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Ecological Significance of Movements and Activity Range for the Sidewinder, *Crotalus cerastes*

STEPHEN M. SECOR

This paper describes the effects of sex, age, and time of year on movements and activity ranges of a desert-adapted viperid snake, the sidewinder (*Crotalus cerastes*). In the eastern Mojave Desert, male sidewinders traveled ($\bar{x} \pm 1$ SE = 185.4 ± 17.1 m) significantly farther than nongravid females ($\bar{x}$ = 122.9 ± 10.1 m) within 24-h periods. This was chiefly a result of lengthy movements by adult males during the spring and fall mating seasons. Subadult sidewinders (2–3 yr old, $\bar{x}$ = 223.1 ± 25.3 m) moved significantly greater distances than neonates (1–3 months, $\bar{x}$ = 125.5 ± 22.0 m), juveniles (6 months–2 yr, $\bar{x}$ = 148.3 ± 14.3 m), and adults (>3 yr, $\bar{x}$ = 123.8 ± 12.1 m). Movements by all snakes were longest during the summer ($\bar{x}$ = 191.2 ± 17.7 m). Actual distances traveled averaged more than twice the straight-line distances between the beginning and end of movements, demonstrating the distinct tortuosity of *C. cerastes* movements. Sidewinders traveled on average 60% of the days monitored during their activity season (April–Oct.), with a resultant mean daily distance traveled of 117.8 ± 11.2 m/day. Although direction of travel was generally random, sidewinders exhibited significant directionality during the fall as they moved eastwardly to the sand-alluvial interface of the study site to overwinter. I speculate that overwintering in rodent burrows at the sand-alluvial interface increases overwintering survival because of decreased likelihood of exposure to freezing subsurface temperatures, greater structural stability of burrows, and lower risk of predation. Activity ranges of *C. cerastes*, calculated by minimum convex polygon ($\bar{x}$ = 23.2 ± 2.8 ha) and harmonic mean ($\bar{x}$ = 20.9 ± 2.6 ha) methods, are among the largest documented for snakes. For this population of sidewinders, there were no significant differences in activity range size between sexes or age classes (subadult vs adult). Core areas of activity (harmonic mean 50% isopleths) averaged 9.2 ± 0.9% of total activity range size (harmonic mean 95% isopleths) and also did not differ in size between sexes and age classes. Activity range size did not correlate with body size (SVL and mass), although it did correlate with the number of locality coordinates used in its calculation. Activity ranges of individual sidewinders overlapped extensively on the study site, and snakes commonly shifted their centers of activity seasonally. Sidewinders moved their activity centers during the fall to the site's sand-alluvial edge and returned to the site's sandy region following emergence from hibernation.

ACTIVITIES, movements, and overall spatial patterns of snakes are influenced by a mosaic of abiotic and biotic features (Gibbons and Semlitsch, 1987; Gregory et al., 1987). Classic examples include increased activity of males during the mating season as they search for females and decreased activity of females while gravid (Viitanen, 1967; Duvall et al., 1985), movements to and from overwintering sites governed by changes in environmental temperatures (reviewed by Gregory, 1982; 1984), and spatial selection determined by prey availability (Duvall et al., 1990). Recent reviews of activity, movement, and habitat selection of snakes (Gibbons and Semlitsch, 1987; Gregory et al., 1987; Reinert, 1993) have noted similar shortfalls in many studies. These include the difficulties of observing free-ranging individuals because of their general secretive nature, the short duration of many studies, the paucity of information on neonates and juveniles, and the lack of knowledge on the precise locality of all activities and paths of movements. To assess how intraspecific variation (sexual, ontogenetic, and temporal) shapes population structure, data must be collected throughout the year from individuals representing both sexes, different reproductive conditions, and all age classes.

This paper analyzes intraspecific differences in movement and activity range of the sidewinder (*Crotalus cerastes*). Sidewinders inhabit sandier regions of the Sonoran and Mojave deserts of North America (Klauber, 1972). In this species, individuals of all age classes are active

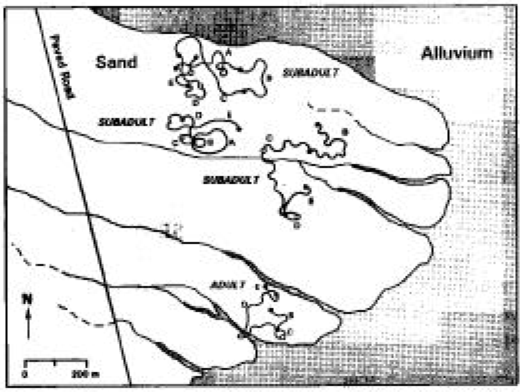

Fig. 1. Movements of four *Crotalus cerastes* (one adult and three subadults) during the nights of 26 (A), 27 (B), 28 (C), 29 (D), and 30 (E) Aug. 1990. Solid circles (●) designate rodent burrows in which snakes spent the day and open circles (○) designate sites where individuals cratered into the sand. The northern, eastern, and southern edges of the study site were bordered by an alluvial fan (shaded). Several arroyos crossed the site from east to west, and a two-lane paved road transected the western portion of the site.

on the surface throughout their activity season, adults are large enough for implanting radiotransmitters, and, most important, sidewinders exist in sandy habitats and leave very distinct tracks in the sand enabling their movements to be accurately measured (Brown and Lillywhite, 1992; Secor, 1992a). In this paper, I address the following questions. Do male sidewinders move greater distances and possess larger activity ranges than females, as observed for other snake populations (Viitanen, 1967; Shine, 1987)? Do larger and older sidewinders travel greater distances and establish larger activity ranges than smaller and younger cohorts (Clark, 1974; Christian and Waldschmidt, 1984)? Do sidewinders exhibit seasonal peaks of activity and seasonal changes in movement direction (Madsen, 1984; Duvall et al., 1985)? Do sidewinders exhibit activity patterns similar to other sit-and-wait foraging species? And finally, because it is common in temperate snakes (Gregory, 1984), do sidewinders migrate to and from communal hibernacula?

MATERIALS AND METHODS

Study site.—This three-year study (spring 1988–spring 1991) was conducted at the northeastern edge of the Kelso Dunes system (Devil's Playground) in the eastern Mojave Desert, San Bernardino County, California. Most of the 120-ha site had a fine-sand substrate and was crossed by several arroyos (Fig. 1). An alluvial fan emanating from the base of the Providence Mountains gradually inundated the loose sand along the southern, eastern, and northern borders of the site (Fig. 1). Over 90% of the perennial vegetation on the site was galleta grass (*Hilaria rigida*), burroweed (*Ambrosia dumosa*), and creosote bush (*Larrea tridentata*). From the northwest corner to the southeast edge of the site, the elevation gently rose from 650–700 m above sea level. I divided the site into 1-ha units and marked the borders of each hectare with surveyor's tape to facilitate mapping snake locations and movements.

Study organism.—I captured 181 sidewinders on the study site and measured [snout-vent length (SVL) and total length], weighed, sexed, and permanently marked (clipping portions of the subcaudal scales; Fitch, 1987) each individual. Captured sidewinders ranged in length from 16.5–61.5 cm SVL and in mass from 5–304 g; and I placed each individual into one of four age-class categories based upon its size (SVL and mass), age (if known), and reproductive potential (based on size of observed mating males and females): neonate (newborn prior to first hibernation, 16.5–23.6 cm SVL, 5–13 g); juvenile (first spring to second year, 21.4–39.5 cm SVL, 10–50 g); subadult (second to third year, 40.0–47.6 cm SVL, 45–77 g); and, adult (>3 years, 44.3–61.5 cm SVL, 75–304 g).

