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Wood Turtle (*Glyptemys insculpta*) Spatial Ecology, Habitat Selection, and Use of Restored Oak-Pine Barrens in Northwestern Michigan

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Dedication

This thesis is dedicated to my friends and family who have always been so loving and supportive of my wild dreams. And to my younger self: We never gave up no matter how hard it got, and we've come so far. All that's left is to go even further.

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Abstract

Habitat fragmentation and loss, predation, and illegal collection are among the many threats plaguing turtle species worldwide which have caused substantial population declines. In the United States and Canada, approximately 38% of turtle and tortoise species are under significant threat. The wood turtle (*Glyptemys insculpta*) a freshwater turtle species experiencing declines and in 2023, the U.S. Fish and Wildlife Service will determine if this species should be listed under the Endangered Species Act. We studied the spatial ecology of wood turtles in northwestern Michigan, USA to fill knowledge gaps that exist throughout their geographic range. Between May 2021 and August 2022, we used VHF radiotelemetry to track 21 wood turtles which allowed us to quantify home ranges and movement patterns, assess habitat selection, and evaluate use of restored oak-pine barrens. Across both field seasons, average home range sizes were not statistically different between gravid females (23.92 ± 16.26 ha), non-gravid females (11.24 ± 3.40 ha), males (12.76 ± 5.68 ha), and juveniles (3.69 ± 1.46 ha). Gravid females averaged farther distances from the river (219.03 ± 13.85 m) compared to non-gravid females (64.86 ± 4.65 m), males (58.08 ± 2.77 m), and juveniles (34.82 ± 2.79 m). Differences between this population and others can be attributed to variations in the availability of resources, quality of habitat, and accessibility of nesting grounds which are inconsistent across their range. Turtles selected lowland riparian and aquatic habitats and avoided upland forest and forested slopes which echoes other wood turtle studies. One gravid female nested in the restored oak-pine barrens habitat indicating this management practice may benefit the reproductive success of this population through an expansion of nesting opportunities. The variability we observed across years in home range sizes, movement distances, and habitat selection among sex and reproductive classes within this population, indicates a need for continued monitoring to

determine long-term patterns. The use of oak-pine barrens by gravid females both years provides preliminary support that this restoration may benefit this wood turtle population.

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Abbreviations

°C – degrees Celsius

aKDE – autocorrelated kernel density estimations

CA – compositional analysis

CBD – The Center for Biological Diversity

CL – carapace length

cm – centimeters

CWD – coarse woody debris

EDA – Euclidean distance analysis

EGLE – Michigan Department of Environment, Great Lakes, and Energy

ESA – Endangered Species Act

f^3/s – cubic feet per second

GPS – Global Positioning System

ha – hectares

HMNF – Huron-Manistee National Forest

IUCN – The International Union for Conservation of Nature

KDE – kernel density estimations

km – kilometers

m – meters

mm – millimeters

MANOVA – multivariate analysis of variance

MCP – minimum convex polygons

NAIP – National Agriculture Imagery Program

RFSS – Regional Foresters' Sensitive Species

SE – standard error

USFS – United States Forest Service

USFWS – The U.S. Fish and Wildlife Service

VES – visual encounter surveys

VHF – very high frequency

Chapter 1: Introduction

Introduction

Turtles and tortoises play important ecological roles in their respective ecosystems throughout the world. They aid in nutrient distribution throughout ecosystems, mineral cycling, seed dispersal and germination, and soil disturbance (Lovich et al. 2018). Worldwide, turtles face many anthropogenic and natural threats including habitat loss and fragmentation, overharvesting, and predation (Rhodin et al. 2018). An estimated 52% of freshwater turtle species are experiencing significant declines worldwide (Böhm et al. 2013). The importance of their ecological contributions, coupled with the magnitude of threats they face, emphasizes the importance of studying and protecting turtles. To develop appropriate conservation strategies to aid these imperiled species, researchers and managers must have a thorough knowledge of turtle spatial ecology and habitat requirements.

Spatial ecology focuses on the analysis of habitat and resource use at different spatiotemporal scales. Plant and animal species use ecosystems and their mosaic of habitats at different scales and over different periods of time depending on their resource requirements, lifespan, and reproductive cycles. The spatiotemporal use of habitat based on availability and resource requirements at different scales is termed habitat selection (Morris 2011). Different classifications of scale have been proposed but many follow Johnson (1980) who defined four levels of spatial selection. First order selection occurs within the species' geographic range. Selection at the second order involves population-wide habitat use versus availability. Third order selection involves habitats selected within an individual's home range. Lastly, fourth order selection encompasses fine scale movements and use of habitat within habitat patches of an individual's home range (such as foraging or nest sites). Scale and taxon dependent factors influence habitat selection complicating efforts to determine the appropriate scale of analysis. The temporal aspect of a study also varies depending on the natural history of the study species and the study objectives (Morris 2011). This variety of factors necessitates a multi-scale approach to quantifying habitat selection (Mayor et al. 2009). Understanding the most ecologically relevant spatiotemporal scale at which a species selects specific resources can aid in the development and implementation of appropriate management plans for that species and their habitat.

Several common methods exist for analyzing the spatial ecology of a species. Within home range selection (fourth order) studies often focus on selection of vegetative communities or key habitat structures used by individuals to understand fine-scale preferences (Kaufmann 1992a, Compton 2002). These findings can be scaled up to the analysis of individual and population home ranges at the third and second order which delineate habitat type preferences. A final scaling to first order selection provides an overall landscape use pattern exhibited by a species throughout their geographic range. All levels of selection involve the specific choice to use certain habitats or resources over others that may be available.

Adding a temporal component into these studies provides information on movements, home range selection, and habitat selection at any indicated time interval (e.g., hourly, daily, diurnal, nocturnal, yearly activities). Long-lived reptiles and large mammals require longer study periods and many years of data to determine patterns in their natural history (Tinkle, 1979).

Collectively, turtles are a long-lived taxonomic group that require long-term studies to understand habitat selection in relation to survival and reproductive success (Harding and Bloomer 1979, Galbraith and Brooks 1989). This information can then be incorporated into management plans. Most turtle species exhibit delayed maturation in which it can take an individual decades before it is able to reproduce however, this strategy often results in improved individual fitness and better resistance to environmental changes (Deevey Jr. 1947, Pianka 1970). However, these animals are also slow moving and survival can be affected by habitat quality and availability. Major changes to habitat structure and declines in population size can harm population viability and reproductive success which might not be quantifiable for many years due to their long and cryptic lives thus indicating a need for long-term population monitoring.

Measures have been taken to protect imperiled species including the development of the international IUCN Redlist which lists species most at risk of extinction. There are also national lists of conservation concern controlled by legislation such as the U.S. Endangered Species Act (ESA) and the Species at Risk Act in Canada both of which provide resources for assessing levels of risk, provide protection from collection and habitat loss, and specify recovery and conservation actions. Species listings and assessments also occur at the state and province level in the United States and Canada, respectively. Many turtle species endemic to the midwestern and northeastern United States are listed as threatened or endangered by the IUCN Redlist and are included in other lists throughout the Unites States (Rhodin et al. 2018). However, we cannot enact appropriate conservation strategies to protect at-risk species and their habitats without adequate knowledge of species distributions, population viability, and responses to anthropogenic disturbance.

Wood turtles are semi-aquatic freshwater reptiles endemic to the Great Lakes region and surrounding midwestern and northeastern United States, as well as southeastern Canada. Due to the various threats they face, populations are declining throughout their native range, and they are being considered for federal protection in the United States (Adkins Giese et al. 2012, U.S.

Fish and Wildlife Service 2016). Internationally, they are listed on the IUCN Redlist as an endangered species, and they are threatened in Canada (van Dijk and Harding 2011, Environment Canada 2016). Throughout their United States distribution, individual states have listed them as at-risk, threatened, or endangered, and they are a species of special concern in Michigan. These statuses are attributed to declines caused by habitat fragmentation via roads and water barriers, habitat destruction through timber harvest, development, and recreational activities, illegal collection for the pet trade, and predation (Adkins Giese et al. 2012, Jones et al. 2015).

Management of habitat for wood turtles can be complicated because they use multiple habitat types throughout the year which can vary by sex and reproductive class. Seasonal habitat use is based on activity and resource availability (Strang 1983, Kaufmann 1992*a*, McCoard et al. 2018). Wood turtles are commonly found in or near moving water and tend to stay within nearby riparian habitat in the spring and fall, summer is often spent farther from water, and winter brumation occurs in rivers or streams. Females may regularly move farther from water in search of nesting sites, so movement and home range estimates reflect these nesting forays. Preferred aquatic habitat tends to be shallow with a sandy bottom and terrestrial habitat preference is for open canopy habitat with complex ground vegetation and woody debris (Compton et al. 2002, McCoard et al. 2018). This species exhibits a preference for habitat edges and efficiently uses both aquatic and terrestrial habitats for thermoregulation, foraging, protection, mating, and nesting which further complicates their habitat requirements (Arvisais et al. 2004).

In Michigan, wood turtles are a species of special concern, and while scientists have been studying some populations in northern Michigan, there is a lack of statewide data. In the northeastern section of the Huron-Manistee National Forest (HMNF), there have been multiple long term population studies of wood turtles, providing scientists with useful information for managing these areas. Willoughby et al. (2013) used genetic analyses of wood turtles at three sites in the northern Lower Peninsula to determine demography and measure genetic diversity and found evidence of population declines. Schneider et al. (2018) used 18 years of radiotelemetry and capture data to create population models, estimate recruitment, and estimate survival in the northeastern HMNF. They found evidence of historically declining populations that have now stabilized in population size, are experiencing growth, and have maintained genetic diversity because of habitat management that included closing unregulated roads. Another wood turtle study from Michigan's Upper Peninsula discovered that soil disturbance was a cue for predators of turtle nests and that nests placed farther from rivers experienced a lower chance of depredation (Rutherford et al. 2016).

Only one published study has quantified wood turtle spatial ecology in Michigan (Remsberg et al. 2006). They determined poor habitat quality or drought may be causing larger average home ranges in Michigan compared to other studies. The collection of movement, home range, and habitat selection information for populations of wood turtles throughout Michigan is essential to continue understanding the dynamics and behaviors of this species and to fill knowledge gaps. This knowledge can then be used to inform current and future management plans to ensure persistence of these populations and this species into the future.

Chapter 2.1 is formatted as a manuscript for submission to *The Journal of Wildlife Management.* This chapter focuses on home ranges, movement, and habitat selection of focal wood turtles. We have also included information on the spatial ecology of this population in relation to oak-pine barrens restored by the U.S. Forest Service (USFS). Chapter 2.2 contains various ecological notes recorded and analyzed during the field season.

Purpose

The wood turtle is listed as a species of special concern in the state of Michigan and a Regional Foresters' Sensitive Species (RFSS) in the HMNF according to the USFS. Due to the variation in habitat availability and quality that exists throughout the wood turtles' range, it is important to study individual populations in all geographic areas. Quantifying movement patterns and habitat use can guide local land management and can be used to compare with other populations which helps to better understand wood turtle natural history. We sought to provide useful information to the local USFS land managers as well as supplement existing knowledge of wood turtle habits in the wider literature.

One objective of this study included collecting and comparing spatial data regarding home range sizes and movements of wood turtles in northwestern Michigan with other wood turtle populations throughout their range. Another objective involved analyzing habitat selection at the second and third order to assess patterns of selection for comparison with other populations. We also sought to determine use of USFS restored oak-pine barrens and how this might affect the wood turtle population into the future. Comparing this population with others will provide valuable information that can assist listing decisions and guide land management of this public forest area.

Scope

The scope of this thesis includes quantifying home ranges of adults and juveniles, assessing movement patterns, analyzing population and individual habitat selection, and determining use of recently restored oak-pine barrens.

Assumptions

- We assume telemetry had no effect on movements or subsequent relocations.

- We assume telemetry from May to August is an accurate representation of each turtle's peak activity period to quantify average home range sizes and movement patterns.
- We assume GPS locations are accurate within a certain degree of error.
- We assume digitized land cover classification is an accurate representation of the habitat types in our study site.
- We assume 95% KDEs are adequate delineations of our study site and home ranges within.
- We assume Euclidean Distance Analysis is an appropriate method of analyzing habitat selection for wood turtles and that all distance ratios were independent of each other among all turtles.

Hypotheses

We hypothesize that these wood turtles will have smaller home ranges than those of other turtles throughout their range based upon the variety of habitat types available within our study site and the low disturbance they experience. We hypothesize wood turtles will primarily be found in the riparian floodplain surrounding the river corridor and will use open canopy habitats with complex ground vegetation like other populations throughout their range. We hypothesize that oak-pine barrens restoration will not affect wood turtles due to timing of restoration activities and the wood turtle's tendency to avoid upland forested areas in other populations.

Significance

This study provides valuable natural history information of wood turtles in northwestern Michigan where there is currently no published information. These data may help the U.S. Fish and Wildlife Service (USFWS) make a listing decision for this species in 2023. The USFS can also use this information to assess management strategies and tailor them to most benefit these wood turtles based on their responses to restoration activities and the timing of their seasonal movements. Our study contributes to the growing body of knowledge on wood turtle spatial ecology throughout their range.

