Modelling territoriality and wolf–deer interactions

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WE propose here a mechanism for territorial pattern formation in wolves (*Canis lupus*) and analyse it using a spatially explicit mathematical model incorporating wolf movement and scent marking. Model results reflect field observations from northeastern Minnesota: buffer zones where wolves are scarce arise between adjacent packs, and near these buffer zones there are increased levels of scent marking[1,2]. Territories are arranged in a spatial mosaic (Fig. 1) which covers the wolf range. In the model formulation no assumptions are made about actual existence or extent of wolf territory and buffer zones; these arise naturally as stable steady-state solutions to the equations. We show mathematically how reduced predation by wolves in the buffer zones provides a refuge for prey species. Field studies support this; distribution of a primary prey species, white-tailed deer (*Odocoileus virginianus*), correlates negatively with that of wolves. Deer are found primarily in buffer zones[3,4] (Fig. 2).

Elaborate spatial patterns of wolf scent marks[5] are used to advertise precise information about territorial claims[6]. Behavioural studies indicate that it is the raised leg urination (RLU) which plays the key role in scent marking[5,7]. Out of a typical pack of 5–15 wolves[8], a few mature dominant members leave RLUs regularly on trails; a travelling wolf may encounter one RLU every two to three minutes[5]. Marking frequency roughly doubles near territorial borders, giving rise to 'bowl-shaped' distributions of RLUs across territories, with the raised edges of the olfactory bowl located at the territorial boundaries[5]. Observations indicate scrutiny of RLUs[7] and some aversion to foreign RLUs made by neighbouring packs[5].

We propose a mechanism for generating the territorial patterns using a mechanistic, spatially explicit mathematical model with simple rules for scent marking and movement. Making no underlying assumptions about the size and extent of the wolf territories themselves, we show how the territorial patterns actually arise naturally as stable steady-state solutions to the equations.

Our key modelling assumption is that wolf movement and behaviour are mediated by the absence/presence of foreign RLUs. In the absence of foreign RLUs: (1) movement is primarily dispersive as individuals search for food and other resources, and (2) RLU-marking occurs at low levels. The presence of foreign RLUs elicits two responses: (1) movement towards an organizing centre for the pack such as a den, above-ground rendezvous site or familiar location[9]; and (2) increase in RLU-marking frequency[5]. The RLU marks are assumed to lose intensity with age.

The expected location of an RLU-marking wolf is described by a probability density function denoting the chance of finding it at point x and time t. For any given pack, these are summed over the number of RLU-marking wolves to yield the expected density of RLU-marking wolves, henceforth referred to as the expected density of wolves in a pack. For a model of two adjacent interacting wolf packs, pertinent state variables are expected densities of wolves in packs 1 and 2 ($u(x, t)$ and $v(x, t)$); and of RLUs from packs 1 and 2 ($p(x, t)$ and $q(x, t)$).

Components of the wolf movement are expressed mathematically by:

$$\frac{\partial u}{\partial t} = -\nabla \cdot \{\mathbf{J}_{d_u} + \mathbf{J}_{c_u}\} \qquad (1)$$

and

$$\frac{\partial v}{\partial t} = -\nabla \cdot \{\mathbf{J}_{d_v} + \mathbf{J}_{c_v}\} \qquad (2)$$

where $\mathbf{J}_{d_u}$ and $\mathbf{J}_{d_v}$ describe dispersive movement via diffusion and $\mathbf{J}_{c_u}$ and $\mathbf{J}_{c_v}$ describe movement towards organizing centres situated at x_u and x_v by convection towards x_u and x_v, respectively.

Specific forms for the fluxes in equations (1) and (2) were derived under the assumptions that dispersive movement is modelled by simple diffusion ($\mathbf{J}_{d_u} = -d\nabla u$, $\mathbf{J}_{d_v} = -d\nabla v$) with diffusion coefficient $d > 0$; and that convective movement is at a rate proportional to the expected density of foreign RLU

$$(\mathbf{J}_{c_u} = -cuq\,(x - x_u)/|x - x_u|, \mathbf{J}_{c_v} = -cvp\,(x - x_v)/|x - x_v|)$$

with convective proportionality constant $c > 0$.

Equations for RLU-marking and decay are:

$$\frac{\partial p}{\partial t} = u(l + mq) - fp \qquad (3)$$

and

$$\frac{\partial q}{\partial t} = v(l + mp) - fq \qquad (4)$$

where $l > 0$ denotes low-level continual RLU marking, $m > 0$ describes increased RLU-marking levels in the presence of foreign RLUs, and $f > 0$ represents first-order RLUs decay kinetics.

