LINEAR APPROACHES TO SPATIAL OPTIMIZATION

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ABSTRACT.—This paper documents formulations for four different spatial optimization problems that use linear (continuous-variable) programming. For more discussion on these problems, the models, and case study results, the reader is referred to our forthcoming papers: Bevers et al (1997), Hof et al. (in preparation), Hof (in review), and Hof and Raphael (in press).

THE BLACK-FOOTED FERRET

Early in 1987 the black-footed ferret (*Mustela nigripes*) became one of the world's most endangered mammals when the last known free-ranging member of the species was taken into captivity. The Wyoming Game and Fish Department was successful in breeding six of the surviving ferrets, setting the stage for a national recovery program of releasing captive-bred ferrets back into the wild. The first release of captive-bred black-footed ferrets occurred in 1991 in Shirley Basin, Wyoming. Two additional reintroduction areas were added in 1994, including the site of our study, the federally managed lands of the Buffalo Gap National Grassland adjacent to the Badlands National Park.

Available evidence strongly supports the conclusion that black-footed ferrets have narrow habitat requirements, living principally in prairie dog burrows and depending primarily on prairie dogs for prey (Linder et al., 1972). The spatial arrangement of prairie dog colonies in a colony complex has important effects on the number of black-footed ferrets that can be supported (Minta and Clark 1989). As prairie dog colonies become smaller or more widely separated, successful ferret dispersal between colonies is less likely and the total population that can be supported is reduced.

Within the reintroduction area, black-footed ferret habitat comprises a complex of active and potential prairie dog colonies (patches) forming distinct habitat "islands" on the landscape. The approach described here is related to earlier biodiffusion models (Skellam 1951, Kierstead and Slobodkin 1953, Okubo 1980), and island biogeography models (Allen 1987). Our spatial optimization model uses discrete time periods and approximates habitat patch configurations with a grid of cells on the landscape. We then incorporate cellular habitat management decision variables so that all potential spatial configurations can be considered (within the resolution of our grid). Ferret population growth and dispersal between cells from year to year is modeled here with an exponential population growth potential and a random dispersal pattern that relates probability of dispersal to distance. With discrete spatial cells and time periods, this reaction-diffusion process can be captured with linear constraints, as described below.

Particular ferret habitat layouts are achieved over time by the prairie dog populations that result from rodenticide treatment-nontreatment schedules applied to each cell across the landscape, on the premise that prairie dog populations will recover rapidly in areas left untreated. Decision variables (X_{ihk}) are defined for each possible schedule (indexed by k) of annual rodenticide treatment or nontreatment in each habitat condition class (indexed by h) for each cell (indexed by i). For example, one schedule could call for rodenticide treatments in the first year and every fourth year thereafter, while another schedule might call for treatments to begin in the second year instead. Adult black-footed ferret populations expected in each cell in any year are limited by either the carrying capacity of that cell, or by the ability of ferrets from nearby cells to successfully reproduce and disperse there, or both.

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Additional decision variables (R_{it}) are used to determine the timing (year t) and location (cell i) for captive-bred ferret releases into the area. Our spatial optimization model is:

[1] Maximize: $\sum_t F_t \quad (1)$

[2] subject to: $F_t = \sum_i S_{it}\ ; \quad t = 1,\ldots,T$

[3] $S_{i0} = N_i \quad \forall i$

[4] $S_{it} \le R_{it} + \sum_j g_{ji}(1 + r_j) S_{j(t-1)} \quad \forall i\ ;\ t = 1,\ldots,T\ ; \sum_i g_{ji} \le 1 \quad \forall j$

[5] $\sum_i R_{it} \le b_t \quad ;\ t = 1,\ldots,T$

[6] $S_{it} \le \sum_{h=1}^{m_i} \sum_{k=1}^{n_{ih}} c_{ihkt} X_{ihk} \quad \forall i\ ;\ t = 1,\ldots,T$

[7] $\sum_{k=1}^{n_{ih}} X_{ihk} = A_{ih} \quad \forall i,h$

[8] $\sum_i \sum_{h=1}^{m_i} \sum_{k=1}^{n_{ih}} c_{ihktp} X_{ihk} \le C_{pt} \quad \forall p\ ;\ t = 1,\ldots,T \quad X_{ihk}, S_{it}, R_{it} \ge 0 \quad \forall i, h, k, t$

