



## ESS Analysis of Mechanistic Models for Territoriality: the Value of Scent Marks in Spatial Resource Partitioning

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In this paper elements of game theory are used to analyse a spatially explicit home range model for interacting wolf packs. The model consists of a system of nonlinear partial differential equations whose parameters reflect the movement behavior of individuals within each pack and whose solutions describe the patterns of space-use by each pack. By modifying the behavioral parameters, packs adjust their patterns of movement so as to maximize their reproductive output. This involves a tradeoff between maximizing prey intake and minimizing conflict with neighbors. Evolutionarily stable choices of the behavioral parameters yields territories that are immune to invasion by groups with alternate behaviors.

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### Introduction

Traditional approaches to understanding home range patterns used optimality theory to examine intra- and inter-specific variation in territorial behavior (Kodric-Brown & Brown, 1978; MacLean & Seastedt, 1979; Hixon, 1980; Myers *et al.*, 1981), reviewed by (Schoener, 1983). These models have sought to understand the functional significance of animal's movement behaviors by examining the costs and benefits of different movement strategies in different environments. Although these models addressed the issue of spatial occupation, their representations of space were largely implicit, with the definition of a territorial strategy usually equating to the statement

that “an individual occupies area of size  $x$ ” (though see also Stamps *et al.*, 1987).

More recently, a new class of models for understanding territorial patterns has emerged, in which explicit patterns of space-use are formally computed from underlying mechanistic descriptions of individual movement and interaction behavior (Benhamou, 1989; Lewis & Murray, 1993; White *et al.*, 1996; Moorcroft *et al.*, 1999). In contrast to the earlier optimization models, the representation of space-use in these models is fully explicit. Patterns of space-use are derived by a mathematical scaling of an underlying mechanistic model comprising of probabilistic rules for an individual's movement behavior. The scaling yields macroscopic equations for patterns of space-use, expressed in terms of a probability density function (pdf) for the expected location of each individual or group with coefficients that reflect the underlying mechanistic rules of individual movement behavior. The scaling approach

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used in spatially explicit models of territoriality has enabled them to successfully address the relationship between the movement and interaction behaviors of individuals and resulting patterns of space-use (White *et al.*, 1996; Lewis *et al.*, 1997). In addition, due to their spatially explicit nature, the models can also be used to perform mechanistic analyses of empirical home range patterns (Moorcroft *et al.*, 1999)—see Fig. 1.

Unlike the earlier optimization models however, the behavioral rules of movement within spatially explicit models of territoriality have, to date, been viewed as fixed properties of individuals. In this paper, we reconcile the optimization and spatially explicit approaches to understanding animal territories, analysing the fitness payoffs of different movement strategies for wolves in north-eastern Minnesota using a spatially explicit model of territoriality proposed by Lewis & Murray (1993).

Wolves (*Canis lupus*) in NE Minnesota live in packs which occupy and defend well-defined territories that are stable over long periods of time (Mech, 1973; Van Ballenberghe *et al.*, 1975) and as in other carnivores, scent marks are an important proximate cue used to indicate home range

occupation (Brown & MacDonald, 1985). Based on these observations, Lewis & Murray (1993) developed a spatially explicit model of territoriality consistent with these empirical observations, in which territories arise as a result of individuals exhibiting an avoidance response to the scent-marks of neighboring packs. In contrast to other wolf populations, the predator-prey dynamics in this region are relatively simple, closely approximating a single-predator, single-prey interaction. Wolf predation accounts for about 90% of known mortality of white-tailed deer (*Odocoileus virginianus*), and the deer provide approximately 70% of the typical wolf diet (Nelson & Mech, 1981).

Using a simplified implementation of the Lewis & Murray (1993) spatially explicit model, we examine the adaptive significance of wolf home-range patterns in NE Minnesota, analysing the costs and benefits that accrue from different movement behaviors when considering a tradeoff between utilization of an underlying prey resource (deer) and avoidance of hostile neighbors. We determine evolutionarily, the stable movement strategy for individuals that yields a pattern of space-use that is uninvadable by packs adopting alternative movement strategies. The results highlight the value of scent-marks as cues in the spatial partitioning of the deer prey resource between neighboring wolf packs. More generally, our work shows how it is possible to integrate mechanistic and functional investigations of animal movement patterns.

## Modeling

### MECHANISTIC HOME RANGE MODEL FOR WOLF PACKS

We analyse a simplified version of the model described in Section 3 of Lewis *et al.* (1997), considering a pairwise interaction between two packs, U and V of equal size in a single space dimension  $x$ . The pertinent state variables are the expected local densities of individuals in the two packs  $u(x, t)$  and  $v(x, t)$ , and their respective distributions of scent-marks  $p(x, t)$  and  $q(x, t)$ . Individuals within each pack exhibit the same movement behavior, having a random component of motion which describes foraging and patrolling behavior, and a directed component of

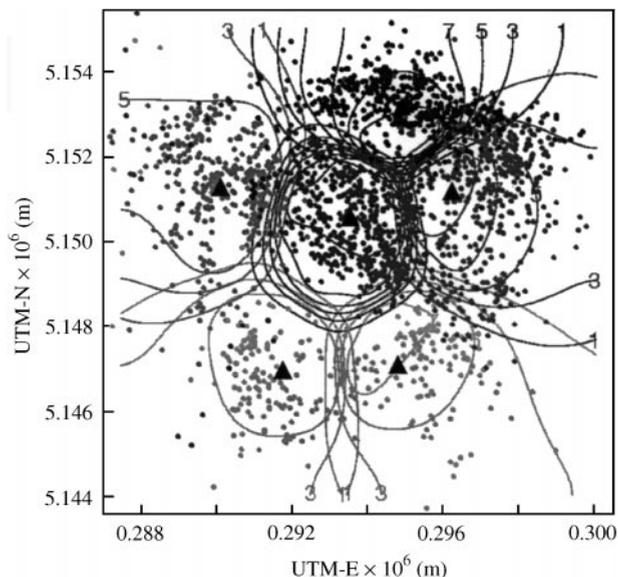


FIG. 1. Contour lines showing fit of the Lewis and Murray (1993) home-range model to relocation data (●) for six coyote packs at Hanford ALE collected by Crabtree (1989). The contour lines indicate the shape of the probability density function for each pack  $u(x, y)$  (contour interval is 2), and the home range centers for each pack are also shown (▲). Based on Moorcroft *et al.*, (1999).

motion towards their den site, located at opposing ends of a one-dimensional domain of length  $L$ . As they move, individuals scent-mark at a constant rate, and depending on the coefficients in model (see below), encounters with foreign scent-marks may increase the magnitude of their directional bias in movement towards their den site (Fig. 2).

