

1-1-2011

Influence of Season and Sex on *Terrapene c. carolina* (Eastern Box Turtle) Movements: An Observation of a Population in West Virginia

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**INFLUENCE OF SEASON AND SEX ON *TERRAPENE C. CAROLINA*
(EASTERN BOX TURTLE) MOVEMENTS: AN OBSERVATION OF A
POPULATION IN WEST VIRGINIA**

A Thesis Submitted to
the Graduate College of
Marshall University

In partial fulfillment of the
requirements for the degree of
Master of Science
Biological Sciences

by
Nathalie Caroline Aall

Approved by
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Marshall University

July 2011

ACKNOWLEDGMENTS

First, I would like to thank my thesis advisor, Dr. Thomas K. Pauley, for his input and support toward the writing of this thesis. I would also like to thank my committee, Dr. Elmer Price and Dr. Frank Gilliam, for their contributions toward the analysis and general structure of my thesis and for encouraging me to voice my opinions. Dr. Gilliam was crucial in the data analysis stage, giving me new ways to look at my raw data and developing questions. I would also like to thank Dr. Price for his unwavering support of the Herpetology Lab. Thanks to the department of biological sciences at Marshall University for my funding without which a radio telemetry project would not have been possible. Zach Felix and Ross Maynard's advice was invaluable toward focusing this thesis and developing questions once faced with the wealth of data I collected. The completion of this thesis would also not have been possible without Ross Maynard due to his diligent editing and thought-provoking advice. Additional editors whose skills have been well utilized in the writing of this thesis include Sarah Wallace and Courtney Richards. I would also like to thank my hardworking and fellow graduate student Derek Bozzell who was a great help in locating tricky turtles rain or shine throughout the field season. With the support of my parents, Chris and Esther Aall, I have always been able to strive toward my goals and without them I would not be where I am now. Last, I would like to thank others who have served essential roles in the completion of this thesis be it as fellow field assistants, data analysis, piece of mind, or a combination of all three, Dr. Jeffrey May, James Spence, James Stanton, Nathan Shepard, Dr. Anita Walz, Aaron Gooley, Whitney Kroschel, and Josh Adkins.

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SE Standard Error

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* Reference Appendix I for ANOVA results

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Ψ No statistical analysis was run and general trends were observed.

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ABSTRACT

Influence of Season and Sex on *Terrapene c. carolina* (Eastern Box Turtle) Movements: An Observation of a Population in West Virginia

Nathalie Caroline Aall

Environmental conditions influence box turtle movements on multiple temporal scales as they navigate their home ranges. This study focuses on the impacts of seasonal shift and sex on straight-line distances traveled, movements along elevations, and home range sizes in the Eastern Box Turtle, *Terrapene c. carolina*. Radio telemetry was used to track nine *T. c. carolina* (5 males; 4 females) from May to October 2010 at Beech Fork State Park in Wayne County, West Virginia. Turtles were tracked once a day at two-day intervals. At each turtle location, microhabitat variables recorded were relative humidity, soil and ground surface temperature, canopy and shrub cover, and substrate type. Results showed seasonal influence ($P < 0.05$) on both home range sizes and distances traveled with no apparent differences between sexes ($P > 0.05$). Movements along elevations were significantly different between sexes ($P = 0.006$) and not strongly influenced by seasonality.

BACKGROUND

TAXONOMY AND DISTRIBUTION

The Eastern Box Turtle is in the genus *Terrapene*, family Emydidae. This genus has four species which are endemic to North America including *Terrapene ornata* (Ornate and Desert Box Turtle), *T. nelsoni* (Spotted Box Turtle), *T. coahuila* (Coahuilan Box Turtle), and *T. carolina* (Eastern Box Turtle). There are currently four subspecies recognized in *T. carolina*: *T. c. carolina* (Eastern Box Turtle), *T. c. bauri* (Florida Box Turtle), *T. c. major* (Gulf Coast Box Turtle), and *T. c. triunguis* (Three-Toed Box Turtle). In the United States, *T. carolina* ranges from Florida north to New Hampshire and west to Texas. The range of *T. c. carolina* is the largest of the subspecies and overlaps with other *T. carolina* subspecies (Minx, 1996). It is also the most northern of the subspecies as its range extends into New Hampshire and Michigan, west to Illinois, and south into Georgia. *Terrapene c. carolina* is the only box turtle found in West Virginia. Green and Pauley (1987) defined the etymology of *Terrapene* as originating from an Algonquin Indian word meaning turtle, while the species name *carolina* is named after the Carolinas. The nomenclature of *T. c. carolina* is shown in the following list.

Kingdom	Animalia
Phylum	Chordata
Subphylum	Vertebrata
Superclass	Tetrapoda
Class	Reptilia
Subclass	Anapsida
Order	Testudines
Suborder	Cryptodira
Family	Emydidae
Genus	<i>Terrapene</i>
Species	<i>carolina</i>
Subspecies	<i>carolina</i>

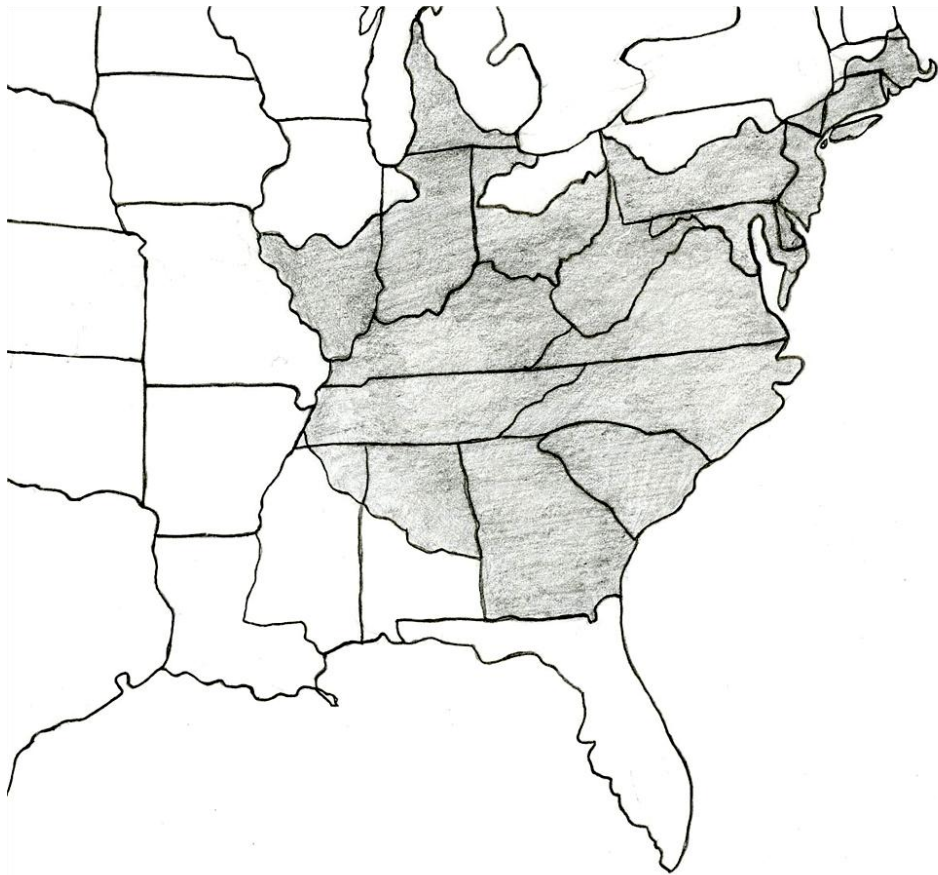


Figure 1. Distribution of the Eastern Box Turtle, *Terrapene c. carolina*, in the United States. Map design by the author.

SPECIES DESCRIPTION AND NATURAL HISTORY

The Eastern Box Turtle, *Terrapene carolina*, is the only true terrestrial turtle in the northeastern United States (Hulse et al., 2001). Although typically diurnal, during the peak of the summer, particularly in populations residing in the southern extent of their range, box turtles are crepuscular and bimodal, active only at dawn and dusk (Legler, 1960; Nieuwolt, 1996; Dodd, 2001; Converse and Savidge, 2003).

Adult *T. c. carolina* have a domed carapace, or dorsal shell, with a slight mid-dorsal keel. Juveniles exhibit a much stronger keel due to their growing shell. The carapace is dark brown in color with variable patterns of yellow, brown, and orange (Figure 2). Overall coloration is usually more intense in adult males as their head, neck, and legs can have strong yellow, orange, and red markings. Maximum adult carapace length for both males and females is around 20cm. The plastron, or ventral shell, is a sexually dimorphic characteristic; females have a reasonably flat plastron, whereas males exhibit a more concave plastron which aids in mounting the female's carapace during copulation. An additional sexually dimorphic feature, although less reliable due to variation, is iris coloration (Dodd, 2001). Males typically have red pigment compared to the browner coloration often seen in females.

The vernacular name, box turtle, is appropriately assigned to the species due to a hinge located on their plastron with which they can completely close their shell. This allows them to encase their limbs for protection from predators. Juveniles do not develop a hinge until they reach the sub-adult life stage. This delay in their hinge development, in conjunction with their underdeveloped and more cartilaginous shells, makes them more susceptible to predation. Common predators of box turtles are raccoons, opossums,

coyotes, skunks, snakes, and ants. An average life span is approximately 50 years, but individuals have been known to live up to 100 years.

Terrapene c. carolina are often associated with woodland habitats such as deciduous, mesic forests as well as meadows and marshes (Schwartz and Schwartz, 1974; Ernst et al., 1994; Dodd, 2001). Box turtles enter a dormant state that begins in late fall and ends in early spring (Dodd, 2001). Following this dormancy, they emerge from burrows to begin mating activities such as the mate search (Ewing, 1933; Legler, 1960). Peaks in mating activity have been associated with times immediately prior to and after winter dormancy (Ewing, 1933; Legler, 1960). Some box turtle populations are reported to mate mainly in the spring (Allard, 1935; Legler, 1960; Dodd, 2001). Other populations have exhibited mating behavior throughout the active season (Williams and Parker, 1987), but this may vary by locality and latitude (Budishak et al., 2006). The act of mate detection for box turtles is not fully understood. Previous research suggests that they stumble upon a mate at random and proceed with the courting ritual (Dodd, 2001). Males may be more proactive in the search for a mate due to their observed searching behavior of scent tracking (Evans, 1953; Stickel, 1978). Male spermatogenesis (the development of sperm cells) occurs from July to October while female ovulation occurs at least twice a year, once mid-May and once mid-June. Repetitive ovulation allows females to lay several clutches within one season (Gibbons, 1968; Congello, 1978; Messinger and Patton, 1995).

Although annual mate detection and courtship are essential for increasing gene flow in a population, they are not essential for a female to produce fertilized eggs immediately. Female box turtles have shown arrested development within their oviducts,

allowing them to store sperm for extended periods of time (Dodd, 2001). Ewing (1943) witnessed female turtles producing fertilized eggs seasonally for four years with no male contact.

There are four phases to egg deposition including nest-site selection, digging, egg deposition, and concealment (Congello, 1978). Nest-site selection usually occurs from May to mid-July followed by egg deposition (Stickel, 1950; Congello, 1978; Ewing, 1933). In a quest to select suitable nest sites, box turtles will traverse their home ranges.

Box turtles are known to have set home ranges although some individuals have been observed to display transient behavior, repeatedly moving through habitats with no indication of a set home range (Kiestler et al., 1982; Dodd, 2001). The non-territorial nature of box turtles results in home ranges of individuals within a population to overlap, particularly if the habitat is favorable (Stickel, 1950; Nieuwolt, 1996). Box turtle movements through home ranges are influenced by a combination of factors. Some factors involved in habitat utilization include physiological needs of the turtle, which are met in varying environmental conditions through thermoregulation and mating activity. How these factors influence *T. c. carolina* movements through their home ranges will be explored in this study.



