Analysis of a model for wolf territories

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Abstract

A mechanism for territorial pattern formation in wolves is analysed using a spatially explicit mathematical model which incorporates wolf movement and scent marking. Model results reflect field observations: buffer zones where wolves are scarce arise between adjacent packs and near these buffer zones there are increased levels of scent marking. It is shown how the precise behavioral response of wolves to foreign scent-marks determines the qualitative form of the spatial territories. Realistic territories in two spatial dimensions require 'switching' of the movement and scent marking behavior in response to foreign scent marks.

1 Introduction

Although territoriality has been the subject of numerous models, until recently (Lewis and Murray 1993; White, Lewis, and Murray 1996) no mathematical investigation has focused on group or pack territories and their dependence on scent marking. We became intrigued by this issue after being made aware of some striking spatial patterns evident in wolf territories (Mech 1973; Van Ballenberghe, Erickson, and Byman 1975) and of how these provide a mechanism for wolves and their prey to coexist in relatively close proximity (White, Murray, and Lewis 1996). Our goal has thus been 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 in northeastern Minnesota.

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 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. An brief report of the model is given by Lewis and Murray (1993) in a previous article. The current paper contains an analysis of the model in detail and focuses on how behavioral responses to foreign scent marks determines the qualitative form of resulting spatial territories.

Models of animal territoriality have been used to determine the optimum shape for territory (Barlow 1974; Covich 1976; Buckley and Buckley 1977), to analyze the effect of resource allocation on group living (Macdonald 1983; Carr and Macdonald 1986), to investigate the effect of a spatially distributed predator upon a prey population (Taylor and Pekins 1991), and to evaluate home range of animals in the absence of interspecific competition. The latter typically employ a random walk with bias towards the 'home base' (Holgate 1971), previously visited areas (Siniff and Jessen 1969) or olfactory gradients (Benhamou 1989). However, very few quantitative models have been derived to explain the spatial dynamics of territories when competition for space is a key factor (Shigesada, Kawasaki, and Teramoto 1979), and, as far as we are aware, the model analysed here, and variations on it (Lewis and Murray 1993; White, Lewis, and Murray 1996), comprise the only spatially explicit formulation designed to show how pack territories form over time based on behavioral interactions. By way of contrast, field studies of pack territoriality have been extensive, and include observations of a variety of predatory mammals such as wolves (Mech 1973; Van Ballenberghe, Erickson, and Byman 1975; Fritts and Mech 1981), lions (Bertram 1978; Schaller 1972; Caraco and Wolf 1975; Rodman 1981), badgers (Kruuk 1989), hyenas (Mills 1990; Kruuk 1972), African wild dogs (Frame, Malcolm, Frame, and Van Lawick 1979), and canids (Moehlman 1983).

2 Biological Background

Wide-ranging radio-marking studies of wolves (*Canis lupus*) in northeastern Minnesota in the last 20 years have greatly facilitated the observation of wolf territories. By following the movements of radio-marked individual members from a pack, or cooperative extended family group, these studies have made it possible to deduce distinct spatial patterns in wolf distribution. Wolves typically remain within well-defined territories (Mech 1973; Van Ballenberghe, Erickson, and Byman 1975) that overlap only along their edges (Fig. 1). These territories may effectively partition jurisdiction over spatially distributed resources such as prey (Messier 1985).

The precise details of wolf behavior and ecology depend upon local habitat conditions. Although we concentrate on northeastern Minnesota, the key results should have applicability to other areas. The wolf activities which we now briefly review occur over various time scales: yearly, seasonally and daily. Thus a key element in modelling these wolf activities is the determination of an appropriate time scale.

Several important events mark each year. Wolves produce young in the spring; pups arrive in April or May and activity centers around the den until summer. The entire 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 northeastern Minnesota wolf packs basically remain in territories ranging from 125 to 310 km^2 (Peters and Mech 1975). Territorial boundaries are usually avoided, primarily to limit confrontation with adjacent packs (Mech 1977b). The resulting buffer zones or 'no-mans-lands' are about 2 km wide and may comprise as much as 25-40% of the available area (Mech 1977b; Mech 1977a).

Based upon many years of field observations, Mech (1991) suggests that wolf territories are formed and maintained by inter-pack 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. It is these scent marks that we now consider.

As with other carnivores, the primary sensory modality for wolves is olfaction (or scent) (Macdonald 1985). As wolves travel, they typically leave olfactory signs. Marks include (1) raised-leg urination (RLU), (2) squat urination, (3) defecation, and (4) scratching. Behavioral studies indicate that it is the RLU which plays the most important role in leaving information for subsequent canine travellers (Peters and Mech 1975; Merti-Millhollen, Goodman, and Klinghammer 1986). Thus, although wolves typically use a spectrum of olfactory stimuli for territory maintenance, we concentrate here upon the RLU as the dominant one. The information available for subsequent travellers includes the identity of the pack from which the RLU originated, the approximate time since the RLU was made and the reproductive status of the pack (Rothman and Mech 1979). Out of a typical pack of 5–15 wolves (Mech 1970), only a few mature dominant members leave RLUs (Peters and Mech 1975). However, these wolves leave RLUs quite regularly upon trails and and a travelling wolf may expect to encounter one RLU every two to three minutes (Peters and Mech 1975). Observations indicate some aversion to the scent from RLUs made by neighboring packs (Peters and Mech 1975). Marking frequency approximately doubles near territorial borders, giving rise to 'bowl-shaped' distributions of RLUs across territories, with the raised edges of the olfactory bowl located at the territorial boundaries (Peters and Mech 1975).

Wolves are capable of moving over 50 km in a 24-hour period (Mech 1966) and thus could cover a large portion of their territory in a single day. The maintenance of pack territory thus occur over a daily to weekly time scale, while seasonal events such as the birth and maturation of pups occurs over a yearly time scale. Our approach to modelling pack territory dynamics neglects the yearly birth and death processes, but concentrates upon the short-term behavioral and movement dynamics.

3 Models for Territorial Pattern Formation

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. We henceforth refer to this quantity as the expected local density of wolves in a pack.

For a model of two adjacent interacting wolf packs, the pertinent state variables thus 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, $q(\mathbf{x}, t)$.

