

---

## CHARACTERIZATION OF DIAMONDBACK TERRAPIN (*MALACLEMYS TERRAPIN*) NESTING AND NEST PREDATION AT A SITE IN NORTHEASTERN USA

RICHARD D. MERCER<sup>1</sup>, TYLER B. DEVOS<sup>2,4</sup>, LIAM S. CORCORAN<sup>2</sup>, SCOTT W. BUCHANAN<sup>2</sup>,  
KATHRYN A. BEAUCHAMP<sup>3</sup>, MADELEINE H. LINCK<sup>3</sup>, AND NANCY E. KARRAKER<sup>1</sup>

<sup>1</sup>University of Rhode Island, Department of Natural Resources Science, 1 Greenhouse Road, Kingston,  
Rhode Island 02881, USA

<sup>2</sup>Rhode Island Department of Environmental Management, Division of Fish and Wildlife, 277 Great Neck Road,  
West Kingston, Rhode Island 02892, USA

<sup>3</sup>Barrington Terrapin Conservation Project, Barrington, Rhode Island 02806, USA

<sup>4</sup>Corresponding author; email: tylerbdevos@gmail.com

**Abstract.**—The Diamondback Terrapin (*Malaclemys terrapin*) plays a keystone role in Saltmarsh ecosystems and is considered a species of conservation concern throughout its range. One major source of terrapin egg mortality is destruction of nests by nocturnal mammalian predators. Although Diamondback Terrapins are listed as State Endangered in Rhode Island, nesting ecology for the species is poorly understood at the local and regional level. To fill this knowledge gap, we identified temporal patterns of Diamondback Terrapin nesting, hatchling emergence, and nest predation during 2 y at a Rhode Island terrapin nesting site. We also used a series of trail cameras to detect and quantify the presence of nocturnal nest predators and tested a solar electric fence as a possible management solution for nest protection. Both predated nest counts and predator detections were highest during the Diamondback Terrapin nesting period, decreasing only after hatchlings began to emerge from nests. We detected Northern Raccoons (*Procyon lotor*) and Striped Skunks (*Mephitis mephitis*) more frequently than other mammalian nest predators; detections of both species were strongly correlated with observed nest predation events, suggesting that these are the main species responsible for Diamondback Terrapin nest predation at our study site. After various modifications, the electric fence succeeded in excluding raccoons from the nesting area but failed to deter skunks. An increased understanding of the dynamics of terrapin nest predation will contribute meaningfully to effective conservation of this keystone species in Rhode Island, USA, and throughout the range of the Diamondback Terrapin.

**Key Words.**—camera trap; conservation; electric fence; Emydidae; endangered; herpetology; keystone species; Rhode Island

---

### INTRODUCTION

The Diamondback Terrapin (*Malaclemys terrapin*) occupies estuaries and Saltmarshes from Massachusetts to the Gulf of Mexico (Roosenburg and Place 1995; Muldoon and Burke 2012; Hart et al. 2014). Within the family Emydidae (the most speciose family of turtles in North America), Diamondback Terrapins are unique in being the only species to inhabit ecosystems characterized by brackish waters (Wood and Herlands 1997; Hart and Lee 2006). Diamondback Terrapins play a keystone role in the Saltmarsh ecosystem by preying on Salt Marsh Periwinkles (*Littoraria irrorata*), a marine invertebrate that can overgraze Salt Marsh Cord Grass (*Spartina alterniflora*) and contribute indirectly to ecosystem erosion when populations are left unchecked by predators like terrapins (Roosenburg et al. 2019). By feeding on Salt Marsh Periwinkles, Diamondback Terrapins aid in maintaining coastal flora, increase

primary production, decrease erosion, and ultimately maintain the health of the estuarine ecosystems in which they live (Giambanco 2002; Roosenburg et al. 2019). The Diamondback Terrapin is classified as Vulnerable on the Red List of Threatened Species by the International Union for Conservation of Nature (IUCN) and is also listed as an Appendix II species by the Convention on International Trade in Endangered Species (Roosenburg et al. 2019), indicating that export from the U.S. is regulated. Although Diamondback Terrapins are not protected federally, they are classified as a species of conservation concern in every state in which they occur (Selman et al. 2014).

Diamondback Terrapins typically nest in areas that have sandy substrates, are located above the high tide line near a Saltmarsh or estuary, and do not contain dense vegetation (Burger and Montevecchi 1975; Palmer and Cordes 1988; Hart and Lee 2006). Sand dunes and beaches are the primary habitats that satisfy

these criteria (Wood and Herlands 1997; Giambanco 2002). Female terrapins tend to nest in open areas exposed to sunlight (Roosenburg 1996) and can nest multiple times within a single season (Seigel 1979, 1980; Feinberg and Burke 2003; Feinberg 2004). Throughout their range, Diamondback Terrapins nest from late April to early August with timing varying geographically; the length of the nesting season for an individual population can range from approximately 44 to 78 d (Burger and Montevecchi 1975; Seigel 1979, 1980; Butler 2000). Existing literature shows that there is also geographic variation in Diamondback Terrapin clutch size, with clutch size increasing as latitude increases (Seigel 1980; Butler 2000; Allman et al. 2012). Reported clutch size averages for populations throughout the U.S. include egg counts of 5.9, 7.2, and 7.9 in Louisiana (Pearson and Wiebe 2018; Donini and Selman 2022), 6.0 in South Carolina (Allman et al. 2012), 10.9 in New York (Feinberg and Burke 2003), 12.2 in Maryland (Allman et al. 2012), and 16.1 in Rhode Island (Allman et al. 2012). The incubation time for Diamondback Terrapin eggs can range from approximately 50 to 120 d (Jeyasuria et al. 1994).

Historically, humans overharvested Diamondback Terrapins for food, leading to substantial population declines (Giambanco 2002; Feinberg 2004; Hart and Lee 2006; Roosenburg et al. 2019). Terrapin consumption decreased during the 20th Century and a reduction of commercial terrapin harvesting followed (Hart and Lee 2006). Although some populations are slowly recovering from overexploitation (Giambanco 2002), Diamondback Terrapins are still threatened by various anthropogenic impacts including habitat destruction, road mortality, boat strikes, commercial fishing and crabbing, and illegal collection (Giambanco 2002; Hart and Lee 2006; Sevin et al. 2022). The greatest risk of mortality for Diamondback Terrapin individuals, however, occurs during the embryonic and hatchling stages (Burke 2015). Throughout their geographic range, terrapin eggs are vulnerable to predation by nocturnal mammals. Nocturnal mammalian predators of the Diamondback Terrapin include the Northern Raccoon (*Procyon lotor*; hereafter, raccoon), Red Fox (*Vulpes vulpes*), and Striped Skunk (*Mephitis mephitis*; hereafter, skunk; Burger 1977; Congdon et al. 2000; Marchand et al. 2002; Butler et al. 2004; Reses et al. 2015). Among these predators, the raccoon is known to be a particularly impactful terrapin nest predator (Ner and Burke 2008). Previous studies indicate that raccoons can predate as many as 87–100% of Diamondback Terrapin nests at monitored nesting sites (Feinberg and Burke 2003; Feinberg 2004; Munscher et al. 2012). It is presumed that mammalian predators locate turtle nests using diverse sensory cues, which include tactile, olfactory, visual, and auditory stimuli

(Riley and Litzgus 2014; Oddie et al. 2015; Buzuleciu et al. 2016; Czaja et al. 2018; Edmunds et al. 2018). Although adult survival is the parameter that is most critical to ensure population viability for most turtle species (Zimmer-Shaffer et al. 2014; Howell and Seigel 2019; Bougie et al. 2022), nest survival has important implications for population recruitment and stability (Mazaris et al. 2005; Murphy et al. 2022). In extreme cases, persistently high rates of nest failure can lead to population collapse (Spencer et al. 2017). Increased nest success by way of nest protection is likely to be particularly important for populations undergoing active recovery (Mitro 2003).

