

BLACK-FOOTED FERRET SPATIAL USE OF PRAIRIE DOG COLONIES IN
SOUTH DAKOTA

by

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ABSTRACT

Endangered black-footed ferrets (*Mustela nigripes*) rely exclusively upon prairie dogs (*Cynomys* spp.) for food and shelter. The details of the relationship between ferrets and their habitat is not well understood. I examined habitat factors that may influence ferret use of prairie dog colonies and ferret home ranges within prairie dog colonies. Using logistic regression and estimated ferret densities I modeled ferret use of prairie dog colonies as related to colony variables including size, prairie dog and prairie dog burrow density, intercolony distance and the proportion of colonies within the landscape. I found ferrets occur more often on larger prairie dog colonies but may not necessarily select for large colonies. Ferret density was negatively associated with colony size ($P < 0.001$, $r^2 = 0.732$) although colony size showed no correlations with relative fitness, prairie dog density or prairie dog burrow density. The potential fitness advantages to lower densities of ferrets on larger prairie dog colonies remains unknown. To investigate ferret spatial use within a prairie dog colony I used spotlighting locations to estimate home ranges for ferrets and assessed factors that may influence range size. Multiple regression models of ferret home ranges indicated a larger range for males ($\bar{x} = 131.8 \pm 40.3$ ha) than females ($\bar{x} = 64.7 \pm 11.6$ ha) but no difference was detected between captive- and wild-born animals. Female home range size was negatively related to male density and male home range size was positively associated with age. Inter-sexual overlap and intra-sexual exclusivity of home ranges was evident, suggesting ferrets conform to a typical mustelid spacing pattern. Core activity areas had higher estimated prairie dog densities than home ranges. Management of prairie dog colonies should focus on a mosaic of colony sizes to

account for the territoriality and reproductive needs to sustain a black-footed ferret population.

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CHAPTER 1

BLACK-FOOTED FERRET SELECTION OF PRAIRIE DOG COLONIES IN SOUTH DAKOTA

ABSTRACT

Black-footed ferrets (*Mustela nigripes*) are obligate predators of prairie dogs (*Cynomys* spp.) and occur only on prairie dog colonies. However, all prairie dog colonies might not represent equally suitable habitat for ferrets. I compared attributes of prairie dog colonies occupied by black-footed ferrets in the Conata Basin portion of the Buffalo Gap National Grassland and Badlands National Park, South Dakota (n=64) with those without ferret presence (n=46). Univariate tests found that ferrets occupied prairie dog towns that were significantly larger ($\bar{x} = 56.7$ ha vs. $\bar{x} = 8.9$ ha), with a higher area-weighted intercolony distance ($\bar{x} = 0.0116$ vs. $\bar{x} = 0.0006$) and that were closer to colonies on which black-footed ferrets were released ($\bar{x} = 840$ m vs. $\bar{x} = 1276$ m) ($P < 0.05$). Although sample sizes were considerably smaller, prairie dog density and burrow densities did not appear to influence selection of colonies. I also used binary logistic regression to construct models of black-footed ferret selection. The resulting models indicated the size of prairie dog colony had the largest influence on black-footed ferret occupation of prairie dog colonies. However, due to passive sampling issues the use of larger colonies may have only been an artifact of the greater likelihood of a ferret encountering the area, not because of selection. To explore the relationship of colony size to ferret selection, I looked at the relationship of ferret density to colony size. Prairie dog colony size was negatively correlated with black-footed ferret density ($P < 0.001$, $r^2 = 0.732$), indicating ferrets are more widely spaced on large colonies. Because the number

of ferret kits per female, prairie dog density, and prairie dog burrow density are no different on large colonies versus small, the decrease in ferret density on larger colonies is difficult to explain. However, because data on survivorship of ferret adults or kits is unavailable, potential fitness advantages to lower ferret densities on larger colonies is unknown and should be investigated further. Management should focus on a mosaic of colony sizes to ensure ferret population persistence.

INTRODUCTION

Black-footed ferrets are a federally endangered species and were reintroduced into the Conata Basin/Badlands (CB/B) area of southwestern South Dakota from 1994-1999. They are obligate predators of prairie dogs (Biggins et al. 1993; 2006a) and occur only on prairie dog colonies (Linder et al. 1972, Hillman et al. 1979), therefore coarse habitat attributes for ferrets are essentially prairie dog colony attributes because the two species occur sympatrically (Forrest et al. 1985). However, repeated observations of ferret occurrence and distribution suggests that all prairie dog colonies do not represent equally suitable habitat for selection and successful use by reintroduced or subsequently wildborn ferrets (Plumb et al. 1996). Consequently, there may be some level(s) of resource selection occurring. Managers suspect that among colonies there may be acceptable levels of habitat “quality” as defined by a suite of habitat variables which will likely increase or decrease the probability of resource selection and use of a colony by ferrets. As of 2001, the CB/B black-footed ferret reintroduction project had resulted in a small, growing population ($N > 200$) of reintroduced and wildborn individuals distributed across a 400-km² black-tailed prairie dog (*Cynomys ludovicianus*) complex. Ferrets were reintroduced into 13 sites across six states and Mexico since 1991 with varied success at

establishing populations (Lockhart et al. 2006). To develop sound management guidelines, managers require a better understanding of the relationship between habitat variation and selection by ferrets.

A number of habitat variables may influence prairie dog colony selection by black-footed ferrets. Forrest et al. (1985) identified seven habitat features for assessing suitability of prairie dog colonies to support ferret populations (in order of descending importance): complex size, colony size, colony distribution, prey density and distribution, vegetation composition and structure, burrow structure, and predators. These habitat features were the basis for a Habitat Suitability Index developed by Houston et al. (1986). Biggins et al. (1993) recommended a minimum size of 400 ha for the combined area of all colonies in a prairie dog complex for consideration as a ferret reintroduction site regardless of prairie dog species. The historic range of black-footed ferrets encompassed three prairie dog species, black-tailed (BTPD), white-tailed (*Cynomys leucurus*; WTPD) and Gunnison's prairie dogs (*Cynomys gunnisoni*; GPD) (Fagerstone 1987). BTPDs generally have a larger body size, higher burrow density and smaller colony size than WTPDs and GPDs (Hoogland 1995).

Distribution of colonies within a complex is important because ferrets are more likely to encounter large, closely spaced colonies than small, distant colonies (Forrest et al. 1985, Houston et al. 1986, Miller et al. 1988). For ferrets, the consequences of occupying small, distant colonies could be reduced gene flow, decreased colonization rates and dispersal success, and decreased mating success (Biggins et al. 1993), leading to higher probabilities of extinction. At Meeteetse, Wyoming, site of the last known wild population of ferrets, the average distance between WTPD colonies was 0.9 km (Clark

1989) compared with 5.2 km for BTPDs at Mellette County, South Dakota (Hillman et al. 1979), which supported the only wild ferret population on BTPDs ever studied.

Colony size may be important for establishment and maintenance of black-footed ferret populations, although smaller colonies incapable of supporting long-term ferret occupancy may be important for dispersal and inter-colony movements (Forrest et al. 1985). At Meeteetse, WTPD colony sizes were 0.5-1,302 ha and the smallest colony supporting an individual ferret was 12.5 ha. Litters were found only on colonies >49 ha (Clark 1989). Hillman et al. (1979) recommended a minimum colony size of 12 ha for an individual ferret and 40 ha for litters, based on observations at Mellette County, South Dakota (BTPDs). In contrast, Stromberg et al. (1983) recommended 167 to 355 ha of prairie dog colony per ferret. Beck and Gebhart (1978) observed ferrets on 17 BTPD colonies averaging 24 ha, compared with 13 ha for colonies where ferrets were not observed. Forrest et al. (1985) found that colonies >180 ha were continuously occupied by ferrets, whereas smaller colonies were used seasonally or not at all.

Within and among prairie dog colonies there is substantial variation in attributes which may influence black-footed ferret selection. Prey availability has been shown to influence habitat selection by other mustelids such as river otters (*Lontra canadensis*; Melquist and Hornocker 1983) and least weasels (*Mustela nivalis*; Erlinge 1974). Since prairie dogs comprise approximately 90% of the ferret diet (Sheets et al. 1972, Campbell et al. 1987), it is likely that prairie dog density influences the quality of habitat for ferrets. Biggins et al. (1993) reported that higher prairie dog densities are required to support ferret reproduction than to sustain individual animals. Average BTPD densities across their historic distribution range from 10-55/ha (O'Meilia et al. 1982, Knowles 1986,

Archer et al. 1987). At Meeteetse, mean WTPD density was 3.8/ha and mean burrow opening density was 37.6/ha (Clark 1989). Among BTPD complexes, Hoogland (1995) noted that burrow opening densities varied from 10-250/ha. Forrest et al. (1985) suggested high burrow densities may be desirable for the added protection they provide to ferrets as escape from predators. Collins and Lichvar (1986) examined the vegetation of the Meeteetse study area and concluded that vegetative parameters were less important in defining ferret habitat than other variables, although, the presence of tall vegetation may influence the ability of a ferret to detect predators.

Carlson (1993) studied habitat selection by black-footed ferrets immediately following release (1-11 days) and found no correlation between ferret use sites and prairie dog density, but concluded ferrets released in the fall may initially exhibit exploratory behavior rather than selecting areas with characteristics beneficial to survival. Managers at CB/B observed further post-release ferret selection of prairie dog colonies during definite periods such as breeding season and parturition, suggesting that some colonies may be selected to fulfill biological requirements. Because the CB/B ferret population was comprised of released animals and their offspring the selection of release colonies by biologists might have influenced colony selection. In essence, biologists made the first colony selection for ferrets and if ferrets did not move to non-release colonies, that influence should remain.

My objective was to examine black-tailed prairie dog colony attributes in relation to black-footed ferret selection of a colony. I constructed logistic regression models with data from the combination of released and wild-born ferrets at CB/B and expected that

ferrets would select prairie dog colonies non-randomly, in a pattern that was predictable from prairie dog colony attributes.

STUDY AREA

I collected prairie dog colony attribute and black-footed ferret location data at the Conata Basin/Badlands area of southwestern South Dakota (Figure 1) on public lands administered by the National Park Service, Badlands National Park, USDA Forest Service, Buffalo Gap National Grassland, and adjoining private lands. Ferrets were reintroduced to prairie dog colonies in CB/B annually from 1994-1999. The climate of the area was semi-arid with an average annual precipitation of 39.9 cm. Mean annual temperature was 10.3 °C and monthly mean temperatures range from -4.6 °C in January to 25.5 °C in July (National Oceanic and Atmospheric Administration 1993).

Topography is level but broken by small drainages generally running north to south.

Soils are young and poorly developed with textural classes dominated by clay. Badlands buttes and formations are scattered throughout the landscape. Vegetation was mixed-grass prairie, dominated by western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloe dactyloides*), and blue grama (*Bouteloua gracilis*) (Severson and Plumb 1998).

