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The Spatial Ecology and Habitat Selection of a Spotted Turtle (Clemmys guttata) Population in Southwest Michigan

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The Spatial Ecology and Habitat Selection of a Spotted Turtle (*Clemmys guttata*) Population in Southwest Michigan

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Thesis Approval Form

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STATE UNIVERSITY

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Dedication

This thesis is dedicated to my parents, Marisa and Tom Coury, who have been my two biggest supporters when it comes to me following my passion for working with the environment. You both have been my inspirations in furthering my education in this field. Thank you for your continuous support and encouragement, your willingness to read my papers, listen to my presentations, and learn all that is to be known about spotted turtles. I love you both unconditionally.

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Abstract

Turtles are arguably the most threatened group of vertebrates on the planet. Anthropogenic influences such as habitat loss and fragmentation, road mortality, subsidized predators, climate change, and illegal collection have contributed to their global decline. Understanding which isolated populations of turtles are viable despite these synergistic threats is crucial for making conservation and management decisions. In Michigan, the spotted turtle (*Clemmys guttata*) is a threatened species subjected to many negative anthropogenic influences that accelerate its rapid population decline. In order to properly sustain their populations, the goal of my research was to investigate relevant factors that help us understand the influences on this population's viability, including their spatial ecology and habitat selection. We trapped and marked turtles within vernal pool and fen habitats in southwest Michigan. VHF radio telemetry and mark-recapture techniques were used to track turtles (*n* =22) across two active seasons (Spring-Fall 2020; Spring-Fall 2021). This allowed us to delineate home ranges, assess habitat selection, and detect influences on their daily movement patterns. Male turtles exhibited larger $\mathrm{wAKDE_c}$ home ranges (3.71 ha SE ± 0.52 ha) than females (2.31 ha SE ± 0.38 ha) across the two field seasons. Home ranges were much smaller than those of turtles from other populations in similar northern latitudes. Smaller home ranges were attributed to easily accessible resources or confinement within the landscape. Precipitation, minimum, and average temperatures significantly influence the turtles' daily movement rates. Habitat selection was evident at both 2nd and 3rd order spatial scales, with emergent wetland as one of the most selected habitats and dry-mesic forest as the most avoided. We recommend that management agencies conduct analyses of this species' habitat selection and spatial ecology at multiple scales. These results can be applied to managing populations in similar latitudes that occur in similar habitats.

Table of Contents

List of Tables

Chapter Two

List of Figures

Chapter Two

Chapter Three

Abbreviations

ACF – autocorrelation function

MDDT – mean daily distance traveled

AIC – Akaike information criterion

ANOVA – analysis of variance

CI – 95% confidence intervals

cm – centimeters

ESA – Endangered Species Act

g – grams

GPS – global positioning system

ha – hectares

HDR – highest density region

ID – Identification number

KDE – Kernel Density Estimation

MANOVA – multivariate analysis of variance

m – meters

mm – millimeters

MCL – midline carapace length

MCP – Minimum Convex Polygon

No. – number

PCA – Principal Component Analysis

pHREML – perturbative Hybrid Residual Maximum Likelihood

SE – standard error

SVF – semi-variance function

UD – Utilized Distributions

USA – United States of America

U.S. – United States

USGS – United States Geological Survey

VHF – very high frequency

wAKDE$_c$ – weighted, area-corrected autocorrelated Kernel Density Estimation

Chapter One: Introduction

Introduction

Turtles are arguably the most threatened group of vertebrates on the planet, with almost two-thirds of the known 365 turtle species listed as threatened, endangered, or extinct (Lovich et al., 2018). Their roles, ranging from nutrient redistribution to stimulating natural energy flow, aid in maintaining trophic balance within their ecosystems (Stanford et al., 2020). One of the most threatened branches of turtles is freshwater turtles, with over 60% of their 159 species considered threatened (Bour, 2008). The United States (U.S.) hosts 18 percent of the world's tortoises and freshwater turtle species (Rhodin et al., 2018). Unfortunately, these species are constantly subjected to negative anthropogenic pressures such as habitat loss and fragmentation, road mortality, illicit collection and trade, and climate change (Malcolm & Markham, 2000). Because of these anthropogenic influences, 40 % of those turtle species in the U.S., such as the Blanding's turtle (*Emydoidea blandingii*), diamondback terrapin (*Malaclemys terrapin*), gopher tortoise (*Gopherus polyphemus*), and spotted turtle (*Clemmys guttata*) are facing extinction (Buhlmann et al., 2009). Furthermore, as these species face accelerated losses in their populations across their geographic range, it becomes critical to devise proper management plans to sustain the remaining populations.

The conservation and management of vulnerable species with low detection probabilities, like many freshwater turtles, requires efficient planning. Expanding our knowledge of the ecological elements that drive a species spatial ecology and habitat selection can offer managers a better understanding of their life histories and habitat requirements (Budischak et al., 2006). Over the past few decades, radio-telemetry has become increasingly used for tracking small, cryptic species (Refsnider et al., 2011). Very high frequency (VHF) radio-telemetry is typical for tracking turtles. Using VHF radio-telemetry in studies affords insight into elements that build up the framework of their spatial ecology (Hulbert, 2020; Millar & Blouin-Demers, 2011; Olivier et al., 2010). For instance, VHF telemetry estimates an individual's movement patterns, home range, and selection of habitats (Fieberg & Kochanny, 2005; Fujisaki et al., 2014).

The spotted turtle is a small, cryptic freshwater turtle species endemic to the Eastern and Midwest U.S. and Southern Ontario, Canada (Litzgus & Mousseau, 2006). This rare turtle is a wetland-dependent species whose populations are subjected to the familiar litany of anthropogenic influences that many other species face, such as poaching, habitat fragmentation, and climate change, directly contributing to their decline (Chandler et al., 2020; Ernst, 1976; Rasmussen & Litzgus, 2010). Within the U.S., spotted turtle populations have declined by over 50 % within the last 75 years (van Dijk, 2011). Contrary to Canada, where they are listed as an endangered species, the spotted turtle lacks federal protection within the United States, and as of 2015, they are under review for federal listing under the U.S. Endangered Species Act (ESA; Chandler et al., 2019; Howell & Seigel, 2018; van Dijk, 2011). Geographical locations such as the eastern U.S. and southern Ontario have well-studied spotted turtle populations (Ernst, 1970, 1976; Litzgus & Mousseau, 2004a, 2004b, 2006; Rasmussen & Litzgus, 2010); however, there is a paucity of knowledge on the more imperiled Midwest U.S. populations (Litzgus & Brooks, 1998; Rasmussen & Litzgus, 2010; Rowe et al., 2013; van Dijk, 2011).

Species that extend across an expansive geographic range vary in their ecological characteristics, habitat selection, spatial ecology, and life-history traits (Iverson et al., 1997; Reeves & Litzgus, 2008). For example, spotted turtles occur in disconnected populations across the eastern Midwest, ranging from Maine down to Florida and throughout the southern shores of the Great Lakes, from Ohio, Illinois, southern Michigan, and Ontario (Lee, 2000; Litzgus &

Mousseau, 2004b). Consequently, management protocols for broad-ranging species, such as the spotted turtle, should be specific to the location. For instance, management guidelines on spotted turtle populations from their southern distribution would not be applicable for populations within the Midwest region due to differences in their ecology (Chandler et al., 2019; Reeves & Litzgus, 2008). Furthermore, expanding study efforts in areas with significant knowledge gaps on habitat selection and spatial ecology could provide efficient conservation tactics for contiguous spotted turtle populations.

In the state of Michigan, the spotted turtle's conservation status is currently listed as threatened (legally protected), with their state ranking labeled as "Imperiled" (S2; Lee, 2000). Despite their threatened status and rapidly declining populations, spotted turtles are understudied in Michigan (Lutz, 2009; Moriarty, 1998), with habitat loss considered one of the greatest threats in this state (Lee, 2000). This species occurs in a wide variety of wetlands that have become increasingly susceptible to habitat degradation and fragmentation (Howell et al., 2019; Oxenrider et al., 2018; Stanford et al., 2020). Agricultural activities and industrial development are some of the root causes of the destruction and pollution of wetlands in the Midwestern United States (Rizkalla & Swihart, 2006). The loss of these wetlands has subsequently led to the decline of many wetland-dependent species, including the spotted turtle (Anthonysamy et al., 2014; Gibbs, 1993). Furthermore, focusing on this species habitat selection and vagility within and between wetlands can help researchers further understand species-habitat relationships while providing long-term population management recommendations, particularly in areas with more significant knowledge gaps, such as Michigan.

Purpose

This project aimed to further our understanding of the factors affecting spotted turtles' spatial ecology, movement patterns, and habitat selection within isolated wetlands. This study focused on a spotted turtle population in Southwestern Michigan, previously studied over ten years ago (Rowe et al., 2012, 2013). We used radiotelemetry to quantify each individual's movement patterns, home range size, and habitat selection at multiple scales to determine weather and individual variation influences. With this study, we seek to develop future conservation management plans for this population and others within similar geographic latitudes.

Scope

Chapter two focuses on a spotted turtle population's spatial ecology and habitat selection at two spatial scales within an isolated wetland in Southwest Michigan. Radio telemetry was used to gather turtle locations throughout their active season across two years to determine home ranges, movement patterns, and habitat selection at the landscape and home range scale.

Assumptions

1. We assume that radiotelemetry has no adverse effects on the turtles and does not inhibit their normal behavior.
2. We assumed that spotted turtle home range sizes were independent for each turtle within the population.
3. We quantified habitat use and availability using a Euclidean distance analysis (EDA) and therefore assumed habitat use was independent for each turtle within the population.
4. We assumed that the spotted turtle's active season would not occur before April or after October.

Objectives

My objectives of this study were to 1) observe and quantify home ranges of spotted turtles across two active seasons (May-September of 2020 and 2021), comparing differences by sex and year, 2) to determine if sex, year, and environmental variables influence movement patterns, 3) to quantify habitat use versus availability at two spatial scales, and 4) provide management recommendations for this population.

Significance

This project's significance focuses on closing the knowledge gap on spotted turtles' general ecology and life histories in Michigan. A long-term study on a spotted turtle population conducted by Howell et al. (2019) revealed that within a protected habitat over a 30- year time frame, populations decreased by 49%. Consequent to the population decline, the researchers reported an increased percentage of larger individuals within the population, demonstrating a lack of recruitment (Howell et al., 2019). This study can be compared to similar declining populations across the species range, highlighting the necessity for active management within their habitats. However, effective active management cannot be accomplished when there is a paucity of information on species ecology and life history, such as in Michigan. Therefore, this study will provide crucial information on spotted turtles' spatial ecology in Michigan, providing insight into their use, thermal tolerance, behavior, and distributions within their rare ecosystems.

Definitions

Anthropogenic Influences

Relating to the influence of human beings on nature

Cryptic

An animal with physical attributes that camouflage them within its natural environment

Endangered

At the serious risk of extinction

Endemic

Native and restricted to a certain environment or habitat

Mark-Recapture Technique

Method used to estimate the population size of wild animals and track movements

Spatial Ecology

The study on the roles of space on ecological processes and its effects on ecological patterns

Chapter Two:

Spatial ecology and habitat selection of a spotted turtle population in southwest Michigan

Abstract

Spotted turtles (*Clemmys guttata*) are small, aquatic turtles whose populations have dramatically declined due to habitat fragmentation, poaching, climate change, and subsidized mesopredation. In Michigan, spotted turtles are listed as a threatened species and are currently under review for federal listing under the U.S. Endangered Species Act. We currently lack information about these more imperiled Midwest U.S. populations than the populations across the eastern U.S. and southern Ontario. The objective of our study was to investigate home ranges, movement patterns, and habitat selection of spotted turtles in Southwest Michigan to help fill in this knowledge gap. We trapped and marked turtles and used VHF radio-telemetry to track 22 turtles (12 males, 10 females) across two active seasons (May-October 2020 and 2021) in a prairie fen. This allowed us to delineate home ranges, assess habitat selection, and assess influences on their daily movement patterns. Male turtles exhibited larger wAKDE_c home ranges (3.71 ha SE ± 0.52 ha) than females (2.31 ha SE ± 0.38 ha) across the two field seasons. Home ranges were much smaller than those of similar northern latitudes. Smaller home ranges were attributed to easily accessible resources or confinement within the landscape. Precipitation, minimum, and average temperatures significantly influence the turtles' daily movement rates. Habitat selection was evident at both 2nd and 3rd order spatial scales, with emergent wetland as one of the most selected habitats and dry-mesic forest as the most avoided. We recommend that management agencies conduct analyses of this species habitat selection and spatial ecology at multiple scales. These results can be applied to managing populations in similar latitudes that occur in similar habitats.

Introduction

Understanding an animal's spatial ecology – its use of space within the dynamics of a landscape – is crucial when managing wildlife. As anthropogenic influences (e.g., habitat fragmentation) continue to modify the composition of a landscape, species' energetic and biological fitness costs are often incurred (Beyer et al., 2010; Rechetelo et al., 2016), and subsequently, species at risk, like many freshwater turtles, are directly impacted (Buhlmann et al., 2009). For instance, due to climate change, severe droughts in temporary wetlands increase transition probabilities between water sources and sharply affect turtle survival rates(Owen-Jones et al., 2015). Furthermore, during these times of drought, individuals are presented with a choice of seeking external water sources or aestivating. Consequently, those searching for water are subjected to higher mortality risks, while those that are aestivating are more susceptible to desiccation (Roe et al., 2009). The responses of an animal to its environment are primarily influenced by its spatial ecology and habitat selection (Buchanan et al., 2017). Therefore, understanding the factors that influence a species spatial ecology and habitat selection can help to mitigate these threats and manage at-risk populations and their habitats effectively.

Home ranges and movement patterns broadly reflect an animal's physiological and ecological needs and make up the framework of their spatial ecology (Millar & Blouin-Demers, 2011; Roe & Georges, 2008). Burt (1943) defines a home range as the extent to which an animal roams and spends most of its time performing "normal activities." Home ranges are also described as an animal's understanding of its environment (Powell & Mitchell, 2012), defined by the most minimal contoured area representing a given percentage of an animal's total utilization (Jennrich & Turner, 1969; Litzgus & Mousseau, 2004a). Understanding an animal's home range can shed light on the elements that drive their use of space while delineating areas where an individual reproduces, acquire resources, and survives (Ross et al., 2019). Furthermore, an animal's home range is inextricably linked to its movement patterns (Manly et al., 2007). Their movement patterns reflect their response to the environmental conditions that satisfy their needs to seek, access, and exploit resources (Van Moorter et al., 2016). Therefore, analyzing patterns in movement reveals underlying factors that constrain their distributions, such as landscape configuration and habitat availability, and highlights essential habitat types that benefit their population's ecology (Millar & Blouin-Demers, 2011; Sindorf et al., 2009).

The study of an animal's use of habitats relative to their availability, also known as habitat selection, elucidates their preference for various landscape features at different spatial scales (Paterson et al., 2012; Rasmussen & Litzgus, 2010). This hierarchal process assesses habitat selection at spatial scales relevant to their ecology, ranging from the species geographical range to an individual's home range (Aebischer et al., 1993; Johnson, 1980; Rozylowicz & Popescu, 2013). Observation of habitat selection at multiple spatial scales is essential when discerning if habitat selection occurs in a given population (Johnson, 1980; Rasmussen & Litzgus, 2010). Respectively, Johnson's (1980) second-order selection – the selection of habitats within the home range from the population range, and third-order selection – the selection of habitats within the home range, provides researchers with an understanding of habitat selection at both coarse- and fine-scales. Studying habitat selection at multiple ecologically relevant spatial scales can assist researchers in characterizing habitats that meet an animal's biological or physical needs and identify noncontiguous habitat patches that can impede dispersal (Conner & Plowman, 2001; Edge et al., 2010; Johnson, 1980). Moreover, these scales can assist conservation practitioners with characterizing habitat quality while offering insight into resources needed to enhance an animal’s habitat (Manly et al., 2007; Rasmussen & Litzgus, 2010).

Freshwater turtles are some of the most threatened vertebrates globally, with over 63% of their species listed as threatened, endangered, or extinct (Lovich et al., 2018). There is an imperative need for conservation planning for many of these species (Tickner et al., 2020), as their populations have declined due to negative anthropogenic influences such as habitat fragmentation, climate change, poaching, and subsidized mesopredation (Sterrett et al., 2015; Yagi & Litzgus, 2012). This study focused on threatened spotted turtles (*Clemmys guttata*), a small freshwater turtle whose range extends throughout the Atlantic Coastal Plain and Midwest states of the U.S. and Southern Ontario, Canada (Ernst & Zug, 1994; Litzgus & Mousseau, 2004a). Spotted turtles occur in a mosaic of rare and threatened wetlands such as bogs, marshes, vernal pools, and prairie fens (Kost et al., 2007; Cohen et al., 2020). They are commonly referred to as semi-aquatic for wetlands and upland habitats and often exhibit high site fidelity between the two habitat types (Buchanan et al., 2017). Unfortunately, over the last few decades, this cryptic species has experienced a decline of more than 50% of its historical population within the United States (U.S.; Dickson, 2013), attributed to poaching, road mortality, climate change, pollution, and urban development (Pittman & Dorcas, 2009; Rizkalla & Swihart, 2006; Russell et al., 2002; Tickner et al., 2020). These factors have resulted in the isolation of populations, limited their dispersion between habitat patches, and increased their susceptibility to subsidized predation and illicit collection (Bennett et al., 2011; Feng et al., 2019). Fortunately, in 2013, the spotted turtle received international protection by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) under CITES Appendix II (CITES, 2013), and are currently under review for federal listing under the United States Endangered Species Act (US Fish and Wildlife Service (USFWS, 2015; van Dijk, 2011).

Although extensive research on the spatial ecology and habitat selection of spotted turtles has been conducted in the Eastern United States and Ontario, Canada (Haxton & Berrill, 1999; Litzgus & Mousseau, 2004a; Rasmussen & Litzgus, 2010; Ward et al., 1976), information on populations in the Midwest U.S. is limited (Feng et al., 2019; Lewis et al., 2004; Rowe et al., 2013; Ward et al., 1976). Spatial ecology and resource selection of spotted turtles varies by population and geographic location, making generalized management problematic (Chandler et al., 2020). Therefore, it is critical to developing strategies tailored to a population's geographic location.

We used radio telemetry to study home ranges, movement patterns, and habitat selection of an isolated spotted turtle population inhabiting a rare prairie fen in southwest Michigan. The objectives of this study were to (1) determine the influence of body size (midline carapace length), sex, and year on home range size, (2) define habitat selection at two different spatial scales (2^{nd} order and 3^{rd} order; Johnson, 1980) and identify overwintering locations, and (3) determine whether turtle movement is governed by sex, time of year, or other weather conditions

Materials and Methods

Study Site

Our study site (53 ha), located in Barry County, Michigan (45° N, 85° W), is characterized by a mosaic of relatively undisturbed palustrine communities, including southern shrub, forested wetlands, emergent wetlands, and vernal pools within state-owned land (Fig.2). Surrounding the site is a landscape matrix of agricultural fields, roads, and developed areas. We are withholding the exact site location to prevent illicit trade and collection.

The central portion of the study site is prairie fen (13 ha), a rare groundwater-fed ecosystem characterized by alkaline organic soils and graminoid-dominated vegetation (Cohen et al., 2020; Kost et al., 2007). This habitat is a hotspot for biodiversity, as it harbors many rare plant and animal species, including willow aster (*Aster praealtus*), Jacob's ladder (*Polemonium reptans*), spike-rush (*Eleocharis radicans*), tamarack tree crickets (*Oecanthus laricis*), eastern massasaugas (*Sistrurus catenatus*), eastern box turtles (*Terrapene carolina carolina*), and spotted turtles (*Clemmys guttata*). Intermittently throughout the spring and summer, this wetland is often submerged in water resulting from heavy snowmelt or precipitation. Deer trails, kettle ponds, and wet depressions within the fen are periodically filled with water greater than 10 cm deep and used by an array of biota for feeding, thermoregulation, and more effortless locomotion (Rowe et al., 2013). In addition, patches of sphagnum moss and scrub/shrub are scattered throughout the fen and used for cover, thermoregulation, aestivation, and overwintering for various species. Encompassing the fen is a closed-canopy, oak-dominated forest (dry-mesic southern forest) that contains multiple vernal pools. These rare ephemeral pools are unique, intermittent wetlands that experience cyclical periods of flooding during the spring and late fall and drought throughout the summer (Thomas et al., 2010). They provide refuge for various functionally specialized organisms that can endure and often rely on the hydrological regime's dramatic changes (Zedler, 2003).

Data Collection

From May-early June of 2020 to 2021, we captured spotted turtles opportunistically throughout the prairie fen and used hoop traps (Promar TR-503) baited with sardines within the vernal pools scattered around the site (Fig. 3). Turtles were marked individually by notching a unique combination of scutes using a triangular file (Cagle, 1939). We collected morphological measurements of each turtle captured and determined sex by secondary sexual characteristics (e.g., males have concave plastrons and relatively long pre-cloacal tail lengths). Midline carapace length (MCL, to the nearest mm) was measured using calipers (150 mm; Vernier Digital Caliper, Edgewood, New York), and turtles were weighed to the nearest gram using a spring scale (Pesola Medio-Line Spring Scale, Forestry Suppliers, Jackson, Mississippi).

Twenty-two turtles (*n*=12 males, *n*=10 females) were outfitted with very high frequency (VHF) radio transmitters (model R1645, Advanced Telemetry Systems, Fish and Wildlife, Isanti, Minnesota, USA) onto the posterior carapace using J-B WaterWeld epoxy (J-B Weld Company, Sulphur Springs, Texas, USA; Fig. 4). Transmitter and epoxy weights were <5% of each individual's body mass. All turtles were released at their initial capture points once epoxy dried and transmitters were secured.

