

SPATIAL ECOLOGY OF PRAIRIE RATTLESNAKES (*CROTALUS VIRIDIS*) ASSOCIATED WITH BLACK-TAILED PRAIRIE DOG (*CYNOMYS* *LUDOVICIANUS*) COLONIES IN COLORADO

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Abstract.—We analyzed movements of three groups of radio-telemetered Prairie Rattlesnakes (*Crotalus viridis*) hibernating in three Black-tailed Prairie Dog (*Cynomys ludovicianus*) colonies within short-grass prairie in Arapahoe County, Colorado. Movements were short and frequent, with mean R values (measuring straightness-of-path) not exceeding 0.6. Mean total distance traveled during the entire active season was 3007 m. On average, snakes moved 0.7 times per day, traveling 89 m per movement. Home range sizes varied from 0.3–31.4 ha. All snakes returned in autumn to the same colony in which they hibernated the previous winter. Increased foraging opportunities in our study site may have supported shorter migrations than have been reported for *C. viridis* in Wyoming. Greater body mass of our rattlesnakes and a Nebraska population of *C. viridis* relative to a Wyoming population of *C. viridis* indirectly supports this idea. We discuss conservation implications of these findings.

Key Words.—*Crotalus viridis*; ecology; Prairie Dog; prairie dog ecosystem

INTRODUCTION

Black-tailed Prairie Dog (*Cynomys ludovicianus*) ecosystems have been well studied, including effects of prairie dog activities on invertebrates and vertebrates associated with the colonies (e.g. Clark et al. 1982; Reading et al. 1989; Lomolino and Smith 2003; Smith and Lomolino 2004). While many reptiles are documented to occur in *C. ludovicianus* colonies (Kretzer and Cully 2001; Davis and Theimer 2003; Shipley and Reading 2006), rattlesnakes are especially common (Campbell and Clark 1981; Clark et al. 1982; Kretzer and Cully 2001; Ceballos et al. 2005), using prairie dog burrows for thermoregulation, predator avoidance, hibernation, and ambush sites (Klauber 1972; Hammerson 1999). Although several studies address Prairie Rattlesnake (*Crotalus viridis*) interactions with prairie dogs and ground squirrels (eg., Halpin 1983; Owings and Loughry 1985; Coss et al. 1993; Owings et al. 2002), little information exists about the spatial ecology of *C. viridis* in prairie dog ecosystems (Ludlow 1981; Holycross 1993). Only Holycross (1993) used radio-telemetry, and movement data from his Nebraska population agree with the results presented here (see Discussion).

We report movements of radio-tracked *C. viridis* from three *C. ludovicianus* colonies during the active seasons of 2005 and 2006. Proximity of these colonies to each other and associated grassland (see below) provided an opportunity to examine rattlesnake home ranges, movement patterns, and site fidelity. In particular, we

tested two hypotheses; that rattlesnake movements would result in intermixing of snakes from the three colonies, and that their movements would reveal lengthy forays outside of the colonies. We compare movements and body condition of our snakes with those of a Wyoming (Duvall et al. 1985) and Nebraska (Holycross 1993) population. Significant differences are hypothesized to arise from differences in resource availability; indirect support for this hypothesis is provided.

MATERIALS AND METHODS

We conducted this study on the Plains Conservation Center (PCC; Fig. 1) in Arapahoe County, Colorado (39° 39' 20" N, 104° 44' 11" W), consisting of 445 ha of short-grass prairie, 1728–1783 m above sea level. No geologic relief exists, such as rock outcrops, arroyos, or canyons. Major soils types are Buick loam, Fondis silt loam, Fondis–Colby silt loam, Renohill–Buick loam, and Renohill–Little–Thedalund complex (Larsen and Brown 1971). Dominant native grasses included Blue Grama (*Chondrosium gracile*), Western Wheatgrass (*Pascopyrum smithii*), and Green Needle Grass (*Stipa viridula*), followed by Needle-and-Thread (*Hesperostipa comata*), Prairie Junegrass (*Koeleria macrantha*), and Buffalo Grass (*Buchloe dactyoides*). Predominant native forbs included broom Snakeweed (*Gutierrezia sarothrae*), Western Wallflower (*Erysimum asperum*), Sand Dropseed (*Sporobolus cryptandrus*), and Gumweed (*Grindelia squarrosa*). Four species of cactus



FIGURE 1. Landscape views of the Plains Conservation Center: A) Short-grass prairie without prairie dogs, B) Prairie dog colony A and western edge of study site showing housing development. (Photographed by Bryon Shipley)

(*Opuntia compressa*, *O. polyacantha*, *Coryphantha vivipara*, *C. missouriensis*) were abundantly distributed as were Rabbitbrush (*Chrysothamnus parryi*) and Fourwing Saltbush (*Atriplex canescens*). Invasive, exotic plants included Cheatgrass (*Bromus tectorum*), Common Mullein (*Verbascum thapsus*), Canada Thistle (*Cirsium arvense*), Kochia (*Kochia scoparia*), and Russian Thistle (*Salsola australis*; Plains Conservation Center staff, unpubl. report).