3.1 Model for a Single Pack

In the simplest possible case, with only one wolf pack, we anticipate that two types of movements will dominate:

1. movement back towards the den as the wolves return to the social organizing center, and

2. dispersal as the wolves search for food and other resources.

We model this situation by a diffusion-convection equation of the following form:

$$\frac{\partial u}{\partial t} = \nabla \cdot [u c_u(r_u) \boldsymbol{\rho}_{\mathbf{u}}] + \nabla \cdot [d_u \nabla u] \,. \tag{3.1}$$

where

$$\boldsymbol{\rho}_{\mathbf{u}} = \frac{(\mathbf{x} - \mathbf{x}_u)}{|\mathbf{x} - \mathbf{x}_u|}$$

is a unit vector pointing towards the den located at $\mathbf{x}_u$. The movement speed towards the den, c_u, is given as a continuous function of the distance from the den $r_u = |\mathbf{x} - \mathbf{x}_u|$ with $c_u(0) = 0$, and the magnitude of the random movement away from the den is given by d_u. A related equation was proposed by Okubo to describe the swarming of insects (Okubo 1980; Murray 1989).

3.2 Territorial Model

Inter-pack competition and subsequent territorial behavior is modelled by changing equation (3.1) to include responses to foreign RLUs from other packs, and by including equations for the RLU densities themselves. 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 effectively constant over the time horizon for the model.

The equation for wolf pack 1 is thus a modification of (3.1)

$$\frac{\partial u}{\partial t} + \nabla \cdot \{\mathbf{J}_{c_u} + \mathbf{J}_{d_u}\} = 0 \tag{3.2}$$

where the fluxes are given by

$$\begin{aligned} \mathbf{J}_{c_u} &= -uc_u(q, r_u)\boldsymbol{\rho}_{\mathbf{u}}, \quad 0 \leq c_u(q, r_u) \leq c_{u\infty} < \infty, \quad \frac{dc_u}{dq} \geq 0 \\ \mathbf{J}_{d_u} &= -d_u \nabla u, \qquad\qquad\qquad\qquad d_u > 0. \end{aligned}$$

Here the rate of movement back to the den (which is situated at $\mathbf{x}_u$) depends on the expected levels of competing RLUs (q) and on the distance from the den (r_u). In the presence of competing RLUs, the wolves retreat towards the den and thus $dc_u/dq \geq 0$. Also, in the spring and summer, when pack movements are focused upon nourishing the pups at the den or rendezvous site, there may be an additional constant rate of movement towards $\mathbf{x}_u$ ($c_u(0, r_u) > 0$). The diffusive flux (d_u) is as described in the earlier simpler model (3.1).

The equation for movement of the second wolf pack mirrors that describing movement of wolf pack 1:

$$\frac{\partial v}{\partial t} + \nabla \cdot \{\mathbf{J}_{c_v} + \mathbf{J}_{d_v}\} = 0 \tag{3.3}$$

where

$$\begin{aligned} \mathbf{J}_{c_v} &= -vc_v(p, r_v)\boldsymbol{\rho}_{\mathbf{v}}, \quad 0 \leq c_v(p, r_v) \leq c_{v\infty} < \infty, \quad \frac{dc_v}{dp} \geq 0 \\ \mathbf{J}_{d_v} &= -d_v \nabla v, \qquad\qquad\qquad\qquad d_v > 0. \end{aligned}$$

Lastly, we require equations to describe the changes in RLU density (p or q) with time. The equation for p is:

Rate of change in expected RLU density (pack 1)

$$
\begin{aligned}
&= \text{Low level of continual marking}\\
&+ \text{Increased marking in the presence of RLUs from pack 2}\\
&+ \text{First order decay of RLUs with time.}
\end{aligned}
$$

Thus

$$\frac{\partial p}{\partial t} = u\left(l_p + m_p(q)\right) - f_p p, \quad 0 \leq m_p(q) \leq m_{p\infty} < \infty, \quad \frac{dm_p}{dq} \geq 0, \tag{3.4}$$

and the equation for q mirrors that for p:

$$\frac{\partial q}{\partial t} = v\left(l_q + m_q(p)\right) - f_q q, \quad 0 \leq m_q(p) \leq m_{q\infty} < \infty, \quad \frac{dm_q}{dp} \geq 0. \tag{3.5}$$

Here l_p and l_q represent low level RLU marking throughout the wolves' territory, m_p and m_q quantify the increase in RLU in the presence of competitive RLUs and f_p and f_q quantify decay dynamics for the RLUs, which are taken here to be first order.

To complete the mathematical formulation of our two-wolf pack model we require boundary and initial conditions. Biologically realistic boundary conditions may involve local migration dynamics. However, the simplest possible boundary conditions result when we assume that wolves neither immigrate to nor emigrate from the domain of interest Ω. This situation is described by zero-flux boundary conditions for u and v, namely

$$\{\mathbf{J}_{c_u} + \mathbf{J}_{d_u}\} \cdot \mathbf{n} = 0 \quad \text{on } \partial\Omega \tag{3.6}$$

and

$$\{\mathbf{J}_{c_v} + \mathbf{J}_{d_v}\} \cdot \mathbf{n} = 0 \quad \text{on } \partial\Omega, \tag{3.7}$$

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

$$u(\mathbf{x},0) = u_0(\mathbf{x}), \quad v(\mathbf{x},0) = v_0(\mathbf{x}), \quad p(\mathbf{x},0) = p_0(\mathbf{x}), \quad q(\mathbf{x},0) = q_0(\mathbf{x}). \quad (3.8)$$

At any given time, the total number of wolves from wolf pack 1 in the domain Ω is

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

For wolf pack 1

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

Thus the zero-flux boundary conditions (3.6)–(3.7) guarantee a constant number of wolves for each pack within the domain Ω. An analogous argument holds true for pack 2.

We calculate the average density of wolves from pack 1 throughout the region Ω as

$$U_0 = \frac{1}{A}\int_\Omega u_0(\mathbf{x})\,d\mathbf{x} \tag{3.9}$$

and the average density of wolves from pack 2 is

$$V_0 = \frac{1}{A}\int_\Omega v_0(\mathbf{x})\,d\mathbf{x}. \tag{3.10}$$

where A is the area of Ω.

