Ecology & Conservation of the Wood Turtle

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Mike Jones and Liz Willey • Editors

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Introduction

The North American Wood Turtle (*Glyptemys insculpta* LeConte 1830[1829]) is a semi-terrestrial riverine and riparian species. Its current distribution includes large portions of the eastern forest from Cape Breton Island and mainland Nova Scotia, throughout New Brunswick, southern Québec, New York, and New England to the mountains and Piedmont of Pennsylvania, New Jersey, Maryland, West Virginia and Virginia. To the west, Wood Turtles are associated with the forested regions of the northern Great Lakes from Ontario, New York, and Michigan to the Upper Mississippi basins of Minnesota, Wisconsin, and Iowa. Wood Turtles are known to occur naturally in twelve of the thirteen northeastern United States, from Maine to West Virginia and Virginia; as such, the Northeast Region comprises the largest contiguous portion of the Wood Turtle's current range.

The Wood Turtle has been identified as an extremely high-value focal species for landscape scale conservation in the northern forest (Beazley and Cardinal 2004). At present, the Wood Turtle is of conservation concern throughout a majority of its natural range, considered "Endangered" by the IUCN and "Vulnerable" by NatureServe (van Dijk and Harding 2011). The Wood Turtle is listed on the Wildlife Action Plan (WAP) of all thirteen northeastern States (NEPARC 2010), and is considered "secure"(S4) in only two states (Maine and Maryland) and as a result is considered a G3 "Vulnerable" species by NatureServe. Biologists have expressed concern for over thirty years that the Wood Turtle appears to be declining throughout its range, and no less so in the northeastern States. Quantifiable evidence of decline has grown substantially since the 1990s but is still lacking, or is insufficiently broadscale to conclusively demonstrate regional collapse.

In a 1995 response to a listing petition the previous year (RESTORE: The North Woods et al. 1994), the U.S. Fish and Wildlife Service (Amaral 1995) rejected a Threatened status listing because of "...the inadequacy of existing data to support the contention that the Wood Turtle has undergone rangewide decline or that the threats identified in the petition are affecting Wood Turtle populations across all or a significant portion of its range to the extent that the species is likely to become an endangered species in the foreseeable future." The USFWS is currently considering a proposal by the Center for Biological Diversity (2012) to list the Wood Turtle as Threatened as part of a proposal to list 53 amphibians and reptiles.

In this document we provide an review of published and technical literature, including a detailed summary of population declines and threats to population persistence.

General Reviews and Major Studies

Excellent summary accounts of the Wood Turtle have been provided by Pope (1939), McCauley (1945); Carr (1952), Ernst (1972), Harding and Bloomer 1979; Ernst et al. (1994); Ernst and Lovich (2009), and others (Compton 1999; Akre and Ernst 2006; COSEWIC 2007).

Intensive, multi-site, or long-term studies of Wood Turtle ecology in the Northeast Region have been undertaken in Maine (Compton 1999; Compton et al. 2002), New Hampshire (Carroll 1991, 1999; Tuttle and Carroll 2003; 2005; Jones 2009), Vermont (Parren 2013), Massachusetts (Jones 2009); Connecticut (Klemens 1993; Garber and Burger 1995), New York (Carroll and Ehrenfeld 1978), New Jersey (Harding and Bloomer 1978; Farrell and Graham 1991; Castellano 2008), Pennsylvania (Kaufmann 1992; Kaufmann 1995; Ernst 2001), Virginia (Akre 2002; Akre and Ernst 2006; Sweeten 2008); and West

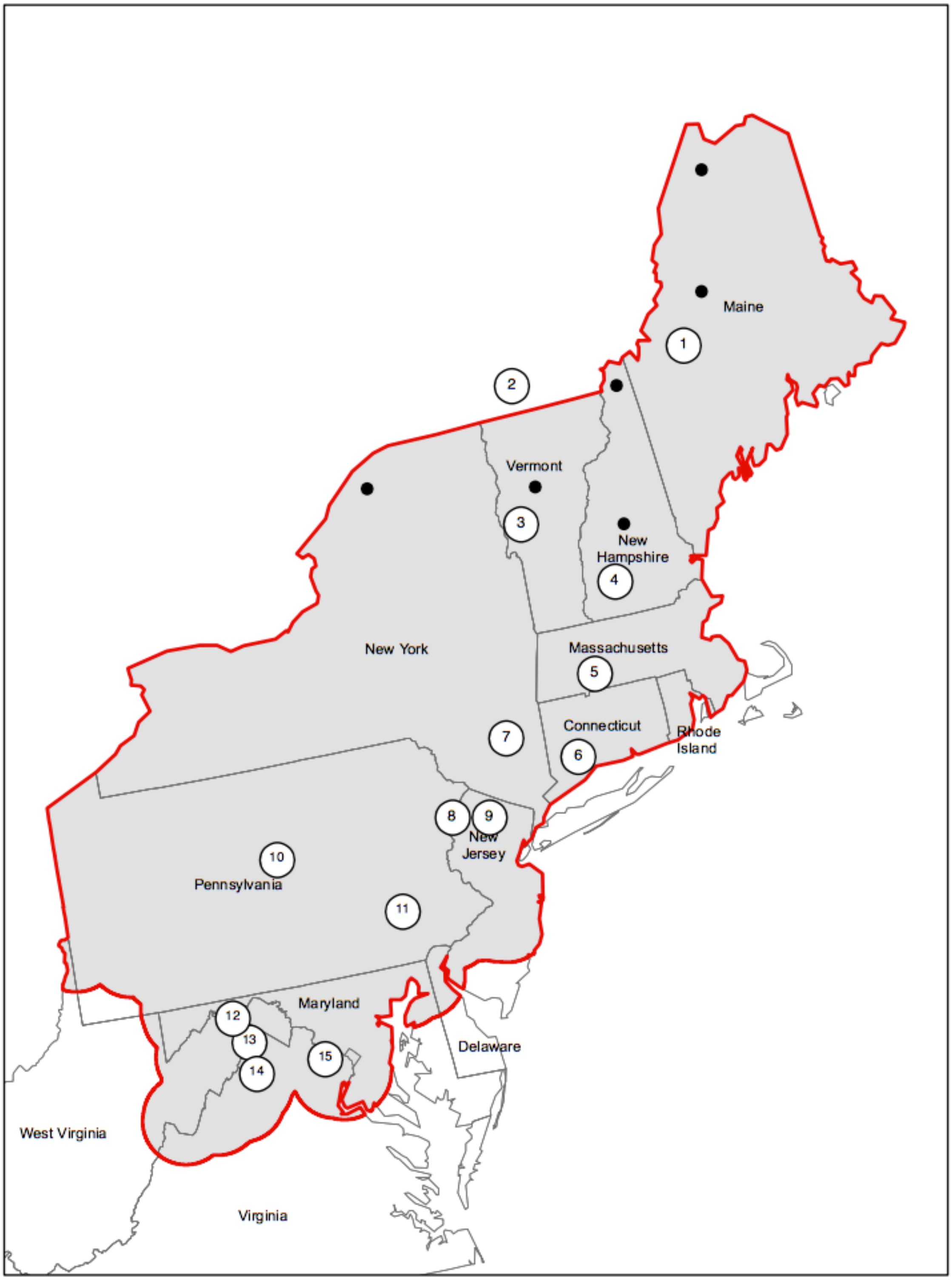

Figure 1. Intensive, long-term, or multi-site studies of wood turtle ecology in the Northeast Region: [1] Maine (Compton 1999; Compton et al. 2002), [2] southern Québec (Saumure 2004; Daigle and Jutras 2005; Saumure et al. 2007); [3] Vermont (Parren 2013); [4] New Hampshire (Carroll 1991, 1999; Tuttle and Carroll 2003; 2005; Jones 2009), [5] Massachusetts (Jones 2009); [6] Connecticut (Klemens 1993; Garber and Burger 1995), [7] New York (Carroll and Ehrenfeld 1978), [8,9] New Jersey (Harding and Bloomer 1978; Farrell and Graham 1991; Castellano 2008; Buhlmann and Osborn 2011), [10,11] Pennsylvania (Kaufmann 1992; Kaufmann 1995; Ernst 2001), [12] West Virginia (Niederberger 1993; Niederberger and Seidel 1999; Breisch 2006; Spradling et al. 2010); [13, 14, 15] Virginia (Akre 2002; Akre and Ernst 2006; Sweeten 2008). Black dots indicate intensive, multi-site, unpublished studies underway. Locations are generalized.

Virginia (Niederberger 1993; Niederberger and Seidel 1999; Breisch 2006). Major published studies and studies underway are shown in Figure 1.

Species Description

The Wood Turtle is medium-sized turtle with a broad, flat, ovate, lightly to strongly keeled carapace (Surface 1908, p. 158; Logier 1939; Ernst and Lovich 2009, p. 251; Figure 2), serrated posteriorly. The scutes of the carapace may be lightly pyramidal and typically number 39 as follows (Storer 1840, p. 210): 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, p. 158), with or without radiating or reticulated yellow-gold and blackish markings, and with or without "concentric and radiating striae (Storer 1840, p. 210)". 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. The posterior margins of the carapace are serrated (Vogt 1981, p. 94), and sometimes strongly flared (Surface 1908, p. 158), especially in males. The plastron is notched posteriorly, yellowish-cream or horn-colored with prominent blackish pigmentation located posteriolaterally on each plastral scute (Surface 1908, p. 158–159; Vogt 1981, p. 94), except in tannin- or iron oxide-stained animals, which may be obscured by reddish brown coloration. Similar black blotches are found on the ventral surface of the marginal scutes (Babcock 1919, p. 403). Like the carapace, the plastron accumulates growth rings visible in the outer layers of keratin. These are added along the medial and cranial edges of each plastral scute. New growth is often evident as lighter-colored annuli along the plastral midline.

The head, outer surfaces of the forelimbs, and tail of Wood Turtles are typically black. The neck, forelimbs, and hind feet are often bright orange to red in both males and females (Ernst 1972, p. 125.1), but may be dull yellowish in some individuals. Color may vary in intensity seasonally or geographically (Harding and Bloomer 1979) or by sex (Ernst and Lovich 2009, p. 251). Wood Turtles from the Great Lakes region are often said to have have light yellow or yellow-orange limbs and neck, with more reddish-orange tones seen in the Appalachian region (Harding and Bloomer 1979; Ernst and Lovich 2009, p. 251). The nape of the neck and throat may be dark gray, and the throat may be adorned with yellow in young individuals. 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 the beak. Some adults possess a prominent golden ring in the iris; the function of which is unknown (Figure 2L and 3C).

Male Wood Turtles are larger than females. Lovich et al. (1990) reported that males are approximately 1.07 to 1.1 times larger than females. Our data from Maine, New Hampshire, and Massachusetts correspond with this estimate (1.1, 1.08, and 1.06, respectively; M. Jones and L. Willey, unpublished data). Additional morphometric data for adult Wood Turtles are presented in Table 1.

Adult males have long, thick tails with the cloacal vent equal to or posterior to the carapace rim, a strongly concave plastron, and heavy scales on the forelimbs (Figure 2). Males have heads that are absolutely and relatively larger than those of adult females (Akre 2002). Ernst and Lovich (2009, p. 251) report that some older males have carapace indentations at the bridge. Jones and Compton (2010, p. 71) report an unusually large male Wood Turtle (SCLmax=251 mm) from northwestern Maine.

Ernst (1972, p. 125.1) provides additional references for technical descriptions of the skull, shell, seam contacts, cervical vertebrae, nasal choanae, arterial canals of the ear, and penis (Romer 1956; Parker 1901 and Zangerl 1939; Tinkle 1962; Williams 1950; Parson 1960 and 1968; McDowell 1961; Zug 1966). Hatchlings may appear to be uniform gray-brown, with a mottled grayish plastron and no carapace keel (Vogt 1981, p. 96). Adult coloration is usually evident by the third year in the wild (Figure 3). Of 500 hatchlings measured by Dragon (unpubl. data) in northwestern Virginia in 2012–2013, the average shell dimensions were as follows: SCL: 35.4 (30.4–39.5) mm; SPL: 29.70 (24.4–34.2) mm; carapace width: 35.0 (25.7–41.0) mm; mass: 9.7 (6.4–12.3) g. These measures appear consistent with those reported throughout the range (Ernst and Lovich 2009).

Key descriptive features of the Wood Turtle are as follow:

- females are typically 170–200 SCLmin; males up to 11% larger; maximum reported SCLmax is 251 mm;
- carapace with low keel, brown to black, solid in color or with radiating or reticulated yellow marks or spots, with or without "sculpted"appearance;
- plastron cream to white with twelve black pigment blotches located on each plastral scute (the plastron may be stained brown with tannins or iron oxide in some areas);
- solid (unstriped) red, orange, or yellow coloration on neck, forelimbs, and hind feet;
- head, outer surfaces of forelimbs, and tail are black.

Table 1. Summarized morphometric data from throughout the Wood Turtle range. In each case, the number in parentheses indicates the number of turtles weighed.

		Females			Males			
State/ Prov.	**Site**	**SCLmin (mm)**	**Mass (g)**	***n***	**SCLmin (mm)**	**Mass (g)**	***n***	**Source**
QC	Mauricie	201.1±10.9	1083±168	83	214.5±4.2	1173±252	55	Walde et al. (2003)
QC	Brome Co.	181.0±5.51	881.7±92.91	12	193.9±9.0	1008±147	15	Saumure & Bider (1998)
QC	Pontiac Co.	200.5±11.6	1061±127	10	215.6±22.3	1219±361	9	Saumure & Bider (1998)
ON	Sudbury Dist.	195±5	1099±127	21(18)	205±19	1152±238	15(13)	Greaves & Litzgus (2009)
MI	Upper Pen.	182	-	105	200	-	86	Harding & Bloomer (1979)
ME	Aroostook Co.	189.1±8.5	1060±145	69	207.2±10.6	1231±156	60	Jones & Willey (2013b)
ME	Somerset Co.	181.1±7.5	1006±100	102	196.2±8.1	1114±119.2	51	Jones & Willey (2013b)
ME	Somerset Co.	193.7±10.3	1121±174	23(29)	201±13.2	1210±179	9(11)	B.W. Compton (unpubl. data)
NH	Coos Co.	184.3±8.6	973±126	37	200.4±10.1	1116±150	28	Jones & Willey (2013a)
NH	Grafton Co.	174.8±9.9	865.9±111	66	189.3±8.9	973±133	54	Jones & Willey (2013a)
MA	Conn. R.	171.8±7.67	875±121	83(12)	182±7.57	872±121	83(15)	Jones et al., unpubl. data
MA	Deerfield R.	170.9±7.0	830±37	37(14)	184.4±7.5	889±102	42(16)	Jones et al., unpubl. data
MA	Berkshire Co.	176.8±10.4	911±160	9(8)	185.4±6.27	939±91	18(16)	Jones et al., unpubl. data
MA	Westfield R.	172±7.6	854±96	64(19)	186±9.6	887±120	49(2)	Jones et al., unpubl. data
NJ	Passaic Co.	165	-	464	178	-	311	Harding & Bloomer (1979)
NJ	Sussex Co.	170.9±9.3	NA	49	177.0±8.9	NA	69	Farrell & Graham (1991)
VA	Fairfax Co.	185±9.5	NA	78	195±12.5	NA	43	Akre (2002)
WV	E. Panhandle	179±9.6	846.7±174	15	190.6±12.2	932±178	16	Breisch (2006)

Figure 2. Appearance of the wood turtle. The carapace of the wood turtle is gray to brown to black when dry (A). Yellow radiating lines, vermiculate markings, or spots may be evident when the shell is wet (B–D). Turtles from iron-rich seeps are occasionally stained from iron oxide (E and J) and tannins may also discolor turtles. The wood turtle plastron is typically horn, cream, yellow, or white with bluish black pigment spots posteriolaterally on each plastral scute (F–H). Young turtles <15–20 years exhibit new growth as light-colored annuli near the plastral midline (H). Old adults may become completely worn and depigmented (I). The limbs and neck are orange, reddish, or yellow, and the head and outer forelimbs and tail are black (K and L). Some adults, especially males, exhibit a golden iris (L). Photos © Michael T. Jones

Figure 3. Male and female wood turtles are strongly dimorphic. Males are approximately 1.1 times larger in shell dimensions and approximately 1.2 more massive. A comparison of a female (L) and male (R) is provided in photo (A). Males have concave plastra (A and B) and large tails with the cloaca posterior to the margin of the carapace (B). Mature males have heads that are proportionally larger than females, and heavy scales on the forelimbs (C). Females have narrower heads and smaller scales on the forelimbs (D). Photos © Michael T. Jones

Figure 4. Hatchling wood turtles are gray or brown with a rough carapace, serrated posterior marginals, and relatively long tail (A). The plastron is mottled bluish-black, black, gray, yellow, or brown (B and E). Adult coloration of the limbs is evident within the first or second year of growth, as pictured in this two- year-old from Maine (C). A profile image of a submerged hatchling is presented in (D). A single clutch of Massachusetts hatchlings is shown in (E). Photos © Michael T. Jones

Taxonomy and Nomenclature

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 species in the genera *Actinemys*, *Clemmys*, *Emydoidea*, *Emys*, and *Terrapene* of North America and Europe (Figure 4). The Wood Turtle was classified in the genus *Clemmys* (Ritgen 1828) for most of the 20th century (Strauch 1862, p. 104; Babcock 1919, p. 403). In the sense of McDowell (1964), *Clemmys* encompassed three North American species in addition to the Wood Turtle: the spotted turtle (*C. guttata*), bog turtle (*C. muhlenbergii*), and western (or Pacific) pond turtle (*C. marmorata*). Holman and Fritz (2001, p. 323) note that McDowell's arrangement of *Clemmys* was based on plesiomorphic (basal) rather than synapomorphic (derived) traits, including the unhinged, buttressed plastron with bony bridges, and the lack of a scapular suspensorium as described by Bramble (1974). Beginning in the late 1980s, several authors critically explored the relationships within *Clemmys* (Gaffney and Meylan 1988; Lovich et al. 1991) and several authors subsequently provided evidence that the traditional genus *Clemmys* was made paraphyletic by not including the sister genera *Emys* and *Emydoidea* (which are more closely related to *Actinemys* [=*Clemmys*] *marmorata* than to either *G. insculpta* or *G. muhlenbergii*) and possibly also *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 2012, p. 75). Burke et al. (1996) speculated on possible reconfigurations of the emydine taxa to reflect the clear paraphyly of *Clemmys*, including 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) and Feldman and Parham (2002) reassigned the Wood Turtle from *Clemmys* to *Glyptemys* (Agassiz 1857) and *Calemys* (Agassiz 1857), respectively. *Glyptemys* and *Calemys* occur on the same page in the original publication by Agassiz (1857, Vol. 1, p. 443), but because the former was selected by Holman and Fritz (2001), it was determined to be the correct genus for both species. Although the final taxonomic schemes reflecting the relationships within the Emydinae are contentious, concerns pertain primarily to the genera *Actinemys*, *Emydoidea*, and *Emys*, and all authors agree that the wood and bog turtles form a living monophyletic clade (Bickham et al. 1996; Burke et al. 1996; Lenk et al. 1999; Holman and Fritz 2001; Feldman and Parham 2002). For further discussion, see Crother (2012, p. 75). The genus *Glyptemys* is described by Holman and Fritz (2001, p. 324; 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 carotico-pharyngeale 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."

The type locality for *G. insculpta* is the northern United States, restricted to New York City vicinity by Schmidt (1953, p. 92). Synonyms follow (adapted and revised from Jones 1865, p. 118; Fowler 1906; Babcock 1919, p. 403; Ernst 1972, p. 125.1; Vogt 1981, p. 94; Bowen and Gillingham 2004, p. 5; Saumure 2013):

Emys pulchella	Sweigger 1814, p. 34
Emys scabra	Say 1825*, 210
Testudo insculpta	LeConte 1830, p. 112
Terrapene scabra	Bonaparte 1830, p. 157
Emys speciosa	Gray 1831, p. 26
Emys speciosa var. *levigata*	Gray 1831, p. 26
Emys inscripta	Gray 1831, p. 26
Emys insculpta	Harlan 1835, p. 152
Clemmys insculpta	Fitzinger 1835, p. 124
Clemmys insculpta	Strauch 1862
Geoclemys pulchella	Gray 1856, p. 18
Glyptemys insculpta	Agassiz 1857, p. 443
Glyptemys pulchella	Gray 1869, p. 196
Chelopus insculptus	Cope 1875, p. 53
Clemmys insculpta	McDowell 1964
Glyptemys insculpta	Holman and Fritz 2001

* Storer (1840, p. 210) and Ernst (1972) report that Say's (1825) *E. scabra* synonymy is erroneous (misidentified and placed with *Testudo scabra* L.)

Habitat

Some of the earliest reports on the suitable habitats of Wood Turtles include those of LeConte (1829; p. 113). Holbrook (1838; p. 19) repeated LeConte's observation that the species resides in ponds and rivers, but frequently leaves the water. Storer (1840, p. 209) also claimed that the species "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.*" Thoreau (2009; many entries between 1855–1860) provided some of the most detailed 19th century observations of Wood Turtle ecology, and was probably the first to notice Wood Turtles' localized preference for copious amounts of sand. By the mid- to late-19th century, many authors recognized the basic amphibious nature of Wood Turtle life history, including Thoreau (2009) in Massachusetts; Jones (1865; p. 118) in Nova Scotia (who reported *G. insculpta* as terrestrial but sometimes ventures into lakes); Allen (1868; p. 175) in Massachusetts; Huse (1901, p. 49) in New Hampshire, and Fowler (1906, p. 243) in New Jersey; although Surface (1908, p. 161) in Pennsylvania, 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" and went on to report instances of turtles hibernating in "comparatively dry woods in Centre County." A complete summary of aquatic, upland, and nesting habitats (which together meet the essential requirements of overwintering, foraging, and reproductive habitat) follows.

General Landscape Considerations

The habitat requirements of Wood Turtles are complex but constant throughout the northeastern range. The range of habitats in which Wood Turtles are found from Maine to Virginia all meet the basic requirements for individual persistence, plus some degree of population development. Minor behavioral differences and differences in microhabitat selection may be noted by sex and age as well as geographic location, stream size, season, and upland habitat composition. But in all circumstances, in order to persist without long-term intensive management (which itself is clearly necessary at some locations), Wood

Turtle populations must have access to stable overwintering locations in streams (see Overwintering, below), upland nesting areas (see Nesting Habitat Requirements, later), and varied upland habitats (including natural or anthropogenic early-successional clearings) for foraging and thermoregulation.

Streams in an intact and unfragmented mosaic of high-integrity riparian habitats including instream nesting areas, stream- or beaver-influenced early successional habitats, and temporary wetlands, juxtaposed with mixed-age floodplain and upland forest appear offer an ideal long-term management context. Because of the compound expenses of intensive management, unfragmented sites with necessary habitat components and minimal human use are most likely to provide cost-effective conservation outcomes. Further, Wood Turtle populations appear to respond to landscape alterations at multiple scales (see Part 4), suggesting that significant populations should be managed as part of much larger landscapes of low-intensity development.

It should be noted that the ideal habitat configuration outlined above is relatively rare on the Northeastern landscape, and to maintain the historic range of the Wood Turtle will clearly require targeted management actions to improve or replace key features that are missing from the landscape, or to artificially boost recruitment where threats to adult persistence and nest/juvenile survival have been addressed (see Part VI for a more in-depth discussion of management scenarios and landscape considerations).

Wetland and Stream Habitat Requirements

Almost all recent studies of known Wood Turtle populations report strong associations with slow-moving sections of clear, cold, woodland streams that otherwise have moderate to fast current, especially with sand, gravel, or rock substrate (Finneran 1948; Vogt 1981, p. 95; Quinn and Tate 1991, p. 219; Kaufmann 1992b; Holman and Clouthier 1995, p. 214; Akre 2002, pp. 3 and 13; Arvisais et al. 2004, p. 392; Ernst and Lovich 2009, p. 253; Table 2; Figure 6). Streams appear to be central to the persistence of most known Wood Turtle populations as they provide essential overwintering habitat (Vogt 1981, p. 95; White et al. 2010; White 2013; *see* Overwintering, later.). In northern areas, Wood Turtles are associated with rivers that have well-developed riparian zones encompassing alder swales, marshes, sedge meadows, emergent and forested wetlands (Quinn and Tate 1991, p. 217; Compton et al. 2002, p. 834; Walde et al. 2003, p. 378), but riparian swales and wetlands are critical throughout the region (Akre and Ernst 2006). In Wisconsin, Wood Turtles occur in forested areas along fast-moving streams (Vogt 1981, p. 95). Buhlmann and Osborn (2011, p. 317) report Wood Turtles from a typical stream in New Jersey: "flowing current, gravel bottom, deep pools, and undercut banks with overhanging trees," the latter of which provide stable overwintering sites. In Virginia, Wood Turtles are associated with clear brooks and streams (Ernst and McBreen 1991).

