

**MICROHABITAT USE BY BLANDING'S TURTLES (*EMYDOIDEA
BLANDINGII*) AND WOOD TURTLES (*GLYPTEMYS INSCULPTA*) IN A
SHARED LANDSCAPE**

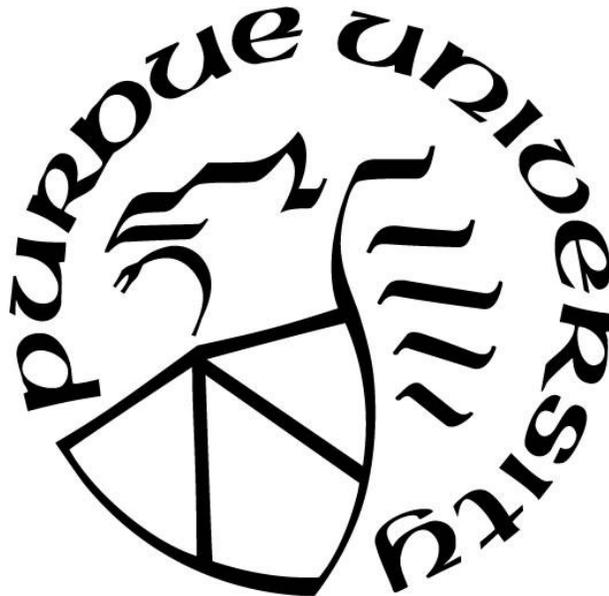
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*Dedicated to my moms
who supported my passion for the scaly since my first “dinosaur phase”
and without whom I would never have made it this far.*

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TABLE OF CONTENTS

LIST OF TABLES	7
LIST OF FIGURE.....	8
LIST OF ABBREVIATIONS.....	9
ABSTRACT.....	10
CHAPTER 1. INTRODUCTION	11
1.1 Habitat Selection and Conservation	11
1.2 Levels of Habitat Selection	12
1.3 Habitat selection in Blanding’s Turtles and Wood Turtles	12
1.4 Project Objectives.....	14
CHAPTER 2. METHODS.....	15
2.1 Field Site.....	15
2.2 Radio Telemetry and Data Collection	15
2.3 Preliminary Data Exploration: Principal Components Analysis	17
2.4 Microhabitat Selection Modeling: Conditional Logistic Regression Fitted with Generalized Estimating Equations	18
2.5 Comparison Between Species: Mann-Whitney U Test and Mood’s Median Test.....	19
CHAPTER 3. RESULTS	21
3.1 Principal Components Analysis	21
3.2 Microhabitat Selection Modeling.....	23
3.3 Interspecific Comparisons	29
CHAPTER 4. DISCUSSION AND CONCLUSIONS	30
APPENDIX. CLR MODEL DETAILS	33
REFERENCES	41

LIST OF TABLES

Table 1. PCA loadings for all principal components with eigenvalues >1	23
Table 2. Model definitions for microhabitat selection in Blanding's Turtles (N=22)	24
Table 3. Model definitions for microhabitat selection in Wood Turtles (N=14)	25
Table 4. Results of conditional logistic regression models fit with generalized estimating equations when analyzing the full dataset (including paired points with different macrohabitat).	26
Table 5. Model averaged coefficients and combined model weights (w_i) for important parameters	27
Table 6. Results of conditional logistic regression models fit with generalized estimating equations when analyzing the limited dataset (excluding paired points with different macrohabitat).	28
Table 7. Model averaged coefficients and combined model weights (w_i) for important parameters when paired points were located within the same macrohabitat.....	28

LIST OF FIGURE

Figure 1. Plot of mean PC1 and PC2 scores per individual per season	22
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LIST OF ABBREVIATIONS

WDEPTH: Depth of water at the center of a 1m² quadrat (cm).

WDIST: Distance to water (m).

TREE: Number of trees within a 10m circular quadrat around the sampling point.

BWD: Number of woody stems ≥ 2 cm within 1m² quadrat.

SWC: Percent of 1m² plot covered with shrubs < 2 cm at the base, visually estimated from above and assigned to ordinal categories (low cover = 0 - 33%, medium cover = 34 - 66%, high cover = 67 - 100%).

HC: Percent of 1m² plot covered with herbaceous vegetation, visually estimated from above and assigned to ordinal categories (low cover = 0 - 33%, medium cover = 34 - 66%, high cover = 67 - 100%).

OC: Overstory canopy cover > 1 m directly above sampling point, visually estimated into one of three ordinal categories (low cover = 0 - 33%, medium cover = 34 - 66%, high cover = 67 - 100%).

TL: Cover at turtle level, < 1 m directly above sampling point (low cover = 0 - 33%, medium cover = 34 - 66%, high cover = 67 - 100%).

SE: Season (pre-nesting, nesting, or post-nesting)

ABSTRACT

Understanding and adequately protecting habitat is at the forefront of modern conservation concerns. Turtles are especially vulnerable to habitat loss, and are therefore a top priority for habitat research. To help meet this need, I used radio telemetry to collect microhabitat data from two imperiled species of turtles that occupy a military base in Michigan. Preliminary data exploration was carried out with principal components analysis (PCA). Microhabitat use was then modeled for each species using conditional logistic regression (CLR), with a generalized estimating equation (GEE) element to limit bias due to individual variation. Finally, I compared habitat use between sympatric Blanding's and Wood Turtles using Mann-Whitney U tests and Mood's median tests to investigate the degree of overlap in microhabitat use when these species occur in sympatry. Evidence for microhabitat selection in Blanding's Turtles was weak, suggesting that they likely do not make habitat decisions at this level. Wood Turtles selected sites that were farther from water and had fewer trees, less overstory canopy cover, and more ground cover. Additionally, the two species differed in several aspects of microhabitat use; Wood Turtles were more terrestrial and more tolerant of tree cover than Blanding's Turtles. Patterns of microhabitat use found in this study match previously observed behavior of turtles in high quality habitat, suggesting that managers should work to maintain the habitat currently available at Camp Grayling. Additionally, because both turtle species were associated with open canopy, selective logging could benefit turtles provided care is given to timing and methods.

CHAPTER 1. INTRODUCTION

1.1 Habitat Selection and Conservation

Habitat is one of the most important aspects of ecological niche for conservationists to understand. In the United States, habitat loss is among the leading threats to imperiled species (Wilcove et al. 1998). Even when land is set aside for wildlife use, encroachment by invasive species or changes to historic patterns of disturbance in an area can destroy movement corridors and critical habitat for resident wildlife (Browne & Hecnar 2007; Markle et al. 2018). Thus, it is necessary not only to set aside land for species of conservation interest, but also to ensure that the available land actually meets the needs of those species.

