2019

Home Range, Habitat Use and Thermal Ecology of the Florida Box Turtle (Terrapene bauri) on an Anthropogenic Island in Southwestern Florida

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Home Range, Habitat Use and Thermal Ecology of the Florida Box Turtle (*Terrapene bauri*) on an Anthropogenic Island in Southwestern Florida

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December 2018

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A Thesis
Presented to the Department of Environmental Studies
Antioch University New England

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

By Christina Demetrio
December 2018

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to my thesis advisor, Liz Willey, for supporting my graduate studies and giving me the opportunity to work with her on this project. Her tremendous dedication to the students is an invaluable asset for Antioch University and I am grateful to have received her generous time and mentorship. I am especially appreciative for her assistance with developing the statistical analyses. I would also like to give special thanks to my other two committee members, Michael Jones and Mark Danaher, for their field work support to the project and for contributing their insightful input on Box Turtle populations in southwestern Florida. My entire committee was instrumental in conceiving and designing the methods for this project.

Funding and support was provided collaboratively by the American Turtle Observatory and the U.S. Fish & Wildlife Service SW Florida Gulf Coast Refuges. I would like to thank the USFWS Biological Science Aids Matthew Grassi, Jared Franklin, and Allyson Genson for contributing over 400 hours of hard work on-site collecting the radio-telemetry data in a very unforgiving landscape with challenging heat and painful cacti spines. Permits to conduct this research were obtained from the U.S. Fish and Wildlife Service (Ten Thousand Islands National Wildlife Refuge), and the Florida Fish and Wildlife Conservation Commission (Permit No. LSSC-10-00103 and LSSC-13-00035A). Research protocols were approved by the University of Massachusetts Institutional Animal Care and Use Committee (protocol 25-02-04).

Several of my fellow graduate students were incredibly helpful in completing this project. Conversations I had with Jess Meck about her analogous Gulf Coast Box Turtle study helped guide this project and I am indebted for her willingness to share her experiences and statistical scripts. I would also like to thank Steven Lamonde for his limitless interest in geography and GIS analysis and the numerous occasions he provided expert advice and helped me check the accuracy of my GIS work.

Lastly, I would like to thank my family and friends for their support during this belated endeavor to pursue my professional aspirations. Going back to school after all these years is nothing short of ambitious and I am grateful for their encouragement, patience, and confidence in me throughout this experience.

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ABSTRACT

Limited information is available on the ecology of *Terrapene bauri* (Florida Box Turtle) in mangrove ecosystems. Radio-telemetry and iButton data loggers were used to study the home range, habitat use, and thermal ecology of ten Florida Box Turtles on an anthropogenic island in the mangrove-dominated region of southwestern Florida. The effects of weather variables on movement and activity were also examined. Home range analysis using Minimum Convex Polygons (MCP) and Kernel Density Estimates (KDE) determined an average home range size of 0.81 ha (MCP) and 2.32 ha (95% KDE). Box Turtles moved an average distance of 6.3 m per day and 46.1 m between weekly locations. Habitat analysis using both field data and Geographic Information Systems (GIS) indicated tropical hardwood hammock as the dominant habitat type used in Box Turtle home ranges. Mangrove forests, shrub-scrub-cactus, and shell barren habitats were also utilized. There were no significant differences in home range size or habitat use between the sexes. Activity appeared to increase during the wet season from May to October. Logistic regression models found humidity and temperature to be significantly correlated to turtle activity. Increases in humidity resulted in increases in turtle activity whereas increases in temperature resulted in decreased activity. Linear regression models found turtle movement significantly increased with precipitation. Larger movements appeared to occur after precipitation that was preceded by drier conditions. Temperature data loggers recorded mean carapace temperatures of 25.3°C as well as temperatures up to 40.1°C, which is close to the critical thermal maximum for turtles in the genus *Terrapene*. These results provide baseline information on Box Turtles near their southern range limit, which may become increasingly important for conservation efforts as changes to southern Florida occur from expected climate change.

CHAPTER 1: THESIS INTRODUCTION

A long-term population assessment was conducted by the American Turtle Observatory (ATO) on *Terrapene bauri* Taylor (Florida Box Turtle) in the northern Ten Thousand Islands, Florida to study its distribution and ecology in relation to mangrove ecosystems. A total of 18 islands (5 natural and 13 prehistoric man-made) were examined from 2010 – 2014 for Florida Box Turtle populations (Jones et al., 2016). Exact site locations have been withheld due to poaching risk for this species. As part of a partnership with the U.S. Fish & Wildlife Service Southwest Florida Gulf Coast Refuges, 10 adult Box Turtles were tracked via radio-telemetry on one of the islands approximately once per week from March 2016 through October 2016 and once additionally in March 2017 to examine the movement, seasonal habitat use, and thermal sensitivity of Box Turtles in tropical hardwood hammock and mangrove forests. In addition to radio transmitters, turtles were outfitted with external iButton Data loggers (Maxim, Dallas, TX) to monitor body temperature.

Florida Box Turtles have a reported distribution throughout peninsular Florida, the Florida Keys, and additionally on barrier islands (Dodd et al., 1994; Farrell et al., 2006). Xeric habitat use of scrub, pine forest, and pine rocklands is consistent with *T. bauri* in its southernmost Florida Key range as well as mesic, hardwood hammocks in central Florida (Farrell et al., 2006; Verdon & Donnelly, 2005). Mangroves are considered an infrequent or non-existent habitat for Box Turtles and have been understudied in Florida at the southern extent of their range (Farrell et al., 2006; Jones et al., 2016). The primary habitat types of the study area are mangroves, shell mound, and hardwood hammock (FNAI, 2010; Wilder and Barry, 2010). The presence of mangroves and a relatively visible *T. bauri* population made this study site of particular interest. In addition, climate change and sea level rise is expected to have a discernible impact on the low lying region of Florida and consequently for *bauri*. In the midst of this vulnerability, documenting baseline information on these populations is important to inform actions for their conservation (L. Willey and M. Jones, personal communication, March 10, 2018).

This thesis presents the results of the 2016–2017 radio-telemetry and iButton data logger collection season. Chapter 2 contains a literature review on the genus *Terrapene* with an emphasis on the natural history of *T. bauri*. Chapter 3 examines *T. bauri* home range and habitat use in a mangrove dominated area of southwestern Florida. Chapter 4 describes their observed movements, activity, and thermal ecology. The specific objectives of this thesis are to: (1) Evaluate home range of the Florida Box Turtle (by both sex and individual) via radio-telemetry in comparison to other *Terrapene* studies; (2) Quantify whether Florida Box Turtle habitat use is related to specific vegetative communities, in particular mangrove ecosystems; 3) Evaluate how Florida Box Turtle movement and activity is influenced by the subtropical weather of their extreme southern range. Chapters 3 and 4 are formatted according to the publishing guidelines of the peer-reviewed scientific journal, The Southeastern Naturalist.

CHAPTER 2: A REVIEW OF THE GENUS TERRAPENE WITH EMPHASIS ON THE FLORIDA BOX TURTLE (*Terrapene bauri*)

Introduction

Terrapene carolina L. (Eastern Box Turtle) is a predominately terrestrial turtle that occurs in North America, Mexico and historically Canada. According to the Turtle Taxonomy Working Group (Rhodin et al., 2014), *Terrapene carolina* is divided into six living subspecies, *Terrapene carolina carolina* L. (Eastern Box Turtle), *Terrapene carolina mexicana* Gray (Mexican Box Turtle), *Terrapene carolina yucatana* Boulenger (Yucatán Box Turtle), *Terrapene carolina triunguis* Agassiz (Three-toed Box Turtle), *Terrapene carolina major* Agassiz (Gulf Coast Box Turtle), and *Terrapene carolina* bauri Taylor (Florida Box Turtle). Frequent intergradation occurs in parts of their range in particular for *T. c. carolina*, *T. c. triunguis*, *T. c. major* and *T. c. bauri* where they coexist together in the Gulf Coast region, along the borders of Georgia and Florida as well as the Florida Panhandle (Butler et al., 2011; Farrell et al., 2006; Kiester & Willey, 2015; Seidel & Ernst, 2017). This coexistence and the resulting hybridized variations of Box Turtles have complicated taxonomic classifications both morphologically and genetically. Butler et al. (2011) suggested *T. c. major* as not a distinct subspecies but rather an intergrade of *T. c. carolina* and the extinct subspecies *T. c. putnami* (Giant Box Turtle) based on phenotypic and genetic analysis. In addition, they proposed the elevation of *T. c. bauri* to species status. Martin et al. (2013) found mitochondrial and nuclear DNA bar coding warranted *T. mexicana* species status containing *mexicana*, *triunguis*, and *yucatana* as its subspecies. They also estimated a divergence of the Florida Box Turtle from *T. carolina* about 10.3 million years ago and acknowledged its potential as a unique group as suggested by Butler et al. (2011). DNA bar codes have been useful in identifying new species previously defined by morphology

(Puillandre et al., 2012) as is the case for *Terrapene*. Interspecific genetic variation may be considered distinct based on thresholds greater than 2–3% (Chapple & Richie, 2013), and levels above 2% for several *Terrapene* subspecies were found by the Martin et al. (2013) study. However, it is recommended as a more valid approach to use aspects of a species' morphology, geography, and ecology in conjunction with genetic analysis due to the biases that exist in DNA barcoding (Puillandre et al., 2012). Therefore, Fritz and Havaš (2014) responded in contrast to Martin et al. (2013) along with recent studies on DNA barcoding and divergence levels (Shen et al., 2013) that thresholds for determining a species are not universal. They argued distinction should not be based purely on these levels alone but rather include additional evidence. Fritz and Havas (2014) also stated that the current taxonomy of the subspecies for *Terrapene carolina* as listed by Rhodin et al. (2014) should remain unchanged. This review acknowledges the taxonomic difficulties associated with the genus *Terrapene.* However, with regards to the Florida Box Turtle, we consider its morphological differences from *T. carolina*, its reported endemism to peninsular Florida, and its agreed divergence of millions of years from *carolina* to suffice as authentication of its status. Therefore from here on we use the binomial *Terrapene bauri* when referring to this species as have other recent authors (see Anderson & Boughton, 2018; Dodd et al., 2012; Iverson et al., 2012).

Despite their complicated and disputed phylogeny, Box Turtles have historically been referred to as a common species for the eastern United States including Florida (Dodd & Franz, 1993). However, they are now considered in decline due to a combination of biological and environmental factors. These include a long lifespan with delayed sexual maturity and low fecundity (Erb, 2012) in conjunction with habitat loss, fragmentation, fatality on roads, pet trade collection, and disease (Kimble et al., 2014). Dodd and Franz (1993) commented on the need for long-term research in Florida on the biology of *T. bauri* where data is lacking for management decisions and determining population declines. This review will address known natural history characteristics, population status, and conservation issues for Box Turtles in the genus *Terrapene* with a particular emphasis on *T. bauri* and its ecology within the state of Florida.

Identification

Morphological features can be distinguishing factors for North American subspecies of Box Turtles (Farrell et al., 2006). Attributes often used are carapace and plastron color, patterning, size and shape; extent of concavity of the male plastron; eye, head, neck, and leg coloration/pattern; and the number of hind toes (Butler et al., 2011). Box turtle size ranges from a straight carapace length (CL) of 115mm to over 200mm for *triunguis* and *major* respectively with averages below 160mm for most other subspecies (Farrell et al., 2006; Kiester & Willey, 2015). Sexual dimorphism in the Florida Box Turtle was examined by Ernst et al. 1998 in a total of 101 individuals with a 127mm mean CL for females and a larger body size for males at 137mm mean CL. The carapace of *T. bauri* (Figure 2.1) is dark brown to black with yellow radiating lines and variable flaring of the rear marginal scutes (Dodd, 2001; Farrell et al., 2006). The skin is dark and also marked with yellow including stripes on the head (Dodd, 2001). Both sexes of Florida Box Turtles exhibit the same bright coloration, a trait usually present in *Terrapene* males (Kiester &Willey, 2015). In addition, *bauri* males often have brown eyes similar to females instead of typical red as in other subspecies (Dodd, 2001).

Geographic Distribution and Habitat Associations

The distribution of the Eastern Box Turtle spans the length of the eastern seaboard from New England down to the Florida Keys, further south to the Mexican states of Yucatán, Quintana Roo, Campeche, San Luis Potosi, Tamaulipas, and Vera Cruz, and west to Michigan, eastern Kansas, Oklahoma, and Texas (Ernst & Lovich, 2009; Farrell et al., 2006; Platt et al., 2010). Although generally considered a woodland species, habitat use varies across their wide range and differs even further in the subtropical climate of Florida. *T. bauri* has been researched in west central Florida in grassy, sea oat meadows and palm-pepper forests on Egmont Key, Hillsborough County (Dodd et al., 1994; Langtimm et al., 1996) and eastern Florida in the mesic forests and palm-oak hammocks of the Volusia County floodplains (Pilgrim et al., 1997). Populations were recorded in the lower Florida Keys within fire adapted pine rockland forests on Big Pine Key, Monroe County (Platt et al., 2010; Verdon & Donnelly, 2005). Recently, *T. bauri* have been reported in southwestern Florida in mangrove and tropical hardwood hammocks on shell work islands within the Ten Thousand Islands National Wildlife Refuge, Collier County (Jones et al., 2016). In the north and throughout the panhandle where intergradation occurs between *bauri*, *carolina* and *major* (Minx, 1996) as well as *triunguis*, distribution descriptions remain muddled and need additional research (Farrell et al., 2006).

Diet

Eastern Box Turtles occupy an omnivorous niche as their dietary strategy. They eat seasonally available vegetation including berries, fruits, mushrooms, mosses, as well as the buds, roots, stems, and leaves of plants (Dodd, 2001; Stone & Moll, 2006). Invertebrate prey is a staple food resource, and they pursue earthworms, all insect life stages, snails and slugs (Dodd, 2001). Carrion, small mammals, and birds may also be consumed (Kiester & Willey, 2015). Florida Box Turtles have been observed group feeding on the ripened fruits of *Coccoloba uvifera* L. (sea grape) and *Opunita sp.* (cactus), in addition to foraging cockroaches on Egmont Key, FL (Dodd et al., 1994; Farrell et al., 2006). Platt et al. (2009) predominately found 92.8% gastropods (snails and slugs) in the diet of Florida Box Turtles on Big Pine Key, FL. They also found seeds of fruits from *Byrsonima lucida* (Mill.) DC. (Long Key Locustberry), *Mosiera longipes* (O. Berg) Small (Mangroveberry), and *Thrinax morrisii* H. Wendl. (Key Thatch Palm), which are readily available in the pine rockland forests on National Key Deer Wildlife Refuge. Given their preference for fleshy fruits, Florida Box Turtles may serve a valuable function as seed dispersers (Farrell et al., 2006) and aid in germination of some plants as seeds pass through the digestive tract and become distributed throughout the turtle's range (Lui et al., 2004). Figure 2.2 is a photograph of a female Florida Box Turtle feeding on *Opunita* (L.) Mill (prickly-pear cactus) fruits in the hardwood hammock forests of the Ten Thousand Islands during the long-term assessment between American Turtle Observatory and the U.S. Fish & Wildlife Service (Jones & Willey, 2017).

Home Range

Box turtles move throughout a home range for biological and environmental purposes such as seasonal habitat changes and food availability, reproduction and nesting, thermoregulation and hibernation (Iglay et al., 2007). Home range size estimates for *Terrepene* may differ geographically between subspecies and habitat types. The minimum convex polygon method (MCP) is a common reporting standard for individual home range. MCP sizes from 0.22 ha to 187.6 ha for the Eastern Box Turtle have been observed (Kiester & Willey, 2015). Kernel density estimation (KDE) is another method for reporting home range. Box Turtles have a reported mean KDE of 5.3 ha in Illinois (Baker, 2009; n = 24), 2.26 ha in Tennessee (Donaldson & Echternacht, 2005; n=13), and 2.08 ha in Georgia (Greenspan et al., 2015; n=23). The use of different tracking methods (i.e., mark recapture, thread-trailing, radio-telemetry), different home range calculators, and the varying number of individuals and lengths of time tracked by various authors produces a wide range of results and complicates their comparisons (Dodd, 2001). A number of home range calculators have been created for use with Geographic Information Systems (GIS) such as Hawth's Tools (Beyer, 2004), Geospatial Modelling Environment (GME) (Beyer, 2010), ArcMET Movement Ecology Tools (Wall, 2014), Home Range Tools (HRT) (Rodgers et al., 2015) as well as the AdehabitatHR package for use with the open-source software Program R (Calenge, 2006). Although software developments such as these are considered advancements in the study of movement ecology, their methods in estimation vary (Laver & Kelly, 2008). Also, home range software are often not maintained to coincide with updated versions of GIS software such as the Animal Movements for ArcView extension (Hooge & Eichenlaub, 1997). This makes them unavailable for future authors to use as a reproducible standard.

There are currently only two reports on Florida Box Turtle movement and home range. *T. bauri* radio-tracked on Big Pine Key, FL (n=11) for one year had an observed mean home range size of 1.4 ha for MCP and 1.8 ha for 95% Kernel Area using the Animal Movements extension (Verdon, 2004). Season affected mean daily movement, with greater travel during the wet season (30.2 m per day) and less travel during the dry (season 9.2 m per day) (Verdon, 2004). A thread-trailing study by Jennings (2003) for juvenile Florida Box Turtles on Egmont Key, FL (n =58) found turtles had a mean distance traveled of 60.3 m in a 24-hr period and ranged from 0 – 200.5m at the largest movement. Most studies for *Terrapene carolina* do not show sex as a significant difference for home range size between males and females (Aall, 2011; Baker, 2009; Cook, 2004; Kapfer et al., 2013; Stickel, 1950; Verdon, 2004).

Reproduction

Documentation on the reproductive and nesting behaviors of Eastern Box Turtles is accessible throughout its range. Cahn and Conder (1932) and Evans (1953) provided detailed observations on mating and courtship phases. Mating can occur during periods of seasonal activity between March and October (Farrell et al., 2006). *T. bauri* females presented gravid with calcified eggs from late March through early August upon radiograph (Dodd, 1997). As with most Box Turtles, *T. bauri* copulate terrestrially however, the subspecies *T. c. major* maintains an aquatic mating habit (Kiester & Willey, 2015).