Figure 2. Top: Male *T. c. carolina* with transmitter. Middle: Female *T. c. carolina*. Bottom: Male *T. c. carolina* burrowing under shrub layer. Photographs by author.

INTRODUCTION

Mating and nesting behavior, home range utilization, and physiological needs have all been shown to play a role in box turtle movements and microhabitat preferences (Dodd, 2001). Box turtles are terrestrial, ectothermic reptiles that move throughout different microhabitats as a way to behaviorally thermoregulate their body temperature, prevent desiccation, search for mates, forage for food, and select nest-site locations (Sturbaum, 1981; Dodd, 2001; Amaral et al., 2002). Box turtle body temperature is shown to be highly correlated with ambient temperatures (Adams et al., 1989) making it important for them to migrate toward microhabitats that will allow them to achieve an optimal body temperature. Movement patterns have been shown to vary seasonally (Reagan, 1974), however, seasonal variation of box turtle movement patterns are understudied. Within the home range and habitat of a box turtle there are available microhabitats that are utilized periodically. Humidity, temperature, and topography likely influence how they selectively migrate between these microhabitats. It is, therefore, important to investigate each of these components relative to a box turtle's movements.

Accurate information on variability in turtle movements, both between seasons and sexes, is necessary to increase our understanding of *T. c. carolina* natural history and habitat preferences. This study aims to provide knowledge about the movements of a population of *T. c. carolina* at Beech Fork State Park, West Virginia. Recent declines in box turtle populations along their entire range emphasize the need for effective mitigation plans for box turtle conservation (Swarth, 2005). If box turtle populations are to continue to persist across their range in the future, studies of their ecology and natural history are

needed to better inform population-based management plans that will be effective in the long-term.

The purpose of this study was to observe a sample of a population of *T. c. carolina* at Beech Fork State Park in Wayne County to gather data on movements in relation to individual home range sizes, movements along elevations, and straight-line distances traveled. More specifically, this study focused on how seasonality and sex impact *T. c. carolina* movements. This study was done in Wayne County, West Virginia (Figure 3) where *T. c. carolina* is listed as common (Uetz and Hallerman, 2011). Furthermore, previous literature guided my decision to collect additional data on box turtle microhabitats, which are included herein as supplemental to my study and will be included in the discussion. These data augment the relevancy of this study and how my study population equates to others across the species' range.

This study assessed whether distances traveled, movements along elevational gradients, and home range size are influenced by sex and/or season. I hypothesized that (1) box turtle movements and home range size would decrease in the fall due to lower ambient temperatures, and (2) seasonal distances traveled would vary between sexes due to differing reproductive behaviors, and (3) box turtle movement would not vary across elevational gradients.

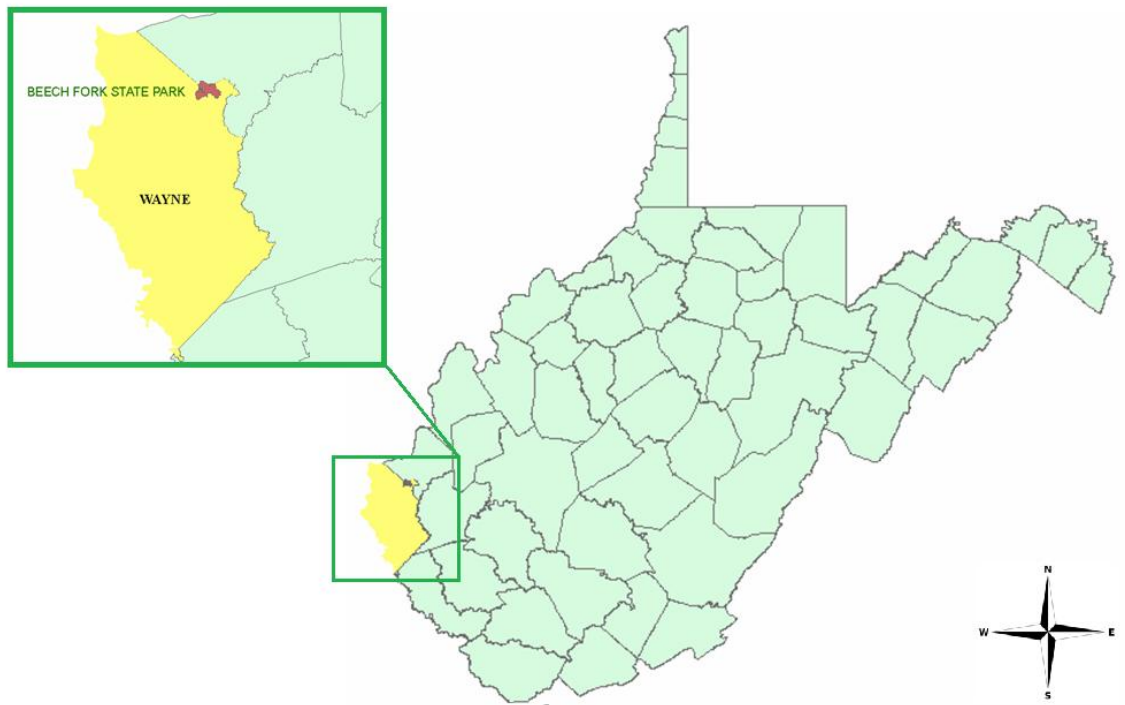


Figure 3. Map of West Virginia highlighting county in yellow and study area in pink.
Map design by author.

MATERIALS AND METHODS

STUDY SITE

The study site was located in Beech Fork State Park (BFSP; 38°18'19"N, 82°20'21"W) adjacent to the campgrounds in Barboursville, Wayne County, West Virginia (Figure 3). Turtles were tracked across a 93,800 m² area with a 680m diameter. The site was selected based on the high box turtle population density and diverse topography. Elevation in the study site ranged from 181m to 263m including two mountain ridges (Figure 4). This study employed radio telemetry, whereby a transmitter is attached to the carapace allowing locations of the turtles to be pinpointed and adjacent environmental measurements to be taken. Radio telemetry allows for a wealth of data collection with regard to individual movements throughout a landscape and within a population (Forsythe et al., 2004; Iglay et al., 2006).

Initial sampling and the adherence of transmitters were done in the lower elevation range (181-190m) of the study site (Figure 4). Weather data for Wayne County, West Virginia were retrieved from AgroClimatic Information Service. The maximum to minimum ambient air temperatures recorded were 29.7 °C in the summer and 11 °C in the fall. Mean temperatures were 22 °C, 26 °C, 18 °C for the spring, summer, and fall, respectively. Total precipitation for the study period was 66cm and 22cm, 36cm, and 8cm during spring, summer, and fall in 2010. Mean precipitation was highest in the summer (0.88cm) and lowest in the fall (0.21cm). Due to high precipitation from July 19th-26th (20cm), extreme flooding occurred at the study site. Flooding filled the seasonally dry

stream bed causing turtles to be impeded from crossing the stream or traversing some lower elevations.

Habitat was characterized by mesophytic eastern deciduous hardwood forest and fragmented by two frequently traveled trails, a seasonally dry stream bed, and open fields cleared and mowed for recreational use (Figure 5). Common overstory vegetation at site comprised of mixed pine (*Pinus* sp.) and hardwood including maples (*Acer* sp.), American beech (*Fagus grandifolia*), hickory (*Carya* sp.), tulip poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), and sassafras (*Sassafras* sp.). Some dominant understory vegetation during the sampling period included autumn-olive (*Elaeagnus umbellata*), honeysuckle (*Lonicera* sp.), Japanese stiltgrass (*Microstegium vimineum*), and a variety of fern species.



Figure 4. Google Earth topography map of study site at Beech Fork State Park. Area outlined in red represents the area in which box turtles were initially tagged in May 2010.

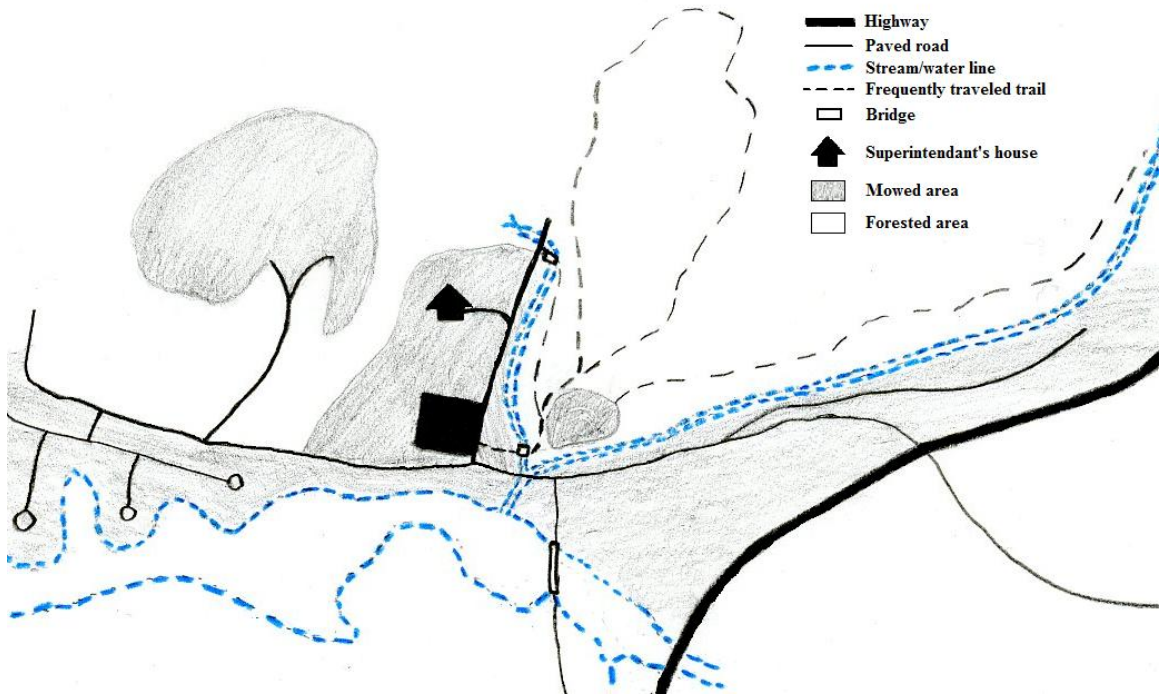


Figure 5. Map of study site at Beech Fork State Park. Map design by author.

FIELD WORK

Ten SOPR-2190 model transmitters (3.0x1.3x0.8cm), a three-prong Yagi antenna, and a TRX-2000 receiver were purchased from Wildlife Materials, Murphysboro, Illinois in March 2010. The dark green transmitters each weighed 5-6g, which was less than three percent of each turtle's body mass, and had a 17cm long flexible antenna (Figure 2). Four adult gravid female (4,8,10,11) and six adult male (1,3,5,6,7,9) *T. c. carolina*, identified by their respective assigned numbers, were tagged with transmitters in mid-May of 2010 and tracked until mid-October 2010 at BFSP. Sampled turtles were all classified as adults because carapace length exceeded 11cm and they exhibited well-defined sex characteristics (Legler, 1960; Converse, 1999). Individual turtle measurements were conducted in the field in concordance with Legler (1960) for plastron and carapace lengths, hinge width, and body mass. Transmitters were attached with five-minute epoxy to the right front costal scute of the carapace after a light cleaning with acetone. This positioning decreased transmitter interference with mating and burrowing.