Habitat selection studies inform conservation efforts by identifying key features that make habitat suitable for a target species, which can then be used to identify suitable habitat in need of protection or to guide restoration of degraded habitat (Alldredge & Griswold 2006). Understanding the process by which species of concern select habitat is equally important, as it gives managers some ability to predict responses to environmental change. With this knowledge, managers can shape conservation efforts to maximize benefits to the target species and take measures to mitigate the impacts of anthropogenic change when necessary. Furthermore, comparing ecological niche elements between syntopic species provides a more holistic context for understanding how each interacts with the greater ecosystem. In doing so, it can highlight interactions, similarities, or distinctions between species that may be relevant to conservation efforts (Herczeg et al. 2007).

The importance of well-informed conservation is heightened when the species in question is in peril. This is the case for many freshwater turtles, whose habitat requirements and life history make them especially vulnerable (Turtle Conservation Fund 2002). A wealth of research has implicated road mortality, subsidized predators, poaching, and habitat loss in the reduction or extirpation of many turtle populations, including those in protected areas (Beaudry et al. 2008; Browne & Hecnar 2007; Markle et al. 2018; Spencer et al. 2017).

To contribute to our understanding of the ecology and conservation of this vulnerable taxon, I explored microhabitat selection in syntopic populations of Blanding's Turtles (*Emydoidea blandingii*) and Wood Turtles (*Glyptemys insculpta*) at a site in central Michigan. Both of these species mature slowly and rely on high survivorship of adults for sufficient recruitment (Congdon

et al. 1993, Schneider 2018). Consequently, they have been among the hardest-hit species in North America, making them a top conservation priority (COSEWIC 2005, 2007). Blanding's Turtles in particular have also been championed as umbrella species because of their need for a variety of connected wetlands and uplands, including ephemeral wetlands, which encompasses the conservation needs of many other wetland species (Congdon et al. 2011). In many habitats, if turtles are adequately safeguarded, the protection of many other species should follow.

1.2 Levels of Habitat Selection

Johnson's (1980) four levels of selection have guided studies of resource selection for decades, and continue to be used in habitat research across a variety of taxa (Bauder et al. 2018; Bergeson et al. 2018; Paterson et al. 2012b). Johnson (1980) defines first-order selection as the species range, second-order selection as the distribution of home ranges within species range, third-order selection as the use of microhabitat within home range, and fourth-order selection as the consumption of food resources within selected microhabitats. Of these, second- and third-order selection are typically most relevant to habitat selection studies for managed populations.

Although there is substantial evidence for hierarchical habitat selection in many species, others appear to focus their selective decisions at certain levels. For example, Harvey and Weatherhead (2006) found evidence that eastern massasauga rattlesnakes select microhabitat (third-order selection) but not macrohabitat (second-order selection). Tew et al. (2000) had similar results with wood mice (*Apodemus sylvaticus*), finding that they were associated with certain weed species but showed no direct preference for crop type at the landscape level. Thus, it is important to consider habitat selection at multiple scales. This thesis will focus on third-order habitat selection in two species of freshwater turtle as part of a larger multi-scale habitat selection study, in order to provide a complete picture of how and why these turtles select habitat.

1.3 Habitat selection in Blanding's Turtles and Wood Turtles

The strength of third-order selection in Blanding's Turtles is somewhat unclear. Edge et al. (2010) observed second-order selection but not third-order selection in a population at Algonquin Park of Ontario, Canada. They propose that large, high quality habitats like Algonquin Park may eliminate the need for microhabitat selection by providing a surplus of suitable habitat. Similarly,

Anthony et al. (2014) found that Blanding's Turtles were microhabitat generalists at a preserve in Illinois. However, Hartwig & Kiviat (2007) observed a preference for shallow water, high vegetation cover, and muck substrate by Blanding's Turtles in Dutchess County, New York, as well as a distinct seasonal pattern in which the turtles moved from warmer constructed wetlands in the first part of the season to deeper, cooler natural wetlands later in the season. This represents a shift in both micro- and macrohabitat. Millar & Blouin-Demers (2011) also noted preference for high vegetation cover in turtles from Ontario, Canada, as well as preference for colder water and avoidance of open water, although their microhabitat data were not separated by season. Unfortunately, microhabitat studies are rarely consistent in which variables are measured and in whether data are divided among seasons. This may contribute to the abundance of contradictory conclusions.

Evidence for third-order habitat selection in Wood Turtles is stronger and more consistent. Arvisais et al. (2004) found that Wood Turtles in Quebec, Canada prefer low overstory canopy cover, moderate shrub cover, and young trees. Compton et al. (2002) also observed selection for low canopy cover among Wood Turtles in Maine, as well as selection for close proximity to water. Females are more likely to venture farther from water than males (Curtis & Vila 2015), possibly as a result of nesting activity.

Habitat use in Wood and Blanding's Turtles is dynamic over time, as turtles seek to satisfy different needs at different times of the year. Blanding's Turtles spend more time basking and foraging early in the active season, from spring until early summer, but often seek refuge in deeper water as temperatures increase later in the summer (Beaudry et al. 2009; Hartwig & Kiviat 2007). Similarly, Wood Turtles primarily bask in the spring, followed by nesting forays for females and upland foraging excursions for both sexes in the summer (Greaves 2007; Quinn & Tate 1991).

Blanding's Turtles and Wood Turtles are syntopic in and around Camp Grayling, a military training base in the northern lower peninsula of Michigan that features large areas of relatively undisturbed wildlife habitat. These species are specifically known to co-occur in several creeks and rivers in that area, and have reasonable access to all of the same landscape features. This presents an opportunity to directly compare habitat use between these species without the need to account for spatial or temporal differences in resource availability. Little is known about how syntopic Blanding's and Wood Turtles interact. One study examined habitat use in hatchlings (Paterson et al. 2012), but there is no previous research on how adult Blanding's and Wood Turtles

may or may not partition resources when occupying the same landscape. Comparing habitat selection between these two imperiled turtles will contribute not only to the broader knowledge of ecology, but also to conservation efforts for both populations on Camp Grayling. Understanding similarities and differences in the habitat needs of both species will allow managers to ensure that both species have the entirety of their habitat needs met.