METHODS

Black-footed Ferret Location Data

During 1997-2004, black-footed ferrets were located on prairie dog colonies using spotlighting methods (Clark et al. 1983, Biggins et al. 2006b). Spotlight surveys occurred throughout the year, with the exception of June, on prairie dog colonies where ferrets were released and surrounding colonies to document dispersal. Snow-track surveys (Richardson et al. 1987) were used to indicate presence of ferrets on outlying

colonies and were followed up by spotlight surveys. Ferret locations were temporarily marked with a driveway reflector and assigned a location using differentially-corrected Trimble® global positioning system (GPS) equipment. Released ferrets were uniquely identified by previously implanted passive integrated transponder (PIT) tags (Fagerstone and Johns 1987, Stoneberg 1996). Wild-born ferrets were live-trapped and implanted with PIT tags (Biggins et al. 2006*b*).

Once the identification number and the location colony of the black-footed ferret was known then sex, location date, and release date data were obtained from release records and spotlighting data. By subtracting the location date from the release date, I estimated the number of known days the ferret had survived in the wild since release. Released ferrets experience an acclimation period when selection is essentially random (Carlson 1993). Survival to 30-days post-release is indicative of a higher probability of long-term survival (D. Biggins, U.S. Geological Survey-Biological Resources Division, Fort Collins, CO, personal communication). Thus data collected prior to 30-days post-release were discarded.

Parturition in the wild is typically in May-June. Kits first come above ground at approximately 60 days of age (July-August), and disperse from their mothers at 90-120 days of age (September-October). Hence, for wild-born animals their 'release date' was considered to be 1 September, and data were used for ferret locations only after 30-days post-release.

Spotlight surveys during the study were considered a complete census and the population closed since it was a reintroduced population in an area containing no ferrets and >90% of the known ferrets present were accounted for after intensive sampling. The

sampling units were prairie dog colonies, with each colony being designated as used by the detection of at least one ferret.

Prairie Dog Colony Variables

Prairie dog colony attributes were compared between colonies that were used and unused by black-footed ferrets. Prairie dog colonies in the study area were mapped in 1999 and 2004 using differentially corrected Trimble GPS (Global Positioning Systems) equipment. A Geographic Information System (GIS) was used to calculate 9 landscape metrics for each prairie dog colony (Table 1). At Meeteetse, a white-tailed prairie dog complex, the longest nightly moves recorded for ferrets were approximately 7 km (Richardson et al. 1987, Biggins et al. 1993). I suspected longest nightly moves for ferrets on black-tailed prairie dog colonies were <7 km since black-tail colonies are more clustered and dense than white-tail (Tileston and Lechleitner 1966). Thus I used a 7-km buffer from the colony edge to calculate the percentage of landscape occupied by prairie dog colony at 1 km increments as “donuts” (%1KM-%7KM). Another measure of patch isolation was developed by taking the harmonic means of distances to all other colonies and weighting them by the size of the colony. This variable, called an area-weighted inter-colony distance (AWIC), was calculated by:

$$AWIC = \frac{\sum_{i=1}^{n-1} \frac{a_i}{d_i}}{n-1},$$

where d is the distance from the closest edge of the target colony to all other colonies ($n-1$), and a is the area (ha) of the distant colony, excluding the target colony. Therefore, a colony with large colonies nearby would have a higher AWIC than a colony surrounded by small, distantly spaced colonies. Variables %1KM-%7KM were all highly correlated

($r \geq 0.5$) with AWIC and with each other, the highest correlations among the closest variables (e.g. %2KM was most correlated with %1KM and %3KM). AWIC was analyzed separately from all %KM variables.

Prairie dog density was estimated 1996-1999 on a random sample of 21 colonies although only data from 8 colonies was able to be used in modeling. Prairie dog density was obtained by visual counts (Fagerstone and Biggins 1986, Menkens and Anderson 1993, Severson and Plumb 1998) on one randomly selected 16-ha plot per colony to yield an estimate of prairie dogs/ha (PDOG DENS). Density of active (ACT BURR) and total (TOT BURR) prairie dog burrows/ha was estimated on 34 colonies using transect methods outlined by Biggins et al. (1993) although only data from 24 colonies was able to be used in modeling. To assess the influence of release colony selection by biologists I measured the minimum edge-to-edge distance in meters from a release colony (RELDIST) with release colonies having a value of zero.

Using prairie dog colony size (HA) in the logistic regression models was problematic because larger colonies effectively represent larger samples and the probability of a ferret occupying a large colony is greater than a small colony by simple random chance. This problem is known as “passive sampling” (Johnson 2001). I avoided the issue of passive sampling by regressing adult female density against prairie dog colony size to assess the influence of colony size on ferret selection as measured by density. Data from 2003-04 were used because reintroduction was no longer occurring and the population was >99% wild-born. Black-footed ferret densities for each colony were calculated by the number of adult females present on a colony in 2003 and 2004. A paired t-test indicated that the densities between years were not significantly different ($P=0.714$), so I averaged both

years to provide one density estimate for each colony. If ferrets were selecting for larger prairie dog colonies I expected to find an increased ferret density in larger colonies. Sampling effort per unit area was not equivalent across all colonies and was generally cumulatively greater on large colonies than on small colonies.

I also assessed the relationship between one measure of fitness, kits per adult female, and colony size. The number of unmarked kits present on a colony was divided by the number of adult females to estimate kits per adult female. I regressed both prairie dog density and prairie dog burrow density against colony size to determine if colony size was related to prey density.

Data Analysis

Attributes of prairie dog colonies used/unused by black-footed ferrets for each gender were compared using Mann-Whitney U-tests and pooled if groups were not significantly different. To determine if selection occurred at a univariate level, Mann-Whitney U-tests were used to compare used and unused prairie dog colony attributes. Variables that were not highly correlated ($r \leq 0.5$) were used in a binary logistic regression model. Models were evaluated for goodness-of-fit using r^2 , Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) and Akaike weights. AIC_c uses log-likelihood and the number of parameters to evaluate the bias and precision of all possible model subsets. The top models had the lowest AIC_c score, highest Akaike weight and evidence and high r^2 . Significance level was $\alpha = 0.05$ for all tests unless noted.

RESULTS

From 1997 to 2001, 110 of 195 prairie dog colonies were sampled for ferrets and 8,309 locations were collected on 501 individual black-footed ferrets (251 females, 250 males) from 66 prairie dog colonies (60 used by females and 61 by males). Data from 1997-2001 were used in logistic regression modeling while data from 2003-04 (115 individual adult females on 17 colonies) were used for density regression. Collection of ferret location data was accomplished by personnel of the U.S. Forest Service, National Park Service and I.

Prairie dog colonies ($N = 195$) had a mean size of 28.4 ha ($SE = 5.2$) with a mean edge-to-edge inter-colony distance of 304.8 m ($SE = 33.4$). Mean prairie dog density on a sample of 21 colonies was 28.7 prairie dogs/ha ($SE = 5.4$) and mean active burrow density on a sample of 34 colonies was 139.6 active burrows/ha ($SE = 7.1$).

There were no significant differences between used colony attributes for females and males for all variables, thus sexes were pooled. Ferrets were found in colonies that were larger in size ($P = 0.005$), had a greater area-weighted inter colony distance (AWIC; $P = 0.049$) and where the distance to a release colony was less (RELDIST; $P = 0.018$) (Table 2).

Logistic regression models indicated HA had a large influence on black-footed ferret selection of prairie dog colonies (Table 3). Despite a generally greater sampling effort on large colonies, density of adult female black-footed ferrets was negatively associated with prairie dog colony size ($P < 0.001$, $r^2 = 0.732$; Fig. 2). The number of kits per female, as a measure of fitness, did not change with colony size ($P = 0.595$, $r^2 = 0.016$; Fig. 3).

Neither prairie dog density ($P = 0.651$, $r^2 = 0.011$; Fig. 4) nor prairie dog burrow density ($P = 0.876$, $r^2 < 0.001$; Fig. 5) were related to colony size.

DISCUSSION

Prairie dog colonies at CB/B were larger than the mean colony size of 151 black-tailed prairie dog colonies in Mellette County, SD ($\bar{x} = 8.5$ ha; Linder et al. 1972) but smaller than 37 white-tailed prairie dog colonies at Meeteetse, WY ($\bar{x} = 80.9$ ha; Clark 1989). Mean edge-to-edge inter-colony distance at CB/B ($\bar{x} = 304.8$ m, $SE = 33.4$) was much smaller than white-tailed prairie dog colonies at Meeteetse ($\bar{x} = 900$ m), due to a larger complex size at CB/B than Meeteetse. Mean prairie dog density on a sample of 20 colonies at CB/B was 29.0 prairie dogs/ha, considerably higher than the 3.8 prairie dogs/ha on white-tailed prairie dogs reported by Clark (1989) for Meeteetse. Mean active burrow density on a sample of 41 colonies at CB/B was 158.3 active burrows/ha and was more than four times greater than the mean white-tailed prairie dog burrow opening density of 37.6/ha at Meeteetse (Clark 1989). The large disparity in mean prairie dog and burrow density between CB/B and Meeteetse is not surprising because black-tailed prairie dogs are typically more clustered and dense than white-tailed prairie dogs (Tileston and Lechleitner 1966). The mean prairie dog and burrow densities at CB/B also fall within the typical range for black-tailed prairie dog densities (10-55/ha; O'Meilia et al. 1982, Knowles 1986, Archer et al. 1987) and burrow opening densities (10-250/ha; Hoogland 1995).

Black-footed ferret selection of prairie dog colonies was slightly influenced by AWIC suggesting colonies in close proximity are preferred by ferrets. The benefits of closely spaced prairie dog colonies for ferrets would be reduced predation risk and energetic

expenditure during inter-colony movements. I did find a negative correlation between adult female ferret density and colony size suggesting female ferrets are more widely spaced on large colonies. In CB/B the smallest colony supporting a litter was 12ha. Hillman et al. (1979) found 5 of 9 litters in Mellette County, SD on colonies <16 ha and Biggins et al. (2006c) reported a female ferret raised two kits on a 5 ha colony in Montana.

The lower density of female ferrets on larger colonies may be the result of several different factors: 1) low density may increase individual female fitness by increasing survivorship rates, or; 2) prey density or burrow density may be more heterogeneous in large colonies, hence larger areas are required for females to meet their energetic demands. Because the number of kits per female, prairie dog density and prairie dog burrow density did not differ with colony size, those factors do not appear to be influencing colony selection. Rigorous survival data was unavailable to assess the relationship between black-footed ferret survival and selection of prairie dog colonies which ultimately would identify the best colonies for ferrets to occupy. While small colonies may meet the biological requirements of individual ferrets, larger colonies are probably needed to sustain a population. The historic Mellette County (BTPD) ferret population had small, isolated prairie dog colonies ($\bar{x} = 8.5$ ha; Linder et al. 1972), more than 3 times smaller than the mean colony size at CB/B and the population ultimately disappeared.

Prairie dog density was untestable in the univariate tests because there was only one unused colony that had prairie dog density calculated. While prairie dog density is expected to be important to ferrets, there is likely a range of densities that influence

colony selection with an upper and lower threshold. At high prairie dog densities ferrets are probably not limited by prey availability thus other variables, such as territoriality, likely influence selection under those circumstances. The high prairie dog and burrow densities found at CB/B may be above the upper threshold of densities that influence colony selection, but obviously I was unable to test for this relationship.

