Nest-Site Characteristics of *Glyptemys muhlenbergii* (Bog Turtle) in New Jersey and Pennsylvania

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Abstract - Nest-site selection can affect both the survival and fitness of female turtles and their offspring. In many turtle species, the nest environment determines the thermal regime during incubation, length of incubation period, sex ratio of the hatchlings, and exposure to predators and other forms of mortality for both mothers and their offspring. Between 1974 and 2012, we collected detailed data on habitat variables at 66 *Glyptemys muhlenbergii* (Bog Turtle) nests in 9 different bogs, fens, and wetland complexes in New Jersey and Pennsylvania. The nests had a mean elevation above the substrate of 8.2 cm, and many were shallow and located in raised tussocks of grass or sedges. Females covered most nests, but we also observed partially or completely uncovered eggs. Some females deposited eggs in communal nests; we found 4 nests with 2 separate clutches, and 2 nests with 3 clutches. Principal component analysis confirmed the importance of cover and vegetation to nest-site selection in this species. Availability of open, shade-free, wet nesting areas is an important habitat requirement for Bog Turtles.

Introduction

Selection of a nest site has important fitness consequences for mothers and offspring of oviparous organisms, as recently reviewed for turtles by Lovich et al. (2015). Female aquatic turtles are at risk because of their exposure to predators when they leave the comparative safety of their wetland environment to nest (e.g., Steen et al. 2006). In addition, because most turtle species do not exhibit parental care (but see Agha et al. 2013), their offspring are left to fend for themselves in the post-ovipositional nest environment where nest predation can be extremely high and variable (Congdon et al. 1994)—up to 100% in some years and species (Ernst and Lovich 2009). The post-ovipositional environment has the potential to affect a number of key aspects of the life history of turtles: developmental rate and duration; hatchling-turtle sex ratios; and phenotype, growth rate, and survival of hatchlings as reviewed by Wilson (1998) and Lovich et al. (2012). As a result, it is expected that nesting turtles would select egg-deposition sites that provide appropriate environmental conditions for hatching success (e.g., solar/thermal exposure and soil-moisture conditions), including protection of eggs and developing embryos from predators (Pignati et al. 2013).

Although most gravid female freshwater-turtles migrate away from their aquatic habitat to locate traditional upland nest sites (Ernst and Lovich 2009), there are

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some species with nesting behaviors that differ substantially from the norm in that they nest within the confines of their wetland habitat. In Australia, *Chelodina rugosa* Werner (Siebenrock's Snake-necked Turtle) actually lays eggs underwater (Kennett et al. 1993). In eastern North America, *Glyptemys muhlenbergii* (Schoepff) (Bog Turtle) remains in its wetland and often selects slightly elevated sites (as opposed to subterranean nests), generally on raised clumps of sedges called tussocks (pedestal-forming vegetation), for nesting within characteristic marshy habitat (Zappalorti 1976a, b). Bog Turtle nesting areas typically have limited canopy closure, support an array of moisture-tolerant plants, and provide ample solar exposure (Ernst and Lovich 2009). The practice of nesting within their wetland habitat may reduce predation risk that might occur in nesting forays to uplands and reduce competition for nest sites used by other turtle species. Bog Turtles are sympatric with as many as 5 aquatic-turtle species in parts of their range (Lovich et al. 2014).

With the exception of unpublished research by Whitlock (2002), few studies have focused on the environmental attributes of Bog Turtle nests in the wild. Information on the species' natural history is needed to guide effective conservation for the recovery of this federally threatened turtle (Lovich and Ennen 2013). In this study, we examined the physical characteristics of nests and proximate-habitat characteristics of nest sites selected by Bog Turtles. We conducted our research episodically between 1974 and 2012 at 9 different bogs, fens, and wetland complexes in New Jersey and Pennsylvania (Table 1). In the absence of similar data for sites without nests, we were unable to specifically address nest-site selection relative to available microhabitats. However, our data allow a quantitative assessment of environmental attributes associated with nest sites used by Bog Turtles in the mid-Atlantic region.

