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A Model for Wolf-Pack Territory Formation and Maintenance

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A model is developed to investigate the formation and maintenance of wolf territories based on the spatial patterns observed in northeastern Minnesota. Initially we simplify the model to consider the movements of a single pack. In this case we obtain steady state density distributions corresponding to territories and determine how the size of a territory depends on the number of wolves in a pack. We suggest how, with sufficient access to the relevant field data, this simplified model could be used to estimate some of the model parameters. The complete multi-pack model shows how interactions between adjacent packs determine the shape of the territory. We investigate the solutions to the mathematical model systems and discuss ecological implications.

1 Introduction

Territorial behaviour is an intrinsic part of the ecology of many mammals and introduces large scale spatial heterogeneity into population interactions. Clearly such heterogeneity can have major effects on the spread of disease and population survival, but despite this there have been very few attempts to model the phenomenon mathematically.

In 1939, Noble defined territory as "any defended area", thus providing a very general and flexible definition for future development. Since then there has been a large number of alternative definitions each with a slightly different emphasis. Emlen (1957) suggested "a space within which an animal is aggressive to and usually dominant over certain intruders", Pitelka (1959) suggested "any exclusive area", Eibl-Ebesfeldt (1970) "a space associated intolerance" and Brown & Orians (1970) "a fixed exclusive area with the presence of defense that keeps rivals out". In all cases the territory is an actively defended fixed area in space (but this can vary over time) and the holder has exclusive use of the space with respect to a certain group of individuals. It is important to reiterate that boundary areas can overlap temporally, allowing them to be used by two different groups at different times (Brown & Orians, 1970). The large number of definitions that have been developed by field ecologists indicates the importance of territoriality in many different natural systems.

The motivation for this paper came from field studies on the ecology of the timber wolf (*Canis lupis*) carried out in northeastern Minnesota over a period of many years (see, for example Mech, 1977*a*; van Ballenberghe *et al*., 1975). Although wolves are highly developed carnivores with a complex social structure, we restrict discussion of wolf behaviour in this paper to those elements most directly related to territoriality.

Wolf packs are extended family groups typically consisting of 3–12 wolves with territories ranging from 125–310 km^2 in northeastern Minnesota (van Ballenberghe *et al*., 1975). Buffer zones which separate adjacent territories can be as wide as 1–2 km covering between 25 and 40% of the available land (Mech 1977*b*, *c*). These buffer regions are areas of potential inter-pack conflict into which wolves rarely trespass, although when prey levels are low within the territory cores, wolves may move into the buffer zones

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to hunt and the levels of inter-pack strife can increase (Mech, 1977*b*).

One pair of wolves, known as the alpha couple, dominate pack activities. This alpha couple is usually the only pair to produce young. Pups are born in the late spring, are reared at the den site for some time after birth, and then move to above ground rendezvous sites. Thus, during the summer months pack activity is centred around the den or rendezvous sites where the pups are fed and cared for. By the end of the summer, the pups have developed sufficiently and are able to move with the pack. In this way, the den loses its focus and the pack can move extensively through the territory.

Olfactory stimuli are well known to be used in a variety of different roles by many mammals. The raised leg urination (RLU) is closely connected with territorial marking and maintenance (Peters & Mech, 1975). These markings are made throughout the territory along wolf trails but, more importantly, they increase significantly around the territory edges giving rise to high concentrations of RLU markings from all packs in the buffer regions. Unlike other olfactory stimuli associated with wolves, the RLU shows little correlation with pack size. In fact, it is the alpha pair which is predominantly responsible for this marking.

Mathematical models describing animal movement have been proposed, for example, by Skellam (1951) in which the idea of modelling animal movement with simple Fickian diffusion was developed. Okubo (1986) investigated mathematical models describing animal groups such as schools and swarms while more recently, Grunbaum & Okubo (1993) reviewed models for social aggregations.

The specific issue of territoriality, however, has been less often considered. Statistical models, both of the univariate and bivariate type were compared by van Winkle (1976) for their ability to predict home range movements. A home range is similar to a territory but there is no element of defense associated with this area so models of home range activity are of limited value when describing territorial behaviours and movements. Don & Renolls (1983) used a more sophisticated model based upon probability distributions to determine home range movement when attraction points were used to represent a nesting or similar site. Benhamou (1989) developed a correlated random walk model to describe animal movement which is governed by olfactory gradients and produced results in agreement with field studies. A probability model concerned specifically with territorial animals was proposed by Bacon *et al*. (1991) to investigate the resource dispersion hypothesis of Macdonald (1983) which suggests that spatial distribution of resources determines territory size and the richness of these resources independently determines group size. They use normal distribution to represent yield from a territory during a feeding period for a habitat of discrete independent food patches. The results show agreement with Macdonald's theory (1983). More generally, Covich (1976) investigated the shape and size of foraging areas using graphical techniques. These simple, non-mechanistic models give an indication of the dependence of foraging areas on ecological constraints such as predation, resource distribution and population density. Another simple model by Possingham & Houston (1990) reconsiders the "marginal value theorem" (Charnov, 1976) in the case of territorial foragers and shows that resource renewal is an important element of foraging strategy for a territorial animal.

Of particular relevance to this paper, Taylor & Pekins (1991) used a modified Lokta-Volterra system of ordinary differential equations to investigate how important the buffer zone is in maintaining the stability of the wolf-deer ecosystem in Minnesota. Here, however, territories were specified as hexagonal shapes and movement between the core and buffer was achieved by splitting the deer population into two subpopulations. As the spatial structure of territory is assigned, nothing can be deduced from this model about the natural development and maintenance of wolf territories.

The recent paper by Lewis & Murray (1993) considers a partial differential equation model with two wolf packs and deer and shows how the system gives rise to territorial patterns and the subsequent spatial segregation of wolves and their prey, the white-tailed deer (*Odocoileus virginianus*). This model has a similar structure to that described below, incorporating dispersive movement to represent wolf foraging activities and a convective term representing movement towards an organising centre. The model described here, however, differs from that one in several ways. In the Lewis & Murray model, convection back towards an organising centre occurs only upon encountering foreign RLU markings. In our model, this component of movement occurs irrespective of any olfactory stimuli and we represent wolf response to friendly and foreign RLUs with chemotactic type terms.

This paper considers territory formation without predator–prey interactions. Subsequent papers will deal with this aspect (White *et al*., submitted). Our primary interest is in summer movement patterns when the den is a focal point of pack activity and thus we are essentially considering a model with a time span of several months. We begin by formulating the mathematical model assuming that there are two wolf packs in a region with plentiful food supply. Analysis is carried out on the simpler single pack model and shows that territories can be formed even in the absence of neighbours. The steady state solution for the single pack model allows us to determine a relation between pack and territory size. The interaction of several packs is shown to introduce spatial heterogeneities into the wolf density distributions about the den location and allows an investigation of RLU density distribution in relation to the wolf density distribution. We also discuss model solutions when the den is no longer a focus of activity in the winter months and show that, in its present form, the model is rather limited in its ability to describe the density distributions in this case.

2 Model Formulation

The behaviour and ecology of the wolf are clearly highly complex but the stability of the territories found in N.E. Minnesota suggest that there are certain mechanisms underlying the movement of the pack members.

To define state variables, we must account for the size of the territory relative to the pack size. As wolf packs are small in size when compared with their territory sizes, there will be large periods of time when no wolf is found in a given location. In view of this, we define the state variables as expected density of wolves using a probabilistic approach. Scent marking is thought to be an important component in maintaining territories—we reflect this in the model by assigning two state variables to each wolf pack, one for expected wolf density and the other for expected RLU density. In this case the state variables for a two pack model are:

$u(\mathrm{x}, t)$ = expected density of scent marking wolves in pack 1

$v(\mathrm{x}, t)$ = expected density of scent marking wolves in pack 2

$p(\mathrm{x}, t)$ = expected density of RLUs from pack 1

$q(\mathrm{x}, t)$ = expected density of RLUs from pack 2.

