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Animal Biotelemetry



Conservation implications of habitat selection by nesting diamondback terrapins (*Malaclemys terrapin*) investigated via an automated radio telemetry system

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Abstract

Background Despite considerable research on nest site selection of diamondback terrapins and the risks that coastal roads pose to populations of this obligate estuarine turtle, there are gaps in our understanding of movements and habitat use by female terrapins during the nesting season. In particular, movements within salt marshes, shallow water habitats, and nest site-adjacent developed habitats remain relatively understudied. To investigate habitat use and risk exposure of this semiaquatic species, we employed an automated radio telemetry system featuring 31 passive receivers. In 2021, concurrent with annual nest surveys, we tracked 60 telemetered female terrapins near a nesting area in southern New Jersey subject to impacts from road mortality. We triangulated terrapin locations based on the relationship between radio signal strength at each receiver and distance, generated utilization distributions using kernel density estimation, and classified habitat using multispectral imagery.

Results We detected differences in habitat use versus relative availability within general (95% KDEs) and core (50% KDEs) use areas at a population level. Core use areas suggested more frequent use of salt pools, marsh, and upland habitats and less frequent use of developed and wide tidal creek habitats than expected based on availability alone. To further characterize variability in habitat use, we compared selectivity between terrapins grouped by proximity of their capture location to a road. Terrapins nesting closer to the road showed relatively more frequent usage of developed habitats and less frequent usage of narrow creeks and regularly flooded marsh throughout the nesting season.

Conclusions Patterns of habitat selection across all terrapins underscore the importance of shallow water habitats such as salt pools near nesting areas. Individuals tended to spend more time in habitat types close to their nesting locations, such that terrapins initially captured near roads spent more time in high-risk developed areas throughout the study period. Road mortality risk may not be homogenous within this nesting population, which may be a critical consideration for demographic modeling. This study expands our understanding of terrapin movements while demonstrating the effectiveness of a novel radio telemetry approach, and contributes to conservation planning in a rapidly changing salt marsh landscape.

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Introduction

Salt marsh ecosystems of the eastern United States have historically experienced, and continue to be threatened with, significant degradation and reductions in area [1-6]. In southern New Jersey, where uninterrupted

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tidal marsh habitat formerly connected the mainland to the dune systems of the barrier islands, anthropogenic shoreline hardening and roads have reshaped the landscape. These features may impact dispersal potential and movements of salt marsh species [7], disrupting gene flow between populations [8] and reducing access to high quality habitats [9].

The diamondback terrapin (*Malaclemys terrapin*, hereafter terrapin) is an estuarine turtle particularly threatened by anthropogenic impacts to salt marsh environments. As with many turtle species, terrapin life history is characterized by site fidelity, both to the home ranges they inhabit and to their nesting areas [10-15]. In the northeast and mid-Atlantic regions, terrapins lay 2–4 clutches of eggs approximately 15–20 days apart from late May to early August [16, 17] in sandy, sparsely vegetated upland habitats.

In many places, these coastal uplands have been anthropogenically modified, bringing nest-seeking terrapins into contact with roads and other barriers to their movements [18] and obstructing safe pathways from the marsh to historical terrapin nesting habitats such as barrier island sand dunes. In much of New Jersey, roadside habitats have become ecological traps, serving as high-risk substitutes for natural nesting habitats above the high tide line. Peak seasonal traffic often corresponds with peak terrapin nesting movements, compounding the threat of vehicle collisions and further limiting safe access to nesting areas [17, 19-23]. Roads can have significant demographic impacts on turtle populations, including terrapin populations, with effects ranging from altered sex ratios due to increased mortality of nesting females to population declines [24-26].

Against this landscape of risk, movements and habitat selection of female terrapins throughout the nesting season are not well-characterized, despite a wealth of knowledge on the terrestrial habitat use of the species during nesting attempts. Females frequently lay each clutch in the same general area [10, 27], and thus make multiple trips between the salt marsh and nesting habitat. There is preliminary evidence that some females remain in close proximity to nesting areas between clutches, while others may travel 2–10 km between nesting habitat and more distant foraging habitats [14, 15, 28, 29]. Between nesting attempts, females may use habitat such as regularly flooded marsh dominated by tall form Spartina alterniflora, tidal creeks, and salt pools for thermoregulation and foraging opportunities on fiddler crabs (Uca spp.), marsh periwinkles (Littoraria irrorata), and small fish [30, 31]. However, there are few comprehensive studies investigating terrapin movements and use of particular habitat types during the nesting season.

