Biological variation, management units, and a conservation plan for the timber rattlesnake (Crotalus horridus)

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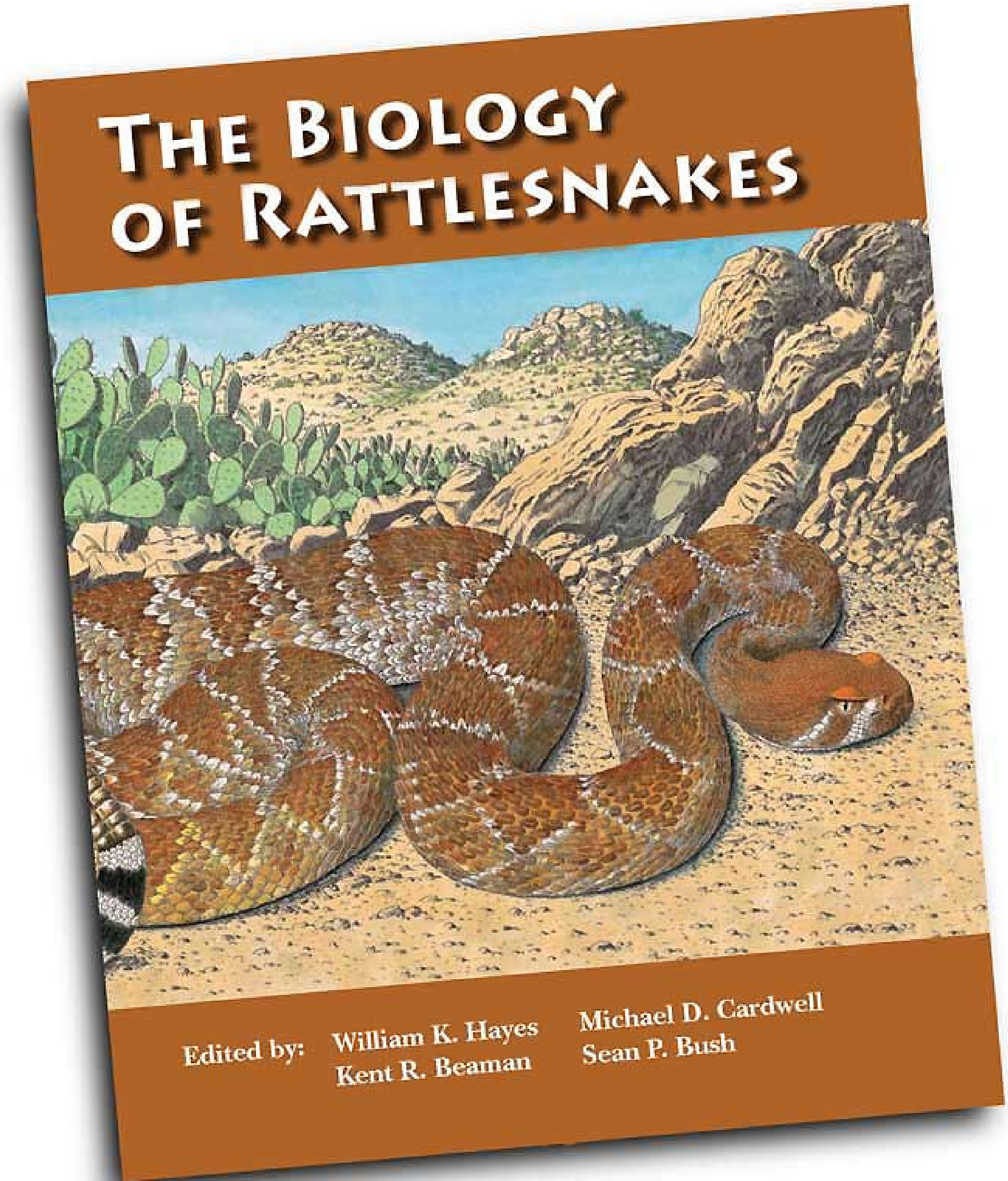

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Biological Variation, Management Units, and a Conservation Action Plan for the Timber Rattlesnake (*Crotalus horridus*)

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Abstract.—Across its wide range in eastern North America, the Timber Rattlesnake (*Crotalus horridus*) is highly variable in phenotype and ecology. All aspects of the life history are affected by seasonal temperatures and the length of the active season, the latter ranging from about 4.6-5.2 months at the northern distributional limits to 9-10 months along the southern edge of the range. In the southern part of its range, the species is associated with heavily wooded hardwood corridors along streams, whereas in the northern and western parts of its range, it is found in the forested mountains and wooded stream bluffs where rock outcrops provide overwintering dens. Denning behavior ranges from solitary overwintering in ephemeral sites (southern range sectors) to communal denning in deep ancestral dens (northern areas). Mean adult size (total length) varies geographically from 86-135 cm for females and from 100-150 cm for males. Mean fecundity varies from 7-12 neonates per litter, with the largest litters produced in the southern Coastal Plain. The modal age of first reproduction in females varies from 4-11 yr and the modal reproductive interval varies from 2-5 yr. Habitat loss and degradation from residential, commercial, agricultural, and highway development are reducing this rattlesnake's populations and fragmenting its habitats, putting severe pressure on its remaining populations all across the northern, eastern, and western edges of the range, as well as in some of the interior regions. An organized group (the Timber Rattlesnake Conservation Action Plan, or TRCAP), composed of federal, state, and private biologists, is developing a conservation action plan to facilitate identifying, coordinating, and implementing actions to minimize further range-wide reductions or possible extirpations of local or regional populations. Here, we identify and list management units (MUs) based on ecoregions and subregions. The major units identified are: Southern, Western, Mid-western, Appalachian/Northeastern, and Mid-Atlantic.

Introduction

The Timber Rattlesnake (*Crotalus horridus*), a widespread woodland rattlesnake of the eastern half of North America, faces serious and varied conservation challenges. Because of differences in climate and habitats, the snake's life history characteristics vary considerably across its wide range. Based on letters from early European settlers, it is apparent that a "war" on the Timber Rattlesnake was well underway soon after Europeans arrived on the continent (Palmer, 1992). In contrast, this species persisted through thousands of years of coexistence with the widespread and diverse aboriginal American tribes (Mann, 2005; Sasaki et al., this volume). An attitude of fear, intolerance, and, in the 19th and 20th centuries, bounties on the snakes followed, as Europeans colonized its habitat in their westward advance.

The range of this rattlesnake in the early 21st century, although still largely intact in the heavily wooded parts of the Coastal Plain and mountainous interior portions of the eastern United States, has become highly fragmented all across its western and northern edges, as well as through most of the Piedmont and the Midwest (Fig. 1). Persecution, habitat fragmentation and degradation, and highway mortality cumulatively pose serious range-wide threats to this rattlesnake. Winter communal denning requirements in significant portions of its range, as well as gravid female basking behavior, allow humans to precisely locate the populations. In addition, long time spans required to attain sexual maturity, long inter-birthing intervals in individual females, and small litter size make this rattlesnake particularly vulnerable to a plethora of threats (summarized in Brown, 1993). While it currently inhabits 31 states, it is unquestionably gone from Delaware and Michigan, and has also probably been extirpated from Maine, Rhode Island, and the Canadian province of Ontario. The Timber Rattlesnake likely occurred in extreme southwestern Quebec (Curran and Kauffeld, 1937), as well. Its distribution and numbers have been reduced in the balance of its range. The species is now imperiled in eight states and critically imperiled in Nebraska, Vermont, and New Hampshire.

Considerable geographic variation in body size and color pattern, as well as in habitats and ecology, exist across the range of this species. In parts of the South, this snake is known as the Canebrake Rattlesnake, and its southern populations were described as a subspecies, *C. horridus atricaudatus* (Gloyd, 1936). The Canebrake Rattlesnake was distinguished from the Timber by a distinctive color pattern,

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higher mid-body and ventral scale counts, and larger size. Pisani et al. (1972) argued against continued recognition of both subspecies, but Brown and Ernst (1986), examining only eastern specimens, argued for continued recognition of the subspecies based on their considerable differences, especially those noted to occur between southeastern Coastal Plain specimens and those from the Appalachians and Northeast. Recent detailed morphological studies (Allsteadt et al., 2006) and genetic analyses (Clark et al., 2003) do not support subspecific recognition for either of these forms. The genetic study, in fact, indicates major eastern and western lineages that are at odds with the traditional north-to-south morphological division between the subspecies. Campbell and Lamar (2004) provided an authoritative systematic review of all the rattlesnakes, including *C. horridus*, with a full synonymy that omitted recognition of subspecies. Similarly, the Committee on Standard English and Scientific Names of the three major herpetological societies rejected recognition of subspecies (Crother, 2008; see also Beaman and Hayes, this volume).

