Space use, Resource Selection and Territoriality of Black-Footed Ferrets: Implications for Reserve Design

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Insight into the spatial ecology of predators might help biologists to design wildlife reserves that maximize conservation success. We investigated the spatial ecology of endangered black-footed ferrets *Mustela nigripes* during the post-breeding seasons (June–October) of 2007 and 2008 on a 452-ha colony of black-tailed prairie dogs *Cynomys ludovicianus* in South Dakota, USA. Ferrets of both sexes frequently used areas with an abundance of active openings to prairie dog burrows, suggesting a positive response to refuge and prey. Densities of active burrow openings were similar in areas of same-sex overlap and areas of exclusive space use, which might suggest limited defense of resources by ferrets. However, this result could be expected in our study because much of the study colony contained high densities of active burrow openings. Same-sex home ranges overlapped in area, but the intensity of space use overlap was low. For male ferrets with overlapping home ranges, both males tended to spend low amounts of time in areas of overlap. In contrast, for pairs of overlapping female home ranges, one female frequently used areas of overlap while the second apparently avoided them, suggesting a dominance hierarchy of some sort. Core areas were essentially exclusive. Our data are consistent with the hypothesis of intrasexual territoriality by ferrets in habitats of high quality, which would limit the number of ferrets a habitat supports. Where wildlife managers aim to maximize densities of free-ranging ferrets, it might be beneficial to create reserves that 1) provide each ferret with sufficient prey and refuge, 2) reduce social conflict and competition for space, and 3) facilitate dispersal.

Evaluations of space use and resource selection by animals can aid in the creation of wildlife reserves, and are therefore of conservation importance (Manly et al. 2002, Kertson and Marzluff 2011, McDonald et al. 2012). From the perspective of predator species, a key question relates to the influence of prey density on the spacing and territoriality of predators. In general, predators are attracted to areas used by prey (Hassell 1978) and might inhabit smaller territories where prey are abundant (Powell 1993, 1994). At least two outcomes are possible as prey densities increase and predators shrink their territories:

Model no. 1. – Given costs associated with defense of space and resources, predators might become less possessive of prey and space, and might tend to inhabit overlapping territories when prey densities increase (Powell 2000), which would increase habitat carrying capacity. This model notes that conservation of predators is best achieved by maximizing the density of prey throughout a reserve, and assumes that patchiness of the habitat might not influence, or weakly influence, habitat carrying capacity because the predators are willing to inhabit overlapping territories.

Model no. 2. – Alternatively, as prey densities increase and predators increase in abundance, the predators might shrink their territories but become crowded and, therefore, reduce space use overlap (Wilson 1980). In this model, although prey is abundant, social conflict would reduce space use overlap, thus reducing the number of predators the habitat supports, unless patches with high densities of prey are spaced in ways that limit social strife.

From a conservation perspective, these models suggest different methods for reserve design, and they require investigation on a species-by-species basis.

Here, we evaluate these models using data on the spatial ecology of black-footed ferrets *Mustela nigripes*, endangered carnivores that inhabit colonies of prairie dogs (*Cynomys* spp.) in western North America. Prairie dog colonies differ in size, and contain varying densities of prairie dogs. In colonies with high densities of prairie dogs, ferrets can shrink their territories (Jachowski et al. 2010) but it is unclear if ferrets tend to inhabit overlapping territories (model 1) or become crowded and compete for space (model 2). Many

studies suggest ferrets exhibit a developmentally fixed predisposition to defend space, perhaps regardless of habitat quality, which would limit the number of ferrets a habitat supports, thus supporting model 2 (Biggins et al. 1985, Paunovich and Forrest 1987, Richardson et al. 1987, Fagerstone and Biggins 2011, Livieri and Anderson 2012). However, in a recent study, Jachowski et al. (2010) reported a few instances of intense same-sex space use overlap during June–October when adult female ferrets were rearing their young (i.e. kits). In explaining the instances of high overlap, Jachowski et al. (2010: 7) suggested that "The relatively high degree of overlap… 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." Thus, those authors hypothesized that in areas with an abundance of prairie dogs, ferrets tend to share space, which would support model 1. That hypothesis has important conservation implications, as discussed by Jachowski et al. (2010: 8): "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."

Given discrepancies among studies of space use and territoriality of black-footed ferrets, and the importance of the competing models for reserve design, a study is needed on another colony of prairie dogs to determine which model is best supported for the ferret. We present an examination of space use, resource selection, and territoriality by adult ferrets during the post-breeding season on a colony of black-tailed prairie dogs (hereafter prairie dogs, *C. ludovicianus*) in the Conata Basin, South Dakota, USA. The study colony was immediately adjacent to, and contained somewhat higher densities of burrow openings (144.7 ha⁻¹) than the colony surveyed by Jachowski et al. (2010: 129.3 ha⁻¹). Overall, we hoped to increase understanding of the spatial ecology of *M. nigripes* and to evaluate the competing models for reserve design. We investigated the following hypotheses for adult ferrets:

1) Ferrets will use less space in areas where resources are abundant (Powell 2000). We concentrated on active burrow openings as a resource because prairie dogs are often abundant where active burrow openings are abundant, and ferrets can use the burrows as refuge (Biggins et al. 1993, Johnson and Collinge 2004, Chipault 2010). We hypothesized that sizes of areas used by ferrets would negatively correlate with densities of active burrow openings in those areas. Because female ferrets (but not males) care for kits, we hypothesized that the negative relationship between area of use and density of active burrow openings would be stronger for females than males.