Turtles were radio-tracked throughout their active seasons (May through September 2020 and 2021). For both years, turtles were located 3-4 times a week from May-July and 1-3 times a week from August to October, using a three-element Yagi antenna and an R410 Scanning radio receiver (Advanced Telemetry Systems Fish and Wildlife, Isanti, Minnesota, USA). Once individuals were located, coordinates were recorded using a handheld GPS and uploaded to RStudio Team (2019) and ArcGIS v. 10.4.1.

Home Range Analysis

Home ranges were estimated for each sex over two activity seasons. We used two different home range estimations: 95% Minimum Convex Polygons (MCPs; Anderson, 1982; Bekoff & Mech, 1984) and autocorrelated kernel density estimation (AKDE) using 95% kernels (Fleming et al., 2015). We estimated the 95% MCP using the '*mcp*' function from the *adehabitatHR* package in R (Calenge, 2006). We chose to use an area-corrected, optimally weighted $AKDE_c$ ($wAKDE_c$) to estimate home ranges and core ranges of this population, as this method corrects for irregular data sampling, small sample size, and temporal sampling bias (Fleming et al., 2018), and outperforms the KDE and MCP home range estimations (Averill-Murray et al., 2020). To assess the $wAKDE_c$ home range and core area for each turtle, we used the *ctmm* R package (Fleming et al., 2019), only including turtles with ≥ 20 relocations to ensure adequate sampling (Paterson et al., 2012). We first checked for each individual's range residency (their tendency to remain within their home range) by calculating the semi-variance function (SVF) through the '*variogram()'* function, which allowed us to unbiasedly observe the autocorrelation structure (Calabrese et al., 2016; Silva et al., 2021) RStudio Team, 2021). We then tested for movement models that would explain the autocorrelated structure of the movement data by using an automated model *'ctmm.select'* with the perturbative hybrid residual maximum likelihood (pHREML) as the default parameter estimation method (AIC_c; Calabrese et al., 2016; Silva et al., 2021). Perturbative Hybrid REML is the most comprehensively implemented method that improves (co)variance for small effective and absolute sample sizes (Silva et al., 2021). Considering that our autocorrelated tracking data was irregularly sampled with a small sample size, the pHREML fitted-weighted optimization was the most suitable home range method to increase spatial resolution and correct irregular sampling (Fleming et al., 2018; Silva et al., 2021). Movement models were selected and fit into a $wAKDE_c$ using the '*akde'* function from the *ctmm* package to estimate individual turtle's home range sizes (ha), extracting 50% and 95% kernels as percentile level ranges for all individuals (±95% CI; Calabrese et al., 2016; Silva et al., 2021). We assumed 50% kernels as the animal's 'core' activity ranges, representing 50% of its highest density region (HDR). The entire home range was represented by the 95% kernel, maintaining 95% of the probability distribution of all possible locations determined from the dispersal of all possible paths (Fleming et al., 2015). Individual turtle home ranges were extracted as spatial polygons and projected into ArcGIS v. 10.4.1 (ESRI, 2021).

We used a simple log-transformed linear regression to determine whether there was a linear relationship between a 95% $wAKDE_c$ home range size and mean carapace length (MCL; mm) and mean mass (g). Home ranges (95% $wAKDE_c$) and core ranges (50% $wAKDE_c$) were analyzed using a two-way analysis of variance (two-way ANOVAs) on log-transformed data to examine the effects of sex, year, and sex X year on mean home range sizes (ha). We used a Tukey HSD test for a post-hoc analysis to identify differences in the variables' outcomes if the results were significant. Percent of 95% $wAKDE_c$ home range overlap was assessed for individuals tracked for both years (*n*=14), and the percent of 95% MCP home range overlap was measured for individuals (*n*=2) that were tracked in our study and a previous study by Rowe et al. (2013). The "Intersect" tool within the Analysis Tools in ArcMap v. 10.4.1, was used to extract the area of overlap between an individual's home range polygons. The formula used to calculate percent overlap was represented by:

$$[\text{Area}_{\text{Intersect}} / (\text{Area}_{\text{Homerange1}} + \text{Area}_{\text{Homerange2}} - \text{Area}_{\text{Intersect}})] \text{ x } 100$$

Mean annual percent home range overlaps were compared by sex using a Mann-Whitney U test. Lastly, we used a Spearman's rank correlation test to determine if there was a relationship between the size of an individual's 95% MCP home range and their 50% $wAKDE_c$ core range, as MCPs are often known to underestimate home ranges (Averill-Murray et al., 2020) and represents as the smallest convex polygon that contains X% of the individual's locations (Noonan et al., 2019). We used the conventional 95% MCP to compare home ranges with past studies, as it is the most conventional and commonly applied home range method, despite its flaws (Averill-Murray et al., 2020). Significance was evaluated at an alpha value of 0.05. We tested for normality violations ($P < 0.05$) and homogeneity of variance using a qqplot and histogram, along with Levene's test and Shapiro Wilk's test in RStudio (RStudio Team, 2021).

Movement Analysis

We estimated movement metrics for each turtle ($n = 22$) by quantifying the straight-line distance (m) and time lag between consecutive relocations along a movement track throughout each active season, using the *move* package in R (Kranstauber et al., 2017). We accounted for the non-normal distribution of movement data through the utilization of Poisson distribution. We calculated each individual's mean daily distance traveled (MDDT) by taking each successive step-length (m) recorded and dividing it by the number of days elapsed since the last location. We then took the mean MDDT for each month across the two years using individuals as replicates. A two-way ANOVA with $\log_{10}$ transformed data was used to observe the effects of date, sex, and sex X date on MDDT.

We followed this by performing a principal components analysis (PCA) to quantify and compare the interrelationship amongst environmental parameters, time of year, and MDDT, using individual turtles as replicates (weather data was retrieved from the Michigan Enviro-weather Automated Weather Station Network, Pierce Cedar Creek Institute, Hastings, MI, USA). Weather stations collected daily data on minimum temperature (°C), maximum temperature (°C), average temperature (°C), precipitation (mm), and solar radiation (kJ/m^2). In previous research, air temperature, solar radiation, and precipitation have all been essential determinants of turtle activity (Clavijo-Baquet & Magnone, 2017; Ficetola et al., 2009; Montero et al., 2018). We took averages of daily environmental data for each month across the two years sampled to use as predictor variables within the ordination. The predictor variables were explored at two temporal scales: active months (May, June, July, August, and September) and years (2020 and 2021).

Points in the ordination represented an individual’s MDDT; with point size increasing with MDDT. To further explore these relationships, we regressed MDDT against the factor scores with PC1 and PC2, using simple linear regressions. All data were tested using R statistical software v. 4.1.1 (R Development Core Team, 2021) for normality using a Shapiro-Wilk's test and equal variance with a Levene’s test setting the alpha level to 0.05, and were transformed if not normal.

Habitat Selection Analysis

We created habitat classification maps for the study site, defined in ArcMap 10.4.1 using the USGS EROS archive ArcGIS data layer, based on 1:12,000 infrared stereo aerial photography (USGS, 2014), along with ground-truthing and measurement using a handheld GPS unit (Garmin, Kansas City, Kansas USA). Habitats were reclassified based on natural community descriptions in Kost et al. (2007). We classified land cover into 10 general land classes in ArcMap 10.4.1: (1) Emergent wetland, (2) Dry-mesic Forest, (3) Scrub/Shrub, (4) Open Water, (5) Coniferous, (6) Open Canopy, (7) Emergent Marshland, (8) Developed, (9) Agriculture, and (10) Vernal Pool (Table 1).

We investigated habitat selection at two biologically relevant spatial scales based on Johnson's (1980) hierarchical selection approach. We considered 2nd order (population range) – selection of home range from within the population range, and 3rd order (home range scale) – selection within the individual’s home range (Edge et al., 2010; Paterson et al., 2012). Habitat selection was analyzed using a Euclidean Distance Analysis (EDA) to measure the straight-line distance of each location to the nearest available habitat type (Conner & Plowman, 2001). This assessment provided an estimate of habitat use vs. availability and determined an individual’s preference or avoidance of a particular habitat type within the spatial scale of interest (Benson, 2013; Conner & Plowman, 2001).

To satisfy the requirements of 2nd order selection, we had to define a population range. We defined the population range by merging all 95% $\mathrm{wAKDE_c}$ home ranges from both field seasons into a single polygon in ArcMap (v. 10.4.1) and buffering that polygon by 250 m (the maximum width of an AKDE home range) to fully encompass the limits of available habitat (Fig. 5). We generated 1,299 random points in a uniform random distribution (Conner & Plowman, 2001), equal to the total number of radio locations for all individuals across both years within the population range boundary (128.4 ha; Paterson et al., 2012). Next, we measured Euclidean straight-line distances from each point to the nearest representatives of each habitat type in ArcMap (Conner & Plowman, 2001). A ratio of use vs. availability was created for each individual (i) for each habitat type (j) for both spatial scales. The ratio formula was represented as,

$$d_i = u_{ij}/r_{ij}$$

where u_{ij} is defined as use and r_{ij} as availability. This ratio allowed us to evaluate if habitats were preferred ($d_{ij} < 1$), avoided ($d_{ij} > 1$), or randomly used ($d_{ij} = 1$; Conner et al., 2003). For selecting home ranges within the population range (second-order), we defined habitat use (u_{ij}) as the mean distance from random points within an individual's home range to the nearest representative habitat type within the population range. We measured habitat availability (r_{ij}) for second-order as the mean distance from random points within the population range to the nearest available habitat type within that same range. Similar to the population range, to quantify habitat selection within individual home ranges (third-order), we merged home ranges of individuals tracked across both field seasons and those tracked for one field season for the analysis. At the third-order scale, we determined habitat use (u_{ij}) as the mean distance from telemetry points within each individual's home range to the nearest available habitat type within their home range. Habitat availability (r_{ij}) was measured as the mean distance from random points within each individual's home range to the nearest available habitat type within the same range. The selection scale was analyzed using a one-way MANOVA on square root-transformed data to test if the mean distance ratios (d_{ij}) for each habitat differed significantly from a vector of 1's, using individual turtles as replicates. The ratios further provided evidence of habitat selection at the selected spatial scale ($d_{ij} \neq 1$; Paterson et al., 2012). If there was evidence of habitat selection, we followed with square root-transformed one-sample *t*-tests using a Bonferroni correction for multiple comparisons (2^{nd} order: $\alpha = 0.05/10$ habitats = 0.005; 3^{rd} order: $\alpha = 0.05/6$ habitats = 0.007), to determine which habitat ratios were significantly different from one. We followed with a Tukey HSD as a pairwise comparison test to produce a relative rank of habitats based on preference.

Lastly, we identified overwintering locations by visual confirmation (77%), or if there was no visual encounter, overwintering sites were determined by the last tracked location (23%). Visual observation of overwintering sites on ArcMap and in the field provided additional insight on possibilities of site fidelity. All reported analyses included a standard error (SE) represented by a plus-minus (±) symbol.

Results

We radio-tracked 22 adult spotted turtles (12 males, 10 females) and collected 1,299 radio-locations across two years. Due to equipment failure and loss of turtles within the early stages of the telemetry surveys, we only considered 17 turtles (*n*= 7 females, *n*= 10 males) for 2020 and 19 turtles (*n*= 10 females, *n*= 9 males) for the 2021 data analyses. Out of the 22 total turtles tracked, 14 of those turtles (*n*= 7 females, *n*= 7 males) were tracked in both years;

however, field seasons were considered independent samples for home range and habitat selection analyses. The number of relocations ranged from 16-40 locations per turtle during each field season, including those with equipment failures (Table 2). Male (*n*=59) midline carapace length (MCL) averaged 90.09 ± 1.18 mm and mass average 118.05 ± 3.41 g. Female (*n*= 73) MCL averaged 83.33 ± 1.27 mm and mass averaged 110.12 ± 4.17 g.

Home Ranges

Spotted turtles (*n*= 22) exhibited a mean 95% wAKDE$_c$ home range of 3.63 ± 0.53 ha for 2020 and 2.53 ± 0.43 ha for 2021. For core ranges (50% wAKDE$_c$), individuals averaged 0.90 ± 0.14 ha in 2020 and 0.54 ± 0.11 ha in 2021. Spotted turtles annual home ranges, represented as 95% MCP, averaged 1.31 ± 0.25 ha for 2020 and 1.26 ± 0.21 ha for 2021. Raw mean home ranges are summarized for male and female turtles in Table 3. For turtles tracked across both field seasons (*n*=14), mean 95% wAKDE$_c$ home ranges averaged 3.24 ± 0.98 ha during 2020 and 2.27 ± 0.47 ha in 2021. Similarly, individuals tracked across both field seasons averaged 0.80 ± 0.11 ha for core ranges (50% wAKDE$_c$) in the year 2020 and 0.47 ± 0.13 ha in 2021. Annual 95% wAKDE$_c$ home range overlap for each individual varied 11 – 68% (mean = 35.6 ± 5.2 %). Mean annual overlap for females (47 ± 8%) differed significantly from males (24.7 ± 3.3 %; Mann – Whitney *U*-test = 42, P= 0.026). Our Spearman's rank correlation test revealed a positive relationship between the mean annual 95% MCP home ranges and 50% wAKDE$_c$ home ranges (r_s= 0.71, P<0.0001; Fig. 6). Therefore, further analyses focused on a mean 50% wAKDE$_c$ representing the core annual home range, as it was comparable with the 95% MCP home ranges.

We found no relationship between body size (MCL) and 95% home range size (R^2= 0.001, $F_{[1,34]}$= 0.02, P= 0.87), nor 50% wAKDE$_c$ core ranges (R^2= .00004, $F_{[1,34]}$= 0.001, P=

0.97). However, home ranges (R^2= 0.14, $F_{[1,34]}$= 5.67, *P*= 0.023; Fig. 7), and core range (R^2= 0.17, $F_{[1,34]}$= 6.95, *P*= 0.012; Fig. 8) increased with body mass. There was no effect of year ($F_{[1]}$ = 3.47, *P*= 0.072), sex ($F_{[1]}$ = 2.54, *P*= 0.12), nor sex X year ($F_{[1,1]}$ = 0.18, *P*= 0.67) on the size of mean annual core ranges. Similarly, annual 95% $wAKDE_c$ home ranges did not differ in size between years ($F_{[1]}$ = 2.046, *P*= 0.162) nor sex X year ($F_{[1,1]}$ = 0.090, *P*= 0.77); however, sex did have a significant influence on the size of mean 95% $wAKDE_c$ home ranges ($F_{[1]}$= 4.55, *P*= 0.041; Fig. 9). Male turtles (3.71 ± 0.52 ha) had a larger mean annual home range than females (2.31 ± 0.38 ha; $F_{[1]}$ = 4.554, *P*= 0.041).

Movement

In 2020, straight-line distance movements between successive locations ranged from 0 – 348.14 m, with 76% of those distances less than 50 m and 14% greater than 100 m. In 2021, straight-line distance movements between successive locations ranged from 0 – 314.6 m, with 81% of those distances less than 50 m, and only 7.4% were greater than 100 m. Total distance traveled during one successive active season ranged from 385.72 – 1774.41 m in 2020 and 623.34 – 2297.71 m in 2021. Mean daily distance traveled (MDDT) during the active season ranged from 0.44 – 43.64 m/day in 2020 to 0 – 39.41 m/day in 2021. Mean daily distance traveled (MDDT) was not significantly affected by sex (two-way ANOVA; $F_{[1]}$= 0.17, *P*=0.69), as males traveled 10.9 ±1.09 m/day on average, and females similarly traveled a mean of 10.6 ±0.98 m/day (Table 4). Sex and its interaction with date also did not have a significant impact on MDDT (two-way ANOVA; $F_{[1,9]}$= 0.50, *P*= 0.874), but date alone did have a significant influence on MDDT ($F_{[9]}$= 8.13, *P*<0.001; Fig. 10).

We saw the majority of the population's movement occurring during May, June, and July for both seasons. During the spring and mid-summer months, the mean daily distance traveled ranged from 12.1 ± 1.34 m/day – 17.0 ± 2.00 m/day across both field seasons. The mean daily distance traveled was significantly reduced during August and September for both field seasons, with average distances ranging 1.17 ± 0.34 m/day – 6.52 ± 1.48 m/day. In 2020, MDDT was significantly higher in June (13.6 ± 2.01 m/day) compared to August (6.52 ± 1.48 m/day, $P < 0.05$), and MDDT was significantly higher in June and July (10.8 ± 1.75 m/day) compared to September (6.89 ±2.63 m/day, $P < 0.05$; Table 5). In 2021, turtles had significantly higher MDDT for May (17.7 ± 2.07 m/day), June (15.7 ± 2.18 m/day) and July (13.3 ± 1 m/day) compared to August (6.02 ± 0.96 m/day) and September (1.17 ± 0.34 m/day, $P<0.05$). When MDDT was compared between months by year, September was the only month that differed significantly between years, with 2020 MDDT averaging 6.89 ± 2.63 m/day and 2021 averaging 1.17 ± 0.34 m/day ($P= 0.002$; Table 5).

We used a PCA to assess correlations between MDDT and weather conditions across a time series. A quarterly breakdown of the weather variables for 2020 and 2021 is found in Table 6. The first two components of the PCA explained 73.3% of the variation in the data (PC1: 43.8%, PC2: 29.6%; Fig. 11). The environmental variables that positively loaded on the PC1 axis were maximum temperature (Max_Temp; C°) and precipitation (Precip; mm), while for the PC2 axis, average temperature (Av_Temp; C°) negatively loaded onto the axis and minimum temperature (Min_Temp; C°) positively loaded onto the axis (Table 7). The PCA revealed that months grouped together, indicating distinct weather conditions for each month. Different environmental variables explained variation within each of the years. The year 2020 was explained mainly by precipitation and average solar radiation and 2021 by maximum and minimum temperatures; average temperature also explained variation among months for both years. July and August 2020 were associated with higher precipitation levels and average solar radiation than September and May 2020. For 2021, August had the highest minimum temperature values, and May had the lowest temperatures, with July and June in between. As indicated by the pattern seen in the size of the points among months, which directly correlates to MDDT values, MDDT decreased from spring to fall.

To further explore the relationship between the explanatory variables and spotted turtles' MDDT, we regressed MDDT values against the factor scores of PC1 and PC2. According to our regression analysis, variables that loaded onto PC1 did not have a linear relationship with MDDT (R^2= 0.0003, $F_{[1,176]}$= 0.046, *P*= 0.83), indicating little association with MDDT. We did, however, see a significant negative relationship with variables that loaded on the PC2 axis (R^2= 0.096, $F_{[1,136]}$= 18.65, *P*= 2.62e-05; Fig. 12), indicating a negative relationship between MDDT and average temperature, and a positive relationship between MDDT and minimum temperature. MDDT was greatest during May and June for both years and was associated with lower minimum temperatures and higher average temperatures. During the remaining months of 2020, there were no significant patterns of rates of MDDT in parallel to weather conditions. We did observe that for 2021, MDDT was the lowest during July, August, and September. July and August of that year were strongly associated with higher minimum temperatures and lower average temperatures.

Habitat Selection

We tested for spotted turtle habitat selection at second-order and third-order scales (Johnson 1980). We found non-random habitat selection of home ranges within the population range (second-order; MANOVA; Pillai's Trace = 0.99, $F_{[10,33]}$ = 385.47, *P*< 0.0001) and selection of habitats within the home range scale (third-order; MANOVA; Pillai's Trace = 0.90, $F_{[7,26]}$ = 33.47, p< 0.0001). For second-order selection, distances from random points within the population range to the nearest habitat type were significantly different from distances of random points within home ranges to the nearest habitat type (α= 0.005; Fig. 13), excluding water (t= -0.42, *P*= 1.00) and emergent marshland (t= -2.62, *P*= 0.16; Table 8). Our pairwise comparisons ranked vernal pool (t= -9.88, *P* <0.0001) and emergent wetland (t= -5.55, *P* <0.0001) as the most preferred habitat types (*d* <1), and agriculture (t=7.23 *P* <0.0001), scrub/shrub (t=3.45, *P*= 0.02), developed (t=26.33, *P* <0.0001), open canopy (t=6.65, *P* <0.0001), coniferous forest (t=7.98, *P* <0.0001), and dry-mesic forest (t=7.03, *P* <0.0001) as the least preferred habitat types (*d* >1; Table 8 & 9)

At the third-order spatial scale, most home ranges did not contain agriculture, developed, and emergent marshland habitat types; therefore, we dropped them from the analysis to avoid null values. We found that distances from random points within the home range to the nearest available habitat type were significantly different from distances of telemetry points to the nearest habitat type within the home range (α= 0.007; Fig. 14) for only emergent wetland (t= -4.42, *P*=0.002) and water (t= -4.30, *P*= 0.002). Our pair-wise comparisons test ranked emergent wetland and water as the preferred habitat types (d<1; Table 8 & 10). Turtles did not show selection nor avoidance for the remaining habitat types classified within the third-order scale.

For both years, three habitat types contained overwintering sites: emergent wetland, scrub/shrub, and dry-mesic forest. We saw similar percentages of overwintering sites in those habitat types across the two years. In 2020, 53% of the total overwintering sites were within emergent wetland habitats, and 47% in 2021. Across the two years, one male turtle overwintered in the dry-mesic forest (5% of the total sites). Lastly, scrub/shrub habitats contained 41% of the overwintering sites in 2020 and 47% in 2021.

