REPTILIAN ACTIVITY, MOVEMENTS AND SPATIAL ECOLOGY WITHIN THE OAK OPENINGS REGION

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ABSTRACT

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Many taxa suffer from habitat loss, spread of invasive species, and climate change; however, reptiles are especially vulnerable because they are constrained physiologically from their ectothermic nature in addition to global population declines. Like other taxa, reptilian basic ecology requirements are influenced by ecological neighborhoods, which shape the abundance of critical resources and their movement patterns. My goal was to better understand reptilian movement patterns across spatial and temporal scales to facilitate conservation efforts within Oak Openings Region (OOR), of northwestern Ohio and southeastern Michigan, using a combination of field surveys, remote sensing data and modeling. My research examined (1) climate change, (2) distribution patterns, (3) habitat use, and (4) movement patterns. At the regional scale, we found moderate increases in suitable habitat for box turtles within the future scenarios based on climatic suitability models. Individuals may be more displaced or vulnerable from temperature change during the driest quarter of the year. Dispersal is feasible; box turtles, based on tracking of individuals, can move large distances within their lifetime but the physical barriers, like roads, on the landscape may greatly hinder these movements. I modeled habitat suitability for a suite of reptiles based on occupancy data and climate, habitat, elevation, and structural features. Currently, suitable habitat was less than half the area within OOR and was more restricted for two species of concern. There is a need for a to examine the range of limitations, i.e., minimum and maximum models, when planning conservation efforts for a suite of species, especially emphasizing the protection of wet and dry forest. At the local scale, I found using radio telemetry that box turtles displayed typical average home range sizes; however, some were much larger than other studies. This is likely a difference in landscape heterogeneity where home range size increased with greater shape complexity and decreased as it became more physical connected. Movements within preferred patch types may be more costly resulting in larger home ranges. Fine-scale tracking for box turtles and garter snakes was conducted using fluorescent powder. I found that they responded differently to the local environment as seen by trail curvature and distance traveled and were distinct from those found in other studies. Multi-species approaches are critical for conservation efforts. Combining field data with spatial modeling provides a dynamic tool for land management and informing conservation decisions.

This research is dedicated to Phillip DeQueiroz, my life partner, to Cynthia and Stanley Martin, my loving and most supportive parents, and Morningstar, my cuddly cat. Without their love and support, I would not have been able to succeed.

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INTRODUCTION

Understanding how organisms interact with their environment is critical for conservation ecology (Howze & Smith 2015; Shew et al. 2012; Roe & Georges 2008). Many taxa suffer from habitat loss, spread of invasive species, and climate change, along with other threats (Gibbons et al. 2000; Greenspan et al. 2015). Reptiles are especially vulnerable to the synergistic impacts of these threats because they are more closely tied their environment for regulating body temperature than their endothermic counterparts. Additionally, reptilian populations are facing large global population declines. Many of their basic ecological requirements are shaped by ecological neighborhoods. Ecological neighborhoods are determined by ecological processes, e.g., foraging, growth, and reproduction, and timing at multiple scales, e.g., day, week, season, year, and activity during the time period (Addicott et al. 1987). Seasonal changes often instigate movement shifts from summer foraging to fall overwintering habitats (Larsen 1987; Web & Shine 1997). It is critical to understand the biotic and abiotic factors that influence distributions and movement patterns at multiple spatial and temporal scales. Abiotic factors such as landscape composition and configuration play a large role in the distribution and abundance of reptiles and their resources.

Mixed-disturbance landscapes, that have a variety of active management and anthropogenic activities, provide an opportunity to examine varying responses to heterogeneity. At larger spatial scales, dispersal is affected by the flow of connectivity across land cover types, while at smaller spatial scales dispersal is affected by the presence of ground cover obstacles. Understanding the relationship between organisms and the factors influencing their movement patterns at fine scale can improve our understanding at larger scale (Peterman & Semlitsch 2013). Delineating the least costly path across these spatial scales is difficult; however, it highlights how organisms interact with their environment and balance energy expenditure with ecological requirements. A highly biodiverse and heterogeneous landscape such as Oak Openings Region, with large ongoing conservation efforts (Schetter et al. 2013; Abella et al. 2017; Root & Martin 2018), provides an opportunity to examine reptilian movement patterns within a variety of contexts to better understand responses to climate change, distribution, habitat selection, and daily movements. Oak Openings Region extends from northwestern Ohio to southeastern Michigan which historically showcased a mosaic of oak savanna and wet prairie on postglacial sandy soils (Brewer & Vankat 2004). European settlement systematically changed this region through drainage, fire exclusion, urban and agricultural development (Schetter et al. 2013). Oak Openings remains a biodiversity hotspot with five globally vulnerable plant communities (Faber-Langendoen 2001) that supports a multitude of potentially threatened, threatened, and endangered species, both plants and animals. This region is unique in landscape structure, in terms of composition and configuration, as the natural habitats are highly fragmented in contrast to other more contiguous protected lands. Local efforts have prioritized conserving five communities of special concern (Root & Martin 2018) and further investigations of specific taxa may provide useful for informing local conservation efforts. These explorations require a variety of techniques from computer modeling to field surveys for both species by species and multi-species approaches.

My goal for this work was to better understand reptilian movement patterns across spatial and temporal scales to facilitate conservation efforts within Oak Openings Region. I focused on how landscape characteristics, in terms of composition and configuration, influence movement patterns for a suite of reptilian species and for eastern box turtles, *Terrapene carolina carolina*, a species of special concern. I investigated how eastern box turtle distributions change in response to climate change and the identified important variables predicting this change across their geographic range. Then I focused on local populations within Oak Openings Region to evaluate the least cost path in response to climate change. I investigated habitat suitability for local populations of several target, representative reptilian species to identify patterns of biodiversity. Building on previous research, which has identified the importance of forest habitats for reptiles (Wilson 2012; Cross 2016), I expanded our knowledge by tracking habitat use within home ranges and fine-scale movement responses to ground cover heterogeneity, especially for male eastern box turtles.

Research Objectives

My research combined field surveys with spatial modeling to examine how reptiles respond to different landscape components across a variety of spatial and temporal scales. I addressed several questions related to (1) the effects of climate change, (2) diversity and distribution patterns, (3) habitat use, and (4) daily movement patterns for reptiles. Oak Openings Region has a mixed-disturbance landscape that provides an opportunity to examine my research questions at multiple spatial and temporal scales from landscape to fine-scale. My research will increase our understanding of ecological requirements, provide a planning tool for reptilian conservation, and make specific land management recommendations. I answered these questions within the following dissertation sections co-authored with Karen Root:

Chapter I

- Published in *Remote Sensing*, Special Issue: Remote Sensing for Monitoring Wildlife and Habitat in a Changing World:

  - Examined eastern box turtle current distribution and responses to different future climate change scenarios. Dynamic evaluation of local-scale dispersal across current and climate change scenarios using different movement capabilities.

Chapter II

- Prepared for submission to *Diversity and Distributions*:
  - Habitat suitability models for combined reptiles and four target, representative species. Examined patterns of diversity by characterizing underlying land cover across low to high species overlap.

Chapter III

- Prepared for submission to *Journal of Herpetology*:
  - Robust distance-based analysis and multiscale approach to better understand habitat use and spatial ecology of eastern box turtles.

Chapter IV

- Prepared for submission to *Herpetological Conservation and Biology*:
  - Tracked eastern box turtles and eastern garter snakes using non-toxic fluorescent powder to estimate and characterize daily movement patterns. Related movement patterns to fine-scale and local scale habitat heterogeneity to make informed land management recommendations.

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CHAPTER I: CHALLENGES AND OPPORTUNITIES FOR TERRAPENE CAROLINA CAROLIN UNDER DIFFERENT CLIMATE SCENARIOS

Abstract

An unprecedented rate of global climate change as a result of human impacts has affected both endotherms and ectotherms. This is of special concern for ectotherms, such as reptiles, as these species are suffering from large population declines and lack the dispersal ability of other taxa. There are many protected areas across the United States; however, these areas are fragmented, which hinders dispersal. We examined species distribution and dispersal capabilities for *Terrapene carolina carolina*, a relatively narrow range, low dispersal, and vulnerable species. We created climatic suitability models to predict changes in suitable habitat and identified important predictor variables. We modeled three time periods using MaxEnt and hypothesized that there would be an increase in northern habitat as a result of increased warming and precipitation. We found that most of the suitable habitat changed at the northern end of the range and that mean temperature within the driest quarter had a larger contribution towards future predictions. Overall, there were relatively moderate changes in suitable habitat, but where these changes occur affects accessibility. As an example, we examined these local scale movements within Oak Openings Region and found that individuals are capable of dispersing to new suitable habitats; however, other physical barriers such as roads, ditches, or streams, can hinder movements. In conclusion, there is a critical need to protect this vulnerable reptilian species and our results suggest that *T. c. carolina* will expand their distribution northward. We suggest that land managers increase connectivity among protected areas to facilitate dispersal, but future studies should incorporate other dynamic ecological factors at finer spatial scale.

Introduction

Global biodiversity is under major threat by a multitude of factors, such as nutrient loading, carbon dioxide enrichment, and invasive species; similar to these other threats, land-use and climate change pose considerable challenges (Sala et al. 2000). Climate change affects both endotherms and ectotherms by varying density, distribution, phenology, morphology, and genetics (Root et al. 2003). Many species are unable to adapt fast enough to the rapid rate of rising global average temperature (Alexander 2003; Jump & Peñuelas 2005; Araujo et al. 2006; Carey & Visser 2008). Although the impacts on endotherms is concerning, there have been relatively few studies examining the decline of less charismatic, but highly vulnerable and climatically sensitive ectothermic species (Gibbons et al. 2000; Carey & Alexander 2003; Araujo et al. 2006; Wake 2007; Sinero et al. 2010; Sahlean et al. 2014). This is especially concerning for reptiles, such as turtles, because these species lack the dispersal ability of other taxa such as some species of birds, mammals, and many fishes (Sinero et al. 2010) and population declines are expected to be expedited (Gibbons et al. 2000). Additionally, ectotherm physiology plays a strong role where it is influenced by thermal conditions, which in turn are often highly affected by the local scale physical characteristics of a habitat (Parmesan 2006). In a changing climate, thermal heterogeneity is crucial for providing both sunny, warm patches and shady, cool patches to move in or out of as needed. However, maintaining optimal thermal physiology can be difficult in thermally variable environments, and consistent sub-optimal conditions can reduce population viability and directly impact dispersal and population persistence (Huey 1976; Niehaus et al. 2012). *Terrapene carolina carolina* has been shown to have a thermal body temperature range of 20 ºC–25 ºC (Erskine & Hutchison 1981; Huey 1991; do Amaral et al. 2002a) or 27 ºC–31 ºC (do Amaral et al. 2002b). They are often found in less optimal temperatures within closed, forested habitat; however, open habitats tend to peak frequently above 35 ºC especially during the active season (Roe et al. 2017). When interacting with temperatures above 35 ºC, turtles often seek to lower their body temperature and avoid their lethal upper limit of 43 ºC (Parlin et al. 2017). Forests may be thermally suboptimal; however, they provide refuge from excessive temperatures, reduced desiccation risk, and provide access to resources (Roe et al. 2017). Rising temperatures will make it more challenging for *T. c. carolina* to behaviorally regulate body temperature and will likely require increased movement to find optimal thermal environments. As with this species, other reptiles will face similar issues with warming climate, such as overheating and will require greater fine-scale heterogeneity.

There are many protected areas across the United States; however, many of these areas are fragmented by the large network of roads and human-dominated land cover, which make it difficult for species to relocate. This reduces connectivity and negatively impacts reptilian populations by reducing gene flow and dispersal. Efforts made to increase connectivity among protected areas can enhance species resilience to factors such as climate change, especially with the expected potential shifts in distribution ranges (Sturbaum 1981). These climatic changes will likely cause species to shift their range, change their population dynamics, adapt to new climates or become extirpated from local sites. It is imperative to understand how they will respond to these changes across multiple scales (Iverson & Prasad 1998; Hughes 2000; McCarty 2002; Matthews et al. 2004; Root et al. 2004; Thomas et al. 2004; Root et al. 2005; Bradshaw & Holzapfel 2006; Skelly et al. 2007; Massot et al. 2008; Sinero et al. 2010; Ziolkowska et al. 2016). It is expected that changes will be concentrated in areas with the largest temperature changes such as higher latitudes and altitudes with fewer changes in other areas (Root et al. 2003). Therefore, it is important to examine expected changes from unsuitable to suitable, or vice versa, across a species distribution range and manage the areas that vary in climate extremes. In other words, there is a need to translate large scale climate changes to local scale habitat alterations to better manage for vulnerable species. Species that live in areas with large changes from current or historical temperature regimes may have increased vulnerability to declines or extirpation.

Species distribution models have become commonplace to predict potential changes from current conditions to varying climate scenarios (Walther et al. 2002; Araujo et al. 2006). These models have been used to infer species distributions or habitat suitability in past, current, and future scenarios for refinement of protected areas for different species, prediction of invasive species distributions, and impacts of climate change on wildlife (Iverson et al. 1999; Hughes 2000; Cowling et al. 2001; Peterson 2001; Pearson & Dawson 2003; Peterson et al. 2003; Wiens 2004; Araujo et al. 2005; Schwartz et al. 2006; Dormann et al. 2007; Papes & Gaubert 2007; Raxworthy et al. 2007; DeMatteo & Loiselle 2008; Massot et al. 2008; Bombi et al. 2009; Moussalli et al. 2009; Puschendorf et al. 2009; Doko et al. 2011; Wiens 2011; Lee et al. 2012; Owens et al. 2012). One major drawback to climatic prediction modeling is that it may solely rely on the correlation between abiotic factors and species presence creating a “bioclimatic envelope” which assumes that the space of climatic variables best matches observed species’ distribution estimations (Araǘjo & Peterson 2012; Sahlean et al. 2014) and selected parameters often include sources of uncertainty (Pearson et al. 2006; Beaumont et al. 2008; Seo et al. 2009; Wilson et al. 2010). However, advances in species distribution modeling have helped to reduce prediction uncertainties by using robust statistical modelling, which can create forecasts at different scales (Thuiller 2004; Elith et al. 2006; Araujo & New 2007). Although these models cannot directly predict species occurrence in the future, we can predict changes in suitability over time using direct connections of occurrence data to habitat and direct habitat alterations linked to climate change. Species dispersal plays a strong role in distributions, which should be included in models to aid identification of future suitable habitat. Predicting suitable habitat is meaningless if the organism is unable to disperse to the location. Therefore, efforts to assess current and projected land use and climate changes are critical to conserve diverse wildlife communities (Hijmans et al. 2005).

In the present study, (a) we used climate suitability models (CSMs) to estimate impact scenarios on the geographic extent of *T. c. carolina*, a species with a relatively narrow range, low dispersal, and population vulnerability, (b) examined changes in suitable climatic habitat between model time periods, and (c) identified dispersal capabilities within a changing climate context. We modeled three time periods (Last Glacial Maximum or LGM, current, and future 2050) using MaxEnt models for habitat suitability. Our study incorporated other studies' methodologies to build our MaxEnt models and evaluate change over time (Tavernia et al. 2013; Sahlean 2014; Yousefkhani et al. 2017); however, our approach to evaluate change over time with least cost pathways is novel. Our main objectives were to model climatic habitat suitability and changes over time while assessing the main climatic variables influencing suitable habitat regions. We hypothesized that there would be an increase in suitable habitat in the northern portion of the range as a result of increased warming and precipitation. Therefore, we predicted that there would be a northward shift in distribution. We predicted that habitat suitability would increase over time with greater gains for higher greenhouse gas concentration scenarios. We hypothesized that mean temperature of warmest quarter and precipitation of driest quarter would drive *T. c. carolina* responses as a result of increased vulnerability to very hot and dry conditions.

Methods

CSMs (Regional Scale)

CSMs were created for the range of *T. c. carolina* by combining (a) species occurrence data with (b) bioclimatic layers from CHELSA to identify past, current, and future distributions of habitat using MaxEnt. These variables are biologically meaningful and represent annual trends, seasonality, and extreme or limiting environmental factors. MaxEnt applies maximum entropy modeling, a machine-learning technique, which includes a set of environmental layers with georeferenced occurrence localities (Phillips et al. 2004). Then the model creates a probability distribution for the species where each grid cell contains a predicted suitability condition. Climate suitability was modeled at different time periods using six bioclimate variable layers. We used presence-only data in MaxEnt version 3.3.3k (Elith et al. 2011; Xu et al. 2018) to build CSMs for each scenario for the *T. c. carolina* distribution range. Presence-only records were randomly subsampled and separated withholding 30% of the records for test data and using 70% as training data, with ten replicates.

(a) Occurrence. Species occurrence data for *T. c. carolina* were obtained from the Global Biodiversity Information Facility (GBIF, https://doi.org/10.15468/dl.ojpmsm) (Phillips et al. 2004) and a current radio telemetry study (Martin & Root, Chapter 3). We downloaded 2579 records (decimal degree) from GBIF across this species range in the United States that were gathered as presence-only records from 1970 to 2019. We used a subset of presence records from the current radio telemetry study in Oak Openings Region. These records were condensed by applying a 75 m spatial buffer (Cross 2016) to reduce sampling bias, improve model performance and reduce spatial autocorrelation (Boria et al. 2014). The methods for tracking individuals were carried out in accordance to approved guidelines and permitted by Ohio

Department of Natural Resources (20-016), Bowling Green State University's Institutional Animal Care and Use Committee (1001429-9), and with permission from Metroparks Toledo.

(b) Bioclimatic layers. Bioclimatic variables represent extremes of limiting environmental factors. Nineteen bioclimatic layers were downloaded from CHELSA (climatologies at high resolution for the Earth's land surface areas) (Karger et al. 2017a; Karger et al. 2017b) for three conditions: LGM (22,000 years ago), current (1979–2013), and future 2050. The future scenarios were taken from the Coupled Model Intercomparison Project Phase 5 Model Community Climate System Model version 4 for four scenarios (Representative Concentration Pathway (RCP) 2.6, RCP 4.5, RCP 6.0, and RCP 8.5). All layers were downloaded in 30 arc-second resolution and clipped to Eastern United States region using the Environmental Systems Research Institute (ESRI) ArcCatalog version 10.2.2. Climatic layers for the current model were examined using band collection statistics tool in ESRI ArcGIS version 10.2.2 to identify highly correlated variables, i.e., $r > 0.80$ (Table 1.S1). We selected variables to minimize correlations; the final set included bioclimatic (BIO) 8 (mean temperature of wettest quarter); BIO9 (mean temperature of driest quarter); BIO10 (mean temperature of warmest quarter); BIO16 (precipitation of wettest quarter); BIO17 (precipitation of driest quarter); and BIO18 (precipitation of warmest quarter) layers (Table 1.1). Each quarter has a temporal resolution of three months of the year.

CSMs Regional Evaluation

We examined the influence of each environmental predictor variable using percent contribution and permutation importance for each climate scenario model. Percent contribution values depend on the pathway taken by the MaxEnt code for the optimal solution and these values may vary depending on the algorithm taken, while permutation importance depends on the final model and is derived from the contribution of each variable from random permutation among the training points (Phillips 2017). The response curves for the average model were examined to explore how the environmental variable affected the MaxEnt model prediction and the jack-knife results for the average model were used to identify the significance of individual environmental variables.

We evaluated our CSMs by building alternative climatic distribution maps for comparison. These models were created from a bioclimatic profile (i.e., the range of values at each occurrence point) of current conditions (Table 1.2). We reclassified the climatic variables as suitable (range from minimum to maximum) and unsuitable (values below the minimum and above the maximum) for LGM, current and future scenarios. Using raster calculator, we added each reclassified binary variable together and created a hotspot distribution map. Low overlap ranged from 0–2 layers, medium overlap ranged from 3–4 layers, and high overlap ranged from 5–6 layers. These maps represent suitable climate conditions based on current thermal usage by *T. c. carolina*.

Occurrence Model (Local Scale)

To place the regional climate results in a local context, we explored a case study within Oak Openings Region in northwestern Ohio. We developed five separate occurrence models for *T. c. carolina* in northwestern Ohio by combining (a) species occurrence data with (b) bioclimatic data, and (c) local environmental data using MaxEnt. We utilized local environmental data that were readily accessible and biologically relevant for *T. c.* carolina. Presence-only records were randomly subsampled and separated withholding 30% of the records for test data and using 70% as training data, with ten replicates. We created five comparison distribution models for Current and Future scenarios. Each model included all six bioclimatic variables, percentage of forest, percentage of early successional, and normalized difference vegetation index (NDVI). Only the six bioclimatic variables varied across models as each set were based on current and the four future emission scenarios.

(a) Occurrence. Species occurrence data for *T. c. carolina* were obtained from the same subset of presence records from a current radio telemetry study (Martin & Root, Chapter 3). We used 47 records (decimal degree) within Oak Openings Region that were gathered as presence-only records from 2016 to 2019. These records were at least 75 m apart to reduce spatial autocorrelation. As stated earlier, the methods for tracking individuals were approved and permitted.

(b) Bioclimatic layers. We used the same six selected bioclimatic variables from our regional scale models for current and future conditions. All layers were clipped to Oak Openings Region using ESRI ArcGIS version 10.2.2.

(c) Local environment data. We created two additional environmental variables, i.e., land cover, and NDVI. We ran a supervised land cover classification using training data. We acquired one image from 19 June 2016 Landsat 8 for Path 20, Row 31, and we clipped the scene to only contain our entire study area (USGS 2019). Training sites were delineated in ENVI 5.5 (Harris Geospatial Solutions, Broomfield, CO, USA) across the study site for four classes, i.e., forests, early successional, human-modified, and water. We used a cropland mask (USDA FSA 2016) and then ran the supervised land cover classification. We merged the cropland layer with the classification map and created a final 5-class land cover map for Oak Openings Region. We converted the categorical land cover map to continuous data in FRAGSTATS version 4.2.1 (McGarigal & Marks 1995). To identify the percentage of landscape for forest and early successional land cover, we ran a moving window analysis with a 120 m buffer, four times the raster cell size (Schetter et al. 2013). A NDVI was created using the 19 June, 2016, Landsat 8 image for our study area in ArcGIS version 10.2.2.

We examined model accuracy using the area under receiver-operating-characteristic curve (AUC) values and converted each average model into a binary suitable and unsuitable distribution map using the logistic threshold for the maximum test sensitivity plus specificity (MSS). Additionally, we examined the influence of each environmental predictor variable using percent contribution and permutation importance for each climate scenario model.

Connectivity Model (Local Scale)

We created our own connectivity model using least cost pathways to examine whether individuals would be capable of dispersal along with changing climatic conditions. We used fine-scale movement data from an ongoing tracking study (Martin & Root, Chapter 4) to create three dispersal distance scenarios (minimum: 10 m/d; average: 35 m/d; and maximum: 200 m/d) to determine if *T. c. carolina* would be able to feasibly migrate within their life time (conservative estimate of 40 years). At this northern portion of the distribution range, we assumed that individuals would be able to travel for 252 days or 36 weeks per year as their active period occurs from mid-March to mid-November, with no movement during overwintering. Individuals in the southern portion of the distribution range would have a longer activity period and we expect they would be able to travel greater distances. Additionally, we would expect variation in movement with changing temperatures; however, we present a conservative estimate with the three dispersal scenarios.

Climate conditions are not the only barriers that *T. c. carolina* face when attempting to disperse, other physical barriers such as roads and streams reduce landscape connectivity. To estimate whether individuals could disperse to predicted novel areas of suitable climate, we built dispersal cost layers for (a) occupancy models, and five physical factors including (b) roads and streams, (c) elevation, and (d) land cover. We combined each cost layer together for four scenarios: Occupancy Model 1 and five physical factors; Occupancy Model 2 and five physical factors; Occupancy Model 3 and five physical factors; and five physical factors only, then we calculated the least cost path for each scenario for comparison. We assumed that our cost layers represent permeability of movement across the landscape and that favorable habitats have less resistance to movement than unfavorable habitats (Gonzales & Gergel 2007). We assigned relative general cost values based on order, which is assumed to be more important than absolute value assignments (Adriaensen et al. 2003). We also assumed that continuous suitable habitat is considered optimal for movements. We created cost raster layers in ESRI ArcGIS 10.2.2 for each occupancy model and each of the five physical layers (Sahlean 2014). To determine actual cost of travel for each physical layer, we used our field data to inform our decision.

(a) Occupancy models. We utilized the three occupancy models that were built in section 2.3. We created a separate cost layer for each occupancy model in ESRI ArcGIS 10.2.2. Each average continuous probability map was converted to a binary suitable and unsuitable map using the MSS threshold. We then assigned a cost of 1 to values above and a cost of 2 for values below the MSS threshold.

(b) Road and streams. We acquired road and stream shapefiles from U.S. Census Bureau (US Census Bureau 2009) and clipped the layers to our study area. We then calculated the Euclidean distance for road and stream layers to create a distance from continuous layer. We created an environmental profile layer using the presence-absence occurrence points, like our bioclimatic profile (Table 1.2), and used the minimum to maximum range values to assign a cost of 1, and a cost of 2 to any values above or below that range.

(c) Elevation. We obtained a digital elevation image courtesy of U.S. Geological Survey Earth Explorer server (USGS 2016) and we derived slope from this digital elevation model. We created an environmental profile layer and used the minimum to maximum range values to assign a cost of 1, and a cost of 2 to any values above or below that range.

(d) Land cover. We utilized an existing land cover map specifically created for the study area (Root & Martin 2018). We estimated how much each land cover would cost for *T. c. carolina*, we assumed that upland prairie, upland savanna, sand barrens, upland deciduous forest, and upland coniferous forest would have the smallest travel cost of 1, followed by wet prairie, swamp forest, floodplain forest, and wet shrubland with a cost of 2, then turf/pasture, Eurasian meadow, and cropland with a cost of 3, then residential/mixed, and dense urban with a cost of 4, and, finally, perennial pond the highest cost of 5. We assumed that wet habitats would be relatively more difficult to travel through than dry habitats as a result of flooded areas and that human-modified land cover types would be more difficult to move through as a result of potentially increased mortality events or human interference. Finally, we assumed that ponds are uncrossable, with the highest relative cost. We caution that these cost assignments are based on static current conditions and that some land cover types may become more favorable or unfavorable under warming conditions.

Our cost raster layers were simplified for practicality with such large-scale data. Fine-scale models could include greater detail for each cost raster if warranted. Each raster was reclassified into a binary cost raster, except land cover which had 5 cost values, and then we calculated the sum for all the values per pixel to create a final comprehensive dispersal cost raster for the least cost path analysis. We used the cost path tool in ArcGIS version 10.2.2 to derive the path of least resistance from the starting point to the destination point. It uses a cost surface raster, i.e., difficulty of travel, a cost distance analysis, i.e., inputs a source or starting point and calculates the accumulative cost to travel to each cell from the source, and a backlink raster, i.e., the direction from each cell to its lowest cost neighbor. The least cost pathway is calculated by backtracking from the destination point using the directions created by the backlink raster and the total cost accumulated from the distance raster to create a pathway to the source. Here, we estimated the best single pathway for each scenario from the starting point in Oak Openings Preserve to the destination point in Wildwood Metroparks, a straight-line distance of 20.6 km. We calculated the length of the least cost paths in km to determine how far *T. c. carolina* would need to travel at a minimum.

Results

CSMs (Regional Scale)

At a large scale, climate changes are likely to have relatively modest impacts on suitable habitat in the future compared to changes in the past. For each scenario the average model (i.e., average of 10 replicates) performed better than random with AUC values greater than 0.8 (ranging from 0.808 to 0.823) (Table 1.3). Using the MSS threshold value obtained for each scenario, suitable habitat ranged from 24.5%–30.3% across scenarios (Table 1.3). Habitat suitability continuous probability maps varied among each time period (Figure 1.1). All models except 2050 RCP 2.6 were largely affected by the environmental variable: mean temperature of the driest quarter based on the percent contribution (Table 1.4). In contrast, 2050 RCP 2.6 distributions were largely affected by mean temperature of the warmest quarter using the percent contribution (Table 1.4). We found that suitable habitat decreased over time, 5.8% from LGM to current conditions (Table 1.3). We found predicted increases in suitable habitat from current to future predictions: 2050 RCP 2.6 (4.6%), 2050 RCP 6.0 (4.4%), 2050 RCP 4.5 (4.7%) and 2050 RCP 8.5 (3.7%) (Table 1.3).

We examined the most influential variable using response curves (Figure 1.S1) and our test data jack-knife results for all our models. We found that for LGM, precipitation of driest quarter had the highest gain, or goodness of fit which indicates how closely the model is concentrated around the presence samples, when used in isolation and mean temperature of warmest quarter decreased the gain the most when omitted. Additionally, for all other models, we found that mean temperature of driest quarter had the highest gain when used in isolation and precipitation of driest quarter decreased the gain the most when omitted.

Over time, 45%–54% of the habitat remained unchanged in suitability across each scenario. Total change varied from 19% to 29% for *T. c. carolina* under the different climate scenarios (Figure 1.2, Table 1.5). The greatest habitat gain occurred between current conditions and 2050 RCP 4.5 with an increase of 39% in suitable habitat; while the greatest loss of suitable habitat occurred between LGM and current, with a decrease of 42%. All four future scenarios ranged from 10% to 17% loss of suitable climatic habitat and ranged from 36% to 39% gain of suitable climatic habitat. Overall, suitable habitat was lost from LGM to current, while future scenarios gained suitable habitat.

Our alternative CSMs supported our hypothesis that suitable habitat for this species would have a northward expansion. This held true for changes from LGM to current model, while suitable habitat both expanded northward and contracted in the south for future models (Figure 1.S2). The predicted suitable habitat losses across low to high categories ranged from 4.3% to 31.7% across all scenarios, while predicted suitable habitat gains ranged from 0.0% to 31.4% (Table 1.6). The greatest habitat gain for future change occurred for 2050 RCP 8.5 medium category with an increase of 31.4% in suitable habitat, while the greatest loss of suitable habitat for future change occurred 2050 RCP 8.5 high category with a decrease of 31.7% (Table 1.6).

Occurrence Model (Local Scale)

At the local scale, changes in suitability were readily detectable as a result of climate changes. We found that Model 1, 78% of the habitat was unsuitable and 22% was suitable (Table 1.7, Figure 1.3a). The model was largely affected by percentage of forest, precipitation of driest quarter, and precipitation of wettest quarter based on the percent contribution (Table 1.8). We found that the probability of presence increased as percentage of forest and precipitation of driest quarter increased (Figure 1.S3). We examined our jack-knife results and found that percentage of forest had the highest gain when used in isolation and precipitation of wettest quarter decreased the gain the most when omitted. In contrast, all future models had less suitable habitat than Model 1, ranging from 14.4% to 18.1% (Table 1.7, Figure 1.3b-e), and except for Model 2, all future models were largely affected by percentage of forest based on percent contribution and as this variable increases so does probability of presence (Table 1.8). Model 2 was largely affected by mean temperature of warmest quarter, followed by percentage of forest, and mean temperature of wettest quarter (Table 1.8). Additionally, our jack-knife results showed that mean temperature of warmest quarter had the highest gain when used in isolation and precipitation of driest quarter decreased the gain the most when omitted. Both Model 3, Model 4, and Model 5, respectively, were secondly largely affected by mean temperature of driest quarter, mean temperature of warmest quarter, and mean temperature of wettest quarter. Our jack-knife results varied across each future scenario; Model 3 had the highest gain for mean temperature of driest quarter, while Model 4 and Model 5 it was mean temperature of warmest quarter. Conversely, the variables that decreased the gain the most when omitted for Model 3 and Model 4, were mean temperature of driest quarter, while for Model 5 it was mean temperature of wettest quarter.

Connectivity Model (Local Scale)

While suitable habitat may be available both now and in the future, the question is whether it is likely to be accessible. We estimated that *T. c. carolina* would be able to disperse 101 km, 353 km, and 2016 km, respectively, per dispersal distance scenario (i.e., minimum, average, maximum) within their lifetime. These dispersal distances were based on feasible movement distances and do not consider physical barriers that would hinder movement. However, we examined constraints on movements in our local study area. We found that the least cost pathway from two protected areas varied across the five scenarios. All models had similar required distances to travel, ranging from 22.95 km to 23.84 km. Both Model 1 and Model 5 had similar pathways, while Model's 2 through 4 were more similar (Figure 1.4). We found that near the upper portion of the pathways, all models converge for the same least cost path. Individuals would have to cross 44 to 49 roads and avoid the Toledo Express Airport that lies in the center between the two parks to get from point A to point B. Even with the minimum dispersal distance, individuals can feasibly migrate despite a multitude of environmental barriers.

Discussion

MaxEnt modeling is a common method for modeling future changes in habitat suitability. Our prediction that this species would have expanding climatic habitat northward was supported with both our MaxEnt and alternative distribution models. Other studies have shown northern expansion for several taxa, such as *Ambrosia artemisiifolia* (Case & Stinson 2018), Lepidoterans (Lemoine 2015), *Dolichophis caspius* (Sahlean 2014), and several mesopredators: *Lontra canadensis*, *Mephitis*, *Canis latrans* (Pandey & Papes 2018). For our study, these changes are based on temperature and precipitation, which are important to reptilian movements. Overall, with warming climate, reptiles will face similar problems such as overheating and will require greater fine-scale heterogeneity which includes more shaded areas provided by more vegetation (Kearney et al. 2009). Forest canopy cover can provide critical structural complexity in its underlying microclimates (Chen et al. 1999) and facilitate fine-scale thermoregulation; however, local movements are limited by other physical barriers such as streams, roads, and human-modified landscapes. Therefore, habitat fragmentation may lead to the isolation of dispersing individuals within habitats that become suboptimal in terms of temperature and precipitation (Stefanescu et al. 2011). Utilizing land surface temperature maps can help identify critical areas of thermal limits for different species and land managers can manage the habitat to increase or decrease temperatures (e.g., manage amount of canopy cover). As with many problems that species face, there will be winners and losers as in Popescu et al. (2013), which found that reptiles show mixed responses to climate change across species. Our study suggests that *T. c. carolina* may benefit from climate change at a landscape scale with increased suitable habitat in the future, assuming that habitat is detectable and accessible, which will be dependent on local scale characteristics.

Our results for LGM, current and future regional models supported mean temperature of driest quarter as the most influential bioclimatic variable driving the model, except for RCP 2.6 scenario where mean temperature of warmest quarter was the most influential. This may have occurred because precipitation patterns may change more drastically at higher temperatures, i.e., RCP 2.6 to RCP 8.5 scenarios or it may be a result of more physiological stress when conditions are both warm and dry. Many climate models for North America have shown that some areas have an increase in precipitation over time (Dore 2005). For more northern areas, this may occur from warmer winter and spring temperatures that lead to more snowmelt and rain-on-snow events that create severe flooding (Yarnal et al. 1997). We found that greatest change occurred between LGM and current conditions; however, the temporal difference between these two scenarios is much greater than between current and future scenarios. Therefore, we caution when making too many conclusions about the change from past to present. Global climate changes are occurring at an unprecedented rate and many of these changes are alterations in temperature and precipitation. Surprisingly, we saw little change among the four future scenarios. Although our results suggest that *T. c. carolina* will have the greatest response to these changes within the driest and warmest quarters of the year, as we predicted based on physiological constraints. We found small percent contributions from precipitation of the wettest and warmest quarters (< 5.7%) across all models. This suggests high vulnerability during the driest and warmest temperatures of the year and declines may be expedited if these quarters become longer or temporally shift. At the local scale, we found an opposite trend for the current model where precipitation of wettest and driest quarters mattered the most and mean temperature was less important. This suggests that currently, temperature is vital for regional suitability, while precipitation matters locally. However, when we examined future models, mean temperature was most important, but varied which quarter mattered the most. At the local scale, *T. c. carolina* utilize a wide range of habitats for thermoregulation; however, when their body temperatures are too high, they seek cover in flooded or wet areas (Fredericksen 2014), spending days in these areas especially during high temperatures and droughts (Donaldson & Echternacht 2005). Therefore, precipitation and where water is located during the driest quarter would result in greater movement displacement. Physiologically, this makes sense because fluctuations in water availability or other fluctuations in the thermal environment exacerbates temperature regulation issues and stress responses (Seebacher 2005), therefore shaded and floodplain areas will become disproportionately more important during the driest season for these vulnerable species. Other studies have utilized different sets of these bioclimatic predictor variables and found that other variables were most important. For example, the most influential variable for *D.* caspius was mean temperature of coldest quarter (Sahlean 2014); for *Pseudopus apodus* it was temperature seasonality and annual precipitation (Nasrabadi et al. 2018). For several coral snake species, they were most affected by annual mean temperature, precipitation of wettest month, and precipitation of warmest quarter (Terribile et al. 2018). Since each study used a different set of bioclimatic factors, it is difficult to effectively compare variable importance. However, each species will be affected differently based on their ecological requirements, physiology, and location of their range. This underscores the need to translate regional climate change effects to the local scale context.

