

Spatial Ecology and Factors Influencing Movement Patterns of Desert Massasauga Rattlesnakes (*Sistrurus catenatus edwardsii*) in Southeastern Colorado

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The Massasauga Rattlesnake (*Sistrurus catenatus*) occurs from extreme southeastern Canada to northern Mexico, and most populations are highly threatened due to habitat loss and fragmentation. Although their range is reduced from historical levels, they may be locally abundant in appropriate habitat. We studied movement patterns, home range and core activity centers, habitat use, and prey abundance in a robust population of Desert Massasauga Rattlesnakes (*S. c. edwardsii*) in southeastern Colorado by radiotracking 36 snakes over four active seasons (May–October). In the spring, snakes made long-distance directed movements (mean = 1.89 km) from the hibernacula (shortgrass, compacted clay soils) to summer foraging areas (mixed-grass/Sand Sagebrush, sandhills). Summer activity was characterized by short distance non-directional movements, and snakes were most often observed at the base of Sand Sagebrush (*Artemisia filifolia*). Home ranges and core activity centers were significantly larger for males than for females, but daily movements, total distance moved, and range length did not differ significantly between sexes. Prey base surveys indicated a significantly higher abundance of both rodents and lizards in summer foraging grounds than at hibernation sites. Snakes returned to the hibernaculum area in October and appeared to hibernate individually in rodent burrows. Migration patterns exhibited by *S. c. edwardsii* are likely resource driven, with the migratory movements observed in the spring resulting in utilization of summer foraging habitat with more abundant prey. Conversely, hibernacula with greater thermal and structural stability in the shortgrass habitat (perhaps due to the compacted clay soils versus loose sandy soils) favor migratory return for torpor in the fall. At present, the main populations in Colorado occur far from developing regions in the state, but due to habitat loss and fragmentation resulting from projected agricultural expansion and urbanization, these populations may be threatened in the future.

THE elucidation of movement patterns and their relation to resource and habitat utilization data can provide insights regarding an animal's ecological niche. Movement increases an animal's risk of predation and incurs energetic costs and therefore should occur primarily in response to environmental challenges or resource needs (Gregory et al., 1987; Bonnet et al., 1999); in some cases, these challenges or needs may drive directional, migratory movements (Dingle, 1996). In snakes, directed movement is usually following a straight-line path in search of patchily distributed potential mates or demes of prey animals (Duvall et al., 1985, 1990) or moving between hibernacula and summer activity ranges (Landreth, 1973; Gregory and Stewart, 1975). An understanding of an animal's habitat requirements, activity patterns, and spatial distribution is critical for making informed ecological management decisions (Weatherhead and Prior, 1992; Durbian et al., 2008). Further, variation in resource dispersion and other environmental factors can promote widely disparate movement patterns among animal populations (Reed and Douglas, 2002). At present, however, there have been no reports on the spatial ecology of the Desert Massasauga (*Sistrurus catenatus edwardsii*).

In Colorado, *S. c. edwardsii* is associated with mesic to xeric grasslands across much of the southeastern portion of the state (Smith et al., 1965; Mackessy et al., 1996; Montgomery et al., 1998; Hobert et al., 2004; Mackessy, 2005) and is currently considered vulnerable to extirpation in many parts of its historical range (Hobert et al., 2004; Anderson et al., 2009). *Sistrurus c. edwardsii* occurs in the southwestern United States (New Mexico and Texas) as well

as disjunct populations in Colorado, Kansas (Hobert, 1997), Arizona (Holycross and Douglas, 1996; Holycross, 2003), and in Coahuila and Nuevo Leon, Mexico (Stebbins, 1985; Hammerson, 1999). Listed as a protected species in Arizona and a species of special concern in Colorado, it is unprotected in other parts of its range. Several populations in Colorado contain the highest snake densities and abundance known for this species, and in these areas *S. c. edwardsii* are also the most common snakes (Mackessy, 2005). However, due to habitat loss and fragmentation resulting from agricultural expansion and urbanization (Greene, 1997), they are likely to become increasingly threatened in the future.

Our primary objective was to investigate the spatial ecology and factors influencing movement patterns of *S. c. edwardsii* in southeastern Colorado to address conservation needs for this subspecies. We report home ranges (100% minimum convex polygons and 95% kernel density), core activity centers (50% kernel density), range length, total distance moved, daily movement, habitat use (above/below ground, microhabitat associations), prey base availability, and the significance of directional movement during migration.

