

LIFE HISTORY CONSTRAINTS ON THE TIMBER RATTLESNAKE (*CROTALUS HORRIDUS*) AT ITS CLIMATIC LIMITS

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ABSTRACT: A population of Timber Rattlesnakes (*Crotalus horridus*) was studied from 1989 to 2001, at a high-elevation (1,075 m) site on the Allegheny Plateau of eastern West Virginia. This study establishes climate and elevation as important demographic constraints for *C. horridus*. Median active season at the study site was 4.7 months (8 May to 29 September). Parturition typically occurred from 11 to 30 September, but during two years of the study females failed to bring embryos to term before hibernation. A proportion of females had partial reproductive failures in three years of the 12-year study, and overall failure was estimated between 25% and 35%. Reproductive failures were correlated with unfavorable weather during the active season. Annual reproduction was highly stochastic, and the number of reproductive females observed was from one to 13 per year. Because the population was dominated by several age-class cohorts, the number of adult snakes in the population was estimated to be from 60 to 120, and the number of breeding females was estimated to be from 25 to 50. On average, females gave birth for the first time at 11 years-of-age (9–14 years-old), and the mean birthing interval was five years. Annual survivorship was high for all age classes, and estimated to range from 68% for first-year juveniles to 92% for adult females. Generation time was calculated at 18 years. Females were estimated to average 2.4 pregnancies during their lifespan, with 1.8 successful lifetime efforts. Two additional populations of *C. horridus* from higher elevations (1,230 to 1,375 m) were found to be predominantly composed of adult males. Among snakes, *C. horridus* represents an extreme case in K-selection, and populations from higher elevations in the Appalachian Mountains are at their climatic limits. Climate during the Pleistocene and its effects on the distribution of *C. horridus* are discussed. In central Appalachian valleys, where *C. horridus* overwintered in limestone structures during Pleistocene glaciations, summer temperatures were probably similar to those that presently occur on nearby ridge tops. High elevation and high latitude populations of *C. horridus* have suffered recent declines and extirpations due to human activities.

INTRODUCTION

Animal populations persist where births and subsequent recruitment equals or exceeds mortality. Long-term climate and immediate weather conditions affect population size, vulnerability to extirpation, and geographic range by constraints placed on reproduction. Populations on the periphery of a species' range are expected to change in density, and are possibly susceptible to extirpation. Thus, from the standpoint of conservation biology, it is important to understand the life history traits of such potentially vulnerable populations.

The Timber Rattlesnake (*Crotalus horridus*) is a late-maturing, long-lived viperid with a low reproductive rate (Gibbons, 1972; Brown, 1991; Martin, 1993). Its distribution in northeastern North America and the Appalachian Mountains is primarily in forested areas with exposed rock. This species has been extirpated from much of its northern range, including all of Maine and Rhode Island, and most of Massachusetts, New Hampshire, and Vermont (Norton, 1929; Palmer, 1946; Breen, 1970; Hunter et al., 1992; Palmer, 1992). Place names and historical documents suggest that *C. horridus* had a much wider distribution when Europeans settled in New England, as well as in Wisconsin (Fobes, 1951; Schorger, 1967). As late as

1957–1958, two rattlesnake bites were reported in New Hampshire (Parrish 1980), a state where today only a single den colony is confirmed. Farther south, resource managers and biologists in the Appalachians report that *C. horridus* has declined at higher elevations during the last half of the 20th century (mail survey in 1981; W. Martin, unpublished). Severe declines and possible local extinctions were reported in New Hampshire, Allegany State Park in southwestern New York and adjoining Allegheny National Forest in Pennsylvania, from higher elevations of the Allegheny Plateau in West Virginia, and from the southern Appalachians in North Carolina, Tennessee, and Georgia.

In the central Appalachian region, *C. horridus* apparently survived Wisconsinan glacial advances by overwintering in limestone caverns (Holman, 1995). Known Pleistocene refugia were located in deep valleys of the Ridge and Valley province. In contrast, the High Allegheny Plateau and mountains above 900 m were probably in the permafrost zone containing tundra vegetation (Pe'we', 1983), beyond the climatic limits of this species. Two opposing views of Pleistocene climate in the Appalachians have been proposed: (1) Mean annual temperatures during the full glacial were at least 15°C cooler than at present with most of the cooling in the winter (Delcourt, 1979), and precipitation was less than half of what is today. (2) Based on an "inharmonious" assemblage of plants and animals,

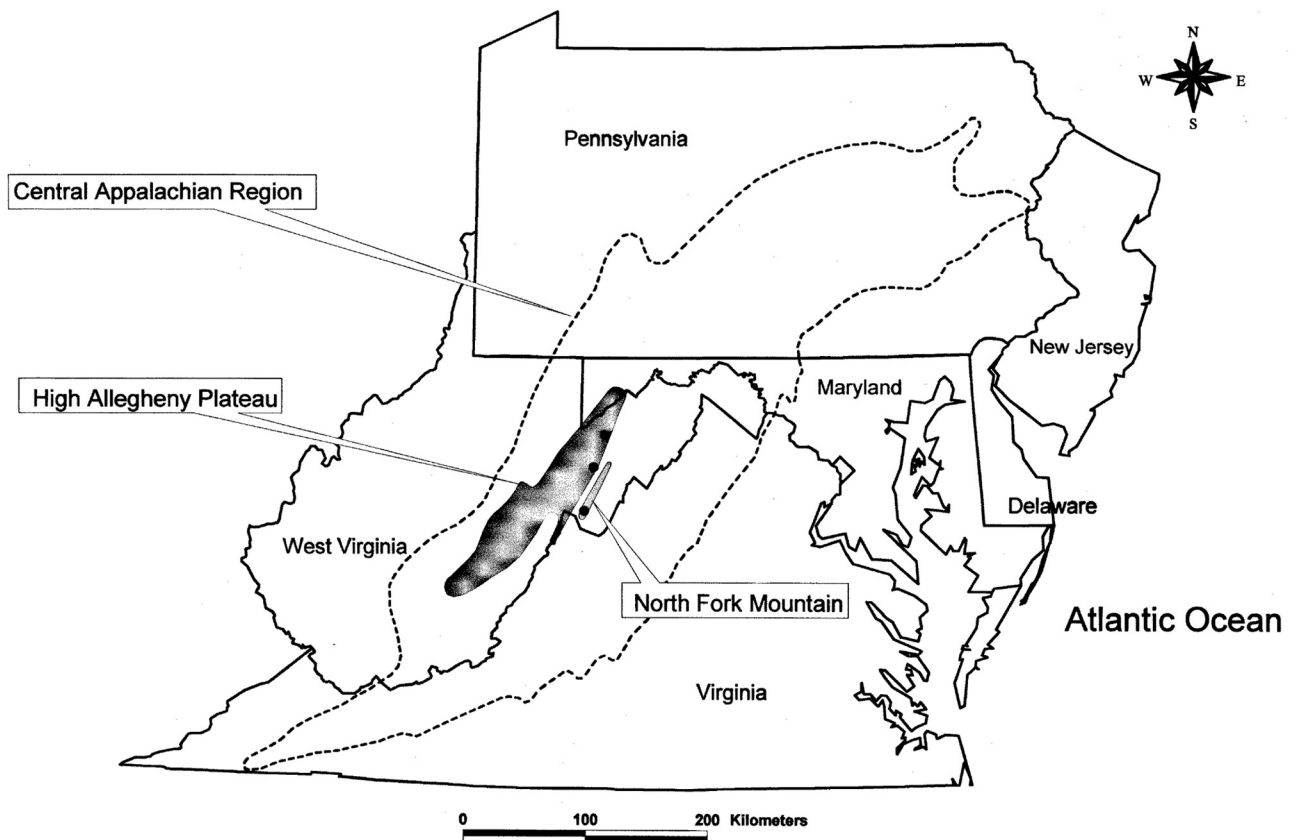


Fig. 1. Map of the central Appalachian region of eastern North America. High Allegheny Plateau and North Fork Mountain indicated by shading. Solid circles are the study sites. Geographic data source; ESRI Inc. Cartography by John Sealy.

Lundelius et al. (1983) proposed the “climatic equability hypothesis,” suggesting that summers were much cooler and winters much warmer than current conditions. Determining the present climatic requirements and ecological limits of widespread, montane, ectothermic vertebrates, such as *C. horridus*, may assist in resolving this debate.

The High Allegheny Plateau (Grossman et al., 1998) of eastern West Virginia was historically dominated by Red Spruce (*Picea rubens*) and Eastern Hemlock (*Tsuga canadensis*) forests from the Allegheny Front to the Allegheny Backbone, 15–27 km west, with Northern Red Oak (*Quercus rubra*) and northern hardwood trees (e.g., maples, *Acer* spp.; birches, *Betula* spp.; American Beech, *Fagus grandifolia*) at the periphery and in dissected areas (Stevenson, 1993). Local distribution of *C. horridus* on the High Allegheny Plateau suggests that this species reaches its ecological limits there because its occurrence is discontinuous and patchy in apparently suitable habitat. *Crotalus horridus* occurs around the periphery

of the High Allegheny Plateau. It is locally common on Fore Knobs and New Creek Mountain–North Fork Mountain to the east, as well as in some dissected areas of the plateau, but occurs sparingly at higher elevations (1,220 to 1,480 m) dominated by heath barrens or dwarf shrublands (*Vaccinium* spp.). *Crotalus horridus* is absent in areas of apparently suitable habitat with exposed ledges and boulder fields, such as interior headwater areas distant from low-elevation valleys.

A site located on the edge of *C. horridus* distribution on the High Allegheny Plateau was chosen for the present study (see Plate 10e). Criteria used in selecting this site included (1) remoteness so as to minimize human disturbance, and (2) a sufficient sized rattlesnake population to permit a meaningful study. Although sparsely inhabited by humans, snake collectors have heavily exploited the High Allegheny Plateau. Compared with much of the Cumberland Plateau and the Ridge and Valley sections of the Appalachians, the terrain here is readily accessible,

and most rattlesnake den sites are known to local people and have been exploited since the 19th century (Browning, 1859).

From 1989 to 2000, I studied *C. horridus* at a remote high-elevation site in the High Allegheny Plateau where the population has not been severely depleted. My primary goals were to determine the climatic conditions experienced by *C. horridus* in the region, as well as the influence of climate on growth and shedding rates, age of maturity in females, frequency of reproduction, and annual age-specific survival rates. To compare life history characteristics (such as birthing dates) along a climatic gradient, I sampled populations of *C. horridus* at both lower and higher elevations on the High Allegheny Plateau.

