Homing Behavior in Response to Displacement and Orientation of the Northern Diamondback Terrapin (Malaclemys terrapin terrapin) in Barnegat Bay, New Jersey

Nicole M. Lainhart
State University of New York Buffalo State, woodnm01@gmail.com

Advisor
Edward Standora, Ph.D., Professor of Biology

First Reader
Harold Avery, Ph.D., Adjunct Faculty of Biology

Second Reader
Christopher Pennuto, Ph.D., Professor of Biology

Third Reader
Daniel Potts, Ph.D., Associate Professor of Biology

Department Chair
Gregory Wadsworth, Ph.D., Associate Professor of Biology

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Homing Behavior in Response to Displacement and Orientation of the Northern Diamondback Terrapin (*Malaclemys terrapin terrapin*) in Barnegat Bay, New Jersey

Increasing urbanization of the Barnegat Bay estuary in New Jersey has subjected northern diamondback terrapins to substantial habitat loss. Understanding whether terrapins have homing behavior, and determining the types of orientation cues they use to aid in this behavior, is important for conservation management. To test their homing behavior, nine non-gravid female terrapins were outfitted with biotelemetry tracking devices and data loggers and were displaced 4 km north and/or south. Eight of nine terrapins successfully returned home; the one terrapin that did not return home was inadvertently captured in a crab pot. Urbanization and shoreline development of the north displacement location may be causing terrapins to make quicker movements home compared to the ‘natural’ south displacement location. A terrestrial arena that blocked terrapins from perceiving visual landmarks was used to test orientation in both male and female terrapins that had been captured to the south or east of the testing site. Only male terrapins captured from the east exhibited apparent homeward orientation, suggesting that terrapins orient toward water rather than home. Terrapins from the south tested under overcast skies and during the afternoon, and females captured from the south, tested separately, had easterly orientation, suggesting there was orientation toward open water as well within these groups. While displaced terrapins were able to return home, terrapins tested in the arena appeared to orient toward water, suggesting that the orientation cues used in homing may not be available to the terrapins on land, within the arena. Understanding both homing behavior and orientation will give managers insight into how terrapin home ranges might be protected. Since terrapins are able to return home after displacement, protection measures will be needed for all potential home ranges of the terrapins and relocation efforts may require the displacement of terrapins to more distant areas.
State University of New York
College at Buffalo
Department of Biology

Homing Behavior in Response to Displacement and Orientation of the Northern Diamondback Terrapin (Malaclemys terrapin terrapin) in Barnegat Bay, New Jersey

A Thesis in
Biology

by
Nicole M. Lainhart

Submitted in Partial Fulfillment
of the Requirements
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Approved by:

Ed Standora, Ph.D.
Professor of Biology
Chairperson of the Committee/Thesis Adviser

Gregory J. Wadsworth, Ph.D.
Chair and Associate Professor of Biology

Kevin J. Railey, Ph.D.
Associate Provost and Dean of the Graduate School
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Chapter 1

Homing Behavior of the Diamondback Terrapin (*Malaclemys terrapin*) in Response to Displacement
Introduction

Homing behavior enables animals to return to their home range if displaced. This behavior has been observed in a wide range of vertebrates including red-backed salamanders (*Plethodon cinereus*, Kleeberger and Werner 1982), northern elephant seals (*Mirounga angustirostris*, Oliver et al. 1998), lemon sharks (*Negaprion brevirostris*, Edrén and Gruber 2005) and sleepy lizards (*Tiliqua rugos*, Freake 2001). Additionally, multiple turtle and tortoise species are able to return home after both short and long displacement distances, indicating homing behavior in these species. Some turtle and tortoise species with homing behavior include Eastern box turtles (*Terrapene carolina*, Gould 1957, 1959), red-eared slider turtles (*Trachemys scripta elegans*, Tucker and Lamer 2008), painted turtles (*Chrysemys picta marginata*, Gould 1959) and Hermann’s tortoises (*Testudo hermanni*, Chelazzi and Francisci 1979), to name a few.

Among the many species of turtles demonstrating homing behavior, studies suggest this ability may be dependent on life history characteristics (i.e., age or sex) or such factors as displacement distance and topography (Hinderle 2011). There seems to be a displacement threshold, a certain distance from home, where a turtle is unable to navigate back to familiar territory (Hinderle 2011). Topographic landmarks may be used as visual cues during homing by some organisms such as neotropical bats (*Phyllostomus hastatus*, Williams et al. 1966), bumblebees (*Bombus terrestris*, Goulson and Stout 2001) and homing pigeons (*Columba livia domestica*, Lipp et al. 2004). In such cases, homing ability is related to the ability to navigate from one topographic landmark to another (Caldwell and Nams 2006). Recognition of topographic landmarks is also important in
homing and has been observed in loggerhead turtles \textit{(Caretta caretta, Standora et al. 1995)}, green turtles \textit{(Chelonia mydas, Luschi et al. 1996)} and painted turtles \textit{(Williams 1952, Emlen 1969)}.

Habitat alteration has been a major result of increased urbanization, threatening many turtle species. Chicken turtles \textit{(Deirochelys reticularia)} experience increased highway mortality due to significant habitat loss from development within their home range \textit{(Buhlmann 1995)}. Animal translocation has been an important strategy in conserving animals inhabiting degraded habitats \textit{(Buchholz 2007, Caro 2007)} and helping them to create new home ranges and populations \textit{(Dodd and Seigel 1991)}. Translocation is a common conservation technique where researchers move animals from a threatened area to one less prone to alteration \textit{(Tuberville et al. 2005)}. Translocated California ground squirrels \textit{(Spermophilus beecheyi)} established new home ranges within 18 days \textit{(Van Vuren et al. 1997)} and translocation of gopher tortoises \textit{(Gopherus polyphemus)} successfully resulted in the creation of new populations \textit{(Tuberville et al. 2005)}. However, translocation has had mixed success as a conservation technique with reptiles and amphibians. Out of 91 reptile and amphibian translocations, homing behavior was one of the leading causes of translocation failure \textit{(Germano and Bishop 2009)}. Additional factors that potentially affect translocation success of turtles include disruption of social structure between populations \textit{(Dodd and Seigel 1991)}, stress \textit{(Field et al. 2007, Tuberville et al. 2008, Dickens et al. 2010)} and natal site philopatry \textit{(Cagle 1944, Doroff and Keith 1990, Smar and Chambers 2005, Bernstein et al. 2007, and Newton and Herman 2009)}. Although little research has been conducted on the
translocation of reptiles, this conservation strategy may prove to be an increasingly important factor in the conservation of many threatened turtles (Turtle Conservation Fund 2002, Tuberville et al. 2005).

Rapid urbanization along the Mid-Atlantic coast of the United States has resulted in alteration of salt marsh ecosystems. These ecosystems serve as critical habitats for many species of animals including northern diamondback terrapins (*Malaclemys terrapin terrapin*), the only North American estuarine turtle. Like many turtles, the diamondback terrapin, which ranges from Cape Cod, Massachusetts to Corpus Christi, Texas (Ernst et al. 1994, Brennessel 2006, Hart and Lee 2006), is vulnerable to anthropogenic disturbances (Bishop 1983, Gibbons et al. 2001, Javioff 2007). There are many anthropogenic factors that have the potential to disrupt terrapins’ abilities to navigate within their home range, including near-shore crabbing (Roosenburg et al. 1999), bulkheading (Winters et al. 2009), road mortality (Wood and Herlands 1997), and boat traffic (Harrison 2011, Lester 2012). Due to the negative effects of increased urbanization, the northern diamondback terrapin has been listed as a species of special concern in New Jersey (Hart and Lee 2006). Throughout the terrapin’s range, each state differs in their regulatory status of the terrapin. For example, Delaware, North Carolina, Georgia, Alabama, Mississippi, and Louisiana also list the terrapin as a species of special concern. Other states throughout its range list this species as threatened (MA), endangered (RI), state regulated (CT) or apparently secure (MD and VA) (Watters 2004).

The purpose of this study is to determine whether terrapins display homing behavior when displaced from their home range. Diamondback terrapins have nest site
fidelity (Roosenburg 1991, Gibbons et al. 2001, Szerlag-Egger and McRobert 2007, Sheridan 2010), returning to the site where they hatched. However, the capabilities and mechanisms of homing have not been studied in diamondback terrapins. With a seven to nine year maturation period and low fecundity, protection of the adult female population is imperative for this species (Bishop 1983). When habitats are no longer available or become significantly altered, terrapin behavior may change. Quantifying long distance movements may provide valuable information about the preferred habitat of the terrapin. Observing terrapin homing behavior could help identify home ranges, potentially leading to protection of critical habitat. Population viability also may change in response to estuarine habitat destruction. I determined whether diamondback terrapins exhibited homing behavior after being displaced from their home range in two different directions and identified possible variables influencing this behavior.

**Methods**

*Diamondback terrapins as a model*

While homing behavior of various freshwater, terrestrial and sea turtle species has been studied, the behavior of estuarine turtles has not yet been researched. The diamondback terrapin’s wide geographic distribution, long lifespan, and high site fidelity make for a model for other studying homing behavior in estuarine ecosystems. Adult females were selected because they are larger than males and thus are better able to carry a transmitter. Additionally, female terrapins tend to leave the water less frequently and are less likely to become entangled in crab pots compared to males (Walters 2008). Female terrapins may travel greater distances than males (Hart and Lee 2006), resulting
in longer displacement distances. Furthermore, females are more important from the standpoint of population viability, as indicated by Bishop (1983). To prevent confounding of homing behavior by nest site fidelity and other reproductive behaviors, non-gravid female terrapins were used.

Study site

Barnegat Bay, New Jersey USA (39.8517°N, 74.1141°W) is an estuary that extends 68 km from Point Pleasant to Little Egg Inlet (Dowhan 2010) and contains an arrangement of barrier beaches that serve as protection from the open ocean (Barnegat Bay National Estuary Program 2010). Barnegat Bay was chosen as a study site due to its high amount of urbanization over the years. For example, a total of 777 hectares of land were altered to urban areas between 1995 and 2006 (Lathrop and Haag 2007), indicating this area would be a good place to study the effects of urbanization on homing. More than 70% of the Barnegat Bay shoreline is altered, with the Edwin B. Forsythe National Wildlife Refuge being a part of the 29% of ‘natural’ land left (Lathrop and Haag 2007). Island Beach State Park is a narrow barrier beach that divides Barnegat Bay from the ocean. The bay has an average depth of 1.5 m, consisting mainly of saltmarsh habitats. The deepest water is usually found in dredged boat channels. Summer water temperatures have been recorded as high as 28°C (Dowhan 2010). Within Barnegat Bay, there were sites of interest: Osprey Cove and Sloop Sedge (Figure 1.1). Both of these sites yielded high terrapin capture rates and had been trapping locations for previous studies, indicating terrapins are continually using these sites year after year. Therefore, these locations were deemed the ‘home’ locations for terrapins in this study.
Capture and release sites

The capture sites (also referred to as the home locations for this study) were Osprey Cove and Sloop Sedge. Both of the home locations were chosen based on the high density of captured terrapins. Based on preliminary data from Walters (2008), more terrapins were captured in Osprey Cove than any other trapping location in the bay. Hoop traps and fyke nets were used to capture terrapins and were checked daily during the summer of 2010 and 2011. Traps were baited with Atlantic menhaden (*Brevoortia tyrannus*) to attract blue crabs, which then attracted terrapins. A float was placed inside each trap to maintain an air pocket to prevent accidental drowning. Hoop traps ranged from 0.6 m to 0.8 m in diameter with a 3.8 cm mesh size. Fyke traps were 0.9 m high and 1 m wide with leaders ranging from 3.0 m to 6.1 m with a 1.27 cm mesh size. Hoop traps and fyke nets were set in Osprey Cove and hoop nets were set at Sloop Sedge (Figure 1.1). In relation to the home locations, each displacement location was half way between the mainland and Long Beach Island. There were two release locations: 4 km north and 4 km south of the home locations (Figure 1.2). Once each terrapin was tracked back home, recapture was not attempted until at least the next day or two for verification that this was the home location rather than an area travelled through while swimming.

