Spatial and demographic patterns of two threatened turtle species in an urban environment

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DEDICATION

This thesis is dedicated to my family and friends. I am incredibly thankful for all of the love and encouragement that they have given me along the way.

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ABSTRACT

Urban development is a global threat to native wildlife. The process of urbanization reduces and degrades the useable habitat of a region, and creates novel “urban ecosystems” that possess new threats and stressors to local species. Turtles are one of the most threatened vertebrate groups worldwide, and are particularly at risk of decline in urban ecosystems due to reduced nesting success, increased road mortality events, altered movement patterns, and increased predation rates. Eastern box and Blanding’s turtles are two at-risk turtle species in the state of Michigan, USA, primarily due to land use change. Presently, there are urban populations of eastern box and Blanding’s turtles in the city of Grand Rapids, Michigan, a major urban center, however little is known about the status of these populations. I studied the urban populations of eastern box and Blanding’s turtles within the city limits of Grand Rapids in order to determine demographic and spatial movement patterns within this developmentally intense environment. I conducted mark-recapture and radio telemetry surveys across 2019 and 2020. A total of 1,041 locations were collected for 20 adult turtles, and 406 trap nights were completed across the 2019 and 2020 seasons. Comparisons of home range estimations were made using minimum convex polygons and kernel density estimators, and habitat use was analyzed using Brownian bridge movement models. Only one instance of mortality was noted from telemetered individuals, and sex ratios did not differ from parity for either focal species, or for other native turtles captured during the study. Age classes were skewed towards adults, and home range sizes were highly reduced (mean = 1.58 ha SE +/- 0.486 for Blanding’s turtles; mean = 2.88 ha SE+/- 0.913 for eastern box turtles) when compared to previous studies in more naturalistic environments. These populations of eastern box and Blanding’s turtles will likely require human intervention in order to continue to persist within this urban landscape.

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ABBREVIATIONS

BBMMs – Brownian Bridge Movement Models

cm – Centimeters

dBBMMs – Dynamic Brownian Bridge Movement Models

GPS – Global Positioning System

ha – Hectares

KDE – Kernel Density Estimator

km – Kilometers

LCSV – Least Squares Cross Validation

m – Meter

MCP – Minimum Convex Polygon

UD – Utilization Distribution

VHF – Very High Frequency

CHAPTER 1

INTRODUCTION

Landscape modification and habitat fragmentation, or the splitting up of continuous habitat into smaller, isolated patches, have long been considered to be threats to native wildlife (Reed 2004, Sala et al. 2000, Foley et al. 2005). In general, habitat fragmentation results in the loss of useable habitat, and wildlife populations become more isolated from one another. If prolonged, this reduction in connectivity between individuals can eventually lead to increased extinction rates (Reed 2004). Urban development is one of the primary drivers of habitat fragmentation and loss, and results in the creation of novel ecosystems that are relatively understudied. Many of the effects of urban development on native wildlife are unknown, or difficult to predict, due to the heterogeneity of urban landscapes, as well as differential responses at the species-level (French et al. 2018).

Urban ecosystems create unique threats to native wildlife, and can result in abnormal or altered behaviors. Urban wildlife may change their movement patterns in order to avoid interactions with humans, experience higher levels of stress from sound or light pollution, and suffer from increased predation rates from mesopredators and domestic animals (French et al. 2018, Knapp and Perez-Heydrich 2012). Although generalist or exotic species may thrive in urban ecosystems, native species typically do not (French et al. 2018). Human-induced landscape changes are often occurring too quickly for wildlife to alter their movement behaviors, such as their willingness to cross between different habitat types, path shape, and movement distances, and continue to persist within the fragmented environment (Fahrig 2007). Rapidly changing environments create conflicting cues to the apparent risks and benefits of moving from one habitat patch to another, resulting in increased probabilities of mortality (Fahrig 2007, Robertson and Hutto 2006, Schlaepfer et al. 2002). The matrix in which the fragmented habitat is situated can also influence the success of a resident species. Species that dispersed further between existing habitat patches prior to the loss of habitat are placed at risk when dispersing through a dangerous matrix, and are more likely to disappear from the remaining patches (Van Houtan et al. 2007). Species that are less vagile however, can sometimes persist in the remaining patches (Van Houtan et al. 2007, Fahrig 2007).

Urban environments are particularly detrimental for turtles (order Testudines). Human-altered landscapes typically undergo rapid change, often creating ‘ecological traps’ for turtles. An ecological trap occurs when positive environmental cues do not match the potential negative outcomes of the selection being made (Robertson and Hutto 2006). This is most commonly displayed in turtles through nesting alongside roadways or other anthropogenically-modified areas, as the thermal conditions and the ease of digging the nest are improved in comparison to more naturalistic areas (Francis et al. 2019). This presents a tradeoff however, of greater risk of mortality during the nesting foray, as well as increased nest depredation (Fahrig 2007, Steen et al 2006).

Demographic vital rates, such as sex ratios, age structure, and age-specific mortality rates have the potential to become skewed for turtles living within urban environments. Low juvenile recruitment, particularly due to nest and juvenile predation, is a threat to turtles globally yet becomes particularly pronounced in urban areas. Urban and fragmented habitats support unnaturally high mesopredator populations, such as raccoons, skunks, and opossums, through the process of mesopredator release and the amount of human-subsidized food resources in urban areas (Soulé et al. 1988, Prugh et al. 2009). The high presence of mesopredators can in turn increase the rate at which turtle nests are predated upon (Engeman et al. 2005, Temple 1987, Congdon et al. 1983). Many turtle life histories are characterized by long generational times and delayed sexual maturity, and a reduction or loss in juvenile recruitment skews the age class distribution of a population towards adults. Long-lived species of turtle require an estimated juvenile survivorship, from age one to sexual maturity, of 70% in order to maintain stable populations (Congdon et al. 1993). Adult mortalities become especially problematic when paired with the loss of juveniles, as it is unlikely for juvenile survivorship to increase past the already high level required to maintain stability in the population. (Congdon et al. 1993, Rubin et al. 2004).

The sex ratios of turtles in developed environments have additionally become a subject of interest, due to the apparent phenomenon of female turtles having a higher risk of mortality than male turtles. It is most commonly hypothesized that female turtles perform large overland movements in order to find suitable nesting sites, and therefore are more likely to cross over roads and become victim to road mortality (Steen and Gibbs 2004, Steen et al. 2006, Aresco, 2005). Male-biased turtle populations in anthropogenically-modified environments have not always been able to be linked to road mortality or the amount of protected area at a site, and could also signal that female turtles are more vulnerable to terrestrial predators during their nesting movements (Vanek and Glowacki 2019, Eskew et al. 2010). The unknown methods in which turtle sex ratios become skewed drive a need for the replication of previous studies across different urban areas in order to best determine localized conservation practices (Vanek and Glowacki 2019).

The movement patterns of turtle species can be greatly influenced by the presence of urban development, particularly roads. Some turtle species display strong road avoidance behaviors, crossing roads much less often than predicted by random chance (Shepard et al. 2008, Proulx et al. 2014, Paterson et al. 2019). Road avoidance behaviors can be beneficial in terms of reducing mortality, however the reduction of movements can lead to a lack of gene flow between populations that are intersected by roads. Most turtles are long-lived species that show delayed sexual maturity, and it may take many generations for the impacts of this isolation to become evident in the population, in turn delaying the timely intervention of conservation initiatives (Shepard et al. 2008). Turtle species do not avoid habitats near roads; instead, they travel longer daily distances while avoiding road crossings (Paterson et al. 2019). Paterson et. al (2019) estimated the energetic cost of this road avoidance behavior to be low for turtle species, leaving vehicle strikes and genetic isolation as greater threats from roads within turtle home-ranges.

Study species: Eastern box and Blanding's turtles

Eastern box turtles (*Terrapene carolina carolina)* and Blanding's turtles (*Emydoidea blandingii)* are two turtle species of special concern in Michigan, USA, as their populations are declining throughout their range. Both species are threatened by residential and commercial development, agriculture, and transportation corridors such as roads (van Dijk and Rhodin 2011, van Dijk 2011).

Blanding's turtles are listed as endangered by the IUCN (International Union for the Conservation of Nature), as a species of special concern by the Michigan Department of Natural Resources, and are under "pre-listing" as a federally endangered species (U.S. Fish & Wildlife 2013). The Blanding's turtle is found primarily in the northern United States, ranging from Nebraska to New York, and as far north as Ontario, Canada. Blanding's turtles are semi-aquatic turtles that typically make large overland movements from wetland to wetland. Blanding's turtles have clutch sizes from 3-15 eggs, and have a life expectancy upwards of 75 years (Congdon et al. 1983, Brecke and Moriarty 1989).

The eastern box turtle is listed as vulnerable by the IUCN, and as a species of special concern by the Michigan Department of Natural Resources (van Dijk 2011). Eastern box turtles are found primarily in the eastern and southeastern United States, and extend north midway into Michigan's lower peninsula, and as far south as Florida. Eastern box turtles are terrestrial in nature, but may use puddles or shallow water bodies such as creeks to thermoregulate. Individual daily movements differ between rainy and dry periods for both sexes, with the highest amount of movement typically following rain showers (Iglay et al. 2007). Eastern box turtles have clutch sizes of 3.0 to 5.87 eggs throughout their range, and have a life expectancy of greater than 50 years (Willey and Sievert 2012, Stickel 1978).

Populations of eastern box and Blanding's turtles exist within the city limits of Grand Rapids, Michigan, USA, however the viability of these populations is unknown. Grand Rapids is the second largest city in the state of Michigan, and the turtles living within this urban area are of particular interest due to the developmentally intense habitat in which they reside. Studying these populations of urban turtles can provide insights for conservation at the local level, as well as provide information as to the specific influence of urban development on these two at-risk turtle species.

Purpose

The purpose of this study is to establish baseline movement and demographic data for the urban population of eastern box and Blanding's turtles within the city limits of Grand Rapids, Michigan, USA. I aim to provide information as to the habitat use and connectivity of individuals through spatial analyses, as well as information on sex ratios, age classes, and survivorship through demographic analyses. These analyses will help to determine the land use and long-term viability of these urban populations of turtles.

Scope

This study focuses on two species of threatened turtles within Grand Rapids, Michigan, USA. These results can inform local and regional conservation of these species, as they are of concern throughout the state of Michigan. Comparing these urban turtle populations to those in more naturalistic environments can be used to further assess the impacts of anthropogenic influence on small populations of threatened species.

Assumptions

- We assume accurate GPS locations of the located individuals – consistent GPS/location error
- We assume that no turtles escaped the traps
- We assume that the markings on the turtle’s marginal scutes are permanent
- We assume that traps did not bias one sex or size of turtle over another
- We assume in the Brownian bridge movement models that the animal’s mobility factor remained constant

Objectives

For chapter 2, my objectives are to (1) estimate home range size and interactions with roads for each individual eastern box and Blanding's turtle, (2) estimate survivorship, sex ratios, and age class distributions, and (3) determine habitat types in both the core and activity areas for each individual.

Significance

The study of the impacts of urbanization on wildlife, particularly on reptiles, is relatively recent, with many spatial and demographic patterns not being fully understood. Few studies have focused on turtles in this developmentally intense of an environment, and primarily study fragmented habitats as opposed to landscapes with significant levels of urban and suburban development. This study is important in order to determine the long-term viability of eastern box and Blanding's turtles within the city of Grand Rapids, Michigan, USA, and the results can be used to inform local and regional level management of these two species.