In this simplified model system, wolf movement is assumed to comprise four components—movement towards the den (during summer) to feed the pups, dispersal to find food and to mark the territory, movement away from regions of foreign RLU marking and movement back towards familiar RLU marking. We assume that there is no starvation or inter-pack conflict during the summer months and hence that there is no wolf mortality. For the adult members of a pack at least, this is not an unreasonable assumption (Mech, 1970).

Each of the movement components is represented by a term in a nonlinear partial differential equation. Movement towards the den is modelled by advection towards a single point in the (x, y) plane—x_u for pack 1 with convection coefficient $C_u(\mathrm{x}-\mathrm{x}_u)$ and x_v for pack 2 with convection coefficient $C_v(\mathrm{x}-\mathrm{x}_v)$. Dispersal is modelled by nonlinear diffusion with coefficient $D_u(u)$ for pack 1 and $D_v(v)$ for pack 2 and the response to familiar and foreign RLU marks is represented by chemotactic-type terms with coefficients $F_u(q)$ and $G_u(p)$ for pack 1 and $F_v(p)$ and $G_v(q)$ for pack 2. They combine together to give the governing equations for each pack (given first in words),

Rate of change = Rate of change because of movement back to the den

(in wolf density) + Rate of change because of dispersal for foraging

+ Rate of change because of avoidance of foreign RLUs

+ Rate of change because of attraction of familiar RLUs

$$\partial u/\partial t = \nabla\cdot[C_u(\mathrm{x}-\mathrm{x}_u)u] + \nabla\cdot[D_u(u)\nabla u] + \nabla\cdot[uF_u(q)\nabla q] - \nabla\cdot[uG_u(p)\nabla(p)] \quad (1)$$

$$\partial v/\partial t = \nabla\cdot[C_v(\mathrm{x}-\mathrm{x}_v)v] + \nabla\cdot[D_v(v)\nabla v] + \nabla\cdot[vF_v(p)\nabla p] - \nabla\cdot[vG_v(q)\nabla q] \quad (2)$$

Typical forms for the movement coefficients are discussed in Section 2.2.

The equations governing the temporal distribution of RLU marking are structurally simple. We assume there is a low level marking in the territory core which increases significantly when foreign marking is encountered. We also assume the strength of the marks decays over time. Combining these gives the two equations governing the temporal variation in RLU distributions as

$$\partial p/\partial t = u[l_p + M_p(q)] - f_p p \quad (3)$$

$$\partial q/\partial t = v[l_q + M_q(p)] - f_q q. \quad (4)$$

The parameters can be interpreted as follows: l_p and l_q denote the rate of low level scent marking throughout the wolf territory, and f_p and f_q indicate the first order rate at which the RLUs decay. Again the model functions $M_p(q)$ and $M_q(p)$ which represent the increase in RLU marking in the presence of foreign RLU markings are discussed in Section 2.2.

To completely specify the problem mathematically, we give the initial expected density distributions,

$$u(\mathrm{x},0)=h_u(\mathrm{x}),\quad p(\mathrm{x},0)=h_p(\mathrm{x}),$$

$$v(\mathrm{x},0)=h_v(\mathrm{x}),\quad q(\mathrm{x},0)=h_q(\mathrm{x}) \tag{5}$$

for arbitrary functions $h_u(\mathrm{x})$, $h_p(\mathrm{x})$, $h_v(\mathrm{x})$, and $h_q(\mathrm{x})$. Typically we set $h_p(\mathrm{x})=h_q(\mathrm{x})=0$ because we are primarily interested here in initial territory formation.

We consider the problem on some domain Ω with zero flux boundary conditions for the expected wolf density distributions; that is,

$$0=[C_u(\mathrm{x}-\mathrm{x}_u)u+D_u(u)\nabla u+uF_u(q)\nabla q- uG_u(p)\nabla(p)]\cdot \mathrm{n} \text{ on } \partial\Omega$$

$$0=[C_v(\mathrm{x}-\mathrm{x}_v)v+D_v(v)\nabla v+vF_v(p)\nabla p- vG_v(q)\nabla(q)]\cdot \mathrm{n} \text{ on } \partial\Omega \tag{6}$$

where n is the outward normal to the domain on its boundry $\partial\Omega$. The zero flux boundary condition effectively imposes the biological constraint that there is no immigration or emigration of wolves across the boundary of the finite study area.

Equations (1) and (2) with the boundary conditions given in (6) are conservation equations and thus the number of wolves in a pack remains constant for all time. To show this we look at just one of the equations, (1) for example, and suppose that the number of wolves in the pack is $Q_u(t)$ where

$$Q_u(t)=\int_\Omega u(\mathrm{x},t)\mathrm{dx}. \tag{7}$$

Using (1), (6), (7) and the divergence theorem, we get

$$\begin{aligned}\frac{\partial Q}{\partial t}&=\int_\Omega \frac{\partial u}{\partial t}\,\mathrm{dx}\\ &=\int_\Omega \nabla\cdot[C_u(\mathrm{x}-\mathrm{x}_u)u+D_u(u)\nabla u+uF_u(q)\nabla q\\ &\qquad -uG_u(p)\nabla(p)]\,\mathrm{dx}\\ &=\int_{\partial\Omega}[C_u(\mathrm{x}-\mathrm{x}_u)u+D_u(u)\nabla u+uF_u(q)\nabla q\\ &\qquad -uG_u(p)\nabla p]\cdot \mathrm{dn}\\ &=0\end{aligned} \tag{8}$$

Thus the number of wolves in the pack does not change with time; that is

$$Q_u(t)=Q_u(0)=Q_u=\text{constant}.$$

Similarly for pack 2,

$$Q_v(t)=Q_v(0)=Q_v=\text{constant}.$$

2.1. NON-DIMENSIONALISATION

We non-dimensionalize the model system to allow comparison between the relative size of model parameters and to reduce the number of parameters in the problem. The area of Ω is given by

$$A=\int_\Omega \mathrm{dx}$$

and we define $L=A^{1/m}$ where m is the dimension of the solution domain (that is, $m=1$ for 1 space dimension and $m=2$ for 2 space dimensions). We use the decay time for the RLUs of pack 1 as a typical timescale. We take U_0 and V_0 to be average expected wolf densities for the respective packs, that is

$$U_0=\frac{Q_u}{L^m}\quad V_0=\frac{Q_v}{L^m}$$

and non-dimensionalize by letting

$$u^*=\frac{u}{U_0},\quad v^*=\frac{v}{V_0},\quad p^*=\frac{f_p}{U_0 l_p}p,$$

$$q^*=\frac{f_p}{V_0 l_q}q,\quad t^*=tf_p,\quad \mathrm{x}^*=\frac{\mathrm{x}}{L}$$

$$C_u^*=\frac{C_u}{Lf_p},\quad C_v^*=\frac{C_v}{Lf_p},\quad D_u^*=\frac{D_u}{L^2 f_{\mathrm{p}}},\quad D_v^*=\frac{D_v}{Lf_p}$$

$$F_u^*=\frac{F_u V_0 l_q}{L^2 f_p^2},\quad F_v^*=\frac{F_v U_0 l_p}{L^2 f_p^2},$$

$$G_u^*=\frac{G_u U_0 l_p}{L^2 f_p^2},\quad G_v^*=\frac{G_v V_0 l_q}{L^2 f_p^2}$$

$$M_p^*=\frac{M_p}{l_p},\quad M_q^*=\frac{M_q}{l_q},\quad \phi=\frac{f_q}{f_p}.$$

For the dimensionless quantities to be well-defined, we require that both wolf packs have a low level of RLU marking ($l_p>0, l_q>0$) and that the RLU intensity decreases over time ($f_p>0$). With this choice of dimensionless variables, and dropping the asterisk for notational simplicity, the model equations for the two wolf packs (1–2) remain unchanged in appearance as do the initial conditions (5) and the boundary conditions (6). The model equations for the RLU density distributions become,

$$\partial p/\partial t=u[1+M_p(q)]-p \tag{9}$$

$$\partial q/\partial t=v[1+M_q(p)]-\phi q \tag{10}$$

The conservation condition (7) now takes the form

$$\int_\Omega u(\mathrm{x}, t)\,\mathrm{dx} = 1 \quad \int_\Omega v(\mathrm{x}, t)\,\mathrm{dx} = 1, \tag{11}$$

and the dimensionless domain for study is an area or length equal to unity. The integral relation (11) shows that we can consider the dimensionless dependent variables $u(\mathrm{x}, t)$, $v(\mathrm{x}, t)$ as probability density functions for the location of the wolves at some time t. We use the non-dimensional form of the system in the analysis below to indicate which parameters are important in determining the qualitative behaviour of the solution.

