Wolf-Deer Interactions: A Mathematical Model

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SUMMARY

Field studies done in northeastern Minnesota indicate that stable wolf (Canis lupus) territories exist separated by buffer regions in which white-tailed deer (Odocoileus virginianus) density is greatest.

We present a mathematical model to describe this interaction based on simple movement rules for the wolf population and basic predation dynamics. Solutions suggest that pack social requirements to care for the young set up differential predation rates causing segregation of high deer and wolf densities. More interestingly, they also suggest that the predator–prey interaction may play an important role in segregating and maintaining the territories.

1. INTRODUCTION

To begin to understand the behaviour of a population from field observation requires many years of work. One population which has received such attention is the wolf (Canus lupus) in northeastern Minnesota: over the past 30 years the research has covered many aspects of its behaviour (Mech & Frenzel 1971; van Ballenberghe et al. 1975; Hoskinson & Mech 1976; Mech 1977 a, c; Mech & Karns 1977; Nelson & Mech 1981; Harrington & Mech 1983; Harrington et al. 1983; Ciucci & Mech 1992) from which one distinct feature of the system appears to be the persistence of territory structure (Mech 1977 b).

The territories in northeastern Minnesota vary in size between 100–300 km², are separated by regions known as buffer zones (Mech 1977 b) which may be up to 2 km wide and are rarely visited by pack members. Wolf packs are highly structured (Mech 1970) with a dominant alpha male and female leading the pack. The alpha female gives birth to pups in late April which are cared for at a den site. As the pups become stronger, they are moved to a series of rendezvous sites (Mech 1970) which again provide a focus for pack activity. Finally in the autumn, these sites are abandoned and the pack moves extensively through the territory.

Relative to the size of their territories, pack size is small (3–15 wolves) and therefore olfactory signals are used to deter intruders. The particular signal that has been associated with territory marking is the raised leg urination (RLU) (Peters & Mech 1975), a mark predominantly produced by the alpha male. Levels of RLU are significantly higher around the buffer zone (despite low wolf presence) but they are also found at kill sites (Peters 1979; L. Schmidt, personal communication).

Recent work by Lewis & Murray (1993), White et al. (1995) and M. A. Lewis, K. A. J. White & J. D. Murray (unpublished data) developed mathematical models to describe these territorial interactions demonstrating that simple behavioural rules could be used effectively to produce the patterns observed in the field.

The main prey species for wolves in northeastern Minnesota is the white-tailed deer (Odocoileus virginianus) (van Ballenberghe et al. 1975), the distribution of which varies seasonally (Nelson & Mech 1981): in the summer months, they are dispersed on large home ranges, but in the winter they congregate in yards. Both locations have been found to lie, to a large extent, around the buffer zone between pack territories as shown in figure 1 (Hoskinson & Mech 1976). This is the case despite a reasonably homogeneous distribution of appropriate food and habitat for the deer and despite the fact that deer do not actively avoid settling in regions of high wolf density (Nelson & Mech 1981). Nelson & Mech (1981) suggested that the heterogeneity in deer density was caused, quite simply, by differential predation rates because of the segregation of wolf territories and the buffer regions between them.

The observations described in Hoskinson & Mech (1976) suggest that the buffer region may act as a prey refuge for the deer. Mathematically, prey refuges have been approached either by assuming that they exist and considering the dynamics of the system (McNair 1986; Sih 1987; Taylor & Pekins 1991) or by determining conditions on the movement and dynamics of the predator and prey to give rise to spatial segregation (Segel & Jackson 1972; Mimura & Murray 1978; Okubo 1980; Murray 1989).

Here we are interested in the role which predator–prey interactions have on the territorial nature of wolf movements. Because reproduction in both species occurs over a period which is short in comparison with a year, we consider a time span during which there is no reproduction and couple deer mortality to wolf

