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Timber Rattlesnakes (*Crotalus horridus*) of the Pine Barrens: Their Movement Patterns and Habitat Preference

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Radiotelemetry was used to monitor the movements and habitat use of timber rattlesnakes (*Crotalus horridus*) in the Pine Barrens of southern New Jersey. Reproductive condition strongly influenced both aspects of behavior. Males generally exhibited the largest activity ranges, and the sizes of their ranges were positively correlated with the number of days the snakes were monitored. This was not true for gravid or non-gravid females. Time series analyses indicated that movement patterns of males and non-gravid females consisted of constantly shifting, non-overlapping activity areas. In most cases these snakes moved in a looping pattern during the active season that returned them to the same hibernation site from which they departed. Gravid females exhibited more static, overlapping activity areas and shorter dispersal distances from hibernacula.

Males and non-gravid females utilized forested habitat with greater than 50% canopy closure, thick surface vegetation (approx. 75%), and few fallen logs. This habitat occurred with high frequency throughout the study area. Gravid snakes utilized less densely forested sites with approx. 25% canopy closure, an equal mixture of vegetation and leaf litter covering the surface, frequent fallen logs, and warmer climatic conditions. This habitat occurred in low frequency on the study area and was largely restricted to the edge of sand roads.

TO the animal ecologist, patterns of movement and habitat use constitute two of the most basic and important aspects of a species' behavior. The lack of such information severely hampers assessment of the relationships among species and limits our understanding of community structure and function. For most snake species information concerning these two parameters is unavailable largely because of their secretive behavior. The difficulty in observing free-ranging snakes is reflected by inadequate and biased samples which, in turn, have resulted in general confusion concerning the pattern of snake movements and erroneous descriptions of habitat preference (Reinert, 1984a; Gregory et al., 1987; Tiebout and Cary, 1987). Only recently have long-term, high resolution studies of snake behavior been possible through the use of radiotelemetry (Brown and Parker, 1976; Reinert, 1984b; Duvall et al., 1985; Tiebout and Cary, 1987). These studies have begun to provide new insight into snake ecology; however, more information must be obtained before meaningful behavioral and ecological generalizations can be made (Gregory et al., 1987).

This paper provides a quantitative evaluation of intraspecific variation in the movements and habitat use of timber rattlesnakes (*Crotalus horridus*) in the Pine Barrens of southern New Jersey. While *C. horridus* populations in mountainous regions have been the subject of several investigations (Galligan and Dunson, 1979; Brown et al., 1982; Reinert, 1984b), no systematic field research has been performed on coastal plain populations of this species. As a result, our knowledge of the ecology and behavior of *C. horridus* in the Pine Barrens of southern New Jersey is limited to a few observations on natural history (Burger, 1934; Kauffeld, 1957; Klauber, 1972). The purpose of this investigation was to examine the effect of sex and reproductive condition on the movements and habitat use of *C. horridus* and to determine whether coastal plain populations exhibit patterns of behavior similar to those reported for upland populations of this species.

MATERIALS AND METHODS

Study area.—The study area encompassed approx. 12.5 km^2 of Atlantic Coastal Plain Pine Barrens in southern New Jersey. Figure 1 indicates the vegetation, general topography, and the position of streams and roads. Elevations ranged from 25–42 m above sea level. The site was drained by one small permanent stream having several seasonally intermittent tributaries. Approximately 10.5 km of sand or gravel roads traversed the study area. Regionally typical forests of pine (*Pinus rigida* and *P. echinata*) and oak (*Quercus marilandica*, *Q. ilicifolia* and *Q. velutina*) dominated the vegetation over most of the site, while forests of second growth cedar (*Chamaecyparis thyoides*) bordered the stream. More complete vegetational descriptions of the Pine Barrens can be found in Forman (1979).

Telemetry.—Fifteen snakes (5 males, 10 females) were monitored using AVM Instrument Company Model SM 1 transmitters equipped with Mallory RM640 1.4 V mercury batteries and 40 cm teflon-coated whip antennas. The transmitter assemblies were coated with a 1:1 mixture of paraffin and beeswax and had a final package mass of 12–15 g. The units were surgically implanted in the body cavity following the procedure of Reinert and Cundall (1982). Transmission distances of transmitters averaged 500 m.

Activity ranges.—Transmitter-equipped snakes were located an average of once every 5 d. Locations were plotted to scale and activity range areas calculated using the method of harmonic mean analysis (Dixon and Chapman, 1980). Harmonic mean measures of activity areas allow for the identification of realistic activity centers and offer a practical method for examining variation in activity areas over time (Dixon and Chapman, 1980; Tiebout and Cary, 1987). The area enclosed by a 95% isopleth was considered to represent the total activity range area of a snake, while the area enclosed by a 50% isopleth was considered to represent the core area of activity. Convex polygon areas are also reported because of the historic prominence of this method, and its ease of comparison with existing data on reptilian activity (Jennrich and Turner, 1969; Rose, 1982; Gregory et al., 1987). Activity range areas were calculated on a Zenith Z-140 PC using Micro-computer Programs for the Analysis of Animal Locations (McPAAL) developed by M. Stuwe and C. E. Blohowiak at the National Zoological Park of the Smithsonian Institution, Front Royal, Virginia. Activity range length was measured as the linear distance between the two most distant location sites within the activity range. The total distance moved was calculated by summing the linear distances between successive relocation sites. The mean distance moved per day was calculated by dividing the total distance moved by the total number of days the snake was monitored during the active season (April–Nov.). Snakes monitored for periods of less than 60 d were not included in any analyses.

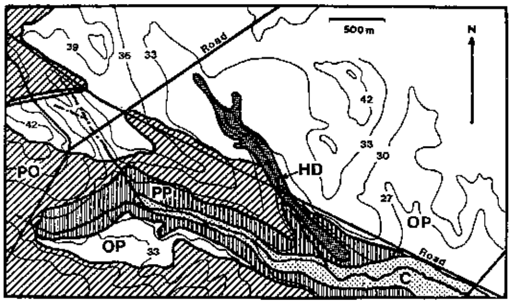

Fig. 1. Base map of study area used in activity range figures showing streams, roadways, elevation contours (in meters), and vegetation. C = Cedar Swamp Forest, HD = Hardwood Swamp Forest, OP = Oak-Pine Forest, PO = Pine-Oak Forest, PP = Pitch Pine Lowland Forest.