Radiotelemetry.—I surgically implanted [modification of the method of Reinert and Cundall (1982)] temperature-sensitive radio transmitters (Telonics, Inc., CHP-2P) into 23 adult *C. cerastes* and monitored those snakes intermittently for spans of 20–521 days ($\bar{x} \pm 1$ SE = 198 ± 33). Transmitters ($\bar{x}$ dimensions = 32.0 ± 0.4 × 14.7 ± 0.2 × 9.2 ± 0.4 mm, $\bar{x}$ mass = 6.1 ± 0.1 g), equipped with whip antennas ($\bar{x}$ length = 279 ± 9 mm), had a reception range of 250–600 m and an operational life of 5–9 months (depending upon pulse interval). Transmitters weighed an average of 4.7 ± 0.2% of snakes' body mass and were replaced every 4–6 months. I also observed younger age-class sidewinders, too small to be implanted with transmitters, for as many continuous days as possible.

Measurements of movements.—I was able to determine the distance and direction of travel of sidewinders by the very distinct tracks they left in the sand (see Mosauer, 1933). I measured the movement of an individual as the distance traveled over a 24-h period (1000–1000) by pushing a measuring wheel (Rolotape Corp., model 394) directly over its tracks from beginning to end. I measured and mapped 805 movements by 155 individuals ($\bar{x}$ SVL = 37.4 ± 0.9 cm, $\bar{x}$ mass = 54.6 ± 3.8 g), of which I identified 67 as males ($\bar{x}$ SVL = 37.3 ± 1.2 cm, $\bar{x}$ mass = 55.5 ± 5.3 g) and 75 as nongravid females ($\bar{x}$ SVL = 37.4 ± 1.2 cm, $\bar{x}$ mass = 53.7 ± 5.4 g). These movements were performed by 17 neonates ($\bar{x}$ SVL = 20.1 ± 0.5 cm, $\bar{x}$ mass = 7.7 ± 0.7 g), 83 juveniles ($\bar{x}$ SVL = 31.2 ± 0.7 cm, $\bar{x}$ mass = 26.8 ± 1.4 g), 35 subadults ($\bar{x}$ SVL = 42.2 ± 0.4 cm, $\bar{x}$ mass = 56.6 ± 1.7 g), and 39 adults ($\bar{x}$ SVL = 51.8 ± 0.7 cm, $\bar{x}$ mass = 125.2 ± 7.2 g). For any individual, I measured 1–43 ($\bar{x}$ = 5.2 ± 0.5) movements.

I also recorded the snake's position and form of nearest vegetation at the beginning and end of each movement. I drew each individual's movements and sighted localities on a scaled map of the study site. I determined the compass direction (north = 0°) of 638 movements (beginning to end) from the scaled maps. I also measured the straight-line distance between the starting and stopping points of 728 movements either directly in the field or calculated it from mapped coordinates of the two points. I quantified how much the actual distance traveled differed from the straight-line measurements as a meander ratio (actual distance divided by straight-line distance; Williamson and Gray, 1975). I calculated both relative frequency of movement (proportion of total days monitored that an individual actually moved) and mean daily distance traveled (total distance traveled divided by number of days) from instances in which individuals were monitored for a minimum of four consecutive days ($\bar{x}$ = 5.2 ± 0.1 days, n = 154). Because of the scarcity of gravid females (two in 1988; Secor, 1992a), only data from nongravid sidewinders were used in this study.

To lessen the effect of individual bias in the ensuing analyses, I pooled movement values (distance traveled, straight-line distance, meander ratio, frequency of movement, and mean daily distance) for each individual and used the resulting means. I used methods of circular statistics to calculate mean angular direction of travel for each individual (Batschelet, 1981). Averaging sine (y) and cosine (x) of compass directions the mean angle of movement ($\bar{\phi}$) was calculated as follows:

$$\arctan(\bar{y}/\bar{x}) \text{ if } x > 0$$
$$\text{or } \arctan(\bar{y}/\bar{x}) + 180 \text{ if } x < 0$$

Length of the mean vector (r), a measure of the spatial concentration of compass directions ($0 \leq r \leq 1$), was as follows:

$$(\bar{x}^2 + \bar{y}^2)^{0.5}$$

Mean angular deviation (s) of compass directions, equivalent to standard deviation of linear statistics, was as follows:

$$180°/\pi[2(1 - r)]^{0.5}$$

I partitioned movement data by sex, age class, and season, with seasonal categories including spring (movements made March–May), summer (June–Aug.), and fall (Sept.–Nov.). Prior to statistical analysis, I subjected data sets to Bartlett's test for homogeneity of variances (Zar, 1974). Because several categories of movement and meander ratio data were heteroscedastic, I log transformed (base 10) all values prior to analyses. I arcsine transformed movement frequencies to normalize their distribution (Zar, 1974). I used a three-way analysis of variance (ANOVA) to simultaneously test the singular and interactive effects of sex, age class, and season on movement distance (log), straight-line distance (log), meander ratio (log), movement frequency (arcsine), and mean daily movement distance (log). Within age class and season categories, a one-way ANOVA tested for differences among categories of the other two main effects. All F-tests were based on conditional (type III) sum of squares (proc GLM in SAS) to control for nonorthogonality. A post hoc Tukey multiple range test determined whether significant differences existed between main effect categories. I employed a Pearson product moment correlation test to determine whether either body mass or SVL was correlated with movement distance. I used a Rayleigh test to determine whether the direction of travel was random (Batschelet, 1981). Randomness was assumed if, based upon mean vector length (r) and sample size, the preassigned probability (P) was >0.05 (Table H in Batschelet, 1981). I utilized a Watson-Williams test to determine whether movement direction differed significantly among and between categories (Batschelet, 1981). I performed most statistical analyses using Statistical Analysis Systems (SAS Institute, Inc., 1988) and designated statistical significance at $P < 0.05$.

Measurement of activity range size.—I calculated the activity range size of each individual from the mapped coordinates (x, y) of its known localities. Many models of activity range size assume that localities are independent of each other (White and Garrott, 1990). To increase the independence of the coordinates used, I applied the following criteria to determine which locality coordinates I would use for analysis: one locality coordinate per day if the snake did not move, coordinates of each sighted locality (direct observation, 2–4/day) when it did move, and one coordinate per month while it hibernated. I calculated activity ranges only for those individuals for which I recorded a minimum of 40 coordinates over a minimum of three months. The resultant data set included 25 individuals (13 females and 12 males) which ranged in SVL from 39.5–59.1 cm ($\bar{x} = 49.5 \pm 1.2$) and in mass from 44–210 g ($\bar{x} = 106.7 \pm 8.7$). Eighteen were adults (16 implanted with transmitters), and seven were subadults. I monitored those sidewinders for an average of 131 ± 24 days (range = 21–521) and, based on my criteria, used an average of 96 ± 14 (range = 42–357) locality coordinates to estimate activity range size.