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Proc. R. Soc. Lond. B (1996) 263, 299–305
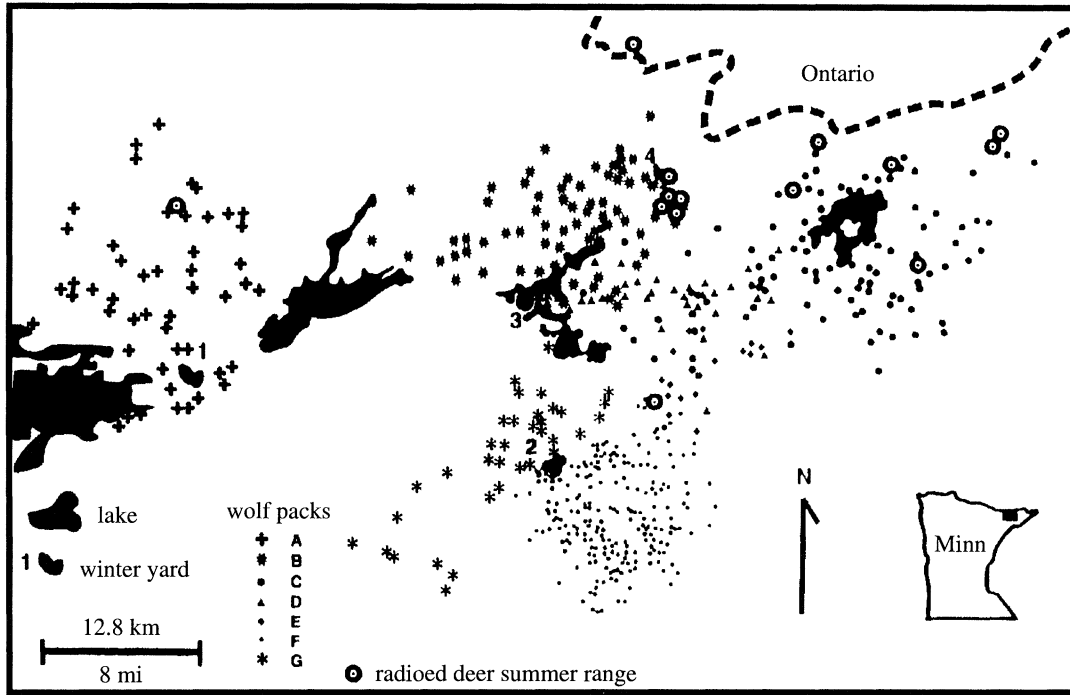Printed in Great Britain

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Figure 1. Winter yards and summer ranges of radio-collared deer in relation to wolf pack territories (Hoskinson &
Mech 1976) with permission of the Wildlife Society (copyright holders).

movements. In the long-term this model clearly breaks
down: the deer population would be driven to
extinction and, with our model formulation, the wolf
pack would congregate, rather unrealistically, at the
den site. However, over a period equivalent to several
months, the model described in §2 is valid and useful in
describing wolf–deer interactions and territorial behav-
iours. In §3 and §4 we describe model predictions, in
§5 we introduce a pulse into the system to represent
deer birth and finally the results are discussed from an
ecological perspective.

2. MODEL FORMATION

Both wolf and deer density in northeastern
Minnesota is low which means that there will be long
periods of time during which no animal is found at a
given location. In view of this we use a probabilistic
approach to define the state variables:

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

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

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

$q(\mathbf{x}, t)$ = expected density of RLUs for pack 2

$h(\mathbf{x}, t)$ = expected density of deer

where $\mathbf{x}$ is position and t is time. The number of packs
is arbitrary.

Although wolf movement is highly complex, we
assume that it is dominated by two fundamental
components: movement towards the den to feed the
pups and movement towards regions of high deer
density in search of food. Because our primary interest

is to determine how wolf movement affects the
distribution of wolves and deer, we assume a constant
population size for each pack by taking zero flux
boundary conditions for the model so that there is no
external effect on the system. Mathematically this
combines to give the nonlinear partial differential
equations:

rate of change in wolf density = rate of change
caused by movement back to the den + rate of change
caused by movement towards deer

$$\frac{\partial u}{\partial t} = \nabla(C_u(\mathbf{x} - \mathbf{x}_u)\, u) - \nabla(u\phi_u\, \nabla h), \tag{1}$$

$$\frac{\partial v}{\partial t} = \nabla(C_v(\mathbf{x} - \mathbf{x}_v)\, v) - \nabla(v\phi_v\, \nabla h), \tag{2}$$

where $\nabla = (\partial/\partial x, \partial/\partial y)$, $C_u(\mathbf{x} - \mathbf{x}_u)$ and $C_u(\mathbf{x} - \mathbf{x}_v)$ are
coefficients describing the rate of movement back to
the dens (located at $\mathbf{x}_u$ and $\mathbf{x}_v$ respectively), ϕ_u and ϕ_v
are constants scaling the rate of movement of each pack
towards the deer and ∇h is the local gradient in the deer
density.