1.4 Project Objectives

The objectives of this thesis are (1) to model microhabitat selection in Blanding's Turtles and Wood Turtles at Camp Grayling and (2) to compare microhabitat selection between these species where they occur in sympatry. If Blanding's Turtles select microhabitat at Camp Grayling, I would expect them to select shallow water and high ground cover. However, if turtle habitat at Camp Grayling is sufficiently high quality, I would expect to see little to no microhabitat selection in Blanding's Turtles (Anthonysamy et al. 2014; Edge et al. 2010). For Wood Turtles, I expect to find selection for low canopy cover, moderate ground cover, and close proximity to water (Arvisais et al. 2004; Compton et al. 2002; Curtis & Vila 2015). I further expect that Wood Turtles and Blanding's Turtles will show differences in microhabitat selection, which would prevent resource conflict in these sympatric populations.

CHAPTER 2. METHODS

2.1 Field Site

Camp Grayling Joint Maneuver Training Center is a National Guard training facility located in the northern lower peninsula of Michigan. Spanning 147,000 acres across three counties, it is the largest National Guard training center in the United States (Michigan National Guard 2020). Much of this land consists of relatively undisturbed natural habitat, which functions primarily as buffer areas around artillery ranges and lightly used training areas. A variety of wetlands are present in these areas, including rivers, streams, lakes, bogs, and scrub-shrub, and support a variety of wildlife.

I chose two specific sites for radio telemetry based on accessibility and initial surveys for target species. The sites are approximately 25 km apart and connected by a system of lakes, rivers, and other wetlands. To protect the exact location of these rare and often exploited turtles, a map has not been included. The first site, hereafter referred to as the “South” site, was centered on a creek bordered by speckled alder (*Alnus incana*) stands and mixed forests. Movements of tracked turtles expanded this site to include a portion of a connected river, several *Salix*-dominated scrub-shrub wetlands, and a large pond, as well as nearby upland forests and speckled alder stands. The South site supports both Wood Turtles and Blanding’s Turtles, which each utilize the creek and the river for at least part of the year. The second site, hereafter referred to as the “North” site, includes several bogs and marshy areas along the edge of a lake, a river that feeds into the lake, and vernal pools in the surrounding mixed and coniferous forests. The North site supports a population of Blanding’s Turtles, but no Wood Turtles have been observed here to date.

2.2 Radio Telemetry and Data Collection

Turtles were collected for radio-telemetry by hand during Visual Encounter Surveys (VES) in 2018. I continued to collect subjects with VES in 2019, and also used hoop net trapping to supplement the number of tracked turtles that year. Additionally, new individuals were added opportunistically during radio-telemetry of telemetered turtles. I collected a total of 38 individuals across both years (24 Blanding’s Turtles and 14 Wood Turtles) for radio telemetry. 15 Blanding’s Turtles and 11 Wood Turtles were collected in 2018, and 9 Blanding’s Turtles and 3 Wood Turtles

were added in 2019. Of these, 9 were male Blanding's Turtles, 13 were female Blanding's Turtles, 6 were male Wood Turtles, and 8 were female Wood Turtles.

For all telemetered turtles, I attached temperature-sensitive transmitters (model RI-2BT, Holohil Systems Ltd.) to a single scute on the carapace with Devcon 5-Minute Epoxy, following methods used by Boarman, Goodlett, Goodlett, and Hamilton (1998) on immature desert tortoises. The collective weight of transmitter and epoxy was less than 5% of the turtle's total body weight. Transmitter attachment was performed in the field, and turtles were released immediately at the point of capture once the epoxy was sufficiently hardened (after about 10 minutes). I also measured shell dimensions to 0.01mm with calipers, weighed turtles to the nearest 5g with an electronic hanging scale, estimated age from annuli, sexed turtles with shell concavity and tail morphology, and determined whether female turtles were gravid with finger palpation. All turtles were marked with a unique notch code following Cagle (1939).

Turtles were subsequently relocated three times per week with a three-element Yagi antenna (Advanced Telemetry Systems, Isanti, MN) and R-1000 receiver (Communications Specialists, Orange, CA). At each relocation, I recorded the time, transmitter pulse rate (related to the temperature of the transmitter), air and water temperature, weather conditions, precipitation in the past 48 hours, exposure to sunlight (full, partial, or none), behavior, macrohabitat, and turtle aspect. UTM coordinates for all turtle locations were recorded with Garmin eTrex 10 GPS units to an average accuracy of three meters.

Once per week, I recorded additional data on each turtle's microhabitat. I collected a suite of variables describing water and vegetation structure within a 10m circular quadrat and a 1m² quadrat centered on the turtle's location. This point was defined as the "used" point. The same data were taken at a paired "available" point 15-50m in a random compass direction from the turtle. This point represented habitat that was available to the turtle but not selected, and was used in subsequent statistical analyses as a spatiotemporally similar point of comparison for turtle-selected microhabitat points (Compton et al. 2002). Distances and directions for available points were determined with a random number generator prior to field data collection.

Within the 10m circular quadrats, I counted the number of trees >10.16 cm diameter at breast height (DBH) by genus, and I used meter tape to measure distance to the nearest water body in meters. Distances >10m were later calculated using the Near command in ArcMap 10.7 (2019). For points in water, I measured water depth at the center of the plot with a meter stick. To

characterize vegetation structure within 1m², I recorded density of woody stems >2cm diameter at base, percent woody cover <2cm diameter at base, and percent herb cover. Percent cover values were estimated visually. All shrubs and other small woody vegetation were identified to species when possible, but due to difficulty distinguishing shrubs in the genus *Salix*, these were recorded only at the genus level. Herbaceous vegetation was categorized into functional groups. Overstory canopy cover and cover at turtle level, the latter of which I defined as the percentage of cover within 1m above the turtle's location, were also estimated visually. Visual estimates of percent cover were later combined into three categories (low = 0 - 33%, medium = 34 - 66%, high = 67 - 100%) to account for inconsistency in estimates between observers.

My protocol for collecting data did not specify that available points had to be in the same macrohabitat as the paired used point. Many recent studies on microhabitat selection place available points exclusively in the same macrohabitat to ensure that only microhabitat use is measured (i.e. Paterson et al. 2012b), but this ignores the possibility that turtles select microhabitat features without regard to macrohabitat. To address this, I later separated my data into two datasets: a full dataset that included all points, and a limited dataset that included only data points where used and available points were in the same macrohabitat. Analyzing both datasets enabled me to investigate whether microhabitat selection was independent of macrohabitat selection, or if turtles merely selected microhabitat features that were common to a certain macrohabitat. In this way, I could clearly distinguish between second- and third-order selection.

