BIOLOGY & CONSERVATION *of the* WOOD TURTLE

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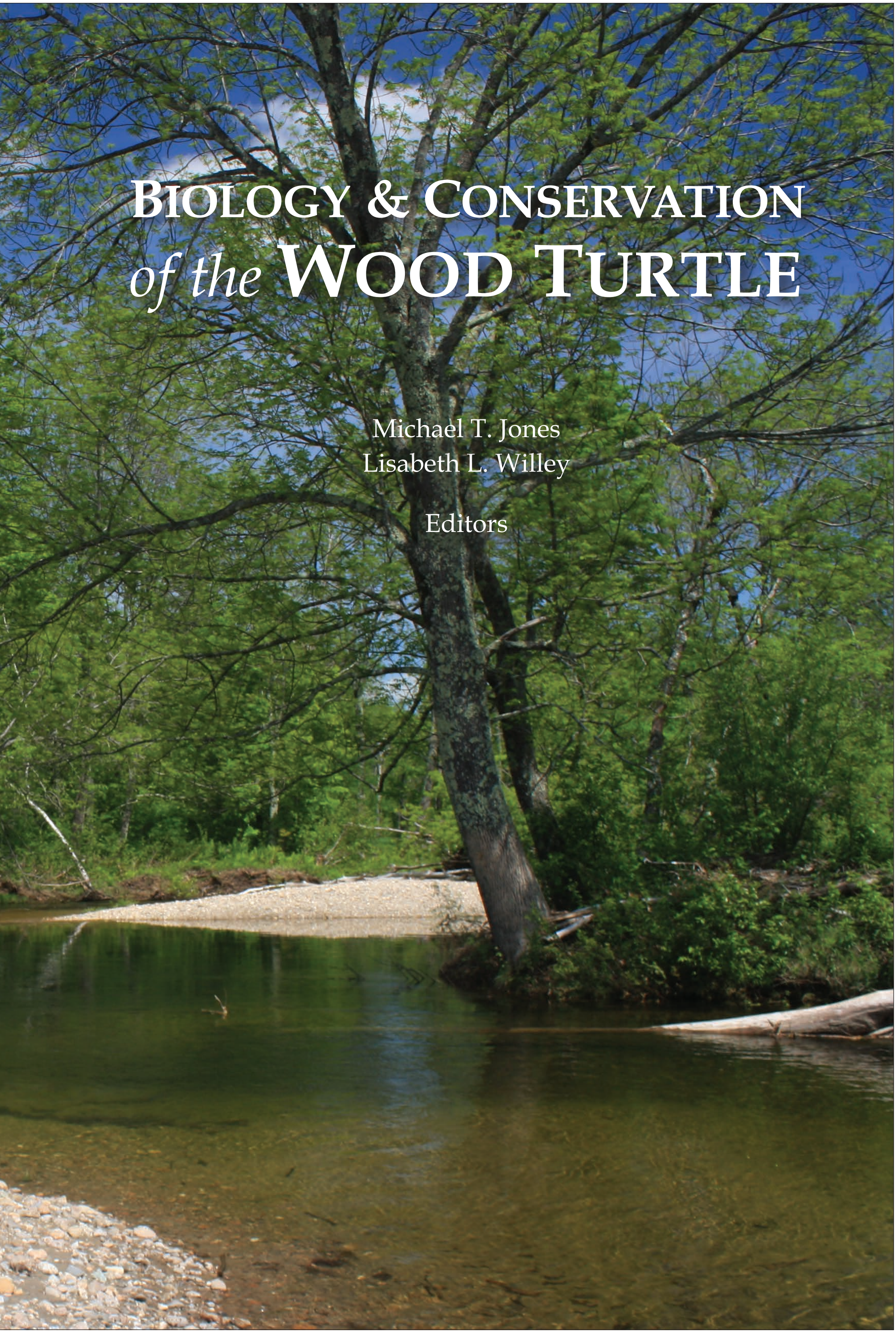

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BIOLOGY & CONSERVATION *of the* WOOD TURTLE

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Biology & Conservation of the Wood Turtle

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Addie, the Labrador, was there for most of our (i.e., the editors') Wood Turtle field surveys from 2005 to 2019, and now her absence on long field days is palpable. The editors also wish to thank their parents, Betty and Tom and Lloyd and Lynn, for tolerating and supporting this endless interest—and their sons, Everett and Lewis.

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Preface

I first encountered Wood Turtles while I was on a canoe trip in northern New England at age 12. They were colorful and aware, basking on gigantic logjams, out of place along the cold brown river. Likewise, their riparian habitats—sun-dappled, bright, green, breezy—stood out in contrast to the dark coniferous forests. In the three decades since those initial encounters, I've been fortunate to cross paths with wild Wood Turtles on roughly 11,000 occasions, often with biologists, managers, and experts who understand the species from years of direct observation in the wild, and whose dedication to Wood Turtle conservation is impressive and inspiring. Along this journey I've been fortunate to study Wood Turtles in a range of environmental contexts, including heavily developed areas—where Wood Turtles often occur at critically low numbers—as well as in agri-forest mosaics typical of many sites from New England to Virginia, and in the braided channels of enormous wild rivers.

Wood Turtles themselves are an accessible focal point through which to reflect upon slow processes and long timeframes, providing insight into evolution, biogeography, phylogenetics, Quaternary science, and physical geography. This unassuming turtle lineage has persisted through millions of years of chaotic upheaval, migrating repeatedly across 15° of latitude (at least) in response to the glacial advances of the Pleistocene epoch, and weathering the collapse of the North American mammalian megafauna (with which Wood Turtles shared the eastern floodplains for several million years, at least). Moreover, the places where Wood Turtles thrive today can (collectively) serve as a valuable lens on the ecological patterns of eastern North America. Studying Wood Turtle populations offers a means by which to evaluate and measure the health of river ecosystems, but correspondingly, often serves as a warning due to the diminishing acreage and degraded condition of remaining habitats.

The Wood Turtle makes for an interesting subject in conservation biology, in part, because of its long lifespan and low dispersal capability: individual Wood Turtles may reside for many decades of their (potentially) long lives within relatively small sections of a single river. They are also uniquely amphibious (thriving both on land and in water): unlike solely aquatic or terrestrial species, the distribution of Wood Turtles is governed both by stream characteristics and upland habitat. Where there are large populations of Wood Turtles, the natural dynamism of the river remains mostly intact, sufficiently so to retain the deep holes, logjams, and sandy banks necessary to sustain the population. Rivers themselves are often an intrinsically useful lens on a natural landscape: in places cutting their way through bedrock, and elsewhere arranging new deposits of sediment. Populations of Wood Turtles thriving naturally represent a snapshot in the long narrative of turtle evolution, and the cool creeks they inhabit tell a similarly complex story of landscape evolution.

Biology and Conservation of the Wood Turtle is a book about Wood Turtles, but also a book about the eastern North American landscape, adaptation and evolution at many timescales, and a challenging evolutionary outlook. This book is based on the premise that this species needs a certain type of functional landscape for multiple generations to survive in the wild, and that worthy goal is still within reach.

The Wood Turtle will probably weather on (as a species) for decades yet. It has survived hazardous and chaotic environmental changes in its recent evolutionary history. But whether it will persist for any length of time that is evolutionarily significant is less clear. It's conceivable that the species has been dealt such a staggering blow it may not regain its post-Pleistocene momentum. We need more wild streams, more forestland, cleaner rivers, fewer miles of roads. We need all of these things and if we achieve this across representative portions of the species' range, the Wood Turtle will gradually recover. However, I remain uneasy because many of the places Wood Turtles seem to do well at present are conserved accidentally—places that simply have been overlooked for some long period of time. It's challenging to design a conservation reserve for Wood Turtles because illegal collectors, development, and recreation can so easily affect them.

This book has several purposes. First and most obvious, I hope, is to provide a summary account of the ecology of the Wood Turtle, drawing upon the experience and ideas of some of the people who know the species very well, and to provide recommendations for its management, conservation, and restoration. We also attempt to frame the Wood Turtle firmly within an evolutionary-ecological context: what trajectory brought the species to its current distribution, from Nova Scotia to the edge of the Prairie and across the southern footprint of the Laurentide Ice? Further—where possible—we try to focus on the intrinsic landscape processes that facilitate the Wood Turtle's persistence today. And lastly, throughout the text, we try to bear in mind the Wood Turtle's evolutionary trajectory forward from this point in time.

Thank you for your interest in this book, and for the part that you will play in the recovery of the Wood Turtle.

Mike Jones
Natural Heritage and Endangered Species Program
Massachusetts Division of Fisheries and Wildlife
May 9, 2021

1. Introduction

Michael T. Jones, Raymond A. Saumure,
Lisabeth L. Willey, H. Patrick Roberts

Adult male Wood Turtle, Maine. Mike Jones

1.1—Wood Turtle populations throughout the range of the species have been negatively influenced by habitat fragmentation and habitat loss. Most of the large, demographically robust, and stable populations are associated with streams in areas that have not been fragmented. American Turtle Observatory

Conservation Context

The Wood Turtle (*Glyptemys insculpta*) has experienced dramatic population declines as a result of habitat loss, road mortality, detrimental anthropogenic land-use practices, and numerous other factors over the past century. Agriculture, textiles, industry, deforestation, and habitat fragmentation have degraded many of the major streams that formerly supported large Wood Turtle populations. The remaining, viable populations of Wood Turtles are mostly found in areas with relatively little development or fragmentation (1.1).[1] In this chapter, we provide a broad overview of the ecology of the Wood Turtle, introducing material that is covered in more detail in later chapters, and we provide a detailed and illustrated overview of the species' appearance.

Wood Turtle populations are typically associated with sections of clear, cold, medium-sized streams and rivers, often situated within a mosaic of mature forest and early-successional habitats (Saumure 2004; Akre and Ernst 2006; Ernst and Lovich 2009; Jones and Sievert 2009a) (1.2).[2] These streams are generally characterized by sand, gravel, cobble, and/or bedrock substrates and significant accumulations of within-stream woody structure such as fallen trees, branches, and root-masses that play a critical role in providing overwintering sites, basking areas, cover, and stability during periods of elevated flows. Although single individuals and small populations may

1 A comprehensive account of the species' distribution is provided in Chapter 4.

2 More detailed descriptions of the species' habitat preferences, common ecological associates, and noteworthy associated taxa are provided in Chapter 5.

1.2—Wood Turtle populations are generally associated with clear, cold, medium-sized streams and rivers within a mosaic of forested and nonforested floodplain and riparian habitats. Streams are often characterized by inorganic substrates and low to moderate stream gradient. Typical habitat in the Lake Huron watershed of southwestern Ontario, Canada is pictured. Joe Crowley

1.3—Although they are fluvial (stream and river) specialists throughout their range, Wood Turtles range extensively in floodplain and upland habitats through most of the warmer months. Floodplain habitat dominated by Silver Maple (*Acer saccharinum*) and Ostrich Fern (*Matteuccia struthiopteris*) in New Hampshire is pictured. Mike Jones

be found with regularity throughout the species' range, it is clear that robust, demographically stable populations are generally found within landscapes and stream systems that sustain dynamic fluvial, geomorphic, and biological disturbance processes. Examples include: (1) seasonal flooding, (2) meandering stream channels, and/or (3) periodic Beaver (*Castor canadensis*) activity. Each of these features allows for frequent deposition of nesting material and maintenance of ephemeral early-successional habitats.

1.4—In many areas, Wood Turtles are limited by the availability of high-quality nesting habitat, which often consists of well-drained sand, gravel, sandy loam, or alluvium. These areas may occur along the bends of larger rivers, as pictured here in southern Wisconsin. Andrew Badje

Although Wood Turtles require streams for overwintering and mating, they also rely upon adjacent terrestrial habitats. They spend much of the warm months of late spring to early fall in the surrounding landscape, sometimes hundreds of meters from their overwintering stream (1.3). Terrestrial habitat preferences vary by geographic region and season, but Wood Turtles will typically occupy a mosaic of habitats including mature forest and early-successional cover types. Ecotones[3] and "edge habitats" serve an important function for Wood Turtles by providing opportunities to balance both thermoregulation and food requirements. Ephemeral pools (especially within river floodplains) and temporary wetlands appear to serve as complementary habitat, but generally do not support overwintering activity.

Prime nesting areas consist of well-drained, elevated, and exposed alluvium, poorly graded sand, fine to medium gravel, or sandy loam, and the availability of such locations limits the Wood Turtles' available habitat (1.4). These areas may be associated with a wide range of natural and anthropogenic settings. Natural nesting areas include sandy point bars on the inside of river bends, cutbanks on the outside of river bends, sand and gravel bar deposits in the stream channel (associated with stream obstructions, constrictions, or directional changes in flow), areas of overwashed sand in open floodplains, and dry stream beds. Anthropogenic nesting features include sand and gravel pits, gravel boat ramps, exposed areas along power line/pipeline corridors and rights-of-way, roadsides, unpaved farm roads near streams, railroad beds, gravel piles in waste areas such as junkyards, golf course sand traps, and nesting areas created specifically for turtles.

Individual movement patterns among Wood Turtle populations vary. In some streams, especially where winter ice cover is low or nonexistent, Wood Turtles may be detected year-round even where activity may be minimal in mid-winter. Broad characterizations of movement and space-use are valuable when contextualizing many of the challenges associated with Wood

3 Ecotones are transitional zones between distinct, adjacent habitats, such as the transitional area between a hayfield and a floodplain forest.

1.5—In much of their range, Wood Turtles overwinter or brumate underwater in streams or associated floodplain channels and oxbows during the coldest months of the year, which may extend from November to April. In Massachusetts (pictured), Wood Turtles may overwinter in deep pools associated with bends in the river (left), or in the roots of large trees such as this Eastern Hemlock (*Tsuga canadensis*) (right). Mike Jones

Turtle conservation.[4] Wood Turtles' "active period" varies with latitude and elevation (i.e., Wood Turtles are generally active for longer periods in warmer regions), but generally spans from April to October in northern or high-elevation areas, and from March to November in more moderate areas. Wood Turtle activity can be subdivided into at least five distinct periods: (1) emergence and pre-nesting, (2) nesting, (3) post-nesting, (4) pre-brumation, and (5) brumation.

Wood Turtles then retreat to streams and settle into overwintering locations within the stream channel (1.5). The overwintering period occurs during the coldest months of the year from November or December to March or April. Wood Turtles remain largely immobile while overwintering, but may make occasional small underwater movements.

Similar to related turtle species, Wood Turtles display delayed sexual maturity and small clutch sizes. In addition, Wood Turtle populations typically suffer high nest predation and juvenile mortality rates even without the presence of anthropogenic pressures. These factors are only offset by their longevity (>70 years in the wild), high adult survival rates, and continued reproduction into old age. In fact, Wood Turtle generation time may exceed 45 years. It is clear from studies of related species with similar life history characteristics that even small increases in the adult mortality rate can lead to steady population decline and local extirpation. Their precarious balance of life history traits—which require adult turtles to have high annual survivorship—coupled with the Wood Turtle's highly terrestrial nature, has made the species particularly susceptible to the broad array of anthropogenic threats affecting streams throughout its range in the United States and Canada.

4 A detailed description of Wood Turtles' spatial ecology is provided in Chapter 6.

1.6—Adult Wood Turtles are medium-sized emydid turtles. The carapace is usually brownish, broad, flat, ovate, and lightly to strongly keeled with a heavily "sculpted" or "engraved" appearance. A typical adult female from western Lake Superior is pictured. Mike Jones

Individual Wood Turtles face numerous threats directly or indirectly associated with anthropogenic development. Habitat loss, fragmentation, and degradation due to development, road mortality, and human land use (e.g., agriculture) are widely considered the primary causes of population declines throughout the range.[5] However, Wood Turtles are also vulnerable to incidental and commercial collection for pet markets, pathogens, human-subsidized predators, pollution, stream bank stabilization, and loss of functional nesting areas from invasive plant species. These factors, which affect Wood Turtle populations in varying combinations and degrees of severity, contribute to the overall decline experienced by the Wood Turtle throughout the global species range.

As a result of perceived rarity, documented population declines, and localized extirpations, agencies and organizations throughout the species' range have listed the Wood Turtle as endangered or threatened. Current levels of protection—and the tools available to the partners working for its long-term conservation—are clearly inadequate for the long-term preservation of the Wood Turtle's evolutionary potential. Meaningful conservation of this elegant and distinctive creature will require a renewed commitment to land conservation at large spatial scales, creative and careful stream restoration efforts, and attention to the unfolding climate crisis.[6]

Appearance

The Wood Turtle is a medium-sized turtle with a broad, flat, ovate, lightly to strongly keeled, brownish carapace (1.6). The carapace may be solid in color or have radiating or reticulated yellow marks or spots, with or without a sculpted or engraved appearance (Surface 1908; Logier 1939;

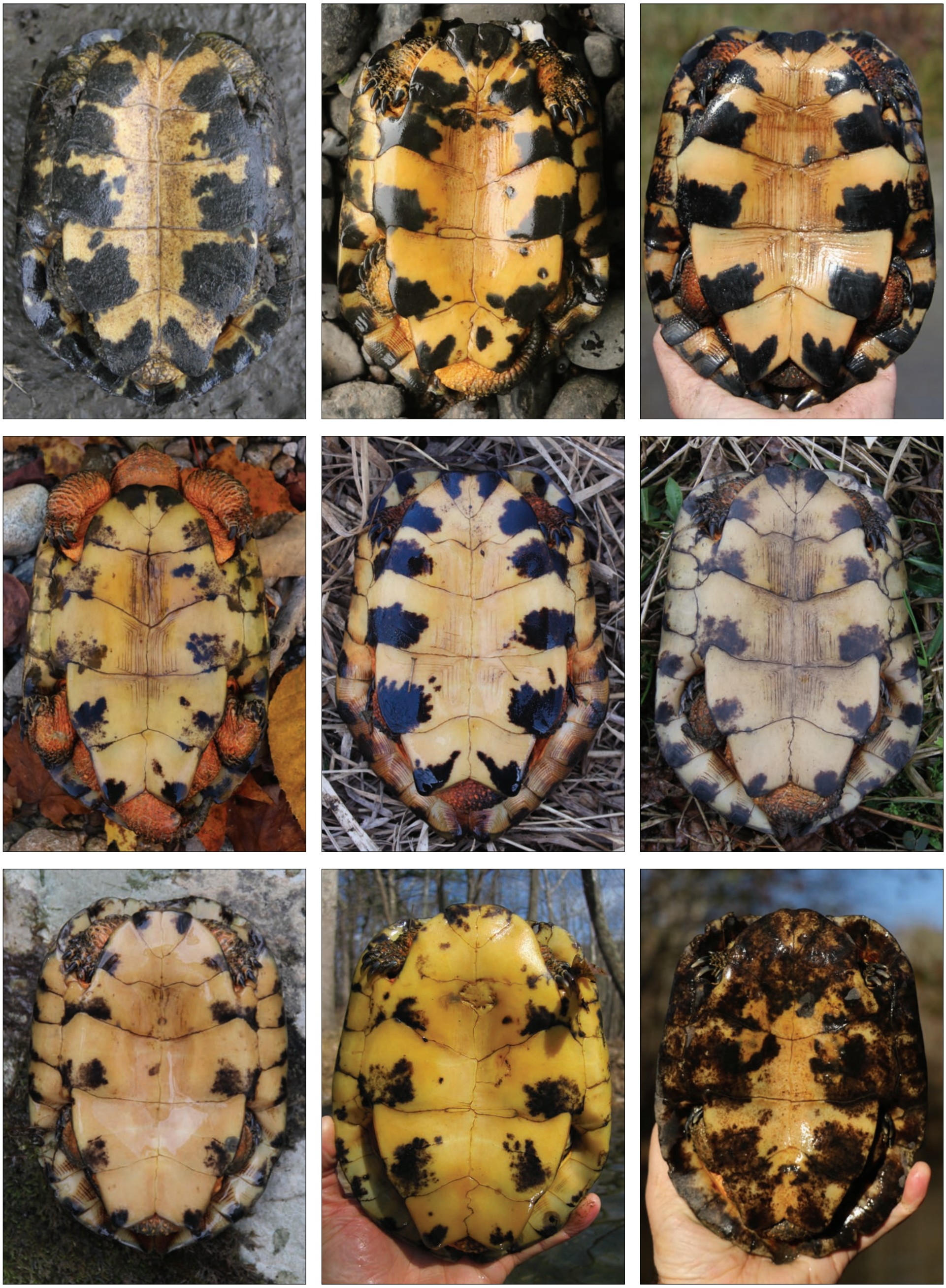
5 The threats influencing Wood Turtle populations are enumerated and described in Chapter 8.

6 Restoration opportunities for Wood Turtle populations are discussed in Chapter 9.

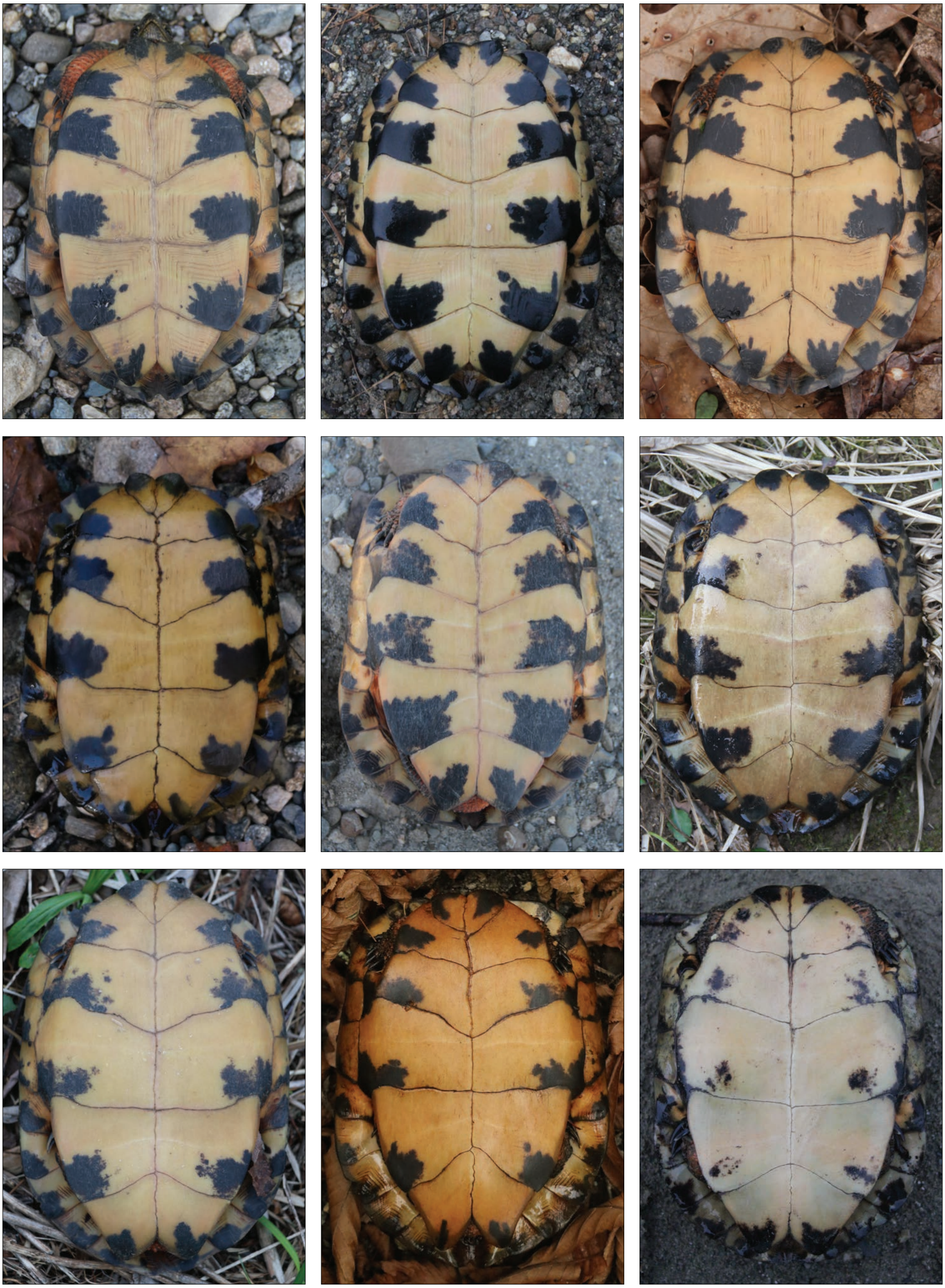
1.7—The Wood Turtle's carapace, while usually brownish, can be highly variable in coloration based on the turtle's age and environment, the season, and whether the animal is wet or dry. Adult male Wood Turtles are pictured from across the range.

1.8—In some adult male Wood Turtles, the posterior margin of the carapace may be strongly flared. An adult male from Vermont is pictured. Mike Jones

1.9—The scutes of the carapace gradually become worn smooth, and the annuli become less distinct in older adult Wood Turtles. The carapace generally takes longer to become completely worn than the plastron. *Top*: females from New York. *Bottom:* females from Maine. Mike Jones



1.10—The Wood Turtle's plastron is usually yellowish-cream or horn-colored, with prominent blackish pigmentation blotches. Adult male Wood Turtles are pictured from across the range.



1.11—The pigment blotches on the Wood Turtle's plastron diminish with age in some populations. Progressive plastral pigment loss is pictured in female Wood Turtles from across the Northeastern United States.

Ernst and Lovich 2009).[7] Carapace scutes typically number 38 following the pattern of most living emydid turtles (Holbrook 1838, 1842; Storer 1840): twelve marginal and four pleural scutes on both sides; five vertebral scutes; a single, narrow nuchal scute. The color of the carapace may be brown, reddish brown, tan, grey, or black in adults (Surface 1908; Ernst and Lovich 2009), with or without radiating or reticulated yellow-gold and blackish markings, and with or without radiating striae (Le Conte 1830; Storer 1840) (1.7). The scutes of the carapace accumulate growth rings in the outer layers of keratin; these may contribute to a sculptured or pyramidal appearance in young adult turtles, but are not strongly reflected in the underlying bone (Phillips 2006).[8] The posterior margins of the carapace are serrated (Vogt 1981), and sometimes strongly flared (Surface 1908), especially in males (1.8). The scutes of the carapace become worn and smooth in older adults (Le Conte 1830; Gray 1831; Jones 2009) (1.9).

The plastron is yellowish-cream or horn-colored, deeply notched posteriorly, with prominent blackish pigmentation located posteriolaterally on each plastral scute (Surface 1908; Vogt 1981) (1.10). Similar black blotches are found on the ventral surface of the marginal scutes (Holbrook 1838; Babcock 1919; Ernst and Lovich 2009). The pigment of the plastral scutes is lost with age (Jones 2009) (1.11). Like the carapace, the plastron accumulates growth rings visible in the outer layers of keratin. Older rings accumulate along the medial and cranial edges of each plastral scute. In younger turtles, areas of new growth on the plastron are evident as lighter-colored annuli along the ventral midline (1.12). Individual turtles may be stained by tannins or iron oxide and thus appear to have a reddish-brown coloration; this condition may affect entire populations or only certain individuals within a population based on individual habitat use. Wood Turtles may also experience discoloration from silt or algae deposited during the winter (1.13).

The head, outer surfaces of the forelimbs, and tail of Wood Turtles are typically black. Both males and females often exhibit bright orange to red neck, forelimbs, and hind feet (Ernst 1972; Ernst and Lovich 2009), while some populations may be dull yellowish. Specifically, Wood Turtles from the Great Lakes region have light yellow or yellow-orange limbs and neck; more reddish-orange tones are native to the Appalachian region (Harding and Bloomer 1979; Ernst and Lovich 2009) (1.14). The nape of the neck and throat may be dark gray, and the throat may be adorned with yellow in young individuals. Skin coloration reportedly varies in intensity seasonally or geographically (Harding and Bloomer 1979) and by sex (Ernst and Lovich 2009).

The upper jaw is strongly hooked and notched at the tip, and the lower jaw is similarly hooked upward. Mottled lines of black, white, blue, and yellow may be present on keratinized surfaces of

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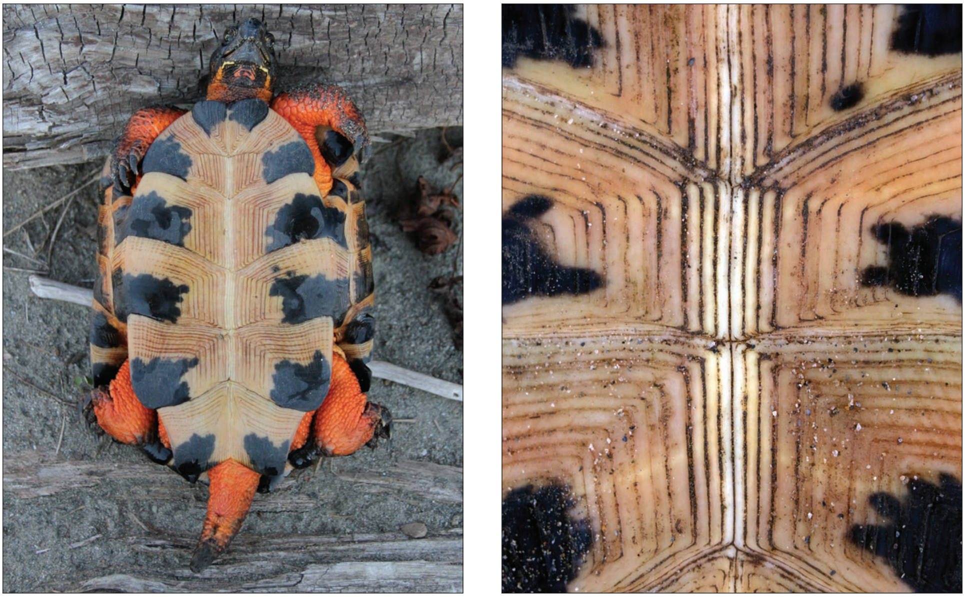
7 John Eatton Le Conte (1830), John Edward Gray (1831), and John Edwards Holbrook (1838) provided most of the defining characteristics of the Wood Turtle during the decade of its initial description. A full account of the Wood Turtle's description and historical biology are provided in Chapter 3.

8 Phillips (2006) provides a uniquely detailed anatomical review of Wood Turtle skeletal remains in the context of paleontological research in Mississippi. On this point, he says: "Individual scutes in [the Wood Turtle] represent a multilayered composite of annually deposited scutes, each new scute attached to the bottom and larger than that of the preceding year's scute. A Wood Turtle scute, or scute growth complex, overlies a less interesting and more subdued corresponding bony substrate, delimited by seam lines, upon which the scute grows. The growth of the Wood Turtle's pyramidal scutes produces an interesting surface texture in which each scute possesses a pattern of regularly spaced radiating ridges. These ridges are combined with and intersect a pattern of equally spaced concentric ridges, the two together producing a peculiar texture on the scute pyramid that is not realized in the underlying, almost featureless bone."



1.12—New growth is evident in younger Wood Turtles as a lighter-colored segment along the midline (medial) and anterior portion of each plastral scute. When observed in the spring, the whitish area of growth closest to the plastral midline represents the previous year's growth. As measurable growth ceases with the onset of maturity, the lighter areas take on the more typical yellowish coloration. Young Wood Turtles from Maine are pictured. Mike Jones

1.13—Tannins, silt, and algae cause temporary discoloration in some Wood Turtle populations. *Top left:* Tannin-stained adult male from New Hampshire. Mike Jones. *Top right:* Tannin-stained adult male from Wisconsin. Andrew Badje. *Bottom right:* Algae-covered adult female Wood Turtle from Massachusetts. Mike Jones. *Bottom left:* Silt-covered adult female from Ontario, Canada. Joe Crowley.

1.14—Wood Turtles from the western Great Lakes region have light yellowish skin. Wood Turtles from the Appalachian regions have a more reddish- or orange-colored skin. Pictured are a female from western Lake Superior (*top*), and a female from northern New England (*bottom*, eating an earthworm). Mike Jones

the beak. Some adults of both sexes possess a prominent golden ring in the iris, the function of which is unknown (1.15).

Size and Sexual Dimorphism

Male Wood Turtles are larger than females in most living populations (Table 1.1). Female Wood Turtles are typically 170–200 mm minimum straight-carapace length (SCLmin); and males typically range from 180–215 mm SCLmin. Lovich et al. (1990) reported that males are

1.15—Some adult Wood Turtles have a prominent golden iris. The trait seems to be more common in adult males and may be progressive with age, although it is sometimes present in females and younger turtles. An adult male Wood Turtle from New England is pictured. Mike Jones

Table 1.1—Wood Turtle morphometric data summarized from across the species' range, with standard errors. Where provided, the number in parentheses indicates the number of turtles weighed.

State/	Females			Males			
Province	SCLmin (mm)	Mass (g)	*n*	SCLmin (mm)	Mass (g)	*n*	Source
QC	201.1±10.9	1083±168	83	214.5±4.2	1173±252	55	Walde et al. (2003)
QC	181.0±5.5	881.7±92.91	12	193.9±9.0	1008±147	15	Saumure and Bider (1998)
QC	200.5±11.6	1061±127	10	215.6±22.3	1219±361	9	Saumure and Bider (1998)
ON	195±5	1099±127	21(18)	205±19	1152±238	15(13)	Greaves and Litzgus (2009)
MI	182	-	105	200	-	86	Harding and Bloomer (1979)
ME	189.1±8.5	1060±145	69	207.2±10.6	1231±156	60	Jones and Willey (2013b)
ME	181.1±7.5	1006±100	102	196.2±8.1	1114±119.2	51	Jones and Willey (2013b)
ME	193.7±10.3	1121±174	23(29)	201±13.2	1210±179	9(11)	Compton (unpubl. data)
NH	184.3±8.6	973±126	37	200.4±10.1	1116±150	28	Jones and Willey (2013a)
NH	174.8±9.9	865.9±111	66	189.3±8.9	973±133	54	Jones and Willey (2013a)
MA	171.8±7.7	875±121	83(12)	182±7.6	872±121	83(15)	Jones et al., unpubl. data
MA	170.9±7.0	830±37	37(14)	184.4±7.5	889±102	42(16)	Jones et al., unpubl. data
MA	176.8±10.4	911±160	9(8)	185.4±6.3	939±91	18(16)	Jones et al., unpubl. data
MA	172±7.6	854±96	64(19)	186±9.6	887±120	49(2)	Jones et al., unpubl. data
NJ	165	-	464	178	-	311	Harding and Bloomer (1979)
NJ	170.9±9.3	-	49	177.0±8.9	-	69	Farrell and Graham (1991)
VA	185±9.5	-	78	195±12.5	-	43	Akre (2002)
WV	179±9.6	846.7±174	15	190.6±12.2	932±178	16	Breisch (2006)

approximately 1.07 to 1.1 times larger than females. Agri-forest and forest populations in Québec both had males 1.07 times that of females in the respective populations (Saumure and Bider 1998). Our unpublished data from Maine, New Hampshire, and Massachusetts correspond with this estimate (1.1, 1.08, and 1.06, respectively; Jones and Willey 2013a and 2013b). Jones et al. (2019) presented limited evidence that male-biased dimorphism may be plastic, based on a review of specimens from the 1850s. Jones et al. (2019) also presented evidence of smaller mean carapace lengths in the 1850s based on a single site in Massachusetts.

1.16—The largest documented Wood Turtles have usually been reported from the northern range-margin. The largest Wood Turtle currently on record, a young male from Maine, is pictured. Mike Jones

Wood Turtle shell dimensions generally increase with northerly latitude. The largest Wood Turtles, on average, are associated with the northernmost populations in Québec. The smallest average Wood Turtles have been reported in New Jersey. Mean body size of Virginia and West Virginia specimens reported by Akre (2002) and Breisch (2006) and the Brome County, Québec population studied by Saumure and Bider (1998) represent notable deviations

1.17—Male Wood Turtles are larger than females, with a concave plastron and a longer, heavier, thicker tail. In the comparison above, the female is on the left and the male is on the right. Adult Wood Turtles are pictured from New England. Mike Jones from an otherwise clear trend. The unexpectedly small body size reported in the Brome County population is perhaps a result of the energy required to heal shell injuries from agricultural machinery (Saumure and Bider 1998; Saumure et al. 2007).

Exceptionally large Wood Turtles may exceed maximum carapace lengths of 250 mm, and are found primarily in the northern portion of the species' range. Jones and Compton (2010) reported an unusually large, 25-year-old male Wood Turtle (SCLmin=240 mm; mass=1895 g) from northwestern Maine (1.16). Subsequently the largest turtle of 1,763 Wood Turtles measured in New England from 2004–2019 by Jones and Willey (unpubl. data) was another Maine male with SCLmin=232.5 mm and mass of 1,340 g. Saumure (1992) presented evidence of two very large male Wood Turtles (SCL=238 mm and SCL=234.5 mm) from Pontiac County, Québec. The latter Québec specimen is equal to the largest *G. insculpta* reported by Conant and Collins (1991). This same Québec forest population had the largest adult female recorded (SCL=227.45 and mass of 1,450g), captured still gravid on a nesting site (Saumure, unpubl. data). Other large females (SCL=225 mm) have been encountered at the northernmost limits of the species' range in Ontario and Québec, Canada (Brooks et al. 1992; Walde et al. 2003). Another large female specimen of unknown origin was recovered during a confiscation event (SCLmin=225 mm) (Northeast Wood Turtle Working Group, unpubl. data).

Adult male Wood Turtles have long, thick tails with the cloacal vent equal to or posterior to the carapace rim (Oliver 1955) and a strongly concave plastron (1.17). Males also have heavier scales on the forelimbs (1.18). Males' heads are absolutely and relatively larger than those of adult females (Akre 2002). Ernst and Lovich (2009) reported that some older males have carapace indentations at the bridge.

Technical Descriptions

Ernst (1972) provided additional references for technical descriptions of the skull, shell, seam contacts, cervical vertebrae, nasal choanae, arterial canals of the ear, and penis (Parker 1901;

1.18—Male Wood Turtles have larger heads than females and heavier scales on the forelimbs. An adult male from New England is pictured. Mike Jones

1.19—Wood Turtle hatchlings are usually gray-brown, with a mottled grayish or slightly peach-colored plastron. Hatchlings are pictured from across New England. Mike Jones & Derek Yorks

Zangerl 1939; Williams 1950; Romer 1956; Parsons 1960; McDowell 1961; Tinkle 1962; Zug 1966; Parson 1968). Phillips (2006) provided a comparative discussion of ancient Wood Turtle skeletal remains from Mississippi. Holman and Fritz (2001) provided detailed shell diagrams.

Hatchlings

Hatchlings are generally uniform gray-brown, with a mottled grayish plastron and no carapace keel (Vogt 1981) (1.19). Hatchlings are typically between 30.4 and 39.5 mm in straight-carapace length and between 6.7 and 12.3 g in mass (Ernst and Lovich 2009; Dragon 2014). Adult skin coloration is usually evident by the second or third year in the wild.

Summary

At this moment in their evolutionary arc, Wood Turtles are a species of wild rivers; seemingly perfectly adapted to the seasonal disturbance regimes of mid-sized streams. Viable, connected, persistent, and resilient populations occur most often in relatively remote areas where key features—such as nesting areas and overwintering sites—occur near one another. The Wood Turtle's long lifespan means that the species may be detected long after the population has ceased normal function. This phenomenon likely hinders long-range conservation efforts—especially those that are of consequence on evolutionary timescales—by redirecting resources to severely impaired sites. These and many other aspects of Wood Turtle natural history and habitat requirements are discussed in later chapters, but the persistence of representative populations of Wood Turtles on the North American landscape—for periods of time beyond what can be easily modeled or imagined—will require adequate preservation of high-quality, remote river and stream environments with minimal human disturbance.

In these streams, Wood Turtles can be remarkably variable in appearance, sometimes imbued with tannins or covered in silt or algae. The Wood Turtle's attractive appearance may be part of their ongoing downfall, as dedicated collectors target an ever-expanding network of sites, undermining well-meaning conservation efforts.

2. Evolution

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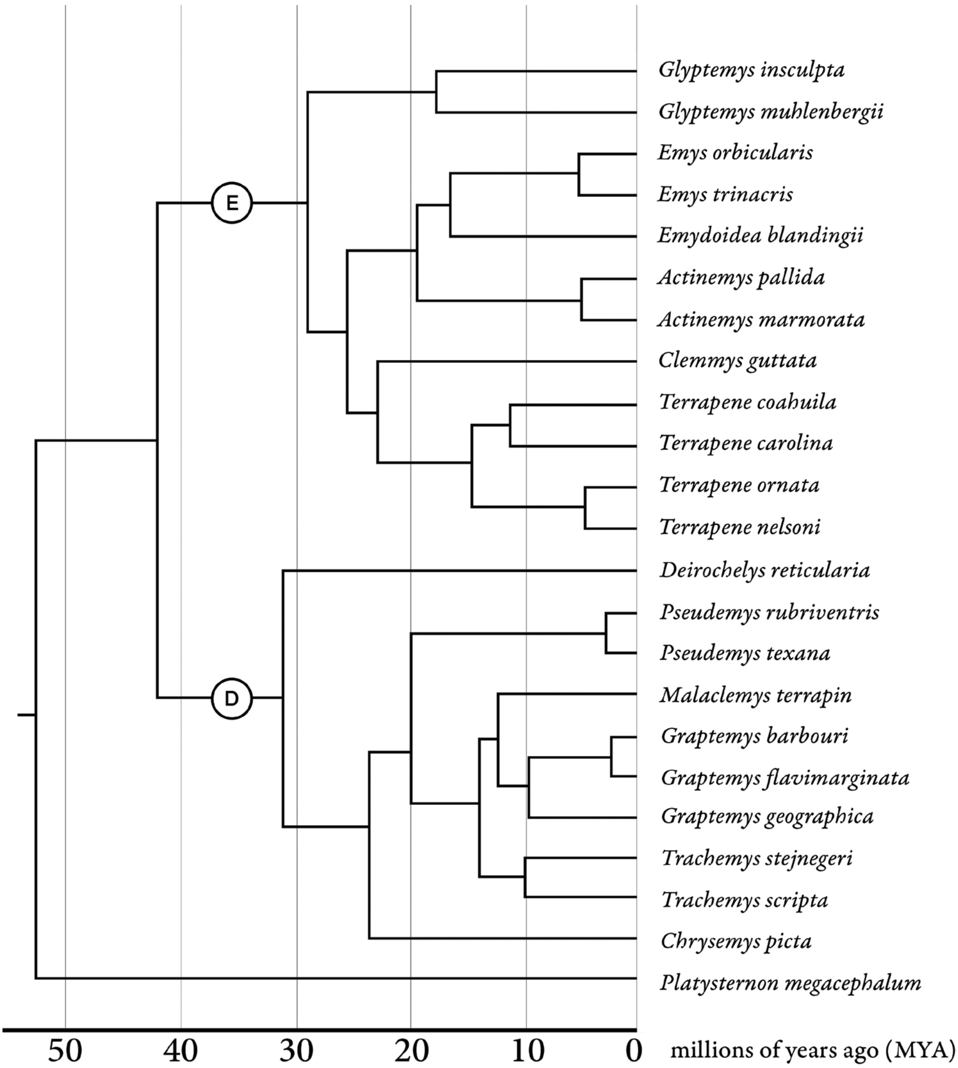
Juvenile Wood Turtle, Massachusetts. Mike Jones

Introduction

The Wood Turtle, *Glyptemys insculpta*, has arrived at a turning point in its evolutionary history, having never previously encountered the suite of environmental challenges that it is currently experiencing. These anthropogenic challenges include: (1) rapid habitat destruction and fragmentation; (2) increased mesopredator abundance; (3) rapidly-changing precipitation and flooding patterns; and (4) decades of intense collection for the biological supply and pet trades. Natural selection—and millions of years of adaptation—have resulted in a species that requires large tracts of unfragmented, variable (yet specific) habitat with naturally low predator density, and high adult annual survivorship rates (Compton et al. 2002; Lapin et al. 2019). Within this adaptive context, the Wood Turtle has evolved a unique suite of survival adaptations. If we are to preserve the evolutionary potential of the Wood Turtle—or, at a pitiable minimum, prevent this species from joining the list of turtles that will disappear during the anthropogenic sixth mass extinction (Barnosky et al. 2011; Ceballos et al. 2015)—we must continue to investigate the species' evolutionary context, while reducing the negative influence of human activity on Wood Turtle populations across its range.

Despite evolving and surviving for millions of years in the presence of procyonines (raccoons), mustelids (e.g., weasels, skunks, otters), and other mesopredators, Wood Turtle populations have likely not encountered mesopredator densities of the current magnitude in the past (Zeveloff 2002; Harding 2008). The assortment of predator defenses that *G. insculpta* has evolved include: (1) morphological features (strong shell, thickened scales on the forelimbs); (2) behavioral responses (head retraction, strong home site fidelity, limited homing ability, responsiveness to river dynamics); and (3) environmental (cryptic basking in dense vegetative cover, hiding in forms and under flood debris in terrestrial habitats, utilizing aquatic habitats, and avoiding exposure to terrestrial predators when there is little thermal benefit to aerial exposure). These adaptations may not be as effective against narrow-snouted mesopredators—which can penetrate a hingeless shell—as they were against larger predators (e.g., canids) that formerly regulated mesopredator populations and kept their densities in check (Harding 2008). Perhaps more importantly, the Wood Turtle's unique evolutionary adaptations do not provide adequate protection from machinery (e.g., Saumure and Bider 1998; Saumure et al. 2007) and people (e.g., Garber and Burger 1995).

The earliest members of the genus *Glyptemys* evolved from an emydine ancestor during the Miocene Epoch (Holman and Fritz 2001; Montiel et al. 2016). Already by that point, the emydine lineage of Wood, Bog, Box, Blanding's, and Spotted Turtles had differentiated from its sister lineage, the Deirochelyinae. The Wood Turtle itself had differentiated well before the ice ages of the Pleistocene epoch, and during the post-glacial Holocene epoch, has maintained a distribution at middle latitudes in eastern North America (Ernst and Lovich 2009). This species has survived numerous climate cycles in its evolutionary past, ice ages and intervening warming periods, new assemblages of competitors and predators, and has responded to the changes associated with the advance and retreat of continental ice sheets by altering its range (Holman 1967; Parmalee and Klippel 1981; Tessier et al. 2005; Amato et al 2007). The Wood Turtle, or its direct ancestors, evolved sex chromosomes during a prior period of global warming; thus, effectively decoupling changes in environmental temperature from population sex ratios (Valenzuela and Adams 2011; Montiel et al. 2016; Literman et al. 2017), differentiating this species from most other living turtles.



2.1—The freshwater turtle family Emydidae—the Pond Turtles—is comprised of two major lineages that likely diverged in the Eocene epoch and diversified throughout the Oligocene and Miocene epochs: subfamily Deirochelyinae, which includes the aquatic genera *Chrysemys, Pseudemys, Graptemys, Malaclemys, Trachemys,* and *Deirochelys*, and the subfamily Emydinae, which includes the semi-aquatic and terrestrial genera *Clemmys, Terrapene, Emydoidea, Emys, Actinemys,* and *Glyptemys*. The two subfamilies are denoted on the tree with a "D" and "E" symbol, respectively. Wood Turtles (*Glyptenys insculpta*) are placed within the subfamily Emydinae on the basis of morphological and molecular characters. According to the most current and most comprehensive evaluation (Spinks et al. 2016), the genus *Glyptemys* (Wood and Bog Turtles) probably diverged from other emydine genera in the Oligocene epoch, toward the end of the Paleogene Period. The placement of the Spotted Turtle (*Clemmys guttata*) remains unresolved, which may in part be caused by short internode lengths early in the emydine lineage. The genera *Emys, Actinemys,* and *Emydoidea* are grouped into a holarctic genus, *Emys*, by Spinks et al. (2016) and others. This tree is based on the divergence analysis provided by Spinks et al. (2016), with modifications based on Angielczyk et al. (2010). For more details and additional discussion, see Spinks et al. (2016).

Phylogeny

The Wood Turtle is placed within the genus *Glyptemys* with a single congener, the Bog Turtle (*G. muhlenbergii*) of the central and southern Appalachian Mountains. The genus *Glyptemys* is placed within the subfamily Emydinae, which encompasses at least 11 North American and European species in the four major clades, roughly corresponding to the genera *Glyptemys, Emys* (including *Emys, Emydoidea,* and *Actinemys*), *Clemmys,* and *Terrapene* (2.1). The genus *Glyptemys* may be the sister taxon to a clade that includes the other emydine genera (Spinks et al. 2016). The Emydinae are the sister group to the Deirochelyinae, which includes the Sliders (*Trachemys*), Cooters (*Pseudemys*), Painted Turtles (*Chrysemys*), Map Turtles (*Graptemys*), Diamondback Terrapins (*Malaclemys*), and Chicken Turtles (*Deirochelys*). Together, these two subfamilies encompass the family Emydidae, which is mostly distributed in North America, with a few representatives in South America and Europe. The emydids are a remarkably diverse group of freshwater turtles, the result of a diversifying trend since the Oligocene (Vlachos 2018). The emydine species differ from the deirochelyines in that they are generally more terrestrial, longer-lived, later to reach maturity, and smaller.

The Wood Turtle was classified in the genus *Clemmys* (Ritgen 1828) for most of the 20th century (Strauch 1862; Babcock 1919). In the sense of McDowell (1964), *Clemmys* encompassed three North American species in addition to the Wood Turtle. These were the Spotted Turtle (*C. guttata*), Bog Turtle (*C. muhlenbergii*), and Western (or Pacific) Pond Turtle (*C. marmorata*). Holman and Fritz (2001) note that McDowell's arrangement of *Clemmys* (in the broad sense) was based on plesiomorphic (basal) rather than synapomorphic (derived) traits, including an unhinged plastron, buttressed bony bridges connecting the plastron to the carapace, and the lack of a scapular suspensorium as described by Bramble (1974).

Beginning in the late 1980s, several authors critically re-evaluated the relationships within *Clemmys* (Gaffney and Meylan 1988; Lovich et al. 1991). Several authors subsequently provided evidence that the traditional genus *Clemmys* was made paraphyletic[1] by not including the sister genera *Emys* and *Emydoidea* (which are more closely related to *Actinemys* [formerly *Clemmys*] *marmorata* than to either *G. insculpta* or *G. muhlenbergii*) and possibly also the Box Turtles, *Terrapene* (Bickham et al. 1996; Burke et al. 1996; Lenk et al. 1999; Holman and Fritz 2001; Ernst 2001a; Feldman and Parham 2002; Seidel and Wood 2002; Stephens and Wiens 2003; Wiens et al. 2010; Fritz et al. 2011; see Crother 2017). Burke et al. (1996) speculated on possible reconfigurations of the emydine taxa to resolve the clear paraphyly of *Clemmys*, as broadly defined. Their recommendations included combining most species (except G. *insculpta* and *G. muhlenbergii*) into *Emys*; although, this would have obscured clearly monophyletic lineages and distinct genera groups. Holman and Fritz (2001) reassigned the Wood Turtle from *Clemmys* to *Glyptemys* (Agassiz 1857) and Feldman and Parham (2002) reassigned the Wood Turtle from *Clemmys* to *Calemys* (Agassiz 1857) without reference to Holman and Fritz. *Glyptemys* and *Calemys* occur on the same page for Wood Turtle and Bog Turtle, respectively, in the original publication by Agassiz (1857, Vol. 1). Although *Calemys* is listed first in Agassiz (1857), *Glyptemys* was selected by Holman and Fritz (2001) based mostly on preference, using the principle of the first reviser.

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1 Paraphyly is an evolutionary concept that describes a taxonomic group of animals (e.g., Class Reptilia) containing a common ancestor and only some (e.g., turtles, lepidosaurs, and crocodilians) of the living descendants. In the case of Reptiles, the group has excluded birds, which are more closely related to crocodilians than either are related to lizards, snakes, Rhychocephalians, or turtles. If a group is paraphyletic, it means that some members of the related group have been placed into another group.

2.2—Wood Turtles have hybridized with Blanding's Turtles (*Emydoidea blandingii*) under rare conditions in captivity. Hybrids appear intermediate between the two species. James Harding

2.3—Bog Turtles (*Glyptemys muhlenbergii*) are the Wood Turtle's closest living relative and the only other living species in the genus *Glyptemys*. The two species likely diverged in the Miocene epoch of the Neogene Period. The two, living *Glyptemys* species historically occurred in close proximity in the northern part of the Bog Turtle's range from Massachusetts to Maryland. *Top left:* an adult female Bog Turtle from North Carolina (Mike Knoerr). *Top right:* adult male Bog Turtle from New Jersey (Mike Jones). *Bottom right:* hatchling Bog Turtle from North Carolina (Mike Knoerr). *Bottom left:* plastron of an adult male Bog Turtle from Massachusetts (Mike Jones).

The current taxonomy of the Emydinae remains unresolved. Most areas of concern pertain primarily to the final status of the genera *Actinemys*, *Emydoidea*, and *Emys*, or to the species-level divisions within the Eastern Box Turtle clade (*Terrapene carolina* sensu lato). All authors agree that the Wood and Bog Turtles form a living monophyletic clade within the subfamily Emydinae (Bickham et al. 1996; Burke et al. 1996; Lenk et al. 1999; Holman and Fritz 2001; Feldman and Parham 2002). Hybridization between a female Wood Turtle and at least one male Blanding's Turtle has been reported by Harding and Davis (1999) (2.2).

Subfamily Emydinae

Genus *Glyptemys*

The genus *Glyptemys* (Agassiz 1857) contains two living species, *G. insculpta* and *G. muhlenbergii*. Wood Turtles being the focus of this entire book, will not be further discussed here. The Wood Turtle's congener and sister taxon, the Bog Turtle (*G. muhlenbergii*) is a much smaller turtle that rarely exceeds 100 mm in carapace length (Ernst and Lovich 2009) (2.3). Bog Turtles have a disjunct distribution, with one primary area of occurrence extending from Massachusetts to Maryland and another extending from Virginia to northern Georgia. Outlying populations occur on the Lake Ontario plain, and formerly in the vicinity of Lake George, New York. Bog Turtles are a species of open, graminoid-dominated bogs and fens, often with a hydrology characterized by groundwater seepages, rills, and springheads (Ernst and Lovich 2009).