T. c. carolina nesting activities take place in the evening, often concurrent with rainfall events. Nests are constructed in open area sites for thermal exposure with bare, sandy soils for ease of digging (Burke & Capitano, 2011; Flitz & Mullin, 2006; Willey & Sievert, 2012; Wilson & Ernst, 2005). The nest site location is an important factor because predation and flooding can impact success and temperature affects how the eggs develop as well as the sex, size, and growth of the hatchlings (Dodd, 2001; Flitz & Mullin, 2006). Cooler nest chamber temperatures have been found to produce more male Box Turtles whereas warmer temperatures result in females (Erb, 2012; Ewert & Nelson, 1991). Female Box Turtles therefore may choose to migrate out of their home range in search of favorable nesting conditions (Stickle, 1950). For *T. bauri*, the extreme environmental temperatures of Florida may influence the nesting behavior of females. Dodd et al. (2012) reported male biased sex ratios for *T. bauri* on Egmont Key. Though nest site observations were rare (n=1 in 16 years), they suggested *bauri* females behaviorally select for the cool, moist soil layers of forest interiors rather than the hot sand of open areas which can reach temperatures up to 50°C (122°F). Thus they may produce more males.

Average clutch size and frequency vary across subspecies and range from 1 to 10 eggs (Kiester & Willey, 2015). Box turtles in northern latitudes tend to have larger less frequent clutches whereas southern Box Turtles may have multiple smaller clutches per season (Burke & Capitano, 2011; Dodd, 2001; Willey & Sievert, 2012; Wilson & Ernst, 2005). Dodd (1997) found *T. bauri* on Egmont Key, FL lay 1-3 clutches per year with an average clutch size of 2.4 eggs. Individual females varied in their clutch number between seasons and may not reproduce consecutively each year. Dodd speculates that food resources are a limiting factor in these variations. Increases in reproduction appear to correlate with an abundance of fruit and invertebrates after rainy winters on Egmont Key. There are currently no published data on the reproductive ecology of Florida Box Turtles in the Ten Thousand Islands region.

Population status

Mark-recapture studies using mathematical models are a common method to assess Box Turtle populations. This technique involves marking a number of individuals for recapture at regular time intervals to record the number of marked vs. unmarked in the population. Statistical programs are then used to estimate population size (Dodd, 2001). Population densities for *T. bauri* in Florida have been calculated at 14.9 turtles/ha on Egmont Key (Langtimm et al., 1996), 16.3 turtles/ha in central Florida (Pilgrim et al., 1997), and 4.8 to 10.2 turtles/ha on Big Pine Key (Verdon & Donnelly, 2005). Most recently, Jones et al. (2016) estimated 2.7–12.2 turtles/ha on four different shell work islands in the Ten Thousand Islands region. Population densities of Box Turtles may remain high where their habitat is unchanged by human development (Kiester & Willey, 2015). However with lack of long-term data for Florida populations (Dodd & Franz, 1993; Verdon & Donnelly, 2005), there is a need for continued research on *bauri* densities and the influence of environmental stressors on its future stability.

Conservation

Terrapene carolina is currently listed as Vulnerable on the IUCN Red List (van Dijk, 2011). Anthropogenic disturbance is a leading cause for Box Turtle decline throughout its range. Humans affect Box Turtle populations through the destruction of habitat for urban development and the building of roads that fragment populations and carry mortality dangers (Budischak et al., 2006). Large landscape changes to natural habitats in Florida for growing communities have led to a decrease in forest area by 22% and herbaceous wetlands by 55%. These are both valuable habitats for Box Turtles (Farrell et al., 2006). In addition, the unregulated trade of Box Turtles for the pet industry has put a strain on already declining populations. The large exportation of Box Turtles to other countries warranted the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to amend Appendix II to include all *Terrapene* species and require permits for export through the U.S. Fish and Wildlife Service (Kiester & Willey, 2015). Commercial collection and sale of Box Turtles is currently prohibited in Florida and state regulations limit possession to two turtles per person (FWC, 2018). However, small scale illegal collections still occur with uncertainty as to how it influences populations (Dodd et al., 1994).

Though Box Turtles may naturally occur in fire adapted habitats (Platt et al., 2010), mortality due to burns can damage populations as well (Dodd, 2001). Prescribed burns for land management should incorporate considerations for Box Turtles such as the severity of the initial burn, the subsequent reduction in ground cover and humidity that Box Turtles require, as well as the reduction in fruiting plants and invertebrates as food resources (Dodd et al., 1994). Incorporating seasonality into management plans may help reduce the negative effects of fire. In winter on Egmont Key, Box Turtles burrow below the surface during colder temperatures making it a preferred time period for controlled burns in small sections. Alternatively, burning in the wet season in the pine rocklands of Big Pine Key was reported as less of a threat to Box Turtles (Farrell et al., 2006).

Florida's government and private conservation lands support a number of potentially viable populations of Florida Box Turtles (Farrell et al., 2006) creating possibilities for its future conservation and research. Dodd and Franz (1993) outline the necessity for proactive, comprehensive monitoring of herpetofauna in Florida rather than fixating solely on endangered species. They suggest a pitfall for many "common" species is that they are often not even considered for management until they become threatened themselves. Reactive approaches such as this may miss signals of irreversible population declines that only long-term research can provide. Areas of strategic direction beneficial to the preservation of *T. bauri* include increasing published data on population dynamics and life history; monitoring the effects of collection on present status; active law enforcement; habitat protection; and redefining land management practices to include conservation based planning.

Conclusion

Though several studies have examined the ecology of various populations of *T. bauri* throughout Florida, few have contributed to the knowledge of home range and habitat use with advanced techniques such a radio-telemetry especially within the mangrove ecosystems of southwestern Florida. Data focused on the biology of *Terrapene* Box Turtle populations in this extreme subtropical range limit are also lacking. Further investigation into these topics would therefore assist in understanding the species which in turn could be used to guide conservation efforts in southern Florida.

Figures

Figure 2.1. Photographs of *Terrapene bauri* male #193 denoting body and shell characteristics. Reprinted with permission. Photo © American Turtle Observatory, March 2016 (Jones & Willey, 2017).

Figure 2.2. Photograph of a female *Terrapene bauri* feeding on *Opunita stricta* (prickly-pear cactus) fruit in the tropical hardwood hammock forests of the Ten Thousand Islands, Florida. Reprinted with permission. Photo © Mike Jones, American Turtle Observatory, November 2015 (Jones & Willey, 2017).

CHAPTER 3: HOME RANGE AND HABITAT USE OF FLORIDA BOX TURTLES (*Terrapene bauri*) IN SOUTHWESTERN FLORIDA

Abstract

We used radio telemetry to assess the home range size and habitat use of *Terrapene bauri* (Florida Box Turtle) on an anthropogenic, shell-work island in southwestern Florida from 2016–2017. Few studies have examined Box Turtles in this mangrove-dominated region. Home range calculated as 100% minimum convex polygons ranged from 0.29-1.52 ha with an average of 0.81 ha, which is consistent with but smaller than other parts of their range. Box Turtles were most commonly located in tropical hardwood hammock forests (53%). Other habitat use included shrub-scrub-cactus (29%), mangrove forest (13%) and shell barren (6%). Males and females did not differ significantly in movement or habitat use though variation among individuals was observed. Habitat associations in this subtropical southern range are important information given the anticipated transitions of Florida's habitats due to global climate change. As temperature and sea level rises, Box Turtles face considerable vulnerability to loss of habitat and being driven further to their thermal limits, which may affect their ability to survive at this extreme latitudinal extent.

Introduction

Understanding the ecology of a species and what drives their choices in habitat can provide strong support for conservation efforts (Rasmussen & Litzgus, 2010). The study of home range has proven beneficial in answering questions involving space use and conservation planning as it refers to the area most used by an individual to perform vital biological functions (Burt, 1943; Litzgus & Mousseau, 2004). For *Terrapene* (North American Box Turtles), important activities such as foraging, sleeping, nesting, and thermoregulating are markedly related to habitat resources (Dodd, 2001). Box Turtles are known to exhibit home range behavior and as a result of their extensive geographic range they have been associated with a variety of environments from mesic woodlands to grasslands to semi-arid deserts (Dodd, 2001; Donaldson & Echternacht, 2005; Greenspan et al., 2015; Iglay et al., 2007; Kapfer et al., 2013; Nieuwolt, 1996, Refsnider et al., 2012; Stickel, 1950). Habitat quality can differ regionally and may influence the size of movements in Box Turtle populations as they explore space and resources to meet their needs. Therefore evaluating home range throughout all regions and habitat types where Box Turtles occur can be informative for their management (Farrell et al, 2006; Greenspan et al., 2015; Stickel, 1989).

Terrapene bauri Taylor (Florida Box Turtle) is a terrestrial turtle restricted to peninsular Florida and the Keys (Ernst & Lovich, 2009). Various studies on Florida Box Turtles have reported information on population size, clutch size, activity, diet, and habitat use primarily within the grassy, sea oat meadows and palm-pepper forests on Egmont Key in Hillsborough County, the pine rockland habitats of Big Pine Key in Monroe County, and mesic hammocks in Volusia County (Dodd, 1997, 1998; Dodd et al., 1994; Jennings, 2007; Langtimm et al., 1996; Pilgrim et al., 1997; Platt et al., 2009; Platt et al., 2010; Verdon & Donnelly, 2005). However, few data are available quantifying the movement and home range size of *T. bauri* in Florida which is essential information for understanding its natural history. Even rarer are accounts of their association with subtropical mangrove ecosystems (Farrell et al., 2006; Jones et al., 2016; Verdon, 2004).

We therefore sought to examine Florida Box Turtles in southwestern Florida within the Ten Thousand Islands National Wildlife Refuge (TTINWR) in Collier County, a region defined by an extensive formation of mangrove islands. We used radio-telemetry to describe the home range size of adult *T. bauri* and to summarize how their habitat selection may differ in a subtropical mangrove-dominated environment. Given that the genus *Terrapene* is generally associated with temperate regions, its spatial ecology and habitat requirements at the southern extent of its range are both interesting and also exceedingly relevant to any management strategy that may be developed for the conservation of its populations.

Field Site Description

The TTINWR is comprised of approximately 35,000 acres of expansive estuaries, mangroves, and marshes located within Collier County, Florida (25.84° N, 81.54° W, Figure 3.1). The refuge provides vital habitat for many species of wildlife and plants and a variety of public recreational activities. The study was conducted on a shell-work island located within the refuge. Exact site location has been withheld due to poaching and conservation concerns.

Currently uninhabited, the island bears unique historical origins as a major shell-work site constructed by the indigenous Calusa between about 1,900 to 900 ybp (Schwadron, 2010). The non-agricultural Calusa monopolized the rich coastal food resources in south Florida and constructed immense settlements from molluscan by-products such as *Crassostrea* spp. (Oysters), *Melongena* spp. (Crown conchs), and *Busycon* spp. (Whelks) shells (Hutchinson et al., 2016; Marquardt, 2004, 2010; Schwadron, 2010; Thompson et al., 2016). The prehistoric shell-work site has an area of approximately 30 hectares that was constructed gradually in phases for both human occupation and societal functions (Schwadron, 2010). Exposed shell substrate or shell barren habitat is still currently present. Coastal hardwood hammock dominates the upland areas of the island. Forest canopies are composed primarily of tropical hardwood species such as

Ficus aurea Nutt. (Strangler fig) and *Bursera simaruba* L. Sarg. (Gumbo limbo). Dense thickets of *Acanthocereus tetragonus* L. Hummelink (Barb-wire) and *Opuntia* spp. (Prickly-pear) cacti as well as *Agave* L. (Agave) occur throughout the island in shrub and ground cover. In addition, mangrove forests dominated by *Rhizophora mangle* L. (Red mangrove), *Avicennia germinans* (L.) L. (Black mangrove), and *Laguncularia racemose* (L.) Gaertn. f. (White mangrove) encompass the perimeter of the island and are present within the recessed inland areas (FNAI, 2010; Jones et al., 2016; Wilder & Barry, 2010). Climate in south Florida is characterized as subtropical with seasonal precipitation differences that distinguish a wet season from May to October and a dry season from November to April (Verdon & Donnelly, 2005). Average annual precipitation ranges from 119–157 cm with 60% of total rainfall occurring in the wet season (Obeysekera et al., 1999).

Methods

Radio-telemetry

Florida Box Turtles were opportunistically captured by hand through visual surveys during a long-term population assessment to determine species distribution and ecology (Jones et al., 2016). In March 2016, a subset of turtles were outfitted with a 12 gram (g) radio-transmitter (R2020, Advanced Telemetry Systems) on their posterior carapace using water weld plumbing epoxy (Figure 3.2). Transmitters weighed < 5 % of the turtle's body mass. Each turtle was assigned a unique number according to the system of Ernst et al. (1974) that was notched into their marginal shell scutes with a triangular file (Cagle, 1939) for future identification. We recorded morphological characteristics during initial capture (e.g., sex and body mass measured to the nearest g using a spring loaded scale [2500 g Medio Line scale; Pesola, Barr, Switzerland]). Body size measurements (mm) were taken using dial calipers (straight carapace length, straight plastron length, plastron width at the hinge, carapace width at the 8th marginal scute, and carapace height at the highest point; Jones & Willey, 2017). Turtles were handled for no more than 15 minutes and released in the location they were captured. We located each turtle using a 148 -174 MHz telemetry receiver (R1000, Communications Specialists Inc.) approximately one day per week from March 2016 through October 2016 and once opportunistically in March 2017 prior to removal of the radio-transmitters. Tracking reflected U.S. Fish and Wildlife Service (USFWS) technician availability. At each turtle radio location, we recorded date, time, identification number, turtle activity, air temperature (°C) and relative humidity (inHg) using a hand-held kestrel unit. Locations were collected using either a Garmin hand held GPS unit (Model Etrex, Garmin International Inc., Olathe, Kansas) with +/- 5 m accuracy or a Trimble hand held GPS unit (Model Juno Series, Trimble Navigation Limited, Westminster, Colorado) with +/- 2 m accuracy. Habitat parameters such as dominant species and percent cover were estimated for canopy, shrub and herbaceous layers within 5m of the telemetry location. Dominant canopy was classified as tropical hardwood hammock forest, mangrove forest, shrub-scrub-cactus, or exposed shell barren. Cactus cover, leaf litter, coarse woody debris, bare shell cover, and bare soil cover within 5m were estimated as low, medium or high. Due to transmitter detachments, two of the turtles (F1052, M193) were not tracked after 10 August 2016 and 23 August 2016 respectively. A single death occurred during the study and therefore turtle F1057 was not tracked after 6 September 2016, leaving a total of seven turtles tracked for the entire time period.

Data Analysis

Home Range and Habitat Use Using Field Assessments

To estimate home range size, we calculated minimum convex polygons (MCP) and fixed kernel density estimators (KDE) for each radio-tagged turtle based on its telemetry points (Appendix B and C). The MCP estimates an animal's area of range based on the connection of peripheral location points (Mohr, 1947) and is commonly used in home range studies for its uniform methodology (Worton, 1987). However, MCPs may encompass unused areas and are biased toward larger sizes. Therefore they may lack details of areas and resources that individuals are selecting for (Litzgus & Mousseau, 2004; Worton, 1985). In contrast, the KDE creates a density estimate through relocation data based on an animal's use of an area (Seaman et al., 1999). This is considered a more accurate representation for an individual's home range. One complication to KDE is the element of user choice in selecting the appropriate bandwidth smoothing factor (h). This choice can considerably impact KDE estimates (Laver & Kelly, 2008; Worton, 1989), creating the potential for inconsistencies that have been reported to affect the accuracy of determining home range in herpetofauna (Row & Blouin-Demers, 2006). In addition, deficient reporting of methods by authors (Laver & Kelly, 2008) and the use of outdated home range software extensions for Geographic Information Systems (GIS) (e.g., Animal Movements for ArcView extension, Hooge & Eichenlaub, 1997; Hawth's Tools, Beyer, 2004; Home Range Tools, Rodgers et al., 2015) challenge the possibility of reproducible standards. Though most recent studies use 95% MCP, we used 100% MCP to estimate each Box Turtle's total home range and to focus our discussions as we credit any outlying movements and habitat use that may be females nesting or males mate searching to be biologically important.

However we also report 95% MCP and KDE at the 95% and 50% contours in efforts to offer comparability with other studies that may use similar estimators and methods to our study.

Location data were also used to evaluate each individual for movement patterns and habitat associations during the study period. The straight line distance between two successive turtle relocations was calculated in Excel to determine the distance since last location in meters (DSLL). Daily movement distances (DPD) were calculated by dividing the DSLL by the number of days between relocations. Distances were averaged by individual, sex, and across all turtles to determine patterns. Habitat use was summarized by calculating the percentage of dominant cover types recorded within 5m at all turtle locations.

All home range calculations and statistical analyses were conducted using RStudio (version 1.1.447) and Program R (version 3.4.4) (R core team, 2018). The level of significance for all tests was set to $\alpha = 0.05$. Home range calculation required projected x,y coordinates therefore turtle locations were converted from decimal degrees to the projected coordinate system NAD 1983 UTM Zone 17N in ArcMap 10.5.1 (ESRI, Redlands, CA), which corresponded to the data layer used in the habitat analysis. Locations were then exported to Excel and loaded into RStudio as spatial points. Home range calculations were conducted using the functions mcp and kernelUD in the adehabitatHR package (Calenge, 2006). The smoothing parameter (h) was calculated for kernel estimations using both the reference default (href) and also a specified h value of 46.15m (the mean distance since last location [DSLL]), which represented a biologically significant value for the turtles at our study site. Least Squares Cross Validation (LSCV) was not utilized due to its sensitivity to sample size and recommendation of $\geq$ 50 observations per individual (Seaman et al., 1999). Home ranges were exported as shapefiles for GIS analysis using the writeOGR function. Home range and movement data were evaluated for normality using histograms, boxplots, q-q Plots and the Shapiro-Wilk test (function shapiro.test). Welch's two sample t-tests (function welch.test) were used to compare male and female home range sizes with unequal variances. A correlation test (function cor.test) was run to evaluate the relationship between body size and home range size using straight carapace length measurements. Due to the small sample sizes, a Fisher's Exact test (function fisher.test) was conducted to determine if habitat associations between males and females were significantly different from each other. Results were further evaluated using mosaic plots.