2) Ferrets will selectively use areas where resources are abundant. We hypothesized that intensity of space use by ferrets in portions of their home ranges and core areas (also called territories) would positively correlate with densities of active burrow openings in those areas.

3) Ferrets will rarely occupy areas used by ferrets of the same sex, but intersexual overlap will be frequent. Thus, we hypothesized that in the colony with high densities of prairie dogs and burrows, the ferrets would be crowded and reduce space use overlap, which would support model 2 for reserve design. Most studies of ferrets suggest that ferrets

limit same-sex overlap (Paunovich and Forrest 1987, Richardson et al. 1987, Livieri and Anderson 2012) and other *Mustela* often exhibit intrasexual territoriality (Powell 1979, King and Powell 2007). However, male *Mustela* often use areas that overlap females and, therefore, intersexual overlap is common (Powell 1979, King and Powell 2007).

4) Active burrow openings will be more abundant in areas of same-sex overlap than in areas of exclusive space use. In portions of a ferret's home range where active burrow openings are abundant, a ferret might be able to acquire sufficient numbers of prey and den sites without excluding other same-sex ferrets (Powell 1993, King and Powell 2007).

5) Female ferrets will be found more in areas of male–male overlap than in areas used by only one male. This trend would suggest that male ferrets tended to overlap in areas where female ferrets are abundant. This hypothesis parallels that in 4), except in this case, females are the 'resource'. We monitored ferrets during the post-breeding season but male ferrets might continue to monitor female ferrets (potential mates) and male kits (future competitors) between breeding seasons.

Material and methods

Study site

We studied wild-born, adult black-footed ferrets during June–October 2007–2008 on the South Exclosure (or SC07), a colony of prairie dogs in the Conata Basin, South Dakota, USA (Fig. 1). In 2007, we recorded the locations of openings to prairie dog burrows, classifying those openings with fresh prairie dog scat as 'active' (Biggins et al. 1993, Eads et al. 2011a, b). The activity of burrow openings was similar in 2007 and 2008 in 192 circular-plots of 20-m radius distributed throughout the study colony, suggesting consistency in burrow activity between years (Eads et al. 2011b). We delineated the boundary of the colony as a polygon that excluded areas > 20 m from a burrow opening (Eads et al. 2011b).

Monitoring ferrets

We used spotlight surveys to monitor and collect coordinates for individually-identifiable black-footed ferrets (Campbell et al. 1985, Biggins et al. 2006a). To limit serial autocorrelation, we included consecutive locations separated by ≥ 12 h (Livieri 2007); however, 88% of consecutive locations were separated by ≥ 24 h (Eads 2009).

Home range and core area estimation

We estimated three areas of space use by ferrets that were located and identified ≥ 30 times, including two home range metrics and a core area metric (Seaman et al. 1999, Millspaugh et al. 2006). One of the home range metrics and the core area metric also estimated intensity of use. In presenting space use metrics for ferrets, we do not intend to suggest that the metrics represent true home ranges or core areas, because space use metrics are limited models of reality
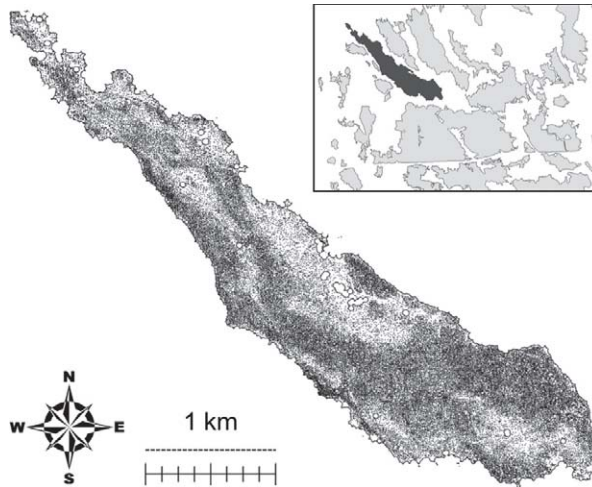
Figure 1. Spatial distribution of active openings (dots) to black-tailed prairie dog *Cynomys ludovicianus* burrows in SC07, a 452-ha colony in the Conata Basin (inset map), South Dakota, USA (North American Datum 1927 UTM: 13N N4848099, E716705). We monitored space use by adult black-footed ferrets *Mustela nigripes* inhabiting the colony during 13 June–10 October 2007, and 11 June–27 September 2008.

(Powell and Mitchell 2012: 950, 956). Instead, we use the space use metrics as models to investigate behaviors and biological processes that might have generated the patterns of space use (Powell and Mitchell 2012: 948).

First, we calculated 100% minimum convex polygon (MCP) home ranges by connecting the outermost locations of a ferret (Mohr 1947). Second, we calculated 95% utilization distribution (UD) home ranges that estimated intensity of space use throughout a system of grid cells (Millspaugh et al. 2006). Third, we used UD grids to calculate area independent method (AIM) core areas (Seaman and Powell 1990). These core areas delineated portions of UD ranges where intensity of space use was most different from a random space use pattern (Seaman and Powell 1990, Powell et al. 1997, Powell 2000).

