

7. DEMOGRAPHY AND REPRODUCTION

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Courting Wood Turtles in a Maine stream. DEREK YORKS



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

Introduction

The Wood Turtle's decline across a majority of its range in the United States and Canada has primarily been caused by human encroachment on its habitat, including the direct and indirect effects of habitat loss, fragmentation, and degradation. As noted in Chapter 8, threats include direct mortality from flooding, agricultural machinery, and motor vehicles, as well as illegal collection for pet markets and subsidized predation by mesocarnivores. Wood Turtles are unable to effectively respond—behaviorally or numerically—to these synergistic threats because they have evolved as extreme bet-hedgers: they are adapted to low (and variable) rates of juvenile survival and very high (and stable) adult survival. This is true of most of the turtles within the subfamily Emydinae,¹ which generally exhibit late maturity and a long, iteroparous² lifespan (7.1). Survival is low for eggs and hatchlings, but apparently increases throughout the juvenile life-stages until the turtle reaches adulthood. At this point, individuals generally experience high annual survival rates, and they often reproduce in most years for many sequential decades, replacing at least themselves and a mate in a stable population. In this chapter, we summarize key aspects of Wood Turtle biology, including lifespan, age of maturity, reproductive output, demography, and population dynamics. We also summarize fundamental demographic parameters including recruitment, survivorship, stage and sex structure, generation time, and population viability, and present published and unpublished information on population size, density, and trends.

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

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

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

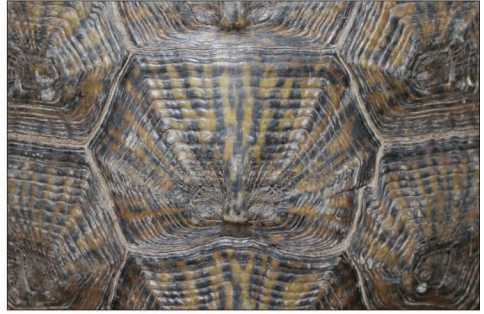
Lifespan

Determining the exact age of mature Wood Turtles is not possible because individuals effectively stop growing (and stop accumulating clear growth annuli) in the years around the onset of maturity. Obtaining a relative age estimate for a mature Wood Turtle is also difficult, and counting annular growth rings on the plastron or carapace is somewhat reliable only for immature or recently mature turtles (younger than ~15–20 years; Harding and Bloomer 1979; Kaufmann 1992a; Parren 2013) (7.2). After the turtle is mature, annual growth rings generally become too small and tightly packed to be counted, if visible at all. In addition, both the plastron and carapace become progressively worn as turtles age, making it even more difficult to see or count annual growth rings. However, there is now abundant evidence that wild Wood Turtles often survive into their fifties (COSEWIC 2007): in Minnesota, recaptures in 2013–2014 of Wood Turtles originally marked as adults in 1990 indicated that at least 11 turtles exceeded 50 years of age (Brown et al. 2015).