Under current conditions, our MaxEnt model predicted that *T. c. carolina* has a concentrated distribution within the middle of the eastern United States which is consistent with known range distributions. We expected that all future scenarios at a regional scale would result in the gain of suitable habitat and our results supported our hypothesis. We found that the proportion of suitable or unsuitable habitat showed moderate changes, i.e., 19% to 27%, it is critical to note, though, that where these changes occur will have large impacts on this species. Most of the changes, both gains and losses, occur on the distribution edge and relatively few changes within the center of the distribution. Although identifying these large-scale changes can help pinpoint critical priority areas for conservation efforts, we need finer-scale data to provide recommendations for on the ground management. Additionally, further examination should be done to identify why some of the southern areas had gains in suitable habitat, such as in Georgia

(Figure 1.2). In the future, suitable habitat may become inaccessible and isolated, therefore these models should distinguish between suitable and accessible locations (Miller & Holloway 2015). Identifying these areas, requires downscaling from regional to local scale maps. Therefore, we compared local scale models across current and future scenarios. We found that suitable habitat decreases over time and is limited (i.e., ~15%). For our case study, percentage of forest was the driving factor for all models except Model 2 which suggests that the availability of shade will drive individual responses. Depending on which emission scenario is used will vary which quarter (i.e., wettest, driest, or warmest) will drive turtle responses. Once again highlighting the need for local scale climatic datasets, especially when modeling future suitable habitat. However, in all cases, suitable habitat is limited and fragmented, which makes dispersal challenging. Warming climate may make forest habitat more suitable; however, it will also make open areas less suitable and costly to cross. This suggests that canopy cover is important for dispersal, although NDVI is a good model for canopy cover, it cannot substitute for measuring canopy cover at a fine scale. Our results, though, support the need to incorporate land cover or other remote sensed data with climate factors, as percentage of habitat and NDVI contribute to habitat suitability. We recognize that projecting changes into the future is challenging and deriving models with more models requires a lot of assumptions. Therefore, a mixture of different techniques that address both changes in spatial and temporal scale are needed to tackle this challenge. From a climatic perspective, *T. c. carolina* may not need to move, especially at the northern part of the distribution, therefore other biological processes (i.e., increased disturbance, fragmentation, competition, predation) will drive local scale movements.

We examined this problem using both our CSMs and finer-scale environmental data in Oak Openings Region to evaluate whether individuals could feasibly disperse despite climatic changes. Based on field data an individual could feasibly disperse to a new area within its lifetime to accommodate a changing landscape. However, this assumes that there are relatively few to no barriers and constant movement each day towards potentially new suitable habitat, as well as an ability to detect these new habitats. For example, in Oak Openings Region, we found that individuals would need to travel a total of 22.95 to 23.84 km to get from one protected area to another (an additional 2 to 3 km from the straight-line distance) using only physical factors on the landscape. It would take individuals approximately 5.5 months to 9.5 years based on our minimum to maximum dispersal scenarios and seasonal activity period to travel this distance. When we incorporated climate suitability combined with the physical environmental layers, we found that it produced a northern route, which did not vary much across different scenarios. We did find that the end portion of all models were the same and we suggest that local managers focus on protecting this route for potential dispersal. Although this distance ranges from 23% to 24% of the minimum dispersal distance scenario, it is unlikely that individuals will take the least costly, straight-line path. Individuals would have to carefully traverse a multitude of suboptimal habitat including roads, rivers, crops, and developed areas. Additionally, individuals would have to traverse a variety of thermal gradients that may become too intolerable in the future. It is worth noting that although better suitable habitat that is distant may be available and accessible, it may not be detectable by turtles. We caution that our cost assignments are based on static current conditions and that land covers may become less or more favorable with changing climate. Therefore, future studies should incorporate a greater range of cost values per environmental layer and consider how land cover permeability may change under warming conditions. For an example, upland prairie, was assigned a relative cost of 1 for current conditions; however, as temperatures increase, this land cover may become thermally challenging to travel through and could be assigned a cost of 2 instead. This type of dynamic modeling could provide greater insight into future movement patterns but should be undertaken cautiously as cost assignments may be difficult to infer. Individuals would be able to travel the required distance; however, when considering other structural features, many individuals would likely perish trying to disperse such large distances. *T. c. carolina* can persist in developed areas and can traverse croplands and flooded areas; however, they are susceptible to road mortality. Deaths on roads often change the population demographic and cause skewed adult sex ratios (Gibbs & Steen 2008). Additionally, this species is more susceptible to road mortality than other turtle species because they tend to close their shell when threatened and remain closed for longer periods of time (Gooley 2010). Increased road traffic will increase the probability of mortality and assuming no further habitat changes, will lead to a threshold effect that causes widespread local extinction (Kiester & Willey 2015). Additionally, another important variable that would influence *T. c. carolina* dispersal would be ditches or culverts, which are abundant throughout northwestern Ohio. These features are likely highly variable temporally with ditches having various levels of water levels which would vary dispersal responses. Currently, too little is known about the dispersal responses to ditches and culverts which are especially likely to be very complicated as it will vary both spatially and temporally. Therefore, we suggest that future models incorporate these factors and investigate dispersal using finer spatial and temporal scales. Although we found that there will be more suitable habitat in the future, it may not do any good with continued habitat fragmentation. We found that this species will face many difficult barriers and potentially have increased mortality when dispersing to future suitable habitat even with expanding suitable habitat, it may not be accessible.

Although *T. c. carolina* may not be as heavily impacted by climatic changes in terms of suitable area at the landscape-scale, it is important to provide a model for local scale context. *T. c. carolina* will remain under threat from a variety of sources, e.g., habitat destruction, invasive species, environmental pollution, disease, unsustainable use (Gibbons et al. 2000). Therefore, models should incorporate other biologically relevant variables (e.g., roads, land cover, elevation, streams/lakes, etc.) to represent the synergistic effects of multiple threats. Such a multifaceted approach is critical because the response of local populations will be dependent on regional weather patterns and local structural characteristics. In addition, climate change interacts with the landscape by altering the configuration and composition of land cover.

For example, lakes are sensitive indicators of climate alterations, this occurs from fluctuating water levels (Williamson et al. 2009) and timing changes in ice formation and thawing (Magnuson et al. 2000). As with many other studies, land-use patterns are often a larger driving factor that influences populations more so than climate alone (Rowe 2007; Hof et al. 2011). Our climatic habitat models illustrate that climatic change may be beneficial for this species; however, there are local scale challenges when other factors are examined that will affect how the species responds to these changes.

Conclusions

There is a critical need to protect and manage a flagship reptilian species such as *T. c. carolina*. We developed CSMs for this vulnerable species and evaluated the climatic variables that are influential in determining the geographic distribution and we predicted changes in potentially suitable habitat between different time periods. Our results predict moderate suitable habitat expansion. Additionally, we have identified areas that are susceptible to loss or gains in habitat within *T. c. carolina* distribution that can be monitored or managed. One of the most important aspects of our approach is to consider climate change impacts across a range of temporal and spatial scales from regional climate models to local occupancy models. Understanding the local context of large- scale changes is necessary to effectively manage for potential impacts on native flora and fauna and can highlight critical priorities. In addition to identifying where suitable habitat is and will be, we suggest that land managers should work towards increasing connectivity among suitable areas to facilitate dispersal. However, to examine these local scales, we need finer scale climatic data in combination with a variety of remotely sensed and locally collected data to inform our models. Finally, we suggest that future studies incorporate other dynamic ecological factors that influence distribution shifts.

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Tables

Table 1.1. The correlation matrix for six selected bioclimatic variables which includes average temperature (ºC) and precipitation (mm) for wettest, driest, and warmest quarters. Abbreviations are: Temperature (T), Wettest (Wet), Driest (Dry), Warmest (Warm), Quarter (Q), and Precipitation (P).

Layer	T of Wet	T of Dry	T of Warm	P of Wet	P of Dry	P of Warm
T of Wet	1.00	-0.06	0.22	0.12	-0.22	0.46
T of Dry	-0.06	1.00	0.78	0.67	0.65	0.29
T of Warm	0.22	0.78	1.00	0.62	0.38	0.33
P of Wet	0.12	0.67	0.62	1.00	0.44	0.78
P of Dry	-0.22	0.65	0.38	0.44	1.00	0.18
P of Warm	0.46	0.29	0.33	0.78	0.18	1.00

Table 1.2. The bioclimatic profile which includes minimum, maximum, and mean of the selected bioclimatic factors for T. c. carolina occurrence data.

Variable	Minimum	Maximum	Mean
Mean Temperature of wettest quarter (ºC)	1.2	27.2	20.3
Mean Temperature of driest quarter (ºC)	-4.0	27.7	8.28
Mean temperature of warmest quarter (ºC)	17.4	27.7	24.4
Precipitation of wettest quarter (mm/quarter)	221	731	351
Precipitation of driest quarter (mm/quarter)	121	448	227
Precipitation of warmest quarter (mm/quarter)	201	569	324

Table 1.3. The maximum test sensitivity plus specificity threshold (MSS) and model area under the curve (AUC) values with standard deviation for the Last Glacial Maximum (LGM), Current conditions, and four future Representative Concentration Pathway (RCP) scenarios. Including the percentage of suitable and unsuitable habitat based on the MSS threshold.

Scenario	MSS	AUC Values	Suitable Habitat (%)	Unsuitable Habitat (%)
LGM	0.3196	0.823 ± 0.004	30.3%	69.7%
Current	0.3598	0.819 ± 0.005	24.5%	75.5%
RCP 2.6	0.3109	0.815 ± 0.004	29.1%	70.9%
RCP 4.5	0.3584	0.811 ± 0.006	28.9%	71.1%
RCP 6.0	0.3260	0.808 ± 0.005	29.2%	70.8%
RCP 8.5	0.3261	0.810 ± 0.002	28.2%	71.8%

Table 1.4. For each climate scenario model is presented the percent contribution (% C) and permutation importance (PI) for each environmental predictor variable with the highest contribution in bold. All temperature variables are in (ºC) and all precipitation variables are in (mm). Abbreviations are: Temperature (T), Wettest (Wet), Driest (Dry), Warmest (Warm), Quarter (Q), and Precipitation (P).

	LGM		**Current**		**RCP 2.6**		**RCP 4.5**		**RCP 6.0**		**RCP 8.5**	
Variable	**% C**	**PI**	**% C**	**PI**	**% C**	**PI**	**% C**	**PI**	**% C**	**PI**	**% C**	**PI**
Mean T of Wet Q	3.0	4.0	15.2	6.9	23.4	23.7	14.4	11.4	19.2	7.8	21.7	12.4
Mean T of Dry Q	**45.1**	23.7	**31.3**	**30.1**	20.3	24.2	**33.7**	**28.8**	**25.5**	**27.7**	**30.2**	**35.0**
Mean T of Warm Q	35.6	**41.6**	30.4	25.2	**27.8**	23.7	27.4	23.3	28.9	23.7	25.3	21.5
P of Wet Q	1.8	6.4	2.2	9.4	2.1	10.4	1.7	6.9	1.9	6.7	2.2	6.4
P of Dry Q	12.5	17.2	19.9	25.6	23.3	**27.5**	18.5	25.8	23.8	32.6	14.9	21.5
P of Warm Q	2.0	6.4	1.0	2.8	3.1	4.1	4.4	3.9	0.6	1.5	5.7	3.3

Table 1.5. Predicted changes in the climatically suitable habitat area of T. c. carolina under varying climate scenarios within their distribution range. Abbreviations: Last Glacial Maximum (LGM) and Representative Concentration Pathway (RCP).

Change Scenario	**Unchanged**	**Gain**	**Loss**	**Total change (= Gain - Loss)[1]**
LGM -> Current	45%	13%	42%	-29%
Current -> 2050 RCP 2.6	54%	37%	10%	27%
Current -> 2050 RCP 4.5	45%	39%	16%	23%
Current -> 2050 RCP 6.0	50%	38%	12%	26%
Current -> 2050 RCP 8.5	47%	36%	17%	19%

Table 1.6. Predicted changes in the percent of climatically suitable habitat for T. c. carolina using hotspot maps based on the number of environmental predictor layers that overlap with one another. We classified low overlap (0–2 layers), medium overlap (3–4), and high overlap (5–6). Abbreviations: Last Glacial Maximum (LGM) and Representative Concentration Pathway (RCP).

# of Layer Overlap	LGM	Current	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
Low	0.0%	0.0%	0.5%	0.3%	0.2%	0.3%
Medium	49.4%	45.1%	54.9%	71.7%	72.3%	76.5%
High	50.6%	54.9%	44.6%	28.0%	27.5%	23.2%

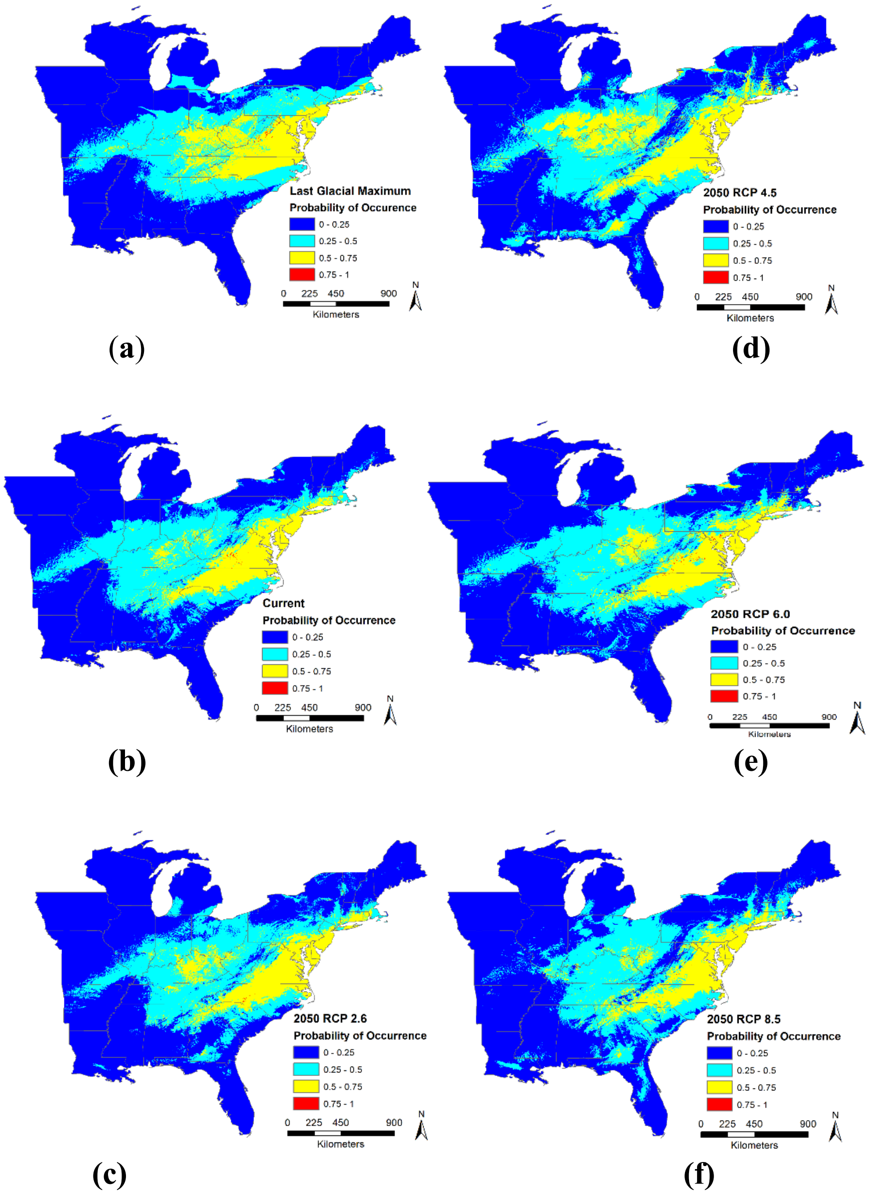
Table 1.7. The maximum test sensitivity plus specificity threshold (MSS) and model area under the curve (AUC) values with standard deviation for Current conditions and four future Representative Concentration Pathway (RCP) scenarios. Including the percentage of suitable and unsuitable habitat based on the MSS threshold.

Model #	Scenario	MSS	AUC Values	Suitable Habitat (%)	Unsuitable Habitat (%)
1	Current	0.3452	0.852 ± 0.076	22.0%	78.0%
2	RCP 2.6	0.4003	0.905 ± 0.039	14.8%	85.2%
3	RCP 4.5	0.4042	0.896 ± 0.0039	14.4%	85.6%
4	RCP 6.0	0.4277	0.883 ± 0.063	13.9%	86.1%
5	RCP 8.5	0.3194	0.860 ± 0.070	18.1%	81.9%

Table 1.8. Presented are the percent contribution (% C) and permutation importance (PI) for each environmental predictor variable with the highest contribution in bold for each Model. All temperature variables are in (ºC) and all precipitation variables are in (mm). Abbreviations are: Mean Temperature (MT), Wettest (Wet), Driest (Dry), Warmest (Warm), Quarter (Q), Percentage (%) Precipitation (P), Early successional (ES), and Land surface temperature (LST).

	Model 1		**Model 2**		**Model 3**		**Model 4**		**Model 5**	
Variables	**% C**	**PI**	**% C**	**PI**	**% C**	**PI**	**% C**	**PI**	**% C**	**PI**
MT of Wet Q	5.3	17.3	12.1	7.7	5.6	3.1	10.8	3.7	22.4	32.2
MT of Dry Q	1.1	2.1	4.9	4.5	24.1	**46.7**	12.9	**23.8**	21.4	14.9
MT of Warm Q	1.0	0.0	**46.6**	**64.7**	10.6	95	0.3	0.5	17.9	**36.3**
P of Wet Q	11.5	**55.3**	0.4	0.6	2.7	0.3	3.8	12.4	0.0	0.0
P of Dry Q	18.2	0.0	11.0	10.3	6.1	15.8	3.8	12.4	3.1	4.6
P of Warm Q	5.1	11.8	0.4	1.5	1.2	0.8	0.0	0.0	4.2	5.4
% of forest	**45.7**	9.0	18.2	5.5	**41.3**	17.8	**37.1**	11.2	**27.7**	4.0
% of ES	6.3	4.5	2.4	2.0	5.3	4.3	4.1	3.1	1.8	0.3
NDVI	5.7	0.0	3.9	3.2	3.1	1.8	6.4	6.2	1.4	2.4

Figures

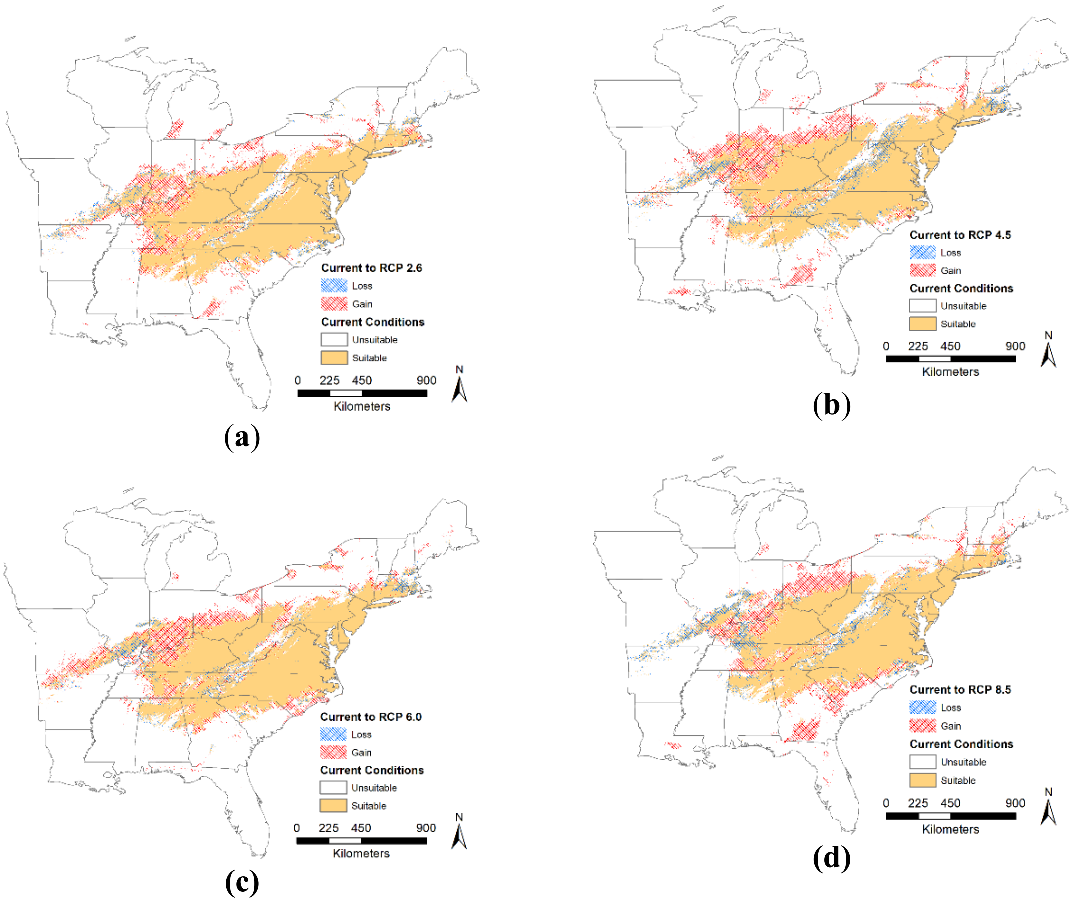


(a) **(d)**

(b) **(e)**

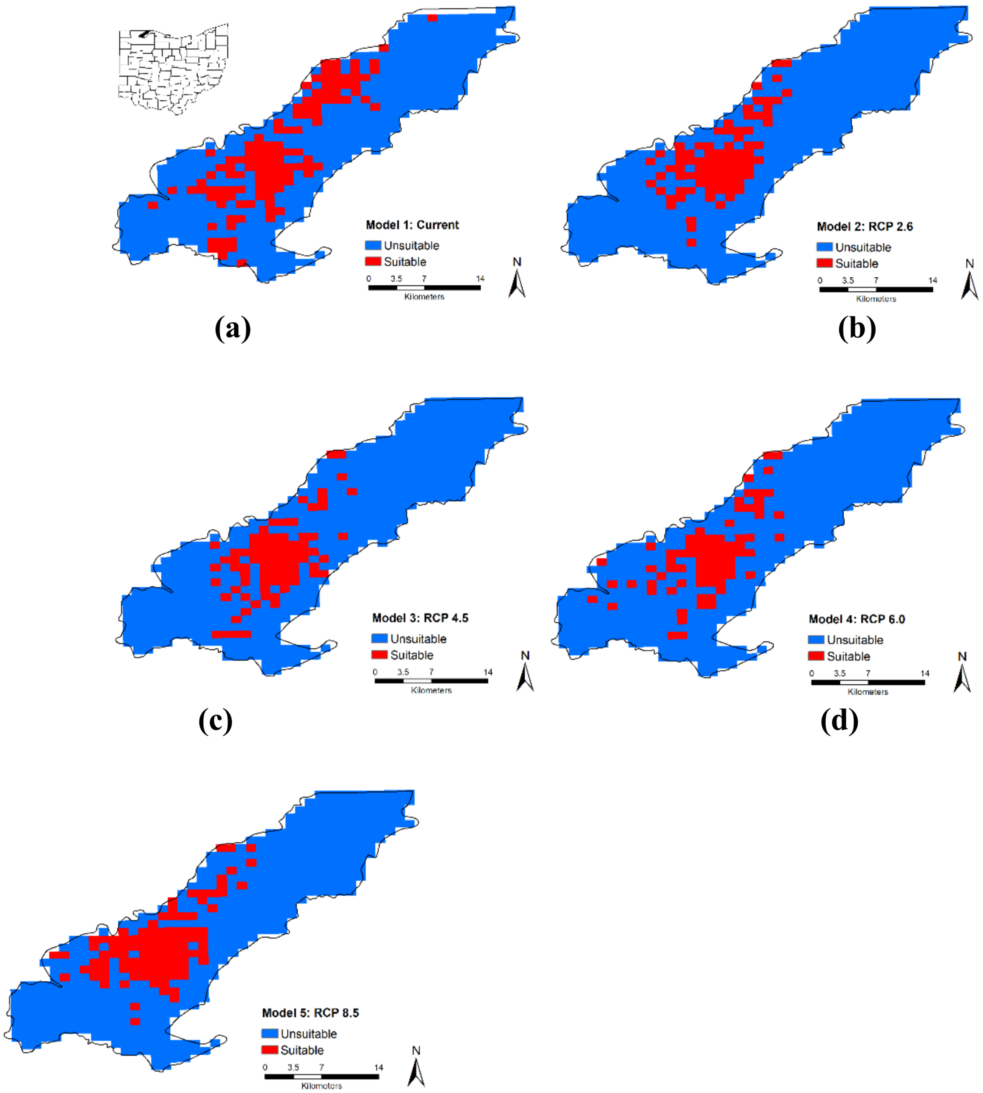
(c) **(f)**

Figure 1.1. Climatic habitat suitability continuous probability maps for T. c. carolina for four different time periods. (a) Last Glacial Maximum (LGM); (b) Current; (c) 2050 Representative Concentration Pathway (RCP) 2.6; (d) 2050 RCP 4.5; (e) 2050 RCP 6.0; (f) 2050 RCP 8.5. Color changes indicate probability of suitability, with blue indicating low to no probability and red indicating high probability.



(a) **(b)** **(c)** **(d)**

Figure 1.2. Predicted current (unsuitable and suitable) combined with future loss (in blue) and gain (in red) habitat for T. c. carolina. Future predictions are based on four emission scenarios for 2050 with changes from current to (a) 2050 Representative Concentration Pathway (RCP) 2.6; (b) 2050 RCP 4.5; (c) 2050 RCP 6.0; (d) 2050 RCP 8.5.



(a) **(b)**

(c) **(d)**

(e)

Figure 1.3. Climatic habitat suitability maps for T. c. carolina for five models, which include six bioclimatic variables, percentage of forest, percentage of early successional, and normalized difference vegetation index (NDVI). (a) Model 1: Current; (b) Model 2: 2050 Representative Concentration Pathway (RCP) 2.6; (c) Model 3: 2050 RCP 4.5; (d) Model 4: 2050 RCP 6.0; and (e) Model 5: 2050 RCP 8.5 for Oak Openings Region in northwestern Ohio.

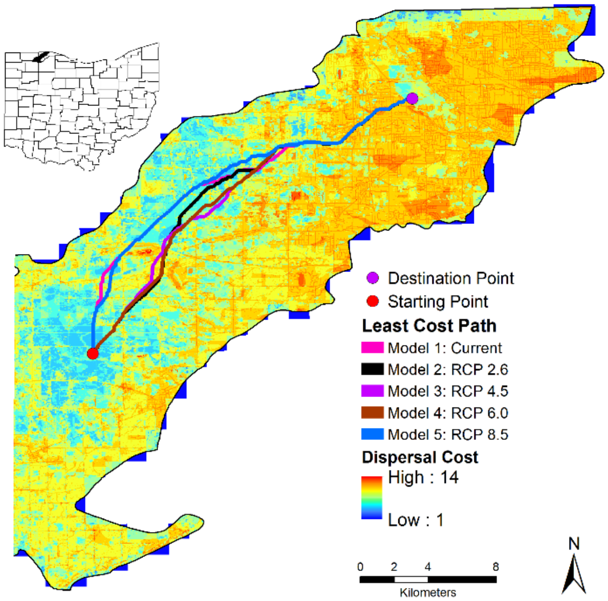


Figure 1.4. The least cost paths that individuals can take from Oak Openings Preserve to Wildwood Metroparks for five scenarios. Model 1: Current, Model 2: 2050 Representative Concentration Pathway (RCP) 2.6, Model 3: 2050 RCP 4.5, Model 4: 2050 RCP 6.0, and Model 5: 2050 RCP 8.5. Least cost paths (colored lines) are overlaid on the cost layer with high travel cost (in red) and low travel cost (in blue) for current conditions.

CHAPTER 2: USING THE PATTERNS OF DIVERSITY AND HABITAT SUITABILITY OF REPTILES AS A PLANNING TOOL

Abstract

Aim: To develop logical multi-species habitat suitability models based on manageable environmental predictor variables and identify patterns of diversity for a suite of reptilian species in northwestern Ohio and extrapolate to southeastern Michigan. Guide management and conservation strategies within a biodiverse region that lies within a human-dominated landscape.

Location: Oak Openings Region extending from northwestern Ohio to southeastern Michigan

Methods: Habitat suitability models were created in MaxEnt for four representative reptilian species and for reptiles using 10 environmental predictor variables. Patterns of diversity were examined with the overlap of suitable habitat for the four target species. Presence data was collected using field surveys in Ohio and supplemented with citizen science research grade data from iNaturalist. We withheld 15% of data as an independent validation set to test model accuracy.

Results: Our models showed that less than half the area was suitable for reptiles with restricted suitable habitat for species of concern, i.e., eastern box turtles and eastern hognose snakes, and more abundant for common species, i.e., midland painted turtle and eastern garter snake. Floodplain forest was an important predictor variable across reptilian species with increasing probability of suitable habitat as floodplain forest habitat increased within a 120 m buffer. Model validation generally improved when changing from minimum to maximum models. Over half the area in Michigan and roughly 20% of the area in Ohio was not suitable for the four target species and there were very limited highly suitable areas, less than 2%.

Main conclusions: Our study highlights the need for a conservation plan that examines the range of limitations for a suite of reptilian species in Oak Openings Region. Conservationists should utilize both generalizable models and species-specific models at multiple scales to make informed management decisions. MaxEnt models can be used to identify important predictor variables that can be altered on the landscape, such as our models where land surface temperatures around 20ºC are more suitable for both midland painted turtle and eastern garter snake. Canopy cover manipulations can be done to increase or decrease land surface temperatures.

Introduction

Many organisms are negatively affected by accelerating anthropogenic activities which alter and degrade many habitats, overexploit natural resources, affect global climate change, and spread invasive species (Brook, Soghi, & Bradshaw, 2008; Hoekstra, Boucher, Ricketts, & Roberts, 2005). Reptiles are currently facing global population declines from a variety of threats (Spotila et al., 2000; Donaldson, & Echternacht, 2005; Lewis et al., 2004; Moore & Seigel, 2006), especially those that stem from human impacts (Gibbons et al. 2000). In order to effectively conserve reptilian species it is critical to understand their spatial ecology to provide stronger management recommendations, i.e., identifying potential restoration sites, increasing connectivity among protected areas. Often natural landscapes are encroached by expanding development by humans (Levia & Page 2000; Lugo 2002), therefore these mixed disturbance environments have a variety of active management and anthropogenic activities, that can influence species distributions. Many efforts have focused on protecting umbrella species within highly charismatic megafauna, such as mammals and birds, in the hope that this will protect other taxa (Sibarani, Marco, Rondinini, & Kark, 2019). These species are often selected since they have large home ranges or potential for dispersal; however, they are not always effective surrogates for regional species conservation (Andelman, & Fagan, 2000). The assumption in this approach is that umbrella species are representative of the surrounding ecosystem and conservation actions made to aid the umbrella species will promote the persistence of many or preferably all other species within the area (Caro et al., 2005). However, studies (Breckheimer et al., 2014; Stewart et al., 2017; Runge et al., 2019) have shown that focusing on one target taxon often excludes others such as herpetofauna. Many taxa operate at different spatial scales and have different ecological requirements (Wellenreuther, Syms, & Clements, 2007); therefore, it is critical to examine a suite of species to make more informed conservation decisions. Currently, though, we lack knowledge of the basic spatial distributions for even the best-studied taxa (Ficetola et al., 2013) and detecting cryptic, threatened and/or rare, and nocturnal species is challenging. Other logistical issues, such as the need for expensive and time-consuming surveys, highlight the utility of analytical techniques, e.g., distribution modeling that can maximize the value of survey data.

Species distribution modeling has allowed researchers to predict distributions and suitable habitat across a broad geographic area while additionally identifying important variables that influence these distributions. Scale-dependent factors play an important role in the selection of these predictor variables, e.g., macroclimate factors have large-scale impacts, while microhabitat selection of breeding sites and biotic interactions shape local-scale distributions (Trumbo et al., 2012; Nams, & Bourgeois, 2004; Mayor et al., 2009). Ecologists have been working on linking these macroclimate and microhabitat factors to better understand their influence on species distributions (Peterson, & Parker, 1998; Turner et al., 2001; Scott et al., 2002; Reunanen et al., 2002; Bowne, Bowers, & Hines, 2006; Kindlmann, & Burel, 2008).

Land cover type has often been a good predictor of animal distributions at regional scales (Scott et al., 2002; Van Buskirk, 2005; Elith et al., 2006). This is helpful for land managers because land cover can be modified through restoration and management to suit the needs of the target species, either by increasing or decreasing specific land cover types to facilitate habitat suitability. Land cover can be managed by focusing on each specific type or can focus on a suite of land cover types. Species often use a variety of land covers and management can manage habitat based on functionality by the target species instead of by the amount. Single species modeling is an excellent tool for examining threatened, focal, umbrella or flagship species within conservation planning. However, as more and more species suffer from increasing urbanization and large-scale population declines, there is a greater need to examine community-level spatial modeling. Multi-species modeling provides useful insight into species distributions and facilitates mapping of biodiversity hotspots. For reptiles, occurrence data are often sparse and restricted to small areas as a result of their highly cryptic nature. Therefore, presence-absence data are often less reliable and obtainable, especially for cryptic reptilian species (Mazerolle et al., 2007). In the absence of large reptilian data sets it is critical to find ways to use limited datasets to identify areas of new populations, habitat suitability, biodiversity hotspots, dispersal patterns, geographical range distributions and predict climatic influences or species invasion risk on species distributions.

In this study we quantified habitat suitability using simple and comparable models for a suite of representative reptilian species within Oak Openings Region, a biodiversity hotspot in northwestern Ohio to southeastern Michigan, to aid local land management and planning. Conceptually, we assumed that site occupancy relates directly to habitat suitability, i.e., that where an individual is detected is suitable. We chose to model habitat suitability using MaxEnt, which has been used to examine reptilian distribution patterns (Rose, & Todd, 2014; Sahlean et al., 2014; Cross, 2016; Stryszowska et al., 2016; Hosseinian Yousefkhani et al., 2017; Maqsood Javed, Raj, & Kumar, 2017). We also sought to identify important predictor variables that can be managed or modified to increase habitat suitability. Our research addressed (1) where the most suitable habitats for reptiles were located within Oak Openings Region; (2) which environmental predictor variables had the greatest influence on habitat suitability; and (3) what features characterized the greatest biodiversity hotspots. Our study area was unique with its focus on a biodiverse and heterogeneous landscape; however, this research provides a successful example of how to utilize sparse data to develop better land use plans for managing complex landscapes for a suite of species.