2.2. CHOICE OF FUNCTIONAL FORMS

Okubo (1980) used the advection-diffusion equation

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(C_u(x)u + D_u(u)\frac{\partial u}{\partial x}\right)$$

to describe the swarming of the insects. In that one-dimensional model he used a density dependent diffusion coefficient of the form

$$D_u(u) = d_u u^n$$

for some positive value of n and the function $C_u(x - x_u)$ was chosen as the piecewise discontinuous function

$$c_u\ \mathrm{sgn}(x - x_u).$$

It can be seen that this model is one that would govern the movements of a pack (in one space dimension) if their movements were unaffected by RLU markings for a general $C_u(\mathrm{x} - \mathrm{x}_u)$. We use these functional forms as a basis, therefore, for the model functions $D_u(u)$, $C_u(\mathrm{x} - \mathrm{x}_u)$ proposed here.

In particular, we use an identical diffusion coefficient chosen to have a non-negative exponent n and compare the cases $n = 0$ and $n > 0$ for which the solution takes different forms. The first case represents standard Fickian diffusion so that, in the absence of the advection term, the wolves move in a random way during their foraging activities. The other represents density dependent diffusion where the rate of random motion, as measured by the diffusion coefficient D_u, is highest in those regions that are used most commonly (u high) and lowest in those regions which are used least (u low). In fact, it is assumed that as a wolf approaches totally unfamiliar regions ($u \to 0$) the rate of random motion approaches zero ($D_u \to 0$). In effect this means that if we begin with a density distribution which is not spatially homogeneous in Ω, (for example a hat or delta function) the leading edge moves outwards with a finite speed. While recognising that this nonlinear diffusion term has not been derived directly from the underlying stochastic process [see, for example, discussion of the Fokker Planck equation in Okubo (1980)], we believe that this term provides an effective means for characterizing movement rates based on familiarity with a region. As this work is the first of its kind to mathematically investigate the movements of territorial carnivores such as wolves using partial differential equations, we have chosen to compare these situations and see what information each can provide.

The convective flux term of the Okubo (1980) model is generalized to a two-dimensional function of the form

$$C_u(\mathrm{x}) = c_u \tanh(\beta r)\frac{\mathrm{x}}{r} \tag{12}$$

where $r = \|\mathrm{x}\|$ is the distance of a point from the den site.

This formation differs from that of Okubo in that $C_u(\mathrm{x})$ is a continuous function of space. The parameter c_u measures the maximum speed of the wolf when moving towards the den and β measures the change in the rate of convective movement as the den is approached. In particular we can see that the above function in one space dimension approaches that of Okubo (1980) as $\beta \to \infty$. In summer when the den is a focus of activity we take $c_u > 0$ and in winter when the den has been abandoned we can set $c_u = 0$.

We assume that when there is no RLU marking at a location, there is no wolf taxis away from foreign or towards familiar RLUs. Moreover, we assume that there is a maximum value for this coefficient which corresponds to the maximum wolf speed. We therefore take $F_u(q)$, $F_v(p)$, $G_u(p)$ and $G_v(q)$ to be monotonic non-decreasing functions with $F_u(0) = 0$, $F_v(0) = 0$, $G_u(0) = 0$, $G_v(0) = 0$ which asymptote to a finite non-zero value.

Finally, the functions $M_p(q)$ and $M_q(p)$ determine the extent to which RLU marking increases in the presence of foreign scent marks. They are also bounded monotonically non-decreasing functions similar in form to $F_u(q)$, $F_v(p)$, $G_u(p)$, $G_v(q)$. Qualitative forms for these functions are shown in Figs 1–2.

3. Single Pack Steady-State Distribution

If we suppose that pack 1, for example, is not affected by the presence of RLU marks (either familiar or foreign) so that $F_u(q) = G_u(p) = 0$, we can determine the steady-state solution for this pack analytically. This situation corresponds to the idea of home range because there is no mechanism of defence involved in the pack activities. Moreover, when the dimensionless distributions are converted back into their dimensional form, we can determine a relationship between pack and territory (home range) size.

A steady state arises when the diffusive flux balances the convective flux so that $\partial u/\partial t = 0$. In one space dimension the dimensionless convective flux (12) simplifies to

$$C_u(x - x_u) = c_u \tanh [\beta(x - x_u)]$$

and the non-dimensional steady state wolf distribution is governed by (1) with $\partial u/\partial t = 0$; that is

$$\frac{\partial}{\partial x}\left(c_u \tanh [\beta(x - x_u)]u + d_u u^n \frac{\partial u}{\partial x}\right) = 0. \qquad (13)$$

We can integrate this once and apply the zero flux boundary condition to obtain

$$c_u \tanh (\beta(x - x_u)) + d_u u^n \frac{\partial u}{\partial x} = 0 \qquad (14)$$

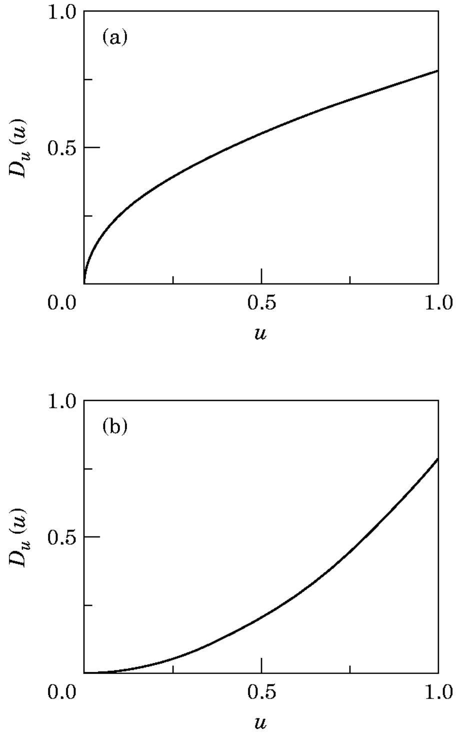

FIG. 1. Typical forms for the diffusion coefficient $D(u) = d_u u^n$ with $d_u = 0.8$ and (a) $n = 0.5$, (b) $n = 2$.

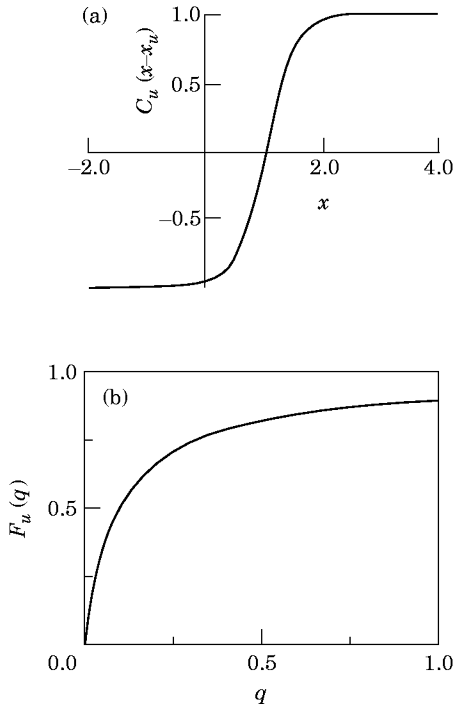

FIG. 2. Typical forms for (a) the convection coefficient in one space dimension, $C_u(x - x_u)$ for $\beta = 2$, $c_u = 1$, $x_u = 1$ and (b) the RLU related coefficient, F_u. The other RLU related coefficients M_p, M_q, F_v, G_u and G_v have a similar form.

