Optimizing habitat location for black-tailed prairie dogs in southwestern South Dakota

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Abstract

A spatial optimization model was formulated and used to maximize black-tailed prairie dog populations in the Badlands National Park and the Buffalo Gap National Grassland in South Dakota. The choice variables involved the strategic placement of limited additional protected habitat. Population dynamics were captured in formulations that reflected exponential population growth combined with the recalcitrant dispersal behavior of this social mammal that is important to many other species. The model results are compared to a previous paper which modeled the black-footed ferret, an aggressive disperser that is dependent upon prairie dogs for food and shelter. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

In the late 1800's, an estimated 283 million ha were occupied by a combined population of North American prairie dogs (*Cynomys* spp.) exceeding some 5 billion individuals (Seton, 1929). By 1971, that area had declined to 600,000 ha (Fagerstone and Biggins, 1986). Loss of habitat, control programs, and plague (*Yersinia pestis*) have continued to reduce populations. More recent estimates suggest that prairie dog populations have been reduced by 98–99% of their former numbers across the western United States (Miller et al., 1994; Mulhern and Knowles, 1997). Ever since Merriam (1902) reported that prairie dogs compete with livestock for forage, they have been targeted for control programs as agricultural pests. More recently, however, prairie dogs have been viewed as keystone species important to many other species that are dependent on them for food, burrows, and their effects on plant communities (Miller et al., 1994). Nonetheless, rodenticide control programs will likely continue because of the competition between prairie dogs and livestock (Roemer and Forrest, 1996; Long, 1998).

The black-tailed prairie dog (*C. ludovicianus*) was historically the widest-ranging of the five prairie dog species in North America, occupying areas from Mexico to Canada. Members of this

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species are the only prairie dogs found on the Great Plains (Wuerthner, 1997). South Dakota is a particularly important location for black-tailed prairie dogs because of the apparent absence of plague epizootics (Barnes, 1993; Fitzgerald, 1993). Thus, public interest is high concerning efforts to expand the prairie dog numbers on public lands in that state (Long, 1998). Previously occupied prairie dog habitat is frequently repopulated if protected from rodenticide treatments, but live-stock grazing may also be necessary to aid in the spread of prairie dog populations by reducing vegetative cover in selected areas (Uresk et al., 1981; Cincotta et al., 1988).

Given that land areas for additional prairie dog colonies will likely be limited under any conserva-tion strategy, an important question is: where should any additional colonies be located? The spatial arrangement of protected habitat has im-portant effects on the ability of the prairie dogs to occupy and utilize that habitat (Hoogland, 1995; Garrett and Franklin, 1982). This paper investi-gates the use of optimization methods to find efficient spatial arrangements of protected habitat for expanding prairie dog populations on the Buffalo Gap National Grassland. Many other models that emphasize spatial relationships have been described recently in this journal (see: Bet-tinger et al., 1997; Jianguo and Levin, 1997; Fahrig, 1998; Batabyal, 1998; Loehle, 2000; Ji and Jeske, 2000; Brooks and Lebreton, 2001).

In a previous paper, we modeled the releases and population recovery of an associated species—the black-footed ferret (*Mustela nigripes*), see Bevers et al. (1997). In that model, prairie dog colony placements were treated as choice variables, and the ferret population response reflected its total dependence on prairie dogs for food and shelter. We characterized the spatial options with a grid of uniform cells and captured the dispersal behavior of the aggressively-dispersing ferret with a set of reaction-diffusion relationships. The prairie dog is much more hesitant to disperse, and will typically only do so if population densities approach habitat patch carrying capacity. Thus, to model the prairie dog we characterized the landscape choice vari-ables with irregular patches of habitat and the dispersal behavior with a population-dependent,

and yet linear, formulation. The two models are therefore quite different in terms of structure and formulation. Results from both models will be compared in the conclusion to investigate the hypothesis that managing for prairie dogs (given their population dynamics) is (or is not) consistent with managing for ferrets (given their population dynamics). We begin by discussing prairie dog habitat and the population dynamics that we wished to capture in the optimization model.

2. A prairie dog population management model

We identified patches of black-tailed prairie dog habitat from maps of prairie dog presence during the time (early 1980s) of highest known popula-tions. These maps were developed from color infrared aerial photographs taken in 1983, using methods described in Schenbeck and Myhre (1986), Uresk and Schenbeck (1987). Those habi-tat patches were assumed to be the only part of the landscape that could support prairie dog popula-tions within the planning time horizon (8 years), and thus they limited our choice variables. The choice variables determine the area within each patch of habitat that is zoned and protected for prairie dog colonies. It was assumed that grazing regimes conducive to prairie dog presence would be applied in the areas zoned for colonies, and poisoning would be eliminated. Areas in the patches of habitat that were not zoned for colonies were assumed to be subject to poisoning and other management actions that make them unsuitable for prairie dog occupation.

In order to model prairie dog populations, we had to make some specific assumptions about their dynamics. First, we assumed 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 protected habitat carrying capacity determined by our choice variables. Second, we assumed that, if un-constrained by rodenticides, prairie dog popula-tions grow exponentially up to habitat capacity with an 'r-value' that indicates a percentage growth rate, accounting for resident natality and mortality.