Each individual turtle (N=10) was tracked once between 10 am-2 pm at two-day intervals. Waypoints were taken with a Garmin GPS with accuracy up to 5 m. Once a turtle was located, ground surface temperature and humidity measurements were taken with a thermo-hygrometer within a 10 cm radius of the turtle's position. A thermometer was also inserted into the soil at 5 cm depth within a 10 cm radius of the turtle to measure soil temperature. The close proximity at which measurements were taken in relation to the turtle allowed for more accurate descriptions of locations. A spherical densitometer was used to estimate canopy cover at arm's length and in kneeling position over each turtle's carapace. Microhabitat characteristics at each location were categorically noted

for type of substrate and presence of shrub cover. Transmitters were removed mid-October due to battery limitations.

DATA ANALYSIS

Box turtle home range area, elevation, and straight-line distances traveled were analyzed using SPSS (2006). Several univariate analyses of variance (ANOVA) and Tukey Post-hoc tests ($\alpha=0.05$) were run to determine significant differences between sex and season. Seasons were selected in concordance with Rossell et al. (2006): spring (May 15th –June 30th), summer (July 2nd –August 29th), and fall (September 1st –October 15th). Results of ANOVAs are located in Appendix I for further reference.

ANOVA's are semi-robust for data with deviations from normal distributions (Zar, 1984). Data for the parameters analyzed had relatively normal distributions, which was determined using the Shapiro Wilke Test. Data for four male (3, 5, 7, 9) and four female box turtles (4, 8, 10, 11) were analyzed. Male box turtle 6 was lost mid-June and male turtle 1 was lost mid-September due to transmitter failures; therefore, the data collected for these turtles were not included in the analysis.

Distance

Mean straight-line distance traveled was calculated in meters by how much a turtle moved from one location to the next within a two-day time period within season and between sexes. A square root of the mean transformation was applied to normalize the data.

Elevation

Elevation was determined by overlaying waypoint data into Google Earth. Mean elevation preference for males and females over time was calculated by taking the average elevation at which turtles were found each season. Additionally, mean elevations

were compared between sexes within each season with a univariate ANOVA and Tukey Post-hoc analyses.

Home range

Turtle waypoints were entered into ArcGIS 9.3 and mapped in ArcMap. Total home range size for each turtle was determined using the minimum convex polygon method in which outer waypoints are connected to form a polygon with no internal angle that exceeds 180 degrees and contains all waypoints (Mohr, 1947; Burgman and Fox, 2003). To calculate seasonal home range size, waypoints for each turtle were categorized by season. Home ranges were compared between four females and four males. Male box turtle 9 showed transient behavior; therefore, home range size data for this individual were not analyzed and male box turtle 1's data were used instead.

Principle Component Analysis

Principle correspondence analysis (PCA) was done to visualize general trends in the data. The PCA was adapted to look at the interrelatedness of multiple parameters (relative humidity, ground surface and soil temperature, canopy cover, elevation and distance traveled) with respect to individual turtles across seasons. Each point represents an individual turtle's microhabitat utilization in each season. Proximity of points signifies similarity between turtles within season according to their proximity to the parameters measured.

Microhabitat Utilization

Microhabitat analysis was conducted at all locations of tagged turtles over the course of the study. Figures and tables for microhabitat data are located in Appendix II for further reference. Relative humidity and soil and ground surface temperatures at turtle

microhabitats were analyzed for seasonal variation through an ANOVA and Tukey Post-hoc analysis. Shrub layer cover was recorded as present (1) or not present (0) for each turtle's location if the vegetation cover greater than 0.25m and less than 1m in height from the turtle's carapace. Downed trees, thickets, dense branches, tall vegetation, and bushes were ruled as shrub layer cover.

Substrate on which the turtles were located was categorized into three variables: leaf litter, bare soil, and dense vegetation. Percent preference for a certain substrate was calculated by counting the number of turtles found on a substrate category in a season and dividing by the total turtle collections within that season. No trend in substrate selection was witnessed between sexes or across seasons; therefore, it was excluded from the discussion.

RESULTS

DISTANCE TRAVELED

Straight-line distances traveled by turtles varied significantly across seasons ($F = 4.97$, $P = 0.019$; Table 2). Turtles traveled significantly greater mean straight-line distances in the spring compared to the fall ($P = 0.015$; Figure 6). One female, BT10, was observed traveling a great distance from her early spring home range over two mountain ridges in late June and returning early to mid-July. No similar behavior was witnessed in the other females. No significant differences in mean straight-line distances traveled were observed between sexes.

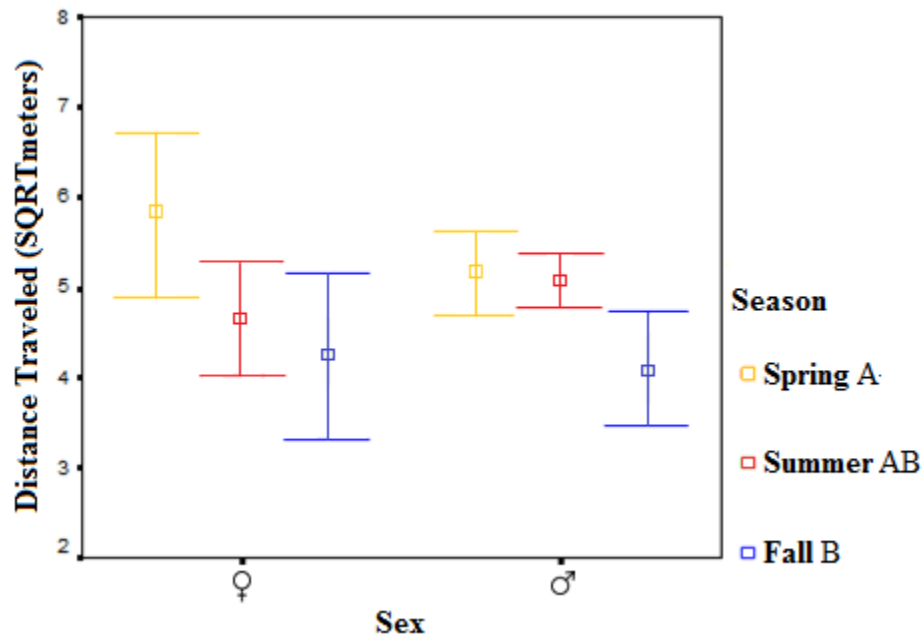


Figure 6. Mean \pm 1SE straight-line distances ($\sqrt{\text{meters}}$) traveled by male and female *T. c. carolina* across seasons. †*

ELEVATION

Turtles were located between 181- 227m in the study site. A male was located at 227m in the summer, marking the highest elevation at which a turtle was tracked. Throughout the study males were found at higher mean elevations than females ($F=9.78$, $P=0.006$; Figure 7). Unlike the other parameters, no significant seasonal differences were witnessed for elevation preference ($P>0.05$; Table 2). Males and females did not significantly differ in mean elevation at which they were located within any season ($P>0.05$); however, the greatest difference was observed between sexes in the fall ($P = 0.057$; Table 3).

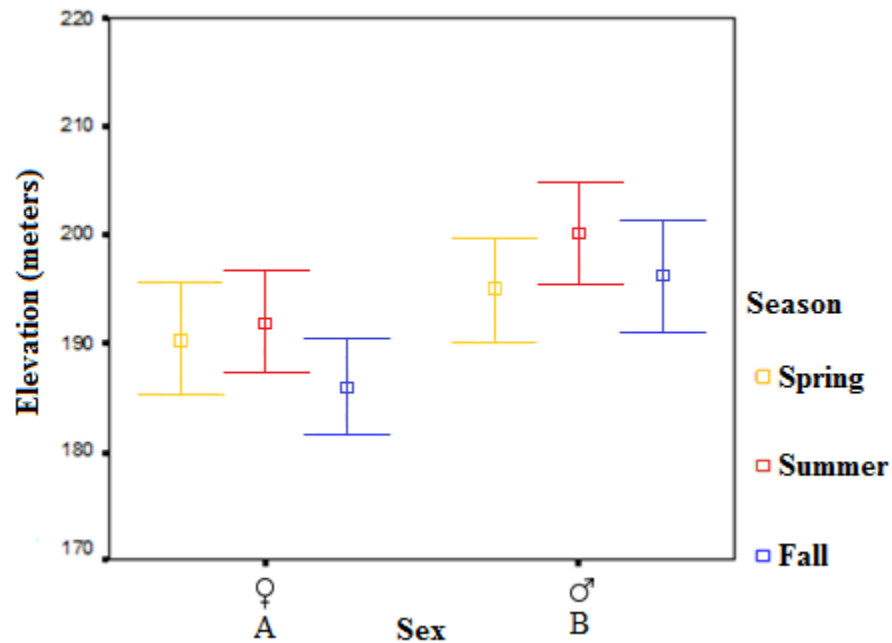


Figure 7. Mean \pm 1SE elevation (meters) for male and female *T. c. carolina*. †*

HOME RANGE

No significant interaction was witnessed between sex and season (Table 2). There was a significant difference between seasons for home range size ($F=13.8$, $P = 0.000$; Figure 8). Mean spring home range size was significantly smaller than mean home range size in the summer for turtles ($P = 0.005$). Mean summer home range size was also significantly larger compared to fall ($P = 0.000$), but there was no difference between spring and fall home range sizes. Home ranges were roughly elliptical in shape (Figure 9). Males had a smaller mean home range (12,012m²; Figure 10) compared to females (18,340m²; Figure 11) across the study, however, sex did not play significant role in determining home range size ($P>0.05$).

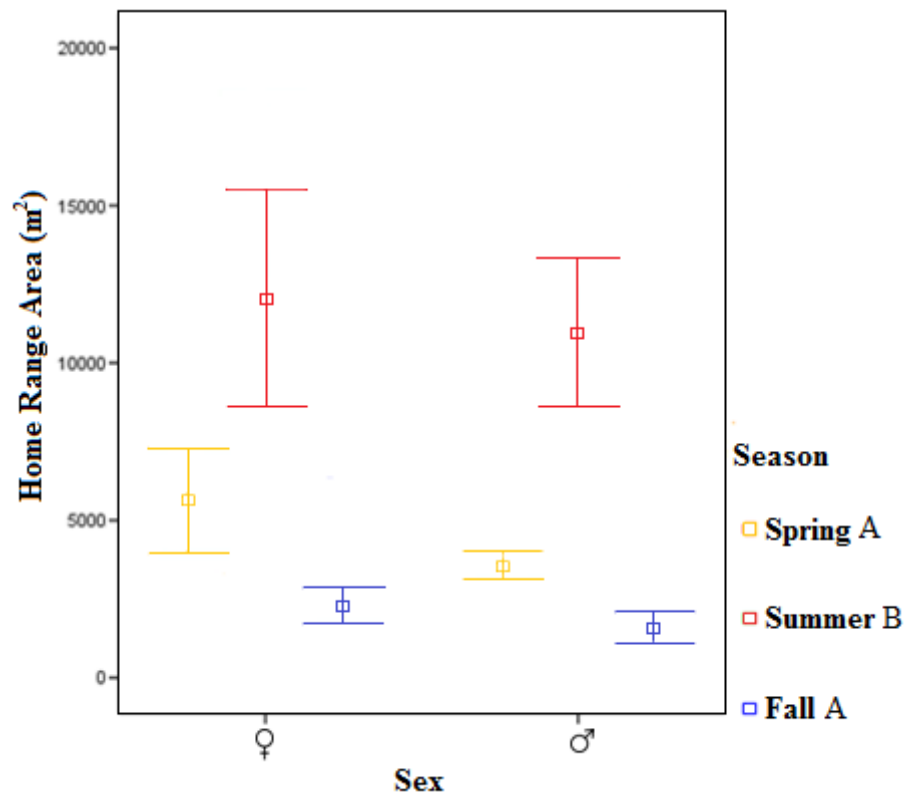


Figure 8. Mean ± 1 SE home range size (meters²) for male and female *T. c. carolina* across seasons. †*

