

SHORT TERM TEMPORAL TRENDS IN ACTIVITY AND HABITAT SELECTION  
OF THE TEXAS DIAMONDBACK TERRAPIN.

by

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## ABSTRACT

### SHORT TERM TEMPORAL TRENDS IN ACTIVITY AND HABITAT SELECTION OF THE TEXAS DIAMONDBACK TERRAPIN.

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The Diamondback terrapin (*Malaclemys terrapin*) is a potential keystone species in the brackish marsh habitat due to its unique standing as the only Emydidae species to reside exclusively in brackish water. Despite this, the species faces many threats, including mortality in crab pots, boat propeller injuries, and alteration of crucial habitat. Little is known about terrapins in Texas, including habitat selection, range, and behavioral and activity trends, and even less is known about the nocturnal habits of the Diamondback terrapin. In this study, we compared the daily range and movement, habitat selection, behavior, and activity over a short term (diel and seasonal) period. We found a high interaction between season and diel period, with higher nocturnal behavioral and activity levels occurring during mating season. Significant interaction between soil, water, and air temperature and terrapin behavior was also detected. We also found significant decreases in distance travelled at night versus during the day as well as a preference for denser and taller vegetation at night. During this study, we documented the first occurrence of large

social burrows outside of brumation periods, with sometimes as many as 22 terrapins per burrow. While these groups exhibited no diel trends in behavior, sex ratios in these burrows changed as the season progressed. These behavioral trends may provide information on the nesting and mating seasons of Texas Diamondback terrapins, of which little is presently known.

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## INTRODUCTION

### *Life history and background information*

The Diamondback terrapin (*Malaclemys terrapin*) is one of the few Chelonian species that exclusively inhabits brackish water habitat. They belong to the *Chrysemys* evolutionary line of Emydidae, which also includes basking turtles such as the painted turtle and map turtle (Orenstein 2001). Their range extends from the Northern Atlantic coast from Cape Cod, MA, down to the Gulf of Mexico and Texas. They are found in a variety of coastal habitats, ranging from *Spartina alterniflora* salt marsh to mangrove forests (Brennessel 2006, Orenstein 2001).

Terrapin preference for estuarine ecosystems is a result of their unique adaptations that allow them to survive in brackish water. The Diamondback terrapin has several specialized adaptations for coping with varying levels of salinity, including the possession of a pair of lachrymal glands that secrete salt in the form of “salty tears”. These glands function as an extra kidney, but their salt secretion capacity as well as activity is much lower than that in sea turtles and is not sufficient for complete osmoregulation in 100% sea water (32 ppt) (Brennessel 2006). To compensate for this, they participate in osmoregulatory behaviors such as drinking fresh water that has accumulated in depressions from rainfall events. They also utilize behavioral osmoregulation when fresh drinking water is unavailable by increasing their basking

activity, which prevents additional salt influx that can occur during immersion in salt water while concurrently allowing salt excretion. Finally, it has been hypothesized that terrapins may minimize salt intake through diet by engaging in hyperphagia, during which they consume a large amount of food in times of high freshwater inflow so that they can fast during periods of high salinity (Davenport and Ward 1993).

The Diamondback terrapin is a highly sexually dimorphic species. Females are much larger overall than males, and have a larger head width and gape. They also possess thinner tails with the cloacal opening anterior to the edge of the plastron in contrast to the males, which have larger tails with the cloacal opening posterior to the edge of the plastron. In some subspecies, males can be more brightly colored than females, with blue skin and orange coloration on the carapace (Brennessel 2006). Sexual maturity is usually attained in 4-7 years for females and even less for males. However, maturity is often more closely correlated with size than age. Females mature at a plastron length of approximately 14 cm, while males mature at 8 or 9 cm. It is also common for southern populations of terrapin to reach sexual maturity at a younger age than northern populations: Females in North Carolina and New Jersey have been found to mature at around 13.5 centimeters in plastron length at approximately 7 years of age, while females in Florida have been found to mature at approximately 4-5 years of age. Similarly, males have been shown to reach maturity at approximately 9.0 cm and 5 years of age in North Carolina, while attaining maturity at 9.5 cm and 2-3 years of age in Florida (Siegel 1984). Small size in males is indicative of sexual selection pressures. In a species in which the males are small, such as the Diamondback terrapin, female sexual selection based on size and aggressive mate defense are not likely. It is more likely that the smaller size of males

is due to a higher investment of energy and resources into sexual reproduction and mating rather than aggression and mate defense. Therefore, a strategy that includes sexual maturation at a younger age and size would increase their reproductive output during their lifetime (Brennessel 2006).

Terrapin exhibit a type III survivorship curve with a clutch size averaging 12 eggs (Roosenburg and Dunham 1997) and a maximum life span of approximately 30-50 years (Roosenburg 1991, Tucker et al 2001), although some studies have calculated the average life span to be closer to 5.7 years based on instantaneous mortality rates in a South Carolina estuary (Tucker et al 2001). A type III survivorship denotes a life history where an organism typically experiences high mortality during the early life stages in contrast to later life stages (Molles 2005). Roosenburg (1991) estimated that in order to replace herself as a hatchling, a female Diamondback terrapin needs to undergo three years of maximum reproduction (Roosenburg 1991). This specific life history leaves terrapin extremely susceptible to local population depletion or extirpation due to human induced breeding female mortality. Females that have survived to reproductive maturity are highly valuable to the population as the limiting factor in offspring production, and their mortality can decimate populations. Furthermore, the time required to reach maturity (generation time) may prevent Diamondback terrapin from being able to quickly adapt to changing environments (Roosenburg 1991), which makes the terrapin especially susceptible to loss due to habitat alteration.

*Interactions with Humans and Conservation Issues*

Diamondback terrapin was a relatively inexpensive source of food until the late 1800's, and over 200,000 diamondbacks were processed in Maryland alone between 1800 and 1936 (Orenstein 2001). Many local and regional populations have still not recovered from historical overharvesting, and the species is now protected in Rhode Island, Alabama, Florida, Connecticut, and Massachusetts, and is considered a "species of concern" in North Carolina, Louisiana, Virginia, Delaware, and Georgia. Diamondback terrapin harvest is state regulated in Connecticut and New Jersey, allowing collection during a specified period of time. Diamondback terrapins are not listed or controlled in New York, South Carolina, and Texas (Brennessel 2006).

Even though terrapin are presently protected from overharvest in directed fisheries, there are still many threats to the survival of the species. These include blue crab fishery, vessel collisions, and destruction of nesting habitat (Roosenburg 1991). The Atlantic and Gulf Coast blue crab fishery has been documented as a major source of terrapin mortality (Roosenburg 1991, Roosenburg 2004, Butler and Heinrich 2007, Crowder et al 2000, Hoyle and Gibbons 2000). Terrapin that are not targeted by the fishery are incidentally captured along with other species of marine life as bycatch. Terrapin, enticed by the bait in the crab traps, enter the traps but are then unable to escape. Drowning in these traps is one of the primary sources of terrapin mortality. In one case, whole shells of 49 terrapin, along with the remains of several others, were recovered from a single crab pot (Roosenburg 1991). More recent data suggests a capture rate of 0.02-0.49 terrapins/trap/day in traps without bycatch reduction devices (BRDs), depending on trap location (Roosenburg 2004). Roosenburg and Dunham (1997)

predicted that, in “active” seasons, 100% terrapin mortality in crab traps would result in a decimation of 78% of the local population each year (Roosenburg and Dunham 1997). A recent study in North Carolina found 58% mortality in experimental crab pots, most of which occurred in May in the shallower waters near shore (Crowder et al 2000). Hoyle and Gibbons (2000) suggest that recreational crabbers rather than commercial crabbers may have the most negative impact on Diamondback terrapin populations as they set traps farther into creeks and shallow waters that overlap with terrapin habitat, and may also check their traps less often and have higher rates of crab trap abandonment (Hoyle and Gibbons 2000). Both recreational and commercial crab fishing are abundant in Texas, and 20% of the Gulf Coast production of blue crabs is from Texas (Perry 1984). This suggests that drowning in crab traps could potentially be a major source of mortality for terrapin in Texas, and further research is needed.

Female Diamondback terrapin are possibly more susceptible to man-made dangers than males in that they display nesting site philopatry. Philopatry is defined in ecological literature as the tendency of an individual to remain or return to their birthplace (Molles 2005). During their migration to these nesting beaches, females increase their range considerably and are vulnerable to boat propeller injury as they swim across open stretches of water to their nesting beaches (Tucker et al 2001). In one case, 19.7% of a studied population’s females had carapace boat propeller scars, while males only exhibited a 2.2% injury rate (Roosenburg 1991). In another study, 27.7% of terrapin in an Everglade population had carapace injuries associated with boat propellers (Hart and McIvor 2008). In addition to boat collisions, Szerlag and McRopert (2006) observed over 600 occurrences of female terrapins crossing roads during reproductive migration,

resulting in an average of approximately 8% mortality (Szerlag and McRopert 2006).

While there have been no published studies on road mortality in Texas, it is possible that road mortality is less of a threat to West Galveston Bay populations. Many potential nesting beaches are accessible by water and do not require crossing roads, so boat collisions may be a more present danger in Texas. However, we have received reports, in addition to our own personal observations, of a few female terrapins found crossing roads. These reports and observations are few in number.

Nesting site fidelity also causes terrapins to be extremely susceptible to destruction of nesting habitat. Altering the coastline to prevent erosion and reduced hurricane damage can alter the microclimate of the nesting area, and consequently alter the sex ratios (see Introduction: Habitat Selection: ESD). Planting beach grasses as erosion control for dunes can increase “grass root predation” on terrapin eggs, a process by which grass roots penetrate the eggs and absorb their nutrients (Roosenburg 1991, Lazell and Auger 1981, Stegmann et al 1988). Bulkheads built to reduce erosion effectively exclude terrapin from historic nesting grounds, causing them to nest in nearby lower elevation sandy habitat that is frequently inundated during high tides. Eggs found in these nests have little chance of hatching due to immersion during high tide and embryo drowning (Roosenburg 1991). Additionally, females will continue to expose themselves to increased risks such as boat collision, human interaction, and predation as they revisit destroyed or altered historic nesting areas (Roosenburg 1991).

Due to the combination of high natural mortality as described by the type III survivorship curve and high human induced mortality, local and regional terrapin populations are at great risk of local extirpation. The significance of increased terrapin

mortality and importance conservation is more evident when we observe their niche within the salt marsh.

### *Trophic Interactions*

Aside from the intrinsic value of being the only turtle within the family Emydidae capable of living constantly in brackish water, terrapin also play an important role in invertebrate population regulation. In the absence of predators, the periwinkle snail *Littorina littorea* becomes overabundant and overgrazes on the senescent (and sometimes living) portions of the marsh grass *Spartina alterniflora*, causing mass *Spartina* die off (Sillimian and Vieman 2001). The damage from the rasping of the snails results in more biomass loss than consumption itself, as well as stimulated microbial infection (Sillimian and Vieman 2001). While much of the top-down control of periwinkle snails is attributed to blue crabs (Sillimian and Vieman 2001), Tucker et al (1995) found that periwinkle snails account for 79% of terrapin diet in a South Carolina estuary. Terrapin may be considered a keystone predator if further studies continue to provide evidence of the regulation of invertebrate community composition within saltmarshes by terrapin.

Several studies have found differing composition of terrapin diet. In Davis marsh, North Carolina, the eastern melampus snail constitute the majority of diet (67.8%), as well as blue crabs and fiddler crabs (Spivey 1993). This study also found that diet largely corresponded to size of the terrapin: the diet of larger terrapins was predominately composed of blue crabs, mud crabs were eaten only by larger terrapins and not smaller terrapins, and fiddler crabs were predominately eaten by small and medium sized

terrapin. Diversity of diet increased with terrapin size. Spivey (1993) also found that prey density varied with distance from water and between low marsh and high marsh: fiddler and blue crabs were found in higher densities closer to water and in low-marsh (Spivey 1993).

The diet of Diamondback terrapin in Texas is unknown, but we have received reports from recreational fishermen of as many as 5 terrapins scavenging on a dead red drum. I have also observed several terrapin eating periwinkle snails. In one case, I found three terrapin in an abandoned crab trap, one of which was dead and had been partially eaten, presumably by the other two terrapins. Further research is needed on the diet and trophic interactions of Diamondback terrapin in Texas.

#### *Habitat Selection*

Terrapin habitat selection is largely influenced by sexual dimorphism and diet. The considerable large difference in gape size between males and females may promote gender-based resource partitioning (Tucker et al 1995). In a South Carolina study, the females' large gape size was found to permit a diet of large and small *Littorina littorea* (or periwinkle snail), as well as crabs and scavenged fish. The smaller gape size of males restricted them to small periwinkle snails (Tucker et al 1995). Because larger periwinkle snails inhabited less dense vegetation at higher elevations further from creeks, it was more common to find females foraging in these areas (Tucker et al 1995). High tide and marsh flooding enabled easy access into the marsh above the creeks and therefore increased foraging opportunities. Males were limited to foraging on the small periwinkle

snails that inhabit the thick, tall vegetation adjacent to creeks (Tucker et al 1995). However, these trends have only been observed on the Atlantic coast, and no research has been done in Texas on tidal influence on prey availability and habitat selection.

Sexual size dimorphism is also strongly correlated with habitat use. Larger females have been found to swim further into open water, and distance from shore is positively correlated with plastron length (Roosenburg et al 1999). They proposed that this may also have to do with gender-based resource partitioning. In the Chesapeake Bay, larger clams are found further from shore, and terrapin may require greater crushing strength associated with larger jaw size to feed on these clams. Roosenburg et al (1999) also found a higher abundance of female terrapin in the upper reaches of the marsh and male terrapin along the edges of the marsh and channels, which supports Tucker's gape size limitation hypothesis.

While terrapin utilize many habitats over the course of their life, including tidal creeks and salt marshes, nesting habitat is regarded as one of the most important habitats for their life cycle, and losing just this part of their habitat range could cause the decimation of their population (Brennessel 2006). Terrapin exhibit environmental sex determination (ESD) that is heavily influenced by temperature. A constant incubation temperature of 28.5°C to 29.5° C is required to produce mixed sex ratios, while temperatures outside this range produce mono-sex clutches (Roosenburg and Place 1995). Maintaining appropriate sex ratios may be difficult for terrapins due to the large daily variation in the temperature of Diamondback terrapin nests as compared to sea turtle nests (2-12° variation) (Burger 1976a). Female terrapins therefore need to have a wide variety of nesting microhabitat choice in order for sex ratios to be balanced

(Roosenburg 1994). Consequently, obtaining a healthy sex ratio is very dependent on nesting site selection. Terrapin nesting habitat is also more variable compared to sea turtles, and includes dike roads, sand dunes, and shell hash beaches (Roosenburg 1994). Only one terrapin nest has been documented in Texas, and so nesting habitat is largely unknown, but nesting is assumed to occur in high elevated shell hash (Hogan 2003).

Very little is known about the first few years of the Diamondback terrapin's life (Gibbons et al 2001). Juveniles and hatchlings appear to be absent from habitats in which most adults are found, suggesting a difference in hatchling habitat preference (Gibbons et al 2001). This different habitat has been largely unknown until recently, although released hatchlings have shown a preference for shore vegetation and tidal wrack rather than water (Burger 1976b). Recent studies have found hatchlings under patches of *Spartina patens* and *Distichlis spicata* in the intertidal zone of the upper marsh (Draud et al 2004), and these hatchlings move toward higher elevated upland marsh in the fall and toward water (away from upland habitats) in the spring (Muldoon 2010). Draud et al (2004) found high nocturnal predation rates on hatchling Diamondback terrapin by the Norway rat in New York, and Muldoon (2010) found possible predation by raccoons, Norway rats, ants, and birds.

As temperature decreases in November through January, terrapin must select locations to hibernate. This involves cessation of foraging, a drop in metabolism, and a retreat into tidal creeks. During hibernation, they burrow in the bottom of deep creeks and in the side of creek banks. Burrowing can either be singular or communal (Yearicks et al 1981). In a 1997-2000 radiotelemetry study in a Florida salt marsh, a radiotagged female was found burrowed in 3-5 cm of mud in low areas near creeks that were flooded at high

tide. From November until January, her burrowing location varied, but from January through February, she remained burrowed in one spot (Butler 2002).

In Texas, our continuing study has found active terrapins (walking and swimming) year round, although the majority of terrapin burrow in late November until late February. Burrowing sites vary in vegetation cover and location, as we've found terrapins burrowed in creeks, creek banks, and terrestrial marshes with 100% vegetation cover and vegetation height of half a meter or more. In one case, a single female terrapin swam a distance of approximately 2.3 km between sites (from South Deer to North Deer) in February, with water temperatures near 18° C.

### *Activity Trends*

Generally, terrapin emerge and breed in the spring, disperse in the summer, retreat into tidal creeks in the fall, and hibernate during winter (Brennessel 2006). In South Carolina, Gibbons et al (2001) observed the highest levels of terrapin activity in April, with a second peak of male activity in October. However, terrapins have been observed to be active from early March until late November in some study locations, such as New Jersey (Butler 2002). Butler (2002) noted the highest terrapin activity at a water temperature of 25°C and a salinity of 20 ppt. Hurd et al (1979) noted a decrease in population size (or capture rate) as the summer progressed. Seasonal variation in activity is most likely due to a temperature response in terrapin. At extreme temperatures, terrapin remain burrowed (Brennessel 2006), while on days with more moderate temperatures, terrapin catch rate is

higher, suggesting higher activity (pers. observation). However, there have been a few observations of terrapin swimming in water less than 14°C (Butler 2002).

During spring emergence, common terrapin activities include foraging, nesting, mating, swimming, basking, and some burrowing. From 1997 until 2000, a radiotelemetry study was conducted on terrapin within a Florida salt marsh (Butler 2002). He observed that during the warmer months (June), some terrapin burrowed in shallow mud, but during March and April, most terrapin observed were swimming and walking in the *Spartina alterniflora* marsh. In one instance, a mating lek was observed in Grice Cove, South Carolina (Estep 2005).

The most prevalent activity during spring emergence is that of mating and nesting. Terrapin display nesting site philopatry, and annual female reproductive migration to nesting sites exposes females to greater risk from open water sources of injury (Roosenburg 1991, Tucker et al 2001) as well as car collisions (Szerlag and McRopert 2006) in comparison to males.

At smaller time scales, terrapin activity on the Atlantic coast is highly influenced by tides. High tide allows females easier access into the upper reaches of the marsh, and is therefore correlated with foraging behavior (Tucker et al 1995, Roosenburg 1991). Although not studied, it is possible that terrapin would display this same high tide foraging pattern at night. High tide is also correlated with swimming activity while at low tide terrapin are more likely to bask or burrow (depending on the temperature) (Tucker et al 1995). However, most studies pertaining to tidal patterns in terrapin behavior and habitat selection have been conducted on the East Coast where tides can have a

considerably higher range of fluctuation. Little is known about how terrapins partition their habitat in regards to tidal levels in Texas and further data is needed.

### *Range*

Terrapin display variable levels of home range and site fidelity. Previous studies have found that on a larger scale, high site fidelity can limit terrapin's ability to re-colonize abandoned creeks (Tucker et al 2001). Similar studies show 5.7% migration rates with a maximum range of 0.7 km (Gibbons et al 2001). In these studies, female migration rates and range were found to be higher than males (Gibbons et al 2001, Tucker et al 2001, Butler 2002, Hogan 2003). Migration rates are most likely correlated with dietary needs, reproduction, and habitat selection, and are ultimately limited by the habitat available and ease of movement. Spivey (1993) calculated a home range of  $305.4 \pm 64.5$  ha for female terrapins in a North Carolina estuary using a Minimum Convex Polygon method, and Butler (2002) calculated a home range of  $54.33 \pm 54.80$  ha in Northeastern Florida. Clearly, estimates of home range vary between regions and studies, and needs to be further researched. Once again, these previous studies have mostly been conducted on the East Coast, and more data is needed on range in Texas. Preliminary data from our ongoing research shows our home ranges to be approximately 25 ha, but our population is insular and may not be an appropriate comparison to larger marsh populations.

### *Nocturnal Behavior*

There has been little research on the nocturnal behavior of Diamondback terrapin. Past studies on the Atlantic coast have suggested that the Diamondback terrapin is a diurnal species that burrows and sleeps at night (Orenstein 2001). The personal observations of Jeff Lovich and Whit Gibbons indicate that terrapin are not captured in overnight traps and seines, and therefore support this diurnal theory (Jeff Lovich and Whit Gibbons – pers. comm. at the Diamondback Terrapin Working Group Conference in 2011).

However, some studies along the Atlantic coast suggest limited activity at night (Roosenburg 1994, Burger and Montivecchi 1975, Hart and McIvor 2008). However, no studies have been conducted in Texas that give any indication to the nocturnal habitats of terrapin. During the course of my study, I have observed female terrapin activity in the saltmarsh cordgrass at night, which may be indicative of foraging activity. Hart and McIvor (2008) have successfully dip netted Diamondback terrapin at nocturnal low tides in the Everglades, indicating nocturnal swimming activity. There have also been several observations of terrapin nesting at nocturnal high tides in Maryland and New Jersey (Roosenburg 1994, Burger and Montivecchi 1975). Based on preliminary observations, I have also observed summer nocturnal group burrowing, which is also associated with hibernation periods (Yearicks et al 1981).

While there has been little research on terrapin nocturnal activity, there has been some nocturnal behavior observed in other species of turtles. Green sea turtles have been found to exhibit nocturnal feeding, swimming, mating, and nesting (Jessop et al 2002). In these occurrences, it was found that nocturnal melatonin and corticosterone levels were

comparable to diurnal levels rather than fluctuating with a diel cycle. It was proposed that these activities under normal hormonal ranges allow green turtles to acquire resources that may be more readily available at night than during the day (Jessop et al 2002). Several species of sea turtle, including the Loggerhead, also hatch and emerge nocturnally (Witherington et al 1990). Our hypothesis is that terrapin exhibit nocturnal behavior for similar reasons, such as habitat partitioning and efficient food acquisition.

Several species that co-inhabit the salt marshes exhibit nocturnal activity, including prey animals such as fiddler crabs. Early research efforts found that fiddler crabs were actually less likely to be disturbed by human intrusion at night (Burkenroad 1947). During the day, fiddler crabs would scatter at even the slightest movement or intrusion, thus making their study difficult. At night, they were much harder to disturb, as when he shone a flashlight on them, they were less likely to disperse. The observer could walk much closer and move a significant amount, even to the point of actually picking them up, before they would disperse (Burkenroad 1947). It is possible that this decrease in predator awareness could provide optimal nocturnal foraging opportunities for terrapin. Juvenile fish have also been shown to partition resources via temporal differences in activity. For example, in a 1977 study in a South Carolina estuary, flounders and grass shrimp were captured mainly at night, while worm eels were only collected during the day (Shenker and Dean 1979). Once again, this temporal partitioning in fish could lead to optimal foraging at night for terrapin.

Understanding the diurnal and nocturnal habits of terrapin is important for conservation and management plans. For example, if terrapin are not found in the water at night, then the potential impacts from nocturnal crab trap deployment would be

minimal. In general, a better understanding of terrapin nocturnal habits is required for management and understanding the ecology of this species.

### *Study Objective and Hypothesis*

The primary objective of this study was to characterize the short term trends (including diel and seasonal trends) in behavior, activity, habitat selection, and daily movement of Texas diamondback within South Deer Island complex, Galveston Bay, Texas. This island complex is representative of many islands found within Texas Gulf coast estuaries.

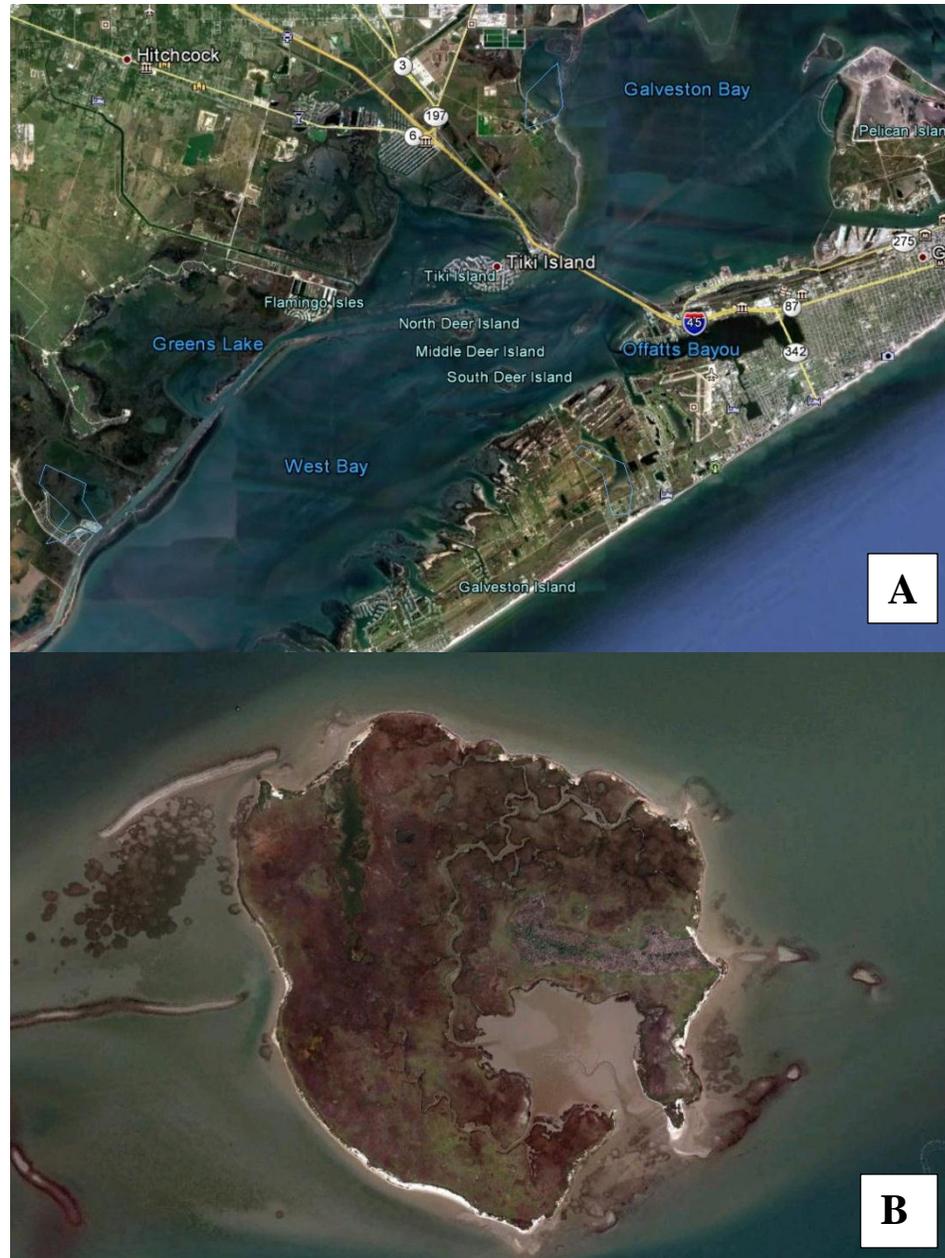
Based on previous literature, during the hottest part of the summer I expected to find some female foraging activity in the marsh at night, and more extensive male foraging at night. However, in the early spring and late summer/fall, I expected to find an increase in the number of terrapin burrowed nocturnally. This change in behavior would also shift nocturnal terrapin habitat selection from intertidal marsh and open water to soft mud in creek beds. Overall, I expected terrapin activity to be more closely correlated with monthly or seasonal trends, temperature, and tide rather than time of day. I also expected to find more site fidelity and less total distance moved during nocturnal activity and burrowing.

## METHODS

### Study Site

South Deer Island has an area of 29 hectares and is characterized by frequently inundated low lying salt marsh dominated by smooth cordgrass (*Spartina alterniflora*) (Figure 1). An extensive tidal creek network is found on the interior of the entire island with outlets connecting to Galveston bay at the North and East ends, and to a large lagoon at the South end. Higher elevations are found along the perimeter of the island, as well as on a narrow, 1 hectare mound on the east side of the island. These areas are characterized by shell hash mounds and a shift in vegetation from *S. alterniflora* to *Iva frutescens*. The only documented terrapin nest in Texas was found in this elevated shell hash habitat (Hogan 2003), indicating that it could be a critical nesting site for the Deer Island complex. This thesis is in conjunction with the Environmental Institute of Houston's ongoing monitoring study that began in 2008 and has continue past the period of my study. At the time of this study, 362 terrapin were already tagged on South Deer and 120 were tagged at the nearby North Deer Island. There have been several instances of individual migrations between these two islands as well as a third study site on Galveston Island, indicating that the population on South Deer is not closed. Although data for terrapin movement existed for the 3 years previous to this study, we did not use any habitat selection or behavioral data before 2011 in order to eliminate additional

variability due to inter-annual patterns in weather and rainfall, since the focus of this study was the comparison of diel rather than annual trends.



**Figure 1. South Deer Island in Galveston Bay, Texas. Top figure shows location of South Deer Island in Galveston Bay (A) and close-up showing major features (B).**

The period of study (February 2011- September 2011) was characterized by an unusually severe drought that ranked as the second driest year in Texas, falling second only to the 1917 drought ([www.noaa.gov](http://www.noaa.gov), National Climatic Data Center). This may have influenced the behavior and habitat selection of terrapin due to their dietary requirement for freshwater. A total of 15 sampling events occurred during the study period. Sampling events consisted of a 24-hour observation period on South Deer Island during which radio-tagged terrapin were tracked every two hours and randomized transect land searches were conducted an hour before and after sunrise, noon, sunset, and midnight.