Definitions

- Ecological trap – occurs when rapid environmental change causes an animal to mistakenly prefer habitats which reduce fitness than other available habitats
- Habitat fragmentation – the splitting of continuous habitat into smaller patches
- Home range – the region which an animal moves and acquires the resources needed to survive and reproduce

- Mesopredator – a mid-tropic level predator

- Urbanization – the conversion of land into cities or towns

CHAPTER 2

Spatial and demographic patterns of two threatened turtle species in an urban environment

ABSTRACT

Urban development is a global threat to native wildlife. The process of urbanization reduces and degrades the useable habitat of a region, and creates novel “urban ecosystems” that possess new threats and stressors to local species. Turtles are one of the most threatened vertebrate groups worldwide, and are at risk of decline in urban ecosystems due to reduced nesting success, increased road mortality events, altered movement patterns, and increased predation rates. Eastern box turtles (*Terrapene carolina carolina*) and Blanding’s turtles (*Emydoidea blandingii*) are two of these at-risk turtle species. I studied urban populations of eastern box and Blanding’s turtles using VHF radio telemetry and mark-recapture surveys to understand the impact of intense urban development on movement patterns and population demography. Surveys occurred within the city limits of Grand Rapids, Michigan, USA from 2019-2020. Surrounding traffic volumes for the telemetered individuals ranged from 1,000-49,000 vehicles daily, making this landscape more developmentally intense compared to many previous studies. Telemetered individuals had reduced home ranges (mean = 1.58 ha SE +/- 0.486 for Blanding’s turtles; mean = 2.88 ha SE+/- 0.913 for eastern box turtles) compared to those described in previous studies in more rural areas. Both turtle species were frequently located within close proximity to high traffic volume roads, and avoided road crossings. One instance of mortality was recorded for telemetered individuals over the course of the study period. Sex ratios did not differ from parity, and age classes were primarily comprised of adults. Continued monitoring of these urban turtles will be necessary in order to determine the long-term viability of these small populations, as well as require significant human intervention for nest-protection and habitat restoration.

Key words: Blanding’s, Eastern box, Urbanization, Habitat fragmentation, Movement, Brownian Bridge

INTRODUCTION

Habitat fragmentation and loss is resulting in species decline and extinction across the globe (Gibbons et al. 2000). Habitat fragmentation is the splitting of continuous patches of habitat into smaller patches through land use change (Fischer and Lindenmayer 2007). Habitat fragmentation can lead to the loss of connectivity among existing populations, particularly if the habitat is fragmented by roads or situated within unsuitable matrices such as agriculture. This loss of connectivity is notably detrimental to small populations, which have a higher probability of extinction with increasing levels of habitat fragmentation (Reed 2004). Loss of habitat eventually occurs through these land use alterations as the habitat is continually divided.

Urban development is one of the primary drivers of habitat fragmentation and loss, and is a global threat to wildlife. Currently, 54.8% of the global human population lives in an urban area (World Bank 2018). This number is projected to grow to 68% by 2050, driving further land use change in the form of urban development (United Nations 2018). Wildlife living within urban areas, or areas undergoing rapid urban development, have shown varying responses to these novel environments, typically due to the heterogeneity of the urban landscape and the species' life history characteristics (French et al. 2018). Generally, species living within urban areas display altered activity patterns, such as increased space use in order to meet resource needs, modified activity cycles in order to avoid human interactions, and higher mortality rates through predation and road strikes, than their less-urban counterparts (Ditchkoff et al. 2006).

Reptile species are declining globally due to urban development and anthropogenic influence (Gibbons et al. 2000). Reptile communities in urban areas show decreases in native species richness, whereas exotic reptile species tend to thrive (French et al. 2018, Nielsen et al. 2014, Cordier et al. 2021). Urbanization causes dramatic changes in abiotic conditions such as air temperature, soil temperature, and degree of light pollution, preventing many native species from thriving in the novel-environment (Cordier et al. 2021). Reptiles also tend to experience increased physiological stress from human interactions, pollutants, and increased predation rates from mesopredators (such as raccoons, opossums, and foxes) and domestic species (French et al. 2018). Cats and dogs can act as predators of many reptile species, especially in areas of increased density of these domestic animals due to human presence (Koenig et al. 2002, Knapp and Perez-Heydrich 2012). Pesticides, heavy metals, and other pollutants present in the soil and water systems of urban areas can lead to altered development or direct mortality of reptile species (Croteau et al. 2008). These compounding stressors, in addition to the loss of habitat, make urban areas highly-unsuitable environments for many reptile species.

Turtles (order Testudines) are an at-risk group of reptiles in urban environments due to their traits of delayed sexual maturity, long generational times, low recruitment rates, and specific habitat requirements (Grgurovic and Sievert 2005, Congdon et al. 1993). Additionally, turtles frequently make overland movements for mate location and nest site selection, making them vulnerable in high-traffic areas. Turtles have recently become the subject of interest in the study of urban ecosystems for these reasons. Turtles living in urban environments experience a number of stressors that can threaten the overall viability of a population, resulting from increased road density and land-use conversion (French et al. 2018, Budischak et al. 2006, Rubin et al. 2004). Female turtles are at an increased risk of road mortality than male turtles due to their overland nesting movements coinciding with commuting traffic hours, resulting in the opportunity for skewed sex ratios in areas of high road density (Steen and Gibbs 2004, Aresco 2005). Increases in road density also have the ability to reduce a turtle's overall movements, as seen in common snapping turtles (*Chelydra serpentina*) (Patrick and Gibbs 2010).

Two at-risk turtle species from urban development are the Blanding's turtle (*Emydoidea blandingii)* and the eastern box turtle (*Terrapene carolina carolina)*, both of which are species of special concern in Michigan, USA. Although these two species of turtle are declining, small numbers of these species still exist in Grand Rapids, the second largest city in the state of Michigan. In unfragmented, more naturalistic environments, eastern box and Blanding's turtles show great variation in the size of their home range; the Blanding's turtle home range is approximately 22 ha in size and the eastern box turtle's home range can stretch from 0.33 ha to 54.7 ha (Grgurovic and Sievert 2005, Greenspan 2015). In extremely dense urban areas, there is potential for these home ranges to decrease in size, reducing or removing the connectivity between populations (Row et al. 2012, Ahlers et al. 2010).

The purpose of this study was to understand the impacts of urbanization on the movement patterns and population demography of eastern box and Blanding's turtles. Studying the populations of eastern box and Blanding's turtles within the city of Grand Rapids, Michigan can provide insights to the impacts of dense urbanization on these two threatened turtle species. Traffic volumes surrounding these populations have average annual daily volumes reaching up to 49,000 cars daily, and road densities upwards of 12 km/km^2, making this environment more developmentally intense than most previous studies of urban turtle populations (State of Michigan 2017). Specifically, we aimed to (1) estimate home range area and interactions with roads for each individual eastern box and Blanding's turtle, (2) estimate survivorship and sex ratios, and (3) determine habitat use in both the core and activity areas for each individual.

METHODOLOGY

Study area

This study was conducted across three sites within the city limits of Grand Rapids, Michigan, USA, which is the second largest city in the state of Michigan (Figure 1). Grand Rapids has a city population of approximately 200,000 and a metropolitan population of over one-million (U.S. Census Bureau 2018). Each site was located within fragmented habitat, and was selected due to having previously recorded sightings of the two focal species.

The first site 'A' was located on the western boundary of Grand Rapids. Site 'A' is approximately 57.8 ha of land, and recently acquired an additional 48.9 ha of a former golf course in 2017. Ecological restoration of the golf course began immediately after its purchase in 2017 with the creation of a single manmade wetland, and three more wetlands the following year. Several turtle species, including Blanding's turtle, used these manmade wetlands within one season of their creation. Habitat types include developed open land, scrub/shrub wetlands, deciduous forest, and emergent wetland. Traffic volumes for this region range from 7,000 to 15,000 cars daily (State of Michigan 2020).

The second site, 'B', was a fragmented landscape at the edge of the downtown area that included a golf course, an active mine, and a wooded lot. Site 'B' is approximately 40 ha of land, and is intersected by Interstate-96, industrial plants to the south, and dense residential areas to the north and east. The site contains habitat types of deciduous forest, developed open space, forested wetland, and grassland/herbaceous openings. Traffic volumes for this area range from approximately 2,400 to 49,000 cars daily (State of Michigan 2020).

The third site, 'C', was a large urban park, located on the southwest side of the city of Grand Rapids. This land previously contained a gypsum mine and a condemned landfill, but has since been restored to become the current county park (Friends of Grand Rapids Parks 2019). The park is primarily grassland/herbaceous habitat and open water, with smaller regions of deciduous forest and wetlands. Site ‘C’ is approximately 566 ha of land and is bordered by Interstate-96 freeway to the south (County of Kent, Michigan 2018). Traffic volumes range from approximately 1,000 to 49,000 cars daily for the surrounding area (State of Michigan 2020).

Survey Methods

Turtle populations were studied using two methods: mark-recapture surveys, and very high frequency (VHF) radio telemetry tracking. Mark-recapture surveys were used at the three study sites in order to estimate sex ratios and age class distributions for each focal species, and capture individuals for VHF telemetry. Four eastern box turtles and four Blanding’s turtles captured during preliminary work in 2018 were included in the 2019-2020 study. Eastern box turtles were located opportunistically via visual encounter, often by visitors, students, and staff members at the three sites, or through the congregation of other eastern box turtles. To capture aquatic turtles, baited hoop nets of both 12 in and 36 in diameter were used, with mesh sizes of 0.25 in and 3 in, respectively. Traps were baited with various foods of interest including canned cat food, sardines, and other chopped fish. Traps were partially submerged and left overnight between April-September 2019, and May-August 2020. Traps were checked at least once every 24 hours, and turtles were processed immediately the following morning regardless of species captured. Aquatic trapping effort was low at site ‘B’ compared to sites ‘A’ and ‘C’ in 2019 due to low water levels throughout the active season, as well as a lack of Blanding’s turtle sightings in the previous year. In 2020, mark recapture surveys of aquatic turtles did not occur at site ‘B’ due to construction obstructing the single body of water at the site during the active season.

All captured turtles were sexed using external secondary sex characteristics, with males possessing plastral concavity and a longer pre-cloacal tail length than females. Turtles were then weighed on a digital scale to the nearest gram, and carapace and plastron length and width were taken to the nearest millimeter using metal calipers. A unique identifying code was assigned to each turtle by filing notches in the marginal scutes with a metal triangular file (as described by Cagle 1939). Any injuries, such as missing limbs or damage to the shell, were also noted. Eastern box and Blanding's turtles were outfitted with a VHF transmitter as detailed below. Turtles were then released at their capture location, and processing equipment was cleaned with 100% ethanol to prevent potential disease transmission.

Radio-telemetry surveys of eastern box and Blanding's turtles were used in order to determine survivorship, home-range estimates, as well as the habitat types in the core and activity areas of each telemetered individual. VHF transmitters (Advanced Telemetry Systems, Isanti, MN. Model R1860 – battery life 796 days) did not exceed 5% of a turtle's body weight to prevent burden to the animal. A single GPS logger was used for a female eastern box turtle who was situated in habitat that was difficult to access regularly. Transmitters were adhered to the turtle's first or second costal scute in order to avoid interference with mating behaviors using a combination of DEVCON 5-minute epoxy (ITW Performance Polymers, Danvers, MA) and PC marine epoxy putty (Protective Coating Company, Allentown, PA). Turtles were held until the epoxy had dried (approximately 1-3 hours) and released at their capture location. Turtles were tracked to their locations 2-3 times weekly during the active season (May-September), and once a month during the inactive season (October-April). Blanding's turtles were observed opportunistically at each relocation, and eastern box turtles were observed at approximately 90% of relocations. GPS location and environmental data (air, water, and soil temperatures, % canopy cover, substrate type, % cloud cover, precipitation, and dominant vegetation) were recorded at each location.

Spatial and demographic analysis

50% and 95% minimum convex polygon (MCP) and kernel density estimator (KDE) home ranges were estimated using the package “rhr” in R Studio (Signer 2019, RStudio Team 2020). Bandwidth selection for KDE home ranges was determined using the least squares cross-validation (LSCV) method. Home range estimates made by KDEs that did not reach bandwidth convergence were removed from analysis.