Genus *Emys*

The genus *Emys* (Duméril 1806) contains three well-defined lineages generally referred to the individual genera *Emys, Emydoidea,* and *Actinemys* (2.4). In this strict sense, *Emys* contains a species complex that includes the European Pond Turtles (*Emys orbicularis*), which extend from the Iberian Peninsula to the Caspian shore of Iran (Fritz et al. 2009), including many of the Mediterranean, Adriatic, and Aegean islands. Throughout this enormous region, *E. orbicularis* may be found in clear-flowing rivers, ephemeral wetlands, ponds and reservoirs, marshes, agricultural ditches, and coastal lagoons. The genus *Emydoidea* contains a single species, Blanding's Turtle (*E. blandingii*), which ranges from Nebraska to Ontario, with outlying populations in the Hudson Valley of New York, east-Central New England, and the Kejimkujik region of southern Nova Scotia (Compton 2007). Blanding's Turtles occur occasionally in large rivers, but are primarily a species of large and deep marshes, shrub swamps, and ephemeral pools. Finally, the genus *Actinemys* contains two recognized species, the Western Pond Turtles (*A. marmorata* and *A. pallida*). These species historically ranged continuously from the Coast Ranges of Oregon to the Sierra Juarez of Baja California, with outlying occurrences near Puget Sound, Washington (Fisher 2018); the Mojave River, California (Lovich and Meyer 2002); and the Sierra San Pedro Mártir of Baja California (Grismer 2002). Recently, an extreme southern outlier was discovered in a palm oasis of the Vizcaino Desert of central Baja California (Valdez-Villavicencio et al. 2016), perhaps the most disjunct and isolated of any North American emydine occurrence. More than its congeners, the Western Pond Turtles are often associated with flowing streams.

Genus *Clemmys*

The genus *Clemmys* (Ritgen 1828) contains a single living species, the Spotted Turtle (*C. guttata*), which ranges along the Atlantic Coastal Plain and adjacent piedmont from southern Maine to north-central Florida, and from western Pennsylvania to Indiana and Illinois (2.5). Within this area, Spotted Turtles occur in a wide range of shallow and ephemeral wetlands, including interdunal swales, vernal pools, and forested swamps dominated by Sweetgum




2.4—The clade *Emys* includes at least two species on the Pacific coast of North America from Washington to Baja California, a single species in east-central North America from Nebraska to Nova Scotia, and a species complex in southern Europe and northern Africa. Three distinct clades within this group are usually referred to the genera *Actinemys, Emydoidea*, and *Emys. Top left:* Western Pond Turtle (*Actinemys pallida*). *Top right:* Western Pond Turtle (*Actinemys marmorata*). *Bottom right:* adult female Blanding's Turtle (*Emydoidea blandingii*). Mike Jones. *Bottom left:* adult European Pond Turtle (*Emys orbicularis*). Alexandre Roux

2.5— The genus *Clemmys* includes a single species, the Spotted Turtle (*Clemmys guttata*), which co-occurs with the Wood Turtle in southern New England, New York, New Jersey, Pennsylvania, and western Michigan. An adult female from Massachusetts is pictured. Mike Jones

(*Liquidambar styraciflua*), tupelo (*Nyssa* spp.), Baldcypress (*Taxodium distichum*), Red Maple (*Acer rubrum*), or Tamarack (*Larix laricina*). Spotted Turtles occur on many offshore and barrier islands from Massachusetts to North Carolina; southern populations are generally found further inland (Ernst and Lovich 2009).

Genus *Terrapene*

The genus *Terrapene* includes 4–8 species of North American Box Turtle (2.6). Well-resolved species include: (1) the Spotted Box Turtle (*Terrapene nelsoni*), which ranges the crest of Mexico's Sierra Madre Occidental (Buskirk and Ponce-Campos 2011); (2) the Ornate Box Turtle (*Terrapene ornata*), a grassland species found from the Sonoran and Chihuahuan grasslands of Arizona, New Mexico, Texas, and Sonora (Legler and Vogt 2013) to a series of isolated relictual occurrences in Wisconsin and Illinois; and (3) the Coahuila Box Turtle (*T. coahuila*), which is known only from marl-pools and springs in the Chihuahuan Desert of Cuatrocienegas, Coahuila, Mexico (Howeth and Brown 2011). Finally, there is a group of about five species that historically grouped within the superspecies *T. carolina* (Dodd 2001). These include: (1) the Florida Box Turtle (*T. bauri*); (2) the Yucatán Box Turtle (*T. yucatana*); (3) the Mexican Box Turtle (*T. c. mexicana*); (4) the Three-toed Box Turtle (*T. c. triunguis*), and (5) Eastern or Woodland Box Turtle (*T. c. carolina*). A very large and mysterious form known as the Gulf Coast Box Turtle (*T. c. major*) occurs in the large river basins near the Gulf of Mexico coast; this may actually be an introgressed form of the Pleistocene Giant Box Turtle (*T. putnami*) (Butler et al. 2011; Martin et al. 2013; Kiester and Willey 2015; Martin et al. 2020).

Fossil Record

Miocene

The genus *Glyptemys* appears first in the middle to Late Barstovian (Middle Miocene) of the Niobrara River Valley of northern Nebraska (ca. 14.5–11.5 million ybp, Holman and Fritz 2001; Ernst and Lovich 2009).[2] The species found in this area has been assigned to *Glyptemys valentinensis* (Holman and Fritz 2001), which may have given rise to *G. insculpta* in the Middle Miocene between the Late Barstovian and Late Hemphillian times (11.5–5.5 million ybp). *Glyptemys valentinensis* differs from *G. insculpta* primarily in its average body size, which is smaller than the modern species, although not as small as the 1850s adult *G. insculpta* measured by Jones et al. (2019). In addition, *G. valentinensis* had a less prominently serrate posterior carapace margin. The holotype for this species, UNSM 76564, is a remarkably complete carapace that was originally identified as Painted Turtle (*Chrysemys picta*) by Holman and Sullivan (1981) (2.7).

Pleistocene

Pleistocene-age fossils suggest that Wood Turtles occupied portions of their contemporary range during interglacial events. Late Pleistocene remains generally support the prevailing hypothesis of a large refugium around the southern terminus of the Appalachian Mountains, from Mississippi to Georgia.

Frankstown Cave.— Early to Middle Pleistocene (Irvingtonian 1.9 million to 250,000 ybp) Wood Turtle remains were recovered from the Frankstown Cave, Blair County, Pennsylvania

2 *Glyptemys* specimens were obtained from the Sand Lizard Quarry, Knox County; Crookston Bridge, Nenzel, Stewart, and Valentine Railway Quarries of Cherry County; Norden Bridge Quarry of Brown County; and the Forked Hills of Hayden in Boyd County (Holman and Fritz 2001).

2.6—The genus *Terrapene*, the North American Box Turtles, includes several distinct lineages with species-level confusion caused by high levels of introgression in the southeastern United States. *Top left:* the Coahuila Box Turtle (*Terrapene coahuila*) occurs only in the desert springs of Cuatro Ciénegas, Coahuila, Mexico. *Middle:* the Florida Box Turtle (*Terrapene bauri*) and Yucatán Box Turtle (*Terrapene yucatana*) are southern-latitude representatives of the Eastern Box Turtle (*Terrapene carolina*) species complex that is distributed from New England to the Yucatán Peninsula. An adult male from Yucatán is pictured at middle right, and an adult male from Florida is pictured at middle left. *Bottom:* the Ornate Box Turtles (*Terrapene ornata*) occur throughout the prairies and warm deserts of the western USA and Mexico. An adult female is pictured at bottom right, and an adult male is pictured at bottom left. Mike Jones

2.7—During the Miocene epoch, a smaller relative of the Wood Turtle, described as *Glyptemys valentinensis*, inhabited the Niobrara River valley of northern Nebraska. Fossils have been recovered from at least eight distinct localities. The holotype specimen, UNSM 76564, is pictured. Ross Secord (Nebraska State Museum)

(Peterson 1926). The Pennsylvania reports provide additional evidence that Wood Turtles occupied at least part of their contemporary range during an interglacial event of the Late Pleistocene (Hay 1923; Parris and Daeschler 1995).

Port Kennedy Cave.—Wood Turtle remains from the Port Kennedy Cave, a limestone solution feature in Montgomery County, Pennsylvania, were dated to the Late Irvingtonian or Middle Pleistocene (850,000–250,000 ybp) (2.8). Here, skeletal remains of *G. insculpta* were found in association with Box Turtles (*Terrapene carolina*), Blanding's Turtle (*Emydoidea blandingii*), and a species of *Hesperotestudo* tortoise (Parris and Daeschler 1995). Noteworthy mammalian associates reported by these authors included Mastodon, Wheatley's Ground Sloth (*Megalonyx wheatleyi*), Lesser Short-faced Bear (*Arctodus pristinus*), Long-nosed Peccary (*Mylohyus nasutus*), Hay's or Giant Tapir (*Tapirus haysii*), skunk (*Brachyprotoma obtusata*), and Eastern Cottontail (*Sylvilagus floridanus*). Plant remains included hickory (*Carya* sp.), beech (*Fagus* sp.), and Pitch Pine (*Pinus rigida*). The remarkable assemblages from Port Kennedy were studied by Cope (1899) and Hay (1908), both of whom noted the

2.8.—During the last interglacial period of the Pleistocene epoch, Wood Turtles occupied at least a portion of their current range. Fossils are known from Nova Scotia and Pennsylvania. Pictured: ASNP 151, fragmentary remains from the Port Kennedy Cave, Pennsylvania, USA, which were studied by Edward Drinker Cope (1899). Photo: Ned Gilmore (Academy of Natural Sciences of Drexel University/ASNP).

presence of Wood Turtles. According to Phillips (2006), Cope (1899) noted that Port Kennedy Wood Turtles exhibited a thicker, more enlarged gular surface of the anterior plastral lobe than found in contemporary specimens.

East Milford Mastodon Site.—Wood Turtle remains were recovered from the East Milford mastodon site near the current Shubenacadie River in Halifax County, Nova Scotia (Holman and Clouthier 1995). The Wood Turtle remains were found preserved in a layer of dark, organic clay deposited in a gypsum sinkhole in association with Mastodon (*Mammut americanum*), Painted Turtle, and Northern Leopard Frog (*Lithobates pipiens*). The East Milford remains are particularly noteworthy, because they represent a rare interglacial occurrence of Wood Turtles from an area where they must have subsequently been displaced by advancing Wisconsinan Ice Sheets. The East Milford remains were dated by Holman and Clouthier (1995) to roughly 70,000 to 80,000 ybp.

Last Glacial Maximum

During the last glacial advance or last glacial maximum (i.e., Wisconsinan glaciation) of the Pleistocene epoch—and immediately thereafter—Wood Turtles occurred well south of the ice margin around the margin of the southern Appalachian Mountains. Molecular studies have hypothesized at least one southern Pleistocene refugium for *G. insculpta* (Amato 2006; see Phylogeography discussion later in this chapter), and supporting fossil evidence has been recovered from sites in Tennessee, Georgia, Alabama, and Mississippi (Phillips 2006).

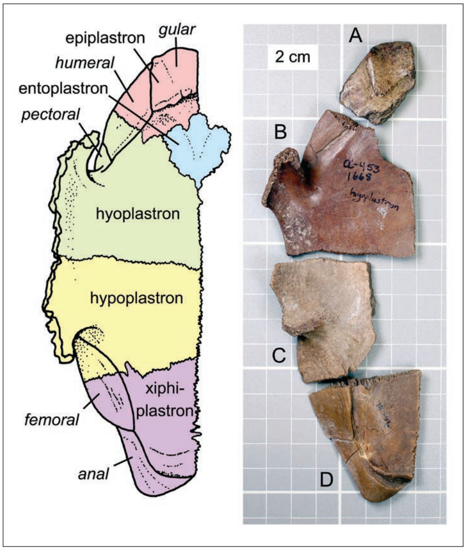
Cheek Bend Cave.—Wood Turtle remains (a partial carapace) from Cheek Bend Cave along the Duck River, Maury County, central Tennessee (Parmalee and Klippel 1981; Klippel et al. 1982) were estimated to have originated in the Late Pleistocene (Rancholabrean, 12,000–16,000 ybp). Wood Turtles from Cheek Bend

2.9.—During the last glacial advance of the Pleistocene epoch, Wood Turtles occurred at the margin of the southern Appalachian Mountains. Fossils from the last glacial maximum have been recovered from Mississippi, Tennessee, and a site near Ladds, Bartow County, Georgia (the stream nearest the quarry is pictured). Mike Jones

2.10.—Map of Pleistocene Wood Turtle localities in the Deep South. The Black Prairie District is generally more fossiliferous than the Loess Hills, but the former has also been sampled more purposefully. Map: George Phillips (Mississippi Museum of Natural Sciences).

were associated with Arctic Shrew (*Sorex palustris*), Yellow-Cheeked Vole (*Microtus xanthognathus*), American Marten (*Martes americana*), and Beautiful Armadillo (*Dasypus bellus*), apparently representing a juxtaposition of boreal and subtropical mammals, as noted by Phillips (2006).

Ladds Quarry.—Wood Turtle remains—consisting of a partial plastron and pleural bones—from Ladds Quarry, Bartow County, Georgia were Late Pleistocene (Rancholabrean) in age (Holman 1967; 1985a; 1985b). These remains provide additional clarity and detail to the geographic extent of the southern refugium occupied by *G. insculpta* during the Late Pleistocene (2.9)



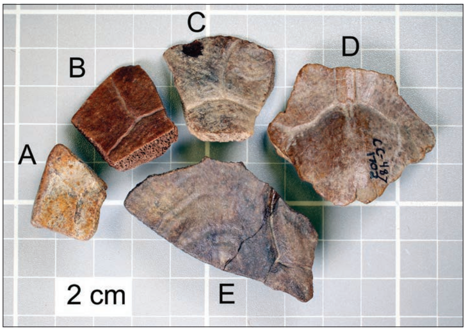
2.11.—*Top:* Wood Turtle plastral elements (left side, dorsal aspect) from the Late Pleistocene of the Mississippi Loess Hills (A) and Black Prairie (B–D). (A) epiplastron (MMNS VP-7982); (B) incomplete hyoplastron (MMNS VP-1668); (C) partial hypoplastron (MMNS VP-1795); and (D) xiphiplastron (MMNS VP-7477). Specimens collected in Warren (A), Lowndes (B, C), and Lee (D) counties and curated at the Mississippi Museum of Natural Science, Jackson, Mississippi. Plastral schematic adapted from Holman and Fritz (2001), with kind permission. Individual bony elements are colored; dorsal presentation of named scutes in *italics*. Photos: George Phillips (Mississippi Museum of Natural Sciences).

Black Prairie.—Dozens of dissociated Wood Turtle shell elements have been recovered from Late Pleistocene alluvial deposits in the Black Prairie (or Black Belt, Barone 2005) of Mississippi and Alabama, as well as the Loess Hills (or Loess Bluffs/Bluff Hills, Krinitzsky and Turnbull 1967) district of western Mississippi (Phillips 2006) (2.10). These physiographic districts exhibit botanical and faunal formations originating in previous Pleistocene interglacials, representing survivorship and reorganization through multiple glacial phases and megafaunal extinction (e.g., Williams et al. 2001). Of the two districts, the most productive single fossil locality lies in the Black Prairie near Mayhew, Mississippi (2.11), where the Wood Turtle represents over 10% of the identified chelonian remains in a rather diverse assemblage (Phillips 2006) (2.12). Blanding's Turtle (*Emydoidea blandingii*) is also present in the Mayhew samples. Thus, both extant cool temperate chelonians—Wood and Blanding's—inhabited the Deep South in the Late Pleistocene (Jackson and Kaye 1974; Phillips 2006). Otherwise, Wood Turtle remains at Mayhew co-occur primarily with chelonian taxa that are extant in the Black Prairie (eight of 13 species, 61.5%),[3] as discussed further below.

Among the deirochelyines, the genus *Pseudemys* (cooters) is well-represented in the fossil assemblage at Mayhew. Some of these specimens are probably attributable to River Cooter (*Pseudemys concinna*), a modern resident; however, a thick-shelled Red-bellied Cooter (*Pseudemys* cf. *rubriventris*)—which no longer inhabits the area—is well-represented (Kaye 1974b; Phillips 2006). Elements of Slider (*Trachemys scripta*), Painted Turtle (*Chrysemys picta*), and Alabama Map Turtle (*Graptemys* cf. *pulchra*) were each less common than Red-bellied Cooter (Phillips 2006).

3 The form of Box Turtle present at Mayhew was the larger subspecies *T. putnami* or *T. c. major* and not the currently resident *T. c. triunguis* (Jackson and Kaye 1974a).

Kinosternid remains were also recovered from the Mayhew deposits. In addition to Common Musk Turtle, the now extralimital Razorback Musk Turtle (*Sternotherus carinatus*) was also present, although the modern resident Stripe-necked Musk Turtle (*Sternotherus minor peltifer*) was absent (Phillips 2006). A single specimen of Gopher Tortoise (*Gopherus polyphemus*) was recovered from the Mayhew site; this is the northern- and inland-most record of this taxon (Franz and Quitmeyer 2005). Spiny Softshell (*Apalone spinifera*) was present, but the Smooth Softshell (*A. mutica*) was not (Kaye 1974b; Phillips 2006). Kaye (1974b) recorded both lineages of extant chelydrids (*Macrochelys*, *Chelydra*), although they were not common (Phillips 2006). The extinct Giant Nearctic Tortoise (*Hesperotestudo crassiscutata*) rounds out the Mayhew assemblage (Kaye 1974b; Jackson and Kaye 1975; Phillips 2006). The absence of Stripe-necked Musk Turtle and Smooth Softshell, species of riverine habitats, is probably environmental. The totality (turtles, other vertebrates, and sedimentology) of the Black Prairie assemblage suggests smaller, occasionally impounded streams and associated riparian habitat.



2.12. Wood Turtle carapacial elements (left side, dorsal aspect) from the Late Pleistocene of the Mississippi Black Prairie (see 2.10). (A) third peripheral (MMNS VP-1707); (B) second peripheral (MMNS VP-1881); (C) first peripheral (MMNS VP-4281); (D) incomplete nuchal (MMNS VP-1702); and (E) first costal (MMNS VP-4123). Specimens collected in Lowndes (A–D) and Monroe (E) counties and curated at the Mississippi Museum of Natural Science, Jackson, Mississippi. Photos: George Phillips (Mississippi Museum of Natural Sciences).

In addition to the chelonian component, the Black Prairie paleofauna included a similarly disharmonious suite of mammals and other vertebrates. Caribou (*Rangifer tarandus*), Meadow Vole (*Microtus pennsylvanicus*), and Southern Bog Lemming (*Synaptomys cooperi*)—all currently higher latitude, cool temperate taxa—are intermixed with Beautiful Armadillo (*Dasypus bellus*), Northern Pampathere (*Holmesina septentrionalis*), and Indigo Snake (*Drymarchon corais*)—species with pre-Pleistocene roots in subtropical and more southern biomes (Kaye 1974b; Frazier 1985; Dobie et al. 1996; McDonald et al. 1996).

Collectively, the composition (diversity, relative abundance, and presence/absence) of Late Pleistocene chelonians at Mayhew suggests an ecosystem of small, sylvan, occasionally impounded, perennial streams with at least seasonally dry, sandy riparian habitat. This is in contrast to an upland Black Prairie fossil assemblage of low chelonian diversity, low aquatic species diversity, and, along with a complementary sedimentology, generally suggestive of intermittent prairie streams with clayey alluvium and lightly wooded riparian habitat (Phillips 2006). The relative abundance of Wood Turtle at lowland sites, like Mayhew, may suggest small glades or openings associated with the riparian habitats.

The co-occurrence of ecologically incongruous chelonian (and other) taxa (at least based on modern distributions) such as the aquatic, cool temperate Blanding's Turtle and terrestrial, subtropical Gopher Tortoise, is suggestive of either a disharmonious fauna (Lundelius 1989) or a time-averaged assemblage (e.g., Behrensmeyer 1982). The components of fluviatile deposits are frequently reworked, in which case older fossils may be reincorporated into younger deposits (with younger fossils), but the extent of this attritional reworking, and thus time-averaging, can sometimes be confined to reasonably narrow intervals. Phillips (2006) summarized the cumulative

2.13.—Wood Turtle remains from the West Nishnabotna River near the city of Malvern, Mills County, Iowa, radiocarbon dated to the Late Pleistocene (10,220 ± 30 B.P., 12,095-11,803 cal B.P.). Photos: Matt Hill (Iowa State University).

evidence for confinement of the Black Prairie assemblage to the Rancholabrean Land Mammal Age, and thus to the Late Pleistocene. However, mixing of previous interglacial (Sangamon) fossils with those of the last glacial phase (Wisconsinan) cannot be completely ruled out.

Nishnabotna River.—The partial shell of a wood turtle (*Glyptemys insculpta*) was collected from the West Nishnabotna River near Malvern, Mills County, southwestern Iowa by Matt Hill of Iowa State University (2.13) (Hill, in prep). This specimen was radiocarbon dated to the Late Pleistocene (10,220 ± 30 B.P.; 12,095–11,803 cal B.P.).

Wood Turtle remains are prominently absent from the Late Pleistocene (roughly 18,530 to 18,940 ybp) Ardis local fauna reported from the Giant Cement Quarry near Harleyville, Dorchester County, South Carolina, USA, by Bentley and Knight (1998). Here, excavations of clay deposits among limestone solution chambers revealed Eastern Mud Turtle (*Kinosternon subrubrum*), Common Musk Turtle (*Sternotherus odoratus*), Snapping Turtle (*Chelydra serpentina*), Alligator Snapping Turtle (*Macrochelys temminckii*), Painted Turtle (*Chrysemys picta*), Chicken Turtle (*Deirochelys reticularia*), Common Slider (*Trachemys scripta*), Cooters (*Pseudemys* sp.), Spotted Turtle (*Clemmys guttata*), Bog Turtle, Blanding's Turtle, Giant Box Turtle (*Terrapene carolina putnami* or *T. c. major*), Giant Tortoise (*Hesperotestudo crassiscutata*), and softshells (*Apalone* spp). The authors suggest that the Ardis turtle fauna represents a "disharmonious" fauna with no modern analog.

The report of a Wood Turtle nuchal bone from Quarternary deposits at McFaddin Beach, Texas (Russell 1975) is undoubtedly in error. As pointed out by Phillips (2006), the description matches exactly that of Diamondback Terrapin (*Malaclemys terrapin*), which is known to inhabit the area today.

Recent Prehistory

Wood Turtle remains and subfossils have been reported from numerous mid- to late-Holocene archaeological sites throughout the United States and Canada.

In Ontario, Wood Turtle remains were recovered from the Roebuck Native American site, Leeds and Grenville United Counties, Ontario (Bleakney 1958a). Adler (1968) reported Wood Turtle remains from the Raddatz Rockshelter, Sauk County, Wisconsin, and the Juntunen site on Bois Blanc Island in the Mackinac Strait, Mackinac County, Michigan. Evidence of a single Wood Turtle was recovered from the Little Ossipee North site in Oxford County, Maine, dating from approximately 1,000 ybp (Sobolik and Will 2000). Wood Turtle fragments accounted for

33% of turtle remains in a midden at the Olsen Site near Cushing, Knox County, Maine—a coastal site, with no currently confirmed populations within 30 km (Downs 1987 in Rhodin 1995; Maine Department of Inland Fisheries and Wildlife, unpubl. data). In southern New Hampshire, Wood Turtle remains accounted for 61% of all turtle remains in shell middens at Sewall's Falls, Merrimack County, New Hampshire (Howe 1988 in Rhodin 1995). By contrast, Wood Turtle remains accounted for only 11% of the large sample from the Concord Shell Heap on the bank of the Sudbury River, Concord, Middlesex County, Massachusetts (Rhodin 1995). Wood Turtle remains are even more rare in the turtle bone fauna at Flagg Swamp, Middlesex County, Massachusetts (Huntington and Shaw 1982) and the Cedar Swamp, Westborough, Worcester County, Massachusetts (Rhodin 1986; 1992).

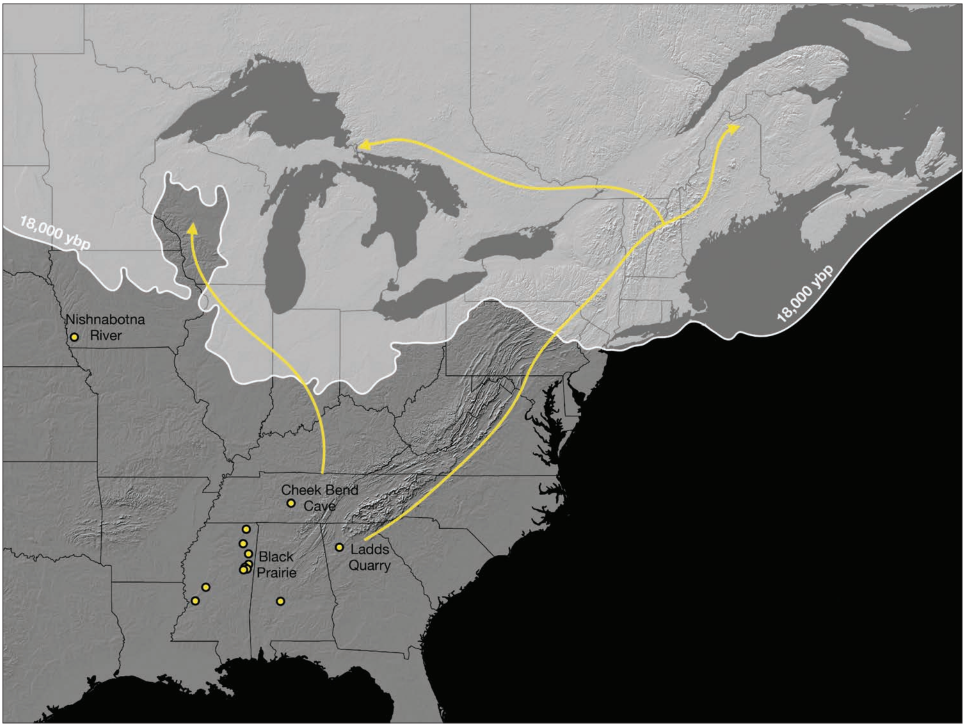
Chromosomal Evolution

Recent genetic and chromosomal studies indicate that the genus *Glyptemys* derived genotypic sex determination (GSD) ~20 million ybp from the ancestral environmental sex determining system (temperature-dependent; TSD) present in a common ancestor that *Glyptemys* spp. shared with other emydid turtles (Montiel et al. 2016, Literman et al. 2017). Molecular data suggest that the two congeners of the genus, *G. insculpta* and *G. muhlenbergii*, split between 8 and 18 million ybp (Montiel et al. 2016), a date that is consistent with the few fossil remains of the genus. *Glyptemys insculpta* possesses a diploid count of 50 chromosomes, distributed as 13 pairs of macrochromosomes and 12 pairs of microchromosomes (Bickham 1975; Montiel 2016). Both *G. insculpta* and *G. muhlenbergii* possess slightly heteromorphic, macrochromosomal XX/XY sex chromosomes that are homologous with chromosome four of *Chrysemys picta*. In *G. insculpta*, the fourth largest pair macrochromosomes in males is characterized by a subtelocentric chromosome and a slightly larger submetacentric chromosome; the fourth pair in females is subtelocentric and homomorphic. Although an earlier cytogenetic study (Bickham 1975) could not differentiate sex chromosomes in *G. insculpta*, Montiel et al. (2016) determined that the XX/XY chromosomes of the Wood Turtle were the result of at least two inversions between the X and Y chromosomes and subsequent intrachromosomal rearrangements of genes that co-localize with the male-specific region of the Y chromosome.

Genotypic sex determining mechanisms have evolved independently in several lineages of turtles, but the ~20 million ybp derived XX/XY system of the genus *Glyptemys* is apparently the youngest known chelonian example, a group characterized by a low rate of chromosomal changes (Bickham 1981; Olmo 2008). This date corresponds to a period of global warming before the Miocene Epoch Ice Age; thus, increasing environmental temperatures may have influenced selective forces that favored a shift from TSD to a GSD system to counter-balance potential female-biased sex ratios (Valenzuela and Adams 2011; Montiel at al. 2016). In this scenario, masculinizing mutations and the associated inversions identified by Montiel et al. (2016) may have limited recombination and increased the divergence of sex chromosomes in members of this genus.

Phylogeography

The most current phylogeographic hypothesis for the modern distribution of the Wood Turtle comes from Amato et al. (2008) and Rödder et al. (2013). Amato et al. (2008) examined variation in a 750 bp segment of the mitochondrial control region in 117 individuals from 29 locations across the range. They identified 21 haplotypes with little genetic variation among



2.14.—Following the Last Glacial Maximum (shown as a white line) at the end of the Wisconsinan phase of the Pleistocene ice ages, Wood Turtles probably colonized their current range from a refugium in the southern Appalachians of Tennessee, Mississippi, Alabama, and Georgia (yellow dots demarcating Late Pleistocene collection sites). The post-Pleistocene collonization hypothesis of Amato et al. (2008) is illustrated by yellow arrows, showing movement into New England and eastern Canada, with continued migration from eastern Canada into the Great Lakes region, as well as direct migration from the southern refugium into the Great Lakes region. Base DEM created by Emmy Whistler / Antioch University New England.

them; the highest pairwise difference was 2%. They suggest that the low level of observed genetic variation can be explained by a severe bottleneck as well as selective sweep when the Wood Turtle was isolated in its southern refugium during the last Pleistocene glacial maximum, from 90,000 to 18,000 years ago. Amato et al. (2008) interpret the presence of fossil Wood Turtles in northwestern Georgia (Holman 1967) and south-central Tennessee (Parmalee and Klippel 1981), about 240 km apart, dating to the Late Pleistocene-Early Holocene as evidence of a refugium in the southern Appalachian region.

Amato et al. (2008) conclude that the Wood Turtle likely exhibited a rapid northward expansion along two major routes from its southern refugium as the Laurentide ice sheet retreated (2.14). In particular, they infer from their analyses that the Wood Turtle experienced rapid population growth beginning approximately 12,000 years ago, which corresponds well with the most recent glacial retreat. They found a significant association of genetic variability and geographical distribution among the haplotypes, as revealed by nested clade analysis. They also found that a large number of intermediate haplotypes were missing, suggesting that they were not sampled or that some were lost to a population bottleneck following glaciation. From this, they inferred that the first route of rapid expansion via long distance dispersal occurred along the Atlantic coast of North America from Virginia to Nova Scotia, with a secondary westward expansion across the top of the Great Lakes region that was characterized primarily by contiguous dispersal, but also some long-distance dispersal and restricted gene flow. The second route, a westward infiltration, occurred from the Georgia-Alabama refugium to western localities south of the Great Lakes in Michigan, Wisconsin, and Minnesota, and was characterized by long-distance dispersal and restricted gene flow, as populations of the Wood Turtle are not found along this Midwestern route. Amato et al. (2008) and the paleophylogeographic models presented by Rödder et al. (2013) suggest that a second refugium, west of the Appalachian Mountains, cannot be discounted as the source of this westward infiltration. Phillips (2006) and the supplementary fossil evidence presented above, which were unknown to Amato et al. (2008) and Rödder et al. (2013), support these models. Based on the paleobotanical and alluvial valley evolution (Delcourt and Delcourt 1996), the Mississippi River Valley and/or adjoining Blufflands is a logical corridor for dispersal of Wood Turtles to and from the Loess Hills. Based on hypothesized alternate paths of the lower Tennessee River (Shaw 1918; Kaye 1974a), a dispersal route between the upper Tombigbee River, which drains the Black Prairie, and the Ohio River may have been available for movement of Wood Turtles during glacial fluctuations. However, considering the Cheek Bend Cave occurrence in Maury County, Tennessee (Klippel et al. 1982), the full extent of the Interior Low Plateaus, bordered by the Tennessee River to the west (and south), would have made for a larger dispersal corridor, at least to the edge of the Gulf Coastal Plain to the southeast (Black Prairie paleofauna, Tombigbee River) and the Appalachian foothills to the southwest (Ladds Quarry paleofauna, Georgia).

A secondary westward expansion north of the Great Lakes is inferred first because some animals from clades that are located along the eastern seaboard of North America are also found in eastern Ontario, Michigan (including the Upper Peninsula) and Minnesota, suggesting a westward infiltration by contiguous range expansion. It is also inferred, again by contiguous westward range expansion, because animals from that same eastern clade, around Lake Ontario, are also found along the northern shore of Lake Huron. Phylogenetic structuring also suggests the presence of at least three more clades that expanded contiguously north of the Great Lakes. Finally, movement southward across the Great Lakes region by long distance dispersal and restricted gene flow is evidenced by the presence of a clade that includes haplotypes from central and southern Ontario as well as southern Minnesota. Amato et al. (2008) conclude that although there is solid evidence of phylogenetic structuring by geography, no clades are distinct enough to warrant conservation status reassessment. However, at the same time, they caution the assignment of conservation units when using neutral genetic markers. In addition, they interpret this to have both positive and negative consequences: (1) loss of location populations may not have severe consequences to species persistence; and (2) the species gene pool may not contain sufficient variation for future adaptation.

Population Genetics

There is currently limited information on variation and structuring within and among populations of the Wood Turtle across its range. Information on patterns of population structure at relatively small spatial scales (i.e., 12, 25, 43.3, 120, and ca. 100–450 km), either within or across major basins, are limited to studies in Québec (Tessier et al. 2005), Pennsylvania (Castellano et al. 2009), Iowa and West Virginia (Spradling et al. 2010), Ontario (Fridgen et al. 2013) and Michigan (Willoughby et al. 2013). Each of these studies has used varying numbers of nuclear microsatellite loci (5–9) to examine intra- and interpopulation genetic variation in the Wood Turtle at the local-to-regional scale. More recently, some studies (e.g. Bouchard et al. 2019, Weigel and Whiteley *in* Jones et al. 2018) have also used microsatellite loci (9 and 16, respectively) to examine genetic variation within and among populations at even larger scales (i.e., watershed basins in eastern Ontario, Québec, and New Brunswick, a ca. 770 km maximum straight line distance and 1,340 km maximum river distance, Bouchard et al. 2019; by state and basin in the northeastern United States from Virginia to Maine over ca. 1,230 km minimum straight line distance). In this section, we present a synthesis of these papers from the regional to the local scale (i.e. from the largest to smallest scale of population clustering and differentiation).

Across the Northeast, from northern Virginia to Northern Maine, Weigel and Whiteley (*in* Jones et al. 2018) suggest that populations of the Wood Turtle cluster into four major population groups based upon a sample of 1,244 individuals from 62 sites. These clusters correspond to population groups in northern Maine, coastal Massachusetts and Rhode Island, New York and New Jersey, and the Potomac Basin. They found that populations from New Hampshire and Pennsylvania were admixed with adjacent population clusters. They also found that sites in the Connecticut, Merrimac and Kennebec River basins indicate mixed ancestry between the coastal Massachusetts and the northern Maine sites should be considered a genetically similar group. Therefore, they suggest five evolutionarily significant units (ESUs) made up of the four distinct clusters and the three-river basin mixed ancestry group. They further suggest that the admixed populations in New Hampshire, New York and Pennsylvania should be grouped with their adjacent clusters. Population genetic structure is best described by an island stepping-stone model where sites are exchanging individuals with neighboring sites creating a gradation of genetic structure over the Northeast. Further, their isolation by distance tests within the major clusters suggested that gene flow among nearest neighbors, with and across watershed boundaries, occurs both by water course, as expected, and also overland, with overland movement being more important for some groups, such as Potomac, but less important others, such as Northern Maine. For example, their full-sibling family tests indicate a maximum distance of 50 km between closely related turtles. Ninety-one percent of pairwise comparisons among sample sites were significant after correction for multiple tests. Not surprisingly then, the northern and southern states were the most distinct with populations from Virginia being among the most divergent in the entire sample. Among populations across the Northeast, genetic diversity as measured by allelic richness, private alleles and heterozygosity was within the range of other Wood Turtle genetic studies (e.g., Tessier et al. 2005; Castellano et al. 2009; Spradling et al. 2010; Fridgen et al. 2013; Willoughby et al. 2013), and did not indicate a loss of diversity. However, due to the very long generation time, relatively low dispersal rates, and low population abundances of the Wood Turtle, current population genetic data may reflect conditions several generations ago, possibly as long as ca. 100 years. Therefore, the effects of anthropogenic population fragmentation may not be detected for some time.

In eastern Canada, across a similar distance from eastern Ontario to northwestern New Brunswick, Bouchard et al. (2019) found that the population structure of 331 turtles from 24 locations in 12 watersheds was optimized at only two clusters, one north and one south of the St. Lawrence River. To test their hypothesis of clustering by watershed further, they found that additional clustering runs revealed five clusters on the North Shore that corresponded directly to their watersheds. On the South Shore, the situation was not as clear, with some clusters containing more than one watershed and others containing only one sample site within a watershed. In all cases, genetic diversity within watersheds was similar and observed heterozygosity was relatively high. These finding are similar to Tessier et al. (2005) who examined genetic diversity in two isolated populations on the North Shore of the St. Lawrence and four relatively proximal populations on the south shore in Québec. They found that all loci were extremely polymorphic and populations were highly variable, and that north and south shore sites were distinct, suggesting independent colonization, but southern sites were not distinct from each other. In fact, Tessier et al.'s (2005) findings on the differences in allelic distribution and genetic variability among their two sampled north shore sites suggested that there were two distinct northern colonization events; with isolation and random drift playing a major role in differentiation. Bouchard et al. (2019) interpret the clear distinction among the North Shore and South Shore sites as arising from an ancient dispersal barrier rather than post-glacial colonization. Yet, surprisingly they conclude that since certain individuals from North Shore sites contain an ancestral genetic signature similar to South Shore individuals, despite the St. Lawrence barrier, anthropogenic movement must be the cause. Overall, similar to Tessier et al. (2005), they found that despite anthropogenic pressures being more severe and population declines occurring on the South Shore, there were no significant different differences in genetic diversity between watersheds on opposite shores of the St. Lawrence. However, contrary to Tessier et al. (2005), they found lower levels of genetic diversity in more isolated watersheds and explain that by founder effect of post-glacial colonization. Despite that, Bouchard et al. (2019) suggest that each site, including the sites in Tessier et al. (2005), should be its own conservation management unit.

In terms of spatial scale, Spradling et al. (2010) is the next largest, with comparison of genetic diversity within and among sites in Iowa, as the extreme western edge of the species' range and West Virginia, some 1,235 km apart. They examined individuals from two localities, 12 km apart in Iowa, and from seven localities with a maximum distance of 25 km between samples in West Virginia. Not surprisingly, they found no structure in either sampling group, suggesting that both the Iowa sample and the West Virginia sample form one group each. However, they did find that genetic diversity was lower in Iowa than West Virginia, with expected heterozygosity being significantly lower. Nevertheless, they did not find evidence for a population bottleneck or inbreeding in Iowa or West Virginia, despite apparent severe population declines in Iowa. Again, this observation may be because of the long generation time of the Wood Turtle coupled with the close proximity of sites leading to gene flow in Iowa. They conclude that fixation indices and private alleles found in Iowa suggest that Iowa is a peripheral isolate that may represent a significant contribution to the genetic diversity of the species, and that both sites may be considered their own conservation management units. Next, in terms of distance between sites is Fridgen et al. (2013), who compared 79 turtles across four populations in three regions some ca. 340 km apart in eastern, southern and central Ontario. They found that the central Ontario population should be its own conservation management unit because it separated from the eastern and southern populations, which were undifferentiated by structure analysis and principal components analysis. Expected heterozygosity was relatively high among the four populations and genetic diversity did not vary much among the populations; however, there was higher heterozygosity and lower evidence of inbreeding in the central and eastern populations compared to the anthropogenically impacted southern population. In fact, despite the observation that heterozygosity in Ontario was generally similar to Québec and Iowa, the southern population, which underwent drastic population declines, had the lowest heterozygosity of any reported population. This observation appears contrary to the suggestion that the signature of anthropogenic disturbance as a loss of genetic diversity is slow to build up because of the long generation time of the Wood Turtle, or it may suggest a long history of population decline in southern Ontario.

Nearby in northern Michigan, Willoughby et al. (2013) examined 68 samples from roughly 20 km on three rivers in the Lower Peninsula, each approximately 120 km from another. They found that clustering identified two distinct populations; a northern cluster comprising the northeastern and northwestern sampling locations and a southern cluster. They do not comment on conservation management units, but considering that measures of genetic diversity were comparable with other studies, it is reasonable to conclude that the northern and southern clusters could be separate conservation management units. Not surprisingly, since the two northern populations clustered, structure analysis also revealed admixed individuals from both groups, suggesting some common ancestry between the northern and southern clusters. Nonetheless, fixation indices indicated that the northern and southern clusters were more isolated than the two northern populations. Overall, genetic diversity was high, but heterozygosity was higher in the northern population. There too, coalescent theory population size models indicated that there had been a demographic decline in both the northern and southern populations; however, loss of genetic diversity was not detected using bottleneck and inbreeding measures. They suggest that genetic diversity may be maintained in these declining populations by the relatively high migration rate between the two clusters. They further infer that the result of two clusters, rather than three, indicates that the historic pattern of urbanization and agriculture may not be sufficient to isolate populations by measurable genetic differentiation. Finally, they speculate that Amato et al.'s (2008) phylogeographic hypothesis may explain the difference between the northern and southern population clusters with the southern population arising from the westward infiltration across the Midwest and the northern population having ancestry in the secondary westward expansion across the top of the Great Lakes.

The smallest spatial scale comparison of population aggregations comes from two studies in the Northeast, Castellano et al. (2009) and Robillard et al. (2019). Castellano et al. (2009) measured genetic diversity among four aggregations in the Delaware Water Gap of Pennsylvania, with a maximum distance of 43.3 km apart. They found very high genetic diversity, among the highest reported heterozygosity values, and no evidence of structure among the aggregations, concluding that the four aggregations are one conservation management unit. This was explained by their high estimates of gene flow among a large overall population size. Indeed, they report that their data suggest that the population has undergone a recent and rapid expansion. Robillard et al (2019) examined the effect of population segregation due to the development of a large highway that bisected historically inhabited creeks in the Susquehanna drainage of south-central New York. Using 38 historic samples collected from 1958–1968 and 26 current samples from 2015–2016 in a study area with sites 15–50 km apart, they examined genetic diversity north and south of the highway with six microsatellite loci. As expected, they found that the historic samples clustered into one population but that current samples clustered into a northern and southern sample, with three additional compelling findings. First, aggregations of turtles from their sampling sites had become more genetically differentiated over the nearly 60-year period, with fixation values dropping from 0.081 to 0.166. Second there had been a marked loss of heterzygosity in the northern population compared to historic values, and third, in a possibly related phenomenon, migration over the study period appeared to be oriented southward, coming from the northern sites to the southern sites. Overall they concluded that there had been the development of genetic fragmentation among the sample sites in the north and the south as a result of the highway, noting that among historic sites the genetic differentiation was similar to those of Tessier et al. (2005) that had comparable distances among (15–50 km), but that contemporary differentiation was comparable to Tessier et al's (2005) sites that were much farther apart (>60 km).

Summary

From its origins in the Miocene, the genus *Glyptemys* radiated to encompass two living forms, *G. insculpta* and *G. muhlenbergii*, the only emydine taxa known to exhibit chromosomal sex determination. Although the extinct form *G. valentinensis* is well-represented from Miocene deposits in Nebraska, most of the fossil record of *G. insculpta* dates to the Pleistocene and later. Considerable fossil evidence indicates two noteworthy patterns in the paleodistribution of the Wood Turtle, namely, that Wood Turtles were present in portions of their current range during previous interglacial periods, and that Wood Turtles weathered part of the last glacial advance near the southern terminus of the Appalachian Mountains in Mississippi, Alabama, Tennessee, and Georgia, with an enigmatic fossil occurrence from extreme southwestern Iowa.

To date, genetic studies provide a somewhat ambiguous interpretation. Some studies demonstrate little effect of modern fragmentation on genetic diversity and differentiation, while others clearly do. In conclusion, clearly more studies are needed under more circumstances to understand how the population size and demographic structure, underlying genetic diversity, and degree and temporal and spatial scale affect genetic fragmentation and depauperation in the Wood Turtle.

3. Historical Biology

Michael T. Jones, Lisabeth L. Willey,
Alan M. Richmond

Within a year of Le Conte's formal description of the Wood Turtle, John Edward Gray published *Synopsis Reptilium; or Short Descriptions of the Species of Reptiles* (1831), in which he provided a redundant description of the Wood Turtle under the epithet *Emys speciosa.* Gray was aware of Le Conte's work the year before—but had not read it. Pictured above is OUM 8491, a three year-old juvenile Wood Turtle and one of three syntypes of Gray's *Emys speciosa* in the Oxford Museum of Natural History. Katherine Child (Oxford Museum of Natural History)

Introduction

Understanding of the fundamental aspects of Wood Turtle biology took shape over a period of about 30 years, from the formal description of the species in 1830 to a series of detailed collections, observations, and treatments in the 1850s. In this way, it mirrored other North American species, which also came into scientific focus in the first half of the 19th century. Still, the Wood Turtle was first described later than other related species such as the Spotted Turtle (*Clemmys guttata*, 1792), Bog Turtle (*Glyptemys muhlenbergii*, 1801), and Eastern Box Turtle (*Terrapene carolina*), the last of which were among the species described by Linnaeus in 1758, 72 years earlier. Some of the earliest technical descriptions of the Wood Turtle included ecological information, forming a valuable record of a fleeting moment before the massive industrialization, degradation, and fragmentation of America's waterways. Early scientific accounts suggest Wood Turtles were more abundant historically, at least in some streams, than they are at any known location today. Wood Turtle densities in some areas may have been artificially elevated in the mid-19th century above a running mean of the previous centuries: widespread predator control and low-intensity agriculture created openings and edge habitat without the high level of turtle mortality caused by today's industrial farm machinery (Saumure 2004; Erb and Jones 2011). But the early accounts provide some basis for comparison and offer a helpful context in the search for a meaningful definition of Wood Turtle baselines.

The 19th-century accounts are interesting and noteworthy for other reasons. In these accounts, we gain perspective on the species in the context of many of the most significant discoveries of the modern era. Two centuries of logical thought were giving way to an avalanche of astonishing discoveries and theoretical frameworks as many curious men and women advanced the cause of reason. Four relevant concepts began to take form, which today frame all studies of the natural sciences in eastern North America: (1) the concept of Uniformitarianism was popularized by Charles Lyell in *Principles of Geology* (1833), stating that Earth's observable, natural processes are subject to immutable physical laws; (2) Charles Darwin's theories of natural selection (*On the Origin of Species*, 1859) led vertebrate anatomists (grudgingly, irreversibly) into the new field of evolutionary biology; (3) Gregor Mendel published the first careful experiments in inherited genetic traits (*Versuche über Pflanzen-hybriden*, 1865); and (4) the basic mechanisms of glacial geology, including the fact of a great North American ice sheet thousands of meters thick, took sharper form (Louis Agassiz, *Études sur les glaciers*, 1840).

The coincidence of the Wood Turtle's range with the highest density of North American academic institutions probably facilitated a disproportionate level of interest and corresponding records at the time. Additionally, the Transcendentalist movement gathered momentum around Boston and Concord, Massachusetts, where Wood Turtles foraged abundantly in the Assabet River, from the 1830s–1850s. As a result, scientists otherwise preoccupied with the great ideas of the day penned accounts of the Wood Turtle in a pre-industrial context.

Original Description and Nomenclature

A Specious Terrapin: Le Conte, Gray, and Holbrook

Wood Turtles gained serious scientific attention following the publication of Major John Eatton Le Conte's monograph, *Descriptions of the Species of North American Tortoises,* in 1830. Le Conte's paper, which was read before the Lyceum of Natural History of New York on December

7, 1829 and was printed in the society's Annals the following year, was the first to clearly and accurately describe the species *Glyptemys insculpta* (which he described as *Testudo insculpta)*.

Within a year of Le Conte's description, John Edward Gray published *Synopsis Reptilium; or Short Descriptions of the Species of Reptiles* (1831), in which he provided a description of the Wood Turtle under the epithet *Emys speciosa*. Gray was aware of Le Conte's earlier work but had not read it; in fact, in his Preface, Gray includes a very self-aware disclaimer that: "I have to regret that after every inquiry and considerable delay on its account, I have not been able to procure the last part of the Annals of the Lyceum of New York, in which I understand M. Le Conte has given descriptions of the American species of Tortoises."[1] Le Conte's account had primacy over Gray's by more than a year, and so we refer to the Wood Turtle today by the formal epithet *Glyptemys insculpta* (Leconte, 1830).[2]

In the decade following Le Conte's description, some confusion arose as to whether the species had actually been first described by Johann David Schoepff (1801) or August Friedrich Schweigger (1812) as *Emys pulchella*. Some of this confusion originated when Duméril and Bibron (1834) categorized the Wood Turtle as *Emys pulchella*—an epithet used by both Schoepff and Schweigger to refer to the European Pond Turtle (*Emys orbicularis*), but equated it to the species account of *Testudo insculpta* provided by Le Conte. As later demonstrated by Holbrook (1838), the *Emys pulchella* of both Schoepff and Schweigger was clearly in reference to the species today assigned to *Emys orbicularis*, not *Glyptemys insculpta*.

Le Conte's account is also one of the first to provide ecological details for the Wood Turtle. In his original description of the species, Le Conte notes that the species "inhabits the northern states in rivers and ponds: is fonder of leaving the water than any other aquatic species, and will remain uninjured in a dry place for some months."

With the distance of a few more years, in the third volume of his monumental *North American Herpetology* (1838b), John Edwards Holbrook, M.D., provided the most detailed physical description of the Wood Turtle to date. Holbrook's description was accompanied by a color lithograph of a young tannin-stained *G. insculpta*, prepared by George Lehman of Lehman & Duval in Philadelphia from a figure drawn by an artist named J. Sera (3.1). Holbrook repeated Le Conte's observation that the species resides in ponds and rivers and frequently leaves the water. Holbrook somewhat casually remarked on the aggressive tendencies of captive New Jersey *G. insculpta* toward captive Diamondback Terrapins (*Malaclemys terrapin*) and Yellow-bellied Sliders (*Trachemys scripta scripta*) that were kept in the same enclosure. Holbrook further clarified the geographic range of *G. insculpta* to include the "Atlantic states from Maine to Pennsylvania," and noted the large size of an adult from Maine, preserved in collections of the Boston Lyceum of Natural History.

Storer and De Kay

Following the serial publication of Holbrook's third volume (and an early list of the native turtles of Massachusetts by Smith in 1833), Dr. David Humphreys Storer (1840), a Boston medical

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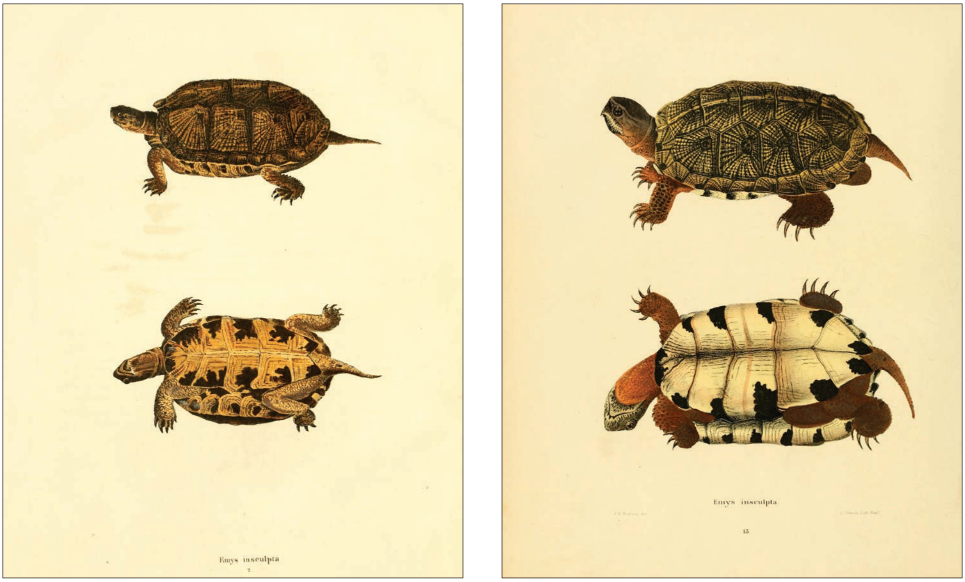
1 Gray includes a terse footnote to his disclaimer about Le Conte's book. "While correcting this proof Mr. Children has kindly put into my hands the above paper [i.e., Le Conte's book]... his *Test. insculpta* is the *Emys speciosa*."

2 Although Le Conte spelled his last name with a space, as two words, as a taxonomic authority his name is usually spelled, "Leconte." Also, see notes below on the origin of the genus name *Glyptemys.*



3.1—In the third volume of his *North American Herpetology* (1838), Dr. John Edwards Holbrook provided the most detailed early description of the Wood Turtle to date. Holbrook's description was accompanied by a color lithograph of a young tannin-stained Wood Turtle, prepared by George Lehman of Lehman & Duval in Philadelphia from a figure drawn by an artist named J. Sera. Slightly different versions of the figure were included in the 1838 edition (left) and the 1842 edition (right).

doctor, provided a brief account of the Wood Turtle from Massachusetts based on specimens received from Walpole, Concord, Amherst, and Andover. Storer considered *G. insculpta* "our most beautiful tortoise," and declared that it was "not uncommon in the ponds" of Massachusetts, but that "this species wanders a great distance from, and remains a long time out of the water, and being oftentimes found in woods and pastures, has received the common name of wood tortoise." Storer's report was followed promptly by an account by James E. De Kay (1842), who provided a species description and new observational data from the Adirondack region of northern New York. "Little is known of its habits," De Kay concluded, although he'd already determined key elements of its life history such as its preference for rivers and a propensity to wander "in woods at some distance from water."