Home Range Composition and Habitat Use using Geographic Information Systems (GIS)

All Box Turtle locations and 100% MCPs were imported into ArcMap for habitat use analysis. We defined the study area as a 37 ha polygon around the island's boundary, hand digitized from a high resolution 2-foot orthophotography image (Florida Department of Environmental Protection, 2015). Peripheral mangroves were excluded from the island boundary. The island's area was calculated using ArcMap tools. Habitat cover type was evaluated using the existing TTINWR Vegetation Types data layer as prepared in Barry (2009) for the USFWS. Habitat types were reclassified based on field data and orthophotography interpretation to account for discrepancies with the data layer and also to group by analogous habitat classes. Reclassifications were based on descriptions from the Data Summary of Working Vegetation Maps of the Ten Thousand Islands National Wildlife Refuge report (Barry, 2009) as well as the correlated USGS Vegetation Classification for South Florida Natural Areas report (Rutchey et al., 2006; Appendix E). Due to the small patch sizes of ecotones, GPS location error, and the differences between the field observations, the data layer and aerial photo perspective, the shrub-scrub-cactus habitat class observed in field was unable to be reclassified effectively remotely. This resulted in the loss of the scrub habitat type for GIS analysis. Therefore, habitats were grouped into the following three classes: Tropical Hardwood Hammock, Mangrove, and Shell. We used the *Dissolve Tool* to generate continuous polygons of each habitat class. We then calculated the area of each habitat type within the island boundary and each turtle MCP using the *Tabulate Area* tool to determine habitat composition. In addition, the *Extract Multi Values to Points* tool was used to determine the habitat class of each turtle relocation point in order to evaluate habitat use. Results were exported to Excel for analysis.

Results

Home Range and Habitat Use using Field Assessments

We tracked 10 adult Florida Box Turtles (5 males and 5 females) with a total of 287 relocations to determine home range sizes. The number of locations per turtle ranged from 23 to 31 (average = 28.6). The individuals with < 30 locations (loss of transmitter n=2, death n=1) were excluded from mean calculations. Average 100% MCP for Florida Box Turtles on the island was estimated as 0.81 ha (range: 0.29 ha –1.52 ha, n = 7, Table 3.1). Home range sizes of males (MCP: 0.39 – 1.52 ha, n = 4) were similar to females (MCP: 0.29 – 1.35 ha, n = 3). There were no significant differences between the sexes ($P = 0.6256$, $t = -0.5$, $df = 4.0$). There were no significant correlations between body size and home range size ($P = 0.8776$, $t = 0.16$, $df = 5$). Overlap in home range occurred both between and among the sexes (Appendix B). The average distance Box Turtles traveled between locations was 46.15 m (range = 33.3 m to 66.1 m, Table 3.1). Average distances traveled per day was 6.3 m (range = 4.3 m to 9.3 m). See Chapter 4 for further details and correlations on movement.

Of the 287 Box Turtle relocations, 53% of all habitat use was associated with hardwood hammock (n=151) and 29% with shrub-scrub-cactus (n=82). Mangrove forest (13%, n=38) and shell barren habitat (6%, n=16) were also utilized (Figure 3.3). Habitat use did not differ significantly between the sexes (P = 0.5, Chisq = 2.3, Figure 3.4). Dominant plant species observed for canopy, shrub, and herbaceous layers can be found in Appendix D.

Home Range Composition and Habitat Use using GIS

After ground-truthing with aerial imagery and field data, the following classes from the TTINWR Vegetation Types data layer were grouped as tropical hardwood hammock: Tropical Hardwood Shell Mound (FHM), buttonwood woodland - succulent mound (WMcSM), and human impacted mound (HIM). The mangrove forest habitat included: mixed mangrove forest (FMX), black and red mangrove (FMXar), buttonwood-red mangrove (FMXcr), white and red mangrove (FMXlr), black mangrove forest (FMa), buttonwood forest (FMc), red mangrove forest (FMr), mud (MUD), and open water (OW). Shell barren habitat included upland woodland mound (WUM). Open water was grouped with mangrove to account for a single telemetry location event within the boundary of the two habitat classes in the data layer. Mud and human impacted mound were grouped based on their spatial locations within mangrove and hammock habitats respectively. In addition, upland woodland mangrove was reclassified as shell barren based orthophotography comparisons.

Florida Box Turtle home ranges were composed primarily of tropical hardwood hammock habitat with an average of 0.57 ha in their MCP's (n=7, Table 3.2), representing an average of 71.9%. The MCPs also averaged 0.10 ha of mangrove forest and 0.14 ha of shell barren habitat (9.6 and 18.4% respectively). The island contained areas of 16.37 ha (43.8%) mangrove, 15.22 ha (40.7%) hammock, and 5.79 ha (15.5%) shell barren. Based on relocation points, Box Turtles on average used 82.3% tropical hardwood hammock, 7% mangrove, and

10.8% shell barren habitats. Hardwood hammock was used more than it was generally available on the island (Figure 3.5).

Discussion

The average home range size we observed for *T. bauri* on the island (0.81 ha) is consistent with literature suggesting adult Box Turtles generally have small home ranges from less than 1 ha to 5 ha (Dodd, 2001). Most studies in the southern United States have examined home range for *Terrapene carolina* L. (Eastern Box Turtle) with reported MCPs of 1.88 ha in Tennessee (Donaldson & Echternacht, 2005), 6.45 ha and 2.68 ha in North Carolina (Hester et al., 2008; Kapfer et al., 2013), and 10.33 ha in Georgia (Greenspan et al., 2015). However, *Terrapene* populations at the extreme southern extent such as *T. bauri* in Florida have received limited attention with regard to home range and movement (but see Farrell et al., 2006; Jennings, 2003; Pilgrim et al., 1997). Verdon (2004) radio-tracked Florida Box Turtles (n=11, 426 captures) in the lower Keys and found an average MCP of 1.4 ha (range 0.26–3.57 ha) and movements of 13.1 m per day in the dry season and 30.0 m in the wet season. By comparison, our results were similar though smaller with *T. bauri* MCPs (n=7) ranging from 0.29–1.52 ha and average movement distances of 6.3 m per day (Table 3.1). However, correlating home range studies among Box Turtles has been regarded as difficult given the many calculation techniques and variation in the habitat types where they are found (Dodd, 2001; Ernst & Lovich, 2009; Keister & Willey, 2015). The relative differences in home range size between our study and Verdon (2004) may be a factor of our smaller sample size, number of relocations, length of time tracked as well as different methods for determining home range and movement (Boyle et al., 2009; Donaldson & Echternacht, 2005; Marchand et al., 2002). There is also a substantial disparity in the size and habitat types of both islands. Although Big Pine Key contains fragmented habitat due to development and residences (Verdon, 2004), the 2,400 ha island is markedly larger than our 30 ha study island and may have more available habitat for Box Turtles potentially allowing larger home ranges. Yet, habitat quality has also proven relevant to the selection of home range (Dodd, 2001; Keister & Willey 2015; Nieuwolt, 1996; Stickel, 1950). The hardwood hammock, scrub, and mangrove habitats at our study site may provide more diverse and favorable conditions for Box Turtles than the xeric pine rocklands at Big Pine Key. This could result in a decreased necessity for movement to locate resources and therefore smaller home ranges. Male and female home range sizes were not found to be significantly different on the island. However, individual variation between Box Turtle home range did occur and this along with small sample sizes has been suggested to influence the significance of results (Kapfer et al., 2013; Verdon, 2004).

Individual variation also occurred in the use of habitat types which is consistent with other studies (Dodd, 2001; Farrell et al., 2006; Frederickson, 2014). Although all Box Turtles in our site used transitional zones between habitat types on the island, some turtles were predominately observed in hardwood hammock, some in shrub-scrub-cactus, and most notably some individuals chose to make use of mangrove forests (Figure 3.3). Given that mangrove habitat use is uncharacteristic for *T. bauri* (Farrell et al., 2006), we consider this a unique observation to our study area and for the species. Though mangroves may be more prevalent in our study area, Verdon (2004) recorded only a single Box Turtle observation in mangrove habitat out of 1884 captures that were primarily in pine rocklands (86.9%). The association of Box Turtles with tropical hardwood hammock is also distinctive as it is a community type endemic to south Florida (Loope & Urban, 1980; Olmstead et al., 1980) and therefore an uncommon occurrence in Box Turtle habitat use within the United States. Rare cacti and agave vegetation are also present on the island and within Box Turtle home ranges (see Figure 3.6 for photographic examples). The underlying shell mound and ancient history of indigenous human occupation further augment these exceptional combinations of habitat associations, making the study site truly a remarkable example of Box Turtle habitat.

Box Turtle use of edge communities is a common documented aspect of their ecology (Keister & Willey, 2015). Movement between different habitat structures allows Box Turtles to access sunlight or shade for thermoregulation, to select for moisture in their microenvironments for desiccation control and also to find food or suitable nesting areas (Converse & Savidge, 2003; Currylow et al., 2013; do Amaral et al., 2002; Ernst & Lovich, 2009; Frederickson, 2014; Reagan, 1974). Our study also found *T. bauri* to behaviorally select for ecotones within their home ranges often having telemetry fixes between the borders of closed canopy forests (hammock and mangrove) and the open habitat classes (scrub and shell barren). These transitional habitat associations posed the most challenging aspect for our GIS habitat analysis due to demarcation issues in the TTINWR Vegetation data layer. The data layer had well defined mangrove boundaries even by tree species based on ground-truthing and GIS analysis in Barry (2009). However, the other habitat classes such as hammock, scrub, and shell lacked such refined delineation, making it difficult to analyze Box Turtle habitat use on the island. Certain classes in the data layer were found to either be assigned codes not previously described in the coordinating Vegetation Classification for South Florida report (Rutchey et al., 2006) or completely lacked classification and delineation all together. For example, options for non-vegetative classes such as mud (MUD) and open water (OW) were present in the reports as descriptors in classification tables (see Barry, 2009; Rutchey et al., 2006; Appendix E). Yet shell mound which is distinguished as a natural community type in Florida (FNAI, 2010) was not assigned a classification code and therefore not present in the data layer. A vegetation class with the acronym WUM (upland woodland mound), previously undescribed by Rutchey et al. (2006), is currently assigned to areas in the data layer where exposed shell barren could clearly be seen in the aerial imagery. We therefore chose to change this code to shell when analyzing turtle habitat use. Additionally, we found the data layer lacked sufficient representation for the shrub-scrub-cactus habitat type we observed. There were many discrepancies with our field data, placing the majority of the points in either hammock or shell habitat. Though hand delineation is an option when dealing with such issues, we believed this could possibly be too arbitrary to be useful for comparisons with other studies. Ultimately, we were compelled to drop the scrub habitat class from the GIS analysis which was unfortunate since it accounted for over a quarter of Box Turtle habitat use according to radio-telemetry field observations (29%, Figure 3.3). While we present quantitative data (Table 3.2) on the habitat composition of *T. bauri* within their home range, we recognize the limitations in the GIS data layer and recommend improvements. The vegetation classification hierarchical scheme in Rutchey et al. (2006) should be updated to reflect the refined descriptions in Barry (2009) for the TTINWR. In addition, line transect surveys with GPS mapping are suggested for the island to further classify the habitat types and authenticate their boundaries in particular for the scrub-cactus habitats and insolated shell barren. Updates could then be performed to the vegetation data layer for future island surveys. Having the ability to adequately describe habitat use based on spatial calculations can have a much more meaningful impact for Box Turtle conservation. For example, based on our results the average 100% MCP of *T. bauri* on the island was comprised of 0.57 ha (1.4 acres) of tropical hardwood hammock. This region in southwestern Florida is dominated by mangrove and few islands contain several acres of upland hardwood hammock. Therefore understanding how much area of this habitat type is necessary to support a Box Turtle home range and population can be useful information for their management. Future field observations should also account for Box Turtle edge habitat use and would benefit from methods that incorporate transition zone measurements in habitat analyses.

Box Turtles commonly occupy mesic woodlands (Dodd, 2001) making the availability of hardwood hammock for *T. bauri* in our study region important. This habitat occurs on slightly elevated uplands and therefore rarely floods, yet it remains moist and cool due to the closed forest canopy structure (USFWS, 2011). The semi-deciduous vegetation also generates an ample layer of leaf litter and soil humus (USFWS, 2011). Several tree species in this habitat type produce fruit as well (Karim & Main, 2004). These characteristics support life history requirements for Box Turtles. They can take refuge from desiccating winds and extreme subtropical temperatures within the microenvironment of tropical hardwood hammocks and also locate food resources. Thus the expected changes and loss of upland forest habitat in southern Florida due to global climate change are of concern. Pearlstine et al. (2010) summarizes the ramifications for habitats in southwestern Florida including the Ten Thousand Islands (TTI) which could incur reduction or complete loss due to sea level rise, drought, increased storm activity as well as the conversion of plant communities from temperature increases, salinity changes, and invasion of exotic vegetation. Island forests rely heavily on precipitation as a freshwater source (Langston et al., 2017), which is then stored in the soil vadose zone (see Saha et al., 2011 and Sternberg et al., 2007 for process descriptions). As sea level rises, soils and groundwater become flooded with sea water and the fresh vadose water decreases. The accumulation of salt and anoxic conditions result in physiological stresses too extreme for tree regeneration and survival (Desantis et al., 2007; Jones & Koptur, 2017; Saha et al., 2011; Ross et al., 1994; Williams et al., 1999). Additionally, the rise in temperature and decrease in rainfall predicted for southern Florida may intensify these effects for vegetation by contributing to soil dryness (Desantis et al., 2007; Pearlstine et al., 2010; Saha et al., 2011). Further, the expected increase of storm intensity may also cause more frequent forest damage by uprooting canopy trees and exposing young undergrowth to storm surged salt water (Langston et al., 2007; Michener et al., 1997). In general, the low lying elevation of Florida increases its susceptibility to the average expected sea level rise (Ross et al., 2016). The risk of full inundation for the lowest shell-work islands in our study region is plausible and larger islands could experience a reduction in the size of upland habitat (Jones et al., 2016). Though climate related changes at the edge of a species range may result in geographical shifts to more habitable environments (Parmesan, 2006), reptiles are often not attributed with movement abilities required for migration (McCallum et al., 2009). As an island population, *T. bauri* at our study site are further restricted by sea water and have even more limitations than other reptiles on the mainland. Additionally, they are functioning close to their physiological tolerances in the subtropical conditions of this extreme southerly range. Therefore hammock habitat loss and accelerated temperature increases in TTI due to climate change may be particularly consequential for Box Turtles because they genuinely lack the opportunity for dispersal and would need to persist in smaller areas with limited resources and less means for thermoregulation. Studies by Dodd et al. (2012) on *T. bauri* at Egmont Key over a 16 year period showed some resilience to large-scale habitat disturbances such as overwash from tropical storms and extensive canopy loss from exotic plant removal. On the larger 180 ha island of Egmont Key, Box Turtles relocated to unaffected areas and were able to maintain population stability provided initial mortality was avoided. However, substantial loss of land from sea level rise would most likely negate such phenomenon for terrestrial turtles.

Continued erosion has already equated to a loss of nearly one half of Egmont Key since the early 1900's (Dodd et al., 2006). The role of mangrove forests as a driver in plant community conversion also poses a question for our study system. Mangroves have the ability to capitalize on sea level rise and warming temperatures. At the northern extent of their range with higher salinity tolerances, mangroves can outcompete other species for expansion which has led to changes in the habitat composition of several coastal Florida areas (Krauss et al., 2011; Langston et al., 2017; Ross et al., 1994; Saha et al., 2011). Though it is relevant that some individual turtles in our study used mangrove forest within their home ranges whether they could solely exist in this habitat structure is yet to be fully understood. Furthermore, mangrove forests can also be sensitive to climate change. Mangroves will succumb to rapid submersion and harsh storm disturbances if canopy damage is extensive and soil surface elevation is not able to be rebuilt (Krauss et al., 2014; Michener et al., 1997; Smith et al., 2009). Due to these complexities in climate research, ultimately only long-term studies documenting the landscape changes of south Florida and subsequent Box Turtle habitat use can assist in answering questions about the future of this unique ecosystem and how Box Turtles populations will respond.

To our knowledge, aside from Verdon's (2004) research at Big Pine Key, our study represents the only other assessment of *T. bauri* using radio-telemetry in southern Florida. This makes our results particularly informative for their life history regarding home range and habitat use in a subtropical region. Given the considerable effects climate change could have on this population and others in Florida, continued monitoring of the movements and habitat associations is recommended not only to determine the ecological requirements of Box Turtles but also to evaluate their level of adaptation or extinction risk in the face of drastic environmental change.

Tables and Figures

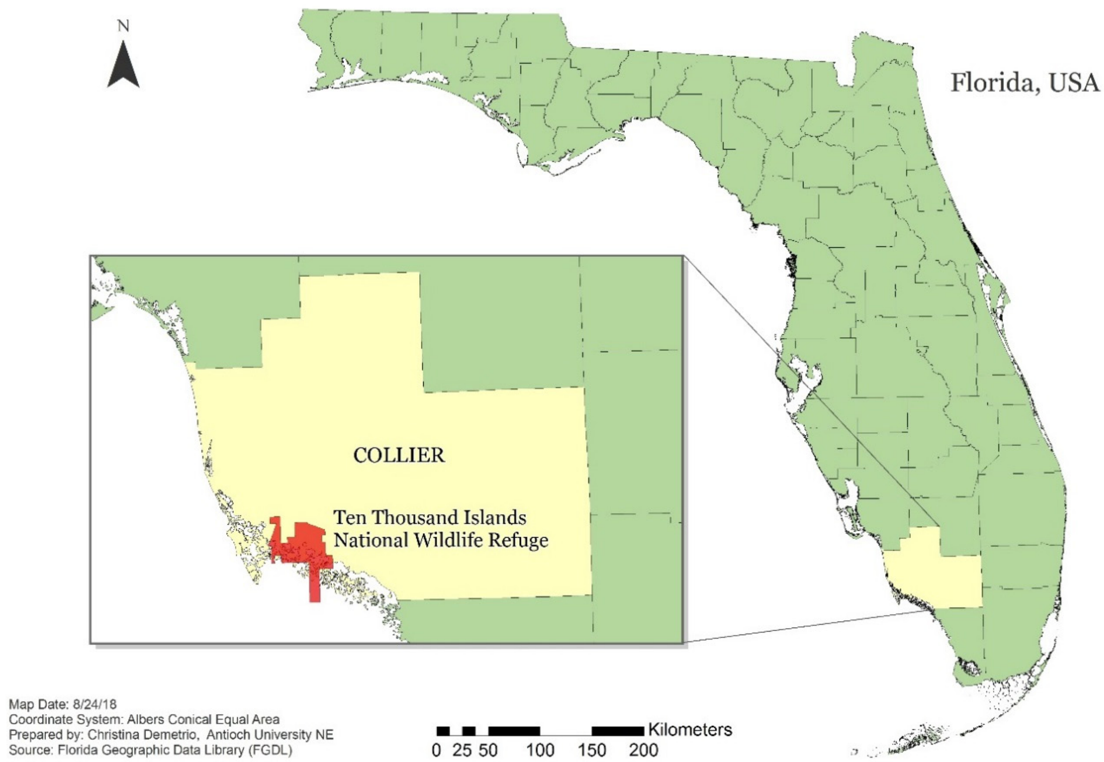

Figure 3.1. Study site for the 2016–2017 *Terrapene bauri* home range assessment located in southwestern Florida within the Ten Thousand Island National Wildlife Refuge, Collier County. Refuge boundaries are delineated in red.