Brownian bridge movement models (BBMMs) were used in order to determine habitat types in both activity areas and core areas of each individual. BBMMs were used as they do not incorporate as much unused areas of land as MCPs (Silva et al. 2018). Although primarily used for GPS telemetry, Brownian bridge based analyses have been shown to work well for herpetofauna who spend significant amounts of time sheltering in one location, and remain accurate with lower sampling regimes using VHF telemetry (Silva et al. 2020). Location error in VHF telemetry is highly variable, particularly with herpetofauna, due to unfavorable terrain and the animal’s ability to burrow itself into the ground. Location error for the BBMM was set at 20m due to this variability. Eastern box turtles and Blanding’s turtles have a period of overwintering (brumation), as well as a defined active season. Because of this, animals were located 2-3 times a week in the active season, but only once a month during the inactive season, resulting in an inconsistent amount of lag time between sampling locations. To the best of our knowledge, BBMMs have not been used for animals that brumate or hibernate, or with an inconsistent sampling regime in VHF telemetry. Because of this variation, max lag was set to one month in order to reflect the longest time possible between successive locations. Utilization distributions (UD) for each turtle were created using Brownian bridge movement models in the package “BBMM” in RStudio at both 50% (core area) and 95% (activity area) (Nielson et al.

2013, RStudio Team 2020). Habitat types in the activity and core areas were determined by overlaying the 50% and 95% UD isopleths over a landcover raster dataset (NOAA Coastal Change Analysis Program (C-CAP) Regional Land Cover Database 2016). Developed habitat types were classified based on the following: developed open space, developed low intensity, developed medium intensity, and developed high intensity (NOAA Coastal Change Analysis Program (C-CAP) Regional Land Cover Database 2016). Developed open space was characterized by managed vegetation in areas developed for recreation or aesthetic purposes, and constructed surfaces were less than 20% of the total land cover. Developed low intensity habitat was characterized by constructed materials accounting for 21-49% of total area, including areas such as rural neighborhoods. Developed medium intensity refers to areas that had 50-79% of the land cover as constructed materials, typical of suburban areas. Developed high intensity land had less than 20% vegetation, and 80-100% of the total land cover was constructed materials, as is typical in urban centers (NOAA Coastal Change Analysis Program (C-CAP) Regional Land Cover Database 2016).

Average distance to roads for each individual turtle was determined through plotting the GPS coordinates in ArcMap (version 10.4.1). Road density was calculated as the total length of roads within a one-kilometer radius of each turtle’s 95% MCP home range using ArcMap (version 10.4.1). The effect of road density on home range area was analyzed using linear regression, separately for each species, using RStudio (RStudio Team 2020). Sex ratios were determined to differ from parity using Chi-squared tests (Zar 1984). Eastern box turtles were determined to be adults if the carapace length was greater than 100mm, and had greater-than or equal to nine annuli, or if growth rings were too worn to be distinctive (Dodd 2002). Eastern box turtles were considered juveniles if the carapace length was less than 90 mm and had less than or equal to seven annuli (Dodd 2002). Blanding's turtles were considered to be adults if they had greater than 14 annuli, or if growth rings were too worn to be distinctive (Congdon et al. 1993). Kaplan Meier known-fates models were used to estimate survivorship of the two focal species using the package "Survival" in RStudio (Therneau 2020, RStudio Team 2020).

RESULTS

Demographic analysis

A total of 406 trap nights were performed during the active season (May-September). Across the three sites, 158 native turtles, and no non-native turtles, were captured between the 2019 and 2020 active seasons, and approximately 24.6% of the turtles were recaptures. Thirty-two turtles were of the two focal species; however, ten of these were hatchlings and unable to be marked (Table 1). Aquatic turtles were captured at a rate of approximately one turtle per every three trap nights. Recaptured individuals were captured at a rate of approximately one recapture per ten trap nights. Blanding's turtles were captured at a rate of approximately one turtle per 37 trap nights.

At site 'A', 14 Blanding's turtles were captured. Five of these Blanding's turtles were hatchlings, one juvenile, and eight were adults (six males and two females). Eleven adult eastern box turtles (five males and six females) and five hatchlings were also located at 'A'. Three adult eastern box turtles (one male and two females) and no Blanding's turtles were captured at site 'B'. No turtles of the focal species were captured at site 'C', although a single Blanding's turtle was sighted by a park staff member. Sex ratios of the Blanding's and eastern box turtles did not differ from parity ($p > 0.05$), and sex ratios also did not differ from parity when all native turtle species were pooled as a whole ($p>0.05$).

A single female eastern box turtle at site ‘A’ died within the first week of the study, due to undeterminable causes, and therefore was not included in home range analyses. This was the only instance of mortality of telemetered individuals over the course of the study. Eastern box turtles had a survivorship of 0.923 (SE +/- 0.0739, 95% CI 0.789-1), and Blanding’s turtles did not experience any mortality.

Home range analysis

A total of 1,041 turtle locations from 20 adult turtles were recorded from October 2018 to August of 2020. Blanding’s turtles had an average of 41 locations each, and eastern box turtles had an average of 59 locations each. Location data were collected from eight adult Blanding’s turtles (six males and two females) and twelve adult eastern box turtles (five males and seven females). No road crossings were recorded for either species, with the exception of low-traffic driveways.

Blanding’s turtle home ranges averaged 1.58 ha (SE +/- 0.486) when determined by 95% MCP, and 0.50 ha (SE +/- 0.210) when determined by 95% KDE (Figure 2). Road density had a significant positive relationship with Blanding’s turtles home range area, with higher road densities corresponding with larger home range areas ($p=0.0211$, $R^2=0.616$) (Table 2). Blanding’s turtles were frequently located within close proximity to roads, with a mean distance of 69.2 m, a minimum of 0.2 m, and a maximum of 218.3 m, per location. Habitat types in the activity areas (95% UD isopleth) for the Blanding’s turtles were dominated by developed open (mean = 42.7% SE +/- 4.61), and developed low intensity habitat types (mean = 22.2% SE +/- 11.2) (Figure 3). Blanding’s turtles core areas (50% UD isopleth) were primarily dominated by developed open (mean = 55.6% SE +/- 10.3) habitat types, however developed low intensity habitats became less prominent (Figure 3).

Eastern box turtles had a mean home range area of 2.88 ha (SE +/- 0.913) when determined by 95% MCP, and a mean area of 1.68 ha (SE +/- 0.290) when determined by 95% KDE (Figure 4). One female eastern box turtle had a dramatically larger home range of 12.23 ha when determined by 95% MCP. Road density had a significant positive relationship with eastern box turtles' home range area, with higher road densities corresponding to larger home range areas, when the outlying female was excluded from analysis ($p=0.000687$, $R^2=0.739$). Road density had no significant relationship with home range area when the outlying female was included in the analysis ($p>0.05$). Eastern box turtles were also frequently located within close proximity to roads, while avoiding road crossings (Figure 5). Eastern box turtles' distance to roads had a mean value of 90.9 m, a minimum value of 2.9 m, and a maximum value of 298.5 m. Habitat types in the eastern box turtle activity areas (95% UD isopleth) were dominated by deciduous forest (mean = 38.0% SE +/- 4.3) and developed open habitat types (mean = 23.1% SE +/- 2.99) (Figure 6). Habitat types in the eastern box turtles' core area (50% UD isopleth) were primarily dominated by deciduous forest (mean = 51.6% SE +/- 1.95) (Figure 6).

DISCUSSION

Home range sizes were constrained within the urban landscape, and road avoidance behaviors were evident for both eastern box and Blanding's turtles. Habitat types in both the core and activity areas of both species contained developed habitat types. Sex ratios did not significantly differ from parity; however, age class distributions were skewed towards adult individuals and juveniles were mostly absent.

Both species were frequently located within close proximity to roads while avoiding road crossings. Proulx et al. (2014) and Paterson et al. (2019) found that Blanding's turtles actively avoid road crossings, regardless of the road type (paved or unpaved), which is consistent with our observations. The number of locations within close proximity to roads, as well as developed habitat types dominating the core and activity areas, is likely due to the lack of significant, un-altered habitat space available to distance themselves from human-dominated environments.

Home range area increased with road density, for both Blanding's and eastern box turtles. It is likely that these individuals are travelling larger distances in order to avoid road crossings, and therefore have larger home ranges as a result of the avoidance behavior, which is consistent with the results of Paterson et al. (2019). To the best of our knowledge, the influence of road density on the home range area of eastern box turtles has not been previously noted. Fortin et al. (2012) found that landscape composition had no strong influence on Blanding's turtles' home range area in low to moderately disturbed sites, yet Grgurovic and Sievert (2005) noted a positive relationship between roadless area and home range area. Variation in traffic densities, resource availability, or environmental factors could lead to these observed differences between studies, and therefore replication of studies in other urban environments should be encouraged. This positive relationship between road density and home range size could also simply imply that as turtles travel more, they encounter roads more frequently.

Overall, calculating home range area by use of KDE yielded notably smaller estimates than when estimated through MCP. This reduction in home range size estimate is likely due to the use of the LSCV method of bandwidth selection, which has previously been shown to greatly underestimate home range sizes for herpetofauna (Hemson et al. 2005, Silva et al. 2018). KDEs have been noted to be inaccurate for herpetofauna, as telemetry data are highly autocorrelated due to the repeated use of refugia, or species low vagility (Row and Blouin-Demers 2006). This autocorrelation violates the assumptions of the LSCV method, and results in poor performance. Conversely, MCPs often include large patches of land that are not actually used by the individual, and they do not depict areas of intense use by the individual **(**Row and Blouin-Demers 2006). Although MCPs can overestimate home range size, a number of bandwidth selections for the KDE home range estimates did not reach convergence. For these reasons, further analyses including home range estimates were performed using 95% MCPs. Minimum convex polygon (MCP) home ranges were smaller for both eastern box and Blanding's turtles compared to previous studies in less urbanized areas. Previous studies of Blanding's turtles home range in more naturalistic settings found mean home ranges of 22 ha in area (Grgurovic and Sievert 2005), which is comparatively much larger than the Blanding's turtles in this study who had a mean home range of 1.58 ha. Eastern box turtle home ranges were within the range of those in less developed environments (mean = 2.88 ha, SE +/- 0.913; or mean = 2.04 ha, SE +/- 0.368 if the outlying female is removed), however they did not exhibit the same degree of variation as seen by Greenspan et al. (2015), who found home range areas that varied from 0.33 ha to 54.7 ha.

Home ranges appear constrained in this heavily modified environment, and road avoidance behaviors are evident for both eastern box and Blanding's turtles. These reduced home range areas and road avoidance behaviors can have a number of consequences for these remnant populations, including a loss of species connectivity and increased rates of extinction (Gibbons et al. 2000). Road avoidance behaviors from adult turtles residing within the urban landscape, in addition to the lack of suitable habitat, constrain these individuals to small, isolated habitat patches within this otherwise highly unsuitable landscape. These habitat constraints, however, could present a tradeoff between reduced mortality risk, and reduced home ranges and connectivity of individuals of reproductive age. Previous studies in urban ecosystems have found that roads cause increased mortality rates for female turtles due to their increased movements to locate nesting sites (Aresco 2005, Steen and Gibbs 2004, Haxton 2000). This trend was not seen in our small sample of turtles, as over the course of this study a single female eastern box turtle experienced mortality due to an unknown cause. These low rates of adult mortality could be the result of remnant individuals who are less prone to movement, a lack of suitable habitat to travel to, or primarily older individuals who are familiar with the risks of this developed landscape. Local level studies of turtle movement within a specific landscape of interest should be encouraged to best inform management strategies due to this variation.

One female eastern box turtle at site 'B' had a dramatically larger home range area than any of the other eastern box turtles. The road density within a one-kilometer radius of this individual's home range was comparable to the other telemetered individuals (7.86 km/km^2 vs a mean road density of 9.45 km/km^2 for all individuals). This particular female was originally located in the school bus drop-off zone at the nearby zoological park. For this reason, we hypothesized that this turtle is a non-resident. Hester et al. (2008) showed translocated eastern box turtles had approximately three times the home range size of resident eastern box turtles when measured by MCP. The difference in observed home range area for this individual compared to the other eastern box turtles in this study, while living within a similar habitat matrix, could therefore suggest that this female is a non-resident turtle.