Where:

t		indexes annual time periods (0,...,T) that begin in late spring when the young emerge from the den
i,j		index habitat management cells in the study area
h		indexes initial habitat condition classes in each cell
k		indexes rodenticide treatment schedules
p		indexes policy constraints (if any) on selection of habitat management variables
X_{ihk}	=	amount of area (in hectares) in cell i and initial habitat condition class h allocated to the kth multi-year habitat management schedule
R_{it}	=	number of captive-bred ferrets released in cell i during year t that are expected to survive adaptation to life in the wild
S_{it}	=	expected adult ferret population (including yearlings) in cell i at the beginning of year t, plus R_{it}
F_t	=	expected adult ferret population for the entire complex in year t
N_i	=	actual or estimated initial number of adult ferrets in cell I
g_{ji}	=	proportion of surviving adult and juvenile ferrets from den areas in cell j in year t-1 expected to disperse and become adult ferrets in cell i at the beginning of year t
r_j	=	an "r-value" for ferrets in cell j reflecting the maximum expected annual net population growth rate (i.e., when habitat is not a limiting factor)
b_t	=	an upper bound on the total number of captive-bred ferrets released during year t expected to survive adaptation to life in the wild
c_{ihkt}	=	expected adult black-footed ferret carrying capacity for cell i and condition class h in year t per hectare allocated to X_{ihk}
m_i	=	number of initial habitat condition classes in cell I
n_{ih}	=	number of habitat management schedules being considered for initial habitat condition class h in cell I
A_{ih}	=	total prairie dog colony area (in hectares) of initial habitat condition class h in cell I
c_{ihktp}	=	c_{ihkt} if X_{ihk} contributes to policy constraint p in time period t, and zero otherwise
C_{pt}	=	amount of total expected black-footed ferret carrying capacity allowed in time period t under policy p from the relevant subset of X_{ihk} habitat management variables.

Equations (1) - (5) define a discrete-time reaction-diffusion system (in this case, population growth and dispersal) for evaluating population persistence within a habitat complex. Equation (1) maximizes total expected adult black-footed ferret population for all time periods, each summed by equation (2). Equation (3) sets initial population conditions. Equation (4) limits the expected adult ferret population in any cell for any year to (at most) the number of captive-bred ferrets released into the cell plus the number of ferrets expected to disperse into the cell from all cells in the complex (including the same cell), after accounting for net reproduction during the previous year. Equation (5) limits the number of ferrets that can be released during any given year.

Our model assumes that organisms relocating into unsuitable regions will perish. This mechanism provides a probabilistic basis for the expectation that, after accounting for births and deaths due to all causes in an abundant habitat setting through the r-value (net annual population growth rate r_j), additional mortality will occur in proportion to the usage of inhospitable surroundings. Equations (6) and (7) account for these habitat dynamics by imposing black-footed ferret carrying capacity constraints in each cell as a function of the selected habitat management (rodenticide treatment) schedules. The expected ferret population in any cell in a given year (S_{it}) is determined by either equation (4) or (6), whichever is limiting. We employed equation (8) to limit the total amount of ferret habitat in the National Grassland in order to examine spatially and temporally efficient tradeoffs between expected adult ferret populations and levels of prairie dog population control. The linear dispersal model (equation 4) is based upon an assumption of purely random diffusion, which is a first-level approximation for highly developed species like the black-footed ferret. In general, biased diffusion enhances the persistence of populations (Allen 1983). Thus, our model provides an estimated lower bound on the size of the expected population. Note that we have identified the r_j growth rates by cell. In some cases, expected net reproduction may be different from one cell to another even with abundant habitat. For example, one cell may lie closer to terrain frequented by predators than another cell.

BLACK-TAILED PRAIRIE DOGS

Once regarded as nothing but pests, the ecological importance of the prairie dog (*Cynomys* sp.) is now more completely understood (Hoogland, 1995; Cincotta et al., 1988). To allow for analysis of black-tailed prairie dog (*C. ludovicianus*) recovery strategies, we are working with the Nebraska National Forest to build a model for the Conata basin area of South Dakota. The formulations presented here reflect our current thinking and will be tested further in this case study. We will identify patches of potential black-tailed prairie dog (simply “prairie dog” hereafter) habitat, based on historic maps of prairie dog presence during a time of high populations. These irregular patches are contrasted with the cellular grid utilized in the previous section. Those patches will be assumed to be the only part of the landscape that can support prairie dog populations, and thus they will limit our choice variables. The choice variables will determine the area within each patch of potential habitat that is zoned for prairie dog habitat. It is assumed that grazing regimes will be applied in the areas zoned for habitat that are conducive to prairie dog presence, and poisoning will be eliminated. Areas in the patches of potential habitat that are not zoned for prairie dogs will be assumed to be subject to poisoning and other management actions that make them unsuitable for prairie dog occupation.