Discussion

Spotted turtles in the southwestern lower peninsula of Michigan have a shorter active season than the more southern and eastern populations across their geographic range (Rowe et al., 2013). This population displayed high site fidelity of home ranges within the prairie fen (emergent wetland) and vernal pools. Male spotted turtles had larger home ranges than females, likely due to the accessible resources provided within the prairie fen and the matrix of unsuitable habitats that confined their movements and home ranges to select core areas. This population's daily movement rates were dictated by weather and time of year. Turtles preferred home ranges and habitats with water, including the prairie fen and vernal pool. Most of the activities, such as foraging, overwintering, and aestivating, occurred within the confines of the fen. Our results indicate that wetlands (e.g., prairie fen and vernal pools) are essential habitats that provide necessary resources for spotted turtles during their active season.

Home Range Estimation

Turtle home ranges often have high intraspecific variability (Averill-Murray et al., 2020; Slavenko et al., 2016), which influenced our predictions on body size, sex, and year affecting the size of the home ranges. The magnitude of variation in home range sizes of spotted turtle populations can be influenced by a myriad of variables such as their geographic location, sexual reproduction, the configuration of habitat patches and distributions of resources, season, and demographics (Buchanan et al., 2017; Rowe et al., 2013). Our findings suggest that spotted turtle body mass is positively linked to home range size. Many other reptile species have similarly demonstrated a positive linear relationship between home range size and body mass (Müller et al., 2019). The males in this population displayed larger body masses on average than the females and produced greater home ranges than females as well, providing additional support for this linear relationship. However, Slavenko et al. (2016) did report that when body mass was used as the sole predictor of a turtle's home range size, it only accounted for 12% of the variation. Therefore, we must also consider other intrinsic mechanisms and environment variables outside of body size to draw a clearer picture of the primary influences on spotted turtle home range sizes.

There are varying reports on the sexual dimorphism of spotted turtle home range sizes, with the majority reporting females producing larger annual home ranges, accrediting this to their reproductive needs (Buchanan et al., 2017; Litzgus & Mousseau, 2004a). In many populations, female spotted turtles tend to display a larger annual home range than males, as they have to travel extensive distances upland to find habitats suitable for nesting (Milam and Melvin, 2001). We, however, documented larger annual home ranges of male spotted turtles than females within our population across the two study years. Our findings were consistent with two populations in Massachusetts (Graham, 1995; Kaye et al., 2005), whose male home ranges were more extensive than the females on average, but these reports are to be interpreted carefully due to their small sample sizes ($n < 6$).

Within our population, females presented a more significant percentage of annual home range overlap than males, with over 60% of the overlap of both sexes concentrated within the prairie fen (Fig. 15 & 16). Spotted turtles tend to favor isolated wetlands (e.g., prairie fens, vernal pools, wet meadows, marshlands) for feeding, copulation (Ernst & Lovich, 2009), and nesting, particularly within endemic wetland microhabitats such as *Sphagnum* moss, root hummocks, and marshy pastures (Beaudry et al., 2010; Ernst & Lovich, 2009; Joyal et al., 2001). Because our female turtles were so small, we could not palpate them to feel for eggs. However, similar to other populations, we can assume that our females reproduced annually (Litzgus & Mousseau, 2003). Although we did not observe any nests during the study, we did find the females often residing in *Sphagnum* moss mounds or within root hummocks within the prairie fen. This suggests that while male turtles still covered more area, most likely in search of mates, females did not need to extend their home ranges upland, as nesting most likely occurred within the confines of the fen.

Across their species geographic range, spotted turtle home range sizes vary from 0.2 – 53.1 ha (95% MCP; Ernst, 1976; Kaye et al., 2005; Milam & Melvin, 2001; Rowe et al., 2013). For historical comparisons, this population's 95% MCP home range sizes ranged from 0.17 – 4.5 ha across the two active field seasons, averaging 1.3 ha for 2020 and 1.26 ha for 2021. Rowe et al.'s (2013) study on the same population found their home range (95% MCP) sizes averaged 0.41 ha (*n*=7) in 2006 and 0.13 ha (*n*=8) in 2007. For our study, we documented larger MCP home range areas than Rowe et al. (2013), likely due to the differences in tracking frequencies (3-5 d/wk: each individual tracked once or three times a day). Nevertheless, the average home range sizes of both males and females from our population are reportedly small compared to many other populations across their geographic range.

Some studies have found that individuals in poorer quality or patchy habitats must increase their range to meet their ecological demands, suggesting that smaller home ranges correlate with higher quality habitats (Fortin et al., 2012; Kaye et al., 2005). The two females tracked in both Rowe et al.'s (2013) study and ours (14 years) demonstrated long-term annual site fidelity and small home ranges that occurred within the prairie fen and vernal pool (Fig. 17). Home range site fidelity has additionally been noted in populations within similar northern latitudes, such as Litzgus et al.'s (1999) population in Ontario, Canada. Home range fidelity reflects the distance of necessary resources to an individual's home range, suggesting again that smaller, more concentrated home ranges could have accessible resources within similar distances

(Litzgus & Mousseau, 2004a). However, it is essential to consider all possibilities. This study site has been embedded in a matrix of agricultural areas for decades, and therefore, an alternative explanation is that small home range sizes and annual site fidelity could be a result of long-term isolation from other available resources. Our results and Rowe et al. (2013) suggest that this population's small home ranges and site fidelity are not just a product of year-to-year variation but are rather a long-term phenomenon.

Movement

Currently, there are no standardized movement measurement protocols for this species, and therefore, comparing movement data can be difficult as results may vary by population and method and must be interpreted with caution (Rowe et al., 2013). Our individuals' mean daily distance traveled ranged (min-max) from 0 – 43.64 m/day, with an average of 10.8 m/day across two years. Rowe et al. (2013) reported similar movement rates from this population fourteen years ago, 0.7 – 35.9 m/day, with a mean distance of 9.5 m/day across 2006 and 2007. Throughout their geographic distribution, spotted turtles in Georgia had similar mean daily movement rates (averaged monthly), ranging from 4.3 – 15.0 m/day, from spring to fall (Chandler et al., 2019), whereas spotted turtles near Lake Huron (Rasmussen & Litzgus, 2010), doubled our population's mean daily movement rates (ca. 12 – 40 m/day), from spring to fall. Such differences in movement may reflect landscape configuration and factors such as demographics, season, and weather (Rowe et al., 2013).

Our population's MDDT varied as a function of environmental changes and time of year rather than sex. Spring aggregations around the vernal pool, nesting availability within the prairie fen, and communal overwintering might clarify the lack of differences in movement rates between sexes, as seen in other northern populations (Rasmussen & Litzgus, 2010). Unlike

Blanding's turtles, whose gravid females travel a significant distance upland to nest (Buchanan et al., 2017; Millar & Blouin-Demers, 2011), gravid spotted turtles are not known to travel as far, especially if there are more available nesting opportunities (Rasmussen & Litzgus, 2010). Most of our turtles' movements remained within the emergent wetland, consistent with what we saw in the home ranges, therefore assuming the turtles nested and copulated within the wetlands as well, constricting their movement rates

We found higher daily movement rates during the spring and mid-summer and shorter daily movement rates during the late summer and fall, consistent with other populations (Beaudry et al., 2010; Ernst, 1976; Rasmussen & Litzgus, 2010). Changing environmental conditions have been extensively reported to modify chelonian distributions, specifically life-history traits like seasonal movement (Butler, 2019). For instance, 2020 experienced higher precipitation levels throughout the early spring (Fig. 18), which inundated the vernal pools in the forests and deer trails within the prairie fen. This increased water availability and promoted movement in the spring, as we saw spotted turtles emerging from their hibernacula in the prairie fen and subsequently aggregating within the vernal pools to thermoregulate, feed, and breed. They additionally would be found in the deer trails when aquatically active, consistent with another Michigan population, who reportedly used deer trails for rehydration and more effortless locomotion (Lutz, 2009).

As water availability decreased and solar radiation increased during the late summer of 2020, our turtles experienced more frequent periods of aestivation and smaller bursts of movement, especially when temperatures approached their critical thermal maximum (41° C, Hutchison et al., 1966). Rowe et al. (2013) supported this hypothesis, as they reported that this population's movements decreased significantly when the wetland dried up correspondingly in the summer ten years ago. This behavioral trend was also seen in other populations within similar northern latitudes who also credited the turtle's reduction of movement to water loss at the end of the summer (Ernst, 1982; Haxton & Berrill, 1999; Rasmussen & Litzgus, 2010). However, in 2021, precipitation levels were too low to fill up the shallow water bodies, and therefore there were no water sources for the turtles to retreat to. Therefore, during 2021, turtle movement became contingent on temperature, as we saw spotted turtles aestivating more frequently during that year or traveling further distances in search of water to prevent desiccation. Chandler et al. (2020) similarly found that a population in the Coastal Plain of southeastern Georgia conformed their behavior to ambient temperatures when water was absent because the turtles became less energetically efficient as the temperatures climbed. Furthermore, as climate change continues to accelerate, the extreme changes in temperatures and the loss of available aquatic habitats could impede chelonian dispersal throughout their habitats. Thus, furthering research on understudied species and creating standardized measurement methods could be beneficial for understanding what influences their movements and biology.

Habitat Selection

Spotted turtles exhibited significant nonrandom habitat selection at both spatial scales. Individuals of this population chose home ranges closer to vernal pools and emergent wetlands than random points and furthest from dry-mesic and coniferous forests than random points within their population range. Similarly, at the home range scale, locations of individuals tended to be closer to emergent wetlands and water than random points and farthest away from the coniferous forest and open canopy forests within their home ranges. The selection of emergent wetlands at both spatial scales is consistent with previous research on spotted turtle habitat selection (Rasmussen & Litzgus, 2010). Permanent wetlands, such as prairie fens and bogs, are critical habitats for this species as they provide opportunities for nesting, thermoregulation, food sources, and hibernacula (Buchanan et al., 2017; Rasmussen & Litzgus, 2010). These types of emergent wetlands are considered the most productive habitats for spotted turtles, as populations ranging from Massachusetts (Kaye et al., 2005) to Ontario, CA (Reeves and Litzgus, 2008) seek these out these habitats for important life cycle activities, such as spring copulation and nesting. Within the large emergent wetland, which is a large prairie fen, we found turtles using characteristic microhabitats, such as basking on top of peat moss (*Sphagnum sp.*), aestivating within the moss, or under matted sedges (*Carex sp.*) and root systems of dogwood trees (*Cornus sp.*). These microhabitats within this wetland acted as essential refugia to avoid desiccation and predation, but as mentioned earlier, they are essential habitats for nesting.

Upland habitats, such as dry-mesic and open-canopy forests, surrounded the prairie fen (emergent wetland) and acted as a buffer zone between other wetlands and developed or agricultural areas. Spotted turtles have been recorded to use forested uplands for travel, nesting, and aestivation (Joyal et al., 2001). Populations native to Ontario, Canada (Litzgus & Brooks, 2000) and Massachusetts (Kaye et al., 2001) used upland habitats the most frequently during the summer for thermal refugia from the summer heat. However, outside of locating two males hidden under forest leaf piles during the fall of both years, these upland habitats were largely avoided. This was surprising as upland habitats naturally border emergent wetlands, like prairie fens (Kost & Hyde, 2009). Rowe et al. (2013) had similar observations of their tracked individuals who avoided upland habitats, stating that upland habitats encircling the emergent wetland might not offer essential resources for spotted turtles, confining the population within the wetland throughout the year, especially when the vernal pools dry up.

Isolated, ephemeral wetlands, such as vernal pools, are often discounted as quality turtle habitats (Kaye et al., 2001). The primary selection of these seasonal pools within the entire population range indicates how our population used them disproportionately over other available habitats. Out of 17 turtles, 13 occupied a sizeable vernal pool within the middle of a dry-mesic forest from May to mid-July of 2020. Our turtles used this pool for basking, cover, and foraging during this period. Milam and Melvin (2001) and Graham (1995) similarly observed spotted turtles using vernal pools for basking and feeding opportunities. Milam and Melvin (2001) explained that pools provide a source for turtles to congregate and find mates.

Contrary to the population range, we did not see spotted turtles significantly selecting vernal pools at the home range scale. We suspect this was due to environmental factors. To illustrate, the year 2020 experienced more rainfall and snowmelt that filled the vernal pool for the spring, whereas in 2021, there was substantially less snowmelt and precipitation, and the vernal pool never filled up for the entire active season (Fig. 18). Consequently, turtles expanded their home ranges to find external water sources or condensed them while remaining solely within the emergent wetland.

Spotted turtles are very dependent on a localized water source and prefer habitats with increased water coverage (O'Bryan et al., 2016; Rasmussen & Litzgus, 2010; Rowe et al., 2013). If vernal pools were not present, spotted turtles would use supplementary water sources for foraging, thermoregulation, and rehydration. While aquatically active, we found spotted turtles in spring-fed ponds, depressions, and intertwining deer trails holding less than 10 cm of water within the emergent wetland. We observed turtles using aquatic vegetation (e.g., *Scheonoplectus sp.*) within the spring-fed ponds to prop themselves up to bask or for cover. When deer trails and depressions were deluged with water, we often found spotted turtles feeding on macroinvertebrates, such as black soldier fly larvae (*Diptera stratiomyidae*; Fig. 19), hiding in the silt from predators, or swimming quickly from one destination to another. Rowe et al. (2013) and Lutz (2009) had similar observations of spotted turtles in northern latitudes, using deer trails for more accessible travel, possible escape routes from predators, and areas to forage.

A large part of a spotted turtle's selection of habitats consists of choosing optimal areas for establishing overwintering sites (Lewis et al., 2004). For both years, most of the overwintering sites were either located within the scrub/shrub or emergent wetland land cover, with one turtle overwintering in the forest as an outlier (Fig. 20). We observed this population overwintering either aquatically under sphagnum hummocks or matted sedges hummocks, or terrestrially under tree root systems, log and leaf decay. Turtles exhibited communal hibernation, with up to 7 individuals observed in one hibernaculum (specifically the aquatic hummocks). Various studies have additionally reported communal overwintering with spotted turtles (Buchanan et al., 2017; Milam & Melvin, 2001; Rasmussen & Litzgus, 2010) and other freshwater turtles as the Blanding's turtles (Newton & Herman, 2009). Most turtles did display fidelity to hibernaculum or fidelity to a cluster of hibernacula used communally. All hibernacula, except for one, remained within scrub/shrub and emergent wetland, thus inferring how critical wetland habitat is to this species.

Conservation Implications

To effectively manage the remaining populations of spotted turtles across their geographic range, we must continue to fill in the knowledge gaps on their spatial ecology and habitat selection. We observed that the majority of this population's activity cycle is spent in either emergent or rare, isolated wetlands, such as prairie fens and vernal pools, similar to other northern populations (e.g., Rasmussen & Litzgus, 2010; Rowe et al., 2013). Additionally, the longevity of their activity cycle seems to be contingent on the presence of water within these wetlands. Therefore, it is of utmost importance that we focus our conservation efforts on preserving these habitats, including prairie fens and vernal pools, as they are highly preferred habitats for this species and are constantly subjected to habitat fragmentation and climate change. We recommend extended long-term studies on this population and other spotted turtle populations within the Midwest. Long-term studies on this population and those within adjacent regions could provide managers with a more efficient guide to localized management. Our results provide valuable insight into spatial ecology and habitat selection of a northern population of spotted turtles.

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Tables

Table 1. Habitat classifications and definitions were used for the habitat selection study of a spotted turtle (*Clemmys guttata*) population in southwest Michigan between 2020 and 2021. The percent (%) extent (availability) of each habitat type within the entire population range is provided for each year.

Habitat Type	**Description**	**% Extent**	**Size (ha)**
Emergent Wetland	Spring fed ecosystem with moderately alkaline organic soil and multiple distinct vegetation zones, such as sedges, bull rush, forbs, and other graminoid species.	9.64 %	12.38
Scrub/Shrub	Ecosystem encompassing the fen, occurring on saturated organic soil with poor drainage conditions. Dominated by dogwoods, tamaracks, poison sumac, winterberry, and bog birch	16.50 %	21.10
Dry-Mesic Forest	Oak or oak-hickory dominated forest that is fire-dependent, occurring in conjunction with wetland communities	41.50 %	53.74
Coniferous Forest	Tall vegetation comprised of cone-bearing, needle-leaved, or scale-leaved evergreen trees	14.4 %	18.31
Open Canopy Forest	Woodlands where tree crowns do not connect nor form a continuous canopy layer	8.0 %	9.94
Open Water	Standing open water that turtles can fully emerge themselves in >1m.	0.38 %	0.22
Emergent Marshland	Herb-dominated wetland, characterized by narrow and broadleaf plants and grasses that float on the surface, including yellow water lily and white plantain.	0.37 %	0.48
Vernal Pool	Seasonal depressional wetlands that are filled with rain and snowfall and dry up during the summer	0.11%	0.14
Agriculture	Pastures, cropland, orchards, groves or confined areas for animal feeding.	7.62%	9.80
Developed	Areas that cannot be classified as natural communities, including residential developments, industrial, paved roads, and commercial services	1.86%	1.86

Table 2. Summary of spotted turtle (*Clemmys guttata*) ID, sex, midline carapace length (MCL; mm), body mass (g), number of fixes, tracking period (2020 and 2021), and home range size (ha), which includes: 50% weighted autocorrelated kernel density estimation (wAKDE$_c$), 95% wAKDE$_c$, and 95% minimum convex polygon (MCP) of all radio tracked turtles with over 20 fixes within a tracking period. *Turtles tracked for two field seasons.

						Home Ranges (ha)		
Turtle ID	**Sex**	**MCL (mm)**	**Mass (g)**	**No. of fixes**	**Tracking Period**	**50% wADKE$_c$**	**95% wADKE$_c$**	**95% MCP**
10	Male	73	118	29	2020	0.40	1.98	0.62
23*	Male	101	134	26	2020	1.10	4.21	1.7
30*	Female	72	118	28	2020	0.31	1.20	0.54
37*	Female	82.3	153	25	2020	0.4	2.44	0.68
52	Female	84	154	14	2020	–	–	–
53*	Female	73	100	25	2020	0.32	1.48	0.58
71*	Female	91	143	24	2020	1.7	6.36	2.21
82	Male	85	161	25	2020	2.56	9.86	4.51
101*	Female	88	98.8	21	2020	1.202	4.10	1.452
102*	Male	78	71.8	24	2020	0.352	2.85	1.804
103*	Male	97	165	25	2020	1.14	4.78	1.42
104*	Female	78	115	24	2020	0.667	2.35	1.64
105	Female	74	112	12	2020	–	–	–
106*	Male	79.4	111	22	2020	0.942	4.65	0.701
107*	Male	86	131	23	2020	0.704	3.23	0.44
108*	Female	87	120	29	2020	0.317	1.29	0.42
110*	Male	89	146	23	2020	0.86	2.04	0.54
111	Male	74	147	25	2020	1.18	4.43	1.06
116*	Male	85	120	29	2020	1.14	4.47	1.98
23	Male	101	125	41	2021	0.49	1.7	0.74
30	Female	88.2	115	38	2021	0.472	2.17	1.2
37	Female	91.1	150	36	2021	0.412	1.69	0.8
50	Female	96.5	115	38	2021	0.233	1.28	0.65
53	Female	81	98	33	2021	0.21	0.879	0.35
71	Female	97.9	148	36	2021	1.1	4.4	2.1
101	Female	88.1	103	37	2021	0.15	0.56	0.24
102	Male	82.8	73	36	2021	0.772	5.62	2.91
103	Male	110	163	37	2021	0.384	3.05	1.72
104	Female	87.5	105	37	2021	0.167	0.72	0.44
106	Male	90	115	38	2021	0.084	1.43	0.71
107	Male	101	125	40	2021	0.114	0.52	0.17
108	Female	90.2	127	38	2021	0.312	1.38	0.55
110	Male	97.9	135	36	2021	1.981	6.67	3.18
116	Male	96.4	140	36	2021	0.12	1.95	0.71
173	Male	87	85	36	2021	0.602	1.3	1.5
181	Female	84.6	104	30	2021	0.657	3.22	1.5
182	Female	93.9	140	35	2021	0.873	3.72	1.53
210	Male	96.8	143	38	2021	1.144	5.81	2.90

Table 3. Raw mean home range estimates (ha) of 50% and 95% area-corrected, weighted autocorrelated kernel density estimations (wAKDE$_c$) and 95% minimum convex polygon (MCP), reporting standard error (±SE) between sexes and across years of a spotted turtle (*Clemmys gutatta*) population in southwest Michigan.

		Home Range (ha)			
Sex	***n***	**Year**	**50% wAKDE$_c$**	**95% wAKDE$_c$**	**95% MCP**
Male	10	2020	0.95 (± 0.21 SE)	4.25 (± 0.79 SE)	1.48 (± 0.38 SE)
Male	9	2021	0.70 (± 0.17 SE)	3.04 (± 0.81 SE)	1.62 (± 0.38 SE)
Female	7	2020	0.68 (± 0.12 SE)	2.64 (± 0.73 SE)	1.08 (± 0.26 SE)
Female	10	2021	0.46 (± 0.21 SE)	2.00 (± 0.42 SE).	0.94 (± 0.20 SE)
Male	19	Overall	0.84 (± 0.14 SE)	3.71 ± 0.52 SE)	1.54 (± 0.26 SE)
Female	17	Overall	0.74 (± 0.10 SE)	2.31 (± 0.38 SE)	1.17 (± 0.15 SE)
Total	**17**	**2020**	0.90 (± 0.14 SE)	3.63 (± 0.53 SE)	1.31 (± 0.25 SE)
	19	**2021**	0.54 (± 0.11 SE)	2.53 (± 0.43 SE)	1.26 (± 0.22 SE)

Table 4. Monthly averages of mean daily distance traveled (m/day), reporting ± SE (*n*= number of individuals) between sexes of a spotted turtle (*Clemmys guttata*) population in southwest Michigan.