MATERIALS AND METHODS

Study Area

Ecological setting.—The High Allegheny Plateau consists of a series of broad plateau-like mountains trending southwest to northeast. These mildly folded ridges are separated by shallow, synclinal plateau-like valleys, and the area is underlain by sediments of Mississippian and Pennsylvanian age, resistant sandstones, conglomerates, and coal-bearing sediments (Stevens, 1993). The main study site is located on the Allegheny Front, which forms the eastern edge of the High Allegheny Plateau in the Central Appalachian Region of eastern North America (Fig. 1). The site, an outlier of the Huckleberry Plains-Dolly Sods ecosystem (Brooks, 1965), is located in Grant County (northeastern West Virginia), near lat. 39°N, long. 79°W. To the east, the Allegheny Front is an escarpment that drops off steeply to the Ridge and Valley Province. To the west it dips gently toward a high intermountain plateau that averages about 1,000 m in elevation. Similar in elevation to the Allegheny Front and located from 15 to 27 km to the west, the Allegheny Backbone rises above the west side of the intermountain plateau. In places, streams incise both the intermountain plateau and Allegheny Backbone. The vegetation from the Allegheny Front to the Allegheny Backbone is a mosaic of northern hardwoods, heath barrens, and scattered Red Spruce, and that of the escarpment and incised areas is a Northern Red Oak-northern hardwood mix. To the east, the Ridge and Valley province consists of steep, narrow ridges separated by relatively wide and deep, largely agricultural lowland valleys. On the east slope of the Allegheny front is a series of short ridges (eroded remnants carved by escarpment streams) known as the Fore Knobs. Across the valleys

of New Creek and the North Fork of the South Branch of the Potomac River is the New Creek-North Fork Mountain complex, a series of narrow, steeply tilted sandstone ridges divided by water gaps. Both the ridge system and Fore Knobs are dominated by Chestnut Oak (*Q. prinus*) woodland, except above 1,200 m on North Fork Mountain where Northern Red Oak is dominant. Although the highest peaks of the Ridge and Valley are within 100 m of the higher parts of the High Allegheny Plateau, the average elevation is much lower.

The main study site is at an elevation of 1,075 m, and encompasses an area of ridge-top ca. 200 x 350 m within 10 km² of mountainside and summit; this area is probably used by the rattlesnake population. Rattlesnakes were collected at two primary dens, 115 m apart and on the edge of the escarpment, each consisting of several crevices in sandstone outcrops at the interface between outcrops and soil. The south den is located in open-canopy Northern Red Oak woodland, at a point where the den aspect changes from east to southeast. The main entrance to the den is a crevice under a small (< 1 m), flat, sandstone outcrop. Additional crevices and holes within 10 m of the main entrance are used by a small number of snakes. The north den is in closed-canopy Northern Red Oak forest and faces almost due east, and its main entrance consists of a large (> 2 m), square-like, sandstone outcrop with several crevices around the edges. Within 15 m north and south of the main entrance, a small number of snakes use additional holes and crevices.

The proportion of individuals using the dens is nearly equal (56.8% north den, 43.2% south den; $t = 1.04$, $df = 70$, $P = 0.30$). A flat above the dens consists of exposed sandstone conglomerate ledges and boulder fields, interspersed with Mesic Scrub Oak (*Q. ilicifolia*)-Scrub Pine (*Pinus pungens*, *P. rigida*)/heath barren (*Kalmia latifolia*, *Vaccinium* spp.), Red Spruce-Eastern Hemlock/Rhododendron (*Rhododendron maximum*), and stunted Northern Red Oak woodland. Elevations of the flat range from 1,065 m on the west to 1,075 m at a high point about 20 m from the edge of the escarpment. I identified nine specific locations on the flat, from 20 to 200 m from the nearest den, that *C. horridus* used for gestating and/or birthing. Neighboring rattlesnake dens are located 3 km north and 6 km south on the Allegheny Front. Five km to the east, New Creek Mountain is well populated with rattlesnakes, but a portion of Fore Knobs (1.5–2 km to the east) was inaccessible and not surveyed. To the west, the contiguous plateau appears to be devoid of

Table 1. Thirty-year (1961–1990) mean temperatures recorded at Canaan Valley State Park, Tucker County, WV. Mean monthly temperatures (°C) from June to October 1998 for Canaan Valley and Kumbrabow State Park (Randolph Co.), the Allegheny Front (Grant Co.), and North Fork Mountain (Pendleton Co.), WV. Temperature data at Canaan Valley for August and September 1998, are not available.

Month	30-yr	NOAA station data		Field data (current study)	
		Canaan Valley	Kumbrabow	Allegheny Front	North Fork Mountain.
		1998	1998	1998	1998
April	7.6	—	—	—	—
May	12.8	—	—	—	—
June	16.6	16.6	16.4	15.2	14.8
July	18.5	18.1	18.3	18.5	17.4
Aug.	17.8	—	18.4	18.3	17.5
Sept.	14.7	—	15.9	17.0	16.0
Oct.	9.0	8.7	9.6	9.9	9.0
Mean	13.9	—	15.7	15.8	14.9

rattlesnakes; the nearest known den is located 24 km west-southwest of the study site.

The nearest weather station is 25 km from the study site at Canaan Valley State Park (988 m). Annual precipitation (30-year average, 1961 to 1990) is 1,320 mm (Owenby and Ezell, 1992; Table 1). Mean July temperatures at the station averaged 18.5°C, with a high-low range from 25 to 11.7°C. Mean January temperatures averaged – 3.9°C, with a high-low range from 1.7 to – 9.4°C. Overall mean temperatures and total precipitation from April to October for the years 1989 to 1999 were recorded. Daily mean temperatures were analyzed for 1989 through 1999 for Canaan Valley State Park. For periods missing from the record, data from Kumbrabow State Park (982 m, Randolph Co., West Virginia) were used. Two temperature-recording devices (Hobologger®) were installed 1.2 m above ground on the north sides of large trees within 10 m of the dens. At the main study site, temperatures were recorded from 19 May 1998 to 16 June 1999, and on North Fork Mountain from 21 May 1998 to 6 June 1999.

Two other study sites, 30 and 70 km south-southwest of the primary study site, were monitored on the Allegheny Front and on North Fork Mountain in the Ridge and Valley province (Pendleton Co., West Virginia), respectively. The ecosystem of the former site, located on the Huckleberry Plains (1,230–1,280 m), is similar to that of the main study site and occupies 0.8 km along the Allegheny Front, rising gently toward the south and dropping off sharply toward the east-southeast. The east slope has rock outcrops, and the vegetation consists of closed-canopy Northern Red Oak-northern hardwood forest. The second site, on North Fork Mountain, ranges from 1,250 to 1,300

m in elevation and occupies 1 km of ridge-top. The habitat consists of talus (broken rock below cliffs), and scree slopes (broken rock not associated with a cliff), sandstone cliffs, boulder and block fields, dry Scrub Oak-Scrub Pine/heath barren, open-canopy scrubby Northern Red Oak/Mountain Laurel (*Kalmia latifolia*), with open-canopy Northern Red Oak woodland on the slopes. Two south-facing dens are located approximately 750 m apart. The north den is at 1,360 m in elevation in exposed sandstone scree, and the south den is at 1,260 m in a talus patch on the south side of a shaded knoll in Northern Red Oak woodland. A neighboring den is located 1.7 km to the south at 1,135 m in elevation. Four den sites on the Allegheny Plateau (Garrett Co., Maryland; 870 m) within 20–40 km north of the primary study site, were sampled at birthing time. One site is an open-canopy sandstone glade, one is a mountaintop ledge, and the other two are outcrops near ridge-tops. The surrounding forests are primarily Northern Red Oak-northern hardwoods.

A nearby weather station (Franklin, West Virginia; 580 m) is lower in elevation than the North Fork Mountain site. The Ridge and Valley province, however, is hotter and drier than comparable elevations on the High Allegheny Plateau. Precipitation and cloud cover are ca. 75% less than that of the plateau (U. S. Dept. Agriculture, 1941; NOAA, 2000), and temperatures are ca. 0.5°C higher at comparable elevations. Precipitation at Franklin averages 848 mm. Mean temperature for July was 21.2°C (high-low range 28.3 to 14.1°C), and mean temperature for January was – 1°C (high-low range 5.4 to – 7.2°C). Based on data extrapolated from local climate records and a 1-year log of actual temperatures, the following climatic features for the North Fork Mountain and Huckleberry Plains

sites are estimated: average active season length based on seasonal passage of the 11.5°C isotherm for North Fork Mountain is 4.3 months (14 May to 23 September), July mean temperature is 17.4°C, and January mean temperature is -4.8°C. The active season for Huckleberry Plains is estimated at 4.4 months (12 May to 24 September), July mean temperature is 17.5°C, and January mean temperature is -4.7°C.

Field Techniques

The study was conducted from May 1989 to June 2001, but data collected during an initial visit on 6 July 1983 are also included. Observations of snakes at the main study site, including initial captures, recaptures, neonates, and others that were counted but not captured totaled 884. Not including same-year recaptures of pregnant females, there were 113 recaptures of 263 snakes marked from 1989 to 2000, as well as the observations made in 1983. Pre-molt neonates (N = 181) located in the field were not marked. Several near-term pregnant females were brought into the laboratory, and offspring born in captivity (N = 99) were marked before they were released. A lack of concordance between totals may be noted. Individuals were counted every time they were seen, but snakes that escaped could not be used for tabulating length, growth, or shedding rates. Reproductive females found more than once in a season were counted only once in a given year. Observations of 27 snakes at the North Fork Mountain site and 16 at Huckleberry Plains were recorded. When groups of snakes were encountered, data on sex, breeding condition of females, coloration, and rattle-segments were sometimes determined without disturbing them (e.g., large adult males and post-partum females with litters were readily identified). Snakes whose sex or breeding condition was uncertain were assigned as adults or juveniles. Marked snakes could often be identified visually. The number of shedding events was determined by counting the unmarked rattle segments. Of 83 reproductive females observed, four could not be assigned a probable age. These included post-partum females with litters, but they escaped before careful examination or hid under rocks where their rattles could not be seen.

Snakes were marked with a black indelible-ink pen by writing a number on the basal segment of the rattle and drawing a line along the crease of the rattle (Martin 1993), and measured (snout to base of rattle) by gently extending them along a ruled snake stick. I noted color phase, sex of adults, and breeding condition

of adult females, but did not routinely sex juveniles (Martin 1993). I also noted rattle-segment count and shape of the rattle (e.g., complete, broken but tapered). Rattle segment counts included the basal segment (representing the most recent molt) and free segments. The button (present at post-natal molt) was noted but not included in shedding frequency calculations (see Aldridge and Brown, 1995). For example, a snake that had shed 10 times had a basal segment, eight free segments, and a button, and was thus designated in one of two ways: 10-shed or 9 + b (button). Photocopies of complete rattle strings were used to estimate the number of lost segments in individuals with broken rattle strings. Although rattle size varies in numbers and size, an average-sized rattle was used as a standard to estimate rattle segment counts.

To facilitate recapture identification, I took color slides and drew sketches of pattern peculiarities. Determination of mass was not routinely performed. For snakes that I was unable to mark, I usually determined color pattern and assigned them to an approximate age-class category. Time, temperature, weather conditions, and exact location were recorded for all snakes. Snakes taken into or born in the laboratory were measured in a squeezebox.

I constructed length and shedding correlations based on recapture data. Snakes were assigned to age classes by rattle segment counts or by total length when the rattle was missing more than one or two segments. New captures were assumed to be the same age as snakes of known age with the same rattle segment count. The first ten segments usually showed a noticeable taper. Although tapering may be detected through the first 14–18 sheds by using calipers, in the field it is difficult to determine differences beyond rattle number 10. Thus, a rattlesnake with a broken string of eight segments approximately uniform in width was assumed to have shed at least 18 times, and was assigned to the > 14-year age class; an 8-segment snake with a slight taper was assigned to the 12–14 year age-class. Rattlesnakes with short (< 5 segments), broken, and non-tapered rattle strings were assigned to an estimated age class based on total length.

I considered snakes adults if they had completed at least 10 sheds (basal segment, eight free segments, a button). The youngest females in this study gave birth after they had shed 11 times (10 segments plus a button), and thus would have been 8 years old when they mated for the first time. Aldridge and Brown (1995) determined male *C. horridus* to be sexually mature at 4–5 years-of-age in northeastern New York,

but those researchers did not present direct evidence that males of that age are effective in mating. Likewise, I have not observed young males from my study (or elsewhere in the Appalachians) to mate at such a young age. Reproduction in males (and females) typically occurs at 10 years-of-age or older, but occasionally some females reproduce at 9 years-of-age. Growth and shedding rates of juveniles of the same cohort found in fall or the following spring were pooled because growth is negligible during hibernation, no shedding was recorded before June, and most shedding takes place before fall.

