

## A Technique for Evaluating Black-footed Ferret Habitat

by

Dean E. Biggins

*U.S. Fish and Wildlife Service  
National Ecology Research Center  
4512 McMurry Avenue  
Fort Collins, Colorado 80525*

Brian J. Miller

*Conservation and Research Center  
National Zoological Park  
Smithsonian Institution  
Front Royal, Virginia 22630*

Louis R. Hanebury

*U.S. Fish and Wildlife Service  
National Ecology Research Center  
4512 McMurry Avenue  
Fort Collins, Colorado 80525*

Bob Oakleaf

*Wyoming Game and Fish Department  
260 Buena Vista  
Lander, Wyoming 82520*

Adrian H. Farmer

*U.S. Fish and Wildlife Service  
National Ecology Research Center  
4512 McMurry Avenue  
Fort Collins, Colorado 80525*

Ron Crete

*U.S. Fish and Wildlife Service  
Fish and Wildlife Enhancement  
301 South Park, P.O. Box 10023  
Helena, Montana 59626*

and

Arnold Dood

*Montana Department of Fish, Wildlife, and Parks  
Montana State University Campus  
Bozeman, Montana 59717*

**Abstract.** In this paper, we provide a model and step-by-step procedures for rating a prairie dog (*Cynomys* sp.) complex for the reintroduction of black-footed ferrets (*Mustela nigripes*). An important factor in the model is an estimate of the number of black-footed ferret families a prairie dog complex can support for a year; thus, the procedures prescribe how to estimate the size of a prairie dog complex and the density of prairie dogs. Other attributes of the model are qualitative: arrangement of colonies, potential for plague and canine distemper, potential for prairie dog expansion, abundance of predators, future resource conflicts and ownership stability, and public and landowner attitudes about prairie dogs and black-footed ferrets. Because of the qualitative attributes in the model, a team approach is recommended for ranking complexes of prairie dogs for black-footed ferret reintroduction.

**Key words:** *Mustela nigripes*, *Cynomys*, habitat evaluation, prairie dogs, habitat model.

We are presenting a technique for evaluating habitat and potential reintroduction sites for the black-footed ferret (*Mustela nigripes*). We incorporated parts of existing models (Houston et al. 1986; Miller et al. 1988) into a new model. Our goal was the development of an easily understood and practical technique for evaluating the potential ability of prairie dog (*Cynomys* sp.) complexes (groups of prairie dog colonies in close proximity) to support black-footed ferrets with data that are easily and inexpensively collected. Our concern is simplicity. When choices of method or concept were available, we selected the simplest. Because ecological models are abstract constructs and simplifications of actual systems, they may approximate (but not duplicate) reality (Horton and Becak 1987). Thus, their value is in a capacity to contain conceptual information without complicating detail.

An evaluation should allow the ranking of habitat that is related to the number of breeding adult ferrets the habitat supports on a sustained basis. Furthermore, if a technique predicts the number of adult ferrets each site supports, progress in the recovery of the species (1,500 breeding adults in 10 or more populations, each with at least 30 adults; U.S. Fish and Wildlife Service 1988) can be rapidly estimated.

The following technique is based on two parts: (1) development of a numeric rating by energetics of ferrets, and (2) integration of the numeric rating with qualitative attributes into a comprehensive evaluation.

## Quantitative Attributes

### *The Formula*

We based quantitative evaluation of black-footed ferret habitat on abundance of prey because

the prey base is fundamentally important to the ferret. Variables are combined as follows into a rating index:

$$R = \sum_{i=1}^n (A_i \times P_i) / 763 \text{ for } (A_i \times P_i) \geq 272.5$$

where

R = the number of ferret family groups that could be supported by the prairie dog complex (prairie dog complex is defined later),

A = the area of the colony with at least 3.63 prairie dogs per ha,

P = the density of prairie dogs in area A (prairie dogs per ha),

763 = the number of prairie dogs, under typical conditions, required to support one ferret family group for 1 year,

272.5 = the minimum number of prairie dogs needed to support one ferret family group for 1 year,

i = colony number, and

n = the number of colonies in the complex.

Individual ratings are calculated for each colony in the complex, and the overall rating is the sum of those individual ratings. The rating, R, for a complex is an estimate of the number of ferret family groups the complex can support. Colonies with fewer than 272.5 prairie dogs do not contribute to the rating of a complex. In South Dakota, ferrets frequently reproduced on small colonies in nonconsecutive years, presumably because of depletion of prairie dogs (Henderson et al. 1969; Hillman and Linder 1973). Colonies with ratings of less than 1.0 are not expected to support family groups of ferrets every year.

Evidence indicates black-footed ferrets are obligate associates of prairie dogs, relying on them for prey and using their burrows for shelter. Anderson et al. (1986) listed 310 museum specimens of black-footed ferrets, only 6 of which were located outside the range of prairie dogs. In the Meeteetse, Wyoming, complex, Biggins et al. (1985) found that 98% of the locations of all radio-tagged ferrets were in prairie dog colonies. Prairie dogs were about 90% of the black-footed ferret's diet in South Dakota and Wyoming (Sheets et al. 1972; Campbell et al. 1987).

Several researchers speculated about the effect resource availability has on spacing strategies and population density (Riebesell 1974; Schoener 1983; von Schantz 1984; Stamps and Buechner 1985; Carr and MacDonald 1986). To reduce factors of environmental variation on small populations prone to extinction, a reserve should be chosen for the availability of the target species' food resources (Goodman 1987). Morris (1987) reported population density of temperate small mammals depended on quality of habitat. In addition, raptor fledgling rates correlated positively with prey levels (Southern 1970; Smith et al. 1981; Janes 1984; Hansen 1987), as did population densities of gray wolves (*Canis lupus*; Messier 1985), lynxes (*Lynx canadensis*; Brand et al. 1976), bobcats (*Lynx rufus*; Litvaitis et al. 1986), weasels (*Mustela* spp.; Robina 1960; Erlinge 1974; Fitzgerald 1977), and coyotes (*Canis latrans*; Clark 1972). Prey availability influenced habitat selection by river otters (*Lutra canadensis*; Melquist and Hornocker 1983) and least weasels (*Mustela nivalis*; Erlinge 1974).

Our approach requires the assumption that prey base determines potential ferret density. Social behavior may dictate a maximum ferret density regardless of prey abundance, but evidence is conflicting. At the Meeteetse complex, more than one family group of ferrets occupying the same area at the same time was not uncommon (Paunovich and Forrest 1987), and density of feral domestic ferrets (*Mustela putorius furo*) increased as prey became more abundant (Moors and Lavers 1981).

### Derivation of Rating Formula

#### Rationale

Recovery of the black-footed ferret depends on the number of breeding adult ferrets (U.S. Fish and Wildlife Service 1988). Thus, our formula is based on the prairie dog biomass that supports one family group of breeding adults and dependent young.

Higher densities of prairie dogs are needed for reproduction than for maintenance of individual ferrets. Erlinge (1974) suggested that in weasels a higher minimum rodent density was necessary for reproduction than for maintenance. Because of the litter, female weasels used a more restricted area when their food requirements were high (East and Lockie 1964). We assumed that female ferrets with litters would likewise restrict their movements during lactation and during the period from post-weaning to dispersal. As a result, they must hunt in the immediate area more intensively and successfully.