Definitions

Anthropogenic – originating in human activity

Endangered – at serious risk of extinction

Endemic – native and restricted to a certain place

Habitat fragmentation – continuous habitat split into smaller patches

Home range – the area where an animal obtains resources and moves to fulfill natural history requirements

Mesopredator – a mid-trophic level predator that preys on smaller animals

Spatial ecology – the ultimate distributional or spatial unit occupied by a species

Threatened – at risk of being endangered

Chapter 2.1:

Wood turtle spatial ecology, habitat selection, and use of restored oak-pine barrens in northwestern Michigan

ABSTRACT Wood turtles (*Glyptemys insculpta*) are experiencing widespread population declines in the face of many threats including habitat fragmentation and loss, predation, and illegal collection. Understanding wood turtle spatial ecology and habitat selection is crucial for managing habitat and to determine the required level of protection needed to ensure the viability and growth of existing populations. In 2023, the U.S. Fish and Wildlife Service will determine if this species should be listed under the Endangered Species Act which presents an immediate need to fill knowledge gaps of unstudied populations. We studied the spatial ecology of wood turtles in northwestern Michigan, USA to help fill these knowledge gaps. Between May 2021 and August 2022, we used VHF radiotelemetry to track 21 wood turtles which allowed us to analyze home ranges, movement patterns, habitat selection, and use of restored oak-pine barrens. We found no statistical difference between the home range averages of gravid females (23.92 ± 16.26 ha), non-gravid females (11.24 ± 3.40 ha), males (12.76 ± 5.68 ha), and juveniles (3.69 ± 1.46 ha). Gravid females averaged farther distances from the river (219.03 ± 13.85 m) compared to non-gravid females (64.86 ± 4.65 m), males (58.08 ± 2.77 m), and juveniles (34.82 ± 2.79 m). These measures differ from other populations which can be attributed to spatially varied resources, variable habitat quality, and the inconsistent accessibility of adequate nesting habitat across their range. These turtles selected lowland riparian and aquatic habitats and avoided upland forests and forested slopes which mirrors other wood turtle studies. One gravid female nested in the restored oak-pine barrens habitat indicating this management may benefit the reproductive success of this population through an expansion of nesting opportunities. The

variability we observed across years in home range sizes, movement distances, and habitat selection among sex and reproductive classes within this population, indicates a need for continued monitoring to determine long-term patterns. The use of oak-pine barrens by gravid females both years provides preliminary support that this restoration may benefit this wood turtle population.

KEYWORDS Euclidean distance analysis; home range; herpetology; radiotelemetry

Spatial ecology explores where, when, and how a species is using habitat. An important determinant of spatial ecology is habitat selection which refers to the use of habitat relative to its availability. A species' natural history influences spatial ecology and habitat selection at different spatiotemporal scales (Mayor et al. 2009). "Scale" is an ambiguous term and there have been many attempts to rigidly define spatial scales that are often complicated by differences in the natural history of various plant and animal species. A commonly used hierarchy of scale was defined by Johnson (1980) who suggested four general scales of selection. These orders of selection scale down from first order selection occurring within the species' geographical range, to second order selection involving population-wide habitat use, to third order selection involving selection within individual home ranges and ending with fourth order selection which incorporates specific resource use on a fine scale within different habitat patches of a home range.

With more complex natural histories and resource requirements, come more challenges to studying certain species. Reptiles can be long-lived and often exhibit complex mating and reproductive strategies and require specific habitat characteristics that can change with ontogeny.

Because of these specific natural history traits, these species can be vulnerable to changes in habitat quality and resource availability. Turtles are an exceptionally vulnerable order as they exhibit long lives, delayed sexual maturation, and complex habitat requirements. An estimated 52% of freshwater turtles are experiencing significant declines worldwide (Böhm et al. 2013). These declines are attributed to threats including habitat loss and fragmentation, overharvesting, and predation (Rhodin et al. 2018). Turtles play important ecological roles throughout the world adding to nutrient cycling and soil disturbance, being predators or prey, and aiding in seed dissemination and germination (Lovich et al. 2018). Protecting and mitigating threats to these species is of utmost importance for conservation scientists. While much is known about the basic natural history of many turtle species, their spatial ecology and habitat selection can be quite complex and varies across their range. Filling knowledges gaps of species distributions, population viability, and habitat requirements is crucial for informing conservation management and affording large scale protection from the many threats they face.

One North American turtle species that is being considered for federal protection in the United States is the wood turtle (*Glyptemys insculpta*). Wood turtles are semi-aquatic freshwater reptiles endemic to the Great Lakes region and surrounding midwestern and northeastern United States, as well as southeastern Canada. They are listed on the IUCN Redlist as an endangered species, and they are threatened in Canada (van Dijk and Harding 2011, Environment Canada 2016). In the United States, they are listed as a species of special concern, species at-risk, threatened, or endangered in the various states they inhabit. The Center for Biological Diversity (CBD) petitioned for this species to be listed as federally endangered under the Endangered Species Act (ESA) in 2012 and wood turtles are currently scheduled for a listing determination by the U.S. Fish and Wildlife Service (USFWS) in 2023 (Adkins Giese et al. 2012, U.S. Fish and

Wildlife Service 2016). The petition by the CBD and the decision to consider federal listing has been caused by the same threats turtles face worldwide with a primary focus on habitat loss. Wood turtle populations in the United States have steadily declined due to human recreation, habitat fragmentation by roads and water barriers, habitat destruction through timber harvest and development, illegal collection, and predation (Adkins Giese et al. 2012, Jones et al. 2015).

Wood turtles use habitat types based on seasonal activities, thermoregulation, foraging opportunities, and reproductive cycles (Harding and Bloomer 1979, Arvisais et al. 2002). This species uses terrestrial habitat throughout late spring, summer, and early fall, and aquatic habitat from late fall to early spring (Arvisais et al. 2004, Brown et al. 2016, McCoard et al. 2018). Movement is centered around their use of river or stream systems and is influenced by sex, reproductive class, and activity period. Male wood turtles are more often found nearer to and in water while females are often captured farther from water during nesting season, depending on habitat quality (Harding and Bloomer 1979, Remsberg et al. 2006, McCoard et al. 2016*a*, Parren 2013). Wood turtles display a preference for complex vegetative structures and habitat edges. They select open canopy habitat and riparian vegetation based on thermoregulation, protection, nesting, and foraging needs (Kaufmann 1992*a*, Compton et al. 2002, Arvisais et al. 2004, McCoard et al. 2016*b*, Wallace et al. 2020).

In Michigan, wood turtles are listed as a species of special concern, and while some published research of Michigan wood turtles exists, there is a lack of statewide data. Only one published study has examined wood turtle spatial ecology in Michigan, and they found that wood turtles in northeastern Michigan had larger home ranges than other populations throughout their range which was attributed to poor habitat quality or drought (Remsberg et al. 2006). A predation study from Michigan's Upper Peninsula revealed that soil disturbance was a leading cause of nest depredation and that nests placed farther from rivers experienced a lower chance of depredation (Rutherford et al. 2016). Some threats to Michigan wood turtles include nest depredation by mesopredators, habitat fragmentation and destruction by continued development, and overharvesting for the illegal pet trade. This lack of published data regarding wood turtle spatial ecology in Michigan necessitates more studies throughout the state.

Collecting spatial and habitat selection data for populations of wood turtles throughout Michigan is essential to continue understanding the dynamics and behaviors of this species and to fill knowledge gaps. This information can be used to advise current and future management plans to ensure persistence of these populations and this species into the future. We studied a population of wood turtles in northwestern Michigan to inform local U.S. Forest Service (USFS) land managers and supplement the existing knowledge of wood turtle habits in the wider literature.

STUDY AREA

Field work took place along ~4 km of a river within northwestern Michigan. The specific location of the site has been withheld to protect this wood turtle population. The study river averages 15 m across and consists of a sandy bottom with minimal submergent or emergent vegetation and occasional woody debris. Annual discharge averages 1500 ft^3/s with lows in the winter months and peaks up to 3200 ft^3/s in early spring (U.S. Geological Survey, Michigan Water Data Support Team 2022). Riverbanks comprise a mix of thick terrestrial vegetation and bare ground. Wetlands, graminoid-dominant habitat, scrub-shrub areas dominated by speckled alder (*Alnus incana*), and northern hardwood forest comprise the surrounding terrestrial habitat. Hardwood forests occur within the riparian areas and dominate the upland. Michigan experiences a humid continental climate under the modified Köppen climate classification which is characterized by hot summers, cold winters, ample precipitation, and regular weather fluctuations (Climate Change in the Midwest: A Synthesis Report for the National Climate Assessment, 2014). This area receives an average of 8.4 cm of precipitation during the summer months (April – August) and 95.11 cm annually. Temperatures peak in July averaging 27 °C (Abatzoglou et al. 2018).

Occurring within a public forest, this site experiences moderate recreational use in the form of fishing, kayaking, and hiking. The USFS actively manages this public forest throughout the year. Some unpaved and partially paved roads run through the surrounding landscape with bridges crossing the river and there is sporadic traffic ranging from small passenger vehicles to large commercial trucks. In 2019, the USFS began focusing on restoring remnant oak-pine barrens around this site using timber harvest, prescribed burns, and native seeding. Timber harvest for oak-barrens consists of opening about 10-60% of the overstory canopy. They are removing undesirable and invasive species such as spotted knapweed (*Centaurea stoebe*), common mullein (*Verbascum thapsus*), foxtail grass (*Alopecurus* spp.), bull thistle (*Cirsium vulgare*), and Canada thistle (*Cirsium arvense*) which is followed by reseeding native graminoid and forb species including June grass (*Koeleria cristata*), big bluestem (*Andropogon gerardi*), little bluestem (*Sarothamnus scoparius*), wild lupine (*Lupinus perennis*), golden rod species (*Solidago nemerosa, Solidago juncea, Solidago speciosa*), rough blazing star (*Liatris aspera*), and wild bergamot (*Monarda fistulosa*), to restore oak-pine barrens (P. Laarman, U.S. Forest Service, personal communication). Long-term management involves the mechanical removal or herbicide treatment of woody encroachment and prescribed burns on a 3–5-year rotation.

METHODS

Data collection

We captured wood turtles during May 2021, using visual encounter surveys along ~4 km of the river ranging 0–200 m perpendicular to the river on both sides (Arvisais et al. 2002, Tuttle and Carroll 2003, Flanagan et al. 2013, Hagani et al. 2021). We captured all individuals by hand and notched the marginal carapacial scutes using a numbering scheme comparable to Cagle (1939). We collected morphological data including age, sex, mass, shell measurements, and physical abnormalities or injuries of all individuals. Turtles were aged by counting growth annuli of the plastral scutes (Harding and Bloomer 1979). Wood turtles in Michigan become sexually mature around a minimum carapace length of 160–180 mm and annuli count of 12–14 so we used these as our baseline measurements to determine sex and reproductive class (Harding and Bloomer 1979). We also used secondary male characteristics for determining sex which include a concave plastron and a thicker pre-cloacal tail with a cloaca posterior to the edge of the plastron (Lovich et al. 1990). Females were examined for eggs by palpating anterior to the rear legs.

Turtles were divided into four groups including gravid (females found gravid anytime during the active season), female (non-gravid females that met the minimum size to sex or were found mating), males (individuals exhibiting secondary male characteristics or were found mating), and juveniles (individuals too small to determine sex based on size and characteristics). We palpated females from spring emergence until the end of the nesting season in case of delayed egg development.

In May 2021, we fitted 23 individuals (3 gravid, 6 females, 9 males, 5 juveniles) with radio transmitters (R1800 or R1600, Advanced Telemetry Systems [ATS], Isanti, MN, USA) using an instant-setting epoxy and a marine putty. Transmitter and epoxy combination weights represented less than 5% of the body weight of the individual turtles to reduce interference with daily and seasonal habits (e.g., swimming, walking, mating, etc.). All turtles were released at point of capture within 2 hours. Turtles were tracked between 07:00 h and 17:00 h every 1–3 days from May to August, 2021-2022, using a 4 MHz receiver [ATS] and a flexible H-type antenna (Telonics Inc., Mesa, AZ, USA). Gravid females were tracked twice per day in the morning and later in the evening, during nesting season, to estimate time and location of nesting. Locations were recorded using a handheld GPSMAP 64x (Garmin LTD., Schaffhausen, Switzerland).

Spatial analyses

We estimated minimum convex polygon (MCPs; 50% and 100%) and kernel density estimation (KDEs; 50% and 95%) home ranges. We used the *mcp* function to calculate MCPs and the *kernelUD* function to calculate KDEs using the adehabitatHR package version 0.4.19 (Calenge 2006) in R (R Core Team 2020). MCPs and KDEs are both commonly used throughout wildlife research to estimate the size of individual home ranges, yet both are prone to issues particularly with herpetofauna. MCPs tend to overestimate home ranges by including too much space that is not necessarily used by the individual (Worton 1987). KDEs have been deemed more accurate estimators of home ranges as they consider the utilization distributions of individuals and place more weight on areas that are more commonly used however, choice of bandwidth is crucial for creating an appropriate kernel (Kie 2013). Many herpetofauna species exhibit site fidelity which can lead to autocorrelation of data and overweighting of frequently used areas in KDEs (Row and Blouin-Demers 2006). We used both methods despite their drawbacks as they are well-represented in previous wood turtle home range studies which provides us the ability to compare across time and space. We used the ad hoc method of bandwidth choice which has been shown to be the most accurate and least likely to over or underestimate KDE home ranges (Kie 2013). We used multivariate analysis of variance (MANOVA) tests to determine if there was a difference in MCP and KDE home ranges between sex and reproductive classes between 2021, 2022, and both years combined. MANOVA was performed using the *MANOVA.wide* function from the MANOVA.RM package version 0.5.3 (Friedrich et al. 2022) in R (R Core Team, 2020).

Turtle movement in relation to the river was calculated using the NEAR tool in ArcMap 10.7.1 (Esri, Redlands, CA, USA) and calculating mean distances of each sex and reproductive class to a Michigan streams shapefile (EGLE Admin 2022). We also visually analyzed turtle locations in relation to oak-pine barrens in ArcMap 10.7.1.

