ECOLOGY AND BEHAVIOR OF THE TIMBER RATTLESNAKE (*CROTALUS HORRIDUS*) IN THE UPPER PIEDMONT OF NORTH CAROLINA: IDENTIFIED THREATS AND CONSERVATION RECOMMENDATIONS

JOHN B. SEALY

ABSTRACT: A disjunct population of the Timber Rattlesnake (*Crotalus horridus*) was studied in the Sauratown Mountains, an upper Piedmont monadnock in north-central North Carolina. Anecdotal evidence suggests that this population is declining. A field study was thus initiated to examine the reproductive ecology, spatial requirements, and possible causes of the population decline in state parks that represent habitat islands surrounded by a fragmented landscape intersected with roads. Of snakes examined (n = 96), ten were implanted with radio transmitters and radio tracked, five for multiple seasons. Mass of pregnant females (n = 11) suggests that a minimum of 500 g is necessary for reproduction. Snakes hibernated as singles or small groups at elevations from 466 to 655 m. Non-random 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 is a significant cause of population decline, causing a skew in the sex ratio (Male:Female, 1:3.7). Our observations show that humans may negatively impact pregnant females and their habitat. Management response to nuisance snakes was examined, and subsequently changed at Hanging Rock State Park. Short-distance translocation (n = 31), for example, was determined to be 100% effective in managing nuisance rattlesnakes. Management recommendations include public education as to the presence and protected status of *C. horridus* in North Carolina state parks, termination of long-distance translocation as a conservation management practice, and restriction of access to sites occupied by pregnant females.

INTRODUCTION

The Timber Rattlesnake (*Crotalus horridus*) once ranged over much of the eastern United States in upland, deciduous forests (Conant and Collins, 1998). Overall, its current range is reduced and severely fragmented (Martin, 1992a). The present distribution of *C. horridus* in North Carolina is from the western mountains to the maritime forests of eastern coastal islands, but is discontinuous (Palmer and Braswell, 1995). Although populations continue to occur in many forested areas of the lowland Coastal Plain, only a few isolated populations persist in the heavily-populated and agricultural, mid-elevation central Piedmont region. In the Sauratown Mountains, which is a small and isolated uplift in the upper Piedmont, a disjunct population of *C. horridus* remains. Populations of *C. horridus* nearest to the Sauratowns occur in the foothills of the Blue Ridge province 30 km to the northwest, as well as 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 *C. horridus*. Indeed, anecdotal information from residents living adjacent to the mountains indicated that sightings of this once-common species have declined precipitously over the past 20 years. In a cooperative research program with personnel of the larger of the two state parks, 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 *C. horridus* with a concomitant focus on the movement patterns and behaviors of selected individuals by radiotelemetry.

1058 Piedmont Springs Rd.
Danbury, NC 27016
jbsealy@earthlink.net

MATERIALS AND 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 lat. 36º 20', 36º25' N, long. 80º13', 80º30' W in Stokes and Surry counties, North Carolina (Fig. 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 7.9ºC and – 2.7ºC for January and 28.3ºC and 17.7ºC for July (NOAA, Asheville, North Carolina).

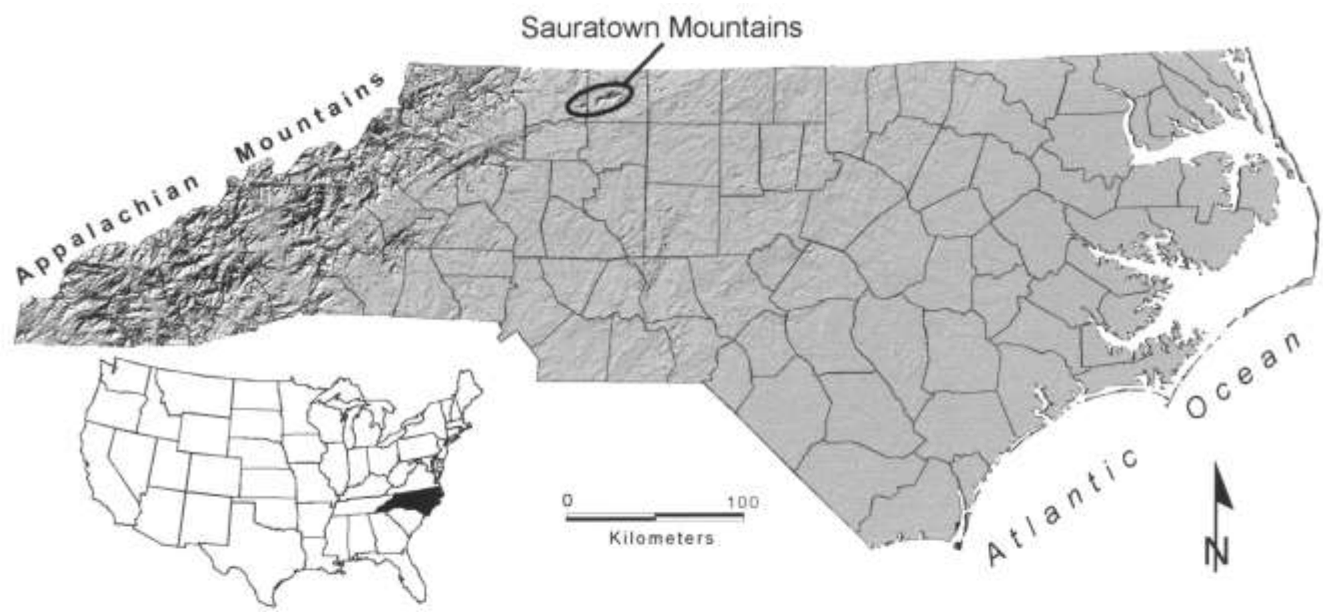

Fig. 1. Location of the Sauratown Mountains in the northern Piedmont of North Carolina. Data Source: U.S.G.S. Prepared by Art Rex, 2001