Annual precipitation averaged 27.2 cm. Average daily maximum and minimum temperature for July 2005 and 2006 were 33.7° C and 16.3° C, respectively (NOAA National Weather Service, Denver/Boulder, Colorado Weather Forecast Office). Peak rattlesnake hibernation egress and ingress from 2001–2004 occurred on 27 ± 2 April and 17 ± 3 October, respectively. Average daily maximum and minimum temperatures for these dates were 22.7° C / 5.9° C and 41.6° C / 5.3° C, respectively. Three colonies of *C. ludovicianus* (labeled A, B, C on Fig. 3) occur on PCC, comprising 25.9, 10.4, and 7.8 ha, respectively, separated by an average of 2.0 km (range 1.3–2.4 km).



FIGURE 2. Prairie Rattlesnake (*Crotalus viridis*) from the study of home range and movements in Aurora, Colorado. The longitudinal black line between successive rattle segment lobes indicates prior capture. (Photographed by Bryon Shipley)

Field methods and data collection.—In 2001–2004 we surveyed each prairie dog colony for *Crotalus viridis* (Fig. 2). We used data from 2003–2004 for calculations of population size estimates because of quality of data gathered. We searched for rattlesnakes during egress and ingress periods, which we define as occurring from April through mid-May and September through October, respectively. We searched each prairie dog colony with 2–5 people, between 1000 and 1800, maintaining even distances between each person. Depending on time schedules and number of volunteers, each colony was searched 14–37 times. Although we attempted to apply similar search effort to each colony, bias was created as volunteers learned to locate and capture rattlesnakes more efficiently, particularly in areas in which rattlesnakes tended to be found with greater predictability. We captured rattlesnakes with tongs and injected Passive Integrated Transponder tags (PIT tags; HomeAgain™ Microchip identification system, Schering-Plough Animal Health Corporation, Omaha, Nebraska, USA) into each snake for identification after we measured, weighed, and determined sex of individuals.

In April of 2005–2006, we captured 14 adult female and 19 adult male rattlesnakes during egress for radio transmitter implantation and processed them as above. Battery failures and predation reduced the number of snakes tracked to five females and eight males in 2005, and four females and two males in 2006. We transported our rattlesnakes to Alameda East Veterinary Hospital where G3-1V transmitters (AVM Instrument Co., LTD., Colfax, California, USA) were implanted following methods of Fitzgerald and Vera (2006). Transmitters never exceeded 4.5% of the mass of a snake. We

released each snake 3 d post-surgery into the same burrow from which it was captured.

Tracking commenced on the day following release, and we used a LA12-Q radio-telemetry receiver with a Yagi 3-element directional antenna (AVM Instrument Co., LTD., Colfax, California, USA). We radio-tracked between 17 April and 8 October in 2005, and 15 May to 23 October in 2006. We recorded locations using a handheld global positioning unit (Garmin eTrex Venture Cx, Garmin International Inc., Olathe, Kansas, USA).

We used movements in analyses if the animal had moved > 3 m since its last observation. We calculated distances and 100% minimum convex polygon (MCP; see Row and Blouin-Demers 2006) home ranges with Hawth's Analysis Tools (Beyer 2004). Home range in our study encompassed all locations between egress and ingress periods. We considered each prairie dog colony as a den (Holycross 1993), reflecting the concept of "diffuse" or opportunistic denning described in coastal plain Timber Rattlesnakes (*Crotalus horridus*; Sealy 2002). Given an abundance of suitable hibernacula within a relatively small area, a snake might occupy a different burrow each year. Hence, we used the term "den colony" to describe the prairie dog colony in which a snake overwintered.

We assessed relative body condition of rattlesnakes by regressing mass on length for a sample of 90 *C. viridis*, 30 from eastern Colorado (18 males, 12 females; this study), 30 from central Wyoming (18 males, 12 females; King 1987), and 30 from Nebraska (18 males, 12 females; Holycross 1993). We calculated residuals, using a positive value to indicate a greater mass than average for snakes of the same length; whereas, a negative value indicated less mass than average. We used these values to test the hypothesis that effects of ecosystem differences on rattlesnake movements between these study sites (prairie dog versus non-prairie dog) could be revealed by comparing body condition of snakes from each area, reflecting potential availability of resources (i.e. prey density) and foraging efficiency. We did not census prey base populations due to time and resource constraints (but see Clark et al. 1982, Lomolino and Smith 2003, Shiple and Reading 2006, Stapp 2007).