Low turtle capture rates, with only 154 native turtles captured across the course of the study, are not unusual in human-modified environments. Low capture rates of Blanding's turtles have been seen over a number of studies, in both human-modified and restored environments

(Rubin et al. 2004, Reid et al. 2016). Rubin et al. (2004) captured only 24-38 Blanding's turtles despite intensive trapping (732-3,181 trap nights at each site) when trapping in suburban Chicago forest preserves. Reid et al. (2016) had very low aquatic trapping success of Blanding's turtles at a restored wetland-upland complex, with a rate of only 0.05 Blanding's turtles per trap night. Juvenile turtle captures are typically low across studies, as juveniles are rare, or occupy habitats that are not surveyed as intensively by researchers (Congdon et al. 1993). The low rate of turtle captures (one turtle per three traps nights, or one Blanding's per 37 trap nights), and visual observations across all species in this study, despite reasonable trapping effort, reflect the small, isolated nature of these populations. For example, the Blanding's turtles that we trapped or observed likely represent a majority of the current population, which is probably a fraction of its size prior to intensive landscape development.

Sex ratios of Blanding's and eastern box turtles did not differ from parity ($p > 0.05$), nor did the sex ratios of all native turtle species captured when pooled together. Because sample sizes and capture rates for each species were low, further sampling will be required to determine whether this trend in sex ratios holds for the greater population of native turtles. Focused, intensive monitoring of more common species of turtles in the area, such as painted turtles (*Chrysemys picta*) or common snapping turtles (*Chelydra serpentina*), would likely be more easily accessible, and produce a more comprehensive snapshot of the overall viability of the urban turtle community.

Eastern box and Blanding's turtles were primarily comprised of adult individuals, with the exception of a single juvenile Blanding's turtle, as well as some hatchlings discovered upon emergence from their nest. This lack of diversity in age structure points to a lack of nest and juvenile survivorship. Survivorship of young individuals is necessary to support any loss of adult individuals, with long-lived species requiring an estimated juvenile survivorship of >70% in order to maintain a stable population (Congdon et al. 1993). Eastern box and Blanding's turtle nests were found within mulched garden beds, as well as in parking-lot planted dividers over the course of the study at site 'A'. Nesting in these areas acted as an ecological trap for the turtles, as there were direct mortalities upon the hatchlings emerging into the parking lot. Protecting these nest sites, and monitoring the sites until emergence, could provide means to reduce both predation and vehicle-induced mortalities, and boost juvenile survivorship.

Continued monitoring of these urban turtles will be necessary to determine the health and status of each population, as well as to inform management strategies. The overall low sample of eastern box and Blanding's turtles indicates that these are likely remnant "ghost populations" that have experienced dramatic decline (Compton 1999). The lack of appropriate, sizable habitat in the area would prevent any further expansion and connectivity of these remnant populations without significant human intervention. Long-term viability of these urban populations is contingent on careful monitoring at the local and regional level, and direct human interventions. Promoting juvenile recruitment, through the protection of nests of both Blanding's and eastern box turtles, would likely support these small populations while habitat is either protected or transformed into usable space. Blanding's turtles living within this urban matrix appear to be the most at risk due to their reduced home range sizes, reliance on aquatic habitats, as well as their low juvenile recruitment. Increasing the amount of usable habitat, or improving corridors between existing bodies of water, would facilitate the connectivity between remaining individuals. Headstarting for the Blanding's turtles could help to alleviate the low recruitment rates, as it appears adult mortality is low, however, the benefits of supplementing this population needs to be weighed with the release of this threatened species into a dangerous and highly developed landscape. Current habitat restoration work at site ‘A’ does signal some hope for these urban turtle populations, however. The creation of man-made wetlands at the neighboring former golf course not only provided additional gains of protected habitat, but turtles species, including the Blanding’s, used these wetlands within one year of their creation. Human interventions such as these can increase the connectivity of individuals, provide usable habitat, and create safer corridors for turtles living within developed environments, helping to support these at-risk populations.

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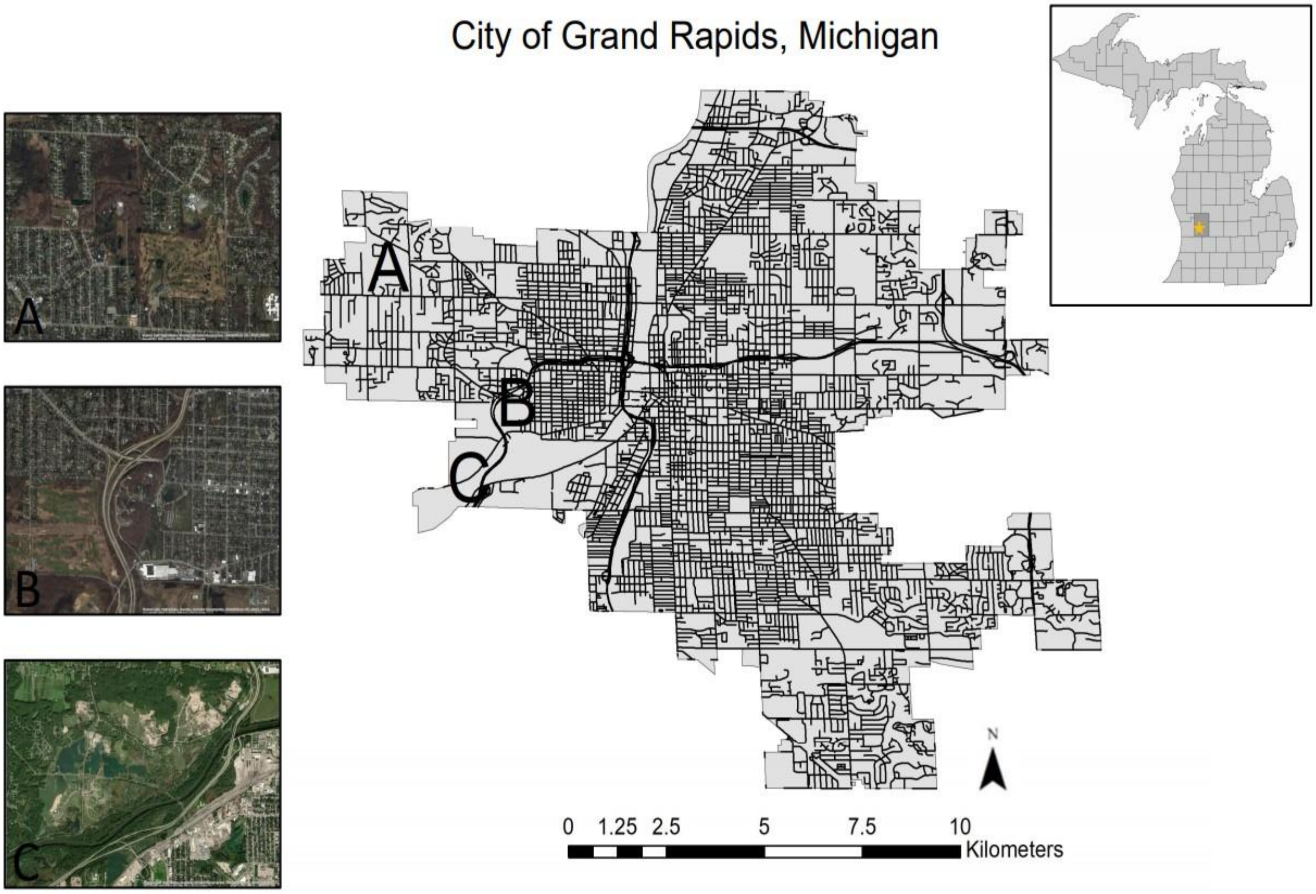
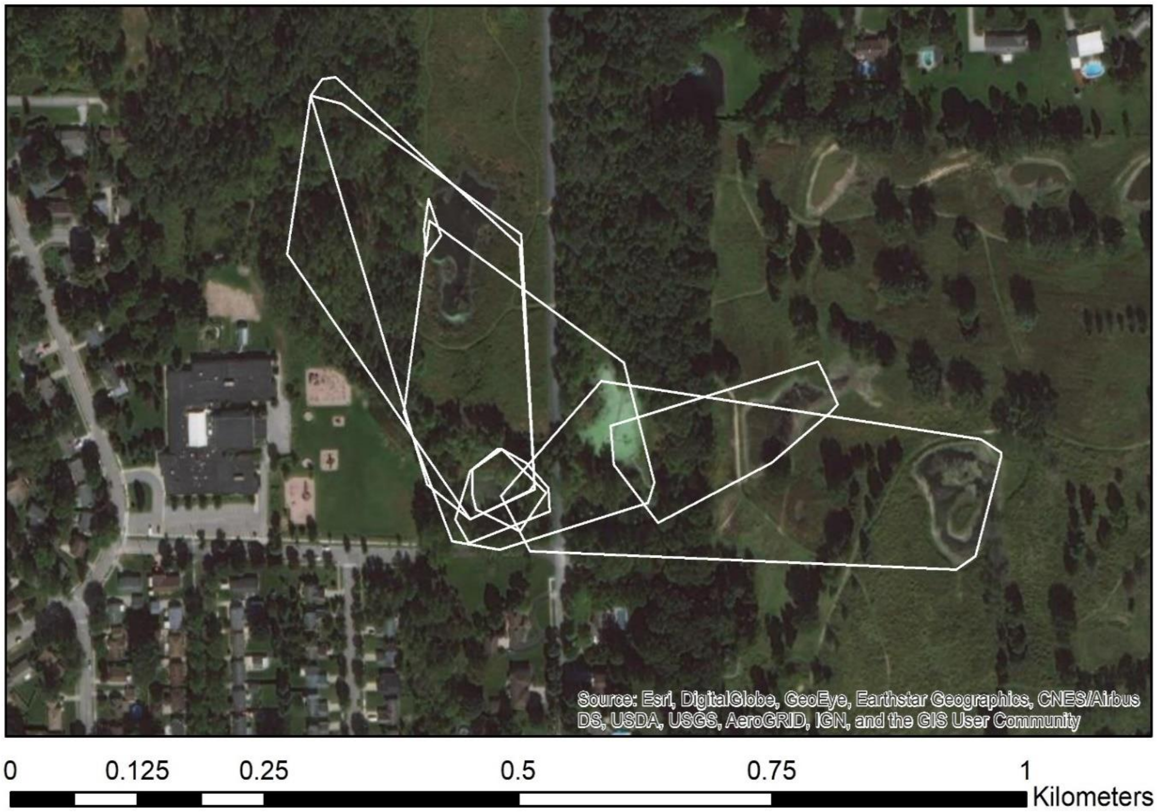


Figure 1. *Study sites located in the city of Grand Rapids, Michigan, USA. Black lines depicted are roads, and heavy black lines are interstates.*

Table 1. *Species counts of unique individuals from each turtle species captured. Eastern box and Blanding's turtles include individuals captured during 2018 preliminary work, and unmarked hatchlings discovered upon emergence from a nest*.

