ASPECTS OF THE REPRODUCTIVE AND MOVEMENT ECOLOGY OF THE TIMBER RATTLESNAKE (*CROTALUS HORRIDUS*) IN THE UPPER PIEDMONT OF NORTH CAROLINA: CONSERVATION MANAGEMENT RECOMMENDATIONS WITH AN EXAMINATION OF THE POTENTIAL VULNERABILITIES TO POPULATIONS THREATENED BY NEW ROADS

A Thesis

by

John Benjamin Sealy III

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ABSTRACT

ASPECTS OF THE REPRODUCTIVE AND MOVEMENT ECOLOGY OF THE TIMBER RATTLESNAKE (*CROTALUS HORRIDUS*) IN THE UPPER PIEDMONT OF NORTH CAROLINA: CONSERVATION MANAGEMENT RECOMMENDATIONS WITH AN EXAMINATION OF THE POTENTIAL VULNERABILITIES TO POPULATIONS THREATENED BY NEW ROADS

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Understanding the dynamics of movement in animals threatened by habitat alterations requires that structures such as roads be considered. I conducted a two-part study to better understand the impact of roads on populations and the conservation management of this species.

A disjunct population of the timber rattlesnake (*Crotalus horridus*) was studied at Hanging Rock State Park located in the Sauratown Mountains in the upper Piedmont of North Carolina. Anecdotal evidence suggested that the population was declining. A telemetric field study was initiated to examine the reproductive ecology, spatial requirements, and possible causes of population decline. Of snakes examined (n=96), ten were radio-tracked, five of these for multiple seasons. Weights of gravid females (n=11) suggest a minimum body mass of 500g as a threshold for reproduction that is unrelated to age. Nonrandom movements, stable home ranges, and site fidelity were observed in telemetered snakes. Males had larger home ranges and on average moved greater distances and more often than females. Disproportionate male mortality primarily due to road-kill is a significant cause of population decline and has skewed the male:female sex ratio 1 to 3.7. Based upon the study findings, the existing management practice of translocating nuisance snakes long distances has been discontinued. The road system in the United States exerts an enormous ecological influence on many species of vertebrates. Studies show that roads negatively affect a wide diversity of species worldwide and that different species are impacted in diverse ways. In a study looking at how roads influenced snake movements and their behavioral response to roads, there were found to be interspecific differences. Indeed, the timber rattlesnake (C. horridus) was at highest risk of road mortality. I thus initiated a subsequent investigation to build upon the findings of the Hanging Rock study. In this study, I contrasted the movement characteristics of the Timber Rattlesnake population at Hanging Rock State Park to individuals in several comparatively roadless populations in the western/mountain region of North Carolina. These comparisons infer that adult males from roadless populations displaying similar movement characteristics to those of adult males at Hanging Rock State Park will show an analogous response, vulnerability, and mortality from roads.

ACKNOWLEDGEMENTS

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I thank Tommy Wagoner, Superintendent of Hanging Rock State Park for his endless support. I benefited from extensive field assistance, advice, and information provided by William H. Martin. I thank W.S. Brown for sharing his advice and expertise with all aspects of radiotelemetric field studies. I am indebted to David Garst for extensive field assistance.

I thank Dr. Vickie Martin, Dr. Linda Bennett, and the Appalachian State University Department of International Studies for financial assistance in attending the Vipers Conference in Uppsala, Sweden.

DEDICATION

I dedicate this thesis and degree to my mother Margaret Vaughn McAlister Sealy.

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Chapter 1

Aspects of the Reproductive and Spatial Ecology of the Timber Rattlesnake (Crotalus horridus) in the upper Piedmont of North Carolina: Conservation Management Recommendations

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INTRODUCTION

The timber rattlesnake (*Crotalus horridus*) once ranged over much of the eastern United States in upland, deciduous forests (Conant and Collins, 1998). The current range of the species is reduced and severely fragmented (Martin, 1992a). In North Carolina, the present distribution is discontinuous; the species ranges from the western mountains to the maritime forests of eastern coastal islands (Palmer and Braswell, 1995). Although populations continue to inhabit many forested parts of the lowland Coastal Plain only a few isolated populations persist in the heavily populated and agricultural, mid-elevation central Piedmont physiographic region of the state. In the Sauratown Mountains, a small and isolated uplift in the upper Piedmont, a disjunct population of the timber rattlesnake persists. Populations nearest to the Sauratowns occur in the foothills of the Blue Ridge physiographic province 30 km to the northwest, and in the Uwharrie Mountains of the central Piedmont 84 km to the southeast.

Two state parks are located in the Sauratowns. Their popularity, combined with an increasingly fragmented terrain surrounding the mountains, has presumably increased unnatural mortality in this population. Indeed, anecdotal information from residents living adjacent to the mountains indicated that sightings of this once-common species have declined precipitously in the previous two decades. In a cooperative research program with personnel of the largest state park, this study was developed to locate critical habitats and to

determine the population's major attributes that could be possible causes of decline. To this end, I initiated a study of reproductive and spatial ecology by combining field captures and measurements of rattlesnakes with a concomitant focus on the movement patterns of selected individuals by radiotelemetry.

METHODS

Study Site

The Sauratown Mountains are a series of small, disjunct monadnocks (resistant rock rising from a large, eroded plain) consisting of Pilot Mountain, Sauratown Mountain proper, and a group of peaks encompassed by Hanging Rock State Park at 36° 20'-36° 25' N lat., 80° 13'-80° 30' W long. in Stokes and Surry Counties, North Carolina (Fig. 1.1). The geologic structure of these monadnocks is described as a monolithic quartzite layer superimposed upon a sublayer of sandstone (Taggart, 1979). Over time, as the supporting sandstone has eroded, sections of the overlying quartzite have sheared off, creating cliff faces above steep slopes of rock rubble and boulders now covered in soil and supporting a diverse, deciduous forest. The climate of the study area is temperate. Annual precipitation averages 120.3 cm and varies little by month. Mean daily maximum and minimum temperatures for Danbury (3 km east of the study area, elevation 256 m) are 7.9° C and -2.7° C for January and 28.3° C and 17.7° C for July (NOAA, Asheville, NC, USA).

Primary data collection occurred within the boundaries of Hanging Rock State Park which makes up the largest section of the Sauratown range (Fig. 1.2).

The Park encompasses 2517 ha with an elevation range of 298 to 785 m inclusive of six peaks: Hanging Rock Bluff, Moores Knob, Cooks Wall, Wolf Rock, Devils Chimney, and Reuben Mountain. Hanging Rock Bluff is the west-

facing terminus of Hanging Rock Ridge that stretches generally east from the bluff and includes three lesser peaks (the "Three Sisters") referred to herein

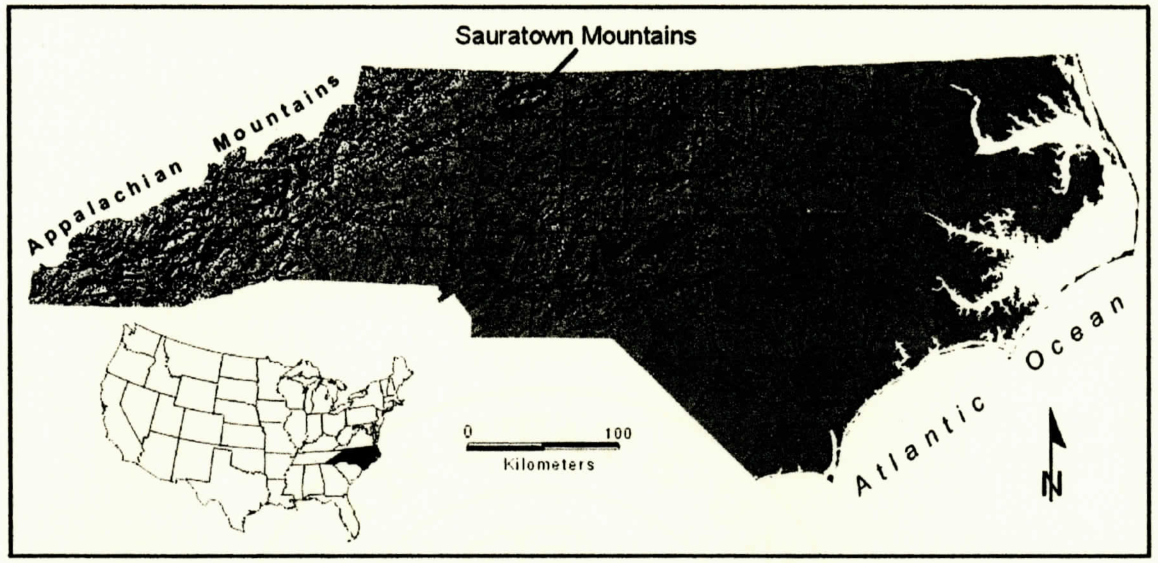

Figure 1.1. Location of the Sauratown Mountains in the northern Piedmont of North Carolina. Data Source: USGS, Prepared by Art Rex, 2001

as the Hanging Rock Mountains. Sauratown Mountain and Pilot Mountain (inclusive of Pilot Mountain State Park) lie 4.5 and 13 km to the west, respectively (Fig. 1.2).

Hanging Rock State Park experiences heavy public use, receiving more than 400,000 visitors and 100,000 vehicles annually with the majority of visitation occurring in the seven-month period from April through October. The park contains 8 km of paved roads and 30 km of hiking trails. Public facilities include a visitor center, a campground containing 81 campsites, six rental cabins, a lake for swimming and boating with a bathhouse, four open-air shelters for large day-groups, and 65 picnic tables. Two parking lots accommodate 682 vehicles and are often filled to capacity during the summer months, especially on weekends.

Facilities for staff include a maintenance area, barracks for seasonal workers, and four full-time residences for permanent staff.

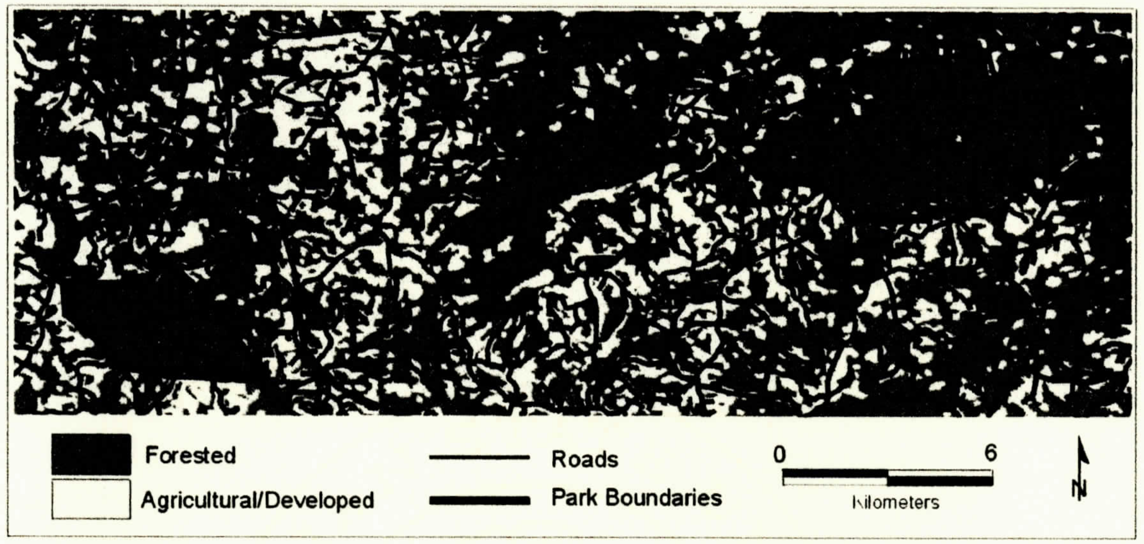

Figure 1.2. Fragmented and road intersected landscape surrounding the Sauratown Mountains in Stokes and Surry Counties, NC. Data Source: NC CGIA. Prepared by Art Rex, 2001

Study Procedures

Snakes were captured from May 1990 to October 1997. Regular searches of exposed rock outcrops allowed rattlesnakes to be located at their hibernacula. As summer progressed and snakes dispersed, searches focused on rock formation types used by gestating females (cf. Martin, 1993). Many snakes were obtained as "nuisance" snakes captured by park personnel on park roads, in campgrounds, and in other public areas while several residents living adjacent to the park provided captured or dead snakes for the study. I collected road kills, canvassed park roads at night for snakes, and in one instance, purchased a snake captured outside the park boundary from a commercial snake collector. An enclosure of 1.2 m high, 2 cm mesh, hardware cloth fencing was

constructed around a hibernaculum entrance to capture emerging snakes (J.B. Sealy, *Unpublished data*).

Sex was determined by tail length and/or subcaudal counts (Gloyd, 1940; Klauber, 1972; Palmer and Braswell, 1995). When necessary I examined the interior of the cloaca for reddish to purplish vascularized tissue of the hemipenis revealed by gently expressing the superficial exterior of the cloaca (W. S. Brown, pers. comm., has used this method for many years). Snakes listed as "sex unknown" were snakes that escaped without physical examination or were severely damaged or decomposed road kills. Two females obtained dead were necropsied to examine reproductive condition. Females were considered reproductive for the year in which they produced a litter. Gravid females, therefore, were considered reproductive in their year of capture. Gravid females were identified by their distended lower abdomens (Fitch, 1987; Martin, 1993) or (rarely) females were palped to detect enlarged follicles and/or embryos. Females diagnosed as postpartum and found in spring and early summer were considered reproductive the previous year (Martin, 1993). Postpartum females were identified by their collapsed abdomens and loose, longitudinal, posterior skin folds (Macartney and Gregory, 1988).