Statistical analysis.—We pooled data from 2005 and 2006, as we detected no differences between the two sets of scores (distance measures, MCP). We calculated population size estimates for each colony with Bailey's correction of the Lincoln-Peterson estimator (Bailey 1951), using mark-recapture results from 2003 and 2004. We report means and population estimates ± 1 SEM. We analyzed data using ANOVA followed by a Tukey's HSD. We analyzed directionality using circular statistics (Fisher 1993) to determine R values for straightness-of-path. When R approaches a value of one,

a snake has traveled on a nearly straight line, while values near zero reflect random changes of direction. We defined cessation of vernal migration as occurring when a snake moved ≤ 10 m on two successive days. For each snake, we used the number of days before reaching this criterion and an equal number of days thereafter to compare migratory and post-migratory movements. Although the data were limited, we analyzed *C. viridis* movements from a Nebraska population (Holycross 1993) because this study represents the only other movement data for *C. viridis* found in prairie dog colonies.

RESULTS

Mean mass of females was 486.7 ± 53.1 g, range 200–720; and mean mass of males was 520 ± 50.9 g, range 300–830. Mean snout-vent length for females was 83.9 ± 3.3 cm, range 67–95; and mean snout-vent length of males was 87.7 ± 2.8 cm, range 73–103. Densities of rattlesnakes on these colonies varied from 2.4 to 16.9 snakes per ha (Table 1). In 2005, 69% of our rattlesnakes immediately moved from their den colonies into fallow agricultural fields, road cuts, and boundary fence lines located off PCC grounds (Fig. 3), instead of adjacent grassland on PCC property. All rattlesnakes released in 2006 remained within the PCC grounds. Despite the relative abundance of prairie dog burrows, we captured rattlesnakes primarily from abandoned prairie dog burrows located beyond the edge of active burrow boundaries where taller, ungrazed grass was still found.

Home range.—Rattlesnake home ranges generally incorporated a large portion of their den colonies, although six rattlesnakes (4 males, 2 females) had home ranges entirely outside their den colonies but returned to those colonies for hibernation. These home ranges were not correlated with smaller den colonies. In contrast, a female that was not gravid in 2005, but was gravid in 2006, maintained a home range entirely on the same den colony in both years, although her home range declined by 33% (13.4 ha) in 2006. Male home range sizes varied from 0.3–31.4 ha, those of non-gravid females varied from 8.1–28 ha, while those of gravid females varied from 0.2–28 ha. Home range sizes of males, non-gravid females, and gravid females (Table 2) differed significantly ($F = 4.313$, $df = 2,16$, $P = 0.031$), with males having a significantly larger home range than those of gravid females ($P = 0.03$). Male and non-gravid female home ranges did not differ significantly ($P = 0.99$), and although non-gravid females had overall larger home ranges compared to gravid females, this difference also was not significant ($P = 0.08$). Home range overlap revealed two points; snakes from different colonies did not overlap, and snakes from the same

TABLE 1. Mark-recapture information for years 2003–2004. Parenthetical values represent total number of hours searching for *Crotalus viridis* during egress / ingress periods 2003–2004. Table is estimated from field notes. Values shown are means \pm 1 SEM.

Colony	Rattlesnake population size estimate	Number of snakes per ha	Recapture rates (%)	Number of snakes captured per search hour	Number of mark-recapture events
A	62.7 \pm 12.7	2.4 \pm 0.5	8.0	0.3 \pm 0.09 (210)	4
B	176.4 \pm 39.6	16.9 \pm 0.3	2.2	0.4 \pm 0.06 (266)	4
C	38.5 \pm 13.5	4.9 \pm 1.7	2.9	0.3 \pm 0.04 (133)	4

colony overlapped, but the amount (3–13.9%) did not differ among the three groups ($F = 0.44$, $df = 2, 16$, $P > 0.05$). Mean amount (ha) of overlap between snakes within each colony was 3.4 ± 1.8 ($n = 7$), 2.6 ± 2.6 ($n = 5$), and 4.2 ± 1.2 ($n = 4$).