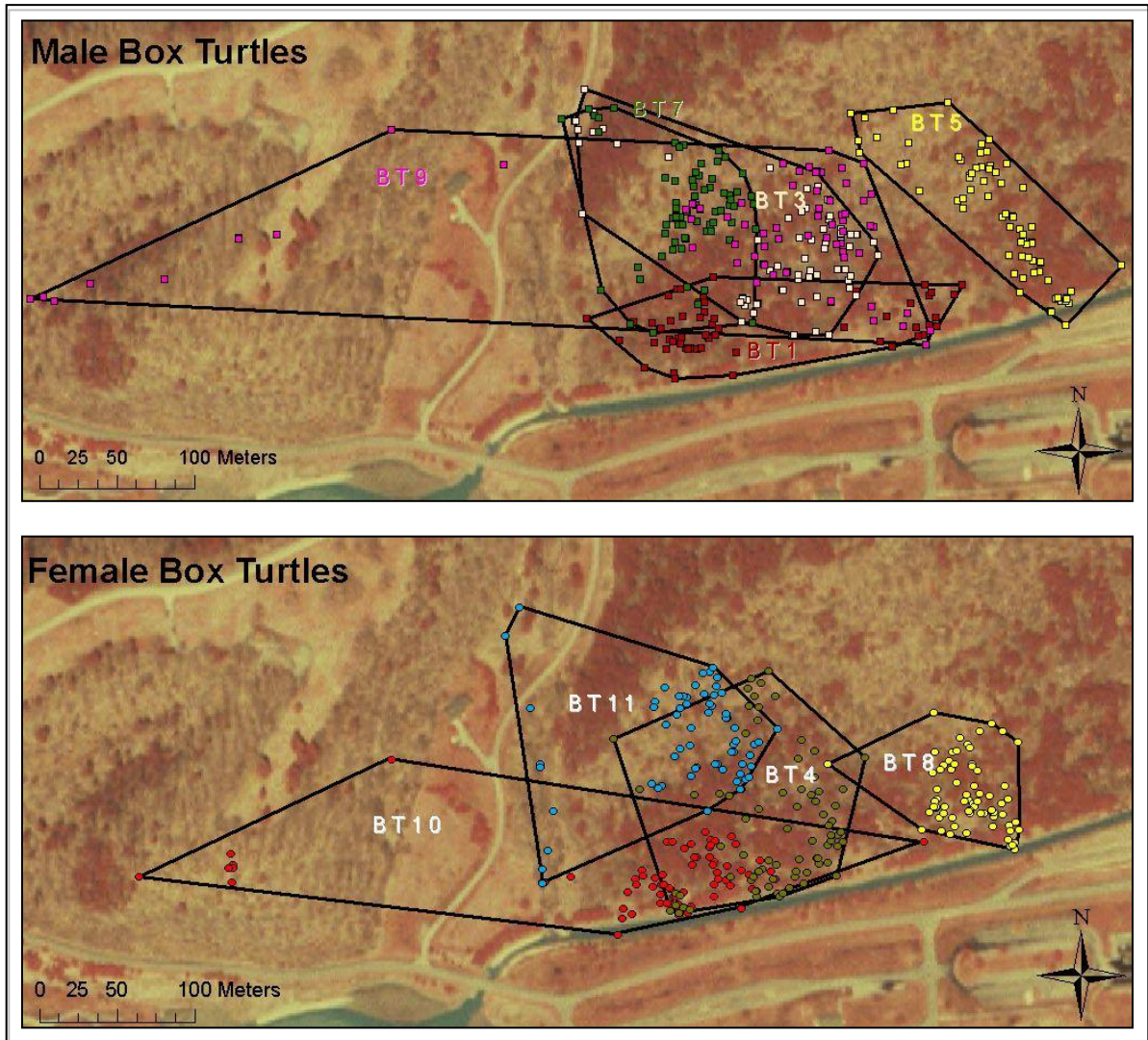


Figure 9. Five male (above: 1, 3, 5, 7, 9) and four female (below: 4,8,10,11) *T. c. carolina* home ranges outlined with a minimum convex polygon and overlain on an aerial view of the study site. Like colors represent locations of individual box turtles. Male box turtle 9 was characterized as transient.

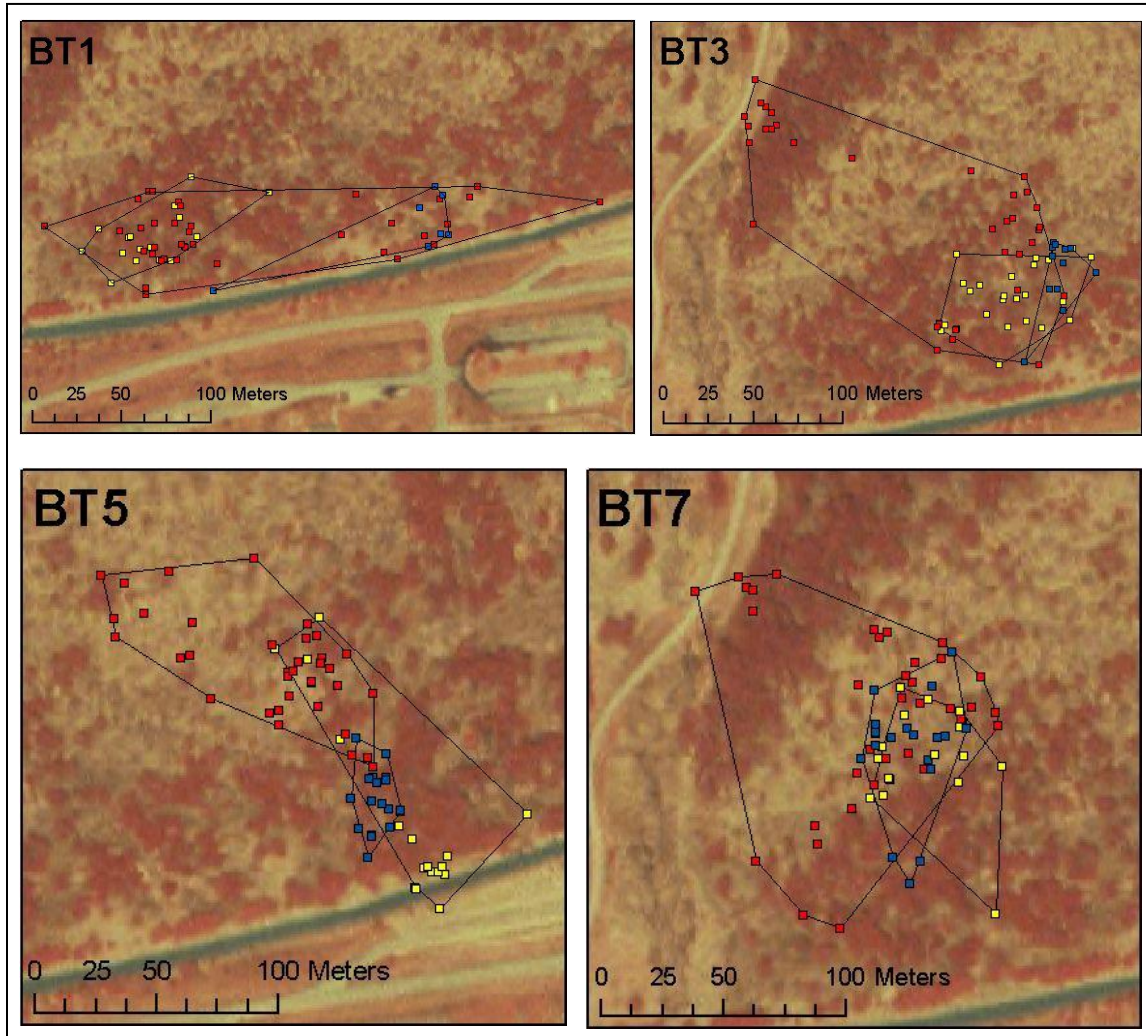


Figure 10. Four male *T. c. carolina* (1,3,5,7) seasonal (spring = yellow, summer = red, fall = blue) home ranges outlined with a minimum convex polygon and overlain on an aerial view of the study site.

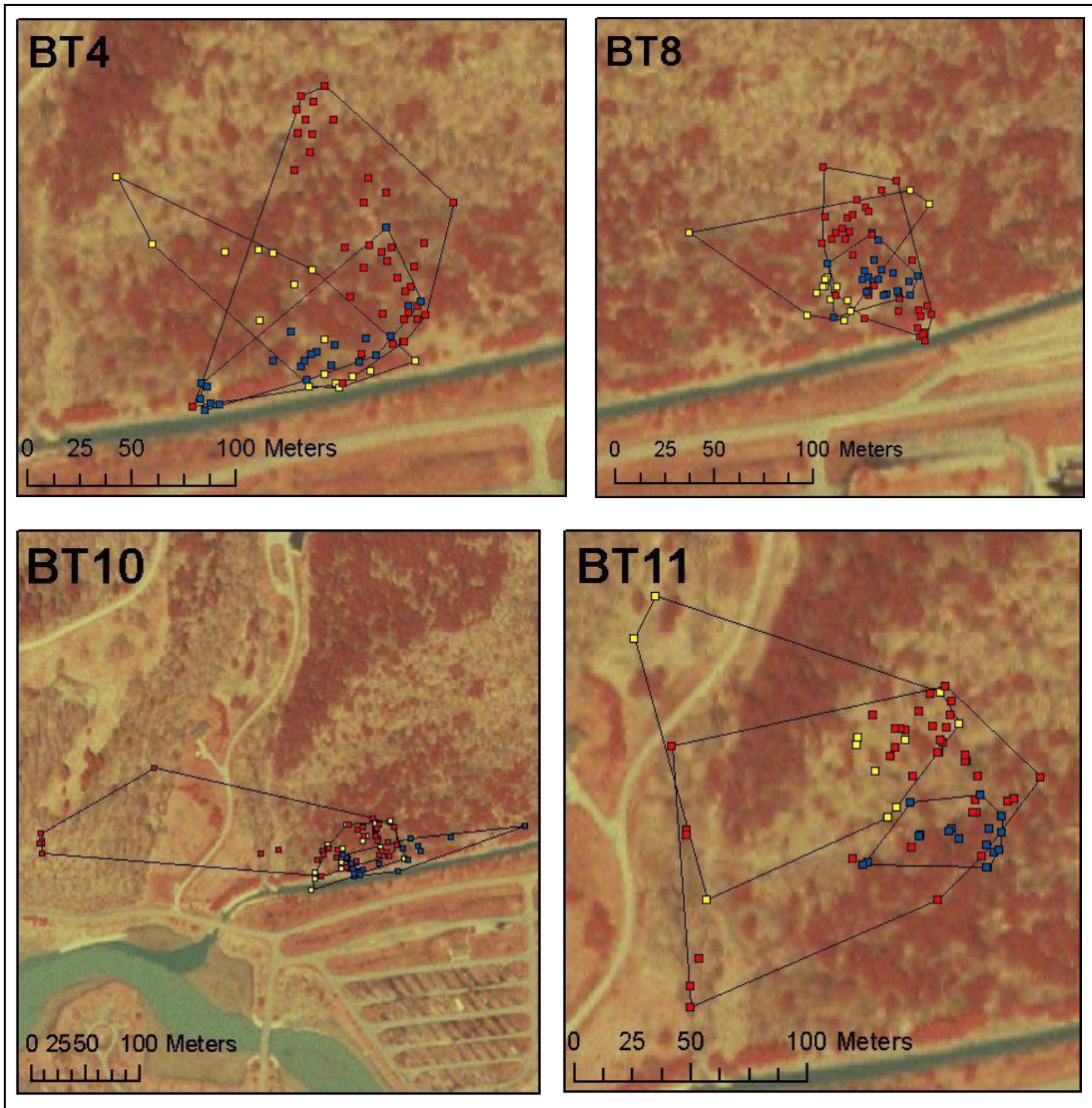


Figure 11. Four female *T. c. carolina* (4,8,10,11) seasonal (spring = yellow, summer = red, fall = blue) home ranges outlined with a minimum convex polygon and overlain on an aerial view of the study site.

