Home-range size and spatial organization of black-footed ferrets Mustela nigripes in South Dakota, USA

Authors: Jachowski, David S., Millspaugh, Joshua J., Biggins, Dean E., Livieri, Travis M., and Matchett, Marc R.

Source: Wildlife Biology, 16(1) : 66-76

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/09-034

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 22 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 16: 66-76 (2010)
DOI: 10.2981/09-034
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Home-range size and spatial organization of black-footed ferrets *Mustela nigripes* in South Dakota, USA

David S. Jachowski, Joshua J. Millspaugh, Dean E. Biggins, Travis M. Livieri & Marc R. Matchett

Effective conservation planning for endangered species depends on an understanding of space use patterns. Black-footed ferrets *Mustela nigripes* depend on prairie dogs *Cynomys* sp. as prey and use their burrow systems for shelter. The availability of areas with high densities of active prairie dog burrows is the major factor thought to affect their selection of sites and resources. However, we have little knowledge about how the spatial distribution of active prairie dog burrows might influence the spatial organization and home-range size of ferrets. We monitored the movements of black-footed ferrets on a black-tailed prairie dog *C. ludovicianus* colony in South Dakota to document ferret space use patterns. Home ranges of female ferrets were 22.9 - 95.6 ha in size ($\bar{x}=56.3$ ha, SE=19.7, N=6), while male ferret home ranges were on average more than twice as large as those of females ($\bar{x}=128.3$ ha, SE=68.5, N=3). The home-range size of female ferrets was correlated with mean active prairie dog burrow utilization distribution (UD) value within ferret home ranges, where home-range size decreased as active prairie dog burrow UD value increased ($r^2=0.974$, $P < 0.001$, N=6). Ferret space use overlapped more extensively than previously reported, with up to 43% UD overlap between a ferret and the nearest adjacent ferret of the same sex. Areas of overlap tended to have higher active prairie dog burrow UD values, suggesting that the spatial distribution of active prairie dog burrows influenced both home-range size and the amount of space use overlap between ferrets. These findings emphasize the potential influence of resource distribution on carnivore sociobiology and the importance of considering that distribution in assessing habitat for the reintroduction of specialized species.

Key words: black-footed ferret, black-tailed prairie dog, Conata Basin, home range, Mustela nigripes, space use, volume of intersection, utilization distribution

David S. Jachowski & Joshua J. Millspaugh, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Natural Resources Building, Columbia, Missouri, 65211 USA - e-mail addresses: djachowski@email.com (David S. Jachowski); millspaughj@missouri.edu (Joshua J. Millspaugh)
Dean E. Biggins, U.S. Geological Survey, Fort Collins Science Center, 2150 Center Avenue, Building C, Fort Collins, Colorado, 80526 USA - e-mail: bigginsd@usgs.gov
Travis M. Livieri, Prairie Wildlife Research, P.O. Box 308, Wellington, Colorado, 80549 USA - e-mail: tlivieri@prairiewildlife.org
Marc R. Matchett, U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, P.O. Box 110, Lewistown, Montana, 59457 USA - e-mail: randy_matchett@fws.gov

Corresponding author: David S. Jachowski

Received 20 April 2009, accepted 11 November 2009

Associate Editor: Shyamala Ratnayeke

Successful conservation of rare or declining carnivores requires management of habitat on a scale appropriate for the biological functions of those species (Woodroffe & Ginsberg 1998, Herfindal et al. 2005). The amount of space required for establishing self-sustaining populations of carnivores varies by species, yet within species the spatial distribution of resources may greatly influence carnivore space use patterns (Macdonald 1981, 1983, Norbury et al. 1998). For formerly extirpated species, such as the black-footed ferret *Mustela nigripes* (hereafter referred to as ferret), there is an urgent need to better understand how habitat conditions influence space use patterns, because such information might help improve reintroduction success (Griffith et al. 1989, Benson & Chamberlain 2007).

Spatial ecology of ferrets has been studied little due to their rarity and typically solitary, nocturnal and subterranean nature (Paunovich & Forrest 1987, Forrest et al. 1988). Ferrets occur exclusively on prairie dog *Cynomys* sp. colonies (Biggins et al. 2006b), rely on prairie dogs as their primary prey source (Sheets et al. 1972, Campbell et al. 1987), and spend most of their lives in underground burrow systems created by prairie dogs (Henderson et al. 1969, Richardson et al. 1987). Male ferrets, similar to other mustelids, do not assist in litter rearing, frequently have multiple female partners and have been hypothesized to select for areas frequented by female ferrets (Biggins et al. 1985, Richardson et al. 1987). Female ferrets are reproductively active immediately prior to one year of age and produce one litter each year throughout their life span (Miller et al. 1996). Female ferrets are solitary and are hypothesized to select and compete for areas with high densities of prairie dog burrows (Richardson et al. 1987, Biggins et al. 2006b, Jachowski 2007b). Yet how the spatial distribution of prairie dog burrows directly influences ferret home range and spacing patterns remains poorly understood (Biggins et al. 2006b).

Prey density is a major determinant of home-range size for predators (Sandell 1989, McLoughlin et al. 2000, Nilsen et al. 2005), and likely influences ferret space use patterns. Macdonald (1983) proposed the resource dispersion hypothesis for explaining variation in home-range size, where home-range size is primarily determined by the spatial distribution of resource patches. Although this hypothesis was developed for social carnivores, similar patterns have been observed for numerous solitary carnivore species (Carr & Macdonald 1986, Johnson et al. 2002, Eide 2004). Male ferret home ranges are typically much larger than those of females, though home-range size also varies greatly even among individuals of the same sex (Biggins et al. 1985, Livieri 2007). Under the resource dispersion hypothesis, such variation likely occurs due to variations in prey availability. The spatial distribution of prairie dogs and their burrows is heterogeneous (Jachowski et al. 2008), thus we hypothesized that ferrets occupying areas with higher densities of prairie dog burrows would have smaller home ranges.