The distance of a prairie dog colony from a ferret-release colony (RELDIST) was significant in univariate tests and appeared in competing models but not the preferred model. Biologists initially chose 17 large prairie dog colonies to release captive-born ferrets or translocate wild-born ferrets. Through reproduction and dispersal, ferrets occupied non-release colonies throughout CB/B. Because this reintroduction of ferrets is relatively recent I expected distance from a release colony (RELDIST) to have a relationship with ferret colony selection. The significance of RELDIST in univariate tests suggested a lingering influence of where biologists initially placed ferrets, although it was not large enough to dominate the logistic model.

MANAGEMENT IMPLICATIONS

My results suggest black-footed ferrets prefer closely spaced prairie dog colonies but may not specifically select for large colonies. Although ferrets may fulfill biological requirements on small colonies it is likely that small colonies are more susceptible to localized extinctions, requiring immigration from large colonies that may serve as source populations. The observed higher density of ferrets on smaller colonies suggest these “islands” of habitat may support more ferrets per unit area by reducing the effects of territoriality (Biggins et al. 2006a). Within a prairie dog colony, black-footed ferrets select for patches of high prairie dog burrow density and prior residency may impart a

competitive advantage (Biggins et al. 2006a). Competition for high burrow density patches among ferrets may lead to higher dispersal rates from large colonies. My results support Biggins et al. (2006a) suggestion that “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.”

While small colonies may meet the biological requirements of individual ferrets, larger colonies are needed to sustain a population. Biggins et al. (2006c) suggest colonies <10 ha may not have sufficient prairie dog numbers to sustain ferret reproduction in consecutive years without a severe depletion of prairie dogs. Biologically, managing prairie dog complexes for black-footed ferret recovery may require a mosaic of colony sizes. Although large prairie dog colonies may not support high densities of ferrets we do not yet understand their role in the population dynamics or their relationship to fitness and long-term persistence of black-footed ferret populations on the landscape.

LITERATURE CITED

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Table 1. Prairie dog colony attributes collected at Conata Basin/Badlands, South Dakota.

Variable	Description	Range
AWIC	Area-weighted inter-colony distance	0.001583 – 0.112343
HA	Size of prairie dog colony in hectares	0.1 – 656.8
%1KM	% area of prairie dog colonies in the landscape within 1km of colony edge	0.0 – 53.8
%2KM	% area of prairie dog colonies in the landscape within 2km of colony edge	0.2 – 37.1
%3KM	% area of prairie dog colonies in the landscape within 3km of colony edge	0.5 – 34.9
%4KM	% area of prairie dog colonies in the landscape within 4km of colony edge	0.9 – 27.6
%5KM	% area of prairie dog colonies in the landscape within 5km of colony edge	1.0 – 20.6
%6KM	% area of prairie dog colonies in the landscape within 6km of colony edge	0.9 – 17.6
%7KM	% area of prairie dog colonies in the landscape within 7km of colony edge	1.1 – 17.4
PDOG DENS	Prairie dog density (prairie dogs/ha)	7.5 – 32.6
ACT BURR	Active prairie dog burrow density (active burrows/ha)	80.9 – 202.5
TOT BURR	Total prairie dog burrow density (total burrows/ha)	84.4 – 217.5
RELDIST	Edge-to-edge distance of nearest ferret release colony (meters)	0.0 – 5999.2

Table 2. Mean and standard error for prairie dog colony variables used and unused by black-footed ferrets at Conata Basin/Badlands, South Dakota.

Variable	Used \bar{x} (SE)	n	Unused \bar{x} (SE)	n
AWIC	0.01168 (0.00206)*	64	0.00653 (0.00062)*	46
HA	56.7 (14.2)*	64	8.9 (1.6)*	46
%1KM	10.3 (1.4)	64	10.0 (1.3)	46
%2KM	12.1 (1.2)	64	9.6 (1.2)	46
%3KM	12.4 (1.0)	64	10.3 (1.1)	46
%4KM	11.8 (0.7)	64	10.3 (0.9)	46
%5KM	10.9 (0.6)	64	9.8 (0.7)	46
%6KM	10.2 (0.5)	64	9.2 (0.6)	46
%7KM	9.4 (0.5)	64	8.5 (0.5)	46
PDOG DENS (dogs/ha)	19.2 (3.9)	7	25.6 (0.0)	1
ACT BURR (per ha)	138.5 (6.7)	20	138.8 (15.0)	4
TOT BURR (per ha)	147.7 (8.0)	20	148.4 (9.3)	4
RELDIST (m)	840.2 (128.6)*	64	1275.7 (194.5)*	46

*Significant difference at $\alpha = 0.05$.

Table 3. All logistic regression candidate models for black-footed ferret selection of prairie dog colonies in South Dakota.

Models	Log-likelihood	K	AIC_c	Delta	Weight	Evidence	r²
HA + %7KM	-60.83	3	127.88	0	0.14		0.207
HA	-62.06	2	128.24	0.35	0.12	1.2	0.190
HA + %6KM	-61.17	3	128.57	0.69	0.10	1.4	0.203
HA + AWIC	-61.20	3	128.62	0.74	0.10	1.4	0.202
HA + %5KM	-61.59	3	129.40	1.52	0.06	2.1	0.198
HA + %4KM	-61.63	3	129.49	1.60	0.06	2.2	0.197
HA + %3KM	-61.74	3	129.71	1.83	0.05	2.5	0.196
HA + RELDIST	-61.75	3	129.73	1.84	0.05	2.5	0.196
HA + RELDIST + %7KM	-60.83	4	130.04	2.15	0.05	2.9	0.208
HA + %1KM	-61.95	3	130.12	2.23	0.04	3.1	0.193
HA + %2KM	-62.00	3	130.22	2.33	0.04	3.2	0.193
HA + AWIC + RELDIST	-61.13	4	130.64	2.76	0.03	4.0	0.205
HA + RELDIST + %1KM	-61.14	4	130.67	2.78	0.03	4.0	0.204
HA + RELDIST + %6KM	-61.17	4	130.72	2.84	0.03	4.1	0.204
HA + RELDIST + %5KM	-61.55	4	131.48	3.59	0.02	6.0	0.200
HA + RELDIST + %4KM	-61.59	4	131.55	3.67	0.02	6.3	0.199
HA + RELDIST + %3KM	-61.66	4	131.71	3.82	0.02	6.8	0.198
HA + RELDIST + %2KM	-61.75	4	131.88	3.99	0.02	7.4	0.197
AWIC	-71.28	2	146.68	18.79	0.00	12057.1	0.061
AWIC + RELDIST	-70.98	3	148.18	20.30	0.00	25536.7	0.066
RELDIST	-72.90	2	149.91	22.03	0.00	60655.2	0.033
%1KM + RELDIST	-72.36	3	150.95	23.06	0.00	101857.9	0.043
%3KM	-73.63	2	151.37	23.48	0.00	125547.2	0.021
%2KM	-73.76	2	151.64	23.75	0.00	143644.9	0.018
%4KM	-73.76	2	151.64	23.75	0.00	143724.9	0.018
%3KM + RELDIST	-72.78	3	151.79	23.91	0.00	155319.4	0.036
%7KM + RELDIST	-72.79	3	151.82	23.93	0.00	157229.8	0.036
%2KM + RELDIST	-72.82	3	151.86	23.98	0.00	160952.6	0.035
%4KM + RELDIST	-72.83	3	151.88	24.00	0.00	162390.3	0.035
%6KM + RELDIST	-72.86	3	151.95	24.06	0.00	168070.7	0.034
%5KM + RELDIST	-72.87	3	151.97	24.08	0.00	169657.3	0.034
%7KM	-73.94	2	152.00	24.11	0.00	172306.3	0.015
%5KM	-73.99	2	152.08	24.20	0.00	179676.7	0.014
%6KM	-74.03	2	152.17	24.29	0.00	188009.6	0.013
%1KM	-74.75	2	153.62	25.73	0.00	387402.0	0.000

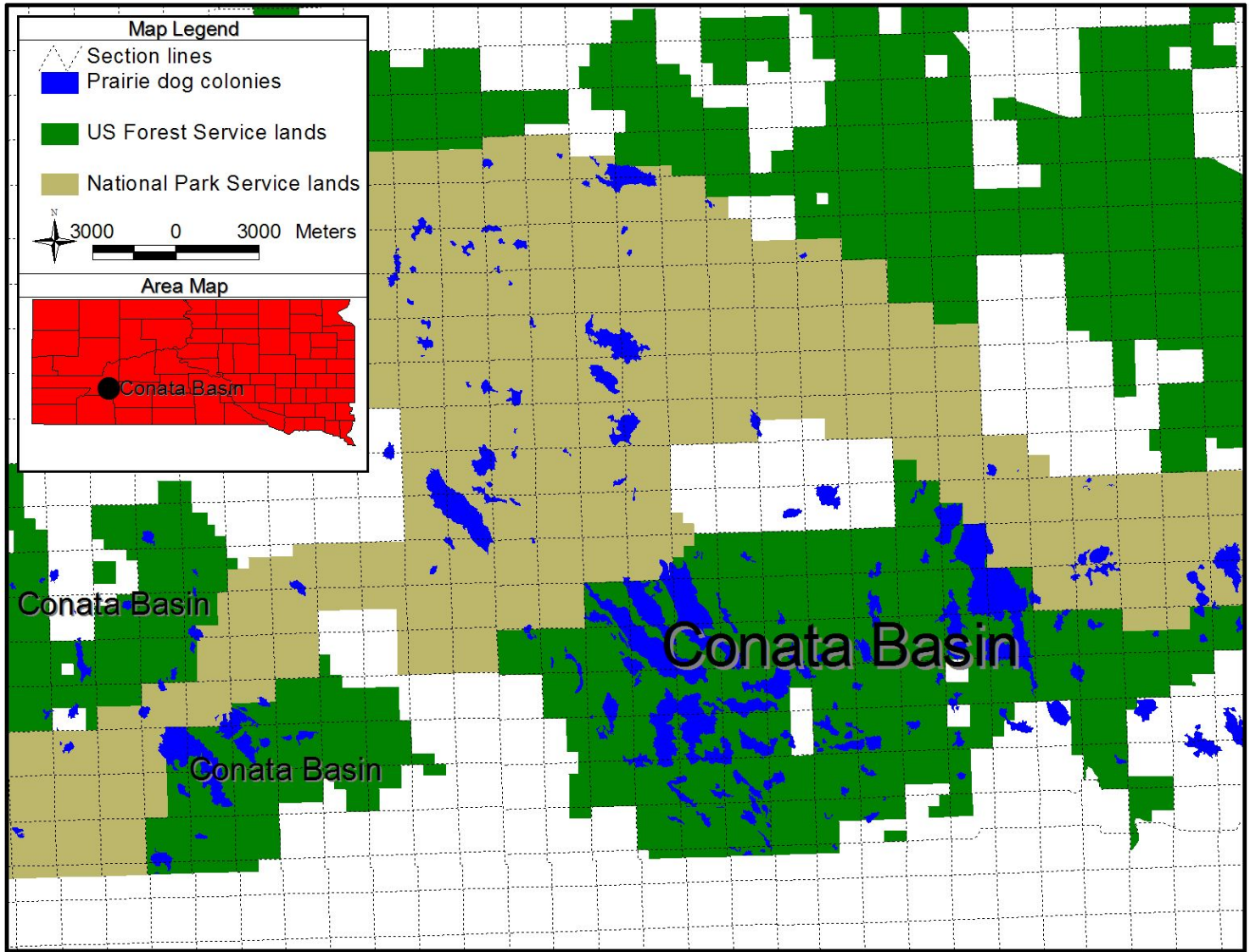


Figure 1. Map of prairie dog colonies in Conata Basin/Badlands, South Dakota, 1999.

