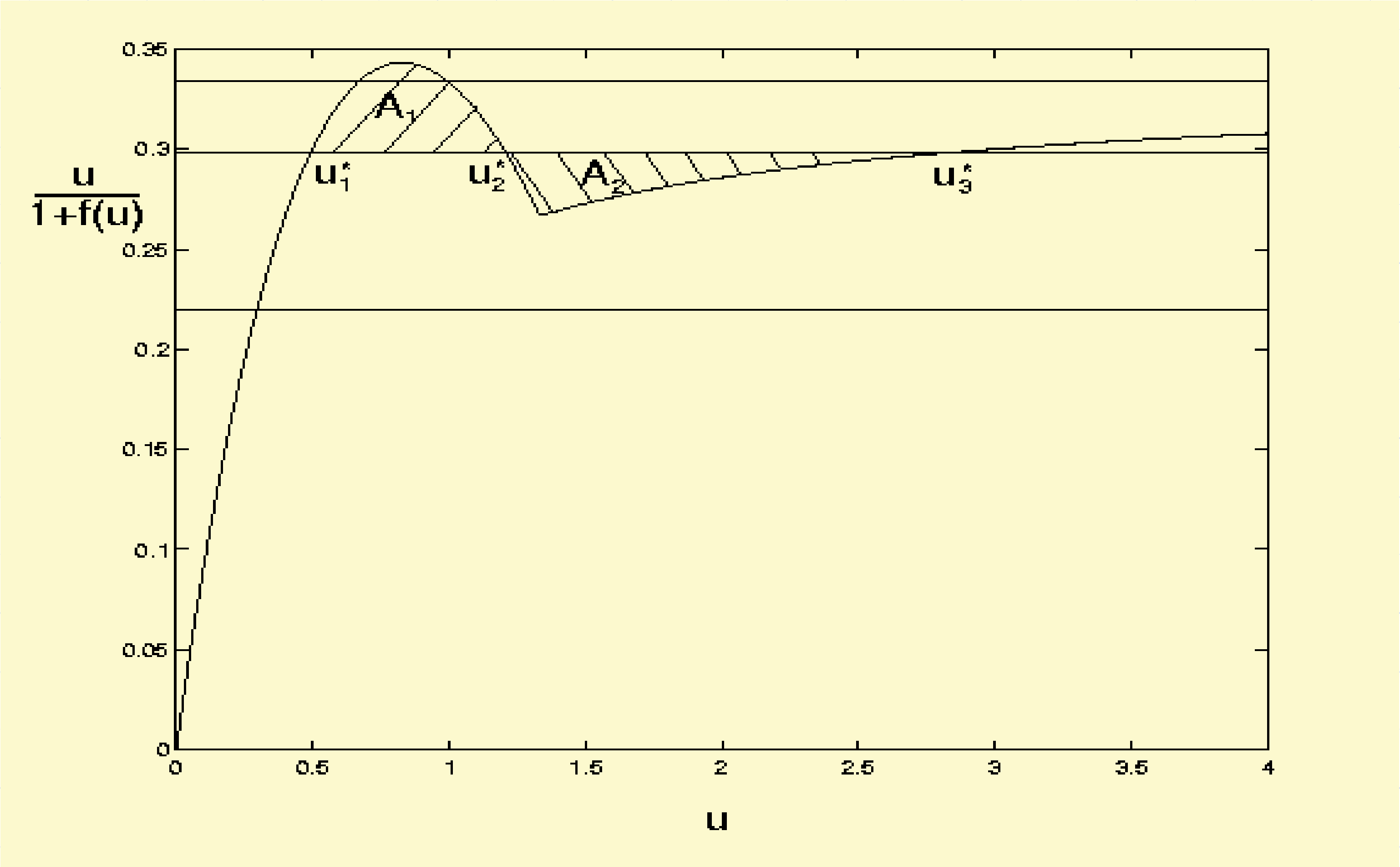
$$\sum_{i-1}^{N} L_i = 1$$

$$U = \sum_{i-1}^{N} L_i u_i = U_0$$

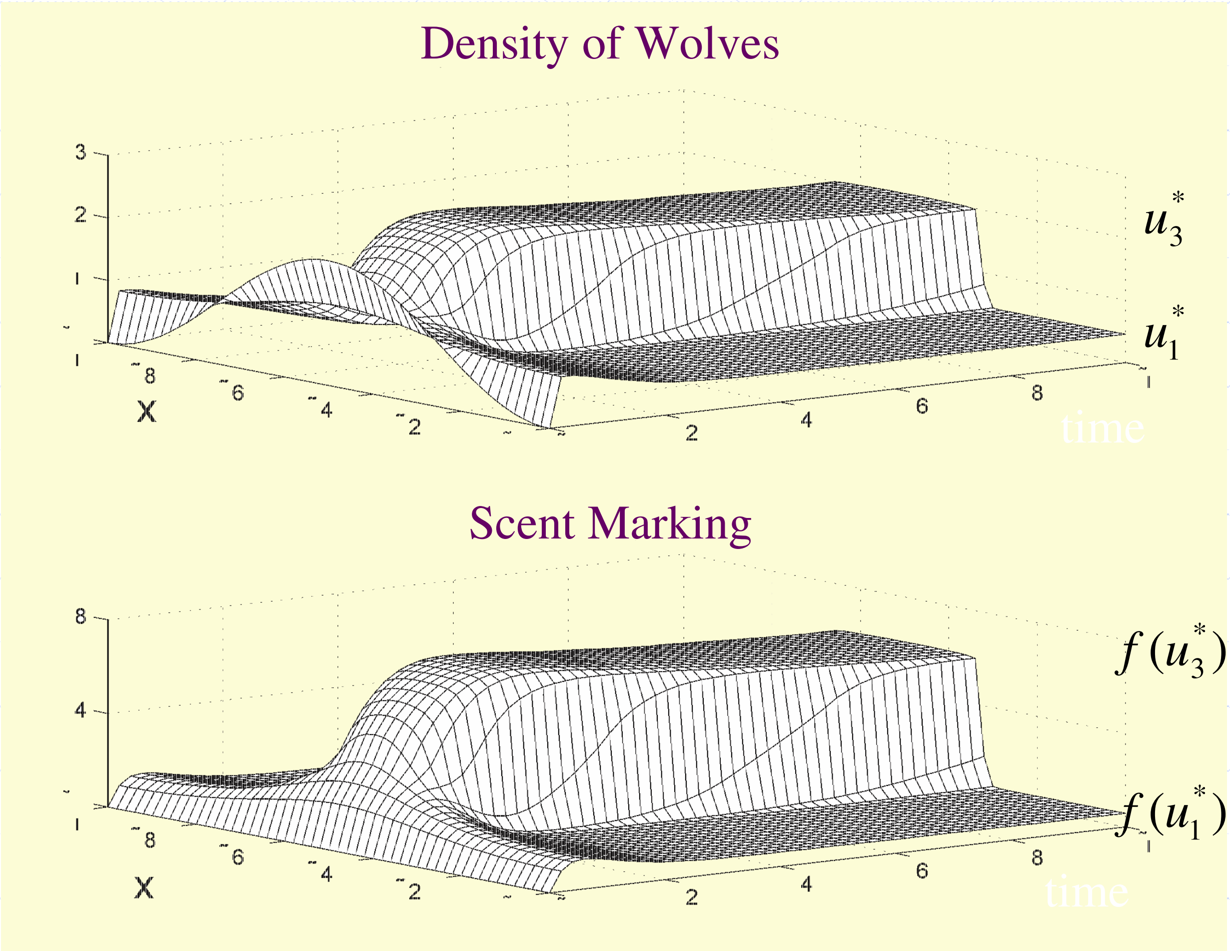
$\lambda = 0$ yields the lowest $E_{\min}$ and a solution with proportion L_1 with value u_1^* and proportion $1 - L_1$ with value u_3^*



"Equal Area" Rule



Home Range

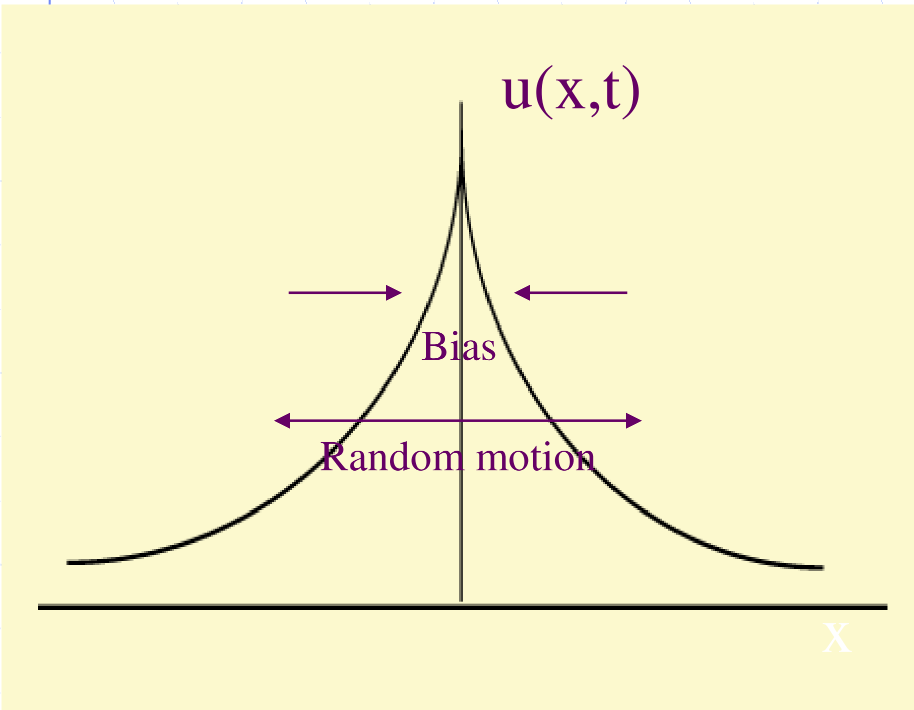

Density of Wolves
3
2
x
2
4
6
8
time
u_3^*
u_1^*
Scent Marking
8
4
x
2
4
6
8
time
$f(u_3^*)$
$f(u_1^*)$

Conclusions

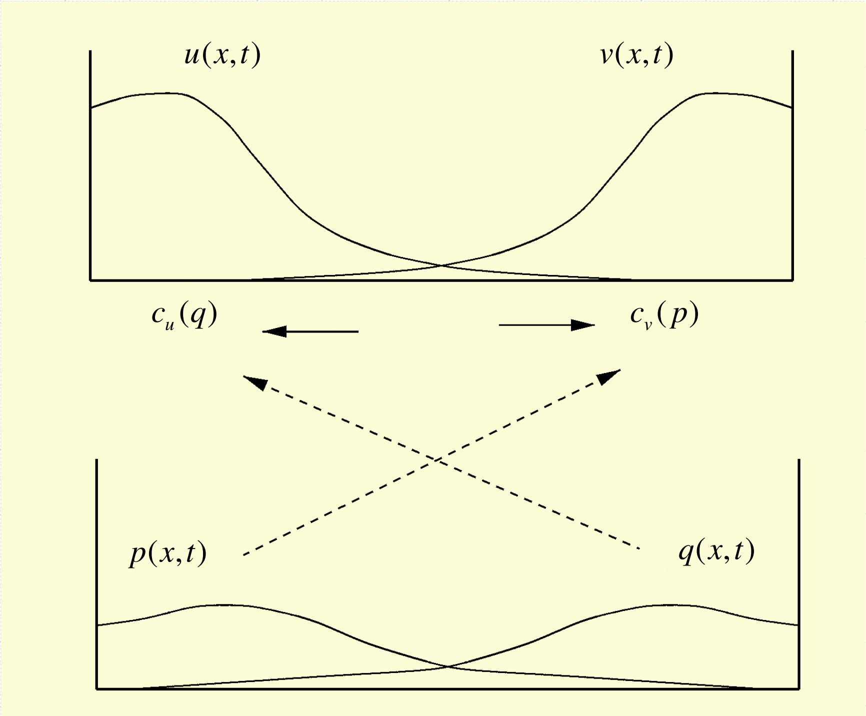
- A simple mechanistic model with (1) positive feedback in scent marking dynamics and (2) reduced movement rates near familiar scent marks gives rise to distinct home range patterns with a core area surrounded by a lower use area.
- Densities in the core and surrounding areas are predicted analytically using the "Equal area rule".
- The model does not predict some field observations (eg, "bowl-shaped" scent mark densities, buffer zones). These observations are for well established territories where (1) there is a den site (2) there are interactions between adjacent packs.