Figure 5. Living representatives of the subfamily Emydinae include the "sculpted turtles" (Ernst and Lovich 2009): wood turtle, *Glyptemys insculpta* (A); and bog turtle, *Glyptemys muhlenbergii* (B); the pond turtles: Blanding's turtle (*Emydoidea blandingii*[C]), western pond turtle (*Actinemys marmorata* [D]), European pond turtle (*Emys orbicularis* [E]); the spotted turtle (*Clemmys guttata* [F]), and box turtles (*Terrapene* spp.) including the eastern box turtles (*Terrapene carolina* complex [G]); the western box turtles (*Terrapene ornata* [H]). All of the emydine species are of conservation concern because of perceived range contraction and population decline. Photos © Michael T. Jones

Stream size.—Although Wood Turtles appear to tolerate a wide range of streamflow conditions, they are most often associated with mid-sized 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, p. 24; Akre and Ernst 2006; White 2013; *but see* detailed discussion in Jones and Willey 2015 and Table 2; illustrated in Figure 4). There are many published and anecdotal reports from smaller streams (Wright 1918, p. 55; Akre and Ernst 2006; Jones 2009; Dragon et al. 2012) and much larger streams (Niederberger 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, riparian clearings; see Habitat Requirements, later) as past landuse history in the watershed. In a number of cases, Wood Turtles have been reported in associated with very large rivers (≥50 m wide), including major rivers in Ontario (Brown 1940), Québec (Denman and Lapper 1964, p. 20); Maine (Maine Department of Inland Fisheries and Wildlife, unpublished occurrence data 2011; J. Mays, ME IF&W, pers. comm.); central New Hampshire (New Hampshire Fish and Game Department, unpublished occurrence data 2011); Pennsylvania and New Jersey (New Jersey Fish and Wildlife, unpublished occurrence data, 2012; Pennsylvania Natural Heritage Program, unpublished data, 2012), Maryland (Cooper 1949; MacCauley 1955, p. 155; E. Thompson, MD DNR, pers. comm.; B. Cukla pers. comm. to S. Smith, MD DNR), Virginia (Henshaw 1907; Brady 1937; Akre and Ernst 2006; Akre, pers. comm.), and West Virginia (K. O'Malley, WV DNR, pers. comm.; T. Akre, pers. comm.). In many cases, Wood Turtles in large rivers appear to be associated with braided channels, sidearms, or tributary streams. Isolated occurrences have been documented in association with beaches of very large rivers in central Massachusetts, possibly representing nesting animals, although these may have originated from any of several smaller streams nearby (Massachusetts Natural Heritage and Endangered Species Program rare species database, 2012; Jones, unpublished data). A quantitative analysis of stream watershed area is presented by Jones and Willey (2015).

Stream substrate.—White (2013) reported Wood Turtles in Nova Scotia in association with primarily cobble stream substrate. Akre (2002, p. 13–14) reported that conditions along the same third-order tributary of the Potomac watershed in Fairfax County, Virginia varied from "clear, moderate-current" with "sand-gravel substrate" to "slow-flowing with suspended sediments and clay-gravel substrate." This stream flowed through the Piedmonth escarpment/fall line into the Potomac river floodplain, and the upper half, outside of the river floodplain, was clear and gravelly while the lower half was clay and often murky. The flow was often slowed down by the Potomac River volume backing up into the tributary (Akre, pers. comm.). Breisch (2006, p. 24) reports Wood Turtles in West Virginia in association with sand- and rocky substrates. However, Parren (2013, p. 183) points out that the population he studied was associated with calcareous bedrock and silt, and cautions that Wood Turtles likely tolerate a wide range of stream conditions. Jones and Willey (unpublished data) observed Massachusetts, New Hampshire, and Maine Wood Turtle stream locations (n=5125) dominated by wide range of stream substrates including organics and muck (3.1%), clay (0.3%), silt (3.6%), silty sand (14%), sand (40.5%), gravel (14.3%), cobble (17.2%), boulders (6.4%), and bedrock (0.3%).

Use of tidal wetlands and estuarine creeks.— Wood Turtles have not been reported from brackish habitats, but there is evidence that individual Wood Turtles occasionally occur in freshwater tidal wetlands. For example, an unusual metapopulation may occur along both banks of the fresh-tidal Hudson River in New York near Dutchess, Greene, and Columbia counties, where a dozen individual turtles were observed in tidal marshes and islands in the Hudson River by researchers during long-term monitoring in the 1980s and 1990s (Kiviat and Barbour 1996). The animals reported here may represent flood-displaced individuals from farther up the Hudson River or the smaller tributaries nearby, or they may represent functional populations. It is possible that a similar arrangement exists, or existed, in tributaries of the Parker River estuary of Essex County, Massachusetts (P. Huckery, Massachusetts Division of Fisheries and Wildlife, pers. comm. to L. Willey; D. Taylor pers. comm. to T. French, Massachusetts Division of Fisheries and Wildlife, *in* Kiviat and Barbour 1996). In New Jersey, there is at least one Wood Turtle record from Beverly, Burlington County, in the lower watershed of the Delaware River (Street 1914), and there are two historic records from 1933 and 1951 from the vicinity of Rancocas Creek, in the records of the New Jersey Endangered Species Program (New Jersey Division of Fish and Wildlife 2012). 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 smaller side streams, and several of the streams on Elk Neck, Cecil County, Maryland, where Wood Turtles were documented between the 1950s and 1970s, are in close juxtaposition with tidal estuaries and Wood Turtles likely had access to tidal systems in recent decades. It is possible that Wood Turtles once occurred in the lower Potomac River in Maryland and Virginia nearly as far as the tidal mouth (Akre, pers. comm.; Akre and Ernst 2006), and in northeastern Virginia historic occurrences in coastal creeks may have encompassed tidal stream reaches (Akre, pers. comm.).

Springs, vernal pools, seeps, and temporary wetlands.—Many authors have observed the tendency of Wood Turtles to exploit the seasonal availability of vernal pools and ephemeral wetlands (Mitchell et al. 2008, in Calhoun and deMaynadier 2008, p. 172). In Maryland, Wood Turtles have been reported from a mountain spring in the Catoctin Mountains (Reed 1956, p. 80), and Abbott (1884, p. 254) provides an account of three Wood Turtles congregating at a forest spring near Trenton, Mercer County, New Jersey. Breckenridge (1958, p. 169) reports Wood Turtles in "spring holes" and "woods ponds," as well as wooded streams, in Minnesota. Surface (1908, p. 161) recounts an individual Wood Turtle in Centre County, Pennsylvania hibernating on a wooded hillside "with a temporary pool only a few yards away". 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. Occasional use of vernal pool habitats was reported from Northampton County, Pennsylvania, and Westchester County, New York by S. Angus (unpublished data). In Massachusetts and New Hampshire, 80 of 7348 active season radiolocations (1.1%) were within vernal pool habitat, and 117 (1.6%) were within 5 m of vernal pool habitat (M. Jones, L. Willey, and P. Sievert, UMass, unpublished data). Springs, seeps, and vernal pools appear to be complementary landscape features that do not support overwintering populations.

Use of channelized rivers and canals.—Multiple individuals have been recorded from an 1890s canal system in Hampshire County, Massachusetts (Massachusetts Division of Fisheries and Wildlife, Natural Heritage and Endangered Species Program, unpublished occurrence data, 2012), and Wood Turtles may be associated with portions of the Chesapeake and Ohio Canal system in Maryland (T. Akre, pers. comm.).

Use of lakes, ponds, and reservoirs.—Although many early authors reported the Wood Turtle to frequent or reside in lakes or "ponds," this statement appears to be suppositional or erroneous (see Logier 1939). For example, Jones (1865, p. 118) reported use of lakes in Nova Scotia. As frequently reported, the Wood Turtle appears to be a stream obligate species in the winter months. However, there are several instances in which Wood Turtles have been found in association with lakes and ponds. There are Wood Turtle element occurrences associated with several large lakes in Québec (Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, unpublished data), and Quinn and Tate (1991, p. 218) presented evidence by at least one individual of seasonal lake use in Ontario (although they stated that most aquatic habitats were streams). There are other numerous records primarily of single animals on

Figure 6. Wood turtles overwinter primarily in clear, cold, sand-, gravel-, or rock-bottomed streams. Stream habitats depicted in spruce-fir forest in northern Maine (A); red maple-white pine upland forest in central New Hampshire (B); abandoned agricultural land in central Vermont (C); spruce-fir forest in western Massachusetts (D), deciduous floodplain forest in northern New Jersey (E); river birch-sycamore-American elm floodplain forest in northern West Virginia (F); and mixed pine-oak upland forest in northern Virginia (G). Photos © Michael T. Jones

roads near lakes in Maine and New Hampshire (Maine Department of Inland Fisheries and Wildlife, unpublished data; New Hampshire Department of Fish and Game and New Hampshire Natural Heritage Bureau, unpublished data; M.T. Jones, unpublished data). In Monroe County, Pennsylvania, two Wood Turtles (one of them dead) were observed in the fall near the outlet of a small reservoir, and the living one was recaptured in March of the following year (S. Angus, pers. comm.), suggesting that the animal had overwintered in the muck-bottomed reservoir. One of the clearest examples of a Wood Turtle population overwintering in a lake or reservoir environment is from Huntingdon County, Pennsylvania, where a population of Wood Turtles, including juvenile and young adults, overwinters in a cove of a large reservoir created in the 1970s (R. Nagle, Juniata College, pers. comm.). Whether the cove is spring-influenced or hydrologically distinct from surrounding areas of lakeshore is unknown. A head-started Wood Turtle overwintered in a manmade pond at Great Swamp NWR in 2012–2013 (C. Osborn, pers. comm.). In Bergen County, New Jersey, one very old female was found nest-searching near the edge of the Monksville Reservoir (and other Wood Turtles were observed in the area; R. Farrell, Herpetological Associates, pers. comm.). In Franklin County, Massachusetts, Jones and Sievert (2009) and Jones (2009) reported that a subpopulation of Wood Turtles resided in the catchment area behind an 1890s power dam that had largely silted in, although radiotracked turtles primarily used riverine and riparian features within the old reservoir area.

pH.—Most authors do not report stream pH associated with Wood Turtle sites (but see Parren 2013), and it is not well known the extent to which stream pH influences the distribution or abundance of Wood Turtles.

Table 2. Summarized characteristics of streams with known Wood Turtle populations.

		Stream Characteristics				
Sta te	Site	Width (m)	Depth	Substrate	Other features	Source
QC	Mauricie	5–10	up to 2 m	sandy to rocky		Arvisais et al. (2002)
NS	Cape Breton	~8	~0.2–2.0	clay, gravel	Gravel bar	Gilhen & Grantmyre (1973)
WI	Wisconsin R.	3–5	0.3–1.5	sandy		Ross et al. (1991)
ME	Aroostook Co.	24–34	-	sand, gravel, cobble		Jones & Willey (2013b)
ME	Somerset Co.	20–27	>2 m	clay, silt, sand, gravel		Jones & Willey (2013b)
NH	Coos Co.	13–15	>1.5 m	silt, sand, and gravel		Jones & Willey (2013a)
NH	Coos Co.	12–15	>1.5 m	sand and gravel		Jones & Willey (2013a)
NH	Grafton Co.	7–10	>1.5 m	sand and gravel		Jones & Willey (2013a)
NH	Grafton Co.	11	>2.5 m	silt, sand, gravel		Jones & Willey (2013a)
VT	Addison Co.	4.5–12	-	silt, gravel, cobble, rock, boulder	≤1% gradient	Parren (2013)
CT	New Haven Co.	4–5	1–1.5			Garber & Burger (1995)
NJ	Morris Co.	4–6	-	gravel	Pools; undercut banks, large trees	Buhlmann & Osborn 2011; Buhlmann, pers. comm.
PA	Centre Co.	5–10	up to 1.5	-		Kaufmann (1995)
VA	Frederick Co.–Shenandoah Co.	3–13	0.1–2.5	silt, sand, gravel, cobble, bedrock	Fairly straight stream with wide floodplain	Akre & Ernst (2006)
VA	Frederick Co.	1–5	0.05–2.0	silt, sand, gravel, cobble, boulders	Narrow floodplain and steep slopes	Akre & Ernst (2006)
VA	Loudoun Co.	5–20	0.1–3.0	silt, sand, gravel, cobble	Variable floodplain width	Akre & Ernst (2006)
VA	Fairfax Co.	2–4	0.1–2.0	clay, silt, sand, gravel	third order	Akre 2002; Akre, pers. comm.

Terrestrial Habitat Requirements

Upland and floodplain habitats used by Wood Turtles varies by geographic region, season, and spatial scale (Harding and Bloomer 1979; Strang 1983, p. 43; Quinn and Tate 1991; Compton 1999; Compton et al. 2002; Walde et al. 2003; Arvisais et al. 2004; Jones 2009). It is clear from corroborating studies that Wood Turtles are often found using upland mosaics of forested and nonforested habitats. Compton et al. (2002) suggested that forest edges may provide opportunities to balance thermoregulation and food requirements.

Forest tree species composition.— Across their range in the Northeast region Wood Turtles are found in a broad range of forest ecoregions and canopy associations (Table 3). Forest associations range from northern coniferous (*Picea glauca, P. rubens, P. mariana*, *Abies balsamea, Thuja occidentalis*) forests and northern hardwood (*Betula* spp*., Acer saccharum, Fagus grandifolia*) associations of northern New England, the Berkshires, and the Adirondacks, to extensive pine and northern hardwood forests of Ontario and the Great Lakes, to Appalachian forests in Virginia, West Virginia, and Maryland in which sycamore (*Platanus occidentalis*), river birch (*Betula nigra*), tulip poplar (*Liriodendron tulipifera*) are abundant in floodplains and oaks (*Quercus* spp.), hickories (*Carya* spp.) and pines (*Pinus* spp.) dominate on adjacent hillsides. Local topography can drive forest composition, including the degree to which floodplain tree species such as silver maple (*Acer saccharinum*), sycamore, and river birch dominate over upland species such as oaks, hickories, and pines. The most common tree genera reported from floodplains and adjacent upland forests near streams with Wood Turtles are presented in Table 3.

At broad spatial scales, Wood Turtles are associated with a range of early and late-successional habitats of the eastern deciduous and mixed forests of the southern boreal zone. Quinn and Tate (1991, p. 217) reported that Wood Turtles in Ontario occur in mixed woods associations of white and red pine (*Pinus strobus* and *Pinus resinosa*), poplar (*Populus* spp.), white birch (*Betula papyrifera*), red maple (*Acer rubrum*), and red oak (*Quercus rubra*), but at finer scales were found frequently in speckled alder (*Alnus rugosa*) swales (30% of terrestrial observations), mixed forest (28%), and grassy openings (12%). In the Mauricie region of Québec, Walde et al. (2003, p. 378) reported Wood Turtles from the boundary of the boreal/Great Lakes St Lawrence lowland forest (Farrar 1995), where forests are dominated by white spruce (*Picea glauca*), white birch (*Betula papyrifera*), and aspen (*Populus tremuloides*) and floodplains are dominated by speckled alder. Arvisais et al. (2004, p. 392) reported a largely forested mosaic of balsam fir (*Abies balsamea*), poplar, birch, and spruce, with alder near watercourses, in which Wood Turtles were strongly associated with alder stands and young (16 years) forest. In an agricultural area of southern Québec (Brome County), Saumure and Bider (1998) reported extensive hay fields and cattle pastures juxtaposed with forest dominated by box elder (*Acer negundo*), American elm (*Ulmus americana*) with willows and speckled alder prevalent. At a largely forested site in southern Québec (Pontiac Co.), Saumure and Bider (1998) report undisturbed floodplain forest dominated by balsam fir, white spruce, aspen, and alder. In Nova Scotia, White (2013) describes a mixed agricultural and forested landscape, with forests dominated by northern hardwood species such as yellow birch (*Betula alleghaniensis*), red maple, white birch, red oak, and black cherry (*Prunus serotina*) with some white pine, balsam fir, and hemlock (*Tsuga canadensis*), and open riparian areas dominated by alder, cherry, elder (*Sambucus* sp.), hawthorn (*Crataegus* sp.), serviceberry (*Amelanchier* sp.), and raspberries (*Rubus* spp.). On Cape Breton Island, Gilhen and Grantmyre (1973) report a mosaic of hayfields, alder, and meadows.

Compton (1999, p. 33) and Compton et al. (2002, p. 834) reported a population in western Maine associated with mixed and coniferous industrial forest. In western Vermont, Parren (2013) reported that his study site was divided amongst the Mesic Clayplain Forest (in floodplain areas) and northern hardwood forest (upland areas). Jones (2009, p. 59–60; unpublished data) reported on populations in central New England occurring in both agricultural landscapes (including dairy farms, hayfields, and row crops) and forested landscapes dominated by upland spruce-fir, northern hardwoods (*Betula alleghaniensis, Acer saccharum,* and *Fagus grandifolia*) and transition hardwoods, and extensive floodplain forests (associated with larger rivers) dominated by silver maple (*Acer saccharinum*). Wood Turtles in New Haven County, Connecticut, were associated with streams in central hardwoods forest (Garber and Burger 1995). In Sussex County, New Jersey, Farrell and Graham (1991, p. 1) reported on a population of Wood Turtles occurring in a mosaic of agricultural land, wet meadows, open pasture, and deciduous fores, and in Morris County, New Jersey, Buhlmann and Osborn (2011, p. 317) reported Wood Turtles from a stream bordered by "riparian hardwood forest" and abandoned pastures with blackberry (*Rubus* sp.) 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 agricultural fields. In Cumberland County, Pennsylvania, Strang (1983, p. 43) reported Wood Turtles in lowland areas dominated by oaks (*Quercus* spp.), black birch (*Betula lenta*), and red maple, and in Centre County, Pennsylvania, Kaufmann (1992a) reported little use of deciduous forest. 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 (*Liriodendron tulipifera*), ironwood (*Carpinus caroliniana*), pawpaw (*Asimina triloba*), river birch (*Betula nigra*), and sycamore; and red maple, sycamore, box elder (*Acer negundo*), slippery elm (*Ulmus rubra*), and ashes (*Fraxinus* spp.). At a site in Loudoun County, Virginia, Akre and Ernst (2006) report typical assemblages of southern floodplain hardwoods (Table 3) but also note the present of a relatively rare co-occurrence of Wood Turtles with the Piedmont Hardpan Forest, which includes Virginia pine (*Pinus virginiana*), eastern redcedar (*Juniperus virginiana*), small oaks, hickories, redbud (*Cercis canadensis*), and sweetgum (*Liquidambar styraciflua*). At a complex of sites in Shenandoah and Frederick counties, Virginia, Akre and Ernst (2006) report that sycamore, red maple, and tulip poplar are common in the floodplain, while oaks and hickories occur on undisturbed floodplain sites and adjacent slopes, where they occur with Virginia pine and pitch pine. White pine is present throughout the site complex. In northern West Virginia, Breisch (2006, p. 24) reported Wood Turtles from a forested stream with floodplain canopy consisting of sycamore, red maple, river birch, and rhododendron (*Rhododendron* sp.) Elsewhere in West Virginia, Niederberger (1993) describes 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 gives way in places to open, savanna-like pastures with black walnut canopy and understory dominated by orchard grass (*Dactylis glomerata*) and other herbs.

The American chestnut (*Castanea dentata*) once reached great densities in the Appalachian forests from Maine to Virginia and undoubtedly was a prominent feature in Wood Turtle community ecology before its collapse from the chestnut blight in the early 20th century.

Nesting Habitat Requirements

The Wood Turtle requires open, well-drained, elevated, exposed areas of sand and/or gravel for nesting (Akre and Ernst 2006; Ernst and Lovich 2009; Jones 2009; Akre 2010), although appropriate nesting areas vary by geographic region (Figure 7–9). 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, p. 50) and sandy loam associated with a very wide range of natural and anthropogenic sites.

Common natural features include sandy point bars on the inside bends of rivers (Buech et al. 1997; J. Harding, Michigan State University, pers. comm.; Saumure and Bider 1998, p. 38; Jones 2010; Parren 2013, p. 180), cutbanks on the outer bend of rivers (Buech et al. 1997); sand and gravel bars deposits in the stream channel associated with stream obstructions, constrictions, or directional changes in flow (Gilhen and Grantmyre 1973; Vogt 1981, p. 96; Compton 1999; Akre 2002; Akre and Ernst 2006; Jones 2009; Parren 2013), and areas of overwashed sand in open floodplains (M.T. Jones and L.L. Willey 2013a) and dry stream beds (Graf et al. 2003; Jones 2008).

Anthropogenic sites include: abandoned, stable, or infrequently disturbed portions of sand and gravel pits (Compton 1999, p. 75; Tuttle and Carroll 2005; Walde et al. 2007, p. 50); gravel boat ramps (Compton 1999; Compton, pers. comm.); powerlines (Jones 2009; Akre 2010); roadsides and roadcuts (Saumure and Bider 1998, p. 38; Akre 2010; Akre et al. 2012); farm roads near streams (Jones 2009; Parren 2013), abandoned railroad beds (Vogt 1981, p. 95; Farrell and Graham 1991, p. 4), active rail beds (J. Foley, pers. comm.), 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), cornfields (Castellano et al 2008; Jones 2009). Of 52 nests primarily detected by radiotelemetry in Massachusetts and New Hampshire (Jones 2009, p. 156), 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. At a site in Morris County, New Jersey, Buhlmann and Osborn (2011) created an artificial nesting mound 18 m long x 8 m wide x 1.5 m tall, 50 m from an occupied Wood Turtle stream and 100 m from a confirmed nesting site threatened by development. In Sussex Co., New Jersey, a >50 year old gravel extraction area was purposefully managed to improve suitability for nesting Wood Turtles (T. Duchak and R. Burke, Hofstra University, pers. comm.). Akre et al. (2012) and Dragon et al. (2012) proposed 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 nesting on well-drained substrates with some elevation above the surrounding landscape, in areas with good solar exposure and strong southern aspect (Akre 2010). Compton (1999, p. 76) also questioned whether anthropogenic nesting areas in Maine may function as ecological traps.

Paterson et al. (2012) reported that the selected, open upland habitats of hatchling Wood Turtles in Algonquin Park, Ontario, were encompassed by the larger-scale nesting areas of adults.

Of 52 nests reported by Jones (2009, p. 156) 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.

Vascular plants associated with Wood Turtle nesting areas in New Hampshire include sweetfern (*Comptonia peregrina*), field hawkweed (*Hieracium pratense*), little bluestem (*Schizachyrium scoparium*), and goldenrods (*Solidago* spp.; Tuttle and Carroll 2005).

Table 3. Canopy tree genera associated with forested habitats near Wood Turtle overwintering streams.

State	Site	*Abies*	*Picea*	*Pinus*	*Tsuga*	*Acer*	*Plantanus*	*Liriodendron*	*Betula*	*Populus*	*Quercus*	*Ulmaceae*	*Prunus*	*Caryaceae*	*Fraxinus*	Source
QC	Mauricie		x		x				x	x						Walde et al. 2003
QC	Mauricie	x	x						x	x						Arvisais et al. 2002; 2004
QC	Brome Co.					x						x				Saumure and Bider 1998
QC	Pontiac Co.	x	x							x						Saumure and Bider 1998
ON	Algonquin			x		x			x	x	x					Quinn & Tate 1991
NS	Cape Breton											x	x			Graf et al. (2003)
NS	Mainland	x		x	x	x			x		x		x			White (2013)
ME	Aroostook Co.	x	x			x			x	x		x			x	Jones and Willey (2013b)
ME	Somerset Co.	x	x			x			x			x				Jones and Willey (2013b)
NH	Coos Co.	x	x			x			x			x				Jones and Willey (2013a)
VT	Addison Co.				x										x	Strang (1983)
MA	Western MA	x	x	x	x	x	x		x		x	x	x	x	x	Jones (2009)
CT	New Haven Co.					x					x			x		Strang (1983)
NJ	Warren Co.					x					x			x		Castellano et al. (2008)
PA	Cumberland Co.					x			x		x					Strang (1983)
PA	Monroe County				x						x					Angus (unpubl. data)
VA	Sites A–C			x	x	x	x	x	x	x	x		x	x	x	Akre and Ernst (2006)
VA	Loudon Co.					x	x	x			x	x		x	x	Akre and Ernst (2006)
VA	Fairfax Co.					x	x	x	x			x			x	Akre (2002)
WV	E. Panhandle					x	x		x							Breisch (2006)
WV	Cacapon R.					x	x	x					x			Niederberger (1993)

Associated Turtle Species

Although the Wood Turtle often co-occurs with the painted turtle (*Chrysemys picta*) at the watershed scale throughout the range of the former, the two species are usually found using different aquatic habitats within a given watershed (Harding and Bloomer 1979). Still, because of its widespread abundance, the painted turtle is probably the turtle species most often found in association with Wood Turtle populations in the northeastern States. The snapping turtle (*Chelydra serpentina*), because of its wide range of habitat tolerances, is perhaps the second most likely to co-occur with Wood Turtles in the Northeast. In fact, across most of northern New England and eastern Canada the Wood Turtle is likely to co-occur only with the painted turtle and the snapping turtle, and in northern Coos County, New Hampshire, and northwestern Maine, the Wood Turtle is sometimes the only turtle species present in a given stream system. In central New Hampshire, Carroll (1991; 1999; pers. comm.) reports that Wood Turtles co-occur in a diverse wetland mosaic with spotted, Blanding's, painted, and snapping turtles; elsewhere in central New Hampshire Wood Turtles occur frequently with painted and snapping turtles (Jones 2008; unpubl. data). Historically in the deltas of certain large rivers of northern Lake Champlain, Wood Turtles likely co-occurred with common map turtles (*Graptemys geographica*) and spiny softshells (*Trionyx spiniferus*).

Similarly in parts of central and southwestern Wisconsin, Wood Turtles co-occur with spiny softshells as well as map turtles (*Graptemys* spp.) and Blanding's turtles (*Emydoidea blandingii*). In Massachusetts, the Wood Turtle occurs frequently with painted and snapping turtles, often sharing nesting sites, and less often in the same wetland complexes as spotted (*Clemmys guttata*), bog (*Glyptemys muhlenbergii*; A. Whitlock, USFWS, pers. comm.), eastern or woodland box (*Terrapene carolina*), and Blanding's turtles (Jones and Willey, unpublished data). In Morris County, New Jersey, the Wood Turtle uses the same nesting areas as the snapping turtle, musk turtle (*Sternotherus odoratus*), painted turtle, and eastern box turtle (Buhlmann and Osborn 2011). In Sussex County, New Jersey, Wood Turtles co-occur with these species as well as bog and spotted turtles (R. Farrell, Herpetological Associates). Wood Turtles seasonally inhabit calcareous fens with bog and spotted turtles in Sussex and Warren counties, New Jersey; southern Orange, Dutchess, and Putnam counties, New York; and Northampton and Monroe counties in Pennsylvania (S. Angus, pers. comm.). In eastern Pennsylvania, Wood Turtles co-occur in stream systems with spotted, bog, box, and snapping turtles (K. Gipe, PFBC, pers. comm.), and occasionally musk turtles in Berks County (J. Drasher, Aqua-Terra Environmental Ltd.). In northern West Virginia, Wood Turtles co-occur with Eastern Box Turtle (K. O'Malley, WV DNR, pers. comm.). In western Maryland, the Wood Turtle co-occurs with Eastern Box Turtle and in Virginia, the Wood Turtle co-occurs with the eastern box turtle as well as common musk turtle (*Sternotherus odoratus*; T. Akre, Smithsonian Conservation Biology Institute, pers. comm.; J. Dragon, George Mason University, pers. comm.).