Snakes captured in the field were stretched along an incrementally marked snake hook and measured for total length (rounded to the nearest centimeter), from the tip of the snout to the base of the rattle (Klauber, 1972). Nuisance snakes captured by park personnel were measured in a portable squeeze box by marking a continuous line on a plastic sheet and measuring its length with a rolling map measurer (cf. Brown, 1991). Snakes receiving transmitters were measured while anesthetized. All snakes were weighed with 1-kg Pesola scales to the nearest 5 g while bagged.

Age estimates were made from rattle-segment counts using data and methods described by Martin (1993). Rattle-segment counts included the basal segment and, when present, the post-natal button. In the Appalachian Mountains with similar climatic regions and habitats as those of the Sauratowns, Martin (1993) found that shedding rates are predictable based on active season length. Thus, age estimates can be made from complete rattle strings representing all of the snake's sheds since birth when the shedding rate is known. The shedding rate varies with age and this must be considered when calculating total age for adults. Shedding rates for juveniles are higher than that of adults. Juveniles typically shed twice every second year and adults twice every third or fourth year, shedding once each season during the intervening years. Based on known-age snakes sampled by Aldridge and Brown (1995) and Martin (1993) coupled with a longer active season in the Sauratowns, I estimate an 11 shed (10 + button) snake to be 6 years old.

When broken rattle strings were tapered, the number of missing segments were determined by comparison with photocopies of complete strings (Martin, this volume) thus facilitating an accurate estimate of age. Martin (1993) reported that the first 10 rattle segments taper, allowing the inference that broken untapered strings are missing at least 10 segments. When estimating ages of snakes with such rattles (typical of older adults), snakes with un-tapered rattle

strings having seven or more segments were assigned to the 10-year or older age class. Snakes with broken un-tapered rattle strings having fewer than 7 segments were placed in age classes of known-age snakes of corresponding total length.

Snakes were uniquely marked with indelible ink by writing a number on both sides of the basal rattle segment and making a dark stripe in the groove on both sides of the rattle (Martin, 1993). The stripe allowed recognition of marked snakes when capture was not possible. Individuals were identified 7 years after their initial capture using this marking technique.

Movements, and habitat-use data were collected using radiotelemetry. Transmitter implantation surgeries were performed using the method described by Reinert and Cundall (1982), anesthesia followed the protocol of Hardy and Greene (1999). Following surgery, snakes were confined for two days to insure that wounds were knitting. Each transmitter-implanted animal was released at its point of capture.

Transmitters (model SM-1, AVM Instruments LTD, Livermore, CA) were powered with two 1.5 V batteries in parallel to give the package a life expectancy exceeding 10 months. The 10-12 g package did not exceed 5% of the subject's body weight (Reinert, 1992). Transmitting antennas (40.5 cm in length) provided a potential range of 500 m. Snakes were located using a receiver (model TRX-1000S, Wildlife Materials Inc. Carbondale, ILL) on a frequency of 150 MHz.

Telemetered snakes were located approximately every other day. Snake locations were marked with surveyor flagging inscribed with the snake's identification number and the date. Distances traveled were measured in the field using a string-line distance measurer (Walktax®) and movement headings were determined with a compass. When movements were < 200 m, distances and movement headings were determined from field locations plotted on United States Geological Survey 7.5 minute topographic maps.

From July 1993 through October 1997, 10 snakes (4 males and 6 females) were monitored telemetrically for periods ranging from 27-345 days. Five of these ten were monitored for multiple seasons resulting in a combined total of 18 activity samples. Measures of spatial activity followed those of Reinert (1992). I calculated "total distance moved" as the sum of all linear movements and the "mean distance moved per day" as the total distance moved divided by the number of days monitored. The "total distance moved in one season" was calculated as the sum of linear distances between all locations from emergence to ingress recorded for five individuals (2 males and 3 females). The "maximum distances from the den" are measures of the straight-line distance from the den to the snake's location of greatest distance from its den for the five full-season animals. Activity area (home range) was determined for these five snakes by plotting each snake's locations for all seasons monitored and constructing convex polygons by connecting the outermost points. Polygon area was calculated using coordinate geometry software (Maptech Inc, 1990). Statistical analyses of movement parameters were conducted using Quattro Pro software (Corel Corp. LTD, 1999) with $p \leq 0.05$.

RESULTS AND DISCUSSION

Morphology

Size Dimorphism

Length, sex, and age were determined for 74% of all snakes examined (n = 71, Table 1.1). Total length of adult males averaged 106.0 ± 16.3 cm (range 86-138, n = 7) and 94.5 ± 7.4 cm (range 83-110, n = 34) for females. On average, adult males achieve a length 12% greater than that of adult females. Males had a greater number of subcaudal scales (mean = 23.8, range 22-26, n = 15) than did females (mean = 19.7, range 16-22, n = 35).

Color Morphology

C. horridus in the Sauratown Mountains exhibit dorsal ground colors of tan, light brown, gray, or pale yellow; crossbands are medium to dark brown and increasingly blackish toward the posterior. One freshly molted two-year-old exhibited a distinctly pink dorsum. Individuals have prominent and often reddish mid-dorsal stripes and distinct post-orbital bars; the latter are diminished in snakes of advanced age. Tails of all juveniles ≤ 2 years-old were banded, whereas tails of adults were uniformly black although an exceptional one had a distinctly banded tail.

The snakes of the Sauratowns exhibit color patterns most closely resembling the canebrake variant (*C. h. atricaudatus*) of the Coastal Plain and

Table 1.1. Mean total length and estimated age (calculated from the number of lifetime sheds) for *Crotalus horridus* in Hanging Rock State Park, Stokes County, North Carolina. Rattle size is given as the number of segments plus the button (b) of a complete (unbroken) string.

Females

Sheds	Rattle	Age (yr)	Total Length (cm) Mean	(Range)	n
1	b. only	neonate	31.9	(29-35)	8
6	5 + b.	3	69.7	(56-82)	3
7	6 + b.	3-4	61.0		1
9	8 + b.	4-5	73.0	(71-76)	3
10	9 + b.	5	91.0		1
11	10 + b.	6	88.3	(83-95)	4
13	12 + b.	7	90.0		1
14	13 + b.	8	91.2	(84-100)	6
15	14 + b.	8-9	93.0	(84-102)	2
16	15 + b.	9	91.7	(87-97)	3
≥17	16 + b.	≥10	97.8	(83-110)	18
				Total	50

Males

Sheds	Rattle	Age (yr)	Total Length (cm) Mean	(Range)	n
1	b. only	neonate	29.7	(29-30)	3
4	3 + b.	1-2	56.5	(52-61)	2
5	4 + b.	2	65.0		1
6	5 + b.	3	69.0		1
7	6 + b.	3-4	84.0	(78-90)	2
8	7 + b.	4	74.0		1
9	8 + b.	4-5	85.7	(78-91)	3
10	9 + b.	5	84.0		1
12	11 + b.	6-7	102.0		1
14	13 + b.	8	95.3	(86-100)	2
15	14 + b.	8-9	100.0		1
16	15 + b.	9	102.0		1
≥17	≥16 + b.	≥10	126.0	(114-138)	2
				Total	21

lower Piedmont of North Carolina (see description of *C. h. atricaudatus* in Palmer and Braswell, 1995). The Sauratown population does not include dark color morphs that occur in the high elevation, western North Carolina mountains. These observations suggest that historical colonization of the Sauratowns may have occurred out of Coastal Plain populations from the south and east.

Table 1.2. Reproductive status, weight, total length, and age of reproductive females (n=12) at Hanging Rock State Park, Stokes County, North Carolina.

Date	Reproductive Status	Weight (g)	Total Length (cm)	Age (yrs)
2 July	Gravid	500	90	7
2 July	Gravid	520	87	9
27 June	Vitellogenic	530	93	>10
7 August	Vitellogenic	540	91	>10
16 June	Gravid	567	91	>10
2 July	Gravid	600	91	9
30 June	Gravid	680	102	8
2 July	Gravid	790	93	>10
18 June	Gravid	820	93	>10
24 June	Gravid	850	107	>10
14 June	Gravid	1049	104	>10
15 August	Vitellogenic	1219	110	>10

Reproduction

Size and Age at Reproduction

Reproductive females whose age could be reliably estimated (n = 23) are shown in Figure 3. The youngest reproductive (gravid) females had rattle-segment counts of 12 and were estimated at 7 years of age. A sample of gravid females whose weight, length and age were determined (n = 12) are shown in Table 1.2. Snakes ≥10 years of age averaged 796 g and made up 67% of this sample. Those 7 to 9 years old averaged 575 g. In another grouping of reproductive and postpartum females (n = 21) where accurate lengths were obtained, snakes ranged from 83 to 110 cm, averaging 96.5 cm.

Seven to nine-year-old females in the Sauratowns are probably producing their first litters, having achieved sexual maturity at age six (Fig. 1.3). Few *C. horridus* younger than six years would have achieved sufficient body mass to support vitellogenesis, and of these, few would be able to produce second litters within the next four years (Martin, 1993). Reproductive maturity and litter production in many ectotherms are both related to body mass, size, and age (Schuett, 1992). Regaining lost body mass invested in reproduction is a daunting task for postpartum females and to do so in one season is improbable (Brown, 1991). The one female weighed before and after giving birth lost 46% of her body mass at parturition. A similar loss of body mass for C. horridus has been reported by Brown (1991) and for C. viridis by Macartney and Gregory (1988). In fact, reproductive frequency is constrained by a female's ability to regain this lost body mass (Macartney and Gregory, 1988; Brown, 1991) as vitellogenesis is evidently protracted in snakes with insufficient fat-body stores.

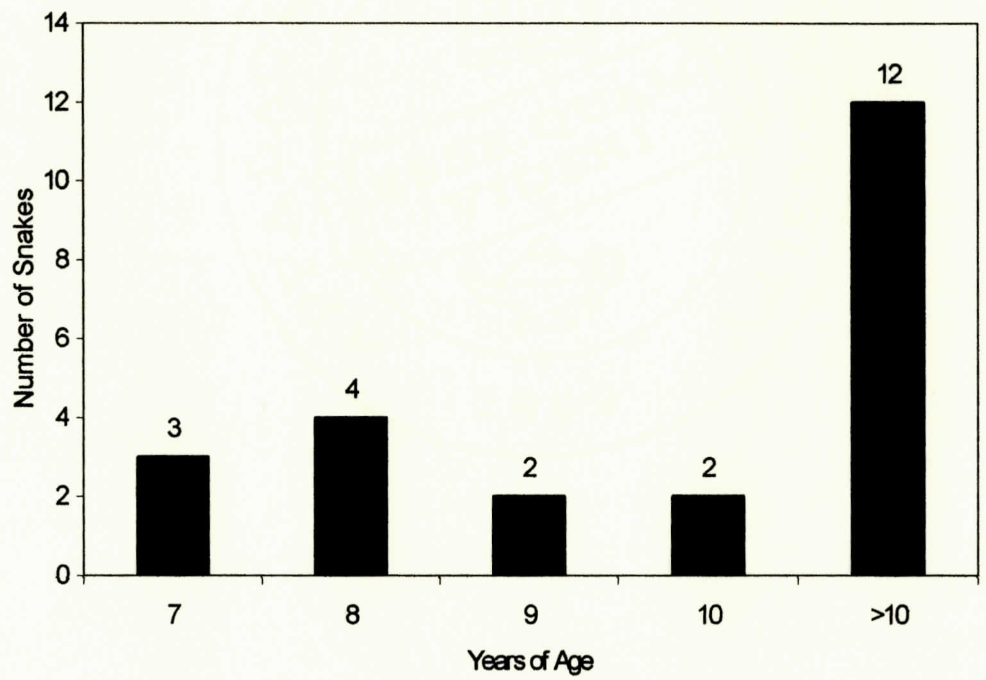

Figure 1.3. Estimated age of reproductive female *C. horridus* at Hanging Rock State Park, Stokes County, NC. Reproductive females ≥ 10 years of age make up 67% of the Sauratown sample. Older, and therefore larger, females have a higher fecundity due to their ability to regain body mass following parturition (Gibbons, 1972; Diller and Wallace, 1984; Macartney & Gregory, 1988; Martin, 1993), thus explaining the higher representation of older females in the Sauratown sample.

It appears, however, that body mass alone may be a more important determinant of sexual maturity than age in *C. horridus* as the lowest body mass of any gravid snake in the Sauratowns was 500 g (Table 1.2). In New York, females < 500 g and/or < 85 cm snout-vent length (approx. 89.4 cm total length) were considered immature. In the Appalachians, the youngest reproducers (5 years of age) were above the average length for their age at 91 cm TL (86-96 cm, n = 6) and I presume above average in body mass as well (Martin, 1993). These data suggest a threshold body mass, rather than age, must be achieved for the onset of sexual maturity in this species.

Mating Season

In the Sauratowns, the mating season extends from late June through August and probably into mid-September; estimated by a marked increase in the frequency and distance of male movements (Rudolph and Burgdorf, 1997), and by dates recorded for vitellogenic females (Table1.2) and mating activity. In the Appalachians, most mating activity occurs from late July to mid-September and seems timed to coincide with follicular yolking (Martin, 1993).

Mating

Four instances of mating activity were observed from mid-July to mid-August. On 14 July, 28 July, and 7 August males were found < 2 m from females. On 11 August a male was observed actively accompanying a female and was in physical contact with her over a 4-day period, culminating in copulation on 15 August (Sealy, 1996).

Parturition

On 30 August a telemetered female gave birth to nine young. The neonates were often observed basking until they molted on 11 September. The mother was always present and coiled in view under the "birth" rock slab within 30 cm of the neonates that were usually aggregated in a pile. Three of the young were captured (1 male, 2 females) and each weighed 25 g and measured 29 cm in total length. The mother and neonates were last observed at the site on 14 September.