Month	**Average Daily Distances Traveled (m/day)**	
	Male	**Female**
May	18.4 m/day ± 3.03 SE (*n*=12)	15.2 m/day ± 2.47 SE (*n*=9)
June	15.2 m/day ± 2.35 SE (*n*=12)	14.1 m/day ± 1.78 SE (*n*=10)
July	10.8 m/day ± 1.38 SE (*n*=12)	13.6 m/day ± 2.36 SE (*n*=10)
August	5.52 m/day ± 1.10 SE (*n*=12)	7.08 m/day ± 1.32 SE (*n*=10)
September	4.57 m/day ± 2.24 SE (*n*=11)	3.21 m/day ± 1.41 SE (*n*=10)
Total	10.9 m/day ± 1.09 (*n*=12)	10.6 m/day ± 0.98 SE (*n*=10)

Table 5. Reported summary of a Tukey HSD test from a two-way ANOVA, observing the interactions between mean daily distance traveled (m/day; MDDT) and date (month and year) of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. Mean monthly MDDT is reported with ± SE for both years. Bold numbers indicate significant values ($P < 0.05$).

Date	**MDDT (m/day)**	**SE**	**Aug 2020**	**Aug 2021**	**July 2020**	**July 2021**	**June 2020**	**June 2021**	**May 2020**	**May 2021**	**Sep 2020**
Aug 2020	6.52	1.48									
Aug 2021	6.02	0.96	0.82								
July 2020	10.8	1.75	0.261	0.334							
July 2021	13.3	1	**0.027**	**0.034**	0.998						
June 2020	13.6	2.01	**0.042**	0.057	1	1					
June 2021	15.7	2.18	**0.002**	**0.003**	0.87	1	1				
May 2020	16.0	3.80	0.323	0.404	1	0.986	1	0.878			
May 2021	17.7	2.07	**0.0002**	**0.0003**	0.516	0.96	0.939	1	0.542		
Sep 2020	6.89	2.63	1	1	**0.046**	**0.0022**	**0.004**	**0.0001**	0.068	**<0.0001**	
Sep 2021	1.17	0.34	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.002**

Table 6. Summary of weather variables: maximum, minimum, and average temperature (C°), precipitation, and solar radiation, for years 2020 and 2021, including quarterly a breakdown, Quarter 1: January – March, Quarter 2: April – June, Quarter 3: July – September, and Quarter 4: October – December. Bold represents average temperatures and total precipitation, and solar radiation for the year.

	Maximum Temperature (C°)	**Average Temperature (C°)**	**Minimum Temperature (C°)**	**Precipitation (mm)**	**Solar Radiation (kJ/m^2)**
2020	**26.98**	**9.65**	**-4.45**	**941.27**	**4484157.6**
Quarter 1	4.40	-0.02	-4.45	174.98	606558.3
Quarter 2	20.00	13.54	7.08	310.88	1671317.4
Quarter 3	26.98	20.09	13.20	253.48	1676301.7
Quarter 4	10.11	4.95	-0.20	201.93	529980.2
2021	**27.35**	**2.15**	**-6.53**	**782.56**	**4444736.4**
Quarter 1	4.11	-1.2	-6.53	84.06	788867
Quarter 2	21.66	14.75	7.67	238.03	1588102.2
Quarter 3	27.35	20.83	14.31	231.9	1597225.9
Quarter 4	10.82	6.17	1.38	228.57	470541.3

Table 7. The principal component analysis (PCA) coefficients and loadings on principal components, one (PC1) and two (PC2), were retained for environmental variables collected for a population of spotted turtles (*Clemmys guttata*) in southwest Michigan across two active field seasons in 2020 and 2021. Environmental variables are represented as: Max_Temp= maximum temperature (C°), Min_Temp= minimum temperature (C°), Av_Temp= average temperature (C°), Precip= precipitation (mm), and Av_srad= average solar radiation (kJ/m^2).

	Loadings		**Coefficients**	
	PC1	**PC2**	**PC1**	**PC2**
Max_Temp	0.610	0.223	-2.200	0.661
Min_Temp	0.437	0.551	-1.542	1.633
Av_Temp	0.168	-0.700	-0.607	-2.07
Precip	0.500	-0.243	-1.68	-0.722
Av_srad	0.448	-0.313	-1.616	-0.929

Table 8. Habitat selection based on a Euclidean distance analysis (EDA) at two spatial scales, second-order (population range) and third-order (home range scale), of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. Habitats were tested using one-sample t-tests with a Bonferroni adjusted p-value, determined by the number of habitat types within that spatial scale (second-order α=0.005; third-order α= 0.007). Rankings were based on a *post hoc* Tukey HSD test, with 1 indicating most preferred and 10 (second-order) or 7 (third-order) as least preferred. Bold numbers indicate statistical significance.

	Second-Order			**Third-Order**		
Habitat type	t-value	*P*-value	Ranking	t-value	*P*-value	Ranking
Vernal Pool	**-9.88**	**<0.0001**	**1**	-2.51	0.162	3
Emergent Wetland	**-5.55**	**<0.0001**	**2**	**-4.42**	**0.002**	**1**
Emergent Marshland	-2.62	0.1604	3	–	–	–
Open Water	-0.42	1.000	4	**-4.30**	**0.002**	**2**
Agriculture	7.23	<0.0001	5	–	–	–
Scrub/Shrub	3.45	0.0234	6	0.34	1.000	5
Developed	26.33	<0.0001	7	–	–	–
Open Canopy	6.65	<0.0001	8	1.09	1.000	7
Coniferous Forest	7.98	<0.0001	9	0.66	1.000	6
Dry-Mesic Forest	7.03	<0.0001	10	-0.59	1.000	4

Table 9. Tukey HSD test, ranking p-values of second-order habitat selection of home ranges from the population range by spotted turtles (*Clemmys guttata*) (n=22) in southwest Michigan using 1,299 random points within the population range. Ranks are based on a Tukey HSD test with a Bonferroni correction of multiple tests (α= 0.05/10; habitats = 0.005). Bold numbers indicate statistical significance (*P*< 0.05).

Habitats	**Mean *d***	**SE**	**Ag**	**Canopy**	**Conif**	**Develop**	**Emerg**	**Marsh**	**Mesic**	**Scrub**	**Vernal**
Ag	1.36	0.5									
Canopy	2.40	0.24	**0.002**								
Conif	2.65	0.24	**0.012**	0.992							
Develop	2.27	0.06	< **0.0001**	1.000	0.986						
Emerg	0.48	0.08	< **0.0001**	< **0.0001**	**<0.0001**	**<0.0001**					
Marsh	0.86	0.05	0.102	**<0.0001**	**<0.0001**	**<0.0001**	**0.013**				
Mesic	3.23	0.36	< 0.0001	0.185	0.804	0.155	**0.002**	**<0.0001**			
Scrub	1.38	0.11	1.000	**0.001**	< **0.0001**	< **0.0001**	**<0.0001**	0.120	**<0.0001**		
Vernal	0.47	0.05	< **0.0001**	**<0.0001**	< **0.0001**	< **0.0001**	1.000	0.090	**<0.0001**	**<0.0001**	
Water	1.00	0.09	0.456	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	1.000	**<0.0001**	0.501	**0.009**

Table 10. Tukey HSD test, ranking of p-values of third-order habitat selection of home ranges from the population range by spotted turtles (*Clemmys guttata*) (n=22) in southwest Michigan. Ranks are based on a Tukey HSD test with a Bonferroni correction of multiple tests (α= 0.05/7; habitats = 0.007). Bold numbers indicate statistical significance (*P*< 0.05)

Habitats	**Mean *d***	**SE**	**Canopy**	**Conif**	**Emerg**	**Mesic**	**Scrub**	**Vernal**
Canopy	1.12	0.08						
Conif	1.11	0.87	1.000					
Emerg	0.58	0.12	**< 0.0001**	**<0.0001**				
Mesic	0.99	0.1	0.919	0.962	0.0002			
Scrub	1.06	0.07	1.000	1.000	**<0.0001**	0.994		
Vernal	0.02	0.02	0.730	0.818	**0.004**	1.000	0.928	
Water	0.04	0.04	0.296	0.386	**0.011**	0.935	0.575	0.998

Figures

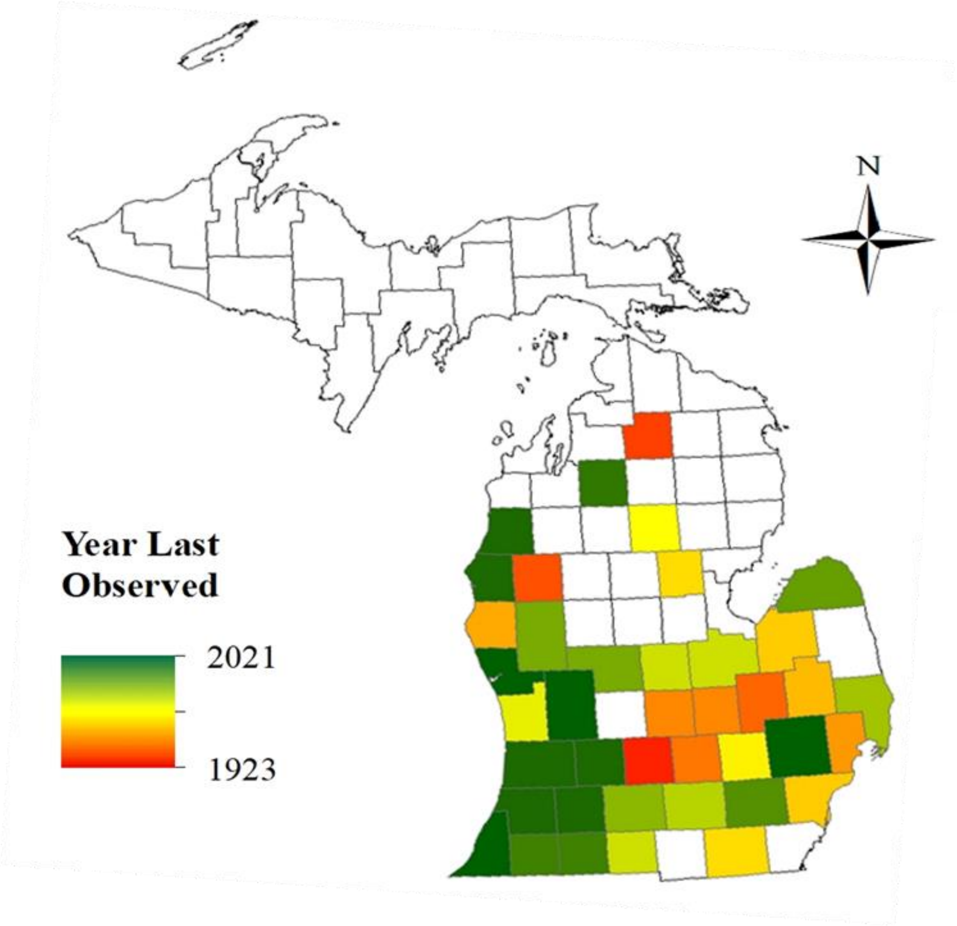

Figure 1. A map of reported spotted turtle (*Clemmys guttata*) sightings from the Michigan Natural Features Inventory (MNFI, 2021), by county, dating back from 1923 to the most current sightings, in 2021. The gradient represents the year a spotted turtle was last observed; red = older dates, green= most recent dates, yellow= in between years.

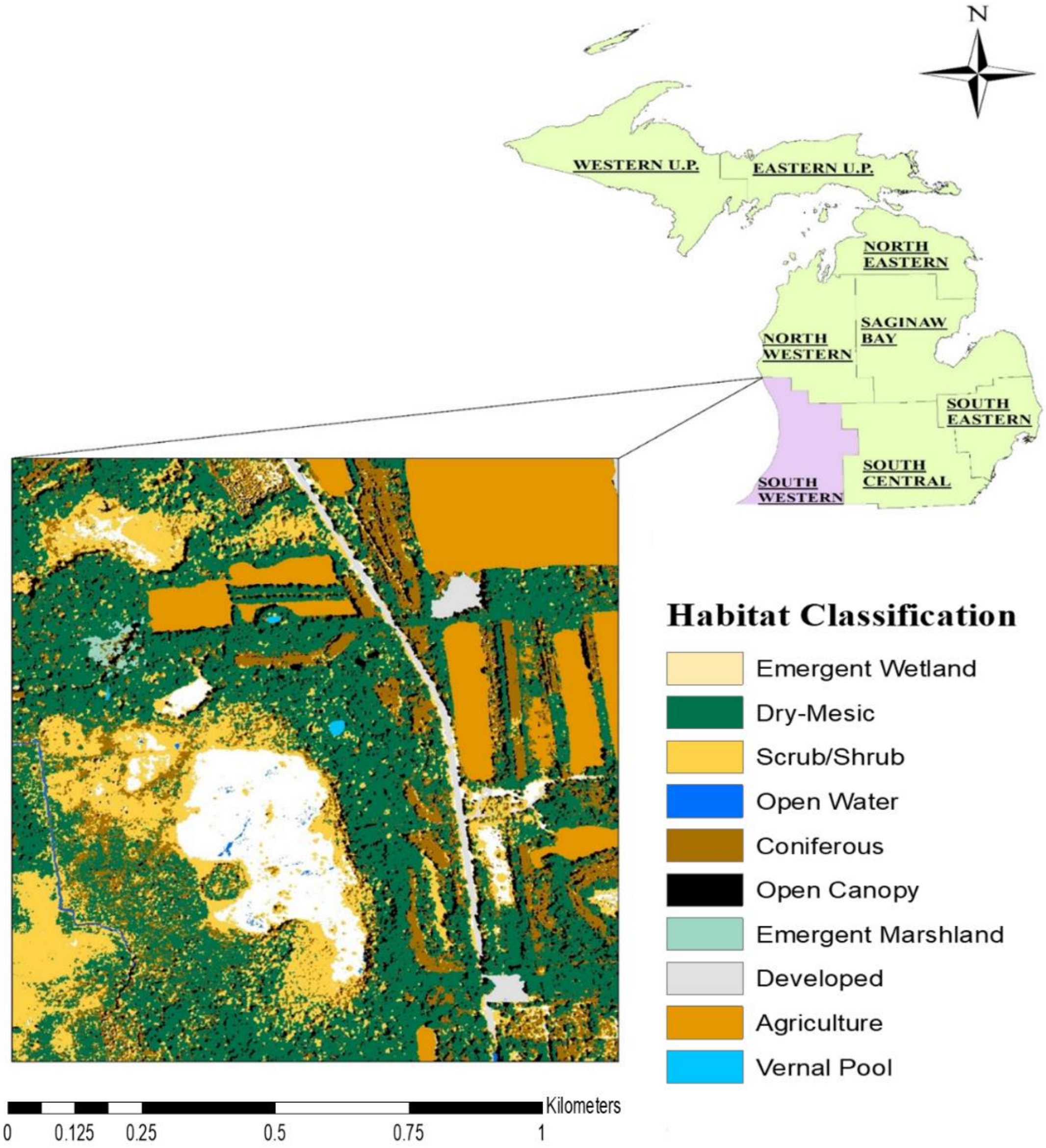

Figure 2. A map of the land cover of the study area of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. Inset is study site in southwestern Michigan, with habitat classifications to the right of the land cover. Habitats are classified as (1) emergent wetland, (2) dry-mesic forest, (3) scrub/shrub wetland, (4) open water, (5) coniferous forest, (6) open canopy forest, (7) emergent marshland, (8) developed area, (9) agriculture, and (10) vernal pool.

Figure 3. An example of a retrieved Pro-mar hoop net trap baited with sardines and set for 24 hours over night. The picture shows five spotted turtles (*Clemmys guttata*) caught within the net.

Figure 4. An example of a VHF transmitter (denoted by the orange circle), fitted on the carapace of a male spotted turtle (*Clemmys guttata*).

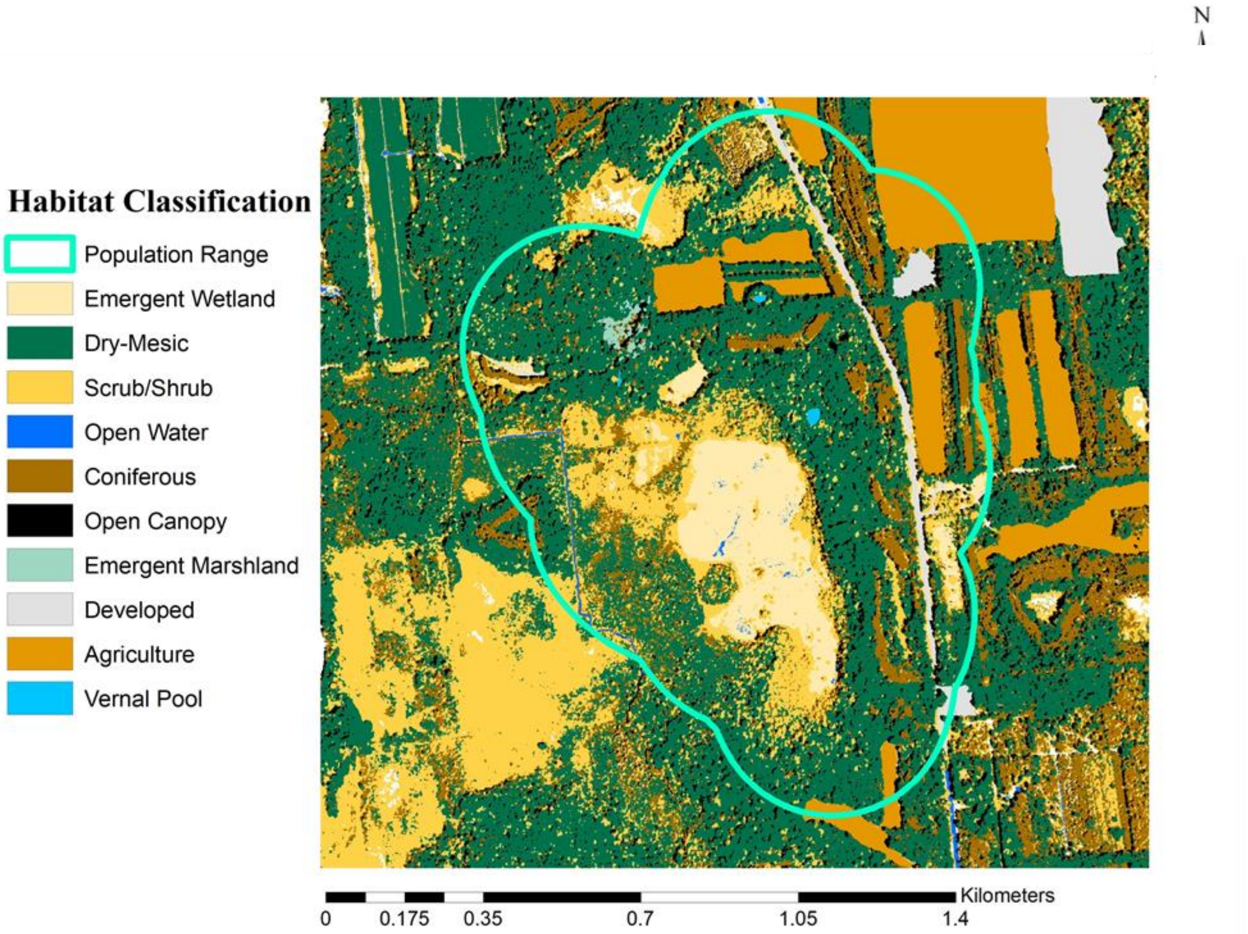

Figure 5. A map of the spotted turtle (*Clemmys guttata*) population range, within the study area located in southwest Michigan. The bright green polygon denotes the population range; comprised of all the 95% wAKDE_c home ranges across both field seasons (2020 and 2021), merged into a single polygon that is buffered by 250 meters. The 10 habitats classified within the study area are left of the population range.

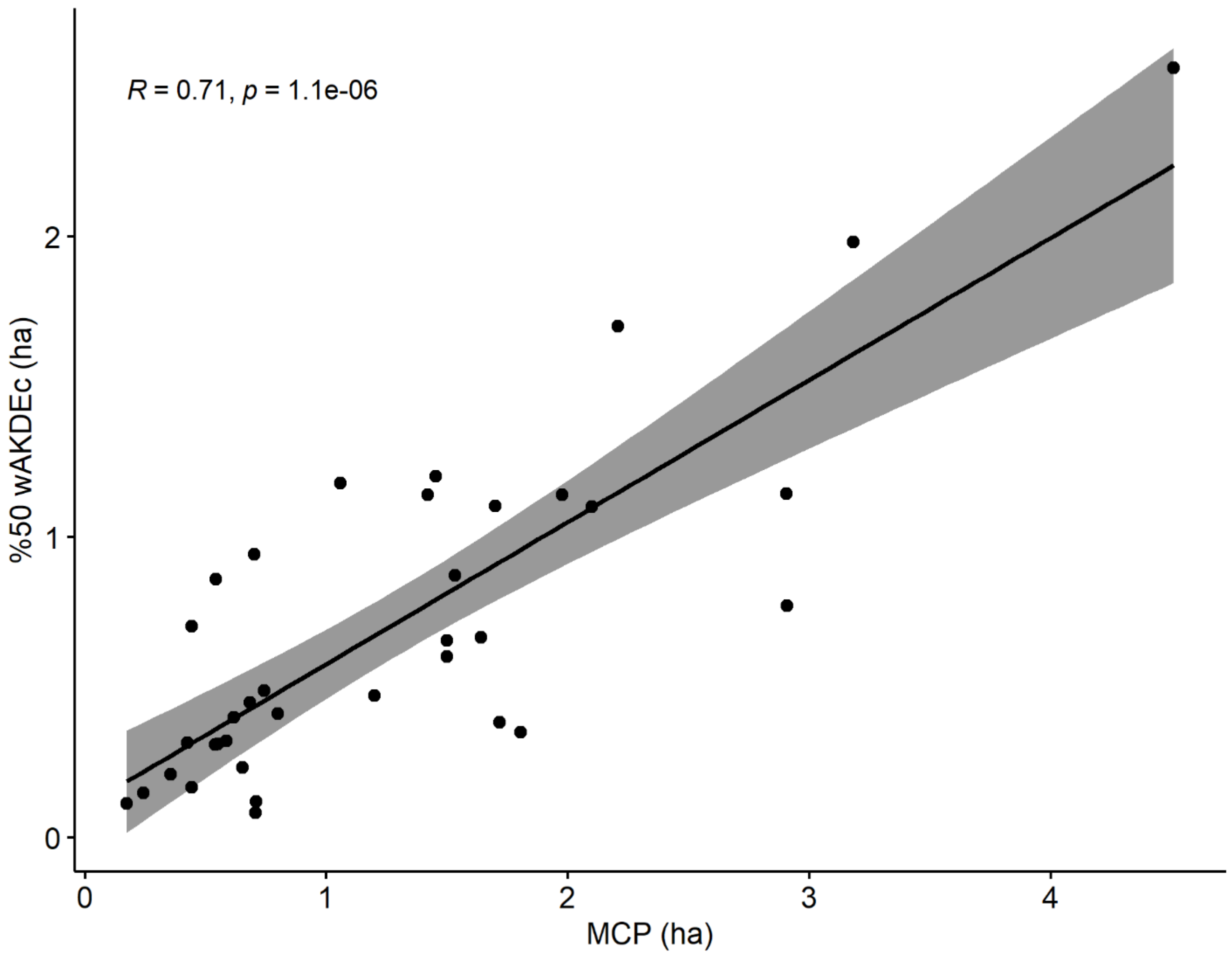

Figure 6. Spearman's rank correlation (*r_s*) of weighted, area-corrected 50% autocorrelated kernel density estimation (AKDE) home ranges (ha) versus minimum convex polygon (MCP) home range (ha) estimates (r_s=0.71). 95% confidence intervals are represented by the shaded areas (CI± 0.47-0.85).