Figure 3.2. Photograph of adult male #1049 Florida Box Turtle with a radio transmitter. Reprinted with permission. Photo © American Turtle Observatory, March 2016 (Jones & Willey, 2017).

Table 3.1. Body mass (g), movement (m), and home range size (ha) for 10 radio-tracked *Terrapene bauri* (Florida Box Turtles) on a shell work island in the Ten Thousand Islands National Wildlife Refuge, Florida, USA, 2016–2017. Movement is represented by average distance per day (DPD) and distance since last location (DSLL). Home range was estimated using minimum convex polygons (95% and 100%) and kernel density (95% and 50% core range). N is the total number of individual turtle locations.

						Minimum convex polygon		KDE (href)		KDE (specified h value)	
Turtle No.	**Sex**	**N**	**Mass (g)**	**DPD**	**DSLL**	**95%**	**100%**	**95%**	**50%**	**95%**	**50%**
1006	F	30	452	8.88	66.12	1.32	1.35	3.50	0.71	6.91	1.53
1009	F	31	441	4.87	34.94	0.28	0.43	1.05	0.23	5.02	1.14
1052[1]	F	23	433	4.38	30.89	0.26	0.35	0.96	0.24	4.86	1.14
1053	F	31	376	4.63	33.97	0.25	0.29	0.78	0.22	4.74	1.11
1057[1]	F	26	383	4.55	31.45	0.51	0.81	1.57	0.28	5.26	1.18
193[1]	M	24	413	2.52	15.86	0.18	0.33	0.70	0.17	4.58	1.06
1034	M	30	546.5	4.32	33.34	0.30	0.39	0.98	0.23	4.89	1.14
1049	M	31	497	5.88	45.99	0.62	1.09	2.45	0.54	6.15	1.45
1054	M	31	486.5	6.16	47.07	0.46	0.64	1.69	0.43	5.49	1.30
1055	M	30	429	9.27	61.61	1.42	1.52	4.04	1.08	7.31	1.83
Mean											
Females				6.13	45.01	0.62	0.69	1.78	0.39	5.56	1.26
Males				6.41	47.00	0.70	0.91	2.29	0.57	5.96	1.43
Total				6.29	46.15	0.66	0.81	2.32	0.49	5.79	1.36

[1] Due to transmitter detachments (193, 1052) and a death (1057), these turtles were not included in the mean calculations.

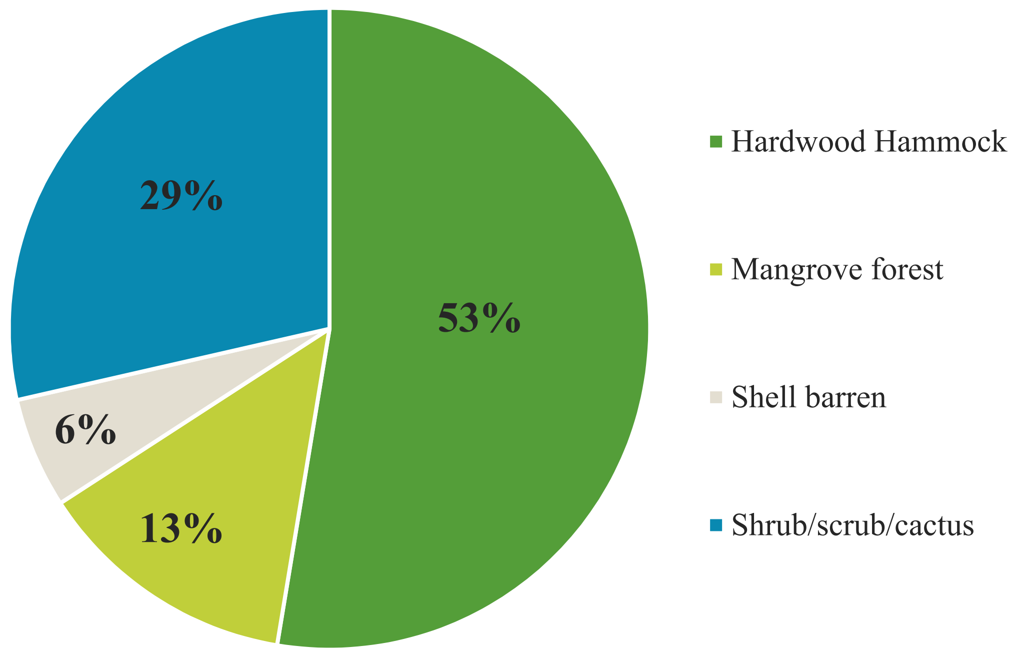

Figure 3.3. Percent dominant cover types within 5m of Florida Box Turtle locations based on field observations during the 2016–2017 study in the Ten Thousand Islands Region, Collier County, FL.

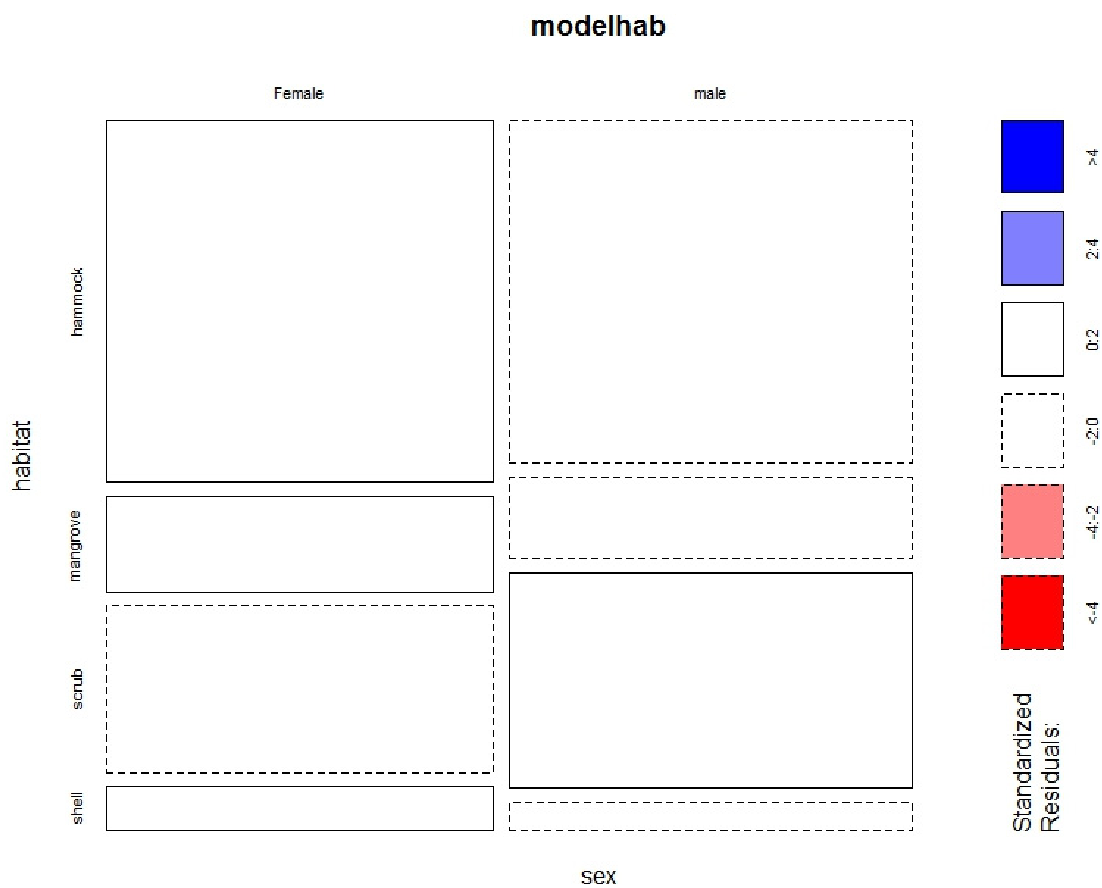

Figure 3.4. Mosaic plots comparing male and female habitat use for 10 radio-tracked Florida Box Turtles. Habitat use did not differ significantly between the sexes.

Table 3.2. Habitat composition of the 100% MCPs created from 10 radio-tracked *Terrapene bauri* on a shell-work island in the Ten Thousand Islands National Wildlife Refuge, Florida, USA, 2016–2017. Habitat areas are calculated in hectares. N is the total number of turtle locations.

			Mangrove		Hammock		Shell barren		
Turtle No.	**Sex**	**N**	**No. locations**	**(ha)**	**No. locations**	**(ha)**	**No. locations**	**(ha)**	**Total (ha)**
1006	F	30	3	0.06	25	1.01	2	0.28	1.35
1009	F	31	0	0.00	29	0.43	2	0.00	0.43
1052[1]	F	23	5	0.08	16	0.27	2	0.00	0.35
1053	F	31	2	0.01	21	0.18	8	0.09	0.29
1057[1]	F	26	5	0.10	11	0.30	10	0.41	0.81
193[1]	M	24	0	0.00	17	0.21	7	0.11	0.33
1034	M	30	0	0.00	26	0.24	4	0.15	0.39
1049	M	31	10	0.63	19	0.36	2	0.09	1.09
1054	M	31	0	0.00	31	0.59	0	0.05	0.64
1055	M	30	0	0.00	25	1.17	5	0.35	1.52
Island				16.37		15.22		5.79	37.37

[1] Due to transmitter detachments (193, 1052) and a death (1057), these turtles were not included in the mean calculations.

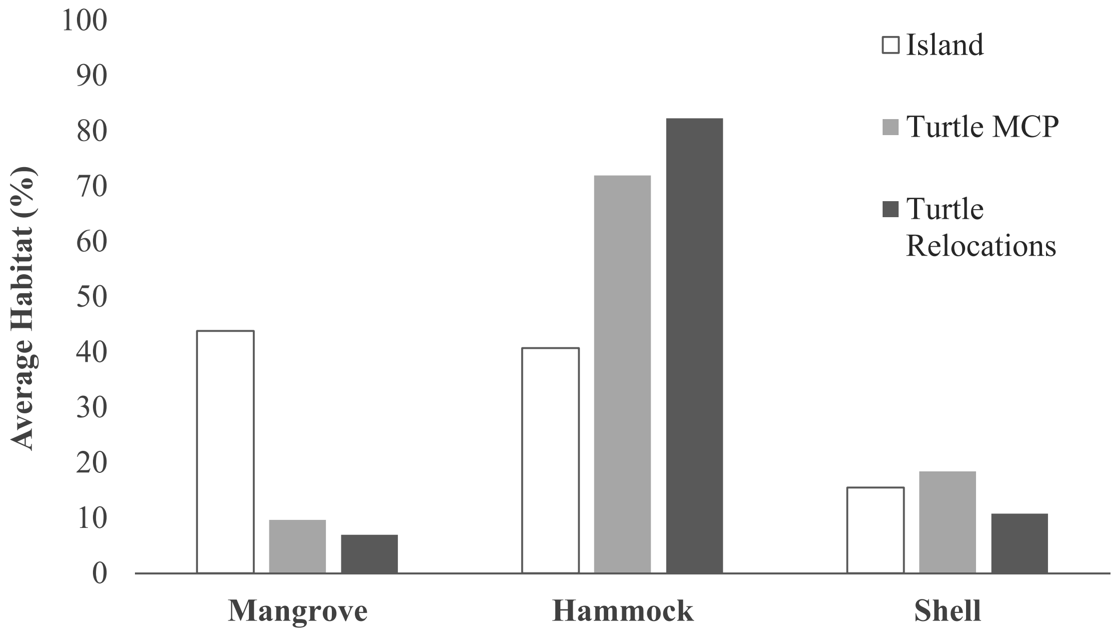

Figure 3.5. Average percent habitat use of Florida Box Turtles in relation to habitat availability on the study island in the Ten Thousand National Wildlife Refuge, FL.

Figure 3.6. Top: Photograph of scrub habitat type on the study island. Bottom: Photograph of Florida Box Turtle with *Agave decipiens* (false sisal or Florida agave) vegetation. Reprinted with permission. Photo © American Turtle Observatory (Jones & Willey, 2017).

CHAPTER 4: NOTES ON THE SEASONAL MOVEMENT, ACTIVITY AND THERMAL ECOLOGY OF FLORIDA BOX TURTLES (*Terrapene bauri)* IN SOUTHWESTERN FLORIDA

Abstract

We studied *Terrapene bauri* (Florida Box Turtles) in southwestern Florida to evaluate their ecology in a subtropical region dominated by mangrove forests. We used radio-telemetry and iButton temperature data loggers to summarize their movements and activity patterns in relation to weather and the extreme thermal characteristics of their environment. Turtles appear to exhibit seasonal behavior with increased activity during the wet season from May to October. Humidity and temperature were both significantly correlated to turtle activity. Average distances traveled per day were 6.3 m and average distances between weekly locations were 46.1 m. Turtle movements significantly increased with precipitation. Turtle carapace temperatures were similar to temperatures recorded in tropical hardwood hammock which is the habitat type where they were most frequently located. Average carapace temperatures were 25.3°C however in this geographic region turtles did experience temperatures close to Box Turtle critical thermal maximums. This locality represents an understudied southern extent of *Terrapene* Box Turtle range, therefore results observed in this study could offer important information about behavior and biological traits previously unrecorded for this species.

Introduction

Thermoregulatory behavior of ectothermic species is often correlated with environmental factors. Turtles in the genus *Terrapene*, like many other reptiles, exhibit variation in activity levels and undertake movements to microenvironments coinciding with changes in temperature, humidity, and precipitation (Nieuwolt, 1996; Parlin et al., 2018; Plummer, 2003; Rossell et al., 2006; Tucker et al., 2015). In the temperate zones of the northern United States, Box Turtles demonstrate dormancy in winter and seasonal activity during warmer periods (DeGregorio et al., 2017; Dodd, 2001). Seasonal rainfall stimulates activity of Box Turtles in Mexico and Arizona that may otherwise be in burrows or forms during the intense dry seasons (Buskirk, 1993; Dodd, 2001; Plummer, 2003). Burrowing in leaf litter or soil "forms" is a common thermoregulatory behavior turtles utilize to endure extreme conditions (Stickel, 1950). During high temperatures or drought, turtles may also soak in shallow water (Donaldson & Echternacht, 2005).

Terrapene bauri Taylor (Florida Box Turtle) is a terrestrial turtle that ranges throughout Florida (Farrell et al., 2006). Studies in central Florida have examined *T. bauri* in environments appreciably different than in the southern part of the state (Dodd, 1994, 1997, 2001; Dodd et al., 1997; Jennings, 2003, 2007; Langtimm et al., 1996; Pilgrim et al., 1997; Verdon, 2004). Areas in north Florida are considered warm-temperate evergreen forests with intermixed deciduous trees. The central regions are characterized by drier pine-oak-palmetto scrub vegetation types (Box et al., 1993). In south Florida however, latitude and meteorological regimes create a climate distinctly more subtropical than in central and northern Florida with a pronounced wet and dry seasonal variation in rainfall (Obeysekera et al., 1999; Verdon, 2004). In the southernmost study at Big Pine Key in the Florida Keys, Verdon (2004) observed *T. bauri* to have seasonal ecology with increased behavior occurring in the wet season. Although additional studies have been conducted in the xeric pine rocklands of the lower Keys (Liu et al., 2004; Platt et al., 2010; Verdon & Donnelly, 2005), few have assessed the behavior of Box Turtles in the south Florida peninsula where they occur in subtropical hammock and mangrove forests (Jones et al., 2016).

We conducted a radio-telemetry study in the Ten Thousand Islands National Wildlife Refuge (TTINWR) in southwestern Florida with the goal of examining Box Turtles near their southern range limit. We gathered new information on *T. bauri* in a complex estuarine mangrove ecosystem. In this current note, we summarize the movement, activity, and thermal ecology observed, comment on how season, sex, and weather influenced their behavior, and discuss the possible effects of climate on their biology and conservation.

Field Site Description

The TTINWR is comprised of approximately 35,000 acres of expansive estuaries, mangroves, and marshes located within Collier County, Florida (Figure 4.1). The refuge provides vital habitat for many species of wildlife and plants and a variety of public recreational activities. The study area was a shell-work island located within the refuge. Exact site location has been withheld due to poaching and conservation concerns.

Currently uninhabited, the island bears unique historical origins as a major shell-work site constructed by the indigenous Calusa between about 1,900 to 900 ybp (Schwadron, 2010). The non-agricultural Calusa monopolized the rich coastal food resources in south Florida and constructed immense settlements from molluscan by-products such as *Crassostrea* spp. (Oysters), *Melongena* spp. (Crown conchs), and *Busycon* spp. (Whelks) shells (Hutchinson et al., 2016; Marquardt, 2004, 2010; Schwadron, 2010; Thompson et al., 2016). The prehistoric shell-work site has an area of approximately 30 hectares that was constructed gradually in phases for both human occupation and societal functions (Schwadron, 2010). Exposed shell substrate or shell barren habitat is still currently present. Coastal hardwood hammock dominates the upland areas of the island. Forest canopies are composed primarily of tropical hardwood species such as *Ficus aurea* Nutt. (Strangler fig) and *Bursera simaruba* L. Sarg. (Gumbo limbo). Dense thickets of *Acanthocereus tetragonus* L. Hummelink (Barb-wire) and *Opuntia* spp. (Prickly pear) cacti occur throughout the island in shrub and ground cover. In addition, mangrove forests dominated by *Rhizophora mangle* L. (Red mangrove), *Avicennia germinans* (L.) L. (Black mangrove), and *Laguncularia racemose* (L.) Gaertn. f. (White mangrove) encompass the perimeter of the island and are present within the recessed inland areas (FNAI, 2010; Jones et al., 2016; Wilder and Barry, 2010). Climate in south Florida is characterized as subtropical with seasonal precipitation differences that distinguish a wet season from May to October and a dry season from November to April (Verdon & Donnelly, 2005). Average annual precipitation ranges from 119–157 cm with 60% of total rainfall occurring in the wet season (Obeysekera et al., 1999).