Ecoregional Divisions or Management Units

Distinctive sets of color morphs among individuals of populations occupying the different parts of the geographic range of *C. horridus* underscore the variability of this rattlesnake (color photos of a variety of specimens are in Brown, 1993). Several ecotypes have evolved in response to the varied ecological conditions in the different parts of the range. Recent genetic studies (Clark et al., 2003) and morphological studies (Allsteadt, 2003; Allsteadt et al., 2006) have elucidated genetic and morphological differences across the range. Because of additional data suggesting that strong regional variation also exists in life history traits, and in the snake's numerical status, threats, and conservation status, we are suggesting dividing the range into management units (MUs) and ecoregional subunits (Fig. 2). The MUs and ecoregional subunits are based on shared geographical characteristics and on the ecological, morphological, and genetic characteristics of the snakes as currently understood or surmised.

A large lowland form, whose range is associated primarily with hardwood stream corridors, occurs across the entire southern part of the range. This is the variant that has traditionally been known as the Canebrake Rattlesnake, and was considered a distinct subspecies (*C. h. atricaudatus*). Both major lineages and most of the haplotypes plotted in Clark et al. (2003) comprise this segment. Each haplotype represents a unique structure of a segment of DNA that differs from other haplotypes by the substi-

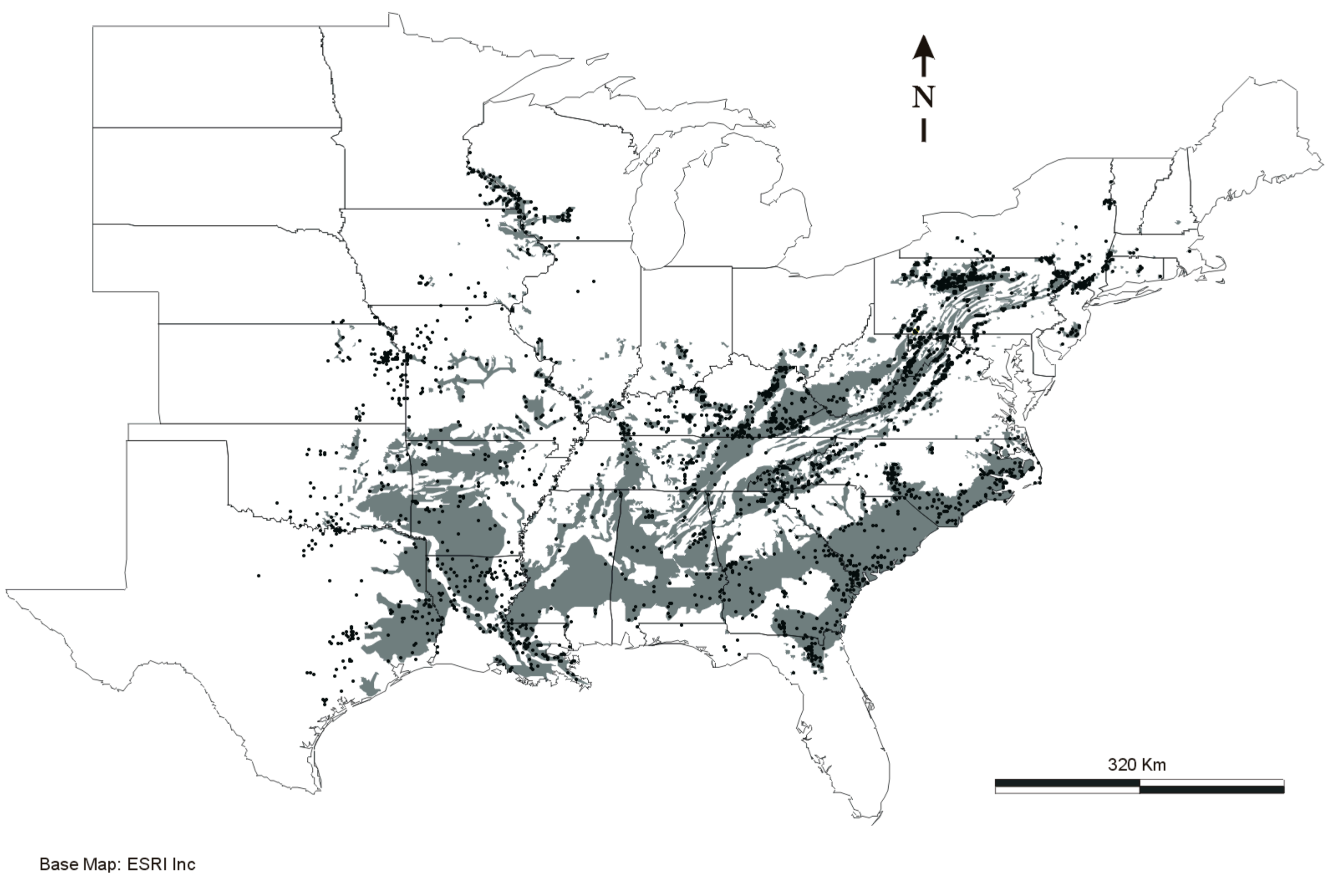

Figure 1. Current range of the Timber Rattlesnake (*Crotalus horridus*). Dots represent locality records. Shading shows presumed distribution.

tution of one or more nucleotide bases. The background dorsum color of individuals ranges from pale whitish pink through various shades of tan and gray to chocolate brown and charcoal gray. A pinkish tinge is often present. A dark postorbital bar and a mid-dorsal orange to reddish-brown stripe is usually present. Occasional individuals with dark heads have been reported in the eastern part of the range of this morphotype.

A western variant, composed primarily of a single haplotype of the western lineage, occurs in the Ouachita Mountain and Ozark Plateau regions of Arkansas and Missouri, as well as along wooded river bluffs through the prairie/woodland transition zone from Oklahoma northward to southeastern Nebraska and up the Mississippi River valley to southeastern Minnesota and west-central Wisconsin. In comparing body sizes to other geographic regions, the vari-