Technology and terrapin behavior have historically limited movement studies, as standard radio telemetry is difficult to use in a salt marsh environment due to attenuation of the radio signal by salt water, and terrapins are difficult to observe directly in aquatic habitats. The attenuation of radio signals when terrapins enter aquatic habitats complicates relocation of telemetered individuals and makes use of a handheld receiver time-consuming and labor-intensive. To overcome these difficulties associated with traditional radio telemetry, we deployed a passive receiver grid that was capable of detecting radio transmitters at all hours, providing consistent relocations whenever terrapins were within range of receivers and above water. Using this system, we evaluated habitat use and selectivity, movement, and exposure to risk as represented by interaction with roads and roadside developed habitats. We studied a subset of female terrapins captured at a nesting area in southern New Jersey where road mortality and nesting activity have been monitored for decades. Despite long-term monitoring of this population, questions remain as to whether individuals that habitually nest in different parts of the site demonstrate predictable differences in habitat selectivity before, between, and after nesting attempts, which may have important implications for survivorship due to high levels of annual road mortality near the nesting area. Terrapins travel a variety of routes to the nesting area and thus may experience different levels of risk depending on the habitats encountered and associated threats. In this study, we address two key questions about terrapin habitat use during the nesting season: (i) which habitat types or specific landscape features are preferentially selected or avoided by adult female terrapins? (ii) Do female terrapins that nest within close proximity to roadways display more frequent use of developed habitats, and therefore increased exposure to road mortality risk, throughout the nesting season compared to terrapins that nest farther from the road?

Methods

Study site and telemetry receiver array

We conducted this study at a known terrapin nesting area and surrounding habitat in Cape May County, New Jersey. The study site (~145.2 ha) includes natural landscape features such as salt marsh, salt pools, and tidal creeks, transitional upland habitat along a wildlife observation trail, and developed features such as grassy lawns, roadsides, paved surfaces, and shellgravel parking lots. Multiple roads intersect the study site, including a main roadway which experiences heavy traffic and is a documented threat to terrapin populations. Sections of the roadway are bordered by barrier fencing in effort to decrease terrapin mortality. The portion of roadway within the study area is interrupted by driveways and intersections, leading to the development of crossing hotspots. From 2019-2024 67 ± 10 (SD) terrapins were killed annually along the 1.4-km roadway segment that falls within our study site. The nesting area and surrounding habitat are also the site of a long-term terrapin population monitoring effort, with surveys for nesting females and roadkilled individuals conducted daily throughout the nesting season. We employed a system of solar-powered receiver nodes (Cellular Tracking Technologies, CTT) to obtain relocations for telemetered terrapins throughout the nesting season. We tilted solar panels at a 45 degree angle, rotated them south to optimize solar exposure, and fixed nodes approximately 2 m high on PVC poles. We arranged 31 nodes spaced roughly 100 m apart in a grid surrounding the nesting area from June 1–August 1, 2021 (Fig. 1A). A radio receiver station (CTT Sensor Station) with yagi antenna positioned ~ 5.0 m high received data from the



Fig. 1 Receiver node grid functional detection range and habitat classification of study area. **A** Study area containing receiver node grid, base station, functional node range where points could be triangulated (within 435 m detection range of at least 3 nodes), and nesting areas where diamondback terrapins (*Malaclemys terrapin*) were captured. A receiver node is pictured in inset. **B** Habitat classification map based on 2019 National Agriculture Imagery Program near infrared imagery and 2015 New Jersey Department of Environmental Protection Land Use layer

nodes. Nodes were 75.0-655.6 m (mean 366.2 ± 146.9 m) from the base station. We assessed node functionality by evaluating health reports provided by CTT and performed routine maintenance of nodes as necessary. Nodes more than 550 m from the base station commonly demonstrated interrupted or patchy transmission of data to the base station. Therefore, we deployed the majority of nodes at shorter distances. We relocated nodes minimally throughout the study to maintain a consistent grid; however, node failures occasionally necessitated shifts to preserve relatively consistent grid coverage and to fill priority locations near nesting areas and the road. Node data were relayed in real time from each receiver to the base station and uploaded hourly to an online repository hosted by CTT. We downloaded base station data using an API [32] implemented in R (v4.2.0; R Core Team 2022) and RStudio (v2022.02.2; RStudio Team 2022).