Movements

Home Range Sizes

Comparing reported home range values is complicated by the wide variety of home range metrics reported, including both area and linear measurements, and by variable telemetry effort. Meta-analysis of home range data is further complicated by strong annual effects and the tendency to report mean rather than median values, which are more sensitive to individual effects (Saumure 2004; Jones 2009, B.W. Compton, pers. comm.). Meta-analyses of the influence of landscape on home range size is now complicated by the ingrained practice of withholding site location information (Litzgus and Brooks 1996).

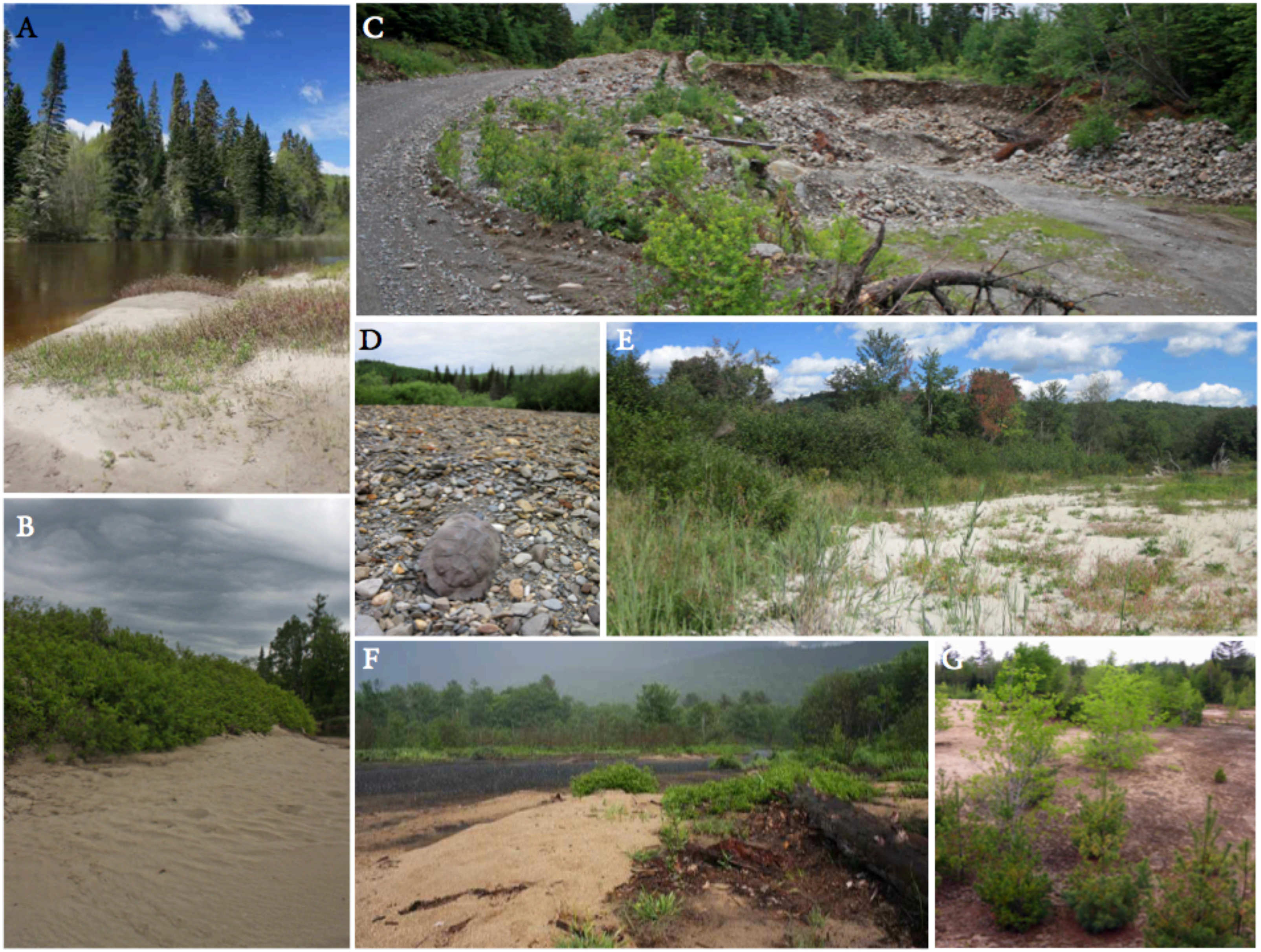

Figure 7. Wood turtle nesting areas in the northern Appalachians. Wood turtles nest primarily in poorly graded sand and gravel, as pictured here on natural river point bars in northern ME (A and B); an abandoned gravel pit in western ME at Compton's (1999) study site (C); a gravel and cobble bar in northern NH (D); a 0.2 ha area of overwashed flood-deposited sand in central NH (E); a sandy delta beach above a hydroelectric reservoir in central NH (F); an abandoned, sand and gravel quarry in central NH (G). Photos © Michael T. Jones and Lisabeth L. Willey

Figure 8. Wood turtle nesting areas in Massachusetts (Jones 2009). Sand pile in farm junkyard (A); powerline near river (B); sand traps in golf course (C); abandoned gravel pit rapidly becoming unsuitable as a result of gray birch and alder colonization (D); overwashed sand associated with major floods in sycamore-dominated floodplain (E); motorbike jumps in horse pasture (F). Photos © Michael T. Jones and Lisabeth L. Willey

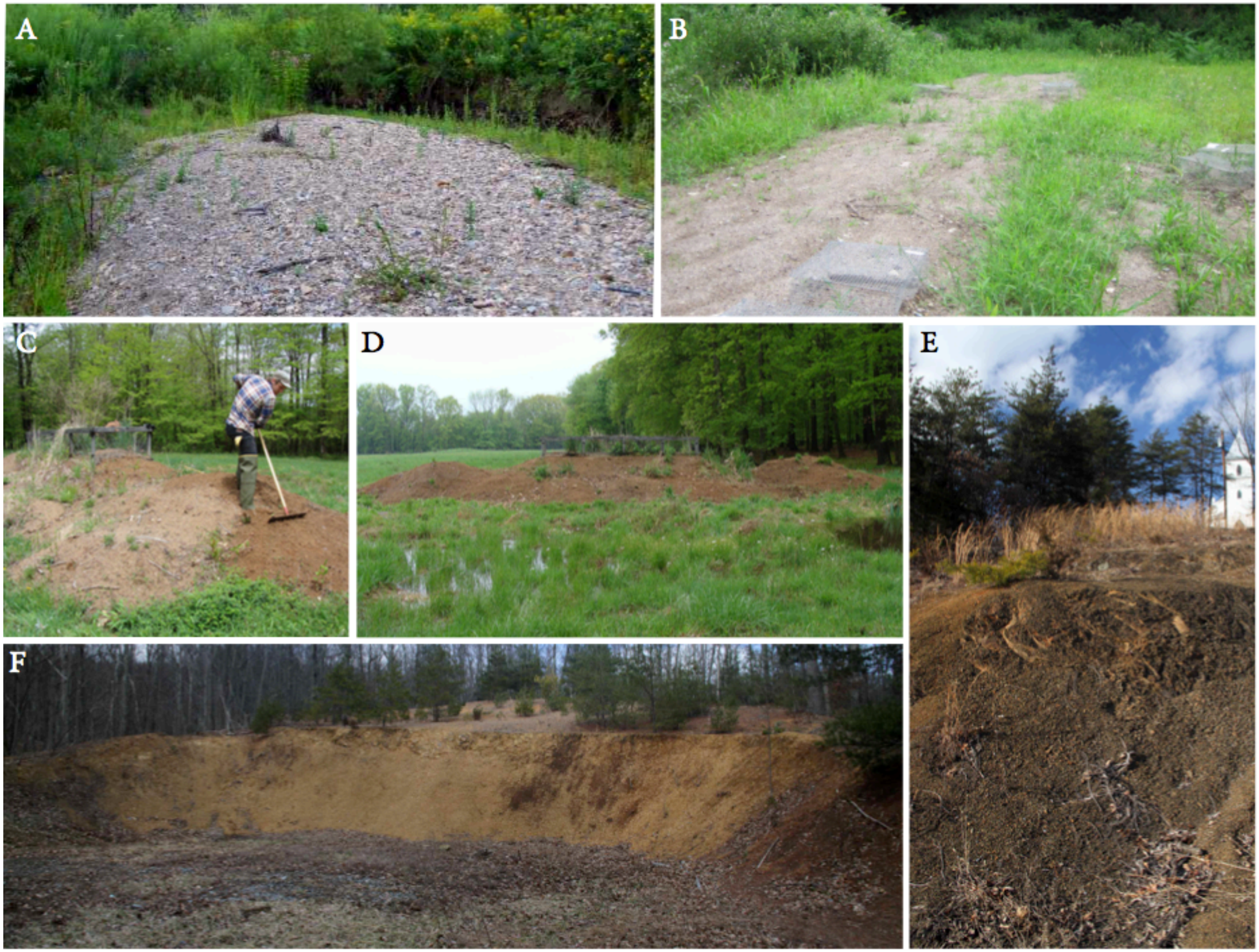

Figure 9. Nesting habitat for the wood turtle in southern New England and the Mid-Atlantic. Nesting habitat in Connecticut, an instream gravel bar (A; Photo by John Foley). A number of sites have been successfully managed to encourage nesting by wood turtles in New Jersey, including a former sand and gravel extraction site that was cleared and has become the primary nesting site at the study site of R. Burke and T. Duchak (B) and a 18 m x 8 m x 1.5 m tall nesting mound was constructed by the U.S. Fish and Wildlife Service in Morris County, New Jersey (C and D; Buhlmann and Osborn 2011; Photos by Colin Osborn). Adjacent to the George Washington National Forest of Virginia, wood turtles nest in powerline cuts (E). On the GMNF, wood turtles nest in roadcuts and borrow pits (F; Akre 2010; Akre et al. 2012). Photos © John Foley (CT), Colin Osborn (NJ), and Michael Jones

Arvisais et al. (2002, p. 406) and Smith (2000) noted that home range size in northern populations appeared to be larger than in southern populations; this observation was supported by data collected in western Maine (B.W. Compton, unpubl. data). Saumure (2004) observed that Wood Turtles at his disturbed, agri-forested site in southern Québec moved less than those observed by Arvisais et al. (2002) in a more intact forested landscape in the Mauricie region of Québec. Both observations have roughly been supported by subsequent studies (e.g., Jones 2009), and both phenomena have conservation implications. Certainly, it is ideal to obtain empirical data on the movements of individual turtles at key conservation sites.

Saumure (2004, Chapter 3) proposed standardized 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 (straight-line distance between the two most widely separated capture locations). In the following summary, we analyze the area and linear space of Wood Turtles representative studies 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. While these measures capture the differences between sites and individuals and shed light on the influence of landscape on movement patterns, they do little to provide regulators with distance data necessary for adequate habitat mapping. The distance traveled along stream corridors has regulatory and biological significance, as does the distance traveled from streams (Jones 2009).

Statistical Range.—Statistical ranges (MCP 95%) of males are typically larger, although the difference is typically not reported to be significant. The mean value of thirteen averaged statistical ranges for males is 18.2 ha (0.3–32.2 ha). The mean value for females from the same studies is 11.6 ha (0.5–29.4 ha; Table 4).

Linear Range.—The linear range, or greatest distance between recorded locations in one year, of males is typically larger than that of females, driven in part by their tendency to use larger lengths of stream. The mean value of averaged linear home ranges from seven studies is 1028 m (481–1531 m) for males and 647 m (435–866 m) for females (Table 4).

Stream Range.—Males spend more time than females in streams during the active season (Akre 2002), and correspondingly have longer stream ranges. Several authors have reported that male Wood Turtles use greater stream lengths than females. Parren (2013) reported that females have a stream range of 659±563 m (range=130–1602 m; *n*=5), slightly less than males (760±445 m; range=287–1521 m; *n*=6), but the difference was not significant. From a sample of 123 adult turtles in Massachusetts and New Hampshire, Jones (2009; unpublished data) reported that males have a stream home range of 1422±1295 m (range=221–6304 m; *n*=56) and females exhibited stream ranges of 757±814 m (range=62–5537 m; *n*=67).

Distance from River.—Generally, females move greater distances away from their overwintering streams (Akre and Ernst 2006; Jones 2009; Wicklow, unpubl. data). Arvisais et al. (2002) reported that all locations were within 300 m in the Mauricie Region of Québec. 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–>1000 m; *n*=56), and females 209±175 m (range=29–933 m; *n*=67). Parren (2013) implied 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. In a sample of five females and six males, the mean maximum distance traveled from the river was 276±86 m (range=209–425 m) and 108±36 m (range=72–151 m), respectively.

Nesting Movements

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, unpublished data; Steen et al. 2012). Jones (2008) documented that most New Hampshire females nested on beaches within the stream corridor, but one moved 600 m from the stream to nest in a residential area. Jones (2009) reported that 35% of females in Massachusetts and New Hampshire nested within the stream channel on beaches and instream bars.

At Great Swamp NWR, New Jersey, three different female Wood Turtles made nesting movements over 1 km from their typical home ranges to deposit eggs (C. Osborn, pers. comm.).

In northwestern Virginia, Dragon and Akre (unpubl. data) report that nests in 2012 and 2013 were an average of 159.2 m (range=54.3–264.2 m) from the stream.

Nest Site Fidelity

Walde (1998) reported that 64% of females nested in the same gravel pit in 1996 and 1997, and that in some cases females nested in the same 1m^2 area in both years. In New Hampshire, B. Wicklow (unpublished data) observed 15 to 20 females returning to the same nesting area each spring for a period of ten years. At a nesting site purposefully created for Wood Turtles in Morris County, New Jersey, Buhlmann and Osborn (2011, p. 315) reported that one female turtle (of nine) returned to the nesting mound in three subsequent years.

Table 4. Summarized characteristics of Wood Turtle home ranges, following Saumure (2004).

State	Site	Sex	Year	Integral	Statistical (MCP 95% [ha])	Linear	Stream	Mean Max Distance	*n*	Source
MA	Connecticut Valley	F	2004	-	5.8±5.6	565±303	514±430	216±194	23	Jones (2009)
MA	Connecticut Valley	F	2005	-	14.8±30.9	823±742	895±1165	218±220	29	Jones (2009)
MA	Connecticut Valley	F	2006	-	13.8±25.0	866±614	1033±902	222±120	26	Jones (2009)
MA	Connecticut Valley	F	2007	-	3.9±3.7	449±137	546±276	135±105	12	Jones (2009)
NH	Merrimack Valley	F	2007	-	7.7±9.5	502±323	611±427	163±195	8	Jones (2009)
ON	Huron Co.	F	1991	6.4±3.7	-	-	-	-	4	Foscarini (1994)
QC	Brome Co.	F	1998	11.6±16.4	9.6±7.2	741±251	-	-	9	Saumure (2004)
QC	Brome Co.	F	1999	16.4±13.3	13.0±10.0	797±397	-	-	11	Saumure (2004)
QC	Mauricie	F	1996	-	25.9±32.9	-	-	-	14	Arvisais et al. (2002)
QC	Mauricie	F	1997	-	29.4±37.8	-	-	-	14	Arvisais et al. (2002)
PA	Centre	F	1988	3.3±0.5	2.6±0.5	435±74	-	-	4	Kaufmann (1995)
VA	Rockingham Site 1	F	2006–07	7.9±6.5	-	-	-	-	6	Sweeten (2008)
VA	Rockingham Site 1	F	2006–07	16.8±27.8	-	-	-	-	14	Sweeten (2008)
WI		F		-	0.5±0.3	-	-	-	-	Ross et al. (1991)

State	Site	Sex	Year	Integral	Statistical (MCP 95% [ha])	Linear	Stream	Mean Max Distance	*n*	Source
MA	Connecticut Valley	M	2004	-	17.8±25.0	1138±938	1670±1498	114±90	18	Jones (2009)
MA	Connecticut Valley	M	2005	-	16.0±17.0	1109±778	1478±1100	97±89	22	Jones (2009)
MA	Connecticut Valley	M	2006	-	20.3±44.8	976±954	1343±1341	97±63	25	Jones (2009)
MA	Connecticut Valley	M	2007	-	24.3±33.8	1014±594	1436±955	85±59	9	Jones (2009)
NH	Merrimack Valley	M	2007	-	6.6±5.5	673±485	921±653	66±59	8	Jones (2009)
ON	Huron Co.	M	1991	5.0±2.9	-	-	-	-	6	Foscarini (1994)
QC	Brome Co.	M	1998	19.4±13.1	16.7±11.3	1301±564	-	-	5	Saumure (2004)
QC	Brome Co.	M	1999	36.0±51.9	32.2±50.0	1531±1412	-	-	9	Saumure (2004)
QC	Mauricie	M	1996	-	32.1±38.7	-	-	-	4	Arvisais et al. (2002)
QC	Mauricie	M	1997	-	29.1±20.0	-	-	-	6	Arvisais et al. (2002)
PA	Centre	M	1988	5.0±1.5	3.8±1.4	481±75	-	-	6	Kaufmann (1995)
VA	Rockingham Site 1	M	2006–07	33.0±34.8	-	-	-	-	8	Sweeten (2008)
VA	Rockingham Site 1	M	2006–07	19.3±34.9	-	-	-	-	15	Sweeten (2008)
WI		M		-	0.3±0.2	-	-	-	-	Ross et al. (1991)

Hatchling Orientation and Movements

The movement, behavior, ecology, and survivorship of hatchling Wood Turtles was studied by Wicklow (unpublished data); Tuttle and Carroll (2005); Castellano et al. (2008); Dragon et al. (2012); and Patterson et al. (2012). Recently, researchers have used radiotelemetry to document fine-scale movements (e.g., Castellano et al. 2008; Dragon et al. 2012; Patterson et al. 2012). In Algonquin Park, Ontario, Patterson 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 report that hatchlings left the nest site in a multidirectional dispersal pattern and headed for the nearest cover. Compton (1999, p. 75) 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 indicate that hatchlings are, in fact, willing to move over large obstacles. 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. Further, 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 (unpublished data) 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 dictated the amount of days taken to reach the stream more 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 max movement of 1112 m. In New Hampshire, Wicklow (unpublished data) demonstrated 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.

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 (to 17 km straight-line; Jones 2009, p. 73; Sweeten 2008), and that adult Wood Turtles are capable of short-range homing movements (Carroll and Ehrenfeld 1978; Barzilay 1980). It is also clear that turtles are occasionally swept downstream by floods and survive the initial displacement, 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 2009). 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 two female Wood Turtles in Massachusetts and New Hampshire 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.

Reproduction

Maturity

Age at maturity has been reported to vary from 11 to 20 depending on sex and geographic area (about 12 years, Akre and Ernst 2006; 12 to 19 years, Harding and Bloomer 1979; 14 years, Farrell and Graham 1991; 14 to 20 years, Ross et al. 1991, p. 363; 17–18 years, Brooks et al. 1992; 12 years, Garber and Burger 1995; 14 to 18 years, Akre 2002, p. 3; 15 years (age of youngest mating male), Parren 2013, p. 179–180; see discussion in Compton 1999, p. 66–67). Documenting the age of onset of reproductive behaviors (mounting, courting) and secondary sex characteristics (plastral concavity, enlarged tail, etc.) is apparently easier and less time-intensive for males, so significant differences in age at maturity between sexes may be masked.

Lifespan and Survivorship

Determining the exact age of adult Wood Turtles is often problematic, but there is now abundant evidence that wild Wood Turtle often survive into their 50s. Continued long-term monitoring will likely indicate much greater lifespans, as have now been demonstrated for related taxa. Most authors agree that counting annular growth rings on the plastron or carapace is appropriate only for immature or recently mature, growing turtles (younger than 15–20 years; Harding and Bloomer 1979; Kaufmann 1992a; Ernst, pers. obs., *in* Ernst and Lovich 2009, p. 259; Parren 2013). Ernst (2001a) reports wild turtles over 40 years old in Pennsylvania. In captivity, Oliver (1955) reported a maximum age of 58 years and Brooks (*in* COSEWIC 2007, p. 13) reports an adult of approximately >50 years. Recaptures of John Kaufmann's (1992a) study animals by Kathy Gipe (PFBC, unpublished data) in 2012–2013 as part of the this regional effort (described in Jones and Willey 2015) provides additional evidence of lifespans exceeding 50 years. Ray Farrell's (unpublished data) recent (2012–2013) recaptures of animals he marked in the 1970s (Farrell and Graham 1991) indicate ages in excess of 55 years. In Virginia, Dragon and Akre (pers. comm.) recaptured two Wood Turtles marked by Buhlmann (pers. comm.) in 1988 as mature adults, indicating minimum ages of 45 years. Jones (2009) estimated from time-lapse (interval) photographs of the carapace of 75 individual Wood Turtles in New England that complete wear of all carapace scutes may require approximately 80 years. A similar analysis of the depigmentation of the characteristic black blotches of the plastron indicated that they were reduced by >50% after approximately 70 years. Because turtles in these wear-class categories are frequently found in that region, the results may indicate natural lifespans exceeding 70 years.

Akre (2002, p. 5) notes that the Wood Turtle appears to exhibit a typical Type III survivorship curve with survivorship positively related to age, and this observation is supported by many reviews and published studies. Compton (1999) reported annual adult survivorship rates of 0.96–1.0 in Somerset County, Maine, but noted these may be as low as 0.92–0.96 if radioed turtles of unknown fate had actually died. In Hillsborough County, New Hampshire, Wicklow (unpubl. data) observed annual adult survivorship rate of 0.93 between 2005–2013. Jones (2009) provided supporting evidence indicating that young adult Wood Turtles sustained mortality rates twice as high as relatively old adults. In northwestern Virginia

(Shenandoah and Frederick counties), Akre and Ernst (2006) reported annual survivorship (for adults and juveniles) of 0.92, 0.92, and 0.80 between 1999–2002.

Hatchling survivorship in the first year appears to be extremely low. Wicklow (unpublished data) reported survivorship data for postemergent hatchlings in southern New Hampshire, and of eight hatchlings with transmitters, only one survived to reach the overwintering stream. Of the remainder four were eaten by chipmunks (*Tamias striatus*), one eaten by a short-tailed shrew (*Blarina brevicaudata*), one was eaten by a striped skunk (*Mephitis mephitis*), and two were unaccounted for. Dragon (unpubl. data) reported survivorship data for postemergent hatchling Wood Turtles in northwestern Virginia. Of the total 68 hatchlings monitored, only 13 survived to overwinter (0.19), and the majority (86%) of deaths occurred within 20 m of the stream. The average lifespan of radiotracked hatchlings between emergence and hibernation was 27 days. Survival varied greatly between the two years studied. Of the 41 hatchlings sampled in 2012, 3 survived to overwinter (0.07). In 2013 a total of 27 hatchlings were sampled and 10 survived to overwinter (0.37). 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 *G. insculpta* was much lower than observed in a similar sample of Blanding's turtle hatchings in Paterson's (2012) study.

Generations

Generation time or length is the average age of parent turtles of the current cohort (in this case, hatchlings of the current year present in the population). As generation time varies by region and from population to population it reflects the approximate turnover rate of breeding adults. Consequently, the generation length in long-lived, iteroparous species, such as the Wood Turtle, is older than the age at maturity and younger than the maximum lifespan of turtles in the population. The IUCN (2013) further specifies that when the generation length is depressed by anthropogenic sources, "the more natural, i.e. pre-disturbance, generation length should be used." According to Pianka (1974) generation length is the age to maturity plus one half the reproductive longevity. According to COSEWIC (2007), the IUCN formula for generation time (gt) is as follows, where (m)=average age at maturity and (am)=adult mortality rate: gt=(m)+(1/am). The generation time provided by COSEWIC (2007, p. 13) is 35 years, and van Dijk and Harding (2011), citing James Harding, suggested that it likely mirrors that of Blanding's turtle (*Emydoidea blandingii*) at approximately 36–47 years. Using an average age at maturity of 15 years, and the range of survivorship estimates of 0.96–1.0 provided by Compton (1999, p. 66–67) for a remote population in Maine, the generation time is >40 years (but may be as low as 32 years if three missing, radioed turtles actually had died). Adult annual survival estimates of 0.88 for 185 adult Wood Turtles of all adult age classes in agri-forested landscapes of Massachusetts and New Hampshire provided by Jones (2009) suggest generation times of 23 years. If these figures are indicative of other regions, generation time may vary from approximately 20 years at sites with high adult annual mortality rates (>0.2) to about 45 years at sites without 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. However, it should be noted that nest success and juvenile survival are probably as important in determining generation time as adult survival.