Movements.—All groups had reduced R scores after the vernal migration, although there was no statistical difference between groups ($F = 0.64$, $df = 2, 16$, $P > 0.05$). Mean R values for males during migration and post-migration were 0.6 ± 0.1 and 0.3 ± 0.0 , respectively ($t = 3.44$, $df = 9$, $P < 0.05$). Only three males had $R \geq 0.9$, indicating nearly straight paths during spring migration. For gravid females, mean R values were 0.5 ± 0.2 during migration and 0.4 ± 0.2 post-migration ($t = 2.10$, $df = 4$, $P > 0.05$). Non-gravid females had migration and post-migration means of 0.5 ± 0.1 and 0.2 ± 0.1 , respectively ($t = 2.37$, $df = 3$, $P > 0.05$). Pooling all females resulted in migratory vs. post-migratory R values of 0.5 ± 0.1 and 0.3 ± 0.1 ($t = 3.14$, $df = 8$, $0.01 > P > 0.05$). No female had $R \geq 0.9$.

The number of tracking days and total number of movements were comparable for male, non-gravid, and gravid female rattlesnakes (Table 2; $F_{\text{days tracked}} = 0.75$, $F_{\text{number movements}} = 0.32$; $dfs = 2, 16$, all P 's > 0.05). Movements per track day (Table 2; $F = 1.25$, $df = 2, 16$, $P > 0.05$), and mean total distance traveled (Table 2) did not differ significantly among the three groups ($F = 2.687$, $df = 2, 16$, $P > 0.05$). However, distance per movement (Table 2) differed significantly between the groups ($F = 7.89$, $df = 2, 16$, $P = 0.004$). Males did not differ from non-gravid females ($P = 0.822$), but both of these groups were significantly higher than gravid females ($P_{\text{M vs GF}} = 0.003$; $P_{\text{NGF vs GF}} = 0.04$).

Another view can be had by calculating the percentage of relatively short (≤ 50 m) movements: 43%, 48%, and 70% for males, non-gravid and gravid females, respectively ($\chi^2 = 27.36$, $df = 2$, $P < 0.05$). Conversely, long movements (≥ 400 m) occurred in both males (5%) and non-gravid females (7%), but were completely absent in gravid females ($\chi^2 = 15.99$, $df = 2$, $P < 0.05$).

Maximum distance from the den that individuals moved after egress, as measured in a straight line (i.e., ignoring meanderings and retracings), never exceeded 812 m (Table 2), with this score trending towards significance among the groups ($F = 3.449$, $df = 2, 16$, $P = 0.058$). Males did not differ from non-gravid females ($P = 0.400$), but the maximum distance traveled between males and gravid females was approaching significance ($P = 0.051$), suggesting that males traveled farther from hibernacula than gravid females. While the two groups of females did not differ significantly ($P = 0.617$), non-gravid and gravid female data combined with males showed a significant difference between sexes ($F = 6.029$, $df = 1, 16$, $P = 0.026$), further indicating that males moved significantly farther from dens than females overall.

Body condition.—Residuals for Colorado and Wyoming snakes were significantly different for males (mean_{co} males = 35.1 ± 24.4 ; mean_{wy} males = -56.3 ± 8.0 ; $t = 3.55$, $df = 34$, $P < 0.05$), but not for females (mean_{co} females = 24.2 ± 32.5 ; mean_{wy} females = -31.3 ± 18.6 ; $t = 1.48$, $df = 22$, $0.10 > P > 0.05$). Because the difference between females from the two populations was of marginal significance, we cast the data into a 2×2 ANOVA (sex \times population) to determine if an interaction existed between sex and population. The main effect for population was significant ($F = 15.96$, $df = 1, 56$, $P < 0.05$), whereas neither the main effect of sex nor the interaction was significant (both F 's < 1.0 , $P > 0.05$). As a further test using a non-parametric method, we applied a 2×2 chi-square, focusing on the number of rattlesnakes from each population and sex that had negative residuals (Colorado males 6 of 18, Wyoming males 17 of 18, Colorado females 4 of 12, Wyoming females 8 of 12). Again, the main effect of population was significant ($\chi^2 = 15.18$, $df = 1$, $P < 0.05$), but neither the main effect of sex ($\chi^2 = 1.13$, $df = 1$, $P > 0.05$), nor the interaction ($\chi^2 = 1.11$, $df = 1$, $P > 0.05$) was significant. All analyses confirm that Colorado males had

