

14. Wolf Territoriality, Wolf–Deer Interaction and Survival

14.1 Introduction and Wolf Ecology

Territoriality is a fundamental aspect in the ecology of many mammals, particularly predatory animals such as wolves, lions, hyenas, African wild dogs and badgers, and it has been widely studied. In the case of wolves, whose prey are mainly moose and deer, an immediate question arises as to how the predator and prey coexist if the land is divided up into predator territories.¹ This in turn leads to the question of how territories are determined and maintained. It is clearly important in the ecology of such predatory animals. In this chapter we consider the question of mammalian territory formation, specifically as it applies to wolves, and its role in wolf–deer survival for which there is a considerable amount of data. In spite of the numerous studies on how pack territories are formed and maintained it was not addressed mechanistically until the mid-1990's with the mathematical modelling work of Lewis and Murray (1993), White (1995), White et al. (1996a,b), Lewis et al. (1997, 1998), Moorcroft et al. (1999) and Lewis and Moorcroft (2001) who studied the spatiotemporal effects on territory formation, territory maintenance and wolf–deer survival. Most of the material we describe in detail in this chapter is based on their work. First we give some background ecology on wolves.

The book (which has many beautiful photographs) by Mech (1991), who has studied wolves for nearly 40 years, is the best general introduction to the biology and ecology of wolves. It gives an excellent overview of the major aspects of wolf behaviour and social organisation; he also discusses some practical aspects of wolf conservation. Through his work, Mech has done much to change the often held traditional (erroneous) view of these splendid animals. He also points out that the stories of wolves attacking humans are mainly myths. He notes 'I have no doubt that if a single wolf—let alone a pack—wanted to kill someone, it could do so without trouble. When I have watched wolves close-up killing prey, they were swift and silent. A few good bites, and a human would be dead. The fact remains, however, that there is no record of an unprovoked, non-rabid wolf in North America seriously injuring a person.'

¹I first became intrigued by this question during a visit to the University of British Columbia in the late 1970's when, over dinner, in a discussion on animal intelligence it was mentioned how particularly clever and intelligent wolves are, as has been noted regularly since at least Roman times. In Canada their main food source is often the moose. I started to wonder how, if wolves are so clever, did the moose manage to survive. It was not until the early 1990's that Mark Lewis and I started to look at the question from a mathematical modelling point of view being joined soon afterwards by Jane White.

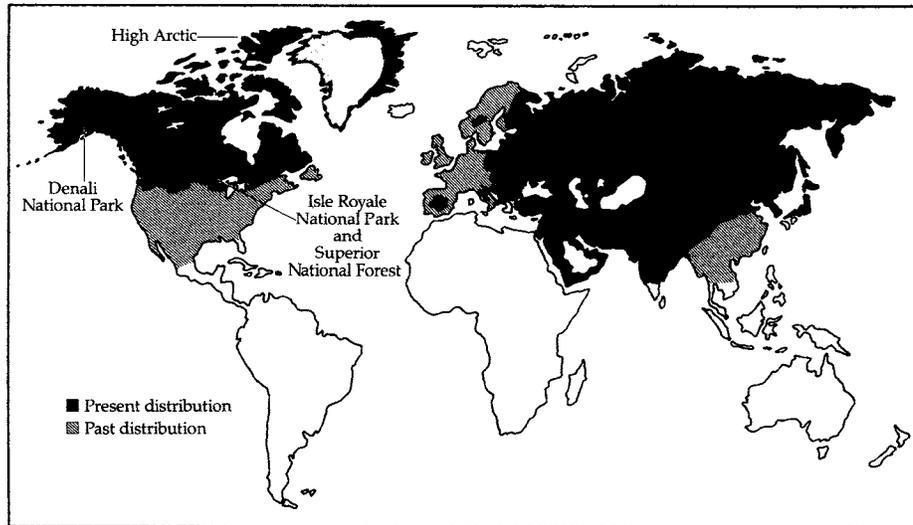


Figure 14.1. The past and present geographic distribution of wolves from Mech (1991). (Reproduced with permission of Voyageur Press Inc. (copyright holder)) With the recent reintroduction of wolf packs into the western U.S., in particular into Yellowstone National Park, the range has been extended below the 49th parallel, which separates Canada and the U.S.

Wolves used to be one of the most widely distributed animals in the northern hemisphere. Figure 14.1 shows the present and past distribution of wolves.

Wolves are social carnivores typically belonging to a pack which is a family unit consisting of 3–15 wolves. The extensive field studies which have been carried out on different packs in northeastern Minnesota, often using radiotracking techniques, have provided information on the land use by wolves from different packs. Pack territories are maintained over several years and are spatially segregated, rarely overlapping in the boundary regions; see Figure 14.2.

Territorial boundaries are usually avoided to lessen the chance of interpack conflict which often leads to death of one or more of the pack leaders (the alpha pair) which, in turn, can result in pack disintegration. In northeastern Minnesota, territories range in size from 100–310 km². These boundary regions between neighboring packs, known as ‘buffer zones’ are rarely visited by pack members. The buffer zones, which are a kind of ‘no-mans-land,’ are about 2 km wide and can account for as much as 25–40% of the available area.

Some of the most striking spatial patterns evident in wolf territories have been described by Mech (1973) and van Ballenberghe et al. (1975) and these provided the modelling basis for a mechanism as to how wolves and their prey may coexist in relatively close proximity (Lewis and Murray 1993, White 1995, White et al. 1996a,b, 1998). Our goal was to develop a mechanistic, spatially explicit model incorporating wolf movement, scent marking and wolf interactions that produces the spatial patterns evident in a wolf ecosystem specifically in northeastern Minnesota. Understanding pack territory formation and home range patterns is crucial if we are to understand the ecol-

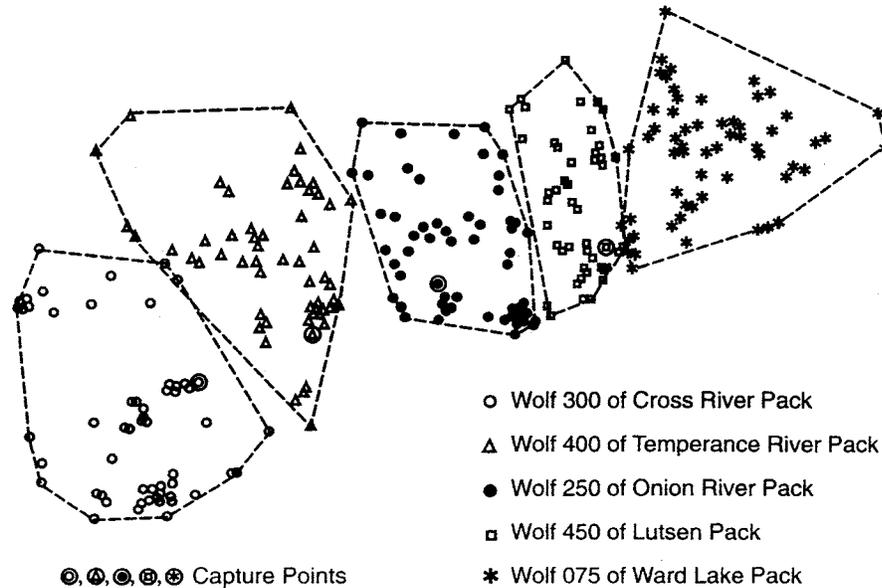


Figure 14.2. Radiolocations and home range boundaries of five adult and yearling timber wolves radiotracked in northeastern Minnesota during the summer of 1971. (Redrawn from van Ballenberghe et al. (1975) and reproduced with permission from the Wildlife Society (copyright holder))

ogy of many mammalian societies. Of course, other aspects are also important such as the social organization, mating and demography (see, for example, Clutton-Brock 1989). The literature is large and diverse; we give only a few references (see the numerous references cited in these). White (1995) gives an extensive review of the literature and modelling studies and the articles by Lewis et al. (1998) and Moorcroft and Lewis (2001) review some of the more recent theoretical studies with the latter presenting some interesting field data on coyotes using the mechanistic models discussed in this chapter.

The biological background and data used in constructing the mechanistic models is largely based on the wide-ranging radiomarking studies of wolves (*Canis lupus*) in northeastern Minnesota over the past 25 years. These have greatly facilitated the observation of wolf territories. The well-known and the most detailed quantitative studies of wolf numbers, however, is from the Isle Royale Project.

The Isle Royale National Park, an island of just over 200 square miles, is in Lake Superior close to the Minnesota–Ontario border. During a particularly cold winter in 1949, when the island was joined to the mainland by ice, some wolves crossed over to the island. They established themselves on the island where their main prey is the moose. Since 1959 the actual wolf and moose numbers, among many other things (such as beaver colonies and otter numbers), have been recorded thereby providing a remarkable data set on the wolf and moose interaction and their survival. Dr. Rolf Peterson (School of Forestry and Wood Products, Michigan Technical University, Houghton, Michigan 49931-1295, U.S.A.) is the director of the project. The report (Peterson 1999)

for the 1998 to 1999 year gives an overview and some quantitative details of the ecology of the island. Some of the data on wolf–moose numbers and wolf pack territories are given below. This long term study of more than 40 years is immensely important and has allowed a wide variety of studies to be carried out. For example, other than wolf population and territorial distribution, the effect of inbreeding, disease pathology and so on are of major current interest as are the dynamics of other animal populations and interactions on the island. The data are an excellent source for modelling investigations of population interactions. Figure 14.3 shows the wolf–moose populations, the wolf pack territories and the moose distribution on Isle Royale in 1999.

Wolves can cover around 50 km in a 24-hour period and so could cover a significant portion of their territory in a day. Even so, relative to pack size, the size of territories in northeastern Minnesota really means that physical presence can not provide a sufficient defensive mechanism to protect the territory. Based on many years of field observations, Mech (1991) suggests that wolf territories are formed and maintained by interpack aggression in conjunction with two warning systems: scent marking and howling, and that the result is a mosaic of territories covering the wolves' range. While howling may provide temporary information on a pack's location, elaborate spatial patterns of scent marks serve to advertise precise information about territorial claims even in the absence of any pack members. We shall include scent marking in our models.

As with other carnivores, olfaction (smell) is the primary sense.² Wolves use a variety of olfactory signs but behavioral studies indicate that raised leg urination (RLU) is the most important one in territory marking and maintenance. RLU markings occur throughout the territory along wolf trails but, more importantly, they increase significantly around the buffer region giving rise to high concentrations of RLU markings from all packs in this region: Figure 14.4 sketches typical RLU markings around a pack territory. Unlike the other olfactory signs used by wolves, RLU shows little correlation with pack size because they are made by only a few mature dominant wolves in each pack. These are primarily the alpha pair who reproduce and who dominate the other pack members: wolf packs are highly structured socially. Observations also indicate aversion to the scent from RLUs made by neighbouring packs.

White-tailed deer are the main prey for wolves in northeastern Minnesota and their distribution varies seasonally. During the summer months, deer are dispersed on large home ranges but in the winter months they tend to congregate in yards as shown in Figure 14.5. In spite of the relative homogeneity in food and habitat across the study region, the deer in both summer and winter tend to remain in the buffer zones between pack territories. It has been suggested that this deer heterogeneity could be due to differential predation rates caused by the territorial nature of the wolf.

As mentioned, the main motivation for the work described here is from the wolf–deer data from northeastern Minnesota. By following the movements of radiomarked individual members from a pack, or cooperative extended family group, it has been possible to deduce distinct spatial patterns in wolf distribution. Wolves typically remain within well-defined territories (Mech 1973, Van Ballenberghe et al. 1975) that, to some

²As noted earlier, the domesticated male silk moth (*Bombyx mori*) uses an optimally designed antenna filter to detect molecules of the sex-attractant chemical, *Bombykol*, emitted by the female. The male silk moth cannot fly so it has to walk up the concentration gradient to find the female: in some experiments it walked upwind as much as a kilometre!

