NESTING ECOLOGY OF SPOTTED TURTLES (*Clemmys guttata*) At an Anthropogenic Site in Massachusetts, USA

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Abstract.—Describing the nesting ecology of an imperiled species is fundamental to developing locally informed management recommendations. Spotted Turtles (Clemmys guttata) are a species of conservation need that use upland habitats for nesting. We conducted terrestrial visual surveys for nesting females throughout late May and June 2021 and 2022, protected nests from depredation using cages, and monitored nests throughout the incubation season until hatchling emergence. Our objectives were to: (1) characterize nesting phenology, including nesting and hatchling emergence dates and incubation period; (2) describe mean clutch size and hatching success; (3) describe nest site preferences at the microhabitat scale; and (4) compare the microhabitat of observed nests with random points using Conditional Logistic Regression. We located 18 Spotted Turtle nests and observed nesting between 30 May and 28 June, with a median nesting date of 9 June. Hatchlings emerged during August and September after a median incubation period of 79 d. Clutch size ranged from 3-6 eggs per clutch, with a mean clutch size of 4.31. The mean hatch success rate for protected nests was 50.0% and hatch failure was due to egg infertility, root and fungal intrusion, flooding, and depredation. We found nests along trail edges and clearings, and nests were associated with herbaceous vegetation, dead vegetation, bare soil, and gravel. Habitat characteristics did not differ between nest sites and random points. Our results provide novel Spotted Turtle nesting data for Massachusetts, USA, that can inform Population Viability Analysis and provide a timeline for when to avoid actively managing nest sites in the state.

Key Words.—conservation; Emydidae; endangered species; management; nest protection; New England; reptiles; right-of-way

INTRODUCTION

Studies of the nesting ecology of oviparous species can provide insight into reproductive biology, nest survival, and nest site preferences, which are essential to understanding the life history of a species (Spencer and Thompson 2003; Steen et al. 2012). Nest success rates are important life-history variables that can inform Population Viability Analyses (PVAs) and management practices (Buhlmann and Osbourne 2011; Roosenberg et al. 2014). Freshwater turtles are oviparous, exhibit delayed sexual maturity, have low rates of juvenile survival, high rates of adult survival, and are among the most imperiled vertebrate clades on earth (Rhodin et al. 2018; Stanford et al. 2020). There are many documented barriers to turtle nests successfully hatching, including subsidized predators that prey upon turtle eggs (Mitchell and Klemens 2000). Habitat degradation and changes in land-use may prompt females to travel further distances to nest sites or force them to use non-preferable sites (Beaudry et al. 2010; Willey et al. 2022). Due to the

amalgam of threats that impede successful nesting of turtles (Byer et al. 2018; Lovich et al. 2018), it is important to conduct nesting studies to understand the best ways to conserve these species.

Spotted Turtles (Clemmys guttata) are a freshwater species endemic to North America, where they are federally listed as Endangered in Canada (Committee on the Status of Endangered Wildlife in Canada 2014) and a Species of Greatest Conservation Need (SGCN) in each U.S. state within which they occur. This species is declining due to mortality on roads, illegal collection, habitat degradation, and depredation by subsidized predators (Ernst and Lovich 2009; Howell et al. 2019). The nesting ecology of Spotted Turtles varies considerably throughout the range (Ernst and Zug 1994; Litzgus and Mousseau 2006), though eggs usually incubate throughout the summer, and hatchlings emerge in the late summer (Ernst 1976; Carroll and Ultsch 2007; Refsnider et al. 2022). Because of regional variability, field studies must take place in various locations to allow for a better understanding of how environmental

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parameters influence reproduction to inform local management decisions and assess status. The objectives of our study were to: (1) characterize nesting phenology, including nesting and hatchling emergence dates and incubation period; (2) describe mean clutch size, hatch success and failure, and describe the fate of failed nests; (3) describe nest site preferences on a microhabitat scale; and (4) compare the microhabitat of observed nests with random points using conditional logistic regression for Spotted Turtles in Massachusetts, USA. Despite several field studies focusing on the nesting ecology of Spotted Turtles, few publications focus on nest site selection or nest success parameters in anthropogenic settings to inform management (Joyal et al. 2001; Beaudry et al. 2010).