Third, the only prairie dog movements that we modeled were 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) were ignored. Hoogland et al. (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." Thus, prairie dogs appear to be reluctant to disperse from patch to patch. Prairie dogs probably begin to disperse to other areas before their colonies become completely saturated, but as a conservative modeling approach, we assumed that no emigration occurs until habitat areas are at carrying capacity, determined with a fixed parameter (per area of habitat).

Fourth, we assumed that once dispersal occurs, it is random. Thus, we identified a probability that a dispersing prairie dog from each patch will successfully disperse to any other patch. This probability can reflect barriers to dispersal (and other landscape features), but is simply a function of the distance between the two patches in this exploratory study (see Garrett and Franklin, 1982). Our model is structured so that dispersal between all patches of habitat is determined simultaneously for each 1-year time period. Implicit in this simultaneous solution is the feature that if prairie dogs attempt to enter a habitat area that is already full, those animals then return to the pool of dispersers and are again subjected to the dispersal mortality associated with moving to other patches.

Fifth, we assumed that, each year, prairie dogs reproduce (and the r-value is applied) before they disperse. The literature also suggests that dispersing prairie dogs will not reproduce during their first year in a 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.' This temporary non-mating behavior is a subtlety that we did not capture in our optimization model. Instead, we assumed that all prairie dogs reproduce similarly. The combination of highly population-dependent dispersal and random dispersal once it does occur creates an otherwise conservative model of prairie dog colonization. The sensitivity of the model to the overall reproduction rate is explored below.

With these assumptions, our model is formulated as follows:

$$\text{Maximize:} \quad \sum_{t=1}^{T} \sum_{i=1}^{M} S_{it} \tag{1}$$

$$\text{Subject to:} \quad X_i \le A_i \quad \forall i \tag{2}$$

$$S_{i1} = N_i \quad \forall i \tag{3}$$

$$Q_{i1} = 0 \quad \forall i \tag{4}$$

$$S_{it} + Q_{it} \le (1+r)S_{i(t-1)} + \sum_{j \ne i} g_{ij} Q_{jt} \quad \begin{array}{l} \forall i \\ t = 2, \ldots, T \end{array} \tag{5}$$

$$S_{it} \le C_i X_i \quad \begin{array}{l} \forall i \\ \forall t \end{array} \tag{6}$$

$$\sum_{i=1}^{M} X_i \le B \tag{7}$$

Indexes: i, indexes patches, as does j; M, the number of patches; t, indexes time periods; and T, the number of time periods.

Variables: S_{it}, the prairie dog population in patch i, time period t; X_i, the number of hectares in patch i zoned for prairie dog colonies; and Q_{it}, a variable used to account for the prairie dogs that leave patch i in time period t to disperse to other patches. The number of prairie dogs that successfully disperse to patch i from other patches ($j \ne i$) is:

$$\sum_{j \ne i} g_{ij} Q_{jt}$$

(see text for more explanation).

Parameters: A_i; the number of hectares of prairie dog habitat in patch i; N_i, the initial population of prairie dogs in patch i; r, the 'r-value' reproduction rate for resident prairie dogs; g_{ij}, the probability of a dispersing prairie dog leaving patch j and successfully reaching patch i; C_i, the carrying capacity of prairie dogs per hectare of protected habitat; B, a limit on the total amount of area zoned for prairie dog colonies (policy parameter).

Eq. (1) is the objective function, and maximizes the total prairie dog population over all patches and time periods. Many other objective functions are also possible, including maximization of the population in a given time period (such as the last one). Eq. (2) limits the zoned colony area to the habitat area in each patch. Eq. (3) sets the population in the first time period to the initial population. Eq. (4) initializes the number of dispersing prairie dogs (Q_{i1}) at zero. The population in each patch and time period, S_{it}, is determined by whichever of constraints (5) or (6) (or (3) for the first time period) is binding. Eq. (5) determines the population of each patch i in each time period t, if it is binding, as follows: The population from the previous time period ($t-1$) for patch i, $S_{i(t-1)}$ is expanded by the reproduction factor $(1+r)$. Then, the prairie dogs successfully immigrating from other patches ($j \neq i$),

$$\sum_{j \neq i} g_{ij} Q_{jt}$$

are added. Eq. (6) limits the prairie dog population to the habitat carrying capacity determined by the solution values for X_i. If, for a given i, Eq. (6) is binding, then the excess population in Eq. (5) is accounted for in the Q_{it} variable, which simultaneously enters into the other equations in Eq. (5) as dispersing prairie dogs. The model solution will always set $Q_{it} = 0$ until Eq. (6) is binding because the sum of the S_{it} is being maximized and $\Sigma_{i \neq j} g_{ij}$ for any patch j is always less than one, reflecting dispersal-related mortality. Thus, no dispersal occurs until allocated habitat (X_i) is full, as desired. Eq. (5) is a simultaneous system of equations which will solve for all Q_{it} and Q_{jt}—accounting for all dispersal between all

patches in the given time period. Eq. (7) limits the total prairie dog colony area across all patches, as a policy constraint.