Overlap of home ranges among ferrets of opposite sexes is believed to be common, with male home ranges overlapping the home ranges of multiple females, but overlap of home ranges among members of the same sex is thought to be less frequent (Richardson et al. 1987). Intra-sexual overlap in home ranges has been documented among males and among females; however, these observed overlaps were considered 'boundary patrol' movements (Richardson et al. 1987:235). Space use overlap for other solitary carnivore species has been reported to vary in response to fluctuations in prey abundance (Eide et al. 2004, Cochrane et al. 2006). For example, when habitat quality or prey availability drops below a certain threshold, there is a net benefit to defending quality areas of food resources (Carpenter & MacMillen 1976, McLoughlin et al. 2000). Female ferrets in particular would be expected to exhibit territoriality similar to other species that bear altricial young (Wolff 1997, Wolff & Peterson 1998). Given this, along with strong evidence that ferrets select for specific areas with high prairie dog abundance (Biggins et al. 2006b, Jachowski 2007b), we hypothesized that intra-sexual space use is uncommon between female ferrets and where it does occur it is likely a function of prey abundance.

We studied a successfully reintroduced ferret population to test hypotheses about ferret space use patterns and the relationship of prairie dog burrow distribution to ferret space use during the non-breeding or litter-rearing (May-October) season. Specifically, we quantified: 1) home-range size of individual ferrets, 2) spatial overlap between adjacent ferrets, and 3) spatial distribution of prairie dog burrows and how it was related to ferret home-range size and space use overlap.

Material and methods

Study area

Given the relatively recent reintroduction of ferrets to the Great Plains of North America (Lockhart et al. 2006, Jachowski & Lockhart 2009), we selected a study area with a long history of occupancy by ferrets. The Conata Basin is a portion of the Buffalo Gap National Grassland in southwestern South Dakota, which has extensive black-tailed prairie

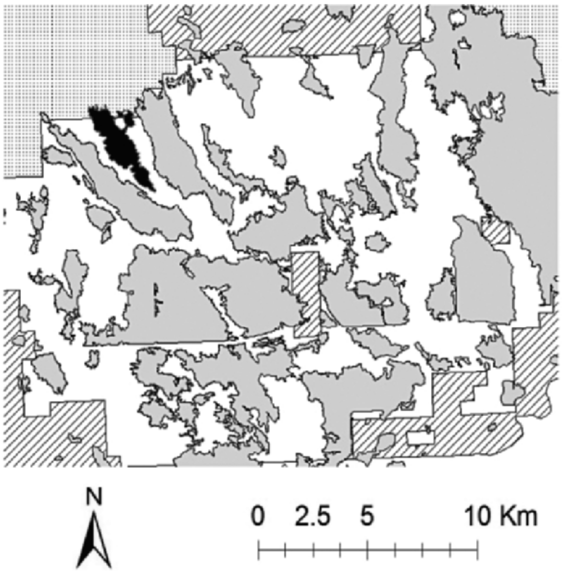

Figure 1. Maximum extent of prairie dog colonies (solid grey) in 2005 within the Conata Basin region of the Buffalo Gap National Grassland managed by the U.S. Forest Service (white), National Park Service (speckled) and private landowners (cross-hatched) in southwestern South Dakota. The North Exclosure prairie dog colony study area is highlighted in black.

dog *Cynomys ludovicianus* colonies (approximately 11,803 ha; Fig. 1; Livieri 2006). From 1996 to 2000, 164 captive-born ferrets were released at Conata Basin (Livieri 2006). The population stabilized at an annual minimum population estimate of 200-290 individuals during 2000-2006 (Livieri 2006).

Within Conata Basin, we selected the distinct North Exclosure prairie dog colony as our study area (see Fig. 1). Prairie dog populations form distinct colonies that are typically defined by the maximum extent of their burrow systems (King 1959). The North Exclosure prairie dog colony was 202 ha in size and comprised 2% of the entire Conata Basin recovery area (see Fig. 1). We selected this colony for the following reasons: 1) the logistical benefits of its size for monitoring ferrets and prairie dog burrows, 2) its geographic isolation from other colonies by ravines of ~ 15 m depth on the east, west and south sides, and 3) the continuous occupancy of the colony by ferrets for eight years prior to the initiation of our study. In 1997, six female and four male ferrets were released into the North Exclosure prairie dog colony. Subsequent annual surveys showed that the colony was occupied continuously by 3-11 adult ferrets since that time without subsequent releases (Livieri 2006). No captive-born animals were present during our study.

Field observations

We collected location data on all ferrets occurring in the study area during nearly consecutive nights from June through October in 2005 and 2006. We used systematic spotlight survey techniques to obtain ferret locations (Biggins et al. 2006a, Jachowski 2007a). We chose spotlight surveys instead of telemetry or other commonly used tracking techniques due to: 1) their logistical benefit for surveying a large flat area with short (< 10 cm) vegetation, 2) their widespread acceptance and use in locating and monitoring ferrets (Campbell et al. 1985, Grenier et al. 2009), and 3) our concern for the endangered status of ferrets and the need to minimize capturing or disturbing females during the litter-rearing period (May through October). We established a survey route that maximized coverage of the colony and minimized overlap. We traveled the route once each hour during the night to sample ferret locations. We drove the survey route with a 4-wheel-drive vehicle using a roof-mounted Lightforce® spotlight of > 1 million candlelight power. We traveled 8-16 km/hour with constant side-to-side scanning of the spotlight to detect ferret 'eye shine'. Upon seeing ferret eye shine, we were able to identify an individual ferret $> 94\%$ of the time by visually identifying the animals or recording the animal's unique transponder number (Grenier et al. 2009). Every individual within our study area was marked with a PIT (passive integrated transponder) implant (Fagerstone & Johns 1987) prior to the start of the study. We captured male individuals upon first encounter to apply unique dye-markings on the front and back of the neck to allow for quick visual individual identification (Grenier et al. 2009). We waited until August to capture and dye-mark female ferrets to limit disturbance to females while they cared for young kits. In subsequent observations, if we were unable to discern clearly the dye mark on an individual, we placed a PIT reader at the burrow entrance for up to three days to record the unique PIT number. We obtained GPS coordinates for the location of each ferret observation using hand-held, Garmin GPS 12XL Personal Navigator units that have an accuracy error of < 7 m. When we observed a ferret more than once a night, we selected the first observation made ≥ 24 hours after the previous observation to allow for one activity-period cycle between observations (Goodrich & Buskirk 1998, Lair 1987).