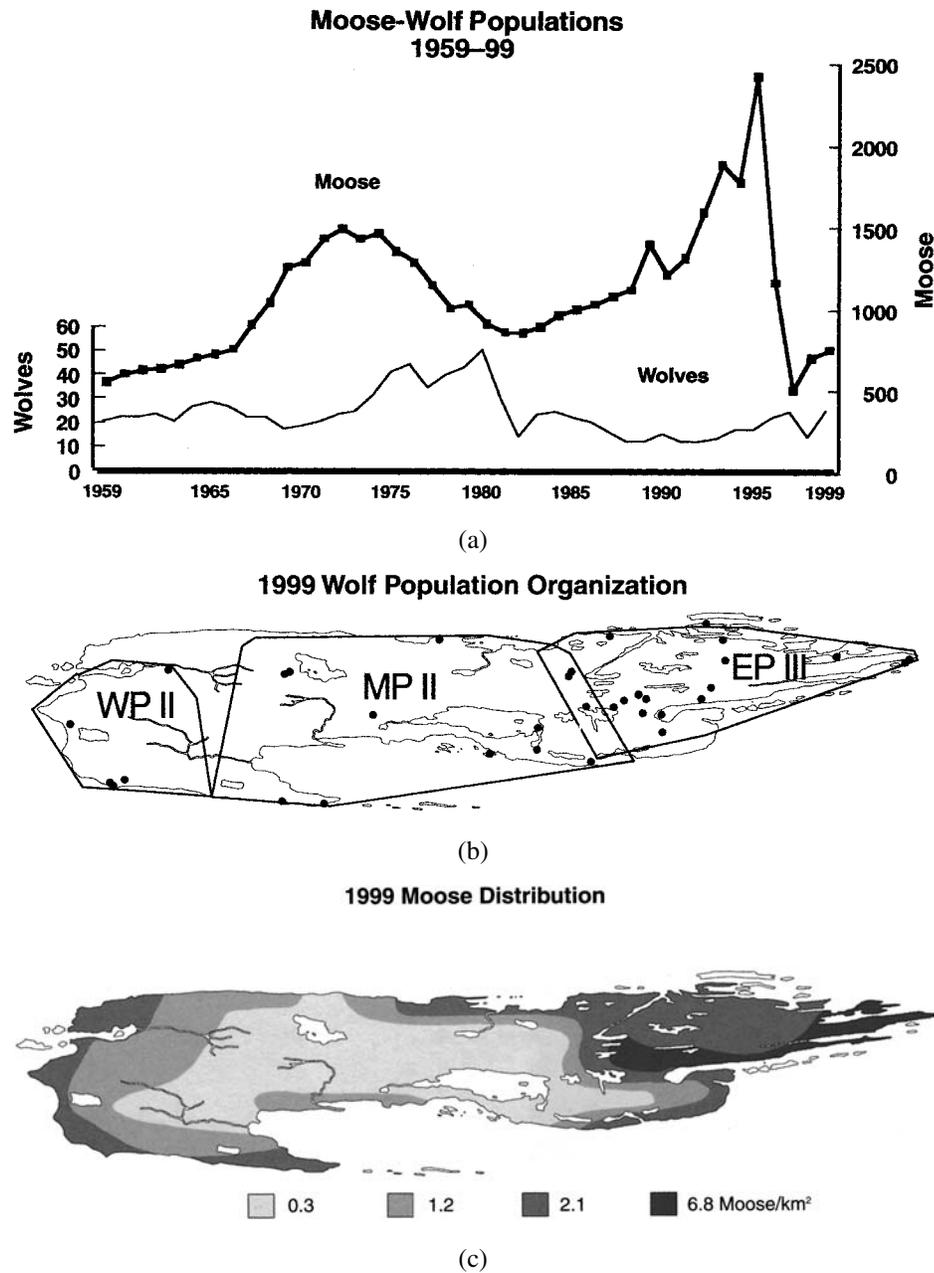


Figure 14.3. Isle Royale National Park: (a) Wolf and moose populations since 1959. (b) Wolf pack territories in the winter of 1999. In that year the sizes of the packs were: 11 in East Pack III (EP III), 10 in Middle Pack II (MP II) and 2 in West Pack II (WP II). (c) Moose distribution in the February 1999 census. (All figures are from Peterson 1999 and reproduced with permission of Dr. Rolf Peterson)

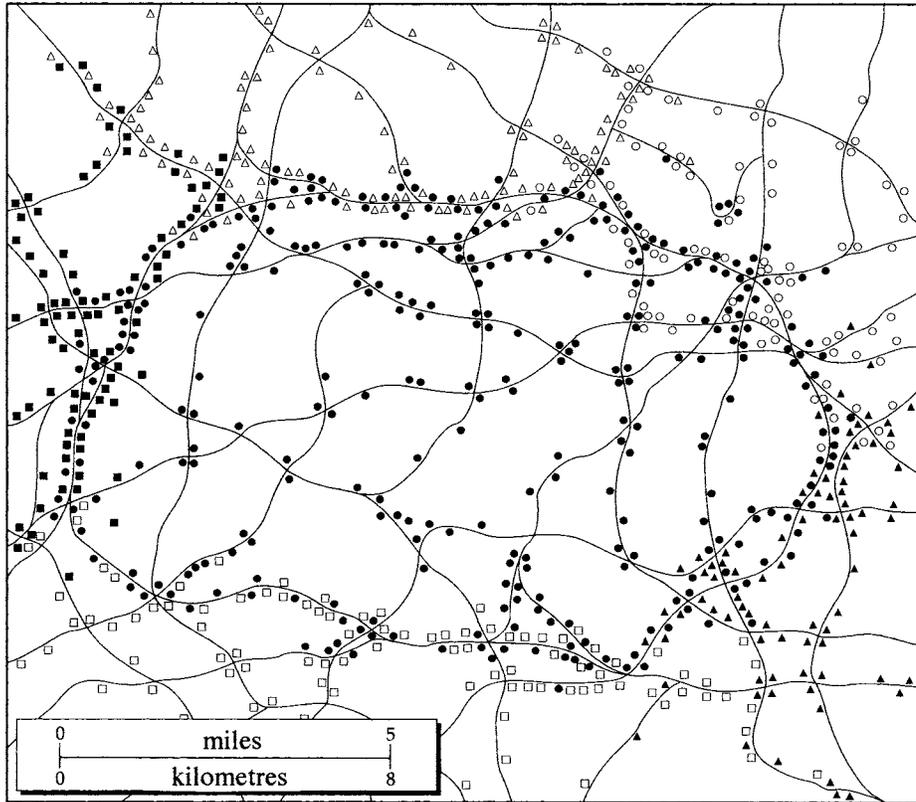


Figure 14.4. Typical distribution of RLU markings in and around a wolf pack territory in northeastern Minnesota. The levels of scent marking both due to the resident pack and its neighbours are greatest around the territory edges. The different shapes (filled squares and circles, open squares, circles and triangles) denote markings from different packs. (From Peters and Mech (1975) and reproduced with permission of Dr. David Mech)

extent, overlap only along their edges as shown in Figures 14.2 and 14.3. These territories effectively partition jurisdiction over spatially distributed prey resources.

The precise details of wolf behavior and ecology depend on local habitat conditions: there are, for example, basic differences between the habitat on Isle Royale and on the mainland. Although we concentrate on northeastern Minnesota, we believe the main results have applicability to other areas and other territorial mammals. This has been shown to be the case in the interesting study by Moorcroft et al. (1999) on coyotes (*Canis latrans*) which we discuss later. Wolf activities occur over various timescales—yearly, seasonally and daily. Thus a key element in modelling these wolf activities is the determination of an appropriate timescale.

Seasonality plays an important role in both wolf and deer ecology as is particularly evident in the reproductive behaviours of both species. Wolves produce young in the spring; pups arrive in April or May and activity centres around the den throughout the summer. Deer produce fawns in the early summer. Throughout the rest of the year,

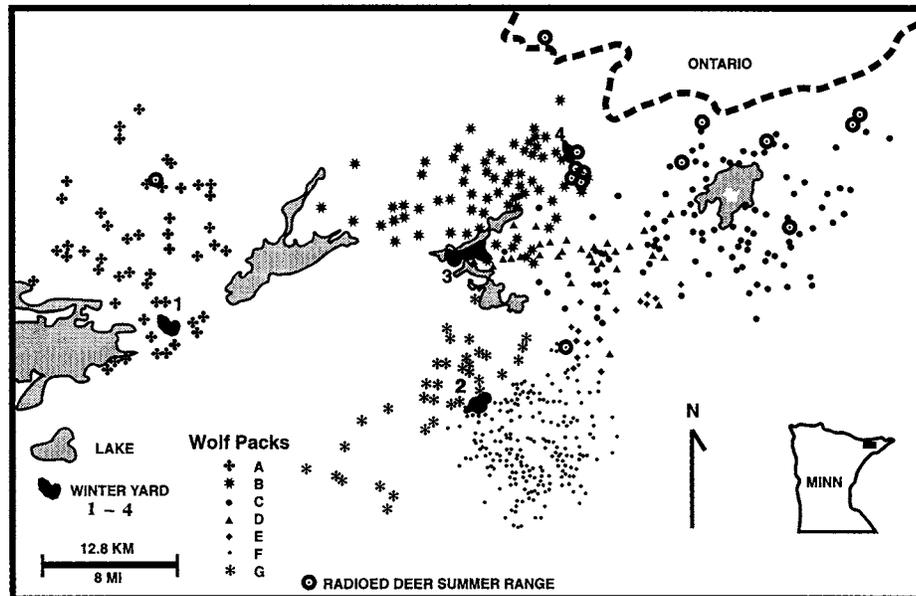


Figure 14.5. Winter yards and summer ranges of radio-collared deer in relation to wolf pack territories. (From Hoskinson and Mech 1976 and reproduced with permission of the Wildlife Society (copyright holder))

any changes in population levels are due to mortality, emigration or immigration. The entire wolf pack helps with feeding the pups (Mech 1970); adults make daily excursions and return with food. In late summer, as the pups become stronger, the den may be abandoned in favor of above-ground rendezvous sites. In the fall and winter, pups are able to move and travel widely with the pack, rarely returning to the den or rendezvous sites. In our modelling of pack territory dynamics we shall not include the yearly birth and death processes (see White 1995), but concentrate on the short term behavioral and movement dynamics.

In formulating the model we make no underlying assumptions about the size and extent of the wolf territories themselves; we show that the territorial patterns actually arise naturally as stable steady state solutions to the model equations. These mathematically generated territorial patterns share key features with field observations including buffer zones between adjacent packs, where wolves are scarce and increased levels of scent marking near territorial boundaries. The material in this chapter develops the model and analyzes it in detail. Among other aspects we show how behavioral responses to foreign scent marks determines the qualitative form of resulting spatial territories.

Very few quantitative models have been derived to explain the spatial dynamics of territories when competition for space is a key factor. As far as we are aware, the model and variations we describe here (Lewis and Murray 1993, White 1995, White et al. 1996a,b) comprise the only spatially explicit formulation designed to show how pack territories form over time based on behavioral interactions. On the other hand, field studies of pack territoriality have been extensive, and include observations of a variety

of predatory mammals other than wolves, such as lions, badgers, hyenas and African wild dogs (references to all of these are given in White et al. 1998).

14.2 Models for Wolf Pack Territory Formation: Single Pack—Home Range Model

Despite the complexity of wolf and deer behaviours and ecology, the stability of the pack territories and wolf–deer distribution observed in northeastern Minnesota suggests that there may be basic mechanisms underlying the spatial structure and dynamics of the ecosystem. The background details provided in the last section form the basis for the modelling we now discuss. The principal modelling motivation is whether or not simple behavioral rules can help elucidate the following questions (not all of which we address here).