Although the Diamondback Terrapin is listed as a State Endangered Species in Rhode Island ([https://rinhs.org/wp-content/uploads/2020/04/ri\\_rare\\_animals\\_2006.pdf](https://rinhs.org/wp-content/uploads/2020/04/ri_rare_animals_2006.pdf)), little is known about the local phenology of terrapin nesting, nest predation, and hatchling emergence, except for limited details provided in a single recent study (Decker et al. 2023). Nest predation is believed to be one of the greatest threats to Diamondback Terrapin survivorship in Rhode Island (Butler et al. 2006), so it is critical to understand when this predation occurs and which predator species are involved. This study fills important knowledge gaps by identifying temporal trends in Diamondback Terrapin nesting and hatchling emergence, describing patterns of nocturnal mammalian nest predation, and determining the main species responsible for nest predation at a nesting site of Diamondback Terrapins in Rhode Island, USA.

## MATERIALS AND METHODS

**Study site.**—We monitored Diamondback Terrapin nesting activity in Bristol County, Rhode Island, USA (specific location details withheld due to risk of illegal collection). In Bristol County, long-term (1991–2021) average temperature and average precipitation during the Diamondback Terrapin nesting and hatching season (June–September) were 20.1° C and 38.3 cm, respectively (<https://www.ncei.noaa.gov/cag/>). Our study site was located on a sheltered brackish-water bay with semidiurnal tidal cycles where adult terrapins congregate to breed each summer. During subsequent nesting events, female turtles emerge from the bay and travel through Saltmarsh and deciduous forest habitat to reach nesting habitats that include areas of open sand, herbaceous meadow, and agricultural fields. Diamondback Terrapin nesting has been monitored at this site by a dedicated group of community science volunteers since 1990.

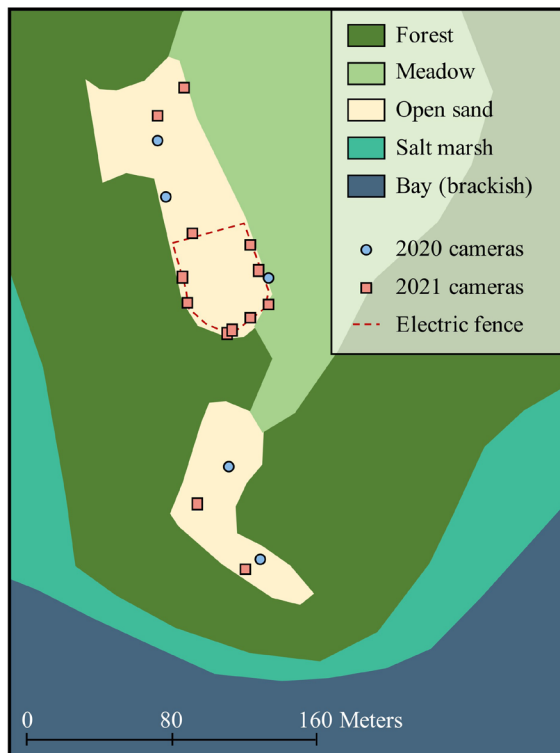
**Data collection and nest protection.**—From the beginning of June through the end of September in 2020 and 2021, we surveyed the nesting areas each day

and recorded counts of nesting females, predated nests, and nests from which hatchlings had emerged. As often as possible, we installed small wire mesh exclosures over individual nests to protect eggs from predators. Counts of predated nests included both protected and unprotected nests. Counts of emerged nests included only nests protected by exclosures, as emergence is rarely observed when a barrier is not present to retain emerging hatchlings. For all protected nests, we also documented clutch size, which was defined as the sum of live hatchlings, dead hatchlings, dead embryos, and nonviable eggs found in a nest on the day of emergence. We excluded from the clutch size dataset all predated nests (whether predated entirely or in part) and nests from which hatchlings escaped prior to exclosure removal.

In addition to Diamondback Terrapin nesting activity, we also monitored nocturnal predator activity using a series of motion-activated trail cameras installed in and around the nesting areas (Fig. 1). We attached cameras to U-channel signposts approximately 0.6 m off the ground and secured each unit in a lock box or with bicycle locks. We programmed the cameras to collect either 10- or 20-sec videos of moving subjects and to require a minimum period of 60 sec to elapse between consecutive

recordings. Because most nest predators are crepuscular or nocturnal, we collected videos only between 1900 and 0700 each night. In 2020, we maintained five cameras from 23 June to 1 September (except between 3–7 August, when we temporarily removed the cameras due to inclement weather). In 2021, we increased this number to 13 cameras; we deployed nine of these on 4 June, the remaining four on 25 June, and maintained all 13 through 17 August 2021. We reviewed camera footage to produce a dataset summarizing the species detected, date, time, and number of individuals observed in each video. To ensure the independence of detections, we applied a 1-h exclusion interval across all camera traps as a single unit (i.e., following an initial detection of a particular species, we did not count subsequent videos of that species as additional detections until an hour had elapsed). The predator count recorded for each detection was the maximum number of unique individuals appearing in any one video captured during the hour-long exclusion interval.

Due to high observed rates of nest predation in 2020, we installed a solar electric fence around an approximately 1,200 m<sup>2</sup> portion (approximately 48%) of the largest nesting area in 2021. The fence incorporated two lines of seven-strand galvanized steel wire cable supported by a series of fiberglass rods (1.3 cm diameter) and was powered by a monocrystalline 5-W Speedrite S500 Solar Energizer solar panel (Datamars, Lamone, Switzerland). The fence was designed to deter nocturnal mammalian nest predators such as the raccoon, skunk, Virginia Opossum (*Didelphis virginiana*), Red Fox (*Vulpes vulpes*), and Coyote (*Canis latrans*). We activated the fence nightly from 27 May through 29 September 2021, except between 23–31 July due to an unanticipated design malfunction. On 25 June, we added a third electrified wire to the bottom of the fence in response to observations of predators passing under the existing wires. Between 7–15 July, we laid 1.3-cm hardware cloth (30.5 cm in width) below the fence to improve grounding. The hardware cloth was centered beneath the lowest wire and secured in the substrate with 15.2-cm sod staples. Throughout the summer we periodically baited the lower and middle fence wires with cat food, peanut butter, or bacon to increase the likelihood that predators foraging near the fence would be shocked and subsequently deterred from the area. We also periodically removed vegetation from below the wires and tested for conductivity with a Wellscroft 5-light wireless fence tester (Wellscroft Fence Systems LLC., Harrisville, New Hampshire, USA).



**FIGURE 1.** Habitat types and locations of camera traps and the solar electric fence we installed at a Diamondback Terrapin (*Malaclemys terrapin*) nesting site in Rhode Island, USA. The electric fence boundary encompassed an approximately 1,200 m<sup>2</sup> of the total 5,500 m<sup>2</sup> of monitored nesting habitat.