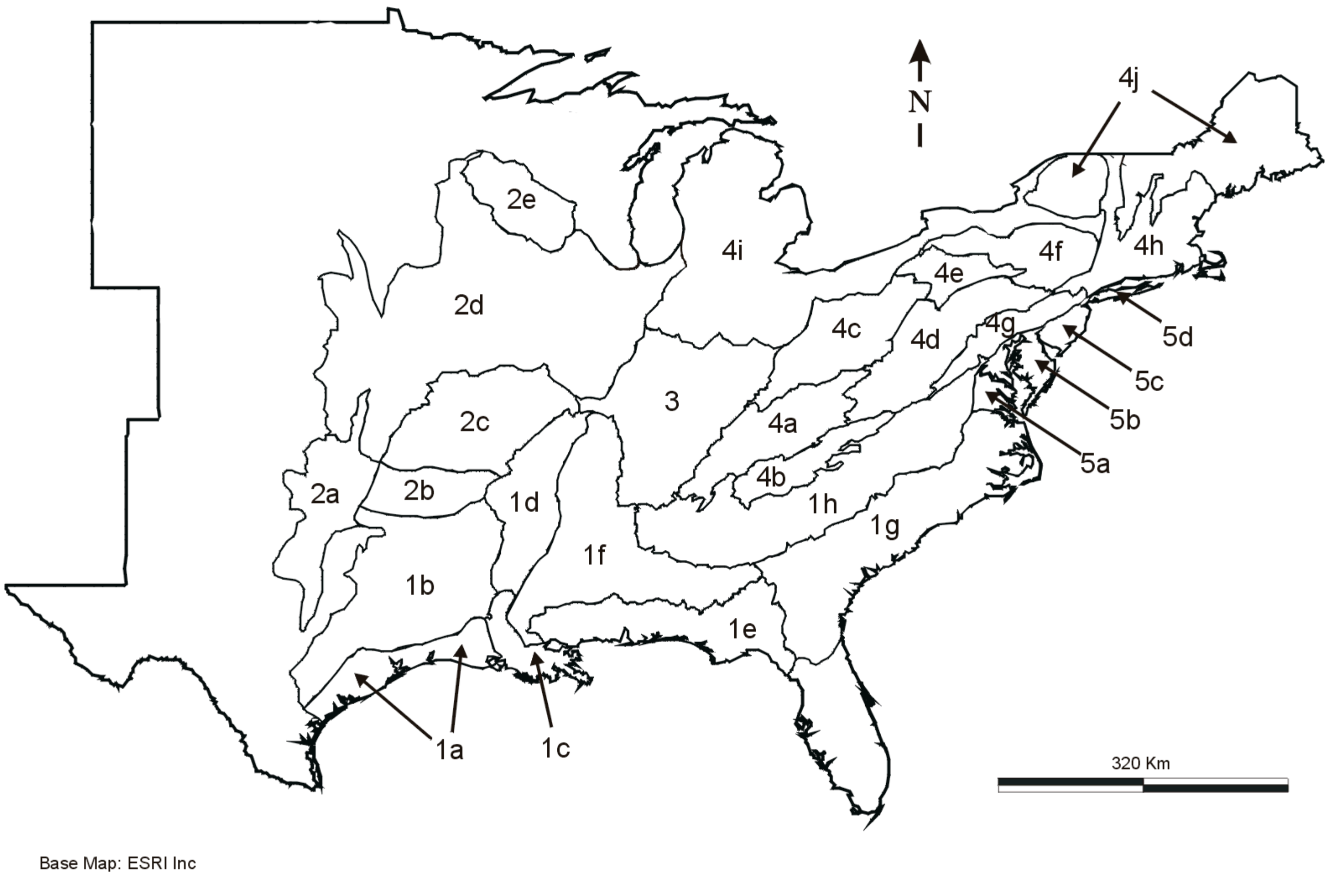

Figure 2. Management units and eco-regional sub-units for *Crotalus horridus*:

1. Southern (Canebrake) Unit
   1a. Lower West Gulf Coastal Plain
   1b. Upper West Gulf Coastal Plain
   1c. Lower Mississippi Embayment
   1d. Middle and Upper Mississippi Alluvial Plain
   1e. Lower East Gulf Coastal Plain
   1f. Upper East Gulf Coastal Plain
   1g. Southeast Atlantic Coastal Plain
   1h. Southeastern Uplands/Southern Piedmont
2. Western Unit
   2a. Cross Timbers
   2b. Ouachita Mountains
   2c. Ozark Plateau
   2d. Prairie/Woodland Transition
   2e. Upper Mississippi Blufflands
3. Midwestern Unit
   3. Interior Low Plateau
4. Appalachian/Northeastern Unit
   4a. Cumberland Mountains
   4b. Southern Blue Ridge
   4c. Western Allegheny Plateau
   4d. Central Appalachian Mountains
   4e. North-central High Allegheny Plateau
   4f. Glaciated Appalachians
   4g. Northern Piedmont
   4h. New England Uplands
   4i. Lake Plains and Till Plains
   4j. Northern Boreal Zone
5. Mid-Atlantic Unit
   5a. Western Shore of the Chesapeake Bay
   5b. Delmarva Peninsula
   5c. New Jersey Pine Barrens
   5d. Long Island

ous western populations range from small to moderate in size. Background color ranges from light tan, gray, and yellow to slate gray or brown. Postorbital bars and mid-dorsal stripes are often evident, but the incidence of post-orbital bars declines to the north. Individuals with black heads have not been reported.

A variant (not previously discussed in the literature) occurs in the rather low but heavily dissected wooded hill country of the Interior Low Plateau (Fenneman, 1938) of the Midwest. Judging from a limited number of samples from the area (Clark et al., 2003), the region is dominated by a single haplotype of the western lineage and this variant may be indigenous to the area. In body size, and in many other respects, including color pattern, this variant is intermediate between the Canebrakes of the South and Timber Rattlesnakes of the northeastern and northwestern parts of the range. Black heads are not uncommon in some parts of the area, and occasional individuals are rather dark in background color. Post-orbital bars and mid-dorsal stripes are often present.

The Appalachian/Northeastern variant is associated primarily with the mountains of the area where exposed rock provides dens and birthing sites. This variant is composed of both major genetic lineages, and while primarily consisting of only two haplotypes, other haplotypes are represented (Clark et al., 2003). Like the western variant, populations range from small to moderate in body size. They are highly variable in color pattern with the background color ranging from very light yellow or tan to jet black with the pattern almost entirely obscured. Post-orbital bars are usually absent, except around the southern and southwestern portions of the region. Mid-dorsal stripes often occur in dark individuals, but only rarely in lighter snakes.

Timber Rattlesnakes of the Mid-Atlantic region survive only in the New Jersey Pine Barrens. They have a very restricted range and have several adaptations, especially regarding hibernation, to an unusual habitat. They, in common with coastal populations from northern South Carolina northward along the eastern edge of the Appalachians to New England, are composed of one haplotype of the eastern lineage. They are moderate in body size and most closely resemble the Appalachian/Eastern populations in color pattern. Yellow, tan, and brown individuals are usual. Dark, but not jet black, individuals occur.

Rattlesnakes of the Southeastern Uplands/Southern Piedmont appear to be clinal in morphological characters, including body size, as well as in habitat between those of the southern Coastal Plain and those of the Appalachian Mountains. These rattlesnakes are associated with both the wooded stream corridors and the scattered small wooded ridges and mountains of the area. Body size, in general, declines as the Appalachians are approached. The color pattern does not differ appreciably from that of Coastal Plain populations, except in the foothills of the Appalachians. The foothills populations are intergradient, and individuals may show characteristics of both Coastal Plain and mountain snakes. Both major genetic lineages occur.

Because of additional data suggesting that strong regional variation also exists in life history traits, and in the snake's population sizes, threats, and conservation status, we have divided the range into ecoregional units and ecoregional subunits (Fig. 2). We suggest that these divisions be considered Management Units (MUs). These ecoregional units and subunits are based on shared geographical characteristics and on the ecological, morphologic, and genetic characteristics of the snakes, as currently understood or surmised. These units, with their ecoregional subunits are as follows:

1. Southern (Canebrake) Unit.—Subunits include:

- Lower West Gulf Coastal Plain
- Upper West Gulf Coastal Plain
- Lower Mississippi Embayment
- Middle and Upper Mississippi Alluvial Plain
- Lower East Gulf Coastal Plain
- Upper East Gulf Coastal Plain
- Southeast Atlantic Coastal Plain
- Southeastern Uplands/Southern Piedmont

The Southeastern Uplands/Southern Piedmont subunit is considered to be transitional between units 1 (above), 3, and 4 (below).

2. Western Unit.—Subunits include:

- Cross Timbers
- Ouachita Mountains
- Ozark Plateau
- Prairie/Woodland Transition
- Upper Mississippi Blufflands

3. Midwestern Unit.—The Interior Low Plateau comprises this unit and no subunits are identified.

4. Appalachian/Northeastern Unit.—Subunits include:

- Cumberland Mountains
- Southern Blue Ridge
- Western Allegheny Plateau
- Central Appalachian Mountains
- North-central High Allegheny Plateau
- Glaciated Appalachians
- Northern Piedmont
- New England Uplands
- Lake Plains and Till Plains
- Northern Boreal Zone

The Northern Boreal Zone subunit lies outside of the current confirmed *C. horridus* range. At the time of European settlement, rattlesnake colonies occurred near some low-elevation stream valleys within this zone.

5. Mid-Atlantic Unit.—Subunits include:

- Western Shore of the Chesapeake Bay
- Delmarva Peninsula
- New Jersey Pine Barrens
- Long Island

Populations have gone locally extinct on Long Island (New York), the Delmarva Peninsula (Delaware, Maryland, Virginia), and Maryland's Western Shore, but remain extant in the New Jersey Pine Barrens.

Our ecoregional map is adapted from maps by Bailey (1998), Omernik (1995), and The Nature Conservancy (1999).