Development of our formula may be summarized in five steps:

1. Calculate the prairie dog biomass that black-footed ferret family groups need during the year.
2. Convert prairie dog biomass to prairie dog numbers by estimating quantity of food that ferrets waste, and average weight of live prairie dogs.
3. Sum mortality of prairie dogs from predation by ferrets and other causes.
4. Estimate number of needed prairie dogs to support mortality in step 3, assuming typical prairie dog reproductive rates.
5. Estimate minimum density of prairie dogs necessary to provide sufficient prey in the largest home range of a female ferret with young.

In steps 3 and 4, we used two approaches that lead to the two numbers in the formula. First, we defined the lower limits of habitat that support reproduction in ferrets by assuming low mortality of prairie dogs from causes other than predation by ferrets and by assuming a high reproductive rate in prairie dogs. Using these optimum conditions assures that potential habitat is not overlooked. Second, we used moderate estimates of prairie dog mortality and reproduction to approximate the ability of prairie dog colonies to support reproducing ferrets under more typical conditions. Application of these two principles defining lower limits of habitat and estimating average carrying capacity are illustrated later.

#### Calculation of Prairie Dog Biomass

Data from captive black-footed ferrets and from published information on other *Mustela* species were used to estimate energetic needs of black-footed ferrets. A single captive ferret ate 50–70 g prairie dog meat / day (Joyce 1988). Similarly, captive Siberian polecats (*Mustela eversmanni*) ate 62 g prairie dog meat / day (Powell et al. 1985).

Although energetic costs of gestation are low, two captive black-footed ferret females increased their consumption two and three times during lactation, and weaned black-footed ferret young ate about 100 g prairie dog meat/day during a period of rapid growth (D. Kwiatkowski, personal communication). In comparison, lactating least weasels increased consumption by a factor of three (East and Lockie 1964) and lactating fishers (*Martes pennanti*), by two to three (Powell and Leonard 1983). Based on field observations, Paunovich and Forrest (1987) speculated that a female black-footed ferret with a weaned litter of five may have been killing 0.6 prairie dogs/day.

We therefore separated a female ferret's energetic requirements into five stages throughout the year and estimated her daily intake during each of those stages. We assumed gestation lasts 42 days, lactation lasts 42 days, postweaning demands on the female and her litter of 3.3 young (average litter size reported by Forrest et al. 1988) last 80 days, replenishing the drain of previous demands by the litter lasts 51 days, and maintenance lasts the remaining 150 days. Thus, annual consumption of prairie dog meat by the female and her young is

#### Female:

|                                 |                               |
|---------------------------------|-------------------------------|
| Maintenance                     | 150 days × 60 g/day = 9,000 g |
| Gestation                       | 42 days × 70 g/day = 2,940 g  |
| Lactation                       | 42 days × 180 g/day = 7,560 g |
| Postweaning                     | 80 days × 75 g/day = 6,000 g  |
| Post-dispersal<br>replenishment | 51 days × 70 g/day = 3,570 g  |

#### Young:

$$3.3 \text{ young} \times 80 \text{ days} \times 100 \text{ g/day/young} \\ = 26,400 \text{ g}$$

Because several home ranges of females are often overlapped by a male's activity area (Fagerstone and Biggins 1984; Richardson et al. 1987), we assumed 0.5 males inhabit the female's area for 1 year, adding the following biomass requirement:

$$\text{Adult male: } 0.5 \text{ male} \times 365 \text{ days} \times 60 \text{ g} = 10,950 \text{ g}$$

$$\text{Total} \dots \dots \dots 66,420 \text{ g}$$

#### Conversion of Biomass to Prairie Dog Numbers

According to Hillman (cited personal communication in Stromberg et al. 1983), black-footed ferrets wasted 20% of the kill. In two studies, average weight of black-tailed prairie dogs (*Cynomys ludovicianus*) was 712 g (King 1955) and of white-tailed prairie dogs (*Cynomys leucurus*), 820 g

(Clark 1977). We assumed the average prairie dog weighs 760 g, therefore, the number of prairie dogs needed to meet annual consumption by black-footed ferrets is

$$\frac{66,420 \text{ g}}{0.8 \times 760 \text{ g/prairiedog}} = 109 \text{ prairiedogs}$$

#### Mortality of Prairie Dogs

Ferrets are not the only cause of mortality in prairie dogs. Results from the Meeteetse complex indicated that biomass of badgers (*Taxidea taxus*) probably exceeded biomass of ferrets, and the badgers fed frequently on prairie dogs. More radio-tagged prairie dogs were killed by raptors and coyotes than by badgers and ferrets (D. E. Biggins, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data). Mortality also may result from disease, parasites, other predators, hunters, and so on. Thus, losses of prairie dogs from other causes are assumed to be at least 50% and more typically 250% of predation by ferrets. The low and moderate estimates of mortality in prairie dogs are

1.  $109 \times 1.5 = 163.5$  prairie dogs / ferret family group / year and
2.  $109 \times 3.5 = 381.5$  prairie dogs / ferret family group / year.

#### Required Population of Prairie Dogs

It was difficult to select low and typical rates of increase for prairie dogs; reported ratios of young to adults vary from nearly 0.0 to more than 3.0. In two longer-term studies, Hoogland et al. (1988) found an average ratio of 0.6 and Menkens (1987) reported an average ratio of 1.4. We use the midpoint (1.0) as the typical rate. Hoogland et al. (1988) showed an inverse relation between density of adults and production of young, leading to our choice of 1.5 at the lower limit of good habitat (where prairie dog density is only 3.6/ha). Combining the low loss estimate (losses from other predators that equal 50% of predation by ferrets) with the high reproductive rate (1.5) and combining moderate loss (250%) with the moderate reproductive rate (1.0) provides estimates of required prairie dog populations. We assumed the population was stable from year to year. Because prairie dogs are routinely counted when population levels peak in summer, the annual production is added to the base population. Thus, the two estimates are

1.  $163.5 / 1.5 + 163.5 = 272.5$  prairie dogs (mid-July) and
2.  $381.5 / 1.0 + 381.5 = 763$  prairie dogs (mid-July)

### Minimum Prairie Dog Density

For the purposes of defining and mapping all habitat capable of supporting reproducing ferrets, low prairie dog population requirements must be converted to a density value. Because a female ferret's moves are especially restricted during litter rearing, we assumed an area of activity no larger than 75 ha (an average of hectares of prairie dogs at the Meeteetse complex divided by number of ferrets during 1983 and 1984). If 272.5 prairie dogs must be present in 75 ha, the minimum density is

$$272.5/75 = 3.63 \text{ prairie dogs/ha}$$

With an observability index of 0.495 (D. E. Biggins and G. E. Menkens, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data), a visual count of 1.8 white-tailed prairie dogs / ha represents an estimated density of 3.63 white-tailed prairie dogs / ha. With an index of 0.566 (D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data), a visual count of 2.06 black-tailed prairie dogs / ha represents an estimated density of 3.63 black-tailed prairie dogs / ha. On nine sites at the Meeteetse complex where black-footed ferrets raised litters, the lowest visual count was 2.59 prairie dogs / ha (D. E. Biggins, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data). The minimum visual count of 1.8 prairie dogs / ha based on energetics thus seems reasonable.

The rating formula is based on breeding habitat of ferrets, defined as having at least 3.63 prairie dogs / ha in mid-July. We recognized that many prairie dog colonies below this threshold value may support nonbreeding ferrets and, in fact, these buffer habitats may be critical to the persistence of ferrets. If two-thirds of the ferret population is lost each year (Forrest et al. 1985), a buffer of replacement animals could be instrumental in maintaining breeding populations for the long term. We initially planned to give buffer habitat some value in our calculations, but after considering the lower energetic demands of nonbreeding ferrets and the demography of the replacement process, we concluded that all complexes have an excess of buffer habitat and the attribute need not be included in the rating.