**Data analysis.**—We smoothed daily counts of nesting females, predated nests, and nests from which hatchlings had emerged using a rolling 5-d average and graphed these values to visualize the temporal

**TABLE 1.** Summary of Diamondback Terrapin (*Malaclemys terrapin*) nests, nest predation, and hatchling emergence at a Rhode Island, USA, nesting site in 2020 and 2021. Successful nests were those from which at least one hatchling emerged.

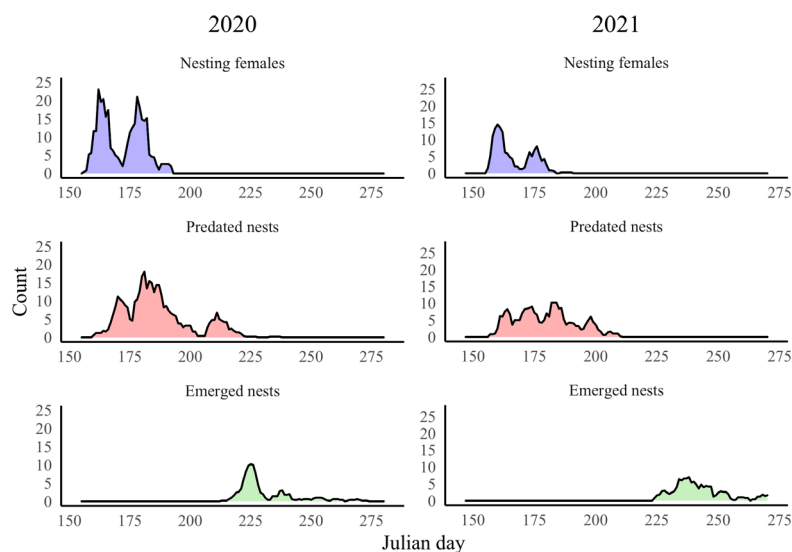
Year	Nests Identified		Predated Nests	Successful Nests	Predator Detections	
	total	per person-hour			total	per night
2020	323	0.76	372	106	143	2.20
2021	149	0.49	254	128	223	3.01
Total	472	0.64	626	234	366	2.63

distribution of nesting-related events. We visualized and assessed nightly predator detection counts (also smoothed using a rolling 5-d average) in relation to terrapin nesting and emergence trends. We also compared predator detections to corresponding counts of predated nest observations via Spearman's Rank Correlation analyses. To identify which nocturnal predators were contributing most significantly to Diamondback Terrapin nest predation at our study site, we generated a series of scatterplots comparing nightly detection counts for individual predator species (raccoon, skunk, Virginia Opossum, Red Fox, and Coyote) to the associated daily counts of predated nests. For frequently observed species, we also performed Spearman's Rank Correlation analyses on these variables. We assessed the efficacy of the electric fence by graphing and comparing patterns of nest predation within the fence boundary to patterns observed beyond the fence, as well as by calculating weekly proportions of predator detections occurring within versus outside of the fence perimeter over time. For these calculations, we did not filter predator detections for independence; this is because we sought to describe the proportion of time spent on either side of the fence by predators rather

than the unique number of visits. We performed all Spearman's Rank Correlation analyses at  $\alpha = 0.05$  and generated all graphs in R v3.5.1 (R Core Team 2018) using the packages ggplot2 (Wickham 2016), ggridges (Wilke 2021), zoo (Zeileis and Grothendieck 2005), and reshape2 (Wickham 2007). We annotated and archived the code used to produce each graph in a public GitHub repository ([https://github.com/tylerdevos/terrapin\\_nest\\_predation\\_2023](https://github.com/tylerdevos/terrapin_nest_predation_2023)).

## RESULTS

Across 2 y, we observed 472 Diamondback Terrapin nesting events, identified 626 predated nests, documented hatchling emergence from 234 nests, and detected 366 predator visits to the study site (Table 1; Fig. 2). Clutch size ranged from one to 19, with an average of 12.2 eggs per nest (standard deviation = 3.50,  $n = 209$  nests; Table 2). In both years, nesting events were bimodally distributed, with nesting peaks occurring on 12 June and 28 June in 2020 and on 9 June and 23 June in 2021. These peaks were highly temporally concentrated, with large numbers of female terrapins emerging synchronously from the bay in



**FIGURE 2.** Temporal distributions of Diamondback Terrapin (*Malaclemys terrapin*) nesting activity, nest predation, and hatchling emergence (protected nests only) at a Rhode Island, USA, nesting site in 2020 and 2021. All count values are rolling 5-d averages.

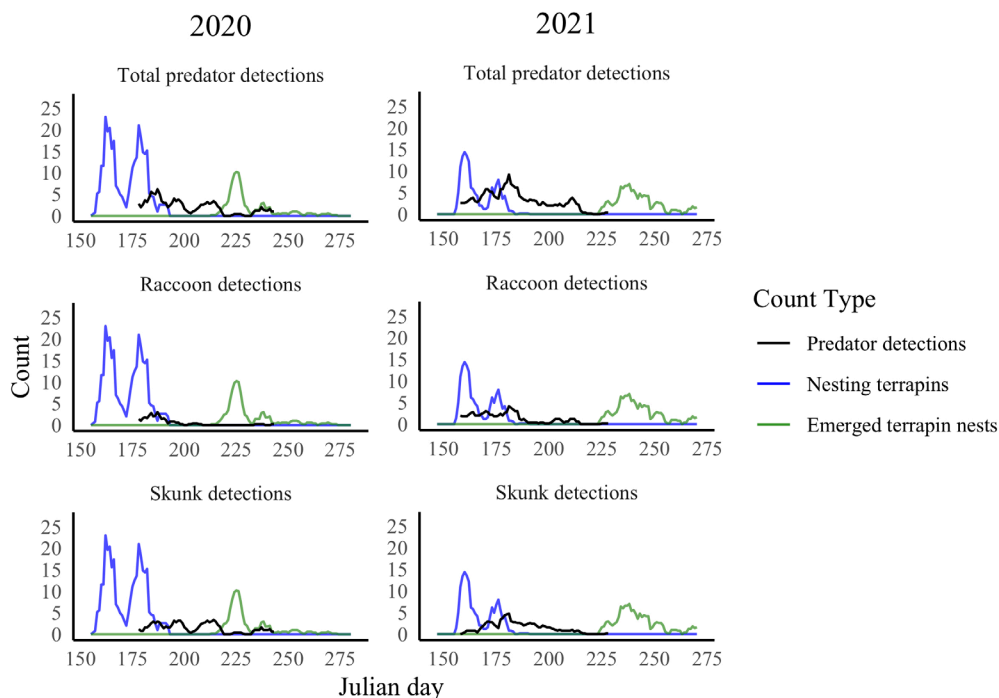
**TABLE 2.** Clutch size and survival summary statistics for protected nests of the Diamondback Terrapin (*Malaclemys terrapin*) at a Rhode Island, USA, nesting site in 2020 and 2021. We defined clutch size as the sum of live hatchlings, dead hatchlings, dead embryos, and nonviable eggs found in a protected nest on the day of hatchling emergence. The abbreviation SD = standard deviation.

Year	n	Clutch Size			% Survival	
		range	mean	SD	mean	SD
2020	97	1–18	11.5	3.8	95.6	14.8
2021	112	1–19	12.8	3.0	82.1	25.7
Total	209	1–19	12.2	3.5	88.3	22.3

arribada-like fashion (e.g., during the first peak in 2020, we documented 59 terrapins nesting on the same day). We observed predated nests 4 d after the first nesting event in 2020 and 1 d after the first nesting event in 2021. In both years, nest predation occurred continually from the beginning of nesting season until the time of hatchling emergence. Hatchling emergence peaked on 12 August in 2020 and on 26 August in 2021. Camera detections of predators reached the highest frequency just after the second nesting peak and dropped to nearly zero during the peak phase of hatchling emergence in both years (Fig. 3). Among the 366 predator visits our cameras detected, 56% were observations of skunks and 36% were observations of raccoons. Only 16 Virginia Opossum visits, 10 Coyote visits, and two Red Fox visits were detected across both years of camera trapping.