Implicitly, prairie dog emigration was modeled as a multi-step process with mortality occurring (accounted for in the g_{ij} coefficient) at each step. The more steps it takes a given prairie dog to find an unoccupied patch, the more mortality risk accumulates (the g_{ij} coefficients apply at each step). We defined a maximum dispersal distance of 5 km (Garrett and Franklin, 1982, as cited by Hoogland, 1995) for each step. Thus, to define the g_{ij} coefficients, we drew a 5 km radius around the centroid of each patch j. We assumed that any patch i whose centroid was within that radius had an equal chance of being located by a prairie dog emigrating from patch j. The actual dispersal process may be affected by a number of factors including corridors of high-visibility which the prairie dogs prefer, the chirping of other prairie dogs that may serve as an attractant, and other biological and landscape variables. These processes are not well understood, and observed prairie dog dispersal behavior is rare (Hoogland, 1995). Thus, random dispersal direction seems to be the most tenable assumption. A mortality rate of 40% in excess of that already accounted for in the r-value (Garrett and Franklin, 1982) was applied to calculate all g_{ij}. In effect then, modeled prairie dogs can disperse farther than 5 km (consistent with Knowles (1985), and others) but with approximately an exponential decay in survival of 40% for each 5 km. The dispersal distance and mortality rate both come from the same study (Garrett and Franklin, 1982) which took place in an area of rapid expansion and plentiful habitat. We thus assumed that these rates were applicable to each step, because in the Garrett and Franklin study only the first step was likely to be observed (few emigrating prairie dogs encountered fully populated patches).

We adopted an r-value of 0.4 (so $1+r = 1.4$) which is at the lower end of the range reported by Hoogland (1995). Given the presence of hunting and many predators (including the black-footed ferret), this seemed appropriate. A carrying capacity (C_i) of 18.4 prairie dogs per hectare was assumed for all habitat patches and all time peri-

ods. This was the average observed population density for mature colonies measured (with repeated trapping) over 2 years on 12 plots in the study area (personal communication, Kieth E. Severson).

Fig. 1 shows the study area with 601 habitat patches covering ~ 20,443 ha. Initial occupancy (unpublished data, Nebraska National Forest, updated summers of 1996 and 1997) covered ~ 7991 ha and is indicated in Fig. 1 with color coding. As noted earlier, the habitat was determined from historically-high populations. The patches in Bad-

lands National Park were assumed to be initially at capacity. Thus, the only choice variables for additional protected habitat were in the National Grassland, but the model includes the Park patches to account for dispersal from that population into other areas. On the National Grassland, prairie dog densities were initially highest in three areas: the red patches labeled 1 in Fig. 1, the red and orange patches labeled 2 in Fig. 1, and the orange patch labeled 3 in Fig. 1. These areas had been previously designated as protected prairie dog habitat. Poisoning had been allowed to vary-
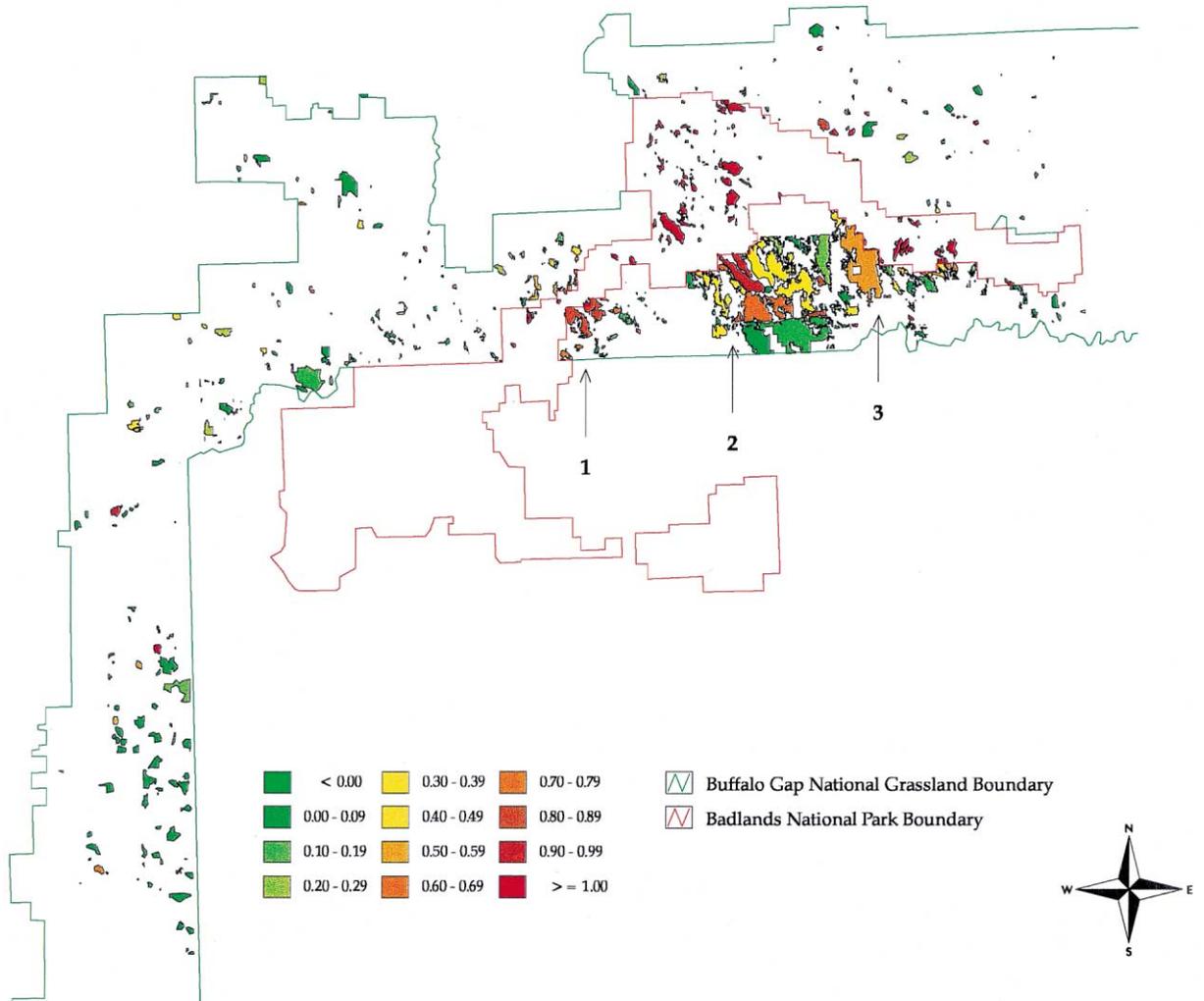