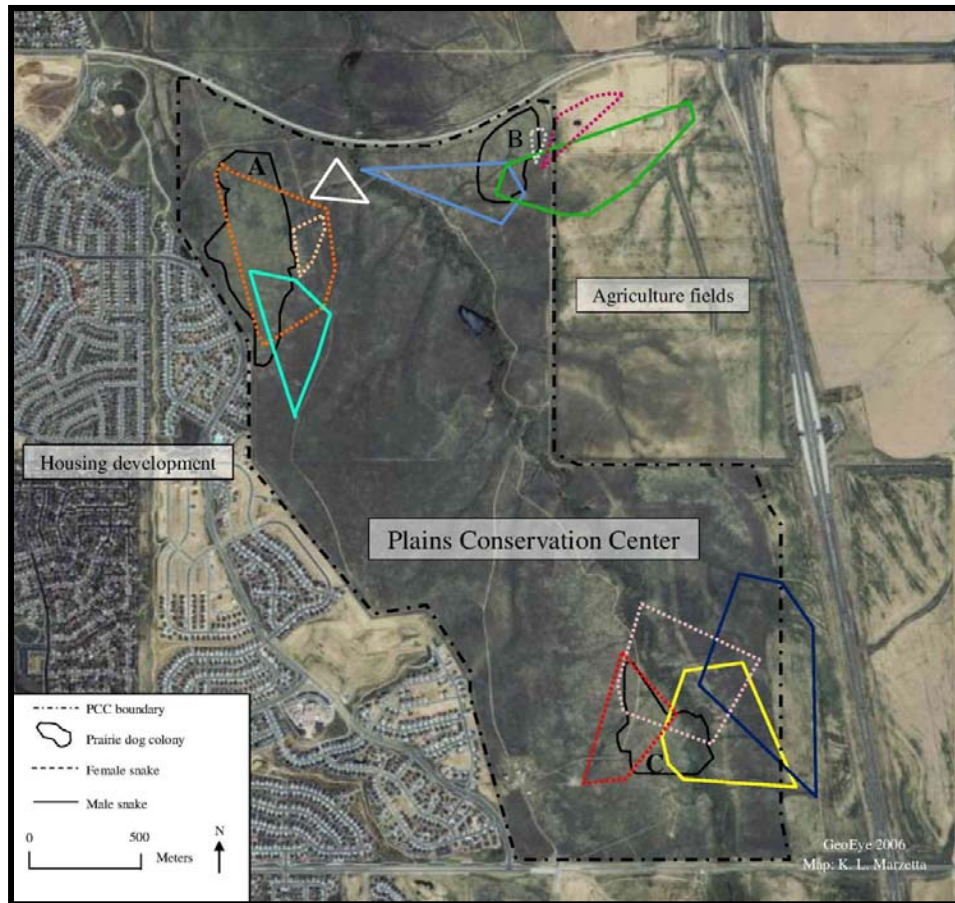


FIGURE 3. Map of the Plains Conservation Center in Arapahoe County, Colorado, USA and home ranges of *Crotalus viridis* relative to three Black-tailed Prairie Dog colonies. For simplification, home ranges of two males and two females per prairie dog colony are illustrated. Active colony boundaries are illustrated with black polygons. Although some home ranges appear to not intersect prairie dog colonies, these ranges exist within areas of abandoned burrows outside of active colony boundaries.

greater mass than Wyoming males. Residuals for Nebraska and Wyoming male rattlesnakes also were significantly different (mean_{ne} males = 46.1 ± 14.1, mean_{wy} males = -40.7 ± 7.9; $t = 5.38$, $df = 34$, $P < 0.05$), whereas females did not differ significantly (mean_{ne} females = 22.6 ± 16.1, mean_{wy} females = -16.9 ± 18.5; $t = 1.61$, $df = 22$, $P > 0.05$). When we recast these data into a 2 × 2 ANOVA, the population difference was robust ($F = 47.68$, $df = 1, 56$, $P < 0.05$), while the sex main effect ($F < 1.0$, $P > 0.05$) and the interaction were not significant ($F = 5.54$, $df = 1, 56$, $P > 0.05$). Analysis by Chi-square tests confirmed the difference between Wyoming and Nebraska snakes ($\chi^2 = 13.16$, $df = 1$, $P < 0.05$), the absence of a main effect of sex ($\chi^2 = 0.92$, $df = 1$, $P > 0.05$), and the absence of an interaction ($\chi^2 = 1.72$, $df = 1$, $P > 0.05$). Residuals for Colorado and Nebraska male snakes (mean_{co} males = 299.4 ± 64.9, mean_{ne} males = 233.4 ± 73.0; $t = 0.67$, $df = 34$, $P > 0.05$) and females

(Mean_{co} females = 66.3 ± 113.2, mean_{ne} females = -33.0 ± 106.8; $t = 1.25$, $df = 22$, $P > 0.05$) were not significant. A 2 × 2 ANOVA revealed no significant effects (all P 's > 0.05). For Colorado males, four of 18 had negative residuals, while seven of 18 Nebraska males had negative residuals; seven of 12 Colorado females and six of 12 Nebraska females had negative residuals. Chi-square analysis revealed no significant effects (all P 's > 0.05). No significant differences were found between Colorado females and Wyoming or Nebraska females. When these groups were pooled with their respective males in ANOVA and Chi-square analysis, the population difference remained robust.

