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Movement Ecology of *Coluber constrictor*  
Near Communal Hibernacula

WILLIAM S. BROWN AND WILLIAM S. PARKER

Several aspects of the spatial biology of the racer, *Coluber constrictor mormon*, were studied in 1971 and 1972 near communal hibernacula in a desert habitat near Grantsville, Tooele County, Utah. *Coluber* is an abundant, winter-aggregating species at this locality. We used radio-telemetry to track free-ranging racers during their spring migrations away from hibernacula and on their summer ranges.

Males dispersed a mean distance of 781 m and females 663 m. The geometric mean dispersal was 383 m, a more meaningful measure of central tendency for this parameter. Maximum dispersals recorded were 1.6 and 1.8 km from two separate den complexes. Because of an apparent increase in dispersal distance in the population since 1966, coupled with a population increase, seasonal remigration of *Coluber* to and from their hibernacula may fit a refuging model where competitive resource acquisition may, in part, govern the extent of these rhythmical movements.

On days when movements occurred during spring dispersal, mean travel rate of four females was 99.7 m/day. Once migratory movements commenced, long unidirectional distances were traversed within several days. Directional shifts at the end of migration, and less frequent and shorter subsequent movements, made a snake's home range distinct from its dispersal route. Mean movement on the home range was 31 m/day, on days when movements occurred. Ten females had home ranges averaging 0.4 ha. After sample size bias correction, mean home range size of 7 non-gravid females was 1.4 ha. Kansas racers, *C. c. flaviventris*, occupy home ranges ca. 7 times larger than Utah *C. c. mormon*. This major intraspecific geographic difference in spatial biology may be related to the larger age-specific body size of Kansas racers. "Total range," embracing all seasonal movements of an animal lacking home range stability, was previously advanced by others for *Coluber* at our study locality. Our findings do not support this concept.

Through 1971, 93% of 283 survivors returned to hibernate in the same den used the previous winter, whereas 7% hibernated in different dens. Such high fidelity to a specific den may have an olfactory basis. *Coluber* homed successfully after displacements of 100–300 m north and south of the main den in autumn, but snakes displaced east, where their return brought them near other dens, used these dens for hibernation and did not home successfully.

One female captured in successive springs at the same den migrated along an identical route and occupied the same home range both years. The orienting mechanisms used during migration are unknown, but dispersal distance and direction, as well as the home range area occupied, may become fixed behavioral attributes in many members of the population.

THE spatial biology of snakes, probably because of their secretive habits, has not received the attention it has with other reptilian groups. Blanchard and Finster (1933), after conducting one of the earliest mark-recapture studies of snakes, concluded that movements of *Thamnophis sirtalis* and *Natrix sipedon* in Michigan were unpredictable. They argued for wandering, rather than home range maintenance, in these species. Hirth et al. (1969) reached similar conclusions for three species of snakes in Utah. Numerous other studies, however, have demonstrated the existence of home ranges or limited movements in snakes (Carpenter, 1952; Clark, 1970; Fitch, 1958; Fitch and Fleet, 1970; Fitch and Shirer, 1971; Fraker, 1970; Platt, 1969; Seibert and Hagen, 1947; Stickel and Cope, 1947; Tanaka, 1973; Wharton, 1969).

Although several authors (Fitch, 1960, 1963a, 1963b, 1965; Lang, 1969; Prestt, 1971; Viitanen, 1967) have recorded dispersal of snakes migrating from hibernacula to summer ranges by recapturing marked snakes, and others (Barbour et al., 1969; Hirth et al., 1969; Naulleau, 1965; Smith, 1972) have recorded movements in radioactivity-tagged snakes, to our knowledge no investigators have attempted to track individual snakes during their long seasonal migrations from winter aggregation sites.

Several aims of this study were to determine 1) whether the duration and extent of a snake's annual remigration movements differ from its summer movements; 2) if a recognizable home range is established or if summer movements are variable and patternless; 3) whether a given dispersal route or home range (if established) is used by the same individual in different years; 4) if changes in population density affect dispersal distances; 5) whether a major intraspecific geographic difference in the home range size of *Coluber constrictor* may be demonstrated.

We used small radio transmitters in western yellow-bellied racers, *Coluber constrictor mormon* Baird and Girard, in northern Utah in 1971 and 1972 to elucidate these problems. We tracked racers in spring as they moved away from hibernacula and in summer after they had dispersed from dens. Recapture records of marked racers provided additional data on dispersal distances from hibernacula, den fidelity and home range occupancy in successive years, movements between adjacent den complexes, and homing to a den following displacement.

#### STUDY AREA

The study area is located 4 km W Grantsville, Tooele County, Utah (40° 36' N, 112° 32' W, elevation 1,580 m), or 58 km WSW Salt Lake City.

Vegetation conforms closely to Shelford's (1963) sagebrush-jackrabbit association. The immediate habitat is predominantly sagebrush (*Artemisia tridentata*) distributed uniformly throughout the area. Cheatgrass (*Bromus tectorum*), an introduced annual, is ubiquitous. Other species of introduced plants occur on disturbed sites (heronsbill, *Erodium cicutarium*; mustard, *Sisymbrium* sp.; bur buttercup, *Ranunculus testiculatus*). Disturbance of the habitat has been largely due to grazing of domestic sheep and cattle around the study site, as has historically occurred in many Great Basin plant communities in Utah (Cottam, 1961). Native desert bunchgrasses (*Agropyron* spp.), and shrubs (rabbitbush, *Chrysothamnus* spp.; snakeweed, *Gutierrezia* sp.; horsebush, *Tetradymia* sp.) constitute lesser site-specific elements of the flora.

Burrows of native mammals (kangaroo rats, *Dipodomys* spp.; antelope ground squirrel, *Ammospermophilus leucurus*) are important to *Coluber* in providing sites for retreat from extreme heat prevailing during summer (Brown, 1973). *C. c. mormon*, *Masticophis t. taeniatus*, *Pituophis melanoleucus deserticola* and *Crotalus viridis lutosus*, are the four most common snakes in the area (Parker and Brown, 1973; Woodbury et al., 1951).

The hibernacula ("dens") communally used by these species for winter hibernation consist of accumulations of rounded quartzite stones, each averaging ca. 30 cm in diameter (Fig. 1). Thickness of the deposits ranged from about 0.5–1.0 m above underlying soil in three places at one den. The hibernacula are of variable sizes (ca. 5 × 6 m to 15 × 18 m) and shapes. Rock piles were probably deposited as outwash material from gullies cut in the Pleistocene Lake Bonneville terrace immediately west of the dens (King, 1968). The nature and depth of hibernating locations within these dens are unknown. Depth, position, and activity of occupants during winter probably are similar to those of snakes excavated from a hibernaculum 23 km SE of our study site (Brown et al., 1974).

#### METHODS

We captured snakes in autumn and spring each year between 1969–1973 by encircling each rock pile with a wire screen fence at two series



Fig. 1. Snake hibernacula along eastern foothills of Stansbury Mountains, Tooele County, Utah, April 1971. Two M-complex rock piles, den 5 (top) and den 3 (bottom) typify several known groups of communal hibernacula in the area.

of closely-situated dens designated "M" (containing dens M, 1, 2, 3 and 5) and "S" (dens S1, S2 and S3) complexes (Parker and Brown, 1973). Individuals were marked following Brown and Parker (1976).