Fig. 1. Map of the ratio of currently occupied prairie dog habitat area to total prairie dog habitat area in the Buffalo Gap National Grassland and the Badlands National Park.
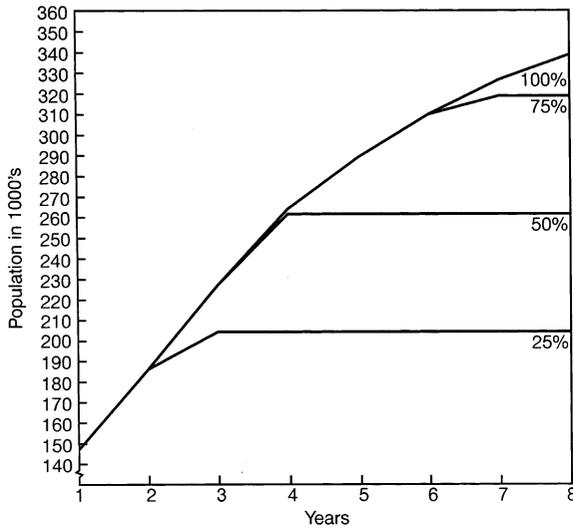
Fig. 2. Prairie dog population trends for four levels of habitat increase (+ 25, + 50, + 75, and + 100% of currently unpopulated habitat).

ing degrees elsewhere in the National Grassland, with the population varying in the initial conditions as indicated. Areas 2 and 3 are at the west and east limits of an area called 'Conata Basin', which will be referenced in Section 3.

The model was built with eight 1-year time periods (with one exception discussed below). With these dimensions, the model had 9626 choice variables and 8424 constraints. The model was built using the high-level programming language GAMS (Brooke et al., 1992) and was solved with

the C-WHIZ solver (Ketron Management Science, 1998).

3. Model results

Four policy alternatives were examined by solving the model with different right-hand side levels (B) in constraint (7) that represent protecting 25, 50, 75, and 100% of the initially unoccupied habitat in addition to what was initially occupied. Each 25% increment amounts to an increase of 3113 ha, which supports 57,280 prairie dogs at a carrying capacity of 18.4 per ha. The population results are given in Fig. 2. With the first three levels of increased prairie dog habitat, all available habitat is occupied within 8 years. With 100% of the habitat protected, all but ∼ 4.5 ha are eventually occupied, but a 21-year model was required before no further population increases occurred. These 4.5 ha are initially unpopulated and are also isolated by the geography and dispersal assumptions in the model. Essentially all of the habitat can be fully occupied with enough time. The optimization model is thus most useful for identifying those patches of additional protected habitat that can be populated by prairie dogs most quickly for a given policy alternative.

Table 1 compares the optimized rates of population increase with the population increases from the model solved with spatially 'neutral' protected locations imposed. For the neutral solutions, the

Table 1
Model prairie dog populations (in 1000s) over time for spatially-optimized and spatially-neutral patch allocations under three increments of habitat increase

Habitat increase:	+25%		+50%		+75%	
Allocation:	Optimum	Neutral	Optimum	Neutral	Optimum	Neutral
Year: 1	147.0	147.0	147.0	147.0	147.0	147.0
2	186.1	175.2	186.1	182.4	186.1	185.0
3	204.3	186.1	227.1	208.0	227.1	220.2
4	204.3	192.5	261.6	222.9	264.1	245.8
5	204.3	195.7	261.6	234.6	289.3	263.9
6	204.3	197.5	261.6	241.9	309.9	279.0
7	204.3	198.7	261.6	245.7	318.9	289.3
8	204.3	199.7	261.6	248.5	318.9	294.7

given percentage (25, 50, or 75%) of the habitat that was initially unpopulated was protected in all patches. This represents a neutral spatial allocation in that an equal proportion of additional habitat in all patches is protected, analogous to the random selections of null models in ecology (Gotelli and Graves, 1996). As can be seen in Table 1, the optimized location of habitat additions supports more rapid prairie dog population increases (at least as indicated by the model itself). We also experimented with objective functions that maximized the population in individual time periods, including the final period and intermediate periods. In all cases, the maximized single-period population equalled the population obtained for that period in Table 1. Thus, for this model, maximizing the population total across all time periods results in as rapid a population recovery as is possible.

