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Spatial Ecology of the Adult and Neonate Eastern Box Turtle in a Forested Landscape

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Spatial ecology of the adult and neonate eastern box turtle in a forested landscape

Patrick B. Laarman

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DEDICATION

This thesis is dedicated to my Gram, Helen “Billie” Hoffman, who inspired me with her love, humor, generosity, and intellect. Gram, I’m sorry my thesis writing took so long as I know how much you were looking forward to attending Graduation. I could not have done this without you.

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ABSTRACT

A thorough understanding of spatial ecology is fundamental when developing and implementing conservation strategies for imperiled turtle species. I investigated spatial ecology of adult and neonate eastern box turtles in the Manistee National Forest (MNF), Michigan. My primary objectives were to evaluate relative habitat preferences of adults and document residency time of neonates in natal openings. I radio-fitted 25 adults, protected 64 nests, and radio-fitted 66 neonates. Mean home range size for adults (n = 25 turtles) was 16.4 ha ± 2.4 SE (100% Minimum Convex Polygon). I detected non-random habitat use by adults (Wilks $\Lambda = 0.202$, df = 4, $P = 0.001$ by randomization) at the home range versus available landscape scale. Upland broadleaf forest ≤250 m to wetland and upland openings were most preferred relative to 5 available habitat types. Most (23/25, 92.0%) adult turtles were initially captured in uplands but 21/25 (84.0%) subsequently maintained home ranges that included wetland habitat. Distances to edge and water within adult home ranges were closer than distances to edge and water within available landscape (Wilcoxon signed-rank tests, $P < 0.001$). Mean nest emergence date was 18 September. Neonates did not move far ($\bar{x} = 19.9$ m ± 2.4 SE) before overwintering and 24/46 (52.1%) overwintered within their natal opening. Neonate dispersal and overwintering habitat use were associated with distance from nest to nearest forest edge and date of nest emergence. In their second activity season, neonates were sedentary in early spring ($\bar{x} = 0.7$ m/d ± 0.1 SE) but movements increased >600.0% in June and July. By 1 July, all radio-fitted neonates had vacated their natal openings. Maintenance of existing nesting habitat and creation additional nesting habitat near wetlands should be a priority when considering conservation approaches for box turtle populations in the MNF. Land managers should be aware neonates reside in or very near natal openings for several months after nest emergence.

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KEY TO SYMBOLS

α

Alpha value in statistical hypothesis tests.

Λ

Wilks lambda statistic.

ΔAIC_c

Rank value of Akaike Information Criterion corrected for small sample size.

w_i

Weight value of Akaike Information Criterion corrected for small sample size.

$\bar{x}$

Mean value in descriptive statistics

ABBREVIATIONS

MNF = Manistee National Forest

GVSU = Grand Valley State University

USDA = United States Department of Agriculture

USFS = USDA Forest Service

RFSS = Regional Foresters' Sensitive Species

HMNF = Huron-Manistee National Forests

MDNR = Michigan Department of Natural Resources

VHF = Variable hertz frequency

GIS = Geographic Information Systems

ID = Identification number

SE = Standard error of the mean

CI = 95% Confidence intervals

NAIP = National Agriculture Imagery Program

MANOVA = Multivariate analysis of variance

km = kilometers

m = meters

cm = centimeters

mm = millimeters

g = grams

y = years

h = hours

d = days

ha = hectares

$\text{ft}^{2 =}$ square feet

CHAPTER I

INTRODUCTION

Many turtle and tortoise populations, including eastern box turtles (*Terrapene carolina carolin*a, hereafter box turtle), have steadily declined in recent decades. Anthropogenic factors are the primary drivers behind population declines and include habitat loss, habitat fragmentation, road mortality, and collection for pets (Dodd 2001, Gibbons 2000, Gibbs and Shriver 2002). As human demand for space and natural resources mounts, effective habitat management on public land will be increasingly important for conservation of this imperiled turtle species. The Manistee National Forest (MNF) includes the largest area of publicly owned box turtle habitat in the state of Michigan. To provide site specific information related to vegetation management projects, Huron-Manistee National Forest (HMNF) personnel surveyed for and radio-monitored box turtles from 2010-2014. Although their data were collected for monitoring purposes and vegetation management project planning, the HMNF graciously provided me access to their data for subsequent analysis in my graduate studies. In addition to this dataset, my Grand Valley State University (GVSU) colleagues and I collected field data from 2013-2016 with the goal of providing new and relevant research results on box turtles. While the GVSU box turtle research was multi-faceted, my focus was the spatial ecology of adult and neonate age classes.

Chapter II was formatted as a journal manuscript for submission to *American Midland Naturalist*. Although a terrestrial species, box turtles are often located near water (Dodd 2001, Donaldson and Echternacht 2005). Chapter II addresses the question: are wetlands a habitat requirement, habitat preference, or neither for box turtles? Home range estimates, relative habitat preferences, seasonal habitat use, and overwintering site fidelity are also included.

Chapter III was formatted for submission to *The Journal of Wildlife Management*. In Michigan and other Midwestern states, box turtles often nest in upland open canopy habitats, some of which are managed with prescribed fire to promote biodiversity and restore rare natural communities (Cohen 2000, Kost et al. 2007). This chapter is an examination of factors associated with neonate dispersal and residency time in natal upland open canopy habitats and includes management implications and recommendations regarding prescribed fire and the neonate age class.

Chapter IV contains a collection of short notes on interesting or unique observations accrued during fieldwork. These notes could not be assimilated into Chapters II or III but may be of interest to someone, somewhere, some day. Chapter V outlines management recommendations specific to box turtle populations inhabiting the MNF. Chapter VI contains a brief literature review of box turtle ecology and supplemental detail on methodologies outlined in Chapters II and III, including schematics for an effective predator exclusion device used to protect box turtle nests. Chapter VI also contains a list of references cited in Chapters I, IV, V, and VI.

PURPOSE

Within the MNF, the United States Department of Agriculture Forest Service (USFS) considers the eastern box turtle a Regional Foresters' Sensitive Species (RFSS). Prior to management decisions, USFS biologists analyze best available information and make determinations regarding potential impacts of proposed management activities to box turtles and other RFSS. During this process, local knowledge pertaining to a species is more informative than research conducted elsewhere, especially if the RFSS has a large geographic range. Knowledge gaps associated with box turtle ecology in the MNF were identified through communication with USFS biologists. The purpose of this research was to investigate aspects of box turtle ecology relevant to promoting long-term population viability in the MNF via effective habitat management.

SCOPE

The scope of this thesis includes spatial ecology of adult and neonate age classes, relative habitat preferences of adult box turtles, overwintering habitat use of adult and neonate age classes, nesting, nest emergence, neonate dispersal, and residency time of neonates in natal openings. This thesis also includes management recommendations for box turtles and their habitat in the MNF.

ASSUMPTIONS

Because riparian and wetland habitat within the study area (Chapter II) was almost exclusively limited to a single river floodplain, but upland habitat was extensive and spanned for several km, I assumed that adult turtles captured and radio-fitted in upland habitats would be less likely to have riparian or wetland habitat within their home ranges if these habitats were not important resources.

HYPOTHESIS

I hypothesized (Chapter III) neonates would remain near their nests during their first year of life (Madden 1975).

SIGNIFICANCE

This research addresses aspects of eastern box turtle ecology relevant for conservation outcomes in the Manistee National Forest. Furthermore, this thesis provides novel insight into early life history of eastern box turtles. Information provided in this thesis may also prove useful in the context of eastern box turtles and management and restoration of early successional and fire dependent vegetation communities in the Midwest and Great Lakes Regions.

DEFINITIONS

Activity Season

Period of eastern box turtle activity after spring overwintering egress and before fall overwintering ingress.

Adult

Age classes of sexually mature eastern box turtles.

Edge

Transition or ecotonal zone between two distinct land cover types.

First activity season

Period of activity between the time neonate eastern box turtles emerge from nests in late summer or fall and their first overwintering period.

Form

A term first mentioned in Stickel (1950) referring to the common behavior of eastern box turtles in which they seek thermal refugia and or concealment in leaf litter or other substrates during the activity season.

Juvenile

Ages classes of sexually immature eastern box turtles which are >1.0 y old.

Natal opening

The specific opening where a neonate eastern box turtle emerged from its nest.

Neonate

Age class of eastern box turtles which are <1.0 y old.

Opening

A broad classification term used by the Huron-Manistee National Forests to reference a suite of upland non-forested (i.e., relatively open canopy) sites of relatively small patch size (0.5 ≤ 50 ha).

Overwintering

A period of torpor allowing box turtles to survive inclement winter climates by burrowing into substrates (Dodd 2001).

Overwintering egress

The beginning of the overwintering period, when box turtles seek refugia by burrowing into substrate.

Overwintering ingress

Emerging from overwintering refugia in spring.

Raster data

A category of GIS data referencing a grid of cells at a specified resolution.

Second activity season

Period of activity for neonate turtles between spring overwintering egress and fall overwintering ingress. Refers to neonates that hatched the previous fall, survived the overwintering period, and resumed activity the following spring.

Stand

Smallest unit of basic forest mapping used by the Huron-Manistee National Forests.

Vector data

A category of GIS data referencing points, lines, or polygons.

CHAPTER II

Riparian associations of a terrestrial turtle? Relative habitat preferences of the adult eastern box turtle in a forested landscape

ABSTRACT

Eastern box turtles are terrestrial and commonly associated with forested habitat, yet are often found near water sources. We monitored habitat use of 25 adult box turtles (19 females, 6 males) via radio telemetry in the Manistee National Forest, Michigan. Our primary objectives were to evaluate relative habitat preferences and examine potential riparian associations. Our study area was large (~ 50 km^2) but wetland habitat was concentrated in a single river floodplain surrounded by extensive upland forest. Adult box turtles were specifically targeted for initial capture in uplands, often at nest sites a considerable distance (up to 990 m) from wetlands. We evaluated relative habitat preferences using compositional analysis. Mean home range size (n = 25 turtles) was 16.4 ha ± 2.4 SE (100% Minimum Convex Polygon). We detected non-random habitat use (Wilks Λ =0.202, df = 4, P = 0.001 by randomization) at the home range versus available landscape scale. Upland broadleaf forest ≤250 m to wetland and upland openings were most preferred relative to 5 available habitat types. Occupancy of upland openings peaked in late May and June. Most (23/25, 92.0%) adult turtles were initially captured in uplands but 21/25 (84.0%) subsequently maintained home ranges that included wetland habitat. Distances to edge and water within adult home ranges were closer than distances to edge and water within available landscape (Wilcoxon signed-rank tests, P < 0.001). Areas where upland openings, upland forest, and wetland habitat occur in close proximity are easily identified with simple GIS exercises and should be a priority for box turtle habitat conservation efforts. Providing upland nesting habitat near wetlands would likely benefit existing populations because gravid females would encounter fewer roads when traversing to and from nesting sites in May and June.

INTRODUCTION

Many turtle and tortoise populations, including eastern box turtles (*Terrapene carolina carolin*a, hereafter box turtle), have declined in recent decades (reviewed in Dodd, 2001). As anthropogenic factors continue to drive declines, comprehensive understanding of spatial ecology and habitat requirements is needed to promote long-term box turtle population viability via effective habitat management.

Forest, ecotones, and upland open canopy nesting sites are consistently identified as primary components of box turtle habitat, yet observations of riparian and wetland use are also common but have received less attention with regards to research investigations or conservation strategies (Overton, 1916, Allard, 1948, Stickel, 1950, Madden, 1975, Dodd, 2001, Donaldson and Echternacht, 2005, Fredericksen, 2014, Cross, 2016). Most reports of aquatic habitat use have been anecdotal (reviewed in Dodd, 2001) although Donaldson and Echternacht (2005) detected 131/166 marked box turtles over a single month at two small ponds in Tennessee. These accounts provided valuable insight into behavioral mechanisms for surviving heat stress or periods of drought. Considering box turtles display high fidelity to small home ranges (reviewed in Currylow *et al.*, 2012), availability and juxtaposition of water sources and wetland habitat may influence distribution of individuals and local populations on the landscape.

It is well known box turtles will use ponds, streams, and other permanent water sources within their home range (reviewed in Dodd, 2001, Donaldson and Echternacht, 2005) yet unknown whether permanent water sources are required habitat components within established home ranges. We investigated spatial ecology, seasonal habitat use, and relative habitat preferences of a box turtle population in a landscape where riparian and wetland habitat was concentrated in a single river floodplain yet upland forested habitat was extensive. The relatively homogeneous landscape and extensive contiguous upland forests provided the ideal study area evaluate potential riparian associations of the resident box turtle population.

STUDY AREA

We conducted our study within the Manistee National Forest (MNF), Michigan. We opted to omit specific coordinates to deter potential poachers from locating the study population. The study area was ~ 50 km^2 and can be generalized as a relatively natural area with few paved roads and no agricultural land use. Ownership was primarily federal (USFS) although fragmented by some private inholdings. USFS lands within the study area were managed for timber production, wildlife habitat, watershed quality improvement, recreation, and fuels reduction (USDA, 2006).

The entire length of the study area was bisected by a cold-water river. Streams and wetlands were concentrated in the river floodplain. Steep slopes marked abrupt transitions from upland forest to lowland floodplain. The floodplain varied in width from ~50-500 meters and was diverse in land cover types including; lowland conifer, lowland hardwoods, wet meadow, and scrub-shrub thickets. Many short first order streams, bayous, ponds, wetlands, and ground water seeps were present in the floodplain.

Uplands adjacent to the floodplain were extensive (outwash plains), generally spanning 5 to 7 km to the next nearest rivers, streams, or wetland complexes. Uplands were primarily second growth dry-mesic northern forest dominated by oaks (*Quercus spp.*), although other species including white pine (*Pinus strobus*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), and red maple (*Acer rubrum*) were often present in the overstory. Mixed and even aged conifer stands (e.g. monoculture plantations) of red pine, white pine, and jack pine were also present in the uplands to a lesser extent. The understory in upland forests was generally underdeveloped but contained the same species found in the overstory as well as shrubs such as cherry (*Prunus* spp.) or witch-hazel (*Hamamelis* spp.). Throughout much of the upland forests there were gaps in overstory canopy closure and mosaics of herbaceous vegetation and leaf litter on the forest floor containing sedges (*Carex* spp.) and grasses (*Andropogon* spp.), low bush blueberry (*Vaccinium angustifolium*), bracken fern (*Pteridium* spp.), and tree seedlings.

Upland openings were interspersed throughout the forest matrix. The term 'opening' is a broad classification used by the Huron-Manistee National Forests to reference a suite of non-forested sites of relatively small patch size (0.5 ≤ 50 ha). Openings are managed under individual prescriptions for wildlife habitat improvement and promotion of biodiversity (USDA Forest Service 2006). Openings represented approximately 4.0% of the uplands within the study area (USFS unpublished data). Many openings were periodically managed by the USFS by mechanical brushing, mowing, non-native invasive species treatments, planting of native grasses and forbs, and prescribed fire. Linear shaped openings resulting from powerline, fuel-break, and road maintenance activities were also present.

METHODS

RADIOTELEMETRY

We located and fitted adult box turtles with radio-transmitters in staggered entry fashion from September 2010 to June 2013. We located turtles by road cruising, surveying historic box turtle occurrences (USFS unpublished data), discovering ‘new’ turtles during telemetry, and surveying potential nesting habitat in May and June. Because our objectives were to evaluate potential riparian/wetland associations and box turtles are known for low vagility (Stickel, 1950, Dodd, 2001, Currylow *et al.*, 2012), we targeted individuals for our sample in upland habitats whenever possible. Because riparian and wetland habitat was concentrated in the river floodplain, but upland habitat was extensive and spanned for several kilometers, we assumed box turtles captured in uplands would be less likely to include riparian or wetland within their home range if these habitats were not important resources.

Following capture, we outfitted each turtle with 15 g VHF radio transmitters (Model RI-2D Holohil Systems Ltd., Ontario, Canada or Model 1555 Advanced Telemetry Systems, Isanti, Minnesota, USA). We tracked and directly observed turtles approximately weekly for at least one complete activity season (the end of the overwintering period in spring to the beginning of the overwintering period in fall) or a minimum of 1 y. During telemetry observations, we recorded Global Positioning System (GPS) location using a Garmin etrex®. Cumulative mass of epoxy and transmitters comprised less than 5.0% of turtle body mass. All handling techniques were approved by the Michigan Department of Natural Resources (Scientific Collectors Permits) and the Institutional Animal Care and Use Committee at Grand Valley State University (protocol 13-03A).

HOME RANGE ESTIMATION

We estimated home ranges using 100% Minimum Convex Polygons (Mohr, 1947) in ArcMap 10.1. The Minimum Convex Polygon (MCP) method has been widely criticized when applied to mobile species such as mammals and birds (Worton, 1987, Worton, 1989, Börger *et al*., 2006) but defended as a reliable estimate of reptilian home ranges (Row and Blouin-Demers, 2006). We opted for 100% (MCP) as opposed to lower percentage (such as 95%) because we did not want to exclude locations indicative of important life history events (e.g., nesting or overwintering). Additionally, using MCP facilitated comparison to recent box turtle home range estimates (Currylow *et al*., 2012, Cross, 2016).

DELINEATION OF AVAILABLE HABITAT WITHIN THE LANDSCAPE

We estimated ‘available’ habitat individually for each box turtle in similar fashion to Row and Blouin-Demers (2006a) and Moore and Gillingham (2006), due to size of our study area and low vagility of box turtles. We buffered the centroid of each home range by the cumulative distance of each seasonal activity range (maximum straight line distance between any two points within the activity season). Because each box turtle in the sample may have differed in physical health, locomotive ability, and behavior, this approach incorporated spatial patterns of each individual.

LANDCOVER CLASSIFICATION AND HABITAT TYPES

We conducted supervised classification of 2012 National Agriculture Imagery Program (NAIP) leaf-on imagery quarter quads 1.0 m^2 resolution raster data in Erdas Imagine® GIS. We classified landcover into one of three basic categories; broadleaf forest, coniferous forest, or open. During grid generalization, the minimum patch size was assigned at 0.1 hectares, patches smaller than the minimum patch size were assimilated into surrounding land cover types. We clarify individual conifers were often present within broadleaf forest stands and vice versa. We inspected supervised classification results using USFS stand level vector GIS data (USFS unpublished data). The USFS vector data (hereafter vector data) contained many useful attributes including stand size, dominant overstory tree species, basal area, and stand age. We also conducted ground truthing in 2014 and reviewed Forest Service management activities and determined no stand conversion (e.g. forest converted to open) activities had taken place on USFS land within the study area from 2010 to 2014 (USFS unpublished data). Finally, we viewed Google Earth® aerial photography of any private lands within each turtle's available habitat polygons and detected no appreciable differences in land cover between 2012 NAIP imagery and the 2014 Google Earth® imagery.

After classifying vegetation into the three categories referenced above, we used vector data to further differentiate between upland and wetland. Because wetlands were almost exclusively limited to the river floodplain and there was an abrupt transition between uplands and floodplain, we used elevation data to differentiate between uplands and river floodplain and created a shapefile for the floodplain. We then merged this shapefile with the vector data containing the few small wetland patches (primarily *Chamaedaphne* bogs) disjunct from the river floodplain. We considered classified vegetation types (broadleaf forest, coniferous forest, and open) occurring in the floodplain and wetland patches a single habitat type (hereafter wetland) during subsequent analyses. The vector data contained permanent water sources but these comprised a very small amount (<0.001%) of the study area (primarily the river, first order streams in the floodplain, and small ponds) and we combined surface water into the wetland category. We then buffered the wetland habitat shapefile by 250 meters and clipped the broadleaf forest polygon within the buffer to create a fifth habitat feature. We elected the 250 m buffer because half of our initial capture locations for radio-fitted turtles were > 250 m from wetland (see Results; Table 2). These processes yielded five discrete habitat types within the study area: upland broadleaf forest ≤250 m to wetland, upland broadleaf forest >250 m from wetland, coniferous forest, upland openings, and wetland (Table 1). For distance based analyses, we identified four areal (linear) habitat features in GIS using the five habitat types outlined above and water features from the vector data: upland/wetland edge, upland opening/forest edge, riparian (water), and all edge. All edge was upland/wetland edge, upland opening/forest edge, and riparian (water) edge merged into a single line shapefile.

RELATIVE HABITAT PREFERENCES AND DISTANCE BASED ANALYSIS

We calculated proportions of habitat types within each turtle's home range and available habitat buffer and used compositional analysis (Aebischer *et al*., 1993) to evaluate relative habitat preference in a use versus availability design. Compositional analysis (CA) is a widely used technique for evaluating relative habitat preferences for Johnson's (1980) second order habitat selection (selection of home range within available landscape) and third order selection (selection of habitat use within home range). If we rejected the null hypothesis (i.e., non-random habitat use), we continued with the CA process which generated a ranking matrix of relative habitat preferences. CA performs best when all habitat types are available to each animal and when all habitat types are used at least once by each animal (Bingham *et al*., 2010). If not all habitat types were available to each animal at a particular order of selection, we did not conduct CA to avoid potential for inflated Type I or Type II error rates (Bingham *et al*., 2007). We substituted 0.01 when a habitat type was available but not used.

For distance based analyses, we calculated the nearest straight line distances from each turtles' telemetry observations to each of the edge habitat categories. As opposed to generating random points within each home range or available habitat, we systematically sampled the entire study area using distance rasters (Benson, 2013). Distance rasters yielded distance (m) from the centroid of each cell (1.0 m^2 resolution) within the study area raster grid to the nearest edge habitat. After creating a study area distance raster for each edge habitat category, we intersected each home range and available habitat polygon with the distance rasters using the ‘clip’ function and repeated the process for each of the four habitat categories. Systematic sampling yielded mean distance to each habitat feature within each box turtles’ respective home range and available habitat polygons. Each box turtle and their respective telemetry observations, home range, and available habitat were considered an individual sampling unit and data were treated as paired during analysis. Because not all data met assumptions of normality, we used Wilcoxon Signed Rank test to compare distances to each habitat type at two scales; box turtle locations versus home ranges (3rd order selection, Johnson, 1980) and home ranges versus available habitat within the landscape (2nd order selection, Johnson, 1980). We conducted statistical analyses using the base package and Adehabitat package (Calenge, 2006) in program R version 2.15.1 (R Development Core Team, 2012). In all hypothesis tests, $\alpha = 0.05$. We reported descriptive statistics as means ($\bar{x}$) ± standard errors (SE).

RESULTS

We radio-fitted 26 adult box turtles (7 male, 19 female) resulting in 1385 total relocations (Table 2). Maximum distance between any two radio-fitted turtles was approximately 20 km (Figure 2). All turtles were alive at transmitter removal. Two box turtles were initially captured and radio-fitted in wetland and 24 turtles were captured in uplands ranging from 7 m to 990 m to the nearest wetland habitat (Table 2). One male turtle, ID 1457, exhibited transitory movements during the study period and his activity range was greater than 3 km during an eight-week period. During this period, he was moving within the river floodplain. Unfortunately, he was collected while crossing a road by a well-intentioned local resident who drove him, ironically, quite near his original capture location and released him into the river, mistaking him for an aquatic species. We acquired this information retrospectively because the local noticed the transmitter and left several messages over the weekend at the USFS office before deciding to release him. We reported data collected male ID 1457 (prior to his citizen-translocation) in Table (2) but censored it from descriptive statistics and further analysis because his home range estimate was an extreme outlier and his movements were likely a function of transitory or dispersal behavior. Home range estimates (*n* = 25 turtles) were $\bar{x}$ = 16.4 ha ± 2.79, range 2.2 ha to 54.5 ha and activity ranges (i.e., maximum diameter of MCP home range) were $\bar{x}$ = 726.5 m ± 76.8, range 207.0 to 1867.0 m (Table 2).