### Data Collection and Evaluation

Ideally, the quantitative rating involves partitioning a prairie dog complex into the maximum

number of ferret activity areas ( $\leq 75$  ha) with at least 273 prairie dogs (with a few added constraints on shape of parcels). The concept is simple, but a map of a partitioned complex is impossible to construct because prairie dogs cannot be economically inventoried on large areas. Instead, sampling schemes that are a compromise between accuracy, precision, and practicality are employed.

### *Occupied Burrows as Indicators of Prey Abundance*

Visual counts of white-tailed prairie dogs underestimate actual densities but correlate with estimated density from mark-recapture (Fagerstone and Biggins 1986; Menkens et al. 1991). Similarly, estimated densities from visual counts of radio-tagged black-tailed prairie dogs are too low (D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data).

Visual counts of prairie dogs are more costly and time-consuming than counts of burrows; therefore, we propose counting burrows to assess quality of the prey (at least during initial screening). The correlation between estimates of prairie dog density and density of total burrows seems weak (King 1955; Menkens et al. 1988; D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data). The correlation is much stronger if only active burrows are used. D. E. Biggins and G. E. Menkens (U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data) found a high correlation ( $r = +0.95$ ) between counts of active burrows of white-tailed prairie dogs and estimates of prairie dog density.

A priori we knew that counts of prairie dogs are zero in the absence of occupied burrows and the relation between counts of active burrows and white-tailed prairie dogs was best described by a regression line through the origin ( $r = +0.94$ ; Zar 1984):

$$\text{prairie dog count} = 0.073 \times \text{number of active burrows.}$$

If 3.63 prairie dogs / ha is the lower limit of good ferret habitat and a population density of 3.63 equals a visual count of 1.8 white-tailed prairie dogs, then good habitat should have at least 25 active burrows / ha (active burrows =  $1.8 / 0.073$ ).

The relation between counts of active burrows and black-tailed prairie dogs was best described by a regression line through the origin ( $r = +0.65$ ; Zar

1984). We obtained the best fit for black-tailed prairie dog counts and active burrows with:

$$\text{prairie dog count} = 0.179 \times \text{number of active burrows.}$$

If 3.63 prairie dogs / ha is the lower limit of good ferret habitat and a population density of 3.63 equals a visual count of 2.06 black-tailed prairie dogs, then good habitat should have at least 12 active burrows / ha (active burrows =  $2.06 / 0.179$ ). A technique for sampling burrow density is described later, but colonies must first be mapped and the complex defined.

### Mapping of Colonies

Inconsistencies in mapping can affect the rating. We attempted to solve this potential problem by (1) further standardizing mapping and (2) choosing a quantitative evaluation that is minimally sensitive to mapping. For the proposed technique, mapping can have a significant effect on defining the complex. Failure to map good habitat can affect calculations, but mapping marginal habitat does not increase the rating because areas of low prairie dog density are defined and excluded by the sampling of burrows. Forrest et al. (1985) defined a colony as a minimum of 10 burrow openings / ha. For our evaluation, a minimum of 20 burrows/ha is more appropriate. Resolution, the choice of the smallest parcel to be mapped, is equally important. We suggest viewing a colony as a group of 5-ha parcels, each of which must contain at least 100 burrows to be placed on the map. This implies that colonies smaller than 5 ha can be ignored.

Colonies of black-tailed prairie dogs have been mapped from black and white aerial photography (Cheatheat 1973; Tietjen et al. 1978) and from color infrared photography (Dalsted et al. 1981; Schenbeck and Myhre 1986). The scale of the photography was from 1:15,000 to 1:24,000. The primary characteristic that photo-interpreters used was the distinctive vegetative change caused by black-tailed prairie dogs; these vegetative ecotones were easily seen on color infrared photos. Costs of photo acquisition and interpretation ranged from \$0.10 to \$3.70/ha. Black and white aerial photography of the white-tailed prairie dog complex at the Meeteetse complex (ASCS, 1:20,000 and 1:40,000) was inadequate for accurate mapping of all colonies. Upland colonies were well defined because the tone of mounds contrasted with the background (the deeper soils were lighter colored than surface soil), but colonies on the alluvial bottomlands were

poorly defined or could not be seen at all. Color infrared photography at a scale of 1:5,000 was acquired at a cost of about \$2.30 / ha and had adequate resolution for the detection of individual burrows and mounds on both soil types. Mapping of white-tailed prairie dog colonies must be based on the distribution of burrows because there seldom is a noticeable difference in vegetation. Aerial photography may not be suitable for the mapping of all complexes but is probably the most efficient aide for the mapping of many areas (especially of complexes of black-tailed prairie dogs. For comparisons of reintroduction sites and broad overviews of complexes (transfer to 1:100,000), the scales of original maps should be standardized (perhaps 1:24,000).

### *Definition of the Complex*

Forrest et al. (1985) described a complex of prairie dog colonies as "a group of prairie dog colonies distributed so that individual black-footed ferrets (and thus genetic material) can migrate among them commonly and frequently." The expression "commonly and frequently" seems to refer to types of moves actually observed at the Meeteetse complex rather than long distance dispersal between widely separated colonies. The longest nightly moves observed in black-footed ferrets were about 7 km (Biggins and Fagerstone 1984; Richardson et al. 1987). We adopted that 7 km distance in the circumscription technique presented below. The process of circumscribing a prairie dog complex is analogous to describing the home range of an animal from a sample of locations. The following set of rules serves as a practical and biologically reasonable procedure for circumscribing a complex of prairie dog colonies (for a diagrammatic example of a simulated complex refer to Fig. 1):

1. Start at the northernmost point of the northernmost colony.
2. Pivot a 7 km-long line segment clockwise from due north until it touches a point on a colony. The line between the initial point and the second point forms the first segment of the polygon.
3. From the second point, superimpose the line over the first segment, then pivot the 7 km line clockwise until it touches a third point on a colony. This forms the second segment of the polygon.
4. If the 7-km line cannot be pivoted to another colony without bisecting the colony on which it is positioned, move clockwise around that col-

- ony's perimeter until step 3 can be accomplished. The convex perimeter can thus become a segment of the boundary of the complex.
5. Continue until the polygon becomes closed.
  6. In rare circumstances, a complex may have one or more large spaces without prairie dogs (diameter at least 7 km). Delete the space from the area of the complex, circumscribing it as follows:
    - (a) start at the southernmost point of the northernmost colony in the empty space;
    - (b) pivot a 7 km-long line counterclockwise from due south until it touches a point on a colony;
    - (c) if the 7-km line cannot be pivoted to another point, move counterclockwise around that perimeter until (b) can be accomplished; and
    - (d) repeat step (b) until the polygon becomes closed.

7. If an impassable barrier (to ferrets) splits the complex, the resulting parts must be redefined as two or more complexes with the method above.
8. Calculate the area with a polar planimeter.

### Sampling of Burrow Density

We offer the following suggestions for sampling burrow densities on prairie dog colonies. A sample data sheet is provided (Fig. 2).

1. Use strip transects 1,000 m  $\times$  3 m and a Rotapete measuring wheel (for length) onto which a 3-m piece of electrical conduit is attached (for width) to establish length and width of these 0.3 ha transects. Wires hanging from ends of the conduit facilitated the occasional decision of whether to include borderline burrows. A burrow was included if more than half of the opening was within the transect swath.