Various survivorship schedules were tested empirically for best fit (Fitch, 1985). Estimates of population size are based primarily on adult females, because females can be most reliably studied. Adult males and adult non-pregnant females spend their active seasons at greater distances from their dens, apparently foraging, and only a small percentage are found in any given year. On the other hand, pregnant females began gestating at well-exposed sites soon after emergence. Because those areas could be readily surveyed, a count of reproductive females was obtained each year through periodic searching of basking sites. The proportion of new vs previously tabulated snakes was used to estimate the number of reproductive females in a given year. Recaptures during the same season were high, suggesting that at least 75% of the reproductive females were tabulated. For each 5-year period (the usual interval between births) annual counts of reproductive females were summed to estimate the total number during each period.

Determining the earliest dates for emergence was not logistically feasible, but visits were timed to coincide with peak den emergence (egress), parturition, and den ingress. When I was early, subsequent visits were made within one or two weeks. I sampled the primary study site on 51 days during the 12-year period as follows: May, 16; June, 6; July, 3; August, 2; September, 16; October, 8. The North Fork Mountain site was checked on 21 days in a 7-year period (1994 to 2000) and the Huckleberry Plains site was visited six times in a 2-year period (1998 and 1999) and once in May 2001. Visits to the primary site on 6 July 1983, and 4, 11 May, and 12 June 2001, were not included in most analyses.

Several snakes (11 adult females, 99 juveniles) from the main study site, including neonates born in the laboratory, were maintained in captivity for various lengths of time (up to six years) in order to obtain data on the following: litter size, neonatal length and mass,

parturition dates, and food intake vs shedding and growth rates of juvenile snakes. The snakes were maintained in a two-tiered enclosure with three compartments. One compartment was a concrete underground chamber accessible through a 75 mm plastic pipe. One of the above ground compartments was maintained at ambient temperatures, and the other was equipped with a heating pad and artificial light set to cycle on a timer. Mid-summer temperature ranged from 15 to 20°C in the underground compartment, and from 30 to 35°C in the heated compartment. Most individuals spent the colder months (October to April) in the underground compartment where temperatures were from ca. 15°C in October to 5°C in December and January, and subsequently rose in spring (ca. 9°C in April).

During the active season snakes were fed laboratory mice and rats, but occasionally they were offered wild mice (*Peromyscus* spp.) and voles (*Microtus* spp.). Neonates were moved to small enclosures after their initial shed and offered 8–12 gm live mice. Most captive-born juveniles were released in fall or in spring, and head-started by feeding them mice.

Median active season was considered the time when ca. 50% of the population had surfaced in spring, and when ca. 50% remained on the surface in fall. Date estimates were based on the numbers of snakes observed at basking sites vs numbers at dens. The overall active season was based on the initiation of egress and ingress.

The following terms define the various classes of snake study:

- *Non-reproductive female*. An adult female that did not reproduce, or would not have reproduced the year she was processed. Yolking females collected in the fall were considered non-reproductive.
- *Reproductive females*. Pregnant females and post-partum females processed in fall.
- *Neonate*. A newborn that has not had its first shed-of-life.
- *Young-of-the-year*. A snake in its first fall (includes pre- and post-shed neonates).
- *First-year juvenile*. A snake in its first fall, spring, or summer.
- *Juvenile*. A snake too young to breed. Snakes that had shed \leq six times (e.g., $\leq 5 + b$) were considered juveniles.
- *Sub-adult*. Snakes potentially old enough to breed, but not known to have done so. Also, snakes that had shed 7 to 9 times).

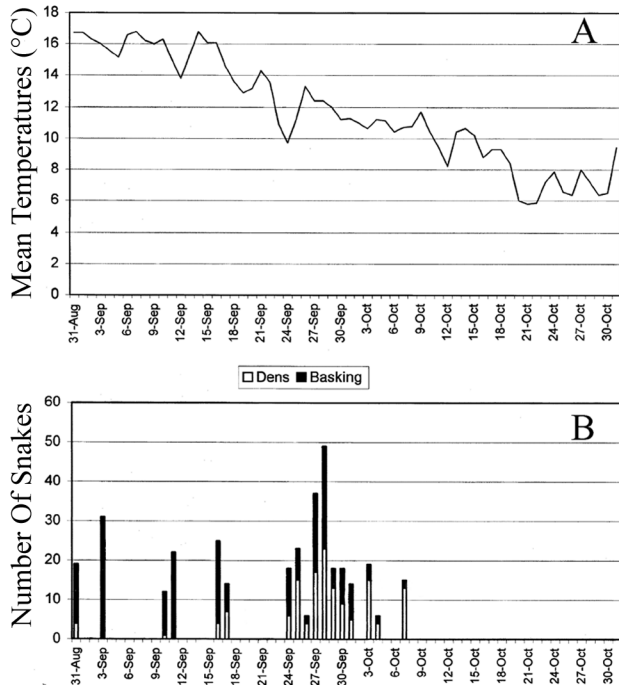


Fig. 2. Fall ingress pattern of *Crotalus horridus* at a site on the Allegheny Front, WV. (A) Average temperatures (°C) recorded 25 km from the main study site from 1989 to 1999. (B) Dates when snakes were observed at the dens and basking areas. Sampling did not occur on all dates.

- **Adults.** Snakes known to have reproduced. Also, snakes that had shed at least 10 times.

Data were analyzed by computing arithmetic means \pm one standard deviation (SD). To test the difference between means of two samples, *t*-tests were used (Quattro Pro 9, Corel Corp., Canada). Alpha significance was set at 0.05.

RESULTS

Phenology

Ingress.—During the 12-year period (1989 to 2000), rattlesnakes were found at dens from 31 August to 7 October. From 24 September to 3 October, 58.4% of the fall total ($N = 346$), excluding neonates, were observed (Fig. 2). No snakes were present on visits on 13 and 15 October. In fall, 40.5% of the snakes observed were at dens. The proportion of snakes at dens from 24 to 28 September was 49.0% ($N = 133$), and from 29 September to 7 October was 65.6% ($N = 90$).

On 31 August 1991, four snakes, including two females with their litters were at dens but not yet in crevices. On 3 September 1989, 30 snakes (mostly juveniles) were at basking areas within 200 m of the

dens. The earliest that a snake was observed in an overwintering crevice was on 10 September 1998. On 16 September 1994, four of 24 snakes were at their dens, but on the same date the following year, 16 snakes seen were away from their dens. Dens with a southern exposure had more visible snakes ($N = 85$) than those with a northern exposure ($N = 65$), but the difference between the two sites was not significant ($t = 1.24$, $df = 40$, $P = 0.22$). Young-of-the-year apparently overwintered at the same dens as adults. Overall, in spite of repeated searches, I was unable to locate snakes hibernating outside of the main denning areas. The latest snake seen at Huckleberry Plains was on 21 September, on its summer range.

On two occasions, young-of-the-year were observed following conspecifics toward the dens in fall (see Reinert and Zappalorti, 1988). Post-partum females typically stayed one to two weeks with their offspring, until their first shed-of-life (see Greene et al., this volume). Females and pre-molt neonates were observed at rookeries as late as 4 October. However, mothers and offspring usually left birthing rookeries in late September and early October whether or not the neonates had shed. On five occasions, from 25 September to 4 October, transient young-of-the-year (4 of 10 pre-molt), were found enroute to dens. On nine occasions during the same time, young-of-the-year (7 of 15 pre-molt), were found at the dens. In three instances, young-of-the-year were noted to trail adult conspecifics.

Egress.—During the 12-year period of study (1989 to 2000), springtime (7 May to 3 June) observations ($N = 330$) showed that egress peaked from 7 to 16 May, with 72.4% of the snakes seen during this period (Fig. 3). The proportion of snakes at dens vs those at basking areas in spring was 37.3%. The proportion of adult and near-adult snakes (≥ 7 years-of-age) was 33.8%. Throughout spring, 8.0% of the snakes at the dens were adults ($N = 108$). A majority of the snakes were found in basking areas within 200 m of their dens, but occasionally up to 700 m.

On 7 May 2000, only 38.6% of snakes ($N = 44$) observed were at dens; some were 200 m from the dens, suggesting that peak emergence had occurred several days earlier. Based on observations at the lower-elevation Blue Ridge dens, emergence was one to two weeks earlier than average in 1990, 1991, and 1998 (W. Martin, unpublished). During spring visits 33 snakes were seen at the south den, and 90 at the north den; this difference is significant ($t = 2.65$, $df = 28$, $P = 0.01$). Because I deliberately visited the site

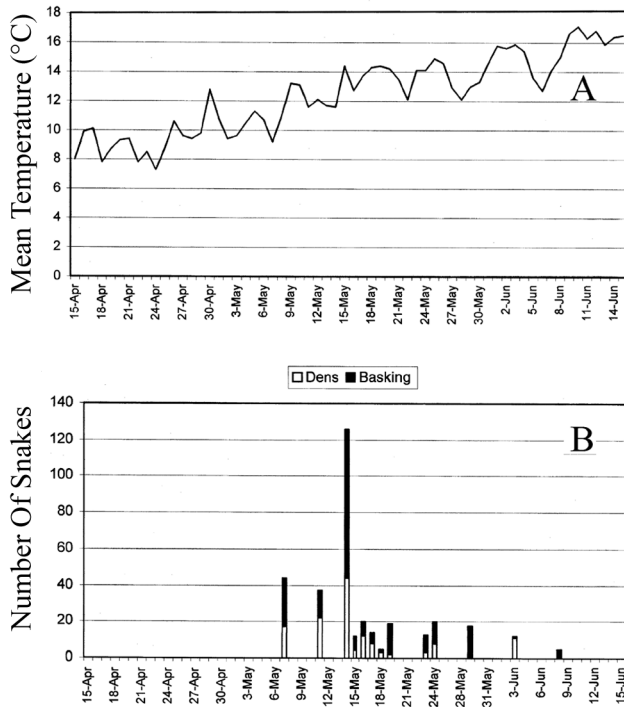


Fig. 3. Spring egress pattern of *Crotalus horridus* at a site on the Allegheny Front, WV. (A) Average temperatures (°C) recorded 25 km from the main study site from 1989 to 2000. (B) Dates when snakes were observed at dens and basking areas. Sampling did not occur on all dates.

after snakes had emerged from both dens, dispersal from the south den usually had occurred, hence the lower number of snakes.

On 14 May 1992, egress appeared to have been in its second day with 16 snakes observed, but below-average temperatures and above-average cloud cover kept some snakes at the dens past the usual time. On 3 June, I observed 11 snakes at the dens, nine of which were first-year juveniles. In 1996, and 1997, spring was delayed about a week past the average time of egress and some snakes did not depart the dens until June.

Snakes were found at the North Fork Mountain dens on 10 May 2000 (N = 1), 21 May 1998 (N = 4), 24 May 1996 (N = 3), 2 June 1996 (N = 2), and 19 June 1997 (N = 4). The earliest of eight visits to the Huckleberry Plains site was on 24 May 2002, and 31 May 2001, and snakes (N = 5) were on their summer range.

Active season.—The extreme dates for observing snakes at the primary study site were 4 May to 7 October. The average individual active time (length of time that a snake was out of hibernation) was estimated to be ca. 4.7 months from the peak of egress (ca. 8 May), until the peak of ingress (ca. 29 September).