*Coluber* were tracked using techniques similar to those of Fitch and Shirer (1971) and Parker and Brown (1972). Thirteen snakes were monitored in the field for periods ranging from 5–78

days. Females, ranging from 60–77 cm snout-vent length and 89.2–146.0 g, were used because of their larger size (most males at the study locality were too small to accommodate a transmitter).

Transmitters used were similar to those described by Osgood and Weigl (1972). Each unit was a 1.3 × 3.5 cm polyethylene-encapsulated cylinder weighing 11. g. Reliable battery



life was  $40 \pm 10$  days. Transmitter frequencies were in the range 26.87–26.94 MHz.

Paraffin-coated transmitters were palpated into stomachs of nine snakes in 1971 and spring 1972. A thin nylon string was tied externally around the animal's body to prevent regurgitation of the unit following the procedure of Fitch and Shirer (1971). Transmitters were inserted surgically into the coelom of four individuals in summer 1972 through a longitudinal incision in the lateral abdominal wall at the stomach region (approximately mid-body). Closure was effected by a single cotton suture through the adjoining ends of each cut ventral scute. Only slight bleeding occurred. Healing in the field seemed complete within two weeks. Transmitter removal was by the same procedure, but on the opposite side from the first cut.

Lafayette "dynacom-12" receivers were used with separate, hand-held directional antennae. Signals could be received at distances of 50–100 m, depending on a snake's location. Each racer was located at least once per day, and, if visible, its activity was recorded. Most observations were brief ( $< 5$  min) to avoid disturbing the animal. Observations were more frequent (up to an average of over 3/day) when a snake was moving. During migration, racers were followed until they had stopped moving for the day (usually in late afternoon).

Snakes were released at the site of their emergence from a den in spring, or at the site of capture in summer. Two individuals in 1971 were tracked in June after being maintained in captivity for 37 and 40 days; five were released with transmitters 1–2 days after they were captured in the field. In 1972, six individuals were tracked in spring and summer beginning 1–11 days after capture. Females moving within limited areas that we considered home ranges were checked for 11 to 65 days; mean duration of home range records was 29 days per snake.

In autumn, snakes were captured when they returned to den M and some were displaced from this den to test their homing ability. Between 22–29 September 1971 on the day following capture, 30 *Coluber* (12 ♂♂, 18 ♀♀) were carried in cloth bags (admitting light but concealing visibility of the landscape) to measured release points 100, 200 and 300 m N, E and S of den M (nine release points in all). Three individuals were released at each distance N and S of the den, and four were released at each distance E of the den. Equal numbers

(9) of each sex were displaced both N and S; three males and nine females were displaced E. Possible effects of both displacement distance and direction on homing ability were tested by chi-square analysis, under the null hypothesis that returning to den M was independent of either factor.

To determine the ability of young racers to follow scent trails of conspecific adults, we conducted laboratory experiments between 11–19 October 1972 in a 1 m<sup>2</sup> test arena (cf. Gehlbach et al., 1971). Lab-reared hatchlings (late August progeny of a den area female) and 2-month-old juveniles (collected in early October at den M) were used. A 200 cm central octagon was marked out lightly in 1 cm increments on a cotton cloth substrate which was washed between trials. A scent trail was made by rubbing the lateral skin of an adult racer along the octagon. Hatchlings were introduced from a central release cylinder and observed for 3 min. Reactions of the snakes upon contacting the scent trail were scored as 1) crossing the trail with no evident reaction to it, 2) a momentary hesitation but with no following response or 3) a hesitation, turn and movement along the trail. The distance of each trail-following movement was measured from the point of contact to the point of departure from the trail.

Shedding locations at dens 1 and 5 in autumn provided additional information on intra-complex movements. Shedding records were based upon 12 snakes in a pre-shed (eye opaque) condition which were assumed to have subsequently shed where captured, and upon 22 marked skins under brush at the edge or on the rocks of a given den. The hibernation site was based on spring emergence. These two dens were not fenced in spring 1973 to verify autumn 1972 den choice of 11 snakes leaving marked skins within M complex. We assumed that the hibernation site of these individuals was the same den from which each had emerged in the previous two successive years.

The term "home range" as used here follows Brown and Orians (1970): "The area in which an animal normally lives, exclusive of migrations, emigrations, or unusual erratic wanderings."

Locations of telemetry-monitored snakes were flagged and measured from field landmarks using a surveying transit. Directions were reckoned from true north. A large-scale location map was prepared from an aerial photograph of the area. Overall accuracy is to within

TABLE 1. DISPERSAL OF 34 *Coluber constrictor mormon* FROM FIVE HIBERNACULA (M COMPLEX), TOOELE COUNTY, UTAH, IN 1971 AND 1972. Records include hand recaptures of 27 marked snakes (15 males, 12 females) and seven females monitored by radiotelemetry (three of which were captured on summer ranges).

Den From Which Snake Emerged	Dispersal Distance (m)*			Dispersal Direction**				Recapture Interval (days)		
	Mean	Range	N	NE	SE	SW	NW	Mean	Range	N†
M	490	15–1,373	8	3	2	2	1	41.4	24–60	5
1	494	40–1,056	10	3	5	1	1	29.7	9–57	7
2	976	206–1,488	3	1	2	–	–	30.6	23–35	3
3	880	124–1,632	3	3	–	–	–	47.3	23–75	3
5	988	8–1,555	10	8	2	–	–	36.6	20–63	10
	713	8–1,632	34	18	11	3	2	36.2	9–75	28

\* From center of hibernaculum to approximate center of home range (telemetered snakes) or to point of recapture.

\*\* Scored as within 90° quadrants from hibernaculum.

† Sample size may be less than number of snakes recaptured because of no spring emergence records for two snakes, and exclusion of time records of four telemetry snakes tracked during dispersal.

± 2 m of a flagged position. Measurements were plotted on graph paper (scale 1 mm = 1 m) and home range sizes were calculated by counting squares within the enclosed convex polygon. The convex polygon method has historical prominence and graphical simplicity, but is not devoid of sample size bias (Jennrich and Turner, 1969). We compensated for the statistical unreliability of this method by using the appropriate correction factor (Jennrich and Turner, 1969) for the number of different daily location points in each home range.

Statistical data reported herein are followed by ± 1 standard error (SE) of the arithmetic mean. Inspection of the distribution of dispersal distances indicated positive skewness, so these data were transformed to logarithmic scale. Geometric means and 95% confidence limits for these retransformed means were calculated following Sokal and Rohlf (1969).

## RESULTS

*Dispersal from hibernacula.*—Recaptures of marked snakes after their release at M-complex hibernacula in spring provided information on extent and direction of dispersal movements (Table 1). These data show considerable variability. Some individuals in the M-complex population traveled considerable distances away from dens, whereas others did not. For example, a male was recaptured 8 m from its den 63 days after release, whereas another male was recaptured after 25 days 1.5 km from the same den.

Dispersal distances from M complex averaged 781 (median 885) m for 15 males, and 663 (median 705) m for 19 females. These data include records of seven females tracked by radiotelemetry, but exclude records of one tele-

metered snake (No. 8) that appeared to establish a home range within M complex itself in spring 1972, but then moved 213 m SW. Whether this individual may be considered to have dispersed before the time of its home range occupancy or afterwards seems equivocal.

Dispersal times (Table 1) should be interpreted as maximum intervals, as four individuals tracked with transmitters reached home ranges within 24 days (see below). For two individuals recaptured the greatest distance in the shortest time interval, greatest rates of movement were 77 m/day from M complex and 62 m/day from S complex. All other minimum rates of dispersal from M complex calculated in this manner averaged 45.8 (24.3–64.7) m/day over distances ranging from 878–1,632 m (n = 10).