PRINCIPLE COMPONENT ANALYSIS

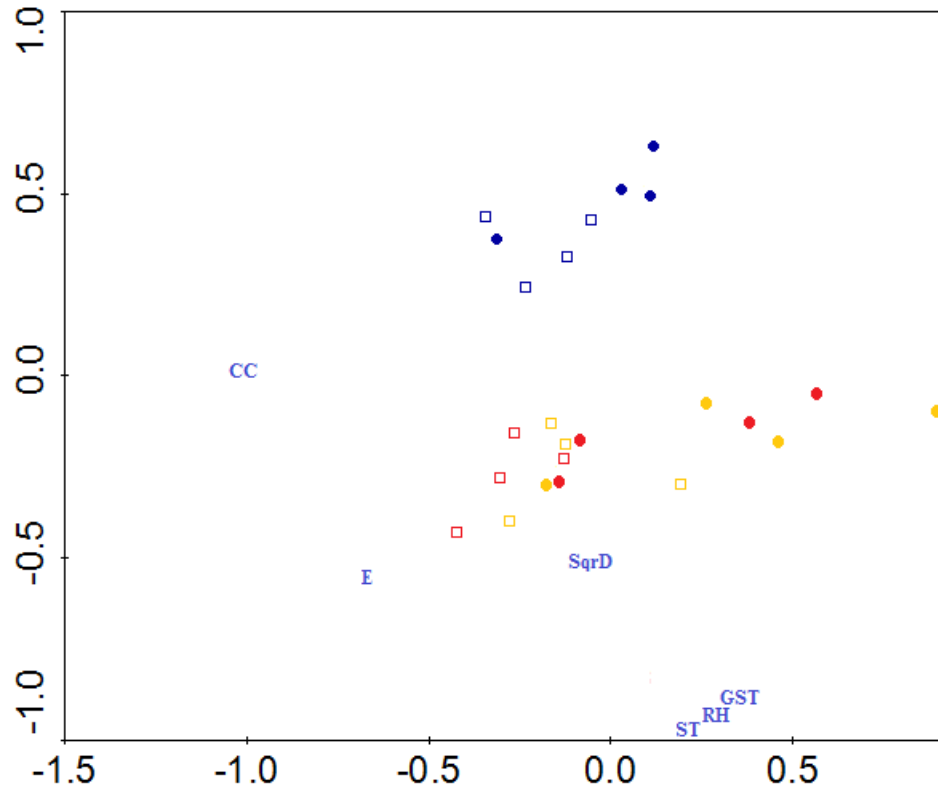


Figure 12. Principle component analysis (PCA) of seasonal (spring = yellow, summer = red, fall = blue) parameters at *T. c. carolina* utilized microhabitats between sexes (squares = males; circles = females) for relative humidity (RH), ground surface (GST) and soil (ST) temperature, square root of distance traveled in meters (SqrD), elevation (E), and canopy cover (CC). Eigenvalue shows that the PCA accounts for 87.5% of variance for both axes.

DISCUSSION

DISTANCE TRAVELED

Active box turtles are shown to move anywhere from a meter to hundreds of meters within a day, where seasonal shift accounts for some of this variation (Stickel, 1950; Penick et al., 2002). Penick et al. (2002) saw that turtles moved on average less than a meter a day during the winter and six to nine meters a day during the active season, spring to early fall, respectively. Whereas seasonal shift is one factor that dictates activity in box turtles, other elements have also been suggested to influence box turtle patterns of movement.

A potential predictor for the amount of straight-line distances moved by box turtles through their habitats is sex, as posited by previous studies (Stickel, 1950; Gibbons, 1968; Strang, 1983; Penick et al., 2002). Penick et al. (2002) found that females have a tendency to travel shorter overall distances within each season compared to males. Additionally, Gibbons (1968) witnessed females traveling greater distances in the summer, potentially moving from their preferred foraging grounds to seek out suitable nest sites. Males and juveniles remained within the same general areas for longer periods.

Guided by these findings, I hypothesized that, due to the different reproductive behaviors that are prompted by seasonal cues, each sex would exhibit seasonal variation in mean distances traveled. That is, females would travel greater distances during oviposition to select for suitable nest sites in the summer. Males, who actively seek mates (Muegel and Claussen, 1994), would instead travel greater distances in the spring. The results of this study rejected my hypothesis, as no significant variation for straight-line distances traveled was observed between males and females. Similar results were

recorded by Donaldson and Echternacht (2005). One possible explanation of these results is that mate searching and nest-site selection activities overlap in some populations causing a lack of differences to be observed between sexes in the amount of distances they traveled. Attributing seasonal movement variations solely to reproductive behaviors is difficult, as variations in many factors such as home range features, climate characteristics, and annual precipitation all likely influence the time line of reproductive behaviors.

Whereas no correlation was found in distances traveled between sexes across seasons, the data indicate a significant seasonal variation in the amount of overall straight-line distances box turtles traveled. Mean straight-line distance traveled by box turtles decreased significantly in the fall compared to the spring (Figure 6). Simultaneously, relative humidity and soil and ground surface temperatures at utilized microhabitats decreased significantly in the fall from the spring and summer seasons (Figure 12). These observed environmental patterns are important to note as high relative humidity encourages higher levels of box turtle activity (Rossell et al., 2006). Therefore, the seasonal drop in relative humidity experienced in the fall potentially triggered shorter bouts of activity during this season, such as those recorded in my study population. As temperature and moisture dropped in the fall, the risk of desiccation would have increased and a need to up-thermoregulate body temperature may have caused turtles to remain within forms. Forms are defined as depressions in the soil in which a turtle remains inactive for a period of time from one day to several weeks. Form locations are said to shift depending on seasons (Stickel, 1950; Reagan, 1974; Dodd, 2001), and they are utilized for longer consecutive periods during the fall and during cooler weather

fronts (Reagan, 1974). They are located in areas with high humidity as a means to decrease evaporative water loss and desiccation (Reagan, 1974; Ernst et al., 1994; Rossell et al., 2006). During the fall, box turtles may have traveled shorter distances to select new form sites or made shorter excursions, returning to previous form sites.

Greater distances can be covered by box turtles that exhibit optimal body temperatures (Adams et al., 1989). As ambient and microhabitat temperatures decreased, turtles were observed traveling shorter mean distances. Achieving optimal internal temperatures during the active and mating season allows turtles to maximize their reproductive output, lessen energy expenditure, and decrease their mortality rate (Dodd, 2001). Box turtles reach optimum body temperatures through behavioral thermoregulation; they select microhabitats that allow them to achieve an optimum body temperature in order to remain active for longer periods during unfavorable conditions (Nieuwolt, 1996). Lower surface temperatures are generally preferred by turtles during high ambient temperatures and low precipitation as a means to dissipate heat (Rossell et al., 2006). During high ambient temperatures, box turtles select cooler microhabitats for forms to lower body temperatures and lessen energy expenditure. This behavioral thermoregulation allows turtles to decrease the time of inactivity and refocus on activities necessary for survival, feeding, and reproduction (Donaldson and Echternacht, 2005).

Behavioral thermoregulation governs box turtle movements, particularly in relation to their activity levels and the resulting seasonal distances traveled throughout their habitats. Combining the analysis of box turtle microhabitat data with seasonal weather shifts while examining more acute differences between sexes in reproductive

behaviors, specifically, time lines of mate searching and nest-site selection within certain populations, is essential towards furthering our understanding of box turtle movements.



Figure 13. Above: Slight incline at higher elevations of the southeast facing slope at study site. Below: Flatter grade and low elevation at study site on the southeast of the adjacent mountain ridge.



Figure 14. Higher elevation on southeast aspect of mountain ridge in October 2010 at study site; note reduced canopy and vegetation cover.

ELEVATION

It is important to understand the impacts of vertical components within box turtle habitats because they influence general box turtle locomotion, distribution, and dispersal (Muegel and Claussen, 1994). Two mountain ridges at the study site were analyzed as vertical components across or adjacent to which box turtles traversed. My hypothesis that no differences would be observed in movements across elevational gradients was rejected because males were located at significantly higher mean elevations compared to females across all seasons (Table 2). Additionally, season did not appear to have an influence on turtle elevational preferences.

Previous studies have investigated movements in relation to slope incline (Stickel, 1950; Strang, 1983; Muegel and Claussen, 1994). Extreme slope inclines can cause a box turtle to deviate from straight-line movement increasing energy expenditure and risk of predation (Stickel, 1950; Metcalf and Metcalf, 1970; Carroll and Ehrenfeld, 1978; Strang, 1983; Muegel and Claussen, 1994). Muegel and Claussen (1994) recorded voluntary movements along differently graded slopes and saw that turtles ascended and descended easily along a slope of $\leq 40^\circ$ and $\leq 51^\circ$, respectively. Claussen et al. (2002) found that steeper slopes typically decreased box turtle speed of locomotion, in turn affecting box turtle intent to travel across different elevational gradients, and that speed decreased by 20 to 30 % at a slope of 20° or greater, whereas a slope of greater than 35° reduced speed by 50 %. In my study, turtles were tagged on the south-eastern slope, which was the less steep aspect of the mountain ridge (Figure 4, 5). The difference in slope incline between each aspect of the ridge may have limited turtle ascension and descension due to the

energy needed to traverse the steeper slope or resulted in avoidance by traveling around it.

Physical attributes of turtles affect energy expenditure and mobility, thus limiting their movements along slopes (Muegel and Claussen, 1994). Studies have documented that turtles with smaller body masses, small adults and juveniles, traverse steeper slopes more effectively, easily ascending and descending ridges compared to individuals with larger body masses (Adams et al., 1990). This adaptation is beneficial for juvenile box turtle dispersal as well as gene flow. Of the individuals sampled in my population, males had an average body mass of 392.5g (range = 340-445g), whereas females averaged 354.5g (range = 303g-405g). As turtles were tracked only once every two days, it was not possible to observe whether the smaller females were able to traverse the higher elevations more effectively than larger males. Without further investigation, data herein may be biased in terms of males favoring higher mean elevations. According to the idea that larger body masses decrease locomotor abilities along slopes, males may have remained at higher elevations for longer periods of time due to increased energy expenditure resulting from their greater body mass compared to females. Furthermore, males would have exhibited greater form establishment behavior at high elevations, particularly in the summer during high ambient temperatures. Males utilizing forms more frequently at high elevation is supported by the critical thermal maximum theory, which states that turtles with greater body masses have lower tolerances to high temperatures owing to their lowered critical thermal point, which when reached, can halt movements and result in death (Cowles and Bogart, 1944; Hutchison et al., 1966). Males, in particular, exhibited frequent burrowing behavior, in which the carapace was completely

covered by live/dead vegetation, debris, or leaf litter, in the summer (Figure 2). This behavior supports their thermal needs as they select microhabitats that allow them to thermoregulate their body temperatures under extreme ambient temperatures (Nieuwolt, 1996).