Methods

Oak Openings Region

Oak Openings Region is a biodiverse hotspot that was sculpted by the same glaciation event that shaped the Great Lakes. The region, expanding from northwestern Ohio to southeastern Michigan, is highly heterogenous despite lying within a human-dominated landscape. Although the region is relatively small, 477 km^2 for Ohio and 1461 km^2 for Michigan, it contains almost a third of Ohio's rare flora and fauna (Schetter et al., 2013). Within midwestern United States, this region contains five globally rare communities (Brewer, & Vankat, 2004), which land managers have identified as conservation targets. Conservation efforts have focused primarily on upland savanna/prairie, wet prairie, upland deciduous forest, floodplain forest, and swamp/flatwood forest and management goals were developed through modeling ecosystems suitability with target representative species (Root, & Martin, 2018). These ecosystems provide critical habitat for a suite of reptilian species including eastern milksnake

(*Lampropeltis triangulum*), spotted turtle (*Clemmys guttata*), eastern box turtle (*Terrepene carolina carolina*), Blanding's turtle (*Emydoidea blandingii*), and eastern massasauga (*Sistrurus catenatus catenatus*) (Gardner, 2016).

Occurrence Dataset and Species Selection

Presence-only records were collected using visual encounter surveys, both line transects and quadrat surveys, and opportunistically within Oak Openings Region from 26 April 2014 to 27 September 2014 (Martin, 2015) and 2017-2019. In 2014, we sampled 189 quadrat surveys, which encompassed a 400 m^2 area per quadrat or 75,600 m^2 area surveyed within Oak Openings Preserve. Additionally, in 2014, we approximately surveyed 82,503 m^2 area using opportunistic visual encounter surveys within Oak Openings Preserve. Opportunistic visual encounter surveys from 2017 – 2019 surveyed roughly 1,200,000 m^2 across six parks. In 2019, we surveyed 87 line transects, 200 m in length, for a total of 87,000 m^2 area across five parks. Additionally, incidental observations were provided from other researchers (unpublished data, 2019). We recorded the GPS coordinates with a handheld GPS unit (Garmin eTrex) when we detected a reptile. The methods for detecting reptilian species were approved and permitted by Metroparks Toledo, Kitty Todd, and Maumee State Forest. We supplemented our data with citizen science records downloaded from iNaturalist database (i.e., research grade) within Oak Openings Region (Table 2.S1). These additional records comprised between 18% and 56% of records for our selected species models. Species were selected based on sample size, ecological status, and variety of ecological niches. We selected two snake species, i.e., eastern garter snake (*Thamnophis sirtalis sirtalis*) with a total of 21 occurrence records and eastern hognose snake (*Heterodon platirhinos*) with a total of 15 occurrence records, and two turtle species, i.e., eastern box turtle (*Terrapene carolina carolina*) with a total of 66 occurrence records, and painted turtle (*Chrysemys picta*) with a total of 21 occurrence records.

We chose two species of special concern, i.e., eastern hognose snake and eastern box turtle, and two common species, i.e., eastern garter snake and eastern snapping turtle, in order to compare similarities and differences in the availability of suitable habitat. Land managers can make more informed decisions by evaluating quality habitat for both common and at-risk species. These community-level models can be used to fit multiple species within a single step or can improve predictions for rare species by utilizing information from common species (Nieto-Lugilde et al. 2018). Additionally, we considered ecological requirements across the suite of present reptilian species within the region. Eastern garter snakes encompass a large breadth of ecological habitats; as a generalist, they are found within meadows, marshes, woodlands, and hillsides and tend to live near water and grassy environments (Behler & King 2000). While eastern hognose snakes are more specialized, mostly found in dry, sandy and near woodland edges. Eastern box turtles are terrestrial habitat generalists, utilizing woodlands, prairies, floodplains and marshy areas, while midland painted turtles are highly aquatic and spend much of their time within lakes and ponds (Behler & King 2000). This selection of species served as a representative sample of reptilian biodiversity across the region.

For our combined model, we included all records of detected reptiles (40 snakes and 99 turtles) within field surveys, which additionally included non-focal snakes, i.e., blue racer (*Coluber constrictor foxii*) with a total of 4 occurrence records, Dekay's brownsnake (*Storeria dekayi*) with a total of 2 occurrence records, northern ring necksnake (*Diadophis punctatus edwardsii*) with a total of 3 occurrence records, northern water snake (*Nerodia sipedon*) with a total of 1 occurrence record, and 4 unidentified individuals to species and non-focal turtles, i.e., Blanding's turtle with a total of 2 occurrence records, eastern spiny softshell (*Apalone spinifera*) with a total of 2 occurrence records, eastern snapping turtle (*Chelydra serpentina*) with a total of 10 occurrence records, northern map turtle (*Graptemys geographica*) with a total of 2 occurrence records and 13 unidentified individuals to species (Table 2.S1). The iNaturalist database records included both focal and non-focal snakes including blue racer with a total of 1 occurrence record, Dekay's brownsnake with a total of 1 occurrence record, eastern garter snake with a total of 10 occurrence records, eastern hognose snake with a total of 15 occurrence records, northern ribbon snake (*Thamnophis sauritus septentrionalis*) with a total of 1 occurrence record, northern ringneck snake with a total of 1 occurrence record, and northern water snake with a total of 1 occurrence record and turtles including eastern box turtle with a total of 13 occurrence records, eastern snapping turtle with a total of 4 occurrence records, and midland painted turtle with a total of 6 occurrence records (Table 2.S1).

Environmental Predictor Variables

Several environmental variables were initially considered for modeling including 19 bioclimatic variables (Karger et al., 2017a, 2017b) and landscape configuration, i.e., edge and heterogeneity. We checked if these predictor variables were highly correlated in ArcGIS vers. 10.2.2 (Earth Systems Research Institute, Redlands, CA, 2002) using band collection statistics within our study region. For variables that were highly correlated with another variable, r > 0.80, we removed one of the pair. Therefore, we only present our final candidate predictor environmental variables.

Our final set of environmental predictor variables described climate (land surface temperature), land cover (percentage of: deciduous forest, swamp forest, floodplain forest, upland savanna, upland prairie, and water), elevation (aspect and percent slope), and structural features (patch cohesion index) at 30-m resolution and were derived from remotely sensed data (Table 2.1). These were selected based on our knowledge of reptilian ecology and relatively comparability to other habitat suitability models (Rizkalla & Swihart 2006; Stryszowska et al. 2016; Massod Javed, Raj, & Kumar 2017; Corovic et al. 2018). For climate, we created a multi-seasonal land surface temperature map in ArcGIS for our study area, derived from three Landsat 8 images using the thermal bands (USGS EarthExplorer): 16 April 2016, 19 June 2016, and 9 October 2016 (Table 2.S2). Both thermal bands were converted into radiance, which is the power per unit that is directed towards a sensor, using raster calculator and then converted to At-Satellite Brightness Temperature, which is a measurement of the radiance traveling upward from the atmosphere to the satellite (USGS, 2019), in ºC. We created a normalized difference vegetation index (NDVI), which is an estimate of the density of vegetation, for each image and used it to calculate land surface emissivity, which is the efficiency for which land surface radiates its thermal energy. Land surface temperature was then estimated for both thermal bands and the average value calculated with cell statistics for each image (Koppad, & Malini, 2018). Finally, we used cell statistics to average each image's land surface temperature to create the final multi-seasonal land surface temperature map for our study area. For land cover, we converted the categorical land cover map created for the study area (Root, & Martin, 2018) into continuous data using FRAGSTATS ver. 4.2.1 (McGarigal, & Marks, 1995). We estimated percentage of land cover within a 120-m buffer using an eight-neighbor rule (i.e., diagonals are included) for each land cover type as shown in Table 2.1. For elevation, we obtained a digital elevation image from the U.S. Geological Survey Earth Explorer server (USGS, EarthExplorer) and derived both aspect and percent slope. Finally, for connectivity, we calculated patch cohesion index, which measures the physical connectedness of the corresponding patch type, from the 15-class land cover map.

Habitat Suitability Modeling

For our combined (all reptiles detected) model and each selected species, suitable habitat was modeled in MaxEnt ver. 3.3.3 (Phillips et al., 2006) by combining presence-only occurrence records with selected environmental predictor variables (Figure 2.1). MaxEnt uses maximum entropy modeling, which is a machine-learning technique that identifies suitable habitat from a set of environmental layers based on georeferenced occurrence localities. We ran 10 replicates with cross-validation, random seed, and a 0.5 regularization parameter. The result of each replicate was a model (i.e., map) of probability of occurrence based on the characteristics found at known occurrences. We examined the minimum, average, and maximum models (i.e., models with the minimum, maximum or average probability value across all cells for the ten replicates) and converted each continuous probability distribution into a binary suitable and unsuitable distribution map using the maximum test sensitivity plus specificity (MSS) threshold. We selected this threshold because it balances the omission or false negative (a species is present but identified as absent) error rates with commission or false positives (a species is absent but identified as present) error rates. We examined the range of habitat suitability by comparing the minimum, average, and maximum models, which provides critical information on the upper and lower limits or the full range of possibilities. Focusing only on the average model may prevent understanding of individual differences within a species. The number of cells for suitable habitat and unsuitable habitat were converted to percentages.

We examined the importance or influence of each predictor variable using two measures: percent contribution and permutation importance produced by MaxEnt program. During model training, the MaxEnt algorithm increases the model gain by modifying the coefficient for a single feature and then assigns the gain increase to the environmental variables that the feature depends on; at the end of the training process, these assignments are converted to percentages, i.e., percent contribution (Phillips 2017). These values depend on the algorithm used and may vary. The second measure of variable contribution is permutation importance which depends only on the final model not the path taken. The contribution of each variable is randomly permutated among the training points and then measuring the resulting decrease in training AUC, normalizing the values to percentages (Phillips 2017). We used the jack-knife function in MaxEnt program as an alternative estimate of variable importance. This function first excludes each variable in turn and creates a model with the remaining variables, then creates a model using each variable in isolation (Phillips 2017). Variables that have the highest gain when used in isolation have the most useful information by itself, while variables that decrease the gain the most when omitted have the most useful information that the other present variables do not have. Gain is a measure of goodness of fit where it indicates how closely the model is concentrated around the presence samples. Finally, we present the response curves for each modeled species of the top two environmental predictor variables based on percent contribution.

We ran a post hoc final model for one example target species (midland painted turtle) to compare differences across spatial scales, i.e., fine- vs. local scale. We found that the 120 m spatial buffer highlighted more suitable habitat than expected for midland painted turtles and we wanted to examine whether a reduced buffer size would reduce the amount of suitable habitat. Therefore, we reduced the spatial buffer from 120 m to 60 m to estimate the percentage of land cover (PLAND) within the region and for patch cohesion index in FRAGSTATS ver. 4.3.2 (McGarigal, & Marks, 1995). In order to run the moving window in PLAND, the buffer size should be in multiples of the raster cell size, i.e., 30 m. We then modeled habitat suitability for midland painted turtle using the derived variables from the 60 m buffer; all other conditions were the same. We convert the continuous probability distribution into a binary suitable (values above threshold) and unsuitable (values below threshold) map using the MSS threshold of 0.416. We examined the response curves and jack-knife results for comparison to the results of the 120 m model. This allowed us to check and compare between the 120 m and 60 m model whether the same or different variables were more influential.

Patterns of Diversity

We examined the patterns of reptilian diversity across the region by combining the four species (i.e., eastern garter snake, eastern hognose snake, eastern box turtle, and midland painted turtle) distribution models together. Here, we identified the areas of least to greatest species diversity by combining each of the suitable/unsuitable species maps together using raster calculator in ArcGIS. Comparisons between Ohio and Michigan were made for protected lands. We calculated the percentage of area within and outside of protected areas for the two states. We then characterized the underlying habitats within each area from least to greatest species diversity. Here, we extracted each attribute, i.e., number of species overlap, from the diversity map and clipped the area from a simplified land cover map (Root & Martin 2018). We calculated the percentage of area for each land cover type for each diversity map category, i.e., overlap of suitable habitat for four species. We tested for significant differences between the number of species overlap (response variable) and the percent area of a given land cover type (predictor variable) using least squares means comparison in JMP ver. 11 (SAS Institute Inc., Car, North Carolina, USA).

Model Evaluation and Validation

Model performance was analyzed using the Areas under the Curve value (AUC) with values greater than 0.75 indicating an informative model (Swets, 1988; Eskildsen et al., 2013). We additionally set thresholds for models using the MSS threshold to discriminate between suitable and unsuitable habitat. To maintain large enough sample size across models, i.e., greater than 10 occurrence points per species, we withheld 15% of our data, i.e., validation dataset, for each species to test our models. The percentage of correctly assigned occurrence points within classified suitable habitat was compared to the percentage of incorrectly assigned occurrence points within classified unsuitable habitat. For our combined (all reptiles detected) model, we used all reptile presence records collected in the field and used the iNaturalist research grade observations as an independent validation dataset.

Results

Habitat Suitability Models

We modeled habitat suitability for our combined (all reptiles detected) and for our four representative species using presence-only records in MaxEnt (Figure 2.2). We used the average MSS threshold value and found that suitable habitat ranged from: 28.5% to 47.2% of the study area for combined (all reptiles detected), 38.8% to 69.7% for midland painted turtles, 10.1% to 19.4% for eastern box turtles, 37.4% to 84.4% for eastern garter snakes, and 15.9% to 59.4% for eastern hognose snakes (Table 2.2; Supplement Figure 2.1 a-e). We found that suitable habitat for combined (all reptiles detected) was mostly influenced by percentage of floodplain forest and upland deciduous forest within a 120 m buffer. All selected species were greatly influenced by percentage of floodplain forest within a 120 m buffer. However, suitable habitat for both midland painted turtle and eastern garter snake were also influenced by land surface temperature, while eastern box turtle was affected by percentage of upland deciduous forest and eastern hognose was affected by percentage of coniferous forest (Table 2.3).

We examined the response curves for the two most influential variables for each species. We found that all species had increasing probability of suitable habitat as the percentage of floodplain forest increased (Figure 2.3 a-e), with similar results for upland deciduous forest (Figure 2.3c) and upland coniferous forest (Figure 2.3e). However, probability of suitable habitat decreased as land surface temperature increased for midland painted turtle (Figure 2.3b) and eastern garter snake (Figure 2.3d). Our jack-knife results were variable across species. Floodplain forest had the highest gain, i.e., how concentrated the model is around the presence samples, when used in isolation for combined (all reptiles detected), eastern garter snake and eastern hognose snake. In contrast, the highest gain when used in isolation was land surface temperature for midland painted turtles and percentage of upland deciduous forest for eastern box turtles. The gain decreased the most when omitting upland deciduous forest for combined (all reptiles detected) and eastern box turtle, land surface temperature for midland painted turtle, percentage of upland savanna for eastern garter snake, and percentage of floodplain forest for eastern hognose snake.

For our alternative post hoc midland painted turtle model, we found that suitable habitat was 6% for the minimum, 11% for the average, and 17% for the maximum models for the total study area (Figure 2.S2). Suitable habitat was changed and was mostly influenced by percentage of swamp forest and conifer forest within a 60 m buffer (Table 2.S3). The response curves showed that as the percentage of these land covers increased, so did habitat suitability. Our jack-knife results showed that land surface temperature had both the highest gain when used in isolation and decreased the gain the most when omitted. The variables response curve showed that as land surface temperature increased, habitat suitability decreased.

Model Evaluation and Validation

Our combined (all reptiles detected) model used 93 training, 11 test and 37 validation points; midland painted turtle with 11 training, 1 test and 3 validation points; eastern box turtles with 40 training, 5 test and 9 validation points; eastern garter snake with 14 training, 2 test and 3 validation points; and eastern hognose snake with 15 training, 2 test and 4 validation points. We found that our models for each turtle species and combined (all reptiles detected) performed better than random with AUC values greater than 0.8, while our models for each snake species performed adequately with values greater than 0.70 (Table 2.2). We found for our combined (all reptiles detected) model and our selected snake species that accuracy improved from minimum to maximum models; however, there was no improvement for our selected turtle species models. The minimum models had the greatest misclassification of suitable habitat for our combined (all reptiles detected) model, while the maximum model correctly classified almost 50% of the validation data. Across all models for each turtle the values were equally accurate, with 33% correctly classified for midland painted turtle and 56% correctly classified for eastern box turtle. Eastern garter snake had the greatest improvement of correctly classified points increasing to 100% for the maximum model. Eastern hognose snake had at most half of the points correctly classified as suitable habitat.

Patterns of Diversity

We modeled hotspots of habitat suitability for our four selected species based on the minimum, average, and maximum models (Figure 2.4). We found 56% to 90% of the region was not suitable for all four species, while 10% to 43% of the region was suitable for one to 4 species

(Table 2.5). Across all models, the most suitable area, i.e., all 4 species, was highly limited comprising less than 2% of the region. We also compared suitable habitat within Oak Openings Region between Ohio and Michigan. We found that over half of the area in Michigan was unsuitable for these four species. Michigan contained slightly more suitable habitat of the region for 1 or 2 species, i.e., 4% to 21% and 1% to 8%, respectively, than the portion in Ohio. However, Ohio contained slightly more suitable habitat for 3 or 4 species, i.e., 0.6% to 3% and 0.3% to 1%, respectively (Table 2.5). Overall, the amount of unsuitable habitat decreased and the most suitable habitat for all 4 species increased as the values ranged from minimum to maximum. For Ohio, only a small portion of unsuitable habitat was inside protected areas across the study region, ranging from 1.7% to 5.2%, while a large portion of unsuitable habitat was outside of protected areas, ranging from 55% to 76% (Table 2.6). Most of the diverse areas of suitable habitat, i.e., suitable for multiple species, though, were located inside protected areas (Figure 2.5).

We characterized the difference between suitable habitat for diversity ranging from zero to four species (Table 2.7, Figure 2.6). We found that both dry and wet forest increased in percentage of area with increasing number of species overlap, with greater percentages for wet forest. In contrast, percentage of area decreased with increasing number of species overlap. There was a bell curve distribution for the amount of water, dry and wet early successional habitat with the greatest percentage of area for overlap of two species. For the least suitable habitat or zero species overlap, we found significant differences between the percentage of human-modified from the other land covers and dry early successional from the other land cover types. For the most suitable habitat, i.e., all four species overlap, we found no significant differences between amount of wet early successional, water, and human-modified, and dry early successional and human-modified; the percentage of area was significantly different for the other land cover types.

Discussion

Habitat Suitability

Our study is one of the first to incorporate the range of habitat suitability to examine the lower and upper limits for a suite of reptilian species. Many studies use the average model to inform conservation; however, broadening our perspective may provide a better understanding of ecological constraints. We found that suitable habitat was highly limited for our combined (all reptiles detected) model, while suitable habitat for individual species varied. Although, we expected that physiologically, the aquatic midland painted turtle would be highly constrained to water sources as wetland connectivity requirements in fragmented landscapes are not well-studied for aquatic turtles (Rizkalla, & Swihart, 2006), while the terrestrial eastern box turtle would have more widespread suitable habitat, using both aquatic and terrestrial (Donaldson, & Echternacht, 2005), as they are less physiologically constrained, as thermal generalists (Parlin et al., 2018); but we found the opposite pattern. The spatial scale of 120 m buffer could potentially have masked this expected constraint. Alternatively, this scale could include functional habitat in and around specifically desirable land cover types, i.e., water bodies. This inclusion reflects the influence of both the composition and configuration of land cover and illustrates that the species have broader ecological requirements that include a mixture of terrestrial and aquatic habitat. Additionally, this highlights how complex, diverse and structurally heterogeneous landscapes can drive ecological processes (Stein, Gerstner, & Kreft, 2014). These mixed results suggest that this approach can better identify the broader patterns of occupancy that may be influenced by more than just physiological constraints (e.g., biotic factors). In other words, these broader habitat use patterns are likely to better approximate functional sets of habitats for these reptiles.

As expected for our selected snake species, eastern garter snakes had the greatest amount of suitable habitat ranging from 37% to 84% of the study area, while eastern hognose snake were limited in suitable habitat, i.e., 16% to 59%. Eastern garter snakes select warm fields over cool forest (Halliday, & Blouin-Demers, 2016), which provides greater fitness benefits (Halliday, & Blouin-Demers, 2018). Warm cropland fields were abundant within Oak Openings Region, comprising 25% of the total land cover, second to residential/mixed land cover (Root & Martin, 2018). In contrast, the eastern hognose snake is considered a species of special concern because they are closely associated with disturbance-dependent pine-scrub oak barrens (Michener, & Lazell, 1989; Therres, 1999); they use open canopy habitat with xeric, sandy soils, and often avoid dense canopy forests (Platt, 1969; Plummer, & Mills, 2000; LaGory et al., 2009). Such habitats in Oak Openings Region were generally confined within protected lands, therefore restricting potential distributions. Our results confirmed that suitable habitat was both widely available outside and within protected areas for eastern garter snakes, while suitable habitat for eastern hognose snakes was primarily constrained within protected areas of northwestern Ohio.

Patterns of Diversity

We examined the region for areas with high biodiversity and then characterized those regions by land cover type. Over half of the region was neither suitable for our target species nor, likely, for other reptiles not modeled here. Despite utilizing occurrence data only from Ohio, we identified slightly more suitable habitat in Michigan. Michigan may have even greater suitable habitat had we included occurrence records from the state. Clearly there is a need to further test our extrapolated models and collaborate across states for monitoring reptilian species. We utilized our diversity map to characterize the underlying habitat of the least suitable or zero species overlap to most suitable or high species overlap. We found very intriguing results: the percentage of wet forest increased as the number of species overlap increased, while, as expected, human-modified habitat decreased. Early successional habitat, both wet and dry, contributed the most to suitable habitat for two species overlap, which suggests that differences in species ecological requirements may drive this response.

Generalizable Modeling for Suites of Species

MaxEnt is an excellent tool for modeling suitable habitat for an array of species; however, it is critical to incorporate species biology when selecting environmental predictor variables. Generalizable models that utilize the same environmental predictor variables across species can inform land managers of specific management targets for conserving a suite of species as opposed to species-specific models which use environmental predictor variables that are relevant to that one species and vary species by species. Our models are general models which provide a starting point to look at important variables across species. Each of these models can be developed further with greater in-depth biological knowledge by building stronger species-specific models. For example, our eastern box turtle model provides similar suitability maps as the species-specific model developed by Cross (2016); however, our model identified less suitable habitat. This suggests that general models are competitive with species-specific models, but they may be more conservative and highlight minimum estimates of suitable habitat.

As with many habitat suitable models, land cover is often a driving factor and it is a manageable or changeable factor. For example, the percentage of land cover within a 120 m buffer can be altered under conservation plans through targetable goals. We found that reptiles were greatly influenced by the percentage of floodplain forest with increased suitable habitat with increasing amount of this land cover. Land managers can actively alter how much floodplain forest occurs within areas by planting more trees and/or affecting local hydrology. Additionally, land surface temperature, an important contributing factor for midland painted turtle and eastern garter snake (for which suitability decreased as temperature increased), can be manipulated either by removing shrubs/trees that provide cool shady patches or planting shrubs/trees that provide refuge from warm sunny patches.

Our study focused on one spatial scale; however, future models can incorporate multi-scale models, which may illuminate how different spatial scales influence community assemblages and ecological niches within species distribution modeling (Trumbo et al., 2012). For example, the buffer for calculating the percentage of land cover from 120 m to 60 m or 180 m can be changed and the results compared. This in turn will allow for flexible conservation plans to create targetable goals for large-, local-, and fine-scale land management. We tested this for one of our target species, i.e., midland painted turtle, using a smaller buffer size of 60 m. Estimated suitable habitat decreased, ranging from 33% to 53%, which suggests that these turtles may be more sensitive to habitat change at a finer spatial scale.

Implications of Model Validation and Improvements

Overall, our models performed adequately with AUC values greater than 0.70 for predicting conditions that were like those occupied based on a limited validation data set. As such, these models provide a useful baseline for comparison and are readily modifiable as additional data becomes available. Data deficiency significantly hinders conservation and management, especially in the face of global population declines for reptiles (Bland, & Böhm, 2016). Therefore, many studies have utilized small sample sizes to inform their habitat suitability model, which still provides important insight for conservation plans (Udyawer et al. 2020; Root,

& Martin, 2018; Mert & Kirac 2019; Almasieh, Mirghazanfari, & Mahmoodi, 2019). Utilizing radio telemetry can boost sample size; however, this is often based on a small subset of individuals that are used to model habitat suitability (Evcin, Kucuk, & Akturk, 2019; Morris et al., 2020) and must be filtered to reduce spatial autocorrelation. Although our model accuracy correct classification rate was lower than expected (one species model with 60% correct identification within classified suitable habitat), we have provided critical information to inform local land managers. Additionally, correct classification improved when we changed from minimum to average or maximum models; this was not surprising because both the average and maximum models resulted in an increase in the area of suitable habitat. As with any model, there should be a constant cycle of refining and improving model accuracy (Figure 2.1). We started with a sparse dataset; however, our study may spark greater involvement of citizen scientists and collaboration among local entities in order to improve the availability, quality and quantity for occurrence datasets.

Remote sensing has widely advanced our ability to examine the effects of environmental heterogeneity for habitat suitability modeling (Bush et al., 2017); however, biodiversity data vary in availability both at fine spatial and temporal resolution across broad extents (Bellard et al., 2012). We caution that using only a few points as validation points likely led to larger misclassifications and that there is a strong need for shared databases among researchers. Reptiles are highly cryptic, and for our study area, in particular, there were not many supplementary independent sightings from citizen scientists using iNaturalist. Outreach programs can be implemented to increase these supplementary sightings to further conservation goals. Citizen scientists detected seven more snakes than turtles. Our field surveys were conducted within protected areas and may not reflect suitable habitat conditions outside of protected areas.

In contrast, most of the citizen science data were collected outside of protected areas. We see this disparity from our overall combined (all reptiles detected) model with 139 occurrence locations, which used our field collected data to build the model and the iNaturalist dataset which had 53 occurrence locations as an independent validation dataset. Despite having a much larger sample size, our prediction success was much lower than expected. Less than 50% of our independent data was predicted to be in suitable habitat and this is likely a result of conducting field surveys only within protected areas. The model is less successful predicting suitable habitat conditions outside of protected areas, where citizen scientists incidentally collect data. Therefore, we suggest that incorporating citizen scientist data are crucial to understanding distribution patterns outside of protected areas because they increase both the spatial and temporal coverage of samples (Poisson et al., 2020). One limitation of our study was the use of data collected in Ohio to extrapolate into Michigan. We found that Michigan contained a large percentage of unsuitable habitat for the 4 species; however, we expect that including samples in Michigan would greatly improve our models.

Management Recommendations

MaxEnt models can be used to identify important predictor variables that can be altered on the landscape. We highly recommend that researchers examine a variety of suitable habitat models per species, including utilizing the minimum and maximum models with average models and testing different spatial scales. From our models we suggest that land managers focus on maintaining thermal refuges, especially areas with land surface temperatures around 20ºC. Land surface temperature maps can identify these and other areas that are above 30ºC which may become even warmer as climate change alters these conditions. Based on our results, efforts can focus towards areas where both midland painted turtles and eastern garter snakes overlap with one another by maintaining or altering canopy cover. This will specifically benefit these species and may benefit other species that have similar ecological needs, such as other aquatic turtles. Maintaining landscape heterogeneity by balancing both forest and early successional habitats will be helpful to reptilian species (Griffin et al., 2009; Hoss et al., 2010). These thermal refuges will also be critical as global average temperatures increase. We suggest that land surface temperature maps be evaluated every 3 – 5 years to identify lethal limit areas for targeted management. In this region a greater percentage of forests, both floodplain and deciduous forest, were important to reptiles, likely serving as thermal refuges, as well as containing important resources. Floodplain forest contributed greatly to our models and we suggest that land managers maintain this land cover. Our patterns of diversity showed that high quality habitat or areas with all four species, had the greatest percentage of wet forest. Therefore, we highly recommend that local land managers continuing preserving and acquiring forest habitat, especially for wet forest (floodplain and swamp forest). Land managers have already identified these two ecosystems as major communities of concern and should keep reptilian ecological requirements in mind.

Our study area, Oak Openings Region, has been the focus of large-scale conservation planning. The Green Ribbon Initiative, a coalition of partners across the region, has focused its efforts on restoring five target ecosystems: upland savanna/prairie, wet prairie, upland deciduous forest, floodplain forest, and flatwoods/swamp forest (Gardner, 2016) with the overarching goal of creating a connected corridor among all of the protected areas. Our combined (all reptiles detected) model, see Figure 2.2a, appears to highlight these efforts as the “ribbon” of suitable habitat following northward throughout the region. We would expect a stronger signature in northern Oak Openings Region if we had included field observations from Michigan to build the model. We suggest that our models continue to be refined with the addition of presence records outside of protected areas and including data from Michigan. These generalizable models provide conservative estimates of habitat suitability for a suite a reptilian species and characterized habitat within hotspots for future land acquisition and management.

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Tables

Table 2.1. Final set of uncorrelated predictor variables separated by category and listed data source.

Category	Variables (units)	Source
Climate	Land surface temperature (ºC)	Derived from Landsat 8 image
Land Cover	% of deciduous forest (%)	Derived from Root & Martin 2018
	% of swamp forest (%)	
	% of floodplain forest (%)	
	% of upland savanna (%)	
	% of upland prairie (%)	
	% of water (%)	
Elevation	Aspect	Derived from DEM
	% Slope	
Connectivity	COHESION	FRAGSTATS

Table 2.2. The maximum test sensitivity plus specificity threshold (MSS) and percentage of suitable and unsuitable habitat based on the MSS threshold for combined (all reptiles detected) and selected species.

Species	Model	MSS	AUC Value	Suitable Habitat (%)	Unsuitable Habitat (%)
Combined	Minimum			28.5%	71.5%
	Average	0.12	0.952±0.025	39.8%	60.2%
	Maximum			47.2%	52.8%
Midland Painted Turtle	Minimum			38.8%	61.2%
	Average	0.38	0.828±0.132	56.9%	43.1%
	Maximum			69.7%	30.3%
Eastern Box Turtle	Minimum			10.1%	89.9%
	Average	0.26	0.921±0.071	15.6%	84.4%
	Maximum			19.4%	80.6%
Eastern Garter Snake	Minimum			37.4%	62.6%
	Average	0.25	0.702±0.702	66.7%	33.3%
	Maximum			84.4%	15.6%
Eastern Hognose Snake	Minimum			15.9%	84.1%
	Average	0.23	0.73±0.73	41.3%	58.7%
	Maximum			59.4%	40.6%

Table 2.3. Percent contribution (% C) and permutation importance (PI) for the explanatory predictor variables for the average models for all combined (all reptiles detected) and each selected species. Top two contributing variables in bold.

	Combined		MPT		EBT		EGS		EHS	
Variable	% C	PI	% C	PI	% C	PI	% C	PI	% C	PI
Aspect	1.1	4.0	0.3	0.0	0.5	2.5	2.3	3.8	9.1	5.6
Slope	0.6	2.3	0.2	0.4	0.2	0.6	4.4	1.4	3.5	2.0
% Conifer	11.6	4.0	15.6	0.0	8.6	2.9	4.3	0.0	**26.1**	0.7
% Deciduous	**26.5**	**30.9**	0.7	0.4	**48.8**	**63.6**	9.3	1.6	3.4	3.0
% Swamp	5.3	5.9	12.2	0.2	2.5	0.5	1.7	0.3	7.2	8.2
% Floodplain	**29.4**	**18.9**	**28.4**	**10**	**36.2**	**9.1**	**37**	1.0	**25.5**	9.7
% Savanna	2.0	3.4	0.5	0.3	0.3	1.5	10.2	**32.1**	2.9	1.0
% Prairie	1.8	8.4	5.2	0.0	2.1	4.4	3.5	**26.9**	8.2	**14.9**
% Pond	4.3	1.1	13.5	4.8	0.1	5.6	7.7	3.1	1.8	11.2
Land surface temperature	14.5	16.5	**23.4**	**83.5**	0.1	2.6	**13.6**	20.4	1.4	9.0
Cohesion	2.8	4.6	0.0	0.5	0.6	6.7	6.0	9.5	11.1	**34.7**

Table 2.4. Validation matrix comparing percentage of presence-only records identified within suitable/unsuitable habitat for average, minimum, and maximum models for all combined (all reptiles detected) and each selected species.

Species	Model	% Suitable	% Unsuitable
Combined	Minimum	11%	89%
	Average	38%	62%
	Maximum	49%	51%
Midland Painted Turtle	Minimum	33%	67%
	Average	33%	67%
	Maximum	33%	67%
Eastern Box Turtle	Minimum	56%	44%
	Average	56%	44%
	Maximum	56%	44%
Eastern Garter Snake	Minimum	33%	67%
	Average	67%	33%
	Maximum	100%	0%
Eastern Hognose Snake	Minimum	25%	75%
	Average	25%	75%
	Maximum	50%	50%

Table 2.5. The percentage of area for the number of species that overlap with one another for the minimum, average, and maximum models for all Oak Openings Region, only Ohio and only Michigan portions.

	Oak Openings Region			Ohio Portion			Michigan Portion		
# of Species Overlap	Min	Average	Max	Min	AVG	Max	Min	AVG	Max
0	90.1%	74.6%	57.4%	20.3%	17.6%	14.2%	69.9%	59.0%	43.2%
1	6.3%	14.0%	24.7%	2.3%	2.6%	4.1%	4.1%	11.4%	20.6%
2	2.6%	6.5%	11.1%	1.4%	2.4%	2.6%	1.2%	4.0%	8.4%
3	0.6%	2.1%	5.2%	0.6%	1.5%	2.5%	0.1%	0.6%	2.7%
4	0.3%	0.9%	1.6%	0.3%	0.8%	1.4%	0.0%	0.1%	0.3%

Table 2.6. Percentage of suitable habitat for 4 species within and outside of protected areas in Ohio.

	Protected Area			Unprotected		
# of Species Overlap	Minimum	Average	Maximum	Minimum	Average	Maximum
0	5.2%	2.8%	1.7%	76.4%	67.8%	55.4%
1	2.6%	2.0%	1.5%	6.5%	8.3%	15.1%
2	1.8%	2.7%	2.3%	4.0%	7.1%	8.3%
3	1.2%	2.1%	3.3%	1.1%	3.8%	6.9%
4	0.8%	1.9%	3.0%	0.3%	1.4%	2.6%

Table 2.7. Habitat characteristics for patterns of diversity. Recorded are percentage of each simplified land cover type (Root & Martin 2018) for the number of species overlap in Oak Openings Region, expanding from northwestern Ohio to southeastern Michigan.