2.3 Preliminary Data Exploration: Principal Components Analysis

Principal component analysis (PCA) was used for preliminary exploration of microhabitat data. This type of analysis is useful for datasets that contain a large number of habitat variables, because it circumvents any potential collinearity and simplifies complex multivariate relationships into a few easily visualized principal components (Anthonysamy et al. 2014; Herczeg et al. 2007). I used PCA to visualize and form hypotheses about microhabitat selection in my turtles. To prevent bias from data-rich individuals, I used destructive sampling to ensure an equal number of observations per individual per season. Because traditional PCAs are only suitable for continuous data (Vaughan & Ormerod 2005) and the purpose of this analysis was merely data exploration, I used percentages rather than ordinal categories for visually estimated cover variables. Ordinal categories were used in all subsequent analyses for these data.

2.4 Microhabitat Selection Modeling: Conditional Logistic Regression Fitted with Generalized Estimating Equations

Conditional logistic regression (CLR) is a popular method for comparing used and available habitat in wildlife telemetry studies (Bauder et al. 2018; Bergeson et al. 2018; Boggie et al. 2018), and is used frequently in studies of freshwater turtles (Compton et al. 2002; Millar et al. 2011; Paterson et al. 2012b). This type of model uses a binary logit link function to relate a linear model of covariates with a dichotomous outcome variable. In most habitat selection studies, the outcome variable is presence (1) or absence (0) of the target animal at a given location, and covariates represent habitat features of interest at a given point. However, traditional CLR models carry an assumption of independent sampling of data points, which telemetry data rarely satisfy (Koper & Manseau 2009).

A solution to this problem exists in the form of generalized estimating equations (GEEs), which manage autocorrelation by separating points into clusters, typically by individual (Koper & Manseau 2009). These clusters are considered the unit of independent sampling. Unlike many other models used for telemetry data, GEEs can incorporate data with different numbers of observations per cluster, which reduces the need to throw out observations or individuals in the interest of equal sample sizes (Prima et al. 2017). On its own, however, a GEE does not account for the spatial and temporal link between pairs of used and available points, which is an important source of statistical power and biological relevance in many use vs. availability studies (Compton et al. 2002).

Fortunately, the best of both models can be combined into one test: a conditional logit model that preserves the association between paired points and accounts for correlation between points from the same individual in a process that approximates a GEE (Criau et al. 2008; Fletcher & Fortin 2018; Prima et al. 2017). Used and available points are considered strata with a unique identification code for each pair, and a clustering argument specifies individuals as statistically independent groups in the manner of a GEE (Criau et al. 2008; Prima et al. 2017). This approach allows researchers with telemetry data to take advantage of the structure of conditional logit models while circumventing their most problematic assumptions (Criau et al. 2008).

I performed these tests with the *survival* package (Therneau 2015) in Program R, following coding instructions by Fletcher & Fortin (2018). Spearman's rank correlations suggested limited collinearity among microhabitat variables, even in pairs with significant correlation ($\rho \leq 0.48$ for

all pairs), so no variables were excluded from models to meet this assumption. I prepared separate models for both sex and species, for a total of four groups (Curtis & Vila 2015, Tingley et al. 2010). Candidate models for each group (Table 2 and 3) were prepared *a priori* based on a literature search, field observations, and results of the preliminary PCA. To account for seasonal differences in behavior (Greaves 2007; Hartwig & Kiviat 2007; Quinn & Tate 1991), I included models with interactions between behavioral activity season and the habitat variables most likely to experience seasonal shifts in selection.

Activity seasons were defined by following methods used by Rasmussen & Litzgus (2010) with radio-tracked Spotted Turtles (*Clemmys guttata*) and by Paterson et al. (2012a) with Common Snapping Turtles (*Chelydra serpentina*). Pre-nesting season was defined as the period between first emergence and first detection of a gravid female of either species. Nesting season occurred between the first detection of a gravid female and the last observed nesting event. Post-nesting season was between the last nesting event and mid-August, when intensive tracking concluded for the year. I only collected microhabitat data for the post-nesting season in 2018, which was from 08 June 2018 to 08 August 2018. In 2019, the pre-nesting season was from 06 May 2019 to 25 May 2019, nesting season was from 26 May 2019 to 26 June 2019, and post-nesting season was from 27 June 2019 to 16 August 2019. Data points from the post-nesting seasons of both years were pooled on the assumption that shifts in microhabitat selection would be similar across years because seasons are defined based on turtle behavior.

For each model, I calculated Akaike's Information Criterion corrected for small sample sizes (AIC_c), ΔAIC_c ($AIC_{ci} - AIC_{cmin}$), and Akaike weight (w_i). I considered models with $\Delta AIC_c \geq 2$ highly probable, and placed all models with $w_i \geq 10\%$ of the top model's weight in a confidence set for model averaging (Burnham & Anderson 2002). Model selection and averaging were carried out in Program R using the package *MuMIn* (Barton 2019). Parameters were considered important predictors of habitat selection if they had a combined model weight ≥ 0.75 .

2.5 Comparison Between Species: Mann-Whitney U Test and Mood's Median Test

Finally, I compared microhabitat use directly between species to explore the question of whether Blanding's Turtles select different microhabitat than Wood Turtles. I used Mann-Whitney U tests to compare distance to water and number of trees (Hong et al. 2012), and Mood's median tests to compare herb cover, overstory canopy cover, and cover at turtle level. I excluded data

related to large and small shrubs based on PCA results. Because these comparisons necessitated the use of multiple tests, one for each microhabitat variable, I used a Benjamini-Hochberg p-value adjustment to avoid inflation of Type I error. All statistical procedures were performed in R, and Mood's median test was performed with the package *RVAideMemoire* (Hervé 2020).

CHAPTER 3. RESULTS

3.1 Principal Components Analysis

Principal component 1 (PC1) explained 25% of variance in the data (Table 1), and it was primarily along this axis that groups differentiated from one another. Variables loading high on this axis were number of trees, overstory canopy cover, water depth, distance to water, and cover at turtle level. Thus, larger positive values of PC1 were associated with open areas in or near water with abundant cover. When all seasons were pooled by species, both Blanding's and Wood Turtles appeared to use these areas disproportionate to their availability. This is evident in Figure 1, which shows displacement of used points toward the positive side of PC1 relative to paired random points for both species. However, overlap between used and random points also suggests that habitat selection on these variables may be weak, or that an abundance of the habitat available to these turtles is suitable, limiting their need to be selective about microhabitat variables.