DISCUSSION

Despite the relatively large area that PCC encompasses, our rattlesnakes only used an estimated 37% of total

TABLE 2. Seasonal movement data of *Crotalus viridis* at PCC. Snakes used were 2 non-gravid (NG) females, 3 gravid (G) females, and 8 males in 2005; 2 (NG) females, 2 (G) females, and 2 males in 2006. Maximum distance from den measured as straight-line distance. Home ranges determined by 100% MCP. Values shown are means \pm 1 SEM.

	Home range (ha)	Days tracked per season	Number of movements	Movements per track day	Total distance traveled (m)	Distance per movement (m)	Maximum distance from den (m)
Males (n = 10)	17.8 (3.2)	41.9 (5.0)	31.0 (4.5)	0.7 (0.0)	3710.0 (675.3)	115.9 (13.0)	568.2 (46.9)
Females (NG) (n = 4)	18.0 (5.1)	53.8 (8.7)	35.3 (3.0)	0.7 (0.1)	3646.9 (181.8)	104.5 (4.3)	437.9 (115.2)
Females (G) (n = 5)	9.2 (4.9)	53.2 (5.1)	32.4 (5.4)	0.6 (0.1)	1662.8 (433.5)	47.2 (7.3)	333.8 (63.8)

available short-grass prairie and did not move far enough to interact with snakes from other den colonies. Snakes maintained a close alliance with their respective den colonies while exhibiting short, frequent movements. It is known, however, that *C. viridis* is capable of much longer movements than were seen at PCC (Duvall et al. 1985; Jorgensen et al. 2008). Upon release, six rattlesnakes (2 females, 4 males) quickly moved a short distance (40 m) from their den colonies into anthropogenically disturbed areas outside of PCC, devoid of prairie dogs, but occupied by Plains Pocket Gophers (*Geomys bursarius*). Four of these snakes remained there until they returned to their den colonies in autumn. Four additional snakes (1 female, 3 males) moved from their den colony to a man-made rock pile created for erosion control (outside PCC). The female stayed for her entire gestation period. Despite the nearness of protected short-grass prairie to den colonies within PCC, these snakes seemed to prefer altered habitat, presumably attracted to prey-enhanced zones and artificial refugia. Because pocket gophers are attracted to soils softened by agricultural activities and other anthropogenic processes, colonies of these rodents can become resource-rich areas for snakes and other vertebrates (Vaughan 1961; Connior et al. 2008), providing high humidity, coolness, and ambush sites.

We show for the first time, based upon repeated captures over a four year period of PIT tagged, non-radio-telemetered rattlesnakes, that snakes never moved to other colonies but often moved among burrows within their den colony. This pattern suggests fidelity to a particular colony, but not to a specific burrow within that colony. Because a burrow has 2–3 entrances on average (Hoogland 1995), it is difficult to determine which entrances are connected to individual burrows. Hence, burrow fidelity might have been underestimated. The most important implication of these data is that they categorically reject the first of the two hypotheses we set

out to test; namely, that there would be mixing of rattlesnakes from the three colonies of *C. ludovicianus*.

Home ranges of rattlesnakes overlapped within colonies, but not between them, even though other colonies were within traveling range (total distance traveled by most rattlesnakes exceeded the average distance to other colonies; Fig. 3). Variability in home ranges appeared to be influenced by habitat features, such as pocket gopher colonies and man-made alterations. Home ranges of our snakes were among the higher values reported for *C. viridis* (Macartney et al. 1988; Parker and Anderson 2007). Brown (1990) reported male *C. viridis* activity ranges of 2.0–9.9 ha with a mean of 7.0 ± 1.7 , and female activity ranges of 1.7–6.9 ha with a mean of 4.4 ± 1.3 . These values are much lower than ours (Table 2) because Brown (1990) did not include migratory movements in home range estimates (see Gregory et al. 1987; Jorgensen et al. 2008). In our study, foraging movements crossed and re-crossed migration paths creating MCP's not readily differentiable into migratory and post-migratory areas.