#### Methods of Terrapin Capture

We employed several capture techniques to maximize effectiveness and minimize bias associated with any single method (Hurd et al 1979). Our methods included passive and active acoustic telemetry, active radio telemetry, trapping, and randomized land searches. While these methods all provide data to answer the same questions, the results from each method were first treated separately because of differences in capture probability, and then combined to identify any overarching pattern and significant differences in the efficiency and information provided by different capture techniques.

### *Randomized Land Searches*

For each 24-hour sampling event, randomized land searches were conducted for a two hour period beginning an hour before and ending an hour after sunrise, noon, sunset, and midnight. Randomized land searches ideally would begin with randomly selecting a portion of the island as a starting position for transects. However, due to the presence of several sensitive species of nesting birds on the island, including the White-faced ibis, White ibis, Caspian and Least terns, and American Oystercatchers, large portions of the island were restricted (Figure 2). This resulted in limited search areas with only one possible base camp and therefore one possible starting position for transects. From this point (Latitude: 29.274423°, Longitude: -94.910994°), the horizon was dissected into equal portions and randomly assigned to the available searchers. Once a transect was assigned, the searchers walked in a straight line toward their reference on the horizon and did not deviate from this line until they could not walk any further (i.e. when they arrived at the edge of the island or when they encountered a restricted avian nesting area). When they encountered an impasse such as this, they turned and walked a new straight line transect at a 45° angle to the right of their previous transect. These transects crossed every habitat type on the island, including dense marsh as well as creeks and lagoons, and resulted in very little selection bias.



**Figure 2. Portions of South Deer Island that were restricted due to sensitive nesting bird species during study period. Red indicates areas that were restricted for the majority or all of the study, and the pink area was restricted only for approximately the first half of the study.**

One potential source of error associated with random land searches arises from differences in terrapin detectability associated with differing habitat. For example, our detection distance in an open area such as a lagoon or creek crossing is much higher than the detection distance in densely vegetated marsh. This could lead to false conclusion that terrapin have a higher preference for areas such as creeks, lagoons, or sparsely vegetated marsh simply because they are easier to detect in these areas. At night, this bias would be reduced because the terrapin detection distance is restrained by the power of the spotlight used and area illuminated, and therefore detection distances in open spaces should be comparable to vegetated areas. This bias is also eliminated during radio-telemetry.

### *Radio Telemetry*

During each sampling period, a few individual terrapins which had been affixed with a radio tag were tracked in two hour intervals over a 24 hour time span. We used the ATS R2001/2100 receiver and R2000 2.5 KHz transmitters that were affixed to the second right carapace scute with marine Epoxy (PC) (Figure 3).



**Figure 3. Female terrapin affixed with ATSR2000 radio tag to second back right scute. With Emma Clarkson.**

We used two different sizes of transmitters for males and females, weighing 12 and 24 grams, respectively. These tags were set at a pulse rate of 40 ppm and a pulse

width of 22 ms. The 12 gram transmitters typically had a battery life of 182 days while the 24 gram transmitter had a battery life of approximately 843 days. Tag size, weight, and pulse rate were specified to maximize battery life while minimizing weight. It has been calculated that terrapin are not affected by tags weighing 5% or less of their bodyweight (Kenward 2001), so only males weighing 0.24 kgs and females weighing 0.48 kgs can be tagged. This caused some bias in the data, as the male tags had a much shorter battery life than the female tags and had ceased emitting signals before the start of this study. Therefore, we only collected radio telemetry data on female terrapin. During the course of this study, there were 14 terrapin radio-tagged on South Deer Island. While we attempted to track the same terrapin during every sampling period, there were sampling events during which only certain terrapin could be located using radiotelemetry. We tracked 2-5 terrapin each 24 hour period and a total of 8 female terrapin during the course of the study.

We conducted a range test for the ATS2001/2100 receiver and found that the detection limit is variable based on depth of submersion in water as well as the tag size. In air, a female (24 gram) transmitter can be detected from over 1.07 km, but the detection limit is drastically reduced to 0.1 km and 0.07 km when submerged at 0.05 m and 0.1 m in salt water, respectively. The receiver was not able to detect the transmitter when submerged past 0.1 m.

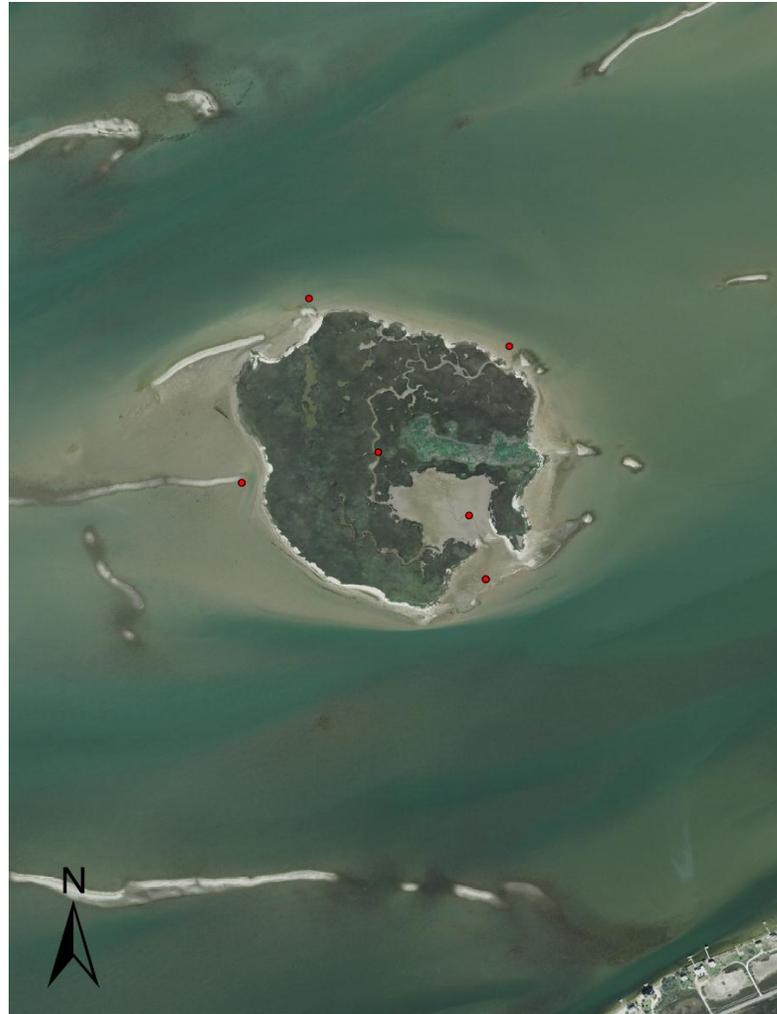
Until August, we were unable to track radio tagged terrapin once they entered the water and submerged below 0.05 m. To determine how to classify absence, I observed a radiotagged terrapin swimming for twenty minutes, and recorded the duration and frequency pattern of the signals received. When a radio tagged terrapin was not found on

land but transmitted a signal characterized by this frequency and duration, we assumed it to be swimming. This signal was typically characterized by several (2-5) strong beeps followed by a few (1-3) attenuated signals and then long periods (several minutes) of no signal. The total absence of a signal was not assumed to be any behavior or habitat selection and was classified as no data.

### *Acoustic Telemetry*

Because of the high salinity of our site (typically 30+ ppt), radio signals are severely attenuated when the transmitter is submerged in only a few inches of water. After approximately half a meter of submersion, they are nearly undetectable. Therefore, we also employed acoustic telemetry, with which we could detect terrapin in water but not on land. We used VEMCO VR2W stationary receivers in conjunction with VEMCO V13-1H pinger transmitters. The receivers were set in an array of 4 around the perimeter of the island and two in the interior water bodies: one in the center of the main creek and one in the center of the inner lagoon (Figure 4). The transmitters had an estimated battery life of 370 days, transmitted at a frequency of 69 kHz, and used A69-1303 coding space (Figure 5). The tags and receivers were set to communicate through the full extent of the study period with no breaks in transmission or reception, and therefore will show any nocturnal vs. diurnal swimming activity from the tagged terrapin who are in the water and vicinity of the receiver. While we had three continuous years of data from these stationary receivers, I only selected data from October 2010- October 2011 so that environmental conditions were nearly identical to and overlapped those at the time of

hand capture and radio-tagged individuals. During this time period, a total of ten terrapin (5 females and 3 males) were tagged with V13-1H.



**Figure 4. Arrangement of Acoustic Receivers around South Deer Island. Red dots indicate location of acoustic receiver.**



**Figure 5. VEMCO V13 acoustic tag affixed to a larger male Diamondback terrapin with marine Epoxy.**

In August 2011, we began active acoustic telemetry tracking using the VEMCO VR100 ultrasonic tracking receiver with a directional hydrophone in conjunction with coded VEMCO V13 transmitters (Figure 6). We used this manual tracker in addition to the stationary receivers because the data it provides is very different: the stationary receivers can only detect and log the data of terrapin that swim within its range, which covers mainly the open bay around the island and the larger creek systems. The manual tracker, however, allows us to actually search smaller creeks and ponds for terrapin that are not appearing on the stationary receivers. We conducted a range test of the VR100 at our study site that showed that the VR100 can detect tags within a 1.015 km radius. This

range was calculated under the following conditions: salinity 31 ppt, water temperature 28 C, and secchi disk turbidity 0.291 m. At the full extent of the range, the transmitter was detected with a 60 DB signal on the “far” setting with gain set to 48. The range can be expected to change based on these parameters; in lower turbidity and salinity, the range could potentially be much higher.



**Figure 6. Using the VR100 manual acoustic tracker. With Emma Clarkson.**

These tags also transmitted at 69 kHz, and so can be detected by both VR2W and VR100 receivers. The four terrapin that were tagged with coded V13 transmitters were also given small radio tags, so that they could be tracked both terrestrially and aquatically (Figure 7). Using these tags, we spent two 24-hours periods focused just on the tracking

and documentation of the behavioral patterns of these four terrapin. Due to the 5% body weight rule mentioned earlier, we could only double tag very large females, so all behavioral observations from this segment of the study is biased toward females. Unfortunately, two of the double tagged terrapin died after the study, with the expected cause of death being old age. I do not think that the cause of death was related to stress from tagging, as we had a high death rate in our South Deer population during normal surveying in the year of study. However, this may negate some of the behavioral data from them, as they may have behaved unusually before death. The results from these two sampling periods were included in general analysis of behavior and habitat selection, but were also analyzed separately and qualitatively.

During the two 24-hour periods that we tracked the double-tagged terrapins, we were unable to perform any additional land search and hand capture transects. We did occasionally capture other individuals during our radio and acoustic telemetry, but because of our focused effort on telemetry, all August data is highly biased towards these four terrapins.



**Figure 7. Large female diamondback terrapin affixed with both a V13 acoustic transmitter tag and a ATSR2000 radio transmitter tag.**

### *Trapping*

Modified crab traps of my own design (Figure 8) were deployed in open bay, tidal creeks, and the lagoons to determine nocturnal and diurnal utilization of these aquatic habitats.

We initially attempted to utilize these traps in every sampling period, but due to logistical and time constraints we had to abandon this method.

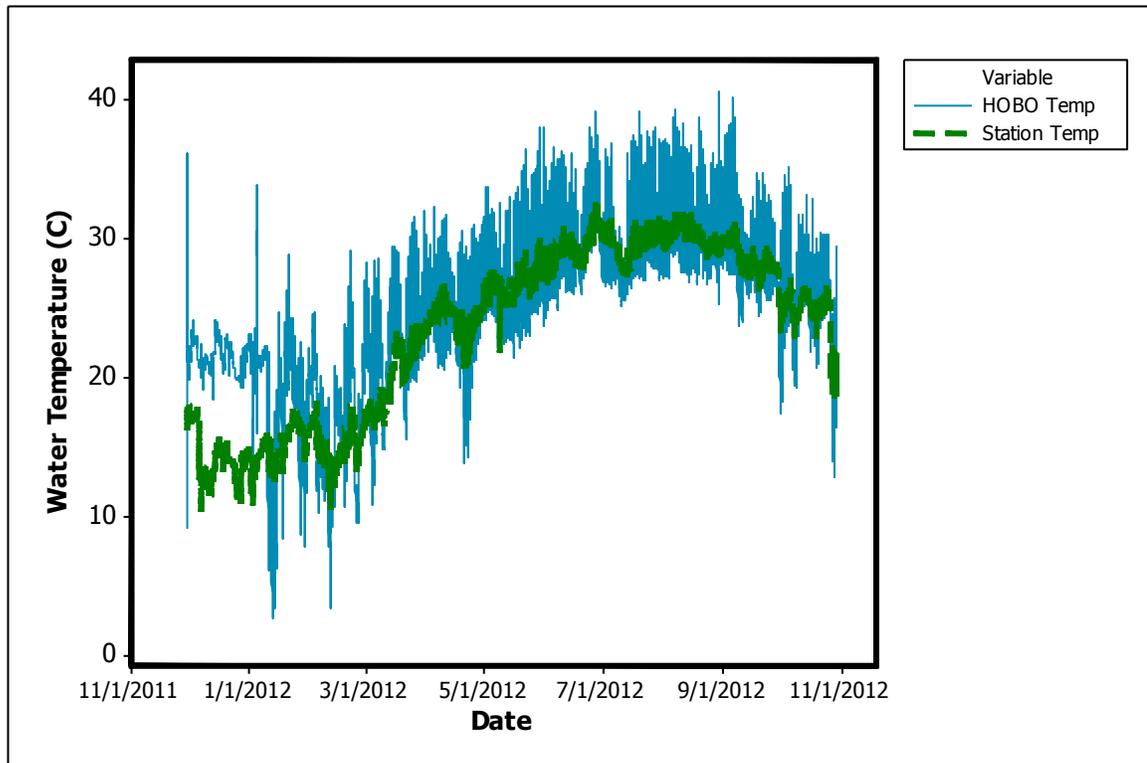


**Figure 8. Modified crab traps, designed by Emma Clarkson. The base of the modified trap is made from two crab traps on top of each other. The top was removed from the bottom trap and the bottom and top were removed from the top trap to create one large open space with 8 points of entry.**

### *Physical-Chemical Data Collection*

Soil temperature was logged hourly during the study using HOBOWare<sup>®</sup> temperature tidbit that was buried 6 inches deep in shell hash on the north beach of South Deer Island. Water temperature was originally set to record on a HOBOWare tidbit that was deployed in shallow water near South Deer Island. However, the tidbit was damaged during the study and no data could be retrieved. Instead, I used water temperature data from the closest NOAA tide gauge, which was at the North Jetty entrance to Galveston Bay. Because this was not ideal for some data, I deployed a HOBOWare tidbit in the main creek of South Deer Island the year following my study. Using the 2012 data from this

tidbit, I created a regression plot between the tide station water temperature data and the actual water temperature from South Deer Island. A comparison of tide station data and HOBOware data for 2012 can be found in Figure 9. I then used this regression equation to extrapolate and predict more accurate temperature data for the period of my study. This extrapolated data was only used in the analysis of aquatic versus terrestrial habitat preference, which will be discussed later. Air temperature was measured at the time of surveys using a Kestral<sup>®</sup> handheld meteorological meter. Tide data was downloaded from the NOAA tide gauge at Pier 21, which is located in West Galveston Bay between Pelican and Galveston Island at latitude 29.31000 longitude -94.79333, approximately 12 km from South Deer Island. We had previously measured turbidity during terrapin sampling events using a Secchi tube, but this was impossible at night and therefore we could not obtain paired data on nocturnal versus diurnal turbidity levels around South Deer Island. Note that when water and soil temperature trends are analyzed, the temperatures reported are ambient temperature not obtained at the exact point of capture of the terrapin. Actual microhabitat temperatures experienced by the individual terrapins (referred to as operative temperatures) can only be predicted and are not presented in my results.



**Figure 9.** Water temperature data from the NOAA tide station (green) and the HOBOWare tidbit on South Deer Island (blue) for 2012. A regression showed the relationship between these two data set to be “HOBO Temp = 6.60 + 0.791 Station Temp” with an R-sq value of 66%.

#### *Utilization and Synthesis of Data from Different Methods*

It has been shown that the utilization of many capture techniques counteracts the bias associated with each individual technique (Hurd et al 1979). Previous studies have compared radio telemetry and hand capture data as well as analyzing them separately and have found an increase in accuracy by combining the data. Powell et al (2005) analyzed Wood thrush nesting habitat selection and as nest survival using hand capture and radio telemetry analysis. They found that radio telemetry revealed extended habitat selection that traditional capture efforts had previously not located. The difference in distribution detected by radio versus hand capture showed that radio capture was effective in

identifying nesting habitat in areas that traditional search may have had a low detection probability (i.e., in higher elevated habitats). They found no difference in behavior or survival rate between individuals with and without radiotags, and identified radio telemetry as an unbiased source of habitat selection data (Powell et al 2005). In another study, Powell et al (2000) found that combining traditional hand mark recapture methods with radio telemetry of Wood thrushes resulted in a more precise description of movement between habitat types and recapture rates, especially in cases where the sample size for hand capture events is small (Powell et al 2000). Conversely, Kooper and Brooks (1998) found that combining hand capture and radio telemetry data did not reduce the amount of error resulting from unequal catchability in painted turtles.

Given the contradictory results in literature from combining methodologies, I identified the most appropriate use of methodologies in my study on an individual basis based on the primary research question. In most cases, small sample size and low detection probability in densely vegetated habitats necessitated combining the data from hand and radio capture for behavior and habitat selection. The major assumption when doing this is that the presence of radio tags does not affect terrapin behavior or habitat selection.

I did not combine passive acoustic telemetry data with hand capture or radio telemetry in any analysis because all acoustic capture events have a theoretical 100% detection probability in water, but a 0% detection limit of terrestrial behavior. This bias would skew the data significantly toward higher aquatic behavior and habitat selection. While similar concerns exist for radiotelemetry and terrestrial monitoring, I was actually able to locate swimming terrapin with radio telemetry, indicating that there is also a

reasonable detection probability for terrapin in water. Some swimming events were inferred from the radio transmission pattern (See Section *Methods of Terrapin Capture: Radiotelemetry*). All passive acoustic data from the stationary receivers was analyzed separately and was compared to hand and radio capture data qualitatively but not quantitatively.

### Measuring and Analyzing the Behavior, Activity, Habitat Selection, and Range

#### *Behavior and Activity*

To document the differences in behavior between diurnal and nocturnal periods, I used an ordinal classification scale to classify and rank the behavior and activity of each terrapin at the time of capture. Using this scale, I assigned a value 1-5 to activities and behavior that increased from burrowing to swimming, respectively. A value of “1” represents a terrapin that is burrowed and inactive, while a value of “2” represents a terrapin that is burrowed in very shallow mud “pocket”, is not completely covered with substrate, and shows signs of recent activity (Figure 10). Signs of recent activity include freshly disturbed mud, identifiable and fresh tracks leading to the terrapin, and general alertness of the terrapin. Values 3-5 represent terrapin that were sitting on the surface of the marsh, walking, and swimming, respectively. Swimming (5) represents the highest level of activity observed. While there is no evidence supporting that swimming is the highest calorically demanding activity, I still considered it as the “highest level” of activity not from a caloric standpoint but rather a functional one: when a terrapin is swimming, it has

no vegetation cover and therefore no protection from predators. Swimming therefore requires constant alertness. Many non-thermoregulatory behaviors also occur during swimming events, such as mating and foraging (see *Activity Trends* section).



Figure 10. A burrowed turtle with a behavioral value of 1 (left) versus a "turtle pocket" and behavioral value of 2 (right).

Ranked data cannot be analyzed using parametric statistics (Lehner 1998).

Therefore, I used the non-parametric Kruskal Wallis one-way ANOVA with the Minitab<sup>®</sup> software package to determine significant differences in behavioral ranks between diel and monthly periods. While running this test, I had to “collapse” month and diel period into a month/diel period variable combination due to unbalanced data and software restrictions. For example, instead of running a two-way test that treated “month” and “diel period” separately, I manually created combinations such as : Jan Day, Jan Night, Feb Day, Feb Night, Mar Day, Mar Night, and so on. From here on, this “collapse” will be referred to as the “month/diel period variable”. This was used to determine if any interactions between month and diel periods could be identified. To further identify environmental factors that may influence functional or thermoregulatory behaviors such

as predator avoidance and basking, I used an One-Way ANOVA to determine if the mean air, soil, and water temperature differed at the time of capture during different behavioral types. I then used Pearson's correlation to compare behavioral rankings of the terrapin with the air, water, and soil temperature at time of capture to determine if there was a clear trend in the correlation.

Due to the potential overlap of some activity patterns, we also used a more clear cut and definitive measure where we divided the behaviors into two groups: active versus inactive. All of the 5 classification categories can be reclassified into static and dynamic behavior. A static behavior is one in which an individual is unmoving with relationship to its environment (for example, burrowed alone), while a dynamic behavior is one in which either an individual is moving with respect to its environment (general) or an individual's body part is moving with respect to its body (localized) (Lehner 1998). For example, using my original ordinal scale, values of 1 in the ordinal scale represent static behavioral units and were recorded as 0, and values of 2-5 represent dynamic individual units and were recorded as 1 for active. In this way, I was able to classify terrapins as "active" (values 2-5 = 1) or "inactive" (value 1 = 0) at the time of capture. Kruskal Wallis showed that the activity and inactivity trends followed the behavioral trends exactly, so I found further analysis of "activity" between diel periods and months null. However, I did describe the water, soil, and air temperature during periods of inactivity versus activity with a histogram depicting at what temperature terrapins can be found active or inactive. A summary of the statistical tests used to analyze behavioral trends can be found in Table 1.

**Table 1. Summary of statistics used to analyze behavioral data.**

Testing for:	Test Used:	Variables Assigned	Data Set	Reasoning
Difference in behavior between Night and Day during Different Months	Kruskal Wallis ANOVA	Month - Diel Variable Collapse as classification factors, behavioral levels 1-5 as sample	All captures (hand, radio, and manual acoustic), tested males and females separately	Behavior is a non-parametric term and therefore cannot be tested with parametric ANOVA. Month and diel period had to be "collapsed" into month/diel combinations due to unbalanced data.
Difference in mean air, water, and soil temperature during differing terrapin behaviors	ANOVA	Behavioral levels 1-5 as classification factors, temperature as sample	All captures (hand, radio, and manual acoustic), tested males and females separately. Air, water, and soil temperatures analyzed separately	Temperature can be tested parametrically, so One-Way ANOVA appropriate
Trends of increasing or decreasing air, soil, and water temperature with increasing/decreasing levels of behavior	Pearson's Correlation	Correlation between behavior, temperature	All captures (hand, radio, and manual acoustic), tested males and females separately.	Because one term was non-parametric (behavior), a non-parametric correlation was required rather than a linear regression model
Descriptive statistic for "activity" levels at different air, soil, and water temperatures	Histogram	"Active" (any behavior with a ranking of 2 or more) and "Inactive" (a behavior with the ranking of 1) as the classes, temperature as the sample	All captures (hand, radio, and manual acoustic), tested males and females separately. Air, water, and soil temperatures analyzed separately	Needed to provide a visual representation and description for what temperatures occur during which levels of activity

When measuring behavior, common sources of variability include the observer effect and inter-observer variability such as differential detection ability. The observer effect occurs when the presence of the observer disturbs the organism being observed, resulting in a non-normal behavior (Lehner 1998). Differential detection ability occurs when several observers may have differential capture efficiency and therefore may miss organisms performing certain behaviors, causing bias in the data (Lehner 1998). Interpersonal error is difficult to avoid in any study, but the small number of researchers and the consistency of the field crews drastically reduced this error in our study. For the most part, only one or two people captured and processed terrapin during the course of this study. The observer effect was minimized through the definition of the classes in the behavioral ordinal scale. For example, a terrapin that is burrowed or in a turtle pocket is

unlikely to have a drastic change in behavior that results in a different classification in the short amount of time that the observer is apprehended by the terrapin. The only categories that may be affected by this error are 3 and 4 (sitting vs. walking), and this must be considered when analyzing the data. However, during all investigations the senior investigator accompanied survey teams to insure consistent methodology.

### *Social Behavior*

During this study, I observed burrows in which two or more terrapins had congregated. I coined these “social burrows” and analyzed these “social” tendencies further. I compared both the total number of terrapin in each burrow and the sex ratio of each burrow (analyzed as % female composition of the burrow) to diel period using a T-test. I then used data from previous years (2010-2011) when social burrows had been observed to determine if there was a difference in both mean number of terrapins in each burrow and sex ratio in each burrow between months. I could not analyze any differences in number of terrapin or sex ratios in social burrows between diel periods or the “month/diel period” variable combination for this ongoing data as the nocturnal effort was not equal to the diurnal effort in 2010. A summary of statistical tests used to analyze social behaviors can be found in Table 2.

**Table 2. Summary of statistical tests used to analyze social behavior data**

Testing for:	Test Used:	Variables Assigned	Data Set	Reasoning
Difference in the mean number of terrapin found in a social burrow at night versus during the day.	T-Test	Night and Day as classification factors, number of terrapin/burrow as sample	All captures (hand, radio, and manual acoustic) found in a social burrow, males and females together, ONLY during the sampling period of thesis work	The number of terrapin in each burrow is a discrete number and can therefore be analyzed parametrically. With only two factors (night and day) the T-Test is most appropriate
Difference in the mean sex ratio of social burrows at night versus during the day	T-Test	Night and day as classification factors, % female composition of burrows (representation of sex ratio) as sample	All captures (hand, radio, and manual acoustic) found in a social burrow, males and females together, ONLY during the sampling period of thesis work	The percent female composition of each burrow is a discrete number and can therefore be analyzed parametrically. With only two factors (night and day) the T-Test is most appropriate
Difference in the mean number of terrapin found in a social burrow between months	One-way ANOVA	Month as classification factor, number of terrapin/burrow as sample	All captures (hand, radio, and manual acoustic) found in a social burrow, males and females together, during ongoing sampling from 2010-2011	Could not analyze diel period or month-diel variable combination as there was not an even, standardized nocturnal effort paired with diurnal efforts during 2010
Difference in the mean sex ratio of social burrows between months	One-way ANOVA	Month as classification factor, % female composition of burrows (representation of sex ratio) as sample	All captures (hand, radio and manual acoustic) found in a social burrow, males and females together, during ongoing sampling from 2010-2011	Could not analyze diel period or month-diel variable combination as there was not an even, standardized nocturnal effort paired with diurnal efforts during 2010

### *Habitat Selection*

To measure habitat selection, we deployed 0.5-m<sup>2</sup> quadrats around the capture location of each terrapin to characterize vegetation cover and species abundance. We recorded the percent coverage of each individual vegetation species, as well total percent vegetative cover. Due to variation in vegetation height in each quadrat, I classified vegetation height in an ordinal ranking scale of 20 cm, increasing from zero to greater than a meter (0-20, 21-40, 41-50...91-100 cm).

Because this ordinal ranking cannot be analyzed parametrically, I used Kruskal Wallis ANOVA to determine if there was a difference in the median vegetation height rank at point of captures between diel periods. I also collapsed “month” and “diel period” terms into a single “month/diel period” variable and used a Kruskal Wallis to test for differences in median vegetation height between this variable combination.

I used parametric general linear ANOVA model to analyze habitat selection via percent vegetation cover. The model included diel period, monthly (seasonal), as well as seasonal diel interaction terms as the classification factors and the percent vegetation cover as the sample. This would demonstrate if there is a difference in habitat selection (specifically, selection of areas with greater or less vegetation cover) at night versus during the day and during different months, and if there is an interaction between month and diel period.

In addition to General Linear Model, I also used a One-Way parametric ANOVA with Tukey’s to determine if there was a difference in mean percent vegetation cover between month and diel period. Due to unbalanced data, I collapsed “month” and “diel period” into a month/diel period variable. While general linear model demonstrates if there is a significant difference between these variables, ANOVA and Tukey’s show more clearly between which factors there is a significant difference. Therefore, I used this in addition to general linear model to clearly demonstrate during which specific months and diel periods terrapins displayed preference for certain vegetation covers.

For further analysis, I classified each capture location as being either aquatic or terrestrial. I then divided the number of terrapins hand-captured on land and in water by

the number of hours of transect effort to produce a CPUE (catch per unit effort) value for each capture location. For example, if I spent 2 hours on a transect searching for terrapins and I captured 4 terrapins on land and 3 terrapins in the water, then that would be an aquatic CPUE of 3 terrapins/2 hours (1.5) and a terrestrial CPUE of 4 terrapins/2 hours (2). I averaged these values by month and used a Two-way ANOVA to identify any differences in CPUE between capture location (land versus water) and month. For this analysis, I used only hand-captured terrapin due to differences in detectability between transect method and radiotelemetry. I then compared terrestrial and aquatic capture to air, soil, and water temperature to identify the functional use of these habitat classes, such as basking or foraging habitats. To do this, I used a T-test to determine if there was a significant difference in air, soil, and water temperature (each a separate T-test) between terrestrial and aquatic captures. I also created a “delta T” in which I subtracted water temperature from air temperature to see if aquatic versus terrestrial habitat selection was a response to a difference in microclimate availability (i.e., selection of a warmer versus cooler available microclimate). I used a T-test to observe significant differences in this Delta T between capture locations (aquatic and terrestrial).

