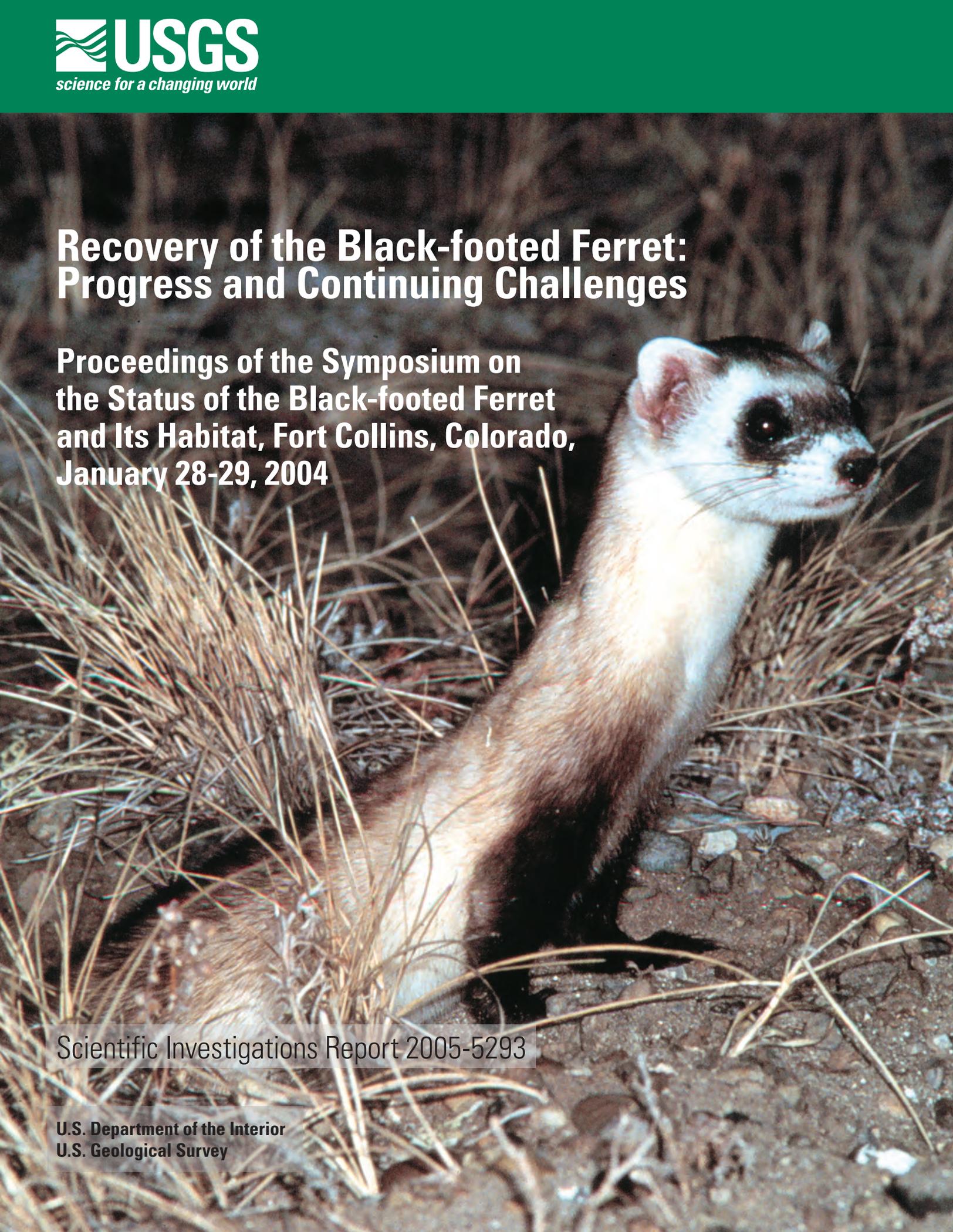


Recovery of the Black-footed Ferret: Progress and Continuing Challenges

Proceedings of the Symposium on
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Habitat Preferences and Intraspecific Competition in Black-footed Ferrets

By Dean E. Biggins,¹ Jerry L. Godbey,¹ Marc R. Matchett,² and Travis M. Livieri³

Abstract

We used radio-telemetry data (28,560 positional fixes) collected on 153 black-footed ferrets (*Mustela nigripes*) to (1) reexamine the assumed obligate relationship of these ferrets to prairie dogs (*Cynomys* spp.), (2) investigate habitat preferences of ferrets at a small scale (<1 ha), and (3) gain insight into competition among ferrets for habitat patches of varying quality. We used densities of prairie dog burrows as an indicator of habitat quality because burrows are presumably valuable to ferrets as cover and because density of burrows is correlated to density of prairie dogs. Burrow density summaries were generated from maps of all burrows on ferret reintroduction sites in Montana and South Dakota. Aboveground movements by ferrets were mostly (89 percent) within the boundaries of prairie dog colonies or associated with circuits involving return to a colony (10 percent), with no evidence that ferrets sought to occupy alternative habitats. Sampling with 0.07-ha plots suggested that dispersion of prairie dog burrows within colonies was neither uniform nor random. Burrows were clumped, and ferrets preferred ($P < 0.001$) patches of habitat with high densities of burrows compared to samples taken at random points on the colonies they occupied. The magnitude of preference (the difference between use and availability) was greatest for resident young ferrets compared to their recently released counterparts, whether the newcomers were compared with residents of 2–4 weeks ($P = 0.039$) or >1 year ($P = 0.048$). Also, preference was stronger for wild-born young ferrets than for young captive-born ferrets released to augment the wild population ($P = 0.040$). This additional evidence for competition among ferrets, and for an advantage of prior residency, raises conservation concerns. The energetics-based model commonly used to predict ferret densities at reintroduction sites does not consider competition, which likely leads to overestimation of the densities of ferrets attainable in high-quality habitat. During sequential releases of ferrets, prior residency may handicap success of newcomers, even though the latter may have higher potential fitness. Although

the manner of initial colonization of available habitat by black-footed ferrets, and their subsequent competition for it, was suggestive of an ideal despotic distribution, we did not assess effects of prey density or burrow density on fitness.