Field-Site Description

All of our study areas were wetland marshes, bogs, or fens with soils (Feaga et al. 2013), hydrology (Feaga 2010), and vegetation (Chase et al. 1989, Zappalorti 1997) typical of Bog Turtle habitat (USFWS 1997, 2001). To protect this popular and imperiled turtle species from exploitation, we do not provide exact localities and specific place names of research areas. Our 9 study sites occurred within emergent, scrub-shrub portions of wetlands. Bog Turtle habitat descriptions are well-documented elsewhere from the landscape (Myers and Gibbs 2013, Rosenbaum and Nelson 2010) to the site-specific level (Carter et al. 1999, Chase et al. 1989, Ernst et. al. 1989, Feaga et al. 2013, Kiviat 1978, Morrow et al. 2001, Pittman et al. 2009, Zappalorti 1976a); thus, we provide only a general description of the habitat features present at most of our study sites. The common habitat features at all of our study areas were wetlands that had year-round spring seeps and soft, muddy substrate (Zappalorti 1978, 1997).

The dominant herbaceous plant species present in the 9 emergent scrub-shrub wetlands (Table 1) we studied included: *Carex stricta* Lam. (Tussock Sedge), *Carex atlantica* spp. *atlantica* L.H. Bailey (Prickly Bog Sedge), *Carex vulpinoides* Michx. (Foxtail Sedge), *Juncus effusus* L. (Soft Rush), *Leersia oryzoides* (L.) Sw. (Rice Cutgrass), *Onoclea sensibilis* L. (Sensitive Fern), *Polygonum sagittatum* L.

(Arrowleaf Tearthumb), *Impatiens* spp. (jewelweed), *Sagittaria latifolia* Willd. (Broadleaf Arrowhead), *Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton (Skunk Cabbage), *Typha angustifolia* L. (Narrowleaf Cattail), *Panicum* spp. (panic grasses), *Eleocharis* spp. (spike-rushes), *Parnassia glauca* Raf. (Grass-of-Parnassus), *Dasiphora fruticosa* (L.) Rydb. (Shrubby Cinquefoil), *Acorus calamus* L. (Sweetflag), *Sagittaria cuneata* Sheldon (Arumleaf Arrowhead), *Polygonum* sp. (smartweed) *Scirpus atrovirens* Willd. (Dark Green Bulrush), *Scirpus cyperinus* (Woolgrass), *Acer rubrum* L. (Red Maple), and *Sphagnum* spp. (sphagnum moss). Common shrub species included *Alnus* spp. (alders), *Viburnum* sp. (viburnum), Red Maple, *Salix* spp. (willows), and *Larix laricina* (Du Roi) K. Koch (Tamarack). The disturbed portions of the wetlands supported invasive plants including *Phragmites australis* (Cav.) Trin. Ex Steud. (Common Reed), *Rosa multiflora* Thun. Ex Murr. (Multiflora Rose), *Phalaris arundinacea* L. (Reed Canary Grass), and *Lythrum salicaria* L. (Purple Loosestrife).

Methods

We conducted our searches during and after the Bog Turtle nesting season in June. Turtles in our study region typically lay their eggs between 8 and 29 June, but we found 1 female nesting on 6 June and another on 1 July (R.T. Zappalorti, pers. observ.). We searched intensively for concealed eggs in canopy-free areas of sedges, sphagnum mosses, and other types of graminoid tussocks. We took great care not to step on tussocks so we did not disturb or crush any unseen eggs in hidden nests. From 1974 to 1993, we carried out ecological and mark–recapture studies in addition to finding eggs and monitoring hatching success in the field and laboratory. Between 1994 and 2012, we concentrated on monitoring nests and eggs in natural habitat (Zappalorti 1997). We marked with a wooden stake and flagged each nest found to prevent researchers from accidently stepping on eggs. Prior to searching for nests and eggs, all researchers thoroughly cleaned their hands with Lysol® dual-action wipes, 70% isopropyl rubbing alcohol, and/or wore latex surgical gloves (Star-Med, Sempermed, Clearwater, FL). We took these steps to reduce human scent at the nest sites and reduce the likelihood of attracting mammalian egg-predators (but see Burke et al. 2005, Tuberville and Burke 1994).