For quality control, I also used predicted water temperature data from a regression between NOAA station temperature and HOBOware tidbit data from the island in 2012 (see Methods: Physical-Chemical Data Collection, Figure 9) to analyze water temperature and Delta temperature between terrestrial and aquatic capture data. For additional quality control, I also re-ran this statistic on data from the ongoing monitoring project from 2012 past the period of this study. The tidbit deployed in the main creek of South Deer island in 2012 collected real data on water temperature that could be

compared to habitat selection data from that year. These additional quality control analyses show whether or not the trends observed during my study period were false due to the distance of the source of water temperature data.

I also calculated the distance from water each terrapin was at time of capture using the latitude and longitude and spatial analyst tools in ArcGIS. I used a T-test to determine if there was a difference in distance from water between diel period, and I used Pearson's correlation to compare distance from water at time of capture to air, water, and soil temperature, and tidal level (in meters). A summary of the statistical tests used to analyze habitat selection can be found in Table 3.

**Table 3. Summary of statistical tests used to analyze habitat selection**

Testing for:	Test Used:	Variables Assigned	Data Set	Reasoning
Differences in median vegetation height (as defined in ordinal ranking) at night versus during the day	Mann-Whitney	Night and Day as the classification factors, vegetation classes 1-6 in increments of 20 cm as the sample.	All captures (hand, radio, and manual acoustic), males and females tested separately	Vegetation height was recorded in ordinal ranked classes 1-6 and therefore could not be tested parametrically
Differences in median vegetation height (as defined in ordinal ranking) between month/diel variable combination	Kruskal Wallis ANOVA	Month/Diel variable combination as the classification factor; vegetation classes 1-6 in increments of 20 cm as the sample	All captures (hand, radio, and manual acoustic), males and females tested separately	Vegetation height was recorded in ordinal ranked classes 1-6 and therefore could not be tested parametrically. The data is unbalanced and therefore "month" and "diel period" are "collapsed" into "month/diel period" variable combination.
Differences in mean vegetation density, or percent cover, between month/diel variable combination	One-Way ANOVA and Tukey's	Month/diel variable combination as the classification factors, percent vegetation cover at point of capture as sample	All captures (hand, radio, and manual acoustic), males and females tested separately	% vegetation cover is an actual, discrete value and is therefore parametric, but the data is unbalanced and therefore cannot have a two-way ANOVA with Month and Diel period separate. These variables had to be "collapsed" into a month/diel combination as one factor in a One-Way ANOVA. Used in addition to General linear model to better demonstrate significant differences in vegetation density between month/diel periods.
To determine if differences in mean vegetation density, or percent cover, are significant between months, diel periods, and a month/diel period interaction factor	General-Linear model	Month + Diel period + Month*Diel period = Vegetation density	All captures (hand, radio, and manual acoustic), males and females tested separately	Used this test in addition to One-Way ANOVA to determine if there is an interaction between month and diel term.
To determine if there is a significant difference in CPUE between capture location (land vs water) and diel period.	Two-Way ANOVA	Diel period and capture location (land vs. water) as classification factors, CPUE as sample.	Hand capture only	Difference in detection probability between transect method and radiotelemetry prevents combination of data from differing methodologies.
To determine if there is a significant difference CPUE between capture location (land vs. water) and month	Two-Way ANOVA	Month and capture location (Land vs water) classification factors, CPUE as sample	Hand capture only	Difference in detection probability between transect method and radiotelemetry prevents combination of data from differing methodologies.
To determine if there is a significant difference in mean air, water, and soil temperatures at time of land versus aquatic capture	T-Test	Land Capture and Water capture as the classification factors; soil, water, and air temperature as the sample	All captures (hand, radio, and manual acoustic), males and females tested separately. Air, water, and soil temperature analyzed separately	Temperature is a discrete number and therefore requires a parametric analysis, and there are only two classifications (land and water), so T-test is appropriate
To determine if the difference between air and water temperature differs significantly at the time of land versus aquatic captures. This will show if terrapins are selection warmer or cooler habitats	T-Test	Land capture and water capture as the classification factors; delta temperature (air temperature - water temperature) as sample.	All captures (hand, radio, and manual acoustic), males and females tested separately. Air, water, and soil temperature analyzed separately	Required this test in addition to previous t-test to better demonstrate if terrapin are selecting warmer versus cooler available habitats, and if habitat selection is a result of delta temperature between land and water habitats versus ambient temperature
Differences in mean distance from water (feet) at point of capture at night versus during the day	T-Test	Night and Day as the classification factors, distance from water (in feet) at point of capture as sample	All captures (hand, radio, and manual acoustic), males and females tested separately	Distance from water (calculated using GIS) is a discrete value and therefore parametric, and with only two classification factors, a T-test is used
To determine if there is a correlation between air temperature, soil temperature, water temperature, and tidal amplitude and distance from water	Pearson's Correlation	Air Temp X Soil Temp X Water Temp X Tidal amplitude X Distance from water	All captures (hand, radio, and manual acoustic), males and females tested separately	Preliminary test before further regressions to determine if there is any correlation between distance from water and these factors.

### *Range*

To obtain an estimation of range, I downloaded all GPS locations of radio capture events (WGS 84 datum) onto ArcGIS 10, using the NAD 1983 coordinate system. I used the ArcGIS spatial analyst to measure the straight line distance between capture events, and classified each of these movements as occurring during a diel period. This measurement represents the minimum distance moved by the terrapin between capture events, and is most likely an underestimation of total movement. If any two capture events spanned multiple diel periods, the exact diel period in which the movement occurred could not be identified and therefore was not included. I divided the straight line distance moved by the amount of time elapsed, and therefore analyzed both minimum rate of movement over time and minimum distance moved during diel periods. Because we only sampled 2-3 times in each diel period per day, there was not enough data to calculate a minimum convex polygon or adaptive kernel estimation of range for each diel period. Instead, I compared distance moved and rate of movement to diel periods using a T-test. I also used a parametric One-way ANOVA to determine if there was a significant difference between both distance moved and rate of movement between month and diel period. Unbalanced design prevented me from using a Two-way ANOVA to detect interaction between these variables, so I collapsed them into the “month/diel period” variable. A summary of statistical tests used to analyze range can be found in Table 4.

**Table 4. Summary of statistical tests used to analyze range**

Testing for:	Test Used:	Variables Assigned	Data Set	Reasoning
If there is a significant difference in mean "minimum straight line distance travelled" at night versus at day	T-test	Night and Day as classification variables; straight line distance travelled as sample	Consecutive radio captures within the same diel period only	Straight line distance is a discrete actual value and is therefore parametric
If there is a significant difference in mean rate of movement at night versus at day	T-test	Night and day as classification variables; rate of movement (in meters/hour) as sample	Consecutive radio captures within the same diel period only	Rate of movement is a discrete value and is therefore parametric
If there is a significant difference in mean "minimum straight line distance travelled" between Month/Diel period combinations	One-Way ANOVA	Month/Diel combination as classification variable; straight line distance travelled as sample	Consecutive radio captures within the same diel period only	Unbalanced design prevents a 2-way ANOVA using month and diel period separately, so month and diel period are "collapsed" into month/diel combination variable. Parametric ANOVA required for discrete, parametric data

### *Acoustic Telemetry*

The acoustic receiver output presents data in a continuous temporal format, and therefore needed to be transformed to discrete data in order to be qualitatively comparable to the habitat and behavioral results. To do this, I classified swimming events as periods of time during which terrapin were transmitting continuously. If a transmitter was not received for a period of time greater than an hour, it was assumed to be "absent". I determined that an hour was the appropriate cutoff time for activity by calculating how long it takes for a continuously swimming terrapin to swim through a "blind spot" between two receivers. For example, if a terrapin was recorded to be swimming continuously from one receiver to the next (ie, South to East to North) and then registered on the West receiver an hour later, I assumed this to be a continuous swimming activity with the hour of inactivity being explained by the "blind spot" between the two receivers in which the terrapin cannot be detected. After defining discrete swimming events, I was able to calculate the minimum percent of time each tagged terrapin spent swimming during each diel period. This is considered a minimum value, since terrapin may have still been in the water but

were not detected by the receivers because they were out of range. This calculation represents the number of hours in each diel period as a percentage of the minimum amount of time that the transmitter was detected by the receiver. For example, if a terrapin was detected for a total of 20 hours in the month of June and 5 of these hours were at night and 15 of these hours were during the day, then the data for that terrapin would show a 25% nocturnal swimming rate and a 75% diurnal swimming rate for June. I compared percentages (in addition to hours spent swimming) so that data would not be biased towards terrapin that swam more hours overall. This metric shows how the terrapin partitions its swimming effort between nocturnal and diurnal periods. Because of this, I could not use general linear model ANOVA to detect any significant differences in this “percent time spent swimming during each diel period” between month or month/diel period interaction: Because this data represents a percentage of time, it will always add up to 100% within each month. Instead, I used a One-Way ANOVA and Tukey’s test to analyze difference in percent time spent swimming between diel periods in each month.

I also similarly analyzed number of hours each individual terrapin spent swimming. This metric (hours) provides different information than the metric aforementioned (percent). While hourly swimming data can be biased toward the terrapins that swim more often or for longer periods of time, it depicts actual aquatic habitat use in each diel period rather than an ambiguous percent of time. I used a One-Way ANOVA to determine if there was a difference in number of hours spent swimming between month/diel periods. Again, unbalanced design prevented the use of a 2-way ANOVA using month and diel period as separate factors and I therefore had to collapse “month” and “diel period” into a single month/diel period variable.

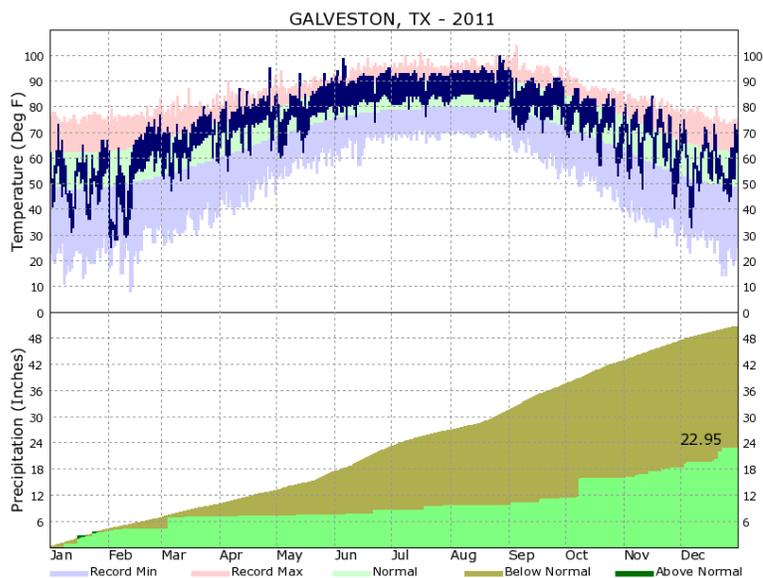
**Table 5. Summary of statistical tests use to analyze stationay acoustic telemetry data.**

Testing for:	Test Used:	Variables Assigned	Data Set	Reasoning
Significant difference in percent time spent swimming at night versus during the day	T-Test	Night and Day as classification factors; percent time swimming as sample. Percent time swimming represents the number of hours a terrapin was swimming during each diel period divided by the total number of hours the terrapin spent swimming during.	Detections from stationary acoustic receivers during the course of thesis work ONLY. Only females analyzed due to small sample size of males.	Time spent swimming can be analyzed parametrically, and with only two factors, a T-test is appropriate.
Significant difference in percent time spent swimming between month/diel period combinations	One-Way ANOVA	Month/Diel period combination as classification factor; percent time spent swimming as sample	Detections from stationary acoustic receivers during the course of thesis work ONLY. Only females analyzed due to small sample size of males.	Unbalanced design prevented using a 2 way ANOVA with month and diel period as separate factors, and therefore month and diel period were "collapsed" into month/diel period variable combination
Significant difference in number of hours spent swimming at night versus during the day	T-Test	Night and day as classification factors; number of hours detected as sample.	Detections from stationary acoustic receivers during the course of thesis work ONLY. Only females analyzed due to small sample size of males.	Time spent swimming can be analyzed parametrically, and with only two factors, a T-test is appropriate.
Significant difference in number of hours spent swimming between month/diel period combinations	One-Way ANOVA	Month/Diel period combination as classification factor; hours spent swimming as sample.	Detections from stationary acoustic receivers during the course of thesis work ONLY. Only females analyzed due to small sample size of males.	Unbalanced design prevented using a 2 way ANOVA with month and diel period as separate factors, and therefore month and diel period were "collapsed" into month/diel period variable combination. Hours and percent time spent swimming represent two DIFFERENT sets of data and different ideas and need to be analyzed separately.

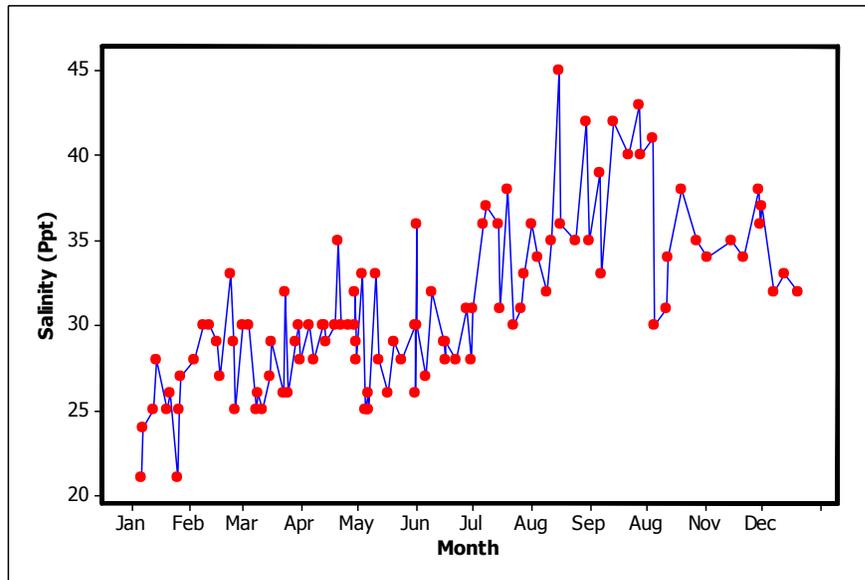
## RESULTS

Over the course of the study, we observed a total of 72 males and 161 females. There were fifteen 24-hour sampling events during the period from February 2011 until September 2011 and approximately 200 hours of cumulative search and tracking effort. Salinity and temperatures are reported in subsequent sections. Our sample size for February and March is smaller than for the period of April through August due to less available manpower. August data is biased toward the four female terrapins we continuously tracked for 24 hours.

### *Environmental Data from Period of Study*



**Figure 11. Rainfall and air temperature data from 2011. From National Weather Service readout at Scholes Field, Galveston TX.**

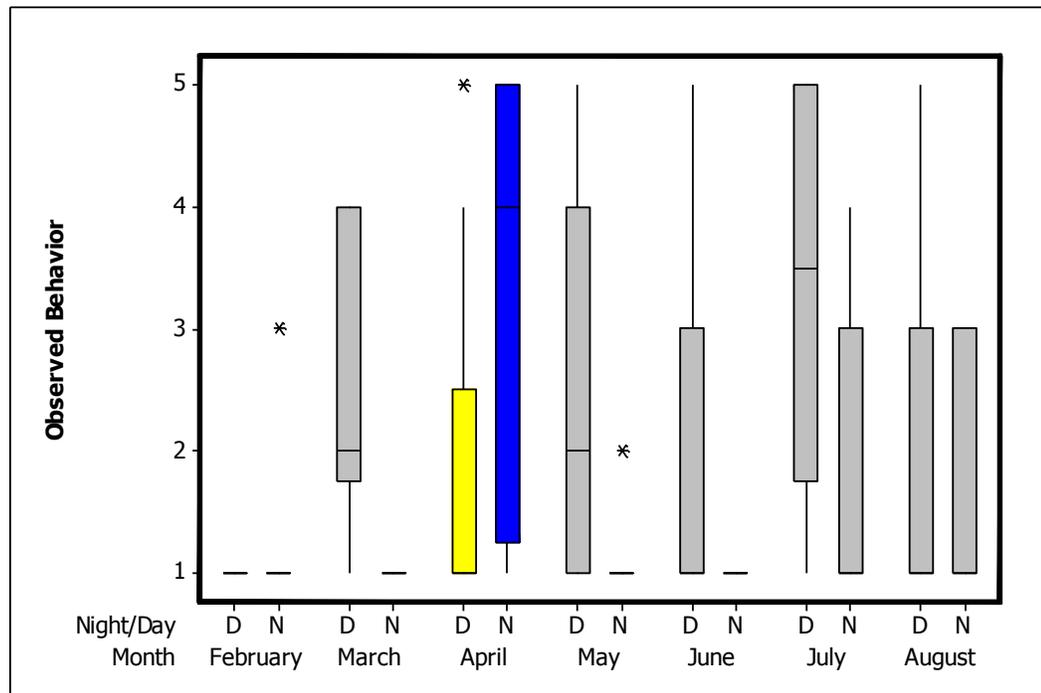


**Figure 12. Salinity levels (in ppt) in 2011. Obtained using refractometer in Galveston Bay in the vicinity of South Deer Island (includes readings from Sportsman’s Road and North Deer Island).**

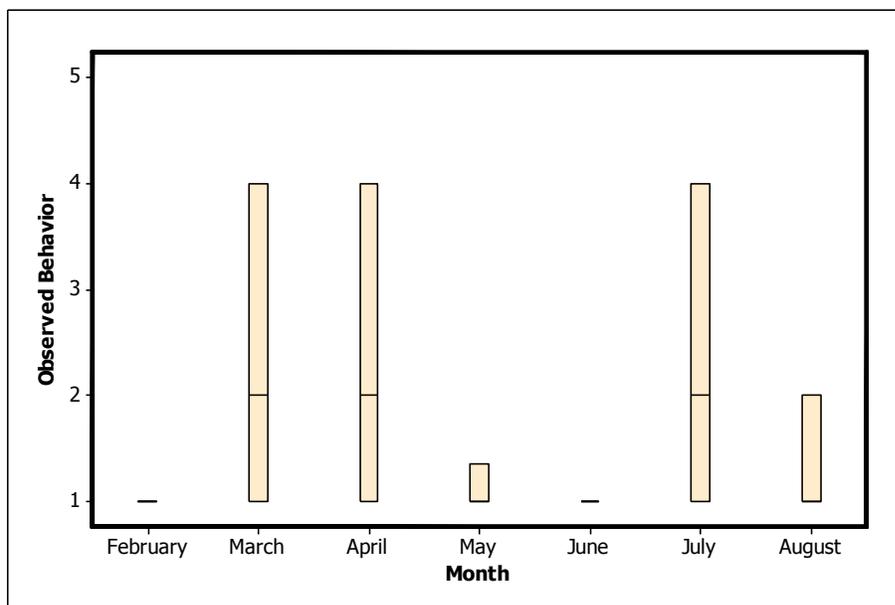
*Behavior: Median Behavioral Levels at Each Month and Diel Period*

There was a significantly higher level of female behavior at night versus during the day during April, but no significant difference in behavioral levels between night and day during any other month (Kruskal Wallis of actively captured females,  $p=0.000$ , Figure 13, Appendix 1 Section 1.1). Male terrapin showed higher levels of behavior during the day versus at night in April and May (Kruskal Wallis ANOVA,  $P=0.003$ , Appendix 1 Section 1.2). There was also a significant trend of higher median levels of female behavior overall in March, May, and July as compared to other months (Kruskal Wallis ANOVA of actively captured females,  $p=0.001$ , Figure 14). Males only showed significant increases in behavior in March and April (Kruskal Wallis ANOVA of actively captured males,  $p=0.003$ , Figure 15). This data shows that the highest levels of activity

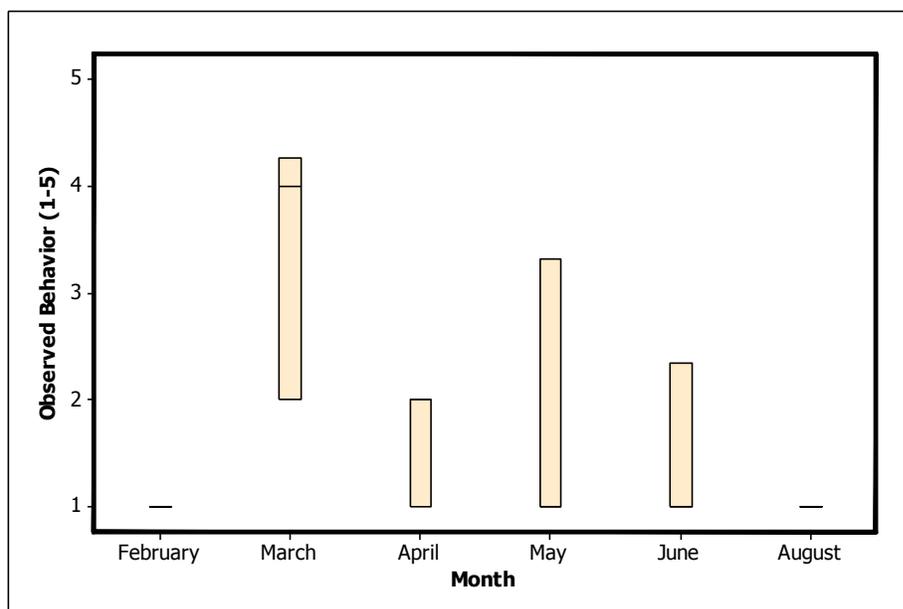
occur in March, May, and July for female terrapins, and that high levels of nocturnal behaviors can be observed in April. Because males do not display this same trend (activity levels highest in only March and April), May and July could represent months during which female-specific behaviors occur, such as nesting and nesting migrations.



**Figure 13. Boxplot of median observed behavior of female terrapins during each diel period and each month of the study. Kruskal Wallis shows a significant difference in median observed behavior between at least one month/diel period combination ( $p=0.000$ ). This data represents all female terrapin actively captured (hand capture, radiocapture, and active acoustic capture). August data is highly biased toward the 4 terrapins that were double-tagged with radio and acoustic tags and followed closely for 24 hours.**



**Figure 14.** Boxplot of median behavior of actively captured female terrapins during each month. Kruskal Wallis showed that May, March, and July coincide with significantly higher levels of behavior when compared to other months ( $p=0.001$ ). This data represents all female terrapin actively captured (hand capture, radiocapture, and active acoustic capture). August data is highly biased toward the 4 terrapins that were double-tagged with radio and acoustic tags and followed closely for 24 hours.



**Figure 15.** Boxplot showing the median behavior of male terrapins between each month of the study. Kruskal Wallis ANOVA showed significant increases in male behavior in March and April ( $p=0.003$ ). This data represents all male terrapin actively captured (hand capture and radiocapture). There is no value for August too few males were captured.

*Behavior: Trends with Abiotic Data (Temperature)*

A parametric one-way ANOVA showed a significant difference between the mean water and soil temperatures at different levels of female behavior ( $p = 0.001$ ,  $p=0.012$ , respectively, Figure 16 -Figure 19, Appendix 1 Section 1.3 and 1.4). Air, soil, and water temperatures at different behaviors can be found in Table 6. Soil and water temperatures were significantly higher during sitting (3) and swimming (5) behaviors than during burrowing (1) behaviors, but were not significantly different between sitting (3) and swimming (5) behaviors and other behaviors that could potentially be viewed as “basking”, ie, “turtle pockets” (2). Further correlation analysis shows that there is a trend of increasing soil and water temperature with increasing female behavioral rankings (Pearson’s correlation,  $p=0.12$ ,  $p=0.001$ , respectively, Appendix 1 Section 1.6). We failed to find any relationship between air temperature and female behavior categories ( $p = 0.549$ , Appendix 1 Section 1.5). As stated in my methods, these values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture. Therefore, the “operative” temperature as experienced by the terrapin may be different than the “environmental”, or ambient temperature, measured by the data loggers (see Discussion for further clarification on operative versus environmental temperatures). This data shows that soil and water temperature may be better indicators for the “operative” temperature experienced by the terrapin rather than air temperature. It also supports my hypothesis that temperature may have a greater influence on behavior than time of day.

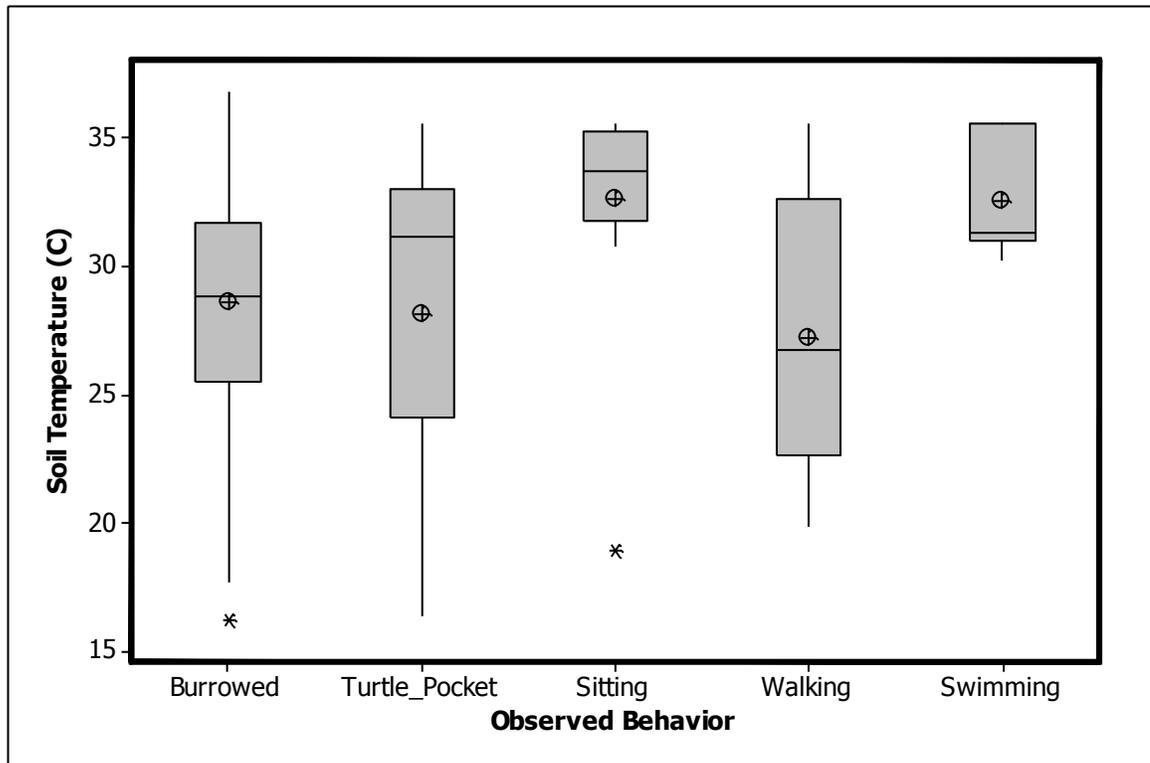
In contrast to female terrapin trends, parametric One-way ANOVA results showed significant differences only between the mean soil temperatures at different male terrapin behavior ranks ( $p = 0.042$ ) (Appendix 1 Section 1.7). Air, water, and soil temperatures at time of different behaviors can be found in Table 7. Pearson's correlation (Appendix 1 Section 1.10) showed that male behavior appeared to decline as soil temperature ( $p = 0.012$ ) and air temperature ( $p = 0.026$ ) increased. However, similar patterns between male terrapin behavior and water temperature were not detected (ANOVA,  $p = 0.785$ , Pearson's  $p = 0.754$ , Appendix 1 Section 1.9-1.10). These correlations suggest that male terrapins become less active in hotter temperature, which is the opposite of female response to increasing temperature. This may have to do with the physiology and size dimorphism between the sexes, which will be discussed later on.