Species	**Female**	**Male**	**Unassigned**
Terrapene carolina carolina	8	5	5
Emydoidea blandingii	2	6	6
Chrysemys picta	30	44	17
Chelydra serpentina	3	1	4



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 2. *95% Minimum convex polygon home ranges for eight adult Blanding's turtles in Grand Rapids, Michigan (2020). Each white polygon represents the home range of one individual at site 'A'.*

Table 2. *Road densities within 1km of each turtle's home range as calculated by 95% MCP.*

Turtle ID	Species	Sex	95% MCP Home Range (ha)	Road Density (km/km2)
ABL	*Blanding's*	Female	0.272	8.18
ABH	*Blanding's*	Female	0.024	8.28
ABK	*Blanding's*	Male	2.450	9.29
ABN	*Blanding's*	Male	0.178	7.96
ABO	*Blanding's*	Male	2.949	9.38
ABP	*Blanding's*	Male	3.349	10.07
ABQ	*Blanding's*	Male	2.540	9.12
ACX	*Blanding's*	Male	0.907	9.79
Blanding's turtle mean			1.584	9.09
ABH	*Eastern box*	Female	1.490	8.03
ABM	*Eastern box*	Female	0.286	8.96
ACH	*Eastern box*	Female	3.823	12.14
ACI	*Eastern box*	Female	2.270	10.18
ACK	*Eastern box*	Female	2.347	10.32
ACM	*Eastern box*	Female	1.308	8.122
MNO	*Eastern box*	Female	12.228	7.08
ABC	*Eastern box*	Male	3.619	11.98

ABV	*Eastern box*	Male	0.781	9.13
ACJ	*Eastern box*	Male	2.423	10.06
ACL	*Eastern box*	Male	3.315	10.67
ACN	*Eastern box*	Male	0.723	9.23
Eastern box turtle mean			**2.884**	**9.66**
Total mean			**2.364**	**9.40**

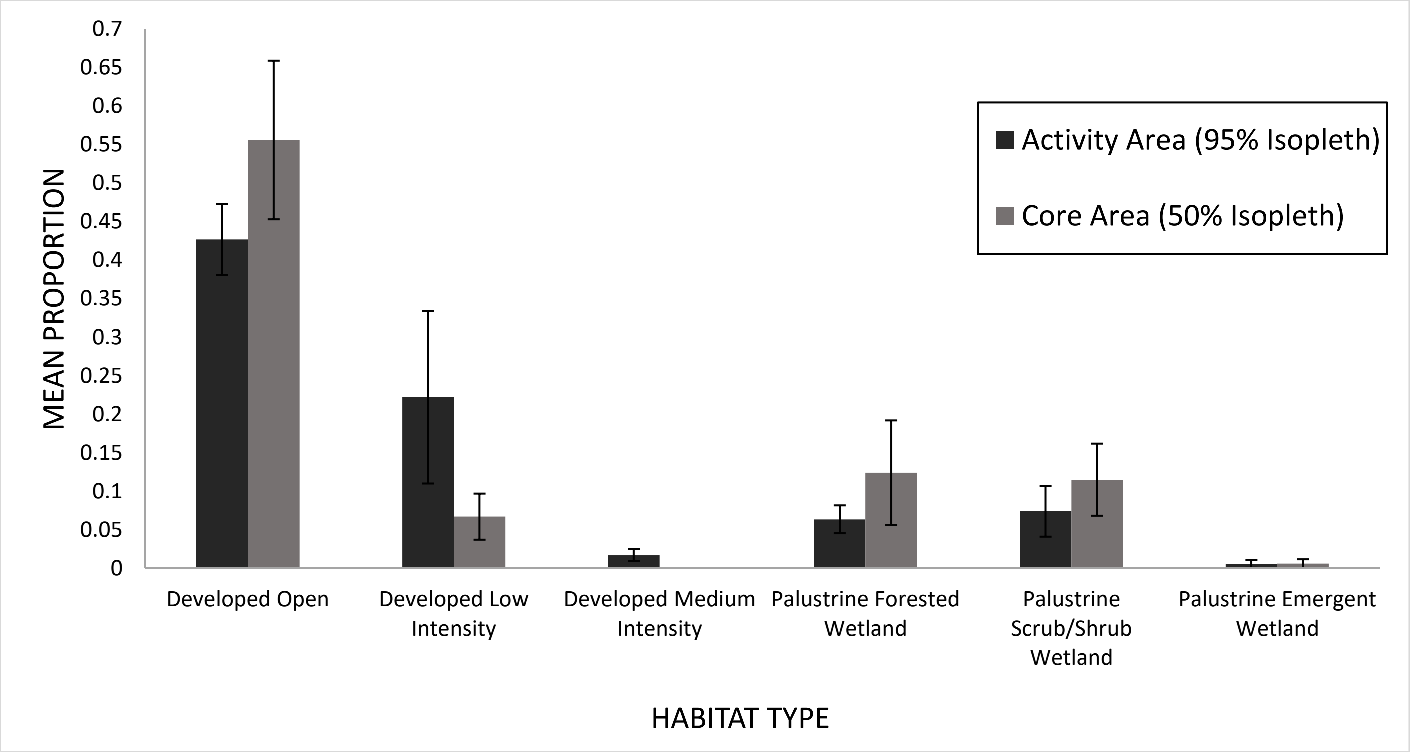


Figure 3. *Dominant habitat types within the activity and core areas of Blanding's turtles. Bars represent standard errors.*

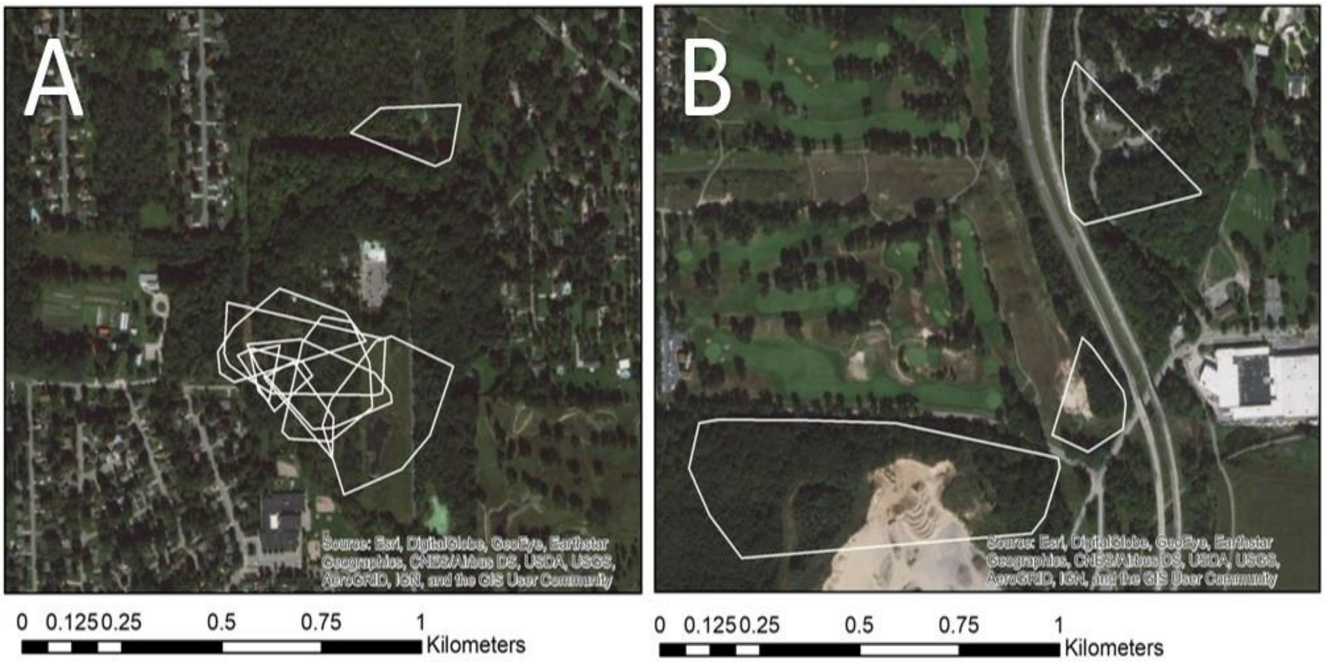


Figure 4. *95% MCP home ranges of eastern box turtles at site 'A' and site 'B', in Grand Rapids, Michigan (2020).*

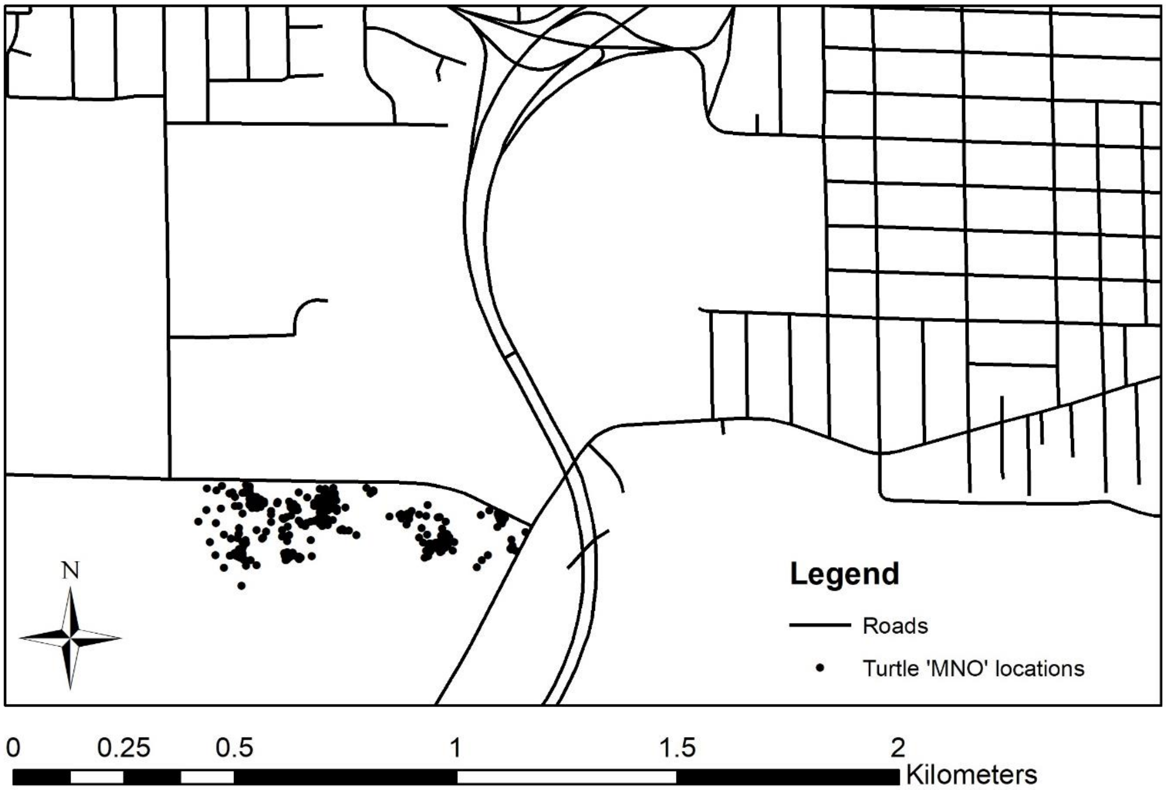


Figure 5. *Road avoidance behavior as demonstrated by a female eastern box turtle (ID = 'MNO'). This turtle avoided road crossings, however, did not avoid the habitats directly alongside roadways.*