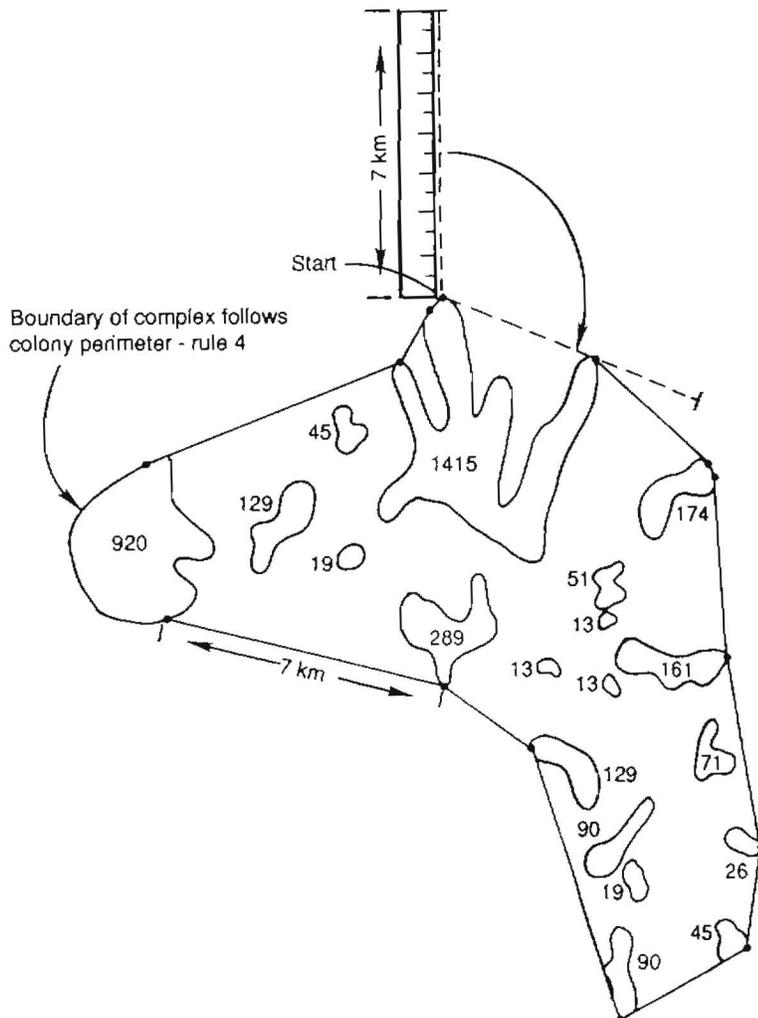


Fig. 1. Circumscribing a complex of prairie dog colonies. The number in or adjacent to a colony is its area in hectares.



Orientation of the transects is determined by compass heading, but a straight line can be maintained by heading toward a distant point identified by a compass heading. The compass heading is important because it must be exactly reversed (after moving over to achieve proper spacing). If the colony border is reached in the middle of a transect, the transect may be continued during the spacing move and subsequently in the opposite direction; thus, some transects may be U-shaped. When approaching the colony boundary (do not let burrow density bias the choice of turning point), the observer must select a meter reading (on the Rolatape measuring wheel) and turn at that reading.

8. Avoid several pitfalls. Keep the transect as straight as possible. Above all, do not let distribution of burrows bias direction of travel. A straight course decreases the chance of divergent and overlapping transects on long, multi-transect hikes. Sampling must be done only in mapped colonies. If Rolatape measuring wheels are used in colonies with very uneven topography or heavy shrub cover, they have to be tested under prevailing conditions and a correction factor has to be developed. Wheels measured distance with less than 1% error on most prairie dog colonies (D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data).
9. Each person can be expected to complete 10–20 transects / day. At the Meeteetse complex, the average was 14 transects / person / day.
10. Sampling should be conducted during mid-June through August after young emerged.

### *Evaluation of Data*

For an evaluation of habitat in each colony in the complex, counts of active burrows have to be available from a sample of 0.3-ha strip transects and colony size must be known. Proceed as follows:

1. Estimate the proportion of good habitat (equal to habitat capable of supporting ferret reproduction) as the number of transects with at least 25 active white-tailed prairie dog burrows / ha divided by the total number of transects or as the number of transects with at least 12 active black-tailed prairie dog burrows / ha divided by the total number of transects.
2. Estimate area of good habitat by multiplying proportion of good habitat by colony size.
3. Calculate average density of occupied burrows for only good habitat. Because each transect

covers 0.3 ha, at least eight occupied burrows of white-tailed prairie dogs must have been counted along each transect (25 occupied burrows / ha multiplied by 0.3 ha) or four occupied burrows of black-tailed prairie dogs along each transect (12 occupied burrows / ha multiplied by 0.3 ha).

4. Convert the density of occupied burrows to density of white-tailed prairie dogs (PD DEN).

$$\text{PD DEN} = (0.073 \times \text{active burrow density}) / 0.495$$

Convert the density of occupied burrows to density of black-tailed prairie dogs (PD DEN).

$$\text{PD DEN} = (0.179 \times \text{active burrow density}) / 0.566$$

5. Estimate the number of prairie dogs on good habitat by multiplying the result of calculation number 2 by the result of calculation number 4.
6. Estimate the number of ferret family groups that the colony supports by dividing the result from calculation number 5 by 763. If the result of calculation number 5 was less than 272.5, the colony receives a rating of zero (0).
7. The rating for the complex is the sum of all colony ratings.

Reintroduction sites for black-footed ferrets should be a minimum of about 400 ha (combined area of all colonies). A group of small complexes requires intensive management as habitat for a metapopulation of ferrets (Clark 1986; Brussard and Gilpin 1989; Harris et al. 1989). Complexes larger than 400 ha are desirable because the degree of human intervention is inversely related to complex size.

The quantitative model is a valuable aid in ranking reintroduction sites for black-footed ferrets, especially if its results are considered in combination with other qualitative criteria to be described later. The usefulness of estimating numbers of ferrets that can be supported in a complex has been emphasized, but the result must be viewed as only an approximation. The accuracies of the original estimated density of active burrows, the conversion from burrows to prairie dog counts, and counts to estimate density are uncertain. Many assumptions were made about energetics and demographic processes. In particular, natality and mortality of prairie dogs from other than predation have profound effects on the estimate, and both are expected to be highly variable.

Our evaluation of varying configurations of prairie dog complexes was hindered by lack of

data. Only two prairie dog complexes with ferrets (Mellette County, South Dakota, and Meeteetse, Wyoming) were studied. These complexes had extremely different configurations and were occupied by different species of prairie dogs. It should not be assumed that the South Dakota or Wyoming complexes were good habitat for ferrets just because ferrets persisted on them longer than elsewhere. The sequence of extinction of ferret populations may have been highly influenced by chance events when habitat became fragmented.

### *The Meeteetse Complex*

Evaluation of the Meeteetse complex in 1988 (Table) illustrates the described computations. A computer spreadsheet (e.g., LOTUS, MULTIPLAN, QUATTRO) is convenient for manipulating data.