We mapped the location of all prairie dog bur-

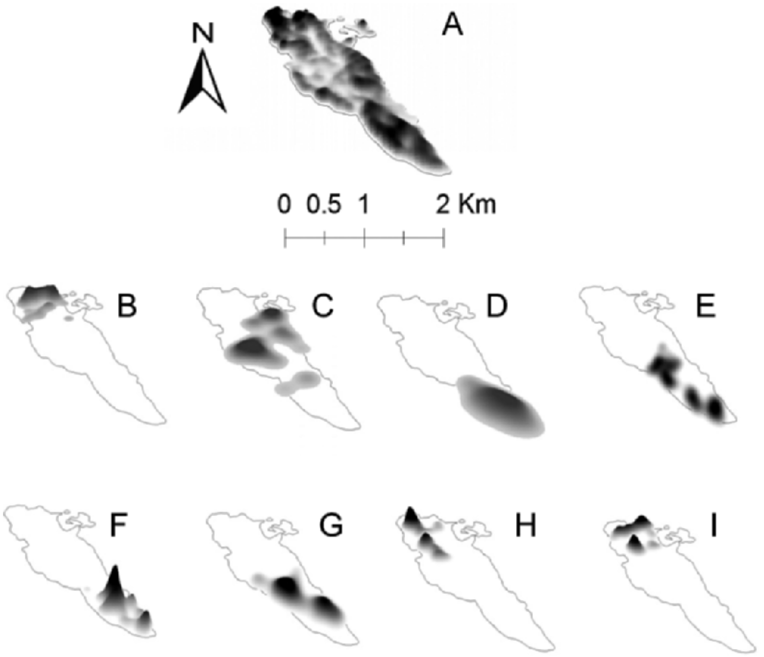

Figure 2. Comprehensive mapping of active prairie dog burrows was used to calculate 95% fixed kernel utilization distribution (UD) of active burrows at the Conata Basin study site in 2005 (A). Areas of high active prairie dog burrow distribution (dark areas) are similar to areas with large UD values for individual female ferrets observed during 2005: F02015 (B), F02047 (C), F03031 (D) and F04019 (E) as well as 2006: F03031 (F), F04019 (G), F05003 (H) and F05005 (I). The height and darkness of the ferret UD indicates areas with a higher probability of use by that individual ferret.

rows in the colony in 2005 using Trimble CMT MC-V GPS data loggers (Trimble Navigation Limited, Sunnyvale, California, USA) mounted on all-terrain vehicles (see Jachowski et al. 2008). We downloaded burrow location data and differentially corrected locations using the nearest base station in GPS Pathfinder® Office 3.0 (Trimble Navigation Limited, Westminster, Colorado, USA). We obtained correction rates of 99-100% and therefore assumed burrow location error to be $\leq$ 1 m. While mapping, we classified burrows as active or inactive based on the presence of fresh scat or recent soil disturbance at burrow entrances (Biggins et al. 1993, Dullum 2001, Jachowski et al. 2008). We used active prairie dog burrows as a measure of the spatial distribution of resources for ferrets based on previous findings that ferrets spend a majority of their lives in prairie dog burrow systems and typically are sighted near active burrow entrances (Jachowski 2007b), that active prairie dog burrows are correlated with the presence of prairie dogs, and that burrow distribution commonly is used to examine patterns of prairie dog spatial distribution and abundance (Biggins et al. 1993, Powell et al. 1994, Johnson & Collinge 2004).

Data analysis

To assess space use by individual ferrets, we used locations to estimate fixed kernel utilization distributions (UDs; Kernohan et al. 2001). Our assumption that the population was effectively closed due to physical barriers and prairie dog colony boundaries was supported by our monitoring, because we regularly relocated all individuals in our study area. Therefore, we included all observed animals in our analyses. We acquired more than the minimum number of observations ($N > 30$; Seaman et al. 1999) on each individual within the 5-month sampling period each year and calculated a 95% fixed kernel UD for each ferret (Fig. 2). We used Matlab (Mathworks Incorporated, Natick, Massachusetts, USA) and 'plug-in' methods for bandwidth selection (Wand & Jones 1995, Gitzen et al. 2006) using the 'Kde folder' (Beardah & Baxter 1995) to create individual UDs. We utilized data from all ferrets observed during each sampling year to analyse space use overlap. To avoid pseudoreplication in our estimates of mean home-range size, we randomly selected one year for each of the three animals observed during both years (Hurlbert 1984).

We assessed space use overlap of ferrets by determining how much overlap existed in the 95% kernel UD of each ferret with all other ferrets observed during the same sampling year. We used the Volume of Intersection (VI) technique to quantify the degree of overlap in volume of two individual ferret UDs as

$$\mathrm{VI} = \iint \hat{f}_A(x, y), \;\; \hat{f}_B(x, y) dx\, dy,$$

where $\hat{f}_A$ is the estimated UD for ferret A and $\hat{f}_B$ is the UD for ferret B (Seidel 1992, Millspaugh et al. 2004). VI scores range from 0 to 1 where a VI score of 1 indicates complete overlap of the UDs.