Data collection

Radio telemetry data were collected between June 3 and August 1, 2021, which spans the majority of the nesting season and the period of peak seasonal traffic when the risk of road mortality to the population is highest. Between June 3 and July 5, 2021, we attached batterypowered PowerTag[™] radio transmitters (CTT, 2022) to adult female terrapins captured by hand during routine surveys of the study site conducted multiple times daily. For all but six of 60 telemetered terrapins, we deployed transmitters within 3 days of their initial encounter in an effort to track terrapins from their first nesting attempt. We palpated turtles to determine if they were gravid, measured body mass and other morphometrics, and affixed transmitters to the carapace using Loctite marine grade epoxy [33], which set for at least 6 h prior to release. To minimize stress to the animals, we attached transmitters only if terrapins had completed nesting (were not gravid). Likewise, to prevent interference with shell growth, we attached transmitters to a single scute and covered scute sutures with medical tape during the application of epoxy to prevent seepage of epoxy across scutes [34]. In total, transmitters and epoxy weighed approximately 6.3 ± 0.3 g (0.5–1.2% of body mass). Each device transmitted a unique code over a common 433 MHz frequency at a rate of one signal every 15 s. All individuals were released at their capture locations.

To assess whether differential risk of road mortality may result from nesting habitat selection, we attached transmitters to an equal number of terrapins captured in nesting areas on opposite sides of the study site. Terrapins captured on roads intersecting the study site or within roadside developed habitats were considered the "road group" (Fig. 1A). Terrapins captured in the nesting area at the farthest distance from the road, in upland habitat close to a wide tidal creek, were considered the "creek group". The creek group included one terrapin captured in an intermediate location of the nesting area who was caught shortly prior in a narrow tidal creek adjacent to creek group territory. We expected that throughout the nesting season, terrapins would return to the same general nesting area where they were encountered. We therefore hypothesized that terrapins would spend more time in habitat types found near the initial nesting area, with terrapins in the road group more frequently using road-adjacent developed habitat than terrapins in the

Triangulation and filtering

creek group.

To translate raw detection data from our receivers into points, we first performed a calibration to relate received signal strength (RSS) and distance in our study area. We taped a transmitter to the bottom of a PVC pole held just above the marsh surface to approximate the height of a terrapin and walked the pole along a transect in the marsh, stopping at 14 known GPS points for six minutes each. We excluded the first and last minute from analysis to prevent bias from transit between points. We calculated the distance between each node and the calibration point as well as the mean RSS for each node during each four minute calibration period. Using the calibration dataset, we also calculated maximum detection range for the nodes to be 435 m, as nodes at greater distances failed to detect the calibration transmitters. Following Paxton et al. [35], we fitted an exponential decay model relating RSS and distance using the nls (nonlinear least squares) function in R stats v3.6.2. We then used this relationship to triangulate terrapin locations from signals received by a minimum of three nodes.

For triangulation, we binned data into 15-min intervals and calculated mean RSS for each transmitternode combination within each interval. To reduce error derived from detections with low signal strength, we then excluded signals with mean RSS less than – 100. We triangulated points using a nonlinear test to optimize locations with respect to the calculated distance between each transmitter-node pair and the pairwise distances between nodes. We calculated estimated error around each point using confidence ellipses generated by the car package in R [32, 36]. We excluded all triangulated points with estimated error greater than 100 m from downstream analysis. This exclusion threshold was selected to mitigate error and balance adequate sample size after preliminary testing against 50 m, 100 m, and 150 m error thresholds.

To reduce spatial autocorrelation among triangulated points, we divided our study period into 6-h intervals centered on the high and low tides, such that each interval included approximately 3 h before and after the tidal extreme. From a maximum of 24 possible triangulated points within each tidal interval, we retained the point with the lowest estimated localization error for further analysis. By setting the intervals to form alternating high and low tide bins, we minimized the probability of over-representing either tidal extreme, and by choosing the point with the lowest estimated error, we ensured that filtering did not compromise accuracy.

Relocations by group

We calculated relocation metrics including the number of relocations per individual, tracking duration (days) per individual, mean localization error, mean time between relocations, and mean straight-line distance between sequential relocations for groups and individual terrapins (see Table 1 and Supplemental Table 1). We then compared group characteristics using Wilcoxon rank sum tests or Student's *t*-tests as appropriate to evaluate the similarity of road group and creek group datasets.