The data from four snakes monitored over complete seasons of activity (from hibernation to hibernation) were separated into time blocks of 4–6 consecutive locations which approximated monthly intervals. Each successive block was subjected to a harmonic mean analysis to determine the position of activity centers and to evaluate whether activity areas shifted over time. Since no gravid females were monitored from spring emergence through to fall hibernation, the data from two gravid snakes tracked for nearly complete seasons were subjected to similar analyses for comparison. Both of these snakes were caught during the first week of June and monitored until entering fall hibernation.

To determine if activity range areas, activity range lengths, total distances moved, or mean distances moved per day differed among males, non-gravid females, and gravid females, one-way analyses of variance (ANOVA, Model I) were performed. Significant ANOVA were followed by a Tukey-Kramer a posteriori test to determine which of the three groups differed. The equality of group variances was evaluated using Bartlett's test and two-tailed F tests. The problem of heteroscedastic variances was rectified where necessary by transforming the data to natural logarithms before parametric statistical comparisons were performed. Pearson product-moment correlations were calculated to assess the relationship between activity variables and the total number of days that a snake was monitored. Comparisons with data taken from the literature were done using t-tests. All statistical analyses were performed in accordance with Sokal and Rohlf (1981).

Structural habitat and climatic factors.—At each relocation during 1985 a series of 15 structural habitat and eight climatic environmental factors was recorded. Of these variables, five proved to be either invariant or highly correlated with other variables ($r > 0.90$) and were deleted to avoid statistical problems associated with linear dependence and singular covariance matrices (Pimentel, 1979).

Sampling methods for habitat factors are described by Reinert (1984a, 1984b) and consisted largely of plotless sampling techniques. Climatic factors were recorded immediately upon location of the snake. Substrate surface temperatures and ambient temperatures (1 m above the snake) were measured with a standard field thermometer, surface and ambient relative humidity was determined with a motor driven Bendix psychrometer, soil moisture at a depth of 5 cm was measured with a Kelway HB-2 soil moisture meter, and light intensity at the snake and maximum light intensity within a 2 m radius were measured with a photographic light meter. Locations at which snakes were observed to be disturbed or actively traveling were not considered selected habitats and were deleted from all analyses pertaining to habitat preference.

To determine if the characteristics of snake locations represented a random selection of available habitat, 100 sites within the confines of the study area were sampled in an identical manner to that described for snake locations with the exception that climatic factors were not recorded. These sites were selected by placing a grid over a map of the study area and selecting coordinates from a table of random numbers.

Structural habitat and climatic factor data sets were analysed separately. The observations in both data sets were separated into sampling groups (i.e., male, non-gravid female, gravid female, and random sites). Multivariate analysis of variance (MANOVA) was used to test if group habitat and climatic centroids (multidimensional means) differed significantly among sampling groups (Pimentel, 1979). Multiple discriminant function analysis (MDFA) was then used to determine which linear combinations of the original environmental variables best distinguished among groups. Linear correlations between discriminant functions and original variables indicated which measured variables contributed most greatly to group separation (Pimentel, 1979). Discriminant scores were then calculated for each sampling site. These scores indicated the position of each site on the discriminant axis. A one-way ANOVA (Model I) of discriminant scores followed by a Tukey-Kramer a posteriori test (Sokal and Rohlf, 1981) was used to determine the significance of the separation of group means along the discriminant axis.

Pairwise group overlap on discriminant axes was calculated using the following equation (Maurer, 1982):

$$a = (2s_1s_2/s_1^2 + s_2^2)^{1/2}\exp[-d^2/2(s_1^2 + s_2^2)]$$

where d is the distance between the mean discriminant score of each group and s_1 and s_2 are the SD of the discriminant scores for each group.

Habitat and climatic analyses were preformed on a VAX computer using SPSSX programs (SPSS Inc., 1983). Two sets of data consisting of raw and log transformed variates (Sokal and Rohlf, 1981) were analysed. Both data sets produced statistical results having identical biologically interpretations. The values reported are for log transformed data because of closer adherence to statistical assumptions.

RESULTS

Activity ranges.—Between 8 Aug. 1983 and 9 June 1986, a total of 15 snakes (5 males, 10 females) were monitored with radiotelemetry for periods of 60–701 d. Five of these snakes (2 males, 3 females) were monitored over two successive years, resulting in a total of 20 sets of activity parameters (Table 1).

Examples of typical activity ranges of snakes are illustrated in Figure 2 (a–c). These figures show the affinity of the snakes in this population for the vicinity of the stream and also for the edges of the sand roads. In particular, all gravid snakes showed core areas (50% isopleths) in the immediate vicinity of one of the roads.

One-way analyses of variance comparisons (Model I) and Tukey-Kramer a posteriori tests involving all 20 samples indicated that there were no differences among males, non-gravid females, and gravid females for mean total distance moved ($F_{s(2,17)} = 2.00$, $P > 0.05$), mean distance moved per day ($F_{s(2,17)} = 2.56$, $P > 0.05$), mean 50% isopleth area ($F_{s(2,17)} = 1.99$, $P > 0.05$),

TABLE 1. ACTIVITY PARAMETERS FOR *Crotalus horridus* MONITORED BY RADIOTELEMETRY (M = MALE, F = NON-GRAVID FEMALE, F_g = GRAVID FEMALE).

Snake number	Sex	Year	Days tracked	Total dist. moved (m)	Dist./day (m)	Range length (m)	Convex polygon area (ha)†	95% isopleth area (ha)	50% isopleth area (ha)
287	F_g	1983	71	971	13.7	600	5.2 (31)	5.18	1.04
017	F_g	1983	148	1242	8.4	936	16.2 (51)	19.10	3.70
287*	F	1984	175	2053	11.7	780	11.9 (25)	19.68	4.85
017*	F	1984	170	2039	12.0	690	11.1 (29)	15.41	1.67
213*	F	1984	164	4246	25.9	1950	46.4 (27)	89.66	25.16
386	F	1984	142	1026	7.2	480	5.4 (22)	9.26	0.58
037	F_g	1984	125	809	6.5	300	1.8 (43)	1.26	0.36
082	M	1984	115	3718	32.3	840	26.3 (20)	28.06	3.47
280	M	1984	77	1085	14.1	828	5.6 (16)	7.99	3.52
238	F	1984	68	974	14.3	600	8.3 (16)	7.99	0.52
082*	M	1985	186	7289	39.2	2142	123.5 (38)	195.63	7.94
280*	M	1985	184	5381	29.2	2610	101.4 (35)	219.24	21.56
238	F	1985	60	2230	39.1	1470	20.3 (14)	75.16	3.38
061	M	1985	60	1937	32.3	1632	21.9 (17)	44.37	4.58
089	F_g	1985	86	1280	14.9	540	3.8 (11)	11.01	0.27
107*	F_g	1985	102	2004	19.6	660	20.4 (19)	25.09	1.79
135	M	1985	81	727	9.0	810	3.5 (14)	21.00	0.47
119	M	1985	137	2496	18.2	1380	58.2 (22)	70.11	2.34
187*	F_g	1985	131	1562	11.9	840	13.8 (20)	19.30	1.95
013	F_g	1985	88	1542	17.5	636	8.2 (20)	18.84	1.27
Mean			118	2231	18.9	1036	27.4	45.17	4.52
(SE)			(9.7)	(380.7)	(2.33)	(139.0)	(4.47)	(13.577)	(1.509)