		# of Species Overlap				
		0	1	2	3	4
MIN	Wet Early Successional	1%	4%	4%	1%	0%
	Dry Early Successional	19%	32%	23%	12%	11%
	Wet Forest	3%	24%	35%	56%	61%
	Dry Forest	1%	10%	10%	22%	19%
	Water	0%	4%	11%	0%	0%
AVG	Human-Modified	76%	27%	18%	10%	8%
	Wet Early Successional	1%	3%	4%	2%	1%
	Dry Early Successional	16%	35%	31%	20%	14%
	Wet Forest	1%	13%	25%	48%	51%
	Dry Forest	1%	3%	9%	17%	26%
	Water	0%	0%	8%	2%	0%
MAX	Human-Modified	81%	24%	24%	12%	8%
	Wet Early Successional	1%	2%	4%	2%	6%
	Dry Early Successional	12%	27%	40%	30%	13%
	Wet Forest	0%	4%	17%	39%	42%
	Dry Forest	0%	1%	4%	13%	30%
	Water	0%	0%	4%	2%	8%
	Human-Modified	87%	66%	31%	14%	2%

Figures

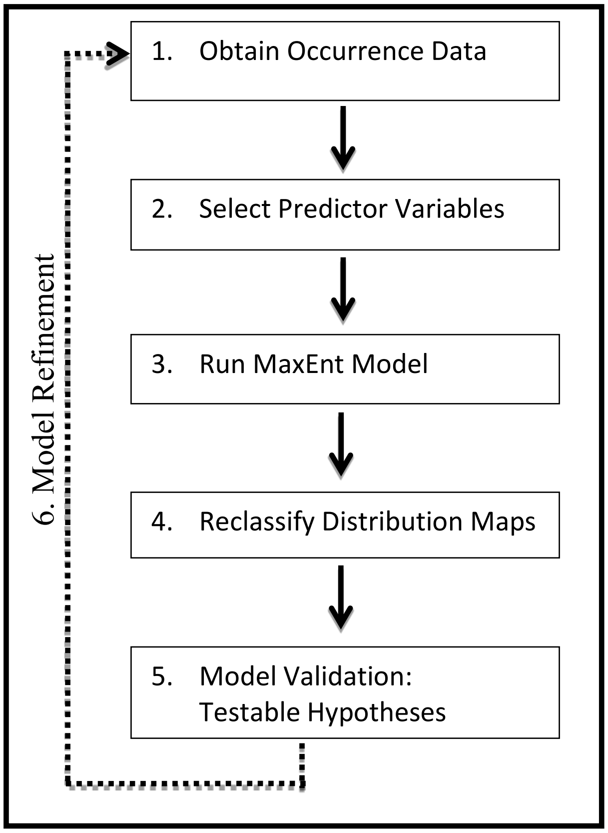
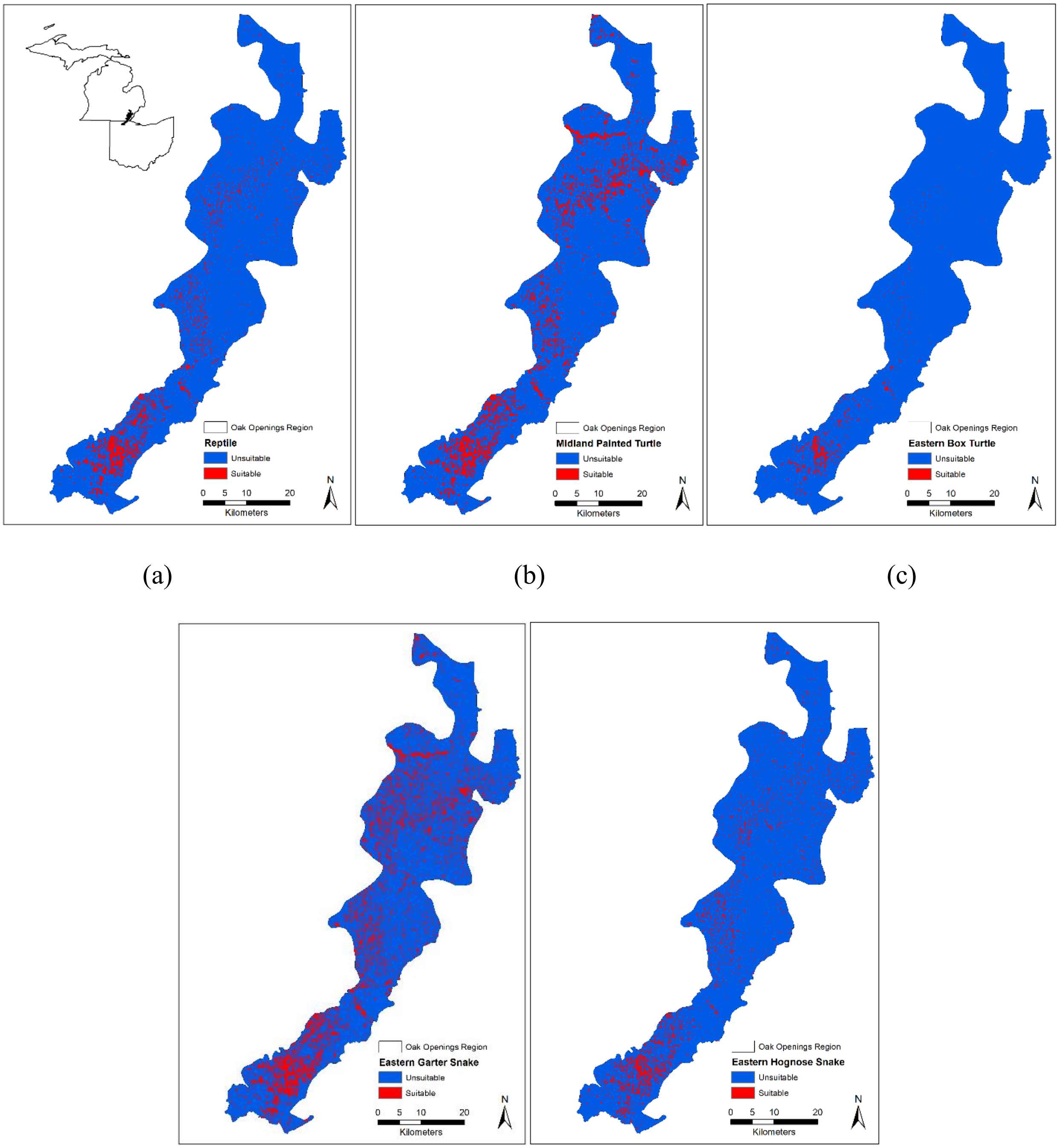


Figure 2.1. Model for predicting species distribution patterns. (1) Acquire species occurrence data from field surveys or known databases; (2) select appropriate predictor variables for model input; (3) run data in MaxEnt after selecting model criteria; (4) reclassify map into suitable/unsuitable habitat using threshold value; (5) test or validate model(s) using independent data and testable hypotheses; (6) refine model as needed.



(a) (b) (c)

(d) (e)

Figure 2.2. Average binary habitat suitability models. For combined (all reptiles detected) (a), midland painted turtle (b), eastern box turtle (c), eastern garter snake (d), and eastern hognose snake (e).

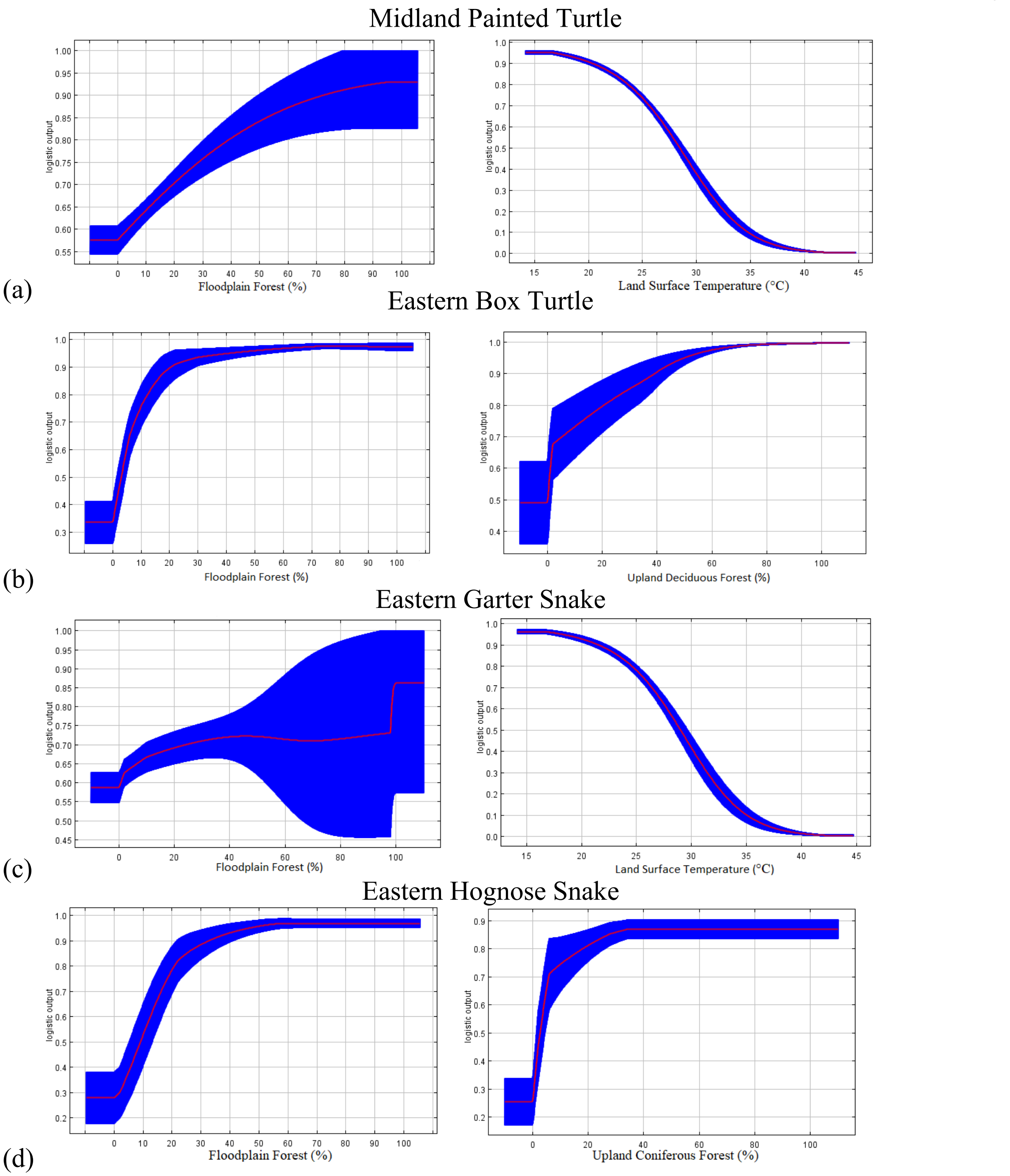
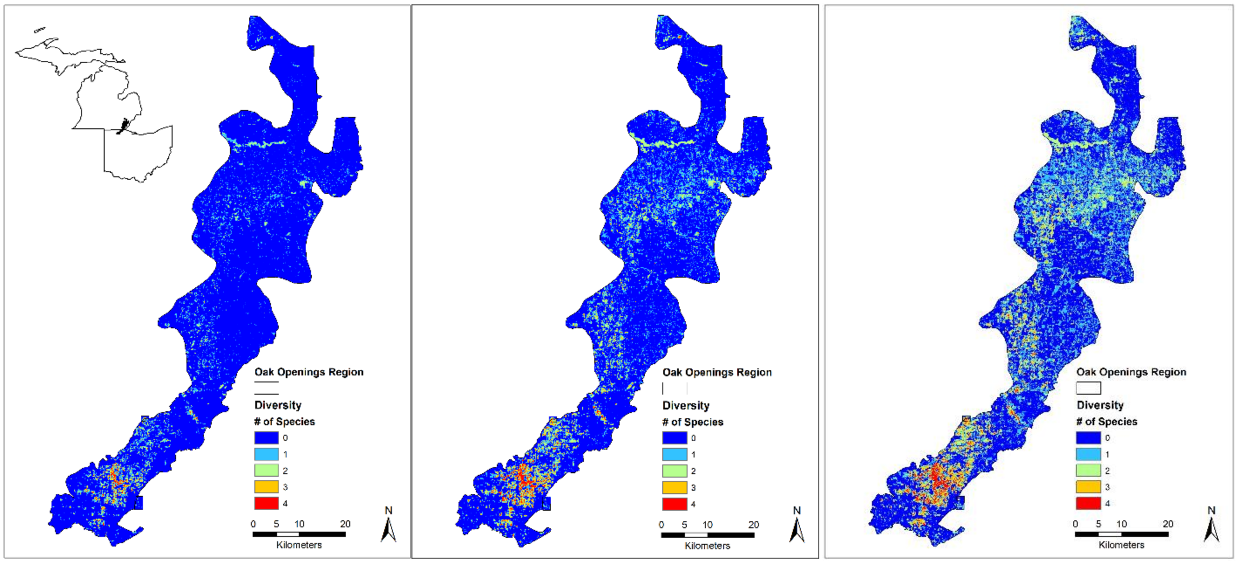
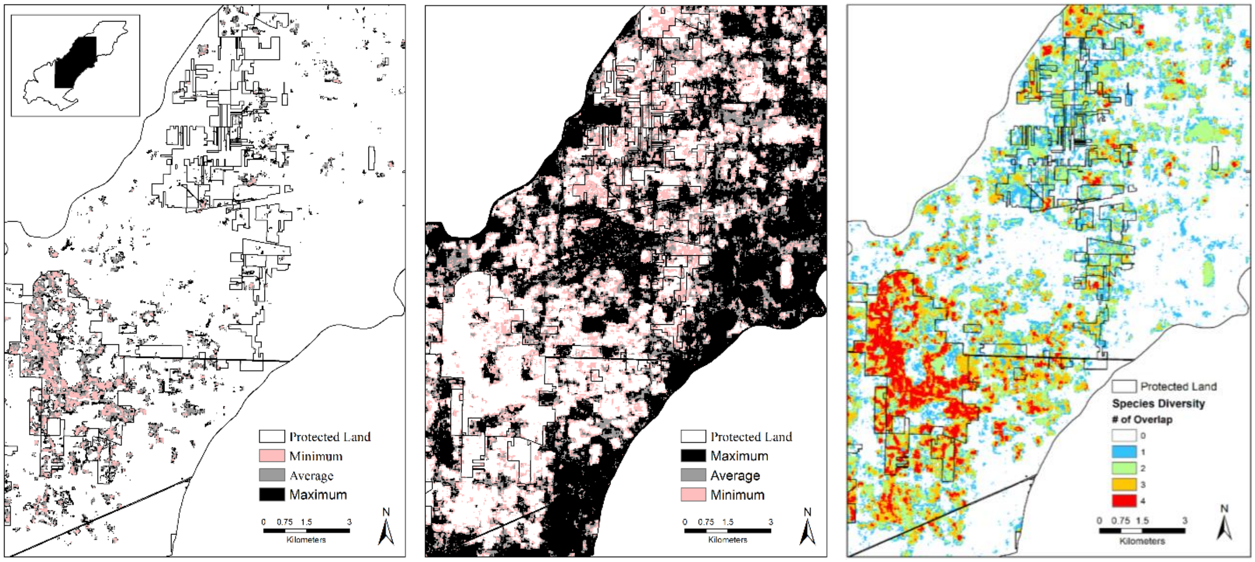


Figure 2.3. Response curves for top two influential variables for midland painted turtle (a), eastern box turtle (b), eastern garter snake (c), and eastern hognose snake (d). The x-axis represents values for the percentage of a given land cover type from 0% to 100% and the land surface temperature in °C. The y-axis represents the probability of suitable habitat with increasing values indicating more suitable habitat conditions.



(a) (b) (c)

Figure 2.4. The habitat suitability for the minimum (a), average (b), and maximum (c) models of four reptile species within Oak Openings Region of southeastern Michigan and northwestern Ohio. Each color shows the number of species that overlap with one another with low overlap (in blue) to high overlap (in red).



(a) (b) (c)

Figure 2.5. A comparison for suitable habitat overlap between all four species and no species between three separate models: the minimum (in pink), average (in gray), and maximum (in black). Presented is the most suitable habitat where all four species overlap with one another (a) compared to the least suitable habitat where all four species did not overlap with one another (b). Finally, the full average model is presented where suitable habitat is shown based on the number of species that overlap with one another (c). Maps show areas within and outside protected areas (black outlines) within northwestern Ohio. Enlarged between two protected areas, Oak Openings Preserve and Kitty Todd.

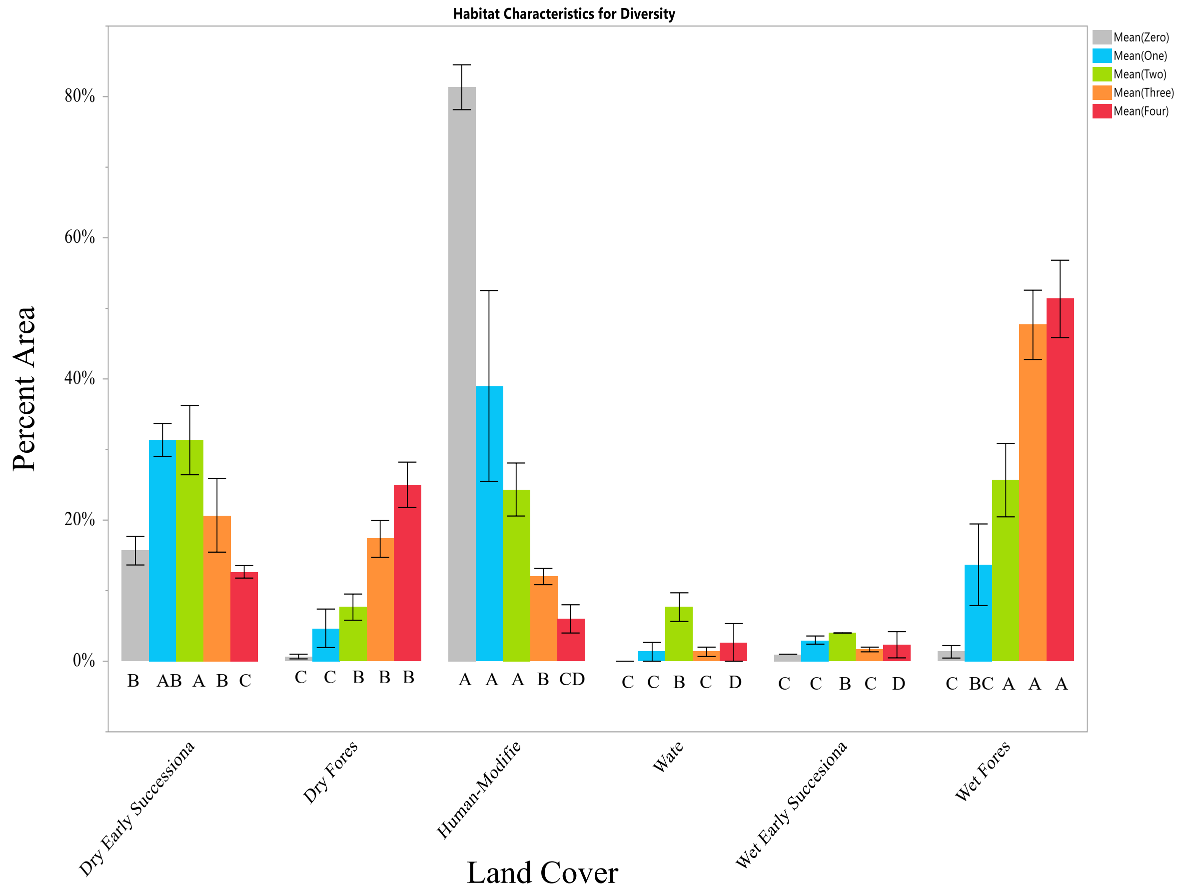


Figure 2.6. Bar graph for percentage of area per land cover type (± 1 SE) for the number of species overlap ranging from zero (in grey, left) to four (in red, right). Land cover types at each level are significantly different if the connecting letter is different.

CHAPTER 3: HOW DOES HETEROGENITY INFLUENCE THE SPATIAL ECOLOGY OF EASTERN BOX TURTLES (TERRAPENE CAROLINA CAROLINA) WITHIN OAK OPENINGS REGION

Abstract

Natural habitats are continually decreasing in size and becoming more fragmented as human-modified land cover increases, which in turn, affects landscape heterogeneity through its composition and configuration. Species are influenced by these local-scale factors as they require landscape heterogeneity for thermoregulation, foraging, and reproduction. As habitats or species ecological neighborhoods become more fragmented, conservation actions require a better understanding of these interactions with environmental context. A mixed-disturbance landscape, such as Oak Openings Region in northwestern Ohio, provides an opportunity to examine species distributions and movements in a variety of contexts. Our study focused on how heterogeneity influences the spatial ecology of eastern box turtles. The main goal was to assess general habitat relationships and the effects of landscape metrics on home range size. We radio tracked a subset of turtles and characterized features of the landscape. We found that turtles were significantly positively associated with upland prairie at the landscape scale in Oak Openings Preserve and negatively associated in Secor. Additionally, turtles were closer to forest and farther away from human-modified land cover. We found that home range size was significantly positively associated with patch shape, i.e., mean fractal dimension index, and negatively associated with contiguity. Landscape metrics varied in relation to home range size across spatial scales. Our top model predicting home range size included fractal dimension and Shannon's Evenness at 400 m spatial buffer. Overall, we found that turtles responded to landscape composition and configuration at different spatial scales and recommend that land managers focus on maintaining

or increasing connectivity among forest habitats. In conclusion, our study informs the spatial ecology of eastern box turtles by using a robust distance-based and multiscale approach for a species of special concern.

Introduction

Understanding the spatial ecology of different species is critical under the current threat of habitat loss and fragmentation. There are declines in agricultural expansion as suitable arable lands are depleted; however urban development is rapidly expanding and encroaches on natural, non-arable, landscapes (Levia & Page 2000; Lugo 2002). These natural habitats are continually decreasing in size and becoming more fragmented as human-modified land cover increases and dominates the landscape. It is especially concerning for ectothermic species, which are more closely tied to their environment than their endothermic counterparts. Species distributions are influenced by landscape composition and abundance of critical resources, which in turn affects local characteristics such as home range size (Hoss et al., 2010) and surrounding ecological neighborhoods (Addicott et al., 1987; Holland and Yang 2016). Landscape heterogeneity, configuration and composition affect individual's space use when thermoregulating, foraging, and reproducing. These interactions with the environment or other organisms often occur across multiple scales. It is critical to examine these interactions and the relevant ecological neighborhoods (Holland and Yang, 2016) they encompass to aid conservation and management of vulnerable species, such as eastern box turtles (*Terrapene carolina carolina*), as in this study.

Delineating ecological neighborhoods requires an understanding of the biotic and abiotic factors that influence the distribution and movement of a reptile, including food resources, thermal refuges, as well as predators and competitors. It has been shown that several reptiles, such as eastern diamond-backed rattlesnakes (*Crotalus adamanteus*) in Georgia, USA (Hoss et al., 2010) and a suite of species in Australia (Garden et al. 2007; Kanowksi et al. 2006)depend on complex habitat structure rather than species composition. Habitat selection may be partly a reflection of an ectotherm's body temperature maintenance as seen in eastern diamond-backed rattlesnakes (Lillywhite and Navas, 2006), garter snakes in California, USA (Huey, 1991), and a suite of species, lizards and snakes, in Australia (Pike et al., 2011), therefore home ranges within highly heterogeneous habitats may be more conducive for thermoregulation.

However, habitat should include the resources that produce occupancy, which additionally includes survival and reproduction (Hall et al., 1997). At a finer spatial scale, vegetation cover is shaped by disturbance regimes, such as fire, as well as soil type, soil depth and drainage (Clarke, 2002; Sankaran et. al. 2005; Pike et al., 2011), and may impact the daily movements of ectotherms. Management can actively target vegetation characteristics by reducing woody vegetation density to increase habitat heterogeneity and patchiness (Pike et al., 2011), especially in areas with altered disturbance regimes. Many reptiles, including box turtles, have site fidelity (Carpenter, 1952; Barbour et al., 1969; Ciofi and Chelazzi, 1994; Web and Shine, 1997; Dodd, 2001; Arvisais et al., 2002; Harms, 2008; Croak et al., 2013), which is advantageous for individuals as it increases familiarity with habitat features to avoid predators, and forage and thermoregulate more effectively (Madsen, 1984). Box turtles spend most of their time in their home range for daily activities, e.g., foraging, thermoregulation, and nesting (Burt, 1943), and may move outside of their home range for new foraging opportunities or mate search (Stickel, 1950; Dodd, 2001). By including a suite of explanatory variables in addition to vegetation associations, researchers can assess their importance in multiple scales (Addicott et al., 1987; Holland and Yang, 2016).

A mixed-disturbance landscape, with a variety of active management and anthropogenic activities, provides an opportunity to examine species habitat associations in a variety of contexts. Our study focused on the influence of heterogeneity on the spatial ecology of eastern box turtles in Oak Openings Region of northwestern Ohio, a highly diverse landscape with 15 unique land cover types (Schetter & Root 2011). This array and configuration of dry and wet habitats, forested and open vegetation resulted in a large variety of unusual flora, including 145 plant species that are potentially threatened, threatened, and endangered (Brewer, & Vankat, 2004). Our objectives were to (1) assess if individuals exhibit nonrandom habitat associations at the landscape and home range spatial scales, (2) compare home range size with previous studies, (3) investigate how landscape heterogeneity affected home range size, and (4) provide land management recommendations. We predicted that eastern box turtles would exhibit nonrandom patterns with positive habitat associations with forest and early successional habitat and negative habitat associations with human-modified land cover. Our expectation was that turtles would have larger home ranges than found in other areas as a result of the region's greater landscape heterogeneity. The results should increase our understanding of the effects of habitat impacts on turtles in patchy noncontiguous forest landscapes heavily altered by human activities.

Methods

Study Site

This study was conducted at multiple protected areas within Oak Openings Region with emphasis in Oak Openings Preserve and Secor Metroparks located in northwestern Ohio. Oak Openings Preserve is characterized by the mixture of early successional (401 ha), wet forest (576 ha), dry forest (455 ha), water (106 ha), and human-modified (1 ha) land cover types, Figure 3.1a (Root and Martin, 2018). Of these land covers, we surveyed approximately 26% of available wet forest, 30% of available dry forest, and 19% of available early successional. It has six major roads bisecting the natural habitat as well as numerous paved and unpaved trails for recreational use. Secor is characterized by the large proportion of wet forest (80 ha), dry forest (455 ha), early successional (401 ha), and human-modified (19 ha) land cover types, Figure 3.1b (Root and Martin, 2018). Of these land covers, we surveyed approximately 52% of available wet forest, 25% of available dry forest, and 36% of available early successional. It has two main roads that bisect the natural habitats and numerous unpaved trails.

Visual Encounter and Radio-Telemetry

We conducted visual encounter surveys within forested habitats to detect eastern box turtles from 1 May 2017 to 2 November 2019, capturing 12 individuals (three female, nine male) for radio transmitter application. Three male turtles were radio tracked at Secor and nine turtles (three female, six male) were radio tracked at Oak Openings Preserve. Two individuals in Oak Openings Preserve, one female and one male, were removed from subsequent analyses as we had less than 10 detection points for each. All detected individuals were scanned for a passive integrated transponder (PIT) tag (AVID(R) MicroChip ID Systems, Folsom, Louisiana, USA) for identification and a PIT tag was implanted in those without one. Sex was determined using secondary characteristics (Ernst & Lovich 2009). We glued a radio transmitter (Model RI-2B or SI-2F; Holohil Systems, Ltd., Ontario, Canada) onto the back-right carapace using 5-minute epoxy of selected turtles. Both the PIT tag and transmitter did not weigh more than 5% of the turtle's total body weight. After application of transmitter and/or PIT tag, subjects were released at their capture site.

We radio-tracked individuals roughly once to three times a week during daylight hours using an R1000 radio-telemetry receiver (Communications Specialists, Inc., Orange, California, USA) and a folding Yagi 3-element antenna (Advanced Telemetry Systems, Isanti, Minnesota, USA). When a turtle was detected, we recorded the Global Positioning System (GPS; eTrex, Garmin International, Inc., Olathe, KS, USA) coordinates in WGS 1984 with a 3-m accuracy. We tested if home range size differed between years and sex using a one-way analysis of variance (ANOVA) in JMP (vers. 11; SAS Institute Inc., Cary, North Carolina, USA).

Part 1: Habitat Associations

Composite home ranges were estimated by merging all observations across years for each individual and then calculating the 100% minimum convex polygons (MCP) in ArcGIS (vers. 10.2.2; Earth Systems Research Institute, Redlands, CA, 2002). We tested whether habitat use differed between parks at both home range and landscape spatial scales using a Wilcoxon two group test in JMP ver. 11 (SAS Institute Inc., Car, North Carolina, USA).

We analyzed habitat associations for *T. c. carolina* at two spatial scales: home range and landscape. All turtle observations were evaluated in ArcGIS with a 15-class land cover map for the local region (Root and Martin, 2018). We measured habitat associations by creating Euclidean distance layers for each land cover type (Conner et al., 2003). The mean distance from observed turtle locations was compared to expected mean distances from random locations for each habitat type within the estimated composite home range and their respective park, i.e., Oak Openings Preserve or Secor. We separated individuals based on parks and randomly subsampled the observed turtle locations based on the lowest number of radio telemetry locations to maximize spatial independence. Random points were populated within ArcGIS based on the number of subsampled observed turtle locations, i.e., 30 points for Oak Openings Preserve and 12 points for Secor. Distance scores of zero represented occupancy of that specific habitat.

For the home range scale, we assessed habitat associations within composite home ranges by comparing random points within the estimated home range to observed locations for each individual. This compared available habitat to utilized habitat within the home range. At the landscape scale, we compared unconstrained random points across the study site to random points equal to the number of turtle observations within each composite home range. This analysis compared the availability of habitats within the home range to availability within the landscape.

Part 2: Home Range Size and Landscape Patterns

We examined the effects of landscape pattern and heterogeneity on the composite home range size for eastern box turtles using a 15-class land cover map (Root and Martin, 2018). We calculated the center point within each home range and overlaid these data on the land cover map. Four spatial scales were delineated around the centroid using 100-, 200-, 300- and 400-m radius buffers that encompassed 3.1, 12.6, 28.3, and 50.3 ha, respectively (Figure 3.2). These spatial scales encompassed the known home range sizes of eastern box turtles and captured multi-scale habitat use.

Using FRAGSTATS (vers. 4.2.1; McGarigal and Marks, 1995) we analyzed composition and configuration within the four spatial scales with each buffer distance for individual turtles across the landscape. Our analysis focused on the FRAGSTATS components: aggregation, area, core, diversity, and shape metrics. Within these groups, we used patch characteristics and calculated metrics at the landscape scale. Additionally metrics can be calculated at the patch or class level.

Home range size was estimated using pooled observations across years for all subsequent analyses. All landscape metrics were checked for multicollinearity using Spearman's correlation coeffficients in JMP ver. 11 (SAS Institute Inc., Car, North Carolina, USA). High colinearity among explanatory variables often leads to higher standard errors and interpretation difficulties for generalized linear models (Graham 2003), therefore we removed highly correlated variables ($r > 0.70$) within our candidate group including varaibles from each category: aggregation, area, core, diversity, and shape. Of the remaining variables within these metric categories, we selected two variables per group for a total of 10 final variables (i.e., area-weighted mean proximity, aggregation index, total area, Shannon's Evenness Index, patch richness density, mean fractal dimesnsion index, mean contiguity index, largest patch index, total core area, and area-weighted mean core area distribution). We used Pearson's correlation coefficients to examine if home range size was significantly correlated with the selected variables at each spatial buffer size. Pearson correlation coefficients were calculated between composite home range size (response variable) and each selected landscape variable (potential predictor variables) by buffer size. We applied a Bonferoni correction to our significance value to account for repeated measures. All statistical analyses were performed using JMP ver. 11.

We further evaluated our remaining predictor variables using a stepwise multiple regression to develop candidate models of home range size at the four spatial buffers. We ran all possible outcomes with indivdiual variables; however, fitting all possible outcomes represented a substantial number of models to consider. Therefore, we limited the model to a maximum of six variables and looked at the top eight models per buffer (Weir et al., 2005). Akaike's Inforation Criteria adjusted for small sample size (AIC_c) was used to select the "best" model among all possible candidate models and we included a null model for comparison. All final model residuals were checked for normaility using Shapiro-Wilks test. We reported the most parsimonous models and assumed that models with AICc changes less than or equal to 2 and the fewest number of variables are more competitive (Burnham and Anderson, 2002; Peng et al., 2002; Sherwood and Wu, 2012; Larm et al., 2020; Pearman-Gillman et al., 2020).

Results

Part 1: Habitat Associations

We tracked 3 female and 9 male individuals with radio telemetry, the total number of observations was 515 (mean = 23, range = 3 – 45 observations; Table 3.1). We did not find a significant effect of sex on home range size, F (1,18) = 0.0103, p = 0.9204, or of year on home range size, F (2,17) = 2.0095, p = 0.1647. Average composite home ranges (± 1SE), i.e., year pooled together, respectively, for all turtles (n = 10), female only (n = 3), and male (n = 8) were 3.62 ha ± 0.49 ha, 4.82 ha ± 0.43 ha, and 3.11 ha ± 1.61 ha.

Across each year from 2017 to 2019 (Figure 3.S1), box turtle home ranges contained floodplain forest (range = 19% – 36%), swamp forest (range = 15% – 23%), upland deciduous forest (range = 28% – 37%), upland coniferous forest (range = 2% – 5%), upland prairie (range = 5% – 16%), upland savanna (range = 1% – 8%), sand barrens (range = 0% – 1%), and residential/mixed (range = 1% – 3%). We found that composite home ranges had an average of 5 different land cover types (range = 2 – 7). Individuals within Oak Openings Preserve had an average of 6 (range = 4 – 7) different land cover types, while individuals within Secor had an average of 2 (range = 2 – 3) different land cover types within the composite home range. We found one significant difference between parks for the habitat association with upland prairie ($\chi^2 = 5.72$, df = 1; $P = 0.0227$), with a positive association within Oak Openings Preserve and a negative association within Secor. We did not find any significant habitat associations at the home range scale. We found that land cover types were highly variable, i.e., being closer to or further away from, at the landscape and home range scale. For Oak Openings Preserve, all human-modified habitats, except residential/mixed at the landscape scale were further away than expected at random, while natural land cover types were highly variable (Figure 3.3a). Seven of the land cover types, which varied in mean distance ratio size, where values increasing up to 1 are further away from a given land cover type and values decreasing down to -1 are closer to a given land cover type, switched across spatial scales from being further away to being closer to a given land cover type. Specifically, for turtles in Secor, the mean distance ratio for floodplain forest was 0.24 (home range) and 0.32 (landscape) compared to the mean distance ratio for swamp forest which was -0.25 (home range) and -0.95 (landscape). Therefore, turtles were more further away from swamp forest at the landscape scale than at the home range scale. For Secor, all human-modified land cover types, except turf/pasture at the landscape scale and cropland at the home range scale, were further away than expected at random, while natural land cover types were highly variable (Figure 3.3b). Four of the land cover types, which varied in mean distance ratio size, switched scales from further away to closer to a given land cover type.

Part 2: Home Range Size and Landscape Patterns

Individuals were monitored, on average, 24 times in 2017 (range = 2 – 38), 17 times in 2018 (10 – 22), and 26 times in 2019 (range 6 – 45). For home range estimates, we had an average of 25 locations (range = 9 – 45) (Table 3.1). We found that home range size was significantly positively correlated with Shannon's evenness index, which measures how even the distribution of the area is among patch types, at the 400 m spatial buffer ($p < 0.0125$). Therefore, larger home ranges had a more even distribution of area among patch types, i.e., the same proportional abundances.

Using linear multiple regression we did not find any significant predictor variables for home range size for the 100 m or 200 m spatial buffers. We found three significant factors that influenced home range size at the 300 m spatial buffer: positive for mean fractal dimension index, negative for mean contiguity index, and negative for area weighted proximity index; however, mean fractal dimension index was not significant under the Bonferroni correction. We found two significant factors that influenced home range size at the 400 m spatial buffer: positive for mean fractal dimension index and positive for Shannon’s evenness index. Fractal dimension index reflects patch shape complexity, mean contiguity index reflects the spatial connectedness of cells, proximity index reflects the spatial context of a habitat patch in relation to its neighbors, Shannon’s evenness reflects dominance or and even distribution among patch types(Table 3.2). Larger home range sizes had greater shape complexity and lower physical spatial connectedness. Neither area-weighted mean proximity nor total core area had a significant influence on home range size.