PC2 primarily represents sub-tree woody vegetation structure, with positive values indicating more small woody vegetation such as lowbush blueberry and sweet gale, and negative values indicating more large woody vegetation, such as speckled alder and Salix shrubs. Broad dispersion of both species along this axis suggests that these variables have little impact on microhabitat selection; given the importance of cover at turtle level suggested by PC1, the availability of cover may be more biologically relevant for Blanding's and Wood Turtles than the type of vegetation providing it.

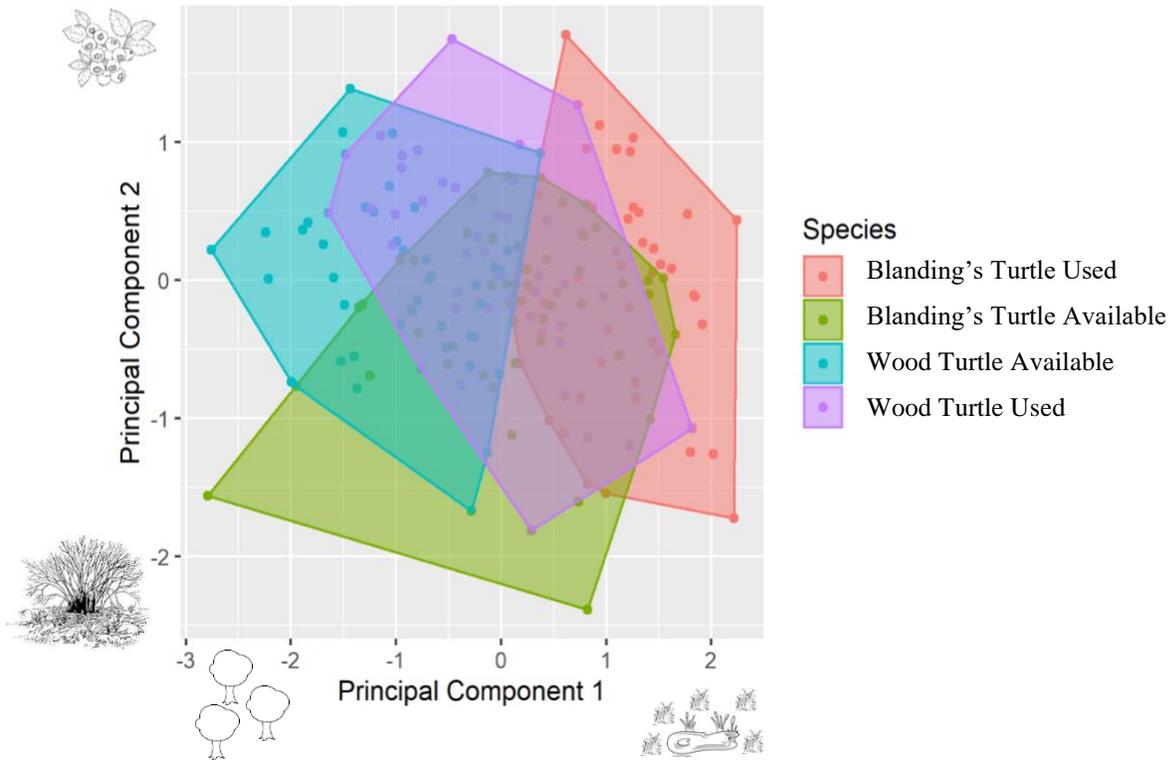


Figure 1. Plot of mean PC1 and PC2 scores per individual per season. The most important contributing variables for PC1 were number of trees, water depth, distance to water, and cover at turtle level, with higher positive values associated with fewer trees, more cover, closer proximity to water, and deeper water. The most important contributing variables for PC2 were number of large woody stems and small shrub cover, with higher positive values associated with abundance of small shrubs and more negative values associated with dominance by large shrubs.

Table 1. PCA loadings for all principal components with eigenvalues >1. PCA included habitat data for both species, both sexes, and paired random points.

	PC1	PC2	PC3	PC4
Proportion of variance explained	0.25	0.17	0.15	0.13
<i>Loadings</i>				
Water depth (cm)	0.461	-0.319	0.131	-0.321
Distance to nearest water body (m)	-0.389	0.367	0.172	-0.068
Number of trees >4" DBH within 10m	-0.538	-0.061	0.001	-0.159
Density of woody stems within 1m	0.013	-0.494	0.350	0.554
Woody cover <2cm base diameter within 1m (%)	0.004	0.522	0.580	0.159
Herbaceous cover within 1m (%)	0.058	0.251	-0.658	0.535
Overstory canopy cover (%)	-0.457	-0.364	0.100	0.316
Cover at turtle level (%)	0.367	0.218	0.228	0.386

3.2 Microhabitat Selection Modeling

I tested a total of 10 models for Blanding’s Turtles (Table 2), 4 of which used exclusively points in aquatic macrohabitats, and 11 models for Wood Turtles (Table 3). Of these, I retained 4 models for Blanding’s Turtles, 1 of which was for aquatic points, and 1 model for Wood Turtles in candidate sets (Table 4). Models based on high-loading variables from the preliminary PCA were consistently successful, while few models incorporating seasonal variation in behavior could be included in the candidate sets.

Model averaging identified several microhabitat variables that were important to selection for each group (Table 5). Blanding’s Turtles selected microhabitats closer to water and with fewer trees than paired random points. Blanding’s Turtles in aquatic environments selected deeper water and high cover. Wood Turtles avoided dense trees and high overstory canopy cover, and selected high cover at turtle level. When the dataset was limited to comparisons between points in the same macrohabitat, most of the same models were supported (Table 6). However, examining the coefficients revealed no evidence for microhabitat selection in Blanding’s Turtles, while Wood Turtles showed the same selection patterns as before (Table 7).

Table 2. Model definitions for microhabitat selection in Blanding's Turtles (N=22). References are listed for models drawn from previous research.