Terrapin Processing

Morphologic measurements were taken of each captured terrapin. Carapace length and width and plastron length and width were measured to the nearest millimeter using calipers. The number of scutes and any shell/body abnormalities and injuries were documented as well. Body mass was measured to the nearest gram using a digital scale.
Scute identification codes were recorded for previously captured and marked terrapins, and scute identification codes were assigned to new captures. Unique identification was assigned by filing v-shaped notches into the marginal scutes (Gibbons 1968). Sex was determined by examining the width of the tail (Brennessel 2006), where the tails of females are more narrow and the cloaca positioned more proximally than in males. Females over 550 g had passive integrated transponders (PIT) tags injected under the skin in the hindlimbs for identification. Female reproductive status was evaluated by hand palpitation through the inguinal wall (Ewert and Legler 1978, The North American Veterinary Conference 2006) and further verified through X-ray radiography. After processing was completed, terrapins were typically held for 24 hours before being returned to their capture site.

**Biotelemetry**

Terrapins (n=9) were tracked using both radio and sonic telemetry. A sonic transmitter (Figure 1.3, Sonotronics, IBT-96-5) was attached to the marginal scutes directly behind the hind limbs, where 2.8 mm holes were drilled into the scutes with a Dremel tool for secure attachment with 0.45 mm diameter nylon fishing line. Ends of the line were looped and attached using 0.65 mm crimping sleeves. Monofilament nylon line was passed through a hole on either side of the transmitter for attachment. The sonic transmitter was tuned to 40 KHz to be detected by a sonic receiver (Dukane underwater acoustic location receiver #N15A235B). The sonic transmitter, 36 x 13 mm, weighed 3.2 g in air, and had a battery life of five months. The radio transmitter (Figure 1.3, Sirtrack, J20147) was adhered to the carapace with PC-7 epoxy while the rest of the
instrumentation was attached using monofilament nylon fishing line and crimping sleeves. Epoxy was shaped to the leading edge of the transmitter to decrease the amount of hydrodynamic resistance and present a more streamlined profile. About halfway through the study, syntactic foam (Emerson and Cuming, Inc.) was placed under the radio transmitter to increase the overall height of the transmitter on the carapace. This allowed for a stronger radio signal when the terrapin was near the surface and decreased the in water weight of the transmitter due to the buoyancy of the foam. The radio transmitter was tuned to 164 MHz, weighed 20 g in air, and had a flexible antenna (~200mm). The signal from the radio transmitter was detected using a two-element yagi antenna for short distances (0.8 km) and a six-element yagi antenna for long distances (2.8 km). Both the two and six-element antennas were attached to a radio receiver (Communication Specialists, R1000).

Terrapin diving behavior was recorded using a temperature and depth recorder (Figure 1.3, TDR, StarOddi, DST milli-L) that was also attached to the posterior half of the vertebral scute of the carapace, using the same method as the attachment of the sonic transmitter (one side of the TDR was attached with a 6.4 mm miniature nylon cable tie and the other side with monofilament line). The dimensions of the data logger were 12.5 mm diameter x 38.4 mm long. The data logger had a mass of 9.2 g in air and 5.0 g in water with a temperature precision of ± 0.1°C. The data logger had a maximum pressure range equal to 20 m water depth with ± 0.8% full-scale accuracy, corresponding to 16 cm. The sampling frequency was set for every 30 seconds, which allowed the data logger to last almost 15 days, storing up to 43,000 data points. All terrapins were held stationary
at the surface of the water for one minute to establish baseline values for calibration of
the TDR prior to release. Each data logger was calibrated prior to each terrapin release
because they were highly sensitive to air pressure changes associated with current
weather conditions.

Terrapin movements were recorded using a GPS data logger (Figure 1.3, i-gotU,
GT-120) to determine the location and time when each turtle surfaced. The dimensions
of the GPS data logger were 44.5 x 28.5 x 13 mm with a weight of 20 g. Each GPS data
logger was waterproofed before attachment to terrapins since its intended purpose was to
provide locations for hikers and runners and therefore was not waterproof.
Waterproofing trials were performed to determine the correct materials necessary to
prevent leakage when submerged underwater. The GPS was first placed into two latex
condoms. Parafilm was then wrapped around the GPS twice in opposite directions to
overlap the seals and a hairdryer was used to melt the parafilm slightly. Electrical tape
was wrapped around the edges of the GPS data logger where fishing leaders were
attached to two miniature nylon cable ties, to prevent abrasion to the parafilm. Six coats
of Plasti-dip were applied to the GPS for waterproofing. The GPS data logger and the
radio transmitter were spray-painted fluorescent orange for easier visualization when the
terrapin surfaced. Since the point locations recorded by the GPS data logger were not
taken continuously, these points were essentially waypoints. These waypoints allowed
the path taken home by each terrapin to be determined. The GPS data logger had a
sampling frequency of two, two-hour intervals daily. Within each two-hour interval, the
GPS data logger determined waypoints every 60 seconds when the animal was at the
surface. With this sampling frequency, the battery life was approximately 20 days. According to Harrison (2010), terrapins tended to surface the most from 10:00-12:00. Therefore, 10:00-12:00 was set as the first sampling interval, with a six-hour gap between sampling intervals, and 18:00-20:00 as the second interval. The six-hour gap in sampling intervals was necessary to maximize the amount of data obtained when terrapins surfaced most frequently. Also, biotelemetry was conducted mainly during the six-hour gap providing data when the GPS data logger was inactive. About halfway through the study (28 July 2010), the sampling interval was changed due to malfunctions in the GPS data logger. Terrapins used during the latter portion of the study had a continuous sampling interval from 10:00-14:00, with waypoints taken every 60 seconds.

Finally, a 7 cm long fluorescent orange pencil float was attached to 2 m of fishing line to the posterior end of the carapace, allowing for high visibility while the terrapin was submerged as most locations in the bay were less than 2 m deep. The mass of all instrumentation attached to each terrapin did not exceed five percent of the animal’s body weight, to prevent interference with terrapin behavior. All instruments were attached to minimize the risk of entanglement with vegetation and other obstructions, and to not interfere with locomotion or other normal activities. All of these precautions were taken following the guidelines of The American Society of Ichthyologists and Herpetologists (Beaupre et al. 2004). Research was conducted under permits by New Jersey Department of Environmental Protection, Division of Fish and Wildlife and Edwin B. Forsythe National Wildlife Refuge. All research protocols (Protocol No. 18296) were approved by Drexel University’s Institutional Animal Care and Use Committee. Outfitted terrapins
were recaptured at the end of each trial to remove all instrumentation. The sonic transmitter, GPS data logger, and the temperature and depth data logger were removed by cutting all the ties with wire cutters. The radio transmitter was removed by prying under the epoxy to detach it from the carapace.

A submersible underwater receiver (SUR, Figure 1.4, Sonotronics, SUR-1) was placed at the capture site to determine if and when terrapins returned home. A SUR was placed in Osprey Cove and at Sloop Sedge. A range test indicated a sonic detection radius of approximately 60 m in both capture locations. The date and time of the terrapin arriving within the radius of the SUR was automatically recorded to indicate when an individual terrapin returned home. The SUR was mounted to a PVC pipe, which was placed on the outside of another PVC pipe. This sliding sleeve design allowed the SUR to be completely submerged and yet easily retrieved for data collection (Figure 1.4). An ID tag and a float were attached to the SUR to ensure visibility and identification if lost. Data were downloaded daily using SurSoft software (Sonotronics, v 3.3.5). The SUR data were downloaded daily to determine if a terrapins was recently in the area. After SUR data were downloaded, daily telemetric tracking commenced.
Figure 1.1. Map of the two capture locations: A. Osprey Cove, B. Sloop Sedge (http://maps.google.com). Hoop traps and fyke nets were set at both of these locations to capture non-gravid females for the displacement study.
Figure 1.2. Barnegat Bay home and displacement locations. A. 4 km north displacement location; B. Osprey Cove home location; C. Sloop Sedge home location; D. 4 km south displacement location. * indicates the point from where the displacement locations were measured, + indicates the location of the SUR, submersible underwater receiver (http://maps.google.com).
Figure 1.3. Terrapin outfitted with: A. GPS data logger, B. radio transmitter, C. sonic transmitter, D. temperature and depth data logger, and orange float (not in photograph) secured by monofilament nylon fishing line. Photo credit A. Dominy.
Figure 1.4. Submerged underwater receiver used to determine whether terrapins returned home by detecting signals from the sonic transmitter. Photograph depicts the downloading of data to a laptop computer. Photo credit E.A Standora.
**Terrapin release procedure**

Optimal tuning frequency of the radio transmitter was determined by holding the terrapin with the attached transmitter at the surface of the water. The signal of the transmitter is heard differently in air than in water, so it was imperative to tune the transmitter to the correct frequency while the terrapin was at the surface of the water. The sonic transmitter was turned on and the pulse rate and frequency were confirmed prior to release. The depth data logger was calibrated immediately prior to release and GPS coordinates of the release location were recorded with a handheld GPS receiver (Magellan, Explorist 400, accuracy up to 3-5 m).

Each terrapin was released at approximately the same location when displaced north and south. Immediately after the release, the initial heading of the terrapin was recorded along with a new waypoint since wind and wave action typically caused the boat to move from the initial location. The initial heading was used to assess their identification of home when released in unfamiliar territory. Directional headings were also taken at five minutes, thirty minutes, and one hour after release using a handheld compass to determine if there was a homeward heading. There were some instances where a terrapin was not sighted at one of these times to record a directional heading. Every telemetric reading and visual sighting was recorded with the time and a new waypoint.
**Terrapin recapture procedure**

Terrapin recapture included the use of both radio and sonic telemetry. Once a terrapin was within range of the sonic receiver, visually locating the terrapin was usually possible because of the high visibility float. GPS coordinates and time were recorded at the recapture site. Once the turtle was recaptured, the TDR and GPS data were downloaded.