MATERIALS AND METHODS

Study site.-We conducted nesting surveys at an anthropogenically disturbed site in Bristol County, Massachusetts, USA (Massachusetts NHESP element occurrence #170). The site is within the Taunton River watershed and consists of low elevation (< 120 m) mixed forests and wetland complexes shifting from gently rolling hills to flatlands (Griffith et al. 2009). We do not report the exact location of our study due to state wildlife agency concerns about illegal collection. Our study occurred in a 3.0 km section of a powerline right-of-way (ROW) surrounded by > 4,000 ha of forested wetland. Within the ROW, a gravel trail, elevated above the water level, was directly adjacent to emergent and scrub-shrub wetlands with several clearings along the trail containing transmission line towers. This site was chosen because Spotted Turtles were known from previous trapping to be relatively abundant (Lisabeth Willey et al., unpubl. report). This species is known to nest at various ROWs in Massachusetts and characterizing its nesting ecology at a ROW can inform its management at similar sites.

Data collection.—We conducted nesting surveys in the evenings (1700-2400) between 23 May and 8 July 2021 and 30 May to 2 July 2022. Surveys consisted of visually searching for nesting females in all areas of the ROW that were not submerged underwater. We captured individuals that were not actively nesting. determined their sex by visual inspection, and manually palpated anterior to the hind leg to determine if a female was gravid (Litzgus and Brooks 1998). We recorded the exact locations of individual captures using a handheld GPS (Garmin GPSmap 78; Garmin Ltd., Olathe, Kansas, USA). We used 150 mm electronic digital calipers (Erebus Company, Zhejiang, China) to record morphometric measurements including midline carapace length (MCL), midline plastron length (MPL), carapace height (CH), carapace width (CW), and

plastron width (PW) to the hundredths place (Iverson and Lewis 2018). We recorded non-gravid body mass (to 1 g) using a Pronto Digital Kitchen Scale (Ozeri Corporation, San Diego, California, USA), counted the lines of arrested growth on an abdominal scute of the plastron, and estimated the percentage of wear on plastron growth rings to the nearest 5% (Lisabeth Willey et al., unpubl. report).

We calculated descriptive statistics (minimum, mean, median, maximum, and standard deviation) for morphometric measurements. Individuals were given a unique identification number and notch on the marginal scutes using a triangular file (Ernst et al. 1974). We attached a cocoon thread bobbin (Imperial Threads Inc., North Brook, Illinois, USA) to the center posterior carapace of gravid females using electrical tape, which allowed for precise tracking of turtle movements and aided in identifying nests (Breder 1927). We wrapped thread bobbins in aluminum foil and electrical tape to contain the thread; each package weighed approximately 4 g and never exceeded 5% of turtle body mass to ensure it did not impede the locomotion or behavior of individuals (Graeter et al. 2013). We tied the thread to the nearest piece of vegetation, released the turtle, and followed the threads every 24-72 h (Knoerr et al. 2021).

Upon finding an individual that was actively nesting, we flagged nearby vegetation to mark the nesting location, took a photograph of the nest site, and continued surveying, monitoring the nesting progress of the turtle periodically. We recorded the nesting date (day of nest completion), nest initiation time (time of first observed digging), nest completion time (time the female left the nest site), and minimum nesting time (total time between nest initiation and nest completion). If the female remained in the nesting area once nesting was completed, we captured her and recorded morphometric measurements and identification number following the methods outlined above. We recorded the exact location of nests (±4 m) using a handheld GPS (Garmin GPSmap 78; Garmin Ltd.) and protected them from depredation using wire mesh cages (0.64 cm galvanized hardware cloth) that were affixed on top of the substrate using landscape pins (Bougie et al. 2020).

Throughout the incubation period, we monitored each nest with one Bushnell Core camera (Bushnell Corporation, Overland Park, Kansas, USA) and observed the nest in person every 1–2 weeks (Riley and Litzgus 2013). We monitored nests every 7 d during the late summer through early fall; and modified nest cages by removing the cage corners in late July, allowing hatchlings to disperse at will. We recorded the minimum nest date (earliest nesting date of the study), the maximum nest date (latest nesting date of the study), and the median nest date (median date of all nests observed during our study). We excavated nests for which young had not emerged after 100 d since oviposition to determine the fate of the nest (Refsnider et al. 2022). If hatchlings were present in the nest chamber, we released them into herbaceous cover within 1 m of the nest. We describe the fate of nests by counting the eggs in the nest chamber after hatchling emergence or upon excavation, dissecting the eggs to determine the cause of failure. We describe the fate of nests as successful if all of the eggs hatch, partially successful if at least one egg hatches, unsuccessful if no eggs hatch, and report descriptive statistics for nest fates. We calculated a success rate for each nest by dividing the number of hatched eggs by the clutch size and calculated the mean success rate across all nests.