Model Name	Variables	References
<i>Full Dataset</i>		
Global	WDIST + TREE + BWD + SWC + HC + OC + TL	
Open wetland	WDIST (-) + TREE (-)	field obs.
PC1 variables	WDIST (+) + TREE (+) + OC (+) + TL (-)	preliminary analyses
Spring basking with overstory cover	OC (-) + SE + OC*SE	Hartwig & Kiviat (2007)
Open wetland with sex differences	WDIST + TREE + SEX	preliminary analyses
PC1 variables with sex differences	WDIST + TREE + OC + TL + SEX	preliminary analyses
<i>Aquatic Dataset</i>		
Global Aquatic	WDEPTH + TREE + BWD + SWC + HC + OC + TLC	
Late season shift to deeper water	WDEPTH + SE + WDEPTH*SE	Beaudry et al. (2009) Hartwig & Kiviat (2007)
PC1 variables	WDEPTH (-) + TREE (+) + OC (+) + TL (-)	preliminary analyses
Typical selection	WDEPTH (-) + TL (+)	Hartwig & Kiviat (2007) Millar & Blouin-Demers (2011)

Table 3. Model definitions for microhabitat selection in Wood Turtles (N=14). References are listed for models drawn from previous research.

Model Name	Variables	References
Association with forest edge	TREE (+) + OC (-)	Dubois et al. (2009)
Association with forests	TREE (+)	field obs.
Global	WDIST + TREE + BWD + SWC + HC + OC + TLC	
Late season optimal foraging habitat 1	HC (+) + SE + HC*SE	Greaves (2007) Quinn & Tate (1991)
Late season optimal foraging habitat 2	TREE (+) + SE + TREE*SE	Greaves (2007) Quinn & Tate (1991)
Late season upland foraging	WDIST (+) + SE + WDIST*SE	Greaves (2007) Quinn & Tate (1991)
PC1 variables	WDIST (-) + TREE (-) + OC (-) + TL (+)	preliminary analyses
Spring basking	OC (-) + SE + OC*SE	Greaves (2007) Quinn & Tate (1991)
Typical selection	WDIST (-) + OC (-) + SWC (med)	Arvisais et al. (2004) Compton et al. (2002) Dubois et al. (2009)
Distance to water with sex differences	WDIST (-) + SEX	preliminary analyses
Basking habitat with sex differences	OC (-) + SEX	Dubois et al. (2009)

Table 4. Results of conditional logistic regression models fit with generalized estimating equations when analyzing the full dataset (including paired points with different macrohabitat).

Model Name	<i>K</i>	$\Delta AICc$	<i>w_i</i>
<i>Blanding's Turtle Microhabitat Selection (N=22)</i>			
PC1 variables*	5	0.00	0.495
Global*	8	0.64	0.359
Open wetland	3	2.45	0.145
Distance to water with sex differences	4	26.35	0.000
Spring basking	4	66.16	0.000
<i>Aquatic Blanding's Turtles (N=21)</i>			
Typical selection*	3	0.00	0.547
Late season shift to deeper water*	4	0.99	0.333
PC1 variables	5	3.04	0.119
Global Aquatic	8	14.59	0.000
<i>Wood Turtle Microhabitat Selection (N=14)</i>			
PC1 variables*	5	0.00	0.896
Global	8	4.31	0.104
Late season optimal foraging habitat	4	28.39	0.000
Association with forest edge	3	18.96	0.000
Association with forests	2	27.53	0.000
Typical selection	4	28.81	0.000
Overstory canopy cover with sex differences	4	36.29	0.000
Spring basking	4	41.83	0.000

Table 5. Model averaged coefficients and combined model weights (w_i) for important parameters. Parameters were considered important if $w_i \geq 0.75$.

Parameter Name	Coefficient	Combined Model	
		Weights	p
<i>Blanding's Turtles</i>			
Number of trees >4" DBH within 10m	-0.17	0.854	0.013
Overstory canopy cover (medium)	-0.73	1.000	0.098
<i>Blanding's Turtle Aquatic</i>			
Water depth (cm)	0.04	1.000	0.009
<i>Wood Turtles</i>			
Number of trees >4" DBH within 10m	-0.06	0.896	0.006
Overstory canopy cover (medium)	-0.77	0.896	0.004
Overstory canopy cover (high)	-0.92	0.896	0.002
Cover at turtle level (medium)	0.55	0.896	0.067
Cover at turtle level (high)	1.18	0.896	< 0.001

Table 6. Results of conditional logistic regression models fit with generalized estimating equations when analyzing the limited dataset (excluding paired points with different macrohabitat).

Model Name	K	$\Delta AICc$	w_i
<i>Blanding's Turtle Microhabitat Selection (N=22)</i>			
Open wetland	2	0.00	0.740
Distance to water with sex differences	3	0.64	0.196
PC1 variables*	4	4.96	0.062
Global*	7	11.34	0.003
Spring basking	3	failed to converge	
<i>Wood Turtle Microhabitat Selection (N=14)</i>			
PC1 variables*	4	0.00	0.979
Global	7	8.49	0.014
Typical selection	3	11.20	0.004
Association with forest edge	2	12.06	0.002
Association with forests	1	13.85	0.001
Late season optimal foraging habitat	3	17.82	0.000
Overstory canopy cover with sex differences	3	19.35	0.000
Spring basking	3	20.45	0.000

Table 7. Model averaged coefficients and combined model weights (w_i) for important parameters when paired points were located within the same macrohabitat. Parameters were considered important if $w_i \geq 0.75$.

Parameter Name	Coefficient	Combined Model Weight	p
<i>Wood Turtles</i>			
Distance to water (m)	-0.01	0.979	0.046
Number of trees >4" DBH within 10m	-0.07	0.979	0.014
Overstory canopy cover (medium)	-0.84	0.979	0.006
Overstory canopy cover (high)	-0.68	0.979	0.089
Cover at turtle level (high)	1.17	0.979	0.008

3.3 Interspecific Comparisons

Wood Turtles and Blanding's Turtles in sympatry had different median distance to water ($U = 8347.00$, $p < 0.001$), number of trees ($U = 7501.50$, $p < 0.001$), overstory canopy cover ($\chi^2 = 7.48$, $df = 1$, $p = 0.008$), and cover at turtle level ($\chi^2 = 9.27$, $df = 1$, $p = 0.004$), but showed no difference in median herb cover ($\chi^2 = 0.11$, $df = 1$, $p = 0.739$).

CHAPTER 4. DISCUSSION AND CONCLUSIONS

PCA was an effective tool for narrowing the available microhabitat measurements to a smaller set of important variables. Models based on high-loading variables from PC1 were among the most successful models in all categories.