**Experimental design**

All captured terrapins (n=5 from the north, n=4 from the south) were displaced 4 km in one direction, either north or south. After recapture, terrapins were displaced in the opposite direction of their previous displacement. Displacement in opposite directions was used to test whether terrapins continuously displayed homing behavior. Comparing the time to return home between the north and south displacement locations assessed potential anthropogenic disturbances. The north location was considered more disturbed (i.e., more boat activity, crabbing, bulkheading and no inlets or coves) and the south location was considered less disturbed and more natural (i.e., mostly inlets and coves with little boating activity). GPS locations along with radio and sonic telemetry data were used to map terrapin movements. Maps for each terrapin indicated the paths taken and areas travelled during homing. Perpendicular distance from shore and depth data from the temperature and depth data logger assessed whether terrapins used the shoreline as a landmark to locate home.
The amount of time spent at the surface and the number of surfacings were calculated to determine if terrapins use landmarks to locate home. More time spent at the surface rather than below the surface might indicate terrapins may be using terrestrial landmarks or other topographic features to locate home. If true, the amount of time spent at the surface and the number of surfacings should be greater the further each terrapin was from home. The TDR was used to assess whether terrapins engaged in basking behavior or other behaviors moving between water and land. Depth data from the TDR would determine if the terrapin was out of the water or at the surface for a prolonged period of time. More time spent at the surface would be indicative of a terrapin was using landmarks (although this was not directly tested). Other factors that may entice terrapins to swim at the surface were not tested (i.e., bottom structure and current). However, terrapins were found to have little response to boat traffic, so minimal anthropogenic noise affected their behavior (Harrison 2010). The nearest available weather station with daily air temperatures was in Toms River, which is approximately 20 km from the study site (www.wunderground.com). Air temperature data from this website are managed by NOAA. The combination of water and air temperatures, along with locational data from the GPS data logger, provided terrapin behavioral information throughout their home journey.

_Determination of homing behavior_

Terrapins were tracked using both radio and sonic telemetry throughout the day to obtain the maximum amount of data as possible to monitor their spatial movements. The GPS data logger was also recording data at the same time as tracking, providing more
precise locational data for every time the terrapin surfaced. Telemetry data were collected every day until recapture.

*Topographic features as indicators of home*

Surfacing data for each terrapin were recorded by the TDR. Surface was defined as a depth of half the body length of each terrapin below the actual water surface. When a terrapin was below this depth, it was considered to be submerged. The number of times terrapins came to the surface and the surface duration were evaluated as each terrapin swam closer to home. If terrapins spent more time submerged than at the surface, it was assumed that they were familiar with the surrounding territory and did not need to surface to identify landmarks associated with home, suggesting that terrapins are able to home visually. Perpendicular distance to shore was also related to the use of landmarks for navigation, specifically the shoreline. If the terrapin spent more time close to shore than away from shore, it was assumed that the terrapin relied more on the use of landmarks to identify home. Again, telemetric readings and GPS locational data were used to compare each perpendicular distance from shore.

*Temperature selectivity*

Water temperature at the location of each terrapin was recorded by the TDR attached to the shell (±0.1°C accuracy), allowing for continuous record of daily temperatures. Water temperatures were measured with i-buttons (HOBOware UA-002-64) in a vented PVC tube at the subsurface (0.1 m) and submerged to the bottom (0.5 m) of Osprey Cove by a floating environmental monitoring station (Figure 1.5). For this
study, bay water temperature was considered water temperatures measured by i-buttons
and terrapin water temperature was considered water temperatures recorded by the TDR.

Statistical analysis of data

All statistical analyses for this study were completed using the SAS statistical
software package (SAS Institute, Inc., version 9.2). Geographic information systems
(ESRI 2008) software was used to map a path for each terrapin that successfully returned
home. These maps allowed for movement comparisons between north and south
displaced terrapins. Time to return home was compared between north and south
displaced terrapins using a t-test to determine from which direction they returned faster.
Circular statistics were used to determine if terrapins were able to identify their
homeward direction after five minutes, thirty minutes, and one hour after release
(Visscher 2003). Orientation of juvenile loggerhead sea turtles was studied in an outdoor
arena by determining a directional heading after ten minutes (Avens and Lohmann 2003).
Initial orientation after release was of particular interest, so a five-minute time period was
justified. Since terrapins were released into open water, tracking at thirty minutes and
one hour after release, rather than at ten-minute intervals, was justified. A weighted
average, or the average of all trap locations, was used for both north and south
displacement locations as indicated as the reference angle on each circular diagram. The
reference angle was referred to as the target home angle since home was defined as the
location of capture for each terrapin. The mean vector bearing (MVB) indicated the
mean chosen directional angle for all terrapins displaced north and south for each test
Figure 1.5. Floating environmental monitoring station. A. i-button temperature data logger mounted at subsurface, B. i-button at the bottom of the water column (not in photo). Photo credit E. A. Standora.
The r-value determined how clustered the data were, where a value of 0 indicated the data were not clustered and a value of 1 indicated that all the data were clustered with the same directional bearing.

The mean number of surfacings and the surface duration were calculated to determine whether terrapins spent more time at the surface and surfaced more often during their travels after displacement. Depth data were divided into six time of day categories, four hours per category with three categories in the AM and three in the PM. These time categories allowed for characterization of trends in surface duration or the number of times the terrapins came to the surface throughout the day. Five terrapins were used in this analysis, where one terrapin had data for both north and south displacements (KNOQW). For mean number of surfacings, surface duration, mean depth and surfacings per each third of trip, one terrapin (HIJPW N) was not included in the analysis due to recording problems of the TDR. Mean depth was compared for all terrapins displaced north and south for all six time of day categories. A GIS shapefile with depth soundings of Barnegat Bay (NOAA 2001) was used to determine the depth of the bay compared to the depth of each monitored terrapin in the water. Each location data point from the terrapin was paired with the nearest depth sounding from the shapefile. The depth sounding data and depth data from the TDR allowed for determination of the terrapin’s depth for a specific time of day. Number of surfacings and surface duration were also compared for the first, second, and last third of their homeward trip. North and south-displaced terrapins were combined to determine if there was a difference in the number of surfacings as they approached home using an ANOVA
(t-test determined there was no difference in surfacings between north and south terrapins, so combining them for this test were justified). For surface duration, north and south terrapins were compared to determine if there were differences between each third as each group approached home using an ANOVA and Tukey test (north and south terrapins could not be combined because there were differences between them using a t-test). Shallow water was defined as 1 m or less.

Cumulative depth frequency diagrams were made to determine what water depths terrapins prefer during their home journey, where probability (P) was plotted against depth. For example, if a depth of 1 m corresponded to a probability of 0.85 that would indicate that the terrapin spent 85% of its time at a depth of 1 m or less from the surface during its trip.

The perpendicular distance of each terrapin from the nearest landmass was determined using Arc Map through GIS. Perpendicular distance data were measured during each third of the terrapin’s trip home to determine if there were any differences in the use of the shoreline as the terrapin moved closer to home.

Temperature profiles were constructed to visualize the temperatures terrapins experienced while making long distance movements back home. Water temperature at the turtle recorded by the TDR, bay water temperature recorded by the water monitoring station, and air temperature recorded by NOAA were all graphed versus date/time to create the temperature profile. Spikes in the temperatures recorded by the TDR on the terrapin were used for determination of basking behavior. These increases in TDR
temperatures were associated with turtle depth, also recorded by the TDR, to ensure accuracy of basking event determination.

**Results**

All eight terrapins returned to their home range within 23.5 to 213.5 hours after displacement of four kilometers (Table 1.1, Figure 1.6, Appendix 1.1A-H), except for one terrapin that was inadvertently captured in a crab trap (only used in initial heading data analysis). Maps of each terrapin’s home journey confirmed their homing behavior. Each map was used to visually validate that a terrapin returned home by evaluating their behavioral movements in relation to their displacement location and home range (Figure 1.6, Appendix 1.1A-H). Terrapins that returned home (Sloop Sedge or Osprey Cove) were intentionally not recaptured for at least one day to determine if they remained home, where movements indicated this was the case for most terrapins. Random movements rather than directed movements were seen on the maps, visually indicating that terrapins may not know the precise location of home (Appendix 1.1A, C, D, E, and G). In some instances, terrapins were not recaptured for up to three days of being within their home range (Appendix 1.1C, D).

Four terrapins displaced from the north remained offshore of Conklin Beach for more than one day (Figure 1.6, and Appendix 1.1A, E, G), where this beach was considered to be a part of their home location. Two terrapins displaced from the north swam toward the shore immediately after release and continued to swim closer to shore as home was reached (<700m for first third and <100m for middle and last third of trip,
Figure 1.6 and Appendix 1.7A) while two other terrapins displaced from the north swam in open water (>700 m) until they reached within 400 m of the shoreline (Appendix 1.1E, G). Terrapins displaced to the south spent more time travelling (t-test, mean north=64.6 hours, mean south=168.5 hours, p=0.03), utilizing the nearby coves and/or inlets of the surrounding area (Appendix 1.1F, G).

Terrapins were not able to identify home based on directional headings after initial release. There were no significant homeward directional headings for north or south displaced terrapins after five minutes (Figure 1.7, north and south p>0.05), thirty minutes (Figure 1.8, north p>0.05, south p>0.2) and one hour after release (Figure 1.9, north and south p>0.5).

The number of times terrapins came to the surface was significantly different among the time of day categories (repeated measures ANOVA, F_{5,143}=9.85, p<0.0001, Figure 1.10), where AM late, PM early, and PM middle had a higher number of surfacings compared to the other time categories (Tukey-Kramer adjusted p<0.05). The surface duration did not significantly differ among terrapins throughout the day (repeated measures ANOVA, F_{5,3165}=1.90, p=0.09, Figure 1.11). There was no significant difference in the number of surfacings between the first, second, and last third of the home journey of all north and south-displaced (ANOVA, F_{2,15}=1.68, p=0.22, Appendix 1.2). North-displaced terrapins had no significant difference in surface duration for each third of their home trip (repeated measures ANOVA, F_{2,1587} = 0.07, p=0.932, Figure 1.12). South-displaced terrapins spent most of their time at the surface per surfacing
during the second third of their home journey (repeated measures ANOVA,
F=2.1578=5.99, p=0.0026, Tukey-Kramer adjusted p<0.05, Figure 1.12).

There were significant differences between all six time of day categories for mean
depth in the water column (ANOVA, F5,72000=524.68, p<0.0001, Tukey-Kramer adjusted
p<0.05, Figure 1.13), where terrapins utilized different depths of the bay during homing.
Terrapins occupied the deepest water during AM late and PM early and the shallowest
water during AM early (Figure 1.13). Due to the shallowness of Barnegat Bay, terrapins
only had a mean depth difference of 10 cm between the six “Time of Day” categories
(Figure 1.13). Terrapins displaced north spent 85% of their time in water less than 1 m
where south displaced terrapins spent 60% of their time in water less than 2 m (Figure
1.14) based on the cumulative frequency diagrams. The mean perpendicular distance for
all displaced terrapins for the first third of the trip was significantly further from shore
where the middle and last third of the trip were significantly closer to shore (ANOVA, F2,
150=71.51, p<0.0001, Tukey-Kramer adjusted p<0.05, Figure 1.15); however, this finding
may be an artifact of the experimental design rather than an actual behavioral response
due to releasing each terrapin in the middle of the bay.