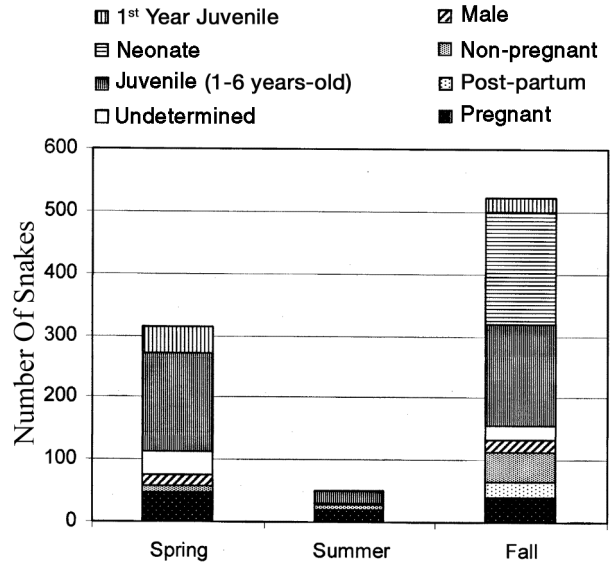


Fig. 4. Sex and age-class distributions are shown for spring, summer, and fall for *Crotalus horridus* at a site on the Allegheny Front, WV, from 1989 to 2000.

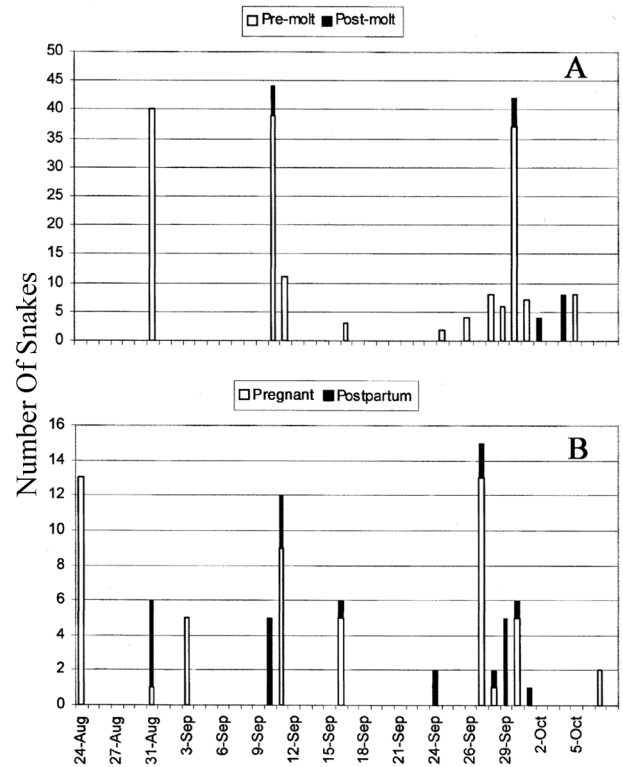


Fig. 5. (A) Distribution by date for pre-shed neonate and post-shed young-of-the-year *Crotalus horridus* at a site on the Allegheny Front, WV, from 1989 to 2000. (B) Distribution by date for pregnant and post-partum females. Sampling did not occur on all dates.

Table 2. Dates of parturition for the main study site on the Allegheny Front (1,072 m) and a site on North Fork Mountain (1,125 m), WV, and for four sites (combined) in Garrett Co., MD (870 m). PR = pregnant, PP = post-partum, L = litter, RS = reproductive status. Mean temperatures and precipitation (when available) are provided for April to October for Canaan Valley State Park, Tucker Co., WV. Most Garrett Co. records are courtesy of Ken Stairs and Doug Walters.

Year	Mean temperature (°C)	Precipitation (mm)	Allegheny Front		North Fork Mountain		Garrett County	
			Date	RS	Date	RS	Date	RS
1989	14.1	1,000	9/3 10/6, 10/13	4 PR,				
1990	14.3	801	9/28	1 PR, 1 PP, 2-3 L				
1991	15.2	586	8/31	1 PR, 6 PP, L				
1992	13.4	656	9/28 10/15	2 PR				
1993	14.4	856	9/5	1 PR			9/12	2 L
1994	14.2	780	9/16	5 PR			9/10	1 PP, 4 L
							9/25	1 L
1995	14.7	762	9/16	1 P, L			8/29	2 PR, 1 L
							9/2	3 PP, L
							9/9	1 PP, L
1996	12.7	1,330	9/30	5 PR, 1 PP, L	9/14	1 PR, 1 PP		
1997	11.1	828	9/27 10/7	7 PR, 1 PP, L 2 PR			9/7	2 PR, 1 PP, L
							9/14	2 PR, 1 PP, L
1998	14.2	767	9/11 9/29	10 PR, 3 PP, L 5 PP, L			9/5	4 L
1999	13.8		9/10	6 PP, L			9/4	1 PR, 1 PP, 2L
2000			9/27, 10/4	5 PR, 2 PP, L	9/21	2 PR, 1PP		

The average active season for the population (beginning of egress until the end of ingress) was estimated to be ca. 5.0 months (from ca. 4 May to 3 October)

Female activity.—Post-partum females apparently departed dens without going to basking areas. None were found in spring (Fig. 4). In contrast, pregnant females typically went to basking areas (rookeries) at egress and were found at nine different locations. On 7 May 2000, I found 10 pregnant females at basking areas.

Pregnant females were difficult to find in early June, but by late June many were observed at the rookeries. The average number of reproductive females located per day was: May (14 visits, 3.2), June (4 visits, 0.75), July (3 visits, 2.3), Aug (2 visits, 9.5), September (16 visits, 3.1), and October (7 visits, 1.4).

Parturition was recorded at eight of nine known rookeries; the most distant one was 200 m from a den. Two birthing sites located near the dens were apparently used only in September and October. Both were located between regularly used rookeries and the dens at distances of 20 to 100 m from the dens. From 1983 to 1994, a large flat slab in a partially open location was used as the main birthing rookery. In later years,

gestating females usually used this slab only early in the season, apparently because of shading over by the canopy trees. However, in 1998, a summer with above average temperatures, three pregnant females were present on 11 September.

Parturition.—I recorded 29 litters of pre-shed neonates from as early as 31 August (1991) to as late as 4 October (2000) (Fig. 5). The latest date on which pregnant females were found was 7 October (1997). During seven of nine years, the range of parturition dates was from 11 to 30 September. Of 29 litters, 16 occurred in this period. Pregnant females (N = 7) taken to the laboratory in late September of 1996, 1997, and 2000, gave birth from 1–19 October. Pre-shed neonates were found at or en route to dens 1990, 1994, 1995, and 1999, from 24 to 28 September. At least three litters, two found 31 August 1991, and one found 25 September 1994, were apparently born at dens.

During three years of the 12-year study (1991, 1998, and 1999) parturition occurred earlier than typical, apparently due to above-average temperatures and below-average cloud cover (Table 2). During the hottest and driest year, 1991, for example, one preg-

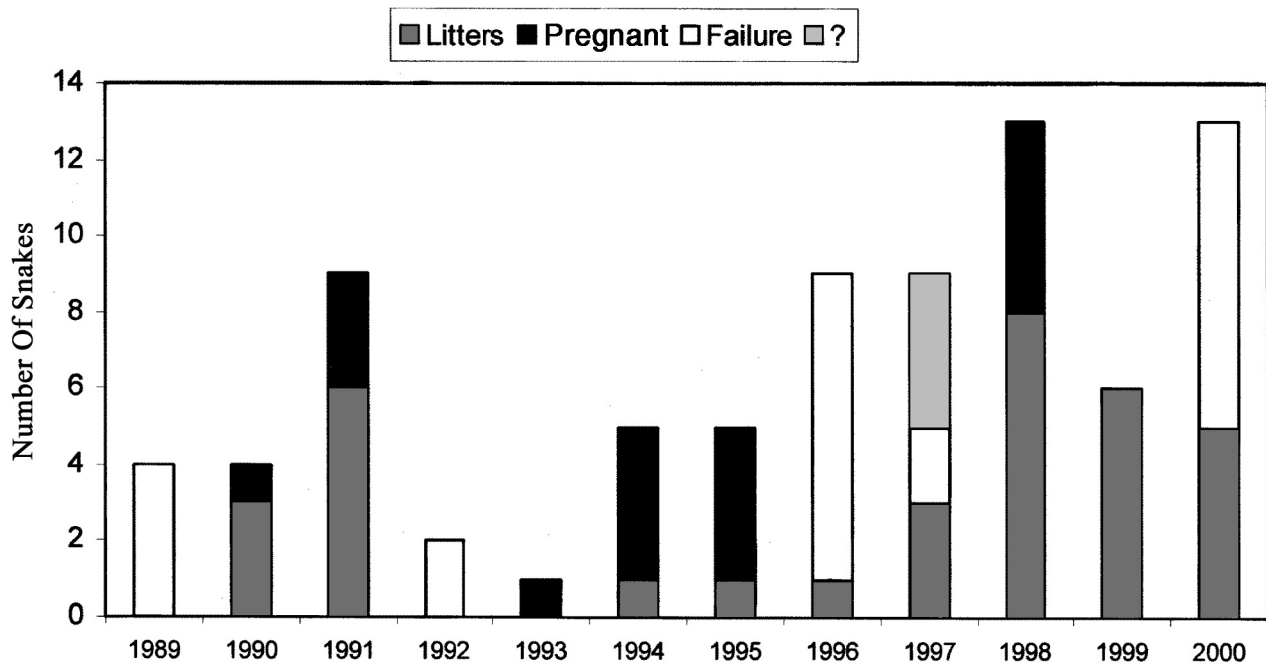


Fig. 6. Reproductive effort by year for *Crotalus horridus* at a site on the Allegheny Front, WV, from 1989 to 2000. The following are shown: number of litters observed; additional pregnant females that probably birthed; pregnant females that failed to bring embryos to term; pregnant females for which outcome of their pregnancy is unknown.

nant female and six post-partum females with litters were found on 31 August.

During this study, 30–36% of known pregnant females ($N = 80$) failed to reproduce (i.e., no offspring). There were two years in which complete failure to reproduce was weather-related. Twenty-two to 28 pregnant females were pregnant when they entered dens for hibernation; presumably, those pregnancies were aborted. During two years with above-average precipitation or below-average temperatures (1989 and 1992), all pregnant females ($N = 4$ and 2, respectively), were apparently “forced” to hibernate before parturition (Fig. 6). During 1996, 1997, and 2000, the first litters of the season were seen between 27 and 30 September, and in 1996 and 2000 a majority of the females failed to give birth. One female from each of the “failure years” was subsequently found post-partum with litters (Table 4).

During summer 1996, precipitation was about 50% above average, and summer 1997 was the coolest recorded in 50 years. On 30 September 1996, I located eight pregnant females and one post-partum female with a litter. I took one female to the laboratory where she gave birth on 10 October. Similarly, in 1997, egress was delayed by cool spring weather with little suitable weather for activity before 12 June.

Parturition was also delayed that year. Summer 2000 had below-average temperatures and above-average precipitation, but these conditions were somewhat mitigated by an early egress, allowing some females to give birth. Two of 13 pregnant females had given birth by 27 September.

