

Evaluating Habitat for Black-footed Ferrets: Revision of an Existing Model

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Abstract

Black-footed ferrets (*Mustela nigripes*) are highly dependent on prairie dogs (*Cynomys* spp.) as prey, and prairie dog colonies are the only known habitats that sustain black-footed ferret populations. An existing model used extensively for evaluating black-footed ferret reintroduction habitat defined complexes by interconnecting colonies with 7-km line segments. Although the 7-km complex remains a useful construct, we propose additional, smaller-scale evaluations that consider 1.5-km subcomplexes. The original model estimated the carrying capacity of complexes based on energy requirements of ferrets and density estimates of their prairie dog prey. Recent data have supported earlier contentions of intraspecific competition and intrasexual territorial behavior in ferrets. We suggest a revised model that retains the fixed linear relationship of the existing model when prairie dog densities are <18/ha and uses a curvilinear relationship that reflects increasing effects of ferret territoriality when there are 18–42 prairie dogs per hectare. We discuss possible effects of colony size and shape, interacting with territoriality, as justification for the exclusion of territorial influences if a prairie dog colony supports only a single female ferret. We also present data to support continued use of active prairie dog burrow densities as indices suitable for broad-scale estimates of prairie dog density. Calculation of percent of complexes that are occupied by prairie dog colonies was recommended as part of the original habitat evaluation process. That attribute has been largely ignored, resulting in rating anomalies.

Keywords: black-footed ferret, burrows, carrying capacity, competition, *Cynomys*, energy, habitat, *Mustela nigripes*, prairie dog, territory

Introduction

By 1988, captive breeding of black-footed ferrets (*Mustela nigripes*) rescued from a failing population in Wyoming was becoming successful (Biggins and others, 1997), and a subcommittee of the Black-footed Ferret Interstate Coordinating Committee (ICC) addressed the challenge of locating, evaluating, and comparing sites for black-footed ferret reintroduction. Habitat for terrestrial species, including prairie dogs (*Cynomys* spp.), is commonly evaluated with respect to vegetative and physiographic features. Although we recognize the crucial link between prairie dogs and their environments, the extreme specialization of the black-footed ferret allows us to equate black-footed ferret habitat with prairie dog colonies. A habitat model now in common use was developed by the ICC to assess the ability of prairie dog colonies and complexes to support populations of black-footed ferrets (Biggins and others, 1993). The model arose from earlier descriptions and models of ferret habitat (Linder and others, 1972; Hillman and others, 1979; Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988), models of ferret energetics (Stromberg and others, 1983; Powell and others, 1985), data on ferret nutrition and food habits (Sheets and others, 1972; Campbell and others, 1987; Joyce, 1988), and information on behaviors of free-ranging ferrets (Hillman, 1968; Biggins and others, 1985; Paunovich and Forrest, 1987; Richardson and others, 1987). Biggins and others (1993) also provided a method for estimating approximate densities of prairie dogs from strip transect samples of active burrows and offered a technique for grouping colonies into complexes. Complexes were defined as clusters of colonies that could be circumscribed with 7-km line segments; colonies are sequentially added to a complex if they are separated by ≤ 7 km. Spaces within a complex that are devoid of prairie dogs are defined similarly.

We herein suggest changes to procedures described by Biggins and others (1993), based in part on information collected during 1991–2003 from reintroduced populations of black-footed ferrets, and we discuss aspects of the existing system needing renewed emphasis. Changes include assessing portions of complexes at a smaller scale (called subcomplexes), incorporating the effects of ferret territoriality

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in assessments of habitat carrying capacity, and limiting the effect of ferret territoriality on small habitat patches where social strife is unlikely to influence ferret use.

Subcomplexes

The initial impetus for considering smaller, more compact clusters of prairie dog colonies as subcomplexes stemmed from de facto procedures used to select and prioritize ferret release sites. Sites were intuitively regarded as high quality if colonies were closely spaced or large and if prairie dog densities were high. Release of ferrets took place on such “core” sites, with much less attention given to the remainder of the complex as defined by the 7-km procedure (Biggins and others, 1993). We describe a process, involving subcomplexes, that has been in practical use since 1999 by the U.S. Fish and Wildlife Service and partners to allocate ferrets.