Paleogeography

To understand the present *C. horridus* distribution, we need to focus not only on current habitats and climate, but also on biogeographical features of the past. Paleontological evidence suggests that *C. horridus* evolved during the Pleistocene, which encompasses approximately the past 2 million yr; the fossil record of *C. horridus* goes back 0.5-1.0 million yr (Holman, 1995). For most of the evolutionary history of the species, the climate was somewhat intermediate between the full glacial climate of 20,000 yr ago and the relatively mild and equable modern climate (Pielou,1991; Delcourt, 2002). Speciation probably occurred south or west of its current southwestern range limit (in present-day Texas; Gloyd, 1940). The species most likely occupied a place niche—deciduous forests—not already filled by other large rattlesnakes. During a moist climatic phase sometime prior to the most recent glacial advance (the Wisconsinan), the species probably expanded its range to the southeastern Coastal Plain, where subsequent xerification across what is now southern Georgia and northern Florida (Bartlein et al., 1998) isolated a segment of the population. For much of the Pleistocene, *C. horridus* ranged as far north as Missouri, southern Indiana (Richards, 1990), and southern Pennsylvania (Holman, 1995). During the time that *C. horridus* is known to have been extant in North America, several advances and retreats of the glaciers have occurred, resulting in constantly shifting distributional limits.

From 80-85% of today's gene pool in both the northern and the southern parts of the range is made up of just two haplotypes from two mitochondrial lineages (Clark et al., 2003). The current distribution of haplotypes and lineages suggests a major population occurred across the lower Mississippi embayment/Gulf region, and that during the glacial maximum this population was restricted to the southernmost part of that region and the associated exposed continental shelf. Here, winter temperatures roughly comparable to those prevailing in southern Virginia today (Bartlein et al., 1998) should have permitted widespread distribution and overwintering in ephemeral sites, such as root holes and small mammal burrows. Coastal Plain distribution then, as today, was probably mainly associated with stream corridors.

Isolated colonies probably survived across the karst regions located mainly in Alabama and Georgia, where the snakes overwintered in limestone structures. Based on vegetation (Delcourt, 2002) and climate (Bartlein et al., 1998) simulations, a few colonies may have survived as far north as extreme southeastern and south-central Tennessee, and at the southeastern edge of the Ozarks and southern edge of the Ouachita mountains in Arkansas. At this latter locality, the east-west orientation of the mountains may have provided some woodland habitat (on north slopes) in spite of the aridity of the period.

Another major refugium contributing to the northeastern gene pool was probably located on the Coastal Plain and exposed continental shelf of what is now South Carolina, where both white cedar swamps (as in the New Jersey Pine Barrens today) and karst features (cf. Neill, 1948) may have provided overwintering refuges. With lower precipitation prevailing during much of the Pleistocene (Bartlein et al., 1998), this rattlesnake's Coastal Plain distribution was probably even more strongly associated with stream corridors than associations would suggest today.

When the climate warmed, the two major populations, Gulf Coast and southeast Atlantic Coast, advanced northward and, by their sheer numbers, probably overwhelmed the small surviving populations that had persisted in isolated pockets of the southern parts of the Ozark and Appalachian regions. Nonetheless, some of the restricted gene pools surviving in southern Appalachian valleys may have contributed to the distinctive color patterns that occur in some of the eastern populations today. The Interior Low Plateau region of Indiana and the central parts of Kentucky and Tennessee (Fig. 2) are dominated by a single haplotype (Clark et al., 2003). A refugium in or near the Tennessee Valley of northern Alabama may have served as a source for the rattlesnakes of the Interior Low Plateau.

Based on climatic (Bartlein et al., 1998) and vegetative (Delcourt, 2002) simulations, by about 6,000 yr ago, *C. horridus* is expected to have occupied most of the forested country as far north as southern Ontario, extreme southwestern Quebec, and southwestern Maine. To the west, the species had probably advanced up the Mississippi River valley as far as southeastern Minnesota and central Wisconsin. With the subsequent cooling of the climate culminating in what is known as the "Little Ice Age" from about 1350-1870 A.D. (Pielou, 1991), the range in the northerly parts contracted around those sites offering suitable overwintering and gestating refugia. These were usually located at prominent topographical features such as fault-block escarpments with talus slides, granitic domes and monadnocks, and rocky bluffs and cliffs along rivers.

Historic and Current Distribution

The higher latitudinal and elevational range limits of this snake are determined primarily by the length and temperatures of the active season. Within these limits, a local distribution is determined chiefly by the distribution of suitable sites for overwintering. Lesser factors affecting persistence are availability of sites for gestating and—as with all species—for foraging. When the European immigrants arrived in North America during the "Little Ice Age" period, they found rattlesnake populations in the Northeast already coalesced around the scattered suitable sites meeting the strict overwintering and gestating requirements (Stechert, 1980). Wherever the settlers went, forested land was cleared (Foster and O'Keefe, 2000), removing not only foraging habitat, but also connective corridors between populations. By the mid-to-late twentieth century, the Timber Rattlesnake had been extirpated from northern Ohio, Ontario, Michigan (where they are poorly documented), and much of New York and New England. Most, if not all, colonies have been extirpated from north-central New Hampshire, Maine (Norton, 1929; Palmer, 1946; Fobes, 1951), and Rhode Island (Breen, 1970). The Timber Rattlesnake probably occurred in extreme southwestern Quebec as well (Curran and Kauffeld, 1937), although this is not certainly documented. They have been extirpated from the Delmarva peninsula (Mitchell, 1994; White and White, 2002), Maryland's Western Shore of the Chesapeake Bay, and the greater part of the Piedmont region from Georgia to New Jersey (WHM, pers. obs). The distribution, already patchy across the entire western and northern parts of the range from Texas to Minnesota and eastward to New England at the time of European settlement, has since become highly fragmented. The one-time nearly continuous distribution in the middle Mississippi embayment and in the southern Piedmont also has become highly fragmented.

The snake's range limits in the West and South correspond roughly with the historical limits of the eastern deciduous forests and closed-canopy mixed pine and hardwood forests. The northern limits are generally located south of the 20°C mean July isotherm. Within these limits, *C. horridus* is restricted to sites providing adequate hibernacula, gestating sites, and foraging grounds, all of which must be sufficiently free from human disturbance to allow the populations to persist. Critical climatic limits in the southern and central Appalachians occur at lower temperatures. This feature is demonstrated at a long-term study site on the High Allegheny Plateau in West Virginia, which has a mean July temperature of about 18°C (Martin, 2002). The presence of nearby low-elevation neighboring dens may enable recovery of the high plateau populations from multi-year periods of poor weather there, or from stochastic events (e.g., human depredations) that are known to severely constrain this population. The narrow range of habitable elevations apparently precludes such refuges in the northern parts of the range (e.g., New England), where the life history constraints are doubtless similar to those described for West Virginia (Martin 2002).

Habitats

Throughout its range, the distribution of *C. horridus* is prominently and consistently associated with deciduous forests. Although nearly all terrestrial habitats, including agricultural lands, may be used occasionally, woodlands are apparently included within the home ranges of all populations thus far studied. It has not been established, however, that the association with woodlands is due to any proclivity of the snake for trees. In northeastern Kansas, the association may simply occur because the rock ledges necessary for hibernation are usually located in thinly wooded habitat (Fitch and Pisani, 2006), as rattlesnakes at a study site there died out apparently due to shading-over. In the open-canopied pinelands of the Coastal Plain, most records are within 1-2 km of hardwood corridors along streams (Mount, 1975; Rudolph et al., 1998). Within alluvial bottomlands and swamps, the snakes occur on higher ground not subject to inundation. Campbell and Lamar (2004) found them in hardwood uplands and higher portions of hardwood bottomlands in northwestern Mississippi, western Tennessee, and eastern Texas. To the west, the range follows wooded streams into the prairies, where the local distribution is associated with bluffs in which snakes use rock crevices as hibernacula. Across the northern part of the range (the Upper Mississippi Blufflands, the New England Uplands) and in the Appalachian Mountains, the distribution is closely tied to wooded hills and mountains where exposed rock is prevalent.

A tract of land for foraging, sufficiently free of human activity to allow persistence of populations, is essential throughout the range of the species. The minimum size of such an area necessary for long-term survival of a population has not been established. In general, females and juveniles use more open habitats than males (Brown et al., 1982; Reinert, 1984a,b; Fitch et al., 2004; Sajdak et al., 2005; Smith et al., this volume), but this may not always be the case (Gibson et al., this volume). In the South Carolina Coastal Plain, males use bottomland hardwoods for foraging, but females are more prone to use mixed pine-hardwood stands, pine savannas, or cultivated and fallow fields (Waldron, 2005, 2006). Likewise, in Wisconsin, males were prone to forage in hardwood swamps (Sajdak et. al., 2005). In northeastern Kansas, the preferred foraging grounds are prairie grasslands (Fitch and Pisani, 2006). In the Pine Barrens of southern New Jersey, rattlesnakes are usually associated with white cedar-dominated swamps that occur along streams, where most hibernacula are located (Smith et al., this volume).