MATERIALS AND METHODS

Study site.—The study area comprised approximately 40,000 hectares on a private ranch (1380 m to 1470 m elevation) in southeastern Colorado, divided along a north/south axis by a dirt road. East of the road, the area is characterized by gently sloping grass-stabilized sandhills and

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loose sandy soils. The dominant vegetation in the sandhills consists of a typical mixed-grass prairie association: Blue Grama Grass (*Bouteloua gracilis*), Buffalo Grass (*Bouteloua dactyloides*), Sand Sagebrush (*Artemisia filifolia*), and dense stands of Bluestem Grass (*Andropogon* sp.). West of the road, the area slopes downward to a small drainage, oriented in a N-NW to S-SE direction, which roughly parallels the dirt road. Immediately east and west of this drainage, the soil is loamy/dense (also called hard-pan due to denser soils) and the vegetation consists of a typical shortgrass prairie habitat: Grama Grass, Buffalo Grass, and Prickly Pear Cactus (*Opuntia* sp.). The hibernaculum area is located approx. 100 m east of the drainage and is within this same soil/vegetation type; hibernacula consist of rodent burrows as well as sink-hole openings which appear to lead to deep, perhaps interconnected cavities. This study area was selected for three reasons. First, this area has been identified as supporting the largest known population of *S. c. edwardsii* in the state (Hobert, 1997; Mackessy, 2005), and we were allowed access to the property. Second, *S. c. edwardsii* in this area show a distinct pattern of migratory movements (west to east, and back), facilitating high capture and recapture rates. Third, the study site experiences only modest impact by cattle ranching, because the owners implement rotational grazing and thus avoid detrimental effects of over-grazing on occupied snake habitat.

Radiotelemetry.—Radiotelemetry of 36 *S. c. edwardsii* was conducted from May through October in 1997–1998 ($n = 12$) and 2005–2006 ($n = 24$) using radios obtained from Holohil Inc., Ontario, Canada (1997–1998 only; model BD2GI, 1.6 g, rated lifetime = 11 weeks), AVM Instrument Co., Livermore, CA (2005; model SM1, approx. 3.5 g, rated lifetime = 12 weeks), and Advanced Telemetry Systems (ATS), Isanti, MN (2005–2006; model R1675, 1.9 g, 20 weeks, and model R1685, 2.8 g, 26 weeks). Radioed snakes were located in the field using an AVM Model LA12-Q portable receiver (148.0–149.9 kHz) with a Yagi 3-element antenna (Custom Electronics, Urbana, IL).

All *S. c. edwardsii* encountered in the study area were captured during their spring emergence, summer foraging, and fall ingress movements by conducting a combination of road surveys, hibernaculum searches, and general habitat searches. We captured snakes via snake hooks and drift fence-funnel traps. We injected all snakes with PIT tags (Avid Inc., Norco, CA) for future identification. Radios (148.0–149.9 MHz) were implanted at the UNC Animal Facility using well-established procedures (Reinert and Cundall, 1982) and isoflurane anesthesia as approved by the UNC-IACUC (protocol #0503). Due to the small size of *S. c. edwardsii*, only adults greater than 50 g body mass were selected for radio implantation, and all transmitter/snake body mass ratios were less than 0.05. All radio-implanted snakes were given 2–3 days to recover from surgery before release. Snakes were released at the site of capture and located daily (when possible) throughout the season.

For all telemetry locations, a GPS unit (1997–1998: Scout II GPS unit, Trimble, Sunnyvale, CA; 2005–2006: Garmin E-trex series, Vista C, Garmin International, Inc., Olathe, KS) was used to record location (UTM: NAD 83), elevation, date, and time. In 1997 and 1998 all GPS data were uploaded to an IBM Pentium computer and differentially corrected (expected to be less than 2 m from actual locations; Trimble Pathfinder Manual, 1996. Geo Explorer II operations

manual. Trimble Navigation Limited, California) and plotted utilizing Pathfinder software (Trimble, Sunnyvale, CA) and the CompassCom base station data available via the Internet. In 2005/2006, all snake locations were recorded with an accuracy of ± 3 meters. Distance and bearing from last movement were also noted (aiding in locating snakes out of signal range).

Data were analyzed using ESRI Geographic Information System (GIS) software (ArcView GIS 3.3 and ArcGIS 9.2) equipped with the Animal Movement Extension (Hooge and Eichenlaub, 1997), which was used to calculate core area, activity area, and significance of migratory travel and direction (circular statistics). All other statistical analyses were calculated using Microsoft Excel or SPSS (Chicago, IL). Means were reported (± 1 standard error), and movement parameters were analyzed using t-tests. Following suggestions of Reinert (1992), the following parameters were also measured: mean distance moved per day (total distance moved divided by the total number of days monitored), range length (linear distance between two furthest location points), total distance moved (sum of all linear distances between locations), and distance between subsequent year hibernaculum sites, used by Patten (2006) to define site fidelity. We also analyzed differences between male and female movement data and home range sizes (t-test).

Home range was calculated using the two most widely used methods: the 100% minimum convex polygon (MCP), and the fixed kernel density estimator (a probability of utilization distribution measurement). The MCP method does not take into account the number of occurrences at specific locations (highly vs. rarely used areas), nor does it allow for any areas outside of the polygon to be included in the activity area. In addition, MCP often significantly overestimates the area used by an animal (Reed and Douglas, 2002). The fixed kernel density estimator is a nonparametric measurement of the activity area of an animal that is constructed using a probabilistic model (Worton, 1989). Although the accuracy of kernel densities for home range estimates has been questioned (Row and Blouin-Demers, 2006), because it is commonly provided in snake spatial ecology studies, we include it here for comparative purposes. The Animal Movement extension of ArcView implements a fixed kernel with the smoothing factor calculated via least-squares cross-validation (LSCV), which is widely considered the most robust technique (Seaman and Powell, 1996). Using the fixed kernel density estimator, the 95% and 50% probability estimates that an individual will be in a given part of its activity range were calculated (Powell, 2000). The 95% fixed kernel was used to estimate the activity range and the 50% fixed kernel was used to delineate the core area (Tiebout and Cary, 1987).