* Samples with complete or nearly complete seasonal activity data.

† Number of locations used to calculate polygon areas are given in parentheses.

or mean 95% isopleth area ($F_{s(2,17)} = 3.42$, $P > 0.05$). Males, however, had a significantly greater mean range length than non-gravid or gravid females (males = 1463.1 m, non-gravid females = 995.0 m, gravid females = 644.6 m, $F_{s(2,17)} = 4.79$, $P < 0.05$). For these statistical comparisons the activity parameters for a snake monitored over two consecutive years were considered two independent samples. Although not statistically rigorous, examination of the data (Table 1) suggested that this approach was reasonable in light of the heuristic nature of this study. Comparisons were also made with the data from repeated specimens removed, and statistically similar results were obtained. Overall means for each activity parameter and uncorrected convex polygon areas (Jennrich and Turner, 1969) are also given in Table 1.

Bartlett's test indicated that males, non-gravid females, and gravid females had equal variances only for mean distance moved per day ($X^2_{s(2)} = 4.52$, $P > 0.05$). For total distance moved, range length, 50% isopleth area, and 95% isopleth area, gravid females were less variable than the other groups (total distance: $X^2_{s(2)} = 13.28$, $P < 0.05$; range length: $X^2_{s(2)} = 7.03$, $P < 0.05$; 50% isopleth area: $X^2_{s(2)} = 15.53$, $P < 0.05$; 95% isopleth area: $X^2_{s(2)} = 19.62$, $P < 0.05$).

Three non-gravid females and two males were monitored over complete seasons of activity (i.e., emergence from hibernaculum in spring through entrance into hibernaculum in fall), while two gravid females were monitored over nearly complete seasons (i.e., from early June until fall hibernation). Despite the rather small sample sizes involved, additional ANOVA and a posteriori comparisons were performed using only the data from these snakes. These analyses indicated that the males moved a greater total distance than gravid females, while non-gravid females were intermediate and did not differ from either group ($F_{s(2,4)} = 9.15$, $P < 0.05$). Males also had a larger mean 95% isopleth area than either gravid or non-gravid females ($F_{s(2,4)} = 23.07$, $P < 0.05$). The groups did not differ in their mean range length ($F_{s(2,4)} = 5.30$, $P > 0.05$), mean distance moved per day ($F_{s(2,4)} = 4.38$, P

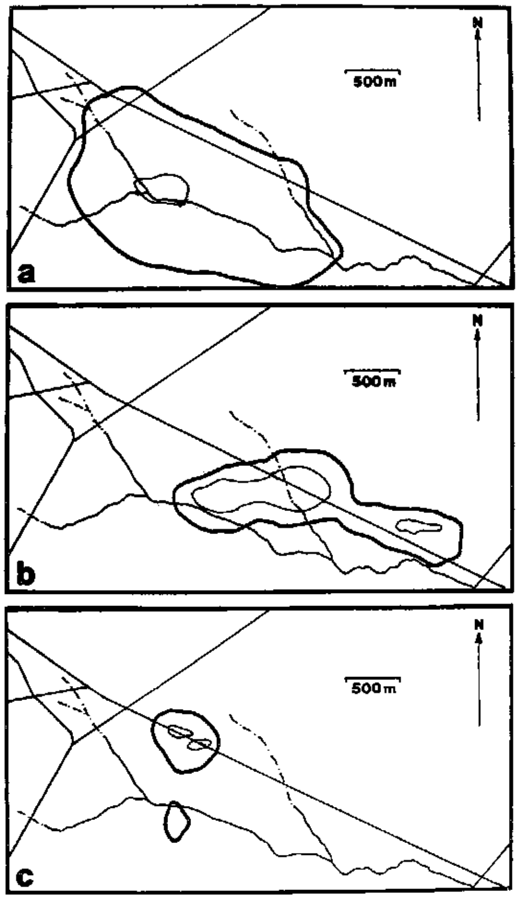

Fig. 2. Typical activity range areas for *Crotalus horridus* in the Pine Barrens: a. male #082 (1985); b. non-gravid female #213 (1984); c. gravid female #187 (1985). Heavy line defines the 95% isopleth and light line defines the 50% isopleth.

> 0.05), or 50% isopleth area ($F_{s(2,4)} = 1.81$, $P > 0.05$). Table 2 reports the group means of activity parameters based upon the specimens having complete seasonal activity data.

Bartlett's tests indicated that the group variances for most activity parameters of snakes monitored over complete seasons were equal (total distance moved: $X^2_{s(2)} = 1.29$, $P > 0.05$; range length: $X^2_{s(2)} = 1.91$, $P > 0.05$; mean distance moved per day: $X^2_{s(2)} = 0.14$, $P > 0.05$; 95% isopleth area: $X^2_{s(2)} = 2.93$, $P > 0.05$). However, gravid females were less variable than the other groups for the 50% isopleth area ($X^2_{s(2)} = 5.99$, $P < 0.05$).

Activity centers (50% isopleths) represented an average of 11.1% (SE = 1.90, n = 20) of the total activity range. This percentage did not differ among gravid females, non-gravid females, and males monitored for more than 60 d ($F_{s(2,17)} = 1.57$, $P > 0.05$) or among the subsamples of these groups tracked over complete seasons ($F_{s(2,5)} = 0.73$, $P > 0.05$). Bartlett's tests indicated that the variances for this parameter were also equal among groups (monitored > 60 d: $X^2_{s(2)} = 4.38$, $P > 0.05$; monitored complete season: $X^2_{s(2)} = 1.04$, $P > 0.05$).