Nest site selection analysis .- To determine the nest site preferences of Spotted Turtles at the microhabitat level, we estimated the proportion of ground cover types in a 1-m² plot centered on the nest, and also in 1-m² random plots (Fig. 1; Kim 2018). We characterized ground cover types (herbaceous, coarse woody debris [CWD], moss/lichen, dead vegetation, gravel, and bare soil) and estimated proportions visually within the frame to the nearest 5% (Kim 2018). We compared the microhabitat of observed nests to random points, which we determined by following a random bearing to a distance between 1-10 m from the observed nest site. This would reflect a random bearing off of wetlands below the upland to keep the assessment within the same macrohabitat type (Compton et al. 2002). We chose a random distance of 1-10 m from observed nests because the uplands of our site are topographically confined and in most locations the uplands are only 5 m in width. We categorized ground cover within 1-m² plots at random points following the same procedure outlined above to compare ground cover between observed nests and random points.



FIGURE 1. We used a 1-m^2 PVC frame to classify ground cover type for our microhabitat analysis by surrounding a Spotted Turtle (*Clemmys guttata*) nest with the nest central to the frame. (Photographed by John Garrison).

We performed all statistical analyses in R Studio (R Core Team 2022) and considered test statistics significant with $\alpha = 0.05$. We used Conditional Logistic Regressions using the function cLogit in the R package Survival to evaluate microhabitat using the proportions of ground cover types within 1-m² plots at nest sites and paired random points (Therneau 2022). We calculated Akaike Information Criterion (AIC) with a correction for small samples (AICc) using the function AICc in the R package MuMIn to rank the Conditional Logistic Regression models (Barton 2022). We ran univariate models in our Conditional Logistic Regression for each cover type that was classified within 1-m² plots at nest sites and paired random points (herbaceous, CWD, moss/lichen, dead vegetation, gravel, and bare soil), ranked them by AICc values, and reported the associated statistics.

RESULTS

Nesting observations.—We observed the exact location of 18 Spotted Turtle nests during our 2-y study. Nesting took place in the late afternoon and throughout the night, with some individuals taking several hours to complete nesting. We saw two females digging nest chambers after nightfall, staying the entire night atop the nest chamber, and finally depositing the eggs in the early morning. We observed nesting between 30 May and 28 June, with a median nesting date of 9 June (Table 1). Hatchlings emerged during August and September with a median incubation time of 79 d (Table 1). We detected most nests by locating females who were actively nesting (n = 16) and two nests via following thread bobbins. Nesting female body size varied among individuals from a low of 99.31 MCL to a high of 118.96 MCL (Table 2).

Clutch size and nest success.—Clutch size ranged from 3–6 eggs per clutch, with a mean clutch size of 4.31 eggs (standard deviation = 0.79; Table 3). Of the 18 nests documented, 33.3% (n = 6) successfully hatched, 33.3% (n = 6) were partially successful, and 33.3% (n = 6) were unsuccessful. The success rate of each nest ranged from 0.0–100.0%, and the mean success rate among all nests

TABLE 1. Minimum, median, and maximum values for nesting date (ND), emergence date (ED), incubation period (IP), nest initiation time (NIT), nest completion time (NCT), and minimum nesting time (MNT) of 10 Spotted Turtle (*Clemmys guttata*) nests in Bristol County, Massachusetts, USA. Abbreviation Aug. = August and Sept. = September.

	ND	ED	IP	NIT	NCT	MNT
Minimum	30 May	22 Aug. ± 7 d	68 d	1727	1909	27.0 m
Median	9 June	2 Sept. ± 7 d	79 d	1957	2329	3.27 h
Maximum	28 June	12 Sept. ± 7 d	99 d	0147	0704	10.53 h

TABLE 2. Descriptive statistics for morphometric measurements including growth rings, midline carapace length (MCL), midline plastron length (MPL), plastron width (PW), carapace width (CW), carapace height (CH), mass, and % wear (deterioration of growth rings estimated to the nearest 5%) of Spotted Turtles (*Clemmys guttata*) that nested during our study in Bristol County, Massachusetts, USA.