Kernel density estimate generation

For terrapins with 10 or more triangulated points retained after filtering, we used the *adehabitatHR* package in R [37] to calculate kernel density estimate (KDE) contours illustrating the area used during the nesting season. We estimated both general use (95% KDE) and core use (50% KDE) areas for (i) all individuals aggregated, for data visualization and (ii) each individual, for analyses. Given that KDEs are not strongly influenced by grid size and placement [38], KDE presents an optimal method for understanding habitat use in our grid despite intermittent node failures. Moreover, because our relocations are estimated, a probabilistic approach to estimate seasonal habitat use is better suited to our dataset than an approach such as fitting a minimum convex polygon which generates range estimates with hard edges and is highly sensitive to relocation error. We used likelihood cross-validation (CVh) in the Animal Space Use [39] program to calculate a unique smoothing parameter (h) for each KDE, as individuals displayed considerable variation in both number and distribution of relocations and CVh provides intermediate values compared to other methods for selecting a smoothing factor [40]. We compared the areas of 95% and 50% KDEs by nesting group using generalized linear models with a Poisson distribution and log link function, and included the number of relocations per individual as a fixed factor in each model to control for the moderate difference in relocations between groups.

Habitat classification

After generating KDEs, we investigated habitat use by nesting female terrapins within the 435 m detection range of at least three nodes. To define available habitat for our study site, we generated 435 m buffers around each node location using the sf package in R [41]; then, we imported these polygons into ArcMap (v10.8.2; Environmental Systems Research Institute 2021), overlaid them using transparency, and traced the boundaries of the area contained by three or more polygons (Fig. 1B).

We classified habitat into seven categories: developed habitat, undeveloped upland, irregularly flooded marsh, regularly flooded marsh, salt pools, narrow tidal creeks, and wide tidal creeks. The developed habitat category included multiple roads, shell and gravel parking lots, and lawns. To generate this layer in ArcMap, we extracted sections of our study site that were identified as "Urban" in the 2015 New Jersey land use/land cover map (NJ Department of Environmental Protection Bureau of Geographic Information System 2020). We classified upland habitat to include a sand and shellgravel wildlife observation trail where terrapins frequently nest, and transitional habitat where salt marsh approaches roads and houses. Irregularly flooded marsh described higher elevation marsh platforms dominated by short form Spartina alterniflora which often surround salt pools or upland areas. In contrast, regularly flooded marsh comprised lower elevation areas dominated by tall form Spartina alterniflora which commonly border tidal creeks and frequently

Table 1 Sample size, tracking duration, and mean relocation metrics ± standard deviation by group for adult female diamondback terrapins (Malaclemys terrapin) fitted with PowerTag radio transmitters near a known nesting habitat in southern New Jersey

Diamondback terrapin summary statistics by group										
Group	n	Duration of tracking period (days)	Mean relocations	Mean error (m)	Mean time between relocations (hours)	Mean straight-line distance between relocations (m)	Mean general use area (ha)	Mean core use area (ha)		
Road	16	29.1±13.8	40.8±30.5	51.9±27.8	15.7±30.9	177.2±134.1	23.2±11.0	4.9±2.4		
Creek	22	30.9 ± 14.3	61.1 ± 40.4	50.7 ± 27.6	11.5±24.6	168.4±125.3	22.1 ± 7.6	4.5 ± 2.0		
Total	38	30.2±13.9	52.6±37.5	51.1±27.7	12.9±26.8	171.2±128.3	22.6±9.1	4.6±2.2		

Table includes data only for those turtles with 10 or more relocations after filtering to reduce error and limit spatial autocorrelation

host terrapin prey species such as fiddler crabs and mud snails (Ilyanassa obsoleta). Salt pools described shallow water ponds in the marsh which retain standing water across all seasons and tide cycles; narrow tidal creeks represented shallow tidal tributaries < 35 m wide; and wide tidal creeks represented wider, deeper channels. To classify these habitats, we used the near infrared band of the New Jersey 2019 4-band multispectral imagery dataset (National Agricultural Imagery Program; USDA-FSA-APFO Aerial Photography Field Office, 2020; raster cell size 0.60 m), validated by visible habitat boundaries and known landscape features. We divided the water layer into salt pools and wide and narrow tidal creeks by comparing against ESRI satellite imagery (Maxar 2022). We clipped the classified habitat polygons to the boundaries of the available habitat area in which it was possible to triangulate points.