- (i) Can we show how pack territories form, determine their size and explain why they are stable for many years?
- (ii) When deer, as prey, are included can we show why they are found mainly in the buffer zones between pack territories?
- (iii) With seasonal changes can we explain winter increase in buffer zone trespass, wolf–wolf altercation, wolf starvation and territory change?
- (iv) Can we predict wolf dynamics with low winter deer populations?
- (v) Can we quantify our predictions of population dynamics, territory and buffer zone sizes and seasonal changes, based on behavioral parameters? How sensitive are these predictions to behavioral changes?
- (vi) Do buffer zones stabilize wolf–deer interactions by providing a refuge for the deer, and if so, does a refuge act to dampen population oscillations or prevent extinction or both?
- (viii) Do biannual migrations act as a stabilizing factor in wolf–deer interactions?

As mentioned there are seasonal changes in wolf ecology. Since we are primarily interested here in territory formation we consider the formation and maintenance of territories during the summer months and so we do not include yearly birth processes. Consequently, the models focus on wolf movement patterns, which in later sections we couple to deer mortality caused by wolf predation, and aspects of the deer movement.

Due to the small numbers of both species there are potentially significant periods of time during which areas of territory are not occupied by a wolf (or deer). In view of this, it makes sense to use a probabilistic approach in which state variables are taken to be expected densities of wolves at a point \mathbf{x} and time t ; direct field observations typically will not yield the exact densities.

In view of the probabilistic approach and the choice of RLU marking as the method of territory delineation, a two wolf pack model could include the following state variables.

- $u(\mathbf{x}, t)$ = expected density of wolves from pack number 1
 $v(\mathbf{x}, t)$ = expected density of wolves from pack number 2
 $p(\mathbf{x}, t)$ = expected density of RLUs from wolf pack number 1
 $q(\mathbf{x}, t)$ = expected density of RLUs from wolf pack number 2.

During the summer months, pack members focus their movements around the den but they must necessarily spend time away from the den foraging for food. At the simplest level, we anticipate that wolf movement, independent of responses to other wolf packs, is dominated by (i) dispersal as the wolves search for food and other activities (like RLU marking) and (ii) movement back towards the den as the wolves return to the social organizing centre, the den, to care for the pups. So, a typical word equation for a single pack without RLU and deer input with this scenario is

- Rate of change in expected wolf density
 = Rate of change due to movement of wolves towards the den
 + Rate of change due to dispersal of wolves away from high density regions in search of food.

The key question is how to model the spatial movements.

Field studies indicate that wolves use cognitive maps and are aware of their relative locations within the territory. Consequently, movement back towards the den site tends to be more or less in a straight line. Mathematically, such movement can be represented by directed motion, or convection, with a flux, \mathbf{J}_u which takes the form, for the u -pack,

$$\mathbf{J}_u|_{\text{convection}} = -c_u(\mathbf{x} - \mathbf{x}_u)u, \quad (14.1)$$

where \mathbf{x}_u denotes the location of the den and $c_u(\mathbf{x} - \mathbf{x}_u)$ is the space-dependent velocity of movement; Okubo (1986) used a similar form in his model for insect dispersal that we discussed in Chapter 11, Volume I in which we used the discontinuous function $c_u(x - x_u) = c_u \text{sgn}(x - x_u)$ where c_u , the speed of movement, is constant. A continuous version of (14.1) which describes slowing and eventual stopping as wolves approach the den site is

$$c_u(\mathbf{x} - \mathbf{x}_u) = c_u \tanh(\beta r) \frac{\mathbf{x} - \mathbf{x}_u}{r}, \quad (14.2)$$

where $r = \|\mathbf{x} - \mathbf{x}_u\|$. The parameter c_u now 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 the limit as $\beta \rightarrow \infty$ (14.2) approaches the discontinuous form. In the presence of foreign RLUs the coefficient describing the speed of movement may be modified to include a response to the foreign RLU marking as described later.

Let us now consider movement due to foraging activity. In the first case we assume a plentiful and homogeneous food supply and in the second, discussed below, the deer density is explicitly incorporated into the model.

In the first case, the simplest assumption is that there is no preferred direction of motion for foraging and so is a random walk process as could occur if the food supply were uniformly distributed throughout the region. An extension to this assumes that movement may be density-dependent. As we now know, mathematically such movement can be represented by a diffusion flux, \mathbf{J}_u , which for the wolf pack u is

$$\mathbf{J}_u|_{\text{diffusion}} = -D(u)\nabla u, \quad (14.3)$$

where $D(u) = d_u u^n$, with constant d_u and $n > 0$, is the density-dependent diffusion coefficient. For n positive, density-dependence can be interpreted as an increased rate of movement in regions which are more familiar to the wolf pack.

Consider the simplest scenario of a single isolated wolf pack. Combining movement back to the den to care for the young, (14.1), with movement away from the den to forage, (14.3), the model conservation equation

$$\frac{\partial u}{\partial t} + \nabla \cdot \mathbf{J}_u = 0 \Rightarrow \frac{\partial u}{\partial t} = \nabla \cdot [c_u(\mathbf{x} - \mathbf{x}_u)u + D_u(u)\nabla u]. \quad (14.4)$$

We now have to consider appropriate initial and boundary conditions. Biologically realistic boundary conditions may involve local migration dynamics. However, the simplest possible boundary conditions are when we assume that wolves neither immigrate nor emigrate from the domain of interest denoted by Ω and which has to be determined. That is, we impose zero-flux boundary conditions for u , namely,

$$\mathbf{J}_u \cdot \mathbf{n} = 0 \quad \text{on the boundary} \quad \partial\Omega, \quad (14.5)$$

where \mathbf{n} is the outward unit normal to the boundary, $\partial\Omega$, of the domain. Initial conditions, describing the expected spatial distributions of wolves at the beginning of a study period, is given by

$$u(\mathbf{x}, t) = u_0(\mathbf{x}). \quad (14.6)$$

At any given time, the total number of wolves, Q , in the domain Ω is

$$Q = \int_{\Omega} u(\mathbf{x}, t) d\mathbf{x}. \quad (14.7)$$

Using (14.4) we see that

$$\frac{\partial}{\partial t} \int_{\Omega} u(\mathbf{x}, t) d\mathbf{x} = \int_{\Omega} \frac{\partial}{\partial t} u(\mathbf{x}, t) d\mathbf{x} = - \int_{\Omega} \nabla \cdot \mathbf{J}_u d\mathbf{x} = - \int_{\partial\Omega} \mathbf{J}_u \cdot \mathbf{n} ds = 0. \quad (14.8)$$

So, the zero-flux boundary condition (14.5) guarantees a constant number of wolves in the pack within the domain Ω .

We obtain the average density, U_0 , of wolves in the pack throughout the region Ω as

$$U_0 = \frac{1}{A} \int_{\Omega} u_0(\mathbf{x}) \, d\mathbf{x}, \tag{14.9}$$

where A is the area of the territory Ω . The mathematical problem is now completely defined.

Suppose we consider the time-independent problem. Equation (14.4) becomes

$$0 = \nabla \cdot [c_u(\mathbf{x} - \mathbf{x}_u)u + D_u(u)\nabla u]. \tag{14.10}$$

By way of illustration let us consider the one-dimensional situation with the zero-flux boundary condition (14.5) and with the continuous convection form (14.2) and obtain the steady state density distribution and territory size as a function of pack size. Let us further take the density-dependent diffusion coefficient to be given by $D_u(u) = d_u u^n$. The last equation then becomes, on integrating with respect to x ,

$$c_u u \tanh \beta(x - x_u) + d_u u^n \frac{du}{dx} = \text{constant}. \tag{14.11}$$

Linear Diffusion, $n = 0$

Here $D(u) = d_u$ a constant. Using zero-flux boundary conditions integration immediately gives the steady state solution, $u_s(x)$, in one space dimension as

$$u_s(x) = \frac{B}{[\cosh \beta(x - x_u)]^{c_u/(d_u\beta)}}, \tag{14.12}$$

where B , a constant of integration, is determined by the conservation condition (14.7) with a given number of wolves, Q , in the pack, namely,

$$B \int_{\Omega} \frac{dx}{[\cosh \beta(x - x_u)]^{c_u/(d_u\beta)}} = Q. \tag{14.13}$$

Nonlinear Diffusion, $n > 0$

Here integration of (14.11) gives

$$u_s(x) = \begin{cases} \left[\frac{c_u n}{d_u \beta} \ln \left[\frac{\cosh \beta x_b}{\cosh \beta(x - x_u)} \right] \right]^{1/n} & |x - x_u| \leq x_b \\ 0 & \text{otherwise,} \end{cases} \tag{14.14}$$

where the range radius of the pack, x_b , is given implicitly by

$$\int_{x_u - x_b}^{x_u + x_b} \left[\frac{c_u n}{d_u \beta} \ln \left[\frac{\cosh \beta x_b}{\cosh \beta(x - x_u)} \right] \right]^{1/n} dx = Q, \tag{14.15}$$

where Q is the number of wolves in the pack as defined above by (14.7). (Equation (14.14) is a weak solution of (14.11), in the sense that it satisfies (14.11) at all points except $x = \pm x_b$.) Similar results were obtained in Chapter 11, Volume I for positive choices of the power of the diffusion coefficient n .

The crucial difference between the two solutions ($n = 0$ and $n > 0$) is that when foraging activity is described using regular Fickian diffusion ($n = 0$) no definite territory boundary is formed whereas with the density-dependent diffusion ($n > 0$), territories with finite boundaries are formed (recall the detailed discussion in Chapter 11, Volume I). Figure 14.6(a) shows an example of the time evolution to the steady state wolf distribution for $n > 0$ obtained by numerically solving (14.4).

Figure 14.6(d) is an example of the relationship between pack and territory size given by equations (14.14) and (14.15) for representative values of the parameters. White (1995) estimated parameter values from field data and showed that values of $0.25 \leq n \leq 0.5$, $0.006 \leq \beta \leq 0.02$, $0.5 \leq d_u \leq 2.08$ were reasonable estimates with the higher diffusion coefficients associated with larger packs and hence larger territories.

The relationship shown in Figure 14.6(d) is reminiscent of ideas of McNab (1963) and Okubo (1980) who suggested that home range size, R , for mammals is related to

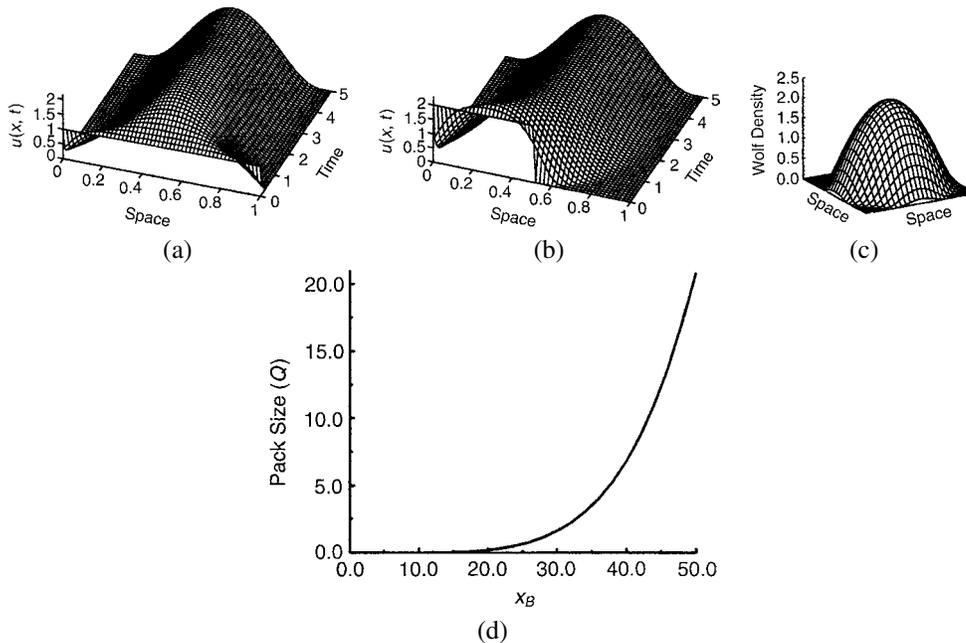


Figure 14.6. Time evolution to the steady state solution for a single pack in one space dimension with a density-dependent diffusion ($n = 0.5$): (a) and (b) have different initial conditions but the steady state solution is the same. Parameter values: $\beta = 1$, $c_u = 1$, $d_u = 0.03$. (c) Radially symmetric steady state solution for a single pack. Parameter values: $n = 1$, $\beta = 1$, $c_u = 1$, $d_u = 0.05$. (d) The relation between the pack territory ($2x_b$) in terms of wolf density obtained from the implicit relation (14.15) with representative parameter values $n = 0.5$, $\beta = 0.001$, $c_u = 1$, $d_u = 2$. (From White 1995)

the energy intake required per animal and hence the body weight, W , through the power law, $R = aW^b$, where a is a constant and $b \approx 0.75$.