Keywords: black-footed ferret, competition, *Cynomys*, endangered species, habitat, ideal despotic distribution, ideal free distribution, *Mustela nigripes*, prairie dog, prior residency

Introduction

Conservation efforts for the highly endangered black-footed ferret (*Mustela nigripes*) include a captive breeding program that rescued the species from a remnant population of 10 animals in Wyoming (fig. 1) during the winter of 1985–86. That captive breeding program currently produces annual surpluses of 200–300 kits for reintroduction (Marinari and Kreeger, this volume). Ferrets have been reintroduced at sites in six U.S. States and Chihuahua, Mexico (Lockhart and others, this volume). Releases of ferrets into unoccupied and occupied habitat, and monitoring of wild-born ferrets, provided unique opportunities to evaluate large-scale habitat

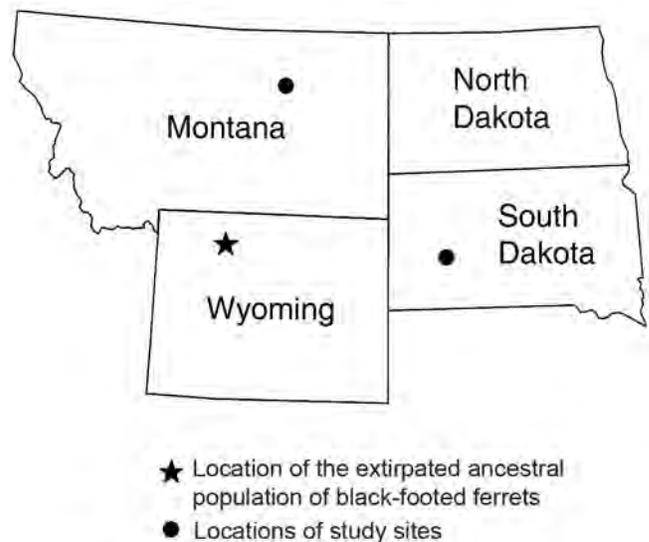


Figure 1. The site near Meeteetse, Wyo., that provided ancestral stock for the captive breeding program, and study sites in Montana and South Dakota where black-footed ferrets (*Mustela nigripes*) were released.

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use by ferrets (objective 1), habitat preferences at small scales (objective 2), and relationships between ferret territoriality and habitat quality (objective 3), all of which are relevant to ferret conservation.

Considerable evidence supports a strong relationship between prairie dogs (*Cynomys* spp.) and black-footed ferrets. A summary by Anderson and others (1986) indicates that almost all recent ferret specimens were collected from areas within the composite ranges of black-tailed prairie dogs (*C. ludovicianus*), white-tailed prairie dogs (*C. leucurus*), or Gunnison's prairie dogs (*C. gunnisoni*), and most of the explicit descriptions of locality, where provided, mentioned prairie dog colonies. The last extant ferret populations were found on prairie dog colonies, and studies of those ferrets revealed intensive use of prairie dog colonies (Hillman and others, 1979; Biggins and others, 1985). Prairie dogs are the predominant prey taken by black-footed ferrets (Sheets and others, 1972; Campbell and others, 1987). Strategies for evaluating black-footed ferret habitat (Linder and others, 1972; Forrest and others, 1985; Flath and Clark, 1986; Houston and others, 1986; Biggins and others, 1993) universally assumed that prairie dog colonies were a primary requirement. Others, however, have questioned the characterization of black-footed ferrets as extremely specialized (Owen and others, 2000). One objective of this study was to further document the use of habitats by ferrets on a large scale, using data from radio tracking and maps of black-tailed prairie dog colonies in Montana and South Dakota, to reexamine the degree of dependence of black-footed ferrets on prairie dogs.

Evaluations of ferret habitat are mostly large scale, conducted on colonies hundreds of hectares in size and on complexes occupying thousands of hectares, leaving the details of how ferrets use their local environments largely unexplored. If black-footed ferrets are obligate predators on prairie dogs and variation exists in densities of prairie dogs and their burrows within their colonies, we predict that intensity of ferret activity will correlate positively with density of prairie dogs when habitat is examined at scales smaller than colonies. Thus, our second objective was to evaluate preferences of ferrets by using sample parcels of land <1 ha in size. To address small-scale habitat preferences and the following objective, we used burrow densities as an indicator of habitat quality. Prairie dog burrow densities should give a suitable measure of habitat quality for black-footed ferrets, in part because they correlate to density of the prairie dog prey (Biggins and others, 1993) and in part because burrows have intrinsic value to ferrets as refuges from predators and adverse weather and as dens to rear young.

Black-footed ferrets, like many other mustelids, appear to be intrasexually territorial (Powell, 1979; Miller and others, 1996). In typical carnivore fashion, females attempt to control access to food resources, while males attempt to control access to females (Ewer, 1973). Although several factors in varying combinations appear to contribute to an organism's resource holding power (e.g., relative size of contestants, age,

experience in former contests), prior residency often confers significant advantages. The residency advantage is widespread among several taxa, including insects (Davies, 1978), arachnids (Riechert, 1978), decapods (Jennions and Backwell, 1996), fish (Harwood and others, 2003), amphibians (Mathis and others, 2000), and mammals (Neumann, 1999). Because many of the ferrets we studied were released into unfamiliar terrain that was either unoccupied by ferrets or occupied by ferrets for known periods of time, it was possible to examine the effect of prior residency.

Release of ferrets into vacant habitat allowed us to assess the sequence of occupancy. If habitat patches are heterogeneous, the order in which they become colonized or abandoned should relate to quality of those patches as perceived by occupants (Wiens, 1976; Krohn, 1992). Ideal free distribution theory predicts such an interrelationship between population density and carrying capacity of patches in heterogeneous habitats (Fretwell and Lucas, 1970). If order of occupancy reflects quality of habitat patches, then assessment of the colonization process also may lead to improved understanding of source-sink dynamics after habitats become fully populated (Howe and others, 1991; Pulliam and Danielson, 1991). To evaluate intraspecific competition for habitat and order of occupancy of habitat patches, we again utilized radio-telemetry data, overlaying ferret locations onto digitized maps of prairie dog burrows within the colonies studied.

Methods

We radio tracked 153 black-footed ferrets on prairie dog colonies at UL Bend National Wildlife Refuge, Mont., and on the Buffalo Gap National Grassland, S. Dak., during September–November 1994–97 (figs. 1 and 2). Some of the resulting 28,560 telemetric fixes were used for multiple studies; the UL Bend data from 1994 and 1995, for example, were also used in the comparisons of adults and kits reported herein (Biggins, Godbey, Livieri, and others, this volume). We affixed transmitters having 20-cm whip antennas to wool collars of 1-cm width, using Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). We weighed and radio collared ferrets that were wild caught or captive bred (while the animals were held under isoflurane anesthesia) and inserted passive integrated transponder chips for long-term identification (Biggins, Godbey, Matchett, and others, this volume). Ferrets from captive breeding facilities were reared under a variety of strategies and released during August–November with no more than 1-day acclimation in onsite cages (Biggins and others, 1998).