Model with den site and pack interactions

- Home range model (Holgate, 1971): individuals move via random motion plus a constant bias towards a den site.
- Territorial model (Lewis and Murray, 1993): individuals move via random motion while scent marking; foreign scent marks bias movement towards a den site.



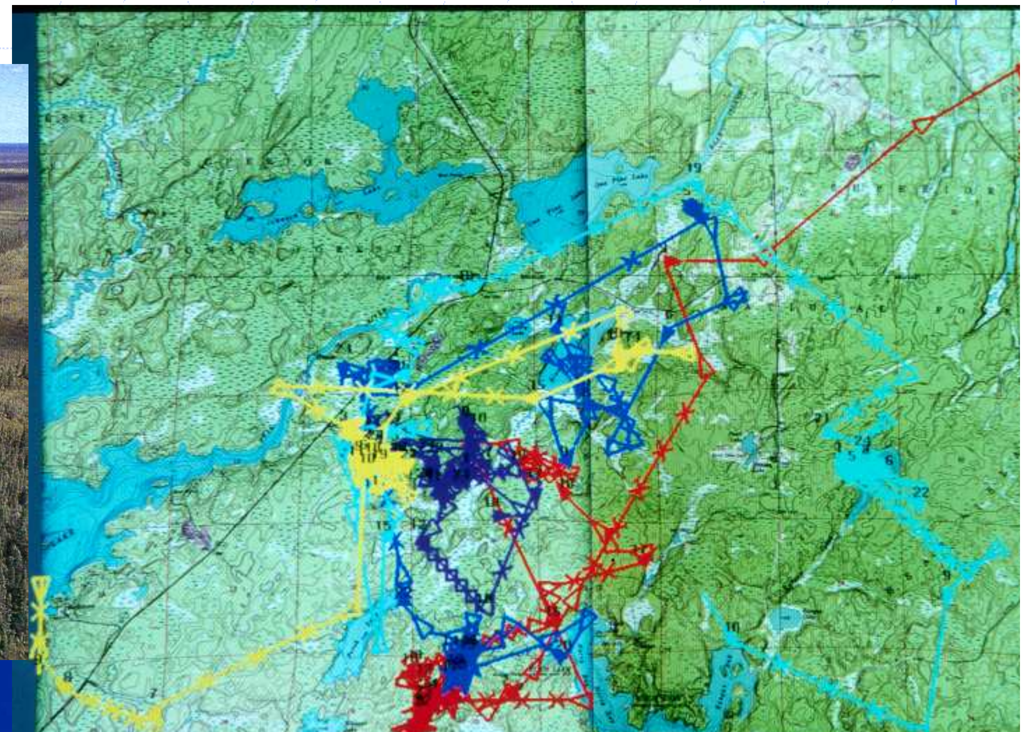
Home range model

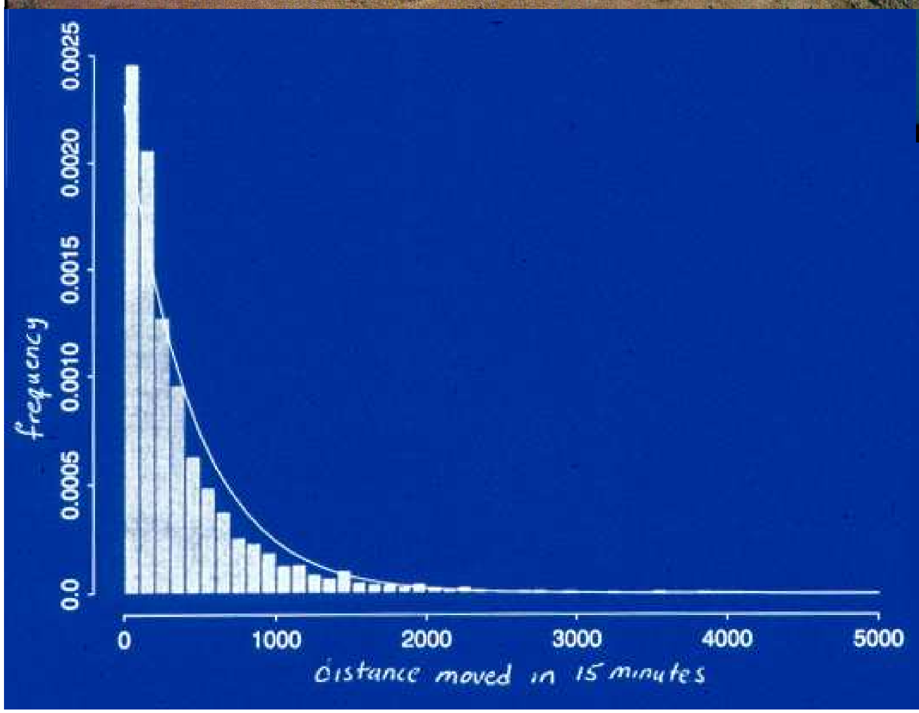


Territorial model

Radiotracking

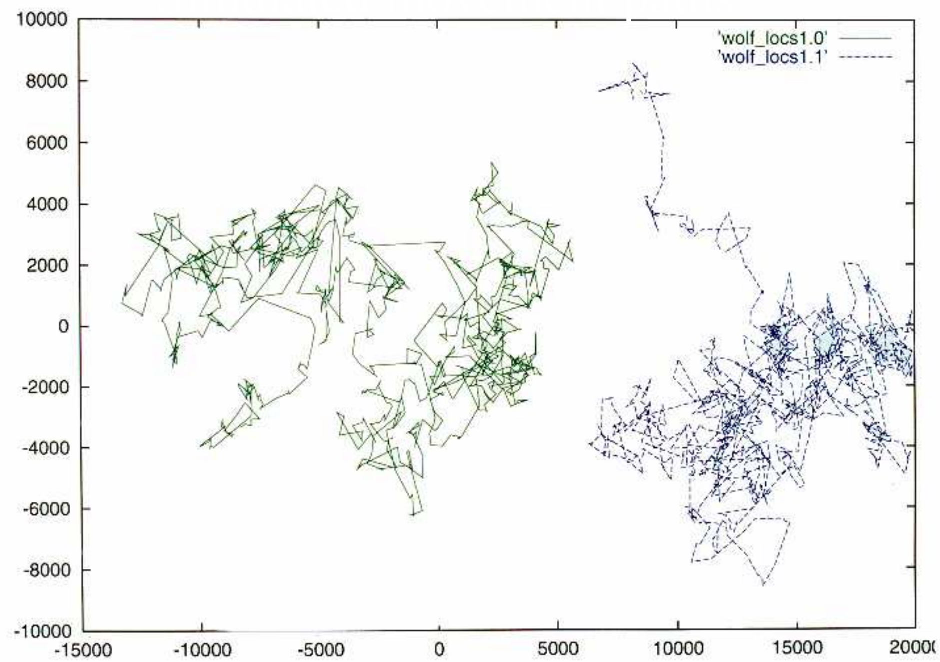
Data from Dan Groebner (unpublished)

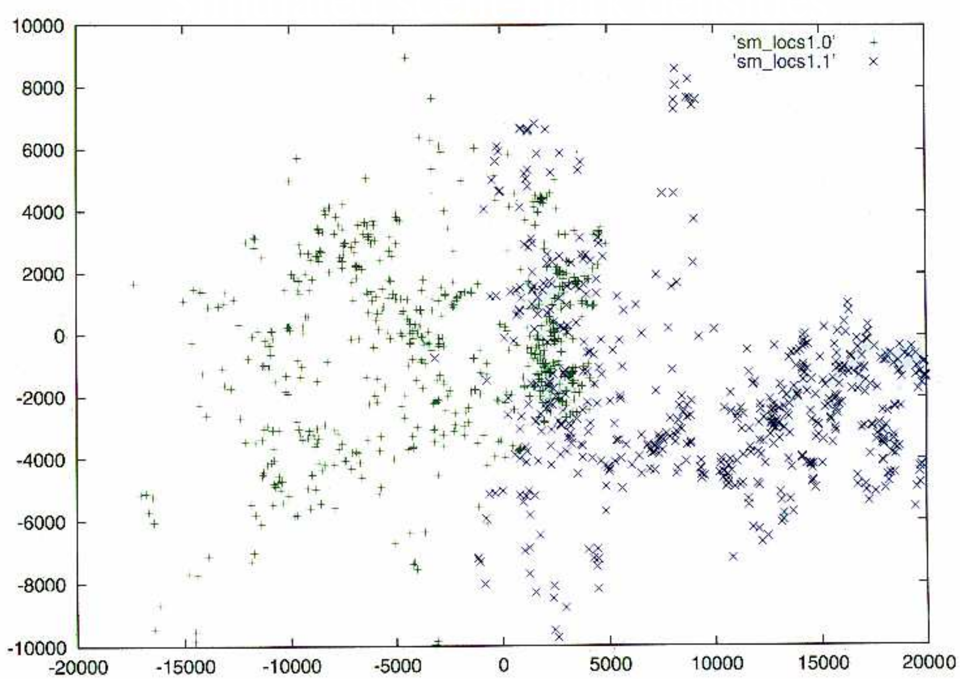




Lagrangian Simulation Model

- Model for individuals based on a modified random walk and observed movement distances
- Foreign scent-marks assumed to cause local increase in scent marking and movement towards den site





PDE Formulation

Movement

$$\underbrace{\frac{\partial u}{\partial t}}_{\text{local density change}} = \underbrace{d_u \frac{\partial^2 u}{\partial x^2}}_{\text{random motion}} + \underbrace{\frac{\partial}{\partial x}\left(c_u(q)u\right)}_{\text{directed motion to den on left}}$$

Pack U density

$$\underbrace{\frac{\partial v}{\partial t}}_{\text{local density change}} = \underbrace{d_v \frac{\partial^2 v}{\partial x^2}}_{\text{random motion}} - \underbrace{\frac{\partial}{\partial x}\left(c_v(p)v\right)}_{\text{directed motion to den on right}}$$

Pack V density

Marking

$$\underbrace{\frac{\partial p}{\partial t}}_{\text{local density change}} = \underbrace{lu}_{\text{deposition by U individuals}} - \underbrace{\phi p}_{\text{decay}}$$

Pack U scent marks

$$\underbrace{\frac{\partial q}{\partial t}}_{\text{local density change}} = \underbrace{lv}_{\text{deposition by V individuals}} - \underbrace{\phi q}_{\text{decay}}$$

Pack V scent marks

Formulation Continued

- Zero-flux boundary conditions

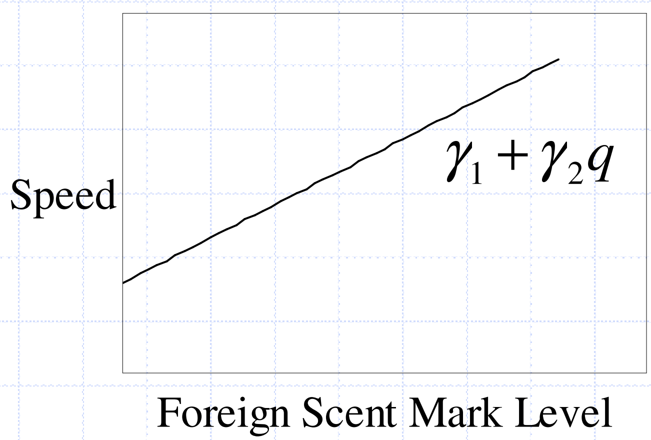
$$d_u \frac{\partial u}{\partial x} + c_u(q)u = 0, \quad d_v \frac{\partial v}{\partial x} - c_v(p)v = 0 \quad \text{at} \quad x = 0, L$$