The described quantitative process seems reasonable when results are compared with data and conclusions from other studies. Forrest et al. (1985) predicted a need for 40–60 ha of habitat per adult ferret at a mean density of 54.5 ha / adult at the Meeteetse complex. The ratio of adult males to adult females was about 2:1 (Forrest et al. 1988),

and male home ranges overlapped those of females (Fagerstone and Biggins 1984; Richardson et al. 1987). If 16.7 males are added to 33.4 females (Table) and the total of 50.1 is divided into 2727 (Table; hectares of good habitat), the result of 54.4 ha / adult ferret is within the predicted 40–60 ha / ferret. Assuming a high density of prairie dogs (30/ha) and using the minimum habitat requirements of our model (272.5 prairie dogs), a stable prairie dog population may support a female ferret's reproduction in a 9-ha area. Black-footed ferret families were raised on colonies as small as 10 ha in South Dakota (Hillman et al. 1979), and female European polecats, a similar species, used small home ranges (12.4 ha) when prey was abundant (Moors and Lavers 1981).

### **Integration of Quantitative and Qualitative Information for an Evaluation**

Some important features of prairie dog complexes are not quantifiable. Miller et al. (1988) attempted to quantitatively incorporate two sociopolitical factors (landownership and

Table. *Attributes of the 1988 evaluation of the Meeteetse prairie dog complex that led to an estimate of black-footed ferret families each prairie dog town can support.*<sup>a</sup>

| Town                 | Transects (No.) | Size (ha)      | % good habitat | Ha             | Burrows / ha | Prairie dogs / ha | Total prairie dogs <sup>b</sup> | R <sub>i</sub> |
|----------------------|-----------------|----------------|----------------|----------------|--------------|-------------------|---------------------------------|----------------|
| Long Hollow          | 52              | 196.5          | 0.519          | 102.0          | 57.5         | 8.5               | 865.5                           | 1.1            |
| Lot 58               | 10              | 48.0           | 1.000          | 48.0           | 86.0         | 12.7              | 608.8                           | 0.8            |
| New Town             | 9               | 55.0           | 0.889          | 48.9           | 65.0         | 9.6               | 468.6                           | 0.6            |
| BLM 10               | 17              | 74.0           | 1.000          | 74.0           | 69.4         | 10.2              | 757.5                           | 1.0            |
| BLM 13               | 39              | 185.5          | 0.795          | 147.4          | 60.1         | 8.9               | 1,305.9                         | 1.7            |
| Rawhide              | 50              | 253.0          | 0.780          | 197.3          | 108.5        | 16.0              | 3,158.6                         | 4.1            |
| Spring Creek         | 71              | 459.5          | 0.944          | 433.6          | 89.2         | 13.2              | 5,706.0                         | 7.5            |
| Pickett / Grave      | 127             | 679.0          | 0.669          | 454.4          | 67.1         | 9.9               | 4,494.0                         | 5.9            |
| Core / Rose          | 268             | 1,901.5        | 0.373          | 709.5          | 38.6         | 5.7               | 4,034.3                         | 5.3            |
| 91 Town              | 13              | 270.0          | 0.538          | 145.4          | 41.8         | 6.2               | 895.2                           | 1.2            |
| Thomas               | 23              | 51.5           | 0.696          | 35.8           | 52.3         | 7.7               | 276.3                           | 0.4            |
| Tonapah              | 11              | 61.0           | 0.000          | 0.0            | 0.0          | 0.0               | 0.0                             | 0.0            |
| Pump Station         | 68              | 363.0          | 0.574          | 208.2          | 56.5         | 8.3               | 1,735.5                         | 2.3            |
| Hogg                 | 17              | 72.0           | 0.941          | 67.8           | 71.9         | 10.6              | 718.3                           | 0.9            |
| L Rawhide            | 7               | 191.0          | 0.286          | 54.6           | 58.3         | 8.6               | 469.5                           | 0.6            |
| <b>Complex total</b> | <b>782</b>      | <b>4,860.5</b> |                | <b>2,727.0</b> |              |                   | <b>25,494.1</b>                 | <b>33.4</b>    |

<sup>a</sup>R<sub>i</sub> = number of prairie dogs / 763

<sup>b</sup>Ha good habitat × (burrows / ha × 0.073) / 0.495)

development potential) into their model. In practice, it may be difficult to assign quantitative ratings to these categories and to some important biological categories. We therefore evaluate several biological and sociopolitical features qualitatively and integrate those rankings with the quantitative data.

### *Spatial Arrangement of Colonies*

The spatial arrangement of colonies in a complex has important ramifications and should be considered in the evaluation (Minta and Clark 1989). Complexes of equal colony area can consist of few closely-spaced large colonies, many widely-separated small colonies, or various combinations thereof. As colonies become smaller and their spacing more distant, ferret populations may suffer the following consequences: (1) reduced gene flow, (2) decreased ability to recolonize prairie dog colonies vacated because of stochastic events, (3) decreased ability to disperse to new colonies after initial reintroduction or to colonize newly established prairie dog colonies, and (4) lowered mating success. Effects of each would probably become serious at different points on the size per distance scale; for example, lowered mating success may only occur at the lower extremes of size and density. Nevertheless, the same morphology of a prairie dog complex that promotes easy moves among colonies also facilitates spread of disease. Thus, an argument can be made for separation of subpopulations of ferrets and prairie dogs.

Houston et al. (1986) proposed two variables to characterize configuration of a complex—intercolony distance and frequency distribution of colony sizes. Intercolony distance is intuitively appealing because it seems to reflect the amount of nonhabitat a ferret might have to cross when moving from colony to colony; the attribute has been referred to elsewhere (Hillman et al. 1979; Forrest et al. 1985). Houston et al. (1986) and Miller et al. (1988) recommend interpretation of intercolony distance with a nearest-neighbor technique (a distance from each colony to its nearest neighbor with distances often used twice). This measurement is influenced by clumping of colonies in a complex; distances between clumps of colonies are ignored. The frequency distribution of colony sizes gives a disproportionately higher value to large colonies than to small colonies. Both frequency distribution and intercolony distance are sensitive to inconsistencies in mapping that can persist despite efforts to

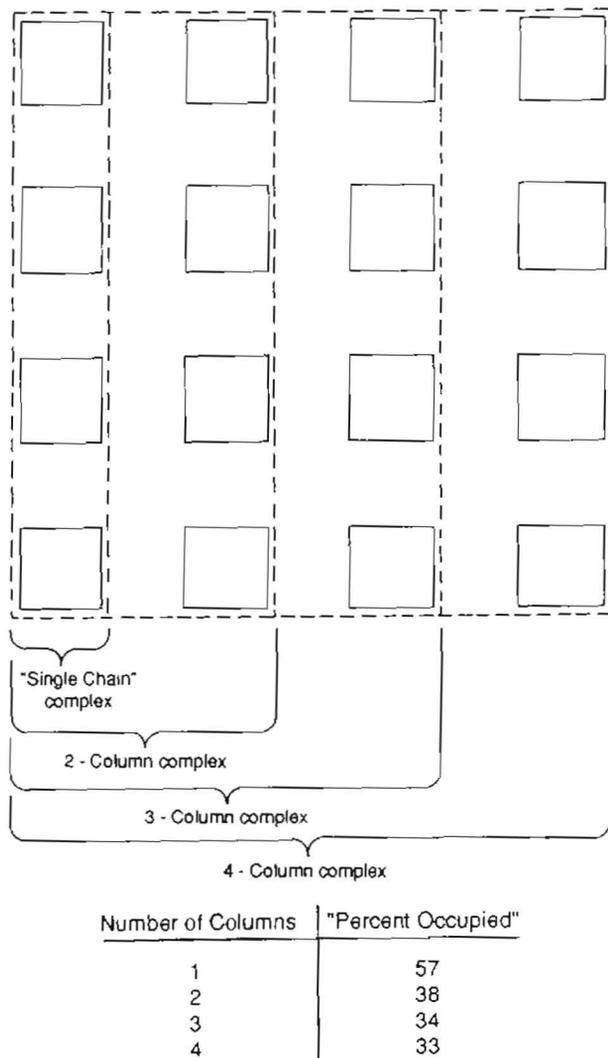
standardize (analogous to the taxonomic debates of lumpers and splitters).