Courtship and Mating

Copulation almost always occurs in water, along the banks of streams, and in pools along the stream course (see review by Ernst and Lovich 2009). The Wood Turtle exhibits a number of noteworthy

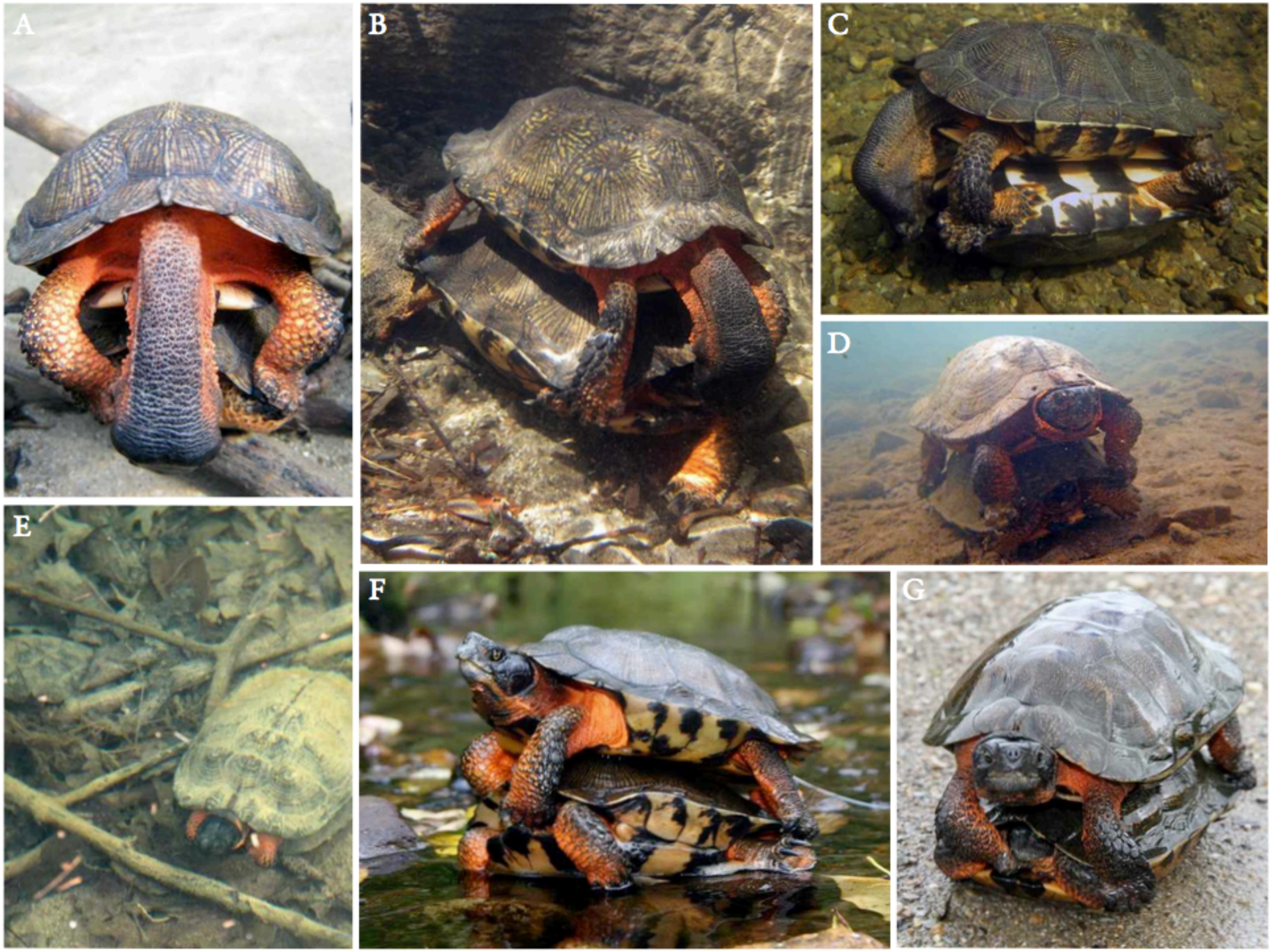

Figure 10. Wood turtles primarily court and mate underwater in quiet sections of streams (A–E), but the pair may be dragged from the water by the female as pictured here in New Hampshire and Maine (F–G). Males exhibit a range of head bobbing, throat pulsations, and biting behavior (A–C). Copulation takes place plastron-to-carapace but plastron-to-plastron also occurs, as pictured here in northern New Hampshire (C). Often mating occurs on the bottom of quiet pools, as pictured here in NW Virginia (D). Mating occurs often in proximity to overwintering sites, as pictured here in western Maryland (note quiescent turtle at left; E). Photos © Michael Jones

courtship rituals. Liu et al. (2013) summarize instances of head-bobbing courtship rituals and "shell clapping," in which the male thumps his plastron against the carapace of the female. Tronzo (1993) and Mitchell and Mueller (1996) report instances of plastron-to-plastron mating, although Kaufmann (1992) reports primarily plastron-to-carapace mating. Several instances of plastron-to-plastron mating were observed during the course of this study in the Fall of 2013 in Aroostook County, Maine (Jones and Willey 2013b); Coos County, New Hampshire (Jones and Willey 2013a); and Monroe County, Pennsylvania (Angus, unpublished data).

Fifty-three of 57 (93%) breeding attempts observed by Parren (2013, p. 180) in Vermont were in the water. Three instances of clasping/mounting were observed on the bank from 1–8 m from the river. Jones (2009, p. 158) observed courting behavior (clasping, mounting) or copulation on 110 occasions, of which 97% were in the water.

Nesting Frequency

All populations studied produce one or fewer clutches of eggs per year (M. Ewert, Indiana University, pers. comm. to T. Akre, *in* Akre 2002, p. 3). Farrell and Graham (1991, p. 4) reported that females did not appear to deposit more than one clutch per year. In Algonquin Provincial Park, Ontario, Brooks (unpublished data provided to T. Akre) found that 75% of females nest in a given year. Remarkably, in one of the most isolated populations of southern Ontario, Foscarini (1994) estimated that 33% of females nest annually. Walde et al. (2007) found that larger females in Québec are more likely to nest in consecutive years than smaller females. Jones (2009) reported that the proportion of adult females nesting in a given year between 2004–2007 ranged from 0.5 to 0.9 (mean=0.7) in Massachusetts and New Hampshire. Of twenty-five Massachusetts female Wood Turtles tracked for multiple years, the proportion of years in which turtles became gravid ranged from 0 to 1 and averaged 0.7. Akre (2002, p. 4) emphasized Kuchling's (1999) point that if females do not nest annually, it may be because they fail to ovulate despite a typical vitellogenic cycle.

Clutch Sizes

Range wide, average clutch sizes contain approximately 7–11 eggs (Table 5). In Ontario, average clutch size range from 8.0 to 10.7 (range=3–15; Brooks et al. 1992; Foscarini 1994; Smith 2002; *in* COSEWIC 2007, p. 1). In the Sudbury District of Ontario, Greaves and Litzgus (2009, p. 302) reported clutch sizes of 8.8±2.2, 9.4±2.3 in 2005 (*n*=5) and 2006 *(n*=11). In the Mauricie region of Québec, clutch size averaged 10.1 (range 5–20; n=58; Walde 1998). Nova Scotia females examined by Powell (1967) had clutch sizes of 8.2 (range=4–11; n=20). Harding (1991) reported clutch sizes to range from 5 to 18 and average 10.5 in Michigan. Wisconsin Wood Turtles studied by Ross et al. (1991) had average clutches of 11 eggs.

In the Northeast, Tuttle and Carroll (1997) reported average clutch size of 7.8±1 (range=6–9; n=9) in New Hampshire. Jones (2009, p. 157) reported a range of 1–14 eggs per clutch and a mean of 7.3 (n=76) in Massachusetts and New Hampshire. Kaufmann (1992a) reported mean clutch size of 8.9 (range=5–12) in Centre County, Pennsylvania, and in Sussex County, New Jersey Harding and Bloomer (1979) reported similar mean and range of 8 and 5–11, respectively. Nearby at another site in Sussex County, Farrell and Graham (1991) reported a mean clutch size of 8.5±1.7 (range 5–11, n=21).

Several studies have report that clutch size is correlated to straight-line carapace length (Brooks et al. 1992; Walde et al. 2007; Jones 2009, p. 157).

Although a strong correlation has been found between female body size and clutch size in Wood Turtles, as noted by Akre (2002), other studies of Emydids and Kinosternids indicate a pronounced influence of environmental parameters. Gibbons et al.'s (1991, 1992) findings demonstrated that environmental conditions influence clutch size more than age class or genetics in populations of slider (*Trachemys scripta*), eastern mud turtle (*Kinosternon subrubrum*), and chicken turtle (*Deirochelys reticularia*). Iverson (1991) and Iverson and Smith (1993) similarly found that yellow mud turtle (*Kinosternon flavescens*) and western painted turtle (*Chrysemys picta bellii*) responded to variable environmental conditions with varied reproductive output.

Table 5. Summarized clutch size data from across the Wood Turtle's range.

		Clutch characteristics				
State	**Site**	**No. eggs**	**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)
MI	-	10.5	5–18	-	-	Harding (1991)
NS	-	8.2	4–11	-	20	Powell (1967)
NH	Merrimack Co.	7.8±1.0	6–9	-	9	Tuttle & Carroll (1997)
MA	Western MA	7.3	1–14		76	Jones (2009)
NJ	Sussex Co.	8.5±1.7	5–11		21	Farrell & Graham (1991)
NJ	Morris Co.	-	7–16	2007–2010	23	Buhlmann & Osborn (2011)
PA	Centre Co.	8.9	5–12	-	-	Kaufmann (1992)

Egg Viability and Nest Predation

Nest viability rates appear to be variable. In Massachusetts and New Hampshire, Jones (2009) found that emergence rate, or nest success (excluding depredation by mammals) ranged from 0 to 1.0 and averaged 0.41. When emergence rate, or nest success, was regressed separately on a shell-wear index and straight-carapace length, no significant model was produced (P=0.72; P=0.56).

Nest depredation rates also appear to be variable, although striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and numerous other midsize carnivores appear to be major factors in some areas (see Significant Threats to Population Stability, later). Raccoon, skunk, and possibly turkey are predators of nests in New Jersey (S. Angus, pers. comm.). Buhlmann and Osborn (2011) noted that raccoons and red fox were significant nest predators in New Jersey. Nest predation by badgers (*Taxidea taxus*) was noted by Cherry et al. (2015), who also reported that striped skunks, raccoons, ravens (*Corvus corax*), and American crows (*Corvus brachyrhynchos*) were observed eating eggs in a Minnesota nesting area.

Incubation

Compton's (1999) degree-day models using field-hatched (n=4) and lab-hatched (n=7) nests from Maine and other reported studies (Ewert 1979; M. Ewert, Indiana University, unpublished data; Vogt 1981; Herman 1991; J. Harding, Michigan State University, unpublished data) predict that a Wood Turtle egg will hatch when it has received 788 (se=10.1) degree-days above a threshold of 12.5˚C. Incubation time of the Maine nests ranged from 67 (at a mean temperature of 24.5˚C) to 113 days (with a mean temperature of 19.5˚C) with a median (n=11) of 89 days. Maine eggs incubated at the same rate as eggs from other localities, although he left open the question of whether incubation rates vary geographically based on low power and lack of replicates from a wide range of latitudes. Based on a soil temperature model built from historical weather data, Compton (1999, p. 20) 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 because of low summer temperatures.

In Warren County, New Jersey, Castellano et al. (2008) reported a mean incubation period of 72.2±3.0 days (range=69–76; *n*=10). In southern New Hampshire, Tuttle and Carroll (2005) reported both synchronous (all hatchlings emerged at the same time; *n*=5) and asynchronous (*n*=2) emergence from 13–29 August between 0820–1805 h.

Most nests emerge in August, but emergence ranges from July to October. Castellano et al. (2008) reported a range of emergence dates from 13 August to 20 August 2002 in Warren County, New Jersey. In Morris County, New Jersey, Buhlmann and Osborn (2011) reported a range of emergence dates from 29 July to 14 September, but noted that most hatchlings emerged in mid- to late-August (K. Buhlmann, pers. comm.). In northern Virginia, Akre (2010) reported emergence dates ranging from 3 August to 22 September 2010 with most hatchlings emerging before 19 August. Parren and Rice (2004) speculated that some Wood Turtle nests may overwinter on land in Vermont, but this has not been reported in other studies (Walde et al. 2007), although Wright (1918, p. 55) observed a turtle of "newly hatched form" in April 1913.

Demographics

A complete understanding of demographics in Wood Turtle populations requires either an intensive sampling effort directed at all age classes, or a long-term sampling effort. Most studies have reported female-biased or equal sex ratios and highly variable juvenile ratios, which range from 0% to 48.0% of captures (Greaves and Litzgus 2009, p. 303; Table 6). In Québec, Walde et al. (2003) reported a female-skewed sex ratio of 1 : 1.51 (males to females), which differed significantly from 1 : 1, but felt the result was biased because of their research emphasis on nesting females. Compton (1999; unpublished data) reported a female-based sex ratio of 1 : 2.7 in western Maine; this also may reflect intensive sampling for nesting females, or increased detectability of females. Jones and Willey (2013b) reported equal sex ratios in Aroostook County, Maine, and female-skewed sex ratios in Somerset County, Maine.

Caution should be used when interpreting absolute juvenile captures because they are detected at lower rates than adults and detection is probably variable across sites and habitats. Walde et al. (2003) reported that immature turtles accounted for 31% of the animals captured in the Mauricie region of Québec, by contrast, Compton (1999; unpublished data) detected only four turtles aged 14 or younger.

Saumure and Bider (1998) detected differences in the demographic structure of two populations in Québec, noting that juveniles were less common at the agricultural site. Jones (2008, p. 11) detected significant differences in age class structure between two populations in the White Mountains, New Hampshire, and Akre and Ernst (2006) report differences in demographic structure across five populations in northern Virginia.

Table 6. Summarized demographic data from selected sites throughout the range of the Wood Turtle.

State	Site	Males	Females	Juveniles	Ratio (M:F)	% Juvenile	Source
QC	Mauricie	55	83	50	1 : 1.51	0.27	Walde et al. 2003
QC	Brome Co.	18	24	10	1 : 1.33	0.19	Daigle (1997)
QC	Brome Co.	16	13	4	1 : 0.07	0.12	Saumure & Bider (1998, p. 39)
QC	Pontiac Co.	10	10	11	1 : 1.0	0.36	Saumure & Bider (1998, p. 39)
ON	Algonquin Park	21	56	13	1 : 2.57	0.14	Brooks et al. (1992)
ON	Sudbury Dist.	15	21	19	1 : 1.40	0.35	Greaves & Litzgus (2009)
ON	Huron Co.	83	136	51	1 : 1.60	0.19	Foscarini (1994)
NS	Mainland	14	20	10	1 : 1.43	0.23	White (2013)
MI	Upper Pen.	86	105	63	1 : 1.22	0.25	Harding & Bloomer 1979
WI	Black R.	20	37	1	1 : 1.85	0.02	Ross et al. (1991)
WI	Wisconsin R.	8	15	0	1 : 1.88	0	Ross et al. (1991)
ME	Aroostook Co.	60	69	37	1 : 1.15	0.22	Jones & Willey 2013b
ME	Somerset Co.	48	102	77	1 : 2.13	0.34	Jones & Willey 2013b
ME	Somerset Co.	10	27	4	1 : 2.7	0.1	Compton, unpubl. data
NH	Coos Co.	28	44	37	1 : 1.57	0.34	Jones & Willey 2013a
NH	Grafton Co.	54	66	112	1 : 1.22	0.48	Jones & Willey 2013a
NH	Merrimack Co.	17	29	36	1 : 1.8	0.44	Tuttle (1996)
MA	Connecticut R.	83	83	27	1 : 1.0	0.14	Jones et al., unpubl. data
MA	Deerfield R.	42	37	16	1 : 0.88	0.17	Jones et al., unpubl. data
MA	Berkshire Co.	18	9	9	1 : 0.5	0.25	Jones et al., unpubl. data
MA	Westfield R.	49	64	27	1 : 1.30	0.19	Jones et al., unpubl. data
NJ	Passaic Co.	311	464	-	1 : 1.49	-	Harding & Bloomer 1979
VA	Frederick-Shenandoah	70	80	27	1 : 1.14	0.15	Akre 2010
VA	Shenandoah Co.	38	44	12	1 : 1.16	0.13	Akre and Ernst 2006
VA	Frederick Co.	23	32	9	1 : 1.39	0.14	Akre and Ernst 2006
VA	Fred.-Shen. Co.	43	42	35	1 : 0.98	0.29	Akre and Ernst 2006
VA	Fairfax Co.	38	64	37	1 : 1.68	0.27	Akre (2002)
WV	Cacapon R.	52	49	86	1 : 0.94	0.46	Niederberger & Seidel (1999)
WV	E. Panhandle	16	16	18	1 : 1.0	0.36	Breisch (2006)

Feeding

The Wood Turtle is an opportunistic omnivore (Surface 1908, p. 161–162; Logier 1939; Oliver and Bailey 1939; Harding and Bloomer 1979, p. 22; Vogt 1981, p. 96; Farrell and Graham 1991, p. 7; Klemens 1993, p. 173) that feeds from April to October (Ernst 2001b). Like many terrestrial or semi-terrestrial turtles, the Wood Turtle is able to feed on land or in water (Castellano et al. 2008).

Surface (1908, p. 161) reported that 76% of turtles examined in Pennsylvania had eaten vegetable material, and 80% had consumed "animal matter." Oliver and Bailey (1939) report that New Hampshire Wood Turtles eat "a variety of vegetable as well as animal food. Berries, seeds, earthworms, and insects are favored articles in this turtle's diet." Lagler (1943) reported that Michigan adults had consumed filamentous algae, mosses, willow leaves (*Salix* sp.), insects (including black flies [Simuliidae], caddisfly [Trichoptera] larvae, and beetles), mollusks, snails, earthworms, bluegill (*Lepomis macrochirus*) and trout (Salmonidae), and tadpoles (*Lithobates* sp.). Countless authors have essentially reported that Wood Turtles opportunistically eat a wide range of green leaves, fruits, arthropods and other invertebrates, eggs, and carrion, including Harding and Bloomer (1979, p. 22), who reported collectively on turtles in natural or semi-natural conditions in Michigan and New Jersey had eaten blueberries (*Vaccinium* spp.), blackberries and raspberries (*Rubus* spp.), strawberries (*Fragaria* sp.), green leaves of willow and alder (Salix and Alnus spp.), as well as grasses, mosses, and algae and a variety of animal matter including molluscs, insects, earthworms, tadpoles, fish carrion, and newborn mice. Gilhen and Grantmyre (1973) and Graf et al. (2003), respectively, reported apparent consumption of blueberries and choke-cherries (*Prunus virginiana*) by Wood Turtles on Cape Breton Island, and Compton et al. (2002) speculated that raspberries were an important food in western Maine. Farrell and Graham (1991, p. 4) observed Wood Turtles eating green leaves of strawberries (*Fragaria* sp.) and strawberry and blackberry (*Rubus* sp.) fruits, fish carrion, and slugs, and Niederberger and Seidel (1999) reported Wood Turtle stomach contents as follows: vegetation (68%); earthworms (46%); other invertebrates (38%) and carrion (23%).

Among the foods taken by multiple individuals reported by Surface (1908, p. 162) were leaves and seeds of flowering plants (including *Ilex verticillata* and *Plantago major*, beetles, snails and slugs, bird carrion (7.6%). Green leaves (including cinquefoil, *Potentilla* sp.; and violets, *Viola* sp.) and fungi were prevalent in the foot items reported by Strang (1983, p. 45). Vogt (1981, p. 96) reported spruce (*Picea* sp.) needles eaten by a female in Wisconsin, and James Harding (pers. comm. to R. Farrell *in* Farrell and Graham 1991, p. 7) reported Wood Turtles feeding on willow (*Salix* sp.) leaves. Jones and Sievert (2009, p. 433), reported 395 recorded instances of identifiable food items in Massachusetts Wood Turtles. Slugs and other invertebrates comprised the majority of known food items (N=246), followed by the green leaves of at least 24 species plants (N=90). Corn, apples, raspberries, blackberries, and dewberries (*Rubus* spp.) and grapes were also eaten. Additional food items reported by Jones and Sievert (2009) included spotted salamander (*Ambystoma maculatum*) eggmassess, trout carrion, bird carrion, and the fungi genera *Russula* and *Lactarius*. In New Hampshire, Wicklow (unpublished data) reports that in early spring adult Wood Turtles feed extensively on bracken (*Pteridium aquilinum*) as well as tadpoles in vernal pools, and in fall Wood Turtles feed heavily on elderberries (*Sambucus* spp.), grapes (*Vitis* spp.)., and silky dogwood (*Cornus amomum*) fruits and drupes.

In Iowa, Tamplin (2006) reports that Wood Turtles routinely feed on prairie ragwort (*Senecio plattensis*), which is a highly toxic plant known to kill fish, lizards, and livestock.

A female Wood Turtle was reported to eat her own egg after depositing it prematurely in a hayfield (Jones and Sievert 2009, p. 434) and captive turtles have been observed to eat the eggs of *Terrapene carolina* (Ernst and Lovich 2009, p. 260). Ernst and Lovich (2009, p. 260) present a complete list of food items and a list of other references (Ernst and Barbour 1972; Czarnowski 1976; Ernst and McBreen 1991; Ernst 2001a; Castellano and Behler 2003).

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, and this behavior was described in depth in wild Pennsylvania adults by Kaufmann (1986; 1989). This has since been reported in Maine (K. Rolih, University of Massachusetts, pers. comm.), New Hampshire (B. Wicklow, St. Anselm College, unpublished data; Tuttle 1996); Massachusetts (M.T. Jones and D.T. Yorks, unpublished data); New Jersey (S. Angus, pers. comm.) and Virginia (T. Akre, Smithsonian Conservation Biology Institute, unpublished data), and in captivity (Kirkpatrick and Kirkpatrick 1996).

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. Patterson 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 (unpublished data) observed hatchlings to eat riffle beetles (Elmidae) and larvae of the caddisfly (Trichoptera) genus *Helicopsyche*.

Seasonal Activity Patterns

Active Season

Wood Turtles are active in streams throughout their northeastern range from March or April to November or December in most years, depending on elevation, latitude, and annual variation in weather. Arvisais et al. (2002) noted pronounced activity periods from May to October, including prenesting, nesting, postnesting, and prehibernation periods. Akre and Ernst (2006) report activity in northern Virginia during the late fall, winter, and early spring in addition to the window from March to November. Based on their data and regional reports, they propose two primary annual periods: hibernation (December–February) and the activity season (March–November). They break 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) prehibernation (October – November).

Below water temperatures of about 6˚C, Wood Turtles are generally inactive in streams (see Overwintering; Harding and Bloomer 1979; Ernst and McBreen 1991; Kaufmann 1992b; Akre 2002; Pulsifer 2012). In the southern portion of their range, Wood Turtles emerge and become active in March and begin feeding when water temperatures reach 4–5˚C and air temperatures reach 12–15˚C (Akre, unpublished data). Niederberger (1993, p. 13) reported that Wood Turtles were typically dormant when water temperatures ranged from 2–9˚C, but observed at least one instance of mounting at water temperature of 1˚C, and noted that while juveniles and females tended to be dormant at low temperatures, males sometimes moved underwater and appeared active. Anecdotal accounts of Wood Turtle moving under the ice of streams in January in northern New Jersey were provided by R. Farrell (Herpetological Associates) and S. Angus (pers. comm.).

Emergence and spring activity in Maine and northern New Hampshire may be determined by ice-out (Jones and Willey 2013b). White (2013) reported no activity between 19 December and 12 March in Nova Scotia. Activity in Michigan is rare after mid-October (Holman 2012, p.128). Graham and Forsberg (1991) reported extended periods of inactivity with only minor repositioning from December–February in Massachusetts. Klemens (1973, p. 172) reports that Wood Turtles become active in Connecticut in late March and early April. In western New York, Wright (1918) noted that Wood Turtles generally emerged and were found in streams around April 20 (a range of dates are reported, from the earliest of 20 March [1915] to 14 May [1906]), and were found again near streams between 20 September–15 October.

Male Wood Turtles generally become active earlier in the season and remain active later (Akre and Ernst 2006). By September in Québec, most turtles have returned to their home streams (Saumure et al. 2007), which is probably representative of autumn seasonality at many northern sites.

Mating Season

Courting and copulation takes places commonly in both the spring and fall in Minnesota (Breckenridge 1958, p. 170); Wisconsin (Brewster 1985); Massachusetts (Jones 2009); New York (Wright 1918, p. 55), New Jersey (Farrell and Graham 1991; Harding and Bloomer 1979); 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 Northeast region, Swanson (1952, p. 47) reports "clasping pairs in trout streams in the middle of April," and reports mating in captivity in March and September. Autumnal mating was reported to be more common in Québec (Walde 1998), Vermont (Parren 2013, p. 179) and Virginia (Akre 2002). Harding (1991) reported that mating is most common in June and September in Michigan. Kleopfer (VDGIF, pers. comm.) reports Wood Turtles mounted under ice in December in Virginia.

Nesting Season

Throughout the Northeast region and adjacent areas, Wood Turtles generally nest in June, although observed dates range from mid-May to mid-July (Thoreau 2009 [entries from 1855–1860, see Historical and Current Distribution, this document]; Harding and Bloomer 1979; Compton 1999; Walde et al. 2007; reviewed by Bowen and Gillingham 2004, Table 2; Akre 2010). Wood Turtles in Ontario observed by Brooks et al. (1992) nested between 7–19 June, and Walde (1998) reported nesting dates between 9–28 June in Québec; this range closely mirrored the dates reported by Harding (1991; 1994) of 10–29 June. In Maine, Compton (1999, p. 21) reported a mean nesting date of 20 June, with half of all nests deposited between 12–25 June. In New Hampshire, Tuttle and Carroll (1997) reported a range of nesting dates from 2–13 June. Parren (2013) recorded most nesting activity between 23 May and 21 June. In Massachusetts, Jones (2009, p. 156) reported nests deposited between 28 May and 4 July. Median deposition dates for each year (2004–2008) ranged from 7–20 June; the average of these was 12 June. Castellano et al. (2008) reported nesting during the last two weeks of May and the first two weeks of June in New Jersey. Buhlmann and Osborn (2011) reported that nesting in a Morris County, New Jersey population ranged from 21 May to 13 June during the period 2007 to 2010. Ernst (2001b) observed a range of nesting from June 4–19 in Lancaster County, Pennsylvania, while in Centre County, Kaufmann (1992) observed nesting from 4–16 June. In Frederick-Shenandoah counties, Virginia, Akre (2010) reported nesting from 23 May–22 June, 2010.

Walde et al. (2008) reported that 38.5% of nests in Québec are initiated between 0500 and 0900 hr. Jones found that 90% of nests in Massachusetts and New Hampshire were initiated in the late afternoon and evening. Akre (2010) 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.

Hatchlings typically emerge in August (Castellano et al. 2008; Akre 2010), but may emerge in September or October (See Incubation, earlier).

Aestivation

Aestivation is not well documented to occur in the Wood Turtle. Most authors report continuous activity throughout the summer months (Strang 1983, p. 43). 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 (Akre 2002; Akre and Ernst 2006), and fine-scale movements appear to decrease during the warmest months of July and August. Some limited evidence of individual turtles becoming inactive on land during hot spells was also reported by S. Angus (unpublished data) in New Jersey.