On occasion, more than one cluster of colonies has been used as a release site, but ferret releases in each year have been conducted on relatively small portions of complexes. Following initial release(s), ferrets rather quickly populated some of these core release areas through natural reproduction; other clusters in a complex defined with the 7-km criterion were mostly populated with additional releases (e.g., Conata Basin, S. Dak.) or natural dispersal over longer time periods (Shirley Basin, Wyo.). Although lines of delineation are arbitrary, ferret movement within clusters where colonies were separated by ≤ 1.5 km was common. At UL Bend National Wildlife Refuge, Mont., for example, there were 88 intercolony moves by radio-tagged ferrets during 1994, 1995, and 1997 (Biggins, Godbey, Matchett, and Livieri, this volume); 77 (85.5 percent) of these moves were between colonies separated by < 1.5 km, but all moves were between colonies separated by < 2.1 km. In the Meeteetse, Wyo., complex of white-tailed prairie dogs (*Cynomys leucurus*) that supported the remnant ancestral population of ferrets, most colonies were interconnected with a 1.5-km maximum distance between them. Based on these experiences and data, we propose defining a subcomplex as a group of colonies that can be linked to one another with a series of line segments ≤ 1.5 km in length. The procedure for outlining a subcomplex will be further standardized by following the method used to circumscribe a complex (Biggins and others, 1993), but substituting a 1.5-km line segment for the 7-km line segment (fig. 1).

Territoriality and Carrying Capacity

Carrying capacity has been traditionally discussed in terms of populations of an organism and their food supply, with implications of sustainability of resources (Leopold, 1933). In that sense, the habitat model of Biggins and others (1993) attempts to estimate carrying capacity of prairie dog colonies for black-footed ferrets. Many organisms, however,

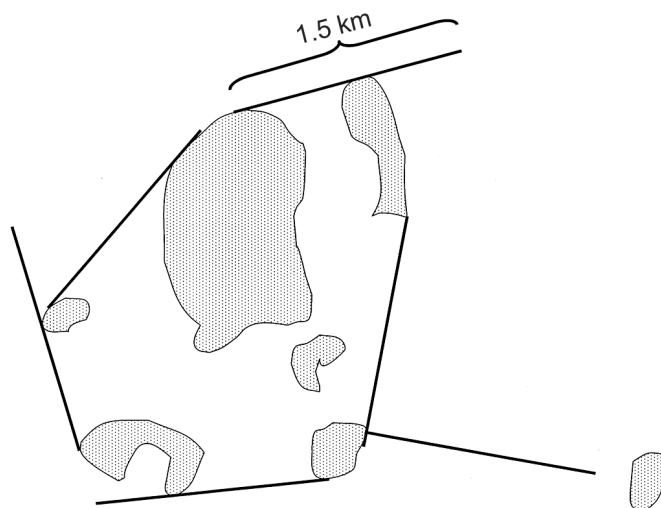


Figure 1. Procedure for circumscribing a subcomplex of prairie dog (*Cynomys* spp.) colonies by using a minimum intercolony distance of 1.5 km. See Biggins and others (1993) for additional details on the methodology.

seem to space themselves within habitat. Carnivores are often intrasexually territorial, but King’s (1990) chapter on “adjustable living spaces” provides evidence that there is an interaction between habitat quality (mainly abundance of prey) and territoriality for other *Mustela* species. The utility of estimating the upper limits of habitat to sustain organisms, whether such limits are imposed by food or other mechanisms, was evident in early attempts to model regulated growth with the logistic equation (Pearl and Reed, 1920) and in Leopold’s (1933) discussions of managing game for sustained yields. More recent efforts at modeling ferret population fluctuations require similar input (Bever and others, 1997).