Henry David Thoreau

Storer's brief account from Massachusetts and De Kay's from New York were followed by a notable flurry of inquiry in Massachusetts in the 1850s led by Henry David Thoreau and Louis Agassiz, who lived only about 20 km apart but very seldom crossed paths.

By 1857, Thoreau had spent many long springs exploring the Assabet River, which winds through West Concord to meet the sluggish Sudbury River at Egg Rock, where the two form the Concord River. It is clear from Thoreau's eloquent journal entries that at the time, Wood Turtles were abundant in the Assabet and some of the smaller tributaries. Despite (or because of) their abundance, Wood Turtles were an object of fascination for Thoreau throughout his later years. Throughout his journals, Thoreau vaguely recounts the actual numbers of Wood Turtles he (or his correspondents) observed in the Assabet watershed, mostly elaborating on single encounters with individual turtles. Various descriptive phrases in his journal, like: "a great many wood turtles on the bank of the Assabet to-day" and "the shores of the Assabet and of ditches are lined with them," today generate improbable images of an extremely common species.

Henry David Thoreau, in many journal entries between 1854 and 1860, provided some of the most detailed and thoughtful 19th-century observations of Wood Turtle ecology from his sojourns around Concord, Middlesex County, Massachusetts. Thoreau was perhaps the first to notice Wood Turtles' localized preference for quick-flowing streams and copious amounts of sand, noting their abundance in the quick-flowing Assabet River and their apparent absence from the stagnant Sudbury River immediately to the east. At the time, Wood Turtles were relatively common, and Thoreau reported many observations. Following the convention of Holbrook and Storer, Thoreau referred to the species as "*Emys insculpta*" or, more frequently, following Storer, "wood tortoise."

Most of Thoreau's observations were centered on the Assabet River and its tributaries, from West Concord to the confluence with the Sudbury River in Concord, Middlesex County, Massachusetts, between 1854 and 1860. Because of their unique historical value as the earliest direct empirical reports of Wood Turtles *in situ*, we have reproduced most of Thoreau's Wood Turtle sightings from his journals here in chronological order (Table 3.1). Collectively, Thoreau's observations from Concord represent the first detailed depiction of the spatial distribution of the Wood Turtle at any scale (3.2), and paint a rare picture of an abundant and ubiquitous animal routinely encountered in the course of normal day-to-day activities. Oddly, Thoreau's famous account of his adventures in Maine in 1846 (published in 1864 as *The Maine Woods*), as well as the corresponding journal entries, do not reveal any encounters with Wood Turtles. It's possible that Thoreau encountered none, but it seems more likely—given the abrupt onset of detailed reports in 1855—that he had simply not yet begun to give them much thought.

Louis Agassiz

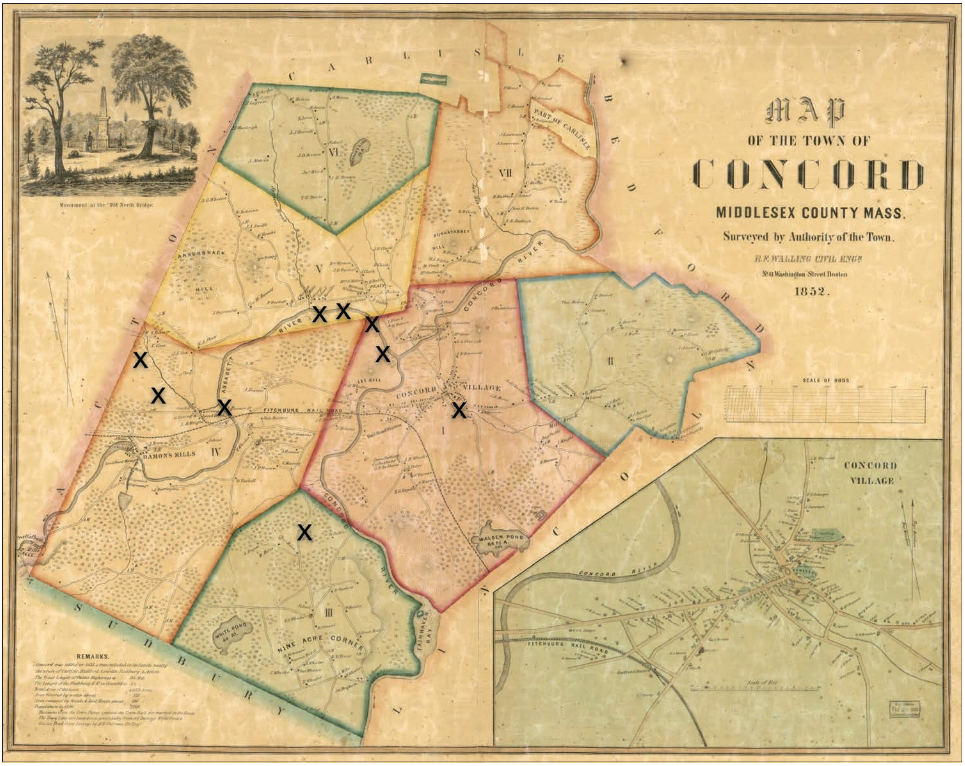
With the possible exception of Thoreau, no other 19th-century scientist or naturalist left a better record of their Wood Turtle investigations than Louis Agassiz.

Agassiz was a Swiss geologist and organismal biologist who emigrated to the United States in 1847 after studying in France, Germany, and Switzerland. Though born and raised in Switzerland (which has no native turtles), Louis Agassiz became quickly fascinated by New England's native species when he came to Harvard in 1848. Through his current, former, and future students, Agassiz extended a broad network of turtle-collectors who sent him specimens from near and far. Like Thoreau, Agassiz made several intriguing statements concerning the Wood Turtles of Lancaster, Massachusetts in his *Contributions to the Natural History of the United States of America*, including: (1) "*Emys [=Glyptemys] insculpta* is so common in the neighborhood of Lancaster, about forty miles from Boston, that I have at times collected more than a hundred specimens in one afternoon, aided by a few friends," and (2) "I am indebted to Mr. [Sanborn] Tenney for hundreds of specimens [of *Glyptemys insculpta*] from Lancaster, Massachusetts."

Within a decade, by 1857 Agassiz had published a four-volume *Contributions to the Natural History of the United States.* The enormous document is detailed, careful, creative, and painstakingly organized. On page 252 of Agassiz' first volume, he suggested that Wood Turtles should be removed from the genus *Emys*, where they had been placed by Gray in 1831, and into

Table 3.1—Wood Turtle observations at Concord, Middlesex County, Massachusetts, compiled from the journals of Henry David Thoreau between 1854–1860 provide intriguing insight into the abundance, landscape associations, and behavior of Wood Turtles during New England's agricultural period.

Date	Thoreau's Wood Turtle Observation
September 16, 1854	Wood Turtle observed in the woods near "Dugan Dessert (sic)," upper Nut Meadow Brook (AKA Dugan Brook).
March 26, 1855	Wood Turtle in "the brook" near "Hubbard's Close," shown by Gleason (1906) to be south of Mill Brook near Concord center.
April 6, 1855	Wood Turtle observed basking on bank of Assabet River.
May 4, 1855	"Yesterday a great many spotted & wood tortoises in the Sam. Wheeler--birch fence mead--pool which dries up..." Note: Samuel Wheeler lived due west of the present-day crossing of Route 2 over the Sudbury River, according to Gleason (1906)
June 19, 1855	Mated pair of Wood Turtles oberved in the Assabet River.
September 15, 1855	Mated pair of Wood Turtles oberved in the Assabet River.
October 14, 1855	Mated pair of Wood Turtles oberved in the Assabet River.
November 9, 1855	Wood Turtle basking along Assabet River near "Merrick's Pasture".
November 11, 1855	Wood Turtle "rustling" on the bank.
April 24, 1856	Wood Turtle observed at "Warren Miles' new mill" in the Dugan Brook watershed.
April 27, 1856	Wood Turtle observed.
May 7, 1856	Wood Turtle observed at "Miles' mill-pond." Note: This observation is interesting because Thoreau discusses the species' abundance: "The water thus suddenly let off, there were many spotted and wood tortoises seen crawling about on the bottom." Note: According to Gleason (1906), this site may be near Nut Meadow/Dugan Brook.
June 3, 1856	Wood Turtle observed southwest or west of Loring's Pond (today the site of Warner's Pond).
July 6, 1856	Wood Turtle eating Wood Sorrel on bank at "Assabet Bath," near the "One Arch Bridge."
March 27, 1857	Wood Turtle oberved on the edge of Dodge's Brook along the Assabet River.
May 14, 1857	13 Wood Turtles observed near the "brush fence pond" in young forest near the Assabet River. Note: This pond is referred to by Thoreau as ½ acre; three floodplain pools of roughly this size are still visible in aerial photographs from 1938, present along the right bank upstream of the confluence. Is this the same pond as on May 4, 1855?
October 21, 1857	Mated pairs of Wood Turtles observed along the lower Assabet River.
November 17, 1857	Wood Turtle observed on the "bank" (of the Assabet River?)
April 17, 1858	Wood Turtle observed basking on "shore" (of the Assabet River?)
May 7, 1858	Wood Turtle by Tarbell's along the Assabet River northeast of West Concord.
May 28, 1858	Wood Turtle observed.
June 6, 1858	3 or 4 Wood Turtles nesting on gravel bank south of "Assabet Bath" along the Assabet River.
June 10, 1858	Nesting female Wood Turtle observed, possibly near the "White Cedar Swamp" near Spencer Brook.
June 10, 1858	Wood Turtle nest near the "Assabet Bath" along the Assabet River.
June 11, 1858	6 Wood Turtles nesting near the "Assabet Bath" along the Assabet River.
June 11, 1858	6 Wood Turtles nesting in Abel Hosmer's rye fields, and 2 nests discovered there. Note: Abel Hosmer evidently owned land on both sides of the Union Turnpike's One Arch Bridge (near present-day Route 2), and Wood Turtles nested in Hosmer's rye fields south of the road and on sandy soils north of the road.
June 17, 1858	"...coming across the level pasture west of E. Hubbard's swamp, toward Emerson's, I find a young *Emys insculpta*...."
July 19, 1858	3 or 4 nests of Wood Turtle and Musk Turtle on sandbank (of Assabet River?)
May 17, 1859	Individual Wood Turtle observed on the "bank" (of the Assabet River?)
June 10, 1860	Wood Turtles present in Hosmer's sandy field north of Assabet River and near the One Arch Bridge.
June 12, 1860	2 or 3 Wood Turtle nests on a sandbank along the Assabet River.
June 14, 1860	Wood Turtle nest observed at "Dugan Desert."



3.2—Henry David Thoreau's Wood Turtle observations from Concord, Middlesex County, Massachusetts in the 1850s represent the first detailed description of the species' ecology and distribution, and paint a rare picture of an abundant animal routinely encountered. Here, some of Thoreau's Wood Turtle observations are reproduced on an 1852 map of Concord. Thoreau frequently observed Wood Turtles in the lower Assabet River but noted their absence from the adjacent Sudbury River, which had a more sluggish flow.

the new genus *Glyptemys*.[3] In the same volume, Agassiz makes wide-ranging observations on Wood Turtles' scute morphology,[4] vocalizations,[5] foot morphology, and ease of captive care in dry terrestrial conditions. Agassiz describes the species as "common in the North-eastern States, and is found only as far south as New Jersey." He notes another specimen from as far north as 47˚N in Maine.

In a terse footnote, Agassiz tries to clarify a point that had interested Holbrook nearly twenty years earlier: "This is the *Emys insculpta* of Major LeConte. Duméril and Bibron have erroneously identified it with Schoepff's *Testudo pulchella*, which is the young of the European *Emys lutaria*.

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3 Earlier on the very same page, Agassiz suggested moving the Bog Turtle (*Glyptemys muhlenbergii*) from *Emys* to the new genus *Calemys*, resulting in some minor confusion more than 140 years later when the two species were together determined to form a monophyletic genus and were placed by Holman and Fritz (2001) into the genus *Glyptemys.*

4 Agassiz notes the tendency of some Wood Turtles to become entirely smoothed, and points out that the *Emys speciosa* of Gray (1831) was based on a smooth specimen of *G. insculpta*.

5 In a passage on vocalizations in turtles, Agassiz claims to have heard Wood Turtles and several other emydid turtles "emit a piping note."

Emys speciosa, Bell, is the smooth variety of the old age."[6] Essentially, Agassiz paused to reiterate that Le Conte had properly first identified the Wood Turtle; but Duméril and Bibron incorrectly thought that Schoepff had described the Wood Turtle as *Testudo pulchella*, when actually Schoepf (and subsequently, Schweigger) had used the name *T. pulchella* with reference to the European Pond Turtle (*Emys orbicularis*). It may seem arcane and circular today, but imagine the excitement and confusion as the North American species were catalogued and given scientific names, coupled with the discouraging communication delays and the ambiguity of the written word.

Volume II of Agassiz's *Contributions to the Natural History of the United States* contains additional detailed and careful observations on the biology of Wood Turtles. In Part III of Volume II, a standalone segment titled *Embryology of the Turtle*, Agassiz provides details of the reproductive biology and egg anatomy gleaned from multiple dissections of reproductive females. Some of Agassiz's (and Sanborn Tenney's) Wood Turtle specimens are still at Harvard University in the Museum of Comparative Zoology (3.3) and the *Staatliches Museum fur Naturkunde* (State Natural History Museum), Stuttgart, Germany (3.4).

In two passages in Volume I, Agassiz leaves an evocative account of the abundance of Wood Turtles at Lancaster, Worcester County, Massachusetts, which lies about 50 km west of Boston. In one passage he reports, "I am indebted to Mr. S. Tenney[7] for hundreds of specimens from Lancaster, Massachusetts." In another, when describing the generally low detection rates of young Emydid turtles (compared to adults of a species) he reports: "…Nothing could prove more directly this difference in the mode of life of the young and the adult than the fact, that though *Emys insculpta* is so common in the neighborhood of Lancaster, about forty miles from Boston, that I have at times collected over one hundred in an afternoon, aided by a few friends, I have never yet been able to obtain a single young specimen of the first year, even though a whole school of young men were called to aid in the search." Even more than the journal entries of Thoreau, these brief passages suggest that Wood Turtles were an abundant species in the Nashua River watershed of the 1850s. More than 160 years later, we (Jones et al. 2019) returned to Lancaster to examine remaining populations of Wood Turtles, and found suitable habitat (3.5) but only a small, vulnerable population that had significantly larger adult body size, greater sexual dimorphism, and faster growth rates compared to the specimens studied by Agassiz (3.6).

Return to Lancaster

Collectively, Agassiz's accounts appear to describe population densities unheard of in New England today, but his generalizations are impossible to directly compare to modern populations. While these references provide some historical context and anecdotal value, the information provided is insufficiently quantitative to infer many details. One hundred and fifty-five years later,

6 Agassiz's original italics are retained here.

7 Sanborn Tenney was a particularly ambitious student of Agassiz'. Following his graduation from Amherst College in 1853, Tenney took an entry-level teaching position at the New England Normal School in downtown Lancaster before later studying under Agassiz at Harvard. The Normal School is situated directly across the street from a meandering, sandy section of the Nashua River, at the confluence of the North Nashua River and the Stillwater River in the Merrimack River drainage of Worcester County. It is very likely that his post at the Normal School on Main Street was Tenney's base of operations as he collected Wood Turtles for Agassiz, although the exact site isn't known.

3.3—The Museum of Comparative Zoology at Harvard University maintains a series of Wood Turtles collected in the 1850s at Lancaster, Worcester County, Massachusetts, USA by Louis Agassiz and Sanborn Tenney. MUSEUM OF COMPARATIVE ZOOLOGY, HARVARD UNIVERSITY

3.4—Two of the Wood Turtles collected in the 1850s at Lancaster, Worcester County, Massachusetts, USA by Louis Agassiz and Sanborn Tenney are juveniles preserved at the State Museum of Natural History Stuttgart (SMNS), Germany. *Top:* SMNS 3794.1; *Bottom:* SMNS 3794.2. Günter Stephan (State Museum of Natural History Stuttgart)

3.5—More than 160 years after the explorations of Louis Agassiz and Sanborn Tenney, the current authors returned to their general study area in Lancaster, Worcester County, Massachusetts, and found plentiful, suitable stream habitat—much of it seemingly unoccupied by the species. Mike Jones

in 2009, we tried to rediscover the Agassiz-Tenney site in Lancaster and to document what had become of it.

Harvard University's sample of Wood Turtles from Lancaster in 1854 represents a collection of animals from an entirely different context than today. In the mid-1800s, the landscape of southern New England was on the verge of industrialization, mostly deforested and lined from the Atlantic to the Hudson River with agricultural fields and small town centers, but farms were rapidly being abandoned as mill communities like Holyoke and Lowell were on the rise. Lancaster itself and the surrounding areas were largely cleared for agriculture.[8] It was in this agricultural context that 19th-century New England biologists began to generate a thorough account of the region's reptile and amphibian fauna, including some of the earliest such accounts in the country.

A century and a half later, not only has the landscape changed, but the abundance of turtles has also changed. We spent 30 days surveying the streams throughout the Lancaster area to find Agassiz and Tenney's population. We began our search by surveying the Nashua River itself, focusing heavily on the area within walking distance of the Normal School. After seven days of searching in March and April by canoe and on foot, we hadn't found a single Wood Turtle. Casting a wider net, we examined aerial photos for likely sites throughout the rest of Lancaster. We found several and explored most of them through May, June, September, and October. In the end, 120 hours of searching yielded exactly 31 Wood Turtles in the entire town of Lancaster and vicinity in 2009, a capture rate about 100 times worse than Agassiz and Tenney's inferred rate.

8 Lancaster, Massachusetts struck Thoreau (1842) as similar to his own native Concord, Massachusetts: "...we found ourselves almost at home again in the green meadows of Lancaster, so like our own Concord, for both are watered by two streams which unite near their centres, and have many other features in common. There is an unexpected refinement about this scenery; level prairies of great extent, interspersed with elms and hop-fields and groves of trees, give it almost a classic appearance... a couple of miles brought us to the southern branch of the Nashua, a shallow but rapid stream, flowing between high and gravelly banks..."

The limited number of Wood Turtles we encountered in 2009 suggests that either: (1) Agassiz and his friends were 100 times better at finding Wood Turtles than we are; (2) Agassiz exaggerated the number he had seen; or (3) in the 155 years following Agassiz's collections, the population had collapsed. While some combination of these might be true, we evaluated each in turn. Our population estimates based on recapture rates from the Lancaster streams suggest that there are, indeed, very low Wood Turtle densities on these rivers. Population decline appears to be the most likely cause for the discrepancy between our numbers and Agassiz'. It is a sobering fact that the populations of these rivers, once consisting of hundreds, or perhaps even thousands of turtles, have collapsed to only a few individuals in the span of fewer than four turtle generations.

3.6—Despite abundant, suitable stream habitat, Wood Turtles are very rare today in Lancaster, Worcester County, Massachusetts. Pictured is male #481, captured within the same watershed as Louis Agassiz' and Sanborn Tenney's likely collection areas. MIKE JONES

Thoreau and Agassiz Share Dinner at Emerson's

On March 20, 1857 Thoreau and Agassiz—two of the most peculiar and noteworthy men of the century—met at Ralph Waldo Emerson's house in Concord, Massachusetts, where the discussion ranged from puffball fungi to the ability of fish and caterpillars to freeze and thaw without injury. A large portion of the conversation, however, focused on the variety of turtles that inhabited 19th-century Concord and nearby Cambridge. The account of that evening, as recorded by Thoreau in his journal, indicates that the two men discussed Painted, Snapping, and Blanding's Turtles, but it's not hard to imagine that they also discussed the abundant "wood tortoises" that inhabited the clean rivers of eastern Massachusetts. It may be surprising to some that two thinkers of such stature and intellect (Thoreau's *Walden; or, Life in the Woods* had been published three years earlier, and Agassiz, the father of glacial theory, was busy completing his sprawling and detailed *Contributions to the Natural History of the United States*) would focus on turtles, of all topics. Of course, anyone who has spent time in the field with New England's turtles can understand why both men were enamored and fascinated by turtles.

Other Significant Contributions

After the landmark contributions of Agassiz (1857) followed a period of detailed syntheses and a few noteworthy local accounts. Strauch (1865) prepared a detailed synthesis, borrowing heavily from Holbrook, Agassiz, Storer, and De Kay. An early local account to follow Agassiz was J. A. Allen (1868), who reported on the abundance and feeding habits of Wood Turtles near Springfield, Massachusetts. Charles Conrad Abbott published *A Naturalist's Rambles About Home* in 1884, providing some light details about the Wood Turtle's ecology in central New Jersey. Abbott was familiar with and heavily quoted from Agassiz, but he referred to the Wood Turtle as the "Rough-backed Terrapin," or "Diamond-back," without addressing the other species commonly called by that name in New Jersey (i.e., *Malaclemys terrapin*). Abbott notes that the Wood Turtle was "considered a great delicacy by epicures, and has been so persistently

3.7—A designated lectotype for John Le Conte's *Testudo insculpta* is a young male specimen in the *Muséum national d'histoire naturelle* (MNHN), Paris, France (MNHN-RA-0.9452), pictured here. *Shell:* Antoine Fraysse; *Head and limbs:* Roger Bour (Muséum national d'histoire naturelle)

3.8—Within a year of John Le Conte's description of the Wood Turtle as *Testudo insculpta*, John Edward Gray described the species as *Emys speciosa*—the Specious Terrapin. Three syntypes of Gray's *Emys speciosa* are preserved in the Oxford University Museum, Oxford, United Kingdom. The Oxford specimens include, from top to bottom: the dry shell of an adult female (OUM 8489), a taxidermied adult male (OUM 8490), and a taxidermied juvenile (OUM 8491). Katherine Child (Oxford Museum of Natural History) hunted that now it is quite scarce." Abbott goes on to describe the behavior of Wood Turtles near a "bubbling spring," where they reportedly would burrow in the mud around the spring in search of invertebrates. Abbott's account is interesting, but includes questionable details that aren't easily substantiated elsewhere, such as the occurrence of Blanding's Turtles in central New Jersey in the 1880s.

A significant, highly detailed, and interesting account of Wood Turtles in Pennsylvania was provided by H.A. Surface (1908) in his *First Report on the Economic Features of Turtles of Pennsylvania*. Surface lists seven regional or local names for the species (including Sculptured Tortoise, Fresh Water Terrapin, Wood Terrapin, Red Bellied Turtle, Rough Back Terrapin, Water Terrapin, and Wood Tortoise), and provides a brief description and a line-art figure. He also provides more than 30 county-level occurrence records and indicates that they have become scarce as the result of collection for food. Surface reported that the species "is liable to be found in any habitat or haunt throughout its range where the conditions are suitable, or where there are damp leaves in rather secluded woods." He presents contrasting information on their overwintering habitat, suggesting (as is most likely) that Wood Turtles hibernate in streams and ponds, and elsewhere stating that he has seen them hibernate in dry woods in Centre County (near a temporary pool). Perhaps the terrestrial turtles were early to emerge or late to brumate. Surface also provides a quantitative summary of the stomach contents collected during dissections, which are described more thoroughly in Chapter 6.

Type Specimens

A designated lectotype for Le Conte's *Testudo insculpta* is a young male specimen in the *Muséum national d'histoire naturelle* (MNHN), Paris (MNHN-RA-0.9452) (3.7). The type locality for *G. insculpta* is the northern United States (Stejneger and Barbour 1923), further narrowed down to the vicinity of New York City by Schmidt (1953).

Three syntypes of Gray's *Emys speciosa* and the holotype of Gray's *Emys speciosa*, var. *levigata,* are preserved in the Oxford University Museum (Nowak-Kemp 2009; Nowak-Kemp and Fritz 2010) (3.8). The Oxford specimens include the dry shell of an adult female (OUM 8489) (holotype of Gray's *Emys speciosa*, var. *levigata*), a taxidermied adult male (OUM 8490), and a taxidermied juvenile (OUM 8491). According to Gray (1831), further syntypes of *Emys speciosa* are in the *Muséum national d'histoire naturelle* (MNHN), Paris (Nowak-Kemp and Fritz 2010).

Etymology

The etymology of *Glyptemys* is based upon the Greek *γλύφειν* or *glyphein* ("to carve") and the Classical Latin *emys*, from the Greek *ἐμύς* ("freshwater tortoise") (Brown 1956). Thus *Glyptemys* refers to the somewhat "carved [or engraved]" appearance of the carapace (Ernst and Lovich 2009). The species name *insculpta* is from the Latin to carve or engrave, again referring to the appearance of the carapacial scutes (Brown 1956; Ernst and Barbour 1972; Ernst and Lovich 2009).

Genus *Glyptemys*

The Wood Turtle was first assigned to the genus *Glyptemys* by Agassiz (1857). Agassiz provided the first full description of the genus *Glyptemys,* as follows:

"III. *Glyptemys*, Ag. The upper jaw projects in the form of a bill, arched downward, notched at the tip, and so compressed sidewise that the margin of the mouth is narrower than the top of the forehead over the nose. The edge of the lower jaw is straight, except the tip, which is greatly arched upward. The horny sheath of the horizontal, alveolar surface is narrow in both jaws. The margin of the shield is very thin and spreading in the young, and the surface of the scales is coarsely granular. In the adult they have radiating ridges, which in very old age are sometimes entirely smoothed down."

The genus *Glyptemys* is described by Holman and Fritz (2001; combined from Ernst 1972; Ernst and Bury 1977; Ward 1980; Ernst et al. 1994 and unpublished data of Holman and Fritz) as follows:

Glyptemys Agassiz, 1857. Small to medium-sized turtles (shell length 8.0–22.5 cm), with an elongated, keeled carapace which may be serrated posteriorly. Premaxillary notch with adjacent tomiodonts. Foramen caroticopharyngeale located anteriorly of articular condyles. Alveolar shelf with lateral ridge. Horney seams between submarginals and pectoral and abdominal scutes located on the hyo- and hypoplastron. Entoplastron elongated to bell-shaped. Xiphiplastral notch moderate to well-developed.

Table 3.2—Selected synonyms of the Wood Turtle's correct scientific binomial epithet, *Glyptemys insculpta*.

Synonym	Author
Testudo insculpta	Le Conte 1830
Terrapene scabra	Bonaparte 1830
Emys speciosa	Gray 1831
Emys speciosa, var. *levigata*	Gray 1831
Emys inscripta	Gray 1831
Emys insculpta	Harlan 1835
Clemmys insculpta	Fitzinger 1835
Geoclemys pulchella	Gray 1856
Glyptemys insculpta	Agassiz 1857
Clemmys insculpta	Strauch 1862
Glyptemys pulchella	Gray 1869
Chelopus insculptus	Cope 1875
Clemmys insculpta	McDowell 1964
Glyptemys insculpta	Holman and Fritz 2001

Synonymy

Synonyms for *Glyptemys insculpta* are provided in Table 3.2 (adapted and revised from Jones 1865; Boulenger 1889; Fowler 1906; Babcock 1919; Ernst 1972; McCoy 1982; Vogt 1981; Bowen and Gillingham 2004.)[9]

Summary

The Wood Turtle was described as *Testudo insculpta* by John Eatton Le Conte in 1830. Le Conte's description narrowly superseded a careful description (as *Emys speciosa*) by John Edward Gray in 1831. In retrospect, given the species' apparent abundance in the mid-19th century, Le Conte's and Gray's descriptions came several decades after the formal descriptions of most other related emydine taxa such as *Terrapene carolina, Clemmys guttata*, and *Glyptemys muhlenbergii*.

Within 20 years—by the 1850s—the Wood Turtle had risen to a prominent position in the published works of Louis Agassiz and the journals of Henry David Thoreau. Agassiz and Thoreau were both based in eastern Massachusetts, and coincidentally provided unusually detailed records

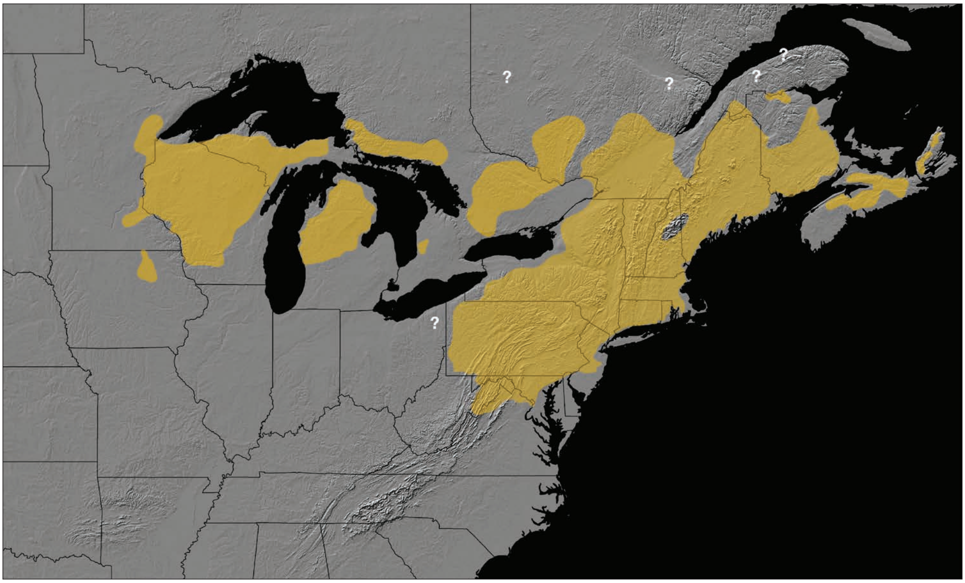
9 Storer (1840) and Ernst (1972) report that Say's (1825) *E. scabra* synonymy is erroneous (misidentified and placed with *Testudo scabra* L.). Holbrook (1838) determined that Schweigger's (1812) *Emys pulchella* is actually *Emys orbicularis*.

of the Wood Turtle's ecology and abundance in the Nashua River and Assabet River watersheds. Unlike Thoreau, who rarely collected live reptiles for scientific collections, Agassiz preserved many of his specimens at Harvard's Museum of Comparative Zoology. These specimens, coupled with the written works of both Agassiz and Thoreau, provide a unique glimpse into the Wood Turtle's status during the height of the agricultural period in the northeastern United States.

4. Distribution

Michael T. Jones, Lisabeth L. Willey, Joe Crowley, Thomas S. B. Akre,
Phillip deMaynadier, Derek T. Yorks, Jeffrey W. Tamplin, Brian Zarate,
Raymond A. Saumure, Andrew Badje, Katharine D. Gipe,
John D. Kleopfer, Michael Marchand, Steve Parren, Maureen Toner

With the exception of the Snapping Turtle, Wood Turtles range north of the 45th parallel more extensively than other freshwater turtle species in eastern North America. In some areas of Maine and eastern Canada, Wood Turtles may be the only freshwater turtle species in fluvial habitats. American Turtle Observatory

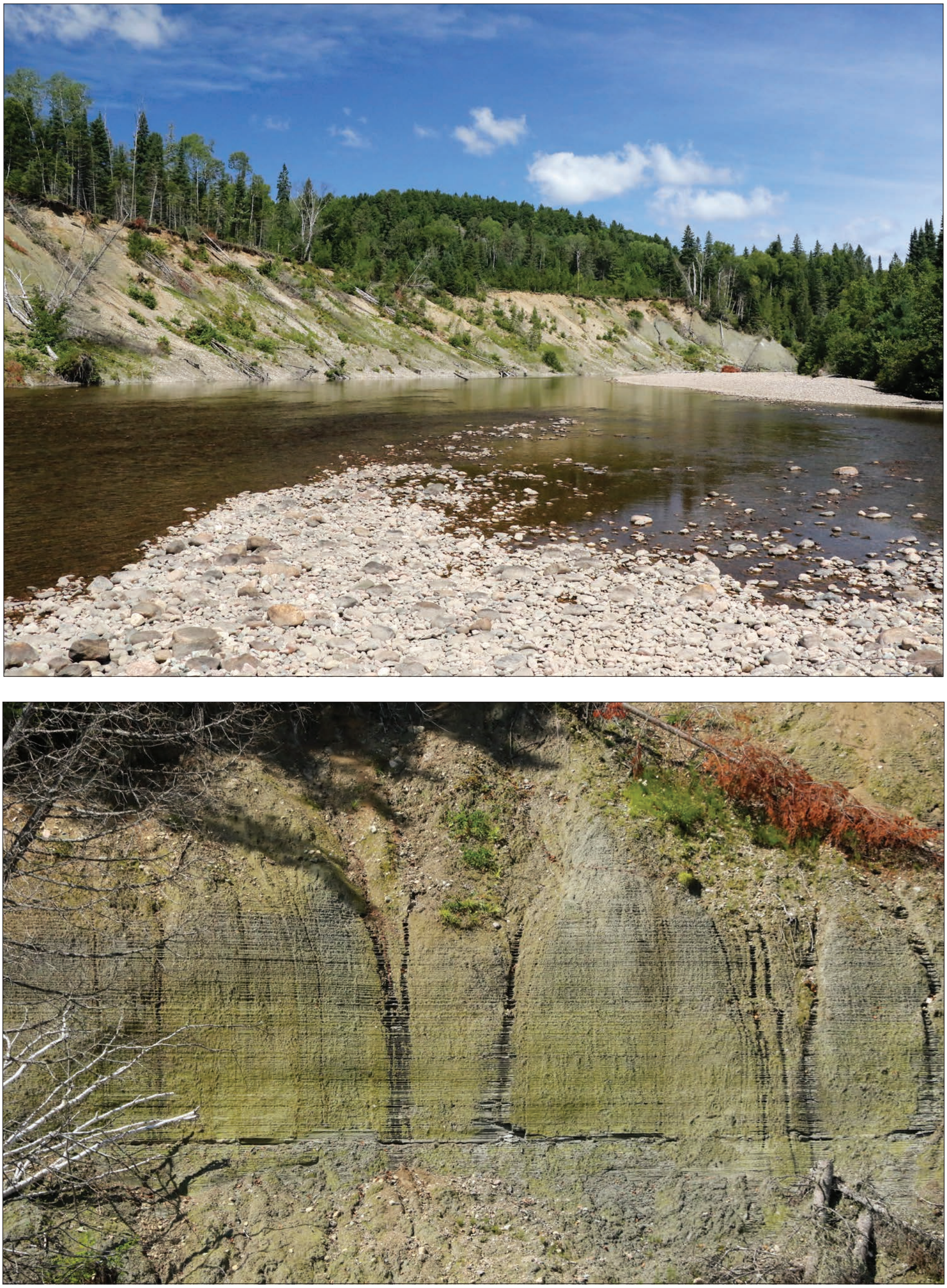


4.1—Recent distribution of the Wood Turtle. Base DEM created by Emmy Whistler / Antioch University New England.

Introduction

Wood Turtles' extent of occurrence spans nearly 9˚ of latitude from the southernmost populations in Virginia and West Virginia (38.6˚N) to the northernmost confirmed populations in Québec and New Brunswick (47.5˚N). The configuration of the Wood Turtle's large distribution provides a unique lens through which to interpret the ecology and biogeography of eastern North America (4.1). For example, the Wood Turtle's current range occurs mostly within the area that was glaciated by the southernmost lobes of the Laurentide Ice Sheet during the final (or Wisconsinan) phase of the Pleistocene glaciation,[1] which ended roughly 18,000 years before the present (ybp) and affected most of the continental regions from Nova Scotia to Iowa. In fact, only about 18% of the Wood Turtle's current range remained unglaciated during the Wisconsinan, and an even smaller fraction was never glaciated during any of the Pleistocene glacial advances. As a result, in most areas, the local distribution of Wood Turtles is strongly influenced by the landforms, alluvium, till, and debris of the post-glacial landscape (4.2). Here we examine the Wood Turtle's distribution across the various ecological gradients and political boundaries of the eastern North American landscape, and consider the commonalities and differences across each of these areas, illuminating the biogeography of the North American continent.

1 The Pleistocene epoch is a geological time period that spanned from about 2.5 million years ago until 11,700 years ago, during which time eastern North America was heavily glaciated by the Laurentide Ice Sheet. The Laurentide ice expanded and contracted from a center of mass in eastern Canada, presumably displacing Wood Turtles to southern refugia (see Chapter 2, Evolution). Laurentide ice eroded mountains, left diverse debris fields of till (unsorted glacial rock, silt, and sand) and outwash (sorted meltwater soils). The glacial retreat rearranged watersheds and streamcourses, providing a footprint for recolonization by the Wood Turtle.



4.2—Less than 20% of the Wood Turtle's current range remained unglaciated during the Late Pleistocene. In most areas, the local distribution of Wood Turtles is strongly influenced by the landforms and debris of the post-glacial landscape. *Top:* A Wood Turtle stream exposes an extensive alluvial deposit from a proglacial lake in Ontario. *Bottom:* Varved sediments along this river in Ontario indicate the former presence of a proglacial lake. Mike Jones

4.3—Wood Turtles occur primarily within two major geological or physiographic provinces, the Canadian Shield and the various ranges of the Appalachian Mountains. *Top:* Wood Turtle habitat in the Adirondacks of New York, a southerly exposure of the Greenville Province of the Canadian Shield. *Bottom:* Wood Turtle habitat in a subsidiary range of the Appalachian Mountains in New England. Mike Jones

4.4—Most extant Wood Turtle populations lie within forested ecoregions of eastern North America. Only the small, isolated Wood Turtle populations in southeastern Minnesota and Iowa lie completely within the Great Plains Ecoregion. Mike Jones

Physiography

Today, Wood Turtles occur primarily within two major geological or physiographic provinces: (1) the Laurentian and Superior Uplands of the Canadian Shield, and (2) various ranges of the Appalachian Highlands (Fenneman and Johnson 1946) (4.3). Wood Turtles occur to a lesser extent on the interior plains, and tend to be quite rare upon, or absent from, the Coastal Plain portions of many eastern states.

Ecography

At a continental scale, Wood Turtle populations are strongly associated with the forested ecoregions of eastern North America. They are widely distributed within the southern tier of the Northern Forest and the northern reaches of the Eastern Temperate Forest (Omernik 1987; CEC 1997). Only the small, isolated Wood Turtle populations in Iowa and southeastern Minnesota are considered to lie completely within the Great Plains ecoregions (4.4). At a finer scale (i.e., USEPA Level II Ecoregions), Wood Turtles are mostly associated with the Atlantic Highlands, Mixed Wood Plains, Mixed Wood Shield, and Appalachian Forests ecoregions, with limited, and likely impaired, populations in the Southeastern Plains ecoregion of Pennsylvania, Maryland, and Virginia. As noted, the populations in Iowa and southeastern Minnesota are noteworthy as the only occurrences within the Temperate Prairies ecoregion.

Hydrography

Wood Turtles occur in streams and watersheds that flow to the Atlantic Ocean, the Gulf of St. Lawrence, and the Gulf of Mexico via the Mississippi River. On the Atlantic slope, Wood Turtles are widely distributed in every major watershed from the St. John River to the Potomac River. In the Great Lakes (St. Lawrence) watershed, extant Wood Turtle populations are associated with the watersheds of southern Lake Superior, northern Lake Michigan, Georgian Bay, portions of Lake Huron, and eastern Lake Ontario. Historically, the species was more widely distributed around Lake Huron, Lake Erie, and Lake Ontario. Streams draining to the Gulf of Mexico that are occupied by Wood Turtles fall into two broad classes: those of the Upper Mississippi River, which include the populations in western Wisconsin, southeastern Minnesota, and Iowa; and those of the Ohio Valley, which include the Allegheny and (to a limited extent) Monongahela watersheds of Pennsylvania and West Virginia (Jones et al. 2015).

Our modern understanding of the Wood Turtle's native range was not firmly in place until the mid-20th century. The only significant, recent range extension—to Cape Breton Island, Nova Scotia—was published in 1973 (Gilhen and Grantmire 1973). Still, a few important biogeographical questions remain unresolved. For example, the current population status of Wood Turtles in Delaware and Ohio is unclear. Wood Turtles are likely native to, but functionally extirpated from, both states. And in Iowa, researchers are continuing to document the full distribution of the species (Tamplin 2019). The Wood Turtle's range has substantially contracted in recent decades (Willey et al. 2022). We know of no watersheds outside of the native range in which Wood Turtles have become established.[2]

Distribution in the United States and Canada

Connecticut

Wood Turtles have been reported from every county in Connecticut (Klemens 1993). Early distributional data were provided by Babcock (1919) and Finneran (1948). Populations seem to be rare in the coastal zone as well as parts of Windham and New London counties, but are more widely distributed in the hills of eastern Connecticut, between the Connecticut River Valley and the Quinebaug River Valley (Klemens 1993).

Delaware

The historical status of Wood Turtles in Delaware is unclear (White and White 2002). Early summaries of reptiles and amphibians from Delaware did not report any specimens of Wood Turtle (Stone 1906, Fowler 1925, Conant 1945). Biologists have surveyed northern Delaware for other turtle species, including Bog Turtles (*Glyptemys muhlenbergii*; Arndt 1977) and Eastern Box Turtles (*Terrapene carolina*; Kipp 2003; Nazdrowicz et al. 2010), but none reported occurrences of Wood Turtles. Wood Turtles very likely occurred naturally within the past few hundred years in New Castle County, which borders Pennsylvania and Maryland, where Wood Turtle records have been reported from neighboring Cecil County, Maryland (Harris 1975), and Chester County, Pennsylvania (Hulse et al. 2001; PARS 2020). Jim White (2002) reported two individuals from New Castle County, but follow-up surveys failed to detect Wood Turtles. A single female turtle captured in New Castle County was radio-tracked for several years by Delaware Division of Fish and Wildlife, but no other Wood Turtles were found (Delaware DFW, unpubl. data). Suitable habitat— albeit fragmented—remains in northern Delaware (Willey et al. 2021), but it appears clear that the Wood Turtle is functionally extirpated from the state (4.5). A noteworthy archeological occurrence of Wood Turtle was reported by the Delaware Department

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2 Note, however, that Witmer and Fuller (2011) include the Wood Turtle in an appendix of vertebrates that have been introduced to novel sites within the United States.

4.5—Although some suitable habitat persists in New Castle County, Wood Turtles appear to be functionally extirpated from Delaware. Mike Jones

of Transportation during excavations near Dover, Kent County: faunal remains recovered from the Tomas Dawson farm at Coopers Corners, Kent County, Delaware, reportedly included one fragment of Wood Turtle. The assemblage was dated to 1740–1780 (Bedell 2002).

Illinois

Wood Turtles are clearly not native to Illinois, but there are several enigmatic records from the state. One series of two specimens from Evanston, Cook County, were shipped to the Museum of Comparative Zoology between 1864 and 1872 (MCZ 4056), but it seems plausible that these turtles were erroneously labeled, given that Evanston is the home of Northwestern University. Another specimen was observed in the Des Plaines River Canal, Cook County (Miller 1993, in Iverson 1992), which is clearly atypical habitat as well as a highly disjunct observation, and does not appear to represent a local population. Cahn (1937) describes a Wood Turtle specimen from the Rock River south of Janesville, Wisconsin, "11 miles" north of the Illinois border, but dismisses it as a likely "transport"; nevertheless, he provides full treatment to the species in his *The Turtles of Illinois.*

Iowa

The Wood Turtle is narrowly restricted to the tributaries of the Upper Cedar River drainage of northeastern Iowa. The Iowa population likely extends across the Minnesota state border into the headwaters of the Upper Cedar River in Dodge, Freeborn, and Mower counties. The first (erroneous) report of Wood Turtles in the state was made by Palmer (1924), who reported a juvenile Wood Turtle from Ames, Story County, which extended the range south and west from recently discovered sites on the Wisconsin-Minnesota border (e.g., Wagner 1922). The location was highly unusual; not only did it constitute a new state record, but it was also near the geographic center of the state, and well within the Temperate Prairies ecoregion. Palmer's record was subsequently incorporated into large-scale compendia, such as Clifford Pope's *Turtles of the United States and Canada* (Pope 1939). Bailey (1941) discredited the observation as a misidentified juvenile Blanding's Turtle (*Emydoidea blandingii*). However, by the mid-1940s, Wood Turtles were well known to occur in the Cedar watershed of northeastern Iowa, and today the species is known to occur in Black Hawk, Bremer, Butler, Cerro Gordo, Floyd, Franklin, and Mitchell counties (Otten 2017). Isolated Natural Area Inventory records in Benton, Delaware, Iowa, and Washington counties from 1989 are likely misidentifications; no other specimens have been reported from these locations and there are no lotic water sources at the indicated localities (Otten 2017). Recent reports of Wood Turtles in the Wapsipinicon River have not been substantiated, but the Wapsipinicon is an adjacent watershed to the Upper Cedar River and small tributaries of these two rivers lie in close proximity in Bremer, Chickasaw, and Mitchell counties (Tamplin, unpubl. data). Populations in Black Hawk and Butler counties are the subject of long-term research by biologists at the University of Northern Iowa (Tamplin et al. 2006a; 2006b; Tamplin et al. 2009; Spradling et al. 2010; Williams 2013; Berg 2014; Otten 2017; and Lapin et al. 2019).

Maine

Wood Turtles occur nearly statewide in Maine with the exception of outlying islands, and have been reported from all but Sagadahoc County (Hunter et al. 1999; Maine Department of Inland Fisheries and Wildlife, unpubl. data). Early accounts of Wood Turtles in Maine include Say (1825), and perhaps Williamson's (1832) account of a "speckled land turtle." Other early reports include those of Agassiz (1857), who reported a northern specimen from Aroostook County, and Fogg (1862). Verrill (1863) noted that Wood Turtles were "common" in the vicinity of Norway, Oxford County, but that the species was apparently uncommon east of the Penobscot River. Boardman (1903) reported Wood Turtles from the vicinity of Calais. The Wood Turtle is not native to any of the many islands of the Maine coast: records from Isle au Haut (Knox County) in 1999 and Mount Desert Island (Hancock County) in 1958 and 1989 (Brotherton et al. 2004; Maine Department of Inland Fisheries and Wildlife, unpubl. data) must represent released or escaped animals. Historical accounts of Wood Turtles (and other turtles) in Maine are summarized by McCollough (1997), who also noted that Wood Turtles are less abundant near the coast.

Maryland

In Maryland, Wood Turtles occur in the Central Appalachians, Ridge and Valley, Blue Ridge, and Northern Piedmont Ecoregions (Conant 1958; Harris 1975; Miller 1993) and in all of Maryland's western counties, with limited evidence of populations near the Coastal Plain. It

4.6—Wood Turtles were reported in the vicinity of the Conowingo Dam in the 1940s, providing additional support for native occurrences of Wood Turtles near the Coastal Plain in Maryland. Mike Jones

4.7—Historically, Wood Turtles were reported from Cecil County, Maryland. These outlying populations on Maryland's Coastal Plain is likely extirpated. Mike Jones

now seems clear that Wood Turtles occurred naturally in the lower Susquehanna and the lower Potomac Rivers very near the Coastal Plain, as well as several creeks in the vicinity of Washington, D.C., and Arlington, Virginia (Akre and Ernst 2006), though this has been a contentious subject. Norden and Zyla (1989) presented a series of 12 records from Coastal Plain counties (including the first for Anne Arundel County) and voiced support for a native population of Wood Turtles on the Coastal Plain. Miller (1993) questioned their conclusions, citing a lack of historical data and museum specimens. Wood Turtles collected near Havre de Grace, Cecil County (e.g., McCauley 1945) were presumed by Reed (1956) to be waifs displaced well into Pennsylvania from upstream in the Susquehanna. However, Wood Turtles were reported in the immediate vicinity of the Conowingo Dam by Cooper (1949), supporting the native occurrence of Wood Turtles in the lower Susquehanna (4.6). There was historically a population reported from Elk Neck, Cecil County (White and White 2002), which is apparently extirpated (4.7). A single record near Easton, Talbot County, Maryland (Reed 1956) is the only record from Maryland's eastern shore. This record was dismissed by McCauley (1945, in Reed 1956) and Conant (1958).

Massachusetts

Wood Turtles occur throughout much of Massachusetts below 610 m in elevation (Jones, unpubl. data) with the exception of the Coastal Plain, outlying islands, and the most urbanized areas (Lazell 1976; MassWildlife NHESP, unpubl. data). Wood Turtles had been well documented in eastern Massachusetts by the 1850s, and were included among the native turtles on the Commonwealth's first reptile list prepared by Smith (1833). Subsequently, Wood Turtles were reported by Storer (1840), Thoreau (many journal reports from 1854–1860), and Agassiz (1857).[3] Allen (1868) reported Wood Turtles to be "common" in the vicinity of Springfield, Hampden County, but Babcock (1919) reported Wood Turtles were not common around Dedham, Norfolk County.

3 A full account of the observations made by Thoreau and Agassiz are provided in Chapter 3.

4.8—Wood Turtles are mostly extirpated from the vicinity of Boston, although a few small populations remain within I-495. One such site in Middlesex County is pictured here. Mike Jones

Today, Wood Turtles occur throughout all mainland counties of Massachusetts (MassWildlife NHESP, unpubl. data) except Suffolk and Barnstable counties (Lazell 1976; Klemens 1993). Lazell (1976) discredited the single record from Mashpee, Barnstable County, on Cape Cod. Wood Turtles have been entirely extirpated from the greater Boston area within the inner beltway of Interstate 95, and they appear to be functionally extinct in many areas within Interstate 495, which encircles the greater Boston area (MassWildlife NHESP, unpubl. data) (4.8).

Michigan

Wood Turtles occur widely throughout the northern half of lower Michigan and much of the Upper Peninsula (Harding and Holman 1990; Harding 1997). The presence of Wood Turtles in Michigan has been known since Ruthven and Thompson (1915) reported the species in Schoolcraft County in the Upper Peninsula and Manistee and Missaukee counties in the Lower Peninsula. The Upper Peninsula of Michigan is ecologically and geologically an extension of the conditions found in northern Wisconsin; with the exception of the Keweenaw Peninsula, Wood Turtles occur continuously throughout the Upper Peninsula from the border of Wisconsin, in Gogebic County, to Schoolcraft County. On the Lower Peninsula, Wood Turtles occur from the northernmost counties (Cheboygan and Presque Isle) as far south as Muskegon, Montcalm, and Saginaw counties (Vogt 1981; Lee 1999). Isolated records from Allegan and Ingham counties in southern Michigan were discredited by Vogt (1981) and Lee (1999).

Minnesota

Wood Turtles are known primarily from three distinct regions in Minnesota: (1) watersheds draining into Lake Superior in St. Louis, Lake, Pine, and Chisago counties in the northeastern part of the state; (2) watersheds associated with tributaries to the Mississippi River in Rice, Goodhue, Steele, Dodge, Olmsted, and Mower counties in the southeastern part of the state;

4.9—Wood Turtles reach their westernmost extent of occurrence in the Mississippi drainage of south-central Minnesota. Mike Jones

(3) tributaries to the Upper Cedar River in Mower County on the Iowa border (Ernst 1973). Wood Turtles reach their westernmost range-wide extent of occurrence in south-central and southeastern Minnesota (Breckenridge 1958; Ernst 1973; Iverson 1992; Ernst and Lovich 2009) (4.9).

New Brunswick

Across the entire range of the species, the Wood Turtle's northernmost confirmed populations are in western New Brunswick. Wood Turtles are distributed patchily through New Brunswick with the exception of low-lying coastal areas in the southern part of the province and the central part of the highland plateau of northern New Brunswick (Bleakney 1958b; McAlpine and Gerrietts 1999). Wood Turtles occur around the periphery of the highland plateau, but populations in this region have not been intensively studied (Heward and McAlpine 1994; McAlpine and Gerriets 1999). Wood Turtles have been documented at low elevations in a very few watersheds in northern New Brunswick.

New Hampshire

Wood Turtles are known to occur naturally in every county in New Hampshire (Taylor 1993; Taylor 1997). Huse (1901) reported Wood Turtles as common in New Hampshire. Oliver and Bailey (1939) provided records from eight of New Hampshire's 10 counties (except Strafford and Carroll counties). Wood Turtles are mostly absent from the White Mountain National Forest, probably due to a combination of climatic exclusion and scarcity of low-gradient stream habitats that are not subject to severe flooding related to steep upstream basins (Bowen and Gillingham 2004; Jones and Sievert 2009a).

New Jersey

The Wood Turtle's historical range included 17 of New Jersey's 21 counties (NatureServe 2021), with a noticeable gap in documentation in Camden County. It is likely that Wood Turtles were historically native to Camden County based upon records to the south in Gloucester (Stone 1906) and along a waterway in Burlington that serves as the county divide with Camden. Absent are any records from Salem, Cumberland, or Cape May Counties, and it's likely the species did not occur there, as with other Coastal Plain counties throughout the species range. Agassiz (1857) erroneously reported that New Jersey encompassed the southernmost range margin of the Wood Turtle. A record from Gloucester County in 1906, and two records from Atlantic and southern Burlington counties in 1945 and 1978, cannot be replicated today (Zarate, unpubl. data). Stone (1906) commented that he knew of no specimens from the Pine Barrens, and this has borne out over time. Today, the Wood Turtle's current distribution is constrained to 13 counties north of the central portions of Burlington and Ocean counties.[4] Wood Turtles are absent from heavily developed Hudson County (NatureServe 2021).