To simplify the analysis we nondimensionalize the model system (3.2)–(3.5) with boundary conditions (3.6)–(3.7) and initial conditions (3.8). This permits us to normalize the wolf density and domain size as well as reduce the number of parameters. Defining $L = A^{1/n}$, where n is the dimension of the solution domain (either $n = 1$ or $n = 2$), we write

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

$$c_u^* = \frac{c_u}{Lf_p}, \quad c_{u\infty}^* = \frac{c_{u\infty}}{Lf_p}, \quad c_{v\infty}^* = \frac{c_{v\infty}}{Lf_p}, \quad c_v^* = \frac{c_v}{Lf_p}, \quad d_u^* = \frac{d_u}{L^2 f_p},$$
$$d_v^* = \frac{d_v}{L^2 f_p}, \quad m_p^* = \frac{m_p V_0 l_q}{l_p f_p}, \quad m_q^* = \frac{m_q U_0 l_p}{l_q f_p}, \quad \phi = \frac{f_q}{f_p}.$$

For the nondimensionalized 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 non-zero low level of RLU marking ($l_p > 0$, $l_q > 0$) and that the RLU intensity decays with time ($f_p > 0$). Dropping the asterisks for notational simplicity, we write the nondimensionalized system as (3.2)–(3.3) together with

$$\frac{\partial p}{\partial t} = u\,(1 + m_p(q)) - p. \tag{3.11}$$

$$\frac{\partial q}{\partial t} = v\,(1 + m_q(p)) - \phi q. \tag{3.12}$$

The boundary conditions (3.6)–(3.7) remain unchanged, and an appropriate nondimensionalization of the initial data,

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

leaves the initial conditions (3.8) unchanged as well, once asterisks have been dropped. Observe that our nondimensionalization of space has rendered Ω an area or length equal to unity. Furthermore, with the nondimensionalization given here,

$$\int_\Omega u(\mathbf{x},t)\,d\mathbf{x} = \int_\Omega v(\mathbf{x},t)\,d\mathbf{x} = 1 \tag{3.13}$$

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

4 Solutions Corresponding to Territories

We show that if m is a convex function the time-independent solutions of (3.2)–(3.3), (3.6)–(3.7), (3.11)–(3.12) satisfy a system of ordinary differential equations (ODEs). The integral conditions (3.13) are transformed into initial conditions for the ODEs.

For simplicity we consider a one-dimensional system with dens at opposing ends of the domain ($x_u = 0$, $x_v = 1$). Thus time-independent solutions to the model (3.2)–(3.3), (3.11)–(3.12) are given by

$$0 = -\frac{\partial}{\partial x}J_u, \quad J_u = -d_u\frac{\partial u}{\partial x} - c_u(q,r_u)u \tag{4.1}$$

$$0 = -\frac{\partial}{\partial x}J_v, \quad J_v = -d_v\frac{\partial v}{\partial x} + c_v(p,r_v)v \tag{4.2}$$

$$0 = u(1+m_p(q)) - p \tag{4.3}$$

$$0 = v(1+m_q(p)) - \phi q \tag{4.4}$$

with boundary conditions (3.6)–(3.7)

$$J_v, J_u = 0 \text{ at } x = 0, 1 \tag{4.5}$$

and conservation conditions (3.13)

$$\int_0^1 u(x)\, dx = \int_0^1 v(x)\, dx = 1. \tag{4.6}$$

For any fixed u and v the convexity assumption on m means that p and q can be uniquely determined as functions of u and v (Figure 2(a)). Furthermore, the construction of a series of contracting rectangles (Smoller 1982) can be used to show that $(p(u,v), q(u,v))$ is a globally stable invariant manifold for (3.2)–(3.3), (3.11)–(3.12). Note that the case where m has an inflection point may yield two distinct locally stable equilibrium values for p and q (Figure 2(b)).

Integration of (4.1)–(4.2) and application of the boundary conditions (4.5) thus yields the following ODEs:

$$\frac{\partial u}{\partial x} = \frac{-1}{d_u} c_u(q(u,v), r_u) u \tag{4.7}$$

$$\frac{\partial v}{\partial x} = \frac{1}{d_v} c_v(p(u,v), r_v) v \tag{4.8}$$

Considering the first of these equations we observe that $0 \leq c_u(q, r_u) \leq c_{u\infty}$ (3.2) implies that

$$\begin{aligned} u > 0 \quad &\Rightarrow \quad 0 \geq \frac{\partial u}{\partial x} \geq -\frac{c_{u\infty}}{d_u} u \\ u < 0 \quad &\Rightarrow \quad 0 \leq \frac{\partial u}{\partial x} \leq -\frac{c_{u\infty}}{d_u} u \\ u = 0 \quad &\Rightarrow \quad \frac{\partial u}{\partial x} = 0 \end{aligned}$$

Thus

$$u(0) > 0 \quad \Rightarrow \quad u(0) \geq u(x) \geq u(0) \exp\left(-\frac{c_{u\infty}}{d_u} x\right) \tag{4.9}$$

$$u(0) < 0 \quad \Rightarrow \quad u(0) \leq u(x) \leq u(0) \exp\left(-\frac{c_{u\infty}}{d_u} x\right) \tag{4.10}$$

$$u(0) = 0 \quad \Rightarrow \quad u(x) = 0. \tag{4.11}$$

This describes three regions where the solutions to (4.7) must lie (Figure 3). However the constraint $\int_0^1 u(x)\, dx = 1$ implies that $u(0) > 0$ and thus the first of these cases (4.9) applies. Coupled with the constraints on $m_p(q)$ (3.4) this in turn means that

$$0 < p(x) = u(x)(1 + m_p(q(x))) \leq u(0)(1 + m_{p\infty}). \tag{4.12}$$

A similar argument holds for $v(x)$ and $q(x)$.

Our assumptions about $c_u(q, r_u)$ (3.2) and $c_v(p, r_v)$ (3.3) along with the fact that $u(x)$, $v(x)$, $q(x)$ and $p(x)$ are strictly positive imply that the right hand sides of (4.7) and (4.8) are nonzero. Thus neither $u(x)$ nor $v(x)$ can have a critical point; $u(x)$ decreases monotonically with x and $v(x)$ increases monotonically with x.