Upland broadleaf forest ≤ 250 m to wetland habitat was the most used habitat type and all turtles used it (Fig. 3). No other habitat type was used by all 25 turtles. Three turtles consistently overwintered in wetland, although their overwintering sites were above the water table in forested stands within the floodplain. The remaining turtles (*n* = 23) overwintered in upland forest (all three categories). Habitat use by males was variable by individual throughout the activity season. Female turtles displayed a more pronounced temporal pattern of habitat use. Following spring overwintering egress, gravid females moved towards upland openings in mid to late May and staged in or near openings until nesting was completed in early to mid-June (Fig. 4, Fig. 5). Several turtles traveled considerable distance to nest, the maximum observed distance from overwintering site to nesting site was 1.9 km. Of the females that we documented nesting (*n* = 15), only two females nested in different openings from one year to the next. After nesting, females vacated openings within a few days. Many females traveled immediately to wetland habitat and remained for several weeks. Most turtles frequented forest and wetland habitat throughout the summer (Fig. 4). Box sexes rarely used openings in summer or fall (Fig. 4). By mid-September, turtles were within 100.0 m from their future overwintering site. Of the turtles monitored for consecutive winters (*n* = 18 turtles), 83.0% overwintered within 100.0 m and 56.0% overwintered within 50.0 m from previous year's overwintering location.

Turtles were only observed in water on five occasions (0.4% of total observations). Transient male (ID 1457) crossed the river on at least two separate occasions. We also observed a focal point of habitat use near a small pond (0.15 ha) which drained into a stream. The pond and stream were located at the bottom of a steep slope within 10.0 m of the upland forest/wetland edge. Although only one turtle was captured and radio fitted at this location, the home ranges of nine turtles overlapped near the pond and stream (Fig. 6). It was common to see aggregations of box turtles (both radio-fitted and non-radio fitted individuals) at this location during summer although we did not observe them in the pond.

The area we estimated as 'available' to each turtle ranged from 60.5 ha to 3066.0 ha (Table 2). All five habitat types and edge categories were 'available' to each turtle but not every habitat type and edge category was included in each turtle's home range or used by each turtle within its respective home range. Because of the potential for increased Type I or Type II error rates when small values are substituted for zero use in the numerator and denominator, we opted to conduct CA only at home range versus landscape scale (2^{nd} order selection Johnson, 1980). We rejected the null hypothesis of random habitat use (Wilks $\Lambda = 0.202$, $df = 4$, $P = 0.001$ by randomization). The order of relative habitat preference was: *upland broadleaf forest ≤250 m to wetland* > *upland openings* > *wetland* > *upland conifer forest* > *upland broadleaf forest >250 m from wetland* (Table 4).

Each box turtle’s available habitat polygon included all four edge categories. All home ranges except for male ID 560 included at least one edge habitat category. We detected significant differences between distances to all edge categories when comparing home ranges to available habitat (Table 5). When comparing distance to nearest edge between telemetry points versus home ranges, we detected no significant differences (Table 5).

DISCUSSION

We examined box turtle spatial ecology and habitat use in a forested landscape where wetland was concentrated to a single river floodplain. Home range estimates were larger than most reported in the literature (see review by Currylow *et al.*, 2012). Gravid females traveled considerable distances (up to 1.9 km) to nest in upland openings. We located and radio-fitted box turtles in uplands yet most individuals (21/25, 84.0%) used wetlands to some extent and maintained a riparian association at the home range versus available landscape scale.

In south-central Indiana, Currylow *et al*. (2012) reported an average home range (100% MCP) of 7.45 ha which at the time (2012) was larger than other published reports. Our mean home range estimate was more than twice that of Currylow *et al*. (2012) but was similar to Cross (2016) who reported mean annual home ranges in Ohio ranged from 13.95 ha to 26.71 ha (100% MCP). Some authors have reported home range size among herpetofauna increases near range extremes (DeGregorio *et al*., 2011) or in areas where quality and availability of resources is low (Arvisais *et al*., 2002). Others have suggested home ranges may be larger in tracts of contiguous high quality habitat (Currylow *et al*., 2012) because box turtles are not frequently contending with or encountering natural or anthropogenic barriers to movement (e.g. paved roads and urban development). Cross (2016) surmised limited availability and distribution of suitable nesting habitat patches resulted in relatively large home ranges. In this study, we attribute large observed home range sizes dually to high connectivity of upland forest habitat and to relatively low availability of upland openings suitable for nesting. The juxtaposition of suitable nesting habitat patches in a large upland forest matrix likely facilitates lengthy movements with relatively low risk for selection against this behavior from anthropogenic induced mortality events (e.g. paved roads).

Seasonal patterns of movement, overwintering habitat use, and nesting were similar to literature accounts (Madden, 1975, Dodd 2001, Kipp, 2003, Gibson, 2009, Wiley, 2010, Burke and Capitano, 2011, Cross 2016). As reported by Stickel (1950) and Kipp (2003), we observed females traversing past suitable nesting areas (as evidenced by other box turtles nesting there) to remote nesting areas. Most females displayed nest-site fidelity but we observed alternating use of nesting habitat patches (distinct openings ~ 450 m apart) by two individual female box turtles. Observations of ecotonal habitat use, upland forest/upland opening and upland/wetland ecotones, were similar to previous accounts (Madden, 1975, Donaldsen and Echternacht, 2005) and are probably a function of microhabitat preferences pertaining to thermoregulation and relative humidity (Penick *et al*., 2001, Rossell *et al*., 2006, Currylow *et al*., 2012, Cross, 2016). Thermoregulatory preferences probably also explain why some males frequented openings in spring and early summer. Decreased movements in fall and fidelity to overwintering sites were also reported by Cross (2016).

Access to wetland habitat was not habitat requirement on the annual temporal scale but wetlands were used by most (21/25, 84%) individuals we monitored. Because our study design targeted individuals in uplands, we likely understated the percentage of box turtles in the population that consistently use wetlands for access to water and other resources. Weekly telemetry observations averaged approximately 15 minutes of direct observation per individual which only represented 0.3% (assuming diurnal movements and an average photoperiod of 14 hours/day) of potential weekly activity (Schwartz and Schwartz, 1974, Dodd, 2001). Certainly, box turtles not observed in wetlands (4/25, 16.0%) could have used them but we failed to detect it. A portion of these box turtles (n = 4) probably frequented wetlands (based on proximity of telemetry locations to wetland) during the study period and we simply did not detect it, but we are confident female ID 450 did not use wetland habitat during the study period. She was observed 78 times over 36 consecutive months, she displayed extremely high fidelity to her 15.7 ha home range each, and was never found within 225 meters of wetland habitat.

We doubt individuals occupying only uplands could have survived the study period without drinking water occasionally. These individuals may have persisted by drinking from puddles in two-track roads after precipitation events, although this behavior was never observed. Perhaps leaf litter in upland forests, particularly oak leaves which are quite recalcitrant (Harrison, 1971), may cup enough water for the occasional drink following heavy precipitation events. Water-filled ground level tree-holes (Kitching, 1971) were present in uplands (pers. obsv.) and could provide a potential water source although we never witnessed box turtles using them. We observed extensive home range overlap near a small pond as did Donaldson and Echternacht (2005) in Tennessee. Box turtles can orientate and return to precise locations within their home ranges (Stickel, 1950, Dodd, 2001) and individuals that have permanent water sources within their home range may have higher long term survival rates than those relying on dynamic and infrequent water sources in uplands.

CA ranked wetland in the middle of the range of relative habitat preference but upland broadleaf forest ≤ 250 meters from wetland was the most preferred habitat type. Maintaining home ranges near wetland facilitates access to water and may be important for long term survival, especially during periods of drought or heat stress (Dodd, 2001, Donaldson and Echternacht, 2005). Box turtles are known to drink copious amounts of water when given opportunity (Bartlett and Bartlett, 1996, Dodd, 2001) but are likely capable of surviving extended periods of time without doing so, although the duration probably varies based upon many factors including ambient temperatures, relative humidity, water content of food sources, physical fitness, etc. (Ernst, 1968, Riedesel *et al*., 1971, Sturbaum and Riedesel, 1977). CA and other use versus availability designs may understate the importance of wetland habitat to box turtles if wetlands are used infrequently but provide valuable resources (water) allowing individuals occupy uplands for extended periods.

Box turtles frequently selected home ranges which included wetland habitat but spent most of their time in upland habitats which were proximal (≤ 250 m) to wetland habitat. Plausible explanations include 1) wetlands are used for infrequent yet important episodes of copious drinking, 2) there is an increasing relative humidity gradient in upland forests as distance to wetland decreases and therefore upland forests adjacent to wetland provide optimum micro-climates, 3) hydric soils and water sources in the wetlands provide thermal refugia for surviving periods of heat stress (Donaldsen and Echternacht, 2005) , and 4) the hard edged ecotone between upland forest and lowland sites provides ideal thermo-regulatory and foraging opportunities and is therefore high quality habitat used by many members of the population.

While we did not elucidate mechanism(s) driving the wetland association in this population, juxtaposition of riparian and wetland habitat in a forest matrix likely has strong predictive value for predicting box turtle occurrence. Areas where upland openings, upland forest, and wetland habitat occur in close proximity are easily identified with simple GIS exercises and should be a priority for box turtle conservation efforts. In the MNF, providing upland nesting habitat near wetlands would benefit existing populations because gravid females would encounter fewer roads when traversing to and from nesting sites in May and June. Furthermore, because a percentage of the population is likely transient (Stickel 1950, Williams, 1961, Kiester *et al*., 1982, Williams and Parker, 1987, Dodd, 2001), females will travel extensively to nest, and some individuals occupy only uplands throughout a given year, there are opportunities to provide habitat connectivity between localized populations. Specifically, creating nesting habitat and/or water sources between disjunct wetland/riparian habitat patches or localized populations may facilitate dispersal, genetic exchange, and colonization over the long term.

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FIGURE LEGENDS

Figure 1. Location of Manistee National Forest in Michigan. We radio-fitted and monitored 26 adult eastern box turtles within a study area approximately 50 km² in the Manistee National Forest (MNF), Michigan, 2010 to 2014. We refrained from providing further spatial reference to the study area to deter potential poachers from locating the study population.

Figure 2. Spatial distribution of 26 adult eastern box turtles depicted by each turtle's 100% Minimum Convex Polygon home range estimate. Turtles were radio-fitted and monitored in staggered entry fashion within the Manistee National Forest, Michigan, 2010-2014. We refrained from including landscape features deter potential poachers from locating the study population.

Figure 3. Mean ± SE proportional habitat use of 25 eastern box turtles radio-fitted and monitored weekly in staggered entry fashion within the Manistee National Forest, Michigan, 2010-2014. Numbers above error bars indicate the ratio of turtles observed using the habitat type at least one time during the telemetry monitoring period. All turtles were monitored for at least one full activity season (spring overwintering egress to fall overwintering ingress) or for one calendar year. UB close = upland broadleaf forest ≤ 250 m from wetland habitat. UB far = upland broadleaf forest > 250 m from wetland habitat. Up Con = upland conifer forest. Up open = upland openings. Wet = wetland.

Figure 4. Mean proportional habitat use ± SE of 25 eastern box turtles (*n* = 19 female, 6 male) by month. Three upland forest habitat types (upland broadleaf forest ≤ 250 meters from water, upland broadleaf forest > 250 meters from water, and upland conifer forest) were combined into a single category for ease of interpretation. All turtles were monitored for at least one full activity season (spring overwintering egress to fall overwintering ingress) or for one calendar year.

Figure 5. Habitat use and movements of radio-fitted female eastern box turtle ID 444 in 2013. Manistee National Forest, Michigan, 2013.

Figure 6. Extensive home range overlap among nine radio-fitted box turtles near a single small pond and stream. Turtles were radio-fitted and monitored in the Manistee National Forest, Michigan, 2010-2014.

TABLES

Table 1. Descriptions of habitat categories used in compositional analysis and distance based tests. Habitat in the study area was delineated using supervised classification in Erdas Imagine software and USFS vector stand level data. Minimum patch size = 0.1 ha.

Habitat type	Description of habitat type	Analysis
Upland broadleaf forest adjacent to wetland	Forest stands dominated by deciduous trees within 250 meters to wetland	Compositional Analysis
Upland broadleaf forest far from wetland	Forest stands dominated by deciduous trees greater than 250 meters to wetland	Compositional Analysis
Upland conifer forest	Forest stands dominated by long-lived conifer, including plantations	Compositional Analysis
Upland opening	Upland openings dominated by grasses, sedges, and forbs.	Compositional Analysis
Wetland	Floodplain forest, shrub-scrub, open canopy sedges, emergent vegetation, and water	Compositional Analysis
Upland/wetland edge	Transition zone (areal line feature) between upland and wetland sites	Wilcoxon signed-rank test
Upland opening/upland forest edge	Transition zone (areal line feature) between all upland forest and upland openings	Wilcoxon signed-rank test
Riparian	Transition zone (areal line feature) between water and terrestrial habitat	Wilcoxon signed-rank test
All edge	Combination of the four edge types described above	Wilcoxon signed-rank test

Table 2. Descriptive statistics for 26 adult eastern box turtles radio-fitted and monitored in staggered entry fashion from September 2010 through August 2014 in the Manistee National Forest, Michigan. Study period activity range represents the maximum distance between any two locations within the estimated home range. Cumulative activity range is the sum of the maximum distances between any two locations for each activity season (spring overwintering egress to fall overwintering ingress). Available habitat was estimated by buffering the centroid of each turtle's home range by the cumulative activity range.

Turtle ID	Sex	Distance from initial capture location to nearest wetland (m)	Number of observations	100% MCP home range estimate (ha)	Study period activity range (m)	Cumulative activity range (m)	Available habitat (ha)
613f	f	7	37	3.7	366	902	255.6
593f	f	31	50	5.4	370	688	148.7
2585f	f	0	54	6.1	371	793	197.6
1458f	f	371	23	6.1	779	901	255.0
587f	f	116	57	7.6	463	1059	352.3
648f	f	431	40	7.9	593	1151	416.2
671f	f	500	23	10.5	761	1109	386.4
1596f	f	368	106	10.6	602	1990	1244.1
24f	f	34	40	12.3	593	1573	776.9
649f	f	357	23	12.4	479	844	223.8
443f	f	19	65	15.0	1016	2204	1526.1
450f	f	240	78	15.7	682	1887	1118.6
573f	f	166	66	16.3	766	1425	637.9
577f	f	198	62	17.8	1098	1589	793.2
562f	f	549	80	27.8	821	2080	1359.2
667f	f	974	30	30.4	1362	1712	920.8
444f	f	392	95	32.3	1196	3124	3066.0

670f	f	974	30	51.9	1867	2990	2808.6
669f	f	990	22	54.5	1036	2027	1290.8
583m	m	15	72	2.2	207	554	96.4
560m	m	162	53	3.5	294	439	60.5
614m	m	191	37	4.8	367	861	232.9
441m	m	0	77	9.9	414	1173	432.3
412m	m	308	51	21.6	755	1105	383.4
579m	m	710	61	24.0	904	2432	1858.1
1457*	m	259	53	222.6	3647	n/a	n/a
Total/Average		321.6	1385	16.4	726	1464	833.7

[*] Male turtle ID 1457 was considered an outlier due to transitory or dispersal movements and information collected on this turtle was censored and thus was not included in totals, averages, or further analysis.

Table 3. Ranking matrix showing results of compositional analysis (Aebischer *et al*., 1993) applied to proportion of habitat types included in 100% MCP home ranges vs. proportion of habitat types within habitat available to each turtle (2nd order selection, Johnson, 1980) for 25 eastern box turtles radio-fitted and monitored in the Manistee National Forest, Michigan, 2010 - 2014. The higher the ranking order, the higher the level of disproportionate habitat use. Significant deviation ($P < 0.05$) from random use is indicated by a triple sign. 'UB Close' refers to upland broadleaf forest ≤ 250 meters to wetland, 'Up Open' refers to upland openings, 'Wet' refers to wetland, 'Up Con' refers to upland conifer forest, and UB Far refers to upland broadleaf forest > 250 meters from wetland.

	Habitat type					Relative habitat preference rank
Habitat type	UB Close	Up Open	Wet	Up Con	UB Far	
UB Close		+	+++	+++	+++	1
Up Open	-		+	+++	+++	2
Wet	---	-		+	+	3
Up Con	---	---	-		+	4
UB Far	---	---	-	-		5

Table 4. Results of univariate non-parametric tests comparing distances (m) to nearest areal edge feature between telemetry points, within home ranges, and within available habitat, respectively. Mean distance from telemetry points to nearest areal edge feature was calculated for each turtle (*n* = 25) and each turtle was treated as an individual sampling unit. Mean distances to edge features within home ranges and available habitat were acquired by systematically sampling a raster grid at a resolution of 1.0 m² following the technique put forth by Benson (2013).

Habitat Feature	Mean Distance (m)		Wilcoxon Signed-Rank Tests
	Within HR (±SE)	Within available landscape (±SE)	*P*
Upland/Wetland Edge	227.4 (32.1)	459.9 (44.1)	< 0.001
Upland Opening/Forest Edge	137.4 (15.0)	171.4 (6.5)	0.042
Riparian (water)	288.8 (37.5)	536.7 (52.0)	< 0.001
All Edge	77.7 (6.5)	122.1 (5.8)	< 0.001
	Telemetry points (±SE)	Within HR (±SE)	*P*
Upland/Wetland Edge	198.1 (27.8)	227.4 (32.1)	0.120
Upland Opening/Forest Edge	147.0 (16.6)	137.4 (15.0)	0.751
Riparian (water)	251.2 (30.2)	288.8 (37.5)	0.071
All Edge	73.5 (8.4)	77.7 (6.5)	0.230

FIGURES

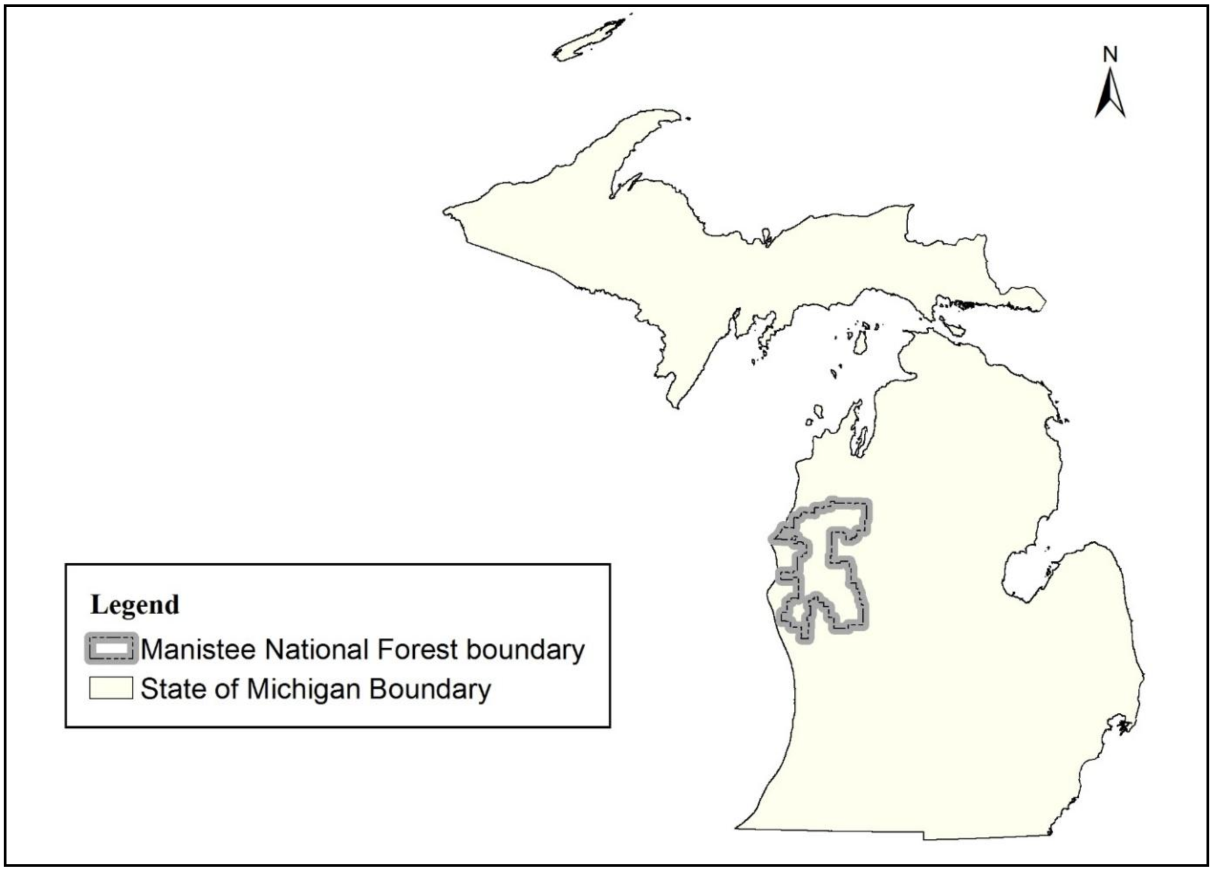

Figure 1.