Temperature, cloud cover, and rainfall have a strong influence on the length of gestation and timing of parturition. Mean April–October temperatures during 1991, when births occurred in late August were 3–4°C higher than temperatures in 1996 and 1997 when the few births that did occur were delayed until the end of September and early October. Cloud cover, because of its effect on basking temperatures, is expected to be an important variable in gestation and parturition phenology, but those data were not available. Lowest April–October rainfall was recorded in 1991, and highest (about 200% of average) in 1996.

No births were recorded at the North Fork Mountain site during the 7-year period of the study, and the youngest age-class recorded at this site was from the 1991 cohort. Females, however, gave birth at a lower elevation site one to two weeks earlier (Table 2). During 1998 and 1999 I recorded no births at the Huckleberry Plains site. In late August 1986, I found a litter of neonates at a rock pile in a meadow

Table 3. Age-cohort distribution of *Crotalus horridus* (N = 637) by year for a site on the Allegheny Front, WV. The first column for each row is age-class cohorts. Snakes ≥ 10 years-of-age were not assigned to age-class cohorts unless they had been marked as younger snakes. The columns represent sampling years. The last column is total snakes in each cohort.

Cohort	Year												N
	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	
≤ 10 yr	7	22	19	8	3	26	14	4	17	11	9		137
'80	2	3	2	1									7
'81													0
'82	3	7	1										11
'83	2	2	2			2							8
'84	1	3	4		1								9
'85	3	9	4	4		3		2					25
'86	9	20	8	6	5	7	5			2			62
'87	3	10	5	7	1	6	2	2	1	2	1		40
'88	3	1	2		4	6	2	3		1			22
'89													0
'90		6				4	3	2	1	1	1	1	19
'91			50	21	10	28	5	1	3	6	1	3	103
'92													0
'93						2		1	2	2	1		8
'94						4		4	2	6	3	3	22
'95							4	5	4	5	3	1	22
'96								7	0	2			9
'97											6	5	11
'98										61	21	16	97
'99											54	18	72
'00												8	8

Table 4. Reproductive interval for adult female *Crotalus horridus* captured more than once at a site on the Allegheny Front, WV. Rows are individual females (numbered for this table). Columns are years from 1989 to 2000. PR = pregnant. PP = post-partum. NR = non-reproductive. The last column is the birthing interval. N = 10 females, 11 cycles.

No.	Year										Interval (years)		
	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98		'99	'00
1	PR					PR					PR		5, 5
2		PR				PR				PR			4, 4
3		PP								PP			8 or (4, 4)
4			PP							PP			7
5			PP				PR						5
6				PR						PP			6
7						PR				NR			
8					PR					PR			5
9						PR					PR		5
10							PP				PP		3

Table 5. Rattle size, number of sheds, total length, and age for *Crotalus horridus* at a site on the Allegheny Front, WV. Total length (mm) from snout to base of rattle is given with 1 SD and range. For snakes whose age was determined by recapture, sample size is given in parentheses. Rattle-segment count includes basal segment. b = postnatal button. Unmarked snakes were assigned to age class that most closely fit their rattle-segment count and age.

Rattle segments	Sheds	Age (yr)	Body Size (mm)		N (recaptures)
			Total length	Range	
1 + b	2	1	400 ± 31	340–460	32 (13)
2 + b	3	1	437 ± 21	410–460	5 (2)
2 + b	3	2	465 ± 36	410–530	27 (9)
3 + b	4	2	470 ± 18	460–480	2 (2)
3 + b	4	3	577 ± 53	480–660	24 (9)
4 + b	5	3	654 ± 48	610–760	12 (7)
4 + b	5	4	677 ± 58	610–710	3 (2)
5 + b	6	4	686 ± 66	610–800	16 (7)
5 + b	6	5	760	—	1 (1)
6 + b	7	5	791 ± 70	660–860	14 (7)
7 + b	8	6	820 ± 58	770–940	19 (13)
8 + b	9	7	841 ± 52	760–910	14 (7)
9 + b	10	8	897 ± 20	860–910	8 (3)
10 + b	11	8	893 ± 52	840–990	9 (3)
10 + b	11	9	900 ± 54	860–940	2 (2)
11 + b	12	9	945 ± 20	890–940	11 (7)
11 + b	12	10	940	—	1 (1)
12 + b	13	10	959 ± 39	860–1070	4 (4)
					238 (98)

(900 m elevation) on the slopes below Huckleberry Plains. Parturition at the Garrett Co. sites, which were 200 m lower elevation than the main study site, occurred about 1–2 weeks earlier (Table 2).

Morphology, Growth, and Shedding

Coloration.—Rattlesnakes at this site are highly variable in color pattern. Pre-shed neonates always have a gray cast, are difficult to categorize as to color morph, and hence were not used in this analysis. Of 611 snakes, the following are the major color morphs distinguished:

- *Pale morph:* 66% were scored as a yellow or pale morph. However, these individuals varied along a continuum from pale tan to yellow. Dorsal blotches varied from pale brown or olive to dark brown and black.
- *Dark morph:* 27% were scored as a dark morph, but these individuals also varied from pale gray to nearly solid black. Dorsal blotches were sometimes outlined in yellow, and some individuals showed a yellow to rusty-brown mid-dorsal stripe.
- *Brown morph:* 6% of the snakes were scored as brown, and varied from pale to medium brown, with

dark brown or black dorsal blotches.

- *Mixed color morphs:* Five individuals were unusual, and can be considered a mixture of the preceding color morphs.

Overall, females were darker than males, especially in the posterior half of the body. Most snakes that were yellow-brown were females (see Plate 10d), and only one adult male was scored as yellow-brown. Pale-morph males often had a pale green hue, which was not observed in females. Dark morph individuals without a trace of pattern were always females (see Plate 10c), and they were at least 12 years old. Although some males were black, their dorsal blotches were outlined with yellow.

Shedding.—Although neonates born in the laboratory (N = 99) had their first shed-of-life within five to 12 days of birth, the interval between birth and shedding was usually longer in nature, presumably due to lower temperatures. Six litters were observed on 10 September 1999, and on 24 September, two neonates from those litters were still pre-shed and the remaining young could not be found. On 3 October, nine neonates of the above litters were found post-shed at or near the dens. When parturition occurred during

Table 6. Survivorship model for *Crotalus horridus* at a site on the Allegheny Front, WV. This model shows estimated survivorship for various age classes starting with 60 neonates at year 0, predicted population distribution in any given year, and actual numbers of *C. horridus* recorded in the 12-year sample (N = 760). Numbers and proportions are shown. Numbers and proportions for multiple years combined are in parentheses. Recaptures were not counted more than once in the same season of the same year.

Age (yr)	Estimated survival rate	Predicted population		Recorded population	
	(%)	N	%	N	%
0	68.2	60.0	19.8	231	28.9
1	70.9	40.9	13.5	49	6.1
2	73.8	29.0	9.6	62	7.8
3	76.7	21.4	7.1	65	8.1
4	79.8	16.4	5.4	35	4.4
5	83.0	13.1	4.3	30	3.8
6	86.3	10.9	3.6	34	4.3
7	89.7	9.4	3.1	30	3.6
8	92	8.4	2.8	27	3.4
9	92	7.8	2.6	(30.9)(≥ 9 yr) (237) (29.6)	
10	92	7.1	2.3		
11	92	6.6	2.2		
12	92	6.0	2.0		
13	92	5.6	1.9		
14	92	5.1	1.7		
≥ 15	92	(55.0)	(18.2)		

late September or early October, many neonates apparently entered the dens while still in the pre-shed state. I found pre-shed neonates at or en route to dens in 1990, 1994, and 1995, from 25 to 28 September. One pre-shed neonate from a litter located on 16 September 1995, was at a den on 28 September, still in a pre-shed state. Neonates produced in 1996, 1997, and 2000, entered hibernation in a pre-shed state. Two litters first seen on 27 September, 2000, were still pre-shed at the birthing rookery on 4 October, the end of the active period. Three recently shed first-year juveniles were observed at the rookery the following June.

The mean shedding rate for snakes of known-age (N = 93) was 1.2 times/yr for the first 9 years-of-life (Table 5). With a median active season of 4.7 months, this equates to one shed every 3.9 months or 0.26 sheds/month. After birth, most juveniles shed once in each of their next two years, and twice during either their third or fourth summer. Adults typically shed once annually.

Only two of 15 juveniles recaptured as 1-year-olds shed twice during their first full year. Only 33% of putative 3-year-olds (N = 36) completed five sheds (4 + b); the remaining shed four times. Of eight 5-year-olds, seven shed seven times (6 + b) and one six times. All 6-year-olds (N = 13) shed eight times, and all 7-year-olds (N = 7) shed nine times. Three 8-year-

old snakes (N = 6) probably shed twice in their eighth year. Twelve sheds was the mode for 9-year-old females (N = 11), but two had only shed 11 times.

Long-term recaptures indicate that most adults ≥ 10 years-of-age (N = 3 males, 11 females) shed once annually, and there was some indication that when egress was early and summer was unusually hot, at least some adults shed twice yearly. Most shedding occurred in June and July. Dates for locating pre-shed snakes were from 8 June to 20 July, and the earliest post-shed individual was seen on 12 June.

On North Fork Mountain in early September 1999, I located one adult male and three adult females recently post-shed, and three opaque pre-shed adult males. An adult male recaptured there on 10 May 2000, had shed six times in four years. The typical shedding rate for that population has not been established, and their shedding schedule may not necessarily conform to that at the main study site on the Allegheny Front.

Feeding rate.—Snakes with obvious gut boli were seen three times from June to early September. An adult male was found 1.6 km from the den on 16 June, 1999, coiled on the forest floor next to an Eastern Chipmunk (*Tamias striatus*) burrow. Neonates apparently did not feed until the spring. Thirty-three percent of neonates (N = 99) maintained in the laboratory accepted food in fall at least once, and most fed readily after hibernation.

Table 7. Age of reproductive female *Crotalus horridus* at a site on the Allegheny Front, WV. Reproductive females were those pregnant or immediately post-partum during the year of capture. The first column is age (yr). N = the number of reproductive females in the corresponding age class, and includes those estimated by rattle-segment count. The third column includes females of known age.

Age (yr)	N	Known age (yr)
9	8	4
10	5	3
11	6	4
12	2	2
13	1	1
14	1	1
12–14	7	
≥ 15	49	
Total	79	15

Adult length and longevity.—Mean total length for adult (= reproductive) females was 980 mm ± 68 (860–1,100 mm, N = 48). The lowest rattle-segment count for a pregnant female was 10 (9 + b) for one collected in May, and the lowest count at parturition was 11 (10 + b). Non-pregnant females with ≥ 10 sheds (9 + b) averaged 925 ± 61 mm total length (830–1,070 mm, N = 42). Adult males with ≥ 10 sheds (9 + b) averaged 1,100 ± 84 mm total length (920–1,270 mm, N = 42). The three largest males ranged from 1,230 to 1,270 mm, and from 1,500 to 1,560 g.

Two females and one male marked from 1989 to 1991 (when ca. 16 years-of-age) and recaptured from 1998 to 1999, achieved a minimum of 24 and 26 years-of-age. The high number of old adults in the population suggests a maximum longevity of at least 35 years (Table 6).

Reproduction

Size and age at maturation.—Thirty to 38% of pregnant females (N = 79) were first-time reproducers. First-time reproducers averaged 910 ± 64 mm (860–960 mm, N = 20). Fifteen pregnant females were aged by recapture, and the remainder by rattle-segment counts, rattle-segment estimates, and body length (Table 7). Among pregnant females, first-time reproducers were estimated to range from nine to 14 years-of-age, but most females of known age reproduced for the first time at 9 to 12 years-of-age. Thus, for most females sexual maturity and first breeding would have occurred between nine and 11 years-of-age. The youngest females known to reproduce were 9 years old (N = 4). Two females, 13 and 14 years-of-age, were probably first-time reproducers.