	Growth rings	MCL	MPL	PW	CW	CH	Mass	% Wear
Minimum	13	99.31	94.30	57.95	82.09	39.31	176.00	0.00
Median	15.5	112.12	99.95	62.12	85.45	43.09	205.00	50.0
Mean	15.9	111.02	100.15	62.26	85.59	43.50	209.85	52.5
Maximum	20.0	118.96	106.24	67.36	91.88	50.37	255.00	90.0
Standard deviation	2.11	5.54	3.98	2.80	4.03	2.70	28.66	27.17
Sample size	12	13	13	13	13	13	13	12

was 50.0% (Table 3). Dissecting the unviable eggs (n = 32, 46.4%) revealed eggs that were unfertilized, had plant roots or fungal hyphae on the exterior of the shell, or contained partially developed hatchlings. One of the dissected eggs in Nest R contained an embryo that appeared to lack normal pigment and had a light-colored carapace and a primarily white plastron (Fig. 2). Camera traps revealed that two nests located on a trail edge were run over by the same truck on the same day, 61 d (Nest K) and 56 d (Nest M) after the nesting date. Upon excavating Nest K, we found five eggs, one of which successfully hatched, two of which were unviable with root and fungal intrusion, two contained

TABLE 3. Descriptive statistics for clutch size, number of hatched eggs, number of failed eggs, and success rate of 18 Spotted Turtle (*Clemmys guttata*) nests observed in Bristol County, Massachusetts, USA. The fate of nests was characterized by examining eggs in the nesting chamber after excavation and the success rate was calculated by dividing the number of successful eggs by the clutch size. The abbreviation SD = standard deviation.

	Clutch size	# of hatched eggs	# of failed eggs	Success rate
Nest A	NA	NA	NA	0
Nest B	4	4	0	1
Nest C	NA	NA	NA	0
Nest D	4	3	1	0.75
Nest E	4	4	0	1
Nest F	4	4	0	1
Nest G	4	1	3	0.25
Nest H	6	4	2	0.67
Nest I	3	3	0	1
Nest J	5	2	3	0.4
Nest K	5	1	4	0.2
Nest L	4	0	4	0
Nest M	4	4	0	1
Nest N	4	3	1	0.75
Nest O	6	0	6	0
Nest P	4	0	4	0
Nest Q	4	4	0	1
Nest R	4	0	4	0
Minimum	3	0	0	0
Median	4	3	1.5	0.53
Mean	4.31	2.31	2	0.50
Maximum	6	4	6	1
SD	0.79	1.7	2	0.44

the remains of partially developed hatchlings with pill bugs (Armadillidiidae) and ants (Formicidae) preying upon the hatchling carcasses. Nest M contained four eggs, all of which successfully hatched.

Nest site selection.—We observed nests constructed in clearings associated with transmission line towers (50%, n = 9) and on the edge of a gravel trail (50%, n =9), all of which were in open canopy settings (n = 18). The microhabitat selection revealed that the herbaceous vegetation model had the lowest AICc value, followed by the models for gravel, dead vegetation, bare soil, CWD, and finally, moss/lichen (Table 4). Spotted Turtle nest sites were negatively associated with herbaceous vegetation, bare soil, CWD, and Moss/Lichen, and positively associated with gravel and dead vegetation (Table 4); however, none of these relationships were significant.

DISCUSSION

Nesting observations.—Spotted Turtle nesting in Massachusetts occurred primarily at night and occurred mainly in June. Nests took several hours for females to complete, similar to elsewhere in the species range (Litzgus and Brooks 1998; Beaudry et al. 2010). Our median observed incubation time of 79 d is comparable to that reported in Pennsylvania (70–83 d; Ernst 1970) and South Carolina (79 d; Litzgus and Mousseau 2006). Understanding the phenology of nesting is essential for informing future research and management. Providing an expected timeline for nesting activity and incubation can inform when land managers should avoid active habitat management in known nesting areas to reduce impacting nesting females and destroying nests.

The use of thread bobbins was not an effective method for locating nests due to the high volume of human activity and all-terrain vehicle use at our study site, which caused most threads to break, making it difficult to follow the lines. We located most nests by conducting visual surveys, similar to nesting research conducted in Pennsylvania, USA (Ernst 1970). Visual surveys were an effective method for locating nesting Spotted Turtles, likely because of the relatively confined upland areas,



FIGURE 2. A dead Spotted Turtle (*Clemmys guttata*) embryo that appeared to lack normal pigment had a light-colored carapace (A) and a primarily white plastron (B) found in a failed nest (Nest R) in Massachusetts, USA. (Photographed by John Garrison).

and the high density of individuals at our study site. Spotted Turtles, however, are known to nest in wetlands and our detection methods might have caused us to overlook nesting outside of the confined uplands and because of this, our results may not be representative of the broader population. Observing nesting through repeat visual surveys is minimally invasive to nesting females because it does not require repeated capture events prior to oviposition to check gravid status via palpation. Using minimally invasive techniques for studying wild animals can significantly reduce the impact of field research on study organisms and may lead to unique ecological observations (Levasseur et al. 2019; Unger and Santana 2019; Zemanova 2020).