The final part of the argument requires translation of the integral constraints (4.6) to initial values for (4.7)–(4.8). Figure 3(b) shows two curves from Figure 3(a) which yield the upper and lower bounds for $u(0)$ that satisfy (4.6). Defining

$$U(u(0), v(0)) = \int_0^1 u(x; u(0), v(0))\, dx \tag{4.13}$$

we observe that $U(u^+(0), v(0)) \geq 1 \geq U(u^-(0), v(0))$. A continuity argument can be used to show that and $U(u(0), v(0)) = 1$ for some intermediate $u(0)$. Defining

$$V(u(0), v(0)) = \int_0^1 v(x; u(0), v(0))\, dx \tag{4.14}$$

a similar argument can be made to show that $v(0)$ lies between the corresponding $v^-(0)$ and $v^+(0)$.

In summary we have shown that if $m_p(q)$ and $m_q(p)$ are convex functions then territories are determined by a system of 2 ODEs with the initial values at $x = 0$ specified. The expected wolf density for pack 1 ($u(x)$) is bounded above and below as described in (4.9) and a similar result holds true for pack 2 ($v(x)$). In turn this means that the expected scent mark density for pack 1 ($p(x)$) is positive and bounded above as described in (4.12) and that a similar result holds for expected scent mark densities for pack 2. Note that 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, at least for certain parameter ranges. This is not surprising biologically as linear m_p and m_q assume that arbitrarily high scent-marking rates are possible. A simple case where m_p and m_q exhibit 'switching' and thus are not convex is considered in Section 6.4. It is shown there that, for this case, p and q are functions of u and v only for certain parameter values.

5 Existence of a Buffer Zone

We now show that a buffer zone, or interior minimum for $u+v$, will arise under fairly general assumptions on the movement response function. For the sake of simplicity we consider two identical interacting packs, with dens at opposing ends of the domain and assume no explicit spatial dependence in the movement response function c. The equations (4.1)–(4.4) are thus given by

$$\frac{\partial u}{\partial x} = -\frac{1}{d}c(q)u \tag{5.1}$$

$$\frac{\partial v}{\partial x} = \frac{1}{d}c(p)v \tag{5.2}$$

$$p = u(1+m(q)) \tag{5.3}$$

$$q = v(1+m(p)). \tag{5.4}$$

subject to the integral constraints (4.6).

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

$$u = v, \quad p = q, \quad 0 > \frac{\partial u}{\partial x} = -\frac{\partial v}{\partial x}, \quad \frac{\partial p}{\partial x} = -\frac{\partial q}{\partial x},$$
$$\frac{\partial}{\partial x}(u+v) = 0, \quad \frac{\partial q}{\partial x} = \frac{\frac{\partial v}{\partial x}(1+m(p))}{1+vm'(p)} > 0.$$

and

$$\begin{aligned}
&(u+v)_{xx} \\
&= \frac{1}{d}\left\{c(p)v - c(q)u\right\}_x
\end{aligned}$$

$$
\begin{aligned}
&= \frac{2}{d}\left\{c'(p)up_x - c(p)u_x\right\} \\
&= \frac{2u^2}{d}\frac{\partial}{\partial x}\left\{\frac{c(p)}{p}\frac{p}{u}\right\} = \frac{2u^2}{d}\frac{\partial}{\partial x}\left\{\frac{c(p)}{p}(1+m(q))\right\} \\
&= \frac{2u^2}{d}\left\{\frac{\partial}{\partial p}\left(\frac{c(p)}{p}\right)(1+m(q))p_x + \frac{c(p)}{p}m'(q)q_x\right\}.
\end{aligned}
$$

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 $u+v$ corresponding to a buffer zone for the interacting packs.

6 Dependence of Territories on Behavioral Responses

In this section we consider the qualitative dependence of the wolf territories on the form of the movement response function c and the scent-marking response function m. Functional responses have been widely analysed in the context of predator-prey dynamics (Holling 1966). The forms we use here for the behavioral responses are analogous to the Holling type II and III functional responses; the former is a convex monotonic function while the latter exhibits switching.

We continue to focus on the model describing two identical interacting pack, with dens at opposing ends of the domain and assume no explicit spatial dependence in the movement response function c (5.1)–(5.4). Using piecewise linear caricatures for the functions we ask how the wolf territories and scent-marking densities depend on the behavioral response.

6.1 Case I: No Marking Response to Foreign RLUs

This case is characterized by no scent marking response of wolves to foreign RLUs ($m = 0$) and a linear increase in the directed movement rate in response to foreign RLUs ($c(q) = \gamma q$) (Figure 4(a)). It is assumed that the function c is none-the-less bounded, but that $q, p \leq c_\infty/\gamma$ (Figure 4(a)). Here (5.3) and (5.4) simply yield $p = u$ and $q = v$. Substitution into (5.1) and (5.2), and addition of these equations subject to the constraint (4.6) yields $u(x)+v(x) = 2$ pointwise on $0 \leq x \leq 1$. Thus the territories are given by solutions to two logistic equations with space as the independent variable:

$$u_x = \frac{-\gamma}{d} u\,(2-u)\,, \quad v_x = \frac{\gamma}{d} v\,(2-v) \tag{6.1}$$

(Figure 5). The initial conditions $u(0)$ and $v(0)$ to this system are chosen to satisfy the integral constraints (4.6). We can construct an energy function on the globally stable invariant manifold $p = u$, $q = v$:

$$F = \int_0^1 \phi^2\, dx, \quad \phi = u + v - 2, \tag{6.2}$$

$$\frac{\partial F}{\partial t} = -2 \int_0^1 \frac{\partial \phi}{\partial x}^2\, dx. \tag{6.3}$$

Thus the territory corresponds to a state of lowest potential, where the potential is measured as the squared deviation of away from a constant cumulative wolf density $u + v = 2$. The function F is not strictly a Lyapunov function because it is semi-definite and is restricted to the stable subspace $p = u$, $q = v$.

The territories calculated in this section (Figure 5) differ qualitatively from results observed in the field in that

1. The total expected wolf density $(u + v)$ remains constant throughout and is not reduced near the inter-pack boundary and

2. The expected density of RLU markings ($p = u$ and $q = v$) is no higher near territorial boundaries than near the den.

We now consider a modification of the above case which rectifies these two discrepancies.