Spatial Ecology

Movement Analyses

In early spring and late fall snakes moved by day. During the summer months when nighttime temperatures rarely fell below 20º C snakes moved at night. In all movement analyses, male *C. horridus* exceeded the spatial movements of females (Tables 1.3 and 1.4). Males traveled greater distances from their dens, had larger activity areas, and moved farther and more often on a daily basis than did females. Mean daily movements of nongravid females averaged 12.1 ± 4.6 m (n = 8) ranging from 6.5 to 19.2 m. Males averaged 28.3 ± 10.1 m (n = 8) with mean daily movements ranging from 13.7 to 42.2 m. Daily movements for gravid females averaged 6.2 m (n = 2).

Table 1.3. Movement data for *C. horridus* monitored with radiotelemetry at Hanging Rock State Park, Stokes County, North Carolina. Mean and SE are calculated across all adult classes (M = male, F = non-gravid female, F_g = gravid).

Snake ID Number	Sex	Year	Total Days Monitored	Total Distance Moved (m)	Mean Distance Moved Per Day (m)
8	F	93	101	1365	13.5
8	F	94	178	1158	6.5
9	F	93	73	1420	19.2
9	F	97	165	3042	18.4
18	F	94	124	1205	9.7
20	F	94	76	740	9.7
23	F	94	102	1108	10.9
23	F	96	170	1512	8.9
23	F_g	95	69	431	6.2
40	F_g	96	88	543	6.2
15	M	93	34	1280	36.5
15	M	94	155	3848	24.8
15	M	95	65	1200	18.5
25	M	94	60	2302	38.4
25	M	95	76	1755	23.1
25	M	96	209	2855	13.7
19	M	94	27	1140	42.2
21	M	94	73	2130	29.2
Mean (SE)			103	1613 (213.0)	18.6 (2.7)

To determine if differences existed in the mean daily movements of males and nongravid females, t-tests were used. In all activity samples, the difference was highly significant ($t = 4.13$, $df = 14$, $p = 0.001$). Due to the loss of sample independence and thus statistical rigor when using data for the same snake in different years, I purposely adjusted the data by removing the lowest value for each multiple-season female and the highest value for each multiple-season male. The difference in mean movement distance remained significant after the adjustment ($t = 2.67$, $df = 9$, $p = 0.027$).

For five snakes (3 females and 2 males) monitored through multiple seasons, a complete season of spatial data was obtained for each individual (Table 1.4). The total linear distance moved in a complete season averaged 1.9 km for females and 3.4 km for males. The greatest distance snakes were found from their dens averaged 0.61 km for females and 1.20 km for males. Range size for males (40.15 ha) was larger, on average, than that of females

Table 1.4. Total distance moved in a season, maximum distances from the den, and home range size for five *C. horridus* monitored a complete season (emergence to ingress) with radiotelemetry at Hanging Rock State Park, Stokes County, North Carolina. Mean and SE are calculated across sex classes (M = male, F = nongravid female).

Snake Number	Sex	Year	Total Distance Moved (km)	Maximum Distance From Den (km)	Home Range Size (ha)
8	F	94	1.10	0.38	11.1
23	F	96	1.51	0.65	10.9
9	F	97	3.04	0.81	20.3
15	M	94	3.85	1.34	64.8
25	M	96	2.86	1.05	15.5
Mean			2.50	0.85	24.5
(SE)			(0.50)	(0.16)	(10.2)

(14.1 ha). These findings mirror results from other studies of the spatial movements of *C. horridus* (Reinert and Zappalorti, 1988; Reinert, 1991, reported in Brown, 1993; Rudolph and Burgdorf, 1997).

One road-killed, non-telemetered male was found 6.4 km from his probable denning habitat and was an anomaly when compared to snakes monitored with telemetry. However, the distance was not aberrant when compared to the maximums found in other studies of C. horridus. Martin (1988) found a male 6 km from its hibernaculum, Reinert and Zappalorti (1988) 2.6 km, and Brown (1993) 7.2 km.

Cessation of Movements

Thermoregulation related to feeding and ecdysis often induced tracked snakes to stop moving for days or weeks in the summer season. The following

observations are representative: (1) Following a meal, a male remained coiled and exposed in one spot on the forest floor for 10 consecutive days. (2) A pre-shed female entered a hollow log and remained for 13 days, emerging freshly shed; and (3) a pre-shed male remained exposed on the surface with no movement for 15 consecutive days until he shed.

Nonrandom Movements

Observations of telemetered snakes indicated that their movements were not merely random wanderings through the landscape. Snakes monitored over multiple seasons showed a marked familiarity with specific natural structures throughout their ranges in successive years, often using nearly identical pathways and taking shelter at specific rocks during their movements. Snakes were observed to actively avoid large, open-canopied areas typical of those created for human uses. In the fragmented and developed habitat of Hanging Rock State Park, encounters with such areas were not uncommon. Although disinclined to enter these sites, snakes frequently remained on their periphery conducting normal activities undetected by humans nearby.

Movements of the male in Figure 1.4 are representative of snakes exhibiting active avoidance of open-canopied areas such as picnic shelter sites, roads, and parking lots, while remaining close to people. This snake was particularly adept at conducting normal behaviors along the edges of open-canopied, developed areas within his familiar home range. When encountering these areas in his migrations, the snake would back away or change directions and move parallel along their periphery. In one instance, having taken a meal, the snake thermoregulated for 10 days in one spot < 4 m from the park's most heavily used trail.

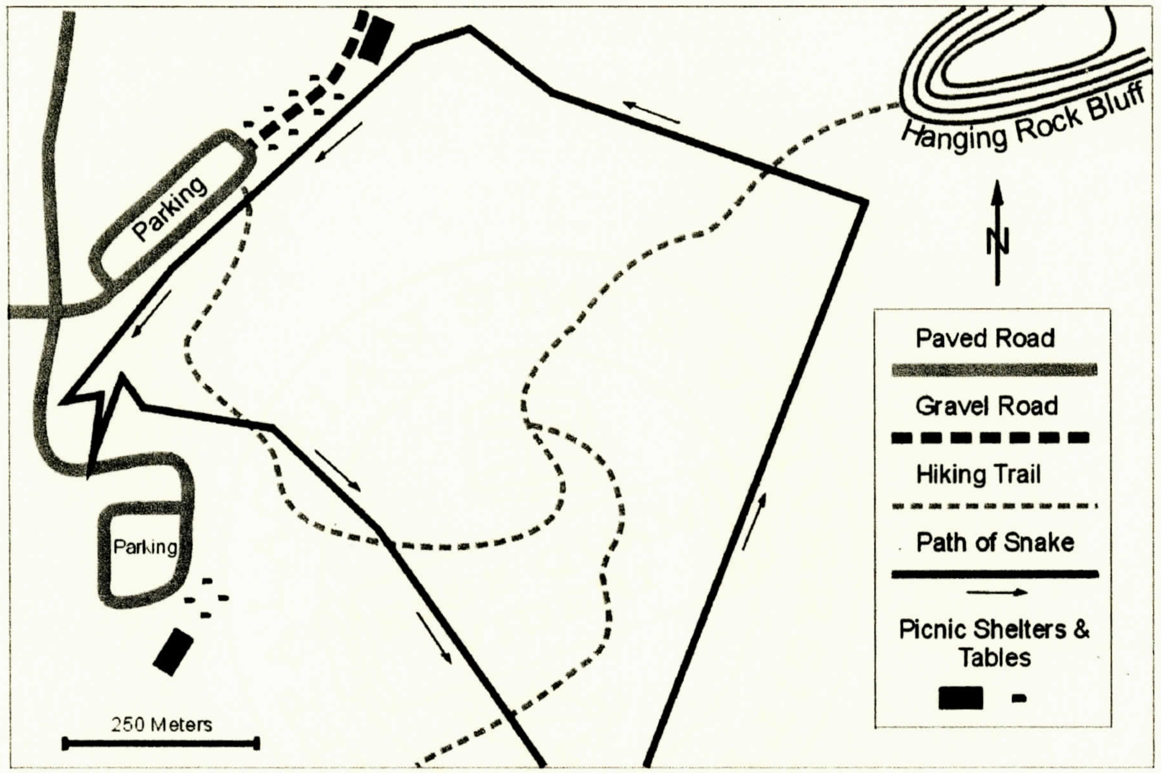

Figure 1.4. Movements of an adult male *C. horridus* from 25 July to 25 September, 1994. This snake's movements demonstrated active avoidance of roads, picnic areas, and parking lots.

In another location this male was adjacent to (< 6 m) and visible from the same trail, yet undetected by hikers. He remained stationary at the site for three days of a September weekend and then crossed the trail at night resuming his fall migration.

Movements of the female in Figure 1.4 are representative of snakes exhibiting site fidelity and home range stability. Initially captured in June 1994

crossing the campground road, this female was relocated (see short-distance translocations) 100 m into the adjacent woodland and monitored with telemetry until October.

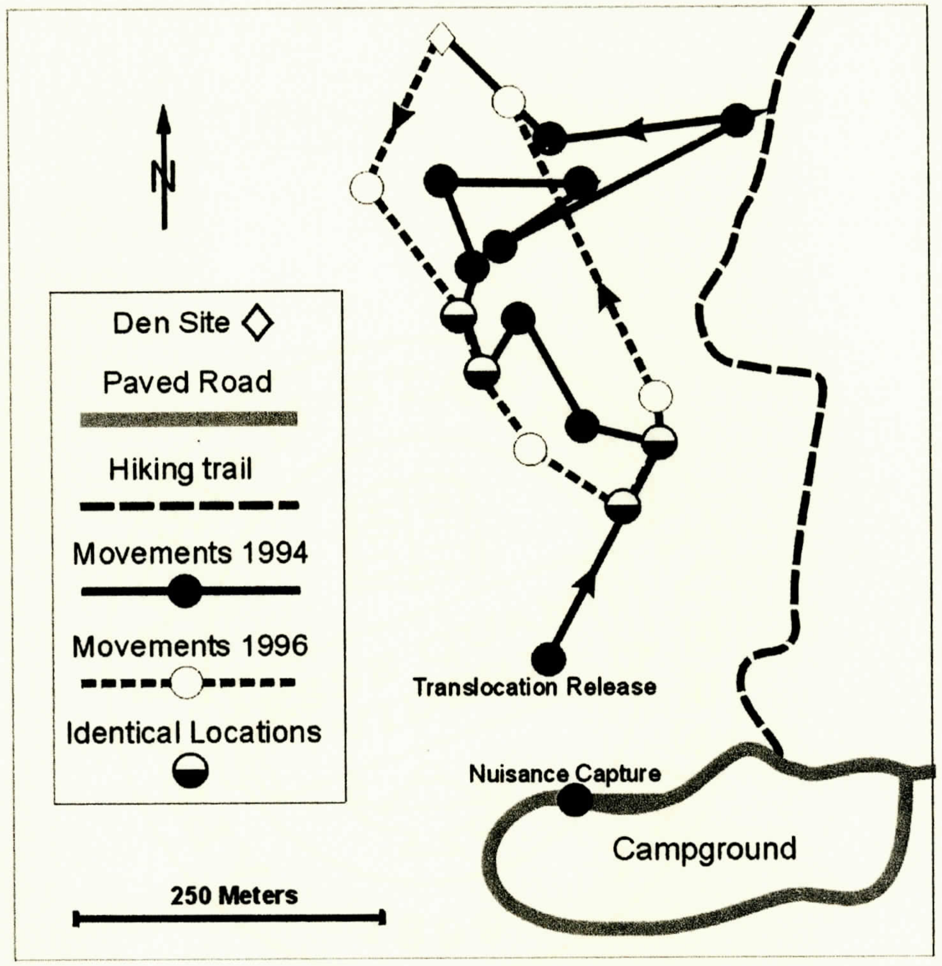

Figure 1.5. Movements of an adult female *C. horridus* during 1994 and 1996 in Hanging Rock State Park, Stokes County, NC. Initially captured in the campground in 1994 and translocated a short distance (100m), this snake demonstrated non-random movements, site fidelity, home range stability, and subsequent avoidance of the campground.

Her whereabouts were unknown the next season, but she was recaptured at her den during ingress of 1995. Monitored the following season (1996), she remained within her familiar home range and was found on four occasions precisely at her flagged locations from 1994.

Habitat Use and Foraging

Males and Nongravid Females

Habitats of deciduous woodlands having nearly closed canopies, sparse to moderate understories, and a dense shrub layer were preferred. Large, open-canopied areas (both natural and man-made) devoid of sufficient cover were avoided. In the behavioral and habitat-use records (n = 244) of telemetered individuals, snakes were in a resting coil on the woodland floor in preferred habitat 66% (n=161) of observations. Snakes were fully exposed and in view 75% of all observations (Table 1.5).

Table 1.5. Diurnal summer range behaviors, habitat use, and surface visibility observations (n = 244) for telemetrically monitored male and nongravid female *C. horridus* at Hanging Rock State Park, Stokes County, North Carolina. Structures used or behaviors exhibited were recorded once at the initial observation for that location. Data include observations of 4 males and 6 nongravid females from 1993 to 1997. Snakes found on roads, trails, or in other areas of human activity are excluded.

Behavior/Habitat Use	(n)	Proportion	Visibility
Resting coil on surface	161	0.66	Visible
Underground or under rocks	38	0.16	Not visible
In hollow log	10	0.04	Not visible
Under leaves	9	0.04	Not visible
Stretched out basking	7	0.03	Visible
Actively moving	7	0.03	Visible
Ambush posture	6	0.02	Visible
In tree (above ground)	3	0.01	Visible
In grass	3	0.01	Not Visible

Gravid Females

Habitats selected by gravid snakes showed a marked difference from those selected by males and non-gravid females. Gravid snakes utilized rockier, less forested, and more open-canopied areas and migrated to these sites during May and June.