We take $C_u(\mathbf{x} - \mathbf{x}_u)$ and $C_v(\mathbf{x} - \mathbf{x}_v)$ to have the form

$$C_u(\mathbf{x}) = c_u \tanh{(\beta r)}\frac{\mathbf{x}}{r}, \tag{3}$$

where $r = \|\mathbf{x}\|$ is the distance of a point from the origin.
The parameter c_u measures the maximum speed of the
wolf when moving towards the den and β measures
how the rate changes as the den is approached. The
form of this function is shown, for the one dimensional
case in figure $2a$; it suggests that the wolves are aware
of their location relative to the den and will try to
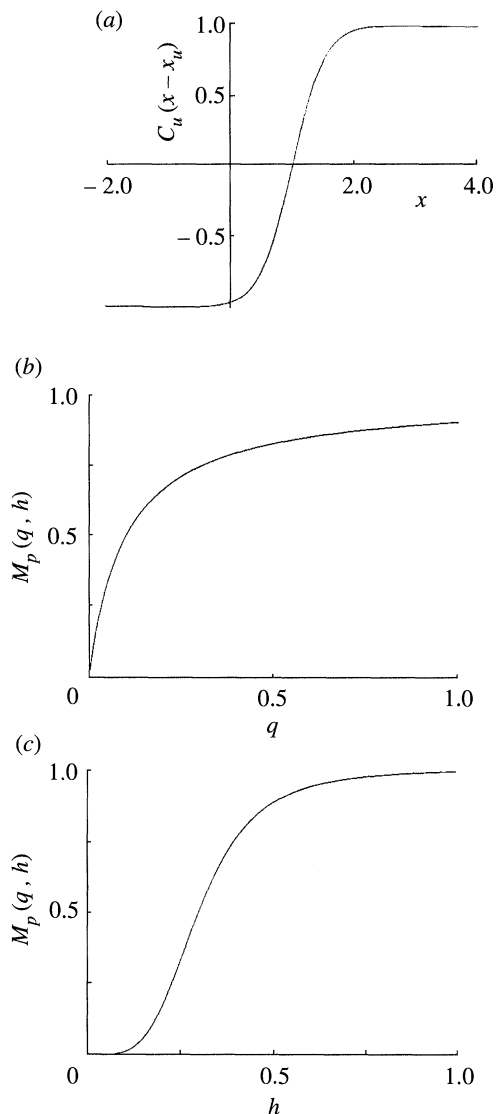return there in a straight line direction (Peters 1979).

Figure 2. Typical qualitative forms for the model functions. In (a) we show the coefficient $C_u(x-x_u)$ (in 1 – d) with the den x_u at $x = 1$. In (b) we show the dependence of function $M_p(q,h)$ on q and in (c) the dependence of $M_p(q,h)$ on h, which is the more important dependence.

The model equation governing expected deer density is somewhat simpler. Given that there is no evidence of active avoidance of wolf populations (except on the scale of escaping attack), we assume that deer do not have any largescale movements (once within their summer ranges–winter yards). Their density distribution is therefore dominated by wolf predation levels and natural mortality so that the model equation takes the form

rate of change in deer density = mortality caused by wolf predation + mortality caused by environmental conditions

$$\frac{\partial h}{\partial t} = -(\alpha_u u + \alpha_v v) h - \mu_h h, \qquad (4)$$

where α_u, α_v and μ_h are constants. In particular μ_h is a parameter which determines the effect of weather conditions on survival of the deer.

The model equations for the density distribution of RLUs are also structurally simple. Wolves mark kill sites extensively (Peters 1979; L. Schmidt, personal communication) both to provide themselves with information in the future and to indicate their presence if the kill site is discovered by other wolves. Wolves are also known to investigate and then overmark foreign RLUs. Thus we assume the model formulation:

rate of change in RLU density = low level RLU marking throughout territory + increase in marking at a kill site or in presence of foreign RLUs + first order decay of RLUs

$$\partial p/\partial t = u(l_p + M_p(q,h)) - f_p p$$
$$\partial q/\partial t = v(l_q + M_q(p,h)) - f_q q, \qquad (5)$$