6.2 Case II: Marking Response to Foreign RLUs

Here we assume that $m(q)$ and $c(q)$ have similar functional forms (Figures 4(a) and 4(b)). The part of the functions of interest are given by $m(q) = \mu q$ and $c(q) = \gamma q$. Although the functions m and c in Figures 4(a) and 4(b) are bounded, we assume that that $q, p \leq c_\infty/\gamma$ and $q, p \leq m_\infty/\mu$ (Figures 4(a) and 4(b)). Here (5.3) and (5.4) yield

$$p = \frac{u(1 + \mu v)}{1 - \mu^2 uv} \qquad (6.4)$$

$$q = \frac{v(1 + \mu u)}{1 - \mu^2 uv} \qquad (6.5)$$

and substitution into (5.1) and (5.2) yields

$$0 = \gamma \frac{uv(1 + \mu u)}{1 - \mu^2 uv} + du_x \qquad (6.6)$$

$$0 = -\gamma \frac{uv(1 + \mu v)}{1 - \mu^2 uv} + dv_x. \qquad (6.7)$$

Defining

$$\Gamma(w) = \int_0^w \frac{d\omega}{1+\mu\omega} = \log(1+\mu w)/\mu$$

we observe from (6.6)–(6.7) that

$$\Gamma(u) + \Gamma(v) = \Gamma(u(0)) + \Gamma(v(0)) = k(u(0), v(0)) \quad \text{(constant)}. \tag{6.8}$$

Thus

$$(1+\mu u)(1+\mu v) = \exp(\mu k) \tag{6.9}$$

describes u in terms of v and vice-versa.

Substitution of (6.9) into (6.7) yields

$$0 = -\gamma \frac{v\left(\frac{\exp(\mu k)}{1+\mu v} - 1\right)/\mu}{1 - \mu v\left(\frac{\exp(\mu k)}{1+\mu v} - 1\right)} + \frac{dv_x}{1+\mu v} \tag{6.10}$$

while substitution into (6.6) yields a similar equation for u. Equation (6.10) is separable, and integration yields an implicit formula for $v(x)$, namely

$$\frac{v(x)}{(E - \mu v(x))(1+\mu v(x))^E} = \frac{v(0)\exp\{\frac{\gamma E x}{d\mu}\}}{(E - \mu v(0))(1+\mu v(0))^E}, \tag{6.11}$$

where we have written $E = \exp(\mu k(u(0), v(0)) - 1$, and the similar u equation can be solved by the same method. For the special case $E = 1$ the solution can be calculated explicitly. Finally, the initial conditions $u(0)$ and $v(0)$ must be chosen so as to satisfy the integral constraints (4.6).

Profiles for the pack and scent mark densities are shown in Figure 6(a) and the cumulative expected densities for both wolf packs and for both scent marks are shown in Figure 6(b). Note that the cumulative wolf-pack density drops near the territorial boundary at $x = 1/2$ and the cumulative RLU density is highest there. Thus this solution reflects the biological observations more accurately than the $m = 0$ case.

We use equation (6.9) to observe that

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

This can be used to simplify expressions for p_x derived from (6.4) and q_x derived from (6.5):

$$\begin{aligned} p_x &= \frac{(1 + \mu u)(\mu u - 1)}{(1 - \mu uv)^2} v_x \\ q_x &= \frac{(1 + \mu v)(\mu v - 1)}{(1 - \mu uv)^2} u_x. \end{aligned}$$

Because $u(x)$ and $v(x)$ have no critical points (Section 4) possible interior maximums for $p(x)$ and $q(x)$ are given when $u(x) = 1/\mu$ and $v(x) = 1/\mu$, respectively. Thus 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 $q(x)$ if and only if $v(0) \leq 1/\mu \leq v(1)$ (Figure 6(a)). In other words, if the behavioral response function m is sufficiently steep then $1/\mu$ will lie in the above interval and bowl-shaped scent marking densities will arise.

6.3 Case III: Switching in Movement Response to Foreign RLUs

We now include 'switching' in the movement response of wolves to foreign scent marks. Specifically, we assume that there is no response at all until the foreign scent mark has reached a critical value q_c at the point x_c, after which there is a return to the den at speed c_∞. The marking response is chosen to be the same as in Case II above. Hence we have $m(q) = \mu q$ (Figure 4(b)) and $c(q) = c_\infty H(q - q_c)$ where $H(\cdot)$ is the Heaviside function (Figure 4(c)).

Using symmetry, equations (5.1) and (5.2) are solved to give

$$u = \begin{cases} u(0) & \text{if } 0 \le x \le x_c \\ u(0)\exp\left(-\frac{c_\infty}{d}(x - x_c)\right) & \text{if } x_c < x \le 1 \end{cases} \tag{6.12}$$

$$v = \begin{cases} u(0) & \text{if } 1 - x_c \le x \le 1 \\ u(0)\exp\left(-\frac{c_\infty}{d}(1 - x - x_c)\right) & \text{if } 0 \le x < 1 - x_c \end{cases} \tag{6.13}$$

where $u(0)$ is given in terms of x_c by the integral constraint (4.6) as

$$u(0)\left(x_c + \frac{d}{c_\infty}\left(1 - \exp\left(\frac{c_\infty}{d}(x_c - 1)\right)\right)\right) = 1. \tag{6.14}$$

The equations for p and q are given by (6.4) and (6.5). Using (6.5) and (6.12)–(6.13) we calculate

$$\begin{aligned} q_c &= q(x_c) = \frac{v(x_c)(1 + \mu u(0))}{1 - \mu^2 u(0) v(x_c)} \\ v(x_c) &= u(0)\exp\left(-\frac{c_\infty}{d}(1 - 2x_c)\right). \end{aligned} \tag{6.15}$$

Simultaneous solution of (6.14) and (6.15) yields the maximum expected density of wolves from a pack ($u(0)$) and the width of the buffer zone ($1-2x_c$) in terms of the parameters c_∞, d, q_c and μ. Whereas some buffer zone is evident without switching (Figure 6(b)), the switching function can greatly enhance the the magnitude of the buffer zone (Figure 7). For any given width, the depth of the buffer zone is an increasing function of the ratio of directed to random motion in the presence of foreign scent marks c_∞/d.