We estimated MCP ranges in program CALHOME (Kie et al. 1996). We estimated UD ranges under a fixed kernel approach (Seaman and Powell 1996) in MATLAB 5.3 with bandwidth selected using plug-in methods (Wand and Jones 1995, Jones et al. 1996, Gitzen et al. 2006) and the 'kde' folder (Beardah and Baxter 1995). These are the same kernel estimators used by Jachowski et al. (2010). We estimated AIM core areas as described in Eads et al. (2011a, 2012). Lastly, we limited the UD estimates to the 95% contour, and then clipped 100% MCPs, 95% UDs and AIM core areas at the colony boundaries because ferrets rarely leave prairie dog colonies (Biggins et al. 2006b) and relatively inhospitable areas should be excluded from space use metrics (Powell and Mitchell 2012). Metrics of space use, such as the sizes of estimated home ranges, can vary depending on the number of observations collected (Seaman et al. 1999). We did not detect a significant correlation between numbers of observations per ferret and sizes of 100% MCP ranges ($r^2 = 0.07$, $F_{1,19} = 1.47$, $p = 0.24$), 95% UD ranges ($r^2 = 0.08$, $F_{1,19} = 1.69$, $p = 0.21$), or AIM core areas

($r^2 = 0.10$, $F_{1,19} = 2.10$, $p = 0.16$); all three correlations were negative.

Data analyses

Analyses were completed in five steps that correspond with the five hypotheses in the Introduction:

1. Do ferrets use less space in areas where active burrow openings are relatively abundant? We counted numbers of active burrow openings in UDs and core areas and converted counts to densities (per ha). Then, we used linear regression to relate densities of active burrow openings to sizes of UDs or core areas. We interpreted r^2-values as effect-sizes.

2. Do ferrets concentrate space use in areas with relatively high densities of resources? We addressed this question in two ways. First, we used paired Wilcoxon signed-rank tests to compare densities of active burrow openings in AIM core areas to densities in the remaining areas of UD ranges (i.e. areas outside the core area). Livieri and Anderson (2012) completed a similar analysis. Second, we related intensity of space use in UD ranges and AIM cores to densities of active burrow openings. For each UD range and AIM core area, we standardized the grid cells (Σ values = 1.00); thus, a grid cell estimated the relative amount of time a ferret spent in the cell. Then, we calculated the density of active burrow openings in each grid cell and used linear regression to relate cell-specific estimates of intensity of space use to densities of active burrow openings in grid cells. To account for potential spatial autocorrelation among neighboring cells, we used Gaussian spatial autoregressive (SAR) models, with inverse distance weighting (Bonham and Reich 1999, Reich and Bonham 2001, Lichstein et al. 2002). In the SAR models, grid cells comprised the sample, with repeated grid cells for a ferret's home range or core area. We fit an SAR model for each individual ferret.

3. In instances of same-sex overlap, what is the estimated area of overlap and how intense is the overlap? As a summary of space use overlap, for each ferret we counted the number of female or male ferrets overlapped. In addition, for UD home ranges and AIM core areas, we calculated areas of overlap, which are presented as proportions of home ranges or core areas. Further, we investigated intensity of space use overlap using the *VI* index (Seidel 1992) as used by Jachowski et al. (2010),

$$ VI = \int \int \min\left[\hat{f}_A(x, y), \hat{f}_B(x, y) \right] dxdy $$

where $\hat{f}_A$ is the estimated UD or core area for ferret *A* and $\hat{f}_B$ is the UD or core area for ferret *B*. The *VI* index measures overlap of kernel volume (i.e. height) and ranges from 0.00 for no overlap to 1.00 for complete overlap (Seidel 1992). We calculated *VI* values for all instances of same-sex overlap. The *VI* estimates for intensity of overlap were over-estimates in the sense that 1) kernel estimators create buffers that can increase estimates of space use overlap (Powell and Mitchell 2012) and 2) we did not consider instances of non-overlap among same-sex ferrets.

A low *VI* index for a pair of ferrets does not necessarily imply avoidance of areas of overlap by both individuals;

one ferret might have avoided the areas of overlap, while the other frequently used the areas. To investigate this possibility, we compared how ferrets used areas of same-sex overlap for UD home ranges. AIM core areas were not included in this analysis because core areas rarely overlapped. The grid cells of a UD summed to 1.00, as noted in analysis no. 2. For each individual ferret in a pair of same-sex overlap, we added the UD grid values in the areas of overlap, thereby estimating the proportion of time that ferret spent in the area of overlap. Then, we used paired Wilcoxon signed rank tests for all same-sex pairs of overlapping UD ranges to compare the amount of time-in-overlap for overlapping ferrets. One analysis was completed for each sex. Differing rank-values would indicate that one ferret tended to spend more time in the areas of home range overlap than their same-sex conspecific.

4. Are resources more abundant in areas of same-sex overlap than in areas of exclusive use? For each sex separately, we used paired Wilcoxon signed-rank tests to compare average densities of active burrow openings in areas of same-sex overlap versus areas of exclusive space use. AIM core areas overlapped very little and were not included in this analysis.

5. Are female ferrets more likely to be found in areas of male–male overlap than in areas of non-overlap? We completed two analyses using UD ranges for males observed ≥ 30 times and locations for all monitored females, including those observed < 30 times. All of the male UDs overlapped at least one other male UD. First, for male ferrets we used a paired Wilcoxon signed-rank test to compare average densities of female locations in areas of male–male overlap versus areas of exclusive space use; thus, in the analysis, each male had two paired values for comparison, one from the areas of overlap and the other value from areas of exclusive space use. Second, we used a paired Wilcoxon signed-rank test to compare counts of unique female ferrets located in areas of male–male overlap versus areas of exclusive use by males; the number of unique females (potential breeding partners) is likely important to a male ferret.