Paths of all snakes became significantly less straight immediately after reaching our criterion (2 days of < 10 m movements) defining the cessation of vernal migration and the beginning of summer foraging. For gravid females, the end of vernal migration meant arrival at appropriate microhabitat for gestation. Mean migration R values of our gravid females were lower than those reported by Graves and Duvall (1993) for gravid females in Wyoming (R = 0.81, n = 3), likely because Wyoming females migrate to established rookeries (Duvall et al. 1985), a feature absent on PCC. Moreover, our gravid females were not found in birthing aggregations as described in other studies of *C. viridis* (Duvall et al. 1985; Graves and Duvall 1993, Holycross 1993, Jorgensen and Nicholson 2007).

Although movements are difficult to compare between

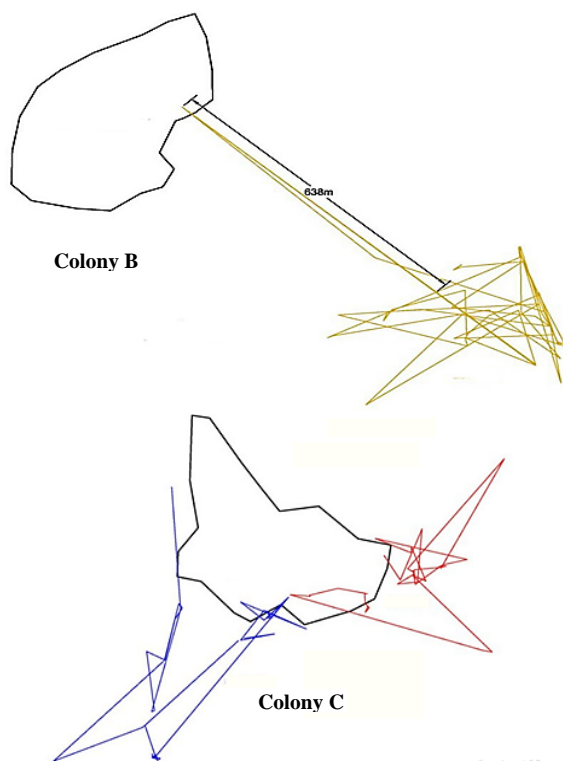


FIGURE 4. Representative individual rattlesnake movements relative to respective den colonies on the Plains Conservation Center. Note: In colony C, there are two different rattlesnakes, denoted by red and blue movement lines.

studies, movements of PCC rattlesnakes per track day were numerically greater than values reported for *C. viridis* (reviewed in Jorgensen et al. 2008), while maximum distance from the den was much less. These differences may be related to particular habitat characteristics of PCC (see below). In addition, two movement patterns appeared to occur in the study. First, 10 snakes moved off the PCC into anthropogenically disturbed areas, some remaining in the areas throughout their active season; second, snakes that remained in the PCC frequently retraced their movements between previously used ambushing sites that were not far apart and not necessarily close to den colonies. Both patterns were consistent with our second hypothesis, which stated that forays considerably beyond den colony boundaries would occur during the foraging season. Such behavior might reduce intraspecific (or, perhaps intra-den colony) competition, considering the competitive situation that would exist if the majority of snakes remained in the immediate vicinity of their respective den colonies. Other potential adaptive consequences include increased resource harvesting efficiency and likelihood of locating mates.

Frequent, short movements made by males and non-

gravid females on PCC may be a function of foraging in an area where prey densities are more concentrated by prairie dog ecosystems (Agnew et al. 1986; Reading et al. 1989; Lomolino and Smith 2003). Moreover, the relatively homogenous distribution of vegetation in short-grass prairie (such as found in Colorado) may reduce the patchy distribution of rodent populations (Duvall et al. 1990). In this context, prolonged prey searches may be unnecessary, instead focusing rattlesnake dispersal in zones within and in close proximity to prairie dog colonies. Similar movements of a Nebraska population of rattlesnakes to ours were found by Holycross (1993). In this study, radio-telemetered rattlesnakes (1 male, 3 females) hibernating in a prairie dog colony were followed after egress and prior to ingress as they moved into sub-habitats peripheral to the colony. Although the data were limited, we calculated that mean total distance traveled, mean distance traveled per day, and mean migratory straightness-of-path R values (4943 m, 96.3 m, and 0.51 m, respectively) were similar to our study. Maps of snake movements were nearly identical to ours, illustrating the ecosystem effect of prairie dog colonies on compacting rattlesnake movements (Fig. 4). Reed and Douglas (2002) and Ashton (2003) found similar movement patterns in canyon habitat with *C. oreganus abyssus* and *C. o. concolor*. In contrast, *C. viridis* in Wyoming shrub steppe/bunch grass zones showed significantly longer foraging movements in response to widely scattered prey distributions (in the absence of prairie dog colonies; Duvall et al. 1985; King and Duvall 1990). An analysis of body condition between rattlesnake populations in Colorado, Wyoming, and Nebraska indirectly supports our supposition that prairie dog ecosystems (with short-grass prairie) may provide comparatively better localized foraging opportunities. Thus, although all females from the three geographical locations were comparable in condition, Colorado and Nebraska male snakes appeared to be in better condition than Wyoming males (the difference mainly due to lower than average mass of Wyoming males); however, Colorado and Nebraska snakes of both sexes were in similar condition, both populations maintaining home ranges inclusive of prairie dog colonies.