6.4 Case IV: Switching in Marking Response to Foreign RLUs

Lastly we consider the case where there is switching in the scent marking behavioral response. The movement response is chosen to be the same as in Case II above. The functional forms are thus $m(q) = m_\infty H(q - q_m)$ (Figure 4(d)) and $c(q) = \gamma q$ (Figure 4(a)). Figure 8 shows the stable time-independent equilibria for (6.4)–(6.5) in terms of u and v. Note that if (u, v) lies within the shaded region of Figure 8 there is not a unique time-independent solution. However, providing this region in $u - v$ phase space is bypassed the solution can be calculated in each sub-region in a manner similar to that used in Case II above. At the transition from Region B to Region D the expected scent mark density for pack 1 ($p(x_m)$) jumps up from $u(x_m)$ to $(1 + m_\infty)u(x_m)$ and at the transition from Region D to Region C the expected scent mark density for pack 2 ($q(1 - x_m)$) jumps down from $(1+m_\infty)v(1-x_m)$ to $v(1-x_m)$ (Figure 8). Using symmetry, the relationship between $u(x)$ and $v(x)$ given in terms of $k = u(0) + (1 + m_\infty)v(0) - m_\infty q_m$ is

$$\begin{array}{rcll} u + v + m_\infty v & = & k + m_\infty q_m & \text{if} \quad 0 \le x \le x_m \\ u + v & = & k & \text{if} \quad x_m < x < 1 - x_m \\ u + v + m_\infty u & = & k + m_\infty q_m & \text{if} \quad 1 - x_m \le x \le 1 \end{array} \tag{6.16}$$

The value of k is chosen so as to satisfy the integral constraints (4.6). A sample trajectory is shown in Figure 8 and the corresponding solution is shown in Figure 9. Here the step function form for $m(q)$ yields a solution which is discontinuous in p and q. In other words, an abrupt jump in p and q at the edge of the buffer zone corresponding to a sharp lip on the bowl of scent marking densities is direct consequence of switching in m.

In summary, our analysis of the piecewise linear system response functions has demonstrated how the functions determine the qualitative nature of the territories. Specifically

1. Territories can form with a convex movement response function and no scent marking response function ($m = 0$) but they typically do not exhibit the bowl shaped scent mark densities and the buffer zones between territories.

2. The addition of a convex scent marking response function can give rise to the bowl shaped scent marking densities and buffer zones. A condition for the bowl shaped scent marking densities is that the scent marking response function (m) is sufficiently steep.

3. Inclusion of switching in the movement response function can give rise to very distinct, wide buffer zones.

4. Inclusion of switching in the scent marking response function can give rise to very distinct, sharp edges on the scent mark bowl.

7 Numerical Solution in Two Spatial Dimensions

The full nonlinear system (3.2)–(3.5) was solved numerically using finite differences in two spatial dimensions. Computation was terminated when the solution had effectively reached a stationary profile. This stationary profile corresponds to territories, as described above. Shown are the two- and three-pack interactions (Figure 10). The numerical solution over a range of smooth movement behavior functions (c) and scent marking behavior functions (m) indicated that switching in c is needed for distinct territories and switching in m is needed for an lip on the bowl of scent marking densities. When there was no switching in m the regions of high scent marking were not localized to the edges of the 'bowl' but formed large two-dimensional hotspots in a 'blotchy' manner. The precise forms of the switching functions was not crucial as long as they were given qualitatively by Holling type III. This contrasts with the 1 dimensional results illustrated in Figure 6; there the bowl-shaped RLU densities arise with a convex m and switching in m only serves to sharpen the lip.

8 Discussion

In this paper we have analysed a simple mechanistic mathematical model which assumes that wolf movement and scent marking is mediated by the presence or absence of foreign scent marks. Specifically, upon encountering a foreign scent mark a wolf is assumed to increase its own scent marking and move toward the organizational center of its pack. The steady states that result correspond to territories. We have shown that, under a wide variety of assumptions about the movement and scent marking response functions, territories are determined uniquely and buffer zones exist between territories. The presence or absence of bowl shaped scent mark densities observed in nature specifically depends upon the shape and steepness of the scent marking response function.

Numerical experimentation in two spatial dimensions indicates that switching in both the movement response function and in the scent marking response function are needed to generate realistic territories with buffer zones and bowl shaped scent mark densities. Although piecewise constant switching functions were used for the mathematical analysis, the numerical solutions with smooth switching functions indicate that it is the qualitative form of the function (switching vs. no switching) that determines the kind of territorial patterns.

While analysis was primarily restricted to the explicit calculation of territories as time-independent solutions, all of our numerical results indicate that the territories are stable configurations. We conjecture that the territories are globally stable when unique, and have local stability properties when switching in m causes loss of uniqueness (see Figures 2(b) and 8). Analytical approaches to stability would be a worthwhile topic for additional research. These could possibly use an energy method similar to that in Section 6.1.

Although nonlinear partial differential equations have been applied successfully to ecological problems (Holmes, Lewis, Banks, and Veit 1994; Okubo 1980) including the spatial segregation of interacting species (Shigesada, Kawasaki, and Teramoto 1979; Mimura and Kawasaki 1980) and understanding social aggregations (Grünbaum and Okubo 1990) the modelling given here represents a new approach to understanding behavioral aspects of territory formation. A significant feature of our study is that the seemingly complex formation of wolf territories can be reduced to a relatively simple set of formulas involving scent marking.

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List of Figures

Figure 1: Radiolocations and home range boundaries of 5 adult and yearling timber wolves radiotracked via aircraft, 27 May – 22 October 1971 in northeastern Minnesota. Redrawn from Fig. 4 in Van Ballenberghe, Erickson, and Byman (1975) with permission from The Wildlife Society (copyright holder).

Figure 2: (a) Scent mark densities $p(u(x), v(x))$ and $q(u(x), v(x))$ are determined uniquely by (4.3)–(4.4) $m_u(q)$ and $m_u(q)$ are convex functions. (b) If $m_u(q)$ and $m_u(q)$ exhibit switching then $p(u(x), v(x))$ and $q(u(x), v(x))$ may not be determined uniquely if $u(x)$ and $v(x)$ are sufficiently small.