Nest data

We recorded 2 sets of variables at each nest. The first set described the actual nest; variables including nest-chamber depth, width, and length, as well as the distance from the bottom of the elevated nest chamber to the water or substrate below. To characterize the habitat around the nest, we recorded distance (m) to the nearest tree with a diameter at breast height (DBH) >7.5 cm and a height > 2 m), distance to nearest woody shrub <2 m in height, height of nearest emergent vegetation, distance to nearest emergent vegetation, distance to nearest surface water, and estimated canopy cover (%) in each cardinal compass direction. We estimated overhead tree- or shrub-canopy cover at each nest by using a black-plastic ocular tube. The ocular tube had 2 central cross-hairs (length = 16 cm, diameter = 4 cm). Looking up from the nest, but without disturbing it, we held the tube at a 45º angle from the egg chamber, looked through the tube, and took a total of 4 readings at each nest—1 in each of the cardinal directions. We estimated up to 25% cover (full cover at a given cardinal direction) at each compass point for a maximum score of 100% for all 4 estimates. Most canopy trees were fully leafed-out by early June when the turtles were nesting. Due to time constraints, we collected habitat data from a subset of all nests found. We used an Oakton pH Tester with BNC Connection (model 35801-00, Oakton Instruments, Vernon Hills, IL) to record nest-substrate pH.

We combined data both within and between states for analysis because 1 study site had a relatively small number of nests. While we recognize there may be site- or state-specific differences, our data represent a range of study sites that might be considered typical for mid-Atlantic Bog Turtle populations.

Statistical tests

We did not collect data from random points without nests; thus, our analysis is a quantitative description of known nest sites, not an analysis of nest-site selection relative to available habitat. We employed principal component analysis (PCA) with varimax rotation as a data-reduction technique to remove redundancy from our intercorrelated environmental variables (Kachigan 1991) and identify important factors and loadings. Chase et al. (1989) used this approach to reduce the number of habitat variables in their analysis of Bog Turtle habitat. A priori, we decided to use only those components with eigenvalues >1 in our presentation of the data. When plotting principal component scores, we used a confidence kernel based on a nonparametric kernel-density estimator that showed where data (nests) are most concentrated in the sample. We generated all analyses and figures with SYSTAT® 13 software. Means are reported ± 1 standard deviation.

Results

We found all Bog Turtle nests in microsites that were elevated above standing water at the time of discovery. Many were in elevated tussocks of grasses or sedges including Tussock Sedge and Prickly Bog Sedge (n = 28). The nests' mean elevation above the substrate was 8.2 cm ± 4.8 (range = 1.4–27.1 cm). Other vegetation found at nest sites included sphagnum mosses (n = 10), jewelweed (n = 1), *Juncus* spp. (rushes; n = 1), Sensitive Fern (n = 1), and Narrow-leaved Cattail (n = 3). Most nests concealed under vegetation were covered with a layer of humus, grass blades, or sphagnum moss (n = 38) at a depth ranging from 0.1–3.5 cm (mean = 1.8 ± 1.1; (Table 1). Some nests contained eggs that were poorly covered by the turtle, or were partially or fully exposed to direct sunlight (n = 6; Fig. 1). We covered these nests with sphagnum moss and all the eggs hatched. We found 2 atypical nests, containing 3 eggs each, atop Red Maple stumps in New Jersey. One nest was in a pocket of soft, rotting wood. Both were covered in sphagnum moss (depth of cover = 2.2–3.5 cm).

Mean nest-chamber measurements (n = 66) were 3.7 ± 0.99 cm deep (range = 1.8–6.5), 5.07 ± 1.69 cm long (range = 2.2–10.0), and 3.8 ± 0.9 cm wide (range = 2.0–6.0). We found evidence of communal-nest sites at 2 Pennsylvania

Table 1. Dominant vegetation types, habitat characteristics, and structure of Bog Turtle nest sites from 9 study areas in New Jersey and Pennsylvania between 1974 and 2012. The Berks County, PA, study site consisted of 3 meta-populations in a large, connected wetland complex. The Northampton County, PA, study site consisted of 6 meta-populations in a large, connected wetland complex, but all nests had the same structure.