Whereas the data suggest no significant difference across seasons, it is interesting to note that males and females were located at their respective highest mean elevation during the summer (Figure 7). A previous study witnessed turtles moving toward a water source at lower elevations in response to high temperatures and low precipitation (Donaldson and Echternacht, 2005). At my study site, precipitation and ambient temperatures were highest during the summer, allowing turtles to move farther from the water sources by traversing higher elevations at a lowered risk of desiccation. This seasonal change in climatic conditions offers a possible explanation as to why both sexes selected higher elevations during the summer.

Parameters at utilized microhabitats for relative humidity and soil and ground surface temperatures all followed similar seasonal trends, decreasing in the fall (Table 4). Sexes did not differ in their utilization of microhabitats in relation to these parameters. Whereas females tended to be found at lower elevations with flatter grades, males were found at higher, and usually steeper, elevations, and it is possible that turtles were selecting similar microhabitats at higher and lower elevations across seasons. In other words, turtles at higher elevations, mainly males, were utilizing microhabitats similar to those of turtles at lower elevations, mainly females, and that elevation preference was independent of humidity and temperatures at utilized microhabitats. This observation

allowed the assumption to be made that other factors, such as reproductive behaviors, were acting upon males and females differently.

Contrary to males, female preference for lower mean elevations during the study period can be associated with nest-site selection. Additionally, lower energy expenditure and a decreased risk of desiccation at lower elevations are also possible explanations for observed box turtle movements. During the mating seasons (spring and early fall) females have to limit energy expenditure before oviposition. Gravidity (a female carrying eggs) has been associated with behavioral adjustments (Seigel et al., 1987). Preferable nest sites are located in either sunny open areas or shadowed areas with limited sunlight within wooded areas, edge habitats, and grassy fields (Messinger and Patton, 1987; Temple, 1987; Forsythe et al., 2004). Sites free of surface debris, which could interrupt or hinder nest excavation, and softer soils are preferable and often found at lower elevations (Legler, 1960; Messinger and Patton, 1995).

In my study site, the mountain ridge adjacent to where turtles were tagged was most traversed along the southeast facing aspect (Figure 4). As a result of aspect, the angle of incidence increases solar radiation on south-facing slopes (McEwan et al., 2005). Therefore, naturally higher temperatures and lower moisture conditions existed on the slope that was most frequently traversed by turtles. The drier resulting conditions on this slope would have discouraged females from higher elevations along this slope aspect due to its lower potential for suitable nest site locations. Higher humidity levels observed at lower elevations are linked with nest site locations (Congello, 1978). In conjunction with unfavorable conditions for nesting along this slope, traversing the slope incline would have unnecessarily increased female energy expenditure, which is essential for

reproduction and associated activities. It is important to note that only mean straight-line distances or minimum distances traveled between successive locations by turtles were measured. It was, therefore, not possible to determine whether females traveled greater total distances, such as winding movements, between successive locations to avoid vertical barriers or if they traveled directly from one location to the next.

Examining cover as a means for thermoregulation at microhabitats can provide useful insight on the observed elevational trends. Moderate mean canopy cover was observed at turtle locations throughout the study (Figure 18), which has been similarly noted by other studies (Dodd, 2001; Rossell et al., 2006). The mixed hardwood dominance of the study site can account for this trend. Box turtles prefer forested areas, particularly during the warmer active season where canopy cover can range from relatively moderate to high (Dodd, 2001). Percent canopy cover depends on a number of variables such as elevation and seasonal shift. Lower canopy cover was observed in the fall at turtle microhabitats (Figure 12). It is important to note that canopy cover increased naturally in the summer and slightly decreased in the fall, reducing my ability to infer true turtle selectivity for microhabitats with specific canopy cover.

Males showed a preference towards higher canopy cover (Figure 12) and had a higher percent presence of shrub cover at microhabitats than females (Figure 19). Since canopy cover was seemingly less at higher elevations in the study site (Figure 13, 14), it is suggested that males may have been exhibiting behavioral thermoregulation by utilizing areas with higher canopy cover and shrub cover more frequently at higher elevations. Rossell et al. (2006) noted in areas where turtles selected for greater canopy cover and shrub layer cover, air circulation was decreased, allowing the turtle to dissipate

heat more slowly during cooler ambient temperatures. Studies also suggest that presence of shrub layer cover (<1 m above turtle) will decrease net radiation and air circulation at ground level, in turn cooling the site during high ambient heat (Plummer, 2003; Rossell et al., 2006). The interaction between over- and understory cover to increase thermoregulatory potential at microhabitats may explain why males were able to traverse higher elevations with lowered risks of desiccation and cooling in the fall and overheating in the warmer seasons.

Interestingly, females were found at lower elevations and lower canopy covered areas than males around the time period that has been shown to correspond with nest-site selection and oviposition (spring and late summer; Figure 7, 13). Lower canopy cover can increase the number of basking sites in a turtle's home range and, therefore, improve their thermoregulatory potential (Muegel and Claussen, 1994; Blázquez, 1995; Penick et al., 2002). Embryonic development and hatchling success have also been positively correlated with nest site incubation temperatures causing a selective pressure towards areas with lower canopy cover and increased surface temperatures (Blázquez, 1995). Therefore, even though canopy cover was naturally higher at lower elevations at the study site, female box turtles may have shown a preference toward lower canopy covered areas due to preferential nest-site selection and to increase their thermoregulatory potential.

Seasonality was not significantly related to box turtle elevation preferences whereas sex showed a significant relationship with box turtle mean elevations. Due to similarities witnessed between environmental data at microhabitats utilized by males and females, it can be inferred that behavioral differences, specifically reproductive

behaviors, between sexes were driving this observed trend. However, in addition to differences in reproductive behaviors, it is important to incorporate slope aspect and incline and microhabitat cover utilization characteristics into future analyses of box turtle movements along elevational gradients. Further investigation into these fields is warranted and could shed light on box turtle movements along both horizontal and vertical components within their home ranges.

HOME RANGE

To understand movements of box turtles, knowledge of temporal (diurnal/seasonal) and spatial (home range area utilization) movement patterns is required. The need to explore, forage, and search for potential mates inspire box turtle movements (Stickel, 1950; Dodd, 2001). Due to the temporal variation in the conditions that motivate movement, both seasonally and daily, home range usage fluctuates (Nieuwolt, 1996). This shift is likely related to habitat quality and seasonal variation (Donaldson and Echternacht, 2005). Changes in home range size across seasons and between sexes are understudied in box turtle populations (Swarth, 2005; Bernstein et al., 2007). Further understanding home range utilization in box turtle populations throughout their range will better enable effective conservation management plans for this long-lived species. For my study population, I hypothesized that home range size, or the area utilized within the total home range, would be significantly smaller in the fall. Turtles had significantly different sized home ranges across seasons, utilizing the largest area of their home range in the summer and the smallest in the fall (Figure 8), supporting my hypothesis.

Reduced home ranges coupled with a reduction in mean distances traveled in the fall, suggest box turtle seasonal adjustment of activity levels toward lower ambient temperatures and humidity. Box turtles usually enter a dormant state in late fall, as changes in microhabitat characteristics signal them to select suitable burrowing sites. Burrows are selected as a means of thermoregulation due to increased burrowing behavior exhibited during extreme temperatures (Doroff and Keith, 1990).

Further results indicate that spring home ranges were significantly smaller than summer home ranges (Figure 8; Table 2). Average and total precipitation peaked in the summer increasing ambient relative humidity. Previous studies suggest that high moisture conditions have more influence on box turtle activity than do variations in temperature within a habitat (Reagan, 1974; Dodd, 2001). Thus, turtles may have been actively foraging more frequently during the summer months, utilizing a larger part of their home range compared to the spring, which had lower precipitation. Seasonal shifts in home range utilization have also been related to nearby water sources. Turtles expanded their home ranges in the summer to include a temporary pond, reiterating the importance of high humidity and moisture levels relative to higher ambient temperatures for box turtle movements and habitat utilization (Donaldson and Echternacht, 2005).

Distances traveled by turtles were not significantly different between spring and summer seasons (Figure 6). Although turtles were traveling similar distances between spring and summer, they were utilizing a significantly greater area of their home range in the summer compared to the spring. Due to higher ambient temperatures, precipitation levels, and extended daytime hours during the summer, a bimodal shift in activity may have influenced box turtle movements throughout home ranges. Box turtle activity could have shifted toward early evening hours increasing evening foraging and exploration behavior allowing them to remain within forms during high, mid-day temperatures. This bimodal behavior may have resulted from an effort to thermoregulate to more optimal body temperatures during high summer temperatures. Although turtles utilized less of their home ranges in the spring, yet traveled similar distances, the lower ambient temperatures observed within this season allowed them to traverse greater distances

during the day within a shorter time compared to the summer. Turtles may have exhibited less exploration behavior and, therefore, less home range usage was observed during the spring.

Concurrent with distances traveled within seasons, vertical components (i.e. elevational gradients) within a habitat can act as potential barriers limiting home range sizes (Stickel, 1950; Strang, 1983). As most turtles were not located on the opposite aspect of the first mountain ridge closest to where they were initially tagged, it can be assumed that this vertical component coupled with adjacent habitat fragmentation such as the dry stream bed, open field, and paved road (Figure 5) limited home range size by forming barriers for box turtle movements.

It is disputed whether or not sex plays a role in determining home range size (Stickel, 1950; Doroff and Keith, 1990; Barron, 1996; Cook, 1996; Donaldson and Echternacht, 2005). My results indicate that there was no significant difference between sexes in their home range sizes (Table 2). Nonetheless, females were observed to have a slightly larger mean home range size compared to males. As males were generally located at higher elevations, and, therefore, on steeper slopes, their relative home range size would have been limited due to the increased energy necessary to traverse habitat at those locations. Additionally, limited movements along steeper slopes at higher elevations can impinge upon the males' ability to search for potential mates, forage for food, distribute, and expand his home range. Consequently, this impediment on turtle locomotor abilities may be why males were observed with lower mean total home range sizes. Females have been shown to take short excursions from their home ranges as a means to select suitable nest sites (Stickel, 1950). This behavior, coupled with utilizing generally lower elevations

and flatter inclines, allowed females to traverse a larger area with less energy expenditure, offering an explanation for their slightly larger home range sizes.

The observed seasonal shift in usage of home ranges from spring to fall suggests that ambient environmental changes in connection with thermoregulatory behavior govern box turtle home range size. Analyzing home range usage patterns and influencing factors is critical to the development of well informed conservation efforts. The analysis of this particular population and how sex and season, along with various microhabitat variables, influence utilization of home ranges contribute toward our understanding of box turtle populations as a whole.

IMPLICATIONS FOR CONSERVATION

Box turtle populations are declining across their range in the United States (Stickel, 1978; Williams and Parker, 1987; Ernst and Lovich, 2009). Box turtles are at a particular risk, due to their low fecundity (Dodd, 1997), longevity (ages ranging from 45 to 100 years; Stickel, 1978), slow maturation rates, and high rates of hatchling mortality (Dodd, 2001). Within turtle populations the loss of adult individuals can be detrimental to the population for almost two decades after loss (Congdon et al., 1994). Individual mortality, particularly of female adults, can impact a population greatly by decreasing potential mates, reproduction, and the addition of new individuals. This individual loss increases pressure on maternal nest-site selection to increase hatchling survival of remaining females to maintain a stable population. Movements throughout habitats and between microhabitats, therefore, become more crucial during the nesting season as females search for nest sites with optimal substrate, incubation temperatures, and high concealment.

Box turtle selection of microhabitat characteristics for nest site locations and thermoregulation require more in depth analyses. In studies involving microhabitat selection, as in Rossell et al. (1996), box turtle selected microhabitats are paired with randomly selected adjacent microhabitat locations. This data collection allowed researchers to make pair-wise comparisons to determine whether turtles selected for specific characteristics within microhabitats. Inferences could then be made about box turtle motivations for movements within home ranges, such as behavioral thermoregulation and reproductive strategies.