Habitat selection during nesting season

We explored third order habitat selection [42] by a nesting population as well as by subsets of that population captured at opposite sides of the study site. To examine habitat use during the nesting season at a population level, we used generalized linear mixed models with a binomial distribution to compare available habitat to the 95% and 50% KDEs of 38 individual terrapins in our filtered dataset (JMP v16.1.0, SAS Institute Inc. 2020-2021). For each terrapin, we selected 2500 random points from within the available habitat area, identified habitat types at each point based on classified habitat polygon layers (Fig. 2A, D), and assigned each of these points a "Use" value of zero. We repeated these steps to generate random points within each terrapin's 95% and 50% KDE contours (Fig. 2B, E, C, F), and assigned these points a "Use" value of one. We determined the number of points



Fig. 2 Conversion of habitat classifications to random points for habitat selection analysis. Polygons represent **A** the functional node range where it was possible to triangulate locations, **B** the 95% kernel density estimate (KDE) contour (general use area), and **C** the 50% KDE contour (core use area) for 38 diamondback terrapins (*Malaclemys terrapin*). To simplify data visualization, the KDEs shown here were generated using all triangulated locations in the final dataset. Analyses were conducted using KDEs generated for each terrapin individually. To compare habitat availability versus habitat use, for each terrapin random points were generated **D** across the functional node range and classified as "Available", and within the **E** general use and **F** core use areas and classified as "Used". Each random point was assigned a habitat type based on its corresponding map location

generated within each KDE contour based on the proportion of the total available habitat area occupied by the KDE area, such that the number of "Used" points varied among individuals but the density of points remained constant. We then tested for evidence of habitat selection by comparing "Used" versus "Available" points across all habitat types and included 'individual' as a random effect to control for individual differences in KDE size and shape that may have derived from variation in number of relocations.

Comparison of habitat use by capture location

To determine the extent to which habitat use by terrapins corresponded to capture location, we examined the number of terrapins from the road group with 95% and 50% KDEs overlapping the creek-adjacent nesting area and vice-versa.

To ascertain whether there were differences in habitat use between road and creek groups, we compared Manly's selectivity measure [43] for each habitat type across all individuals in each group. We calculated habitat selectivity as the proportion of a terrapin's KDE contour occupied by a given habitat type divided by the proportion of the total available habitat area occupied by that habitat type. Manly's selectivity measure is equal to one when habitat type use is in exact proportion to availability; values less than one suggest avoidance, while values greater than one suggest preference [43]. We compared habitat selectivity separately at general and core use scales using generalized linear models with an exponential distribution. Models included group and habitat type as categorical variables, and an interaction term for habitat type and group.

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Results

Relocations by group

Of 60 nesting terrapins (30 per group) captured and fitted with transmitters, 38 terrapins (road group, n = 16; creek group, n=22; Table 1) met the criteria to be included in analyses, with 10 or more relocations in the filtered dataset. We obtained a total of 1,998 relocations for this sample over 60 possible tracking days. Individual terrapins had 11-154 relocations and were tracked for 3.4-59.6 days. The number of relocations per individual, mean localization error, and mean straight-line distance between sequential relocations did not differ significantly between groups (Z = -1.8, p = 0.08;Z = 0.8, p = 0.41; Z = 1.0, p = 0.29, respectively; Table 1). The mean time between sequential relocations was significantly smaller for terrapins in the creek group (Z=3.5, p<0.001), although the total duration for which individuals were tracked did not differ between groups ($t_{36} = 0.4$, p = 0.70; Table 1).

Within the total available habitat area (145.2 ha), the mean general use area occupied by individual terrapins was 22.6 ± 9.1 ha, and the mean core use area was 4.6 ± 2.2 ha. Comparisons of use area by group that controlled for the number of relocations per individual were significant (95% KDE: X^2_2 =16.6, p < 0.001; 50% KDE: X^2_2 =6.3, p=0.04), largely due to the effect of relocations (95% KDE: X^2 =16.1, p < 0.001; 50% KDE: X^2 =6.0, p=0.01) rather than group (95% KDE: p=0.69; 50% KDE: p=0.90; Table 1). Seventeen individuals (6 in road group, 11 in creek group) exhibited multimodal distributions at the core use scale (Fig. 3).