14.3 Multi-Wolf Pack Territorial Model

Response to neighboring packs occurs primarily through RLU marking. The particular nature of the response (in terms of wolf movement) is not well understood and has been investigated in two different ways. In the first, the presence of foreign RLU marks increases the speed of movement back towards the den (central territory) area while increasing the production of familiar RLUs. In the second, wolves respond to gradients in foreign RLU markings by moving away from regions of high density at the same time increasing production of their own scent marks. Although similar behaviours are observed with both these scenarios there are some differences which we come back to below.

Because RLUs are made by a few mature dominant wolves in each pack, the location of these wolves is key in determining the RLU marking patterns. For the purposes of this model we can describe the location of such a dominant wolf by a probability density function denoting the chance of finding the wolf at point \mathbf{x} and time t . For any given pack, we sum these probability density functions over the number of RLU-marking wolves. This provides a measure of the *expected* density of RLU-marking wolves in the pack at a point \mathbf{x} and time t . From now on we refer to this quantity as the expected local density of wolves in a pack.

For a model involving two adjacent, interacting (in effect competing) wolf packs, the relevant state variables are the expected local densities of wolves in pack number 1, $u(\mathbf{x}, t)$; wolves in pack number 2, $v(\mathbf{x}, t)$; RLUs from pack number 1, $p(\mathbf{x}, t)$; and RLUs from pack number 2, $q(\mathbf{x}, t)$.

We must now include equations for the RLU densities which reflect the wolf responses to foreign RLUs from other packs. Based on the above, we assume that when members of a pack encounter RLUs from an adjacent pack, they move away from these foreign RLUs and back towards the den while also increasing their rate of RLU marking. Although mortal strife may occur when adjacent packs interact, for the purpose of modelling the populations we assume that such fatal interactions are very rare and that the number of wolves remains constant over the time period of the model. Remember that we are only considering the summer months.

The word equation for the wolf dynamics (of pack 1) is now

$$\begin{aligned} & \text{Rate of change in expected density of wolves (pack 1)} \\ &= \text{Rate of change due to movement of pack 1 wolves towards their den} \\ & \quad + \text{Rate of change due to dispersal of pack 1 wolves} \\ & \quad + \text{Rate of change due to movement of pack 1 wolves away from the RLUs} \\ & \quad \quad \text{made by pack 2} \end{aligned}$$

the terms of which we must now quantify. Let us first consider movement in response to foreign RLU markings. We consider two ways to model movement induced by RLU

levels. In the first, the response is assumed to increase the rate of movement back towards the den site. At the most extreme, this movement is assumed only to occur in the presence of competing RLUs but can be modified to allow movement independent of neighboring packs. In either of these, the convection flux, \mathbf{J}_{c_u} , described in the last section, (14.1) is modified to

$$\mathbf{J}_{c_u} = -c_u(\mathbf{x} - \mathbf{x}_u, q)u, \quad (14.16)$$

where, to show the dependence on foreign RLUs, q , we write as $c_u(\mathbf{x} - \mathbf{x}_u, q)$ which is a function of q such that $dc_u/dq \geq 0$ since in the presence of foreign RLUs, the wolves retreat towards the den site. The function $c_u(\mathbf{x} - \mathbf{x}_u, q)$ is typically a bounded monotonically increasing function of q ; a function qualitatively like $Aq/(B + q)$ with A and B constants is reasonable.

In the second case, the response to RLUs is to make the wolves move down gradients of foreign RLU density. In this case, the movement is modelled mathematically by a flux, \mathbf{J}_{a_u} given by

$$\mathbf{J}_{a_u} = a_u(q)u\nabla q, \quad (14.17)$$

where $a_u(q)$ is another monotonically non-decreasing function. Gathering these together we now have the conservation equation for the wolves in pack 1 as

$$\frac{\partial u}{\partial t} + \nabla \cdot [\mathbf{J}_{c_u} + \mathbf{J}_{d_u} + \mathbf{J}_{a_u}] = 0, \quad (14.18)$$

where the fluxes are given by

$$\begin{aligned} \mathbf{J}_{c_u} &= -uc_u(\mathbf{x} - \mathbf{x}_u, q), & c_u(0) &\geq 0, & \frac{dc_u}{dq} &\geq 0 \\ \mathbf{J}_{d_u} &= -d_u(u)\nabla u, & d_u(0) &\geq 0, & \frac{dd_u}{du} &\geq 0 \\ \mathbf{J}_{a_u} &= a_u(q)u\nabla q, & a_u(0) &\geq 0, & \frac{da_u}{dq} &\geq 0. \end{aligned}$$

The equation for movement of the second wolf pack mirrors that for wolf pack 1 and is given by

$$\begin{aligned} &\text{Rate of change in expected density of wolves (pack 2)} \\ &= \text{Rate of change due to movement of pack 2 wolves towards their den} \\ &\quad + \text{Rate of change due to dispersal of pack 2 wolves} \\ &\quad + \text{Rate of change due to movement of pack 2 wolves away from the RLUs} \\ &\quad \quad \text{made by pack 1} \end{aligned}$$

and is represented mathematically as

$$\frac{\partial v}{\partial t} + \nabla \cdot [\mathbf{J}_{c_v} + \mathbf{J}_{d_v} + \mathbf{J}_{a_v}] = 0, \quad (14.19)$$

where

$$\begin{aligned} \mathbf{J}_{c_v} &= -vc_v(\mathbf{x} - \mathbf{x}_v, p), & c_v(0) &\geq 0, & \frac{dc_v}{dp} &\geq 0 \\ \mathbf{J}_{d_v} &= -d_v(v)\nabla v, & d_v(0) &\geq 0, & \frac{dd_v}{dv} &\geq 0 \\ \mathbf{J}_{a_v} &= a_v(p)v\nabla p, & a_v(0) &\geq 0, & \frac{da_v}{dp} &\geq 0. \end{aligned}$$

We must now model the changes in the RLU densities p and q . Spatial distribution of RLU marks is a direct consequence of the spatial location of RLU-marking wolves. Field studies indicate that there is some low level of continuous RLU marking throughout the territory (along wolf trails) and that foreign RLU marking induces an increased rate of marking in the vicinity of the alien mark. (There is also an increase in the vicinity of a kill.) In addition, the strength of the RLU decays over time and although a first-order kinetics decay rate is assumed here, this rate will also depend fundamentally on the environmental conditions (such as rainfall, heat, snow cover and so on). Combining these three components gives the governing equation for RLU density distribution for pack 1 as

$$\frac{\partial p}{\partial t} = u[l_p + m_p(q)] - f_p p, \quad (14.20)$$

where l_p and f_p are constants describing low-level RLU marking and first-order decay kinetics respectively. The function $m_p(q)$ is plausibly assumed to be a bounded and monotonically nondecreasing function, again typically like $Aq/(B + q)$ with A and B constants. This means that there cannot be an infinite rate of urine production and a greater level of foreign RLU elicits a stronger response, at least at low levels. A similar equation holds for pack 2, namely,

$$\frac{\partial q}{\partial t} = v[l_q + m_q(p)] - f_q q. \quad (14.21)$$

To complete the mathematical formulation of our two-wolf pack model we require boundary and initial conditions. As in the single pack model biologically realistic boundary conditions may involve local migration dynamics. The simplest possible boundary conditions result, however, when we again assume that wolves neither immigrate to, nor emigrate from, the region Ω . Again we have zero-flux boundary conditions for u and v on the boundary, $\partial\Omega$, that is,

$$[\mathbf{J}_{c_u} + \mathbf{J}_{d_u} + \mathbf{J}_{a_u}] \cdot \mathbf{n} = 0 \quad \text{on } \partial\Omega \quad (14.22)$$

and

$$[\mathbf{J}_{c_v} + \mathbf{J}_{d_v} + \mathbf{J}_{a_v}] \cdot \mathbf{n} = 0 \quad \text{on } \partial\Omega, \quad (14.23)$$

where \mathbf{n} is the outward unit normal to the boundary, $\partial\Omega$, of the solution domain. Initial conditions describe the expected spatial distributions of wolves and RLU markings at the beginning of a study period and are given by

$$u(\mathbf{x}, 0) = u_0(\mathbf{x}), \quad v(\mathbf{x}, 0) = v_0(\mathbf{x}), \quad p(\mathbf{x}, 0) = p_0(\mathbf{x}), \quad q(\mathbf{x}, 0) = q_0(\mathbf{x}). \quad (14.24)$$

We can again show that the zero-flux boundary conditions (14.22) and (14.23) guarantee a constant number of wolves for each pack within the domain Ω . At any given time, the total number of wolves from wolf pack 1 in the domain Ω is

$$\int_{\Omega} u(\mathbf{x}, t) \, d\mathbf{x}.$$

Then, from (14.18) and an application of the divergence theorem, for wolf pack 1 we have

$$\begin{aligned} \frac{\partial}{\partial t} \int_{\Omega} u(\mathbf{x}, t) \, d\mathbf{x} &= \int_{\Omega} \frac{\partial}{\partial t} u(\mathbf{x}, t) \, d\mathbf{x} \\ &= - \int_{\Omega} \nabla \cdot [\mathbf{J}_{c_u} + \mathbf{J}_{d_u} + \mathbf{J}_{a_u}] \, d\mathbf{x} = - \int_{\partial\Omega} [\mathbf{J}_{c_u} + \mathbf{J}_{d_u} + \mathbf{J}_{a_u}] \cdot \mathbf{n} \, ds = 0. \end{aligned}$$

An analogous argument holds for pack 2.