Although somewhat conflicting evidence precluded considering ferret territoriality in their earlier model, Biggins and others (1993, p. 75) suggested that “social behavior may dictate a maximum ferret density regardless of prey abundance.” There is increasing evidence that black-footed ferret territoriality does indeed constrain predictions of the energetics model when prey may not be limiting. First, reintroduced ferret populations in South Dakota habitats seldom had average densities exceeding about 1 female per 30 ha, even though the energetics-based model often predicted 1 female per 20 ha or less. Additional evidence from ferrets released in Montana and South Dakota suggests that there is competition for good quality habitat (Biggins, Godbey, Matchett, and Livieri, this volume). These recent results are consistent with observations that female ferrets generally do not use overlapping areas (Richardson and others, 1987) and evidence of spacing in other *Mustela* species (Powell, 1979; King, 1990). The mounting evidence is sufficiently compelling that we here suggest adding a function to the simple linear relationship between densities of black-footed ferrets and prairie dogs that

will have increasing impact as ferret density rises. A guiding principle is parsimony; we do not suggest adding complexity that is unsupported empirically.

We revised the energetics-based model (Biggins and others, 1993) to allow an effect of territoriality that is initiated at densities of 18 prairie dogs per hectare, gradually increases in intensity, and reaches an asymptote of 0.04 ferret families per hectare at a prairie dog density of 42/ha (fig. 2). Because a black-footed ferret family includes one female, we are discussing female ferret density. A quadratic equation ($Y = a + bX + cX^2$) adequately approximates the proposed curvilinear relationship within the range 18–42 prairie dogs per hectare, where: Y = predicted density of female ferrets, X = density of prairie dogs, $a = -0.00456329$, $b = 0.00193283$, and $c = -0.00002083$. If there are <18 prairie dogs per hectare, the equation for the straight line segment of the graph remains $Y = 0.00131062X$, a slope determined by the existing energetically based estimates and a linear relationship between ferret density and prairie dog density. Although white-tailed prairie dogs occasionally have been found at densities >20/ha, the graph suggests (correctly, we believe) that density of female ferrets seldom will be limited by territoriality on white-tailed prairie dog habitat. In contrast, we believe that territorial behavior of female ferrets will commonly influence their spac-

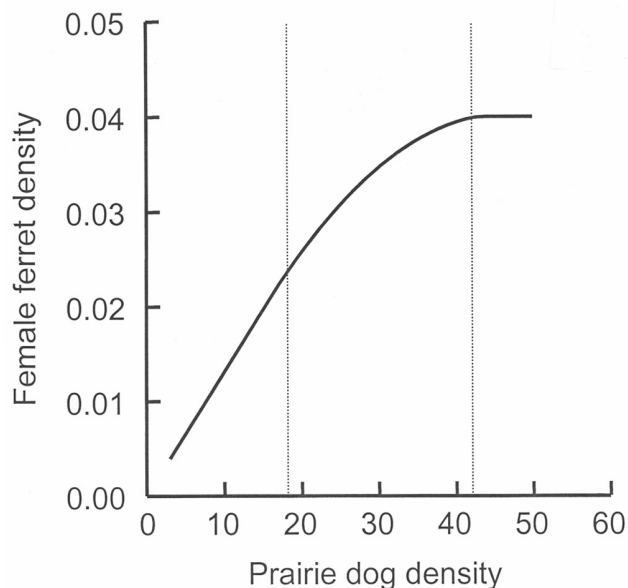


Figure 2. Hypothetical relationship between densities of prairie dogs (*Cynomys* spp.) and densities of female black-footed ferrets (*Mustela nigripes*) (individuals/ha), allowing territoriality to modify the linear relationship predicted by the energetics-based equation ($Y = X/763$) of Biggins and others (1993) at prairie dog densities >18/ha but defining an upper limit of 0.04 ferrets/ha. At intermediate prairie dog densities (18–42/ha), the increasing influence of territoriality is approximated by the quadratic equation $Y = a + bX + cX^2$, where Y = density of ferrets, X = density of prairie dogs, $a = -0.00456329$, $b = 0.00193283$, and $c = -0.00002083$.

ing on most black-tailed prairie dog (*Cynomys ludovicianus*) habitat. Under our proposed relationship, that influence will increase until female ferrets reach densities of about 1 ferret per 25 ha of habitat (the maximum density of 0.04 ferrets per hectare). We predict that prairie dog densities above 42/ha will not result in increased densities of territorial female ferrets, but these higher densities of prairie dogs may affect other population attributes such as ferret survival and productivity.