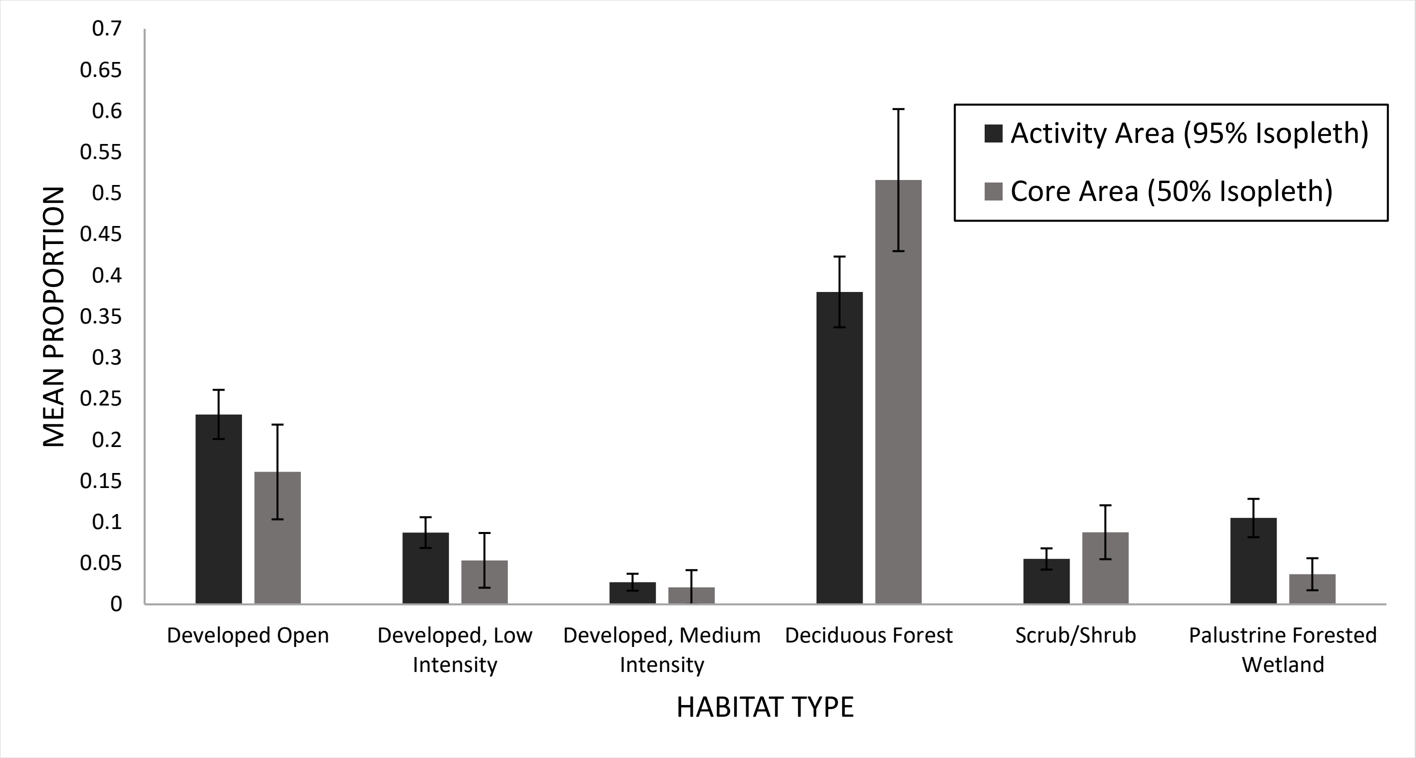


Figure 6. *Dominant habitat types within the activity and core areas of eastern box turtles. Bars represent standard errors.*

CHAPTER 3

EXTENDED REVIEW OF LITERATURE

Landscape modification and habitat fragmentation, or the splitting up of continuous habitat into smaller, isolated patches, have long been considered to be threats to native wildlife (Reed 2004, Sala et al. 2000, Foley et al. 2005). In general, habitat fragmentation results in the loss of useable habitat, and wildlife populations become more isolated from one another. If prolonged, this reduction in connectivity between individuals can eventually lead to increased extinction rates (Reed 2004). Urban development is one of the primary drivers of habitat fragmentation and loss, and results in the creation of novel ecosystems that are relatively understudied. Many of the effects of urban development on native wildlife are unknown, or difficult to predict, due to the heterogeneity of urban landscapes, as well as differential responses at the species-level (French et al. 2018).

Urban ecosystems create unique threats to native wildlife, and can result in abnormal or altered behaviors. Urban wildlife may change their movement patterns in order to avoid interactions with humans, experience higher levels of stress from sound or light pollution, and suffer from increased predation rates from mesopredators and domestic animals (French et al. 2018, Knapp and Perez-Heydrich 2012). Although generalist or exotic species may thrive in urban ecosystems, native species typically do not (French et al. 2018). Human-induced landscape changes are often occurring too quickly for wildlife to alter their movement behaviors, such as their willingness to cross between different habitat types, path shape, and movement distances, and continue to persist within the fragmented environment (Fahrig 2007). Rapidly changing environments create conflicting cues to the apparent risks and benefits of moving from one habitat patch to another, resulting in increased probabilities of mortality (Fahrig 2007, Robertson and Hutto 2006, Schlaepfer et al. 2002). The matrix in which the fragmented habitat is situated can also influence the success of a resident species. Species that dispersed further between existing habitat patches prior to the loss of habitat are placed at risk when dispersing through a dangerous matrix, and are more likely to disappear from the remaining patches (Van Houtan et al. 2007). Species that are less vagile however, can sometimes persist in the remaining patches (Van Houtan et al. 2007, Fahrig 2007).

Urban environments are particularly detrimental for turtles (order Testudines). Human-altered landscapes typically undergo rapid change, often creating 'ecological traps' for turtles. An ecological trap occurs when positive environmental cues do not match the potential negative outcomes of the selection being made (Robertson and Hutto 2006). This is most commonly displayed in turtles through nesting alongside roadways or other anthropogenically-modified areas, as the thermal conditions and the ease of digging the nest are improved in comparison to more naturalistic areas (Francis et al. 2019). This presents a tradeoff however, of greater risk of mortality during the nesting foray, as well as increased nest depredation (Fahrig 2007, Steen et al 2006).

Demographic vital rates, such as sex ratios, age structure, and age-specific mortality rates have the potential to become skewed for turtles living within urban environments. Low juvenile recruitment, particularly due to nest and juvenile predation, is a threat to turtles globally yet becomes particularly pronounced in urban areas. Urban and fragmented habitats support unnaturally high mesopredator populations, such as raccoons, skunks, and opossums, through the process of mesopredator release and the amount of human-subsidized food resources in urban areas (Soulé et al. 1988, Prugh et al. 2009). The high presence of mesopredators can in turn increase the rate at which turtle nests are predated upon (Engeman et al. 2005, Temple 1987, Congdon et al. 1983). Many turtle life histories are characterized by long generational times and delayed sexual maturity, and a reduction or loss in juvenile recruitment skews the age class distribution of a population towards adults. Long-lived species of turtle require an estimated juvenile survivorship, from age one to sexual maturity, of 70% in order to maintain stable populations (Congdon et al. 1993). Adult mortalities become especially problematic when paired with the loss of juveniles, as it is unlikely for juvenile survivorship to increase past the already high level required to maintain stability in the population. (Congdon et al. 1993, Rubin et al. 2004).

The sex ratios of turtles in developed environments have additionally become a subject of interest, due to the apparent phenomenon of female turtles having a higher risk of mortality than male turtles. It is most commonly hypothesized that female turtles perform large overland movements in order to find suitable nesting sites, and therefore are more likely to cross over roads and become victim to road mortality (Steen and Gibbs 2004, Steen et al. 2006, Aresco, 2005). Male-biased turtle populations in anthropogenically-modified environments have not always been able to be linked to road mortality or the amount of protected area at a site, and could also signal that female turtles are more vulnerable to terrestrial predators during their nesting movements (Vanek and Glowacki 2019, Eskew et al. 2010). The unknown methods in which turtle sex ratios become skewed drive a need for the replication of previous studies across different urban areas in order to best determine localized conservation practices (Vanek and Glowacki 2019).

The movement patterns of turtle species can be greatly influenced by the presence of urban development, particularly roads. Some turtle species display strong road avoidance behaviors, crossing roads much less often than predicted by random chance (Shepard et al. 2008, Proulx et al. 2014, Paterson et al. 2019). Road avoidance behaviors can be beneficial in terms of reducing mortality, however the reduction of movements can lead to a lack of gene flow between populations that are intersected by roads. Most turtles are long-lived species that show delayed sexual maturity, and it may take many generations for the impacts of this isolation to become evident in the population, in turn delaying the timely intervention of conservation initiatives (Shepard et al. 2008). Turtle species do not avoid habitats near roads; instead, they travel longer daily distances while avoiding road crossings (Paterson et al. 2019). Paterson et. al (2019) estimated the energetic cost of this road avoidance behavior to be low for turtle species, leaving vehicle strikes and genetic isolation as greater threats from roads within turtle home-ranges.

Eastern box turtles (*Terrapene carolina carolina)* and Blanding's turtles (*Emydoidea blandingii)* are two turtle species of special concern in Michigan, USA, as their populations are declining throughout their range. Both species are threatened by residential and commercial development, agriculture, and transportation corridors such as roads (van Dijk and Rhodin 2011, van Dijk 2011).

Populations of eastern box and Blanding's turtles exist within the city limits of Grand Rapids, Michigan, USA, however the viability of these populations is unknown. Grand Rapids is the second largest city in the state of Michigan, and the turtles living within this urban area are of particular interest due to the developmentally intense habitat in which they reside. Studying these populations of urban turtles can provide insights for conservation at the local level, as well as provide information as to the specific influence of urban development on these two threatened turtle species.

Urbanization and reptiles

Urbanization is the development of land into cities or large towns. The current world population is growing at a rate of 1.2% annually (The World Bank, 2018 “Population Growth”), and 54.8% of the world’s population currently lives in urban areas (The World Bank, 2018 “Urban Population”). This number is expected to grow to 68% by 2050 (The United Nations 2018) resulting in the need for further land development and construction of urban areas. The characteristics and extent of urban development is different in every region, and therefore can positively or negatively affect a species depending on their ecological needs and life history characteristics (French et al. 2018). Most reptile species, however, are impacted negatively by urban development (French et al. 2018).

Urban development can affect multiple facets of a reptile’s ecology. High levels of land development decrease reptile species richness and abundance, allow exotic reptile species to thrive, and have even resulted in species extinctions (French et al. 2018, Nielsen et al. 2014, Cordier et al. 2021). Aquatic habitats that have experienced damming or pollution inputs have led to the decline of aquatic or semi-aquatic species (French et al. 2018, Gibbons et al. 2000). Increased levels of stress due to pollution, noise, and interactions with humans have the ability to suppress a reptile’s immunity, interfere with mate acquisition, and the shift the timing of breeding events (Ditchkoff et al. 2006). The presence of humans, even without high levels of land-use change, can create a disturbance for reptile species and increase mortality rates (French et al. 2010, Gibbons et al. 2000, Garber and Burger 1995). Humans inappropriately handle wild reptiles, produce food waste that attracts natural predators, and cause mortality of terrestrial reptile species due to road-collisions (Gibbons et al. 2000).

Human-induced landscape changes can indirectly influence the predation rates of reptiles through the creation of habitats that support large numbers of mesopredators that act as predators of reptiles and their nests. Apex predators become less abundant as habitat loss increases, resulting in a lack of top-down control of mid-level trophic predators (Prugh et al. 2009). Mesopredators can then become unnaturally abundant, and place significant pressure on prey populations (Prugh et al. 2009). The term “mesopredator release” was created by Soulé et al. (1988) to describe this abnormal growth in the populations of smaller predators due to the lack of top-down control.

Although mesopredator release refers to the loss of apex predators in a habitat, mesopredators can also become unnaturally abundant in human-dominated environments through other methods, such as habitat fragmentation, and increased levels of food resources and trash products (Crooks and Soulé 1999, Prugh et al. 2009). Human-induced landscape changes, and the influence of human presence, is a chronic threat to wildlife and can be expected to increase in conjunction with the human population (Sala et al. 2000).

Urbanization and turtles

Turtle species are particularly impacted by urban development, and the habitat loss that coincides with it. It is estimated that 61% of turtle species are threatened or are already extinct, many of these species due to habitat destruction (Lovich et al. 2018). For long-lived reptiles such as turtles, population-level impacts of urbanization can take years to become evident due to their long generational times (Congdon et al. 1993, Knapp and Perez-Heydrich 2012). Urban ecosystems can alter a turtle’s behavioral responses through changes in movement patterns, as well as skewing the demographic patterns of a population through increased mortality and predation.

The influence of urbanization on a turtle's movements differs depending on the species of turtle, as well as with the overall habitat matrix. In general, the rate at which habitats are changing due to anthropogenic influence is too fast for species to adapt (Fahrig 2007). This is particularly true for turtles, who have long generational times and delayed sexual maturity. A turtle's movement behaviors, such as their willingness to cross boundaries into new habitat types, as well as daily distances moved, may or may not appropriately align with the risk of traveling through an urban or suburban matrix (Fahrig 2007). Some species, such as the Eastern long-necked turtle (*Chelodina longicollis*) travel larger distances in fragmented suburban environments than on larger, more contiguous nature reserves (Rees et al. 2009). These turtles likely had to travel longer distances in order to acquire necessary resources in the suburban environment, whereas the nature sanctuaries were able to sufficiently support these turtles within a smaller area (Ditchkoff et al. 2006). In this case, the need for adequate resources was a motivator for the turtles to travel through a potentially dangerous suburban matrix. Common snapping turtles *(Chelydra serpentina)* however, reduce their association with developed areas when living in more urbanized environments (Ryan et al. 2014). Blanding's turtles (*Emydoidea blandingii)* and eastern box turtles (*Terrapene carolina carolina*) display a strong boundary response by avoiding road crossings, even travelling longer distances in order to avoid road crossings, but do not avoid the habitats alongside roads (Paterson et al. 2019, Weigand et al. 2019). Due to these differential responses to boundaries or developed habitat types, it is important to replicate studies across a wide range of urban environments as the heterogeneity of urban landscapes, as well as the rate of environmental change, could influence a species' persistence in the habitat over time.