Overwintering

Despite 19th and early 20th century accounts of terrestrial brumation (e.g., Surface 1908), all recent telemetry studies have documented overwintering in streams, rivers, and associated aquatic habitats (Farrell and Graham 1991; Tuttle and Carroll 1997; Niederberger and Seidel 1999; Ultsch 2006; Akre and Ernst 2006; Greaves and Litzgus 2008; White 2013). Many authors have noted the propensity of Wood Turtles to overwinter, or brumate, in association with deep pools, rootmasses of large trees, and undercut banks. In New Hampshire, Wicklow (pers. comm.) reports that Wood Turtles keep their heads free of debris when hibernating even when much of the shell may be covered with leaves, sticks, or sand.

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 used, and that Wood Turtles overwintered at a mean water depth of 0.67±0.35 m. Most turtles overwintered in reaches dominated by fine sediments. Wood Turtles often overwintered in close proximity to large woody structure 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 are likely to protect turtles from potentially lethal scouring ice sheet flows and/or being washed downstream during spring run-off events (Saumure, pers. comm.; Jones and Sievert 2009). Most turtles (16 of 19 and 21 of 24 in years one and two, respectively) overwintered within 2.0 m from shore. In White's study, the mean dissolved oxygen (DO) across all overwintering sites for 20 turtles (year one) and 29 turtles (Year 2), 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 and on the gravel bottoms of pools in woodland streams (Farrell and Graham 1991), and amongst tree roots (Klemens 1993, p. 172). Farrell and Graham (1991) report an important overwintering site associated with the roots of a large sycamore (*Platanus occidentalis*) at a bend in a stream in Sussex County, New Jersey. 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 such as sycamore (*Platanus occidentalis*).

Aggregations.—The Wood Turtle is noted for its large aggregations associated with late fall and early winter, often near overwintering sites (Bloomer 1978). Klemens (1993, p. 172) reported an aggregation of 20 Wood Turtles in Tolland County, Connecticut. Farrell and Graham (1991) reported an aggregation of 28 Wood Turtles in a New Jersey stream. Niederberger (1993) reported an aggregation of 80 turtles, with 35 turtles visible on a pool bottom and others scattered under banks with their carapaces visible.

Daily activity patterns

With the exception of nesting females, which are frequently active well after dark throughout the region, Wood Turtles are primarily diurnal, although whether their activity patterns are unimodal (peak mid-day) or bimodal (more active in mornings and afternoon) appears to vary by season, geographic location, and weather conditions. Ernst and Lovich (2009) report that Wood Turtles in Virginia may use creeks on a daily basis.

Thermoregulation

Thermoregulation is a critical component of Wood Turtle behavior and activity, especially during emergence from brumation in the spring (Dubois et al. 2009). Thermoregulation in the Wood Turtle reflects the interaction of temperature, humidity, and weather. When Wood Turtles become active in the spring, they are first unimodal (active during the warmest part of the day), moving to bimodal with increasing temperatures and greater risk of water loss, and moving back to unimodal with decreasing temperatures in the fall. Combined with foraging opportunities, access to basking sites probably drives Wood Turtle habitat selection at the fine scale (Compton et al. 2002; Saumure 2004).

Paleontological, Prehistoric and Archaeological Records

The genus *Glyptemys* is known from the middle to Late Barstovian of Nebraska (ca 14.5–11.5 million ybp, Holman and Fritz 2001; Ernst and Lovich 2009, p. 251). *Glyptemys valentinensis* may have given rise to *G. insculpta* between the Late Barstovian and Late Hemphillian times (11.5–5.5 million ybp).

Molecular studies indicate at least one southern United States Pleistocene refugium for *G. insculpta* (Amato 2006), but fossil evidence is rare (Ernst and Lovich 2009, p. 251). Evidence suggests that some populations of Wood Turtles ranged south along the Appalachians during the Pleistocene. Late Pleistocene (Rancholabrean, 12,000–16,000 ybp) Wood Turtle remains (a partial carapace) were recovered from Cheek Bend Cave along the Duck River, Maury County, central Tennessee (Parmalee and Klippel 1981, p. 413). Wood Turtle remains (partial plastron and pleural bones) from Ladd Quarry, Bartow County, Georgia were also believed to be late Pleistocene (Rancholabrean) in age (Holman 1967 in Parmalee and Klippel 1981, p. 414). Together, these remains provide additional evidence for a southern Appalachian refugium occupied by *G. insculpta* during the late Pleistocene.

Several Pleistocene fossil records suggest that Wood Turtles occupied at least part of their modern range during interglacial events. These include Rancholabrean (70,000–80,000 BP) remains of *G. insculpta* from the East Milford mastodon site near the current Shubenacadie River in Halifax County, Nova Scotia (Holman and Clouthier 1995), Middle Pleistocene (Late Irvingtonian) Wood Turtle remains from the Port Kennedy Cave, Montgomery County, Pennsylvania, and Pleistocene (Irvingtonian) Wood Turtle remains recovered from the Frankstown Cave, Blair County, Pennsylvania (Peterson 1926)—all in watersheds where they are historically reported (Pennsylvania Natural Heritage Program, unpublished data). These data suggest that Wood Turtles occupied at least part of their modern range during interglacial events of the Pleistocene (Hay 1923; Parris and Daeschler 1995, p. 564).

Wood Turtles have been reported from numerous mid- to late-Holocene archaeological sites throughout the northeastern United States. In Ontario, Wood Turtle remains were recovered from a Native American site near Roebuck, Leeds and Grenville counties (Bleakney 1958, p. 4). Adler (1968) reported Wood Turtle remains from archaeological sites in Raddatz rockshelter, Sauk County, Wisconsin; and Juntunen, Mackinac County, Michigan. In Maine, evidence of a single Wood Turtle was recovered from the Little Ossipee North site in Oxford County, dating from approximately 1000 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, unpublished data, 2012). 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—a region of the Merrimack River still occupied by the species (Howe 1986 *in* Rhodin 1995; New Hampshire Natural Heritage Bureau and New Hampshire Fish and Game Department, unpublished occurrence data, 2012). By contrast, Wood Turtles account 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), and are even more rare in the turtle bone fauna at Flagg Swamp, Middlesex County, Massachusetts (Huntington and Shaw 1982) and the Cedar Swamp, Middleborough, Plymouth County, Massachusetts (Rhodin 1992).

Historical and Current Distribution

Here follows a brief summary of the recent (1850–present) range of Wood Turtles. Extant populations span at least 9˚ of latitude from the southernmost populations in the northern third of West Virginia and Virginia (38.5˚N) to the northernmost confirmed populations in Québec and New Brunswick (47.5˚N). Witmer and Fuller (2011) include the Wood Turtle in an appendix of vertebrates that have been introduced to portions of the United States, but we have not found corroboration of successful introduction to a new site. Despite strong interest in the species by 19th century scientists and naturalists, a complete picture of the Wood Turtle's native range was not firmly in place until the mid-20th century. In fact, a major range extension to Cape Breton Island, Nova Scotia—the only confirmed offshore occurrence of Wood Turtles —was only published in 1973 (Bleakney 1958b, p. 28 [reports absence of turtle sightings on Cape Breton]; Gilhen and Grantmire 1973; Gräf et al. 2003). Question remains as to the recent native status, and current population status, of Wood Turtles in at least two states (Delaware and Ohio; see Part 2 in Jones and Willey 2015).

The Wood Turtle's general extent of occurrence now strongly overlaps with the regions glaciated by the Laurentide glacial advances of the Pleistocene epoch. This is—and certainly was, three centuries ago— a heavily forested region of about 725,000 km^2 (280,000 mi^2), straddling the northern reaches of the Eastern Temperate Forest ecoregion and the southern tier of the Northern Forest ecoregion. Just over half of this area, occurs within the Northeast Region from Virginia to Maine, encompassing some of the most densely populated areas in North America, including dozens of large cities from New York and Washington, D.C. to Albany, Harrisburg, and Rochester, New York (the latter is approximately the geographic center of the Wood Turtle's range).

Northeastern United States

A complete analysis of the distribution of Wood Turtles in the Northeastern United States is presented in Part 2 of Jones and Willey (2015). We find that a descriptive summary of our current knowledge provides useful context, and so we here summarize the knowledge of the range of the Wood Turtle at the outset of this cooperative project. A descriptive account of the distribution of the Wood Turtle further provides context for the following sections, which contain original analyses. In New England, the Wood Turtle's range encompasses most of the five large New England states but is absent from much of the coastal plain in Connecticut, Rhode Island and Massachusetts—especially in the vicinity of Buzzards Bays and Cape Cod—and are evidently absent from all of the major offshore islands, including Martha's Vineyard, the Elizabeth Islands, and Nantucket in Massachusetts and Mount Desert Island in Maine (but see discussion under Maine, later). Wood Turtles are absent from mountain areas, but few isolated populations occur within the uplifted massifs of the White Mountains and in the vicinity of Baxter State Park, but they are generally absent from these high-elevation and high-relief regions. Wood Turtles are also now absent from the greater Boston area.

Wood Turtles are prominently absent from most major islands within their generalized range, including Anticosti, Prince Edward Island (Logier and Toner 1961, p. 51), Martha's Vineyard, Nantucket, and Long Island. The only major island in North America with confirmed occurrences of Wood Turtle is Cape Breton, Nova Scotia.

Maine.—Wood Turtles have been reported from all but Sagadahoc County (Hunter et al. 1999; Maine Department of Inland Fisheries and Wildlife, unpublished occurrence data 2012). Early accounts of Wood Turtles in Maine include Say (1825) and perhaps Williamson's (1832) account of "speckled land turtle," and the reports of Agassiz (1857, p. 443), who reported a northern specimen from the Little Madawaska River in Aroostook County, Fogg (1862), and Verrill (1863, p. 196), who noted that Wood Turtles were "common" in vicinity of Norway, Oxford County, but that it was apparently uncommon east of the Penobscot River. Boardman (1903) reported Wood Turtles from Calais. The Wood Turtle is not native to the islands of the Maine coast: records from Isle au Haut (Knox County) in August 1999 and Mount Desert Island (Hancock County) in 1958 and 1989 (Brotherton et al. 2004, p. 98; Maine Department of Inland Fisheries and Wildlife, unpublished occurrence records 2012), almost certainly represent released or escaped animals. Historical accounts of Wood Turtles (and other species) in Maine are summarized by McCollough (1997), who also noted that Wood Turtles are less abundant near the coast.

New Hampshire.—Wood Turtles are known from every county in New Hampshire (Taylor 1993; Taylor 1997; New Hampshire Department of Fish and Game and New Hampshire Natural Heritage Bureau, unpublished data 2012). Huse (1901, p. 49) reported Wood Turtles as common in New Hampshire. Oliver and Bailey (1939) provided records from eight of New Hampshire's ten counties (except Strafford and Carroll). Wood Turtles are known from only four occurrences within the White Mountain National Forest (WMNF) proclamation boundary, which includes large portions of Carroll County. At nearly 304,000 hectares, the WMNF is the largest block of federal land in New England—probably the result of a combination of climatic exclusion (the White Mountain region is largely above 500 m) and scarcity of low-gradient stream habitats not subject to severe flooding related to steep upstream basins (Bowen and Gillingham 2004; Jones and Sievert 2009).

Vermont.—Wood Turtles are reported from all of Vermont's fourteen counties, in both the Champlain Valley (St. Lawrence watershed) and the Connecticut watershed, along both the west and east slopes of the Green Mountains (Vermont Reptile and Amphibian Atlas, unpublished data 2013; J. Andrews, unpublished data). The earliest confirmed specimen from Vermont maybe an animal collected at Sharon in Windsor County in 1900 by M. Parker (CAS 54480), although Wood Turtles were reported from Vermont by Thompson (1853), together with painted and snapping turtles. A specimen collected in South Hero, Grand Isle County on July 29, 1934 by L.H. Babbitt (Boston Museum of Natural History 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. DesMeules (1997) notes that Wood Turtles are found throughout the state but that little more is known about its distribution or abundance.

Massachusetts.—Wood Turtles occur throughout all mainland counties of Massachusetts (Massachusetts Natural Heritage and Endangered Species Program, unpublished occurrence data 2012), but are not known from Cape Cod, Barnstable County (Klemens 1993); or the islands of Martha's Vineyard (Dukes County) or Nantucket Island, Nantucket County (Lazell 1976). Lazell (1976) discredited a single recordsfrom Mashpee, Barnstable County, on Cape Cod.

Several nineteenth century accounts of Wood Turtle populations in Massachusetts are among the earliest such records available. The Wood Turtle was included in the early list of seven native turtles of Smith (1833). Storer (1840, p. 27) reported the Wood Turtle from Walpole (Norfolk County), Concord (Middlesex County), Amherst (Hampshire County), and Andover (Essex County). Louis Agassiz (1857) described Wood Turtles as common near Lancaster, Worcester County, circa 1854; Henry David Thoreau (2009) provided many accounts of abundant Wood Turtles in Concord, Middlesex County, circa 1855–1860; and J.A. Allen (1868, p. 175) reported Wood Turtles to be "common" in the vicinity of Springfield, Hampden County, in the 1860s. Through the 20th century, anecdotal reports appear to indicate a gradual decline. Babcock (1919, p. 404) indicates that is not common around Dedham, Essex County.

Connecticut.—Wood Turtles have been reported from every county in Connecticut, but are rare in the coastal zone and in eastern Windham and New London counties (Klemens 1993, p. 171–172). They are reported to reach their greatest abundance in the hills of eastern Connecticut, between the "eastern escarpment of the Central Connecticut Lowland and the Quinebaug Valley (Klemens 1993, p. 172)." Early data were provided by Babcock (1919) and Finneran (1948). The species historically was broadly distributed throughout the entire state.

Rhode Island.—The Wood Turtle has been consistently reported as rare in Rhode Island (e.g., Drowne 1905, p. 5; Klemens 1993, p. 172), where it is known to occur in Providence, Kent, and Washington counties. There is a single record from Bristol County in 1983 (C. Raithel, Rhode Island Department of Environmental Management, unpublished data) and an anecdotal account of a dead Wood Turtle on a beach in Newport County ca. 1991–92 (D. Yorks, Maine Department of Inland Fisheries and Wildlife, pers. comm.) Consistent with regional trends, there are no records from the islands of Narragansett Bay.

New York.—Wood Turtles range throughout New York from the Hudson Valley to Lake Erie and eastern Lake Ontario with the exception of Long Island (Klemens 1993). Corroborated occurrences of multiple turtles, or population data, are rare in some westernmost counties such as Chautauqua, Orleans, Gennessee, Monroe, Livingston, Yates, and Seneca (New York Herp Atlas 2013), and the lake plain south of Lake Ontario. Wood Turtles appear to be rare on the southern lake plain of Lake Ontario, but evidently occur in most of the suitable drainages on the west shores of Lake Champlain as well as throughout the entire Hudson Valley. Although many distribution maps (e.g., Ernst and Lovich 2009, p. 251) 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 (G. Johnson, SUNY Potsdam, unpublished data; NY Herp Atlas, unpublished data; see Part 3 of Jones and Willey 2015). Wood Turtles were described as "common" in the Hudson Highlands of southeastern New York by

Mearns (1898, p. 329) and as "fairly common" in Essex County, between Lake Placid and Tahawus in the Adirondacks, in the 1920s (Weber 1928). Wright (1918, p. 54–56) described Wood Turtles as relatively common in the vicinity of Ithaca, New York, at the southern end of Cayuga Lake. Ditmars (1905, p. 137; 1907, p. 53) vaguely reports Wood Turtles from the vicinity of New York City but does not provide specific locality data. Clausen (1943) reports three specimens from Tioga County on the Pennsylvania border.

Wood Turtles have been reported on at least three occasions from Long Island but none of these reports are sufficient to demonstrate that a population occurred there (Murphy 1916, p. 57). Five Wood Turtles found washed ashore at Orient, Mattituck, Riverhead, and East Marion, eastern Long Island, between 1919–1926 may have originated from the Connecticut River watershed of New England, displaced during floods (Latham 1971). An individual collected from the Southern State Parkway northwest of Islip, Suffolk County, in the 1980s, may have been a released captive (Price 1982). No further specimens from Long Island have been documented (Al Breisch, New York State Department of Environmental Conservation [retired], pers. comm.)

New Jersey.—Wood Turtles range throughout all of northern New Jersey north of Camden, southern Burlington, and southern Ocean counties. Agassiz (1857, p. 443), reported that New Jersey encompassed the southernmost records of Wood Turtle and subsequently Stone (1906, p.169) noted specimens from Delaware Gap, Warren County, and Woodbury, Gloucester County, New Jersey. The record from Gloucester County in 1906, and two records from Atlantic and southern Burlington counties in 1945 and 1978, cannot be replicated today. Stone (1906, p. 169) commented that no specimens from the Pine Barrens were known to him.

Pennsylvania.—The Wood Turtle ranges across almost all of central and eastern Pennsylvania. Surface (1908, p. 160–161) provided records from 22 counties ranging as far west as Venango County. Typical range depictions and descriptions (e.g., Surface 1908, p. 160; McCoy 1982; Ernst and Lovich 2009, p. 251) suggest that the Wood Turtle ranges west nearly to the Ohio border. In fact, there are historic records from Erie Harbor and the Presque Isle peninsula at Erie (CM 6880, Collections of S.H. Williams, Carnegie Museum of Natural History, Pittsburgh; McKinstry et al. 1987). However, from the information provided, it is impossible to confidently assign the Erie County records to typical stream habitats. Reportedly, small streams once entered Lake Erie where the city of Erie is now situated, and the historic records in the region may reflect populations formerly present along the Erie shore (M. Lethaby, Tom Ridge Center for the Environment, Erie, PA, pers. comm.) Interestingly, there is a record in the Royal Ontario Museum from Long Point, Norfolk County, Ontario, 40 km due north across Lake Erie and possibly encompassing a similar dune ridge island environment (Logier and Toner 1961, p. 52), although this specimen is believed to represent a released captive animal (R.A. Saumure, pers. comm.). The nearest record to Erie, and one of the westernmost specimens from south of the Great Lakes, was collected at Linesville, Crawford County, by Daniel A. Atkinson (who collected Wood Turtles across Pennsylvania in the spring of 1906) on June 9, 1906 (CM2985, Coll. D. Atkinson). The Shenango River, which flows along the Pennsylvania-Ohio border and was dammed in 1934 to create the Pymatuning Reservoir, may have supported one of the most western population of Wood Turtles in our region. Other early reports of the Wood Turtle from Pennsylvania include Stone (1906, p. 169), 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) 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.

Delaware.—The historic status of Wood Turtles in Delaware is not clear and is poorly substantiated (NatureServe 2012; H. Niederitter, pers. comm. 2012; Nazdrowicz, pers. comm. 2018; but see Part 2 of Jones and Willey 2015). Stone (1906, p. 169), in his summary of reptiles and amphibians from Pennsylvania, Delaware, and New Jersey, and who reported the earliest records of Wood Turtle from adjacent Chester County, did not report any specimens of Wood Turtles from Delaware. Several turtle biologists have surveyed northern Delaware for other turtle species, including Bog Turtles (Arndt 1977) and Eastern Box Turtles (Kipp 2003; Nazdrowicz et al. 2010) and did not report the occurrence of Wood Turtles. A noteworthy archeological occurrence of Wood Turtle was reported by the Delaware Department of Transportation during excavations near Dover: faunal remains recovered from the Thomas Dawson farm at Coopers Corners, Kent County, Delaware, reportedly included one fragment of Wood Turtle. The assemblage was dated to 1740–1780 (Bedell 2002, Ch. 3). If confirmed, this occurrence is remarkable because it is one of only two records from the Delmarva Peninsula. Wood Turtles very likely occurred naturally in New Castle County, along the borders with Pennsylvania and Maryland, where there have been recent unconfirmed reports and negative follow-up surveys (H. Niederriter, pers. comm.). Suitable habitat, albeit fragmented, remains in northern Delaware (see Part 2 and Part 3 in Jones and Willey 2015). It appears clear that the Wood Turtle is functionally extirpated from the state.

Maryland.—In Maryland, as in Pennsylvania and Virginia, Wood Turtles evidently occurred naturally in the Central Appalachians, Ridge and Valley, Blue Ridge, and Northern Piedmont Ecoregions (Conant 1958; Harris 1975; Miller 1993). Wood Turtles occur through all of the western counties, reaching into portions of the Piedmont ecoregions in the east.

Norden and Zyla (1989) presented a series of 12 records from Coastal Plain counties, including the first for Anne Arundel County, voicing support for a native population of Wood Turtles on the Coastal Plain. Their conclusions were questioned by R.W. Miller four years later (1993), largely on the grounds of a lack of historical data and museum specimens. However, it remains clear that Wood Turtles were once native to the lower Susquehanna in Maryland and the lower Potomac in Maryland and Virginia, and several creeks in the vicinity of Washington, D.C., and Arlington, Virginia (Akre and Ernst 2006; T. Akre, SCBI, pers. comm.). Wood Turtles collected from near Havre de Grace, Cecil County (e.g., McCauley 1955, p. 55) were presumed by Reed (1956) to be waifs displaced from farther upstream in those respective watersheds (in the case of the Susquehanna, well into Pennsylvania); these were considered feasible by Miller (1993) because of “strong” support for the occurrence of Wood Turtles upstream in the Susquehanna watershed. According to Scott Smith (MD DNR, pers. comm.), Wood Turtle populations have been recently confirmed from the vicinity of Aberdeen, and Wood Turtles were reported in the vicinity of the Conowingo Dam by Cooper (1949), strongly indicating their native occurrence in the lower Susquehanna. These stations, as well as the population reported from Elk Neck, are biogeographically significant because of their proximity to Delaware and the Delmarva Peninsula, where the native status of Wood Turtles is problematic. The Elk Neck population is probably extirpated (Scott Smith, Maryland Department of Natural Resources, pers. comm.).

A single record near Easton, Talbot County, Maryland, has prompted much discussion because of its potential biogeographical significance as the only record from Maryland’s eastern shore (NHSM R-529). The record was dismissed by McCauley (1955, p. 155 in Reed 1956, p. 80). Conant (1958, p. 51) agrees with McCauley’s dismissal of this record. Reed (1956, p. 80) argued that the Talbot County Wood Turtle location also supports some plants typical of the Piedmont Plateau, and that the vicinity of Easton may have similarly supported a natural occurrence of Wood Turtles; this line of logic was summarily dismissed by Miller (1993; p. 90) on many points, among them that the localized occurrence of Piedmont plants is insufficient grounds to validate such an isolated and unusual record, and that the Wood Turtle is not a piedmont species in Maryland but rather a montane species, and so the connection is more tenuous. Miller (1993, p. 90) is also skeptical of the Talbot County record and of the tendency for authors to repeat the anomalous location without critical review or corroborating evidence. The current opinion of state managers is that Wood Turtles are not native to the eastern shore and Delmarva Peninsula (Scott Smith, MD DNR, pers. comm.). Historic records in the vicinity of Great Falls, Fairfax County, VA, apparently represent a natural historic 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 that there was once a network of populations that lived in sidestreams on both sides of the Potomac River, both up- and downstream of Great Falls. The quantity of historic sightings and records along the lower Potomac River (as well as evidence that Wood Turtles nest on the river) suggests that some individuals did live on the Potomac itself, in addition to sidestream areas.

Washington, D.C.— Although reliable documentation of Wood Turtles within the District of Columbia, and adjacent Anne Arundel County, Maryland, is minimal, substantial evidence from Maryland, Virginia, and the District of Columbia indicate that Wood Turtles were native to Washington, D.C. Wood Turtles are now considered “possibly extirpated” by the District Department of the Environment. There have been no recent confirmed reports, although there have been unconfirmed sightings (L. Rohrbaugh, wildlife biologist, District Department of the Environment, pers. comm.). A specimen from Washington in the National Museum (USNM 62556) was believed by Miller (1993) to be an animal referred to by Shufeldt (1919) as originating near Bennings in eastern Washington, D.C.

Two sight records from the Anacostia watershed along the eastern border district in Maryland (Norden and Zyla 1989) may provide additional support for the natural historic occurrence of Wood Turtles in the Anacostia drainage, but these were questioned by Miller (1993, p. 91). Suitable (though fragmented) habitat still exists at several locations in the District.

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 (K. O’Malley, WV DNR, unpublished data) are noteworthy. Bond (1931, p. 54) reports Wood Turtles as “not uncommon” in Monogalia County, although this record was discounted by Breisch (2006). Recent sightings in Beaver County, Pennsylvania, suggest that Wood Turtles may have occurred in neighboring Hancock County, West Virginia, and surveys may be warranted here.

Virginia.—Wood Turtles occurred historically throughout most of Virginia’s northernmost counties, including Fairfax, Loudoun, Clarke, Frederick, Warren, Shenandoah, Page, and Rockingham (Akre 2002, p. 2; Akre 2010, p. 3). An early record from Fairfax County was provided by Dunn (1940, p. 8). In the 1980s, Wood Turtles were reported by U.S. Forest Service personnel in the southern part of Rockingham County (Buhlmann and Mitchell 1989). A recent record from the Blue Ridge Parkway in Nelson County was judged to be a released or escaped captive (T. Akre, pers. comm.). Extensive areas of formerly suitable habitat in Virginia have become unsuitable and fragmented by urban sprawl from the Washington, D.C. metropolitan area (see Part 4), and only one population is known to persist in the area east of the Blue Ridge (Akre 2010, p. 3). The majority of records and populations known to be reasonably large come from west of the Blue Ridge and the Shenandoah River (Akre 2010, p. 3). An Arlington record from the mouth of Four Mile Run near the Potomac River and US-1 in 1953 (USNM 136639) is substantiated by a recent (1993) record in the records of the Virginia Department of Game and Inland Fisheries from approximately 8 km upstream. Much of the discussion of Wood Turtles in the Lower Potomac under Maryland, earlier, applies to Virginia as well.