**Table 6. Air, water, and soil temperatures during different behaviors at time of female terrapin capture**

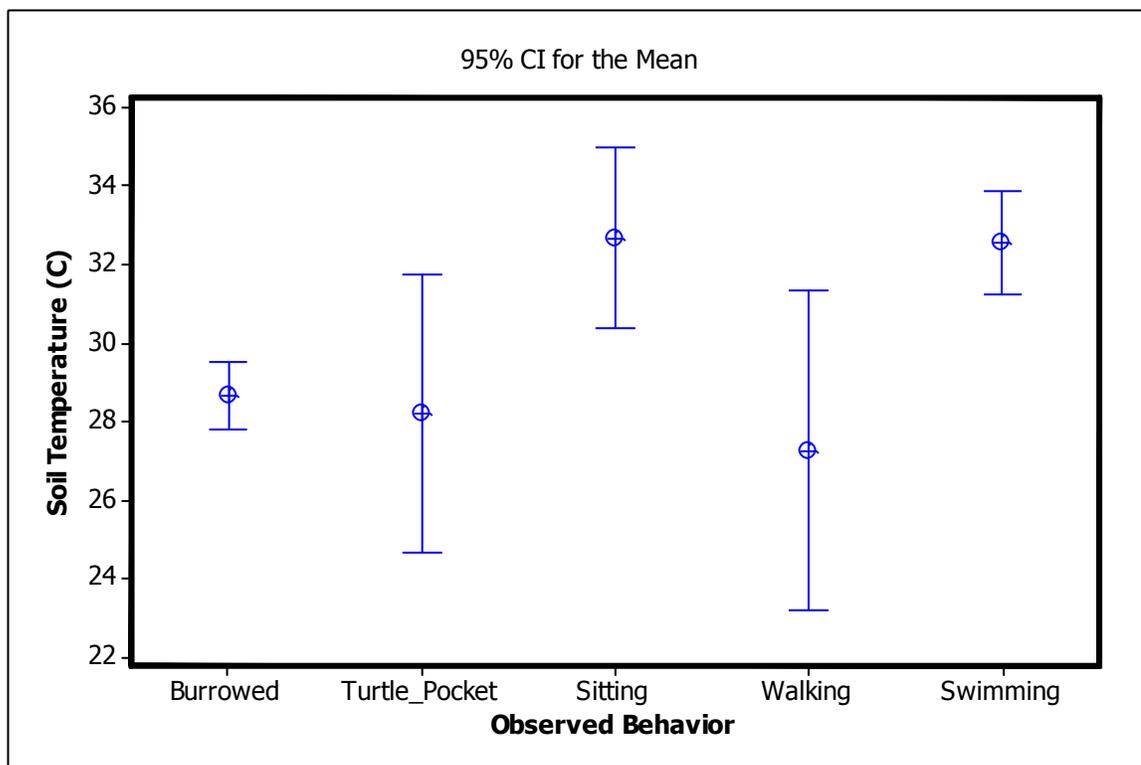
Variable	Behavior Rank	N	N*	Mean	SE Mean	StDev	Minimum	Q1	Median	Q3	Maximum
Air Temperature (C)	1	102	4	26.8	0.6	5.6	14.0	23.4	28.2	29.2	37.1
	2	16	0	25.4	1.4	5.5	17.5	18.6	29.0	29.5	33.0
	3	15	0	28.7	1.1	4.3	15.0	29.0	29.5	31.0	33.0
	4	10	0	26.4	2.1	6.7	13.0	21.5	29.4	31.6	33.2
	5	9	4	27.7	1.5	4.4	18.5	25.5	29.0	30.0	33.0
Water Temperature (C)	1	89	17	28.1	0.3	3.0	22.2	24.5	28.5	30.5	32.2
	2	11	5	29.9	0.7	2.3	23.3	30.1	30.5	31.1	31.6
	3	14	1	31.1	0.3	1.0	29.1	30.5	31.1	32.0	32.2
	4	6	4	27.9	1.5	3.6	23.4	23.5	29.5	30.6	31.0
	5	13	0	30.3	0.2	0.7	29.0	30.0	30.5	30.8	31.6
Soil temperature (C)	1	106	0	28.6	0.4	4.5	16.2	25.5	28.9	31.7	36.8
	2	16	0	28.2	1.7	6.7	16.3	24.1	31.1	33.0	35.6
	3	15	0	32.7	1.1	4.2	18.9	31.8	33.8	35.3	35.6
	4	10	0	27.2	1.8	5.7	19.8	22.6	26.8	32.6	35.6
	5	13	0	32.5	0.6	2.2	30.2	31.0	31.3	35.6	35.6

**Table 7. Air, water, and soil temperatures during different behaviors at time of male terrapin capture.**

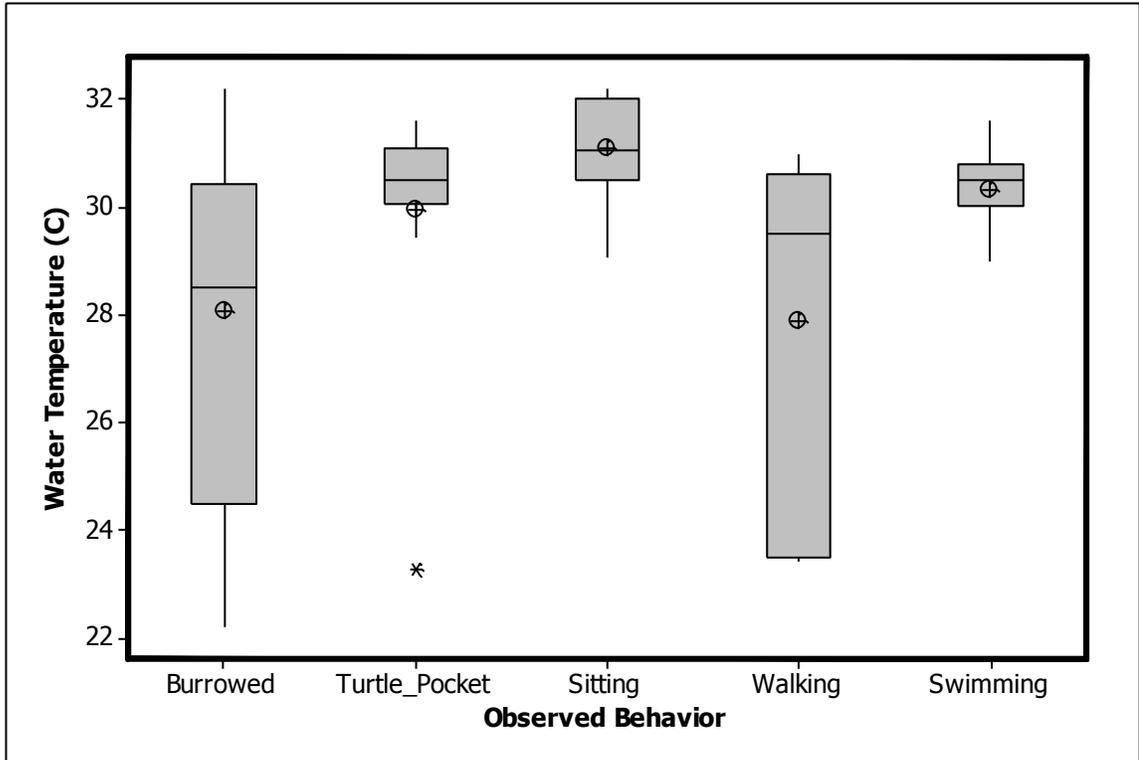
Variable	Behavior		N*	Mean	SE Mean	StDev	Minimum	Q1	Median	Q3	Maximum
	Rank	N									
Air temperature ( C )	1	36	0	27.9	1.0	6.0	19.1	22.9	28.0	29.5	38.5
	2	17	0	25.0	0.8	3.3	18.8	22.4	24.5	27.8	31.0
	3	7	0	26.2	1.6	4.3	21.0	22.7	24.0	31.0	31.3
	4	10	0	24.3	1.7	5.4	18.8	18.8	23.8	29.5	33.2
	5	2	0	23.1	5.6	7.9	17.5 *		23.1 *		28.7
Water temperature (C)	1	21	15	25.8	0.7	3.1	22.6	23.3	23.7	29.8	30.3
	2	3	14	25.2	1.4	2.5	23.7	23.7	23.8	28.0	28.0
	3	2	5	25.8	2.2	3.1	23.6 *		25.8 *		28.0
	4	2	8	23.5	0.0	0.0	23.5 *		23.5 *		23.5
	5	1	1	28.0 *		*	28.0 *		28.0 *		28.0
Soil temperature ( C )	1	36	0	25.7	0.6	3.7	18.8	22.9	25.6	28.1	31.8
	2	17	0	23.9	0.8	3.3	16.0	23.9	24.1	25.4	28.9
	3	7	0	25.8	0.8	2.1	23.7	24.0	25.2	28.6	28.9
	4	10	0	21.7	1.5	4.7	16.2	16.4	22.7	26.7	27.4
	5	2	0	23.0	5.9	8.3	17.2 *		23.0 *		28.9



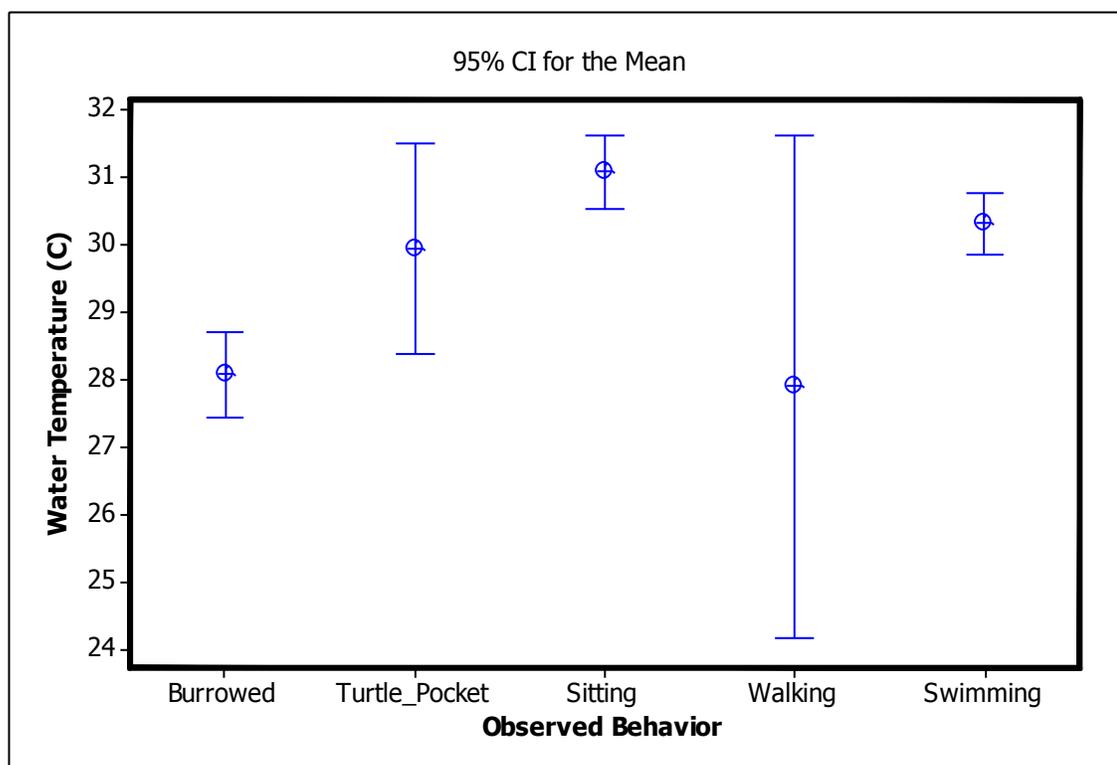
**Figure 16.** Boxplot of the median and mean soil temperature recorded at time of female terrapin capture exhibiting different behavior types. Circles with crosshairs represent the mean of the data. One-Way parametric ANOVA showed a significant difference in mean soil temperatures at the time of capture between different behavioral ranks ( $p=0.012$ ). This data represents all female terrapin actively captured (hand capture, radiocapture, and active acoustic capture). August data highly biased toward the 4 terrapins that were double-tagged with radio and acoustic tags and followed closely for 24 hours. As stated in my methods, these values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture. Therefore, the “operative” temperature as experienced by the terrapin may be different than the “environmental”, or ambient temperature, measured by the data loggers (see Discussion for further clarification on operative versus environmental temperatures).



**Figure 17. Interval plot showing 95% confidence interval of the mean soil temperature at the time of female capture during differing behaviors. One-Way parametric ANOVA showed a significant difference in mean soil temperatures at the time of capture between different behavioral ranks ( $p=0.012$ ). This data represents all female terrapin actively captured (hand capture, radiocapture, and active acoustic capture). August data highly biased toward the 4 terrapins that were double-tagged with radio and acoustic tags and followed closely for 24 hours. As stated in my methods, these values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture. Therefore, the “operative” temperature as experienced by the terrapin may be different than the “environmental”, or ambient temperature, measured by the data loggers (see Discussion for further clarification on operative versus environmental temperatures).**



**Figure 18. Boxplot of water temperature at time of female terrapin capture during different behaviors. Circles with crosshairs represent the mean of the data. One-Way parametric ANOVA showed a significant difference in mean water temperatures at the time of capture between different behavioral ranks ( $p=0.001$ ). This data represents all female terrapin actively captured (hand capture, radiocapture, and active acoustic capture). August data highly biased toward the 4 terrapins that were double-tagged with radio and acoustic tags and followed closely for 24 hours. As stated in my methods, these values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture. Therefore, the “operative” temperature as experienced by the terrapin may be different than the “environmental”, or ambient temperature, measured by the data loggers (see Discussion for further clarification on operative versus environmental temperatures).**



**Figure 19. Interval plot of showing the 95% confidence interval of the mean water temperature at time of female terrapin capture exhibiting different behaviors. One-Way parametric ANOVA showed a significant difference in mean water temperatures at the time of capture between different behavioral ranks ( $p=0.001$ ). Water temperatures were significantly lower during periods when female terrapin were exhibiting behavior pattern 1 in comparison to specimens exhibiting behaviors 3 and 5. This data represents all female terrapin actively captured (hand capture, radiocapture, and active acoustic capture). August data highly biased toward the 4 terrapins that were double-tagged with radio and acoustic tags and followed closely for 24 hours. As stated in my methods, these values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture. Therefore, the “operative” temperature as experienced by the terrapin may be different than the “environmental”, or ambient temperature, measured by the data loggers (see Discussion for further clarification on operative versus environmental temperatures).**

### *Behavior: Activity and Temperature*

Soil, water, and air temperature descriptive statistics at differing levels of activity can be found below (Table 8, Table 9, Figure 20). With little known about the activities of Texas

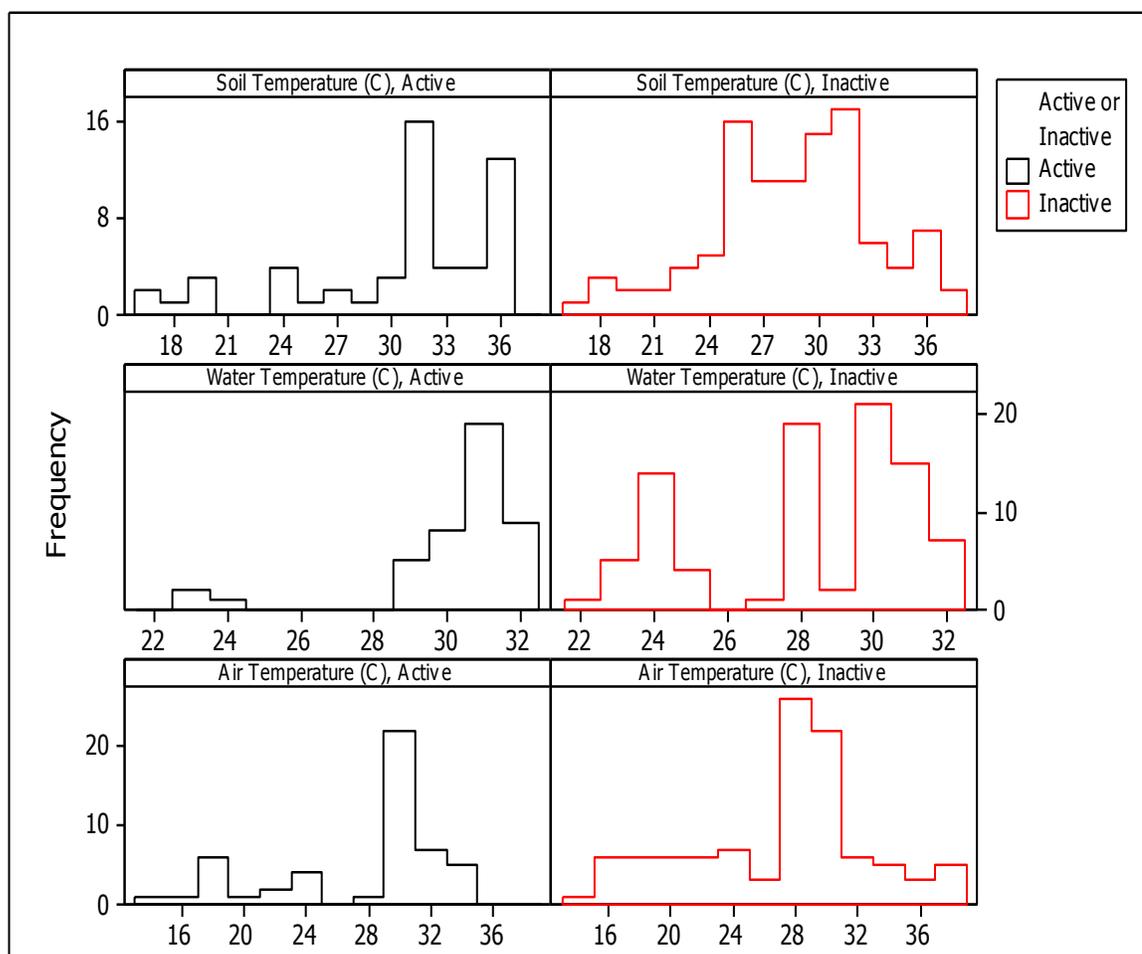
Diamondback terrapin, this descriptive data can provide insight to when we can expect to observe activity (and subsequently active behaviors such as migrations, nesting, and mating) during differing temperatures. We could use such data to predict activity trends in Texas terrapin and suggest temporal and spatial restrictions on crabbing in areas and times of high terrapin activity, therefore reducing crab trap mortality.

**Table 8. Descriptive statistics for air, water, and soil temperature at time of capture for active and inactive female terrapin.**

Variable	Activity Level	N	N*	Mean	SE Mean	StDev	Minimum	Q1	Median	Q3	Maximum
Air Temperature (C)	Inactive	102	4	26.8	0.6	5.6	14.0	23.4	28.2	29.2	37.1
	Active	50	4	27.0	0.7	5.3	13.0	23.2	29.0	30.3	33.2
Water Temperature (C)	Inactive	89	17	28.1	0.3	3.0	22.2	24.5	28.5	30.5	32.2
	Active	44	10	30.1	0.3	2.0	23.3	30.1	30.5	31.1	32.2
Soil temperature (C)	Inactive	106	0	28.6	0.4	4.5	16.2	25.5	28.9	31.7	36.8
	Active	54	0	30.3	0.7	5.5	16.3	28.0	31.5	35.1	35.6

**Table 9. Descriptive statistics for air, water, and soil temperature at time of capture for active and inactive male terrapin.**

Variable	Activity Level	N	N*	Mean	SE Mean	StDev	Minimum	Q1	Median	Q3	Maximum
Air temperature (C)	Inactive	36	0	27.9	1.0	6.0	19.1	22.9	28.0	29.5	38.5
	Active	36	0	24.9	0.7	4.3	17.5	22.4	24.5	28.6	33.2
Water temperature (C)	Inactive	21	15	25.8	0.7	3.1	22.6	23.3	23.7	29.8	30.3
	Active	8	28	25.3	0.8	2.3	23.5	23.5	23.7	28.0	28.0
Soil temperature (C)	Inactive	36	0	25.7	0.6	3.7	18.8	22.9	25.6	28.1	31.8
	Active	36	0	23.6	0.7	3.9	16.0	22.2	24.2	26.4	28.9



**Figure 20. Histogram showing the frequency of observation of inactive versus active female terrapin at different air, soil, and water temperatures. This data represents all female terrapin actively captured (hand capture, radiocapture, and active acoustic capture). August data highly biased toward the 4 terrapins that were double-tagged with radio and acoustic tags and followed closely for 24 hours. As stated in my methods, these values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture. Therefore, the “operative” temperature as experienced by the terrapin may be different than the “environmental”, or ambient temperature, measured by the data loggers (see Discussion for further clarification on operative versus environmental temperatures).**

### *Behavior: Social or Group Burrowing*

I also observed social burrowing behavior in the terrapin during this study. These

burrows typically contained anywhere from 3 – 15 inactive terrapin. A T-Test failed to

detect any statistically significant relationships between number of terrapins in a burrow and diel period ( $p = 0.642$ ) or sex ratios and diel period ( $p = 0.549$ , Figure 21, Appendix 1 Section 1.11 and 1.12). I examined the data collected from the ongoing mark recapture project (years 2010-2011) using a one-way ANOVA and Tukey's range test and found that the sex ratios in the burrow shift from male dominant in March and April to female dominant in May – August ( $p = 0.01$ ), with sex ratios being very near 1:1 for the rest of the year (Figure 22, Appendix 1 Section 1.13). These trends may suggest a shift in activity or mating patterns as the year progresses, and is discussed in detail later on. One-way ANOVA showed no significant difference in total number of terrapin in a burrow between months ( $p = 0.275$ , Figure 23, Appendix 1 Section 1.14). As noted in the methods, I could not use 2010-2011 data to observe diel or diel-monthly interaction trends in social burrow data as there was not an equal nocturnal effort in 2010. Therefore, these two data sets were analyzed separately due to the unequal sampling effort and no analysis of month/diel period interaction could be performed.

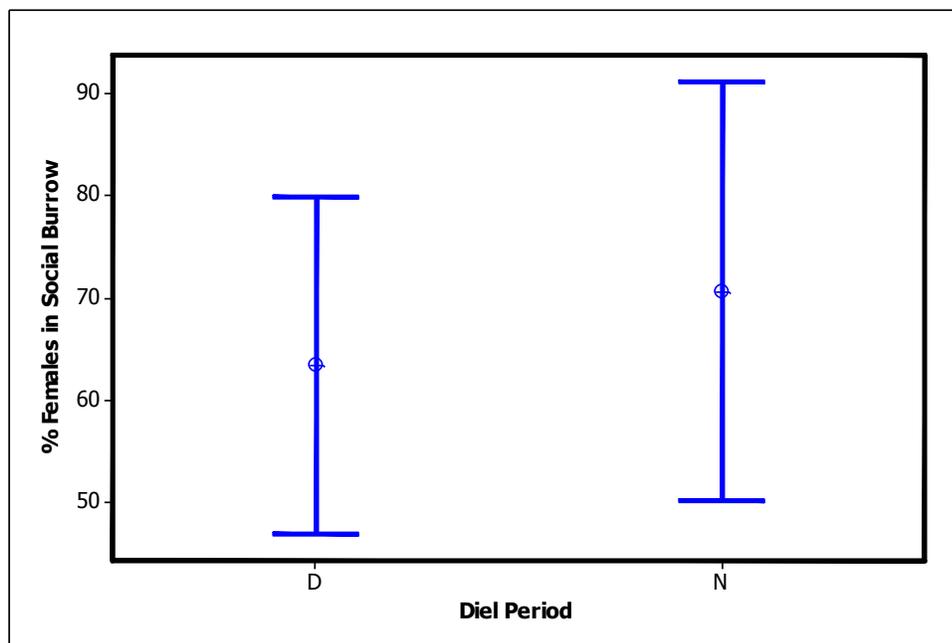


Figure 21. Interval plot showing the 95% confidence interval of the mean percent female composition in social burrows between diel period. Insignificant T-Test ( $P= 0.549$ ). This data represents all terrapins captured in social burrows during the paired nocturnal-diurnal search effort during the course of this thesis, regardless of capture methodology.

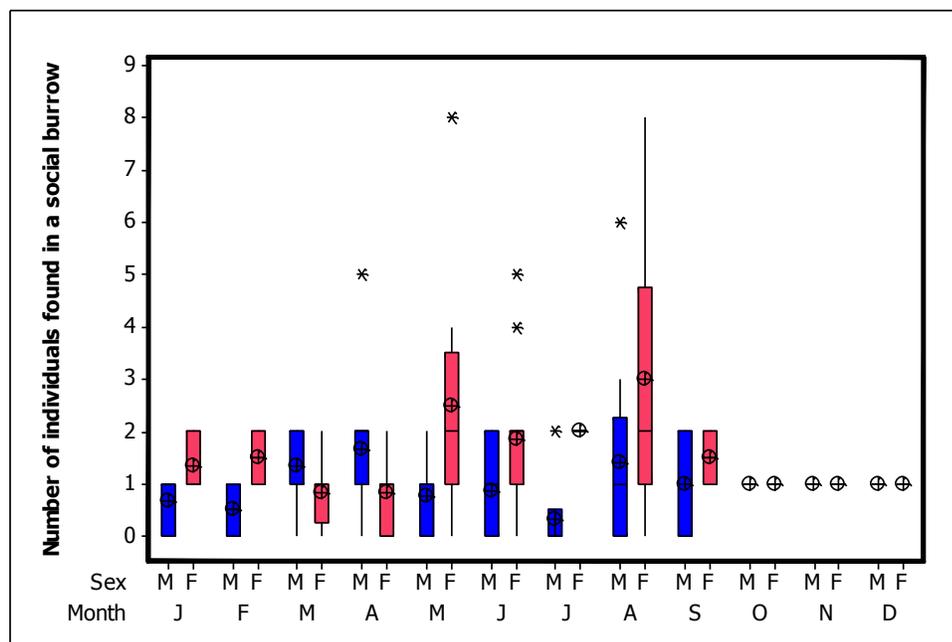
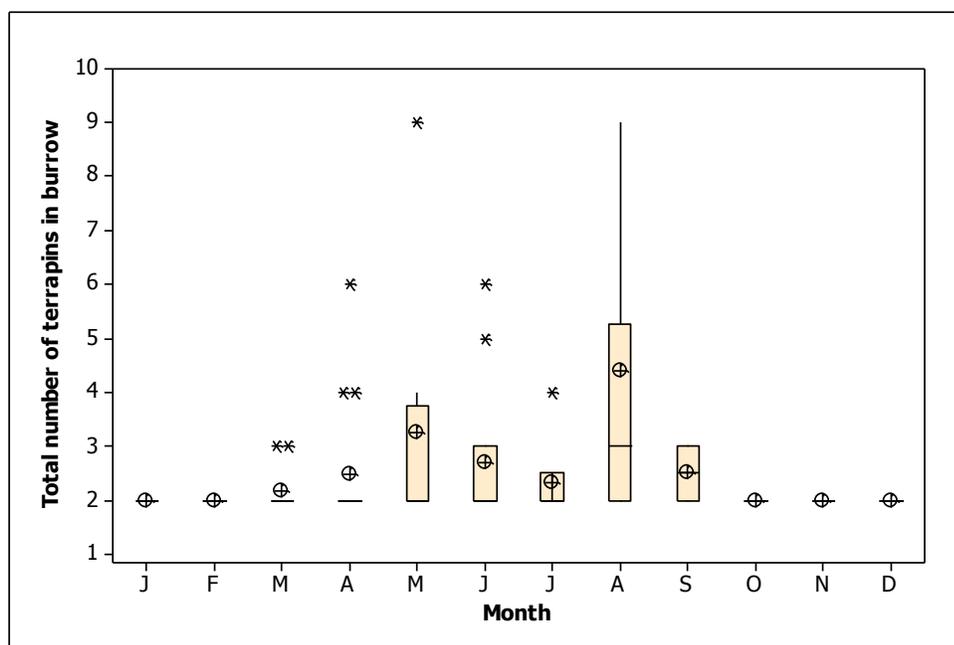


Figure 22. Boxplot of number of terrapins (males versus females) found in social burrows during each month. Parametric One-Way ANOVA found a significant difference in the male:female ratio of terrapins in social burrows between months ( $p=0.001$ ). Circles with crosshairs represent the mean of the data. This data represents all terrapins captured in social burrows during 2010-2011, regardless of capture methodology.