I calculated activity range size using the minimum convex polygon method (Jennrich and Turner, 1969) and the harmonic mean method (Dixon and Chapman, 1980). The former technique has been used most frequently to estimate activity ranges of snakes (Macartney et al., 1988); therefore, it allows the broadest comparison of my results with other studies. The harmonic mean method, a nonparametric statistical technique, estimates an activity range size strongly influenced by the relative distribution of localities. The size of an individual's activity range is the area isopleth that encloses a predetermined percentage of those localities. In this study, the area enclosed by the 95% isopleth represented the total activity range, whereas the 50% isopleth represented the core area of activity (Tiebout and Cary, 1987). This technique, which may provide a more accurate measure of activity range size, has been used in several recent studies of snake populations (Tiebout and Cary, 1987; Reinert and Zappalorti, 1988a). I entered locality coordinates into the microcomputer program MCPAAL (Microcomputer Programs for the Analysis of Animal Locations, National Zoological Park, Smithsonian Institute) and used it to calculate activity range size based on either model.

I used a two-tailed *t*-test to determine whether activity range size differed between sexes, age classes, and individuals located continuously with telemetry and those found intermittently without telemetry (Zar, 1974). Because larger sidewinders may be expected to establish larger activity ranges (Clark, 1974; Christian and Waldschmidt, 1984), I tested for the possible correlation (Pearson product moment correlation) of body size (SVL and mass) with activity range size. Because I had earlier found a significant correlation between number of localities used and activity range size for this population (Secor, 1992a), I again tested whether such a relationship existed for this larger data set. I expected that individuals that travel greater distances and are more active would possess larger activity ranges; thus, I also tested for possible correlations between individual activity range size and movement variables.

To detect shifts in centers of activity over time, I conducted time series analyses (Reinert and Zappalorti, 1988a) on 13 individuals, whose known localities spanned a minimum of three nonwinter seasons. I used locality coordinates, subdivided by season, to generate seasonal activity ranges (95% isopleths). The change in position of seasonal ranges and their degree of overlap provide an indication of vagility of snakes from one season to the next. I used these data to determine the proportion of the total activity range that included the combined areas (excluding overlapping segments) of the seasonal ranges.

RESULTS

Movement behavior.—*Crotalus cerastes* were chiefly nocturnal and typically began their movements soon after sunset from either rodent burrows (80% of movements) or coiled positions on the sand surface (20%). Occasionally, at the onset of a movement, *C. cerastes* traveled the first several meters ($\bar{x} = 4.7 \pm 0.5$ m, range = 1.0–13.1, n = 42) using rectilinear locomotion (Edwards, 1985) and then switched to sidewinding for the remainder of the movement. Individuals varied their movement behavior; in some instances they traveled in a fairly unidirectional path at a nearly constant pace (3–6 m/min), whereas in others they traveled more slowly (1–3 m/min), changed direction frequently, and repeatedly stopped to investigate the base of vegetation and rodent burrows. Figure 1 illustrates typical patterns of movement by *C. cerastes*.

During many movements, the sidewinder stopped, coiled, and worked the outer edges of its coil into the sand [see Brown and Lillywhite (1992) for description]. This "cratering" behavior provided a cryptic position from which to ambush prey and may have also served a thermoregulatory role (Cowles and Bogert, 1944; Brown and Lillywhite, 1992). Sidewinders often formed several craters in an evening, commonly near the mouth of rodent burrows. In many such instances, the sidewinder had investigated the burrow's entrance before cratering next to it (determined by the tracks left in the sand).

A movement ended in one of three ways: (1) the snake entered a rodent burrow during the evening and remained there until the next day (54.4% of movements); (2) it remained cratered or coiled throughout the evening and moved directly into a nearby burrow several hours after sunrise (16.9%); or (3) it remained cratered or coiled on the surface throughout the following day (28.7%). This third scenario occurred only during the spring and fall when daytime shaded-air temperatures seldom exceeded 35 C.

Movements usually ended near one of the major forms of vegetation occurring on the study site. The distribution of plant species closest to where snakes ceased their movements was significantly different (chi-square, $X^2_7 = 19$, $P < 0.01$) from that predicted from the relative occurrence of those plants on the study site (calculated from four 800-m transects). Sidewinders terminated their movements more often than expected close to *Larrea tridentata* (observed: 117, expected: 96) and *Krameria parvifolia* (ratany, observed: 46, expected: 33). Both plants typically had rodent burrows at their base and *K. parvifolia* had low, thick, foliage beneath which *C. cerastes* commonly cratered or coiled.

Movement distance.—For all 805 measured movements, the mean distance traveled was 146.7 ± 5.6 m (range = 2.0–963.3). After averaging the data for each individual, the mean distance traveled was 150.3 ± 9.5 m (Table 1). A three-way analysis of variance demonstrated that sex, age class, and season each had a significant effect (sex, $F_{1,184} = 7.19$, $P < 0.01$; age class, $F_{3,184} = 3.50$, $P < 0.05$; season, $F_{2,184} = 3.61$, $P < 0.05$) on movement distance. A significant interaction did occur between age class and season ($F_{5,184} = 2.59$, $P < 0.05$). Overall, male sidewinders moved significantly greater distances than females, and this occurred specifically for adult snakes (male $\bar{x} = 169.5 \pm 19.7$ m, $\bar{x}$ female $= 84.3 \pm 8.4$ m; $F_{1,55} = 13.4$, $P < 0.001$). Only during the spring did males ($\bar{x} = 141.5 \pm 13.5$ m) and females ($\bar{x} = 93.4 \pm 12.8$ m) differ in movement distance ($F_{1,66} = 6.51$, $P < 0.05$).

Subadults moved significantly greater distances than neonates, juveniles, and adults (Tukey multiple range test; Ps < 0.05). There were no significant differences in the distance traveled among or between age classes during the spring. Differences among age classes existed during the summer ($F_{3,88} = 4.89$, $P < 0.01$) and fall ($F_{3,55} = 4.10$, $P < 0.05$), because subadults traveled significantly (Ps < 0.05) greater distances than adults during the summer and farther than juveniles during the fall. For this population, neither SVL ($r = 0.02$, $P = 0.783$) nor mass ($r = 0.06$, $P = 0.432$) correlated with movement distance. Summer movements (all individuals) were significantly longer (Ps < 0.05) than those made during the spring or fall. Only juveniles differed significantly among seasons in movement distance ($F_{2,89} = 8.17$, $P < 0.001$), because they undertook significantly (Ps < 0.05) longer movements during the summer than during the spring or fall.

Straight-line distance.—Sidewinders seldom traveled in a straight path (Fig. 1). Straight-line distances between the start and stop of movements were significantly less than actual distances traveled (paired *t*-test, $t_{140} = 17.7$, $P < 0.001$). Only sex had a significant effect ($F_{1,173} = 5.09$, $P < 0.05$) on straight-line distances, because such measures from male movements overall were significantly longer than those from female movements. There were no significant (Ps > 0.05) interactions of main effects on this movement variable. Among age classes, only adults exhibited significant differences ($F_{1,55} = 13.4$, $P < 0.001$) in the straight-line distances of movements between males ($\bar{x} = 129.2 \pm 17.0$ m) and females ($\bar{x} = 61.8 \pm 5.9$ m). Among seasons, only movements made during the spring differed ($F_{1,68} = 5.13$, $P < 0.05$) between males and females in their straight-line distances. During the fall, straight-line distances differed among age classes ($F_{3,51} = 3.31$, $P < 0.05$) because such distances of neonate movements exceeded those of juvenile movements.