The following is the age-class distribution for probable first-time reproducers. The first value in each group is the total whose age was estimated by rattle-segment count (or total length), and the parenthetical values denote ages known from recaptures. These are: 9 year, 8 (4); 10 year, 4 (2); 11 year, 6 (4); 12–14 year, 10. The total number of first-time reproducers ranged from 23 to 30, and 49 females were likely > 14 years old and pregnant for their second to fourth time.

Mating season.—Mating was not observed at the main study site, but on 20 July, two adult male-female pairs were observed in close contact. On North Fork Mountain, I found four adult male-female pairs, one in coitus, from 7 to 11 September 1999. The pair was copulating in a fern-covered forested area next to a fallen log, ca. 550 m from the presumed den of the female. The male was relatively young (8–9 years old) and had been marked at a den 2.4 km from the site of mating (see Coupe, this volume).

Reproductive effort and number of offspring.—In the field, the average number of offspring per litter was 8.8 ± 2.5 (range 6–14, N = 14). Litters born in the laboratory also averaged 8.8 ± 2.2 (range 7–14, N = 11). Females typically lost ca. one-third of their body mass at parturition. Pregnant females (N = 11) brought into the laboratory averaged 780 ± 140 g (range 563–1,005 g). Immediately following birth they averaged 538 ± 98 g (range 380–675 g). Neonates (N = 99) averaged 21.1 ± 2.7 g (range 13–27 g), and 300 ± 20 mm in total length (range 230–330 mm).

Reproductive interval.—Birthing intervals were 3 to 8 years, with a mode of 5 years (\bar{x} = 5.2 years). Ten females were reproductive in two or more years (Table 4). Applying Brown's (1991) criteria, eight of 10 females fit a definitive cycle (i.e., one in which an undetected pregnancy could not have occurred during the interval between captures). One female was non-reproductive four years after parturition. Because reproductive intervals of three years are rare in females, I conclude that 6- or 7-year intervals recorded are actual, and that no reproduction occurred between captures.

One female was pregnant three times, and was at least a second-time reproducer when initially processed. Of 11 reproductive females that were recaptured, only two were first-time reproducers at their initial capture. With a mean birthing interval of 5.2 years, the remaining nine females were probably at least 15–17 years old on their initial capture, and at least 20–22 years old when recaptured.

Annual variation in reproduction.—The number of pregnant and post-partum females totaled 80, and averaged 6.7/yr (range 1–13; Fig. 5). Three pregnant females were recorded on the initial visit in 1983. The total number of litters recorded in the field was 34, and they averaged 2.8/yr (range 0–8).

Lowest numbers of reproductive females occurred in 1992 (N = 2) and 1993 (N = 1). Judging from the numbers of the 1993 cohort (Table 3), no more than a total of two litters were produced that year. Highest recorded reproduction occurred in 1998, with 13 pregnant females and 8 litters confirmed. The number of females that reproduced in 1991 and 1999, judging from the high numbers of those two cohorts seen in subsequent years (Table 3), may have been higher than the nine and six recorded, respectively.

As noted, during 1989 and 1992, none of the pregnant females had litters, and in 1996, only one of nine pregnant females produced a litter. Failure in reproduction was also recorded in 1997 and 2000, with three of nine pregnant females producing litters in 1997, and five of 13 producing litters in 2000.

Age-class distribution.—On the basis of 884 snakes, the overall age composition was determined to be 33.7% adults, 43.3% juveniles, and 23.0% neonates and young-of-the-year (Fig. 5). If neonates are excluded, adults made up 43.8% of the remaining sample (N = 681). In spring (7 May to 3 June), 36% of all snakes observed were adults (N = 314). In late summer and fall (31 August to 7 October), age composition was made up of 30% adults, 31% juveniles, and 39% young-of-the-year (N = 522).

Survivorship.—The most plausible survival rates are 68% for the first year, and up to 92% for adults \geq 8 years-of-age (Table 6). This pattern of survivorship would result in a population distribution composed of one to 6-year-old juveniles (54.5%), 7-year-old sub-adults (4.0%), and adults \geq 8 years-of-age (41.5%).

Sex and reproductive condition.—Of the adult snakes (N = 299), 44.2% were reproductive females, 22.4% were non-pregnant females, 13.0% were males, and in 20.4% the sex was not determined. Neonates that were sexed in the laboratory did not vary from a 1:1 ratio (48 males, 51 females).

Cohort distribution.—The age-class structure was dominated by several cohorts (Table 3). From 1994 to 1998, cohorts from 1985 to 1988, especially those from 1986 and 1987, dominated the adult population. These cohorts were augmented by a 1991 cohort that began reproducing in 2000. When recruited into the adult population in 2007 to 2011, the reproductive

cohorts of 1998 and 1999 should figure prominently, augmenting the previously dominant but declining cohorts of 1986, 1987, and 1991.

North Fork Mountain.—From 1994 to 2000, 19 observations were made on 15 *C. horridus* at the north den. Two snakes were juveniles (1991 cohort), seven were adult females (nine observations) and six were adult males (eight observations). At the south den, I made 12 observations on 10 adult males ranging in size from 1,070 to 1,260 mm in total length. No females or juveniles were observed at this den, although two females were found on the summer range south of this den. No births have been recorded at the site.

Huckleberry Plains.—Sixteen *C. horridus* (11 males, 5 females) were found at the Huckleberry Plains site from 1998 to 2001. The age-class distribution included juvenile and young adult females, and adult males.

DISCUSSION

Phenology.—Data in fall and spring were pooled and indicate a strong correlation between the passage of the 11.5°C isotherm and both egress and ingress. For the Canaan Valley station, the mean 30-year dates for passage of the 11.5°C isotherm were 10 May and 1–2 October; peak egress and termination of ingress conformed closely to those dates. As expected, there was some minor year-to-year variation in timing of egress and ingress. From 1989 to 1999, mean temperatures were ca. 12°C from 28 September to 1 October, and from 8 to 15 May; peak ingress and egress occurred at these times. Brown (1991) studied *C. horridus* at the edge of the Adirondacks in northeastern New York. Although summer temperatures there were higher than those on the High Allegheny Plateau, and precipitation was lower, spring and fall temperature profiles of these two regions were similar. My findings and those of Brown (1991) are nearly identical with respect to the spring peak (7 to 14 May), but fall observations in the Adirondacks peaked earlier than mine. In fall, *C. horridus* in northeastern New York show ingress earlier and do not stay on the surface. They arrived at dens from 14 September to 1 October, and the majority of snakes were observed from 20 to 25 September. Peak ingress for the Allegheny Front, however, was four to eight days later, from 24 September to 3 October. Selection probably favors an early ingress at more northern sites with colder winters. Compared to snakes at the Blue Ridge sites (Martin 1992), which had longer active seasons and experi-

enced higher temperatures, *C. horridus* from the Allegheny Plateau spend more time on the surface in the fall. Thus, egress and ingress thresholds appear to show clinal variation with respect to seasonal temperatures and precipitation.

In contrast to the Blue Ridge sites (Martin, 1992), where I sometimes found solitary or small groups of neonates hibernating separately from the adults, nearly all age classes at the Allegheny site overwintered in the same dens. In *Crotalus viridis* (= *C. oreganus*; see Douglas et al., this volume) in British Columbia, Charland (1989) found that neonates overwintered with adults.

On the Allegheny Plateau, I occasionally found neonates (pre-molt) leaving rookeries and moving to dens. Apparently selection favors reaching dens vs successful molting at the rookeries. Typically, neonates stay at the rookeries with their mother until their first shed (Martin, 1992; see Greene et al., this volume). In a laboratory experiment, Brown and Maclean (1985) noted a strong tendency of the post-molt young-of-the-year to scent-trail conspecifics. In the Pine Barrens of New Jersey, Reinert and Zappalorti (1988) had evidence of post-molt young-of-the-year scent-trailing adults to the dens.

Feeding.—In contrast to the Blue Ridge and other lower-elevation areas, there was no indication that neonates on the High Allegheny Plateau feed before hibernation (Martin, 1992). I found no neonates with food boli in fall. Overall, captive neonates from this site typically refused to feed in the fall. Even when births occurred in late August to early September, neonates had only two or three weeks of marginal temperatures to shed and find dens. Selection probably does not favor fall feeding in neonates that occur at high elevations. In British Columbia, Charland (1989) found *C. viridis* (= *C. oreganus*) neonates in British Columbia did not feed prior to hibernation. Schuett et al. (2002), however, found a neonatal *C. cerberus* from a high elevation (2,172 m) site in northern Arizona that had recently consumed an adult male *Sceloporus undulatus* just prior to ingress (late September).

Size, growth, and shedding.—The size of mature females from the present study area did not differ significantly from values reported from populations in southwestern Wisconsin (Keenlyne 1978), northeastern New York (Brown 1991), the Blue Ridge (Martin 1993), and the upper Piedmont of North Carolina (Sealy, this volume). Compared to High Allegheny populations, growth rates reported for *C. horridus* in northeastern Kansas (Fitch, 1985) were about 15%

greater, and females first reproduced at a length ca.10% greater. In populations of *C. horridus* in coastal South Carolina (Gibbons, 1972) and northeastern Florida (Diemer-Berish, 1999), growth rates were found to be ca. 30% greater than in females from the High Allegheny populations.

Sexual maturity and reproductive interval.—On the High Allegheny Plateau, *C. horridus* is characterized by late age to sexual maturity and long (multiple years) intervals between pregnancies. Undoubtedly, this is a result of the low temperatures during the active season. In the northern Blue Ridge, which has a longer active season than the High Allegheny Plateau, Martin (1993) found that the usual age of first reproduction was eight years, and the usual interval between births was three years. In northeastern New York, where the active season is similar in length to the High Allegheny Plateau but has higher summer temperatures and lower rainfall, Brown (1991) found that the average age of first reproduction was 9.3 years, and the interval between births was 3–5 years. Similarly, populations in Wisconsin and Minnesota experienced a short active season (4.6 months), but higher summer temperatures and lower rainfall than northeastern New York. Thus, because of relatively high summer temperatures and low rainfall, climate is not expected to be a serious constraint on reproduction in those areas inhabited by *C. horridus*.

When cumulative active months were compared for northeastern New York (Brown, 1991) and the Blue Ridge (Martin, 1993), age of first reproduction and reproductive interval were similar. This, however, was not the case when comparisons were made between the high Allegheny Plateau and northeastern New York populations.

In sharp contrast to northeastern populations of *C. horridus*, especially in the High Allegheny Plateau, youngest females in populations from northeastern Kansas reproduce at 4 years-of-age, and at intervals as short as two years (Fitch, 1985). Interestingly, the age of first reproduction in South Carolina populations of *C. horridus* is believed to occur at 6 years-of-age, and the reproductive interval is 2–3 years (Gibbons, 1972). The youngest reproductive females in northeastern New York (Brown 1991) gave birth at 7 years-of-age, and thus would have mated the previous fall at 6 years-of-age. In Wisconsin, the youngest pregnant females probably bred at 5 years-of-age (Keenlyne 1978). In the Blue Ridge the youngest females that gave birth had shed nine times and were likely 5 years old (Martin, 1993). Growth rates, maturation, and

reproductive intervals are influenced by climate, temperature, and energy (i.e., food). With the shorter and cooler active seasons of the Appalachians, the age of first reproduction and birthing interval is extended beyond that of populations in more equable climates.