Canada

New Brunswick.—Wood Turtles are patchily but widely throughout New Brunswick with the exception of southwestern portions of the province and the highland plateau of northern New Brunswick (McAlpine and Gerrietts 1999; McAlpine 2010; D.F. McAlpine, pers. comm.). In the north, Wood Turtles have been documented from the Restigouche watershed near Cambellton and the St. Francis basin near the Maine border. Wood Turtles have also been documented throughout the Miramichi drainage on the Gulf of St. Lawrence coast (M. Toner, New Brunswick Department of Natural Resources, pers. comm.; Atlantic Canada Conservation Data Centre Rare Species Database 2013). Wood Turtles were reported by Bleakney (1958, p. 66 & 69) from south-central and northern New Brunswick. Wood Turtles are apparently rare on the highland plateau of northern New Brunswick, although they apparently occur in many streams around the periphery of this highland massif. It seems likely that New Brunswick harbors some of the most intact and productive Wood Turtle habitat remaining in Canada—and all of North America—but the populations in this region have not been intensively studied (Heward and McAlpine 1994; McAlpine and Gerriets 1999).

Nova Scotia.—On the peninsula of 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, p. 127; Bleakney 1958b; Bleakney 1963; Nova Scotia DNR 2003) and Guysborough County (Bleakney 1958b; Pulsifer et al. 2006; White et al. 2010). Wood Turtles occur in several drainages of the southern third of Cape Breton Island, where they were only documented in the 1970s (Logier and Toner 1961, p. 51; Gilhen and Grantmire 1973; Gräf et al. 2003). Wood Turtles are not native to Prince Edward Island or Newfoundland (Bleakney 1958b).

Ontario.—Wood Turtles are widely distributed in watersheds throughout central Ontario from those draining into Lake Superior near Sault Ste. Marie (Algoma District) in the west (Logier and Toner 1961, p. 51), to basins draining into Gore Bay on Lake Huron to the St. Lawrence Valley east of Lake Ontario (Ontario Wood Turtle Recovery Team 2009), although Logier (1939) suggested the east (Appalachians) and west (Great Lakes) populations may be isolated from one another because of land conversion in southern Ontario. They are known throughout eastern portions of Algonquin Provincial Park and adjacent areas, where they have been intensively studied (Quinn and Tate 1991; Brooks and Brown 1992 *in* Foscarini and Brooks 1997; Brooks et al. 1992; COSEWIC 2007). Relatively isolated occurrences have been documented near Midland on Georgian Bay and in Huron County on Lake Huron (Logier 1939; Oldham and Weller 1989). Greaves and Litzgus (2009) studied the demographic structure of a Wood Turtle population in the Sudbury District. In south-central Ontario Wood Turtles formerly occurred along the north shore of Lake Erie (Logier and Toner 1961), but populations near Wheatley, Hamilton, Burlington, Mississauga, Toronto, and Oshawa have apparently been extirpated (COSEWIC 2007). Farther north, historic occurrences near Ottawa, Midland, Brechin, and Georgina have also been extirpated (COSEWIC 2007).

Québec.—Wood Turtles occur widely throughout Québec south of the 48th parallel (Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, unpublished occurrence data 2013), on both sides of the St. Lawrence River, a vast saltwater gulf. Bleakney (1958b) reported that Wood Turtles reach their northernmost range limit in the "St. Maurice" Valley. Biogeographically, various regions of southern Québec share affinities with the eastern Great Lakes Region of Ontario and New York, with which western Québec shares vast exposures of Precambrian shield rock as part of the Mixed Wood Shield ecoregion; the St. Lawrence and Champlain Valleys of New York and Vermont, composing the northern tier of the Mixed Wood Plains ecoregion; the Green and White Mountains of Vermont and New Hampshire; and the Madawaska watershed of western New Brunswick (encompassing part of the Atlantic Highlands ecoregion). Denman and Lapper (1964) report Wood Turtles from Mont St. Hilaire, Rouville County. Isolated northern occurrences (above the 48th parallel) have been reported from the vicinity of Val-d'Or in western Québec, La Tuque, Sanguenay, and Cap-Chat on the north coast of the Gaspé Peninsula, although Provancher (1874) reports an absence of turtles in the Sanguenay Region (Bleakney 1958b) and the northern Gaspésie record is highly questionable (W. Bertacci and Y. Dubois, Québec Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, pers. comm.). Québec populations are primarily constrained to the watersheds of the Ottawa River, the lower St. Lawrence River (including the Missisquoi and Lake Champlain basin of Vermont and the Restigouche watershed of New Brunswick), and St. John River near the Maine and New Brunswick borders. In several cases, streams shared by both Québec and the United States, and in some cases forming the border itself, harbor populations of Wood Turtles. In the past two decades, Québec has established itself as a leading supporter of Wood Turtle research (Arvisais et al. 2002; Walde et al. 2003; Arvisais et al. 2004; Saumure et al. 2007). Wood Turtles do not occur on Anticosti Island (Bleakney 1958b).

Great Lakes Region

Wood Turtles occur throughout small regions of eastern Minnesota, and as a disjunct population in northeastern Iowa, and occur across relatively large areas of northern Wisconsin, Michigan and southern Ontario. Despite the enormous area of suitable habitat surrounding the Great Lakes and Upper Mississippi River watershed—it is some 1,100 km from western Lake Ontario to the isolated Iowa populations—Wood Turtles went largely unnoticed by scientists until the 1920s–1940s. This is not surprising given that the major cities of Detroit, Chicago, and Milwaukee lie outside the range of the Wood Turtle.

Ohio.—The natural history and distribution—and even the 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, p. 30) and repeated by Ditmars (1907, p. 53) and Surface (1908, p. 160). Conant (1938, p. 8) considered the native status of Wood Turtles in Ohio to be "doubtful", although 13 years later, Conant (1951, p. 13) states of northeast Ohio that "probably *Clemmys insculpta* and *Clemmys 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) include northeastern Ohio is his range description. 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 large stream 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, pers. comm. to Iverson 1992). A record in Stark County, Ohio in Iverson (1992) is a mislabeled record from Butler County, Pennsylvania (CM31215). Conant (1951) searched for Wood Turtles unsuccessfully in the northeast corner of Ohio, but determined that Wood Turtles likely occur in that part of the state. As noted above, a specimen from Linesville, Crawford County, Pennsylvania, provides limited evidence of a historic population in the Linesville Creek–Shenango River Watershed (since 1934, flooded by the Pymatuning Dam), which straddles the Pennsylvania–Ohio border. Conant's (1951, p. 13) 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 County, Pennsylvania (PA NHP 2013) bear relevance to determining the native status of Wood Turtles in Ohio.

Illinois.—There are at least two enigmatic records of Wood Turtle from Illinois. One series of two specimens were from Evanston, Cook County, where shipped to the MCZ between 1864 and 1872 (MCZ 4056). As Evanston is the location of Northwestern University, it seems possible that these records were either released captives or mislabeled with the University of origin rather than the capture site. Another specimen was observed in the Des Plaines River Ship Canal, Cook County (Miller 1993, pers. comm. to Iverson 1992), which is clearly atypical habitat in addition to being widely disjunct, and must represent an anomalous occurrence.

Iowa.—The Wood Turtle is narrowly restricted to the Cedar River drainage of northeastern Iowa. In 1924, E.L. Palmer of Cornell University reported a juvenile Wood Turtle from Ames, Story County, Iowa, extending the range south and west from recently discovered sites on the Wisconsin-Minnesota border (Wagner 1922; Palmer 1924). This unusual occurrence—not only a new state record, but near the geographic center of the state, and squarely within the Temperate Prairies ecoregion—was subsequently repeated in large-scale compendia, such as Clifford Pope's Turtles of the United States and Canada (Pope 1939). The observation was discredited (Bailey 1941) as a misidentified juvenile Blanding's turtle (*Emydoidea blandingii*). Nonetheless, by the mid-1940s, Wood Turtles were well-known to occur in the Cedar watershed of northeastern Iowa, and the populations in Black Hawk and Butler counties are the subject of long-term research by biologists the University of Northern Iowa (Tamplin et al. 2006; Tamplin et al. 2009; Spradling et al. 2010; Tamplin, pers. comm.). These populations, and those in extreme southeastern Minnesota and southwestern Wisconsin, represent the only occurrence of Wood Turtles within the prairie ecoregions of the middle United States—noteworthy for what is otherwise a creature of cool, northern forests. In these peripheral prairie regions it is common for the floodplains of larger rivers to support heavily forested floodplains.

Minnesota.—Wood Turtles reach their westernmost extent of occurrence in the Mississippi drainage of south-central Minnesota (Breckenridge 1958; Ernst 1973; Iverson 1992; Ernst and Lovich 2009). In this state, Wood Turtles are known primarily from three distinct regions: (1) watersheds draining into Lake Superior in St. Louis and Lake counties; (2) those from Pine and Chisago counties in the St. Croix watershed; and (3) those along the Cannon and Mississippi Rivers in Rice, Goodhue, Steele, Dodge, Olmsted and Mower counties in the southern part of the state, reaching almost to the Iowa border in Mower County (Ernst 1973).

Wisconsin.—Wood Turtles occur widely throughout the forested regions of northern and western Wisconin (Vogt 1981). Though known from the state for less than a century—first confirmed near St. Croix Falls in Polk County by George Wagner (1922) and subsequently reported by Edgren (1944) from Bayfield County. Wood Turtles are now known to occur throughout the northern two-thirds of Wisconsin, including Douglas and Bayfield counties on the shores of Lake Superior, and known from at least seven major drainages within the Chequamegon National Forest (St. Pierre (2008). Wood Turtles occur in southwestern Wisconsin in portions of the Wisconsin River watershed, but they are absent entirely from the southeastern part of the state and southern Lake Michigan drainages, including Door, Kewaunee, Fond du Lac, Green Lake, Dane, and Lafayette counties (Wisconsin Herp Atlas 2011). 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 (e.g., HerpNet 2012), which would lend weight to Illinois 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. A single record from the Rock River, south of Janesville in Rock County, has not been replicated and is an unusual outlier (Cahm 1937).

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 established at least since 1915, when Alexander Ruthven and Crystal Thompson reported the species from Schoolcraft County in the Upper Peninsula as well as Manistee and Missaukee counties in the Lower Peninsula (Ruthven and Thompson 1915). The Upper Peninsula of Michigan is ecologically and geologically an extension of 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 counties. 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 1985; Lee 1999). Isolated records from Allegan and Ingham counties in southern Michigan were discredited (Vogt 1985; Lee 1999).

Population Estimates and Status

Population Status and Trends and Northeast Occurrence Data

As with other Northeastern turtles (Compton 2007, p. 30), quantifying the size and trend of Wood Turtle populations in the Northeastern United States is made difficult by the broad distribution across at least twelve states, prevalence of Wood Turtle occurrence on private lands, cost of standardized surveys and travel between sites, and a lack of a coordinated effort with centralized data analysis. There is also a clear lack of quantitative historical data. A complete analysis of Northeastern United States occurrence data is presented in Part 2. A pilot effort to standardize survey protocols and begin a regionwide monitoring effort is presented in Part 3.

Population Size and Density

Wood Turtle populations have been quantitatively assessed, or minimum population sizes reported, 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); 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, p. 204), turtles per linear km (or m) of meandering river ("river-km," e.g., Jones 2009, Ch. 4) and turtles per km (or m) of linear floodplain transect (Pulsifer et al. 2006; M. Pulsifer, Nova Scotia Department of Natural Resources, pers. comm. to M.T. Jones). 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, and are made further confusing because researchers variably report population estimates for both adults and juveniles or only adults. Foscarini and Brooks (1997, p. 204) proposed that density estimates be standardized by stream surface area (stream length x average stream width). Population density estimates from throughout the Northeast are summarized in Table 7.

Density per hectare of available habitat.—Density estimates provided as turtles per hectare of available habitat (usually extent of floodplain vegetation) range from 0.4/ha (for 538 ha) in the Mauricie region of Québec (Walde 1998, p. 9), to 4.4/ha in Pennsylvania (Ernst 2001b); 10.6/ha for 62 ha in Sussex County, New Jersey (Farrell and Graham 1991), and about 12.5/ha for an unspecified area in Passaic County, New Jersey (Harding and Bloomer 1979, p. 18). Again, these figures are problematic because of the difficulty in standardizing measures of available habitat.

Stream-based density estimates.—For stream-based density estimates, Daigle (1997) and Daigle and Jutras (2005) reported densities of 9.7 turtles/river-km. Brooks and Brown (1992, in Foscarini and Brooks 1997) estimated densities of 35.0 turtles/river-ha and 35.5 turtles/river-km, Jones (2009, Ch. 4) 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 per kilometer of meandering stream, and reported several streams where repeated surveys could not reveal sufficient animals for recapture analysis, suggesting extremely low population size. Pulsifer et al. (2006; M. Pulsifer, Nova Scotia Department of Natural Resources, pers. comm. to M.T. Jones) reported estimated minimum densities of 2.5–11.3 Wood Turtles per transect km in Nova Scotia. The highest density estimates reported are probably Farrell and Graham (1991; R. Farrell pers. comm. to M.T. Jones), whose estimates are equivalent to about 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. The largest known population in the Wood Turtle's range may be found in the St. Mary's River of Nova Scotia, where extrapolated estimates suggest a population size of between 1083–4000 turtles (Pulsifer et al. 2006; M. Pulsifer, pers. comm.).

Total population size.—No estimates have been generated for the total North American or United States population (van Dijk and Harding 2011). The total population size for the four eastern Canadian provinces has been roughly estimated at 6,000–12,000 adults based on estimates from Canadian researchers (COSEWIC 2007, p. v).

Historical references.—Limited historical data indicates that some populations in the 19th century may have been relatively large. In Massachusetts in the 1850s, Wood Turtles were reported by Louis Agassiz (1857) and Henry David Thoreau (ca. 1855–1860) to be relatively abundant in certain streams in Worcester and Middlesex counties. Subsequently, J.A. Allen (1868, p. 175) reported Wood Turtles as "common" in the vicinity of Springfield, Hampden County. Nash (1908, p. 18) reports the Wood Turtle "tolerably common" in western Ontario, less frequently found eastward." Oliver and Bailey (1939) reported the Wood Turtle to be one of the most common turtle species in New Hampshire. In New Jersey, however, Fowler (1906, p. 243) reports the Wood Turtle to be "scarce".

Population Viability Analysis

Undertaking a regionwide, spatially explicit Population Viability Analysis (PVA) is not a straightforward undertaking because of the small proportion of known sites that have been sampled, the long-standing tendency to select study sites and study animals nonrandomly, the expense of radiotelemetry, the short term of radiotelemetry studies, temporal and spatial variation in nest depredation rates, and the difficulty assessing hatchling and juvenile life stages without influencing survival rates. Compton (1999, Ch. 3) built a demographic model for a theoretical Wood Turtle population in Maine, and modeled the effect of harvesting or removing of 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 (Compton 1999, p. 73).

Direct Evidence for Population Decline

Several studies in the Northeast or adjacent regions have presented quantitative evidence of decline of Wood Turtles. Almost all studies with a long-term component appear to report detectable or apparent declines. In the Missisquoi watershed of Québec, which is shared with Vermont, Daigle and Jutras (2005) reported a 50% decline in the estimated adult population over 7 yr. 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, p. v) status assessment, the overall trend in Wood Turtle abundance across Canada has been a decline. Approximately ten historic occurrences near the Ontario shores of Lakes Erie, Huron, and Ontario have been extirpated, which represents a major range contraction in that part of Canada (COSEWIC 2007, p. 18). The single remaining 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, p. 18).

In Michigan, Harding (1991) reported population declines in remote and relatively undisturbed areas, and proposed that illegal collection may have contributed to the declines.

In Maine, Verrill (1863) reported Wood Turtles to be common near Norway in Oxford County, where Wood Turtles are today relatively uncommon (T. Akre, pers. comm.).

In central Massachusetts, Jones (2009) reported that several populations appeared to be declining and presented limited evidence of significant declines at three long-term study sites over periods of up to 5 years. Jones and Sievert (2009b) presented evidence that Wood Turtles in western Massachusetts were declining by as much as 11.2% annually. Jones and Sievert (2009b) presented evidence that Wood Turtles 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, p. 54) reported that the Wood Turtle had declined nearly to extirpation, although approximately five individuals have been observed in that town since the 1990s (Windmiller 2009, p. 2; Windmiller, pers. comm.; M.T. Jones, unpublished data). In 2009, researchers reassessed the streams in Lancaster, Worcester County, Massachusetts, where Agassiz (1857) reported capture rates of >100 turtle per afternoon, and had capture rates nearly 1/50th those reported by Agassiz (M.T. Jones, L. Willey, A. Richmond, P. Sievert, University of Massachusetts, unpublished data), suggestive of a localized decline.

In Connecticut, Garber and Burger (1995) interpreted their long-term (1974–1993) survey results as evidence of total 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 present 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, p. 1–4) considers the Wood Turtle functionally extinct. Burger and Garber (1995) emphasize widespread decline but do not present evidence beyond that summarized in Garber and Burger (1995).

Harding and Bloomer (1979) note 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 provide 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 provide a detailed analysis of the probable range contraction of Wood Turtles on the coastal plain.

Monitoring and Inventory

Existing Monitoring Protocols

Visual encounter surveys.—As outlined in the literature review in the proceeding pages, the Wood Turtle has been intensively studied at sites widely distributed throughout the northeastern States. However, sampling procedures vary. Typically, researchers report searching for Wood Turtles on foot in streams and riparian areas in the spring and fall in groups of one to four.

Boat surveys.—Some researchers (e.g., Saumure and Bider 1998; Walde 1998) report searching for Wood Turtles within one observer in a canoe and one observer on each bank, or with two observers alternately in a canoe or small motorboat or searching upland bank habitats (Jones and Willey 2013b).

Trapping.—Trapping is infrequently reported as an effective sampling method, but has been implemented in Virginia (Akre and Ernst 2006) and Maine (Jones and Willey 2013b), with varied success. Akre and Ernst (2006) describe an interruption-type setup with wing fences constructed from fyke nets, rock walls, or other materials.

Other Sampling Techniques

Viewing underwater.—To improve detection rates, teams throughout the Northeast variably use underwater viewing scopes (Akre, pers. comm., Dragon, pers. comm., Lemmon, pers. comm.), polarized eyeglasses, or facemasks and snorkles (T. Pluto, USACE, pers. comm.; Jones and Willey 2013a; 2013b). The effectiveness of these probably varies in different stream systems based on the type of structural habitats present underwater, the volume of water in the system, and the clarity of the water.

Cameras.—With the recent advent of low-cost, high quality time-lapse models, it has become possible to use cameras to assess relative densities of Wood Turtles at known features within high-density sites.

Wingscapes PlantCams, programmed to record images every five minutes between 1700 h and 2100 h, have been used to assess the relative use of different nesting beaches in New England, and GoPro cameras have been used to record fine-scale, short-term nesting behaviors (Jones and Willey 2013a; 2013b) and may also be used to monitor use and behavior at overwintering sites (faced north, with a polarized lens). The PlotWatcherPro may be a more versatile option for a range of applications including nest- and basking-site behavior and has been used successfully to monitor gopher tortoise activity (T. Radzio, Drexel University, pers. comm.). Motion-sensing cameras have also been used to detect nest predators (Akre 2011).

Decontamination of Field Gear

Although it is generally not mentioned in recent studies of Wood Turtles, decontamination of field equipment and sampling gear has become part of standard operating procedure in light of widespread outbreaks of *Ranavirus* in wild box turtle populations and unidentified pathogens in bog turtle populations (see Threats to Population Stability, later). Standard decontamination protocols include the following components (Miller and Gray 2009; Appendix I):

1. Remove mud, sand, and debris from equipment, boots, waters, bins, tires and rinse with local or sterile water;
2. Apply disinfectant (3% household bleach; 0.75% Nolvasan [Fort Dodge Animal Health]; or 1% Virkon [DuPort Animal Healthy Solutions]) to equipment and tools for five minutes and rinse with sterile water;
3. Avoid unnecessary contact between turtles during processing (when possible, house turtles in separate sterile bins) and wear gloves during processing.

Other Considerations

Study Design.—In a comprehensive review of sampling design considerations for the western pond turtle (*Actinemys marmorata*), Ashton et al. (2012) note the following major themes that apply equally to monitoring efforts for Wood Turtle:

1. Clear statement of hypothesis;
2. Appropriate use of available information to frame the question;
3. Rigorous data collection and management standards;
4. Emphasis on sampling all size- (age-) classes using a range of methodologies;
5. Study site selection with consideration for accessibility, elevation, stream size, and habitat suitability;
6. Randomized site selection if all sites cannot be sampled;
7. Classification of sites to allow stratification by human influence and habitat features.

Safety.—On the surface, most Wood Turtle sites do not appear to pose clear risks to human safety. However, working in streams and rivers pose risks ranging from hypothermia to drowning. It is important that researchers identify potential safety risks and take measures to minimize them. For instance, snorkeling and boating should be undertaken only by qualified and trained personnel. Snorkeling should not occur near potentially unstable structures such as logjams. Surveys should not be conducted during high flows or flood conditions that may result in unsafe conditions for observers. Other safety considerations are enumerated by Bury et al. (2012) for western pond turtle, and these apply equally to Wood Turtle surveys.

Legal Status and Regulatory Protections

Legal Status in the United States and Canada

The Wood Turtle was upgraded to "endangered" from "vulnerable" by the IUCN in 2011 (van Dijk and Harding 2011). NatureServe recently (2010) upgraded the Wood Turtle from G4 to G3 (vulnerable). The Wood Turtle is listed as "endangered" in Iowa; as "threatened" in Minnesota, New Jersey, Virginia, and Wisconsin; and as a species of special concern/interest in Connecticut, Maine, Massachusetts, New Hampshire, Vermont, Rhode Island, New York, and West Virginia. The Wood Turtle is not listed, but a protected nongame species, in Maryland and Pennsylvania. In Canada, the Wood Turtle is listed as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the Species at Risk Act (SARA), and is further listed as "rare" in Ontario, "threatened" in Québec (Y. Dubois, Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, pers. comm.), and as "vulnerable" in Nova Scotia. The Wood Turtle has no formal status in New Brunswick although individuals are protected under the Fish and Wildlife Act and under federal legislation.

Lacey Act.—Because the Wood Turtle is not federally listed and has no federal protected status, most of the laws and regulations protecting Wood Turtles and their habitats are enacted and promulgated at the state level. However, the U.S. Lacey Act (18 USC 42–43; 16 USA 3371–3378) applies to the interstate transportation and sale of Wood Turtles that were collected in violation of state law or regulation. Captive-bred specimens are not exempt from the Lacey Act if the parent stock was illegally harvested. The law applies to living and dead specimens. Private citizens engaged in the sale of Wood Turtles may be subjected to investigations under the Lacey Act, and prosecuted if it is found they did not exhibit "due care" in determining the legal status of the Wood Turtles (U.S. Fish and Wildlife Service Office of Law Enforcement 2006). Several recent cases of poaching (see Significant Threats to Population Persistence, below) were successfully prosecuted under the Lacey Act, although the penalties have been arguably minor.

CITES.—Wood Turtles are afforded some protection internationally as an Appendix II list species under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which is currently (2013) adhered to by 179 sovereign states. International trade in CITES Appendix II species is moderately controlled. Exportation may be authorized by the granting of an export permit or re-export certificate, but no import permit is necessary for these species. According to the U.S. Fish and Wildlife Service (2003), which is the United States' managing authority for CITES, export permits for Appendix II species are only be granted if trade will not be detrimental to the species' survival, and that specimens were legally acquired.

U.S. Forest Service.—Wood Turtles are designated Regional Forester sensitive species on the White Mountain, Green Mountain, Allegheny, George Washington, and Jefferson National Forests. Under this designation, habitat for this species must be conserved, although not every acre must be protected. When a management action is proposed, a review is completed to analyze potential effects to Wood Turtles and their habitat. If the analysis indicates a likely adverse impact, then generally the project is modified to avoid the impact or does not proceed (L. Prout, USFS White Mountain National Forest, pers. comm.; F. Huber, USFS George Washington National Forest, pers. comm.). When the White Mountain National Forest revised its management plan ("Forest Plan") in 2005, an extensive review was conducted, which included a compilation of known occurrences, expert opinion, and an evaluation of implementing the Forest Plan on Wood Turtle viability.

Critical Review of Regulatory Status by State

In this section, we provide a comprehensive state-by-state summary of regulatory measures in effect to protect Wood Turtles and Wood Turtle habitat in the 13 northeastern States (Table 8).

Table 8. Summarized regulatory protections in effect for the Wood Turtle in the Northeastern United States. Y=yes; N=no; SR=state river or wetland regulations only; L=limited.

	ME	NH	VT	MA	CT	RI	NY	NJ	DE	PA	MD	WV	VA
Listing status	SC	SC	SC	SC	SC	SC	SC	T	SR	-	-	SC	T
Possession legal	Y	N	N	N	N	N	N	N	Y	N	Y	N	N
Commercial trade legal	N	N	N	N	N	N	N	N	N	N	N	N	N
Import legal	N	N	N	N	N	N	N	N	N	N	N	N	N
Take legal	N	N	N	N	N	N	N	N	N/A	N	N	N	N
River habitat protected	SR	L	L	Y	L	SR	SR	L	SR	SR	SR	SR	L
Nesting habitat protected	N	L	L	Y	L	N	N	L	N	N	N	N	L
Upland habitat protected	N	L	L	Y	L	N	N	L	N	N	N	N	L
Qualified wood turtle observers are regulated	N	N	N	Y	Y	N	N	L	N	N	N	N	N

Maine.—The Wood Turtle is a Species of Special Concern in Maine, which is a category assigned by policy and not regulation. Maine Department of Inland Fisheries and Wildlife considers Species of Special Concern "...any species of fish or wildlife that does not meet the criteria of an endangered or threatened species but is particularly vulnerable, and could easily become, an endangered, threatened, or extirpated species due to restricted distribution, low or declining numbers, specialized habitat needs or limits, or other factors." This status is used for planning and informational purposes. The Maine Department of Inland Fisheries and Wildlife "reviews the list of special concern species at the beginning of each calendar year, and, based on criteria in the Maine Endangered and Threatened Species Listing Handbook (ME DIFW 2009), revises the list as appropriate." Large development projects may be reviewed to protect Wood Turtle habitat under Site Location of Development law (Title 38, Chapter 3, Subchapter 1, Article 6, § 481 and 484; P. deMaynadier, ME DIFW, pers. comm.)