Clutch size and nest success.—Our mean observed clutch size of 4.31 is generally greater than studies that took place further south in the range of Spotted Turtles (Table 5) and most similar to the mean clutch sizes in Pennsylvania (3.58; Ernst 1970), Ontario, Canada (5.30; Litzgus and Brooks 1998), and in Ohio and Michigan, USA (3.70; Refsnider et al. 2022). Our study supports the hypothesis that Spotted Turtles in higher latitudes produce more eggs per clutch than individuals in the southern part of the range (Litzgus

and Mousseau 2006). Documentation of mean clutch size allows for comparisons between populations and exploring trends in reproductive output over time and space, and provides improved parameter estimates for PVAs (Walde et al. 2007; Willey and Sievert 2012; Duchak and Burke 2022).

Our mean observed nest success rate (50%) is comparable to other studies conducted on Spotted Turtles in Georgia, USA (50%; Chandler et al. 2022), Maine, USA (33%; Beaudry et al. 2010), and Pennsylvania (68%; Ernst 1970); however, we caged nests to prevent depredation, while these other studies did not. Other nesting studies of closely related species reported similar rates of nest success among caged nests (Wilson and Ernst 2005; Willey and Sievert 2012; Zappalorti et al. 2017). The low success rate of caged nests may be due to infertility or environmental factors such as root and fungal intrusion (Stegmann et al. 1988; Duchak and Burke 2022). An unknown predator depredated one of the two nests because the cage was not properly centered over the nest, and flooding inundated the other. The observations of two of our nest cages that were run over by a truck raises concerns for the survival of turtle nests in areas that receive high volumes of vehicle traffic, although the two nests run over by a truck had similar

TABLE 4. Outputs from conditional Logistic Regression models comparing microhabitat characteristics at observed Spotted Turtle (*Clemmys guttata*) nests with paired random points, ranked from lowest to highest Akaike's Information Criterion corrected for small sample sizes (AICc) values (n = 36; 18 nests and 18 random points). Cover types include herbaceous vegetation (Herb), gravel, dead vegetation (DV), bare soil, coarse woody debris (CWD), and moss/lichen. The abbreviation Coef = coefficient, LCI = lower confidence interval and UCI = upper confidence interval.

Cover Type	Coef	Odds ratio	P-value	Ζ	LCI	UCI	AICc
Herb	-0.025	0.975	0.095	-1.670	0.947	1.004	23.846
Gravel	0.035	1.035	0.133	1.502	0.990	1.083	23.983
DV	0.027	1.027	0.156	1.419	0.990	1.065	24.343
Bare soil	-0.022	0.978	0.257	-1.133	0.941	1.016	25.492
CWD	-0.015	0.986	0.553	-0.593	0.939	1.034	26.843
Moss/lichen	-0.009	0.991	0.600	-0.524	0.959	1.025	26.919



FIGURE 3. (A) Example of a clearing at our study site in Massachusetts, USA, and (B) a Spotted Turtle (*Clemmys guttata*) nesting in a clearing. (C) Example of a trail edge at our study site and (D) and *C. guttata* nesting along the trail edge. (Photographed by John Garrison).

nest success rates to all other nests observed. Therefore, further research on nest success rates in Spotted Turtles and the role that human recreation plays in this process is warranted.

Nest site selection.—All observed nests were constructed in clearings associated with transmission line towers or on trail edges elevated above the nearby wetlands, receiving total sun exposure (Fig. 3). These results are similar to a study conducted in Hampshire and Franklin counties in Massachusetts, where nesting occurred in upland fields with sparse vegetation and total sun exposure (Milam and Melvin 2001). Similar to other studies in northerly latitudes (Litzgus and Brooks 1998; Refsnider et al. 2022), our results indicate that

TABLE 5. Mean clutch sizes (MCS) of Spotted Turtles (*Clemmys guttata*) from nesting studies throughout the range in the USA and Ontario, Canada, arranged by lowest (top) to highest (bottom) clutch size.