*Movement Equations*

The macroscopic equations for the pattern of space use resulting from these underlying movement rules are as follows:

The parameters  $d_u$  and  $d_v$  govern the strength of random movement and  $c_u(q)$  and  $c_v(p)$  are non-decreasing, nonnegative functions describing the directed component of movement towards the den site. As shown in an earlier analysis, these parameters are related to the characteristics of individual movement; in particular the first and second moments of the joint distribution of movement speed and times between turns, and the sensitivity of an individuals distribution of turning angles to encounters with foreign scent-marks (Moorcroft, 1997).

Pack U density: $\underbrace{\frac{\partial u}{\partial t}}_{\text{local density change}} = \underbrace{d_u \frac{\partial^2 u}{\partial x^2}}_{\text{random motion}} + \underbrace{\frac{\partial}{\partial x} c_u(q)u}_{\text{directed motion}}.$ (1)
Pack V density: $\underbrace{\frac{\partial v}{\partial t}}_{\text{local density change}} = \underbrace{d_v \frac{\partial^2 v}{\partial x^2}}_{\text{random motion}} - \underbrace{\frac{\partial}{\partial x} c_v(p)v}_{\text{directed motion}}.$ (2)

with boundary conditions

$$d_u \frac{\partial u}{\partial x} + c_u(q) = d_v \frac{\partial v}{\partial x} - c_v(p)v = 0 \quad \text{at } x = 0, L \tag{3}$$

indicating that the movements and interaction occur in the finite enclosed region between  $0 \leq x \leq L$ . These ‘zero-flux’ boundary conditions conserve the total number of individuals so that

$$\int_0^L u(x, t) dx = U_0 \quad \int_0^L v(x, t) dx = V_0, \tag{4}$$

where  $U_0 = V_0$  are the fixed number of individuals in packs U and V.

Lewis *et al.* (1997) considered generalized functions for the directed components of motion back to the den sites  $c_u(q)$  and  $c_v(p)$ . Here, we consider the simple case where  $c_u(q)$  and  $c_v(p)$  are linear functions of foreign scent mark density (Fig. 3).

$$c_u(q) = \gamma_{u1} + \gamma_{u2}q, \tag{5}$$

$$c_v(p) = \gamma_{v1} + \gamma_{v2}p, \tag{6}$$

*Scent-mark Equations*

For simplicity we assume that individuals mark at a constant rate  $l$ . Thus, at every point  $x$  in spaces the following ordinary differential equations describe production and decay of marks:

Pack U marks: $\underbrace{\frac{\partial p}{\partial t}}_{\text{local density change}} = \underbrace{lu}_{\text{deposition by U individuals}} - \underbrace{fp}_{\text{decay}}.$ (7)
Pack V marks: $\underbrace{\frac{\partial q}{\partial t}}_{\text{local density change}} = \underbrace{lv}_{\text{deposition by V individuals}} - \underbrace{fq}_{\text{decay}},$ (8)

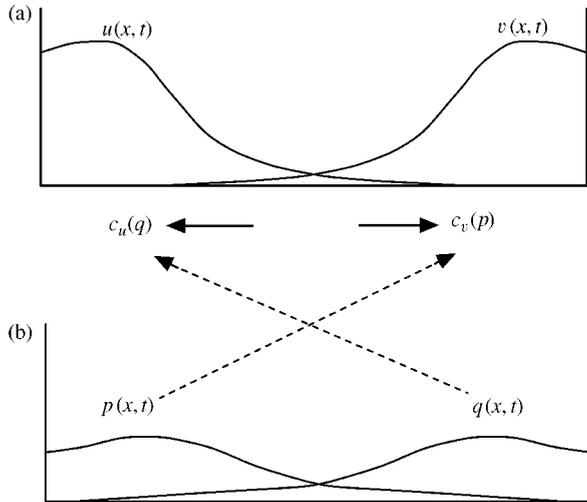


FIG. 2. Schematic illustrating the movement and interaction rules of the underlying Lewis and Murray (1993) spatially explicit territoriality model (eqns (1) and (2)), shown for the simple case of a pair of packs, U and V moving on a one-dimensional landscape. The expected location of the individuals in the two groups is indicated by the probability density functions  $u(x, t)$  and  $v(x, t)$ . The movement of individuals comprises both a random component and an avoidance response arising from encounters with foreign scent marks. The density of scent marks by the two groups at each point in space is given by the functions  $p(x, t)$  and  $q(x, t)$ , respectively. As individuals move, their avoidance response to foreign scent marks increases their probability of turning towards their respective den-sites, located at opposing ends of the domain. This response results in the U and V packs having directed component of motion  $c_u(q)$  and  $c_v(p)$  that act towards their home range centers, the strength of the directed motion varying in magnitude depending on the local density of foreign scent-marks encountered ( $q$  or  $p$ , respectively).

where parameters  $l$  and  $f$  are the rate of scent-mark production by individuals and the rate of scent-mark decay, respectively.

PATTERNS OF SPACE-USE

Solutions  $u(x, t)$ ,  $v(x, t)$ ,  $p(x, t)$  and  $q(x, t)$  for eqns (1)–(6) reach a time-independent steady state which depends only upon spatial location  $x$ :  $u(x)$ ,  $v(x)$ ,  $p(x)$  and  $q(x)$ . The solutions of eqns (7) and (8) show that the expected scent-mark density faithfully reflects the expected density of individuals ( $p(x) = lu(x)/f$  and  $q(x) = lv(x)/f$ ) and thus constitute ‘honest’ signals of space use (Johnstone, 1997). Integration of eqns (1) and (2), application of the boundary conditions (3) and the prescribed movement functions (5) and (6) and non-dimensionalization yield the following