A majority (85%) of recapture records and movements of radio-equipped snakes were east of the M-complex hibernacula (Fig. 2). Ten recaptures after 9–36 days averaged 432 (374–556) m E or ESE of S complex. In addition, nine racers marked in this area in summer 1971 subsequently emerged from S-complex dens the following spring. Mean dispersal distance was 426 (341–556) m.

Our collecting efforts and recapture records of S-complex snakes were strongly clustered around an abandoned farm area which appeared to be attractive to *Coluber* and to two other species (*M. taeniatus* and *P. melanoleucus*), possibly because of an abundance of small mammal burrows that served as oviposition sites (Parker and Brown, 1972) and perhaps shelter. Considering the large population overwintering at den S-3 (272 *Coluber* captured in spring 1972), the sample of 10 recaptured in summer 1972 indicates that only

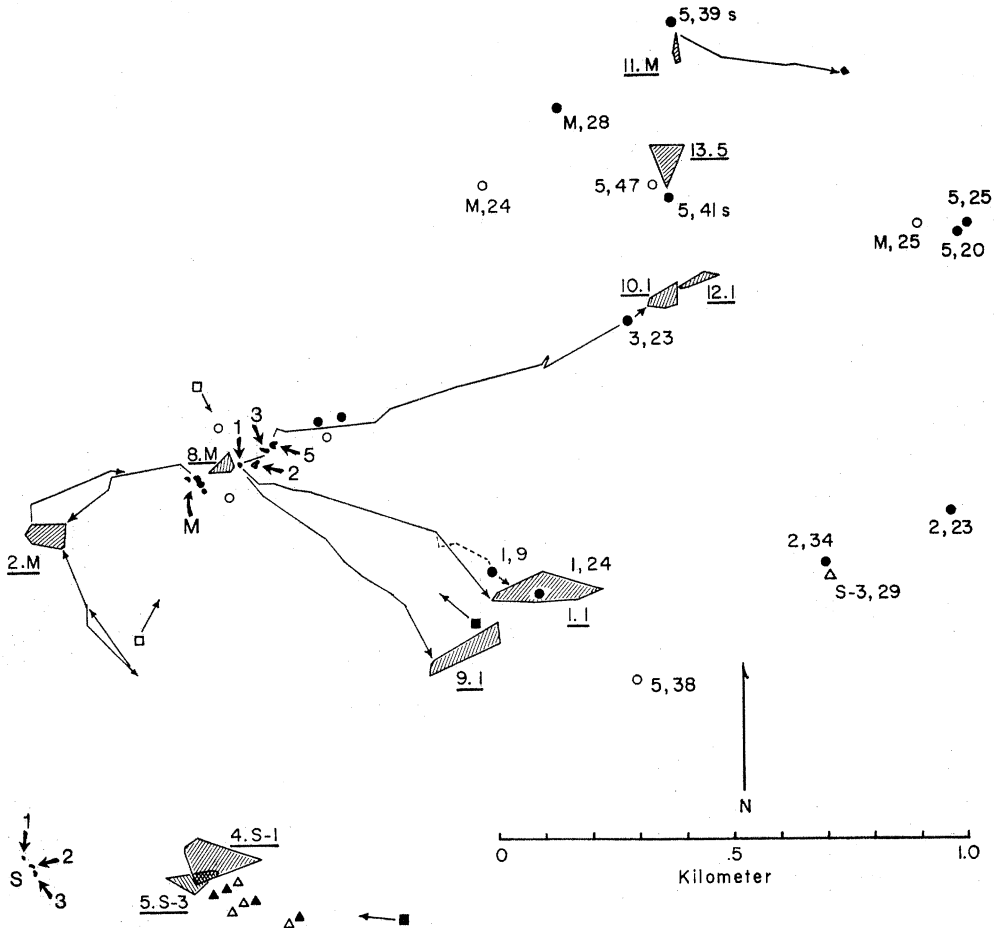


Fig. 2. Location of M and S-complex hibernacula and selected dispersal records of *Coluber constrictor mormon* in 1971 and 1972. Large arrows point to specific numbered dens. Circles indicate recapture points of snakes from M complex, triangles snakes from S complex; squares indicate autumn recaptures, with arrows indicating presumed direction of movement based on known hibernation records. Solid symbols represent males, open symbols females. Numbers beside points of location indicate den from which snake emerged, followed by interval (days) between date of release and date of recapture. Two records based on recovery of marked skins are indicated by "s." Home ranges of 10 snakes monitored by radiotelemetry are indicated by shaded areas, denoted by their sequence number (cf. Table 3, Fig. 3), followed by their den number (underlined). Routes of migration from hibernaculum to home range in spring and a route of ingress in autumn are shown for four females (1, 2, 9 and 10).

a small portion of the population dispersed to the homestead area. One record suggests that snakes from S complex may disperse distances comparable to those from M complex. A female was recaptured 1.8 km NE of den S-3 after 29 days.

*Movements during dispersal.*—Considerable variation between telemetered individuals occurred in the total time of migration and in the proportion of days that movements occurred (Table 2). Frequency of movement days ranged from 39–80% of migration time. On 31 days

when movements occurred, mean distance moved was 99.7 (8.0–304.0) m/day. Each migration included at least one day when a movement of over 100 m occurred; the 5 maximum daily movements averaged 223 m/day.

Individual differences in migration are best illustrated by comparing three snakes (Table 2). Snakes 9 and 10 each delayed long unidirectional movements until periods of 9 and 16 days after release. During this "pre-migratory" interval, snake 9 initially moved 82 m SE of her release point on the second day, and

TABLE 2. FREQUENCY AND EXTENT OF DISPERSAL MOVEMENTS FROM HIBERNACULA TO HOME RANGES OF FOUR FEMALE *Coluber constrictor mormon* TRACKED BY RADIO-TELEMETRY IN TOOELE COUNTY, UTAH.

Snake No.	Date Released to Date Arrived at Home Range	Migration Interval (days)	No. Days Movements Recorded	Mean Distance Moved per Day (m)*	Total Migration Distance (m)**
1.	12-16 June 1971†	5	4	156.7 (47.0-304.0)	627
1.	15-18 May 1972	4	3	215.3 (166.0-275.0)	654
2.	22 June-1 July 1971††	10	5	57.2 (16.0-104.0)	286
9.	24 April-6 May 1972	13	5	120.0 (36.0-203.0)	600
10.	26 April-20 May 1972	24	14	73.3 (8.0-229.0)	1,025

\* Calculated for days when movements occurred.

\*\* Measured from point of release to edge of home range along course traveled by snake.

† Released 40 days after emergence.

†† Released 37 days after emergence.

remained there and at a nearby location (twice shifting back and forth) for 7 days. Extensive movements began on 3 May and continued through 6 May when the snake arrived at her home range, covering 518 m in four days. An abrupt directional shift occurred on 6 May as the snake turned directly east from its SSE migratory course (Fig. 2).

Individual 10 initially moved 189 m (7 moves) between 26 April-11 May, generally in a NE direction (Fig. 2). Sustained lengthy movements began on 12 May. The nearly due-east portion of her migration route was in a gully, but on 15 May her direction shifted toward NE and the snake moved across homogeneous sagebrush terrain. Home range arrival was on 20 May. Movements during the active phase of migration averaged 119.5 m/day.