- Pack size conserved

$$\int_0^L u(x,t)dx = U_0, \qquad \int_0^L v(x,t)dx = V_0$$

- Movement response to foreign scent marks

$$c_u(q) = \gamma_{u1} + \gamma_{u2} q, \qquad c_v(p) = \gamma_{v1} + \gamma_{v2} p$$



Steady-state Analysis

- Nondimensionalize
- Look for time-independent solutions which vary with space
- Solve scent marking equations for $p(u,v)$ and $q(u,v)$
- Substitute $p(u,v)$ and $q(u,v)$ into time-independent movement equations to get a system of coupled ODEs

Steady-state Analysis

Pack 1 density $\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial}{\partial x}\left((\gamma_{u1} + \gamma_{u2} q)u\right)$

Pack 2 density $\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - \frac{\partial}{\partial x}\left((\gamma_{v1} + \gamma_{v2} p)v\right)$

Pack 1 scent $\frac{\partial p}{\partial t} = u - p$

Pack 2 scent $\frac{\partial q}{\partial t} = v - q$

$\Rightarrow$

$$\underbrace{-\frac{\partial u}{\partial x}}_{\text{rate at which pack 1 density drops off with distance from den}} = \underbrace{(\gamma_{u1} + \gamma_{u2} v)u}_{\text{nonlinear function of pack 1 density and pack 2 density}}$$

$$\underbrace{\frac{\partial v}{\partial x}}_{\text{rate at which pack 1 density drops off with distance from den}} = \underbrace{(\gamma_{v1} + \gamma_{v2} u)v}_{\text{nonlinear function of pack 1 density and pack 2 density}}$$

$$\underbrace{\int_0^1 u(x)dx = 1, \quad \int_0^1 v(x)dx = 1}$$

distance between den sites is rescaled to equal 1; *u* and *v* can be interpreted as probability density functions for wolf locations from packs 1 and 2

γ_{*1} : rate of intrinsic movement towards den site

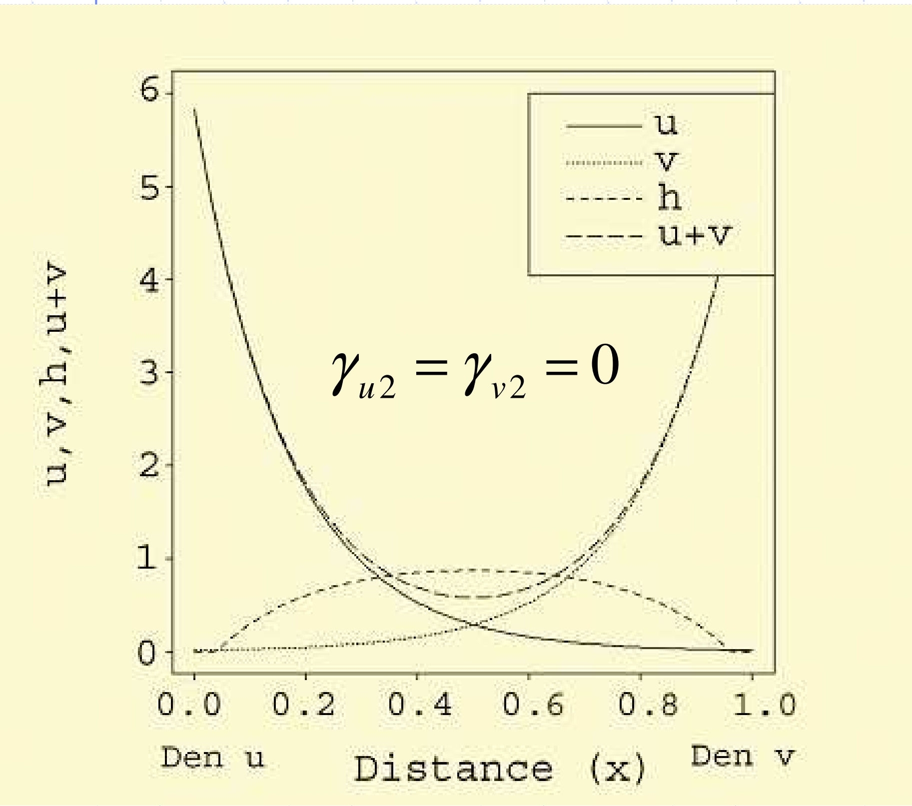
γ_{*2} : rate of movement towards den site in response to foreign scent marks

Territorial Interactions

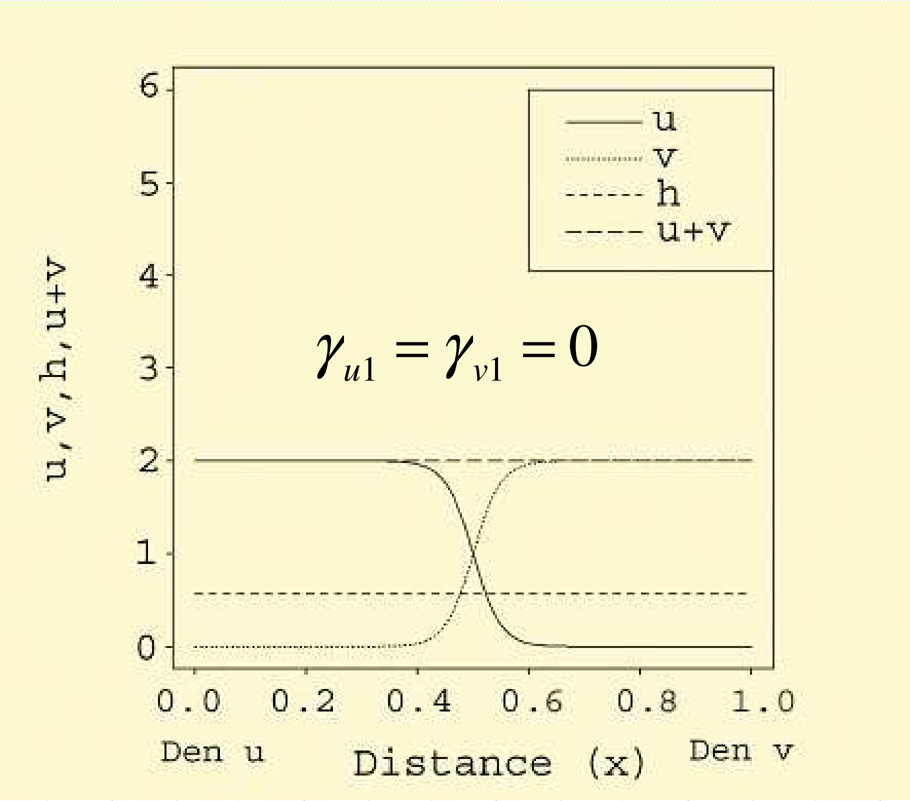
- Steady state analysis

$$\frac{\partial u}{\partial x} = -(\gamma_{u1} + \gamma_{u2} v)u$$

$$\frac{\partial v}{\partial x} = (\gamma_{v1} + \gamma_{v2} u)v$$

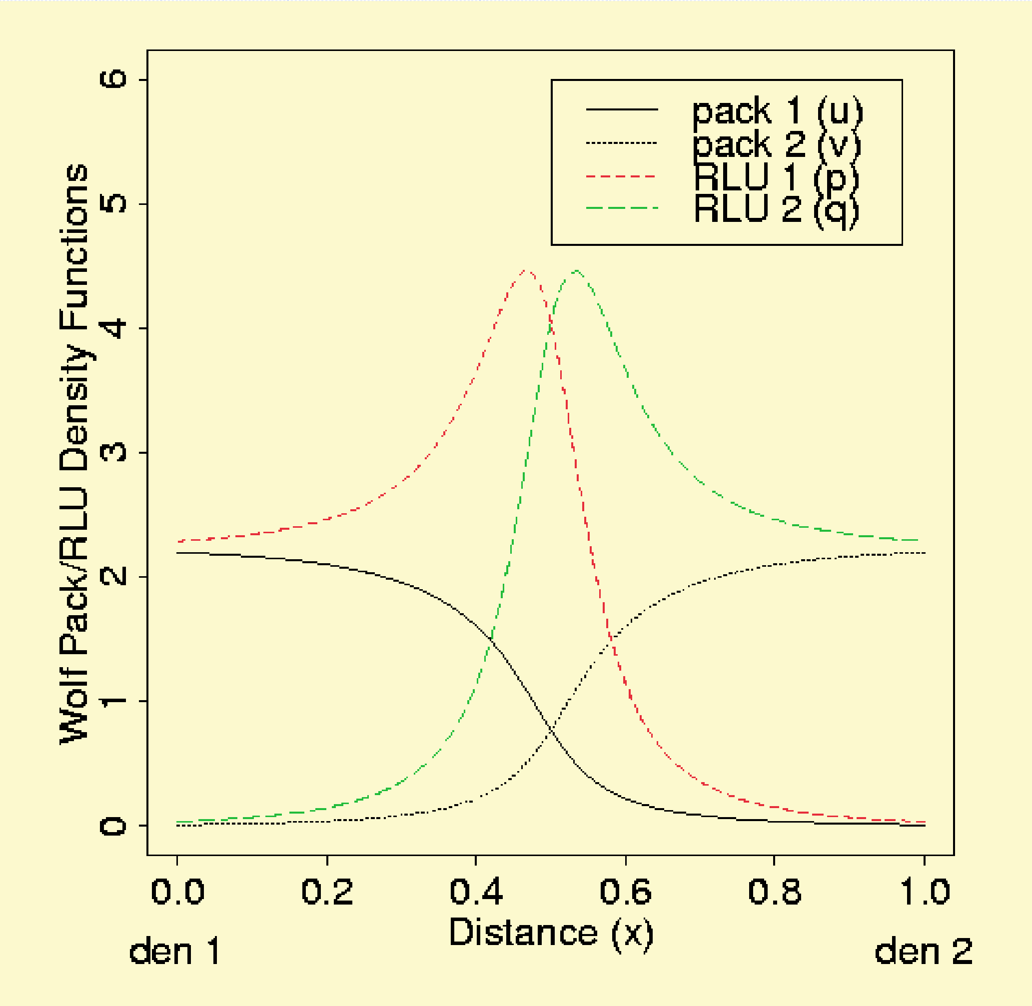


Holgate home range model



Pure territorial model

Complex Scent Marking

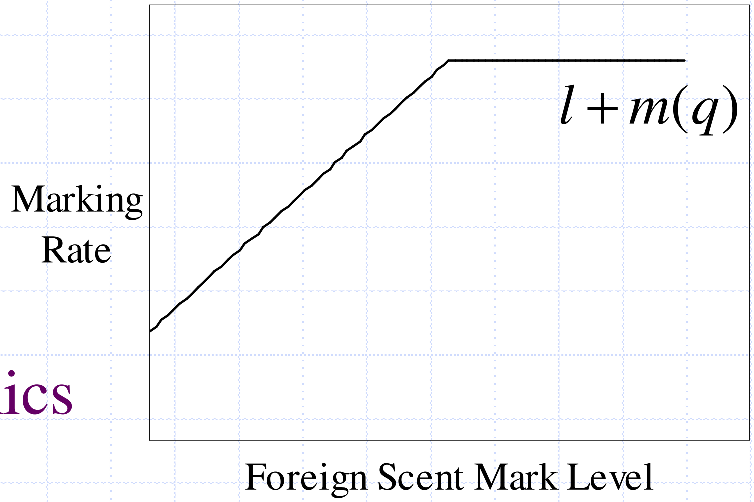


$$\frac{\partial u}{\partial t} = d_u \frac{\partial^2 u}{\partial x^2} + \frac{\partial}{\partial x} c_u(q)u$$

$$\frac{\partial v}{\partial t} = d_v \frac{\partial^2 u}{\partial x^2} + \frac{\partial}{\partial x} c_v(p)v$$