Fig. 3 Polygons show three representative diamondback terrapin (*Malaclemys terrapin*) core use areas with multimodal distributions where one activity center is located on narrow tidal creeks and another encompasses salt pools. Among *n* = 38 terrapins in our final dataset, 44.7% demonstrated multimodal core use areas, and 34.2% demonstrated core use areas overlapping narrow tidal creek and salt pool habitats as shown here

Habitat selection during nesting season

When controlling for individual effects, we found population-level differences in the habitats used versus availability at the 95% KDE ($F_{6, 100,000}$ = 67.4, p < 0.001) and the 50% KDE scale ($F_{6, 97,997}$ = 101.9, p < 0.001; Table 2). General use areas included salt pool and upland habitats significantly more than expected, and encompassed marsh and tidal creek habitats significantly less than expected based on availability. Developed habitat was used in proportion to availability. At the core use scale, upland, salt pool, and marsh habitats were used more than expected, developed and wide tidal creek habitats were used less than expected, and narrow tidal creek habitats were used in proportion to availability (Table 2).

Comparison of habitat use by nesting areas

Our investigation of habitat use indicated that most terrapins were detected over a wide portion of the available habitat, with 86.8% of all terrapins including both road-adjacent and creek-adjacent nesting habitat in their general use areas. Use of the creek group area was very common, with general use KDEs of every terrapin overlapping this region. Use of the road group area was also widespread (road group: 93.8%, creek group: 77.2%).

At the core use level, however, only 18.4% of terrapins coincided with the other group's nesting area, with only one creek group individual including road-adjacent nesting habitat. Four road group terrapins and one creek group terrapin exhibited core use KDEs coinciding with both road and creek nesting areas. Core use KDEs of 39.5% of terrapins did not overlap nesting areas associated with either group and instead centered on nearby salt pools, small tidal tributaries, and adjacent regularly flooded marsh.

At the general use level, we observed a significant difference in Manly's selectivity measure $(X_{13}^2=39.8,$

Table 2 Test results for population-level comparisons ofused versus available habitat types for diamondback terrapins(Malaclemys terrapin) fitted with PowerTag radio transmitters neara known nesting habitat in southern New Jersey

	95% KD	E	50% KD	E
	t Ratio	<i>p</i> -value	t Ratio	<i>p</i> -value
Developed	- 1.2	0.24	- 8.3	< 0.001
Upland	8.1	< 0.001	6.0	< 0.001
Irregularly flooded marsh	- 2.8	0.01	2.5	0.01
Regularly flooded marsh	- 3.7	< 0.001	3.4	< 0.001
Salt pool	10.8	< 0.001	17.0	< 0.001
Narrow tidal creek	- 4.6	< 0.001	1.2	0.23
Wide tidal creek	- 16.0	< 0.001	- 17.3	< 0.001

Results are presented for 95% and 50% KDEs

p < 0.001) with a significant interaction term between group and habitat type ($X_6^2 = 12.6$, p = 0.05) and a significant effect of habitat type ($X_6^2 = 29.3$, p < 0.001), but not group ($X^2 = 0.5$, p = 0.50). Road group terrapin general use areas contained significantly more developed habitat than those of creek group terrapins (p < 0.01; Figs. 4, 5A-B). Usage of marsh, tidal creek, salt pool, and upland habitats did not vary between groups (p > 0.10 for all).

For 50% KDEs, we also observed a significant difference in habitat selectivity ($X_{13}^2=232.7$, p < 0.001) with a significant interaction term ($X_6^2=60.1$, p < 0.001) and main effects (group: $X^2=8.4$, p < 0.01, habitat type: $X_6^2=190.9$, p < 0.001). Core use areas of the road group included more developed habitat (p < 0.001), and less narrow tidal creek and regularly flooded marsh habitat (p < 0.01 and p=0.05, respectively) than the creek group (Figs. 4, 5C, D). The groups did not differ significantly in usage of irregularly flooded marsh, salt pool, upland, or wide tidal creek habitats ($p \ge 0.10$ for all).

Discussion

While the dependency of terrapins on salt marshes is long-established [31, 44], this study explored use of distinct habitat features within marshes by female terrapins during the nesting season, offering new insights into terrapin habitat selectivity during this critical period. When we examined habitat selection at a population level, regularly and irregularly flooded marsh, upland areas, and salt pools functioned as core habitat for adult female terrapins between, during, and after nesting attempts. While marsh and upland habitats are understood to be vital for nest-seeking terrapins, use of salt pools has been relatively unexplored. Terrapins are frequently observed in salt pools close to nesting areas from June to August at our site, but such observations are much less common at other times of year, as has been noted elsewhere [45]. Therefore, while we detected disproportionately high use of salt pools by terrapins, due to the temporal and spatial constraints of our study these observations may not be applicable to locations farther from nesting habitat, or to periods outside of the nesting season. Continued telemetry work following the conclusion of this study, however, has revealed that a smaller number of terrapins linger in salt pool habitats into the fall.