We identified a significant, positive correlation between the total number of predators detected on a given night and the number of predated nests observed the following morning in 2020 ( $r_s = 0.691$ ,  $df = 60$ ,  $P < 0.001$ ) and 2021 ( $r_s = 0.601$ ,  $df = 57$ ,  $P < 0.001$ ; Fig. 4). When we performed similar correlation analyses on sets of predator detection counts split by species, we found that detections of raccoons and skunks were strongly correlated with nest predation (raccoons:  $r_s = 0.452$ ,  $df = 119$ ,  $P < 0.001$ ; skunks:  $r_s = 0.644$ ,  $df = 119$ ,  $P < 0.001$ ; Table 3). Scatterplots comparing predator detections to predated nest counts indicated that Virginia Opossums, Red Foxes, and Coyotes were not important nest predators at our study site (Fig. 5). Because these three predator species were observed at such low frequencies, we did not statistically evaluate the associated count distributions.

Throughout the summer of 2021, we observed nest predation within and beyond the boundary of the electric fence. Peaks and dips in predation did not correspond to dates on which we conducted fence maintenance and temporal patterns of predation did not differ between the fenced and unfenced (Fig. 6) regions of the nesting site. Modifications made to the fence during the study, however, were followed by corresponding changes in the proportions of predators detected within versus beyond the fence boundary (Fig. 6). Prior to installation of the third and lowest wire on 25 June 2021, 44 of 134 (33%) raccoon videos captured by the trail cameras



**FIGURE 3.** Temporal distribution of camera trap predator detections as they relate to Diamondback Terrapin (*Malaclemys terrapin*) nesting activity at our Rhode Island, USA, study site in 2020 and 2021. All count values are rolling 5-d averages.

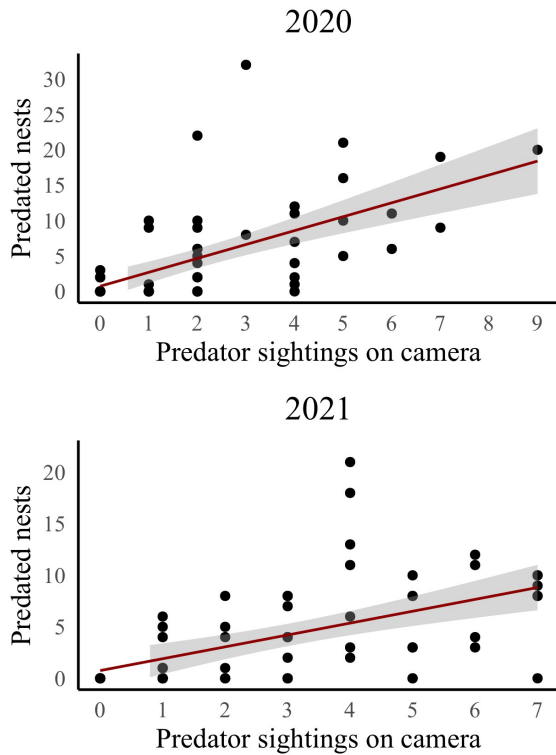


FIGURE 4. Scatterplots comparing daily counts of predated nests to camera trap detections of nocturnal predators at a Diamondback Terrapin (*Malaclemys terrapin*) nesting site in Rhode Island, USA, in 2020 and 2021. Red lines and grey shading indicate the lines-of-best-fit and corresponding 95% confidence intervals identified by Linear Regression analyses, respectively.

showed raccoons located inside of the fence or crossing under the fence; after the addition of the extra wire, only two of 72 (3%) raccoon videos involved animals within the fence boundary. Skunks were regularly observed passing through the electric fence with no sign of shock before and after the installation of the third wire. Although the fence did not effectively exclude skunks at any point during the summer, the proportion of skunks detected within the fenced region of the sandpit did decrease after hardware cloth was laid below the fence between 7–15 July. Trail cameras occasionally captured footage of predators receiving an electric shock from the fence (instances included 11 raccoons, three skunks, one Coyote, and one Virginia Opossum). On 23 July 2021, we found and immediately removed a single female

Diamondback Terrapin wedged under the lowest fence wire. It was unclear whether the turtle had received an electric shock, but no sign of injury was evident. Finally, the protective wire exclosures installed over individual nests were highly effective at preventing mammalian nest predation (considerably more so than the electric fence). In 2020, only 11 of 119 (9%) nests protected with wire exclosures were predated. In 2021, only one of 134 (<1%) protected nests was lost to predation.

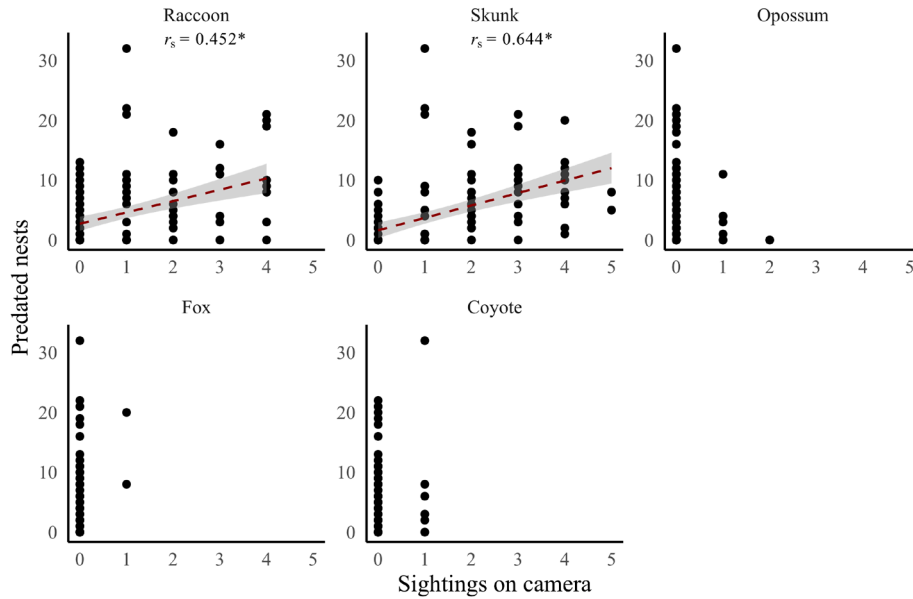
DISCUSSION

Overall, trends in Diamondback Terrapin nesting and hatchling emergence in our study population followed a consistent seasonal pattern. The bimodal distribution of nesting events observed each year indicates that most females at our study site nested twice per season and that nesting activity was highly synchronous. Nest predation and predator visits to the nesting site occurred most frequently during the nesting period and persisted until the peak of hatchling emergence. The greater quantity of trail camera detections for raccoons and skunks in comparison to trail camera detections for other nocturnal mammalian predators suggest that raccoons and skunks are the main species preying Diamondback Terrapin nests at our study site. Conversely, the small counts of trail camera detections for Red Fox and Coyote in both years indicate that these species rarely visited the nesting site and are thus responsible for little to none of the observed nest predation during the study period. Compared with 2020, we observed more predator visits per night in 2021, likely due to our installation of eight additional motion-activated trail cameras. This increase, however, was relatively small and was not proportional to the increase in number of cameras, suggesting that beyond a certain camera density, the return in detections from incorporating additional cameras may be limited.