In order to model the prairie dog, we must make some specific assumptions about its population dynamics. First, we assume that at any point in time, prairie dog populations in any colony are determined by whichever is limiting: population growth and dispersal processes or the habitat carrying capacity determined by our choice variables. Second, we will assume that, if unconstrained by habitat, prairie dog populations grow exponentially with an “r-value” that indicates a growth rate net of natality and mortality.

Third, the only prairie dog movements that we will model are those that result in net dispersal between habitat patches. This means that intra-patch movements and animal “exchanges” between patches for breeding purposes (which roughly balance out) will be ignored. Hoogland (1995, pp.87-88) states “Emigration to, and colonization of, new colony sites probably is expensive and dangerous for prairie dogs...However, expansion of already existing colonies should be easier and safer.” Also, Cincotta et al. (1988, p.31) state that “Results indicated that prairie directly adjacent to the study colony was likely to be colonized if it was near a dense population of prairie dogs...High population densities may force prairie dogs to expand into new territory.” Prairie dogs probably begin to

disperse to other areas before their colonies become completely saturated, but as a conservative modeling approach, we will assume that no dispersal emigration occurs until habitat areas are at carrying capacity, determined with a fixed parameter (per unit of habitat).

Fourth, we will assume that once dispersal occurs, it is random. Thus, we will identify a probability for each pair of patches that a dispersing prairie dog from the first patch will successfully disperse to the other patch. This probability can reflect barriers to dispersal (and other landscape features), but will primarily be a function of the distance between the two patches (Garrett and Franklin, 1981). Our model will be structured so that dispersal between all patches of potential habitat will be determined simultaneously. Implicit in this simultaneous solution will be a feature that if prairie dogs attempt to enter a habitat area that is already full, those animals will then return to the pool of dispersers and will again be subjected to the probabilities of successful dispersal to the other patches.

Fifth, we will assume that dispersing prairie dogs will not reproduce during their first year in the new colony. As Cincotta, et al. (1987, p.341) state: "There was no observed reproductive success during either 1982 or 1983 among the newly established populations of prairie dogs on the treated site. This suggests that female black-tailed prairie dogs disperse after the mating season and do not bear young during their first year in a newly established territory."

The combination of highly population-dependent random dispersal and zero reproduction during the first year in a new territory, creates a model of spatial prairie dog recovery that can be contrasted with the population dynamics assumed for the black-footed ferret in the first section.

Our model is formulated as follows:

[9] Maximize: $$\sum_{t=1}^{T}\sum_{i=1}^{M} S_{it}$$

[10] Subject to: $$X_i \le A_i \quad \forall\, i$$

[11] $$S_{i1} \le N_i \quad \forall\, i$$

[12] $$Q_{i1} = O \quad \forall\, i$$

[13] $$S_{it} + Q_{it} \le (1+r)S_{i(t-1)} - \sum_{j\neq i} r g_{ij}\, Q_{j(t-1)} + \sum_{j\neq i} g_{ij}\, Q_{jt} \qquad \forall\, i,\ t=2,\ldots,T$$

[14] $$S_{it} \le C_{it} X_i \ \forall\, i\ \forall\, t$$

[15] $$\sum_{i=1}^{M} X_i \le B$$

Where:

i		indexes patches, as does j
M	=	the number of patches
t		indexes time periods
T	=	the number of time periods.
S_{it}	=	the prairie dog population in patch i, time period t
X_i	=	the number of acres in patch i zoned as prairie dog habitat
Q_{it}	=	a variable used to account for the prairie dogs that leave patch i in time period t to disperse to other patches.
A_i	=	the number of acres in patch i. Patches are defined as areas of <u>potential</u> prairie dog habitat.
N_i	=	the initial population of prairie dogs in patch i.
r	=	the "r-value" for resident prairie dogs.
g_{ij}	=	the probability of a dispersing prairie dog successfully leaving patch j and inhabiting patch i.