The optimized protected habitat locations chosen by the model for the three habitat expansion levels in Table 1 are presented in Figs. 3–5. Fig. 3 shows the habitat additions selected for each patch as proportions of total patch sizes, for the +25% solution. The highest priority area for habitat expansion was indicated to be in Conata Basin. The yellow area surrounding area 2 in Conata Basin was the area with the largest habitat increases in solution (compare with Fig. 1). Thus, the top priority indicated was to expand the size of area 2 to the east and south. This top priority area does not go all the way south to the National Grassland boundary, so a buffer between large colonies and other land ownerships could probably be maintained without much loss. The next priority indicated was to increase the level of protection in areas 1 and 3 (note that it was impossible to expand the size of area 1 very much). Also, it was clearly desirable to connect areas 2 and 3 more than they were initially. It is actually surprising that, even with a recalcitrant disperser such as this animal, it was still optimal to expand the habitat significantly outside of Conata Basin. In particular, the area north and east of the Park, the area due west of Conata Basin, the area due east of area 3, and the middle part of the southwestern leg of the study area all were increased in the optimal solution. The areas

in the extreme southwest and northwest of the Grassland were not indicated to be high priority. This solution thus suggested a strategy where: we try to protect some additional habitat in the southwest grassland, northwest grassland, and the grassland northeast of the Park; we give high priority to expanding area 2 into a nearly round, coterminous area in Conata Basin that will serve as the 'core area' for the population; and we also try to connect area 1 enough to make it a part of this core area. Area 3 is probably also very important for connecting this core area to the west and southwest fringe areas. The Park serves this purpose for the northeast grassland. As one might expect, the population trends and locations followed the patterns of habitat location, with all available habitat fully occupied by year 3 (Table 1).

Fig. 4 shows the habitat added to each patch as a proportion of total patch size for the +50% solution. This solution is almost the same as the +25% solution west of the core area around area 2, though there is some additional protected habitat in the southwest leg of the study area. The emphasis in this solution is on increasing the density in the core area and expanding it to the point that it encompasses area 3 and the patches east of there. Some priority is also given to the northeast part of the study area.

Fig. 5 shows the habitat added to each patch as a proportion of total patch size for the +75% solution. This solution expands the core area south to the National Grassland boundary. The core area is now expanded to the limits of the habitat locations. Area 1 is still not given high priority, and the northwest areas are still at very low densities. Some high densities are now protected in the far southwest, however, as well as the patches due west of the core area. The patches in the northeast part of the National Grassland now have protected densities as high as 100%, especially close to the Park boundary and the initial high densities found there.

In summary, all three solutions emphasized the core area, but not completely at the expense of expanding the overall size of the total population area. Obviously, as the prairie dog expansion levels increase, so do the conservation opportuni-
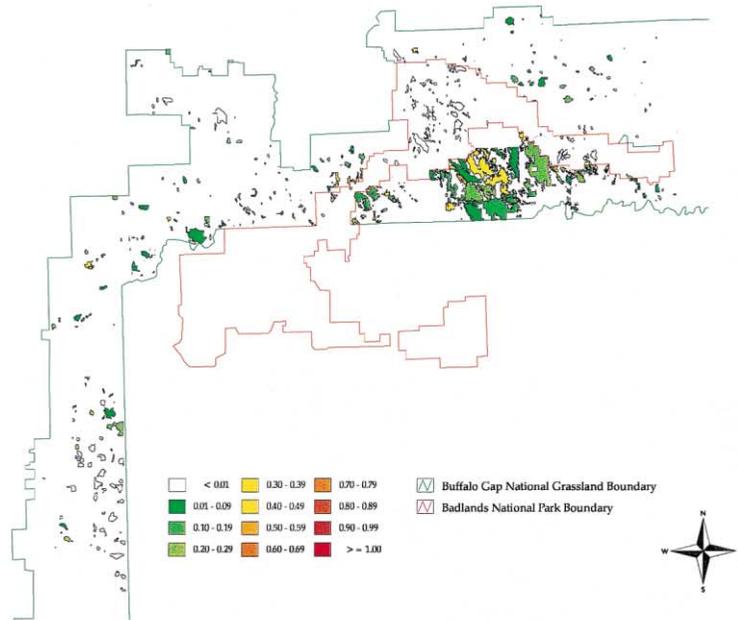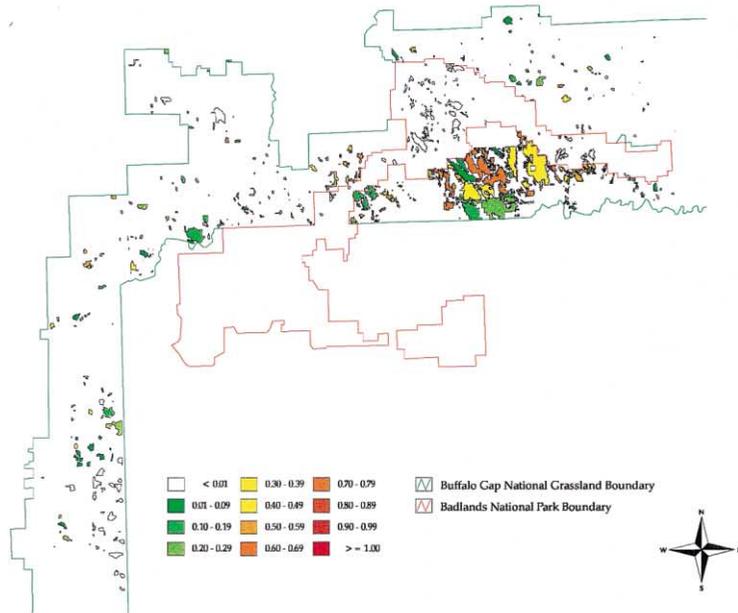
Fig. 3