The area of Ω is given by

$$A = \int_{\Omega} d\mathbf{x}.$$

The average density of wolves from pack 1 and pack 2 throughout the region Ω is then given by

$$U_0 = \frac{1}{A} \int_{\Omega} u_0(\mathbf{x}) \, d\mathbf{x}, \quad V_0 = \frac{1}{A} \int_{\Omega} v_0(\mathbf{x}) \, d\mathbf{x}. \quad (14.25)$$

We now nondimensionalise the model system (14.18)–(14.21) and their boundary and initial conditions (14.22)–(14.24). This lets us normalise the wolf density and domain size as well as reduce the number of parameters in the usual way. Defining a length $L = A^{1/m}$, where m is the dimension of the solution domain ($m = 1$ or $m = 2$), we introduce dimensionless quantities, denoted by an asterisk, by

$$u^* = \frac{u}{U_0}, \quad v^* = \frac{v}{V_0}, \quad p^* = \frac{pf_p}{U_0 l_p}, \quad q^* = \frac{qf_p}{V_0 l_q}, \quad t^* = tf_p, \quad \mathbf{x}^* = \frac{\mathbf{x}}{L}, \quad (14.26)$$

$$c_u^* = \frac{c_u}{Lf_p}, \quad c_v^* = \frac{c_v}{Lf_p}, \quad d_u^* = \frac{d_u}{L^2 f_p}, \quad d_v^* = \frac{d_v}{L^2 f_p} \quad (14.27)$$

$$a_u^* = \frac{a_u V_0 l_q}{L^2 f_p^2}, \quad a_v^* = \frac{a_v U_0 l_p}{L^2 f_q^2}, \quad m_p^* = \frac{m_p}{l_p}, \quad m_q^* = \frac{m_q}{l_q}, \quad \phi = \frac{f_q}{f_p}. \quad (14.28)$$

For the nondimensionalised quantities to be well defined, we implicitly assume that wolves from both packs are present originally ($U_0 > 0$, $V_0 > 0$), that the domain Ω has a size greater than zero ($L > 0$), that both wolf packs have a nonzero low level of RLU marking ($l_p > 0$, $l_q > 0$) and that the RLU intensity decays with time ($f_p > 0$, $f_q > 0$). Dropping the asterisks for notational simplicity, we then have the nondimensionalised system as

$$\frac{\partial u}{\partial t} + \nabla \cdot [\mathbf{J}_{c_u} + \mathbf{J}_{d_u} + \mathbf{J}_{a_u}] = 0, \quad (14.29)$$

$$\frac{\partial v}{\partial t} + \nabla \cdot [\mathbf{J}_{c_v} + \mathbf{J}_{d_v} + \mathbf{J}_{a_v}] = 0, \quad (14.30)$$

$$\frac{\partial p}{\partial t} = u[1 + m_p(q)] - p, \quad (14.31)$$

$$\frac{\partial q}{\partial t} = v[1 + m_q(p)] - \phi q, \quad (14.32)$$

where the fluxes are given by

$$\mathbf{J}_{c_u} = -uc_u(\mathbf{x} - \mathbf{x}_u, q), \quad \mathbf{J}_{d_u} = -d_u(u)\nabla u, \quad \mathbf{J}_{a_u} = a_u(q)u\nabla q \quad (14.33)$$

$$\mathbf{J}_{c_v} = -vc_v(\mathbf{x} - \mathbf{x}_v, p), \quad \mathbf{J}_{d_v} = -d_v(v)\nabla v, \quad \mathbf{J}_{a_v} = a_v(p)v\nabla p \quad (14.34)$$

and where the functions c_u , c_v , d_u , d_v , a_u , a_v are all nonnegative functions (or constants) as described above.

The boundary conditions (14.22) and (14.23) are unchanged and an appropriate nondimensionalisation of the initial data is

$$u_0^* = \frac{u_0}{U_0}, \quad v_0^* = \frac{v_0}{V_0}, \quad p_0^* = \frac{p_0 f_p}{U_0 l_p}, \quad q_0^* = \frac{q_0 f_q}{V_0 l_q},$$

which leaves the initial conditions (14.24) also unchanged after omitting the asterisks. Note too that the nondimensionalisation of space has made the dimensionless domain Ω equal to unity. Also, with this nondimensionalisation

$$\int_{\Omega} u(\mathbf{x}, t) d\mathbf{x} = \int_{\Omega} v(\mathbf{x}, t) d\mathbf{x} = 1 \quad (14.35)$$

and so, at any given time, $u(\mathbf{x}, t)$ and $v(\mathbf{x}, t)$ are probability density functions for the location of wolves.

We now have to specify appropriate forms for the interaction functions in the model equations. Lewis et al. (1997) showed that if the increased marking function m is typically as we described above (specifically a concave down function for the scent-marking density) then the time-independent solutions of (14.29)–(14.32) satisfy a system of ordinary differential equations with space as the independent variable. The integral conditions (14.35) are transformed into initial conditions for the ordinary differential equations. The resulting expected wolf density functions decrease mono-

tonically with distance away from the den site. A sufficient condition for the buffer zone (that is, a minimum in the value of $u + v$ between the den sites) is that the movement function, c_u , is also a concave down function of foreign scent-mark density.

For analytical simplicity and demonstration they considered a one-dimensional system with dens at opposite ends of the domain ($x_u = 0$, $x_v = 1$) and the movement response to foreign RLUs omitted. So, steady state solutions of (14.29)–(14.32) satisfy

$$0 = [J_u]_x, \quad J_u = -d_u u_x - c_u(r_u, q)u, \quad (14.36)$$

$$0 = [J_v]_x, \quad J_v = -d_v v_x + c_v(r_v, p)v, \quad (14.37)$$

$$0 = u[1 + m_p(q)] - p, \quad (14.38)$$

$$0 = v[1 + m_q(p)] - \phi q, \quad (14.39)$$

where r_u, r_v are distance measured from the respective dens. Boundary conditions (14.22) are now

$$J_v, J_u = 0 \text{ at } x = 0, 1 \quad (14.40)$$

and conservation conditions (14.35)

$$\int_0^1 u(x) dx = \int_0^1 v(x) dx = 1. \quad (14.41)$$

Generally, for any fixed values of u and v the assumption on the functional dependence of the m means that p and q can be uniquely determined as functions of u and v .

In summary what they proved is that if $m_p(q)$ and $m_q(p)$ are concave down functions then territories are determined by a system of two ordinary differential equations with the initial values at $x = 0$ specified. They showed that the expected wolf density for each pack is bounded above and below which, in turn, means that the expected scent mark density for each pack is positive and bounded above. One has to be careful with the choice of the form of these functions. The case described previously by Lewis and Murray (1993), where m_p and m_q are linear functions, can result in ‘blow-up’ for p and q , for certain parameter ranges. This is not surprising biologically since linear m_p and m_q imply that arbitrarily high scent marking rates are possible.

Existence of a Buffer Zone Between the Packs

We now show that a buffer zone, that is, an interior minimum for $u + v$, will arise under fairly general assumptions on the movement response function. For the sake of algebraic simplicity and illustration we consider one space dimension and two identical interacting packs (that is, $d_u = d_v = d$, $\phi = 1$ and so on), again with dens at opposite ends of the domain and we assume no explicit spatial dependence in the movement response function c . We also reasonably assume the same form for the marking functions m . Equations (14.36)–(14.39) are then, on integrating (14.36) and (14.37) and applying

the boundary conditions (14.40),

$$\begin{aligned}\frac{du}{dx} &= -\frac{1}{d}c(q)u, & \frac{dv}{dx} &= \frac{1}{d}c(p)v, \\ p &= u[1 + m(q)], & q &= v[1 + m(p)],\end{aligned}$$

subject to the integral constraints (14.41).

The solution to this system is invariant when $x \rightarrow 1 - x$, $u \leftrightarrow v$, $p \leftrightarrow q$ and so is symmetric about the midpoint $x = 1/2$. Thus, at $x = 1/2$ we have

$$\begin{aligned}u = v, p = q, \quad 0 > \frac{du}{dx} &= -\frac{dv}{dx}, \quad \frac{dp}{dx} = -\frac{dq}{dx}, \\ \frac{d(u+v)}{dx} &= 0, \quad \frac{dq}{dx} = \frac{1+m(p)}{1+vm'(p)} \frac{dv}{dx} > 0,\end{aligned}$$

and

$$\begin{aligned}&(u+v)_{xx} \\ &= \frac{1}{d} \{c(p)v - c(q)u\}_x \\ &= \frac{2}{d} \{c'(p)up_x - c(p)u_x\} \\ &= \frac{2u^2}{d} \frac{d}{dx} \left\{ \frac{c(p)}{p} \frac{p}{u} \right\} \\ &= \frac{2u^2}{d} \frac{d}{dx} \left\{ \frac{c(p)}{p} (1+m(q)) \right\} \\ &= \frac{2u^2}{d} \left\{ \frac{d}{dp} \left(\frac{c(p)}{p} \right) [1+m(q)]p_x + \frac{c(p)}{p} m'(q)q_x \right\}.\end{aligned}$$

A sufficient condition for the right-hand side of the last line to be positive is that $c(p)$ is convex. In this case $x = 1/2$ is a minimum for $u + v$ and this corresponds to a buffer zone for the interacting packs.

Lewis et al. (1997) discuss other analytical aspects of these models, for example, the dependence of territories on behavioral responses such as: (i) no marking response to foreign RLUs, (ii) marking response to foreign RLUs, (iii) switching in movement response to foreign RLUs and (iv) switching in marking response to foreign RLUs. By switching we mean, in the case of movement, for example, that there is essentially no movement back to the den (that is, $c(\mathbf{x} - \mathbf{x}_u, q) = 0$) until the foreign scent mark has reached a critical value, q_c say, after which c jumps up to a final value. In this situation we can take $c(q) = c_\infty H(q - q_c)$. A similar switching response to foreign RLUs can be incorporated by a comparable marking response function $m(q)$. These forms are alternatives to the constant slope type functions for $c(q)$ and $m(q)$ in Figure 14.7. White (1995), White et al. (1996a,b) and Lewis et al. (1997) also investigate in some

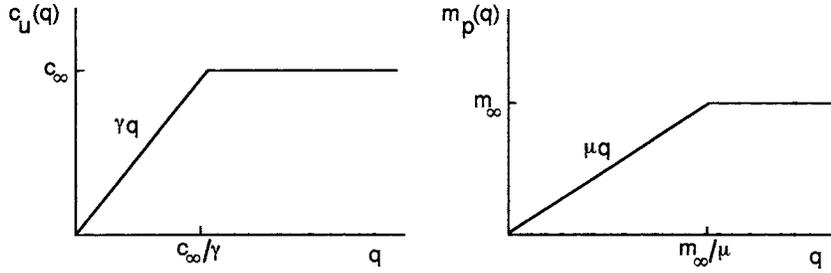


Figure 14.7. Piecewise linear forms for the movement functions $c_u(q)$, with a similar form for $c_v(p)$, and the RLU-marking functions $m_p(q)$, with a similar form for $m_q(p)$.

detail the numerical solutions of these model systems in both one and two dimensions. Some of their numerical results we give in Figure 14.9 below and the following section.

Let us now consider two specific examples, based on these general forms, discussed by White et al. (1998).

Foreign RLUs Influence Movement Back to the Den

Here we consider an encounter with foreign RLU markings causes increased movement back towards the den location in addition to increased RLU production. We also assume simple diffusion as the dispersal effect for foraging for food. With his scenario equations (14.29) to (14.32) become

$$\frac{\partial u}{\partial t} = \nabla \cdot [c_u(\mathbf{x} - \mathbf{x}_u, q)u + d_u \nabla u], \quad (14.42)$$

$$\frac{\partial v}{\partial t} = \nabla \cdot [c_v(\mathbf{x} - \mathbf{x}_v, p)v + d_v \nabla v], \quad (14.43)$$

$$\frac{\partial p}{\partial t} = u[1 + m_p(q)] - p, \quad (14.44)$$

$$\frac{\partial q}{\partial t} = v[1 + m_q(p)] - \phi q. \quad (14.45)$$

We consider a simplified case, where c and m are given by piecewise linear functions as shown in Figure 14.7 and again dens are at opposing ends of a one-dimensional domain ($x_u = 0, x_v = 1$). Steady state solutions to (14.42)–(14.45) with zero-flux boundary conditions and the functional forms in Figure 14.7 are given by

$$p = \frac{u(1 + \mu v)}{1 - \mu^2 uv}, \quad q = \frac{v(1 + \mu u)}{1 - \mu^2 uv} \quad (14.46)$$

and, after integrating (14.42) and (14.43),

$$0 = \gamma \frac{uv(1 + \mu u)}{1 - \mu^2 uv} + du_x, \quad 0 = -\gamma \frac{uv(1 + \mu v)}{1 - \mu^2 uv} + dv_x, \quad (14.47)$$

where μ and γ are the slopes of the functions defined in Figure 14.7. If we write

$$\Gamma(w) = \int_0^w \frac{dw}{1 + \mu w} = \frac{1}{\mu} \log(1 + \mu w) \quad (14.48)$$

we see from (14.47) that

$$\Gamma(u) + \Gamma(v) = \Gamma(u(0)) + \Gamma(v(0)) = k(u(0), v(0)), \quad \text{a constant.} \quad (14.49)$$

So

$$(1 + \mu u)(1 + \mu v) = \exp(\mu k) \quad (14.50)$$

gives u in terms of v and vice versa. In the special case $\mu = 0$, (14.47) implies

$$0 = \gamma uv + du_x, \quad 0 = -\gamma uv + dv_x \Rightarrow du_x + \gamma u(K - u) = 0,$$

where $K = [u(0) + v(0)]/d$ is a positive constant. This equation has solution

$$u(x) = \frac{L}{1 + Me^{\gamma Kx/d}},$$

where M and $L = (1 + M)u(0)$ are constants; this solution is a monotonically decreasing function of x .