Analysis indicates the existence of a stable, spatially heterogeneous steady-state solution to equations (1) to (4). Describing territorial patterns and corresponding levels of the spatially distributed RLUs, this solution (Fig. 3) can be found analytically by integrating steady-state versions of equations (1) to (4) subject to zero-flux boundary conditions for u and v. The solution predicts the partitioning of available space into territories and the formation of territorial boundaries near which there are low levels of expected wolf density and high levels of expected RLU density (Fig. 3). This clearly reflects the field observations regarding territorial patterns, interpack buffer zones and bowl-shaped RLU densities. Thus, the simple rules for scent marking and movement given here are sufficient to explain territorial patterns.

Here, scent marks are crucial to the formation of territories; if scent marking is not included ($l, m = 0$ in equations (3) and (4)) then $p, q \to 0$ and equations (1) and (2) are reduced to diffusion equations so that the territories do not form. It can also be shown that a necessary condition for the bowl-shaped
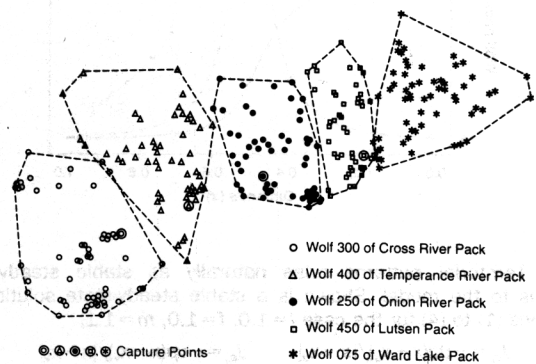

FIG. 1 Radiolocations and home range boundaries of five adult and yearling timber wolves radiotracked by aircraft, 27 May–22 October 1971 in northeastern Minnesota. Redrawn from Fig. 4 of ref. 2 with permission.

○ Wolf 300 of Cross River Pack
△ Wolf 400 of Temperance River Pack
● Wolf 250 of Onion River Pack
□ Wolf 450 of Lutsen Pack
✳ Wolf 075 of Ward Lake Pack

⊙.⊙.⊙.⊙.⊙ Capture Points

RLU patterns with interior maxima for p and q (Fig. 3) is that foreign RLUs elicit a sufficiently large increase in the RLU-marking rate. Mathematically, this condition is met when m exceeds a critical value.

We now consider an extension of the above model which can be used to predict the negative correlation between wolf territories and the white-tailed deer distribution (Fig. 2). For the purposes of illustration, we assume: (1) wolf territories are stationary and stable (Fig. 3); (2) Holling type 1 functional response of deer to wolf predation; (3) Beverton–Holt density-dependent population dynamics for the deer in the absence of wolf predation. Denoting $h(x, t)$ as the expected density of deer, we have

$$\frac{\partial h}{\partial t} = -\psi(u(x) + v(x))h \qquad (5)$$

where $u(x)$ and $v(x)$ denote the expected densities of pack 1 and pack 2 wolves, ψ is the predation rate and $0 \le t \le T$, the year being T time units long. Steady-state solutions, yielding constant values when deer densities are compared from one spring to the next, satisfy the Beverton–Holt dynamics:

$$h(0, x) = \frac{\lambda h(T, x)}{1 + (\lambda - 1)h(T, x)/K} \qquad (6)$$

where $\lambda > 1$ and K measure the population growth rate and carrying capacity of the deer in the absence of predation, respectively. Solving equation (5) subject to the condition of equation (6) gives steady-state solutions as

$$h(0, x) = \max \{0, K(\lambda - \exp \{[u(x) + v(x)]\psi T\})/(\lambda - 1)\} \qquad (7)$$

FIG. 2 Winter yards and summer home ranges of radio-tagged deer in relation to wolf-pack territories. Wolf-pack territories: A, Glenmore L. pack; B, Newton L. pack; C, Ensign L. pack; D, Greenstone L. pack; E, Pagami L. pack; F, Harris L. pack; G, Birch L. pack in northeastern Minnesota. Redrawn from Fig. 4 in Hoskinson and Mech[3] with permission. (Roads have been removed and colour has been added.)