All recaptured terrapins occupied bay water temperatures between 20-30°C
(Figure 1.16, Appendix 1.3A-G). Water temperature at the terrapin was cooler than the
bay water temperature, which was monitored in a shallow water cove, on the first day of
release for two terrapins displaced to the north (Figure 1.16, Appendix 1.3C) and one
terrapin displaced to the south (Appendix 1.3B). Since the release sites were located in
the middle of the bay, cooler water temperatures were associated with the deeper depth of
the bay. Also, the sensor of the monitoring station was located in Osprey Cove, where bay water temperatures would be warmer because the average saltmarsh depth in Barnegat Bay is 1.5 m. Peaks in water temperature at the terrapin were seen for five recaptured terrapins, where the water temperature at the terrapin were at least 3°C higher than the bay water temperature (Figure 1.16, Appendix 1.3B, D, F, G). Water temperature at the terrapin peaked between 12:00 and 15:00, when the sun would be at a position for ideal basking thermoregulation. These peaks in water temperature at the terrapin also occurred within the last two days of recapture, suggesting these terrapins were basking when they were closer to home (Figure 1.16, Appendix 1.3B, D, F, G). Interestingly, one terrapin was actually recaptured basking with other terrapins on Sloop Sedge, with steep peaks in water temperature compared to the bay water temperature (Figure 1.16). Four out of the five recaptured terrapins with increases in water temperature at the terrapin were displaced from the north (Figure 1.16, Appendix 1.3D, F, G). Cyclic patterns in water temperature and air temperature were apparent as well (Appendix 1.3E, F, G).
Table 1.1. Day and time of release, return and recapture of all 4 km displaced terrapins. Osprey Cove and Sloop Sedge were the two capture/home locations for all terrapins. All recaptured terrapins displaced north and south successfully displayed homing behavior. One terrapin was recaptured in a crab pot (as indicated with an *) and another terrapin returned home successfully as indicated by the submersible underwater receiver but was not recaptured (not included in any of the data analyses **). Four terrapins were left at their home location after returning until recapture a few days later. South-displaced terrapins took significantly more time to return home than north-displaced terrapins (mean for north and south=64.6, 168.5, respectively, p=0.03).

<table>
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<tr>
<th>Home Location</th>
<th>Date Released</th>
<th>Time Released</th>
<th>Date Returned</th>
<th>Time Returned</th>
<th>Returned Site</th>
<th>Recapture Date</th>
<th>Recapture Time</th>
<th>Recapture Location</th>
<th>Return Hours</th>
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<td>n/a</td>
<td>n/a</td>
<td>23-Jun-10</td>
<td>13:20</td>
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<td>30-Jul-10</td>
<td>9:35</td>
<td>2-Aug-10</td>
<td>14:30</td>
<td>Osprey Cove</td>
<td>6-Aug-10</td>
<td>15:00</td>
<td>Conklin Beach</td>
<td>77</td>
</tr>
<tr>
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<td>10:03</td>
<td>1-Aug-10</td>
<td>9:48</td>
<td>Osprey Cove</td>
<td>6-Aug-10</td>
<td>11:29</td>
<td>Sloop Sedge</td>
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</tr>
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<td>17-Aug-10</td>
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<td>Osprey Cove</td>
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<td>Osprey Cove</td>
<td>75</td>
</tr>
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<td>n/a</td>
<td>n/a</td>
<td>21-Aug-10</td>
<td>12:26</td>
<td>Sloop Sedge</td>
<td>73</td>
</tr>
<tr>
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<td>n/a</td>
<td>n/a</td>
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<td>Osprey Cove</td>
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<td>Island</td>
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<td>n/a</td>
<td>27-Aug-10</td>
<td>10:30</td>
<td>Ghost Trap</td>
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Figure 1.6. Path taken home by BCJOP when displaced to the north. A. Initial release at 10:37, B. Last tracking location at 15:32 near Conklin Beach, C. Recapture at 13:20, * indicates the initial capture location. Gap in path indicates missing data. This terrapin swam towards the mainland and may have used the shoreline as a reference to home. The lines connecting the points do not necessarily reflect the actual path taken.
Figure 1.7. Directional headings (bearings) of north (A) and south (B) displaced terrapins after five minutes from initial release. The reference angle was referred to as the target home angle. The mean vector bearing (MVB) indicated the mean chosen directional angle towards the reference angle. The r-value determined how clustered the data were and N is the sample size. There were no significant homeward headings made by north and south-displaced terrapins (p>0.05).
Figure 1.8. Directional headings (bearings) of north (A) and south (B) displaced terrapins after 30 minutes from initial release. The reference angle was referred to as the target home angle. The mean vector bearing (MVB) indicated the mean chosen directional angle towards the reference angle. The r-value determined how clustered the data were and N is the sample size. Neither north nor south displaced terrapins made significant homeward directional headings 30 minutes after initial release (p>0.05).
Figure 1.9. Directional headings (bearings) of north (A) and south (B) displaced terrapins after one hour from initial release. The reference angle was referred to as the target home angle. The mean vector bearing (MVB) indicated the mean chosen directional angle towards the reference angle. The r-value determined how clustered the data were and N is the sample size. Neither north nor south displaced terrapins made homeward directional headings after one hour from initial release (p>0.05).
Figure 1.10. Mean number of surfacings per time period (+/- standard error) for five displaced terrapins (KNOQW was included for north and south displacement directions, so six data sets) as a function of time of day. Time of day category is defined as a four-hour time period, where six time of day categories covered a 24-hour day. The highest number of surfacings occurred during AM late, PM early, and PM middle (repeated measures ANOVA, $F_{5,143}=9.85$, $p<0.0001$, Tukey-Kramer adjusted p-value<0.05).
Figure 1.11. Surface duration (min/surfacing, mean +/- standard error) for five terrapins (KNOQW was included for north and south displacement directions, so six data sets) as a function of time of day. Time of day category is defined as a four-hour time period, where six time of day categories covered a 24-hour day. There were no significant differences among all time of day categories (repeated measures ANOVA, $F_{5,3165} = 1.90$, $p=0.09$).
Figure 1.12. Duration at surface for displaced terrapins for each third of their home journey. North-displaced terrapins did not differ in surface duration for each third of their home journey (repeated measures ANOVA, $F_{2,1587}=0.07, p=0.93$). South-displaced terrapins spent most of their time at the surface during the second third portion of their home journey (repeated measures ANOVA, $F_{2,1578}=5.99, p=0.0026$, Tukey-Kramer adjusted $p$-value<0.05). Data are means ± standard error. Five terrapins used in the analysis (KNOQW was included for north and south displacement directions, so six data sets).
Figure 1.13. Mean depth (± standard error) in the water column of all terrapins (five terrapins but KNOQW was displaced both north and south, so six data sets) for different time of day categories. Time of day category is defined as a four-hour time period, where six time of day categories covered a 24-hour day. Terrapins occupied the deepest water during AM late and PM early and the shallowest water during AM early (repeated measures ANOVA, $F_{5,72000}=524.68$, $p<0.0001$, Tukey-Kramer adjusted $p$-value<0.05.
Figure 1.14. Cumulative depth frequency diagram for north and south displaced terrapins. North displaced terrapins spent 85% of their time in water less than 1 m whereas south displaced terrapins spent 60% of their time in water less than 1 m.
Figure 1.15. Mean perpendicular distance (+/- standard error) from the nearest landmass for all terrapins displaced north and south for each third of their home journey (six terrapins total, two displaced both north and south, so eight data sets). The number of data points used for each third of the trip (n) is provided. Terrapins were significantly further from the shore during the first third of their home journey, where the last two thirds were significantly closer to shore (repeated measures ANOVA, $F_{2,150}=71.51$, $p<0.0001$, Tukey-Kramer adjusted $p$-value$<0.05$).
Figure 1.16. Temperature profile of BCJOP displaced to the north. At first release, the water temperature at the terrapin was lower than the bay water temperature. The sharp peaks in water temperature at the terrapin at the end of the track correlated with basking behavior since she was recaptured basking with other terrapins.
Discussion

Eight monitored terrapins returned home after four-kilometer displacement north, south or in both directions (only three of eight terrapins were displaced in both directions because not all terrapins were recaptured). The one terrapin that did not return home was recaptured trapped in a crab pot close to the shoreline. Successfully recaptured terrapins returned home between one and nine days. One non-recaptured terrapin also returned home as indicated by the SUR. These successful homing findings were similar to loggerhead sea turtles (Standora et al. 1993), suggesting turtles are able to compensate for displacement. All terrapins remained in the vicinity in which they were recaptured for at least one day and four of the nine terrapins remained there for approximately three days, further indicating that this was home. One terrapin displaced to the north remained in her home range for six days until recapture (KNOQW). Terrapins most likely stay in their home range for maintaining necessary daily activities such as feeding, basking and mating. It may be possible that terrapins do not use compass orientation in homing, which is why no directional headings were seen in this study. Future studies should look at directional headings after longer time periods to determine if a homeward heading is made.

This study suggests that terrapins may have different behavioral responses to displacement when there is variation in shoreline structure and anthropogenic development. When terrapins were displaced to the south, they spent significantly more time travelling home than terrapins displaced to the north. The south displacement location had many shallow water inlets and coves, where the north displacement location
was mostly open water. The south location may serve as appropriate feeding grounds due to the shallow water areas that would delay terrapins in returning home. The shoreline to the south may also be less threatening to terrapins compared to the north due to less urbanization and human activity (i.e., many shallow water areas prevent accessibility to boats and crabbing), so the southern location may be indicative of a more ‘natural’ habitat. The open bay, prone to boating, crabbing and shoreline development, suggests the north location may be a more ‘disturbed habitat’. Rapid development to the Charlotte-Metropolitan area of North Carolina has lowered the survivorship rate of mud turtles (Eskew et al. 2010) where terrestrial habitats within these anthropogenically-disturbed areas have proved to be essential for the survival of these turtles (Harden et al. 2009). Mud turtles were still able to traverse disturbed areas, suggesting these areas may be a refuge from threats associated with heavy urbanization (Harden et al. 2009). As a result, terrapins may make quicker movements to return home, still traversing areas exposed to human disturbance, to reduce their vulnerability to negative impacts and to reach an undisturbed habitat. This is suggested because between 2002-2007, the Barnegat Bay watershed gained 12.2 square miles of urban land while losing 0.8 square miles of wetlands (Kauffman and Cruz-Ortiz 2012).