In terms of depth, spacing, permanence, and population size, hibernacula evidently range along a continuum. At one end of the continuum (northern part of range where winters are cold), widely spaced ancestral dens with large populations are the norm (Stechert, 1980; Brennan, 1995; Brown, this volume; Cochran, this volume); in such dens, a single crevice may provide entrance to a hibernaculum in which an entire colony of over 100 snakes overwinters. In northeastern New York, Brown (this volume) has noted a number of so-called "den pockets," or hibernating concentration points within a den, whose intra-den number varies among dens and correlates with the physical size of a den, affecting the apparent inter-den snake abundance. At the other end of the continuum (i.e., in the southern part of the range where winters are mild), a so-called ephemeral den (e.g., a root hole) may house a solitary overwintering snake. Most dens in the southern Coastal Plain and lower Mississippi embayment fall in this latter category, but communal ancestral dens are known to occur there (Neill, 1948; WHM, unpubl. data). Across the balance of the range, most

C. horridus dens fall somewhere in between these extremes (Sealy, 2002; Fitch et al., 2004; Cobb, 2005; Fogell and Fawcett, 2005; Gibson et al., this volume). In the southern New Jersey Pine Barrens, where rock ledges are lacking, most denning is in association with streams (Smith et al., this volume). In summary, where winters are severe, deep permanent dens are obligatory, whereas in the mild climatic zones, deep permanent dens are optional.

Across the northern part of the range and extending south through the higher Appalachians, because of the necessity of maintaining a high temperature during gestation, an essential element of the habitat is an availability of rocks that are exposed to the sunlight; these open rocks are used for shedding and gestating (Keenlyne, 1978; Brown et al., 1982; Reinert 1984a,b; Martin, 1992, 2002; Bielema, 2004; Cochran, this volume; McGowan and Madison, this volume). Rocks along utility-line rights-of-way are favored, as well as rocks in naturally occurring forest openings. In many areas of level-lying sedimentary rocks, such as the unglaciated Upper Mississippi Blufflands and in parts of the unglaciated Appalachians (WHM, unpbl. obs.), open and exposed ledges and slabs are a relatively scarce habitat; this is a major constraint on distribution. In contrast, in the New England Uplands of eastern New York and the New England states, due to glaciation, open rocky woodlands with numerous surface slab rocks used as shelters are abundant; thus, exposed rocks, per se, often may not present a significant constraint on the snake's local distribution there (WSB, unpubl. obs.).

Avoiding excessive heat and low humidity may be an additional function of these gestating shelters. In the southern part of the range, where summer temperatures are consistently high, the major requirement for gestation is simply shelter, which can be provided by mammal burrows, root holes, or logs (Conner et al., 2003), although females do select more open habitats than males (Waldron, 2005). Between these two extremes, as in southern Indiana (Gibson et al., this volume) and southern New Jersey (Reinert and Zappalorti, 1988), logs in forest clearings, whether natural or man-caused, are typically used for gestation.

Crotalus horridus occurs from sea level along the southeastern Atlantic and Gulf Coasts to well over 1,800 m in the southern Appalachians. The elevational limit at which the species can reproduce decreases from south to north; much of the wildest country in both the southern Appalachians and in the Northeast lies above the known elevational limits of *C. horridus*. Greatest occupied elevations are reached in the southern Blue Ridge Mountains of western North Carolina and eastern Tennessee. Although uncommon in such locations, occasional snakes have been recorded on or near some of the highest peaks in the Great Smoky Mountains, including Mount Guyot (elevation 2,012 m), and specimens are commonly recorded at Gregorys Bald (elevation 1,508 m; Huheey and Stupka, 1967). Snakes are frequent during the summer in the Great Craggy and Black Mountain ranges up to 1650 m elevation, and gestating females have been found up to 1400 m (WHM, unpubl. obs.). The elevational limits at which they are able to reproduce evidently decline to the north. In western Virginia, reproduction occurs up to 1200 m, and on the High Allegheny Plateau in West Virginia, up to 1100 m (Martin, 2002), with individual snakes reaching the highest elevations of the state on Spruce Knob (elevation 1481 m). Pregnant females are recorded up to 670 m in the Catskill Mountains of southeastern New York (R. Stechert, pers comm.) and at 485 m in the southeastern Adirondack Mountains of northeastern New York; at the latter site, denning occurs up to 400 m and snakes regularly occur at 700 m during the summer (WSB, unpubl. obs.). Elevations at the northwestern range limits apparently do not exceed the limits of the species; in Minnesota and Wisconsin, the dens and gestating sites occur up to the highest available elevations (350 m, Oldfield and Keyler, 1989).

Movements

Adults typically travel greater distances than do juveniles. Males travel greater distances than do the females, and non-gravid females travel farther than do gravid females; the latter have the most restricted movement distances and summer range. Individuals apparently establish their home ranges in their early years, and most apparently maintain the same general range throughout their lives. Movements generally involve a looping movement away from the den, followed by a return loop in the fall, but not necessarily on the same path (Reinert and Zappalorti, 1988; Reinert and Rupert, 1999; Sealy, 2002). Occasional shifts to a new den occur (Martin, 1992; Brown, this volume). Most studies have found that males and non-gravid females have home ranges of 1-2 km at their greatest width (Brown et al., 1982; Reinert and Zappalorti, 1988; Reinert and Rupert, 1999; Sealy, 2002; Tyning, 2005; Smith et al., this volume). Individuals, especially males, have been found as far as 7 km distant from the den (Brown, 1993). No consistent geographic trends in distances traveled are apparent, but movement distances recorded in the North Carolina Piedmont (Sealy 2002), southern South Carolina, and southeastern Virginia Coastal Plain (Savitzky and Petersen, 2004) were less than travel distances reported for northeastern New York (Brown, 1993), southern New Jersey (Reinert and Zappalorti, 1988b), and Massachusetts (Tyning, 2005). In southeastern Nebraska, the mean migratory distance was 3.4 km (Fogell and Fawcett, 2005). Perhaps the linearity of the habitat at this latter locality influences the population's movements, where the best habitat is found along streams. Gestating females, which normally do not feed during the 3 months or so prior to parturition, typically travel no more than 500 m away from their dens, but some have been recorded to move over a distance of 1 km to basking sites (Reinert and Zappalorti, 1988; Martin 1992; Reinert and Rupert, 1999; WSB, unpubl. obs.). In eastern Pennsylvania, open rock exposures had a considerable effect on snake movements, as the snakes apparently oriented their summer foraging travels in concert with the location of basking sites (Bushar et al., 1998). The distribution of roads and other barriers, as well as that of basking habitat and feeding grounds and the distance to near-neighbor populations, all may be factors in distances traveled.

Food and Feeding

Numerous studies indicate that small mammals, especially rodents, are the major food of *C. horridus*, with birds taken occasionally. Lizards and amphibians are taken occasionally by juveniles, at least in the southern part of the range (Surface, 1906; Uhler et al., 1939; Clark, 1949; Hamilton and Pollack, 1955; Parmley and Parmley, 2001; Platt et al., 2001; Clark, 2002). White-footed Mice (*Peromyscus leucopus*) and Deer Mice (*P. maniculatus*) are the main prey across most of the range in the North and the Appalachians, with voles (*Clethrionomys* and *Microtus*) and Eastern Chipmunks (*Tamias striatus*) figuring prominently in some areas. Mice (*Peromyscus*) and Cotton Rats (*Sigmodon hispidus*) dominate the diet in much of the South. Rabbits (*Sylvilagus*) of an appropriate size are taken opportunistically, especially in the South. Only the largest males, and primarily in southern populations, are capable of taking a full-grown rabbit. Squirrels (*Sciurus*) are also important items, especially in the South, and more so for males (Sealy, 2002; Waldron et al., 2006). In southeastern Virginia, individual telemetered snakes obtained from 0-5 large squirrel-sized meals per year (Savitzky and Petersen, 2004). Red Squirrels (*Tamiasciurus hudsonicus*) are of ideal size for an adult Timber Rattlesnake, and are frequently taken where they occur (e.g., northeastern New York, WSB, upubl. obs.), but their distribution is spotty across the Northeast. Likewise, the woodrat (*Neotoma*) is of ideal size, but has not been reported as an important item except in Kansas (Fitch et al., 2004). Shrews (*Sorex*, *Blarina*), because of their small size and abundance, are probably important items for young-of-year snakes prior to hibernation and for first-year juveniles after their initial hibernation (Clark, 2002).