Urban environments skew age classes in turtle species due to increased nest predation from mesopredators, resulting in populations primarily made up of adult individuals (Gibbons et al. 2000, Knapp and Perez-Heydrich 2012). Rubin et al. (2004) found that only 5% of Blanding's turtles captured over a five-year period in suburban Chicago were juveniles, as opposed to 18% juveniles in a forest preserve in Wisconsin. Urban populations such as these with age classes skewed towards adults are likely to experience decline as a result of turtles' long-generational times and delayed sexual maturity (Congdon et al. 1993).

Nesting success for turtle species in urban areas can vary depending on the density of predators, the habitat in which the nest was laid, as well as other chronic disturbances. Nesting sites closer to edge habitats tend to experience more depredation, as demonstrated for painted turtles (*Chrysemys picta*) (Strickland et al. 2010). Increased amounts of edge habitat in fragmented urban or suburban areas could therefore increase the rate of nest predation when compared to nests in a more naturalistic environment. Anthropogenically-modified sites, such as edge habitat, may also provide some benefits for nesting, however. Anthropogenically-modified areas support nests that are 3.3℃ warmer than natural nests during the incubation process, and embryos likely experience twice as much development in the human-altered nesting sites (Francis et al. 2019). These anthropogenically-modified sites could act as an ecological trap however, if there is frequent disturbance from humans or an increased presence of predators. The benefits of laying a nest in a significantly warmer environment must be weighed by the risk of adult mortalities and nest predation (Francis et al. 2019).

In addition to age class, sex ratios can be skewed by urban development due to the increased risk of mortality from road collisions or predation, which can disproportionately affect female turtles. Female turtles travel long overland distances when attempting to locate a nesting site, and therefore would be more likely to cross over roads and suffer from vehicle collisions, or become exposed to predators (Steen et al. 2006). These skewed sex ratios have been seen for many species of semi-aquatic turtle, including the common snapping turtle (*Chelydra serpentina),* and the painted turtle (*Chrysemys picta)* (Piczak et al. 2019, Patrick and Gibbs 2010, Vanek and Glowacki 2019). Populations biased towards one sex will be at greater risk of decline or extinction due to the difficulty of acquiring a mate, and the loss of sexually mature individuals.

Eastern box turtles

The eastern box turtle (*Terrapene carolina carolina)* is a turtle native to the eastern United States. The eastern box turtle is currently listed as vulnerable by the International Union for the Conservation of Nature (IUCN), and as a species of concern in multiple states throughout its range (van Dijk 2011). Current threats to the eastern box turtle include urban development, climate change, and transportation corridors (van Dijk 2011). Eastern box turtles typically live to be 50 years old, reaching their full size after approximately 20 years (Stickel 1978). Male and female eastern box turtles display sexual dimorphism: males typically have bright red eyes and a concave plastron, and the females typically have brown eyes and a flat plastron. The eastern box turtle is recognizable by its domed shell and bright yellow and orange markings. The namesake of these turtles is due to their hinged plastron, which allows them to completely close their appendages into their shells like a ‘box’.

The eastern box turtle is in the pond turtle family Emydidae, yet is primarily terrestrial in nature. The eastern box turtle may use puddles or other shallow bodies of water during warmer periods, and tend to have larger daily movements following rain showers (Iglay et al. 2007). As the weather cools, eastern box turtles overwinter within the bounds of their home range, digging themselves underground (Stickel 1989). Both male and female eastern box turtles are terrestrial, and therefore both sexes can have equal potential for mortality due to vehicle collisions, grass mowing, or other negative human-wildlife interactions (Nazdrowicz et al. 2008). Eastern box turtle home ranges can show great variation in area, stretching from 0.33 ha to 54.7 ha of land (Greenspan et al. 2015). Resident eastern box turtles and translocated eastern box turtles, either moved by the public or as a part of a conservation initiative, have demonstrated differences in home range behaviors. Eastern box turtles who have been relocated have home ranges three-times larger than resident turtles when measured by minimum convex polygon (MCP), as well as higher mortality rates and greater daily movements (Hester et al. 2008).

Eastern box turtles lay their nests in open canopy areas, with clutch sizes of 3.0 to 5.87 eggs throughout their range (Willey and Sievert 2012). Eastern box turtles may show a preference for anthropogenically-modified environments for nesting, as Flitz and Mullin (2006) found all of their eastern box turtles to select disturbed clearings. This is likely due to the increase in temperatures in anthropogenic nest sites, providing a more beneficial thermal environment for egg incubation (Francis et al. 2019). This preference for anthropogenically-modified nesting environments could act as an ecological trap for this species, reducing the reproductive success if the amount of human or predator disturbance is too great in these areas (Robertson and Hutto 2006). Towards the northern end of their range, nest success rates are approximately 55% without the influence of depredation (Willey and Sievert 2012). Nest predation, however, remains a significant threat to this species. Flitz and Mullin (2006) determined that 87.5% of eastern box turtle nests in Illinois experienced depredation within the first 72 hours of deposition. Moderate nest success rates paired with high levels of predation would cause significant losses of recruitment for eastern box turtles, particularly those in urban and suburban areas where mesopredator density is significantly higher than in a more naturalistic environment.

Blanding's turtles

The Blanding's turtle (*Emydoidea blandingii)* is part of the pond turtle family, Emydidae. The Blanding's turtle is semi-aquatic, and native to Michigan, Wisconsin, Illinois, and parts of Canada. Blanding's turtles are identifiable by their bright yellow necks and characteristic grins. The Blanding's turtle is currently listed as endangered by the IUCN, and this endangered status is due to similar threats as the Eastern box turtle: urban development, climate change, and transportation corridors (van Dijk and Rhodin 2011).

Blanding's turtle's home range area can vary from 3.7 to 27 hectares of land, as these turtles frequently travel between ephemeral pools (Innes et al. 2008, Grgurovic and Sievert 2005). Seasonally, female Blanding's turtles may travel longer distances than males in order to reach suitable nesting areas, which could place them at increased risk for road mortality (Grgurovic and Sievert 2005, Steen et al. 2006). Blanding's turtles enter their overwintering spot in late fall, typically submerged in mud, soil, or under the water.

The Blanding's turtle has a life expectancy upwards of 75 years (Brecke and Moriarty 1989) and females become sexually mature between the ages of 14-20 years old (Congdon 1993). This delayed sexual maturity is beneficial for increased levels of reproductive success over the span of a lifetime, however these long generational times, and high mortality before the animal is able to reproduce, have led to the decline of many Blanding's turtle populations (Congdon 1993). Congdon et al. (1993) estimated generational times of 37 years for the Blanding's turtles, and predicted that juvenile survivorship needed to be approximately 72% in order to support a stable population. Mortality of adult or older juvenile Blanding's turtles would reduce the number of sexually mature individuals, and the long generational times would prevent these populations from rebounding at a sufficient rate. Clutch sizes for this species range from 3-15 eggs (Congdon et al. 1983). Nest success rates are low for the Blanding's turtle, with nests in southeast Michigan experiencing predation rates of 42-93% (Congdon et al. 1983).

Home range analyses (MCPs, KDEs, BBMMs, dBBMs)

A home range is the area used by an animal during a specific duration of time. An animal's home range includes areas for finding mates, refuge, foraging or hunting, and reproductive processes. Home ranges have been studied for many years, using a number of different techniques such as VHF and GPS telemetry. Very high frequency (VHF) radio telemetry studies have been used across a wide number of species, and require manual location of the telemetered individual by the researcher. VHF transmitters can be small or surgically implanted, which makes them more commonly used in reptile studies. GPS telemetry is the most recent advancement, however the large transmitter size as well as the high cost make them less commonly used for reptiles who frequently shed their skin or scutes. GPS transmitters also require areas of open canopy to fix locations, which is not conducive for herpetofauna who commonly burrow beneath the soil, or use areas of dense canopy and other coverage.

Much like the tracking technology, the method in which the locations are constructed into a home range estimate has a number of potential options. First, and the most popular for herpetofauna, is the minimum convex polygon (MCP) method. MCPs use the smallest possible polygon, with no internal angles being greater than 180 degrees, that encompasses the known locations. MCPs can be reported as a percentage, which determines the number of outlying locations excluded as exploratory movements. MCPs are the most widely used home range analysis for herpetofauna, as they are simple and more easily comparable from one study to another (Row and Blouin-Demers 2006). MCPs however, often include large patches of land that are not actually used by the individual, and they do not depict areas of intense use by the individual **(**Row and Blouin-Demers 2006).

A second popular method of home range estimation are kernel density estimators (KDEs). Kernel home range estimators are non-parametric, and produce a likelihood distribution of finding an animal at any given location. KDEs have been preferred over MCPs in situations where an analysis of the intensity of use of an area is desired. The most difficult component of using a kernel density estimator, however, is the accurate selection of an ‘h’ value, known as the smoothing factor. Choosing the smoothing factor ‘h’ has the ability to greatly alter the size of the home range that is calculated. The least-squares cross-validation (LSCV) is the most common method of selecting a value for the smoothing factor due to its effectiveness with a variety of situations, and lower error and bias than the reference bandwidth method (Row and Blouin-Demers 2006, Seaman and Powell 1996). LSCV however does not perform well for data that is highly autocorrelated, which is typical of herpetofauna telemetry data. Herpetofauna tend to use the same locations for refugia within their home range, and these repeated locations are what drives the data to be more autocorrelated, even if significant time is allowed between sampling events (Row and Blouin-Demers 2006). Row and Blouin-Demers (2006) compared home ranges estimated by kernels at a range of smoothing factors to home ranges calculated by minimum convex polygon (MCP) for *Lampropeltis triangulum*. The range of home-range sizes calculated by kernel density was twice that of those calculated by MCP. In addition, the amount of variation due to the smoothing factor selected was inconsistent from on individual to another, making it difficult to select an appropriate smoothing factor value. Although KDEs remain a common method of home range estimation for herpetofauna, their drawbacks should be noted when analyzing and interpreting telemetry data.

The more recently developed method of space-use analysis is the Brownian bridge movement model (BBMM). It is worth noting that BBMMs and dBBMMs are considered to not be suitable for estimations of home range size rather it should be used to answer questions of space usage (Silva et al. 2020). A Brownian bridge models an animal's movement by producing probabilities that an animal will be in a given area across the time surveyed. Brownian bridges do this by taking into consideration the time elapsed between successive points, as well as each individual's unique mobility factor (σ^2_m) (Horne et al. 2007, Calenge 2006, Bullard 1999). Using Brownian bridges to model animal movements was proposed by Bullard (1999), and software was then developed by Calenge (2006). Horne et al. (2007) extended these ideas by developing a method to estimate the animal's mobility factor. The most recent iteration of the BBMM is the dynamic Brownian Bridge movement model (dBBMM), which allows the animal's mobility factor (σ^2_m) to adjust based on changes in movement patterns (Kranstauber et al. 2012). This dBBMM is particularly useful for animals who exhibit distinctive changes in activity throughout the day, such as nocturnal species (Silva et al. 2020).

Brownian bridge movement models have grown in popularity due to their ability to provide a probability of occurrence within a region, similar to a KDE, however it does not contain the problematic 'h' value, or smoothing factor. In addition, the methods detailed by Horne (2007) incorporate an adjustable value for location uncertainty that is decided by the researcher. In general, there are no guidelines as to the maximum lag time between successive locations for a

BBMM to maintain its confidence, however it is assumed that the BBMM will decrease its confidence as time increases between sampling events (Horne 2007).