Conservation implications.—Prairie dog colonies contribute to increased landscape heterogeneity and grassland biodiversity (Kretzer and Cully 2001), and at least 117 species of vertebrates are known to associate with prairie dog colonies (Kotliar et al. 1999). For example, Northern Grasshopper Mice (*Onychomys leucogaster*) and Northern Deermice (*Peromyscus maniculatus*) are more abundant around prairie dog colonies and may attract Prairie Rattlesnakes (Johnsgard 2005). Home ranges and movements of our rattlesnakes suggest that they are closely tied to the ecology of the

prairie dog ecosystem. In particular, Prairie Rattlesnakes (Kretzer and Cully 2001; Shipley and Reading 2006) and Lesser Earless Lizards (*Holbrookia maculata*; Davis and Theimer 2003) are strongly attracted to prairie dog burrows and favor the shorter, sparser vegetation characteristic of prairie dog colonies. Moreover, numerous other reptiles and amphibians have been found in prairie dog colonies (Clark et al. 1982, Kretzer and Cully 2001, Lomolino and Smith 2003, Shipley and Reading 2006) and are described as having a facultative dependency on colonies.

Perhaps the singular ecological factor in our study site is the absence of rock outcrops and rock crevices necessary for snake hibernacula. Prairie dog burrows become important sources of hibernacula because they provide structurally and thermally stable hibernation environments in soils containing high clay content (Wastell and MacKessy 2011), such as found on the PCC. Although burrows of other rodent species exist, the nature of prairie dog burrows as being spatially fixed and permanent means that they are a principal source of hibernacula that consistently meet the long term physiological needs of snakes in hibernation (Holycross 1993). Further, rattlesnakes in our study site appear to prefer prairie dog burrows with openings to the northwest (pers. obs.), and these elongated, sloping burrows may provide functional advantages for thermoregulation and in-burrow temperature moderation throughout the season into late fall; advantages that could support gravid females, pre-hibernatorial digestion, immune system charging, and other reproductive processes. Alternative rodent burrows, such as that of Plains Pocket Gophers, although numerous and widespread in our study site, may be effective as summer refugia, but not provide the necessary depth required for snakes to avoid freezing in the winter.

Destruction of prairie dog populations through loss of habitat or other causes may result in a cascade of negative changes affecting vegetation and vertebrate fauna associated with colonies, leading to a rapid loss of landmarks and resources important to rattlesnakes. Plague infections can decimate prairie dog populations (Pauli et al. 2006), causing long term degradation of prairie dog ecosystems. For example, burrows may erode and collapse from lack of maintenance by prairie dogs, creating shortages of hibernacula and refugia, and may contribute to the movement of rattlesnakes and other herpetofauna into anthropogenically disturbed areas. Management of prairie dogs frequently involves the application of poisons, which are lethal to rattlesnakes (Travis Taggart et al., unpubl. report) and other non-target organisms.

Rattlesnakes hibernating in prairie dog colonies tend to be concentrated around select prairie dog burrows prior to egress and ingress. This concentration can lead

to over-collection of snakes for commercial purposes and is a potential means for more efficient eradication of snakes (Holycross 1993, Ernst and Ernst 2012). Protection of prairie dogs would mitigate this loss while preserving grassland biotic diversity.

Our work illustrates that *C. viridis* movements in prairie dog colonies differ from rattlesnake movements in non-prairie dog inhabited areas, such as in Wyoming (Duvall et al. 1985), with respect to: (1) amount of available hibernacula; (2) influences of prairie dog activities on a landscape level; and (3) managing for conservation of rattlesnakes by effectively conserving prairie dogs and the short-grass prairie. Further research is needed to examine the response of rattlesnake populations to loss of prairie dogs. These questions remain: Do rattlesnakes move away from dead colonies and then return when the colony is repatriated with prairie dogs? How long do these changes take, and can they be influenced by management practices?

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