Foraging commences with the first warm weather, usually 1-2 wk after emergence. Postpartum females are among the earliest feeders (WHM, unpubl. obs.). Feeding peaks in the late spring and early summer, when rodent populations are usually at a high point following their concentrated bout of spring breeding (Wolff 1996a,b). Feeding among males decreases with the onset of the mating season in late summer, but may resume again briefly in the early fall (WHM, unpubl. obs.). Young-of-year snakes and postpartum females disperse after the young have completed the postnatal molt, and both age groups in most areas forage prior to hibernation. In the South, the fall is an important time for foraging, especially for the young-of-year snakes. Fall feeding by young-of-year snakes and postpartum females seems to decline to the north and at the highest elevations because of the short interval between birth and denning (Martin, 2002). In a sample of 43 post-shed young-of-year snakes found in September and October at a high-elevation West Virginia site, none had stomach boli which would otherwise suggest previous feeding (WHM, pers. obs.). Similarly, in northeastern New York, where births usually occur a little earlier (first two weeks of September, WSB, unpubl. obs), occasional feeding by young-of-year snakes takes place, as 19% of these snakes had gut boli (Brown, this volume).

Food availability is a fundamental factor driving individual and population responses of Timber Rattlesnakes (Beaupre, this volume). Under conditions of low food intake, snakes spend more time foraging and experience reduced growth, lower field metabolic rates, poorer body condition, and reduced reproductive activity. Conversely, under conditions of high food intake, snakes forage less, grow faster, experience higher field metabolic rates and improved body condition, and exhibit extensive mate search and courtship behaviors.

Growth and Shedding

Establishing an average shedding rate for the earlier years of a rattlesnake's life is important, because it enables the age class of individual snakes to be estimated. The growth rate and shedding rate vary with age and sex, length of the active season, and prevailing summer temperatures. Juveniles grow at a much faster rate than do sexually mature adults. Males grow a little faster and for a longer period of time than females (Brown, 1991), and thus males ultimately reach a maximum length that exceeds females by 20% or more (WHM, unpbl. obs.). The rattle provides a record of shedding. A shedding event shortly after birth (the postnatal shed) produces the first permanent rattle segment, the button. We advocate consistency in rattle-segment counts, and recommend that the basal segment should be included in all rattle counts because it clearly represents a shed. The button (b) should be noted because it indicates a complete string, but it is not included in shedding-rate calculations because it is acquired soon after birth in all snakes.

Where summer temperatures are high, shedding typically occurs at intervals of 2-3 months for juveniles and declines to about 3-4 month intervals for adults. The average shedding rate declines to as low as one shed every 4-5 months at higher elevations. The lowest growth and shedding rates observed in any population occur at the higher elevations of the Appalachians. Snakes from a population on the High Allegheny Plateau in West Virginia, where the active season lasts just over 5 months, averaged 1.2 sheds per year for the first 9 yr, and typically only one shed per year thereafter (Martin, 2002). Females from this Allegheny population had rattle-segment counts of 10+b or 11+b at 9 yr, and males typically had counts of 11+b at this age. In northeastern New York, where the active season is of similar length but summer temperatures are higher, a slightly higher rate of 1.4 sheds per year for females and 1.5 sheds per year for males was recorded (Brown, 1991). A shedding rate of 1.54 sheds per year for females and 1.80 sheds per year for males was recorded in Wisconsin (Berg et al., 2005), where the active season is about 4.8 months long but summer temperatures exceed those of northeastern New York. Females from the northern Blue Ridge (west-central Virginia to southern Pennsylvania) of the central Appalachian region, with an active season of 5.5-6 months, shed at a rate of 1.4 times per year; individuals typically had rattle-segment counts of 12+b at an age of 8 yr (Martin, 1993). Males in this region averaged 1.5 sheds per year (WHM, unpubl. obs.). In northeastern Kansas, females typically had rattle-segment counts of 7+b at 4 yr and males 8+b at 4 yr (Fitch, 1985; Fitch et al., 2004), a shedding rate of 1.75 per year for females and 2.0 per year for males. The shedding rate in the southern Coastal Plain, with an active season of 8-10 months, has not been established by mark-recapture of juveniles. However, first-year juveniles often emerge from the first hibernation with the button and a basal segment (1+b), providing evidence for a birth-year shedding event in addition to the obligatory postnatal shed. Based on the long active season and high summer temperatures, juveniles in this region might be expected to shed up to three times per year through their third year and twice per year thereafter.

Newborn size also varies geographically, with the average size known ranging from 25 to 35 cm total length and a mass ranging from 20-30 g. The largest newborns apparently occur in the southern Coastal Plain populations. Juveniles from the southeastern Coastal Plain in South Carolina approximately double their length by the age of 1 yr and triple their lengths at 3 yr (Gibbons, 1972). Juveniles on the High Allegheny Plateau required, at minimum, about 2 yr to double their lengths and 8 yr to triple their lengths (Martin, 2002). In northeastern New York, first-year juveniles approximately triple their weights in the first year (Brown, this volume).

The normal maximum total length (NML; i.e., the size at which growth ceases and/or natural death occurs) depends on genetics and food intake, and varies considerably across the range. The smallest adult size apparently occurs in some of the ridges around certain interior Appalachian valleys, where the NML for females is only 86-100 cm and for males 103-120 cm (WHM, unpubl. obs). The greatest NML is reached in the lower Mississippi embayment (Klauber, 1956) and adjacent Gulf Coastal Plain (Tennant, 1985), where the NML for females is 135-158 cm and that for males is 163-188 cm (Allsteadt, 2003; WHM, unpubl. obs.). A Louisiana specimen captured as a juvenile and fed on a rather spartan schedule of three or four meals per year eventually reached a total length of 177 cm (Cavanaugh, 1994). Interestingly, these data, along with additional data sets from Berish (1998), Gibbons (1972), Mitchell (1994), Palmer and Braswell (1995), and Savitzky and Petersen (2004), suggest that the largest sizes are reached in parts of the South where the species is not in sympatry with *C. adamanteus* (c.f. Martin and Means, 2004). Geographical variation in body size remains an important area of research, as we have observed apparently large interpopulational differences within the same ecoregion. Competition, as well as the size and density of prey, may be among factors contributing to the source or maintenance of this variation, and its adaptive significance would be a worthwhile avenue of study.

Size and Age at Maturity

The age at which sexual maturity is reached depends on the length of the active season, ambient temperature, and nutrition. Sexual maturity is reached when snakes have approximately tripled their birth lengths (WHM, unpubl. obs.). Males and females reach sexual maturity at around the same size, but males typically reach this size at a younger age. Across the range, maturity in males probably varies from about 2-3 yr in the southern Coastal Plain to 6-8 yr at the highest elevations of the Appalachians. Occasional fast-growing males might reach sexual maturity at 2 yr in the extreme southern part of the range. South Carolina males evidently matured at 3 yr and a total length of 97-108 cm (Gibbons, 1972). Males in northeastern New York reached sexual maturity, as determined by gonadal cellular development, at 4-7 yr at a mean total length of 84 cm (Aldridge and Brown, 1995).