Habitat-induced Isolation

“Islands” or “peninsulas” of habitat with high densities of prairie dogs may support more ferret families than would large blocks of uniform habitat because some configurations of habitat can reduce among-female interaction. An “island” arrangement with a colony small enough to support just one female and her litter (figs. 3 and 4) seems likely to eliminate any potential for limiting effects of territoriality. A “peninsula” configuration removes that effect on two sides, but territorial spacing comes into play for end-to-end territories along linear habitat. The example of 20 ha of prairie dog colony needed to support a female and her litter (fig. 3) is somewhat conservative. Five of the nine ferret litters reported by Hillman and others (1979) in Mellette County, S. Dak., were raised on colonies <16 ha in area (one was 10 ha). A female ferret raised two kits on a 5-ha colony in Montana (fig. 4); however, it seems doubtful that the Montana female could have accomplished that feat without seriously depleting the prairie dog population, and her small litter suggests that conditions may have been suboptimal. At Meeteetse, Wyo., the smallest colonies that supported females with litters were about 50 ha, but white-tailed prairie dogs at Meeteetse occurred at much lower densities (about 7.7/ha, calculated from the visual count density of Clark and others (1985) divided by the sightability adjustment of 0.495 of Biggins and others (1993)) than did the black-tailed prairie dogs discussed above (Hillman and Linder, 1973). We accommodate the most extreme of these influences of colony sizes and shapes into the evaluation procedure with a provision that removes the effect of territoriality if a colony is sufficiently small and isolated to support just a single female. To facilitate evaluation of prairie dog complexes as habitat for black-footed ferrets, a spreadsheet with appropriate formulae is available from the authors.

Colonies as small as the minimum mapping unit (5 ha) suggested by Biggins and others (1993) may support a female and her litter. Usually, however, colonies <10 ha will not have sufficient numbers of prairie dogs to sustain both themselves and a ferret family. Depletion of prairie dogs can be expected on colonies <10 ha if they are occupied by a ferret family, and it seems unlikely that such small colonies will support ferret reproduction in consecutive years. Nevertheless, we propose allowing colonies as small as 5 ha to contribute to the family rating of a complex by using the direct linear equation (Biggins and others, 1993), without the influence of