Figure 3: (a) Three regions where solutions to equation for wolf pack 1 (4.7) must lie. These are given by (4.9)–(4.11). (b) The maximum and minimum values for $u(0)$. The area under each curve integrates to unity and thus satisfies (4.6).

Figure 4: Functional forms for the movement behavior function $c(q)$ and the marking behavior function $m(q)$: (a) convex $c(q)$, (b) convex $m(q)$, (c) switching in $c(q)$ and (d) switching in $m(q)$.

Figure 5: Time-independent solution to (3.2)–(3.3), (3.6)–(3.7), (3.11)–(3.12) with $m_u = m_v = 0$ and $c_u(q) = \gamma q$, $c_v(p) = \gamma p$, $\gamma = 1$, (Figure 4(a)) and $d_u = d_v = 0.1$. Shown is the large-time numerical solution with

the expected density of wolves from pack 1 ($u(x)$) and the expected density of wolves from pack 2 ($v(x)$). This corresponds to the analytical solution to the system of logistic equations (6.1). Note that $u(x) + v(x) = 2$ pointwise across the domain so there is no buffer zone. The expected scent mark densities are identical to the expected wolf densities. Numerical solution used the Method of Lines and Gear's Method.

Figure 6: Time-independent solution to (3.2)–(3.3), (3.6)–(3.7), (3.11)–(3.12) with $c_u(p) = \gamma p$, $c_v(q) = \gamma q$ (Figure 4(a)) and $m_u(q) = \mu q$, $m_v(p) = \mu p$, (Figure 4(b)) and $\gamma = 1$, $d_u = d_v = 0.333$, $\mu = 1.1$. (a) Shown is the large-time numerical solution with the expected density of wolves from pack 1 ($u(x)$), the expected density of wolves from pack 2 ($v(x)$), the expected scent mark density from pack 1 ($p(x)$) and the expected scent mark density from pack 2 ($q(x)$). This corresponds to the analytical solution to equation (6.11) and the similar equation for u. Note the bowl shaped scent mark densities. Intersection of the line $u = 1/\mu$ with $u(x)$ yields the location of the maximum value for $p(x)$ which corresponds to the edge of the bowl (6.12). (b) The corresponding cumulative expected wolf density ($u(x) + v(x)$) and cumulative scent mark density ($p(x) + q(x)$). The function $(1 + \mu u)(1 + \mu v)$ is constant across the domain as predicted by (6.9). Note the the elevated scent mark density and buffer zone at $x = 0.5$. Numerical solution used the Method of

Lines and Gear's Method.

Figure 7: Analytical solution to the territoriality ODEs (5.1)–(5.4) subject to the integral constraints (4.6) with $c(q) = c_\infty H(q - q_c)$ (Figure 4(c)) and $m(q) = \mu q$ (Figure 4(b)). The solution for $u(x)$ and $v(x)$ is given by (6.12)–(6.13) with $u(0)$ and x_c determined by (6.14)–(6.15). The corresponding solutions for $p(x)$ and $q(x)$ are given by (6.4)–(6.5). Note the width of the buffer zone.

Figure 8: Stable time-independent equilibria for (5.4)–(5.4) with $m(q) = m_\infty H(q - q_m)$. Region A: $(p, q) = (u, v)$, region B: $(p, q) = (u, (1 + m_\infty)v)$, region C: $(p, q) = ((1 + m_\infty)u, v)$ and region D: $(p, q) = ((1 + m_\infty)u, (1 + m_\infty)v)$. Note that if $q_m/(1 + m_\infty) < u, v < q_m$ then the equilibrium cannot be determined uniquely, being either case A or B above. If parameters are chosen so that $k = u(0) + (1 + m_\infty)v(0) - m_\infty q_m > q_m$ (6.16) then the indeterminate region can bypassed in phase space. A sample trajectory is shown with three legs of the trajectory as given in (6.16).

Figure 9: An analytical solution to the territoriality ODEs (5.1)–(5.4) subject to the integral constraints (4.6) with $m(q) = c_\infty H(q - q_m)$ (Figure 4(d)) and $c(q) = \gamma q$ (Figure 4(a)). The corresponding solution trajectory is given in Figure 8. The solution method is the same as described in Section 6.1 except with the relationship between $u(x)$ and $v(x)$ in each subregion given by (6.16). Note the abrupt jumps in $p(x)$ and

$q(x)$.

Figure 10: Two dimensional territories. Each surface describes a group of wolves and their scent marks. The height of the surface describes the expected density of wolves and the color of the surface describes the expected scent mark density. The shading follows colors of the rainbow with red being low and violet being high. Solutions were generated by solving (3.2)–(3.3), (3.6)–(3.7), (3.11)–(3.12) numerically using finite differences and an alternating direction implicit method until the a stationary solution was effectively reached. The domain size is $[0, 1] \times [0, 1]$ and the mesh size is 40×40. The movement function is given by

$$c(q, r) = \frac{c_\infty}{2} \left(1 + \tanh(\gamma(q - q_c))\right) \tanh(\alpha r)$$

and the scent marking function is given by

$$m(q) = \frac{m_\infty}{2} \left(1 + \tanh(\mu(q - q_m))\right).$$

In the case with three interacting packs, an additional wolf movement and scent marking equation is added and the functions m and c are modified to depend on the cumulative foreign scent mark density. (a) Two interacting packs with dens at opposite corners of the domain ($d = 0.3$, $c = 3$, $\alpha = 100$, $\gamma = 2$, $m_\infty = 1.5$, $c_\infty = 1$, $\mu = 10$, $q_c = 1$, $q_m = 1$ and the color scale ranges from 0 to 4). (b) The cumulative expected wolf density and expected scent mark density surface for (a) above. (c) Three interacting packs with dens in two adjacent corners and at the midpoint of the opposite side ($d = 0.3$, $c = 3$, $\alpha = 100$, $\gamma = 2$, $m_\infty = 1.5$, $c_\infty = 1$, $\mu = 7$, $q_c = 0.75$, $q_m = 1$ and the color scale ranges from 0 to 5). (d) The cumulative expected wolf density and expected scent mark density surface for (c) above.

References

Barlow, G. W. (1974). Hexagonal territories. *Anim. Behav. 22*, 876–878.

Benhamou, S. (1989). An olfactory orientation model for mammals' movements in their home ranges. *J. Theor. Biol. 139*, 379–388.