Study area location	Dominant vegetation at nest site	Secondary vegetation 30-cm around nest site	Nest site structure or substrate	Type of cover over the eggs	Number of nests
New Jersey					
Sussex County	Sphagnum moss, Prickly Bog Sedge,	Tussock Sedge, Sensitive Fern	Elevated earth and root hummock	Sphagnum moss	6
Morris County	Sphagnum moss, Red Maple	Tussock Sedge, Common Rush	Old Red Maple stump	Sphagnum moss	1
Monmouth County	Sphagnum moss, Red Maple,	Prickly Bog Sedge, Tussock Sedge	Old Red Maple stump	Sphagnum moss	1
Pennsylvania					
Lancaster County – A	Tussock Sedge, Prickly Bog Sedge	Reed Canary Grass, Sweetflag	Elevated earth and root hummock	Twisted blades of sedge leaves	10
Lancaster County – B	Tussock Sedge, Prickly Bog Sedge	Fox Sedge, Common Rush	Elevated earth and root hummock	Twisted blades of sedge leaves	12
Berks County	Tussock Sedge, Narrow-leaved Cattail	Fox Sedge, Sweetflag	Elevated earth and root hummock	Twisted blades of sedge leaves	11
Northampton County	Tussock Sedge, Prickly Bog Sedge	Grass-of-Parnassus, Sensitive Fern	Elevated earth and root hummock	Twisted blades of sedge leaves	5
Monroe County	Tussock Sedge, Prickly Bog Sedge	Fox Sedge, Sensitive Fern	Elevated earth and root hummock	Twisted blades of sedge leaves	19
Lehigh County	Tussock Sedge, Narrow-leaved Cattail	Sensitive Fern, Red Maple	Elevated earth and root hummock	Twisted blades of sedge leaves	1

study sites. Some nests had 2 clutches (n = 4), and we observed 2 nests with 3 clutches. At 1 communal-nest site, a clutch of 4 eggs appeared to have been dislodged by another nesting female. The substrate pH of the 66 nests ranged from 4.8 to 7.0 (mean = 6.3 ± 0.5). We observed nest-site fidelity in some females. In Pennsylvania, a radio-tracked female nested in a sheep meadow at the same Prickly Bog Sedge tussock for 2 consecutive years. Circumstantial evidence suggests similar behavior in New Jersey—we recaptured gravid females in 2 consecutive years (n = 4) and 1 turtle for 3 consecutive years at the same nesting area.

Other environmental attributes of nest locations are summarized in Table 2. PCA of 9 habitat-characteristic variables identified 3 components with eigenvalues >1. The first component was most strongly related to canopy cover in the west and distance to the nearest woody shrub, both negatively (Fig. 2). The second component was related primarily to canopy cover (north and east, respectively), both positively. The third component was strongly related (positively) to distance to the nearest tree (Table 3). Collectively, these components explained 65.8% of the total variance. Four extreme outliers are shown in Figure 2. These nests were characterized by higher canopy-cover values and/or nearer distances to trees than the means for the majority of nests. They were also located closer to the nearest emergent

Figure 1. A Bog Turtle nest as found by researchers on 24 June 2012 in Sussex County, NJ. Three eggs are visible and 1 is partially visible. After the female oviposited, the eggs were not fully covered. It is not clear if the female left the eggs uncovered after oviposition or if another turtle or animal disturbed them. After discovering the nest, we covered the eggs with damp moss to prevent dehydration. All four eggs successfully hatched in the nest. Photograph © Robert Zappalorti.

vegetation (including Narrow-leaved Cattails and invasive Purple Loosestrife) than the mean for the other nests, and one was very low to the substrate. The outlier nests had variable hatching success. All 3 eggs from a nest located in sphagnum on a Red Maple stump hatched after we took them to the laboratory. Only one egg hatched in 2 of the nests, and 3 out of 5 eggs hatched in another. We determined that some eggs were either infertile or contained an embryo that died during development. The correlation between factor 1 scores and canopy cover to the west was negative, showing that as canopy cover increased, the associated factor-scores decreased. The other 2 factor-score correlations with their respective variables with high loadings were positive.

Table 2. Summary of environmental attributes associated with Bog Turtle nest sites in New Jersey and Pennsylvania. Height = height of nearest emergent vegetation (cm), and Emerg veg = emergent vegetation.