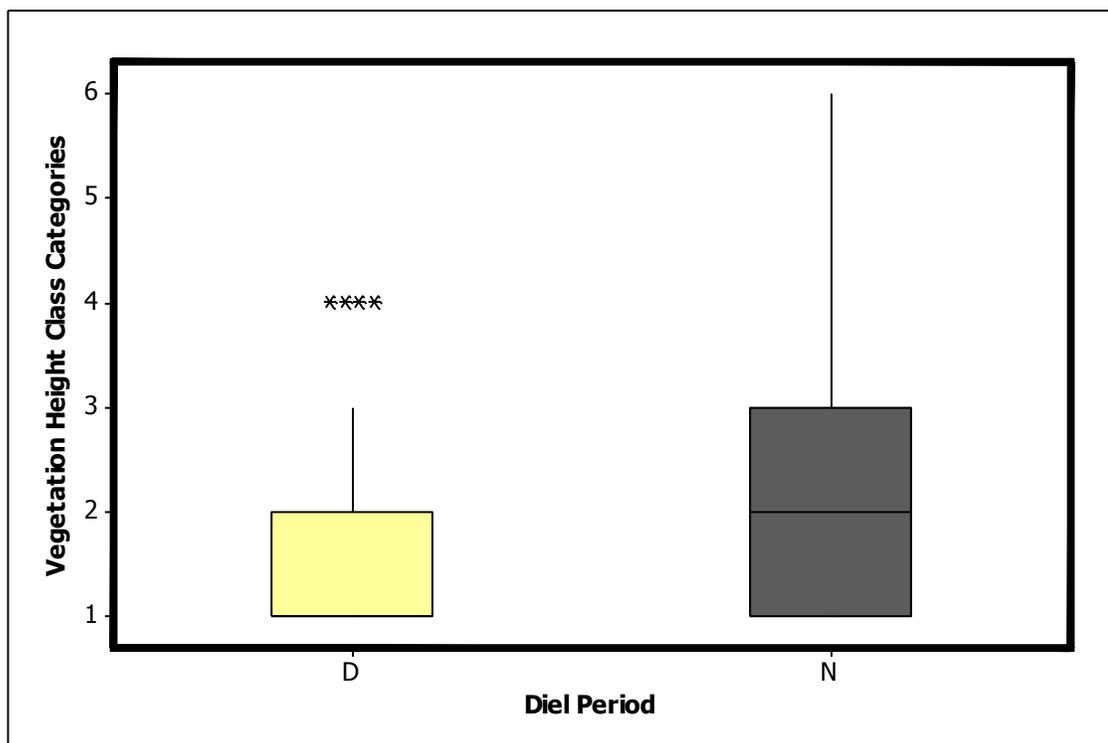


**Figure 23. Boxplot of total number of terrapins found in social burrows between months. Parametric One-Way ANOVA showed no significant difference in total number of terrapins in a social burrow between months ( $p=0.275$ ). Circles with crosshairs represent the mean of the data. This data represents all terrapins captured in social burrows during 2010-2011, regardless of capture methodology.**

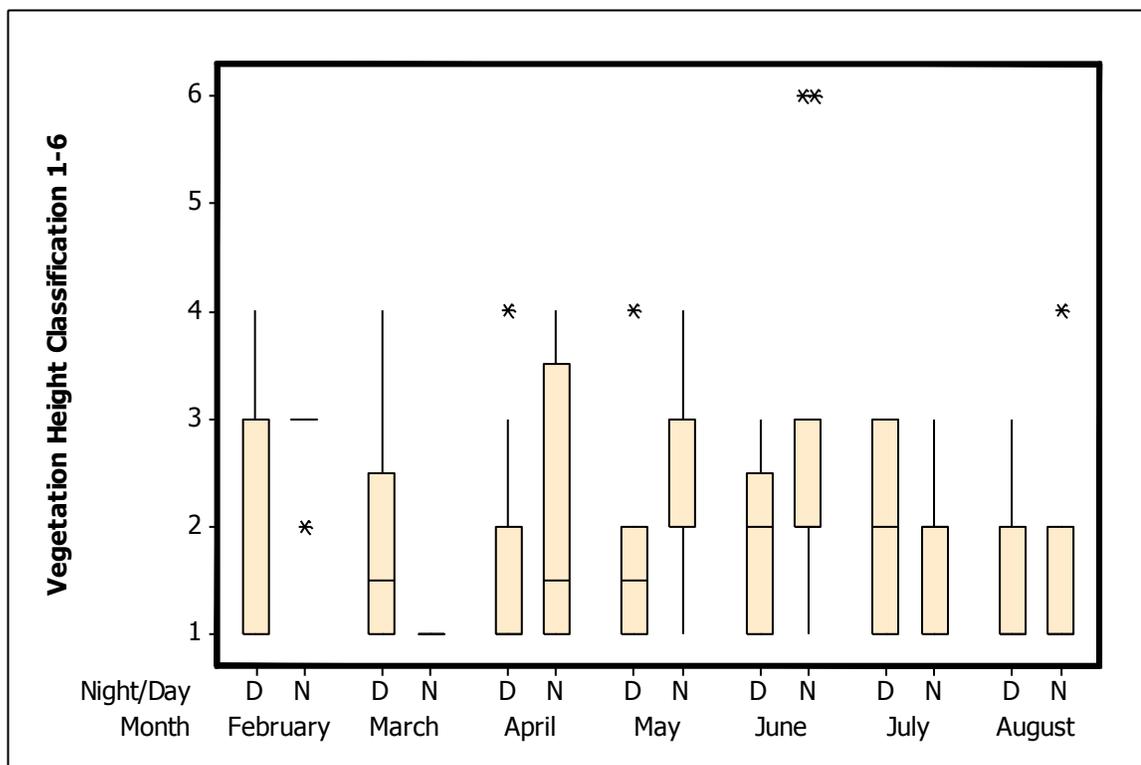
#### *Habitat Selection: Vegetation Height*

A Mann-Whitney test of all actively-captured female terrapins showed that females displayed a significant preference for taller vegetation during the night versus the day ( $p=0.0010$ , Figure 24, Appendix 1 Section 2.1). Males showed no significant difference in vegetation height preference during the night versus the day (Mann Whitney,  $p = 0.10$ , Appendix 1 Section 2.2). A Kruskal Wallis ANOVA testing month/diel variable showed that female terrapins display a significant preference for taller vegetation overall in February, June, and July, and a preference for taller vegetation at night versus during the day in May ( $p=0.001$ , Figure 25, Appendix 1 Section 2.3.) Males showed no significant difference in their preference for vegetation height between monthly and diel periods

(Kruskal Wallis,  $p=0.228$ , Appendix 1 Section 2.4). Preference for taller vegetation at night by females could indicate either predator avoidance or selection of an optimum-temperature microhabitat, and will be discussed in detail later on.



**Figure 24.** Boxplot showing the median vegetation height class at the point of female terrapin capture between diel periods. Class categories are ordinal intervals of 20 cm. 1 = 0-20 cm, 2 = 21-40 cm, 3 = 41-60 cm, 4 = 61-80 cm, 5 = 81 -100 cm, 6 = > 1 meter. Mann Whitney T-Test showed that vegetation at the point of female terrapin capture was significantly higher at night versus during the day ( $p=0.001$ ). This data represents all terrapins caught using active methods (hand capture, radio telemetry, manual acoustic telemetry). Mean not displayed as the test is non-parametric.



**Figure 25. Boxplot showing median vegetation height (recorded in classes 1-6 in increments of 20 cm) at point of female terrapin capture at night versus during the day between months. Kruskal Wallis ANOVA shows increased median vegetation height in February, June, and July ( $p=0.001$ ). This data represents all terrapins caught using active methods (hand capture, radio telemetry, manual acoustic telemetry). Mean not displayed as the test is non-parametric. August data highly biased towards the 4 terrapins being radiotracked continuously.**

#### *Habitat Selection: Vegetation Density, or Percent Vegetation Cover*

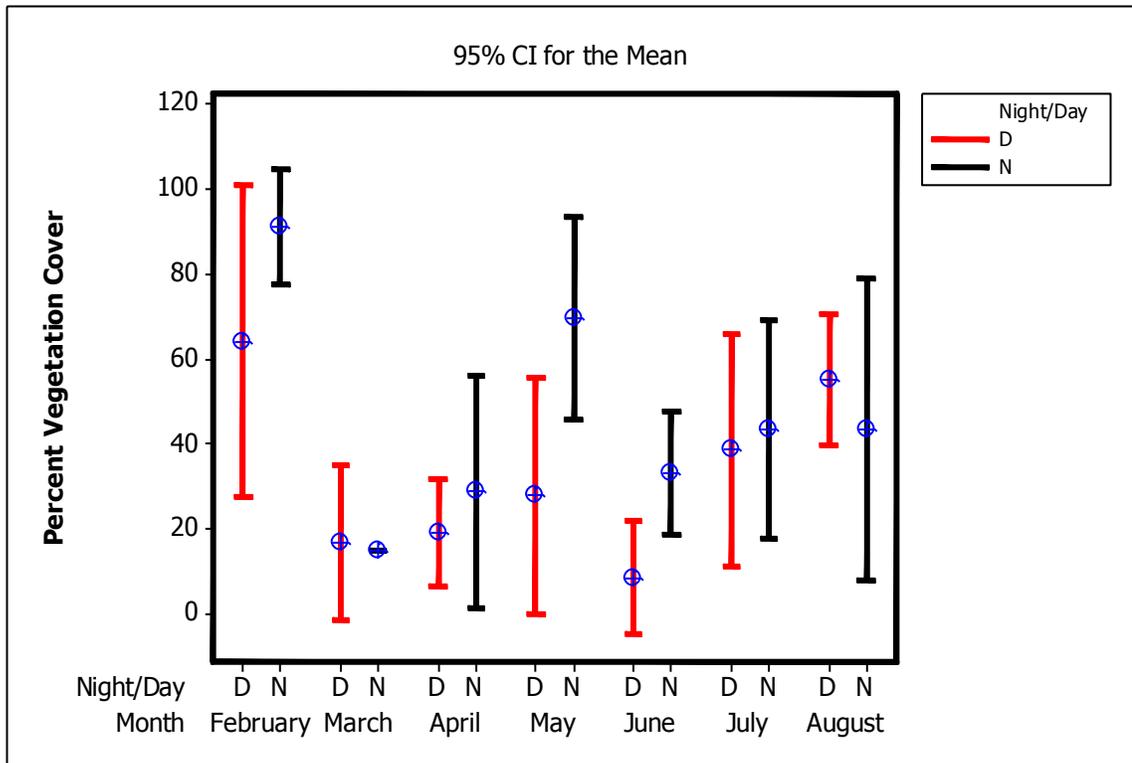
Parametric One-Way ANOVA and multiple range test results suggest that females have a preference for more dense vegetation cover during the night versus the day in May and June, but not during any other month (Figure 26, Appendix 1 Section 2.5,  $p=0.000$ ).

However, the general linear model test showed that the majority of variation in vegetation preference is due to month ( $p=0.00$ ) fluctuations rather than diel period (“barely” insignificant,  $p = 0.057$ ), and that there was no interaction between these two variables ( $p$

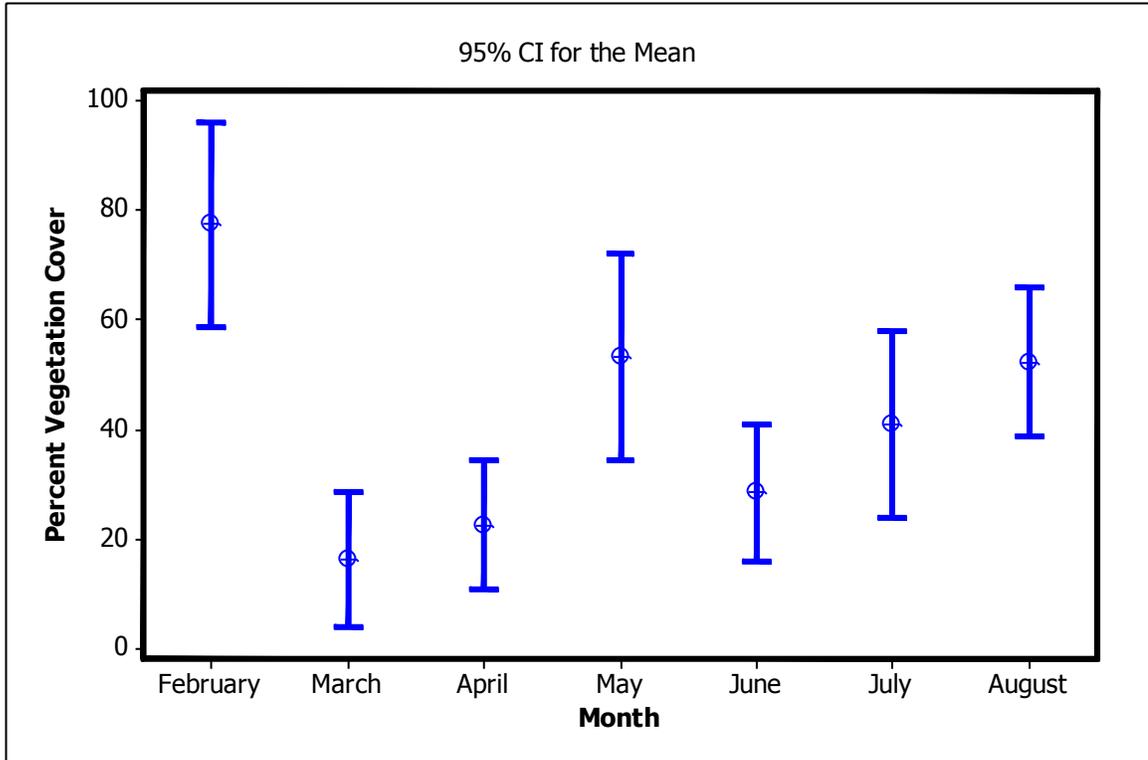
=0.207, Appendix 1 Section 2.6). Tukey's multiple range test showed that females selected denser vegetation in February, May, and August as compared to March and April ( $p=0.000$ , Figure 27). This data suggests female selection of more open habitat for mating in March and April, and possibly nocturnal nesting in May and June. Males showed no significant preference for different vegetation cover densities during the night versus day, but they did show a significant preference for less dense vegetation overall during March and more dense vegetation in August (ANOVA,  $p=0.001$ , Figure 28, Appendix 1 Section 2.7). Once again, selection of less dense vegetation in March could indicate a preference for open mating habitat. There was no interaction between diel period and month for male vegetation cover preference. Table 10 shows the overall percent cover of vegetation at point of female terrapin capture during each month, as well as vegetation species presence and percent cover.

**Table 10. Description of percent cover as explained by each species at point of female terrapin capture each month.**

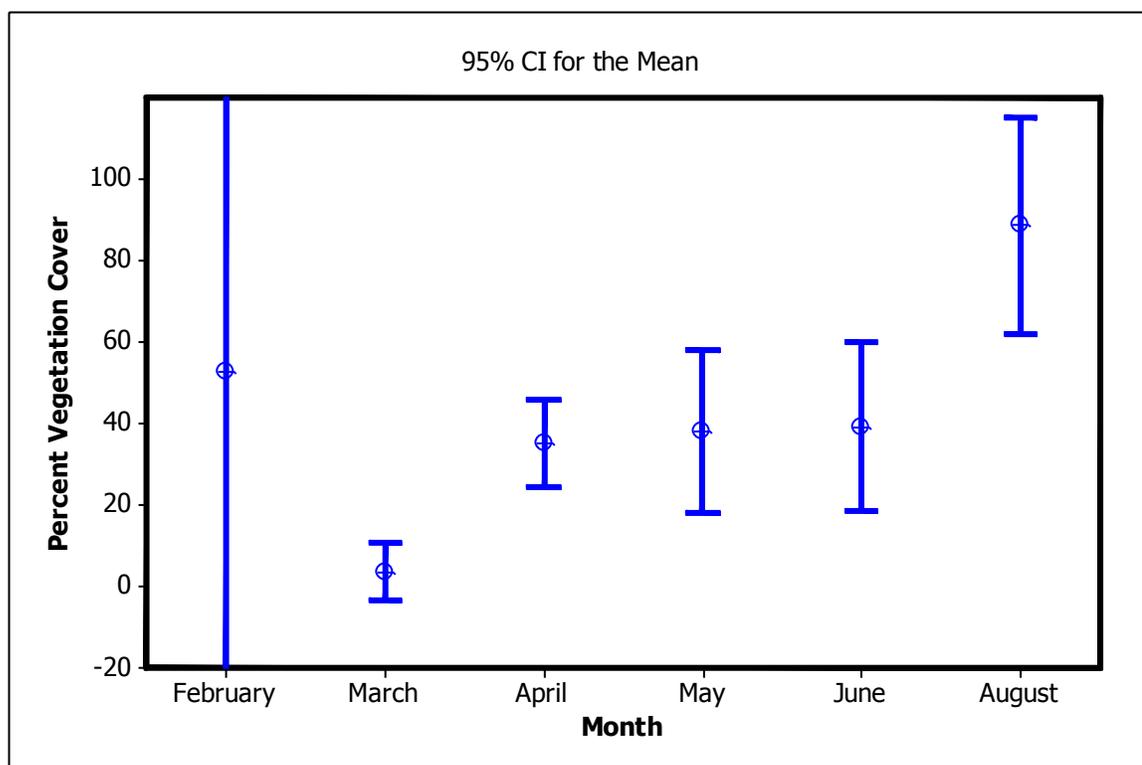
Variable	Month	Mean	StDev	Minimum	Median	Maximum
% Ground Cover that is <i>Spartina alterniflora</i>	Feb	20	25.7	0	5	60
	Mar	16	16.4	0	10	40
	Apr	25	27.7	0	10	80
	May	51	47.8	0	30	100
	Jun	32	35.6	0	15	100
	Jul	30	28.1	0	15	60
	Aug	33	30.9	0	30	100
% Ground Cover that is <i>Batis maritima</i>	Feb	4	10.2	0	0	25
	Mar	3	6.7	0	0	15
	Apr	0	1.4	0	0	5
	May	0	0.5	0	0	2
	Jun	3	8.6	0	0	35
	Jul	20	27.4	0	0	50
	Aug	45	46.3	0	30	100
% Ground Cover that is <i>Salicornia</i>	Feb	11	17.4	0	0	40
	Mar	1	2.2	0	0	5
	Apr	1	1.9	0	0	7
	May	0	0.0	0	0	0
	Jun	0	0.0	0	0	0
	Jul	4	5.5	0	0	10
	Aug	0	0.0	0	0	0
% Total Vegetation Cover	Feb	33	34.0	0	32.5	70
	Mar	20	17.0	0	25	40
	Apr	26	26.9	0	10	80
	May	51	47.7	0	30	100
	Jun	34	34.5	2	20	100
	Jul	54	31.1	0	60	75
	Aug	78	23.5	40	80	100



**Figure 26. Interval plot showing the 95% confidence interval of the mean percent vegetation cover at point of female terrapin capture at night versus at day during different months. One-Way ANOVA showed a significant difference in mean percent vegetation cover between month/diel period variable combinations ( $p=0.000$ ) and General Linear Model ANOVA showed that this variation is mostly due to monthly factors ( $p=0.000$ ) rather than diel influence ( $p=0.057$ ). This data represents all female terrapins actively captured (using hand capture, radio telemetry, and manual acoustic telemetry). August data highly biased towards the 4 terrapins being radiotracked continuously.**



**Figure 27. Interval plot showing the 95% confidence interval around the mean percent vegetation cover at point of female terrapin capture between months. Based on Tukeys multiple range tests, February, May and August levels were significantly different ( $P < 0.05$ ) from March and April values. This data represents all female terrapins actively captured (using hand capture, radio telemetry, and manual acoustic telemetry). August data highly biased towards the 4 terrapins being radiotracked continuously.**

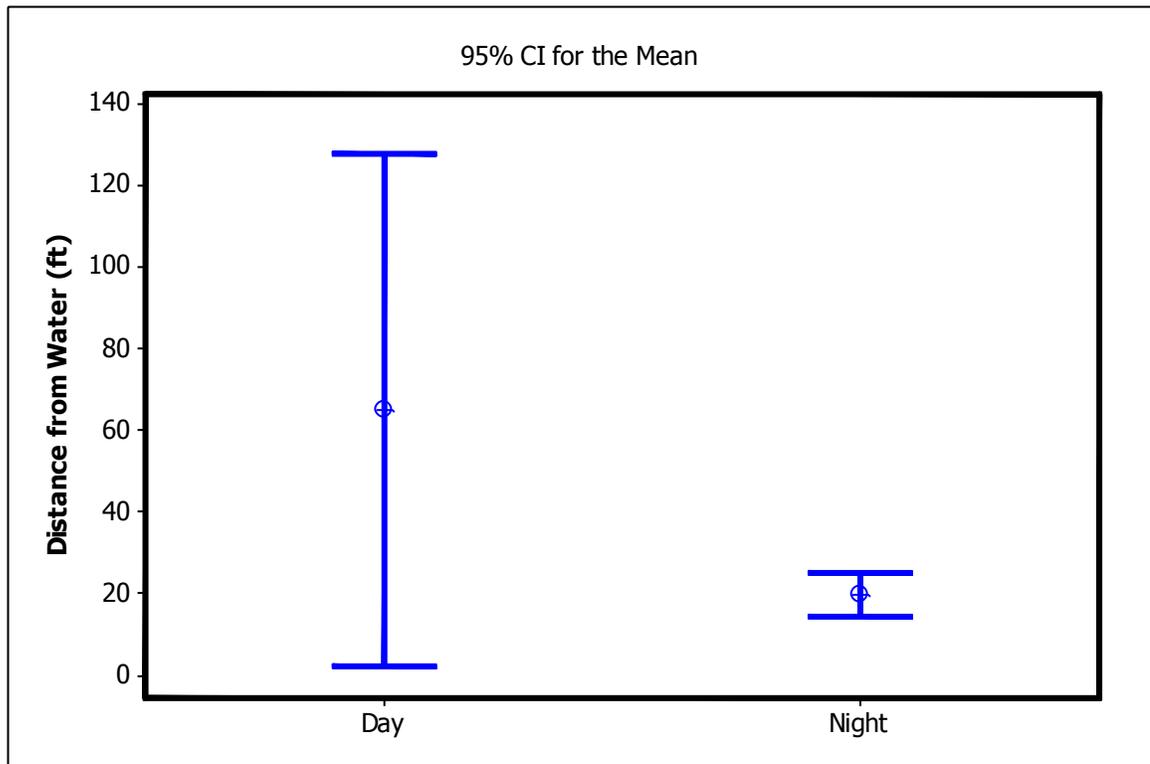


**Figure 28. Interval plot showing the 95% confidence interval around the mean percent vegetation cover at the point of male terrapin capture during different months. The large CI around the mean vegetation cover in February is due to very little, highly variable data. One-Way ANOVA showed that male terrapin captured in March were found in significantly lower mean vegetation cover when compared to all other months ( $p=0.001$ ). This data represents all male terrapins actively captured (using hand capture, radio telemetry, and manual acoustic telemetry). August data highly biased towards the 4 terrapins being radiotracked continuously.**

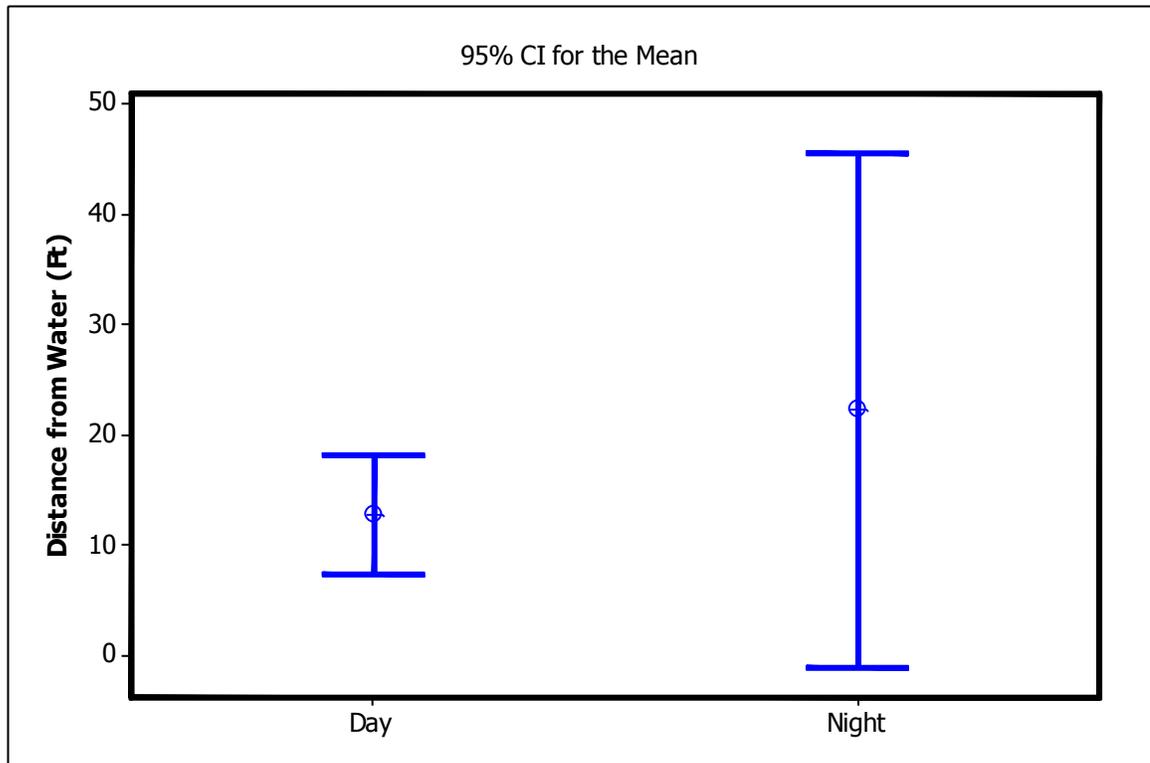
#### *Habitat Selection: Distance from water*

A T-test showed that there was no significant difference in proximity to water at time of capture between night and day for female and male terrapin ( $p=0.159$ , Figure 29, Appendix 1 Section 3.1,  $p=0.423$ , Figure 30, Appendix 1 Section 3.2, respectively). A Pearson's correlation test also showed that there was no correlation between proximity to water and tidal amplitude (females  $p=0.866$ , males  $p=0.956$ ), water temperature

(females  $p = 0.403$ , males  $p = 0.515$ ), soil temperature (females  $p = 0.082$ , males  $p = 0.115$ ), or air temperature (females  $p = 0.466$ , males  $p = 0.421$ ) (Appendix 1 Section 3.3 and 3.4). This data exemplifies the difference in Texas environments versus those on the East Coast: because we experience less variation in tidal amplitude, resources may be more evenly distributed, resulting in less of a drastic habitat partitioning between males and females. This is discussed in detail later on.



**Figure 29.** Interval plot showing the 95% confidence interval of the mean of distance from water at the point of female terrapin capture. Distances were not significantly different between both time periods (t-test:  $p = 0.159$ ). This data represents all female terrapins actively captured (using hand capture, radio telemetry, and manual acoustic telemetry).

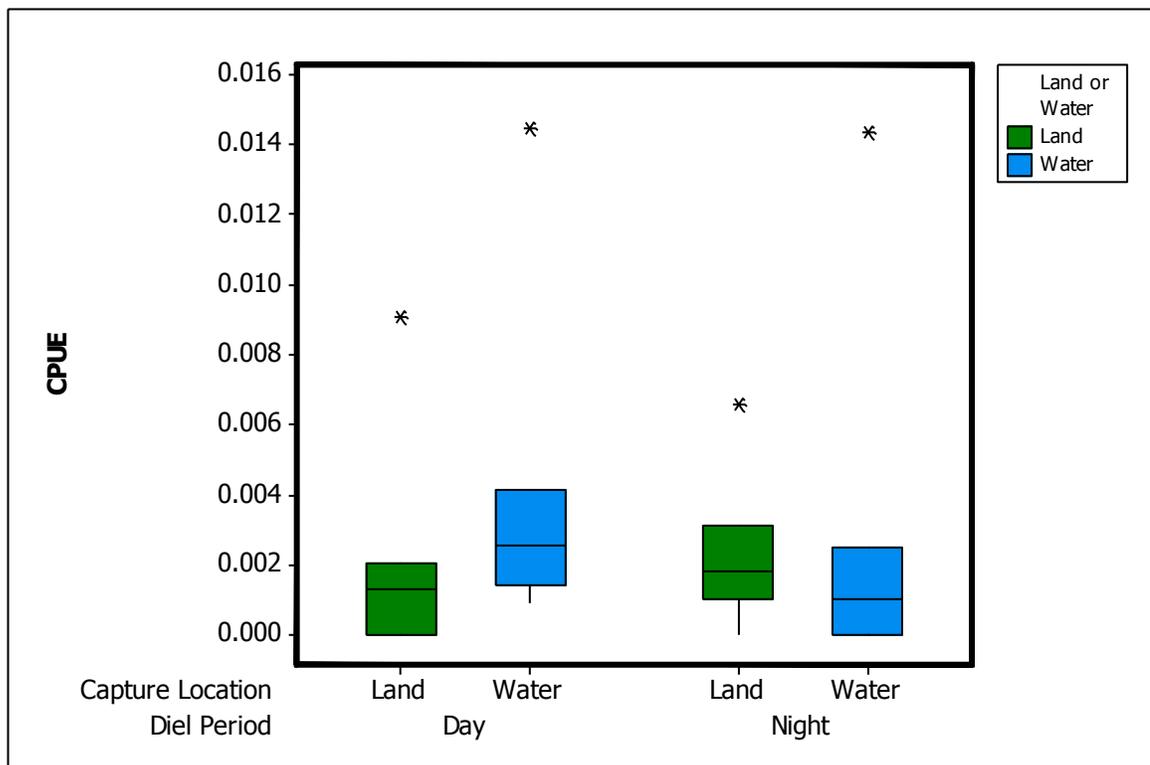


**Figure 30. Interval plot showing the 95% confidence interval of the mean distance from water at point of male terrapin capture at night versus day. The T-test showed no significant difference in distance from water between diel periods ( $P = 0.423$ ) This data represents all male terrapins actively captured (using hand capture, radio telemetry, and manual acoustic telemetry).**

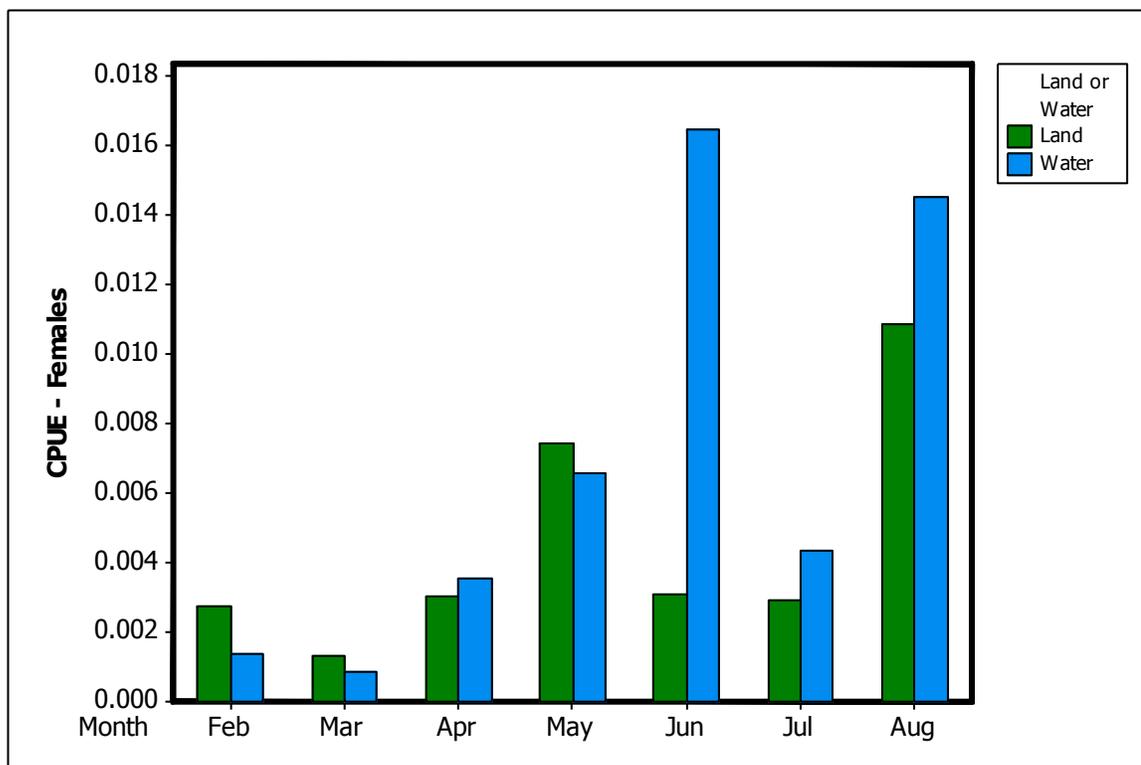
#### *Habitat Selection: Aquatic versus Terrestrial Habitat Use*

A two-way ANOVA of the CPUE of hand captured terrapin showed that there was no significant difference between capture location (terrestrial and aquatic) for different diel periods (night and day) (Figure 31, Females  $p=0.602$ , Appendix 1 Section 4.1 and Males  $p=0.364$ , Appendix 1 Section 4.2). Although this relationship is insignificant, there is a trend that may indicate female terrapin utilize terrestrial habitat more than aquatic habitats during the night, and vice versa during the day. There was higher overall aquatic

habitat use in June, July, and August, although this was insignificant (two-way ANOVA of CPUE of hand captured female terrapins,  $p = 0.117$ , Figure 32). While this data was statistically insignificant, it is possible that these trends are still biologically significant: due to the increased difficulty of capturing a terrapin in the water versus on land, the number of terrapins found in the water should realistically be much higher. At any time, we could observe several terrapins swimming but were unable to catch them, so the number of terrapins utilizing aquatic habitat is most likely much higher than the number of terrapins actually captured. This suggests that the data could potentially show a significant trend of greater aquatic habitat selection in peak summer months by female terrapins.