To assess the relationship between the distribution of active prairie dog burrows and ferret home-range size, we established the home-range size for each individual ferret by measuring the maximum extent of each ferret's 95% fixed kernel UD. We then quantified the spatial distribution of prairie dog burrows by using the comprehensive location data of active burrows to create a UD of all active prairie dog burrows in the study area using the fixed kernel approach described above (Jachowski et al. 2008). We used Spatial Analyst tools within ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, California, USA) to clip the active prairie dog burrow UD by the maximum extent of each ferret's 95% fixed kernel home range. We then measured the mean active prairie dog burrow UD value within each ferret's home range. Using linear regression, we then assessed the relationship of home-range size to mean active burrow UD value within the home range for each ferret.

We also assessed the relationship between home-range overlap and active prairie dog burrow density. We paired individual ferrets of the same sex that had the highest degree of UD space use overlap (i.e. highest VI values). We randomly selected 200 locations from within the area where space use overlap occurred to measure active burrow UD values and compared those values to 200 randomly selected locations from the area within the selected ferret's home range where no overlap occurred. We then calculated the mean and standard errors for the UD values at those locations and compared the distribution of values by sex.

Results

We collected > 30 observations on each of nine individual ferrets in our study area (three males and six females) during our study period ($\bar{x} = 47.6$, SD = 11.1, range: 32-71; Table 1). We did not observe other adult ferrets at any point during our study, supporting our assumption that the population was closed and that we measured space use for all animals present in the study area. Of the nine individuals, three (one male and two females) were present in both years (Table 2).

Ferret home-range size was related to the spatial distribution of active prairie dog burrows (see Fig. 2). Home-range estimates for female ferrets ranged from 22.9 to 95.6 ha ($\bar{x} = 56.3$ ha, SE = 19.7, N = 6; see Table 1). Home-range estimates of males averaged more than twice the size of female home ranges ($\bar{x} = 128.3$ ha, SE = 64.5, N = 3). Because of few individuals, we omitted males when assessing the influence of resource distribution on home-range size. Female ferret home-range size showed a negative relationship to mean active burrow UD values within the home range ($r^2 = 0.974$, $P < 0.001$, N = 6; Fig. 3), indicating that female ferrets had smaller home ranges in areas with the highest relative burrow density.

We observed considerable overlap in space use

Table 1. Number of locations and home-range estimates (perimeter of 95% of UD by volume) for male and female ferrets monitored in 2005 and 2006 (year of observation) at the Conata Basin, South Dakota.

Females[1]				Males[1]			
Ferret ID	No. of locations	Home-range size (ha)	Year	Ferret ID	No. of locations	Home-range size (ha)	Year
F02015	46	44.1	2005	M04006	47	59.7	2005
F02047	49	95.6	2005	M04013	46	187.8	2006
F03031	38	47.4	2005	M05014	64	137.6	2006
F04019	49	56.9	2006				
F05003	32	47.0	2006				
F05005	42	46.8	2006				
Mean	42.7	56.3			52.3	128.3	
SE	6.7	19.7			10.1	64.5	

[1] Note that three individuals (two females and one male) were sampled during both 2005 and 2006, so we randomly removed one year of these three animals for the calculation of home-range metrics (resulting in N = 9).

Table 2. Amount of overlap between ferret utilization distributions, as measured through volume of intersection scores (Seidel 1992, Millspaugh et al. 2004) for all ferrets present on the study area during 2005 (A) and 2006 (B) at the Conata Basin, South Dakota. Volume of intersection scores range from 0 to 1, with 1 representing complete overlap in space use between two ferrets.

A)

Ferret ID	F02015	F02047	F03031	F04019	M04006	M04013
F02015	-	0.01	0.00	0.00	0.18	0.28
F02047	0.01	-	0.04	0.04	0.19	0.09
F03031	0.00	0.04	-	0.39	0.00	0.02
F04019	0.00	0.04	0.39	-	0.00	0.01
M04006	0.18	0.19	0.00	0.00	-	0.32
M04013	0.28	0.09	0.02	0.01	0.32	-

B)

Ferret ID	F03031	F04019	F05005	F05003	M04013	M05014
F03031	-	0.18	0.00	0.00	0.01	0.13
F04019	0.18	-	0.00	0.00	0.00	0.40
F05005	0.00	0.00	-	0.42	0.13	0.04
F05003	0.00	0.00	0.42	-	0.14	0.00
M04013	0.01	0.00	0.13	0.14	-	0.17
M05014	0.13	0.40	0.04	0.00	0.17	-

between ferrets of the same and opposite sex. Although space use overlap between females varied widely (range of VI values: 0.01-0.43), six of the eight females monitored had at least 0.18 or 18% overlap in volume of their UD with another female (range: 0.18-0.42; see Table 2). Similarly, six of eight females had at least 0.13 or 13% overlap in the volume of their UD with another male (range: 0.13-0.40; see Table 2). The presence of only two males during each year of our study restricted our analyses to two measures of overlap (one for each pair each year).

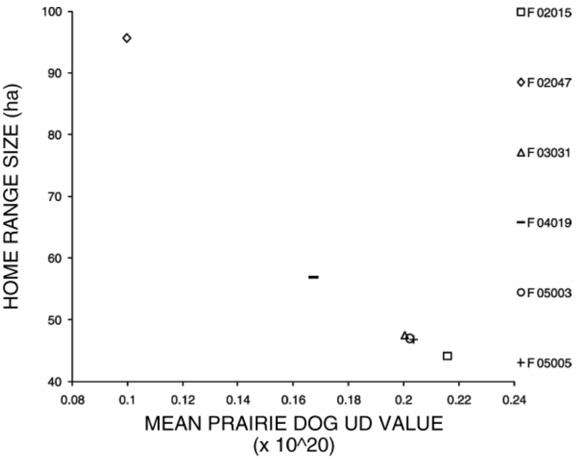

Figure 3. Home ranges of individual female ferrets (N = 6) as a function of mean active prairie dog burrow utilization distribution (UD) value at the Conata Basin in 2005 and 2006. Standard error values for all ferrets were < 0.006. The mean prairie dog UD value for the entire study area was 0.05 (SE = 0.02).