We radio tracked ferrets from fixed stations fitted with dual-beam, 11-element Yagi antennas on 6-m masts and used null-peak direction finding and triangulation to fix each ferret's position at intervals of 7–60 minutes while the animals

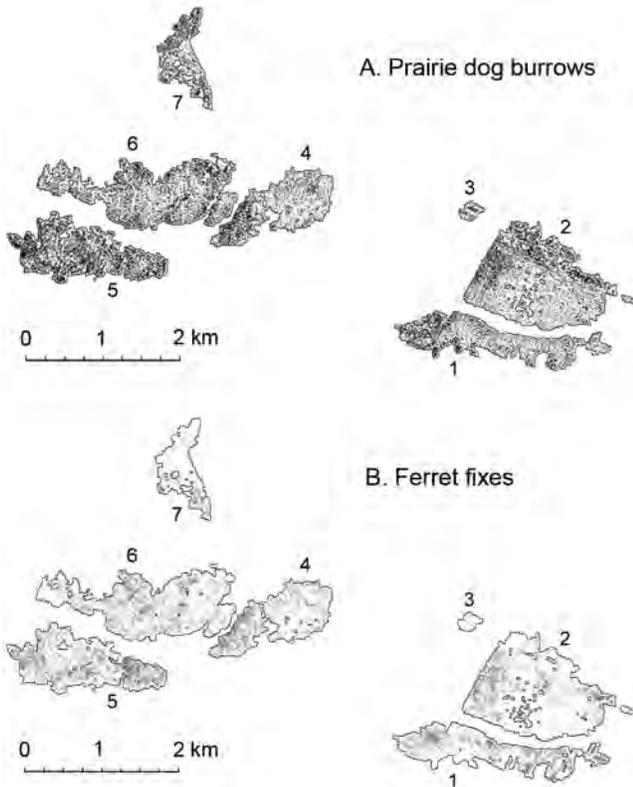


Figure 2. Distribution of black-tailed prairie dog (*Cynomys ludovicianus*) burrows (A) and black-footed ferret (*Mustela nigripes*) telemetric fixes (B) on colonies at UL Bend National Wildlife Refuge, Mont. Each dot is a burrow opening or telemetric fix; density of resulting stippling thus reflects density of burrows or fixes. Attributes for numbered colonies are summarized in table 1.

were active above ground (Biggins and others, 1999; Biggins, Godbey, Livieri, and others, this volume). We developed station-specific error estimates from test data by using differences between telemetry-derived azimuths and azimuths to transmitters of known location (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). Aboveground activity of black-footed ferrets is mostly nocturnal (Biggins and others, 1986; Biggins, 2000), so we limited monitoring of ferrets to hours of darkness for 2 weeks to 2 months postrelease. We recorded estimated locations of ferrets and associated error polygons as Universal Transverse Mercator coordinates derived from paired azimuths with program TRITEL (Biggins, Godbey, Miller, and Hanebury, this volume).

We recorded locations of prairie dog burrow openings (henceforth, such openings will be referred to as burrows) with Global Positioning System (GPS) receivers, differentially corrected to provide point estimates with errors of <1 m. ArcInfo® Version 8.2 (Environmental Systems Research Institute, Inc., Redlands, Calif.) was used for all vector processing, and the GRID module was used for all raster modeling. The vector point data for all prairie dog burrows and ferret loca-

tions in the study were consolidated into the Universal Transverse Mercator Zone 13 projection using the North American Datum of 1927. The GRID module was used to convert the vector points to 1-m² cells. To create a map of each prairie dog colony, cells were expanded by 10 m in every direction. Thus, the maps of colonies (fig. 2A,B; table 1) can be envisioned to include a buffer of 10 m beyond the outermost burrows and to exclude spaces within the outer boundary that are >10 m from the nearest burrow.

Use of Habitats Other than Prairie Dog Colonies

To investigate the broad-scale preference of black-footed ferrets for prairie dog colonies, we examined ferret use of the colonies as defined above and their use of noncolony areas. Ferret fixes were classified as being on or off colonies. Because there were nearby colonies in the South Dakota complex that were not mapped with the system described, ferret fixes that were not on mapped colonies could have been on other colonies. Thus, we did not use South Dakota data for these large-scale assessments. Similarly, a subset of ferrets in Montana (14 animals living near the eastern boundary of the subcomplex) had access to colonies that were not mapped with this system and were likewise eliminated from the analysis. The remaining data used for this overview included 24,512 fixes on 108 radio-tagged animals, including released and resident adults and kits. Because ferrets presumably must make exploratory moves to assess the distribution of prairie dogs, and because some ferrets traversed noncolony areas during routine travels between colonies, fixes that were off colonies do not necessarily imply that ferrets were actually living in areas not occupied by prairie dogs. We estimated the relative use of noncolony areas attributable to these phenomena, defining an off-colony excursion as a movement involving ≥2 fixes

Table 1. Black-tailed prairie dog (*Cynomys ludovicianus*) colonies where prairie dog burrows were mapped. Numbers for Montana colonies correspond to the numbered colonies of figure 2.

Colony	Area (ha)	Burrows/ha
Montana		
1. South Locke	90.1	57.9
2. North Locke	166.0	48.9
3. Small	5.0	64.1
4. Sagebrush	79.8	49.8
5. South Hawley	102.4	79.4
6. North Hawley	144.0	54.6
7. Wilderness	42.2	62.1
South Dakota		
North Sage Creek	160.1	138.9

away from a colony, followed by return to a colony. We also tallied the number of fixes associated with intercolony moves and dispersal moves (movement with no return to a colony).