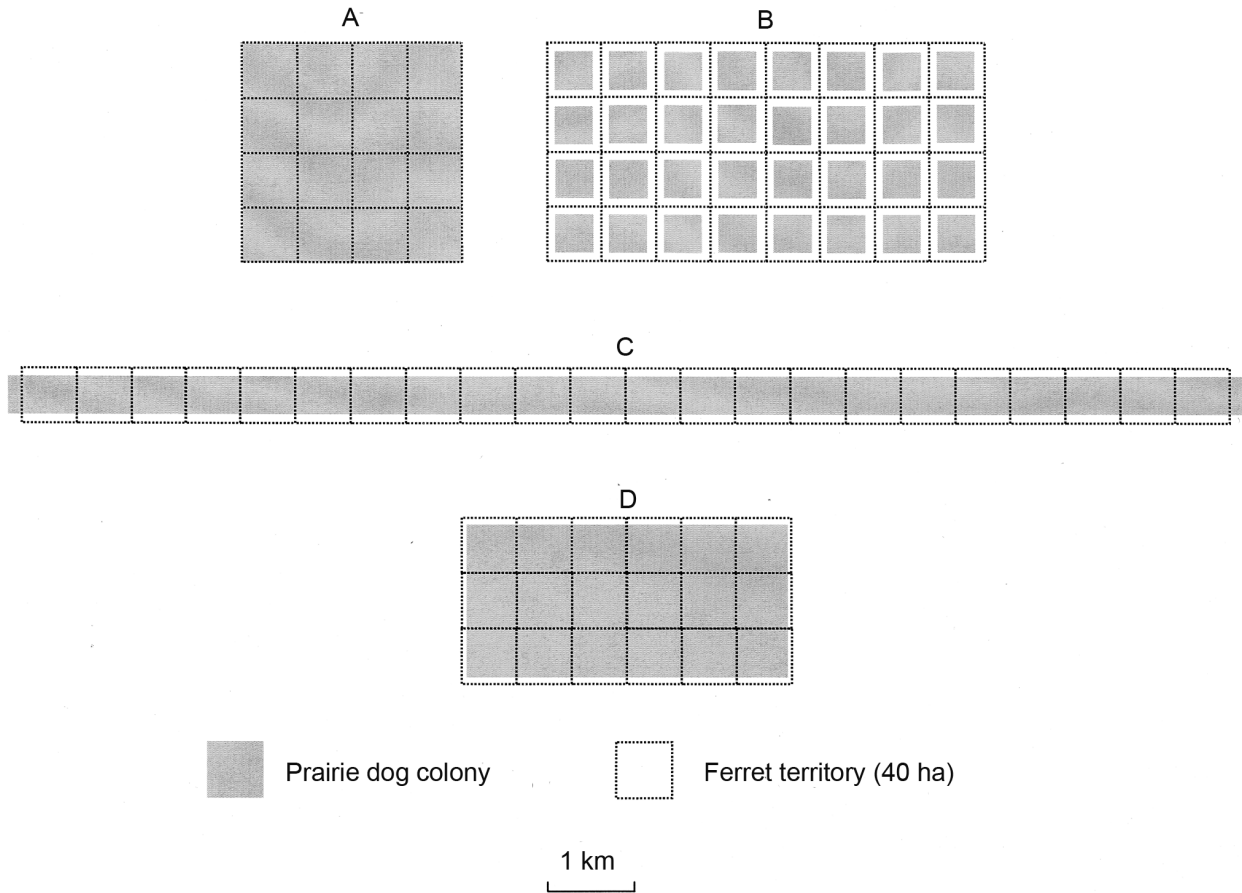


Figure 3. Comparison of female black-footed ferret (*Mustela nigripes*) numbers supported by hypothetical prairie dog (*Cynomys* spp.) complexes occupying 640 ha: (A) a complex with a single square colony ($n = 16$ ferrets); (B) a complex with 20-ha colonies at sufficient spacing to allow separate ferret territories ($n = 32$ ferrets); (C) a complex with a single linear colony (22 ferrets); and (D) a complex with a single rectangular colony (18 ferrets). These predictions are based on the following assumptions: (1) ferret territories are 40-ha squares, (2) a patch of prairie dog habitat occupying at least 20 ha is centered in the territory, and (3) a habitat patch of 20 ha has sufficient prairie dogs to sustain a ferret family while maintaining its prairie dog population.

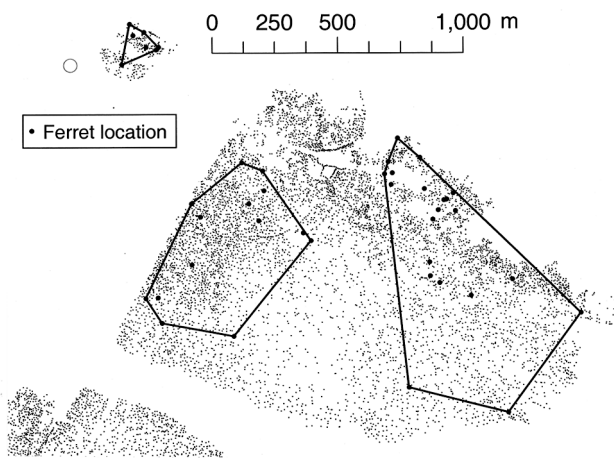


Figure 4. Activity areas (circumscribed by minimum convex polygons) for three female black-footed ferrets (*Mustela nigripes*) with litters. These females and their litters were repeatedly relocated during summer 1998 at UL Bend National Wildlife Refuge, Mont. Heterogeneity in dispersion of black-tailed prairie dog (*Cynomys ludovicianus*) burrows (small dots) is evident. The female ferret on the small colony is relatively insulated from repeated contact with other females. In this example, areas of dense prairie dog burrows do not form true “islands” of good habitat, but low densities of prairie dog burrows in the central portion of the larger colony may have influenced separation of ferret activity areas.

territoriality. If the rating using the linear equation is less than two female ferrets, then a single colony, regardless of size or prairie dog density, may be evaluated with the linear relationship (even if the result is a rating <1.0).