Male and non-gravid female snakes monitored over complete seasons demonstrated shifting, non-overlapping activity areas as illustrated in Figures 3–4. This was determined by separating the relocation sites into subsets of 4–6 consecutive locations and subjecting each set to a harmonic mean analysis. In all cases, samples consisting of spring and fall locations had activity areas in the immediate vicinity of the main stream where hibernation occurred. From late spring through summer, the two males (#082, #280) and two of the non-gravid females

TABLE 2. MEANS AND STANDARD ERRORS (IN PARENTHESES) OF ACTIVITY PARAMETERS FOR MALE, NON-GRAVID FEMALE, AND GRAVID FEMALE *Crotalus horridus* MONITORED FOR COMPLETE ACTIVE SEASONS. Parameter means that share the same superscript within a column do not differ significantly among groups, on the basis of Tukey-Kramer a posteriori comparisons ($P = 0.05$).

Group	Total dist. moved (m)	Dist./day (m)	Range length (m)	95% isopleth area (ha)	50% isopleth area (ha)
Male	6335.0^{a}	34.2^{a}	2376.0^{a}	207.43^{a}	14.75^{a}
(n = 2)	(945.00)	(4.97)	(234.00)	(11.805)	(6.810)
Non-gravid	2779.3^{a,b}	16.5^{a}	1140.0^{a}	41.58^{b}	10.56^{a}
female (n = 3)	(733.34)	(4.68)	(405.83)	(24.070)	(7.357)
Gravid female	1783.0^{b}	15.7^{a}	750.0^{a}	22.19^{b}	1.87^{a}
(n = 2)	(221.00)	(3.85)	(90.00)	(2.895)	(0.080)

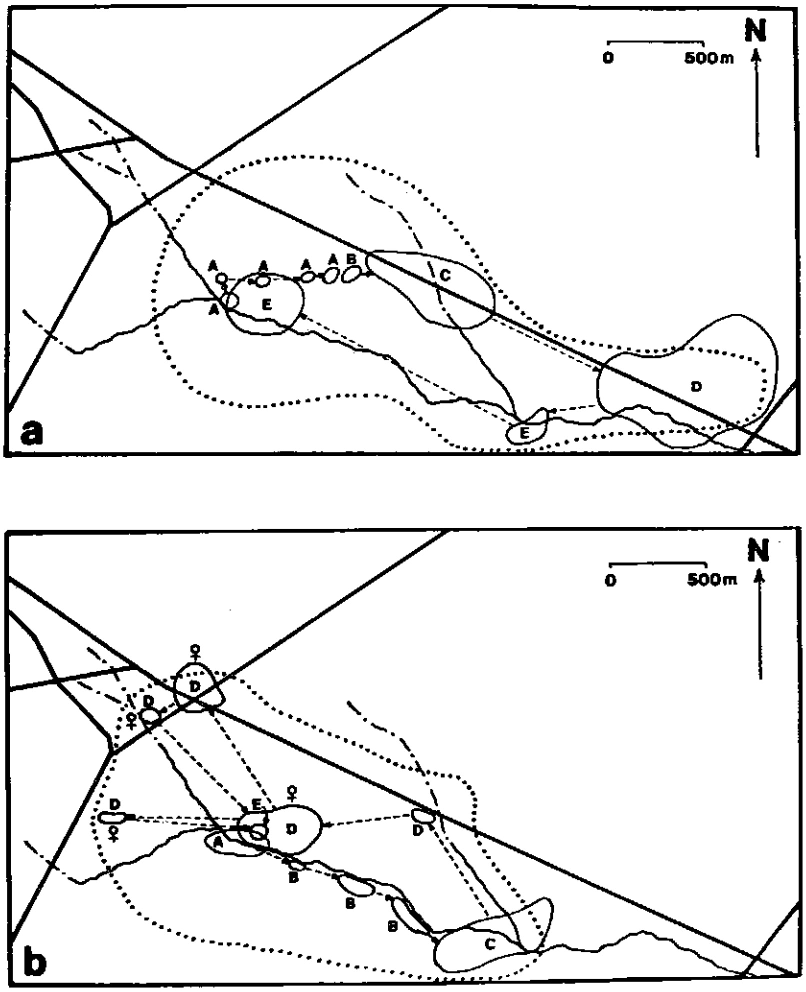

Fig. 3. Activity range areas (95% isopleths) derived from analysis of successive subsamples of locations from males #280 (a) and #082 (b) during 1985. Dotted line indicates comparative 95% isopleth obtained from an analysis of combined data. Dashed line indicates direction of movement. A = April 30 to June 1; B = June 2 to June 30; C = July 1 to July 31; D = Aug. 1 to Aug. 31; E = Sept. 1 to Oct. 9. Female symbols indicate the concurrent presence of a female snake within the range area.

(#213, #287) demonstrated extensive shifting with practically every subsample of locations, resulting in a new, non-overlapping activity area. The remaining non-gravid female (#017), however, showed greatly overlapping activity areas during the summer active season. With the exception of male #082, these snakes shifted away from the stream in the spring in a northeasterly direction toward the road and utilized small patches along a looped pathway which eventually brought them back to the same hibernation area by fall (Fig. 3a, 4). Male #082 stayed close to the stream and followed it in a southeasterly direction until early Aug. Throughout the month of Aug., when mating occurs, this snake displayed five widely separated activity centers which were not on a looped pathway. Four of these areas were known to also be frequented by females during this same time period. At the activity area near the intersection of the two roads he was found in the same burrow as a monitored gravid female (Fig. 3b).