Terrapins were not found to use tidal creeks more frequently than available. The relatively small extent of narrow tidal creek habitat within our node grid, as well as high localization error, likely limited our ability to accurately perceive use of these habitats. In addition, due to the attenuation of radio signals by salt water, we were only able to detect terrapins in aquatic habitats when they had surfaced or were basking on adjacent creek banks or pool edges, which likely decreased the number



Fig. 4 Manly selectivity ratios are shown for both general use areas (**A**) and core use areas (**B**). Boxplots represent mean selectivity, interquartile ranges, and outliers for diamondback terrapins (*Malaclemys terrapin*) captured in each nesting area. Asterisks indicate significant differences in habitat selectivity by group for a given habitat type. The gray horizontal line at one indicates a habitat type used in proportion to availability. Values greater than one suggest that a habitat type is used more than expected based on its availability; values less than one suggest that a habitat type is used less than expected



Fig. 5 General use areas (A, B) and core use areas (C, D) are shown for diamondback terrapins (*Malaclemys terrapin*) in the road group (A, C) and creek group (B, D). These KDEs were generated using the aggregated relocations of all individuals in each group in order to visualize differences in habitat selectivity between groups. Habitat selectivity analyses were conducted using KDEs generated for each individual terrapin in each group. Habitat types for which selectivity varied significantly by group are highlighted in color. For example, at the general use scale, developed habitat was selected significantly more by road group terrapins, so developed habitat is pictured in color in A and B. Habitat types that were selected equivalently across groups are shown in greyscale. While they were considered as part of developed habitat for all analyses, roads are visualized separately to illustrate the degree to which road crossings may have varied between terrapin nesting groups

of detections we received. Nevertheless, core use areas for 31 terrapins (81.6%) included narrow tidal creeks and adjacent regularly flooded marsh, and 13 terrapins displayed multimodal core use areas with one activity center located on a network of narrow tidal creeks and surrounding regularly flooded marsh and another in salt pool habitats (Fig. 3). This consistent result observed across multiple individuals underscores our conclusion that salt pools are highly used, and suggests that narrow tidal creeks and the immediately adjacent marsh are valuable habitat for female terrapins during the nesting season. Terrapin use of tidal creeks is supported by previous studies [31, 45, 46] as well as field observations of terrapins at our site. Shallow aquatic habitats found in close proximity to nesting areas may serve similar ecological roles, as they may host terrapin prey species such as crabs, mollusks, and small fish, provide opportunities for thermoregulation, and offer refuge from predation.

In addition to improving our understanding of selection of landscape features by terrapins during the nesting season, this study was designed to provide insight into whether habitat use patterns of the nesting population may result in differential risk from road mortality associated with developed areas. Although nesting and road crossing surveys conducted at the study site have identified that terrapins occasionally nest on roadsides throughout the study area, at the population level terrapins appeared to avoid developed habitats. This suggests that while some terrapins may nest in developed areas, forays into these habitats do not comprise the majority of habitat use during the nesting season. When we examined terrapin habitat selectivity by original capture location, however, we found that terrapins nesting near the road showed higher usage of developed habitats throughout the nesting season than creek group terrapins, particularly at the core use scale. Similarly, at the core use scale, the creek group was significantly more likely to spend time in narrow tidal creeks. These results support our hypothesis that individuals may more frequently use habitat features found near their nesting location, and by extension may experience different levels of road mortality risk.

Roads are a major threat to terrapin populations in several locations throughout their range, including our study site [21, 26]. Given the life history characteristics of terrapins, which include delayed maturity (6-8 years for females) and low offspring survival, additive mortality from vehicle strikes to females on roads is a significant conservation concern. Studies have predicted that even relatively low levels of road mortality (>3.1%) may lead to negative population growth and shifts in sex ratio in habitats proximate to highly trafficked roads [24, 26]. Although additional study is needed, our results suggest that survival rates of terrapins may not be uniform within a population using a given nesting habitat, even for individuals encountered < 1 km from each other. This difference in risk occurs over a relatively small spatial scale given that terrapin movements during the nesting season may exceed 2 km [14]. At locations where road mortality is a known threat to nesting females, such as our study site, terrapins that use different areas may be exposed to varying degrees of risk. We suggest that efforts to model survival rates or other population parameters consider terrapins that frequently use high-risk areas differently than individuals that habitually use less risk-prone habitats.