3.1. CASE 1: $n = 0$

The solution to (14) when $n = 0$ is

$$u_s(x) = \frac{A}{[\cosh \beta(x - x_u)]^{c_u/d_u\beta}} \qquad (15)$$

where A is a constant of integration determined by the conservation condition (11) such that

$$A \int_\Omega \frac{\mathrm{d}x}{[\cosh \beta(x - x_u)]^{c_u/d_u\beta}} = 1 \qquad (16)$$

Note that $u_s(x_u) = A$, so A can be interpreted biologically as the ratio of probability of finding a wolf near the den site versus the probability of finding a wolf at a randomly selected point in space. This is effectively a measure of the aggregation about the den site. In Fig. 3(a) we show how the value of A varies with the parameter d_u for typical values of the parameters c_u and β and in Fig. 3(b) with the parameter β for typical values of c_u and d_u. The results are indeed reasonable, as they suggest that the probability density function for the wolves within a pack at the den location increases with increasing convection back to this location and decreases as the diffusion away in search of food increases. These results are verified in Fig. 4, where we show two steady-state density distributions—again, by increas-

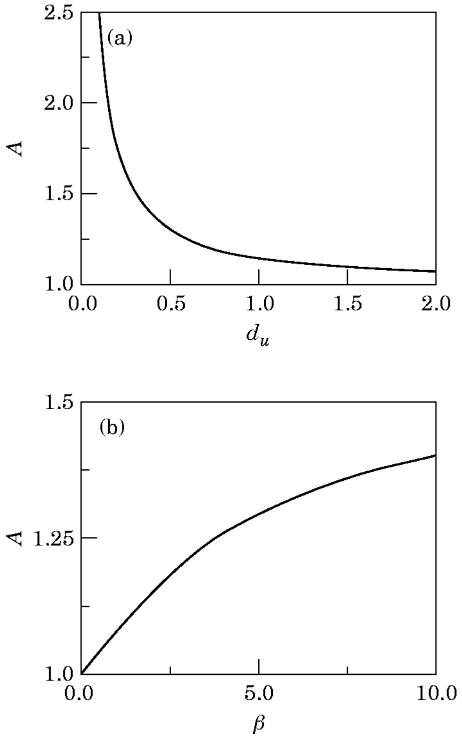

FIG. 3. The parameter A calculated from eqn (16) as a function of (a) d_u when $\beta=5$ and (b) β when $d_u=0.5$. In both cases, $c_u=1$.

ing the strength of the convection coefficient relative to the diffusion coefficient, we localize pack activity around the den site.

Although in theory the density given in (15) is never zero ($u_s(x)\rightarrow 0$ as $x\rightarrow \pm\infty$), $u_s(x)$ can become very small particularly if the convective flux is large. This suggests that the probability of finding a pack member beyond some finite distance from the den approaches zero and a territory has, in some sense, been established. When $n>0$, the boundaries are definite and can be calculated from the model solution.

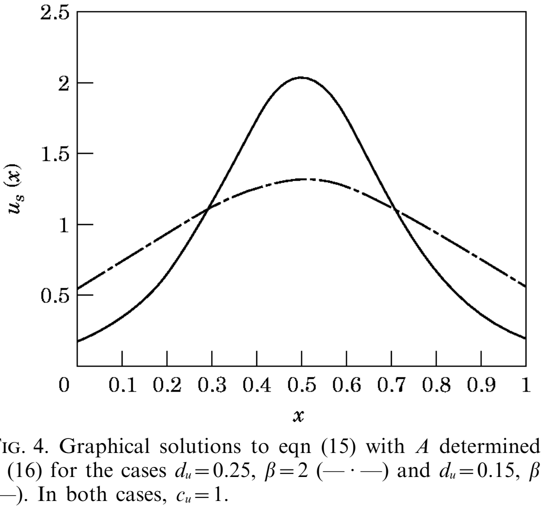

FIG. 4. Graphical solutions to eqn (15) with A determined by eqn (16) for the cases $d_u=0.25$, $\beta=2$ (— · —) and $d_u=0.15$, $\beta=5$ (——). In both cases, $c_u=1$.

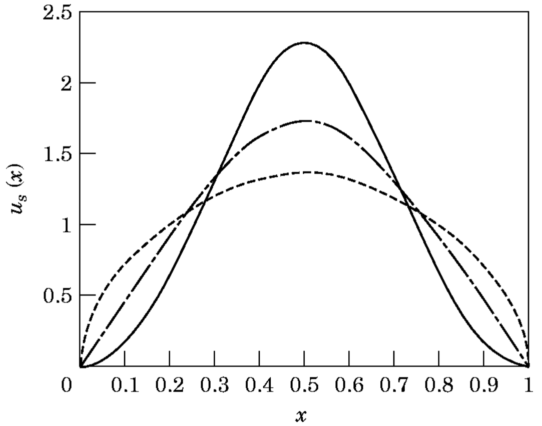

FIG. 5. Graphical solutions of eqn (17) with k determined by eqn (18) for the cases $n=0.5$, $d_u=0.12$ (——) $n=1$, $d_u=0.21$ (— · —) and $n=2$, $d_u=0.39$ (— —) and with $\beta=5$, $c_u=1$.

3.2. CASE 2: $n>0$

As $u_s(x)$ is a probability density function satisfying (11) it cannot become negative or grow without bound. As a result, by integrating (14) we obtain the steady state solution

$$u_s(x)=\begin{cases}\left(k-\dfrac{c_u n}{d_u\beta}\ln\{\cosh[\beta(x-x_u)]\}\right)^{1/n} & \\ 0 \quad \text{if } k>\dfrac{c_u n}{d_u\beta}\ln\{\cosh[\beta(x-x_u)]\} & \\ & \text{otherwise}\end{cases} \tag{17}$$

where k is the constant of integration given by the conservation condition

$$\int_{\Omega}\left(k-\frac{c_u n}{\beta}\ln\{\cosh[\beta(x-x_u)]\}\right)^{1/n}=1 \tag{18}$$

This integral equation is used to determine k uniquely once the model parameters have been specified and is used in the next section to determine the territory boundaries. In Fig. 5 we show the solution (17) for the three different cases of n and fixed choices of c_u, β and d_u.

4. Estimation of Territory Boundaries

The steady-state distributions (15–16) and (17–18) have one fundamental difference, namely the possibility of having a definite territory boundary.

4.1. CASE 1: $n=0$

In the first case where we are using ordinary Fickian diffusion, $u_s(x)=0$ only when $x=\pm\infty$. There is no definite region in space beyond which the probability of spotting a wolf from the pack is zero although this probability becomes immeasurably small at large distances from the den. The spatial heterogeneity that arises in the solution demonstrates a form of territoriality and, if we assume some threshold density within which there is an 80% chance of finding an individual, then we obtain territories with $n=0$. When there is no den, however, the territory breaks down completely as we show in Section 8.1.

4.2. CASE 2: $n\neq 0$

When n is non-zero, the density distribution becomes zero at a finite distance from the den. Now $u_s(x)=0$ when $k=n/d_u\beta\ \ln\{\cos \mathrm{h}[\beta(x-x_u)]\}$. If this occurs at $x=x_u\pm x_b$ then x_b can be determined uniquely by

$$k=\frac{c_u n}{d_u\beta}\ln[\cosh(\beta x_b)],\quad x_b>0,$$

[see eqn (17)]. The spatial points $x_u\pm x_b$ define the limits of the wolf territory. Figure 5 shows that there is a difference in the shape of the leading edge between the cases $0<n<1$, $n=1$ and $n>1$ and this arises in the gradient of the system. Rearranging (14) we have

$$\frac{\partial u}{\partial x}=-\tanh[\beta(x-x_u)]u^{1-n}.$$

At the leading edge, $u=0$ so that if $0<n<1$, $\partial u/\partial x=0$, if $n=1$, $\partial u/\partial x=-\tanh[\beta(x_b-x_u)]$ and if $n>1$, $\partial u/\partial x=\infty$. Ecologically this distinguishes the cases where there is a gradual or an abrupt end to the territory. In all cases, the result is a non-dimensional steady state expected wolf density distribution given by (17) as

$$u_s(x)=\begin{cases}\left[\dfrac{c_u n}{d_u\beta}\ln\left(\dfrac{\cosh\beta x_b}{\cosh\beta(x-x_u)}\right)\right]^{1/n} & |x-x_u|\leqslant x_b\\ 0 & \text{otherwise.}\end{cases}\tag{19}$$

This non-negative function of x satisfies the boundary conditions. Moreover we can see that the steady state has boundaries at a fixed and finite distance from the den.