Fig. 4

Fig. 3. Additional protected habitat area ÷ total habitat area in the + 25% optimization solution.
Fig. 4. Additional protected habitat area ÷ total habitat area in the + 50% optimization solution.

ties associated with those animals. However, conflicts with adjoining land ownership's can also be expected to increase with expanded prairie dog

presence on public lands. Our model indicated that optimally-located habitat additions could be more rapidly utilized to expand prairie dog popu-

lations than a neutral locational scheme (Table 1). The initial areas protected from rodenticide use were well-located for this potential, especially areas 2 and 3.

We previously noted that our model formulation is not able to capture the subtlety that female prairie dogs do not appear to bear young during their first year in a newly established territory. Instead, our model applies the same r-value to all prairie dogs. In order to explore the sensitivity of our model to the reproduction rate, we replicated Table 1 with the r-value

halved (so $1 + r = 1.2$). These results are reported in Table 2. The population recovers more slowly in the Table 2 results than in Table 1, but not as differently as one would expect if the population was 'r-limited.' Comparing the two tables suggests that the prairie dog is habitat-limited in at least part of the study area, but not all of it (or the two tables would be identical). Overall, comparing the two tables suggests that the gains from spatial optimization over a neutral spatial allocation are similar for the two r-values examined.
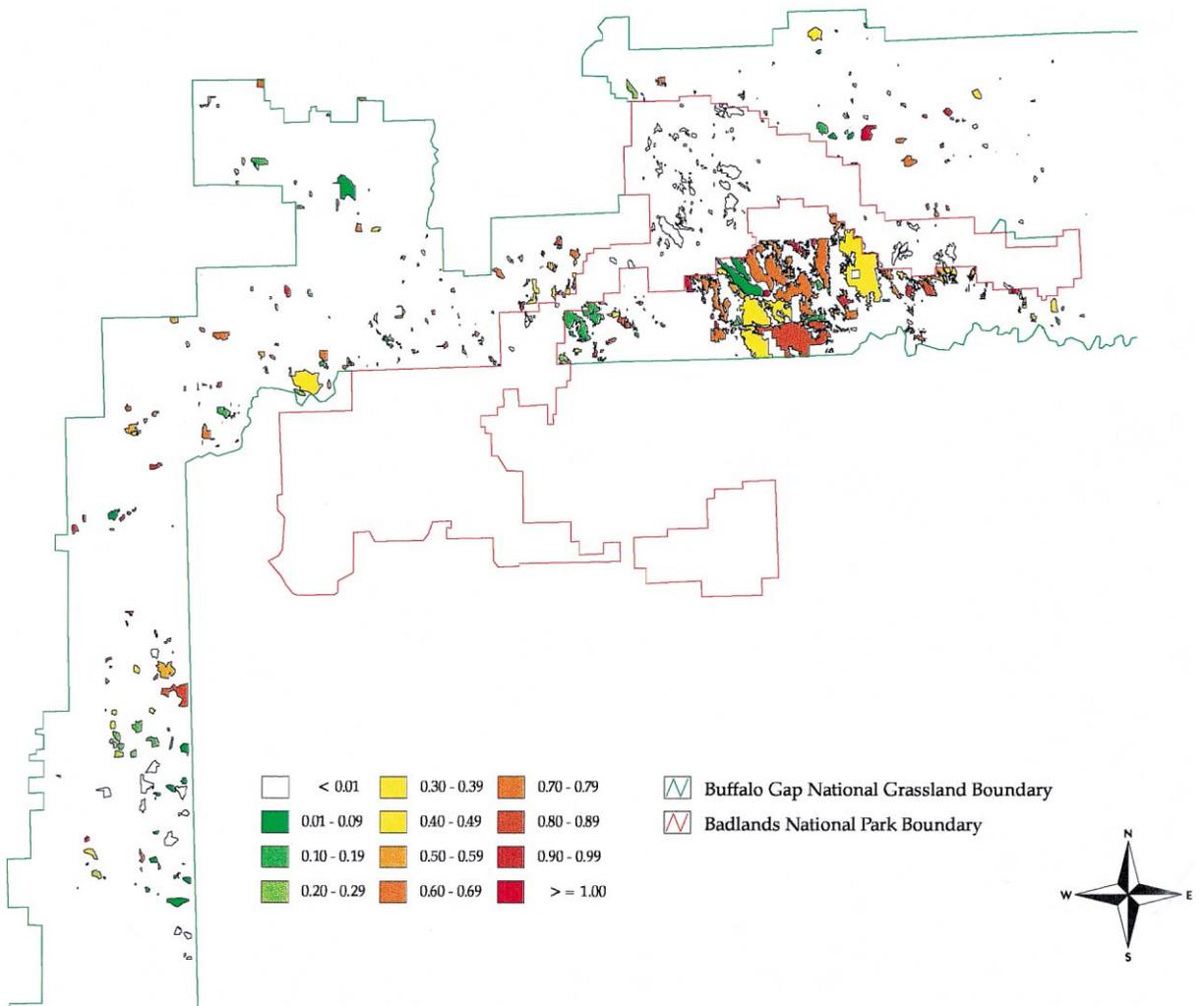