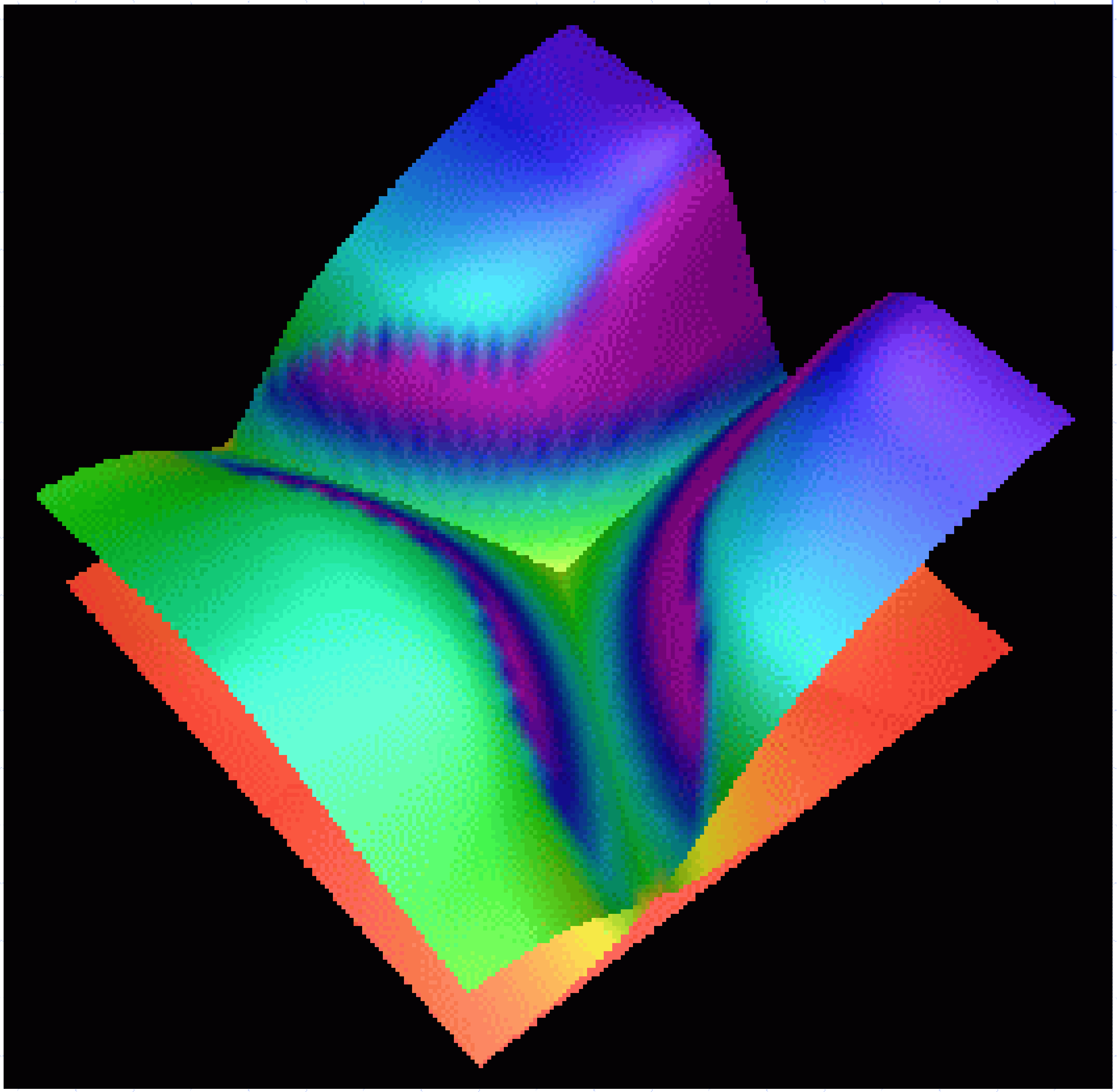
$$\frac{\partial p}{\partial t} = u(l + \underbrace{m(q)}_{\text{increased marking}}) - fp$$

$$\frac{\partial q}{\partial t} = u(l + \underbrace{m(p)}_{\text{increased marking}}) - fq$$



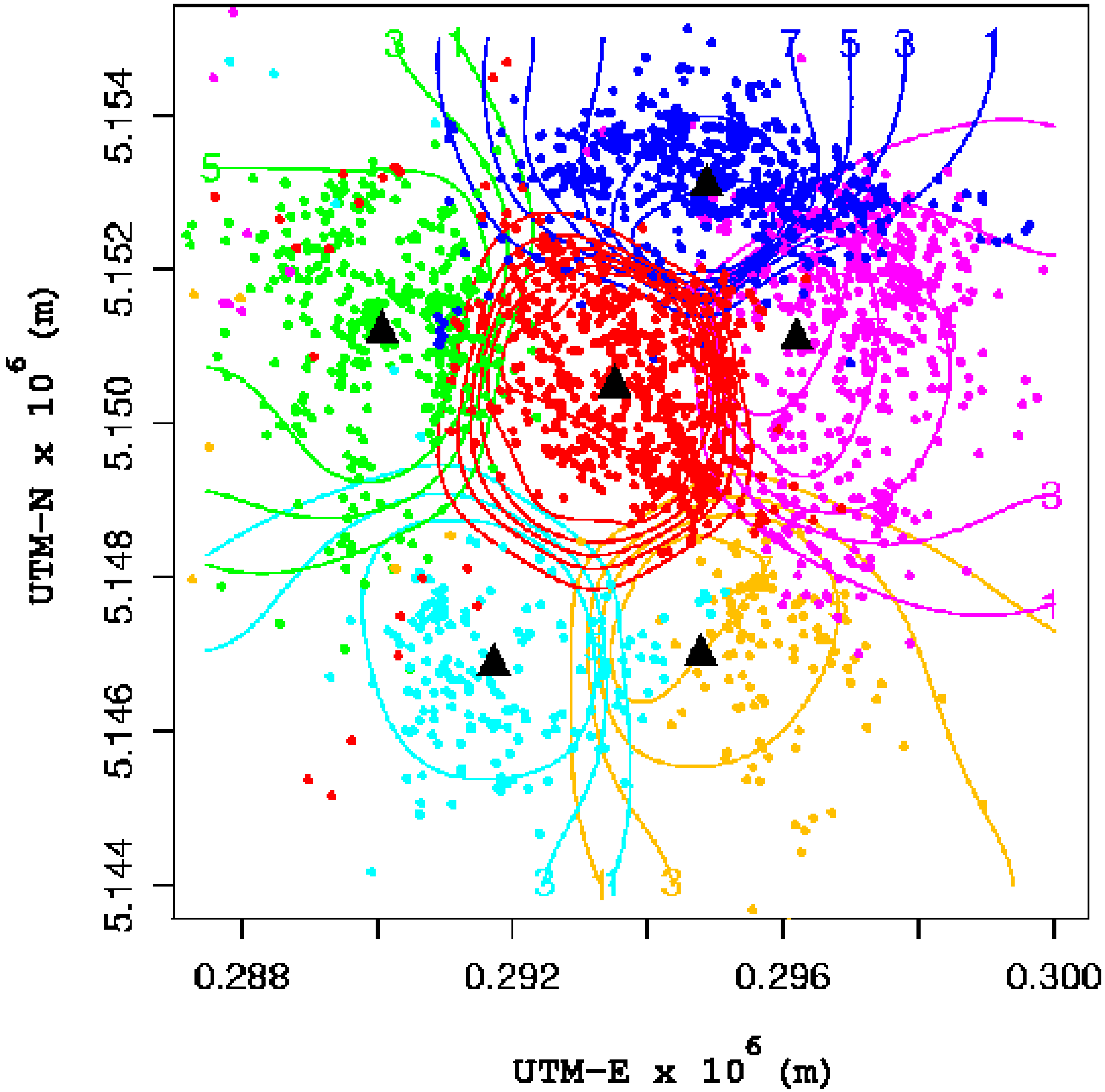
Positive feedback in scent-marking dynamics gives “bowl” shape scent-mark densities

Complex Scent Marking



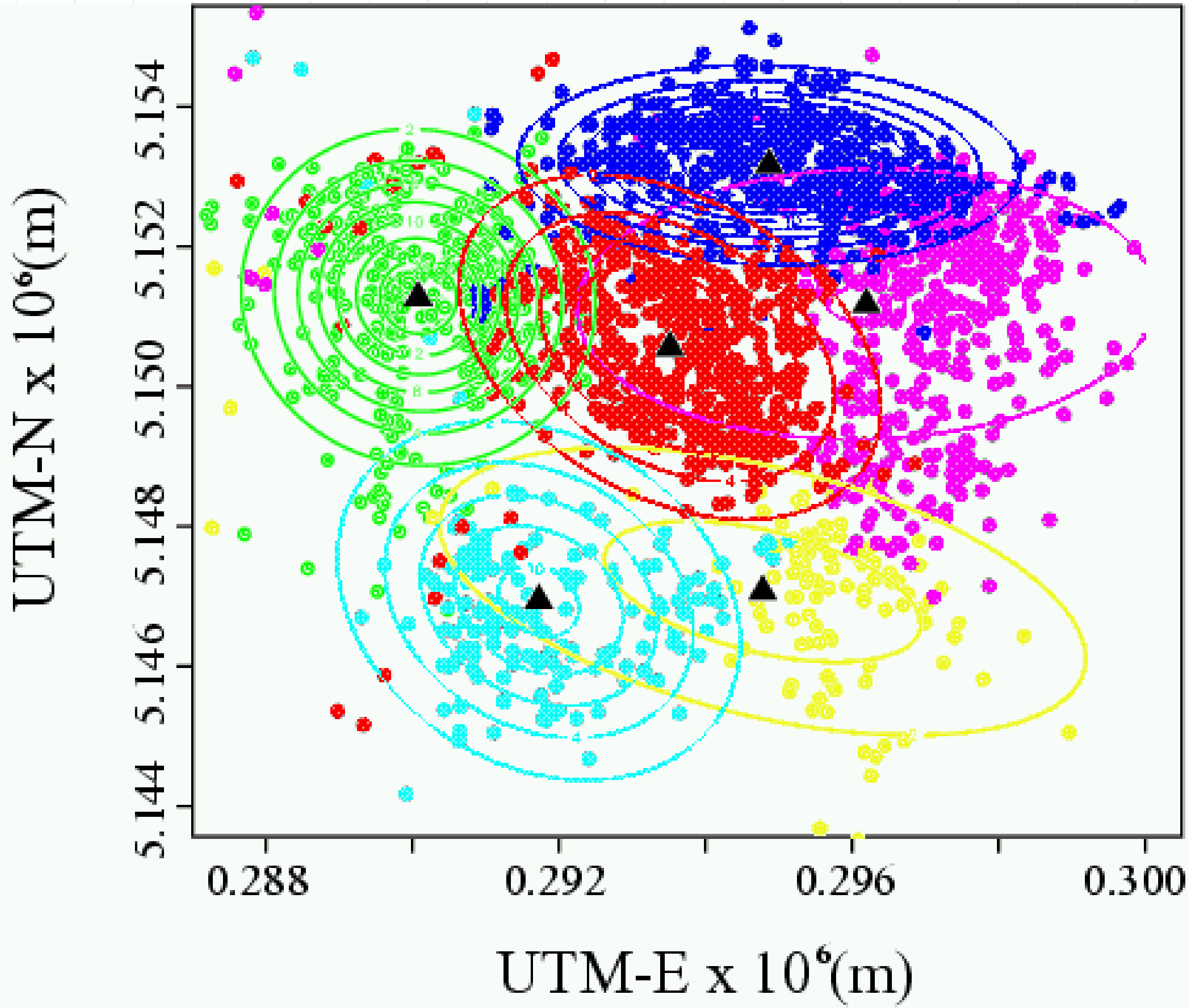
Lewis, White and Murray (1997)