The time series activity plots for the two gravid females (#107, #187) that were tracked from early June until entering fall hibernation showed patterns of activity similar to non-gravid female

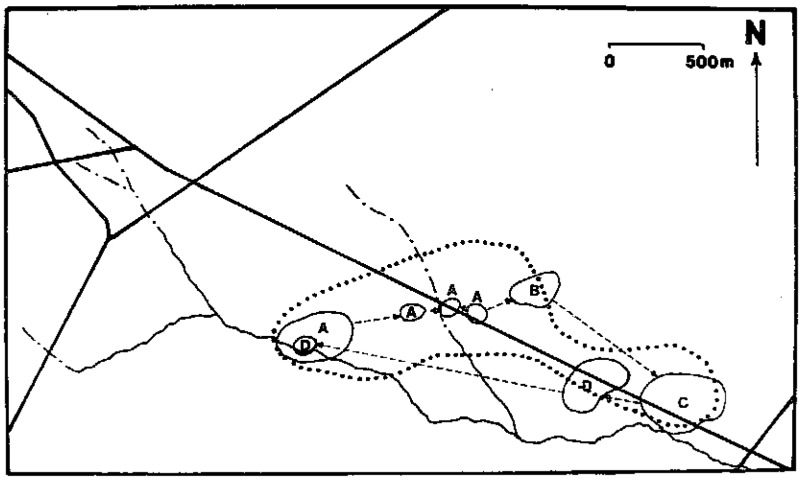

Fig. 4. Activity range areas (95% isopleths) derived from analysis of successive subsamples of locations from non-gravid female #213 during 1984. Dotted line indicates comparative 95% isopleth obtained from an anaysis of combined data. Dashed line indicates direction of movement. A = June 2 to June 30; B = July 1 to July 31; C = Aug. 1 to Aug. 31; D = Sept. 1 to Sept. 30.

#017. In both cases these snakes had greatly overlapping activity ranges in the vicinity of roadways throughout the spring and summer followed by a late season movement to the border of the main stream where they both hibernated in burrows that extended to the water table (Fig. 5).

Table 3 reports the sums of successive activity range areas from the time series analysis minus areas of overlap for the five snakes monitored over complete seasons and the two gravid snakes monitored over nearly complete seasons. These values are more realistic estimates of the actual areas used by snakes than are the total range areas since the latter include large portions of the study site that the snakes never actually occupied or just rapidly traversed (Tiebout and Cary, 1987). This table also indicates the pro-

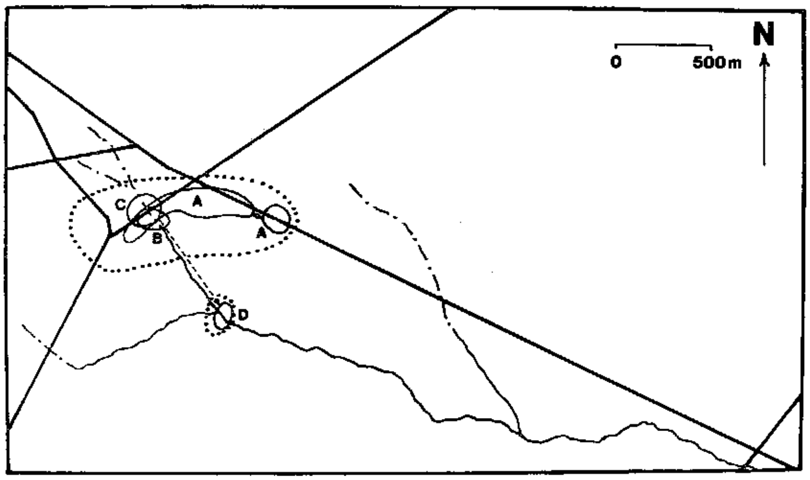

Fig. 5. Activity range areas (95% isopleths) derived from analysis of successive subsamples of locations from gravid female #107 during 1985. Dotted line indicates comparative 95% isopleth obtained from an analysis of combined data. Dashed line indicates direction of movement. A = June 2 to June 30; B = July 1 to July 31; C = Aug. 1 to Aug. 31; D = Sept. 1 to Oct. 9.

TABLE 3. ACTIVITY RANGE AREAS OF SPECIMENS MONITORED FOR COMPLETE SEASONS COMPUTED BY SUMMING SUCCESSIVE 95% ISOPLETH AREAS FROM TIME SERIES ANALYSIS AND SUBTRACTING AREAS OF OVERLAP (TS). Total range areas (T) calculated from a single analysis using all data are given for comparison (M = male, F = non-gravid female, F_g = gravid female).

Snake number	Sex	Time-series activity range (ha) TS	Total activity range (ha) T	TS/T × 100 (%)
082	M	36.60	195.63	18.7
280	M	77.29	219.24	35.3
287	F	2.96	19.68	15.0
017	F	10.22	15.41	66.3
213	F	26.66	89.66	29.7
107	F_g	5.11	25.09	20.4
187	F_g	3.66	19.30	19.0

portion of the total activity range that this summed value represents. The activity range areas estimated in this manner from the time series data average 29.2% (SE = 6.74, n = 7) of the total activity range areas.

Males showed significant positive correlations between the number of days monitored and the total distance moved (r = 0.89) and the number of days monitored and the 95% isopleth area (r = 0.90). Both groups of females showed no significant correlations between the length of monitoring period and measured activity parameters. These results support field observations and time series analyses that indicate the continual movement of male snakes throughout the active season, and the long distance shifting of activity centers.

Structural habitat.—A total of 38 relocation sites for five male *Crotalus horridus*, 18 sites for four non-gravid female *C. horridus*, 33 sites for six gravid female *C. horridus*, and 100 randomly selected sites were used to evaluate habitat utilization.

A MANOVA for four groups with 10 structural habitat variables showed that there were significant differences among the group habitat centroids (Wilks lambda = 0.495, $F_{s(30,517)} = 4.66$, $P < 0.05$). This indicates that the structural habitats of the groups differed, but it does not indicate which groups differed.

TABLE 4. GROUP MEANS AND STANDARD ERRORS (IN PARENTHESES) FOR HABITAT VARIABLES AND DISCRIMINANT SCORES (df 1) FROM HABITAT ANALYSIS.

Variable	Random (n = 100)	Male (n = 38)	Non-gravid female (n = 18)	Gravid female (n = 33)
% canopy closure	63.4 (2.91)	68.4 (3.73)	54.7 (5.95)	25.9 (4.66)
% surface vegetation	72.5 (2.62)	74.0 (4.58)	69.9 (7.09)	44.1 (5.34)
% fallen log cover	1.0 (0.28)	1.1 (0.40)	0.6 (0.56)	4.7 (1.27)
% leaf litter cover	25.4 (2.53)	24.7 (4.54)	29.2 (7.17)	42.0 (5.63)
Diameter of nearest log (cm)	8.5 (0.98)	9.8 (0.58)	7.4 (0.54)	11.0 (0.75)
Distance to log (m)	3.3 (0.28)	2.7 (0.47)	6.1 (1.15)	2.6 (0.79)
Distance to overstory tree (m)	2.0 (0.13)	1.4 (0.15)	1.7 (0.26)	2.5 (0.25)
DBH of overstory tree (cm)	16.0 (0.59)	14.9 (0.98)	15.7 (1.28)	13.4 (0.77)
Distance to understory tree (m)	2.5 (0.34)	1.1 (0.14)	2.2 (0.46)	1.9 (0.18)
DBH of understory tree (cm)	4.3 (0.19)	4.0 (0.30)	3.5 (0.47)	4.0 (0.29)
Scores on df 1 of habitat data	0.37 (0.103)	0.14 (0.112)	0.66 (0.144)	−1.65 (0.229)