Ferrets were more likely to exhibit space use overlap in areas of relatively high active prairie dog burrow density during the litter-rearing season. Active burrow UD values within areas of overlap between a female ferret and its nearest same-sex neighbour were higher ($\bar{x} = 0.06$, SE = 0.00, range: 0.00-0.10) than in areas without overlap ($\bar{x} = 0.04$, SE = 0.00, range: 0.00-0.11). In contrast, active burrow UD values of a male ferret and its nearest same-sex neighbour were similar within areas of overlap ($\bar{x} = 0.04$, SE = 0.00, range: 0.00-0.11) and in areas without overlap ($\bar{x} = 0.04$, SE = 0.00, range: 0.00-0.12).

Discussion

As predicted, ferret home-range size varied among individuals based on sex and the spatial distribution of resources, a pattern which exists for other solitary carnivore species (Sandell 1989, Eide et al. 2004). Sex-specific differences in home-range estimates during the litter-rearing season in our study were similar to annual home-range estimates of 132 ha for males and 65 ha for females previously reported by Livieri (2007) for ferrets in our study area. The strong inverse relationship between female ferret home-range size and the availability of active prairie dog burrows that we observed provides unique support for the hypothesis that the spatial distribution of this critical resource likely explains most of the variation in home-range size observed among individuals of the same sex.

In contrast to previous hypotheses regarding female ferret territoriality, we found that where resources were more abundant, home ranges of female ferrets tended to overlap. Generally, when habitat quality is high, individuals exhibit less territoriality (Carpenter & MacMillen 1976, McLoughlin et al. 2000). For example, Eide et al. (2004) observed weaker territoriality and increased sociality among arctic foxes *Alopex lagopus* where resources were clumped, highly abundant and predictable. Similarly, female ferrets in our study exhibited decreased territorial behaviour in areas of high quality habitat or where prey were more abundant. These findings contradict previous hypotheses that predict relatively exclusive territories among female ferrets (Clark 1989), and provide novel support for the hypothesized relationship between habitat quality and space use overlap that has been suggested to occur in ferrets (Biggins 2000, Biggins et al. 2006b, Livieri 2007). The relatively high degree of overlap (up to 42%) that we observed among female ferrets goes beyond previous observations of occasional or exploratory overlap among ferret territories (Paunovich & Forrest 1987, Richardson et al. 1987), and suggests that for female ferrets rearing young where prey and burrows are relatively abundant, the cost of defending exclusive territories might outweigh any potential benefit from defending exclusive territories.

Our findings support application of the resource dispersion hypothesis (Macdonald 1983) to solitary carnivore species. Sandell (1989) proposed that the resource dispersion hypothesis could be extended beyond social carnivores. Broadly applied to solitary carnivores, females would have exclusive ranges when food resources are 'stable and evenly distributed' and would have overlapping ranges when food distribution and timing varied. Support for this hypothesis has been mixed (Herfindal et al. 2005), where a direct relationship between habitat quality and home-range size or space use overlap has not been universally observed in social (Creel & Creel 2002) or solitary (Bixler & Gittleman 2000) carnivore species. Clear support of the importance of resource distribution on ferret spatial ecology was likely due to 1) the importance of active prairie dog burrows to highly specialized ferrets, 2) the heterogeneous distribution of resources, and 3) the fine scale measures of resource distribution that we employed. Similar to other mustelid species, ferrets are likely primarily concerned with locating prey, limiting vulnerability to predators and conserving energy (King & Powell 2007). For ferrets, these three factors are associated with active prairie dog burrows. Where Bixler & Gittleman (2000) found no relationship between home-range size and habitat conditions for omnivorous striped skunks *Mephitis mephitis,* which likely viewed their site as having a uniform distribution of resources, active prairie dog burrows are heterogeneously distributed within colonies (Jachowski et al. 2008) and are occupied by populations of prairie dogs which can fluctuate annually due to biotic and abiotic factors (Hoogland 1995). Previous failures to detect a close association between a critical resource and carnivore space use patterns could also be due to poor classification of habitat quality (Herfindal et al. 2005). By precisely mapping locations of active prairie dog burrows throughout a colony and taking a utilization distribution approach which measures the relative distribution of those burrows, we quantified the fine-scale distribution of resources available to ferrets within our study area.

Although the spatial distribution of prairie dog burrows likely influenced home-range size and space use overlap between individual ferrets, factors such as season, rank, kinship, physiological condition and age also have been identified as influencing space use patterns of other carnivores (Rolls et al. 2001, Boydston et al. 2003, Støen et al. 2005). While our small sample size and season of study did not allow for analysis of these factors, we suspect that seasonality, in particular, is likely to affect space use by ferrets. Our period of study occurred during the litter-rearing season, but ferret space use likely differs between breeding and non-breeding times in a pattern similar to that of other mustelids (Erlinge 1977, Johnson et al. 2000, King & Powell 2007). Female ferrets might have smaller home ranges during the litter-rearing period (Robitaille & Raymond 1995) and males might be less territorial during that period than during the winter breeding season (Richardson et al. 1987). Additionally, ferret populations typically experience high turnover within and between years because of their relatively short life span and high reproductive rate (Grenier et al. 2007). This, too, has the potential to affect ferret spatial organization through the frequency with which newly vacated habitat becomes available.