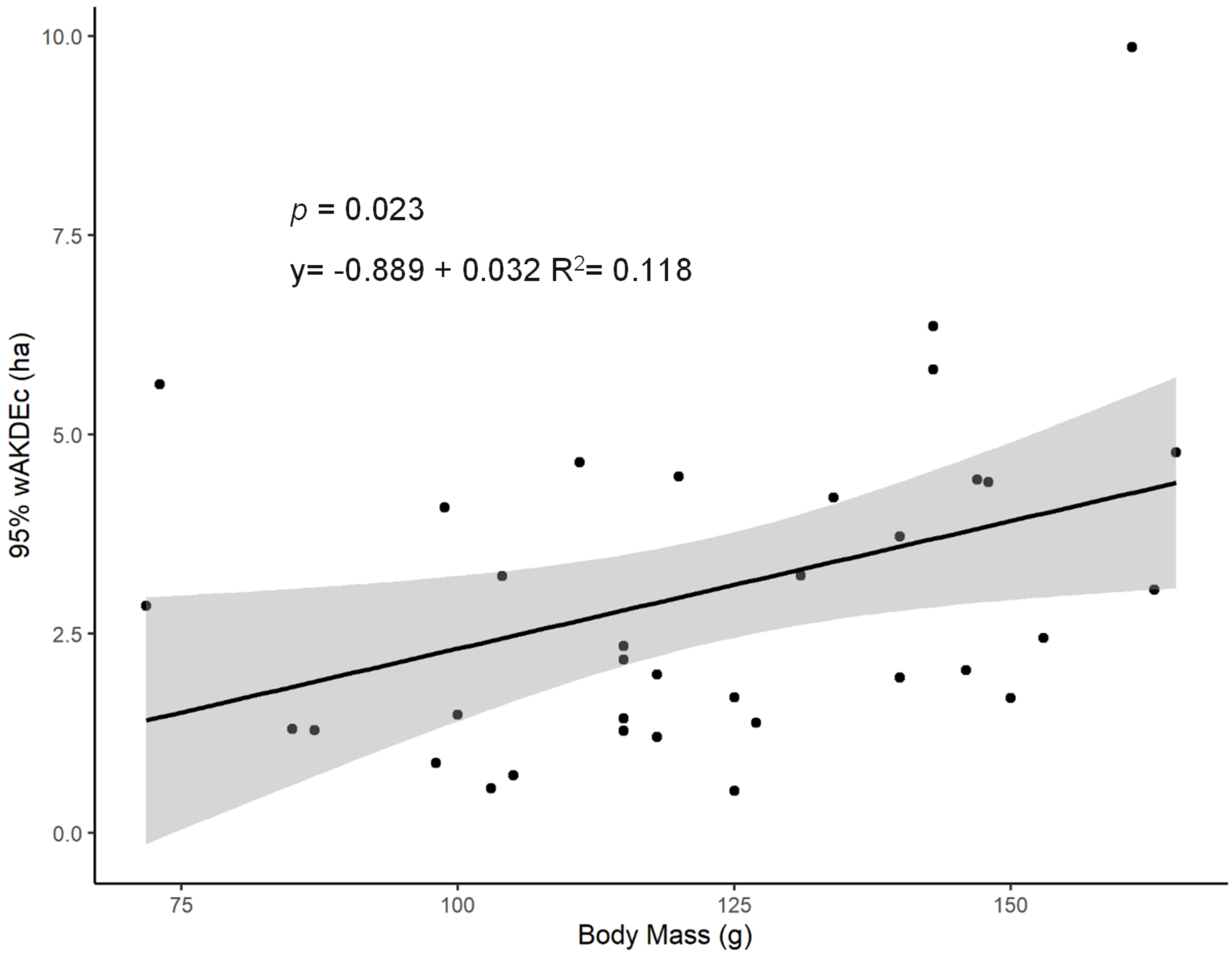

Figure 7. Simple linear regression analysis of weighted, area-corrected 95% autocorrelated kernel density estimation (AKDE) and Body Mass (g) of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. 95% confidence intervals are represented by the shaded areas (CI ± 0.47-5.93).

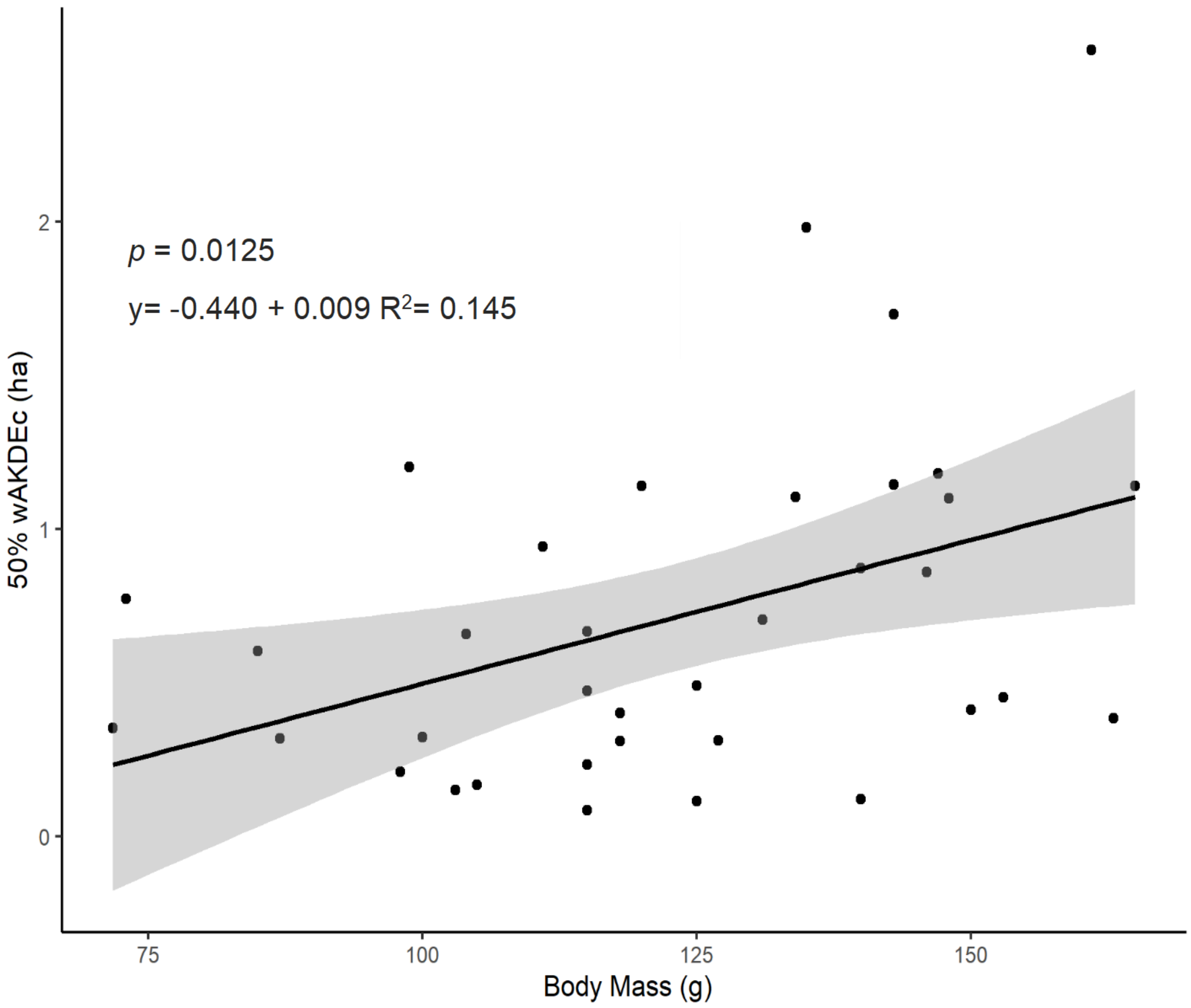

Figure 8. Simple linear regression analysis of weighted, area-corrected 50% autocorrelated kernel density estimation (AKDE; ha) versus Body Mass (g) of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. 95% confidence intervals are represented by the shaded areas (CI ± 0.21-1.65).

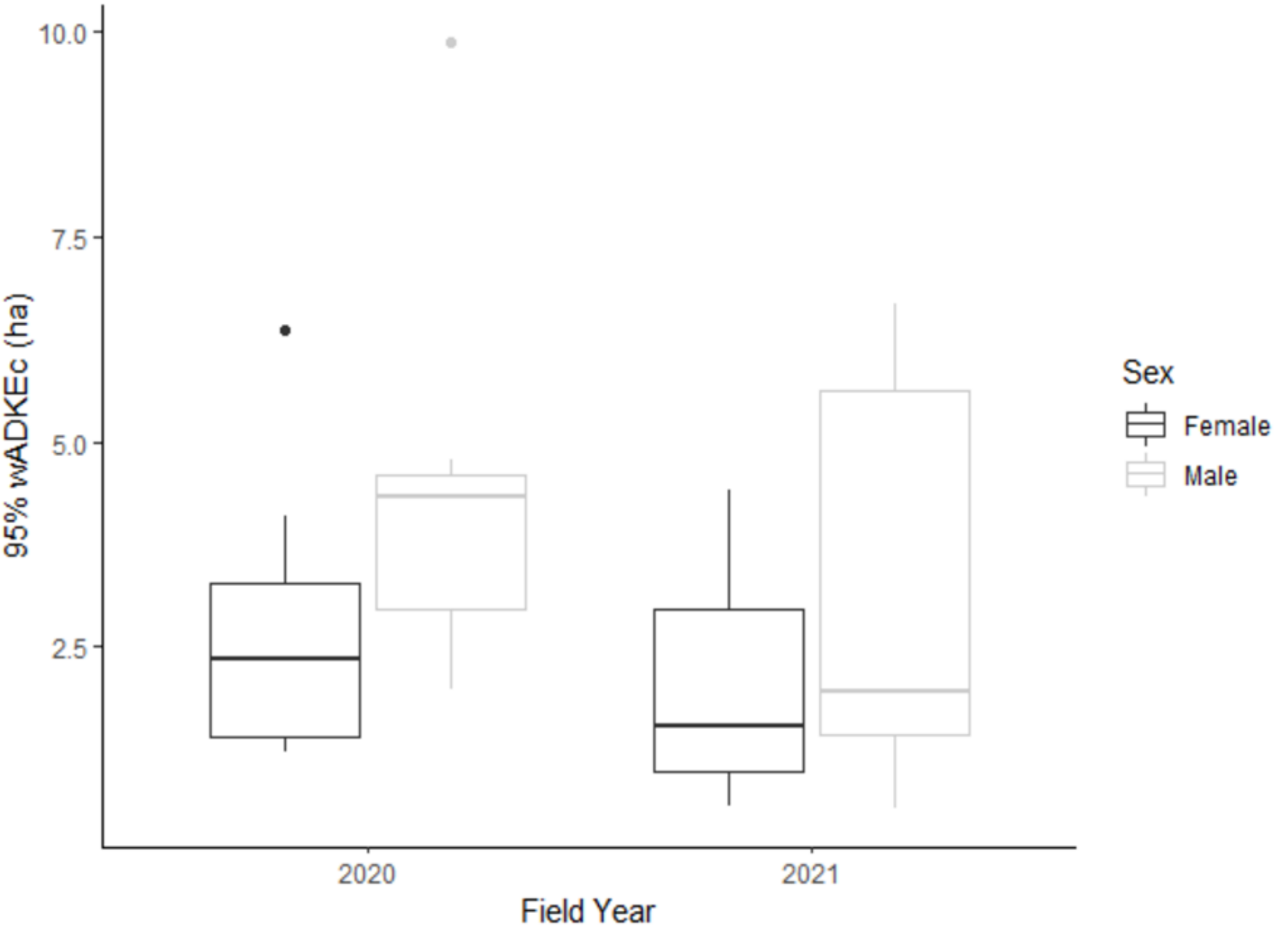

Figure 9. Boxplot of a spotted turtle (*Clemmys guttata*) population's weighted, area-corrected 95% autocorrelated kernel density estimated home ranges between sexes across two years. The dark line in the center of the box represents the interquartile range (IQR), with the bolded horizontal line in the center of the box representing as the median value, and lines extending outside of the box denoting as the standard error (± SE), with dots signifying as potential outliers.

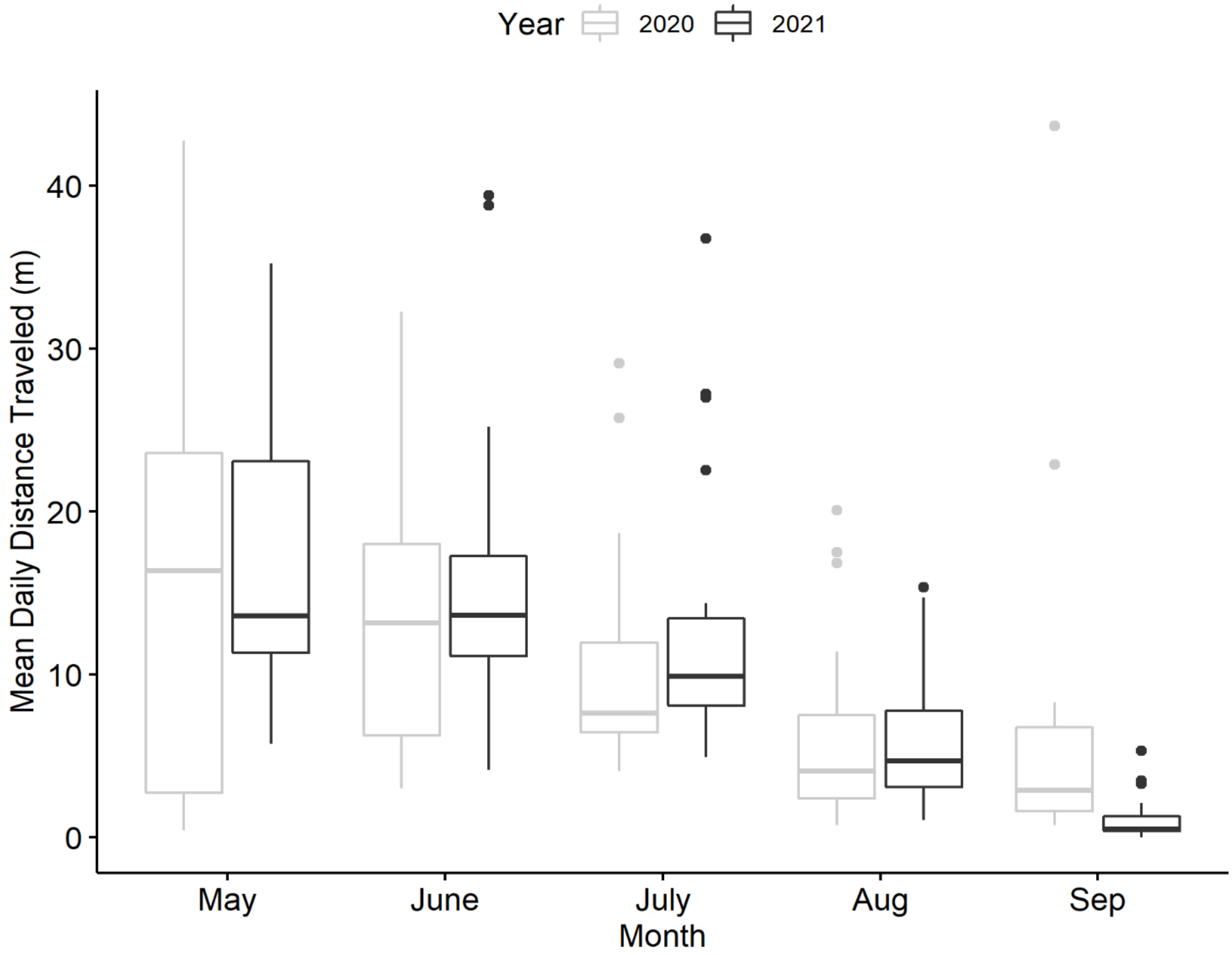

Figure 10. Boxplot of a spotted turtle (*Clemmys guttata*) population's mean daily distance traveled (m) during their active season across two field seasons. The mean traveled distance was separated by months surveyed throughout their active season, and divided into years, 2020 (light grey) and 2021 (black). The dark line in the center of the box represents the interquartile range (IQR), with the bolded horizontal line in the center of the box representing the median value, and lines extending outside of the box denoting the standard error (± SE), with dots signifying as potential outliers.

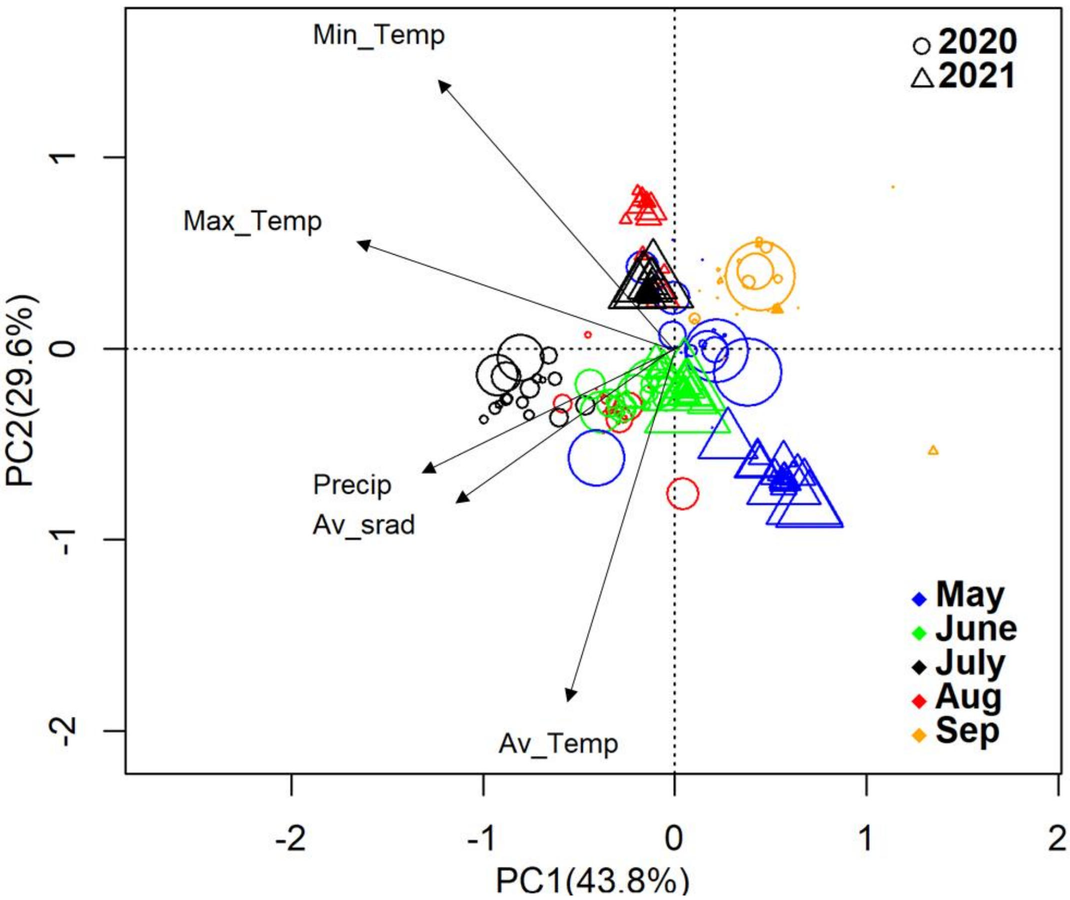

Figure 11. Principal component analysis (PCA) of mean daily distance traveled (MDDT; m/day), collected monthly across two field seasons; PC1 =43.8%, PC2=29.6%. Cumulative proportion of variation explained by both PCs= 73.3%. Sites (months): Blue diamond = May, Green diamond = June, Black diamond= July, Red diamond = August, and Orange diamond = September. Date (years): circle = 2020, triangle= 2021. Size of the data points reflect the mean distance traveled per day, the larger the point size the greater distance traveled per day, and the smaller the point size the less distance traveled per day. Vectors represent environmental data: Min_Temp = Minimum Temperature (C°), Max_Temp = Maximum Temperature (C°), Av_Temp = Average Temperature (C°) and Precip = Precipitation (mm), and Av_srad= Average Solar Radiation.