FIG. 4 Deer are found primarily in the narrow corridors between the territories of adjacent wolf packs. Shown is the steady-state distribution of deer in the spring given by equation (7) and $u(x)$ and $v(x)$ given as in Fig. 3, and $\psi T = 0.3$, $\lambda = 2.0$ and $K = 5.0$.
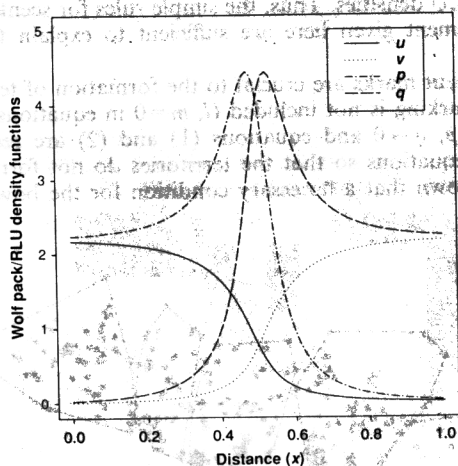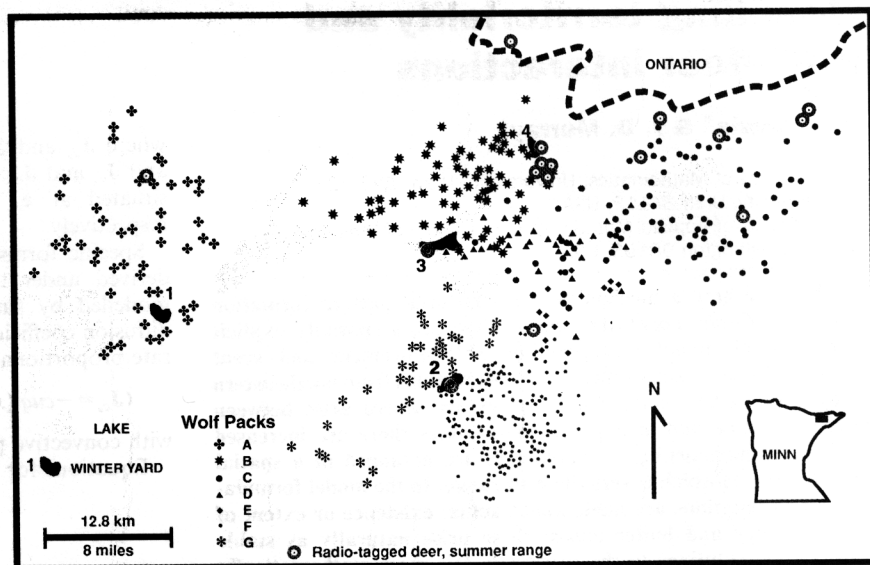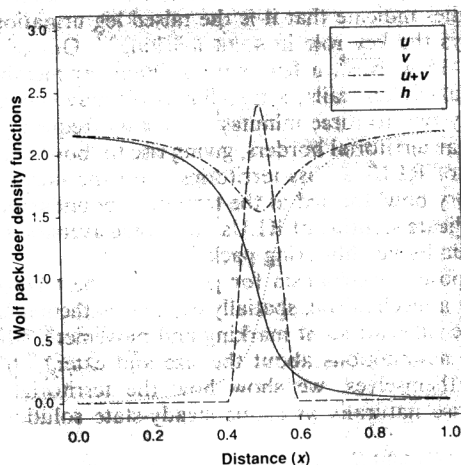

FIG. 3 Territorial patterns arise naturally as stable steady-state solutions to the model. Shown is a stable steady-state solution for equations (1) to (4) for the case $l = 1.0$, $f = 1.0$, $m = 1.1$,

$$J_{c_u} = -uq(x - x_u)/|x - x_u|, \qquad J_{c_v} = -vp(x - x_v)/|x - x_v|$$
$$J_{d_u} = -0.3\nabla u, \qquad J_{d_v} = -0.3\nabla v$$

$x_u = 0$ and $x_v = 1$. A territorial boundary is found at the point $x = 0.5$. Near this boundary the expected wolf-densities, $u(x)$ and $v(x)$, are low and expected RLU densities, $p(x)$ and $q(x)$, are high. Numerical solution used the method of lines and Gear's method.

Thus deer are found primarily where the combined wolf densities are lowest, in the buffer zones between packs (Fig. 4).

As noted by Mech[10], evidence for a similar situation involving deer and human societies is given by Hickerson's study of Sioux and Chippewa Indians in 1780–1850[11]. Warfare between the two tribes gave rise to a buffer zone which was normally unoccupied. In turn, reduced hunting pressure in this buffer zone effectively provided a refuge for the deer. But when a long truce was maintained, the buffer zone was destroyed and famine ensued. □

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