Fit to Radio-tracking Data

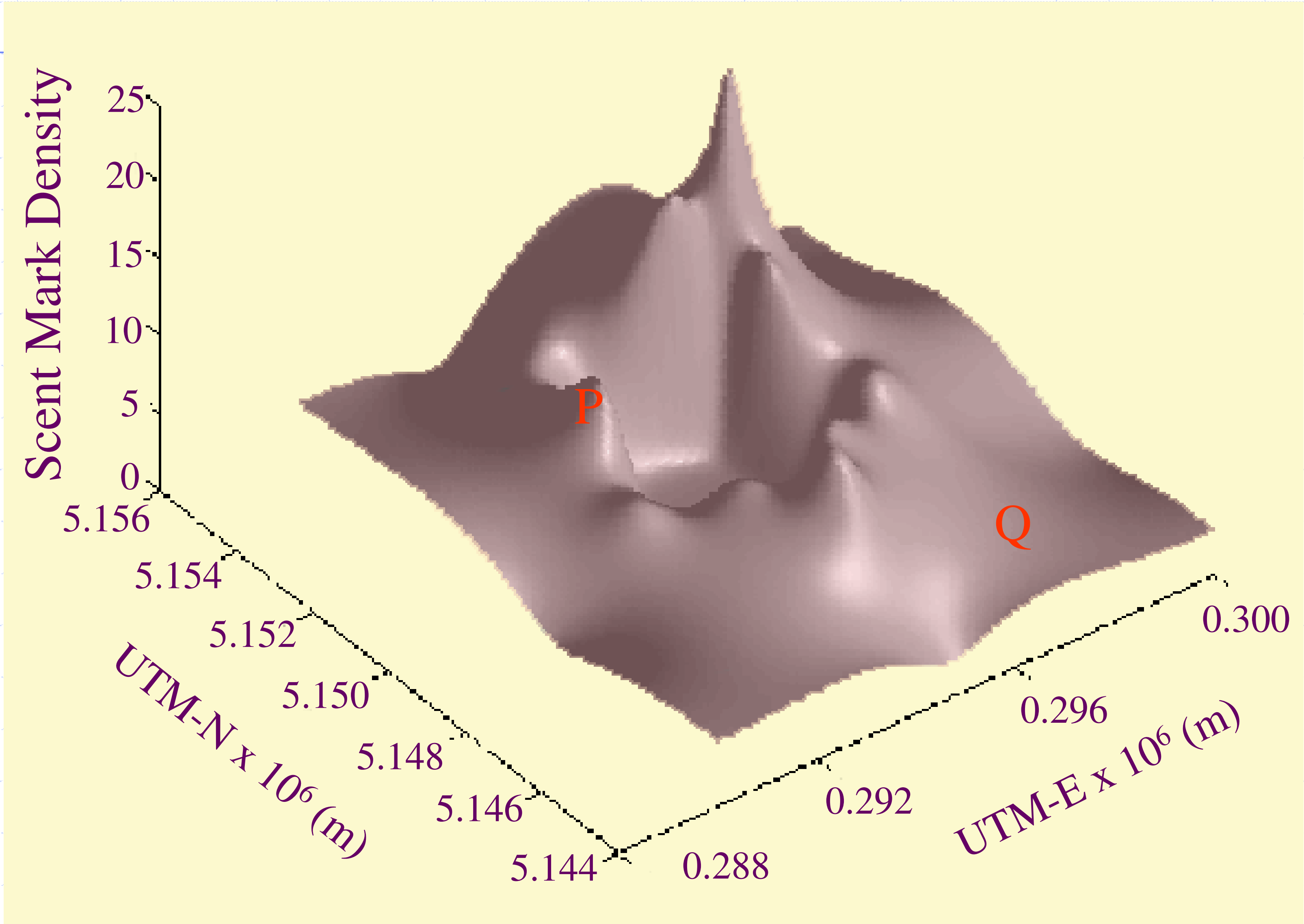


Moorcroft, Lewis and Crabtree (1999)

Fitting probability density functions: Bivariate Gaussian

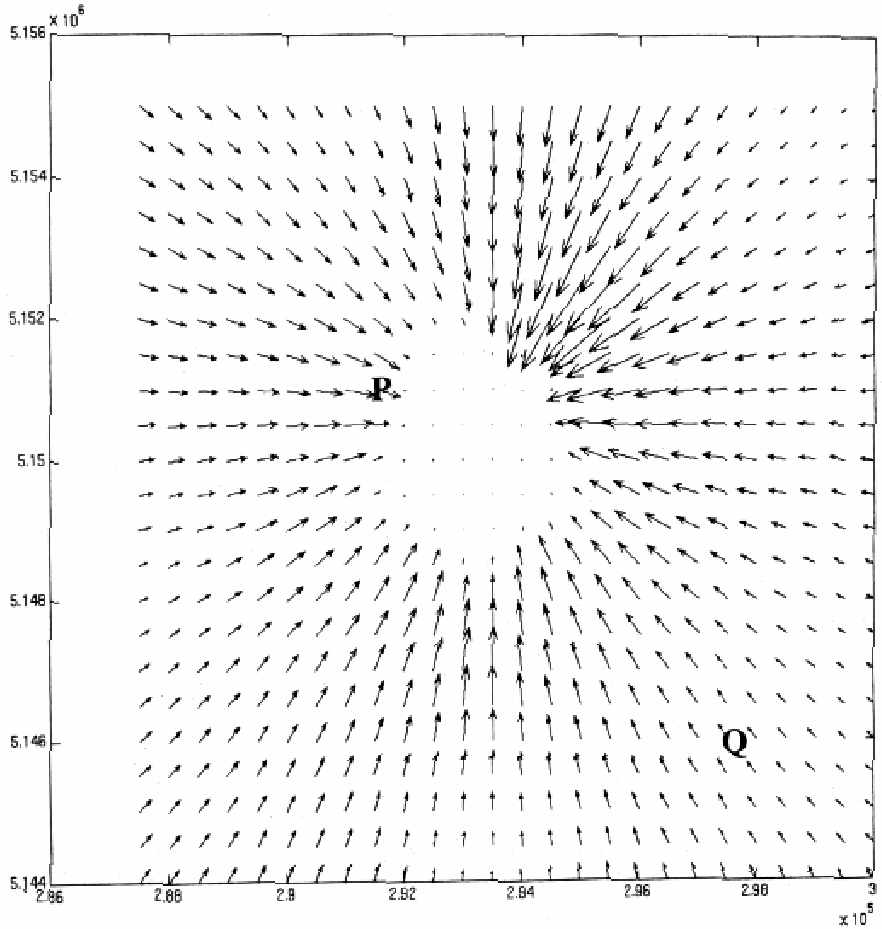


Fit to Radiotracking Data

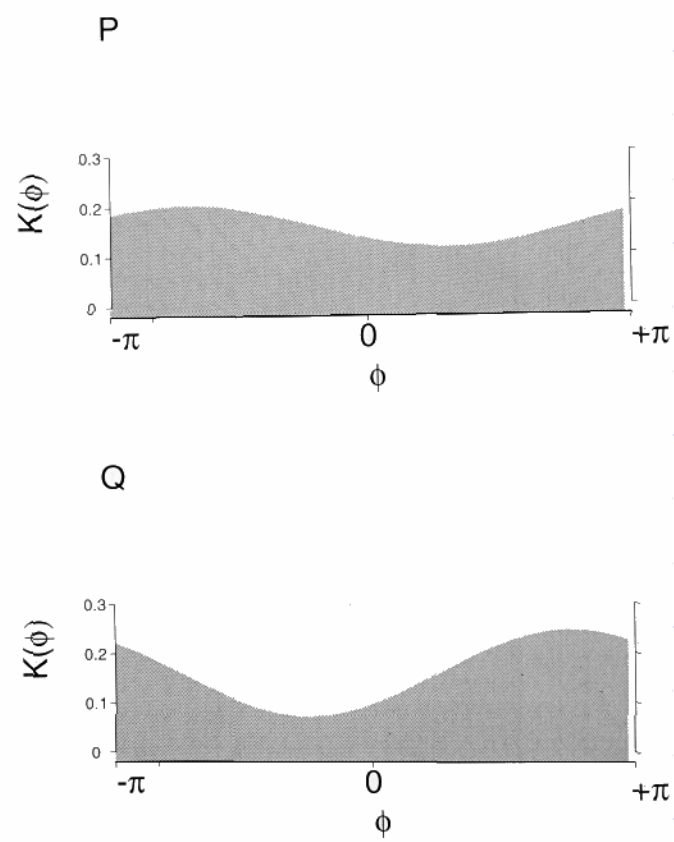


Relationship to Random Walk Model

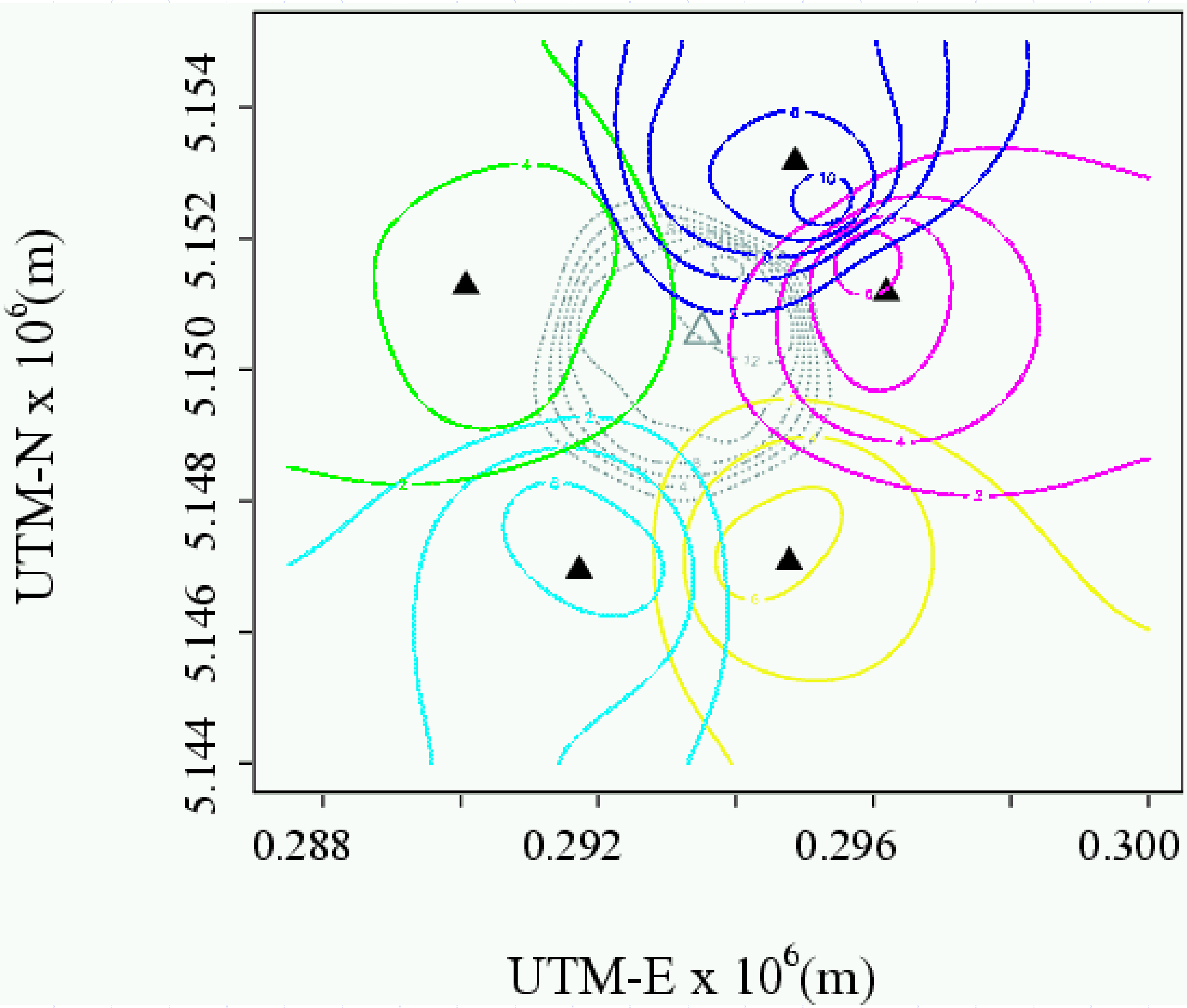
- The nonlinear PDE model for densities can be related to a complex random walk model for individuals