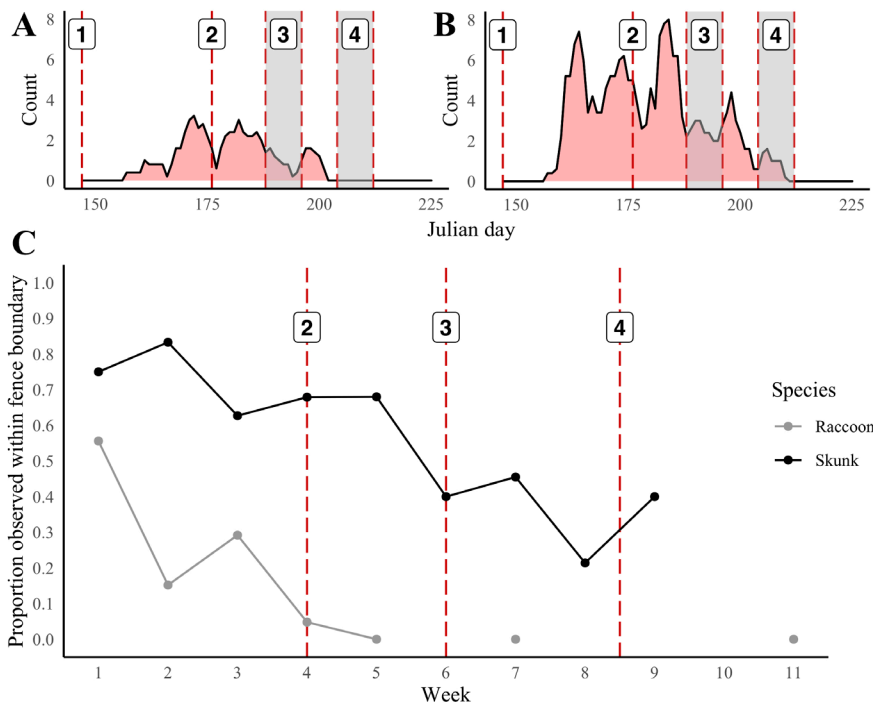
Previous literature indicates that most terrapin nest predation occurs within 24 to 48 h after a nesting event (Congdon et al. 2000; Feinberg and Burke 2003; Butler et al. 2004; Burke et al. 2005; Reses et al. 2015) and in soil that was recently excavated or disturbed by nesting females (Burke et al. 2005; Geller 2015; Buzuleciu et al. 2016). Predators use olfactory and tactile cues to identify nest locations, and these cues are most obvious in the hours immediately after a nest has been

TABLE 3. Results of Spearman’s Rank Correlation analyses relating daily predated Diamondback Terrapin (*Malaclemys terrapin*) nest counts at a Rhode Island, USA, site to associated nightly counts of Northern Raccoons (*Procyon lotor*) and Striped Skunks (*Mephitis mephitis*) from camera detections.

Species	2020 (df = 60)			2021 (df = 57)			combined (df = 119)		
	n	$r_s$	P-value	n	$r_s$	P-value	n	$r_s$	P-value
raccoon	35	0.503	< 0.001	79	0.360	0.005	114	0.452	< 0.001
skunk	86	0.603	< 0.001	82	0.700	< 0.001	168	0.644	< 0.001



**FIGURE 5.** Scatterplots comparing the relative association of five nocturnal mammalian predator species with Diamondback Terrapin (*Malaclemys terrapin*) nest predation observed across two years of study (2020–2021) in Rhode Island, USA. Predators were the Northern Raccoon (*Procyon lotor*), Striped Skunk (*Mephitis mephitis*), Virginia Opossum (*Didelphis virginiana*), Red Fox (*Vulpes vulpes*), and Coyote (*Canis latrans*). Dashed red lines and shaded polygons indicate the lines-of-best-fit and corresponding 95% confidence intervals, respectively, identified by correlation analyses relating counts of predated nests to camera detections of Northern Raccoons (*Procyon lotor*) and Striped Skunks (*Mephitis mephitis*) at the terrapin nesting site. An asterisk (\*) indicates a  $P$ -value  $< 0.001$ . Linear Regression analyses were not performed on count distributions for the Virginia Opossum, Red Fox, or Coyote due to low numbers of positive detections for these species.



**FIGURE 6.** Daily distribution of predated Diamondback Terrapin (*Malaclemys terrapin*) nests within (A) and beyond (B) the boundaries of a solar electric fence designed to deter nocturnal mammalian nest predators during the 2021 nesting season at a Rhode Island, USA site. (C) Weekly proportions of raccoon and skunk observations occurring within the fence perimeter. All counts in graphs A and B are 5-d averages. Vertical dashed lines indicate the day(s) on which modifications were made to the electric fence: (1) electric fence installed; (2) third wire added to fence; (3) hardware cloth added below fence to improve grounding; and (4) fence temporarily inactivated.

created (Feinberg and Burke 2003; Burke et al. 2005; Geller 2015; Edmunds et al. 2018). At our survey site, the majority and peak counts of predated nests in 2020 and 2021 occurred during the terrapin nesting period; however, we detected nest predation events at continuously high levels until hatchlings emerged and there were no longer nests to predate, suggesting that nests remain vulnerable to mammalian predation for weeks, rather than hours, after eggs are deposited. Predator detection counts followed the same trends as nest predation, indicating that nocturnal predators visit the nesting site frequently both during and after terrapin nesting season.

At the species level, camera detections of raccoons were most numerous during and just after the Diamondback Terrapin nesting period, while skunk detections peaked at the end of nesting season and continued until the time of hatchling emergence. This suggests that skunks may be more efficient than raccoons at finding nests in the absence of fresh scent or texture cues, possibly due to an enhanced ability to detect nests using auditory cues created by hatching turtles, and that skunks are likely responsible for much of the predation observed after the nesting period concludes. Prior studies have identified raccoons as the most important predator of terrapin nests (Burger 1977; Roosenburg 1992; Butler 2000; Feinberg and Burke 2003; Butler et al. 2004). For example, at Winyah Bay National Estuarine Research Reserve in South Carolina, USA, cameras detected more raccoons than other mammalian predators (Buzuleciu et al. 2016). Although raccoons were commonly observed at our study site and were likely responsible for large numbers of predated nests, our cameras detected more skunks than raccoons during both study years. Nightly skunk detections were also more strongly related to corresponding counts of predated nests than were raccoon detections, likely in part because skunks were better at passing through the electric fence than raccoons. Collectively, these findings strongly suggest that skunks were the most important predator of Diamondback Terrapin nests at our site during the study period. To our knowledge, this study is the first in which skunks (rather than raccoons) have been identified quantitatively as the most important terrapin nest predator (Butler 2000; Butler et al. 2004; Ruzicka 2006).