Fig. 5. Additional protected habitat area ÷ total habitat area in the +75% optimization solution.

Table 2
Model prairie dog populations (in 1000s) over time for spatially-optimized and spatially-neutral patch allocations under three increments of habitat increase, with a diminished *r*-value ($1 + r = 1.2$).

Habitat increase:	+25%		+50%		+75%	
Allocation:	Optimum	Neutral	Optimum	Neutral	Optimum	Neutral
Year: 1	147.0	147.0	147.0	147.0	147.0	147.0
2	167.9	164.7	167.9	166.6	167.9	167.4
3	189.6	176.4	189.6	184.7	189.6	188.4
4	204.3	182.9	213.0	200.2	213.0	207.5
5	204.3	187.5	233.5	210.9	233.5	225.9
6	204.3	191.2	254.8	219.2	254.8	239.7
7	204.3	193.6	261.6	226.1	270.7	250.9
8	204.3	195.3	261.6	232.7	284.3	260.3

4. Conclusion

Our model required many assumptions regarding the population dynamics of the black-tailed prairie dog, and did not explicitly account for random variation in those dynamics. Of particular importance is the possibility of a plague epizootic or other catastrophic event that could completely invalidate our model results. As such, our results should be regarded as an initial estimate of the expected population levels for the optimized habitat arrangements. While the indicated improvements in total population from using a spatial optimization model are modest (Table 1), the arrangement strategies suggested by our results appear to be useful in hastening the utilization of habitat additions by prairie dogs.

We contrasted the formulations in this paper with those in our previous paper that modeled the black-footed ferret (Bevers et al., 1997). The management strategies emerging from the two models are really quite consistent, however. Our ferret model used dynamic (scheduled) choice variables as opposed to the fixed zoning choice variables in the prairie dog model, and the ferret model only covered the northern part of the area modeled for the prairie dogs. Still, both models indicate that initially protected prairie dog colony areas are well-selected, but should be expanded if increased populations are desired. The strategy from the ferret model was to add a little habitat everywhere

at first and then later to concentrate the habitat in Conata Basin. Though fixed, the strategy suggested here is similar—create a core area in Conata Basin, but also increase other areas to expand the geographic extent of the population. Thus, it appears that locating prairie dogs to maximize ferret populations taking ferret population dynamics into account does create a similar strategy to maximizing prairie dog populations taking prairie dog population dynamics into account. This is encouraging, because it implies that our strategy in managing for ferret recovery is plausible given prairie dog dynamics, and managing for the prairie dogs themselves is not inconsistent with our objectives of supporting ferrets. Hopefully, this is also true for the other species that rely on the prairie dog as well—that managing for the keystone species is spatially tenable for the species that it supports.

Clearly, there is much that we do not yet know about prairie dogs. As more is learned about them and the species that they support, we anticipate that our model(s) could be used as part of an adaptive management process (Walters, 1986). Spatial optimization offers a capability for combining specific habitat and population information as it becomes available with management options and constraints. Further research is needed to understand the complexities of prairie dog population dynamics and to account for those complexities in optimization models.

References

Barnes, A.M., 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. In: Oldemeyer, J.L., Biggins, D.E., Miller, B.J., Crete, R. (Eds.), Proceedings of the Symposium on the Management of Prairie Dog Complexes for the Reintroduction of Black-Footed Ferrets. US Fish and Wildlife Service, Biological Report no. 13, Washington DC, pp. 28–37.

Batabyal, A.A., 1998. An optimal stopping approach to the conservation of biodiversity. Ecol. Modell. 105 (2-3), 293–298.

Bettinger, P., Sessions, J., Boston, K., 1997. Using tabu search to schedule timber harvests subject to spatial wildlife goals for big game. Ecol. Modell. 94 (2-3), 111–123.

Bevers, M., Hof, J., Uresk, D.W., Schenbeck, G.L., 1997. Spatial optimization of prairie dog colonies for black-footed ferret recovery. Oper. Res. 45 (4), 495–507.