Five gestation sites were confirmed in the Hanging Rock Mountains, ranging in elevation from 411 to 707 m. In each instance, the sites were on a south slope or flat area on a ridge that received full sun exposure much of the day. These sites were typified by one to several rock slabs surrounded by, or in close proximity to, low shrubs and grasses. The snakes took shelter under slabs during the heat of the day as well as on days of cool and/or rainy weather. In the morning and late afternoon, females were found basking near the shelter rocks in the filtered sunlight afforded by vegetation.

Gestation sites were used communally. An aggregation of 4 gravid females was found at one site and aggregations of 3 snakes were found at three other gestation sites. When more than one snake was found, they often were lying in contact with each other. In some years, single gestating females were seen at all of these same sites. In two instances in early summer, postpartum females (having produced litters the previous fall) were found with gravid snakes. The earliest date I found snakes at gestation sites was on 29 May and the latest 14 September.

Identified Threats and Management Recommendations

Road Mortality and a Skewed Sex Ratio

Of the total sample (n = 96), there were 63.5% females (n = 61), 26.0% males (n = 25), and 10.5% unknown (n = 10). Females represented 84% of all adults examined (n = 55). These data undoubtedly reflect a sampling bias due to the relative ease of finding gravid females (Brown, 1992; Martin, 1993). Indeed, females found at gestation sites represented 24% of the total sample and 38% of all females examined. This sampling bias did not, however, account fully for the skewness toward females when data were adjusted for the effect of gravid snakes at gestation sites. Of 59 snakes encountered randomly, (road kills, nuisance snakes, and incidental finds) females comprised 63% (n = 37), males 34% (n = 20), and unknowns 3% (n = 2). The exclusion of subadults resulted in

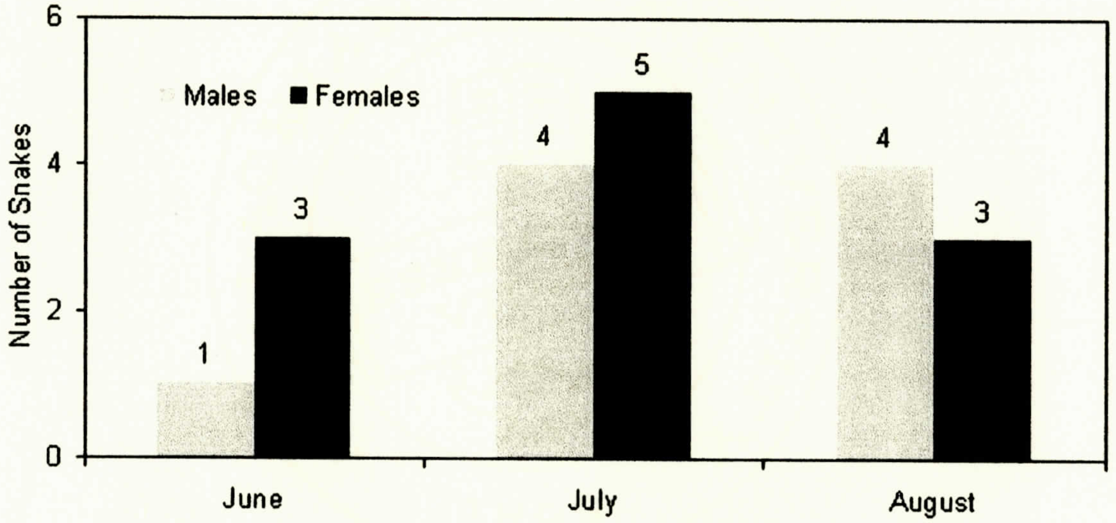

Figure 1.6. Combined road mortality data of C. horridus males and females in the Sauratown Mountains, Stokes County, NC. Data are shown for a total of 20 specimens retrieved in three months from July 1992 to July 1997. The months of April, May, September, and October did not yield road-killed specimens.

a sample of 33 sexually mature snakes randomly encountered. Of this sample, females composed 79% (n = 26), and males 21% (n = 7). Thus the male:female sex ratio of the adult random sample was 1.00 to 3.70.

An explanation of the Sauratown population's skewed sex ratio can be found in the road mortality data (Figure 1.6) and spatial ecology of males (Tables1.3 and 1.4; see Rudolph et al., 1998). Twenty rattlesnakes were recorded dead on roads from July 1992 through July 1997, however, 17 of these were recorded in but three years (1995-97) when an effort was made to collect these data. Road-kills (n = 20) represented 21% of all the snakes examined (n = 96) through 1997. Males represented 45% of all road mortalities.

Numerous studies of *C. horridus* have demonstrated that adult males are substantially more vagile than females (Tables 1.3 and 1.4; cf. Brown, 1982, 1993; Reinert and Zappalorti, 1988; Martin, 1992b; Stechert, 1996; Rudolph and Burgdorf, 1997), thus any sample of random encounters should favor adult males. Road mortality, as a sampling method, is highly biased to males (Aldridge and Brown, 1995; Rudolph and Burgdorf, 1997; Rudolph et al., 1998) as they travel more often and greater distances into fragmented and rattlesnake-hostile terrain that may be intersected with roads, farms, and residences (Fig. 1.2). Indeed, this study's road-kill data reflect this bias in that males are represented at a higher proportion (45%) in road mortality than in other of the population's samples. However, if sex ratios were not skewed in the Sauratowns, male road mortality would be expected to be disproportionately higher than that of females (cf. Aldridge and Brown, 1995). In New York, Brown's (1992) 8-year sample of *C. horridus* showed that the sex ratio of all age classes was nearly one-to-one (51.7% female), but male mortality during summer was 13 times higher than that of females (Aldridge and Brown, 1995). In a study of *C.*

viridis in Utah, a sex ratio favoring males was interpreted as a result of higher mortality on females (Parker and Brown, 1973) and, in Idaho, Diller and Wallace (1984) considered a one-to-one sex ratio an indication of equal mortality in the sexes. I conclude that my findings of essentially equal male-female road mortality and the under-representation of males in the catch samples to be a result of excessive male attrition due to disproportionate male mortality.

Road mortality, clearly the leading threat to this population, is a difficult factor to address; however, the continued viability of this population may depend upon finding solutions to this relentless drain on adults. Any serious conservation efforts must make road mortality a priority. In the short-term, efforts must be made to educate park visitors that rattlesnakes are present, are protected, and that killing them on roads with automobiles is illegal and carries penalties. Long-term solutions must provide snakes a means to cross roads safely. There is a pressing need for research into the types of structures snakes will utilize as safe passage under roads. If suitable structures were developed, "snake" fencing (see Brown, 1993) could be used to direct snakes to the passage. It would not be necessary to erect fencing along entire roadways. There are areas often called "snake crossings" where a disproportionate number of snakes are killed on roads. Indeed my first rattlesnake viewing was in the 1950s on a 100 m stretch of road that remains today a site of high road mortality. Efforts to reduce road mortality could concentrate on these specific areas and yield a significant reduction in road mortality while keeping costs low.

Long-distance Translocation of Nuisance Rattlesnakes

Large numbers of people recreate at Hanging Rock State Park and as a result there are numerous opportunities for human/rattlesnake encounters. Rattlesnakes discovered in areas of human activity are considered a dangerous hazard and must be dealt with by park personnel. The resolution of encounters with these "nuisance" snakes was to relocate (translocate) the offending animal long distances to a remote area > 3 km distant. Long-distance translocation (LDT) of timber rattlesnakes is a widespread management response to "nuisance" rattlesnakes (Reinert and Rupert, 1999) and was a common practice at Hanging Rock and in other North Carolina State Parks as well. In a 1995 survey conducted as part of this study, North Carolina parks reporting a nuisance rattlesnake problem (n=10) translocated snakes an average of 4 km (range 0.8 to 8 km). The goals of this well-intentioned practice were to: (1) remove the threat to human safety, (2) protect the snake from accidental or malicious killing, and (3) prevent recurrence as a nuisance (Sealy, 1997). However, research has shown that LDT ignores the spatial biology of the species and is detrimental to the snake's survival. In Pennsylvania, timber rattlesnakes translocated long distances into unfamiliar terrain displayed aberrant movement behaviors (Reinert and Rupert, 1999), presumably searching for their familiar home range. The translocated snakes suffered a mortality rate 5 times that of resident non-translocated snakes (Reinert and Rupert, 1999). These data demonstrate that long-distance translocations are a threat to populations and should be terminated.

Short-Distance Translocation of Nuisance Snakes

Maximum distances traveled by snakes from their dens (Table 1.4) indicated that translocated snakes at Hanging Rock State Park were being moved outside their familiar range. Nonrandom movements, (demonstrated as site fidelity, home range fidelity, and active avoidance of open-canopied/human-use areas) indicated that timber rattlesnakes have developed a spatial familiarity with their home ranges and further suggested that moving snakes outside familiar range could disrupt their normal behaviors, if not be detrimental to their survival.

When monitoring snakes telemetrically it was evident that rattlesnakes, undetected and close to people, continued to behave normally. Undiscovered rattlesnakes, however close to humans, are not a nuisance. From these observations I hypothesized that short-distance translocations, at distances surely within the snakes' familiar ranges, might successfully accomplish the goals of long-distance translocations (Sealy, 1997).

From July 1992 to August 1998, park personnel and I began short-distance translocations to test the efficacy of the practice. Short-distance translocations (SDT) were defined as those ≤ 200 m. Translocations were considered successful if individuals did not recur as nuisance snakes in the same season. Most snakes translocated long distances (≥ 400 m) were those removed from private property with the requirement that snakes be returned to park property. Release locations for all translocated snakes were chosen by

considering the animals direction of movement when found, and the proximity of structures and areas of human activity nearby. Nuisance snakes were released to available cover such as hollow logs, thickets of fallen limbs, or rock slabs. Snakes captured in areas of intense human activity were held and released at dusk on Sundays when park visitorship minimal. Snakes found on roads or trails were processed and released immediately.

In a six year period, we recorded 31 short-distance translocations (8 males and 23 females) and 12 long-distance translocations (6 males and 6 females). One same-season recurrence occurred in the LDT group. The success rate for short-distance translocations was 100% (Table 1.6).

Table 1.6. Results of translocations of nuisance rattlesnakes at Hanging Rock State Park in Stokes County, North Carolina. Recurrences are individuals repeating as a nuisance in the same season.

	n	Mean (m)	Range (m)	Recurrences
Short Distance	31	87	30-200	0
Long Distance	12	721	400-1600	1

Seven telemetered animals, initially captured as "nuisance" snakes, provided an opportunity to assess the movements and behaviors of translocated rattlesnakes. Five of these were translocated short distances and each quickly resumed normal behaviors of foraging, mate searching, and mating. Subsequently all of these five located hibernacula and over-wintered successfully. The quick resumption of normal behaviors by snake No. 23 (Fig. 1.6) is typical of snakes moved short distances. Seventeen days after her 100 m translocation, she was found accompanied by a male and four days later was observed copulating (Sealy, 1996). The outcomes for the two telemetered snakes translocated long distances could not be assessed as one was preyed upon and the other was lost due to premature transmitter failure. For a narrative of the movements of these seven snakes see Sealy (1997).

Why are short-distance translocations successful? If the snakes were moving away from release sites randomly, occasional recurrences would be expected. My observations of telemetered snakes indicate that avoidance of their capture site may be a tactic consistent with predator avoidance behaviors. *C. horridus* relies primarily on its natural coloration and secretive behaviors (procrypsis) as protection from predators. Indeed the habitat use data (Table 1.5) support this assertion having shown that the snakes were visually exposed in 75% of observations. This combination of cryptic coloration and behavior is so effective that even telemetered snakes are often difficult to find when in full view to a visually oriented human "predator." When approached in woodlands, timber rattlesnakes do not move or rattle and rarely flick their tongues until disturbed. If stretched out while basking or moving, they do not coil, but lay motionless (cf. Duvall et al., 1985). Telemetered snakes on the forest floor may be visited repeatedly and closely, yet remain in one spot, sometimes for two weeks. It was necessary at times to physically touch the snakes by gently lifting their tails to examine their surgical sites. When disturbed in this manner the snakes did not demonstrate overt defensive behaviors, yet no matter how briefly or gently examined, subsequent visits would find the snake some meters away. Galligan and Dunson (1979) noted identical behavior in a Pennsylvania population of *C. horridus*. This unfailing response indicates an association with the site and the disturbance (Brown 1993).

Open canopied areas may represent an increased vulnerability to predators and are actively avoided by rattlesnakes in this population. Nuisance snakes are often discovered when exposed away from cover in open canopied areas. These snakes, in contrast to those approached in woodlands, invariably exhibit behaviors of flight, defensive coiling, and/or rattling. In a very few instances, the snakes attempt to bite human captors. I hypothesize that snakes experience nuisance captures as an encounter with a large predator when they are most vulnerable; creating a memorable and negative association to the capture location. Upon release, having "escaped" into familiar terrain the snakes can then avoid the site of the frightening experience. Thus the success of short-distance translocations.