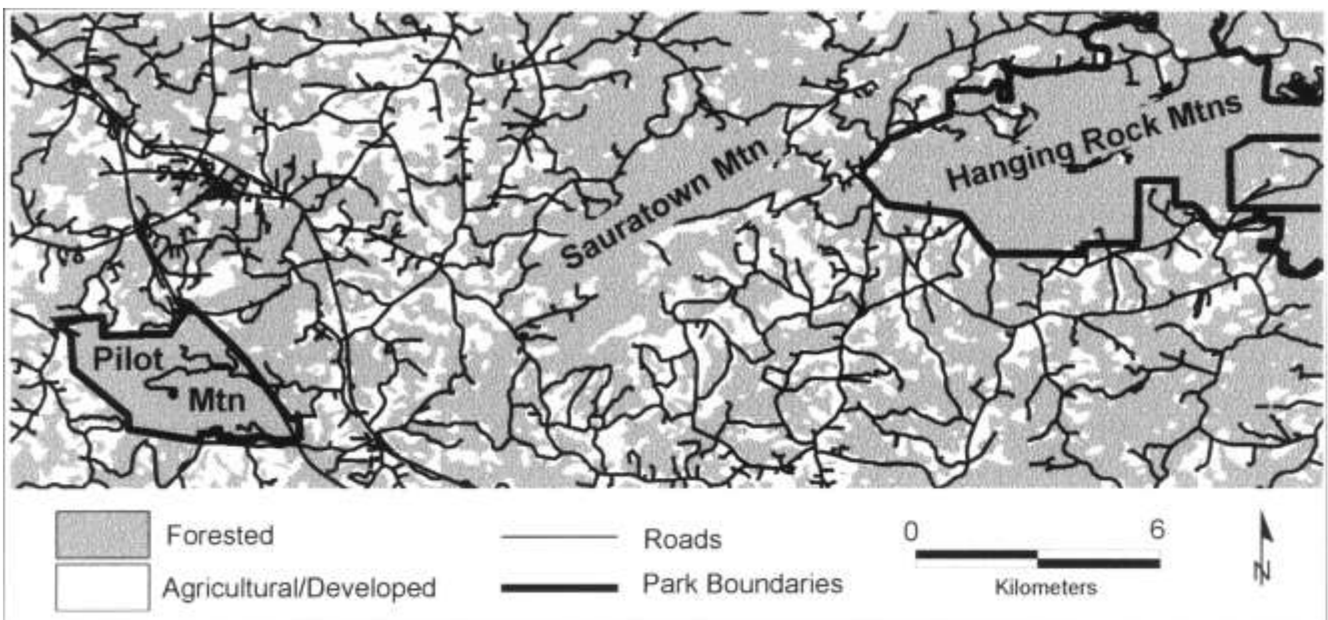

Fig. 2. Fragmented and road intersected landscape surrounding the Sauratown Mountains in Stokes and Surry Counties, NC. Data Source: NC CGIA. Prepared by Art Rex, 2001

Data collection primarily occurred within the boundaries of Hanging Rock State Park, which constitutes the largest section of the Sauratown range (Fig. 2). The park encompasses 2,517 ha and has an elevational range of 298 to 785 m including 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 as the Hanging Rock Mountains. Sauratown Mountain and Pilot Mountain (including Pilot Mountain State Park) lie 4.5 and 13 km to the west, respectively (Fig. 2).

Hanging Rock State Park experiences heavy public use, receiving more than 400,000 visitors (100,000 vehicles) annually with the majority of visitors 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, a bathhouse, four open-air shelters for large day-groups, and 65 picnic tables. Two parking lots can 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.

Study Procedures

Timber Rattlesnakes were captured from May 1990 to October 1997. Regular searches of exposed rock outcrops allowed individuals to be located at their hibernacula. As summer progressed and they dispersed, my searches focused on rock formation types used by pregnant females (Martin, 1993). Park personnel captured many "nuisance" rattlesnakes on park roads, in campgrounds, and in other public areas, and 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. Sealy, unpublished).

Sex was determined by tail length and/or subcaudal counts (Gloyd, 1940; Klauber, 1972; Palmer and Braswell, 1995). Where 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 (this method has been used by W. Brown, pers. comm.). Snakes listed as "sex unknown" were individuals 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 they produced a litter. Pregnant females, therefore, were considered reproductive in their year of capture, and were identified by their distended lower body (Fitch, 1987; Martin, 1993) or (rarely) females were palped to detect enlarged follicles and/or embryos. Females diagnosed as post-partum 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).

Following capture, individuals were stretched along an incrementally marked snake hook and measured for total length (rounded to the nearest centimeter), from tip-of-snout to base-of-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 (Brown, 1991). Snakes receiving radiotransmitters were measured while anesthetized. All snakes were weighed with 1-kg Pesola® scales to the nearest 5 g while secured in bags.