New York

Wood Turtles historically ranged throughout mainland New York from the Hudson and Mohawk Valleys to Lake Erie and eastern Lake Ontario. The original specimens that formed the basis of Le Conte's (1830) description were likely obtained from New York (Schmidt 1953). Early records from the Adirondack region were provided by De Kay (1842), who reported observations from tributaries of the St. Lawrence River, Lake Champlain, and the Hudson River. Wood Turtles were described as "common" in the Hudson Highlands of southeastern New York by Mearns (1898). Ditmars (1907) vaguely reported Wood Turtles from the vicinity of New York City but did not provide specific locality data. Wright (1918) described Wood Turtles as relatively common in the vicinity of Ithaca, Tompkins County, at the southern end of Cayuga Lake. Clausen (1943) reported three specimens from Tioga County on the Pennsylvania border. Confirmed Wood Turtle populations are rare in some westernmost counties such as Chautauqua, Orleans, Gennessee, Monroe, Livingston, Yates, and Seneca, and the lake plain south of Lake Ontario (Jones et al. 2015). Wood Turtles appear to be rare on the southern lake plain of Lake Ontario, but they evidently occur in many of the suitable drainages of Lake Champlain and the Hudson Valley. Although many distribution maps (e.g., Ernst and Lovich 2009) indicate that Wood Turtles are absent from a large portion of the Adirondacks, especially central Essex County, scattered populations have been confirmed throughout the Adirondack massif (Breisch, unpubl. data). Wood Turtles were described as "fairly common" in Essex County—in the Adirondacks—in the 1920s (Weber 1928). Wood Turtles have been reported from Long Island on multiple occasions, but none of these reports are sufficient to demonstrate that a population occurred there (Murphy 1916). Five Wood Turtles found washed ashore at Orient, Mattituck, Riverhead, and East Marion, eastern Long Island, between 1919–1926 may have been displaced during floods from the Connecticut River watershed in Connecticut (Latham 1971), and an individual found northwest of Islip, Suffolk County, in the 1980s, may have been a released captive.

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4 A recent (2018) outlier observation of a Wood Turtle from central Ocean County—a coastal location—was genetically assigned to a Midwestern population and is not considered a valid state record (Zarate, unpubl. data).

4.10—Wood Turtles reach their extreme easternmost distribution in Nova Scotia. Mike Jones

Nova Scotia

On the peninsula of mainland Nova Scotia, Canada's easternmost mainland province, Wood Turtles occur throughout the northern half of the mainland including Cumberland, Halifax, Hants, and Kings counties (Bleakney 1952; Bleakney 1958b; Bleakney 1963) and Guysborough County (Bleakney 1958b; Pulsifer et al. 2006; White et al. 2010). Wood Turtles reach their extreme easternmost distribution on Cape Breton Island, where they were not documented until the 1970s (Gilhen and Grantmire 1973; Gräf et al. 2003) (4.10).

Ohio

The natural history, distribution, and native status of Wood Turtles in Ohio is poorly understood, and supported by very few observations. The species was attributed to Ohio by Smith (1899) and repeated by Ditmars (1907) and Surface (1908). Conant (1938) considered the native status of Wood Turtles in Ohio to be "doubtful," although 13 years later, Conant (1951) stated of northeast Ohio that "probably *Clemmys* [=*Glyptemys*] *insculpta* and *Clemmys* [=*Glyptemys*] *muhlenbergii* occur in this region; they have been found in the adjacent part of Pennsylvania but repeated search for them in Lake, Geauga, and Ashtabula counties has resulted in failure." Ernst (1972) includes northeastern Ohio in his range description for *G. insculpta*. There have been at least two, and possibly three individuals observed in the Rocky River watershed near Cleveland in Cuyahoga County (Thompson 1953; Rice, pers. comm. to J. Iverson, in Iverson 1992). Rocky River is a large stream that enters Lake Erie about 150 km (90 mi) west of the nearest corroborated occurrences in Pennsylvania, and is otherwise isolated from the continuous main range in Ontario. Anecdotal accounts of Wood Turtles from Greene and Suit counties are unconfirmed (Salzberg, in Iverson 1992). A record in Stark County, Ohio in Iverson (1992) is a mislabeled record from Butler County, Pennsylvania (CM 31215). Conant (1951) searched for Wood Turtles unsuccessfully in the northeast corner of Ohio, but determined that Wood Turtles likely occurred naturally in that part of the state. As noted above, a specimen from Linesville, Crawford County, Pennsylvania, provides limited evidence of a historical population in the Linesville Creek–Shenango River watershed (since 1934, flooded by the Pymatuning Dam), which straddles the Pennsylvania–Ohio border. Conant's (1951) repeated searches in the northeasternmost counties, and Thompson's (1953) report of two Wood Turtles in Rocky River, Cuyahoga County, may indicate the recent persistence of an isolated relict population not contiguous with populations in Pennsylvania. Recent sightings in Beaver, Mercer, Crawford, and Erie Counties, Pennsylvania (PARS 2019) bear relevance to determining the native status of Wood Turtles in Ohio. At present, it appears likely that Wood Turtles occurred naturally in eastern Ohio within the past few hundred years, but the species is functionally extinct.

4.11—Wood Turtles are distributed in isolated watersheds along the north shore of Lake Huron and Lake Superior in Ontario's Algoma and Sudbury Districts. Mike Jones

Ontario

In central Ontario, Wood Turtles are distributed in isolated watersheds along the north shore of Lake Huron in southern Algoma and Sudbury Districts (as far west as watersheds draining into Lake Superior near Sault Ste. Marie) (4.11), as well as several watersheds in the eastern portions of Algonquin Provincial Park and adjacent areas (Nipissing District and Renfrew County; COSEWIC 2018). In southern Ontario, Wood Turtles formerly occurred along the north shore of Lake Erie (e.g., near Wheatley, Hamilton, Burlington, Mississauga, Toronto, and Oshawa; Logier and Toner 1961), but these populations have been extirpated (COSEWIC 2007). Historical occurrences near Ottawa, Midland, Brechin, and Georgina have also been extirpated (COSEWIC 2007). The only remaining population in southern Ontario occurs in Huron County near the southeastern shore of Lake Huron (Logier 1939; Oldham and Weller 1989), but the long-term viability of this population is currently dependent on extensive and ongoing management efforts (i.e., headstarting, predator control, habitat creation/restoration; Mullin 2019). Ontario's Wood Turtle populations are isolated from those south of the Great Lakes in New York and Pennsylvania due to extensive habitat loss and fragmentation throughout southern Ontario, but there is potential for connectivity between eastern Ontario populations and those in Québec along the Ottawa River. The species has been extensively studied throughout most of its Ontario range, including populations in Algonquin Provincial Park and the surrounding area (Quinn and Tate 1991; Brooks and Brown 1992 *in* Foscarini and Brooks 1997; Brooks et al. 1992; COSEWIC 2018), Algoma District (Wesley 2006; Thompson et al. 2018), Sudbury District (Greaves and Litzgus 2007; 2008; 2009; Hughes et al. 2016), and Huron County (White and Mullen 2017; COSEWIC 2018; Mullin 2019).

4.12—Isolated Wood Turtle records from the northern coast of Québec's Gaspé Peninsula probably do not represent natural occurrences. Mike Jones

Pennsylvania

The Wood Turtle has been recorded statewide in Pennsylvania with the notable exception of the four westernmost counties (McCoy 1982; PARS 2020). Surface (1908) provided records from 22 counties ranging as far west as Venango County. Typical range depictions and descriptions (e.g., Surface 1908; McCoy 1982; Ernst and Lovich 2009) indicate that the Wood Turtle ranges west nearly to the Ohio border. In fact, there are historical records from Erie Harbor and the Presque Isle peninsula at Erie (Carnegie Museum of Natural History CM6880; McKinstry et al. 1987; 1991). However, from the information associated with these records, it is not possible to confidently assign the Erie County records to typical stream habitats. Historical records in the region may reflect populations formerly present along the Erie shore in an area that has been dramatically converted to urban and agricultural development. Interestingly, there is also a record in the Royal Ontario Museum from Long Point, Norfolk County, Ontario, 40 km due north across Lake Erie and encompassing a similar dune ridge island environment (Logier and Toner 1961), although this specimen is believed to represent a released captive animal (Saumure, unpubl. data). The nearest record to Erie, and one of the westernmost specimens from south of the Great Lakes, was collected at Linesville, Crawford County. Daniel A. Atkinson discovered this specimen on June 9, 1906 (CM2985), and he collected Wood Turtles across Pennsylvania throughout the spring of 1906. The Shenango River, which flows along the Pennsylvania-Ohio border, was dammed in the 1930s to create the Pymatuning Reservoir (McCoy 1982). It may have supported one of the westernmost populations of Wood Turtles south of Lake Erie. Other early reports of the Wood Turtle from Pennsylvania include Stone (1906), who reported specimens from Chester and Fulton Counties, Bristol, Bucks County, and Round Island, Clinton County; Dunn (1915), who reported two individuals from Delaware County; and Evermann (1918), who reported three individuals from Pike County. Conant (1942) reported anecdotal sightings from Dutch Mountain, Sullivan County. A series of excellent behavioral studies by John Kaufmann

(1986; 1992a; 1992b; 1995) were conducted in Centre County; and important studies by Carl Ernst (1986; 2001b) were conducted in Lancaster County. Strang (1983) studied Wood Turtles in Cumberland County.

Québec

Wood Turtles occur widely throughout Québec south of about 47.5°N (Ministère des Forêts, de la Faune et des Parcs, unpubl. occurrence data; Giguère et al. 2011), on both sides of the St. Lawrence River (Tessier et al. 2005). Québec Wood Turtle populations are primarily constrained to the watersheds of the Ottawa River, the lower St. Lawrence River (including the Lake Champlain basin of Vermont), and Atlantic-draining watersheds shared with Maine and New Brunswick. Two early records from the vicinity of Mont-Tremblant were provided by D'Urban and Bell (1860). Bleakney (1958b) reported that Wood Turtles reach their northernmost range limit in the St. Maurice Valley, but isolated northern occurrences have been reported as far north as La Tuque. Extreme northerly records (near or north of 48°N) have been reported from the vicinity of Val-d'Or, Saguenay, and Cap-Chat (on the north coast of the Gaspé Peninsula). Of these, only the reports from Saguenay seem to be climatically appropriate for Wood Turtles (Giguère et al. 2011), but these are isolated by more than 150 km from La Tuque. The northern Gaspésie records are highly questionable because the climate is not conducive to Wood Turtles, and there are no confirmed occurrences within 100 km (4.12).

Rhode Island

The Wood Turtle has been consistently reported as rare in Rhode Island (e.g., Drowne 1905; Klemens 1993), where it is known to occur in Providence, Kent, and Washington counties. Yorks (unpubl. data) found a dead Wood Turtle on a beach near the saltwater Sakonnet River in Newport County in 1992. Consistent with regional trends, there are no records of Wood Turtles from any of the islands of Narragansett Bay.

Vermont

Wood Turtles are reported from all of Vermont's 14 counties, in both the Champlain Valley (St. Lawrence watershed) and the Connecticut watershed, and along both the west and east slopes of the Green Mountains (DesMeules 1997; Vermont Reptile and Amphibian Atlas 2020). Wood Turtles in Vermont were reported by Thompson (1853), together with Painted (*Chrysemys picta*) and Snapping Turtles (*Chelydra serpentina*). The earliest documented specimen from Vermont may be an animal collected at Sharon in Windsor County in 1900 by M. Parker (CAS 54480). A single specimen collected in South Hero, Grand Isle County in 1934 by L.H. Babbitt (BMNH 51-8451) is the only record from the Hero Islands (Grand Isle County) and one of relatively few from an island anywhere in the range.

Virginia

Wood Turtles occurred historically throughout much of the Potomac and Shenandoah River drainages in Virginia's northernmost counties, including Fairfax, Loudoun, Clarke, Frederick, Warren, Shenandoah, Page, and Rockingham (Akre 2002; Akre and Ernst 2006). The earliest published record of the Wood Turtle in Virginia was an individual collected by E.A. Preble in 1918 from Little Pimmit Run, Fairfax County, Virginia (Dunn 1920). Though the Wood Turtle was not on an early list of reptiles from the District of Columbia (D.C.) and vicinity (Hay 1902), Henshaw (1907) extended the known range southward to the shore of the Potomac River, less

4.13—Wood Turtles reach their southernmost distribution in Rockingham County, Virginia. Mike Jones

than 1 km from Virginia. Clark (1930) then added several records from the D.C. area, including three from Fairfax County near the Potomac River. Few additional localities were added until the 1970s when records collected over the following two decades established their presence in Loudoun County and the northern Shenandoah Valley (Simpson and Simpson 1977; Tobey 1985; Mitchell 1994; Mitchell and Reay 1999). However, an Arlington record from the mouth of Four Mile Run near the Potomac River and US-1 in 1953 (USNM 136639) was substantiated by a relatively recent (1993) record in the database of the Virginia Department of Wildlife Resources from approximately 8 km upstream. Simpson and Simpson (1977) found the Wood Turtle to be reasonably common in Frederick and Shenandoah counties. Surveys in the 1980s and 1990s added several records from Fairfax, Loudoun, and Frederick Counties, and at the same time, U.S. Forest Service personnel reported Wood Turtle records from the southern part of Rockingham County (Buhlmann and Mitchell 1989). Rockingham County today represents the species' southernmost extent of occurrence (4.13). The majority of records and populations come from west of the Blue Ridge and the Shenandoah River (Akre and Ernst 2006). Historical records in the vicinity of Great Falls, Fairfax County, Virginia, apparently represent a natural historical population, and numerous small creeks on the Virginia side of the lower Potomac once provided suitable habitat for Wood Turtles (Akre and Ernst 2006). The Potomac River has many sidearms and sidestreams that reduce the average flow volume and may have provided better habitat than the main channel. Available evidence suggests there was once a network of populations living in sidestreams on both sides of the Potomac River, both up- and downstream of Great Falls.

Washington, D.C.

Wood Turtles probably occurred naturally in the area that is now Washington, D.C., as suggested by substantial evidence from adjoining Maryland and Virginia. A specimen from Washington, D.C. in the National Museum (USNM 62556) may have originated near Bennings in eastern Washington, D.C. (Shufeldt 1919; Miller 1993). Two sight records from

4.14—Wood Turtles persist in the Driftless Area of southwestern Wisconsin, which was left unglaciated by successive advances of the Laurentide Ice Sheet. Mike Jones

the Anacostia watershed along the eastern border district in Maryland (Norden and Zyla 1989) provide additional support for the natural historical occurrence of Wood Turtles in the Anacostia drainage, but these were questioned by Miller (1993). Wood Turtles are now considered "possibly extirpated" by the District Department of the Environment.

West Virginia

Wood Turtles occur in the panhandle of West Virginia including Jefferson, Berkeley, Morgan, Mineral, Hampshire, and Hardy counties, reaching the southernmost confirmed populations in Pendleton County (38.6°N). Outlying occurrences in Grant County (WV DNR, unpubl. data) are noteworthy. Bond (1931) reports Wood Turtles as "not uncommon" in Monongalia County, although this report was discounted by Breisch (2006). Recent sightings in Beaver County, Pennsylvania (PARS 2020), suggest that Wood Turtles may have occurred in neighboring Hancock County, West Virginia.

Wisconsin

Wood Turtles occur widely throughout northern, western, and south-central Wisconsin (WDNR 2015), and they are associated with forested regions adjacent to clear, moderate- to fast-moving streams and rivers (Vogt 1981), including the Driftless Area of southwestern Wisconsin (4.14).[5] Despite their widespread distribution, their full extent in Wisconsin has yet to be delineated, due in part to a lack of thorough statewide survey efforts (WDNR, unpubl. data). There is general agreement that the species is not present in the southeast and extreme southern portions of Wisconsin, due to the lack of data confirming existing wild populations. Wood Turtles

5 Wisconsin's Driftless Area remained unglaciated during all of the major glaciations of the Pleistoeene.

were first confirmed in 1917 in Wisconsin near St. Croix Falls in Polk County, the westernmost record at the time (Wagner 1922). Casper (1996) noted that the sporadic reports from urban areas in the southern Lake Michigan drainage counties were likely "released or escaped pets." A single record from the Rock River, south of Janesville in Rock County, has not been replicated and is an unusual outlier (Cahn 1937). Casper (1996) also questioned the legitimacy of the Dane and Rock County records, describing both as being possibly "displaced" individuals. Records from the Wisconsin Department of Natural Resources (unpubl. data) suggest northern Wood Turtle populations are more viable (e.g., more abundant, robust, and less fragmented); whereas populations in western (Driftless Area) and south-central Wisconsin (Lower Wisconsin River watershed) are more vulnerable to population decline, characterized by smaller populations, increasing isolation, and a general decline in suitable habitat. Two Wisconsin specimens collected in the "Fox River" (UA R107 and UA R108) in 1951 by W.A. Lemberger have been attributed to Kenosha County on the Illinois border, which would lend weight to Illinois and southern Lake Michigan specimens (see discussion of Illinois records, earlier), but these more likely originated in a different Fox River watershed, such as the one that flows through Outagamie and Brown counties to reach Lake Michigan at Green Bay. Additional locality data are provided by Casper (1996). Several distributional updates have been published in recent years for Dunn County (Schuler and Badje 2019), Clark County (Badje 2019), and Langlade County (Arrowwood et al. 2019). Johnson et al. (2015) provide a brief discussion of the documentation for Wood Turtle occurrence in Vernon County.

Summary

Wood Turtles occur broadly throughout the forested regions of eastern North America south of the 48th parallel, from southern Minnesota to Cape Breton, Nova Scotia and south to West Virginia and Virginia. The northernmost populations are in New Brunswick, although they have been questionable reports farther north in Québec. Ecologically, the Wood Turtle's current distribution is divided between the Canadian Shield, the Appalachian Mountains, and the interior basin areas. Ecologically, the species is found in coniferous, transition, and hardwood forests, with marginal populations extending into the Great Plains and prairie ecoregions. Finally, hydrologically the Wood Turtle is distributed between the watersheds of the Atlantic Coast, the Gulf of St. Lawrence, and the Mississippi River. Consequently, extant populations differ substantially in terms of ecological and geopolitical context.

5. Habitat

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Matthew R. Burne, John D. Kleopfer, Andrew Badje

A summer thunderstorm in Wood Turtle habitat, Massachusetts. Mike Jones

5.1—Riparian habitat mosaics often include sandy nesting areas, stream-influenced early successional habitats, downed trees, and temporary floodplain pools, juxtaposed with mixed-age floodplain forest. Pictured: Wood Turtle habitat in New England. American Turtle Observatory

Introduction

Wood Turtles are fluvial (flowing water) specialists and riparian generalists, found primarily in mid-sized streams and rivers that flow through a broad range of upland habitats. Across the Wood Turtle's large geographic range, the major structural habitat components required by the species remain relatively consistent. For example, all functional Wood Turtle populations must have access to: (1) suitable in-stream habitat for overwintering, courtship, and foraging; (2) suitable upland nesting areas; and (3) varied upland habitats (including early-successional habitats) for foraging and thermoregulation. Localized differences in habitat selection, as well as by region, stream size, and physical geography, are relatively minor.

Today, the ideal configuration of habitats for long-term Wood Turtle conservation would include mid-sized streams within a mosaic of high-integrity riparian and upland habitats unfragmented by roads or recreational features. The riparian mosaic would include in-stream nesting areas, stream-influenced early successional habitats, and temporary wetlands, juxtaposed with mixed-age floodplain and upland forest (5.1). Unfragmented sites with supporting disturbance regimes that maintain these characteristics—and minimal human use—are most likely to provide cost-effective conservation outcomes. Multiple streamcourses with independent flow and disturbance regimes, and within a few kilometers of one another, facilitate long-term population connectivity and stability at longer time scales. There is clear evidence that Wood Turtle populations are negatively affected by roads and agriculture even at broad landscape scales, suggesting that wherever feasible, Wood Turtle populations should be managed as part of much larger landscapes of high integrity forests or low-intensity development and land use. This ideal habitat scenario is startlingly rare on the American landscape today. Maintaining the evolutionary potential of representative Wood Turtle populations will require sustained efforts to insulate

5.2—Wood Turtle populations are generally associated with slow-moving sections of clear, cold streams with sand, gravel, rock, or bedrock substrate in woodland and agricultural areas, interspersed among areas of moderate to fast current. *Clockwise from top:* New England; Maryland; New Brunswick; New Jersey ((Joe Crowley & Mike Jones)

5.3—Wood Turtles tolerate a wide range of stream flow conditions, but they are most often associated with mid-sized streams between between 3 and 20 m wide. *Clockwise from top:* New Hampshire; Upper Mississippi watershed; New Jersey; northern Minnesota (Mike Jones & Donald Brown) functional stream systems from the effects of overuse. And elsewhere, minimizing Wood Turtle population decline will require targeted actions to improve or replace key habitat features missing from the landscape and to lessen the annual mortality risks to individual turtles.

Aquatic Habitat

Wood Turtle populations are strongly associated with relatively slow-moving sections of clear, cold, woodland or agricultural streams—often interspersed with areas of moderate to fast current—and especially those with sand, gravel, rock, or bedrock substrate (Finneran 1948; Vogt 1981; Quinn and Tate 1991; Kaufmann 1992b; Holman and Clouthier 1995; Akre 2002; Arvisais et al. 2004; Ernst and Lovich 2009; Jones 2009; Buhlmann and Osborn 2011) (5.2). Suitable streams are critical to the persistence of most known Wood Turtle populations as they provide essential overwintering habitat (Vogt 1981; White et al. 2010; White 2013) and the preferred context for courtship and mating.

Stream Size

Wood Turtles and Wood Turtle populations can tolerate a wide range of stream flow conditions, but they are most often associated with mid-sized or mid-order streams between about 3 and 20 m wide (Brooks and Brown 1992 in Foscarini and Brooks 1997; Foscarini and Brooks 1997; Arvisais et al. 2004, Breisch 2006; Akre and Ernst 2006; White 2013) (5.3). Wood Turtle populations may occur in even smaller streams (Wright 1918; Akre and Ernst 2006; Jones 2009; Akre, unpubl. data) and much larger streams (Niederberger 1993; Niederberger and Seidel 1999), and the extent to which Wood Turtles reside in both may be as much a function of the availability of key structural features (pools, logjams, cutbanks, root structures, and riparian clearings) as past land-use history in the watershed.

In a number of cases, Wood Turtles have been reported in association with very large rivers (≥50 m wide), including major rivers in Ontario (Brown 1947), Québec (Denman and Lapper 1964); Maine (Jones and Willey, unpubl. data); central New Hampshire (NHFG, unpubl.

5.4—Wood Turtles in very large rivers are often associated with braided channels or tributary streams. Algoma District, Ontario. Mike Jones

5.5—Wood Turtles are often associated with inorganic substrates including clay, sand, gravel, and cobble, although some populations occur in areas of deep organic sediment accumulation. Prevailing substrates associated with Wood Turtle streams are pictured here. *Top left:* Algoma District, Ontario; *Top right:* Minnesota; *Bottom left:* New Hampshire; *Bottom right:* New Hampshire. MIKE JONES

data); Pennsylvania and New Jersey (NJ DFW, unpubl. data; PA NHP, unpubl. data); Maryland (Cooper 1949; MacCauley 1955); Virginia (Henshaw 1907; Brady 1937; Akre and Ernst 2006); and West Virginia (Akre, unpubl. data). In many cases, Wood Turtles in very large rivers appear to be associated with braided channels or tributary streams (5.4). Isolated Wood Turtles have been documented in association with beaches along very large rivers in central Massachusetts, possibly representing nesting animals, although these may have originated from a smaller river nearby (MassWildlife NHESP, unpubl. data; Jones, unpubl. data). A quantitative analysis of stream watershed area is presented by Jones et al. (2015), which suggested that Wood Turtles are associated with stream habitat that is generally of lower gradient, higher sinuosity, and higher flow than randomly available streams, though specific associations vary locally.

Stream Current and Substrate

Wood Turtles are most often associated with streams characterized by variable inorganic substrates including clay, sand, gravel, and cobble, although some populations occur in areas of deep organic sediment accumulation (5.5). White (2013) reported Wood Turtles in Nova Scotia in association with primarily cobble stream substrate. Akre (2002) reported that conditions along a third-order tributary of the Potomac watershed in Fairfax County, Virginia, which flows across the Atlantic Seaboard Fall Line into the Potomac River floodplain, varied from “clear, moderate-current” with “sand-gravel substrate” to “slow-flowing with suspended sediments and clay-gravel substrate.” Breisch (2006) reported that Wood Turtles in West Virginia were associated with sand and rocky stream substrates. By contrast, Parren (2013) reported a population in Vermont associated with calcareous bedrock and silt, and noted that Wood Turtles likely tolerate a wide range of stream conditions. In a series of 5,125 stream locations in Maine, New Hampshire,

5.6—Wood Turtles often overwinter in deep pools, undercut banks, or in association with the root masses of large trees. Known overwintering sites associated with large trees are pictured above. *Top left:* Silver Maple (*Acer saccharinum*) in New Hampshire; *Top right:* Yellow Birch (*Betula alleghaniensis*) in Massachusetts; *Bottom left:* Eastern Hemlock (*Tsuga canadensis*) in Massachusetts; *Bottom right:* American Sycamore (*Platanus occidentalis*) in Massachusetts. Mike Jones

and Massachusetts, Jones and Willey (unpubl. data) found that stream substrates included sand (40.5%), cobble (17.2%), gravel (14.3%), silty sand (14%), boulders (6.4%), organics and muck (3.1%), silt (3.6%), clay (0.3%), and bedrock (0.3%).

Stream Alkalinity

Parren (2013) reported a Wood Turtle site in Vermont that was associated with calcareous underlying bedrock. McCoard et al. (2016) found a positive association of Wood Turtles with higher soil pH in West Virginia. Most authors do not report stream pH associated with Wood Turtle sites, and it is not well known the extent to which stream pH influences the distribution or abundance of Wood Turtles.

Instream Overwintering Habitat

Wood Turtles spend the coldest months underwater. They primarily overwinter in streams, rivers, or connected floodplain features such as abandoned rivers meanders, oxbows, and tributary streams. Nearly all recent telemetry studies have documented overwintering in streams, rivers, and associated aquatic habitats. Many authors have noted the propensity of Wood Turtles to overwinter in deep pools, undercut banks, or in association with the root masses of large trees such as American Sycamore (*Platanus occidentalis*), Eastern Hemlock (*Tsuga canadensis*), Eastern White Pine (*Pinus strobus*), and Yellow Birch (*Betula alleghaniensis*) (Farrell and Graham 1991;

5.7—Wood Turtles will overwinter in proximity to large logjams, such as this site in New Hampshire. Mike Jones

Tuttle and Carroll 1997; Niederberger and Seidel 1999; Ultsch 2006; Akre and Ernst 2006; Greaves and Litzgus 2008; White 2013) (5.6).[1]

Radio-equipped Wood Turtles in Ontario (Greaves and Litzgus 2008) overwintered entirely in the stream rather than adjacent wetland habitats and generally chose areas with muck substrate, available structure (vegetation, woody debris, and logs), and an average depth of 91.2±34.8 cm. White (2013), in a study of overwintering site selection in Nova Scotia Wood Turtles, reported that most telemetered Wood Turtles overwintered in riverine habitats, although marsh and oxbow habitats were also used, and that Wood Turtles overwintered at a mean water depth of 67±35 cm. Most turtles overwintered in reaches dominated by fine sediment substrates. Wood Turtles often overwintered in close proximity to structures such as log jams, single logs, large branches, woody material, and root balls, as well as undercut banks, underwater rock ledges, and boulders. In northern populations, such structures likely shelter turtles from potentially lethal scouring ice sheet flows and/or being washed downstream during spring run-off events (Jones and Sievert 2009; Saumure, unpubl. data). In Greaves and Litzgus' study (2008), turtles were observed overwintering at dissolved oxygen (DO) concentrations averaging 12.39±0.92 ppm, and in White's (2013) study, the mean DO across all overwintering sites for 20 turtles (year one) and 29 turtles (year two), respectively, was 13.12±1.56 ppm (n=88 measurements) and 11.97±3.50 ppm (n=133 measurements), although turtles were observed overwintering in an oxbow at DO of 9.65±2.25 ppm.

Graham and Forsberg (1991) reported aquatic oxygen uptake by overwintering Wood Turtles in central Massachusetts, and noted that turtles typically rested on the stream bottom, near submerged logs or rocks, in 0.3–0.6 m of water. In Connecticut, Wood Turtles hibernate in muskrat dens, on the gravel bottoms of pools in woodland streams (Farrell and Graham 1991), and amongst tree roots (Klemens 1993). Farrell and Graham (1991) reported an important overwintering site associated with the roots of a large sycamore at a bend in a stream in Sussex County, New Jersey, and Parren (2013) reported overwintering sites associated with tree stubs and

1 There are a few 19th- and early 20th-Century accounts of terrestrial overwintering or brumation (e.g., Surface 1908).

logs including Eastern Hemlock, as well as the use of small “bank coves” in streams in Vermont. In Virginia, Akre and Ernst (2006) reported a range of key overwintering features including leaf packs in deep pools, undercut banks, logjams, and large deadfalls of tree species such as American Sycamore; an anecdotal association with logjams is evident throughout the range of the species (5.7).

Rare Aquatic Habitats

Tidal Rivers.—Infrequently, Wood Turtle populations may occur outside of a strictly fluvial context. For example, a noteworthy Wood Turtle metapopulation occurs along the fresh-tidal Hudson River in Dutchess, Greene, and Columbia Counties, New York, where a dozen individual turtles were observed in tidal swamps along the Hudson River by researchers in the 1980s and 1990s (Kiviat and Barbour 1996).[2] In neighboring New Jersey, there is at least one older Wood Turtle record in the lower watershed of the Delaware River (Street 1914) in Beverly, Burlington County, and two historic records from the vicinity of lower Rancocas Creek in 1933 and 1951 (New Jersey Division of Fish and Wildlife 2019). However, in a review of validated New Jersey occurrence records from 1980 to 2019, there are currently known Wood Turtle occurrences within freshwater tidal marshes or tidal rivers (NatureServe 2021).

Records from the mouth of the Susquehanna River in Harford County, Maryland (Cooper 1949) may represent individuals from populations associated with tidally-influenced streams or, more likely, associated with smaller side streams. Several streams on Elk Neck, Cecil County, Maryland, where Wood Turtles were documented between the 1950s and 1970s, are in close juxtaposition with tidal estuaries. Therefore, Wood Turtles likely had access to tidal systems in recent decades. Wood Turtles are known to have occurred in the Potomac River and its tributaries upstream of the Atlantic Seaboard Fall Line, and it is possible that they once occurred in the lower Potomac River in Maryland and Virginia nearly as far as the tidal mouth (Akre and Ernst 2006). In any event, Wood Turtles likely used the tidal Potomac as a corridor because historic populations are known from streams that flow through the fall line into tidal sections where they enter the tidal Potomac in northeastern Virginia (Mitchell and Pilcicki 2000; VDGIF FWIS 2019; Akre, unpubl. data).

Ephemeral Pools.—Wood Turtles appear to be opportunistic or facultative users of temporary, seasonal, or fishless aquatic habitats, especially abandoned river meanders but also vernal and autumnal pools or other confined depressions. Wood Turtles exploit the seasonal availability of vernal pools and ephemeral wetlands (Mitchell et al. 2008, in Calhoun and deMaynadier 2008), but the importance of seasonal or ephemeral pools likely varies regionally. In Massachusetts and New Hampshire, only 80 of 7,348 active season radiolocations (1.1%) were within “vernal pool” habitat, and 117 (1.6%) were within 5 m of vernal pool habitat (Jones and Willey, unpubl. data).

Seeps and Springs.—Akre and Ernst (2006) report consistent use of seepage areas in deciduous forest in Virginia and report that small wetlands may be attractors on the landscape. Springs, vernal pools, and seeps appear to be complementary landscape features that do not support overwintering populations. Wood Turtles were reported from a mountain spring in the Catoctin Mountains of central Maryland (Reed 1956), and Abbott (1884) provided an account of three Wood Turtles congregating at a forest spring near Trenton, Mercer County, New Jersey.

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2 French, in Kiviat and Barbour (1996), also reported an observation of a single Wood Turtle from a tidal context in Newbury, Essex County, Massachusetts.

Breckenridge (1958) reported Minnesotan Wood Turtles in "spring holes" and "woods ponds," as well as wooded streams.

Canals.—Wood Turtles are generally more abundant in naturally sinuous sections of stream, but may occur in lower densities in channelized rivers, and, very rarely, in canal systems. Multiple individual Wood Turtles have been reported from an 1890s canal system associated with the Springfield Reservoir in Hampshire County, Massachusetts (MassWildlife NHESP 2019), and Wood Turtles are associated with portions of the Chesapeake and Ohio Canal system in Maryland (Akre, unpubl. data).

5.8—Alder (*Alnus* spp.), pictured here in New England, is an important tall shrub in Wood Turtle sites throughout the range of the species. Mike Jones

Lacustrine Habitats.—Although many early authors reported the Wood Turtle to frequent or reside in lakes or "ponds," these statements appear to be suppositional (Logier 1939). There are many credible accounts (both historic and modern) of Wood Turtles from lentic habitats, though lotic habitats are more the norm for almost all populations studied at length. Jones (1865) reported that Wood Turtles were found in lakes in Nova Scotia. There are documented Wood Turtle occurrences associated with several large lakes in Québec (MDEFP, unpubl. data). Quinn and Tate (1991) presented evidence of seasonal lake use in Ontario by at least one individual (although they stated that most aquatic habitats were streams). A head-started Wood Turtle overwintered in a manmade pond at Great Swamp NWR in 2012–2013 (Osborn and Buhlmann, unpubl. data). In Franklin County, Massachusetts, Jones and Sievert (2009) reported that a subpopulation of Wood Turtles resided in the catchment area behind an 1890s power dam that had largely silted in, although radio-tracked turtles primarily used riverine and riparian features within the old reservoir area. Akre (unpubl. data) observed one Wood Turtle overwinter in a farm pond in Virginia.

Beaver-Influenced Habitats.— The relationship between beaver-caused habitat modifications and Wood Turtle spatial ecology is complex and in need of further study.[3] At the larger watershed scales in unfragmented river systems, North American Beavers (*Castor canadensis*) are an important driver of structural complexity within Wood Turtle-occupied waterways from Minnesota to Nova Scotia. For example, beavers create openings in northern, coniferous forests through tree removal and flooding, and create deeper pools for overwintering (Saumure, unpubl. data). In states and regions where beavers have been aggressively controlled or hunted, these disturbance regimes are no longer present and can be difficult to replicate. At most of the remote, isolated sites studied by Jones and Willey (2013b), turtles exhibited heavy use of beaver-created openings and clearings. Beaver dams may also play a major role in the creation of suitable nesting habitat in Virginia and elsewhere: as beaver dams deteriorate or are blown out by major rain events, what often remains behind are large sandbars that may be suitable for Wood Turtle nesting (Kleopfer, unpubl. data).

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3 Further discussion of the interactions between beavers and Wood Turtles is provided in Chapter 9.

5.9—As much as any other freshwater turtle, if not more, Wood Turtles near their northern range-margin are found in association with northern conifers, including: (*clockwise from top left*): Northern White Cedar (*Thuja occidentalis*), White Spruce (*Picea glauca*), Red Spruce (*Picea rubens*), Black Spruce (*Picea mariana*), Tamarack (*Larix laricina*), and Balsam Fir (*Abies balsamea*). Mike Jones

Riparian and Floodplain Habitat

Riparian Habitats

Riparian swales and floodplain wetlands are components of Wood Turtle habitat throughout the region (Vogt 1981; Ernst and McBreen 1991; Akre and Ernst 2006; Jones 2009; Buhlmann and Osborn 2011). In more northerly areas, Wood Turtles are frequently associated with rivers that have well-developed riparian zones encompassing alder swales, marshes, sedge meadows, and emergent and forested wetlands (Quinn and Tate 1991; Compton et al. 2002; Walde et al. 2003).

Grey or Speckled Alder (*Alnus incana*) is an important tall shrub within riparian areas along Wood Turtle streams throughout the species' range (Saumure and Bider 1998; Walde et al. 2003)

5.10—Silver Maple (*Acer saccharinum*), pictured here in flower in Maine in early May, is a common component of floodplain forests throughout the entire range of the species. In more northerly areas, Silver Maple often shares floodplain habitat with American Elm (*Ulmus americana*) or Black Ash (*Fraxinus nigra*). Mike Jones

5.11—Eastern Cottonwood (*Populus deltoides*) is a dominant component of floodplain forests in southeastern Minnesota, southern Wisconsin, and Iowa, and along larger rivers from New England to Virginia. Mike Jones

(5.8). Box Elder (*Acer negundo*) is locally abundant in open riparian habitats throughout the southern Great Lakes and St. Lawrence Valley (Saumure and Bider 1998).

Floodplain Canopy Composition

In northern streams, floodplain forests may be composed substantially of conifers, including White Spruce (*Picea glauca*) in the Great Lakes, Maritimes, and extreme northern New England, with Black Spruce (*Picea mariana*) found sparingly throughout the northern range on poorly drained (or nutrient-poor) sites. Red Spruce (*Picea rubens*) is more typically found on upland sites through the Appalachian Mountains but may be a component of floodplain swamps in New York and New England. Other common conifer associates in northern floodplain forests include Balsam Fir (*Abies balsamea*), Tamarack (*Larix laricina*) and localized areas of Northern White-Cedar (*Thuja occidentalis*) (5.9). The northern conifers often give way to floodplain forests of Silver Maple (*Acer saccharinum*), which is a common species in floodplains across much of the Wood Turtle's range (5.10), along with Red Maple (*Acer rubrum*), American Elm (*Ulmus americana*), and Black Ash (*Fraxinus nigra*). Floodplain trees in the western Great Lakes include associations of Silver Maple, Black Ash, Basswood (*Tilia americana*), Swamp White Oak (*Quercus bicolor*), Green Ash (*Fraxinus pennsylvanica*), and River Birch (*Betula nigra*).[4] Eastern Cottonwood (*Populus deltoides*) is a dominant component of floodplain forests in southeastern Minnesota, southern Wisconsin, and Iowa, and throughout the transitional area (5.11).

In unglaciated Appalachian streams from Pennsylvania to Virginia, floodplain tree species include Silver Maple, Sycamore, River Birch, and Tulip Poplar (*Liriodendron tulipifera*) (5.12). In eastern Virginia, Akre (2002) reported Wood Turtles from a third-order stream near the Potomac River in floodplain forests dominated by Red Maple, Tulip Polar, Ironwood (*Carpinus caroliniana*), Pawpaw (*Asimina triloba*), River Birch, Box Elder, Slippery Elm (*Ulmus rubra*), and ashes (*Fraxinus* spp.).

4 Kordiyak (1981) reported floristic associations within Wood Turtle habitat in the Driftless Area of southwestern Wisconsin, noting that Silver Maple, Swamp White Oak, Slippery Elm, River Birch, and Green Ash were dominant canopy trees in the floodplain; these associations are common across central Wisconsin.

5.12—Typical Appalachian forests prevail from near the southern New England coast and throughout Pennsylvania, Maryland, Virginia, and West Virginia. Here, floodplain and riparian tree species include: *Left:* River Birch (*Betula nigra*); *Middle:* Tulip Poplar (*Liriodendron tulipifera*)*; Right:* American Sycamore (*Platanus occidentalis*). Mike Jones

At a complex of sites in Shenandoah and Frederick counties, Virginia, Akre and Ernst (2006) reported that Sycamore, Red Maple, and Tulip Poplar were common in the floodplain, while oaks and hickories occured on undisturbed floodplain sites. In northern West Virginia, Breisch (2006) reported Wood Turtles from a forested stream with floodplain canopy consisting of Sycamore, Red Maple, River Birch, and rhododendron (*Rhododendron* spp.). Elsewhere in West Virginia, Niederberger (1993) described a similar floodplain forest of Sycamore, Tulip Poplar, and Red Maple, with Red Maple, Black Walnut (*Juglans nigra*) and hickory (*Carya* spp.) increasing at the "outer edge" of the riparian area. The floodplain forest gave way in places to open, savanna-like pastures with Black Walnut canopy.

Upland Habitat

Upland habitats used by Wood Turtles vary by geographic region, season, and spatial scale (Harding and Bloomer 1979; Strang 1983; Quinn and Tate 1991; Compton 1999; Compton et al. 2002; Walde et al. 2003; Arvisais et al. 2004; Jones 2009; Parren 2013). Wood Turtles are often found using upland mosaics of forested and non-forested habitats, both in and out of the riparian floodplain (which may be seasonally dry). Within largely forested landscapes, forest edges provide opportunities to balance thermoregulation and food requirements (Compton et al. 2002).

Upland Canopy Composition

Across their range, Wood Turtles are found in a broad range of upland forest conditions and canopy associations. These can be broadly divided between: (1) the coniferous forests of the northern range-margin; (2) transitional communities of the Great Lakes, New England, and Nova

Scotia); and (3) the southern hardwood and pine assemblages of the central Appalachian Mountains.[5]

5.13—Young or recently disturbed forests in northern regions from Minnesota to Nova Scotia, and south as far as Vermont, may be dominated by stands of Balsam Poplar (*Populus balsamifera*), pictured here in Maine. Mike Jones

Northern Range-Margin.—In a broad swath of the continent from Nova Scotia and New Brunswick, across northern New England, Québec, New York, Ontario, Michigan, Wisconsin, and Minnesota, canopy tree associations may be comprised of northern conifers in the pine (Pinaceae) and cypress (Cupressaceae) families, predominately Red Spruce in the northern Appalachian regions and White Spruce in the upper Midwest and Great Lakes regions. Balsam Fir is present in upland forests from Minnesota to Nova Scotia and south to Massachusetts and northern Pennsylvania. Young forests in the boreal regions from Nova Scotia to Minnesota, and south as far as Massachusetts, may be dominated by stands of Black Cherry (*Prunus serotina*), Quaking Aspen (*Populus tremuloides*) or Balsam Poplar (*Populus balsamifera*) (5.13).[6]

Throughout the Great Lakes from northeastern Minnesota to Michigan's Upper Peninsula and Ontario, Wood Turtles occur occasionally within fire-dependent communities dominated by Jack Pine (*Pinus banksiana*) and Red Pine (Greaves and Litzgus 2008) (5.14).

Transitional Communities.—South of the northern coniferous forests, northern hardwood species predominate, including Yellow Birch, Sugar Maple (*Acer saccharum*), and American

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5 Wood Turtles in New Haven County, Connecticut, were associated with streams in central hardwood forests (Garber and Burger 1995). In Morris County, New Jersey, Buhlmann and Osborn (2011) reported Wood Turtles from a stream bordered by "riparian hardwood forest" and abandoned pastures with blackberry (*Rubus* spp.) and invasive multiflora rose (*Rosa multiflora*). In Warren County, New Jersey, Castellano et al. (2008) reported Wood Turtles from a deciduous forested landscape interspersed with row crop (mostly corn) agricultural fields. A separate analysis of 1,379 radio-telemetry points representing 70 unique Wood Turtles in New Jersey found that the largest percentage of observations of turtles in non-stream habitats were in deciduous forested wetlands followed by cropland and pastureland (Zarate, unpubl. data). In Cumberland County, Pennsylvania, Strang (1983) reported Wood Turtles in lowland areas dominated by oaks, Black Birch, and Red Maple, but in Centre County, Pennsylvania, Kaufmann (1992a) reported little use of deciduous forest.

6 In the Mauricie region of Québec, Walde et al. (2003) reported Wood Turtles from the boundary of the boreal/Great Lakes St. Lawrence lowland forest (Farrar 1995), where forests are dominated by White Spruce, White Birch, and Quaking Aspen, and floodplains are dominated by Speckled Alder. In the same system, Arvisais et al. (2004) reported a largely forested mosaic of Balsam Fir, poplar, birch, and spruce. In an agricultural area of southern Québec (Brome County), Saumure and Bider (1998) reported Wood Turtle habitat as extensive hayfields and cattle pastures juxtaposed with forest dominated by Box Elder and American Elm with willows (*Salix* spp.) and Speckled Alder prevalent. In Nova Scotia, White (2013) described a mixed agricultural and forested landscape, with forests dominated by northern hardwood species such as Yellow Birch, Red Maple, White Birch, Northern Red Oak, and Black Cherry, with some White Pine, Balsam Fir, and Eastern Hemlock.

Beech (*Fagus grandifolia*) (5.15). Northern Red Oak (*Quercus rubra*) is a locally important canopy tree from New Brunswick to Virginia. Within this transitional area of northern New England, the Berkshires, the Adirondacks region, and portions of Québec, Ontario, and the northern Great Lakes states, younger forests may be composed of birch species (*Betula papyrifera* and *Betula populifolia*).[7]

5.14—Throughout the Great Lakes from northeastern Minnesota to Michigan's Upper Peninsula and Ontario, Wood Turtles occur occasionally within fire-dependent communities of Jack Pine (*Pinus banksiana*), such as this site in Ontario. MIKE JONES

Central Appalachian Mountains.—The transitional forests of the Great Lakes and New England transition to more typical Appalachian forests near the New England coast and in Pennsylvania, Maryland, Virginia, and West Virginia. A multitude of oaks (*Quercus* spp.) and hickories (*Carya* spp.) are common components in adjacent upland forests. White Pine is nearly ubiquitous in many areas from the Great Lakes and Maritimes to Virginia; Virginia Pine (*Pinus virginiana*) is a more localized component from Pennsylvania to Virginia. Local topography drives forest composition, including the degree to which floodplain tree species dominate over upland species such as oaks, hickories, and pines.

At a complex of sites in Shenandoah and Frederick counties, Virginia, Akre and Ernst (2006) reported oaks and hickories on adjacent slopes, along with Virginia Pine and Pitch Pine (*Pinus rigida*), with White Pine present throughout. At a site in Loudoun County, Virginia, Akre and Ernst (2006) reported an occurrence of Wood Turtles within the Piedmont Hardpan Forest,

5.15—South of the northern coniferous forests, northern hardwood species predominate on upland slopes adjacent to Wood Turtle streams, including: *Left:* American Beech (*Fagus grandifolia*); *Right:* Sugar Maple (*Acer saccharum*) . MIKE JONES

7 Quinn and Tate (1991) reported that Wood Turtles in Ontario occur in mixed woods associations of White Pine and Red Pine, poplar (*Populus* spp.), White Birch, Red Maple, and Northern Red Oak, but at finer scales were found frequently in Speckled Alder. In western Vermont, Parren (2013) reported that his study site was surrounded by northern hardwood forest in upland areas.


5.16—Wood Turtles rarely live within the Piedmont Hardpan Forest of eastern Virginia, which supports: *Left:* Sweetgum (*Liquidambar styraciflua*); *Right:* Eastern Redbud (*Cercis canadensis*). Mike Jones

which supports Virginia Pine, Eastern Redcedar (*Juniperus virginiana*), small oaks, hickories, Redbud (*Cercis canadensis*), and American Sweetgum (*Liquidambar styraciflua*) (5.16).

Within the Wood Turtle's large range, several historically important canopy tree species have suffered substantial or complete decline within the past two centuries. For example: (1) the American Chestnut (*Castanea dentata*) undoubtedly influenced Wood Turtle ecology from Maine to Virginia before its collapse from the chestnut blight in the early 20th Century; (2) American Elms have been decimated by Dutch Elm Disease; (3) Eastern Hemlocks have suffered declines as a result of Hemlock Woolly Adelgid (*Adelges tsugae*, Foster 2014); and (4) the three native ashes (*Fraxinus* spp.) are facing widespread decline associated with Emerald Ash-Borer (*Agrilus planipennis*) (5.17).




5.17—Several historically important canopy tree species have suffered substantial or complete decline within the past two centuries within the core of the Wood Turtle's range: *Top left*: American Chestnut (*Castanea dentata*) collapsed due to chestnut blight; *Top right:* American Elms have been decimated by Dutch Elm Disease ; *Bottom right:* Eastern Hemlocks have suffered declines as a result of Hemlock Woolly Adelgid (*Adelges tsugae*); *Bottom left:* the three native ashes, including Green Ash (*Fraxinus pennsylvanica*, pictured here), have been declining due to the Emerald Ash-Borer (*Agrilus planipennis*). Mike Jones

Nesting Habitat

Wood Turtles require open, well-drained, elevated, exposed areas of sand and/or gravel for nesting (Akre and Ernst 2006; Ernst and Lovich 2009; Jones 2009; Akre and Ruther 2015), although appropriate nesting areas vary by geographic region. Over much of their range, Wood Turtles preferentially select nesting sites in coarse alluvium, poorly graded sand, or fine to medium gravel (Akre and Ernst 2006; Walde et al. 2007; Jones 2009) and sandy loam associated with a very wide range of natural and anthropogenic sites. Of 52 nests reported by Jones (2009) in Massachusetts, 64% were deposited in sand, 29% were deposited in mixed sand and gravel; 6% were deposited in organic materials or mixed organics and sand, and 2% were deposited in gravel (5.18).

Common natural features include sandy point bars on the inside bends of rivers (Buech et al. 1997; Saumure and Bider 1998; Jones 2009; Parren 2013); cutbanks on the outer bend of rivers

5.18—Wood Turtles typically nest in inorganic substrates of sand and mixed sand and gravel. Substrates of known nest locations in New England are pictured. Mike Jones

(Buech et al. 1997); sand and gravel bar deposits in the stream channel associated with stream obstructions, constrictions, or directional changes in flow (Gilhen and Grantmyre 1973; Vogt 1981; Compton 1999; Akre 2002; Akre and Ernst 2006; Jones 2009; Parren 2013); and areas of overwashed sand in open floodplains (Jones and Willey 2013a) and dry stream beds (Gräf et al. 2003; Jones 2008) (5.19).

Anthropogenic sites include: abandoned, stable, or infrequently disturbed portions of sand and gravel pits (Compton 1999; Tuttle and Carroll 2005; Walde et al. 2007), gravel boat ramps (Compton 1999), powerlines (Jones 2009; Akre and Ruther 2015), roadsides and roadcuts (Saumure and Bider 1998; Akre 2010; Akre and Ruther 2015), farm roads near streams (Jones 2009; Parren 2013), abandoned railroad beds (Vogt 1981; Farrell and Graham 1991), active rail beds (Franek and Ruziecki 2018), gravel and cobble piles (Akre and Ernst 2006), sandy pastures (Jones 2009), junkyards and outdoor storage areas with sand piles (Jones 2009), golf course sand traps (Jones 2009), and corn fields (Castellano et al 2008; Jones 2009). Of 52 nests primarily detected by radio-telemetry in Massachusetts and New Hampshire (Jones 2009), 35% were deposited on beaches along the stream in which the turtle over-wintered, 27% were deposited in gravel pits, 19% were deposited on sand piles or along dirt roads in pastures, 4% were deposited under powerlines, and 2% each were deposited along dirt roads and in a corn field. Wood Turtles also use nesting areas anthropogenically created specifically for turtle nesting (Buhlmann and Osborne 2011) (5.20).

Akre et al. (2012) and Dragon (2014) suggested that roadcut banks may function as ecological traps on the George Washington National Forest in northwestern Virginia, where Wood Turtles occur in small, forested stream systems with limited natural nesting areas. Here, Wood Turtles nest on well-drained substrates with some elevation above the riparian landscape, in areas with good solar exposure and strong southern aspect (Akre and Ruther 2015). In that setting, only 4% (N=9) of 214 nests located by a combination of radio-telemetry, thread-spooling, and surveillance from 2010–2014 were deposited in streamside sand banks, while 96% (N=195) were deposited in anthropogenically created and maintained habitats—the majority of which (55% of 214; N=18) were road cut banks. Compton (1999) also questioned whether anthropogenic nesting areas in Maine may function as ecological traps. However, Akre and Ruther (2015) found that absent predation (i.e., among protected nests), 75% of nests monitored over five years had some hatchling emergence and 66% had 50–100% emergence of hatchlings. The effect of predation on nests in this unusual setting remains to be studied directly.

Vascular plants associated with Wood Turtle nesting areas in New Hampshire include Sweetfern (*Comptonia peregrina*), hawkweeds (*Hieracium* spp.), Little Bluestem (*Schizachyrium scoparium*), and goldenrods (*Solidago* spp., Tuttle and Carroll 2005). These plants are also commonly associated with Wood Turtle nesting areas in New England (Jones, unpubl. data). In Ontario, nesting beaches also support Atlantic Ninebark (*Physocarpus opulifolius*), Field Wormwood (*Artemisia campestris*), and Balsam Poplar. Common Mullein (*Verbascum thapsus*) is often present in anthropogenic and roadside nesting areas throughout the Wood Turtle's range. Sassafras (*Sassafras albidum*) is present in disturbed habitats from New England to Virginia (5.21).

Other Associated Plant Species

Commonly associated herbaceous species in floodplains and streamside habitats include Ostrich Fern (*Matteuccia struthiopteris*), Interrupted Fern (*Osmunda claytoniana*), Trout Lily

5.19—Natural nesting features used by Wood Turtles include sandy point bars on the inside bends of rivers, cutbanks on the outer bend of rivers, sand and gravel bar deposits in the stream channel, and areas of overwashed sand in open floodplains.

5.20—Anthropogenic sites used by Wood Turtles include abandoned sand and gravel pits, powerlines, roadsides and roadcuts, farm roads near streams, abandoned railroad beds, gravel and cobble piles, sandy pastures, junkyards with sand piles, golf course sand traps, and cornfields.

5.21—Some of the many plants associated with Wood Turtle nesting areas include, *clockwise from top left:* Sweetfern (*Comptonia peregrina*); Common Mullein (*Verbascum thapsus*); Atlantic Ninebark (*Physocarpus opulifolius*); Sassafras (*Sassafras albidum*). Mike Jones

(*Erythronium americanum*), American False-Hellebore (*Veratrum viride*), and Tall Meadow-Rue (*Thalictrum pubescens*). In the Potomac River watershed, Wood Turtles occur occasionally with Golden Club (*Orontium aquaticum*) (5.22). In the Driftless Area of Wisconsin, Canada Nettle (*Laportea canadensis*) is one of the most common herbaceous species. The Common Prickly-Ash (*Zanthoxylum americanum*) is a shrub species commonly associated with Wood Turtle habitat in Driftless Area floodplains (Kordiyak 1981). A radio-telemetry study in the central Appalachians found that Wood Turtle plots were more closely associated with bedstraw (*Galium* spp.) while random points were more closely associated with Reed Canary Grass (*Phalaris arundinacea*) (McCoard et al. 2016). White (2013) described open riparian areas in Nova Scotia dominated by alder, cherry, elder (*Sambucus* spp.), hawthorn (*Crataegus* spp.), serviceberry (*Amelanchier* spp.), and raspberries (*Rubus* spp.).