All statistical tests were completed in Program R ver. 2.11.1 for the years combined (2007–2008) under a significance threshold (α) of 0.050. Three adult ferrets (two females, one male) inhabited the colony both years. For these three ferrets, we assumed independence of the 2007 and 2008 samples in data analyses (Eads et al. 2011a).

Results

During 13 June–10 October 2007 and 11 June–27 September 2008 we collected ≥ 30 observations ($\bar{x} = 39.14$, range $= 30$–55, SD $= 5.93$) of 11 (eight females, three males) and 10 (five females, five males) adult ferrets respectively (three monitored both years). Insufficient numbers of observations inhibited estimation of space use for one female in 2007 and four females in 2008. For the female in 2007, we did not locate her until 20 August, and she inhabited an area in the northern portion of the colony where, in past field seasons, female ferrets had extended their areas of space use outside of our study colony into a smaller, adjacent colony. Perhaps this female was an occasional resident of our study colony, or a "floater" as defined by Wilson (1980:

136). For the four females in 2008, one female was not observed after 20 June and another female was not observed after 2 July (these females might have died or moved to another colony) and the remaining two females were observed sporadically during the field season but in numerous areas (suggesting transient space use). Thus, our results are limited to 'resident' adult ferrets as defined.

1. Do ferrets use less space in areas where active burrow openings are abundant? We failed to detect a relationship between female UD range size and density of active burrow openings ($r^2 = 0.16$, $F_{1,11} = 2.06$, $p = 0.179$) but the negative slope was suggestive (Fig. 2). We failed to detect a relationship between male UD range size and densities of active burrow openings ($r^2 = 0.004$, $F_{1,6} = 0.02$, $p = 0.880$). For core areas, we did not detect a relationship between core area size and density of active burrow openings for females ($r^2 = 0.18$, $F_{1,11} = 2.48$, $p = 0.143$), although the correlation again was suggestive (Fig. 3). We did not detect a relationship for male core areas ($r^2 = 0.004$, $F_{1,6} = 0.02$, $p = 0.883$). For UD ranges and AIM core areas, the female r^2-value was 40- to 45-times greater than the male r^2-value, suggesting that, although not statistically significant in any model, the relationship between area of use and density of active burrow openings was stronger for females.

2. Do ferrets concentrate space use in areas with relatively high densities of resources? Rank values for densities of active burrow openings were greater in AIM core areas than the remaining UD area for females ($V = 11$, $p = 0.013$) and males ($V = 1$, $p = 0.016$). Thus, within UD ranges, ferrets established core areas in patches with high densities of active burrow openings.

Regarding intensity of space use in home ranges, female and male ferrets () concentrated space use in areas with high densities of active burrow openings (females, $p \leq 0.003$ for all 13 SAR F-tests; males, $p \leq 0.005$ for all eight SAR F-tests).
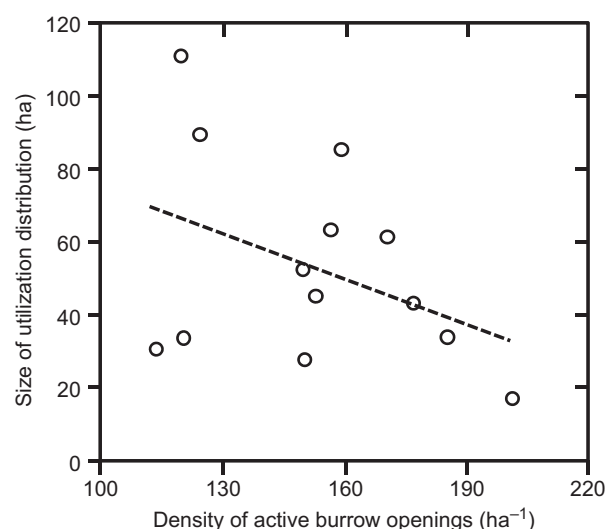

Figure 2. The sizes of utilization distribution home ranges for adult female black-footed ferrets *Mustela nigripes* relative to densities of active burrow openings in those ranges. The regression line was derived from a least-squares linear model. Ferrets were monitored on SC07, a 452-ha colony of to black-tailed prairie dogs *Cynomys ludovicianus* in the Conata Basin, South Dakota, USA, June–October 2007–2008.
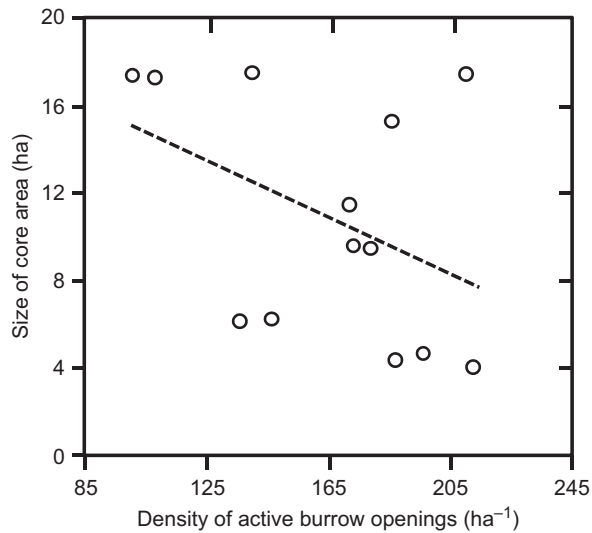
Figure 3. The sizes of area independent method core areas for adult female black-footed ferrets *Mustela nigripes* relative to densities of active burrow openings in those areas. The dotted line was derived from a least-squares linear model. Ferrets were monitored on SC07, a 452-ha colony of black-tailed prairie dogs *Cynomys ludovicianus* in the Conata Basin, South Dakota, USA, June–October 2007–2008.

