

# 6. SPATIAL ECOLOGY AND SEASONAL BEHAVIOR

Lisabeth L. Willey, Thomas S. B. Akre, Michael T. Jones,  
Donald J. Brown, Jeffrey W. Tamplin



Wood Turtle habitat in the Appalachians. MIKE JONES





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

## Introduction

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

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

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

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

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

## Seasonal Activity

### Activity Periods

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



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

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

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

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

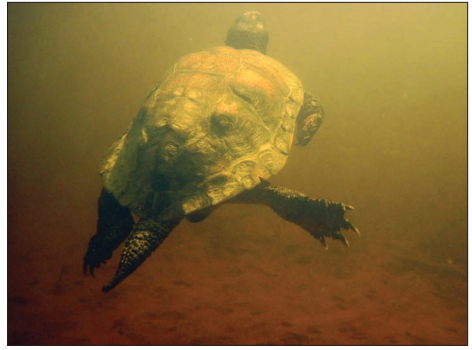
4 Male Wood Turtles may become active earlier in the season and remain active later (Akre and Ernst 2006).

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

### Winter Dormancy or Brumation

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

In northern areas, Wood Turtles exhibit more pronounced periods of dormancy, although observation is often hindered by snow and ice cover. White (2013) reported no Wood Turtle



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



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

activity between 19 December and 12 March in Nova Scotia. Emergence and spring activity in northern New England may be determined by ice-out (Jones and Willey, unpubl. data). Graham and Forsberg (1991) reported extended periods of inactivity with only minor repositioning from December–February in Massachusetts, and Klemens (1993) reported that Wood Turtles become active in Connecticut in late March and early April. Activity in Michigan is rare after mid-October (Holman 2012).

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

### **Summer Dormancy or Aestivation**

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

### **Daily Activity and Thermoregulation**

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

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

## Courtship and Mating

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

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



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



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

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

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



6.7—The courtship ritual of the Wood Turtle includes a prolonged period of “head-bobbing” (left), in which the male extends his throat and head in front of the female’s face and sways his head from side to side while “clapping” his plastron to her carapace. This sound is audible from several meters away. Rarely, the courtship convolutions will result in an overturned pair. DEREK YORKS & MIKE JONES



whistle.” Brewster and Brewster (1987) described nine different behaviors—including lateral rocking, biting, and mounting—in an enclosure setting. Liu et al. (2013) summarized instances of head-bobbing courtship rituals and “shell clapping,” in which the male thumps his plastron against the carapace of the female. The mating posture is typically plastron-to-carapace (Kaufmann 1992a), but Tronzo (1993) and Mitchell and Mueller (1996) reported instances of plastron-to-plastron mating. In addition, several instances of plastron-to-plastron mating were observed during the course of studies for this volume in Aroostook County, Maine and Coos County, New Hampshire (Jones and Willey, unpubl. data) (6.8).



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

### Nesting Season and Timing

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

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

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

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

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

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

### Incubation

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

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

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



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



6.10—Wood Turtle hatchlings usually emerge from the nest in August, but emergence can occur from July to October. Emerging hatchling Wood Turtles are pictured in New England. DEREK YORKS & MIKE JONES

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

### Hatchling Emergence

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

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

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

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

## Social Behavior

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

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

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

## Aggregations

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



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

## Foraging

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

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

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



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

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

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

### Hatchling Diet

Hatchling Wood Turtles are probably opportunistic omnivores, although most observations of feeding suggest invertebrate carnivory. Castellano et al. (2008) reported seven instances

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

### Oophagy

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

### Worm Stomping

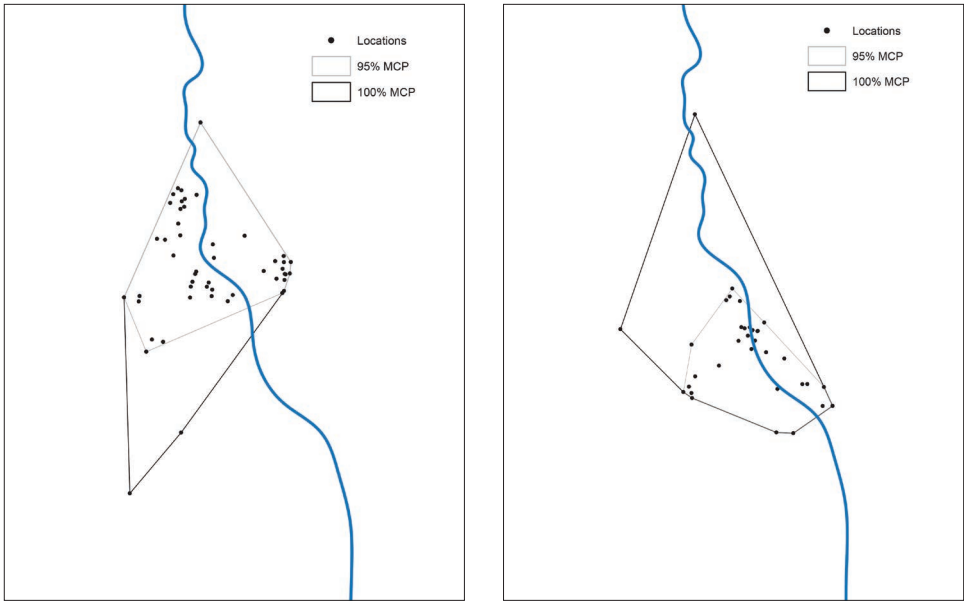
Zeiller (1969) first reported “worm-stomping” foraging behavior in captive Wood Turtles, in which adult turtles use their front feet and plastron to drum worms to the surface. This behavior was described in depth in wild Pennsylvania adults by Kaufmann (1986) and Kaufmann et al. (1989). This has since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