Noteworthy Plants

Wood Turtles are also frequently associated with plants of regional or conservation interest. Near their western range-margin in southeastern Minnesota, Wood Turtles are associated with the Minnesota Dwarf Trout Lily (*Erythronium propullans*), the Prairie Bush-Clover (*Lespedeza leptostachya*), Green Dragon (*Arisaema dracontium*), and more than 50 additional rare or protected species in Minnesota (MNDNR 1979). In northern Maine, Wood Turtles occur in relatively close proximity to significant populations of Furbish Lousewort (*Pedicularis furbishae*), Labrador Indian Paintbrush (*Castilleja septentrionalis*), Bird's-Eye Primrose (*Primula mistassinica*), Alpine Sweetvetch (*Hedysarum alpinum*, var. *americanum*), and at least seven other unusual or rare plants (Richards 1976; Jones, unpubl. data), and elsewhere occur with Canadian Burnet (*Sanguisorba candensis*). Wood Turtles in New Hampshire are occasionally associated

5.22—Commonly associated herbaceous species in floodplains and streamside habitats include, *clockwise from top left:* Ostrich Fern (*Matteuccia struthiopteris*); Interrupted Fern (*Osmunda claytoniana*); Trout Lily (*Erythronium americanum*); American False-Hellebore (*Veratrum viride*); Tall Meadow-Rue (*Thalictrum pubescens*); Golden Club (*Orontium aquaticum*). Mike Jones

5.23—Some noteworthy plants of local or regional conservation interest that are associated with Wood Turtle streams include, *clockwise from top left*: Dwarf Scouring-Rush (*Equisetum scirpoides*); Threadfoot (*Podostemum ceratophyllum*); Canadian Burnet (*Sanguisorba canadensis*); Butternut (*Juglans cinerea*). Mike Jones

with rare floodplain forests of Butternut (*Juglans cinerea*, Jones, unpubl. data). In Massachusetts, some noteworthy plants that occur in association with Wood Turtles include Arctic Sweet Coltsfoot (*Petasites frigidus*), Threadfoot (*Podostemum ceratophyllum*), Dwarf Scouring-Rush (*Equisetum scirpoides*), Canadian Burnet, and Balsam Poplar (5.23). Noteworthy streamside species associated with important Wood Turtle sites in the Potomac watershed include Atlantic River Harperella (*Ptilimnium viviparum*).

Noteworthy Faunal Associates

Insects.—Wood Turtles occur in comparable and overlapping habitats with a multitude of rare or at-risk insects. For example, Wood Turtle populations may co-occur with several species of dragonflies and damselflies (Odonata) including the Green-faced Clubtail (*Gomphus viridifrons*) in Maryland and Virginia; the Spine-Crowned Clubtail (*Hylogomphus abbreviatus*) in Maine, Massachusetts, and Maryland; the Boreal Snaketail (*Ophiogomphus colubrinus*), Pygmy Snaketail (*Ophiogomphus howei*), Cobra Clubtail (*Gomphurus vastus*), and Arrow Clubtail (*Stylurus spiniceps*) in Maine. Wood Turtles also share riparian habitats with rare beetles (Coleoptera) throughout the Northeast including the White Mountain or Appalachian Tiger Beetle (*Cicindela*

5.24—Wood Turtles share riparian habitats with the rare Cobblestone Tiger Beetle (*Cicindella marginipennis*) from New Brunswick to Massachusetts. Jonathan Mays

5.25—Wood Turtles share aquatic habitats with freshwater mussels, some of which are of local or regional conservation interest, including, *clockwise from top left*: Plain Pocketbook (*Lampsilis cardium*); Pink Papershell (*Potamilus ohiensis*) (Mike Jones); Eastern Floater (*Pyganodon cataracta*); Brook Floater (*Alasmidonta varicosa*) (Amy Maynard); Triangle Floater (*Alasmidonta undulata*) (Chris Buelow); Eastern Pearlshell (*Margaritifera margaritifera*) (Chris Buelow).

ancocisconensis) and the Cobblestone Tiger Beetle (*C. marginipennis*). Wood Turtles have been reported from one of the remaining sites for Puritan Tiger Beetle (*C. puritana*) (5.24). Wood Turtles overlap with the Tomah Mayfly (*Siphlonisca aerodromia*, order Ephemeroptera) in Maine and New York.

Mussels.—Wood Turtles co-occur with a wide array of freshwater mussels, including several of regional conservation interest (5.25). Wood Turtles co-occur with Green Floater (*Lasmigona subviridis*) in New Jersey, Maryland, and Virginia, and with Brook Floater (*Alasmidonta varicosa*) in Nova Scotia, New Brunswick, Maine, New Hampshire, Massachusetts, Connecticut, New York, Pennsylvania, Virginia, and West Virginia. Wood Turtles co-occur with Triangle Floater (*Alasmidonta undulata*) in New England, and may be found in association with Dwarf Wedgemussels (*Alasmidonta heterodon*) or Eastern Pondmussels (*Sagittunio nasutus*) in New Hampshire, Massachusetts, Connecticut, and Virginia. Wood Turtles co-occur with Eastern Pearlshell (*Margaritifera margaritifera*) over most of their range in Nova Scotia and New Brunswick, and in high-quality coldwater habitats from Maine to Connecticut. In the upper

5.26—Wood Turtles are very often found in association with Eastern Elliptio (*Elliptio complanata*), so often that they are occasionally found with Elliptios attached to their feet. Mike Jones

Mississippi River watershed, Wood Turtles co-occur with Plain Pocketbook (*Lampsilis cardium*) and Pink Papershell (*Potamilus ohiensis*). Over much of their range, Wood Turtles are found in frequent association with Eastern Floater (*Pyganodon cataracta*) and Eastern Elliptio (*Elliptio complanata*), which occasionally attach themselves to Wood Turtles' feet (Jones et al. 2020) (5.26).

Fish.—In certain areas of the Northeastern United States, Wood Turtles may co-occur with the following fish species of local or state-level conservation interest: American Brook Lamprey (*Lethenteron appendix*), American Eel (*Anguilla rostrata*), Bridle Shiner (*Notropis bifrenatus*), Eastern Brook Trout (*Salvelinus fontinalis*), Slimy Sculpin (*Cottus cognatus*), Tessellated Darter (*Etheostoma olmstedi*), and Longnose Sucker (*Catostomus catostomus*). On the Ontario shore of Lake Superior, several Wood Turtle streams historically supported breeding Lake Sturgeon (*Acipenser fulvescens*) populations. Anecdotally, the association between Wood Turtles and Eastern Brook Trout seems to be strong. Historically, Wood Turtles co-occurred with spawning Atlantic Salmon (*Salmo salar*) from Nova Scotia and New Brunswick at least as far south as the tributaries of the Housatonic and Connecticut Rivers in New York, Vermont, New Hampshire, Massachusetts, and Connecticut, as well as tributaries to Lake Ontario (Fuller et al. 2020). Today however, the southernmost wild Atlantic Salmon are found in the lower portions of the Penobscot

5.27—Wood Turtles share streamside alder and scrub habitats with nesting American Woodcock (*Scolopax minor*). Mike Jones and Kennebec River watersheds of Maine (Gephard and McMenemy 2004; USFWS and NMFS 2018).

Birds.—Wood Turtles are found in association with a wide range of birds, including neotropical migrants and raptors. A brief list follows: American Woodcock (*Scolopax minor*), Louisiana Waterthrush (*Parkesia motacilla*), Willow Flycatcher (*Empidonax traillii*), Blue-Gray Gnatcatcher (*Polioptila caerulea*), Yellow-Throated Vireo (*Vireo flavifrons*), Northern Harrier (*Circus hudsonius*), Osprey (*Pandion haliaetus*), and Bald Eagle (*Haliaeetus leucocephalus*) (5.27).

Mammals.—In New Brunswick and Maine, Wood Turtles are found in association with Canada Lynx (*Lynx canadensis*) and American Marten (*Martes americana*) (5.28). From Massachusetts to Pennsylvania and New Jersey, Wood Turtle habitat may overlap with that of the Northern Water Shrew (*Sorex palustris*). From Minnesota to the Upper Peninsula of Michigan, Wood Turtles are found in association with Gray Wolves (*Canis lupus*).[8]

Amphibians.—Wood Turtles may locally share habitats with Northern Leopard Frog (*Lithobates pipiens*) and Four-toed Salamander (*Hemidactylium scutatum*) across New England, New York, and much of the northern Great Lakes Region. In northern Maine, New Hampshire, and Ontario, Wood Turtles are often found with Mink Frogs (*Lithobates septentrionalis*). Wood Turtles in Maine are associated with Northern Spring Salamander (*Gyrinophilus porphyriticus*), and are known to co-occur with Hellbenders (*Cryptobranchus alleganiensis*) in Pennsylania and Maryland (5.29).

Reptiles.—In Minnesota, Wood Turtles are found in close proximity to noteworthy populations of Timber Rattlesnake (*Crotalus horridus*), Massasauga (*Sistrurus catenatus*), and Six-lined Racerunner (*Aspidoscelis sexlineatus*, MNDNR 1979). Over portions of the

5.28—From Minnesota to Nova Scotia, including portions of New York, Maine, and New Hampshire, Wood Turtles occur in proximity to American Marten (*Martes americana*). Mike Jones

5.29—Wood Turtles locally share riparian habitats with Northern Leopard Frog (*Lithobates pipiens*) and Mink Frogs (*Lithobates septentrionalis*) across much of the Northern Forest from Minnesota to Nova Scotia, including much of the northern Great Lakes, northern New York, and New England. *Top:* Northern Leopard Frog. *Bottom:* Mink Frog. Mike Jones

8 Historically (of course) Wood Turtles occurred with wolves across most of their range.

Northeastern United States, Wood Turtles may co-occur locally with Eastern Ribbon Snake (*Thamnophis sauritus*, both Common and Northern sub-species), Short-headed Garter Snake (*Thamnophis brachystoma*), Queen Snake (*Regina septemvittata*), and Smooth Greensnake (*Opheodrys vernalis*) (5.30).

5.30—Wood Turtles co-occur locally with Smooth Greensnake *(Opheodrys vernalis)* from Ontario to Nova Scotia, including northern New England. Mike Jones

Associated Turtle Species

With the exception of a few notable areas in New Brunswick, Maine, and Québec, where Wood Turtles are the only freshwater turtle present in fluvial systems, Wood Turtles generally co-occur with one or more other native freshwater turtle. In fact, Wood Turtles are known to occur naturally in microsympatry with at least thirteen species of freshwater turtle in four families, and in close proximity to at least three additional species, suggesting that there may have been regular contact within the historical period.

5.31—Eastern Box Turtles (*Terrapene carolina carolina*) overlap with Wood Turtles in riparian areas from New Jersey to Virginia. This adult female Box Turtle was found during a Wood Turtle survey in Maryland. Mike Jones

Emydinae

Perhaps the best-documented associations are those with its most close living relatives, the other genera in the subfamily Emydinae. Wood Turtles historically occurred in the same habitats with their congener the Bog Turtle (*Glyptemys muhlenbergii*) from Berkshire County, Massachusetts (Jones, unpubl. data) as far south as Cecil County, Maryland (Cooper 1949), including portions of Sussex and Warren Counties, New Jersey (Zarate, unpubl. data) and much of the lower Hudson Valley and throughout southeastern Pennsylvania (Gipe, unpubl. data).

Wood Turtles co-occur in microsympatry with Eastern Box Turtles (*Terrapene carolina carolina*) over a broad area from Middlesex County, Massachusetts (Jones, unpubl. data) to northern Virginia and West Virginia (Akre and Kleopfer, unpubl. data), and in a small portion of west-central Michigan between Manistee and Muskegon Counties. Wood Turtles may be found with Eastern Box Turtles in Morris County, New Jersey (Buhlmann and Osborne 2011), throughout southern Pennsylvania (Gipe, unpubl. data), and in western Maryland (Akre, unpubl. data) (5.31).

Spotted Turtles (*Clemmys guttata*) co-occur with Wood Turtles in localized areas of southern New England, the Hudson Valley and Finger Lakes of New York, and south to Maryland. Narrow areas of range overlap with Spotted Turtles also occur in western Pennsylvania and west-central Michigan.

Blanding's Turtles (*Emydoidea blandingii*) co-occur with Wood Turtles in east-central New England (Carroll 1991; 1999), eastern Ontario, northern Michigan, and portions of Wisconsin (Badje, unpubl. data), Minnesota (MNDNR 1979), and Iowa (Tamplin, unpubl. data). At the present time, no co-occurring populations of Wood Turtles and Ornate Box Turtles (*Terrapene*

5.32—Notably, Wood Turtles are found in close association with only two Deirochelyine turtle species, the Painted Turtle *(Chrysemys picta)* and the Common Map Turtle *(Graptemys geographica)*. *Left:* Painted Turtle. *Right:* Common Map Turtle. Mike Jones

ornata) are known (Badje, unpubl. data). However, there are documented occurrences of both species in at least four of the same southwestern Wisconsin counties (WI DNR 2019), and it is possible these species overlapped occasionally in the lower Wisconsin River of Wisconsin in historic times.

Deirochelyinae

Notably, Wood Turtles are found in close association with only two Deirochelyine turtle species, the Painted Turtle (*Chrysemys picta*) and the Common Map Turtle (*Graptemys geographica*) (5.32). Wood Turtles may be found in microsympatry with Painted Turtles in every portion of its range except Cape Breton Island, Nova Scotia, northern New Brunswick, and northwestern Maine, and north of the St. Lawrence River in Québec. The two species are usually found using different aquatic habitats within a given watershed (Harding and Bloomer 1979), but are often found sharing nesting areas throughout their range. Wood Turtles are associated with Eastern Painted Turtles (*C. p. picta*) in New England, Midland Painted Turtles (*C. p. marginata*) in Ontario, Québec, and New York, and Western Painted Turtles (*C. p. bellii*) in Iowa (Tamplin, unpubl. data).

Historically, Wood Turtles very likely co-occurred with the Common Map Turtle near the mouths of certain large tributaries of northern Lake Champlain in Vermont, Québec, and New York. Elsewhere in the eastern part of the range, Wood Turtles rarely co-occur with Map Turtles, although they have been observed sharing basking sites (Hartzell 2017) and stream habitats (T. Pluto, unpubl. data, in Jones et al. 2015) in the Susquehanna watershed of Pennsylvania. Wood Turtles occur more regularly with *G. geographica* in the Great Lakes region. In the Upper Mississippi Region of Wisconsin, Minnesota, and Iowa, Wood Turtles may occur with Ouachita Map Turtles (*G. ouachitensis*), and False Map turtles (*G. pseudogeographica*) in addition to *G. geographica*. In southeastern Minnesota, Wood Turtles co-occur with Common Map Turtles and False Map Turtles (MNDNR 1979). In Iowa, Wood Turtles occur in stream systems that harbor Northern Map Turtles, Ouachita Map Turtles, and False Map Turtles (Tamplin, unpubl. data). All three *Graptemys* species occur with Wood Turtles in western Wisconsin (Vogt 1981; Badje, unpubl. data).

Wood Turtles rarely occur in larger streams with Northern Red-bellied Cooters (*Pseudemys rubriventris*) in Virginia and Maryland (Kleopfer and Jones, unpubl. data), but these two species do not co-occur in Massachusetts (Jones, unpubl. data; MassWildlife NHESP 2019). We know of no co-occurring populations of Wood Turtles and Diamondback Terrapins (*Malaclemys terrapin*), and their strict habitat preferences would seem to preclude them from frequent contact or shared habitats, but they occur in close proximity where small streams reach the eastern shore of Narragansett Bay in Rhode Island and Massachusetts (Yorks and Jones, unpubl. data).

Wood Turtles also co-occur in close proximity to introduced populations of Common Sliders (*Trachemys scripta*) in Massachusetts, New Jersey, and Virginia (Jones, Zarate, and Kleopfer, unpubl. data).

Chelydridae

Wood Turtles co-occur with Common Snapping Turtles (*Chelydra serpentina*) throughout their range with the exception of large areas of northwestern Maine and northern New Brunswick where Common Snapping Turtles are absent (5.33). The two species commonly share nesting areas in New Hampshire (Carroll 1991; Jones, unpubl. data), Massachusetts (Jones, unpubl. data), New Jersey (Buhlmann and Osborn 2011), Virginia (Kleopfer, unpubl. data), Iowa (Tamplin, unpubl. data), and Wisconsin (Badje, unpubl. data).

Kinosternidae

Wood Turtles occur rarely in microsympatry with Common Musk Turtles (*Sternotherus odoratus*) in central and eastern New England (Jones, unpubl. data), in Morris County, New Jersey (Buhlmann and Osborn 2011), in Virginia (Kleopfer, unpubl. data), and elsewhere between these locations. Wood Turtles co-occur with Eastern Mud Turtles (*Kinosternon subrubrum*) in eastern Virginia (Akre, unpubl. data) (5.34).

Trionychidae

Wood Turtles occur in microsympatry with two trionychid turtles, the Smooth Softshell (*Apalone mutica*) and Spiny Softshell (*A. spinifera*), primarily in the Upper Mississippi tributaries of Wisconsin, Minnesota, and Iowa (Tamplin, unpubl. data; MNDNR 1979; Badje, unpubl. data). Wood Turtles may also be found in association with *A. spinifera* in Michigan, Pennsylvania, and possibly western New York (5.35).

5.33—Wood Turtles co-occur frequently with Common Snapping Turtles *(Chelydra serpentina)* throughout their range with the exception of large areas of northwestern Maine and northern New Brunswick where Common Snapping Turtles are absent. An adult male is pictured. Mike Jones

5.34—Wood Turtles co-occur with Common Musk Turtles (*Sternotherus odoratus*) from New England to Virginia. An adult male is pictured. Mike Jones

5.35—Wood Turtles occur in microsympatry with two trionychid turtles, the Smooth Softshell *(Apalone mutica)* and Spiny Softshell *(A. spinifera),* in tributaries to the Upper Mississippi River. *Left:* Smooth Softshell. *Right:* Spiny Softshell. Mike Jones

Summary

Wood Turtles are uniquely adapted to the habitats in which they occur, the mid-sized flowing streams of North America's eastern forests. Here, they occur with a wide range of species representative of different regions of the North American continent, and often occur with species of conservation interest.

6. Spatial Ecology and Seasonal Behavior

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Wood Turtle habitat in the Appalachians. Mike Jones

6.1—Because of their long lifespan and need for disparate resources ranging from instream habitats to riparian areas to upland nesting and foraging sites, as well as their tendency to travel large distances over land to access those resources, Wood Turtles respond to landscape heterogeneity at a range of spatial scales. American Turtle Observatory

Introduction

Ethology—the study of animal behavior—examines the ways that an individual animal interacts with its environment, combining evolutionary, genetics, developmental, ecological, and mechanistic approaches to study both the proximate and ultimate drivers of observable behaviors (Rubenstein and Alcock 2018). Animal behavior is an expansive field of study, which includes (at a minimum) communication and social interactions, foraging, defense, and reproductive behavior, among many other elements. One of the most important aspects of animal behavior, particularly as it relates to wildlife ecology and conservation, is the way animals move and use space on a landscape.

The field of spatial ecology has grown rapidly over the last several decades as ecologists increasingly recognize the importance of scale, as well as the relationship between ecological processes and landscape composition and heterogeneity (Fletcher and Fortin 2018). As global environments become increasingly fragmented and dominated by anthropogenic drivers, the interaction between ecological systems and spatial heterogeneity becomes all the more important to understand and incorporate into ecological studies and biodiversity conservation efforts alike. Wood Turtles are an interesting case study, because they are reliant upon certain disturbed habitats for nesting, foraging, and thermoregulation, but they are also highly vulnerable to most anthropogenic methods of creating early-successional habitats. From a recent evolutionary perspective, it seems that Wood Turtles thrived in the riparian habitat mosaics created by intermediate levels of riverine disturbance.

It is clear now that Wood Turtles respond to landscape change and landscape heterogeneity at a range of spatial scales that may even exceed an animal's lifetime movement distance (6.1). Because of their long lifespan,[1] need for disparate resources (riparian areas, upland nesting, foraging, and thermoregulatory habitats),[2] and their ability to travel large overland distances to access resources as they shift over time, a Wood Turtle's lifetime movements can encompass relatively large areas within—or across—watersheds (Jones and Willey 2020).

6.2—Though they require instream habitats to overwinter, Wood Turtles are the most terrestrial of the subfamily Emydinae with the exception of Box Turtles. In many areas, Wood Turtles will spend weeks to months in upland habitats as they seek foraging opportunities. Here, an old male Wood Turtle forages on Jewelweed (*Impatiens capensis*) in Maine. Derek Yorks

Although Wood Turtles require instream habitats to overwinter, they are also among the most terrestrial of the Emydidae, leaving streams in the spring to spend weeks and often months in adjoining upland areas (6.2).[3] Most studies have found that Wood Turtles use relatively constrained areas along streams, but they are capable of moving long distances (i.e., several kilometers) to nesting sites and summertime activity centers in riparian and upland areas. The capability and willingness to move large distances in search of nesting sites and feeding areas—in combination with a suite of bet-hedging life history characteristics—leaves them particularly vulnerable to the anthropogenic changes to the landscape that elevate mortality rates associated with large movements, or to disturbances that result in ecological traps.

In this chapter, we explore the Wood Turtle's seasonality, behavior, and their use of space and the landscape, with a particular emphasis on movement patterns (including seasonal, annual, and dispersal patterns). Indeed, Wood Turtles tend to move large distances—and generally operate at larger spatial scales—than other emydid turtles (e.g., Bog, Spotted, or Box Turtles). However, their use of space varies considerably by age and sex, as well as across latitude and climate gradients, habitat composition, site, and level of habitat fragmentation.

Seasonal Activity

Activity Periods

Wood Turtles generally become alert and active between March and April and become mostly dormant in November or December, depending on elevation, latitude, and annual variation in weather (6.3), as well as individual characteristics such as body condition, age, or sex.[4] At northern latitudes, Wood Turtles may be inactive for more than half the year. For example, in a Québec

1 See Chapter 7 for a more detailed discussion of the Wood Turtle's lifespan.

2 See Chapter 5 for a more complete description of the Wood Turtle's habitat requirements.

3 The basic components of the Wood Turtle's seasonal ecology have been well understood since the mid-19th century. For more discussion, see Chapter 3.

4 Male Wood Turtles may become active earlier in the season and remain active later (Akre and Ernst 2006).

study, Arvisais et al. (2002) reported activity from May to October. By contrast in northern Virginia, Akre and Ernst (2006) reported regular activity from March to November, but Akre (unpubl. data) has also reported occasional winter activity in the same stream systems. Akre and Ernst (2006) identified two primary biological periods: brumation (December–February) and active season (March–November). They divided the latter season into five distinct periods of activity: (1) emergence, March; (2) prenesting, April–May; (3) nesting, June; (4) postnesting, July–September; and (5) prebrumation, October–November. With some modifications to account for earlier or later emergence and brumation, this framework is useful for evaluating Wood Turtle activity across their range.

6.3—Wood Turtles may be found active in streams from March or April to November in most years, with regional variation based on elevation and latitude. A male Wood Turtle in northern New England is pictured. Mike Jones

Winter Dormancy or Brumation

Below water temperatures of about 6˚C, Wood Turtles are generally inactive in streams (Harding and Bloomer 1979; Ernst and McBreen 1991; Kaufmann 1992b; Akre 2002; Pulsifer 2012) (6.4). In West Virginia, Niederberger (1993) reported that Wood Turtles were typically dormant when water temperatures ranged from 2–9˚C (but noted at least one instance of mounting at water temperature of 1˚C) and observed that while juveniles and females tended to be dormant at low temperatures, males sometimes moved underwater and appeared active. Virginia Wood Turtles emerge and become active in March and begin feeding when water temperature reaches 4–5˚C and air temperatures reach 12–15˚C (Akre and Ernst 2006); Akre and Ernst (2006) also observed Virginia Wood Turtles alert and marginally active at water temperatures of 1˚C. In West Virginia, thermochrons revealed that Wood Turtles became active at about 5˚C in mid-March and ceased activity in late October at approximately 10˚C (Curtis and Vila 2015).

6.4—Below water temperatures of about 6˚C, Wood Turtles are generally inactive in streams. At higher elevations and northerly latitudes, streams may become partially to entirely ice-covered. Snow-covered habitat is shown in eastern Canada in February (*top*). Brumating Wood Turtles in the Appalachians (*bottom*). Mike Jones

In northern areas, Wood Turtles exhibit more pronounced periods of dormancy, although observation is often hindered by snow and ice cover. White (2013) reported no Wood Turtle activity between 19 December and 12 March in Nova Scotia. Emergence and spring activity in northern New England may be determined by ice-out (Jones and Willey, unpubl. data). Graham and Forsberg (1991) reported extended periods of inactivity with only minor repositioning from December–February in Massachusetts, and Klemens (1993) reported that Wood Turtles become active in Connecticut in late March and early April. Activity in Michigan is rare after mid-October (Holman 2012).

In Pennsylvania, Kaufmann (1992a; 1992b) reported that turtles became active in very late March or early April, and that daytime activity during this emergence period was primarily limited to the stream, with occasional forays onto the bank for basking or feeding. Kaufmann further noted that during April in the year the studies were conducted, when the temperature fell below 10˚C on 94% of nights, 84% of turtles spent the night in the creek, whereas an average of 54% spent the night in the creek on warmer nights during this time. In addition, in that same time, maximum air temperature did not exceed 20˚C on 83% of days and an average of 90% of turtles remained in the creek compared to an average of 39% on warmer days. Then, as temperatures dropped in the early autumn, turtles began returning to the creek after spending most of their time on land since late April (Kaufmann 1992a; 1992b). For example, in October, all nights were 10˚C or lower and an average of 91% of turtles returned to or remained in the creek overnight. Again, during that same time, maximum air temperature on 85% of days never exceeded 20˚C. On those days, 87% of turtles entered or remained in the water, compared to 71% on warmer days (Kaufmann 1992a; 1992b). In central New York, Wright (1918) noted that Wood Turtles generally emerged and were visible in streams around April 20, though a range of dates were reported from 20 March (1915) to 14 May (1906).

Summer Dormancy or Aestivation

It is not well documented whether or not wild Wood Turtles experience periods of heat-related dormancy. Most authors have reported continuous activity throughout the summer months and do not describe periods of aestivation (Strang 1983; Ernst 1986; Jones 2009). In Pennsylvania, Kaufmann (1992b) recorded no observations of aestivation during the summer months in his wild study population, though several of his penned captives aestivated for 7–29 days in July and August. Even in the southern part of their range and at low elevations, Wood Turtles remain active through the summer, although they move much less than during the spring. Fine-scale movements appear to decrease during the warmest months of July and August (Akre 2002; Akre and Ernst 2006).

Daily Activity and Thermoregulation

Wood Turtles are primarily diurnal, with the exception of nesting females (which may be active well after dark). Their daily activity cycle, however, appears to vary by season, geographic location, and weather conditions. Thermoregulation is a critical component of Wood Turtle behavior and activity, especially during emergence from brumation in the spring, and appears to drive diurnal activity patterns (Ernst 1986; Dubois et al. 2009; Curtis and Vila 2016). Thermoregulatory behaviors in the Wood Turtle are driven by interactions between temperature, humidity, and season. When Wood Turtles become active in the spring, their activity cycle is first unimodal (active during the warmest part of the day), but becomes bimodal with increasing temperatures and greater risk of water loss, transitioning back to unimodal with decreasing temperatures in the fall. Access to basking sites partially drives Wood Turtle habitat selection at fine scales (Compton et al. 2002; Saumure 2004). In the only experimental thermoregulatory studies to date, Wood

Turtles in southern Québec—near the northern limit of the species' range—were shown to imprecisely regulate their body temperature by basking to achieve an optimal temperature of 30°C (Dubois et al. 2008; 2009). This upregulation of body temperature and metabolism was more important for juveniles that had recently fed than it was for unfed juveniles or adult males. The authors further demonstrated that wild Wood Turtles exhibited a unimodal thermoregulatory activity cycle by basking in mostly open habitats on sunny days and shuttling between sun and shade between 0900 and 1600 hr to regulate their body temperature toward the 30°C optimum. This optimal temperature was only achievable for a 5-hour window from 1100–1600 hr at that location (Dubois et al. 2009).

Courtship and Mating

Wood Turtles court throughout the active period, usually with peaks in spring and fall (Harding and Bloomer 1979). Courtship and/or copulation occurs in both the spring and fall in Minnesota (Breckenridge 1958); Wisconsin (Brewster 1985); Massachusetts (Jones 2009); New York (Wright 1918); New Jersey (Harding and Bloomer 1979; Farrell and Graham 1991); Pennsylvania (Kaufmann 1992a; Ernst 2001b); Virginia (Ernst and McBreen 1991); and West Virginia (Niederberger and Seidel 1999). In Venango County, Pennsylvania, near the western margin of the Wood Turtle's range in the Northeast region, Swanson (1952) reported "clasping pairs in trout streams in the middle of April," and reported mating in captivity in March and September. Autumnal mating was reported to be more common in Virginia (Akre 2002); Québec (77% of 35 courtship events, Walde et al. 2003); Vermont (84% of 57 observed mating events, Parren 2013); and West Virginia (64% of 28 courtship events, McCoard et al. 2018). Harding (1991) reported that mating is most common in June and September in Michigan. Kleopfer (unpubl. data) observed a mounted pair of Wood Turtles under ice in early December in Virginia. Like many related species, Wood Turtles are able to store viable sperm for at least two years (Figueras and Burke 2017), so the specific timing of mating may not be a significant driver of clutch fertilization rate.

Copulation typically occurs in water, along the banks of streams, in pools along the stream course, or within logjams and woody debris (Ernst and Lovich 2009) (6.5). Fifty-three of 57 (93%) breeding attempts observed by Parren (2013) in Vermont were in the water, with three instances of clasping/mounting observed on the bank 1–8 m from the river (6.6). In a radio-telemetry study in Massachusetts and New Hampshire, Jones (2009) observed courtship behavior (e.g., clasping, mounting) or copulation on 110 occasions, of which 97% were in the water. McCoard

6.5—Wood Turtles usually court and copulate underwater in pools along the stream course. Courting Wood Turtles are shown in New England (left) and Virginia (right). Mike Jones

6.6—Wood Turtles occasionally will court on land, usually within a few meters of the stream course, and often because the female has dragged the pair out of the water. The Wood Turtle pairs pictured here were photographed as found—on land or at the water's edge—in various New England streams. Mike Jones

et al. (2018) observed 28 mating events in West Virginia, of which 18 (64%) were in the water. Ernst (1986) noted that all observed mating events at his study area in Pennsylvania were aquatic.

Wood Turtles exhibit a number of noteworthy courtship rituals (6.7). Carr (1952) provides an early summary of some common courtship behaviors, relying heavily on the detailed observations of J.G. Knowlton, and enigmatically reported that "several observers" had reported a "courtship

6.7—The courtship ritual of the Wood Turtle includes a prolonged period of "head-bobbing" (left), in which the male extends his throat and head in front of the female's face and sways his head from side to side while "clapping" his plastron to her carapace. This sound is audible from several meters away. Rarely, the courtship convolutions will result in an overturned pair. Derek Yorks & Mike Jones whistle." Brewster and Brewster (1987) described nine different behaviors—including lateral rocking, biting, and mounting—in an enclosure setting. Liu et al. (2013) summarized instances of head-bobbing courtship rituals and "shell clapping," in which the male thumps his plastron against the carapace of the female. The mating posture is typically plastron-to-carapace (Kaufmann 1992a), but Tronzo (1993) and Mitchell and Mueller (1996) reported instances of plastron-to-plastron mating. In addition, several instances of plastron-to-plastron mating were observed during the course of studies for this volume in Aroostook County, Maine and Coos County, New Hampshire (Jones and Willey, unpubl. data) (6.8).

6.8—The mating posture of Wood Turtles is typically plastron-to-carapace, as illustrated in Figures 6.5 and 6.6, but numerous observers have reported instances of plastron-to-plastron mating, such as this pair in New Hampshire. MIKE JONES

Nesting Season and Timing

Throughout their range, Wood Turtles generally nest in June, with observed nesting dates ranging from mid-May to mid-July (Thoreau 2009;[5] Harding and Bloomer 1979; Compton 1999; Bowen and Gillingham 2004; Walde et al. 2007; Jones 2009; Akre and Ruther 2015) (6.9) (Table 6.1). An early account of Wood Turtle nesting was provided by Gammons (1871), who described the female preparing the nest site with her front limbs, and whose account was dismissed by Carr (1952). In our New England study areas (western Massachusetts to northern Maine), we found that the median date of nesting activity between 2004 and 2017 was 6 June (Jones and Willey, unpubl. data); the earliest and latest confirmed nests were 21 May (2013) and 4 July (2006), respectively.

Daily timing of nesting seems to vary widely throughout the range. In Québec, Walde et al. (2008) reported that 38.5% of nests were initiated

Table 6.1—Reported dates of nesting activity in Wood Turtle populations throughout their range.

State/ Province	Range of Nesting Dates	Source
QC	9–28 June	Walde (1998)
ON	7–19 June	Brooks et al. (1992)
MI	10–29 June	Harding (1991; 1994)
ME	12–25 June	Compton (1999)
ME, NH, MA	21 May–4 July	Jones and Willey, unpubl. data
NH	2–13 June	Tuttle and Carroll (1997)
VT	23 May–21 June	Parren (2013)
MA	28 May–4 July	Jones (2009)
NJ	15 May–15 June	Castellano et al. (2008)
NJ	21 May–13 June	Buhlmann and Osborn (2011)
PA	4–19 June	Ernst (2001b)
PA	4–16 June	Kaufmann (1992)
VA	23 May–22 June	Akre (2010)

5 For entries from 1855–1860, see Chapter 3.

between 0500 and 0900 hr. Jones (2009) reported that 90% of nests in Massachusetts and New Hampshire were initiated in the late afternoon and evening. In an extended sample from the same study, but including field sites in Maine, we found that more than half of observed nesting activity occurred between 1800 and 2000 hr (Jones and Willey, unpubl. data), with occasional nesting activity extending well after dark. Akre and Ruther (2015) reported that in northwestern Virginia, nesting activity is most common in the early morning, late afternoon, and evening, with some nesting activity continuing through the night.

6.9—Throughout their range, Wood Turtles generally nest in June, as pictured here in eastern Canada (top). Nest-searching and nesting female Wood Turtles will often become covered with sand, as seen in this New England female (middle). Females will sometimes prepare the nest site with their front limbs, as shown here in Massachusetts (bottom). Mike Jones

Incubation

Wood Turtle nests generally hatch after about 70–90 days of incubation. In Maine, incubation duration ranged from 67 (mean temperature=24.5˚C) to 113 days (mean temperature = 19.5˚C) with a median of 89 days (*n*=11) (Compton 1999). In New Jersey, Castellano et al. (2008) reported a mean incubation period of 72.2±3.0 days (range=69–76; *n*=10). In northern Virginia, Akre and Ruther (2015) reported that incubation averaged 82 days based upon a mean nesting date of 7 June and a mean emergence date of 27 August.

Compton (1999) predicted that Wood Turtle eggs hatch when they receive 788±10.1 degree-days above a threshold of 12.5˚C, a model derived from field-hatched (*n*=4) and lab-hatched (*n*=7) nests from Maine. Compton also built a soil temperature model from historical weather data and inferred that there is a broad area in the northern half of the Wood Turtles' range in which nest failure is likely to occur in some years as a result of low summer temperatures. In their study near the Wood Turtle's northern range-margin in Québec, Walde et al. (2007) found that nest failure was positively correlated with date of nesting, consistent with Compton's (1999) predictions that Wood Turtle nests at extreme northerly latitudes are limited by the total amount of accumulated warming.

Rising summer temperatures throughout the species range will likely influence nest-site selection, incubation duration, and nest success rates, especially near the Wood Turtle's northern


6.10—Wood Turtle hatchlings usually emerge from the nest in August, but emergence can occur from July to October. Emerging hatchling Wood Turtles are pictured in New England. Derek Yorks & Mike Jones

and southern range-margins. Because they appear to exhibit chromosomal or genetic sex determination—a trait otherwise unknown in the Emydidae outside of the genus *Glyptemys*—Wood Turtles may have an advantage over related turtle species in that they likely will not experience altered sex ratios as a direct result of warming trends. Toward the southern extent of the Wood Turtle's range, warmer summer temperatures might actually increase rates of lethal nest desiccation (Deeming 2004), or alternatively, promote more rapid embryonic development with hatchings emerging at smaller sizes with slower growth rates (e.g., Brooks et al. 1991; Deeming 2004). It is not clear (under the projected warming scenario) if smaller Wood Turtle hatchlings would grow more slowly or have lower survival—two studies found higher survival in smaller Wood Turtle hatchlings (Paterson et al. 2014; Dragon 2014)—but slower growth could have long lasting implications for size and age at maturity and reproductive output, and thus demography (Congdon and van Loben Sels 1991). In the northeastern United States and adjacent Canada, warmer summer temperatures have brought both greater precipitation and more extreme precipitation events (e.g., Huang et al. 2017), which are likely to influence incubation and/or embryonic development and growth in addition to elevating rates of lethal flooding.[6] How these changes are affecting the development of Wood Turtle eggs—and emergence rates of nests—is not known.[7]

Hatchling Emergence

Hatchling Wood Turtles generally emerge from the nest in August, but emergence can occur from July to October (6.10). In New Jersey, Castellano et al. (2008) reported emergence dates from 13–20 August, and Buhlmann and Osborn (2011) reported emergence dates from 29 July to 14 September, but noted that most hatchlings emerged in mid- to late-August. In northern Virginia, Akre and Ruther (2015) reported emergence dates from 1 August to 25 September between 2010–2014, with a mean emergence of 27 August (±12 days). In southern New Hampshire, Tuttle and Carroll (2005) documented synchronous (n=5) as well as asynchronous (n=2) emergence from 13–29 August, with all emergence events occurring from 0820–1805 h.

6 The risks associated with extreme flooding events are explored further in Chapter 8.

7 Wood Turtles often deposit nests in near-shore sand and gravel banks, so increased flooding frequency and magnitude will locally result in increased nest failure from drowning and erosion; see Chapter 8.

Parren and Rice (2004) speculated that some Wood Turtle nests may overwinter on land in Vermont. Overwintering by hatchling Wood Turtles in the nest has not been reported in other studies, although Wright (1918) observed a turtle of "newly hatched form" in New York in April 1913, and Akre (unpubl. data) found a live hatchling, mostly emerged from the egg, while excavating a previous year's nest in April 2012. Jones and Willey (unpubl. data) observed underdeveloped Wood Turtle hatchlings emerging in response to inundation during a flood in late August 2004.

Social Behavior

Wood Turtles are generally solitary during the active period, although they may be frequently found in small groups. We've noticed that individual pairs of Wood Turtles may be found in close proximity at various times over multiple years (Jones and Willey, unpubl. data). Wood Turtles do not seem to keep and defend territories (Kaufmann 1992a), but aggressive interactions are common and dominance hierarchies have been documented. Kaufmann (1992a) conducted an intensive six-year study on social behavior of Wood Turtles in Pennsylvania, and found that agonistic (combative) encounters between adult females were rare, but male-female and male-male agonistic encounters were common. In Kaufmann's study, males won 18 of 21 putatively non-courtship related agonistic encounters with females, with some encounters involving physical contact (e.g., biting, nudging). Kaufmann (1992a) observed that male-male encounters were nearly always agonistic, with only 12% of 560 observed events being non-agonistic. Male-male combat events were most common during the spring and fall breeding periods, and the larger male usually seemed to defeat the smaller male. Barlizay (1980) documented two male-male agonistic encounters in New York; one included no physical interactions, and the other involved both mounting and biting. McCoard et al. (2018) described five male-male antagonistic interactions in West Virginia. Dinkins (1954) observed biting behavior between two males in an enclosure. On two occasions in Massachusetts in 2004 and 2013, we observed a male Wood Turtle aggressively trying to interrupt the courtship of a clasped/mounted pair by biting the mating male (Jones and Willey, unpubl. data). On twelve additional occasions throughout New England, we observed male-male aggressive encounters, which often involved biting and/or mounting; the majority of these encounters occurred in the fall (8 of twelve, or 66.7%). We also observed clearly aggressive encounters between (1) an adult female and a juvenile; (2) two subadult males; and (3) a male and a subadult male (Jones and Willey, unpubl. data).

Female Wood Turtles appear to exhibit dominance hierarchies during the nesting season. In Wisconsin, Fischer et al. (2017) documented a female-female agonistic interaction during the nesting period. This encounter included one female chasing another female off a partially excavated nest, then continuing to excavate the nest, but ultimately leaving the site without laying eggs. In the Upper Peninsula of Michigan, Rutherford (2012) also documented agonistic behavior between females during the nesting period, where one female chased two females off of a nesting site.

In addition to intraspecific social interactions, Wood Turtles have been documented sharing basking sites with other turtle species including Common Map Turtles (*Graptemys geographica*; Hartzell and Hartzell 2016; Hartzell 2017) and Painted Turtle (*Chrysemys picta*; Jones and Willey, unpubl. data).

Aggregations

6.11—Wood Turtles are opportunistic omnivores, able to capture food and feed on land or in the water. This nest-searching female paused to capture and eat a slug. Mike Jones

The Wood Turtle has been noted for its large aggregations near overwintering sites (Bloomer 1978). Harding and Bloomer (1979) documented groups of 5–70 Wood Turtles in the same overwintering feature in New Jersey. Sizable aggregations of Wood Turtles have also been reported in New Jersey (28 individuals, Farrell and Graham 1991) and Tolland County, Connecticut (20 individuals, Klemens 1993). Niederberger (1993) reported an aggregation of 80 turtles in West Virginia, with 35 turtles visible on a pool bottom and others scattered under banks with their carapaces visible. Parren (2013) documented several communal overwintering sites in Vermont, and we have observed the tendency for Wood Turtles to cluster or aggregate near overwinter sites at many sites in Maine, New Hampshire, Massachusetts, New York, and Maryland (Jones and Willey, unpubl. data).

Foraging

The Wood Turtle is an opportunistic omnivore (Surface 1908; Logier 1939; Oliver and Bailey 1939; Harding and Bloomer 1979; Vogt 1981; Farrell and Graham 1991; Klemens 1993) that typically feeds from April to October (Ernst 2001b). Like other semi-terrestrial emydine turtles, the Wood Turtle is able to feed on land or in water (Castellano et al. 2008) (6.11). Many authors have reported that Wood Turtles opportunistically eat a wide range of green leaves, fruits, fungi, arthropods and other invertebrates, eggs (including turtle eggs), and carrion—in fact, this aspect of the Wood Turtle's life history has evidently captured the interest of a surprising number of investigators.

Reports of the Wood Turtle's omnivorous and terrestrial feeding tendencies came early. Allen (1868) reported Wood Turtles eating dandelions (*Taraxacum* sp.) and a low *Rubus* sp. in Massachusetts. Surface (1908) reported that 76% of Pennsylvania Wood Turtles had eaten vegetable material, and 80% had consumed "animal matter;" among the foods taken by multiple individuals in Surface's study were leaves and seeds of flowering plants (including Winterberry Holly [*Ilex verticillata*] and the exotic Broadleaf Plaintain [*Plantago major*]), beetles, snails and slugs, and bird carrion. Oliver and Bailey (1939) also reported that New Hampshire Wood Turtles were omnivorous: "Berries, seeds, earthworms, and insects are favored articles in this turtle's diet." Lagler (1943) reported that Michigan adults consumed filamentous algae, mosses, willow leaves (*Salix* spp.), insects (including black flies [Simuliidae], caddisfly [Trichoptera] larvae, and beetles), mollusks, snails, earthworms, Bluegill (*Lepomis macrochirus*) and trout (Salmonidae), and tadpoles (*Lithobates* spp.), though some of the items observed might have been scavenged. Harding and Bloomer (1979) reported that turtles in natural or semi-natural conditions in Michigan and New Jersey had eaten blueberries (*Vaccinium* spp.), blackberries and raspberries (*Rubus* spp.), strawberries (*Fragaria* spp.), green leaves of willow and alder (*Salix* and *Alnus* spp.), as well as grasses, mosses, and algae and a variety of animal matter including mollusks, insects, earthworms, tadpoles, fish carrion, and newborn mice.

Green leaves (including cinquefoil [*Potentilla* spp.] and violets [*Viola* spp.]) and fungi were prevalent in the food items reported by Strang (1983). Vogt (1981) reported spruce (*Picea* spp.) needles eaten by a female in Wisconsin, and Harding (*in* Farrell and Graham 1991) reported Wood Turtles feeding on willow leaves. Gilhen and Grantmyre (1973) and Gräf et al. (2003), respectively, reported apparent consumption of blueberries and Choke-cherries (*Prunus virginiana*) by Wood Turtles on Cape Breton Island, Nova Scotia. Compton et al. (2002) speculated that raspberries were an important food in western Maine. Farrell and Graham (1991) observed New Jersey Wood Turtles eating green leaves of strawberry, raspberry, blackberry fruits, fish carrion, and slugs. Niederberger and Seidel (1999) reported that Wood Turtles in West Virginia had stomach contents as follows: vegetation (68%), earthworms (46%), other invertebrates (38%), and carrion (23%).

6.12—Some of the plants eaten most frequently by Wood Turtles in New England include the green leaves of Jewelweed (*Impatiens capensis*) (top) as well as the fruits of several species of blackberries, such as Black Raspberry (*Rubus occidentalis*) (bottom). Mike Jones

In Iowa, Tamplin (2006b) reported that Wood Turtles routinely feed on Prairie Ragwort (*Senecio plattensis*), which is a highly toxic plant known to kill fish, lizards, and livestock. In West Virginia, Tamplin et al. (2009) reported Wood Turtles feeding on adult Ringneck Snakes (*Diadophis punctatus*) and the shed skin of a garter snake (*Thamnophis* spp.). Tamplin et al. (2009) observed a Wood Turtle eating a dried Scarlet Oak leaf (*Quercus coccinea*) in West Virginia.

Jones and Sievert (2009b) reported 395 instances of wild Massachusetts Wood Turtles eating identifiable food items. Slugs and other invertebrates comprised the majority of food items (*n*=246), followed by the green leaves of at least 24 species of plants (*n*=90), one-third of which were Jewelweed (*Impatiens capensis*). The fruits of raspberries and blackberries and strawberries were frequently eaten (6.12). Corn, apples, and grapes (*Vitis* spp.) were also eaten. Additional food items reported by Jones and Sievert (2009b) included Spotted Salamander (*Ambystoma maculatum*) egg masses, trout carrion, bird carrion, and the fungi *Russula* spp. and *Lactarius* spp. In New Hampshire, Wicklow (in Jones et al. 2015) reported that in early spring, adult Wood Turtles feed on Bracken (*Pteridium aquilinum*) as well as tadpoles in vernal pools, and in fall Wood Turtles feed heavily on elderberries (*Sambucus* spp.), grapes, and Silky Dogwood (*Cornus amomum*) drupes.

Hatchling Diet

Hatchling Wood Turtles are probably opportunistic omnivores, although most observations of feeding suggest invertebrate carnivory. Castellano et al. (2008) reported seven instances of radio-equipped hatchlings eating slugs (*Arion subfuscus*); six of these events were during overcast weather with light to heavy rain. Tuttle and Carroll (2005) also reported hatchling Wood Turtles eating slugs, as well as green leaves. Paterson et al. (2012) did not observe foraging or feeding behavior in 295 behavioral observations of radioequipped hatchling Wood Turtles in Ontario. Based on fecal analysis, Wicklow (in Jones et al. 2015) observed hatchlings to eat riffle beetles (Elmidae spp.) and larvae of the caddisfly (Trichoptera, genus *Helicopsyche*).

6.13—Wood Turtles occasionally exhibit cannibalistic oophagy, or an occasional tendency to eat the eggs of their own species. The Massachusetts female pictured here was interrupted eating her own egg in a hayfield. Mike Jones

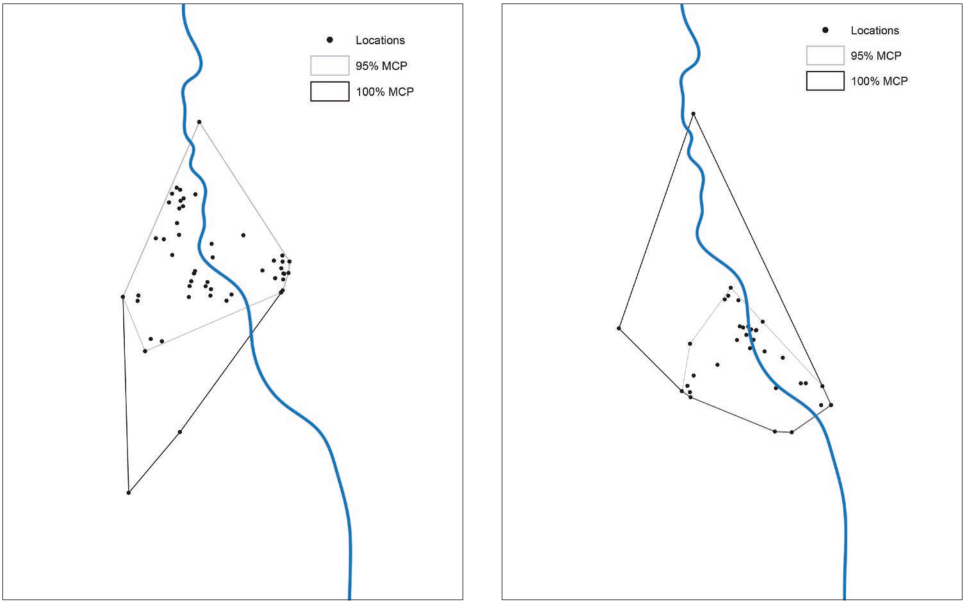
Oophagy

Wood Turtles occasionally eat the eggs of their own species, a phenomenon we refer to here as cannibalistic oophagy, although other terms might be more appropriate. Tamplin (unpubl. data) observed several cases of Wood Turtles in Iowa eating the eggs of other Wood Turtles in captivity (in aquatic and terrestrial contexts). A female Wood Turtle in Massachusetts ate her own egg after depositing it prematurely in a hayfield (Jones and Sievert 2009c) (6.13). Captive Wood Turtles have been observed to eat Box Turtle (*Terrapene carolina*) eggs (Ernst and Lovich 2009).

6.14—Radio-telemetry studies of Wood Turtles' use of space and habitats proliferated in the 1990s. Methods of attaching radios to the carapace have varied, but usually the antenna is left trailing from a posterolateral position on the carapace. Mike Jones

Worm Stomping

Zeiller (1969) first reported "worm-stomping" foraging behavior in captive Wood Turtles, in which adult turtles use their front feet and plastron to drum worms to the surface. This behavior was described in depth in wild Pennsylvania adults by Kaufmann (1986) and Kaufmann et al. (1989). This has since been reported in Maine (Rolih, in Jones et al. 2015), New Hampshire (Wicklow, in Jones et al. 2015; Tuttle 1996); Massachusetts (Jones and Yorks, unpubl. data); New Jersey (S. Angus, unpubl. data, in Jones et al. 2015); Virginia (Akre, unpubl. data); West Virginia (Tamplin, unpubl. data); and in captivity (Kirkpatrick and Kirkpatrick 1996). Tamplin (unpubl. data) has never observed this behavior in Iowa, despite many years of direct observations of hundreds of wild individuals.



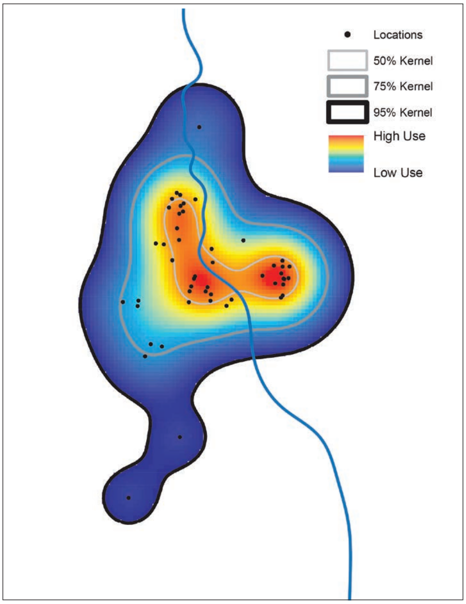
6.15—Space used by Wood Turtles is often estimated using minimum convex polygons (MCP) built from all or a subset of radio-telemetry locations. Two individual Wood Turtle home ranges are depicted here, female #20 (left) and male #103 (right). In both cases, the 95% and 100% MCP home ranges are depicted. Liz Willey

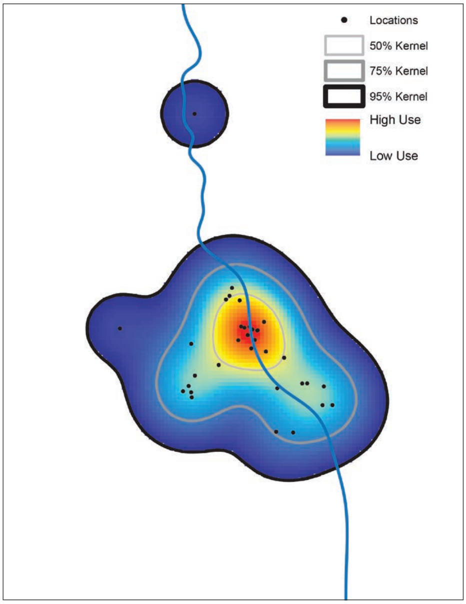
Movement

Home Range

The concept of home range was classically defined by Burt (1943) as: "that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range." Because of the relative ease of measuring space, this concept is often translated to a measure of space use, rather than a focus on the resources Burt defined. Though perhaps less ecologically meaningful to focus on spatial metrics rather than resources, the measure of the amount of space used by an organism, particularly a mobile vertebrate, is certainly useful from both an ecological and conservation standpoint for many reasons.