We analyzed migration paths and summer foraging movements exhibited by adult *S. c. edwardsii* via circular statistics (Batschelet, 1981) to determine travel directions (from sequential animal location points) and the significance of straightness and direction of travel. We calculated the mean angle of movement (compass bearing), angular concentration (r : spatial concentration of movement directions on a compass circle; possible r -value = 0 to 1, where 1 = all angles are the same), and angular deviation (s : equivalent to standard deviation in linear statistics). Z -values were used to compare a sample to a standard normal deviate (standard normal distribution, with $\mu = 0$ and $\sigma = 1$), though they can be defined without assumptions of

normality. Movement segments (movement between daily observed locations) in the movement path during the spring and fall, where snakes made long-distance movements over a short period of time (15 April–1 June and 15 August–15 October), were analyzed separately from the movement path during the summer, where snakes made short distance movements over a longer period of time (1 June–15 August). These dates were based on field observations of over 750 PIT-tagged non-radioed *S. c. edwardsii* and on the average movements of radioed snakes.

At each snake location, the general habitat description (road side, erosion “blow-out” of sandhills, shortgrass prairie, Sand Sagebrush/mixed grass, etc.) was noted for approx. 10 m around the snake. We recorded the microhabitat in which the snake was observed as Sand Sagebrush, grass, cactus, or other (bare ground, uncommon forbs). In addition, glass mercury thermometers ($\pm 0.5^\circ\text{C}$; Weksler, Boca Raton, FL) were used to measure ambient temperature (shaded, 1 m above ground), microhabitat temperature (shaded, 10 cm above ground, as close as possible to the snake’s location), and substrate temperature (shaded, 1 cm under the substrate, as close as possible to the snake’s location). Temperature data were then correlated with surface vs. underground activity/occurrence. All Universal Transverse Mercator (UTM) coordinates for radiotelemetry locations were overlain onto National Agriculture Imagery Program maps and Colorado Vegetation Classification Project maps (provided by the Colorado Division of Wildlife), and Department of Soil Conservation Maps (USDA, 1965; USDI, 1967) of the study site. Individual snake locations and Imagery maps were employed to define habitat use.

Prey base surveys.—Surveys were conducted to determine whether differences in relative prey abundance existed between the hibernaculum habitat (shortgrass/hardpan) and that of summer foraging grounds. In 1997 and 1998, only rodent surveys were conducted in the shortgrass habitat and in the mixed-grass prairie habitat (summer foraging grounds); in 2005 and 2006, surveys were conducted for both lizard and rodent species in both areas. For rodent surveys, 40 Sherman traps (with cotton balls for insulation) were baited with oatmeal and set at 10 m intervals (40 m \times 100 m grids) in both habitat types. Trapping was conducted simultaneously in both habitat types for five continuous days during each of three periods (early summer, mid-summer, and fall). For lizard surveys, 500 m continuous line transects with visual observations were conducted throughout the season at randomly chosen locations in the two habitat types. For each habitat type, time of year and time of day were equally represented. At each location, the observer walked continuously for 500 m in the same direction, recording all lizard species encountered within approximately 2 m of the transect line. A hand-held GPS unit (Garmin E-trex series, Vista C) was used to determine the distance walked.

Rodent and lizard relative abundance estimates in the summer and hibernaculum habitats were analyzed using Chi-square tests (presence/absence). Rodent population estimates were determined using the closed population capture–recapture model in the program MARK (White and Burnham, 1999). Within the model, the data type used was closed captures (Otis et al., 1978), which are based on full likelihood parameterization with three types of parameters;

p is the probability of first capture, c is the probability of recapture, and n is abundance.

RESULTS

General observations.—All 36 radioed snakes were included in analysis of habitat use and activity variables. However, only snakes that were monitored for a full active season (May to October; $n = 12$) were included in analysis of movement and home range; because the 1997–1998 sample included only two snakes, we did not analyze these data sets separately. For the 12 individuals that were radiotracked for an entire active season, the number of tracking days per snake averaged 143.1 and ranged from 104–168 days (Table 1). The number of relocations for radiotelemetered snakes averaged 85.3 and ranged from 46–102. Maximum signal distance was approx. 100 meters, and this maximum was negatively affected by power lines, electric fences, and occasionally weather conditions such as high winds. Eighteen of the 36 radiotransmitters failed between two and 12 weeks, and three snakes were lost to predators (two to Long-tailed Weasel, *Mustela frenata*; one to an unknown predator).