Short-distance translocations have proven to be a successful management practice at Hanging Rock State Park. The public's fears are alleviated when the offending snake is removed, the animals soon resume normal behaviors, and there have been no same-season recurrences in snakes translocated short distances. No matter how intrusive, the activities of humans do not appear to induce snakes to alter their home ranges. Four snakes moved short distances have erred as nuisance snakes in subsequent seasons (one as long as 6 years later), however, this was considered confirmation of SDT success and demonstrated that snakes were continuing to thrive in their familiar home ranges. On average, 7 rattlesnakes were translocated from human use areas each year in the park and it is unreasonable to believe that all snakes in these areas were discovered. Rattlesnakes seem ubiquitous in Hanging Rock State Park and there appears to be a significant degree of serendipity associated with their discovery. The snakes are there and seem to expend some effort to avoid human use/open areas. Short-distance translocations have not increased human/rattlesnake encounters in the park, however, by managing snakes within their home ranges managers can expect to encounter individuals repeatedly over the years. SDTs are not a perfect remedy, but more a compensation and compromise to the intrusion of man into rattlesnake habitat. Snakes moved a short distance are in effect being escorted safely out of what is surely a maze of human structures in hostile territory. SDTs do disrupt the activity of snakes, but the evidence demonstrates that the disruption is brief and, unlike LDT, creates no lasting affect on the animals. Short-distance translocations render moot the legion of ecological, genetic, and disease transmission concerns associated with various forms of long-distance translocation of reptiles and amphibians into novel habitats (Dodd and Seigel, 1991; Reinert, 1991).

Conservation Summary

The Sauratowns are small islands of wilderness in seas of human habitation and fragmented habitat. Despite being protected in many respects, this population is impacted negatively by human activity. The two state parks provide this area with significant habitat protection, but at the same time each park receives more than 400,000 visitors and 100,000 automobiles per year.

Indeed, 50% of the recorded road deaths occurred within park boundaries. Some researchers suggest there is no harvestable surplus of adult timber rattlesnakes (Brown, 1993), yet the Sauratown population loses many adults each year. The findings of this study demonstrate, however, that timber rattlesnake populations can benefit from active management if guided by a knowledge and understanding of the species biology. Indeed, if rattlesnakes are provided a small measure of assistance, combined with a willingness of communities and the public to attempt some degree of coexistence, rattlesnakes populations can survive and thrive safely in close proximity to man.

LITERATURE CITED

Aldridge, R. D., and W.S. Brown. 1995. Male reproductive cycle, age at maturity, and cost of reproduction in the timber rattlesnake (*Crotalus horridus*). Journal of Herpetology, Vol. 29, No. 3, pp. 399-407.

Brown, W.S., D. W. Pyle, K. R. Greene, and J. B. Friedlaender. 1982. Movements and Temperature Relationships of Timber Rattlesnakes, *Crotalus horridus*, in Northeastern New York. Journal of Herpetology, Vol. 16., No. 2, pp. 151-161.

_____. 1991. Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. Herpetologica 47: 101-115.

_____. 1992. Emergence, ingress, and seasonal captures at dens of northern timber rattlesnakes, *Crotalus horridus*. In J.A. Campbell and E. D, Brodie Jr. (eds.), Biology of the Pitvipers. Selva Press, Tyler, Texas, pp. 251-258.

_____. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. SSAR Herpetological Circular No. 22: 1-78.

_____. 1995. Heterosexual groups and the mating season in a northern population of timber rattlesnakes, *Crotalus horridus*. Herpetological Natural History, 3(2), pp. 127-133.

Conant, R., and J. T. Collins. 1998. A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Boston: Houghton Mifflin Co.

Coupe, B. 2001. Arboreal behavior in timber rattlesnake (*Crotalus horridus*). Herpetological Review, Vol. 32(2), 83-85.

Diller, L. V., and R. L. Wallace. 1984. Reproductive biology of the northern pacific rattlesnake (*Crotalus viridis oreganus*) in northern Idaho. Herpetologica, 40(2), 182-193.

Dodd, C. K., and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47:336-350.

Duvall, D., M.B. King and K.J. Gutzwiller. 1985. Behavioral ecology and ethology of the prairie rattlesnake. National Geographic Research 1:80-111.

_____, S. J. Arnold, and G. W. Schuett. 1992. Pitviper mating systems: ecological potential, sexual selection, and microevolution. In J. A. Campbell, E. D. Brodie Jr. (eds.), Biology of the Pitvipers. Selva Press, Tyler, Texas, pp. 321-336.

Fitch, H. S. 1987. Collecting and life history techniques. In Richard A. Seigel, Joseph T. Collins, and Susan S. Novak (eds.), Snakes: Ecology and Evolutionary Biology, pp. 335-365. McGraw-Hill, New York.

Galligan, J.H., and W. A. Dunson. 1979. Biology and status of timber rattlesnake (*Crotalus horridus*) populations in Pennsylvania. Biological Conservation 15:13-58

Gibbons, J. W. 1972. Reproduction, growth, and sexual dimorphism in the Canebrake Rattlesnake *Crotalus horridus atricaudatus*. Copeia (2): 222-226.

Gloyd, H. K. 1940. The rattlesnakes, genera *Sistrurus* and *Crotalus*. Chicago Academy of Science, Special Publication 4: 1-266.

Graves, B. M., D. Duvall, M.B. King, S. L. Lindstedt, and W. A. Gern. 1986. Initial den location by neonatal prairie rattlesnakes: functions, causes and natural history in chemical ecology. Pp. 285-304 in D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, eds. Chemical Signals in Vertebrates 4. Ecology, Evolution, and Comparative Biology. Plenum, New York.

_____. 1989. Defensive behavior of female prairie rattlesnakes (*Crotalus viridis*) changes after parturition. Copeia (3): 791-794.

Gregory, P. T., J. M. Macartney, and K. W. Larsen. 1987. Spatial Patterns and Movements. In Richard A. Seigel, Joseph T. Collins, and Susan S. Novak (eds.), Snakes: Ecology and Evolutionary Biology, pp. 366-394. McGraw-Hill, New York.

Hardy, D.L., and Greene H. W. 1999. Surgery on rattlesnakes in the field for implantation of transmitters. Sonoran Herpetologist 12 (3): 26-28.

Kaufield, C. 1957. Snakes and Snake Hunting. Hanover House, Garden City, New York.

Klauber, L. M. 1972. Rattlesnakes: their habits, life histories, and influence on mankind. 2nd ed. Univ. California Press, Berkeley.

Macartney, J. M., and P. T. Gregory. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. Copeia (1):47-57.

Martin, W.H. 1992a. The timber rattlesnake: Its distribution and natural history. Pp. 13-22 in T. F. Tynning (ed.), Conservation of the timber rattlesnake in the northeast. Massachusetts Audubon Soc., Lincoln, MA.

_____, 1992b. Phenology of the timber rattlesnake (*Crotalus horridus*) in an unglaciated section of the Appalachian Mountains. In J. A. Campbell, E. D. Brodie Jr. (eds.), Biology of the Pitvipers. Selva Press, Tyler, Texas, pp. 259-277.

_____, 1993. Reproduction of the Timber Rattlesnake (*Crotalus horridus*) in the Appalachian Mountains. Journal of Herpetology 27:133-143.

Neill, W. T. 1948. Hibernation of amphibians and reptiles in Richmond County, Georgia. Herpetologica 4:107-114.

Palmer, W. M., and A. L. Braswell. 1995. Reptiles of North Carolina. University of North Carolina Press, Chapel Hill, North Carolina, pp. 260-266.

Parker, W. S., and W. S. Brown. 1973. Species composition and population changes in two complexes of snake hibernacula in northern Utah. Herpetologica 29; 319-326.

Reinert, H.K. and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 1982: 702-705.

Reinert, H.K. 1984. Foraging behavior of the timber rattlesnake *Crotalus horridus*. Copeia 1984: 976-981.

_____. 1991. Translocation as a conservation strategy for amphibians and reptiles: Some comments. concerns, and observations. Herpetologica 47:357-363.

_____. 1992. Radiotelemetric field studies of pitvipers: data acquisition and analysis. In J. A. Campbell, E. D. Brodie Jr. (eds.), Biology of the Pitvipers. Selva Press, Tyler, Texas, pp. 185-198.

_____, and R.T. Zappalorti. 1988. Timber Rattlesnakes *Crotalus horridus* of the Pine Barrens: their movement patterns and habitat preference. Copeia 1988: 964-978.

_____, and R. R. Rupert. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus.* Journal of Herpetology 33:45-61.

Rudolph, D. C., S. J. Burgdorf, R. N. Conner, and J. G. Dickson. 1998. The impact of roads on the timber rattlesnake, (Crotalus horridus), in eastern Texas. Proceedings of the International Conference on Wildlife Ecology and Transportation. Ft. Myers, Florida.

_____, and S. J. Burgdorf. 1997. Timber rattlesnakes and the Louisiana pine snakes of the west gulf coastal plain: hypotheses of decline. Texas Journal of Science 49(3) Supplement: 111-222.

Savitzky, A. H., and B. A. Savitzky. 1995. Movement Patterns and Habitat Associations of *Crotalus horridus* in Southeastern Virginia. Abstract from the Symposium on Eastern Rattlesnakes. Annual meeting of the Society for the Study of Amphibians and Reptiles, Boone, NC.

Schuett, G. 1992. Is Long-term Sperm Storage an Important Component of the Reproductive Biology of Temperate Pitvipers? In J. A. Campbell, E. D. Brodie Jr. (eds.), Biology of the Pitvipers. Selva Press, Tyler, Texas, pp. 259-277.

Sealy, J. B. 1996. *Crotalus horridus* (Timber Rattlesnake). Mating. Herpetological Review, Vol. 27: 23-24.

_____. 1997. Short-distance translocations of timber rattlesnakes in a North Carolina state park: a successful conservation and management program. Sonoran Herpetologist 10:94-99.

_____, 2002. Ecology and behavior of the timber rattlesnake (*Crotalus horridus*) in the upper Piedmont of North Carolina: Identified threats and conservation recommendations. *In* G. W. Schuett, M. Hoggren, M. E. Douglas, and H. Greene (eds.) Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, UT. pp. 561-578.

Settle, L. R., and M.D. Greene. 1995. Notes on the Ecology of Timber Rattlesnakes *Crotalus horridus* in a maritime habitat. Symposium on Eastern Rattlesnakes. Annual meeting of the Society for the Study of Amphibians and Reptiles, Boone, NC. (Abstract)

Stechert, R. 1980. Observations on Northeastern Snake Dens. Bulletin of the New York Herpetological Society. Vol. 15, No. 2.

_____. 1996. Timber Rattlesnake Telemetry Study at West Point Military Reservation. Report to the Natural Resources Department, United States Military Academy.

Taggart, J. B. 1979. Hanging Rock Park Natural Areas. Report compiled for N.C. Div. of Parks and Recreation.

Chapter 2:

Timber Rattlesnake vulnerability to roads:
The characteristics of timber rattlesnake movements in a population experiencing high road mortality infers similar impacts to populations threatened by new roads

INTRODUCTION

The road system in the United States exerts an enormous ecological influence (Forman, 2000) and significantly impacts many species of vertebrates (Rudolph et. al., 1998). Indeed, affects from roads may be the rule rather than the exception in most of the U.S. The road system in the conterminous U.S. covers an area equal to that of South Carolina. Twenty percent of U.S. land area is within 127 m of a road and 83% is within 1,061 m. In fact, only 3% of the total U.S. land area is greater than 4.8 km from a road (Ritters and Wickham, 2003). These data suggest that as the human population grows the affect on entire ecosystems is more likely to increase than decline, thus calling for greater attention to how existing and planned road networks effect wildlife populations (Forman, 2000).

Studies show that roads negatively affect a wide diversity of species worldwide and that different species are impacted in diverse ways. In Montana, grizzly bears (*Ursus arctos*) avoided areas of high road densities, truncating their seasonal migrations and thus preventing full utilization of their already reduced habitat (Mace, et. al., 1999). Amur tigers (Siberia, Russia) were found to die prematurely as well as to have reduced cub survival compared to individuals occurring in roadless areas (Kerley et al., 2002). European researchers noted that road-kills were a minor part of any ungulate population's annual mortality (1%) yet concluded that roads can decrease population viability because of habitat fragmentation (Groot and Hazebrock, 1996). Interestingly, Groot and Hazebrock (1996) contend that salt applied to roads as a de-icer attracted deer and moose to roadways, in essence exacerbating the road deleterious affects

Roads' diverse affects include small vertebrates as well. Canadian researchers identified species differences in how roads effect small vertebrates (Clevenger et. al., 2003). These data showed that small mammal road-kills were greatest on roads with the slowest speeds, but high speed roads produced higher mortality rates for birds.

Amphibian populations seem particularly vulnerable to roads. In fact, it has been suggested that road mortality is a factor in the worldwide decline in amphibians (Hels and Buchwald, 2001). In Denmark, researchers found that 10% of frog populations in ponds located within 250 m of a road were killed annually (Hels and Buchwald, 2001). In the same study, of those individuals attempting to cross a road, mortality rates were 98%.

It seems evident that roads have some affect on any vertebrate species occurring within any roads' "road-effect zone," the area extending 250 meters from each roadside (Forman, 2000). Consider a one-year study of a 3.2 km section of a road in Florida (Smith and Dodd, 2003). A total of 1821 vertebrates representing 62 different species were found dead on the road. The species ranged from dogs to turkey vultures to frogs, but 623 individuals (34%) were snakes. Snakes, however, represented only 24% (n=15) of the 62 species found. Thus, snakes were being killed on the road at a rate higher than their representation in the species sample. The higher kill rate for snakes might be

expected since snakes provide a larger, linear profile when crossing a road compared to most tetrapod species. However, in addition to a higher road-kill rate, 50% of the entire sample was represented by only two of the 15 snake species. These data infer that different taxa, as well as different species, may exhibit varying levels of vulnerability to roads. In fact, vulnerability to human induced mortality may also be discriminate within a single species based on differing behaviors related to age, sex, or season (Bonnet et al., 1999).

In a study looking at how roads influenced snake movements and behavioral response to roads, Andrews and Gibbons (2005) found interspecific differences. Nine indigenous species were tested along a closed road at the Savannah River Ecology Laboratory near Aiken, SC. Of the nine species tested, *C. horridus* was most likely to avoid the road, but when crossing the road, crossed the slowest and was most immobilized (up to one minute) by each approach and passing of a test vehicle. From these data the researchers surmised that species with a high immobilization response would significantly prolong their crossing of the road and would thus increase the threat of mortality. The study concluded that of the nine species tested, *C. horridus* was at highest risk of road mortality (Andrews and Gibbons, 2005), a distinction the species can ill afford.