Animals' use of space and habitats has been measured using radio-telemetry across vertebrate taxonomic groups for decades. In emydid turtles, the radio is usually attached to the posterior margin of the carapace (6.14). Methods used to quantify the space used by emydine turtles range from Euclidean measures of distance (Saumure 2004) to minimum convex polygons (Mohr 1947) (6.15), to kernel density estimators (6.16) popularized by Worton (1989), to more sophisticated movement analyses facilitated by the advent of new technologies such as GPS tags and advanced computing power. While GPS tags capture finer spatial resolution information, allowing less biased (i.e., less researcher interference and less time of day bias) and more precise understanding of resource use (Kie et al. 2010), they are (at present) rarely used due to continued limits on battery life and relatively high costs of GPS equipment. Consequently, very high frequency (VHF) radio-telemetry remains the most often-used technology for studying home ranges in most studies of emydine turtle ecology, though traditional telemetry studies are known to underestimate both cumulative movement and the extent/number of important resources (Harless et al. 2010).





6.16—Space used by Wood Turtles is often estimated using kernel density estimators (KDE) built from all or a subset of radio-telemetry locations. Two individual Wood Turtle home ranges are depicted here, female #20 (left) and male #103 (right). In both cases, thresholds showing 50%, 75%, and 95% density of use are depicted. Here, the h value, or smoothing parameter, is set to the reference bandwidth and is specific to this dataset. Liz Willey

Even when evaluating relatively simple telemetry results, comparing home range values across studies is complicated by the wide variety of home range metrics reported in the literature (including both area and linear measurements, Saumure 2004) and by variable telemetry effort (in frequency and duration, e.g., Harless et al. 2010). Meta-analysis of home range data is further complicated by strong latitudinal, annual, site-specific, and individual effects and the tendency to report mean rather than median values, which are more sensitive to individual effects (Saumure 2004; Jones 2009). Meta-analyses of the influence of landscape on home range size is also now complicated by the ingrained and necessary practice of withholding site location information (Garber and Burger 1995; Litzgus and Brooks 1996) to protect important populations of vulnerable turtles from collection.

Studies spanning multiple years have also observed significant differences in home range size between years (e.g., Remsberg et al. 2006), which have in some cases been attributed to weather patterns. Despite challenges in comparing across studies, patterns in movement emerge over broad spatial scales. Arvisais et al. (2002) and Smith (2002) noted that home range size in northern populations appeared to be larger than in southern populations. Saumure (2004) observed that Wood Turtles at his disturbed, agri-forest site in southern Québec moved less than those observed by Arvisais et al. (2002) in a less fragmented, forested landscape in Québec's Mauricie region. Both observations have been borne out as more telemetry studies have been conducted in the years since (e.g., Compton 1999; Compton et al. 2002; Jones 2009), and both phenomena have conservation implications. Due to the range of variation observed over space, time, and individual, it is ideal to obtain empirical data on the movements of individual turtles at key conservation sites in order to make site-specific conservation recommendations.

Table 6.2—Summarized home range and annual movement statistics reported from Wood Turtle populations throughout the species' range, separated by sex where possible. Integral, Statistical, and Linear range concepts follow Saumure (2004).

State/ Province	Sex	Year	Integral Range (ha)	Statistical Range (ha)	Linear Range (m)	Stream Range (m)	Max Distance (m)	*n*	Source
ON	Both	1990	-	24.3	-	-	-	8	Quinn and Tate (1991)
MI	Both	1998–2000	30.2	-	-	-	-	29	Remsberg et al. (2006)
QC	Female	1998	11.6±16.4	9.6±7.2	741±251	-	-	9	Saumure (2004)
QC	Female	1999	16.4±13.3	13.0±10.0	797±397	-	-	11	Saumure (2004)
QC	Female	1996	-	25.9±32.9	435±74	-	-	14	Arvisais et al. (2002)
QC	Female	1997	-	29.4±37.8	-	-	-	14	Arvisais et al. (2002)
ON	Female	1991	6.4±3.7	-	-	-	-	4	Foscarini (1994)
ON	Female	2012–2015	-	6.4	-	-	-	15	Thompson et al. (2018)
ON	Female	2012–2015	-	21.6	-	-	-	14	Thompson et al. (2018)
WI	Female	ND	-	0.5±0.3	-	-	-	-	Ross et al. (1991)
IA	Female	2014–2015	8.6±7.1	5.3±7.1	750±550	870±700	118±37	9	Otten (2017)
IA	Female	2014–2015	8.7±4.4	6.9±4.4	520±240	590±330	97±17	13	Otten (2017)
IA	Female	2011–2012	-	9.5 ± 11.9	-	-	-		Williams (2013)
VT	Female	ND	-	-	-	-	276±86 m	5	Parren (2013)
NH	Female	2007	-	7.7±9.5	502±323	611±427	163±195	8	Jones (2009)
MA	Female	2004	-	5.8±5.6	565±303	514±430	216±194	23	Jones (2009)
MA	Female	2005	-	14.8±30.9	823±742	895±1165	218±220	29	Jones (2009)
MA	Female	2006	-	13.8±25.0	866±614	1033±902	222±120	26	Jones (2009)
MA	Female	2007	-	3.9±3.7	449±137	546±276	135±105	12	Jones (2009)
PA	Female	1988	3.3±0.5	2.6±0.5	-	-	-	4	Kaufmann (1995)
NJ	Female	ND	-	-	-	-	236	~35	NJDEP (unpublished data)
WV	Female	2009–2011	-	11.03 ± 3.68	-	-	-	10	McCoard et al. (2016)
WV	Female	2010–2011	2.7±1.4	-	-	-	-	5	Curtis and Vila (2015)
VA	Female	2006–2007	7.9±6.5	-	-	-	-	6	Sweeten (2008)
VA	Female	2006–2007	16.8±27.8	-	-	-	-	14	Sweeten (2008)
WV	Juvenile	2009–2011	-	4.04 ± 2.39	-	-	-	6	McCoard et al. (2016)
QC	Male	1998	19.4±13.1	16.7±11.3	1301±564	-	-	5	Saumure (2004)
QC	Male	1999	36.0±51.9	32.2±50.0	1531±1412	-	-	9	Saumure (2004)
QC	Male	1996	-	32.1±38.7	-	-	-	4	Arvisais et al. (2002)
QC	Male	1997	-	29.1±20.0	-	-	-	6	Arvisais et al. (2002)
ON	Male	2012–2015	-	30.96	-	-	-	9	Thompson et al. (2018)
ON	Male	2012–2015	-	35.6	-	-	-	10	Thompson et al. (2018)
ON	Male	1991	5.0±2.9	-	-	-	-	6	Foscarini (1994)
WI	Male	ND	-	0.3±0.2	-	-	-	-	Ross et al. (1991)
IA	Male	2011–2012	-	13.3 ± 9.6	-	-	-	11	Williams (2013)
IA	Male	2014–2015	23.5 ± 26.4	20.0 ± 23.1	1150 ± 570	1420 ± 790	174 ± 42	10	Otten (2017)
IA	Male	2014–2015	26.1 ± 13.1	21.5 ± 11.8	1200 ± 370	1750 ± 590	199 ± 33	8	Otten (2017)
VT	Male	ND	-	-	-	-	108±36 m	6	Parren (2013)
NH	Male	2007	-	6.6±5.5	673±485	921±653	66±59	8	Jones (2009)
MA	Male	2004	-	17.8±25.0	1138±938	1670±1498	114±90	18	Jones (2009)
MA	Male	2005	-	16.0±17.0	1109±778	1478±1100	97±89	22	Jones (2009)
MA	Male	2006	-	20.3±44.8	976±954	1343±1341	97±63	25	Jones (2009)
MA	Male	2007	-	24.3±33.8	1014±594	1436±955	85±59	9	Jones (2009)
PA	Male	1988	5.0±1.5	3.8±1.4	481±75	-	-	6	Kaufmann (1995)
NJ	Male	ND	-	-	-	-	104	~35	NJDEP (unpublished data)
WV	Male	2009–2011	-	4.29 ± 0.78	-	-	-	15	McCoard et al. (2016)
WV	Male	2010–2011	2.6±0.5	-	-	-	-	5	Curtis and Vila (2015)
VA	Male	2006–2007	33.0±34.8	-	-	-	-	8	Sweeten (2008)
VA	Male	2006–2007	19.3±34.9	-	-	-	-	15	Sweeten (2008)

Saumure (2004) proposed standardizing Wood Turtle home range metrics into three categories: integral (100% minimum convex polygon [MCP]); statistical (95% MCP, locations most distant from harmonic mean are removed), and linear ranges (straight-line or Euclidean distance between the two most widely separated capture locations). The distance traveled along stream corridors and the distance traveled from streams have both biological and regulatory significance (Jones 2009). Consequently, we summarize the annual space use of Wood Turtles at representative study sites throughout the range, using "statistical" range as an estimate of the total area required in a given year, and "linear" range to estimate the linear space requirements (Table 6.2). These measures capture the differences between sites and individuals and shed some light on the influence of landscape on movement patterns. Due to the variation noted above, however, they unfortunately do little to provide regulators with distance data necessary for adequate habitat mapping. They also ignore the underling drivers of movements: the resources themselves. Consequently, concurrent analyses of habitat and resource use or finer-scale movement data collected via GPS or thread trailing (e.g., Saumure et al. 2010) or broader scale movement across watersheds measured via genetic information are important complements to this information.

Statistical Range

Statistical ranges (95% MCP) of males are typically larger, although whether or not this difference is significant varies by study. The mean value of 16 averaged statistical ranges for males is 19.2 ha (0.3–35.6 ha); the mean value for females from the same studies is 12.7 ha (0.5–29.4 ha; Table 6.2).

Linear Range

The linear range of males is typically larger than that of females, driven in part by their tendency to use longer lengths of stream. The mean value of averaged linear ranges from seven studies is 1,028 m (481–1,531 m) for males and 647 m (435–866 m) for females (Table 6.2). Although again site specific, this difference is often observed to be significant.

Stream Range

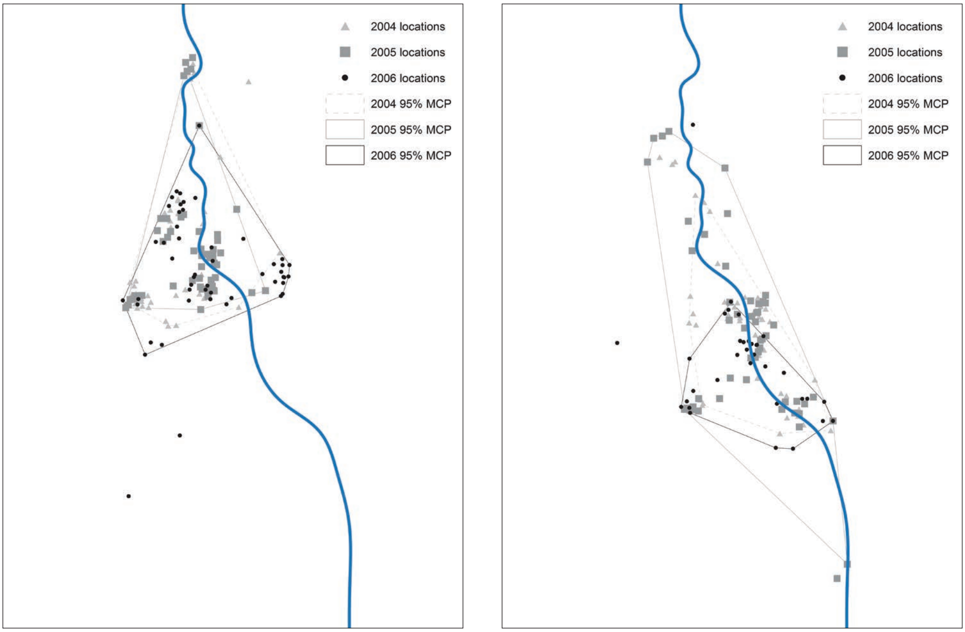
Males spend more time than females in streams during the active season (e.g., Akre 2002; Jones 2009), and correspondingly several authors have reported that male Wood Turtles use greater stream range lengths than females (e.g., McCoard et al. 2016). Parren (2013) reported that females have a stream range of 659±563 m (range=130–1,602 m; n=5), slightly less than males (760±445 m; range=287–1,521 m; n=6), but the difference was not significant. From a sample of 123 adult turtles in Massachusetts and New Hampshire, Jones and Willey (2020) reported that males have a stream range of 1,422±1,295 m (range=221–6,304 m; n=56) and females exhibited stream ranges of 757±814 m (range=62–5,537 m; n=67). Otten (2017) determined that mean stream range of adult male wood turtles in Iowa (1,570±710 m; range=590–3,250 m; n=18) was significantly larger than mean stream ranges of adult females (710 ± 520 m; range=190–2,280 m; n=22) and juveniles (560±180 m; range=350–790 m; n=5).

Distance from River

Allard (1909) noted that Wood Turtles "may frequently be found wandering through dry woods and fields far from any water." Generally, females move greater distances away from their overwintering streams (Akre and Ernst 2006; Jones 2009; McCoard et al. 2016; Thompson et al. 2018; Table 6.2). In Massachusetts and New Hampshire, Jones (2009) reported the mean value of maximum distances traveled by male Wood Turtles away from the river to be 117±146 m (range=4–1,000+ m; *n*=56), and females 209±175 m (range=29–933 m; *n*=67). Average distances from the stream in West Virginia were found to be 85.67 m±19.67 for males and 139.8 m±25.79 for females (McCoard et al. 2016).

Arvisais et al. (2002) reported that all of their observed locations were within 300 m of the stream in the Mauricie Region of Québec. Similarly, Compton et al. (2002) found that 95% of activity areas were within 304 m of the stream in Maine. In addition, McCoard et al. (2016) found that all but two of their 1,443 locations of 31 radio-tracked turtles from 2009–2011 in West Virginia were within 300 m of the stream. In Michigan, 92.5% of 955 locations were within 200 m of the stream (Remsberg et al. 2006). Conversely, maximum distances from streams have been reported that about double the aforementioned distances, with Kauffman (1992) reporting a maximum distance of 600 m and Compton (1999) reporting 500 m. Parren (2013) noted that most radiolocations were within 90 m of the overwintering stream, but forays beyond this distance ranged up to 54 days and extended 425 m from the river.

Based upon a dataset of 3,223 terrestrial locations of 138 Wood Turtles recorded by Tamplin (unpubl. data) in Iowa from 2003–2019, maximum distance from water was 350 m, but only four turtle locations exceeded 300 m. Of these four (331, 340, 350, 350 m), three were associated with one adult female turtle who spent two weeks in the same area in 2014. Mean distance from water of all turtles in this Iowa population was 37.12±47.82 m (range=0.1–350 m; *n*=138); mean distance to water of 71 females at 2,307 terrestrial locations was 46.26±54.54 m (range=0.1–350 m). Mean distance to water of 10 juveniles at 135 locations (26.86±29.86 m; range=0.10–148 m) and of 57 males at 1,051 locations (mean distance=20.71±26.28 m; range=0.1–232 m) were each less than half of the mean value for adult females. Few additional data exist for the movements of



6.17—Wood Turtles often exhibit clear fidelity to home range, nest site, terrestrial habitats, and overwintering sites, although extreme inter-annual variation and even dispersal from sites has been reported. Multi-year home ranges for two turtles are depicted here, female #20 (left) and male #103 (right), showing a high degree of overall inter-annual home range fidelity. Liz Willey juvenile Wood Turtles. Tuttle and Carroll (2005) noted that one eight-year-old juvenile moved 865 m from a stream, whereas another 11-year-old only moved only 60 m from the stream.

Some female Wood Turtles may move greater distance from the water in search of nest locations (see below). Given the seasonal timing of observed movements, this does not entirely explain the difference, and females have been observed foraging and basking at distant terrestrial locations over periods ranging from weeks to months. Males may remain closer to the water, and move farther along the river, in search of mates throughout the year. Regardless of the mechanisms behind the difference, this behavioral difference between the sexes has conservation and management implications, especially related to differential survivorship due to roads along streams (e.g., Desroches and Picard 2005) and land-use and habitat management both within and beyond riparian corridors.

Home Range Fidelity

Wood Turtles exhibit fidelity to home range (Kaufmann 1995; Arvisais et al. 2002; Jones 2009), nest site (see below), terrestrial habitat (Kaufmann 1995; Arvisais et al. 2002; Walde et al. 2003; Remsberg et al. 2006; Parren 2013; Thompson et al. 2018), and overwintering site (Sweeten 2008); although, annual variation has also been reported (Remsberg et al. 2006) (6.17).[8] Few studies have evaluated home range fidelity, or multi-year space-use, in a quantitative way. Arvisais et al. (2002) observed an average overlap between consecutive year MCPs of 60.7±27.8% (range 4.5–98.8%). Analyses suggested that only two of the turtles had significantly different home range centroids in subsequent years, whereas 88.8% of turtles tracked exhibited no significant difference in centroids over the two years. In addition, Thompson et al. (2018) in Ontario found that core areas (70% utilization distribution) used over multiple years (23.92±12.01 ha) were consistent, and not significantly different from the size of a single year's 95% MCP (32.18±14.71 ha).

Nesting Movements

Though females appear to nest in riparian corridors when suitable nesting habitat is available,[9] nests can also be placed in distant locations. It is unclear whether the choice of nest location relates to lack of suitable habitat or is a dispersal mechanism. In Massachusetts and New Hampshire, the median distance of confirmed nests (n=60) from the nearest river was 25.6 m (range=0.2–600.0 m; Jones, unpubl. data; Steen et al. 2012). Although 35% of females in Massachusetts and New Hampshire nested within the stream channel on beaches and instream bars, one moved 600 m from the stream to nest in a residential area (Jones 2009). In northwestern Virginia, Dragon and Akre (unpubl. data) reported that nests in 2012 and 2013 were an average of 159.2 m (range=54.3–264.2 m) from the stream. Long-distance movements by females to access nesting locations have also been observed across studies. Quinn and Tate (1991) and Walde et al. (2007) reported 3.6 km and 3.7 km movements associated with nesting, respectively, in Ontario and Québec.

Nest Site Fidelity

Under certain circumstances, Wood Turtles can exhibit high site fidelity to nesting locations. Walde (1998) reported that 64% of females nested in the same gravel pit in 1996 and 1997, and in some cases females nested in the same $1 m^2$ area in both years. In New Hampshire, B. Wicklow

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8 For more detailed discussions of habitat use, see Chapter 5.

9 A more detailed description of nesting habitat is provided in Chapter 5.

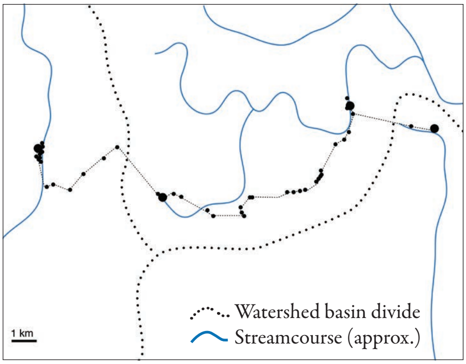
(in Jones et al. 2015) observed 15 to 20 females returning to the same nesting area each spring for a period of 10 years. At a nesting site purposefully created for Wood Turtles in Morris County, New Jersey, Buhlmann and Osborn (2011) reported that one female turtle (of nine) returned to the nesting mound in three subsequent years.

Hatchling Movements and Orientation

The movement, behavior, ecology, and survivorship of hatchling Wood Turtles was studied by: Tuttle and Carroll (2005); Castellano et al. (2008); Paterson et al. (2012); Dragon et al. (2013); Wicklow (in Jones et al. 2015); and Otten et al. (Otten and Tamplin, unpubl. data). As noted earlier in this chapter, hatchling Wood Turtles usually emerge in late summer, regardless of latitude. Recently, researchers have used radiotelemetry to document fine-scale movements (e.g., Castellano et al. 2008; Paterson et al. 2012; Dragon et al. 2013). In Algonquin Park, Ontario, Paterson et al. (2008) observed that hatchling Wood Turtles moved toward brooks, selecting cooler sites with less leaf litter than generally available, and apparently overwintered near the shore. In central New Hampshire, Tuttle and Carroll (2005) reported total nest-to-river movements of 131.7±119.7 m (27–445 m) over 6.2±6.3 days (range=1–24 days) and suggested that hatchlings navigate to streams using "olfaction, vision, positive geotaxis, and auditory cues." One hatchling (of twelve to arrive at a stream) moved overland to arrive in a different brook than the one used by the parent female. The authors reported that hatchlings left the nest site in a multidirectional dispersal pattern and headed for the nearest cover. Compton (1999) also reported that hatchlings appeared to use geotaxis (downslope movements) to navigate, and suggested that deep gravel pits with no low-elevation exit may function as traps. Subsequent studies seem to indicate that hatchlings are, in fact, willing to move over large obstacles. In New Hampshire, Wicklow (in Jones et al. 2015) reported (through field and lab experiments) that hatchlings exhibit phototaxis (navigating toward light). In the field, hatchlings appeared to navigate toward lighter (more open) areas. In the lab, hatchlings navigated toward full-spectrum light sources regardless of compass direction.

In an agricultural landscape in Warren County, New Jersey, Castellano et al. (2008) reported that radioequipped hatchlings remained in upland agricultural fields for several days or weeks following emergence, foraging and growing. While in upland habitats, hatchlings moved less often and occupied sites with lower air and substrate temperatures than adult turtles. The authors noted that agricultural harvest could be detrimental to hatchlings that are still in the fields. In northwestern Virginia, Dragon et al. (2012) reported that hatchling Wood Turtles emerged from their nests and followed the topography of the landscape by moving down in elevation while taking the shortest route from the nest to the stream. Hatchlings from the same nest "patch" displayed similar patterns in direction and movements. Hatchlings took an average of 9.0 days (range=1–28) to reach the stream. Hatchlings that emerged from nest patches with a nearby seep complex (characterized by mucky soils and herbaceous growth) took longer (10.6–11.9 days) to reach the stream than those that emerged in nest patches without a nearby seep (4.6–8.8 days). The presence of a seep was more closely associated with the number of days taken to reach the stream than the distance of the nest from the stream, suggesting certain habitat features may act as a "nursery" and provide shelter for the journey from nest to stream. Hatchlings in Dragon's study moved an average of 253.8 m from emergence to hibernation, with a maximum movement of 1,112 m.

In Iowa, Otten et al. (Otten and Tamplin, unpubl. data) monitored nine hatchlings from a single clutch via radio telemetry from early September through late October 2015 (152 total locations). Hatchlings were outfitted with radio transmitters and released at the nest site, approximately 8 m from water. Upon release, only a single hatchling entered the stream, while eight hatchlings remained on land and either sought cover on the nesting beach or moved into vegetation farther inland. During the two-month monitoring period, the hatchling that initially entered the stream remained in aquatic locations and spent the first several weeks wedged into a large logjam before eventually moving ~200 m downstream to hibernate. The other eight hatchlings remained on land, often buried under sticks, leaves, and dried grass within 150 m of the nest site. One hatchling was depredated approximately one week after release; seven of the eight surviving hatchlings remained along the same stream bank as the nest site. Ultimately, the hatchlings hibernated within 100 m of the nest site, and only 5 of the 152 radio-locations occurred on the opposite bank.



6.18—Wood Turtles are capable of long distance overland or cross-watershed movements exceeding 10 km, although this appears to be a rare phenomenon exhibited by less than 1% of adult turtles annually. Limited evidence suggests males may be more prone to inter-basin dispersal as adults. The multi-year, cross-watershed movement of Massachusetts male #268 is pictured here.

Dispersal

Dispersal in Wood Turtles is poorly understood and poorly documented. It is clear that individual Wood Turtles are capable of long distance, overland movements (6.18), which have been observed via radiotelemetry (to 17 km straight-line, Jones and Willey 2020; to 19.8 km total movement, Sweeten 2008) and GPS technology from studies in Ontario (Thompson et al. 2018), Virginia, and Minnesota (VanDoren and Akre, unpubl. data). It is also clear Wood Turtles are capable of short-range homing movements. When exposed to anthropogenic or natural tests of learning (Tinklepaugh 1932) or displacement and spatial orientation (Harding and Bloomer 1979; Carroll and Ehrenfield 1978; Barzilay 1980), Wood Turtles perform well, with individuals often returning to their source location. Wood Turtles displaced downstream by floods can survive the initial displacement (Sweeten 2008; Jones and Sievert 2009), and in some cases may subsequently either contribute to the genetic pool at the downstream location or at sites encountered while seeking suitable habitat in the years following the flood (Jones and Sievert 2009a) (6.19).

Tuttle and Carroll (2005) reported an instance of a New Hampshire hatchling moving to a neighboring stream system upon emergence from the nest, and Jones (2009) observed female Wood Turtles in Massachusetts and New Hampshire, respectively, nesting near a watershed divide more than 600 m from her overwintering stream, suggesting that some small-scale dispersal may occur at very early life stages.

Recent genetic work suggests populations are, in fact, connected at fairly broad-scales,[10] providing another line of evidence that Wood Turtles regularly make long-distance or between-

10 See Chapter 2.

6.19—Wood Turtles displaced by floods will sometimes survive the initial displacement and may be temporarily integrated into the downstream population. Alternatively, flood-displaced Wood Turtles may temporarily interact with unrelated Wood Turtle populations as they seek appropriate habitat. The adult male pictured here was displaced more than 17 km into a novel habitat, coming to rest within a subpopulation of Wood Turtles it probably had not interacted with previously. It spent the subsequent two years exploring new habitats. Mike Jones

watershed movements. Indeed, such movements may be more common than reported from telemetry or GPS studies. Large movements and connectivity between populations has important conservation implications for Wood Turtles, including the need for broad-scale conservation of habitats (which has been suggested for this species since the 1990s; Quinn and Tate 1991), as well as connectivity between occupied riparian areas in order to maintain historical metapopulation dynamics.

Summary

Because Wood Turtles rely on both instream and terrestrial habitats, and are dormant for nearly half the year along the northern range limit, they exhibit a particularly complex seasonal and spatial ecology. In most areas, Wood Turtles are dormant in streams during the winter, progressing through a highly predictable sequence of biological periods during their constrained active season. During mild winters at low elevation or near the southern range limit, Wood Turtles may be active during the winter months. Wood Turtles are one of most amphibious emydid turtle species, and perhaps among the most amphibious of the living turtles; equally at home in water or upland/terrestrial habitats. They are able to easily navigate deep, cold, flowing water and also spend months on land. They are capable of navigating several kilometers along streams, or moving overland between watersheds. Accordingly, they are extremely flexible omnivores that take a range of terrestrial and aquatic food items. Because of their seasonal habitat needs, which may be widely dispersed, as well as their reliance on disturbed upland habitats and vulnerability to machinery and heavy equipment, Wood Turtle populations are most secure along moderately dynamic streams, within large and unfragmented landscapes, with minimal human influence.

7. Demography and Reproduction

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Courting Wood Turtles in a Maine stream. Derek Yorks

7.1— Like other emydine turtles, Wood Turtles generally exhibit late maturity and a long, iteroparous lifespan without reproductive senescence. Here, an old female Wood Turtle covers her nest in northern New England. Mike Jones

Introduction

The Wood Turtle's decline across a majority of its range in the United States and Canada has primarily been caused by human encroachment on its habitat, including the direct and indirect effects of habitat loss, fragmentation, and degradation. As noted in Chapter 8, threats include direct mortality from flooding, agricultural machinery, and motor vehicles, as well as illegal collection for pet markets and subsidized predation by mesocarnivores. Wood Turtles are unable to effectively respond—behaviorally or numerically—to these synergistic threats because they have evolved as extreme bet-hedgers: they are adapted to low (and variable) rates of juvenile survival and very high (and stable) adult survival. This is true of most of the turtles within the subfamily Emydinae,[1] which generally exhibit late maturity and a long, iteroparous[2] lifespan (7.1). Survival is low for eggs and hatchlings, but apparently increases throughout the juvenile life-stages until the turtle reaches adulthood. At this point, individuals generally experience high annual survival rates, and they often reproduce in most years for many sequential decades, replacing at least themselves and a mate in a stable population. In this chapter, we summarize key aspects of Wood Turtle biology, including lifespan, age of maturity, reproductive output, demography, and population dynamics. We also summarize fundamental demographic parameters including recruitment, survivorship, stage and sex structure, generation time, and population viability, and present published and unpublished information on population size, density, and trends.

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1 See Chapter 2 for a treatment of the subfamily Emydinae.

2 Iteroparity is the ability or tendency of an animal to reproduce throughout its life.

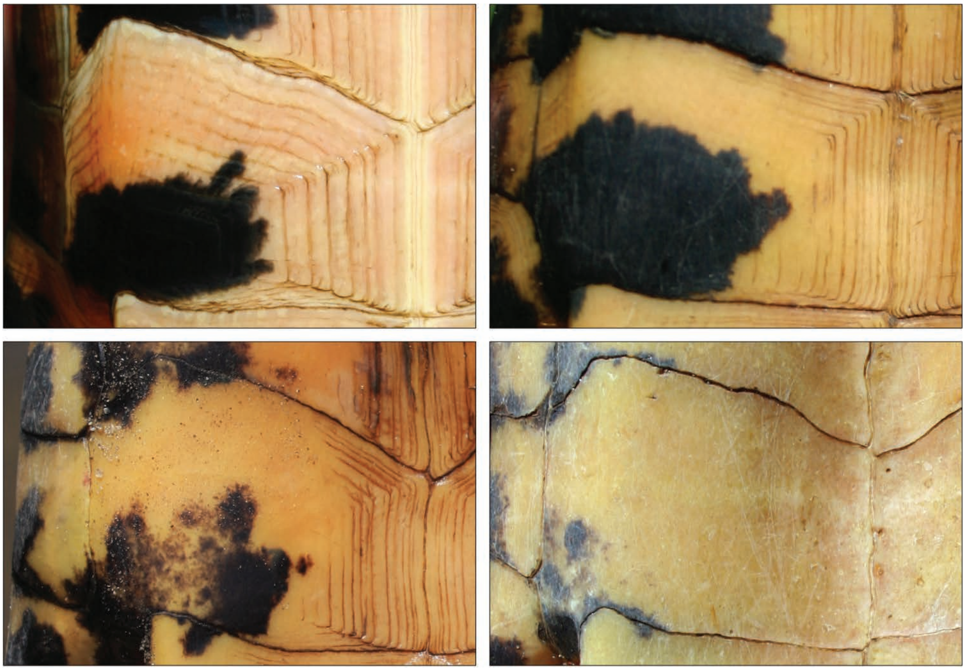
Where feasible, we also compare and contrast historical data with contemporary assessments of the same populations.

Lifespan

Determining the exact age of mature Wood Turtles is not possible because individuals effectively stop growing (and stop accumulating clear growth annuli) in the years around the onset of maturity. Obtaining a relative age estimate for a mature Wood Turtle is also difficult, and counting annular growth rings on the plastron or carapace is somewhat reliable only for immature or recently mature turtles (younger than ~15–20 years; Harding and Bloomer 1979; Kaufmann 1992a; Parren 2013) (7.2). After the turtle is mature, annual growth rings generally become too small and tightly packed to be counted, if visible at all. In addition, both the plastron and carapace become progressively worn as turtles age, making it even more difficult to see or count annual growth rings. However, there is now abundant evidence that wild Wood Turtles often survive into their fifties (COSEWIC 2007): in Minnesota, recaptures in 2013–2014 of Wood Turtles originally marked as adults in 1990 indicated that at least 11 turtles exceeded 50 years of age (Brown et al. 2015). In Pennsylvania, Ernst (2001a) reported wild Wood Turtles over 40 years old, and recaptures of Kaufmann's (1992a) study animals by Kathy Gipe (unpublished data) in 2012–2013 provided evidence of ages exceeding 50 years. In New Jersey, recaptures by Ray Farrell (unpubl. data in Jones et al. 2015) of Wood Turtles marked in the 1970s by Farrell and Graham (1991) indicated ages in excess of 55 years. In Virginia, Akre and Ruther (2015) recaptured two Wood Turtles marked by Kurt Buhlmann in 1988 as mature adults, indicating minimum ages of at least 47 years. In captivity, Oliver (1955) reported a maximum confirmed age of 58 years, and Barker (1964) indicated that a Wood Turtle was in residence at the London Zoological Gardens for 100 years from 1839 to 1939. In New England, Jones (2009) estimated that carapace scutes may require approximately 80 years to become completely worn, based on time-lapse (interval) photographs of the carapace of 75 individual Wood Turtles (7.3), and reported turtles in this category of shell wear. A related analysis of the depigmentation of the characteristic black blotches of the plastron predicted that they would be reduced by >50% after approximately 70 years (Jones 2009) (7.4). Depigmentation of the plastral scutes may also be influenced by injuries that penetrate the keratin layer, or accelerated by limb loss that results in localized wear (Jones, unpubl. data) (7.5). Because turtles in these wear-class categories (with corresponding rates of plastral depigmentation) are frequently found in New England,

7.2—Age estimates produced by counting annular growth rings on the plastron is somewhat reliable only for immature or recently mature turtles, such as this (roughly) 9-year old female from Massachusetts. As a general rule, the count is more reflective of the animal's true age when there is clear evidence of new, medial growth, pictured here as a pale line down the plastral midline. Also, we assume a couple of years of error—even in age estimates for young turtles. Mike Jones

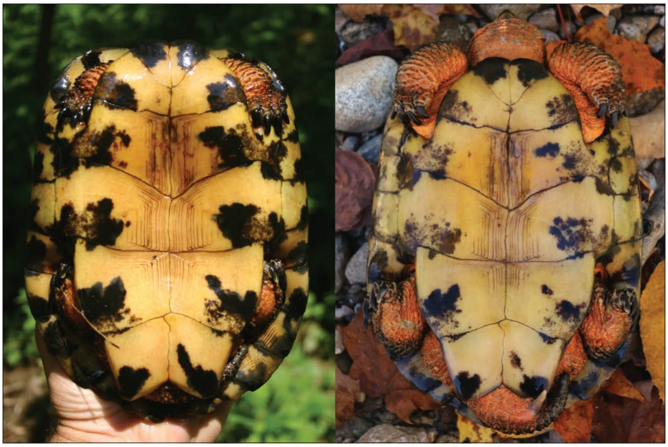
7.3—A study in New England estimated the Wood Turtles' carapace scutes may require approximately 80 years to become completely worn, based on time-lapse (interval) photographs of 75 individuals. Here, four wear classes are shown from left to right, top to bottom, with the least-worn at top left. These figures correspond to the four wear classes utilized in the analysis by Jones (2009). Mike Jones



7.4—A study in New England predicted that Wood Turtles' characteristic black plastral blotches would be reduced by >50% after approximately 70 years. Shown here from left to right, top to bottom, are four classes of depigmentation, corresponding to the depigmentation classes utilized in the analysis by Jones (2009). Mike Jones

7.5—Depigmentation of the plastral scutes may also be influenced and accelerated by injuries that either penetrate the keratin layer (*left*) or limb loss that results in localized wear on the affected side (*right*). In the righthand image, note the turtle's missing hind right foot and the corresponding reduction in pigment on the proximal scutes. Two different males are pictured. Mike Jones

7.6—Pictured here are time-lapsed photos of six New England Wood Turtles taken more than a decade apart, with the original photograph on the left and the most recent photograph at right. Six pairs of images are shown of six different turtles; each pair of images show the same turtle. Three female Wood Turtles pictured at left (from top to bottom) were photographed in 2005 and 2018, 2006 and 2019, and 2006 and 2018, respectively. Three male Wood Turtles pictured at right (from top to bottom) were photographed in 2006 and 2016, 2004 and 2019, and 2005 and 2015, respectively. Mike Jones



Jones' results indicate natural lifespans exceeding 70 years (7.6).[3] It is very likely that continued long-term monitoring will document even greater lifespans. With so many individually marked Wood Turtles on the landscape, long term monitoring represents a feasible and important area of research. It can be aided by applying new technologies to estimate minimum ages in living turtles and evaluating landscape associations and demographic implications of extreme longevity.

7.7— Like all turtle species, Wood Turtle eggs are fertilized internally by at least one male; the female deposits the eggs in the ground, and there is no known parental care after nest deposition. Tracks of a nest-searching female are shown in New England. Mike Jones

Sexual Maturity

Onset of reproductive maturity has been reported to vary from about 11–20 years depending on sex and geographic area, with more southern populations generally maturing sooner. In Ontario, Brooks et al. (1992) estimated the youngest mature female was 18 years old. Walde et al. (2003) found that the smallest reproductive male (as evidenced by secondary sexual characteristics) had an SCL of 170 mm. In Wisconsin, the youngest gravid female observed was estimated to be 14 years old, and the youngest male observed mating was 20 years old (Ross et al. 1991). In the Upper Peninsula of Michigan, the youngest female observed mating was 12 years old, while the youngest female observed laying eggs was 19 years old (Harding and Bloomer 1979). The youngest male observed mating in Vermont was 15 years old (Parren 2013). Garber and Burger (1995), without separating the sexes, stated the average age of maturity was 12 in Connecticut. Farrell and Graham (1991), reporting on conditions in the 1970s, documented mating males and nesting females as young as 14 years old in New Jersey, and speculated that both sexes reached maturity at this age. In Virginia, Akre and Ernst (2006) estimated that maturity was generally reached beginning at 12 years of age, and Akre (2002) reported that the youngest, apparently primiparous, female was 11 years old. Akre (2002) also reported that the youngest male with conspicuous secondary sex characteristics was only seven years old, with a straight-line carapace length (SCL) of 160 mm; the smallest male with secondary sex characteristics was nine years old with a SCL of 156 mm. Both of these individuals were substantially smaller than the average sized adult male (195±12.5 mm SCL), suggesting that secondary sex characteristics begin to develop long before individuals are large enough to be active in the reproductive population.

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3 However, one limitation to Jones' (2009) shell-wear analysis is the possibility that wear-rates are influenced by rare stochastic events, such as flooding (Jones and Sievert 2009), which could theoretically result in accelerated rates of shell wear.

Reproduction

7.8—Generally, more than half of the mature female Wood Turtles in a given population will nest in any given year, but the proportion is spatiotemporally variable. Here, a Wood Turtle deposits an egg along a river in Massachusetts. MIKE JONES

The reproductive biology of *Glyptemys insculpta* is similar in many respects to other freshwater turtle species. Like all turtle species, Wood Turtle eggs are internally fertilized by at least one male; the female deposits the eggs in the ground in terrestrial habitats, and there is no known parental care after nest deposition (7.7). Female Wood Turtles are known to store sperm (Galbraith 1993; Figueras and Burke 2017). Microsatellite analysis of 38 clutches in a Québec population over two years revealed multiple paternity (i.e., the clutch was fertilized by multiple different males) in 37% of clutches and repeat paternity (i.e., a female is fertilized by the same male two years in a row) in 88% of clutches (Bouchard et al. 2018). One prominent way that turtles in the genus *Glyptemys* (including both *G. insculpta* and *G. muhlenbergii*) differ from other emydid genera is that they exhibit chromosomally-dependent sex-determination (also called genetic sex determination or GSD), rather than temperature-dependent sex determination (TSD) as exhibited by related genera such as *Terrapene*, *Emys*, and *Clemmys* (Bull et al. 1985; Ewert and Nelson 1991; Burke 1993; Literman et al. 2017).

Nest Site Fidelity

Wood Turtles in some populations and habitat contexts exhibit pronounced nest-site fidelity. Walde et al. (2007) found that 95% of females nested in the same site in Québec in two consecutive years. Buhlmann and Osborn (2011) provided evidence that fidelity to nesting areas—in this case, a nesting mound described further in Chapter 5—varied among females.

Nesting Frequency

Generally, more than half of the mature female Wood Turtles in a given population will nest in any given year, but the proportion is spatiotemporally variable (7.8). Walde et al. (2007) reported that for 62 females monitored at a nesting site in Québec for two years, a minimum of 64% laid clutches in both years. By contrast, Foscarini (1994) estimated that only 33% of females nested annually in a population in Ontario, Canada, while Mullin et al. (2020) reported 47% and 64% of females reproduced annually in the same region of Ontario from 1993–2017. Jones (2009) found the proportion of monitored adult females (n=76) nesting in a given year between 2004 and 2007 ranged from 0.54–0.88 (mean = 0.74) in Massachusetts and New Hampshire. In addition, of the 25 females tracked for multiple years, the mean proportion of years in which turtles became gravid was 0.71. Akre and Ruther (2015) estimated that the average proportion of females nesting annually in a sample from 2010–2014 was 0.918 (range = 0.86–0.97), though they later found evidence that annual nesting rates may be even higher.

Wood Turtles rarely lay multiple, independent clutches within a year (Harding and Bloomer 1979; Farrell and Graham 1991). Akre (2002) and Akre and Ruther (2015) found no direct evidence of multiple independent clutches produced by a single female within a year despite repeated observations of 117 individuals during the nesting season over nine years. However, Akre

(2002) did observe four instances, confirmed by radiography, where a female appeared to split a clutch into two nests at different sites. Similarly, Jones (2009) observed a single instance in which a female (of 76 monitored females) deposited one clutch in two groups of eggs five days apart.

7.9—Depredation rates of Wood Turtle nests are spatially and temporally variable, but can result in very low egg survival rates. A New England Wood Turtle nest depredated in September—upon emergence—is pictured. Mike Jones

Clutch Size

Individual clutch size is positively correlated with carapace length (Brooks et al. 1992; Walde et al. 2007; Jones 2009). Average clutch size varies geographically, potentially in relation to geographic differences in average female size (Marchand et al. 2018). Distribution-wide, average clutch size ranges from 7–11 eggs (Table 7-1). In general, like adult body size, reported average clutch sizes are largest in northern populations and decrease in size to the south. The largest reported clutch size of 20 was reported from one of the northernmost populations in Québec by Walde (1998) and Walde and Saumure (2008).

Survivorship

Egg Survivorship.—The proportion of eggs laid per female that survive to hatching is dependent on fertility and mortality rates. The viability of each egg is influenced or determined by a number

Table 7.1—Summarized clutch information from Wood Turtle nests range-wide.

		Clutch Metrics				
State / Province	**Site**	**Mean Clutch Size**	**Range**	**Year**	***n***	**Source**
QC	Mauricie	10.1	5–20	-	58	Walde (1998)
ON	Sudbury District	8.8±2.2	-	2005	5	Greaves & Litzgus (2009)
ON	Sudbury District	9.4±2.3	-	2006	11	Greaves & Litzgus (2009)
NS	-	8.2	4–11	-	20	Powell (1967)
WI	-	12	3–17	2012–2013	154	Kapfer and Brown (in press)
MI	-	10.5	5–18	-	-	Harding (1991)
IA	-	10.33	6–13	2003–2019	15	Tamplin (unpublished data)
NH	Merrimack Co.	7.8±1.0	6–9	-	9	Tuttle & Carroll (1997)
MA	Western MA	7.3	1–14		76	Jones (2009)
PA	Centre Co.	8.9	5–12	-	-	Kaufmann (1992)
NJ	Sussex Co.	8.5±1.7	5–11		21	Farrell & Graham (1991)
NJ	Morris Co.	-	7–16	2007–2010	23	Buhlmann & Osborn (2011)

of both internal (lack of fertilization, genetic mutation) and external (climate, ant predation, mold growth, etc.) factors that may influence its survival. As is the case with most biological parameters, these rates are highly variable. Bob Hay (in Kapfer and Brown, in press) artificially incubated 1,792 eggs from 154 naturally laid clutches in Wisconsin and found that 369 (20.6%) of the eggs were infertile. In contrast, Walde et al. (2017) documented infertility for only 12 of 572 eggs (2.1%) in Québec. Tuttle and Carroll (1997) reported a hatching success of 77% for 70 eggs in New Hampshire, but did not determine if the unhatched eggs were fertile. Jones (2009) reported that the emergence rate of live hatchlings from the first observed and protected nest of 39 female Wood Turtles in Massachusetts and New Hampshire ranged from 0–1, with a mean of 0.41. In Virginia from 2010–2014, 75% of nests had some emergence of hatchlings, and like Massachusetts and New Hampshire, the proportion of hatchlings that emerged from non-depredated nests (i.e., protected) ranged from 0–1, with an average of 0.56±0.04.

7.10—Wood Turtle survival probability follows a sigmoid function (i.e., S-curve), or a form of Type III survivorship, with survival probability increasing with body size as turtles grow and then reaching a plateau associated with size at maturity. Juvenile Wood Turtles are expected to exhibit survival rates lower than adults, but key size thresholds are not well established. A juvenile Wood Turtle is pictured in Massachusetts. MIKE JONES

Nest depredation rates are spatially and temporally variable, but can result in very low egg survival rates because entire clutches are lost (7.9). Brooks et al. (1992) reported 15 of 17 monitored nests were depredated in Ontario. In Minnesota, 94% of 105 monitored nests were depredated (Cochrane et al. 2017). In New Hampshire, four of 13 (30.7%) monitored nests were depredated (Tuttle and Carroll 1997). In Virginia, Akre and Ruther (2015) report that only six of 53 (11%) nests monitored in 2013–2014 were depredated and speculated that continuous human presence suppressed predation activity. Therefore, in 2015, they monitored all nest banks by camera without physically searching for nesting activity or protecting any nests. During that year they recorded 20 depredated nests and calculated predation rate as 37% based upon an estimate of 53±2 nests per year from data from the prior five years.

Additional environmental factors, such as nest flooding or inundation and suboptimal temperature, can also result in egg mortality or nest failure. Walde et al. (2007) found that 30% of 57 nests in Québec failed to hatch, and hypothesized that unsuitable nest temperatures may have caused the mortality. In Iowa, 9 of 14 (64.3%) monitored nests were flooded, with the remaining five depredated (Spradling et al. 2010). Very low, sustained incubation temperatures can also result in nest failure by delaying emergence beyond the activity season. Compton (1999) fit a degree-day model from seven lab-incubated Wood Turtle nests that predicted a Wood Turtle egg will hatch after it receives 788 (se = 10.1) degree-days above a 12.5°C threshold, and also reported that the mean incubation temperature was the best explanatory variable to predict incubation duration. Compton further provided evidence that the northern range extent for the Wood Turtle is influenced by the availability of nesting areas that are sufficiently warm to successfully hatch a Wood Turtle egg, indicating that nest success may be dependent on summer temperatures in some parts of the species range, and very cool summers along the northern range-margin will result in nest failure.

Hatchling Survivorship.—Most studies of hatchling survival are based upon the period of time from nest emergence until individuals enter their overwintering stream, and not over the first winter. Paterson et al. (2012) monitored survival of 45 hatchlings in Ontario, and confirmed that at least 11% survived to overwinter (56% were predated, 9% drowned, and 24% were lost). Tamplin (unpubl. data) documented high hatchling survival at a suburban location in Iowa, with 8 of 9 (88.8%) monitored hatchlings surviving to overwinter. Wicklow and Clark (unpubl. data) used radiotelemetry to monitor survival of 20 hatchlings in New Hampshire, and found that at least one survived to overwinter. Ten were predated, with known predators including short-tailed shrews, chipmunks, and skunks, one was crushed by a four-wheeled vehicle, and eight were unaccounted for, disappearing suddenly from last known locations. Dragon (2014) and Akre and Ruther (2015) monitored the survival of 88 hatchlings by radio-telemetry from 2012–2014 in Virginia, with at least 23 individuals (26%) surviving to the onset of winter.

Juvenile Survivorship.—We do not have a strong empirical understanding of how survival probability changes as Wood Turtles grow from hatchlings to adults. We expect that survival probability follows a sigmoid function (i.e., S-curve), with survival probability increasing with body size as turtles grow and then reaching a plateau associated with size at maturity (7.10). Based on a 13-year capture-recapture study in Connecticut, Garber (1989b) concluded juveniles reach adult-level survival rates at a carapace length of approximately 10.5 cm, corresponding to 6 years of age in their population.

Headstart Survivorship.— Michell and Michell (2015) monitored survival of 10 head-started Wood Turtles for two years post-release in the wild, with six and four turtles released in their first and second year, respectively. All 10 turtles survived through the two-year monitoring period. Mullin et al. (2020) introduced 490 head-started Wood Turtles to two populations during the last 15 years of a 30-year capture-recapture study in Ontario, Canada. The survivorship of post-release turtles in the first year was 36% in population A and 52% in population B. Six of the head-started turtles eventually reproduced. The introduction of head-started turtles was intended to augment the populations after a dramatic population size reduction attributed to poaching. The recovery was hampered by predation (58% of 105 confirmed mortalities were due to predation, 40% of mortalities were unknown) and possibly by diseases introduced with the head-started turtles (mycotic shell disease, ranavirus, and the herpesvirus GlyHV-2). The authors concluded that headstarting without predator management would not be enough to rescue either population from extinction.

Adult Survival

As noted above, the Wood Turtle exhibits a Type III survivorship curve, with low survival in early life stages and high survival of adults (reviewed by Akre 2002), though survival varies across populations. Mullin et al. (2020) reported adult survivorship of 0.89 and 0.93 at two sites in Ontario, Canada from 1993–2017. Lapin et al. (2019) estimated adult annual survival rates using monitored turtles in Iowa ($n = 52$), Minnesota ($n = 29$), and Wisconsin ($n = 32$). Annual survival ranged from 0.874–0.946, 0.775–1.0, and 0.61–1.0 at the three sites, and probably represents the relative proportion of juveniles in the sample: 12.7%, 14%, and 29% respectively. Mean annual survival rate in Iowa was 0.86, and ranged from 0.72–0.94 among four monitoring years. Annual survival for two monitoring years in Minnesota was 0.87 and 0.94, respectively, while annual survival rate for two monitoring years in Wisconsin was 0.63 and 0.95, respectively. Compton (1999) reported adult annual survival rates of 0.96–1.0 in Maine, but noted survival rates may have been as low as 0.92–0.96 if monitored turtles of unknown fate had actually died. In New

Table 7.2—Raw demographic information reported from Wood Turtle populations range-wide, with the ratio of males to females and the proportion of juveniles confirmed in the population.

State/ Province	Site	Males	Females	Juveniles	Ratio (males per femle)	% Juvenile	Source
QC	Mauricie	55	83	50	0.66	0.27	Walde et al. (2003)
QC	Brome Co.	18	24	10	0.75	0.19	Daigle (1997)
QC	Brome Co.	16	13	4	1.23	0.12	Saumure and Bider (1998)
QC	Pontiac Co.	10	10	11	1.00	0.35	Saumure and Bider (1998)
ON	Algonquin Park	21	56	13	0.38	0.14	Brooks et al. (1992)
ON	Huron Co.	83	136	51	0.61	0.19	Foscarini (1994)
ON	Sudbury Dist.	15	21	19	0.71	0.35	Greaves and Litzgus (2009)
NS	Mainland	14	20	10	0.70	0.23	White (2013)
MI	Upper Peninsula	86	105	63	0.82	0.25	Harding and Bloomer (1979)
MI	-	88	146	26	0.60	0.10	Schneider et al. (2018)
WI	-	20	37	1	0.54	0.02	Ross et al. (1991)
WI	-	8	15	0	0.53	0.00	Ross et al. (1991)
WI	-	16	10	1	1.60	0.04	Ross et al. (1991)
WI	-	8	15	0	0.53	0.00	Ross et al. (1991)
MN	Northeast MN	17	23	4	0.74	0.09	Cochrane et al. (2018)
MN	Northeast MN	10	30	10	0.33	0.20	Cochrane et al. (2018)
MN/WI	-	3	23	3	0.13	0.10	Ewert (1985)
IA	Black Hawk Co	16	16	3	1.00	0.09	Williams (2013)
IA	Butler Co	24	36	1	0.67	0.02	Berg (2014)
ME	Somerset Co.	10	27	4	0.37	0.10	Compton, unpubl. data
ME	Aroostook Co.	60	69	37	0.87	0.22	Jones and Willey (2013b)
ME	Somerset Co.	48	102	77	0.47	0.34	Jones and Willey (2013b)
NH	Coos Co.	28	44	37	0.64	0.34	Jones and Willey (2013a)
NH	Grafton Co.	54	66	112	0.82	0.48	Jones and Willey (2013a)
NH	Merrimack Co.	17	29	36	0.59	0.44	Tuttle (1996)
MA	Connecticut Valley	83	83	27	1.00	0.14	Jones et al., unpubl. data
MA	Franklin Co.	42	37	16	1.14	0.17	Jones et al., unpubl. data
MA	Berkshire Co.	18	9	9	2.00	0.25	Jones et al., unpubl. data
MA	Hampshire-Franklin	49	64	27	0.77	0.19	Jones et al., unpubl. data
NJ	Passaic Co.	311	464	-	0.67	NA	Harding and Bloomer (1979)
VA	Fairfax Co.	38	64	37	0.59	0.27	Akre (2002)
VA	Frederick-Shenandoah	70	80	27	0.88	0.15	Akre (2010)
VA	Shenandoah Co.	38	44	12	0.86	0.13	Akre and Ernst (2006)
VA	Frederick Co.	23	32	9	0.72	0.14	Akre and Ernst (2006)
VA	Frederick-Shenandoah	43	42	35	1.02	0.29	Akre and Ernst (2006)
WV	E. Panhandle	16	16	18	1.00	0.36	Breisch (2006)
WV	-	137	88	59	1.56	0.21	McCoard et al. (2016)
WV	-	52	49	86	1.06	0.46	Niederberger and Seidel (1999)
WV	E. Panhandle	137	88	59	1.56	0.21	McCoard et al. (2018)

Hampshire, Wicklow and Sirois (unpublished data) observed a mean annual adult survival rate of 0.93 from 2004–2012 ($n = 55$). Jones (2009) estimated an annual survivorship of 0.88 for 185 adult Wood Turtles tracked in Massachusetts and New Hampshire. In Virginia, Akre and Ernst (2006) reported mean annual survivorship (for adults and juveniles) of 0.92 ($n = 94$), 0.92 ($n = 64$), and 0.80 ($n = 120$) at three different sites between 1999 and 2002.

Stage Structure and Adult Sex Ratio

Several studies have reported stage structure (i.e., proportion of juveniles and adults) and adult sex ratio based on survey data (Table 7-2). Most studies have reported female-biased or equal sex ratios and highly variable juvenile ratios, ranging from 0–48% of captures (Greaves and Litzgus 2009). However, these estimates should be treated with caution because juveniles are detected at lower rates than adults, and detection of all age classes is spatially and temporally variable. For example, terrestrial habitat surrounding 12 sites (linear stream distance = 0.63–3.37 km) in northeastern Minnesota was surveyed during the pre-nesting period in 1990 and 2015, with a male:female sex ratio of 1:1.3 and 1:3.0 in the two survey years, respectively (Cochrane et al. 2018). In contrast, annual surveys (1997–2014) conducted during the nesting period and primarily targeting nesting areas in the same study area, resulted in a cumulative male:female sex ratio of 1:7.7 (Cochrane et al. 2018).