For 624 movements, in which the straight-line distance was greater than 0 m (Fig. 2), the meander ratio averaged 2.4 ± 0.2 (range = 1.0–72.2). For an additional 104 movements ($\bar{x} = 28.1 \pm 3.3$ m, range = 3.0–173.3), sidewinders returned to the same location from which they began their movements (straight-line distance = 0). Age class and season, but not sex, had significant effects (age class, $F_{3,173} = 3.08$, $P < 0.05$; season, $F_{2,173} = 8.47$, $P < 0.001$) on meander ratios. Additionally, there were no interactions of these main effects (Ps > 0.15). Meander ratios of neonates were significantly (Ps < 0.05) less than those of juveniles, subadults, and adults; ratios of juveniles were less than those of subadults. During the summer, meander ratios were significantly greater (Ps < 0.05) than those calculated from either spring or fall movements.

Movement direction.—The mean angle of direction (ϕ) for 638 movements was 87.8° [angular deviation (s) = 77.7°]. Males possessed a mean vector of travel (east-northeast) that differed significantly ($F_{1,132} = 4.87$, $P < 0.05$) from that of females (east-southeast), although neither sex

TABLE 1. DESCRIPTIVE STATISTICS (MEAN ± 1 SE, RANGE, N) OF MOVEMENT PARAMETERS FOR *Crotalus cerastes* COMPILED FOR THE TOTAL DATA SET AND FOR EACH SEX, AGE CLASS, AND SEASON.

		Sex		Age class				Season		
	Total	Male	Female	Neonate	Juvenile	Subadult	Adult	Spring	Summer	Fall
Movement distance (m)										
Mean ± 1 SE	150.3 ± 9.5	185.4 ± 17.1	122.9 ± 10.1	125.5 ± 22.0	148.3 ± 14.3	223.1 ± 25.3	123.8 ± 12.1	118.6 ± 9.5	191.2 ± 17.7	145.4 ± 17.1
Range	16.4–902.6	16.4–902.6	17.8–518.3	17.8–409.4	16.4–902.6	21.8–606.6	32.6–331.5	18.6–337.5	16.4–902.6	10.8–606.6
n	155	67	75	17	83	35	39	73	88	57
Straight-line distance (m)										
Mean ± 1 SE	98.2 ± 5.4	113.1 ± 8.4	84.6 ± 6.8	119.7 ± 19.8	96.6 ± 8.3	109.3 ± 13.7	94.4 ± 10.6	91.3 ± 8.1	109.2 ± 8.7	95.8 ± 9.0
Range	13.9–428.4	13.9–311.2	14.7–428.4	14.7–299.7	13.9–258.0	20.4–428.4	16.1–311.2	13.9–295.4	9.9–428.4	14.7–299.7
n	141	66	69	14	75	31	38	68	77	55
Meander ratio (movement distance/straight-line distance)										
Mean ± 1 SE	2.1 ± 0.1	2.1 ± 0.2	2.1 ± 0.2	1.1 ± 0.2	2.0 ± 0.2	2.7 ± 0.3	2.1 ± 0.2	1.6 ± 0.1	2.7 ± 0.2	1.7 ± 0.2
Range	1.0–12.7	1.0–7.7	1.0–12.7	1.0–1.3	1.1–12.7	1.1–7.3	1.1–7.8	1.1–4.3	1.1–12.7	1.0–10.9
n	141	66	69	14	76	31	37	68	77	55
Direction of movement (°)										
Mean ϕ	94.7	67.9	12.0	88.9	179.0	242.6	94.5	234.7	3.7	93.7
s	72.7	73.3	71.8	17.0	78.4	76.4	67.9	73.0	76.9	52.7
r	0.20	0.18	0.22	0.96	0.07	0.11	0.30	0.19	0.10	0.58
n	139	65	69	14	76	31	36	68	75	55
Movement frequency (days move/days monitored)										
Mean ± 1 SE	0.60 ± 0.04	0.64 ± 0.06	0.57 ± 0.06	—	0.78 ± 0.06	0.82 ± 0.06	0.41 ± 0.05	0.54 ± 0.06	0.69 ± 0.05	0.35 ± 0.08
Range	0.0–1.0	0.0–1.0	0.0–1.0	—	0.2–1.0	0.46–1.0	0.0–1.0	0.0–1.0	0.0–1.0	0.0–1.0
n	58	27	31	—	16	12	30	29	37	16
Mean daily movement distance (m/day)										
Mean ± 1 SE	117.8 ± 11.2	134.6 ± 17.1	102.1 ± 14.5	—	133.2 ± 25.1	152.3 ± 22.6	94.1 ± 13.5	101.0 ± 16.0	138.2 ± 14.2	97.8 ± 28.5
Range	0.0–373.6	0.0–331.6	0.0–373.6	—	19.2–323.9	11.9–317.4	0.0–373.6	0.0–373.6	16.6–331.6	0.0–364.8
n	56	27	29	—	16	12	28	29	35	13

SE = standard error, n = number of individuals.
ϕ = vector angle (°), s = mean angular deviation (°), r = mean vector length.

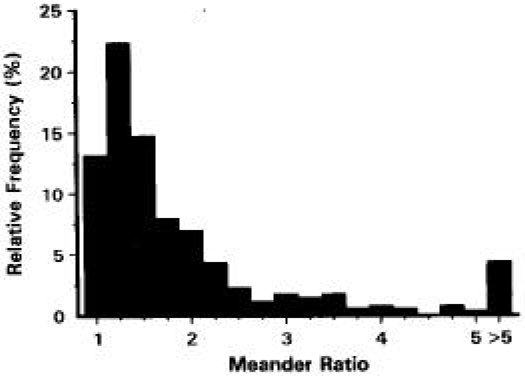

Fig. 2. The relative frequency of meander ratios (actual distance/straight-line distance ± 0.125) for 624 movements by *Crotalus cerastes* in which straight-line distances were greater than 0.

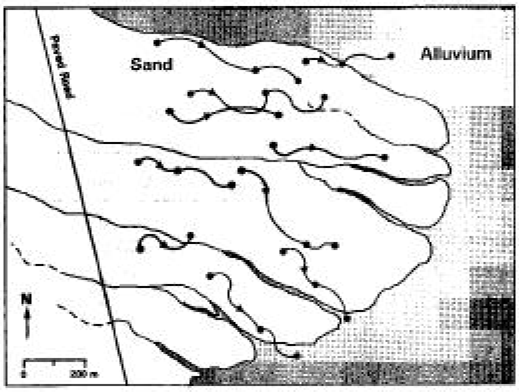

Fig. 3. Nocturnal movements of ten neonate (< 2 months old) *Crotalus cerastes* made during the fall of 1989 and 1990. The solid circles (●) designate rodent burrows that individuals sought refuge in during the daylight hours.

exhibited statistical evidence of movement directionality (Table 1). Sexual differences in movement direction occurred specifically for juveniles ($F_{1,74} = 32.2$, $P < 0.001$) and subadults ($F_{1,29} = 10.8$, $P < 0.01$) and for movements made by all individuals during the spring ($F_{1,65} = 15.3$, $P < 0.001$). Direction of travel (Table 1) differed significantly among age classes ($F_{3,133} = 9.19$, $P < 0.001$), because subadults traveled (westerly) in a significantly (Ps < 0.05) different direction than neonates (easterly), juveniles (southerly), and adults (easterly). Direction of travel by juveniles also differed significantly (Ps < 0.01) from those of neonates and adults. Only neonates exhibited significant directionality in their movements [mean vector length (r) = 0.96, $P < 0.001$] as illustrated in Figure 3. Movement direction differed significantly among seasons ($F_{2,198} = 31.8$, $P < 0.001$) and between seasons (Ps<0.001) because the mean vector of movement was directed toward the west during the spring, toward the north during the summer, and toward the east during the fall (Table 1). Fall movements exhibited significant directionality ($r = 0.58$, $P < 0.001$), resulting from the directness of movements by adults ($r = 0.54$, $P < 0.001$) and neonates ($r = 0.95$, $P < 0.001$; Fig. 3) during that season.