Overall trends varied per category/metric and spatial buffer (Table 3.2). Within the aggregation category, home range size generally increased with an increasing aggregation index, which reflects how the landscape is spread apart or clustered, except at the 400 m buffer, while decreasing as area-weighted mean proximity increased, except for the 100 m buffer. Within the area category, home range decreased with greater total area and largest patch index. Within the core category, home range decreased with larger total core area and area-weighted mean core area distribution at both 100 m and 400 m buffer but increased at the 200 m and 300 m buffer. Within the diversity category, home range increased with increasing Shannon’s evenness index at the 100 m and 400 m buffer and decreased at the 300 m buffer, while increasing with greater patch richness density except at the 100 m buffer. Within the shape category, home range increased with larger mean fractal dimension index at all buffers, while decreasing with larger mean contiguity index except for the 400 m buffer.

Multiple Logistic Regression Modeling

All models met assumptions of normality. We present the best models for each spatial buffer using stepwise regression (Table 3.3 – Table 3.6). Top models included seven variables, i.e., total area, aggregation index, largest patch index, mean contiguity index, Shannon's evenness index, mean fractal dimension index, and patch richness density (all models shown in Table 3.S1). Out of all our models, the 400 m model had the most explanatory power (R^2_{adj} = 0.90) with mean fractal dimension index and Shannon's evenness index (Table 3.6), followed by the first 100 m model (R^2_{adj} = 0.85) with total area, aggregation index and largest patch index (Table 3.3).

Discussion

General

We examined the context of habitat selection and factors influencing home range size for eastern box turtles within Oak Openings Region. We found that turtles had typical average home range size, i.e., 1 – 5 ha, like many studies have shown before in Maryland, (Stickel, 1950), Tennessee (Donaldson and Echternacht, 2005), North Carolina (Kapfer et al., 2013) and Virginia, USA (Fredericksen, 2014); however, some individuals displayed much larger home ranges than typical, i.e., 9.2 ha. Previous studies within this region have found similar results (Wilson, 2012; Martin, 2015; Cross, 2016).

We suggest that this region's high heterogeneity and how it is configured on the landscape are likely driving these turtles' movement patterns. For example, we found that home range size was negatively correlated with mean contiguity index, i.e., spatial connectedness. Larger home ranges were less spatially connected, which suggests that resources may be further away or that movement within preferred patch types is more costly. Turtle home ranges were more heterogenous, especially between parks. On average, home ranges contained five different land cover types; however, turtles in Oak Openings had more land cover types within their home ranges, i.e., four to seven, compared to turtles in Secor, i.e., two to three. The percentage of area for these land covers varied, but the greatest area within home ranges was for upland deciduous and floodplain forest. This was similar as Fredericksen (2014) study which found frequent use of mature hardwood forest, the most predominant habitat within the study area, followed by edge habitat. These turtles tended to use stream habitats during July (28.1°C) and August (28.3°C), the hottest months of the year (Fredericksen 2014). We also found similar habitat use with Kapfer et al. (2013) where turtles were frequently relocated within upland and lowland deciduous forest and least associated with disturbed habitats, grasslands, and edges. Here, average proportional habitat use was similar to average proportional availability and on average, home ranges contained 3 out of 6 available land cover types. We caution that at this spatial scale, we do not account for with-in variation of land cover types, such that fine-scale variations will affect the quality of different floodplain forest patches. Therefore, future studies should utilize additional layers, such as LIDAR, in order to examine these fine-scale variations within a land cover type. The delineation of temporary wetlands likely influence habitat selection at smaller spatial scales than landscape or home range. This suggests that while forests are important, they may not be sufficient. Box turtle habitat selection is flexible while generally focusing on forest habitat, although it also depends on season, ecological requirements, daily movements, and even across life stages (Dodd, 2001).

Habitat Associations

We did not find significant habitat associations between parks at either the landscape scale or within-home ranges scale, except for upland prairie at the landscape scale. Random points within home ranges were significantly closer to upland prairie than random points across the study area within Oak Openings Preserve and are significantly farther away in Secor. We caution that comparing between parks may not be desirable as the amount of each land cover type and configuration differed. Therefore, our results should focus on the changes in habitat associations within parks across scales; however, future studies could consider comparing habitat use between parks based on availability. General trends in Oak Openings Preserve showed that random points within home ranges were closer to natural land covers except for wet prairie, upland savanna, and sand barren than random points across the study site. This suggests that box turtles maintained heterogeneous home ranges in habitat composition, especially in forest land cover types. Individuals were much closer to dry forest than wet forest in Oak Openings Preserve; these habitats may provide better or easier thermoregulation opportunities such as basking in cooler locations. Wet forests reduce desiccation risks and may only be needed during hotter temperatures, such as in June or July (Donaldson and Echternacht, 2005), although habitat utilization is likely to adjust with climate change (Martin and Root, 2020). Adaptations or shifts in species distributions within forest ecosystems are expected as climate changes (Iverson and Prasad, 1998; Parmesan, 2006). These differences are likely the result of different habitat structures, which hinder or facilitate thermoregulation opportunities.

Unsurprisingly, random points within home ranges were further away from both savanna and sand barrens than random points across the study area. These open areas are thermally challenging for reptiles with higher temperatures and may expose turtles to more predators. For sand barrens, it is highly likely that our skewed sex ratio towards males was driving our results. When radio tracking, 44% of our turtle observations occurred during the nesting season, i.e., May-June, while we only had 12% of female turtle observations during the nesting season. Sand barren is critical for nesting females and males likely never travel outside their home range searching specifically for this land cover. The difference between sexes, such as inclusion of searching for open sunlit nesting habitats (Congello, 1978; Hall et al., 1999), suggests there is differential habitat selection, which should be investigated further. On the other hand, random points within home ranges at Secor were closer to upland savanna, wet shrubland, water, swamp forest, conifer and deciduous forest. The turtles in this park utilized swamp forest and upland savanna more. Regardless, Oak Openings Preserve has more total area across land cover types than Secor, for example, there was four times as much swamp forest and eight times as much upland prairie in Oak Openings Preserve than Secor (Figure 3.S2). This explains the differential habitat use between parks because available land covers vary in area and configuration between them.

Eastern box turtles are generally considered a forest dwelling species and our results suggest that turtles at Secor are likely more representative of this association than turtles within Oak Openings Preserve. Upland savanna, though, which has open canopy stands on well drained soils and a well-developed herbaceous layer, is structurally different than upland prairie, which has no trees with mesic to dry prairies and sparse shrub layer (Schetter and Root, 2011). These results suggest that tree structure and herbaceous and/or shrub layers are more important for turtles in Secor than in Oak Openings Preserve. Overall, our study highlights the importance of maintaining heterogeneous landscapes where home ranges that provide a mixture of different land covers will benefit box turtles. Additionally, more homogeneous areas with greater intact, contiguous forests may drive turtle forest usage, whereas more heterogeneous areas with fragmented forests force individuals to use an array of land cover types.

We found shifts in habitat associations when we considered a smaller spatial scale. In Oak Openings, large shifts to further away from landscape to home range scale occurred for upland prairie, floodplain and swamp forest. This suggests that these land covers were less likely to be utilized on a daily basis or turtles were using the habitats more evenly within their home range. Wet forest, such as floodplains, are important resources for thermoregulation in eastern box turtles, but may not be needed constantly at these finer spatial scales; however, at larger scales it is critical for these land cover types to be available and accessible. Wet forests may also play a vital role in foraging because their diet consists of many species that are found in wet or moist areas, such as snails, slugs, earthworms, beetles, fungi, and mosses (Surface, 1908). Other habitats, like open canopy or edges, are important for foraging berries, seeds, grasshoppers, crickets, and caterpillars (Surface, 1908). In Secor, turtles were relatively consistent in habitat associations across scales, except for turf/pasture and wet prairie. We may have found significant differences had we simplified land cover types; however, since the area was highly heterogenous, i.e., 12 land cover types within Oak Openings Preserve and 10 land cover types in Secor out of 15 land cover types in Oak Openings Region, it is important that we differentiated these land covers as structure can play a large role in habitat associations. For example, swamp forests have closed canopy deciduous swamps and flatwoods with semi-permanence on poorly drained soils, while floodplain forests have both closed and open canopy deciduous forests that were poorly to moderate well drained and were often near stream channels (Schetter and Root, 2011). In general, we found that random points and observed locations were further away from human-modified land covers. This was not surprising because other studies have found similar results for reptiles (Hoss et al., 2010; Hibbitts et al., 2013).

The composition complexity of these turtles' home ranges in Oak Openings illustrates the how ecological requirements may vary habitat associations. Ecological neighborhoods for foraging are driven by when food resources are available, such as timing of ripening blueberries, or where these are located, such as finding slugs or snails, within an environment, while ecological neighborhoods for thermoregulation may be so transitory, i.e., moving in and out of shaded areas, that it does not drive the pattern. The issue of scale of operation for foraging vs. thermoregulation or even reproduction requires examining different spatial or temporal scales when we measure habitat utilization.

Home Range Size

Individuals, both female and male, exhibited typical home range sizes (~5 ha). Although, we did find that some turtles exhibited slightly larger home ranges than expected, such as Turtle #4 (male; 7.94 ha; 2018), Turtle #7 (female; 6.46 ha; 2018), and Turtle #8 (male; 9.20 ha; 2019). We noticed that our study sites were wetter in 2018 compared to 2017 or 2019 for these turtles and at the end of 2018, land managers removed a portion of upland coniferous forest within the home range of several turtles in Oak Openings. The extra flooding and land management may have displaced some of our individuals resulting in larger home ranges than typical. Variations across temporal scales may complicate our understanding of habitat associations; however, extensive data collection would be necessary to investigate these differences.

Turtles in Secor had smaller home range sizes than most of our Oak Openings Preserve turtles and these differences were likely the result of different spatial configuration of habitats. Hoss et al. (2010) found for eastern diamond-back snakes that heterogeneity was more important in configuration rather than composition; however, other studies suggest that it may be opposite for several different species such as suites of anurans (Fahrig, 1995) and salamanders (Guerry and Hunter, Jr., 2002) and diurnal breeding birds (Cushman and McGarigal, 2004). Examining both allows us to account for variation across study regions. We did have several limitations to our study such that number of relocations varied across individuals and between parks. Additionally, individuals were not tracked all three years of the study. We recommend some caution as these differences make some interpretations more difficult. Future studies should expand and integrate data from a variety of locations across the parks and either focus on a larger sample size with fewer detections per turtle or focus more intently on a smaller sample size with more consistent tracking across years and multiple parks.

Landscape Pattern

We found that home range size was significantly correlated to mean fractal dimension index, positively at 400 m, and mean contiguity index, negatively at 300 m. Fractal dimension index refers to shape complexity where approaching the low end, i.e., 1, represents very simple perimeters such as squares, while approaching the high end, i.e., 2, represents convoluted perimeters. We found that larger home ranges were more convoluted and smaller home ranges were simpler; however, all our estimated home ranges were on the low end (less than 1.1), suggesting that they were, overall, more simple than convoluted. Contiguity index assesses the spatial connectedness of cells within a grid-cell patch, which provides an index of patch boundary configuration or patch shape. High values, i.e., 1, represent increased connectedness, while low values, i.e., 0, represent disconnectedness. Although we found that smaller home ranges were more spatially connected than larger home ranges, all our values were above 0.80. This suggests that eastern box turtle home ranges were, overall, highly disconnected.

All other landscape metrics were not significant but varied in association across spatial scales. For example, patch richness density, which measures the number of different patch types per area, was negatively correlated with home range size at the 100 m scale but it was positively correlated from 200 – 400 m scales. In other word, at the fine-scale greater patch richness decreased home range size, while at larger scales greater patch richness increased home range size. One explanation may be resource distribution, such that resources were closer together at the fine-scale and farther away at local or landscape scales. Conversely, we found the opposite trend for area-weighted mean proximity index, which measures the proximity of like patch types or spatial arrangement of patch types. For 100 m, home range size increased as the proximity of similar patch types and contiguity of those patch types increased but decreased as this metric decreased from 200 – 400 m scales. At larger scales, eastern box turtles maintained smaller home ranges with greater similar patch proximity. Our study repeated the methodology employed by Hoss et al. (2010) but many of our landscape metrics were different. Therefore, comparisons between eastern box turtles and eastern diamond-back rattlesnakes are difficult to make. However, both studies used area-weighted mean proximity and found the same result that smaller home ranges have greater similar patch contiguity, even with the large difference between spatial scales 250 m to 1,000 m.

We recommend that future studies examine these metrics beyond the landscape FRAGSTATS level, e.g., examining class levels. For example, we found that eastern box turtles showed significant differences between parks for use of upland prairie. Therefore, examining the composition and configuration of upland prairie within home ranges may provide critical information to inform land managers. It may be important for upland prairie to be dispersed within home ranges or it may even more valuable to have greater similar patch proximity. Our results suggest that future studies should incorporate varying spatial scales when examining landscape patterns as many species operate at different scales to meet their various ecological needs. Additionally, our study focused on the influence of landscape on home range size; however, this could be applied to other factors such as total distance traveled within a home range. Future studies may also consider examining multiple temporal scales, within a season and multi-seasonal, even though this requires extensive data collection, it would likely explain some of the heterogeneity that we found.

Modeling Home Range Size using Landscape Patterns

We examined how heterogeneity can predict home range size at multiple spatial scales for eastern box turtles in Oak Openings Region using multiple logistic regression models. We found that our top two models across spatial scales included variations of total area, aggregation index, largest patch index, mean contiguity index, Shannon's evenness index, mean fractal dimension index, and patch richness density. Both our top 100 m, i.e., total area, aggregation index and largest patch index, and 400 m, i.e., mean fractal dimension index and Shannon's evenness index, models had the greatest predictive power ($R^2 = 0.90$) and lowest change in AIC_c. The other models had slightly lower predictive power and models beyond the top two generally had change in AIC_c greater than 2, suggesting weaker models. Eastern box turtles appear to operate and respond to different variables across spatial scales, like many species-habitat relationships (Morris, 1987; Wiens et al., 1987; Wiens, 1989). Our results like many others support considering the context of the environmental setting by including both landscape composition and configuration for study species.

Land Management Recommendations

When examining landscape composition and configuration metrics, there is strong support for careful variable selection. For our study, we considered several variables that are physically modifiable on the landscape. This is important for land managers because they can manipulate the landscape to either facilitate of hinder species movements based on their goals and action plans. For example, based on our results we suggest that land managers should increase the physical connectedness of upland deciduous forest for turtles with home ranges greater than 5 ha in order to reduce home range size. This type of management would be beneficial for turtles because they would spend less time and energy moving around if their habitat was less disconnected. We do caution that landscapes should maintain varying levels of heterogeneity, i.e., two to three land covers as opposed to six to seven, as turtles often utilize both forest and early successional habitats.

Overall, our study addressed the spatial ecology of eastern box turtles, a species of special concern, by using a robust distance-based analysis and multiscale approach. Our results are important for future conservation planning and we found that turtles were, in general, positively associated with forest land covers and negatively associated with human-modified land covers. We suggest that land managers focus on preserving forests but also maintain a mosaic of available land covers. Additionally, some land cover associations did switch in direction of influence between scales, landscape to home range. This is important for managers to consider because at one scale the land cover may be important, while at the other scale it is not. Our results support the use of multiscale approaches that consider landscape composition and configuration in species-habitat relationships, especially for conservation management (Rushton et al., 2004; Guisan and Thuiller, 2005).

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Tables

Table 3.1. Summary of observations for subset of individuals tracked with radio telemetry in Oak Openings Preserve (OOP) and Secor (SEC) from 2017-2019. Home range size (ha) was calculated using minimum convex polygons (MCP).

				# of observations (Home range size)		
Turtle ID	PIT tag Id	Sex	Park	2017	2018	2019
T1	031*023*850	M	OOP	32 (3.75)	24 (3.32)	45 (4.33)
T2	095*118*878	F	OOP	3 (0.02)	---	---
T3	031*036*585	M	OOP	31 (0.10)	---	---
T4	031*007*836	F	OOP	38 (2.70)	10 (7.94)	---
T5	030*879*268	M	OOP	38 (1.96)	21 (5.03)	---
T6	030*083*579	F	OOP	20 (2.79)	10 (1.86)	---
T7	030*892*850	F	OOP	36 (3.69)	20 (6.46)	33 (3.55)
T8	845*003*562	M	OOP	9 (2.55)	24 (4.47)	45 (9.20)
T9	306.1D59537914	M	SEC	---	15 (0.78)	24 (4.18)
T10	845*015*266	M	OOP	---	---	6 (0.04)
T11	3D6.1D595379B7	M	SEC	---	---	12 (3.51)
T12	3D6.1D5953799D	M	SEC	---	---	19 (2.99)

Table 3.2. A comparison between home range size and selected landscape metrics displaying the Pearson correlation coefficients for adult eastern box turtles at four spatial scales. Significant variables are noted by superscript (*).

		Spatial scale			
Category	Metric	100 m	200 m	300 m	400 m
Aggregation	Aggregation index	0.11	0.46	0.19	-0.56
	Area-weighted mean proximity	0.12	-0.58	-0.58*	-0.29
Area	Total area	-0.52	-0.53	-0.47	0.00
	Largest patch index	-0.26	-0.09	-0.11	-0.58
Core	Total core area	-0.03	0.07	0.16	-0.12
	Area-weighted mean core area distribution	-0.03	0.01	0.08	-0.12
Diversity	Shannon's evenness index	0.29	0.00	-0.07	0.73*
	Patch richness density	-0.26	0.25	0.56	0.56
Shape	Mean fractal dimension index	0.16	0.63	0.66*	0.81*
	Mean contiguity index	-0.13	-0.63	-0.79*	0.12

Table 3.3. The null and best models with change in AIC_c values ≤ 2 for eastern box turtle home range size at the 100 m spatial buffer.

K	Predictor variable	Parameter estimate	Prob > F	R^2	AICc	Δ AICc
3	Total area	-592.16	0.0020	0.90	38.10	0
	Aggregation index	9.97				
	Largest patch index	-0.14				
2	Aggregation index	11.36	0.0094	0.74	38.96	0.87
	Largest patch index	-0.15				
1	Intercept	3.62	<0.0001	0	42.00	3.9

Table 3.4. The null and best models with change in AIC_c values ≤ 2 for eastern box turtle home range size at the 200 m spatial buffer.

K	Predictor variable	Parameter estimate	Prob > F	R^2	AICc	Δ AICc
2	Total area	-255.04	0.0130	0.71	39.88	0
	Mean contiguity index	-29.25				
2	Shannon's evenness index	17.84	0.0144	0.70	40.17	0.29
	Aggregation index	6.67				
2	Mean Contiguity Index	-26.46	0.0174	0.69	40.71	1.00
	Mean Proximity Index	-0.29				
1	Mean Fractal Dimension Index	91.98	0.0506	0.40	41.21	1.33
1	Mean Contiguity Index	-28.17	0.0517	0.39	41.26	2.00
1	Intercept	3.62	<0.0001	0	42.00	2.12

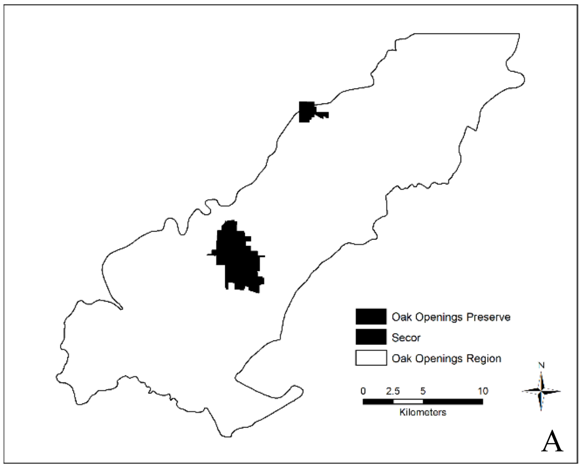
Table 3.5. The null and best models with change in AIC$_c$ values ≤ 2 for eastern box turtle home range size at the 300 m spatial buffer.

K	Predictor variable	Parameter estimate	Prob > F	R^2	AICc	Δ AICc
1	Mean contiguity index	-53.24	0.0070	0.62	36.66	0
2	Mean fractal dimension index	84.47	0.0056	0.77	37.45	0.79
	Patch richness density	0.17				
2	Mean Contiguity Index	-46.72	0.0067	0.76	37.99	1.33
	Patch Richness Density	0.11				
2	Mean Contiguity Index	-45.62	0.0079	0.75	38.47	1.81
	Mean Proximity Index	-0.12				
1	Intercept	3.62	<0.0001	0	42.00	5.34

Table 3.6. The null and best model with change in AIC$_c$ values ≤ 2 for eastern box turtle home range size at the 400 m spatial buffer.

K	Predictor variable	Parameter estimate	Prob > F	R^2	AICc	Δ AICc
2	Mean fractal dimension index	124.90	0.0001	0.90	26.38	0
	Shannon's evenness index	16.33				
1	Intercept	3.62	<0.0001	0	42.00	15.62

Figures



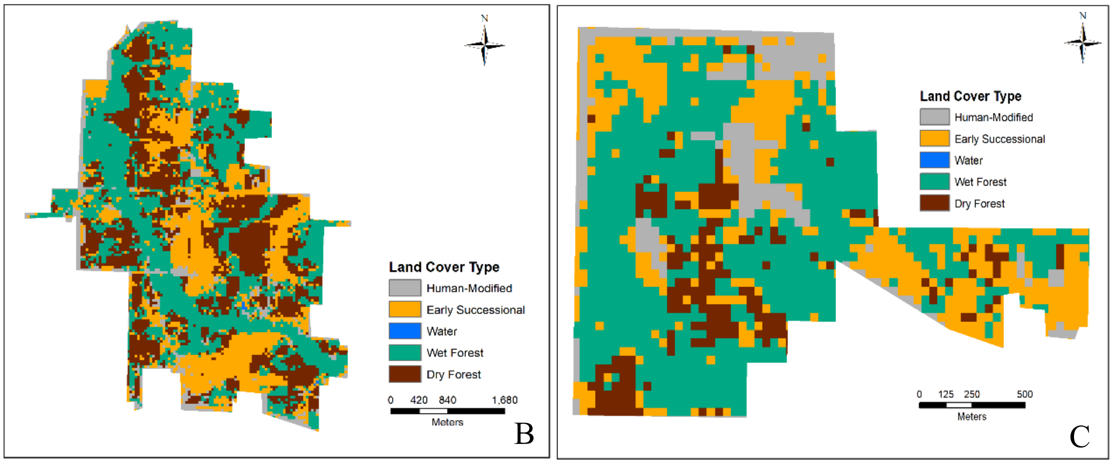


Figure 3.1. Oak Openings Region with the two study areas (in black) (A). Simplified land cover for study sites: Oak Openings Preserve (B) and Secor (C) (Root & Martin 2018).

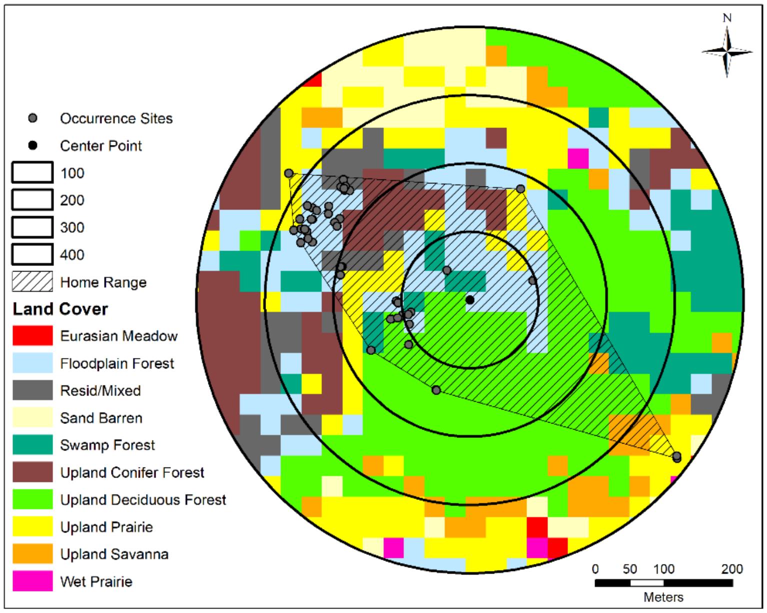


Figure 3.2. A home range (striped lines) for a male eastern box turtle encircled by four spatial buffers with increasing radii (150-, 300-, 450-, and 600-m) overlaid onto a land cover map (Root & Martin 2018).

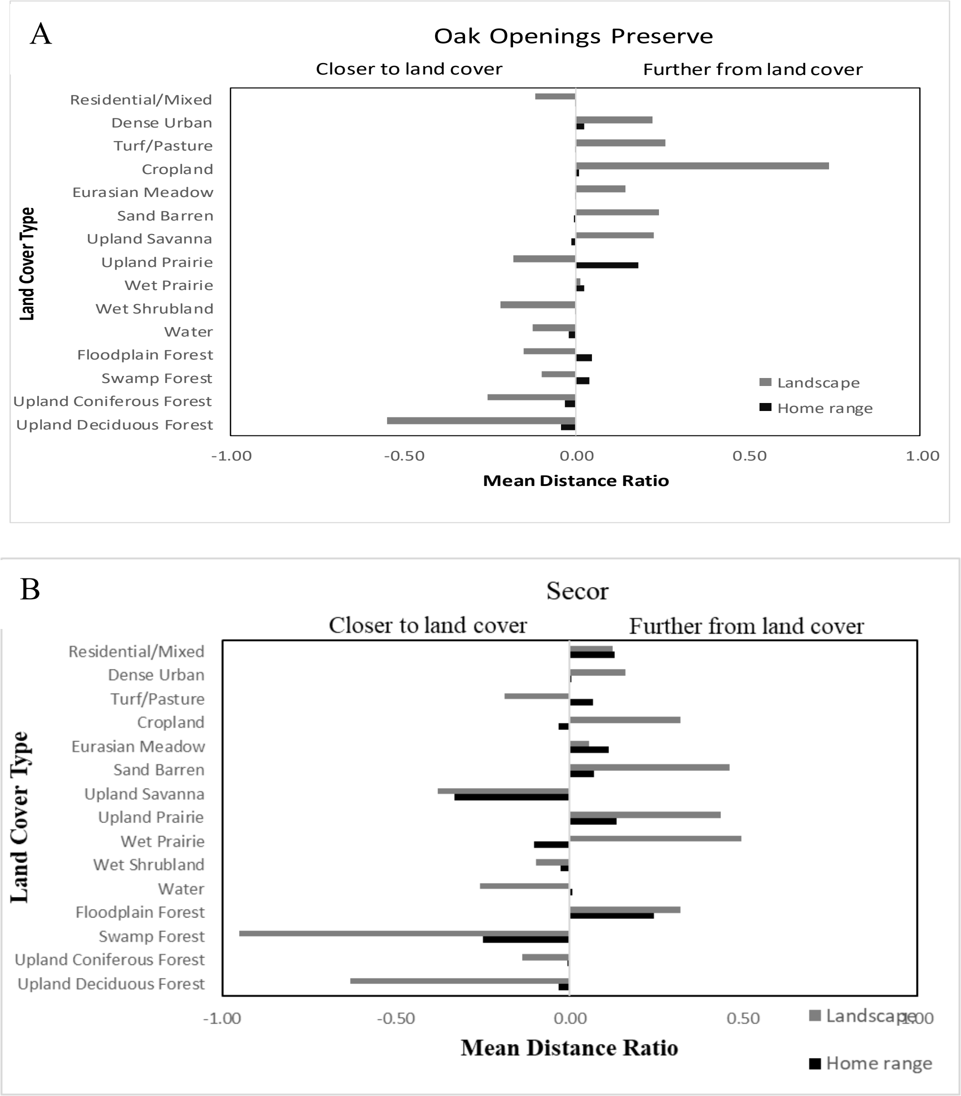


Figure 3.3. The mean distance ratios across individuals for land cover types at the landscape (in light grey) and within-home range (in black) spatial scales for Oak Openings Preserve (A) and Secor (B). The distance ratio was calculated by dividing the mean distance of turtle locations (landscape) or random points (home range) by the mean distance of random locations for each land cover type, then subtract by 1. Distance ratios below zero are considered as closer to a land cover type than expected or at random, while distance ratios above zero indicate that a land cover type is farther away than expected or at random. Separated are natural habitats (below) and anthropogenic (above) the dotted line.

CHAPTER 4: FINE-SCALE MOVEMENT OF TERRAPENEN CAROLINA CAROLINA AND THAMNOPHIS SIRTALIS SIRTALIS WITHIN A FRAGMENTED AND HETEROGENEOUS LANDSCAPE

Abstract

Oak Openings Region, a regional biodiversity hotspot, hosts endangered, threatened and potentially threatened species, including vulnerable herpetofauna. Currently, research on short-range animal movements relative to fine-scale environmental characteristics is scarce. Our objective was to examine fine-scale reptilian movement patterns and link them to ecological and environmental processes. We hypothesized that individuals would travel greater distances in more homogeneous habitats based on ground cover because travel difficulty should be reduced with fewer obstacles. We expected that a greater frequency of short movement distances would occur in more heterogeneous habitats with more ground cover types because of challenges moving from one ground cover to another. Based on different modalities of movement, we expected that snakes would have more tortuous pathways and travel greater distances than turtles. We tracked *Terrapene carolina carolina* and *Thamnophis sirtalis* using fluorescent powder in protected areas from 2017-2019. Hand captured individuals were treated with fluorescent powder then released. Powder trails were measured and analyzed by placing flag markers at directional changes greater than 10°, and we recorded GPS coordinates and ground cover at each flag marker. Using class and landscape metrics in FRAGSTATS we examined the habitat structure within known and expected home ranges. Eastern box turtles traveled around 32 m/d, while snakes traveled 30 m/d on average. We found that increased homogeneity in ground cover was associated with increased distance traveled as well as increased numbers of turns for turtles, as predicted, but the opposite trend was found for snakes. Home ranges had low

connectivity for turtles that traveled more linear trails, while snakes had more tortuous trails. These results provide critical information on the importance of heterogeneity, i.e., local habitat factors do impact fine-scale movement patterns, to maintain diverse taxa such as reptiles. In addition, as management actions are applied at a local scale, fluorescent powder can be an invaluable tool as it highlights the least costly pathways providing a local scale view of connectivity, unlike the regional scale of most habitat modeling.

Introduction

Insight into animal movement patterns is critical for conservation ecology. Reptiles are suffering from large global population declines from human impacts, including increased road mortality, habitat loss, illegal/commercial harvesting and global climate change (Gibbons et al. 2000). These factors play a strong role in large-scale patterns of distribution and abundances; however, how these factors influence fine-scale movements or day to day activities is often understudied. Fine-scale movements are usually closely related to microhabitat and microclimate conditions, which in turn impact larger scale distributions and abundances (Peterman & Semlitsch 2013). In addition to these impacts, movement capability and perception of the environment are different for individuals. Therefore, the spatial scale (i.e., fine, local, landscape) depends on the organisms' lifetime experience (Baker 1978; Nathan et al. 2008). Scale is also influenced by the landscape structure, such that intact, homogenous landscapes are easier for monitoring movements, while it is more difficult to monitor within fragmented, heterogeneous landscapes. Today's landscapes are often heterogeneous mosaics that mix relatively intact ecosystems with residential and agriculture (Hobbs et al. 2014). Therefore, it is critical to examine animal movements across these complex, heterogeneous landscapes. Several studies have found that reptiles, such as northern map turtles (*Graptemys geographica*) (Bennett et al.

2010) and California kingsnake (*Lampropeltis californiae*) (Anguiano & Diffendorfer 2015) have smaller home ranges, more restricted movements and higher spatial overlap with other individuals within fragmented landscapes. In heterogeneous landscapes, these habitat components affect fine-scale movements through vegetation characteristics and topography. Vegetation characteristics affect food and cover availability and often result from trade-offs between reducing energy costs and increasing energy gains (Leblond et al. 2010) and topography affects physical energetic costs when moving.

We can improve our understanding of this relationship at finer scales by examining daily movements and microhabitat use. At the local scale, we can examine movements related to home range size and structure. Small-bodied terrestrial mammals that have relatively low mobility and more restricted home range and habitat requirements, such as marsupials, murid rodents, and introduced mouse in Australia, are an ideal group to examine the influence of habitat heterogeneity (Recher, Lunney, & Matthews 2009). Therefore, reptiles may provide even greater insight into fine-scale movement patterns in response to habitat heterogeneity because they have lower mobility than many mammals and tend to have more restricted home ranges. Additionally, reptiles are linked directly with the environment for thermoregulation (Stevenson 1985; Blouin-Demers et al. 2003; Whitaker & Shine 2002) making it increasingly important to understand the fine-scale nature of this regulation through tracking techniques (Gardiner et al. 2014).

Scale matters when exploring these movement patterns; however, we expect that animals will take the least costly pathway more often to balance their ecological requirements. Complex or heterogeneous environments may reduce energy costs because the varied resources an individual depends upon may be more readily available, requiring less movement to acquire these resources (Hoss et al. 2010). Inferring dispersal can be difficult; however, a simple model such as least cost path (LCP) can help identify likely patterns. LCP models suggest that dispersing individuals will only respond to the environmental context and are constrained by the elements of the landscape. This in turn drives the cost of dispersal and therefore chosen directions are based on minimizing the cumulative displacement costs (Baguette, Stevens & Clobert 2014). LCP assumes individuals make an informed choice, one cell at a time and therefore do not need a perfect understanding of their overall landscape when dispersing. Many reptiles are known to have high site fidelity and often return to the same areas repeatedly over the season, which suggests that they are familiar enough within their home range to reduce travel costs. This may be especially important to long-lived species, such as eastern box turtles (*Terrapene carolina carolina*), which have time to accumulate knowledge of their surrounding environment. Many studies have shown that home range estimates for this species vary slightly from year to year (Stickel 1950; Cross 2016; Dodd 2001), therefore likely in response to environmental stochasticity.

Many studies have focused on local-scale movement patterns such as home range analysis and habitat selection for reptiles because of the wide use of radio transmitters (*Crotalus adamanteus*, Hoss et al. 2010; *Terrapene carolina carolina*, Iglay, Bowman & Nazdrowicz 2007; *Emydoidea blandingii*, Refsnider & Linck 2012; *Pituophis catenifer sayi*, Kapfer, Coggins & Hay 2008). Turtles are prime candidates for radio telemetry because of the relative ease to glue a radio transmitter onto their shell. Snakes have been radio tracked with variable attachment methods such as surgical implanting (Croak et al. 2013; Kapfer, Coggins & Hay 2008; Shew, Greene & Durbian 2012), sewing, and duct taping (Tozetti & Martins 2007). Radio telemetry has been shown to be an excellent method for relocating individuals; however, it provides points in time where individuals are detected and does not indicate the path the individual took to get there. In order to examine these fine-scale movements, researchers have utilized methods such as automatic GPS data loggers (Allan et al. 2013; Price-Rees, Brown & Shine 2013), thread trailing (Stickel 1950; Metcalf & Metcalf 1970; Strang 1983; Donaldson & Echternacht 2005; Tozetti & Martins 2007) and a relatively new method, fluorescent powder (Furman, Scheffers and Paszkowski 2011; Williams et al. 2014). Automatic GPS loggers and radio transmitters are expensive, although thread trailing is a cheaper alternative; all these methods are invasive and require attachment methods for the device. In contrast, fluorescent powder tracking is relatively cheap and releases the individual from carrying a device. Additionally, it provides detailed short-range movements for terrestrial species that can be easily related to environmental characteristics.

These fine-scale environmental characteristics are especially important in forests and serve important ecological functions that provide opportunities in prey detection, protection and avoidance, thermoregulation, rest, and brumation (Godbout & Ouellet 2010). Our study of fine-scale movement patterns is important because it helps us better understand ecological movements (e.g., constraints, influencing factors) and provides better guidance for local on-the-ground management (e.g., what is needed for thermoregulation, refuge). For an example, management of coarse woody debris can affect fine-scale movements that remain undetected at larger scales (i.e., home range, landscape). Yet, changes in fine-scale environmental characteristics can have significant consequences in survival of acute impacts (e.g., fire, storm events) and on daily energy budgets. In order to make informed decisions on reptilian conservation, we need to increase our understanding of fine-scale movement patterns and ecological requirements in order to better manage the habitat.