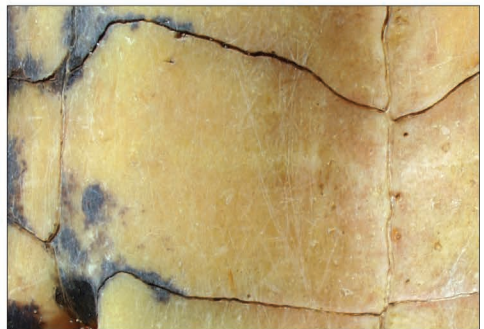
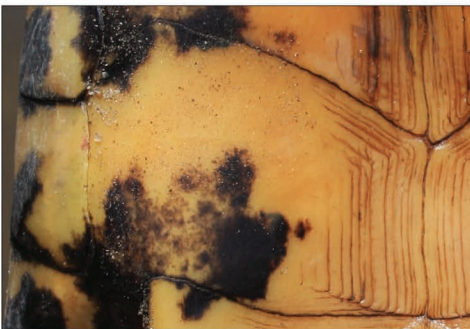
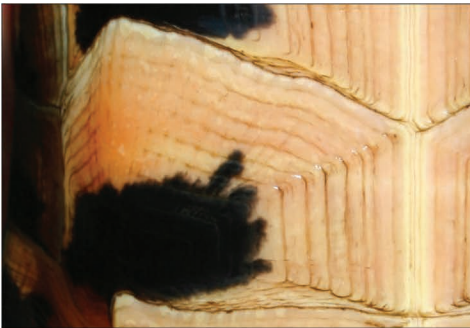
In Pennsylvania, Ernst (2001a) reported wild Wood Turtles over 40 years old, and recaptures of Kaufmann's (1992a) study animals by Kathy Gipe (unpublished data) in 2012–2013 provided evidence of ages exceeding 50 years. In New Jersey, recaptures by Ray Farrell (unpubl. data in Jones et al. 2015) of Wood Turtles marked in the 1970s by Farrell and Graham (1991) indicated ages in excess of 55 years. In Virginia, Akre and Ruther (2015) recaptured two Wood Turtles marked by Kurt Buhlmann in 1988 as mature adults, indicating minimum ages of at least 47 years. In captivity, Oliver (1955) reported a maximum confirmed age of 58 years, and Barker (1964) indicated that a Wood Turtle was in residence at the London Zoological Gardens for 100 years from 1839 to 1939. In New England, Jones (2009) estimated that carapace scutes may require approximately 80 years to become completely worn, based on time-lapse (interval) photographs of the carapace of 75 individual Wood Turtles (7.3), and reported turtles in this category of shell wear. A related analysis of the depigmentation of the characteristic black blotches of the plastron predicted that they would be reduced by >50% after approximately 70 years (Jones 2009) (7.4). Depigmentation of the plastral scutes may also be influenced by injuries that penetrate the keratin layer, or accelerated by limb loss that results in localized wear (Jones, unpubl. data) (7.5). Because turtles in these wear-class categories (with corresponding rates of plastral depigmentation) are frequently found in New England,



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



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



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



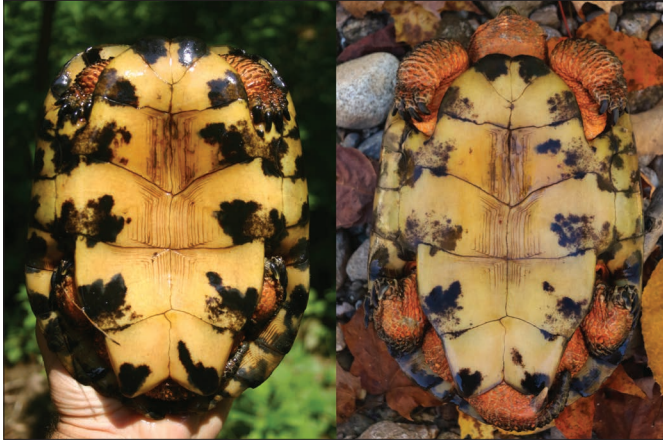
7.5—Depigmentation of the plastral scutes may also be influenced and accelerated by injuries that either penetrate the keratin layer (*left*) or limb loss that results in localized wear on the affected side (*right*). In the righthand image, note the turtle's missing hind right foot and the corresponding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





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

MIKE JONES



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

Sexual Maturity

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



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

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

Reproduction

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



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

Nest Site Fidelity

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

Nesting Frequency

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

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

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

Clutch Size

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



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

Survivorship

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

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

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

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



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

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

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

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

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

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

Adult Survival

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

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

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

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

Stage Structure and Adult Sex Ratio

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

Generation Time

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

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

The Wood Turtle's long lifespan and generation time present implications for the conservation and study of the species. Because they live so long, it is theoretically possible for a few individuals to persist for long periods of time in habitats that are no longer conducive to either successful reproduction or recruitment. This tendency may have been adaptive in an evolutionary sense, because certain areas may be prone to recurring disturbances that rejuvenate key habitats. In today's fragmented landscape, however, the ability for individual Wood Turtles to persist for

decades in suboptimal habitats can confound conservation efforts, as a single observation or occurrence record cannot be reliably used to identify suitable stream habitat. Rather, multiple surveys are necessary to demonstrate the persistence of a viable or recruiting population (though some populations in the first example may be suitable targets for restoration).

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

Population Viability Analyses

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

Population Size and Density

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

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

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

Density for Available Habitat

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

Stream-based Density

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

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

Total Population Size

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

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

Population Trends

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



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

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

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

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

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

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

Summary

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

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

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