**Figure 31.** Catch per unit effort of female terrapins caught on land versus in water at night versus during the day throughout the study period. Two Way ANOVA of actively captured female terrapins showed no significant difference in CPUE of land captures versus water captures between diel periods ( $p=0.602$ ).



**Figure 32. CPUE of females captured by hand on land versus in water, displayed by month. Two-Way ANOVA of hand captured terrapins shows an insignificant trend of increasing aquatic habitat selection in peak summer months ( $p=0.134$ ). This data shows only hand captured terrapin.**

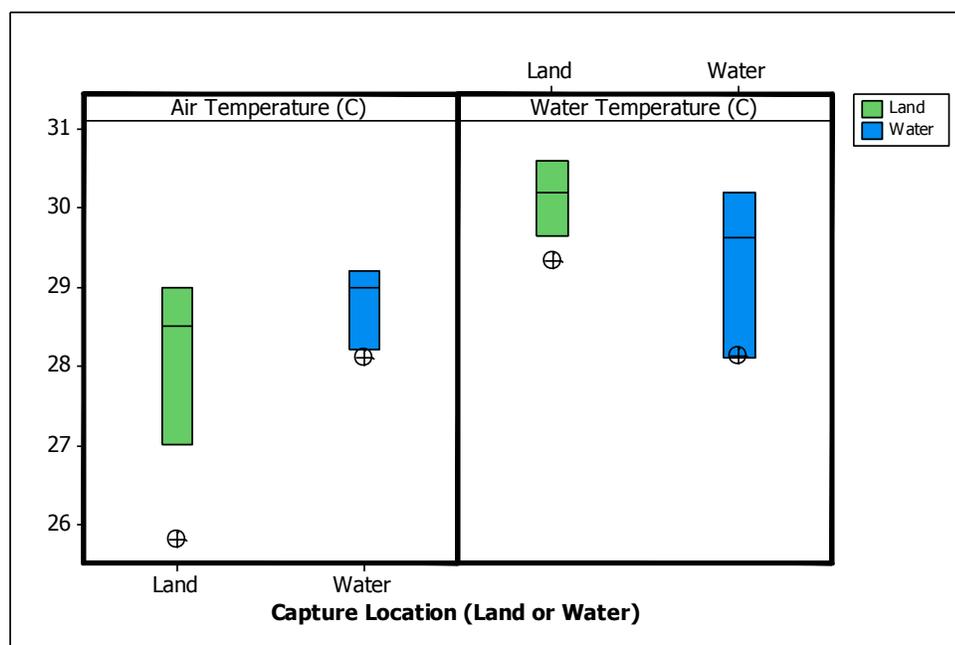
To determine if temperature was a factor in aquatic versus terrestrial habitat selection, I used a T-Test, which employed “land” and “water” as subscript classes and temperature (air and water) as the sample, on all actively captured terrapin. As stated in my methods, these temperature values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture. Therefore, the “operative” temperature as experienced by the terrapin may be different than the “environmental”, or ambient temperature, measured by the data loggers (see Discussion for further clarification on operative versus environmental temperatures). Results of our T-test show that aquatic capture of female terrapins

coincided with higher air temperature and lower water temperature ( $p=0.009$ , Figure 33, Appendix 1 Section 4.3 and 4.4) and capture on land significantly coincided with higher water temperatures and lower air temperature ( $p=0.009$ , Figure 33, Appendix 1 Section 4.3 and 4.4). When this data was re-analyzed using the corrected temperature from the regression (see Methods: Physical-Chemical data Collection), the data still showed the same trend (T-test,  $p=0.044$ , Appendix 1 Section 4.5).

To clarify this data, I subtracted water temperature from air temperature at time of capture to establish a “delta temperature”. A T-Test showed that delta temperature was significantly closer to 0 when female terrapins were captured in water (when water temperature equals or is less than air temperature) and delta temperature was significantly more negative (meaning water temperature was much greater than air temperature) when female terrapins were captured on land ( $p=0.004$ , Appendix 1 Section 4.6). Figure 34 and Figure 35 shows that when mean water temperature exceeds air temperature by  $4^{\circ}\text{C}$ , female terrapin are more likely to be found on land. When water temperature is approximately the same or slightly cooler than air temperature, female terrapins are more likely to be found in the water. This shows that female terrapins are showing preference for the cooler available habitats, which could mean that terrapins are employing cooling rather than basking or heating thermoregulatory behavior. Additional analysis of this data using the corrected water temperature (See Methods: Physical-Chemical Data Collection) showed the same trend in delta temperature and female habitat selection (T-test,  $p=0.012$ , Appendix 1 Section 4.7, Figure 36).

When I re-analyzed the delta temperature trends using 2012 data from the ongoing monitoring project (See Methods: Habitat Selection), there was no significant

difference in delta temperature between habitat types (aquatic versus terrestrial) for female terrapin capture (T-test,  $p=0.241$ , Appendix 1 Section 4.8). However, there was a significant difference in delta  $t$  at time of capture on land versus in water for male terrapins, in contrast to the 2011 data set (T-test,  $p=0.007$ , Appendix 1 Section 4.9). In summary, analyzing the 2011 water temperature data from both the tide station and the corrected temperature regression showed that only females were selecting habitats with lower delta temperatures. The 2012 data from the ongoing monitoring project showed that only males were showing significant preference for habitats with lower delta temperatures. In 2012, no significant difference was observed in female habitat selection and delta temperature.



**Figure 33. Boxplot showing the mean and median water and air temperatures at time of female terrapin capture on land versus in water. A T-test of actively captured terrapins show that water temperature was significantly higher when terrapins were caught on land versus in the water ( $p=0.015$ ). A T-test of actively captured terrapins show that air temperature was significantly higher during aquatic captures versus terrestrial captures ( $p=0.01$ ). Circles with crosshairs represent the mean of the data. As stated in my methods, these values represent the ambient temperature as detected by a data-logger at a specified site, and NOT the micro-habitat temperature at the point of terrapin capture.**

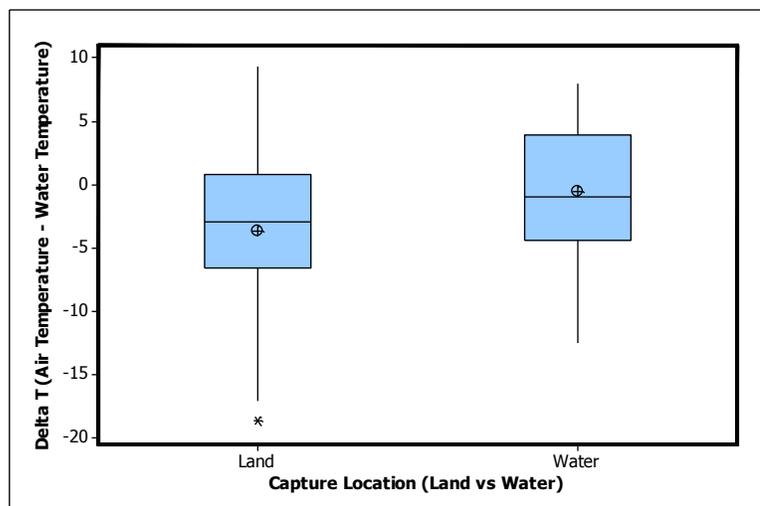


Figure 34. Boxplot showing the median and mean delta temperature (Air temperature - Water temperature) at the time of female terrapin capture on land versus in water. A T-test of actively captured terrapin showed delta temperature was significantly less negative (air temperature exceeding water temperature) when terrapins were found in the water and was significantly more negative (water temperature exceeding air temperature) when terrapins were found on land ( $p=0.000$ ). Circles with crosshairs represent the mean of the data.

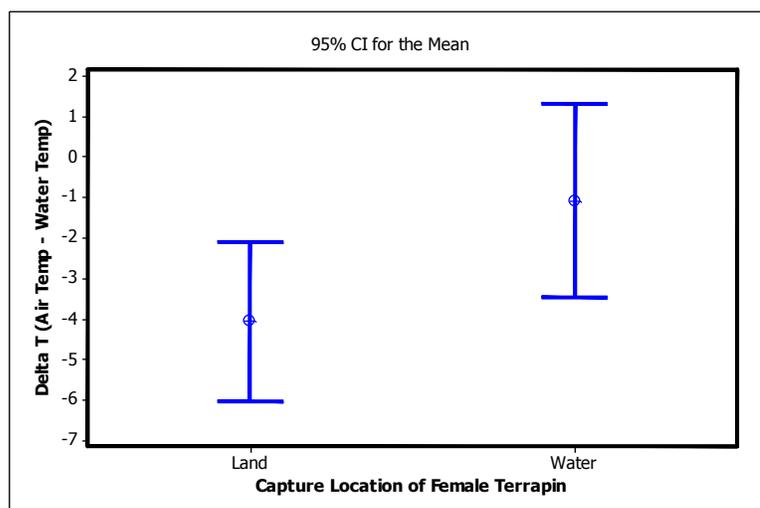
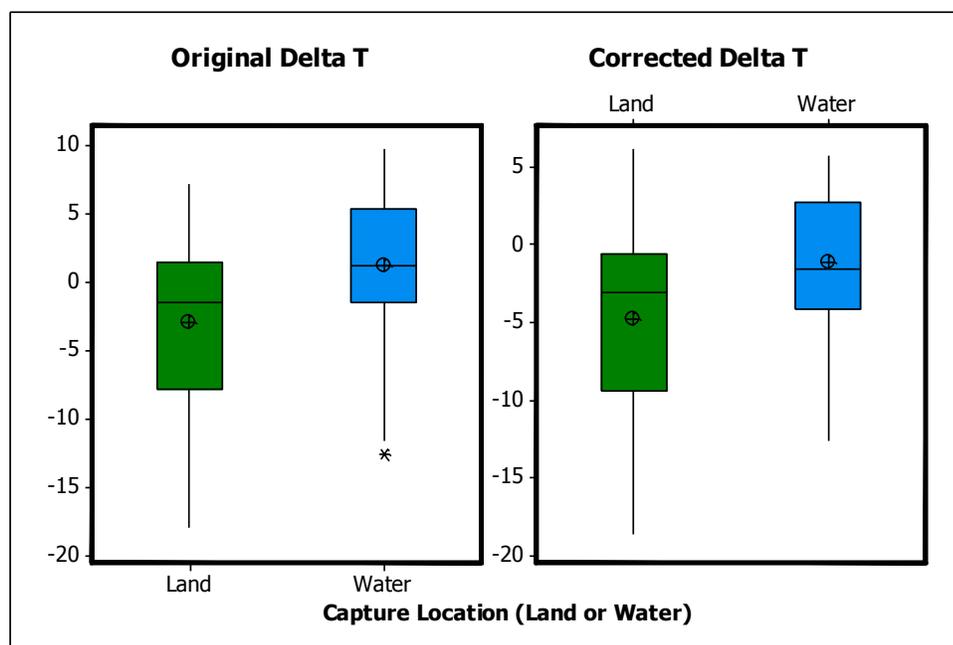


Figure 35. Interval plot showing 95% confidence interval of the mean delta temperature (water temperature subtracted from air temperature) at time of female terrapin capture when on land versus in water. Delta temperature was significantly less negative (Air temperature exceeding water temperature) when terrapins were found in the water and was significantly more negative (water temperature exceeding air temperature) when terrapins were found on land ( $p=0.000$ ).



**Figure 36. Boxplot showing median and mean delta temperature (water temperature subtracted from air temperature) at the time of female terrapin capture on land versus in water. The figure on the right shows the delta temperature as calculated using the “corrected water temperature” from the regression between the 2012 probe data and the 2012 tide station data (see Methods: Physical-chemical data collection). The figure on the left shows the delta t with the original water temperature as measured from the tide station.**

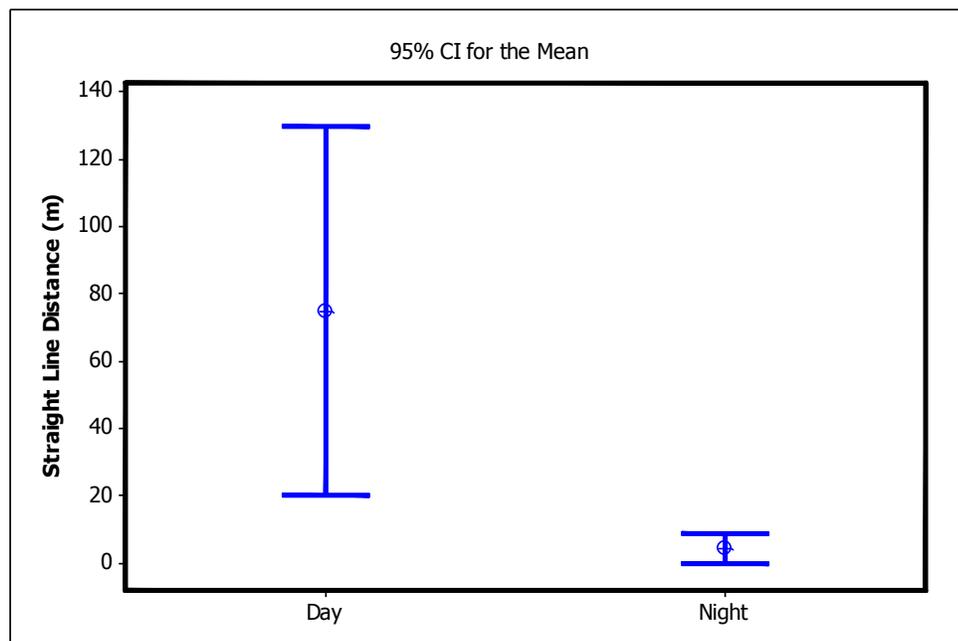
### *Range*

The maximum overall distance travelled in one sampling event was 401 meters, which occurred over a 2-hour period during the day in July. The average distance moved during the day was 75 meters, with a standard deviation of 122 meters. The maximum distance travelled during nocturnal sampling was 55 meters, with the average nocturnal movement being less than 5 meters with a standard deviation of 11 meters (Figure 39).

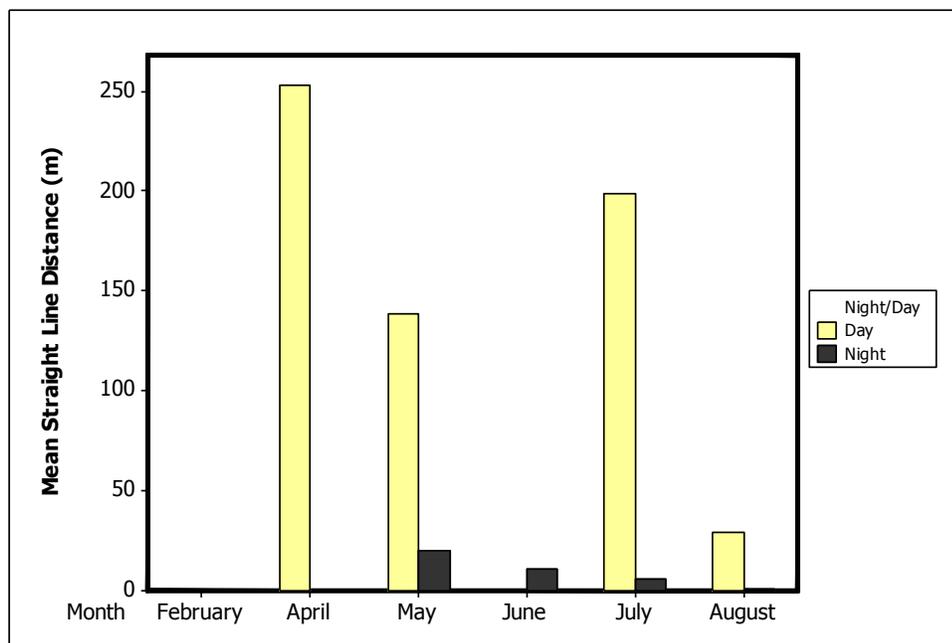
A T-test of radiotracked female terrapins showed that female linear movement was significantly greater overall during the day than at night ( $p = 0.014$ , Figure 37,

Appendix 1 Section 5.1), as was rate of movement ( $p = 0.036$ , Appendix 1 Section 5.2).

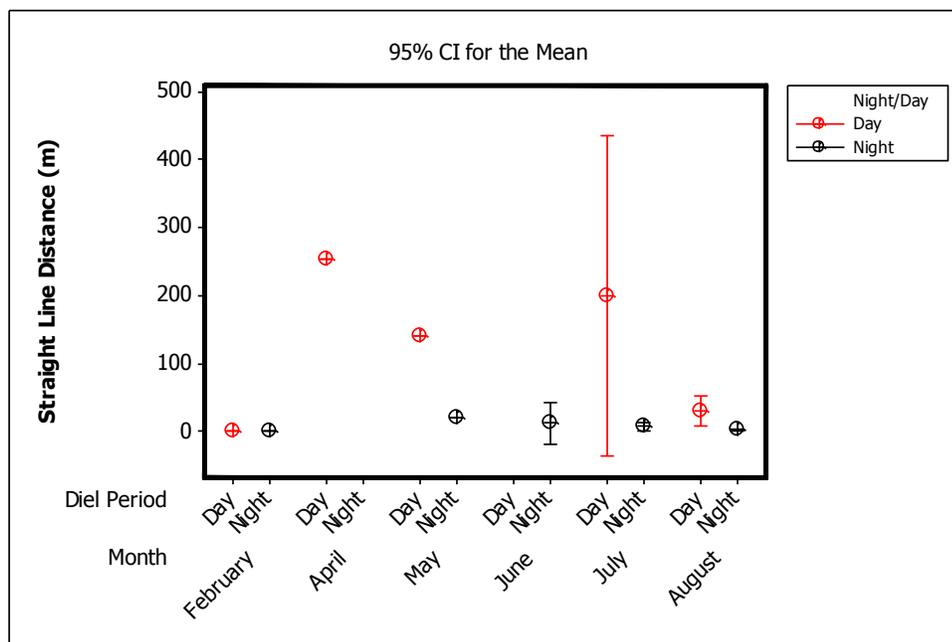
A parametric one-way ANOVA of radiotracked female terrapins showed that, on a month to month basis, significantly greater rates of diurnal linear movement were only observed in April and July ( $p = 0.000$ , Figure 38, Appendix 1 Section 5.3 and 5.4), which could indicate possible nesting or mating migrations. A decrease in nocturnal movement may suggest predator avoidance, which is discussed in detail later on.



**Figure 37. Interval plot of 95% confidence interval of the mean of minimum straight line distance travelled at night versus day. (T-test of radiotracked female terrapins,  $P = 0.036$ ).**



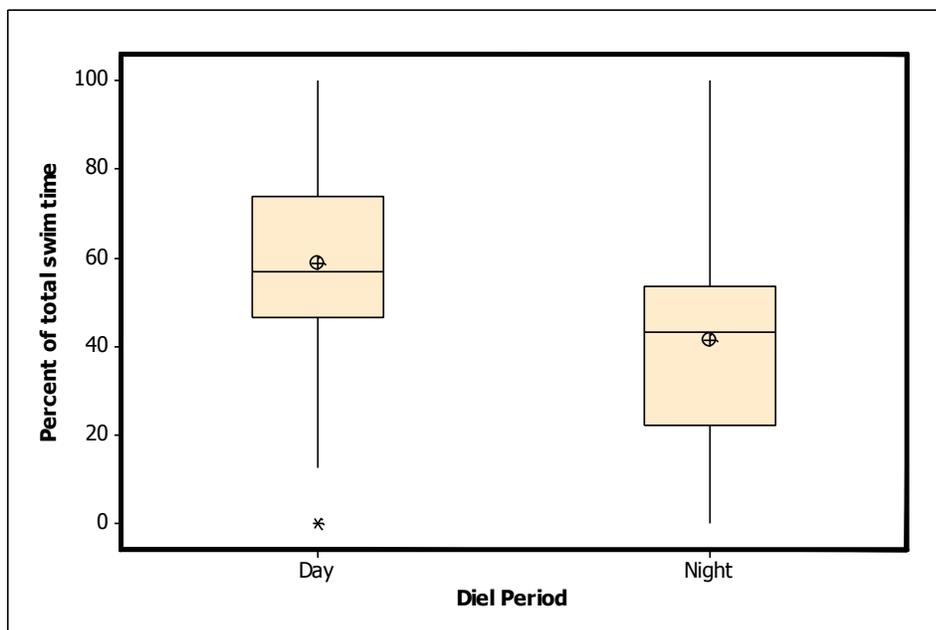
**Figure 38. Mean of straight line distance travelled in each diel period, by month. Blank spaces do not indicate missing data but rather straight line movement of 0 meters. One-way ANOVA of radiotacked female terapins showed significantly higher values of straight line distance travelled during the day versus during the night in April, August, and July ( $p=0.000$ ).**



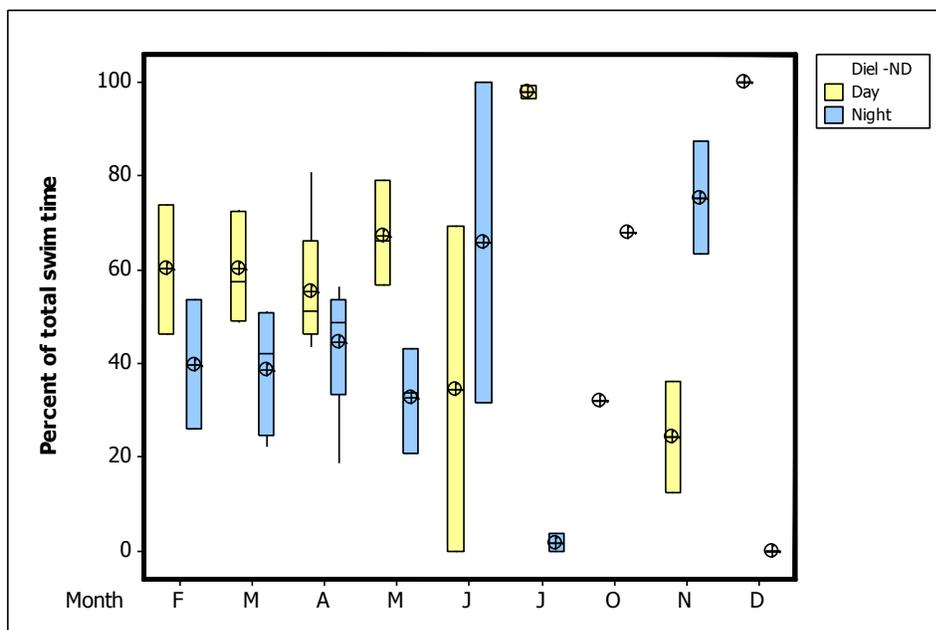
**Figure 39. Interval plot showing the 95% confidence interval around the mean of straight line distance travelled during each diel period between months. One-way ANOVA of radiotacked female terapins showed significantly higher values of straight line distance travelled during the day versus during the night in April, August, and July ( $p=0.000$ ).**

### *Acoustic Data*

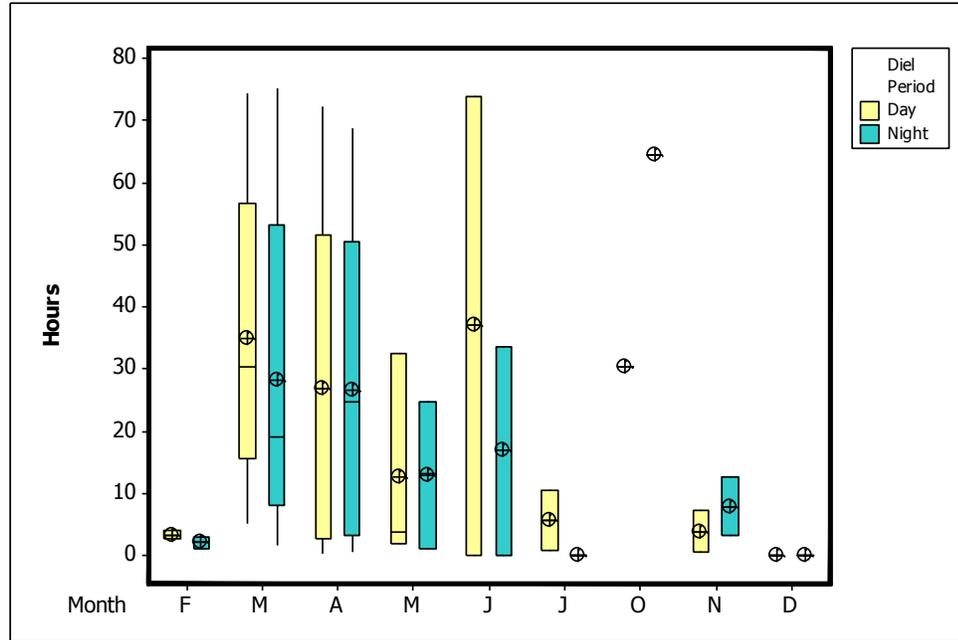
Based on T-Test results, female terrapins detected by the acoustic receivers spent a significantly higher percentage of their time swimming during the day versus at night ( $p=0.025$ , Figure 40, Appendix 1 Section 6.1). One-way ANOVA using the month/diel period variable collapse showed that this diel difference is significant in December and July ( $p=0.000$ , Figure 41, Appendix 1 Section 6.2). A t-test analyzing the number of hours a tagged terrapin was detected by the receivers (rather than percent time) between diel periods found that number of hours detected at night were not significantly different than number of hours detected during the day ( $p=0.773$ , Appendix 1 Section 6.3). A one-way ANOVA showed no significant difference in hours detected by the receiver between the month/diel period ( $p = 0.575$ , Figure 42, Appendix 1 Section 6.4). These results are not unusual: Because there is so much variability in the number of hours spent swimming between individual terrapins, it is expected that the trends of swimming hours between diel periods and months would be insignificant. When these highly variable hours are converted into percentages, however, it reduces the amount of variability and leads to a significant trend. For example, if one terrapin spends 50 hours swimming at day and 50 hours swimming at night (100 hours total), and another terrapin spends 3 minutes swimming at day and 3 minutes swimming at night (6 minutes total), the data within a single diel period is more varied than the data between diel periods and the trends will be insignificant. When this is converted to a percentage, however, it shows both swimming efforts as 50% occurring at night and 50% occurring during the day, variability is reduced, and the trend becomes significant.



**Figure 40.** Boxplot showing the median and mean percent of total swim time that female terrapins tagged with acoustic transmitters swam at night versus at day. T-test showed a significant higher percent of time was spent swimming during the day versus at night ( $p=0.025$ ). Circles with crosshairs represent the mean of the data.



**Figure 41.** Boxplot showing the mean and median percent of total swim time that female terrapins tagged with acoustic transmitters swam at night versus during the day in each month. Circles with crosshairs represent the mean of the data. One-way ANOVA shows that of the time a female terrapin was swimming, it spent a larger percentage of that time swimming at day versus night in December and July ( $p=0.000$ ).



**Figure 42. Boxplot of the mean and median total number of hours that each acoustically tagged female terrapin was detected by the stationary receivers between diurnal periods and month. Circle with crosshairs represents the mean of the data. One-way ANOVA showed no significant difference in the number of hours that tagged females were detected by the acoustic receiver between diel periods and months ( $p=0.575$ ).**

### *Qualitative Observations from 24-hour monitoring*

For two sampling periods, I closely followed the behavior and movement of four terrapin that were double tagged with acoustic and radio tags so that both their terrestrial and aquatic movements could be followed. Our first observation period occurred on July 28<sup>th</sup> – July 29<sup>th</sup>, during which we observed two terrapin. We arrived at 9 am and found both of our tracked terrapin either swimming or buried in the tidal creeks, and during the course of the day we observed high levels of travelling in these creek systems. By evening, two of the observed terrapin had moved into terrestrial habitats and still displayed slightly reduced rates of movement. By 3:00, the terrapins were terrestrial and all travelling had

ceased. By sunrise, the terrapins had re-entered the creek system and had resumed swimming long distances (Figure 43).