Female 2 was released on 22 June 1971. She remained at one location near den M for 6 days before making long movements W up a gently-sloping gully. On 30 June she approached the end of the gully, then turned sharply south before stopping (Fig. 2). On 1 July, she moved 46 m SW to her home range. Movements during the last four active days of her migration averaged 67.5 (45.5-104.0) m/day. Twelve days later (after an excursion from the home range [see below]) this snake moved 114 m NNE, then turned E back down the gully and was captured near her original release point. On 30 July she was again released at her last location in the gully. Her subsequent movements were again west, then south-

west as before, and she returned to one of her previous home range locations. Total distance traveled in four days during the second "migration" was 206 m.

*Individual remigration in successive years.*—In 1971, female 1 moved 153.5 m on the day of release (12 June). On 13 June she did not move, but on the following three days she moved 47, 122.5 and 304 m respectively, arriving at her home range on 16 June. At the end of the last day's migration an abrupt change in direction from a direct SE course to a NE course took place. This turning point was considered the first position of her home range (Fig. 3).

This snake was recaptured in 1972 after emerging from the same hibernaculum. After her release on 15 May she moved 275, 166 and 205 m between 16-18 May and arrived at the same home range area.

In both years the migratory routes were nearly identical. Exact locations marked along the route were different each year because of different distances moved, but the direction taken (105° E of N) during the first two-thirds of the migration was essentially the same both years (Fig. 2).

At a spot 449 m SE of the den the snake's direction shifted toward S by about 37° in 1971 and by about 67° in 1972. This directional change occurred 33.5 m after movement commenced on 16 June 1971, whereas in 1972 it occurred during the first movement on 18 May. At the "turning point" the snake was at an identical spot in both years. In 1972 subsequent



TABLE 3. HOME RANGE SIZE AND MOVEMENTS OF 10 FEMALE *Coluber constrictor mormon* TRACKED BY RADIOTELEMETRY IN TOOELE COUNTY, UTAH.

Snake No.	Inclusive Dates on Home Range	Total No. Days on Home Range	No. Days Movements Recorded	Maximum No. Consecutive Days at One Location	Mean Distance Moved per Day (m)	Max. Distance Between Farthest Outer Points of Home Range (m)	Area of Home Range (ha)
1.	16 Jun-15 Jul 1971 18-24 May 1972	36	13	16	47.2 (4.0-133.0)	248	1.041
2.	2-6 Jul, 7-30 Aug, 1 Sep-6 Oct 1971	65	18	13	20.4 (3.0-51.0)	94	.323
4.	4 Aug-14 Sep 1971	41	19	6	31.1 (7.0-88.5)	177	.868
5.	6 Aug-3 Sep 1971	29	6	13	25.1 (5.5-69.0)	101	.221
8.	26 Apr-16 May 1972	21	9	8	22.4 (5.0-45.0)	64	.141
9.	6-30 May 1972	25	10	7	55.7 (7.5-164.5)	182	.539
10.	20-24 May, 1-6 Jun 1972	11	7	3	32.4 (7.0-63.0)	72	.153
11.	8-18 Jun 1972*	11	8	3	21.9 (5.0-45.5)	60	.065†
12.	8 Jun-8 Jul 1972	31	9	8	47.1 (21.5-98.0)	97	.114
13.	18 Jun-9 Jul 1972	22	10	12	25.6 (5.5-91.0)	101	.374

\* Initial home range before shift to oviposition site.  
† Combined area of both regions occupied.

movements over the final 205 m (dashed line, Fig. 2) were erratic compared to a direct heading toward the home range area in 1971.

*Mating activity during spring dispersal.*—Two different male *Coluber* were captured while we monitored female 1 in 1972 (Fig. 2). The first male crawled directly underneath one of us on 18 May as the female was moving, approaching her home range. Previously, another racer (about the same size) was seen along the path of the female. If the captured male was the same individual, it had traveled at least 93 m, presumably in pursuit of the female. Two days later in the female's home range a different male was with her. We observed courtship behavior between them.

A 2-day interruption in movements of snake 10 took place on 17 and 18 May (jagged inflection in migration path, Fig. 2), when she was seen on both days with another racer (presumably a male). Mating activity may have occurred at this point. On 19 May the female

moved farther NE, and on that day a marked male was coiled closely beside her.

*Spatial dispersion of home ranges.*—As only a small percentage of the racer population could be tracked, home ranges of telemetry-monitored snakes were rather broadly dispersed. Spatial overlap between two home ranges was noted once (Fig. 2). Overlap was synchronous in mid-August 1971 when the two snakes were located 15 m from each other. Thereafter, distances between them diverged.

The group of recapture records of S-complex racers in the homestead area E of the dens, although reflecting our collecting efforts there, indicated a strong possibility of home range overlap in summer (Fig. 2). Between 2-4 June 1972, seven marked snakes (3 ♂♂, 4 ♀♀) were captured 21-32 days after release. In both time (3-day capture interval) and space (maximum separation 58 m), these individuals would likely have overlapped given a mean home range movement rate of 31 m/day (see below).