Age estimates were made from rattle-segment counts using data and methods described by Martin (1993). Rattle segment counts included the basal segment and, where present, the post-natal button. In the Appalachian Mountains, which are similar in climate and habitat to the Sauratowns, Martin (1993) found that shedding rates in *C. horridus* 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 must be considered when calculating the total age for adults. Shedding rates for juveniles are higher than those for adults. Juveniles typically shed twice per season every year, whereas adults shed twice per season every third or fourth year. Further, adults shed once per season during intervening years. Based on known-age snakes sampled by Martin (1993), Aldridge and Brown (1995), and data on a longer active season in the Sauratowns, I estimate an 11-shed (10 + button) snake to be at least 6 years old.

When broken rattle strings were tapered, the number of missing segments was determined by comparison with photocopies of complete ones (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 individual snakes with such rattles (typical of older adults), those with untapered rattle strings having seven or more segments were assigned to the 10-year-old or older age class. Individuals with broken untapered rattle strings having fewer than seven segments were placed in age classes of known-age snakes of corresponding total length.

Subjects 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 seven years after their initial capture using this marking technique.

Movement 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 48 h to ensure that the incisions were healing properly. Each transmitter-implanted animal was released at its site of capture.

Radiotransmitters (model SM-1, AVM Instruments LTD, Livermore, California) 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 mass (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, Illinois) on a frequency of 150 MHz.

Telemetered snakes were located approximately every other day, and 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 individuals (4 males, 6 females) were monitored telemetrically for periods from 27 to 345 days. Five of these 10 snakes 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 (two males and three 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 (e.g., home range) was determined for these five individuals 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 ⟨= 0.05.

RESULTS AND DISCUSSION

Morphology and Shedding

Size dimorphism.—Length, sex, and age were determined for 74% of all snakes examined (n = 71, Table 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.—In the Sauratown Mountains *C. horridus* exhibits 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 one individual had a distinctly banded tail.

In general, the snakes of the Sauratowns exhibit color patterns most closely resembling the Canebrake variant (*C. h. atricaudatus*) of the Coastal Plain and lower Piedmont of North Carolina (see description of *C. h. atricaudatus* in Palmer and Braswell, 1995; Plate 10b). Dark color morphs of *C. horridus* (Plate 10c) do not occur in the Sauratown populations, unlike high-elevation populations in western North Carolina, to the south and east. These observations suggest that historical colonization of the Sauratowns by *C. horridus* may have occurred from Coastal Plain populations to the southeast.

Ecdysis.—Ecdysis (shedding) records (n = 42) peaked in June when 57% of snakes (n = 24) underwent ecdysis. Several snakes (n = 3) shed in July, and many more (n = 15 or 36%) shed in August. Pregnant snakes at gestation sites (n = 23) made up 96% of all shedding observations in June.

Rattle segment counts from two individuals (long-term recapture data) and shedding records from three

Table 1. Mean total length and estimated age (calculated from the number of lifetime sheds) for male and female *Crotalus horridus* in Hanging Rock State Park, Stokes County, NC. Rattle size is given as the number of segments plus the button (b) of a complete (unbroken) string.

Ecdysis	Rattle	Age (yr)	Total length (cm) Mean	(Range)	Sample size n
FEMALES					
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
					50
MALES					
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
					21

telemetered snakes monitored for multiple years indicated that snakes shed 28 times in a combined total of 23 snake active seasons, for a mean adult shedding rate of 1.22 sheds per year. With an average active season of 5.9 months per year, this equals one shed every 4.8 months for adults. One adult male was observed to shed twice in the same season (on 22 June and 15 August). On average, adult snakes were observed to shed once per year in each of three or four successive years and twice in the fourth or fifth season, averaging 1.2 sheds per year.

Ecdysis records indicate that shedding rates in *C. horridus* are somewhat predictable, and that adults shed twice in some years (Martin, 1993); however, the distribution of shedding observations may reflect a sampling bias. For example, in my study, shedding observations coincided with peaks in snake activity (June and August), when 66% of all snake records occurred. Shedding records for non-pregnant and non-telemetered snakes are sparse. Of the 15 sheds recorded in August (10 females, 5 males), 12 were of telemetered snakes that would have been otherwise undetected.

All pregnant females in the Sauratowns completed one shed by the end of June. In New York, Aldridge and Brown (1995) likewise determined that both sexes completed a shed-cycle in June. The heavy representation of pregnant females in this study's shedding data is undoubtedly an artifact of the sampling skew favoring gestating females. Non-pregnant females do not necessarily shed in June, but pregnant females undergo obligatory ecdysis at the onset of gestation.

Two vitellogenic (i.e., they possessed yolked follicles) females shed in mid-August. One shed immedi-

Table 2. Reproductive status, mass, total length, and age of reproductive females (n = 12) at Hanging Rock State Park, Stokes County, NC. P = pregnant. V = vitellogenic.

Date	Reproductive status	Mass (g)	Total length (cm)	Age (yr)
2 July	P	500	90	7
2 July	P	520	87	9
27 June	V	530	93	> 10
7 August	V	540	91	> 10
16 June	P	567	91	> 10
2 July	P	600	91	9
30 June	P	680	102	8
2 July	P	790	93	> 10
18 June	P	820	93	> 10
24 June	P	850	107	> 10
14 June	P	1049	104	> 10
15 August	V	1219	110	> 10

ately prior to copulation, and the other was pre-shed when found accompanied by a male. As with the gestational shed, this "pre-mating" shed in *C. horridus* seems obligatory as a prelude to courtship and copulation (Brown, 1995). In this species and other pitvipers, ecdysis enhances female attractiveness (Macartney and Gregory, 1988; Duvall et al., 1992; Schuett, 1992; Brown, 1995), and it is an important cue to initiate male courtship (Schuett, 1992).