Reference	Location	MCS	# of nests
Chandler et al. 2022	Georgia	2.10	41
Litzgus and Mousseau 2006	South Carolina	2.80	33
Ernst 1970	Pennsylvania	3.58	12
Refsnider et al. 2022	Ohio and Michigan	3.70	36
Current study	Massachusetts	4.31	16
Litzgus and Brooks 1998	Ontario	5.30	24

Spotted Turtles require open areas that provide adequate sunlight for incubation. Studies of Spotted Turtle nesting ecology in southerly latitudes have reported a majority of nests in closed canopy settings (Chandler et al. 2022; Litzgus and Mousseau 2006). The nest site selection of Spotted Turtles in our study is similar, yet different to, the nest sites described in other studies, which provides more evidence of the dynamic nesting ecology throughout the range (Litzgus and Mousseau 2006). Nesting may occur in other areas of our study site, such as within the forested wetlands; however, our study design focused on elevated, anthropogenically disturbed habitats. None of the models in our microhabitat selection analysis yielded significant results, therefore, we did not find evidence that the variables we measured differed between nests and random points. Increasing the sample size of nests would allow for more advanced and powerful statistical analysis, which would help determine the predictors of nest success.

While our study provided insight into the nesting ecology of Spotted Turtles in Massachusetts, there is still much to be learned about the nesting ecology of this species in the state. Other studies have described multiple clutching in Spotted Turtles (Litzgus and Mousseau 2003; Chandler et al. 2022), and it is unknown whether this occurs in Massachusetts individuals. Tracking individuals daily via radio telemetry (Chandler et al. 2022), in concert with locating nests via thread bobbins (if not in areas with vehicle traffic), may provide insight into the possibility of multiple clutching in Massachusetts Spotted Turtles.

In conclusion, our study revealed the peak nesting season and incubation period for Spotted Turtles in Massachusetts, and we suggest that land managers avoid active management at known nesting sites from late May through September. The incubation period for Spotted Turtles in Massachusetts can inform future studies that aim to better understand hatchling ecology and survival and can be used as a reference for captive rearing projects for the purpose of head starting turtles for later release. We described clutch size and the fate of nests, which allows for an assessment of how these parameters vary over space and time and can inform PVAs. Our nest site selection analysis did not discern a difference between the nest sites and random points, which may be due to small sample size, the variables we measured, and the scale at which the variables were measured. Future studies should conduct nest site selection analysis for this species and measure different variables at the microhabitat scale (e.g., soil moisture, soil grain size, microtopography, and temperature) with a larger sample size to better understand nest site preferences.

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LITERATURE CITED

- Barton K. 2022. MuMIn: Multi-model Inference. R package version 1.47.1. https://cran.r-project.org/ package=MuMIn.
- Beaudry, F., P.G. deMaynadier, and M.L. Hunter, Jr. 2010. Nesting movements and the use of anthropogenic nesting sites by Spotted Turtles (*Clemmys guttata*) and Blanding's Turtles (*Emydoidea blandingii*). Herpetological Conservation and Biology 5:1–8.
- Bougie, T.A., N.W. Byer, C.N. Lapin, M.Z. Peery, J.E. Woodford, and J.N. Paulie. 2020. Wood Turtle

(*Glyptemys insculpta*) nest protection reduces depredation and increases success, but annual variation influences its effectiveness. Canadian Journal of Zoology 98:715–724.