**Figure 43. Chronological map of location of individual terrapins throughout a close-up observation of behavior and movement over a 24- hour period from 9:00 a.m. July 28th to 9:00 a.m. July 29th. Individual terrapins are represented by different colors.**

During the second period (August 11<sup>th</sup>), we observed four terrapins. During the day, we found terrapin behavior to be varied, but habitat selection was restricted to creeks or marshes directly adjacent to creeks. By midday, we found two of our tracked terrapin buried socially with 12 additional terrapin at the edge of the creek bed. Later in the evening, we found all terrapins to be still actively swimming or travelling through creeks or the marshes on the edges of the creeks. By 20:00, all terrapins had ceased motion and remained in their locations until 0600 the following morning. At this time, all terrapins had resumed swimming activity (Figure 44 and Figure 45).



Figure 44. Chronological map of location of individual terrapins throughout a close-up observation of behavior and movement over a 24- hour period from 9 a.m. August 11th – 9 a.m. August 12th on the north side of South Deer Island. Individual terrapins are represented by different colors.



Figure 45. Chronological map of location of individual terrapins throughout a close-up observation of behavior and movement over a 24- hour period from 9 a.m. August 11th – 9 a.m. August 12th on the north side of South Deer Island. Individual terrapins are represented by different colors.

## DISCUSSION

### *Diel Period versus Temperature and the Effects on Behavior*

The results of my study support the hypothesis that terrapin activity and behavior is primarily influenced by temperature and less with time of day, while short term range and movement may be more affected by diel period.

Poikilotherms have minimal capabilities for temperature homeostasis and therefore must utilize behavioral and physiological regulation of temperature as well as select habitat and microclimate that maximizes their operative environmental temperature. Operative environmental temperature is the temperature as experienced by the organism, and can be predicted by air temperature or, more appropriately, substrate temperature (Crawford et al 1983). The location of the individual in the salt marsh largely influences operative environmental temperature. Vertical movements in the water column can expose terrapin to differing temperatures, as can differing levels of vegetation cover and sun exposure. In this way, substrate temperature and water temperature can be a much more accurate indicator of operative environmental temperature than air temperature, which can explain why we saw a significant correlation between female behavior and water and soil temperature but no relationship between behavior and air temperature. The “voluntary minimum” operative environmental temperature is the

temperature at which an organism voluntarily emerges from refuge and resumes activity, and can be regarded as the lowest temperature at which an organism will be active. In this study, we found active terrapin at air temperatures as low as 16-19°C, but the majority of terrapins did not resume high levels of activity until closer to 28°C. Terrapins resumed activities at soil temperatures as low as 16-19°C, but the majority of increased activities occurred at soil temperatures 21-27°C. The 95% confidence interval around the mean soil temperature during “active” behaviors showed a voluntary minimum temperature occurring at 23° soil temperature. The “voluntary maximum” is the temperature at which an organism retreats to refuge such as shade or burrow, and can be regarded as the highest temperature at which an organism will be active. We found cessation of activity at soil temperatures of 36°C, during which we found many terrapin retreated to burrows in the sides or bottoms of creek banks. The “optimum temperature” is the temperature at which organisms will engage in normal active behaviors such as foraging and mating (Harless and Morlock 1979). Optimum temperature was highly varied in this study, and both inactive and active terrapins were observed at intermediate soil temperatures (21-36°C). Diel trends in behavioral thermoregulation can represent the trade-off between thermoregulatory and normal behaviors. Since air and substrate temperature are predictors of operative environmental temperature, and light intensity based on the time of day influences air and substrate temperature, time of day can have a great effect on thermoregulatory versus normal active behaviors (Crawford et al 1983). Terrapins can also experience varied sensitivity to environmental temperatures based on the time of day. Turtles that have been exposed to natural photoperiods and temperature gradients have shown to have more thermal tolerance during late morning-evening and more

sensitivity to high temperatures during the late night or early morning (Crawford et al 1983). In this way, diel period and temperature are not mutually exclusive factors, and it may be difficult to discern the exact causality (diel period versus temperature) for changes in behavior as there is significant interaction between these two factors. The only significant difference in female terrapin behavior between diel periods during this study occurred in the month of April. There is little difference in soil temperature at night versus day in April, and this shows that soil temperature may not best explain this trend in variation in female terrapin behavior during diel periods in April. This could indicate that some significant difference in “normal” behaviors (ie, non-thermoregulatory, such as nesting or foraging) is occurring between diel periods in April.

On the east coast, terrapins are observed basking in either shallow water or on the marsh surface the majority of the time, especially when water temperatures are cooler than the air, and particularly in May (Harden et al 2007, Tucker et al 1995). While basking, terrapins achieved carapace temperatures of 16 – 37 °C, while air temperatures ranged from 22-26°C. These temperatures are common during the day in February and March in Texas, but by April and May, night time is characterized by temperatures ranging from 22-25°C and day time is characterized by temperatures 28° C and higher. By mid-summer, daytime temperatures can exceed 38° C. We found that female terrapins exhibited “basking” behavior (which can be explained by a behavior of 2, 3, and in some cases, 5) at soil temperatures ranging from 25-35°C and air temperatures from 23-31°C (95% confidence interval of mean soil and air temperatures). We found that terrapins are more likely to be found swimming or burrowed in the water when the water temperature is cooler than the air temperature, and are more likely to be found on land when air

temperature is cooler than water temperature. A related trend was also observed by Crawford et al (1983) in the case of *P. scripta*, where basking frequency was correlated with a difference between air and water temperature (Crawford et al 1983). This suggests that terrapin are showing preference for the coolest available habitat and may be exhibiting both cooling thermoregulatory behavior and heating (basking) behavior. With respect to diel patterns, this manifests as a higher percentage of swimming activities observed during the day in the hottest months (June, July). Higher percentages of swimming activity were also observed in May despite a lack of extremely hot temperatures, and may represent “normal activities” such as mating or reproductive migrations rather than thermoregulatory behaviors as temperatures are still relatively cooler, and terrapins mate in the water during April-May in Texas (personal observations). The CPUE for the acoustic receivers also showed increased swimming activities in March and April, which also support mating rather than thermoregulatory behaviors during this time. We also observed an increase in the capture rate of terrapins in water versus on land in late summer (June-August). While this could also indicate cooling behavior and habitat selection, it is possible that this is a response to increased prey availability in the creeks during these months. However, further research is needed into the diet and prey availability in the Galveston Bay populations of terrapins before this hypothesis can be supported.

Boyer (1965) tested the heat tolerance for several species of turtles in a lab setting and found that turtles showed physical discomfort and agitation at 30°C, “gaping mouths” and signs of “distress” at 34-37°C, watering eyes, limp limbs, and a cessation of struggling at 34-37°C, and death at 42.1°C for *Sternotherus spp.* and 44.5°C for *P.*

*elegans*. While lab tests on other species may not be the most accurate representation for the expected thermoclines in the field, it can help suggest at what temperature and possibly diel period terrapin may be utilizing cooling thermoregulatory behaviors.

Even at these high temperatures, it is likely that some basking occurs. Previous studies have observed basking behavior at air temperature of 28°C (operative environmental temperature approximately 38-41°C). Although these temperatures can be near lethal levels, basking duration and frequency can be greatly reduced at higher temperature due to a higher speed of body temperature elevation (Crawford et al 1983). With a smaller amount of time allotted to basking, terrapins would be able to allocate more energy to foraging and mating while maintaining the positive effects of a short basking period such as increased digestion rate, stimulation of the production of vitamin D, and the combat of algal growth and parasites (Harless and Morlock 1979). In this study, basking would be represented by behavioral values of 2 (turtle pocket – exposed to sun and covered by a thin layer of mud) or 3 (sitting on marsh surface). Behavioral values of 2 corresponded to soil temperatures ranging from 24-33°C with outliers ranging from 16-35°C and behavioral values of 3 corresponded to soil temperatures of 31-35°C with outliers as low as 30°C. These temperatures occur during both day and night periods during the summer, but with an increased sensitivity to thermoclines at night and early morning, we would expect to see more thermoregulatory behavior during these time periods.

Basking on land is also used as an osmoregulatory behavior in times of drought to prevent saltwater influx (See Introduction). It is possible that the high variability we observed in temperature at time of basking can be explained by this osmoregulation: this

year of study experienced a severe drought, and we may have been observing higher/more variable rates of basking in response.

We also observed an overall increase in female terrapin behavior with increasing soil and water temperature, but a decrease in male behavior with increasing air and soil temperature. Spotila (1980) showed that heat loss is greater in smaller organisms versus larger ones due to convection. If this is the case in Diamondback terrapin, males (which are smaller than females due to sexual size dimorphism) would need to increase thermoregulatory behavior at less extreme temperatures more than females to retain desired body temperatures. For example, as temperatures increase, males will need to display cooler regulatory behaviors at a lower temperature, while larger females can wait until much higher temperatures before employing cooling behavior. In cooler climates, males would exhibit basking at less extreme temperatures to prevent body heat loss. In this study, however, the decrease in male behavior at these high temperatures may show that males are experiencing high enough body temperatures to not necessitate further thermoregulatory behaviors. Once again, this points to probable cooling behavior rather than heating behavior.

#### *Habitat Selection and Temperature versus Diel Period*

The temperature experienced by a Diamondback terrapin can be highly dependent on microhabitat selection. For example, increased soil and water temperature may cause terrapins to actively swim in the cooler parts of the water column or seek more covered terrestrial habitat (resulting in a higher behavioral ranking or “walking” or “swimming”).

However, Pearson's correlation shows no relationship between air temperature and percent vegetation cover at point of female terrapin capture ( $p = 0.943$ ). A parametric one-way ANOVA showed that there was no significant difference in air temperature at differing heights of vegetation at point of female capture ( $p = 0.063$ ). Trends between soil temperature and vegetation cover and vegetation height were not analyzed because soil temperature data was obtained from a data-logger buried at a single point on the island and therefore did not represent instantaneous soil temperature at point of capture. This shows that terrapin show no differential preference for vegetation density or height at differing air temperatures. Future research needs to be conducted on the instantaneous soil temperature at point of capture to see if any trends exist between soil temperature and habitat selection (in terms of vegetation density and height).

Terrapins did, however, display preference for differing vegetation densities and heights based on diel period. The selection of taller and denser vegetation may indicate habitat selection that maximizes predator avoidance. Seigel (1980b, 1984) observed high levels of adult female terrapin mortality resulting from raccoon attack. The majority of these attacks occurred during mating season when terrapins came onshore to nest. Seigel observed one attack in which the raccoon had severed the hind limbs and pulled the innards of the turtle out through the open leg-hole. While we have never actually observed raccoons or raccoon tracks on South Deer Island, we have found several terrapin with limbs missing. Previous literature has also shown a very low rate of raccoon predation on male terrapin (Seigel 1980b, 1984), and we concurrently found a lack of male terrapin preference for increased vegetation cover at night in our study. This could support the hypothesis that nocturnal raccoon predation could account for decreased

movement of female terrapin and selection of taller vegetation cover at night in that this preference was only seen in female terrapin, and only female terrapin are at higher risk of raccoon predation. However, we have no evidence of predation to support this.

Alternatively, female terrapins could be selecting taller vegetation at night as a thermoregulatory behavior: it is possible that the taller vegetation may hold heat after sunset, while more open habitats may cool more quickly. As stated previously, more research is needed on instantaneous soil temperatures at the point of capture to support this hypothesis.

While we found no significant difference in distance from water at point of terrapin capture between diurnal and nocturnal captures, there was a trend showing shorter distances from water and much less variability during the night as compared to the day for females. Contrary to this, males showed shorter distances and much less variability in distance from water during the day as compared to night.

According to a study by Tucker et al (1995), larger periwinkle snails on the east coast inhabit less dense vegetation at higher elevations further from creeks, and therefore it is more common to find females foraging in these areas. High tide and marsh flooding enable easy access into the marsh above the creeks and therefore increased foraging opportunities. Males are constricted to foraging on the small periwinkle snails that inhabit the thick, tall vegetation adjacent to creeks (Tucker et al 1995). However, tidal fluctuations on the Gulf Coast are much less extreme than on the Atlantic, and these trends of periwinkle distribution may be different. And, because flooding at high tide is less extreme, tidal fluctuations may not provide easy access into upper marsh. Instead, wind-driven tides may cause a greater fluctuation on a monthly basis versus a daily tidal

basis, and any habitat selection trends may therefore be more influenced by month than diel period. This is supported by the fact that we saw no significant difference in distance from water between diel periods in both males and females.

At night, the lower variability in female habitat selection (as pertains to distance from water, Figure 29) may correspond to less variable nocturnal behaviors. Nocturnal periods outside mating season may be a time for decreased variability and range of activities and habitat selection for females, while diurnal periods may be a time for an increased range of activities such as mating, nesting, reproductive migrations, and foraging.

Males, on the other hand, showed an increase in variability of distance from water at night versus day (Figure 30) while showing no significant difference in nocturnal versus diurnal behavior. This increased variability in distance from water is unexplained by any of the behaviors that I have classified, but may be related to foraging. I was unable to classify “foraging” in any one of my classes as the observer effect typically prevented observation of these behaviors. From the few instances I have observed a terrapin foraging, I have noticed that they quickly cease foraging as soon as my presence is detected, which makes “foraging” very hard to classify as a behavior without large error. Because of this, it is difficult to address the first part of my hypothesis, in which I propose that we would observe more nocturnal foraging in the hottest parts of the summer. Further research on diet and foraging patterns is needed in Texas, as many habitat selection trends may be explained by prey availability.

Based on acoustic data and qualitative observations, females spend a lower percentage of time swimming at night versus during the day, and typically spend the nights terrestrially. This coincides with personal comments from Jeff Lovich and Whit Gibbons (personal comments at the DTWG Conference 2011) stating that terrapins are not typically caught in seines or traps overnight. Therefore, nocturnal selection of terrestrial habitat may be a pattern throughout their range. Further studies need to be conducted on the Atlantic coast to verify this.

### *Range and Diel Period*

In the case of range and distance travelled, time of day had more of an effect than temperature. We found highly decreased rates of movement at night versus during the day, but we found no significant correlation between air temperature and distance travelled or rate of movement (Pearson's Correlation,  $p=0.211$ ,  $p=0.289$ , respectively). Furthermore, previous literature states that as the body cools (as in during the night), some reptiles metabolism is actually greater than as the body warms (as in during the day) due to an increase in oxygen consumption and heat production (Bennett 1982). This delays cooling, increases metabolism, and supposedly increases activity and muscular use during cooling environmental conditions (Bennett 1982). This would supposedly result in an increase of movement during the night or early evening, while we observed a decrease in movement at night and an increase in movement during the day.

Therefore, the trends we observed most likely reflect the habitat preferences and predator avoidance mentioned in the previous section. Female Diamondback terrapins

experience nocturnal predation by raccoons (Segel 1980b, 1984), and therefore may decrease their movement and settle into more densely vegetated habitats during the night to avoid predation.

Terrapins could also be made highly vulnerable to nocturnal predation by a decrease in vision and consequently a decrease in ability to detect predators. It has been found that sea turtles use simple light reception rather than color vision to find the ocean upon hatching. Sea turtles have much less sensitivity to red light than freshwater turtles, but relatively good near-ultraviolet vision. Ehrenfeld (1968) speculates that this may be due to the short-wavelength transmittance of seawater (Ehrenfeld 1968). Because Diamondback terrapin inhabit high salinity water, it is likely that their vision is more structurally similar to sea turtles than other freshwater turtles. Therefore, their vision is more dependent on photoreception rather than color. This could explain why they travel shorter distances and decrease movement at night: their visibility is greatly reduced by lack of light. My personal observations support this explanation: at night, I am able to observe terrapin from a much closer distance without being detected by the individual I am observing.

#### *Implications for Mating and Nesting*

Females showed an increased level of nocturnal behavior during April. The peaks of activity and range in April-May followed by a second peak in July could indicate two mating seasons. According to the optimal egg size theory (OES), the optimal

reproductive output is typically a trade-off between number of eggs in a clutch, number of clutches in a year, and size of the eggs. In the north east, data shows that terrapins typically lay clutches of 7-9 eggs once a year, while terrapins have been known to lay two or three clutches of 6 eggs a year in warmer climates such as Florida (Seigel 1980a). My data suggests a second mating and clutching period in Texas. The only nest to have ever been found in Texas was discovered in April at South Deer Island (Hogan 2003), which is much earlier than in some north eastern states. This coincides with the peak in overall activity I observed in April, and the higher rate of nocturnal activity could be preparation for nocturnal nesting. Nocturnal nesting has been observed in Maryland and New Jersey (Roosenburg 1994, Burger and Montevecchi 1975), and would be more likely to occur in this warmer climate. Terrapins have not been typically shown to nest at temperatures above 35°C (Feinberg and Burke 2003), and 90% of terrapins typically nest between 29 – 33°C (Seigel 1980a). These temperatures are consistent with both nocturnal and diurnal temperatures observed in April and May during this study. Unfortunately, the presence of sensitive nesting bird species on South Deer Island prevented us from surveying the nesting beaches, so we can only observe mating and foraging behavior.

The documentation of social burrowing may also point to potential mating later in the season. Social burrows were characterized by a higher male to female ratio in March and April, and a higher female to male ratio in May – July, after which the ratios leveled off to 1:1. The highest peak in number of terrapins in a burrow occurred in August. Several instances of “mating aggregations” have been observed in Diamondback terrapin, but are typically aquatic and only described as “hundreds of terrapin heads...in a relatively small area” (Hauswaldt and Glenn 2005, pg728). There have even been reports

of lekking, during which males congregate and females selectively mate with the males based on skin and shell color (Estep 2005). Mating systems can be classified as either polyandrous (in which females have several male mates), polygynous (in which males have several female mates), or monogamous, depending on sex ratios, population stressors, and the distribution of resources (Molles 2005). Typically, populations characterized by a higher or equal male to female sex ratio display polygyny as females serve as a limited resource and male competition is necessary for mating. As sex ratios switch to female-dominant, polyandry and multiple paternity become more common. In a polyandrous system, inbreeding can be reduced and overall effective population size can be maximized. It is also common for females to utilize sperm storage as the chance of encountering a male can be decreased in this scenario (Sheridan 2010). Sheridan (2010) observed a significant number of transient male terrapin migrating through mating habitats in the spring, after which males maintained high site fidelity. This could cause a male-dominant population in spring and a female-dominant population in late summer. Data from the ongoing study at South Deer Island shows a shift in population sex ratios from male dominance in March and April to female-dominant in May-December. This shift was also reflected in the social burrows: Social burrows were dominated by males in March and April, and then dominated by significantly more females in May – September. I am proposing that this shift in sex-ratios causes sexual selective pressure and results in a shift from male dominance polygyns in the spring (March and April) to female defense polygyns in late summer.

Male dominance polygyns typically occur when resources are abundant but highly dispersed, and population density is high, and results in male to male defensive

encounters (Emlen and Oring 1977). Our population satisfies these requirements: the main food sources of terrapins, mainly periwinkle snails and fiddler crabs, are abundant and widely distributed on the island. As for density, we have over 600 terrapin marked on this 29 ha island, and continue to find new captures every time we survey. I have also personally seen several instances of two or more male terrapins “fighting” (which included biting and scratching) over a female terrapin in early spring. These observations typically occur just as hibernation and overwintering inactivity ceases and mating and spring activity just begins, but I have never observed this in late summer. The beginning of spring mating season seems to be characterized by male defense lekking, and subsequent mating encounters are characterized by female defense polygynys, as seen in the shift of sex ratios in these social burrows. Female defense polygyny occurs when females “clump” for reasons other than mating, such as information exchange, observational learning, and predatory defense, but the clumping can result in greater male potential for mating with several females (Emlen and Oring 1977). The other situation in which females clump is resource defense polygyny, in which superior habitats or resources are defended by males, so females must mate with already mated males to acquire this resource or habitat (Emlen and Oring 1977). It is unlikely that the latter is the case, as the habitats in which these burrows are found are not clumped or limited on South Deer. Also, Diamondback terrapins are opportunistic feeders and are highly sexually dimorphic, which could prevent males from defending female food sources such as larger crabs. I suggest that these late summer social burrows are exemplary of a female defense polygyny. It is possible that the increases in activity and behavioral levels later in summer could reflect increases in mating aggregations and nesting activities as well. The

shift to female defense polygynys in the summer would be beneficial as second and third clutches sired by different fathers would minimize inbreeding and increase effective breeding population size.

### *Future Research*

I found that my hypothesis was supported in that I found more site fidelity and less distance moved nocturnally and that behavior seemed to be more related to temperature rather than diel period, but my hypothesis postulating increased female foraging activity at night in the summer was not supported. With the exception of the months mentioned in my discussion, the data showed no difference in activity levels between diel periods. The lack of significant difference in most cases is due to very high individual variability in behavioral patterns and habitat selection. This variability points to the fact that much more research is needed. One thing that needs to be addressed is the source of this variability: is true individual variability being observed, or is there a sampling bias that is not being overcome? As mentioned earlier, when relying only on visual searches and not telemetry, the trends we see in habitat selection may be inaccurate due to difference in detection probability. We can reduce this factor with telemetry (radio and acoustic), but extensive creek systems prevent us from being able to pinpoint terrapin during their active swimming times. We found that our modified traps were not efficient, and we have had no success with seining due to the size and shape of the creeks, and therefore are less able to capture terrapin that are utilizing aquatic habitats (turbidity can sometimes be too high to catch terrapin in the water by hand in the summer months). In my personal

observations, there is a decrease in CPUE from land searches during the hottest summer months, but terrapins are still observed swimming in the bays and creeks. More research needs to be conducted in unbiased and affordable sampling methodologies with which we can detect and capture terrapin in these difficult habitats, such as deep water or very thick vegetation. Furthermore, it is apparent that few studies on the east coast employ extensive terrestrial searching. Many methodologies seem to focus more on seining, fyke nets, and trapping, and therefore there is little available data to compare foraging habitat selection between the east coast and Texas. More telemetry and non-nesting terrestrial studies need to be conducted, as our research indicates there is differential habitat selection and distribution within the foraging habitats (low-lying salt marshes). This may attribute more importance to these areas than before.

My data did not support my hypothesis that Diamondback terrapins increase foraging activity at night during the hottest parts of the summer. This is largely due to the lack of an obvious definition of “foraging behavior”; as I stated earlier, it is incredibly hard to define this behavior as most terrapins detect the observer and cease any foraging behavior. I have rarely (2-3 times) observed a terrapin foraging, and foraging typically occurs during swimming events when the marsh is flooded. While we did see an overall higher level of female activity and behavior during the night in April, there was no difference in male activity between diel periods. Therefore, it is difficult to clearly demonstrate foraging patterns through my ordinal behavioral scale. There has been no research conducted on the diet and foraging habits and behaviors of Texas terrapin. Defining these habits could greatly increase our ability to continue in behavioral studies of Texas terrapin in the field. Furthermore, an increased understanding of their prey could

greatly increase our understanding of terrapin movement, habitat selection, and behavior. It is probable that these variables are based on prey availability as well as thermoregulatory requirements rather than predatory pressure as I have never observed predators on South Deer Island. However, research into the predatory influences on terrapin is also necessary, as little is known about predation in Texas.

While my data can suggest possible clutching and mating times based on activity levels and habitat selection, there has only been one documented Diamondback terrapin nest in Texas (Hogan 2003), which points to a vast deficit in knowledge of nesting habits of Texas terrapins. The peak of nocturnal and diurnal activity, as well as the sex ratio shifts in the social burrows, suggests that several mating and nesting periods may occur on South Deer Island, but without proper nesting research, we can only speculate. Unfortunately, South Deer Island is home to several sensitive species of birds that are protected under the Migratory Bird Act, including the Reddish Egret, the White Faced Ibis, and the Brown Pelican. These birds nest extensively on the same higher-elevated beaches that we presume terrapin would nest, and where the only terrapin nest has been located. Therefore, we are prevented from doing typical nesting surveys on South Deer Island. Recently, we have begun to monitor fecundity in our population using SonoSite Vet 180 Plus Ultrasound, which can provide some information on clutch size, egg size, and nesting times, but much more research is needed.

Nesting research may also provide some answers as to why terrapins tend to burrow socially at the end of the summer, and why the sex ratio shifts from male dominated in the spring to female dominated in late summer. With the little data we have, we can only speculate that these burrows are even related to mating or nesting at all,

when in fact they may be completely independent of mating systems. We plan to investigate these social tendencies further by analyzing spatial distribution and habitat classification at the point of these burrows to determine if it is in fact “social” or is instead more tied to resource and habitat availability. If there is no trend in spatial or habitat distribution, then more research is needed to determine how the terrapins are communicating the need for social burrows (ie, olfactory, vocalizations, etc.).

Terrapins displayed selection of “cooler” habitats, or habitats with a lower Delta temperature, during the summer. While it is possible that selection of aquatic habitats could be related to prey availability, the significant difference in delta temperature between habitats selected suggest that this is a cooling thermoregulatory behavior rather than a diet-based selection. This “cooling behavior” trend could have serious implications for conservation and climate change. If these terrapins are already employing cooling behaviors and are at risk of overheating, a rise in temperature associated with climate change could potentially push this species further north in its range. More research is needed at the micro-habitat scale to verify these trends, and more research is needed to investigate the effects of climate change on the southern populations of Diamondback terrapin.

Unfortunately, I was unable to continue research into September and through the winter due to physical injuries. In our continuous research, we have noted high variability in migration patterns, range, and habitat selection throughout the year. For example, we have several hundred individuals that can be found year-round on South Deer Island, and several hundred others that appear only during mating season every couple of years. We have a few individuals who have been captured at different sites that are several miles

apart, and other individuals that never leave a small area on one creek. Temporal patterns of migration and habitat selection need to be further researched along the Texas coast to better understand the species' ability to re-inhabit extirpated areas and overcome habitat alteration and destruction.

While this study has provided valuable information on Texas terrapin habitat preference, behavior, and range, it is clearly evident that much more research is needed in Texas estuaries. Our unique climate and habitats provide an excellent opportunity for new information and a better understanding of Diamondback terrapin ecology.