Conservation implications

Current coarse-scale techniques used to evaluate the distribution of critical resources might be insufficient to determine the suitability of reintroduction sites for extirpated species. With the advancement of computer mapping software, the use of spatially explicit techniques to assess resource distribution has become a valuable tool in assessing reintroduction site suitability for extirpated carnivore species (Mladenoff & Sickley 1999, Schadt et al. 2002). For carnivores in particular, field surveys of prey density are logistically demanding and rarely are made at a fine spatial scale (Nilsen et al. 2005). Currently, prairie dog populations at ferret reintroduction sites are assessed by measuring the maximum spatial extent of active prairie dog burrows as well as the average density of active burrows (based on counting the number of active burrows on approximately 10% of a colony) within each area on an annual or semi-annual basis (Biggins et al. 1993). These measurements are used by the U.S. Fish and Wildlife Service in assessing and ranking the biological suitability of reintroduction sites in a competitive process of allocating a limited number of captive and wild-born ferrets for release into the wild (Jachowski & Lockhart 2009). Using such an approach, the release or relocation of > 3,000 ferrets into 18 reintroduction sites over the last 18 years has resulted in establishing only four relative large (100-300 individuals), self-sustaining populations (Jachowski & Lockhart 2009). While our findings generally support the use of prairie dog burrow distribution and density as a coarse indicator of habitat suitability, the dynamic nature of prairie dog populations within colonies and the influence of active burrow density on ferret space use suggest that finer-scale and more spatially explicit measurements of the spatial distribution of prairie dogs might help to predict the suitability of sites for reintroduction of ferrets. By identifying areas of high prairie dog density that are likely to serve as high quality habitat for ferrets, managers could more effectively prioritize potential reintroduction sites and more accurately focus efforts to protect prairie dog populations from human influences or disease outbreaks.

Given the role of habitat quality in ferret space use requirements, managers might be able to increase the number of ferrets within a reintroduction site and improve reintroduction success by enhancing prairie dog population density. Reintroduced ferret populations have persisted without augmentation at four of the largest prairie dog complexes (Lockhart et al. 2006, Jachowski & Lockhart 2009), but few remaining prairie dog colonies or complexes of such a size exist (Forrest 2005). To achieve recovery goals, self-sustaining ferret populations will have to be established in smaller prairie dog colonies. It might be possible to maintain more ferrets in a relatively small area if that area is able to maintain a high population density of prairie dogs. This would minimize the total area required for each ferret and maximize the amount of tolerated space use overlap. Management by altering vegetative cover (Milne-Laux & Sweitzer 2006), reducing shooting pressure (Pauli & Buskirk 2007) and prairie dog translocation (Truett et al. 2001, Dullum et al. 2005) could enhance prairie dog abundance at reintroduction sites. Encouraging such management practices could improve the ability of sites to maintain higher densities of ferrets and increase the likelihood of self-sustaining ferret populations.

Acknowledgements - funding and logistical support for this project were provided by the U.S. Fish and Wildlife Service, U.S. Forest Service, Prairie Wildlife Research, National Fish and Wildlife Foundation (Grant number 2006-0058-0000), South Dakota Department of Game, Fish and Parks Small Grants Program, South Dakota Department of Game, Fish and Parks Competitive Grants Program, Disney Centennial Refuge Scholarship, Missouri Chapter of the Wildlife Society and the University of Missouri. This study was funded in part by federal funding through State Wildlife Grant T-35-R, Study #2435, administered through the U.S. Fish and Wildlife Service. We thank R. Jachowski and D. Hanson for help with fieldwork. We also thank K. Atchley and D. Sargent who provided valuable assistance in support of this project. We thank R. Jachowski, C. Bodinof, D. Eads, C. Rittenhouse, T. Bonnot, C. Hansen, J. Kolar, B. Keller and B. Dijak for comments that improved the manuscript. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Beardah, C.C. & Baxter, M.J. 1995: MATLAB routines for kernel density estimation and the graphical representation of archaeological data. - Anelecta Prehistorica Leidensia, 28th edition. Leiden University Press, Rapenburg, Netherlands, 8 pp.

Benson, J.F. & Chamberlain, M.J. 2007: Space use, survival, movements, and reproduction of reintroduced Louisiana black bears. - Journal of Wildlife Management 71: 2393-2403.

Biggins, D.E. 2000: Predation on Black-footed Ferrets (*Mustela nigripes*) and Siberian Polecats (*M. eversmanni*): Conservation and Evolutionary Implications. - PhD dissertation, Colorado State University, Fort Collins, Colorado, USA, 185 pp.

Biggins, D.E., Godbey, J.L., Matchett, M.R., Hanebury, L., Livieri, T.M. & Marinari, P.E. 2006a: Monitoring black-footed ferrets during reestablishment of free-ranging populations: discussion of alternative methods and prescription of minimum standards. - In: Roelle, J.E., Miller, B.J., Godbey, J.L. & Biggins, D.E. (Eds.); Recovery of the black-footed ferret - progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293, Fort Collins, Colorado, USA, pp. 155-174.

Biggins, D.E., Godbey, J.L., Matchett, M.R. & Livieri, T.M. 2006b: Habitat preferences and intraspecific competition in black-footed ferrets. - In: Roelle, J.E., Miller, B.J., Godbey, J.L. & Biggins, D.E. (Eds.); Recovery of the black-footed ferret - progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293, Fort Collins, Colorado, USA, pp. 129-142.

Biggins, D.E., Miller, B., Hanebury, L., Oakleaf, R., Farmer, A., Crete, R. & Dood, A. 1993: A technique for evaluating black-footed ferret habitat. - In: Oldemeyer, J., Miller, B. & Crete, R. (Eds.); Management of Prairie Dog Complexes for Reintroduction of the Black-footed Ferret. U.S. Fish and Wildlife Service Biological Report 13, pp. 73-78.

Biggins, D.E., Schroeder, M., Forrest, S.C. & Richardson, L. 1985: Movements and habitat relationships of radio-tagged black-footed ferrets. - In: Anderson, S.H. & Inkley, D.B. (Eds.); Black-footed ferret workshop proceedings. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA, pp. 11.1-11.7.

Bixler, A. & Gittleman, J.L. 2000: Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). - Journal of Zoology (London) 251: 525-533.

Boydston, E.E., Kapheim, K.M., Szykman, M. & Holekamp, K.E. 2003: Individual variation in space use by female spotted hyenas. - Journal of Mammalogy 84: 1006-1018.