where the parameters are defined as follows: l_p and l_q denote the low level marking throughout the territory and f_p and f_q the first order decay rate of the RLUs. The functions M_p and M_q are monotonically increasing functions of both arguments which asymptote to some finite non-zero level reflecting the biological restrictions on amounts of urine per unit time which can be produced. We show qualitative forms for these functions in figure 2 b, c. In particular we used the idea of a threshold mechanism to describe the effect of deer density on urination marking so that marking increases significantly when the deer density is above some critical level. Ecologically this could arise if regions become significantly more profitable for a wolf pack once prey levels are above the critical level. This assumption makes the distribution of RLU markings more pronounced (and was therefore chosen for this theoretical exercise), but is not necessary to obtain the wolf and deer distributions described below.

(a) Non-dimensionalization

With our choice of dimensionless variables (described in the appendix) we reduce the number of parameters in the system. The model equations (1)–(2), (4) remain unchanged in appearance but (5) becomes,

$$\partial p/\partial t = u(1 + M_p(q,h)) - p \qquad (6)$$
$$\partial q/\partial t = v(1 + M_q(p,h)) - \phi q \qquad (7)$$

and the dimensionless domain Ω is an area or length equal to unity with

$$\int_\Omega u(\mathbf{x},t)\,\mathrm{d}\mathbf{x} = 1, \qquad \int_\Omega v(\mathbf{x},t)\,\mathrm{d}\mathbf{x} = 1. \qquad (8)$$

3. SINGLE PACK SYSTEM

By investigating a single pack model we can determine which model properties are intrinsic to isolated pack activity. Suppose that there is a constant deer distribution in some region, that is $h(\mathbf{x},t) = H$ (where H is a non-negative constant), then we can solve (1) in one space dimension (and (2) similarly) because it reduces to the linear equation

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}[C_u(\mathbf{x}-\mathbf{x}_u)u]. \qquad (9)$$

The solution to (9) is obtained using the method of characteristics (see Kevorkian 1989) and has the form

$$u(x,t) = u(\xi,0)\frac{e^{c_u\beta t}\cosh\beta(x-x_u)}{\cosh[\sinh^{-1}(\sinh\beta(x-x_u)e^{c_u\beta t})]}, \quad (10)$$

where

$$\xi = x_u + \frac{\sinh^{-1}[\sinh\beta(x-x_u)e^{c_u\beta t}]}{\beta}. \quad (11)$$

If $x = x_u$,

$$u(x_u,t) = u(\xi,0)e^{c_u\beta t} \to \infty \quad \text{as} \quad t \to \infty$$

and if $x \neq x_u$

$$u(x,t) \to u(\xi,0)e^{c_u\beta t}e^{-e^{c_u\beta t}}\cosh\beta(x-x_u) \to 0$$

$$\text{as} \quad t \to \infty,$$

which suggests that all the wolves in a pack would aggregate at the den site as time progresses, an ecologically unrealistic scenario. Annual mortality rates for deer are about 30–40% (Nelson & Mech 1981) and thus extinction is unlikely to occur. Furthermore, because wolf distributions are spatially heterogeneous, predation on the deer will also be spatially heterogeneous, deer gradients will be formed ($\nabla h \neq 0$) and this solution is no longer valid (it requires $\nabla h = 0$). In general we solve the complete problem with an initial deer density which is spatially homogeneous and then (10) is a small time approximation to the solution.

Numerical solutions to the complete system are shown in figure 3 and verify that (10) indeed reflects the initial behaviour. Increased wolf activity in the den region means that there is a greater predation rate here and thus a gradient in prey density is established and the wolf density will spread outwards (figure 3*a*, *b*). The symmetry of density distributions about the den location shown here become radial symmetry in two space dimensions. Finally we see that RLU marking can be found along territory boundaries even in the absence of foreign marking (figure 3*c*) caused by the heterogeneous prey density. Unlike previous models where interaction between neighbouring packs was necessary to get RLU distributions consistent with field observations, here interaction between the wolf and deer is all that is necessary.

4. THE MULTI-PACK SYSTEMS

The symmetry of wolf and deer distributions about the den site is destroyed when the model is extended to include movements of several packs as illustrated in figure 4. More importantly, there is a corridor between pack territories where deer are at high density: we interpret this region as the buffer zone between territories.