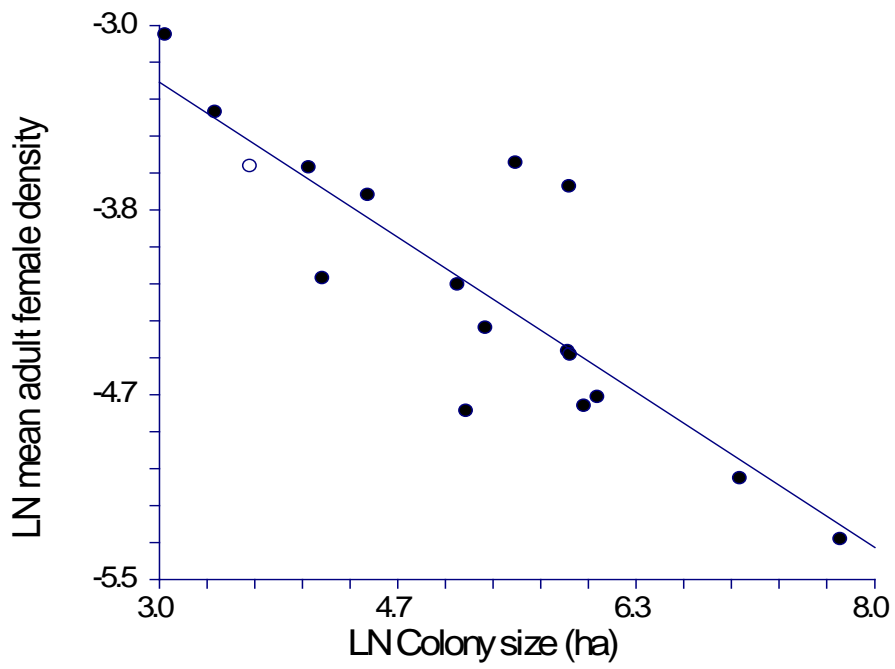


Figure 2. Relationship between adult female black-footed ferret density and prairie dog colony size at Conata Basin/Badlands, South Dakota, 2003-2004.

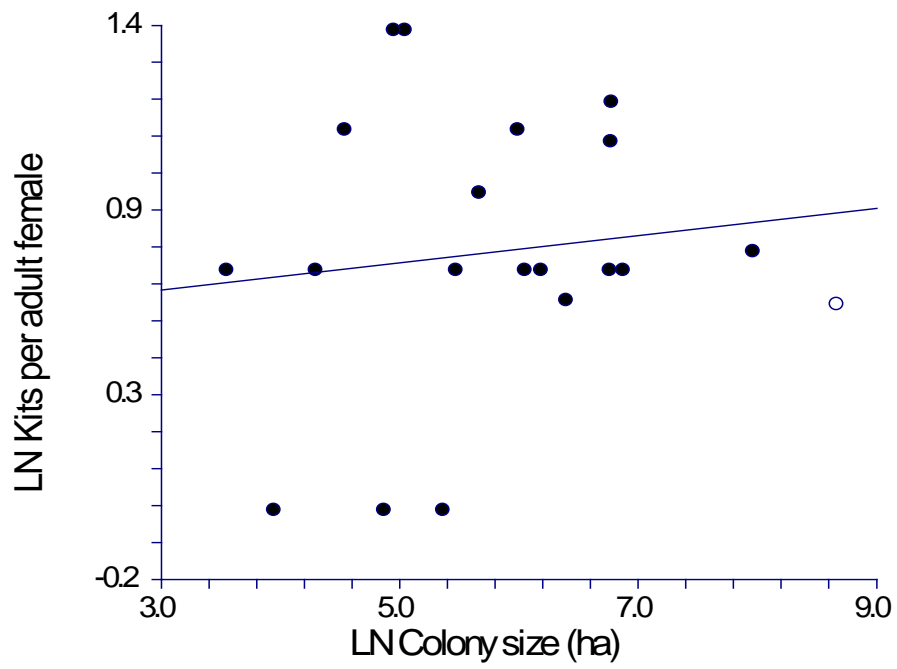


Figure 3. Relationship between kits per adult female black-footed ferret (relative fitness) and colony size in South Dakota, 2003-2004.

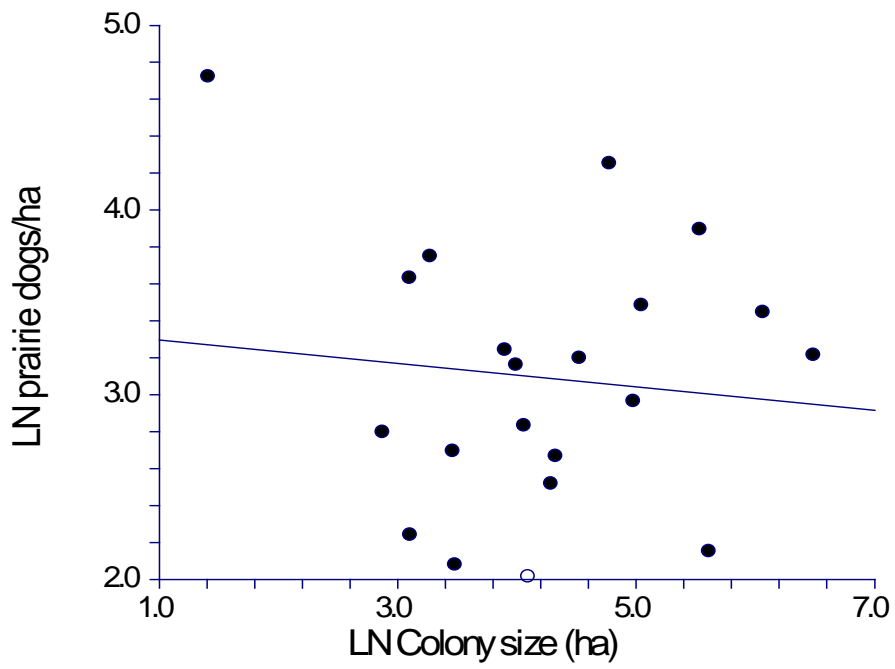


Figure 4. Relationship between prairie dog density and prairie dog colony size in South Dakota, 1997-1999.

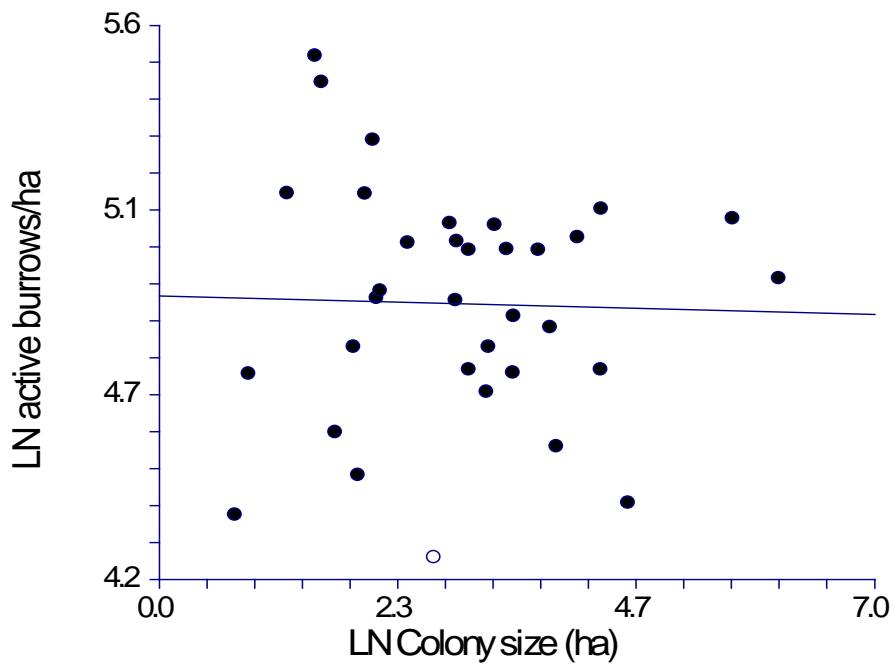


Figure 5. Relationship between active prairie dog burrow density and prairie dog colony size in South Dakota, 1997-1999.

CHAPTER 2

BLACK-FOOTED FERRET HOME RANGES IN CONATA BASIN, SOUTH DAKOTA

ABSTRACT

Estimates of black-footed ferret (*Mustela nigripes*) spatial use of prairie dog (*Cynomys* spp.) colonies are needed for planning prairie dog reserves and ferret reintroductions. Few previous published estimates of ferret home range size exist and were based upon ferrets inhabiting white-tailed prairie dog (*Cynomys leucurus*) colonies, which are spatially unlike black-tailed prairie dog (*Cynomys ludovicianus*) colonies. I collected ferret locations in the Conata Basin of South Dakota through spotlighting methods and used kernel methods to estimate home range size at the 95 and 50% contours and 100% minimum convex polygon for both sexes. Amount of inter- and intra-sexual overlap was calculated by overlaying individual home ranges. A minimum of 23 locations was sufficient to estimate home ranges of 28 ferrets (20 female, 8 male). Mean (\pm SE) 95% and 50% fixed kernel annual home range size of females (64.7 ± 11.6 ha and 12.7 ± 3.0) was significantly smaller than males (131.8 ± 40.3 and 35.6 ± 16.5). Minimum convex polygon home range estimates also differed between females (41.9 ± 6.5 ha) and males (86.3 ± 21.3 ha). Female home range size was negatively related to male density and male home range size was positively associated with age. Inter-sexual overlap and intra-sexual exclusivity of home ranges was evident, suggesting ferrets conform to a typical mustelid spacing pattern. 50% Fixed kernel areas had higher estimated prairie dog densities than 95% areas suggesting core areas are centered around high prairie dog

densities. The large home range and low intra-sexual overlap of ferrets suggest large areas are needed for conservation of the species.