Adult box turtles are said to have stable home ranges, the act of having similar home range sizes from year to year (Legler, 1960; Schwartz et al., 1984; Doroff and Keith, 1990). However, decreased annual stability in home range sizes has been observed in box turtles. Individual home ranges that exhibit annual variations in home range size are observed to have a loss in habitat quality and diversity (Stickel, 1950; Stickel, 1989; Madden, 1975). Habitat quality and diversity are negatively influenced by overcrowding, fragmentation, and destruction, decreasing the number of previous areas used for thermoregulation and foraging. Box turtles have been seen to increase their home ranges to encompass more quality habitat (Stickel, 1948; Madden, 1975; Stickel, 1989). Studies have also shown that turtle movements in severely disturbed and altered habitats remain within constrained home range areas, causing overcrowding (Doroff and Keith, 1990). Constrained home ranges as well as expansions of home ranges within a low quality, fragmented habitat can increase individual mortality rates. Due to high site fidelity observed in box turtles (Stickel, 1989), it is not surprising that individuals remain within severely disturbed habitats to mate, forage, and reproduce exposing themselves to altered climatic conditions and more subsidized predators. Turtles that expand their home ranges to encompass more quality habitat in turn may encounter higher road mortality. Pauley (1992) did a survey on road kills in West Virginia and found that almost 70 % of reptilian road kill were box turtles.

To further strengthen my study, I would analyze annual home range sizes to see whether the observed interannual shifts were related to varying annual environmental conditions, such as precipitation. Additionally, I would explore whether habitat fragmentation, degradation, or destruction from natural and anthropogenic factors are

having an influence on home range sizes. Due to the limited knowledge about annual variations in box turtle movements, the need for long-term studies is emphasized (Somers and Matthews, 2006).

Results of this study demonstrate the interrelatedness between elevational gradients, distances traveled, and home range sizes in box turtle movement. Previous studies suggest that thorough knowledge of box turtle natural history in conjunction with preferential habitat characteristics is imperative toward developing effective conservation efforts (Dodd, 2001; Rossell et al., 2006). Understanding the variations in home range size and population density throughout seasons and annually can be useful in the development of protection protocols for certain areas within the range of *T. c. carolina*.

Box turtle habitats have little-to-no enforced protection (Somers and Matthews, 2006). Currently, box turtle trade with other member nations is the only regulation set in place by the Convention on International Trade in Endangered Species (CITES) (Dodd, 2001). Information on box turtle movements within home ranges will allow for informed decisions on size and location of protected habitats for box turtles by incorporating adjustments for movements in relation to thermoregulatory, foraging, nesting, and mate searching behaviors. To effectively stem box turtle population decline, Doroff and Keith (1990) suggest that 100ha areas should be set aside in habitats that are favorable to box turtles, excluding roads and individual collection. Other studies suggest that the established area of protected land should take into account the seasonal variation of home ranges and seasonal activity (Donaldson and Echternacht, 2005).

In conclusion, it is vital to study movement behaviors of individual populations across *T. c. carolina*'s range as it contributes to a greater understanding of their natural

history and importance within ecological communities (Somers and Matthews, 2006). Additionally, natural history lays the groundwork for future ecological and behavioral studies and can be utilized toward the development of box turtle conservation management plans. These plans include well informed decision-making for potential protected habitats in relation to box turtle movements and behaviors (Morrison et al., 1992; Belzer and Steisslinger, 1999).

NATURAL HISTORY NOTES

The following are noteworthy observations of *T. c. carolina* natural history throughout the study period. Box turtles, both tagged and untagged individuals, were witnessed copulating throughout the study. More frequent copulations were observed in the spring and fall. Spring copulations were observed earlier in the day (9-11 am), whereas fall copulations were witnessed in the later part of the day (1-2pm). During the summer season two tagged male individuals (3 and 7) were observed burrowing in a damp mud pit at the base of the north-western slope aspect (the opposite aspect from which they were initially tagged) within 1 m of one another and adjacent to three other burrowed box turtles whose sexes were not identified. They remained within this mud pit, moving no further than 1 m, for an average of seven days. This observed proximity suggests that box turtles group together during particularly warm periods if favorable habitat is available as a means to thermoregulate. Additionally, this behavior supports the theory that box turtles are non-territorial due to their close proximity during these observations. During a flooding event at the study site in late July, box turtles were observed at higher elevations compared to the previous elevations at which they were usually found.

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APPENDIX I. Tabular data for ANOVAs on distances traveled, elevation, and home range area across seasons and between sexes. Additionally, means \pm 1Standard Error across seasons and between sexes for above parameters are included.

Table 1. Mean \pm 1SE of home range area (m²), elevation (m), and straight-line distances traveled (\sqrt{m}) at utilized microhabitats across seasons, for all turtles, and between sexes for tagged *T. c. carolina*.

Season	Spring			Summer			Fall		
Sex	Male	Female	Turtles	Male	Female	Turtles	Male	Female	Turtles
<i>Home Range Area</i> (meters ²)	3546 \pm 448	5631 \pm 1644	4589 \pm 882	10949 \pm 2366	12013 \pm 3474	11481 \pm 1956	1554 \pm 450	2295 \pm 608	1924 \pm 377
<i>Elevation</i> (meters)	195.1 \pm 2.9	190.1 \pm 3.3	192.6 \pm 2.3	200.2 \pm 2.9	192.1 \pm 2.9	196.2 \pm 2.5	196.1 \pm 3.2	186.1 \pm 2.8	191.1 \pm 2.7
<i>Distance Traveled</i> (\sqrt{m} eters)	5.18 \pm 0.3	5.80 \pm 0.6	5.50 \pm 0.3	5.09 \pm 0.2	4.68 \pm 0.4	4.88 \pm 0.2	4.09 \pm 0.4	4.26 \pm 0.6	4.18 \pm 0.3

Table 2. Univariate analysis of variance (ANOVA) including degrees of freedom, *F*-test, correlational coefficient (*R*) squared and probability (*P*) of variables measured, home range area, square root of distance traveled, and elevation across season and between sexes. Sources with asterisks (*) signify significant relationships.

Dependant Variable	Source	df	<i>F</i>	<i>R</i>²	<i>P</i>
<i>Home Range Area</i> (m ²)	Season*	2	13.8	0.61	0.000
	Sex	1	0.7	-	0.409
<i>Distance Traveled</i> (\sqrt{m})	Season*	2	5	0.39	0.019
	Sex	1	0.2	-	0.699
<i>Elevation</i> (m)	Season	2	1.5	-	0.247
	Sex*	1	9.8	0.43	0.006

Table 3. Movements along elevations within seasons and between sexes for *T. c. carolina*.

		Spring		Summer		Fall	
	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>MaleXFemale</i>	1	1.27	0.300	3.91	0.095	5.51	0.057

APPENDIX II. Figure and tables (ANOVA and mean \pm 1 SE) for microhabitat variables: relative humidity, soil and ground surface temperatures, canopy cover, shrub cover, and substrate.

Table 4. Mean \pm 1SE of relative humidity (%) , ground surface and soil temperatures ($^{\circ}$ C), and canopy cover (%) at microhabitats across seasons, for all turtles, and between sexes for tagged *T. c. carolina*.

Season	Spring			Summer			Fall		
Sex	Male	Female	Turtles	Male	Female	Turtles	Male	Female	Turtles
<i>Relative Humidity</i>	74.3 \pm 0.3	74.3 \pm 1.0	74.3 \pm 0.5	72.3 \pm 0.2	73.4 \pm 0.5	72.9 \pm 0.3	58.1 \pm 0.8	59.1 \pm 0.6	58.6 \pm 0.5
<i>Ground Surface Temperature ($^{\circ}$C)</i>	27.9 \pm 0.3	28.4 \pm 0.4	28.2 \pm 0.3	27.7 \pm 0.1	28.1 \pm 0.2	27.9 \pm 0.2	23.6 \pm 0.3	24.0 \pm 0.6	23.8 \pm 0.3
<i>Soil Temperature ($^{\circ}$C)</i>	21.3 \pm 0.2	21.3 \pm 0.1	21.3 \pm 0.1	20.6 \pm 0.1	20.7 \pm 0.1	20.6 \pm 0.1	16.6 \pm 0.3	16.5 \pm 0.2	16.6 \pm 0.2
<i>Canopy Cover(%)</i>	88.9	74.2	81.5	93.4	80.2	86.8	88.4	86.7	87.6

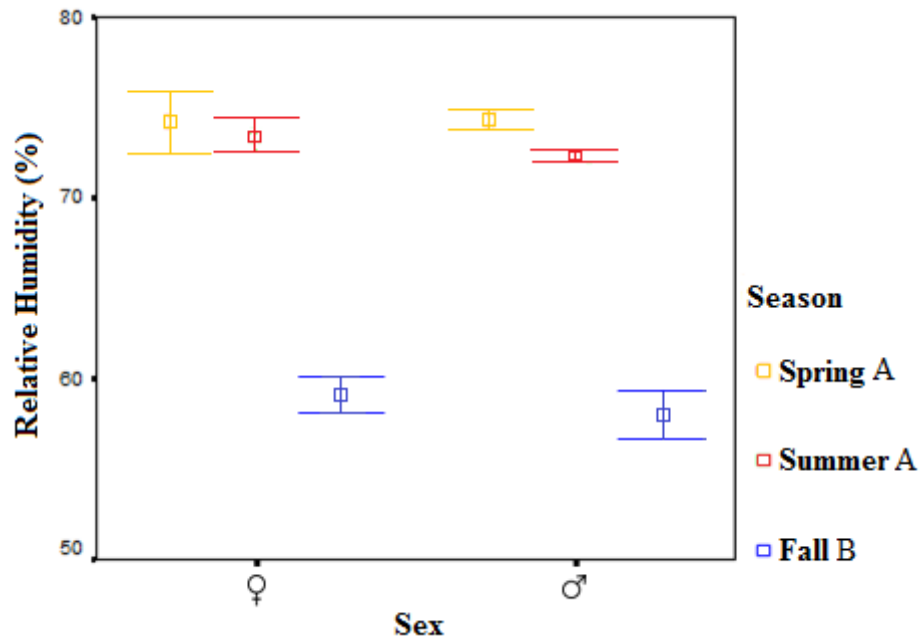


Figure 15. Mean \pm 1SE relative humidity at utilized microhabitats for male and female *T. c. carolina* across seasons. † ◊

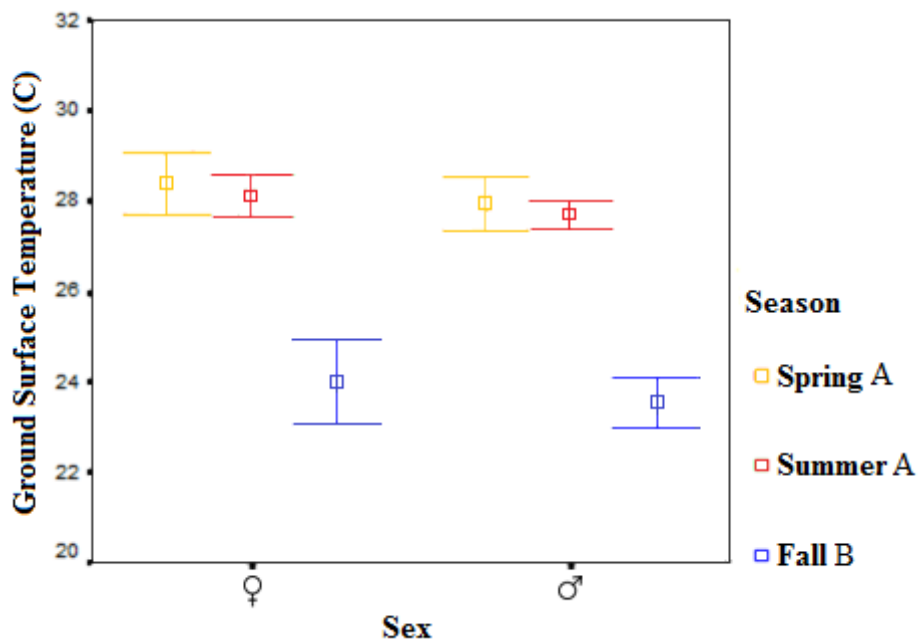


Figure 16. Mean \pm 1SE ground surface temperatures at utilized microhabitats for male and female *T. c. carolina* across seasons. † ◊