In the case of sexual maturity in females, a necessity of their storing large amounts of fat usually delays first reproduction well past the time at which they likely reach sexual maturity. Well-fed captive Appalachian females have reproduced initially at 5 yr while maintained on a 6-month simulated active season (WHM, unpubl. obs.). North Carolina Piedmont and southeastern Coastal Plain captives maintained on a simulated 8-month active season reproduced at 5 and 4 yr, respectively (Z. Orr, pers. comm.). Occasional breeding at 2 yr and reproduction at 3 yr of age cannot be ruled out in the extreme southern parts of the range. However, we surmise that the modal reproductive age of females across the southern distribution ranges from 4-7 yr. Gibbons (1972) stated that first reproduction typically occurs at 6 yr in the South Carolina Coastal Plain. The smaller, and presumably younger, one-third of reproductive females averaged about 120 cm total length in the southeastern Coastal Plain (Gibbons, 1972; Berish, 1995; Palmer and Braswell, 1995). In eastern Texas, Conner et al. (2003) radio-tracked “head-started” females released as first-year and second-year juveniles and, although much larger in size than comparable wild snakes of these ages, they were not observed mating until they were 6 yr old. The modal age and total length for first reproduction in the northern Blue Ridge is 8 yr and 88 cm, with a range for known-age snakes of 6-11 yr (Martin, 1993). Rattle-segment counts (8+b) of a few postpartum or near-term pregnant females suggest that some might reproduce at 5 yr. In northeastern New York, most females were 9 and 10 yr old at first reproduction, and the youngest were 7 yr (Brown, 1991). On the High Allegheny Plateau, the latest age for first reproduction in the species was recorded, where the youngest reproductive females were 9 yr of age and the modal age for first reproduction was 11 yr (Martin, 2002). The modal age of first reproduction in Wisconsin is estimated at 8 yr (Berg et al., 2005), but B. Oldfield (pers. comm.) recorded a near-term pregnant female in the upper Midwest that had a rattle-segment count of only 7+b, and was thus probably 5 yr old. Higher summer temperatures and higher food availability in Wisconsin may shorten the time to maturity as compared to northeastern New York and the High Allegheny Plateau. Fitch (1985) and Fitch et al. (2004) reported females being pregnant at rattle-segment counts of 6+b and total lengths averaging 93 cm at spring emergence, and we estimate that these females were probably 4 yr old at birthing, when they would have had rattle-segment counts of 7+b.

Reproductive Interval

The interval between births by a given female is influenced by the length of the active season, active-season temperatures, and food consumption. The modal interval range apparently varies from 2-5 yr. Captives supplied with abundant food sometimes reproduce during consecutive years (Z. Orr, pers. comm.; c.f. Clark and Antonio, this volume; Taylor and DeNardo, this volume). Back-to-back (annual) reproductive events have not been confirmed in nature, and certainly this frequency is highly unlikely to occur in the northern parts of the range. Even in South Carolina (Gibbons, 1972) and northeastern Florida (Berish, 1998), the proportion of females that are reproductive suggests that 2 yr is the usual inter-birthing interval, whereas sometimes the interval may be even longer. An interval range of 3-5 yr was recorded in southeastern Virginia (Petersen and Savitzky, 2004). A 2-yr interval between births has been recorded in northeastern Kansas (Fitch, 1985) and 2- and 3-yr intervals were recorded in northwestern Illinois (Beilema, 2004). The recorded reproductive interval ranged from 2-5 yr in the northern Blue Ridge of the central Appalachians, where the mode was 3 yr (Martin, 1993). Berg et al. (2005) likewise recorded 2-5 yr intervals in Wisconsin, with a mean of 3.14 yr. In northeastern New York, the usual reproductive interval range was 3-5 yr, with a mode of 4 yr (Brown, 1991), but several 2-yr intervals have been recorded only within the past 5 yr of the 30-yr study at the same site (WSB, unpubl obs.). The longest modal interval (5 yr) was recorded on the High Allegheny Plateau, where only one 3-yr interval, the shortest, was recorded, with the balance of the observed intervals ranging from 4 yr to as long as 7 yr (Martin, 2002).

Survivorship

Annual survivorship is evidently high, ranging from 50-70% for the first year to around 90% for adults (Martin, 2002; Reinert and Rupert, 1999; Brown et al., 2007; Brown, this volume). Fitch (1985) estimated the first-year survival rate at 55% and thereafter at 75% per year in northeastern Kansas. The longer active seasons of the South could be predicted to result in a still lower annual survival rate. The generation time, calculated as the average age of mothers at parturition, has been estimated at 13-18 yr for mountain populations (Martin, 2002, and unpubl. data). Supporting this estimate, we note that some individuals survive into their thirties. A captive survived 36 yr (Cavanaugh, 1994). Age-class distributions suggest some High Allegheny snakes were in their thirties (Martin, 2002), and Brown (this volume) provides direct evidence of similar maximum ages based on recaptures of adults. Fitch and Pisani (2002) recaptured a male almost 24 yr after he was marked as an adult; they estimated the minimum age at 28 yr.

Phenology

The active season—the time period commencing with the beginning of general emergence and ending when most of the population has entered hibernation—varies across the range from 4.6-5.2-months (Brown, 1992; Cochran, this volume) in the northernmost parts of the range to 9-10 months across the southern edge of the range, where individuals are occasionally on the surface during winter. Thus, ingress can range from September to as late as November or early December, and the onset of general emergence ranges from late February to the second week of May. Migration to summer feeding grounds can occur from late March or early April in the South to late May and early June in the North. At least some individuals, however, do not appear to have a summer range that is clearly separated from the overwintering site (Waldron, 2005). Migration toward the overwintering dens can range from late August to early November.

The length of the foraging season ranges from as little as 3-4 months at the high elevations and the more northerly parts of the range to as much as 7-9 months in the more southerly areas. On the High Allegheny Plateau, movement to foraging areas occurred from mid-May to early June, and foraging was not noted later than mid-September (WHM, unpubl. obs.). In the Coastal Plain of South Carolina, Waldron et al. (2006) noted that most foraging was from April-October, with occasional individuals commencing in March or continuing into November.

Gestation centers approximately on the warmest time of the year, and thus occurs over a shorter range of dates geographically than do either emergence or ingress. A short active season with its cooler temperatures lengthening the gestation period might, therefore, favor selection of an early onset to gestation. Where summer temperatures are consistently high (i.e., the southern parts of the range), parturition typically occurs during the last half of August and the first 10 d of September. Farther north and at higher elevations, parturition is delayed because of cooler summer temperatures and greater cloud cover. Across the northern part of the range, most births occur from the very end of August through mid-September (WSB unpubl. obs.; Cochran this volume). The latest parturition dates occur at the higher elevations of the Appalachians, where they typically occur during the middle 2-3 wk of September (Martin, 2002). Births are delayed until late September or early October during some years by poor gestating conditions. At the higher elevations, females sometimes fail to bring the young to term (Martin 2002).

In most areas, newborns and postpartum females typically stay together at the birthing site until the young have completed the postnatal shed (Martin, 1992; Reinert, 2005). The interval between birthing and postnatal shedding varies with the weather and ambient temperatures at the birthing sites. When parturition occurs in August at high temperatures, postnatal shedding typically occurs within 7-10 d. At the higher elevations of the Appalachians, the interval between birth and shedding is usually 2-3 wk (Martin, 2002; WHM, unpubl. obs.), and postnatal shedding can be further delayed when births are late. Females typically stayed with their young only 4-5 d in Wisconsin, and then departed the birth site (Sajdak and Berg, 2005), probably to seek a meal in the short period of time available before hibernation. Preshed young and postpartum females will migrate toward the overwintering dens if cold temperatures arrive before the young have shed; thereafter, the young will continue to bask at the dens in an attempt to shed before hibernation (WHM, unpubl. obs.). The young-of-year snakes are able to trail conspecifics, and not necessarily the mother, to the overwintering dens (Neill, 1948; Brown and MacLean, 1983; Reinert and Zappalorti, 1988; Martin, 2002; Cobb et al., 2005; Reinert, 2005).

The usual mating season is in late summer to early fall (Martin, 1992), beginning with mate searching by the males at or after the mid-point of summer and continuing until near hibernation time. The onset of the mating season from north to south ranges from mid-July to mid August. In New York, mating or heterosexual pairing is reported from mid-July to late September (Aldridge and Brown, 1995; Brown, 1995; McGowan and Madison, this volume), and in Texas from mid-August to late October (Rudolph et al., 1998). Waldron et al. (2006) noted mating from August to October, with a few individuals starting mate-searching as early as late July and with some mating observed to occur into early November. Copulation may begin with shedding by vitellogenic females, as reported by Merrow and Auberton (2005), who observed both inter-male rivalry and courtship that began as soon as a female started to shed, while a second smaller male was chased away by the dominant (mating) male. Males have not been reported copulating with pre-shed females, but they have been observed accompanying and courting pre-shed females (Sealy, 1996; McGowan and Madison, this volume; WHM, unpubl. obs.). Inter-male rivalry (i.e., combat or fighting) may occur before the mid- to late-summer female shedding has occurred (WHM, unpubl. obs.), though its occurrence is rarely observed (McGowan and Madison, this volume). Males are known to make relatively long-distance mate-searching movements during the mating season (McGowan and Madison, this volume; Sealy, 2002), and this may lead to increased mortality by road kills and other encounters with humans (Aldridge and Brown, 1995).