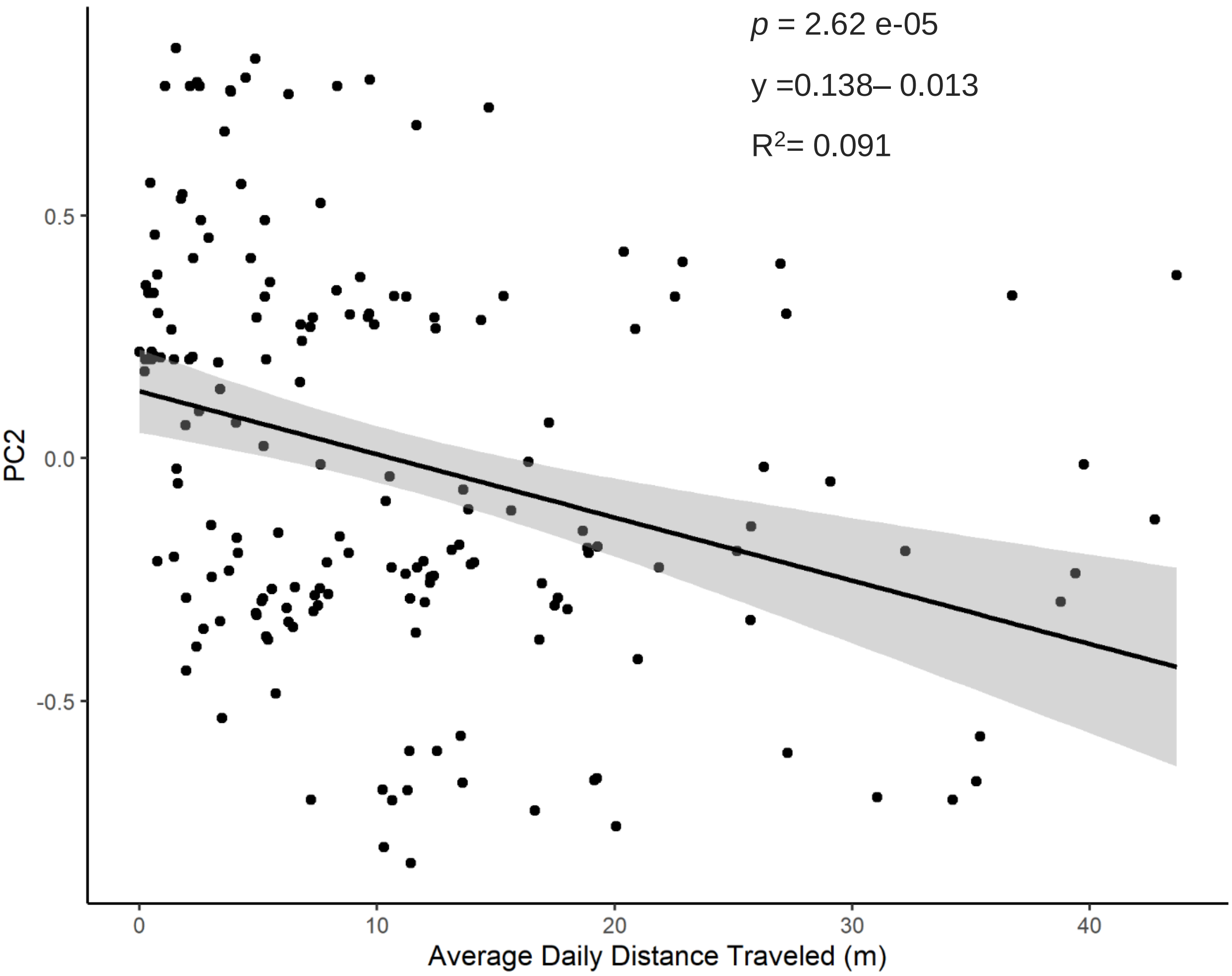

Figure 12. Simple linear regression analysis of a southwest Michigan spotted turtle (*Clemmys guttata*) population's mean daily distance traveled (m) and its relationship to a principal component analysis's PC2 axis factor scores. 95% confidence intervals are represented by the shaded areas (CI ± 0.71-1.9)

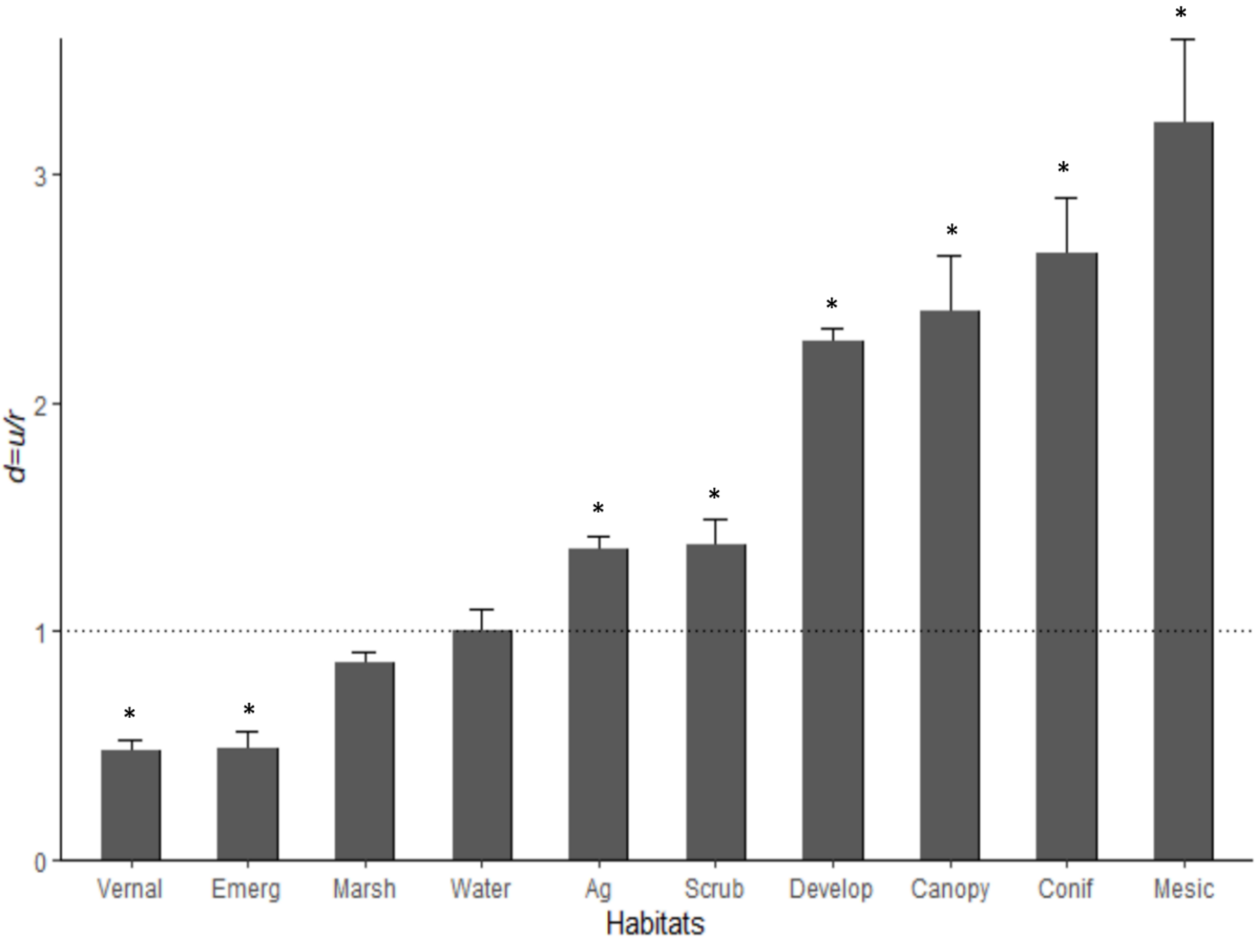

Figure 13. Distance ratios *d=u/r;*mean+*SE*) for second-order habitat selection from a spotted turtle (*Clemmys guttata*; n=22) population's AKDE home range level, during 2020 and 2021, using 1299 random points. Habitats are ranked from most preferred to least preferred, starting from left to right. Asterisks represents values of *d*, significantly different than 1 (corrected α=0.005), indicating preference of the type of habitat.

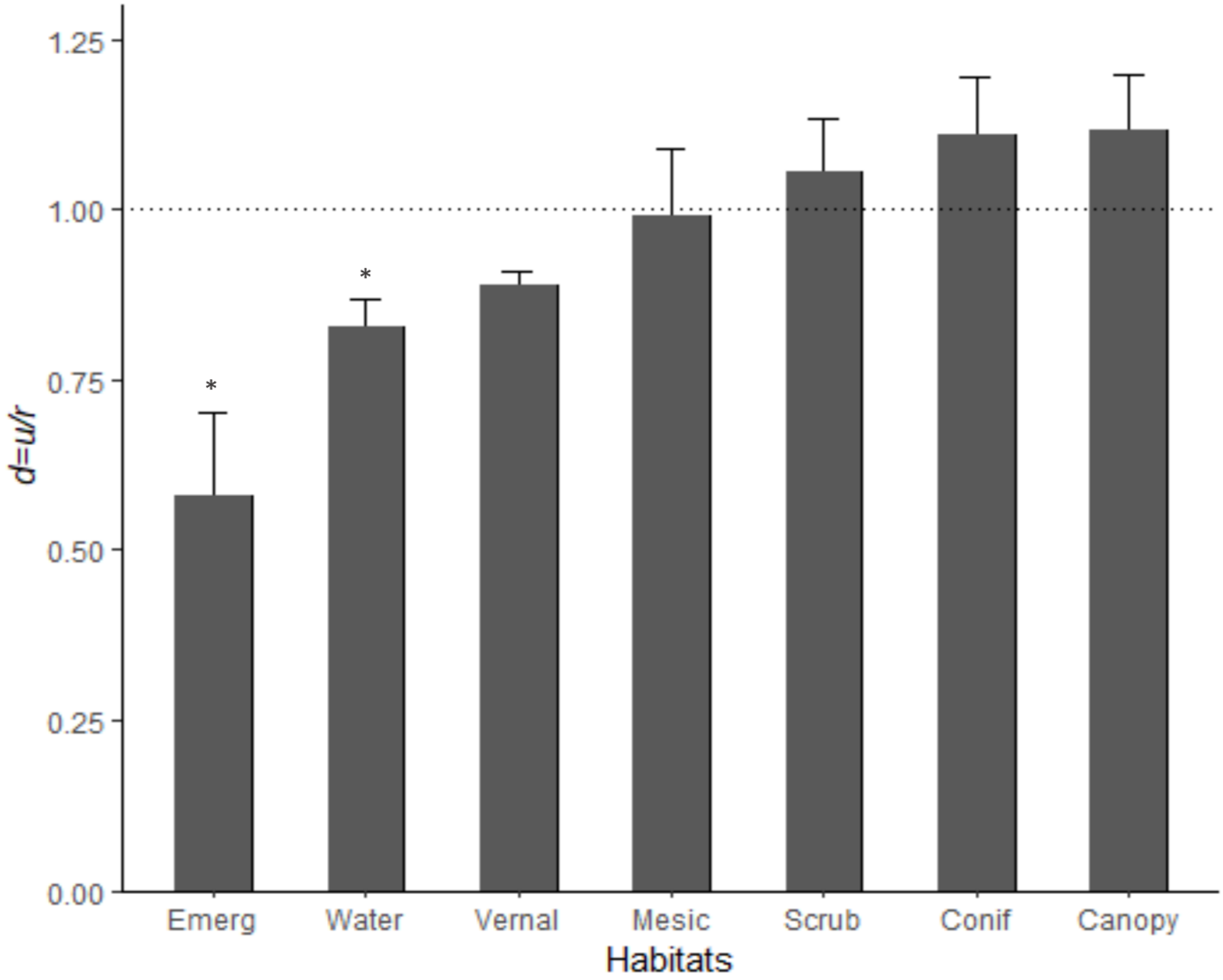

Figure 14. Distance ratios (*d=u/r;*mean+*SE*) for third-order habitat selection from a spotted turtle (*Clemmys guttata*; n=22) population's home range level, during 2020 and 2021. Habitats are ranked from most preferred to least preferred, starting left to right. Asterisks represents values of *d*, significantly different than 1 (corrected α=0.007), indicating preference of the type of habitat.

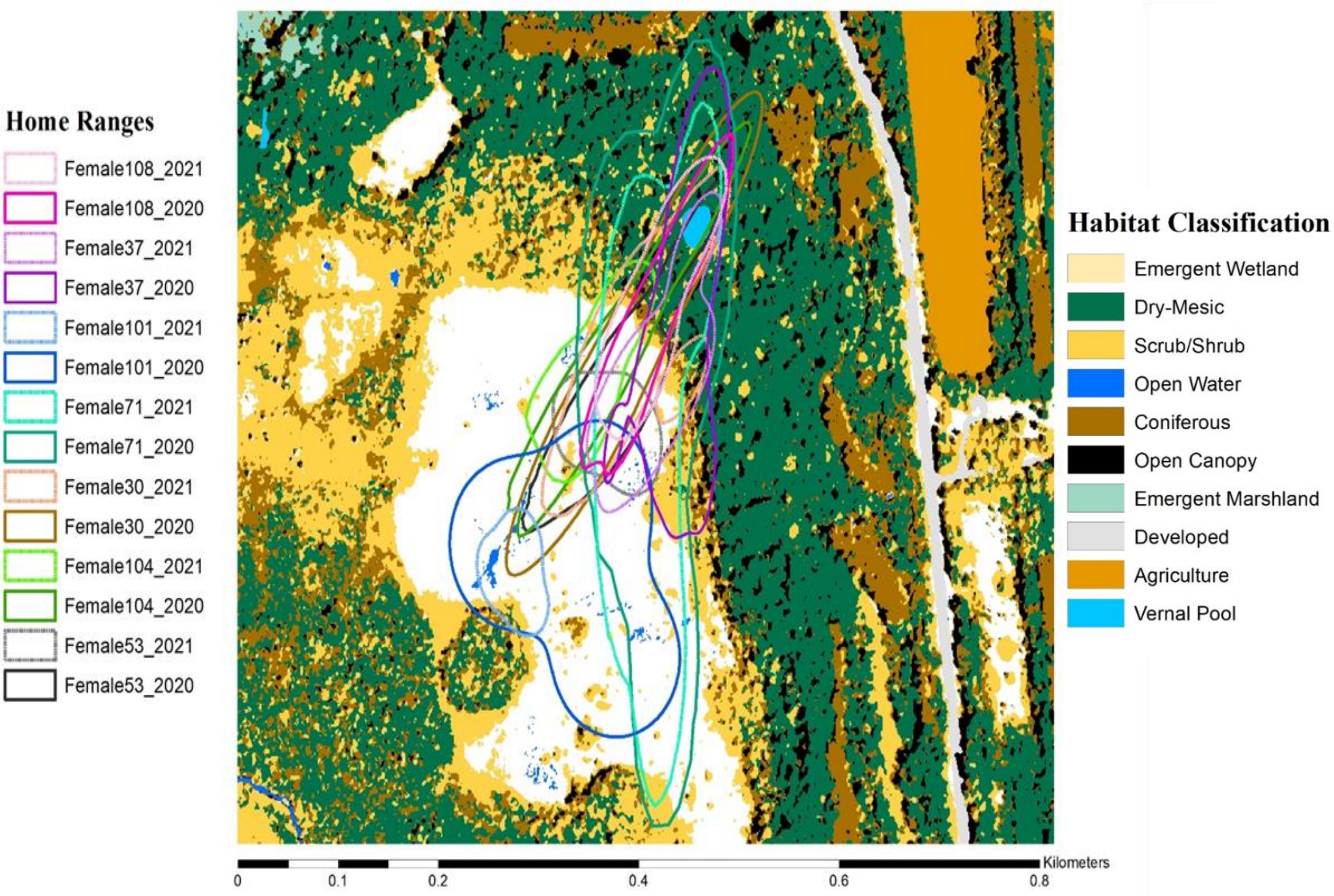

Figure 15. A map of the study area of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. The map includes 95% wADKE$_c$ home ranges of female spotted turtles tracked for both field seasons. The home ranges for each individual are denoted by colored IDs left of the map, to the right of the map are 10 habitats classified within the study area.

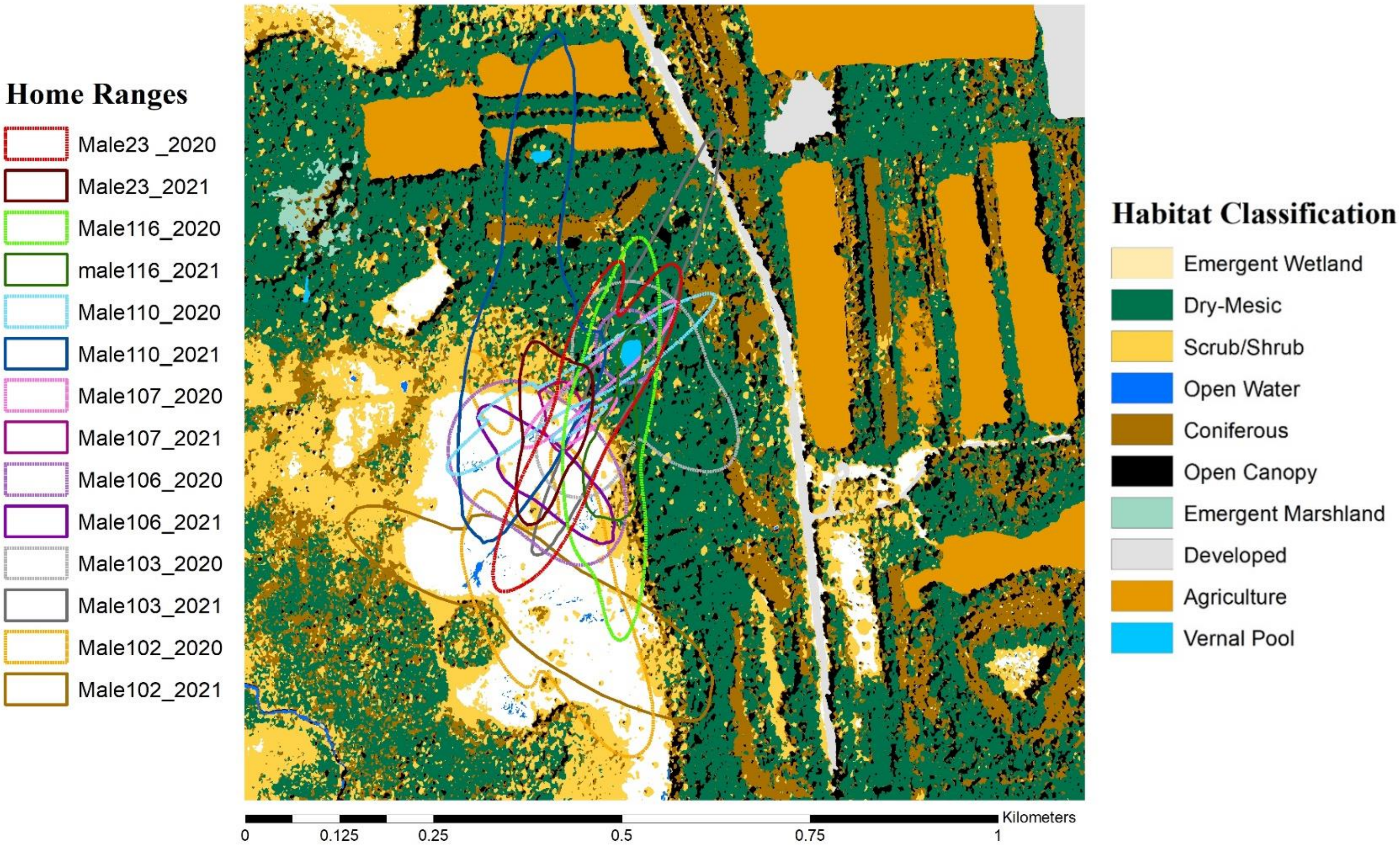

Figure 16. A map of the study area of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. The map includes 95% wADKE$_c$ home ranges of male spotted turtles tracked for both field seasons. The home ranges for each individual are denoted by colored IDs left of the map, to the right of the map are 10 habitats classified within the study area.