Movement and home range.—Snake daily movements for the entire season (April–October) averaged 32.3 m (range 0–493 m), with no significant difference between male and female average daily movements (Table 1; $P = 0.104$, t-test). Due to small sample size, gravid (4) and non-gravid (1) females were not analyzed separately. Further, the home ranges for the non-gravid female vs. gravid females were similar in size. In the spring (15 April–1 June), snakes made long-distance linear movements (Fig. 1) to the east, from the hibernaculum (shortgrass prairie/compact clay soils) to summer foraging areas (mixed-grass/Sand Sagebrush and sandhills); the transition between these habitats is very abrupt in this part of Colorado. In late summer/early fall (15 August–15 October) snakes reversed these long-distance linear movements back to the hibernaculum; mean daily movement during spring and fall migration was 89.7 m, and total migratory movement averaged 1.89 km (range 1.02–3.46 km). There was no significant difference between male and female movement length. Summer activity (1 June–15 August) was characterized by short-distance movements ($\bar{x} = 15.3$ m). The total distance moved throughout the season averaged 4527 m (range 3156.8–7112.3 m). There was no significant difference found between males and females for total distance moved throughout the season (Table 1) or during the summer foraging period. There was an obvious difference in summer foraging movements between males and gravid females shortly before parturition. For approximately three weeks prior to giving birth, females became highly stationary at birthing sites, basking near (or just inside) the same rodent burrow. Females left the birth site five to seven days ($n = 6$; $\bar{x} = 5.7$) after giving birth.

Average ambient temperature when snakes were found above ground was 26.4°C (range 12 – 44°C). During the entire active season, when snakes were observed above ground, they were most often observed in close association with Sand Sagebrush (50.3% of all above-ground observations; total $n = 951$). When ambient temperatures were higher (32.4°C , $n = 586$, SE: 0.35), snakes were observed underground in subterranean refugia (typically beneath Sand Sagebrush). When migrating, snakes moved at lower ambient temperatures (22.5°C , $n = 133$, SE: 0.27) than

Table 1. Individual and Means (± 1 SE) for Movement and Home Range Parameters for 12 *S. c. edwardsii* in Southeastern Colorado. Home range is reported as 100% MCP and 95% KD, and core activity area is reported as 50% KD. * Indicates significant difference between males and females ($P \leq 0.05$). 97/98—two males tracked during 1997–1998.

Snake ID	# Days tracked	# Relocations	Mean dist. moved/day (m)	Range length (km)	Total distance (m)	100% MCP (ha)	95% KD activity area (ha)	50% KD core area (ha)
371 F (Gravid)	124	84	27.6	1.61	3424.8	17.18	24.68	4.81
551 F	168	100	35.0	2.13	5881.0	30.66	37.92	7.51
731 F (Gravid)	166	98	20.3	1.93	3373.9	31.21	86.39	9.48
661 F (Gravid)	139	79	22.7	1.51	3156.8	20.85	34.31	4.38
452 F (Gravid)	112	99	30.9	1.85	3458.6	23.81	12.53	2.69
Mean F (SE)	141.8 (30.9)	92 (9.8)	27.31 (7.40)	1.81 (0.31)	3859.2 (1410.8)	24.74 (7.60)	39.17 (34.97)	5.77 (3.35)
521 M	165	101	27.6	1.84	4551.0	29.69	98.12	18.37
581 M	168	97	25.7	1.02	4315.2	15.21	25.14	5.51
612 M	165	102	33.7	1.16	5556.1	26.75	125.29	43.41
632 M	104	71	44.7	2.24	4647.0	65.32	174.79	47.37
691 M	117	76	42.8	2.23	5003.9	82.92	166.59	30.39
0A9 M (97/98)	137	70	51.9	3.46	7112.3	108.89	373.41	88.23
0B2 M (97/98)	152	46	25.3	1.69	3839.9	51.36	86.09	22.54
Mean M (SE)	144.1 (23.6)	80.4 (20.7)	35.94 (9.79)	1.95 (0.76)	5004.0 (992.7)	54.31 (31.19)	149.92 (102.56)	36.55 (24.94)
Mean both sexes	143.1	85.3	32.3	1.89	4526.7	41.99	103.77	23.72
P-value F:M (t-test)	—	—	0.104	0.677	0.106	0.061	*0.039	*0.023

during movements within the summer foraging grounds (26.1°C , $n = 109$, SE: 0.60). A two-tailed t-test showed a significant difference between ambient temperatures during migratory (cooler) and summer (warmer) movements ($P < 0.05$; $t_{\text{crit}} = -1.96 > t_{\text{obs}} = -7.12$), though operative body temperatures of snakes are likely higher than ambient (Kapfer et al., 2008).

Based on Colorado Vegetation Classification Project maps and field observations, there is an obvious and sudden vegetative compositional difference between the shortgrass habitat at the hibernacula and the mixed-grass habitat of the

summer foraging grounds. These vegetation differences also correlate with differences in dominant soil types (according to Department of Soil Conservation Maps; USDA, 1965; USDI, 1967). Areas used by snakes in the late spring and summer are typified by valent/sandy soils, in contrast to areas used for hibernation in early spring, fall, and winter, which are alkaline/loamy type (compacted clay) soils. The transition from one vegetation type to the other is abrupt and occurs over a very short distance, so radioed snakes were observed in either one or the other type, with no snakes observed in compacted clay/shortgrass in late spring/summer or in sandy soils during fall/winter.