Habitat selection

To quantify landcover types, we created a landcover shapefile using various data sources and ground truthing in ArcMap 10.7.1. We used 2020 National Agriculture Imagery Program (NAIP) imagery (OCM Partners 2022), a Michigan streams shapefile (EGLE Admin 2022), a Michigan road shapefile (Center for Shared Solutions and Technology Partnerships 2014), the 2005 EGLE (Department of Environment, Great Lakes, and Energy) National Wetland Inventory (Ducks Unlimited 2021), an elevation contour shapefile (U.S. Geological Survey, National Geospatial Technical Operations Center 2020), and oak-pine barrens shapefiles from the USFS Cadillac-Manistee Ranger District (P. Laarman, personal communication). Ground-truthing consisted of surveying on foot and taking note of various habitat types throughout the study site and recording habitat associations at turtle locations. We delineated ten categories for use in habitat selection calculations (Table 1).

We used Euclidean Distance Analysis (EDA) to examine habitat use versus availability (i.e., habitat selection) (Connor and Plowman 2001). This method compares the distances of telemetry locations (used points) and random locations (available points) to all habitat types to determine selection. A ratio for each habitat type is created using the average “used” and “available” distances. These ratios are individually compared to a vector of 1s using MANOVA. Ratios <1 indicate selected habitat, >1 indicate avoided habitat, and =1 indicate random use. We chose to analyze population level (second order) and individual level (third order) habitat selection according to Johnson’s hierarchy of selection (Johnson 1980). Due to changes in habitat composition resulting from restoration, we analyzed 2021 and 2022 habitat selection separately for all individuals.

To define available habitat at the second order (population level), we merged our 95% KDE home ranges for each year. To calculate second order “available” distances, we generated random points within our available habitat range equal to the total telemetry points for that year (674 in 2021; 575 in 2022) and measured the distance to each habitat type for each year. We calculated “used” distances by generating random points equal to the number of telemetry points for each individual within the bounds of their 95% MCP and measuring the distance to each habitat type for each year.

For third order (home range level) available habitat, we analyzed individual 95% MCP home ranges for each year. Third order “available” distances were determined by generating random points equal to the number of telemetry points for each individual within the bounds of their 95% MCP and measuring the distance to each habitat type within the combined 95% KDEs for each year. Third order “used” distances were determined by measuring distance from actual telemetry points to each habitat type within the combined 95% KDEs for each year.

For both second and third order, used distances were divided by available distances to create our habitat selection ratios. We used MANOVA to compare our ratio vectors to a vector of 1s to determine if there was non-random habitat selection occurring. If non-random selection did occur (i.e., the MANOVA was significant), we used pairwise t-tests with Bonferroni correction to determine which habitat types were being selected, avoided, or randomly used.

Microhabitat use and turtle behavior

We analyzed microhabitat data collected during telemetry. This included turtle behavior, presence of coarse woody debris (CWD), and identifying items foraged. Turtle activity included basking (sitting in direct sunlight), feeding (actively eating anything), mating, resting (not in direct sunlight or performing another activity), swimming, walking, and unknown (no visual of turtle to assess activity). Presence of CWD was determined by visual observation of woody debris (downed trees or branches and decaying logs large enough for turtles to move in or under) within ~1 m of the turtle. Foraging materials were identified by visually observing food on or in a turtle's mouth.

RESULTS

Spatial analysis

Of the initial 23 wood turtles with transmitters, we tracked 21 (3 gravid, 6 females, 8 males, 4 juveniles) individuals in 2021 and 19 (3 gravid, 6 females, 6 males, 4 juveniles) individuals in 2022 . During 2021, one male and one juvenile were unable to be relocated after stopping movement in a deep part of the river and likely dropped their transmitters or were river mortalities and were excluded from home range analysis. At the beginning of the 2022 season, two males dropped their transmitters and only one field season was included for their home range analyses. Individuals were relocated an average of 62 times (range 46–75) across both field seasons.

Home range sizes statistically did not differ between sex or reproductive classes for 2021, 2022, or both years combined (MANOVA, $MATS_{36}$= 93.702, p=0.237). Across both years, gravid females' 95% MCPs ranged from 2.08 to 55.70 ha, non-gravid females ranged from 1.68 to 25.03 ha, males ranged from 0.99 to 40.24 ha, and juveniles ranged from 1.13 to 7.54 ha. For 95% KDEs, gravid females ranged from 7.08 to 236.59 ha, non-gravid females ranged from 4.50 to 151.00 ha, males ranged from 4.14 to 198.22 ha, and juveniles ranged from 4.33 to 16.72 ha. 50% MCPs ranged from 0.15 to 7.16 ha for gravid females, 0.15 to 7.16 ha for non-gravid females, 0.27 to 5.80 ha for males, and 0.28 to 0.98 ha for juveniles. 50% KDEs ranged from 1.35 to 37.65 ha for gravid females, 0.88 to 23.60 ha for non-gravid females, 0.87 to 38.16 ha for males, and 0.67 to 2.63 ha for juveniles (Table 2).

Distance to the river across both years averaged 219.03 ± 13.85 m (± SE) for gravid females, 64.86 ± 4.65 m for non-gravid females, 58.08 ± 2.77 m for males, and 34.82 ± 2.79 m for juveniles. Monthly averages for both years varied with gravid females found farther from the river than non-gravid females, males, or juveniles during the months of June, July, and August (Figures 1, 2). All sexes and reproductive classes maintained similar distances from the river during the month of May for both 2021 and 2022. Non-gravid females averaged 15.13 ± 1.58 m farther distances from the river than non-gravid females in May. However, gravid females were farther from the river than non-gravid females by 68.69 ± 9.63 m in June, 94.07 ± 14.24 m in July, and 87.10 ± 17.36 m in August. Of all telemetry points, 79% and 86% were within 150 m of the river while 90% and 92% of telemetry points were within 300 m of the river for 2021 and 2022, respectively.

Turtles used both the edges and openings of restored oak-pine barrens (Figure 3). 33% (2021) and 69% (2022) of telemetry locations in the barrens were from one gravid female using coarse woody debris and dead leaves for cover in the opening. We presume this female nested in the oak barrens in 2021 based upon presence of palpable eggs in the morning and absence of eggs later in the day (we could not locate the nest). In 2022, we confirmed this female nested in the barrens by locating her nest. The nest was covered with a predator-proof exclosure and monitored for hatchlings. One other gravid female, four non-gravid females, four males, and one juvenile also used edges of the oak-pine barrens but not the open canopy areas.

Habitat selection

Turtles used habitats non-randomly, at the second order (population), in 2021 (MANOVA, $MATS_{10}$= 1842.24, $p<0.001$) and 2022 (MANOVA, $MATS_{10}$= 715.54, $p<0.001$). In relation to availability at the second order in both 2021 and 2022, developed habitat was used randomly, mesic northern forest was avoided, and all other habitat types were selected for (Table 3). Patterns of second order habitat selection did not differ between years (MANOVA, $MATS_{10}$=8.95, p=0.45). Habitat selection also occurred at the third order (home range) for both 2021 (MANOVA, $MATS_{10}$=34.44, p=0.013) and 2022 (MANOVA, $MATS_{10}$=35.07, p=0.012). In 2021, northern shrub thicket, forested slope, and river were avoided while all other habitat types were used randomly. In 2022, mesic northern forest and forested slope were avoided, river was selected, and all other habitat types were used randomly (Table 4). Third order habitat selection did not differ between years (MANOVA, $MATS_{10}$=15.40, p=.173).

Microhabitat use and activities

Activities including basking, feeding, mating, resting, swimming, and walking were similar among females (gravid and non-gravid combined), males, and juveniles for each month

(Figure 4). During June and July of 2021, feeding (actively eating anything) was the most common behavior while in June and July of 2022, resting (not in direct sunlight or performing another activity) was the common behavior across groups. Nesting was not included in the graphs but there was one instance of a female nesting in each year. We observed two mating events in June 2021 and July 2022. 93.7% (2021; n=261) and 92% (2022; n=112) of feeding events involved consumption of the red slug (*Arion rufus*) which could be identified by its orange color. In addition, turtles were found consuming unidentified green plants, insects, mushrooms, blueberries, and fish remains. Two identifiable feeding instances included consumption of a spongy moth caterpillar (*Lymantria dispar*), and an eastern skunk cabbage fruit (*Symplocarpus foetidus*).

We also recorded the use of CWD in various habitat types. This debris results from dropped branches, tree blowdowns, and mechanical removal left in the form of scattered debris or slash piles. All sex and reproductive classes were found beneath or near (~1m) CWD throughout both field seasons. Gravid females were found under or near CWD during 26.7% (2021) and 31.5% (2022) of observations. Non-gravid females were found 18.7% (2021) and 19.6% (2022) of the time. Males were found near CWD during 15.7% (2021) and 19.9% (2022) of observations. Juveniles were observed near CCWD 22.6% (2021) and 39% (2022) of the time. There were also many instances of turtles found buried under dead, matted grasses and sedges.

DISCUSSION

Wood turtles in northwestern Michigan varied in their home range sizes and movements compared to other populations throughout their range (Tuttle and Carroll 2003, Remsberg et al. 2006, McCoard et al. 2016*a*, Hagani et al. 2021, Otten et al. 2021). There was no statistical difference in home range averages using either estimation method between gravid females, non-gravid females, males, and juveniles. Gravid females moved farther distances from the river, in search of nesting habitat and foraging opportunities. Males, non-gravid females, and juveniles all stayed near the river using primarily riparian habitat throughout the active season indicating there are may be suitable resources within these habitat types. There was some used of oak-pine barren edge habitat and we found one female actively nesting there. At the second order, wood turtles randomly used developed habitat, avoided upland forest, and selected for all other habitat types for both years. At the third order in 2021, turtles avoided shrubby lowland and forested slope habitats while in 2022, they avoided upland forest and forested slope.

River habitat was avoided in 2021 but selected for in 2022. This species is typically found in or near rivers however, there was heavy use of terrestrial habitat and locating a turtle in the river was often dependent on timing of tracking which may have skewed results differently for both years. Our results indicate that there is variation in the habitat types used among these turtles and gravid females use more terrestrial upland habitat far from the river which may have implications for timing of management actions.

Spatial analysis

Wood turtle home range sizes, in northwestern Michigan, statistically do not differ based on sex or reproductive status, and our estimates contribute to the variable patterns seen across their range. Males often average larger home ranges than females which has been attributed to male dominance hierarchies and differing mating strategies (Harding and Bloomer 1979, Kaufmann 1992*b*, Pearse and Avise 2001). However, strictly analyzing numerical differences, gravid females did average larger home range sizes than non-gravid females or males though non-gravid females and males averaged similar home range sizes. These differences may be caused by gravid females searching farther distances for adequate nesting grounds if none are found closer to riparian areas (Steen et al. 2012).

There was a notable lack of low canopy, sandy areas for prospective nesting sites aside from small sandy patches along the river, on walking paths, in unpaved parking areas, and along roadsides. Current nesting options increase risk of nest depredation or destruction, as well as female mortality, as they are easily accessible by humans, predators, and vehicles which may be influencing the inland movements, and resultant large home ranges, of gravid females in this study. The great variability in home ranges sizes seen among both sexes and reproductive classes of this population may indicate there is much variation in movement and habitat selection on an individual scale which can make it difficult to summarize seasonal habits of the entire population.

Movement patterns of our wood turtles were consistent across years with gravid females moving out of riparian habitat at the end of May and staying upland at least until the end of August. Males, non-gravid females, and juveniles tended to stay closer to the river. Movement is related to home range size and the same reasons for variation in home ranges can be applied to differences in movement. Individual turtle habits, habitat quality, and forage availability can contribute to differences seen among the sex and reproductive classes of this population. However, compared to the variation seen between our home range averages and other studies, we found that wood turtles in northwestern Michigan averaged farther distances from the river than other recent studies (Kaufmann 1992*a*, Arvisais et al. 2002, Tuttle and Carroll 2003, Remsberg et al. 2006, Parren 2013, Curtis and Vila 2015, Brown et al. 2016, Hagani et al. 2021).

Other studies have noted a significant difference between male and female distances to the river which we also see when comparing gravid females to males (Kaufmann 1992*a*, Tuttle and Carroll 2003, Curtis and Vila 2015). However, non-gravid females and males did not significantly differ in average distance to the river throughout the active season which may be caused by non-gravid females that did not need to move far to fulfil their foraging and habitat requirements and had no need of nesting grounds. We do note that other wood turtle studies do not specify the reproductive status of female individuals for analyses, so other studies may report larger home ranges and farther distances from the river for females than our averages if they are including both non-gravid and gravid females in the same category.

90% of all turtle locations occurred within 300 m of the river. Our findings are similar to a Pennsylvania study that found 95% of points within 300 m of the river (Kaufmann 1992*a*). However, most other studies found 90-95% of their turtle locations within 200 m of the river (Tuttle and Carroll 2003, Remsberg et al. 2006, Brown et al. 2016). The differences in distance moved from the river among wood turtle studies may have serious implications for wood turtle habitat management. Most land management strategies delineate areas of essential habitat for focal species and former wood turtle studies indicate 300 m as an appropriate distance from the river to protect important riparian habitat (Jones et al. 2015). As seen in our results, 10% of turtle locations were found >300 m from the river, and typically involved gravid females, so 300 m from the river may not be far enough to protect essential habitat for these individuals.

We found some use of edge and inner barrens habitat. Most locations were concentrated along the edges of this habitat in upland forest with one gravid female found using the cleared barrens areas for basking and nesting. Wood turtles prefer edge habitats because closed canopy habitat provides more protection and foraging options while open canopy habitats provide basking opportunities (Arvisais et al. 2004). Restoration of the barrens areas leaves much woody debris behind as scattered branches and slash piles which provides protection when exposed in open barrens habitat. While one telemetered gravid female used the barrens, we also incidentally found a non-telemetered female that had been found gravid in that area in 2021, using the barrens edge in 2022. Few studies have quantified turtle response to oak barrens restoration; however, Reid et al. (2016) monitored Blanding's turtle (*Emydoidea blandingii*) responses to oak barrens restoration aimed at creating Karner blue butterfly (*Lycaeides samueli*) habitat in Wisconsin. Over 24 years, the population showed growth with a trend toward females becoming reproductive at smaller sizes. This shift to smaller nesting females increases the reproductive and recruitment rates of the population thus ensuring a greater ability for the population to persist despite potential high mortality or nest predation events (Reid et al. 2016). Additional movement studies are needed to assess the effects of restoration on the survival and recruitment of this population to see if these wood turtles respond similarly to the Blanding's turtles in Wisconsin.