Terrapins displaced to the north spent 85% of their time in water at a depth of less than 1 m compared to 60% for south displaced terrapins. Terrapins showed similar water depths for all time of day categories, as noted by the very small standard error bars. This suggests that terrapins were selecting shallow (< 1 m) water depths throughout the day. Interestingly, north displaced terrapins spent more time in shallow water given the open
bay characteristics of the north displacement location, showing their affinity to shallow water areas. Since terrapins may be using the shoreline, this finding further implies that terrapins prefer shallow water areas. Diamondback terrapins tracked in South Carolina similarly spent more time in shallow water marsh areas rather than open water (Harden et al. 2007). Shallow water habitats provide feeding opportunities, areas for thermoregulation, and refuge against predators (Harden et al. 2007). Prey availability has been found to play a major role in the habitat use of diamondback terrapins (Roosenburg et al. 1999, Harden et al. 2007) and may be a factor in terrapin shallow water navigation. These areas are also important for thermoregulation, so protection from human activities is vital in terrapin’s shallow water home ranges in Barnegat Bay.

Although terrapins in this study were initially released in the center of the bay, they moved closer to shore as they approached home. As a result, terrapins may be using the shoreline as indicator of home based on their perpendicular distance from shore. However, future studies should release terrapins at varying distances from shore to determine in fact that the shoreline is being utilized in homing. The use of the shoreline could suggest that terrapins were either using the shoreline as a landmark to identify home or as an indicator of shallow water areas. The use of shoreline as a landmark for homing has been observed in the Northern elephant seals (Mirounga angustirostris, Matsumura et al. 2011), green turtles (Luschi et al. 1996), painted turtles (Chrysemys picta, Williams 1952), and musk turtles (Sternotherus odoratus, Williams 1952), whereas use of shoreline to identify areas with shallow water has been observed in spiny soft-shell turtles (Galois et al. 2002, Apalone spinifera). In this study, terrapins appeared to use the
shoreline as they approached home, but since the turtles were captured in hoop traps near the shoreline and released in the middle of the bay, this finding may be an artifact of the experimental design and requires further study.

South-displaced terrapins spent more time at the surface during the second third of their home journey compared to north-displaced terrapins. The total time at the surface during these afternoon times of day categories also suggests that terrapins were basking and/or feeding since terrapins came to the surface the highest number of times during AM late, PM early, and PM middle. While loggerhead sea turtles spend 90% of their time submerged, a female sea turtle was found spending hours at the surface for basking and feeding (Lushi et al. 2003). Additionally, more time spent at the surface for south-displaced terrapins is indicative of longer hours to return home. This may again be related to the topography of the south displacement location.

Basking is a form of thermoregulation used to increase body temperature for metabolism, growth and daily activity (Harden et al. 2007, Harden et al. 2009). Increases in water temperature at the terrapin were at least 3°C higher than the bay water temperature during 12:00-15:00, indicating terrapins were basking during these times although cloud cover data is lacking. Another population of diamondback terrapins was found basking under the same conditions as those in Barnegat Bay, 3°C higher than the water temperature, showing their preference for marsh habitats rather than open water (Harden et al. 2007). Increases in water temperature at the terrapin associated with thermoregulation occurred within the last two days before recapture, suggesting this population of diamondback terrapins prefer to bask in shallow water habitats compared to
the open bay as well. Basking behavior occurred when the bay water temperature was cooler than the air temperature. Terrapins have been suggested to bask during these times to raise their body temperature above the water temperature (Harden et al. 2007). Thermoregulation had been associated with seasonal variation as well. For example, bog turtles were found to have a higher basking frequency in May-June compared to virtually non-existent basking in August when the wetland dried (Pittman and Dorcas 2009).

Similarly, only one recaptured terrapin (BCJOP displaced north, Appendix 1.3C) was released in June and spent more time basking compared to all other recaptured terrapins released in late July- mid-August. This terrapin was the only one sighted and recaptured basking in its home range as well. The cyclic pattern in water and air temperature was seen for only three terrapins that had a home journey lasting about a week while the others were shorter and a pattern could not be easily identifiable in such a short time frame.

Cyclic diel patterns in hawksbill and green turtles were associated with food acquisition (Schmid et al. 2002) and could be attributed to terrapins as well. Future studies should investigate terrapin behavior throughout the year to determine seasonal water temperature preference since our study was limited to June-August.

The homing behavior results presented here suggest that terrapins have site fidelity, as reported by others (Roosenburg 1991, Gibbons et al. 2001, Szerlag and McRobert 2007, Sheridan 2010). Male and female terrapins have been recaptured within several meters of their original capture location for up to three years (Lovich and Gibbons 1990) and similar results were seen for 16 years (Gibbons et al. 2001). Homing behavior may be hindered by localized anthropogenic disturbances and continued urbanization. A
study comparing the population declines of the wood turtle, diamondback terrapin, and sea turtles concluded that anthropogenic causes of mortality were apparent for all three species. In diamondback terrapins specifically, decreased nesting habitat (due to the construction of roads and highways) positively correlated with declined populations as well as increased incidents with boats and capture in crabbing and fishing gear. For example, the number of female terrapins on Little Beach Island in Barnegat Bay decreased from 1973-1990 while anthropogenic disturbances increased (Burger and Garber 1995). Crabbing in high-density terrapin home ranges should be minimized to reduce negative effects on homing behavior. Specifically, the terrapin recaptured in the crab pot would have died if not for being radio tracked, demonstrating the direct effects of humans on this species. Shoreline development enhanced homing capability, since the north-displaced terrapins returned home quicker than the south-displaced terrapins. However, useful landmarks in homing may be eliminated with continued development (i.e., nesting beaches, specific terrestrial landmarks along the shoreline), affecting terrapin behavior if landmarks are indeed necessary. If urbanization continues in Barnegat Bay, relocation of terrapins may be needed to sustain the population. Suggested relocation of terrapins for conservation should be greater than 4 km from their original home site since all terrapins returned home after this displacement distance. Further research is needed to determine the threshold translocation distance necessary for successful homing behavior if relocation was to be used (i.e., greater displacement distances from their home range). For example, box turtles (Gould 1957) and musk turtles (Smar and Chambers 2005) were able to home after displacement of 500 m, where
Conclusion

Results from this study strongly indicate that diamondback terrapins in Barnegat Bay exhibit homing behavior and return home when displaced 4 km (either to the north or to the south) from their original home site. Homing may occur with longer displacement distances, as seen with many other turtle species, but further research is needed to determine how far a terrapin could be displaced without returning home for successful relocation. As suggested by these findings, terrapins displaced to the north had increased homing efficiency compared to those displaced to the south, possibly due to differences in the development of the shoreline between the north (developed shoreline) and south (natural shoreline) displacement locations. If urbanization of Barnegat Bay continues to increase, protection of terrapin home ranges needs to be mandated or relocation of terrapins should be considered. Although this experiment exclusively tested females, future displacement studies should include males to evaluate the homing behavior of the species as a whole.
Chapter 2

Orientation of the Northern Diamondback Terrapin \((M. \ terrapin)\)
**Introduction**

Orientation in numerous turtle species has been well documented, especially pertaining to displacement (Iverson et al. 2009). Displacement to unfamiliar territory requires animals to have orientation mechanisms and orientation cues to help them locate home and resources (Able 1991). Griffin (1952) identified three mechanisms (or types) of orientation. Type I involves the use of landmarks while in familiar territory and random movement while in unfamiliar territory. Type II involves directed movement regardless of the homeward direction. Finally, type III, or homing, is the ability to choose a corrected direction in unfamiliar territory (Griffin 1952).

**Orientation in turtles**

Homeward orientation has been studied in multiple turtle species with differing results. The soft-shell turtle (*Trionyx spinifer*), the box turtle (*Terrapene carolina*), and the painted turtle (*Chrysemys picta*) exhibited significant homeward orientation while located inside a terrestrial arena (DeRosa and Taylor 1980). Box turtles and painted turtles showed the greatest ability to orient in the homeward direction; this may be explained since movements have been seen up to 0.75 km outside of their home range compared to relatively inactive soft-shell turtles, where movements outside of their home range normally do not exceed 100 m (DeRosa and Taylor 1980). When box turtles and painted turtles were displaced to distances ranging from 0.1 km to 4.5 km, they were able to orient toward home when placed in unfamiliar territory (Gould 1959). Turtles can locate the direction of home, and even other aquatic habitats, outside of their home range (Emlen 1969). For example, European pond turtles (*Emys orbicularis*) were able to
orient toward home using aquatic habitats as landmarks when displaced 80-1920 m, suggesting Type I orientation (Leboroni and Chelazzi 2000). Yellow-bellied pond slider turtles (*Trachemys scripta*) were observed to orient toward the nearest aquatic habitat when displaced in unfamiliar territory, showing a water-finding ability when placed within 400m of an aquatic habitat (Yeomans 1995). Orientation ability in yellow-margined box turtles enables them to return to the same area during over-wintering each year (Lue and Chen 1999). Juvenile semiaquatic turtles (*Kinosternon flavescens*) navigated along the same migration path after brumation using compass cues demonstrating Type II orientation (Iverson et al. 2009).

*Mental map and visual cues*

The use of landmarks, along with a compass mechanism, can be used to locate aquatic habitats only if there is knowledge (i.e., mental map) of local surroundings. For instance, a mental map with landmarks would allow an animal to navigate from one landmark to another until home was reached (Gould 1998, Gould 2004, Caldwell and Nams 2006). Eastern painted turtles were proposed to have a compass mechanism but lacked a mental map of home while in unfamiliar territory (Caldwell and Nams 2006). Previous studies indicate that the sun is an important and frequently used reference point for orientation. For an animal to use the sun, the animal must know how the sun moves relative to the rotation of the earth (Justis and Taylor 1976). Box turtles (*Terrapene carolina*, Gould 1957), Florida cooters (*Pseudemys floridana*), snapping turtles (*Chelydra serpentina*), red-bellied turtles (*Pseudemys nelsoni*) and gopher tortoises (*Gopherus*
polyphemus) all have been observed using the sun as a cue in orientation (Gibbons and Smith 1968).

**Magnetic cues in orientation**

Loggerhead sea turtles use magnetic compass orientation to establish correct headings and maintain courses using the earth’s magnetic field while swimming (Lohmann 1991, Lohmann and Lohmann 1993, Irwin and Lohmann 2003, 2005, Merrill and Salmon 2011). Juvenile loggerhead sea turtles have two mechanisms of maintaining a directional heading. When magnetic cues are disrupted, loggerhead sea turtles can compensate by using visual cues for orientation and vice versa. However, when both magnetic (swimming in disrupted magnetic fields) and visual cues (wearing goggles) are blinded at the same time, orientation was disrupted (Avens and Lohmann 2003, 2004). Near the coastline, green turtle hatchlings use oceanic waves for orientation by maintaining headings due to wave refraction (Lohmann and Lohmann 1992), but in deeper waters (where waves are not refracted); hatchling green turtles use a magnetic compass to maintain headings (Lohmann and Lohmann 1991, 1993, Goff et al. 1998, Avens and Lohmann 2003). Other sea turtles have been found to have a magnetic compass as well, such as leatherback hatchlings (*Dermochelus coriacea*, Kloc et al. 1996). The role that the earth’s magnetic field plays as an orientation cue in terrestrial, freshwater and estuarine turtles is currently unknown.
Landmarks used in orientation

Trees, and other easily identifiable landmarks, are visible at great distances and have been suggested as potential cues in orientation (Emlen 1969). Box turtles often use paths formed by wooded areas, roads, streambeds and other landmarks for orientation (Lemkau 1970). The European pond turtle has been hypothesized to use physical landmarks, such as trees, hills and meadows, as cues in their waterward orientation since these water areas were associated with easily recognizable landmarks (Leboroni and Chelazzi 2000).