The solar electric fence installed in 2021 was not initially an effective predator deterrent, but as we modified the fence throughout the summer, its efficacy gradually increased. Proportions of raccoons observed within the fenced area decreased following the addition of a third wire and dropped to zero after grounding was improved with hardware cloth. Although skunks appeared capable of passing through any configuration of wires due, we suspect, to shock protection afforded

by their thick fur, they were slightly more likely to avoid the fence after grounding was improved. Based on our observations, we recommend that other conservation groups interested in using an electric fence to protect turtle nests from mammalian predators should install hardware cloth below the entire fence perimeter and position the lowest electrified wire as close to the ground as possible while permitting just enough space for a turtle to pass underneath. It is important to maintain strong tension in all electrified wires such that wires do not cause electrical shorts by contacting one another (or the ground) on windy days or when animals interact with the fence. We also recommend using strips of raw bacon wrapped tightly around the electrified wires to increase the likelihood of mammals receiving a contact shock. Other studies have found that installation of electric fencing is an effective management strategy for reduction of turtle nest predation by raccoons (Geller 2012; Quinn et al. 2015), although total predator exclusion has yet to be achieved by any fence design.

At our study site, wire exclosures placed over individual turtle nests were a more effective means of nest protection than the electric fence, but also required a notably greater expenditure of time and labor. Installation of exclosures and subsequent monitoring for emerging hatchlings required hundreds of person-hours. Further refinement of our electric fence will be necessary before it will constitute an acceptable replacement for individual nest exclosures. If continued improvements are made, the electric fence has the potential to protect an even greater number of nests using considerably fewer resources than the individual nest exclosure method. In addition to protecting terrapin nests, electric fencing could benefit several additional turtle species susceptible to mammalian nest predation. Other studies have tested electric fencing as a potential conservation tool for the Spiny Softshell (*Apalone spinifera*; Parren et al. 2021), Wood Turtle (*Glyptemys insculpta*; Bougie et al. 2020), and Ouachita Map Turtle (*Graptemys ouachitensis*; Geller 2012).

A few miscellaneous observations made during our study suggest that continued research will be necessary to fully understand the dynamics of Diamondback Terrapin nesting and nest predation in Rhode Island. First, on two occasions, trail cameras documented nocturnal terrapin nesting activity (12 July 2020 at 0515 and 9 June 2021 at 0135). Second, embryos in several protected terrapin nests were killed by predatory fly larvae, red ants, wasps, and root invasion; these forms of nest mortality are cryptic but likely common. Additional studies designed to investigate terrapin nesting at night and the relative contributions of invertebrates and plants to embryonic mortality within wire exclosures will meaningfully enhance our ability to conserve Diamondback Terrapins.



Ultimately, our study demonstrates that Diamondback Terrapin nests are predated during and after the nesting season and that skunks, followed by raccoons, are the most important predators. In response to these findings, we suggest that it is critical to protect terrapin nests throughout the summer, rather than for just a few days after eggs are deposited. We also recommend the continued use of individual wire exclosures to prevent nest predation by mammals. We emphasize that electric fencing represents a promising future alternative but, as deployed in our study, is not as effective as the wire exclosure method, especially in regions where skunks are a major nest predator.

Although many terrapin populations are thought to be slowly recovering from severe historical overharvest, most remain greatly reduced in size due to road mortality, habitat loss, bycatch mortality, predation, and illegal collection (Giambanco 2002; Hart and Lee 2006; Sevin et al. 2022). It is well understood among biologists that protecting adult turtles is preeminent when implementing conservation measures for the stability and viability of a turtle population (Heppell and Crowder 1996). A failure to do so will often ensure the eventual extirpation of a population. Nonetheless, without recruitment it is only a matter of time before even the largest population experiences extirpation. We must be careful not to discount the fundamental importance that recruitment plays in population dynamics. Though it may take a sustained effort over some years to yield measurable returns, buttressing early life stages from increased rates of mortality is a proven strategy for turtle population recovery (Mitro 2003; Shaver et al. 2016; Wijewardena et al. 2023). The continued development and implementation of strategies that enhance nest protection should play a central role in the effort to further restore Diamondback Terrapins from their collapse a century ago.

*Acknowledgments.*—We conducted all research under Scientific Collector permits 2020-36-W and 2021-22-W of the Rhode Island Division of Fish and Wildlife. We thank Jen Brooks, Gabby DeMeillon, Kate Eller, Kyra Higgins, Pete McCalmont, T.J. McGreevy, Carolyn Pralle, and the many volunteers who assisted with nest monitoring and protection efforts for contributing their time, resources, and talents. This work was partially funded by a grant from the Rhode Island Department of Environmental Management to Nancy Karraker and an Undergraduate Research Award to Richard Mercer from the Department of Biological Sciences, University of Rhode Island.

#### LITERATURE CITED

Allman P.E., A.R. Place, and W.M. Roosenburg. 2012. Geographic variation in egg size and

- lipid provisioning in the Diamondback Terrapin *Malaclemys terrapin*. *Physiological and Biochemical Zoology* 85:442–449.
- Bougie, T.A., M.Z. Peery, C.N. Lapin, J.E. Woodford, and J.N. Pauli. 2022. Not all management is equal: a comparison of methods to increase wood turtle population viability. *Journal of Wildlife Management* 86:e22234. <https://doi.org/10.1002/jwmg.22234>.
- Bougie, T.A., N.W. Byer, C.N. Lapin, M.Z. Peery, J.E. Woodford, and J.N. Pauli. 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.
- Burger, J. 1977. Determinants of hatching success in Diamondback Terrapin, *Malaclemys terrapin*. *American Midland Naturalist* 97:444–464.
- Burger, J., and W.A. Montevecchi 1975. Nest site selection in the terrapin *Malaclemys terrapin*. *Copeia* 1975:113–119.
- Burke, R.L. 2015. Head-starting turtles: learning from experience. *Herpetological Conservation and Biology* 10:299–308.
- 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 Diamond-backed Terrapin sign. *Journal of Herpetology* 39:312–215.
- Butler, J.A. 2000. Status and distribution of the Carolina Diamondback Terrapin, *Malaclemys terrapin centrata*, in Duval County. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA. 52 p.
- Butler, J.A., C. Broadhurst, M. Green, and Z. Mullin. 2004. Nesting, nest predation and hatchling emergence of the Carolina Diamondback Terrapin, *Malaclemys terrapin centrata*, in northeastern Florida. *American Midland Naturalist* 152:145–155.
- Butler, J.A., G.L. Heinrich, and R.A. Seigel. 2006. Third workshop on the ecology, status, and conservation of Diamondback Terrapins (*Malaclemys terrapin*): results and recommendations. *Chelonian Conservation and Biology* 5:331–334.
- Buzuleciu, S.A., D.P. Crane, and S.L. Parker. 2016. Scent of disinterred soil as an olfactory cue used by Raccoons to locate nests of Diamond-backed Terrapins (*Malaclemys terrapin*). *Herpetological Conservation and Biology* 11:539–551.
- Congdon, J.D., R.D. Nagle, O.M. Kinney, M. Osenioski, H.W. Avery, R.C. van Loben Sels, and D.W. Tinkle. 2000. Nesting ecology and embryo mortality: implications for hatchling success and demography of Blanding's Turtles (*Emydoidea blandingii*). *Chelonian Conservation and Biology* 3:569–579.
- Czaja, R.A., A. Kanonik, and R.L. Burke. 2018. The effect of rainfall on predation of Diamond-backed Terrapin (*Malaclemys terrapin*) nests. *Journal of*