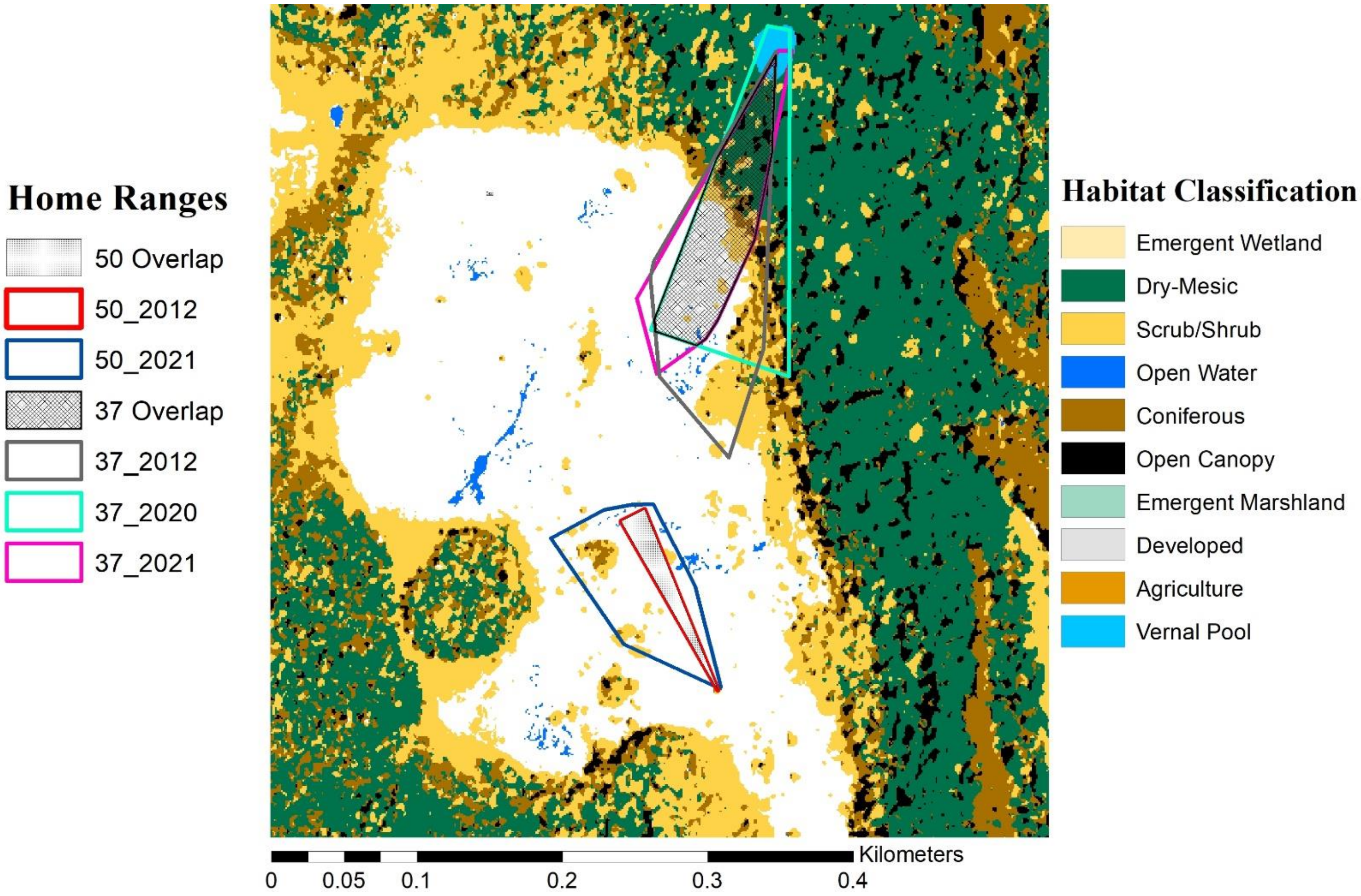

Figure 17. A map of the study area of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. The map includes 95% MCP home ranges of two individuals tracked during this study and Rowe et al. (2013). To the left of the map, home ranges are denoted by colors and home range overlap is denoted by the hash marks. To the right of the map are 10 habitats classified within the study area.

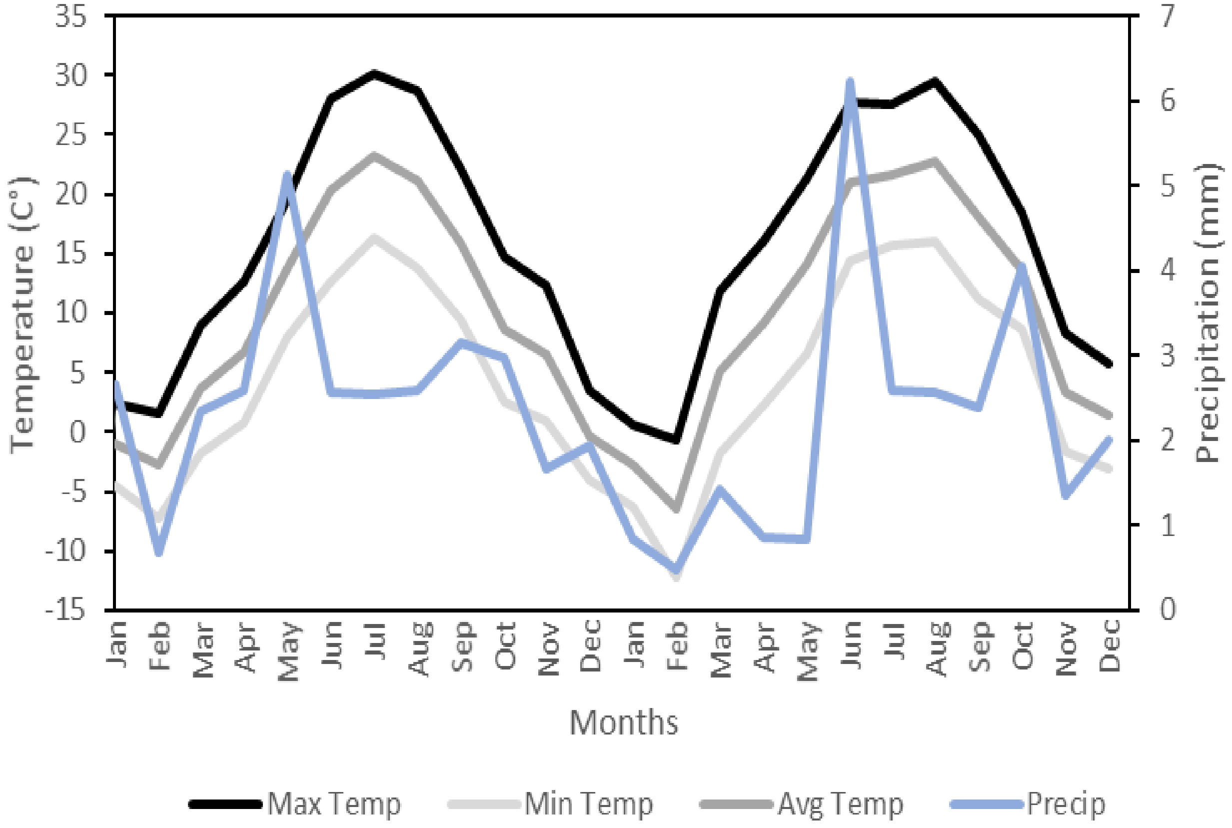

Figure 18. Time-series display of mean minimum, maximum, average, temperatures and precipitation across the span of two years (2020 and 2021). Retrieved from a weather station near the study are of a spotted turtle (*Clemmys guttata*) population in southwest Michigan. Colors lines are denoted as: Black= Average Maximum Temperature (C°), Medium Grey= Average Temperature (C°), Light Grey= Average Minimum Temperature (C°), and Blue= Average Precipitation (mm).

Figure 19. A female spotted turtle (*Clemmys guttata*) found eating black soldier fly larvae (*Diptera stratiomyidae*) within an emergent wetland in southwest Michigan.

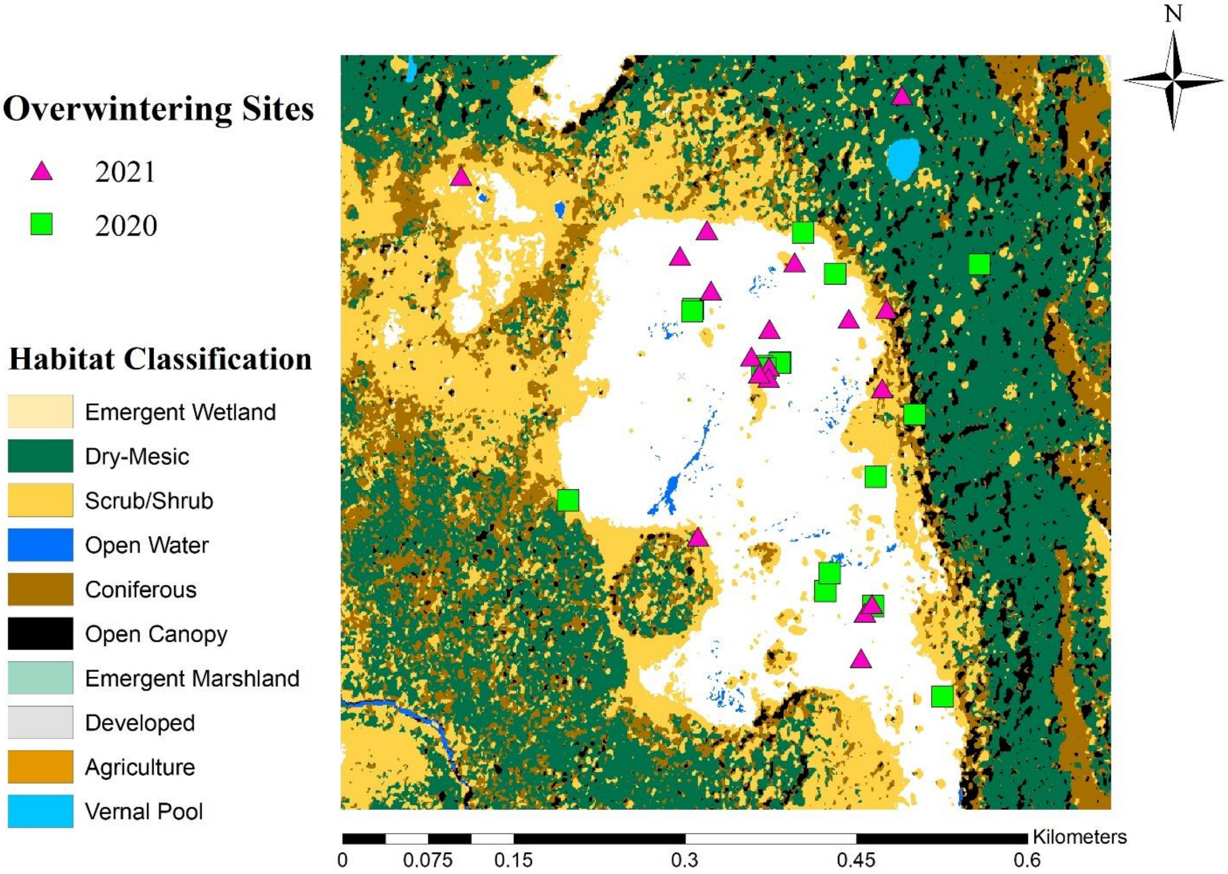

Figure 20. A map of the overwinter sites for each year. On the left of the map, the triangle represents the sites from 2021, and the squares represent the sites from 2020. The habitat classifications are demarcated into 10 categories to represent the map's landcover.

Chapter Three: Extended Review of Literature and Extended Methodology

Extended Review of Literature

Introduction

Reptiles with shells are just an umbrella term to describe the most unique, long-lived, and ubiquitously recognized animals: tortoises, terrapins, and turtles. Turtles, commonly identified by their exceptional morphological architecture, are currently facing a global decline. These reptiles are considered one of the most imperiled vertebrates; almost two-thirds of the 365 extant species are considered vulnerable or on the brink of extinction (Lovich et al., 2018). Turtles' natural delays in sexual maturity, narrow geographic distributions, and low neonatal survival rates have negatively predisposed them to anthropogenic influences such as habitat fragmentation, the introduction of non-native species, poaching, and climate change (Lovich, 1995; Lovich et al., 2018). These reptiles play various roles in their ecosystems, such as contributing to seed dispersal, redistribution of nutrients and energy, and mineral cycling and bioaccumulation (Lovich, 1995). Furthermore, the decline of their populations accompanies grave consequences to their ecosystems. With over half of the world's turtle species either threatened, endangered or extinct (Mali et al., 2014; Lovich et al., 2018), there is a subsequent push for global efforts to prioritize their conservation and prevent the total collapse of their populations and their inhabited ecosystems.

Out of all Testudines, freshwater turtles are the most imperiled branch, with 46-57% of their species listed as highly threatened (Buhlmann et al., 2009; Todd et al., 2010). Despite their vast global range, there are significant gaps in knowledge on their life histories and ecologies, especially when compared to more conspicuous species such as mammals and birds. Preventing further extirpations of these species requires managers to address extinction threats, recognize early detections of their decline, and preserve the habitats in which they occur. However, their disjunctive distributions, low richness, and uncommon life-history traits make conservation strategizing difficult (Buhlmann et al., 2009). Therefore, to succeed in the long-term success in conserving their remaining populations requires data acquisition on their habitat management, spatial ecology, demography, and genetics to close the knowledge gap and form management plans indicative of each species' needs (Stanford et al., 2020).

Life History and Ecology of Spotted Turtles (*Clemmys guttata*)

The spotted turtle (*Clemmys guttata*) is a rare, semi-aquatic, freshwater turtle species that is a member of the family Emydidae and in the Suborder Cryptodira. This species is relatively small, ranging from 9 to 13.7 cm in carapace length (CL; Powell et al., 2016). They are uniquely distinguished by a keelless, smooth black carapace covered in yellow spots, with one to multiple spots per scute, and a hingeless orangish-yellow plastron with black or brown blotching (Lee, 2000). The adult males are identifiable by their secondary sexual characteristics: brown chin, brown eyes, concave plastron, and a cloacal opening on the underside of their thick tail, extended beyond the shell (Ernst, 1972; Appendix Fig. 1). Conversely, female spotted turtles' secondary characteristics are tan chins, yellow eyes, convex plastron, and a cloacal opening on their thinner tail, located under the edge of the shell when fully extended (Ernst, 1976; Appendix Fig. 2).

Spotted turtle populations occur in disjunct locations throughout the Eastern and Midwest states of the United States and the southern end of the province of Ontario, Canada (Litzgus, 2006). This species inhabits aquatic and terrestrial habitats, including isolated wetlands, upland forests, and shallow bodies of slow-flowing water with aquatic vegetation (Lee, 2000). During their active season, which lasts around April – October, depending on geographic location

(Rasmussen et al., 2009), these turtles are dependent on these habitats for essential life cycle activities, such as thermoregulation, mating, aestivation, over-wintering, and foraging (Milam & Melvin, 2001). These turtles are well-developed scavengers with an omnivorous diet, extending from aquatic grasses, macroinvertebrates, small crustaceans, tadpoles (e.g., *Bufo americanus*), and fish (Ernst, 1976). Additionally, these small reptiles use microhabitats, including deer trails, grasses, depressions, vernal pools, or *Sphagnum* mounds, for more effortless movement, prevention of desiccation, or escape from predators (Lutz, 2009; Rowe et al., 2013a).

Spotted turtles, similar to the common box turtle (*Terrapene carolina carolina*), are known for their extremes in longevity, with females living up to 110 years and males up to 65 years of age (Litzgus, 2006, p. 200; Rowe & Gradel, 2013). Their extended life expectancy, similar to most turtles, has been observed as an offset to their delayed sexual maturity, small clutch sizes, low nest survival rates, and environmental stochasticity (Litzgus, 2006). Their survival rates are based on the bet-hedging life history strategy, where turtles' increase in survival, longevity, and fecundity success is positively correlated to their increase in age (Congdon et al., 2001) and quick attainment of total body size (Feng et al., 2019; Tucker et al., 1999). In addition, delayed sexual maturity in spotted turtles ensures a fitness payoff, for they generally face harsher weather conditions across their geographic distribution (Litzgus, 2006; Litzgus & Brooks, 1998).

Spotted turtles are known for their docile disposition and colorful exterior, resulting in their high demand within the domestic pet trades and subsequent vulnerability to illicit collection and trade (Lutz, 2009). In addition to this, their populations are susceptible to genetic bottlenecking and extirpation due to habitat fragmentation and loss, overgrazing, road-crossing mortalities, and climate change (Davy & Murphy, 2014; Ernst, 1976; Lutz, 2009). Consequent to these negative anthropogenic influences, spotted turtles' historical abundance levels have declined by over 50% within the past few decades and thus have been classified as globally endangered (Davy & Murphy, 2014; Litzgus, 2006; van Dijk, 2011). In Canada, this species is granted federal protection and listed as a Species of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Litzgus & Mousseau, 2004); however, within the United States, their conservation status varies by state and lacks overall federal protection (CITES, 2013). In 2012, they were proposed to be listed under the U.S. Endangered Species Act but are still under review by the United States Fish and Wildlife Service (USFWS; Adkins Giese et al., 2012; Feng et al., 2019). Threatened populations in the U.S., such as in Michigan, whose populations have a paucity of studies on their ecology and life-history traits, are highly vulnerable to extirpation. Furthermore, with the lack of federal protection within the United States, it is essential to fill in these knowledge gaps in areas like Michigan, to form proper management plans that will sustain their remaining populations.

Thesis and Research

This study aims to fill in the various knowledge gaps on the spatial ecology and habitat selection of spotted turtles in the Midwest, United States, specifically focusing on a population located in southwest Michigan. Though much of Michigan has not been thoroughly surveyed, 40 counties have tentatively had sightings of this species, dating back to 1921 (MNFI, 2021). Unfortunately, only a handful of those counties are left, consequent of anthropogenic influences (Fig. 1). The remaining populations occupy an array of habitats, many of which are found within our study location, including wetlands like prairie fens and vernal pools and upland habitats such as woodlands and open fields (Lee, 2000). Many vulnerable freshwater turtle species rely upon wetlands, especially isolated wetlands such as vernal pools, prairie fens, bogs, and wet meadows

(Ernst, 1976). For example, Kaye et al. (2001) found that over 96% of their observations of spotted turtles occurred solely in wetlands. Moreover, conservation practitioners need to become better educated on these rare ecosystems to understand habitat requirements for this species more transparently.

This spotted turtle population inhabits two specific wetlands, vernal pools and a prairie fen. Prairie fens are shallow, spring-fed wetlands found throughout the upper Midwest, U.S., hosting a broad range of wildlife (Kost & Hyde, 2009). These aquatic ecosystems are considered a biodiversity hotspot for many threatened and endangered species, such as pitcher plants (*Sarrancenia purpurea*), eastern massasauga rattlesnakes (*Sistrurus catenatus*), Blanding's turtle (*Emydoidea blandingii*), Downy woodpeckers (*Picoides pubescens*), Blanchard's cricket frogs (*Acris crepitans blanchardi*), and spotted turtles (Kost & Hyde, 2009; Lincoln, 2018). Like the prairie fen, emergent wetlands are critically important ecosystems as they deliver ecological services that include removing greenhouse gases, relieving streams and lakes from storm water runoff pollution, and serving as a connection between people and nature (Lincoln, 2018). Spotted turtles utilize these types of wetlands for a large percentage of their activity cycle, such as reproductive activities like nesting and mating, and biological activities like foraging, aestivating, and overwintering (Buchanan et al., 2017; Joyal et al., 2001; Rowe & Gradel, 2013).

Surrounding the prairie fen at the study site is a dry-mesic forest with several vernal pools scattered throughout. These unacknowledged ecosystems are essential for these reptiles as they offer high-quality habitats that support thermal advantages, diverse assemblages, and promote efficient reproductive strategies (Ernst, 1976; Graham, 1995; Litzgus & Mousseau, 2004; Milam & Melvin, 2001). Vernal pools are embedded throughout the upland forests of the field site; these fishless aquatic ecosystems are isolated wetlands that vary in size and are characterized by their cyclical periods of inundations of water (Burne & Griffin, 2005). Vernal pools are filled with water from snowmelt or precipitation in the spring and remain flooded until desiccated from summer heat (Zedler, 2003). During these hydroperiods, these seasonal pools host a unique assemblage of amphibians and rare reptiles and provide essential resources for feeding, rehydration, thermoregulation, courtship, and mating (Burne & Griffin, 2005). These isolated wetlands promote high rates of biological productivity and support a wide array of taxa that have specific life history requirements contingent on the functions within that ecosystem (Leibowitz, 2003). Spotted turtles have a strong association with vernal pools. These seasonal pools play a significant role in their life cycle, as they heavily rely on the provided resources from these pools as a ‘stepping stone’ for starting their activity period (Marsh & Trenham, 2001).

Wetlands hold great intrinsic value for this species; however, they are experiencing a significant decline, with an estimated 53% of wetland habitats lost between 1780 to 1980 in the U.S. (White et al., 2021). Anthropogenic influences like deforestation, climate change, and wetland drainage have severely jeopardized these habitats and their occupants. Spotted turtles are highly susceptible to wetland loss (Buchanan et al., 2017). For example, extreme weather patterns can lead to permanent drought, impeding breeding success and facilitating mass mortalities from loss of food sources and cover (Van Dyke et al., 2019). Therefore, it is essential to establish a baseline understanding of spotted turtle occupancy and wetland habitat selection. Moreover, studying spotted turtles’ spatial ecology and selection of these critical habitats can afford researchers insight into the quality of their habitats and the acute details of their life history and population ecologies needed for management.

As spotted turtle's historic ranges continue to decline, management plans are endlessly being proposed to conserve and restore the remaining populations to better understand their life histories. However, there is still a significant knowledge gap about the spotted turtle's population viability, habitat selection at various spatial scales, and overall spatial ecology in Michigan. Therefore, it is crucial to target these gaps in knowledge by referring to past studies and current studies and survey methods to understand what measures need to be implemented to determine effective conservation strategies.

Spatial Ecology and Habitat Selection

Determining the influences on the spatial ecology of a turtle species can provide researchers with a better insight into population dynamics and demography and can further mitigate imposed threats. However, collecting spatial data on these rare, cryptic species is often limited due to their low detection probability (Crane et al., 2021). Fortunately, advances in technology such as radiotelemetry have permitted researchers greater detection probabilities on population abundance and individual identification and locations within their study area (Refsnider et al., 2011). Traditionally conducted on larger animals, VHF radiotelemetry has only been recently introduced for smaller herpetofauna but has subsequently provided researchers a better perception of their behavioral patterns, foraging strategies, habitat requirements, movement, and home ranges (Crane et al., 2021; Refsnider et al., 2011).