The timber rattlesnake once ranged over much of the eastern United States (Conant and Collins, 1998). Throughout most of its upland range the species over-winters at ancestral hibernacula in aggregations that include all individuals of a den colony (Martin, 1988). Snakes migrate extensive distances seasonally to their summer/home ranges in search of prey and mates, moving out in spring and returning in autumn (Martin, 1988; 1992). Individuals have been found 7.2 km from their hibernaculum, but the majority of individuals spend the summer within 2.4 km of their den (Reinert and Zappalorti 1988; Brown 1993).

Timber Rattlesnakes achieve sexual maturity at approximately eight years-of-age and give birth to a litter averaging 8-10 young. Mating occurs in late summer, usually from mid-July through early September (Martin, 1993; Sealy, 1996). Females store the sperm through hibernation and conceive upon leaving the hibernaculum in April or May, a time immediately prior to the warmest months of the year. Now pregnant, females migrate to critical habitats which exhibit thermal and structural characteristics conducive to the gestation of developing embryos and as shelter from adverse weather and predators. The females remain at these sites until they give birth approximately three months later in late August to early September (Martin, 1988, 1993; Sealy 2002). The newborns remain at the birth site for 10 to 14 days accompanied by their mother until their first ecdysis (Sealy, 2002; Cobb et al 2005), then mother and young leave to forage and locate the winter den (Sealy 2002; Cobb et al., 2005). These reproductive characteristics preclude annual litter production (Gibbons, 1972); indeed Timber Rattlesnakes most frequently reproduce at three or four year intervals due to their need to replenish fat stores necessary to initiate and support vitellogenesis (Brown, 1991, 1993; Martin, 1993; Sealy, 2002). Due to predation and an inability of many to find suitable over-wintering refuge, only

15% of newborns achieve sexual maturity (Martin, 1993). Annual, natural mortality of adults is estimated at 10 to 15%, thus recruitment and natural adult mortality are essentially equal (Martin, 1993). Consequently, there is no harvestable surplus of adult Timber Rattlesnakes (Brown, 1993).

In summary, Timber Rattlesnakes are late to reach sexual maturity, reproduce infrequently, and experience high, natural mortality of their small litters (Brown, 1993; Martin, 1993). These migratory, habitat-use, and reproductive characteristics make this species particularly vulnerable to human activities (Brown, 1993) and the "costs" of these vulnerabilities are becoming increasingly evident.

The current range of the Timber Rattlesnake is reduced and severely fragmented (Conant and Collins, 1998) with six states listing the species as Endangered, and two states as Threatened. The species has been extirpated from Rhode Island, Maine, and Michigan (Brown, 1993; Conant and Collins, 1998). Population size in the remaining den colonies of other states has declined (Brown, 1993). Habitat loss and fragmentation from rampant development is a clear and increasing obstacle to continued population viability rangewide (Martin, 1992). In addition, road construction and increased traffic associated with new development undoubtedly exacerbates these threats to viability (Rudolph et al., 1998). North Carolina populations are not exempt from these processes, especially in the heavily developed western mountains and in the agricultural, central Piedmont physiographic region of the state (Sealy and Martin, *Unpublished data*; Sealy, 2002). In May of 2000 the Timber Rattlesnake was elevated to the status of "Species of Special Concern" in North Carolina based on the recommendation of the North Carolina Wildlife Resource's Commission (North Carolina Administrative Code, Sub Chapter I, Endangered and Threatened Species, 15A NCAC 10I).

It is increasingly important to understand how the movements and behaviors of individual snakes in a population may be influenced by anthropocentric factors and how these factors impact populations. Human activities can threaten the viability of populations indirectly through subtle and not so subtle habitat modifications or directly by wanton killing and/or poaching (Bonnet et al., 1999). In fact, habitat modifications such as roads may expose Timber Rattlesnakes to wanton and purposeful killings unrelated to road mortality from vehicles by exposing migrating snakes that would otherwise remain unseen (Andrews and Gibbons, 2005). Only with an understanding of the full impact of human influences and related intraspecies vulnerabilities may we be able to develop management responses to ameliorate negative consequences to populations (Bonnet et al., 1999).

I studied the movements and population dynamics of a disjunct Timber Rattlesnake population in Hanging Rock State Park, a heavily used state park in the upper Piedmont of North Carolina (Sealy, 2002). I found that: 1) average daily distances moved by males were greater than those of females, 2) park roads were taking a high toll on the population's adults, and indications were 3) the population's sex ratio was skewed 3.7 to 1 in favor of females (Sealy, 2002) instead of a normal or expected ratio of 1 to 1 (Brown 1995). My conclusions

were that high, male vagility across a habitat bisected by heavily traveled, paved roads exposed males to roads' lethal effects at higher rates. Thus, males suffered disproportionate road mortality than that experienced by less vagile females (Sealy, 2002).

These findings raised questions: 1) were the different movement characteristics between the sexes a species specific trait that in the presence of roads creates disproportionate male mortality, or 2) were the movement characteristics within this small population an artifact of high male mortality where a reduced number of males traveled greater distances in search of scarce females? The answers to these questions would require a comparison of Hanging Rock data to populations that are not subjected to the same lethal, road affects. I thus initiated the current investigation to build upon the findings of the Hanging Rock study by comparing the movement characteristics of the Timber Rattlesnake population at Hanging Rock to individuals in several comparatively roadless populations in the western/mountain region of North Carolina.

If the movement characteristics of "roadless" populations were similar to those found at Hanging Rock State Park, I might surmise that when roads are constructed in any population's habitat that similar mortal effects may be inferred. If the comparison reveals that roadless populations exhibit different movement characteristics than those at Hanging Rock State Park then my conclusions would suggest that the Hanging Rock State Park population's movement characteristics are in response to the roads' deleterious effects.

To make the comparisons I developed three hypotheses:

H_1: males from roadless populations display similar mean daily movements to males at Hanging Rock State Park and thus their movements will infer a response and vulnerability to roads similar to that of the Hanging Rock State Park population.

H_2: the mean daily movements of the roadless populations' reproductive females is similar to that of the Hanging Rock State Park reproductive snakes and thus have a lesser vulnerability to roads than males.

H_3: in the roadless populations, non-reproductive females exhibit no propensity to travel greater distances than Hanging Rock State Park non-reproductive females and thus have less vulnerability to roads than males.

METHODS

Study Sites

Hanging Rock State Park (Site A, Figure 2.1) located in the upper Piedmont region of North Carolina, is characterized as a series of small, disjunct, quartzite monadnocks (resistant rock rising from a large, eroded plain), (Taggart, 1979). Annual precipitation at Hanging Rock State Park averages 122 cm. Mean daily maximum and minimum temperatures for the area are 8.7° C and 3.5° C for January and 31.2° C and 18.2° C for July (NOAA, Asheville, NC). The highest elevation at Site A (Hanging Rock State Park) is 786 m.

The Site A rattlesnakes suffer from the proximity of the population's critical habitats to paved roads. The park has eight km of paved roads within the park boundaries, bisecting the study area. In addition, the park is completely encircled by state and county paved highways. There is no critical habitat (dens and gestation sites) greater than 1.6 km from a paved road. During the period of data collection, the interior five miles of park road received more than 100,000 vehicles bearing 400,000 visitors annually (Sealy 2002), a popularity created primarily by its proximity to Greensboro and Winston-Salem. The majority of this visitorship occurs in June through October, the five months coinciding with the active season of the resident rattlesnake population (Sealy 2002).

Four sites were chosen within the Blue Ridge region of North Carolina based upon their relative roadlessness or lack of proximity to paved highways, thus their contrast to the characteristics of Site A. These sites were designated B1-B4 (Figure 2.1); all sharing in an isolation from paved roads. The snakes from these sites collectively are designated a single "population" for comparisons to the Site A.

Site B1 (Figure 2.1) is within Stone Mountain State Park in northern Allegheny and Wilkes Counties. This site is one of monolithic, granitic domes reaching 702 m of elevation. Annual precipitation is 144 cm. Mean daily maximum and minimum temperatures for the area are 4.9° C and -7.5° C for January and 26.5°C and 13.2° C for July (NOAA, Asheville, NC). All park roads at site B1 were single lane and gravel. In addition, Stone Mountain State Park (16,000 acres) enjoys nearly twice the acreage of Hanging Rock State Park and is bordered by the roadless, 6000 acre, Thurmond Chatham Wildlife Management Area.

Site B2, (Figure 2.1) is a series of monolithic domes in northern Alexander County. Much of this study site is owned, managed, and protected by the North Carolina Nature Conservancy. The highest elevation reaches 612 m with annual precipitation of 135 cm. Mean daily maximum and minimum temperatures for the area are 8.2° C and 1.7° C for January and 30.9° C and 17.4° C for July (NOAA, Asheville, NC).

Site B3 (Figure 2.1) occurs within the South Mountains of Rutherford County near the base of the Blue Ridge escarpment. This is the only site occurring on private land, however, the area of study is remote and isolated from paved roads. The highest elevation reaches 651 m with annual precipitation of

137 cm. Mean daily maximum and minimum temperatures for the area are 8.7° C and -3.6° C for January and 30.3° C and 18.6° C for July (NOAA, Asheville, NC).

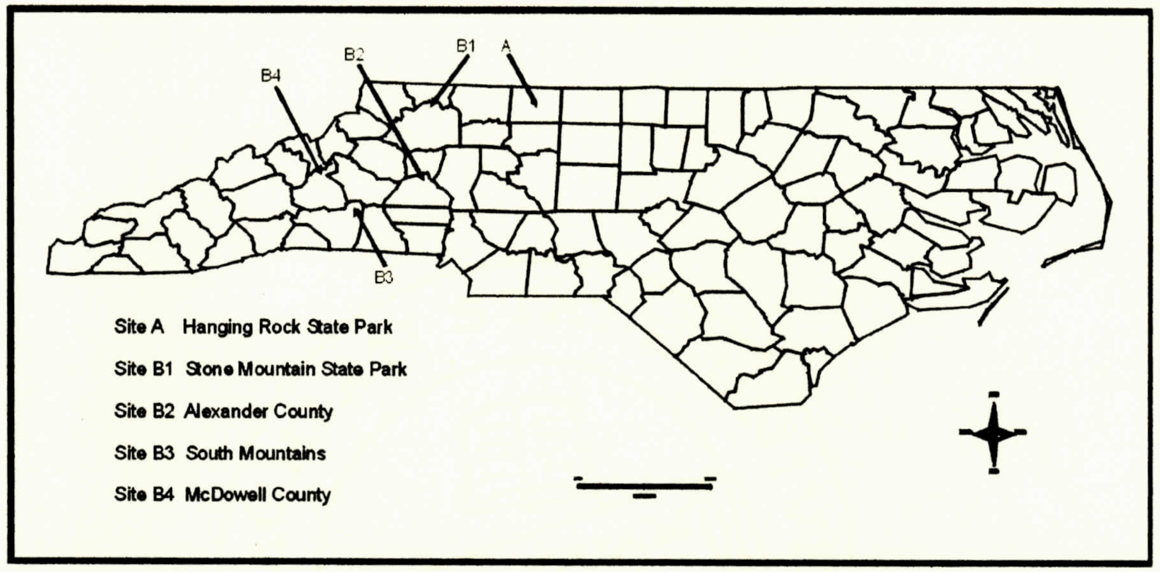

Figure 2.1. Hanging Rock State Park and mountain population's study sites. Note the relatively large distances separating the different sites/populations compared in the study.

Site B4 (Figure 2.1) occurs on the Blue Ridge escarpment, is within the Pisgah National Forest, and is 1/2 miles from a remote section of the Blue Ridge Parkway in McDowell County. The population at Site B4 has available the largest area of roadless habitat as well as being the largest and most robust population in the study. Elevation at this site reaches 3680 feet with annual precipitation of 149 cm. Mean daily maximum and minimum temperatures for the area are 7.8°C and 5.7° C for January and 27.7° C and 14.3° C for July (NOAA, Asheville, NC, USA).

Study Animals

A total of eleven (n = 11) individual adult snakes were monitored telemetrically for movement data (Table 2.1). Six individuals were from Site A (two males, two non-reproductive females, and two reproductive females) and five individual snakes (two males, one non-reproductive females, and two reproductive females) were selected from the four Blue Ridge sites.

Study animals were obtained at hibernacula by making searches of exposed rock outcrops in spring. As summer progressed and snakes dispersed, searches focused on rock formation types used by gestating females (cf. Martin, 1993). Capture permits were obtained from all pertinent agencies for the different sites.

Sex was determined by subcaudal scale counts (Table 2.1; Gloyd, 1940; Klauber, 1972; Palmer and Braswell, 1995). Females were considered reproductive for the year in which they produced a litter. Gravid females were identified by their distended lower abdomens (Fitch, 1987; Martin, 1993) or (rarely) females were palped to detect enlarged follicles and/or embryos.

Study Procedures

Snakes were uniquely marked with indelible ink by writing a number on both sides of the basal rattle segment and making a dark stripe in the groove on both sides of the rattle (Martin, 1993). The stripe allowed recognition of marked snakes when capture was not possible or when snakes were found with others of the species. Snakes were located using radio telemetry. Transmitters (Model K0A 1L0) were powered with two 1.5 V batteries in parallel to give the package a

life expectancy exceeding 10 months. The 10-12 g package did not exceed 5% of the subject's body weight (Reinert, 1992). Transmitting antennas (40.5 cm in length) provided a potential range of 500 m and snakes were located using a receiver (Model TRX-1000S, Wildlife Materials Inc. Carbondale, ILL) on a frequency of 150 MHz.