5. Two-Dimensional Single Pack Problem

We have shown that the steady-state density distribution for a single wolf pack in one space dimension is symmetric about the den location. In two space dimensions the solution maintains this symmetry and in fact the solution is radially symmetric about the den. This is illustrated in Fig. 6, where we solve the model system numerically using explicit finite difference schemes with upwinding for the convection term. Symmetry is lost when there is interaction between neighbouring packs.

6. Relationship Between Pack and Territory Size

For non-zero n we have shown that territories with definite boundaries can be formed. We now convert (19) back into dimensional terms and show how the number of animals in a pack can affect the size of the territory. McNab (1963) suggested that the size of the

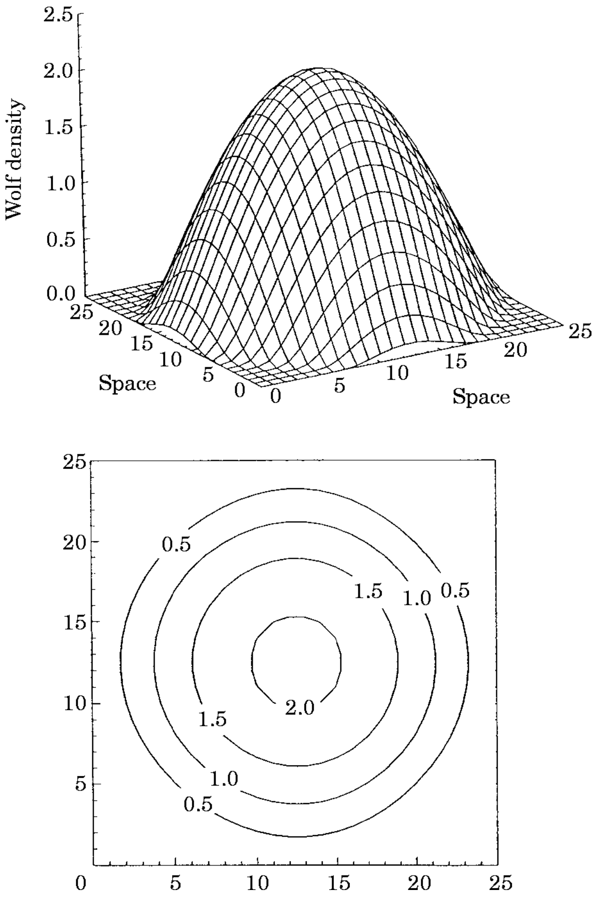

FIG. 6. Two-dimensional single pack solution with $n=1$, $\beta=1$, $c_u=1$ and $d_u=0.05$. The solution domain is the unit square and the solution obeys the conservation requirement (11). The steady- state solution is not dependent on initial conditions and is radially symmetric about the den location. In (a) we show the surface plot and in (b) the contour plot.

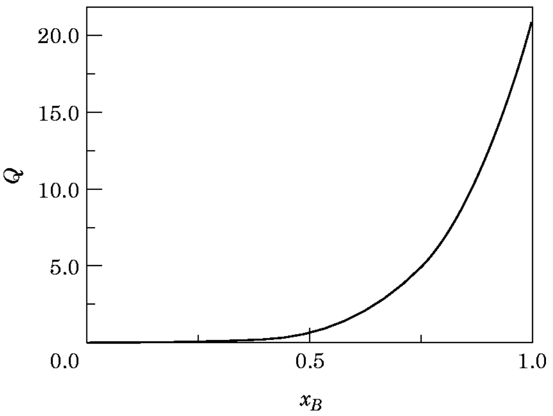

FIG. 7. Number of wolves in a pack as a function of the territory length ($2x_B$) for $n=0.5$, $\beta=0.001$ and $d_u=2$.

home range for mammals is directly related to the rate of energy intake required per animal. Okubo (1980) continued this idea and suggested that the size of the home range R is related to the body weight W through the expression

$$R=aW^b$$

where a and b are constants. For mammals, b was estimated to be approximately 0.75. More recently, Calder (1984) has a thorough discussion of the relation between home range size and body weight.

Imposing the conservation condition on (19) gives

$$\int_{x_u-x_b}^{x_u+x_b}\left[\frac{c_u n}{d_u\beta}\ln\left(\frac{\cosh(x_b)}{\cosh(x-x_u)}\right)\right]^{1/n}\mathrm{d}x=1 \qquad (20)$$

which, in dimensional form becomes

$$\int_{x_u-x_B}^{x_u+x_B}\left[\frac{c_u n}{d_u\beta}\ln\left(\frac{\cosh\beta(x_B)}{\cosh\beta(x-x_u)}\right)\right]^{1/n}\mathrm{d}x=Q=Q(x_B) \qquad (21)$$

where $x=x_u\pm x_B$ are the positions of the territory boundaries in dimensional form.

In Fig. 7 we show the relation of pack size to territory size for selected parameters β, d_u and n. We estimated the maximum value for the convection coefficient $c_u=5\text{ km h}^{-1}$; Mech (1970) suggests that a wolf travels at speeds 5–8 km h^{-1}, we use the lower value because we are interested in speeds that could be maintained for several hours. The relationship between the size of the territory $2x_B$ and number of animals Q in the pack is nonlinear and monotonically increasing, as would be expected. This suggests that smaller packs will, on average, occupy more area per capita than larger packs, a result that could be verified with field data. For use with field data the steady-state solution in the two-dimensional radially symmetric case should be used. With sufficient data on pack and territory sizes one could attempt to fit this model solution to the field data using nonlinear least squares estimation. The results suggested here, however, are for packs that do not respond to the presence of neighbours. Clearly this will have some effect on the size of the territory and the estimation of parameters from the actual field data.

7. Interaction Between Neighbouring Packs

When two packs interact we must consider the complete model system (1–2) and (9–10). Analytical results are now more difficult to obtain unless we simplify the model by considering, for example, that one pack is unaffected by the presence of the other. This type of analysis is useful for predicting possible model behaviours that can be verified by solving the complete system numerically. For the purposes of this paper we show only the numerical solutions—at least in one space dimension, the behaviours that they exhibit are also shown in the mathematical analysis of the simpler systems.

7.1. ONE-DIMENSIONAL PROBLEM

The one-dimensional simulations are used to demonstrate the ability of the model to describe the buffer region and to show the effect of RLU avoidance on pack density distributions. In Fig. 8 we show the steady-state density distributions for two packs with dens located at $x=0.205$ and at $x=0.795$. The initial densities for each pack are uniform and identical. In Fig. 8(a) there is no avoidance of foreign RLU marks ($F_u=F_v=G_u=G_v=0$), although marking is increased in these regions ($M_p, M_q>0$). In Fig. 8(b) packs do avoid foreign marks. The results are striking; they show quite clearly that the region of shared land is significantly reduced when packs avoid the RLUs of other packs. Moreover, they show that asymmetries in the wolf density distribution occur. When there is inter-pack interaction, the densities are no longer symmetrical about the den unless, (of course) one pack is surrounded by packs on both sides and response to them is identical. The levels of RLU marking are directly related to the density of the packs, which explains the higher levels when there is no avoidance. Note that the solution domain was not sufficiently large to show the entire territories of both packs. In the case of no avoidance, however, the wolf density would be symmetrical about the den analogous to the results for the single pack model.