Movement frequency.—On average, individual sidewinders traveled three times every five days ($\bar{x}$ frequency = 0.60 ± 0.04; Table 1) with periods of inactivity commonly occurring after ingestion of a meal (5–10 days) and prior to ecdysis (3–5 days). Age class and season had singular effects (no interactions) on the frequency of movement (age class, $F_{3,66} = 14.7$, $P < 0.0001$; season, $F_{2,66} = 7.86$, $P < 0.001$). Adult sidewinders traveled significantly (Ps < 0.05) less often than either juveniles or subadults, and all sidewinders moved significantly (Ps < 0.05) more frequently during the summer than during either the spring or fall. Movement frequency differed significantly among age classes during the spring ($F_{2,26} = 4.64$, $P < 0.05$) and summer ($F_{2,84} = 14.4$, $P < 0.0001$), as adults traveled significantly (Ps < 0.05) less often than juveniles during both of these seasons and less frequently than subadults during the summer. Subadults differed among seasons ($F_{2,16} = 5.18$, $P < 0.05$) in frequency of travel, moving more often during the summer than the spring.

Daily movement distance.—Mean distance traveled per day, calculated from days of continuous observations, ranged from 0–331.6 m/day (Table 1). The maximum value was for an adult male that traveled 154.7, 18.4, 852.0, and 301.1 m, respectively, for four consecutive days. Only season had a significant effect ($F_{2,61} = 3.58$, $P < 0.05$) on mean daily distance traveled, because sidewinders traveled greater distances per day during the summer than fall. If movement is energetically expensive, then sidewinders that traveled farther than normal would be expected to move a relatively shorter distance the following day. Individuals exhibited no tendencies to travel a relatively short distance (< its mean daily distance) after traveling a relatively long distance (> its mean daily distance) and vice versa (chi-square test, $X^2_1 = 0.46$, $P = 0.50$).

Activity range.—Activity ranges varied in size from 7.3–61 ha (Table 2). Ranges calculated by the minimum convex polygon method did not

TABLE 2. ACTIVITY RANGE SIZE OF *Crotalus cerastes* CALCULATED BY THE MINIMUM CONVEX POLYGON (MCP) AND THE HARMONIC MEAN (HM) METHODS. Harmonic mean 50% and 95% isopleths represent the core area of activity and the total activity range, respectively. Noted for each individual is its age class, sex, snout–vent length (SVL), mass, the number of coordinates that were used to calculate its activity range size, and the number of days that it was monitored.

Age class	Sex	SVL (cm)	Mass (g)	No. of coordinates	No. of days	MCP	HM 50% isopleth	HM 95% isopleth
A*	M	49.7	116.0	90	192	20.9	0.6	19.3
S	F	41.0	50.3	64	43	8.4	1.3	7.5
A*	F	53.3	119.0	95	167	25.0	2.4	19.3
A*	F	54.7	118.0	76	87	7.3	0.4	8.8
A*	M	50.8	118.5	357	521	61.0	5.0	33.3
A*	M	53.8	139.5	42	116	13.0	1.0	7.7
A*	F	56.0	135.0	125	93	16.0	1.2	17.8
A*	F	54.1	138.0	170	250	37.5	1.6	37.5
S	M	42.1	60.6	66	35	32.9	2.1	48.1
S	F	43.6	65.0	42	21	15.6	3.0	24.8
A*	F	55.4	121.0	185	313	19.2	2.0	20.0
S	M	42.1	53.7	75	48	38.0	1.7	18.7
S	F	42.3	56.8	116	79	32.4	4.8	31.8
A*	F	47.5	93.8	98	217	28.0	0.6	36.0
A	M	44.6	75.7	46	22	17.0	1.5	12.7
A*	M	59.0	210.0	149	276	55.3	3.6	54.0
A*	F	52.0	107.0	44	91	25.7	1.1	11.6
S	M	41.8	63.7	47	22	19.1	2.0	16.2
A*	F	53.2	130.0	121	208	8.9	0.3	12.0
A	M	47.6	74.5	69	40	30.6	2.2	30.6
S	M	39.5	44.3	48	24	16.2	1.6	9.3
A*	M	55.4	158.5	91	63	9.7	0.6	7.7
A*	F	59.1	190.5	105	155	8.7	1.1	8.9
A*	F	48.0	99.5	43	66	11.3	0.8	11.3
A*	M	50.0	130.0	42	124	22.8	1.3	16.7
Mean		49.5	106.7	96.3	130.7	23.2	1.8	20.9
SE		1.2	8.7	13.6	23.7	2.8	0.3	2.6

F = female; M = male; A = adult; S = subadult; MCP = minimum convex polygon method; HM = harmonic mean method.
* = transmitter implanted.

differ significantly in size (paired *t*-test, $t_{24} = 1.72$, $P = 0.183$) from those calculated by the harmonic mean method (Table 2). I used harmonic mean values (95% isopleths) in the ensuing analyses because they provide more accurate estimates of activity range size (Tiebout and Cary, 1987). Activity range size did not differ significantly ($Ps > 0.05$) between males ($\bar{x} = 22.9 \pm 4.5$ ha, $n = 12$) and females ($\bar{x} = 19.0 \pm 2.9$ ha, $n = 13$) nor between subadults ($\bar{x} = 22.3 \pm 5.4$ ha, $n = 7$) and adults ($\bar{x} = 20.3 \pm 3.1$ ha, $n = 18$). Additionally, activity range size did not differ significantly between snakes with radiotransmitters implanted ($\bar{x} = 20.1 \pm 3.3$ ha, $n = 16$) and those without ($\bar{x} = 22.2 \pm 4.4$ ha, $n = 9$).

Core areas of activity (50% isopleths) also did not differ significantly ($Ps > 0.05$) in size between sexes or age classes. The core area represented on average 9.2 ± 0.9% (range = 1.7–17.6%) of the total activity range (95% isopleths; Fig. 4). Neither SVL nor mass correlated with activity range size ($Ps > 0.7$), although the number of locality coordinates used did correlate ($r = 0.40$, $P < 0.05$). Activity range size did not correlate ($Ps > 0.05$) with movement distance, mean daily distance, or movement frequency, but it did with straight-line distances ($r = 0.44$, $P < 0.05$).