In core areas, four females concentrated space use in areas of high densities of active burrow openings ($p \leq 0.020$). However, we failed to detect relationships for the remaining nine female core areas ($p \geq 0.100$). Four males (50%) concentrated space use in parts of core areas with high densities of active burrow openings ($p \leq 0.001$) whereas we detected no such contraction of space use for the remaining four males ($p \geq 0.080$).

3. In instances of same-sex overlap, what is the area of overlap and how intense is the overlap? Female-female and male–male UD range overlap was evident in area but limited in intensity of use (Table 1, 2). In 2007, a female's UD partly overlapped, on average, 2.75 females (SD = 0.89), while the UD of each male partly overlapped the remaining two males. The UDs of three males partly overlapped, on average, six females (SD = 1.73). In 2008, female and male

Table 1. Space use overlap of 95% utilization distribution (UD) home ranges and area independent method (AIM) core areas adult female and male black-footed ferrets *Mustela nigripes*. These estimates are limited to ferrets located ≥ 30, exclude same-sex pairs with no overlap, and are presented as proportions of home ranges or core areas. Lower estimates of overlap suggest larger areas of exclusive space use. Ferrets were monitored on SC07, a 452-ha colony of black-tailed prairie dogs *Cynomys ludovicianus* in the Conata Basin, South Dakota, USA, June–October 2007–2008. Home ranges and core areas were clipped at the colony boundary.

Sex	UD home range % overlap ± SD	AIM core area % overlap ± SD
2007		
Female	0.49 ± 0.23	0.06 ± 0.09
Male	0.55 ± 0.32	0.31 ± 0.29
2008		
Female	0.52 ± 0.20	0.15 ± 0.24
Male	0.45 ± 0.27	0.15 ± 0.27

Table 2. Summary of volume of intersection (*VI*) values describing intensity of 95% utilization distribution (UD) and area independent method (AIM) core area overlap for same-sex adult black-footed ferrets *Mustela nigripes*. Ferrets were monitored on SC07, a 452-ha colony of black-tailed prairie dogs *Cynomys ludovicianus* in the Conata Basin, South Dakota, USA, June–October 2007–2008. Home ranges and core areas were clipped at the colony boundary. These estimates exclude same-sex pairs with no overlap, and are limited to ferrets located ≥ 30 times.

Sex	n	UD $\overline{VI} \pm$ SD	AIM $\overline{VI} \pm$ SD
2007			
Female	8	0.08 ± 0.07	0.02 ± 0.01
Male	3	0.16 ± 0.11	0.05 ± 0.03
2008			
Female	5	0.15 ± 0.01	0.09 ± 0.14
Male	5	0.11 ± 0.10	0.01 ± 0.00

UDs partly overlapped an average of 2.40 same-sex UDs (SD = 0.89). The UDs of five males partly overlapped 3.40 females, on average (SD = 0.55).

Regarding time-in-overlap for home ranges, female ferrets spent disparate amounts of time in areas of overlap ($V = 29$, p = 0.006). In contrast, for males, rank values for time-in-overlap did not differ significantly ($V = 31$, p = 0.359); each male spent similarly low amounts of time in areas of overlap (median = 18%).

For core areas, female-female and male–male overlap was limited in area (Table 1) and intensity of use (Table 2). That is, core areas were essentially exclusive. For females with core area overlap, the core area partly overlapped, on average, 2.00 females in 2007 (SD = 0.82) and 1.20 females in 2008 (SD = 1.10). For males with core area overlap, the area partly overlapped two males in 2007 and 0.67 males in 2008 (both SD = 0.52).

4. Are resources more abundant in areas of same-sex overlap than in areas of exclusive use? Rank values for densities of active burrow openings did not differ significantly in areas of female UD overlap and non-overlap ($V = 54$, p = 0.588). Similarly for males, rank values for densities of active burrow openings were not significantly different in areas of UD overlap and non-overlap ($V = 21$, p = 0.742).

5. Are female ferrets more likely to be found in areas of male overlap than in areas of non-overlap? This analysis included observations of all females (2007: n = 9 females, ($\bar{x} = 38.78$ locations, range = 12–47, SD = 10.67; 2008: n = 9 females, ($\bar{x} = 26.33$ locations, range = 2–55, SD = 17.10). Rank values for densities of female locations were greater in areas of male–male overlap than areas of exclusive space use ($V = 32$, p = 0.055). Thus, male ferrets tended to overlap each other in areas often used by females (Fig. 4). Rank values for counts of unique females (potential breeding partners) did not differ significantly in areas of male overlap and non-overlap ($V = 19.5$, p = 0.888).