Campbell, T.M., Biggins, D.E., Forrest, S.C. & Clark, T.W. 1985: Spotlighting as a method to locate and study black-footed ferrets. - In: Anderson, S. & Inkley, D. (Eds.); Proceedings from the black-footed ferret workshop. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA, pp. 24.1-24.7.

Campbell, T.M., Clark, T.W., Richardson, L., Forrest, S.C. & Houston, B.R. 1987: Food habits of Wyoming black-footed ferrets. - American Midland Naturalist 117: 208-210.

Carpenter, F.L. & MacMillen, R.E. 1976: Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. - Science 194: 639-642.

Carr, G.M. & Macdonald, D.W. 1986: The sociality of solitary foragers: a model based on resource dispersion. - Animal Behavior 34: 1540-1549.

Clark, T.W. 1989: Conservation biology of the black-footed ferret *Mustela nigripes*. - Wildlife Preservation Trust Special Scientific Report No. 3, Wildlife Preservation Trust International, Philadelphia, Pensylvania, USA, 175 pp.

Cochrane, J.C., Kirby, J.D., Jones, I.G., Conner, L.M. & Warren, R.J. 2006: Spatial organization of adult bobcats in a longleaf pine-wiregrass ecosystem in southwestern Georgia. - Southeastern Naturalist 5: 711-724.

Creel, S. & Creel, N. 2002: The African wild dog: behaviour, ecology and conservation. - Princeton University Press, Princeton, New Jersey, USA, 341 pp.

Dullum, J.L.D. 2001: Efficacy of translocations for restoring populations of black-tailed prairie dogs in north-central Montana. - M.Sc. thesis, University of Montana, Missoula, Montana, USA, 52 pp.

Dullum, J.L.D., Foresman, K.R. & Matchett, M.R. 2005: Efficacy of translocations for restoring populations of black-tailed prairie dogs. - Wildlife Society Bulletin 33: 842-850.

Eide, N.A., Jepsen, J.U. & Prestrud, P. 2004: Spatial organization of reproductive Arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. - Journal of Animal Ecology 73: 1056-1068.

Erlinge, S. 1977: Spacing strategy in stoat *Mustela erminea*. - Ibid 28: 32-42.

Fagerstone, K.A. & Johns, B.E. 1987: Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife. - Journal of Wildlife Management 51: 294-297.

Forrest, S.C. 2005: Getting the story right: A response to Vermeire and colleagues. - BioScience 55: 526-530.

Forrest, S.C., Biggins, D.E., Richardson, L., Clark, T.W., Campbell, T.M., Fagerstone, K.A. & Thorne, E.T. 1988: Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981-1985. - Journal of Mammalogy 69: 261-273.

Gitzen, B.A., Millspaugh, J.J. & Kernohan, B.J. 2006: Bandwidth selection for fixed-kernel analysis of animal utilization distributions. - Journal of Wildlife Management 70: 1334-1344.

Goodrich, J.M. & Buskirk, S.W. 1998: Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex. - Journal of Mammalogy 79: 171-179.

Grenier, M.B., Buskirk, S.W. & Anderson-Sprecher, R. 2009: Population indices versus correlated density estimates of black-footed ferret abundance. - Journal of Wildlife Management 73: 669-676.

Grenier, M.B., McDonald, D.B. & Buskirk, S.W. 2007: Rapid population growth of a critically endangered carnivore. - Science 313: 779.

Griffith, B., Scott, M.J., Carpenter, J.W. & Reed, C. 1989: Translocation as a species conservation tool: status and strategy. - Science 245: 477-485.

Henderson, F.R., Springer, P.F. & Adrian, R. 1969: The black-footed ferret in South Dakota. - South Dakota Department of Game, Fish and Parks Technical Bulletin 4: 1-37.

Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. 2005: Prey density, environmental productivity and home range size in the Eurasian lynx (*Lynx lynx*). - Journal of Zoology (London) 265: 63-71.

Hoogland, J.L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. - University of Chicago Press, Chicago, Illinois, USA, 557 pp.

Hurlbert, S.H. 1984: Pseudoreplication and the design of ecological field experiments. - Ecological Monographs 54: 187-211.

Jachowski, D.S. 2007a: Notes on black-footed ferret detectability and behavior. - The Prairie Naturalist 39: 99-104.

Jachowski, D.S. 2007b: Resource selection by black-footed ferrets in relation to the spatial distribution of prairie dogs. - M.Sc. thesis, University of Missouri, Columbia, Missouri, USA, 61 pp.

Jachowski, D.S. & Lockhart, J.M. 2009: Reintroducing the black-footed ferret *Mustela nigripes* to the Great Plains of North America. - Small Carnivore Conservation 41: 58-64.

Jachowski, D.S., Millspaugh, J.J., Biggins, D.E., Livieri, T.M. & Matchett, M.R. 2008: Implications of black-tailed prairie dog spatial dynamics to black-footed ferrets. - Natural Areas Journal 28: 14-25.

Johnson, D.D.P., Kays, R., Blackwell, P.G. & Macdonald, D.W. 2002: Does the resource dispersion hypothesis explain group living? - Trends in Ecology and Evolution 17: 563-570.

Johnson, D.D.P., Macdonald, D.W. & Dickman, A.J. 2000: An analysis and review of models of the sociobiology of the Mustelidae. - Mammal Review 30: 171-196.

Johnson, W.C. & Collinge, S.K. 2004: Landscape effects on black-tailed prairie dog colonies. - Biological Conservation 115: 487-497.

Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. 2001: Analysis of animal space use and movements. - In: Millspaugh, J.J. & Marzluff, J.M. (Eds.); Radio tracking and animal populations. Academic Press, San Diego, California, USA, pp. 126-166.

King, C.M. & Powell, R.A. 2007: The natural history of weasels and stoats. - Oxford University Press, United Kingdom, 464 pp.