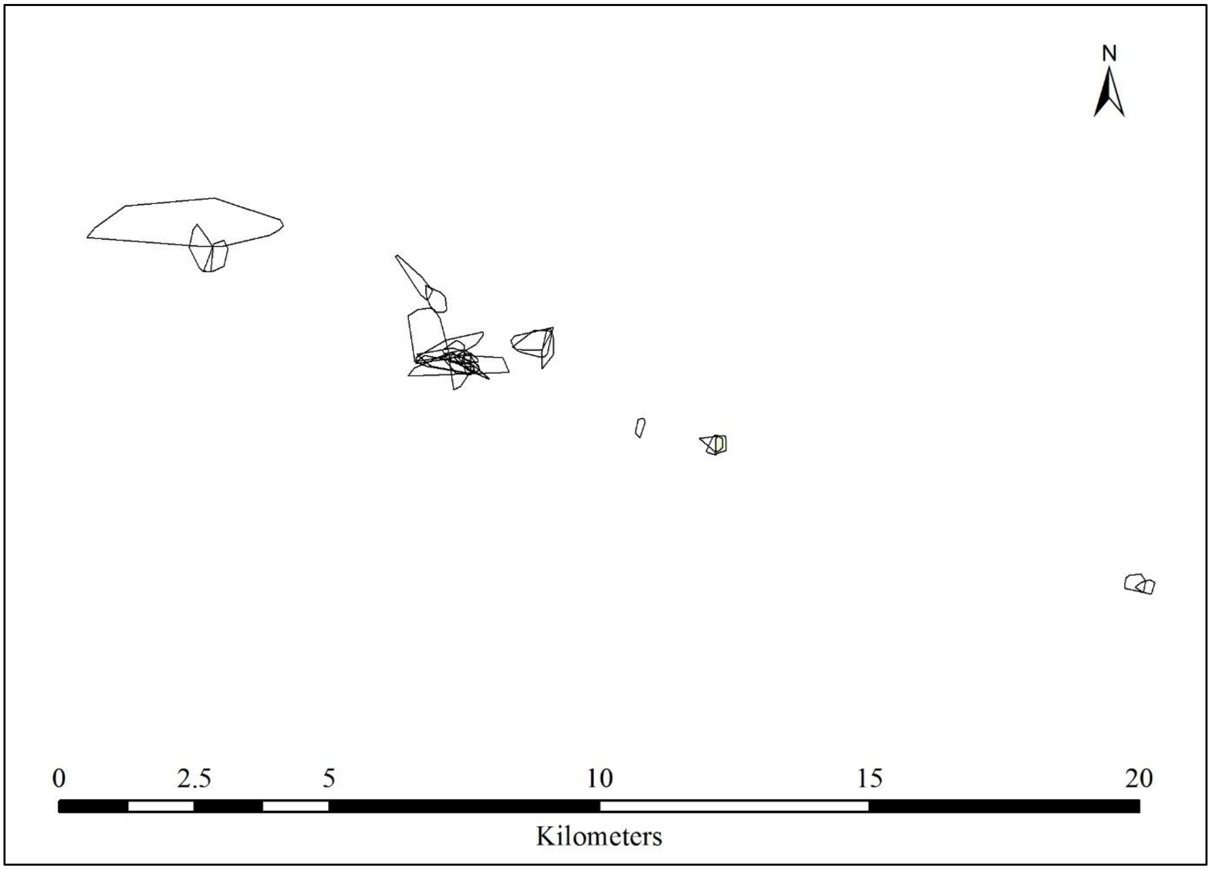

Figure 2.

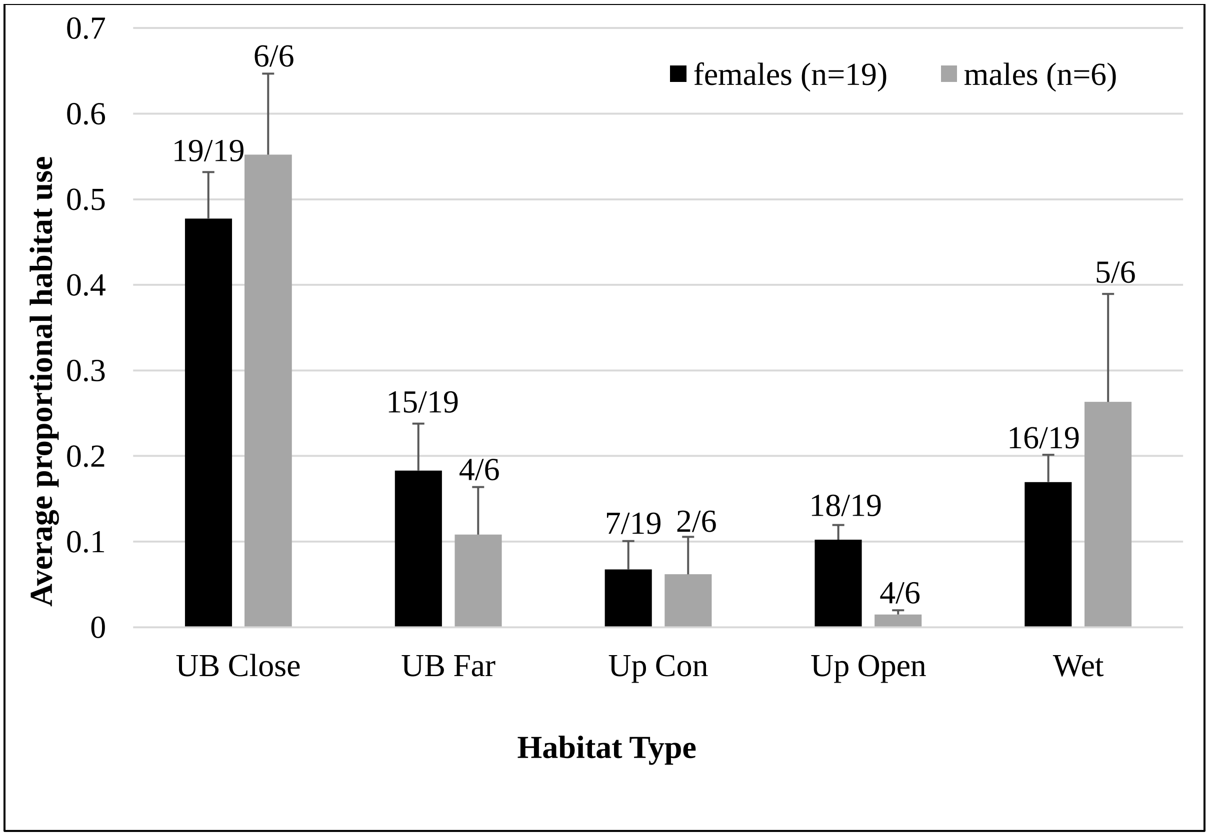
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Average proportional habitat use
■ females (n=19)
■ males (n=6)
19/19
6/6
15/19
4/6
7/19
2/6
18/19
4/6
16/19
5/6
UB Close
UB Far
Up Con
Up Open
Wet
Habitat Type

Figure 3.

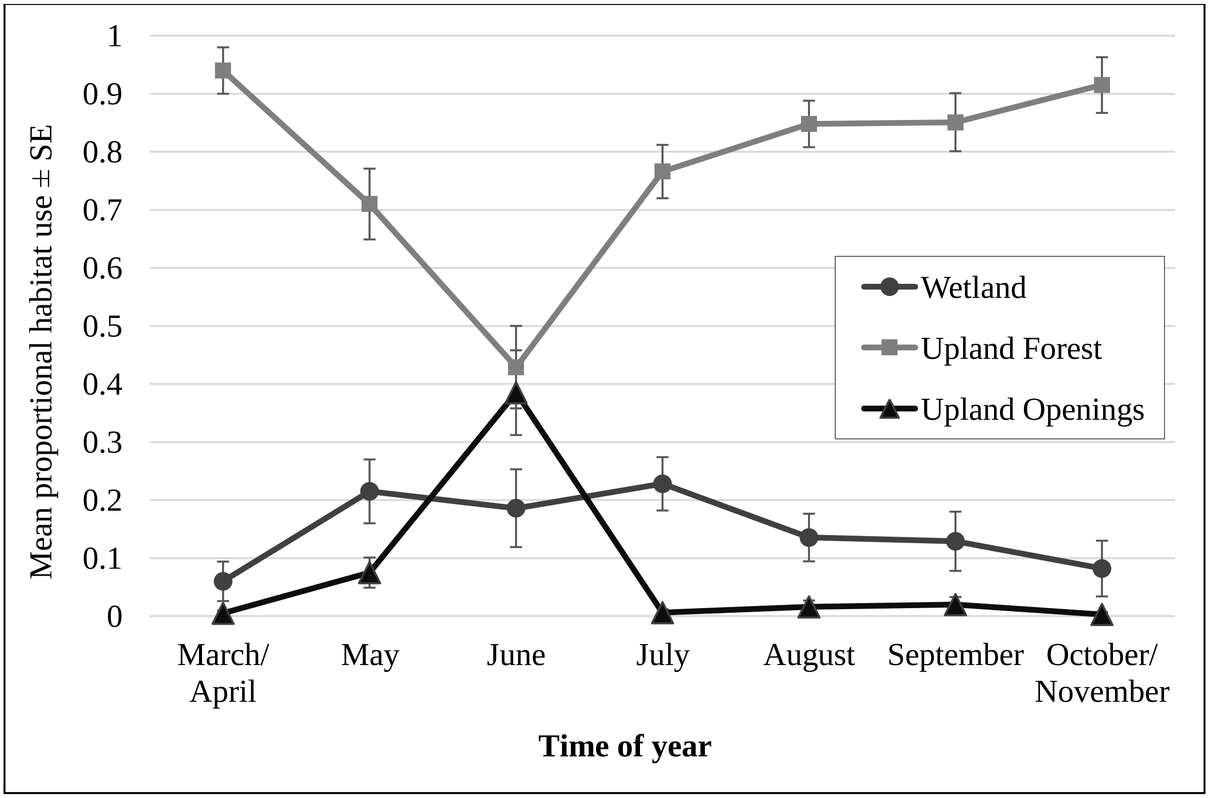
Mean proportional habitat use ± SE
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
March/ April
May
June
July
August
September
October/ November
Time of year
Wetland
Upland Forest
Upland Openings

Figure 4.

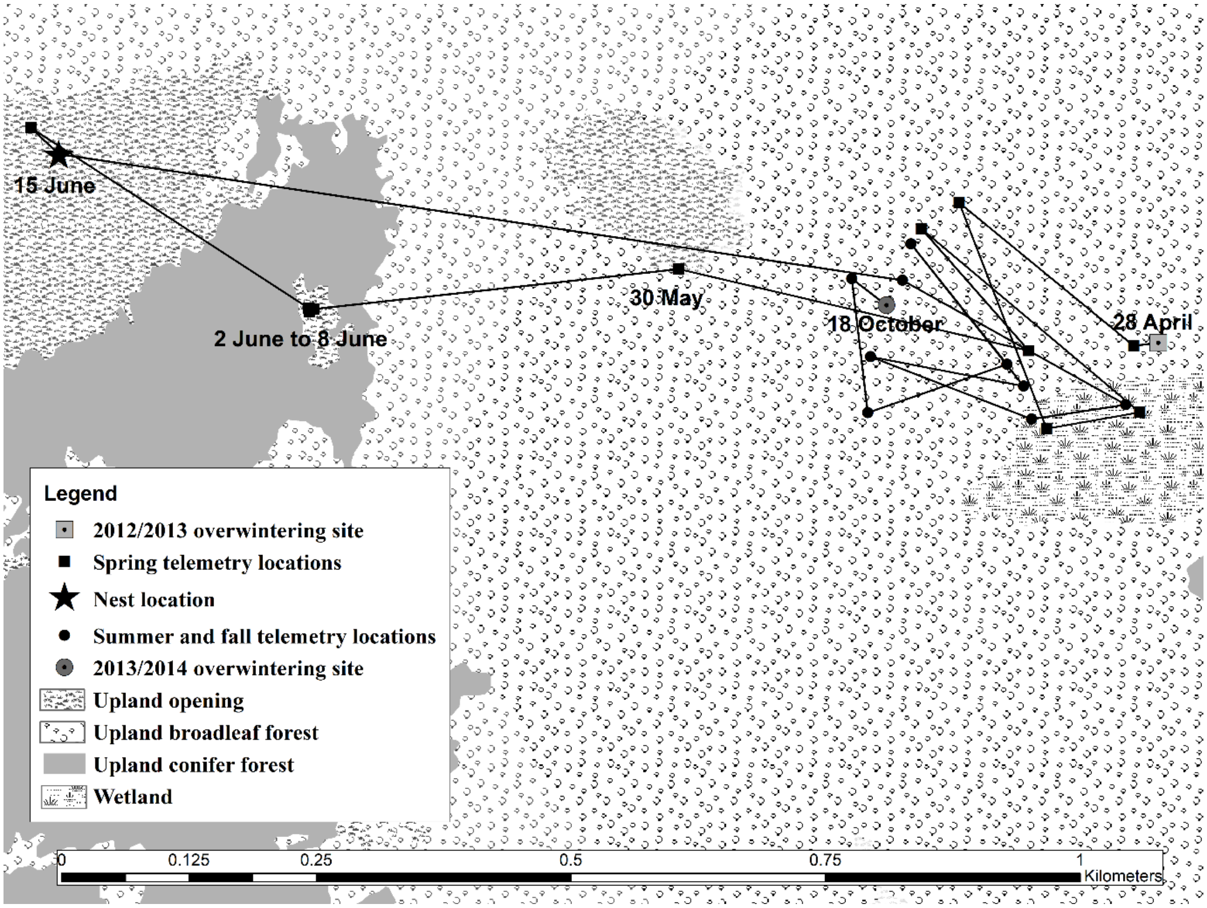
15 June
2 June to 8 June
30 May
18 October
28 April
Legend
2012/2013 overwintering site
Spring telemetry locations
Nest location
Summer and fall telemetry locations
2013/2014 overwintering site
Upland opening
Upland broadleaf forest
Upland conifer forest
Wetland
0
0.125
0.25
0.5
0.75
1
Kilometers

Figure 5.

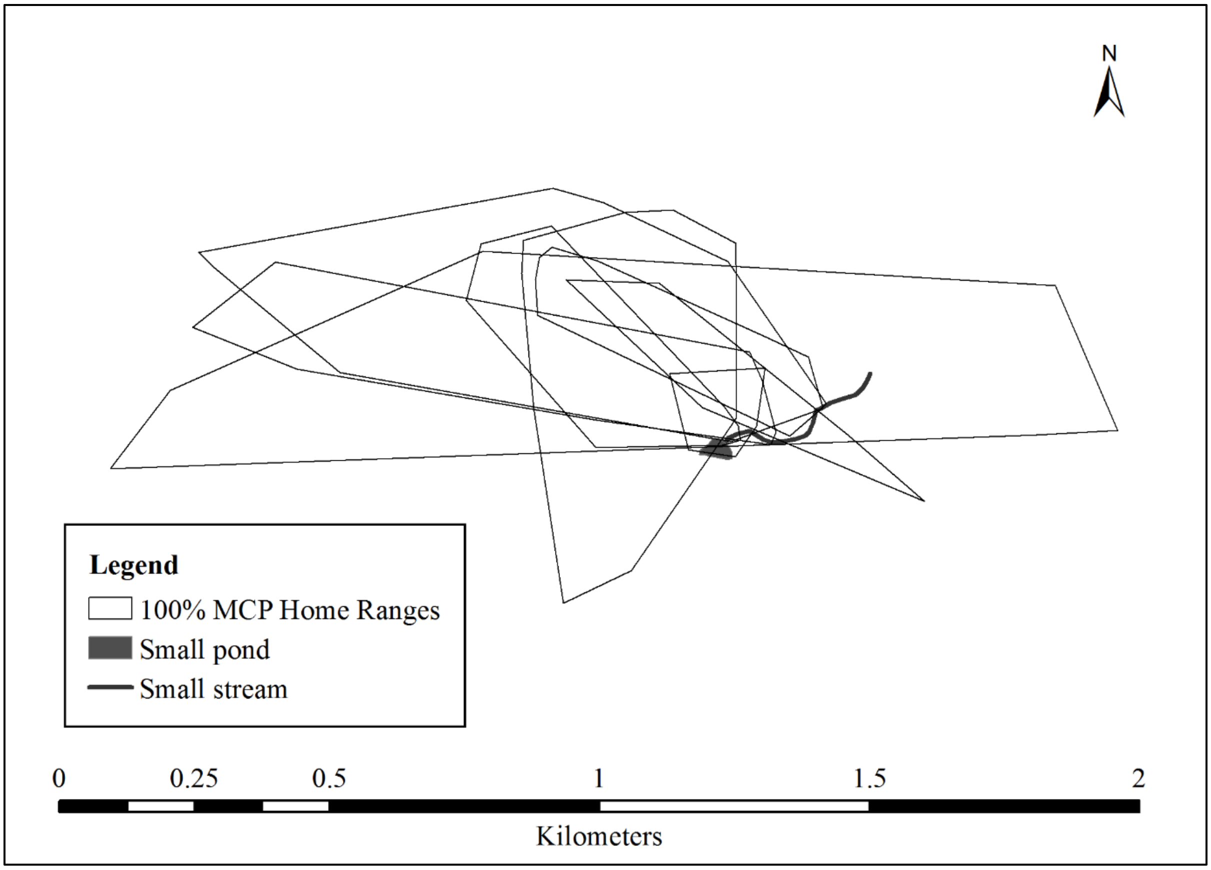
N
Legend
100% MCP Home Ranges
Small pond
Small stream
0
0.25
0.5
1
1.5
2
Kilometers

Figure 6.

CHAPTER III

Spatial ecology of the neonate eastern box turtle with implications for prescribed burning

ABSTRACT

Eastern box turtles *Terrapene carolina carolina* often nest within sites actively managed to promote early successional, grassland, or savanna vegetation communities (hereafter openings). We investigated the spatial ecology of neonate eastern box turtles at four openings in the Manistee National Forest, Michigan. Our objectives were to document nesting, emergence, habitat use, dispersal rates, and residency time of neonates in natal openings. We protected 64 nests using mesh exclosures and radio-fitted 66 neonates from 4 cohort years. Nest emergence varied considerably in different years (16 August to 25 October, 2012-2016) but no neonates dispersed more than 50 m beyond the boundary of their natal opening before onset of winter. Dispersal (distance from nest to overwintering site) was extremely limited in the first activity season (n = 46 neonates, $\bar{x}$ = 19.9 ± 2.4 SE, range 1.9 to 83.2 m). Probability of overwintering within the natal opening increased as distance from nest to nearest forest edge and as date of nest emergence increased. By 1 June of their second activity season, all neonates were still present in or within 50 m of their natal opening but all vacated openings by 1 July. Land managers should be aware neonates reside in or very near their natal openings for several months after nest emergence. We recommend excluding the forest edge during implementation and relaxing the interval (years) between prescribed burns to allow neonates time to disperse between treatment intervals.

INTRODUCTION

Turtle nests require specific environmental conditions for successful development of embryos, which often requires gravid female turtles to travel considerable distances (Gibbons 1986) and deposit eggs in habitats differing their primary habitat. Thus, neonate turtles often emerge from nests into environs for which they are not physiologically adapted to survive for extended periods of time and must disperse into more hospitable habitats (Iverson 1991, Kolbe and Janzen 2002). Differences between primary habitat and nest sites are of course greater for aquatic and semi-aquatic species than terrestrial turtles. Some terrestrial chelonians, including the eastern box turtle *Terrapene carolina carolin*a, also commonly nest in land cover types differing from their primary habitats (Stickel 1950, Stubbs and Swingland 1985, Flitz and Mullin 2006).

In temperate regions of their geographic range, gravid eastern box turtles (hereafter box turtles) travel to upland open canopy sites to deposit eggs but retreat to primary habitat (forest) shortly after nesting (this Thesis Chapter II, Stickel 1950, Wilson and Ernst 2005, Madden 1975, Dodd 2001, Willey and Sievert 2012). Although box turtles are often associated with fire-dependent natural communities (Cohen 2000, Kost 2004) due to seasonal ecotonal and nesting habitat preferences (Rossell et al. 2006, Fredericksen 2014), adult box turtles do not appear to possess behavioral or physiological traits allowing them to consistently escape or withstand flames (Gibson 2009, Howey and Roosenburg 2013, Cross 2016). In southern Michigan (Gibson 2009) and Ohio (Cross 2016), 10.7% and 27.2% respectively, of radio-fitted adult box turtles present within burn units died as a direct result of injuries sustained in low intensity prescribed fire.

Although survival rates of neonates subjected to low intensity fire have not been evaluated in field studies, it is reasonable to assume fire-related mortality events occur (Gibson 2009, Epperson and Heise 2003, Perry and McDaniel 2015, Cross 2016) and would impact the neonate age class at equal or higher rates than those experienced by adults. Mortality of individual neonates during prescribed burning conducted at appropriate intervals may be compensatory or even be offset by increased nest survival rates due to increases in nest habitat suitability resulting from the management action (Reid et al. 2016). Conversely, in scenarios where fire induced mortality is additive, intensively managed sites could function as reproductive sinks if they become increasingly attractive to gravid females but little or no recruitment occurs. In these scenarios, information regarding neonate dispersal would be useful when considering species-specific risk factors associated with timing, layout, and frequency of prescribed burns and other common management activities.

Neonates emerging from nests in relatively open canopy, xeric, fire-dependent systems would be expected to eventually vacate their natal habitat patch given adult age classes seek out humid microclimates (Rossell et al. 2006) and inhabit mesic forested or lowland sites for much of the year (Stickel 1950, Fredericksen 2014). Despite considerable advances in radio-telemetry products and concern regarding viability of box turtle populations (reviewed in Dodd 2001), very few investigators have reported on this age-class. In New York, Madden (1975) radio-fitted and monitored 2 neonates from fall nest emergence to overwintering (17-20 days) and reported one individual overwintering in the open canopy field where it hatched and the other overwintered in adjacent forest. Burke and Capitano (2011), also in New York, monitored 4 neonates from nest emergence to overwintering and reported ~ 10 m as the maximum distance dispersed from the nest. Because box turtles often nest in areas managed with fire and dispersal from nests may be delayed due to onset of winter, additional information is needed to address current knowledge gaps and management implications regarding prescribed burning and the neonate age class.

We conducted a multi-year field study on spatial ecology of neonate eastern box turtles at four open canopy nesting areas and surrounding forested habitat in the Manistee National Forest, Michigan. Our primary objectives were to 1) monitor dispersal rates and habitat use for neonates age 0-1y and 2) identify abiotic and biotic factors potentially associated with dispersal and residency time in natal habitats. Our goal was to identify potential mitigation measures for prescribed burning and other management activities in the context of temporal occupancy of natal open canopy habitats by the neonate age class. We hypothesized neonates would remain near their nests during their first year of life (Madden 1975).

STUDY AREA

We conducted our research at four upland openings and surrounding forest matrix within a 3.0 km^2 area of the Manistee National Forest (MNF), Michigan (Figure 1). We opted not to include specific coordinates of the study area due to issues associated with illegal collection across the species range (Dodd 2001). The term ‘opening’ is a broad classification used by the Huron-Manistee National Forest to reference a suite of non-forested sites of relatively small patch size ($0.5 \leq 50$ ha). Openings are managed under individual prescriptions with the objectives of wildlife habitat improvement and promotion of biodiversity (USDA Forest Service 2006). Fire dependent barrens and dry-sand prairies communities were historically present in this portion of the Manistee National Forest but much of the area converted to second growth forest or was converted into *Pinus resinosa* plantations in the last century (Albert et al. 2008). Geology of the study area was outwash plains and the openings were typified by well drained soils of the Plainfield and Grattan Series (mixed, mesic Typic Udipsamments and Entic Haplorthods, websoilsurvey.nrcs.usda.gov). Ecotones along opening boundaries were relatively hard edged and generally transitioned within a few meters from relatively open canopy settings to forest. Structural characteristics (basal area, % overstory canopy cover, % ground cover) of the study area were sampled in September, 2016 (See Chapter VI, Extended Methodology). Hereafter we refer to the four openings using the fictional names; Savanna, Turtle Bowl, Gravel Pit, and East West.