Preferences Within Prairie Dog Colonies

We examined habitat preferences of ferrets within colonies at a small scale by comparing counts of the number of mapped burrows in circular plots of 0.07 ha (radius = 15 m) surrounding ferret fixes with counts in similar plots surrounding random points on colonies (fig. 3), sampling with replacement (plots were allowed to overlap). To be included in the analysis, the boundary of a sample plot was required to be entirely within a colony as defined above. Ferrets with ≤ 3 fixes were excluded. To characterize densities of prairie dog burrows on the Montana colonies, we sampled 20,328 plots at random points and compared those to plots centered on 21,185 fixes for 110 ferrets. In South Dakota, we counted burrows within plots surrounding 427 fixes (for 19 ferrets) and 465 random points. Because many ferret fixes for individual animals were serially autocorrelated (e.g., the sequential fixes of fig. 3), we summarized density of burrows within plots as

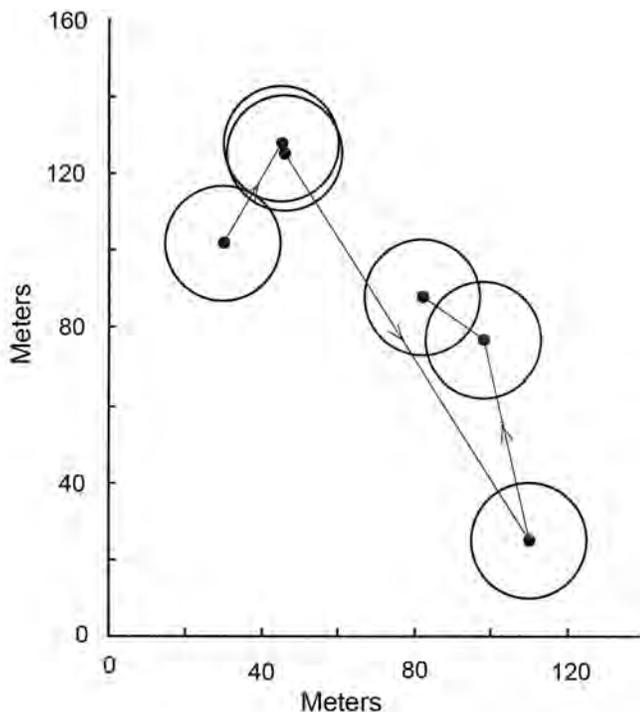


Figure 3. Example of encircling a series of telemetric fixes with plots of 15-m radius, within which black-tailed prairie dog (*Cynomys ludovicianus*) burrow entrances were counted, for black-footed ferret (*Mustela nigripes*) no. 32, North Sage Creek, S. Dak., on the night of October 26–27, 1997. Overlapping plots were allowed for both ferret fixes and random points (sampling with replacement).

mean densities for each animal and used those means in all subsequent analyses. Thus, sample sizes became numbers of animals (not numbers of fixes). We further restricted this data set to include only those ferrets radio tracked >3 days; estimates for animals radio tracked for shorter periods were deemed unreliable.

A patchy distribution of habitat (burrows) within prairie dog colonies is a prerequisite for allowing choice by ferrets. Frequencies of counts within the plots described above would be expected to follow a Poisson distribution if dispersion of burrow openings on colonies were random (Ricklefs, 1990). For a Poisson distribution, the variance in counts is equal to the mean; evenly spaced burrow openings will produce a variance less than the mean, and clumped burrow openings will result in variance greater than the mean. We examined the variance:mean ratios for the counts within our samples of circular plots to provide an indication of dispersion of burrow openings in each colony.

Intraspecific Competition for Habitat

To assess intraspecific competition for habitat, we compared habitats occupied by groups of black-footed ferrets that were expected to differ in competitive standing. We predicted that (1) resident adult ferrets would have a competitive advantage over their wild-born kits, (2) wild-born kits would have an advantage compared to released kits, (3) kits released first would be more competitive than kits released subsequently into the same area in the same year, (4) larger kits would have an advantage over smaller kits, and (5) kits released into unoccupied habitat during the first year of reintroductions at a site would have an advantage over kits released in subsequent years to augment a population. As outlined above, we assumed burrow density correlated positively with habitat quality. We thus expected dominant ferrets to occupy areas of higher burrow density compared to their less competitive counterparts. We assessed burrow densities estimated from the sample of 0.07-ha plots described above.

As implied by the groups in comparisons 1–5 above, various overlapping subsets of animals were used for analyses. Montana data were best suited for this assessment because ferrets were released in multiple years on several colonies, they were released in several consecutive groups in the same colonies during 2 years, and resident ferrets were monitored during 1 year. As with the broader analysis above, we included only those ferrets radio tracked >3 days. Within the Montana data set, the comparison of adult and young resident ferrets (1 above) was limited to the 1997 subset of data collected on Hawley and associated colonies, as was the comparison of wild-born and released young ferrets (2). We compared groups of young ferrets released sequentially during the same years at the same sites (3) within the 1994 and 1995 data sets at all colonies. Measures of mass (4) were available for Montana animals released in 1994 and 1995, and that variable

was included in the assessment of within-year sequential releases. Because sexes are dimorphic, we included sex in the model to interact with mass. Finally, we compared young ferrets released into vacant habitat at Hawley and associated colonies in 1995 with young ferrets released into that habitat in 1997, when portions of it were occupied by resident ferrets (5 above). That 368.3-ha area of prairie dog colonies (the four western colonies of fig. 2A,B) was occupied by at least 8 adults and 19 kits that we marked (not all were monitored via the radio tracking of this study).

To provide additional evidence on the effect of competition, we assessed numbers of released ferrets that moved between colonies in 1995, when these ferrets were released into habitat without a resident population of ferrets, and in 1997, when ferrets were released into the same prairie dog colonies to augment an existing population.

Statistical Evaluation

For statistical comparisons, we reduced burrow density data to animal-specific estimates for habitat they used, paired with colony-specific estimates for colonies they occupied. If an animal occupied more than one colony, we calculated separate pairs of estimates (use and availability) for each colony. We used multivariate general linear modeling (repeated measures) to evaluate differences between burrow densities for colonies and for habitat used by ferrets, assuming that all habitat on the colony occupied by a ferret was potentially available to that ferret. General models were reduced to more parsimonious versions by backward elimination using partial F -tests, when appropriate. Comparisons were judged as significant if the probability of committing a Type I error was ≤ 0.05 . Exact chi-square analyses (Berry and Mielke, 1985) assisted in evaluation of proportions of ferrets engaging in intercolony movements.

Results

Use of Habitats Other than Prairie Dog Colonies

Of the 24,512 total fixes used, 2,744 (11.19 percent) were off colonies. There were 88 instances of intercolony movement. Some of the off-colony locations were solitary telemetric fixes that could be the result of radio-tracking error. Because clusters of sequential fixes provide information on pattern of movement, we assessed off-colony moves using groups of ≥ 2 consecutive fixes away from a colony. The number of clustered fixes off colonies was 2,010 in 474 bouts of movement made by 87 animals with 1 to 24 bouts per ferret; 1,767 of these (87.91 percent) were associated with exploratory excursions involving returns to the

colony of origin (fig. 4) and intercolony moves (fig. 5). If these cluster-based estimates are applied to the total of 11.19 percent of fixes away from prairie dog colonies, it appears that only about 1.4 percent ($0.1119 * 0.1209 = 0.0135$) of the total number of off-colony fixes may involve dispersal (fig. 6) without known return to the colony of origin or travel to another colony.