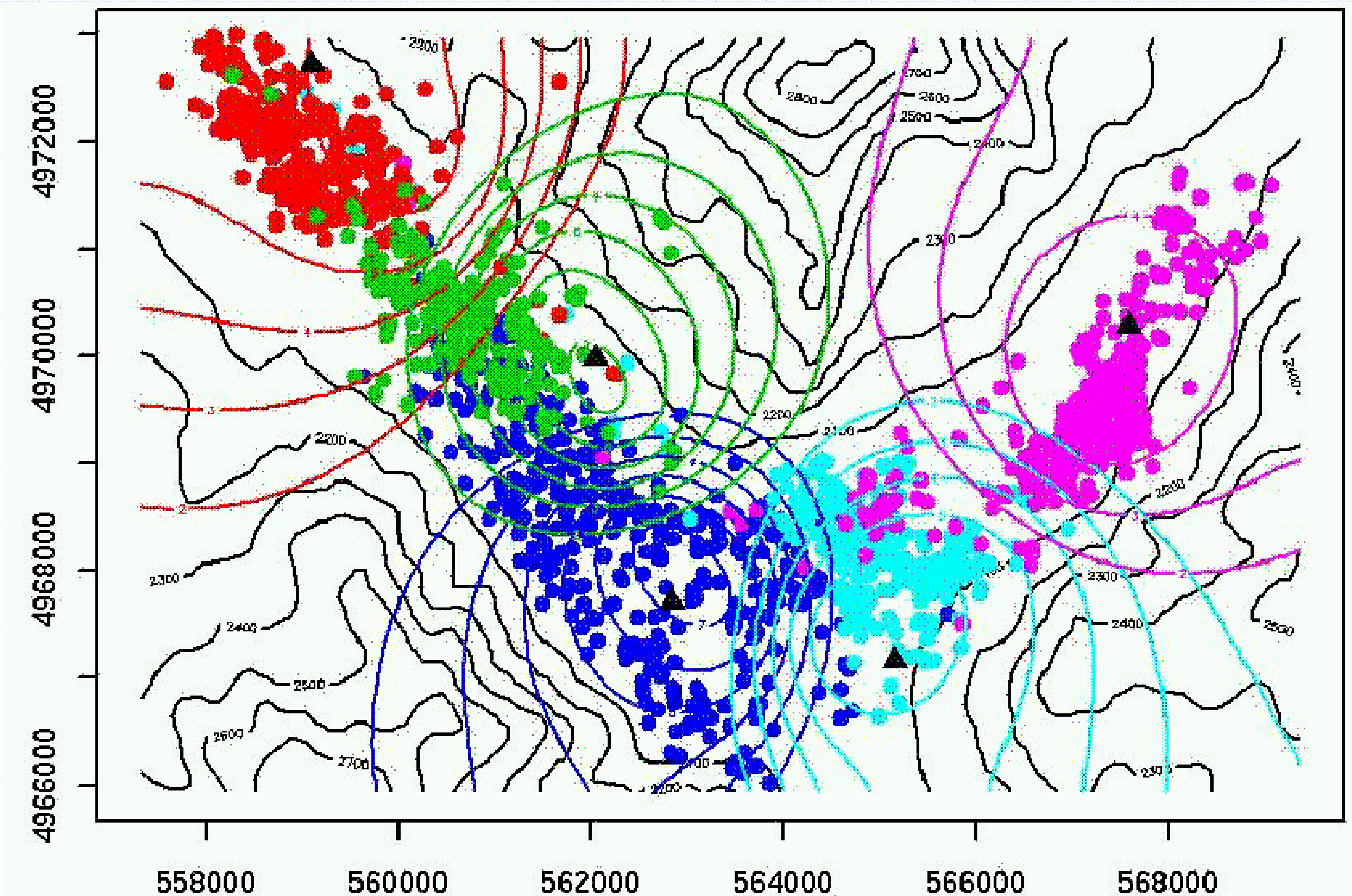
Preferential movement direction



Pack removal prediction

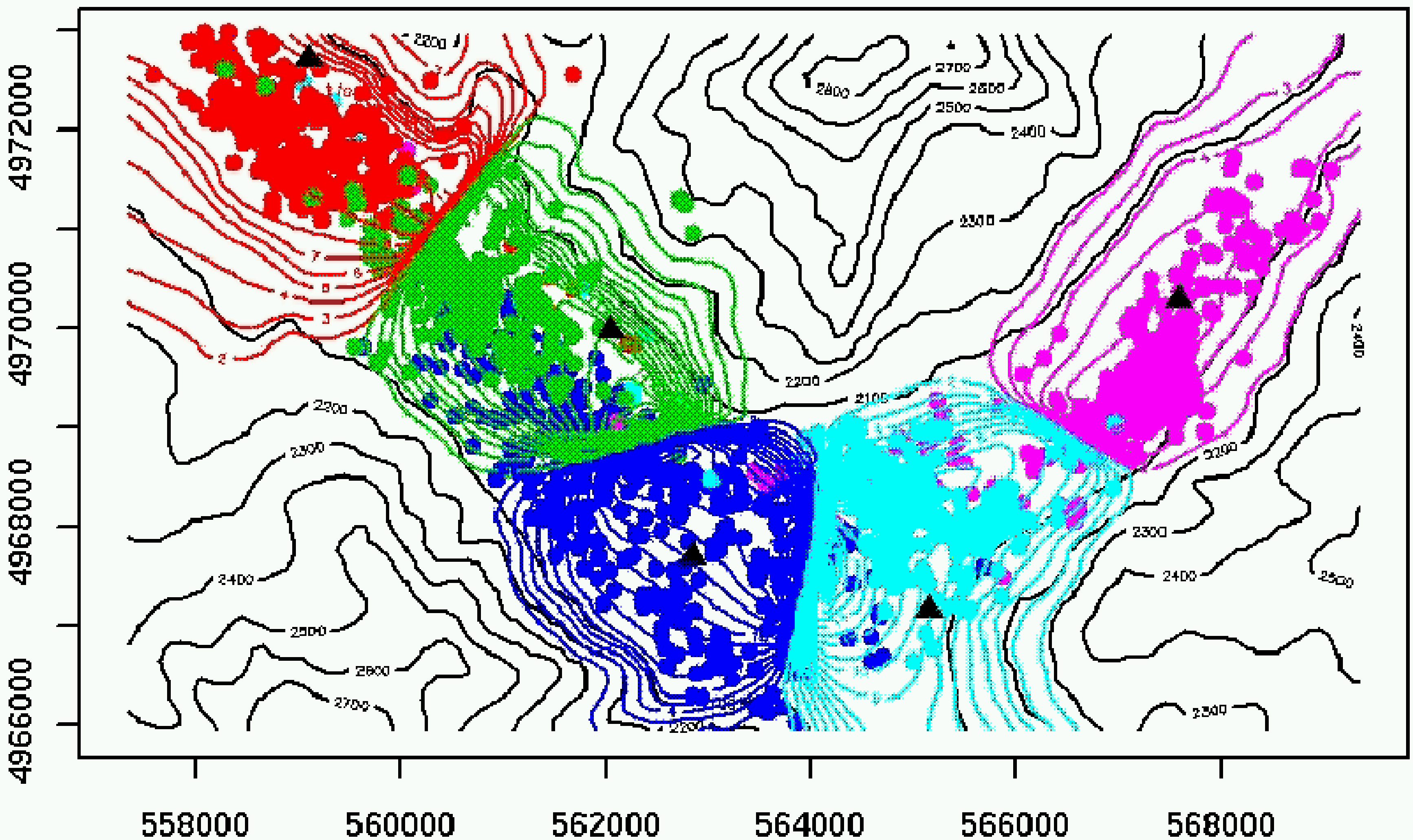


Model fit to Yellowstone Coyote locations



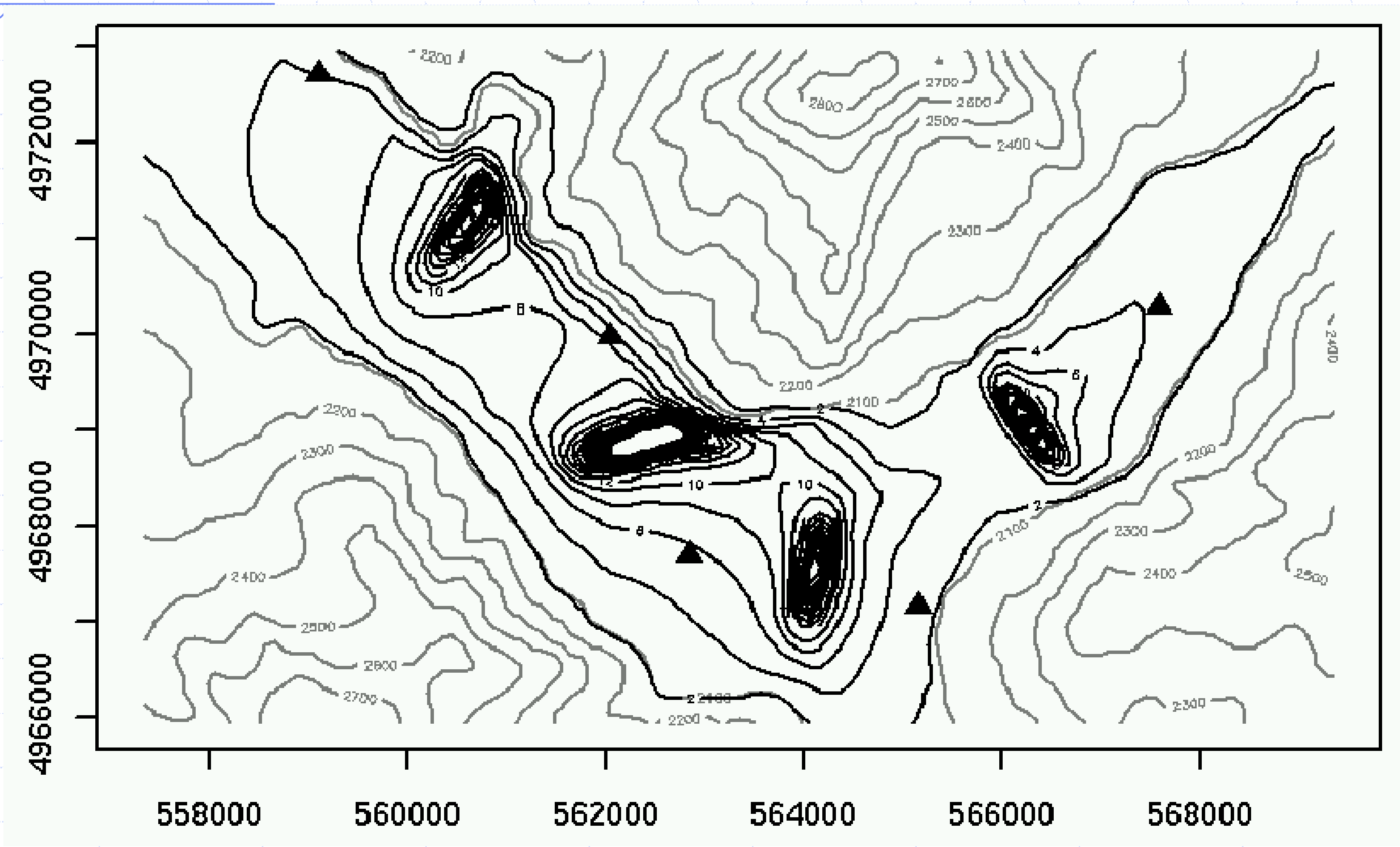
Moorcroft and Lewis (2004)

Model with added "terrain taxis"