Additional laws in effect protect riparian and riverine habitats, including Shoreland Zoning Rules and the Natural Resources Protection Act (Statutory sections: Title 38, Chapter 3, §§ 480–Z). Other state laws provide specific protections for the Allagash Wilderness Waterway (Title 12, Chapter 206).

Wild Maine Wood Turtles are protected from export, sale, and commercial use (Title 12, Part 13, SubPart 4, Chapter 915, §12159), and are protected from collection for personal use by Maine residents (P. deMaynadier, ME DIFW, pers. comm.).

New Hampshire.—The Wood Turtle is a Species of Special Concern, a category not outlined in the endangered species statute (Title XVIII, Chapter 212-A, Endangered Species Conservation Act). Rules are allowed under the Nongame Act (RSA 212-B). Special Concern Species are determined by the Fish and Game Department following a guidance document (NHFG 2009), which outlines Species of Special Concern in two categories, of which the Wood Turtle is category A1 (High risk in much of southern NH; vulnerable to development, collection, roads, stream alterations and life history traits. Northeast Regional Conservation Concern):

> "Category A: 'Near-threatened Species': Species that could become Threatened in the foreseeable future if action is not taken.
>
> > Sub-category 1) Existing threats are such that the species could decline to Threatened status if conservation actions are not taken. In some cases, further survey work may support removing a species from the 'special concern' list but existing information must indicate a sufficient level of threat or concern.
> >
> > Sub-category 2) Species which were recently down-listed (i.e. recovered) from the state endangered and threatened species list and where conservation action is desired to ensure the species continues towards full recovery.
>
> Category B: 'Responsibility Species': Species for which a large portion of their global or regional range (or population) occurs in New Hampshire and where actions to protect these species habitat will benefit the species' global population. Species were candidates for being included as Category B if they scored as 'Very High' (>8% of species Northeast range occurs in New Hampshire) in the Species Responsibility vs. Threat Matrix (Hunt 2007) or in subsequent analyses using similar methodologies."

While the presence of a special concern species in an area may improve its competitiveness for land acquisition or grant allocation, and "should be considered when making habitat management decisions," and NHFG may provide recommendations to reduce impacts from proposed activities (e.g., developments, bridge construction or repair) and the NHDES makes a determination on the issuance of permits and appropriate conditions to include (M. Marchand, NHFG, pers. comm.). Special concern species are candidates for consideration in environmental review under the NHDES Wetlands Bureau Dredge and Fill Rules (Env-Wt 302.04(7a), which "require applicants to address impacts to Special Concern species."

Additional protections for Wood Turtle habitat may be accomplished through the NHDES Wetlands Dredge and Fill permit process (Federal Clean Water Act § 404) and the NHDES Shoreland Protection Act (RSA 483-B), but upland habitat protection is reportedly difficult (M. Marchand, NHFG, pers. comm.).

Further, the Wood Turtle may not be possessed (as defined in RSA 207:1), sold, or imported (NHFG FIS 800) without a permit (NHFG FIS 804.02). The possession or take of Wood Turtles, Wood Turtle eggs, or any part thereof is prohibited (NHFG FIS 1400).

Vermont.—The Wood Turtle is listed by the Vermont Fish and Wildlife Department as a Species of Special Concern, a designation that appears to carry relatively little consistent regulatory weight.

It is theoretically possible to specifically protect Wood Turtle habitat under Act 250, the Land Use and Development Act (S. Parren, Wildlife Diversity Program, VT Fish and Wildlife Department, pers.

comm.). Act 250 applies to development projects larger than 4 ha (10 acres), or more than 1 acre in towns without zoning bylaws. Nine District Environmental Commissions have the power to deny or permit large-scale development based on a series of 10 criteria, several of which, if implemented, protect Wood Turtle habitat, such as water quality (#1); erosion control (#4); aesthetics and endangered species (#8). Subcriterion 8a allows protection of "necessary wildlife habitat." To protect Wood Turtle habitat, the Vermont Fish and Wildlife Department would have to apply to the relevant District Environmental Commission. To do this consistently, Wood Turtle habitat would need to be estimated and mapped.

It is illegal to import any wild animal into Vermont without a permit from the Commissioner, including Wood Turtles (Title 10 Appendix, Chapter 10, §18). It is further illegal to possess, capture, collect, or breed wild animals without a permit, and hence under federal regulations it is illegal to remove Wood Turtles from Vermont to another state without a state permit in both states. The Wood Turtle is not protected under the Vermont endangered and threatened species rule (10 V.S.A. App. § 10) because it is not formally listed. However, the regulatory infrastructure for habitat protection and "take" prohibition is in place, and is based on avoidance, minimization, and mitigation for regulatory review. The most likely use of Act 250 to protect Wood Turtle habitat, a non-listed species in Vermont, would be using subcriterion 8a (necessary wildlife habitat; S. Parren, pers. comm.). Unless the regulatory protections for habitat are improved under the state endangered species statute, this method is likely the most effective for the protection of Wood Turtle habitat.

Massachusetts.—Under the authority of the Massachusetts Endangered Species Act ("MESA," M.G.L. c. 131A) the Wood Turtle is regulated as a Species of Special Concern (321 CMR 10.00, revised and implemented October 15, 2010). Unlike endangered species laws in adjacent states, which generally allow stringent protections for Endangered and Threatened Species, the MESA prohibits the "take" of Endangered, Threatened, and Special Concern species. "Take" is defined as, "in reference to animals to harass, harm, pursue, hunt, shoot, hound, kill, trap, capture, collect, process, disrupt the nesting, breeding, feeding or migratory activity or attempt to engage in any such conduct, or to assist such conduct, and in reference to plants, means to collect, pick, kill, transplant, cut or process or attempt to engage or to assist in any such conduct. Disruption of nesting, breeding, feeding or migratory activity may result from, but is not limited to, the modification, degradation or destruction of Habitat." The Division of Fisheries and Wildlife's Natural Heritage and Endangered Species Program (NHESP) maintains a database of element occurrences, from which it develops "Priority Habitat" maps designating riparian and upland landscapes in which all non-exempt development activities and land use conversions are reviewed for the likelihood of a "take."

"Conservation and Management Permits" (CMPs) may be issued to allow a "take" if the applicant meets a standard of "no significant impact" to regional populations, and if the applicant can demonstrate a regional "net benefit" to the Wood Turtle population. More often, the NHESP provides comments that are incorporated into project design to avoid the necessity of a CMP. Under the take provisions of the MESA, but also under the regulations regarding possession and collection (321 CMR 3.05 [2] and [6]) the Wood Turtle may not be disturbed, harassed, taken, sold, or possessed.

Connecticut.—As a Species of Special Concern, Wood Turtles are afforded limited protection under the Connecticut Endangered Species Act (GSC Title 26, Chapter 495) and its regulations (§§ 25-306-3 and 26-306-7 of the *Regulations of Connecticut State Agencies*). According to H. Gruner (CT Museum of Science, pers. comm.), in an environmental review context, a Wood Turtle site may be identified when a developer requests information from the State Department of Energy and Environmental Protection

(DEP) on the presence of state-listed species. In the case of Wood Turtle, the DEP issues a letter confirming the species' potential presence with a recommendation for the developer to engage an expert to confirm presence and recommend conservation strategies. Developers typically hire consultants to follow-up and then present to the appropriate municipal commission as part of a permit application process. The Department of Energy and Environmental Protection (DEP) is required to review the designation of species as endangered, threatened, or of special concern every five years.

Stream and riparian habitat is afforded protection under the Inland Wetlands and Watercourses Act (GSC §§ 22a-36 through 22a-45).

The Wood Turtle is a restricted species under DEP regulations (26-55-3), which state that no person shall possess any Wood Turtle at any time (Conn. Code Sec. 26-55-3-C). No Wood Turtles may be collected within Connecticut (Conn. Code Sec. 26-66-14-A) at any time.

Rhode Island.—Rhode Island has enacted an endangered species act (Gen. Laws, 1956, 20-37-1–5) Endangered species may be designated by the Director of the Department of Environmental Management. The Wood Turtle is a Species of Concern, which are defined as: "Native species not considered to be State Endangered or State Threatened at the present time, but are listed due to various factors of rarity and/or vulnerability. Species listed in this category may warrant endangered or threatened designation, but status information is presently not well known."

The sale of native wildlife is prohibited in Rhode Island, and the Wood Turtle is further covered under regulations of the Rhode Island Division of Fish and Wildlife as a protected species. Under these regulations, Wood Turtles may not be possessed at any time with out a permit issued by the Rhode Island Division of Fish and Wildlife as provided by Rhode Island General Law, Title 20, Chapters 20-1-18, 20-1-22, and 20-37-3.

New York.—The Wood Turtle is a Species of Special Concern (as defined in §182.2(i) of 6NYCRR Part 182, Endangered and Threatened Species Regulations) and (as with other native turtles except the snapping turtle, *Chelydra serpentina*) as a small game species with no open season may not be collected, pursued, taken, wounded, killed, sold, transported, or possessed (Environmental Conservation Law [ECL] Article 11, Title 1, §11-0107, and DEC promulgated regulations of the ECL, Chapter 1: Fish and Wildlife, Section 3.2: Native Turtles). In essence, the Wood Turtle may not be collected or possessed but there are no strong protections for habitat (A. Ross, NYS DEC, pers. comm.). Under these regulations and the federal Lacey Act, between 2006–2009, New York State Department of Environmental Conservation conducted "Operation Shellshock," an undercover investigation of the reptile trade in New York State, which led to seizures of Wood Turtles and criminal charges against 17 people, including members of the "turtle conservation community" (A.G. Sulzberger, *State officials charge 17 in illegal animal trade*, New York Times, March 19, 2009). Wood Turtle habitat is not afforded specific, formal protections from development, forestry, or agricultural activities. Limited protections to riverine habitats, and special provisions for the Adirondack region, exist under the Stream Protection Act (ECL, Title 5, Article 15), Freshwater Wetland Act (ECL, Title 23, Article 71), Solid Waste Disposal Act (Laws of 1988, Chapter 70), State Environmental Quality Review Act ((8 NYCRR Part 314; A. Breisch, NYS DEC, pers. comm.) The presence of Wood Turtles in a proposed project area is noted, but barring other factors lends little weight to the decision to issue a development permit (A. Breisch, NYS DEC [ret.]).

Interestingly, in 1905, New York State amended its "Forest, Fish, and Game" law to prohibit the "taking, killing, or exposing for sale of all land turtles or tortoises, including the box and Wood Turtle," becoming the first state to enact legislation to protect the species (Breisch 1997; Gibbs et al. 2007, p. 293).

New Jersey.—The Wood Turtle is protected as a Threatened species under the Endangered and Nongame Species Conservation Act ("State Act," or ENSCA; New Jersey Statutes Annotated 23:2A-1, et seq.), implemented in 1973, under which the Commissioner of the Department of Environmental Protection may promulgate and periodically review a list of endangered species, and adopt regulations with respect to the taking, possession, transportation, exportation, processing, and sale of endangered and threatened species (New Jersey Administrative Code 7:25-4). "Take" is defined as "harass, hunt, capture, kill, or attempt to do so (N.J.S.A. 23:2A-3(e)). Regulations designed to protect critical habitat for listed species were promulgated in 2003. The regulations require Habitat Management Plans when development will result in degradation of habitat for state-listed threatened or endangered species, extending the regulatory authority beyond wetlands, floodplains, coastal zones, and the Pinelands. Habitat for Threatened and Endangered Species is depicted on "Landscape Project" maps. All validated occurrences of Wood Turtle are used to model critical wildlife habitat, which is a base layer for environmental review. All projects that intersect critical habitat for Wood Turtle are reviewed by the state when there may be impacts to wetlands or wetland buffers (B. Zarate, NJ DFW, pers. comm.).

Other statutes providing protections for riverine and riparian habitats used by the Wood Turtle in New Jersey include the Freshwater Wetlands Protection Act (N.J.S.A. 13:9B-1, et. seq.) and its implementing Rules (N.J.A.C. 7:7A-1.1, et. seq.), which restrict landowners' ability to "destroy, jeopardize, or adversely modify a present or documented habitat for threatened or endangered species." Wetlands with critical habitat for rare species are classified as of exceptional resource value. Under the Flood Hazard Area Control Act (N.J.S.A. 58:16A-50, et. seq.) and its enabling regulations (N.J.A.C. 7:13-1.3 and N.J.A.C. 7:13-3.9), the Wood Turtle is considered at "water dependent species" (S. Angus, pers. comm.) and the NJ DEP is authorized to regulate development activities in flood prone areas and to control stream encroachments with consideration for threatened and endangered species habitat (B. Zarate, NJ DFW, pers. comm.). Last, the Highlands Water Protection and Planning Act ("Highlands Act," N.J.S.A. 13:20-1 et seq.) and its rules (N.J.A.C. 7:38) regulates development in the northwestern Highlands region.

As noted above, the possession of threatened and endangered species, including Wood Turtle, is regulated, and is prohibited without a permit (N.J.A.C. 7:25-4.10 and N.J.A.C. 7:25–4.14).

Pennsylvania.—The Wood Turtle is not listed by Pennsylvania and is not afforded habitat protections except those provided to streams through regulations promulgated by the Department of Environmental Protection (PA Code Title 25, including Chapters 91, 92, 93, 95, 96, 102, and 105) under the Pennsylvania Clean Streams Law (35 P.S. §691.1 et seq.). Regulations allow for the designation of "High Quality (HQ)" and "Exceptional Value (EV)" waters, as defined in PA Code Title 25 §93.4b. HQ waters are based either on geochemistry indicating long-term water quality better than threshold standards for dissolved oxygen, iron and dissolved metals (copper, arsenic, lead, nickel, cadmium, zinc), temperature, pH, etc., 99% of the time; or on biological data indicating a "high quality aquatic community" based on benthic macroinvertebrate and fish communities. Further, streams may be designated as HQ waters if they have been designated a Class A wild trout stream by the PA Fish and Boat Commission. EV Waters must first qualify as HQ waters, and also meet additional criteria, such as location within a wildlife refuge, state park of forest, of national significance, or qualification as a Wilderness Trout Stream (another designation given by PFBC; PA DEP 2003). Streams may also meet the EV criteria by demonstrating elevated biological parameters or "exceptional ecological significance" (J. Drasher, Aqua-Terra Environmental Ltd., pers. comm.)

The Wood Turtle is protected from harvest and possession with no open season under the Fish and Boat Code (30 Pa. C.S. § 2102) regulations (58 Pa. Code §§ 79.2 and 79.3). These state:

- It is unlawful to damage or disrupt the nest or eggs of a reptile or to gather, take or possess the eggs of any reptile in the natural environment of this Commonwealth (i.e., Pennsylvania).
- It is unlawful to take, catch, kill or possess for the purposes of selling or offering for sale, importing or exporting for consideration, trading or bartering or purchasing an amphibian or reptile whether dead or alive, in whole or in parts, including the eggs or any life stage that was taken from lands or waters within this Commonwealth.
- It is unlawful to transport or import into or within this Commonwealth a native species from another jurisdiction. It is also unlawful to receive a native species that was transported or imported into or within this Commonwealth from another jurisdiction.

Delaware.—The Wood Turtle is not currently considered a native species in Delaware, no populations or occurrences are known or confirmed, and the species is not afforded protection.

Maryland.—The Wood Turtle is not listed in Maryland. According to the Reptile and Amphibian Possession and Permit regulations, Wood Turtles may not be collected from the wild. Maryland residents are allowed to possess 1 Wood Turtle.

In western Maryland, Wood Turtle habitat is considered in management decisions on state forest lands (E. Thompson, MD DNR, pers. comm.)

Virginia.—The Wood Turtle is state-listed as a threatened species under the Endangered Species Act (VA ST §§ 29.1-563–570); it was listed in 1992 (Akre 2010). Two state agencies have authority for administering and implementing the Act: the Department of Game and Inland Fisheries has authority for the protection and management of listed wildlife species the Department of Agriculture and Consumer Service (VDACS) has authority for the protection and management of listed plants and insects.

Under the authority of §§ 29.1-103 and 29.1-521 of the Code of Virginia it shall be unlawful to take, possess, import, cause to be imported, export, cause to be exported, buy, sell, offer for sale, or liberate within the Commonwealth any wild animal unless otherwise specifically permitted by law or regulation.

The Department of Environmental Quality (DEQ) also regulates wetland, open water, and stream impacts associated with development projects under the Virginia Water Protection (VWP) permit program (authorized by § 62.1-44.15:20). If the activity requires a permit from the DEQ, the permit writers will coordinate review of the project with a number of consulting agencies including DGIF and DCRNH to determine whether there are Threatened or Endangered Species documented within two miles of the proposed project. If it is determined that Wood Turtles have been documented from the project area and that the project may resulting impacts upon them, VDGIF may recommend to the DEQ that project activities adhere to time of year restrictions (TOYR), and/or other actions, to avoid or minimize impacts to Wood Turtles and the resources upon which they depend. DEQ makes the final decision about which, if any, of VDGIF's recommendations become permit requirements. If there are no water resources to be impacted by the proposed development, VDGIF would only have an opportunity to review the project if it falls under other regulatory process such as SCC projects, large state projects, NEPA, transportation or energy projects, etc. (J.D. Kleopfer, DGIF, pers. comm.).

West Virginia.—The Wood Turtle is not listed in West Virginia, and West Virginia does not have state-level Endangered Species legislation. Chapter 20 of the West Virginia Code includes "reptiles" in the definition of Wildlife and, as such, the West Virginia Department of Natural Resources (WVDNR) is authorized to promulgate laws and/or regulations. In April 2013, the West Virginia Natural Resource Commission passed an amendment (under the authority to WV Code §20-1-17) prohibiting the take and possession of Wood Turtles, which goes into effect on January 1, 2014. Prior to the implementation of this regulation, the regulation had been amended in 1992 to prohibit commercial collection of turtles. Prior to that, individuals were allowed to collect up to 100 turtles in West Virginia provided they had a valid fishing license.

Significant Threats to Population Stability

Summary of factors affecting the species

There are numerous documented threats to adult Wood Turtles, and it appears extremely likely that many populations have been impaired as a result of urbanization and its associated effects (Part 4). It is apparent that the major threats, causes for decline, or other factors affecting the extant populations are the combined effects of habitat fragmentation and degradation, namely: roadkill of adults; mortality associated with agricultural machinery; collection (especially of adults) for commercial and personal trade; dams; severe floods; stream stabilization; aggressive beaver control; pollution, and disease. As noted by Klemens (1997, p. 23), "Too little is done to sustain adult longevity. Habitat fragmentation, roads, commercial collecting, education/museum collecting are major problems for adults; usually a combination of these."

Destruction and modification of Wood Turtle habitat

Habitat fragmentation and degradation.—Although it takes many forms, and the proximate causes of decline may be roadkill, crushing by agricultural machinery, or collection, the greatest ultimate threat facing most Wood Turtle populations is habitat fragmentation and degradation (Vogt 1981, p. 96). Because Wood Turtles primarily occupy broad, level valleys, their habitats have been converted to agriculture and development at high rates throughout the region (see Part 4 for an original analysis of land conversion). Historically, widespread declines or extirpations must have been caused by the major dam projects of the 19th and 20th centuries. Subsequently, widespread declines have been facilitated by road networks and urbanization. In the following sections we have outlined a brief summary of factors associated with habitat destruction or modification that are known or strongly suspected to negatively influence the distribution and abundance of Wood Turtles.

Roadkill.—Roadkill of adults, juveniles, and hatchlings is a major factor negatively affecting the species throughout its range (Jones and Willey 2015 for an original analysis of road density within known and estimated Wood Turtle habitat). Breckenridge (1958, p. 169) speculated that roadkill ("traffic") caused Wood Turtle mortality, but noted an absence of roadkill records in Minnesota, which he attributed to the species' relative rarity. Akre and Ernst (2006) attributed most of their observed mortalities (5 of 7) to roadkill in Virginia, and remaining mortalities to crushing by vehicles under powerlines, and further considered roadkill one of the most severe threats facing Wood Turtles in Virginia. Although there is a distinct lack of baseline data, roadkill is the likely proximate cause of population declines throughout the urbanized areas of the east coast. Further, where roads serve as nesting areas, as on the George Washington National Forest of northwestern Virginia, the nesting sites themselves may function as ecological traps (Kleopfer, VDGIF, pers. comm., Akre 2011).

Agricultural Machinery.—Abundant evidence strongly suggests that mortality of adults resulting from crushing injury by agricultural machinery is a leading threat to many rural populations and a serious management challenge (Saumure 2004; Saumure et al. 2007; Castellano 2007; Tingley and Herman 2008; Tingley 2009; Jones 2009; Erb and Jones 2011). Saumure and Bider (1998) first noted the potentially 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, and juveniles and adults were less common, at the agricultural site.

Based on bivariate tests, Jones (2009, Chapter 4) in Massachusetts reported that instream Wood Turtle density was associated with low crop cover and higher forest cover at riparian and watershed scales (228 m and 1000 m, respectively), suggesting that densities are depressed in heavily farmed areas.

Forestry.—Although small-scale or selection forestry may create valuable microhabitats for disturbance-dependent Wood Turtles, most authors caution that the negative effects of large-scale cutting, or conducting forestry activities during the active season, would likely far outweigh the benefits through crushing of individuals and degradation of the stream (Akre and Ernst 2006; Tingley and Herman 2008).

Nest and hatchling predators.—Depredation of nests and hatchlings by mesopredators (mid-sized carnivores) such as raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and foxes (*Vulpes vulpes*) is a complex and major threat in many regions (Brooks et al. 1992; Klemens 2000; Buhlmann and Osborn 2011; NatureServe 2013; K. Buhlmann, pers. comm.). In some areas, certain mammalian mesopredators have been subsidized by human development (Klemens 2000). In New Hampshire, Tuttle and Carroll (2005) reported apparent depredation of hatchlings by chipmunks (*Tamias striatus*) and birds, and speculated that great blue herons (*Ardea herodias*) eat hatchlings. Wicklow (pers. comm.) repeated observations of chipmunk depredation, and Jones and Sievert (2012) reported heavy chipmunk depredation of Blanding's Turtle hatchlings in nearby northeastern Massachusetts. At some sites where adult survivorship is relatively high, or the adults are at least provided some level of protection from cars, mowers, and collection, recruitment may be minimal. Akre and Ernst (2006) speculate that raccoons (*Procyon lotor*), red fox (*Vulpes fulva*), striped skunk (*Mephitis* sp.) and opossum (*Didelphis virginiana*) depredate Wood Turtle nests in Virginia.

Predators of adults.—Although the primary risk of elevated depredation rates appears to affect nests and hatchlings disproportionately, several authors have noted that mid-sized predators pose risks to adult Wood Turtles by mutilating them or killing them outright (Harding and Bloomer 1979; Saumure and Bider 1998; Walde et al. 2003; Akre and Ernst 2006; Jones 2009). This appears to vary by site and region, but depredation of adult Wood Turtles by carnivores is a major conservation concern in many areas and warrants consideration in management planning.

Streambank stabilization.—Massive bank collapse and failure can threaten roads, structures, agricultural fields, and energy infrastructure. Where these resources are at risk, aggressive bank stabilization is common throughout the Northeast region. Streambank stabilization takes many forms, and can range from the historical use of debris, broken cement, and boulders, to recent use of gabion and riprap, to bioengineering techniques. A wide range of streambank stabilizations occurred widely in New England

and New York in the wake of Hurricane Irene in 2011 and Tropical Storm Sandy in 2012 (Murphy 2013), many of which were undertaken under emergency authorization. Extensive bank stabilization appears to degrade Wood Turtle habitat in several ways. Illegal bank stabilization has been shown to kill individual turtles through crushing or entombment (Saumure 2004; Saumure et al. 2007). Banks hardened with large riprap (>20 cm) are probably of low habitat quality for several decades (Jones and Sievert 2011, p. 4). By slowing or obstructing the development of sandy or gravelly point bars on the inner bends of wide meanders, the overall site quality is degraded (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) found that 7.5% of the streambanks had been converted to hardened structures of little ecological value to Wood Turtles, and over 3% of the river bank was exhibiting evidence of massive collapse suggesting that stream stabilization might be employed. However, the effects of stabilizing structures on floodplain habitat quality for Wood Turtles have not been empirically tested.

Pollution.—Although the Wood Turtle is often reported from clear, clean streams (Ernst and Lovich 2009), little work has specifically examined the influence of pollution on Wood Turtle populations. Northern Wood Turtle populations are frequently associated with streams high in tannins (R.A. Saumure, pers. comm.). Akre and Ernst (2006) note the potential for poultry farms and logging in Rockingham County, Virginia, to degrade stream quality for Wood Turtles through point-source nutrient pollution and flow-rate degradation.

Dams and reservoirs.—Dams have negatively influenced the distribution and abundance of Wood Turtles by converting suitable stream habitat to deep reservoirs, and through a broad suite of downstream effects. In Part 4, we present an original analysis of the potential effect of dams on Wood Turtles throughout the Northeast Region. More than 1,400 major dams, and many thousands of smaller dams, remain in place on streams and rivers of the Northeastern United States (National Dam Inventory, U.S Army Corps of Engineers 2009), including those with the primary purpose of storing drinking water, generating power, and providing flood protection. Habitat loss associated with dam construction was among the highest threats to Wood Turtles identified by Castellano et al. (2009, p. 1783), and Compton (1999) reported that dams were a major threat to Wood Turtle populations in Maine by starving sediments that would build downstream gravel bars, moderating high springtime flows that would scour nesting areas and deposit new gravel, but generating midsummer high flows that flood low-lying nests. In other cases, 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. There at least 125 hydropower dams in Maine (D. Mirch, Maine Department of Environmental Protection, pers. comm. to B. Compton, *in* Compton 1999, p. 58). There are also many thousands of smaller dams, including a total of 1,602 dams in Massachusetts alone (National Dam Inventory, U.S Army Corps of Engineers 2009). In some instances, it is possible to demonstrate, or confidently infer, that native Wood Turtle populations were displaced by flooding associated with dam construction or maintenance, but in most cases, the negative influence of a large dam on Wood Turtle populations are poorly supported by empirical data.