- Herpetology 52:402–405.
- Decker, C.E., S.W. Buchanan, and N.E. Karraker. 2023. Post-emergence movements and habitat use by hatchling diamondback terrapins. *Journal of Wildlife Management* 87:e22343. <https://doi.org/10.1002/jwmg.22343>.
- Donini, J., and W. Selman. 2022. Clutch size, clutch frequency, and egg characteristics of Diamond-backed Terrapins (*Malaclemys terrapin*) in southwestern Louisiana. *Southeastern Naturalist* 21:235–245.
- Edmunds, S.E., C.N. Kasparov, J.B. Yoon, A.K. Kanonik, and R.L. Burke. 2018. Twelve years later: reassessing visual and olfactory cues Raccoons use to find Diamondback Terrapin nests. *Journal of Herpetology* 52:307–312.
- Feinberg, J.A. 2004. Nest predation and ecology of terrapins, *Malaclemys terrapin terrapin*, at the Jamaica Bay Wildlife Refuge. Pp. 5–12 *In Conservation and Ecology of Turtles of the Mid-Atlantic Region: A Symposium*. Swarth, C.W., W.M. Roosenburg, and E. Kiviat, (Eds.). Biblomania!, Salt Lake City, Utah, USA.
- Feinberg, J.A., and R.L. Burke. 2003. Nesting ecology and predation of Diamondback Terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. *Journal of Herpetology* 37:517–526.
- Geller, G.A. 2012. Reducing predation of freshwater turtle nests with a simple electric fence. *Herpetological Review* 43:398–405.
- Geller, G.A. 2015. A test of substrate sweeping as a strategy to reduce Raccoon predation of freshwater turtle nests, with insights from supplemental artificial nests. *Chelonian Conservation and Biology* 14:64–72.
- Giambanco, M.R. 2002. Comparison of viability rates, hatchling survivorship, and sex ratios of laboratory and field incubated nests of the estuarine, emydid turtle *Malaclemys terrapin*. M.Sc. Thesis, Hofstra University, Hempstead, New York, USA. 83 p.
- Hart, K.M., and D.S. Lee. 2006. The Diamondback Terrapin: the biology, ecology, cultural history, and conservation status of an obligate estuarine turtle. *Studies in Avian Biology* 32:206–213.
- Hart, K.M., M.E. Hunter, and T.L. King. 2014. Regional differentiation among populations of the Diamondback Terrapin (*Malaclemys terrapin*). *Conservation Genetics* 15:593–603.
- Heppell, S.S., and L.B. Crowder. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* 6:556–565.
- Howell H.J., and R.A. Seigel. 2019. The effects of road mortality on small, isolated turtle populations. *Journal of Herpetology* 53:39–46.
- Jeyasuria, P., W.M. Roosenburg, and A.R. Place. 1994. Role of P-450 aromatase in sex determination of the Diamondback Terrapin, *Malaclemys terrapin*. *Journal of Experimental Zoology* 270:95–111.
- Marchand, M.N., J.A. Litvaitis, T.J. Maier, and R.M. DeGraaf. 2002. Use of artificial nests to investigate predation on freshwater turtle nests. *Wildlife Society Bulletin* 30:1092–1098.
- Mazaris, A.D., O. Fiksen, and Y.G. Matsinos. 2005. Using an individual-based model for assessment of sea turtle population viability. *Population Ecology* 47:179–191.
- Mitro, M.G. 2003. Demography and viability analyses of a diamondback terrapin population. *Canadian Journal of Zoology* 81:716–726.
- Muldoon, K.A., and R.L. Burke. 2012. Movements, overwintering, and mortality of hatchling Diamond-backed Terrapins (*Malaclemys terrapin*) at Jamaica Bay, New York. *Canadian Journal of Zoology* 90:651–662.
- Munscher, E.C., E.H. Kuhns, C.A. Cox, and J.A. Butler. 2012. Decreased nest mortality for the Carolina Diamondback Terrapin (*Malaclemys terrapin centrata*) following removal of Raccoons (*Procyon lotor*) from a nesting beach in northeastern Florida. *Herpetological Conservation and Biology* 7:176–184.
- Murphy, R.E., A.E. Martin, and L. Fahrig. 2022. Reduced predation on roadside nests can compensate for road mortality in road-adjacent turtle populations. *Ecosphere* 13:e3946. <https://doi.org/10.1002/ecs2.3946>.
- Ner, S.E., and R.L. Burke. 2008. Direct and indirect effects of urbanization on Diamond-backed Terrapins of the Hudson River Bight: distribution and predation in a human-modified estuary. Pp. 107–117 *In Urban Herpetology*. Mitchell, J.C., R.E. Jung Brown, and B. Bartholomew (Eds.). Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.
- Oddie, M.A.Y., S.M. Coombes, and C.M. Davy. 2015. Investigation of cues used by predators to detect Snapping Turtle (*Chelydra serpentina*) nests. *Canadian Journal of Zoology* 93:299–305.
- Palmer, W.M., and C.L. Cordes. 1988. Habitat suitability index models: Diamondback Terrapin (nesting) - Atlantic Coast. Biological Report 82 (10.151), U.S. Fish and Wildlife Service, Washington, D.C., USA. 27 p.
- Parren, S.G., M.K. Parren, and K.D. Gieder. 2021. Nest counts and hatchling emergence timing the Spiny Softshell (*Apalone spinifera*) and associated turtle species at managed sites in Vermont, USA. *Herpetological Conservation and Biology* 16:194–202.
- Pearson, S.H., and J.J. Wiebe. 2018. Considering Diamond-backed Terrapin (*Malaclemys terrapin*) nesting habitat and reproductive productivity in the