Generation Time

Generation time represents the average age of parent turtles to a cohort of hatchlings, and reflects the approximate turnover rate of breeding adults (Cooke et al. 2018). Generation time is typically estimated using life tables, which account for age-specific reproductive rates (Rockwood 2015). However, accurate life tables are difficult to construct for very long-lived, iteroparous species, such as the Wood Turtle. In the absence of a life table, generation time can be loosely estimated as the age of maturity plus one half the reproductive longevity (Pianka 1974), or as age of maturity + 1/adult mortality rate, which is the calculation used by the IUCN according to COSEWIC (2007).

The generation time for Wood Turtle populations provided by COSEWIC (2007) is 35 years, and van Dijk and Harding (2011) suggest it likely mirrors that of Blanding's Turtle (*Emydoidea blandingii*) at approximately 36–47 years. Assuming an average age at maturity of 15 years, and the range of survivorship estimates of 0.96–1.0 provided by Compton (1999) for a remote population in Maine, the generation time is >40 years (but may be as low as 32 years if three unknown-fate turtles had died). Adult annual survival estimates of 0.88 for 185 adult Wood Turtles in agri-forested landscapes of Massachusetts and New Hampshire provided by Jones (2009) indicate a generation time of 23 years. If these figures are indicative of other regions, generation time may vary from approximately 20 years at sites with very high adult annual mortality rates (>0.2) to about 45 years at sites with fewer anthropogenic sources of mortality. Based on these available data, we propose that 45 years is likely an adequate representation of generation time in undisturbed contexts.

The Wood Turtle's long lifespan and generation time present implications for the conservation and study of the species. Because they live so long, it is theoretically possible for a few individuals to persist for long periods of time in habitats that are no longer conducive to either successful reproduction or recruitment. This tendency may have been adaptive in an evolutionary sense, because certain areas may be prone to recurring disturbances that rejuvenate key habitats. In today's fragmented landscape, however, the ability for individual Wood Turtles to persist for decades in suboptimal habitats can confound conservation efforts, as a single observation or occurrence record cannot be reliably used to identify suitable stream habitat. Rather, multiple surveys are necessary to demonstrate the persistence of a viable or recruiting population (though some populations in the first example may be suitable targets for restoration).

In addition, because of Wood Turtles' long lifespans, relatively low vagility, and dependence on early-successional features for nesting and thermoregulation, Wood Turtles can easily outlive the suitability of ecologically fleeting landscape features. Prehistorically, rivers themselves, through seasonal flood events, likely provided the dynamic disturbance regimes necessary to maintain early-successional habitats for successful foraging and reproduction, as well as overwintering habitats. Today's rivers and streams have generally been so altered by dams, bank stabilization, stream straightening, impervious surfaces in the watershed, and precipitation changes associated with global climate change, that these key disturbance regimes are fundamentally disrupted.

Population Viability Analyses

While adult survival and reproductive output are fairly well studied, additional field research to estimate hatchling and juvenile survival rates is needed to ensure population viability analysis (PVA) models accurately represent population vital rates. Given the uncertainty in the survival parameters in the hatchling and juvenile stages and the large variability in adult parameters across both space and time, uncertainty would likely swamp viability estimates for a PVA at a range-wide scale. Rather, site- or population-specific analyses that account for uncertainty around these parameters may be more appropriate and would prove useful for management decisions at the local level. Compton (1999) constructed a demographic model for a theoretical Wood Turtle population in Maine, and modeled the effect of removing one, two, and three adults annually from a starting population of 100 turtles. The three-turtle harvest resulted in extinction within 50 years, the two-turtle harvest model resulted in extinction in 75 years, and the one-turtle harvest model had declined by over 60% in 100 years. This indicates high adult survivorship is critical for long-term viability of Wood Turtle populations.

Population Size and Density

Wood Turtle populations have been quantitatively assessed in Nova Scotia (Pulsifer et al. 2006), Québec (Daigle 1997; Walde 1998; Walde et al. 2003; Daigle and Jutras 2005), Ontario (Brooks and Brown 1992; Foscarini and Brooks 1997), Michigan (Schneider et al. 2018), Minnesota (Brown et al. 2017; Cochrane et al. 2018), Iowa (Williams 2013), New Hampshire (Tuttle and Carroll 1997; Jones 2009), Vermont (Parren 2013), Massachusetts (Jones 2009), Connecticut (Garber and Burger 1995), New Jersey (Harding and Bloomer 1979; Farrell and Graham 1991), Virginia (Akre and Ernst 2006), and West Virginia (Niederberger 1993; Niederberger and Seidel 1999). Estimates of population density are typically provided as one of four metrics: turtles per hectare of available habitat (e.g., Farrell and Graham 1991), turtles per hectare of river surface area ("river-ha," e.g., Foscarini and Brooks 1997), turtles per linear km (or m) of meandering river ("river-km," e.g., Jones 2009), or turtles per km (or m) of linear floodplain transect (Pulsifer et al. 2006).[4] Often, model estimates are provided for discrete areas that form coherent management units or natural landscapes (Akre and Ernst 2006). Comparisons across these different estimation techniques are difficult, so we detail the most common below. In addition, some studies report

4 Mark Pulsifer provided additional description of survey methods to the authors at a meeting in Fredericton, New Brunswick.

estimates based only on adult detections, while others report estimates based on adult and juvenile detections, further complicating comparability.

Density for Available Habitat

Density estimates provided as turtles per hectare of available habitat (usually extent of floodplain vegetation) range from 0.1/ha (for 469 ha) in Iowa (Williams 2013), to about 12.5/ha for an unspecified area in Passaic County, New Jersey (Harding and Bloomer 1979). Walde (1998) reported a density of 0.4/ha for 538 ha in the Mauricie region of Québec. Farrell and Graham (1991) reported a density of 10.6/ha for 62 ha in Sussex County, New Jersey. Ernst 2001b reported a density of 4.4/ha in Pennsylvania (Ernst 2001b).

Stream-based Density

Daigle (1997) and Daigle and Jutras (2005) reported densities of 9.7 turtles/river-km in Québec. Brooks and Brown (1992, in Foscarini and Brooks 1997) estimated densities of 35.0 turtles/river-ha and 35.5 turtles/river-km in Ontario. Pulsifer et al. (2006) estimated minimum densities of 2.5–11.3 Wood Turtles per transect km in Nova Scotia. Brown et al. (2017) estimated abundance at 8 sites in northeastern Minnesota based on replicated surveys in terrestrial habitat surrounding streams (linear stream distance = 0.38–0.56 km). Site-specific estimated abundances ranged from 5–76 Wood Turtles, corresponding to approximately 12–174 turtles/river-km (mean = 72 turtles/river-km). However, Cochrane et al. (2018) estimated that total abundance at these eight sites decreased by 54% the following year, which was supported by a 44% reduction in unique individuals encountered, as well as discovery of 30 mortality events. Jones (2009) provided density estimates at 31 stream segments in Massachusetts and New Hampshire ranging from 0.4–52.3 adult Wood Turtles/ha of stream surface area and 0.6–40.4 adult Wood Turtles/km of meandering stream, and reported several streams where repeated surveys could not reveal sufficient animals for recapture analysis, suggesting low population sizes and corresponding densities.

The highest density estimates reported are probably those of Farrell and Graham (1991),[5] whose estimates are equivalent to 545 turtles per river-ha and 284.3 turtles per river-km, or Niederberger and Seidel (1999), whose estimate of 337 turtles appears to translate to 198.2 turtles per river-km. Another large population was reported in Nova Scotia, where extrapolated estimates suggest a population size of 1,083–4,000 turtles (Pulsifer et al. 2006). Other estimates of population density, generally at the scale of 1 linear km of meandering stream, were summarized by Jones et al. (2018).

Total Population Size

No quantitative estimates have been generated for total abundance of Wood Turtles across their range in North America or solely for the United States (van Dijk and Harding 2011). Total abundance for the four eastern Canadian provinces has been roughly estimated at 6,000–12,000 adults (COSEWIC 2007).

5 Ray Farrell graciously provided the extent and configuration of the original study location in New Jersey.

Population Trends

7.11—Wood Turtles' iteroparous life history is dependent on continuous high adult survival for population viability. Courting Wood Turtles are pictured in a conifer forest in New Brunswick, covered in needles of spruce (*Picea* spp.) and Balsam Fir (*Abies balsamea*). Damien Mullin

Several studies have presented quantitative evidence for Wood Turtle population declines, including almost all studies with a long-term component. In the Québec portion of the Missisquoi watershed, which is shared with Vermont, Daigle and Jutras (2005) reported a 50% decline in estimated abundance between 1995 and 2002. The study took place in the same stream as the studies undertaken by Saumure and Bider (1998), Saumure (2004), and Saumure et al. (2007), and the combined conclusion of these four studies is that the population is declining because of adult mortality associated with hay mowing and other agricultural activities. According to the most recent COSEWIC (2007) status assessment, the overall Wood Turtle abundance trend across Canada is negative. Populations near the Ontario shores of Lakes Erie, Huron, and Ontario—represented by at least 10 known occurrences—have apparently been extirpated, representing a major range contraction in that part of Canada (COSEWIC 2007). An isolated, remnant population in southern Ontario has shown clear signs of decline since it was first studied by Dina Foscarini in 1991–1992 (Foscarini 1994; COSEWIC 2007; Mullin 2019; Mullin et al. 2020).

In the Upper Peninsula of Michigan, Harding (1991) reported population declines in remote and relatively undisturbed areas, and proposed that illegal collection may have contributed to the declines. However, Schneider et al. (2018) found that a population on protected land in the Lower Peninsula of Michigan was stable from 1998–2015. Cochrane et al. (2018) reported a potential decline in Wood Turtle abundance in northeastern Minnesota since 2006, with a large observed decrease in abundance between 2016 and 2017, which was validated by additional population surveys in 2018 (Brown, unpublished data).

Based on occurrence records and recent surveys, Jones et al. (2015) estimated 58% of suitable habitat in the northeastern U.S. has been impaired as a result of land use conversion. In central Massachusetts, Jones (2009) reported that most populations appeared to be declining and presented limited evidence of significant declines at three study sites over periods of up to 5 years. Jones and Sievert (2008) presented evidence that Wood Turtles in western Massachusetts were declining by as much as 11.2% annually, and among other threats, they were negatively affected by severe floods, which apparently caused population declines in northwestern Massachusetts. Jones (2010) noted that Wood Turtles have become very rare inside the Interstate 95 corridor near Boston. Elsewhere in Massachusetts, in Concord, Middlesex County, Henry Thoreau observed Wood Turtles to be common in the late 1850s, and Rickettson (1911) reported them to be "common in the brooks" in the early 20th century, but Greer et al. (1973) reported Wood Turtles to be "infrequent" by the 1970s. Further, Windmiller and Walton (1992), Windmiller (2009), and Cook et al. (2011) reported that the Wood Turtle had declined nearly to extirpation in Concord, although approximately five individuals have been observed in that town since the

1990s. In 2009, researchers reassessed the streams in Lancaster, Worcester County, Massachusetts, where Agassiz (1857) reported capture rates of >100 turtles per afternoon, and had capture rates nearly $1/50^{th}$ those reported by Agassiz (Jones et al. 2019), suggestive of a localized decline.

In Connecticut, Garber and Burger (1995) interpreted their long-term (1974–1993) survey results as evidence of population collapse associated with human recreation. Following the allowance of passive recreation near the study site in 1982, two subpopulations in the same stream declined from apparent peaks of 106 and 51 captured turtles, respectively, to 6 and 8 detected in 1991 and none in 1992 or 1993. The authors presented a compelling summary of population collapse, although detection rates were not estimated and survey effort by year was not presented. In southwestern Connecticut and adjacent Westchester County, Klemens (1989) considered the Wood Turtle functionally extinct. Burger and Garber (1995) emphasized a widespread decline but do not present evidence beyond that summarized in Garber and Burger (1995).

Harding and Bloomer (1979) noted the collapse of Wood Turtle populations in eastern and central New Jersey since the 1950s. In Virginia, Ernst and McBreen (1991) reported the extirpation of three Wood Turtle occurrences in Fairfax and Loudoun counties since 1979, and noted that 33% of known localities were threatened by development. Akre and Ernst (2006) and Akre (2010) reported that two populations persist on the Piedmont east of the Blue Ridge. Of these, one site in Fairfax County appears stable, but the authors provided evidence of decline at a known site in Loudoun County. Akre and Ernst (2006) resampled three streams in the coastal plain of northeastern Virginia where Wood Turtles had been reported historically, but detected no turtles. Further, they provided a detailed analysis of the probable range contraction of Wood Turtles on the Coastal Plain.

Summary

Demographic parameters estimated from wild populations, available models, empirical observation, and anecdote all suggest widespread recent declines and a discouraging future for the Wood Turtle in North America. The demographic and life history data that have emerged from studies across the range for more than 40 years demonstrate the predictions of life history theory: that the Wood Turtle exhibits demographic parameters in line with bet-hedging theory (Stearns 1976). The Wood Turtle's evolution in environments where egg clutches and juveniles had low but variable survival, and high rates of adult survival, enabled the development of a long-term iteroparous life history that is dependent on continuous high adult survival for population viability (7.11).

While it is clear from the accounts above that there are streams throughout the range where relatively high density, high abundance, and/or connected populations remain, it is also clear that there are as many, if not more locations where Wood Turtle populations do not appear viable. These include areas where Wood Turtles were apparently formerly abundant, suggesting evidence for an overall decline across the range. Although there are a few important gaps in our knowledge of Wood Turtle demography that are in urgent need of filling, including hatchling and juvenile survival rates, decades of research by generations of biologists allow us to understand many of the important parameters around the lifespan, reproductive biology, and demography of the Wood Turtle, which can be used to assess threats (Chapter 8) and inform management and restoration (Chapter 9).

8. Threats and Predators

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Phillip deMaynadier, Lisabeth L. Willey, Brian Zarate,
Raymond A. Saumure, Michael Marchand, Steve Parren

This female Wood Turtle in New England lost both front limbs to a mammalian predator. Mike Jones

8.1—Floodplain ecosystems preferred by Wood Turtles have historically provided rich soils for agriculture, clearly illustrated at this site in New England. Kiley Briggs

Introduction

For most of its evolutionary history, the lineage that led to modern *Glyptemys* thrived (and survived) in environments unimaginable to us today.[1] Today, we see a delicate animal undergoing ecological collapse across much of its recent range. However, the serious threats that imperil Wood Turtle populations today are wholly different from anything the species has experienced during most of its evolutionary history, which must have been heavily influenced by now-extinct megafauna species ranging from mastodons (*Mammut* spp.) to short-faced bears (*Arctodus* spp.) and the chaotic disruptions of continental glaciations. Consider that for almost all of the species' evolutionary history, since it diverged from Bog Turtle, for example, human beings were absent from the North American continent.[2] By contrast, Wood Turtles are now most influenced by urbanization, vast networks of roads, a massive agricultural footprint, countless reservoirs, a landscape mostly devoid of large predators, and a climate that's taken on a different sort of volatility. In fact, countless Wood Turtle populations have been extirpated—or at least severely compromised—by a combination of agriculture, urbanization, habitat loss and fragmentation, and their associated effects (Garber and Burger 1995; Daigle and Jutras 2005; COSEWIC 2007; Jones et al. 2015; Roberts et al. 2017; Willey et al. 2021).

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1 Chapter 2 provides a more detailed examination of the Wood Turtle's evolutionary history.

2 Even if humans have been present in North American for 20,000 years, their overlap with the Wood Turtle, or its direct ancestor, accounts for less than 0.2% of the estimated time since *Glyptemys valentinensis* ranged the Niobrara River of Nebraska 11.5 million years ago.

In this chapter, we broadly outline and discuss the proximate causes of Wood Turtle population decline within the following categories: (1) habitat loss and fragmentation, including road mortality and agricultural mortality; (2) hydrological degradation, including dams and stream alterations; (3) collection and harvest; (4) disease; (5) climate-related environmental change, including floods and drought; and (6) predation. As already described in detail, the life history characteristics of Wood Turtles make reproductive adults particularly important to population persistence (Compton 1999). Many of today's most significant threats are those that disproportionately affect Wood Turtles.[3]

Habitat Loss & Fragmentation

Conversion and fragmentation of Wood Turtles' riparian habitats and adjoining upland areas comprise one of the greatest threats to the persistence of the species. While Wood Turtles primarily occupy floodplains, much of the upland habitat adjoining floodplains in the species' range has been converted to agriculture or development. In the Northeastern United States, over 50% of historically suitable stream habitat is estimated to have been impaired by fragmentation and/or land use changes (Jones et al. 2015; Willey et al. 2021). Many of the low and mid-elevation riverine ecosystems preferred by Wood Turtles have historically provided strategic real estate for the manufacture and transportation of goods, rich soils for agriculture, or, more recently, attractive water-frontage for residential development (8.1). The distinct factors associated with habitat loss, fragmentation, or modification are known or strongly suspected to negatively influence the distribution and abundance of Wood Turtles.

Road Mortality

Road mortality of adults, juveniles, and hatchlings is a major threat to the species throughout its range (Jones et al. 2015) (8.2), and is the likely the single most significant cause of population declines throughout urbanized areas of the Northeastern United States (Gibbs and Shriver 2002). Akre and Ernst (2006) considered road mortality one of the most severe threats facing Wood Turtles in Virginia, and attributed most of their observed mortalities to automobiles. In New Jersey, nearly 10% of validated Wood Turtle occurrence points are live and dead on-road observations (NatureServe 2021). Further, where roads serve as attractive areas for egg-laying, as on the George Washington National Forest of northwestern Virginia, the roadside nesting sites themselves may function as ecological traps (Akre 2010). Heavily trafficked forest management roads in otherwise remote landscapes can also be potentially hazardous features, where few other anthropogenic threats are present. Newly created forest roads can also open otherwise unfragmented habitat, allowing poachers and collectors to access sites more readily. In recent years, as abandoned railway lines have been

8.2—Road mortality of adult, juvenile, and hatchling Wood Turtles is a major threat to the species throughout its range. This adult male was killed along a state highway that closely parallels what must formerly have been an exceptional Wood Turtle river in central New England. Mike Jones

3 Chapter 7 describes the Wood Turtle's life history in detail.

8.3—Agricultural machinery—including mowers and tractors—cause significant mortality in rural Wood Turtle populations throughout their range, and is often the most important cause of adult Wood Turtle mortality. Most reported mortality has been observed in eastern Canada and New England. The adult female pictured here (*top*) was killed in a horse pasture during a radio-telemetry study in New England (*bottom*). Mike Jones

converted to recreational trails, reports have increased of Wood Turtles nesting along these trails (Franek and Ruziecki 2018), putting nesting females at risk of collection and nests at risk of stress or failure due to the incompatibility of the substrate, causing rock falls.

Breckenridge (1958) speculated that automobile traffic resulted in Wood Turtle mortality in Minnesota, but noted an absence of road mortality records, which he attributed to the species' relative rarity. This speculation is supported by data from Québec, where only 2 of 60 (3.3%) road-killed turtles in one study were Wood Turtles (Desroches and Picard 2005), and from central New England, where only 5 of 364 (1.4%) road-killed turtles were Wood Turtles (Jones, unpubl. data).

Agricultural Machinery

Wood Turtle mortality from crushing injury by agricultural machinery is a leading threat to many rural populations inhabiting both hay- and row-crop production areas (Saumure 2004; Daigle and Jutras 2005; Saumure et al. 2007; Castellano et al. 2008; Tingley et al. 2009; Jones 2009; Erb and Jones 2011) (8.3). Saumure and Bider (1998) first noted the severe effects of agricultural machinery on Wood Turtle survival. At their paired agricultural and forested sites in Québec, they noted that shell injuries were twice as common at the agricultural site. Jones (2009) reported that instream Wood Turtle density in Massachusetts was associated with low crop cover and higher forest cover at multiple landscape scales, suggesting that Wood Turtle densities are depressed in heavily farmed areas. Erb and Jones (2011) reported a substantial portion of the mortality associated with mowers is probably caused by tractor tires.

8.4—Active-season forestry operations can result in significant mortality or injury to Wood Turtles. Wood Turtles with serious shell fractures are regularly observed in remote areas of managed forestland. These older female Wood Turtles were found in relatively remote areas of New England forestland with severe—but healed—carapace fractures that were likely caused by forestry operations, forestry-associated vehicles, or mowing. Derek Yorks & Liz Willey

Forestry

The influence of forestry on Wood Turtles is complex, but can be either beneficial or detrimental to Wood Turtle viability depending on the scope, scale, configuration, seasonality, and methodology of the cutting operations, as well as the geographic position within the Wood Turtle's range. Historically, Wood Turtle populations probably centered around natural openings in the forest canopy, caused either by natural riverine disturbance processes or upland forest disturbances caused by fires, beaver, and severe wind blowdowns. Without such natural disturbances, Wood Turtles seek out their anthropogenic equivalents, such as areas cleared for timber harvest.

Some carefully planned riparian forestry practices (e.g., smaller harvest openings and shelterwood cuts) may create valuable basking and foraging microhabitat for Wood Turtles. However, active-season harvests can result in significant mortality or injury to turtles. Indeed, there is at least one report of a crushed adult Wood Turtle from a harvested location in northern Maine (deMaynadier, unpubl. data), and the authors of this chapter have observed Wood Turtles with serious shell fractures in remote areas of commercial forestland throughout New England

8.5—Japanese Knotweed (*Reynoutria* [=*Fallopia*] *japonica*)—appearing here as an orange understory shrub layer in a floodplain forest of American Sycamore (*Platanus occidentalis*) in Massachusetts (*left*), and along stream banks elsewhere in New England *(right)*—is probably the most ecologically problematic invasive plant species affecting Wood Turtle populations. Dense and established knotweed populations can impair the function of Wood Turtle nesting beaches. Mike Jones

(Jones, Yorks, and Willey, unpubl. data) (8.4). In addition, the elimination of a forested stream buffer due to timber harvesting can result in increased stream bank erosion, water quality and flow degradation, and reduced in-stream habitat heterogeneity from fallen trees and other riparian organic inputs (Akre and Ernst 2006; Tingley and Herman 2008). Structured or experimental research into the response of Wood Turtle populations to various forestry practices, including prescribed fire, is warranted.

Invasive Plants

Invasive vascular plant species are present throughout the larger floodplains of eastern North America. Their dispersal and colonization is facilitated by the dynamic nature of riparian systems, but in general, the negative effects of invasive plant species on Wood Turtles are poorly documented. The greatest risk posed by invasive vascular plants is likely reduced light availability for thermoregulation, reduced natural ground cover and forage availability, and loss of previously open, friable substrates for nesting. However, it is important to note that in some cases the process of controlling invasive species may involve greater risk for adult Wood Turtles than the plants themselves (e.g., Sparling et al. 2006), depending on the timing and mechanism for control.

The relative threat posed by invasive plant species probably varies geographically and according to the past land use and disturbance history of the site, as well as current management techniques. Invasive plant species influence the habitat quality of floodplain areas in different ways, depending on their density and growth form. Perhaps the most problematic invasive species for the Wood Turtle is Japanese Knotweed (*Reynoutria* [=*Fallopia*] *japonica*), which is known to overtake open, sandy nesting areas within the floodplain in Maine, New Hampshire, Vermont, Massachusetts, and Pennsylvania (Gipe and Jones, unpubl. data) (8.5). Multiflora Rose (*Rosa multiflora*) is also widespread and common in Wood Turtle habitats from Massachusetts (Jones 2009) to West Virginia (Niederberger 1993) and Virginia (Akre and Ernst 2006), and appears to present a threat to Wood Turtles only if aggressive efforts are made to control the species with heavy machinery during the active season. Other invasive plant species that may exert a negative influence on vegetation structure or sunlight availability in the river corridor include Autumn and/or Russian Olive (*Eleagnus* spp.), which has colonized Wood Turtle streams from New England to Virginia (Jones, unpubl. data; Sweeten 2008) and Mile-a-minute (*Persicaria perfoliata*), which has become problematic in Wood Turtle habitat from Pennsylvania to Virginia

8.6—Coltsfoot (*Tussilago farfara*), shown here in its flowering and vegetative stages, is a Eurasian species now commonly found in Wood Turtle habitats range-wide. Although it is widespread, there is no evidence to suggest that Coltsfoot negatively influences the function of Wood Turtle habitat. Mike Jones

(Akre and Ernst 2006). At Great Swamp National Wildlife Refuge in New Jersey, Wood Turtle nesting areas are also negatively affected by Common Mugwort (*Artemisia vulgaris*) (Buhlmann and Osborn 2011). Wood Turtles actually feed upon some invasive plant species including Autumn Olive berries (Kleopfer, unpubl. data.) in Virginia and Japanese Knotweed, Reed Canary Grass (*Phalaris arundinacea*), and Bishop's Goutweed (*Aegopodium podagraria*) in Massachusetts (Jones and Sievert 2009b).

Other vascular plant species that may become problematic in riparian habitats include: Common Reed (*Phragmites australis*), Japanese Stiltgrass (*Microstegium vimineum*), several species of honeysuckle (*Lonicera* spp.), Garlic Mustard (*Alliaria petiolata*), Purple Loosestrife (*Lythrum salicaria*), Glossy Buckthorn (*Frangula alnus*), and Oriental Bittersweet (*Celastrus orbiculatus*) (PDEP 2004; Akre and Ernst 2006). Despite widespread concern, quantitative studies of the effects of invasive plant species on habitat quality for Wood Turtles are lacking. Many exotic species do not appear to negatively influence Wood Turtles, such as Coltsfoot (*Tussilago farfara*) or hawkweeds (*Hieracium* spp.), although there have not been any fine-scale studies to confirm this (8.6). Wood Turtles will occasionally bask in areas of dense Common Reed (Robillard et al. 2016).

Aquatic Pollution

The Wood Turtle is strongly associated with clear, clean streams (Harding 1991; Ernst and Lovich 2009). There have been few, if any, quantitative studies of the influence of aquatic pollution on Wood Turtle populations. Akre and Ernst (2006) indicated that poultry farms and logging in Rockingham County, Virginia, are degrading stream quality for Wood Turtles through point-source nutrient pollution and flow-rate degradation. Wood Turtles occur at least occasionally in streams affected by Acid Mine Drainage in western Pennsylvania, where they may be stained orange with ferric hydroxide (Williams 2009). Wood Turtles are largely absent from the mainstem of rivers that were used heavily during the textile boom of the 19th Century in Massachusetts (MassWildlife NHESP, unpubl. data; Jones, unpubl. data); however, these areas also tend to be heavily urbanized. More research into the effects of chemical and nutrient contamination on Wood Turtles is clearly warranted.

 

8.7—Bank stabilization or hardening is a common practice to minimize loss of residential or agricultural property caused by streambank erosion. Often, bank stabilization reduces the quality of bank and riparian habitat for Wood Turtles. Large, hardened structures can also influence downstream deposition patterns and can result in direct mortality of turtles during construction. Some rivers are heavily influenced by centuries of bank stabilization efforts, such as these sites in Massachusetts. Mike Jones

Hydrological Alterations

Stream Bank Stabilization

Stream bank alterations to control or contain streamflow have occurred in the eastern United States since European settlement. Artificial bank stabilization is common along rivers throughout the Wood Turtle's range wherever roads, buildings, agricultural fields, and energy infrastructure are at risk from flooding and massive bank failure. In many areas, a majority of available stream habitat has already been significantly altered or hardened. Bank stabilization ranges in form from the historical use of debris, broken cement, and riprap, to more recent applications of boulders, gabion, and bioengineering techniques (8.7).

Large-scale bank stabilization efforts can result in direct turtle mortality. Even small-scale bank stabilization has been documented to result in Wood Turtle mortality through crushing or entombment (Saumure 2004; Saumure et al. 2007). Bank stabilization projects can also degrade habitat for Wood Turtles in several ways depending on the materials used, extent of stabilization, and downstream hydrological changes. For example, riprap is also known to trap turtles of other species between the rocks as they try to navigate across the material (Kleopfer, unpubl. data). Banks hardened with large riprap (>20 cm) are probably of low habitat quality for Wood Turtles for several decades (Jones and Sievert 2011).

Large hardened structures can impair, impede, or influence natural depositional processes. Long sections of hardened bank can impair the natural dynamic movement of the river, slowing or obstructing the development of sand and gravel beaches on the inner bends of wide meanders. In this way, overall nesting-site quality can be degraded over the course of decades (Buech et al. 1997; Bowen and Gillingham 2004). In one large stream system totaling 17.1 km in length in western Massachusetts, Jones and Sievert (2011) reported that 7.5% of the streambanks had been converted to hardened structures of little ecological value to Wood Turtles, and an additional 3% of the river bank was exhibiting evidence of massive collapse, suggesting stream stabilization might be employed in the near future. The effects of bank stabilization on habitat quality for Wood Turtles merits further study, especially in the context of riparian and stream restoration programs.

8.8—Anthropogenic dams, including hydroelectric facilities, flood-control reservoirs, and drinking water reservoirs, have negatively influenced the distribution and abundance of Wood Turtles range-wide by converting suitable, free-flowing stream habitat to deep reservoirs and starving downstream beaches through altered flow regimes. The total effect is difficult to estimate, but is clearly enormous. The Conowingo Dam on the Susquehanna River in Harford County, Maryland, is pictured at left. One of thousands of defunct New England dams—in this case, a 19th-century power dam—is pictured at right. Mike Jones

Widespread stabilization projects occurred throughout New England and New York in the wake of Hurricane Irene (2011) and Tropical Storm Sandy (2012), many of which were implemented under emergency authorization (Murphy 2013). The effects of intensive stream stabilization on Wood Turtle habitat usage and suitability should be a priority for field evaluation.

Anthropogenic Dams

Anthropogenic dams, including hydroelectric facilities, have negatively influenced the distribution and abundance of Wood Turtles by converting suitable stream habitat to deep reservoirs, influencing downstream flow regimes, and other effects (8.8). The influence of dams on habitat suitability for Wood Turtles depends on other habitat resources available, the size of the dam, and the landscape configuration. According to the National Dam Inventory (2018), more than 10,000 dams remain in place on streams and rivers within the Wood Turtle's recent range in the United States alone, including 1,934 in New York, 1,514 in Pennsylvania, 1,327 in Massachusetts, and more than a thousand in Minnesota, Wisconsin, and Michigan. Distributed throughout this area, more than 1,600 large dams serve the primary purpose of: (1) storing drinking water; (2) generating hydroelectric power; and/or (3) providing flood protection.

Habitat loss associated with dam construction was among the highest threats to Wood Turtles identified by Castellano et al. (2009). Compton (1999) reported that a very large dam in western Maine posed several long-term threats to Wood Turtle persistence by: (1) starving the river of sediments that would otherwise build downstream gravel bars; (2) moderating high springtime flows that would scour nesting areas and deposit new gravel, resulting in overgrown nesting areas; and (3) generating midsummer high flows that flood low-lying nests.

In some instances, it is possible to confidently infer from historical reports that Wood Turtle populations were displaced by flooding associated with reservoir construction. For example, in the Catskill Mountains of southern New York, numerous drinking-water supply reservoirs such as the Blenheim-Gilboa and Schoharie Reservoirs have completely flooded valleys that probably contained optimal Wood Turtle habitat prior to flooding in the 1920s but, like most cases involving older impoundments, this can no longer be demonstrated empirically. A nearby dam, which forms the Pepacton Reservoir of the interior Catskills, impounded a major section of the East Branch of the Delaware River. Reeve Bailey collected Wood Turtles in the footprint of the future reservoir in July of 1935, prior to its flooding between 1954–1955. And, to the south of the Catskill massif, the Ashokan Reservoir flooded Esopus Creek (and other small creeks) between 1912–1914. In summary, Wood Turtles were distributed throughout the Catskill Mountains during the era of the reservoir construction, and individual turtles were probably displaced into less optimal habitats by the flooding.

Quabbin and Wachusett Reservoirs in Franklin, Worcester, and Hampshire counties, Massachusetts, flooded extensive areas of suitable Wood Turtle habitat associated with the major branches of the Swift River and Nashua River Valleys when construction began in the 1930s, evidenced by recent Wood Turtle records in tributaries to both reservoirs (MassWildlife NHESP, unpubl. data; Jones, unpubl. data).

Numerous reservoirs in the Highlands of northern New Jersey probably eliminated large, contiguous areas of occupied stream habitat for Wood Turtles. One specific example is the Monksville Reservoir, which flooded portions of the Wanaque River.

The Conowingo Dam is situated on the Susquehanna River in Cecil County, Maryland, where Wood Turtles were documented in the 1940s (Cooper 1949). Likely, some of the tributary streams affected by the Conowingo Dam were inundated.

Flood control facilities maintained by the U.S. Army Corps of Engineers are strategically placed to minimize property damage and loss of life within flood-prone communities. Army Corps flood storage projects include both reservoirs that are permanently flooded and many that are flooded only during major storm events, and both may negatively influence local Wood Turtle populations (Dickerson et al. 1999). Although it has not been studied, it is possible that large flood control projects can negatively influence Wood Turtle populations by creating dramatic shifts in water levels during the winter dormancy period, as well as by changing the downstream redistribution of sand, gravel, and woody material. Permanent flood-storage reservoirs located in close proximity to extant populations, it may be inferred, have likely resulted in long-term loss of free-flowing riverine habitat for local Wood Turtle populations, and in some cases may have caused interruptions in gene flow by serving as partial barriers to movement.

The local influence of smaller dams on riparian habitats is less clear. In Massachusetts, a small subpopulation of 10–15 adults was found to occur in free-flowing stream habitat immediately upstream of a late-19th century power dam, which had filled in with sediment and no longer formed a large reservoir (Jones and Sievert 2009). The dam appeared to create suitable riparian habitat for wood turtles upstream. However, individual turtles within this population were frequently displaced downstream and over the dam by repeated flood events. This appeared to result in reduced survival and reproductive output. The small reservoir remaining behind the dam also occasionally "captured" flood-displaced turtles (Jones and Sievert 2009). A similar situation occurred on a stream in New Hampshire (Jones, unpubl. data), suggesting that in some instances smaller dams can create suitable Wood Turtle habitat upstream after the resulting reservoir fills with sediment, which functionally reduces stream gradient and creates sandy bank structures. As dams are removed throughout the Wood Turtle's range, new opportunities will arise not only for stream and population restoration, but also to learn more about how such infrastructure may have affected Wood Turtle populations in the flooded areas.

Beavers

The relationship between habitat manipulations by American Beaver (*Castor canadensis*) and Wood Turtle population persistence is complex, highly variable at local scales, and not fully understood. Beavers are ecosystem engineers, keystone species that drive structural complexity (e.g., slower, deeper pools, basking and hibernation sites) within Wood Turtle streams. Beaver populations were once ubiquitous in eastern North America, as evidenced by the writings of early surveyors, naturalists, and fur trade records (Goldfarb 2018). Beaver populations periodically saturated the pre-Colonial American landscape, and they co-existed with Wood Turtles at least since the end of the Pleistocene ice ages. Beavers create mosaics of successional wetland communities by building and maintaining dams (8.9). Beaver populations in New England, however, had begun to decline due to human intervention by the mid-1600s and, by the 18th Century, beaver had been extirpated from Massachusetts (Goldfarb 2018). In Canada, the beaver fur trade peaked in 1875, when the Hudson's Bay Company traded over 270,000 pelts (Goldfarb 2018).

8.9—Beavers create mosaics of successional wetland communities by building and maintaining dams. Prior to their extirpation from many areas of eastern North America, beavers were undoubtedly a significant driver of vegetation dynamics within Wood Turtle river systems. A beaver-impounded Wood Turtle stream in New England is pictured. American Turtle Observatory

Today—especially within heavily fragmented or isolated Wood Turtle sites—beaver dam construction more often degrades site quality for Wood Turtles. Without adequate riparian connectivity to other areas of free-flowing lotic habitats, local Wood Turtle populations could be negatively affected. In the course of several radio-telemetry studies, we've noticed apparent avoidance of large beaver impoundments by Wood Turtles, in areas that were heavily used during periods when the beaver dams were defunct (Jones and Willey, unpubl. data).

As with many ecological processes the effects of beavers on Wood Turtle populations is likely a question of scale and may be similar to the patterns observed in fishes (Snodgrass and Meffe 1998); it is clear that in large landscape contexts, beavers can play an important role in the alteration and creation of various components of Wood Turtle habitat.

Collection and Harvest

Throughout their recorded history, Wood Turtles have been collected variously for food, scientific and museum collections, biological supply, and as pets. Today, Wood Turtles continue to be collected to satisfy a burgeoning international market in North American turtles (8.10). Many populations have been affected by collection, and most populations are vulnerable. Federal and state authorities lack the necessary resources and legal authority to put a meaningful end to the trade.

Wood Turtles were collected as a food item in the 19th and early 20th Centuries, contributing to population declines (Klemens 1993; Breisch 1997). By the mid-1900s, biological supply

8.10—Wood Turtles have been collected variously for food, scientific and museum collections, biological supply, and—more recently—as high-end pets. Today, Wood Turtles continue to be collected to satisfy a burgeoning, illegal international market in North American turtles, undermining efforts to protect and conserve otherwise functional populations. Until there is a more coordinated federal approach to regulate interstate and international trade in this species in the United States, many important wild Wood Turtle populations will remain at risk. The Wood Turtles pictured here were confiscated by wildlife agencies, and they represent populations throughout the eastern part of their range. John D. Kleopfer & Mike Jones

houses became a major detrimental cause of Wood Turtle population collapse (Vogt 1981), reflecting a trend that probably extends back several decades earlier (Jones et al. 2015).

In recent decades, illegal collection for domestic and foreign pet markets has become a major, unpredictable, regrettable threat (Compton 1999; NatureServe 2013). While the corrected, real price of Wood Turtles in the early 1960s was about $20.00, the price charged on online markets has climbed to more than $900 per turtle as of this writing.[4] The more than 45-fold increase likely reflects a decline in abundance (and availability).[5] Large-scale collection has been documented in

8.11—Wood Turtles are occasionally shot from their basking sites, as was this female in Iowa. Jeff Tamplin

4 In 2020, one dealer on Kingsnake.com lists adult Wood Turtles for $900 each, retail price (Saumure, unpubl. data).

5 The price of Wood Turtles has increased nonlinearly. A substantial increase occurred in the 1990s, when Wood Turtles were reported to sell for $125 in the early 1990s (RESTORE: The North Woods 1994), $131 in 1996 (Hoover 1998), $175 in 1997 (Compton 1999), and $250 in the late 1990s (McCollough 1997).

Maine,[6] Vermont,[7] New York,[8] New Jersey,[9] Pennsylvania,[10] Maryland,[11] Virginia, West Virginia,[12] Québec,[13] and Ontario.[14]

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6 The Maine Department of Inland Fisheries and Wildlife recorded at least two incidents of large-scale illegal collection of Wood Turtles from the wild. In 1994, approximately 44 Wood Turtles (mostly nesting females) were brought to the Portland waterfront to be sold (ME IFW, unpubl. data). In 1995, 54 Wood Turtles were confiscated from a dealer in Virginia who had obtained the animals in Maine (ME IFW, unpubl. data).

7 Vermont Fish and Wildlife undertook a sting operation in 2003 when it was reported that Wood Turtles were being advertised for sale on the internet; nine turtles were seized and released into their native stream (Parren 2013).

8 According to the New York Conservation Officers Association, Wood Turtles were one of the species most frequently collected and traded illegally as exposed by "Operation Shellshock," an undercover law enforcement action taken by the New York State Department of Environmental Conservation from 2006–2009. According to New York State Department of Environmental Conservation (Breisch, unpubl. data), a major confiscation of Wood Turtles occurred in Cattaraugus County in 2018.

9 In 2008, New Jersey environmental law enforcement, assisted by the Pennsylvania Fish and Boat Commission, raided the home of a commercial reptile breeder and found >20 Wood Turtles in his possession after he purchased four Wood Turtles from undercover agents (United States vs. Albert Roach, USDOJ/ECS 2011).

10 The Pennsylvania Fish and Boat Commission supported "Operation Herp Scam," which in 1998 detected a widespread network of trade in Wood Turtles (Sajna 1998) through which >290 Wood Turtles were taken from western and southwestern Pennsylvania (Blankenship 1999). Kaufmann (reviewing CITES listing in NatureServe 2013) reported that collectors from Canada illegally collected hundreds of Wood Turtles from a stream in Pennsylvania over the course of a few days.

11 Large-scale collection is suspected to have occurred in western Maryland in the early-2010s (Thompson, in Jones et al. 2015).

12 In 2008, the U.S. Fish and Wildlife Service contacted the Virginia Department of Game and Inland Fisheries to be on the lookout for a suspect of a surveillance operation in West Virginia. This effort led to the recovery of 108 illegally collected Wood Turtles. The Wood Turtles were released back at the reported point of capture in West Virginia. There have been other instances of commercial collection in West Virginia as far back as 1992. In 2013, a resident of Ontario, Canada was fined for possession and transportation of Wood Turtles from West Virginia. The investigation, conducted by the USFWS in conjunction with the West Virginia Division of Natural Resources Law Enforcement Section, determined that the Wood Turtles had been obtained from an undercover agent and transported to Ontario in violation of the Lacey Act and CITES (WV DNR, unpubl.data).

13 In order to promote the repatriation of confiscated Wood Turtles in Québec, all mark-recapture projects use the same numerical notching system using the posterior scutes per Saumure and Bider (1998). In addition, the anterior scutes are notched with a sequential population code, first instituted by the late Dr. Bider. Thus, a confiscated Wood Turtle notched as #27 with population code 3 can theoretically be verified based on sex and morphology, the poacher prosecuted, and the turtle returned to its home river.

14 An estimated 70% of a Wood Turtle population in Ontario was collected in a mass poaching event in the mid 1990s (White et al. 2016; Mullin 2019). Saumure (unpubl. data) recalls visiting a turtle hobbyist in Ontario in the mid-1980s who had over a hundred Wood Turtles collected in the United States.

Incidental collection of adult Wood Turtles contributed to the collapse of local populations in Connecticut (Garber and Burger 1995) and Virginia (Akre and Ernst 2006). Although not a widespread practice, Wood Turtles still appear at local turtle derbies (or races). In 2018 and 2019, Wood Turtles were unknowingly used for a turtle derby at the Frederick County Fair in Virginia (Kleopfer, unpubl. data). These turtles were wild-caught and housed with several Eastern Box Turtles (*Terrapene carolina*) in suboptimal conditions.

Clearly, incidences of Wood Turtle collection are widespread, and possibly increasing as the prices of animals continue to climb. As observed by Garber and Burger (1995) and modeled by Compton (1999), the loss of just a few individual adults from a population over time can lead to extirpation. It is fortunate that all extant range states currently prohibit commercial and/or personal collection of Wood Turtles. Better-integrated communication is needed between state wildlife agencies, law enforcement, and researchers. Wood Turtle populations would benefit from stronger deterrents such as higher penalties for collection of wild-caught Wood Turtles and a nexus for federal law enforcement to determine the legal status of captive Wood Turtles in any state. Most confiscations, particularly those that occur at the state level, lead to minor charges and penalties, much less than the market cost of the animals being trafficked. This does little to deter future collection.

There is no legal harvest of Wood Turtles anywhere in the species' range, though turtles are occasionally shot off their basking sites (Tamplin, unpubl. data) (8.11).

Pathogens

Disease has not yet been reported as a major problem influencing Wood Turtle population status (Smith and Anderson 1980; Upton et al. 1995), though emerging pathogens clearly warrant strong precautions by researchers. The presence of *Ranavirus* in captive and wild populations of Eastern Box Turtles, which are often sympatric with Wood Turtles from Massachusetts to West Virginia, is a growing concern (De Voe et al. 2004; Johnson et al. 2008; Allender et al. 2011; Kiester and Willey 2015). Although *Ranavirus* prevalence seems to be low in Eastern Box Turtles (Allender et al. 2011), several die-offs of unknown cause have occurred (Rossell et al. 2002), and incidents in New York, Pennsylvania, Georgia, and Florida may have been caused by *Ranavirus* (Johnson et al. 2008). In New Jersey, an individual headstarted Wood Turtle that was being monitored at its release site in the wild was found dead and tested positive for *Ranavirus* in 2015 (K. Conley, WCS, unpubl. data).

Several dead Wood Turtles and Eastern Box Turtles were found in Pennsylvania in 2014; samples subsequently taken of Wood Frog (*Lithobates sylvaticus*) tadpoles at the site tested positive for *Ranavirus* (Gipe, unpubl. data), though there was no diagnostic link to the turtle mortalities. A mass die-off of about a dozen Wood Turtles and 18 Bog Turtles (*Glyptemys muhlenbergii*) was reported in Monroe County, Pennsylvania in 2014, but the cause could not be determined (Gipe, unpubl. data), and an unidentified pathogen may be causing mortality in wild Bog Turtle populations in Massachusetts and New York (USFWS 2009).

Several instances of limb paralysis, thinning skin, and emaciation in Wood Turtles have been reported by the public. In these cases, the sick captive Wood Turtles were being housed with asymptomatic Box Turtles (Saumure, unpubl. data).

Parasites

Wood Turtles are susceptible to ectoparasites, including biting flies (Grogan et al. 2009) and leeches (*Placobdella parasitica* or *P. ornata,* Koffler et al. 1978, Harding and Bloomer 1979; Hulse and Routman 1982; Routman 1982; Farrell and Graham 1991; Saumure and Bider 1996; Niederberger and Seidel 1999; Walde et al. 2003; Breisch 2006; Parren 2013). The severity of leech infestations varies seasonally (Koffler et al. 1978; Brewster and Brewster 1986; Farrell and Graham 1991; Walde et al. 2003), with most occurring in the spring and fall and fewer during summer months (8.12). Leeches may be detrimental to the turtles in concert with other disease or injury (Saumure and Bider 1996). Although there is no evidence that ectoparasites are a widespread threat to this species, *Placobdella* are known to transmit blood parasites in other sympatric turtle genera (Siddall and Desser 2001). Brown et al. (1994), however, did not find that *P. parasitica* had an effect on Common Snapping Turtle (*Chelydra serpentina*) reproductive output. Nevertheless, it is possible that Wood Turtles actively work to remove leeches and other parasites through behavioral processes such as basking or anting (Hughes et al. 2016). Though there is limited evidence for these behaviors to date, anti-parasite behavior is a potentially unexplored area of research.

8.12—Wood Turtles are often parasitized by harmless leeches in the genus *Placobdella*. A relatively old adult male Wood Turtle is pictured from central New England. Mike Jones

Climate-Related Threats

Flooding

The influence of severe flooding on Wood Turtle habitat quality, reproduction, survivorship, and dispersal is complex. Flooding, a naturally occurring phenomenon in most Wood Turtle streams, may improve or degrade habitat quality based on extent, magnitude, and seasonality. For example, floods may alter or rearrange channel geomorphology, damage floodplain vegetation, rearrange woody structure in the stream channel, or redistribute sand, gravel, and other sediments (Compton 1999), which in turn may either augment or decrease the available nesting habitat (8.13).

8.13—Severe flooding—especially floods in mountainous terrain resulting from spring rain on a heavy snowpack (*top*)—may alter or disrupt channel geomorphology, damage floodplain vegetation, and redistribute sand and gravel deposits used for nesting (*bottom*). Mike Jones

8.14—Severe flooding during the summer can directly result in nest failure if rising water inundates nesting areas for lengthy periods of time. Late-summer floods can result in complete nest failure by drowning hatchlings in the eggs (*left*) or cause young turtles to hatch and emerge prematurely from the nest (*right*). Mike Jones

Flooding can also be a cause of nest failure, particularly mid-summer floods that over-wash sand bars, inundating low lying nests. While Wood Turtle eggs can sometimes survive flood events of several days (Vraniak and Geller 2017), late-season inundation can also prompt hatchlings to emerge prematurely from the nest (Jones 2009; Jones and Willey, unpubl. data) (8.14). Flooding is among the most important factors in the decline of Wood Turtle populations in Iowa, where Wood Turtles frequently nest on sandy stream banks and on riverbank sand bars below the high water line. Flooding has caused complete nest failure among known Iowa nests in 12 years out of approximately 15 years of monitoring (Tamplin, unpubl. data), and Spradling et al. (2010) reported 65% nest failure due to flooding from 2003–2006 in Butler County, Iowa.

Depending on the seasonal activity level of Wood Turtles at the time of the flood event, floods may directly entomb turtles through rapid deposition of sediment and debris, or displace them downstream (8.15). Severe floods may displace individual Wood Turtles from resting places within the stream channel, resulting in drowning or injury (Sweeten 2008; Jones and Sievert 2009). In a study of a western Massachusetts sream system, Jones and Sievert (2009) observed 17 displacements of 12 turtles ranging from 1.4 to 16.8 km during large floods, and they reported elevated mortality rates and depressed reproductive rates in flood-displaced animals. The smallest flood resulting in displacement observed in this study was approximately 14.5 times the average daily flow, or 24.4 m^3/s, although flows exceeding 248.0 m^3/s were observed. Disruptive floods in this system occurred at a rate of 1.7 per year during the study (2004–2008), higher than the

8.15—Floods during the winter inactivity season may directly displace or entomb dormant Wood Turtles. Displaced Wood Turtles may suffer limb or shell injuries, as pictured on this flood-displaced Massachusetts male (*left*). Wood Turtles may also be lethally entombed by rapid deposition of flood debris or by massive bank collapse, which trapped this Virginia female (*right*). Tom Akre & Mike Jones annual rate (0.5) of similar floods over the 38 years previous (1966–2004). The authors report that most turtles displaced more than 2 km did not return to their primary activity area within one year.

Sweeten (2008) observed likely flood displacement of three (of 36) adult Wood Turtles in November 2006 at a site in northwestern Virginia. Two males were displaced 13.6 and 19.8 km into the main stem of a larger river downstream, and one female was displaced 1 km. The author speculated that the displacement occurred because the turtles had returned to the river but had not yet "embedded" themselves for the winter in the rootmasses or undercut banks. Both males subsequently made large upstream movements; neither returned to their original capture location within one year.

8.16—Increasing anecdotal evidence suggests that prolonged droughts, which affect perennial streamflows, can subject Wood Turtles to elevated rates of depredation by mesopredators. This mature female was killed by an otter or mink during a prolonged drought in Concord, Middlesex County, Massachusetts—where the Wood Turtle has been functionally extirpated. Mike Jones

Flooding in Iowa has caused adult Wood Turtle mortality, as the turtles were buried under several feet of sand during extreme flooding events. Several other adult Wood Turtles were found dead shortly after major flooding receded in Iowa (Tamplin, unpubl. data). Lapin et al. (2019) further documented effects of flooding on mortality and survivorship in Iowa.

Recent observations of significant displacement or mortality during floods from Massachusetts, West Virginia, and Iowa—across the range of the Wood Turtle—may in part be caused by increasing precipitation severity, combined with increased impervious surface cover and bank stabilization within Wood Turtle watersheds. Indeed, flood severity is increasing as the result of more intense precipitation events, streambank stabilization projects, and the presence of increased impervious surface area in the watershed (Jones and Sievert 2009). Floods can also be exacerbated by the removal of beavers and their dams that create large wetlands that slow the downstream rate of floodwaters (Green and Westbrook 2009; Goldfarb 2018).

Latham (1971) reported five dead adult Wood Turtles washed ashore at four beaches on Long Island between 1919–1926, clustered in a small area directly across Long Island Sound from the mouth of the Connecticut River. Sightings occurred in May, June, July, and August, the inverse of the range of displacements observed by Jones and Sievert (2009), who reported most displacements in late fall, winter, and early spring in the upper portion of the Connecticut River. Latham reported that the sightings corresponded to "freshets," in which "trash, logs, broken trees" were washed from the rivers of Connecticut. Additionally, a single Wood Turtle was collected at Kingstown, Washington County, Rhode Island, on the shore of Narragansett Bay, circa 1980 (MCZ 166324), and a dead turtle was observed on a saltwater beach at Little Compton, Newport County, Rhode Island, in the 1990s (Yorks, unpubl. data). These last two locations are dozens of kilometers from the nearest confirmed location and may represent flood-displaced individuals from the Taunton River watershed in Massachusetts, or another coastal drainage.

In addition, floods can exacerbate the downstream colonization of aggressive vascular plant species such as Japanese Knotweed, mentioned above as one of the most problematic invasive species for Wood Turtles. This species can be particularly invasive in flood-prone ecosystems because of its propensity to root from plant fragments containing live nodes, and a deep root system (Colleran et al. 2020).

By contrast to the above-listed threats, floods may also positively influence genetic structure within watersheds. Flooding can provide a source of connectivity between lower-watershed populations and isolated subpopulations in the upper watershed.

Drought

As anthropogenic climate change causes more drastic climate events, not only are floods projected to increase, but drought events are also expected to become more frequent and severe. Such effects could alter habitat quality, change streams from permanent to ephemeral, reduce vegetation and foraging quality, or overheat nests. It could also reduce survival rates across all age classes, from nests and hatchlings to adults. In addition to direct mortality, drought could also alter movement patterns and behavior, which might have consequences for population connectivity; Remsberg (2006) found that turtles had smaller home ranges during two drought years compared to a more average year. Droughts can subject Wood Turtles to elevated rates of depredation, as Windmiller et al. (2017) reported in eastern Massachusetts in 2016 (8.16).

Flooding and drought have clearly been a part of the evolutionary context of the Wood Turtle, but anthropogenic climate change has exacerbated these natural phenomena. Floods and droughts are occurring with increased frequency and magnitude. Coupled with landscape change that has increased fragmentation and impervious surface and decreased habitat connectivity, continued increased severity of flooding and drought in future years will lead to increased pressure on individuals and populations of Wood Turtles. As a result, maintaining landscapes that are resilient to these changes is increasingly important to consider in habitat conservation and management plans. Well-designed landscape- and watershed-scale conservation strategies can buffer the species from these increasing threats and make continued population persistence more likely.