Methods

Data Collection

Florida Box Turtles were opportunistically captured by hand through visual surveys during a long-term population assessment to determine species distribution and ecology (Jones et al., 2016). In March 2016, a subset of turtles were outfitted with a 12 gram (g) radio-transmitter (R2020, Advanced Telemetry Systems) on their posterior carapace using water weld plumbing epoxy. Transmitters weighed < 5 % of the turtle's body mass. Each turtle was assigned a unique number according to the system of Ernst et al. (1974) that was notched into their marginal shell scutes with a triangular file (Cagle, 1939) for future identification. We recorded morphological characteristics during initial capture (e.g., sex and body mass measured to the nearest (g) using a spring loaded scale [2500 g Medio Line scale; Pesola, Barr, Switzerland]). Body size measurements were taken using a dial calipers (straight carapace length, straight plastron length, plastron width at the hinge, carapace width at the 8th marginal scute, and carapace height at the highest point; Jones & Willey, 2017). Turtles were handled for no more than 15 minutes and released in the location they were captured. We located each turtle using a 148 -174 MHz telemetry receiver (R1000, Communications Specialists Inc.) approximately one day per week from March through October 2016 and once opportunistically in March 2017 prior to removal of the radio-transmitters. Tracking reflected U.S. Fish and Wildlife Service technician availability. At each turtle radio location, we recorded date, time, identification number, air temperature (°C) and relative humidity (inHg) with a handheld kestrel unit. Locations were collected using either a Garmin hand held GPS unit (Model Etrex, Garmin International Inc., Olathe, Kansas) with +/- 5m accuracy or a Trimble hand held GPS unit (Model Juno Series, Trimble Navigation Limited, Westminster, Colorado) with +/- 2 m accuracy. Turtle activity was documented as alert at surface, walking, or in a form (Table 4.1). Activity was then categorized as active (alert, walking) or quiescent (in partial or full form). Habitat parameters such as dominant species and percent cover were estimated for canopy, shrub and herbaceous layers within 5m of the telemetry location. Dominant canopy was classified as tropical hardwood hammock forest, mangrove forest, shrub-scrub-cactus, or exposed shell barren. Due to transmitter detachments, two of the turtles (F1052, M193) were not tracked after 10 August 2016 and 23 August 2016 respectively. A single death occurred during the study and therefore turtle F1057 was not tracked after 6 September 2016, leaving a total of seven turtles tracked for the entire time period.

In conjunction with radio-transmitters, turtles were outfitted with external Thermochron iButton Data loggers (MAXIM Integrated Products Ltd., Dallas, TX) on their carapace using Water Weld (J-B Weld) plumbing epoxy to monitor for temperature. Studies have shown carapace temperature collected in small bodied turtles using this method is sufficiently representative of internal body temperature (Grayson & Dorcas, 2004; Pittman & Dorcas, 2009; Shen et al., 2013). Ambient habitat temperatures were also obtained concurrently with turtle monitoring by placing iButton sensors on the ground in the primary island habitat types: hardwood hammock, shell barren, and mangrove. All data loggers were set to record a timestamped temperature reading at equal time intervals of every 4 hours. The data were internally stored and later downloaded upon removal of the data logger at the end of the study in March 2017. We attempted to obtain iButton temperature data for all radio-tracked individuals however turtles M193 and F1057 do not contain the full dataset due to loss of transmitter (n=1) and death (n=1). The iButton for turtle F1052 detached and was lost on the island resulting in a lack of data for that turtle. Additionally, water inundation and damage rendered the mangrove sensor unsalvageable for use in analysis.

Data Analysis

Location data were used to evaluate each individual for activity, movement patterns, and habitat associations during the study period. The straight line distance between two successive turtle relocations was calculated in Excel to determine the distance since last location in meters (DSLL). Daily movement distances (DPD) were calculated by dividing the DSLL by the number of days between relocations. Distances were averaged by individual, sex, and across all turtles to determine patterns. Temperature and precipitation data from the nearest weather station approximately 10 miles away was also obtained through the NOAA National Centers for Environmental Information (NOAA, 2018). Monthly averages were calculated for each variable to determine the effects of local meteorological conditions on activity. Total precipitation 3 days prior to each turtle relocation was also calculated to determine its effects on movement.

Following Fredrickson (2014), temperature data from both the turtle and habitat iButton sensors were averaged into 24-hr time intervals of early morning (0600–1000hrs), mid-day (1000–1400hrs), late afternoon (1400–1800hrs), evening (1800–2100hrs), and night (2100–

0600hrs). Data were summarized and plotted by time to assess any seasonal patterns or differences.

All statistical analyses were conducted in RStudio (version 1.1.447) and Program R (version 3.4.4) (R core team, 2018). The level of significance for all tests was set to $\alpha = 0.05$. Movement data were evaluated for normality using histograms, boxplots, q-q Plots and the Shapiro-Wilk test (function shapiro.test). DSLL failed the assumption of normality therefore a nonparametric Wilcoxon rank sum test (function wilcox.test) was used to compare male and female distances. A Welch's t-test (function t.test) was used to compare male and female DPD with unequal variances. Due to the small sample sizes, a Fisher's Exact test (function fisher.test) was conducted to determine if males and females exhibited activities significantly different from each other. Results were further evaluated using mosaic plots. To assess the effect of weather variables on turtle activity, we conducted logistic regression models using the glm function in R. Predictor variables of temperature, humidity, and pressure were run with a binary response (active or non-active) and turtle identification as a fixed effect. We compared models using Akaike's Information Criterion (AIC) to determine the best model. Models within three AIC values of each other were considered equivalent. The model with both the simplest design and lowest AIC score was then chosen as the best model. The resulting model was evaluated using the goodness of fit (function pR2, package pscl). Linear regression models using the lm function were conducted to determine the effect of weather variables on turtle movement (DSLL). Date, total precipitation three days before the turtle relocation, average temperature three days before the relocation, and the change in precipitation within the 6 day period before the relocation were used as predictor variables. Precipitation three days before the relocation was log transformed to normalize the data. AIC scores were again used to determine the best model. The resulting model was further evaluated using residual plots and the Shapiro-Wilk test.

Results

We tracked 10 adult Florida Box Turtles (5 males and 5 females) from March to October 2016 and once opportunistically in March 2017 prior to removal of the radio-transmitters with a total of 287 relocations. Individuals lacking the full data set were excluded from mean calculations and not included in all analyses. The data sets were also truncated to exclude observations that were missing variables such weather or activity depending on the analysis.

Activity patterns and weather: individual based analysis

Of the 284 Box Turtle activities observed, we most commonly found turtles either buried in a partial form (n = 108, 38%) or alert on the surface (n = 106, 37.3%). In addition, 13% of turtles were found in complete form (n = 37) and 11.6% walking (n = 33). A single mating observation of a radio-tracked male was recorded in June and was grouped in the alert at surface category for analysis. There were no significant differences between the sexes regarding activity (P = 0.9012, Chisq = 0.2813, Figure 4.2).

Box Turtle activity varied monthly with changes in environmental variables. Following Verdon (2004), average monthly temperature and precipitation from the NOAA weather station and average humidity recorded at turtle locations (n = 179) were plotted against monthly percentages of turtle activity (Figure 4.3). Turtles were more active during periods of higher temperature, relative humidity, and precipitation within the wet season months of May to September. Although turtles were tracked less frequently in the dry season, they were observed less active in the cooler, drier months of March and April.

At Box Turtle locations (n= 249), the ambient conditions during turtle activity were marked by slightly lower temperatures (29.2°C) and higher relative humidity (84.7%) in contrast to when turtles were inactive at an average temperature of 30.5°C and an average humidity of 72.4%. Average pressure was relatively consistent at 30.1 inHg throughout the study period. We conducted a logistic regression which indicated the best fitting model describing the relationship between turtle activity and weather contained the variables of temperature and humidity (McFadden's pseudo-r^2 = 0.2, Table 4.2). Temperature (P = 0.00328) and humidity (P = 3.5e-06) were significantly associated with turtle activity. Of the two variables, humidity (estimate = 0.05128, SE = 0.01105) presented as the strongest relationship with a positive estimate and thus as humidity increased the probability of turtles being active also increased (Figure 4.4). Temperature (estimate = -0.24578, SE = 0.08360) had a negative relationship and therefore as temperature increased the probability of turtle activity decreased (Figure 4.4).

Movement and precipitation: population based analysis

The average distances Box Turtles traveled between locations ranged from 33.3 m to 66.1 m (mean = 46.1 m, SD = 13.4). Average distances traveled per day ranged from 4.3 m to 9.3 m (mean = 6.3 m, SD = 2.0). Between the sexes (males n = 4; females n = 3), there were no significant differences in DSLL (P = 1, W = 6) or DPD (P = 0.8785, t = -0.1, df = 4.0). Linear regression models indicated the best fit describing the relationship between turtle movement and weather contained the single variable of total precipitation three days before relocations (R^2 = 0.2523, Table 4.3). There was a significant positive relationship between DSLL and precipitation and therefore as precipitation increased the probability of turtle movement increased (P = 0.005, estimate = 3.544, Figure 4.5). Peaks in Box Turtle movement appeared to correspond with changes in rainfall although the model did not find it significant. From March to October 2016, total precipitation three days prior to turtle relocation events (n = 204) was plotted against average weekly DSLL (Figure 4.6). The largest average DSLL of 92.2 m occurred between the weeks of 18 September and 25 September 2016 when total rainfall increased from 0 cm to 5.9 cm. Similarly, movement peaked at 56.8 m between the weeks of 8 May and 15 May 2016 with a 0 cm to 4.6 cm change in rainfall. Note, however, the amount of rain three days before location events was not truly indicative of average monthly rainfall and whether turtles moved may not simply be a factor of rain. The month of August had the most rain during the study with a total of 29.9 cm, though Box Turtles had the smallest average DSLL of 30.9 m (Figure 4.7). Given that food resources are abundant in August on the island, turtles may exhibit smaller movement patterns as they spend increased time feeding.

Thermal ecology: seasonal turtle shell temperature vs. ambient temperature

The iButton Data Loggers ran from approximately March 2016 to February 2017. Results from all recovered sensors are presented in Table 4.4. The average temperature Florida Box Turtles (n = 7) experienced on the island was 25.3°C (range: 14.5°C – 40.1°C). The average temperatures occurring for hardwood hammock and shell barren habitats were 25.3°C (range: 14.5°C – 33°C) and 26.8°C (range: 14.5°C – 46.4°C) respectively. During the wet season from May to October, average turtle carapace temperatures of 27.7°C (range: 15°C – 37.1°C, SD = 2.9) were similar to that of hammock forests with shaded canopy rather than the warmer exposed shell barren (Figure 4.8). Within these months, radio-tracked Box Turtles were mostly located in tropical hardwood hammock forests (n = 94 of 154 locations, 61%) and rarely in shell barren (n = 5, 3%, Figure 4.9). In addition, they were periodically observed in shrub-scrub-cactus (n = 43, 28%) and mangrove forest (n = 12, 8%). Temperatures were similar for carapace and habitat sensors except during mid-day and late afternoon when the shell barren sensor reached 5-12°C higher than the turtle and hammock forest sensors (Figure 4.8). During the dry season from November to January, turtle carapace sensor temperatures were slightly cooler on average at 22.5°C (range: 14.5°C–38.8°C, SD = 4.2). Turtles experienced temperatures approximately 2.5°C higher than the hardwood hammock habitat during mid-day and late afternoon suggesting a possible shift in habitat use, though turtles were not radio-tracked in the dry season to directly confirm (Figure 4.8).

Discussion

Box Turtles on the island were found to be most active during months that occur in the wet season. In other parts of their range, Box Turtles have been known to become less or completely inactive during dry periods but resume with the return of precipitation (Dodd, 2001; Plummer, 2003; Stickel, 1950; Strang, 1983; Tucker et al., 2015). Studies in central Florida on *T. bauri* have reported they remain active throughout the year (Dodd et al., 1994; Pilgrim et al., 1997). In north central Florida seasonal behavior was not observed (Pilgrim et al., 1997). While we conducted the majority of our study during the wet season and therefore were unable to test for significance, the dry season observations visually suggest a pattern of activity congruent with Verdon (2004) who found Florida Box Turtle activity seasonally correlated to the precipitation of south Florida with an increase in active turtles during the wet season.

We found Box Turtle activity and movement to be significantly influenced by environmental factors. *Terrapene* distributions occur over a range of latitudes and their ecology is defined by the varied ambient conditions where they exist (Dodd, 2001). Temperature, humidity and precipitation are common variables that constrain Box Turtle behavior (Adams et al., 1989; Converse & Savidge, 2003; Dolbeer, 1969; Frederickson, 2014; Stickel, 1950; Sturbaum, 1982). Northern populations contend with freezing winters by becoming inactive in underground chambers until temperatures warm (Dodd, 2001; Ultsch, 2006). In the arid climate of tropical Mexico, *T. c. yucatana* (Yucatán Box Turtle) may be relatively absent for most of the year in small caves and cracks underground but becomes active during humid wet season rains (Buskirk, 1993; Willey et al., 2016). Seasonal or bimodal activity where the hottest parts of the day are avoided to prevent desiccation has been observed (Converse & Savidge, 2003; Dodd et al., 1994; Nieuwolt, 1996). Though *T. bauri* generally responds to the warm temperatures of Florida with year-round activity, behavioral peaks on Egmont Key (Dodd et al., 1994) and Big Pine Key (Verdon, 2004) occur with warm temperatures, high humidity, and high rainfall. Our results support this research (Figure 4.3). Dodd (1994) and others (e.g. Reagan, 1974) found relative humidity to be an important limiting factor for Box Turtle activity. Our logistic regression model also found humidity to be most significant (Figure 4.4). Relevantly, the highest percentage of activity (82%) occurred in September within the wet season when average monthly temperature (28.8°C), humidity (92.5%) and precipitation (22 cm) created favorable Box Turtle conditions (Figure 4.3). Of the survey months in 2016, September exhibited the highest humidity. In addition, Box Turtle movement was significantly influenced by precipitation (Table 4.3). Our linear regression model found Box Turtles increased their movements with increases in precipitation (Figure 4.5). This is consistent with other observations made for adults (Dodd, 2001; Donaldson & Echternacht, 2005; Reagan, 1974; Stickel, 1950; Strang, 1983). Large movements by Box Turtles in our study area also appear to be stimulated by rainfall events after dry periods (Figure 4.6). However, it should be noted that factors other than rain itself may play a role in *T. bauri* behavior and movement. Although August had the most rain during the study, we observed the lowest average DSLL from turtles during this month (Figure 4.7). August was distinguished as a time of plentiful food resources and congregations of Box Turtles could often be found clustered around certain trees. Therefore this may be a seasonal period of sedentary behavior as Box Turtles spend their day centered on particular resources that are readily available (L. Willey, personal communication, October 26, 2018).

Box Turtle activity was equally distributed between active and quiescent related behaviors. Compared to our study, Verdon (2004) found a greater overall percentage of Box Turtles (85%) buried in forms throughout the year. If we had tracked turtles for an entire year including the dry season, we may expect Box Turtles in the TTINWR to have a greater proportion of decreased activity than what we observed. However, the Verdon (2004) pine rockland site in the lower Keys has a much more exposed habitat structure with drier conditions. The closed canopy of the hardwood hammock and mangrove forests at our study site may provide higher humidity levels and cooler substrates and reduce the frequency with which turtles seek full forms. Thus they may generally be found alert at the surface more often. Box turtles actively self-regulate within a narrow range of microclimates to meet their preferred physiological needs. Habitat structure and ground cover choice play a significant role in this process (Reagan, 1974). Since the majority of Box Turtles were relocated in hardwood hammock stands with high percentages of leaf litter, we assume this habitat class is providing an important component to their thermoregulatory functions. Keister and Willey (2015) detail the wide range of reported habitat types for *Terrapene carolina* (Eastern Box Turtle) and its subspecies which can vary considerably between and among populations. Due to these differences and the rarity of tropical hardwood hammocks in the United States (Loope & Urban, 1980; Olmstead et al., 1980), further examination into the association of *T. bauri* with hardwood hammock habitat and how its microenvironments provide thermal protection could offer valuable information on Box Turtle natural history and requirements especially in the temperature extremes of their southern range. Other studies have highlighted the importance of fostering a more bottom-up approach to Box Turtle conservation in their utmost locations (Converse & Savidge, 2003; Curtin, 1998; Currylow et al., 2013; Milanovich et al., 2017; Parlin et al., 2017; Roe et al., 2017; Rossell et al., 2006). Juveniles in particular are under surveyed and may differ in their use of these habitats and micro-variables (Jennings, 2007).

Behavioral thermoregulation is the primary mechanism for controlling heat stress and desiccation in Box Turtles provided that adequate microenvironments are available (Dodd, 2001). As generalists of forest and open habitats (Farrell et al., 2006; Keister & Willey, 2015), Box Turtles capitalize on mosaics in the landscape and move between habitat parameters to avoid extreme conditions (do Amaral et al., 2002). While turtles at our site frequently selected for forested habitat presumably as a means to manage for moisture and heat in this system, it is noteworthy that the iButtons recorded turtles experiencing temperatures near 40°C during the study (Table 4.4). This is close to the lethal thermal maximums for the genus *Terrapene* (43°C, Sturbaum, 1981; 41°C, Plummer, 2003). Although latitudinal variation for temperature preferences has been shown to occur (Curtin, 1998; Ellner & Karasov, 1992), the question of whether Box Turtles are thermally stressed in this region of southwestern Florida is of interest. An environment consistently challenging the thermal ecology of a species can affect all aspects of its biology from body condition and growth rates to activity cycles for important behaviors such as feeding, mating, and nesting. These stressors in turn may decrease survival rates and population growth (Dodd, 2001; Huey & Stevenson, 1979; McCallum et al., 2009; Parlin et al., 2017; Roe et al., 2017; Tucker et al., 2015). This is especially concerning as rising temperatures from global climate change are expected to impact ectothermic species (McCallum et al., 2009) particularly in tropical regions where they are already functioning close to their critical thermal maximums (Huey et al., 2009; Walters et al., 2012). Climate change is also expected to alter the habitat structure of low lying forested islands in coastal Florida. Stronger hurricanes combined with sea level rise cause erosion, flooding, tree blow-downs, and dry soils from salt deposits of seawater over-wash. These factors can contribute to suppressed regeneration and forest decline (Desantis et al., 2007; Langston et al., 2017; Ross et al., 1994; Williams et al., 1999). Large canopy openings from wind thrown trees and an overall reduction in patch size of upland hardwood hammock may leave Box Turtles vulnerable to the temperature extremes of the island. This may subsequently shift their focus to engaging in avoidance behaviors for overheating and desiccation more often than performing other valuable biological activities. Further, thermal exposure from canopy loss has the potential to influence *T. bauri* on the island demographically. Box turtles have temperature dependent sex determination (TSD) during egg incubation with cooler temperatures producing males and warmer temperatures producing females (Dodd, 2001; Ewert & Nelson, 1991). There is a noted concern among literature for reptiles with TSD that increasing temperatures from global warming will not only skew sexes toward female-only populations but will also warm nest incubations too high for survival (Gibbon et al., 2000; Janzen, 1994; Hawkes et al., 2007; Wyneken & Lolavar, 2015). Both factors could lead to extreme decline and lack of ability to maintain future populations. Though measures such as shifting the pivotal temperatures for sex determination, selecting behaviorally for shaded nest sites, and adjusting the start of seasonal nesting could be evolved to offset the effects of a warming climate, it is unclear whether long-lived turtles could achieve such adaptations fast enough to counter rapid climate change (Gibbon et al., 2000; Hawkes et al., 2007; Janzen, 1994; Janzen & Morjan, 2001; Morjan, 2003; Refsnider & Janzen, 2012). Answers to such complex climate related questions can only be derived through long-term research. However, there is currently a lack of published information available on the thermal and nesting ecology of *T. bauri*.