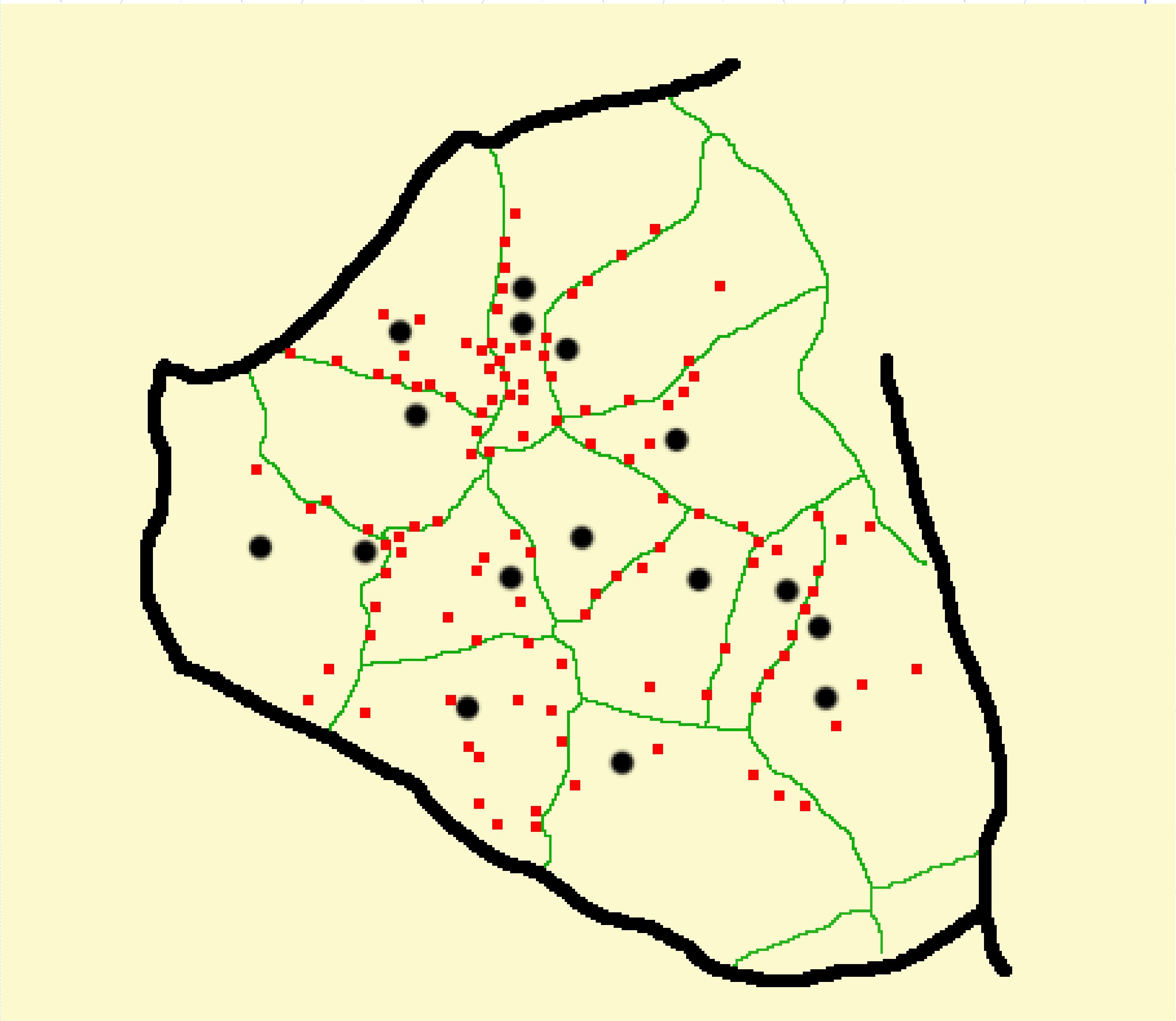
Moorcroft and Lewis (2004)

Scent mark density prediction



Moorcroft and Lewis (2004)

Other Territorial Patterns



Badger territories near Oxford (based on Kruuk)

Conclusions and Discussion

- Simple mechanistic models based on movement about the den site can give rise to complex territorial patterns that fit observed data, including realistic bowl-shaped scent-marking densities.
- Models can be modified to include spatial heterogeneity, such as variable terrain and spatially distributed prey.
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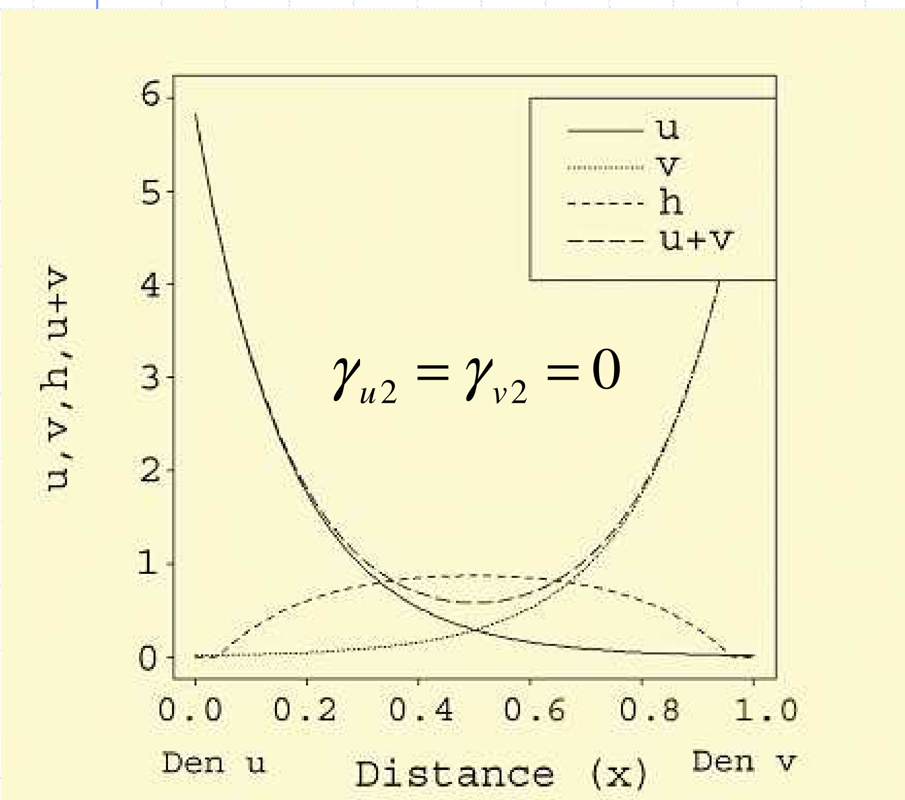
Territorial Interactions

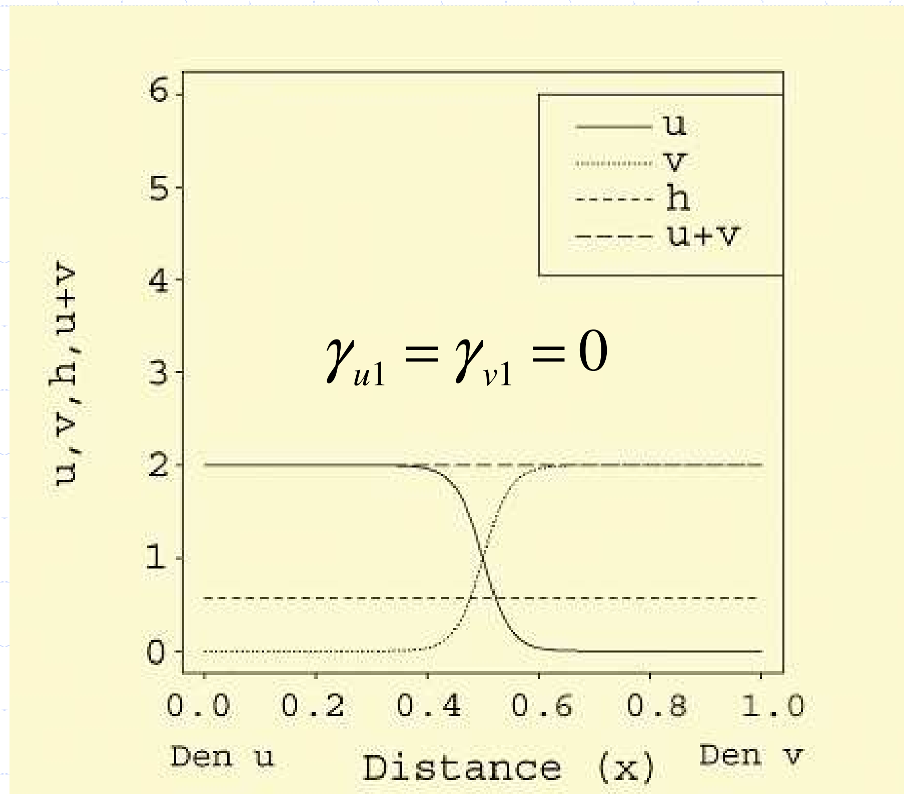
- Steady state analysis

$$\frac{\partial u}{\partial x} = -(\gamma_{u1} + \gamma_{u2} v)u$$

$$\frac{\partial v}{\partial x} = (\gamma_{v1} + \gamma_{v2} u)v$$



Holgate home range model

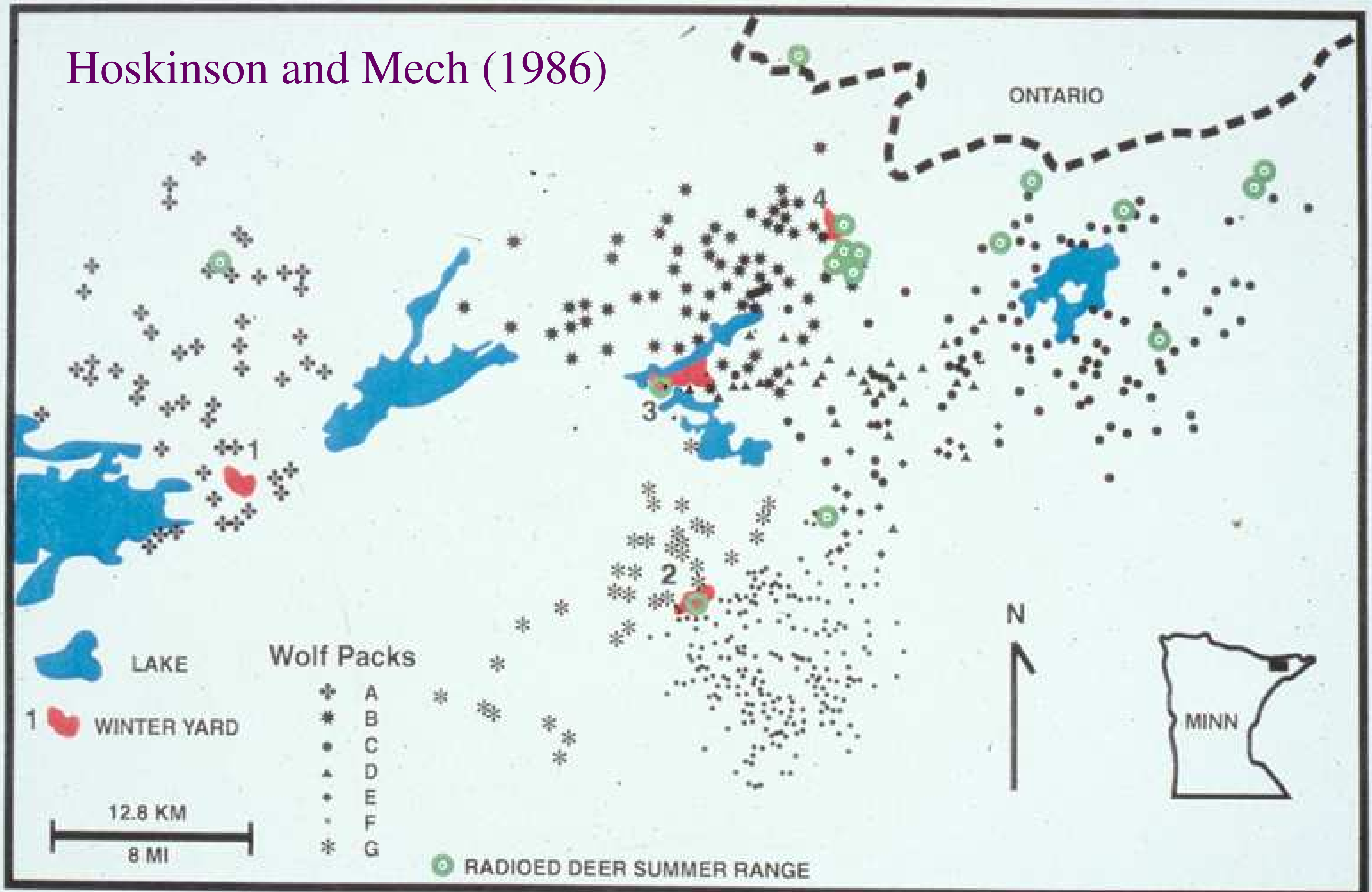


Pure territorial model

Interactions With White-tailed Deer

- Strong predator-prey interaction
- Deer locations correlate negatively with wolf locations in radiotracking studies