Evidence for microhabitat selection in Blanding's Turtles at Camp Grayling is limited. When the full dataset was analyzed, Blanding's Turtles appeared to select microhabitats with low tree density and close proximity to water. This is consistent with habitat commonly available in emergent wetland macrohabitats, suggesting that selection for macrohabitat may be more important than selection for microhabitat in this species. Repeating the analyses with only paired points from the same macrohabitat confirmed this: no microhabitat variables were significant predictors of Blanding's Turtle use, demonstrating that apparent microhabitat selection in the full dataset was likely an artifact of macrohabitat selection. Edge et al. (2010) had similar results when testing for microhabitat selection in Blanding's Turtles at Algonquin Park, and suggested that Blanding's Turtles may not select microhabitat when the surrounding habitat is of sufficient quality.

Wood Turtles showed stronger evidence for microhabitat selection. Regardless of which data set was analyzed, CLR modeling found that points used by Wood Turtles were farther from water and had fewer trees, less overstory canopy cover, and more ground cover. Aside from distance to water, these factors are the same as what previous researchers have found to be important in Wood Turtle microhabitat selection (Arvisais et al. 2004; Compton et al. 2002). Unlike Blanding's Turtles, preference for open canopy in Wood Turtles appears contradictory to their typical association with forests. Compton et al. (2002) suggest that this pattern indicates a compromise between thermoregulation in open areas and foraging in more food-rich closed-canopy forest, which causes Wood Turtles to primarily inhabit the edge between forested and open habitats.

Contrary to previous studies (Compton et al. 2002; Curtis & Vila 2015), I did not observe selection for close proximity to water in Wood Turtles of either sex. In fact, CLR models suggest a slight avoidance of water in Wood Turtles at Camp Grayling. I may not have sampled random points far enough away from Wood Turtles to detect a difference between used and available points, although Compton et al. (2002) followed the same general study design as this and had the same

maximum distance from turtle to random points (50m). This difference could also be explained by behavioral variation among Wood Turtle populations.

I also did not identify any interactions between microhabitat variables and season for either species or dataset, despite strong evidence for seasonal behavioral shifts in the literature (Beaudry et al. 2009; Greaves 2007; Hartwig & Kiviat 2007; Quinn & Tate 1991) and in my personal observations. Microhabitat sampling may not have been frequent enough to observe seasonal differences in selection. Alternatively, habitat quality at Camp Grayling may be sufficiently high to prevent the need for obvious shifts in microhabitat selection as behavioral priorities change from season to season.

Blanding's Turtles and Wood Turtles had strong differences in microhabitat preference, selecting different median distances to water, numbers of trees, overstory canopy cover, and cover at turtle level. Blanding's Turtles preferred microhabitats closer to water and with fewer trees, while Wood Turtles were more likely to be found in dry upland habitat away from water and in more heavily forested areas. This likely limits conflict over resources between the two species, even when they occur within the same wetland. Conversely, these differences in microhabitat selection may reflect the fact that Blanding's Turtles spent part of their time in scrub-shrub and other wetlands that Wood Turtles do not use. If this is the case, then apparent differences in microhabitat could be artifacts of differences in macrohabitat selection.

The extent to which conclusions can be drawn from these models is limited by the small sample size used to generate them. Due to time and resource constraints, I was unable to meet the desired minimum of 30 individuals per species (Prima et al. 2017). These long-lived turtles are especially prone to individual variation in selection as a result of learned behaviors (Compton et al. 2002), making habitat selection studies on them especially vulnerable to bias by atypical individuals. However, despite these drawbacks, this initial modeling effort provides a valuable first look at how Camp Grayling's rare turtles compare to each other and to conspecific populations in other areas in terms of microhabitat use.

In addition to refining these models with the addition of more data, further research on the Wood and Blanding's Turtles of Camp Grayling is necessary to ensure that they receive adequate conservation measures. Although this project provided baseline data and insights into habitat use of adult turtles, future research should give special attention to hatchlings and juveniles. It is currently unknown whether hatchling and juvenile Blanding's and Wood Turtles use the same

habitat as adults at Camp Grayling; although previous research suggests their requirements are largely the same (Paterson et al. 2012b), some hatchlings were found during my study in areas that adults had never been observed. Tracking hatchlings after they emerge from the nest would reveal whether they move directly to habitat used by adults at Camp Grayling or spend time in other areas until they reach a larger size.

Overall, my findings suggest that Blanding's Turtles and Wood Turtles at Camp Grayling have similar microhabitat needs, although Wood Turtles show stronger evidence for selection at this scale. Both species selected areas with fewer trees and less overstory canopy cover. Although this may be an artifact of selection for open wetland macrohabitat in Blanding's Turtles, Wood Turtles were often found in or near forested macrohabitats and thus appear to be selecting open-canopy microhabitats within these areas. This pattern of microhabitat selection is typical for Wood Turtles and may represent a balance between the need for access to sunlight for thermoregulation and the foraging opportunities presented by closed-canopy forests (Arvisais et al. 2004; Compton et al. 2002). Conversely, Blanding's Turtles appear able to meet both needs at once in typical high-quality marsh habitat, so they may experience less pressure to be selective about microhabitat (Anthonysamy et al. 2014; Edge et al. 2010). Additionally, Wood Turtles selected high ground cover, while Blanding's Turtles showed no selection for this variable. Wood Turtles, including those in my study, typically venture farther from water bodies than Blanding's Turtles (Arvisais et al. 2004; Compton et al. 2002; Edge et al. 2010), and may rely more heavily on ground cover for predator avoidance while they are too far from water to dive to safety.

The selection patterns observed in this study were typical for both species in high-quality habitat, suggesting that habitat at Camp Grayling is extremely suitable for them. This is an encouraging sign for land managers, suggesting that at least adult turtles already have what they need at Camp Grayling to thrive. Management that creates additional areas of open canopy could also be beneficial to both species, especially Wood Turtles that appear to select open areas of forested macrohabitats. This type of management is already conducted on base, particularly through selective logging, and it would be simple to guide these efforts in a way that will benefit both humans and turtles. However, it would be important to refer to other studies when determining timing and methods of logging, to avoid directly harming the turtles with equipment in the process.