We concur in principle with those who emphasize the potential importance of size, shape, and interspersed colonies in a complex (Forrest et al. 1985; Houston et al. 1986; Miller et al. 1988; Minta and Clark 1989). However, we remain troubled by the mentioned quantitative difficulties. Consequently, spatial arrangement of colonies is not incorporated into the quantitative section of the model but is represented in a qualitative assessment of biological features.

To aid in the qualitative evaluation, we suggest calculation of the percent of complex area occupied by prairie dog colonies as a partial descriptor of size and juxtaposition of prairie dog colonies in a complex (Miller et al. 1988). We tested the attribute of percent occupancy on simulated and actual complexes representing many combinations of complex and colony shape, intercolony distance, and colony size and found it reflected our concept of suitable habitat in a prairie dog complex configuration for ferrets. The treatment of the percent occupancy concept by Miller et al. (1988) had two problems: (1) the procedure for circumscribing a complex to calculate its overall area was not well described and (2) long, narrow chains of colonies greatly inflated the percentage. The first problem addressed in the previously described procedure for circumscribing a group of colonies.

The second problem occurs when the complex (or part of it) consists of a long narrow chain of single colonies, causing opposite sides of the same colonies to form opposite boundaries of the complex. An example can be illustrated (Fig. 3) by calculating percent occupied for a single string of four colonies, adding a second column of four more colonies with the same intercolony spacing and recalculating percent-occupied, and so on. Our primary concern is with large percent-occupied values calculated from single chains of colonies; the change rapidly became inconsequential with adding the third and fourth columns of colonies. Thus, an additional rule (9) was added to the method of circumscribing a complex, to be used only when calculating the percent-occupied attribute. The following rule upwardly adjusts areas of complexes with single chains of colonies.

**Rule 9.** If opposite sides of two or more consecutive colonies define opposite sides of a complex or part thereof, add to total area of complex the amount of area determined by the following expression:



**Fig. 3.** An example of the effect on percent-occupied caused by progressing from a single chain of colonies to a block of equally spaced colonies.

Adjustment = (average intercolony distance between colonies in the chain)  $\times$  (curvilinear length of chain)

Curvilinear length of chain is the length of a line through the approximate center of each colony extending continuously from the beginning of the first colony to the end of the last colony.

Rule 9 is an approximation to avoid extreme overrating of percent-occupied because of single chains of colonies and ignores narrow complexes that are more than a single colony wide. The technique, however, is repeatable and should function well in practice.

In the Mellette County complex, only about 1% of the complex was occupied by prairie dog colonies, but the area supported ferrets. The configuration of the Mellette County complex seems far from optimum; perhaps this contributed to ultimate failure of that ferret population. Nevertheless, existence of black-footed ferrets on the Mellette County complex suggests that we limit the influence of percent-occupied on the rating. All actual complexes we examined to date were less than 40% occupied by prairie dog colonies; 22% of the Meeteetse complex was occupied (Houston et al. 1986).

### *Other Biological and Sociopolitical Factors*

Quantification of the following biological and sociopolitical factors is also difficult (Fig. 4).

#### **Plague**

Factors of plague to consider are known occurrences of prairie dog die-offs and documentation of plague by the centers for disease control or others. Also consider the ratio of active to total burrows. If less than 50% of the burrows are active and no other significant causes of prairie dog mortality can be identified (e.g., poisoning), further investigate the possibility of plague (collect flea samples from prairie dog burrows, analyze blood samples from other carnivores such as badgers (Fitzgerald 1993), and look for prairie dog carcasses that can be examined.

#### **Canine Distemper**

Demonstration of canine distemper serum antibodies in other carnivores on or near potential reintroduction sites is cause for concern. An abundance of domestic or other wild carnivores may increase the probability of introduction and spread of canine distemper.

#### **Potential for Expansion of Prairie Dog Populations**

Assess the effects of other nearby prairie dog complexes and potential for prairie dog expansion inside and beyond present boundaries. Are other complexes sufficiently near to allow natural dispersal and consequent genetic exchange? Can other prairie dog colonies or small complexes between larger complexes serve as stepping stones for migration? Can prairie dog populations expand? Have prairie dog colony and complex size been controlled by poisoning or are limitations imposed by uncontrollable factors such as physiography? In short,

| FACTOR  | COMPARISON                 |   |
|---|----------------------------|---|
|   | Complex 9 versus Complex 5 |   |
| <u>Quantitative Biological:</u>                                 |                            |   |
| 1. Result from model  | +                          | 0 |
| <u>Qualitative Biological:</u>                                  |                            |   |
| 1. Arrangement of colonies                                      | +                          | 0 |
| 2. Plague potential   | 0                          | + |
| 3. Canine distemper potential                                   | +                          | 0 |
| 4. Other nearby complexes                                       | +                          | 0 |
| 5. Potential for prairie dog expansion                          | +                          | 0 |
| 6. Abundance of other predators                                 | 0                          | + |
| <u>Sociopolitical:</u>  |                            |   |
| 1. Future resource conflicts and ownership stability            | +                          | 0 |
| 2. Public and landowner attitudes and their potential to change | +                          | 0 |
| Overall rating and comments:                                    |                            |   |

Fig. 4. A sample checklist for comparing pairs of complexes.

consider the present situation and potential changes.

### Barriers

Are partial barriers to moves by ferrets in the complex? Rivers may not be completely impassable barriers but may seasonally interrupt moves. Little is known of its swimming ability, but a ferret can cross ice-covered bodies of water. Lines of cliffs and congested highways can also impede free moves of ferrets.

### Predators

Assess abundance and possible influences of other predators. Mammalian predators probably influence the dynamics of disease (Barnes 1993). Mammalian and avian predators prey on ferrets directly (Fagerstone and Biggins 1984) and compete for the same food. Presence of numerous great horned owls (*Bubo virginianus*), ferruginous hawks (*Buteo regalis*), golden eagles (*Aquila chrysaetos*), coyotes, badgers, and so on may make a site less appealing (than another site with fewer such animals) for reintroductions of ferrets, although control of predators during establishment of ferrets could partially compensate.

## Integration

We found agreement on factors of quality of potential habitat for ferrets (models by Houston

et al. 1986; Miller et al. 1988). The model presented here weights those factors differently than the other two models. To minimize disagreements in rating complexes and hence the weighting of each in the final evaluation, a democratic strategy by a team is probably the best solution. Team members can be nominated by the Interstate Coordinating Committee (ICC) and include (but not necessarily be limited to) present ICC participants. The only prerequisite should be familiarity with the ecology of black-footed ferrets and prairie dogs. We envision that (1) each team member independently rates all complexes (Fig. 4), (2) ratings are discussed in an open forum, (3) team members have the opportunity to change individual ratings, and (4) the individual ratings are combined. Individual ratings are made before collective discussions take place because some people have more aggressive, dynamic, and persuasive personalities than others; it seems preferable to have each evaluator's initial rating uninfluenced by the biases of others. On the other hand, diverse expertise and background may be represented on the team, and collective interchange of ideas would be beneficial.