Though our study provides a baseline examination of Florida Box Turtles in southwestern Florida, it would be informative to perform finer scale research into their daily or hourly activity and thermal regimes to better understand their associations with this extreme range subtropical environment. Future studies should include year-round data collection in both the wet and dry seasons that address behavior, movement, habitat use including micro-habitats, and even population demographics. Data such as this may help determine Box Turtle physiological and ecological requirements in mangrove dominated ecosystems and what challenges they may undergo with future climate change.

Tables and Figures

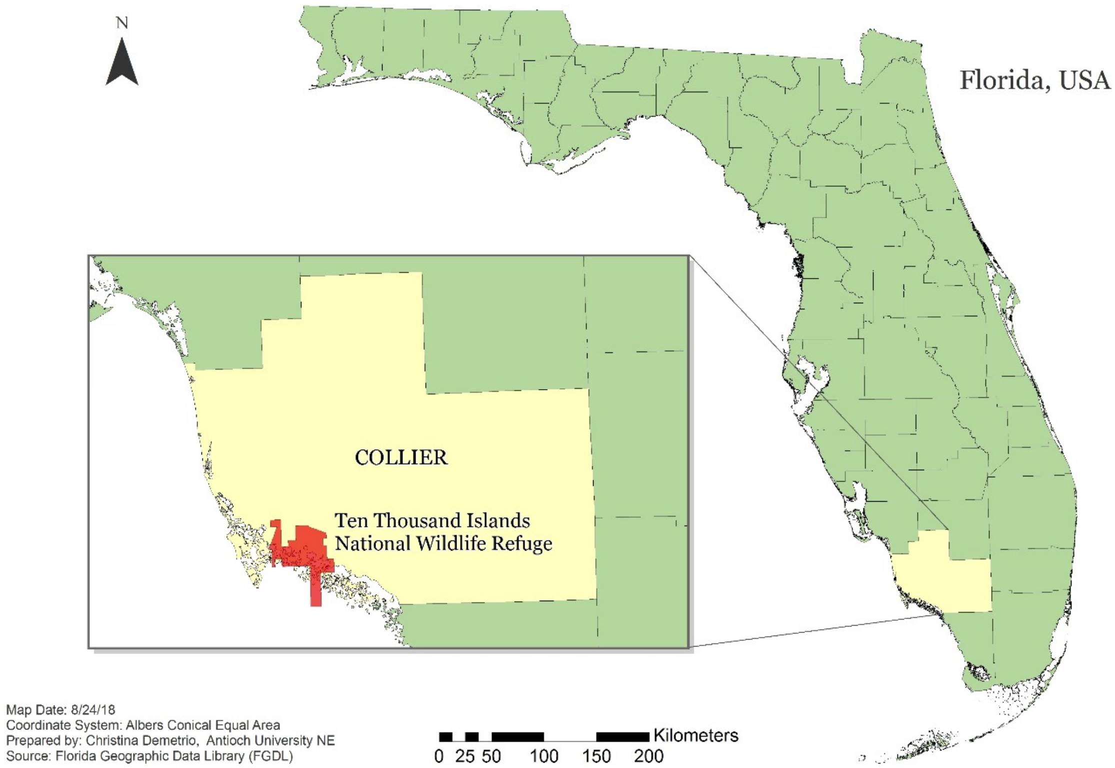

Figure 4.1: Study site for the 2016–2017 *Terrapene bauri* home range assessment located in southwestern Florida within the Ten Thousand Island National Wildlife Refuge, Collier County. Refuge boundaries are delineated in red.

Table 4.1: Descriptions of turtle activities during the 2016–2017 telemetry study.

Activity	**Description**
Alert at Surface	Turtle is alert and above ground with undetermined actions of resting or walking
Complete form	Turtle has carapace completely covered with leaf litter or other substrate
Partial Form	Turtle has carapace partially covered with leaf litter or substrate
Walking	Turtle is walking before or during observation event

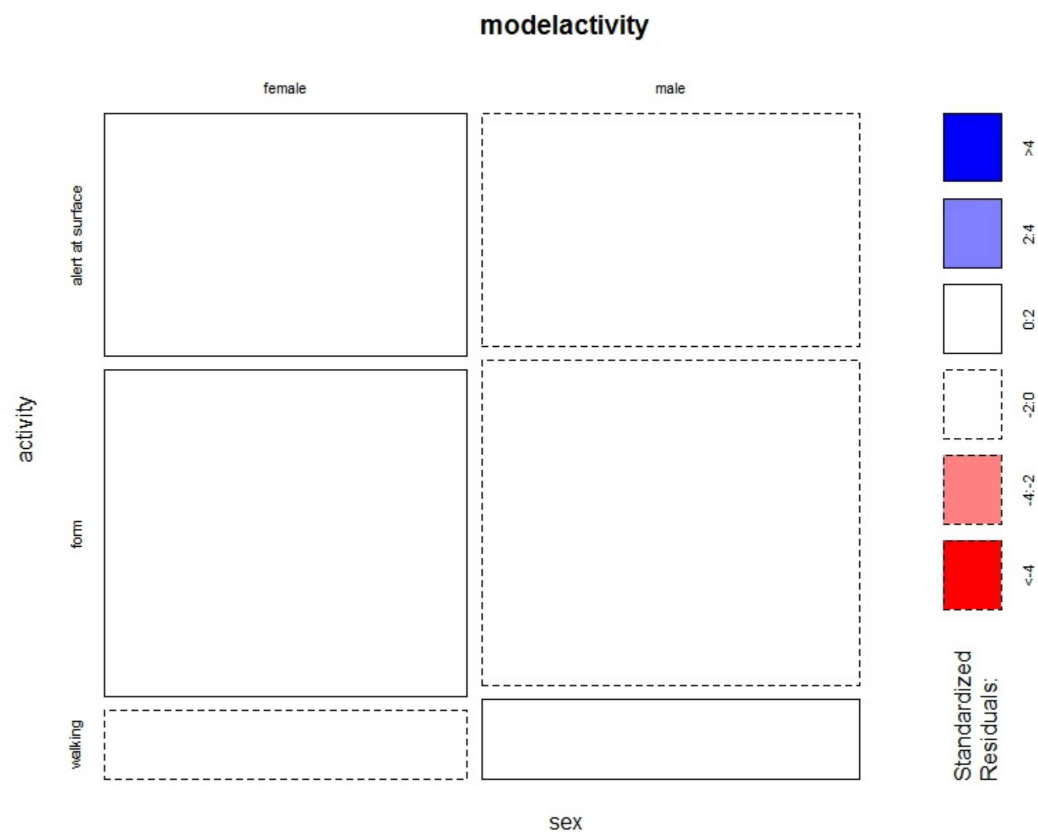

Figure 4.2: Chi-square mosaic plots comparing male and female activity for 10 radio-tracked Florida Box Turtles. Turtle activity did not differ significantly between the sexes.

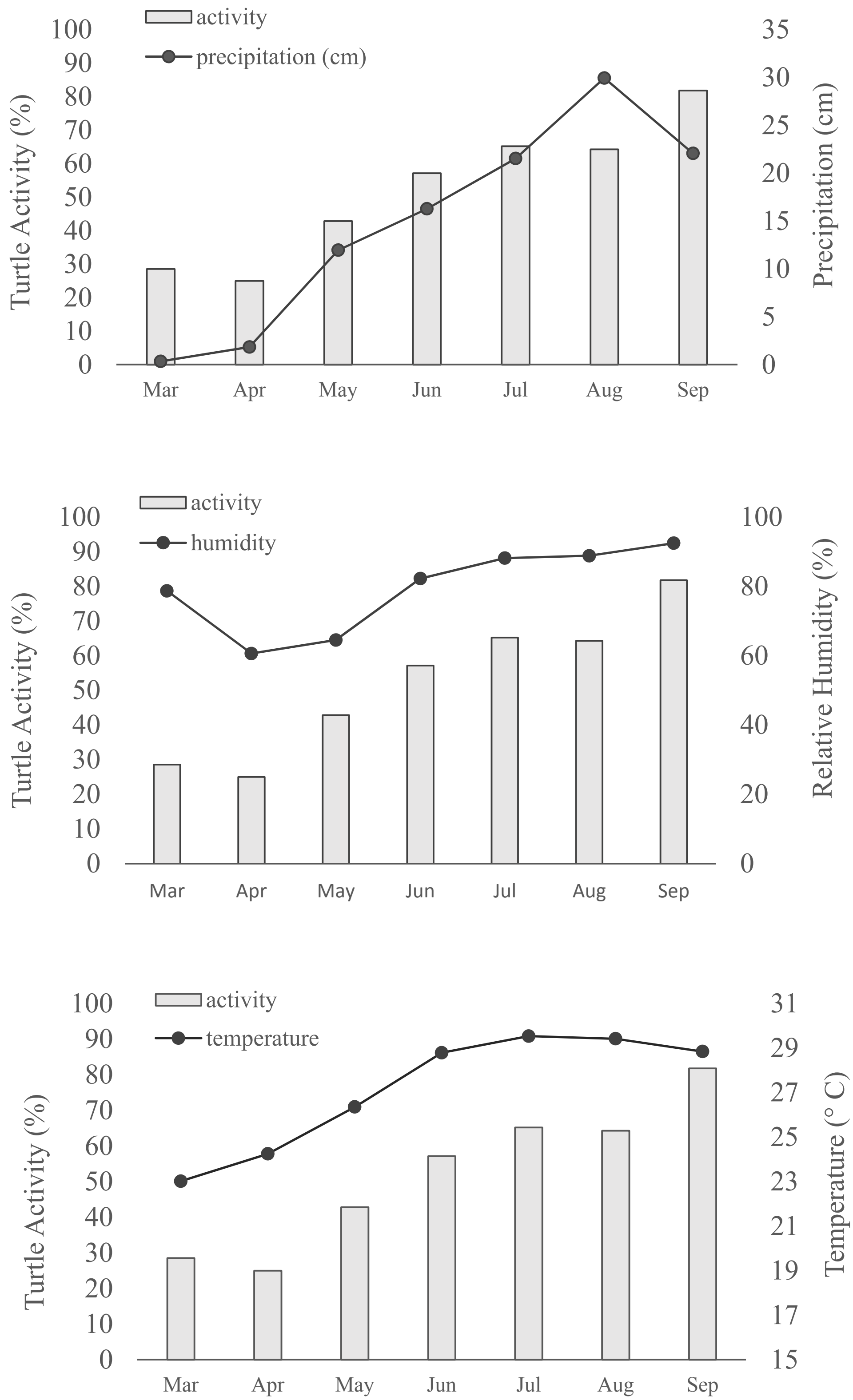

Figure 4.3: Percent activity of Florida Box Turtles in relation to average temperature, humidity, and precipitation in southwestern Florida within the Ten Thousand Islands National Wildlife Refuge, March–September 2016.

Table 4.2. Results of AIC analysis to evaluate model fit for logistic regression models assessing the relationship between weather variables and Florida Box Turtle activity in southwestern Florida, USA, 2016. Best model is indicated in bold.

Model	No. Par	AIC	Δ AIC
Temperature, Humidity, Pressure	3	296.55	0
Temperature, Humidity	**2**	**297.09**	**0.54**
Humidity, Pressure	2	300.36	3.81
Humidity	1	304.44	7.89
Humidity^2	1	306.16	9.61
Temperature	1	320.27	23.72
Temperature, Pressure	2	322.17	25.62
Temperature^2	1	322.17	25.62

Akaike's Information Criterion (AIC) value, change in AIC value from the top model (ΔAIC), and number of parameters (No. Par); models with quadratic terms are represented by (^2).

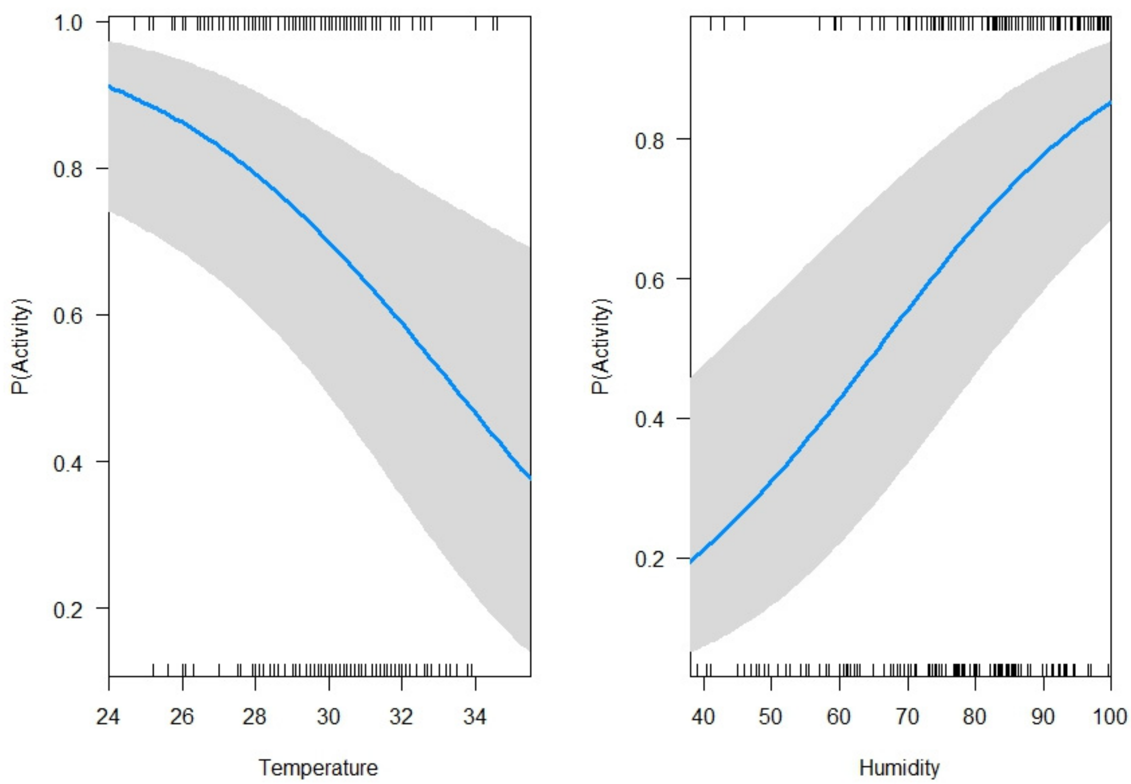

Figure 4.4. Florida Box Turtle probability of activity in relation to weather variables of temperature and humidity in southwestern Florida within the Ten Thousand Islands National Wildlife Refuge, March–October, 2016.

Table 4.3. Results of AIC analysis to evaluate model fit for linear regression models assessing the relationship between weather variables and Florida Box Turtle movement in southwestern Florida, USA, 2016. Movement was represented as distance since last relocation. Best model is indicated in bold.

Model	No. Par	AIC	Δ AIC
log(Precipitation)+Date	2	243.77	0
log(Precipitation)+Temperature	2	244.60	0.83
log(Precipitation)*Temperature	2	244.72	0.95
log(Precipitation)	**1**	**245.29**	**1.52**
log(Precipitation)*Date	2	245.60	1.83
Temperature*Date	2	246.26	2.49
log(Precipitation)+Temperature+Change	3	246.58	2.81
log(Precipitation)+Change	2	247.23	3.46
Date	1	247.69	3.92
Change+Date	2	247.73	3.96
Change+Temperature	2	248.54	4.77
Temperature+Date	2	248.86	5.09
Change	1	252.83	9.06

Akaike's Information Criterion (AIC) value, change in AIC value from the top model (ΔAIC), and number of parameters (No. Par); Variables log transformed are represented by (log).

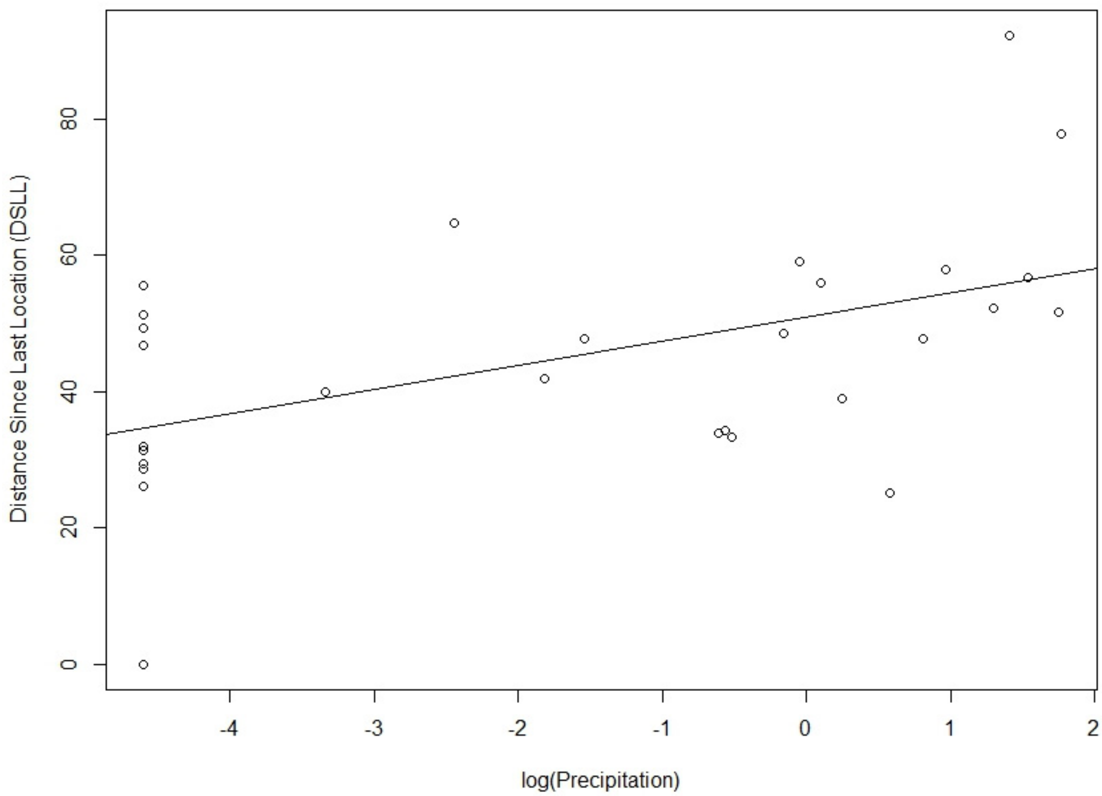

Figure 4.5. Florida Box Turtle probability of movement in relation to precipitation in southwestern Florida within the Ten Thousand Islands National Wildlife Refuge, March–October, 2016.