APPENDIX. CLR MODEL DETAILS

Blanding's Turtle Global (n = 576, df = 11, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	-0.04	0.02	0.226
TREE	-0.17	0.04	0.008
BWD	0.02	0.04	0.763
SWC 2	0.33	0.33	0.255
SWC 3	-0.78	0.35	0.088
HC 2	0.33	0.32	0.337
HC 3	-0.14	0.26	0.676
OC 2	-0.90	0.38	0.020
OC 3	-0.56	0.37	0.067
TLC 2	0.05	0.34	0.853
TLC 3	0.61	0.26	0.014

Blanding's Turtle Open Wetland (n = 576, df = 2, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	-0.05	0.02	0.175
TREE	-0.20	0.04	0.005

Blanding's Turtle PC1 Variable (n = 576, df = 6, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	-0.05	0.02	0.193
TREE	-0.16	0.04	0.017
OC 2	-0.81	0.36	0.008
OC 3	-0.35	0.32	0.309
TLC 2	0.10	0.33	0.680
TLC 3	0.49	0.24	0.031

Blanding's Turtle Spring Basking with Overstory Cover (n = 576, df = 6, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
OC 2	-3.12	1.31	0.004
OC 3	-2.41	1.12	0.057
SE 2	NA	0.00	NA
SE 3	NA	0.00	NA
OC 2 : SE 2	3.10	1.42	0.015
OC 3 : SE 2	1.95	1.23	0.162
OC 2 : SE 3	1.69	1.37	0.126
OC 3 : SE 3	1.26	1.17	0.258

Blanding's Turtle Distance to Water with Sex Differences (n = 576, df = 2, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	-3.12	1.31	0.004
Sex 1	-2.41	1.12	0.057
WDIST : Sex 1	1.26	1.17	0.258

Blanding's Turtle Aquatic Global (n = 224, df = 11, p = 0.002)

Variable	Coefficient	Standard Error	<i>p</i>
WDEPTH	0.03	0.01	< 0.001
TREE	-0.19	0.13	0.069
BWD	-0.02	0.06	0.708
SWC 2	0.19	0.67	0.639
SWC 3	-0.13	0.62	0.801
HC 2	0.01	0.50	0.976
HC 3	-0.03	0.48	0.931
OC 2	0.09	0.59	0.873
OC 3	0.47	0.70	0.362
TLC 2	0.19	0.47	0.582
TLC 3	0.65	0.39	0.099

Blanding's Turtle Aquatic Late Season Shift to Deeper Water (n = 224, df = 3, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDEPTH	0.05	0.02	0.017
SE 2	NA	0.00	NA
SE 3	NA	0.00	NA
WDEPTH : SE2	-0.04	0.03	0.138
WDEPTH : SE3	-0.01	0.03	0.833

Blanding's Turtle Aquatic PC1 Variables (n = 224, df = 6, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDEPTH	0.03	0.01	< 0.001
TREE	-0.18	0.13	0.066
OC 2	0.04	0.56	0.948
OC 3	0.38	0.57	0.509
TLC 2	0.20	0.44	0.545
TLC 3	0.66	0.38	0.091

Blanding's Turtle Aquatic Typical Selection (n = 224, df = 3, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDEPTH	0.03	0.01	< 0.001
TLC 2	0.24	0.43	0.458
TLC 3	0.77	0.37	0.056

Wood Turtle Association with Forest Edge (n = 512, df = 3, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
TREE	-0.08	0.02	0.001
OC 2	-0.65	0.27	0.020
OC 3	-0.86	0.27	0.001

Wood Turtle Association with Forests (n = 512, df = 1, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
TREE	-0.10	0.02	< 0.001

Wood Turtle Global (n = 512, df = 11, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	< -0.01	< 0.01	0.236
TREE	-0.07	0.02	0.004
BWD	0.06	0.07	0.355
SWC 2	0.59	0.34	0.074
SWC 3	0.14	0.36	0.703
HC 2	0.30	0.32	0.404
HC 3	-0.04	0.29	0.874
OC 2	-0.82	0.29	0.002
OC 3	-0.97	0.30	0.002
TLC 2	0.36	0.33	0.241
TLC 3	1.23	0.29	< 0.001

Wood Turtle Late Season Optimal Foraging Habitat 1 (n = 512, df = 6, p = 0.372)

Variable	Coefficient	Standard Error	<i>p</i>
HC 2	0.62	0.87	0.498
HC 3	-0.76	0.50	0.134
SE 2	NA	0.00	NA
SE 3	NA	0.00	NA
HC 2 : SE 2	-0.94	0.98	0.280
HC 3 : SE 2	0.01	0.71	0.990
HC 2 : SE 3	-0.48	0.93	0.664
HC 3 : SE 3	0.87	0.59	0.135

Wood Turtle Late Season Optimal Foraging Habitat 2 (n = 512, df = 3, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
TREE	-0.15	0.06	0.014
SE 2	NA	0.00	NA
SE 3	NA	0.00	NA
TREE : SE 2	< 0.01	0.07	0.995
TREE : SE 3	0.07	0.06	0.199

Wood Turtle Late Season Upland Foraging (n = 512, df = 3, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	-0.09	0.04	0.134
SE 2	NA	0.000000	NA
SE 3	NA	0.000000	NA
WDIST : SE 2	0.08	0.04	0.174
WDIST : SE 3	0.09	0.04	0.140

Wood Turtle PC1 Variables (n = 512, df = 6, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	< -0.01	< 0.01	0.215
TREE	-0.07	0.02	0.006
OC 2	-0.77	0.28	0.004
OC 3	-0.92	0.29	0.002
TLC 2	0.55	0.31	0.067
TLC 3	1.18	0.28	< 0.001

Wood Turtle Spring Basking (n = 512, df = 6, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
OC 2	-1.07	0.62	0.039
OC 3	-1.84	1.13	0.063
SE 2	NA	0.00	NA
SE 3	NA	0.00	NA
OC 2 : SE 2	-0.42	0.86	0.661
OC 3 : SE 2	0.27	1.24	0.817
OC 2 : SE 3	0.42	0.69	0.598
OC 3 : SE 3	0.71	1.16	0.497

Wood Turtle Typical Selection (n = 512, df = 5, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	-0.91	0.26	< 0.001
SWC 2	-1.25	0.25	< 0.001
SWC 3	0.75	0.31	0.032
OC 2	0.54	0.32	0.033
OC 3	< -0.01	< 0.01	0.109

Wood Turtle Distance to Water with Sex Differences (n = 512, df = 2, p = 0.011)

Variable	Coefficient	Standard Error	<i>p</i>
WDIST	< -0.01	< 0.01	0.039
Sex 1	NA	0.000000	NA
WDIST : Sex 1	< 0.01	< 0.01	0.613

Wood Turtle Basking Habitat with Sex Differences (n = 512, df = 4, p < 0.001)

Variable	Coefficient	Standard Error	<i>p</i>
OC 2	-0.60	0.31	0.001
OC 3	-1.10	0.29	< 0.001
Sex 1	NA	0.00	NA
OC 2 : Sex 1	-0.95	0.56	0.024
OC 3 : Sex 1	-0.71	0.55	0.096

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