Average distance between spring emergence site and fall ingress sites, a measure of hibernation site fidelity, was 126.2 ± 94.3 m ($n = 6$; range = 7.3–223.9). A summary of snake movement patterns (Fig. 2) demonstrates year to year consistency in migration paths of *S. c. edwardsii* to and from hibernation sites. Radioed *S. c. edwardsii* ($n = 15$) utilized rodent burrows as hibernaculum sites, and they appeared to occupy them individually. However, within 50 meters of individual *S. c. edwardsii* hibernacula, numerous large “sinkhole” openings occur, and multiple snake species were observed entering these sites in the fall, exiting in the spring and basking in the immediate vicinity shortly before ingress and following egress. Other snake species observed at hibernacula sites included Prairie Rattlesnakes (*Crotalus viridis viridis*), Coachwhips (*Masticophis flagellum*), Racers (*Coluber constrictor*), Milk Snakes (*Lampropeltis triangulum*), Western Hognosed Snakes (*Heterodon nasicus nasicus*), Plains Garter Snakes (*Thamnophis radix*), and Bull Snakes (*Pituophis catenifer*). Further characteristics of this mixed assemblage hibernaculum will be addressed in a separate report.

Home range estimates (Table 1) averaged 42.0 ha (range = 15.2–108.9 ha) for MCP and 103.8 ha (range = 12.5–373.4 ha) for 95% KD. Male MCPs tended to be larger than female MCPs, but no statistically significant difference was found ($t[11] = 2.201$, $P = 0.061$). The 95% KD home range

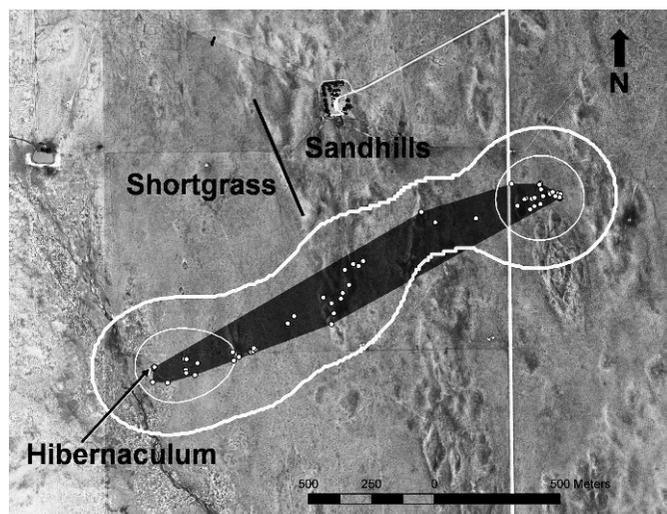


Fig. 1. Representative seasonal activity range, home range, and core use areas for snake 521 overlain on a satellite image of the habitat. Small white circles indicate individual localities; minimum convex polygon is shown as a black transparency (=29.7 ha), 95% activity area (95% KD) is shown as a thick white line (=98.1 ha), and 50% core areas are shown as thin white ovals (=18.4 ha).