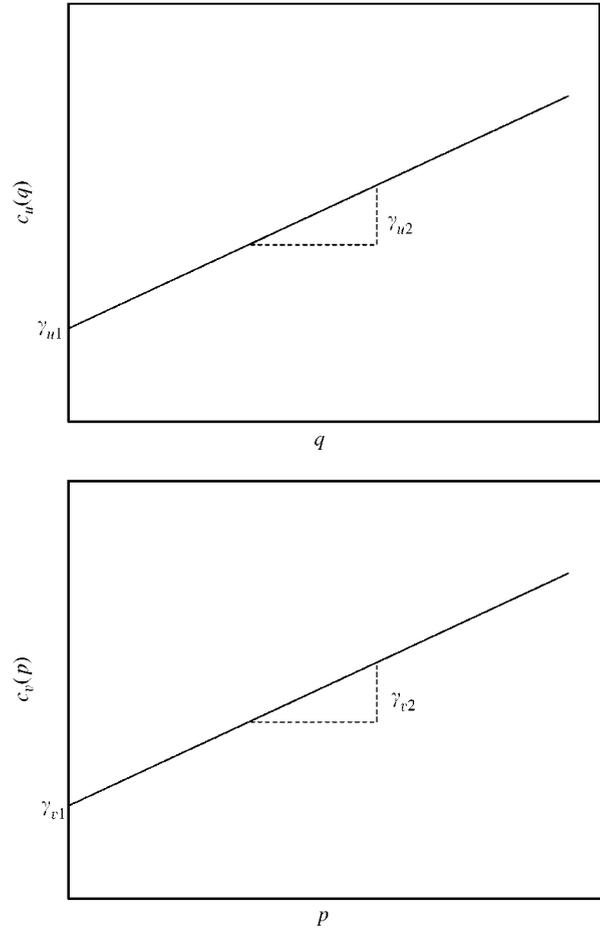


FIG. 3. Functional forms for the directed movement responses  $c_u(q)$  and  $c_v(p)$ . The parameters  $\gamma_{u1}$  and  $\gamma_{v1}$  govern the magnitude of the fixed bias movement direction of individuals in packs U and V, respectively while the parameters  $\gamma_{u2}$  and  $\gamma_{v2}$  govern the sensitivity to scent-marks of the other pack [eqns (5) and (6)]. In the non-dimensionalized equations [eqns (9) and (10)] the magnitude of the movement terms is scaled by the strength of the pack’s random component of motion (given by the values of  $d_u$  and  $d_v$ , respectively).

ODEs of the pattern of space-use by the two groups:

$$\frac{\partial u}{\partial x} = -(\gamma_{u1} + \gamma_{u2}v)u, \tag{9}$$

$$\frac{\partial v}{\partial x} = (\gamma_{v1} + \gamma_{v2}u)v, \tag{10}$$

where

$$u^* = \frac{u}{U_0}, \quad v^* = \frac{v}{V_0}, \quad x^* = \frac{x}{L},$$

$$\gamma_{u1}^* = \frac{L\gamma_{u1}}{d_u}, \quad \gamma_{u2}^* = \frac{L\gamma_{u2}l}{d_u f U_0},$$

$$\gamma_{v1}^* = \frac{L\gamma_{v1}}{d_v}, \quad \gamma_{v2}^* = \frac{L\gamma_{v2}l}{d_v f V_0}$$

and asterisks have been dropped in eqns (9) and (10) for notational simplicity.

Parameters  $\gamma_{u1}$ ,  $\gamma_{v1}$ ,  $\gamma_{u2}$  and  $\gamma_{v2}$  describe the movement behaviors of the individuals within the two packs. In the non-dimensionalization, parameters,  $\gamma_{u1}^*$  and  $\gamma_{v1}^*$  reflect the magnitude of the fixed bias in an individual's movement direction ( $\gamma_{u1}$  and  $\gamma_{v1}$ ) relative to the strength of its random motion ( $d_u$  and  $d_v$ ). Similarly,  $\gamma_{u2}^*$  and  $\gamma_{v2}^*$  reflect the magnitude of the bias in an individual's movement direction caused by encounters with foreign scent-marks ( $\gamma_{u2}$  and  $\gamma_{v2}$ ) relative to the strength of its random motion ( $d_u$  and  $d_v$ ). The constraints (3) and (4) retain the same form, but the constants  $L$ ,  $U_0$  and  $V_0$  in the equation are now unity. Under this non-dimensionalization,  $u(x)$  and  $v(x)$  become probability density functions for the expected location of individuals in the two packs, and the size of the region has been rescaled to be length 1. Thus, the probability density functions  $u(x)$  and  $v(x)$  for expected space-use are determined by solving eqns (9) and (10) subject to the non-dimensionalized integral conditions (11),

$$\int_0^1 u(x) dx = \int_0^1 v(x) dx = 1. \quad (11)$$

It is interesting to consider some special cases of solutions to eqns (9) and (10). First, if there is no increase in movement towards the den in the presence of foreign scent-marks ( $\gamma_{u2} = \gamma_{v2} = 0$ ), then the solution to eqns (9) and (10) and eqn (11) is given by

$$u(x) = \gamma_{u1} \exp(-\gamma_{u1}x)/(1 - \exp(-\gamma_{u1})), \quad (12)$$

$$v(x) = \gamma_{v1} \exp(-\gamma_{v1}(1-x))/(1 - \exp(-\gamma_{v1})). \quad (13)$$

This solution, in which individuals exhibit a constant bias in movement direction toward their home range center and do not respond to foreign

scent-marks, is Holgate's (1971) home range model. We refer to this as the 'pure home range' case (Fig. 4).

Second, if there is no bias in movement towards the den site in the absence of foreign scent-marks then eqns (9) and (10) become

$$\frac{\partial u}{\partial x} = -\gamma_{u2}uv, \quad (14)$$

$$\frac{\partial v}{\partial x} = \gamma_{v2}uv. \quad (15)$$

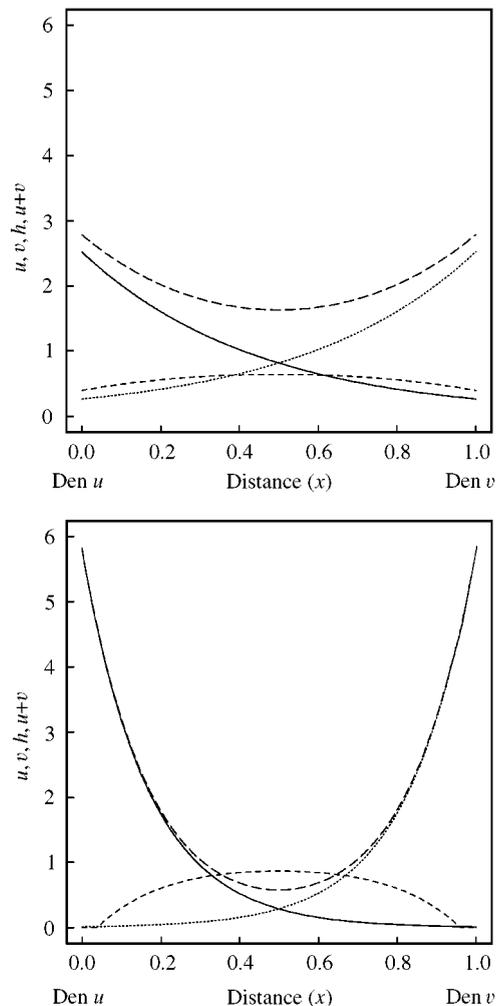


FIG. 4: Pure home range model. Shown are solutions to the Holgate model eqns (12) and (13) with  $\gamma_{u1} = \gamma_{v1} = 2.26$  (top) (—)  $u$ ; (---)  $v$ ; (.....)  $h$ ; (-.-)  $u + v$  and  $\gamma_{u1} = \gamma_{v1} = 6$  (bottom), (—)  $u$ ; (---)  $v$ ; (.....)  $h$ ; (-.-)  $u + v$ , and the resulting spring distributions of deer  $h(x, 0)$ , calculated by (A.4) with  $\lambda = 2$  and  $\psi = 0.15$ . Note that the deer distribution  $h(x)$  is lowest where the total wolf density is highest—near the densites at either end of the domain.