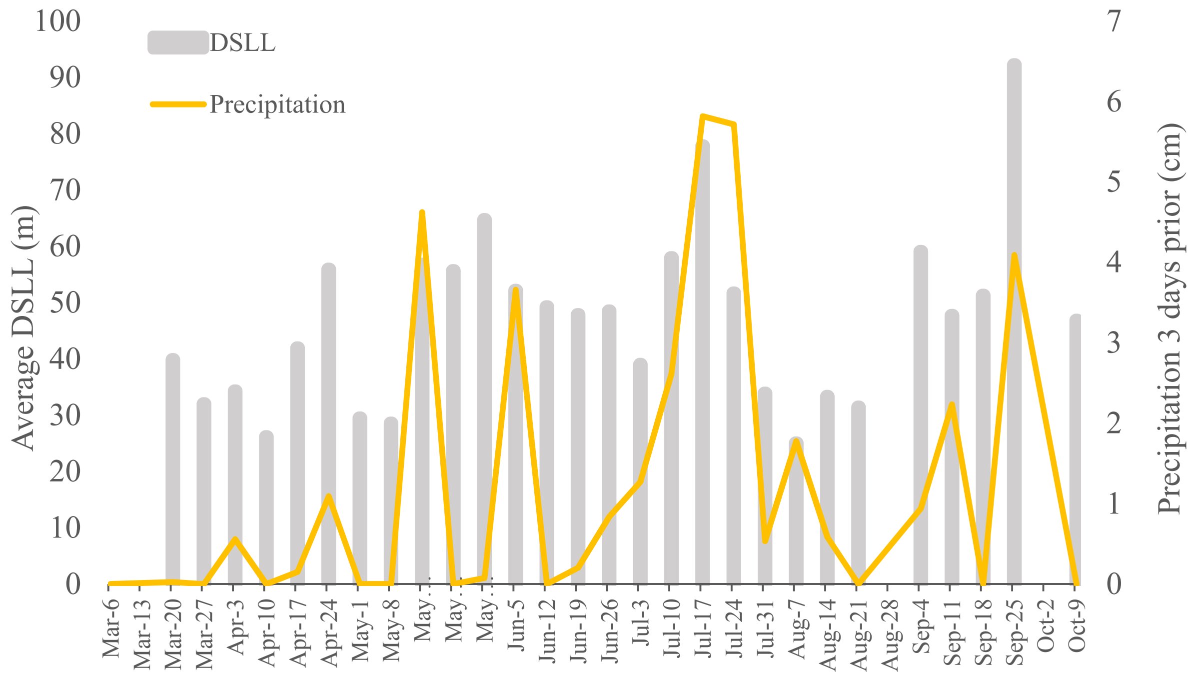

Figure 4.6. Florida Box Turtle movement and precipitation by week in southwestern Florida, March–October 2016. Movement is represented by distance since last location (DSLL). Precipitation was totaled three days prior to location events. Analysis excludes individuals without the full dataset. Turtles were not tracked during the weeks of March 13, August 28, and October 2, 2016.

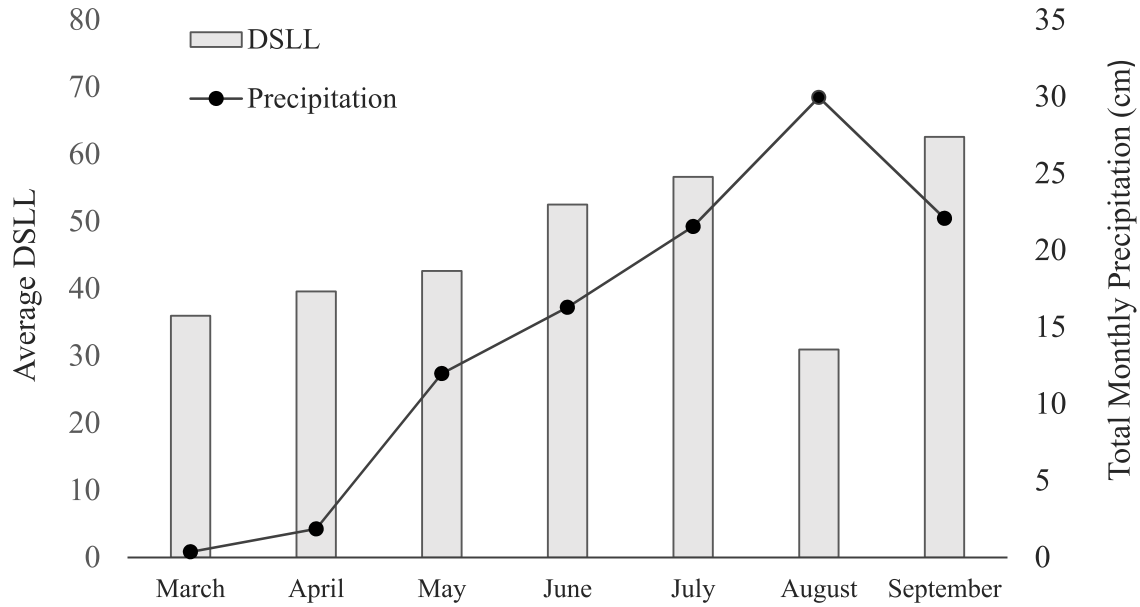

Figure 4.7. Precipitation and Florida Box Turtle movement by month in southwestern Florida, March–September 2016. Movement is represented by average distance since last location (DSLL).

Table 4.4. Summary statistics of average temperature (°C) using iButton data loggers for 9 radio-tracked *Terrapene bauri* (Florida Box Turtles) and two primary habitat types on a shell work island in the Ten Thousand Islands National Wildlife Refuge, Florida, USA, 2016–2017. Maximum temperature, minimum temperature, and standard deviations are also displayed. N is the total number of observations.

Identification	Sex	Mass (g)	N	Average Temperature (°C)	STDEV	Max	Min
193	M	413	1002	27.1	3.9	45.1	16.3
1034	M	546.5	2039	25.8	4.4	37.0	14.5
1049	M	497	2039	24.9	4.2	36.1	14.5
1054	M	486.5	2039	25.3	4.2	40.1	14.5
1055	M	429	2039	25.2	3.9	34.5	14.5
1006	F	452	2039	25.3	4.6	37.1	14.5
1009	F	441	2039	25.3	4.2	36.0	14.5
1053	F	376	2039	25.1	4.5	35.5	14.5
1057	F	383	1002	27.4	4.1	40.0	14.5
Hammock			2039	25.3	3.3	33.0	14.5
Shell barren			2039	26.8	8.5	46.4	14.5

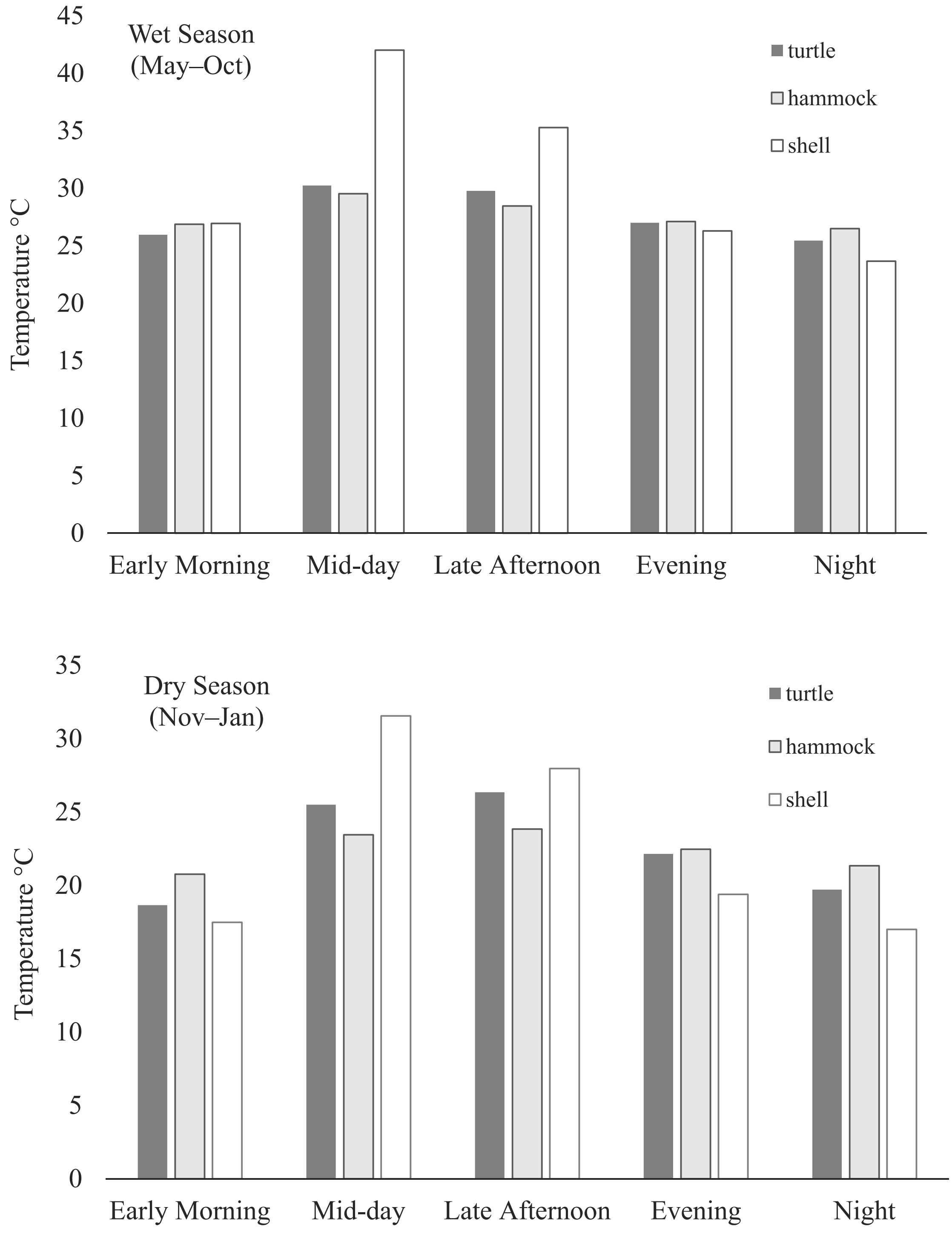

Figure 4.8. Average temperatures from Florida Box Turtle carapace iButton sensors compared to hammock forest and shell barren habitat sensors in southwestern Florida within the Ten Thousand Islands National Wildlife Refuge. Wet season data are from May–October 2016. Dry Season data are from November 2016–January 2017. Data were averaged in 24-hr intervals of early morning (0600–1000hrs), mid-day (1000–1400hrs), late afternoon (1400–1800hrs), evening (1800–2100hrs), and night (2100–0600hrs).

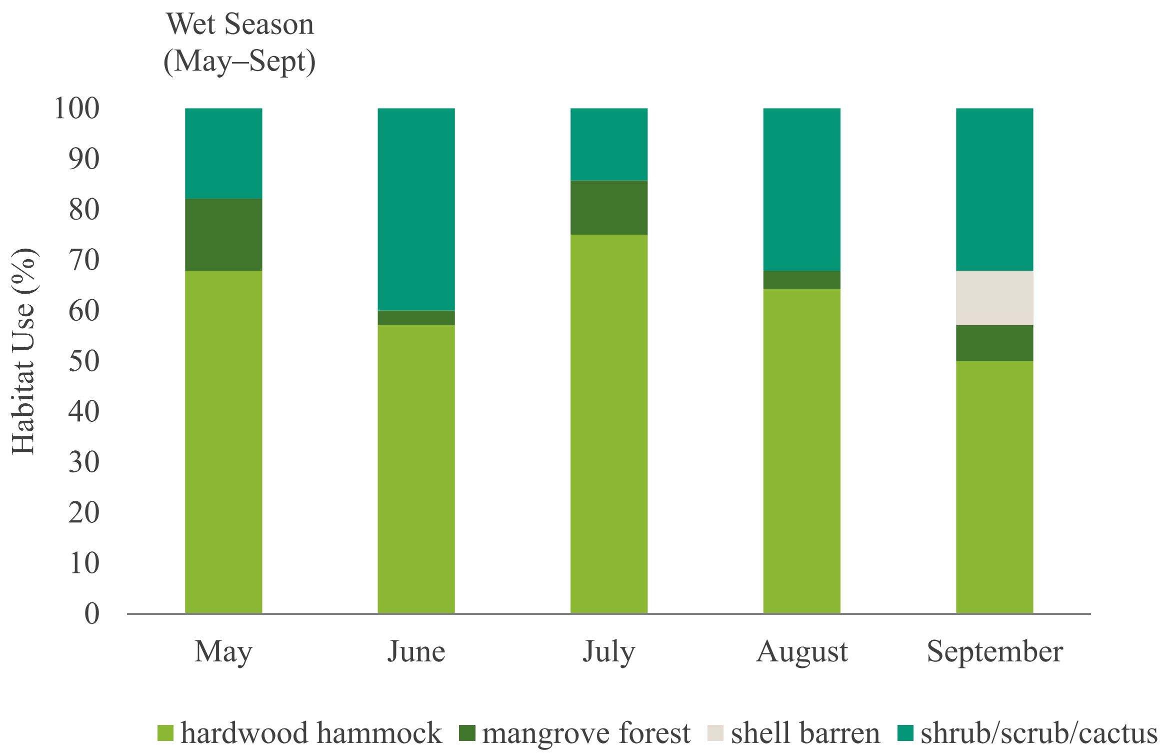

Figure 4.9. Wet season habitat use by Florida Box Turtles in southwestern Florida within the Ten Thousand Islands National Wildlife Refuge, May–Sept 2016.

CHAPTER 5: CONCLUSIONS

Home range size of Box Turtles at our study site in the Ten Thousand Islands National Wildlife Refuge (TTINWR) is consistent with, yet smaller than, studies in other parts of their range, which may be related to the fact that this is an island population. *Terrapene bauri* use tropical hardwood hammock more frequently than other habitats types, which provides them with the food and shelter resources necessary to endure the subtropical conditions of their environment. Notably, mangroves are also utilized, which is contrary to most reports for the species. Box Turtles respond to the increase in temperature, humidity, and rainfall of the wet season in southern Florida with more activity and movement. Average body temperatures of 25.3°C are maintained behaviorally through habitat use. However, the temperatures in this extreme southern latitude drive them close to their critical thermal maximum, which may have implications for their longevity.

Further study of *T. bauri* in the Ten Thousand Islands is recommended not only to remedy the lack of natural history information of Box Turtles in this subtropical mangrove-dominated region but also to document their populations in Florida among the continued natural and anthropogenic changes of the landscape. For example, in September 2017 Hurricane Irma made direct landfall through southwestern Florida as a Category 3 hurricane. This caused extensive damage with maximum winds of 100 kt and storm surge inundations of 6 to 10 ft above ground level within the TTINWR (Cangialosi et al., 2018). The succeeding conditions of the islands and Box Turtle populations after this natural disaster are of interest. The data from Jones et al. (2016) and this accompanying study can help serve as baseline information for comparison with future research. Long-term studies have proven beneficial for documenting drastic change in other Box Turtle populations in Florida. After an extensive fire in 2016 on

Egmont Key as well as raccoon predation, a survey conducted in March 2017 noted more than 250 mortalities and only 11 live Box Turtles from the once abundant population (Dodd, 2017; Jones et al., 2017). It is only with the numerous years of past research on Egmont Key that a decline like this could be appreciated and accounted for from a conservation standpoint. It also makes the population of Box Turtles on our study island in southwestern Florida potentially even more important. Accordingly, long-term studies with large samples sizes in both the wet and dry seasons examining home range, habitat use, micro-environment requirements, and population dynamics are encouraged for Florida Box Turtle populations in the Ten Thousand Islands.

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APPENDICES

APPENDIX A: RADIO-TELEMETRY DATA COLLECTION FORM

APPENDIX B: MAP OF HOME RANGES USING 100% MINIMUM CONVEX POLYGONS (MCP)

APPENDIX C: MAP OF HOME RANGES USING 95% KERNEL DENSITY ESTIMATES (KDE-href)

APPENDIX D: DOMINANT FLORA RECORDED AT STUDY SITE

APPENDIX E: VEGETATION CLASSIFICATIONS DEFINITIONS FOR SOUTH FLORIDA NATURAL AREAS

APPENDIX F: PERMISSION FOR FIGURE 2.1

APPENDIX G: PERMISSION FOR FIGURE 2.2

APPENDIX H: PERMISSION FOR FIGURE 3.2

APPENDIX I: PERMISSION FOR FIGURE 3.6

APPENDIX A: RADIO-TELEMTRY DATA COLLECTION FORM

Box Turtle Location Form (2016) *Complete one form for all box turtles encountered.*

Observer(s): Site Name:

Date:	Time:	Turtle Notch Code:

Air Temp. ˚C:	RH:	PB and tendency:

Sex: ☐ Male ☐ Female ☐ Juvenile ☐ Unknown | ☐ Initial Capture ☐ Recap.

☐ Toenail collected ☐ Measured (first capture only) | ☐ Dead

CL (mm):	
CW (mm):	
PL (mm):	
APL (mm):	
PPL (mm):	
PW (mm):	
Shell height (mm):	
Mass (g):	

Camera & Photo #s:

GPS and Point: **Coordinates** (Lat/Long):

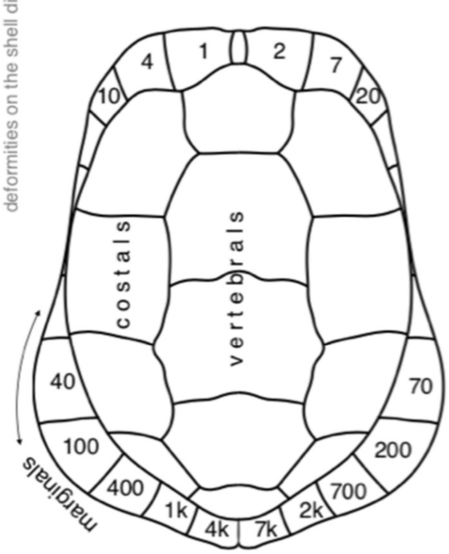
How was the turtle detected?