Preferences Within Prairie Dog Colonies

Patchiness in dispersion of burrow openings was highly evident, as indicated by variance:mean ratios $\gg 1.0$ for all colonies (fig. 7) sampled by 0.07-ha circular plots. Overall, black-footed ferrets preferred patches of habitat with densities of prairie dog burrows higher than the averages for colonies they occupied (fig. 8). Our general statistical model evaluated overall differences between ferret plots and random plots (hereafter referred to as preference) and the effects of sex and colony. Sex accounted for relatively little variation ($F_{1,149} = 0.130$, $P = 0.719$) and was removed from the model. Preference of sites with elevated densities of burrows was consistent ($F_{1,154} = 16.996$, $P < 0.001$) among colonies (fig. 8), but the magnitude of the differences between burrow densities in

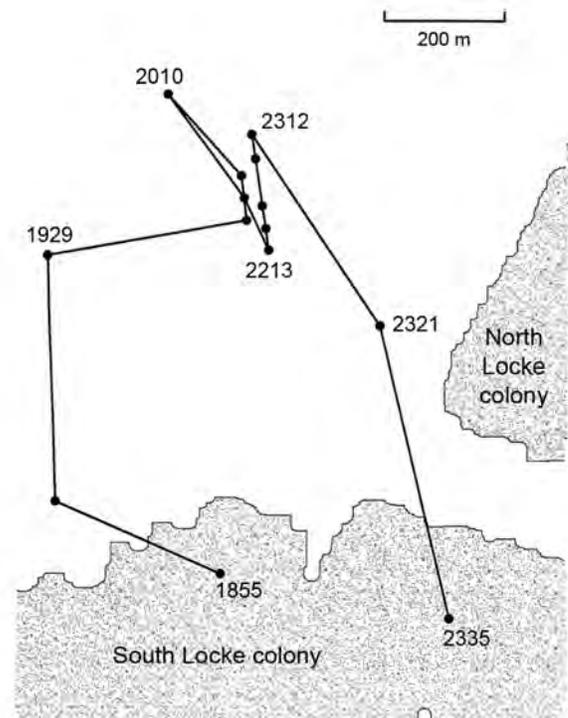


Figure 4. An example of an exploratory excursion away from a black-tailed prairie dog (*Cynomys ludovicianus*) colony by young male black-footed ferret (*Mustela nigripes*) no. 24, UL Bend National Wildlife Refuge, Mont., October 20, 1994. Numbers associated with points are times of day.

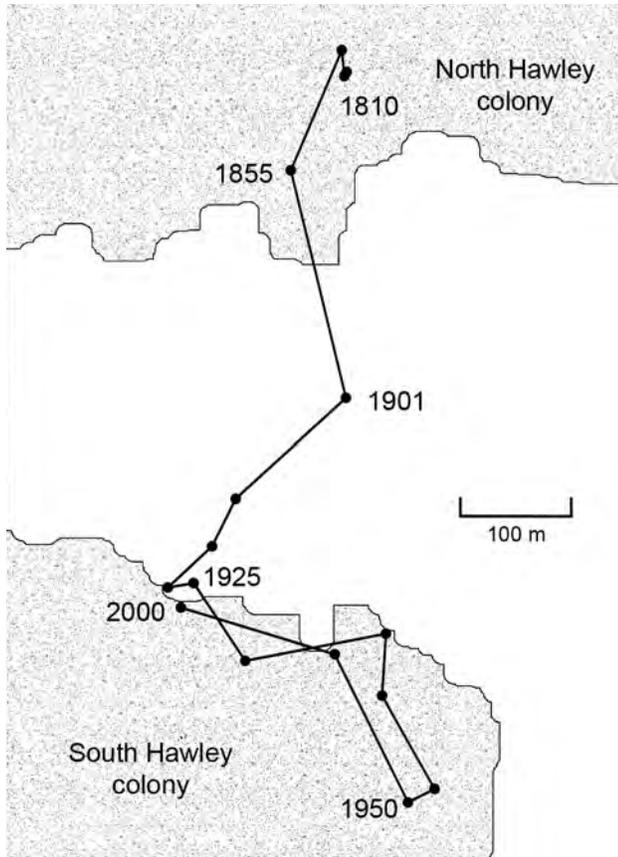


Figure 5. An example of an intercolony move by young female black-footed ferret (*Mustela nigripes*) no. 71, UL Bend National Wildlife Refuge, Mont., November 5, 1995. Numbers associated with points are times of day.

ferret and random plots appeared to vary (preference \times colony interaction; $F_{7,154} = 2.144, P = 0.042$).

Intraspecific Competition for Habitat

Three of the four general models in these analyses had only class of animal in the repeated measures comparison of random and ferret-centered estimates of burrow density; these three models were not further reduced. Failure of sex and mass (in the 1994 and 1995 Montana data) to explain significant variation ($P > 0.160$) resulted in reduction of that model to a simpler submodel resembling the others used to evaluate competition. Each of these subsets of data reflected the significant habitat preferences of ferrets ($P \leq 0.010$) that were documented in the more general treatment above. Our primary focus in evaluations of competition was centered on the interaction term of each model that tested whether classes of ferrets influenced variation in differences between habitat used and habitat available (preference). In that regard, only the comparison between habitat preferences of resident adult ferrets and their resident young failed to explain significant variation (preference \times age interaction; $F_{1,31} = 0.579, P = 0.452$). As predicted, wild-born resident young ferrets were

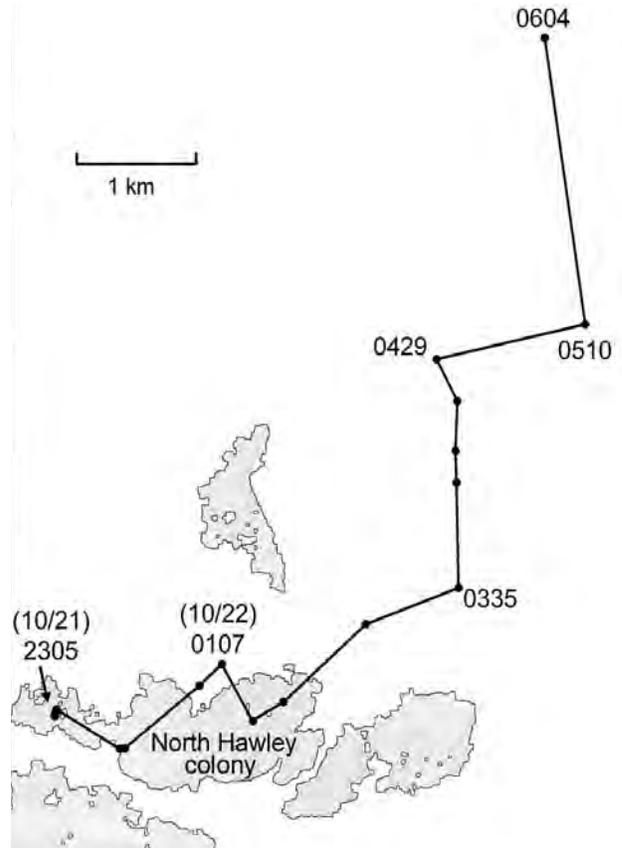


Figure 6. An example of dispersal away from black-tailed prairie dog (*Cynomys ludovicianus*) colonies by young male black-footed ferret (*Mustela nigripes*) no. 213, October 21–22, 1997. Numbers associated with points are times of day.