If we now return to the $\mu \neq 0$ case, substituting (14.50) into (14.47) gives a pair of decoupled differential equations for u and v which can then be solved. Differentiating (14.50) gives

$$0 = \frac{v_x}{1 + \mu v} + \frac{u_x}{1 + \mu u}$$

which can be used to simplify the expressions for p_x and q_x , derived from (14.46), which become

$$p_x = \frac{(1 + \mu u)(\mu u - 1)}{(1 - \mu uv)^2} v_x, \quad q_x = \frac{(1 + \mu v)(\mu v - 1)}{(1 - \mu uv)^2} u_x. \quad (14.51)$$

Since $u(x)$ and $v(x)$ are monotonically decreasing functions of distance away from their den sites, interior maxima for $p(x)$ and $q(x)$ are given only when $u(x) = 1/\mu$ and $v(x) = 1/\mu$ respectively. So, there is an interior maximum for p if and only if $u(0) \geq 1/\mu \geq u(1)$ and there is an interior maximum for q if and only if $v(0) \leq 1/\mu \leq v(1)$. In other words, if the behavioral response function m is sufficiently steep then $1/\mu$ is sufficiently large and bowl-shaped scent marking densities arise as illustrated in Figure 14.8.

In the second illustrative model discussed by White et al. (1998) they incorporate a movement response to foreign RLU markings using chemotaxis with respect to foreign RLUs, movement back to the den and foraging movement based on diffusion. The

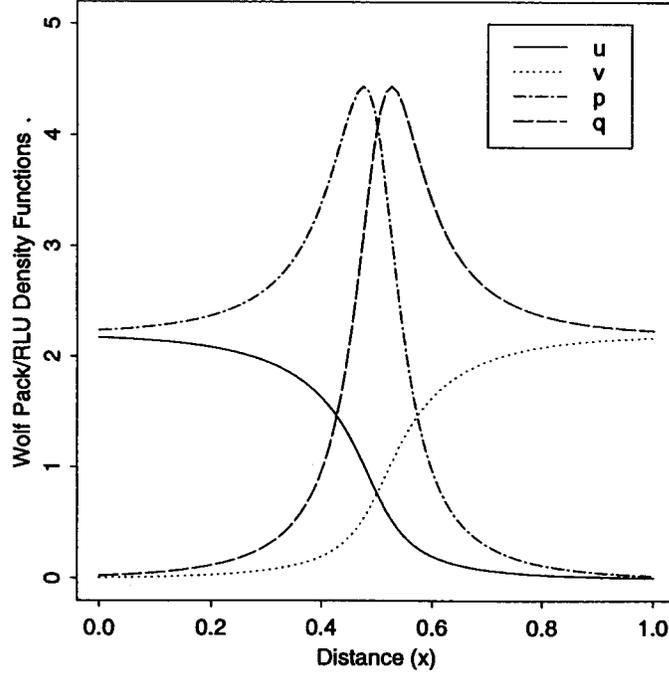


Figure 14.8. Steady state solutions of (14.42)–(14.45) with the piecewise linear functional forms shown in Figure 14.7. The solutions correspond to the analytical solutions of (14.46) and (14.47) for the wolf and the RLU densities. Note the increased scent marking near the pack boundaries. From the last equation the intersection of the line $u = 1/\mu$ with $u(x)$ gives the location of the maximum value for p , the RLU of the u -pack. Similarly the intersection of $v = 1/\mu$ with $v(x)$ gives the maximum for q , the RLU density of the v -pack. Model parameters used were $d_u = d_v = 0.333$, $\mu = 1.1$ and $\gamma = 1$ where γ is the slope of the $c(\cdot)$ -functions in Figure 14.7. (From Lewis et al. 1997)

model they examined is given from (14.29)–(14.34) by

$$\begin{aligned}
 \frac{\partial u}{\partial t} &= \nabla \cdot [c_u(\mathbf{x} - \mathbf{x}_u)u + D_u(u)\nabla u - a_u(q)u\nabla q], \\
 \frac{\partial v}{\partial t} &= \nabla \cdot [c_v(\mathbf{x} - \mathbf{x}_v)v + D_v(v)\nabla v - a_v(p)v\nabla p], \\
 \frac{\partial p}{\partial t} &= u[l_p + m_p(q)] - f_p p, \\
 \frac{\partial q}{\partial t} &= v[l_q + m_q(p)] - f_q q.
 \end{aligned} \tag{14.52}$$

We use the same nondimensionalisation given in (14.26)–(14.28) and get

$$\frac{\partial u}{\partial t} = \nabla \cdot [c_u(\mathbf{x} - \mathbf{x}_u, q)u + d_u\nabla u - a_u(q)u\nabla q], \tag{14.53}$$

$$\frac{\partial v}{\partial t} = \nabla \cdot [c_v(\mathbf{x} - \mathbf{x}_v, p)v + d_v \nabla v - a_v(p)v \nabla p] \quad (14.54)$$

$$\frac{\partial p}{\partial t} = u[1 + m_p(q)] - p, \quad (14.55)$$

$$\frac{\partial q}{\partial t} = v[1 + m_q(p)] - \phi q. \quad (14.56)$$

Once again analysis of the time-independent system produces a set of ordinary differential equations and generates certain criteria for the evolution of a buffer region between the two packs. Further investigation indicates that the above form of movement response to RLU markings shifts the location of the maximum expected wolf density from the den location to a position farther from the neighbouring pack.

The model also illustrates how pack splitting may occur as a response to foreign RLU markings so as to avoid overlap with neighbouring territories. This can be illustrated in a simplified case where only one pack, pack 2 say, responds to foreign RLU marking through movement avoidance, and neither pack increases its RLU marking in the presence of foreign RLU marks. If we take

$$a_u(q) = 0, \quad a_v(p) = \chi_v, \quad m_p(q) = 0, \quad m_q(p) = 0, \quad d_u(u) = d_u, \quad d_v(v) = d_v \quad (14.57)$$

we get, for the one-dimensional time-independent system (from (14.55) and (14.56))

$$p(x) = u(x), \quad q(x) = \frac{v(x)}{\phi},$$

and, using (14.2), from (14.53) and (14.54),

$$\begin{aligned} 0 &= c_u u \tanh \beta(x - x_u) + d_u u_x \\ 0 &= c_v v \tanh \beta(x - x_v) + d_v v_x + \chi_v v u_x \end{aligned} \quad (14.58)$$

the solutions of which are

$$u(x) = \frac{A}{[\cosh \beta(x - x_u)]^{c_u/(\beta d_u)}}, \quad (14.59)$$

$$v(x) = e^{-\psi[\cosh \beta(x - x_u)]^{-\gamma_u}} \frac{C}{[\cosh \beta(x - x_v)]^{\gamma_v}}, \quad (14.60)$$

with

$$\psi = \frac{A \chi_v}{d_v}, \quad \gamma_u = \frac{c_u}{d_u \beta}, \quad \gamma_v = \frac{c_v}{d_v \beta}. \quad (14.61)$$

Conservation of wolf pack size (14.35) then gives

$$\int_{\Omega} \frac{A}{[\cosh \beta(x - x_u)]^{c_u/(\beta d_u)}} dx = 1,$$

$$\int_{\Omega} e^{-\psi \cosh^{-\gamma_u} \beta(x - x_u)} \frac{C}{\cosh^{\gamma_v} \beta(x - x_v)} dx = 1. \quad (14.62)$$

The function $v(x)$ can take one of two forms as shown in Figures 14.9(a) and (b) with either one or two maxima; in both cases there is a maximum value for some $x > x_u$ (assuming that $x_u < x_v$). Note that the distribution for pack 1 remains symmetric about the den location. A single maximum for pack 2 is ensured if

$$A = u(x_u) < \frac{c_v d_u}{c_u \chi_v}$$

which suggests that there is a critical relative strength of adhesion between packs beyond which packs which have the greater response to foreign RLU marking could be forced to split their territories.

Figures 14.9(c) and (d) show the steady state solution of (14.53)–(14.56) for three equal packs together with the cumulative RLU density (from all three packs) which clearly highlights the area of high RLU markings along the pack boundaries.

14.4 Wolf–Deer Predator–Prey Model

We must now include the deer as a dynamic variable. With the explicit inclusion of a deer population, we can be more specific about wolf foraging which we modelled earlier by random diffusion. Here we represent movement associated with foraging by a response of the wolves directly to the deer density. In the simplest form, the prey-taxis describes a local response of the wolves to a ‘deer gradient.’ In other words, wolves move towards regions of higher deer density (which assumes that there is a higher probability of a successful hunt when the deer population is more dense). This is clearly a gross simplification but it provides an initial framework from which more realistic responses to the deer can be formulated. Mathematically, this form of taxis is expressed as a flux; for example, for wolves in pack 1 (u)

$$J_{\text{deer}} = \sigma_u u \nabla h, \quad (14.63)$$

where h is the expected density of the deer and σ_u is a parameter quantifying the strength of the taxis.

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. Their density distribution is therefore dominated by wolf predation levels and so the deer population can be modelled by

$$\frac{\partial h}{\partial t} = -(\alpha_u u + \alpha_v v)g(h), \quad (14.64)$$