We refer to this as the ‘pure territorial’ case, since space partitioning is governed only by interactions via foreign scent-marks. Note that for the symmetric behavior case ( $\gamma_{u2} = \gamma_{v2} = \gamma_2$ ), adding these equations and applying the conservation condition (11) shows that  $u(x) + v(x) = 2$  for all  $0 \leq x \leq 1$ . Thus, the territories are given by solutions to two logistic equations with space  $x$  as the independent variable:

$$\frac{\partial u}{\partial x} = -\gamma_2 u(2 - u), \quad \frac{\partial v}{\partial x} = \gamma_2 v(2 - v) \quad (16)$$

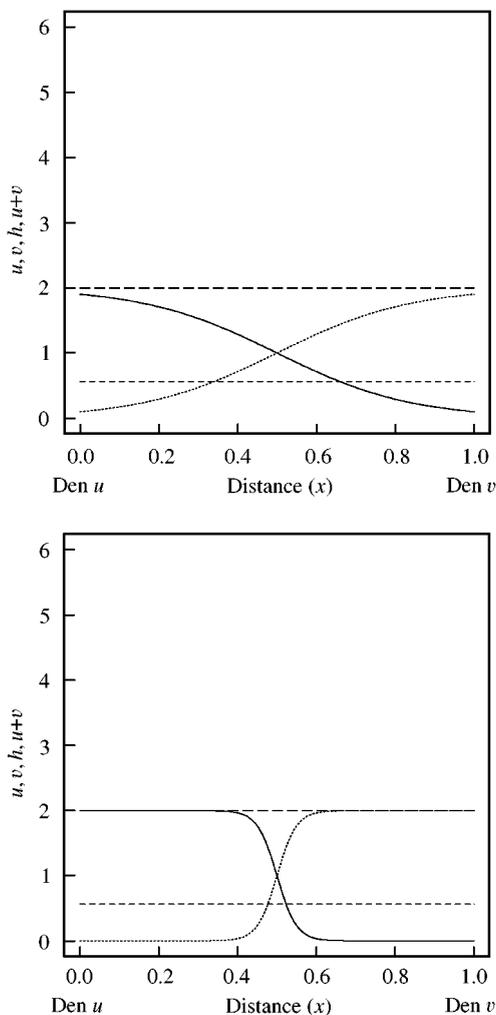


FIG. 5. Pure territorial model. Shown are territorial solutions for  $u(x)$  and  $v(x)$  given eqns (11) and (16) with  $\gamma_2 = 2.95$  (top) (—)  $u$ ; (.....)  $v$ ; (-----)  $h$ ; (- - -)  $u + v$ , and  $\gamma_2 = 20.0$  (bottom) (—)  $u$ ; (.....)  $v$ ; (-----)  $h$ ; (- - -)  $u + v$ , and the resulting spring distribution of deer  $h(x, 0)$ , calculated by (A.4) with  $\lambda = 2$  and  $\psi = 0.15$ . Notice that the deer distribution  $h(x)$  is uniform throughout the domain.

(Fig. 5). The initial conditions  $u(0)$  and  $v(0)$  to this system are chosen to satisfy the integral constraints (11).

FITNESS FUNCTION

We assume that the costs and benefits associated with individuals adopting a particular movement strategy are determined by the effect of the resulting pattern of space-use on resource acquisition and on the frequency of aggressive interactions with neighboring packs. As in many carnivore societies, wolf packs have strong dominance hierarchies with alpha females and males dominating the behavior of subordinates (Sheldon, 1992). While intra-pack interactions can be complex, we propose that a reasonable initial assumption is to assume that the packs operate as cohesive units, maximizing the expected number of offspring produced single year by the alpha female. Although subordinates may attempt to mate, this is rarely successful and females typically retain the alpha status for several years (Mech, 1966; Peterson *et al.*, 1984; Ballard *et al.*, 1987; Fuller, 1989).

The expected number of offspring produced in a single year by a pack alpha female with space-use  $u(x)$  is given by her geometric growth rate  $R_u$  where

$$R_u = \underbrace{S}_{\text{survivorship}} \cdot \underbrace{N_u}_{\text{offspring produced}} \quad (17)$$

where  $S$  is the probability that the alpha female survives the year to breed in spring, and  $N_u$  is the number of offspring surviving weaning, given that the alpha female breeds.

Given the spatial distribution of prey  $h(x, t)$  (A.3), we assume that yearly offspring production  $N_u$  is a simple function of prey intake

$$N_u = \sigma\psi \int_0^1 u(x)H(u(x), v(x)) dx, \quad (18)$$

where  $\sigma$  is the rate of conversion of prey into offspring,  $\psi$  is the prey encounter rate and  $H(u(x), v(x))$  is the average prey density during the year given the packs have patterns of space use  $u(x)$  and  $v(x)$ .  $H(u(x), v(x))$  is calculated using a simple

model for the spatial dynamics of the white-tailed deer population, the major prey species in this region (see eqn A.5 in Appendix A).

We assume that the probability of a wolf being killed as a result of inter-pack aggression as being proportional to the local encounter rate between individuals in the two packs  $\alpha u(x)v(x)$ .

The overall death rate  $\mu$  is then given by

$$\mu = \mu_0 + \alpha \int_0^1 u(x)v(x) dx, \quad (19)$$

where  $\mu_0$  is the natural mortality rate.