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## APPENDIX I Minitab Readouts

### 1. Behavior and Activity

#### 1.1. Kruskal-Wallis Test: Preprocessing Behavior versus Month/ Diel Variable Combination for Female Terrapins

Kruskal-Wallis Test on Preprocessing Behavior

Month Diel	N	Median	Ave Rank	Z
AprilD	13	1.000	88.0	0.61
AprilN	8	4.000	121.1	2.54
AugustD	29	1.000	83.4	0.37
AugustN	9	1.000	87.5	0.47
FebruaryD	9	1.000	53.5	-1.80
FebruaryN	9	1.000	62.0	-1.23
JulyD	10	3.500	122.5	2.96
JulyN	11	1.000	83.6	0.23
JuneD	5	1.000	73.6	-0.34
JuneN	23	1.000	53.5	-3.02
MarchD	6	2.000	113.7	1.79
MarchN	2	1.000	53.5	-0.83
MayD	10	2.000	107.3	1.89
MayN	16	1.000	57.3	-2.11
Overall	160		80.5	

H = 38.56 DF = 13 P = 0.000

H = 54.57 DF = 13 P = 0.000 (adjusted for ties)

\* NOTE \* One or more small samples

#### 1.2. Kruskal-Wallis Test: Preprocessing Behavior versus Month /Diel Variable Combination for Male Terrapins

Kruskal-Wallis Test on Preprocessing Behavior

Month Diel	N	Median	Ave Rank	Z
AprilD	20	2.000	43.3	1.70
AprilN	12	1.000	31.5	-0.90
AugustD	8	1.000	18.5	-2.58
FebruaryD	2	1.000	18.5	-1.23
JuneD	3	1.000	18.5	-1.52
JuneN	7	1.000	35.4	-0.15
MarchD	5	4.000	62.6	2.89
MarchN	2	3.000	55.3	1.28
MayD	7	2.000	46.2	1.29
MayN	6	1.000	24.9	-1.42
Overall	72		36.5	

H = 25.12 DF = 9 P = 0.003  
H = 29.26 DF = 9 P = 0.001 (adjusted for ties)

### 1.3. One-way ANOVA: Water Temperature (C) versus Preprocessing Behavior for Female Terrapins

Source	DF	SS	MS	F	P
Preprocessing Behavior (	4	168.22	42.05	5.85	0.000
Error	128	920.29	7.19		
Total	132	1088.51			

S = 2.681 R-Sq = 15.45% R-Sq(adj) = 12.81%

Level	N	Mean	StDev
1	89	28.076	2.987
2	11	29.936	2.309
3	14	31.082	0.950
4	6	27.900	3.552
5	13	30.315	0.749

Individual 95% CIs For Mean Based on Pooled StDev

26.0 28.0 30.0 32.0

Pooled StDev = 2.681

### 1.4. One-way ANOVA: Soil temperature (C) versus Preprocessing Behavior for Female Terrapins

Source	DF	SS	MS	F	P
Preprocessing Behavior (	4	412.6	103.2	4.74	0.001
Error	155	3376.8	21.8		
Total	159	3789.4			

S = 4.667 R-Sq = 10.89% R-Sq(adj) = 8.59%

Level	N	Mean	StDev
1	106	28.642	4.490
2	16	28.181	6.665
3	15	32.666	4.179
4	10	27.234	5.689
5	13	32.530	2.192

Individual 95% CIs For Mean Based on Pooled StDev

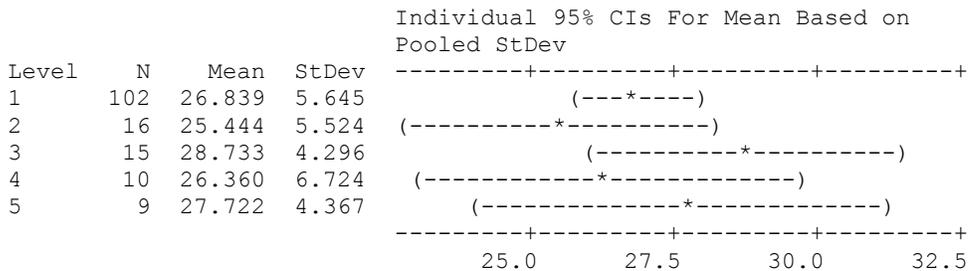
27.0 30.0 33.0 36.0

Pooled StDev = 4.667

### 1.5. One-way ANOVA: Air Temperature (C) versus Preprocessing Behavior for Female Terrapins

Source	DF	SS	MS	F	P
Preprocessing Behavior	93.7	23.4	0.77	0.549	0.549
Error	147	4494.2	30.6		
Total	151	4587.9			

S = 5.529 R-Sq = 2.04% R-Sq(adj) = 0.00%



Pooled StDev = 5.529

### 1.6. Correlations: Preprocessin, Air Temperat, Water Temper, soil temp (C)

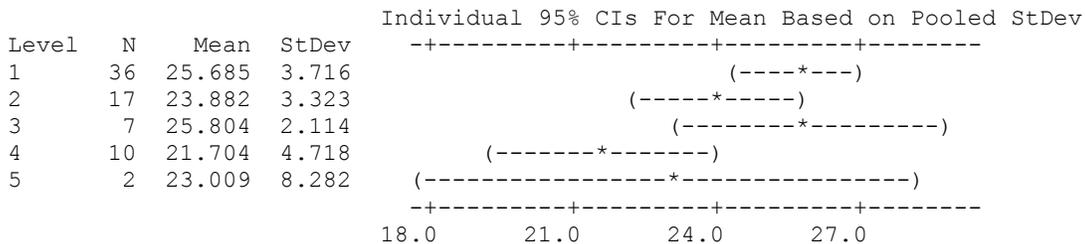
	Preprocessing Be	Air Temperature	Water Temperatur
Air Temperature	0.044 0.589		
Water Temperatur	0.281 0.001	-0.004 0.967	
soil temp (C)	0.199 0.012	0.338 0.000	0.863 0.000

Cell Contents: Pearson correlation  
P-Value

### 1.7. One-way ANOVA: Soil temperature (C) versus Preprocessing Behavior for Male Terrapins

Source	DF	SS	MS	F	P
Preprocessing Behavior	4	150.1	37.5	2.63	0.042
Error	67	955.7	14.3		
Total	71	1105.8			

S = 3.777 R-Sq = 13.57% R-Sq(adj) = 8.41%



Pooled StDev = 3.777

### 1.8. One-way ANOVA: Air temperature versus Preprocessing Behavior for Male Terrapins

Source	DF	SS	MS	F	P
Preprocessing Behavior (	4	185.2	46.3	1.66	0.168
Error	67	1863.5	27.8		
Total	71	2048.7			

S = 5.274    R-Sq = 9.04%    R-Sq(adj) = 3.61%

Individual 95% CIs For Mean Based on Pooled StDev

Level	N	Mean	StDev
1	36	27.939	5.982
2	17	25.000	3.291
3	7	26.157	4.298
4	10	24.290	5.420
5	2	23.100	7.920

Pooled StDev = 5.274

### 1.9. One-way ANOVA: Water temperature (C) versus Preprocessing Behavior for Male Terrapins

Source	DF	SS	MS	F	P
Preprocessing Behavior (	4	15.73	3.93	0.43	0.785
Error	24	218.89	9.12		
Total	28	234.62			

S = 3.020    R-Sq = 6.71%    R-Sq(adj) = 0.00%

Individual 95% CIs For Mean Based on Pooled StDev

Level	N	Mean	StDev
1	21	25.750	3.139
2	3	25.150	2.469
3	2	25.800	3.111
4	2	23.500	0.000
5	1	28.000	*

Pooled StDev = 3.020

### 1.10. Correlations: Water temperature (C), Soil temperature (C), Air temperature, Preprocessing Behavior : Male Terrapins

	Water temp (C)	soil temp (C)	air temperature
soil temp (C)	0.777 0.000		
air temperature	0.754 0.000	0.617 0.000	
Preprocessing Be	-0.042 0.830	-0.293 0.012	-0.262 0.026

Cell Contents: Pearson correlation  
P-Value

### 1.11. Two-Sample T-Test and CI: % Females in a Social Burrow, Night vs Day

Two-sample T for % Females in a Social Burrow

N or D	N	Mean	StDev	SE Mean
D	9	63.4	21.4	7.1
N	14	70.6	35.5	9.5

Difference = mu (D) - mu (N)

Estimate for difference: -7.2

95% CI for difference: (-32.0, 17.5)

T-Test of difference = 0 (vs not =): T-Value = -0.61 P-Value = 0.549 DF = 20

### 1.12. Two-Sample T-Test and CI: Total Number of Terrapins in a Social Burrow, Night vs Day

Two-sample T for Total Number of Terrapin in Burrow

N or D	N	Mean	StDev	SE Mean
D	9	3.56	3.61	1.2
N	14	2.93	1.94	0.52

Difference = mu (D) - mu (N)

Estimate for difference: 0.63

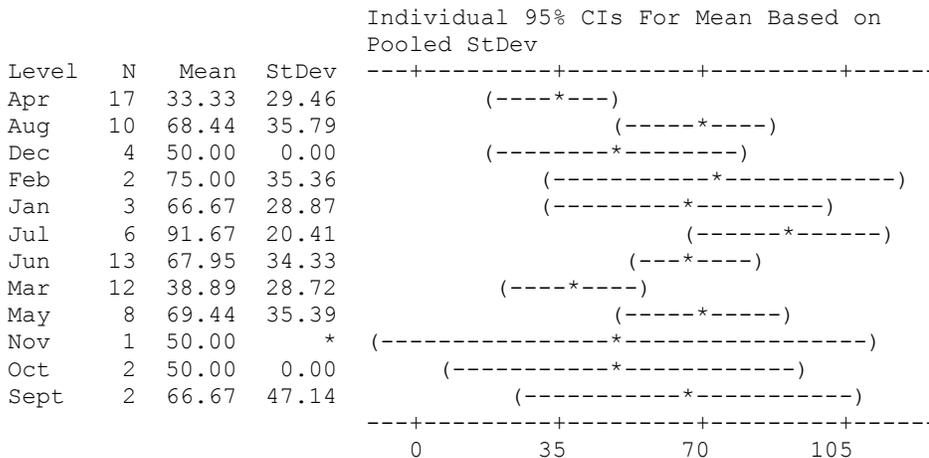
95% CI for difference: (-2.26, 3.51)

T-Test of difference = 0 (vs not =): T-Value = 0.48 P-Value = 0.642 DF = 11

### 1.13. One-way ANOVA: % Females in a Social Burrow versus Month

Source	DF	SS	MS	F	P
Month	11	26228	2384	2.51	0.010
Error	68	64625	950		
Total	79	90853			

S = 30.83    R-Sq = 28.87%    R-Sq(adj) = 17.36%

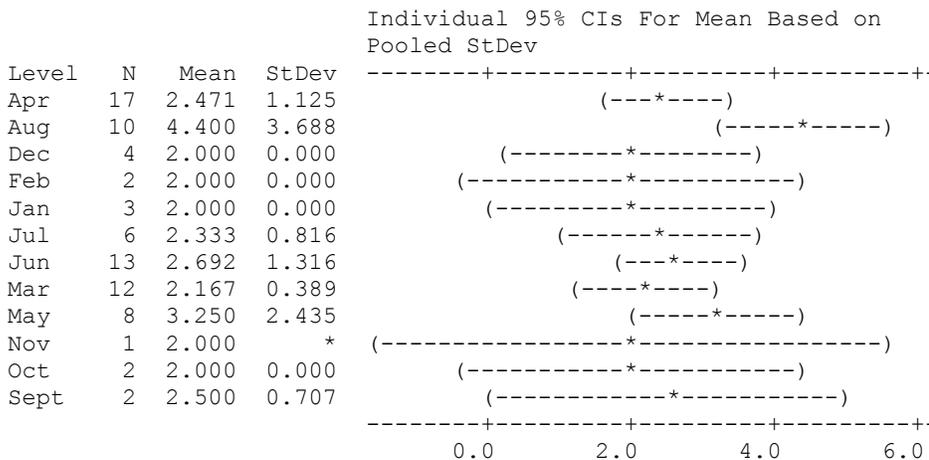


Pooled StDev = 30.83

### 1.14. One-way ANOVA: Total Number of Terrapin in a Social Burrow versus Month

Source	DF	SS	MS	F	P
Month	11	42.40	3.85	1.25	0.275
Error	68	210.40	3.09		
Total	79	252.80			

S = 1.759    R-Sq = 16.77%    R-Sq(adj) = 3.31%



Pooled StDev = 1.759

## 2. *Habitat Selection: Vegetation Cover and Height*

### 2.1. Mann-Whitney Test and CI: Vegetation Class at Night, Vegetation Class at Day for Female terrapins

	N	Median
Vegetation Class N	78	2.0000
Vegetation Class D	82	1.0000

Point estimate for ETA1-ETA2 is 1.0000  
 95.0 Percent CI for ETA1-ETA2 is (0.0002,1.0000)  
 W = 7187.5  
 Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0019  
 The test is significant at 0.0011 (adjusted for ties)

### 2.2. Mann-Whitney Test and CI: Vegetation Class at Day, Vegetation Class at Night for Male Terrapins

	N	Median
MannWhit Veg D	45	1.000
MannWhit Veg N	27	2.000

Point estimate for ETA1-ETA2 is 0.000  
 95.1 Percent CI for ETA1-ETA2 is (-1.000,-0.000)  
 W = 1501.0  
 Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.1010  
 The test is significant at 0.0781 (adjusted for ties)

### 2.3. Kruskal-Wallis Test: Vegetation Height Class versus Month/ Diel Variable Combination for Female Terrapins

Kruskal-Wallis Test on Vege Heigh Bins

Month Diel	N	Median	Ave Rank	Z
AprilD	13	1.000	62.0	-1.50
AprilN	8	1.500	76.6	-0.24
AugustD	29	1.000	60.5	-2.56
AugustN	9	1.000	58.3	-1.48
FebruaryD	9	3.000	99.5	1.27
FebruaryN	9	3.000	123.8	2.89
JulyD	10	2.000	77.7	-0.20
JulyN	11	2.000	69.8	-0.79
JuneD	5	2.000	73.5	-0.34
JuneN	23	2.000	98.2	1.97
MarchD	6	1.500	71.0	-0.51
MarchN	2	1.000	33.0	-1.46
MayD	10	1.500	66.5	-0.99
MayN	16	3.000	115.2	3.16

Overall 160 80.5

H = 35.29 DF = 13 P = 0.001  
 H = 39.35 DF = 13 P = 0.000 (adjusted for ties)

\* NOTE \* One or more small samples

### 2.4. Kruskal-Wallis Test: Vegetation height class versus Month/ Diel Variable Combination for Male terrapins

Kruskal-Wallis Test on Vegetation height (cm)\_1

Month Diel	N	Median	Ave Rank	Z
AprilD	20	1.500	36.4	-0.02
AprilN	12	2.000	41.3	0.87
AugustD	8	1.000	22.9	-1.94
FebruaryD	2	2.000	39.3	0.19
JuneD	3	2.000	50.3	1.17
JuneN	7	2.000	44.9	1.12
MarchD	5	1.000	23.0	-1.50
MarchN	2	1.000	17.5	-1.30
MayD	7	1.000	34.9	-0.21
MayN	6	2.000	47.0	1.28
Overall	72		36.5	

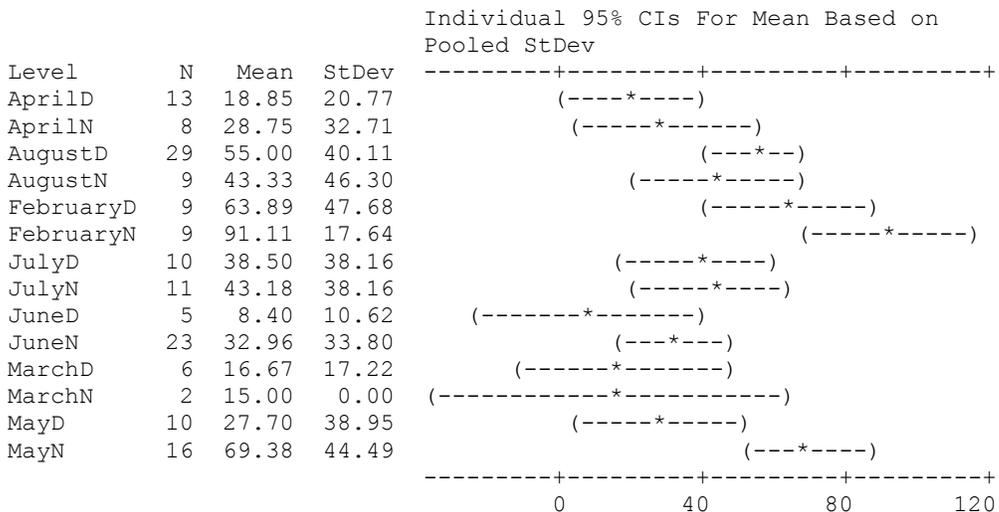
H = 11.75 DF = 9 P = 0.228  
 H = 13.56 DF = 9 P = 0.139 (adjusted for ties)

\* NOTE \* One or more small samples

### 2.5. One-way ANOVA: % vegetation cover versus Month/ Diel Variable Combination for Female Terrapins

Source	DF	SS	MS	F	P
Month Diel	13	65709	5055	3.81	0.000
Error	146	193632	1326		
Total	159	259342			

S = 36.42 R-Sq = 25.34% R-Sq(adj) = 18.69%



Pooled StDev = 36.42

### 2.6. General Linear Model: % vegetation cover versus Month, Night/Day for Female Terrapins

Factor	Type	Levels	Values
Month	fixed	7	February, March, April, May, June, July, August
Night/Day	fixed	2	D, N

Analysis of Variance for % vegetation cover, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Month	6	47670	43234	7206	5.43	0.000
Night/Day	1	6651	4892	4892	3.69	0.057
Month*Night/Day	6	11388	11388	1898	1.43	0.207
Error	146	193632	193632	1326		
Total	159	259342				

S = 36.4177 R-Sq = 25.34% R-Sq(adj) = 18.69%

Unusual Observations for % vegetation cover

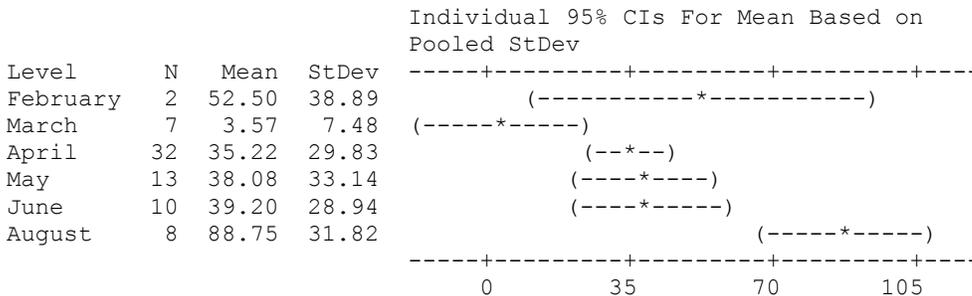
Obs	% vegetation cover	Fit	SE Fit	Residual	St Resid
93	15.000	15.000	25.751	-0.000	-0.00 X
94	15.000	15.000	25.751	-0.000	-0.00 X

X denotes an observation whose X value gives it large leverage.

### 2.7. One-way ANOVA: % vegetation cover versus Month for Male Terrapins

Source	DF	SS	MS	F	P
Month	5	29391	5878	6.78	0.000
Error	66	57238	867		
Total	71	86629			

S = 29.45 R-Sq = 33.93% R-Sq(adj) = 28.92%



Pooled StDev = 29.45

### 3. *Habitat Selection: Distance from Water*

#### 3.1. Two-Sample T-Test and CI: Distance from Water in Feet, Night vs Day : Female Terrapins

Two-sample T for Distance from Water, Feet

Night_Day	N	Mean	StDev	SE Mean
D	79	65	281	32
N	76	19.8	23.1	2.7

Difference = mu (D) - mu (N)

Estimate for difference: 45.2

95% CI for difference: (-18.0, 108.3)

T-Test of difference = 0 (vs not =): T-Value = 1.42 P-Value = 0.159 DF = 79

#### 3.2. Two-Sample T-Test and CI: Distance from Water in Feet, Night vs Day : Male Terrapins

Two-sample T for Distance from Water, Feet

Night_Day	N	Mean	StDev	SE Mean
D	45	12.8	18.1	2.7
N	27	22.3	58.7	11

Difference = mu (D) - mu (N)

Estimate for difference: -9.4

95% CI for difference: (-33.2, 14.3)

T-Test of difference = 0 (vs not =): T-Value = -0.81 P-Value = 0.423 DF = 29

#### 3.3. Female Terrapin: Correlations: Distance from Water, air\_temper, Water\_Temp, soil\_temp, Tide\_\_m\_

	Distance from Wa	air_temper	Water_Temp
air_temper	-0.059 0.466		
Water_Temp	0.075 0.403	-0.038 0.666	
soil_temp	-0.140 0.082	0.167 0.038	0.887 0.000
Tide__m_	-0.014 0.866	-0.008 0.921	-0.241 0.006

Cell Contents: Pearson correlation  
P-Value

### 3.4. Male Terrapins: Correlations: Distance from Water, air\_temper, Water\_temp, soil\_temp, Tide\_\_m\_

	Distance from Wa	air_temper	Water_temp
air_temper	-0.096 0.421		
Water_temp	-0.126 0.515	0.754 0.000	
soil_temp	-0.188 0.115	0.617 0.000	0.777 0.000
Tide__m_	-0.007 0.956	-0.142 0.235	-0.801 0.000

Cell Contents: Pearson correlation  
P-Value

## 4. Habitat Selection: Land versus Water

### 4.1. Two-way ANOVA: Female terrapin CPUE versus Land or Water, Night or Day

Source	DF	SS	MS	F	P
Land or Water	1	0.0000095	0.0000095	0.59	0.449
Night or Day	1	0.0000017	0.0000017	0.11	0.749
Interaction	1	0.0000045	0.0000045	0.28	0.602
Error	24	0.0003839	0.0000160		
Total	27	0.0003995			

S = 0.003999 R-Sq = 3.91% R-Sq(adj) = 0.00%

### 4.2. Two-way ANOVA: Male CPUE versus Land or Water, Night or Day

Source	DF	SS	MS	F	P
Male Land or Water	1	0.0000145	0.0000145	2.06	0.164
Male Night or Day	1	0.0000115	0.0000115	1.63	0.214
Interaction	1	0.0000060	0.0000060	0.85	0.364
Error	24	0.0001694	0.0000071		
Total	27	0.0002014			

S = 0.002656 R-Sq = 15.91% R-Sq(adj) = 5.40%

### 4.3. Two-Sample T-Test and CI: Air Temperature (C), Land vs Water, for Female Terrapins

Two-sample T for Air Temperature (C)

Land or Water	N	Mean	StDev	SE Mean
Land	79	25.79	5.92	0.67
Water	73	28.10	4.79	0.56

Difference = mu (Land) - mu (Water)

Estimate for difference: -2.304  
 95% CI for difference: (-4.024, -0.583)  
 T-Test of difference = 0 (vs not =): T-Value = -2.65 P-Value = 0.009 DF = 147

#### 4.4. Two-Sample T-Test and CI: Water Temperature (C), Land vs Water , for Female Terrapins

Two-sample T for Water Temperature (C)

Land or					
Water	N	Mean	StDev	SE Mean	
Land	69	29.34	2.48	0.30	
Water	64	28.13	3.14	0.39	

Difference = mu (Land) - mu (Water)  
 Estimate for difference: 1.207  
 95% CI for difference: (0.230, 2.184)  
 T-Test of difference = 0 (vs not =): T-Value = 2.45 P-Value = 0.016 DF = 119

#### 4.5. Two-Sample T-Test and CI: Corrected Water Temp, Land or Water

Two-sample T for Corrected Water Temp

Land or					
Water	N	Mean	StDev	SE Mean	
Land	75	30.91	2.43	0.28	
Water	86	30.00	3.24	0.35	

Difference = mu (Land) - mu (Water)  
 Estimate for difference: 0.909  
 95% CI for difference: (0.024, 1.794)  
 T-Test of difference = 0 (vs not =): T-Value = 2.03 P-Value = 0.044 DF = 155

#### 4.6. Two-Sample T-Test and CI: Delta Air Water, Land, Water : Female Terrapins

Two-sample T for Delta Air Water

Land_or_Wa	N	Mean	StDev	SE Mean	
Land	63	-2.97	6.59	0.83	
Water	59	1.36	4.59	0.60	

Difference = mu (Land) - mu (Water)  
 Estimate for difference: -4.33  
 95% CI for difference: (-6.36, -2.30)  
 T-Test of difference = 0 (vs not =): T-Value = -4.23 P-Value = 0.000 DF = 111

#### 4.7. Two-Sample T-Test and CI: Delta T corrected, Land or Water

Two-sample T for Delta T corrected

Land or

Water	N	Mean	StDev	SE Mean
Land	75	-5.69	8.70	1.0
Water	86	-2.20	8.80	0.95

Difference = mu (Land) - mu (Water)

Estimate for difference: -3.49

95% CI for difference: (-6.22, -0.76)

T-Test of difference = 0 (vs not =): T-Value = -2.53 P-Value = 0.012 DF = 156

#### 4.8. Two-Sample T-Test and CI: 2012 Delta -F, Land or Water - F

Two-sample T for Delta -F

Land or

Water - F	N	Mean	StDev	SE Mean
Land	63	0.86	2.47	0.31
Water	36	1.42	2.10	0.35

Difference = mu (Land) - mu (Water)

Estimate for difference: -0.553

95% CI for difference: (-1.485, 0.379)

T-Test of difference = 0 (vs not =): T-Value = -1.18 P-Value = 0.241 DF = 82

#### 4.9. Two-Sample T-Test and CI: 2012 Delta -M, Land or Water -M

Two-sample T for Delta -M

Land or

Water -M	N	Mean	StDev	SE Mean
Land	37	0.87	2.37	0.39
Water	20	2.54	1.98	0.44

Difference = mu (Land) - mu (Water)

Estimate for difference: -1.670

95% CI for difference: (-2.858, -0.481)

T-Test of difference = 0 (vs not =): T-Value = -2.83 P-Value = 0.007 DF = 45

5. Range

5.1. Two-Sample T-Test and CI: Straight Line Distance Travelled, Night vs Day (Female Terrapins Only)

Two-sample T for Straight Line Distance

Night/Day	N	Mean	StDev	SE Mean
Day	22	75	123	26
Night	27	4.4	11.4	2.2

Difference = mu (Day) - mu (Night)  
 Estimate for difference: 70.6  
 95% CI for difference: (15.9, 125.3)  
 T-Test of difference = 0 (vs not =): T-Value = 2.69 P-Value = 0.014 DF = 21

5.2. Two-Sample T-Test and CI: Meters/hour movement, Night vs Day (Female Terrapins Only)

Two-sample T for m/hour

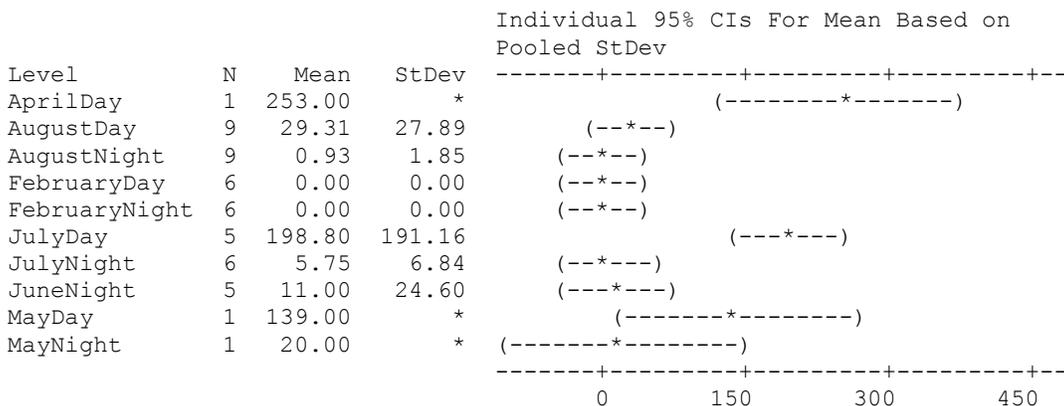
Night/Day	N	Mean	StDev	SE Mean
Day	22	16.5	31.6	6.7
Night	27	1.38	3.04	0.59

Difference = mu (Day) - mu (Night)  
 Estimate for difference: 15.13  
 95% CI for difference: (1.05, 29.21)  
 T-Test of difference = 0 (vs not =): T-Value = 2.23 P-Value = 0.036 DF = 2

5.3. One-way ANOVA: Straight Line Distance versus Month /ND Variable Combination

Source	DF	SS	MS	F	P
Month ND	9	226110	25123	6.32	0.000
Error	39	155072	3976		
Total	48	381182			

S = 63.06 R-Sq = 59.32% R-Sq(adj) = 49.93%



#### 5.4. One-way ANOVA: Straight Line Distance versus Month

Source	DF	SS	MS	F	P
Month	5	113765	22753	3.66	0.008
Error	43	267417	6219		
Total	48	381182			

S = 78.86    R-Sq = 29.85%    R-Sq(adj) = 21.69%

Individual 95% CIs For Mean Based on Pooled StDev

Level	N	Mean	StDev	CI
February	12	0.00	0.00	(---*---)
April	1	253.00	*	(-----*-----)
May	2	79.50	84.15	(-----*-----)
June	5	11.00	24.60	(-----*-----)
July	11	93.50	157.49	(---*---)
August	18	15.12	24.10	(--*--)

0                      120                      240                      360

Pooled StDev = 78.86

## 6. Acoustic Data

### 6.1. Acoustic Data: Two-Sample T-Test and CI: Percent of Time Spent Swimming, Night versus Day :Females

Two-sample T for percent -ND

Diel -ND	N	Mean	StDev	SE Mean
Day	23	58.5	25.2	5.3
Night	23	41.2	25.4	5.3

Difference = mu (Day) - mu (Night)

Estimate for difference: 17.29

95% CI for difference: (2.22, 32.35)

T-Test of difference = 0 (vs not =): T-Value = 2.31    P-Value = 0.026    DF = 43



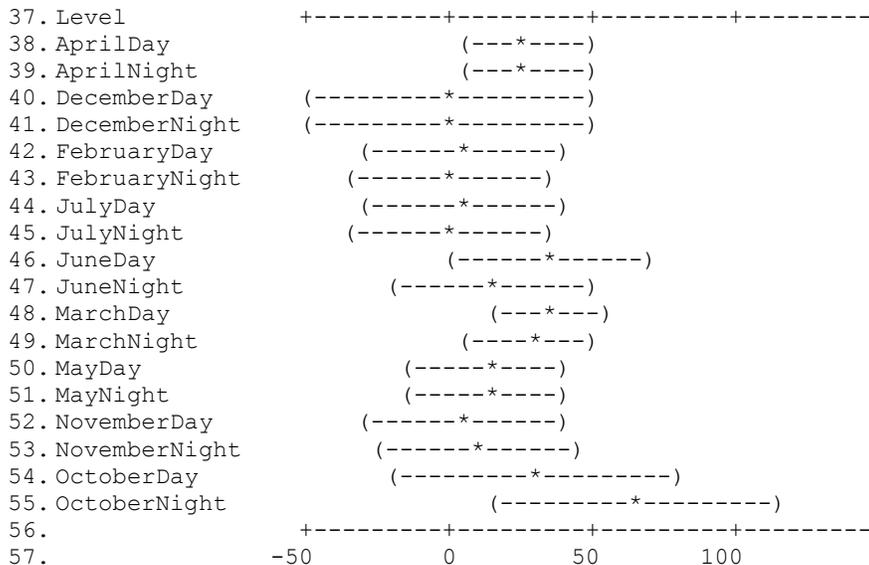
6.4. One-way ANOVA: Number of Hours Detected versus Month /ND Variable Combination (Females)

7. Source	DF	SS	MS	F	P
8. Diel Month ND	17	8929	525	0.91	0.575
9. Error	28	16244	580		
10. Total	45	25172			

11.  
 12. S = 24.09    R-Sq = 35.47%    R-Sq(adj) = 0.00%

16. Level	N	Mean	StDev
17. AprilDay	5	27.04	28.55
18. AprilNight	5	26.55	27.01
19. DecemberDay	1	0.13	*
20. DecemberNight	1	0.00	*
21. FebruaryDay	2	3.34	0.94
22. FebruaryNight	2	2.16	1.29
23. JulyDay	2	5.70	6.76
24. JulyNight	2	0.02	0.03
25. JuneDay	2	37.05	52.39
26. JuneNight	2	16.89	23.84
27. MarchDay	5	34.99	25.33
28. MarchNight	5	28.33	28.29
29. MayDay	3	12.71	17.14
30. MayNight	3	12.97	11.88
31. NovemberDay	2	3.88	4.82
32. NovemberNight	2	7.98	6.69
33. OctoberDay	1	30.52	*
34. OctoberNight	1	64.45	*

36. Individual 95% CIs For Mean Based on Pooled StDev



59. Pooled StDev = 24.09