In Fig. 9 we show the variation in the cumulative RLU and wolf densities in time, again verifying that the model can predict the observations made in the field. The maximum cumulative RLU density is found midway between the dens where (for ecological realism) the cumulative wolf density is a minimum. Comparison between this and Fig. 8(b) also shows that the individual pack RLU attains a maximum at a different location to the cumulative RLU marking. These results suggest that, at least in one space dimension, the model solutions are in agreement with the field observations.

7.2. TWO-DIMENSIONAL PROBLEM: THREE WOLF PACKS

The model is particularly interesting in two space dimensions because of its capacity to develop spatial asymmetries. In view of this we simulated the model equations (1–4) for three packs in two dimensions starting with spatially homogeneous initial expected wolf densities and with no RLU marking.

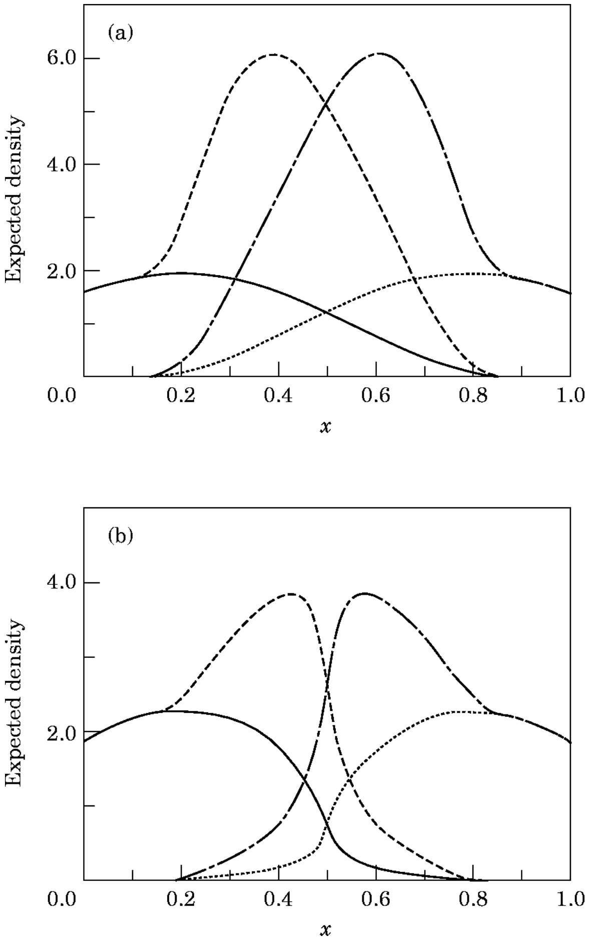

FIG. 8. Steady-state density distributions for two interacting packs showing the differences between avoidance of foreign marks and no avoidance. We use the parameter values, $x_u=0.205$, $x_v=0.795$, $n=0.5$, $d_u=0.05$, $c_u=c_v=0.7$, $\beta=1$. In (a) $F_u(q)=0$ so there is no avoidance of foreign marks and in (b) the avoidance coefficient takes the form $F_u(q)=0.025q/(1+q)$.

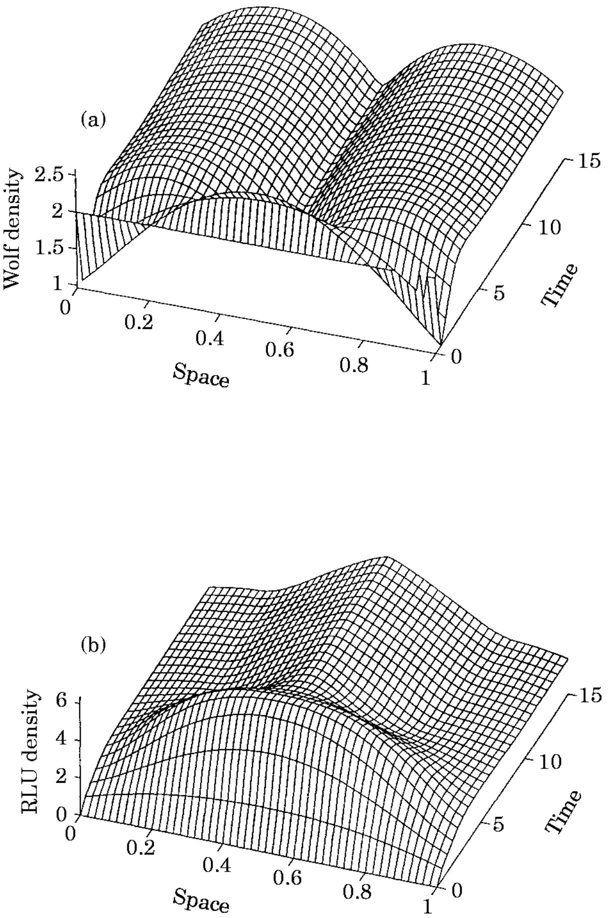

FIG. 9. Time dependent cumulative wolf (a) and RLU (b) density distributions for the model solutions shown in Fig. 8(b). Parameters and functions are those given for Fig. 8.

The surface plot in Fig. 10(a) shows the steady-state cumulative wolf density distributions. Clearly wolf densities are greatest in the den regions as in the case of the single pack. The contour plot in Fig. 10(b) shows that the density distribution for a single pack is no longer symmetrical about the den. That is, the effect of wolf response to olfactory stimuli is to shift wolf activity away from regions of potential conflict. These results are in agreement with the idea of a buffer region between wolf packs. The RLU density distributions are not as well described by this model. It appears that more complex functional forms are required to give realistic RLU densities in two space dimensions (Lewis, White & Murray, submitted).

8. Wolf Distribution in Winter

During the winter months, the den is no longer a focal point for the pack and wolves move more extensively through their territories. The territory, nonetheless, is maintained and for most of the time the wolves are found within the region.

8.1. SINGLE PACK SOLUTION

To solve the time dependent problem for a single pack, we choose the study domain Ω to be infinite with the requirement that both u and ∇u approach zero as $x \longrightarrow \infty$. This choice allows an exact solution the nature of which is easier to see than for the finite domain. The simplified model in which pack 1 is unaffected by the presence of any other packs is the density dependent diffusion equation

$$\partial u/\partial t = \nabla \cdot (d_u u^n \nabla u). \tag{22}$$

which can be solved exactly in one space dimension and in the radially symmetric case for the particular initial condition

$$u(x, 0) = \delta(x - x_u).$$

This initial condition represents the ecological case where the entire wolf pack abandons the den together at the start of the winter period.

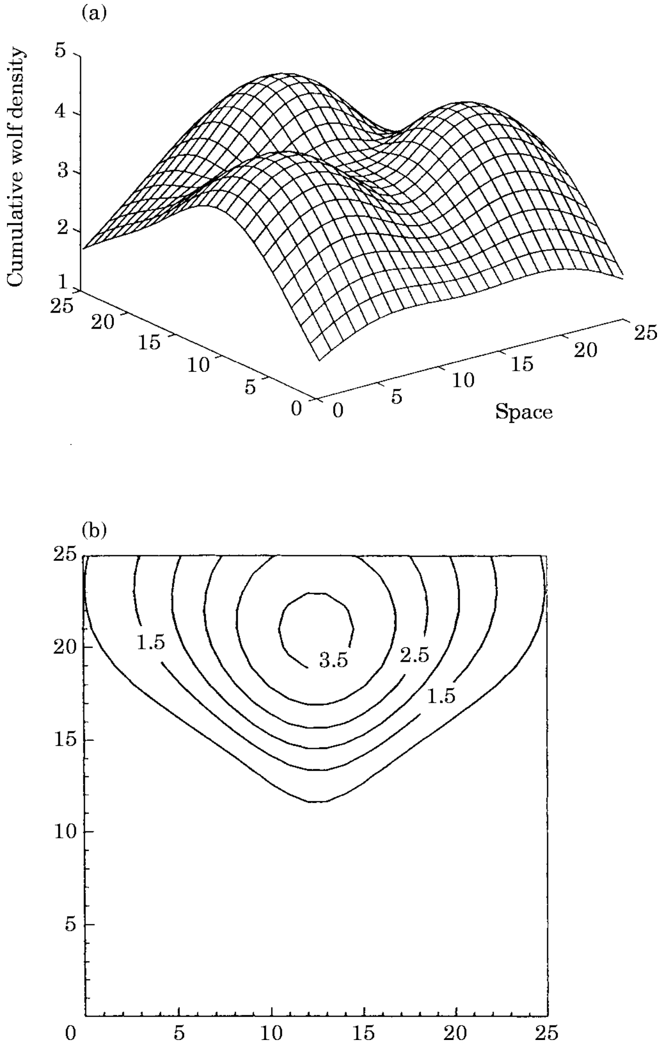

FIG. 10. In (a) we show the steady-state cumulative wolf density distributions when there are three wolf packs in two space dimensions. The parameters used here are identical for each pack, so we give only those for pack 1 ($u(x, t)$: $c_u = 0.5$, $d_u = 0.05$, $n = 0$, $F_u(q) = 0.025q/(1+q)$, $M_p(q) = 2q/(5+q)$. The dens are positioned at (5.5, 10.5), (19.5, 10.5), (12.5, 19.5). The mesh grid size is 0.04 so that we are solving the problem on the unit square and each pack obeys the conservation condition (11). In (b) we show the contour plot for one of the wolf packs.