The concept of islands and peninsulas discussed above creates an image of prairie dog colonies within landscapes that have areas devoid of prairie dogs. Islands with high densities of prairie dogs, however, may also be situated within intervening habitat of low prairie dog density. Thus, the island effect may be operative within colonies that have heterogeneous densities of prairie dogs. The mosaic of prairie dog densities is reflected by nonuniform densities of prairie dog burrows. Heterogeneity in distribution of burrows may influence separation of activity areas of at least some female ferrets (fig. 4).

Another Look at Burrow Densities as Indicators of Prairie Dog Density

Biggins and others (1993) suggested that densities of active burrows were significantly correlated with densities of prairie dogs determined from visual counts. Severson and Plumb (1998, p. 864), however, failed to detect a relationship between densities of prairie dogs and their burrows, concluding that “burrow counts . . . should not be used to estimate or index prairie dog numbers.” This theme has a rather long history of debate extending to species other than prairie dogs, and a full discussion is outside the intended scope of this paper. Nevertheless, an overview of the topic and brief discussion of the specific criticism noted above are appropriate because working groups responsible for monitoring ferret reintroduction sites have made wide use of burrow sampling to calculate indices of habitat quality for ferrets. The need remains for a practical technique to monitor prairie dog status and trends over large scales of space (thousands of hectares) and time (decades). Decisions to use some form of capture-recapture method, visual counts, or burrow indices to estimate prairie dog abundance and density depend in part on objectives and available resources (Biggins and others, 2006). In addition, choice of method will be affected by precision and accuracy required.

Biggins and others (1993) provided only correlation coefficients for regression relationships between data from burrow transects and visual counts. To enhance comparisons with other data sets, more information is needed. Their data sets were generated from counts and transects on 30 white-tailed prairie dog plots and 39 black-tailed prairie dog plots. Using regression models with constants (Biggins and others [1993] reported regression through the origin), the relationships between densities of active burrows and density of prairie dogs as determined by visual counts were highly significant for both species (white-tailed prairie dogs, $F_{1,28} = 86.282$, $P < 0.001$, $R^2 = 0.755$; black-tailed prairie dogs, $F_{1,37} = 29.390$, $P < 0.001$, $R^2 = 0.443$). A comparison of the studies done by Severson and Plumb (1998) and Biggins and others

(1993) reveals differences in several key features that collectively may affect the power to detect correlations (table 1). Collectively, the relative ranges of values and various levels of sampling intensity (e.g., plot size, number of plots, geographic coverage) should have given an advantage to the data sets of Biggins and others (1993). Intensity of transect sampling to estimate burrow density is as important as other features but was not reported by Severson and Plumb (1998).

Evidence of the utility of the burrow transect technique is also provided by data generated from its use. The overall collapse of the Meeteetse complex of white-tailed prairie dogs was documented by using densities of active burrows derived from strip transect sampling (fig. 5). It would be difficult to imagine that the downward trend during the 10-year study was an artifact of the sampling procedure, even without the corroborative evidence that exists from visual counts (D.

Table 1. Attributes of two studies on the relationship between densities of black-tailed prairie dogs (*Cynomys ludovicianus*) and densities of their active burrows.

	Severson and Plumb (1989)	Biggins and others (1993)
Number of States	1	3
Number of plots	24	39
Plot size (ha)	4	9
Area sampled (ha)	96	351
Burrow transects (km)	?	248
Lowest prairie dog density (no./ha)	8	0.8
Highest prairie dog density (no./ha)	46	54.2