Our results may be useful in guiding the construction and enhancement of nesting areas for terrapins, a conservation approach that is becoming more widely used, particularly in the face of sea level rise and habitat destruction [26, 47, 48]. While nest site fidelity of female terrapins is well-established [14, 15, 28, 29], nesting habitat created through natural habitat migration, succession, or human intervention may be quickly adopted, with terrapins using it one year following construction [26, 47, 48]. Construction of alternative nesting areas in uplands close to salt pool habitats and farther from roadways and developed areas may be a significant tool for improving survival rates. When enhancing natural nesting areas, our results suggest enhancements should occur on undeveloped upland habitats in proximity to salt pools and incorporate mitigation fencing or culverts where appropriate to reduce any risk of road mortality.

While this study has improved our understanding of terrapin habitat selection during the nesting season and the threats posed by adjacent roadways, our methods were not without limitations. Our study design relied on a node grid with limited detection range and relatively high localization error, and because female terrapins may travel relatively long distances to nesting habitat [15, 29] we were unable to gain a complete understanding of their movements and total home range. Furthermore, when signals were not being received, we were unable to discern whether this was due to a terrapin leaving the range of our grid or being submerged. This uncertainty prevented us from fully quantifying terrapin movements or behavior in deeper aquatic habitats. Given that some terrapins were not recaptured in the study site after transmitter attachment, we were also unable to classify relocations as having occurred between nesting attempts or after the completion of nesting, and unable to identify exact paths taken to nesting areas. Additionally, several of our nodes failed during the course of the study due to damage to antennas and solar panels from birds. We recommend that researchers seeking to use this technology consider wildlife impacts and routine maintenance of receiver nodes in project planning. Advances in technology are gradually making cellular and satellite telemetry more useful for tracking terrapins, and although both face limitations in aquatic systems, we recommend the use of these techniques instead for studies where wildlife damage is a concern and high precision and long range are required.

Despite its limitations, the novel radio telemetry method trialed in this study may be valuable for investigating movements, habitat use, and nest site selection for a variety of species. This method may be particularly well-suited for small-bodied species with relatively limited home range or territory sizes, or species whose behavior makes them difficult to track using traditional methods, especially those that live in sensitive or remote ecosystems. Radio transmitters are typically smaller, lighter, and more cost-effective than GPS transmitters; however, limited field access or personnel may make manual relocations infeasible or restrict sample sizes. Using a grid of receiver nodes provides a short-range, low effort alternative to GPS tracking. This technology may be most effective in predominantly open landscapes where receivers experience high solar exposure and little interference, such as meadows, deserts, river systems, and freshwater wetlands. Thus far, this method has been tested in salt marsh and urban ecosystems, and has been applied to diamondback terrapins, brown tree snakes (*Boiga irregularis*), and Micronesian starlings (*Aplonis opaca*) (this study, [35]). Our study is among the first completed using this technology, and demonstrates its applicability for examining habitat selection in a wetland environment.

Conclusions

Our results suggest that terrapins preferentially use shallow water habitats such as salt pools and narrow tidal creeks during the nesting season, providing important context for restoration of nesting areas and surrounding marsh. Moreover, this work illustrates that even within one nesting population, individuals may experience differences in mortality risk from localized threats, which may be a critical consideration when estimating survival rate and demographic trends. By using a novel application of an automated radio telemetry system to investigate habitat use of a small-bodied animal in a sensitive marsh environment, we present a foundation for future work applying this method to other species and ecosystems. This study provides a step toward examining diamondback terrapin habitat use in greater detail and will contribute to more informed conservation planning in the face of ongoing population stressors.

Supplementary Information

The online version contains supplementary material available at https://doi. org/10.1186/s40317-024-00391-0.

Supplementary Material 1. Table S1. Relocation summary statistics for final filtered dataset of telemetered diamondback terrapins (*Malaclemys terrapin*) in southern New Jersey.

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Author contributions

BW and AL contributed equally to this work. LMF and BW conceptualized the study. All authors participated in study design, methodology development, field work, data analysis and interpretation. AL led script development and data visualization. BW and AL led writing of the original draft. All authors contributed to review and editing of the manuscript and gave approval to the final manuscript.

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Availability of data and materials

The datasets generated and analyzed during the current study are not publicly available due to sensitivity of diamondback terrapins. Scripts and generated locations are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

The study was conducted under Scientific Collecting Permit #2021093 granted by the State of New Jersey Department of Environmental Protection Division of Fish and Wildlife.

Competing interests

The authors declare no competing interests.

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