Hoskinson and Mech (1986)



Evolutionarily Stable Strategies

- How should packs modify movement and scent-marking parameters so as to maximize fitness?

$$R_u = \underbrace{\exp\left(-\mu_0 - \alpha \int_0^1 u(x)v(x)\,dx\right)}_{\text{survivorship}} \underbrace{\sigma\psi\left(\int_0^1 u(x)H(u(x),v(x))\,dx\right)}_{\text{offspring produced}}$$

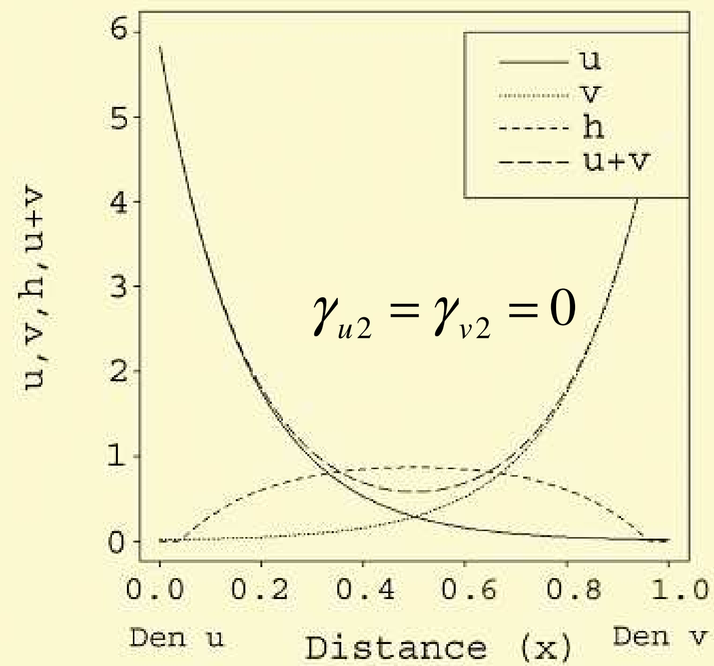
u : pack 1 density
v : pack 2 density
$H(u,v)$: deer density averaged over year
μ_0 : density-independent mortality
α : interaction-dependent mortality
$\sigma\psi$: translates food into offspring

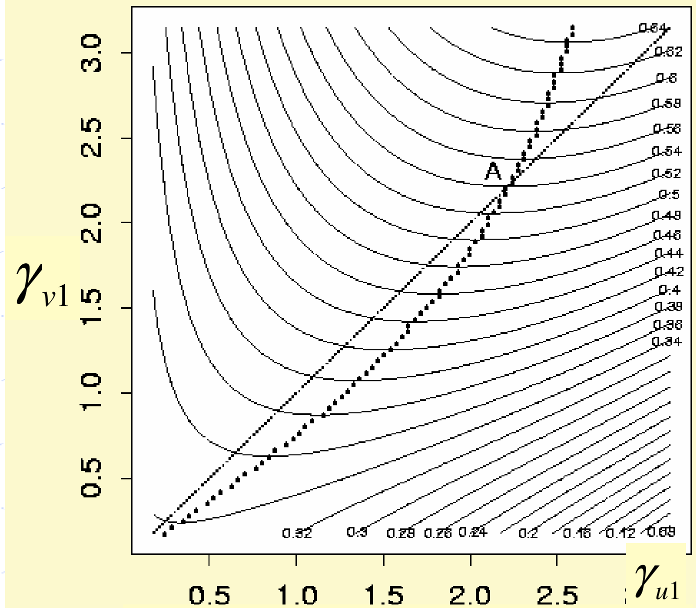
ESS : movement rules for intrinsic bias (γ_{1*}) and response to foreign scent marks (γ_{2*}) that are uninvadable in that a pack digressing from these rules will reduce its "fitness" ($r_u = \log(R_u)$ or $r_v = \log(R_v)$).

Lewis and Moorcroft (2001)

ESS in Home-range Case

Contours indicate constant values of $r_u = \log(R_u)$





home range ESS $(\gamma_{u2} = \gamma_{v2} = 0)$

$$\frac{\partial u}{\partial x} = -(\gamma_{u1} + \gamma_{u2} v) u$$

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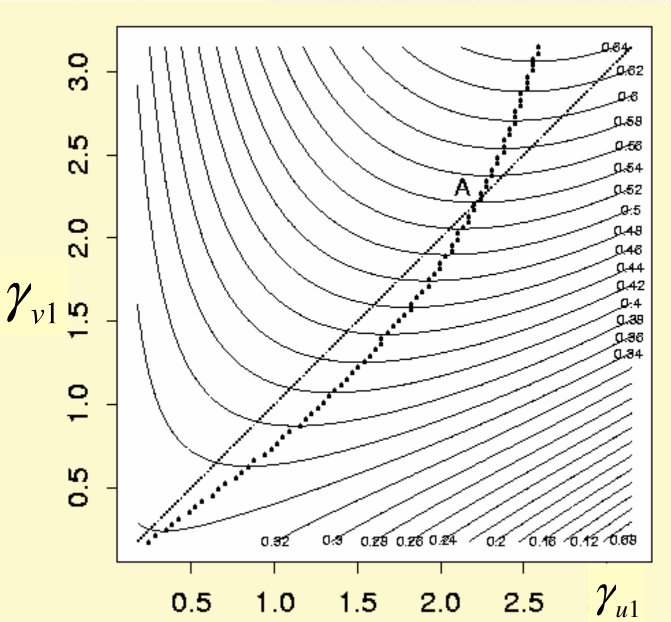
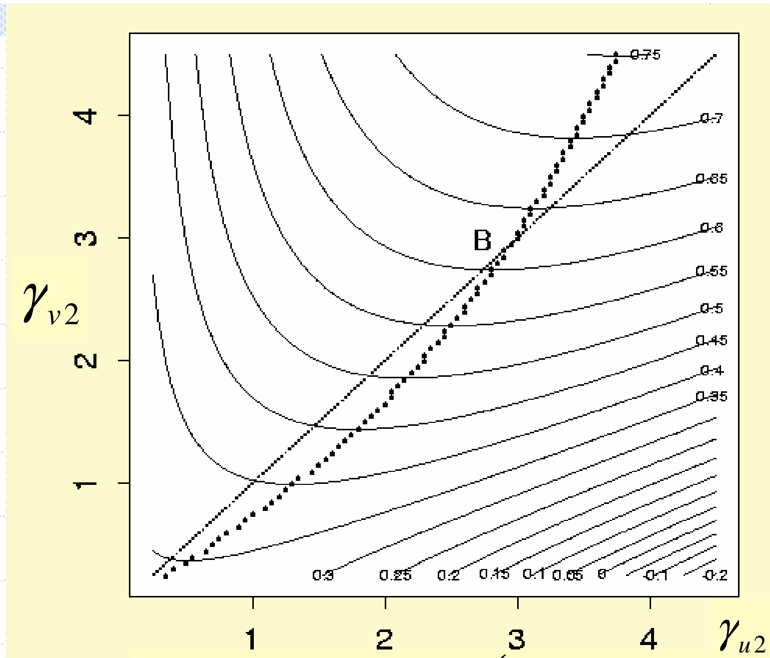
$$R_u = \underbrace{\exp\left(-\mu_0 - \alpha \int_0^1 u(x) v(x)\, dx\right)}_{\text{survivorship}} \underbrace{\sigma \psi \left(\int_0^1 u(x) H(u(x), v(x))\, dx\right)}_{\text{offspring produced}}$$

ESS for mixed model shows pure territorial behaviour with an interaction zone



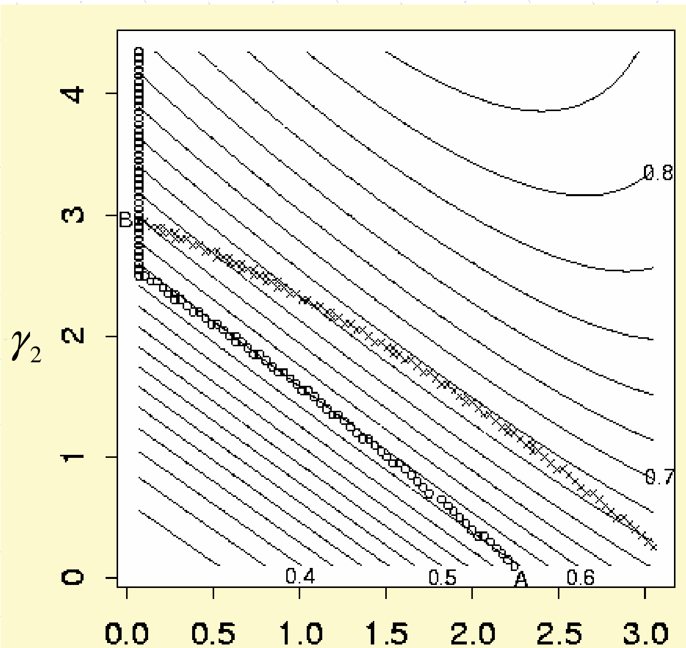
home range ESS $(\gamma_{u2} = \gamma_{v2} = 0)$



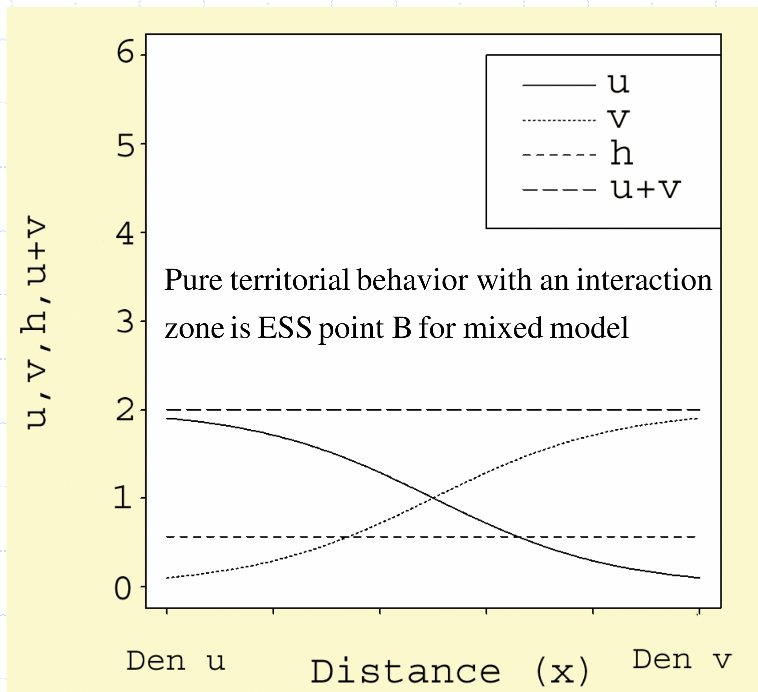
pure territory ESS $(\gamma_{u1} = \gamma_{v1} = 0)$

o: ESS value for γ_1, given fixed γ_2 values

x: ESS value for γ_1, given fixed γ_2 values



ESS for mixed model γ_1



Conclusions and Discussion

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