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



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



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

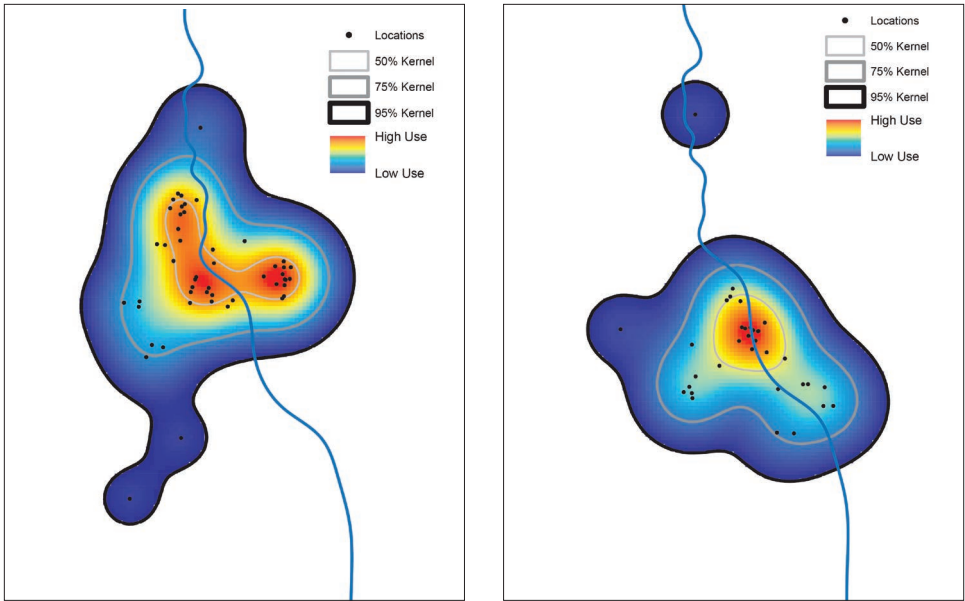
## Movement

### Home Range

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

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





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

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

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

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

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

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

### **Statistical Range**

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

### **Linear Range**

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

### **Stream Range**

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

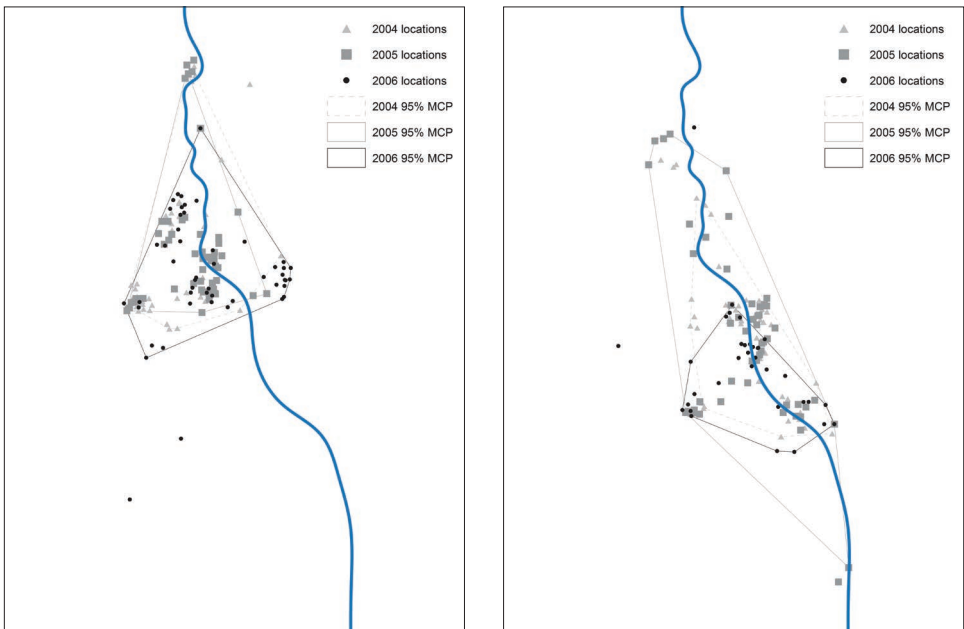
### **Distance from River**

Allard (1909) noted that Wood Turtles “may frequently be found wandering through dry woods and fields far from any water.” Generally, females move greater distances away from their overwintering streams (Akre and Ernst 2006; Jones 2009; McCoard et al. 2016; Thompson et al. 2018; Table 6.2). In Massachusetts and New Hampshire, Jones (2009) reported the mean

value of maximum distances traveled by male Wood Turtles away from the river to be  $117 \pm 146$  m (range=4–1,000+ m;  $n=56$ ), and females  $209 \pm 175$  m (range=29–933 m;  $n=67$ ). Average distances from the stream in West Virginia were found to be  $85.67 \text{ m} \pm 19.67$  for males and  $139.8 \text{ m} \pm 25.79$  for females (McCoard et al. 2016).

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

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



6.17—Wood Turtles often exhibit clear fidelity to home range, nest site, terrestrial habitats, and overwintering sites, although extreme inter-annual variation and even dispersal from sites has been reported. Multi-year home ranges for two turtles are depicted here, female #20 (left) and male #103 (right), showing a high degree of overall inter-annual home range fidelity. LIZ WILLEY

juvenile Wood Turtles. Tuttle and Carroll (2005) noted that one eight-year-old juvenile moved 865 m from a stream, whereas another 11-year-old only moved only 60 m from the stream.

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

### Home Range Fidelity

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

### Nesting Movements

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

### Nest Site Fidelity

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

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

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