		% canopy cover				Distance (m) to nearest			
	Height	North	South	East	West	Tree	Woody shrub	Emerg veg	Surface water
n	47	66	66	66	66	50	52	61	58
Minimum	1.9	0.0	0.0	0.0	0.0	0.27	0.3	0.0	0.1
Maximum	150.0	25.0	50.0	70.0	75.0	40.0	10.5	30.0	37.0
Mean	61.9	4.1	4.8	8.0	7.9	89.9	3.4	2.1	7.5
SD	31.3	6.5	9.1	12.2	13.5	8.6	2.2	6.1	9.7

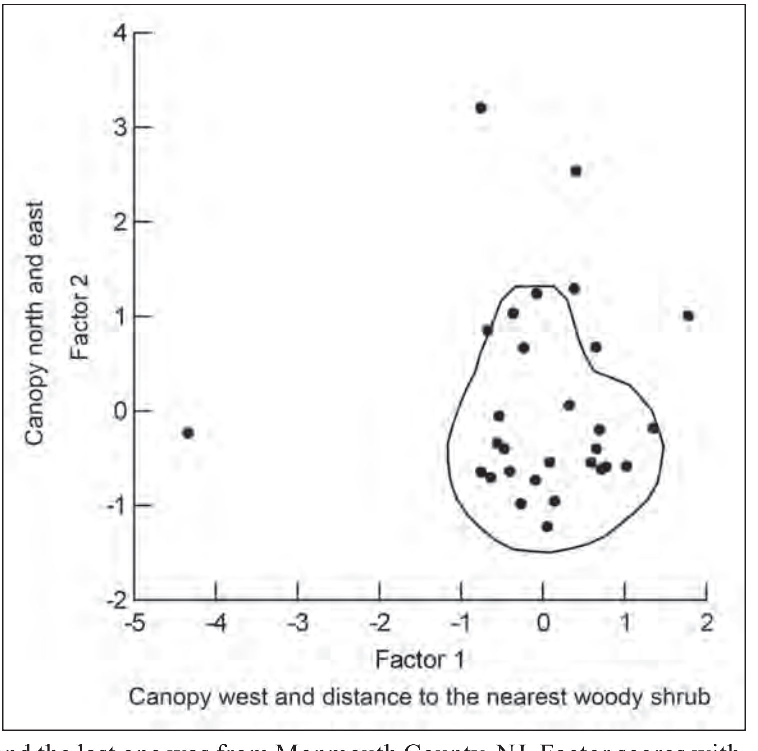

Figure 2. Plot of the first 2 factor scores from principal component analysis of 9 environmental variables listed in Table 3. Components with highest loadings are shown in axis labels. The enclosed area is a confidence kernel based on a nonparametric kernel-density estimator that shows where data (nests) are most concentrated in the sample. The bounds are 1 SD from the mean. The 4 extreme outliers are discussed in the text. From left to right the first 3 were from nests in Monroe County, PA, and the last one was from Monmouth County, NJ. Factor scores with missing data are excluded, leaving only 33 nests (some as overlapping points).

Discussion

Our results, based on the largest sample of Bog Turtle nests previously analyzed, confirm earlier reports of nesting-site characteristics and nesting behavior (see summary in Ernst and Lovich 2009). Unlike most other semi-aquatic turtles, Bog Turtles do not need to leave their wetland habitat and travel to dry upland areas to deposit their eggs. Instead, they select slightly elevated sites, often on Tussock Sedge mounds, for nesting. Only a handful of largely anecdotal publications describe Bog Turtle nesting under natural conditions, although there are numerous reports of nesting in captivity (e.g., Arndt 1972, Herman 1986, Zovickian 1971). Barton and Price (1955) may have been the first to note a preference for elevated nest locations. At a study site in Lancaster County, PA, they noted a nest that was "… quite shallow and was 4 or 5 inches above the surface of water in the swamp." Holub and Bloomer (1977) also noted elevated nests stating, "Regardless of the particular nest site chosen, all nesting females have 2 things in common. The nesting site is always uphill, or on ground that is high and dry such as in the top of a sedge clump." Later, still others confirmed the tendency of Bog Turtles to nest in elevated locations like sedge tussocks and sphagnum hummocks (Wilson et al. 2004). Bog Turtles occasionally nest in unusual locations like stumps (Table 1), a phenomenon also observed by Fahey and Jensen (1999) in Georgia. The authors speculated that ecological succession at the bog they studied limited open areas, thereby forcing turtles to nest in alternative locations.

Barton and Price (1955) further noted, "It appeared that the female had buried herself in the moss and, after depositing the eggs, crawled out and allowed the moss to cover the eggs." Their observation provides a possible explanation for why some nests are covered haphazardly or not at all, unlike the nests of most other turtle species. We observed 6 clutches that were partially or fully exposed to direct sunlight. Had we not covered the exposed eggs with moss, they may not have hatched, given their dehydrated appearance, but this assumption needs to be tested further. The behavior of sometimes leaving the eggs uncovered is poorly understood and requires additional study.