Savanna was the largest (5.6 ha) and most structurally complex opening (Figure 2A). This opening had relatively flat topography. Mean basal area was 5.9 m^2/ha ± 0.7 SE (25.5 ft^2/acre ± 3.0 SE). Overstory canopy cover was greatest at Savanna opening compared to the other three openings (Figure 2A). Overstory tree species included: *Quercus alba Pinus* *banksiana* and *Pinus strobus*. The shrub and herbaceous layer was a mosaic of *Prunus virginiana, Vaccinium angustifolium, Andropogon spp., and Carex Pennsylvania.* Savanna has been periodically managed with low intensity prescribed burning, most recently in 2010.

Turtle Bowl was 1.9 ha, oval shaped, and was a geologic frost pocket with bowl shaped topography. There were few overstory trees (*Quercus alba, Pinus banksiana,* and *Pinus strobus*) and mean basal area was 1.8 m^2/ha ± 0.6 SE (8.0 ft^2/acre ± 2.4 SE). There were a few small patches of shrubs (*Prunus virginiana* and *Vaccinium angustifolium*) but ground layer vegetation was dominated by graminoids (*Andropogon spp.*) including many species indicative of the dry-sand prairie community (Kost 2004). There was also a considerable amount of relatively open ground much of which was colonized by lichens or bryophytes (Figure 2A). Turtle Bowl has been periodically managed with low intensity prescribed burning, most recently in 2010.

Gravel Pit was a 0.7 ha oval shaped opening with bowl shaped topography. This opening was perpetually disturbed by illegal off road vehicle use during the study period. There was one super canopy *Pinus strobus* tree near the center of the opening but it was otherwise devoid of trees and shrubs. Due to off road vehicle use, exposed mineral soil and cobble were prevalent (Figure 2A). Vegetation was sparse and invasive species (*Centaurea maculosa, Hypericum perforatum, and Verbascum thapus*) were dominant.

East West was a 0.9 ha linear shaped opening of moderate structural complexity. This opening had a south-facing approximately 30° slope running its entire length. Mean basal area was 3.1 m^2/ha ± 0.7 SE (13.5 ft^2/acre ± 2.8 SE) and overstory trees were *Quercus alba, Quercus velutina, and Pinus banksiana.* There was also a considerable amount of relatively open ground much of which was colonized by lichens or bryophytes (Figure 2A).

The shrub and herbaceous layer was largely dominated by *Andropogon spp.*, but there were some patches of *Vaccinium angustifolium* as well. *Cirsium hillii*, a relatively rare plant species indicative of dry sand prairie and barrens communities (Cohen 2000), was also present.

The forest surrounding the openings can be generally classified as dry-mesic northern forests (Kost et al. 2007). Forest structure was similar across the study area with respect to overstory canopy cover and ground cover (Figure 2B). Mean basal areas in forests surrounding each opening were 25.7 m^2/ha ± 1.5 SE (112.0 ft^2/acre ± 6.5 SE) at Savanna, 26.8 m^2/ha ± 1.7 SE (116.7 ft^2/acre ± 7.2 SE) at Turtle Bowl, 30.0 m^2/ha ± 1.7 SE (130.8 ft^2/acre ± 7.3 SE) at Gravel Pit, and 24.5 m^2/ha ± 1.9 SE (106.6 ft^2/acre ± 8.2 SE) at East West. At each site, the overstory was primarily comprised of *Quercus velutina*, *Quercus alba*, *Pinus banksiana*, and *Pinus strobus* although *Pinus resinosa* plantation bordered one side of Savanna. The forest mid-story and shrub layers were generally sparse but contained primarily *Pinus strobus*, *Quercus alba*, *Pinus banksiana*, or *Prunus virginiana*. The herbaceous layer within the forest contained primarily *Carex pensylvanica*, a mosaic of *Vaccinium angustifolium*, and *Pteridium aquilinum* was common at low densities. A river floodplain with diverse land cover types including emergent vegetation, wet meadow, scrub-shrub, and lowland conifer was present within 1.0 km of all openings and was immediately adjacent to Gravel Pit opening.

METHODS

Nest Protection and Telemetry

We surveyed openings during late morning or midday from May 25-June 25, 2012 to 2016 to locate gravid adult females. Following capture, we affixed 15 g VHF radio transmitters (Model RI-2D Holohil Systems Ltd., Ontario, Canada or Model 1555 Advanced Telemetry Systems, Isanti, Minnesota, USA) to the rear portion of the carapace. We returned to openings between 1900-2100 hours to monitor radio-fitted turtles for nesting activity and conducted surveys to locate additional nesting turtles. After females covered their eggs, we protected each nest with a 61.0 cm x 61.0 cm x 30.5 cm wooden framed mesh predator exclosure (see Chapter VI, Extended Methodology). We recorded nest locations with a Trimble® Geo 7x Global Positioning System unit (hereafter Trimble) which consistently provided sub-meter accuracy after data had been differentially corrected during post processing. We monitored nest exclosures every 24 to 72 h from 1 August to 5 November. We placed a handful of moist sphagnum moss or leaf litter in the corner of each exclosure to provide refugia options for neonates in the event they emerged in the hours prior to nest checks. Neonates from the same clutch did not always emerge from their nest on the same day and these dates were considered separate nest emergence events when calculating nest emergence statistics. Conversely, when multiple neonates emerged from the same nest on the same day we considered it a single emergence event.

Neonate radio-telemetry

After we detected nest emergence events, we soaked neonates in a shallow dish of distilled water for approximately 5 minutes to minimize stress and remove any debris accumulated during nest emergence. Following soaking, we dried each neonate and collected a morphometric information including; mass (g), carapace length, carapace height, carapace width, plastron length, and plastron height. We used quick setting 2-part epoxy to attach series R1605 radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) to the anterior of the carapace. Radio transmitters were customized to lowest possible pulse rates during production and signal range was approximately 50 m. After epoxy set, we hydrated neonates by dabbing a wet cotton swab on the skin and carapace. We then immediately released neonates at their nest site with exception of a few individuals that had emerged in evening without adequate time for workup and release before nightfall. These individuals were kept in the nest exclosures overnight and released the following morning.

We released each radio-fitted neonate at a random corner of exclosures so not every neonate was orientated the same direction during release. Following release at nests, we tracked neonates 1 to 3 times per week. During telemetry observations, we recorded macrohabitat type (opening, forest, or wetland) and marked each location with small drab colored flag labeled with the neonate ID and date of observation. Flagging allowed us to determine whether the neonate was in the same exact form (sensu Stickel 1950) it had been during the previous observation. We used the Trimble to record location of each neonate flagged location. We monitored neonates until they either disappeared, were depredated, or began overwintering (hereafter referred to as overwintering ingress). We defined the period from nest emergence to overwintering ingress as the first activity season. After overwintering ingress, we placed the same exclosures used to protect nests around the overwintering neonates. When neonates emerged from overwintering refugia in spring (hereafter referred to as overwintering egress), we noted characteristics of the overwintering refugia, removed the exclosure, collected morphometric data, affixed new transmitters, and released neonates at their overwintering sites. We defined the period after spring overwintering egress as the second activity season. We tracked neonates on a weekly basis until we lost contact or mortality occurred. If we could not obtain a transmitter signal for a specific neonate, we scoured last known location looking under leaf litter and other refugia. If that proved unsuccessful, we meandered for 1 to 2 hours scanning for a signal.

All carapace fixtures remained under 8.0% total body mass (Beaupre et al. 2004). All handling techniques were approved by the Michigan Department of Natural Resources (Scientific Collectors Permits) and the Institutional Animal Care and Use Committee at Grand Valley State University (protocol 13-03A).

Analysis

We delineated boundaries of each opening by walking the perimeter and recording positions on the Trimble. We buffered each opening boundary by 2.5 m and considered this edge habitat. We chose a 2.5 m buffer because each opening was relatively hard edged and this metric captured the transition zone between relatively closed canopy forest and the relatively open canopy structure of each opening.

Following the systematic sampling technique of Benson (2013), we obtained mean distance to nearest forest edge within each opening (hereafter distance raster mean) by generating distance rasters (1.0 m^2 resolution) and clipping the raster datasets using the boundaries of the openings. Distance rasters essentially yield a population mean of raster cell centroids (i.e., distance from each 1.0 m^2 raster cell to nearest forest edge) within a polygon. For each opening, we calculated the distance from each box turtle nest to nearest forest edge in GIS. We divided distance to nearest forest edge for each nest by mean distance to forest edge within that opening (obtained from distance rasters) and compared these ratios to a mean of 1.0 using one-sample t-tests (Conner and Plowman 2001). We tested for differences among distances from nests to nearest forest edge between sites using Moods test and conducted 6 pair-wise Mann-Whitney *U*-tests.

For each neonate, we calculated straight line distances between sequential telemetry locations, angles between sequential telemetry locations, distances from nests to overwintering sites, and maximum distances from nests. We pooled the movement rates (m/day) of all neonates and reported descriptive statistics regarding movement rates by season. We applied Mann-Whitney *U*-tests to compare maximum observed distances from nests for neonates which survived to overwinter and the neonates that we lost contact with (i.e., mortality or disappeared) before overwintering. We evaluated associations between distances from nests to overwintering sites and date of nest emergence as well as distances from nests to overwintering sites and body mass at hatching with Spearman rank correlation tests.

We tested for non-random mean directionality of movements for individual neonates and pooled movements of neonates belonging to the same clutch using Rayleigh’s tests (Zar 1984). Rayleigh’s tests do not take length of movements into account, only movement direction. We reviewed telemetry data and subsequently considered fine scale movements between consecutive locations indicative of microhabitat selection (e.g., thermoregulation or concealment) rather than movements related to macrohabitat selection or dispersal. Therefore, when testing directionality of movements, we only included the directions of between consecutive movements > 2.0 meters. We applied Rayleigh’s test if we observed at least 6 movements meeting our criteria because this was the lowest sample size for which Zar (1984) provided critical values of the *z* statistic.

We used binomial logistic regression to model potential relationships between the type of overwintering habitat used by neonates and three biotic and abiotic predictor variables. The binary response variable was overwintering habitat type used by each neonate, either natal openings or surrounding forest or edge habitat. We combined the forest edge overwintering events and forested habitat overwintering events into a single category. We coded overwintering events in openings 1's and overwintering events in forest and edge 0's. Explanatory variables included distance (m) from nest to nearest forest edge, Julian day of nest emergence, and body mass (g) of neonates at nest emergence. We constructed 7 candidate models using all possible combinations of variables. Prior to model construction, we inspected the dataset for multicollinearity using Pearson's correlation coefficients. We calculated Akaike's Information Criterion for small sample sizes (AIC_c), AIC_c rank (ΔAIC_c), and AIC_c weight (w_i) for all candidate models (Akaike 1973, Burnham and Anderson 2002). We considered models equally supported if they differed <2 AIC_c. After selecting the most parsimonious model(s) based on AIC_c rank, we evaluated model fit using McFadden's pseudo R^2 (McFadden 1974) and by inspecting the ratio of residual deviance to degrees of freedom (i.e., dispersion estimate). After model selection and evaluation, we converted the β-coefficients to odds ratios and their 95% confidence intervals and generated predicted probabilities of neonates overwintering in natal openings by holding predictor variables constant at various biologically relevant values.

Prior to parametric tests, we evaluated assumptions of normality and homogeneity of variances using Shapiro-Wilk and Bartletts tests. When conducting post-hoc pair-wise comparisons, we adjusted α using Bonferroni correction. Because of increased probability of type II errors associated with very small sample sizes, and the biological relevance potentially associated with directionality of lengthy dispersal movements, we set α at 0.10 for Rayleigh's tests (Toft and Shea 1983). In all other hypothesis tests, α = 0.05. We used program R version 2.15.1 (R Development Core Team, 2012) for statistical analyses.

RESULTS

Nesting Activity and Proximity to Forest Edge

During the five nesting survey years (2012-2016), we documented 64 nests from late May to mid-June. Nest locations were farthest from nearest forest edge at Savanna (Figures 3, 4). Mean distances to forest edge generated from distance rasters were very close (<3.0 m difference) to mean distances from nests to nearest forest edge at Savanna, East West, and Gravel Pit (Figure 4). Mean distance to forest edge generated from the distance raster was 9.0 m greater than mean distance from nests to nearest forest edge at Turtle Bowl. Differences between mean distances from nests to nearest forest edge and mean distances to forest edge generated from distance rasters were significant at Turtle Bowl ($t = -9.04$, $P < 0.001$) as well as Gravel Pit ($t = -2.18$, $P = 0.049$) but no difference was detected at Savanna ($t = 0.57$, $P = 0.578$) or East West ($t = -0.26$, $P = 0.795$). We detected an overall significant difference ($z = 3.26$, $P = 0.001$) in distances from nests to nearest forest edge between sites. Distances from nests to nearest forest edge at Savanna differed significantly from each of the other three sites ($P < 0.001$ in all comparisons) but distances from nests to nearest forest edge did not differ significantly between Turtle Bowl and Gravel Pit ($W = 246$, $P = 0.042$), Turtle Bowl and East West ($W = 214$, $P = 0.035$), or Gravel Pit and East West ($W = 70$, $P = 0.954$).

First Activity Season

Nest emergence

Nest emergence events occurred between 16 August to 25 October, 2012-2016. The mean nest emergence date was 18 September ± 2.5 days SE ($n = 31$ nests, $n = 42$ nest emergence events, all sites, 2012-2016). Nest emergence ranged from 16 August to 26

August in 2012 (*n* = 3 nests, *n* = 3 nest emergence events), 22 August to 10 October in 2013 (*n* = 7 nests, *n* = 15 nest emergence events), 14 September to 22 October in 2014 (*n* = 4 nests, *n* = 4 nest emergence events), 19 September to 25 October in 2015 (*n* = 7 nests, *n* = 10 nest emergence events), and 23 August to 13 September in 2016 (*n* = 10 nests, *n* = 10 nest emergence events).

Neonate radio-telemetry

We radio-fitted 64 neonates from 20 clutches, during 2012 to 2015 (Table 1). We did not radio-fit neonates from 2016 nests and released them after nest emergence. We successfully determined fates (i.e., mortality or survived to overwintering ingress) for 59 of 64 neonates (92.3%) during the first activity season.

Habitat use and movements

During telemetry observations, neonates were commonly hidden in forms (sensu Stickel 1950) within duff or leaf litter, root systems of graminoids and forbs, or next to coarse woody debris. Movement rates (m/d) were lower in August and September than October and November (Figure 5). The cumulative movement trajectories for individual neonates were relatively linear and neonates did not return to former activity areas after movements >2.0 m (Figures 6, 7, 8). Of the 24 neonates that moved to the forest edge before overwintering, only 2 (8.3%) returned to openings on subsequent telemetry observations. Sample size limitations (movements per neonate) prohibited testing directionality of movements for individual neonates in the first activity season but we did detect non-random directionality (Rayleigh's *Z*, $P \leq 0.1$) in pooled within-clutch movements for 8 of 10 clutches (Table 2). Directional means of movements for these 8 clutches were oriented towards forest edges rather than interior portions of the openings (Table 2, Figures 6, 7, 8).

Dispersal distance

We tracked 46 radio-fitted neonates from nest emergence to overwintering ingress (Table 1). No individuals dispersed more than 50 m beyond the boundary of their natal opening before overwintering (Figures 6, 7, 8). Straight line distances (m) from nests to overwintering sites ($n = 46$ neonates, $\bar{x} = 19.9 \pm 2.4$, range 1.9 to 83.2) were close to maximum observed distances (m) from nests ($n = 46$ neonates, $\bar{x} = 20.6 \pm 2.4$, range 1.9 to 83.2) and overwintering sites were equivalent to the maximum observed distance from nests for 29 (63.0%) neonates. Maximum observed distances (m) from nest for neonates we lost contact with but provided ≥ 1 telemetry location post nest release ($n = 15$ neonates, $\bar{x} = 12.1 \pm 3.2$, range 1.7 to 52.4) were significantly less (Mann-Whitney *U*-test, $P = 0.012$) from maximum observed distances from nest for neonates ($n = 46$ neonates, $\bar{x} = 20.6 \pm 2.4$, range 1.9 to 83.2) which survived to overwinter. Distance (m) from nest to overwintering site was significantly negatively correlated (Spearman rank, *rho* = -0.668, $P < 0.001$) with Julian day of nest emergence. Distance (m) from nest to overwintering site was not significantly correlated (Spearman rank, *rho* = -0.206, $P = 0.169$) with distance (m) from nest to nearest forest edge. Distance (m) from nest to overwintering site was not significantly correlated (Spearman rank, *rho* = -0.182, $P = 0.224$) with body mass (g) at nest emergence.

Overwintering Habitat Use Models and Predictions

Model construction

We documented 46 overwintering events. Twenty-four neonates overwintered in openings, 4 neonates overwintered along the forest edge, and 18 neonates overwintered in forest (Table 1). We detected no issues associated with multicollinearity between any predictor variables ($r \leq -0.164$, $P \geq 0.274$). Overwintering in edge and forest ($n = 22$ events) was the least common and thus the least common event per variable ratios were 7:1 in the full model, 11:1 in models with two predictors, and 22:1 in models with a single predictor (Vittinghoff and McCulloch 2007).

Model selection

We found no evidence body mass (g) at nest emergence was associated with overwintering habitat use, the deviance of the candidate model *Overwintering habitat use ~ body mass at nest emergence* was nearly identical to that of the intercept only model (Table 3). Based on AIC_c rank (ΔAIC_c), we selected *Overwintering habitat use ~ distance from nest to nearest forest edge + date of nest emergence* as the most parsimonious model from the set of candidate models (Table 3). We considered this model to be supported because it had the greatest difference between residual deviance and deviance of the intercept only model, the McFadden R^2 value was within the range suggested in Hensher and Stopher (1979) as excellent model fit, and the ratio of deviance to degrees of freedom (e.g., estimated dispersion) was closest to 1.0 (Table 3).

Model predictions

Using the selected model, we generated a matrix of predicted probabilities of overwintering in natal openings using distance from nest to nearest forest edge values ranging from 1.0 to 110.0 (m) and nest emergence dates ranging from 15 August to 30 October (Table 4). When nest emergence was held constant at 18 September (i.e., mean nest emergence date for all nests we monitored from 2012 to 2016), the predicted probabilities of overwintering in natal openings increased when distance from nest to nearest forest edge increased (Table 4). Similarly, when distance from nests to nearest forest edge values were held constant, the probability of overwintering in natal openings increased as date of nest emergence increased (Table 4). When distance from nests to nearest forest edge exceeded 70.0 m, predicted probabilities of overwintering in natal openings approached 1.0 regardless of nest emergence dates. Conversely, for nest emergence dates on 15 October or later, predicted probabilities of overwintering in openings approached 1.0 for all nests > 5.0 meters from the forest edge (Table 4).

Overwintering period

Neonates (*n* = 46) overwintered in excavated burrows in duff or mineral soil or created shallow circular depressions in mineral soil or duff. Mean vertical depth of overwintering refugia into mineral soil was 29.9 mm ± 2.9 (range 0.0 to 101.8). Seven neonates created shallow (<17.0 mm) circular depressions in mineral soil but their carapace was covered only in duff and leaf litter, and the remaining neonates burrowed into mineral soil at approximately 30° to 50° angles relative to the surface.

Second Activity Season

Habitat use in spring

We re-fitted 28 neonates with transmitters after overwintering egress (*n* = 2 in 2013, *n* = 18 in 2014, and *n* = 8 in 2016) and monitored them weekly. Most neonates (27 of 28) emerged from overwintering refugia during the last week in April through the first two weeks in May and one emerged in the last week of May. Half (*n* = 14 neonates) had overwintered within their natal openings. Throughout April and May, 7 of these individuals remained in the openings, 2 dispersed into the edge, 1 dispersed into surrounding forest, and we lost contact with 4 while they were still in openings (Figures 9, 10, 11). We did not observe any neonates which had previously dispersed into edge or forest returning to openings during April or May.

Of the 28 spring radio-fitted neonates, 4 had overwintered in edge habitat. Three dispersed from edge into forest during May and we lost contact with the other while it was still in edge habitat. We did not observe any of these individuals returning to openings during April or May. Of the 10 neonates that had overwintered in forest, 9 remained in forest throughout April and May and 1 individual returned to Savanna opening in late May (Figure 10). No individuals dispersed more than 50.0 m beyond the boundary of their natal opening by the end of May.

Habitat use in summer

We monitored 24 neonates for portions of the summer period (June, July, August) but we eventually lost contact with all neonates after 17 August (333 days post nest emergence). One neonate had not emerged from its nest in fall, overwintered in the nest, and was detected in the nest exclosure the following spring on 1 June, 2016. This individual was radio-fitted but disappeared before the next tracking interval. We also encountered and opportunistically radio-fitted a natural recruit (i.e., wild neonate from previously undetected nest) on 11 June 2014 at Turtle Bowl. We lost contact with 5 neonates in June while they were still in openings. All neonates vacated the openings by 1 July, including the natural recruit and the 1 neonate which had returned to its natal opening in late May. None of the neonates which had dispersed into forest in spring or the previous fall returned to openings in June or July although 1 neonate returned briefly to edge at Turtle Bowl (Figure 9). We observed no use of openings in July or August (Figures 9, 10) although sample size during this period had diminished to 6 individuals.

Movements and dispersal

Mean movement rate in April and May was less than 1.0 m/day, slightly lower than the first activity season (Figure 5). Mean movement rate in June and July increased > 600% from April and May (Figure 5). We documented extensive movements away from the openings in June and July for 8 neonates which had dispersed >100.0 m away from their nest and overwintering sites before we lost contact (Table 6, Figures 9, 10). We detected non-random directionality (Rayleigh's Z, $P \leq 0.1$) of pooled first and second activity season movements for 11 of 17 neonates (Table 5). When we viewed movement paths of second year neonates cumulatively, dispersal trajectories were best described as a wheel spoke pattern. Natal openings formed the wheel hub and dispersal trajectories of individual neonates formed the wheel spokes into adjacent forest or wetland macro habitats (Figures 9, 10).

DISCUSSION

We collected evidence indicating dispersal is extremely limited during the first activity season in our study area. Because we monitored multiple neonate cohorts from nest emergence to overwintering at four different openings, we likely captured most of the individual annual variation with regards to dispersal distance and nest emergence at our study area. We do not suspect the 5 neonates which simply disappeared in the first activity season had moved out of transmitter range. None were exhibiting atypical movement patterns and waning temperatures considerably slowed overall movement rates. We failed in our objective to monitor neonates during the entire second activity season. Unlike the first activity season, we lost contact with most individuals without determining a fate. We experienced numerous instances of early transmitter failure during the second activity season but we also suspect some of the disappearances resulted from predation (transmitters carried away) and extensive neonate movements. In latter instances, our weekly tracking interval probably allowed neonates to move beyond the limited transmitter range between tracking sessions.