Mesopredators

Nest Predators

Depredation of Wood Turtle nests and hatchlings by mesopredators (mid-sized carnivores) is a complex and major threat in many regions (Harding and Bloomer 1979; Brooks et al. 1992; Klemens 2000; Walde et al. 2003; Akre and Ernst 2006; Buhlmann and Osborn 2011; Cherry et al. 2015; Cochrane et al. 2015; Vraniak et al 2017; Marchand 2020) (8.17). Nest depredation rates appear highly variable: in some areas, mammalian mesopredators such as Raccoons (*Procyon lotor*) have been subsidized by anthropogenic development (Klemens 2000). At some sites

8.17—Depredation of Wood Turtle nests and hatchlings by mesopredators such as Raccoons (*Procyon lotor*) are a significant factor limiting recruitment in many regions. Nest depredation often occurs within the first few nights following egg deposition in late Spring, but may occur in August or September as hatchlings begin to emerge from the nest. Pictured: Raccoon scat intermixed with depredated Wood Turtle eggs on a nesting beach in Maine. Mike Jones where adult survivorship is relatively high, recruitment may nevertheless be minimal due to nest depredation and hatchling predation. In some well-studied Wood Turtle populations, egg depredation reaches 100% at some sites in some years (Harding and Bloomer 1979; Brooks et al. 1992).

Buhlmann and Osborn (2011) noted that Raccoons and Red Fox (*Vulpes vulpes*) were significant nest predators in New Jersey. Nest predation by American Badgers (*Taxidea taxus*) was noted by Vraniak et al. (2017) in Wisconsin. Cochrane et al. (2015) reported Badger depredation of nests in Minnesota, and also observed Striped Skunks (*Mephitis mephitis*), and Raccoons eating eggs in a Minnesota nesting area. Other mammalian nest predators include Virginia Opossum (*Didelphis virginiana*) and Coyote (*Canis latrans*).

8.18—Adult Wood Turtles are able to survive mesopredator attacks under some conditions, as evidenced by frequent (but highly variable) rates of limb loss in populations throughout their range. This female Wood Turtle in Massachusetts has survived and nested for at least fifteen years with a missing hind foot—which, for a Wood Turtle, is an extremely minor injury. MIKE JONES

Cochrane et al. (2015) also reported Common Ravens (*Corvus corax*) and American Crows (*Corvus brachyrhynchos*) eating eggs in a Minnesota Wood Turtle nesting area.

Hatchling Predators

Predators of hatchling Wood Turtles probably include every carnivorous animal larger than a Green Frog (*Lithobates clamitans*). In New Hampshire, Tuttle and Carroll (2005) report apparent depredation of hatchlings by Eastern Chipmunks (*Tamias striatus*) and birds, and speculate that Great Blue Herons (*Ardea herodias*) also eat hatchling Wood Turtles. In Ontario, Paterson et al. (2012) reported extremely high post-emergent mortality of hatchling Wood Turtles; only 11% survived from emergence to their first winter dormancy period. The authors inferred that most hatchlings had been eaten by small mammals. The mortality rate sustained by Wood Turtle hatchlings was much lower than observed in a similar sample of Blanding's Turtle hatchings in Paterson's (2012) study. Of 68 hatchling Wood Turtles monitored by Dragon (2014) in northwestern Virginia, only 17 survived to overwinter (25%), and the majority (66.7%) of deaths were due to predation, representing 50% of all hatchlings tracked. Wicklow (unpubl. data in Jones et al. 2015) reported that four monitored Wood Turtle hatchlings were eaten by Eastern Chipmunks, one was eaten by a Northern Short-tailed Shrew (*Blarina brevicauda*), one was eaten by a Striped Skunk, and two were unaccounted for.

Predators of Adults

Mammalian and avian predators can mutilate adult Wood Turtles or kill them outright (Harding and Bloomer 1979; Farrell and Graham 1991; Saumure and Bider 1998; Walde et al. 2003; Akre and Ernst 2006; Jones 2009; Parren 2013). Adult Wood Turtles are preyed upon by Raccoons (Mullin et al. 2018; Lapin et al. 2019), Snapping Turtles (Tetzlaff and Ravesi 2015), and Ravens (McCullum 2016). Adult Wood Turtles are clearly able to survive predator attacks under some conditions, as evidenced by observed limb loss in populations throughout

8.19—Adult Wood Turtles are sometimes found missing all or part of two limbs (often their front limbs). Under some circumstances these turtles can evidently survive for several years in the wild. The turtles pictured here from New England. Mike Jones

their range: 9.7% in Michigan (Harding and Bloomer 1979); 16.8% in New Jersey (Farrell and Graham 1991), 32.3% and 15.2% at two sites in Québec (Saumure and Bider 1998), 48% at two populations in Massachusetts (Jones 2009), 43.5% of males and 5.5% of females in Vermont (Parren 2013) (8.18). Rarely, adults are found missing two limbs (8.19). Often though, the attack is lethal: three of 183 turtles radio-tracked by Jones (2009) were killed by mammalian predators, which represented 15.8% of the observed mortalities. Fourteen of the 36 mortalities observed on 141 transmitting Wood Turtles in the Midwestern U.S. were the result of predation, most thought to be Raccoon attacks (Lapin et al. 2019) (8.20).

Predation of adult Wood Turtles by corvids (primarily American Crows and Common Ravens) appears to vary by site and region, and in some locations is a major conservation concern and warrants consideration in

8.20—Most mesopredator depredation is probably caused by Raccoons (*Procyon lotor*), but American Mink (*Mustela vison*) and North American River Otter (*Lontra canadensis*) are also likely mammalian predators of Wood Turtles. Sometimes, various threats can act synergistically— to lethal effect. Here, an adult female is pictured on a New England river beach after being attacked by a mink or otter. The predator removed all of the turtle's limbs and most of its face after it was displaced by a major flood in 2007. Mike Jones

8.21—Predation of adult Wood Turtles by corvids appears to vary by site and region, but in some locations is a major conservation concern. Corvid depredation warrants consideration in management planning and additional targeted research. An adult Common Raven (*Corvus corax*) from Ontario is pictured (*top*), along with several adult Wood Turtles depredated by Ravens in New Brunswick (*bottom*). Deanna McCullum & Mike Jones

management planning. In New Brunswick, McCullum (2016) observed over 48 mortalities attributed to depredation by Ravens. More than 60 dead Wood Turtles were found at two nearby sites, attributed to the same cause (8.21). Marchand (2019) observed American Crows killing adult Painted Turtles (*Chrysemys picta*) in New Hampshire.

Many of the mesopredators causing mortality in Wood Turtles across age classes are "human commensals" (Klemens 2000); that is, their populations tend to be larger in anthropogenic landscapes. Although Wood Turtles co-evolved with these species and healthy turtle populations are likely able to withstand low levels of predation of all age classes, because today's landscape supports much greater numbers of mesopredators as a result of human subsidy and lack of apex predators in most parts of the Wood Turtle's range, predation rates are likely much higher than prior to European settlement.

Summary

Wood Turtle populations throughout their range are subject to increasing, interacting, and compounding threats that suppress population viability, causing the many observed population declines and extirpations. Where these threats are relatively minimal, it is important to implement a landscape-based conservation strategy that insulates turtle populations from excessive human influence and use. Where these threats are deeply entrenched and intractable, it is sometimes more appropriate to employ site-specific and stop-gap management efforts, which can buy time if well-designed.

9. Restoration and Management

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An adult Wood Turtle rests in a New Brunswick hayfield. Shaylyn Wallace

9.1—Wood Turtle populations may be classified along gradients of habitat impairment that should be considered when deciding where, how, and when to manage for the species. This site is heavily used by farm machinery. It is bordered on one side by a railroad line and on the other by a busy commuter road. Mike Jones

Introduction

Wood Turtle habitat has been fundamentally altered by human beings throughout the species' range. No streams remain uninfluenced by anthropogenic change; even the most remote watersheds are experiencing interacting effects of climate change, invasive plant species, large carnivore collapse, or mesocarnivore release. Wood Turtles are highly sensitive to human activities including development, road construction, and recreation; therefore the most robust and stable populations persist in landscapes where there is minimal human presence (Garber and Burger 1995; Saumure et al. 2007; Jones et al. 2018; Willey et al. 2021). Although habitat impairment is widespread and even pervasive in many areas, landscapes with minimal degradation still remain. Functional populations could persist in these areas for the foreseeable future without immediate human intervention, provided the landscapes are adequately buffered from human activity (Jones et al. 2018; Willey et al. 2021). A combination of land protection and strategic monitoring of populations and habitat would benefit these noteworthy populations more than active, on-the-ground management. In these (relatively) intact systems, particularly those large and undisturbed enough to maintain regimes of moderate disturbance from flooding and beavers, habitat protection that allows the systems to function as naturally as possible is the most urgent path forward.

However, meaningful land protection for Wood Turtles—at sufficient levels to ensure the species' persistence in a given watershed for any evolutionarily significant timeframe—is often riddled with challenges and practical problems that reduce the long-term feasibility of adequate preservation (e.g., Browne and Hecnar 2007; Carroll 2018). Some of these challenges include disclosures of site-specific details as a necessary component of publicly funded real estate transactions, the prohibitive cost of preserving landscapes of sufficient size, and the societal pressure to promote and facilitate public access, which can lead to rapid attrition of turtles through collection (Garber and Burger 1995). It follows, then, that managers should strategically pursue opportunities to restore and manage Wood Turtle habitat as a realistic hedge against some failures on the land protection front, especially where it is possible to leverage local or specialized resources for projects. Strategic restoration geared toward restoring fluvial disturbance processes may also help to offset the immeasurable loss of Wood Turtle nesting habitat and overwintering habitat in streams associated with development, dams, and hydrologic alterations.

Gradients of Impairment.—Wood Turtle populations may be classified along gradients of habitat impairment that should be considered when deciding where, how, and when to manage for the species (9.1).[1] Within a management jurisdiction such as a state or a federal land agency, restoration activities should generally be directed toward sites that appear to have some reasonable chance of continued persistence without continuous management. Severely impaired populations may not be a priority to organizations and entities whose scope of work has a regional or range-wide focus, but may be the most noteworthy natural resource in a town, county, or state park. In these cases, it often makes sense to attempt interventionist management. Ultimately, habitat management initiatives geared toward restoring function to ecosystem processes will maximize the cost-benefit ratio of Wood Turtle restoration, while also benefiting other species in the system. In any case, some level of strategic planning is helpful in order to identify restoration activities that restore the greatest function within the focal site.

Delayed Population Response.—Habitat restoration for Wood Turtles is further complicated by the species' low annual reproductive output, late maturity, slow life history, and long generation time, generally meaning that population responses to any management actions will be slow (Klemens 2000; Mullin et al. 2020). Determining the real effect of restoration for any emydine turtle species will usually require years—if not decades—before detectable changes can be measured.[2] Partly for this reason, there is a notable dearth of peer-reviewed, empirical studies quantifying population-level responses of freshwater turtles to prescribed management actions (Mullin et al. 2020). This lack of direct evidence should not deter management for Wood Turtles and post-management monitoring, but rather serve as point of caution that, given the unique context and myriad factors influencing any given population, managers should take care when considering when, where, and how to manage for Wood Turtles. Monitoring frameworks should consider the practical limitations associated with a delayed population response (i.e., a necessity for long-term studies).

In this chapter we summarize the available research on restoration and management prescriptions for Wood Turtle populations. We also discuss some general considerations for planning management actions or a restoration program. We put some additional emphasis on those management actions most likely to effectively promote Wood Turtle population persistence by restoring ecosystem function such as natural stream-channel processes. We attempt to seek some congruence between the many documents already available at the state and regional level. However, we underscore two additional notes of caution: (1) without a meaningful evaluation of

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1 The precise seasonal timing—as well as distances most appropriate for management—vary across the species range, as well as from site to site, so we intentionally generalize that discussion here.

2 Note that relatively fast population response to strategic management was reported in a European Pond Turtle (*Emys orbicularis*) in southern France (Ficheux et al. 2014).

the needs of the target population, as well as the broader landscape context, improper habitat management can undermine population recovery or even promote further population decline; and (2) effective restoration will require sustained support over time, and can require immense investment of monetary resources and human effort. If management actions are supported primarily with funds that would otherwise support landscape conservation at large scales (relative to the spatial needs of Wood Turtle populations), they can easily misdirect valuable conservation resources and undermine a larger vision for regional Wood Turtle conservation.

9.2—Nesting habitats often provide some of the clearest opportunities for management, ranging from light scarification to tree removal. Here, volunteers work to scarify plots within a concentrated Wood Turtle nesting area in Massachusetts. Mike Jones

Nest Area Management

Nesting habitats often provide some of the most straightforward opportunities for Wood Turtle management, ranging from light scarification to tree removal (9.2), but are probably most effective when they are part of a management strategy geared toward increasing adult survival. Wood Turtles generally require well-drained, elevated, and exposed areas of sand and/or gravel (or other, primarily inorganic substrates) for nesting (Buech et al. 1997; see Chapter 5), but the acceptable range of nesting conditions seems to vary somewhat throughout the species' range. In relatively natural and unmanaged systems, Wood Turtles often select nesting sites that are generated and maintained by natural stream dynamics and seasonal flooding, such as instream point bars. In more cases than not, however, hydrologically altered stream systems characterized by dams, bank stabilization, and river channel alteration have disrupted the dynamism and depositional patterns of the stream such that natural nesting conditions are rare or non-existent.

9.3—In some cases, especially in areas where natural nesting features are lacking, Wood Turtle nesting areas can be improved upon by depositing piles of sand and gravel, as pictured here in New Jersey. Colin Osborn

Wood Turtle nesting areas can, in some cases, be restored, augmented, or created by clearing land to expose underlying deposits of poorly graded sand and gravel, or by depositing piles from offsite (Buhlmann and Osborn 2011) (9.3). Nesting mounds have also been constructed for other freshwater turtle species (Dowling et al. 2010; Paterson et al. 2013). Paterson et al. (2013) found that nesting mounds built for

Snapping (*Chelydra serpentina*) and Painted Turtles (*Chrysemys picta*) experienced higher use than expected—and higher nest success—compared to more natural nesting areas. Optimal artificial nesting mound dimensions have not been identified; however, a utilized nesting mound created for Wood Turtles in New Jersey by Buhlmann and Osborn (2011) was 18.2 m long, 7.6 m wide, and 1.5 m tall. Artificial nesting areas should be situated in open-canopy areas with ample sun exposure (e.g., a field or scrub/shrub mosaic) and provide a direct, unfragmented path (no intervening roads or structures) to suitable stream habitat. Spatial replication of nesting features at a site will provide turtles with a range of environmental conditions to choose from, and may reduce depredation rates, which have been shown to be higher when nests are spatially concentrated (Marchand and Litvaitis 2004).

9.4—Instream features such as point bars, sand and gravel bars, beaches, and cutbanks can be improved by proactively attempting to eradicate invasive plant species such as Japanese Knotweed (*Reynoutria* [*Fallopia*] *japonica*), or clearing openings to allow nesting at sites where invasive species are already well established. Mike Jones

Instream nesting features such as point bars, sand and gravel bars, beaches, and cutbanks in more fragmented habitats are frequently invaded by introduced plant species such as Japanense Knotweed (*Reynoutria* [=*Fallopia*] *japonica*) (Colleran and Goodall 2014; 2015), Spotted Knapweed (*Centaurea stoebe*), Multiflora Rose (*Rosa multiflora*), Autumn and Russian Olive (*Elaeagnus umbellata* and *E. angustifolia*), and Glossy Buckthorn (*Frangula alnus*), which can degrade otherwise suitable nesting areas as a result of shading, lack of open substrates, and root invasion of Wood Turtle nest cavities (9.4). Each of these species requires a specific management approach, and some eradication efforts may be impractical. In all cases, invasive and introduced plant removal efforts involving machinery, heavy equipment, or vehicles should occur outside of the Wood Turtle activity window.[3]

Managers should avoid landscape configurations that result in attractive nuisances or ecological traps, in which female Wood Turtles are attracted to nesting areas that either result in decreased adult survival rates (because of predation, road mortality, or collection), decreased nest success, or decreased hatchling survivorship. For example, it is not ideal to have suitable or attractive nesting habitat located across the road from the primary watercourse, even if the road is infrequently traveled. Nest area restoration efforts may be monitored via remote sensing cameras, providing immediate feedback about the effectiveness of management and guiding the improvement of future actions (Buhlmann and Osborn 2011; Jones, unpubl. data).

Predator Deterrents and Control.—In landscapes that support exceptionally high densities of mammalian and avian predators, rates of predation on nests, hatchlings, and/or adult Wood Turtles are known to be unsustainably high (9.5). Several management strategies have been

3 For additional discussion of the Wood Turtle activity season, see Chapter 6.

employed across the species range to reduce mammalian predation rates on turtle nests. For example, individual Wood Turtle nests can be protected with a physical transparent structure such as hardware cloth or chicken wire to reduce mammalian predation rates, often by researchers attempting to measure demographic parameters such as clutch size (Compton 1999; Jones 2009) (9.6). These protective exclosures can cause hatchling mortality if not monitored daily beginning well prior to the expected emergence of hatchlings. These exclosures are generally only permitted to be installed in coordination with state or provincial wildlife agencies. More recently, larger-scale, electric fence exclosures have been utilized to surround entire nesting areas in order to exclude mammalian predators (Wisconsin: Lapin et al. 2015; Vraniak et al. 2017; Minnesota: Markle et al. 2019). Electric fences require substantial effort to set up, might attract unwanted attention by recreationists, and have proven to be only moderately effective in some locations for protecting nests of related turtle species. In their evaluation of a long-term headstarting program, Mullin et al. (2020) noted that predator control would likely result in greater positive impact on population growth rates than headstarting young turtles. The effectiveness of predator control on the nest-success rate of wild Wood Turtles has not been specifically tested, but should be targeted for future experimental research.

9.5—In landscapes that support high densities of mammalian predators such as Red Fox, rates of predation on nests, hatchlings, and/or adult Wood Turtles are known to be unsustainably high. Mike Jones

9.6—Several management strategies have been employed to reduce mammalian predation rates on turtle nests, including individual nest protection with exclosures. Here, a Virginia Wood Turtle nest protected by a hardware cloth exclosure is shown with the lid open. Generally, the use of nest exclosures is closely regulated by wildlife agencies because some designs can easily result in hatchling mortality. John D. Kleopfer

Agricultural Land Management

Upland habitats used by Wood Turtles vary geographically and seasonally, but most Wood Turtles annually utilize land-cover mosaics that include forested and early-successional cover types, including agricultural fields. Vegetation ecotones, or edge habitats, that support structural diversity appear to play an important role for Wood Turtles by providing opportunities to balance both thermoregulation and food requirements (Compton 1999; Saumure 2004; Jones 2009). Before the intensification of agricultural machinery, agricultural lands were sources of early-successional habitat that provided areas for foraging, thermoregulation, and localized nesting opportunities.

Wherever agricultural fields are situated near Wood Turtle watercourses, machinery such as mowers, combines, tractors, plows, and harrows can pose a significant threat to Wood Turtle populations by elevating rates of adult and juvenile mortality and injury throughout the species range (Saumure and Bider 1998; Saumure 2004; Jones et al. 2018). Mortality events have been regularly documented within mowed fields (e.g., Saumure and Bider 1998; Saumure et al. 2007; Tingley et al. 2009; Jones 2009) and plowed fields (Saumure 2004; Sweeten 2008; Jones 2009). Under certain landscape configurations and times of year, relatively large mortality events can occur. Below we summarize the available research geared toward minimizing Wood Turtle mortality within active agricultural landscapes. Management of Wood Turtles in agricultural sites is particularly challenging, as resource managers must reconcile their necessity for societal means of food production.

9.7—Research in New Brunswick, Québec, and Massachusetts indicates that sickle-bar mowers result in lower rates of expected Wood Turtle mortality when compared to disc and rotary mowers, but they are less efficient and have largely fallen out of use. Hayfield mowing is pictured at Wallace et al. (2020)'s research site in New Brunswick. Shaylyn Wallace

Mowing Reduction.—Increasing the width of unmowed riparian buffers will likely benefit resident Wood Turtle populations, though these buffers need to be managed/mowed periodically during the Wood Turtle inactive season to maintain the site as early successional habitat (Tingley et al. 2009; Wallace et al. 2020). Further reducing machinery use around the margins of fields near rivers may be an effective method for reducing agricultural mortality. Wood Turtles have been observed congregating along the edges of field and shrub habitats with good solar exposure (i.e., facing south and southwest; Jones, unpubl. data). These congregation areas are often close to abandoned river meanders, ditches, damp areas, or the river itself. Wood Turtles are well-documented to heavily use both forb- and graminoid-dominated meadows and hayfields (see Chapter 5), so turtle presence should be assumed wherever hayfields, pastures, or abandoned farmland provides the most accessible early-successional habitats within a few hundred meters of the margin of a watercourse with high densities of overwintering Wood Turtles. Once fallow, fields should be mowed every one to two years during the Wood Turtle inactive season.

Type of Machinery.—Although less efficient than disc and rotary mowers (Saumure 2004), sickle-bar mowers have been shown to significantly lower expected mortality rates in proxy studies (Erb and Jones 2011; Wallace et al. 2020) (9.7). Raising mower blades above 20 cm when mowing in fields occupied by Wood Turtles may slightly reduce the overall mortality and injury rate, although there is some variability in the exact recommended mowing height. Erb and Jones

(2011) found no further reduction in expected injury rates (to proxies for real turtles) when mower heads were set below 15 cm. Wallace et al. (2020) estimated that raising the mower head to ≥17 cm might reduce mower-caused mortality by 50% (15 cm for smaller turtles). Mitchell et al. (2006) suggested 20 cm as a rough target. Even with blades set high, tractor tires may result in crushing mortality up to 46% (Erb and Jones 2011). Saumure (2004) inferred from carapace fractures that Wood Turtles head for rivers when they detect vibrations from a mower and postulated that mowing progressively from the edge of the field farthest from the river could allow some turtles to move toward the river and out of harm's way. However, the only study to specifically test this assumption found that Wood Turtles did not move from fields during mowing trials (Wallace et al. 2020). As with other methods of agricultural land management, mowing trials (and behavioral studies) would be helpful.

Grazing.—Livestock grazing has the potential to maintain upland, non-riparian areas as diverse, open-canopy, early-successional habitats, and may have value in some areas as an alternative management method to heavy machinery. Grazing areas should be located away from streams to avoid water quality degradation (9.8). The effects of large animal grazing on Wood Turtle habitat use or recruitment have not been specifically evaluated, but there is evidence that low- to intermediate-density livestock grazing is associated with an improved demographic response in Bog Turtle (*Glyptemys muhlenbergii*) populations (Tesauro and Ehrenfeld 2007). However, livestock trampling is associated with reduced recruitment rates in the European Pond Turtle (*Emys orbicularis*) in France (Olivier et al. 2010; Ficheux et al. 2014), suggesting that livestock should be excluded from nesting areas. This suite of effects—including the effects of river, stream, and brook degradation—should be specifically evaluated where feasible.

9.8—Livestock grazing has the potential to maintain large areas as diverse, open-canopy habitats, and for Bog Turtles (*Glyptemys muhlenbergii*) has been a practical management alternative to heavy machinery, but needs further study as a management technique for Wood Turtles. A dairy farm that supports a relatively large Wood Turtle population in New England is pictured. Mike Jones

9.9—Row crop agriculture can result in Wood Turtle mortality depending on the harvest date and other machinery use during the season. Rotation of a given field from corn or potatoes to a late-season crop such as pumpkins could result in annual variation in Wood Turtle mortality rates. Two radio-equipped female Wood Turtles were killed in this Massachusetts potato field in midsummer. Mike Jones

Row Crop Harvest.—Many authors have noted that the potential for row crop agriculture to result in Wood Turtle mortality is partly a function of the harvest date (Saumure and Bider 1998; Castellano et al. 2008) (9.9). Late-season crop varieties that require harvest in fall (rather than summer) may result in lower risk to Wood Turtles because many turtles will have already returned to their overwintering habitat. For this reason, the annual rotation sequence of crops with different harvest schedules (e.g., corn vs. pumpkins) will influence mortality rates in unpredictable and complex ways. Castellano et al. (2008) recommended a harvest schedule that would minimize mortality to nests and hatchlings. In the Ontario system studied by Mullin et al. (2020), the watercourse was bordered by rotational crops of soy, corn, and hay (Mullin, unpubl. data). Of these crops, hay probably posed the greatest risk to the local Wood Turtle population because of its near-monthly harvest, while corn and soy were harvested relatively late in the season.

9.10—Roads near rivers occupied by Wood Turtles seem to be associated with increased probability of extinction of local Wood Turtle populations. This New England juvenile was killed on a state highway where the road parallels the suitable stream habitat for several kilometers—a long-term management challenge for this particular population. Mike Jones

Timber Management

Logging operations near occupied Wood Turtle rivers pose several threats to Wood Turtle populations, the most significant of which is direct adult mortality resulting from the use of heavy machinery (tractors, skidders, or other equipment) during the active season (deMaynadier, unpubl. data). However, we note that the heavy machinery associated with logging operations is likely less of a potential threat than agricultural machinery, given that forests are harvested on the order of multiple decades and hayfields (for example) are harvested multiple times per year. Intensive forest management can also degrade aquatic and terrestrial habitat quality by promoting soil erosion, altering conditions in the watercourse, and introducing invasive species. Intensive forestry can alter the thermal landscape available to Wood Turtles, increasing their exposure to extreme temperatures (Hughes and Litzgus 2019). In addition, centuries of forestry have changed the structural configuration of rivers and streams (Dolloff and Warren, Jr. 2003). In some cases the extensive removal of large wood from riparian areas immediately adjacent to streams through logging has likely decreased the total availability of large wood in the form of instream logjams and other structural features such as debris dams (Silsbee and Larson 1983), a phenomenon discussed in more detail later in this chapter (see River and Stream Management).

Creation of new logging roads can increase direct mortality by vehicle strikes, while also allowing access to otherwise remote unfragmented habitat, which can facilitate the intrusion of poachers or invasive plants into the site. However, smaller-scale forestry operations such as shelterwood cuts, group selection, and patch cuts may provide opportunities to enhance Wood Turtle habitat if conducted during late fall and winter (i.e., while Wood Turtles are underwater, see Ch. 6). The indirect benefits of forest harvest may be variable across the species' range, as northern turtles may benefit more from the creation of early successional habitat. At the present moment, intensive forestry is relatively commonplace within northern Wood Turtle habitats from Minnesota to Nova Scotia, including very large areas of Ontario, Québec, and Maine. Carefully planned research should examine the spatial response of individual Wood Turtles to newly cleared habitats and the population-level response to forestry near Wood Turtle streams.

9.11—Perched culverts, such as these two sites in New England, interfere with instream Wood Turtle movements and appear to prompt turtles to move onto the roadway surface. Wood Turtles have been killed at these culvert crossings on several occasions. Mike Jones

Roadway Management

Although rates of road mortality in Wood Turtles have not often been examined, roads near occupied rivers seem to be associated with increased probability of extinction of local Wood Turtle populations (Willey et al. 2021). Roads that parallel Wood Turtle streams are particularly detrimental (9.10), especially if there are attractive early-successional habitats or nesting features on the opposite side of the road from the watercourse.

Perpendicular road crossings can also result in elevated rates of road mortality near stream and river crossing points if suitable habitat is located near the road shoulder, or if the culvert is undersized or "perched" (i.e., elevated above the low-flow waterline on the downstream end). In these cases, Wood Turtles traveling along the stream may be forced to cross existing road surfaces in order to access key resources, risking collision with cars. Numerous road-killed Wood Turtles have been found on state highways associated with perched culverts in New England (Jones, unpubl. data) (9.11). In those cases where a road already crosses a Wood Turtle stream, it is important to consider practices and redesigns of road features, including culverts or bridges, to accommodate the movements of Wood Turtles. In addition to replacing perched culvert in order to facilitate turtle passage, it is important to avoid situations where the road surface, shoulder, and/or side slopes attracts nesting females.

9.12—Full span bridges that approximate natural stream habitats, with high amounts of available light, will best accommodate Wood Turtle passage under roadways, such as this site in New England. Mike Jones

Wherever feasible, natural bank habitats will best accommodate turtle passage under roadways (9.12). In some site-specific instances, fencing or a similar barrier may be installed off the road shoulder to minimize Wood Turtle intrusion onto the roadway and encourage the use of existing culverts or bridges to travel under the road. However, subsequent monitoring of fence integrity is important because any gaps that allow passage of turtles may substantially reduce the effectiveness of the entire effort (Markle et al. 2017). In a study of related species, Yorks (2015) found evidence that opaque fencing is more effective at getting turtles to move along the fence; turtles tend to keep trying to get to the other side if the fencing is transparent and seem to take longer to move along the fencing to a passageway. This may be important for predation and desiccation/overheating risk. One study of Painted Turtles, Spotted Turtles (*Clemmys guttata*), and Blanding's Turtles (*Emydoidea blandingii*) found that turtles are more likely to use tunnels that are larger and well lit (Yorks 2015). There is a growing trend of using turtle crossing signs at road mortality hot spots, though the effectiveness of these signs has not been thoroughly evaluated (Seburn and McCurdy-Adams 2019). In some cases, these signs may facilitate the detection of Wood Turtle sites by poachers.

Roads increase the ease of human access into otherwise unfragmented habitats, allowing poachers to more easily reach population centers and potentially facilitating the spread of invasive plants. New road and stream crossings should be avoided in all possible cases near extant Wood Turtle populations.

Recreational Access Management

Wood Turtles occur on numerous scenic waterways with high value to canoeists and boaters, and are often found along coldwater trout streams that are frequently traveled by anglers. Collection of Wood Turtles for pets, even at infrequent intervals, can cause population decline and pose a long-term conservation challenge for the species (Congdon et al. 1993; Garber and Burger 1995; Compton 1999). Further, Wood Turtles are occasionally hooked by anglers (Jones and Yorks, unpubl. data; Saumure, unpubl. data in the Canadian Museum of Nature). In order to minimize encounters between recreationists, recreational access points should be relocated away from regionally significant Wood Turtle watercourses.

River and Stream Management

Wood Turtles require moderately dynamic fluvial and adjacent terrestrial habitats in order to maintain viable populations. The most important fluvial characteristics are also those that are not easily re-engineered in a restoration context: flow volume, channel slope, flooding propensity, substrate, sinuosity, and depositional tendencies.

Dam Removal.—Dams have eliminated Wood Turtle habitat by turning low-gradient stream habitat into unsuitable reservoirs and altering the downstream flow regime, which degrades nesting habitat and/or floods nests near rivers (Compton 1999; Lenhart et al. 2013). Dam managers should consider minimizing large water releases between late May and the estimated date of nest emergence (generally throughout August) on rivers with Wood Turtles and known or suspected low-lying nesting areas in order to prevent nest inundation. High flows should be allowed during early spring, before nesting, to encourage natural scouring of vegetation and redistribution of sand and gravel sediments. During dam re-permitting near Wood Turtle streams, managers should map essential resource areas and key features and determine whether nest-site creation or management is necessary as a result of the dam-induced flow regime.

Over 1,000 dams have been removed in the United States since 1970 (O'Connor et al. 2015), most within the range of the Wood Turtle in the northeastern states and upper Midwest (Foley et al. 2017), and that number is growing every year. As historic and defunct dams are removed from throughout the Wood Turtle's range, there may be rare opportunities to restore the integrity of some river systems. In these cases, returning the stream or river to its natural flow and dynamic hydrological regime will support the persistence of the natural nesting and overwintering features (9.13). Removing hardened banks and restoring sinuosity are some actions that might reduce extreme flooding and restore natural nesting features. Though such actions are expensive and difficult to undertake logistically, as part of a larger restoration effort they may be feasible. Managers and conservationists should engage in conversation with collaborative stream restoration projects throughout the species range to ensure that Wood Turtle habitat and management needs are considered as part of broader ecological restoration efforts.

9.13—In some cases, dam removal provides opportunities to restore the natural flow of Wood Turtle rivers, returning the stream to a dynamic hydrological regime (top). However, some dams counter-intuitively provide habitat in their upstream delta channels, such as this site in New England (bottom). MIKE JONES

Large Wood.—The importance of woody material—including large wood and coarse, woody debris—in stream systems has been a focal point of research in fisheries science for decades (Gregory and Davis 1992; Roni and Beechie 2012; Roni et al. 2014). Large wood in the form of fallen trees can dramatically alter the channel dynamics of small- to midsize streams, increasing the availability of deeper instream pools. However, its influence on the distribution of stream-dwelling turtles has only been suggested and not critically examined (Dolloff and Warren 2003). Nevertheless, the role of large wood in Wood Turtle streams can be inferred—at least so far as to inform a research study and some preliminary management—from decades of research on salmonids and other coldwater fish (Dolloff and Warren 2003; Floyd et al. 2008) (9.14). Floyd et al. (2008) found that the addition of large woody structures (digger logs and deflectors) improved salmonid habitat by narrowing the stream channel, scouring pools, and creating bank undercuts. By diversifying the substrates, flow patterns, and habitats within the stream channel it is likely that the addition of woody debris benefits Wood Turtles. Further, Wood Turtles will actively bask on logjams (9.15). In general, as noted by Gregory and Davis (1992) for more general applications of river restoration, management of Wood Turtle streams should maximize the diversity of instream conditions while minimizing disturbance to natural channel dynamics. Streams with extensive riparian areas devoid of mature forest are more likely to have depauperate accumulations of large wood in the stream channel, and may benefit from the direct addition of large trees (Floyd et al. 2008), though all wood should be locally sourced to limit the spread of invasive pests and diseases. Researchers should consider evaluating the association of Wood Turtles with large wood and/or accumulations of coarse, woody debris, as well as the response of Wood Turtles to experimental and controlled additions of large wood.

Beaver Control.—As ecosystem engineers, Beavers (*Castor canadensis*) can dramatically alter Wood Turtle streams in ways that are both positive and negative. Overall, the presence of beavers in large and unfragmented landscapes should be considered neutral or positive unless specifically assessed otherwise. Within landscapes that are anthropogenically unaltered, and contain ample fluvial (i.e., river or stream) habitats, beavers likely benefit Wood Turtles by generating open, early-successional conditions ideal for thermoregulation, foraging, and potentially even nesting (under certain circumstances) via tree removal, flooding, and vegetation removal. However, in relatively fragmented landscapes and/or isolated patches of Wood Turtle stream habitat where suitable nearby conditions do not exist, beavers may negatively affect Wood Turtles by degrading local fluvial habitat quality through associated increases in organic material, water temperature, and hypoxic conditions. However, the influence of beaver impoundments on the instream distribution and habitat selection of Wood Turtles has not been directly examined. Anecdotally, Wood Turtles seemed to avoid a 0.5-ha beaver impoundment in Massachusetts, but overwintered within small (<0.1 ha) beaver impoundments at several sites in New England (9.16).

9.14—Large wood can diversify substrates, flow patterns, and habitats within the stream channel, and likely benefits Wood Turtles. The role of large wood in Wood Turtle streams warrants further research as a restoration technique. Mike Jones

9.15—In addition to general instream habitat improvements associated with large wood, Wood Turtles likely benefit from the addition of large wood by actively bask on logjams and seeking shelter in the accumulated logjam. Basking Wood Turtles are pictured in northern New England. Mike Jones

In areas where beavers are not actively controlled, large areas of free-flowing stream may become impeded and sluggish with organic substrate deposition. Outright dam removal may be appropriate in some cases, or installation of flow control structures (beaver deceivers). However, managers should take into account local stream and flood dynamics before implementing dam removal or beaver management. Strong annual or interannual spring floods may naturally remove dams that impound free-flowing stream habitat. The negative impact of beaver residency on local Wood Turtle populations should be gauged as a function of impoundment duration and proportion of available, connected Wood Turtle habitat that is flooded. If Wood Turtle habitat is typically only flooded sporadically (with intervening periods of beaver inactivity), and free-flowing, instream overwintering habitat is still available, the net effects for the local turtle population are likely positive. If flooded conditions are maintained for extended periods (e.g., >2 years) and impounded areas represent the majority of available Wood Turtle habitat, managers should consider active management. For example, a population decline in the related Bog Turtle was caused by sustained beaver flooding of nesting and overwintering habitat (Sirois et al. 2014).

In heavily altered but otherwise unfragmented (e.g., by roads) stream systems, restoring natural flow regimes through dam removal and/or stream channel restoration will likely promote the availability of important habitat features within Wood Turtle streams. Most applied research involving Wood Turtles has been directed toward some manipulation of the upland environment to support nesting or foraging, but we lack rigorous evaluations of Wood Turtle response (at the individual or population level) to stream restoration efforts.

9.16—Anecdotally, Wood Turtles in Massachusetts seemed to avoid relatively large (0.5 ha) beaver impoundments, but elsewhere in New England Wood Turtles occasionally overwintered within small (<0.1 ha) beaver impoundments. The influence of beavers is probably net positive for Wood Turtles in large areas of continuous habitats, but may pose local management challenges where habitats have been severely fragmented. Here, a small beaver dam impedes a New England Wood Turtle stream. Mike Jones

9.17—In cases where confiscated Wood Turtles appear to be of wild origin, they can be genotyped to their approximate watershed basin of origin and returned to the jurisdictional state wildlife agency to determine the best possible conservation outcome. Mike Jones

Captive Management

The overarching, guiding philosophy of this book—indeed, the whole reason to write it—is the apparent fact that Wood Turtles can still be managed and conserved as wholly functional populations upon dynamic natural landscapes throughout representative portions of their native range in Canada and the United States. From this perspective, it is important to ensure adequate protections for remaining stream systems that are relatively remote from human influence and frequent human traffic. However, as a part of landscape-scale restoration activities, to restore connectivity between important Wood Turtle populations, or to "buy time" to achieve long-term management or conservation actions, it is sometimes feasible to headstart young Wood Turtles. Mullin et al. (2020)—in the only study to critically evaluate this method for Wood Turtles—found that even with headstarting, an Ontario Wood Turtle population would likely continue to decline without predator control. We recommend caution when beginning headstarting initiatives, as their real costs are immense when compounded over multiple decades. Here we essentially pass the discussion over to others who are more invested in this particular management strategy.

Regrettably, it is also the case that Wood Turtles are confiscated from illegal trade networks with some regularity by state and federal law enforcement (see Chapter 8). In our experience, the origin of these turtles is often not immediately clear (Jones and Willey, unpubl. data; Weigel and Whitely 2018). Also from our experience, it is clear that the costs of handling large confiscations can be high (Akre, Jones, and Willey, unpubl. data). Despite the high cost of captive care and uncertain outcomes or conservation value of these animals, some new tools are emerging that will improve our ability to confidently genotype animals of wild origin (Weigel and Whiteley 2018). For the time being, we recommend that seized or confiscated Wood Turtles are maintained in large outdoor enclosures separated by confiscation event and by sex to prevent uncoordinated breeding events and drowning of females by males. In cases where animals appear to be of wild origin, they should be genotyped to basin of origin and returned to the jurisdictional state wildlife agency to determine the best possible conservation outcome (9.17).

Summary

Across their range, important Wood Turtle populations have not yet been afforded sufficient protection from development, fragmentation, or human traffic. For Wood Turtle populations to persist as evolutionarily functional components of the North American landscape without decades of expensive intervention, protecting these exceptional landscapes should be the paramount priority. At present, it is not clear that this is feasible. Given the vast extent of Wood Turtle habitat lost to (or degraded by) habitat fragmentation and hydrological alterations, it follows that restoration activities should be pursued aggressively where the potential benefit outweighs various risks to the local or regional population. Some methods of managing upland habitat—such as minimizing machinery use in fields, or rejuvenating nesting areas—are likely to work in the short term. Management costs over longer durations will remain high in the long term, however, since these strategies do little to restore ecosystem function. Long-term restorative management actions, such as stream channel restoration, large wood additions, and—where practical and with some awareness of larger food supply chains—strategic retirement of agricultural fields near important Wood Turtle streams are generally cost-prohibitive, but are likely to improve the long-term viability of local Wood Turtle populations without the need for constant management. Where these actions are feasible—even if they are principally geared toward landscape restoration and not Wood Turtle conservation—researchers should endeavor to study, monitor, and evaluate Wood Turtles' individual- and population-level response to management, as well as the response of associated species of conservation concern.

10. A Conservation Vision

Michael T. Jones, Lisabeth L. Willey,
H. Patrick Roberts, Thomas S. B. Akre

Adult male Wood Turtle in New England. Mike Jones

10.1—Relictual and remnant Wood Turtle populations—as well as individual Wood Turtles—may still be found in a wide variety of stream conditions from Nova Scotia to Minnesota to Virginia, conveying an appearance of versatility and adaptability and masking the extent of recent decline. An isolated population has persisted for more than 15 years at extremely low population levels—evidently fewer than five adult Wood Turtles—in this small stream in central New England, but it is generally not an ideal target for regional conservation resources. Mike Jones

Despite startling levels of recent habitat loss and troubling demographic trends throughout much of the historic range, we remain hopeful there is a strategic path forward to ensure the survival of the Wood Turtle as an evolutionary lineage *in the wild*. We conclude this book with suggestions for a conservation vision aimed at protecting the evolutionary potential of the species. We emphasize conservation measures that reflect temporal and spatial scales relevant to the life history, ecology, and behavior of this unusual species.

Wood Turtles are still regularly found throughout their pre-colonial geographic range, superficially conveying the appearance of versatility and adaptability to human-dominated environments (10.1). In reality, however, the majority of occurrences seem to represent relictual and remnant populations that continue to persist on the landscape due to the remaining individuals' longevity, but which may be functionally extinct from an ecological and demographic perspective. In general, it is a mistake to presume that Wood Turtles can be easily conserved—through land protection or through the application of best management practices—within relatively small sections of those streams where Wood Turtles have been simply documented to occur.

Successful conservation of Wood Turtle populations—as for any threatened vertebrate—will be imagined and measured in multiple generations, a difficult proposition considering the rapid pace of anthropogenic change. At more than 30 years, the Wood Turtle's generation time is relatively long among terrestrial North American vertebrates. Therefore, conservation and management of this species will require a temporal outlook of a century or more, rather than a decade. This often-overlooked time horizon can prove challenging for conservationists to envision (van Dijk and Harding 2011; Jones and Willey 2015), but must be central to any conservation plan or management strategy at the scale of the entire species' range. Management actions will have little positive influence on local Wood Turtle populations unless they are fundamentally long-term (i.e., multi-decade) in nature.

Furthermore, demographically stable and resilient Wood Turtle populations require long-term landscape complementarity. That is, a configuration of landscape features that reliably maintains important resources within close spatial proximity. Wood Turtle survival and recruitment are generally higher where there is pronounced convergence of suitable stream geomorphology and substrate, nesting site availability, stable in-stream overwintering sites, abundant in-stream woody structure and terrestrial basking areas, and upland vegetation consisting of diverse mosaics of varying successional stages. When these conditions coincide with low levels of roads, development, human recreation, and intensive agriculture in the surrounding uplands (i.e., low mortality across age classes), Wood Turtle populations will generally show demographic resilience necessary for long-term persistence (Chapter 7). Among stream-dwelling or fluvial North American turtles (10.2), the Wood Turtle is unusual in its tendency to spend many months active on land; among the terrestrial North American turtles, the Wood Turtle is noteworthy for its tendency to spend many months underwater (10.3).

10.2—Other North American turtles that are primarily stream-dwelling (i.e., they exhibit fluvial habitat requirements), such as (*from the top*) Western Pond Turtles (*Actinemys* spp.), Sonoran Mud Turtles (*Kinosternon sonoriense*), and Flattened Musk Turtles (*Sternotherus depressus*), do not generally forage extensively on land. Mike Jones

Fortunately, adult Wood Turtles appear to exhibit pronounced fidelity to these locations over decades with minimal rates of inter-annual home range drift or dispersal away from familiar areas (Compton 1999; Compton et al. 2002; Jones 2009), suggesting that documented areas of Wood Turtle occurrence will remain relatively stable over time, allowing for the implementation of long-term conservation or restoration programs. However, it is abundantly clear that landscape complementarity for Wood Turtles is not maintained naturally without unimpeded disturbance dynamics (e.g., seasonal flooding that periodically generates and maintains critical nesting, foraging, overwintering, and basking areas). Thus, the conditions that generally promote robust, stable, or resilient Wood Turtle populations are often influenced by conditions upstream in the

10.3—Other strongly terrestrial North American species such as the box turtles (e.g., *Terrapene carolina carolina,* pictured at left) and gopher tortoises (e.g., *Gopherus polyphemus*, pictured at right) utilize varied upland habitats that are not further constrained by the need to be near a suitable stream or river. Mike Jones

watershed—including areas that may not support Wood Turtles. Indeed, relative Wood Turtle abundance has been shown to be best-predicted by variables at broad scales (e.g., greater than 5 km; Jones et al. 2018) reflective of watershed habitat integrity. While the spatial footprint of a typical Wood Turtle subpopulation may appear relatively small in comparison to the watershed, it is clear that protection of the broader landscape and associated ecological processes must be central to Wood Turtle conservation initiatives if they are to be sustainable in the long-term without intervention.

While landscape-oriented conservation is a challenging task, permanently protecting critical habitat and preserving stream disturbance dynamics in areas that still support robust populations represents a longer-lasting and more cost-effective approach than continual deployment of intensive management actions that are short-term in nature and challenging to assess. Relatively intact landscapes still exist that support self-sustaining Wood Turtle populations. Given this reality, we argue that it is essential that resources devoted to range-wide and/or regional conservation are used to identify and protect those rare watersheds that are: (1) not fragmented or otherwise degraded by roads, development, recreation, or agriculture, particularly within 300 m of streams (but see Carroll 2018); (2) characterized by natural flood dynamics (i.e., limited human impoundments, bank stabilization, and channelization); and (3) documented to support robust Wood Turtle subpopulations that ideally exhibit typical metapopulation dynamics (i.e., varying reproductive and survival rates, successful immigration and emigration). Through targeted land protection and conservation easements of key locations within priority watersheds, and a successful landscape-scale conservation strategy within the basin, it can be possible to achieve not only population persistence over multiple Wood Turtle generations, but also levels of gene flow to sustain genetic connectivity and diversity. Because comprehensive protection of entire watersheds will be unfeasible in nearly all cases, conservation efforts within watersheds will require a multi-pronged strategy that: (1) prioritizes as much land protection as possible within optimal habitat; (2) minimizes anthropogenic stressors; and (3) restores or maintains natural fluvial dynamics to Wood Turtle streams.

Though large landscape protection can achieve a variety of conservation goals for this species, an additional challenge at the forefront of Wood Turtle conservation is that of collection by humans. The removal of Wood Turtles from the wild will continue to undermine conservation efforts directly, through the loss of adult turtles, but also indirectly, by discouraging open sharing of spatially explicit site information, even for conservation purposes. Illegal collection should

10.4—The strategic protection of functional, core wetland and riverine habitats and surrounding uplands must remain the priority for regional conservation partnerships. While true for Wood Turtles, it is also the case for related species across North America such as (*clockwise from top left*) the Bog Turtle (*Glyptemys muhlenbergii*), Spotted Turtle (*Clemmys guttata*), Blanding's Turtle (*Emydoidea blandingii*), and the western pond turtles (e.g., *Actinemys pallida*, pictured), among others. Mike Jones

remain a high priority for federal and state law enforcement, and we highlight that the primary emphasis should remain on preventing the *original collection*, and less on how to manage the individual turtles that are seized or confiscated. The Wood Turtle could benefit from a federal permitting system that places the burden of proof for legal acquisition on the seller/buyer/owner rather than law enforcement officers. At present, the species is easily laundered in and out of states that do not protect the species under state law. Neither land protection or management actions can counter the effects of removing reproductive adult Wood Turtles from populations. Ultimately, if progress is not made in curtailing the expansion and continuation of illegal collection, our general conservation approach will be undermined.

While we contend that landscape-oriented conservation actions outlined thus far represent the most promising actions for preserving the evolutionary potential and long-term persistence of the Wood Turtle, we recognize they are not realistic possibilities for conservationists within portions of the species range where landscapes and fluvial systems are more degraded. Too much emphasis on the highest-quality habitats does not adequately represent the importance of less intact habitats that provide important connectivity between intact or dynamic landscapes. We maintain that valuable actions can still be implemented within human-dominated portions of the range that can have a positive impact for Wood Turtle conservation as a whole (and see Wiedenfeld et al. 2021). For example, in degraded streams, progress can be made through restoration of the original river channel, experimental addition of large wood, nest area management, time-of-year restrictions for machinery in hayfields and pastures, and/or targeted law enforcement efforts (Chapter 9). It is important to acknowledge, however, that while these options may be locally sustainable, they are often expensive and require nearly constant maintenance when compared to the theoretical ideal of conserving naturally functioning fluvial systems within unfragmented landscapes. Furthermore, when considering the monetary and logistic challenges of these management actions within the context of the life history of the Wood Turtle (extremely slow population growth even under favorable conditions), it becomes clear that such strategies require a long-term (multi-decade) outlook to achieve positive outcomes. However, despite our emphasis on large-landscape conservation—and our insistence that individuals not be confused for functional populations—based on our own experience with many extremely small Wood Turtle populations in urbanized landscapes, we acknowledge the value of attempting restoration efforts with local resources.

Of course, there are also strategies that aim to actively manage the populations themselves, such as captive breeding, repatriation of confiscated turtles (Jones et al. 2018), and headstarting juveniles from wild nests (Mullin et al. 2020). On one hand, many of the contributing authors to this book have been involved in such intensive population management, but these methods are not central to the range-wide stability of the species. While these methods may eventually prove valuable in buying time for small populations within areas of marginal habitat suitability and may have important educational or support-building outcomes, scientific evidence for such a strategy remains lacking. On the other hand, if population management is conducted responsibly and effectively, based on a sound understanding of the local population, there may be value in bringing public attention to the conservation needs of the species. There may also be meaningful applications of population management as part of a landscape-focused conservation program, but actions should be taken to ensure such efforts do not distract and pull resources from the landscape-level needs of the species. The best possible outcome of direct population management through headstarting, in our judgment, is leveraging the headstarting program for meaningful landscape-level habitat restoration programs.

But in the end, the ultimate factors that will influence sustainable Wood Turtle conservation outcomes on evolutionary timescales are mostly related to the strategic conservation and restoration of large landscapes that encompass whole rivers and their floodplains. In our experience, some of the best examples of effective landscape-level conservation for Wood Turtles have been stitched together accidentally from patchworks of public and private land. Strategic protection of functional core habitats and surrounding upland must remain the priority for regional conservation partnerships. While large landscape conservation, management, and restoration informed by natural disturbance regimes is clearly the driving conservation need for Wood Turtles in most of their range, it is also a necessary component of successful conservation strategies for related, widespread, semi-terrestrial turtles, such as the Bog Turtle (*Glyptemys muhlenbergii*), Spotted Turtle (*Clemmys guttata*), Blanding's Turtle (*Emydoidea blandingii*), and western pond turtles (*Actinemys* spp.)(10.4), as well as countless other wetland-dependent species.

We close this volume with an acknowledgment of the proverbial elephant in the room: the climate conditions that have prevailed over the past several decades of Wood Turtle inventory and monitoring and research are not what we should expect in coming decades. Some perennial streams will seasonally run dry. Many will flood severely at inopportune times. Coldwater streams will transition to warmwater habitats. Invasive plant species will continue to proliferate in sensitive riparian areas. The specific effects of climate change at the site level are largely unpredictable, and this uncertainty further argues for dedicated efforts to conserve large, dynamic, diverse, and resilient landscapes where feasible to mitigate these changes (see Anderson et al. 2014; Baldwin et al. 2018).

Biology and Conservation of the Wood Turtle provides information for the interpretation, study, and conservation of the Wood Turtle and associated ecosystems. It is our hope that the collaborative and interdisciplinary nature of this book will provide guidance at the federal, state, and local level to accelerate appropriate land conservation, management, and restoration efforts. With this volume, we primarily provide generalized recommendations derived from years of field experience and a review of the existing scientific literature; however, given the broad geographic range of the species, which spans numerous ecological and jurisdictional zones, we urge all managers and conservationists to develop local and site-specific strategies. Last, because incidental and commercial collection of Wood Turtles remains a pervasive, accelerating, and often underperceived threat to local populations and the species as a whole, it is important that the conservation community continue to think creatively about this issue in addition to best methods for sharing important spatial information about conservation priorities without further compromising priority populations (10.5).

10.5—As conservation biologists and managers, we must continue to think creatively about how to share important spatial information about conservation priorities without further compromising priority Wood Turtle populations. It is also essential to continue to pursue the conservation and restoration of large, forested landscapes centered on suitable streams and rivers. Pictured: Wood Turtle habitat in West Virginia. Donald Brown

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BIOLOGY & CONSERVATION *of the* WOOD TURTLE

"Wood Turtles are one of the most iconic and beautiful reptile species of the northern United States, and they are rapidly disappearing. Jones and Willey have brought together the latest information on the species' ecology and conservation status in this wonderful edited volume. It belongs on every turtle lover's bookshelf."

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The Wood Turtle has experienced significant population declines across its range in the United States and Canada, where it is a species emblematic of cool, remote, clean rivers from Nova Scotia to Minnesota and south to Virginia. This richly illustrated book is the first solely dedicated to the natural history, ecology, and conservation of the Wood Turtle. More than 20 scientists and managers from across the species' range have collaborated in this volume to explore the Wood Turtle's evolution, landscape ecology, distribution, habitat, biology, and behavior, and to evaluate its conservation needs and outlook.

Michael T. Jones, Ph.D., is currently the state herpetologist with the Massachusetts Division of Fisheries and Wildlife. Lisabeth L. Willey, Ph.D., is a faculty member at Antioch University New England. Mike and Liz have studied Wood Turtles throughout New England for 18 years.

The Northeast Wood Turtle Working Group was formed in 2009 within the Northeast Partners in Amphibian and Reptile Conservation (NEPARC) to collaboratively pursue conservation planning and management for this widespread species of conservation need.

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