Reproduction

Size and age at reproduction.—Ages of reproductive females (n = 23) are presented in Figure 3. The youngest reproductive (pregnant) females had rattle-segment counts of 12, and were estimated at 7 years-of-age. A sample of pregnant females whose weight, length and age were determined (n = 12) are shown in Table 2. Snakes ≥ 10 years-of-age averaged 796 g and made up 67% of this sample. Those 7–9 nine 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.

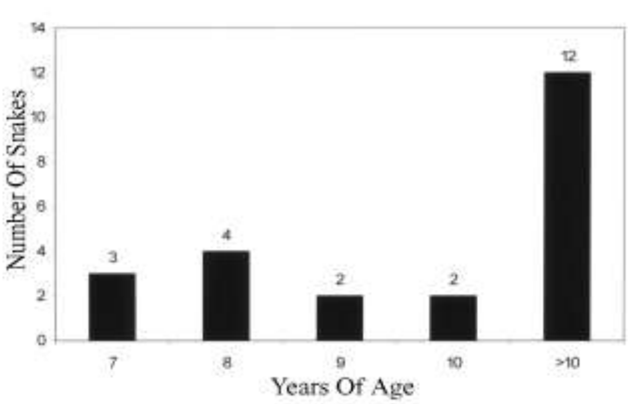

Fig. 3. Estimated ages of reproductive female *C. horridus* at Hanging Rock State Park, Stokes County, NC.

Seven to 9-year-old females in the Sauratowns are probably producing their first litters, having achieved sexual maturity at age six (Fig. 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 related to body mass, size, and age (Schuett, 1992; Beaupre, this volume; Bonnet et al., this volume). 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). One female lost 46% of her body mass at parturition. Magnitude of body mass loss for female *C. horridus* and *C. viridis* has been reported by Brown (1991) and Macartney and Gregory (1988), respectively. Reproductive frequency is constrained by a female's ability to regain lost body mass (Macartney and Gregory, 1988; Brown, 1991) as vitellogenesis is evidently delayed in snakes with insufficient fat reserves (see Bonnet et al., this volume). Reproductive females ≥10 years-of-age made up 67% of the Sauratown sample (Fig. 3). Older and larger females have a higher fecundity due to their ability to regain body mass following parturition (Gibbons, 1972; Diller and Wallace, 1984; Macartney and Gregory, 1988; Martin, 1993), which would explain 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 female *C. horridus* as the lowest body mass of any pregnant snake in the Sauratowns was 500 g (Table 2). In New York, females < 500 g and/or < 85 cm snout-vent length (ca. 89.4 cm total length) were considered immature (Brown, 1991). In the Appalachians, the youngest pregnant females (5 years-of-age) were above the average length for their age at 91 cm total length (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 (see Beaupre, this volume; Bonnet et al., this volume).

Mating season.—In the Sauratowns, mating behavior of *C. horridus* may occur as early as late June and continue through August, probably into mid-September. This was based on a marked increase in the frequency and distance of male movements (see Rudolph and Burgdorf, 1997), dates for vitellogenic females (Table 2), and observations of sexual activity. In the Appalachians and elsewhere, seasonal timing of mating is from late July to mid-September, and appears to be coincident with follicular yolking (Schuett, 1992; Martin, 1993, this volume). In the Sauratowns, four instances of sexual 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 accompanying a female and was in physical contact with her for four days, culminating in copulation on 15 August (Sealy, 1996; see Coupe, this volume).

Follicle size.—Two necropsies of adult females yielded data on follicle size and number. On 15 August, a female (110 cm, 1219 g, > 10 years-of-age) was found to have follicles (n = 21) ranging in length from 7.5 to 25 mm. Nine of these, ranging from 20 to 25 mm, were considered yolked (Macartney and Gregory, 1988). An adult non-pregnant female (87 cm, 520 g, 8 years-of-age) obtained on 9 September was found to have follicles (N = 16) ranging in length from 7 to 12 mm.

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 (see Greene et al., this volume; Plates 10 c, 11 a, b). Three of the young were captured (1 male, 2 females), and each was 25 g and measured 29 cm in total length. The mother and neonates were last observed at the site on 14 September.

Hibernation

Descriptions of dens.—Over-wintering hibernacula (dens) spanned 6.4 km in the primary study area and were located on the lower slopes of the mountains. These rocky slopes, covered in soil and supporting woodlands of mature oak (*Quercus* spp.), hickory (*Carya* spp.), and pine (*Pinus* spp.), provide suitable structures for winter refuge. Deciduous trees dominate each site, and entrances to hibernacula are associated with a break in the soil surface provided by a protruding rock or tree growing into the slope. Five of the nine dens identified were on south or southeast facing slopes. Four dens were on north-facing slopes with two facing east and two facing west. Den elevations ranged from 466 to 655 m.

Five dens were adjacent to and < 5 m from permanent, small streams or temporary drainage courses where surface flow was visible during periods of rain. Three individuals that used separate dens emerged covered with mud and is testament to the hydric conditions underground. Similar observations have been reported elsewhere (Stechert, 1980; Reinert and Zappalorti, 1988). Ground water and/or subsurface flow may benefit hibernating snakes in several ways. Subsurface water may moderate temperatures in the dens and prevent desiccation (Kauffeld, 1957; Stechert, 1980). Apparently, in the Sauratowns, subsurface flow creates interstitial spaces in subsurface rock rubble, providing suitable winter refuge. One telemetered male entered his den in a dry temporary drainage course and traveled 10 m underground and upslope to a location where he remained until spring.