Differences in habitat size and quality contribute to the large variation in home ranges and movement seen among recent wood turtle studies (Curtis and Vila 2015, Wallace et al. 2020, Otten et al. 2021, Hagani et al. 2021). Wood turtles live along rivers and streams which can be surrounded by various plant and habitat associations depending on the local community and land uses. Comparisons between studies conducted near recreationally or agriculturally disturbed land (Kaufmann 1992*a*, Remsberg et al. 2006, McCoard et al. 2018, Wallace et al. 2020) and mostly undisturbed land (Arvisais et al. 2002, Compton et al. 2002, Hagani et al. 2021, Otten et al. 2021) can be difficult to appropriately quantify since differences in available habitat must be considered when comparing home ranges and movements between locations. Fine scale variation in movements, home ranges, and habitat selection may be attributed to habitual movements and habitat use that has occurred over the long lifespans of these individuals despite seasonal variation in habitat quality or availability (Szabo et al. 2021). Care must be taken when comparing different populations and researchers must thoroughly study local populations before developing management plans for the habitats wood turtles inhabit.

Habitat selection

Wood turtles use a variety of habitat types throughout their active season and this site consists of a diverse array of habitat types surrounding the river. The mosaic of habitat types available close to the river might contribute to the shorter movements and smaller home ranges of some of the individuals in this study as they are able to acquire appropriate resources within a small area. Similarly, wood turtles are primarily present within habitats of diverse, complex vegetative structure in other parts of their range (McCoard et al. 2016*b*). Wood turtles avoided mesic northern forest at the population level (second order) for both years and at the home range level (third order) in 2022 though on an individual scale, two gravid females, four non-gravid females, four males, and one juvenile frequently used this habitat type. Similar to our results, forested habitat was the most abundant yet least preferred habitat in a New Brunswick, Canada study (Wallace et al. 2020).

Turtles used developed habitat randomly at the population level (second order). Developed habitat was limited and consisted of roads and small sandy parking areas. While turtles were often not found on roads, they did use roadsides which might contribute to this random use. Forested slope was avoided both years at the home range level (third order) which might be due to quick transit times through this habitat type. While turtles were occasionally found on steep slopes, this habitat type was probably traversed while moving between upland and lowland habitat by the two gravid females, four non-gravid females, four males, and one juvenile that frequented mesic northern forest in the uplands.

Interestingly, river habitat was avoided in 2021 at the home range level (third order). The reason for this difference can be attributed to our telemetry methods. Turtles were randomly found on different days and times during both field seasons. Some turtles overnight in the river while others spend their nights on land. During telemetry, it was evident when a turtle had recently emerged from the river as their shell was still dark and wet however, if they were not physically found in the water, they were marked as a terrestrial observation. A slight change in timing of telemetry could have resulted in finding these individuals in the river. Yearly differences in preference of river habitat differs from other studies that have found specific selection for shore and river buffer habitat at the third order and riparian edge habitat near water at the fourth order (within home range) (Arvisais et al. 2002, Compton et al. 2002, Wallace et al. 2020). Variation in habitat and resource availability throughout their geographic range could be the drivers for this difference in use of riverine habitats. Additional studies of habitat selection at multiple scales in similar geographic areas would be necessary to appropriately compare habitat selection between this population and others.

Microhabitat use and activities

Feeding preferences for wood turtles in this study are similar to those found throughout their range. This species is omnivorous feeding on various grasses, sedges, and other plants as well as invertebrates such as slugs and worms. Seasonal varieties of berries and various mushroom species are also consumed (Compton et al. 2002). There have also been instances of feeding on bird, mammal, or fish carcasses and consuming small snake species (Tamplin et al. 2009). Wallace et al. (2020) found berries to be an important forage item for females, and we had similar observations. We noted females moving into upland forested habitats (~510m from river) and a leatherleaf bog (~445m from river) to take advantage of seasonal blueberries. The location of foraging resources and the timing of their availability influences movement patterns. Individual turtles had selective preferences for foraging areas which was noted by their movements to the same areas for foraging in both years despite the long distance traversed to get there. Anecdotally, we observed turtles moving onto land and into upland forested areas after or during rainy days actively eating slugs which may be due to ease of finding invertebrate prey and resistance to desiccation in terrestrial habitat on those days.

Our turtles used various microhabitats, including CWD, as refugia. Turtles used downed tree limbs and brush in upland habitat while overnighting on land. On slopes and in lowland forests, the ground is typically covered in a thick layer of fallen and decaying leaves which were also used by turtles. In open grassy areas and along riverbanks, dead, matted grasses and sedges also provided refugia for turtles. In Pennsylvania, wood turtles were often found under dead leaves and grass when staying overnight on land (Kaufmann 1992*a*). Habitat selection studies at the fourth order have also shown a positive correlation between turtle presence and CWD presence (Wallace et al. 2020). CWD is a major biproduct of many restoration projects that involve heavy logging and is an important habitat feature for many animal species. In Tennessee, eastern box turtles (*Terrapene carolina*) selected habitats with thicker brambles and more CWD (Harris et al. 2020). Box turtles are also common in our study site and have undergone long-term population monitoring. So, the CWD left behind by logging will provide useful refugia for multiple turtle species in this area.

CONSERVATION IMPLICATIONS

Successful management of wood turtle populations requires continued monitoring of spatial ecology and demography. While some areas with wood turtles have been thoroughly studied, there are other places throughout their range where there is a severe lack of information.

A comprehensive understanding of the wood turtle's status in all parts of its range is necessary to inform conservation actions including legal protection and habitat management. Wood turtles are a long-lived species with delayed sexual maturation which makes their status difficult to assess within brief time frames so studies should be of longer duration to make appropriate conclusions (Harding and Bloomer 1979). We demonstrate that gravid females move far distances in search of nesting grounds while males, non-gravid females, and juveniles stay close to the river. Limited nesting opportunities and higher risks involved with larger movements have contributed to high female mortality and low recruitment in several freshwater turtle species (Steen et al. 2006, 2012). Limited opportunities and elevated risk living in low quality habitat establishes a need for high quality habitat within riparian areas for freshwater turtles, especially nesting females.

Through management to restore remnant oak-pine barrens, new nesting habitat will be created that should positively impact nest survival and recruitment in this area however, more research is necessary to understand the full impact. Maintenance of high-quality riparian habitats will ensure there are adequate resources for males and sexually immature females to stay close to the river where there is better protection and more foraging opportunities in the various habitat types. High-quality riparian habitats should consist of a variety of plant associations to provide variation in vegetative layers for protection and plant forage, plentiful woody debris in various stages of decay which can provide refugia and support an assortment of invertebrate prey, patches of sandy areas to provide options for nesting sites, and minimal disturbance by humans. Further study of movements from the river is necessary to appropriately delineate critical habitat for this population as our short study indicates these turtles move different distances compared to other populations. We recommend a continuation of population monitoring in this area to better assess the status of these turtles, quantify home ranges, define movement patterns, and evaluate habitat selection. Emphasis should be placed on studying females to ascertain an exact age at maturity and to monitor nesting movements in relation to the restored oak-pine barrens. Restoration should continue to occur during the winter and early spring while all age and reproductive classes are safely in the river or nearby riparian habitat. Continued monitoring will ensure management plans and protective measures are tailored to maximize benefits for this wood turtle population.

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ETHICS STATEMENT

All wood turtles were handled with care and disturbed only to the limit needed to collect data in the pursuit of completing study objectives. Turtles were captured and handled under permit FSCP02232021125400 from the Michigan Department of Natural Resources – Fisheries Division and IACUC protocol 19-23-A through Grand Valley State University.

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TABLES

Table 1. Habitat types classified using National Agriculture Imagery Program (NAIP) aerial imagery, streams, roads, 2005 Michigan Department of Environment, Great Lakes, and Energy (EGLE) National Wetland Inventory, U.S. Geological Survey (USGS) elevation contour, and U.S. Forest Service (USFS) oak-pine barrens shapefiles and ground-truthing. Area was delineated by combining 95% KDEs for each year. Area is presented in hectares (ha) with percent of total area in parentheses. Collected in Michigan, USA, 2021-2022.

Habitat type	Description	2021 area	2022 area
River	Open water river with some submergent vegetation along edges and sporadic coarse woody debris	10.13 (1.70%)	7.87 (2.03%)
Emergent marsh	Inundated wetland with emergent and submergent vegetation	3.24 (0.54%)	3.03 (0.78%)
Mixed bog	Mixed dry and wet bog dominated by *Chamaedaphne calyculata* and sphagnum moss	2.26 (0.38%)	1.02 (0.26%)
Northern wet meadow	Semi-dry areas of grasses and sedges within the riparian zone that experience occasional flooding due to seasonal rains and groundwater fluctuation	13.15 (2.21%)	11.43 (2.94%)
Northern shrub thicket	Dense shrubby areas dominated by speckled alder (*Alnus incana*)., grasses, and sedges surrounding northern wet meadow; typically, a transitional area between habitat types	25.77 (4.32%)	16.36 (4.21%)
Hardwood-conifer swamp	Forested sections throughout the riparian zone, characterized by mixed hardwoods and conifers with coarse woody debris and fern species dominating the ground layer	75.45 (12.66%)	55.49 (14.29%)
Forested slope	Mixed hardwood and conifer dominated slope separating riparian and upland habitats, characterized by rapid increase in elevation	82.06 (13.77%)	54.41 (14.01%)
Oak-pine barrens	Areas of upland forest cleared for barrens restoration as of spring 2021; characterized by open canopy, coarse woody debris, sparse shrubs, grasses, and forbs; logged, burned, and native seeding	33.75 (5.66%)	35.45 (9.13%)
Mesic northern forest	Mixed hardwood and conifer forest in upland areas outside of riparian zone; mixed shrub and open understory; dense canopy cover	334.26 (56.09%)	190.64 (49.09%)

Developed	Paved and unpaved roads, parking areas, and human populated areas	15.89 (2.67%)	12.67 (3.26%)
	Total area (ha):	**595.96**	**388.37**

Table 2. 95% and 50% minimum convex polygon (MCP) and kernel density estimation (KDE) wood turtle home range averages for 2021, 2022, and combined years. Mean ± standard error. *n* = number of turtles included in calculations. Calculations performed in R. Data collected in Michigan, USA, 2021-2022.

			MCP		KDE	
		n	95	50	95	50
Non-gravid female	2021	6	9.63 ± 3.95	2.79 ± 1.09	87.37 ± 62.98	15.69 ± 10.04
	2022	6	7.33 ± 3.37	1.54 ± 0.88	34.37 ± 18.47	8.35 ± 5.06
	Combined	6	11.24 ± 3.40	3.16 ± 1.24	54.28 ± 22.24	10.75 ± 3.57
Gravid female	2021	3	10.69 ± 6.94	3.33 ± 1.92	94.04 ± 71.24	15.69 ± 10.26
	2022	3	20.94 ± 14.44	2.36 ± 1.40	117.03 ± 92.00	20.22 ± 13.70
	Combined	3	23.92 ± 16.26	5.49 ± 2.40	94.11 ± 71.83	16.25 ± 10.97
Male	2021	8	9.72 ± 4.03	3.14 ± 1.20	49.30 ± 23.38	11.86 ± 5.89
	2022	6	4.18 ± 1.17	0.64 ± 0.20	39.23 ± 20.77	7.66 ± 4.23
	Combined	8	12.76 ± 5.68	2.29 ± 0.81	48.16 ± 24.04	10.05 ± 4.86
Juvenile	2021	4	1.76 ± 0.71	0.24 ± 0.10	6.77 ± 2.23	1.28 ± 0.37
	2022	4	2.68 ± 0.97	0.67 ± 0.44	12.70 ± 2.96	2.49 ± 0.75
	Combined	4	3.69 ± 1.46	0.51 ± 0.16	9.72 ± 2.96	1.63 ± 0.49

Table 3. Multivariate analysis of variance (MANOVA) results for second order (population) habitat selection using Euclidean Distance Analysis (EDA). Mean of ratios tested ± standard error (SE). Use was determined using post-hoc t-tests with Bonferroni correction. Bold values indicate significance ($P<.05$) t = test statistic p = p-value Data collected in Michigan, USA, 2021-2022.

	2021 second order (population)			
Habitat Type	***t***	***p***	**Use**	**Mean ± SE**
Mesic northern forest	5.234	**≤ 0.001**	avoided	2.35 ± 0.26
Hardwood-conifer swamp	-12.48	**≤ 0.001**	selected	0.24 ± 0.06
Northern wet meadow	-16.27	**≤ 0.001**	selected	0.28 ± 0.04
Northern shrub thicket	-14.82	**≤ 0.001**	selected	0.25 ± 0.05
Forested slope	-17.1	**≤ 0.001**	selected	0.30 ± 0.04
Emergent marsh	-16.72	**≤ 0.001**	selected	0.39 ± 0.04
Mixed bog	-12.34	**≤ 0.001**	selected	0.54 ± 0.04
Oak-pine barrens	-15.43	**≤ 0.001**	selected	0.30 ± 0.05
Developed	-1.106	0.2817	random	0.88 ± 0.11
River	-14.55	**≤ 0.001**	selected	0.26 ± 0.05
	2022 second order (population)			
Habitat Type	***t***	***p***	**Use**	**Mean ± SE**
Mesic northern forest	3.532	**0.0024**	avoided	1.80 ± 0.23
Hardwood-conifer swamp	-8.037	**≤ 0.001**	selected	0.27 ± 0.09
Northern wet meadow	-10.9	**≤ 0.001**	selected	0.30 ± 0.06
Northern shrub thicket	-11.59	**≤ 0.001**	selected	0.24 ± 0.07
Forested slope	-9.238	**≤ 0.001**	selected	0.33 ± 0.07
Emergent marsh	-6.467	**≤ 0.001**	selected	0.52 ± 0.07
Mixed bog	-4.592	**≤ 0.001**	selected	0.63 ± 0.08
Oak-pine barrens	-10.94	**≤ 0.001**	selected	0.43 ± 0.05
Developed	0.548	0.5905	random	1.08 ± 0.15
River	-10.83	**≤ 0.001**	selected	0.29 ± 0.07

Table 4. Multivariate analysis of variance (MANOVA) results for third order (home range) habitat selection using Euclidean Distance Analysis (EDA). Mean of ratios tested ± standard error (SE). Use was determined using post-hoc t-tests with Bonferroni correction. Bold values indicate significance (P<.05) *t* = test statistic *p* = p-value Data collected in Michigan, USA, 2021-2022.