INTRODUCTION

Black-footed ferrets (*Mustela nigripes*) are federally endangered mustelids that rely upon prairie dogs (*Cynomys* spp.) for food and shelter (Biggins et al. 2006c). Because of their secretive, nocturnal habits and rarity, only two populations of ferrets were previously studied. The first population was studied between 1964 – 1974 in Mellette County, South Dakota and subsequently disappeared in 1974. There was also a population in Meeteetse, Wyoming that was discovered in 1981 (Forrest et al. 1988). After a catastrophic decline in the population due to disease, the last 18 individuals were rescued from the wild and a successful captive breeding program began (Miller et al. 1996). Enough “excess” ferrets were produced in captivity that reintroductions into the wild began in 1991 and continue to the present in six states and Mexico (Lockhart et al. 2006). Relatively little is known about spatial use of prairie dog colonies by ferrets, the only habitat they occupy. In the course of planning prairie dog reserves and managing for black-footed ferret reintroduction an understanding of ferret spatial use is vital to estimating the size of prairie dog colonies needed to sustain a viable population of ferrets.

There are few previous published estimates of ferret home range size. Indeed, a vast majority of the previous data on ferret movements came from the Meeteetse, Wyoming population, which survived on white-tailed prairie dogs (*Cynomys leucurus*). Tileston and Lechleitner (1966) found black-tailed prairie dogs (*Cynomys ludovicianus*) are more clustered and dense than white-tailed prairie dogs, hence ferret movement estimates from Meeteetse may not apply in South Dakota, which contains only black-tailed prairie dogs.

At Meeteetse, snow-tracking revealed a young female used 16.0 ha from December to March and was overlapped by a male that used 136.6 ha (Forrest et. al 1985). Biggins et al. (1985) used minimum convex polygon (MCP; Mohr 1947) to estimate that a radio-collared female and male used 12.6 and 27.5 ha respectively over a 15-day period and the female continued to use an MCP range of 53 ha after the first 15 days. Fagerstone (1987) reported monthly (Aug – Dec) MCP areas for a juvenile female and an adult male at Meeteetse as 1.2 – 106.8 ha and 13.1 – 257.8 ha respectively.

Evidence from Meeteetse suggests male black-footed ferrets have larger home ranges than females, a pattern typically observed in solitary polygynous animals (Baker 1978, Sandell 1989). Forrest et al. (1985) suggest male ferrets select home ranges to primarily maximize access to females and only secondarily to maximize food resources. Female range sizes, however, are driven more by the area needed to meet their and their offspring's physiological needs. Ferrets likely conform to a typical mustelid spacing pattern with inter-sexual overlap and intra-sexual exclusion (Powell 1979, Forrest et al. 1985).

In addition to gender, several biological and environmental factors may influence black-footed ferret home range size. Ferrets born in captivity may exhibit difference in home ranges, due to lingering influences from captivity, compared to their wild-born counterparts such as differences in exploratory behaviors or increased time spent above-ground. Age may affect home range size and Biggins et al. (2006a) postulated older age may confer a greater social status to males that competitively exclude younger males. Ferrets have been observed year-round on colonies as small as 17.8 ha in South Dakota (T. Livieri, unpublished data), thus colony size may influence home range size. Sandell

(1989) found density of conspecifics highly negatively correlated with home range size in solitary carnivores and density is likely related to food abundance. Thus density of ferrets as a function of prairie dog abundance may influence home range size. Prey density has been shown to influence home range size of other mustelids, including; martens (*Martes americana*; Thompson and Colgan 1987), long-tailed weasels (*Mustela frenata*) and short-tailed weasels (*Mustela erminea*; Fagerstone 1987). Although ferrets are territorial, the duration of their lifespan may influence home range size as their range occasionally shifts annually. I have observed several adult female black-footed ferrets abandoning their home range after weaning their kits, presumably to allow the kits to inherit her range (T. Livieri, unpublished data).

The objective of this study was to estimate black-footed ferret home range size, identify factors that may influence home range size, and estimate inter- and intra-sexual overlap in home range. To achieve this objective ferret locations from Conata Basin, a portion of the Buffalo Gap National Grassland in southwestern South Dakota, were used to estimate home range size, and to examine the effects of gender, origin (captive-born or wild-born), age (1-year old or >1-year old), prairie dog colony size, prairie dog density, inter- and intra-sexual ferret density and number of locations on range size, as well as calculating overlap. Annual and lifetime home ranges were estimated.

STUDY AREA

The Conata Basin is a 29,000 ha mixed-grass prairie located on the Buffalo Gap National Grassland in eastern Pennington County, South Dakota and administered by the USDA Forest Service. Vegetation was dominated by western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloe dactyloides*), and blue grama (*Bouteloua gracilis*) and

primary land uses were permitted cattle grazing and recreation. The area contained 4,050 ha of prairie dog colonies, mapped in 1999 by driving the perimeter of the colony with a differentially corrected Global Positioning System (GPS) and imported into ArcView 3.1. Black-footed ferrets were extirpated from South Dakota by 1974 (Fagerstone 1987) until 146 captive-born animals were reintroduced into Conata Basin from 1996-1999. The ferret population in this study was comprised of captive-born released individuals and their wild-born offspring, totaling approximately 200 individuals annually from 2000-2006 (T. M. Livieri, Prairie Wildlife Research, unpublished report).

METHODS

Black-footed ferret locations

Black-footed ferrets are nocturnal and were located by spotlighting methods on prairie dog colonies (Clark et al. 1983, Campbell et al. 1985, Biggins et al. 2006*b*). Locations were recorded with differentially corrected GPS with a location error of less than one meter. All animals were marked with passive integrated transponder (PIT) tags (Fagerstone and Johns 1987, Stoneberg 1996) prior to release or shortly after birth in the wild. Ferrets were identified using a passive reader at the occupied prairie dog burrow. Spotlighting occurred throughout the year with the exception of June and the most effort expended was from September-January during dispersal. Ferret kits typically become independent of their mothers in September-October and disperse to find their own territories (Henderson et al. 1969, Biggins et al. 1986, T. Livieri, unpublished data).

Black-footed ferret density was estimated as the maximum number of “resident” ferrets occupying the same colony in spring and summer divided by the colony size (Forrest et al. 1985). I defined “resident” ferrets as animals occupying a colony from

October 1 through March 1 or beyond, concurrent with breeding, parturition, and whelping.

I explored the relationship between home range size and prairie dog density using the GPS locations of all prairie dog burrows of one colony overlaid with ferret home ranges. Prairie dog burrows were mapped using differentially-corrected GPS units and classified as active, inactive or plugged based upon presence of fresh scat (Biggins et al. 1993). Active prairie dog burrow numbers within each ferret home range were converted to number of prairie dogs to estimate prairie dog density following the calculations of Biggins et al. (1993; $\text{Prairie dog density} = 0.179 \times \text{active burrow density} / 0.566$).

Data analysis

Black-footed ferret location data were screened by multiple colony moves, total number of locations, and temporal distribution. Ferrets that used multiple prairie dog colonies in a year were removed from analysis because such movement suggests a non-stationary home range. I used an area-per-observation curve (Odum and Kuenzler 1955) for 8 ferrets to estimate the minimum number of locations needed to assess home range size. Locations within the first 30 days post-release or post-dispersal were eliminated to allow for establishment of a territory after the initial exploratory/dispersal period. For annual home range estimates I used only ferrets that had one location in at least 6 different months to ensure accurate representation of annual home ranges. Lifetime home ranges of the same animals were estimated using all locations over the known duration of life for each animal.

Home range size was estimated using the Animal Movement Extension v2.0 (Hooge et al. 1999) in ArcView 3.1. Three estimators were used; fixed kernel (FK) at 95% and

50% contours (Worton 1989) and 100% MCP (Mohr 1947). Fixed kernel estimates used least-squares cross-validation. I considered the 95% contour the extent of the range and the 50% contour as the core area of ferret use. Because ferrets only use prairie dog colonies (Biggins et al 2006c) resulting home ranges were clipped to include only prairie dog colonies (Figure 6). MCP was included for comparison to earlier studies despite the drawbacks of the method for assessing home range size (White and Garrott 1990, Fuller et al. 2005). I calculated the overlap of home ranges for all methods (95% FK, 50% FK, MCP) within and between sexes as a percentage of each animal's range. Only ferrets whose 95% FK ranges overlapped by more than 1% and all core area overlaps of those animals were reported. Because not all ferrets identified were used in home range analyses and some ferrets may not have been located, the estimated degree of overlap is likely an underestimate of the actual overlap.

Black-footed ferret home range estimates were tested for normality using Shapiro-Wilk W (Shapiro and Wilk 1965) and normalized using natural logarithm transformations when necessary. A two-way ANOVA with Tukey-Kramer Multiple Comparison test was used to compare home range size between gender and origin (captive- or wild-born). Multiple linear regression was used to determine factors that may influence black-footed ferret home range size (Table 4). Models were evaluated for goodness-of-fit using r^2 , Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) and Akaike weights. AIC_c uses log-likelihood and the number of parameters to evaluate the bias and precision of all possible model subsets. The top competing models had Akaike evidence <3 and high r^2 . Significance was $\alpha=0.10$ for all analyses because of the small sample sizes.

RESULTS

Sample size

I constructed an area-per-observation curve (Odum and Kuenzler 1955) to assess minimum number of locations needed to estimate black-footed ferret annual home range size. The first 30 independent locations of 8 ferrets (7 female, 1 male) were used. Time to independence (TTI) was considered 12 hours, ample time for a ferret to traverse its home range. Seaman et al. (1999) recommended a minimum of 30 observations when using kernel methods. Mean percent change in 95% fixed kernel home range size for successive locations showed <3% increase in home range size with ≥ 23 locations (Figure 7). Hence, 23 independent locations were considered as the minimum number of locations needed to describe ferret home ranges. If an animal had ≥ 23 independent locations I then used all locations for home range estimates, regardless of independence because TTI has little influence on kernel or MCP estimates (Swihart and Slade 1997). Others have also reported autocorrelated locations do not influence home range estimates or provide a more accurate estimate (Andersen and Rongstad 1989, Gese et al. 1990, Reynolds and Laundre 1990, DeSolla et al. 1999). For MCP, increase in home range size also appeared to slow after 23 locations (Figure 8), but does not plateau (<3% change) until 27-28 locations, suggesting 23 locations likely underestimates total home range size by the MCP technique.

Annual home range

Spotlight population monitoring of black-footed ferrets occurred from 1 October 1997 – 30 September 2000 and identified 306 individual ferrets (160 females, 146 males) 4,540 times. Search effort was 239 spotlight nights with the highest effort in the summer

and fall months during litter emergence and ferret dispersal (Hillman and Clark 1980, Clark 1989). Personnel and equipment limitations did not allow for spotlight searches of all occupied colonies on a given night therefore not all ferrets were available to be sampled on each search night. Twenty-eight ferrets (4 adult female, 16 juvenile female, 3 adult male, 5 juvenile male; Appendix 1) occupying 6 prairie dog colonies with a total of 834 locations met the data screening criteria and were included in home range analyses. Locations from 1 Jul – 31 Dec comprised 80.1% of all locations analyzed.