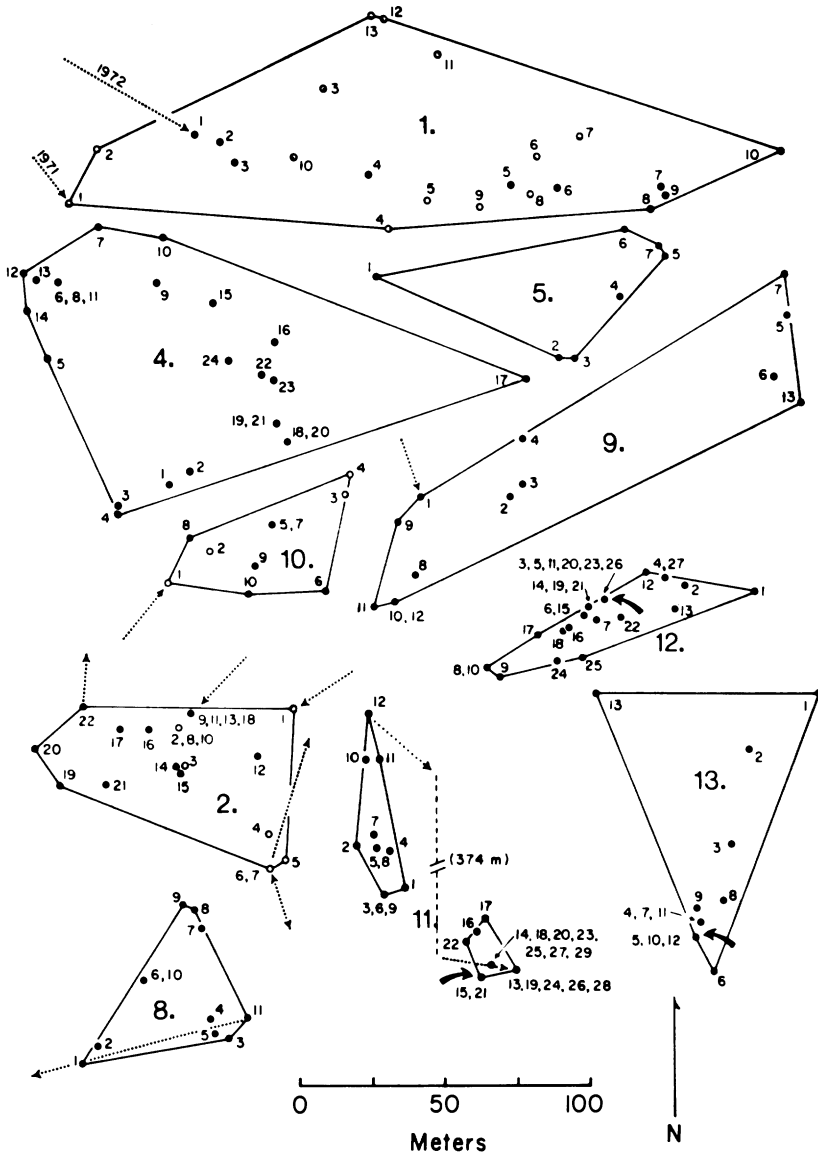


Fig. 3. Home range maps of 10 female *Coluber constrictor mormon* tracked by radiotelemetry. Large numeral indicates snake number (cf. Table 3, Fig. 2). Numbered points indicate positions of successive movements for each snake. Locations plotted were mostly, but not necessarily, on different dates. Dotted lines indicate movements to or from home range. Open circles for snake No. 1 represent locations in 1971, solid circles for snake No. 2 represent locations between 1-11 July 1971, solid circles between 8 Aug.-6 Oct. 1971. Heavy curved arrows for three gravid females (Nos. 11, 12 and 13) denote oviposition sites.

Two home ranges were contiguous (Fig. 2) but did not overlap in space or time. On 22-23 May 1972 one racer occupied a burrow entered by another 17 days later. After investigating the burrow, the second individual moved away from the site.

*Home range size.*—Mean home range movement was 30.6 m/day (109 movement days) (Table 3, Fig. 3). Frequency of movement was 37% of 292 home range days. Time spent at one location ranged from 3-16 consecutive days; proportion of home range time spent consecutively

at one location ranged from 15–55% (mean 31%) of the times that individuals were tracked.

Unadjusted home range areas ranged from 0.06–1.04 ha (mean  $0.38 \pm 0.11$  ha,  $n = 10$ ). However, non-corrected home ranges of 7 non-gravid females were notably larger ( $\bar{x} = 0.47$  ha) than those of 3 gravid females ( $\bar{x} = 0.18$  ha), possibly because the latter restricted themselves to a smaller area while searching for a suitable oviposition site. Employing Jennrich and Turner's (1969) sample size bias corrections, mean home range size for the 7 non-gravid females was  $1.45 \pm 0.81$  ha. For these individuals, 95% confidence limits were 0.64–2.26 ha. Based on this sample, one can be 95% confident that the mean home range size for the female *Coluber* population at the study locality would lie within these limits if similar tracking techniques, observation times, and sampling bias compensations were employed.

*Excursions from the home range.*—Between 1–5 July 1971, daily movements of female 2 were short (5–42 m/day) and were concentrated within a small area. On 6 July the snake made an unexpected long move 141 m SSE, and by 8 July she was far from her home range. In the next two days she moved 188 m back to precisely her second location of 6 July and returned to her original home range departure point by 11 July. The entire trip “out” (341 m) and “back” (329 m) took 6 days (see arrows depicting this movement, Fig. 2).

Female 11 was gravid when captured on 5 June 1972, 1.35 km NE of den M. She was released carrying a transmitter on 8 June. For the next 11 days she remained in a relatively small (473 m<sup>2</sup>) area (Figs. 2 and 3). On 19 June the snake undertook a long (374 m) journey eastward, moving underground into a small mammal burrow system (presumably antelope ground squirrel) where she oviposited on 21 June. The “shift” in home range seemingly was correlated with reproductive activity (i.e., locating an oviposition site).

*Autumn aggregation.*—Snake 2 began to move back to den M on 6 October 1971. The first of this series of movements was 27 m NW within the home range (location 21 to 22, Fig. 3). On 7 October she moved 43 m N, and on 8 October turned E and moved 92 m to the gully that had been the site of her earlier migration movements. She continued another 62 m E in the gully, reaching a point 135 m from den M (her presumed goal) on 13 Octo-

TABLE 4. DEN SHIFTS BY *Coluber constrictor mormon* > 1 YEAR OLD WITHIN M COMPLEX IN 1971. Shifts involve use of a different hibernaculum in two successive winters (1970–71 vs. 1971–72). Percentages in each den-sex category are based on the total number of known survivors for that category.

Den	Males				Females			
	Returned to Same Den		Returned to Different Den		Returned to Same Den		Returned to Different Den	
	N	%	N	%	N	%	N	%
M	53	94.6	3	5.4	55	96.5	2	3.5
1	29	96.7	1	3.3	25	86.2	4	13.8
5	55	91.7	5	8.3	45	88.2	6	11.8
	137	93.8	9	6.2	125	91.2	12	8.8

ber where she remained until collected on 5 November.

*Home range occupancy in successive years.*—The same home range area may be occupied in successive years. The strongest case for this was provided by the telemetered female which in 1972 reached the same area occupied in 1971 (see above). Recaptures of three snakes (1 ♂, 2 ♀♀) in summer 1972 at the abandoned farm area were within 50 m of previous capture locations a year earlier. A male in September 1971 (square symbol with arrow, bottom Fig. 2) was recaptured at this spot in May 1972, nine days after spring emergence. A female with no hibernation records at dens was recaptured in June 1973 and 1974 within 50 m of her 1972 capture location (1.4 km NE of M complex).

*Intra-complex den fidelity.*—Three dens (M, 1 and 5) within M complex were sampled in two successive years. Through 1971, 283 survivors were recaptured the second year; of these, 262 (93%) returned to hibernate in the same den used during the previous winter, whereas 21 (7%) hibernated in a different den the next year.

Inter-den shifts were tabulated by den and sex (Table 4). Females were slightly less prone to return to the same den than were males. Most pronounced proportions of snakes shifted from dens 1 (8.9%) and 5 (8.5%). Dens 2 and 3 were not sampled in both years. Two-way exchanges occurred between dens M, 1 and 5 in all three possible combinations between them, but exchanges involving dens 2 and 3

TABLE 5. RESULTS OF LABORATORY TRAIL-FOLLOWING TESTS OF 11 YOUNG *Coluber constrictor mormon* IN OCTOBER 1972.

Subjects (n)	Number of Contacts with Trail	Response to Adult Scent-trail		
		Crossed Trail, No Response	Hesitated & Crossed Trail	Followed Trail
Lab-reared hatchlings (4)	16	4 (25%)	5 (31%)	7 (44%)
2-month-old field juveniles (7)	27	9 (33%)	2 (7%)	16 (59%)

with others occurred only between the closely situated dens 1 and 5 (it was not possible to record reciprocal shifts between dens 2 and 3).

Den fidelity of hatchlings in 1971, although based on limited data because of low survivorship in this age class, also indicated a tendency to return to the same den. Among seven surviving hatchlings recaptured as 1-year-olds (2 of 18 at den M, and 5 of 10 at den 5), 5 (71%) returned to their original den and 2 (29%) shifted to another den after one year.

We identified a number of shed *Coluber* skins found in the field as skins from marked snakes. Most were at or near dens of M complex in autumn and represented a snake's final exuviation prior to hibernation. Of 34 snakes providing such evidence of shedding location within M complex and known to have used either dens 1 or 5 for hibernation, 17 (50%) shed at locations away from their "home" den. Snakes using den 1 shed at that den more often (60% of 15 shedding records) than did snakes using den 5 (42% of 19 records). Den 1 snakes most frequently (27% of records) used den 2 as a shedding site, whereas den 5 snakes most frequently (47% of records) used the adjacent den 3 for shedding. In autumn 1970 and 1971, when we knew for certain what den a snake had used for hibernation, 5 of 11 (46%) den 1 snakes had shed at dens 2 or 3, and 7 of 12 (58%) den 5 snakes had shed at den 3 or elsewhere in the complex. When 11 autumn 1972 shedding records were compiled, data for dens 1 and 5 combined in 1970–71 (52% shedding away from hibernation den) were compatible with the result of 50% shedding elsewhere in all three years.