Discussion

Space use and resource selection

Like males of other *Mustela*, in this and other studies male black-footed ferrets used areas around female ferrets (Paunovich and Forrest 1987, Richardson et al. 1987,
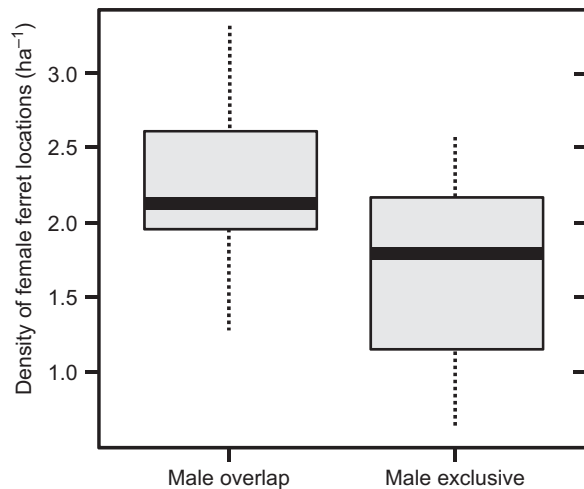
31

Figure 4. Box-plot for densities of observations of female black-footed ferrets *Mustela nigripes* in areas of male–male home range overlap (overlap) and areas of exclusive space use by males (exclusive). Ferrets were monitored on SC07, a 452-ha colony of black-tailed prairie dogs *Cynomys ludovicianus* in the Conata Basin, South Dakota, USA, June–October 2007–2008.

Jachowski et al. 2010, Livieri and Anderson 2012). In our study, male–male overlap was greater in areas frequently used by females, although the male ferrets spent little time in those areas. In the post-breeding season, male ferrets might behave in ways to increase future breeding opportunities. For instance, by continuing to use and monitor areas around female ferrets, perhaps even just on occasion, a male ferret might retain access to the females and surrounding space into the next breeding season. Indeed, in some species, resident males can outcompete intruders (Davies 1978, Krebs 1982) and this residency advantage seems to apply to ferrets (Biggins et al. 2006b).

While male ferrets may benefit from monitoring areas used by females, the females might also benefit. Indeed, females might gain information about males (e.g. from scent markings) and, perhaps, use that information when selecting a breeding partner (Johansson and Jones 2007). Perhaps male ferrets occasionally monitor multiple females to increase breeding opportunities and, in doing so, provide females with opportunities to proactively select mates. Such mate selectivity might be favored by natural selection because female ferrets would seemingly benefit from an ability to distinguish among (and monitor) males, perhaps before the breeding season (Miller et al. 1996).

Predators, including *Mustela*, often concentrate space use in areas where resources are abundant (Hassell 1978, Powell 1979). In our study, both adult female and male ferrets frequently used areas of their home ranges with high densities of active burrow openings where prairie dogs and refuges are abundant (Jachowski et al. 2011, Livieri and Anderson 2012). The similarity between sexes in resource selection and the commonality of intersexual space use overlap might suggest that the two sexes compete for areas where active burrow openings (and prey) are abundant. However, while male UD ranges collectively overlapped areas frequently used by females, the males rarely used those

areas. These patterns of space use would reduce intersexual competition (Powell 1994) while allowing male ferrets to monitor females and, perhaps, periodically monitor other males (i.e. competition for mates). Regardless of whether or not female and male ferrets compete for prey, male ferrets prey on prairie dogs and their resource demands add to those that are required for female ferrets and kits. As a consequence, current habitat evaluations for ferrets sometimes involve calculations of the number of 'ferret families' a site might support based upon indices for prairie dog abundance (family = 1 adult female, the average litter of 3.3 kits, and 0.5 adult males) (Biggins et al. 1993, 2006c).

Ferret core areas had higher densities of active burrow openings compared to other parts of their home ranges (see also Livieri and Anderson 2012). However, less than half of the ferrets frequently used portions of their core areas with high densities of active burrow openings. Perhaps the remaining ferrets did not further increase intensity of space use in portions of their core area with high densities of active burrow openings because active burrow openings were abundant throughout their core areas; habitat homogeneity does not favor selective behavior (Johnson 1980).

As discussed by Powell (1979, 1994), *Mustela* often use less space where resources are abundant. In our study, we did not detect a significant association between sizes of ferret home ranges or core areas and densities of active burrow openings in those areas. Nonetheless, the negative correlation between sizes of UD ranges and densities of active burrow openings in the UDs was suggestive for female ferrets (Fig. 2), but not males. In addition, the negative correlation between sizes of UD ranges and densities of active burrow openings was significant for female ferrets in the study of Jachowski et al. (2010). Therefore, these two studies collectively suggest that female ferrets tend to use smaller areas where active burrow openings are abundant, a trend that agrees with studies of other *Mustela* and the hypothesis that female *Mustela* are most concerned with acquisition of resources to support young, whereas males are more concerned with breeding (Erlinge and Sandell 1986, Sandell 1986, 1989).

Do the patterns of space use and resource selection in our study indicate a direct response by ferrets to prairie dogs? At our site, densities of active burrow openings positively correlated with densities of total burrow openings (active + inactive). Thus, prairie dogs and routes of escape from predators were both abundant in the areas most frequently used by ferrets and, consequently, we could not distinguish between selection for densities of prey or refuge. We hypothesize that ferrets respond to distributions of both resources, given ferrets prey almost exclusively on prairie dogs, and predation is a major source of mortality for ferrets (Sheets et al. 1972, Campbell et al. 1987, Biggins et al. 2011).

Territoriality

We found that same-sex home ranges overlapped considerably in area. As discussed by Powell (2000), home range overlap is to be expected, perhaps in most or all territorial species. For instance, home ranges can overlap due to patrol outside of core areas, as suggested for ferrets by Richardson et al. (1987). Biggins et al. (unpubl.) found

that radio-collared ferrets exhibited "excursions" from core areas, at times into another ferret's home range; the movements were brief, but sometimes distant. In our study, ferrets might have exhibited similar excursions, which would have resulted in home range overlap. In addition, home range estimates can overlap due to the procedure used in delineating home ranges, especially for MCPs that often include large areas not observably used by animals, or kernel methods that sometimes produce large buffers around location data (Powell and Mitchell 2012).