- Breder, R.B. 1927. Turtle trailing: a new technique for studying the life habits of certain Testudinata. Zoologica 9:231–243.
- Buhlmann, K.A., and C.P. Osborn. 2011. Use of an artificial nesting mound by Wood Turtles (*Glyptemys insculpta*): a tool for turtle conservation. Northeastern Naturalist 18:315–334.
- Byer, N.W., B.N. Reid, R.A. Seigel, and M.Z. Peery. 2018. Applying lessons from avian ecology to herpetological research: techniques for analyzing nest survival due to predation. Herpetological Conservation and Biology 13:517–532.
- Carroll, D.M., and G.R. Ultsch. 2007. Emergence season and survival in the nest of hatchling turtles in south central New Hampshire. Northeastern Naturalist 14:307–310.
- Chandler, H.C., B.S. Stegenga, and J.D. Mays. 2022. Compensating for small body size: the reproductive ecology of southern Spotted Turtle (*Clemmys guttata*) populations. Ichthyology and Herpetology 110:268–277.
- Compton, B.W., J.M. Rhymer, and M. McCollough. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83:833–843.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2014. COSEWIC assessment and status report on the Spotted Turtle *Clemmys guttata* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 74 p.
- Duchak, T.J., and R.L. Burke. 2022. Hatchling failure in Wood Turtle (*Glyptemys insculpta*) is linked to maternal identity. Frontiers in Ecology and Evolution 10:836800. https://doi.org/10.3389/ fevo.2022.836800.
- Ernst, C.H. 1970. Reproduction in *Clemmys guttata*. Herpetologica 26:228–232.
- Ernst, C.H. 1976. Ecology of the Spotted Turtle, *Clemmys guttata* (Reptilia, Testudines, Testudinidae), in southeastern Pennsylvania. Journal of Herpetology 10:25–33.
- Ernst, C.H., and J.E. Lovich. 2009. Turtles of the United States and Canada. 2nd Edition. John Hopkins University Press, Baltimore, Maryland, USA.
- Ernst, C.H., and G.R. Zug. 1994. Observations on the reproductive biology of the Spotted Turtle, *Clemmys guttata*, in southeastern Pennsylvania. Journal of Herpetology 28:99–102.
- Ernst, C.H., M.F. Hershey, and R.W. Barbour. 1974. A new coding system for marking hard-shelled turtles.

Transactions of the Kentucky Academy of Science 35:27–38.

- Graeter, G.J., K.A. Buhlmann, L.R. Wilkinson, and J.W. Gibbons. 2013. Inventory and monitoring: recommended techniques for reptiles and amphibians. Technical Publication IM-1, Partners in Amphibian and Reptile Conservation, Birmingham, Alabama, USA. 322 p.
- Griffith, G.E., J.M. Omernik, S.A. Bryce, J. Royte, W.D. Hoar, J.W. Homer, D. Keirstead, K.J. Metzler, and G. Hellyer. 2009. Ecoregions of New England. U.S. Geological Survey, Reston, Virginia, USA. 1 p.
- Howell, H.J., R.H. Legere, Jr., D.S. Holland, and R.A. Seigel. 2019. Long-term turtle declines: protected is a verb, not an outcome. Copeia 107:493–501.
- Iverson, J.B., and E.L. Lewis. 2018. How to measure a turtle. Herpetological Review 49:453–460.
- Joyal, L.A., M. McCollough, and M.L. Hunter. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15:1755– 1762.
- Kim, J. 2018. Important habitat characteristics in Blanding's Turtle nesting behavior in eastern Massachusetts. M.Sc. Thesis, Antioch University New England, Keene, New Hampshire, USA. 53 p.
- Knoerr, M.D., A.M. Tutterow, G.J. Graeter, S.E. Pittman, and K. Barrett. 2021. Population models reveal the importance of early life-stages for population stability of an imperiled turtle species. Animal Conservation 25:53–64.
- Levasseur, P., S. Sterrett, and C. Sutherland. 2019. Visual head counts: a promising method for efficient monitoring of Diamondback Terrapins. Diversity 11:101. https://doi.org/10.3390/d11070101.
- Litzgus, J.D., and R.J Brooks. 1998. Reproduction in a northern population of *Clemmys guttata*. Journal of Herpetology 32:252–259.
- Litzgus, J.D., and T.A. Mousseau. 2003. Multiple clutching in southern Spotted Turtles, *Clemmys guttata*. Journal of Herpetology 37:13–23.
- Litzgus, J.D., and T.A. Mousseau. 2006. Geographic variation in reproduction in a freshwater turtle (*Clemmys guttata*). Herpetologica 62:132–140.
- Lovich, J.E., J.R. Ennen, M. Agha, and J.W. Gibbons. 2018. Where have all the turtles gone, and why does it matter? Bioscience 68:771–781.
- Milam, J.C., and S.M. Melvin. 2001. Density, habitat use, movements, and conservation of Spotted Turtles (*Clemmys guttata*) in Massachusetts. Journal of Herpetology 35:418–427.
- Mitchell, J., and M. Klemens. 2000. Primary and secondary effects of habitat alteration. Pp. 5–32 *In* Turtle Conservation. Klemens, M. (Ed.). Smithsonian Institute Press, Washington, D.C., USA.