King, J.A. 1959: The social behavior of prairie dogs. - Scientific American 201: 128-140.

Lair, H. 1987: Estimating the location of the focal center in red squirrel home ranges. - Ecology 68: 1092-1101.

Livieri, T.M. 2006: Ten-year history of the Conata Basin black-footed ferret population: 1995-2005. - Prairie Wildlife Research, Wall, South Dakota, USA, 50 pp.

Livieri, T.M. 2007: Black-footed ferret spatial use of prairie dog colonies in South Dakota. - M.Sc. thesis, University of Wisconsin, Stevens Point, USA, 61 pp.

Lockhart, J.M., Thorne, E.T. & Gober, D.R. 2006: A historical perspective on recovery of the black-footed ferret and the biological and political challenges affecting its future. - In: Roelle, J.E., Miller, B.J., Godbey, J.L. & Biggins, D.E. (Eds.); Recovery of the black-footed ferret - progress and continuing challenges. U.S. Geological Survey Scientific Investigations Report 2005-5293, Fort Collins, Colorado, USA, pp. 6-20.

Macdonald, D.W. 1981: Resource dispersion and the social organization of the red fox (*Vulpes vulpes*). - In: Chapmand, J.A. & Pursely, D. (Eds.); Proceedings of the worldwide furbearer conference, Frostburg, Maryland, USA, pp. 918-949.

Macdonald, D.W. 1983: The ecology of carnivore social behavior. - Nature 301: 379-384.

McLoughlin, P.D., Ferguson, S.H. & Messier, F. 2000: Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. - Evolutionary Ecology 14: 39-60.

Miller, B., Reading, R.P. & Forrest, S. 1996: Prairie night: Black-footed ferrets and the recovery of endangered species. - Smithsonian Institution Press, Washington D.C., USA, 254 pp.

Millspaugh, J.J., Gitzen, R.A., Kernohan, B.J., Larson, M.A. & Clay, C.L. 2004: Comparability of three analytical techniques to assess joint space use. - Wildlife Society Bulletin 32: 148-157.

Milne-Laux, S. & Sweitzer, R.A. 2006: Experimentally induced colony expansion by black-tailed prairie dogs (*Cynomys ludovicianus*) and implications for conservation. - Journal of Mammalogy 87: 296-303.

Mladenoff, D.J. & Sickley, T.A. 1999: Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. - Journal of Wildlife Management 62: 1-10.

Nilsen, E.B., Herfindal, I. & Linnell, J.D.C. 2005: Can intra-specific variation in carnivore home range size be explained using remote-sensing estimates of environmental productivity? - Ecoscience 12: 68-75.

Norbury, G.L., Norbury, D.C. & Heyward, R.P. 1998: Behavioral responses of two predator species to sudden declines in primary prey. - Journal of Wildlife Management 62: 45-58.

Pauli, J.N. & Buskirk, S.W. 2007: Risk-disturbance overrides density dependence in a hunted colonial rodent, the black tailed prairie dog *Cynomys ludovicianus*. - Journal of Applied Ecology 44: 1219-1230.

Paunovich, R. & Forrest, S.C. 1987: Activity of a wild black-footed ferret litter. - Prairie Naturalist 19: 159-162.

Powell, K.L., Robel, R.J., Kemp, K.E. & Nellis, M.D. 1994: Above-ground counts of black-tailed prairie dogs - temporal nature and relationship to burrow entrance density. - Journal of Wildlife Management 58: 351-355.

Richardson, L., Clark, T.W., Forrest, S.C. & Campbell, T.M., III. 1987: Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming. - American Midland Naturalist 117: 225-239.

Robitaille, J.F. & Raymond, M. 1995: Spacing patterns of ermine, *Mustela erminea* L., in a Quebec agrosystem. - Canadian Journal of Zoology 73: 1827-1834.

Rolls, K., Pilgrim, K.L., White, P.J., Paxinos, E.E., Schwartz, M.K. & Fleisher, R.C. 2001: Kinship, social relationships, and den sharing in kit foxes. - Journal of Mammalogy 82: 858-866.

Sandell, M. 1989: The mating tactics and spacing patterns of solitary carnivores. - In: Gittleman, J.L. (Ed.); Carnivore behavior, ecology, and evolution. Volume 1. Cornell University Press, Ithaca, New York, USA, pp. 164-182.

Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Červeny, J., Koubek, P., Huber, T., Staniša, C. & Trepl, L. 2002: Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. - Journal of Applied Ecology 39: 189-203.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. 1999: Effects of sample size on kernel home range estimates. - Journal of Wildlife Management 63: 739-747.

Seidel, K.D. 1992: Statistical properties and applications of a new measure of joint space use for wildlife. - University Press, University of Washington, Seattle, Washington, USA, 54 pp.

Sheets, R.G., Linder, R.L. & Dahlgren, R.B. 1972: Food habits of two litters of black-footed ferrets in South Dakota. - American Midland Naturalist 87: 249-251.

Støen, O-G, Bellemain, E., Sæbø, S. & Swenson, J.E. 2005: Kin-related spatial structure in brown bears *Ursus arctos*. - Behavioral Ecology and Sociobiology 59: 191-197.

Truett, J.C., Dullum, J.L.D., Matchett, R., Owens, E. & Seery, D. 2001: Translocating prairie dogs: a review. - Wildlife Society Bulletin 29: 863-872.

Wand, M.P. & Jones, M.C. 1995: Kernel smoothing. - Chapman and Hall, London, UK, 212 pp.

Wolff, J.O. 1997: Population regulation in mammals: an evolutionary perspective. - Journal of Animal Ecology 66: 1-13.

Wolff, J.O. & Peterson, J.A. 1998: An offspring-defense hypothesis for territoriality in female mammals. - Ethology, Ecology & Evolution 10: 227-239.

Woodroffe, R. & Ginsberg, J.R. 1998: Edge effects and the extinction of populations inside protected areas. - Science 280: 2126-2128.