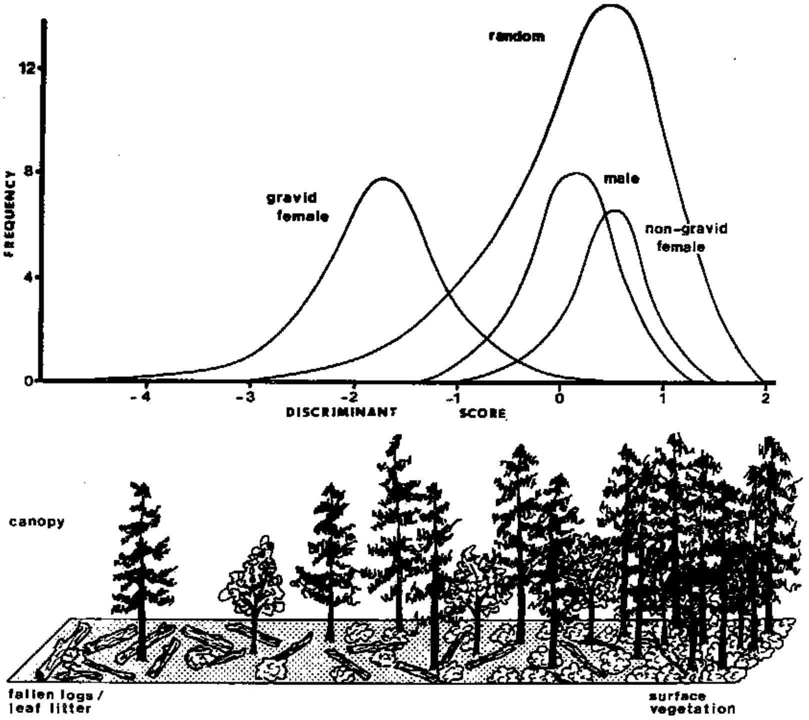

Fig. 6. Frequency curves of discriminant scores and pictorial interpretation of the first discriminant axis of habitat data for *Crotalus horridus* and random site samples.

A MDFA was used to determine which group(s) differed. The MDFA produced two significant discriminant functions (DF 1: eigenvalue = 0.609, $X^2_{(30)} = 127.08$, $P < 0.05$; DF 2: eigenvalue = 0.201, $X^2_{(18)} = 41.01$, $P < 0.05$; DF 3: eigenvalue = 0.044, $X^2_{(8)} = 7.85$, $P > 0.05$). Each function accounted for a successively smaller proportion of the total variance of the data and decreased in its power to distinguish among groups. The remaining analyses and discussion are limited to the first discriminant function which accounted for 71.3% of the total variance and is biologically the most meaningful. Table 4 presents the means and standard errors of discriminant scores for each group on the first discriminant function. One-way analyses of variance and a posteriori comparisons of these scores indicated that gravid female *C. horridus* differed significantly from the random sample and other *C. horridus* groups with respect to structural habitat utilization ($F_{s(3,132)} = 46.19$, $P < 0.05$). Gravid females were most distant from non-gravid females and these two groups had the least overlap on the habitat axis (24.6%). Males and gravid females showed an overlap of 43.9%. Males and non-gravid females were very similar to each other in their habitat use (85.2% overlap) and also did not differ from the random sample.

From the correlations (r) between the original variables and the discriminant functions it is possible to derive a biological interpretation for the discriminant axis. Such interpretations are simplifications based upon only the most highly correlated variables. The first discriminant function was most highly correlated with the following variables: percent canopy closure ($r = 0.591$), percent surface vegetation cover ($r = 0.505$), and percent fallen log cover ($r = -0.479$). The negative or positive signs associated with the r are interpreted as signifying opposite patterns of response. Consequently, this first discriminant function describes a situation where the percent canopy closure increases along with surface vegetation as fallen log cover decreases. This discriminant function represents a structural habitat gradient from forested sites with dense surface vegetation and few fallen logs to open sites with sparse surface vegetation and more fallen logs in evidence. The axis clearly distinguishes gravid specimens from the other sampling groups (Fig. 6).

Generalized habitat descriptions for each sampling group can be derived using the information obtained from the discriminant functions and the mean habitat vectors for each group (Table 4). The typical random habitat site in the study area was characterized as forested with better than 50% canopy closure, thick surface vegetation (approx. 75%), and few fallen logs. Male and non-gravid female *C. horridus* utilized habitat that did not differ from the average random site. Gravid *C. horridus* occupied vastly different habitat from the typical random site. Preferred habitat for this group was open (approx. 25% canopy closure) with a nearly equal percentage of vegetation and leaf litter covering the ground surface and frequent fallen logs.

The position of group centroids in discriminant space relative to a centroid representing available resources (i.e., the random sample) can be considered a measure of habitat (or niche) position (Shugart and Patten, 1972; Dueser and Shugart, 1979). Using the mean discriminant score of the random sample on the first discriminant axis as a representation of available habitat (Carnes and Slade, 1982; Reinert, 1984b), it is clear from Figure 6 that the habitat used by gravid females was the most distant from the random sample and thus had the lowest availability on the study site. The overlap of the gravid female sample with the random sample was only 48.1%. The habitat used by male and non-gravid specimens was closest to the random sample, and overlapped it by 100%.

Measures of habitat width were derived from the variances (s^2) of discriminant scores about group means (Carnes and Slade, 1982). These variances indicate the degree of specialization in habitat used by each group (males: $s^2 = 0.475$; non-gravid females: $s^2 = 0.375$; gravid females: $s^2 = 1.737$). The results of statistical comparisons of habitat widths using two-tailed F tests (Sokal and Rohlf, 1981) indicated that gravid *C. horridus* exhibited a wider range of habitat use than males ($F_{s(32,37)} = 3.65, P < 0.05$) or non-gravid females ($F_{s(32,17)} = 4.63, P < 0.05$). Males and non-gravid females did not differ in their habitat widths ($F_{s(37,17)} = 1.27, P > 0.05$).