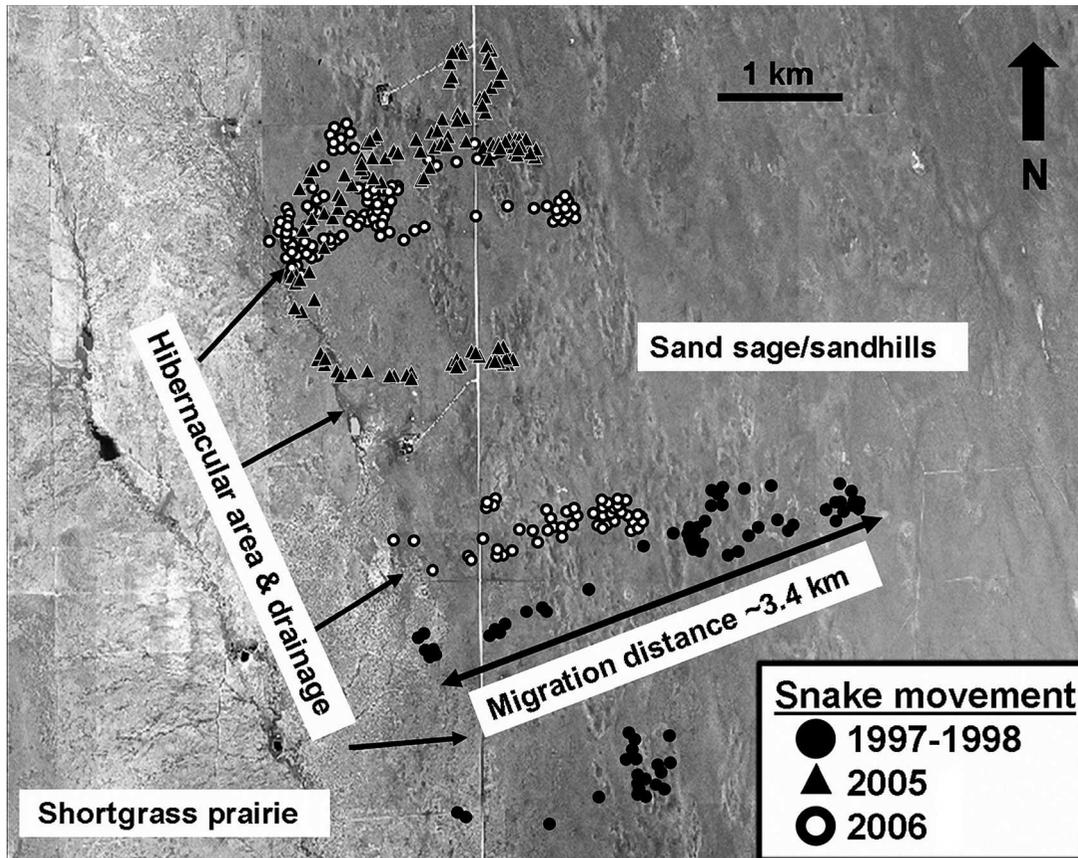


Fig. 2. Combined full season movement data for 12 *S. c. edwardsii* in southeastern Colorado overlain on a satellite image of the habitat. Symbols indicate individual observations.

indicated that male home ranges were significantly larger than female home ranges ($t[11] = 2.201$, $P = 0.039$); however, because most (4/5) of our female data are based on gravid snakes, it is possible that non-gravid females could have home ranges comparable to those of males. Activity center estimations (50% KD) averaged 23.7 ha and ranged from 5.5–88.2 ha, and male activity centers were significantly larger than female activity centers ($t[11] = 2.201$, $P = 0.023$). A typical home range (MCP and 95% KD) and core activity center (50% KD) map is shown in Figure 1.

Circular statistics (Batschelet, 1981) indicated a significant degree of directionality for seasonal movements to and from hibernacula ($n = 10$; Table 2). The average Z-value was 8.62 (range 4.4–13.5; $Z > 2.0 = \text{significant}$, $P < 0.05$). The average r-value (angular concentration, or average angle of all movement segments) was 0.79 (range 0.51–0.92; possible r-value = 0 to 1, where 1 = all angles are the same), demonstrating that movements were linear and directional. Conversely, the same analysis of summer foraging movements of *S. c. edwardsii* ($n = 10$) indicated little to no degree of directionality of movement, with an average Z-value of 0.60 and an average r-value of 0.128 (Table 2).

Prey base surveys.—Based on 2340 total trap nights in each area, a significant difference existed (Table 3) in overall rodent abundance between the two habitat types ($\chi^2 = 118.53$; $df = 1$, $n = 163$, $P < 0.01$). Based on 28 500-m transects, a significant difference also existed in lizard abundance (Table 3) between the two habitat types ($\chi^2 = 92.35$; $df = 1$, $n = 104$, $P < 0.01$). Analysis of rodent abundance surveys conducted in 1998 (based on 549 total

trap nights in each area) showed a significant difference in rodent abundance between the two habitat types ($P < 0.05$; $t_{\text{crit}} = 4.032 < t_{\text{obt}} = 5.4$; $df = 4$), with abundance greater in the summer foraging area. In addition, we calculated (using the program MARK) a substantially higher abundance of mammals in Sand Sagebrush/sandhills (summer foraging grounds) as opposed to shortgrass habitat (hibernacula area) for both 2005 and 2006. However, population estimates varied between years: in 2006 population numbers of rodents were greatly depressed (Sand Sagebrush: 23; shortgrass: 2) relative to 2005 (Sand Sagebrush: 141; shortgrass: 65), but abundance was still much higher in Sand Sagebrush habitat.

DISCUSSION

Individual *S. c. edwardsii* in our study area showed very similar trends in annual movement patterns. In the spring, following emergence in late April to early May, snakes made long-distance, directional, linear movements to the east, from hibernacula to summer foraging areas (Fig. 1). During the summer, in July and August, average daily movements decreased significantly and were non-directional. In the fall, in September and October, snakes reversed the spring movements and made long-distance linear movements back to hibernacula. This bimodal movement pattern represents migration between the hibernation area and summer habitat and is similar in some respects with movement patterns reported in other populations of massasaugas (Eastern Massasauga, *Sistrurus catenatus catenatus*: Reinert and Kodrich, 1982; Johnson, 2000; Western Massasauga,

Table 2. Analysis of Spring and Fall Migration Paths for Ten *S. c. edwardsii* Using Circular Point Statistics (Z-values > 2.0 = significant, $P < 0.05$, based on angular concentration, r).

Snake ID	# Movement segments	Mean bearing (degrees)	Angular conc. (r)	Angular dev.	Z-value	P-value
Spring migration						
551	12	18.97	0.918	23.66	10.1	<0.001
A9	9	19.29	0.912	24.79	7.5	<0.001
521	13	24.47	0.869	36.38	8.7	<0.001
612	12	58.75	0.876	29.52	9.2	<0.001
632	20	64.08	0.721	46.34	10.4	<0.001
mean	13.2	37.11	0.859	32.14	9.18	<0.001
Fall migration						
731	14	192.14	0.814	33.82	9.3	<0.001
452	18	199.52	0.867	30.61	13.5	<0.001
661	19	200.61	0.511	67.84	4.7	<0.001
371	8	203.93	0.744	44.06	4.4	<0.001
691	21	238.73	0.633	54.82	8.4	<0.001
mean	16	206.99	0.714	46.23	8.06	<0.001
Summer foraging movements						
612	31	94.75	0.110	120.52	0.2	>0.9
521	34	18.76	0.058	136.67	0.1	>0.9
551	57	92.42	0.118	118.35	0.5	>0.9
731	52	247.94	0.260	94.03	1.4	0.437
371	63	80.18	0.160	109.68	0.6	0.546
452	68	179.29	0.176	106.83	1.6	0.279
661	66	204.08	0.052	139.54	0.1	>0.9
581	47	9.43	0.093	124.90	0.3	0.728
295	49	161.40	0.165	108.78	1.0	0.279
376	66	71.78	0.087	126.49	0.4	>0.9
mean	53.3	116.00	0.128	118.58	0.63	0.677