An animal's home range is defined as the area an animal occupies and conducts its "normal activities" (Burt, 1943). By studying an animal's home range, researchers can infer an animal's habitat use, site fidelity, and movement patterns (R. Powell, 2000). Spotted turtle home range analyses are often estimated by radio relocating individuals across their active season and calculating home range size using a minimum convex polygon (MCPs). The MCP is the most conventional home range estimate; it consists of forming a convex hull around the peripheral points of the data set (Worton, 1987). MCPs can be problematic as they are susceptible to outliers and small sample sizes, and assumes data points as independent and identically distributed (Fleming et al., 2015). Despite the flawed outcome when using this home range estimator, many reptile studies, including present studies on spotted turtles, still use this method. Researchers often justify using the MCP for its comparability with a broader array of reptile spatial ecology literature, despite newer and more applicable methods, such as the autocorrelated kernel density estimation (AKDE; Crane et al., 2021).

The recently developed AKDE is a home range estimate that incorporates movement effects using an autocorrelation function (ACF; Noonan et al., 2019). Thus, it accounts for autocorrelation, smaller sample sizes, and predicts future space use throughout the individual's life period (Fleming et al., 2015; Fleming & Calabrese, 2017). This method has proven beneficial for many animals, including relatively sedentary species, such as the Sonoran Desert tortoise (*Gopherus morafkai*; Averill-Murray et al., 2020). Furthermore, applying an AKDE as a home range estimate for spotted turtle spatial ecological studies can provide a predictive component linked to an animal’s movements and shed light on missed population behavior and habitat use that an MCP fails to depict.

Understanding how an animal chooses to disperse itself throughout the landscape is crucial in its ecology. An animal’s use of habitats over what is available within its range affords researchers insight into habitat quality and available resources. Furthermore, as anthropogenic influences continuously alter habitat composition, it can have magnified consequences on an animal’s habitat selection (Arthur et al., 1996). Therefore, examining an animal’s selection of habitats within the landscape can provide insight into their changes of dispersal throughout the landscape and habitat affinities.

Unfortunately, there is an absence of studies on habitat selection by spotted turtles in Michigan, and only within the past decade have researchers begun to conduct analyses on spotted turtles' selection of habitats across their geographic range (Yagi & Litzgus, 2012). Past studies on spotted turtle habitat selection have been used to look at the effects of selection of habitats post-flood, responses to early-successional habitat, temporal analyses, selection of available resources, iteroparity, and habitat use across an individual's long-life span (Buchanan et al., 2017; Rasmussen & Litzgus, 2010; Yagi & Litzgus, 2012). These studies are an essential baseline for other spotted turtle selection analyses as they observe their selection of habitats at multiple scales.

When investigating habitat selection, it is critical to consider selection at multiple scales, for individuals use different criteria that define their use of habitats disproportionate to their availability (Johnson, 1980). Hierarchical habitat selection consists of scales that pertain to a specific spatial scale. For instance, second and third-order selection scales reflect the use of habitats in terms of their availability within the home range from the population range and selection of habitats within the home range (Johnson, 1980; Rasmussen & Litzgus, 2010). Observing habitat at multiple scales also teases out movement influences, dispersal strategies, energetics, and foraging (Mayor et al., 2009). Furthermore, researchers have observed variation and thorough characterization of habitat use patterns when studying habitat selection at multiple scales, producing a habitat utilization rank order that ranks habitats from most preferred to avoided (Degregorio et al., 2011; Mayor et al., 2009). However, methods to quantify habitat selection must be carefully chosen based on the study species to determine habitat selection at specific spatial scales.

Two fundamental methods are used to quantify habitat selection: Compositional Analysis (CA) and Euclidean Distance Analysis (EDA; Degregorio et al., 2011). EDA is a distance-based analysis that compares the mean distance of an animal's location to the nearest available habitat type to determine if they are closer or farther to that habitat than expected. In contrast, the CA is a classification-based analysis that looks at the percentage of the habitats within an animal's range versus what is available (Miller et al., 2012). EDA relies on random points and is more tolerant of radio-tracking and GPS location errors than a CA, and can tease apart distinctions among habitat use at a smaller spatial scale (Degregorio et al., 2011; Markle & Chow-Fraser, 2018). The EDA is thus the more preferred method, as it is more successful at distinguishing preference versus avoidance of habitats. However, this method relies on viewing habitat selection on multiple spatial scales and is dependent on an individual's home range to determine available habitats. Furthermore, habitat selection research is inextricably tied to an animal's home range as it permits individual assessments of habitat availability (Mitchell et al., 2019). Therefore, utilizing AKDE for estimates on habitat selection, especially for spotted turtles, can provide better measurements of habitat use than more conventional home range estimates, as its boundaries consist of future movements that collectively incorporate future habitat use (Fleming & Calabrese, 2017).

This study aims to determine this spotted turtle population's spatial ecology and habitat selection within an emergent wetland in southwest Michigan. In addition, we aim to determine influences on movement, habitat selection, and home range size to influence management decisions on this population and others within similar latitudes. As spotted turtle populations continue to decline drastically, it is imperative to fill in the knowledge gaps on their life history and population ecology, especially in understudied regions such as Michigan. Henceforth, I have used an innovative home range estimate, AKDE, and an EDA to determine the influences of their dispersal and movement patterns throughout the landscape. My results will aid in management decisions and conserving this threatened species and its rare habitats.

Extended Methodology

Study Site

Our study site (53 ha), located in Barry County, Michigan (45° N, 85° W), is characterized by a mosaic of relatively undisturbed palustrine communities, including southern shrub, forested wetlands, emergent wetlands, and vernal pools within state-owned land (Fig.2). Surrounding the site is a landscape matrix of agriculture fields, roads, and developed areas that slowly fragment the remaining untouched habitats within the area. To protect the study species and other vulnerable ones that occupy the study area, we are withholding the exact site location to prevent illicit trade and collection.

The central portion of the study site is a type of emergent wetland known as a prairie fen (13 ha), a rare groundwater-fed ecosystem characterized by alkaline organic soils and graminoid-dominated vegetation (Cohen et al., 2020; Kost et al., 2007). This habitat is a hotspot for biodiversity as it holds a diverse range of rare plant and animal species, including willow aster (*Aster praealtus*), Jacob's ladder (*Polemonium reptans*), spike-rush (*Eleocharis radicans*), tamarack tree crickets (*Oecanthus laricis*), eastern massasaugas (*Sistrurus catenatus*), eastern box turtles (*Terrapene carolina carolina*), and spotted turtles (*Clemmys guttata*). Intermittently throughout the spring and summer, this wetland is often submerged in water resulting from heavy snowmelt or precipitation. In particular, deer trails, kettle ponds, and wet depressions within the fen are filled with water greater than 10 cm deep and used by an array of biota for feeding, thermoregulation, and more effortless locomotion (Rowe et al., 2013). In addition, patches of sphagnum moss and scrub/shrub are scattered throughout the fen and used for cover, thermoregulation, aestivation, and overwintering for various species. Encompassing the fen is a closed-canopy, oak-dominated forest (dry-mesic southern forest) that contains multiple vernal pools. These rare ephemeral pools are unique, intermittent wetlands that experience cyclical periods of flooding and drought concurrent with seasonal climate (Thomas et al., 2010). They provide refuge for various functionally specialized organisms that can endure and often rely on the hydrological regime's dramatic changes (Zedler, 2003). These ecosystems presently support an extant spotted turtle population with >100 individuals known and marked.

Data Collection

From May-early June of 2020 and 2021, we captured spotted turtles opportunistically throughout the prairie fen or by using hoop traps (Promar TR-503), baited with sardines within the vernal pools scattered around the site (Fig. 3). Turtles were marked individually by notching a unique combination of scutes using a triangular file (Cagle, 1939). Markings were accorded to a definite system that was based on a number combination (1-100), beginning with the anterior marginal on each side and counting from the nuchal (Cagle, 1939). The marginal plates on the junction of the carapace were not marked. We collected morphological measurements of each turtle captured and determined sex by secondary sexual characteristics (e.g., males were identified by a concave plastron and long pre-cloacal tail length). Midline carapace length (MCL, to the nearest mm) was measured to the nearest mm using calipers (150 mm; Vernier Digital Caliper, Edgewood, New York) and weighed to the nearest gram using a spring scale (163 g; Pesola Medio-Line Spring Scale, Forestry Suppliers, Jackson, Mississippi). We were unable to assess the reproductive status of individual females because we did not use x-ray equipment to detect eggs, and the turtles were too small for inguinal palpations.

Twenty turtles (n=10 males, 10 females) were outfitted with very high frequency (VHF) radio transmitters (model R1645, Advanced Telemetry Systems, Fish and Wildlife, Isanti, Minnesota, USA) onto the posterior carapace using J-B WaterWeld epoxy (J-B Weld Company, Sulphur Springs, Texas, USA; Fig. 4). Transmitter and epoxy weights were less than <5% of each individual's body mass. All turtles were released at their initial capture points once epoxy dried and transmitters were secured.

Turtles were radio-tracked throughout their active seasons (May to October 2020 and 2021). For both years, turtles were located 3-4 times a week from May-July and 1-3 times a week from August to October, using a three-element Yagi antenna and an R410 Scanning radio-receiver (Advanced Telemetry Systems Fish and Wildlife, Isanti, Minnesota, USA). Once individuals were located, coordinates were recorded using a handheld GPS and uploaded to RStudio Team (2019) and ArcGIS v. 10.4.1.

Home Range Analysis

Studies that focus on herpetofauna and species with cryptic behavior have lacked a consensus in selecting an appropriate home range estimation (Silva et al., 2018). The minimum convex polygon (MCP) has been the most traditional home range, formed by a convex hull encompassing all recorded locations for that individual (Anderson, 1982; Millar & Blouin-Demers, 2011). However, current herpetofauna studies only use MCPs as references to past studies (Bowers, 2021) and estimate home ranges using a non-parametric kernel density estimator (KDE; Worton, 1989); which uses the GPS locations of an individual and constructs a continuous intensity surface of their utilized distribution (U.D.; Downs & Horner, 2007). Despite the frequent usage of KDEs and MCPs, studies have found these home range estimations to be highly unreliable (Averill-Murray et al., 2020; Fleming et al., 2019; Fleming & Calabrese, 2017). They rely on independent and identically distributed data (IID; a violation of current tracking data) and do not account for temporal autocorrelation, varying sampling frequency, or correction of small effective sample sizes (Averill-Murray et al., 2020).

Most recent herpetofauna home range studies have transitioned over and used the autocorrelated density estimation (AKDE) to estimate home range size and U.D. in place of KDE and MCPS. An AKDE is an innovative home range estimator that considers temporal autocorrelation and accurately exemplifies the long-term space use through statistically rigorous predictions of future movements, avoiding type I and type II errors (Fleming et al., 2015; Montano et al., 2021; Silva et al., 2021). This method uses Akaike information criterion (AIC) theoretic models to select the most appropriate autocorrelation model and optimizes the smoothing bandwidth (*'h'*) under an autocorrelated Gaussian reference function approximation (Calabrese et al., 2021; Fleming et al., 2019).

For our study, we calculated home ranges for each turtle by collecting radio locations throughout their active season and uploading the GPS locations into RStudio. Home ranges were estimated for each sex over two activity cycles. We used two different home range estimations: 95% Minimum Convex Polygons (MCPs; Anderson, 1982; Bekoff & Mech, 1984) and autocorrelated kernel density estimation (AKDE) using 95% kernels (Fleming et al., 2015). The MCP home range is a standard parametric method that uses the outermost locations of the dataset to create a convex polygon with angles no greater than 180° to represent the animal's home range (Worton, 1987). As mentioned prior, there is a tendency for MCPs to underestimate portions of an animal's home range (Worton, 1987); however, we still chose to include MCP estimates for comparison with past studies (Rowe et al., 2013; Smith & Cherry, 2016). Minimum convex polygons (95%) were estimated using the '*mcp'* function in the *adehabitatHR* package in RStudio v.0.9.0-351 (Calenge, 2006; RStudio Team, 2021).

We chose to use an area-corrected, optimally weighted AKDE$_c$ (wAKDE$_c$) to represent the true home ranges and core ranges of this population, as this method corrects for irregular data sampling, small sample size, and temporal sampling bias (Fleming et al., 2018), and outperforms the KDE and MCP home range estimations. To assess the $wAKDE_c$ home range and core area for each turtle, we used the *ctmm* R package (Fleming et al., 2019), only including turtles with ≥ 20 relocations to ensure adequate sampling (Paterson et al., 2012). We first checked for each individual's range residency (their tendency to remain within their home range) by calculating the semi-variance function (SVF) through the '*variogram()*' function, which allowed us to unbiasedly observe the autocorrelation structure (Calabrese et al., 2016; Silva et al., 2021) RStudio Team, 2021). Followingly, we tested for movement models that would explain the autocorrelated structure of the movement data by using an automated model *'ctmm.select'* with the perturbative hybrid residual maximum likelihood (pHREML) as the default parameter estimation method (AIC_c; Calabrese et al., 2016; Silva et al., 2021). Perturbative Hybrid REML is the most comprehensively implemented method that improves (co)variance for small effective and absolute sample sizes (Silva et al., 2021). Considering that our autocorrelated tracking data was irregularly sampled with a small sample size the pHREML fitted-weighted optimization was the most suitable home range method to increase spatial resolution and correct irregular sampling (Fleming et al., 2018; Silva et al., 2021). Movement models were selected and fit into a $wAKDE_c$ using the '*akde'* function from the *ctmm* package to estimate individual turtle's home range sizes (ha), extracting 50% and 95% kernels as percentile level ranges for all individuals (±95% CI; Calabrese et al., 2016; Silva et al., 2021). We assumed 50% kernels as the animal's 'core' activity ranges, representing 50% of its highest density region (HDR). The entire home range was represented by the 95% kernel, maintaining 95% of the probability distribution of all possible locations determined from the dispersal of all possible paths (Fleming et al., 2015).

Individual turtle home ranges were extracted as a spatial polygon and projected into ArcGIS v. 10.4.1 (ESRI, 2021).

We used a simple log-transformed linear regression to determine whether there was a linear relationship between a 95% $\mathrm{wAKDE_c}$ home range size and mean carapace length (MCL; mm) and mean mass (g). Home ranges (95% $\mathrm{wAKDE_c}$) and core ranges (50% $\mathrm{wAKDE_c}$) were analyzed using a two-way analysis of variance (two-way ANOVAs) to examine the effects of sex, year, and sex X year on mean home range sizes (ha). We used a Tukey HSD test for a post-hoc analysis to identify differences in the variables' outcomes if the results were significant. Percent of 95% $\mathrm{wAKDE_c}$ home range overlap was assessed for individuals tracked for both years (*n*=14), and the percent of 95% MCP home range overlap was measured for individuals (*n*=2) that were tracked in a previous study by Rowe et al. (2013). The "Intersect" tool within the Analysis Tools in ArcMap v. 10.4.1, was used to extract the area of overlap between an individual's home range polygons. The formula used to calculate percent overlap was represented by:

$$[\mathrm{Area_{Intersect}} / (\mathrm{Area_{Homerange1}} + \mathrm{Area_{Homerange2}} - \mathrm{Area_{Intersect}})] \times 100$$

Mean annual percent home range overlaps were compared by sex using a Mann-Whitney U test.

Lastly, we used a Spearman's rank correlation test to determine if there was a relationship between the size of an individual's 95% MCP home range and their 50% $\mathrm{wAKDE_c}$ core range, as MCPs are often known to underestimate home ranges and only include the central locations. Minimum convex polygon home ranges were taken and compared with historical studies. We tested for normality violations ($P < 0.05$) and homogeneity of variance using a qqplot and histogram, along with Levene's test and Shapiro Wilk's test in RStudio (RStudio Team, 2021).

Movement Analysis

We estimated movement metrics for each turtle (n= 22) by quantifying the Euclidean straight-line distance (m) and time-lag between consecutive relocations along a movement track throughout each active season, using the move package in R (Kranstauber et al., 2017). We accounted for the non-normal distribution of movement data through the utilization of Poisson distribution. We calculated each individual's mean daily distance traveled (MDDT) by taking each successive step-length (m) recorded and dividing it by the number of days elapsed since the last location. We then took the mean MDDT for each month across the two years using individuals as replicates. A two-way ANOVA with $\log_{10}$ transformed data was used to observe the effects of date, sex, and sex X date on MDDT.

We followed this by performing a components analysis (PCA) to quantify and compare the interrelationship amongst environmental parameters, sites, and MDDT, using individual turtles as replicates (weather data was retrieved from the Michigan Enviro-weather Automated Weather Station Network, Pierce Cedar Creek Institute, Hastings, MI, USA). Variables used in this ordination included minimum temperature (°C), maximum temperature (°C), average temperature (°C), precipitation (mm), and average solar radiation kJ/m^2. Sites reflected months (May, June, July, August, and September) and plotted over time (2020 and 2021). Points in the ordination were represented as individuals' MDDT; the larger-sized points demonstrated greater distances traveled on average, whereas smaller-sized points represented less distance traveled on average. To further explore these relationships, we regressed MDDT against the factor scores with PC1 and PC2, using simple linear regressions. All data were tested using R statistical software v. 4.1.1 (R Development Core Team, 2021) for normality using a Shapiro-Wilk's test and equal variance with a Levene's test setting the alpha level to 0.05, and were transformed if not normal.

Habitat Selection Analysis

We created habitat classification maps for the study site, defined in ArcMap 10.4.1 using the USGS EROS archive ArcGIS data layer, based on 1:12,000 infrared stereo aerial photography (USGS, 2014), along with ground-truthing and measurement using a handheld GPS unit (Garmin, Kansas City, Kansas USA). Habitats were reclassified based on natural community descriptions in Kost et al. (2007). We classified land cover into ten land classes in ArcMap 10.4.1: (1) Emergent wetland, (2) Dry-mesic Forest, (3) Scrub/Shrub, (4) Open Water, (5) Coniferous, (6) Open Canopy, (7) Emergent Marshland, (8) Developed, (9) Agriculture, and (10) Vernal Pool (Table 1).

We investigated habitat selection at two biologically relevant spatial scales based on Johnson's (1980) hierarchal selection approach. We considered 2nd order (population range) – selection of home range from within the population range, and 3rd order (home range scale) – selection within the individual's home range (Edge et al., 2010; Paterson et al., 2012). Habitat selection was analyzed using a Euclidean Distance Analysis (EDA) to measure the straight-line distance of each location to the nearest available habitat type. This assessment provided an estimate of habitat use vs. availability and determined an individual's preference or avoidance of a particular habitat type within the spatial scale of interest (Benson, 2013; Conner & Plowman, 2001).

To satisfy the requirements of 2nd order selection, we had to define a population range. We determined a population range by merging all 95% wAKDE$_c$ home ranges from both field seasons into a single polygon in ArcMap (v. 10.4.1) and buffering that polygon by 250m (the maximum width of an AKDE home range) to fully encompass the limits of available habitat (Fig. 5). Within ArcMap, we used “Data Management Tools” to generate 1,299 random points in a uniform random distribution (Conner & Plowman, 2001), equal to the total number of radio locations for all individuals across both years within the population range boundary (128.4 ha; Paterson et al., 2012). Next, we selected the “Near” tool in ArcMap to measure Euclidean straight-line distances from each point to the nearest representatives of each habitat type (Conner & Plowman, 2001). A ratio of use vs. availability was created for each individual (i) for each habitat type (j) for both spatial scales. The ratio formula was represented as

$$d_i = u_{ij}/r_{ij}$$

where u_{ij} is defined as use and r_{ij} as availability. This ratio allowed us to evaluate if habitats were preferred ($d_{ij} < 1$), avoided ($d_{ij} > 1$), or randomly used ($d_{ij} = 1$) (Conner et al., 2003).

For selection within the population range (second-order), we defined habitat use (u_{ij}) as the mean distance from random points within an individual’s home range to the nearest representative habitat type within the population range. We measured habitat availability (r_{ij}) for second-order as the mean distance from random points within the population range to the nearest available habitat type within that same range. Similar to the population range, to quantify habitat selection within individual home ranges (third-order), we merged home ranges of individuals tracked across both field seasons and those tracked for one field season for the analysis. At the third-order scale, we determined habitat use (u_{ij}) as the mean distance from telemetry points within each individual’s home range to the nearest available habitat type within their home range. Habitat availability (r_{ij}) was measured as the mean distance from random points within each individual’s home range to the nearest available habitat type within the same range. The selection scale was analyzed utilizing a one-way MANOVA on square root-transformed data to test if the mean distance ratios (d_{ij}) for each habitat were significantly different from a vector of 1's, using individual turtles as replicates. The ratios further provided evidence of habitat selection at the selected spatial scale ($d_{ij} \neq 1$; Paterson et al., 2012). If there was evidence of habitat selection, we followed with square root-transformed one-sample *t*-tests using a Bonferroni correction for multiple comparisons (2nd order: $\alpha = 0.05/10$ habitats = 0.005; 3rd order: $\alpha = 0.05/6$ habitats = 0.007), to determine which habitat ratios were significantly different from one. We followed with a Tukey HSD as a pairwise comparison test to produce a relative rank of habitats based on preference.

Appendices

Chapter Three Figures

Appendix Figure 1. Examples of male spotted turtle (*Clemmys guttata*) secondary sexual characteristics. The picture on the left shows a male spotted turtle's concave plastron and thick tail. The picture on the right focuses on the male's brown iris and dark chin.

Appendix Figure 2. Examples of female spotted turtle (*Clemmys guttata*) secondary sexual characteristics. The left picture shows a female spotted turtle's convex plastron and thin tail with the cloaca lining the edge of the carapace. The picture on the right focuses on the female's yellow iris and tan chin.

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