This yields the basic reproductive ratio  $R$

$$R_u = \underbrace{\exp\left(-\mu_0 - \alpha \int_0^1 u(x)v(x) dx\right)}_{\text{survivorship}} \underbrace{\left(\sigma\psi \int_0^1 u(x)H(u(x), v(x)) dx\right)}_{\text{offspring produced}} \quad (20)$$

and hence

$$r_u = -\mu_0 + \ln(\sigma\psi) - \alpha \int_0^1 u(x)v(x) dx + \ln\left(\int_0^1 u(x)H(u(x), v(x)) dx\right) \quad (21)$$

describes the fitness payoff, in terms of a reproductive rate, for pack U. The payoff for pack V,  $r_v$ , is given by interchanging  $u(x)$  and  $v(x)$  in the above formula.

We refer to  $r_u$  and  $r_v$  as ‘fitness functions’. A more complete measure of fitness would account for relatedness between the offspring and the alpha female, the future reproductive potential of the alpha female (due to reproduction in later years) and variation in population size. However, since these would further complicate the model, we do not pursue them further.

PARAMETER VALUES

The fitness payoffs  $r_u$  and  $r_v$  depend on the density of the deer population, the relationship between resource intake and offspring production and the costs of aggressive interactions between individuals in neighboring packs. We parameterized the model of deer density and spatial

distribution to give realistic estimates for the mortality due to predation and the deer recruitment rate (see Appendix A). The value of the mortality parameter  $\alpha$  is difficult to estimate directly, since the overall mortality rate will depend on the level of home-range overlap, however recent empirical studies have shown that the costs of inter-pack aggression are high (Mech, 1994). We assume that if the two packs interacted uniformly over the region with no avoidance behavior then each alpha female would have a 50% chance of surviving aggressive interactions [ $\alpha = 0.69$  in eqn (19)]. For typical degrees of overlap obtained in the ESS analysis, this gives

mortality rates consistent with empirical estimates which suggest that inter-pack aggression accounts for  $\sim 10\%$  of adult deaths (Mech, 1994).

The natural mortality rate  $\mu_0$  and the rate conversion of prey into offspring  $\sigma\psi$  yield additive constants in formula (21) and hence their values do not affect the evolutionarily stable values of  $\gamma_1$  and  $\gamma_2$ . However we can estimate  $-\mu_0 + \ln(\sigma\psi)$  by calculating reasonable values for the fitness function (21). Suppose the deer are at carrying capacity  $H = 1$  and there are no interactions with hostile neighbors  $\alpha = 0$ . Under these conditions we estimate that the basic reproductive ratio is approximately 5 (Van Ballenberghe *et al.*, 1975; Fuller, 1989). Substituting this value and the value  $\mu$  into eqn (20) gives  $-\mu_0 + \ln(\sigma\psi) = \ln(5)$ . This is the value that we use when calculating the fitness surfaces (see below).

Analysis

We assume that the parameters describing predator-prey interactions, wolf-wolf mortality and conversion efficiency from deer into offspring are fixed. We then determine the values of the movement parameters,  $\gamma_1$  and  $\gamma_2$ , that maximize the fitness payoff functions  $r_u$  and  $r_v$ , subject to

these constraints, assuming a competitive game between the two packs. Increasing space-use by either pack involves a tradeoff between foraging widely for deer (facilitated by low  $\gamma_1$  and  $\gamma_2$ ) and avoiding neighbors (facilitated by high  $\gamma_1$  and  $\gamma_2$ ).

We first determine the evolutionarily stable strategies for the pure home range [eqns (12) and (13)] and pure territorial [eqns (14) and (15)] models.

PURE STRATEGIES

The evolutionarily stable strategy arising for the pure home range case ( $\gamma_{u2} = \gamma_{v2} = 0$ ) is defined by a single value  $\gamma_{1*}$ , such that if individuals in both packs have movement behavior  $\gamma_{1*}$  (i.e.  $\gamma_{u1} = \gamma_{v1} = \gamma_{1*}$ ), a change in behavior by a pack (i.e a change in either  $\gamma_{u1}$  or  $\gamma_{v1}$ ) will result in reduced fitness for that pack. In this sense, the value  $\gamma_{1*}$  is uninvadable by other  $\gamma_1$  values and therefore represents a evolutionarily stable strategy or ESS (Maynard-Smith, 1974) of movement behavior. In a similar way, the evolutionarily stable movement strategy for the pure territorial model ( $\gamma_{u1} = \gamma_{v1} = 0$ ) is defined by individuals in both packs having movement behavior  $\gamma_{u2} = \gamma_{v2} = \gamma_{2*}$ , and that a change in the value of  $\gamma_2$  by a pack will result in reduced fitness for that pack.

Note that in technical terms, our ESS criterion is for a ‘game against the field’ as opposed to a pairwise game in which packs attempt to maximize a fitness differential ( $r_u - r_v$ ). Since in natural populations, packs may have up to six neighboring packs (Peters & Mech, 1975; Peterson *et al.*, 1984; Ballard *et al.*, 1987; Fuller, 1989), we propose that ‘a game against the field’ is the more appropriate caricature of the natural system where a game is being waged in space two dimensions against multiple neighbors.

We calculated the evolutionarily stable movement strategies for the pure home-range case ( $\gamma_{u2} = \gamma_{v2} = 0$ ), and pure territorial case ( $\gamma_{u1} = \gamma_{v1} = 0$ ) by numerically evaluating the fitness function (21) subject to eqns (12,13) and (14,15) respectively (Figs 6 and 7). The ESSs were determined in the following way. For each value of  $\gamma_{vi}$  (where the subscript  $i$  indicates the pure home range ( $i = 1$ ) or pure territorial case ( $i = 2$ )), the maximum value of the fitness function for pack U,  $r_u$  [eqn (21)], is shown with a dot. The

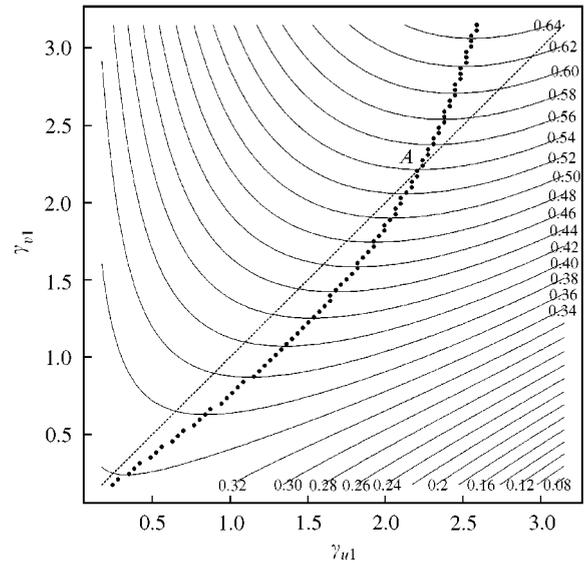


FIG. 6. Evolutionarily stable strategy for Holgate’s (1971) pure home-range model [eqns (12) and (13)]. Isoclines show the level curves of the fitness payoff function for the U pack  $r_u$  [eqn (21)] as a function of the movement strategy of the individuals of the V pack  $\gamma_{v1}$  and the movement strategy for the individuals in the U pack  $\gamma_{u1}$ . Solid dots indicate values of  $\gamma_{u1}$  yielding the maximum value of  $r_u$  for each value of  $\gamma_{v1}$ . The point at which the ridge delineated by solid dots crosses the 1:1 line defines the evolutionarily stable strategy (ESS). Thus the ESS is  $\gamma_{1*} = 2.26$  (Point A) which yields a fitness payoff of  $r = 0.55$ . The resulting pattern of home ranges are shown in Fig. 4(a).