The aim of this study was to understand reptilian (i.e., *Terrapene c. carolina* and *Thamnophis sirtalis sirtalis*) movement in the context of a diverse and fragmented landscape. Understanding movements is relatively straightforward in an intact, homogenous environment; however, our study represents an opportunity to better understand the nuances of movements in a fragmented, heterogeneous environment, an increasingly common context for these species in an urbanizing world. These landscapes are not only challenging for land managers, but for reptiles as well. Our overall goal was to understand how difficult it may be for reptiles, e.g., turtles and snakes, to find food, mates, thermoregulate and avoid predators within their daily movement patterns and make comparisons between these two taxa. From an ecological perspective, we expected that eastern garter snakes would travel greater distances than eastern box turtles because they hunt for prey, have active thermoregulation, and utilize more narrowly distributed resources, such as feeding on worms, slugs, amphibians, and fish. These responses are likely to vary across different land cover types such as between forest and early successional. For example, floodplain forest are critical thermal refuges for eastern box turtles during hotter months (Wilson 2012), while these semi-aquatic areas provide ample foraging opportunities, i.e., fish, aquatic insects and amphibians (Drummond 1983), for eastern garter snakes. Given the differences in locomotion and general needs between turtles and snakes, we expected that they would vary in their fine-scale movement and snakes would be likely to encounter more challenges resulting in more convoluted or tortuous paths. We hypothesized that individuals would travel greater distances in more homogeneous habitats based on ground cover because travel difficulty should be reduced with fewer obstacles. We expected that a greater frequency of short movement distances would occur in more heterogeneous habitats with more ground cover types because of challenges moving from one ground cover to another. To test these expectations, we radio-tracked a subset of *Terrepene carolina carolina*, applied non-toxic fluorescent powder to selected individuals of our two study species, and characterized movement patterns and structural characteristics of the environment.

Methods

Study Species and Study Sites

Eastern box turtles are a terrestrial species and depend on forest habitat; within Ohio box turtles are a species of special concern (Ohio Department of Natural Resources Division of Wildlife. 2012. Woodland Box Turtle-*Terrapene carolina carolina*. Available from http://wildlife.ohiodnr.gov/species-and-habitats/species-guide-index/reptiles/woodland-box-turtle [Accessed 17 August 2017]). Eastern garter snakes are small to medium sized snakes that are commonly found throughout Ohio. We conducted this research from 1 May 2017 to 21 August 2019 during the active season until brumation in several protected areas within the Oak Openings Region in northwestern Ohio. Our study areas varied in size from Blue Creek with 141 ha (the smallest) to Oak Openings Preserve with 973 ha (the largest). We used a land cover map (Root & Martin 2018) for the region to examine habitat use at the local scale. The region itself is highly heterogeneous, i.e., 15 land cover types, including wet and dry forest (swamp, floodplain, conifer, and deciduous), wet and dry early successional (wet prairie, wet shrubland, upland savanna, upland prairie, and sand barren), water, and human-modified land cover types (turf/pasture, residential/mixed, dense urban, cropland, and Eurasian meadow) (Root & Martin 2018). The composition and configuration of habitat with our study sites varied; however, they were similar in the amount of heterogeneity (Table 4.1, Figure 4.1).

Species Capture and Handling

We used a combination of different field techniques to survey for our target reptilian species including 39 wooden cover boards spread across five parks (12 in Oak Openings Preserve, 9 in Secor, 6 in Kitty Todd, 6 in Maumee State Forest, and 6 in Blue Creek), 87 line transects spread across five parks (56 in Oak Openings Preserve, 10 in Secor, 8 in Kitty Todd, 10 in Maumee State Forest, and 3 in Wildwood), and opportunistic visual encounter surveys, rough approximation of 120 ha (~75 ha in Oak Openings Preserve, ~33 ha in Secor, ~6.2 ha in Maumee State Forest, ~2.3 ha in Kitty Todd, and ~4.2 ha in Blue Creek). All individuals were processed quickly to reduce stress and unique pairs of gloves were worn when handling individuals. For eastern box turtles, we scanned individuals for a passive integrated transponder (PIT) tag (AVID(R) MicroChip ID Systems, Folsom, Louisiana, USA) for individual identification, and we implanted a PIT tag in individuals without one. We inserted a PIT tag into individuals that did not have one. A PIT tag was injected using a 12-gauge needle under the skin of the lower abdomen just in front of the rear leg, following our IACUC protocol #1001429-10. A subset of individuals (n = 7) were tracked using radio telemetry. A radio transmitter (Model RI-2B or SI-2F; Holohil Systems, Ltd., Ontario, Canada) was glued onto the back-right carapace using 5-minute epoxy. Sex was identified by secondary characteristics (Ernst & Lovich 2009). The PIT tag and radio transmitter were limited to no more than 5% of the individual’s total body weight. We applied a coating of a non-toxic fluorescent powder (Radiant Color Series T1, DayGlo Color Corporation, Cleveland, Ohio) in one of four colors and mineral oil mixture with a 3:1 g ratio to the plastron of each individual (Figure 4.2a). Eastern garter snakes (n = 5) were hand captured after detection. We did not insert a PIT tag nor attach radio transmitters to these individuals. The bodies of individuals were coated with one of four colors of non-toxic fluorescent powder

(Radiant Color Series T1, DayGlo Color Corporation, Cleveland, Ohio) and mineral oil mixture with a 3:1 g ratio (Figure 4.2b).

Local-Scale and Fine-scale Tracking

We tracked 14 eastern box turtles (6 female, 8 male), and five eastern garter snakes using fluorescent powder in Oak Openings Region. We tracked 7 eastern box turtles using radio telemetry (a 3-element folding Yagi antenna (Advanced Telemetry Systems, Isanti, Minnesota, USA) attached to a R1000 Receiver (Communications Specialists, Inc., Orange, California, USA)) roughly one to three times per week during daylight hours for local-scale tracking. These individuals were monitored closely and were consistently tracked with fine-scale fluorescent powder throughout the active season. Seven additional individuals were detected opportunistically and tracked briefly (e.g., 1 or 2 days) at the fine scale. All six snakes were each tracked for 1 day at the fine scale after initial detection and capture.

At the detection site, we marked the location with a flag and released individuals after processing. A trail was left as the individual traveled throughout the environment by leaving small flakes of powder that rubbed onto the ground cover and vegetation. We returned at night, approximately 34 hours following release starting around 2100; however, heavy rainfall on assigned nights pushed back some of our night work to three to seven days later. This allowed individual(s) to travel during the day and provided enough low light levels to track the fluorescent trail. At night, we returned to the release site and for each trail we overlaid a thin rope on the fluorescent trail (Figure 4.2c). We followed trails until power was depleted or we detected the individual. The following day, we placed flag markers at directional changes greater than 10° (Furman et al. 2011) and the measured the flagged trails. The Global Positioning System (GPS; eTrex, Garmin International, Inc., Olathe, KS, USA) coordinates in WGS 1984 were recorded for each flag marker on the trail (3-m accuracy). We additionally recorded angle of directional change, distance traveled between flag markers using a tape measure, and ground cover vegetation at each positioned flag marker. For ground cover, we took a photograph held at chest-height to create a quadrat sample around each flag marker, i.e., the center point, and estimated the percentage within the quadrat for nine ground cover types, e.g., leaf litter, grass, non-grass plants, coarse woody debris, logs, soil, trees, sand, and water (Figure 4.S1).

Home Range Estimations

We merged radio telemetry observations per year for each eastern box turtle and estimated home range size using the 100% minimum convex polygon (MCP) calculated in ArcGIS 10.2.2. For the individuals not tracked with radio telemetry, we used the average home range size delineated from our home range estimates and, for simplicity, created a circular buffer around the first detection point, assuming the point was near the center of a home range. For snakes, we used the average home range size from the literature as a rough estimation and created a circular buffer around the first detection point, using a similar simplifying assumption.

Analysis of Movement Patterns and Habitat Structure

Data were compiled in ArcGIS ver. 10.2.2 (Environmental Systems Research Institute, Redlands, California, USA) to create detailed path reconstructions. Total distance traveled per trail was measured by adding the distance for each segment between flag markers. We assumed that each trail per individual represented one day of travel. We based this assumption on several observations using radio telemetry that showed complete fluorescent powder depletion between two consecutive detections. For eastern box turtles, we ran statistics for all turtles collectively, separated by sex and by year. We compiled all data for eastern garter snakes and did not run statistics separated by sex or year. We calculated tortuosity, i.e., how many twists/turns or how linear a trail is, to examine general movement patterns. Tortuosity values closer to zero represented trails with more twists and turns and values closer to 1 represented more linear trails. We examined directionality using percentage of travel for each of the cardinal directions. The frequency of distance traveled was calculated by counting the number of times an individual traveled within the movement categories of 0 – 2 m, 2.01 – 4 m, 4.01 – 6 m, 6.01 – 8 m, 8.01 – 10 m, 10.01 – 12 m, 12.01 – 14 m. We additionally used these movement categories to identify differences between average ground cover encounters. We used non-metric multi-dimensional scaling to plot average ground cover and compared total distance traveled as a vector to examine the relationship between these variables.

We examined the influence of local-scale habitat using land cover within a 30 m buffer of the trails and land cover structure within estimated home range. Patches were identified as unique landscape elements that are measured within home ranges. We created our home range habitat characteristics using class level and landscape level metrics in FRAGSTATS ver. 4.2.1 (McGarigal & Marks 1995) including largest patch index, total edge, contagion index, cohesion, patch richness, interspersion and juxtaposition. Largest patch index is a measure of dominance, it measures the percentage of total landscape that is encompassed by the largest patch. Total edge is the length of total edge within the home range. Contagion measures how disaggregated or interspersed the landscape is, where low values represent disaggregation or many patch types. Cohesion represents connectivity and measures how physically connected the landscape or corresponding patch type is. Patch richness measures landscape composition and identifies the number of different patch types present. Finally, interspersion and juxtaposition use patch adjacencies, not cell adjacencies like the contagion index, and measures the intermixing of patch types. As this metric approaches zero, the distribution among unique patch types becomes uneven.

We ran one-way Analysis of Variance (ANOVA) to test for differences between our predictor variables and our response variables for movement patterns at multiple scales (i.e., fine-scale, local-scale). Additionally, we tested for interaction effects between sex and year for total distance traveled, tortuosity, and frequency of short, medium, and long distance movements. We conducted post-hoc Tukey's test to evaluate for significant differences between groups. All statistics were run in JMP ver. 11 (SAS Institute Inc., Car, North Carolina, USA).

Results

Eastern Box Turtle General Movements

Trails were tracked until the fluorescent powder was depleted, from distinct lines which degraded into small flecks of powder. The end of the trail often came before relocating the individual; therefore, we present minimum distances traveled. We tracked individual eastern box turtles two to nine times in 2017, one to five times in 2018 and one to six times in 2019. Fine-scale movements were highly variable within their home range across years (Table 4.2, Figure 4.3a). Eastern box turtle distance traveled per day ranged from 3 m to 177.17 m and averaged 31.73 m/d. We found that females averaged 27.82 m/d, ranging from 3 m to 71.47 m, while males averaged 33.73 m/d, ranging from 3 m to 177.17 m. Trail curvature varied; on average trail tortuosity was 0.61 or more linear, but ranged from 0.07 or twisted to 0.99 or highly linear. We found a significant difference in our one-way ANOVA for trail tortuosity by sex (F(1,72) = 8.3964, *p* = 0.0050) where females had more linear trails than males. We did not find significant difference for trail tortuosity by year (F(2,71) = 1.5303, *p* = 0.2235) nor among individuals (F(13,60 = 1.7589, *p* = 0.0716). There was a significant difference for sex by year interaction term (F(5,68) = 2.9313, $p = 0.0187$) where males in 2018 were significantly different from females in 2017 ($p = 0.0021$) and 2018 (0.0249). We also found that females in 2017 were significantly different than males in 2017 ($p = 0.0171$) and males in 2018 were different from males in 2019 ($p = 0.0211$).

We did not find significant differences in our one-way ANOVA for total distance traveled per trail among individuals (F(13,60) = 0.7013, $p = 0.7545$), nor between females and males (F(1,72) = 0.8214, $p = 0.3678$). We found that the total distance traveled per trail for all turtles per year was significantly different (F(2, 71) = 7.1828, $p = 0.0014$) and a post hoc Tukey's test of distance traveled per trail by all turtles was significantly different in 2018 from 2017 ($p = 0.0010$) and 2019 ($p = 0.0182$). We found a significant difference effect of sex and year interaction term (F(5,68) = 3.0490, $p = 0.0153$) for total distance traveled. Total travel distance significantly differed between females in 2017 and males in 2018 ($p = 0.0121$) and between males in 2017 and 2018 ($p = 0.0093$). Both females and males traveled greater total distance in 2018 than 2017 or 2018. We found similar results when examining the average total distance traveled per trail by individual which had significant differences for year (F(2,18) = 4.3904, $p = 0.0280$) between 2018 from 2017 ($p = 0.0384$). We did not find significant differences for average total distance traveled by individual for sex (F(1,19) = 0.3268, $p = 0.5742$) nor individual (F(13, 7) = 0.4663, $p = 0.8886$.

Eastern Box Turtle Within Trail Movements

We found that collectively, individuals most often traveled southeast, and southwest (15%). Females most often traveled southwest (20%), whereas males generally traveled southeast (15%). We found significant difference for by year when individuals traveled east (F(2, 68) = 0.0494, $p = 0.05$), south (F(2, 68) = 0.0325, $p = 0.05$), and southeast (F(2, 28.979) = 11.0337, $p = 0.0003$). For all turtles, our post-hoc Tukey's test revealed that frequencies of traveling south was significantly different between 2018 from 2017 ($p = 0.0266$. While for all turtles, frequency of traveling southeast 2019 was significantly different from 2017 ($p = 0.0210$) and 2018 ($p = 0.0210$). We did not find any significant differences for directionality between females and males.

We examined the frequency of distance traveled before changing turning angle within each trail and categorized movements as short (< 6 m), medium (6.01 m to 12 m) and long (> 12 m) for turtles (Figure 4.4). We found that individuals primarily make short movements (95.7%) when traveling, followed by medium (3.9%) and long (0.4%). We found that the average distance traveled before making a turn > 10° was 2.62 m with the minimum distance moved before turning as 0.25 m and maximum 13.25 m. We compared female to male movements and found that both females (97.5%) and males (94.8%) frequently traveled in short distance segments, followed respectively by medium movements (2.5%) and (4.6%) and long movements (0.0% and 0.6%). Females averaged 2.18 m before turning, with a minimum distance of 0.40 m and maximum of 12.00 m. While males averaged 2.52 m before turning, with a minimum of 0.25 m and maximum of 13.25 m. From our one-way ANOVA for each categorized distance based on individual, sex, and year, we found no significant differences on short or long distance movements for sex or individual. We found that medium movements were significantly different for year ($F(2, 71) = 15.6472$, $p < 0.0001$). We found that 2018 was significantly different from 2017 ($p < 0.0001$) and 2019 ($p < 0.0001$). We did not find a significant effect of sex by year interaction term for frequency of short movements nor long movements. We found a significant sex by year interaction term ($p < 0.0001$) for frequency of medium movements and a Tukey's test showed that males in 2018 were significantly different from females in 2017 (0.0001) and

2019 (*p* = 0.0182) and from males in 2017 (*p* = 0.0019) and 2019 (0.0017). Both female and male turtles had higher frequency of medium movements in 2018 than 2017 or 2019.

We examined the influence of fine-scale habitat using ground cover. Turtles encountered a variety of ground cover types including leaf litter, grass, plants, coarse woody debris, logs, soil, trees, sand and water. On average, there were four different ground cover types per trail, ranging from 2 – 6. Turtles had seven movement distance categories ranging from 0 – 2 m to 12 – 14 m. We found that average ground cover encountered slightly varied across movement categories (Figure 4.5a). We did not find a significant difference between average distance traveled and average ground cover percentage (F(1,70) = 2.46, p = 0.065). We followed up the PERMANOVA for several potential explanatory variables and found that average percentage of logs (*p* = 0.0082) and coarse woody debris (*p* = 0.0009) were significant with negative associations.

Eastern Box Turtle Local Scale Habitat Characteristics

We examined the local characteristics of known home ranges for eastern box turtles. We found that turtles had an average home range size of 4.2 ha, which contained dry and wet forest (conifer, deciduous, floodplain, and swamp), human-modified, early successional (sand barren, savanna, and prairie) habitat. Within the known home range of turtles, we found an average of 9 patches (range 4 – 14), and on average, the largest patch encompassed 53% of the home range (range 22% – 88%). Home ranges contained, on average, 924 m of edge (range 120 m – 1,980 m) and many small, dispersed patches (contagion index: avg 38%, 16% – 68%). We examined several factors within land cover classes and found that patch connectivity and largest patch index were variable (Figure 4.7a-b); both upland deciduous forest followed by floodplain forest had the greatest connectivity and largest patches. We found that the total edge was greatest for floodplain forest, followed by upland deciduous forest (Figure 4.7c). Forest habitat had the greatest interspersion and juxtaposition, for which it is closer to being equally adjacent to all other patch type, i.e., maximally interspersed (Figure 4.7d). In our one-way ANOVA for each habitat characteristic based on year we found significant differences in total area (F(2, 18) = 4.9889, *p* = 0.0189) where 2017 was significantly different from 2018 (*p* = 0.0212) and 2019 (*p* = 0.0095) and frequency of short movements (F(2, 18) = 4.6890, *p* = 0.0230) was significantly different for 2017 from 2019 (*p* = 0.0075). We did not find significant differences for number of patches, largest patch index, total edge, cohesion, contagion nor patch richness. The Pearson correlation between the habitat characteristics and average distance traveled, average tortuosity, and frequency of categorized movements showed positive correlations between average tortuosity and total area (r = 0.49, n = 21, *p* = 0.0245) and number of patches (r = 0.53, n = 21, *p* = 0.0129). We found negative correlations between frequency of short movements with total area of the home range (r = 0.49, n = 21, *p* = 0.0228) and cohesion (r = 0.50, n = 21, *p* = 0.0202).

Easter Garter Snake General Movements

Trails were tracked until the fluorescent powder was depleted, from distinct lines which degraded into small flecks of powder. The end of the trail came before relocating the individual; therefore, we present minimum distances traveled. We tracked five eastern garter snakes, three in 2017 and two in 2018 and each individual was only tracked once. Snake movement patterns were more consistent with many twists and turns (Figure 4.2b). Eastern garter snake distance traveled per day ranged from 3.95 m to 58.97 m and averaged 30.15 m/d. Trail curvature was twisted or curvy; on average trail tortuosity was 0.28 ranging from 0.09 to 0.53. Average snake trails were curvier and remained curvy across their range of movements. We did not find any significance for total distance traveled per trail (F(1,3) = 1.4527, *p* = 0.3145), number of direction changes

(F(1,3) = 6.0618, *p* = 0.0907), frequency of short movements (F(1,3) = 3.3145, *p* = 0.1662), or frequency of medium movements (F(1,3) = 0.8660, *p* = 0.4207) (Figure 4.6d-f) compared to the average composite ground cover per trail. We found a trend, though, that increasing ground cover or homogeneity decreased the total distance traveled, number of direction changes, and frequency of short and medium movements.

Eastern Garter Snake Within Trail Movements

We found that snakes most often traveled northeast and northwest (23%) and traveled south, east, and southeast the least (6%). We examined the frequency of distance traveled before changing turning angle within each trail and found that snakes used three categorized movement distances, from 0 – 2 m to 4.01 to 6 m (Figure 4.4). The average distance moved before turning was 1.91 m with the minimum distance moved before turning as 0.38 m and maximum 5.87 m. We examined the influence of fine-scale habitat using ground cover. Snakes encountered a variety of ground cover including leaf litter, grass, plants, coarse woody debris, logs, soil, and around trees. On average, snakes encountered 4 ground cover types and ranged from 2 to 5 ground cover types per trail. We found that snakes most frequently traveled through leaf litter across each categorized movement distance, although the range of use varied (Figure 4.5b). There was no significant difference between average ground cover encountered per trail across the movement categories. We examined how ground cover influenced movements within trails and compared the composite ground cover at each flag marker within a trail to the straight-line distance between flag markers. There were no significant differences between ground cover and the straight-line distance between flag markers within trails (F(1,77) = 0.2593, *p* = 0.6121).

Eastern Garter Snake Local Scale Habitat Use

We examined the local characteristics of expected home ranges for eastern garter snakes. We estimated that snakes would have a home range size of 14 ha, one of the largest estimates (DeGraaf & Rudis 1983) containing dry and wet forest (conifer, deciduous, floodplain, and swamp), human-modified, early successional (sand barren, savanna, prairie and wet prairie) habitat. We found an average of 19 patches (range 11-25), with the largest patch index averaged at 43% (range 33% - 53%). Home ranges contained on average 3,131 m of edge (range 2,190 m – 3,869 m) and contained, on average, many small, dispersed patches (contagion index: avg 38%, 30% - 44%). We examined several factors within land cover class and found that patch connectivity and largest patch index were less variable than eastern box turtles (Figure 4.7a-b), where upland deciduous forest followed by sand barrens had the greatest connectivity and largest patches. We found that the total edge within home ranges was greatest for sand barren, followed by floodplain forest, while upland prairie habitat had the greatest interspersion and juxtaposition (Figure 4.7c-d). A Pearson correlation between the habitat characteristics and average distance traveled, average tortuosity, and frequency of categorized movements found no significance differences across the habitat characteristics, except for a negative significance relationship between tortuosity and patch richness (F(1,3) = 13.8912, p = 0.0336). As patch richness increases, tortuosity decreases.

Discussion

General Movements

Our study, like many others, have characterized the general movement patterns for our target species (Ward et al. 2013; Furman et al. 2011, Stickel 1950, Claussen et al. 1997; Parlin et al. 2018; Tozetti et al. 2009; Iglay et al. 2006). However, our study is quite novel in incorporating these general movements with fine-scale and local-scale habitat characteristics within a heterogeneous and fragmented environment. We explored a variety of factors that land managers can influence in order to facilitate or hinder reptilian movements. Our results suggest that snakes and turtles were not responding similarly to the local environment and that some of the movement patterns were distinctly different from those found in other studies. For example, snakes traveled a maximum of 6 m before making a turn, while turtles traveled up to 14 m before making a turn. Additionally, Furman et al. (2010) found that of three different garter snake species, total travel distances within a day had a maximum of 203 m/d, while Cross (2016) found that eastern box turtles traveled on average 18.29 m/d to 24.42 m/d. However, this assumes that snakes and turtles are operating at the same spatial scales and that we should see similar patterns as other studies.

We found that eastern box turtles had a wide variety of daily movements, ranging anywhere between 3 m to 177 m. This was similar to Iglay et al. (2007) study where box turtles traveled 0 m to 203 m using thread trails in a fragmented landscape. This is likely a result from responses to varying ecological requirements. Smaller movements distances should be related to thermoregulation, moving in between sunny and cooler patches. While medium sized movements are likely foraging responses such as locating vegetation, i.e., fungi, mosses, berries, leaves, roots, buds, and seeds or arthropods, i.e., earthworms, snails, slugs, millipedes, grasshoppers, crickets, beetles, and caterpillars (Surface 1908). Larger movements may be displacement responses to environmental features, such as flooding events or prescribed fires, or are more likely for reproduction such as mate searching from males or nest searching for females. Previous research has shown that females in Oak Openings Preserve travel large distances during nesting season (Cross 2016) and critical nesting areas, such as sand barrens are not widely available (Root & Martin 2018), only centrally located within the park. We found a higher average daily distance, i.e., 31 m/d, than several studies that have monitored eastern box turtles (Iglay et al. 2007; Cross 2016). This is likely a result of the advantage of using fluorescent powder technique, which highlights exactly where the turtle went immediately following application, where thread trail tracking may deviate producing straight-line pathways, rather than following the curvy trail (see Figure 4.4 in Martin 2015). Previously we have shown that although thread trailers may be less accurate, they still provide valuable information, such that turtles tracked with fluorescent powder on average traveled 46 m/d, while turtles tracked with thread trailing on average traveled 28 m/d (Martin 2015).

We tested our technique with eastern garter snakes, as very few studies have attempted this (Furman et al. 2011). Individual snakes had similar movement patterns, especially in their response to powder application. Two individuals traveled in a medium sized circle before continuing forward after application which was also seen in Furman et al. (2011) study. However, snake movement patterns were affected temporarily after acclimatization of handling. Surprisingly snakes traveled on average 30 m/d ranging from 4 m/d to 59 m/d. We expected that snakes, as a more mobile species and active hunters, would travel greater distances. This reduced scale of movement is in contrast to Furman et al. (2011), which found that across three garter snake species, they traveled from 3.08 m to 203.4 m. It is possible that the application of the powder coating was insufficient to capture the full travel length within a day or that as small-bodied species, faster paced snakes do not need to travel as far to obtain their necessary ecological requirements in Oak Openings Region, USA compared to Alberta, Canada. Eastern garter snakes are likely spending more time thermoregulating than eastern box turtles which would account for the larger frequency of short ranged movements. Additionally, they utilize a different foraging strategy and likely these short ranged and tortuous pathways could be responses to prey movements. As active hunters, most snakes must chase their prey which may require a lot of twists and turns within the trail. Future studies should consider laboratory experiments to tease apart the ecological and environmental responses within these movement patterns.

One intriguing result was the difference in trail curvature; snakes had curvy pathways, while turtles varied greatly between curvy to linear pathways based on tortuosity. On average, turtles had more linear pathways; however, the paths varied greatly, likely in response to local environmental cues. This suggests that snakes likely utilized less area with smaller distances traveled and more tortuous pathways within their home range, while turtles utilized the full extent of their home range with a wide range on daily travel paths. There have not been many studies focused on home range size for eastern garter snakes. For comparison of a larger snake, Kapfer et al. (2010) found that adult bullsnakes had home ranges of 26 ha for females and 36 ha for males, with 2.41 and 2.65 ha of preferred habitat and 12.07 ha and 21.49 ha of avoided habitat area, respectively for females and males. Conversely, eastern indigo snakes (*Drymarchon couperi*) have been shown to have much larger home range sizes from 41 to 812 ha (Breininger et al. 2011; Hyslop et al. 2014). Snakes utilize a more challenging locomotion style and may not be able to fully utilize their home range as eastern box turtles do.

Fine-scale Within Trail Movements

Our analysis of these short-range movements provides information that complements many static habitat selection analyses and provides insight into the spatial variations in individuals' distributions through time. It is especially important for land managers to understand reptilian responses within their general or overall daily movements, e.g., within the daily trail patterns for eastern box turtles and eastern garter snakes. We found that eastern box turtles most often traveled southwest (most for females) and southeast (most for males); however, the variation was relatively spread out across the cardinal directions. Eastern garter snakes were the opposite, traveling northeast and northwest the most. We do not know why there would be this difference in direction traveled between turtles and snakes, but it is presumably related to the difference in the way the two species respond to local conditions.

On average individuals traveled 2.62 m (eastern box turtles) and 1.91 m (eastern garter snakes) before changing their turning angle. This suggests that reptiles frequently made short movements when traveling from place to place. We found that snakes more frequently made shorter range movements than turtles before changing direction. Our results suggest that turtles are responding differently than snakes when moving within their environment. There are a number of plausible explanations for these detected differences. Each species may utilize different resources, which may be distributed in different patterns (e.g., patchy versus evenly dispersed). Frequent use of short movements could result from thermoregulation and the differential need to move from shade to sun, which may be more critical for snakes rather than turtles. Unlike turtles, snakes do not have a shell to withdraw in when predators approach and may rely more heavily on the presence of coarse woody debris, herbaceous layers or holes in the ground for protection. Reptiles need to maintain their body temperature, and this can be difficult in thermally variable environments. The use of short-range movements to get from cool, shady patches to warm, sunny patches is quite useful. The shorter movements of snakes may also simply reflect the increased challenges that they face in terms of moving through an environment without legs, e.g., any impediments such as coarse woody debris would be less traversable than for a turtle. Greater movement distances are likely reserved for other needs such as foraging and reproduction. Eastern box turtles are generalists and their long-lived nature may allow them to learn where vital resources are, as well as map stable obstacles to allow for more efficient movement. This could account for fewer, but more medium to long range movements to move in a straight-line distance to these resources.

It is difficult to directly measure ecological processes without interfering with movement patterns, therefore we hypothesized that within-trail movements are a response to ground cover heterogeneity. Both turtles and snakes encountered the same variety of ground cover types, with leaf litter as the most frequent type encountered. Overall, ground cover was similar across categorized movement distances for both turtles and snakes. Cover objects are likely to be more abundant for the small-bodied snakes that can easily hide underneath leaf litter, unlike some of the larger turtles. We suggest that further investigations be conducted for eastern garter snakes and expanding to other species with different body structures. Fewer obstacles, such as logs, shrubs, or trees, allow individuals to travel greater distances and may increase exploration. However, we do not suggest that land managers start removing understory or reduce ground cover complexity. With higher homogeneity, turtles may have to search farther to find the necessary resources, such as a log for cover when creating a night form (Stickel 1950) or thorny plants for protection from predators. Higher homogeneity may lead to greater predation as turtles are left out in the open when moving from area to area. Other studies have found that turtles in more developed and diverse habitats travel shorter distances than those within more homogenous and less fragmented habitats (Kipp 2003; Iglay et al. 2007; Willey 2010). Since Oak Openings Region is more diverse and fragmented, our results showcase these larger travel distances.

Local Scale Habitat Characteristics

One of the major strengths of our study is the focus on understanding fine-scale movements within the larger context. Fine-scale movements are not only a response to microhabitats, but also to macrohabitats such as overall land cover composition and configuration. While thermoregulation requirements may rely on the hourly movements, foraging and reproduction rely on larger scale habitat characteristics. Reptiles utilized a wider variety of habitats with variations of dry and wet forest, early successional and human-modified. We expected eastern garter snakes to have larger home ranges as seen with other snakes (Kapfer et al. 2010; Breininger et al. 2011; Hyslop et al. 2014), than eastern box turtles. Turtle home range had far fewer, but more patches and less total edge than snakes. Both species had many small, but dispersed patches and upland deciduous forest had the greatest connectivity and largest patches. This suggests that at a local scale, eastern box turtles home ranges are composed of more intact and homogeneous habitat. Eastern garter snakes may be at more risk than eastern box turtles based on this assessment of habitat characteristics. Although the habitat may be more intact for turtles than for snakes, it is still highly fragmented with a range of 120 m – 1980 m of total edge within home ranges.

Finally, we tested if these habitat characteristics impacted daily movements. We found for eastern box turtles that increasing total home range area and number of patches increased trail tortuosity, while increasing total area and cohesion, decreased the frequency of short movements. For eastern garter snakes, we found that increasing patch richness decreased trail tortuosity. These results suggest that local habitat factors do impact fine-scale movement patterns and that land managers should focus on balancing landscape heterogeneity. Land managers could target factors such as number of land cover types within a specified buffer, increasing/decreasing upland deciduous forest connectivity by connecting isolated patches or reducing hard edges between two land cover types.

Other Factors

One final note for our study, we were able to explore other factors for eastern box turtles that we were unable to do for eastern garter snakes. We had a larger sample size, easier identification for sex, and continued relocation technique for multiple years. It would be helpful for future studies to explore similar factors for snakes for better comparisons. Male turtles generally followed the same patterns as females with a few exceptions. Females did not travel as far as males, an opposite pattern found from a previous study (Cross 2016), likely a result from the previous study's larger number of females and methodology differences. In our study, within trail movements were mostly similar, both females and males frequently made short distance movements, averaging, respectively, 2.18 m and 2.52 m before changing direction. The greatest difference between females and males occurred for the total distance traveled and number of direction changes, which were positively correlated for females. Females may be more sensitive than males to ground cover homogeneity, especially in relation to nesting requirements. Land managers should be cautious when managing ground cover, especially during the nesting season. Males on the other hand, did not appear to be affected by increased ground homogeneity; they may utilize different resources than females and not rely on ground cover structure as much. We did find some significant differences across years, which suggest that environmental stochasticity, e.g., weather patterns, may have played a role in complicating our overall pooled results, such that total distance traveled, traveling east and south, and frequency of medium movements were significantly different in 2018. For our local scale habitat characteristics, we found that 2017 differed significantly for total area and frequency of short movements. This suggests that year to year variations may change eastern box turtle and other reptilian responses at the fine-scale.

Conclusions

We examined fine-scale movement patterns for two reptilian species within a heterogeneous, yet fragmented landscape. Movement patterns were impacted by a variety of factors at different spatial and temporal scales. Monitoring fine-scale patterns provides a broader perspective on movements. We found that at this fine-scale that habitat was complicated and these species frequently made short movements in response to structural features on the landscape. We did find that female eastern box turtles increased the total distance traveled with increasing fine-scale ground cover homogeneity and strongly caution against managing ground cover during the nesting season. Finally, management can target these structural elements in order to facilitate or hinder reptilian movements. For an example, maintaining ground cover heterogeneity can facilitate access to resources.

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Tables

Table 4.1. Characteristics of each surveyed protected area within Oak Openings Region based on approximate size, heterogeneity or number of different land cover types, and composition or percentage of area per simplified land cover type.

Protected Area	Size	Heterogeneity	Land Cover Type	Composition (% area)
Oak Openings Region	47774 ha	15	Early Successional	14.3%
			Forest	14.7%
			Water	0.5%
			Human-Modified	70.5%
Maumee State Forest	826 ha	12	Early Successional	20.2%
			Forest	70.0%
			Water	0.0%
			Human-Modified	9.8%
Blue Creek	141 ha	12	Early Successional	52.8%
			Forest	1.0%
			Water	2.7%
			Human-Modified	43.6%
Oak Openings Preserve	973 ha	12	Early Successional	25.9%
			Forest	67.3%
			Water	0.1%
			Human-Modified	6.7%
Secor	157 ha	10	Early Successional	25.9%
			Forest	61.7%
			Water	0.0%
			Human-Modified	12.3%

Table 4.2. Linear regression between response variables (total distance traveled, number (#) of turns, and frequency of short movements) and average (AVG) composite ground cover per trail for adult eastern box turtles. Significant p-values are in bold and (+) represents a positive and (-) represents a negative relationship.