Table 2.1. Physiological data for the 11 Timber Rattlesnakes from populations A and B. Note greater length and weight of males compared to females.

Snake No.	Sex	Population	Length (cm)	Weight (g)	Subcaudals
15	M	A	138	1921	26
25	M	A	114	875	25
12	M	B	135	1285	25
17	M	B	104	850	26
23	F	A	91	600	18
8	F	A	93	650	21
182	F	B	102	680	18
122	F	B	92	670	20
20	F	A	93	530	16
18	F	A	90	500	18
137	F	B	104	710	20

Radio-transmitter implantation surgeries were performed guided by the protocol described by Reinert and Cundall (1982), and anesthesia followed the protocol of Hardy and Greene (1999). Prior to surgery the transmitter and surgical instruments are placed in sterilizing solution (Nolvasan) for 1 hour and all equipment is prepared and arranged. The snake is guided into a clear acrylic tube which has been covered on one end by a latex sheet (dental dam) held in place by a large rubber band. The interior diameter of the tube is slightly larger that the width of the snake's head to prevent its turning around in the cylinder.

When approximately 1/3 of the snake's body is in the cylinder the snake and cylinder are grasped gently but firmly where the body enters the cylinder. Once this is accomplished the snake can move neither forwards nor backwards in the tube. The snake and tube are placed upon a stainless steel tray draped with clean cotton cloth.

Three to 4 ml of isoflurane are placed on cotton sponges in a 500 ml, plastic, squeeze bottle that has a small plastic tube extending 30 cm from the end. The tube is inserted through a slit in the latex sheet. The anesthetic vapor is mixed with the air inside the cylinder by repeatedly squeezing the pliable bottle. Since concentrations may reach moderately high levels (up to 33%) the snake's reactions are monitored carefully. If the snake is too depressed the color of oral mucous membranes will tend to gray. Pink indicates acceptable circulation. If membranes are gray anesthesia is stopped and the snake is ventilated by gentle, intermittent, dorsal compression.

Surgery does not begin until the snake has achieved an adequate plane of surgical anesthesia as indicated by the lack of withdrawal response to tail pinching. Rarely will additional anesthetic vapor be required once this state is achieved and the snake can be expected to maintain a surgical plane of anesthesia for at least 30 minutes. The surgical procedure usually takes approximately 20 minutes. The tube/chamber is opened to room air 10 min. prior to completion of the surgery to speed ventilation of anesthetic from the blood. When surgical anesthesia has been attained the snake is turned on its left side and the body is extended horizontally. No part of the snake's body is in a

dependent position during the surgical procedure. The transmitter and instruments are sterilized in Nolvasan solution in excess of 1 hour. The snake's skin is cleaned with Nolvasan solution and rinsed with sterile saline. All instruments and the transmitter are rinsed in sterile saline prior to use.

An incision approximately 25 mm in length is made between lateral scale rows two and three and at a distance 75% of the snake's total body length posterior to the snout. The rib cage is gently elevated with the blunt end of the scalpel holder to reveal the peritoneum. The peritoneum is incised and reveals fat bodies indicating the intraperitoneal cavity. The transmitter is inserted into the cavity with the 40 cm antenna remaining outside the body. A fine bore surgical stainless steel tube is inserted subcutaneously and in an anterior direction. When the tip of the tube is 40 cm from the incision, scissors are used to snip a small incision sufficient for the tube to exit the skin. The antenna wire is then inserted into the tube at the 25 mm incision until fully within the tube. The tube is then removed from under the skin by way of the small incision thus leaving the antenna wire extended anteriorly from the transmitter under the snake's skin. The small incision is not sutured. The 25 mm incision is closed using a simple interrupted stitch with absorbable 4-0 polyglycolic acid suture (Dexon). The peritoneum is not sutured. Care is taken not to overlap the skin/scale edges. Swelling is less a problem in snakes and the absorbable suture remains intact for at least two months after snakes are released in the field.

Once the surgery is complete the snake is maintained in the open tube until the snake regains all sensory abilities. The snakes rise and fall as to anesthesia level and must be monitored carefully during recovery. Regular and gentle, dorsal compression hastens anesthesia out-gassing. The return of the tail pinch reflex, tongue flicking, and attempts at forward movement in the tube indicate that the snake is returning to full consciousness. Once this is achieved the snake can be returned to its cage where it is maintained at a temperature ~ 80 degrees F and with fresh water. The snake remains in captivity for a minimum of 48 hours to insure that healing has begun and no infections are evident. Within the first ten days of an animal's return to its point of capture the snake's surgical wound is checked to insure no problems have developed.

Captive maintenance of snakes awaiting surgeries, their transport to and from the field, and surgical protocols were approved by the Appalachian State University IACUC (Institutional Animal Care and Use Committee). Implanted snakes were located at varying intervals in the field, ranging from each day to three weeks between "locations". A recorded "location" represents an actual field observation of the animal in the habitat. All snake locations were marked with surveyor flagging inscribed with the snake's identification number and the date. Universal Transverse Mercator (UTM) coordinates of each snake location were taken using a Garmin XL12 GPS receiver. Distances (m) traveled were measured in the field using a string-line distance measurer (Walktax®) and movement headings were determined with a compass. When movements were >200 m, distances and movement headings were determined from field locations plotted on United States Geological Survey 7.5 minute topographic maps using the UTM coordinates.

Study snakes from Hanging Rock State Park (Site A) were monitored over a period extending from May 1993 to October 1997. Monitoring of snakes in the Blue Ridge populations (B Sites) occurred from June 1999 to October 2002. The movements of some individuals at Site A were recorded for multiple seasons, thus sample sizes are generally larger for individuals at Site A than those in the B sites. The movements of two females at Site A monitored during reproductive and non-reproductive years appear in both reproductive and non-reproductive comparison groups (Figure 2.2).

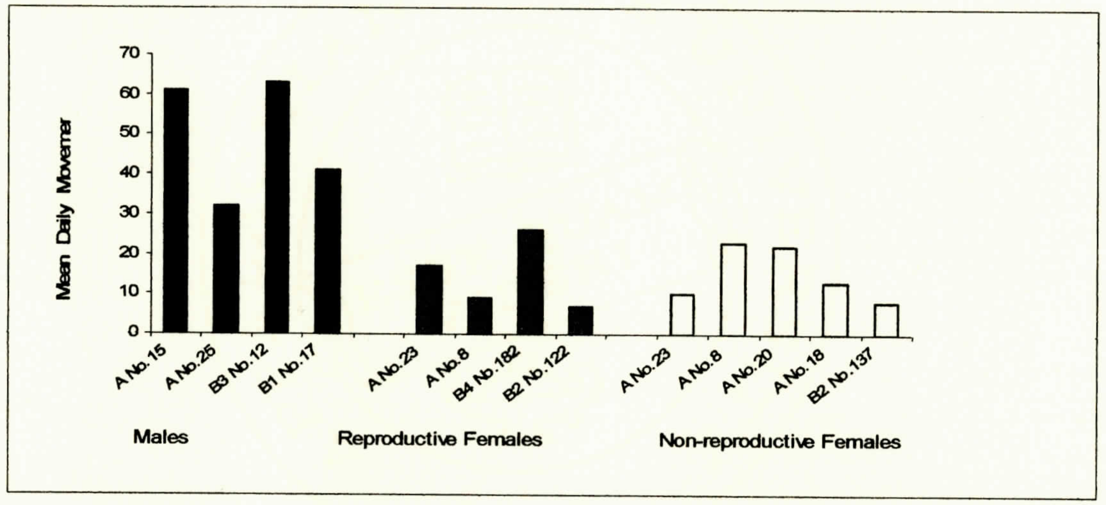

Figure 2.2. Calculated "Mean Daily Movement" data for study Timber Rattlesnakes (n = 11). Study subjects are grouped by adult sex class. Individuals are identified by population ID as well as individual number. Study sites for each individual are designated as follows: Hanging Rock State Park A, Stone Mountain State Park B1, Alexander County B2, South Mountains B4, and McDowell County B5 (see Figure 2.1). Note that females A 23 and A 8, monitored for multiple years, are represented in both female classes.

Data Collected

"Mean daily movement" is an important and common measure of spatial activity (Reinert, 1992) and thus was chosen as the measure of spatial activity for comparisons of the "B" Sites roadless population to the Site A (Hanging Rock

State Park) population. A "mean daily movement" data point represents the total distance moved in the interval between "locations" divided by the days in the interval. For example, if an individual moved 120m in eight days, a mean daily movement for that interval would be calculated as 15 m. This process was repeated for each snake at each field location to develop a sequence of mean movement data points.

Statistical Analyses

For my comparisons, snakes were grouped by the three adult classes; males, non-reproductive and reproductive females. I first determined if intrapopulation differences existed within either of the two populations, thus males were compared to males, non-reproductive females were compared to reproductive females, and males were compared to both classes of females for each of the two populations. To address the existence of interpopulation differences, Site A males were compared to Site B males, Site A reproductive females were compared to Site B reproductive females, and Site A non-reproductive females were compared to Site B non-reproductive females.

Mean movement data were contrasted using non-paired, two-tailed (non-directional) "T" distribution (Zar, 1999) with $\alpha = 0.05$ using Microsoft Excel statistical software.

RESULTS

Within Site A, reproductive females compared to non-reproductive females and males compared to males in the population were not significantly different in daily movement (Table 2.2, Figure 2.3a). However, as expected, the comparison of males and the two classes of females (reproductive and non-reproductive) revealed a highly significant difference (Table 2.2, Figure 2.3a).

Table 2.2. Significance values (P) and *df* for comparisons of mean daily movements of males and female Timber Rattlesnakes between and across study sites. Mean movement data were contrasted using non-paired, two-tailed "T" distribution (Zar, 1999). Values of $P < 0.05$ appear in **bold type**.

Sites	Comparisons	*df*	P
A	Males to Females	159	**0.0001**
	Females (r) to Females	84	0.47
	Males to Males	73	0.09
B	Males to Females	30	**0.00098**
	Females (r) to Females	20	0.447
	Males to Males	8	0.322
A to B	Males to Males	83	0.956
	Females (r) to Females (r)	35	0.603
	Females to Females	69	0.318

Within the B sites "population," the characteristics of daily movements were similar to those of the Site A population. Comparisons of reproductive females to non-reproductive females and those comparing males to males (Figure 2.3b) were not significant. The comparison of males to both classes of females was alone significant (Table 2.2, Figure 2.3b).

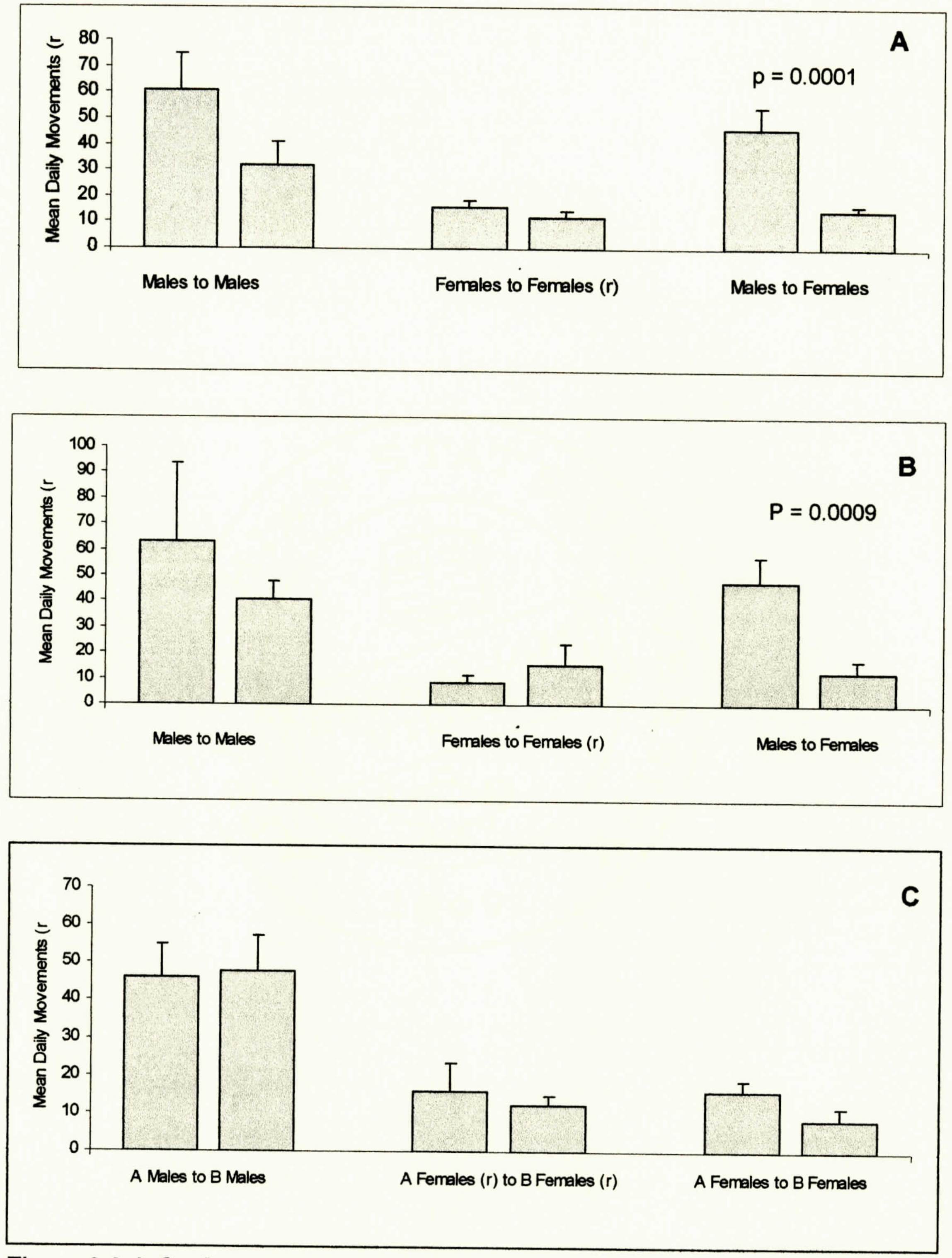

Figure 2.3 A-C. Comparisons of average daily movements within Sites A, B, and A and B. P values are superimposed above significant comparisons within groups. (r) = reproductive.