In the model formulation, wolves move up deer gradients: because deer attain their maximum densities between packs, wolf movement away from the den will be stopped in the buffer. Therefore if a pack is surrounded on all sides by other packs, a territory will be formed because the deer distribution will not allow continued outward movement of the wolf packs. There is no advantage in moving beyond regions of high deer density into ones of lower density where there is the

additional danger of attack by neighbouring packs. Thus wolf–deer interactions may be fundamental in determining the formation of territories.

The width of the corridor is smaller than that of a real buffer because we have no long-range effects in the model: wolves can only respond to local gradients and thus are attracted close to the buffer edge where the steepest deer gradients exist. However, it may be important for wolves to be around the buffer even if deer are at low densities because they are regions of potential territory invasion.

The long-term solution to this model is deer extinction. We overcome this by using a discrete-time pulse to represent seasonal deer reproduction because this period is short when compared with a year.

5. ANNUAL DEER REPRODUCTION

Assuming that seasonal reproduction occurs at times $t = T$ ($T = 0, 1, 2, ...$) we take

$$h(\mathbf{x}, T_+) = h(\mathbf{x}, T_-) + h(\mathbf{x}, T_-)R_h(h(\mathbf{x}, T_-)), \quad (12)$$

where R_h is a density dependent reproduction factor. In this form we are assuming that all adults survive the brief reproductive period and we choose the function R_h as

$$R_h(h(\mathbf{x}, T_-)) = \frac{\lambda_h}{1 + d_h h(\mathbf{x}, T_-)}. \quad (13)$$

where λ_h is the maximum number of offspring per adult and d_h determines the extent of density dependent effects on reproduction.

If we assume that the wolf packs have attained steady state density distributions, that is if $u(x,t) = U(x)$ and $v(x,t) = V(x)$, we can solve (4) on $T_+ < t < T+1_-$ to obtain the stable annual deer population cycles

$$h(x,t) = H(x)e^{-(F(x)+\mu_h)(t-T_+)} \quad T_+ < t < T+1_-$$
$$h(x, T+1_+) = H(x), \quad (14)$$

where $F(x) = \alpha_u U(x) + \alpha_v V(x)$ and
$H(x) =$

$$\begin{cases} e^{(F(x)+\mu_h)}\left[\dfrac{\lambda_h+1-e^{(F(x)+\mu_h)}}{d_h(e^{(F(x)+\mu_h)}-1)}\right] & F(x) < [\ln(1+\lambda_h)-\mu_h] \\ \quad 0 & \text{otherwise.} \end{cases}$$

$$(15)$$

Thus to maintain a deer population at some location x requires that

$$F(x) \leqslant \ln(1+\lambda_h)-\mu_h, \quad \ln(1+\lambda_h) \geqslant \mu_h. \quad (16)$$

This pair of inequalities mean that deer will become extinct in regions of high wolf density and that fawn production must at least compensate mortality from external factors. The interesting feature of the solution (14)–(15) is that it indicates the importance of spatial heterogeneity for maintaining both species within a region. Suppose we have some wolf density distribution $W(x)$ such that

$$\int_\Omega W(x)\,dx > \ln(1+\lambda_h)-\mu_h;$$

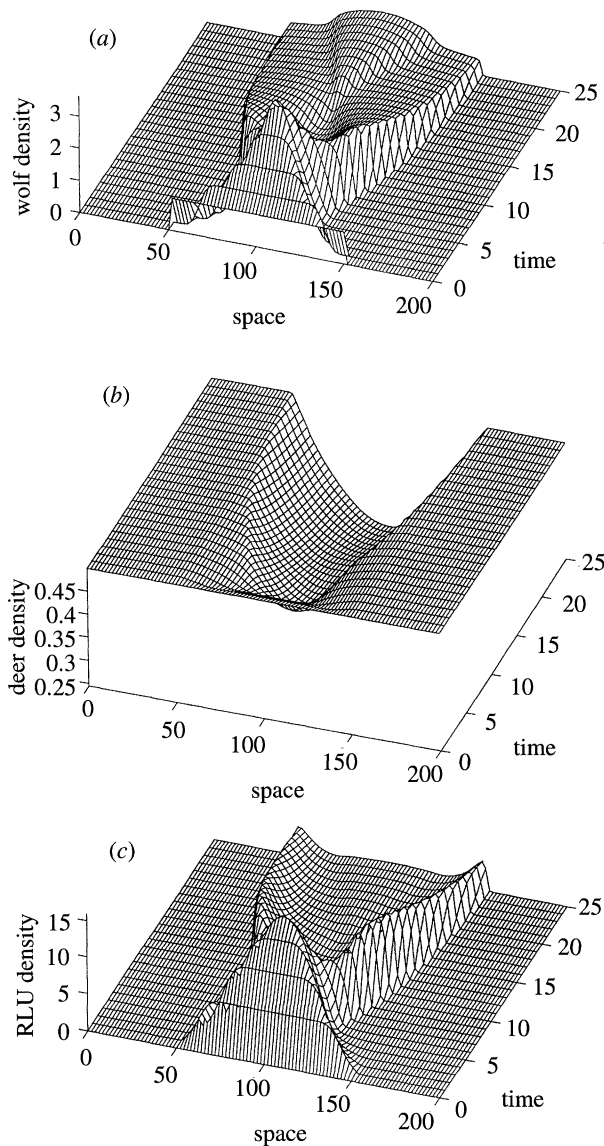(where $\|\Omega\| = 1$), that is, average wolf density is