	2021 third order (home range)			
Habitat Type	***t***	***p***	**Use**	**Mean ± SE**
Mesic northern forest	1.54	0.139	random	1.40 ± 0.26
Hardwood-conifer swamp	1.402	0.176	random	1.24 ± 0.17
Northern wet meadow	1.684	0.108	random	1.10 ± 0.06
Northern shrub thicket	2.91	**0.009**	avoided	1.25 ± 0.09
Forested slope	2.886	**0.009**	avoided	1.30 ± 0.10
Emergent marsh	0.947	0.355	random	1.06 ± 0.06
Mixed bog	-0.676	0.507	random	0.98 ± 0.02
Oak-pine barrens	1.161	0.259	random	1.07 ± 0.06
Developed	1.621	0.121	random	1.10 ± 0.06
River	2.267	**0.035**	avoided	1.14 ± 0.06
	2022 third order (home range)			
Habitat Type	***t***	***p***	**Use**	**Mean ± SE**
Mesic northern forest	3.148	**0.006**	avoided	1.51 ± 0.16
Hardwood-conifer swamp	0.986	0.337	random	3.26 ± 2.29
Northern wet meadow	-0.205	0.840	random	0.99 ± 0.07
Northern shrub thicket	-0.019	0.985	random	1.00 ± 0.11
Forested slope	3.522	**0.002**	avoided	1.51 ± 0.15
Emergent marsh	0.716	0.483	random	1.04 ± 0.06
Mixed bog	-0.193	0.849	random	1.00 ± 0.02
Oak-pine barrens	1.569	0.134	random	1.07 ± 0.05
Developed	2.004	0.060	random	1.10 ± 0.05
River	-2.172	**0.044**	selected	0.89 ± 0.05

FIGURES

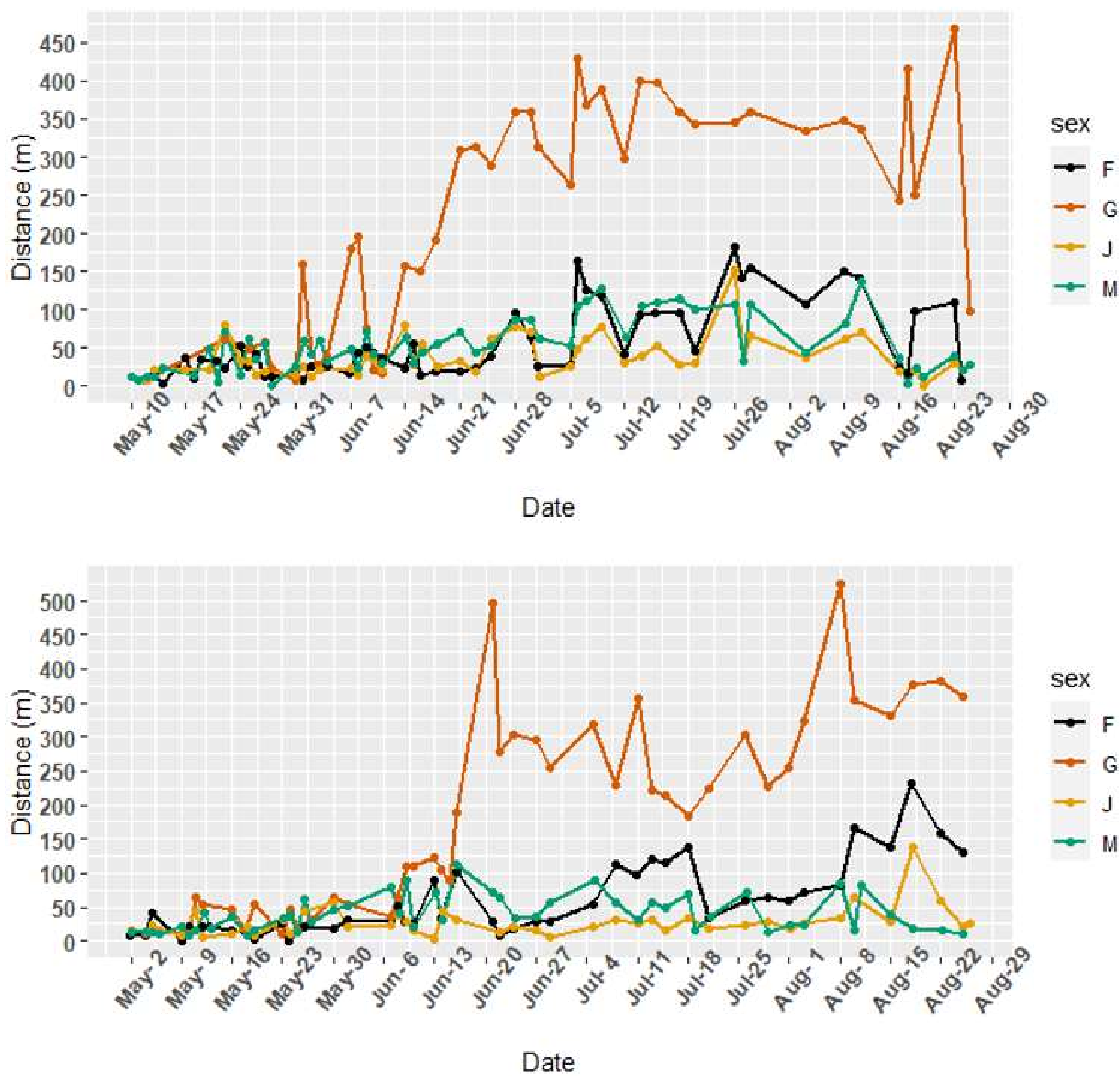

Figure 1. Average daily distances wood turtles were located from the main river during 2021 and 2022. Distances varied from 0 m to 500 m. Note the slight difference in the y-axis scale for each graph. F denotes non-gravid females, G denotes gravid females, J denotes juveniles, M denotes males. Data collected in Michigan USA.

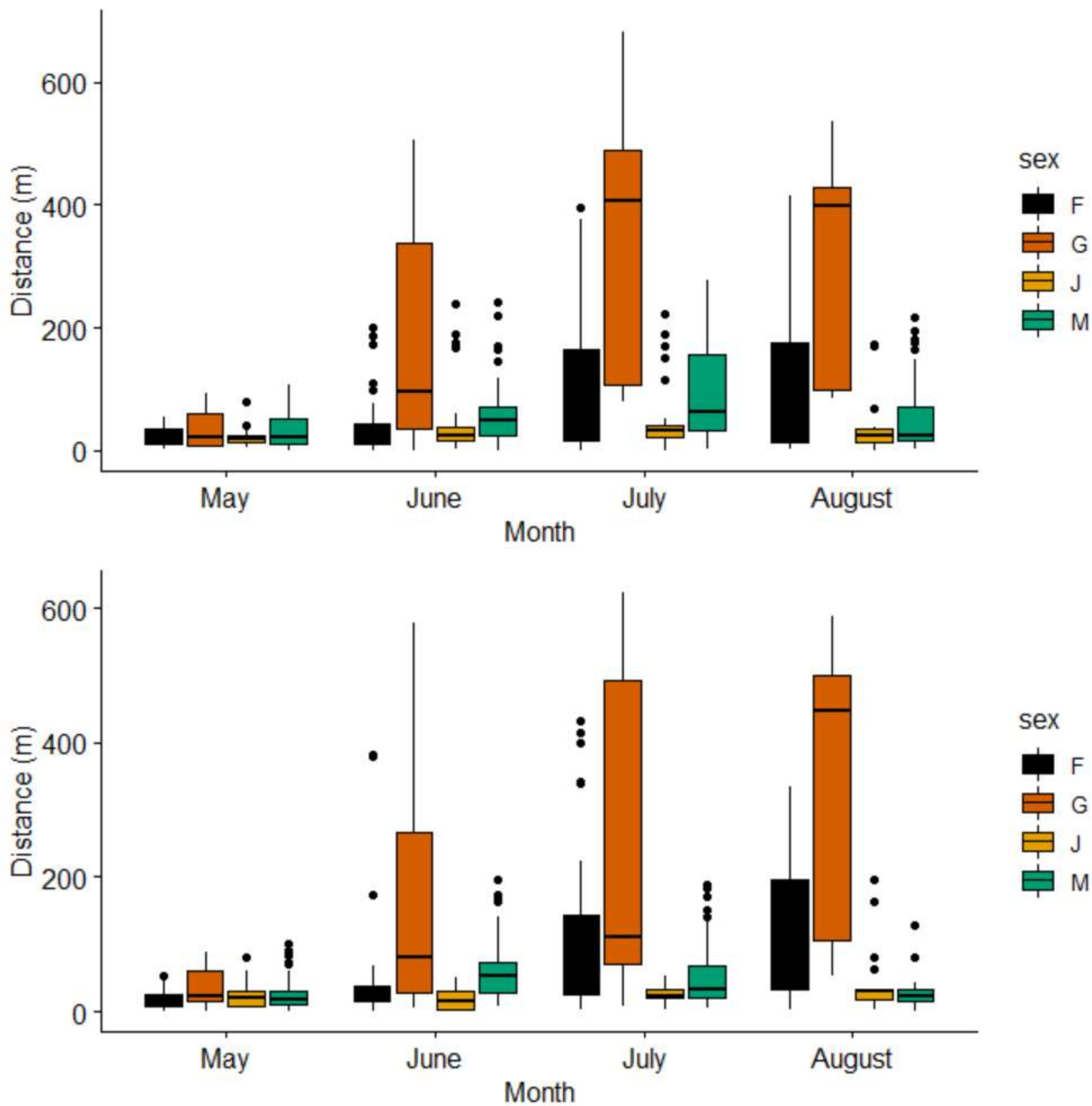

Figure 2. Average monthly distances wood turtles were located from the river during 2021 and 2022. Distances varied 0 m to 600 m. F denotes non-gravid females, G denotes gravid females, J denotes juveniles, M denotes males. Data collected in Michigan USA.

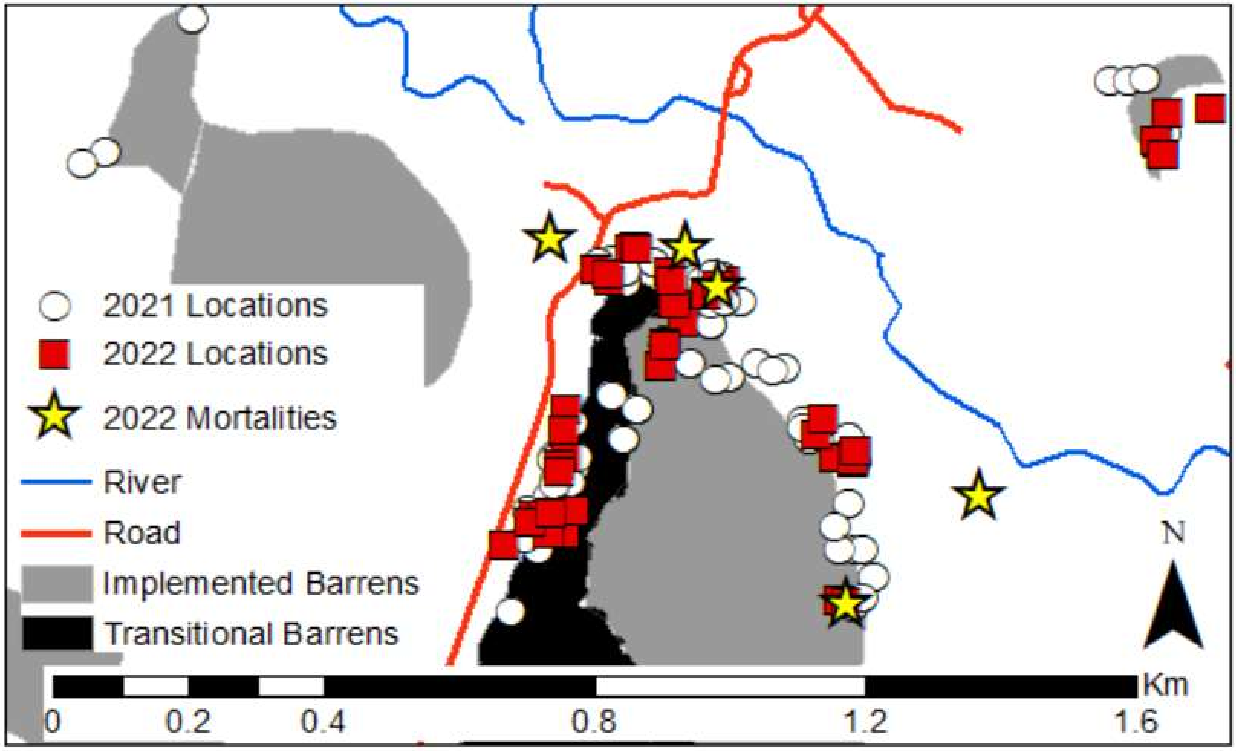

Figure 3. Wood turtle telemetry points in relation to implemented and transitional restored oak-pine barrens within our study site in northwestern Michigan. Implemented barrens were logged and burned in 2019 prior to the beginning of this study. Transitional barrens were logged mid-study during winter 2021. Data collected in Michigan, USA, 2021-2022.