In *Mustela*, same-sex home ranges often overlap in area, but a male or female infrequently uses areas used by another individual of the same sex (Powell 1979, King and Powell 2007). Indeed, in mustelids and other carnivores there is often "no benefit to sharing a territory with a member of the same sex" (Powell 1993: 178). We found that intensity of same-sex overlap, measured with the *VI* index, was limited. This result is striking for at least two reasons. First, we evaluated overlap using UD home ranges that can include boundary areas never used, or actually avoided by animals (Powell and Mitchell 2012). Second, adjacency of home ranges is difficult to define concisely, so we concentrated on overlapping ranges, which provided a consistent definition. By excluding non-overlapping ranges, we limited *VI* values to those > 0, which guarantees a positive bias for *VI* values. If we had considered as neighbors all animals with adjacent home ranges whether or not they overlapped, then the *VI* indices for overlap would have been even smaller. Therefore, the ferrets might have been more territorial than our results suggest.

Using the *VI* method, Jachowski et al. (2010) found limited same-sex overlap but a few instances of high same-sex overlap for adult ferrets. Here, we discuss mean *VI* values because they provide a measure of central tendency. Restricting data from the Jachowski et al. (2010) study to instances of same-sex overlap in area (using their Table 2 and Fig. 2), mean *VI* values from both studies were generally low (combined $\overline{VI} = 0.16$), suggesting much exclusive use of ranges by ferrets in both studies. Thus, these two studies, and all other studies of space use overlap in ferrets suggest these carnivores tend to limit the intensity of overlap with same-sex conspecifics (Biggins et al. 1985, Paunovich and Forrest 1987, Richardson et al. 1987, Fagerstone and Biggins 2011, Livieri and Anderson 2012).

In our study, male ferrets spent little time in areas of male–male overlap. Perhaps the areas of overlap were not of great importance to the males we monitored (King and Powell 2007: 171) or the high densities of females in the areas of male–male overlap induced males to hunt elsewhere. Alternatively, infrequent use of an area of overlap by either male might suggest that the areas of overlap were highly contested, and neither male had acquired primary access to the areas. Although males rarely used the areas of male–male overlap, the males might have occasionally monitored females in those areas. After our field season, as the breeding season approaches, male ferrets are likely to defend access to mates and commonly use areas used by females (Erlinge and Sandell 1986).

Unlike home ranges of males, when two female ferret home ranges overlapped, one female often spent more time in the area of overlap than the other female did. These results could support the findings of Biggins et al. (2006b), who suggested a dominance hierarchy among ferrets sequentially released to prairie dog colonies. In our study, two scenarios seem plausible. First, in a pair of overlapping female ferrets, the female that rarely used the areas of overlap might have been subordinate to the female that spent more time in the areas of overlap, because dominant females might gain primary access to areas of female–female overlap. Alternatively, dominant female ferrets might be those individuals that spend the least amount of time in areas of overlap. We could not rigorously evaluate these two scenarios, but hypothesize that if female ferrets exhibit dominance hierarchies, the dominant individuals tend to spend less time in areas of overlap because prey in those areas might have detected ferret cues (e.g. scent) and ferrets might benefit from hunting unsuspecting prey in areas of their home range that do not overlap another ferret (see also Powell 1993, Roth and Lima 2007).

Dominance seemingly confers opportunities for access to a relatively large home range. If dominant female ferrets inhabit relatively large home ranges, the density of resources in a female's home range might not clearly reflect her social status. Indeed, because of the patchiness of openings to burrows in prairie dog colonies (e.g. Fig. 1), a large home range can have more patches with high densities of active burrow openings (good habitat) but also more intervening spaces with low densities of active burrow openings (poorer habitat). Thus, the ratio of good to poorer habitat can result in lower overall densities of active burrow openings in large home ranges used by dominant females, relative to small home ranges used by subordinate females. Perhaps dominant female ferrets inhabit relatively large home ranges with low overall densities of active burrow openings, but the dominant females have primary access to portions of their home range where resources are extremely abundant.

If some ferrets are dominant and same-sex ferrets compete, then why were densities of active burrow openings similar in areas of same-sex overlap and non-overlap? These results might be expected because our study colony contained large patches with high densities of active burrow openings. Yet, spacing patterns of ferrets suggested competition of some sort; the intensity of home range overlap was low and core areas were essentially exclusive.

Ferrets could limit same-sex overlap due to factors other than contemporary prey availability or, for males, access to females. First, ferrets might have minimum space requirements that are set to maximize access to resources in worst-case scenarios (given temporally fluctuating resources) and therefore simply compete for space (Biggins et al. 2006b). Analogous behavior is exhibited in most animals (Burt 1943), including animals in captive environments where food is provided (Hediger 1955). Second, ferrets use and might compete for complex burrow systems that provide multiple routes of escape from predators (Biggins 2012). Third, ferrets might rarely use areas used by another ferret if prairie dogs have already been alerted to the other ferret (e.g. by detecting ferret cues). Indeed, as noted previously, a ferret might benefit by using and hunting in areas not used, or infrequently used, by another ferret (or itself) (Powell 1993, Roth and Lima 2007). We emphasize that

these multiple explanations are not necessarily mutually exclusive.