A rating from all the variables without following some orderly process is difficult. Two formats for ranking complexes are offered.

1. Evaluate pairs of complexes by progressing down a checklist of factors (Fig. 4), again picking the best for each factor. Although we believe

biological attributes are the critical elements in identifying reintroduction sites, sociopolitical factors may be influential in the survival of ferrets. The final analysis must involve weighting of the individual factors according to relative importance and consideration of the margin of difference for each factor.

- Evaluate all possible pairs of complexes, identifying the best of each pair. The complex with the most wins has the highest rating, and so on. A matrix can be helpful (Fig. 5).

Results from evaluation of a group of complexes may remain valid for a short time. Prairie dog ecosystems are dynamic. Irrespective of anthropogenic control of prairie dogs, numbers of prairie dogs can change rapidly. Plague can rapidly eliminate prairie dog colonies (Lechleitner et al. 1968), but the number of prairie dogs in a colony can double annually (Knowles 1986), and colony area can expand by more than 80% per year (Dalsted et al. 1981). Other biotic components of the ecosystem and the sociopolitical aspects may also undergo changes. Thus, periodic reevaluation of sites

| A \ B     | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|-----------|---|---|---|---|---|---|---|---|---|
| 1         |   | + | + | + | + | 0 | 0 | 0 | 0 |
| 2         | 0 |   | + | 0 | 0 | 0 | 0 | 0 | 0 |
| 3         | 0 | 0 |   | 0 | 0 | 0 | 0 | 0 | 0 |
| 4         | 0 | + | + |   | + | 0 | 0 | 0 | 0 |
| 5         | 0 | + | + | 0 |   | 0 | 0 | 0 | 0 |
| 6         | + | + | + | + | + |   | + | + | + |
| 7         | + | + | + | + | + | 0 |   | + | + |
| 8         | + | + | + | + | + | 0 | 0 |   | 0 |
| 9         | + | + | + | + | + | 0 | 0 | + |   |
| Total +'s | 4 | 7 | 8 | 5 | 6 | 0 | 1 | 3 | 2 |

Fig. 5. Matrix for comparing complexes. If a complex identified in a column has a higher black-footed ferret rating than a complex in a row, place a plus sign (+) in the appropriate column and row block. Otherwise place a zero (0) in the block. When all pairs of complexes are rated, determine the number of plus sign (+) scores for each column. The column-complex with the most plus sign (+) scores has the best reintroduction potential based on black-footed ferret families it can support. In this example, nine complexes are compared. Column-complex 8 has a higher black-footed ferret rating than rows-complexes 6, 7, and 9; thus, it has a total score

is necessary until black-footed ferrets are released. Subsequent to release, monitoring is essential.

## Acknowledgments

We are indebted to Brent Houston for the long hours he spent testing measures of spatial arrangement. We thank Steve Minta and Steve Woodis, for helpful suggestions during that process. Tim Clark gave assistance at several stages in the development of this report. Many members of the Interstate Coordinating Committee provided constructive reviews of earlier drafts. Maps of actual prairie dog complexes were extracted from unpublished reports by the Utah Division of Wildlife Resources, Colorado Division of Wildlife, Wyoming Game and Fish Department, and National Park Service (Badlands National Park).

## References

- Anderson, E., S. C. Forrest, T. W. Clark, and L. Richardson. 1986. Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851. Great Basin Naturalist Memoirs 8:11-62.
- Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pages 27-36 in J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, editors. Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. U.S. Fish and Wildlife Service, Biological Report 93(13).
- Biggins, D. E., and K. A. Fagerstone. 1984. Movements and activity of black-footed ferrets (*Mustela nigripes*). American Society of Mammalogists, 64th Annual Meeting. Abstract.
- Biggins, D. E., M. H. Schroeder, S. C. Forrest, and L. Richardson. 1985. Movements and habitat relationships of radio-tagged black-footed ferrets. Pages 11.1-11.17 in S. H. Anderson and D. B. Inkley, editors. Proceedings of the black-footed ferret workshop. Wyoming Game and Fish Department, Cheyenne.
- Brand, C. J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. Journal of Wildlife Management 40:416-428.
- Brussard, P. F., and M. E. Gilpin. 1989. Demographic and genetic problems associated with small population size, with special reference to the black-footed ferret *Mustela nigripes*. Pages 37-48 in U. S. Seal, E. T. Thorne, M. A. Bogan, and S. H. Anderson, editors. Conservation biology of the black-footed ferret. Yale University Press, New Haven, Conn.

- Campbell, T. M., III, T. W. Clark, L. Richardson, S. C. Forrest, and B. R. Houston. 1987. Food habits of Wyoming black-footed ferrets. *American Midland Naturalist* 117:208-210.
- Carr, G. M., and D. W. MacDonald. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behavior* 34:1540-1549.
- Cheatheam, L. K. 1973. Censusing prairie dog colonies using aerial photographs. Pages 78-88 in R. L. Linder and C. N. Hillman, editors. *Proceedings of the black-footed ferret and prairie dog workshop*. South Dakota State University Publications, Brookings.
- Clark, T. W. 1972. Influence of jackrabbit density on coyote population. *Journal of Wildlife Management* 36:343-356.
- Clark, T. W. 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Milwaukee Public Museum Publication in Biology and Geology 3. 97 pp.
- Clark, T. W. 1986. Some guidelines for management of the black-footed ferret. *Great Basin Naturalist Memoirs* 8:160-168.
- Dalsted, K. J., S. Sather-Blair, B. K. Worcester, and R. Klukas. 1981. Application of remote sensing to prairie dog management. *Journal of Range Management* 34:218-223.
- East, K., and J. D. Lockie. 1964. Observations on a family of weasels (*Mustela nivalis*). *Proceedings of the Zoological Society of London* 114:339-349.
- Erlinge, S. 1974. Distribution, territoriality, and number of weasel, *Mustela nivalis*, in relation to prey abundance. *Oikos* 25:308-314.
- Fagerstone, K. A., and D. E. Biggins. 1984. Home range and mortality of a population of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming. *American Society of Mammalogists, 64th Annual Meeting*. Abstract.
- Fagerstone, K. A., and D. E. Biggins. 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.
- Fitzgerald, B. M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *Journal of Animal Ecology* 46:367-397.
- Fitzgerald, J. P. 1993. The ecology of plague in Gunnison's prairie dogs and suggestions for the recovery of black-footed ferrets. Pages 50-59 in J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, editors. *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret*. U.S. Fish and Wildlife Service, Biological Report 93(13).
- Forrest, S. C., T. W. Clark, L. Richardson, and T. M. Campbell, III. 1985. Black-footed ferret habitat: some management and reintroduction considerations. Wyoming Bureau of Land Management Wildlife Technical Bulletin 2. 49 pp.
- Forrest, S. C., D. E. Biggins, L. Richardson, T. W. Clark, T. M. Campbell, III, K. A. Fagerstone, and E. T. Thorne. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981-1985. *Journal of Mammalogy* 69:261-273.
- Goodman, D. 1987. How do any species persist? Lessons for conservation biology. *Conservation Biology* 1:59-62.
- Hansen, A. J. 1987. Regulation of bald eagle reproductive rates in southeast Alaska. *Ecology* 68:1387-1392.
- Harris, R. B., T. W. Clark, and M. L. Shaffer. 1989. Extinction probabilities for isolated black-footed ferret populations. Pages 69-82 in U.S. Seal, E. T. Thorne, M. A. Bogan, and S. H. Anderson, editors. *Conservation biology of the black-footed ferret*. Yale University Press, New Haven, Conn.
- Henderson, F. R., P. F. Springer, and R. Adrian. 1969. The black-footed ferret in South Dakota. *South Dakota Department of Game, Fish and Parks Technical Bulletin* 4:1-37.
- Hillman, C. N., and R. L. Linder. 1973. The black-footed ferret. Pages 10-20 in R. L. Linder and C. N. Hillman, editors. *Proceedings of the black-footed ferret and prairie dog workshop*. South Dakota State University Publications, Brookings.
- Hillman, C. N., R. L. Linder, and R. B. Dahlgren. 1979. Prairie dog distributions in areas inhabited by black-footed ferrets. *American Midland Naturalist* 102:185-187.
- Hoogland, J. L., D. K. Angell, J. G. Daley, and M. C. Radcliffe. 1988. Demography and population dynamics of prairie dogs. Pages 18-22 in Eighth Great Plains wildlife damage control workshop. U.S. Forest Service General Technical Report RM-154.
- Horton, J. C., and C. J. Becak. 1987. Modeling for biologists. *BioScience* 37:808-809.
- Houston, B. R., T. W. Clark, and S. Minta. 1986. Habitat suitability index model for the black-footed ferret: A method to locate transplant sites. *Great Basin Naturalist Memoirs* 8:99-114.
- Janes, S. W. 1984. Influences of territorial competition and interspecific competition on red-tailed hawk reproductive success. *Ecology* 65:862-870.
- Joyce, S. L. 1988. Feeding behavior and water requirements of black-footed ferrets (*Mustela nigripes*). M.S. thesis, University of Wyoming, Laramie. 82 pp.
- King, J. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog colony in the Black Hills of South Dakota. *Contributions from the Laboratory of Vertebrate Biology of the University of Michigan* 67. 123 pp.
- Knowles, C. J. 1986. Population recovery of black-tailed prairie dogs following control with zinc phosphide. *Journal of Range Management* 39:249-251.
- Lechleitner, R. R., L. Kartman, M. I. Goldenberg, and B. W. Hudson. 1968. An epizootic of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in south-central Colorado. *Ecology* 49:734-743.