Seasonal activity ranges differed in size among the four seasons (one-way ANOVA, $F_{3,37} = 3.63$, $P < 0.05$). Summer ranges ($\bar{x} = 9.0 \pm 2.6$ ha, $n = 12$) were significantly larger (Tukey multiple range test, $P < 0.05$) than winter ranges ($\bar{x} = 0.11 \pm 0.07$ ha, $n = 5$) but did not differ in size from either spring ($\bar{x} = 2.7 \pm 1.2$ ha, $n = 12$) or fall ($\bar{x} = 2.8 \pm 1.6$ ha, $n = 12$) ranges. Individuals regularly shifted their centers of activity from one season to the next resulting in little overlap among seasonal ranges. Beginning in late summer and continuing through the fall, the majority of sidewinders shifted their centers

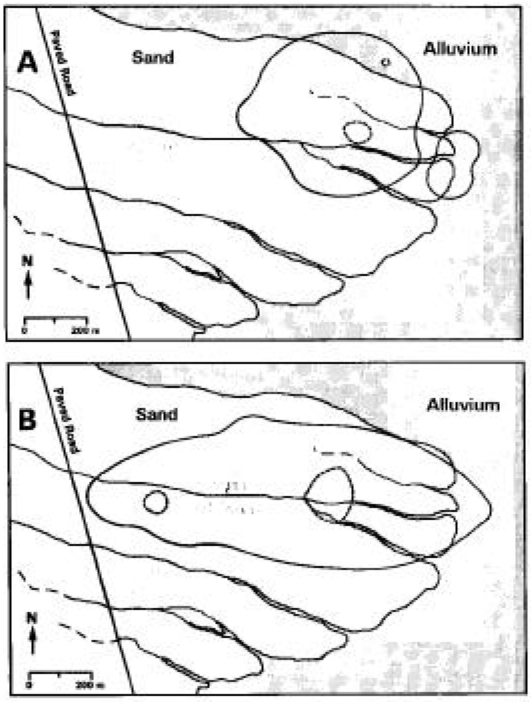

Fig. 4. Total activity range (solid line) and core areas of activity (dashed line) isopleths of (A) adult male and (B) adult female *Crotalus cerastes*. Total activity ranges and core areas of activity were calculated by harmonic mean method and represent 95% and 50% area isopleths, respectively, of individual's localities.

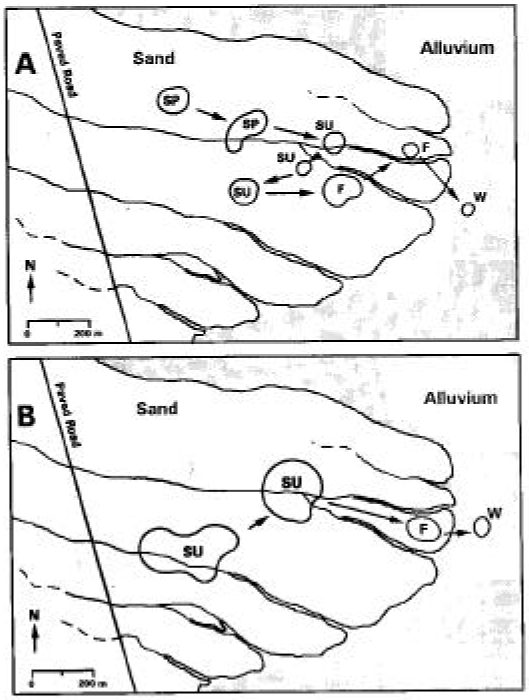

Fig. 5. Easterly shifts in seasonal activity ranges (95% isopleths, sp = spring, su = summer, f = fall, w = winter) by an adult male (A) and female (B) *Crotalus cerastes* during 1990.

eastwardly toward the sand-alluvial interface (Fig. 5). Sidewinders overwintered in this area and shifted their activity centers back to the sandier region of the site after spring emergence.

The combined nonoverlapping area of seasonal ranges averaged 53.0 ± 5.6% of the area of total activity ranges (Table 3). Total activity ranges commonly included areas that were never occupied and were excluded from seasonal ranges. Total activity ranges overlapped extensively on the study site, and each snake's total range overlapped those of 18.3 ± 0.9 (range = 7–23, n = 25) other individuals. Seasonal activity ranges overlapped markedly less. During fall 1989, spring 1990, and fall 1990, each seasonal activity range of 10 sidewinders overlapped, respectively, an average of 1.0 ± 0.3 (range = 0–3), 1.6 ± 0.5 (range = 0–4), and 2.9 ± 0.4 (range = 1–5) seasonal activity range(s) of other individuals. During summer 1990, each seasonal activity range of 14 sidewinders overlapped an average of 5.6 ± 0.9 (range = 1–11) seasonal ranges of other individuals.

Discussion

At the northeast edge of the Kelso Dunes in the eastern Mojave Desert, *C. cerastes* move freely in their search for foraging sites, thermal refugia, and mates. There, male sidewinders travel greater distances than females, subadult snakes are the most active, and activity peaks during the summer. Traditionally, individuals move to the sand-alluvial interface to overwinter and return to the loose-sand region following spring emergence. These movements result in activity ranges that typically are 20–30 ha in size.

Movement behavior.—Earlier researchers commented on the sidewinder's propensity for movement, its mode of locomotion, habitat, and cratering behavior. Mosauer (1933) observed sidewinders using lateral undulation-like movements in the early phase of their travel and suggested that they did so because their body temperatures (T_bs) had not increased enough for proficient sidewinding. I occasionally observed sidewinders using rectilinear locomotion, but not lateral undulation, at the start of

TABLE 3. SUM OF SEASONAL ACTIVITY RANGES (EXCLUDING OVERLAPPING AREAS) AND TOTAL ACTIVITY RANGE SIZES OF 13 *Crotalus cerastes* MONITORED FOR THREE NONWINTER SEASONS. The percentage of the total activity range that includes the sum of seasonal ranges is calculated.

Age class	Sex	Sum of seasonal ranges (ha)	Total activity range (ha)	Sum of seasonal/ total range (%)
A	M	4.4	19.3	22.8
S	F	5.0	7.5	66.7
A	M	16.9	33.3	50.8
A	F	9.8	17.8	55.1
A	F	26.7	37.5	71.2
S	M	6.6	48.1	13.7
A	F	6.2	20.0	31.0
A	F	20.8	31.8	65.4
A	F	21.3	36.0	59.2
A	M	33.7	54.0	62.4
A	M	5.8	12.7	45.7
A	M	18.2	30.6	59.5
S	M	7.9	9.3	84.9
Mean ± 1 SE		14.1 ± 2.6	27.5 ± 4.0	53.0 ± 5.6

M = male; F = female; A = adult; S = subadult.

movements. Sidewinders emerging from burrows possessed T_bs ($\bar{x}$ = 31.5 ± 0.2 C, range = 26.9–35.3 C, n = 75) that commonly exceeded the average T_b (27.9 ± 0.1 C, n = 341) of moving individuals (pers. obs.). Sidewinders may use an alternative locomotory mode at the beginning of a movement to "stretch" locomotory muscles prior to sidewinding, rather than using it until their T_bs had increased enough for efficient sidewinding. Tracks laid at the beginning of movements were commonly irregular and connected, suggesting that individuals were "stretching and warming up" locomotory muscles for several meters before sidewinding proficiently.

In addition to *C. cerastes*, other small desert-dwelling viperids (*Bitis*, *Cerastes*, and *Eristicophis*) bury themselves in the sand (Mosauer, 1933; Mendelssohn, 1965; Louw and Seely, 1982). This convergent trait is considered important for camouflaging these ambush foragers from prey and predators. For nocturnal *C. cerastes*, and possibly for other cratering species, it may also serve to increase optimal foraging time. Snakes cratered in the warm sand in the early evening, while the air and surface were rapidly cooling, may have maintained warmer T_bs for several hours longer than individuals simply coiled on the sand surface (Cowles and Bogert, 1944). In the morning, as surface temperatures quickly increase, snakes cratered in the cooler sand may have remained on the surface longer because it took more time for them to reach their voluntary maximum T_b.