resulting ridge of dots crosses the  $\gamma_{vi} = \gamma_{ui}$  line at a point whose coordinates define the competitively stable value of  $\gamma_1$  or  $\gamma_2$ . By symmetry, the equivalent ridge describing the best movement behavior for individuals in pack V in response to U pack individuals having movement strategy  $\gamma_{u1}$  crosses the 1:1 line at the same point. At this intersection point, individuals in both packs will do worse if they adopt an alternative behavior and therefore the intersection point constitutes an evolutionarily stable movement strategy and the resulting pattern of space-use.

TERRITORIAL VERSUS HOME RANGE  
MOVEMENT STRATEGIES

Comparison of the evolutionarily stable patterns of space-use for the two models shows that a pure territorial movement strategy results in higher fitness for both packs than a pure home range movement strategy ( $r_u, r_v = 0.62$  vs.  $r_u,$

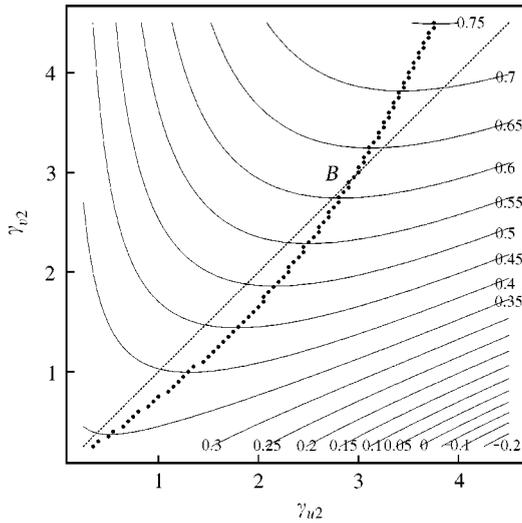


FIG. 7. Evolutionarily stable strategy for pure territorial model [eqns (14) and (15)]. Isoclines show the level curves of the fitness payoff function of pack U  $r_u$  (21) as a function of the movement strategy of individuals in pack V ( $\gamma_{v2}$ ) and the movement strategy of individuals in pack U ( $\gamma_{u2}$ ). Solid dots indicate the values of  $\gamma_{u2}$  that maximize the value of  $r_u$  for  $\gamma_{u2}$  value. The point at which the ridge delineated by the dots crosses the 1 : 1 line defines the evolutionarily stable movement strategy for the two packs. Thus the ESS is  $\gamma_{2*} = 2.95$  (Point B) which yields a fitness payoff  $r_u = 0.62$ . The resulting pattern of home ranges is shown in Fig. 5(a).

$r_v = 0.55$ , see Figs 6 and 7). This is in part due to a more complete utilization of the available prey resource than the pure home-range model [see Figs 4(a) and 5(a)]. However, in addition, the pure territorial movement strategy yields sharper edges in the  $u(x)$  and  $v(x)$  profiles, reducing home-range overlap between the two packs that lowers the rate of interaction between the packs, increasing survivorship [see Figs 4(a) and 5(a)]. As a result of these two effects, the fitness of individuals in both packs is higher if individuals adopt a territorial movement strategy in which the magnitude of directed movement varies in relation to foreign scent-marks, rather than having a directed component of motion of fixed magnitude.

We next consider whether these pure strategies are invasable by a more general strategy that combines a fixed component of motion with a territorial response to scent-marks. This procedure is more complex as it involves potential changes in two components of movement behavior by each pack. In order to determine whether any  $\gamma_1, \gamma_2$  combinations are an ESS, we need

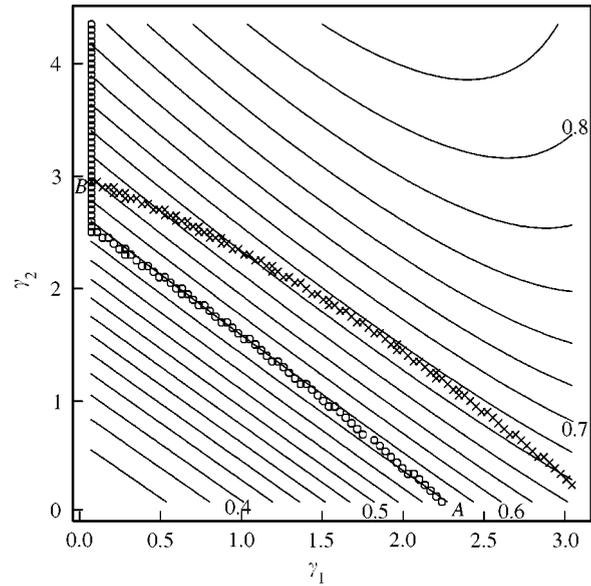


FIG. 8. The necessary condition for an ESS for the combined strategy model [eqns (9) and (10)], is that the ridges of “x”s and “o”s intersect. The ridge of “o”s shows values of  $\gamma_1$  and  $\gamma_2$  for which the fitness of the pack will decrease if it changes its  $\gamma_1$  and the ridge of “x”s shows values for which the fitness of the pack will decrease if it changes its  $\gamma_2$ . The two ridges intersect at  $\gamma_1 = 0, \gamma_2 = 2.95$ , which is marked by the letter B. Refer also to points A and B in Figs. 6 and 7.

to consider the fitness consequences of individuals in either of the packs changing their values of  $\gamma_1$  and  $\gamma_2$ . Two necessary (though not sufficient) criteria for a combined ESS are that the pack’s fitness decreases if it changes its value of  $\gamma_1$  and its fitness decreases if it changes its value of  $\gamma_2$ .