Although ferrets appear to exhibit intrasexual territoriality, the degree of territoriality is likely to vary by context and time of year. Indeed, spatial organization varies within species, home range boundaries are dynamic, and resource abundance/configuration and nepotism might influence the likelihood and degree of space use overlap (Wilson 1980, Biggins et al. 2006b, c, King and Powell 2007). For instance, D. S. Jachowski (Virginia Polytechnic Institute and State University, pers. comm.) informed us that at least one occasion of intensive overlap during his research on adult female ferrets (Jachowski et al. 2010) involved a mother and her daughter, suggesting a potential importance of nepotism (but this topic requires investigation).

In some instances, space use overlap could be high for non-kin, but overlap does not preclude competition or imply tolerance or sharing of space. For instance, in some species categorized as highly territorial and "intolerant" of conspecifics, which we believe is the case for unrelated ferrets at least, individuals can trespass on a same-sex conspecific's home range to acquire resources (Randall 2007: 375). These intrusions might be most frequent when the territory owner is in another part of its home range and an agonistic interaction is unlikely. Richardson et al. (1987) and Jachowski (2007) found that ferret home ranges overlap, but ferrets used the areas of overlap at different times.

Our analyses investigated overlap in space use but considerations of territoriality are more complex (Maher and Lott 1995). For instance, consistent areas of occupancy of ferrets (Forrest et al. 1988) and competitive advantages of prior residency (Biggins et al. 2006b) suggest dominance hierarchies. Our results suggested dominance hierarchies for female ferrets in the post-breeding season (though additional research is needed on this topic). Ferrets can also use scent to communicate with competitors or actively fight ferrets of the same sex, and these behaviors appear to relate to dominance hierarchies in other *Mustela* (Clark et al. 1986, Miller 1988, Hutchings and White 2000). For example, Stoneberg (1997: 13) observed agonistic interactions and "mortal combat" between two male ferrets in Montana, an apparently rare and dangerous territorial behavior (Rubenstein 1982). Even in captivity, where ferrets are well provisioned, same-sex ferrets have been observed to exhibit agonistic behaviors (Miller 1988, Poessel 2009: 17–18) and inadvertent contact among individuals has resulted in fights (P. Marinari, US Fish and Wildlife Service, pers. comm.).

Thus, cumulative evidence suggests that same-sex ferrets do not tend to willingly share space or tolerate one another. Instead, it seems ferrets exhibit a developmentally fixed predisposition to defend home ranges, which corresponds with model 2 in the Introduction. From an evolutionary perspective, defense of home ranges seems adaptive for both sexes alike because defense of a territory can allow continued occupancy of a familiar area where locations of prey, refuge, and potential breeding partners can be monitored and, perhaps, memorized (King and Powell 2007).

Implications for reserve design

Colonies of prairie dogs should be restored and preserved to provide habitat for ferrets and to provide other conservation values to grassland species (Miller et al. 1990, Miller and Reading 2006, 2012). When restoring or evaluating prairie dog habitat, we encourage managers to consider not only sizes of colonies, but local densities of prairie dogs and territoriality by ferrets so conservation actions are directed at scales pertinent to individual ferrets (Biggins et al. 2006b, Eads et al. 2011b).

In general, we believe that numbers and densities of prairie dogs (prey) influence densities and survival rates of ferrets (Biggins et al. 1993), as found for other carnivores (Fuller and Sievert 2001). These factors might also influence territoriality. One theory predicts that ferrets will reduce the sizes of their territories in high quality habitat where resources are abundant. Nevertheless, as ferrets increase in density in high quality habitat, they can become crowded and likely compete for space (Biggins et al. 2006b, see also Wilson 1980: 144). That is, ferret densities could be mostly influenced by prey densities in low quality habitat and by social conflict and territoriality in high quality habitat. Indeed, in our study, ferrets exhibited behaviors consistent with territoriality in a large, high quality colony, with high densities of refuge and prey.

To maximize densities of free-ranging ferrets in managed habitat, it might be beneficial to create habitats that provide each ferret with sufficient prey while reducing social conflict and competition for space, especially among females. For an experiment, in areas capable of sustaining high densities of prairie dogs, managers might attempt to maintain complexes consisting of many colonies each smaller than the average home range of female ferrets in a saturated population on a large colony of prairie dogs (Biggins et al. 2006b). In the experiment, individual colonies should have enough prairie dogs to supply a surplus of prey to support a female ferret and her kits. We hypothesize that an optimum size and spacing of colonies would 1) allow colony boundaries to serve as territory boundaries and, thereby, limit social contact among female ferrets, 2) allow male ferrets to move among several colonies, and 3) facilitate dispersal of young ferrets.

We emphasize that we are not encouraging reductions of prairie dog populations or the areas they occupy. Rather, we are encouraging conservation of remaining colonies of prairie dogs and restoration of additional colonies, regardless of size or configuration, and future research to test our hypothesis. Such research could involve investigation of space use and territoriality by ferrets inhabiting colonies of differing size, shape, and species of prairie dogs, perhaps during different seasons but with similar densities of prairie dogs in the colonies as a control. If the aforementioned hypothesis is supported, then conservation actions at sites might be designed to maximize densities of prairie dogs in as many colonies as possible, with colonies sized and spaced in ways to facilitate ferrets and, more generally, grassland ecosystem functioning (Soulé and Simberloff 1986).

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