Sidewinders occasionally undertook lengthy nonmigratory movements. I recorded movements of 963.0, 903.0, and 902.6 m, accomplished by individuals with SVL (mass) of 38.2 cm (37 g), 40.3 cm (48 g), and 29.1 cm (18 g), respectively. Brown and Lillywhite (1992) estimated, by counting paces, that an adult had traveled 1269.2 m in one evening. Activities and movements of sit-and-wait foraging snakes are generally considered to be less than those of widely foraging species (Gibbons and Semlitsch, 1987). In fact, the average straight-line distance of sidewinder movements is greater than those of many of the species, including wide foragers, documented by Macartney et al. (1988). On the other hand, a sidewinder traveled only 60% of the days it was monitored, whereas a wide forager may move more frequently and average greater distances traveled per day. On the same study site, the mean daily distance of travel by the widely foraging colubrid *Masticophis flagellum* ($\bar{x}$ = 186 ± 37 m/day, n = 8; Secor, 1992b) was twice that of adult sidewinders.

Crotalus viridis become completely exhausted and experience a fourfold increase in blood lactate after five minutes of vigorous stimulated activity (Ruben, 1976). I found no evidence that sidewinders alternate long movements with short or no movements. The energetic cost of sidewinding by *C. cerastes* is comparatively low (Secor et al., 1992). For example, an adult sidewinder (125 g) traveling at 0.25 km/h (a speed I commonly observed in the field) for 500 m expends 1.28 kJ (calculated from Secor et al., 1992), equivalent to only 25% of its mean daily energetic expenditure (4.96 kJ/d; Secor, 1992b). Furthermore, an adult sidewinder traveled 4800 m while moving continuously on a treadmill at a speed of 0.60 km/h (Secor et al., 1992). Long-distance movements do not appear to be energetically taxing to *C. cerastes* (possibly involving a low anaerobic contribution); thus, individuals can easily move such distances repeatedly.

Ecological significance of movement.—Viitanen (1967), Duvall et al. (1985), and Shine (1987) have noted that adult male snakes increased their movements during the mating season and that gravid females exhibited lower levels of activity than nongravid females. In *C. cerastes*, only adult males moved significantly greater distances than nongravid adult females. This population of *C.*

cerastes mated during the spring (April–May) and fall (Sept.–Oct.). It was only during these two seasons that adult males travel significantly ($Ps < 0.05$) greater distances than adult females, presumably because males were searching for females in addition to new foraging sites. Earlier I reported that reproductive state influenced the activities of female sidewinders; gravid sidewinders traveled significantly shorter distances prior to parturition than after, and shorter distances than nongravid females (Secor, 1992a).

It has been suggested that larger and older individuals of a population may move greater distances than smaller and younger individuals (Clark, 1974). However, *C. cerastes*, like *Acrochordus arafurae* (Shine and Lambeck, 1985), shows no relationship between body size and distance traveled. In fact, younger sidewinders moved greater distances and were active more often than adults. If younger snakes were less familiar with the area, it may have taken them more time and longer movements to find suitable foraging sites or refuges (Secor, 1992a). Additionally, young sidewinders may have been foraging more intensively because they are less experienced and have higher mass-specific food requirements than adults (S. M. Secor and K. A. Nagy, unpubl.).

For most sidewinder movements, the straight-line distance between the starting and stopping points clearly underestimated the actual distance traveled. In this study, an adult male traveled 317.8 m and stopped 4.4 m from where it had started. Brown and Lillywhite (1992) calculated a mean "Curvature Index" (= meander ratio of this study) of 1.8 for 69 movements by sidewinders on the same site. That study, mine, and earlier observations (Mosauer, 1933) clearly document the distinct tortuosity of *C. cerastes* movements. Although it is impossible in many habitats to measure an individual's exact path (Madsen, 1984; Shine and Lambeck, 1985), the discrepancy between actual and straight-line distances in *C. cerastes* illuminates the potential underestimation of true movement distances when only straight-line values are presented.

Sidewinders return to the same location from which they began in 12.9% of movements. In such instances, a sidewinder typically exited a burrow at sunset, traveled a relatively short distance (typically <20 m), cratered into the sand or coiled on its surface, and returned to the burrow the following morning. Individuals occasionally repeated this action for several consecutive days, cratering or coiling in the same spot and returning to the same burrow. The majority of burrows on the site were those of the kangaroo rat *Dipodomys merriami*, a common prey species, and most prey captures were made close to these burrows. I suspect that sidewinders had determined those particular locations to be potentially profitable for prey capture by chemoreception (Halpern and Kubie, 1984) of prey activity. Establishing an ambush position, presumably after the detection of prey, has also been observed for the boid *Morelia spilota* (Slip and Shine, 1988a) and the viperids *Crotalus atrox* (Landreth, 1973), *Crotalus horridus* (Reinert et al., 1984), and *Crotalus viridis* (Duvall et al., 1985; Diller, 1990).

Sidewinders exhibited significant differences in the direction of travel with respect to sex, age class, and season. I have no explanations for differences resulting from either sex or age class, whereas movements to and from overwintering sites probably explain seasonal differences. During the summer, sidewinders traveled in seemingly random directions and shifted their direction of travel daily (little directionality). Beginning in mid-Sept., sidewinders moved in a more directional (same direction for consecutive movements) and linear (low meander ratio) fashion as they traveled easterly toward the site's alluvial edge. Brown and Lillywhite (1992) also noted the distinct easterly movements of sidewinders on this site during Oct. Sidewinders overwintered in this sand-alluvial border and returned (westerly) to the sandy region of the site following spring emergence.

Yearly migrations to and from communal hibernacula are common phenomena for many snake populations (Gregory, 1982, 1984). Hibernacula are selected presumably because they provide protection from freezing temperatures (Gregory, 1982). I never observed sidewinders to hibernate communally; instead they overwintered solitarily typically within burrows of *Dipodomys merriami.* Those burrows provided adequate thermal protection for hibernating snakes because subzero temperatures, measured at several depths (5–50 cm) with a digital thermometer (Omega model HH-99A-T2), seldom reached below the sand surface (unpubl.).

Hibernating within burrows of the sand-alluvial interface could increase overwinter survival for three reasons. First, temperature in these burrows may not drop as low as in burrows of the sandy region. The gravel and rocks of the alluvial surface are dark in coloration because of a thin covering of manganese oxide ("desert varnish"; Dorn, 1991). The alluvial surface may absorb more solar radiation than the lighter sand and possibly result in higher temperatures reached in its burrows, thus minimizing snakes freezing during hibernation.

Second, in the sandy region of the site burrows not actively maintained by rodents become sealed by wind-blown sand and eventually collapse. During the activity season, sidewinders were moving frequently enough that burrow degradation was usually not a problem. During hibernation, when snakes were inactive for 2–3 months, closure or collapse of burrows could possibly result in the snakes' death. Burrows of the sand-alluvial border maintained their integrity for many months because the substrate was firmly packed and consisted of sand, gravel, and rocks. Therefore, sidewinders benefited from overwintering in the more stable burrows of the alluvial edge compared to the relatively short-term burrows of the site's sandier region.