Annual variation in the proportion of reproductive females.—The proportion of sexually mature and potentially reproductive females that were pregnant varied greatly between years. Lowest numbers of reproductive females in 1992 and 1993 occurred when mature females were believed to be at their lowest numbers, perhaps 30 individuals. Thus, 3% to 6% of the adult females were pregnant in those years. By 1998, the number of mature females in the population was likely up to ca. 50 individuals. About 33% were reproductive in 1998, and the proportion was possibly higher in 1986. The proportion of females reproductive in northeastern New York averaged 51% of all female captured (Brown, 1991). In the Blue Ridge sites, 60% of adult females were reproductive during their year of capture (Martin, 1993).

As noted, during 1989 and 1992, no litters were produced, possibly due to embryonic death. During other years, there was high variation in the number of offspring produced. Wet weather in 1989 and 1992 may have influenced the number of females to become reproductive in 1990 and 1993. A causal relationship cannot be demonstrated, but the high proportion of females pregnant in 2000 followed two hot, dry summers, indicate the possible influence of temperature. A likely explanation is that cloudy, wet weather may hamper digestion and assimilation of food, thereby lowering the rate of nutrient storage (fat). Thus, fewer snakes would mate and give birth the following year. The possibility that a wet summer, while delaying breeding, might enhance future food availability and thus lead to increased breeding the following summer, should be considered.

Following 1985 to 1987, after apparent high reproduction, my adult populations began declining in 1988, and reached their lowest levels in 1992 and 1993. A temporary upward spike in 1991 was probably the result of what remained of the 1986 reproductive cohort that reproduced in concert five years later. The relatively low numbers of reproductive females found from 1988 to 1993 may be a result of previous reproductive failures and thus a lack of recruitment of nine to 12-year-old first-time reproducers. Females from the large 1985 to 1987 birthing cohorts appeared in 1994, and might have peaked in 1997 had it not been for unfavorable weather in the 1996 active season.

Even so, nine females were known to be pregnant in 1997, and reproduction was unusually high in 1998. In fact, I recorded pregnant females from several age class cohorts that year. The population probably will undergo another downturn in reproduction in the 2001 to 2004 period due to a tendency of low birthing, as noted from 1988 to 1993.

High reproduction in 1986 and 1991 were each followed two years later by low reproduction, but a cause-effect relationship cannot be demonstrated. Those two years were favorable for gestation with higher-than-average temperatures and lower-than-average precipitation. Such conditions, when they coincide with a year of high pregnancy rates, result in successful reproduction. There appears to be a tendency among short-season, high-elevation populations of *C. horridus* for high levels of reproduction, to be followed by another high level of reproduction four to six years later (the usual reproductive interval).

Reproductive failure.—All reproductive failures observed were the result of embryos not completing development due to weather. During the 12 years of the study, between 22 and 28 of the 80 recorded reproductive females recorded contained embryos when they entered dens, where they were presumably aborted.

Failure of embryos to fully develop has not been reported as a typical feature of rattlesnake life history. Brown (1991, 1992), with intensive long-term fieldwork, did not report any birthing failures in northeastern New York. In Wisconsin and Minnesota, typical parturition dates are approximately late August to early September, but birthing failures were not reported (Keenlyne, 1978). Reinert and Rupert (1999) reported that due to low temperatures, a female *C. horridus* from eastern Pennsylvania aborted at a den entrance on 14 October 1992. Also, that same fall, a pregnant female was found basking on 23 October, about 45 days beyond the average birthing time. In Garrett Co., Maryland, on the High Allegheny Plateau, Browning (1859) discovered embryos in female *C. horridus* when they entered their dens in October. Macartney and Gregory (1988) retained female *C. viridis* (= *C. oreganus*) that gave birth in the laboratory in late October, well past the typical time for ingress in British Columbia. Viitanen (1968) noted that *Vipera berus* in Finland sometimes entered hibernation carrying embryos, and he believed they birthed the following spring. The evidence for this assertion, however, was based on a single apparent neonate found in July. Saint Girons (1975) noted that *Vipera aspis* at the northern edge of its range in north-

western France suffered from "thermal shortage." Females normally reproduce at an interval not less than three years, and the normal date for parturition at this locality occurs close to the beginning of winter. Parturition there normally occurs in September or early October, but when gestation extends past the beginning of October, pregnant females enter hibernation without giving birth (Saint Girons 1992, 1997). Rubber Boas (*Charina bottae*) in Idaho complete gestation in most years, but were unable to do so during an unusually cool summer (Dorcas and Peterson 1998).

On the High Allegheny Plateau, selection should favor the earliest possible parturition time. Thus, the factors affecting the variable timing of parturition noted at the primary study site are: (1) the time of egress, (2) active season temperatures, (3) active season cloud cover, (4) the time of cessation of mild weather, and (5) individual differences due likely to individual variation in egress and basking habits. If these factors are in an acceptable range, most births occurs from 11 to 30 September. When egress occurs earlier than average, active season temperatures are above average, precipitation is below average, and births occur at the end of August and the beginning of September. With late egress, below-average temperatures, and above-average cloud cover, parturition is delayed and mothers are forced into hibernation still carrying embryos. At the highest elevations, average conditions may not be sufficient to allow pregnant females to fully develop embryos. Perhaps only rarely are conditions suitable at those elevations, and two consecutive years of favorable weather (one for yolking and breeding, the other for gestation) are necessary for reproduction. As noted, reproduction was not observed at the North Fork Mountain site during seven years of observation, nor at Huckleberry Plains site in a two-year period. However, reproduction occurred at a nearby lower-elevation North Fork Mountain site and was recorded prior to the study at a low-elevation site below Huckleberry Plains. Selection probably favors females that move to warmer, lower elevations for gestation.

Age-class distribution, survivorship, and reproduction.—The high proportion of pregnant females (59.5%) with uniform-sized rattle segments suggests an annual adult survivorship ca. 92%. According to my estimates, the population size immediately prior to parturition should be ca. 242 individuals with 100 adults (≥ 8 years) and 142 juveniles and sub-adults 1–7 years-of-age. About 50% of the adults should be females. With a mean birthing interval of five years, an average of 20% of females will breed each year,

and 75% of the time offspring are produced (average litter size is nine). The estimated annual number of neonates produced would be ca. 60, but annual reproduction is highly variable ranging from zero to 125 (or more) offspring in the population. As presented earlier, 10 to 12 individuals at any time in the population will exceed 30 years-of-age, and a maximum longevity of 40 years is expected.

The mean age of first-time reproducers was 11 years-of-age, and the mean birthing interval was five years. Second-time reproducers were estimated to be 16 years-of-age. The population model presented herein suggests that generation time (calculated as the average age of female parents) is ca. 18 years, and this age represents the life expectancy for an 11-year-old female. This average life expectancy, coupled with a reproductive success rate of 75%, would result in 1.8 successful pregnancies out of 2.4 lifetime attempts. Thus, with an average litter size of about nine offspring, lifetime reproductive effort would be ca. 16 offspring per female. In northeastern New York, Brown (1995, 1997), estimated lifetime reproductive effort at only 1.5 to 2.0 litters. Compared to the High Allegheny Plateau and the Adirondacks, *C. horridus* in northeastern Kansas matured earlier, reproduced more frequently, but had lower survivorship (Fitch, 1985). Fitch estimated first year survival at 55% and 75% thereafter, compared to the 68% first-year and 92% adult survival that I report here.

I expect that there are sampling biases in my analysis. The fall sample is expected to consist of an over-representation of pregnant and post-partum females, as well as neonates. The spring sample probably under-represents post-partum females, as none were observed. Low numbers of adult males recorded at all seasons suggest they are under-represented as well. Juveniles (1–3 years old) are over-represented compared to older juveniles (4–7 years old). These biases probably result from their dissimilar habits. Younger juveniles, for example, tend to arrive at dens earlier and exhibit egress later than other age classes. Perhaps these rattlesnakes increase the size of their home ranges as they age, and thus return later to their dens in fall. Pregnant females and pre-shed neonates apparently spend more time basking than other age-classes.

Post-partum females are readily found in fall because they usually remain with their offspring for one to two weeks before they return to dens. Upon emergence in spring, post-partum females apparently leave the dens immediately, which is probably due to

their increased need to forage. My data suggest that females outnumber males by at least two to one, but this ratio may be affected by potential sampling error. Although a slightly higher mortality rate might be expected among the more vagile adult males, the magnitude of the mortality difference is difficult to explain. Recaptures of adult males were too few to draw any firm conclusions in this regard, but recaptures were also low for adult females, except for years when they reproduced. Only one adult female was recaptured when not pregnant or post-partum. Males are likely prone to go directly to dens rather than to nearby basking areas in fall, and move directly toward their summer range in spring. Human-caused mortality on the summer range is probably negligible because of the remoteness of the site. The nearest resident, now deceased, lived about 1.6 km from the site, and while he reported killing an occasional rattlesnake, it was seldom more than one per year. He reported three rattlesnakes, an unusually high number, killed on the road during the summer of 1991.

I estimated that 40 to 45 different females were reproductive from 1986 to 1990, 25 to 30 from 1991 to 1995, and 45 to 50 from 1996 to 2000. In 1993, the effective population of breeding females appears to have declined to 25 to 30 individuals. With a 92% survival rate and recruitment to equal mortality, an average of over two females should replace the number lost each year. However with an annual replacement rate of about one-third of mortality, 40 females would decline to ca. 27 in seven years. By 1994, the adult population size began to increase as the first survivors of the 1985 to 1988 cohorts were recruited, and reproduction peaked during the next three years culminating in high reproduction in 1998. The large numbers of juveniles in this sample may be an artifact of the timing of this study. Reproduction was high in 1985 to 1988, resulting in a high proportion of juveniles in early years. Low reproduction in 1989 to 1993, resulted in a lower proportion of juveniles for the next several years, and a relatively high reproduction in 1997 to 1999.

Above average rainfall during the active season in 1974, 1979, and 1981, may have contributed to delayed birthing in the High Allegheny Plateau (Martin 1992). Reproductive failures during those years may have also affected recruitment. The 1979 and 1981 birthing cohorts should have been reproducing for the first time from 1989 to 1993. Additionally, the 1981 cohort was likely a large one. The highest level of reproduction occurred in 1991,

and it was probably the result of the 1986 reproductive cohort reproducing again at a 5-year interval. First-time reproducers in 1986 were probably born from 1973 to 1976, second-time reproducers from 1968 to 1971, and third time reproducers from 1963 to 1966. Perhaps conditions of food and climate particularly favored reproduction during those years, thus giving rise to the large 1986 cohort.

Although data for the North Fork Mountain and Huckleberry Plains populations are somewhat scant, they are significant in that data on high-elevation populations of *C. horridus* are rare. These two sites have abundant habitat for basking, high populations of adult males, moderate numbers of adult females, few juveniles, and old males dominate both populations. While assortative den use based on size and age class presumably is due to physical constraints of dens (Martin, 1992), dens composed of all (or nearly all) males, as observed at one of the North Fork Mountain sites, has not been reported elsewhere. The explanation for the high proportion of adult males in these populations is not clear, and additional studies are needed to understand their abundance, survival, and reproductive dynamics. The sites that satisfy the requirements of adult males and adult non-pregnant females, appear to be sub optimal for pregnant females. The mostly shaded south den on North Fork Mountain is entirely (or nearly so) composed of males, lends support to this idea. Significantly, the composition of the Huckleberry Plains population is similar to the population at North Fork Mountain. It is possible that these two sites lie outside the climatic limits for regular reproduction in *C. horridus*. Perhaps such high-elevation sites require nearby lower-elevation sites for females to migrate and gestate, and the discovery of a litter in a meadow below Huckleberry Plains lends support to this idea. Also, the distribution of *C. horridus* on the High Allegheny Plateau suggests that this is possible. All high-elevation sites known to support *C. horridus* are on (or near) steep gradients that provide access to relatively low elevation areas within 1 km. Nearby low-elevation sites may serve as refugia when climatic conditions are suboptimal for persistence of rattlesnakes from the high elevation sites. If this is the case, it may explain recent extinctions in northern parts of the range, where historically *C. horridus* was found at low elevation sites due to climate.