Distances moved from nests to overwintering sites were virtually analogous to maximum observed distance from nests, indicating that distance from nest to first overwintering site is a reasonable proxy for maximum dispersal distance in the first activity season. Our observations of limited dispersal in the first activity season were similar to anecdotal accounts from New York (Madden 1975, Burke and Capitano 2011). In northern portions of the species' range, thermal constraints limit movement and activity in the short period between nest emergence and first overwintering. Dispersal distance was associated with date of nest emergence but not distance from nest to nearest edge or body mass. In addition to date of nest emergence, nest site selection by gravid females greatly influences which habitat types are proximally ‘available’ to neonates for overwintering. Although we collected considerable evidence suggesting neonates dispersed towards the forest edge, some neonates successfully overwintered within each opening indicating adaptive flexibility. Even if they are orientating towards the edge, neonates emerging from nests located away from forest edges may simply not have time (i.e., locomotive limitations and thermal constraints to movement) to vacate natal openings before onset of winter. Madden (1975) also observed variation in overwintering habitat use, one radio-fitted neonate overwintered within its natal field and one overwintered in adjacent forest. Thermal constraints in the first activity season probably also limit or exclude feeding opportunities and thus conserving yolk sac energy reserves (Congdon 1989, Nagle et al. 2003, Constanzo et al. 2004, Willette et al. 2005) is probably of greater consequence than dispersal during the first activity season.

Movement rates in early spring of the second activity season were similar to Forsythe et al. (2004) who monitored 3 radio-fitted neonates for one month (30 March to 27 April) in Central Illinois and reported the mean cumulative distance moved was 21.94 m. Remarkably, Madden (1975) maintained contact with one individual for 3 activity seasons after nest emergence and never observed the juvenile dispersing beyond 100.0 m from the nest. Our observations of extensive movements in June and July were quite different than Madden (1975). Although Madden (1975) did not suspect transmitter mass (~ 20.0% body mass) affected movements, our transmitters (< 8.0% body mass) were less taxing on individual neonates than transmitters available in the early 1970’s. Neonates exhibited linear dispersal trajectories and did not return to former activity areas, while adults usually maintain fidelity to a home range and revisit certain activity areas consistently (Stickel 1950, Stickel

1989, Cross 2016). The openings, forest, and wetlands in our study area were frequently used by radio-fitted adults (this thesis, Chapter II) thus we do not attribute the extensive neonate movements to poor habitat quality. Similar to our observations, increased dispersal distance during the second activity season has been reported for other terrestrial chelonians (Epperson and Heise 2003, Pike 2006).

Because we lost contact with some neonates before they vacated their natal openings, we cannot be certain if they vacated (or would have vacated) openings by July as did the remaining individuals we monitored. Openings were dominated by graminoids with very low forb densities thus we speculate increased temperatures and low relative humidity common during summer renders openings less suitable for neonates than does surrounding forest and wetland (Fredericksen 2014). Due to logistical constraints, we did not evaluate neonate micro-habitat or micro-climate preferences as potential mechanisms driving neonates to disperse from natal openings into adjacent habitat. At some unknown habitat quality threshold, the same openings supporting nesting may provide patches of habitat suitable for year-round occupancy by neonates. Nests were not clustered near the forest edge at Savanna opening. The same structural characteristics (i.e., tree and shrub density, % leaf litter, herbaceous vegetation etc.) potentially driving females to nest farther from forest edge may provide security cover and thermoregulatory options for neonates which could explain, in addition to distance from nests to forest edge, why 7 of 8 neonates overwintered in this opening.

Openings in our study area were relatively small. In large patches of nesting habitat, neonates may occupy their natal openings for much longer periods than we observed. Future studies are needed to further examine relationships between habitat structure, nest site selection, and neonate habitat preferences. Radio-telemetry projects involving neonate turtles are relatively rare because they are challenging, time consuming, and expensive but are warranted considering uncertainties surrounding long-term population viability of many turtle species. We recommend those planning similar radio-telemetry investigations involving neonate box turtles consider experimental release locations within openings of various sizes and complexities while controlling for variability in nest emergence timing and or proximity to edge.

MANAGEMENT IMPLICATIONS

We expect biologists or land managers interested in stand level predictions of neonate box turtle dispersal or overwintering locations will often be aware of nesting hotspots within their area of interest. At similar latitudes to our study area, simply buffering known nesting locations by 50 m would likely provide a reliable estimate as to whereabouts of most neonates during fall, winter, and early spring. In situations where spatial distribution of nests is unknown, buffering opening boundaries by 50 m would provide conservative estimates as to whereabouts of neonates in fall, winter, and early spring.

If the primary management objective is improving eastern box turtle nesting habitat but the selected implementation technique has associated mortality risks, the optimum seasonal window is after nesting and before nest emergence (25 June through 15 August at our study area) because neonates and adults are least likely to occupy openings during this period. When the goal is restoring fire dependent plant communities and the primary tool is prescribed burning, we expect the optimum management window for box turtles may often prove incompatible with fuel conditions, floristic objectives, or seasonal restrictions in place to protect other species of conservation priority. In these scenarios, the following information may prove useful for mitigating or reducing potential for direct impacts on box turtles during implementation.

By nesting season (June in our study area), a portion of the second activity season neonates will probably have already dispersed from openings into surrounding forest yet some neonates may still be present and gravid adult females are likely to be aggregated in openings for nesting purposes. Therefore, burning openings during nesting season could impact adult and neonate age classes. When fire is used in eastern box turtle nesting habitat in spring or fall, we caution that prescribed burns encompassing the entire opening and adjacent forest (≤ 50 m from opening) have the potential to directly impact 100% of the neonate cohort produced at the site during the prior nesting season. In late fall, winter, or very early spring burns, perhaps the overwintering site itself offers some refugia, although the average depth of the overwintering burrow provided less than 5 mm of mineral soil between the carapace and duff layer (see Perry and McDaniel 2015). Increasing the time (years) between burns may allow neonate cohorts to disperse from the sites between treatments. Excluding the forest edge and adjacent forest from the burn unit would decrease potential for impacts, especially in small, or linear shaped openings, or openings where nesting is concentrated relatively near the forest edge. In larger openings, if nesting is not likely to be concentrated near the forest edge, splitting the opening into multiple burn units and burning no more than one unit each year may reduce potential for impacts.

Considering neonates remain in or very near natal openings for months after hatching, this age class is probably quite vulnerable to mortality during implementation of the same management activities often used to maintain and improve nesting habitat. The issue of fire and box turtle population response is likely complex, and has not yet been adequately addressed. Reaching an appropriate level of concern regarding potential impacts to individual neonates during project implementation is an issue of scale and requires the proper context. Clearly, short term perturbations in neonate survival rates during stand level management would not impact long term population growth rates in the same fashion as landscape scale failures to maintain and restore suitable open canopy nesting habitat.

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FIGURE LEGENDS

Figure 1. Location of Manistee National Forest in Michigan.

Figure 2. Mean structural characteristics + SE of study area including four upland openings (A) and the forested habitat surrounding each upland opening (B) in the Manistee National Forest, Michigan. We sampled 30 random locations at each opening and 30 random locations within the forest surrounding each openging ($2.5 \leq 50$ m from opening) from 20 September to 25 September, 2016. We estimated overstory canopy cover (%) using a sperical densiometer and used a 1.0 m^2 pvc frame to estimate ground cover.

Figure 3. Spatial distibution of eastern box turtle nests ($n = 64$ nests) relative to the forest edge at Savanna opening (A), Turtle Bowl opening (B), Gravel Pit opening (C), and East West opening (D), Manistee National Forest, Michigan, 2012-2016. Grey-scale color ramps indicate maximum, minimum, and mean distances (m) of raster cell centroids (1.0 m^2 resolution) within each opening relative to the nearest forest edge (Benson 2013).

Figure 4. Mean distance (m) + SE from eastern box turtle nests to nearest forest edge within four openings in our study area, Manistee National Forest, Michigan, 2012-2016. We used distance rasters to obtain mean distances (m) of raster cell centroids (1.0 m^2 resolution) within each opening relative to the nearest forest edge (Benson 2013). An "≠" sign indicates mean distance from nests to nearest forest edge was significantly different (*t*-tests) than distance raster mean. An "=" sign indicates no significant difference between mean distance

from nest to nearest forest edge and distance raster mean (*t*-test). Different letters above error bars denotes significant differences in distances from nests to nearest forest edge between sites (Mann-Whitney *U*-tests).

Figure 5. Mean movement rates + SE of 64 radio-fitted neonate eastern box turtles monitored up to 333 d post nest emergence (n = 642 telemetry locations) by time of year in the Manistee National Forest, Michigan, 2012-2016.

Figure 6. Movements and overwintering sites of 29 radio-fitted neonate eastern box turtles monitored from nest emergence to overwintering at Turtle Bowl opening, Manistee National Forest, Michigan, 2012-2015. Nest emergence occurred in August, September, or October and neonates began overwintering in October or early November. Labels next to nest locations indicate the year and clutch ID. Due to scale of map, many fine scale movements are obscured.

Figure 7. Movements and overwintering sites of 8 radio-fitted neonate eastern box turtles monitored weekly from nest emergence to overwintering at the Savanna opening, Manistee National Forest, Michigan, 2012, 2013, and 2015. Nest emergence occurred in August, September, or October and neonates began overwintering in October or early November. Labels next to nest locations denote year and clutch ID. Due to scale of map, many fine scale movements are obscured and upland opening habitat is displayed as solid white on map insets.

Figure 8. Movements and overwintering sites of 9 radio-fitted neonate eastern box turtles monitored weekly from nest emergence to overwintering at the East West (EW) and Gravel Pit (GP) openings, Manistee National Forest, Michigan. Nest emergence occurred in September in 2014 October in 2015. Neonates began overwintering in October or early November, 2014-2015. Due to scale of map, many fine scale movements are obscured and upland opening habitat is displayed as solid white on map insets.

Figure 9. Movements of 17 radio-fitted neonate eastern box turtles (Age 7 to 11 months) monitored weekly after emerging from overwintering sites in spring at Turtle Bowl opening, Manistee National Forest, Michigan, 2013, 2014, and 2016. Neonates had hatched from nests within the opening during a previous year and dispersed to their respective overwintering locations. Neonates emerged from overwintering refugia in the fourth week of April through the first two weeks of May. We also encountered and opportunistically radio-fitted a natural recruit on 11 June 2014. Due to scale of map, most fine scale (< 2.0 m) movements are obscured. We eventually lost contact (i.e., mortality or disappearance) with all 17 radio-fitted neonates after 17 August. Underlined dates at the end of movement paths indicate the last observation before we lost contact.

Figure 10. Movements of 8 radio-fitted neonate eastern box turtles (Age 7 to 10 months) monitored weekly after emerging from overwintering sites in spring at Savanna opening, Manistee National Forest, Michigan, 2013, 2014, and 2016. All neonates had hatched from nests within the opening during a previous year and dispersed to their respective overwintering locations. Seven neonates emerged from overwintering refugia in the fourth

week of April through the first two weeks of May and one neonate emerged the last week in May. Due to scale of map, symbols obscure the fine scale movements we observed and upland opening habitat is displayed as solid white on map insets. We eventually lost contact (i.e., mortality or disappearance) with all 8 radio-fitted neonates after 4 July. Underlined dates at the end of movement paths indicate the last observation before we lost contact.

Figure 11. Movements of 3 radio-fitted neonate eastern box turtles (Age 7 to 9 months) monitored weekly after emerging from overwintering sites in spring at Gravel Pit opening (GP) and East West (EW) opening, Manistee National Forest, Michigan, 2016. All neonates had hatched from nests within the opening during the previous year and dispersed to their respective overwintering locations. Due to scale of map, symbols obscure the fine scale movements we observed and upland opening habitat is displayed as solid white on map insets. Underlined dates at the end of movement paths indicate the last observation before we lost contact.

TABLES

Table 1. Dispersal distance and overwintering habitat use of all radio-fitted neonates monitored during their first activity season at four openings in the Manistee National Forest, Michigan, 2012-2015. OW refers to overwintering. Dispersal distance refers to the straight line distance (m) from nest to overwintering site.

Table 1.

Opening	Year	Clutches	Radio-fitted neonates	Survived to OW	Dispersal distance (m)				OW in opening	OW in edge	OW in forest
					$\bar{x}$	SE	min	max			
Turtle Bowl											
	2012	2	2	1	44.2	-	-	-	-	-	1
	2013	4	20	15	25.6	2.8	8.0	45.2	4	3	8
	2014	2	11	10	11.0	2.0	1.9	20.4	8	-	2
	2015	2	4	3	14.9	0.4	14.4	15.8	-	1	2
Total/Average:		10	37	29	20.1	2.2	1.9	45.2	12 (41.3%)	4 (13.8%)	13 (44.8%)
Savanna											
	2012	1	1	1	28.4	-	-	-	1	-	-
	2013	2	6	3	29.8	26.7	2.9	83.2	2	-	1
	2015	2	5	4	5.9	1.1	2.7	7.8	4	-	-
Total/Average:		5	12	8	27.8	9.8	2.7	83.2	7	-	1
East-West											
	2013	1	1	0	-	-	-	-	-	-	-
	2014	1	7	6	28.1	6.1	17.3	49.2	2	-	4
	2015	2	4	2	3.3	0.4	2.9	3.6	2	0	-
Total/Average:		4	12	8	21.9	6.1	2.9	49.2	4	0	4
Gravel Pit											
	2015	1	3	1	16.8	-	-	-	1	-	-
All Sites											
	2012	3	3	2	36.3	11.2	28.4	44.2	1	-	1
	2013	7	27	18	26.3	4.4	2.9	83.2	6	3	9
	2014	3	18	16	17.4	3.3	1.9	49.2	10	-	6
	2015	7	16	10	9.2	1.8	2.7	16.8	7	1	2
Total/Average:		20	64	46	19.9	2.4	1.9	83.2	24 (52.2%)	4 (8.7%)	18 (39.1%)

Table 2. Results of Rayleigh's tests of mean directionality of pooled first activity season movements for 10 clutches of neonate eastern box turtles monitored at three openings in the Manistee National Forest, Michigan, 2013, 2014, and 2015. Only movements ≥ 2.0 m were included in analysis. Directional means of clutch movements only reported for clutches with significant non-random ($\alpha = 0.10$) directionality of movements.

Clutch ID	Opening	Neonates	n^a	z	P	Directional Mean
2013A	Turtle Bowl	4	8	2.30	0.098	279.4°
2013B	Turtle Bowl	5	16	2.70	0.065	94.1°
2013C	Turtle Bowl	5	18	10.32	< 0.001	86.6°
2013E	Turtle Bowl	5	17	4.87	0.006	302.7°
2014C	Turtle Bowl	5	12	2.84	0.055	250.7°
2014E	Turtle Bowl	4	6	0.88	0.433	
2015B	Turtle Bowl	3	11	5.67	0.002	357.5°
2014A	East-West	7	40	6.27	0.002	15.1°
2013F	Savanna	4	9	2.57	0.073	329.1°
2015L	Savanna	3	6	0.10	0.909	

[a] Number of movements ≥ 2.0 m.

Table 3. Binomial logistic regression models and model selection criteria used to examine potential associations between three predictor variables and overwintering in habitat use (natal opening versus adjacent forest). We monitored 46 radio-fitted neonate eastern box turtles from nest emergence to overwintering period in the Manistee National Forest, Michigan, 2012-2015. AIC_c = Akaike's Information Criterion for small sample sizes, ΔAIC_c = AIC_c rank, w_i = AIC_c weight, *Nestedge* = distance (m) from nest to nearest forest edge, *Emgdate* = date of nest emergence, *Mass* = body mass (g) of neonate turtles at nest emergence, β = estimates of coefficients from parameters in selected model, OR = odds ratios from exponentiated estimated coefficients.

Table 3.

Candidate models	Deviance $_{df}$	AIC$_c$	ΔAIC$_c$	w_i	McFadden's R^2
Nestedge + Emgdate	46.626_{43}	53.197	0.000	0.694	0.267
Nestedge + Emgdate + Mass	46.614_{42}	55.589	2.392	0.209	0.268
Emgdate	54.582_{44}	58.860	5.663	0.040	0.142
Nestedge	55.216_{44}	59.494	6.297	0.033	0.132
Emgdate + Mass	54.307_{43}	60.878	7.681	0.014	0.147
Nestedge + Mass	55.082_{43}	61.653	8.456	0.010	0.135
Mass	63.677_{44}	67.677	14.480	0.000	0.000
Intercept only (Null) model	63.683_{45}				
Variables[a]	β	SE	OR	95% CI	
Intercept	-27.180	11.509	<0.001		
Nestedge	0.094	0.039	1.099	1.026-1.209	
Emgdate	0.098	0.043	1.028	1.028-1.226	

[df] Degrees of freedom.

[a] Parameters included in model selected as best supported from candidate models.

Table 4. Predicted probabilities of neonate eastern box turtles overwintering within their natal openings for various nest emergence dates and distances from nests to nearest forest edge, Manistee National Forest, Michigan. We derived each prediction probability from a binomial logistic regression model with three parameters including an intercept, distance from nest to nearest forest edge (m), and date of nest emergence.

Table 4.

Distance from nest to forest edge (m)	Nest emergence date					
	15 Aug	1 Sept	18 Sept[a]	1 Oct	15 Oct	30 Oct
1.0	0.009	0.050	0.220	0.504	0.803	0.947
5.0	0.014	0.071	0.291	0.598	0.856	0.963
10.0	0.022	0.109	0.397	0.704	0.904	0.978
15.0	0.035	0.164	0.514	0.792	0.938	0.985
20.0	0.055	0.239	0.629	0.859	0.960	0.991
25.0	0.086	0.335	0.731	0.907	0.975	0.994
30	0.131	0.448	0.814	0.940	0.984	0.996
35.0	0.195	0.565	0.875	0.962	0.990	0.998
40.0	0.279	0.676	0.918	0.975	0.993	0.999
50.0	0.500	0.843	0.967	0.990	0.997	
60.0	0.720	0.932	0.988	0.996	0.999	
70.0	0.868	0.972	0.995	0.998	0.999	
80.0	0.944	0.989	0.998	0.999		
90	0.978	0.996	0.999			
100.0	0.991	0.999				
110.0	0.999					

[a] Mean day of nest emergence events (n = 31 nests, n = 41 nest emergence events), Manistee National Forest, Michigan, 2012-2016.

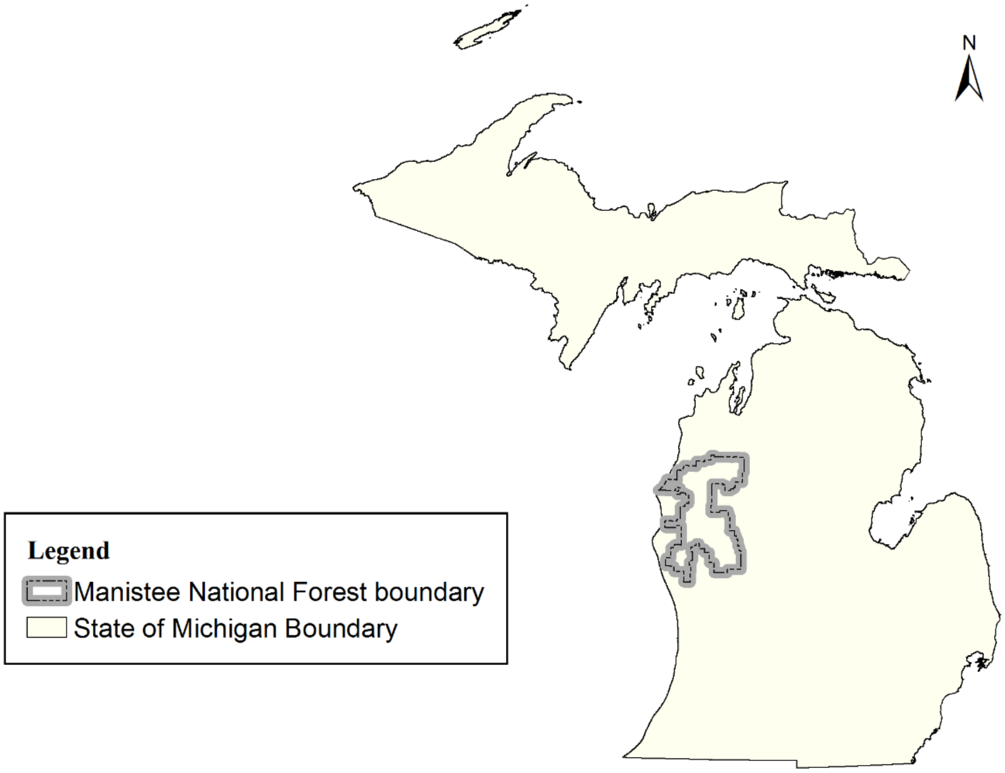
Table 5. Results of Rayleigh's tests of mean directionality of movements for 17 radio-fitted neonate eastern box turtles monitored at two openings in the Manistee National Forest, Michigan, 2012-2016. Only angles between movements ≥2.0 m were included in analysis. Directional means only reported for neonates with significant non-random (α = 0.10) directionality of movements. TB = Turtle Bowl Opening. SAV = Savanna opening.

Neonate ID	Site	Nest emergence	Last contact	Dispersal[a] *(m)*	*n*[b]	*z*	*P*	Directional mean
2012A1	TB	26 Aug 2012	7 Jul 2013	367.3	10	7.16	< 0.001	49.7°
2013A2	TB	9 Sep 2013	27 Jun 2014	322.1	11	1.57	0.212	-
2013A4	TB	16 Sep 2013	18 Jul 2013	111.8	11	1.99	0.136	-
2013B1	TB	18 Sep 2013	11 Jun 2014	79.8	7	3.50	0.024	77.3°
2013B3	TB	18 Sep 2013	17 Aug 2014	397.7	19	2.75	0.062	151.1°
2013B4	TB	18 Sep 2013	10 Jun 2014	33.0	7	1.68	0.190	-
2013C4	TB	15 Sep 2013	24 Jun 2014	355.2	11	2.52	0.078	86.2°
2013C5	TB	18 Sep 2013	16 Jun 2014	70.8	11	2.40	0.089	57.0°
2013E1	TB	14 Sep 2013	2 Jul 2014	193.1	10	3.72	0.020	255.6°
2013E3	TB	14 Sep 2013	21 Jun 2014	100.7	8	4.04	0.012	287.2°
2013E4	TB	14 Sep 2013	3 Jun 2014	80.1	7	3.38	0.028	317.4°
2013E5	TB	15 Sep 2013	5 Jun 2014	35.0	7	2.89	0.049	324.2°
2015B2	TB	19 Sep 2015	28 Jun 2016	65.0	10	10.14	< 0.001	6.9°
2015B4	TB	19 Sep 2015	22 May 2016	17.2	6	1.51	0.229	
2012B1	SAV	26 Aug 2012	27 May 2013	56.7	6	3.95	0.012	316.8°
2013F2	SAV	19 Sep 2013	4 Jul 2014	352.5	12	0.19	0.832	
2015 L2	SAV	18 Sep 2015	28 Jun 2016	27.3	8	0.80	0.463	

[a] Straight-line distance (m) from nest to location of last contact.

[b] Number of movements ≥2.0 m.