8.1.1. CASE 1: $n = 0$

When $n = 0$, (22) reduces to the simple Fickian diffusion equation the time dependent solution to which is

$$u(x, t) = \frac{1}{2\sqrt{(d_u \pi t)}} \exp^{-(x-x_u)^2/(4d_u t)} \tag{23}$$

This solution extends to infinity for all time and thus it suggests the breakdown of the territory. This scenario is unlikely to occur either for well-established wolf packs or for the newly established ones which may not den for several seasons.

8.1.2. CASE 2: $n \neq 0$

In this case, (22) is the porous media equation, the solution of which is given by a radially expanding wave moving outwards. Unlike the density independent diffusion equation, the speed of the leading edge is finite depending upon t. An exact solution to this equation is known for the initial condition above and is given as,

$$u(x, t) = \begin{cases} [\lambda(t)]^{-1} \left[1 - \left(\dfrac{x - x_u}{r_0 \lambda(t)} \right)^{1/n} \right]^{1/n} & |x - x_u| \leqslant r_0 \lambda(t) \\ 0 & \text{otherwise} \end{cases} \tag{24}$$

where

$$\lambda(t) = \left(\frac{t}{t_0} \right)^{1/(2+n)}, \qquad r_0 = \frac{\Gamma(1/n + 3/2)}{\pi^{1/2} \Gamma(1/n + 1)}, \qquad t_0 = \frac{r_0^2 n}{2d_u(n+2)}$$

and Γ is the Gamma function. In this case the territory boundary is not fixed in time but moves continually outwards covering an ever increasing region; at the same time, the density within the region becomes more uniformly distributed. Clearly the long-term solution suggests breakdown of territories as in the density independent case. Restricting the solution to a timescale of a few months only, we can propose this as a possible description of wolf winter movement.

8.2. TWO PACK SYSTEM

When there is no longer convection back to the den location, the only steady-state solution for the complete model system, (1–2) and (9–10) with zero flux boundary conditions is spatially homogeneous. We now analyse the stability of this spatially homogeneous solution.

To simplify the model we assume that the functions in (1–2), are constants and that the wolf packs are identical so that similar coefficients take on the same values, that is

$$D_u(u)=D_v(v)=d \quad F_u(q)=F_v(p)=\phi_1$$

$$G_u(p)=G_v(q)=\phi_2.$$

In addition, we suppose that the coefficients in the RLU governing equations are equal and thus set

$$\phi=1.$$

Moreover we choose the simplest linear functions for M_p and M_q namely

$$M_p(q)=mq \quad M_q(p)=mp \tag{25}$$

where m is a constant. Providing that m is not too large, the spatially homogeneous steady-state distribution can be written as

$$[u_s(x), v_s(x), p_s(x), q_s(x)]=(U_0, V_0, P_0, Q_0) \tag{26}$$

where

$$P_0=\frac{U_0(1+mV_0)}{1-m^2U_0V_0} \quad Q_0=\frac{V_0(1+mU_0)}{1-m^2U_0V_0} \tag{27}$$

with the constraint $m^2U_0V_0<1$. To simplify the system further, we assume that the average density of wolves in each pack is the same so that $U_0=V_0=W$, which means that $P_0=Q_0=W$ where

$$R=\frac{W}{1-mW}.$$

To investigate the stability of this steady-state solution we consider the effect of imposing small perturbations proportional to $\exp(\sigma t+ikx)$ to the homogeneous distribution. Using standard techniques from linear analysis (see, for example, Murray, 1989) we obtain the dispersion relation

$$\sigma^4+f(k^2)\sigma^3+g(k^2)\sigma^2+h(k^2)\sigma+s(k^2)=0 \tag{28}$$

where

$$f(k^2)=2+2dk^2$$

$$g(k^2)=d^2k^4+k^2[4d-2\phi_2W(1+mR)]+1-m^2W^2$$

$$h(k^2)=2d^2k^4+2dk^2(1-m^2W^2)$$
$$-2Wk^2(1+mR)(\phi_2-\phi_1mW+\phi_2dk^2)$$

$$s(k^2)=k^4[d^2-d^2m^2W^2-2Wd(1+mR)$$
$$\times(\phi_2-\phi_1mW)+W^2(1+mR)^2(\phi_2^2-\phi_1^2)].$$

Solutions $\sigma(k^2)$ of (28) determine whether the small perturbations will grow ($\mathrm{R1}\sigma>0$) in time and, if so, for which wavelengths.

We are interested in the possibility of spatio-temporal oscillations so we set

$$\sigma(k^2)=p(k^2)+iq(k^2).$$

where both p and q are real functions of k^2. When we compare the real and imaginary parts of the subsequent expression the imaginary part gives

$$q=0 \text{ or } q^2=(h+2gp+3fp^2+4p^3)/(4p+f). \tag{29}$$

The case $q=0$ corresponds to the case where σ is real, then any instabilities in space do not change with time. The other case corresponds to the possibility of temporal oscillations of any instability. Substitution for q^2 into the real part of the dispersion relation gives an equation for p, namely

$$(4p+f)^2(p^4+fp^3+gp^2+hp+s)$$
$$+(h+2gp+3fp^2+4p^3)^2-(4p+f)$$
$$\times(h+2gp+3fp^2+4p^3)(g+3fp+6p^2)=0. \tag{30}$$

The important property exhibited by this dispersion relation is that the curve only cuts the k^2 axis at the origin. This means that either the curve is wholly below the k^2 axis, in which case the steady state is stable, or it is above in which case small perturbations of all wave numbers will grow. Figure 11 shows two typical curves for $p(k^2)$—in the first the disturbance will die out (as $p=\mathrm{Re}\,\sigma<0$) and the steady state is stable and in the second the perturbation will grow ($p=\mathrm{Re}\,\sigma>0$). Moreover, the latter case also has a non-zero value for $q(k^2)$ which gives rise to spatio-temporal oscillations.

The instability can be found for many parameter combinations, but for fixed f, l, m and W it occurs when the diffusion coefficient is not sufficient to overcome the destabilizing terms from the movement in response to the urination marking.