Sistrurus catenatus tergeminus: Patten, 2006). However, the average range length (1.89 km) and total distance moved during the active season (4.5 km) for *S. c. edwardsii* are greater than those for both *S. c. catenatus* (Marshall et al.,

Table 3. Relative Abundance of Small Mammals and Lizards by Habitat Type (2005–2006). * Total trap nights = 2340 per habitat type; numbers include only unique individuals. † Abundance based on 28 500-m transects/habitat type.

Species	Sand	
	sagebrush	Shortgrass
Mammals*		
<i>Peromyscus maniculatus</i>	4	46
<i>Perognathus flavescens</i>	23	0
<i>Perognathus flavus</i>	0	2
<i>Dipodomys ordii</i>	95	1
<i>Onychomys leucogaster</i>	26	2
<i>Spermophilus spilosoma</i>	4	0
<i>Spermophilus tridecemlineatus</i>	0	3
<i>Neotoma cinerea</i>	2	0
Lizards†		
<i>Holbrookia maculata</i>	33	0
<i>Aspidoscelis (Cnemidophorus) sexlineatus</i>	30	1
<i>Sceloporus undulatus</i>	38	2

2006) and *S. c. tergeminus* (Patten, 2006). There was no significant difference found in movement parameters between male and female *S. c. edwardsii*, despite the fact that most females in our study were gravid. The lack of a sex-biased difference is consistent with reports on *S. c. catenatus* (Reinert and Kodrich, 1982) and *S. c. tergeminus* (Patten, 2006); however, in these other studies, gravid females did move shorter distances than non-gravid females, and this may also be true of *S. c. edwardsii* in our population.

Home ranges and core activity centers, as well as range length, of *S. c. edwardsii* appear to be much larger than those determined from radiotelemetry studies of *S. c. catenatus* in the Midwest and Ontario (Reinert and Kodrich, 1982; Weatherhead and Prior, 1992; Durbian et al., 2008), and recent studies of *S. c. tergeminus* in Nebraska (Patten, 2006). For example, *S. c. edwardsii* at our study site had activity areas which were approximately seven times larger than *S. c. tergeminus* in Nebraska (Patten, 2006), and range length was nearly four times greater. Because the eastern and the western subspecies show considerably shorter range lengths, it is likely that the considerably larger range lengths exhibited by *S. c. edwardsii* during migration (due to distances between the two habitats) account for the difference in activity areas.

In the relatively homogeneous, flat terrain of the short-grass/mixed grass prairie of the study site, there are no topographical features which would otherwise influence direction of movement. Circular statistical analysis of spring and fall movements showed that *S. c. edwardsii* exhibit a

high degree of directionality only during migratory movements between hibernacula and summer foraging grounds. In contrast, the same analysis of summer foraging movement showed extremely low directionality. These findings differ from reports on *Crotalus oreganus abyssus* (Grand Canyon Rattlesnake), which exhibited very low directionality of movements throughout the active season (Reed and Douglas, 2002). Directed movement is typically observed in snakes which are either following a straight-line path in search of potential mates or demes of prey animals which are patchily distributed (Duvall et al., 1985, 1990), or moving between summer foraging habitat and hibernacula (Landreth, 1973; Gregory and Stewart, 1975). This directed straight-line movement prior to and immediately following hibernation appears to be migratory in nature, similar to those seen in migratory bird species (Dingle, 1996): that is, they are stereotypic, occurring during the same periods each year, and they result in the snake moving from one distinct habitat (mixed-grass sandhills) to another distinct habitat (shortgrass prairie). These movements are quite different than foraging and ranging movements in that they occur at lower temperatures (22.5°C), are much longer, and are more directed (i.e., they are straight).

Following fall migration, which typically started around the beginning of September and lasted through early October, *S. c. edwardsii* had a brief ingress, but snakes were observed basking near hibernacula as late as 12 November. *Sistrurus c. edwardsii* commonly utilized rodent burrows as hibernacula and showed a high degree of fidelity toward these hibernation sites, returning to nearly the same location from emergence to ingress. Patten (2006) showed that *S. c. tergeminus* in Nebraska exhibited a similar degree of hibernation site fidelity.