FIGURES



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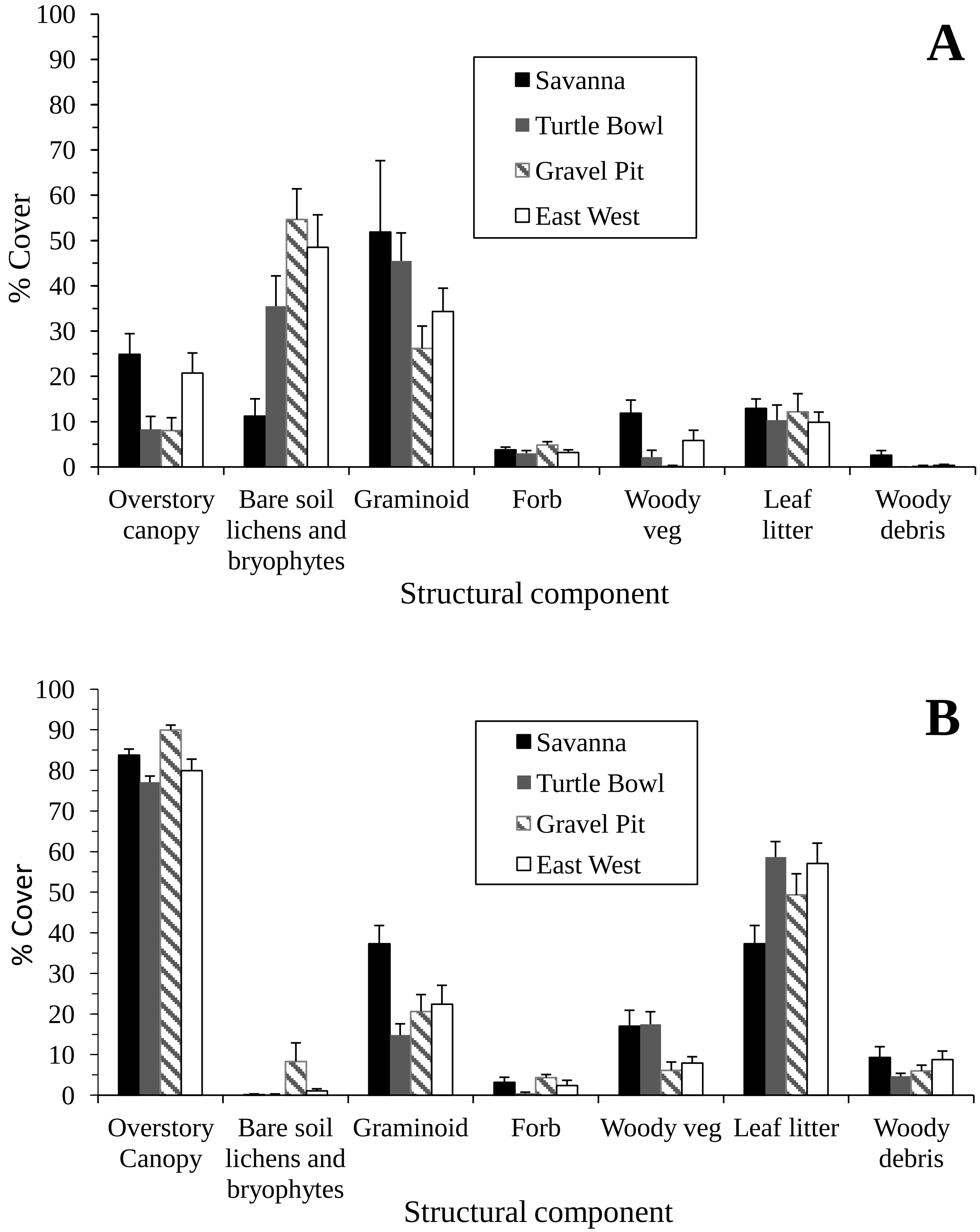
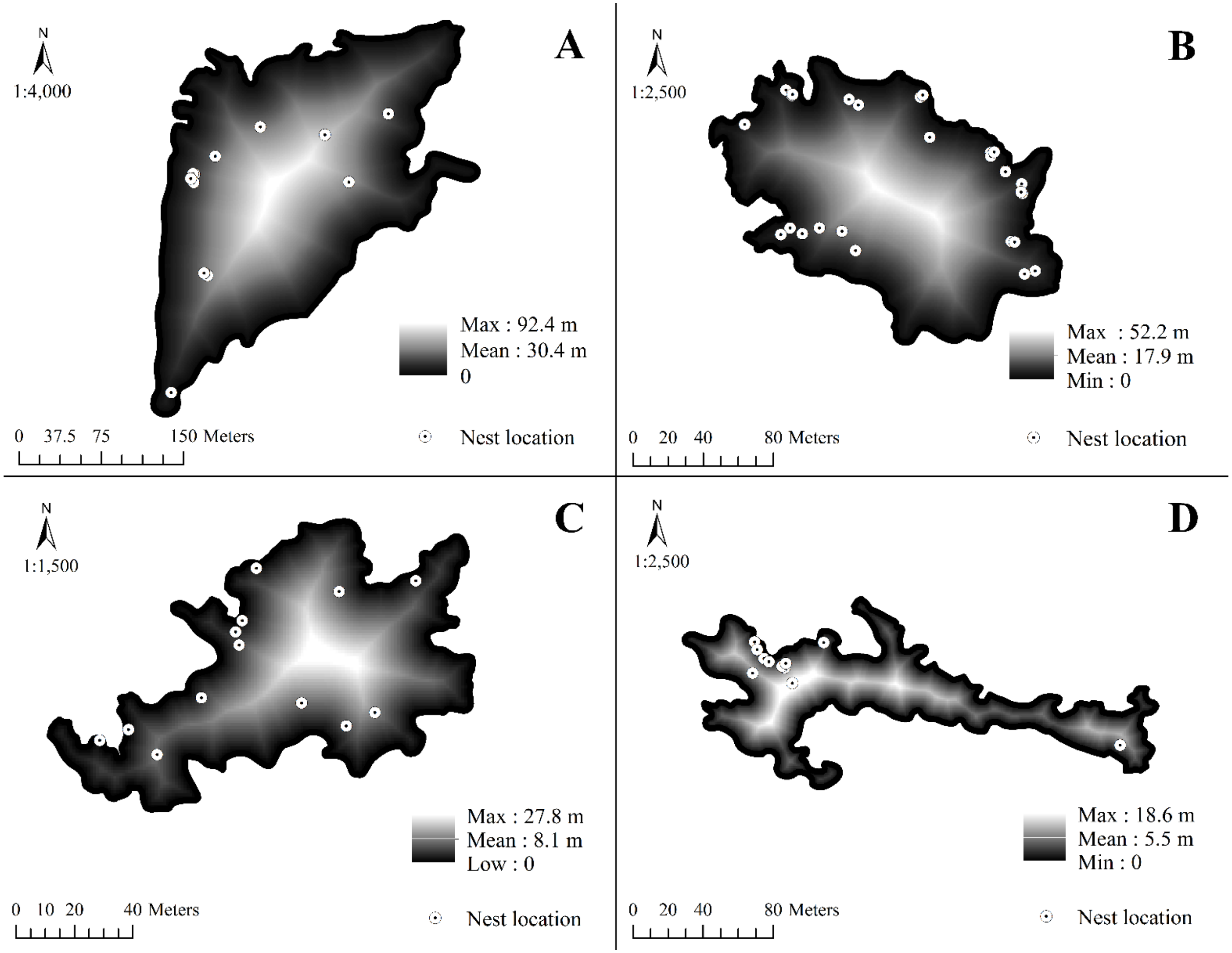
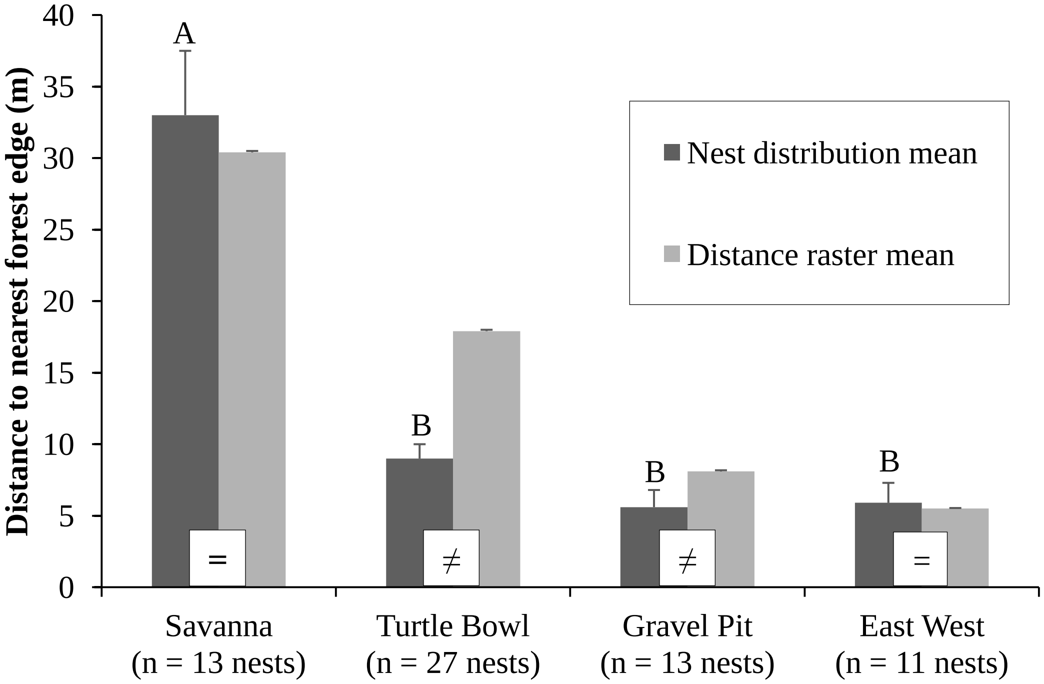

A
% Cover
100
90
80
70
60
50
40
30
20
10
0
■ Savanna
■ Turtle Bowl
▨ Gravel Pit
☐ East West
Overstory canopy
Bare soil lichens and bryophytes
Graminoid
Forb
Woody veg
Leaf litter
Woody debris
Structural component
B
% Cover
100
90
80
70
60
50
40
30
20
10
0
■ Savanna
■ Turtle Bowl
▨ Gravel Pit
☐ East West
Overstory Canopy
Bare soil lichens and bryophytes
Graminoid
Forb
Woody veg
Leaf litter
Woody debris
Structural component

Figure 2.



A
N
1:4,000
Max : 92.4 m
Mean : 30.4 m
0
0 37.5 75 150 Meters
Nest location
B
N
1:2,500
Max : 52.2 m
Mean : 17.9 m
Min : 0
0 20 40 80 Meters
Nest location
C
N
1:1,500
Max : 27.8 m
Mean : 8.1 m
Low : 0
0 10 20 40 Meters
Nest location
D
N
1:2,500
Max : 18.6 m
Mean : 5.5 m
Min : 0
0 20 40 80 Meters
Nest location

Figure 3.



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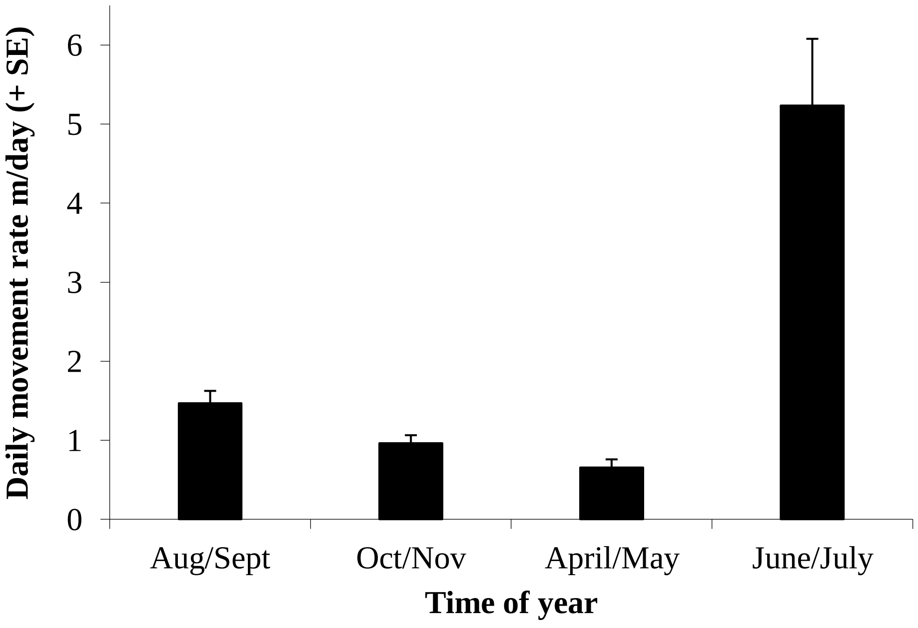

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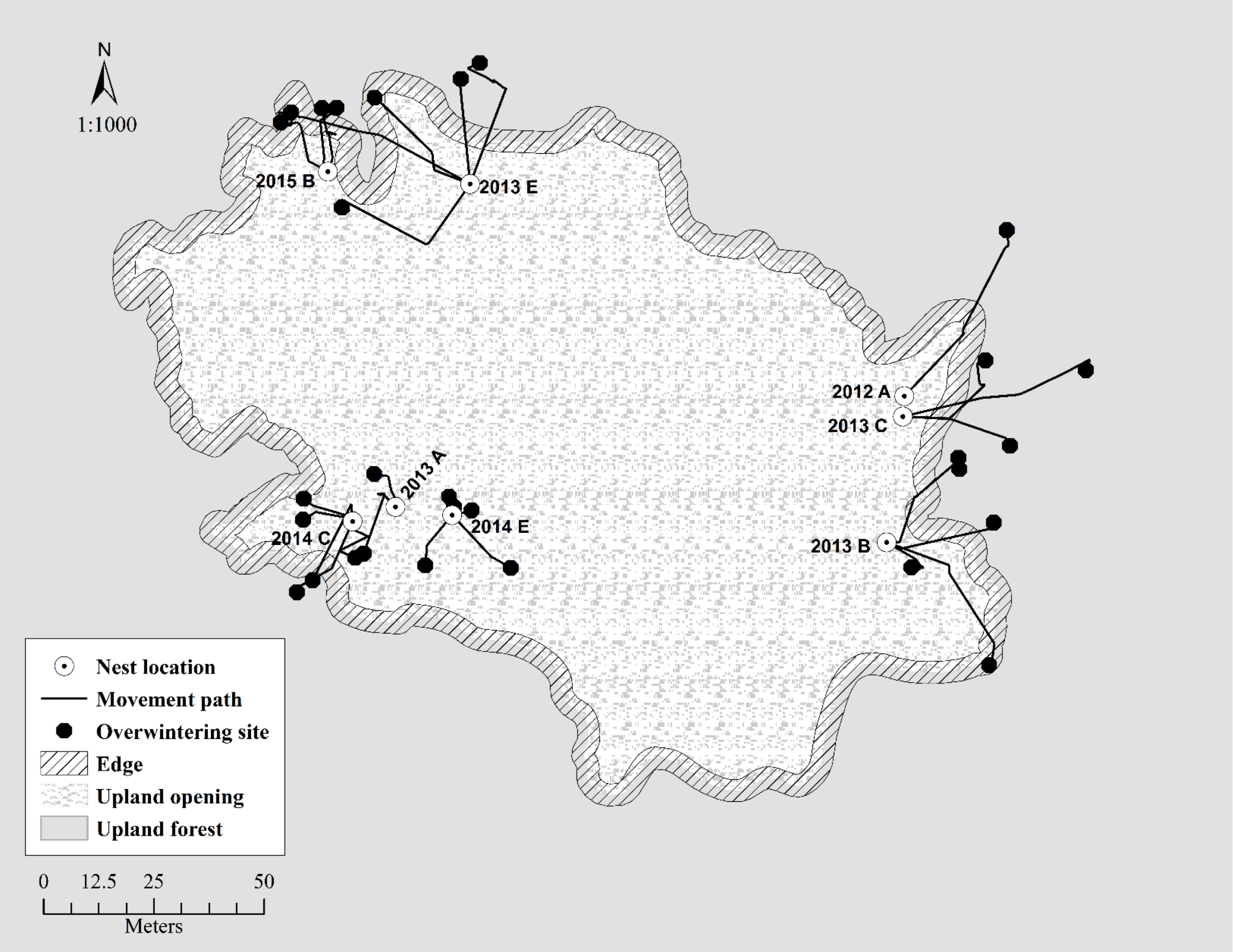

N
1:1000
2015 B
2013 E
2012 A
2013 C
2013 A
2014 C
2014 E
2013 B
Nest location
Movement path
Overwintering site
Edge
Upland opening
Upland forest
0
12.5
25
50
Meters

Figure 6.

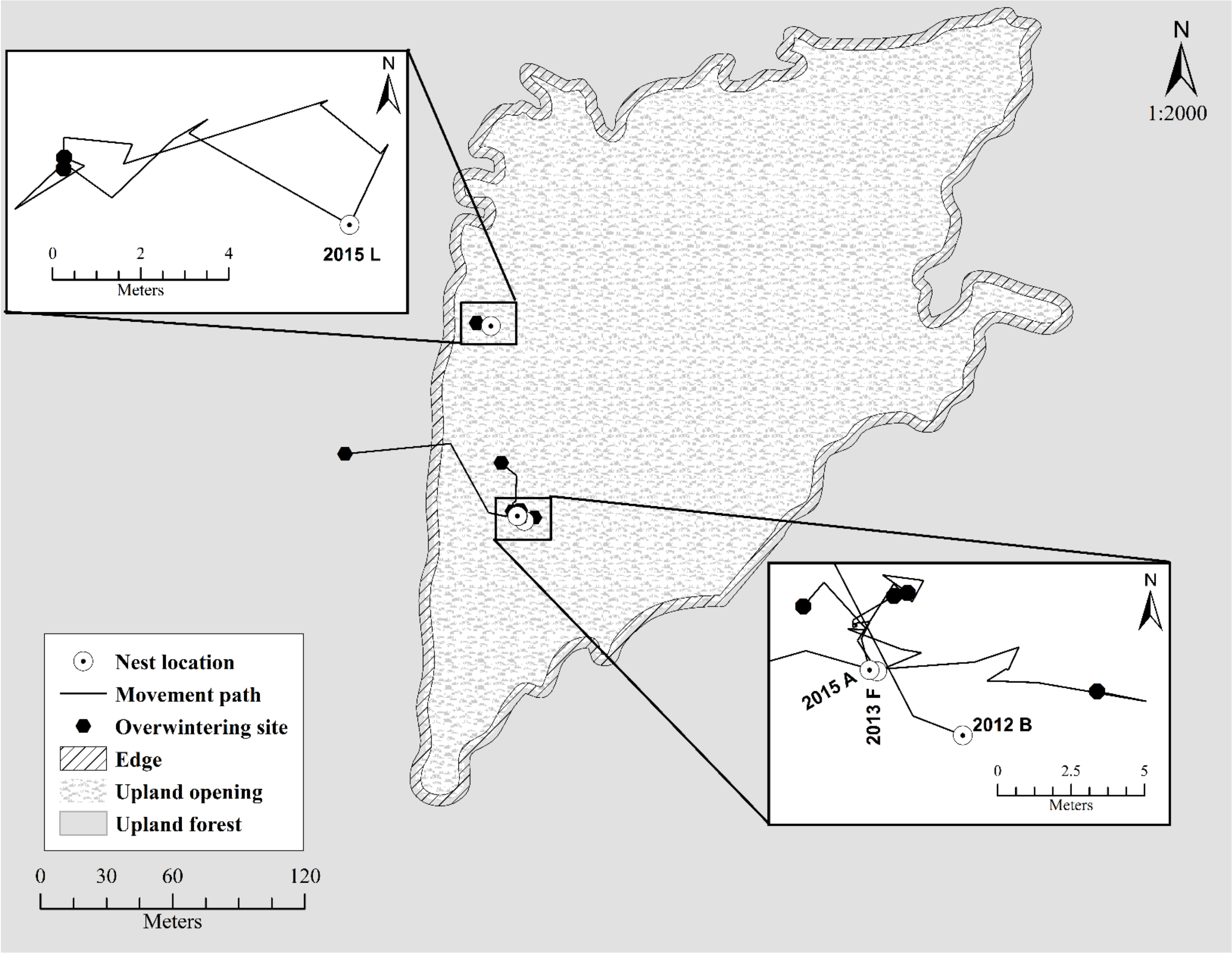

N
1:2000
N
0
2
4
Meters
2015 L
N
2015 A
2013 F
2012 B
0
2.5
5
Meters
Nest location
Movement path
Overwintering site
Edge
Upland opening
Upland forest
0
30
60
120
Meters

Figure 7.

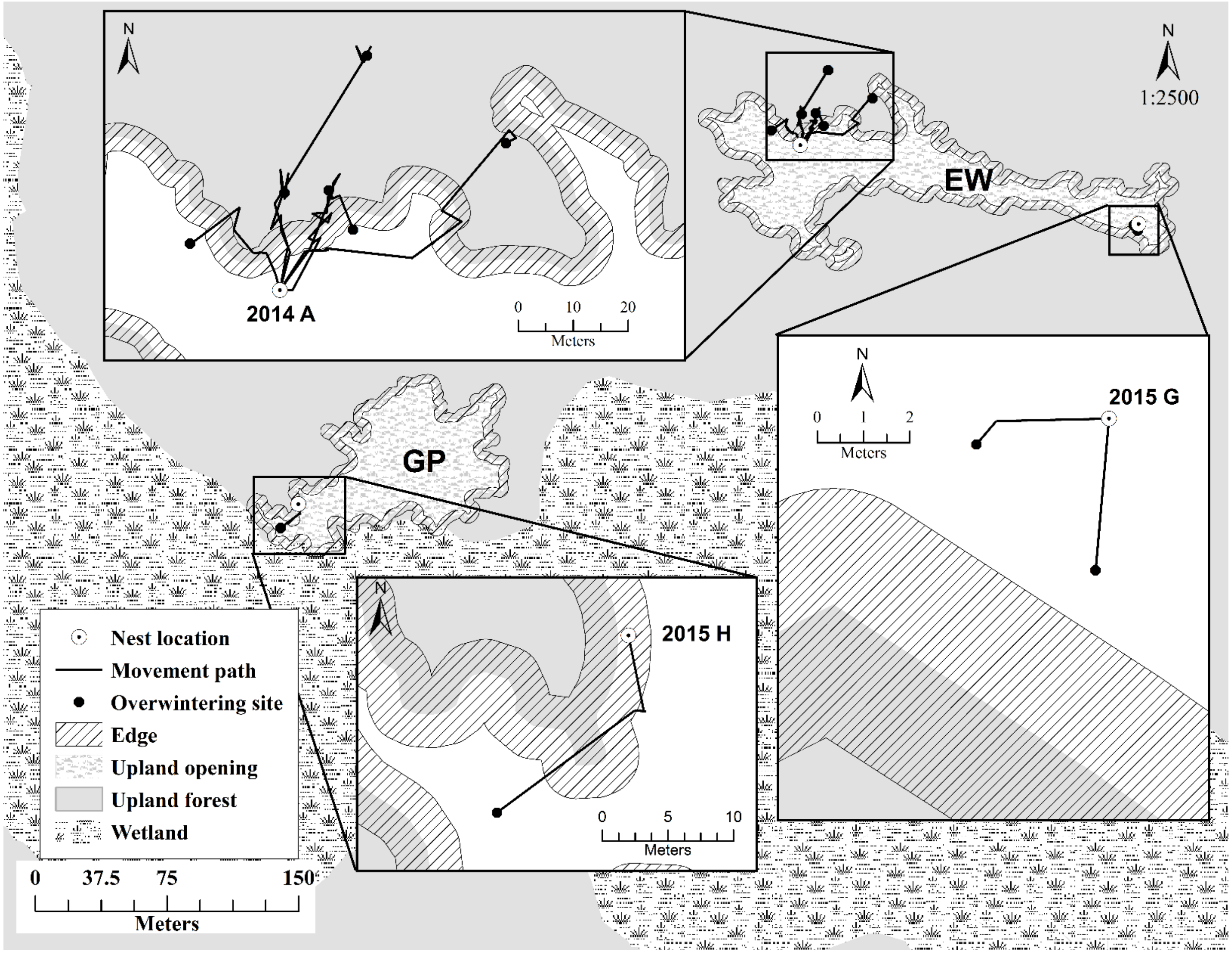

N
1:2500
EW
GP
2014 A
0 10 20
Meters
2015 G
0 1 2
Meters
2015 H
0 5 10
Meters
Nest location
Movement path
Overwintering site
Edge
Upland opening
Upland forest
Wetland
0 37.5 75 150
Meters

Figure 8.