Figure 8 shows potential symmetric strategies  $\gamma_{u1} = \gamma_{v1} = \gamma_1$  and  $\gamma_{u2} = \gamma_{v2} = \gamma_2$ . The ridge of “o”s shows values for which the fitness of pack U will decrease if it changes its  $\gamma_{u1}$  value incrementally and the ridge of “x”s shows values for which the fitness of pack V will decrease if it changes its  $\gamma_{u2}$  value incrementally. Allowable incremental changes for the  $\gamma_{u1}$  value are (i) a small increase in  $\gamma_{u1}$  along boundary  $\gamma_{u1} = 0$  and (ii) a small increase or decrease in  $\gamma_{u1}$  elsewhere. Allowable incremental changes for the  $\gamma_{u2}$  value are (i) a small increase in  $\gamma_{u2}$  along boundary  $\gamma_{u2} = 0$  and (ii) a small increase or decrease in  $\gamma_{u2}$  elsewhere.

The ridges of “o”s and “x”s intersect at  $\gamma_1 = 0, \gamma_2 = 2.95$ , the pure territorial ESS (point B on Fig. 8—see also Fig. 7), suggesting that this is the

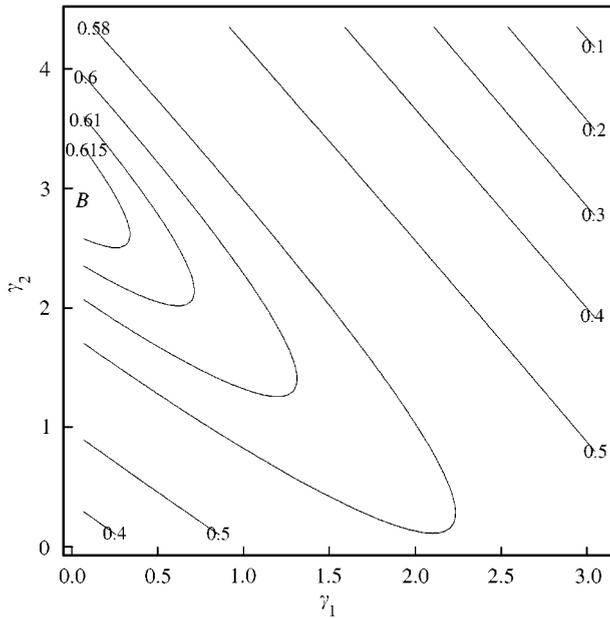


FIG. 9. Fitness payoff  $r_u$  for pack U as a function of  $\gamma_{u1}$  and  $\gamma_{u2}$  given that pack V has the pure home range strategy identified in Fig. 7 ( $\gamma_{v1} = 0$ ,  $\gamma_{v2} = 2.95$ ). Point B ( $\gamma_{u1} = 0$ ,  $\gamma_{u2} = 2.95$  in the figure) corresponds to B in Fig. 8. At B, the strategy and fitness of pack U matches that of pack V so that  $r_u = r_v = 0.62$ . All other possible strategies by pack U however yield lower fitness, demonstrating that pure home range strategy  $\gamma_1 = 0$ ,  $\gamma_2 = 2.95$  is stable to invasion and thus an ESS for the combined strategy model, [eqns (9) and (10)].

ESS for the combined strategy model. Figure 9 confirms this, showing how the fitness payoff to Pack U varies a function of  $\gamma_{u1}$  and  $\gamma_{u2}$  given that pack V has the pure territorial strategy defined by point B ( $\gamma_{v1} = 0$ ,  $\gamma_{v2} = 2.95$ ). In all points other than point B, pack U has a reduced fitness payoff confirming that the pure territorial strategy ( $\gamma_1 = 0$ ,  $\gamma_2 = 2.95$ ) is an ESS for a combined strategy model (Fig. 7).

### Discussion

In our analysis of a simple, mechanistic model of wolf home ranges, the evolutionarily stable movement strategy for individuals uses foreign scent-marks to modulate movement towards interior of the home range ( $\gamma_{1*} = 0$ ,  $\gamma_{2*} = 2.95$ ). Alternative strategies that include a ‘built in’ bias towards the den site ( $\gamma_1 > 0$ ) cannot invade this ‘pure territorial’ strategy.

The ESS for the pure territorial model [eqns (14) and (15)] satisfies the logistic model [eqn

(16)] with ( $\gamma_2 = \gamma_{2*} = 2.95$ ). Here  $u(x) + v(x) = 2$ , so that the prey density  $h(x)$  is uniform in space. This pattern of space-use yields higher fitness than the simple home range strategy ( $r_u, r_v = 0.62$  versus  $r_u, r_v = 0.55$ ). Note that the optimal, as opposed to evolutionarily stable, strategy would be to allow  $\gamma_2 \rightarrow \infty$  so that overlap in the solutions to eqn (16) approaches zero and the solutions approach

$$u(x) = 2(1 - H(x - 0.5)), \quad v(x) = 2H(x - 0.5),$$

where  $H(\cdot)$  is the Heaviside step function ( $H(x) = 0$  for  $x < 0$ ,  $H(x) = 1$  for  $x \geq 0$ ). Under this scenario, there are no aggressive interactions with neighboring packs, space is completely and equitably partitioned and both packs have higher fitness ( $r_u = r_v = 1.03$ ). However, at least for parameters given here for wolves, this optimal strategy is not stable and can be invaded by a  $\gamma_2 > 0$  strategy. The territorial overlap that arises from the evolutionarily stable movement strategy shown in Fig. 7, gives rise to aggressive encounters which confer stability on the patterns of space-use by the two packs.

A heuristic explanation for the pure territorial movement strategy ESS, is that, in the absence of foreign scent-marks, packs with this ESS movement behavior expand their space-use [via simple diffusion see eqns (1) and (2)] to fill the room available. In contrast, alternate ‘pure home range’ or ‘combined’ strategies with a built-in bias towards the den site, stop expanding when the directed and random components of motion balance, even in the absence of foreign scent-marks [see eqns (12) and (13) and Fig. 4 for appropriate functional forms for the pure ‘home-range’ pattern of space use]. In this senses ‘home range’ and ‘combined’ strategies do not fully avail themselves of the opportunity to utilize space that is relatively unoccupied by neighbors.