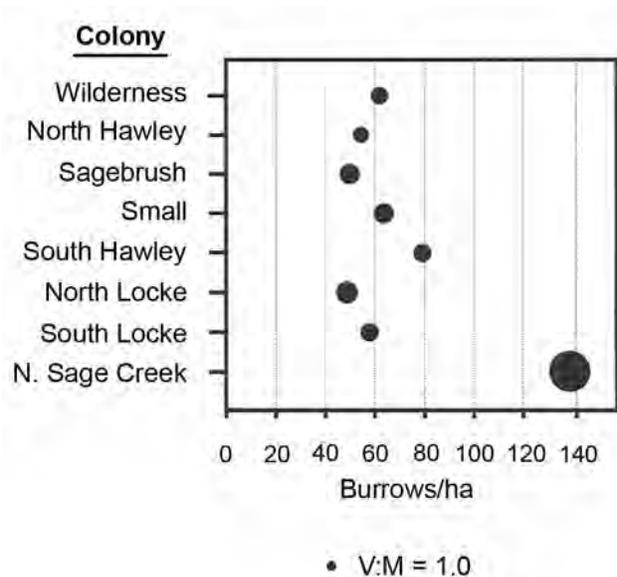


Figure 7. Densities of burrows on study colonies and variance to mean ratios (V:M) estimated from samples of 0.07-ha plots. Diameter of symbol is proportionate to V:M ratio within sample of plots.

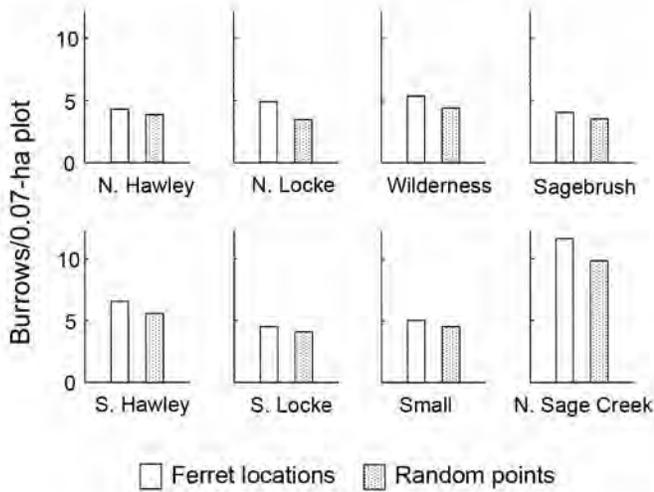


Figure 8. Burrow densities within plots encircling telemetric fixes of black-footed ferrets (*Mustela nigripes*) and within plots at random points on black-tailed prairie dog (*Cynomys ludovicianus*) colonies.

able to exercise a higher level of preference than did released young (fig. 9) (preference × origin interaction; $F_{1,51} = 4.445, P = 0.040$), first-released young ferrets were more selective than were young released later the same year (fig. 10) (preference × sequence interaction; $F_{1,67} = 4.430, P = 0.039$), and young ferrets released into vacant habitat were more selective than were young used to augment the population in that habitat during a later year (fig. 11) (preference × year interaction; $F_{1,62} = 4.063, P = 0.048$).

Most (12/13 = 92.3 percent) young ferrets added to the resident population in the western colonies of the UL Bend complex in 1997 moved between colonies. That proportion was significantly different ($X^2 = 13.789, df = 1, P < 0.001$) from the corresponding proportion for 1995 (8/27 = 29.6 percent), when young ferrets were released into the same colonies that were then vacant.

Discussion

Use of Habitats Other than Prairie Dog Colonies

The term “preference” suggests that use is compared to availability, but we made no explicit attempt to define or measure availability of habitat not occupied by prairie dogs. Noncolony areas, however, were much more available to ferrets (on a large scale at least) than were prairie dog colonies. Thus, the extremely high use of prairie dog colonies by black-footed ferrets does indeed suggest strong preference, and there was no need to delve into more rigorous analyses of preference at that large scale.

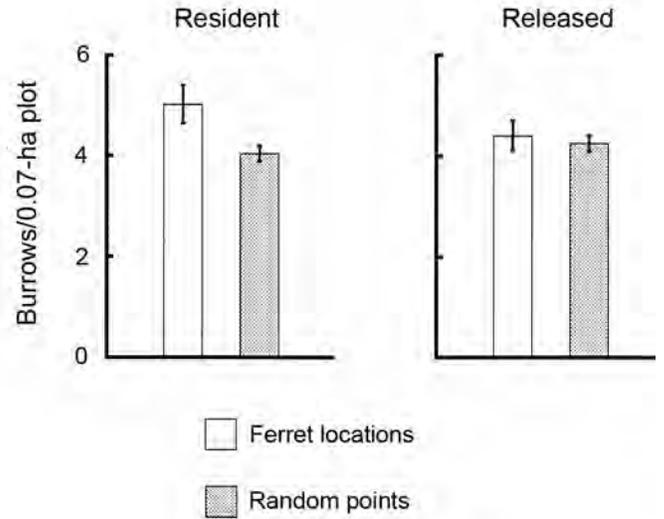


Figure 9. Densities of burrows (mean ± SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-occupied habitat at Hawley Flats Mont., in 1997, and densities of burrows in habitat used by (and available to) the resident wild-born ferret kits at that site.