Bertram, B. C. R. (1978). *Pride of lions*. London: J.M. Dent.

Buckley, P. A. and F. G. Buckley (1977). Hexagonal packing of royal tern nests. *Auk 94*, 36–43.

Caraco, T. and L. L. Wolf (1975). Ecological determinants of group sizes of foraging lions. *Am. Nat. 109*, 343–352.

Carr, G. M. and D. W. Macdonald (1986). The sociality of solitary foragers: a model based on resource dispersion. *Anim. Behav. 34*, 1540–1549.

Covich, A. P. (1976). Analysing shapes of foraging areas: some ecological and economical theories. *Annu. Rev. Ecol. Syst. 7*, 235–257.

Frame, L. H., J. R. Malcolm, G. W. Frame, and H. Van Lawick (1979). Social organization of African wild dogs *lycaon pictus* on the Serengeti Plains, Tanzania, 1967–1978. *Zeit. Tierpsychol. 50*, 225–249.

Fritts, S. H. and L. D. Mech (1981). Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern minnesota. *Wildlife Monographs 80*, 1–77.

Grünbaum, D. and A. Okubo (1990). Modelling social animal aggregations. In S. A. Levin (Ed.), *Frontiers in Mathematical Biology, Springer*

Lecture notes in Biomathematics, Volume 100, pp. 296–325. Berlin: Springer-Verlag.

Holgate, P. (1971). Random walk models for animal behavior. In G. P. Patil, C. Pielou, and W. W. E. (Eds.), *Statistical Ecology: Sampling and modeling biolgical populations and population dynamics*, pp. 1–12. University Park: Pennsylvania State University Press.

Holling, C. S. (1966). The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada 48*, 1–86.

Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit (1994). Partial differential equations in ecology: Spatial interactions and population dynamics. *Ecology 75*, 17–29.

Kruuk, H. (1972). *The Spotted Hyena: a Study of Predation and Social Behavior*. Chicago: University of Chicago Press.

Kruuk, H. (1989). *The Social Badger: Ecology and Behaviour of a Group-living Carnivore (Meles meles)*. Oxford: Oxford University Press.

Lewis, M. A. and J. D. Murray (1993). Modelling territoriality and wolf-deer interactions. *Nature 366*, 738–740.

Macdonald, D. W. (1983). The ecology of carnivore social behavior. *Nature 301*, 379–384.

Macdonald, D. W. (1985). The carnivores: order *carnivora.* In R. E. Brown and D. W. Macdonald (Eds.), *Social Odours in Mammals*, Volume 2, pp. 619–722. Oxford, U.K.: Clarendon Press.

Mech, D. L. (1991). *The Way of The Wolf.* Stillwater, Minnesota: Voyageur Press.

Mech, L. D. (1966). *The Wolves of Isle Royale.* U.S. Natl. Park Serv. Fauna Ser. 7.

Mech, L. D. (1970). *The Wolf: The Ecology and Behavior of an Endangered Species.* Garden City, New York: The Natural History Press.

Mech, L. D. (1973). Wolf numbers in the superior national forest of minnesota. Technical report, US Forest Service Research Paper NC-97.

Mech, L. D. (1977a). Population trend and winter deer consumption in a Minnesota wolf pack. In R. L. Phillips and C. Jonkel (Eds.), *Proceedings of the 1975 Predator Symposium*, Missoula, Montana. University of Montana.

Mech, L. D. (1977b). Wolf-pack buffer zones as prey reservoirs. *Science 198*, 320–321.

Merti-Millhollen, A. S., P. A. Goodman, and E. Klinghammer (1986). Wolf scent marking with raised leg urination. *Zoo Biology 5*, 7–20.

Messier, F. (1985). Social organization, spatial distribution, and population density of wolves in relation to moose density. *Can. J. Zool. 85*, 1068–1077.

Mills, M. G. L. (1990). *Kalahari Hyaenas: the Behavioural Ecology of Two Species*. London: Unwin Hyman.

Mimura, M. and K. Kawasaki (1980). Spatial segregation in competitive interaction- diffusion equations. *J. Math. Biol. 9*, 49–64.

Moehlman, P. D. (1983). Socioecology of silverbacked and golden jackals *canis mesomelas* and *c. aureus*. In J. F. Eisenberg and D. G. Kleinman (Eds.), *Recent advances in the study of mammalian behavior*. Am. Soc. Mammal. Special Publication, No. 7.

Murray, J. D. (1989). *Mathematical Biology*. Berlin: Springer-Verlag.

Okubo, A. (1980). *Diffusion and Ecological Problems: Mathematical Models*. Berlin: Springer-Verlag.

Peters, R. P. and L. D. Mech (1975). Scent-marking in wolves. *Amer. Sci. 63*, 628–637.

Rodman, P. S. (1981). Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. *Am. Nat. 118*, 275–188.

Rothman, R. J. and L. D. Mech (1979). Scent marking in lone wolves and newly formed pairs. *Anim. Behav.*, 750–760.

Schaller, G. B. (1972). *The Serengeti Lion: a Study of Predator-prey Relations*. Chicago: University of Chicago Press.

Shigesada, N., K. Kawasaki, and E. Teramoto (1979). Spatial segregation of interacting species. *J. Theor. Biol. 79*, 83–99.

Siniff, D. B. and C. R. Jessen (1969). A simulation model of animal movement patterns. *Adv. Ecol. Res. 6*, 185–219.

Smoller, J. (1982). *Shock Waves and Reaction-Diffusion Equations.* Berlin: Springer Verlag.

Taylor, R. J. and P. J. Pekins (1991). Territory boundary avoidance as a stabilizing factor in wolf-deer interactions. *Theor. Pop. Biol. 39*, 115–128.

Van Ballenberghe, V., A. W. Erickson, and D. Byman (1975). Ecology of the timber wolf in northeastern minnesota. *Wildlife Monographs 43*, 1–43.

White, K. A. J., M. A. Lewis, and J. D. Murray (1996). A model for wolf-pack territory formation and maintenance. *J. Theor. Biol. 178*, 29–43.

White, K. A. J., J. D. Murray, and M. A. Lewis (1996). Wolf-deer interactions: a mathematical model. *Proc. Roy. Soc. Lond. B 263*, 299–305.