In the Catskills of southern New York, numerous drinking water supply reservoirs have flooded valleys that likely contained optimal Wood Turtle habitat prior to flooding. For example, on the north side of the Catskills, where the New York Herp Atlas indicates scattered occurrences in non-dammed portions of the Schoharie watershed, major reservoirs were created at North Blenheim and Gilboa in the 1920s (Blenheim-Gilboa Reservoir and Schoharie Reservoir). It appears likely that populations extended throughout the Schoharie Reservoir system prior to the 1920s, but like most cases of impoundment this can't be demonstrated empirically. A nearby case with better empirical support, the Pepacton Reservoir of the interior Catskills now occupies what was once apparently a free-flowing stream supporting Wood Turtles: in July of 1935, Reeve Bailey collected Wood Turtles along the East Branch of the Delaware River, which was subsequently flooded between 1954–1955. To the south of the Catskill massif, the Ashokan Reservoir flooded numerous small creeks and Esopus Creek between 1912–1914. Wood Turtles were abundant in this wooded section of the Catskill Mountains during the era of the reservoir construction and individual turtles were probably constrained into less optimal habitats by the flooding (Chase 1989).

Quabbin Reservoir in Franklin, Worcester, and Hampshire counties, Massachusetts, likely flooded extensive areas of suitable Wood Turtle habitat associated with the major branches of the Swift River Valley when it was completed between 1930–1939, evidenced by more than 20 recent (≤30 years) Wood Turtle records in several tributaries to Quabbin Reservoir and confirmed occurrences downstream in the watershed (Massachusetts Natural Heritage and Endangered Species Program, unpublished occurrence data 2012; M.T. Jones and L.L. Willey, unpublished data). Wachusett Reservoir in Worcester County, which with Quabbin Reservoir forms most of Boston's water supply—must have similarly displaced Wood Turtles residing in the Nashua River, the watershed of which was historically known to support extant demes both up- and downstream of the reservoir (Massachusetts Natural Heritage and Endangered Species Program, unpublished occurrence data 2012; M.T. Jones and L.L. Willey, unpublished data).

In New Jersey, numerous reservoirs in the Highlands and adjacent regions clearly displaced what were probably large, contiguous areas of occupied stream habitat. An example is the Monksville Reservoir, which flooded portions of the Wanaque River (R. Farrell, Herpetological Associates, pers. comm.).

As already noted in the stream habitat section, earlier, a major reservoir project in Huntingdon County, Pennsylvania, is situated on what was once very likely a large Wood Turtle stream, as evidenced by historic data downstream and current records from the reservoir (T. Pluto, USACE; R. Nagle, Juniata College).

Major power dams have likely exerted strong negative influences on upstream and downstream riparian areas. An example of a power dam with a large ecological footprint is the Conowingo Dam on the Susquehanna River in Cecil County, Maryland, where Wood Turtles were documented in the 1940s (Cooper 1949.). In western Maine, Compton (1999) reported several ways in which a large power dam affected downstream Wood Turtles: by reducing springtime flows, downstream beaches were starved of sediments and overgrown. By increasing the rate and severity of summer floods, the dam caused low-lying downstream nests to flood.

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 urban areas. 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 likely that large flood control projects negatively influence Wood Turtle populations by creating dramatic shifts in water levels during seasonal periods of high sensitivity to water fluctuations (late winter) and changing the downstream redistribution of sand and gravel. 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 (e.g, sites in Cheshire County, New Hampshire; New Hampshire Fish and Game Department and New Hampshire Natural Heritage Bureau, unpublished occurrence data, 2012). Temporary flood-storage facilities with known Wood Turtle populations nearby are also numerous on the New England landscape (M.T. Jones, unpublished data) and include several designed to protect the major cities of New England from seasonal flooding.

The local influence of smaller dams on riparian habitats can be counterintuitive. In Massachusetts, at least one small subpopulation (deme) 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 reservoir (M.T. Jones, unpublished data; Jones 2009; Jones and Sievert 2009). Individual turtles within this population were frequently displaced downstream and over the dam by repeated flood events, which appeared to result in reduced survival and reproductive output, although the small reservoir remaining behind the dam appeared to "capture" turtles being displaced by floods (Jones and Sievert 2009). A similar configuration, in which a 1930s power dam had partially filled in, and braided deltaic channels were occupied by a deme of ca. 50 adults, was observed by Jones (2008) in northern New Hampshire.

Beavers.—While it seems clear that at heavily fragmented, isolated sites, dam construction and stream-channel flooding by beavers may degrade site quality for Wood Turtles, at the watershed scale in unfragmented systems, beavers are an important driver of structural complexity within Wood Turtle waterways. For example, beavers create openings in northern, coniferous forests through tree removal and flooding, and create deeper pools for overwintering (R.A. Saumure, pers. comm.). 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 studies by Jones and Willey (2013b), turtles exhibited heavy use of beaver-created openings and clearings.

Invasive plant species.—Several species of invasive vascular plants are present in the major watercourses (HUC4) of the Northeast region, but the negative effects of invasive species on Wood Turtles are poorly documented, and the relative threat posed by these 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 also influence the habitat quality of floodplain areas in different ways, depending on their growth form. The most problematic invasive species for Wood Turtle is probably Japanese knotweed (*Fallopia japonica*), which is known to overtake sandy nesting areas within the floodplain in Vermont and Massachusetts (M. Powell, Vermont Adult Learning, pers. comm.; M.T. Jones, unpublished data). Multiflora rose (*Rosa multiflora*) is widespread and common in Wood Turtle habitats from Massachusetts (Jones 2009) to West Virginia (Niederberger 1993, p. 11) and Virginia (Akre and Ernst 2006), and appears to present a threat to Wood Turtles mostly when landowners to undertake intensive land-clearing operations that may crush or injure Wood Turtles if undertaken during the active season. Other invasive plant species that may exert negative influence on vegetation structure or sunlight availability in the river corridor include autumn olive (*Eleagnus umbellata*), which has colonized Wood Turtle streams in Virginia (Sweeten 2008), greenbrier (*Smilax* sp.), which is present in riparian areas in West Virginia (Niederberger 1993, p. 27); and mile-a-minute (*Persicaria perfoliata*), which has become problematic in Wood Turtle habitat in Pennsylvania (J. Drasher, pers. comm.) and Virginia (Akre and Ernst 2006). At Great Swamp NWR in New Jersey, Wood Turtle nesting areas are negatively affected by common mugwort (*Artemisia vulgaris*). Other potentially problematic species in important Wood Turtle riparian habitats include: phragmites (*Phragmites australis*), reed canary grass (*Phalaris arundinacea*), Japanese stiltgrass (*Microstegium vimineum*), several species of honeysuckle (*Lonicera* x *bella*, *L. japonica*, *L. morrowii*, and *L. tatarica*), garlic mustard (*Alliaria petiola*), bishop's goutweed (*Aegopodium podagraria*), purple loosestrife (*Lythrum salicaria*), glossy buckthorn (*Frangula alnus*), and oriental bittersweet (*Celastrus orbicularis*) (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, although the greatest risk posed by invasive vascular plants may occur when they reduce light availability and aggressively colonize open, friable substrates in nesting areas. However, it is important to reiterate that in many cases the process of controlling invasive species may involve greater risk for adult Wood Turtles than the plants themselves. Seasonal habitat use by Wood Turtles, potential impacts to sensitive species, and proper implementation methods should be determined prior to any invasive control actions.

Kleopfer (VDGIF, pers. comm.) reports instances of Wood Turtles feeding on autumn olive berries and considers the negative impact of autumn olive on Wood Turtles to be minimal. Jones and Sievert (2009b) report instances of Wood Turtles feeding on a wide variety of plants considered invasive in Massachusetts.

Overcollection for commercial, recreational, scientific, or education purposes.—Collection for food was apparently an important local factor that led to perceived declines in the 19th and early 20th century (Klemens 1993; Breisch 1997). In the mid-1900s, biological supply houses became a major factor influencing the abundance of Wood Turtles (Vogt 1981, p. 96; A. Richmond, University of Massachusetts, pers. comm.). In recent decades, collection for domestic and foreign pet trades has become a major threat (Compton 1999; NatureServe 2013). Incidental take of adults was identified as a severe threat to the persistence of Wood Turtles in Virginia (Akre and Ernst 2006) and has been noted in most Northeastern States (see Appendix VI).

Wood Turtles were heavily collected by biological supply houses across the country in the mid-20th century, reflecting a trend that probably went back several decades. The real price of Wood Turtles in the early 1960s was about $20.00 (details and sources are provided in Table 9). This has climbed to more than $300.00 as of this report writing, an increase of more than 15 fold and possibly reflecting the perceived decline in abundance (and availability). According to NatureServe (2013), the Chelonian Advisory Group of the American Association of Zoological Parks and Aquariums has adopted a resolution ceasing the collection of the former *Clemmys* spp. complex (*Glyptemys, Emys, Emydoidea, Actinemys*)—a move that was overdue and likely symbolic.

Recent commercial collection of Wood Turtles has been documented in most states in the Northeast, and there is widespread evidence of illegal collection and trade throughout the range (Harding, pers. comm. *in* NatureServe 2013). In Maine, collectors removed ≥44 Wood Turtles from the St. John watershed of northern Maine in 1994 and attempted to sell them on the waterfront at Portland (P. deMaynadier, ME DIFW; McCollough 1997), and in 1995 55 Wood Turtles were confiscated in Virginia after being collected from Maine (McCollough 1997). No instances of commercial collection are known in New Hampshire, but incidental or casual collection has been documented (M. Marchand, NHFG, pers. comm.) and commercial collection suspected (B. Wicklow, St. Anselm College, pers. comm.). 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; the turtles were seized and released in their native stream (VT DFW 2004; Parren 2013; S. Parren, pers. comm.). Recent commercial collection is suspected, but poorly documented, in Massachusetts and Connecticut (L. Erb, MA DFW, pers. comm.; J. Dickson, CT DEEP, pers. comm; H. Gruner, CT Science Center, pers. comm.), although collection for sale by biological supply houses was common in the 1960s and 1970s (A. Richmond, University of Massachusetts Amherst, pers. comm.). In New York, 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 New York State Department of Environmental Conservation (A. Breisch, NYS DEC [ret.], pers. comm.). New

Jersey environmental law enforcement recently (2008) raided the home of a commercial reptile breeder and found >20 Wood Turtles in his collection after he purchased four Wood Turtles from undercover agents (B. Zarate, NJ DFW, pers. comm.; United States v.s Albert Roach, USDOJ/ECS 2011, p. 15). This enforcement action against a New Jersey resident was assisted by efforts from the Pennsylvania Fish and Boat Commission. The Pennsylvania Fish and Boat Commission itself supported “Operation Herp Scam,” which in 1998 detected a widespread network of trade in Wood Turtles (Sajna 1998) through which >290 Wood Turtles taken from western and southwestern Pennsylvania (J. Drasher, Aqua-Terra Environmental Ltd., pers. comm.; T. Akre, pers. comm.). Researchers in eastern Pennsylvania have reported direct evidence of incidental collection within high-density sites (S. Angus, pers. comm.). Kaufmann (reviewing CITES listing *in* NatureServe 2013) reports that Canadian collectors had illegally collected hundreds of specimens from a stream in Pennsylvania over the course of a few days.

Recent (ca. 2010) commercial or large-scale collection is suspected in western Maryland (E. Thompson, MD DNR, pers. comm.). Commercial collection has occurred in Virginia, but the extent and frequency is unknown (J.D. Kleopfer, VDGIF, pers. comm.).

There have been multiple instances of commercial collection in West Virginia. In 1992, two individuals from Indiana were arrested in the eastern panhandle of West Virginia for possession of a “large number of aquatic turtles without a fishing license (WVDNR 1992),” including approximately five Wood Turtles (K. O’Malley, WV DNR, pers. comm.). In 2008, Michael P. Ellard of Estero, Florida, and his associates Kelly Stoops II and Eric Diana, were arrested in Virginia with 108 Wood Turtles he had captured illegally in Hampshire County, West Virginia. In December 2009 Ellard was sentenced to five years probation and ordered to pay restitution in the amount of $12,000 (Jividen 2009; USDOJ ESC 2010, p. 17). The Wood Turtles were released at the reported capture location. In November 2013, David C. Matton, a resident of Windsor, Ontario, paid >$2,200.00 in fines for violations including possession and transportation of Wood Turtles from West Virginia. The investigation was conducted by the USFWS in conjunction with the West Virginia Division of Natural Resources Law Enforcement Section, who determined that Matton had purchased Wood Turtles from an undercover agent and transported them to Ontario in violation of the Lacey Act and CITES (WV DNR 2013).

During the course of this project, a pair of Wood Turtles was confiscated in Hong Kong with notches (K. Buhlmann, University of Georgia, pers. comm.). These animals subsequently were identified as possibly from New York (S. Poirier, Wildlife Enforcement Directorate, Environment Canada, pers. comm.).

As this document was finalized in December 2013, three open classified advertisements on kingsnake.com announced the sale or purchase of adult Wood Turtles, for which the rate was $350.00 per adult turtle was listed; no evidence is presented or requested that the animals are legally obtained. According to McCollough (1997), Wood Turtles were selling for $250 in the late 1990s, representing twice the price at the time of the RESTORE (1994) petition to list Wood Turtles as federally Threatened. Compton (1999, p. 54), pairs of Wood Turtles were sold for $350 in late 1997, which may have represented an increase since 1996, when the average cost per Wood Turtle was $131 (Hoover 1998). In 2008, federal undercover agents sold Albert Roach three Wood Turtles for $375, indicating a price per Wood Turtle of $125 (USDOJ/ESC 2011, p. 15), and suggesting that the price for Wood Turtles is highly variable (Figure 12, Table 9).

Table 9. Prices for Wood Turtles traded openly, 1961–2014, adjusted to the present relative value.

Year	Source	Size	Qty	Price	Price per turtle	Real price, 2012–2013	Real value, 2012–2013	Labor value, 2012–2013	Income value, 2012–2013
1961	Quivira	n/a	1	$2.50	$2.50	$19.20	$22.50	$21.70	$42.20
1961	Quivira	n/a	12	$24.00	$2.00	$15.30	$18.00	$20.90	$33.70
1962	CT Valley Biol. Supply	8–10"	1	$2.50	$2.50	$19.00	$21.80	$25.00	$39.80
1962	CT Valley Biol. Supply	8–10"	12	$25.00	$2.08	$15.08	$18.20	$20.80	$33.20
1964	CT Valley Biol. Supply	8–10"	1	$2.50	$2.50	$18.50	$20.00	$23.50	$36.20
1964	CT Valley Biol. Supply	8–10"	12	$25.00	$2.08	$15.40	$16.70	$19.50	$30.10
1972	Midwest Supply	yearling	1	$20.00	$20.00	$30.80	$33.40	$39.00	$60.20
1972	Midwest Supply	hatchling	1	$10.00	$10.00	$54.90	$53.20	$59.10	$84.60
1973	Midwest Supply	6–8"	1	$15.00	$15.00	$77.50	$79.90	$71.50	$115.00
1973	Midwest Supply	2–4"	1	$20.00	$20.00	$103.00	$106.00	$110.00	$153.00
1996	Hoover (1998)	adult	1	$131.00	$131.00	$192.00	$196.00	$211.00	$225.00
1997	McCullough (1997)	adult	1	$250.00	$250.00	$358.00	$364.00	$363.00	$410.00
1997	Compton (1999)	adult	2	$350.00	$175.00	$250.00	$255.00	$262.00	$287.00
1998	New England Reptile	hatchling	1	$125.00	$125.00	$176.00	$178.00	$187.00	$196.00
1999	Glades Herp	adult	1	$250.00	$250.00	$345.00	$342.00	$362.00	$373.00
1999	RESTORE (1994)	adult	1	$125.00	$125.00	$194.00	$200.00	$205.00	$233.00
1999	Glades Herp	hatchling	1	$125.00	$125.00	$172.50	$171.00	$181.00	$186.50
2000	Glades Herp	adult	1	$250.00	$250.00	$333.00	$333.00	$351.00	$355.00
2000	Glades Herp	adult (CB)	1	$275.00	$275.00	$367.00	$366.00	$386.00	$390.00
2001	Glades Herp	adult	1	$225.00	$225.00	$292.00	$288.00	$315.00	$312.00
2001	Glades Herp	4"	1	$175.00	$175.00	$227.00	$224.00	$245.00	$243.00
2001	Glades Herp	hatchling	1	$125.00	$125.00	$162.00	$160.00	$175.00	$173.00
2002	Glades Herp	adult	1	$225.00	$225.00	$287.00	$280.00	$291.00	$305.00
2002	Glades Herp	4"	1	$175.00	$175.00	$223.00	$218.00	$226.00	$237.00
2004	Glades Herp	hatchling	1	$95.00	$95.00	$115.00	$111.00	$112.00	$117.00
2008	USDOJ (2011)	adult	3	$375.00	$125.00	$133.00	$125.00	$131.00	$134.00
2010	Glades Herp	6"	1	$350.00	$350.00	$369.00	$368.00	$359.00	$375.00
2010	Glades Herp	4"	1	$225.00	$225.00	$237.00	$237.00	$231.00	$241.00
2013	Kingsnake (2013)	adult	1	$350.00	$350.00	$350.00	n/a	n/a	n/a
2014	TurtleSource	4"	1	$395.00	$395.00	$395.00	n/a	n/a	n/a
2014	TurtleSource	juvenile	1	$199.95	$199.95	$199.95	$199.95	n/a	n/a
2014	TurtleSource	yearling	1	$249.95	$249.95	$249.95	$249.95	n/a	n/a
2014	TurtleSource	2 year old	1	$295.00	$295.00	$295.00	$295.00	n/a	n/a

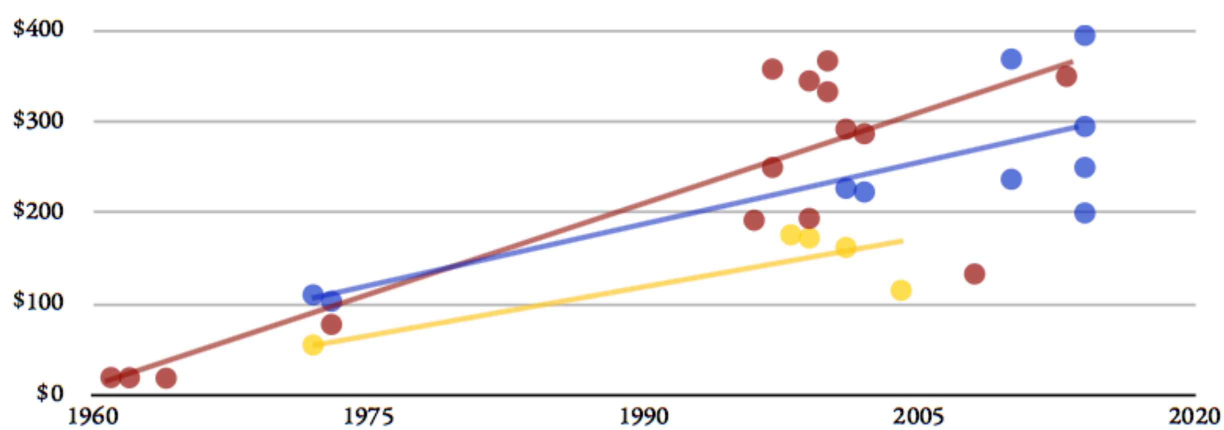

Figure 12. Real price (adjusted by year using algorithm of measuringworth.com) for adult (red), juvenile (blue), and hatchling (yellow) wood turtles traded openly by biological supply houses and reptile companies or as reported in the literature (see Table 9). Additional data from the late 1970s and 1980s would clarify trends in real price. The increasing trend in all groups may suggest increasing demand and/or scarcity.

Disease.—Disease has not yet been reported to be a major problem influencing Wood Turtle population status (but see Smith and Anderson 1980 and Upton et al. 1995). Emerging pathogens clearly warrant strong precautions by researchers. An unidentified pathogen may be causing mortality in wild bog turtle populations in Massachusetts and New York (USFWS 2009).

The presence of *Ranavirus* in captive and in wild box turtle (*Terrapene carolina*) populations, which co-occur with Wood Turtles from Massachusetts to West Virginia, is becoming a growing concern (De Voe et al. 2004; Johnson et al. 2008; Allender et al. 2011; USGS 2013; Kiester and Willey 2015). Although prevalence seems to be low (Allender et a. 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). Several instances of limb paralysis, thinning skin, and emaciation have been reported by the public (R. A. Saumure, pers. comm.). In these cases, the sick captive Wood Turtle were being housed with asymptomatic *Terrapene carolina*.

A mass die-off of about a dozen Wood Turtles was reported in Monroe County, Pennsylvania during the course of this project (S. Angus, pers. comm.) but the cause has not been determined, although bog turtles were also affected (K. Gipe, PFBC, pers. comm.). Diseases and epidemics appear to have the potential to become a major conservation challenge for Wood Turtles at some sites. Researchers should take extreme caution not to introduce pathogens into wild Wood Turtle populations by sterilizing equipment (especially calipers and scales, which may contact the face and tail of multiple turtles), not removing turtles from the wild to the laboratory, restraining wild turtles individually in sterile containers during processing in the field, and following all recommended decontamination protocols (see Appendix I, Miller and Gray 2009, SEPARC Decontamination Procedures).

Inadequacy of existing regulatory mechanisms.—The level of regulatory protections provided to Wood Turtle habitat in the Northeast are surprisingly minimal and do not appear to correspond to the high level of regional concern for Wood Turtle conservation, the widespread evidence of decline and extirpation, and the documented aspects of Wood Turtle life history that render populations susceptible to unregulated land conversion (late maturity, low reproductive output, long lifespan, high site fidelity). The three critical aspects of Wood Turtle habitat—nesting, foraging, and overwintering habitat—are strongly protected under state-level endangered species legislation in only one Northeastern state, Massachusetts. Limited protections for Wood Turtle habitat are in effect under endangered species legislation in Connecticut, New Jersey, and Virginia. Wood Turtle habitat is functionally protected only by state and federal wetland regulations, and not endangered species legislation, in Maine, New Hampshire, Vermont, New York, Pennsylvania, Maryland, and West Virginia.

Fortunately, all states in the Northeast (except Delaware and the District of Columbia, which have no extant documented Wood Turtle populations) prohibit commercial collection. Until 2017, Maine still apparently allows collection by residents (note that Compton [1999] considered this “clearly inadequate”). Life history studies and recent population studies in Maine indicate that even incidental harvest by Maine residents would be a major conservation challenge (as noted later).

Only two or possibly three states appear to actively screen biologists conducting mitigation- or development-related Wood Turtle surveys, which may result in improperly completed habitat assessments or population assessments.

Other natural or manmade factors affecting the Wood Turtle’s continued existence

Floods.—Flood severity in the northeast region may be increasing as a combined result of volatile precipitation and landuse changes such as streambank stabilization and increased impervious surface area in the watershed. Floods may exert strong influences on habitat quality for Wood Turtles, and depending on the season and whether Wood Turtles are inactive in the stream, may directly harm or displace turtles. Severe flooding can influence Wood Turtle habitat in several important ways. Floods may alter or disrupt channel geomorphology, damage floodplain vegetation, or redistribute sand, gravel, and other sediments (Compton 1999)—which may either augment or decrease the available nesting habitat.

Severe floods may also displace individual Wood Turtles from their resting places in the stream channel, resulting in drowning or injury. Recent observations of long-distance displacement or mortality during floods from across the range of Wood Turtles may be a result of increased impervious surfaces and bank stabilization within Wood Turtle watersheds, or the removal of beavers (R.A. Saumure, pers. comm.). Jones and Sievert (2009) observed 17 displacements of 12 turtles ranging from 1.4 to 16.8 km during large large floods in a large stream system in western Massachusetts, and reported that mortality rates were elevated and reproductive rates depressed in flood-displaced animals. The smallest flood that resulted in displacement was approximately 14.5 times the average daily flow, or 24.4 m3/s, although flows exceeding 248.0 m3/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 annual rate (0.5) of similar floods over the the 38 years previous (1966–2004). On the other hand, floods may influence genetic structure within watersheds and provide a source of connectivity between lower-watershed populations and isolated demes in the upper watershed. The authors report that most turtles displaced more than 2 km did not return to their home stretch within one year. In the system studied by Jones and Sievert (2009), beaver populations appeared to be robust during the study period.

Sweeten (2008, p. 27) 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, several km into the mainstem of a larger river downstream, and one female displaced 1 km. The author speculated that the displacement occurred because the turtles had returned to the river but had not yet “embedded” themselves in the rootmasses or undercut banks. Both males subsequently made large upstream movements, although neither returned to their home stream within one year and one eventually ended up at a different site—coincidentally, one of the author’s other study sites.

Severe floods in the winter of 1996 displaced Wood Turtles in at least two basins in western Maryland, depositing moribund turtles onto the floodplain (T. Akre and E. Thompson, pers. comm.). In the same flood, displaced Wood Turtles were observed in the Shenandoah watershed (F. Frenzel to T. Akre, pers. comm.).

Latham (1971, p. 32) reported five large adult Wood Turtles washed ashore dead 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. Latham reports that the sightings correspond to “freshets” in Connecticut, 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 the beach at Little Compton, Newport County, Rhode Island, in the 1990s (D. Yorks, Maine Department of Inland Fisheries and Wildlife, pers.

comm.) This location is several dozen kilometers from the nearest confirmed location and may represent a flood-displaced individual from the Taunton River watershed or another coastal drainage.

Further, floods can exacerbate the downstream colonization of aggressive vascular plant species (see Invasive Species, above, and control recommendations in Part 6) such as Japanese knotweed (*Fallopia japonica*), which can be particularly invasive in flood-prone ecosystems because of its propensity to root from plant fragments containing live nodes, and its deep root system (B. Colleran, Invasive Species Biologist, Vermont Agency of Natural Resources, Department of Fish and Wildlife, pers. comm.). Japanese knotweed appears to reduce overall habitat quality for Wood Turtles by reducing structural diversity and crowding out nesting areas near streams (M. Powell, Vermont Adult Learning Center, pers. comm.; M.T. Jones, unpublished data).

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Literature and References

For a complete list of references and a living, comprehensive list of Wood Turtle publications, see Appendix VIII of the Northeast Wood Turtle Conservation Plan at northeastturtles.org.