The mean \pm SE 95% FK areas for females and males were 64.7 ± 11.6 ha and 131.8 ± 40.3 ha, respectively, and were significantly different ($F_{1,24} = 4.39$, $P = 0.047$) although no difference was found between wild and captive-born animals ($F_{1,24} = 1.06$, $P = 0.313$). Estimates for the 95% contour ranged from 13.9 – 202.7 ha for females and 31.7 – 361.4 ha for males. Mean 50% FK areas for females and males were 12.7 ± 3.0 ha and 35.6 ± 16.5 ha, respectively, and were also significantly different ($F_{1,24} = 4.67$, $P = 0.041$) while there was no difference between captive- and wild-born animals ($F_{1,24} = 1.22$, $P = 0.280$). Core areas (50% FK) ranged from 1.7 – 56.0 ha for females and 3.9 – 142.9 ha for males. Mean MCP areas for females and males were 41.9 ± 6.5 ha and 86.3 ± 21.3 ha, respectively, and differed significantly ($F_{1,24} = 5.22$, $P = 0.031$). There were no differences based on captive versus wild-born ferrets ($F_{1,24} = 0.29$, $P = 0.593$). Estimates for MCP ranged from 9.0 – 119.1 ha for females and 20.2 – 180.7 ha for males.

In the absence of prairie dog density as a variable, multiple linear regression models revealed increasing female black-footed ferret home range size was most strongly associated with decreasing male density for all three models (95% FK, 50% FK, MCP; Tables 5-7). A positive association with colony size was also present in the top

competing models for the 95% and 50% FK. For males, age alone was positively related to home range size for 95% FK and MCP models. The competing 50% FK models identified colony size and age as positively related to male home range size, and negatively related to densities of males, females and combined genders (Tables 8-10).

Overlap

Intra-sexual overlap of annual home ranges (95% FK and MCP) was evident in both genders. Core areas had very little intra-sexual overlap (Table 11). Males overlapped a higher proportion of female ranges than females overlapping males. Core areas for males had no intra-sexual overlap and only 2 females had core area intra-sexual overlap suggesting a high level of intra-sexual territoriality. Home range overlap was most likely underestimated because several animals that were present within the range of another ferret did not meet the minimum number of locations to estimate their home ranges and were excluded from the analysis.

Lifetime home range

All locations over the known lifetimes of the same 28 black-footed ferrets were used to estimate lifetime home ranges. Mean 95% FK home range sizes were 81.7 ± 14.2 ha and 157.4 ± 51.9 for females and males, respectively, but not significantly different between gender ($F_{1,24} = 2.68, P = 0.114$) nor origin ($F_{1,24} = 0.44, P = 0.515$). Estimates of 95% FK area ranged from 16.2 – 263.0 ha for females and 30.6 – 419.8 ha for males. For 50% FK, mean home range sizes were 15.1 ± 4.0 ha and 42.9 ± 18.4 ha for females and males respectively and were significantly different ($F_{1,24} = 3.24, P = 0.085$), ranging from 2.0 -79.6 ha for females and 4.1 – 129.8 ha for males. I found no difference in origin ($F_{1,24} = 1.00, P = 0.327$) for 50% FK ranges. MCP mean home range size was 63.2

± 10.2 ha for females and 125.1 ± 44.2 ha for males and was not different between genders ($F_{1,24} = 2.75$, $P = 0.111$) nor origin ($F_{1,24} = 0.16$, $P = 0.696$). MCP area ranged from 11.6 – 181.6 ha and 24.7 – 401.2 ha for females and males, respectively.

Lifetime home range size was significantly larger than annual home range for male MCP ranges ($P = 0.017$) but not for 95% FK ($P = 0.152$) or 50% FK ($P = 0.689$). Home range size of female ferrets was significantly different for 95% FK ($P = 0.003$) and MCP ($P < 0.001$) but not for 50% FK ($P = 0.199$). Not surprisingly, both male and female lifetime home range regression models were positively associated with duration of life.

In 1999 I mapped 21,800 prairie dog burrows (19,105 active, 2,307 inactive, 388 plugged) on one prairie dog colony. The home ranges of 4 ferrets (1 male, 3 female) were overlaid on burrow distribution to estimate burrow density and prairie dog density per range (Table 12). The small sample size of ferret home ranges (4) precluded a meaningful regression analysis of the relationship between prairie dog density and ferret home range size. Using a paired t-test I found a significantly higher prairie dog density in 50% FK areas than 95% FK areas ($P = 0.047$), suggesting core area may be concentrated in areas of higher prairie dog density (Table 13).

DISCUSSION

Annual home range

At Conata Basin male black-footed ferret home ranges were significantly larger than females similar to the findings of Biggins et al. (1985) and Fagerstone (1987) at Meeteetse. The MCP estimates of 16.0 ha and 136.6 ha for a female and male ferret respectively at Meeteetse (Biggins et al. 1985) both fall within the range of estimates at Conata Basin. Although my research did not attempt to measure prairie dog density in

relation to home range size, females may select home ranges to maximize resources such as high prey density whereas males may be maximizing access to females (Baker 1978, Sandell 1989, Miller et al. 1996). Ferrets in Montana and Conata Basin preferred areas with higher prairie dog density (Biggins et al. 2006c) which may explain some of the variation in home range size at Conata Basin, although Forrest et al. (1985) found white-tailed prairie dog burrow density did not appear to influence activity area size for 21 unidentified ferrets.

Male ferret density was negatively related to female ferret home range size, while colony size was positively related. This suggests that as prairie dog colonies become larger and as male density decreases, female home range size increases.

Age influenced male 95% FK and MCP home range size suggesting older males may be more dominant and willing to travel further to extend their breeding opportunities. They may also be more successful at excluding younger males as suggested by Biggins et al. (2006a). Forrest et al. (1988) found adult ferrets exhibited annual site fidelity, implying established older animals can successfully defend their home ranges from younger ferrets. Biggins et al. (2006c) found prior residency of ferrets imparted an advantage in selecting areas with higher burrow density (habitat quality) over newcomers. Colony size positively influenced male 50% FK area sizes.

Overlap

Ferrets seem to conform to a typical mustelid spacing pattern of inter-sexual overlap and intra-sexual exclusion (Powell 1979, Forrest et al. 1985) although there is some tolerance of intra-sexual overlap at the 95% FK and MCP levels. The relatively high male-male overlap observed in the 95% FK is likely due to 3 locations of one ferret in

another male territory during one night in April 2000. When these 3 locations are removed from the data set the mean male-male overlap at 95% FK falls to 1.4% and MCP to zero. These locations might have been exploratory or an attempt at breeding a female outside the normal territory. Individual males overlapped a higher proportion of individual female ranges than individual females overlapped on individual males which is a consequence of males having larger ranges than females.

Lifetime home range

Duration of lifetime positively influenced the 50% FK range size in females indicating ranges may shift over time. This may be a possible response to temporary depletion of prairie dogs by a ferret or may be the result of competitive interactions with adjacent female ferrets. Occasionally an adult female will abandon her range to her kits and establish a new range (T. Livieri, personal observation), which would inflate range size over a longer life span rather than a typical sedentary pattern.

MANAGEMENT IMPLICATIONS

Ferguson and Lariviere (2004) suggest mustelids in general occupy highly seasonal environments, have larger home ranges and lower population densities than other terrestrial carnivores. In the absence of catastrophic factors, such as sylvatic plague (*Yersinia pestis*), black-footed ferrets occupy a relatively stable environment compared to the conspecific Siberian polecat (*Mustela eversmannii*; Biggins 2000) and other mustelids but the home range of ferrets is large in relation to energetic needs. Converting active burrow densities to number of prairie dogs (Biggins et al. 1993), the 50% FK home range of 4 ferrets in Conata Basin had higher prairie dog density than the 95% FK area suggesting a relationship between prairie dog density and location of core activity areas.

The 95% FK area encompassed more than several times the 272.5 – 763 prairie dogs modeled by Biggins et al. (1993) estimated to sustain a ferret family (Table 12) implying prairie dog density may not influence the size of the 95% FK range. However, the difference between prairie dog density in the 50% FK and remaining 95% FK suggests prairie dog density may influence the location of core (50% FK) areas. The low amount of intra-sexual overlap and large home range of ferrets suggest large areas are needed for conservation of the species. My home range estimates of black-footed ferrets could be used with habitat suitability models to estimate carrying capacity and provide needed data for recovery planning and prairie dog reserve designs.

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Table 4. Biological and environmental variables measured in association with black-footed ferret home ranges.

Variable	Range	Mean	SE
Gender	Male, Female	--	--
Origin	Captive, Wild-born	--	--
Age ^a	Juvenile, Adult	--	--
Colony size (ha) ^a	94.5 – 656.8	364.5	41.2
BFF density (BFFs/ha) ^a	0.06 – 0.49	0.13	0.02
Duration (days) ^b	320 – 1,522	708.8	58.5

^a Analyzed in annual home range models only

^b Analyzed in lifetime home range models only

Table 5. All candidate multiple regression models of female black-footed ferret 95 % fixed kernel annual home range size in South Dakota. Model parameters in italics had a negative correlation and in bold had a positive correlation with home range size.

Model	RSS	K	AIC_c	Delta	Weight	Evidence	r²
<i>Male density</i>	5.69	3	-17.63	0.00	0.290		0.433
<i>Male density</i> + Colony size	5.18	4	-16.35	1.28	0.153	1.90	0.484
Colony size	6.23	3	-15.82	1.81	0.118	2.47	0.379
<i>Male density</i> + Age	5.53	4	-15.03	2.60	0.079	3.66	0.449
<i>Total BFF density</i> + Colony size							
size	5.54	4	-15.00	2.63	0.078	3.72	0.448
<i>Total density</i>	6.52	3	-14.92	2.71	0.075	3.87	0.351
<i>Female density</i> + Colony size	5.72	4	-14.39	3.24	0.057	5.05	0.431
<i>Female density</i>	7.07	3	-13.31	4.32	0.033	8.67	0.296
Age + Colony size	6.07	4	-13.20	4.43	0.032	9.16	0.396
<i>Male density</i> + Age + Colony size							
size	5.18	5	-12.74	4.89	0.025	11.52	0.484
<i>Total BFF density</i> + Age	6.22	4	-12.70	4.93	0.025	11.75	0.381
<i>Total BFF density</i> + Age +							
Colony size	5.54	5	-11.38	6.24	0.013	22.70	0.448
<i>Female density</i> + Age	6.71	4	-11.17	6.45	0.012	25.18	0.332
<i>Female density</i> + Age +							
Colony size	5.71	5	-10.77	6.85	0.009	30.79	0.431
<i>Age</i>	10.01	3	-6.34	11.29	0.001	282.67	0.003

Table 6. All candidate multiple regression models of female black-footed ferret 50 % fixed kernel annual home range size in South Dakota. Model parameters in italics had a negative correlation and in bold had a positive correlation with home range size.