C_{it}	=	the density, or carrying capacity, of prairie dogs, per acre of habitat.
B	=	a limit on the total amount of area zoned for prairie dog habitat (policy parameter).

Equation (9) is the objective function, and maximizes the total prairie dog population over all patches and time periods. Equation (10) limits the zoned habitat to the potential habitat in each patch. Equation (11) limits the population in the first time period to the initial population. Equation (12) initializes the number of dispersing prairie dogs to zero. The population in each patch and time period, S_{it}, is determined by whichever of constraints (13) or (14) (or (11) for the first time period) is binding. Equation (14) simply limits the prairie dog population to the habitat carrying capacity determined by the solution values for X_i. Equation set (13) determines the population of each patch i in time period t, if it is binding, as follows: The population from the previous time period for patch i, $S_{i(t-1)}$ is expanded by a factor of (1+r). In order to account for the dispersing prairie dogs <u>not</u> reproducing during their first year in a new colony,

$$\sum_{j_1} rg_{ij}\ Q_{j(t-1)}$$

is deducted from $(1+r)S_{i(t-1)}$.

Then, the prairie dogs successfully immigrating from other patches ($j \neq i$),

$$\sum_{j_i} g_{ij}\ Q_{jt}$$

are added. If, for a given i, Equation (14) is binding, then the excess population in (13) is accounted for in the Q_i variable, which simultaneously enters into the other equations in (13) as dispersing prairie dogs. The model solution will always set $Q_{it} = 0$ until Equation (14) is binding because the sum of the S_{it} is being maximized and $\sum_{j_i} g_{ij}$ is always less than one. Thus, no dispersal occurs until allocated habitat (X_i) is full, as desired. Equation

set (13) is a simultaneous system of equations which will solve for all Q_{it} and Q_{jt} -- simultaneously accounting for all dispersal between all patches in the given time period. Equation (15) limits the total of the X_i across all patches, as a policy constraint.

EXOTIC PEST CONTROL

Recent literature documents the important and expanding problem of exotic pests invading forest ecosystems. As Haack and Byler (1993) summarize, “most native insects and pathogens reach a dynamic state of equilibrium with their hosts and natural enemies. However, this situation may not be true for ... newly introduced exotic insects and pathogens.” These authors also state “Exotic insects and pathogens have dramatically altered forest ecosystem diversity, function, and productivity. More than 20 exotic fungal pathogens and 360 exotic insects now attack woody trees and shrubs in North America ...” This section will investigate the possibility of using optimization methods to assist in developing a spatial management strategy for an invading pest once it has arrived and has at least minimally established itself.

In order to construct a solvable optimization formulation, we use discrete time periods and discrete units of space as in the ferret model -- square cells located in a north-south coordinate system. Liebhold et al. (1995) (originally Skellam, 1951) suggest “Fick’s law of diffusion” to model the dispersal of an invading organism. An exponential population growth model is then combined with Fick’s model in Liebhold et al. In order to apply this approach with discrete time periods and cells, we treated each time period as a “time of release” and each cell as a “point of release.” Any diffusion model (such as Fick’s) can then be used to predict the dispersal into other cells during the length of one time period. We can thus calculate a matrix of coefficients, g_{nh}, that indicate the proportion of population that disperses from each cell, indexed with n, to each other cell, indexed with h, during one time period

(and using cell centroids to calculate distances). The diagonal of this coefficient matrix, where n = h, indicates the proportion of the population that remains in each cell during each time period. With those coefficients calculated, we can then model the population in each cell h in each time period as:

[16]
$$S_{ht} = \sum_{n} g_{nh} [(1 + r_n) S_{n(t-1)}] \qquad t = 1,\ldots,T \; \forall \, h$$
$$S_{no} = N_n \qquad \forall \, n$$

Where:

h and n both index cells

t indexes time periods (t=0 for initial conditions)

r_n = the r-value for cell n

S_{ht} = the pest population in cell h in time period t

$S_{n\,(t-1)}$ = the pest population in cell n in time period t-1

N_n = the initial pest population in cell n

This combines an exponential growth function with the diffusion coefficients for discrete time periods and discrete space units (cells) in a linear, convex formulation. The g_{nh} coefficients in (16) can be varied to reflect spatial variation across the landscape but must be assumed constant over time (more precisely, across all time periods). This means that no limits to host capacity are included in (16); just as they are not included in Liebhold et al., 1995. If it is possible to reduce pest population through spatially-specific management actions, then (16) could be augmented as:

[17]
$$S_{ht} + a_h \; y_{ht} = \sum_{n} g_{nh} \; [\,(1 + r_n) S_{n\,(t-1)}] \qquad t = 1,\ldots,T \; \forall \, h$$
$$S_{no} = N_n \qquad \forall \, n$$

where:

Y_{ht} = the amount of management effort in cell h and time period t

a_h = the pest population exterminated per unit of Y_{ht} in cell h

Any number of economic or biological objective functions could be utilized, but for simplicity let us assume that we wish to minimize the total exotic pest population over T time periods. Let us also assume that our management resource limitation can be captured by a simple constraint that specifies that we are only able to apply K_t units of management in each time period t. The problem, then, is to optimally locate the management-induced pest mortality over time, given the initial pest infestation location and subsequent growth and dispersal (as it is affected by the management actions).

The basic optimization model is then:

Minimize:

[18] $$\sum_{t=1}^{T} \sum_{n} S_{ht}$$

Subject to:

[19] $$S_{no} = N_n \qquad \forall h$$

[20] $$S_{ht} + a_h \; Y_{ht} \geq \sum_{n} g_{nh} \left[(1 + r_n) S_{n(t-1)} \right] \qquad t = 1,....,T \quad \forall h$$

[21] $$\sum_{h} Y_{ht} \leq K_t \qquad t = 1,...,T$$

Equation (20) is written as an inequality in the model, because that aided in avoiding numerical problems in model solution.

This model assumes that management (Y_{ht}) can be meaningfully related to the exterminated pest population. In situations where management options must be related to host elimination (e.g., sanitation cutting of a host tree species), the reader is referred to the approaches in Hof et al. (1997). The host-based problem appears to require integer programming approaches, which severely limits model size and therefore spatial resolution. If management effort can be directly related to pest mortality, but with diminishing returns, this can be included in the optimization model above through piece-wise approximation.

THE NORTHERN SPOTTED OWL

For more than a decade, conservation of the northern spotted owl (*Strix occidentalis caurina*), hereafter referred to simply as "the owl," has been a central issue in management of forests in the Pacific Northwest. We used a simulation model to construct an optimization model with a simplified formulation of the spatial biological processes and relationships that allows linear optimization. We then used the simulation model to "check" the conclusions drawn from optimization--thus recapturing the biological detail and reliability that might be compromised in the simplified optimization formulation. Following Holthausen et al. (1995), we divided the Olympic Peninsula into hexagonal 1500-ha cells, the size of which represents a core area or territory for an owl pair. This yielded a model with 1681 cells (41 x 41), with the carrying capacity set at zero for any cell that does not currently contain any habitat. To simulate the spotted owl population, we used OWL (version 2.01, described by McKelvey et al. 1992).

The basic variables in this problem are the amount of habitat in each cell that is retained (or protected). Because habitat for the northern spotted owl is low-elevation late-successional and old-growth forest, which take hundreds of years to develop, the decision to retain habitat in any cell or not is semi-permanent. Thus, we used a static optimization model to try to take advantage of this simplifying characteristic. This implies that the dynamic processes of birth, dispersal, and death modeled in the simulation model had to be captured in an equilibrium sense with static relationships in the optimization model.

The dynamics of owl population growth and dispersal captured in the simulation model are complex, but we assume that at any point in time, the population in any cell is limited by either the amount of habitat, the connectivity to other cells' owl populations, or both. A simple characterization of connectivity would be that each cell's population is potentially limited by the population in the cells immediately surrounding it. For each cell i, we will then define the set of immediately-surrounding cells as set Ω_i. This simple relationship is analogous to a first-order spatial autocorrelation; and, because each cell in each Ω_i is affected by its surrounding cells, this relationship implies a cascading effect beyond the Ω_i set for each cell i. The combination of potentially limiting factors could then be formulated as:

[22] $$p_i \leq f\left(\sum_{k \in \Omega_i} p_k\right) \quad \forall i$$

[23] $$p_i \leq g\left(C_i\right) \quad \forall i$$

Where:

i indexes the cells.

p_i = the population in the ith cell.

Ω_i = the set of cell indexes that surround cell i.

C_i = the proportion of cell i that is retained as habitat.