			AVG composite ground cover			
Category	Type	Response	r	R^2_{adj}	P value	Correlation
All turtles		Total Distance Traveled (m)	0.33	0.10	**0.0046**	+
		# of Direction Change (> 10°C)	0.26	0.05	**0.0288**	+
		Frequency of Short Movements	0.25	0.05	**0.0377**	+
Year	2017	Total Distance Traveled (m)	0.46	0.19	**0.002**$^{+}$	+
		# of Direction Change (> 10°C)	0.34	0.09	**0.0261**	+
		Frequency of Short Movements	0.33	0.08	**0.0334**	+
	2018	Total Distance Traveled (m)	0.10	0.03	0.26	+
		# of Direction Change (> 10°C)	0.25	-0.02	0.39	+
		Frequency of Short Movements	0.23	-0.03	0.44	+
	2019	Total Distance Traveled (m)	0.23	-0.02	0.41	+
		# of Direction Change (> 10°C)	0.25	-0.01	0.36	+
		Frequency of Short Movements	0.23	-0.02	0.40	+
Sex	Female	Total Distance Traveled (m)	0.46	0.18	**0.0193**	+
		# of Direction Change (> 10°C)	0.46	0.18	**0.0198**	+
		Frequency of Short Movements	0.44	0.16	**0.0267**	+
	Male	Total Distance Traveled (m)	0.28	0.06	0.06	+
		# of Direction Change (> 10°C)	0.16	0.00	0.28	+
		Frequency of Short Movements	0.14	0.00	0.34	+
Year and Sex	Female, 2017	Total Distance Traveled (m)	0.81	0.64	< **0.0001**	+
		# of Direction Change (> 10°C)	0.77	0.56	< **0.0001**	+

	Frequency of Short Movements	0.77	0.57	< **0.0001**	+
Female, 2018	Total Distance Traveled (m)	1.00	0.99	**0.04**	**-**
	# of Direction Change (> 10°C)	0.95	0.79	0.21	-
	Frequency of Short Movements	0.98	0.92	0.13	-
Female, 2019	Total Distance Traveled (m)	0.99	0.96	0.09	+
	# of Direction Change (> 10°C)	0.99	0.97	0.01	+
	Frequency of Short Movements	0.99	0.97	0.07	+
Male, 2017	Total Distance Traveled (m)	0.26	0.02	0.22	+
	# of Direction Change (> 10°C)	0.04	-0.04	0.85	+
	Frequency of Short Movements	0.03	-0.04	0.90	-
Male, 2018	Total Distance Traveled (m)	0.60	0.29	0.05	+
	# of Direction Change (> 10°C)	0.53	0.20	0.09	+
	Frequency of Short Movements	0.51	0.18	0.11	+
Male, 2019	Total Distance Traveled (m)	0.38	0.06	0.22	+
	# of Direction Change (> 10°C)	0.36	0.04	0.25	+
	Frequency of Short Movements	0.35	0.03	0.27	+

Table 4.3. Fine-scale movement distance (m) per trail (TR) collected for eastern box turtles and eastern garter snakes using fluorescent powder.

Year	ID	TR A	TR B	TR C	TR D	TR E	TR F	TR G	TR I	TR J
2017	T1	17.91	6.16	28.33	12.45	16.03	42.78	39.26	53.4	----
	T2	38.27	4.50	----	----	----	----	----	----	----
	T3	38.05	4.64	3.00	7.41	24.76	9.02	8.85	38.24	----
	T4	9.36	19.27	31.61	54.19	12.52	44.51	----	----	----
	T5	22.49	31.35	26.50	14.35	15.61	38.42	34.36	51.89	64.71
	T6	26.33	27.65	----	----	----	----	----	----	----
	T7	10.45	24.06	6.73	48.51	28.19	32.29	16.86	7.45	38.39
2018	T1	30.66	35.75	89.91	177.17	13.72	----	----	----	----
	T4	33.95	----	----	----	----	----	----	----	----
	T5	64.95	29.09	52.76	----	----	----	----	----	----
	T7	71.47	14.78	----	----	----	----	----	----	----
	T8	52.2	----	----	----	----	----	----	----	----
	T9	83.7	31.62	----	----	----	----	----	----	----
2019	T1	27.7	15.4	----	----	----	----	----	----	----
	T8	11.55	95.98	43.75	4.32	3.69	13.72	----	----	----
	T9	44.24	----	----	----	----	----	----	----	----
	T13	39.13	41.17	----	----	----	----	----	----	----
	T14	13.82	----	----	----	----	----	----	----	----
	T15	43.51	46.79	----	----	----	----	----	----	----
	T16	10.24	----	----	----	----	----	----	----	----
	T17	7.03	----	----	----	----	----	----	----	----
2017	EGS 1	34.08	----	----	----	----	----	----	----	----
	EGS 2	3.95	----	----	----	----	----	----	----	----
	EGS 3	28.26	----	----	----	----	----	----	----	----
2018	EGS 4	58.97	----	----	----	----	----	----	----	----
	EGS 5	25.47	----	----	----	----	----	----	----	----

Figures

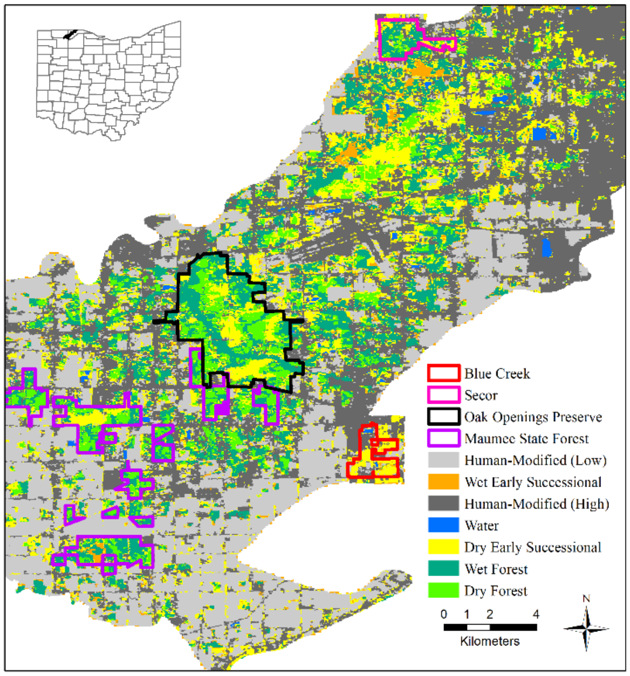


Figure 4.1. Study sites (colored) in Oak Openings Region of northwestern Ohio with a simplified 7-class land cover map (Root & Martin 2018). Combined land cover classes features: dense urban and residential/mixed (Human-Modified Low), cropland, turf/pasture, and Eurasian meadow (Human-Modified High), wet prairie and wet shrubland (Wet Early Successional), perennial pond (Water), upland savanna and prairie (Dry Early Successional), floodplain forest and swamp forest (Wet Forest), and upland deciduous and coniferous forest (Dry Forest).

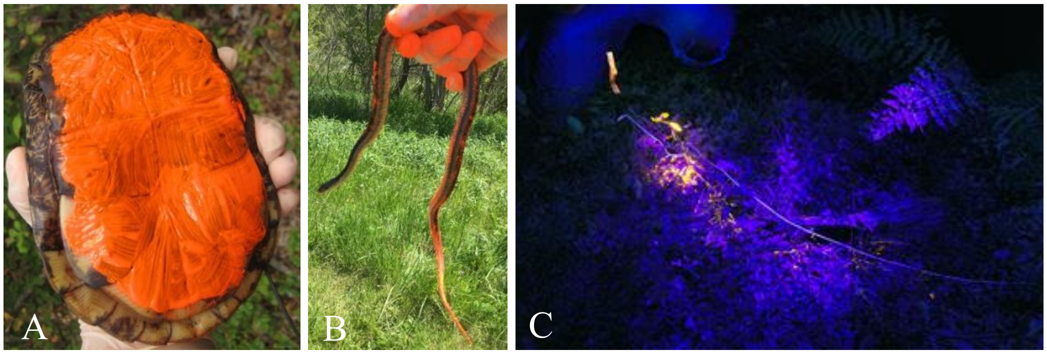


Figure 4.2. Application of the fluorescent powder and mineral oil mixture for a eastern box turtle (A), and eastern garter snake (B). Photographed by Amanda K. Martin. An illuminated orange powder trail at the starting flag marker for an eastern box turtle, Photographed by Anthony A. Kappler.

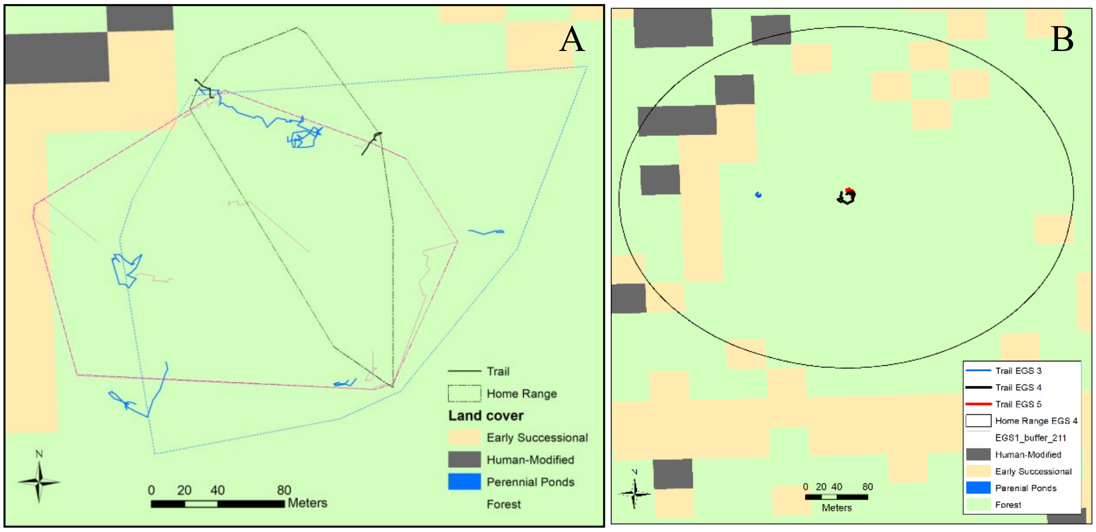


Figure 4.3. Estimated home range size and daily paths traveled for reptiles. The estimated home range size for an eastern box turtle from 2017-2019 (polygon) and its associated daily pathways (lines) (A) and estimated home range from literature (polygon) for three eastern garter snakes (lines) (B) with simplified land cover (Root & Martin 2018).

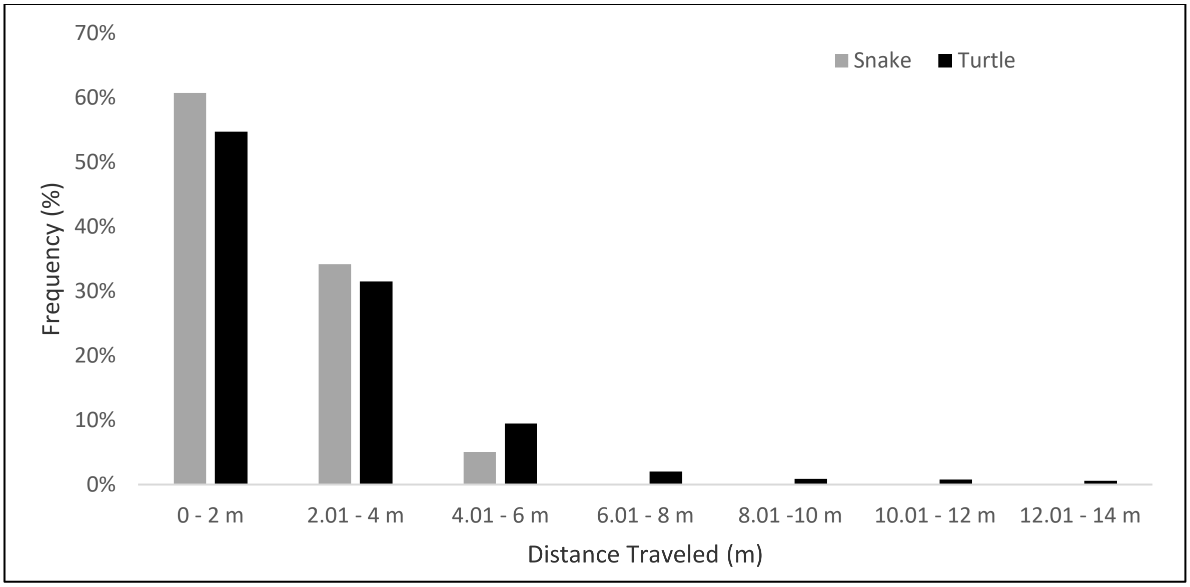


Figure 4.4. The frequency of straight-line movement distances (%) between flag markers for eastern garter snakes (light bars) and eastern box turtles (dark bars).

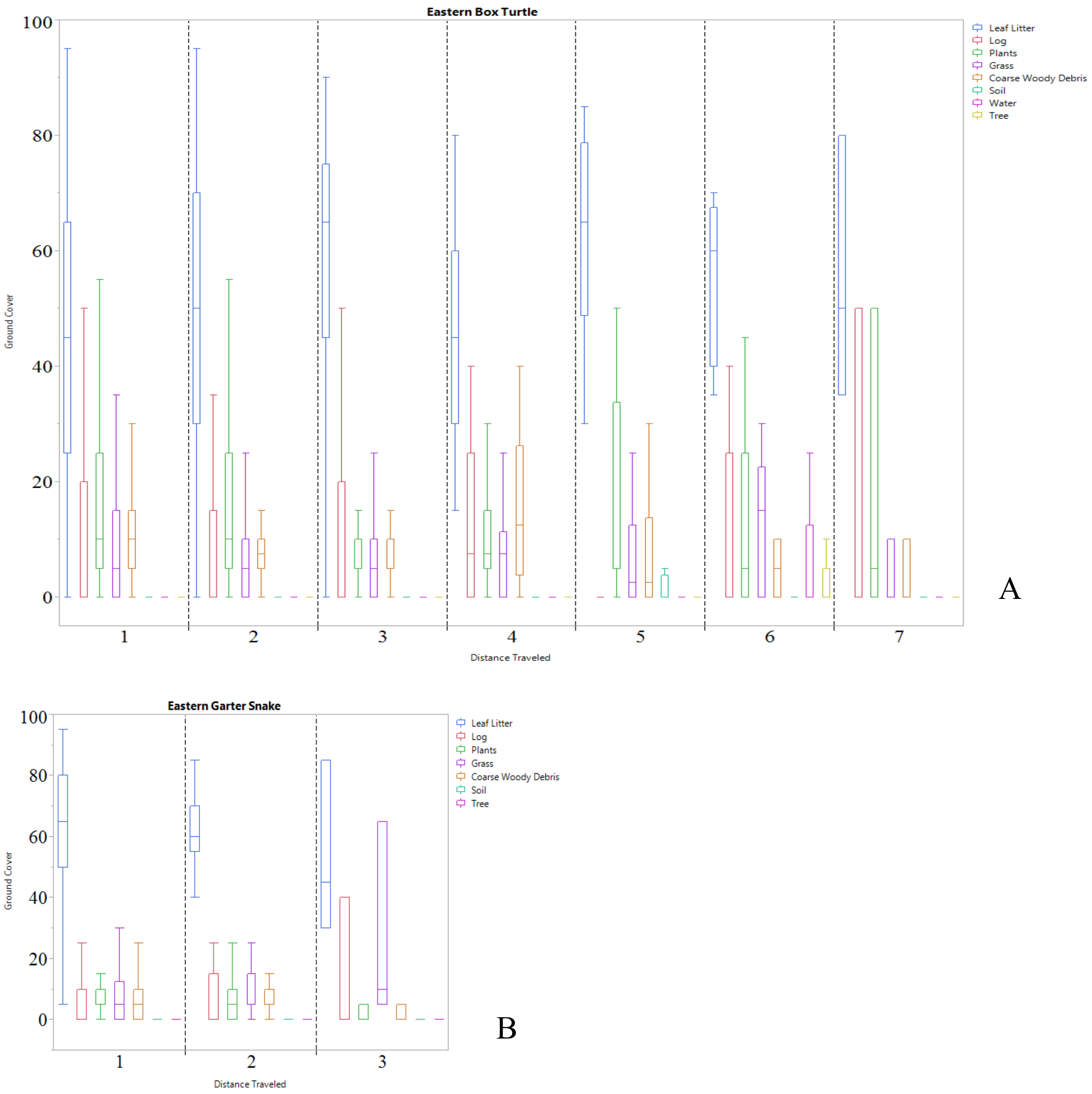


Figure 4.5. Box-and-whisker plots of the average percentage of ground cover, i.e., leaf litter, log, plants, grass, coarse woody debris, soil, tree, and water, encountered during movement distances tracked by fluorescent powder separated by categorized distance traveled (1 = 0 – 2 m; 2 = 2.01 m – 4 m; 3 = 4.01 – 6 m; 5 = 6.01 – 8 m; 6 = 8.01 – 10 m; 7 = 10.01 – 12 m) for eastern box turtles (A) and eastern garter snakes (B). This shows the average values plus range and standard error.

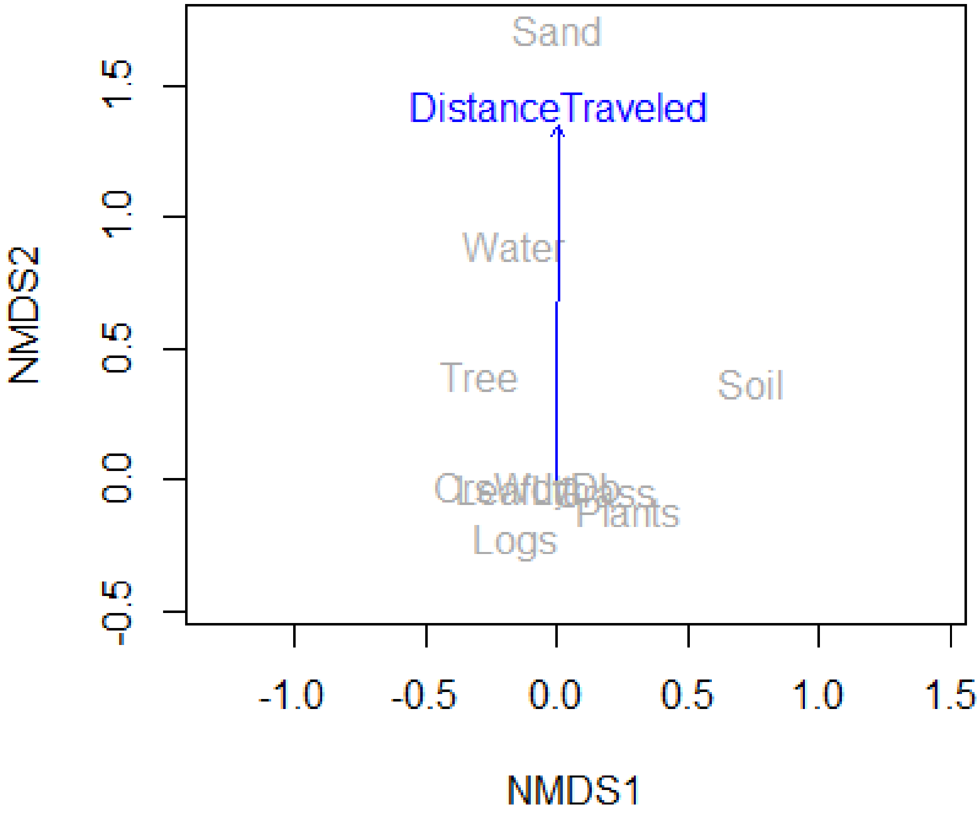


Figure 4.6. Graphical representation using Non-metric multidimensional scaling of the relationship between average distance traveled and average ground cover percentage for eastern box turtles in Oak Openings Region.

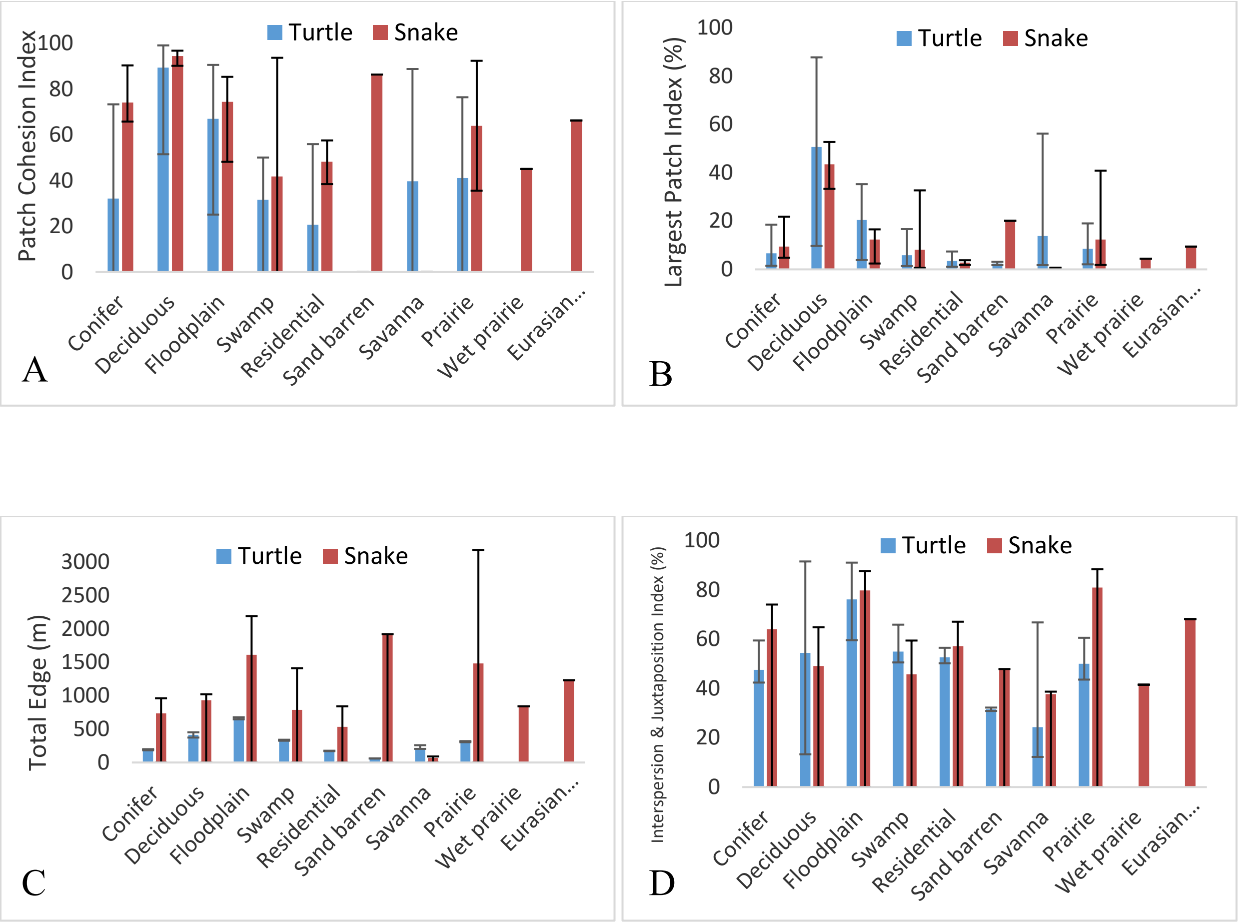


Figure 4.7. Habitat characteristics for eastern box turtle (blue) and eastern garter snake (red) home ranges. For patch cohesion (A), largest patch index (B), total edge (C) and interspersion and juxtaposition index (D) across land cover types.

CONCLUSIONS

In my dissertation, I explored reptilian movement patterns at multiple spatial and temporal scales and related it to landscape structure in terms of composition and configuration. To examine these movements, I utilized a combination of field surveys, remote sensing data, and modeling. My first chapter examines eastern box turtles across their geographic range and identifies how this species responds to climate change within the next fifty years. Utilizing climatic suitability models and occupancy data, I found that at the landscape spatial scale, under predicted climate changes eastern box turtles had increased suitable habitat that expanded northward. These patterns were largely driven by temperature and precipitation. At the local scale based on tracking, individuals can feasibly disperse in response to climate change; however, the physical factors, e.g., barriers such as roads, on the landscape make dispersal difficult. These findings highlight the need to examine dispersal at multiple scales and responses at the fine-scale will influence the overall success in species responses to climate change.

In the second chapter, I examined habitat suitability for several target, representative reptilian species within Oak Openings Region extending from northwestern Ohio to southeastern Michigan. I then identified the characteristics of high diversity areas to inform local conservation plans. I used MaxEnt modeling to build habitat suitability models including reviewing the minimum and maximum models, and then I combined models to examine patterns of diversity. I found that two species of concern, eastern box turtle and eastern hognose snake, have limited suitable habitat, while two common species, midland painted turtle and eastern garter snake, were less restricted. More importantly, I found that suitability increased for multiple species as the percentage of forest habitats increased. Interestingly, I found a bell curve for early successional habitat for multiple species, which suggests that only considering one or two species at a time omits valuable information on habitat suitability for reptiles more broadly. These results provided critical information for land managers and will help inform future conservation plans.

In the third chapter, I examined habitat selection for a single species, eastern box turtle, within two protected areas in Oak Openings Region. I used a robust-distance based analysis and multiscale approach to inform land mangers about habitat use based on tracking surveys. While forests were important across the landscape, I found that upland prairie use significantly differed between parks, indicating that turtles in Oak Openings Preserve utilize prairie, while turtles in Secor do not. I found that home range size increased as shape complexity increased, while home range size decreased as it became more disconnected. Overall, I found that turtles responded to landscape composition and configuration at different spatial scales and recommend that land mangers focus on maintaining connectivity within forest habitats.

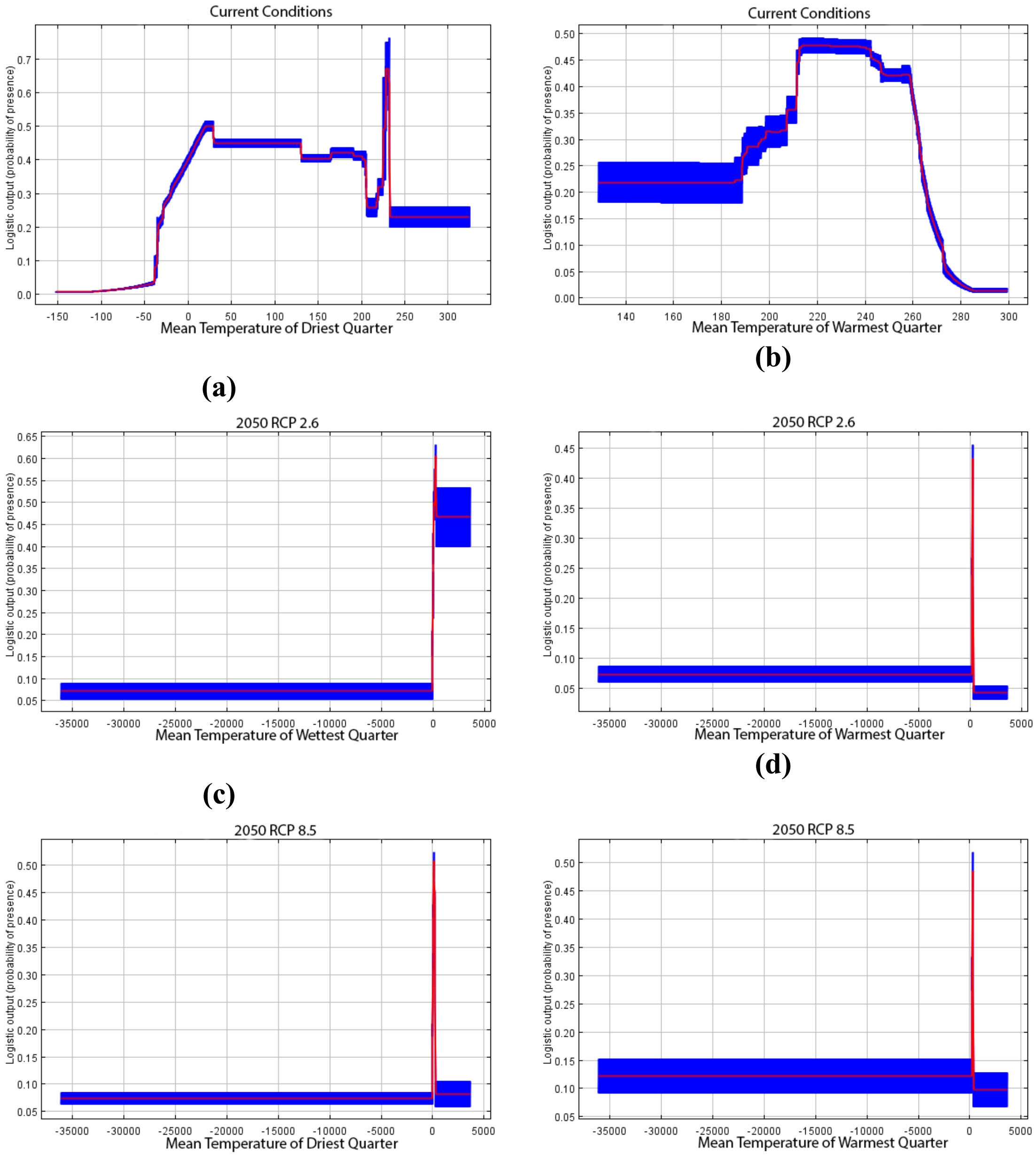
In the fourth chapter, I examined reptilian movements at a fine spatial scale, extending much of the previous knowledge. I utilized a relatively novel method, fluorescent powder, to track the daily movements for eastern box turtles and eastern garter snakes and compared these movements to the local spatial scale. I found that that turtles traveled on average 27.82 m/d, ranging from 3 m to 177 m. These trails ranged in curvature, from nearly completely linear trails to curvy ones. Turtles displayed typical average home range size, but some individuals had slightly larger than expected. Snakes traveled on average 30 m/d, ranging from 3 m to 59 m. Trails were curvy and individuals frequently make short movements. Here, I explored a variety of factors that land managers can influence in order to facilitate of hinder reptilian movements. Overall, my results suggest that turtles and snakes respond differently to the local environment and that it is important to evaluate heterogeneity across multiple scales and its impact on reptile movement.

This work contributes to the growing knowledge of spatial ecology, especially expanding multispecies responses. Conservation efforts for reptiles should focus primarily on improving connectivity for forest habitats, followed by early successional habitats. This is especially important as urbanization expands and continues to fragment large continuous tracts of natural habitats.

APPENDIX A: CHAPTER 1 SUPPLEMENT

Table 1.S1. The correlation matrix for nineteen bioclimatic (BIO) variables. Highly correlated layers (r > 0.80) are in bold.

Variable	**BIO 1**	**BIO 2**	**BI O 3**	**BIO 4**	**BIO 5**	**BIO 6**	**BIO 7**	**BIO 8**	**BIO 9**	**BIO 10**	**BIO 11**	**BIO 12**	**BIO 13**	**BIO 14**	**BIO 15**	**BIO 16**	**BIO 17**	**BIO 18**	**BIO 19**
BIO 1	1.00	0.02	**0.84**	**-0.85**	**0.81**	**0.97**	**-0.80**	0.23	**0.86**	**0.94**	**0.98**	0.72	0.76	0.47	-0.04	0.76	0.50	0.51	0.64
BIO 2	0.02	1.00	0.31	0.33	0.47	-0.16	0.47	-0.09	0.00	0.22	-0.11	-0.08	-0.13	-0.12	0.07	-0.12	-0.12	-0.30	0.02
BIO 3	**0.84**	0.31	1.00	-0.78	0.67	**0.82**	-0.68	0.13	0.73	0.73	**0.85**	0.66	0.69	0.39	0.00	0.69	0.42	0.47	0.58
BIO 4	**-0.85**	0.33	-0.78	1.00	-0.40	**-0.94**	**0.99**	-0.17	-0.78	-0.62	**-0.94**	-0.75	-0.76	-0.56	0.16	-0.75	-0.59	-0.61	-0.64
BIO 5	**0.81**	0.47	0.67	-0.40	1.00	0.67	-0.30	0.21	0.64	**0.95**	0.69	0.43	0.47	0.24	0.05	0.47	0.26	0.18	0.41
BIO 6	**0.97**	-0.16	**0.82**	**-0.94**	0.67	1.00	**-0.91**	0.22	**0.85**	**0.84**	**1.00**	0.75	0.76	0.53	-0.11	0.76	0.56	0.55	0.66
BIO 7	**-0.80**	0.47	-0.68	**0.99**	-0.30	**-0.91**	1.00	-0.16	-0.74	-0.55	**-0.89**	-0.72	-0.72	-0.55	0.17	-0.72	-0.57	-0.61	-0.62
BIO 8	0.23	-0.09	0.13	-0.17	0.21	0.22	-0.16	1.00	-0.06	0.22	0.22	-0.13	0.11	-0.22	0.30	0.12	-0.22	0.46	-0.31
BIO 9	**0.86**	0.00	0.73	-0.78	0.64	**0.85**	-0.74	-0.06	1.00	0.78	**0.86**	0.78	0.67	-0.22	0.30	0.67	0.65	0.29	**0.80**
BIO 10	**0.94**	0.22	0.73	-0.62	**0.95**	**0.84**	-0.55	0.22	0.78	1.00	**0.86**	0.58	0.62	0.36	0.01	0.62	0.38	0.33	0.54
BIO 11	**0.98**	-0.11	**0.85**	**-0.94**	0.69	**1.00**	**-0.89**	0.22	**0.86**	**0.86**	1.00	0.75	0.78	0.52	-0.09	0.77	0.56	0.56	0.66
BIO 12	0.72	-0.08	0.66	-0.75	0.43	0.75	-0.72	-0.13	0.78	0.58	0.75	1.00	**0.82**	**0.82**	-0.34	**0.82**	**0.85**	0.50	**0.89**
BIO 13	0.76	-0.13	0.69	-0.76	0.47	0.76	-0.72	0.11	0.67	0.62	0.78	**0.82**	1.00	0.40	0.21	**0.99**	0.44	0.78	0.57
BIO 14	0.47	-0.12	0.39	-0.56	0.24	0.53	-0.55	-0.22	0.62	0.36	0.52	**0.82**	0.40	1.00	-0.77	0.41	**0.99**	0.16	**0.86**
BIO 15	-0.04	0.07	0.00	0.16	0.05	-0.11	0.17	0.30	-0.24	0.01	-0.09	-0.34	0.21	-0.77	1.00	0.21	-0.76	0.35	-0.56
BIO 16	0.76	-0.12	0.69	-0.75	0.47	0.76	-0.72	0.12	0.67	0.62	0.77	**0.82**	**0.99**	0.41	0.21	1.00	0.44	0.78	0.57
BIO 17	0.50	-0.12	0.42	-0.59	0.26	0.56	-0.57	-0.22	0.65	0.38	0.56	**0.85**	0.44	**0.99**	-0.76	0.44	1.00	0.18	**0.88**
BIO 18	0.51	-0.30	0.47	-0.61	0.18	0.55	-0.61	0.46	0.29	0.33	0.56	0.50	0.78	0.16	0.35	0.78	0.18	1.00	0.18
BIO 19	0.64	0.02	0.58	-0.64	0.41	0.66	-0.62	-0.31	**0.80**	0.54	0.66	**0.89**	0.57	**0.86**	-0.56	0.57	**0.88**	0.18	1.00



(a) (b) (c) (d) (e) (f)

Figure 1.S1. Response curves of the top two bioclimatic predictors for (a) current conditions; (b) 2050 Representative Concentration Pathway (RCP) 2.6; (c) 2050 RCP 8.5. The values shown are averaged from ten replicate runs with ±1 standard deviation (blue margins). Note that x-axis should be divided by 10 to showcase in °C for mean temperature.