Denning aggregations.—In the Hanging Rock Mountains, *C. horridus* hibernates singly or in small groups. The greatest number of rattlesnakes found in one den was three, as determined by captures in an enclosure around the den entrance. *Crotalus horridus* shared over-wintering sites with the colubrid *Elaphe obsoleta*, and the pitviper *Agkistrodon contortrix*.

Ingress and egress.—Dates of ingress (n = 6) ranged from 5 October to 7 November, with a median date of 18 October. Dates of egress (n = 13) ranged from 8 April to 5 May with a median of 12 April. Snakes remained in hibernation for 177 days, calculated from the median dates of ingress to egress.

The first movements of emerging snakes were < 30 m from the hibernaculum. At the time of egress, snakes often were fossorial, using logs, rocks, dense deadfall, and leaves for concealment. Emerging snakes typically used the same pathways each year in their out-migrations and were found at specific structures repeatedly in separate years.

In early to mid-September, all snakes began movements back to dens. The pathways used by migrating snakes when approaching their den sites were the same as those used during their initial spring out-migrations (egress). Incoming snakes remained on the surface within 10 to 100 m of the den with little if any movement for up to 14 days, evidently delaying ingress until low temperatures forced them to take refuge in their hibernaculum.

One male (850 g, 114 cm) was found with a large stomach bolus on 17 October and he delayed ingress until 7 November. The size and shape of the bolus indicated that it was likely an adult Gray Squirrel (*Sciurus carolinensis*). For the next 19 days, he increased basking and used a route to his den that was different from that used in the previous two seasons. This different route was on a south-facing slope presumably more conducive to thermoregulation. On 6 November, he was found moving toward his den in mid-afternoon (air temperature was 13ºC). On 7 November, with an air temperature of 7ºC, he was located underground where he remained for the winter.

Den changes.—Two of five telemetered individuals monitored for multiple seasons used different den sites. A female moved to a site 60 m from her previous den. Subsurface access at this new site was created by a recently toppled, living oak tree (15 cm dbh). A male found refuge 80 m from his usual den when cold temperatures interrupted his migration during ingress. Both of these snakes survived and emerged the following spring.

It was difficult to determine whether new den sites chosen by snakes were occupied by other individuals, but I suspect they did not. Considering the mountainous environs of the Sauratowns, *C. horridus* was predicted to aggregate at scarce hibernation sites and show high fidelity to these sites, as occurs in mountains (Klauber, 1972; Brown, 1992; Martin, 1992b). In high elevations and mountainous habitats, *C. horrridus* has been found to change dens, but such snakes moved to other communal den sites occurring within their migratory ranges (Brown, 1992; Martin, 1992b). Opportunistic den selection, or diffuse denning, is a characteristic associated with Coastal Plain populations where there is a relatively shallow frost line, winters are mild, and refugia are numerous. In the pinelands of southern New Jersey and Coastal Plain of North Carolina and Virginia, *C. horridus* den individually or in small groups (Reinert and Zappalorti, 1988; Savitzky and Savitzky, 1995; Settle and Greene, 1995). Individuals may choose sites opportunistically, although communal denning and site fidelity have been reported in these habitats as well (Neill, 1948).

How snakes determine novel winter refugia to be suitable is unknown; however, in the Sauratowns, relatively mild winter temperatures (mean January air temperature 1.7ºC) and profuse underground access provided by the rocky denning habitat may be factors that reduce risks associated with opportunistic den selection in this population.

Spatial Ecology

Movement analyses.—In early spring and late fall, snakes moved primarily by day. During summer when night temperatures rarely fell below 20ºC, snakes moved primarily at that time. In all movement analyses, male *C. horridus* exceeded the spatial movements of females (Tables 3–4). Males traveled greater distances from their dens, had larger activity areas, and moved farther and more often on a daily basis than females. Mean daily movements of non-pregnant 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 pregnant females averaged 6.2 m (n = 2) (see Coupe, this volume).

Differences in daily movements of males and non-pregnant females were 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, 2 males) monitored through multiple seasons, a complete season of spatial data was obtained for each individual (Table 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 (14.1 ha). These findings mirror results from other studies of the spatial movements of *C. horridus* (Reinert and Zappalorti, 1988; Brown,

Table 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
			$\bar{x}$ =103	$\bar{x}$ =1613	$\bar{x}$ =18.6
				(±213.0)	(±2.7)

Table 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 ID 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
			$\bar{x}$ =2.50	$\bar{x}$ =0.85	$\bar{x}$ =24.5
			(±0.50)	(±0.16)	(±10.2)

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. The distance, however, was not aberrant when compared to the maximums found in other studies of *C. horridus*. Martin (1988), Reinert and Zappalorti (1988), and Brown (1993) found male *C. horridus* 6 km, 2.6 km, and 7.2 km, respectively, from hibernation sites.

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 there for 13 days, and emerged freshly shed. (3) A pre-shed male remained exposed on the surface, and showed no movement for 15 consecutive days until he shed.