Table 3. Principal component analysis for 9 variables describing the habitat characteristics of Bog Turtle nest sites. Loadings for factors with an eigenvalue >1 are shown. Variance explained for principal components 1–3 was 25.0%, 23.1% and 17.7%, respectively.

	Principal component		
Environmental attribute	1	2	3
Canopy north	0.022	0.718	-0.086
Canopy south	-0.331	0.557	0.481
Canopy east	0.175	0.866	0.105
Canopy west	-0.793	0.269	0.218
Distance to nearest woody shrub	-0.792	-0.308	0.101
Distance to nearest emergent vegetation	0.211	0.083	0.669
Distance to nearest surface water	0.516	-0.411	0.472
Distance to nearest tree	-0.302	-0.064	0.768
Height of nearest emergent vegetation	0.668	0.184	0.393

Nesting areas typically have limited canopy closure, support an array of moisture-tolerant, low-growing vegetation, and provide ample solar exposure (Ernst and Lovich 2009). Our analysis supports this characterization in that the variables with the highest loadings in our PCA were canopy cover (west and east) and distance to the nearest tree. Cardinal directions of nest exposure have been demonstrated to influence nest temperatures and thus sex ratios of hatchling turtles; southern and western exposures have more influence on nest temperatures than do northern or eastern exposures (Janzen 1994). The high loading scores for canopy cover in factors 1 and 2 may be a reflection of solar exposure of nest sites.

We observed atypical nesting behavior at 5 nests that we measured. The distance from the top of the nest to the wet ground-surface below ranged from 6.5 cm to 9.0 cm in these unusually low nests, which may be the reason why only 1 out of those 19 eggs hatched. It appears that most of the remaining 18 eggs were lost from water saturation from repeated rain inundation, causing the embryos to drown. Those eggs may have hatched during a drought year, but because of high groundwater levels from excessive rain, the nest sites selected by 5 gravid females were a poor choice and most eggs did not hatch. Selection of nest sites with excessive cover and proximity to vegetation including trees can lead to reduced hatching success as suggested in data for outliers in our PCA analysis.

By selecting nest sites on elevated tussocks or hummocks above the substrate or water, Bog Turtles protect their eggs from flooding in wetlands. Limited site availability may explain why multiple females nest in the same tussock (Holub and Bloomer 1977) and some display nest-site fidelity (see review of nest site fidelity in turtles in Lovich et al. 2015).

Maintenance of favorable environmental conditions for Bog Turtle nesting is a significant conservation challenge due to ecological succession of the habitats they prefer, exacerbated by invasion by exotic plant species (Ernst and Lovich 2009). Canopy closure due to ecological succession compromises access to the open areas female Bog Turtles prefer for nesting, as shown by our analysis (Feaga and Haas 2015). Recent studies suggest that low-intensity, pasture-based grazing by livestock assists in maintaining the conditions that Bog Turtles prefer as nesting habitat (Tesauro and Ehrenfield 2007). Heavy grazing by too many hoofed stock and associated nutrient inputs create favorable conditions for invasive plants to become established; however, these plants may be kept in check by grazing (Tesauro and Ehrenfield 2007). Careful habitat management, including limited grazing by hoofed livestock, selective girdling of bark or cutting of trees and shrubs in nesting areas, and protecting nests with predator-excluder cages may be required to maintain optimum conditions necessary for nest sites, and ultimately, the survival of Bog Turtle populations throughout their range (Frier and Zappalorti 1983, Kiviat 1978, Sirois et al. 2014, Tesauro and Ehrenfield 2007).

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Literature Cited

Agha, M., J.E. Lovich, J.R. Ennen, and E. Wilcox. 2013. Female nest guarding in Agassiz's Desert Tortoise (*Gopherus agassizii*) at a wind-energy facility near Palm Springs, California. Southwestern Naturalist 58:254–257.

Arndt, R.G. 1972. Additional records of *Clemmys muhlenbergii* in Delaware, with notes on reproduction. Bulletin Maryland Herpetological Society 8:1–5.

Barton, A.J., and J.W. Price Sr. 1955. Our knowledge of the Bog Turtle, *Clemmys muhlenbergii*, surveyed and augmented. Copeia 1955:159–165.