The comparisons across the Site A and B populations were not significantly different in any of the groupings, indeed the male to male comparison was nearly unity (Table 2.2, Figure 2.3c). Comparisons of reproductive females to reproductive females and non-reproductive females to non-reproductive females (Table 2.2, Figure 2.3c) were not significant.

DISCUSSION

The results obtained in the comparisons of the two populations clearly demonstrate that the differences observed in the movements between males and females are a common trait of the species and not an affect of the disproportionate male mortality observed in the Site A population. Neither males nor females in the Site B population demonstrated significant differences in mean daily movements to the corresponding road-dense Site A population snakes, thus demonstrating a high probability that different populations of this species will respond to new roads in similar ways. Where roads are constructed in Timber Rattlesnake habitats, we can predict a pattern of heightened vulnerability and mortality specific to males based on previous studies (Aldridge and Brown, 1995; Rudolph 1998; Sealy 2002). Moreover, the disproportionate mortality of males will skew the normal sex ratio heavily in favor of females (Sealy 2002).

At first glance the effects of disproportionate male mortality may seem less than alarming. This unnatural mortality added to the 10-15% natural adult mortality (Martin 1993) would undoubtedly decrease population size. However, since males will mate with more than one female in a season (Martin, 1993; Brown 1995), relatively less plentiful males would have available a larger pool of receptive females. Individual males would have less competition for receptive females and we might expect individual males to experience an increase in reproductive success. We might also argue that the population's

reproductive outcome or litter production would show little change. I contend, however, that heightened male mortality is but a harbinger of more pervasive effects from roads.

With all the discussion centering on male mortality it must not be overlooked that roads do not harvest males alone (Sealy 2002). The toll is on males and females (Bonnet 1999, Sealy 2002), although males suffer greater mortality. This unnatural elevation of a population's adult mortality from roads in addition to the 10-15% natural adult mortality (Martin, 1993) undoubtedly decreases population size. As Brown (1993) noted however, due to low fecundity, there is no surplus of adults in Timber Rattlesnake populations. Thus, a decrease in population size, combined with a reduction of reproductive potential due to the loss of adult females, would lead to population decline (Brown 1995). As population decline continued, the combined effects of relentless road mortality, low fecundity, and reduced reproductive potential would preclude any chance of recovery (Brown, 1995), thus pushing populations to extirpation (Rudolph, 1997).

With the emphasis on road mortality it might be surprising to learn that snakes and timber rattlesnakes in particular are reluctant to cross roads (Andrews and Gibbons 2005, Sealy 2002). We know that snakes attempt to cross roads because we find them there both dead and alive. It seems that snakes, including timber rattlesnakes, avoid the open space of roads unless critical, life history functions such as mate searching or migration to their den compels them to cross a road (Bonnet et al, 1999; Sealy, 2002; Shine et al, 2004; Andrews and Gibbons, 2005). When monitoring timber rattlesnakes it becomes clear that the snakes are aware of the roads. Indeed roads and parking lots are but another feature within their habitat and are treated with the same avoidance as naturally open-canopied areas such as the rock monoliths at Site B1 (Figure 1.2). It is believed that timber rattlesnakes avoid these areas due to a vulnerability to avian predators such as Great-Horned Owls (Bubo virginianus) (Sealy, 2002) and Red-tailed Hawks (*Buteo jamaicensis*), (H. K. Reinert, *Unpublished data*). Some monitored individuals at road-dense Site A showed a particular hesitancy to cross roads, moving parallel to roads and at times backing away from the road edge to seek new directions in their travels (Figure 2.4). It seems clear that roads as permanent, structural features in the habitat are modifying movement patterns of snakes (Shine et al, 2004) and may affect gene flow patterns between populations (Mader, 1984).

In a study of gene flow between timber rattlesnake den colonies, it was found that due to structural habitat features such as open-canopied rock outcrops, gene flow between den colonies was not necessarily the greatest between those colonies occurring the least distance apart as would be expected (Bushar et al, 1998). I contend that snakes view roads as a large, linear, open-canopied, rock outcrop and these "structures" undoubtedly influence and modify snake migrations as well, potentially altering population genetic structure (Reh and Seitz, 1990).

Roads are having a powerful and measurable negative impact on timber rattlesnake populations. As we build increasingly complex road networks,

this knowledge necessitates greater attention to how roads both existing and planned may affect all resident wildlife populations (Forman, 2000). How might

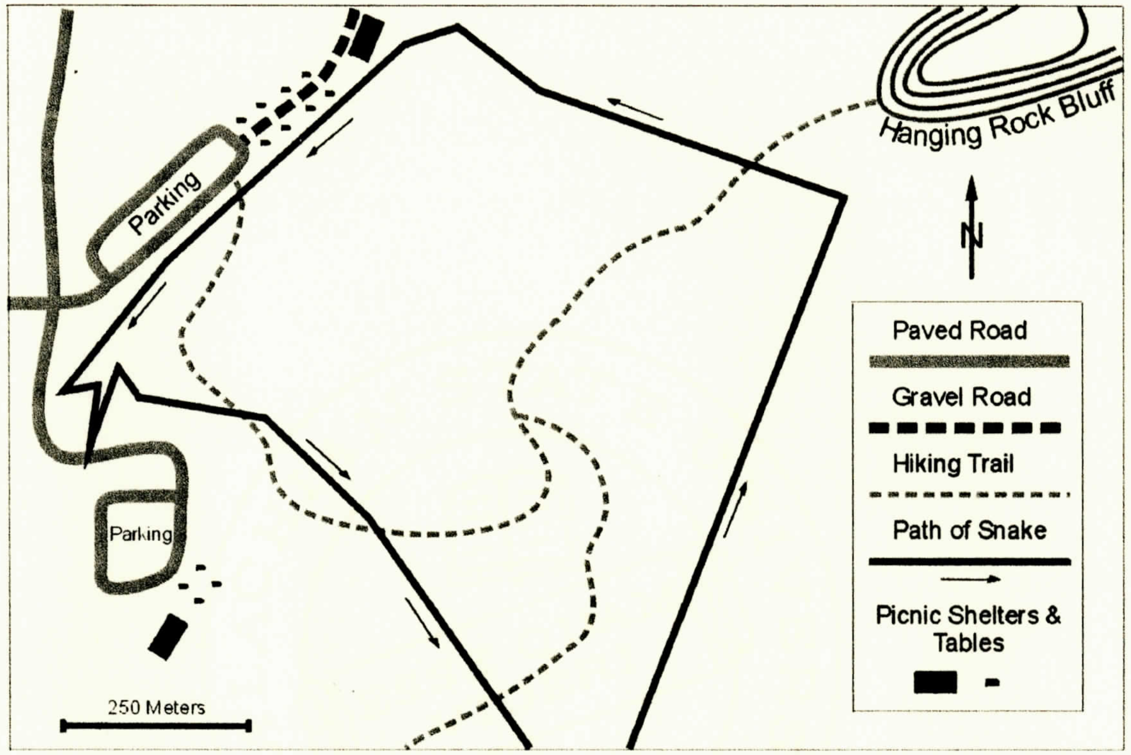

Figure 2.4. Movements of an adult male *C. horridus* from 25 July to 25 September, 1994. This snake's movements demonstrated active avoidance of roads, picnic areas, and parking lots (from Sealy 2002).

we minimize roads' impacts? Barriers barring access to roads are not the answer since these might prevent deaths, but would severely limit the migrations of snakes and other species. For many species, culverts and tunnels constructed under highways have proven successful (Dodd, 1993). Might they be successful for timber rattlesnakes as well? Only future research combined with a willingness of various publics to consider the consequences of roads on rattlesnake populations may address this problem. Without this consideration many timber rattlesnake populations will be pushed to extirpation.

LITERATURE CITED

Andrews, Kimberly M. and J. W. Gibbons, 2005. How do highways affect snake movements? Behavioral response to roads and vehicles. Copeia, 2005 (4), pp. 772-782.

Bonnet, Xavier, G. Naulleau, and R. Shine, 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89 (1999), 39-50.

Brown. W.S. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. SSAR Herpetological Circular No. 22: 1-78.

_____. 1995. Heterosexual groups and the mating season in a northern population of timber rattlesnakes, *Crotalus horridus*. Herpetological Natural History, 3(2), pp. 127-133.

Bushar, L. M., H.K. Reinert, and L. Gelbert. 1998. Genetic variation and gene flow within and between local populations of the timber rattlesnake, *Crotalus horridus*. Copeia, 1998(2), pp. 411-422.

Clevenger, A.P. and B. Chruszczc, K. E. Gunsonc, 2003. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. Biological Conservation 109 (2003),15–26.

Cobb, V.A., and J.J. Green, T. Worrall, J. Pruett, and B. Glorioso. 2005. Initial den location behavior in a litter of neonate *Crotalus horridus* (Timber Rattlesnake). Southeastern Naturalist, 4(4): 723-730.

Conant, R., and J. T. Collins. 1998. A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Boston: Houghton Mifflin Co.

Dodd, C. K. 1993. Strategies for snake conservation. In Richard A. Seigel, Joseph T. Collins (eds.), Snakes: Ecology and Behavior. pp. 363-393. McGraw-Hill, New York.

Forman, R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14 (1): 31-35.

Gibbons, J. W. 1972. Reproduction, growth, and sexual dimorphism in the Canebrake Rattlesnake *Crotalus horridus atricaudatus*. Copeia (2): 222-226.

Groot Bruinderink, G.W.T.A., and E. Hazebroek. 1996. Ungulate traffic collisions in Europe. Conservation Biology 10: 1059-1067.

Hels, T. and E. Buchwald, 2001. The effect of road kills on amphibian populations. Biological Conservation 99 (2001), 331–340.

Kerley, L.L., J. M. Goodrich, D. G. Miquelle, E. N. Smirnov, H. B. Quigley, and M. G. Hornocker. 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology, 16 (1), 97–108.

Reinert, H.K., and R.T. Zappalorti. 1988. Timber Rattlesnakes *Crotalus horridus* of the Pine Barrens: their movement patterns and habitat preference. Copeia 1988: 964-978.

Riitters, K. H., and J. D. Wickham. 2003. How far to the nearest road? Frontiers in Ecology and the Environment 1(3):125–129.

Rosen, P.C., and C. H. Lowe. 1994. Highway mortality of snakes in the Sonoran Desert of Southern Arizona. Biological Conservation 68: 143-148.

Mace, R.D., J.S. Waller, T.L. Manley, K. Axe, and W.T. Wittinger. 2002. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology, 13(2) 97–108

Mader, H.J., 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29 (1984) 81-96.

Martin, W.H., 1992. Phenology of the timber rattlesnake (*Crotalus horridus*) in an unglaciated section of the Appalachian Mountains. In J. A. Campbell, E. D. Brodie Jr. (eds.), Biology of the Pitvipers. Selva Press, Tyler, Texas, pp. 259-277.

_____, 1993. Reproduction of the Timber Rattlesnake (*Crotalus horridus*) in the Appalachian Mountains. Journal of Herpetology 27:133-143.

Sealy, J. B. 1996. *Crotalus horridus* (Timber Rattlesnake). Mating. Herpetological Review, Vol. 27: 23-24.

_____, 2002. Ecology and behavior of the timber rattlesnake (*Crotalus horridus*) in the upper Piedmont of North Carolina: Identified threats and conservation recommendations. *In* G. W. Schuett, M. Hoggren, M. E. Douglas, and H. Greene (eds.) Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, UT. pp. 561-578.

Shine, R., M. Lemaster, M. Wall, T. Langkilde, and R. Mason. 2004. Why did the snake cross the road? Effects of roads on the movement and location of mates by garter snakes. (Thamnophis sirtalis parietalis). http://www.ecologyandsociety.org/vol9/iss1/main.html

Smith, L. and K. Dodd. 2003. Wildlife mortality on U.S. Highway 441 across Paynes Prairie, Alachua County, Florida. Florida Scientist. 66 (2):128-140.

Zar, J. H., 1999. Biostatistical Analysis. Prentice-Hall, Inc., Simon & Schuster, Upper Saddle River, New Jersey.

BIOGRAPHICAL INFORMATION

John Benjamin Sealy III was born in Greensboro, North Carolina, on September 27, 1952. He attended elementary school in Madison, North Carolina and graduated from Madison-Mayodan Senior High School in June of 1970. The following autumn Mr. Sealy entered Elon College and in May of 1975 was awarded the Bachelor of Arts degree in Social Science. He spent 20 years climbing the ladder of success before realizing that his ladder was leaning against the wrong wall. In 1995 Mr. Sealy entered the University of North Carolina at Greensboro to pursue a degree in biology and was awarded a Bachelor of Arts degree in December of 1997. In August of 1998 he entered Appalachian State University to pursue a Master of Science degree and was awarded the degree in December of 2006. Mr. Sealy is presently employed as an Environmental Health Specialist with the Rockingham County Department of Public Health in Wentworth, North Carolina and is a North Carolina Registered Sanitarian.

Mr. Sealy and his wife Kathryn reside at 160 Woodsong Dr. in Stokesdale, North Carolina. His parents are Mr. John B. Sealy Jr. and Margaret Vaughn McAlister Sealy of Greensboro.