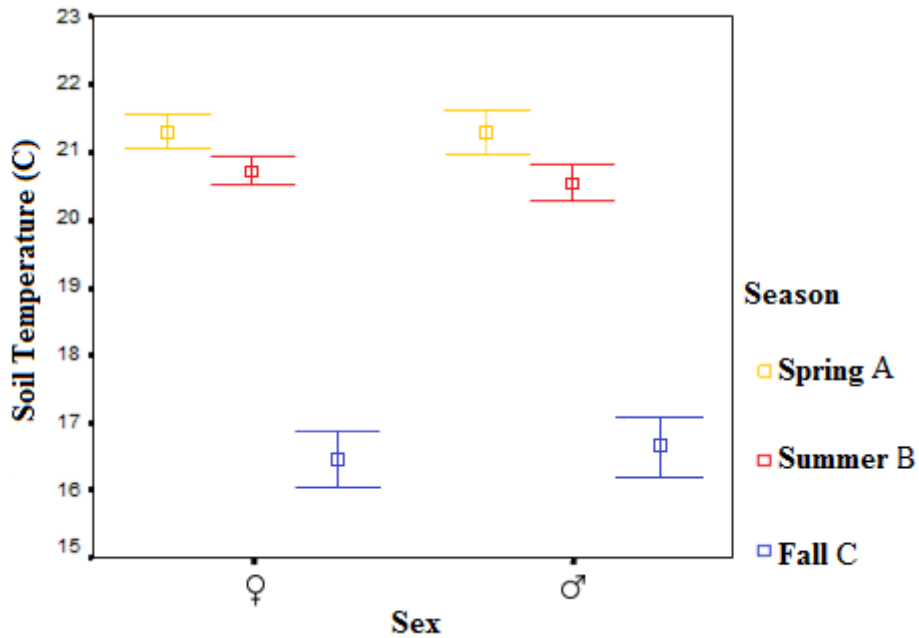


Figure 17. Mean \pm 1SE soil temperatures at utilized microhabitats for male and female *T. c. carolina* across seasons. † ◊

Table 5. Univariate analysis of variance (ANOVA) including degrees of freedom, *F*-test, correlational coefficient (*R*) squared and probability (*P*) of variables measured, home range area, square root of distance traveled, elevation, relative humidity, ground surface and soil temperatures across season and between sexes. Sources with asterisks (*) signify significant relationships.

Univariate Analysis of Variance					
Dependant Variable	Source	df	<i>F</i>	<i>R</i> ²	<i>P</i>
<i>Relative Humidity</i> (%)	Season*	2	382.6	0.98	0.000
	Sex	1	1.8	-	0.199
<i>Ground Surface Temperature</i> (°C)	Season*	2	98.3	0.92	0.000
	Sex	1	2.6	-	0.126
<i>Soil Temperature</i> (°C)	Season*	2	450	0.98	0.000
	Sex	1	0	-	0.968

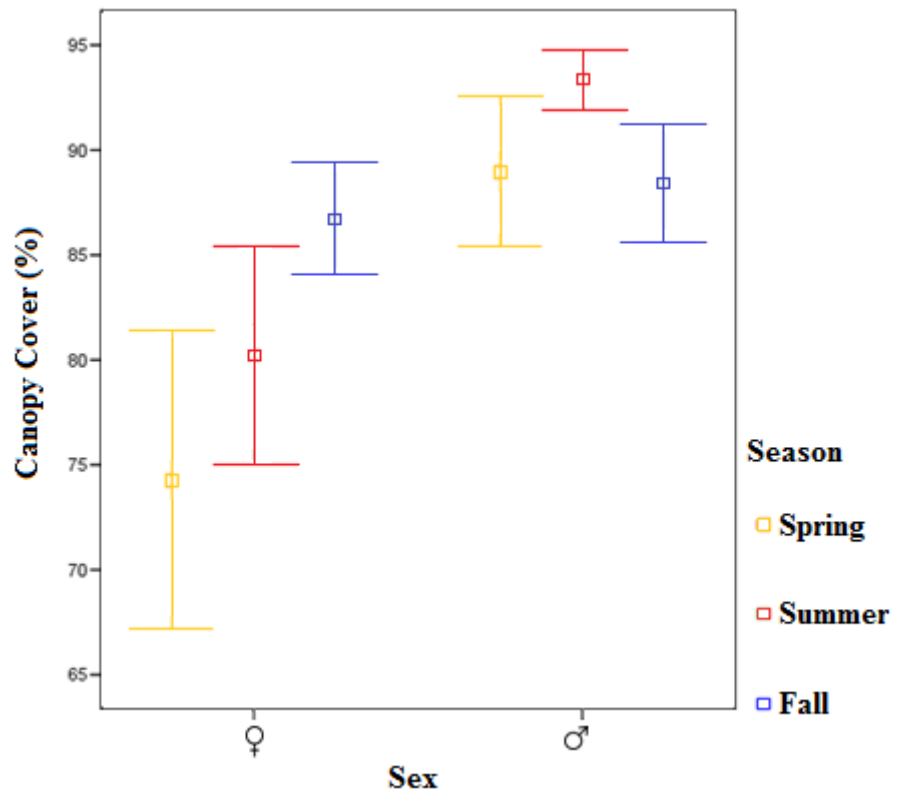


Figure 28. Mean \pm 1SE canopy cover (%) for male and female *T. c. carolina* microhabitats across seasons. Ψ

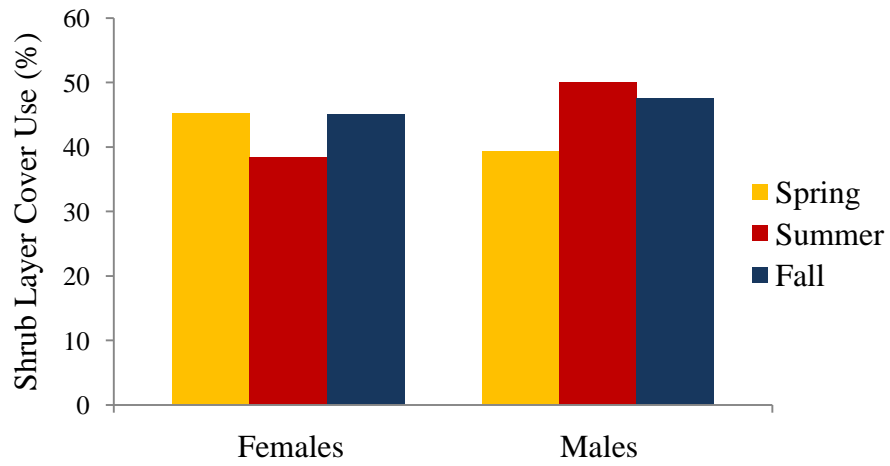
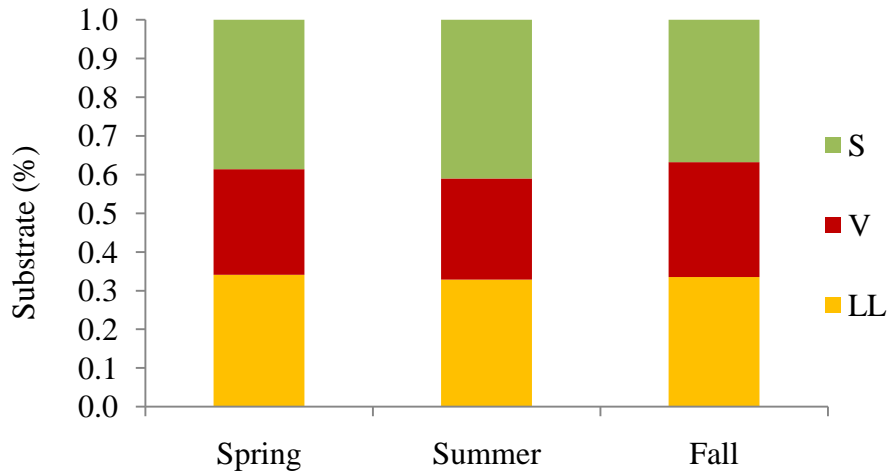


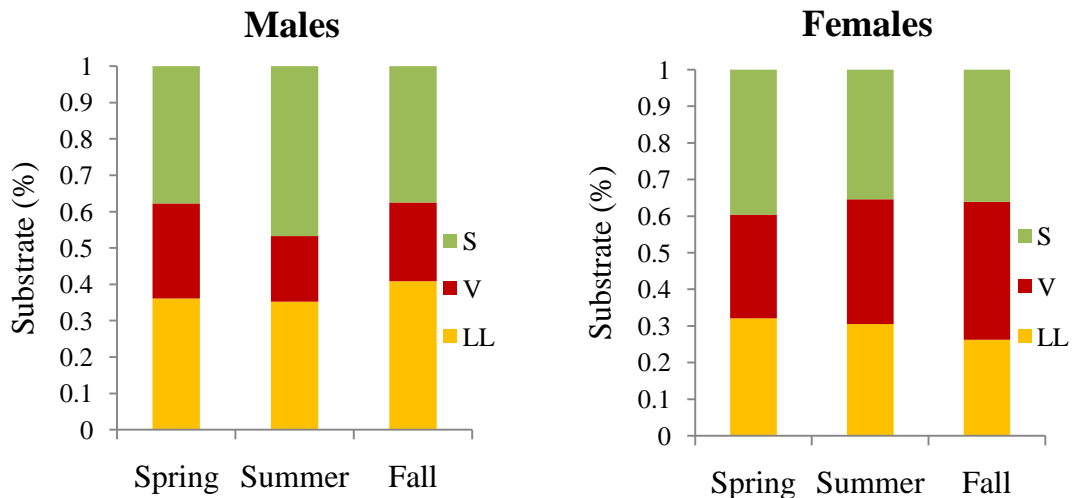
Figure 19. Shrub layer cover (%) use by male and female *T. c. carolina* across seasons. ψ

Table 6. Shrub layer cover use (%) by male (M) and female (F) *T. c. carolina* and the average use for all turtles across seasons.

Season	M	F	Mean
<i>Spring</i>	39.3	45.2	42.25
<i>Summer</i>	50	38.3	44.15
<i>Fall</i>	47.5	45	46.25



(A)



(B)

(C)

Figure 20. Substrate (leaf litter, vegetation, and soil) use (%) by (A) all turtles, (B) male, and (C) female *T. c. carolina* across seasons. ψ

Table 7. Substrate (leaf litter, vegetation, and soil) (%) use by male (M) and female (F) *T. c. carolina* and average use for all turtles across seasons.

Substrate	Leaf Litter			Vegetation			Soil		
	M	F	Mean	M	F	Mean	M	F	Mean
Spring	0.36	0.32	0.34	0.26	0.28	0.27	0.38	0.40	0.39
Summer	0.35	0.30	0.33	0.18	0.34	0.26	0.47	0.36	0.41
Fall	0.40	0.26	0.34	0.22	0.39	0.30	0.38	0.35	0.36