Model	RSS	K	AIC_c	Delta	Weight	Evidence	r²
<i>Male density</i>	9.03	3	-8.40	0.00	0.459		0.482
<i>Male density</i> + Colony size	8.58	4	-6.25	2.15	0.157	2.93	0.508
<i>Male density</i> + Age	8.71	4	-5.97	2.43	0.136	3.38	0.501
<i>Total BFF density</i>	11.29	3	-3.94	4.46	0.049	9.29	0.353
Colony Size	11.31	3	-3.90	4.50	0.049	9.47	0.351
<i>Total BFF density</i> + Colony size	9.91	4	-3.38	5.02	0.037	12.33	0.432
<i>Male density</i> + Age + Colony size	8.51	5	-2.80	5.60	0.028	16.42	0.512
<i>Female density</i> + Colony size	10.43	4	-2.36	6.04	0.022	20.54	0.402
<i>Female density</i>	12.56	3	-1.80	6.60	0.017	27.08	0.280
<i>Total BFF density</i> + Age	10.72	4	-1.80	6.60	0.017	27.10	0.385
Age + Colony size	11.07	4	-1.15	7.25	0.012	37.44	0.365
<i>Total BFF density</i> + Age + Colony size	9.89	5	0.20	8.60	0.006	73.86	0.433
<i>Female density</i> + Age	11.93	4	0.33	8.73	0.006	78.56	0.316
<i>Female density</i> + Age + Colony size	10.43	5	1.26	9.66	0.004	125.44	0.402
<i>Age</i>	17.38	3	4.69	13.09	0.001	695.21	0.003

Table 7. All candidate multiple regression models of female black-footed ferret minimum convex polygon annual home range size in South Dakota. Model parameters in italics had a negative correlation and in bold had a positive correlation with home range size.

Model	RSS	K	AIC_c	Delta	Weight	Evidence	r²
<i>Male density</i>	4.45	3	-22.57	0.00	0.353		0.418
<i>Total BFF density</i>	4.98	3	-20.29	2.28	0.113	3.13	0.348
<i>Male density</i> + Colony size	4.26	4	-20.29	2.29	0.112	3.14	0.443
<i>Male density</i> + Age	4.44	4	-19.43	3.15	0.073	4.83	0.419
Colony Size	5.26	3	-19.22	3.35	0.066	5.34	0.312
<i>Total BFF density</i> + Colony size	4.54	4	-18.98	3.59	0.059	6.03	0.406
<i>Female density</i>	5.34	3	-18.92	3.65	0.057	6.21	0.302
<i>Female density</i> + Colony size	4.68	4	-18.38	4.20	0.043	8.15	0.388
Age + Colony size	4.72	4	-18.22	4.35	0.040	8.81	0.383
<i>Male density</i> + Age + Colony size	4.15	5	-17.18	5.40	0.024	14.87	0.457
<i>Total BFF density</i> + Age	4.98	4	-17.14	5.43	0.023	15.11	0.349
<i>Total BFF density</i> + Age + Colony size	4.42	5	-15.92	6.66	0.013	27.90	0.422
<i>Female density</i> + Age	5.33	4	-15.80	6.78	0.012	29.62	0.303
<i>Female density</i> + Age + Colony size	4.52	5	-15.44	7.13	0.010	35.43	0.408
Age	7.57	3	-11.92	10.66	0.002	206.03	0.009

Table 8. All candidate multiple regression models of male black-footed ferret 95% fixed kernel annual home range size in South Dakota. Model parameters in italics had a negative correlation and in bold had a positive correlation with home range size.

Model	RSS	K	AIC_c	Delta	Weight	Evidence	r²
Age	1.80	3	-6.94	0.00	0.334		0.671
<i>Male density</i>	2.55	3	-4.13	2.81	0.082	4.07	0.532
Age + Colony size	1.77	4	-4.05	2.89	0.079	4.24	0.675
Male density + Age	1.79	4	-3.99	2.95	0.077	4.36	0.673
Total BFF density + Age	1.79	4	-3.96	2.98	0.075	4.43	0.672
Female density + Age	1.80	4	-3.95	2.99	0.075	4.46	0.671
<i>Female density + Colony size</i>	1.80	4	-3.92	3.02	0.074	4.53	0.670
<i>Total BFF density + Colony size</i>	1.91	4	-3.47	3.46	0.059	5.65	0.651
Colony Size	3.09	3	-2.62	4.32	0.039	8.65	0.435
<i>Total BFF density</i>	3.27	3	-2.15	4.79	0.030	10.95	0.401
<i>Male density + Colony size</i>	2.34	4	-1.83	5.11	0.026	12.86	0.571
<i>Female density + Age + Colony size</i>	1.73	5	-0.75	6.19	0.015	22.11	0.683
Male density + Age + Colony size	1.76	5	-0.62	6.32	0.014	23.52	0.678
<i>Total BFF density + Age + Colony size</i>	1.77	5	-0.58	6.36	0.014	24.02	0.677
<i>Female density</i>	4.72	3	0.77	7.71	0.007	47.26	0.137

Table 9. All candidate multiple regression models of male black-footed ferret 50% fixed kernel annual home range size in South Dakota. Model parameters in italics had a negative correlation and in bold had a positive correlation with home range size.

Models	RSS	K	AIC_c	Delta	Weight	Evidence	r²
<i>Female density</i> + Colony size	1.38	4	-6.08	0.00	0.183		0.851
<i>Total BFF density</i> + Colony size	1.39	4	-6.01	0.08	0.176	1.04	0.849
Age + Colony size	1.45	4	-5.65	0.43	0.147	1.24	0.842
Colony Size	2.24	3	-5.19	0.89	0.117	1.56	0.757
<i>Male density</i> + Colony size	1.60	4	-4.88	1.21	0.100	1.83	0.826
Age	2.61	3	-3.96	2.12	0.063	2.89	0.717
Female density + Age	1.92	4	-3.41	2.67	0.048	3.80	0.792
<i>Female density</i> + Age + Colony size	1.37	5	-2.63	3.45	0.033	5.62	0.852
<i>Total BFF density</i> + Age + Colony size	1.38	5	-2.57	3.52	0.031	5.81	0.850
Total BFF density + Age	2.16	4	-2.49	3.59	0.030	6.03	0.766
<i>Male density</i>	3.23	3	-2.26	3.82	0.027	6.76	0.650
<i>Male density</i> + Age + Colony size	1.44	5	-2.24	3.84	0.027	6.82	0.844
<i>Male density</i> + Age	2.55	4	-1.14	4.95	0.015	11.86	0.723
<i>Total BFF density</i>	6.54	3	3.39	9.47	0.002	113.87	0.290
<i>Female density</i>	8.98	3	5.92	12.01	0.000	405.27	0.025

Table 10. All candidate multiple regression models of male black-footed ferret minimum convex polygon annual home range size in South Dakota. Model parameters in italics had a negative correlation and in bold had a positive correlation with home range size.

Model	RSS	K	AIC_c	Delta	Weight	Evidence	r²
Age	2.09	3	-5.73	0.00	0.305		0.536
Male density + Age	1.94	4	-3.32	2.41	0.092	3.34	0.569
<i>Male density</i>	2.91	3	-3.10	2.63	0.082	3.73	0.355
Total BFF density + Age	2.08	4	-2.79	2.94	0.070	4.36	0.539
Age + Colony size	2.09	4	-2.74	2.99	0.068	4.46	0.536
Female density + Age	2.09	4	-2.73	3.00	0.068	4.48	0.536
Colony Size	3.06	3	-2.69	3.04	0.067	4.58	0.321
<i>Total BFF density</i>	3.15	3	-2.44	3.29	0.059	5.17	0.300
<i>Female density + Colony size</i>	2.19	4	-2.38	3.35	0.057	5.35	0.515
Total BFF density + Colony size	2.33	4	-1.87	3.86	0.044	6.88	0.483
<i>Male density + Colony size</i>	2.72	4	-0.62	5.11	0.024	12.90	0.395
<i>Female density</i>	3.98	3	-0.59	5.14	0.023	13.10	0.117
Male density + Age + Colony size	1.93	5	0.14	5.87	0.016	18.85	0.571
Total BFF density + Age + Colony size	2.07	5	0.69	6.43	0.012	24.85	0.540
<i>Female density + Age + Colony size</i>	2.08	5	0.73	6.46	0.012	25.34	0.538

Table 11. Percent of black-footed ferret annual home range inter-sexual and intra-sexual overlap in Conata Basin, South Dakota.

Estimator	% of home range	Overlapped by	n	Mean % of home range	Range
50% FK	Female	Female	2	4.1	3.7 - 4.6
95% FK	Female	Female	18	15.6	1.0 - 34.0
MCP	Female	Female	10	13.2	3.4 - 31.0
50% FK	Female	Male	4	40.7	21.9 - 54.0
95% FK	Female	Male	11	65.6	8.7 - 100.0
MCP	Female	Male	9	60.1	16.1 - 100.0
50% FK	Male	Female	4	11.0	5.2 - 14.1
95% FK	Male	Female	11	30.5	2.7 - 57.3
MCP	Male	Female	9	26.9	11.0 - 51.1
50% FK	Male	Male	0	0	0
95% FK	Male	Male	4	19.3	1.3 - 57.4
MCP	Male	Male	2	7.6	2.9 - 12.4

Table 12. Density of active prairie dog burrows and number of prairie dogs encompassed by the annual home range of 4 black-footed ferrets.

Animal ID	#2118 (M)	#2127 (F)	#2135 (F)	#99-046 (F)
50% FK				
Area (ha)	14.4	4.6	8.9	3.7
Active burrows/ha	146.5	213.9	150.2	167.8
No. prairie dogs	667	311	422	196
Prairie dog density	46.3	67.6	47.4	53.0
95% FK				
Area (ha)	95.3	25.5	47.7	22.9
Active burrows/ha	115.9	174.7	136.7	131.0
No. prairie dogs	3,495	1,409	2,063	948
Prairie dog density	36.7	55.2	43.2	41.4
MCP				
Area (ha)	87.5	17.0	36.8	20.4
Active burrows/ha	114.0	205.6	120.8	119.6
No. prairie dogs	3,156	1,105	1,406	771
Prairie dog density	36.1	65.0	38.2	37.8

Table 13. Prairie dog density within the home range of 4 black-footed ferrets in South Dakota.