The dominant habitat type used by *S. c. edwardsii* for hibernation is a shortgrass prairie association (adjacent to an intermittent stream), with a dense clay soil type. This differs from the habitat used by *S. c. edwardsii* for summer foraging, which is dominated by upland mixed-grass/Sand Sagebrush association and sandy soils. Similar seasonal habitat shifts have been reported in *S. c. catenatus*. Reinert and Kodrich (1982) described a population of *S. c. catenatus* in western Pennsylvania hibernating in low-lying wet areas and preferring high-dry areas throughout the summer and fall. Seigel (1986) reported a population of *S. c. catenatus* in northwestern Missouri that utilized low-lying wet areas (crayfish burrows) for hibernation, moved to dry upland areas in the summer and fall, and then returned to low-lying wet areas before hibernating.

Surveys to determine differences in relative abundance of rodents and lizards between hibernacula and summer foraging areas indicated a much higher abundance of mammals and lizards in the summer foraging habitat. There was significantly greater prey availability in the sand sagebrush habitat than in the shortgrass habitat, particularly of lizards (*Sceloporus*, *Holbrookia*, *Aspidoscelis*), which make up approx. 59% of the diet of *S. c. edwardsii* (Holycross and Mackessy, 2002). We noted significant differences in overall abundance of small mammals in 2005 and 2006, and this fluctuation in population density is commonly observed among rodents (Bradley et al., 2006; Previtali et al., 2009). Birth of young, which occurred in the Sand Sagebrush habitat, appeared to coincide with emergence of neonate lizards, particularly *Sceloporus undulatus* (late August; Hammerman, 1999; pers. obs.). Considering the relatively small

size of neonate *S. c. edwardsii* (average SVL = 155 mm; mass = 3.97 g; $n = 9$), neonate lizards are likely a primary food item. Similarly, when taking into account appropriate mammal prey size for adult *S. c. edwardsii*, the mixed-grass/Sand Sagebrush habitat had a higher abundance of appropriately sized mammal species such as *Perognathus flavescens*, which constitutes approximately 5% of their diet (Holycross and Mackessy, 2002). Additionally, the availability of suitable cover/shade (small shrubs such as Sand Sagebrush) in shortgrass habitat of the hibernacula was much less than in the Sand Sagebrush habitat of summer foraging grounds; appropriate thermal gradients should be most important during the summer, when temperatures are higher and feeding activity is greatest. Structurally and thermally stable hibernation conditions are likely the limiting resource attracting snakes to the hibernacular area. Results demonstrated the importance of not only summer foraging habitat, but also the winter hibernaculum habitat for the persistence of this diminutive species in Colorado.

The migratory patterns of *S. c. edwardsii* in southeastern Colorado appear to be influenced by seasonal differences/constraints in resource utilization. Summer habitat is exclusively Sand Sagebrush/mixed-grass vegetation in sandy soils, with abundant rodent burrows, and this habitat provides an adequate temperature gradient (cover/shade) for above-ground thermoregulation. Conversely, winter hibernation in the shortgrass prairie (compacted clay soils) should provide more stable hibernacula and contains burrows/sinkholes with better insulative and structural qualities than burrows in the loose sandy soils of the mixed-grass/Sand Sagebrush habitat. Further, Smith (2007. Hibernation ecology of the Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*) in Michigan. Abstracts, American Society of Ichthyologists and Herpetologists Joint National Meeting. St. Louis, MO) noted that *S. c. catenatus* in Michigan appeared to be utilizing hibernacula which access the water table and suggested that temperature stability provided by water (above freezing) was the desirable resource. Although we have no direct evidence that *S. c. edwardsii* at our site are exposed to water during hibernation, the water table at the hibernacular site is very shallow, and most snakes recently emerged from hibernation were covered in mud (pers. obs.). Observations of hibernating *S. c. edwardsii* in captivity also suggested that standing water is important during winter, and snakes spent extended periods partially immersed in water bowls (Greene, 1997). In contrast, in the sandhills habitat favored by *S. c. edwardsii* during the active foraging season, the water table is much deeper, and standing water is highly transient at best. It is possible that utilization of a damp or semi-aquatic refugium during hibernation is a shared characteristic among Massasaugas, even in the generally more xeric western habitats frequented by *S. c. edwardsii*.

The greatest constraint in conservation planning for snakes is the fundamental lack of basic biological information for most species (Dodd, 1987, 1993; Reinert, 1993; Greene, 2005), and implementing a conservation program without regard to or in ignorance of the specific biological constraints on a given species has little chance of success (Dodd and Seigel, 1991; Scott and Seigel, 1992). Since 1995, in southeastern Colorado we have documented over 1,000 locality records of *S. c. edwardsii*, PIT-tagged approximately 900 snakes, and shown that several populations in Colorado appear to be relatively large and stable (Mackessy, 2005; this

study). Because populations of *S. c. edwardsii* elsewhere are either poorly known (Texas, New Mexico, and Mexico) or in decline (Arizona), the Colorado populations are particularly important to the continued persistence of this diminutive species. By extensively monitoring a well-documented population of *S. c. edwardsii* in southeastern Colorado, we have made significant progress addressing the many aspects of basic biology/ecology which are fundamental for future conservation approaches. Efforts are underway to facilitate the establishment of a conservation easement to protect the hibernacular area, which benefits a variety of amphibian and reptile species, as well as the summer foraging habitat.

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