As we noted earlier, since individuals scent-mark at a constant rate, the spatial distribution of scent-marks is an accurate reflection of the pattern of space-use and therefore constitutes an ‘honest signal’ (Johnstone, 1997). A variation on eqns (7) and (8), proposed by Lewis and Murray (1993), allows for increased scent-marking rates in the presence of foreign scent-marks. The result

is a 'bowl-shaped' scent-mark distribution with the edges of the scent-mark 'bowl' at the interaction zone between territories. This in turn, gives rise to a 'buffer zone'—an area of low space use between the packs. In this case, scent-marks are no longer an accurate reflection of space-use: scent-mark levels are highest at the edge of the territories where space-use declines (Fig. 10). We are now investigating whether the 'pure territorial' strategy remains an ESS in this situation. It may be that increased sensitivity of marking rates to foreign scent-marks will heighten scent levels in the interaction zone between territories and 'bluff' neighboring packs into retreating.

More generally, our study shows how mechanistic home range models can be used to investigate the adaptive significance of animal home range patterns. In contrast to earlier costs and benefit analyses in which concepts of space were implicit, mechanistic ESS analyses take explicit account of the relationships between movement behavior, resulting patterns of space-use and the subsequent fitness of individuals. In addition, the spatially explicit nature of the models used in

mechanistic ESS analysis permits direct comparison to empirical home range patterns (for example Fig. 1), offering a promising way to integrate theoretical investigations into the functional significance of home range patterns with empirical measurements of animal movement.

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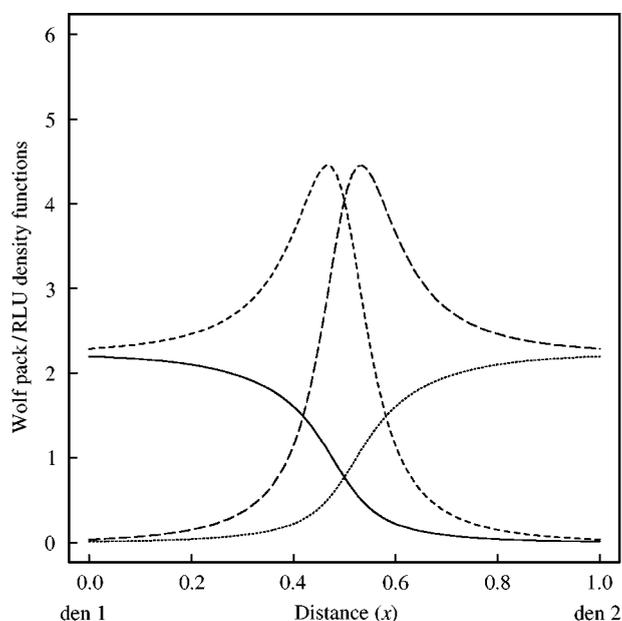


FIG. 10. The expected patterns of space-use [ $u(x)$ ,  $v(x)$ ], and scent mark distributions [ $p(x)$ ,  $q(x)$ ] when scent-marking rate increases in response to foreign scent-marks [based on Lewis *et al.* (1997)]. Note that this gives rise to a bowl-shaped scent-mark distribution in which scent-marks no longer an "honest" pattern of space-use. (—) Pack 1 ( $u$ ); (.....) pack 2 ( $v$ ); (-----) RLU 1 ( $p$ ); (---) RLU 2 ( $q$ ).

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## APPENDIX A

### A Model for the Spatial Distribution of Deer

The major prey species for wolf populations in Minnesota are white-tailed deer *Odocoileus virginianus*. Wolf predation is a major factor affecting white-tailed deer densities across the region, accounting for 90% of all known deaths (Nelson & Mech, 1981). We use the model proposed by Lewis and Murray (1993) for the spatial distribution of the deer population which makes the following assumptions: (i) wolf territories are stationary and stable; (ii) Holling Type I (linear) functional response of wolf predation to local deer density

$$\frac{\partial h}{\partial t} = -\psi(u(x) + v(x))h, \quad (\text{A.1})$$

where  $h(x, t)$  is the deer density,  $u(x)$  and  $v(x)$  are the expected densities of space-use by pack U and pack V wolves, and  $\psi$  is the predation rate. (iii) production of deer each spring given by Beverton-Holt density-dependent population dynamics

$$h(T^+, x) = \frac{\lambda h(T^-, x)}{1 + (\lambda - 1)h(T^-, x)/K}, \quad (\text{A.2})$$

where  $h(T^-, x)$  and  $h(T^+, x)$  are the local density of deer immediately prior to and after the spring birth, and  $\lambda > 1$  and  $K$  are the growth rate and carrying capacity of the deer in the absence of predation.

During the year, predation by wolves according to eqn (A.1) reduces deer numbers such that the population immediately prior to the spring birth in the following year is

$$h(T + 1^-, x) = h(T^+, x) \exp(-\psi[u(x) + v(x)]), \quad (\text{A.3})$$

A ‘steady-state’ solution, which gives no change in density from spring to spring, satisfies  $h(T + 1^+, x) = h(T^+, x)$ . Substituting eqns (A.1) and (A.2) into eqn (A.3) and satisfying this condition yields the spring deer density immediately after birth as

$$h(T^+, x) = \max \left\{ 0, \frac{\lambda - \exp(\psi[u(x) + v(x)])}{\lambda - 1} \right\}, \quad (\text{A.4})$$

where  $h^* = h/K$  is the non-dimensionalized deer density and the asterisk on  $h^*$  has been dropped for notational convenience.

Integrating (A.4) from  $T$  to  $T + 1$  yields the average deer density  $H(u(x), v(x))$  throughout the year

$$H(u(x), v(x)) = \max \left\{ 0, \frac{(\lambda - \exp([u(x) + v(x)]\psi))}{\lambda - 1} \times \frac{(1 - \exp(-\psi(u(x) + v(x))))}{\psi(u(x) + v(x))} \right\}. \quad (\text{A.5})$$

### PARAMETERS

The growth ratio  $\lambda$  in eqn (A.2) was chosen as  $\lambda = 2$  giving recruitment rates consistent with empirical estimates of 30% per annum (Nelson & Mech, 1981) at approximately 60% of carrying capacity (the typical equilibrium population level, for example see Fig. 5).

The predation rate  $\psi$  was estimated assuming that deer have a mean lifespan of approximately

seven years, consistent with empirical estimates (Nelson & Mech, 1981), and giving individual deer a 10–15% chance of being killed each year. The precise probability upon location of the deer in relation to the wolf home ranges. For the case where the interactions are pure territorial and symmetric [eqn (16)], the predation pressure is uniform across the region ( $u(x) + v(x) = 2$ ). Here,

a choice of  $\psi = 0.15$  yields the probability of surviving a year as

$$\frac{1 - \exp(-\psi(u(x) + v(x)))}{\psi(u(x) + v(x))} \approx 0.86, \quad (\text{A.6})$$

and thus a 14% chance of being killed each year.