- ☐ Visual survey only (no telemetry)
- ☐ Radio telemetry (turtle was purposefully tracked)
- ☐ Incidental to telemetry (found while tracking another)
- ☐ On the road
- ☐ Other (specify:)

Turtle **activity** when found:
☐ alert on surface ☐ complete form ☐ partial form
☐ walking ☐ fighting ☐ mating ☐ feeding

Turtle first observed from _________ meters away

Note notches, injuries, & deformities on the shell diagram



Dominant cover type (5 m)

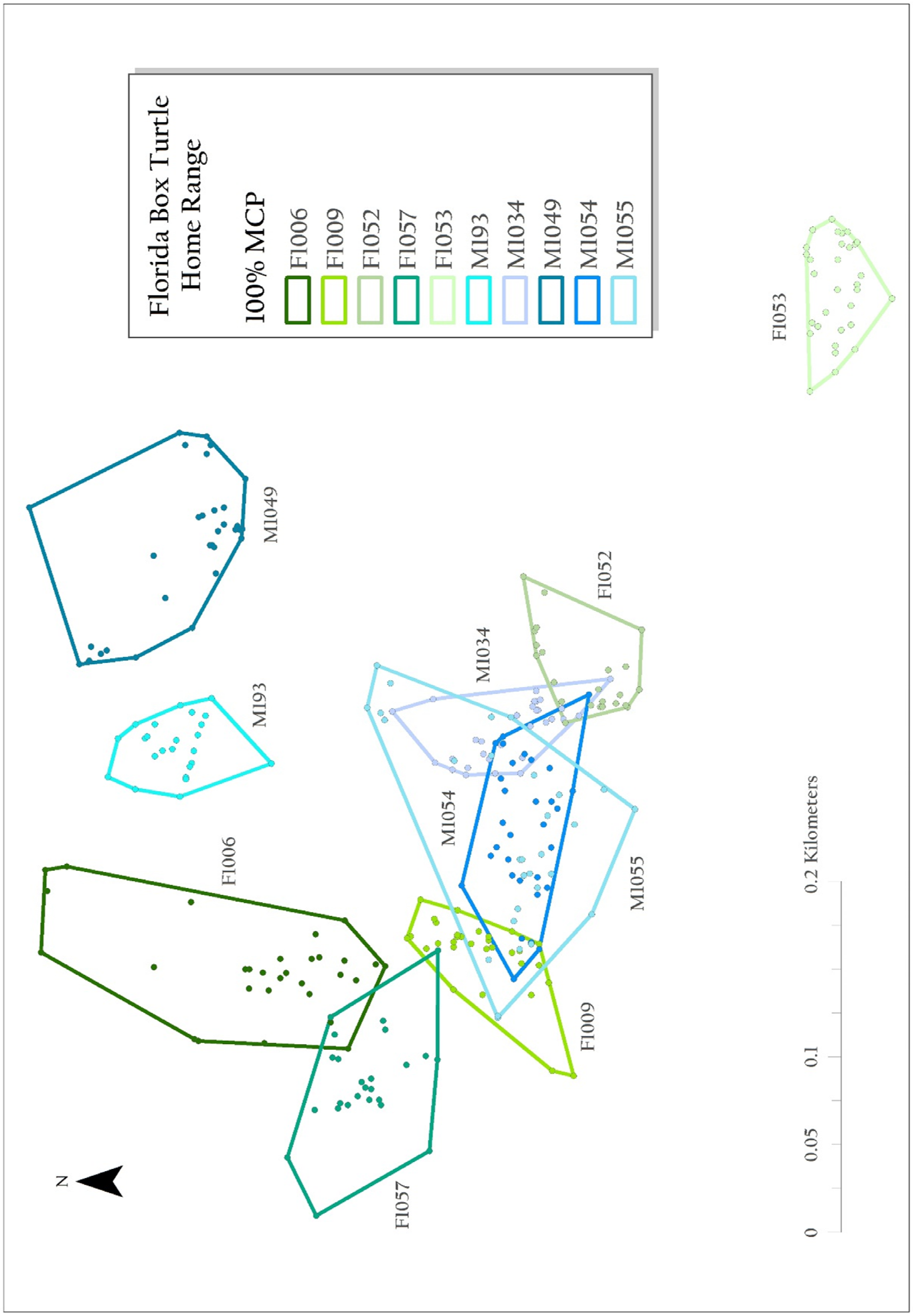
☐	Hardwood hammock	1st	2nd
☐	Mangrove forest	1st	2nd
☐	Shell barren	1st	2nd
☐	Cactus	1st	2nd
☐	Shrub/scrub	1st	2nd

	%	dom. sp.
Canopy cover:		
Shrub cover:		
Herb cover:		

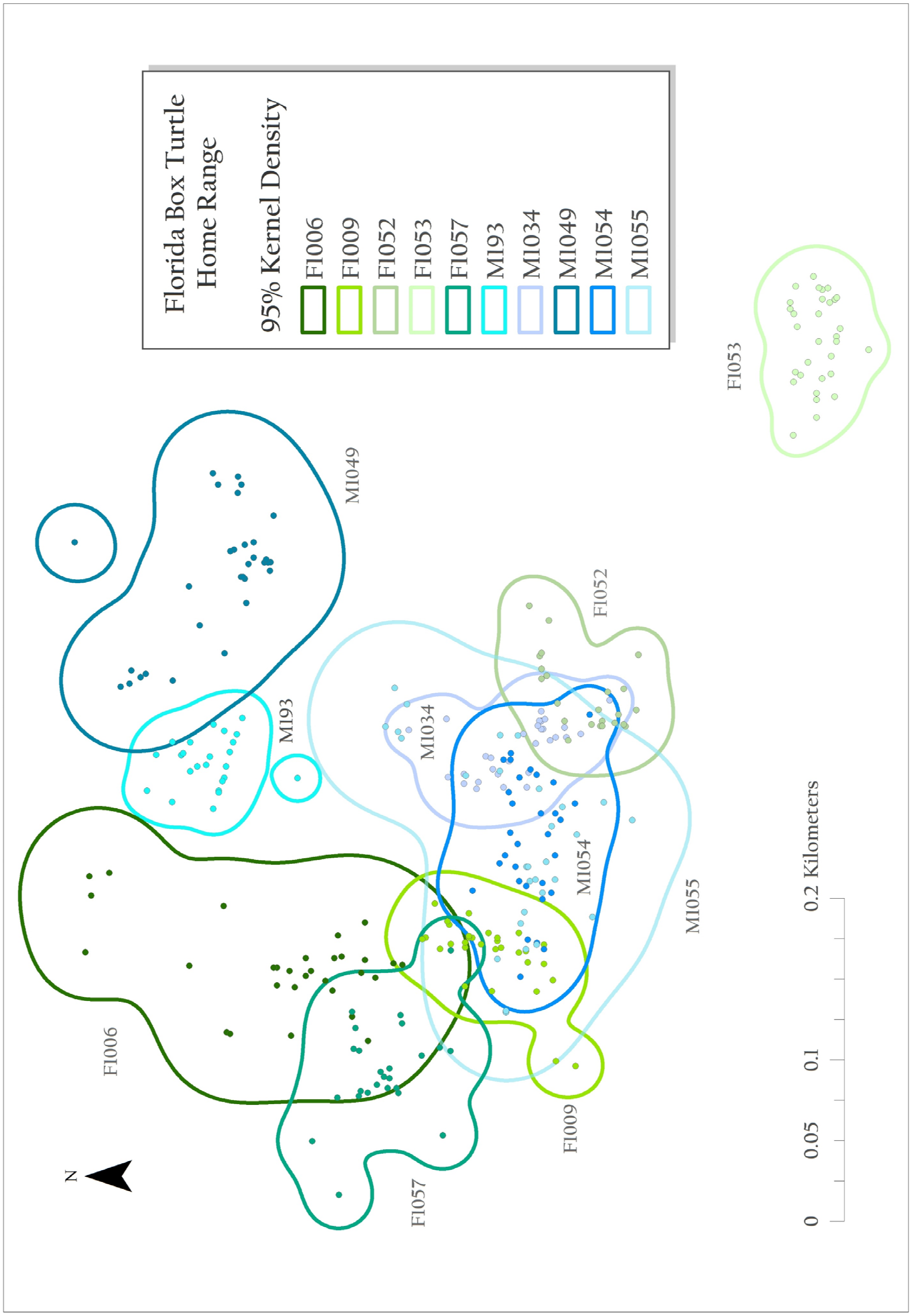
Cactus:	H	M	L	0
Agave:	H	M	L	0
Leaf litter:	H	M	L	0
Coarse woody debris:	H	M	L	0
Bare shell:	H	M	L	0
Bare soil:	H	M	L	0

Comments:

APPENDIX B: MAP OF HOME RANGES USING 100% MINIMUM CONVEX POLYGONS (MCP)



APPENDIX C: MAP OF HOME RANGES USING 95% KERNEL DENSITY ESTIMATES (KDE-href)



APPENDIX D: DOMINANT FLORA RECORDED AT STUDY SITE

Species	Common Name	Growth Habit
Agave spp.	Agave species	Herbaceous/Shrub
Acanthocereus tetragonus	Barbed-wire cactus	Cactus
Ardisia escallonioides	Marlberrry	Shrub
Avicennia germinans	Black mangrove	Tree
Batis maritima	Saltwort	Shrub
Bursera simaruba	Gumbo limbo	Tree
Capparis spinosa	Caper	Shrub
Chrysophyllum oliviforme	Satinleaf	Tree
Coccoloba diversifolia	Pigeon plum	Tree
Conocarpus erectus	Buttonwood mangrove	Shrub/Tree
Coreopsis spp.	Tickseed species	Herbaceous
Dicliptera sexangularis	Sixangle foldwing	Herbaceous
Erythrina herbacea	Coralbean	Shrub
Eugenia axillaris	White stopper	Shrub/Tree
Ficus aurea	Strangler fig	Tree
Ficus spp.	Fig species	Tree
Hymenocallis spp.	Spiderlily	Herbaceous
Ilex glabra	Inkberry	Shrub
Kalanchoe spp.	Kalanchoe species	Herbaceous
Laguncularia racemosa	White mangrove	Shrub/Tree
Lantana involucrata	Buttonsage	Shrub
Ligustrum spp.	Privet species	Shrub/Tree
Mentzelia floridana	Poorman's patch	Herbaceous
Myrsine cubana	Colicwood	Shrub/Tree
Opuntia stricta	Prickly-pear cactus	Cactus
Pithecellobium unguis-cati	Cat's-claw	Shrub
Psychotria spp.	Wild coffee species	Shrub
Randia aculeata	White indigoberry	Shrub
Rhizophora mangle	Red mangrove	Shrub/Tree
Sapindus saponaria	Soapberry	Shrub/Tree
Schinus terebinthifolius	Brazilian pepper	Tree
Sesuvium portulacastrum	Sea purslane	Herbaceous
Sideroxylon foetidissimum	False mastic	Tree
Sideroxylon lanuginosum	Bumelia	Tree
Suaeda maritima	Seablite	Herbaceous
Xanthorhiza simplicissima	Yellowroot	Shrub

APPENDIX E: VEGETATION CLASSIFICATIONS DEFINITIONS FOR SOUTH FLORIDA NATURAL AREAS

Black Mangrove Forest (FMa): "Black Mangrove (*Avicennia germinans*) dominant forest. Found along coastal Florida. Predominates in the upper part of the intertidal zone and into the irregularly flooded higher elevations; sometimes found on higher drier soils than the red or white mangrove. However, it can be found amongst any of the other Mangrove communities."

Black Mangrove-Red Mangrove Forest (FMXar): "Co-dominant mix (60/40% split) of either Black Mangrove (*Avicennia germinans*) or Red Mangrove (*Rhizophora mangle*) dominant mix."

Buttonwood Forest (FMc): "Buttonwood (*Conocarpus erectus*) dominant forest with variable understory composition. Generally coastal in distribution, normally found along the landward edge of the mangrove zone and along the edges of hammocks bordering the transition zone between freshwater and saltwater environments; thriving in areas that are only occasionally subjected to tidal washing (e.g., elevated ridges in or near the tidal zone); southern Florida and the Keys; However, it can be found amongst any of the other Mangrove communities."

Buttonwood – Red Mangrove Forest (FMXcr): "Co-dominant mix (60/40% split) of either Buttonwood (*Conocarpus erectus*) or Red Mangrove (*Rhizophora mangle*) dominant mix."

Buttonwood Woodland – Succulent, Mound (WMcSM): Acronym present in data layer as proposed by Barry (2009) but currently undescribed in the Rutchey et al. (2006) report.

Human Impacted, Mound (HIM): "Areas impacted by human disturbance." Habitat acronym present in data layer as proposed by Barry (2009) but currently undefined in the Rutchey et al. (2006) report.

Mixed Mangrove Forest (FMX): "Mix of mangrove species with no particular species of dominance."

Mud (MUD): "Moist or dry open ground."

Open Water (OW): "Open water areas such as ponds, lakes, rivers, bays, and estuaries."

Red Mangrove Forest (FMr): "Red Mangrove (*Rhizophora mangle*) dominant forest. Found along coastal Florida primarily in the middle and lower portions of the intertidal and upper subtidal zone. However, it can be found amongst any of the other Mangrove communities."

Tropical Hardwood Shell Mound (FHM): Habitat acronym present in data layer as proposed by Barry (2009) but currently undescribed in the Rutchey et al. (2006) report.

Upland Woodland Mound (WUM): Habitat acronym present in data layer as proposed by Barry (2009) but currently undescribed in the Rutchey et al. (2006) report.

White Mangrove – Red Mangrove Forest (FMXlr): "Co-dominant mix (60/40% split) of either White Mangrove (*Laguncularia racemosa*) or Red Mangrove (*Rhizophora mangle*) dominant mix."

Citation

Barry, M.J. (2009). *Data summary of working vegetation maps of the Ten Thousand Islands National Wildlife Refuge*, (Grant Agreement No. 401817J105). Summary Report submitted to the U.S. Fish and Wildlife Service by The Institute for Regional Conservation. Retrieved from www.regionalconservation.org

Rutchey, K., T.N. Schall, R.F. Doren, A. Atkinson, M.S. Ross, D.T. Jones, M. Madden, L. Vilchek, K.A. Bradley, J.R. Snyder, J.N. Burch, T. Pernas, B. Witcher, M. Pyne, R. White, T.J. Smith III, J. Sadle, C.S. Smith, M.E. Patterson, and G.D. Gann. (2006). *Vegetation Classification for South Florida Natural Areas* (Open-File Report 2006–1240). Retrieved from https://archive.usgs.gov/archive/sites/sofia.usgs.gov/publications/ofr/2006-1240/OFR_2006_1240.pdf

APPENDIX F: PERMISSION FOR FIGURE 2.1

Christina Demetrio
[redacted]

12/20/18

Lisabeth Willey, Ph.D.
Michael Jones, Ph.D.
American Turtle Observatory
[redacted]

Dear Lisabeth and Michael,

I am completing a master's thesis at Antioch University New England entitled "Home Range, Habitat Use and Thermal Ecology of the Florida Box Turtle (*Terrapene bauri*) on an Anthropogenic Island in Southwestern Florida". I would like your permission to reprint images collected during the following research:

Jones, M.T., and L.L. Willey. 2017. Distribution and population structure, and movement patterns of Florida Box Turtles (*Terrapene carolina bauri*) in the northern Ten Thousand Islands, Florida. Summary report submitted to the National Park Service, U.S. Fish and Wildlife Service, and FL Department of Environmental Protection. 21 pp.

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Figure 2.1. Photographs of *Terrapene bauri* male #193 denoting body and shell characteristics. Photo © American Turtle Observatory, March 2016 (Jones and Willey 2017).

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Sincerely,
Christina Demetrio

[redacted]

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By: [redacted]

Title: Photographer

Date: 12/31/18

APPENDIX G: PERMISSION FOR FIGURE 2.2

Christina Demetrio
[redacted]

12/20/18

Lisabeth Willey, Ph.D.
Michael Jones, Ph.D.
American Turtle Observatory
[redacted]

Dear Lisabeth and Michael,

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The image to be reproduced is:

Figure 2.2. Photograph of a female *Terrapene bauri* feeding on *Opunita stricta* (prickly-pear cactus) fruit in the tropical hardwood hammock forests of the Ten Thousand Islands, Florida. Photo © Mike Jones, American Turtle Observatory, November 2015 (Jones and Willey 2017).

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Sincerely,
Christina Demetrio

[redacted]

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American Turtle Observatory

By: [redacted]

Title: Photographer

Date: 12/31/18

APPENDIX H: PERMISSION FOR FIGURE 3.2

Christina Demetrio
[redacted]

12/20/18

Lisabeth Willey, Ph.D.
Michael Jones, Ph.D.
American Turtle Observatory
[redacted]

Dear Lisabeth and Michael,

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The image to be reproduced is:

Figure 3.2. Photograph of adult male #1049 Florida Box Turtle with a radio transmitter. Photo © American Turtle Observatory, March 2016 (Jones and Willey 2017).

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Sincerely,
Christina Demetrio

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By: [redacted]

Title: Photographer

Date: 12/31/18

APPENDIX I: PERMISSION FOR FIGURE 3.6

Christina Demetrio
[redacted]

12/20/18

Lisabeth Willey, Ph.D.
Michael Jones, Ph.D.
American Turtle Observatory
[redacted]

Dear Lisabeth and Michael,

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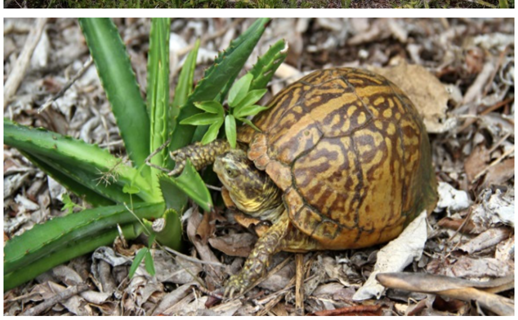

Figure 3.6. Top: Photograph of scrub habitat type on the study island. Bottom: Photograph of Florida Box Turtle with *Agave decipiens* (false sisal or Florida agave) vegetation. Photo © American Turtle Observatory (Jones and Willey 2017).

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Sincerely,
Christina Demetrio

[redacted]

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American Turtle Observatory

By: [redacted]

Title: Photographer

Date: 12/31/18