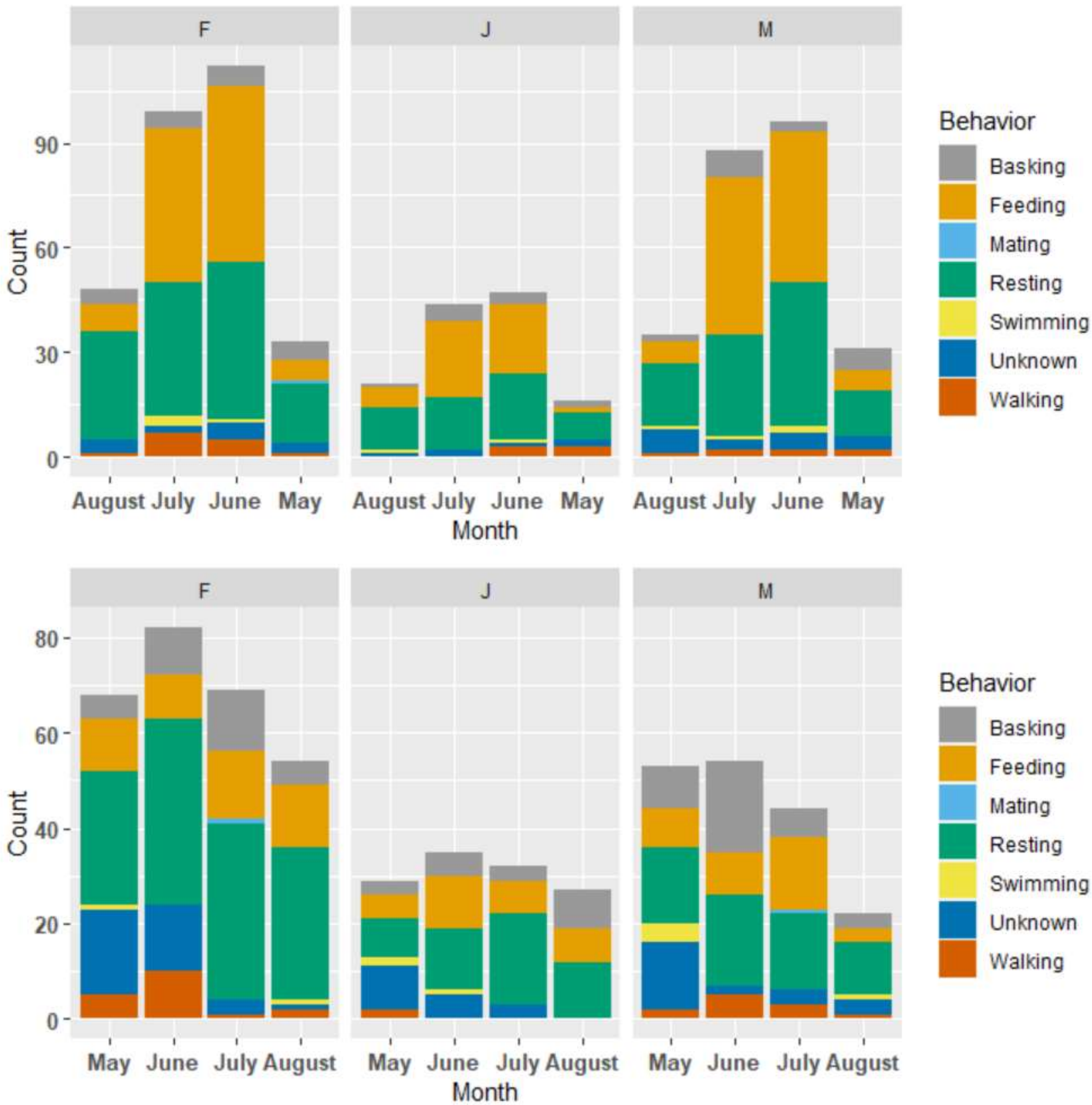

Figure 4. Wood turtle behavior grouped my month for 2021 and 2022. Note the difference in y-axis scale. Fewer turtles in 2022 resulted in fewer telemetry points. F denotes female, including both gravid and non-gravid, J denotes juveniles, M denotes males. Data collected in Michigan, USA.

Chapter 2.2: Ecological Notes

This chapter comprises field data collected during both field seasons that did not directly contribute to the objectives of this study. Data was collected during each turtle encounter. We report this information in the hopes that it can be useful in future data assemblage and analysis to observe trends in wood turtle natural history that may need further study.

Morphology

We collected 63 unique wood turtles (9 gravid females, 14 non-gravid females, 16 males, and 24 juveniles) during both field seasons. The youngest male with clear secondary sexual characteristics had 10 growth annuli and a carapace length of 172 mm while the youngest female found gravid or mating had 13 growth rings and a carapace length of 162 mm. Reproductive female annuli count, mass, and carapace length were similar to males (Table 5). According to our frequency counts, there are many subadults between 10 – 15 annuli which would indicate there should be several individuals that will soon become sexually reproductive (Figure 5). A spread of age classes indicates that there is recruitment however, this does not confirm population growth or viability.

Nesting

Six of the gravid females were captured on roadsides during the nesting season in June of both years while in search of a nesting site as they had palpable eggs, and nesting season was beginning. Three of the gravid females were part of the radiotelemetry study and were gravid both years as we palpated each female for eggs during every recapture. Gravid females averaged 17 growth rings (range 13-23) and a mean carapace length of 180 mm (range 162-200 mm). We observed several instances of females digging nests in 2021 however, all but one of the nests were determined to be false nests when searched after the female moved on. The confirmed nesting event occurred on 14 June 2021 at approximately 13:00 h in a sandy parking area near the river. The eggs were carefully relocated to a secluded area and protected with a predator-proof exclosure. Four of the eight eggs hatched on 7 September 2021 after an incubation period of approximately 12 weeks. The hatchling turtles were released near the river. In 2022, we observed one nesting event that occurred 16 June 2022 at approximately 10:00 h in the restored barrens habitat. The female had recently nested and was found covered in sandy dirt standing on the nest. We confirmed the presence of eggs in the nest. This nest occurred in a safe location, so we did not excavate the eggs. We placed a predator-proof exclosure over the nest and monitored it. The nest did not hatch before the winter months and will be excavated in the spring of 2023 to obtain the eggs or hatchlings.

Mortality and injury

We found one non-telemetered gravid female that was killed by a vehicle on a paved road during June 2022. This individual had been found gravid on the road the previous year and it was likely she was moving to find nesting grounds. During the 2022 field season, five telemetered turtles were depredated including three males and two non-gravid females. These events occurred in June, July, and August. Four of the predated turtles were frequently found in upland forested areas that consisted of dense canopy cover, sparse ground vegetation, and occasional CWD. These four were predated in upland forests and near barrens edges 218 ± 64 m from the river while the fifth turtle was predated in lowland forest within the riparian zone 74 m from the river. All recovered shells were visually inspected and found to have no teeth or scratch marks and were completely intact. The amount of remaining turtle flesh and limbs varied among the turtles with some having all limbs and organs removed and others with internal organs but missing some limbs or tail. All individuals were decapitated and only one head was recovered near the shell.

Raccoons, opossums, and river otters have been observed in lowland and upland habitats through our study site. We speculate that it may be likely that one of these species predated the turtles as they are small enough that they would not cause shell damage. The American mink (*Mustela vison*) also occurs in northern Michigan, so it is possible this species was the offending predator however we have no evidence to support these suppositions. During the 2021 field season, no mortality was observed. Several older individuals were found during our study that had previously lost limbs and recovered. It is possible that travelling predators opportunistically find vulnerable turtles in easily accessible areas and take advantage of this which could also explain why three of the mortalities occurred within weeks of each other. A map of the mortalities in relation to the barrens restoration, roads, and river is depicted in Figure 6. We observed 35% of turtles with stub tails and 10% missing one or more limbs (n = 63). Turtles missing limbs had a 19–25+ annuli. These healed injuries may suggest predators have previously moved through this site and attacked turtles. All injured turtles appeared to be able to move through their habitat as easily as uninjured turtles suggesting they have had time to adapt. Other studies have also found incidences of limb and tail amputation among wood turtle populations (Harding and Bloomer 1979 and Brooks et al. 1992).

Tables

Table 5. Average annuli, mass, and carapace length (CL) ± standard error (SE) for wood turtles captured 2021-2022. Gravid females were gravid at some point either year. Data collected in Michigan, USA, 2021-2022.

	n	Mean Annuli ± SE	Mean Mass ± SE	Mean CL ± SE
Gravid female	9	17 ± 1	897.77 ± 56.77	180.11 ± 3.56
Non-gravid female	14	15 ± 1	688.57 ± 39.96	165.69 ± 2.76
Male	16	16 ± 1	868.33 ± 44.96	184.08 ± 3.46
Juvenile	24	6 ± 1	254.09 ± 35.96	107.46 ± 8.27

Figures

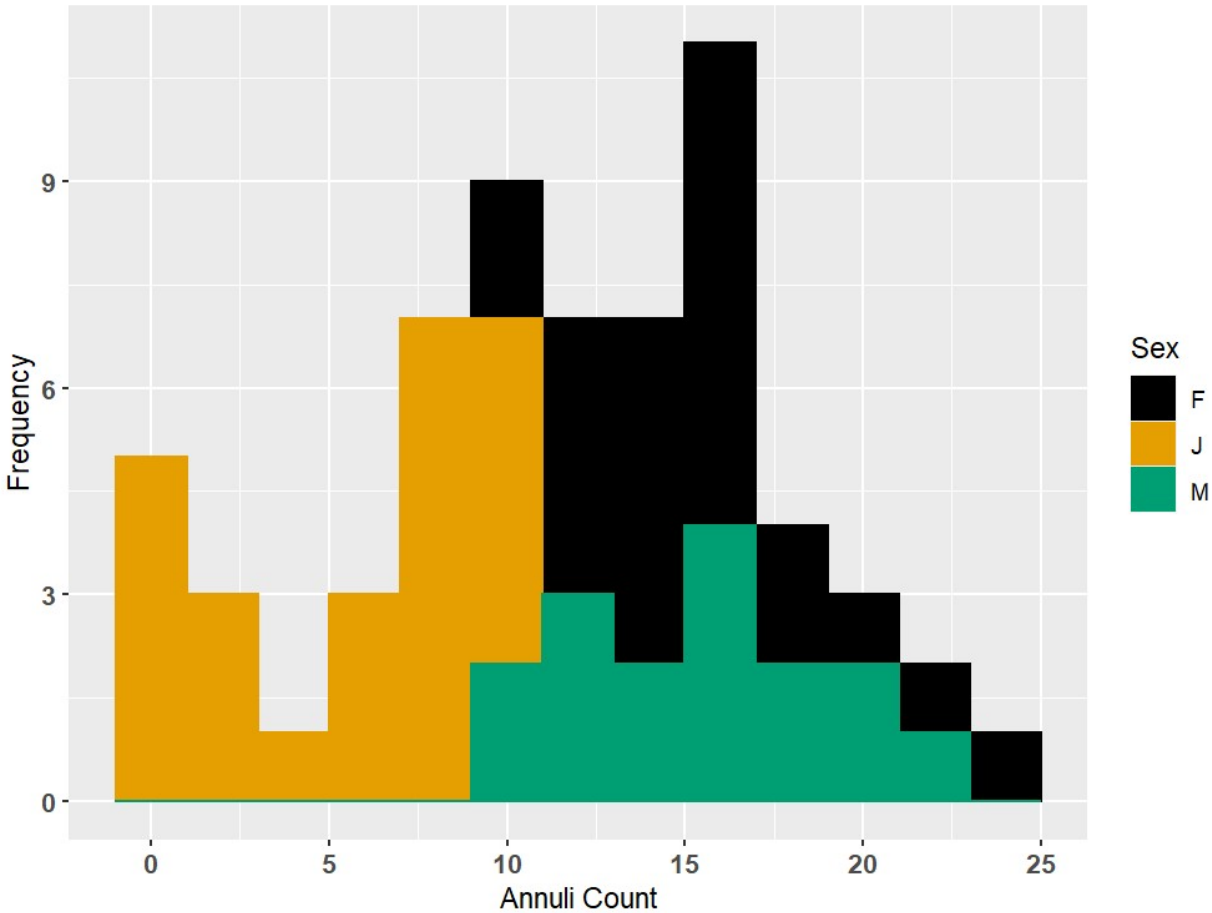

Figure 5. Annuli frequencies for all wood turtles captured during 2021 and 2022 field seasons. F denotes females, including gravid and non-gravid. J denotes juveniles. M denotes males. Data collected in Michigan, USA.