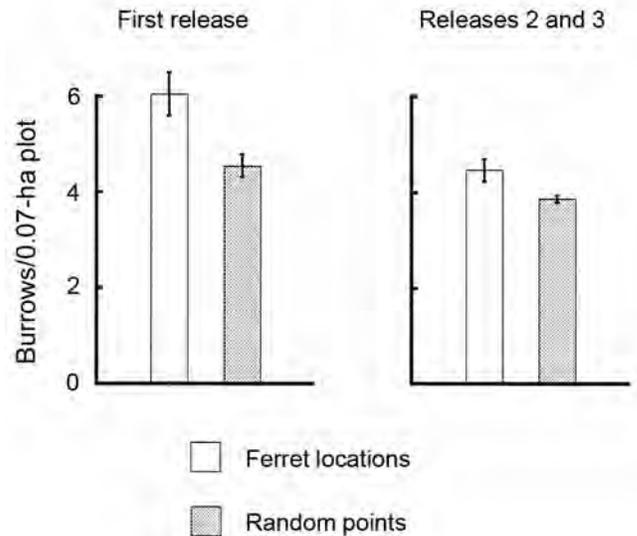


Figure 10. Densities of burrows (mean ± SE) in areas used by (and available to) the first black-footed ferret (*Mustela nigripes*) kits released at Locke Ranch and Hawley Flat, Mont., in 1994 and 1995, and densities of burrows in areas used by (and available to) ferret kits after subsequent releases during those years at those sites.

Most ferrets tracked during this study were young of the year, and many were captive-born ferrets released onto prairie dog colonies. To learn about their new surroundings, these naive animals must explore, and some may adopt home ranges that include multiple colonies. Thus, the small proportion of telemetric fixes away from prairie dog colonies is mostly explained by behaviors that should be expected even for a species fully dependent on prairie dogs. Also, a greater proportion of off-colony fixes occurred in the 1997 animals

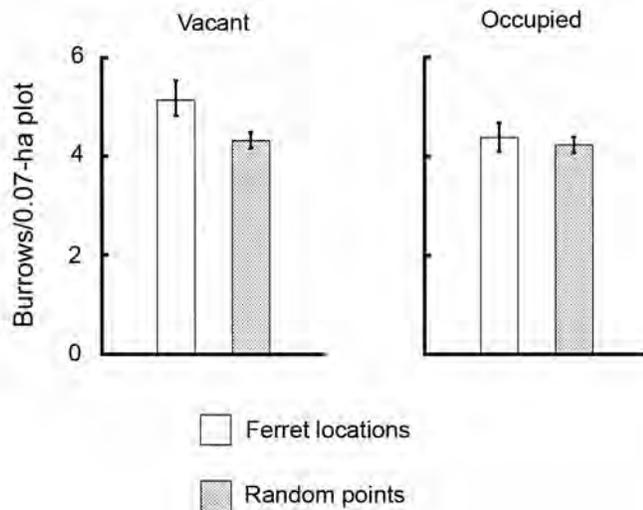


Figure 11. Densities of burrows (mean \pm SE) in areas used by (and available to) black-footed ferret (*Mustela nigripes*) kits released into ferret-unoccupied habitat at Hawley Flat, Mont., in 1995, and densities of burrows in areas used by (and available to) ferret kits released to augment the extant population in 1997.

(16.7 percent), which were subjected to potentially more intense intraspecific competition than were the ferrets released into unoccupied habitat in 1994 and 1995. Considering that the remaining small proportion of “unexplained” off-colony moves also involved (1) ferrets that were killed by predators and carried away from colonies, (2) ferrets with whom telemetric contact was lost, rendering their future travels and fates unknown, (3) predominantly captive-reared ferrets that may behave erratically at times, and (4) dispersal that ultimately may lead ferrets to other prairie dog colonies, there was little indication that ferrets will attempt to live on habitat other than prairie dog colonies, let alone successfully colonize other habitats. We documented a high degree of preference for prairie dog colonies by ferrets, which weakens the contention that there should be a “broader range of possibilities for conservation of the black-footed ferret” (Owen and others, 2000, p. 422), an argument implying broader habitat tolerances based on similarities between black-footed ferrets and Siberian polecats (*Mustela eversmannii*) and the hypothetical niches of North American Pleistocene and Holocene ferrets (or polecats). Our data and those of others (e.g., Biggins, 2000) suggest that natural selection has resulted in considerable divergence of behaviors and nonskeletal features in these two extant species of *Mustela* and that they are “ecological equivalents” (Hoffman and Pattie, 1968, p. 57; Lincoln and others, 1998, p. 94) only in the broadest sense. Attempts to release each species on varying habitats further test this hypothesis. Reproductively sterile Siberian polecats persisted for only short periods when released on prairie dog colonies in Wyoming (16 percent survival for 15 days) and Colorado (16 percent survival for 1 day) (Biggins, 2000), and some of the polecats used habitats other than the prairie dog colonies.

Release of Siberian polecats and black-footed ferrets into colonies of larger species of North American ground squirrels (*Spermophilus*) has not been attempted but could be informative.

Preferences Within Prairie Dog Colonies

For analyses of habitat preference within colonies, we defined as available to a ferret all of the prairie dog colony on which it resided. Definitions of availability are always somewhat arbitrary but are important because they affect the outcome of preference analyses (Johnson, 1980). Prior studies of ferret movements (Biggins and others, 1985, 1999; Biggins, 2000), coupled with the relatively small sizes of the colonies of the present study, helped justify our definition. We believe that the subjects of our study would not have been physically impeded from accessing any portion of the colonies on which they resided and were influenced primarily by the variables targeted for study (quality of habitat and competition for it). Even within the boundaries of prairie dog colonies, therefore, ferrets consistently preferred areas with relatively high densities of prairie dog burrows.

The preference of black-footed ferrets for areas on prairie dog colonies with high densities of prairie dog burrows was made possible by the clumped dispersion of burrows at our study sites. This nonrandom and nonuniform arrangement of burrow openings may be due to phenomena at several scales. Habitat quality for prairie dogs themselves may vary within the boundaries of their colonies, resulting from variation in soil type, soil depth, slope, and aspect. Vegetative mosaics are apparent on some colonies, resulting from these edaphic and physiographic attributes and other influences (e.g., plant competition) and from grazing by prairie dogs. Thus, the patchiness we observed at the scale of our plots (707 m²) is likely a reflection of the patchiness at intermediate scales (measured in hectares) resulting from the factors mentioned above coupled with variation at finer scales caused (at least in part) by the social organization of black-tailed prairie dogs into coterries and by interconnected burrow openings within coterries (Hoogland, 1995). We believe that attention to these considerations of scale will be increasingly important in gaining a more complete understanding of ferret ecology. Former evaluations of habitat for black-footed ferrets (e.g., Hillman and others, 1979; Forrest and others, 1985; Houston and others, 1986; Miller and others, 1988; Biggins and others, 1993) heavily emphasized the larger scales of colonies and complexes and may have led us to overlook details important to ferrets. Ferret preferences for areas of relatively high densities of prairie dog burrows, and the apparent intraspecific competition for those areas, imply qualities that may be related to fitness. We hypothesize that the value of clusters of burrow openings lies not only in their correlation to clusters of prairie dogs as prey but also in the immediacy of protective cover from predators during aboveground movements by

ferrets. Predation appears to be a substantial hazard for ferrets (Forrest and others, 1988; Biggins, 2000), causing by far the most losses during the repatriation program (Biggins, Godbey, Livieri, and others, this volume). Because of the positive association between safety and resources, ferrets are not forced into tradeoffs requiring choices between “a productive, but risky habitat and a less productive, safer habitat” (Grand and Dill, 1999, p. 389).