Burke, R.L., C.M. Schneider, and M.T. Dolinger. 2005. Cues used by Raccoons to find turtle nests: Effects of flags, human scent, and Diamondback Terrapin sign. Journal of Herpetology 39:312–315.

Carter, S.L., C.A. Haas, and J.C. Mitchell. 1999. Home range and habitat selection of Bog Turtles in southwestern Virginia. Journal of Wildlife Management 63:853–860.

Chase, J.D., K.R. Dixon, J.E. Gates, D. Jacobs, and G.J. Taylor. 1989. Habitat characteristics, population size, and home range of the Bog Turtle, *Clemmys muhlenbergii,* in Maryland. Journal of Herpetology 23:356–362.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1994. Demographics of common Snapping Turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.

Ernst, C.H., and J.E. Lovich. 2009. Turtles of the United States and Canada (2nd Edition). Johns Hopkins University Press, Baltimore, MD. 827 pp.

Ernst, C.H., R.T. Zappalorti, and J.E. Lovich. 1989. Overwintering sites and thermal relations of hibernating Bog Turtles, *Clemmys muhlenbergii*. Copeia 1989:761–764.

Fahey, K.M., and J.B. Jensen. 1999. Life-history notes: *Clemmys muhlenbergii* (Bog Turtle) oviposition. Herpetological Review 30:39.

Feaga, J.B. 2010. Wetland hydrology and soils as components of Virginia Bog Turtle (*Glyptemys muhlenbergii*) habitat. Ph.D. Dissertation. Virginia Polytechnic Institute and State University, Blacksburg, VA.

Feaga, J.B., and C.A. Haas. 2015. Seasonal thermal ecology of Bog Turtles (*Glyptemys muhlenbergii*) in southwestern Virginia. Journal of Herpetology 49(2):264–275.

Feaga, J.B., J.A. Burger, and C.A. Haas. 2013. Bog Turtle (*Glyptemys muhlenbergii*) wetland habitat: An emphasis on soil properties. Natural Areas Journal 33:404–412.

Frier, J., and R.T. Zappalorti. 1983. Reptile and amphibian management techniques. Transactions of the North American Wildlife Society 40:142–148.

Herman, D.W. 1986. Life-history notes: *Clemmys muhlenbergii* (Bog Turtle) reproduction. Herpetological Review 17:24.

Holub, R.J., and T.J. Bloomer. 1977. The Bog Turtle, *Clemmys muhlenbergii*: A natural history. Herpetological Bulletin of the New York Herpetological Society 13:9–23.

Janzen, F.J. 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. Ecology 75:1593–1599.

Kachigan, S.K. 1991. Multivariate Statistical Analysis: A Conceptual Introduction. Radius Press, New York, NY. 303 pp.

Kennett, R., K. Christian, and D. Pritchard. 1993. Underwater nesting by the tropical freshwater turtle *Chelodina rugosa* (Testudinata: Chelidae). Australian Journal of Zoology 41:47–52.

Kiviat, E. 1978. Bog Turtle habitat ecology. Bulletin of the Chicago Herpetological Society 13:29–42.

Lovich, J.E., and J.R. Ennen. 2013. A quantitative analysis of the state of knowledge of turtles of the United States and Canada. Amphibia-Reptilia 34:11–23.

Lovich, J.E., M. Agha, M. Meulblok, K. Meyer, J. Ennen, C. Loughran, S.V. Madrak, and C. Bjurlin. 2012. Climatic variation affects clutch phenology in Agassiz's Desert Tortoise (*Gopherus agassizii*). Endangered Species Research 19:63–74.

Lovich, J.E., C.H. Ernst, E.M. Ernst, and J.L. Riley. 2014. A 21-year study of seasonal and interspecific variation of hatchling emergence in a Nearctic freshwater turtle community: To overwinter or not to overwinter? Herpetological Monographs:93–109.

Lovich, J.E., M. Agha, C.B. Yackulic, K. Meyer, C. Bjurlin, J.R. Ennen, T.R. Arundel, and M. Austin. 2015. Nest-site characteristics and lack of long-term nest-site fidelity in Agassiz's Desert Tortoises (*Gopherus agassizii*) at a wind-energy facility in southern California. California Fish and Game 100:404–416.

Morrow, J.L., J.H. Howard, S.A. Smith, and D.K. Poppel. 2001. Habitat selection and habitat use by the Bog Turtle (*Clemmys muhlenbergii*) in Maryland. Journal of Herpetology 35:545–552.