Silva et al. (2020) has shown that Brownian bridge based models outperform MCPs and KDEs across a number of different tracking regimes for reptiles when using VHF telemetry data, as opposed to GPS logger data. Silva et al (2020) used VHF data from active hunters, ambush foragers, and ambush predators, and simulated sampling regimes that ranged from four locations a day to one location per month. Overall, MCPs and KDEs produced higher error rates than Brownian bridge based analyses across all sampling regimes as well as reptile activity types (Silva et al 2020).

Bias in mark-recapture analyses

Mark-recapture surveys for aquatic turtles most commonly include setting baited hoop nets within water bodies, and checking these hoop nets periodically (e.g., every 12-24 hours) in order to capture individuals. Although the use of baited hoop nets is the most common and preferred method of turtle trapping, it is important to acknowledge that hoop nets can add a degree of bias to a mark-recapture survey.

Potential bias in different turtle capture methods was analyzed by Tesche and Hodges (2015) using hoop nets, dip nets, and basking traps. Dip nets involve the researchers to wade or canoe around a water body, and scoop the turtles out by hand using a net. Basking traps are a more passive form of turtle capture, and require a basking platform to be built in the water in order to attract turtles. Turtles use the false “log” or platform for their basking, and then must fall directly into a basket-style trap below the platform when startled or exiting the platform. Turtle surveys were conducted using these three trapping methods in order to determine their impacts on estimates of populations size, and sex and age class ratios. In this particular study, hatchlings and juveniles were primarily caught in dip nets, and it was hypothesized that the large meshing of the hoop nets allowed these individuals to escape (Tesche and Hodges 2015). Using all three methods of trapping combined (hoop, dip, and basking) yielded population estimates with smaller confidence intervals 2/3 of the time, and the authors recommended using multiple techniques when attempting to survey turtle populations (Tesche and Hodges 2015).

Hoop nets have additionally been criticized for their potential for turtles to escape through the funnel design, as well as their male-biased capture rates. Brown et al. (2011) documented the rate of escape from hoop nets by red eared sliders (*Trachemys scripta elegans*). Over the course of their study only five out of 139 red-eared sliders escaped from hoop nets, and these five individuals were all female turtles. Therefore, the male bias in captures that are seen in some studies may be due to escapes as opposed to a differential preference for trap type, although this rate of escape is very low. Although it is important to acknowledge the potential bias towards adult turtles when using hoop nets, baited traps still remain the most commonly used survey method due to their portability, ease of use, and are readily compared amongst other studies.

EXTENDED METHODOLOGY

Study area

This study was conducted across three sites within the city limits of Grand Rapids, Michigan, USA, which is the second largest city in the state of Michigan (Figure 1). Grand Rapids has a city population of approximately 200,000 and a metropolitan population of over one-million (U.S. Census Bureau 2018). Each site was located within fragmented habitat, and was selected due to having previously recorded sightings of the two focal species.

The first site ‘A’ was located on the western boundary of Grand Rapids. Site ‘A’ is approximately 57.8 ha of land, and recently acquired an additional 48.9 ha of a former golf course in 2017. Ecological restoration of the golf course began immediately after its purchase in 2017 with the creation of a single manmade wetland, and three more wetlands the following year. Several turtle species, including Blanding’s turtle, used these manmade wetlands within one season of their creation. Habitat types include developed open land, scrub/shrub wetlands, deciduous forest, and emergent wetland. Traffic volumes for this region range from 7,000 to 15,000 cars daily (State of Michigan 2020).

The second site, ‘B’, was a fragmented landscape at the edge of the downtown area that included a golf course, an active mine, and a wooded lot. Site ‘B’ is approximately 40 ha of land, and is intersected by Interstate-96, industrial plants to the south, and dense residential areas to the north and east. The site contains habitat types of deciduous forest, developed open space, forested wetland, and grassland/herbaceous openings. Traffic volumes for this area range from approximately 2,400 to 49,000 cars daily (State of Michigan 2020).

The third site, ‘C’, was a large urban park, located on the southwest side of the city of Grand Rapids. This land previously contained a gypsum mine and a condemned landfill, but has since been restored to become the current county park (Friends of Grand Rapids Parks 2019).

The park is primarily grassland/herbaceous habitat and open water, with smaller regions of deciduous forest and wetlands. Site ‘C’ is approximately 566 ha of land and is bordered by Interstate-96 freeway to the south (County of Kent, Michigan 2018). Traffic volumes range from approximately 1,000 to 49,000 cars daily for the surrounding area (State of Michigan 2020).

Survey Methods

Turtle populations were studied using two methods: mark-recapture surveys, and very high frequency (VHF) radio telemetry tracking. Mark-recapture surveys were used at the three study sites in order to estimate sex ratios and age class distributions for each focal species, and capture individuals for VHF telemetry. Four eastern box turtles and four Blanding’s turtles captured during preliminary work in 2018 were included in the 2019-2020 study. Eastern box turtles were located opportunistically via visual encounter, often by visitors, students, and staff members at the three sites, or through the congregation of other eastern box turtles. To capture aquatic turtles, baited hoop nets of both 12 in and 36 in diameter were used, with mesh sizes of 0.25 in and 3 in, respectively. Traps were baited with various foods of interest including canned cat food, sardines, and other chopped fish. Traps were partially submerged and left overnight between April-September 2019, and May-August 2020. Traps were checked at least once every 24 hours, and turtles were processed immediately the following morning regardless of species captured. Aquatic trapping effort was low at site ‘B’ compared to sites ‘A’ and ‘C’ in 2019 due to low water levels throughout the active season, as well as a lack of Blanding’s turtle sightings in the previous year. In 2020, mark recapture surveys of aquatic turtles did not occur at site ‘B’ due to construction obstructing the single body of water at the site during the active season.

All captured turtles were sexed using external secondary sex characteristics, with males possessing plastral concavity and a longer pre-cloacal tail length than females. Turtles were then weighed on a digital scale to the nearest gram, and carapace and plastron length and width were taken to the nearest millimeter using metal calipers. A unique identifying code was assigned to each turtle by filing notches in the marginal scutes with a metal triangular file (as described by Cagle 1939). Any injuries, such as missing limbs or damage to the shell, were also noted. The air temperature, water temperature, and time of day at which the turtle was captured was noted, as well as the capture method, trap number, and GPS location. Annuli definition was grouped by well-defined, somewhat well-defined, somewhat smooth, and very smooth. Annuli definition and a visible number of annuli count was used in order to estimate age class, as detailed below. Eastern box and Blanding's turtles were outfitted with a VHF transmitter as detailed below. Turtles were then released at their capture location, and processing equipment was cleaned with 100% ethanol to prevent potential disease transmission.

Radio-telemetry surveys of eastern box and Blanding's turtles were used in order to determine survivorship, home-range estimates, as well as the habitat types in the core and activity areas of each telemetered individual. VHF transmitters (Advanced Telemetry Systems, Isanti, MN. Model R1860 – battery life 796 days) did not exceed 5% of a turtle's body weight to prevent burden to the animal. A single GPS logger was used for a female eastern box turtle who was situated in habitat that was difficult to access regularly. Transmitters were adhered to the turtle's first or second costal scute in order to avoid interference with mating behaviors using a combination of DEVCON 5-minute epoxy (ITW Performance Polymers, Danvers, MA) and PC marine epoxy putty (Protective Coating Company, Allentown, PA). Turtles were held until the epoxy had dried (approximately 1-3 hours) and released at their capture location. Turtles were tracked to their locations 2-3 times weekly during the active season (May-September), and once a month during the inactive season (October-April). Blanding's turtles were observed opportunistically at each relocation, and eastern box turtles were observed at approximately 90% of relocations. GPS location and environmental data (air, water, and soil temperatures, % canopy cover, substrate type, % cloud cover, precipitation, and dominant vegetation) were recorded at each location. Canopy cover was estimated using a spherical densiometer to the nearest percentage. Substrate types were grouped into multiple categories: leaves, grass, brambles, soil, moist area, gravel/road, basking log, in water/not visible, and unknown/other. Cloud cover was estimated to the closest percentage: 0%, 25%, 50%, 75%, or 100% cover. Precipitation was categorized by none, drizzle, moderate rain, heavy rain, fog, or snow. Precipitation occurring in the past 24 hours was noted.

Spatial and demographic analysis

50% and 95% minimum convex polygon (MCP) and kernel density estimator (KDE) home ranges were estimated using the package "rhr" in R Studio (Signer 2019, RStudio Team 2020). Bandwidth selection for KDE home ranges was determined using the least squares cross-validation (LSCV) method. Home range estimates made by KDEs that did not reach bandwidth convergence were removed from analysis.

Brownian bridge movement models (BBMMs) were used in order to determine habitat types in both activity areas and core areas of each individual. BBMMs were used as they do not incorporate as much unused areas of land as MCPs (Silva et al. 2018). Although primarily used for GPS telemetry, Brownian bridge based analyses have been shown to work well for herpetofauna who spend significant amounts of time sheltering in one location, and remain accurate with lower sampling regimes using VHF telemetry (Silva et al. 2020). Location error in VHF telemetry is highly variable, particularly with herpetofauna, due to unfavorable terrain and the animal's ability to burrow itself into the ground. Location error for the BBMM was set at 20m due to this variability. Eastern box turtles and Blanding's turtles have a period of overwintering (brumation), as well as a defined active season. Because of this, animals were located 2-3 times a week in the active season, but only once a month during the inactive season, resulting in an inconsistent amount of lag time between sampling locations. To the best of our knowledge, BBMMs have not been used for animals that brumate or hibernate, or with an inconsistent sampling regime in VHF telemetry. Because of this variation, max lag was set to one month in order to reflect the longest time possible between successive locations. Utilization distributions (UD) for each turtle were created using Brownian bridge movement models in the package "BBMM" in RStudio at both 50% (core area) and 95% (activity area) (Nielson et al. 2013, RStudio Team 2020). Habitat types in the activity and core areas were determined by overlaying the 50% and 95% UD isopleths over a landcover raster dataset (NOAA Coastal Change Analysis Program (C-CAP) Regional Land Cover Database 2016). Developed habitat types were classified based on the following: developed open space, developed low intensity, developed medium intensity, and developed high intensity (NOAA Coastal Change Analysis Program (C-CAP) Regional Land Cover Database 2016). Developed open space was characterized by managed vegetation in areas developed for recreation or aesthetic purposes, and constructed surfaces were less than 20% of the total land cover. Developed low intensity habitat was characterized by constructed materials accounting for 21-49% of total area, including areas such as rural neighborhoods. Developed medium intensity refers to areas that had 50-79% of the land cover as constructed materials, typical of suburban areas. Developed high intensity land had less than 20% vegetation, and 80-100% of the total land cover was constructed materials, as is typical in urban centers (NOAA Coastal Change Analysis Program (C-CAP) Regional Land Cover Database 2016).

Average distance to roads for each individual turtle was determined through plotting the GPS coordinates in ArcMap (version 10.4.1). Road density was calculated as the total length of roads within a one-kilometer radius of each turtle's 95% MCP home range using ArcMap (version 10.4.1). The effect of road density on home range area was analyzed using linear regression, separately for each species, using RStudio (RStudio Team 2020). Sex ratios were determined to differ from parity using Chi-squared tests (Zar 1984). Eastern box turtles were determined to be adults if the carapace length was greater than 100mm, and had greater-than or equal to nine annuli, or if growth rings were too worn to be distinctive (Dodd 2002). Eastern box turtles were considered juveniles if the carapace length was less than 90 mm and had less than or equal to seven annuli (Dodd 2002). Blanding's turtles were considered to be adults if they had greater than 14 annuli, or if growth rings were too worn to be distinctive (Congdon et al. 1993). Kaplan Meier known-fates models were used to estimate survivorship of the two focal species using the package "Survival" in RStudio (Therneau 2020, RStudio Team 2020).

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