Effects of Weather

The effects of weather are both direct and indirect. Weather undoubtedly affects snakes by influencing plant growth, and thus the snakes' primarily herbivorous prey base. This indirect weather-related effect seems to occur range-wide and may be responsible for the surprisingly long reproductive intervals in areas where the climate appears suitable for more frequent reproduction, as in the southeastern Coastal Plain (Gibbons, 1972; Savitzky and Petersen, 2004). Where the summers are relatively cool, as in the Appalachians and the northern parts of the range, the effects of weather are direct. Migration to feeding grounds, ambush feeding behavior, digestion, assimilation, growth, mating, and gestation are all inhibited by below-average temperatures and by above-average cloud cover that accompanies rainy weather. During years when rainfall is high and temperatures below average, snakes exhibit poor body condition (WHM, unpubl obs.); at such times, little mating activity has been noted. Thus, adverse weather conditions are observed to influence both a given year's reproduction as well as the following year's reproduction. During a year of adverse weather, births are delayed, and parturition often does not take place until near hibernation time. Interestingly, at higher elevations many females fail to bring the young to term when temperatures are well below average (Martin, 2002). At least two females are known to have carried embryos into hibernation and survived, and another was observed to abort in a den crevice (WHM, unpubl. obs.). In some cases, the female herself may be unable to survive such intrauterine holding through the winter. During the year following adverse weather, a population's reproductive output is low. On the other hand, in southern and western regions where summer temperatures are expected to be high, below-average temperatures apparently have little direct effect on growth or reproduction (Beaupre, this volume); in this situation, any impact of weather is indirect and is mediated primarily through the food supply.

Current Status and Threats

Crotalus horridus apparently remains common on public lands through much of the swampy lower southeastern Coastal Plain, the lower Mississippi Embayment and nearby Loess Hills, the Ouachita Mountains, the southern Ozark region, and through the Appalachian Mountains from Alabama to Pennsylvania. Its distribution in the Gulf Coastal Plain and middle and upper parts of the Mississippi Embayment has been adversely affected by agricultural development, roads (Rudolph and Burgdorf, 1997; Rudolph et al., 1998), and silviculture. The range has become highly fragmented along the western edge from north-central Texas to southeastern Nebraska (Fogell and Fawcett, 2005), southern Iowa, and Illinois. The distribution in the western part of the range is associated primarily with lightly wooded stream corridors with rocky bluffs, habitat that never represented more than a small fraction of the snakes' range in the prairie-woodland transition regions. In the upper Mississippi blufflands of the non-glaciated region of northeastern Iowa, extreme northwestern Illinois, western Wisconsin, and southeastern Minnesota, the species was formerly common and dens were large (Schorger, 1967; Oldfield and Keyler, 1989), rivaling those in the Appalachians and the Northeast, whose dens often have been considered to have harbored the largest populations. The range was fairly continuous along streams, but in recent decades has been somewhat fragmented by roads and agricultural development. Years of bounty hunting in the Upper Mississippi Blufflands—only recently ended—have severely reduced most populations, and few have recovered. Likewise, across the Interior Plateau of the middle portions of Tennessee and Kentucky and the southern parts of Illinois and Indiana, the range has been highly fragmented by agricultural development. The Northeast north and east of Pennsylvania historically had a patchy distribution, and the range has become further fragmented. Historically, the dens of the Northeast were large, many were geographically isolated, and consequently most became well known to the local inhabitants. Organized or opportunistic persecution led to the extirpation of the majority of the isolated denning populations in New England and western and central New York. Collecting in the mid-twentieth century, some of it for bounties, was a cause of the depletion of many of the dens in New York and western New England (Brown et al., 1994). Across the greater part of the Piedmont, from Georgia to New Jersey, as well as on the Delmarva Peninsula, agriculture and urbanization have eliminated much of the habitat; rattlesnakes have been completely extirpated from much of this mid-Atlantic region, including all of the Delmarva Peninsula. The rattlesnake populations of the southern New Jersey Pine Barrens survive today, but are under serious development pressure resulting in loss of genetic diversity (Bushar et al., 2005).

Considered on a state by state (and province) basis, we offer an assessment of the current status of *C. horridus* using the following categories and criteria:

Extirpated.—*Crotalus horridus* is believed to be locally extinct within the state (or province) due to human activities. The historical occurrence is well documented for Maine, Ontario, and Rhode Island, but poorly so for Delaware, Michigan, and Quebec. Unsubstantiated reports of rattlesnakes persist in Maine (Hunter et al., 1992) and Rhode Island.

- Delaware
- Maine
- Michigan
- Ontario
- Quebec
- Rhode Island

Critically imperiled.—The following states have fewer than five known *C. horridus* denning colonies:

- Nebraska
- New Hampshire
- Vermont

Imperiled.—Less than 5% of the state is occupied by *C. horridus*, or the range has been reduced to <15% of historical levels.

- Connecticut
- Illinois
- Indiana
- Iowa
- Kansas
- Massachusetts
- Ohio
- Texas

Vulnerable or of restricted range.—*Crotalus horridus* occupies 5-15% of the state, or the range has been reduced to 15-50% of historical levels.

- Maryland
- Minnesota
- New Jersey
- New York
- Wisconsin

Apparently secure.—*Crotalus horridus* is uncommon but not rare. It may be widespread but uncommon, or occupying 5-15% of a state but still common in some areas.

- Florida
- Mississippi
- Missouri
- Oklahoma

Secure.—*Crotalus horridus* is widespread in the state, occupying 15-50% of the state and over 50% of its historic range, and is common in parts.

- Alabama
- Arkansas
- Georgia
- Kentucky
- Louisiana
- North Carolina
- Pennsylvania
- South Carolina
- Tennessee
- Virginia
- West Virginia

The Timber Rattlesnake Conservation Action Plan

In response to the fragmentation of habitat and continuing threats that we have surveyed here, a major national effort, known as the Timber Rattlesnake Conservation Action Plan (TRCAP), was initiated by a team of over 40 concerned rattlesnake biologists from federal, state, university, and private institutions, as well as private citizens. The United States Fish and Wildlife Service has provided leadership and support for this effort, although TRCAP is not officially part of any federal or state agency. The purposes of the plan are: (1) to assess and identify problems confronting *C. horridus*; (2) to identify conservation actions needed; (3) to inform state and federal resource agency decision-makers and land managers; (4) to highlight and focus attention on critical conservation issues; (5) to develop a conservation network of workers on *C. horridus*; and (6) to promote and inspire appropriate management actions. This plan includes components on: (1) biological and ecological characteristics and requirements; (2) range-wide distribution and population status; (3) state accounts, with maps of specific state-level distribution, and summarized regional threats and conservation needs; (4) range-wide threats and conservation needs; and (5) appendices with survey protocols and forest management guidelines. Critical rangewide issues and conservation actions identified thus far for *C. horridus* are the following: (1) long-term habitat protection for major populations for each region; (2) identification and protection of corridors for gene flow within populations and throughout the range; (3) assessments of genetic diversity of isolated populations; (4) management plans that ensure maintenance of viable *C. horridus* populations on public lands; and (5) legal protection at the state level throughout its range.

Crotalus horridus is a highly variable snake morphologically, and it is apparently quite plastic in regards to habitats utilized and adaptive life history traits. Increasing awareness by the public, and legal protection granted in some states, have been helpful in establishing a basic conservation approach to management of this rattlesnake. At the same time, there are increasing threats to the species. For example, the fairly recent conversion of natural forests to pine plantations and the exclusion of fire have been detrimental. Shading-over of basking ledges is a major problem in many parts of the range. Invasion by exotics (including plant pathogens) and climate change present possibly the greatest potential threats to the species (e.g., Brown, this volume). Inadequate range-wide legal protection, and extreme vulnerability due to life history factors, will result in further extirpation of populations of this rattlesnake and a significant reduction of its range. Concerted conservation efforts by state and federal resource agencies, as well as private conservation organizations, and a gradual but noticeable improvement in a conservation ethic by the public, may counteract these dire trends to some extent. We are hopeful about the snake's future, but remain realistic in the face of an unknown coalescence of environmental factors brought on by the pressures on all resources by humankind.

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