Myers, A.T., and J.P. Gibbs. 2013. Landscape-level factors influencing Bog Turtle persistence and distribution in southeastern New York state. Journal of Fish and Wildlife Management 4:255–266.

Pignati, M.T., L.F. Fernandes, P.S. Miorando, P.D. Ferreira, and J.C.B. Pezzuti. 2013. Nesting site and hatching success of *Podocnemis unifilis* (Testudines: Podocnemididae) in a floodplain area in lower Amazon River, Pará, Brazil. 2013. South American Journal of Herpetology 8:175–185.

Pittman, S.E., and M.E. Dorcas. 2009. Movements, habitat use, and thermal ecology of an isolated population of Bog Turtles (*Glyptemys muhlenbergii*). Copeia 2009:781–790.

Rosenbaum, P.A., and A.P. Nelson. 2010. Bog Turtle habitat on the Lake Ontario Coastal Plain of New York state. Northeastern Naturalist 17:415–436.

Sirois, A.M., J.P. Gibbs, A.L. Whitlock, and L.A. Erb. 2014. Effects of habitat alterations on Bog Turtles (*Glyptemys muhlenbergii*): A comparison of two populations. Journal of Herpetology 48:455–460.

Steen, D.A., M.J. Aresco, S.G. Beilke, B.W. Compton, E.P. Condon, C.K. Dodd Jr., H. Forrester, J.W. Gibbons, J.L. Greene, G. Johnson, T.A. Langen, M.J. Oldham, D.N. Oxier, R.A. Saumure, F.W. Schueler, J.M. Sleeman, L.L. Smith, J.K. Tucker, and J.P. Gibbs. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:269–273.

Tesauro, J., and D. Ehrenfeld. 2007. The effects of livestock grazing on the Bog Turtle [*Glyptemys* (= *Clemmys*) *muhlenbergii*]. Herpetologica 633:293–300.

Tuberville, T.D., and V.J. Burke. 1994. Do flag markers attract turtle-nest predators? Journal of Herpetology. 28:514–516.

US Fish and Wildlife Service (USFWS). 1997. Endangered and threatened wildlife and plants: Final rule to list the northern population of the Bog Turtle as threatened and the southern population as threatened due to similarity of appearance. Federal Register 62:59,605–59,623.

USFWS. 2001. Bog Turtle (*Clemmys muhlenbergii*) northern population recovery plan. Hadley, MA. 103 pp.

Whitlock, A.L. 2002. Ecology and status of the Bog Turtle (*Clemmys muhlenbergii*) in New England. Ph.D. Dissertation. University of Massachusetts, Amherst, MA. Available from Proquest. Paper AAI3039402. Available online at http://scholarworks.umass.edu/dissertations/AAI3039402. Accessed 13 June 2013.

Wilson, D.S. 1998. Nest-site selection: Microhabitat variation and its effects on the survival of turtle embryos. Ecology 796:1884–1892.

Wilson, T.P., S.A. Dinkelacker, and J.H. Howard. 2004. Nesting and nest-site selection in a Maryland *Clemmys muhlenbergii* metapopulation. P. 112, *In* C.W. Swarth, W.M. Roosenburg, and E. Kiviat (Eds.). Conservation and Ecology of Turtles in the Mid-Atlantic Region: A Symposium. Bibliomania, Salt Lake City, UT.

Zappalorti, R.T. 1976a. The Amateur Zoologist's Guide to Turtles and Crocodilians. Stackpole Books, Harrisburg, PA. 208 pp.

Zappa1orti, R.T. 1976b. The status of the Bog Turtle (*Clemmys muhlenbergii*) in North Carolina. Bulletin of the Maryland Herpetological Society 12(2):69.

Zappalorti, R.T. 1978. The Bog Turtle: Smallest of North American turtles. Bulletin of the Chicago Herpetological Society 13(3):75–81.

Zappalorti, R.T. 1997. Turtles of New Jersey and the Bog Turtle in the Northeast. Pp. 15–22, *In* T. Tyning (Ed.). Status and Conservation of Turtles of the Northeastern United States. Serpent's Tale Natural History Book Distributers, Lanesboro, MN. 53 pp.

Zovickian, W.H. 1971. Captive nesting of Bog Turtles. International Turtle and Tortoise Society 5:14–15, 37.