Delayed maturity and 2-year or longer intervals of reproduction have been reported for some rattlesnake species (e.g., *C. horridus*, *C. viridis*) and other viperids (e.g., *V. aspis*, and *V. berus*) (see Brown,

1991). None, however, have been reported to show such a late age of maturity and long reproductive interval as *C. horridus* occupying high elevations in the Appalachian Mountains. These rattlesnakes are at the extreme of K-selection (K-end of the r-K continuum), which is characterized by late maturity, infrequent reproduction, and extreme longevity (MacArthur and Wilson, 1967). Late maturity and infrequent reproduction were initially reported in the Arafura File Snake (*Achrochordus arufuræ*) in Australia, where females were thought to reproduce at 5–7 years-of-age, and the reproductive interval was 8–10 years (Shine, 1991). Recently, however, Madsen and Shine (2001), found conflicting data on these same populations based on a long-term (10 years) mark-recapture study. Briefly, females matured at 3 years-of-age, and their reproductive interval was 3–4 years. Madsen and Shine (2001) demonstrate the utility of long-term studies on snakes.

Regular, but not annual, reproduction is possible in a relatively high-rainfall, high-cloud cover region with an active season of 4.7 months and a mean July temperature of 18.5°C. That this site is located near the ecological limits of *C. horridus* is indicated by the fact that when temperatures were slightly below average and precipitation was above average, reproduction failed. The North Fork Mountain site may be on the cool side of the climatic limit. Whether or not this small population is able to survive by infrequent reproduction, reproductive augmentation from lower-elevation sites, or using nearby low-elevation sites for gestation and birthing, has not been established. Similar conditions apparently prevail at the Huckleberry Plains site. The evidence presented here for timing of parturition along an elevational gradient suggests that females reproduce successfully only rarely at these high elevation sites. Significantly, the one successful reproductive year at both sites was 1991, the year with the longest active season and highest active season temperatures recorded during the study. Even then, birthing may have been limited to lower elevations. The apparent high reproductive success could have resulted if some of that cohort migrated to higher elevations.

Implications

Pleistocene climate.—Assuming that the fossil record is accurate, *C. horridus*, as well as many other temperate-zone reptile species, survived the Wisconsinan glacial advance by overwintering in limestone caverns located in relatively low valleys of

the central Appalachian region (Holman 1995). Fossils of *C. horridus* indicate that the climate in the valleys, at least in terms of summer weather, must have been similar to current conditions on the higher peaks. With periglacial features at high elevations of the Appalachians indicating a cooler climate than is present today, the temperature difference must have been mainly in winter, as suggested by Delcourt (1979). The active season in the valleys may have been slightly shorter than the current high-elevation active season, whereas it was positively compensated by drier weather. Lack of cloudy weather (more sunlight) would have enhanced thermoregulation, thus enabling females to reproduce with a shorter gestation period.

Conservation.—Climactic factors may be used to predict populations of *C. horridus* at potential risk. Based on my studies and those of others, populations of *C. horridus* in areas of relatively cool climate and/or high rainfall are at especial risk. They survive in a delicate balance without a source population to act as a demographic cushion. Stochastic events, such as bad weather or human predation, may cause local populations (especially those that are relatively isolated) to decline toward extinction. Where the habitable zone for *C. horridus* is broad, as in the central and southern Appalachians, repatriation is probably facilitated by the presence of nearby low-elevation populations. Recorded extinctions have been much greater in the northeastern mountains (Maine, New Hampshire, New York, and Vermont) when compared to the central Appalachians. This may be due to the narrow habitable zone and greater historical isolation of dens in the northeast. Finally, current global climate change may cause an increase in cloudy weather in the Appalachians, thus putting high-elevation and high latitude populations of *C. horridus* in that area at increased future risk.

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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*). *J. Herpetol.* 29:399–407.
- BREEN, J. F. 1970. Rhode Island's declining rattlers. *Narragansett Naturalist* 13:36–38.
- BROOKS, M. 1965. *The Appalachians*. Houghton Mifflin, Boston.
- BROWN, W. S. 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*. Pp 251–258. *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- . 1995. The female timber rattlesnake: a key to conservation. *Reptile and Amphibian Magazine*. Sept./Oct.:12–19.
- . 1997. Lifetime reproduction in the timber rattlesnake: a progress report. *Texas Herpetol. Soc. Tyler Abstract*.
- , AND F. M. MACLEAN. 1983. Conspecific scent-trailing by newborn timber rattlesnakes, *Crotalus horridus*. *Herpetologica* 39:430–436.
- BROWNING, M. 1859. *Forty-four Years of the Life of a Hunter*. Winston Printing, Winston-Salem, North Carolina.
- CAVANAUGH, C. J. 1994. *Crotalus horridus* (timber rattlesnake). Longevity. *Herpetol. Rev.* 25:70.
- CHARLAND, M. B. 1989. Size and winter survivorship in neonatal western rattlesnakes (*Crotalus viridis*). *Can. J. Zool.* 7:1620–1625.
- DIEMER-BERISH, J. E. 1998. Characterization of rattlesnake harvest in Florida. *J. Herpetol.* 32:551–557.
- DELCOURT, H. R. 1979. Late Quaternary vegetational history of the eastern Highland Rim and adjacent Cumberland Plateau. *Ecol. Monogr.* 49:255–280.
- DORCAS, M. E., AND C. R. PETERSON. 1998. Daily body temperature variation in free-ranging rubber boas. *Herpetologica* 54:88–103.
- FITCH, H. S. 1985. Observations on rattle size and demography of prairie rattlesnakes (*Crotalus viridis*) and timber rattlesnakes (*Crotalus horridus*) in Kansas. *Occ. Pap. Kansas Mus. Nat. Hist.* 118:1–11.
- FOBES, C.B. 1951. Rattlesnake mountains in Maine and New Hampshire. *Appalachia* 17:530–534.
- GIBBONS, J. W. 1972. Reproduction, growth, and sexual dimorphism in the canebrake rattlesnake (*Crotalus horridus atricaudatus*). *Copeia* 1972:222–226.
- GROSSMAN, D. H., D. FABER-LANGENDOEN, A. S. WEAKLEY, M. ANDERSON, P. BOURGERON, R. CRAWFORD, K. GOODIN, S. LANDAAL, K. METZLER, K. PATTERSON, M. PYNE, M. REID, AND L. SNEDDON. 1998. *Terrestrial vegetation of the United States, Vol 1. The National Vegetation Classification System: Development, Status, and Applications*. The Nature Conservancy, Arlington, Virginia.
- HOLMAN, J. A. 1995. *Pleistocene amphibians and reptiles in North America*. Oxford University Press, New York.
- HUNTER, M. L., JR., J. ALBRIGHT, AND J. ARBUCKLE (Eds.). 1992. *The Amphibians and Reptiles of Maine*. University of Maine, Orono.
- KEENLYNE, K. D. 1978. Reproductive cycles in two species of rattlesnakes. *Amer. Midl. Nat.* 100:368–375.
- LUNDELIUS, E. L., R. W. GRAHAM, E. ANDERSON, J. GUILDAY, J. A. HOLMAN, D. W. STEADMAN, AND S. D. WEBB. 1983. Terrestrial vertebrate faunas. Pp. 311–353. *In* H. E. Wright (Ed.), *Late Quaternary Environments of the United States, Vol. 1: The Late Pleistocene*. University of Minnesota Press, Minneapolis.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- MACARTNEY, J. M., AND P. T. GREGORY. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. *Copeia* 1988:47–57.

- MADSEN, P., AND R. SHINE. 2001. Conflicting conclusions from long-term versus short-term studies on growth and reproduction of a tropical snake. *Herpetologica* 57:147–156.
- MARTIN, W. H. 1992. Phenology of the timber rattlesnake (*Crotalus horridus*) in an unglaciated section of the Appalachian Mountains. Pp. 259–277. In J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- . 1993. Reproduction of the timber rattlesnake in the Appalachian Mountains. *J. Herpetol.* 27:133–143.
- NOAA. 2000. Climate Atlas of the United States. U. S. Dept. Commerce, National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, North Carolina (CD-Rom).
- NORTON, A. H. 1929. The rattlesnake in Maine. *Maine Naturalist* 9:25–28.
- OWENBY, J. R., AND D. S. EZELL. 1992. Climatology of the United States no. 81. Monthly Station Normals of Temperature, Precipitation, and Heating and Cooling Degree Days 1961–1990. NOAA, Asheville, North Carolina.
- PALMER, R. S. 1946. The rattlesnake in Maine. *Nat. Hist. Misc., Chicago Acad. Sci.* 2:1–3.
- PALMER, T. 1992. *Landscape with Reptile: Rattlesnakes in an Urban World*. Ticknor & Fields, New York.
- PARRISH, H. M. 1980. *Poisonous Snakebite in the United States*. Vantage Press, New York.
- PE'WE', T. L. 1983. The periglacial environment in North America during Wisconsinan time. In H. E. Wright, Jr. (Ed.), *The Vegetational History of the Eastern United States 25,00 to 10,000 Years Ago*. University of Minnesota Press, Minneapolis.
- REINERT, H. K., AND R. R. RUPERT, JR. 1999. Impacts of translocation on behavior and survival of the timber rattlesnake (*Crotalus horridus*) *J. Herpetol.* 33:155–177.
- , AND R. ZAPPALORTI. 1988. Field observation of the association of adult and neonatal timber rattlesnakes, *Crotalus horridus*, with possible evidence for conspecific trailing. *Copeia* 1988:1057–1059.
- SAINT GIRONS, H. 1975. Coexistence de *Vipera aspis* and *Vipera berus* en Loire Atlantique: un probleme de competition interspecificque. *Rev. Ecol.* 29:590–613.
- . 1992. Strategies reproductrices des *Viperidae* dans les zones temperees fraiche et froides. *Bull. Soc. Zool. France* 117:276–278.
- . 1997. Utilization de l'espace vital par *Vipera aspis* (Reptilia, Viperidae) dans une region de bocage de l'ouest de la France. *Bull. Soc. Herpetol. France* 84:5–14.
- SCHORGER, A. W. 1967. Rattlesnakes in early Wisconsin. *Wisconsin Acad. Sci., Arts and Letters* 1967:29–48.
- SCHUETT, G. W., E. M. NOWAK, AND R. A. REPP. 2002. Natural History Notes. *Crotalus cerberus* (Arizona Black Rattlesnake). Diet and prey size. *Herpetol. Rev.* 33:210–211.
- STEVENSON, S. L. 1993. *Upland Forests of West Virginia*. McClain Printing, Parsons, West Virginia.
- UNITED STATES DEPARTMENT OF AGRICULTURE. 1941. *Climate and Man. Yearbook of Agriculture*. U. S. Government Printing Office, Washington, D.C.
- VIITANEN, P. E. 1967. Hibernation and seasonal movements of the viper, *Vipera berus* (L.) in southern Finland. *Ann. Zool. Fenn.* 4:472–546.