Third, burrows of the sand-alluvial interface provided greater protection than those of the loose sand. During this study, four sidewinders were dug out of their burrows within the loose-sand region and preyed upon by either coyotes (*Canis latrans*) or kit foxes (*Vulpes macrotis*). During the winter, sidewinders are susceptible to predation if removed from their overwintering refuge. I never observed any sidewinders dug from burrows of the alluvial edge, probably because the hard-packed rocky substrate was very difficult for a predator to dig through.

The ability of snakes to locate overwintering sites and return yearly to communal hibernacula has puzzled researchers for years. Visual (Viitanen, 1967; Parker and Brown, 1980), celestial (Landreth, 1973; Newcomer et al., 1974), and olfactory (Klauber, 1972; Parker and Brown, 1980) cues have been postulated as the means by which snakes locate hibernating sites. Older sidewinders may have used one or several cues, based upon their earlier experiences, to locate the overwintering region. Traveling mostly at night, they may have used the outline of the Providence Mountains, southeast of the site, to orient their movements toward the sand-alluvial edge. They may have also used the easterly rise in elevation to direct their movements.

The distinct easterly movements of neonate *C. cerastes* during the fall are difficult to explain (Fig. 3) because they have had no previous experience in locating overwintering sites. From laboratory experiments (Brown and MacLean, 1983; Graves et al., 1985) and observations in the field (Reinert and Zappalorti, 1988b), it has been suggested that neonates use chemoreception to follow adults to overwintering refugia. I found no evidence of neonates ever following adults. Neonates were never in the presence of older snakes after dispersing from their place of birth, their tracks were never found alongside tracks of older snakes, and they never changed direction to follow older snakes after encountering their tracks. I speculate that a behavioral trait has evolved in this population which directs neonates, possibly by changes in elevation or substrate texture, to and from the overwintering region.

Determinants of activity range size.—Macartney et al. (1988) tabulated published activity range sizes of 32 species of snakes. Mean activity range size (minimum convex polygon) of *C. cerastes* surpassed mean values of all species (25 species by minimum convex polygon, two by circle method, two calculated as length x width, two by unknown methods, and one by corrected minimum convex polygon) except *Crotalus horridus* (Reinert and Zappalorti, 1988a). However, activity ranges of *C. horridus* were not significantly larger (Kruskal-Wallis test, $Ps > 0.05$) than those of *C. cerastes* calculated by either the minimum convex polygon or harmonic mean method. Activity ranges of eight other viperids reported by Macartney et al. (1988) were considerably smaller ($\bar{x} = 0.01–12.1$ ha) than those of *C. cerastes*. The smaller activity ranges of those species and others tabulated by Macartney et al. (1988) may result from different methodologies and lengths of studies. More recently, Slip and Shine (1988b) reported activity ranges of *Morelia spilota* (minimum convex polygon, $\bar{x} = 42.8 \pm 8.8$ ha, n = 15) that were significantly larger than those of *C. cerastes* (Kruskal-Wallis test, $X^2 = 3.94$, $P < 0.05$).

Core areas of activity (50% isopleths) constituted small percentages of the total activity ranges of *C. cerastes*, as they did for *Crotalus horridus* ($\bar{x} = 11.1 \pm 1.9\%$, n = 20; Reinert and Zappalorti, 1988a) and *Nerodia sipedon* ($\bar{x} = 8.9 \pm 2.1\%$, n = 10; Tiebout and Cary, 1987). Core areas may have contained higher densities of prey and burrows that sidewinders used repeatedly. Duvall et al. (1990) demonstrated that *Crotalus viridis* cease vernal migrations when they encountered the presence of deer mice (*Peromyscus maniculatus*) and remained in close vicinity to the rodents for up to several weeks.

Although male sidewinders moved significantly greater distances than females, they did not possess significantly larger activity ranges. Sexual differences in activity range size were also absent for two other viperids, *Crotalus horridus* (all individuals; Reinert and Zappalorti, 1988a) and *Sistrurus catenatus* (Reinert and Kodrich, 1982), although larger activity ranges in males occur in some colubrids (Weatherhead and Hoysak, 1989), boids (Slip and Shine, 1988b), and elapids (Shine, 1987).

Activity ranges of adults would predictably be larger than those of younger age classes (see Ralph and Pearson, 1971). Shine (1987) noted a significant positive correlation between SVL and activity range size (corrected minimum convex polygon) for the elapid *Pseudechis porphyriacus*. Sidewinders, together with *Morelia spilota* (Slip and Shine, 1988b), exhibited no positive relationships between body size and activity range size. In fact, subadult sidewinders averaged larger activity ranges than did adults.

Sidewinders shifted their activity centers from one season to the next. For most shifts, the new seasonal activity range had little overlap with that of the previous season. Similar shifts in activity ranges have been illustrated for *Natrix natrix* (Madsen, 1984), *Nerodia sipedon* (Tiebout and Cary, 1987), *Crotalus horridus* (Reinert and Zappalorti, 1988a), and *Morelia spilota* (Slip and Shine, 1988b). During the activity season, most movements probably served to locate new foraging sites. Late fall and early spring spatial shifts were associated with movements to and from hibernating sites. Following spring emergence from hibernation, sidewinders shifted their activities back to the sandy region of the site. Possible benefits of the sandy region may include higher prey density, more preferable thermal environment, and greater efficiency in sidewinding over sand than over the rocky alluvial surface (Gans and Mendelssohn, 1972).

Combining the areas of temporal activity ranges may provide more realistic values of activity range size because it excludes areas that the snake did not use, areas normally included in the total activity range. This approach has yielded values of combined seasonal activity ranges that average 29.2–73.9% of total activity ranges (Madsen, 1984; Reinert and Zappalorti, 1988a; Slip and Shine, 1988b; this study). This method is preferable if some habitats included in the total activity range are completely unsuitable (Weatherhead and Hoysak, 1989). In my study, all parts of each individual's total activity range were accessible and suitable, with the exception of a two-lane paved road that passed through the western edge of the site (Fig. 1).

Activity ranges of snakes commonly overlap, especially where individuals exhibit similar habitat preferences (Reinert and Kodrich, 1982; Slip and Shine, 1988b) and/or use a common resource such as food (Wharton, 1969; Andrén, 1982), summer refugia (Weatherhead and Hoysak, 1989; Ciofi and Chelazzi, 1991), oviposition sites (Fitch and Shirer, 1971; Graves and Duvall, 1993), or hibernacula (Gregory, 1982; Duvall et al., 1985; Reinert and Zappalorti, 1988a). Whereas territoriality is a prominent feature of many lizard populations (Stamps, 1977), snakes are noted for their pronounced lack of mutually exclusive ranges and territorial behavior (Gregory et al., 1987). The extensive overlap of total activity ranges of sidewinders resulted from the large size of their ranges (greater chance for overlap) and from their congregation along the sand-alluvial border to overwinter.

The value of this study is that it is an unprecedented analysis of intraspecific variation in movement and activity range of a snake population. The data are unique because they are not biased by sex, age class, or season; and movements were measured as the actual distances traveled. This was possible largely because sidewinders live in sandy habitats, and their distinct tracks were readily followed. This information on the activities and spatial patterns of this desert-adapted reptile will hopefully benefit future inquiries of population energetics, community structure, and habitat management.

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ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

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