Intraspecific Competition for Habitat

Several lines of previous evidence suggest that territoriality is an important feature in the social lives of black-footed ferrets. Although direct agonistic encounters between free-ranging individual ferrets are rarely seen (Clark and others, 1986), two adult males were observed in what was described as “mortal combat” at the UL Bend in 1997 (Stoneberg, 1997, p. 13). Play behaviors in juveniles that may be precursors to such behaviors in adults (Poole, 1966, 1967, 1974) were commonly seen in free-ranging (Hillman, 1968; Clark and others, 1986) and captive (Miller, 1988; Vargas, 1994) litters. Agonistic behaviors between captive adult black-footed ferrets resembled agonistic interactions of domestic ferrets (Miller, 1988). General spacing patterns suggest that ferrets occupy somewhat distinct territories (Clark, 1989). Scent marking is a common behavior in ferrets and is particularly evident for males during the breeding season (Miller, 1988). Our understanding of competition among ferrets (especially females) for resources or space is nevertheless incomplete. Although free-ranging ferrets tend to occupy space that is not used by other ferrets of the same sex, occasional sharing of space by females during winter (Richardson and others, 1987) and even by females with litters (Paunovich and Forrest, 1987) raises doubts about exclusiveness of areas of activity. Captive Siberian polecats have been held in large cages for prolonged periods as same-sex and mixed-sex groups, but, on other occasions, aggression has been immediate and severe when multiple polecats were introduced into the same space (D. Biggins, unpub. data, 1995). Individual black-footed ferrets have severely injured their neighbors in conflicts through the wire mesh that separated their adjacent outdoor pens, and female ferrets have even killed their prospective mates (A. Vargas, oral commun., 1995). Simple rules seem inadequate for predicting outcomes of interactions. For females especially, activity area sizes and their exclusivity in time and space may be influenced by habitat quality and variation among individuals (Biggins, 2000), and perhaps nepotism at times masks the central tendency of ferrets to defend territories.

Nonetheless, the general theme of competition among black-footed ferrets for possession of space was supported by our study; the group that was predicted to be subordinate based on prior residency consistently occupied the habitat of lower quality. Large body size may be an advantage in contests, but we did not detect a significant effect of mass

in the competition for high-quality habitat among sequentially released young ferrets. Ferrets seemed to follow the “bourgeois strategy” (Ramsay and Ratcliffe, 2003, p. 120) in which prior residency overwhelms effects of size and other factors. The duration of prior residency also may have an effect (Harwood and others, 2003). In an experiment involving releases of white-throated sparrows (*Zonotrichia albicollis*) into outdoor aviaries, Dearborn and Wiley (1993) noted a gradual increase in effect of prior residency from 2–45 days, but the increase was most dramatic during the first 14 days. Duration of prior residency for ferrets in our sequential release experiment was fairly brief, with 2–4 weeks between the first and subsequent releases, but duration of residency was >1 year for individuals in the extant population that was augmented in 1997.

As ferret populations are assembled through progressive releases and additions of wild-born animals, intraspecific competition appears to result in sequential occupation of habitat patches by descending order of burrow (and prey) density. As available habitat becomes filled, the additional occupancy of sites with lower densities of burrows and prairie dogs is expected to increase the variance in burrow density of occupied sites. At sites with low burrow densities, areas of activity of ferrets may be largest. These phenomena outwardly resemble the characteristics associated with an ideal free distribution or an ideal dominance (despotic) distribution (Fretwell and Lucas, 1970). Explorations by released ferrets may be sufficient to impart “ideal” knowledge regarding availability of habitat, but territoriality of resident ferrets may prevent “free” choice (*sensu* Fretwell and Lucas, 1970). Further assessment of processes involved in ferret habitat occupancy in relation to theoretical distributions (Fretwell and Lucas, 1970; Fretwell, 1972) must consider relative fitness (Messier and others, 1990; Beckman and Berger, 2003), a topic we will address separately with other data sets.

Commonly used habitat evaluation systems for black-footed ferrets (e.g., that of Biggins and others, 1993) likely overestimate ferret densities attainable on the best habitats. As acknowledged by Biggins and others (1993, p. 75) in the introduction to their suggested model, “Social behavior may dictate a maximum ferret density regardless of prey abundance.” Mounting evidence regarding territoriality in ferrets does indeed suggest that models used to predict carrying capacity of habitat for ferrets should include an increasing effect of social exclusion of ferrets at high densities of prairie dogs. Because the best quality habitats as rated by the model of Biggins and others (1993) are presently sustaining ferrets at densities almost double those of low-quality habitats, we suggest retention of the fundamental structure of the model, with modifications recently suggested (Biggins, Lockhart, and Godbey, this volume). Although our comparative data suggest that competitiveness varies among individuals and has an important influence on population assembly (groups varied in their ability to control space and resources), we are unable to estimate the strength of territoriality at varying prey densities.

Additional studies on territoriality in male and female ferrets could help refine predictions of the model at high prairie dog densities. The model also would benefit from an improved understanding of habitat limitations for reproductive female ferrets inhabiting colonies with low prairie dog densities, a subject beyond the scope of this study.

The prior residency advantage raises other issues of conservation concern. Quality of ferrets released may vary because of prerelease experience (Biggins and others, 1998, 1999) and age (Biggins, Godbey, Livieri, and others, this volume). Preliminary releases of lower quality animals may reduce the amount of good habitat available for higher quality animals subsequently released if the first animals become established. Even if those first residents succumb rather quickly to predation, their initial presence could elevate the risk to newcomers during the first critical days postrelease. Thus, we recommend careful consideration be given to choice of sites and sequence of release when habitat will receive groups of ferrets varying in prerelease experience, origin, and age.

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