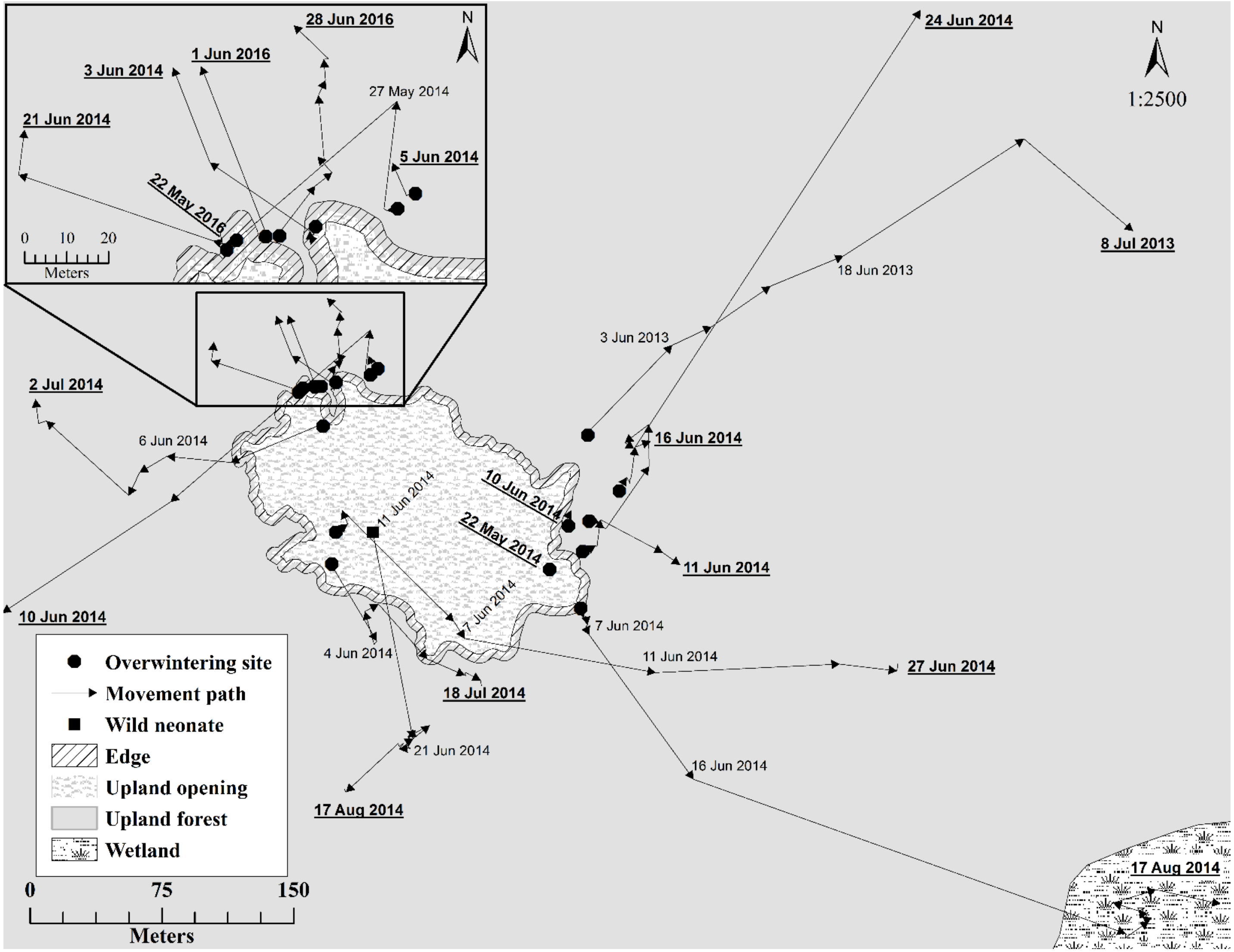

28 Jun 2016
N
1 Jun 2016
3 Jun 2014
27 May 2014
21 Jun 2014
5 Jun 2014
22 May 2016
0 10 20
Meters
24 Jun 2014
N
1:2500
8 Jul 2013
18 Jun 2013
3 Jun 2013
2 Jul 2014
6 Jun 2014
16 Jun 2014
10 Jun 2014
11 Jun 2014
22 May 2014
11 Jun 2014
10 Jun 2014
7 Jun 2014
7 Jun 2014
4 Jun 2014
11 Jun 2014
27 Jun 2014
18 Jul 2014
21 Jun 2014
16 Jun 2014
17 Aug 2014
17 Aug 2014
● Overwintering site
Movement path
■ Wild neonate
Edge
Upland opening
Upland forest
Wetland
0 75 150
Meters

Figure 9.

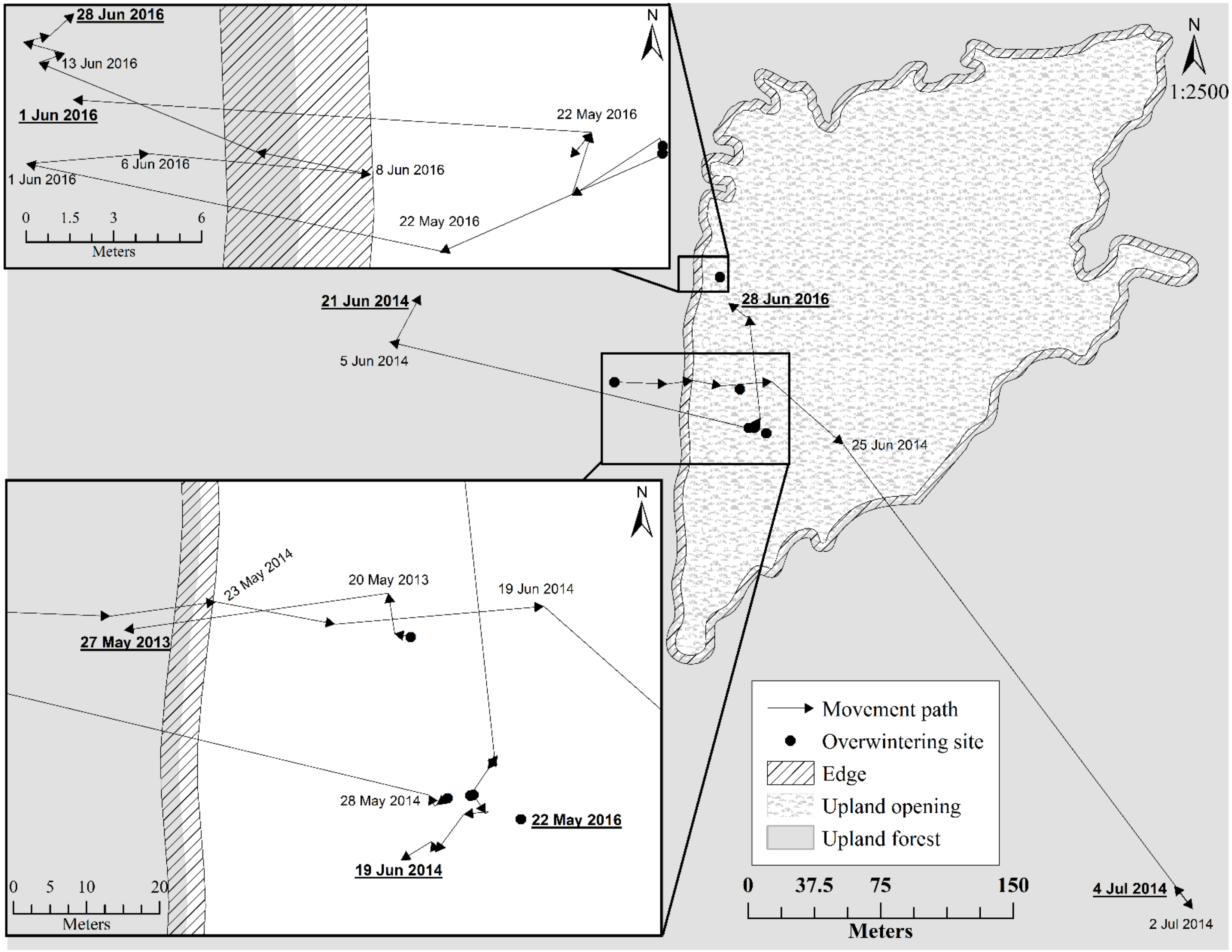

28 Jun 2016
13 Jun 2016
1 Jun 2016
22 May 2016
6 Jun 2016
8 Jun 2016
1 Jun 2016
22 May 2016
N
0 1.5 3 6
Meters
N
1:2500
21 Jun 2014
28 Jun 2016
5 Jun 2014
25 Jun 2014
N
23 May 2014
20 May 2013
19 Jun 2014
27 May 2013
28 May 2014
22 May 2016
19 Jun 2014
0 5 10 20
Meters
Movement path
Overwintering site
Edge
Upland opening
Upland forest
0 37.5 75 150
Meters
4 Jul 2014
2 Jul 2014

Figure 10.

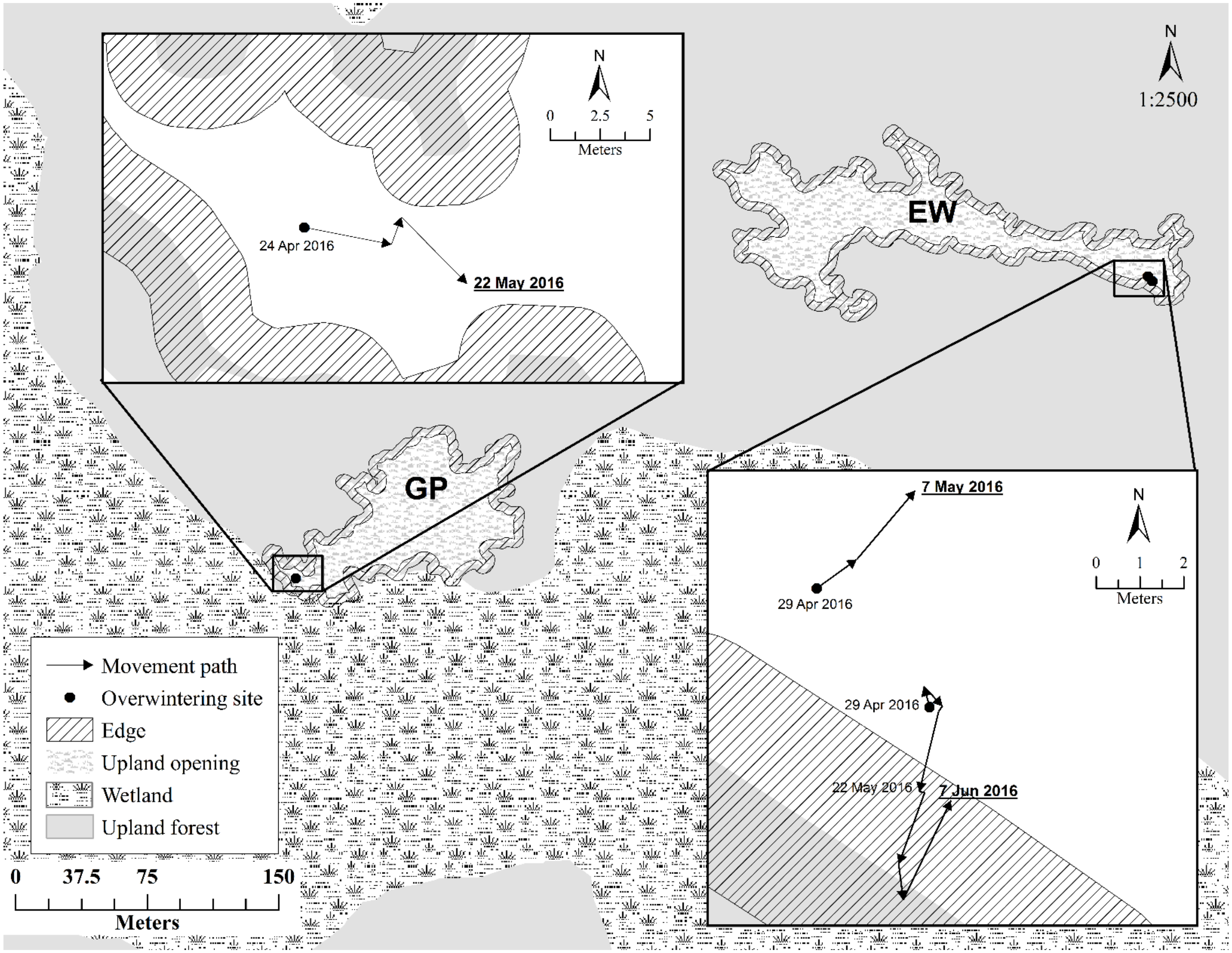

N
1:2500
EW
GP
N
0 2.5 5
Meters
24 Apr 2016
22 May 2016
7 May 2016
N
0 1 2
Meters
29 Apr 2016
29 Apr 2016
22 May 2016
7 Jun 2016
Movement path
Overwintering site
Edge
Upland opening
Wetland
Upland forest
0 37.5 75 150
Meters

Figure 11.

CHAPTER IV

Management recommendations for eastern box turtle populations in the Manistee National Forest, Michigan

NOTES ON EASTERN BOX TURTLE POPULATION STATUS IN THE MNF

Anthropogenic factors, including habitat loss, habitat fragmentation, road mortality, and collection are the primary drivers behind widespread declines in most turtle populations (Dodd 2001, Gibbons et al. 2000, Gibbs and Shriver 2002). In the MNF, many of these populations stressors are probably less acute for resident box turtle populations considering the large land base and relatively low densities of paved roads. In addition, there are reproducing populations of eastern box turtles present in several counties within the MNF, including localized populations with relatively high densities (turtles/ha). High annual survival rates (> 0.90) of adult age classes are generally assumed to be required for stabile population growth rates of *Emydid* turtles (Currylow et al. 2011, Congdon et al. 1993, Heppell 1998). Based on mark-recapture and telemetry data, annual survivorship rates in the MNF appear, albeit anecdotally, very high. Preliminary results from GVSU's investigation of box turtle genetics are favorable and indicate genetic diversity of MNF populations is relatively high (J. Moore pers. comm. 2017). In addition, extensive dry-mesic forested habitat is available to box turtles in the MNF. Recent management activities such as timber harvest and thinning, savanna and barrens restoration/creation, opening creation/maintenance, and road closures (USDA Forest Service 2006) have likely provided indirect beneficial impacts to box turtles and their habitat in the MNF. Thus, barring circumstances beyond control of HMNF land managers (e.g., disease, poaching, stochastic events, etc.), evidence suggests HMNF biologists have excellent potential to maintain the long-term viability of box turtle populations in the MNF.

OUTLINE OF A 3-PHASE EASTERN BOX TURTLE CONSERVATION APPROACH

Wildlife management has long since been analogous to habitat management and many wildlife species will respond relatively quickly, and in detectable fashion, to changes in habitat quality or availability. Conversely, turtle populations respond rather slowly to positive changes in habitat quality yet are especially sensitive to increased losses of adult individuals due to their reproductive strategy (Congdon et al. 1993, Heppell 1998, Reed et al. 2002). Thus, conservation approaches for turtles pose a rather unique suite of challenges. Although individuals are sometimes vulnerable to mortality or injury during management activities, eastern box turtle populations would not be expected to respond favorably to "land preservation" (i.e., no action) over the long term because many disturbance regimes (particularly fire) which historically provided landscape mosaics of suitable nesting habitat, are no longer intact.

Promoting long-term viability of eastern box turtle populations in the MNF will likely hinge upon vegetation management outcomes. Slow population declines would be expected if oak or oak-pine stands adjacent to floodplain and wetlands undergo succession and convert to closed canopy climax communities. Declines would also be expected if availability and suitability of nesting habitat diminishes due to forest succession. Forest succession due to fire suppression has likely concentrated nesting activities to small openings where nest depredation rates are probably extremely high (this Thesis Chapter III, Temple 1987). Thus, effective strategies for promoting long-term population viability in the MNF will likely involve creating or restoring, and subsequently maintaining, suitable upland nesting habitat while mitigating potential for mortality or injury whenever possible during vegetation management. If the volume and suitability of nesting habitat increases, population growth rate would be expected to follow (Reid et al. 2016) and stand level concerns associated with potential impacts to individuals during management actions may become less pertinent in the future. This will be a slow process, however, considering their age at first reproduction is > 10 years.

The following sections outline a 3-phase conservation approach for promoting long-term viability of populations inhabiting the MNF. Phases 1 and 2 are designed to maintain and improve habitat suitability in areas currently inhabited by local box turtle populations. Phase 3 is a longer-term approach which may result in favorable population responses by facilitating colonization (or re-colonization) of additional sites, improving habitat connectivity, and promoting geneflow across the landscape (Figure 1). In general, the approach outlined here would be compatible with conservation strategies specific to the recovery efforts of several federally endangered and threatened species, particularly the karner blue butterfly *Plebejus melissa samuelis* and eastern massasauga rattlesnake *Sistrurus catenatus catenatus*. This approach is consistent with the 2006 Land and Resource Management Plan (USDA Forest Service 2006) direction regarding desired volumes of openings, barrens, and savannas in the MNF.

Phase 1

Objectives:

- Maintain and or improve the existing nesting habitat patches currently used for thermoregulation and reproduction by resident box turtle populations.

Relevant biological information:

- Existing box turtle nesting habitat in the MNF is likely to be associated with Land Type Association 1 (LTA 1) and relatively near (< 1.5 km) wetland or lowland LTA's.
- Upland open canopy sites with recent occurrences records of adult females [in June] can be considering existing nesting habitat.

Prescriptions for existing nesting habitat:

- See Table 1 for desired condition of box turtle nesting habitat.
- Restrict off-road vehicle access if possible.
- Consider enlarging patch size if possible.

Selecting which nesting habitat patches to maintain:

- Prioritize management efforts in existing nesting habitat patches in locations where gravid female turtles do not have to cross paved roads when traversing between primary habitat and nesting habitat patches.
- In general, prioritize larger patch sizes over small patch sizes

Potential concerns and mitigations during implementation:

- Avoid intensive management of occupied nesting habitat from 25 May to 25 June to protect gravid females.
- See Management Implications in Chapter III for additional information regarding neonate occupancy of nesting habitat.

Monitoring:

- A standardized survey protocol for monitoring site use by gravid females and for a sub-set of known nesting areas would provide valuable trend information. Due to their long generation time and high annual survival rates, surveys conducted approximately every 5 to 10 years would probably suffice.
- When surveying the sites, opportunistic carapace marking is recommended to evaluate long-term survival, site fidelity, and dispersal.

Phase 2

Objective:

- Improve nest survival rates and recruitment by increasing volume of available nesting habitat in areas currently inhabited by local box turtle populations.

Relevant biological information:

- Nest depredation rates are often highest near edges (Temple 1987).
- Adult age classes overwinter in forested stands (this Thesis, Madden 1975, Cross 2016).

Selecting sites for nesting habitat creation:

- Prioritize creation of new nesting habitat patches in areas where turtles will not have to cross paved roads when traversing between primary habitat and nesting habitat patches.
- In general, prioritize larger patch sizes over small patch sizes.
- Create new nesting habitat patches within 1.5 km to wetland or water and attempt to create some patches <250 meters from wetland or water sources, if possible.
- Whenever possible create new nesting habitat patches <0.5 km from known nesting areas or recent box turtle occurrence records.

Prescriptions for creating and maintaining nesting habitat:

- See Table 1 and Figures 2, 3 for desired condition of box turtle nesting habitat.
- Restrict off-road vehicle access if possible.

Potential concerns and mitigations during implementation:

- If considering converting forested stands to nesting habitat, conduct surveys in the project planning phase to determine if the proposed site has aggregations of overwintering adults and avoid converting these areas. Surveys conducted on sunny warm days in early May or Late September would provide that information.
- Avoid intensive management of occupied nesting habitat from 25 May to 25 June.
- See Management Implications in Chapter III for additional information regarding neonate occupancy of nesting habitat.

Monitoring:

- Post treatment monitoring will be necessary to evaluate vegetation response and is recommended to assess presence/absence of gravid females.
- Optimum survey period to assess presence/absence is early June during warm, humid days or immediately after a precipitation event.
- Radio-telemetry monitoring of nearby adult females would also yield valuable information regarding the utilization of newly created nesting habitat.

- Opportunistic carapace marking is recommended to evaluate long-term survival, site fidelity, and dispersal.

Phase 3

Objective:

- Promote gene flow and habitat connectivity between populations separated by extensive upland forest.

Relevant biological information:

- Streams, rivers, and small ponds are often visited frequently by box turtles, especially in periods of heat stress or drought (Dodd 2001, Donaldson and Echternacht 2005).
- Box turtles in the MNF will use artificially created, lined waterholes, if available.

Selecting optimum corridors for landscape connectivity via nesting habitat and waterholes:

- If natural permanent water sources or wetlands are present between two known box turtle populations, for example lentic systems between lotic systems, target these general areas for creation of nesting habitat provided road densities are not an issue.
- If water sources or wetlands do not exist between two known populations, augmenting nesting habitat with lined waterholes may improve habitat connectivity by providing important resources to dispersing or stressed individuals, and may facilitate home range establishment as well.
- In general, when identifying optimal placement for dispersal corridors target the shortest distance between two riparian areas currently inhabited by localized box turtle populations unless juxtaposition of paved roads prohibits.

- Create new nesting habitat patches within 0.5 km of other nesting habitat patches whenever possible.

Prescriptions for creating nesting habitat:

- See Table 1 and Figures 2, 3 for desired condition of box turtle nesting habitat.
- Restrict off-road vehicle access if possible.
- Because water sources may be important resources during periods of drought or heat stress, place the waterholes just inside the forest edge rather than a location in receiving full sun.