*Scent-trailing ability.*—Snakes moved from the central release point of the trailing chamber to or across the surrounding scent trail in 43 of 52 trails. In 23 instances where the trail was followed (Table 5), mean distance moved along it was  $55.9 \pm 10.4$  (2–196) cm. The longest movement involved turning a corner along the octagon 7 times. When a snake's head crossed

the trail the most common response was to hesitate with rapid tongue flicking. This occurred whether the snake crossed the trail or turned and followed it. One individual reacted by undergoing rapid anteriorly-directed, reverse muscular waves of the forebody. These wriggling movements lasted about 5 sec and preceded trail-following in five trials.

*Inter-complex movements.*—As M and S complexes are located 875 m apart, and some *Coluber* disperse up to 1.6 and 1.8 km from each, exchanges between these two groups of dens is to be expected. Only in 1972, however, were two such movements recorded. Both instances involved hatchling snakes that moved from M to S after a single intervening activity season.

Two dispersal records for adults may indicate possible genic exchange between the two populations on their summer ranges. An S-complex female and an M-complex male were captured together on 7 June 1972 (Fig. 2). The female had motile spermatozoa in her cloaca, indicating possible recent mating with the male.

*Displacement and homing.*—Thirteen racers (6 ♂♂, 7 ♀♀) returned to den M within a mean time of 9.5 days after displacement (Table 6). There was no correlation between distance displaced and return time ( $r = -0.02$ ,  $P = 0.05$ ). Three snakes returned in 4–8 days, whereas most (77%) returned after 9–12 days, between 3–8 October. Two individuals were later captured at den M the following spring (1972); in all, 15 of 30 (50%) displaced snakes homed successfully. An independence test indicated that a racer's ability to return was not significantly impaired by the distance of displacement ( $\chi^2 = 0.20$ ,  $P = 0.90$ ).

Of the remaining 15 snakes that did not return, 14 were captured in spring 1972 at other M-complex dens. A snake's ability to return to den M was significantly dependent on the direction of displacement, as an independence test did not support the null hypothesis for this factor ( $\chi^2 = 7.63$ ,  $0.025 < P < 0.01$ ).

TABLE 6. RETURNS OF *Coluber constrictor mormon* DISPLACED FROM DEN M IN SEPTEMBER 1971. Numbers indicate displaced snakes recaptured either in the same season (autumn 1971) or the following spring (1972) at emergence from hibernation.

Direction	Displacement		Den Returned To				
	Distance (m)	N	M*	1	2	3	5
N	100	3	2	1	-	-	-
N	200	3	3	-	-	-	-
N	300	3	2	-	-	-	1
S	100	3	3	-	-	-	-
S	200	3	1	2	-	-	-
S	300	3	2	-	-	-	-
E	100	4	1	2	-	1	-
E	200	4	1	2	-	-	1
E	300	4	-	-	1	-	3

\* Presumed goal of displaced snakes.

Among 18 N and S displacements, there were four (22%) returns to other M-complex dens (one snake displaced 300 m S was not recovered) (Table 6). Of 12 displacements E of den M, there were only two (17%) successful returns, and 10 (83%) to the four major dens located 100–150 m E of den M. The next year (autumn

1972 and/or spring 1973 recaptures), four of these 10 individuals returned to den M.

Homing to den M was unsuccessful in three transmitter individuals displaced, although long unidirectional movements were exhibited (Table 7). Two individuals displaced 300 m N and S of den M each moved long distances in approximately the correct direction (SE and WNW, respectively), but subsequently seemed lost, moving W and NW instead of E and SE toward den M. The third snake, displaced 200 m N, headed directly W rather than S as expected. Two of the same individuals were captured, transported in cloth bags, and re-displaced to the east where homing was again unsuccessful.

#### DISCUSSION

*Dispersal and the refuging model.*—Dispersal of several species of colubrid and viperid snakes from hibernacula to summer ranges has been reported by several authors. In Kansas, *T. sirtalis*, *Elaphe obsoleta* and *Agkistrodon contortrix* dispersed mean distances of 347–656 m (Fitch, 1960, 1963b, 1965). *Storeria occipitomaculata* dispersed 152–305 m in Minnesota (Lang, 1969) and *S. dekayi* 817 m in New York (Noble and Clausen, 1936). In Utah, *M. taeniatus* dispersed a maximum of 3.6 km (Hirth et al., 1969) and *P. melanoleucus* 875 m

TABLE 7. SUMMARY OF HOMING MOVEMENTS OF THREE FEMALE *Coluber constrictor mormon* DISPLACED FROM DEN M IN AUTUMN 1971 AND TRACKED BY RADIOTELEMETRY. Number of days involved in each movement in parentheses.

Snake No.	Date Displaced	Location Released from den M	Distance (m) and Direction		
			Movement	Snake's Location from den M	
6.	16 Sep	300 N	245 SE (1)	175 NE	
			60 W (2)	135 NNE	
			40 N (16)	170 NNE	
			60 NW (7)	190 NNE	
			65 W (4)	180 N	
7.	16 Sep	200 N	320 W (3)	365 NW	
			65 SW (1)	375 WNW	
	19 Sep	200 E	50 NW (1)	150 ENE	
			30 NE (1)	170 NE	
8.	26 Sep	300 S	95 WSW (1)	370 WSW	
			95 SE (9)	380 S	
			380 WNW (2)	180 WSW	
				180 W (2)	360 WSW
	9 Oct	300 E	80 N (3)	305 ENE	
			20 E (1)	325 ENE	



TABLE 8. MIGRATORY DISTANCES FROM HIBERNACULA TO SUMMER RANGES OF *C. c. flaviventris* (KANSAS) AND *C. c. mormon* (UTAH) AND FOR TWO TIME PERIODS 5 YEARS APART IN UTAH. All Utah dispersal data pertain to snakes recaptured > 15 days after release at hibernacula; 95% confidence limits for geometric means in parentheses.

Locality & Investigator	N	Method	Dispersal Distance (m)		
			Median	Mean	Geometric Mean
Kansas (Fitch, 1963a)	124 (55 ♂♂, 69 ♀♀)	hand captures, live traps	314	339	...
Utah 1966 (King, 1968)	14 (5 ♂♂, 9 ♀♀)	radioactive tags	247	289	211 (127–351)
Utah 1971–72 (present study)	32 (14 ♂♂, 18 ♀♀)	hand captures, biotelemetry	882	739	383 (225–657)

(Parker, 1974). European *Vipera berus* disperse 300 m–1.9 km, depending on locality (Prestit, 1971; Viitanen, 1967). Oklahoma *Crotalus atrox* are known to disperse up to 3.5 km (Landreth, 1973) and *C. viridis* dispersed up to 1.2 km in Utah (Hirth et al., 1969).