Animal ID	#2118 (M)	#2127 (F)	#2135 (F)	#99-046 (F)
50% FK	46.3	67.6	47.4	53.0
95% FK*	34.9	52.5	42.3	49.4

*Excludes the 50% FK area

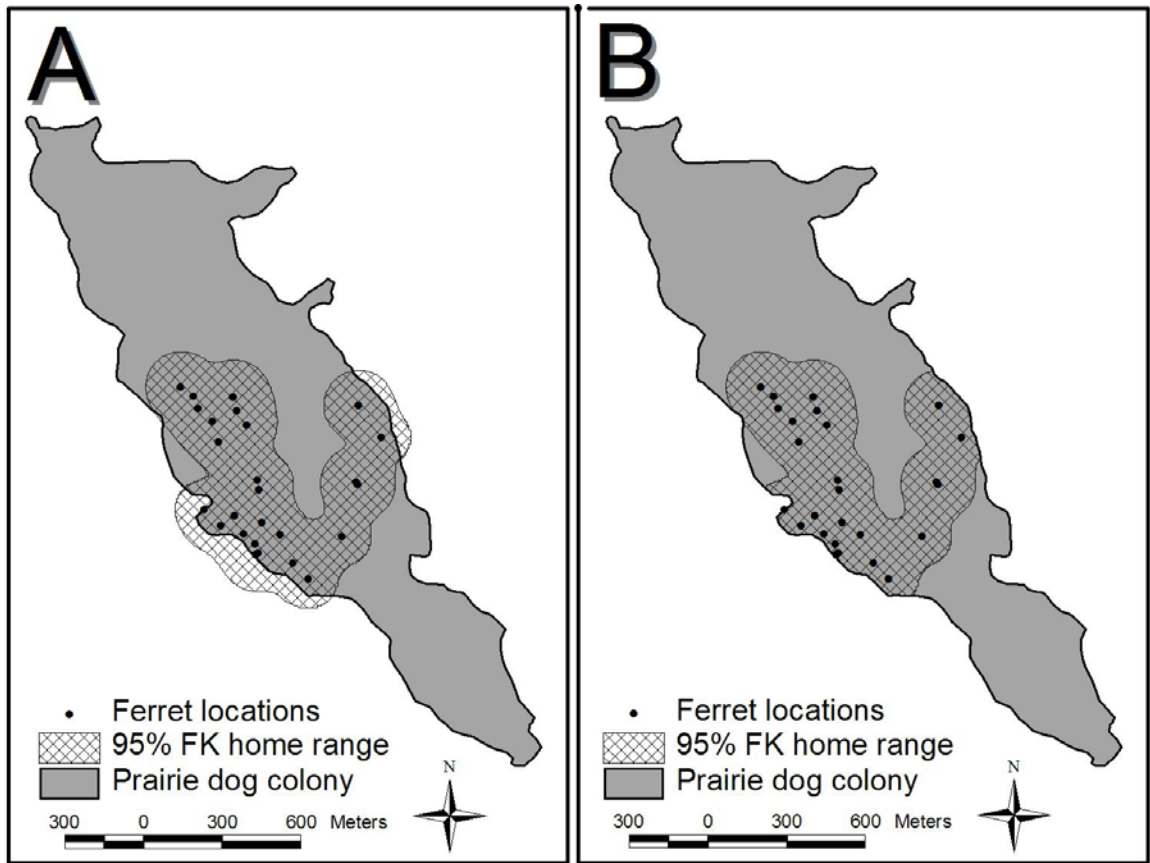


Figure 6. Example of an unclipped black-footed ferret home range (A) and a home range clipped to include only prairie dog colony (B).

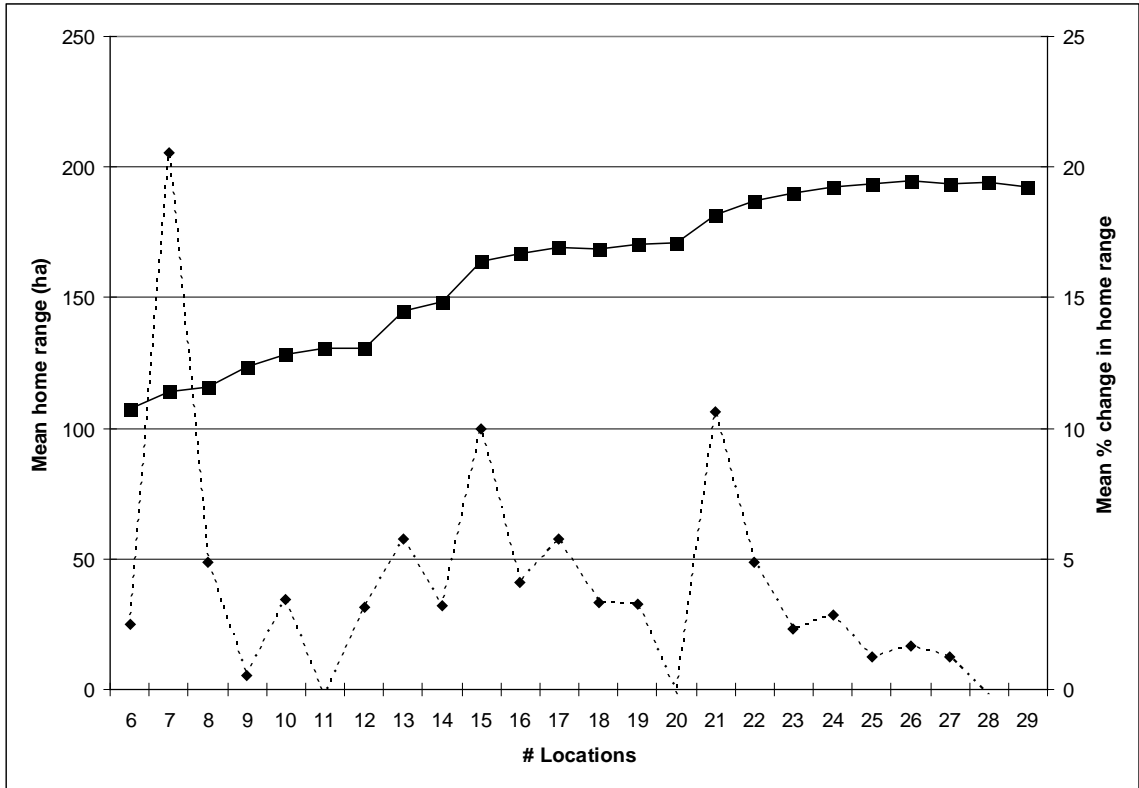


Figure 7. Area-per-observation curve for 95% fixed kernel home range of 8 black-footed ferrets. Solid line-squares represent mean home range size with successive locations. Dashed line-diamonds represent mean percent change in home range size with successive locations.

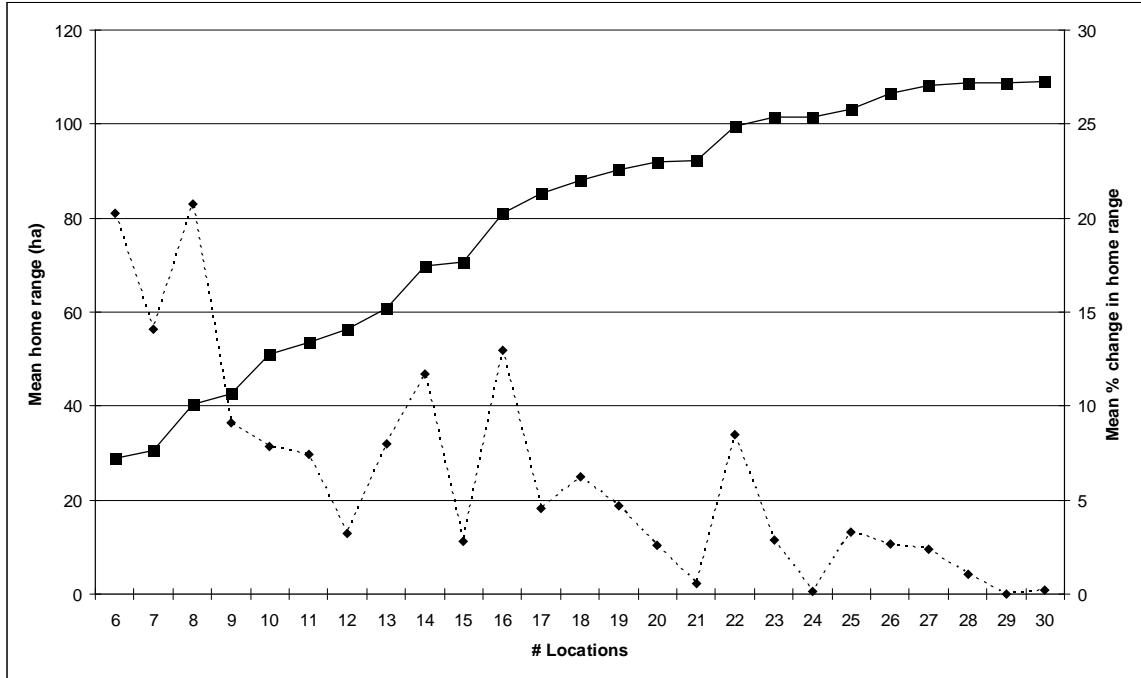


Figure 8. Area-per-observation curve for 100% minimum convex polygon home range of 8 black-footed ferrets. Solid line-squares represent mean home range size with successive locations. Dashed line-diamonds represent mean percent change in home range size with successive locations.

Appendix 1. Summary of black-footed ferret home ranges (ha) in this study.

Studbook#	Sex	Origin	95% fixed kernel		50% fixed kernel		MCP	
			Annual	Lifetime	Annual	Lifetime	Annual	Lifetime
2756	Fem	Captive	13.9	16.2	1.7	2.0	9.0	11.6
2516	Fem	Captive	24.1	66.7	2.1	6.1	30.4	55.0
2127	Fem	Captive	25.5	27.3	4.6	2.5	17.0	25.8
2914	Fem	Captive	33.2	36.4	5.7	5.1	21.7	27.4
2919	Fem	Captive	35.1	41.2	4.3	7.8	25.1	34.8
2483	Fem	Captive	39.6	47.7	10.5	15.5	27.7	33.2
2135	Fem	Captive	47.7	57.6	8.9	5.7	36.8	55.2
2521	Fem	Captive	57.9	55.1	16.1	10.0	48.5	48.5
1750	Fem	Captive	157.2	201.0	34.3	33.4	119.1	161.7
99-046	Fem	Wild	22.9	40.2	3.7	6.0	20.4	32.4
99-010	Fem	Wild	24.0	50.6	2.3	9.8	18.8	40.6
99-004	Fem	Wild	34.6	34.1	3.1	3.9	24.5	27.6
99-025	Fem	Wild	40.6	44.2	6.6	10.3	27.2	34.2
99-005	Fem	Wild	43.8	83.6	9.6	14.0	31.2	69.6
98-005	Fem	Wild	64.2	99.7	13.2	12.8	43.9	94.9
98-030	Fem	Wild	83.1	84.8	12.4	9.1	38.4	61.6
99-008	Fem	Wild	86.4	83.0	12.7	11.7	61.0	61.0
99-029	Fem	Wild	115.5	263.0	15.1	79.6	69.3	181.6
98-007	Fem	Wild	142.6	146.7	31.1	18.1	61.3	86.6
99-047	Fem	Wild	202.7	155.6	56.0	37.9	106.2	120.0
2911	Male	Captive	35.4	45.4	10.0	11.1	28.4	38.5
2336	Male	Captive	45.6	60.4	3.9	4.7	37.4	47.6
2118	Male	Captive	101.3	100.5	14.4	10.4	88.0	91.6
2109	Male	Captive	140.1	154.8	29.7	38.2	83.9	106.7
2498	Male	Captive	231.5	419.8	57.9	120.3	166.7	401.2
99-007	Male	Wild	31.7	30.6	8.0	4.1	20.2	24.7
99-014	Male	Wild	107.4	97.6	17.8	24.9	85.1	85.1
97-006	Male	Wild	361.4	350.0	142.9	129.8	180.7	205.6