Non-random movements.—My observations of telemetered *C. horridus* indicated that their move-

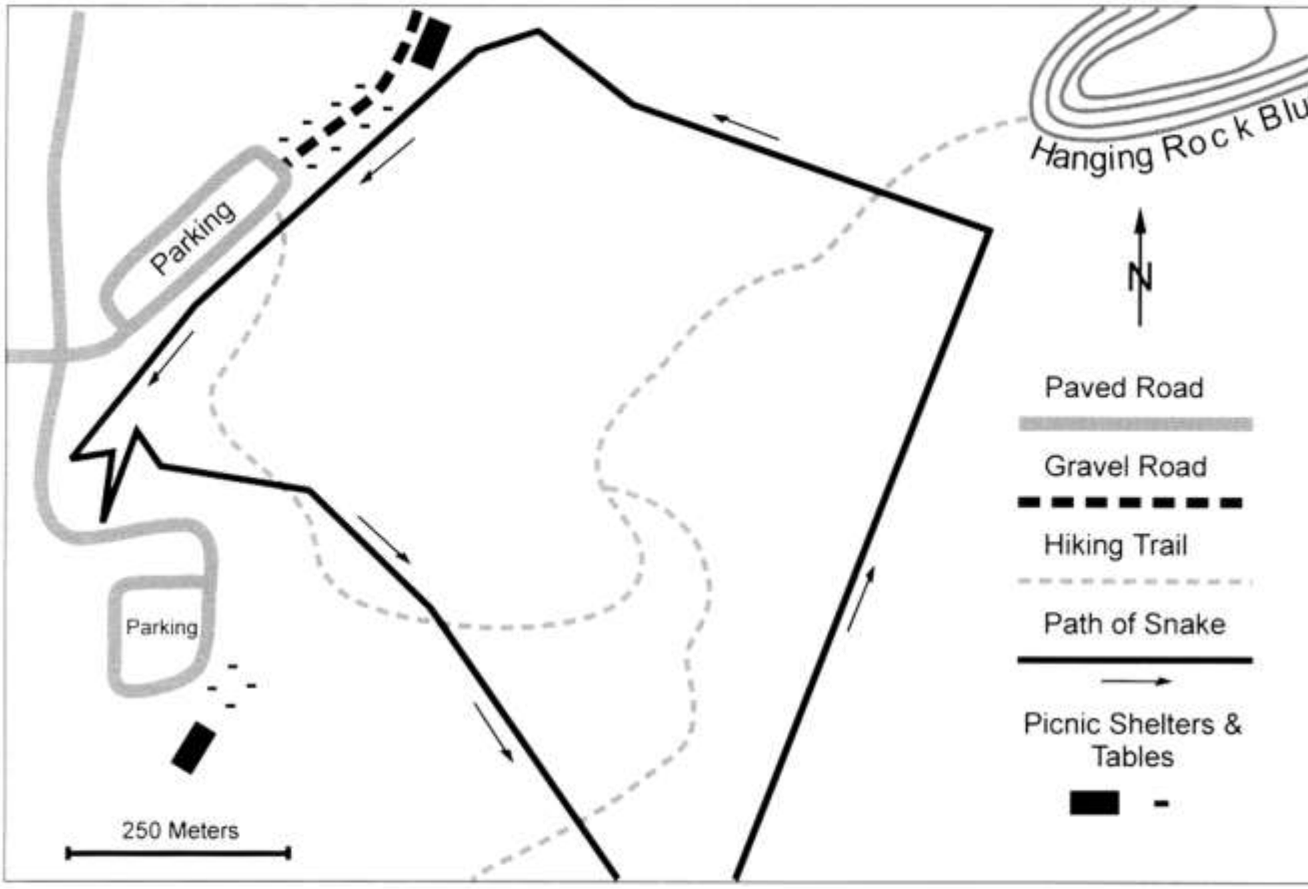

Fig. 4. Movements of an adult male *C. horridus* from 25 July to 25 September, 1994. This snake's movements demonstrated active avoidance of roads, picnic areas, and parking lots.

ments were not merely random wanderings through the landscape (see Coupe, this volume). 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 at their periphery and conducted normal activities undetected by humans nearby.

Movements of the male in Figure 4 are representative of snakes exhibiting active avoidance of open-canopied areas such as picnic shelter sites, roads, and parking lots, yet 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, he would back away or change directions and move parallel along their periphery. In one instance, with a recent meal, he thermoregulated for 10 days in one spot < 4 m from the park's most heavily used trail. In another location this male was adjacent to (< 6 m) and visible from the same trail, but undetected by hikers. He remained stationary at the site for three days in September 1994, then crossed the trail at night resuming his fall migration.

Movements of the female in Figure 5 are representative of snakes exhibiting site fidelity and home range stability. Initially captured in June 1994, crossing the campground road, she was relocated (see Short-Distance Translocations below) 100 m into the adjacent woodland and monitored with telemetry until October. Her whereabouts were unknown the next season, but she was recaptured at her den during ingress of 1995. She was monitored the following season (1996), and remained within her familiar home range; she was found on four occasions precisely at her flagged locations from 1994.

Table 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

Habitat Use and Foraging

Males and non-pregnant females.—Habitats of deciduous woodlands having nearly closed canopies, sparse to moderate understories, and dense shrub layers 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 on the surface and fully exposed in 75% of all observations (Table 5).