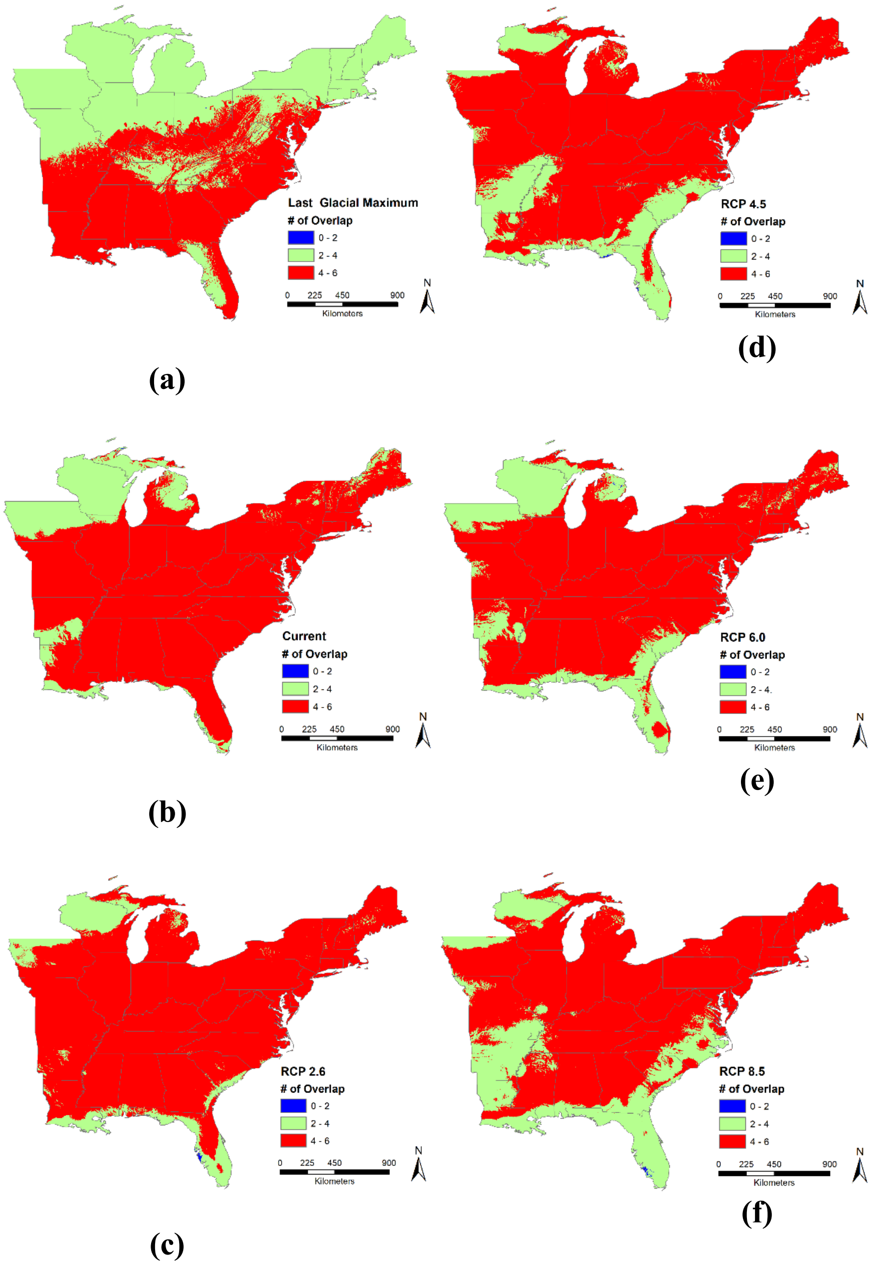
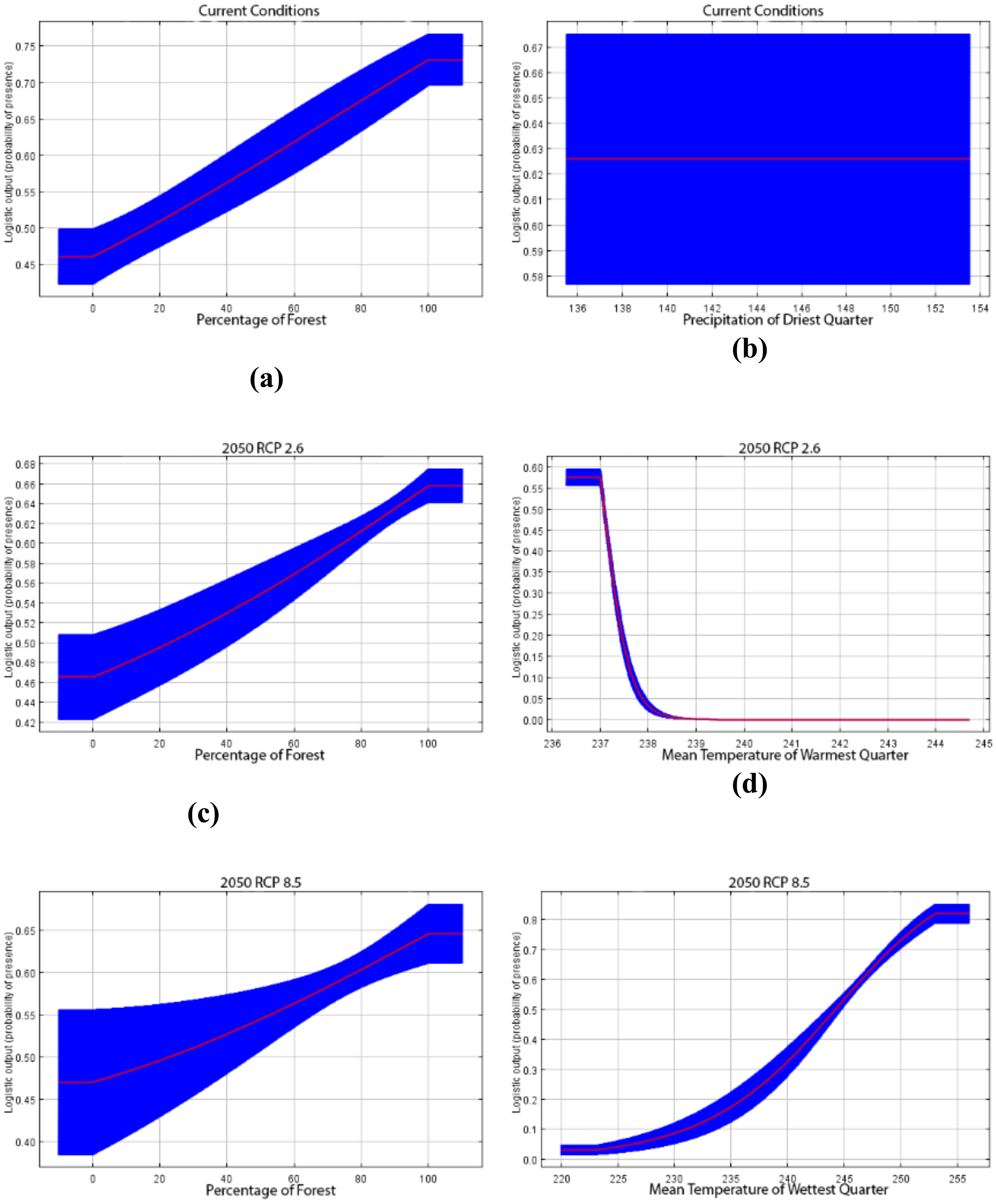


Figure 1.S2. Alternative climatic suitability maps for T. c. carolina for four different time periods: (a) Last Glacial Maximum; (b) Current; (c) 2050 Representative Concentration Pathway (RCP) 2.6; (d) 2050 RCP 4.5; (e) 2050 RCP 6.0; (f) 2050 RCP 8.5. The colors represent climatically suitable habitat based on the bioclimatic profile of current conditions and the overlap between the six bioclimatic variables for each scenario with high overlap or most suitable habitat (in red) and low overlap least suitable habitat (in blue).



(a) **(b)** **(c)** **(d)** **(e)** **(f)**

Figure 1.S3. Response curves of the top two bioclimatic predictors for (a-b) current conditions; (c-d) 2050 Representative Concentration Pathway (RCP) 2.6; (e-f) 2050 RCP 8.5. The values shown are averaged from ten replicate runs with ±1 standard deviation (blue margins). Note that x-axis should be divided by 10 to showcase in °C for mean temperature.

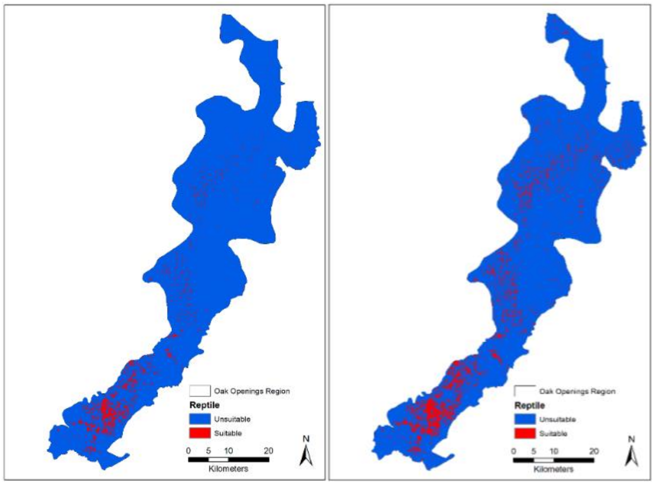
APPENDIX B: CHAPTER 2 SUPPLEMENT

Table 2.S1. Sample size and sources of data collected for habitat suitability models.

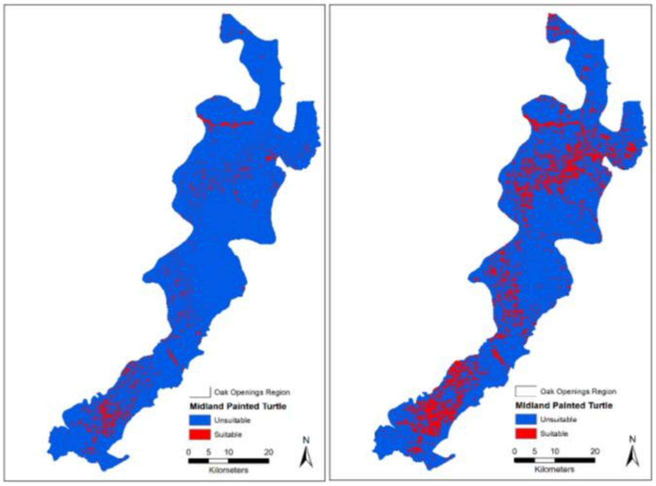
Species	Field Surveys	iNaturalist
Combined Model	139	53
Midland Painted Turtle	16	5
Eastern Box Turtle	54	12
Eastern Garter Snake	14	10
Eastern Hognose Snake	12	15

Table 2.S2. Flow Table for each step calculating land surface temperature for multi-seasonal images. Abbreviations: Thermal (TH), Band (B), Radiance (RAD), At-Satellite Temperature (AST), Proportion of Vegetation (PV), Land Surface Emissivity (LSE), Land Surface Temperature (LST), Multi-Seasonal (MS).

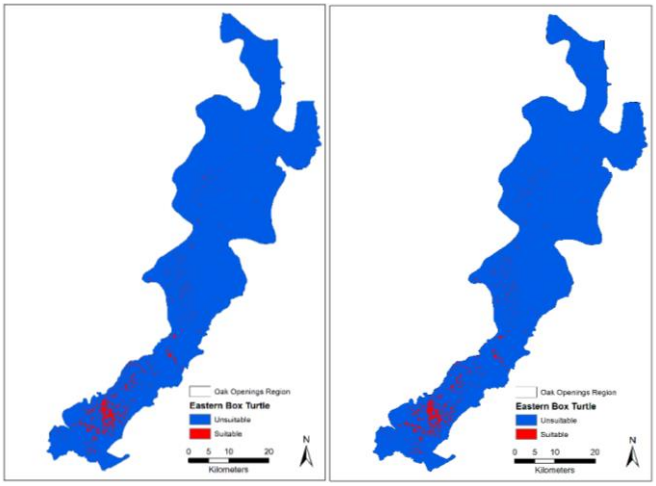
		Step 1	Step 2	Step 3	Step 5	Step 6	Step 7
Landsat Image	TH B	B R	AST	P_V	LSE	LST	MS LST
March	B10	B10 RAD	B10 AST	March P_V	March LSE	March LST	Multi-LST
	B11	B11 RAD	B11 AST				
June	B10	B10 RAD	B10 AST	June P_V	June LSE	June LST	
	B11	B11 RAD	B11 AST				
October	B10	B10 RAD	B10 AST	October P_V	October LSE	October LST	
	B11	B11 RAD	B11 AST				


Oak Openings Region
Reptile
Unsuitable
Suitable
0 5 10 20
Kilometers
N
Oak Openings Region
Reptile
Unsuitable
Suitable
0 5 10 20
Kilometers
N

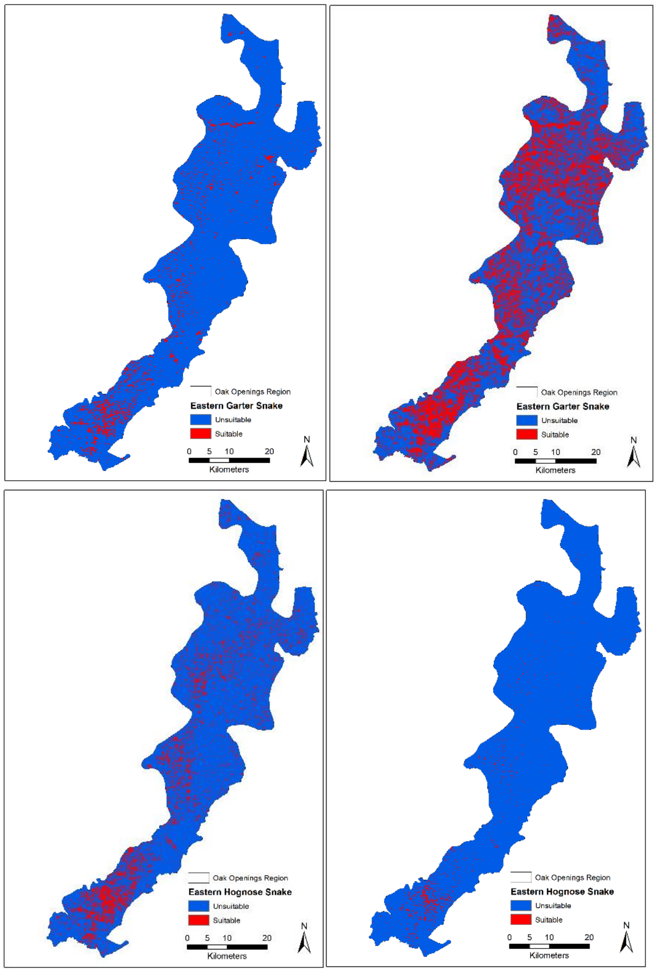
(a)


Oak Openings Region
Midland Painted Turtle
Unsuitable
Suitable
0 5 10 20
Kilometers
N
Oak Openings Region
Midland Painted Turtle
Unsuitable
Suitable
0 5 10 20
Kilometers
N

(b)


Oak Openings Region
Eastern Box Turtle
Unsuitable
Suitable
0 5 10 20
Kilometers
N
Oak Openings Region
Eastern Box Turtle
Unsuitable
Suitable
0 5 10 20
Kilometers
N

(c)



(d)

(e)

Figure 2.S1. The minimum (left) and maximum (right) habitat suitability models for: combined (a), midland painted turtle (b), eastern box turtle (c), eastern garter snake (d), and eastern hognose snake (e).

APPENDIX C: CHAPTER 3 SUPPLEMENT

Table 3.S1. Full stepwise logistic regression models for predicting home range size at four spatial buffers.

Buffer Size	K	Predictor Variable	Parameter Estimate	Prob>F	R2	AIC$_c$	Δ AICc
100	3	Total area	-592.16	0.0020	0.90	38.10	0.00
		Aggregation index	9.97				
		Largest patch index	-0.14				
100	2	Aggregation index	11.36	0.0094	0.74	38.96	0.87
		Largest patch index	-0.15				
100	1	Intercept	3.62	<0.0001	0.00	42.00	3.90
100	1	Total Area	-720.16	0.1217	0.27	43.10	5.01
100	1	Patch Richness Density	-0.01	0.3226	0.12	44.98	6.89
100	1	Shannon's Evenness Index	1.96	0.4179	0.08	45.41	7.31
100	2	Shannon's Evenness Index	8.49	0.0945	0.49	45.54	7.45
		Aggregation Index	6.74				
100	1	Largest Patch Index	-0.02	0.4733	0.07	45.60	7.50
100	3	Mean Proximity Index	-0.33	0.0202	0.78	45.96	7.87
		Aggregation Index	12.05				
		Largest Patch Index	-0.17				
200	2	Total area	-255.04	0.0130	0.71	39.88	0.00
		Mean contiguity index	-29.25				
200	2	Shannon’s evenness index	17.84	0.0144	0.70	40.17	0.29
		Aggregation index	6.67				
200	2	Mean Contiguity Index	-26.46	0.0174	0.69	40.71	1.00
		Mean Proximity Index	-0.29				
200	1	Mean Fractal Dimension Index	91.98	0.0506	0.40	41.21	1.33
200	1	Mean Contiguity Index	-28.16954	0.0517	0.39	41.26	2.00
200	1	Mean Proximity Index	-0.31	0.0774	0.34	42.14	2.26
200	1	Intercept	3.62	<0.0001	0.00	42.00	2.12
200	2	Total Area	-185.02	0.0376	0.61	42.91	3.00
		Mean Fractal Dimension Index	83.49				
200	1	Total Area	-213.86	0.1114	0.29	42.92	3.04
300	1	Mean contiguity index	-53.24	0.0070	0.62	36.66	0.00
300	2	Mean fractal dimension index	84.47	0.0056	0.77	37.45	0.79
		Patch richness density	0.17				

300	2	Mean Contiguity Index	-46.72	0.0067	0.76	37.99	1.33
		Patch Richness Density	0.11				
300	2	Mean Contiguity Index	-45.62	0.0079	0.75	38.47	1.81
		Mean Proximity Index	-0.12				
300	2	Patch Richness Density	0.29	0.0107	0.73	39.33	2.67
		Aggregation Index	4.93				
300	1	Mean Fractal Dimension Index	81.4	0.0393	0.43	40.65	3.99
300	2	Mean Proximity Index	0.09	0.0208	0.67	41.22	4.56
		Shannon's Evenness Index	7.75				
300	2	Total Area	-33.45	0.0215	0.67	41.31	4.65
		Mean Contiguity Index	-47.96				
300	1	Intercept	3.62	<0.0001	0.00	42.00	5.34
400	2	Mean fractal dimension index	124.90	0.0001	0.90	26.38	0.00
		Shannon’s evenness index	16.33				
400	3	Mean Fractal Dimension Index	112.96	0.0005	0.94	33.53	7.15
		Mean Contiguity Index	16.37				
		Shannon's Evenness Index	18.33				
400	3	Total Area	15.28	0.0007	0.93	34.71	8.33
		Mean Fractal Dimension Index	121.61				
		Shannon's Evenness Index	19.54				
400	3	Mean Fractal Dimension Index	124.85	0.0008	0.93	34.84	8.46
		Shannon's Evenness Index	19.05				
		Aggregation Index	0.55				
400	3	Mean Fractal Dimension Index	125.40	0.0009	0.93	35.31	8.93
		Shannon's Evenness Index	17.08				
		Largest Patch Index	0.01				
400	3	Mean Fractal Dimension Index	123.88	0.0009	0.93	35.36	8.98
		Patch Richness Density	-0.02				
		Shannon's Evenness Index	17.27				
400	3	Mean Fractal Dimension Index	124.28	0.0009	0.93	35.37	8.99
		Mean Proximity Index	0.00				
		Shannon's Evenness Index	16.56				
400	1	Intercept	3.62	<0.0001	0.00	42.00	15.62

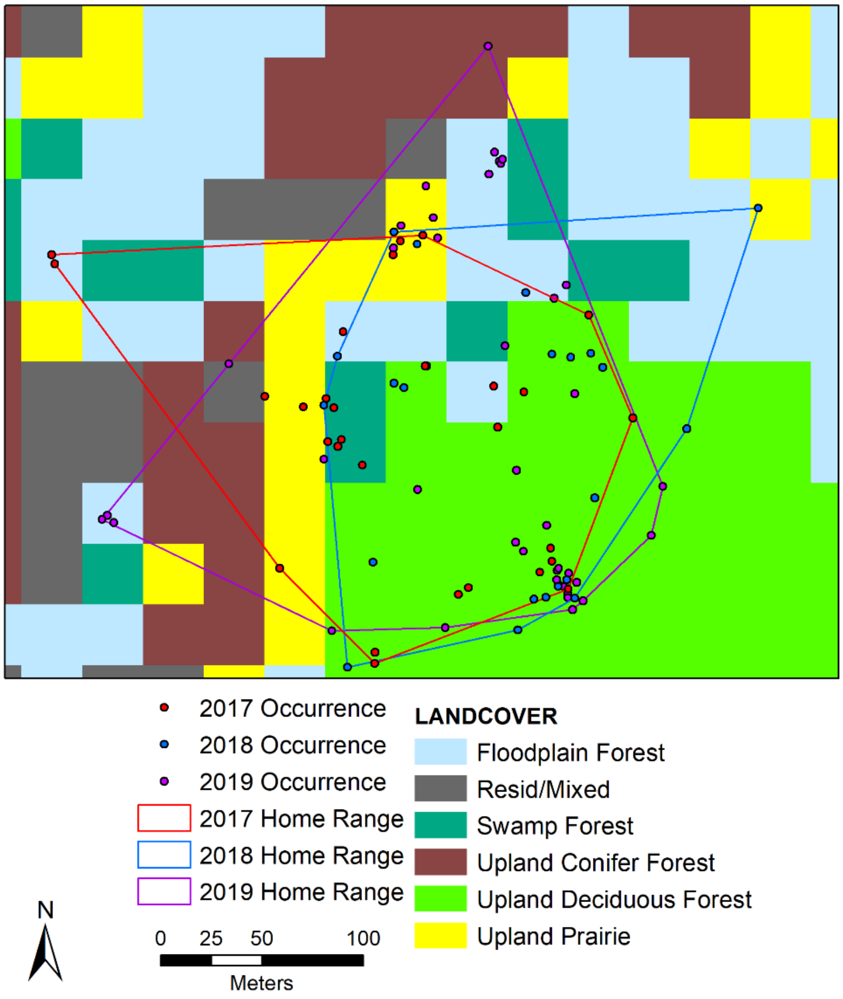


Figure 3.S1. Location points within estimated home range (same color for corresponding year) overlaid on land cover map (Root & Martin, 2018) for a male eastern box turtle from 2017 to 2019 in Oak Openings Preserve of northwestern Ohio.

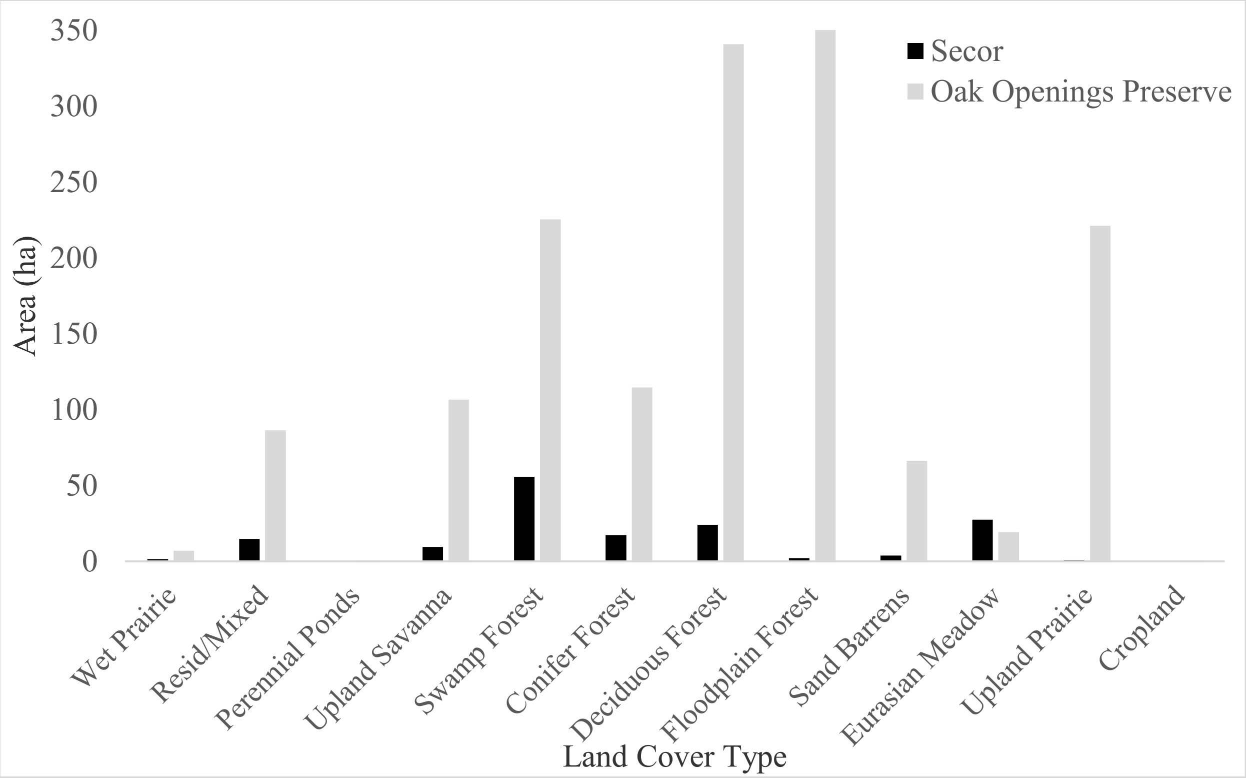


Figure 3.S2. The total amount of area (ha) for land cover types within Oak Openings Preserve (in light gray) and Secor (in black).

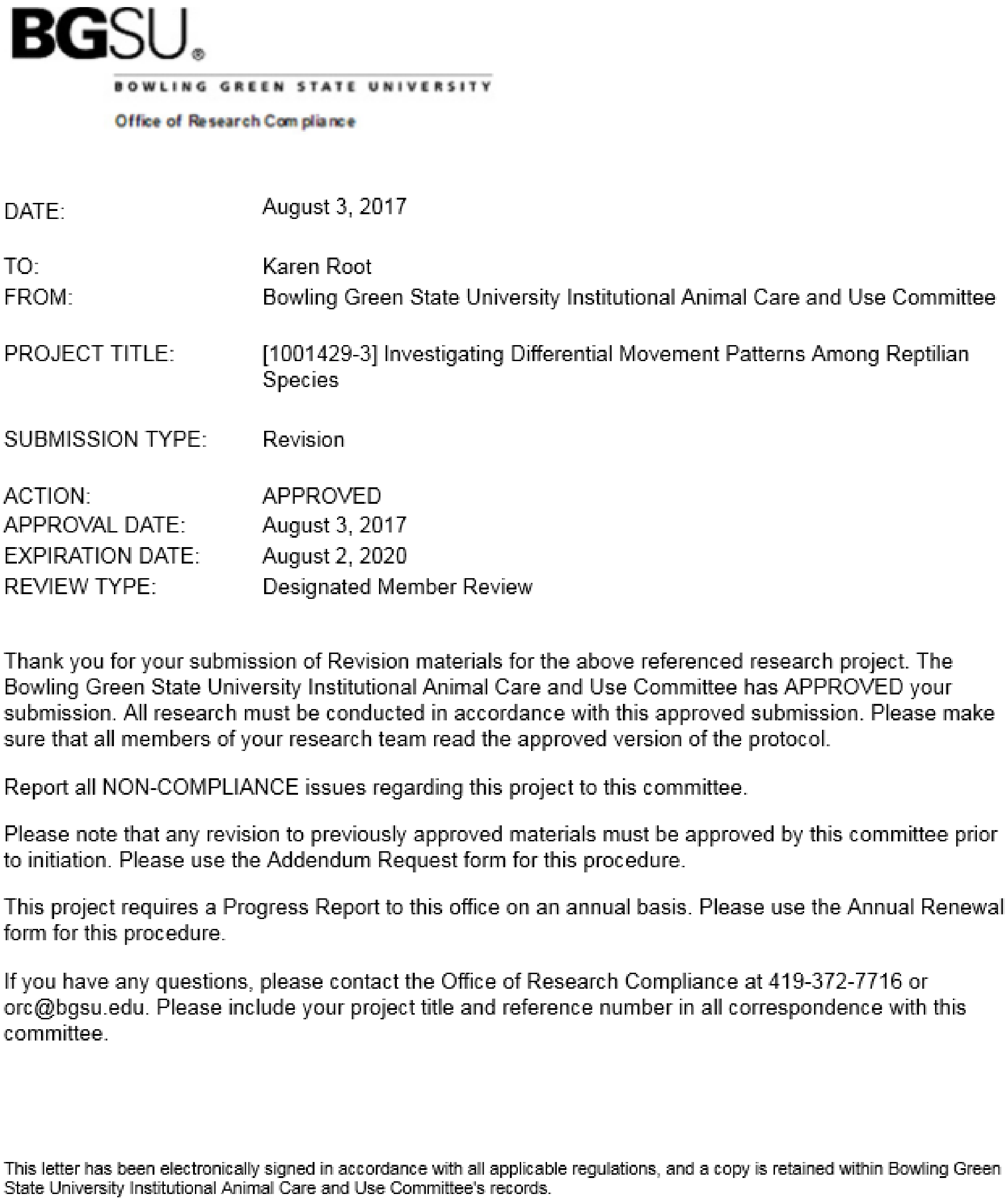
APPENDIX D: CHAPTER 4 SUPPLEMENT

Table 4.S1. An example for a male eastern box turtle of combining percent ground cover at each flag marker (B1 to B10) for one trail to create the composite ground cover predictor variable. Abbreviations: leaf litter (LL), grass (G), plants (P), coarse woody debris (CWD), log (L), soil (So), trees (Tr), and principal component (PC).

	Ground Cover (%)							Eigenvector							
Trail	LL	G	P	CWD	L	So	Tr	PC LL	PC G	PC P	PC CWD	PC L	PC So	PC Tr	Sum of Product
B1	70	5	5	20	0	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	49.86
B2	50	0	0	0	50	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	33.39
B3	35	0	5	0	50	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	26.63
B4	45	5	0	0	50	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	30.99
B5	75	0	5	0	20	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	52.10
B6	45	0	5	0	50	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	33.13
B7	45	0	5	0	25	0	25	0.65	0.17	0.60	0.03	0.02	0.30	0.16	36.62
B8	70	0	5	20	50	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	49.89
B9	20	0	5	25	50	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	17.51
B10	35	0	0	20	45	0	0	0.65	0.17	0.60	0.03	0.02	0.30	0.16	24.06

Figure 4.S1. An example quadrat survey of ground cover for reptilian tracking. The individual encountered logs, plants, grass, tree, and leaf litter.

APPENDIX E: INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL



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BOWLING GREEN STATE UNIVERSITY
Office of Research Compliance

DATE:	August 3, 2017
TO:	Karen Root
FROM:	Bowling Green State University Institutional Animal Care and Use Committee
PROJECT TITLE:	[1001429-3] Investigating Differential Movement Patterns Among Reptilian Species
SUBMISSION TYPE:	Revision
ACTION:	APPROVED
APPROVAL DATE:	August 3, 2017
EXPIRATION DATE:	August 2, 2020
REVIEW TYPE:	Designated Member Review

Thank you for your submission of Revision materials for the above referenced research project. The Bowling Green State University Institutional Animal Care and Use Committee has APPROVED your submission. All research must be conducted in accordance with this approved submission. Please make sure that all members of your research team read the approved version of the protocol.

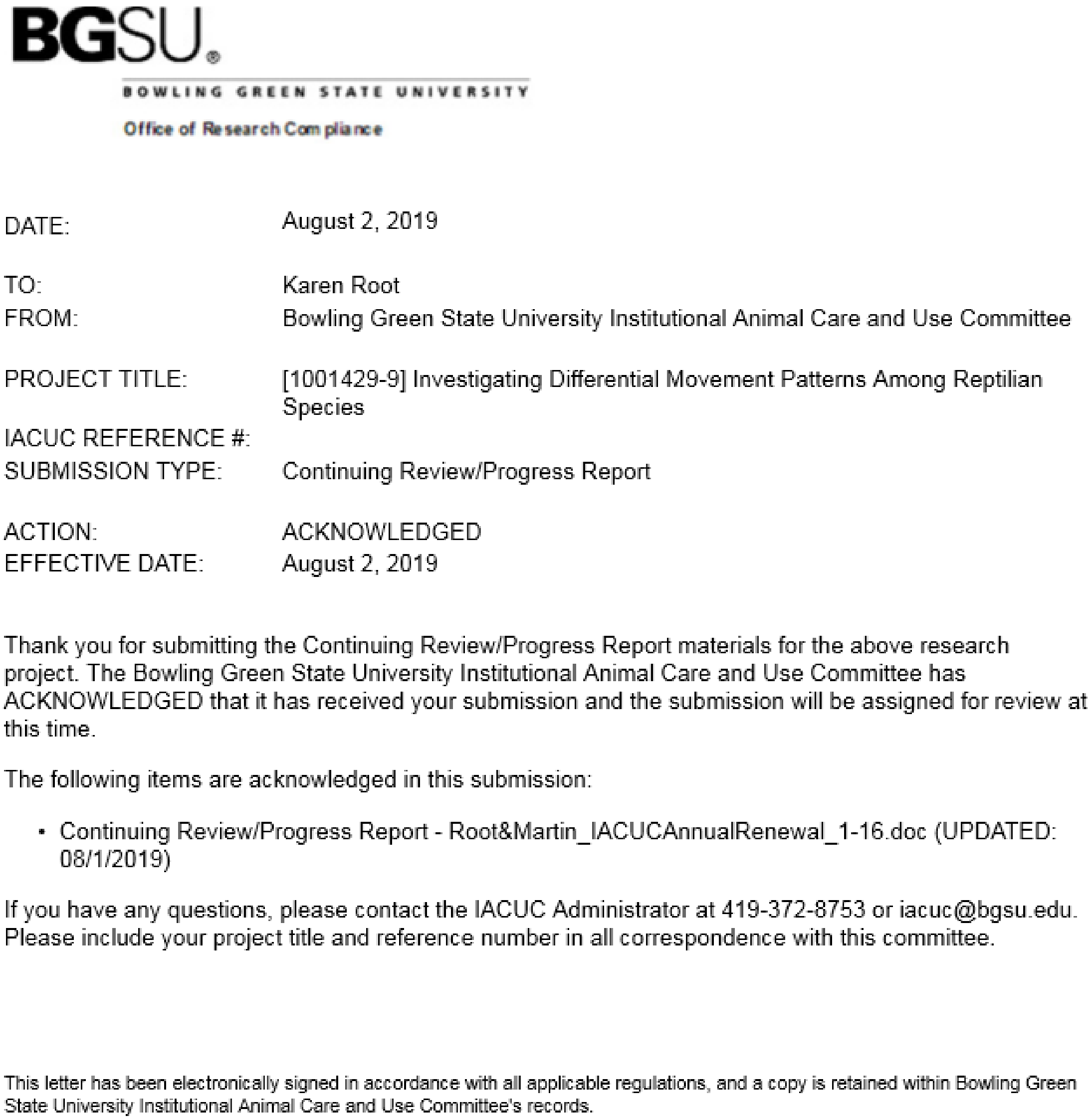
Report all NON-COMPLIANCE issues regarding this project to this committee.

Please note that any revision to previously approved materials must be approved by this committee prior to initiation. Please use the Addendum Request form for this procedure.

This project requires a Progress Report to this office on an annual basis. Please use the Annual Renewal form for this procedure.

If you have any questions, please contact the Office of Research Compliance at 419-372-7716 or orc@bgsu.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Bowling Green State University Institutional Animal Care and Use Committee's records.



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BOWLING GREEN STATE UNIVERSITY
Office of Research Compliance

DATE: August 2, 2019

TO: Karen Root
FROM: Bowling Green State University Institutional Animal Care and Use Committee

PROJECT TITLE: [1001429-9] Investigating Differential Movement Patterns Among Reptilian Species
IACUC REFERENCE #:
SUBMISSION TYPE: Continuing Review/Progress Report

ACTION: ACKNOWLEDGED
EFFECTIVE DATE: August 2, 2019

Thank you for submitting the Continuing Review/Progress Report materials for the above research project. The Bowling Green State University Institutional Animal Care and Use Committee has ACKNOWLEDGED that it has received your submission and the submission will be assigned for review at this time.

The following items are acknowledged in this submission:

- Continuing Review/Progress Report - Root&Martin_IACUCAnnualRenewal_1-16.doc (UPDATED: 08/1/2019)

If you have any questions, please contact the IACUC Administrator at 419-372-8753 or iacuc@bgsu.edu. Please include your project title and reference number in all correspondence with this committee.