- Litvaitis, J. A., J. A. Sherburne, J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. *Journal of Wildlife Management* 50:110-117.
- Melquist, W. E., and M. G. Hornocker. 1983. Ecology of river otters in west central Idaho. *Wildlife Monographs* 83. 60 pp.
- Menkens, G. E. 1987. Temporal and spatial variation in white-tailed prairie dog (*Cynomys leucurus*) populations and life histories in Wyoming. Ph.D. dissertation, University of Wyoming, Laramie. 167 pp.
- Menkens, G. E., B. J. Miller, and S. H. Anderson. 1988. White-tailed prairie dog ecology in Wyoming. Pages 34-38 in Eighth Great Plains wildlife damage control workshop. U.S. Forest Service General Technical Report RM-154.
- Menkens, G. E., D. E. Biggins, and S. H. Anderson. 1991. Visual counts as an index of white-tailed prairie dog density. *Wildlife Society Bulletin* 18:290-296.
- Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Canadian Journal of Zoology* 63:1068-1077.
- Miller, B. J., G. E. Menkens, and S. H. Anderson. 1988. A field habitat model of black-footed ferrets. Pages 98-102 in Eighth Great Plains wildlife damage control workshop. U.S. Forest Service General Technical Report RM-154.
- Minta, S., and T. W. Clark. 1989. Habitat suitability analysis of potential translocation sites for black-footed ferrets in north-central Montana. Pages 29-46 in T. W. Clark, D. Hinckley, and T. Rich, editors. *The prairie dog ecosystem: Managing for biological diversity*. Montana Bureau of Land Management, Billings.
- Moors, P. D., and R. B. Lavers. 1981. Movements and home range of ferrets (*Mustela furo*) at Pukepuke Lagoon, New Zealand. *New Zealand Journal of Zoology* 8:413-422.
- Morris, D. W. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- Paunovich, R., and S. C. Forrest. 1987. Activity of a wild black-footed ferret litter. *Prairie Naturalist* 19:159-162.
- Powell, R. A., and R. D. Leonard. 1983. Sexual dimorphism and energy requirements for reproduction of female fisher (*Martes pennanti*). *Oikos* 40:166-174.
- Powell, R. A., T. W. Clark, L. Richardson, and S. C. Forrest. 1985. Black-footed ferret (*Mustela nigripes*) energy expenditure and prey requirements. *Biological Conservation* 34:1-15.
- Richardson, L., T. W. Clark, S. C. Forrest, and T. M. Campbell, III. 1987. Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming. *American Midland Naturalist* 117:225-239.
- Riebesell, J. F. 1974. Paradox of enrichment in competitive systems. *Ecology* 55:183-187.
- Robina, M. A. 1960. Some features of weasel (*Mustela nivalis* L.) ecology based on observations in the Moscow region. *Bjulleten Otbel Biology* 65:27-34.
- Schenbeck, G. L., and R. J. Myhre. 1986. Aerial photography for assessment of black-tailed prairie dog management on the Buffalo Gap National Grassland, South Dakota. U.S. Forest Service Report 86-7. Fort Collins, Colo.
- Schoener, T. W. 1983. Simple models of optimal feeding—territory size: A reconciliation. *American Naturalist* 121:608-629.
- Sheets, R. G., R. L. Linder, and R. B. Dahlgren. 1972. Food habits of two litters of black-footed ferrets in South Dakota. *American Midland Naturalist* 87:249-251.
- Smith, D. G., J. R. Murphy, and N. D. Woffinden. 1981. Relationships between jackrabbit abundance and ferruginous hawk reproduction. *Condor* 83:52-56.
- Southern, H. N. 1970. The natural control of a population of tawny owls, *Strix aluco*. *Journal of Zoology* 162:197-285.
- Stamps, J. A., and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *Quarterly Review of Biology* 60:155-181.
- Stromberg, M. R., R. L. Rayburn, and T. W. Clark. 1983. Black-footed ferret energy requirements: an energy balance estimate. *Journal of Wildlife Management* 47:67-73.
- Tietjen, H. P., J. F. Glahn, and K. A. Fagerstone. 1978. Aerial photogrammetry: A method for defining black-tailed prairie dog colony dynamics. Pages 244-247 in PECORA IV symposium on application of remote sensing data to wildlife management. Sioux Falls, S.Dak.
- U.S. Fish and Wildlife Service. 1988. Black-footed Ferret Recovery Plan. U.S. Fish and Wildlife Service, Denver, Colo. 154 pp.
- von Schantz, T. 1984. Spacing strategies, kin selection, and population regulation in altricial vertebrates. *Oikos* 42:48-58.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Hills, N.J. 708 pp



Biological Report 13  
July 1993

Proceedings of the Symposium on the  

---

**Management of Prairie Dog Complexes  
for the Reintroduction of the  
Black-footed Ferret**

Edited by

John L. Oldemeyer, Dean E. Biggins, and Brian J. Miller

*U.S. Fish and Wildlife Service  
National Ecology Research Center  
4512 McMurry Avenue  
Fort Collins, Colorado 80525*

and

Ronald Crete

*U.S. Fish and Wildlife Service  
4401 N. Fairfax Drive, Room 400  
Arlington, Virginia 22203*

U.S. Department of the Interior  
Fish and Wildlife Service  
Washington, D.C. 20240