$\sum_{k \in \Omega_i} p_k$ = the total population in all of the cells in set Ω_i

f and g = empirical functions

The f and g functions do not describe dynamic processes, but are, instead, static, deterministic relationships estimated from empirical or simulated observations. The f and g functions would, in general, be nonlinear, but can be approximated in a linear optimization model, so long as they exhibit diminishing returns. We thus formulate a model to maximize owl population as:

[24] Maximize: $$\sum_{i=1}^{I} p_i$$

Subject to:

[25] $$p_i \leq \sum_{j=1}^{J} a_j X_{ij} \quad \forall i$$

[26] $$X_{ij} \leq S_j \quad \forall i \forall j$$

[27] $$\sum_{j=1}^{J} X_{ij} = \sum_{k \in \Omega_i} p_k \quad \forall i$$

[28] $$p_i \leq \sum_{h=1}^{H} b_h Y_{ih} \quad \forall i$$

[29] $$Y_{ih} \leq Q_h \quad \forall i \forall h$$

[30] $$\sum_{h=1}^{H} Y_{ih} = C_i \quad \forall i$$

[31] $$O \leq C_i \leq B_i \quad \forall i$$

Where:

j indexes the J segments that approximate f

h indexes the H segments that approximate g

a_j = a coefficient that approximates the f function for the jth segment of $\sum_{k e \Omega_i} p_k$

b_h = a coefficient that approximates the g function for the hth segment of C_i.

X_{ij} = the jth segment of $\sum_{k e \Omega_i} p_k$

Y_{ih} = the hth segment of C_i

S_j = the segment size limit of X_{ij}

Q_h = the segment size limit of Y_{ih}

B_i = the fixed proportion of habitat currently existing in cell i, and thus available for retention

Equation (24) is simply an owl population-maximizing objective function. Equation (25) approximates the (f) connectivity functions with the X_{ij} segments, defined in Equations (26) and (27). Equation (28) approximates the carrying capacity functions (g) with the Y_{ih} segments, defined in Equations (29) and (30). Equation (31) limits the habitat retention variables, C_i, to be less than or equal to the amount of habitat in each cell that is available for retention (B_i). The expected population in each cell (p_i) is determined by whichever (or both) of Equations (25) and (28) are limiting.

To estimate the connectivity (f) function, we began by selecting cells from the study area where spotted owls were least likely to be habitat-limited. Available evidence suggests that owl survival (and hence, likelihood of occupancy of a cell) does not increase when habitat exceeds 60% of a cell (Bart 1995). There were 100 cells that had > 60% habitat, which we included for the function estimation. Given that these 100 cells are not habitat-limited, we assume that the populations observed in the simulation runs are determined by the presence of population in surrounding cells. Next, we ran 50 replications of 100-year simulations. We estimated "population" of each cell as mean occupancy, the number of years the cell was occupied by a pair of owls divided by the total years in the simulation (100). Using average simulated population numbers across all replications for each of the 100 selected cells, we then regressed each cell's mean population against the total mean population of the six cells surrounding it. We tried several functional forms, but settled on a log-log transformation that yielded an exponential function. The statistical confidence in these equations was quite good with R^2 values of ≈0.9. We also inspected plots to assure that the functions were reasonable relative to the plotted data. These functions were then approximated in Equations (25) - (27).

As with the connectivity (f) functions, we used simulation model results to estimate the carrying capacity (g) functions to be as consistent as possible with the assumptions that were used in the simulation model. We plotted mean owl occupancy per cell against percent habitat in each cell from simulation replications based on retention of all current habitat, thus maximizing connectivity within the limits of the study area. We approximated this relationship with three segments that have diminishing slopes (in Equations (28) - (30)). We did not statistically regress these relationships because of the logical requirements that the intercept term had to be non-negative, and the function had to be "convex" (exhibiting diminishing returns). Based on visual examination of the plots, the functions assumed are good approximations, but it is possible that the carrying capacity (g) functions are somewhat sigmoidal (e.g., logistic). Unfortunately, this functional form would create a nonconvex program in the optimization model, and the approximation of the carrying capacity function would require integer methods (mixed integer programming or separable programming). This nonconvex model would not be solvable with nonheuristic methods that ensure optimality at the scale of our case study. This is a good example of the simplifications necessary to make the optimization model solvable, even given the basic simplicity of the formulation in the first place.

LITERATURE CITED

ALLEN, L.J.S. 1983. Persistence and extinction in single-species reaction-diffusion models. *Bulletin of Mathematical Biology* 45:209-227.