This result highlights the importance of the den, or some other such organizing centre (a rendezvous site, for example), to produce a stable territory. When

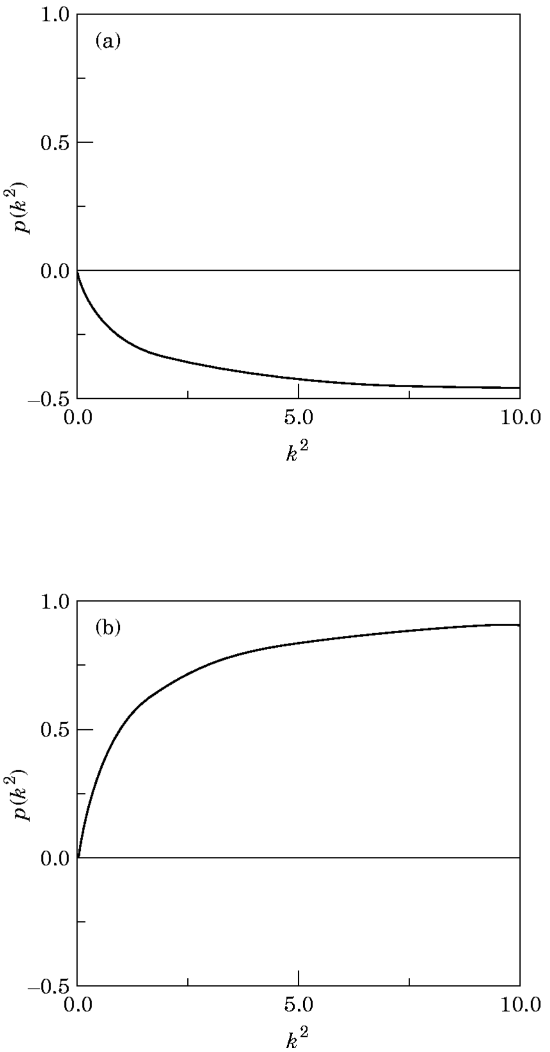

FIG. 11. Solution to eqn (30), the dispersion relation when $W=1$, $m=0.5$, $\phi_1=\phi_2$ and (a) $d=4$ and (b) $d=1$.

there is no den, even in the simplest case described here, a small perturbation to the steady-state wolf distribution can lead to spatio–temporal oscillations and thus no formation of territories. In fact, in contrast to the case where there is a den, the distribution is dependent upon the initial wolf and RLU distribution.

9. Discussion

In this paper we have presented a new mathematical model system to describe the territorial nature of movement. The research was motivated in part by the extensive field studies carried out on wolves in N.E. Minnesota (see, for example, Mech, 1970; van Ballenberghe *et al.*, 1975). Several aspects of the field ecology have been captured by the model solution.

We began by analysing a simplified model which considers the formation of a wolf territory when there are no external constraints such as neighbouring packs. In view of this, the model is perhaps of interest to the issue of wolf reintroduction presently being considered in several areas of northern America such as Yellowstone.

A report on the wolf recolonization of the Glacier National Park (Ream *et al.*, 1991) provides some interesting observations both for future recolonizing policy and, from our point of view, for model validation and adaptations. Wolf packs observed in the study showed a preference for colonizing areas which had already been investigated by lone wolves. The reason for this is unclear, although olfactory stimuli left by the pioneers may provide useful information as to the potential of a region. The wolf packs in the study are thought to be closely related, but despite considerable inter-pack associations (over short time intervals) and the availability of suitable unoccupied regions, there was clear evidence of strong pack adhesion. Our single pack model agrees with this observation as it suggests that packs will form territories even in the absence of any mechanism (such as foreign RLU marking) for territory maintenance. Pack adhesion in this case may be related to the optimal pack size necessary both to hunt large prey and to provide sufficient social interactions for these highly social carnivores (Mech, 1970).

The convective flux term which describes movement back to the den during the summer months assumes that the wolves know their position relative to the den site and will return to the den using a straight line path as observed by Mech (1970). As the convective flux suggests that wolves know their position relative to the den, it can also be interpreted as one component of a wolf's cognitive map. Peters (1979) interpreted field observations by suggesting that wolves develop a mental map of their territory which is continually being reinforced. Within the territory, RLU markings are found most often along wolf trails (Peters & Mech, 1975), indicating that olfactory stimuli may play an essential role in maintaining and updating this cognitive map.

The importance of the cognitive map is highlighted by the analysis in Section 8.2 which showed that, in the absence of a den, the only steady state solution was spatially homogeneous. That is, that steady-state spatial heterogeneity, which represents the maintenance of pack territories, only occurs when the convective flux is non-zero. Thus long-term winter behaviour indicates territory breakdown. On a shorter time scale of several months, however, the model can be reasonably used to describe winter distributions, as shown in the results of Section 8.1.1 where the winter wolf distribution consists of a radially expanding wave moving outwards with some finite speed. This suggests that the pack is moving more extensively through the territory (expected density becomes more homogeneous) and that there is a greater chance of a wolf trespassing into the buffer zone or some neighbouring territory. Field observations indicate that when the rendezvous sites are abandoned, the pack moves extensively throughout the territory (van Ballenberghe *et al*., 1975) which agrees with the more uniform use of land predicted by the model. Clearly one drawback of this model is that there is no form of cognitive map associated with the winter wolf behaviour. We are investigating ways to amend the present model systems to maintain some form of cognitive map during the winter months. One possible scenario is that the wolves move back to more familiar regions during the winter so that a convective flux can be based on the centre of mass of the expected wolf density (Lewis, White & Murray, submitted).

When considering the interaction of several packs, scent marking is thought to have an important role in maintaining territories. The role of scent marking in the model solutions was to break the symmetry of wolf density distributions about the den locations. In this way it allowed for the possibility of buffer regions where wolves are scarce but where RLU marking is at its highest density. In one space dimension, the model solutions showed good agreement with the field ecology. In two dimensions, however, although buffer regions were formed with low wolf densities, the cumulative RLU density did not increase significantly in this region. We are now investigating other forms for the functions related to wolf response to scent marking. In particular we are considering the idea of a threshold phenomena where response to foreign (or friendly) marks is only significant when the density exceeds some critical level. Preliminary results (with a slightly different model formulation) indicate that if we use functional forms of this nature, the cumulative RLU density may attain its maximum value in the buffer region (Lewis, White & Murray, submitted). The importance of the functional response of wolves to scent marking is very interesting—moreover, it is one which could be investigated further by controlled field experiments.

Movement back to an organizing centre (which can be interpreted as a response to a cognitive map) was clearly very important for obtaining a spatially heterogeneous steady-state solution (territory). There are, however, several other possible mechanisms for maintaining territory structure without a focal point. For example, newly formed wolf pairs may form a territory for 2 years before producing young (and thus constructing a den site); similarly for sterile pairs and established pairs or packs who maintain their territories even in years where there is no reproduction (David L. Mech, pers. comm.).

If surrounding territories already exist, then the non-reproductive pair will be subject to some form of foreign RLU spatial patterning. In this case, the territories may be formed or maintained merely by a response to local densities of scent marks. A more long range form of territorial behaviour is that of howling. Harrington & Mech (1983) present results of a field study which show that wolf response to howling, both in terms of reply and movement, is independent of wolf position within the territory and depends rather on the immediate social and ecological circumstances, such as the presence of a prey kill or that of young pups. This mechanism for territory maintenance differs from scent marking both in its spatial and temporal properties but, along with wolf preference for familiar regions, seems capable of maintaining exclusive territories without the need for an organizing centre. Clearly it would be interesting to compare the territory structures formed in the case of a short range, long lasting mechanism (RLU marking) and for a long range, short time mechanism (howling).

In another study, Ciucci & Mech (1992) showed that dens situated within the central portion of territories were randomly located relative to the territory centres although, in larger territories, the dens did tend to be more centrally located. In the numerical simulations shown in Section 7, the den positions were chosen arbitrarily. The resulting wolf distributions were such that the den was positioned somewhere in the central region of the wolf territory, suggesting some agreement with the field work. Further investigation is necessary to determine the extent of model agreement.

The discussion would not be complete without some comparison of the model presented and analysed here with that of Lewis & Murray (1993). As mentioned in the introduction, the forms of the two models are similar, both being nonlinear partial differential equations with diffusive and convective fluxes. The qualitative behaviours differ, however, in the way in which territories form because the model of Lewis & Murray (1993) requires the presence of foreign wolf packs (or at least foreign RLU markings) in order to obtain a territory. In the absence of such olfactory stimuli, their model reduces to the diffusion equation which suggests that the territory mechanism breaks down and wolves from all packs move randomly around. In the model proposed here, the formation of a territory depends only upon the pack itself (supported by van Ballenberghe *et al*., 1975) and foreign markings serve to determine the size, shape and maintenance of the territory.

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