(a)

(b)

(c)

Figure 3. Solution to (1)–(4) with $c_u = 3.5$, $\beta = 0.001$, $\phi_u = 0.2$, $\alpha_u = 0.02$ and $M_p(h) = 10h^{10}/(0.45^{10} + h^{10})$. The simulation ran for the equivalent of 24 weeks and gave a deer mortality rate of about 18.5% over this period. In (a) we show the time dependent wolf density distribution, in (b) the time dependent deer distribution and in (c) the time dependent RLU density distribution.
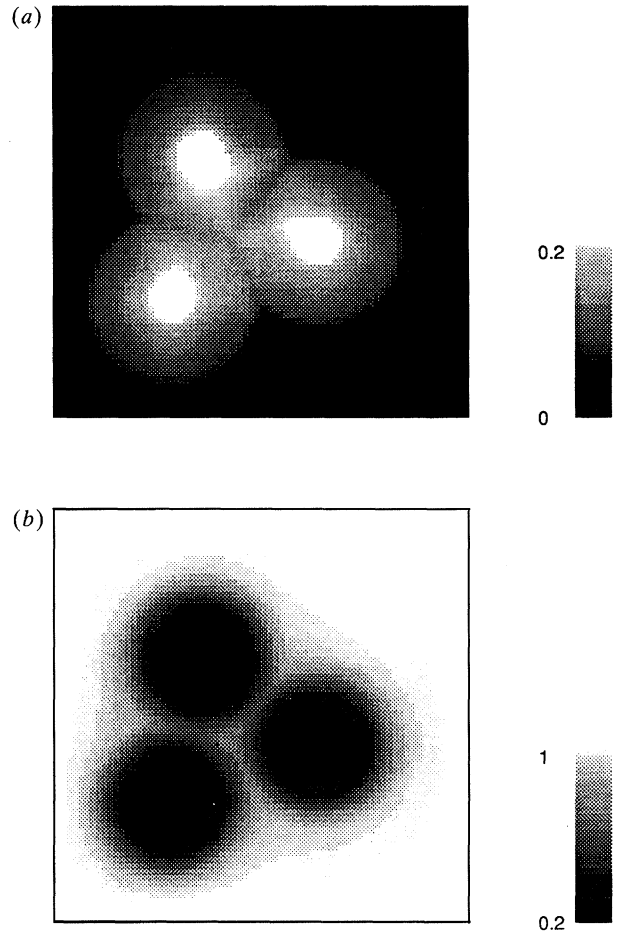

(a)

(b)

Figure 4. Simulation of three wolf packs and a deer herd in two space dimensions. Parameter values are identical for each pack: $c_u = 0.2$, $\beta = 0.5$, $\alpha_u = 0.25$. Dens are located at (19.5, 19.5) (24.5, 44.5) and (44.5, 29.5) on a 70 × 70 grid.

greater than the value for which no deer can be maintained. If the wolves are distributed in a heterogeneous manner we will maintain deer in regions of low wolf density but they will be driven to extinction in other regions. However if the wolves are uniformly distributed extinction will occur for all deer.