Potential concerns and mitigations during implementation:

- Because most box turtles are unlikely to be more than 1.5 km from a water source, even during nesting season, it is unlikely turtles will be present when converting forested stands to open canopy nesting habitat. Management concerns regarding box turtles will not likely be a necessary consideration when initially creating these patches.
- When the sites are eventually discovered and used by gravid females, avoid intensive management of occupied nesting habitat from 25 May to 25 June.
- If the site begins to receive use from gravid females, see Management Implications in Chapter III for additional information regarding neonate occupancy of nesting habitat.

Monitoring:

- A low level of post treatment monitoring will be necessary to evaluate vegetation response and is recommended to assess presence/absence of gravid females.
- Optimum survey period to assess presence/absence of gravid females is early June during warm, humid days or immediately after a precipitation event.
- Radio-telemetry monitoring of nearby adult females would also yield valuable information regarding individual response to newly created nesting habitat and artificial water sources.
- When visiting or surveying these sites, opportunistic carapace marking is recommended to evaluate long-term survival, site fidelity, and dispersal.

FIGURE LEGENDS

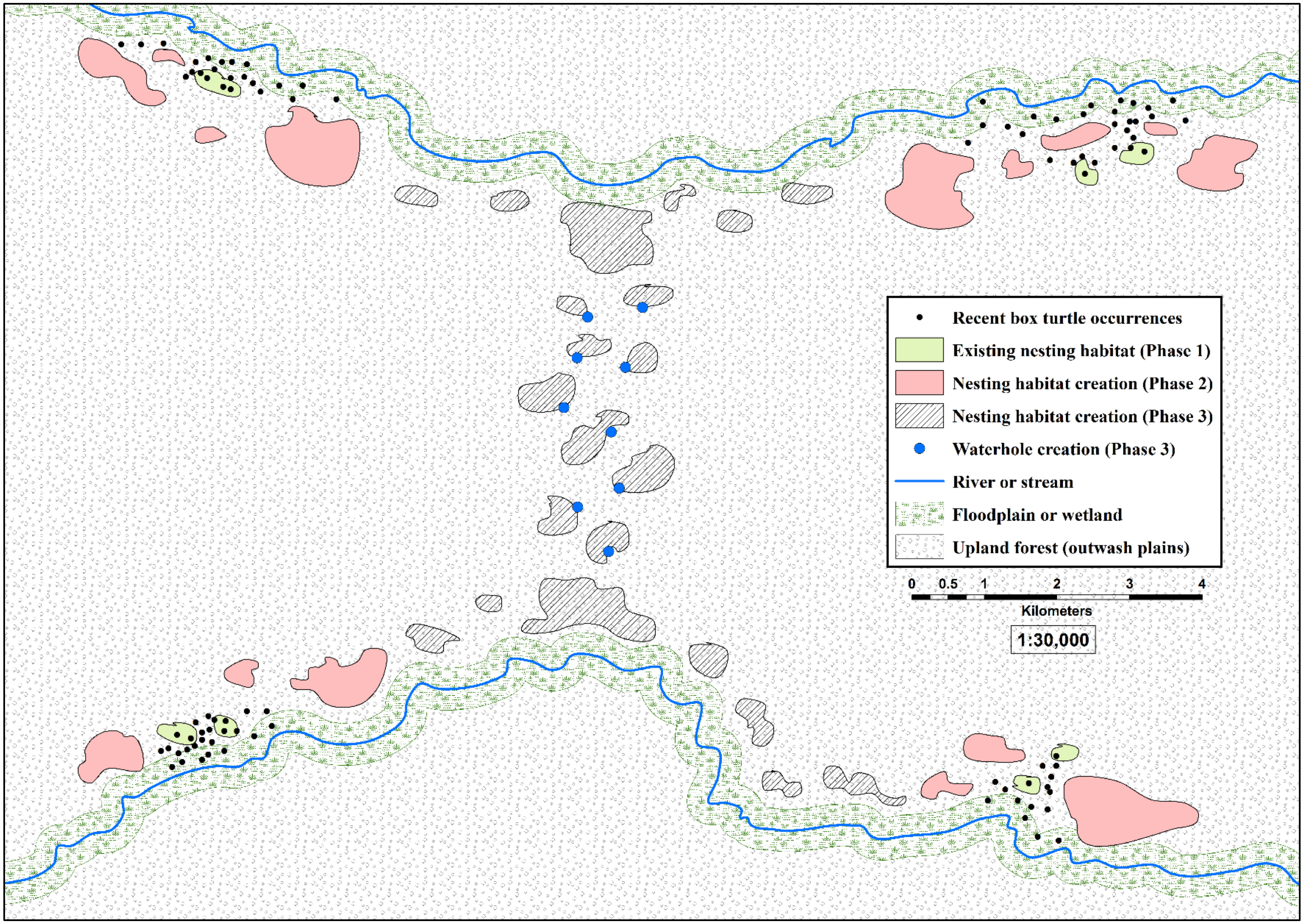
Figure 1. Illustration depicting 3-phase conservation approach for eastern box turtles in forested landscapes. Phase 1 involves maintaining and improving habitat patches currently being used by localized populations for nesting and thermoregulation. Phase 2 involves converting forested stands to patches of suitable nesting habitat near (optimum distance < 0.5 km between patches, maximum 1.5 km) existing patches of nesting habitat. Phase 3 is designed to promote gene flow and connectivity of habitat between localized populations. This phase involves designing a “corridor” through extensive upland forest by creating new nesting habitat patches and man-made water sources. This figure depicts simulated box turtle occurrences in a fictional landscape but is drawn to scale based my observations and analyses of box turtle movement patterns, home range size, relative habitat preferences, and riparian associations.

Figure 2. Upland opening (“Turtle Bowl”, see Chapter III) used by many box turtles for nesting purposes in the Manistee National Forest, 2012-2016. Turtle Bowl was 1.9 ha and had many plant species indicative of dry-sand prairie community. Mean distance from nest to forest edge was 9.0 m (*n* = 27 nests) and 41.4% of radio-fitted neonates overwintered within the opening after emerging from nests in late summer and fall.

Figure 3. Upland opening (“Savanna”, see Chapter III) used by many box turtles for nesting purposes in the Manistee National Forest, 2012-2016. Savanna was structurally complex 5.6 ha opening. Mean distance from nest to forest edge was 32.9 m (*n* = 13 nests) and 87.5% of radio-fitted neonates overwintering within the opening after emerging from nests in late summer and fall.

Table 1. Recommended ranges of structural composition within upland open canopy box turtle nesting habitat. Desired condition is based on vegetation sampling conducted within the four openings used by nesting females in the Manistee National Forest, 2012-2016. Within nesting habitat, box turtles will often nest at locations with very low overstory canopy cover and very little ground vegetation.

Structural Component	**Desired Condition**
Basal area (ft^2/acre)	0-30
Overstory canopy cover (%)	0-30
Graminoids, forbs, lichens, bare soil (% ground cover)	75-100
Woody plants and shrubs (% ground cover)	<25



Recent box turtle occurrences
Existing nesting habitat (Phase 1)
Nesting habitat creation (Phase 2)
Nesting habitat creation (Phase 3)
Waterhole creation (Phase 3)
River or stream
Floodplain or wetland
Upland forest (outwash plains)
0
0.5
1
2
3
4
Kilometers
1:30,000

Figure 1.

Figure 2.

Figure 3.

CHAPTER V

Short field notes

DIET

“After watching box turtles eat and after reviewing their diets as summarized in the literature, I have concluded that they must not have any taste buds.” – Dodd 2001

During telemetry outings, I commonly observed adult box turtles feeding on terrestrial gastropod molluscs, *Vaccinium angustifolium* berries, and fungi fruiting bodies. On 24 May 2013, while conducting a survey for box turtles on a different watershed within the MNF (i.e., not my telemetry study area) I encountered an adult male swimming in an artificially created waterhole (USFS had excavated and lined this waterhole in 2003). The waterhole was round, approximately 5 by 5 m and was less than 0.5 m deep at the center. There were thousands of *Anaxyrus americanus americanus* tadpoles present and the male was actively pursuing them. I watched for a few minutes but did not see him succeed in his attempts at predation. In summer 2011, I observed a radio-fitted adult female scavenging a *Sciurus niger* carcass. By far the most bizarre feeding episode I witnessed took place on 26 June 2012. Ecologist David Dister and I observed a radio-fitted adult female attempting to consume a desiccated *Strix varia* pellet (Figure 1).

I never observed any neonates feeding or pursuing prey during their first activity season (nest emergence in summer or late fall to first overwintering). Based upon the morphometric information I collected and the relatively cool temperatures during this period, I strongly suspect that neonates in northern Michigan rarely, if ever, consume food items in the period after nest emergence and before overwintering.

Figure 1. Adult female eastern box turtle consuming desiccated owl pellet on 26 June, 2012, Manistee National Forest, Michigan.

COURTSHIP AND COPULATION

I observed courtship and mating events regularly during fieldwork and documented these behaviors in every month during the activity period (overwintering egress to overwintering ingress). During courtship, males would chase the female while erratically nipping at the marginal scutes generating audible and unusual clicking noises. After mounting the female, males usually tipped backwards onto their carapace and were sometimes dragged several meters. Duration of courtship and copulation events was several hours.

FALSE NESTING BEHAVIOR

False nesting was a common behavior for most gravid females and frustrated the human observers. Females would often dig late into the night, actively excavating a hole only to abandon it for no obvious reason. After abandoning the false nest, they would not begin excavating a new hole the same night. Some would leave the openings for days before returning and engaging in any new nesting behaviors. Most radio-fitted females false nested multiple times before finally depositing eggs ultimately nested in the same opening but female ID 444 false nested in the Turtle Bowl opening on 2 June 2012 and subsequently deposited her eggs ~450 meters away in the Savanna opening on 8 June 2012.

DEMOGRAPHY

While afield, I opportunistically marked 193 individual eastern box turtles within the study area, 2011 to 2014. I also recorded the number of carapace annuli, if present. The mark-capture data during this period included 176 adults, 16 juveniles, 1 neonate. The youngest adult turtle was a male with 13 annuli, I observed him engaged in copulation with several females. I also captured a juvenile female with 12 annuli (Figure 2) which I would classify as a juvenile based on its appearance and size.

Figure 2. Juvenile female eastern box turtle (top) with 12 carapace annuli. Placed next to adult for size reference. Manistee National Forest, Michigan, 28 April 2013.

CHAPTER VI

EXTENDED REVIEW OF LITERATURE

Species description and geographic range

Eastern box turtles, *Terrapene carolina carolina*, are small terrestrial turtles of the family Emydidae. Adult *Terrapene carolina carolina* (hereafter *T. c. carolina*) possess a fully functional plastral hinge which facilities complete withdrawal of appendages and thus adult age classes have few predators (Dodd 2001). They are slow to reach maturity and extremely long-lived (Williams and Parker 1987, Dodd 2001). Geographic distribution encompasses much of the eastern united states, ranging from Georgia in the south to Michigan and Southern Maine as a northern extremes (Dodd 2001). In Michigan, *T. c. carolina* occurs only in Lower Peninsula extending north to Grand Traverse County (Dodd 2001).

Habitat

T. c. carolina prefers humid micro-climates and thermoregulates by basking and seeking cover in leaf litter and other refugia (Stickel 1950, Rossell et al. 2006, Fredericksen 2014). Because of their thermoregulatory obligations and wide geographic distribution, *T. c. carolina* have been documented in a wide range of macrohabitats including upland forest, floodplain forest, early successional, and wetlands (Stickel 1950, Madden 1975, Dodd 2001). For much of the year, *T. c. carolina* inhabits forests but seasonal habitat shifts are common and *T. c. carolina* often uses ecotones and canopy gaps for basking, feeding, and thermoregulation in spring (Stickel 1950, Madden 1975, Dodd 2001, Fredericksen 2014). Nesting usually occurs in June but may occur in May or July as well and many females travel considerable distances (over 1.0 km in some instances) to locate suitable upland open canopy nest sites (Stickel 1950, Kipp 2003, Willey and Sievert 2012, Fredericksen 2014). In temperature regions, *T. c. carolina* burrows into soil substrates to overwinter (reviewed in Dodd 2001).

Nesting Ecology and Nest Emergence

T. c. carolina nests in relatively open canopy sites and usually select micro-sites with little overstory canopy cover and low densities of ground layer vegetation (Willey and Sievert 2012, Flitz and Mullin 2006, Kipp 2003). In Massachusetts, Willey and Sievert (2012) observed nesting in "abandoned gravel pits, right-of-way's, backyards, old fields, and forest clearings." They detected 34 nests and reported nesting was concentrated in June but dates ranged from 27 May to 10 July. They protected nests in 2005 and 2006 and reported nest emergence (55% success rate) occurred from 20 August to 9 October. In New York, Burke and Capitano (2011A) detected 11 nests in mid-June, 2001 and 2002. Three of these nests were in open fields and 8 nests were deposited along dirt roads. They reported neonates emerged from nests from 22 August to 22 September (Burke and Capitano 2011B). Also in New York, Madden 1975, documented 14 nests and reported 23 June was the mean date of nesting (range 11 June to 4 July). In Virginia, Kipp (2003) documented 39 nests, primarily in open fields, between 27 May to 11 July, 2001-2002. She reported that the 11 successful nests hatched between 2 September and 23 September.

Recommendations for creating eastern box turtle nesting habitat

Willey and Sievert (2012), recommended "canopy openings should be at least 1200 m^2 and probably larger to attract nesting box turtles".

EXTENDED METHODOLOGY

Trimble Accuracy (Chapter III)

Accuracy reports from differentially corrected post-processed Trimble data indicated that ~ 50% of positions (50-150 positions collected during each telemetry observation) were accurate to within 0.0 to 0.5 meters and ~75% of positions were within 0.0 to 1.0 meters. Because positions were averaged together during differential correction process, the resulting location for each telemetry observation was highly accurate (sub-meter).

Habitat Sampling (Chapter III)

I generated 30 (> 2.5 m from the forest edge) non-overlapping random points in GIS for Savanna, Turtle Bowl, Gravel Pit, East West openings and 30 random points in the forest surrounding each opening (> 2.5 m from the opening edge). I conducted plot sampling at each randomly generated location from 20 September to 25 September, 2016 to document habitat conditions during the seasonal time frame when neonate turtles were present at the sites. I estimated overstory canopy cover using a spherical densiometer and basal area using a 10-factor prism. I used a 1.0 m^2 pvc frame to estimate percent cover of bare soil, lichen and bryophytes, leaf litter, graminoids, forbs, woody plants, and down woody debris. I recorded cover class estimates as 0%, 1-10%, 11-20%, 21-30%, 31-40%, 41-50%, 51-60%, 61-70%, 71-80%, 81-90%, or 91-100%.

Nest Detection (Chapter III)

I surveyed the each of four openings for gravid females between 1000 and 1500 hours and fitted them with transmitters. The onset of nesting activity occurs under waning daylight hours (Kipp 2003, Wilson and Ernst 2005, Willey 2010) and I conducted nesting surveys under this assumption arriving to the openings between 1900-2100 hours during late May and June from 2012 to 2016. When I observed a female nesting, I briefly assessed her progress (e.g. digging, depositing, or concealing) from ~10 m away. To avoid disturbing nesting turtles, I rarely spent more than a few minutes monitoring nesting behavior during daylight hours and quickly evacuated the immediate vicinity after marking the location with a thin, non-descript 20 cm piece of stiff wire wrapped in reflective tape. I monitored each female's progress intermittently after dark by locating the reflective wire with a red spectrum headlamp. When a female covered her eggs (often between 0100 and 0400 hours), I placed a wooden framed mesh exclosure over the nest and temporarily secured it using tent stakes, rocks, and/or woody debris. I returned to each nest after sunrise the following morning to install the robust predator exclosure by seating them into 20 cm into the mineral soil.

Nest exclosure design (Chapter III)

I constructed four wooden framed nest exclosures in the 2012 field season and in 2103 the design was greatly improved by Janice and Tim Sapak who custom built 20 exclosures for this project and provided the instructions outlined below. Despite many documented attempts, no potential predators were ever able to purge the exclosures and destroy our hard-earned nests. The dimensions of the exclosures were 61.0 cm x 61.0 cm x 30.5 cm (Figures 1, 2). Figure 2 contains a complete materials list and cutting diagram. We used ordinary 2" x 4" (3.8 cm x 8.9 cm) and 1" x 4" (1.9 cm x 8.9 cm) dimensional lumber. We used ½" (1.3 cm) mesh screen hardware cloth. We ripped the 2" x 4"s and 1" x 4"s lengthwise on a table saw. We painted lumber prior to cutting and assembly which saved considerable time. We constructed the lid by cutting a rabbet in each end of all four frame pieces and joining the corners with a half-lap joint for extra strength. We then stapled a 61.0

cm x 61.0 cm piece of hardware cloth to the underside of the lid using 1.3 cm staples. We constructed the box frame by attaching the top and bottom outer frame pieces to the four interior corner posts, piloting screw holes first and then using 3.8 cm drywall screws. We sandwiched the hardware cloth between the corner posts and the outer frame on each side as the enclosure was assembled. In the field, we secured the lid to the frame using cable ties. Materials for the enclosure, including all fasteners and paint cost approximately $30.00 US per unit. When we purchased material for 4 or more exclosures cost was reduced to approximately $20.00 US per unit.

SUPPLEMENTAL FIGURES

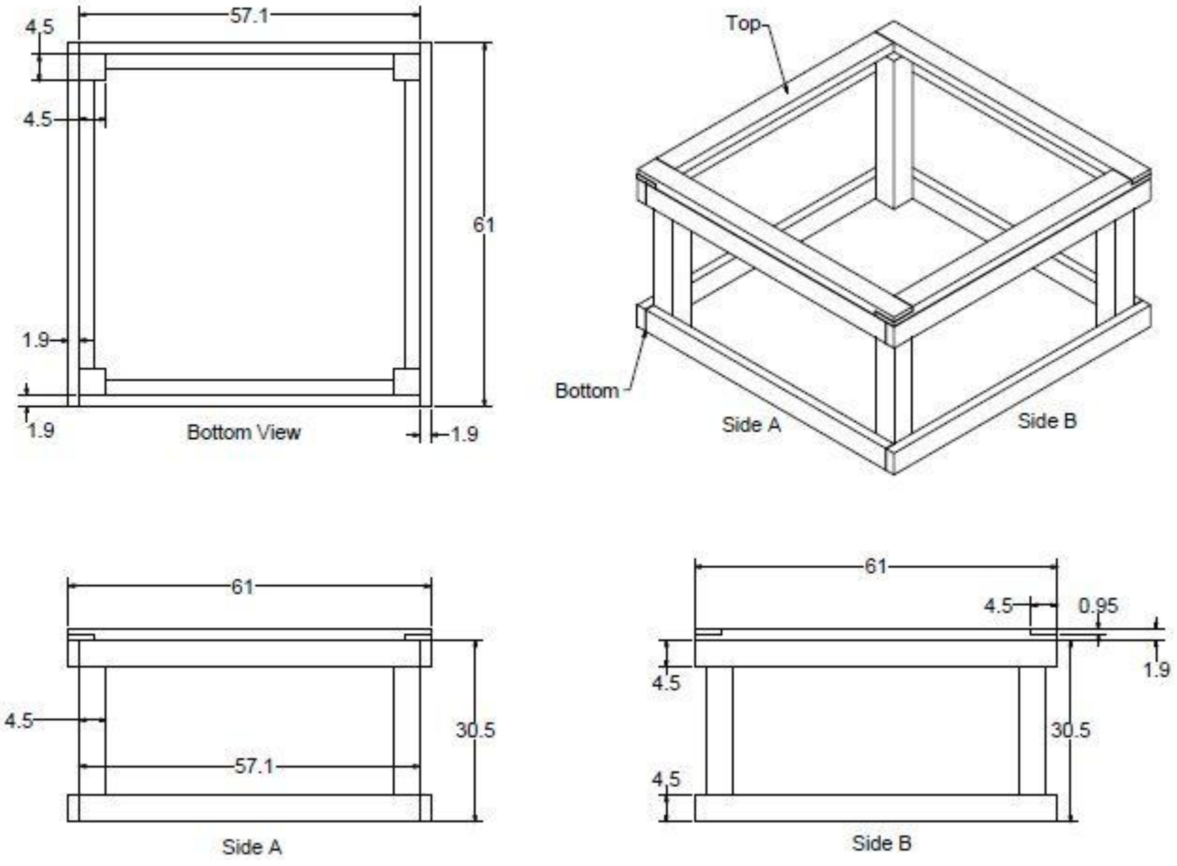


Figure 1. Schematic design of the predator exclosure device used to protect eastern box turtle nests in the Manistee National Forest, 2012 to 2016. Units are in cm. Diagram provided curtesy of Janice Sapak and Alan Finder. Materials cost approximately 20$/unit when four or more units were built at the same time.

Figure 2. Predator exclosures used to protect 64 eastern box turtle nests (top image) and 46 overwintering neonates (bottom image) in the Manistee National Forest, 2012-2016. We seated the exclosures approximately 20 cm into the mineral soil. Many unsuccessful predation attempts were documented (top image, bottom left corner) but we lost no nests due to predation.

Materials, Supplies, & Cutting Diagram

Letter ID	Description	Quantity	Size (inches)
A	Corner Posts	4	1.75 x 1.75 x 12
B	Lid Frame	4	.75 x 1.75 x 24
C	Exclosure Side Frames	4	.75 x 1.75 x 24
D	Exclosure Front/Back	4	.75 x 1.75 x 22.5
E	1/2" Hardware Cloth	1	24 x 24
F	1/2" Hardware Cloth	2	12 x 48
G	1 1/2" Drywall Screws	16	
H	5/8" Brads	16	
I	1/2" Staples		

0.75" x 3.5" x 96" Pine/Spruce Lumber

A	A
A	A

0.75" x 3.5" x 96" Pine/Spruce Lumber

B	B	C	D
B	B	C	D

0.75" x 3.5" x 48" Pine/Spruce Lumber

C	D
C	D

24" x 72" Hardware Cloth (1/2" Mesh)

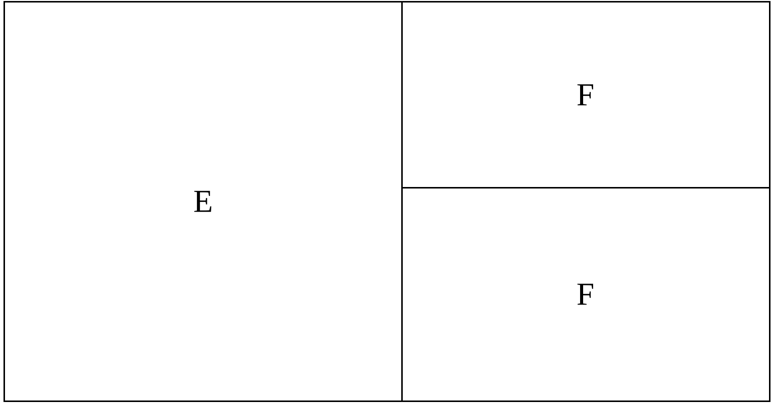


Figure 3. Materials list and cutting diagram used by Jan Sapak to construct exclosures.

Figure 4. A neonate eastern box turtle disperses from its nest in the Turtle Bowl opening, Manistee National Forest, 26 August 2012.

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