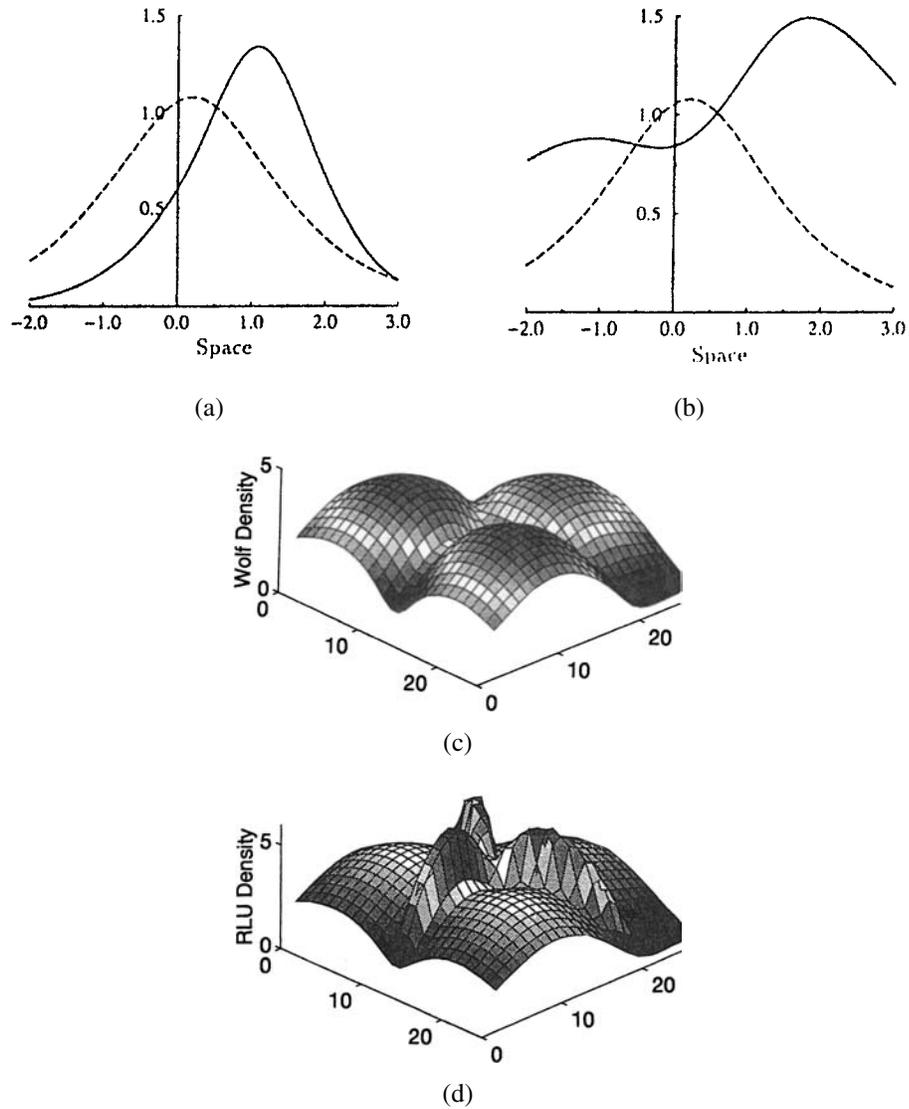


Figure 14.9. Steady state solutions of (14.53)–(14.56) where pack 2 (with den at location $x_v = 0.8$) only responds to foreign RLU marking through movement. The distribution of pack 1 is therefore unaffected by the presence of pack 2 and is symmetric about the den location at $x_u = 0.2$. In (a) the relative strength of adhesion of pack 1 is not strong enough to split pack 2 and hence there is a single maximum density for pack 2 located near the den for pack 2. In (b), however, the density distribution for pack 2 admits two maxima corresponding to the idea of pack splitting. Model parameters: $c_u = d_u = d_v = \chi_v = \beta = 1$ and in (a) $c_v = 2$, in (b) $c_v = 0.5$. The dashed line shows $u(x)$ and the solid line, $v(x)$. (c) and (d) Three-dimensional graphs of the steady state wolf and RLU densities for three identical packs obtained from a numerical simulation of the three-pack version of (14.53)–(14.56) with $c_u = 0.5$, $\beta = 0.5$, $n = 0$, $\alpha_u(q) = 0.25q/(1 + q)$, $\phi = 1$, $m(q) = 2q/(5 + q)$. Note the high levels of RLUs in the pack boundary regions. (From White et al. 1996a, 1998)

where α_u and α_v are constants and $g(h)$ is some typical nonlinear saturating function such as $g = ah/(1 + bh)$ or $g = ah^m/(1 + bh^m)$, $m > 1$ with a and b positive constants. We could add a natural mortality term (like $-kh$, for example) but natural mortality during the summer months is dwarfed by the wolf predation (mainly of the fawns).

We can now write down a basic model for wolf–deer interactions and their role in territoriality. We combine elements of the above wolf–wolf interaction models with the last two equations involving the deer. In the case of two wolf packs we obtain (in dimensional form)

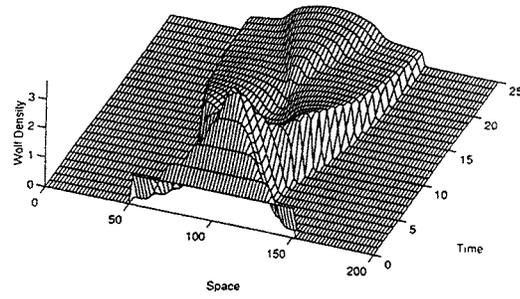
$$\begin{aligned}\frac{\partial u}{\partial t} &= \nabla \cdot [c_u(x - x_u)u - \sigma_u u \nabla h], \\ \frac{\partial v}{\partial t} &= \nabla \cdot [c_v(x - x_v)v - \sigma_v v \nabla h], \\ \frac{\partial p}{\partial t} &= u[l_p + m_p(q, h)] - f_p p, \\ \frac{\partial q}{\partial t} &= v[l_q + m_q(p, h)] - f_q q, \\ \frac{\partial h}{\partial t} &= -(\alpha_u u + \alpha_v v)g(h).\end{aligned}\tag{14.65}$$

This model differs further from the general forms given above in that we include a response to deer density in the production of RLU markings. This comes from the field observations which suggest that there is an increase in RLU marking at kill sites (Peters and Mech 1975, Schmidt, personal communication 1994).

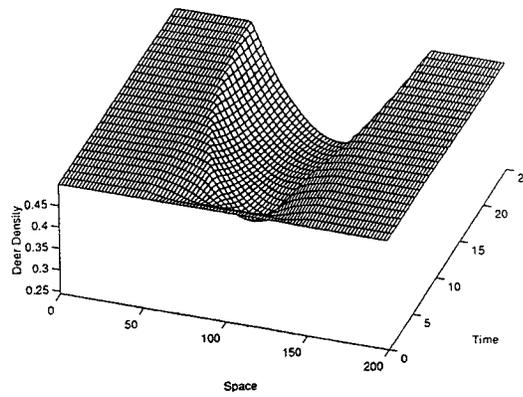
As with the deer, we could reasonably add other terms to the equations, for example, terms representing wolf death due to starvation and interpack conflict. In the u -equation, for example, these could be of the form $-\alpha_u u f_u(h)$ (f_u is a positive decreasing function of h) and $-k_u u v$ respectively added to the right-hand side. The models we have been considering in this chapter, however, have been for the summer period when starvation and interpack conflict are rare so it is reasonable to set these terms to zero in the analysis. The simulations presented below show the time evolution of the solutions for only a limited period. From the last equation in (14.65) it is clear that the deer population decreases with time and eventually would simply die out. For example, the simulation in Figure 14.10 is equivalent to a 24-week period. A fuller model which includes seasonal deer reproduction is discussed by White et al. (1996a); in this context they also discuss the question of deer extinction.

Parameter Estimation

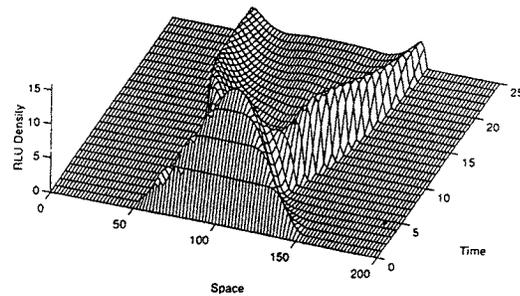
The parameters play a crucial role in the wolf–deer interaction with respect to both territoriality and survival. Estimation—even a rough estimation—of some of the parameters is difficult since it involves a knowledge of behavioral response and the social organization of the animals. White (1995) obtained some estimates from the extant literature.



(a)



(b)



(c)

Figure 14.10. Solutions to (14.65) (with $v = q \equiv 0$) for a single wolf pack in one space dimension with $c_u = 3.5$, $\beta = 0.001$, $\sigma_u = 0.2$, $\alpha_u = 0.02$ and $m_p(h) = 10h^{10}/(0.45^{10} + h^{10})$. 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. The simulation ran for the equivalent of 24 weeks and gave a mortality rate of approximately 18.5% over this period. (From White et al. 1996a)

We have reasonable estimates of pack size, approximately 3–15 wolves, which give a range of values for Q in (14.7) and territories, from 100–300 km², which give the area $A = (100 - 300)n$ where n is the number of wolf packs.

From field data (Peters and Mech 1975) the fresher an RLU the more likely it is to elicit further RLUs. This suggests that RLUs are typically detectable for about a week and so an estimate for the decay rate parameter is $f_p \approx (1/7)/\text{day}$. Wolves often travel at speeds of 5–8 km/hour. Since the timescale we consider is in days we get an estimate for $c_u \approx 5\text{--}30$ km/day: it is unlikely that a wolf will travel farther than the territory diameter in a day. We can also reasonably suppose that, except for the actual kill, the speed of the movement back to the den is not very different to the speed of movement in search of deer. This implies that we can take the prey-taxis parameter, σ_u , to be small since prey-taxis is probably not large on the scale of km²/day.

To estimate the deer mortality rate, α_u , suppose we take $g(h) = h$ and $v = 0$ in (14.64) in which case

$$h(\mathbf{x}, t) = h(\mathbf{x}, 0) \exp[-\alpha_u \int_0^t u(\mathbf{x}, s) ds].$$

Summer deer survival is relatively high but fawn survival is low. Using the data of Nelson and Mech (1991) an overall mortality rate in the summer months of 30% is a reasonable estimate. Taken on a daily basis this gives a mortality rate of about 0.002%. If we assume a constant pack size this gives $\alpha_u = O(10^{-2})$. This, of course, is an estimate for the case of a single pack preying on the deer. It has to be scaled to account for the number of packs considered.

We should reiterate that these estimates are only rough guides to the size of the parameters. They are used in some of the numerical simulations below. Parameter estimates, from detailed field studies of territoriality among coyotes, have been obtained by Moorcroft et al. (1999); we briefly discuss their work below.

White (1995), White et al. (1996a,b, 1998) and Lewis et al. (1997) carried out extensive numerical simulations of the various model equation systems discussed above. An example of such a simulation for a single wolf pack with deer prey and RLU marking, that is, the model obtained from the first, third and fifth equations of (14.65), is shown in Figure 14.10.

To get a clear picture of how territories evolve and are delineated as well as the essential features of wolf–deer interaction and their respective survival it is necessary to consider at least three wolf packs and the deer population. This means that we require 7 coupled partial differential equations in time with two space dimensions: there are three for the expected wolf densities, three for their associated RLU densities and one for the deer population. Figure 14.11 shows one such simulation with three (identical) wolf packs and clearly shows the spatial distribution of territories together with where the deer are primarily found. They mainly stay in the buffer zones between the mutually antagonistic wolf packs.

What is clearly suggested from Figure 14.10 is that food resources play an important role in forming and maintaining territorial structure and add strong support to the explanation for survival of both the wolves and the deer. Extensive numerical simulations of this wolf–deer system were carried out by White (1995), White et al. (1996a,b)

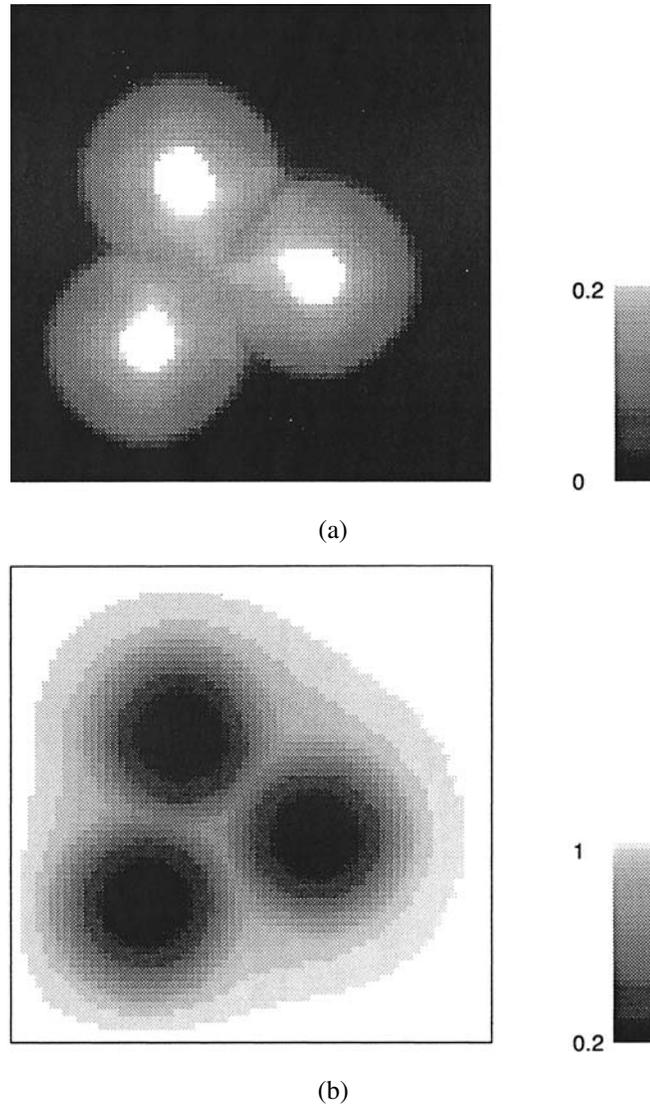


Figure 14.11. Numerical simulation of three wolf packs and a deer herd in two space dimensions showing the cumulative densities of wolf, in (a), and deer, in (b). The equations are the three-pack equivalent of (14.65) together with the form (14.2) for the movement back to the den. Note how the deer primarily congregate in the buffer zones which are regions of high cumulative RLUs from all packs. Parameter values are identical for each pack: $c_u = 0.2$, $\beta = 0.5$, $\alpha_u = 0.25$, $\sigma_u = 0.1$, $m(p, h) = 10h^{10}/(0.45^{10} + h^{10})$. Dens are located at (19.5, 19.5), (24.5, 44.5) and (44.5, 29.5) on a 70×70 grid. (From White et al. 1996a)

and Lewis et al. (1997) and indicate the following interesting features of wolf–deer systems.