- R Development Core Team. 2022. R: a language and environment for statistical computing. R
- Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.
- Refsnider, J.M., S.E. Carter, A. Diaz, A.C. Hulbert, G.R. Kramer, P. Madden, and H.M. Streby. 2022. Macroand microhabitat predictors of nest success and hatchling survival in Eastern Box Turtles (*Terrapene carolina carolina*) and Spotted Turtles (*Clemmys guttata*) in Oak Savanna landscapes. Frontiers in Ecology and Evolution 9:788025. https://doi. org/10.3389/fevo.2021.788025.
- Rhodin, A.G.J., C.B. Stanford, P.P. van Dijk, C. Eisemberg, L. Luiselli, R.A. Mittermeier, R. Hudson, B.D. Horne, E.V. Goode, G. Kutchling, et al. 2018.
 Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conservation and Biology 17:135–161.
- Riley, J.L., and J.D. Litzgus. 2013. Evaluation of predator-exclusion cages used in turtle conservation: cost analysis and effects on nest environment and proxies of hatchling fitness. Wildlife Research 40:499–511.
- Roosenburg, W.M., D.M. Spontak, S.P. Sullivan, E.L. Mathews, M.L. Heckman, R.J. Trimbath, R.P. Dunn, E.A. Dustman, L. Smith, and L.J. Graham. 2014. Nesting habitat creation enhances recruitment in a predator-free environment: *Malaclemys* nesting at the Paul S. Sarbanes Ecosystem Restoration Project. Restoration Ecology 22:815–823.
- Stanford, C.B., J.B. Iverson, A.G.J. Rhodin, P.P. van Dijk, R.A. Mittermeier, G. Kuchling, K.H. Berry, A. Bertolero, K.A. Bjorndal, T.E.G. Blanck, et al. 2020. Turtles and tortoises are in trouble. Current Biology 30:721–735.
- Steen, D.A., J.P. Gibbs, K.A. Buhlmann, J.L. Carr, B.W. Compton, J.D. Congdon, J.S. Doody, J.C. Godwin, K.L. Holcomb, D.R. Jackson, et al. 2012. Terrestrial habitat requirements of nesting freshwater turtles. Biological Conservation 150:121–128.
- Stegmann, E.W., R.B. Primack, and G.S. Ellmore. 1988. Absorption of nutrient exudates from Terrapin eggs by roots of *Ammophila breviligulata* (Gramineae). Canadian Journal of Botany 66:714–718.
- Spencer, R.J., and M.B. Thompson. 2003. The significance of predation in nest site selection of turtles: an experimental consideration of macro- and microhabitat preferences. OIKOS 102:592–600.
- Therneau T. 2022. A package for survival analysis in R. R package version 3.3–1. https://cran.r-project.org/ package=survival.
- Unger, S. and A. Santana. 2019. Turtles and trail cameras: non-invasive monitoring using artificial platforms. Basic and Applied Herpetology 33:93–100.

- Walde, A.D., J.R., Bider, D. Masse, R.A. Saumure, and R.D. Titman. 2007. Nesting ecology and hatching success of the Wood Turtle, *Glyptemys insculpta*, in Québec. Herpetological Conservation and Biology 2:49–60.
- Wilson, G.L., and C.H. Ernst. 2005. Reproductive ecology of the *Terrapene carolina carolina* (Eastern Box Turtle). Southeastern Naturalist 4:689–702.
- Willey, L.L., and P.R. Sievert. 2012. Notes on the nesting ecology of Eastern Box Turtles near the northern limit of their range. Northeastern Naturalist 19:361–372.
- Willey, L.L., M.T. Jones, P.R. Sievert, T.S.B. Akre, M. Marchand, P. deMaynadier, D. Yorks, J. Mays,

J. Dragon, L. Erb, et al. 2022. Distribution models combined with standardized surveys reveal widespread habitat loss in a threatened turtle species. Biological Conservation 266:109437. https://doi.org/10.1016/j.biocon.2021.109437.

- Zappalorti, R.T., A.M. Tutterow, S.E. Pittman, and J.E. Lovich. 2017. Hatching success and predation of Bog Turtle (*Glyptemys muhlenbergii*) eggs in New Jersey and Pennsylvania. Chelonian Conservation and Biology 16:194–202.
- Zemanova, M.A. 2020. Towards more compassionate wildlife research through the 3Rs principles: moving from invasive to non-invasive methods. Wildlife Biology 2020(1): (2020). https://doi.org/10.2981/wlb.00607.



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