Comparisons of seasonal dispersal between widely separated populations of *C. constrictor* (Kansas and Utah), and between recent time periods within one population in Utah, reveal several differences (Table 8). In Kansas, *C. c. flaviventris* dispersed mean distances of 435 (♂♂) and 372 m (♀♀) (Fitch, 1963a). Hirth et al. (1969) stated that *C. c. mormon* at our Utah study locality in 1966 dispersed distances similar to those in Kansas. Most dispersal points shown by Hirth et al. (1969) were within a 750 m radius of den M; only one of 40 snakes was located a maximum of ca. 900 m away. To approach a normal distribution in the dispersal records, we calculated geometric means for some of the 1966 dispersals (available in King, 1968) and for our own records. Although not statistically different ( $t = 1.37$ ,  $0.20 > P > 0.10$ ), the geometric mean dispersal distance in 1971–72 was 1.8 times greater than in 1966.

Why has an increase in dispersal distance apparently occurred in the population during the intervening five years at our study locality? Data of Hirth et al. (1969) applied only to den-M *Coluber*, whereas our records include snakes from other dens of M complex unknown to these workers and not sampled in their study. We do not know whether racers from these dens dispersed farther than did den-M snakes in 1966. Our data indicate that such was not the case in 1971 and 1972.

Recaptures of radioactivity-tagged racers from

den M in 1966 generally ran in a broad NW-SE pattern from the den (Hirth et al., 1969). Most of our recaptures were in an area generally NE and SE of M complex (our sampling efforts were primarily concentrated in eastern sectors). These included individuals from den M along with snakes from other dens. Based on our recent observations of dispersal from dens 1–5, directions of dispersing racers from den M may have differed from those of other dens in 1966.

There may be a similarity of dispersing *Coluber* around M complex to a refuging model, defined as “the rhythmical dispersal of groups of animals from and their return to a fixed point in space” (Hamilton and Watt, 1970). The system involves a fixed core or central place from which radial dispersal is initiated; some well-defined limit of dispersal; and the arena where resource acquisition takes place. Control of distance from the core is based on the ideas that 1) intraspecific competition declines with greater distances, thus compensating those individuals that disperse farthest, and 2) the additional energy and time required to reach more distant but less heavily exploited ranges act to limit dispersal distances (Hamilton and Watt, 1970).

A snake hibernaculum may be likened to a core at the center of a dispersal arena which differs in its time component from bird roosts or mammal watering areas in that dispersal is an annual, rather than a daily, event.

Three facets of our data may provide empirical bases in support of a refuging model involving snake hibernacula: 1) There is a gradation of migratory distances undertaken by individual racers, some remaining near hibernacula (presumably throughout the sum-

mer), and some dispersing relatively long distances in the same season. This observation supports the predicted energy balance mechanism. 2) Between 1966 and 1971 the *Coluber* population at den M nearly tripled in size (Brown, 1973; Parker and Brown, 1973). If this increase in population density caused greater resource utilization pressure in areas closer to the core dens, intraspecific competition would increase and individuals should disperse farther. 3) All three measures of central tendency (median; arithmetic and geometric means) of dispersal distances in our study are considerably greater than those reported in 1966.

*Orientation and den fidelity.*—Clearly, several individual *Coluber* tracked during dispersal exhibited unidirectional courses which involved more extensive movements than were observed at any other time. Once migratory movements commenced, long distances were traversed within a few days.

The orienting mechanisms used during migration remain unknown at present. It is well established that snakes have a keen sense of smell (Burghardt, 1970; Noble, 1937) and can use this sense to aggregate (Dundee and Miller, 1968; Gehlbach et al., 1971; Noble and Clausen, 1936). Solar cues were used by rattlesnakes (*C. atrox*) to follow fixed directional paths after displacement (Landreth, 1973) and by aquatic snakes (*Natrix sipedon* and *Regina septemvittata*) to orient with respect to a shore line (Newcomer et al., 1974).

Sun-compass orientation may operate to guide adult *Coluber* in their denning migrations in some cases exceeding 1 km. It would appear improbable that snake pheromones could remain sufficiently permanent to enable trail-following from long distances, although scent trails may be important near dens. Two individuals we tracked during migration utilized gullies as pathways for part of their trips, then left them and moved in different directions. One of these snakes utilized the same gully between its den and home range on four occasions. Although our experimental techniques may have affected the snake's motivational state, producing the repetition of these movements, this individual certainly seemed familiar with its route. Two other individuals took directed courses in undistinctive shrub habitat to reach home ranges.

Our results on den fidelity, where more than 90% of snakes returned to the same hibernaculum within M complex, indicate that not only can *Coluber* remigrate back to the com-

plex over long distances in autumn, but that they seek out the particular den within the complex that may be considered their "home den." The phenomenon of regularly returning to a certain denning area is well documented in snakes (Fitch, 1960, 1963a, 1965; Prestt, 1971; Viitanen, 1967; Woodbury et al., 1951), but usually this involves returning to a series of dens, rather than to a specific den within a complex. The several dens immediately east of den M are located within 85 m of one another, and none is separated from its nearest neighbor by more than 35 m. In view of their proximity, and of the long dispersals of racers, the discriminative ability of these snakes seems remarkable, but not undocumented in other species. Lang (1969) reported greater than 90% returns of *S. occipitamaculata* to the same ant-mound hibernacula in successive winters, and Kelleher and Tester (1969) noted a similar high degree (88–95%) of natural homing returns of toads, *Bufo hemiophrys*, to specific hibernation mounds.

Homing ability has been shown previously for two other snake species (*M. taeniatus* and *C. viridis*) at den M (Hirth, 1966), and displaced *N. sipedon* can return to home ponds (Fraker, 1970). Neither study provided evidence for the homing mechanism(s). One experimentally blinded *M. taeniatus* displaced 235 m from den M by Parker (1974) homed, as did all of 13 others from 100–300 m. Olfaction and familiarity with local landmarks around the den were considered important in the homing ability of whipsnakes (Parker, 1974).

The ability to home successfully to den M after displacement in autumn from distances up to 300 m north and south of the den demonstrates an orientation capability in racers. We do not know whether random search, known landmarks, olfaction, or some combination of these was involved in this homing. Certainly this would be a fruitful line of further research. Considering that a racer's locating the "correct" den may occur after skin shedding at another nearby den in autumn, the high degree of natural den fidelity would seem to provide circumstantial evidence for olfaction as a possible cue.

Racers displaced from den M to the east had to pass near four other dens in returning to den M. Most behaved opportunistically to a "strange" den after displacement: they wintered and survived in dens other than their supposed "preferred" den. Possible explanations for this may be: 1) a presumed olfactory-

based site memory and/or the snakes' motivation to return were disrupted experimentally by the act of displacement itself; or 2) the stimulus of another den's presence temporarily suppressed any motivation to seek the home den when failure to find it could have resulted in winter mortality. Of 14 displaced snakes that were recovered in other dens, six came back to den M naturally the next year. Evidence of preference for den M was available for four of these snakes by at least two successive years' capture records at den M preceding displacement.

Each of the three snakes we displaced carrying transmitters also had at least one year's prior history of returning naturally to den M. Thus, each may have been familiar with a route back to the den. Although they did not home successfully, direct headings were taken initially, appearing to demonstrate a directional choice that could possibly reflect an individually distinct migratory route maintained after displacement.

The unique record of one racer that moved along the same spring dispersal course in successive years suggests that a migratory route "fixation" becomes established in some, perhaps in many, members of the population. The directional shift noted both years at the same location during this snake's migrations may argue for a memory associated with both distance and direction.