Effects of cloud cover on orientation

Overcast skies may disrupt orientation abilities for animals that use the sun or polarized light as a cue. Soft-shell turtles, painted turtles, box turtles, yellow-bellied pond slider turtles, and eastern long-necked turtles have all been shown to have the ability to orient homeward on clear days but not on overcast days, indicating the use of the sun as a primary cue (Gould 1957, Gibbons and Smith 1968, DeRosa and Taylor 1980, 1982, Yeomans 1995, Graham et al. 1996). Indices of movement straightness were compared for turtles under sunny and overcast conditions. Findings suggest that turtles wandered (i.e., travelled in less of a straight line) more often on overcast days than sunny days (Yeomans 1995, Graham et al. 1996, Bowne and White 2004). However, many aquatic organisms travel long distances regardless of sky conditions and thus may rely on magnetic cues as a secondary orientation input (Gould 1998).
Purpose and justification of the study

Findings from Chapter 1 demonstrate that diamondback terrapins have homing behavior and, therefore, must have some form of orientation ability, to migrate long distances or locate home. Currently, no research has been conducted on orientation behavior in this species. Understanding this species’ orientation behavior may provide a better understanding of terrapin homing behavior as well as more precise management strategies. Increased habitat destruction and urbanization of terrapin home ranges makes it difficult for this species to exist, especially considering terrapins have natal site fidelity (Sheridan et al. 2010). Orientation capabilities, combined with homing behavior, would make it easier to conserve this species since protection could be enhanced in areas most utilized by terrapins.

The purpose of this study was to determine the orientation capability of Northern diamondback terrapins (*Malaclemys terrapin*). Since terrapins are able to locate home after being displaced, they must demonstrate some type of orientation. The ability of turtles to traverse unfamiliar territory, or homing, has been known for years. The homing and orientation cues used to locate home while in unfamiliar territory remains unknown in diamondback terrapins. This study will identify orientation capabilities in terrapins, as well as the use of the sun and landmarks as orientation cues.

I hypothesize that diamondback terrapins will have orientation capabilities used to locate home. Based on my findings of homing behavior (Chapter 1), I expect that terrapins use environmental cues (i.e., sun and landmarks) for orientation. I hypothesized that there would be no difference in orientation between those turtles captured from the
south or the east of our field station, suggesting these turtles would have orientation regardless of directional displacement. I also hypothesized that terrapins have reduced orientation capabilities on overcast days and at night compared to clear days, suggesting that the sun was being used as an orientation cue. Additionally, there would be no difference in orientation between males and females and gravid and non-gravid females based on varying sex difference results in turtle activity and movement experiments (Morreale et al. 1984, Doody et al. 2002).

Methods

Terrestrial orientation arena

An orientation arena, located 11 m from the water of Barnegat Bay, NJ on the property of the Lighthouse Center in Waretown, NJ (field station), was used to determine orientation capability of diamondback terrapins. The location of the arena and wall height eliminated the visibility of landmarks that could possibly influence terrapin orientation; the only visual aid available to each terrapin was the sky. However, olfactory and sound cues could not be eliminated since the arena was located close to the vicinity of the water. Terrestrial movements by terrapins justify the use of a terrestrial arena (Roosenburg 1991, Walters 2008).

Orientation arena construction

Orientation of the diamondback terrapin was studied using a 16 square meter octagon arena (Figure 2.1). The walls of the arena were constructed using 5 cm X 10 cm lumber and were approximately 2 m in height. Each wall section was 205 cm in length.
An opaque brown and silver tarp was used as the walls of the arena, with the silver side facing towards the inside. The tarp walls were secured using cinder blocks to minimize wall movement due to wind action. The arena was constructed on level terrain to exclude possible geotactic cues. The substrate was uniform and consisted of sand with some small pebbles.

*Orientation arena procedure*

Terrapins from two different capture locations were used in this study. Testing terrapins from two different capture locations was important because it would indicate whether terrapins have homeward orientation regardless of their capture location. From a total of 221 sampled terrapins, those with a capture location to the south (n=180) were studied in the summer of 2010 and those captured to the east (n=41) were studied in the summer of 2011 (Figure 2.2). Terrapins captured from the south were captured from the same locations as those captured from the south in Chapter 1, ranging from 4.17-8.16 km from the study site. Those captured from the east were captured from both North Sedge Island and Spizzle Creek, ranging from 6.60-8.06 km from the study site (Figure 2.2).

Each terrapin was placed in the center of the arena at the beginning of each trial (Figure 2.3). Testing was initiated by placing each terrapin under a black bucket to blind them from the external environment. Each terrapin was placed facing the north wall to maintain consistency, reduce bias and control for initial orientation in the direction they were facing, upon bucket removal. Each terrapin was left under the bucket for one minute before beginning each trial. Two ropes were tied to the bucket, which enabled
Figure 2.1. Terrestrial arena used to test orientation of Diamondback Terrapins. Photo credit E. A. Standora.
two people to quickly pull the bucket up in the air away from the arena (Figure 2.4). To limit any possible influence of observer presence, a periscope (Rainbow Resource Center 041570) was used to determine when a terrapin chose a direction (Figure 2.5). Each trial lasted until a direction was chosen or for a maximum of five minutes. A chosen direction was defined as the first wall touched by a terrapin. Any terrapin that took longer than five minutes to select a wall was not considered in the study, since the interest of the study pertained to initial orientation in the homeward direction. The five-minute duration for orientation used in trials was appropriate because only seven percent (12 out of 180) of the south-captured terrapins and only five percent (2 out of 41) of east-captured terrapins took greater than five minutes to choose a direction by hitting the wall. The total time of the trial, arena wall chosen, and directional angle chosen were recorded for each terrapin. Directional angles were determined visually for each wall. The ground of the arena was raked between individual terrapin trials to eliminate possible odors cues from previously tested conspecifics.

Similar methods were used in summer of 2010 and in the summer of 2011. Visual judgments of each angle were made in 2010; however, more precise quantitative measurements of the wall were calculated to obtain the chosen directional angle in 2011. The directional wall chosen was defined as the point at which the terrapin was approximately one body length from contacting the wall after removal of the bucket. The chosen directional angle was calculated by measuring the distance from the location on the wall to a corner of the arena. Time to reach the directional wall was also measured using the same method as in 2010 data collection. Orientation behavior was measured
Figure 2.2. Visual representation of arena trap locations (green circles) both to the east and south of the study site (yellow star). Highlighted areas show the range of potential homeward angles for terrapins captured at the trap locations.
Figure 2.3. Terrapins were placed under a black bucket with two ropes attached. The ropes were draped over the side of the arena to easily lift the bucket away from the terrapin. Each terrapin was placed under the bucket facing the north wall. Photo credit E. A. Standora.
Figure 2.4. After one minute, the bucket was flipped over the wall of the arena. Photo credit E. A. Standora.
Figure 2.5. A periscope, used by an Earthwatch volunteer, to identify when a terrapin selected a specific directional preference. Photo credit E. A. Standora.
three times (i.e., repeatability trials) for each terrapin (n for the south=32, n for the east=33) to ensure that I was observing orientation movements and no other random movements in 2011. Repeatability trials were not conducted in 2010.

Data analysis

Initial bearings of each terrapin were converted into initial bearings relative to home using the standard methods of circular statistics (Zar 1996). The Rayleigh’s test ($\alpha=0.05$), V-test ($\alpha=0.05$) and 95% confidence intervals were used to test for orientation in the homeward direction. Bonferonni correction was used to account for multiple testing bias and to minimize Type I error. The Rayleigh’s test was used to assess for any directional bias, since it determined whether a population clustered in a specific direction (i.e., non-clustered indicated that terrapins were evenly spaced in all directions around the arena). The V-test was used to determine whether the mean vector bearing (MVB), or mean direction taken by all terrapins, differed from the reference angle, or home target angle. The r-value determined how clustered the data were, where a value of 0 indicated the data were not clustered and a value of 1 indicated the data were clustered with the same directional bearing. The V-test was only conducted when there was significance with the Rayleigh’s test. A template constructed in Microsoft Excel 2011 was used to make the circular statistic diagrams (Visscher 2003). A weighted average, based on the number of terrapins caught at each trap, was used as the reference or home angle; the south home angle was 170° and the east home angle was 81°. South and east captured terrapins were compared to determine if terrapins with different capture locations had different home target directions. Differences in orientation were compared between
sexes, under clear and overcast days, and between south versus the east captured terrapins. Orientation behavior was also compared at different times of the day for terrapins captured from the south (morning 06:00-11:59, afternoon 15:00-19:59, and night 20:00-0:00). The same south-captured terrapins were tested at three different times of day to determine any orientation differences in relation to the position of the sun. During the morning, there was complete shade and no sun in the arena while the afternoon provided complete sun. Terrapins from the east were not tested at different times of the day due to time and weather constraints in 2011. Differences in gravid and non-gravid females were compared for east terrapins; however, the sample size of gravid females from the south was too small for any comparisons to be made.

Diagrams were made in Microsoft PowerPoint 2010 to depict the number of terrapins that oriented toward each wall, so the direction that was chosen by the greatest number of terrapins was easily identified. Arrows were drawn proportionally to the number of terrapins in each directional compartment (e.g., north, northeast, east, etc.). The longest arrow corresponds to the compartment with the most terrapins. These diagrams were made to visually complement the circular diagrams and no statistical testing was conducted using these diagrams (B, D in Figures 2.6-2.11, B, D, and F in Figure 2.10).

In 2011, the Kolmogorov-Smirnov Goodness of Fit (K-S) test for discrete data (α=0.05) was used to determine whether the distribution of turtles in each group differed from an expected distribution (Zar 1996). This test was conducted by creating a table listing the number of turtles that were observed orienting in cardinal (north, south, east...
and west) and sub-cardinal (north-east, south-east, south-west and south-east) directions for the same test groups as previously mentioned. The observed numbers of terrapins were compared to a calculated, expected distribution. The distribution of terrapins among the directional heading categories was expected to be uniform. Again, Bonferonni correction was used to account for multiple testing bias and to minimize Type I error.