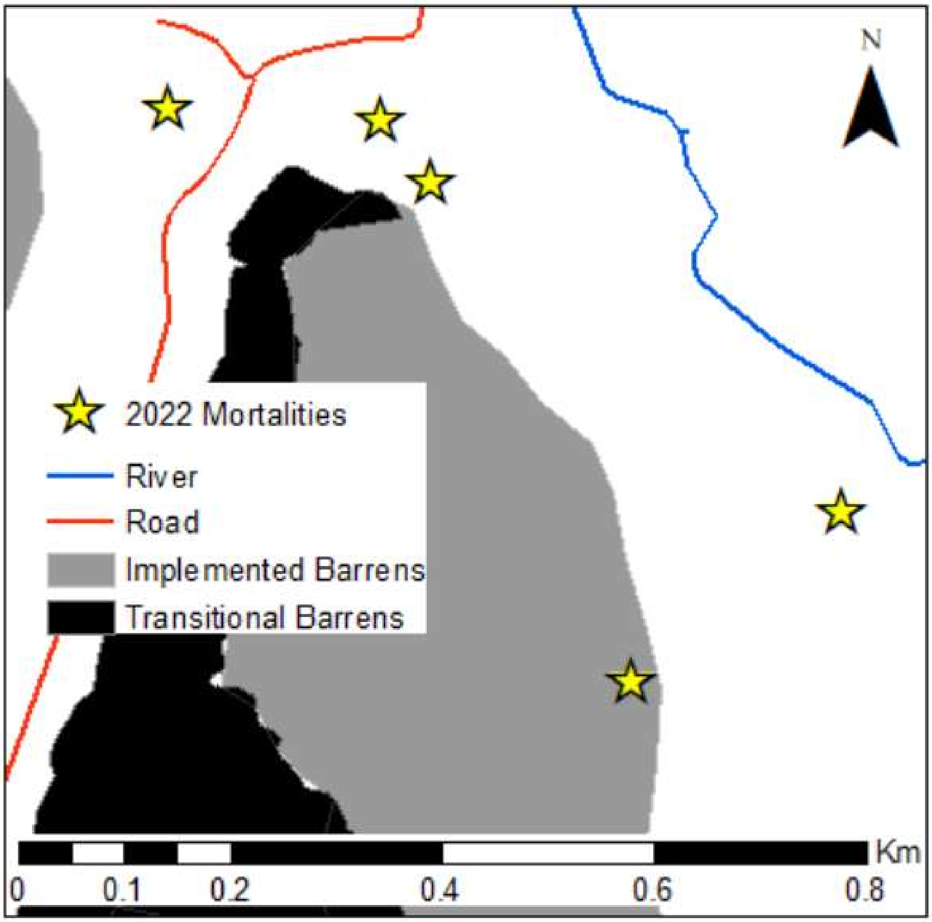

Figure 6. Wood turtle mortality locations within our study site in northwestern Michigan during the 2022 field season. Implemented barrens were logged and burned in 2019 prior to the beginning of this study. Transitional barrens were logged mid-study during winter 2021. Data collected in Michigan, USA.

Chapter 3: Extended Review of Literature and Extended Methodology

Extended Review of Literature

Natural history

The wood turtle's range spans the northeastern United States and parts of southeastern Canada. Studies throughout their range have recorded various use of habitat types based on seasonal activities, thermoregulation, foraging opportunities, and reproductive cycles. A West Virginia population spent spring and summer in terrestrial habitats and the fall and winter seasons in the river (McCoard et al. 2018). Conversely, a Minnesota population stayed in or near moving water throughout the summer months (Brown et al. 2016). In Canada, wood turtles spent early spring and late fall in streams, brooks, wet meadows, marshes, swamps, and beaver ponds while in late spring and summer, they used a variety of different aquatic and terrestrial habitat types including those previously mentioned and various stand types with a focus on alder stands (Arvisais et al. 2004). Their habitat use typically correlates with their annual activity periods including prenesting (May), nesting (June), postnesting (July through September) and prehiberation and brumation (October through April) (Harding and Bloomer 1979, Arvisais et al. 2002, McCoard et al. 2018).

Wood turtle movement is centered around their use of river or stream systems and is typically sex and activity period dependent. Male wood turtles are more often found nearer to and in water while females are often captured farther from water during nesting season, depending on habitat quality (Harding and Bloomer 1979, Remsberg et al. 2006, McCoard et al. 2016*a*, Parren 2013). Wood turtles have also exhibited edge preference and habitat selection for open canopies and riparian vegetation due to thermoregulation, protection, and foraging needs (Kaufmann 1992*a*, Compton et al. 2002, Arvisais et al. 2004, Wallace et al. 2020). Because of the specificity in habitat selection and movement within their home range, it is imperative that we understand how human activities and habitat structure affect wood turtle populations.

Threats

While turtles live quiet, hidden lives, they face many threats to their survival with most being caused by humans. Recreational activities, roads, habitat fragmentation, and illegal collection are all common causes of wood turtle decline (Jones et. al 2015). A 20-year study in Connecticut found a consistent negative correlation between the number of people permitted to use a recreational area each year and the number of turtles captured during surveying (Garber and Burger 1995). Dam building and pollution can also reduce population viability (Harding and Bloomer 1979, Garber and Burger 1995). Road mortality causes considerable female mortality since some individuals travel long-distances for nesting (Steen et al. 2006). Larger road networks also fragment habitat and are impenetrable for most land and semi-aquatic pond turtles (Gibbs and Shriver 2002). Agricultural practices cause mortality in rural areas as Saumure et al. (1998, 2007) show 20% of mortality was caused by agricultural activities. Burger and Garber (1995) and Harding (1990) advise that illegal collection has also been a continued threat for many turtle species being collected as rare novelties for the pet trade.

Death and mutilation by predation are common threats for wood turtles. Harding and Bloomer (1979) first found approximately 10% of marked wood turtles in Michigan were missing at least one limb. Brooks et. al (1992) found approximately 68% of females, 56% of males, and 29% of juveniles were missing all or part of a limb or their tail which was echoed in Lapin et al. (2019) where 39% of adult turtles died due to predation and Farrell and Graham (1991) where 17% of their turtles in a 4-year study had limb injuries, head loss, and shell deformities from predation. Mesopredators are the most probable cause and there has been photographic evidence of raccoons and foxes predating turtles and their nests. Predation is a difficult variable to manage for, so it is important to try to mitigate other threats where possible.

Conservation status

The wood turtle is listed as a species of concern, at risk, threatened, or endangered in different states and provinces throughout its range in the United States and Canada. Burger and Garber (1995) advised that immediate intervention to mitigate the threats to wood turtle populations was necessary to ensure species survival. While there have been many land management strategies to reduce these threats, this species was still listed as endangered on the IUCN Redlist in 2011 (van Dijk and Harding 2011). Based on a petition by the Center for Biological Diversity (CBD), the U.S. Fish and Wildlife Service (USFWS) added the wood turtle to their 7-year National Listing Workplan to decide in if this species should be listed in the Endangered Species Act (ESA) in fiscal year 2023 (Adkins Giese et al. 2012, U.S. Fish and Wildlife Service 2016). Regardless of listing, continued implementation of conservation strategies is essential if we are going to attempt the recovery of this species across its range.

There have been several published studies documenting positive population growth and recovery in response to various land management strategies. Schneider et al. (2018) used 18 years of wood turtle capture data in Michigan to model population changes. They found a decline in population size that appeared to rebound after noted land management plans were implemented that closed specific roads in the riparian zone in the 1980s and 1990s.

Despite conservation efforts, it is possible that certain populations will never be able to recover as some threats can be difficult or impossible to manage. Browne and Hecnar (2007) found that despite conservation efforts in an Ontario, Canada national park, their population showed a decline and a shift in age structure to an older population due to nest predation and population isolation. Willoughby et al. (2013) performed genetic studies and found loss of genetic diversity in populations of wood turtles in northern Michigan. Multiple studies have considered that continued population declines can be attributed to unmanageable threats and population declines going undetected by conservationists due to the long lives of wood turtles and lack of data in some parts of their range (Burger and Garber 1995, Browne and Hecnar 2007). Bowen and Gillingham (2004) confirm that current management practices are not enough as we have seen recorded declines of wood turtle populations across their range.

A lack of consistent population estimates, survival rates, and recruitment rates makes it difficult to fully assess the status of this species throughout its range in the United States and Canada. It is important that more information is collected that can help lawmakers and land managers to determine the appropriate levels of protection this species may need and how scientists can help to stabilize or recover declining populations. To quantify population estimates as well as survival and recruitment rates, scientists perform population surveys. These surveys typically include quantifying home ranges, movement, and habitat selection to better understand the habitat requirements for the population which is all used in conjunction to inform management plans. To understand the composition of preferred wood turtle habitat types, vegetation surveys are the most common method for collecting habitat data. Radiotelemetry studies are the best method for estimating wood turtle movement, home range size, and habitat use, availability, and selection.

Survey and radiotelemetry

Visual encounter surveys (VES), mark-recapture, and very high frequency (VHF) radiotelemetry are the most common methods used for collecting spatial data and population estimates. VES are the most effective method for the capture of wood turtles with most surveyors walking along riverbanks (Brown et al. 2017) and some using a canoe in the river at the same time surveyors search the banks (Saumure and Bider 1998, Schneider et al. 2018). Due to their use of moving water and terrestrial habitat, trapping is not an appropriate capture method for this species. Mark-recapture studies are used in combination with VES for estimating population counts and recruitment when performed yearly over many years. VHF radiotelemetry is used to track individuals to estimate various aspects of spatial ecology including home ranges, movement distances, and habitat selection. Radiotelemetry can be advantageous when tracking individuals throughout a single season when vegetation changes and seasonal movements cause individuals to be difficult to find (Farrell and Graham 1991).

While VES are the most reliable method of wood turtle capture, the distance from the river in which these surveys should occur, varies. Flanagan et al. (2013) argued that most effective surveying can be performed within 10 m of a waterway before July as this is where they found the highest probability of turtle capture. Of wood turtle captures throughout a season, 95% were captured within 300m (Kaufmann 1992*a*), 304m (Compton et al. 2002), 235m (Tingley et al. 2009), <200m (Remsberg et al. 2006), 160m (Brown et al. 2016), or within 150m (Harding and Bloomer 1979) of a waterway in previous studies. Because of this variation, survey distance is study-dependent and should be based upon geographic location, previous knowledge of local wood turtle habits, and riparian habitat structure.

Radiotelemetry is a useful tool for tracking individuals of various animal species, especially turtles. This data can be used to estimate movement distances and home ranges. Radiotelemetry involves the use of a transmitter that is attached to an individual which is then tracked at some consistent interval throughout a specified period. Location and other habitat data is recorded during each tracking event and later used for analyses. In wood turtle studies, transmitters are applied to the posterior part of the shell in males and anterior in females which reduces the chances of disrupting mating (Arvisais et al. 2002). Attachment of transmitters may consist of using an epoxy glue or cement (Remsberg et al. 2006, Parren 2013, Curtis and Vila 2015, Lapin et al. 2019), or researchers can screw or bolt transmitters directly to the shells (Arvisais et al. 2002, Compton et al. 2002, Walde et al. 2003).

Morphological data collection

Upon capture, turtles are typically notched using a systematic shell notching system following the standards of Cagle (1939) which ensures proper identification upon recapture. Various measurements are commonly taken including length and width of carapace and plastron, shell height, weight, and annuli count which can be used to determine sex and estimate age. Sex is commonly determined per Harding and Bloomer (1979) by examining tail length and thickness, distance of cloaca from the plastral edge, and identifying concave characteristics of the plastron. Males have thicker tails with cloacal openings farther from the plastron and develop concave plastrons. Incorrect sexing of wood turtles is common as there are some geographical discrepancies of their size at maturity which can vary greatly. Harding and Bloomer (1979) in Michigan found the smallest female in courtship behavior had a carapace length (CL) of 158 mm and 12 annuli and the smallest male recorded had a CL of 192 mm. In Canada, Brooks et al. (1992) noted the smallest gravid female had a CL of 185 mm and 18 annuli while the smallest male had a CL of 199 mm and 22 annuli. In another Canadian study, Daigle et al. (1997) observed the smallest identifiable male had a CL of 176 mm and 10 annuli. Due to this variation, the use of measurements and observations from captured individuals exhibiting plastron concavity, copulatory behavior, gravidity, or nesting behavior can aid researchers in estimating the minimum size at maturity for a given population or geographic area.

Growth annuli are often counted to determine a turtle's age however, Harding and Bloomer (1979) advised that annuli counts may only be dependable age estimators up to 15 annuli. Wilson et al. (2003) claims aging using growth annuli is unjustified for most studies and requires species calibration between age and annuli count. However, this technique is widely used throughout the literature and is the most comparable among studies. Annuli counts can also vary depending on the different observers performing the counts which increases bias and reduces effectiveness of this aging method (Galbraith and Brooks 1989). Wood turtles have been recorded living long lives (>45 years) and growth annuli can be worn down or grow at an indeterminate rate depending on environmental and individual health conditions so actual turtle age can only reliably be known if recaptured since hatching (Harding and Bloomer 1979).

Home range analysis

Scientists often study an individual's or population's use of habitat over time and space to assess conservation concerns which includes analyzing home ranges. A home range is the space used by an individual over time and is an important part of their natural history. Home ranges can be measured for an individual's active season or for an entire year and they can be compared over time to understand the full utilization of habitat in the individual's range. The two most common and simplest methods for estimating home range size are minimum convex polygons (MCPs) and kernel density estimations (KDEs). Both methods specify an explicit number of data points to include in calculations (e.g., 95% or 50% of points) but MCPs create a convex polygon around the points while KDEs create a rounded kernel around each data point within a specified radial distance. In KDEs, all rounded kernels are combined to form the home range. Both methods have shown various levels of success in estimating wood turtle home ranges (Tuttle and Carroll 2003, Remsberg et al. 2006, Curtis and Vila 2015, McCoard et al.

2016*a*, Wallace et al. 2020). Researchers have now developed adaptations of these classic models that have been used to account for autocorrelation of data points and to adjust for movement and Global Positioning System (GPS) error as many species are not fixed in specific locations and frequent certain habitats or areas. Advances in GPS and telemetry technology have also caused a need for more accurate home range estimators one of the newest being Autocorrelated Kernel Density Estimations (aKDE) which is a KDE method that accounts for location autocorrelation (Fleming et al. 2015).