- restoration of Gulf of Mexico coastal ecosystems. *Ocean and Coastal Management* 155:8–14.
- Quinn, D.P., S.M. Kaylor, T.M. Norton, and K.A. Buhmann. 2015. Nesting mounds with protective boxes and an electric wire as tools to mitigate Diamond-backed Terrapin (*Malaclemys terrapin*) nest predation. *Herpetological Conservation and Biology* 10:969–977.
- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Reses, H.E., A.R. Davis Rabosky, and R.C. Wood. 2015. Nesting success and barrier breaching: assessing the effectiveness of roadway fencing in Diamondback Terrapins (*Malaclemys terrapin*). *Herpetological Conservation and Biology* 10:161–179.
- Riley, J.L., and J.D. Litzgus. 2014. Cues used by predators to detect freshwater turtle nests may persist late into incubation. *Canadian Field-Naturalist* 128:179–188.
- Roosenburg, W.M. 1992. Life history consequences of nest site choice by the Diamondback Terrapin, *Malaclemys terrapin*. Ph.D. Dissertation, University of Pennsylvania, Philadelphia, Pennsylvania, USA. 218 p.
- Roosenburg, W.M. 1996. Maternal condition and nest site choice: an alternative for the maintenance of environmental sex determination. *American Zoology* 36:157–168.
- Roosenburg, W.M., and A.R. Place. 1995. Nest predation and hatchling sex ratio in the Diamondback Terrapin: implications for management and conservation. Pp. 65–70 *In* *Toward a Sustainable Coastal Watershed: The Chesapeake Experiment, Proceedings of a Conference*. Hill, P., and S. Nelson (Eds.). Publication Number 149, Chesapeake Research Consortium, Norfolk, Virginia, USA.
- Roosenburg, W.M., P.J. Baker, R. Burke, M.E. Dorcas, and R.C. Wood. 2019. *Malaclemys terrapin*, Diamondback Terrapin. The IUCN Red List of Threatened Species 2019. International Union for Conservation of Nature. <http://www.iucn.org>.
- Ruzicka, V.A. 2006. The influence of predation on the nesting ecology of Diamondback Terrapins (*Malaclemys terrapin*) in the lower Chesapeake Bay. M.Sc. Thesis, College of William and Mary, Williamsburg, Virginia, USA. 124 p.
- Seigel, R.A. 1979. The reproductive biology of Diamondback Terrapin, *Malaclemys terrapin tequesta*. M.Sc. Thesis, The University of Central Florida, Orlando, Florida, USA. 52 p.
- Seigel, R.A. 1980. Nesting habits of Diamondback Terrapins (*Malaclemys terrapin*) on the Atlantic coast of Florida. *Kansas Academy of Science* 83:239–246.
- Selman, W., B. Baccigalopi, and C. Baccigalopi. 2014. Distribution and abundance of Diamondback Terrapins (*Malaclemys terrapin*) southwestern Louisiana. *Chelonian Conservation and Biology* 13:131–139.
- Sevin, J., K. Wixted, L. Kisonak, B. Macdonald, J. Thompson-Slacum, S. Buchanan, and N. Karraker. 2022. Turtles in trouble: trafficking poses conservation concerns for America’s turtles. *Wildlife Professional* November/December 2022:26–31.
- Shaver, D.J., C. Rubio, J.S. Walker, J. George, A.F. Amos, K. Reich, C. Jones, and T. Shearer. 2016. Kemp’s Ridley Sea Turtle (*Lepidochelys kempii*) nesting on the Texas coast: geographic, temporal, and demographic trends through 2014. *Gulf of Mexico Science* 2:158–178.
- Spencer, R.J., J.U. Van Dyke, and M.B. Thompson. 2017. Critically evaluating best management practices for preventing freshwater turtle extinctions. *Conservation Biology* 31:1340–1349.
- Wickham, H. 2007. Reshaping data with the reshape package. *Journal of Statistical Software* 21:1–20. <https://doi.org/10.18637/jss.v021.i12>.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, New York, USA.
- Wijewardena, T., M.G. Keevil, N.E. Mandrak, A.M. Lentini, and J. Litzgus. 2023. Evaluation of headstarting as a conservation tool to recover Blanding’s Turtles (*Emydoidea blandingii*) in a highly fragmented urban landscape. *PLoS ONE* 18(3):e0279833. <https://doi.org/10.1371/journal.pone.0279833>.
- Wilke, C.O. 2021. *ggridges: ridgeline plots in ‘ggplot2’*. R package version 0.5.3. <https://wilkelab.org/ggridges/>.
- Wood, R.C., and R. Herlands. 1997. Turtles and tires: the impact of roadkills on northern Diamondback Terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May Peninsula, southern New Jersey, USA. Pp. 46–53 *In* *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles-An International Conference 1997*. Van Abbema, J. (Ed.). New York Turtle and Tortoise Society, New York, New York, USA.
- Zeileis, A. and G. Grothendieck. 2005. zoo: S3 infrastructure for regular and irregular time series. *Journal of Statistical Software* 14:1–27. <https://doi.org/10.48550/arXiv.math/050527>.
- Zimmer-Shaffer, S.A., J.T. Briggler, and J.J. Millsbaugh. 2014. Modeling the effects of commercial harvest on population growth of river turtles. *Chelonian Conservation and Biology* 13:227–236.

## Herpetological Conservation and Biology



**RICHARD D. MERCER** works on inland fisheries management projects for the Connecticut Department of Energy and Environmental Protection, USA. He received a Bachelor of Science in Biological Sciences and a Bachelor of Science in Marine Affairs from the University of Rhode Island, Kingston, Rhode Island, USA. He has worked on fish and wildlife conservation and management projects for the University of Rhode Island, Rhode Island Department of Environmental Management, USA, and U.S. Fish and Wildlife Service, Charlestown, Rhode Island, USA. (Photographed by Rhode Island Department of Environmental Management).



**TYLER B. DEVOS** is the Gopher Tortoise Biologist for Florida Natural Areas Inventory, USA, where she conducts and manages field surveys for Gopher Tortoises (*Gopherus polyphemus*) and other native wildlife throughout the state of Florida. She received her B.S. in Zoology from Northern Michigan University, Marquette, USA, and her M.S. in Biological and Environmental Sciences from the University of Rhode Island, Kingston, USA. Tyler has a passion for all things herpetological and has worked with a wide variety of reptile and amphibian species through past research and field positions in Michigan, Alabama, the Bahamas, and Rhode Island. (Photographed by Tyler DeVos).



**LIAM CORCORAN** is a M.Sc. candidate at the University of Rhode Island, Kingston, USA, where he is studying the movement ecology of early successional forest birds. He received his B.Sc. in Wildlife and Conservation Biology from the University of Rhode Island, Kingston, USA. Prior to pursuing graduate school, Liam worked as a field technician for the Rhode Island Division of Fish and Wildlife (Rhode Island, USA) herpetology program for 3 y. His main areas of interest are ornithology, herpetology, movement ecology, and applied management. (Photographed by Sarah Petrarca).



**SCOTT BUCHANAN** is a Biologist with the Rhode Island Division of Fish and Wildlife, West Kingston, USA, where he leads the Herpetology Program. He received his B.Sc. in Ecology and Natural Resources from Rutgers University, New Brunswick, New Jersey, USA, his M.Sc. in Ecology from Montclair State University, Montclair, New Jersey, USA, and his Ph.D. in Biological and Environmental Science from the University of Rhode Island, Kingston, Rhode Island, USA. His work focuses on the conservation and management of amphibians and reptiles in Rhode Island and the northeastern U.S. (Photographed by Scott Buchanan).



**KATHRYN A. BEAUCHAMP** is co-leader of the Barrington Terrapin Conservation Project in Rhode Island, USA. Since 1990, this community-based, citizen-scientist volunteer group has been studying the population of the Diamondback Terrapin in Barrington. She received her B.S. in Nursing from Rhode Island College, Providence, USA, and her M.S. as a Pediatric Critical Care Nurse Practitioner from the University of Pennsylvania, Philadelphia, USA. Following her retirement from nursing, she began her conservation work with the terrapin project. She is an active member of the Diamondback Terrapin Working Group. (Photographed by Kathryn A. Beauchamp).



**MADELEINE LINCK** received a B.A. from University of New Hampshire, Durham, USA, and a M.S. from Worcester State University, Massachusetts, USA. She studied the ecology of the Blanding's Turtles (*Emydoidea blandingi*) at Great Meadows National Wildlife Refuge, Concord, Massachusetts, USA. As a Wildlife Technician for 30 y in Minnesota, USA, she conducted reptile and amphibian, bat and bird surveys, worked with Trumpeter Swans (*Cygnus buccinator*), and managed Purple Martin (*Progne subis*) colonies. Retired in Massachusetts, Madeleine manages Purple Martin colonies, co-leads a Diamondback Terrapin conservation project in Barrington, Rhode Island and volunteers for Massachusetts Fish and Wildlife surveys of Eastern Spadefoot Toads (*Scaphiopus holbrookii*) and Blue Spotted Salamanders (*Ambystoma laterale*). (Photographed by Anna Kelchlin).



**NANCY KARRAKER** is a Professor in the Department of Natural Resources Science at the University of Rhode Island, Kingston, USA, where she teaches Herpetology, Wetland Ecology, and Wildlife Trafficking. She received a B.Sc. and M.Sc. in Wildlife Ecology and M.A. in English from Humboldt State University, Arcata, California, USA, and a Ph.D. in Conservation Biology from SUNY College of Environmental Science and Forestry, Syracuse, New York, USA. Her research focuses on the conservation of amphibians, reptiles, and wetlands in Southeast Asia and the USA. (Photographed by Dana Drake).