ALLEN, L.J.S. 1987. Persistence, extinction, and critical patch number for island populations. *Journal of Mathematical Biology* 24:617-625.

BART, J. 1995. Amount of suitable habitat and viability of northern spotted owls. *Conservation Biology* 9:943-946.

BEVERS, M., J. HOF, D.W. URESK, AND G.L. SCHENBECK. 1997. Spatial optimization of prairie dog colonies for black-footed ferret recovery. *Operations Research* (in press).

CINCOTTA, R.P., D.W. URESK, AND R.M. HANSEN. 1987. Demography of black-tailed prairie dog populations reoccupying sites treated with rodenticide. *Great Basin Naturalist* 47(2): 339-343.

CINCOTTA, R.P., D.W. URESK, AND R.M. HANSEN. 1988. A statistical model of expansion in a colony of black-tailed prairie dogs. In *Eighth Great Plains Wildlife Damage Control Workshop Proceedings*, 30-33.GTR RM-154. U.S. Department of Agriculture, Forest Service.

GARRETT, M.G., AND W.L. FRANKLIN. 1981. Prairie dog dispersal in Wind Cave National Park: Possibilities for control, In *Proceedings: Fifth Great Plains Wildlife Damage Control Workshop*, 185-198. University of Nebraska.

HAACK, R.A., AND J.W. BYLER. 1993. Insects and pathogens: regulators of forest ecosystems. *Journal of Forestry* 91(9), 32-37.

HOF, J., M. BEVERS, AND B. KENT. 1997. An optimization approach to area-based forest pest management over time and space. *Forest Science* 43: 121-128

HOF, J., M. BEVERS, D.W. URESK, AND G.L. SCHENBECK. (in preparation). *Spatial optimization of habitat location for black-tailed prairie dogs in southwestern South Dakota.*

HOF, J. (in review). *Optimizing spatial and dynamic population-based control strategies for invading forest pests.*

HOF, J. AND M.G. RAPHAEL. (in press). Optimization of habitat placement: A case study of the northern spotted owl in the Olympic Peninsula. *Ecological Applications*.

HOLTHAUSEN, R.S., M.G. RAPHAEL, K.S. MCKELVEY, E.D. FORSMAN, E.E. STARKEY, AND D.E. SEAMAN. 1995. *The contribution of federal and nonfederal habitat to persistence of the northern spotted owl on the Olympic Peninsula, Washington.* Gen. Tech. Rep. PNW-GTR-352. U.S. Department of Agriculture, Pacific Northwest Research Station.

HOOGLAND, J.L. 1995. *The black-tailed prairie dog: Social life of a burrowing mammal*. University of Chicago Press, 557 p.

KIERSTEAD, H., AND L. B. SLOBODKIN. 1953. The size of water masses containing plankton blooms. *Journal of Marine Research*, 12:141-147.

LIEBHOLD, A.M., W.L. MACDONALD, D. BERGDAHL, AND V.C. MASTRO. 1995. Invasion by exotic pests: A threat to forest ecosystems. *Forest Science Monograph* 30.

LINDER, R.L., R.B. DAHLGREN AND C.N. HILLMAN. 1972. Black-footed ferret - prairie dog interrelationships, In *Symposium on Rare and Endangered Wildlife of the Southwestern United States*, 22-37. September 22-23, Albuquerque, NM, New Mexico Dept. of Game and Fish, Santa Fe.

MCKELVEY, K., B.R. NOON, AND R.H. LAMBERSON. 1992. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl, In *Biotic interactions and global change*, eds. P. Kareiva, J. Kingsolver, and R. Huey. Sinauer Assoc., Sunderland, MA, pp. 424-450.

MINTA, S., AND T.W. CLARK. 1989. Habitat suitability analysis of potential translocation sites for black-footed ferrets in north-central Montana, In *The prairie dog ecosystem: Managing for biological diversity*, T.W. Clark, D. Hinckley and T. Rich (eds.), Montana Bureau of Land Management, Billings, MT pp. 29-46.

OKUBO, A. 1980. Diffusion and Ecological Problems: Mathematical Models. *Biomathematics 1*0. Springer-Verlag, Berlin.

SKELLAM, J.G. 1951. Random dispersal in theoretical populations. *Biometrika*, 38:196-218.

VARLEY, G.C., G.R. GRADWELL, AND M.P. HASSELL. 1973. *Insect population ecology*. Blackwell Sci. Pub., Oxford, UK.