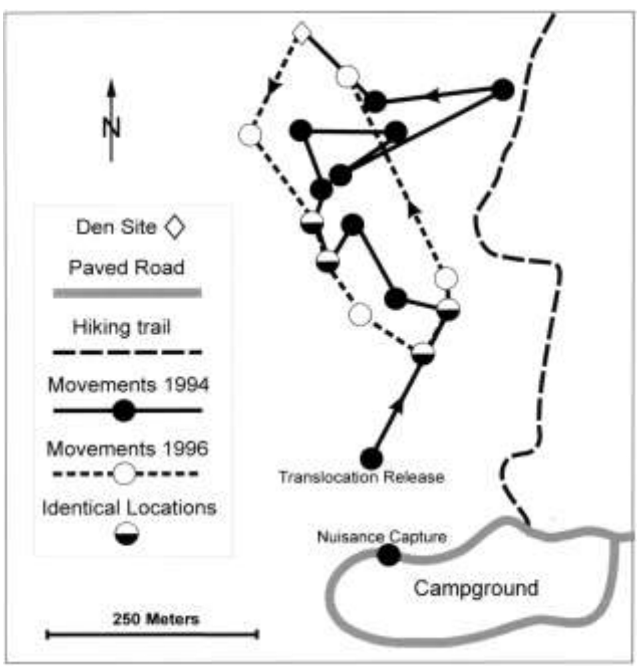

Fig. 5. Movements of an adult female *C. horridus* during 1994 and 1996 in Hanging Rock State Park, Stokes County, NC. Initially captured in the campground in 1994 and translocated a short-distance (100 m), this snake demonstrated non-random movements, site fidelity, home range stability, and subsequent avoidance of the campground.

Pregnant females.—Habitats selected by pregnant females showed a marked difference from those selected by males and non-pregnant females. Pregnant 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 by *C. horridus*. An aggregation of four pregnant females was found at one site, and aggregations (of three snakes each) 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 observed at all of these same sites. In two instances in early summer, post-partum females (having produced litters the previous fall) were found with pregnant snakes. The earliest date I found snakes at gestation sites was on 29 May, and the latest 14 September.

Tree Climbing.—An adult female was found on 17 July, 1994, stretched along a 3.5 cm diameter limb 2.0 m above the ground, she was quite visible and apparently vulnerable to avian predators. The reason for

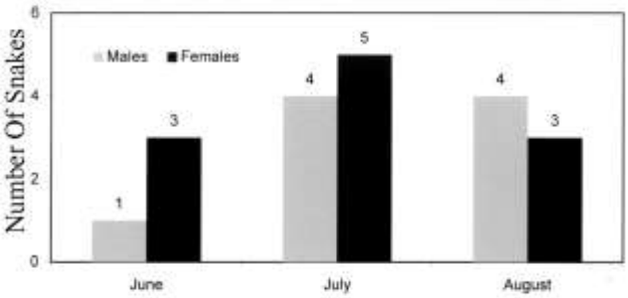

Fig. 6. Combined road mortality data of *C. horridus* males and females in the Sauratown Mountains, Stokes County, NC. Data are shown for a total of 20 specimens retrieved in three months from July 1992 to July 1997. The months of April, May, September, and October did not yield road-killed specimens.

this behavior was not evident. The arboreal perch appeared too precarious for grasping prey and there were several sites on the ground within a few meters of the tree where the snake had recently basked. The same individual was located on 9 June 1995, 2.5 m above ground, coiled on a 20 cm diameter, horizontal limb of a recently fallen tree. She tolerated a severe thunderstorm with heavy rain, and remained at the arboreal perch for at least five days.

Why rattlesnakes climb trees remains open to speculation. The above observations do not suggest basking and/or foraging as a motive (Klauber, 1972; Coupe, 2001). Apparently, however, arboreal behavior in *C. horridus* is not uncommon. Klauber (1972) reported *C. horridus* as one of the more "persistent climbers" and the behavior has been reported in this species in other telemetric studies (e.g., Saenz et al., 1996, Coupe, 2001).

Concealment in leaf-litter.—The conditions under which snakes were found completely concealed beneath leaves (n = 9) were so varied that no single interpretation can be offered. In September and October, snakes were found under leaves on cool days, in May on days of moderate temperatures, and in June on a day above 35ºC. One observation indicated that "leaf-hiding" might at times be a foraging strategy. A large male (138 cm, 1,921 g), known to consume Gray Squirrels (*S. carolinensis*), was completely concealed under loose leaves among the limbs of a fallen tree crown where squirrels were observed foraging. Leaf-hiding behaviors in *C. horridus* have been observed in New York (Stechert, 1996) and southeastern Virginia (A. Savitzky, pers. comm.).

Foraging and diet.—Six instances of ambush posture (Reinert, 1984) were noted, but rarely could I determine whether meals were obtained. Prey items were identified in five individuals, and several of these were observed while feeding. An adult female was observed eating an Eastern Chipmunk (*Tamias striatus*) and two large males ate adult Gray Squirrels (*S. carolinensis*). In May, a yearling (born the previous fall) was found consuming an adult mouse (*Peromyscus* spp.). Two snakes held for radiotransmitter surgeries defecated remains of unidentified birds.

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 pregnant 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 skew toward females when data were adjusted for the effect of pregnancy. 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 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 1:3.7.

An explanation of the Sauratown population's skewed sex ratio can be found in the road mortality data (Fig. 6) and spatial ecology of males (Tables 3–4; 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 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 3–4; Brown et al., 1982; Reinert and Zappalorti, 1988; Martin, 1992b; Brown, 1993; 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

Table 6. Results of translocations of nuisance rattlesnakes at Hanging Rock State Park in Stokes County, NC. Recurrences are individuals repeating as a nuisance in the same season.