For the three repeatability trials, the time to choose a directional heading for the first and second trial was compared to the second and third trial angle to determine if there was a learning curve (Mathis and Moore 1998) or fatigue factor in wall selection for south and east terrapins. For orientation time, the absolute difference was taken between the first and second trial and again for the second and third trial. These differences were then compared using a paired t-test. A difference between the angles selected was also compared for all three trials for south and east terrapins using an ANOVA. Statistical analysis was completed using the SAS statistical software package (SAS Institute, Inc., version 9.2).

Results

Terrapins displaced to the south

Adult females and adult males

South-captured females had a clustered distribution around the arena (Rayleigh’s p<0.001) but not in the homeward direction (V test p>0.10, Table 2.1, Figure 2.6A, B). South-captured males had a non-clustered distribution (Rayleigh’s p>0.2, Table 2.1, Figure 2.6C, D).
Clear and overcast days

On clear days, south-captured terrapins (both females and males) had a clustered distribution around the arena (Rayleigh’s p<0.05) but not in the homeward direction (V test p>0.05, Table 2.1, Figure 2.7A, B). South-captured terrapins had a clustered distribution on overcast days (Rayleigh’s p<0.02), but not in the homeward direction (V test p>0.25, Table 2.1, Figure 2.7C, D).

Effects of time of day

Different times of the day were compared for south-captured terrapins (both females and males) from 2010. A non-clustered distribution was seen in the morning (Rayleigh’s p>0.05, Table 2.1, Figure 2.8a A, B) and at night (Rayleigh’s p>0.1, Table 2.1, Figure 2.8b E, F). Despite a non-clustered distribution at night, the mean direction was 151.4° compared to a homeward direction of 170° (Table 2.1, Figure 2.8b E). During the afternoon, the distribution was clustered (Rayleigh’s p<0.001), but not in the homeward direction (V test p>0.10, Table 2.1, Figure 2.8a C, D).

Actual and expected distributions (K-S tests)

South-captured females (K-S p=0.005, Table 2.2), south-captured terrapins under overcast sky conditions (K-S p=0.01, Table 2.3) and south-captured terrapins tested during the afternoon (K-S p<0.001, Table 2.4) had a significantly different distribution, with the east contributing the most to the test statistic. South-captured terrapins under clear sky conditions had a significantly different distribution, with the south-east contributing most to the test statistic (K-S p=0.05, Table 2.3).
Terrapins displaced to the east

Adult females and adult males

East captured females had a non-clustered distribution (Rayleigh’s p>0.5, Table 2.1, Figure 2.9A, B) and therefore no directional preference. East captured males displayed a clustered distribution (Rayleigh’s p<0.05) with non-random directional preference toward home (V test p<0.01, Table 2.1, Figure 2.9C, D). Additionally, both non-gravid (Rayleigh’s p>0.5, Figure 2.10A, B) and gravid (Rayleigh’s p>0.2, Figure 2.10C, D) females had non-clustered distributions. Non-gravid and gravid females did not significantly differ from an expected distribution either (K-S p>0.5, Table 2.5).

Clear and overcast days

East captured terrapins (both females and males) were non-clustered on both clear days (Rayleigh’s p>0.2, Table 2.1, Figure 2.11A, B) and overcast days (Rayleigh’s p>0.5, Table 2.1, Figure 2.11C, D).

Terrapins with homeward orientation

Males captured from the east (p<0.01) had significant homeward orientation. The mean direction of the males captured from the east (58.1°) was toward the northeast and was not within the range of their capture locations (Figure 2.12).

Repeatability trials

There were no statistically significant differences in the angle chosen between all three trials for both south (ANOVA, p=0.47) and east captured terrapins (ANOVA,
p=0.88). The time to choose a directional heading was not significant for the first and second trial compared to the second and third trial for both south (paired t-test, p=0.43) and east captured terrapins (paired t-test, p=0.43).
Table 2.1. Results of Rayleigh’s and V-test for various orientation variables.

<table>
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<td>z</td>
<td>p-value</td>
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<tr>
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<tr>
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<td>9.072</td>
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</tr>
<tr>
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<td>72</td>
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<td>2.292</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>EAST</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>31</td>
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</tr>
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<td>Non-gravid</td>
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</tbody>
</table>
Figure 2.6. Orientation and arena counts of females (A and B, respectively) and males (C and D, respectively) captured from the South. MVB indicates the mean vector bearing (mean direction taken by all terrapins), r determines the clustering, and n is the sample size and reference angle is the home target angle.
Figure 2.7. Orientation and arena counts on clear days (A and B, respectively) and overcast days (C and D, respectively) for south captured terrapins. MVB indicates the mean vector bearing (mean direction taken by all terrapins), r determines the clustering, n is the sample size and reference angle is the home target angle.
Figure 2.8a. Orientation and arena counts of South captured terrapins during the morning (A and B, respectively), afternoon (C and D, respectively), and night (E and F, respectively). MVB indicates the mean vector bearing (mean direction taken by all terrapins), r determines the clustering, n is the sample size and reference angle is the home target angle.
Figure 2.8b. Orientation and arena counts of South captured terrapins during the morning (A and B, respectively), afternoon (C and D, respectively), and night (E and F, respectively). MVB indicates the mean vector bearing (mean direction taken by all terrapins), r determines the clustering, n is the sample size and reference angle is the home target angle.
Figure 2.9. Orientation and arena counts of females (A and B, respectively) and males (C and D, respectively) captured from the East. MVB indicates the mean vector bearing (mean direction taken by all terrapins), r determines the clustering, n is the sample size and reference angle is the home target angle.
Figure 2.10. Orientation and arena counts of East captured non-gravid (A and B, respectively) and gravid (C and D, respectively) females. MVB indicates the mean vector bearing (mean direction taken by all terrapins), r determines the clustering, n is the sample size and reference angle is the home target angle.
Figure 2.11. Orientation and arena counts on clear days (A and B, respectively) and overcast days (C and D, respectively) for East captured terrapins. MVB indicates the mean vector bearing (mean direction taken by all terrapins), r determines the clustering, n is the sample size and reference angle is the home target angle.
Figure 2.12. Visual representation of arena trap locations (green circles) both to the east and south of the study site (yellow star), as in Figure 2.2. The dotted line represents the mean bearing of males captured to the east (58.1°). This group had statistically significant Rayleigh’s and V tests, indicating these terrapins displayed homeward orientation.
<table>
<thead>
<tr>
<th></th>
<th>337.6-22.5 (N)</th>
<th>22.6-67.5 (NE)</th>
<th>67.8-112.5 (E)</th>
<th>112.6-157.5 (SE)</th>
<th>157.6-202.5 (S)</th>
<th>202.6-247.5 (SW)</th>
<th>247.6-292.5 (W)</th>
<th>292.6-337.5 (NW)</th>
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<th>d&lt;sub&gt;max&lt;/sub&gt;</th>
<th>p-value</th>
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<tbody>
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<td><strong>Male (S)</strong></td>
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<td>12 (9.5)</td>
<td>9 (9.5)</td>
<td>15 (9.5)</td>
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<td>11 (9.5)</td>
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<td>9 (13)</td>
<td>34* (13)</td>
<td>12 (13)</td>
<td>10 (13)</td>
<td>9 (13)</td>
<td>9 (13)</td>
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<td>15</td>
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<td>1 (1.25)</td>
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<td>1 (1.25)</td>
<td>0 (1.25)</td>
<td>0 (1.25)</td>
<td>1 (1.25)</td>
<td>8.10</td>
<td>3.50</td>
<td>&gt; 0.10</td>
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<tr>
<td><strong>Female (E)</strong></td>
<td>3 (3.875)</td>
<td>4 (3.875)</td>
<td>4 (3.875)</td>
<td>5 (3.875)</td>
<td>2 (3.875)</td>
<td>4 (3.875)</td>
<td>4 (3.875)</td>
<td>5 (3.875)</td>
<td>8.31</td>
<td>1.375</td>
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</table>

Table 2.2. Results of K-S test for females and males. Numbers in ( ) are expected values, d<sub>max</sub> is the test statistic. * is the cell that contributed the most to the test statistic. Both the df (degrees of freedom and d<sub>max</sub> are used when determining the p-value, using critical value tables.
<table>
<thead>
<tr>
<th></th>
<th>337.6-22.5 (N)</th>
<th>22.6-67.5 (NE)</th>
<th>67.8-112.5 (E)</th>
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<th>247.6-292.5 (W)</th>
<th>292.6-337.5 (NW)</th>
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<td>17 (11.5)</td>
<td>20* (11.5)</td>
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<td>10 (11.5)</td>
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<td>10 (11.5)</td>
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<td>11</td>
<td>0.05</td>
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<tr>
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<td></td>
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<td></td>
<td></td>
<td>8.88</td>
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<td>8 (11)</td>
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<td>7 (11)</td>
<td>9 (11)</td>
<td>9 (11)</td>
<td>8 (11)</td>
<td>8 (11)</td>
<td>8.13</td>
<td>2.125</td>
<td>&gt; 0.50</td>
</tr>
<tr>
<td><strong>(S)</strong></td>
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<td></td>
<td></td>
<td></td>
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<td>8.28</td>
<td>2</td>
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</table>

Table 2.3. Results of K-S test for terrapins under clear and overcast sky conditions. Numbers in ( ) are expected values, d<sub>max</sub> is the test statistic. * is the cell that contributed the most to the test statistic. Both the df (degrees of freedom and d<sub>max</sub> are used when determining the p-value, using critical value tables.
Table 2.4. Results of K-S test for south captured terrapin during different times of the day. Numbers in ( ) are expected values, $d_{\text{max}}$ is the test statistic. * is the cell that contributed the most to the test statistic. Both the df (degrees of freedom and $d_{\text{max}}$ are used when determining the p-value, using critical value tables.

<table>
<thead>
<tr>
<th></th>
<th>337.6-22.5 (N)</th>
<th>22.6-67.5 (NE)</th>
<th>67.8-112.5 (E)</th>
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<th>157.6-202.5 (S)</th>
<th>202.6-247.5 (SW)</th>
<th>247.6-292.5 (W)</th>
<th>292.6-337.5 (NW)</th>
<th>df</th>
<th>$d_{\text{max}}$</th>
<th>p-value</th>
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<tbody>
<tr>
<td><strong>Morning</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Afternoon</strong></td>
<td>11 (7.25)</td>
<td>8 (7.25)</td>
<td>19* (7.25)</td>
<td>6 (7.25)</td>
<td>3 (7.25)</td>
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<td>5 (7.25)</td>
<td>8.58</td>
<td>16.25</td>
<td>&lt; 0.001</td>
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<tr>
<td><strong>Night</strong></td>
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<td>7 (9)</td>
<td>12 (9)</td>
<td>11 (9)</td>
<td>8 (9)</td>
<td>16 (9)</td>
<td>6 (9)</td>
<td>5 (9)</td>
<td>8.72</td>
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Table 2.5. Results of K-S test for gravid and non-gravid females captured to the East. Numbers in ( ) are expected values, $d_{max}$ is the test statistic. Both the df (degrees of freedom and $d_{max}$) are used when determining the p-value, using critical value tables.