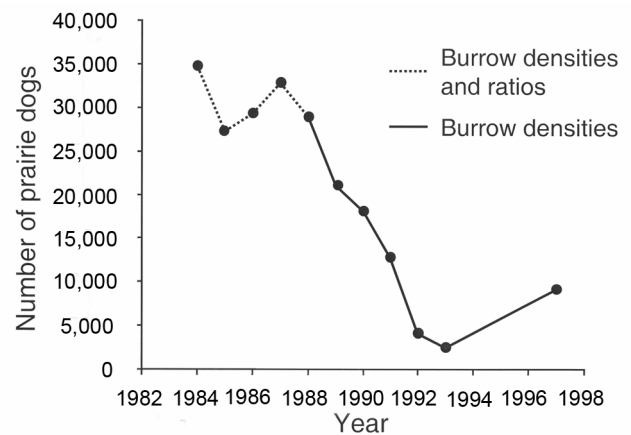


Figure 5. Estimates of white-tailed prairie dogs (*Cynomys leucurus*) on the Meeteetse, Wyo., complex, derived from estimates of active burrow density (Biggins and others, 1993). (Adapted from Biggins and Kosoy, 2001. Reprinted with permission of the *Journal of the Idaho Academy of Science*, Pocatello, Idaho.)

Biggins, unpub. data, 1988–93) that were repeated annually over most of that time period.

The purpose of the foregoing discussion is simply to provide evidence that burrow indices are a useful tool for indexing prairie dog abundance. This does not imply superiority of the technique compared to other tools; methods must be matched to objectives, size of area to be sampled, local conditions, and available funding.

Reemphasizing Percent of a Complex Occupied by Prairie Dog Colonies

Spatial relationships and shapes of prairie dog colonies were discussed above in the context of small islands and peninsulas of habitat with high prairie dog densities. Others (Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988; Biggins and others, 1993) have discussed spatial arrangements of prairie dog colonies at larger scales, implying that some measure of colony arrangement or density within a complex is necessary to adequately evaluate habitat quality for black-footed ferrets. The 7-km limitation to intercolony spacing (Biggins and others, 1993) was a partial solution, but, without additional criteria, vast complexes that are thinly populated with prairie dog colonies may provide the same rating as complexes with more compact arrangements of colonies (fig. 6). There have been theoretical problems with measures of colony dispersion such as intercolony distances (Biggins and others, 1993), ultimately leading the ICC to adopt the conceptually simple tactic of using percent occupied ($100 \times \text{sum of colony area} / \text{total area of complex}$) proposed by Miller and others (1988). During the first decade of ferret reintroductions, however, the spatial arrangement of prairie dog colonies within complexes largely has been ignored. Few participants have bothered to calculate the percent occupied attribute suggested as an overview of dispersion of colonies. By invoking the new procedure for defining subcomplexes of colonies spaced at 1.5 km or less, the consequences of this oversight are diminished (but not eliminated). It will be possible to examine how much of a complex consists of high-quality “core” subcomplexes. Subcomplexes should be rated separately from 7-km complexes; they should no longer be considered as having equal quality to complexes with the same cumulative area occupied by prairie dog colonies (fig. 6C versus 6A and 6B). Nevertheless, calculation of the proportion of complexes and subcomplexes occupied by prairie dog colonies will provide useful additional information (e.g., to distinguish between complexes such as A and B of fig. 6), and we continue to recommend that management teams at all reintroduction sites make these simple measurements. The technique will allow improved comparisons of complexes and subcomplexes among and within ferret reintroduction sites and may help characterize the potential for colony expansion.

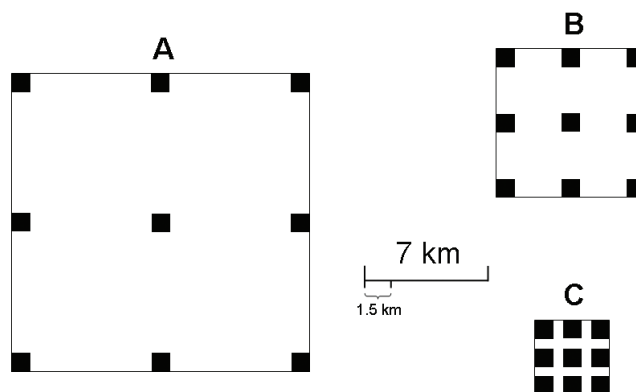


Figure 6. In these three hypothetical complexes, total area occupied by prairie dog (*Cynomys* spp.) colonies (shaded squares) is the same (1,000 ha), but the percentages of each complex occupied by colonies are 4%, 14%, and 57% for A, B, and C, respectively. Are the complexes of equal quality as habitat for black-footed ferrets (*Mustela nigripes*)? Arrangement C qualifies as a subcomplex because of intercolony spacing of <1.5 km.