A downside of using MCPs is the inclusion of unused habitat. Connecting the outermost points to create a polygon can include areas within that are not or cannot be used by the individual (Worton 1987). A limitation to using KDEs is ensuring the correct radial distance, or "bandwidth," is chosen, which is the functional shape and width of a kernel around a telemetry point. Inappropriate choice of bandwidth can result in overestimations or underestimations of home ranges (Kie 2013). Another common inconsistency in home range comparisons using both methods is the percentage of points used to calculate the home ranges. The number of points used in calculations varies from 100% of points to determine the entire area within an individual's home range, to 95% which excludes 5% of random movements, or 50% which is classified as the core area used by the individual. The exclusion of 5% points, as with the 95% method, can unintentionally remove key habitat used by individuals including seasonal movements for mating, nesting, or foraging. Whereas, including those 5% of points, as with the 100% method, can include large areas of unused habitat and overestimate home range sizes. Inconsistent methods and specified percentages make it difficult to compare wood turtle home range studies across time and space which can hinder appropriate management actions in areas with unstudied populations.

Habitat selection

Habitat selection is a complex combination of an individual's preferences based upon their life history and environmental cues, as well as the available habitat (Northrup et al. 2022). Selection can be estimated based upon habitat use versus availability which can be divided into multiple scales. There are several methods of classifying habitat and quantifying the available versus used habitats for an individual or population.

There are several definitions of habitat selection that can be followed but most use Johnson's (1980) hierarchy of selection which includes first order (geographic range), second order (population range), third order (individual home range), and fourth order (selection within home range). Landscape, population, and home range-level classification often occur using aerial imagery, ground truthing (confirming vegetation structure at ground level), and radiotelemetry data (Arvisais et al. 2004, Dubois et al. 2009). Assessing macro and micro-habitat selection within a home range typically involves ground surveys and vegetative sampling to measure specific habitat characteristics including canopy cover, temperature, vegetation associations, coarse woody debris (CWD), and forage (McCoard et al. 2016*a*,*b*; Wallace et al. 2020). However, some limitations can affect estimations including subjective land cover classification, lack of ground truthing, and inappropriate use of land cover data based on objectives.

Analysis of Johnson's second order (population) and third order (individual home range) habitat selection are useful for making management decisions based on population and individual movement patterns and habitat use. To analyze habitat selection at these levels, scientists collect telemetry data for individuals in a population and analyze these locations in spatial relation to habitat that is "used" versus habitat that is "available." "Available" habitat is often classified as habitat found within a specified range that an individual could use if they chose to. "Used" habitat is typically in immediate proximity to telemetry points or an individual's home range. There are multiple methods for analyzing used and available habitat to determine if there is random or targeted habitat selection occurring.

One of the most common methods of analyzing habitat selection is compositional analysis (CA). This method uses percentages of habitat used and habitat available and compares log-ratios of the data (Aebischer et al. 1993). While this method can be successfully used at the first and second order of habitat selection (geographic and population), it fails at assessing habitat selection at finer scales when all habitat types are not used or available to all individuals (Bingham and Brennan 2004). Substitutions of small values for non-used or non-available habitat types has been suggested but inherently establish type one and type two error into analyses (Connor et al. 2003, Bingham and Brennan 2004). Other suggestions include combining lesser-used habitat types into more common habitats, but this reduces the variety and specificity of habitat types that may be available or used within a landscape (Aebischer 1993). Due to the probability of inflated error at fine-scale levels of habitat selection, other methods should be used to evaluate habitat selection at the third and fourth order (individual home range and within home range).

Euclidean Distance Analysis (EDA), similarly to CA, uses habitat types and telemetry points to determine habitat selection however, EDA measures the distance of random or recorded locations to specific habitat types while CA approximates proportions of habitat types within a specified area. Distances to each habitat type are calculated for both used and available habitats. These distances are used to create a ratio of used to available habitat and these ratios are tested for significance and often ranked in order of selection or avoidance. Unlike CA, EDA distances are not limited by log-ratio errors for missing or true zero data. This leaves distance ratios open to use in multivariate analyses including multivariate analysis of variance (MANOVA), which is the most employed. DeGregorio et al. (2011) found that CA proved to be a useful tool for landscape-level habitat selection for snakes, but EDA proved more useful at finer-scales of habitat selection which can be extended to other reptilian species. It is important to determine the appropriate scale for studies based on species natural history and study objectives and to use appropriate statistical methods for assessing selection and avoidance of certain habitats depending on the scale. Using proper methods for a study ensures replicability across a geographic range and verifies the appropriateness of conclusions drawn from the data collected.

Extended Methodology

Study area

Field work took place along ~4 km of a river within northwestern Michigan. The specific location of the site has been withheld to protect this wood turtle population. The study river averages 15 m across and consists of a sandy bottom with minimal submergent or emergent vegetation and occasional woody debris. Annual discharge averages 1500 ft^3/s with lows in the winter months and peaks up to 3200 ft^3/s in early spring (U.S. Geological Survey, Michigan Water Data Support Team 2022). Riverbanks comprise a mix of thick terrestrial vegetation and bare ground. Wetlands, graminoid-dominant habitat, scrub-shrub areas dominated by speckled alder (*Alnus incana*), and northern hardwood forest comprise the surrounding terrestrial habitat. Hardwood forests occur within the riparian areas and dominate the upland. Michigan experiences a humid continental climate under the modified Köppen climate classification which is characterized by hot summers, cold winters, ample precipitation, and regular weather fluctuations (Climate Change in the Midwest: A Synthesis Report for the National Climate Assessment, 2014). This area receives an average of 8.4 cm of precipitation during the summer months (April – August) and 95.11 cm annually. Temperatures peak in July averaging 27 °C (Abatzoglou et al. 2018).

Occurring within a public forest, this site experiences moderate recreational use in the form of fishing, kayaking, and hiking. The USFS actively manages this public forest throughout the year. Some unpaved and partially paved roads run through the surrounding landscape with bridges crossing the river and there is sporadic traffic ranging from small passenger vehicles to large commercial trucks. In 2019, the USFS began focusing on restoring remnant oak-pine barrens around this site using timber harvest, prescribed burns, and native seeding. Timber harvest for oak-barrens consists of opening about 10-60% of the overstory canopy. They are removing undesirable and invasive species such as spotted knapweed (*Centaurea stoebe*), common mullein (*Verbascum thapsus*), foxtail grass (*Alopecurus* spp.), bull thistle (*Cirsium vulgare*), and Canada thistle (*Cirsium arvense*) which is followed by reseeding native graminoid and forb species including June grass (*Koeleria cristata*), big bluestem (*Andropogon gerardi*), little bluestem (*Sarothamnus scoparius*), wild lupine (*Lupinus perennis*), golden rod species (*Solidago nemerosa, Solidago juncea, Solidago speciosa*), rough blazing star (*Liatris aspera*), and wild bergamot (*Monarda fistulosa*), to restore oak-pine barrens (P. Laarman, U.S. Forest Service, personal communication). Long-term management involves the mechanical removal or herbicide treatment of woody encroachment and prescribed burns on a 3–5-year rotation.

Data collection

We captured wood turtles during May 2021, using visual encounter surveys along ~4 km of the river ranging 0–200 m perpendicular to the river on both sides (Arvisais et al. 2002, Tuttle and Carroll 2003, Flanagan et al. 2013, Hagani et al. 2021). We captured all individuals by hand and notched the marginal carapacial scutes using a numbering scheme comparable to Cagle (1939). We collected morphological data including age, sex, mass, shell measurements, and physical abnormalities or injuries of all individuals. Turtles were aged by counting growth annuli of the plastral scutes (Harding and Bloomer 1979). Wood turtles in Michigan become sexually mature around a minimum carapace length of 160–180 mm and annuli count of 12–14 so we used these as our baseline measurements to determine sex and reproductive class (Harding and Bloomer 1979). We also used secondary male characteristics for determining sex which include a concave plastron and a thicker pre-cloacal tail with a cloaca posterior to the edge of the plastron (Lovich et al. 1990). Females were examined for eggs by palpating anterior to the rear legs.

Turtles were divided into four groups including gravid (females found gravid anytime during the active season), female (non-gravid females that met the minimum size to sex or were found mating), males (individuals exhibiting secondary male characteristics or were found mating), and juveniles (individuals too small to determine sex based on size and characteristics). We palpated females from spring emergence until the end of the nesting season in case of delayed egg development.

In May 2021, we fitted 23 individuals (3 gravid, 6 females, 9 males, 5 juveniles) with radio transmitters (R1800 or R1600, Advanced Telemetry Systems [ATS], Isanti, MN, USA) using an instant-setting epoxy and a marine putty. Transmitter and epoxy combination weights represented less than 5% of the body weight of the individual turtles to reduce interference with daily and seasonal habits (e.g., swimming, walking, mating, etc.). All turtles were released at point of capture within 2 hours. Turtles were tracked between 07:00 h and 17:00 h every 1–3 days from May to August, 2021-2022, using a 4 MHz receiver [ATS] and a flexible H-type antenna (Telonics Inc., Mesa, AZ, USA). Gravid females were tracked twice per day in the morning and later in the evening, during nesting season, to estimate time and location of nesting. Locations were recorded using a handheld GPSMAP 64x (Garmin LTD., Schaffhausen, Switzerland).

Spatial analyses

We estimated minimum convex polygon (MCPs; 50% and 100%) and kernel density estimation (KDEs; 50% and 95%) home ranges. We used the *mcp* function to calculate MCPs and the *kernelUD* function to calculate KDEs using the adehabitatHR package version 0.4.19

(Calenge 2006) in R (R Core Team 2020). MCPs and KDEs are both commonly used throughout wildlife research to estimate the size of individual home ranges, yet both are prone to issues particularly with herpetofauna. MCPs tend to overestimate home ranges by including too much space that is not necessarily used by the individual (Worton 1987). KDEs have been deemed more accurate estimators of home ranges as they consider the utilization distributions of individuals and place more weight on areas that are more commonly used however, choice of bandwidth is crucial for creating an appropriate kernel (Kie 2013). Many herpetofauna species exhibit site fidelity which can lead to autocorrelation of data and overweighting of frequently used areas in KDEs (Row and Blouin-Demers 2006). We used both methods despite their drawbacks as they are well-represented in previous wood turtle home range studies which provides us the ability to compare across time and space. We used the ad hoc method of bandwidth choice which has been shown to be the most accurate and least likely to over or underestimate KDE home ranges (Kie 2013). We used multivariate analysis of variance (MANOVA) tests to determine if there was a difference in MCP and KDE home ranges between sex and reproductive classes between 2021, 2022, and both years combined. MANOVA was performed using the *MANOVA.wide* function from the MANOVA.RM package version 0.5.3 (Friedrich et al. 2022) in R (R Core Team, 2020)**.**

Turtle movement in relation to the river was calculated using the NEAR tool in ArcMap 10.7.1 (Esri, Redlands, CA, USA) and calculating mean distances of each sex and reproductive class to a Michigan streams shapefile (EGLE Admin 2022). We also visually analyzed turtle locations in relation to oak-pine barrens in ArcMap 10.7.1.

Habitat selection

To quantify landcover types, we created a landcover shapefile using various data sources and ground truthing in ArcMap 10.7.1. We used 2020 National Agriculture Imagery Program (NAIP) imagery (OCM Partners 2022), a Michigan streams shapefile (EGLE Admin 2022), a Michigan road shapefile (Center for Shared Solutions and Technology Partnerships 2014), the 2005 EGLE (Department of Environment, Great Lakes, and Energy) National Wetland Inventory (Ducks Unlimited 2021), an elevation contour shapefile (U.S. Geological Survey, National Geospatial Technical Operations Center 2020), and oak-pine barrens shapefiles from the USFS Cadillac-Manistee Ranger District (P. Laarman, personal communication). Ground-truthing consisted of surveying on foot and taking note of various habitat types throughout the study site and recording habitat associations at turtle locations. We delineated ten categories for use in habitat selection calculations (Table 1).

We used Euclidean Distance Analysis (EDA) to examine habitat use versus availability (i.e., habitat selection) (Connor and Plowman 2001). This method compares the distances of telemetry locations (used points) and random locations (available points) to all habitat types to determine selection. A ratio for each habitat type is created using the average "used" and "available" distances. These ratios are individually compared to a vector of 1s using MANOVA. Ratios <1 indicate selected habitat, >1 indicate avoided habitat, and =1 indicate random use. We chose to analyze population level (second order) and individual level (third order) habitat selection according to Johnson's hierarchy of selection (Johnson 1980). Due to changes in habitat composition resulting from restoration, we analyzed 2021 and 2022 habitat selection separately for all individuals.

To define available habitat at the second order (population level), we merged our 95% KDE home ranges for each year. To calculate second order "available" distances, we generated random points within our available habitat range equal to the total telemetry points for that year (674 in 2021; 575 in 2022) and measured the distance to each habitat type for each year. We calculated "used" distances by generating random points equal to the number of telemetry points for each individual within the bounds of their 95% MCP and measuring the distance to each habitat type for each year.

For third order (home range level) available habitat, we analyzed individual 95% MCP home ranges for each year. Third order "available" distances were determined by generating random points equal to the number of telemetry points for each individual within the bounds of their 95% MCP and measuring the distance to each habitat type within the combined 95% KDEs for each year. Third order "used" distances were determined by measuring distance from actual telemetry points to each habitat type within the combined 95% KDEs for each year.

For both second and third order, used distances were divided by available distances to create our habitat selection ratios. We used MANOVA to compare our ratio vectors to a vector of 1s to determine if there was non-random habitat selection occurring. If non-random selection did occur (i.e., the MANOVA was significant), we used pairwise t-tests with Bonferroni correction to determine which habitat types were being selected, avoided, or randomly used.

Microhabitat use and turtle behavior

We analyzed microhabitat data collected during telemetry. This included turtle behavior, presence of coarse woody debris (CWD), and identifying items foraged. Turtle activity included basking (sitting in direct sunlight), feeding (actively eating anything), mating, resting (not in direct sunlight or performing another activity), swimming, walking, and unknown (no visual of turtle to assess activity). Presence of CWD was determined by visual observation of woody debris (downed trees or branches and decaying logs large enough for turtles to move in or under) within ~1 m of the turtle. Foraging materials were identified by visually observing food on or in a turtle's mouth.

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