Brooke, A., Kendrick, D., Meerans, A., 1992. GAMS: A User's Guide. The Scientific Press Series, Boyd and Fraser, Danvers, MA.

Brooks, E.N., Lebreton, J., 2001. Optimizing removals to control a metapopulation: Application to the yellow legged herring gull (*Larus cachinnans*). Ecol. Modell. 136 (2-3), 269–284.

Cincotta, R.P., Uresk, D.W., Hansen, R.M., 1987. Demography of black-tailed prairie dog populations re-occupying sites treated with rodenticide. Great Basin Naturalist 47, 339–343.

Cincotta, R.P., Uresk, D.W., Hansen, R.M., 1988. A statistical model of expansion in a colony of black-tailed prairie dogs. In: Uresk, D.W., Schenbeck, G.L., Cefkin, R. (Eds.), Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, South Dakota, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-154, pp. 30–33.

Fagerstone, K.A., Biggins, D.E., 1986. Comparison of capture-recapture and visual count indices of prairie dog densities in black-footed ferret habitat. Great Basin Naturalist Memoirs 8, 94–98.

Fahrig, L, 1998. When does fragmentation of breeding habitat affect population survival? Ecol. Modell. 105 (2-3), 273–292.

Fitzgerald, J.P., 1993. The ecology of plague in Gunnison's prairie dogs and suggestions for the recovery of black-footed ferrets. In: Oldemeyer, J.L., Biggins, D.E., Miller, B.J., Crete, R. (Eds.), Proceedings of the Symposium on the Management of Prairie Dog Complexes for the Reintroduction of Black-Footed Ferrets. US Fish and Wildlife Service, Biological Report no. 13, Washington DC, pp. 50–59.

Garrett, M.G., Franklin, W.L., 1982. Prairie dog dispersal in Wind Cave National Park: Possibilities for control. In: Timm, R.M., Johnson, R.J. (Eds.), Fifth Great Plains Wildlife Damage Control Workshop Proceedings, Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln, pp. 185–197.

Gotelli, N.J., Graves, G.R., 1996. Null Models in Ecology. Smithsonian Institution Press, Washington and London.

Hoogland, J.L., 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal. The University of Chicago Press, Chicago.

Ji, W., Jeske, C., 2000. Spatial modeling of the geographic distribution of wildlife populations: A case study in the lower Mississippi River region. Ecol. Modell. 132 (1-2), 95–104.

Jianguo, W., Levin, S.A., 1997. A patch-based spatial modeling approach: Conceptual framework and simulation scheme. Ecol. Modell. 101 (2-3), 325–346.

Ketron Management Science, 1998. C-WHIZ Linear Programming Optimizer, Version 3. The Bionetics Corporation, Arlington, VA, p. 131.

Knowles, C.J., 1985. Observations on prairie dog dispersal in Montana. Prairie Naturalist 17 (1), 33–40.

Loehle, C., 2000. Optimal control of spatially distributed process models. Ecol. Modell. 131 (2-3), 79–95.

Long, M.E., 1998. The vanishing prairie dog. National Geographic 193(4), 116–131.

Merriam, C.H., 1902. The prairie dog of the great plains. Yearbook of the US Department of Agriculture 1901. US Government Printing Office, Washington DC, pp. 257–270

Miller, B., Ceballos, G., Reading, R., 1994. The prairie dog and biotic diversity. Conserv. Biol. 8, 677–681.

Mulhern, D.W., Knowles, C.J., 1997. Black-tailed prairie dog status and future conservation planning. In: Uresk, D.W., Schenbeck, G.L., O'Rourke, J.T. (Eds.), Conserving Biodiversity on Native Rangelands Symposium Proceedings, USDA, Rocky Mountain Research Station, Fort Collins, CO, pp. 19–29.

Roemer, D.M., Forrest, S.C., 1996. Prairie dog poisoning in the northern Great Plains: an analysis of programs and policies. Environ. Manage. 20, 349–359.

Schenbeck, G.L., Myhre, R.J., 1986. Aerial Photography for Assessment of Black-tailed Prairie Dog Management on the Buffalo Gap National Grassland, South Dakota. USDA Forest Service FPM-MAG Report No. 86-7.

Seton, E.T., 1929. Lives of Game Animals. Doubleday, Doran and Co., Garden City, New York.

Uresk, D.W., MacCracken, J.G., Bjugstad, A.J., 1981. Prairie dog density and cattle grazing relationships. In: Timm, R.M., Johnson, R.J. (Eds.), Fifth Great Plains Wildlife Damage Control Workshop Proceedings, Institute of Agricultural and Natural Resources, University of Nebraska, Lincoln, pp. 199–201.

Uresk, D.W., Schenbeck, G.L., 1987. Effect of zinc phosphide rodenticide on prairie dog colony expansion as determined from aerial photography. Prairie Naturalist 19, 57–61.

Walters, C., 1986. Adaptive Management of Renewable Resources. Macmillan, New York.

Wuerthner, G., 1997. Viewpoint: the black-tailed prairie dog—headed for extinction? J. Range Manage. 50 (5), 459–466.