Climatic conditions.—A total of 119 relocation sites for five male *C. horridus,* 50 relocation sites for four non-gravid female *C. horridus,* and 88 relocation sites for six gravid female *C. horridus* were used to evaluate microclimate utilization. A MANOVA for three sampling groups with eight climatic variables indicated that there were significant differences among the climatic centroids of the groups (Wilks lambda = 0.7658, $F_{s(16,494)} = 4.41, P < 0.05$). As with the habitat analysis, this result indicates that the climatic factors measured differed among the three groups of snakes.

The MDFA for the climatic factors produced one significant discriminant function which accounted for 91.6% of the total data variance (DF 1: eigenvalue = 0.274, $X^2_{(16)} = 66.85, P < 0.05$; DF 2: eigenvalue = 0.025, $X^2_{(7)} = 6.25, P > 0.05$). Table 5 reports the means and standard errors of the discriminant scores for each group on this discriminant function. One-way analyses of variance and a posteriori comparisons of these scores indicated that the gravid female *C. horridus* differed from male and non-gravid female specimens with respect to the climatic factors measured ($F_{s(2,254)} = 34.76$; $P < 0.05$). However, group overlap on the climatic axis was more extensive than for habitat. Males and non-gravid females showed 100% overlap along this gradient. Gravid females overlapped males by 69.6% and non-gravid females by 72.0%.

The first discriminant function was most highly correlated with temperatures (surface temperature, $r = -0.685$; ambient temperature, $r = -0.656$; soil temperature, $r = -0.560$), soil moisture ($r = 0.652$), and maximum surface illumination ($r = -0.511$). This represents a climatic gradient from sites with high temperatures, dry soil, and bright surface illumination to sites with low temperatures, water logged soil, and shaded surface conditions. This axis clearly distinguished the preference of gravid specimens for warmer, dryer, and brighter climatic conditions (Fig. 7). Table 5 indicates the mean climatic vectors for each group.

As with habitat, measures of climate width were derived from the variances (s^2) of discriminant scores about the group climatic means. Such variances indicate the degree of specialization in the climatic conditions selected by each group (males: $s^2 = 1.14$; non-gravid females: $s^2 = 1.28$; gravid females: $s^2 = 0.65$). Comparisons using two-tailed F tests (Sokal and Rohlf, 1981) indicated that gravid females used a narrower range of climatic conditions than males ($F_{s(118,87)} = 1.75; P < 0.05$) and non-gravid females ($F_{s(49,87)} = 1.96$; $P < 0.05$). Males and non-gravid females did not differ in their climate widths ($F_{s(49,118)} = 1.12$; $P > 0.05$).

Table 5. Group Means and Standard Errors (in Parentheses) for Climatic Variables and Discriminant Scores (df 1) from Climate Analysis.

Variable	Male (n = 119)	Non-gravid female (n = 50)	Gravid female (n = 88)
Surface temperature (C)	25.6 (0.45)	25.9 (0.69)	29.1 (0.39)
Ambient temperature (C)	24.8 (0.45)	25.8 (0.73)	28.3 (0.37)
Soil temperature (C)	18.2 (0.31)	18.1 (0.40)	21.0 (0.41)
Soil moisture (%)	35 (2.4)	35 (3.7)	19 (1.1)
Surface relative humidity (%)	67.3 (1.50)	65.4 (2.79)	65.5 (1.62)
Ambient relative humidity (%)	59.9 (1.45)	59.4 (2.54)	59.0 (1.60)
Max. surface illumination (lux)	20,129 (2228.2)	23,143 (3401.5)	36,276 (3197.0)
Illumination at snake (lux)	5382 (1044.1)	4198 (850.4)	9042 (1883.7)
Scores on df 1 of climate data	0.38 (0.098)	0.35 (0.160)	−0.72 (0.086)

Discussion

Significant intra-population variation in the spatial biology and habitat preference of *C. horridus* is linked to reproductive condition and its associated physiological constraints or requirements. Gravid females tended to disperse the shortest distances from winter refugia and centered their activity in a limited area until parturition and their subsequent return to hibernacula. Unlike males and non-gravid females, gravid females selected less densely forested habitat and warmer, less variable, climatic conditions. The low vagility of gravid females within relatively warmer habitats reflects selection of environmental conditions that may enhance embryonic development (Osgood, 1970, 1978; Sanders and Jacob, 1981) and reduce energy expenditure. The latter contention is supported by the observed lack of feeding and foraging behavior in gravid *C. horridus* (Keenlyne, 1972; Reinert et al., 1984). An almost identical habitat response was reported for *C. horridus* in mountainous areas of Pennsylvania (Reinert, 1984b), while several other viviparous snake species inhabiting temperate climates have been found to exhibit similar habitat shifts and decreased vagility when gravid (Viitanen, 1967; Brown and Parker, 1976; Reinert and Kodrich, 1982).

Curtailed foraging activity and the limited availability of preferred habitat are plausible explanations for the decreased vagility of gravid *C. horridus*. However, reasons for differences between the movement patterns of males and non-gravid females are less clear, since both are feeding and occupying the same habitat. We suggest that this disparity is related to the breeding system of these snakes. The movements of males are more extensive because, in addition to looking for food, they also search for receptive females. Females, on the other hand, appear to be passive participants in the process of mate location. They search for food, but wait for males to find them during the late summer breeding season. Higher energy costs associated with the female reproductive cycle and the low energy intake during gravid seasons may leave non-gravid females with consistently lower energy reserves than males. Consequently, a breeding system requiring the least energy expenditure by females could have a strong selective advantage over one in which females actively participate in mate location. The larger activity ranges of males tend to increase the probability of locating one or more receptive females simply by chance alone. The consistent movement of one monitored male between widely separated areas occupied by different fe-

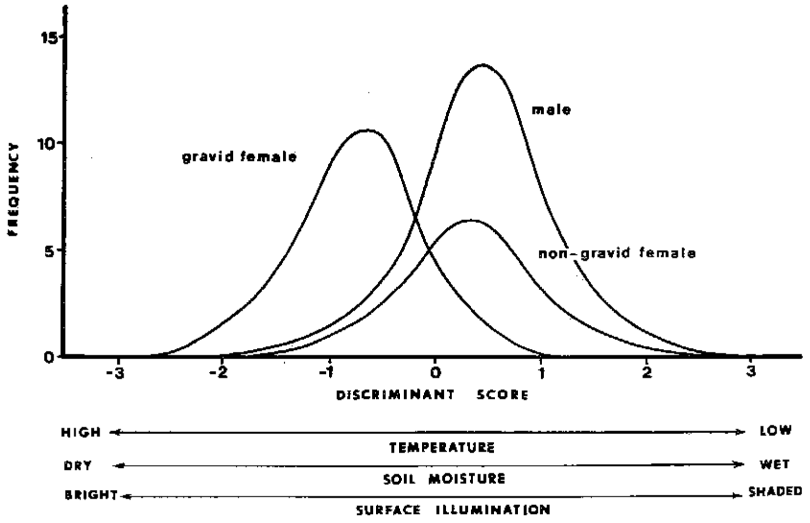

Fig. 7. Frequency curves of discriminant scores and diagrammatic interpretation of the first discriminant axis of climatic data for *Crotalus horridus.*

males, however, suggests that mate location may involve more than chance encounters (i.e., scent trailing).