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

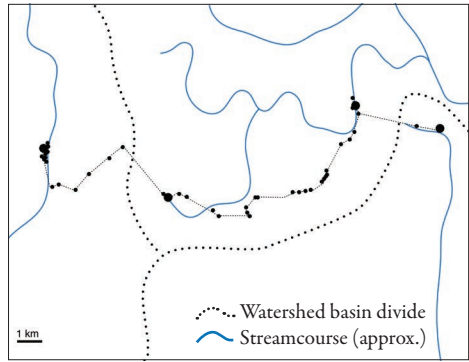
## Hatchling Movements and Orientation

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

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

In Iowa, Otten et al. (Otten and Tamplin, unpubl. data) monitored nine hatchlings from a single clutch via radio telemetry from early September through late October 2015 (152 total

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



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

## Dispersal

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

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

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



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

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

## Summary

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



**BIOLOGY & CONSERVATION**  
*of the* **WOOD TURTLE**

Michael T. Jones  
Lisabeth L. Willey

Editors

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Published by Northeast Association of Fish and Wildlife Agencies, Inc., 2021

Printed in USA on FSC certified paper

Designed and typeset by Matthew R. Burne

ISBN: 978-0-9883535-2-7 (Paperback)

ISBN: 978-0-9883535-3-4 (eBook)

Library of Congress Control Number: 2021904217

This publication was supported by State Wildlife Grants, including the Northeast Association of Fish and Wildlife Agencies, Inc. (NEAFWA) Regional Conservation Need (RCN) program and the Competitive State Wildlife Grant program. This project was also made possible by key contributions from American Turtle Observatory ([www.americanturtles.org](http://www.americanturtles.org)), the Wood Turtle Working Group ([www.northeastturtles.org](http://www.northeastturtles.org)), and Northeast Partners for Amphibian and Reptile Conservation ([www.northeastparc.org](http://www.northeastparc.org)). Early drafts of portions of this book appeared in Part I of *Status and Conservation of Wood Turtle* (2015).

#### Publisher's Cataloging-in-Publication data

Names: Jones, Michael T., editor. | Willey, Lisabeth L., editor.

Title: Biology and Conservation of the Wood Turtle / Michael T. Jones ; Lisabeth L. Willey, editors.

Description: Includes bibliographical references. | Petersburg, NY: Northeast Association of Fish & Wildlife Agencies, Inc., 2021.

Identifiers: LCCN: 2021904217 | ISBN: 978-0-9883535-2-7 (paperback) | 978-0-9883535-3-4 (ebook)

Subjects: LCSH Wood turtle. | Turtles--North America. | Forest animals. | Animals--Habits and behavior. | Reptiles--North America. | Natural history--North America. | Wildlife conservation--North America. | BISAC NATURE / Animals / Reptiles & Amphibians

Classification: LCC QL651 .B56 2021 | DDC 597.9/097--dc23



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