Summary of the Procedure for Evaluating Ferret Habitat

The following steps for evaluating habitat for black-footed ferrets summarize the approach suggested by Biggins and others (1993) and the modifications presented herein.

1. Map the complex of prairie dog colonies.
2. Circumscribe the complex by using the 7-km criterion.
3. Circumscribe high-quality subcomplexes by using the 1.5-km criterion.
4. Estimate areas of complex, subcomplexes, and colonies with geographic information system (GIS) software if maps are digital. Use polar planimeter or other methods (e.g., dot grid) to estimate areas if only hard copies of maps are available.
5. Calculate percent of complex and subcomplexes occupied by prairie dog colonies.
6. Estimate prairie dog densities on colonies by using burrow density transects or visual counts.
7. Enter density and area estimates for each colony into separate spreadsheets for the overall complex and all subcomplexes.
8. Calculate ferret family ratings by using modified formulae (example spreadsheets with formulae are available from the authors).

Assumptions and Unresolved Questions

We believe that the suggested modifications discussed above will improve the existing model but reiterate that any model is only an approximation of reality (Biggins and others, 1993). Reflection on the basic assumptions involved in this exercise serves as a reminder of its inexact nature. Assumptions include (1) the average prairie dog weighs 760 g, (2) a ferret wastes 20 percent of each prairie dog it kills, (3) the several steps involved in estimating caloric demands of ferrets are correct, (4) losses of prairie dogs to other causes are 250 percent of losses caused by ferret predation, (5) the intrinsic rate of growth for prairie dog populations (λ) is 1.0, and (6) prairie dog populations remain stable. A sobering fact is that some of these attributes vary widely (e.g., numbers 4 and 5) and are in need of further study. The earlier model implicitly assumes that all prairie dogs, regardless of sex or age, are equally available as prey. If female ferrets selectively prey upon juvenile prairie dogs, their own productivity may be more closely correlated with prairie dog productivity than with prairie dog density. This possibility leads to questions about links between forage production, prairie dog production, and ferret production and highlights the potential importance of local and annual variation in precipitation.

A better understanding of prairie dog torpor (Lehmer and Biggins, 2005), burrow-plugging behavior, and energetics of ferret digging behavior could also improve the quality of these models. Is the digging involved in excavating hibernating prey more energetically costly than hunting of nonhibernating prey (Harrington and others, 2003)? What is the balance in tradeoffs between energetic costs of accessing prey and risk of injury in killing prey when comparing hibernating and nonhibernating prairie dogs? Does the presumably lower risk involved in killing hibernating prey allow use of larger prairie dogs that might not otherwise be available?

Territoriality in ferrets also remains poorly understood. Key questions include the following: (1) At what densities of prey does control of minimum space take precedence over control of prey resources? Can our proposed curve be further refined? (2) Does nepotism affect territory size and overlap (i.e., are females more tolerant of their female offspring than of less closely related females)? (3) How do shapes and arrangements of high-quality patches within and among colonies affect territorial behavior?

Some related topics would be appropriate for additional investigation. The earlier attempt to define minimum habitat attributes necessary to sustain female ferret reproduction (Biggins and others, 1993) may be questioned. Further study of female ferret behavior on white-tailed prairie dog or Gunnison's prairie dog (*Cynomys gunnisoni*) colonies, where prey densities are low, would help establish the lower limits. Preliminary data suggest a positive correlation between productivity of female ferrets and density of burrows in the

habitat they occupy (D. Biggins, M. Matchett, and T. Livieri, unpub. data, 1997–2000), a relationship that also suggests further research on habitats with low prey densities. Territorial behavior of male ferrets has been ignored but may be an important factor in extinction risk for small populations (Conservation Breeding Specialist Group, 2004). Increasing numbers of black-footed ferrets in reintroduced populations are providing more opportunity to investigate these and other important aspects of ferret ecology.

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