- (i) Initially the wolves tend to congregate in the den region before spreading farther as illustrated in Figure 14.10. This occurs because the initial density distribution of the deer is uniform and in this case the equation governing the wolf movement is dominated by the convective term back towards the den. If this did not set up a gradient of deer, the wolves would aggregate at the den location. In this sense the interaction between the wolves and deer provides a mechanism to produce the wolf pack territory.
- (ii) The RLU density is greatest around the edge of the territory. This occurs because of the greater density of deer in this region and consequently a greater chance of deer kill, locations of which are often scent marked. Although it is unlikely that kill sites are the reason that greater levels of RLU marking are found around the territory edge, it may play some role in this spatial distribution.
- (iii) The symmetry in density distributions which is observed for the single pack model is destroyed when several packs interact as shown in Figure 14.11 for three neighboring packs. The interesting outcome in this case is the occurrence of a buffer region between the pack territories where deer density is greatest. In fact, the interaction between the packs and deer is sufficient to produce this pattern without the presence of RLU marking. This occurs in such a model because wolves move up local deer gradients and when two neighbouring packs approach a deer population from different sides this sets up such a gradient with its peak between the packs. Ecologically, there is no reason why a wolf from one pack would then move across this prey gradient because deer density would be lower on the other side and moreover there would be greater risk of interpack conflict.

14.5 Concluding Remarks on Wolf Territoriality and Deer Survival

The mechanistic models we have discussed up to now have primarily been motivated by the well-documented wolf–deer interactions and wolf territoriality in northeastern Minnesota. All of the various models were based on simple behavioral rules for the animals and the solutions were compared with field observations regarding territory formation, shape, size and maintenance. Further analysis on these models and other variants are given in the references listed throughout the chapter. There are still many different aspects that warrant further study.

One of the major aspects of the explicit spatiotemporal nature of the partial differential equation models is that territories form naturally without prescribed boundaries. When an isolated pack moves both towards and away from a den site the simplest model (14.4) discussed in Section 14.2 predicts the size of the home range as a function of pack size (Figure 14.6). This result is of potential interest in the process of wolf reintroduction currently being considered or underway in many parts of North America such as in Yellowstone National Park. There is field evidence which suggests that strong pack adhesion still occurs for all isolated packs. The single pack home range model mimics this observation and the adhesion which occurs may be explained by optimal pack sizes

which are both large enough to hunt large prey and still provide the necessary social interactions. With this simple model, of course, the territories formed are symmetric about the den site.

We also discussed several multi-pack models which differ in the nature of wolf responses to RLU marking. In all cases, interpack interactions break the territorial symmetry observed in the single pack system. Perhaps the most important aspect in these models is their capacity to produce the buffer regions between pack territories. Detailed analysis (some of it in the papers cited by White et al. 1996a,b and Lewis et al. 1997) shows that the presence or absence of this zone depends upon the shape and steepness of the scent mark response function. Also, numerical simulations in two space dimensions indicate that switching in both the movement and scent marking response functions are necessary to produce realistic territories with buffer zones in which higher densities of scent mark are present. These results suggest that field experiments might usefully be carried out to investigate responses of wolves to different RLU levels both in RLU production and aversion to foreign marks. If these responses are indeed important in territory formation, switching behavior should be observed in the field in both cases with wolves already familiar with foreign marks.

The analysis of the prey-taxis model discussed in Section 14.3 shows how the models can be used to investigate differences between packs in their responses to RLU marking. In the example there, it appears that a pack can be divided if it responds to foreign RLU marking at a significantly higher level than a strongly adhesive neighboring pack (one where there is a high probability of being found at the den site). Further theoretical study on this is presented by White (1995).

Although scent marking plays an important role in territory maintenance, howling, as we have mentioned before, is also important as a mechanism for territory defense. Future investigation concerning the effects of this short-lived, long-distance signal would clearly add to our understanding of territoriality and could be incorporated in more sophisticated models.

Our analysis of wolf–deer interactions suggests that much of the territorial structure observed in northeastern Minnesota can be explained by them. The movement of wolves towards regions of higher deer density results in spatial segregation of competing predators (neighboring packs) and their prey (deer) by setting up prey gradients between the packs. Moreover, the increase in RLU marking around the buffer region may be due, in part, to the increased deer density and hence wolf kill (which induces some level of RLU marking). In keeping with the philosophy in this book we have tried to keep the initial models to well-documented behavioral features with a view to gaining some understanding of the possible processes involved. Although these models involve some fairly basic assumptions they still lack much sophistication. Nevertheless they do pose highly relevant questions to the field ecologist regarding the interaction of predators and prey when the predators are territorial. More sophisticated models can be constructed once we have some idea of what is required and what needs further ecological study.

Of course, as we have seen in this book, nonlinear partial differential equations have been used in a variety of ecological contexts. However, we feel that the modelling described in this chapter presents a new approach to describing and understanding the behavioral aspects of territoriality. The choice of model components was influenced by other ecological studies rather than from a derivation based on individual movements.

Some of the current work along these lines with a more quantitative bent is described in the following section. The models presented here, although involving some fairly general assumptions, suggest that the apparently complex nature of wolf territory formation and maintenance and wolf–deer survival can be explained by the application of a few relatively simple behavioral rules. The work described in the next section on coyotes, based on the above modelling, lends strong support to this view. A new ingredient has been introduced in an interesting article by Lewis and Moorcroft (2001) who introduce aspects of game theory into the above mechanistic theory for home range models in wolves. They estimate relevant parameters and show that appropriate choices of the parameters result in territories that guard against invading groups with alternative behaviours.

14.6 Coyote Home Range Patterns

Although the qualitative features of land distribution between wolves and deer as predicted by the model analyses is in broad agreement with field observations, a more quantitative practical application of the above modelling has been carried out in the seminal paper by Moorcroft et al. (1999; see also Moorcroft 1997) who studied the home range patterns of the coyote (*Canis latrans*). Their work also provides further evidence that the distribution of the land plays a significant role in the spatial distribution of both the predator animals and their prey. It is the first application of the theory to empirical home range models in which the parameters can be estimated from the field studies and tends to confirm the general mechanistic approach we have described above.

Moorcroft et al. (1999) point out several advantages of such combination (theory and empirical) studies. One advantage is that model fits can be used to evaluate various hypotheses made with regard to the spatial distribution of the land resources and dynamics of the species studied. Another is to be able to predict the effects of external perturbations on the animal societies and resource use.

Moorcroft et al. (1999) used the above models, specifically the one proposed by Lewis and Murray (1993), to characterize the home ranges of coyote in the Hanford Arid Lands Ecological Reserve in Washington State, U.S.A. Basically what Moorcroft et al. (1999) did was to show what the key model ingredients which influenced the coyote movement were, namely, that encountering foreign RLUs had the effect of making them move back towards the den and that the effect of these foreign RLUs was to make them increase their own RLU production. A detailed analytical and ecological study specifically associated with the coyotes is given by Moorcroft (1997).

Moorcroft et al. (1999) carried out two separate analyses. In the first, using radio-tracking, they followed individual coyote movements of a single pack and fitted the data to the Lewis and Murray (1993) model for its home range. In the second study they again used the Lewis and Murray (1993) model to study the spatial patterns of six contiguous packs. They used the fit of the single pack solutions to predict the expected distribution of scent markings throughout the territory, the spatial patterns of individual movement and the effect of removing the pack from its home range. They showed that the model captures the observed spatial pattern of home ranges including the location and boundaries between adjacent packs. As we saw in Figure 14.9(d) in the case of three

packs we expect the highest concentration of scent markings to lie in the central region. This was also observed by Moorcroft et al. (1999).

The modelling framework discussed in this chapter and the analytical results derived for home ranges, RLU marking and spatial distribution of the land between the carnivore predators and their prey as they apply to wolf–deer systems gives reasonable qualitative results when compared with observations. The importance of the work of Moorcroft et al. (1999) is that they show that ‘a mechanistic framework for home range analysis provides a method for directly integrating theoretical and empirical studies of animal home range patterns. Formulating and applying models, in which predicted patterns of space use are formally scaled from an individual-level description of movement and interaction behavior, in contrast to earlier descriptive approaches, provides a methodology for directly testing hypotheses regarding the factors governing home range patterns. This in conjunction with an ability to make predictions for individual behaviour and changes in home range patterns following perturbation, allows for the development of a quantitative, reductionist understanding of animal home range patterns.’ A discussion of this work and related mechanistic models for territories is given in Moorcroft and Lewis (2001).

14.7 Chippewa and Sioux Intertribal Conflict c1750–1850

There is a well-documented human application of the general mechanistic theory we have proposed in this chapter which tends to justify intertribal warfare as a traditional means of survival. Morgan (1887) suggested that buffer zones or disputed areas between tribes was a universal feature of tribal societies.³ These buffer zones between accepted tribal territories were not generally occupied by members of either tribe and tended to be entered only by hunting groups of considerable strength (15 to 20 men) since the risk of intertribal conflict was high. The interesting article by Hickerson (1965) discussed the situation specifically as it applied to intertribal buffer zones in the upper Mississippi valley in the second half of the 18th century and the first half of the 19th century with the Virginia deer as the game. It is from his work that the following has been extracted.

In the case of the traditional enemies the Chippewa and Sioux in Wisconsin and Minnesota there was an extensive wooded buffer zone which gave refuge to the animal prey, in particular the Virginia deer. Figure 14.12 shows the approximate intertribal boundaries and buffer zone between the Chippewa and Sioux villages: the buffer zone was generally wider than 20 miles. It was only during the rare times of truce that hunters could enter the buffer zone to hunt and trap. As pointed out by Hickerson (1965) even during times of economic and ecological stasis before the reservation period these zones were probably not occupied by either group for more than a few days. The buffer zone between the Chippewa and Sioux was an area of abundant game.

As noted by Hickerson (1965) this buffer zone was very stable and was in existence from about 1750 to 1850 which is roughly from the time of the Chippewa settlement to the time of the reservations. Hickerson (1965) suggests that it was the deer that deter-

³As a small boy growing up in rural Scotland a remnant of mediaeval territory marking and boundary maintenance occurred every year with the formal ‘Riding of the Marches’ in which a group of local horsemen rode around the official boundaries of the small town.

What is clear is that during periods of truce of any length of time the game—mainly the Virginia deer because they were easier to catch—in the buffer zone quickly became depleted and famine ensued. Hostilities were then resumed and the buffer zone restored. As long as the buffer zone existed, which was maintained essentially by continuous intertribal warfare, deer were able to survive in large enough numbers in this disputed area to provide enough food for both tribes on each side of the disputed area. As Hickerson (1965) concludes ‘The maintenance of the buffer, that is, the warfare which kept a large portion of the best deer habitat a buffer, was a function of the maintenance requirements of the Chippewa and Sioux. During times of extended truce, even in very limited regions like the St. Croix River valley, when hunting was carried out in the buffer, the supply of deer meat became depleted and the war was revived as a response to famine.’



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Mathematical Biology II
Spatial Models and Biomedical Applications
Murray, J.D.
2003, XXV, 814 p., Hardcover
ISBN: 978-0-387-95228-4