6. DISCUSSION

Field work done to study the wolf population in northeastern Minnesota provided motivation for the theoretical model described here. Lewis & Murray (1993) and White *et al.* (1995), also motivated by the wolf–deer interactions in northeastern Minnesota, used model structures similar to the one described here but concentrated on the territorial interactions between

neighbouring packs. In Lewis & Murray (1993), foreign RLU marks were necessary to produce and maintain territory structure whereas in White *et al.* (1995) RLU marking shaped territories which could be formed even in the absence of neighbouring packs. White-tailed deer were not included in the models.

Wolves are known to mark kill sites (Peters 1979; L. Schmidt, personal communication): because deer are found predominantly around the edge of the territory, the increase in RLU density here may be caused, in part, by the predator–prey interaction. Furthermore, the model solutions with several packs suggested that the wolf–deer interaction could help maintain segregated territories. This arises in the model solution because wolves move up deer gradients. Ecological interpretation of the result is that little benefit would be gained by a pack moving beyond a region of high prey density to one of lower density. The result is spatial segregation not only of predator (wolf) and prey (deer) but also of competing predators (neighbouring packs).

The buffer region is intrinsic to the model solution and, unlike previous reaction–diffusion systems (Okubo 1980) spatial segregation of the wolf and deer did not require special conditions on the population dynamics. One assumption made in formulating the model was that deer do not actively avoid regions of high wolf density. This hypothesis has been suggested

by field workers in northeastern Minnesota (Nelson & Mech 1981); given that model solutions are consistent with field observation, this hypothesis is clearly feasible. There are, however, other possible scenarios which should be mentioned. The first assumes that deer actively move to avoid regions of high wolf density. This means however that deer should move to areas of high RLU density. Little is known about the response of white-tailed deer to such olfactory stimuli although there is some evidence that deer will avoid predator urine (Mueller-Schwarze 1972). A second hypothesis is that wolves may form territories such that existing variations in the deer density fall between the territories. Such a hypothesis was proposed for the spatial patterning of wolves and moose (Messier 1985). The very high energy costs, which could be involved in maintaining a territory with rich supply of prey, makes this hypothesis plausible. However, in northeastern Minnesota, the vegetation is thought to be reasonably homogeneous for the deer (at least on a scale of home ranges–territories).

We have restricted our discussion here to the wolf–deer interactions observed in northeastern Minnesota. There is no reason why the results could not be extended to similar systems where the predator has a fixed den site, but we are not aware of other field studies documenting the spatial patterning discussed here. Despite the gross generalizations made in this model (now being refined by M. A. Lewis (unpublished data)), this model system has raised issues about the role of wolf–deer interactions in the formation of wolf territories and theoretically, it has provided a new basis from which more realistic models can be developed.

APPENDIX. NON-DIMENSIONALIZATION

To non-dimensionalize the system (1)–(2), (4), (5) we define $A = \int_{\Omega} d\mathbf{x}$ to be the area of the study domain Ω and let $L = A^{1/m}$ where m is the spatial dimension of the problem. Taking Q_u and Q_v to be the number of wolves in pack 1 and pack 2 respectively, we write U_0 and V_0 as the average expected wolf densities for the respective packs, that is $U_0 = Q_u/L^m$, $V_0 = Q_v/L^m$. Moreover, if we let Q_h be the initial number of deer in the domain then we have an initial average density for the deer as $H_0 = Q_h/L^m$. We non-dimensionalize by letting

$$u^* = \frac{u}{U_0}, \quad v^* = \frac{v}{V_0}, \quad h^* = \frac{h}{H_0}, \quad p^* = \frac{f_p}{U_0 l_p}p, \quad q^* = \frac{f_p}{V_0 l_q}q,$$

$$t^* = tf_p, \quad \mathbf{x}^* = \frac{\mathbf{x}}{L},$$

$$C_u^* = \frac{C_u}{Lf_p}, \quad C_v^* = \frac{C_v}{Lf_p}, \quad \phi_u^* = \frac{\phi_u H_0}{L^2}, \quad \phi_v^* = \frac{\phi_v H_0}{L^2 f_p},$$

$$\alpha_u^* = \frac{U_0}{f_p}\alpha_u, \quad \alpha_v^* = \frac{V_0}{f_p}\alpha_v, \quad \mu_h^* = \frac{\mu_h}{f_p}, \quad M_p^* = \frac{M_p}{l_p},$$

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

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