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

and rattlesnake-hostile terrain that may be intersected with roads, farms, and residences (Fig. 2). Indeed, road-kill data in my study 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 (Aldridge and Brown, 1995). In New York, Brown's (1992) study of *C. horridus* over eight years showed that the sex ratio of all age classes was nearly unity (51.7% female). Male mortality during summer, however, was 13 times higher than that of females (Aldridge and Brown, 1995). In a study of *C. viridis lutosus* (see Douglas et al., this volume) in Utah, a sex ratio favoring males was interpreted as a result of higher mortality on females (Parker and Brown, 1973). Diller and Wallace (1984) considered a 1:1 sex ratio to be an indication of equal mortality in the sexes in a population of *C. v. oreganus* (= *C. oreganus*) in northern Idaho. 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, and the continued viability of this population may depend upon finding solutions to this relentless drain on adults. Any serious conservation efforts must make reduction in road mortality a priority. In the short-term, efforts must be made to educate park visitors that *C. horridus* 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 about 3 km distant. Long-distance translocation (LDT) of *C. horridus* 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, *C. horridus* 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 (see Nowak et al., this volume).

Short-distance translocation of nuisance snakes.—Maximum distances traveled by snakes from their dens (Table 4) indicated that translocated snakes at Hanging Rock State Park were being moved outside their familiar range. Non-random movements, (demonstrated as site fidelity, home range fidelity, and active avoidance of open-canopied/human-use areas) indicated that *C. horridus* has developed a spatial familiarity with home ranges and further suggested that moving snakes outside familiar range could disrupt normal behavior and could be detrimental to their survival.

When monitoring rattlesnakes using telemetry, it was evident that those individuals that were undetected and close to people continued to behave normally. Undiscovered rattlesnakes that are close to humans, however, 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 was minimal. Snakes found on roads or trails were processed and released immediately.

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

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. 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 individuals 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. *Crotalus horridus* relies primarily on its natural coloration and secretive behaviors (procrypsis) as protection from predators. Indeed the habitat use data (Table 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 (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 negative 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. Despite the level of intrusive actions, 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 six 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, seven 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 actively avoid the open areas associated with human use. 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. Short-distance translocations are not a perfect remedy, but rather a compensation and compromise to the intrusion of humans into rattlesnake habitat (see Nowak et al., this volume). Snakes moved a short distance are in effect being escorted safely out of what is surely a maze of human structures in hostile territory. Short-distance translocations 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 LDT of reptiles and amphibians into novel habitats (Dodd and Seigel, 1991; Reinert, 1991).

Disturbance at gestation sites.—In early summer, pregnant females could be located at gestation sites, but I was unable to relocate these females after mid-July. To learn of their location, I monitored a pregnant female with telemetry. Released at her point of capture on 2 July, the female moved frequently using 16 different locations over a 55-day period. She was often hidden from view under rock slabs, in stump holes, and in deadfall debris ≤ 30 m from her original point of capture. Although some of her cryptic nature was related to thermoregulation behavior, this may not account fully for her propensity to move and to remain hidden. Many observations convince me that males and non-pregnant females rely primarily on their coloration and cryptic behavior as protection from predators, spending the majority of their time in full view on the forest floor (Table 5). When approached, males and non-pregnant females rarely move, rattle, or even flick their tongues until disturbed. In contrast, pregnant females at gestation sites display a strong proclivity to move quickly for cover (Graves, 1989). Gestation rocks serve several functions, e.g., thermoregulation, protection from the elements, and from predators (Graves et al., 1986; Martin, 1993). Indeed, Gregory et al. (1987) surmise that the movements between basking sites may make a snake's location less predictable to predators. I infer that the pregnant snake I monitored "thought" of me as a large predator (Brown, 1993) and exhibited a heightened sensitivity to my presence (Graves, 1989). I observed a change in her behavior after she gave birth. Having moved into the surrounding woodlands, her response to my approach was now identical to that of other non-pregnant females. This female apparently responded to the frequent presence of humans as a threat, and altered use of the gestation site by moving to numerous locations and remaining cryptic. This behavior may thus explain why I was unable to locate females in this population at gestation sites in late summer.

These observations strongly infer that visits to gestation sites, however benevolent, are disruptive to pregnant females (Brown, 1992, 1993). Understanding that gestating females show a heightened sensitivity to repeated human intrusions reveals an area where populations can benefit from management intervention. Four gestation sites in Hanging Rock State Park are intersected with spur trails (created by hikers), providing ample opportunity for rattlesnake/human encounters, the resulting disruption, and occasional wanton killings of gestating females. These trails are often evidence of repeated visits by poachers. The location of gestation sites must be kept confidential and access to these areas should be prohibited during the period from June through September.

In Hanging Rock State Park, the park superintendent closed one spur trail in an effort to curtail hiker traffic through a gestation site. This was quite possibly the first action in North Carolina that restricted human activity to benefit rattlesnakes.

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 annually. Half of the recorded road deaths occurred within park boundaries. Some researchers suggest there is no harvestable surplus of adult *C. horridus* (Brown, 1993), yet the Sauratown population loses many adults each year. The findings of this study demonstrate, however, that *C. horridus* can benefit from active management if guided by an understanding of its biology. Indeed, if this species is provided a small measure of assistance, combined with a willingness of communities and the public to attempt some degree of coexistence, their populations can survive and perhaps thrive in close proximity to humans.

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