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<th></th>
<th>337.6-22.5 (N)</th>
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<th>157.6-202.5 (S)</th>
<th>202.6-247.5 (SW)</th>
<th>247.6-292.5 (W)</th>
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<th>$d_{max}$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
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<td>3 (1.75)</td>
<td>3 (1.75)</td>
<td>2 (1.75)</td>
<td>1 (1.75)</td>
<td>1 (1.75)</td>
<td>2 (1.75)</td>
<td>1 (1.75)</td>
<td>8.14</td>
<td>2</td>
<td>&gt; 0.50</td>
</tr>
<tr>
<td><strong>Non-gravid</strong></td>
<td>2 (2.125)</td>
<td>1 (2.125)</td>
<td>1 (2.125)</td>
<td>3 (2.125)</td>
<td>1 (2.125)</td>
<td>3 (2.125)</td>
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<td>4 (2.125)</td>
<td>8.17</td>
<td>2.625</td>
<td>&gt; 0.50</td>
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</table>
Discussion

Only males captured from the east had significant homeward orientation. Although the mean direction was outside the range of their capture location, this suggests these terrapins were water-orienting. Additionally, females captured from the south and south terrapins under overcast days and during the afternoon differed from an expected distribution with an easterly orientation. The location of the bay to the east strongly suggests that these terrapins were orienting towards the bay as well. These results do not provide strong evidence that terrapins have the ability to orient towards home while in the arena, but do suggest that terrapins may orient to nearest water rather than to home.

Similar behavior, referred to as a water-finding ability, has been documented in yellow-bellied pond slider turtles (Yeomans 1995). Likewise, a recent study found that hatchling snapping and painted turtles oriented easterly toward a river not visible from a terrestrial arena, suggesting these turtles may locating water rather than home (Congdon et al. 2011). Based on these results, terrapins orient towards the water and must be using orientation cues available to them while in the water rather than on land.

South-captured terrapins tested during overcast sky conditions had an easterly orientation, with a south-east directional preference on clear days. This was marginally significant, but was not confirmed by the Rayleigh’s test. East orientation during overcast days and south-east orientation on clear days were contrary to my hypothesis since the sun suggested being an orientation cue. This finding would contrast painted turtles (same subfamily as diamondback terrapins, Gould 1959, DeRosa and Taylor 1980), soft-shell turtles (DeRosa and Taylor 1980), box turtles (DeRosa and Taylor 1980)
and Eastern long-necked turtles \textit{(Chelodina longicollis, Graham et al. 1996)}. All four of these turtle species were able to home under clear sky conditions with a lack of homeward orientation under overcast sky conditions. In contrast, another study concluded that painted turtles were able to maintain their homeward orientation under complete cloud cover through the use of topographic landmarks (Emlen 1969). Additionally, directed orientation was observed during the afternoon for south-captured terrapins compared to the morning and evening with a mean directional preference towards the east rather than home. Terrapins may be utilizing different orientation cues, such as landmarks, olfaction or sound to locate the direction of the water. It is possible that diamondback terrapins are similar to painted turtles with respect to the use of landmarks for orientation. Visual landmarks were suggested to explain the difference in orientation between open field and arena tests in the Eastern long-necked turtle (Graham et al. 1996). The use of olfactory cues has been demonstrated in red-eared slider turtles \textit{(Trachemys scripta elegans, Boycott and Guillery 1962)} and has been suggested in Eastern long-necked turtles as well \textit{(Chelodina longicollis, Graham et al. 1996)}. As for the use of sound, terrapins have been found to hear low frequency tones less than 1,000Hz (Lester 2012), so they may be able to hear the wave action of the bay from the arena. However, there was a reduction in the number of olfactory receptor genes in aquatic turtles compared to terrestrial turtles (Vieyra 2011), so terrapins may not be able to hear the waves from the bay. To assess whether terrapins use landmarks, the arena could be moved to a location where trees and other landmarks (i.e., the Barnegat Bay lighthouse) could be easily visible. Projection of images on the arena wall could also be an option to test for landmarks as a cue in orientation. Future studies should also
investigate the possible use of polarized light (Yeomans 1995, Wehner 2001) and olfaction (Boycott and Guillery 1962) by terrapins for orientation as proposed for some aquatic turtles.

Most orientation studies have involved displacement of turtles outside of their home range while observing homeward orientation. Gopher tortoises, snapping turtles, Florida cooters, and juvenile loggerhead sea turtles were all observed orienting towards home after displacement (Gibbons and Smith 1968, Avens and Lohmann 2004). In this study, terrapins captured from the east were tested approximately 6-8 km from their capture locations, whereas south-captured terrapins were tested approximately 3-8 km from their capture locations. Future studies should test terrapins at shorter distances from their capture location to determine if they have orientation. It is possible that the capture locations are too far away from the arena for terrapins to have homeward orientation since homing behavior was seen after 4 km displacement (Chapter 1).

**Conclusion**

Overall, males from the east demonstrated a general homeward orientation. Females captured from the south and all south terrapins on overcast days and during the afternoon had non-random orientation towards the east as well, providing further evidence that locating the water first before orienting towards home is of primary importance. Therefore, this study did not support the hypothesis that terrapins have homeward orientation. Based on these findings, along with my findings from the biotelemetry study in Chapter 1, terrapins have homing behavior, but are unable to orient towards home while inside a terrestrial arena. Apparently, terrapins are utilizing an
orientation cue available to them while free-ranging in the Bay but not in the arena.

Orientation cues not available to terrapins in the arena but available when in the Bay include: landmarks, sound, and olfaction. Specifically, if landmarks are being used as cues in orientation, urbanization and development may impact the behavior of this species of special concern.
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Appendix 1.1A. Path taken home by AJNOW when displaced to the north. A. Initial release at 12:35, B. Last tracking location at 15:40, C. First tracking location at 11:28, D. Last tracking location at 12:36 near Conklin Beach, E. First tracking location at 11:51, F. Last tracking location at 18:10 near Conklin Beach, G. First tracking location at 10:20, H. Last tracking location at 15:32, I. Recapture on 19 Aug 2010 at 11:30, * indicates the initial capture location. The open circle indicates the location of the water monitoring station. The lines connecting the points do not necessarily reflect the actual path travelled.
Appendix 1.1B. Path taken home by AJNOW when displaced to the south. A. Initial release at 13:49, B. Last tracking location at 16:52, C. First GPS tracking location at 11:12, D. Last GPS tracking location at 13:56, E. First GPS tracking location at 10:20, F. Recapture in crab trap at 10:30 by local fisherman, * indicates initial capture location. Note: the long distance between points C and D may be due to malfunctions in the GPS since there were no tracking or visual locations for this day. The open circle indicates the location of the water monitoring station. The line connecting these points does not necessarily reflect the actual path traveled.
Appendix 1.1C. Path taken home by BCJNW when displaced to the south.  A. Initial release at 14:26, B. Last tracking location at 14:31, C. First tracking location at 13:32, D. Last tracking location at 13:44, E. First tracking location at 15:01, F. Last tracking location at 15:03, G. First tracking location at 15:02, H. Last tracking location at 15:15, I. First tracking location at 12:00, J. Recapture at 12:50, * indicates the initial capture location. The open circle indicates the location of the water monitoring station. The lines connected the points do not necessarily reflect the actual path taken.
Appendix 1.1D. Path taken home by CJKOW when displaced to the north. A. Initial release at 11:20, B. Last tracking location at 13:18, C. First tracking location at 10:46, D. Last tracking location at 17:14, E. First tracking location at 11:09, F. Recapture at 12:26, *indicates the initial capture location. The open circle indicates the location of the water monitoring station. The lines connecting the points do not necessarily reflect the actual path taken.
Appendix 1.1E. Path taken home by HIJPW when displaced to the north. A. Initial release at 9:35, B. Last tracking location at 16:44 near Conklin Beach, C. Visual sighting at 15:21 near Conklin Beach, D. First tracking location at 12:30, E. Last tracking location at 12:37 near Conklin Beach, F. Visual sighting at 10:36, G. Recapture at 15:00, * indicates initial capture location. The open circle indicates the location of the water monitoring station. The lines connecting the points do not necessarily reflect the actual path taken.
Appendix 1.1F. Path taken home by HIJPW when displaced to the south.  A. Initial release at 11:32, B. Last tracking location at 14:18, C. GPS tracking location at 10:32, D. Recapture at 17:07, * indicates initial capture location. The open circle indicates the location of the water monitoring station. The lines connecting the points do not necessarily reflect the actual path taken.
Appendix 1.1G. Path taken home by KNOQW when displaced to the north. A. Initial release at 10:03, B. Last tracking location at 15:43 near Conklin Beach, C. First tracking location at 10:48, D. Last tracking location at 16:46, E. First tracking location at 12:02, F. Last tracking location at 12:38, G. First tracking location at 11:03, H. Last tracking location at 15:28, I. First tracking location at 10:55, J. Recapture at 11:29. * indicates the initial capture location. The open circle indicates the location of the water monitoring station. The lines connecting the points do not necessarily reflect the actual path taken.
Appendix 1.1H. Path taken home by KNOQW when displaced to the south.  A. Initial release at 12:59, B. Last tracking location at 13:34, C. First GPS tracking location at 11:05, D. Last GPS tracking location at 12:46, E. First tracking location at 10:43, F. Recapture at 11:25, * indicates initial capture location.  The open circle indicates the location of the water monitoring station.  The lines connecting the points do not necessarily reflect the actual path taken.
Appendix 1.2. The number of surfacings for north and south displaced terrapins for each third of their home journey. There was no statistically significant difference between any third for number of surfacings (ANOVA, $F_{2,15} = 1.68$, $p=0.22$).
Appendix 1.3A. Temperature profile of AJNOW displaced to the south. This terrapin was recaptured in a crab trap as indicated with water temperatures at the terrapins lower than the bay water temperature towards the end of the track. Water temperature was correlated with air temperature.
Appendix 1.3B. Temperature profile of BCJNW displaced to the south. At the release, water temperature at the terrapin was lower than that of the bay. Two peaks in water temperature at the terrapin correlated with air temperature, occurring around noon, suggesting this terrapin was basking during these times.
Appendix 1.3C Temperature profile of AJNOW displaced to the north. Both the bay water temperature and the water temperature at the turtle were similar with only one peak where the water temperature at the turtle was higher than the bay water temperature.
Appendix 1.3D. Temperature profile of CIJKOW displaced to the north. Small decreases in water temperature at the terrapin correlated with air temperature. Increase in water temperature at the terrapin on day three suggested basking.
Appendix 1.3E. Temperature profile of KNOQW displaced to the south. The bay water temperature and water temperature at the terrapin are cyclic.
Appendix 1.3F. Temperature profile of KNOQW displaced to the north. Bay water temperature and water temperature at the terrapin are cyclic. Increase in water temperature at the terrapin on day four suggested basking behavior.
Appendix 1.3G. Temperature profile of HIJPW displaced to the north. Bay water temperature and water temperature at the turtle were cyclic. On day seven, greatest increase in water temperature at the terrapin for entire track suggested basking behavior.