It is also possible that the utilization of different prey and/or foraging strategies results in the disparate movement patterns of males and non-gravid females. Sexual divergence in foraging behavior could be selectively advantageous by reducing intraspecific competition for food resources. Such sexual variation in prey utilization has been reported for copperheads (*Agkistrodon contortrix*) by Garton and Dimmick (1969) but remains unexamined in *C. horridus.*

The forested habitat utilized heavily by males and non-gravid females undoubtedly serves as foraging habitat, and the constant shifting of activity centers may be indicative of foraging behavior in a patchy environment (Charnov, 1976; Duvall et al., 1985). In such habitat, specimens were often observed coiled in close proximity to stump holes, burrows, and small mammal runways. The use of fallen logs as ambush sites and the highly stylized ambush position reported for *C. horridus* in Pennsylvania (Reinert et al., 1984) were not observed during this study. Different behavior patterns by small mammals on the study area may be responsible for the lack of this ambush position. Like specimens in Pennsylvania, however, *C. horridus* in the Pine Barrens appear to be forest floor ambush predators that are morphologically and behaviorally adapted to woodland habitats (Reinert, 1984a, 1984b).

Despite shifting activity centers, complete seasonal data indicate that *C. horridus* are not nomadic wanderers that constantly travel farther and farther from any given location (vs Blanchard and Finster, 1933). On the contrary, snakes that were monitored for portions of two active seasons demonstrated overlapping activity ranges, and all monitored snakes returned to the same general area (and occasionally the same burrow) within their activity range to hibernate each winter (Brown et al., 1982). Snakes may, of course, move randomly during the active season and still return to the same hibernaculum. Studies of other crotalid species suggest non-random, highly directed movements, at least during periods of dispersal (Landreth, 1973; Duvall et al., 1985). In view of the substantial longevity of rattlesnakes (ca 20 yr [Klauber, 1972]), it is possible that they are capable of learning the location of prime foraging sites and suitable pathways of travel (Kamil, 1983). Conspecific chemical signals also may strongly influence movement patterns and may be important in locating mates and winter refugia (Brown and MacLean, 1983; Graves et al., 1986; Reinert and Zappalorti, 1988), or possibly avoiding intraspecific contact in foraging areas (King et al., 1983). Whether movement patterns are static or show significant yearly variation, however, could not be adequately evaluated because no snakes were monitored over two complete seasons of activity.

Tiebout and Cary (1987) reported shifting activity centers and positive correlations between the tracking period and activity area for three of four female water snakes, *Nerodia sipedon.* They concluded that *N. sipedon* "continued to explore new areas and leave old ones behind." Although not specifically addressed, intrapopulation differences similar to those shown by *C. horridus* also may exist for *Nerodia* as evidenced by a specimen that did not appreciably shift its activity center over time (Tiebout and Cary, 1987). As our results indicate, comparative monitoring of both male and female *Nerodia* in varying reproductive conditions over complete active seasons may be necessary to accurately assess such variation.

Comparison of our results with existing information concerning the movements of *C. horridus* is also hampered by small samples, short monitoring periods, and the added problem of snake displacement. Fitch and Shirer (1971) monitored three *C. horridus* in Kansas. Tracking periods, however, were less than 1 mo, and two of the snakes had been displaced from their original capture site. Similarly, Galligan and Dunson (1979) monitored the movements of six *C. horridus* in Pennsylvania, all of which were displaced specimens. Brown et al. (1982) radiotracked five resident adult *C. horridus* (4 females and 1 male) as they dispersed from a den in northeastern New York. The male moved 1400 m and the females moved an average of 280 m. These reported dispersal distances are comparable to the value of 1036 m obtained for overall range length in the Pine Barrens ($t_{s(19)} = 1.21$, $P > 0.05$, for comparison with 280 m; $t_{s(19)} = 0.57$, $P > 0.05$, for comparison with 1400 m). However, all of these snakes were tracked less than 50 d and may not have completed dispersal movements (Brown et al., 1982).

Although most telemetry studies of free-ranging snakes have had the analysis of movement patterns as their major goal, comparisons between studies are severely hampered by several factors involving methodology and samples (Gregory et al., 1987). However, the extensive variation in movement behavior among individual specimens is the greatest impediment to the formulation of meaningful generalizations regarding the spatial biology of snakes (Reinert and Kodrich, 1982). Adequate assessment of such variation and statistically sound comparisons both within and among populations require data collected over long time periods (complete seasons in many cases) from a large number of specimens that are representative of the population's phenotypic and physiological variation. Although such extensive field work is time consuming and expensive, it contributes more to our understanding of activity ranges and movement patterns than do studies that monitor few snakes over short time intervals. However, less extensive telemetry studies can clearly provide valuable information if a greater emphasis is placed upon problems involving habitat selection, species interactions, behavior, and physiology (Reinert, 1984a; Duvall et al., 1985; Peterson, 1987).

The pattern of movement and habitat use described for *C. horridus* in the Pine Barrens has important consequences for the population examined during this investigation. The results indicate that the habitat conditions preferred by male and non-gravid *C. horridus* are readily available and occur in high frequency at the study site. In contrast, the habitat utilized most heavily by gravid specimens occurs in low frequency and is largely limited to the edges of several sand roads that traverse the area. Due to the proximity of the roads to the hibernating sites, most other snakes in the population frequently cross the roadways during their normal seasonal movements. By utilizing areas of high human activity, substantial numbers of snakes are subjected to accidental death, wanton killing, and illegal collecting. Consequently, this project has provided basic ecological information which has direct practical application in the design of conservation and management strategies.

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