*Ontogeny of denning aggregations.*—The development of den-seeking behavior in hatchlings is another fundamental problem in the spatial orientation of *Coluber*. Compared to the ingress of adults, hatchling racers consistently were among the last to arrive at den M in each of four autumns, and each year many unmarked individuals were newly-arrived 1-year-olds (Brown, 1973). Thus, although some of the annual crop of hatchlings may overwinter at communal hibernacula, many spend their first hibernation elsewhere, not utilizing communal dens until they are yearlings.

The consistently late arrival of hatchling *Coluber* may have three possible explanations: 1) there may be selection against arriving when the bulk of adults are present because of predation on hatchlings by older snakes; 2) hatchlings may not be motivated to seek out a communal hibernaculum, or if they are so motivated, they can find a den only after many scent-trails of older racers have been "laid down"; 3) hatchlings, because of their smaller

size, may require a longer time to travel the same distance to reach a den as an adult snake.

We have no direct evidence to support the first hypothesis. Although Fitch (1963a) reported that cannibalism on young *Coluber* was fairly frequent in Kansas, we found no evidence of intraspecific predation in Utah. Further, although some racers remained on the surface for several days near a den to shed before moving underground, most seemed to go into hibernation soon after their arrival at a den minimizing an opportunity to prey on hatchlings. Rather, either or both of the last two hypotheses given above would seem to be more realistic in explaining the late arrival of hatchlings.

Our preliminary results on trail-following demonstrate that young racers reacted to, and in some cases followed, a scent-trail of a conspecific adult. Parker (1974) also obtained laboratory evidence for trail-following by young *M. taeniatus* and *P. melanoleucus* from M complex. Dundee and Miller (1968) showed that *Diadophis punctatus* newly-introduced in a test arena aggregated preferentially under discs which other snakes had previously used for shelter.

*Home range biology.*—In contrast to the vagility of migrating racers, less frequent and shorter movements, combined with a clear directional shift at the end of migration in two individuals, made it possible to distinguish a snake's home range.

Hirth et al. (1969), using radioactive tags, studied spring dispersal patterns and summer movements of two colubrids (*C. c. mormon*, *M. t. taeniatus*) and a rattlesnake (*C. v. lutosus*) at our study locality in 1966. For all three species, they favored a concept of "total range" which embraced the snakes' hibernacula, their migratory routes, and their summer ranges, on which they stated (p. 339): ". . . their movements are random and triggered by their physiological needs." These workers thus reopened a possible controversy regarding home range stability in snakes.

Several factors may be responsible for the apparent discrepancy between our finding that *Coluber* did establish home ranges following dispersal and Hirth et al.'s (1969) statements to the contrary: 1) Hirth et al. were able to detect tagged snakes with gamma scintillometers from distances of only 9 m on the surface and 3 m when a snake was underground; thus, a racer averaging 31 m/daily move on its home range in unpredictable directions, and spending

TABLE 9. HOME RANGE SIZE OF *Coluber constrictor* IN KANSAS AND UTAH.

Parameter Compared	<i>C. c. flaviventris</i> (Kansas)§		<i>C. c. mormon</i> (Utah)
	♂♂	♀♀	♀♀
Circular Home Range (mean recapture distance as radius)	10.6 ha	9.6 ha	...
Convex Polygon (outer location points)	2.9 ha*	1.8 ha*	0.4 ha†, 1.4 ha**
Maximum Distance Separating Farthest Locations	294 m	...	134 m
Mean Individual Distance Moved per Day	...	41 m	31 m

§ Data from Fitch (1963a) and Fitch and Shirer (1971).

\* Reported mean size unadjusted for number of location points.

† Mean size determined by radiotelemetry, unadjusted for number of loci.

\*\* Mean size after sample size bias correction (Jennrich and Turner, 1969).

considerable time underground, could easily have escaped detection; 2) with two workers attempting to locate 64 tagged racers in a 1,000-ha area daily, the probability of recording successive daily movements must have been extremely low. By closely following two or three *Coluber* at a time with long-range radiotelemetry, we have been able to surmount the technical difficulties Hirth et al. (1969) encountered.

From *Coluber* recaptured in successive years, racers may establish and maintain the same summer home ranges and use them year after year. Barbour et al. (1969) reported that several *Carphophis amoenus* occupied the same home ranges in successive years. Radio-tracking and recaptures at our study site showed that three *Pituophis* returned to the same home range area in different years and two *Masticophis* migrated in similar directions in spring (Parker, 1974).

Home range size estimates for *C. c. flaviventris* in Kansas and *C. c. mormon* in Utah are shown in Table 9. As the capture radius index is insensitive to the actual shape of the home range, the convex polygon estimates are compared here. Fitch (1963a) reported a mean home range size of 2.7 ha (both sexes) for 20 Kansas racers with an average of 4.7 outer location points each. Using the appropriate correction factor (Jennrich and Turner, 1969), the mean home range adjusts to ca. 20 ha, vastly greater than the size of the adjusted Utah home range. However, the necessity of sampling bias corrections may be less with radiotelemetric tracking than with recapture procedures, and the small number of capture loci for Kansas

snakes may introduce an unnecessarily large error. Comparing actual measurements, Kansas racers appear to occupy home ranges roughly 7 times larger than their conspecifics in Utah.

The geographic difference in home range size reflects several other major clinal changes in life history of *C. constrictor* (Brown, 1973; Brown and Parker, 1974). The divergent spatial biology between Kansas and Utah may be related chiefly to body size. *C. c. flaviventris* at all ages (except hatchlings) and both sexes average 2-3 times larger (age-specific body weight) than *C. c. mormon*. Body size of snakes as a group is relatively insensitive to latitudinal change (Lindsey, 1966), whereas it decreases from east to west in *Coluber*.

*C. c. mormon* in Utah cold desert is almost entirely a secondary consumer (Brown, 1973), whereas *C. c. flaviventris* in Kansas tall grass prairie is a secondary-tertiary consumer (Fitch, 1963a). Racer food habits separate well from those of other sympatric snake species in each locality (Henderson, 1974; Parker, 1974). Summer conditions in Utah are often unfavorable for diurnal surface activity and much of the insect food is apparently obtained by racers underground.

The more productive Kansas habitat would seem to enable *C. c. flaviventris* to pick from a more diverse food supply and therefore to have a smaller home range than *C. c. mormon*. Paralleling a pattern of interspecific correlation between body size and home range size in lizards (Turner et al., 1969), an intraspecific relationship between these two variables argues for varied roles of a single species in distinct communities.

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## Population Structure, Life History and Evolution of Paedogenesis in the Salamander *Eurycea neotenes*

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The distribution of body size according to reproductive condition was analyzed in samples of the paedogenetic salamander *Eurycea neotenes* taken at two localities in Kerr County, Texas, in the summer of 1970. Males of this species have lobed testes, and apparently add lobes annually upon attaining sexual maturity in their second year. Females also mature in their second year, and probably oviposit initially at two years of age. Annual survivorship appears to be low (0.10) in the first year but increases thereafter, especially among males. It is suggested that paedogenesis in *E. neotenes* has evolved under conditions of uncertain aquatic and hostile terrestrial environments, wherein selection has favored early maturity but not a lowering of metamorphic body size.

*EURYCEA neotenes* is the most widely-distributed of the several hemidactyliine plethodontid salamanders endemic to the Edwards Plateau of Texas (Baker, 1961; Brown,

1967; Mitchell and Smith, 1972). This assemblage includes four troglobitic and three spring-dwelling, epigeal species. Brandon (1971), in reviewing the literature and providing new data