



FINE-SCALE MOVEMENT ECOLOGY OF WOOD TURTLES (GLYPTEMYS INSCULPTA)  
BASED ON GPS TAG DATA AND MOVEMENT MODELING

by

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A Thesis submitted in partial fulfillment of the requirements for the degree of Master of  
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## **DEDICATION**

This work is dedicated to the turtles. Without their patience and intrigue I could not have done any of this. They deserve all the credit in the world.



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## TABLE OF CONTENTS

	Page
List of Tables .....	vii
List of Figures .....	viii
List of Abbreviations and/or Symbols .....	ix
Abstract .....	x
Chapter I: Introduction.....	1
Background and Rationale .....	1
Natural History .....	1
Movement Ecology.....	3
Study Areas .....	6
Virginia.....	6
Minnesota .....	7
Objectives.....	8
Methodology .....	9
Virginia.....	9
Minnesota .....	12
Chapter II: Wood turtle home range sizes and movement speeds in a Minnesota and a Virginia population .....	14
Introduction: .....	14
Methodology: .....	18
Results: .....	21
Discussion: .....	31
Chapter III: A temporal moving window analysis of wood turtle movement throughout an active season .....	33
Introduction .....	33
Methods.....	34
Results .....	35

Discussion .....	45
Chapter IV: Long-distance Movements of wood turtles in Virginia .....	47
Introduction: .....	47
Methods: .....	51
Nesting Movement .....	51
Flood Displacement.....	52
Dispersal Movement.....	53
Results: .....	54
Nesting Movement .....	54
Flood Displacement.....	56
Dispersal Movement.....	58
Discussion: .....	62
Nesting Movement .....	62
Flood Displacement.....	63
Dispersal Movement.....	64
Appendix A.....	67
Virginia Sampling Schedules .....	67
Minnesota Sampling Schedules .....	69
Appendix B .....	70
Virginia Home Range Estimates .....	70
Minnesota Home Range Estimates .....	72
Appendix C .....	73
Virginia Speed Estimates .....	73
Minnesota Speed Estimates.....	75
References .....	76

## LIST OF TABLES

Table	Page
Table 1 AKDEs pooled by sex and state .....	27
Table 2 Speed estimates pooled by sex and state .....	28
Table 3 Virginia turtle sampling schedules .....	67
Table 4 Minnesota turtle sampling schedules .....	69
Table 5 Home Range estimates for Virginia turtles.....	70
Table 6 Home Range estimates for Minnesota turtles .....	72
Table 7 Speed estimates for Virginia turtles .....	73
Table 8 Speed estimates for Minnesota turtles .....	75

## LIST OF FIGURES

Figure	Page
Figure 1 A wood turtle in Virginia with equipment attached .....	12
Figure 2 AKDEs pooled by sex .....	23
Figure 3 Average speed pooled by sex .....	24
Figure 4 AKDEs pooled by state .....	25
Figure 5 Average speeds pooled by state.....	26
Figure 6 AKDEs pooled by sex and state .....	27
Figure 7 Speed estimates pooled by sex and state .....	28
Figure 8 Mean and median home range area estimates for all turtles .....	29
Figure 9 Mean and median home range area estimates for all randomly selected, non-dispersing turtles .....	30
Figure 10 Pooled AKDEs for Virginia wood turtles throughout 2018 .....	36
Figure 11 Pooled speed estimates for Virginia wood turtles throughout 2018.....	37
Figure 12 AKDEs for Virginia wood turtles throughout 2018 pooled by sex.....	38
Figure 13 Speed estimates for Virginia wood turtles throughout 2018 pooled by sex.....	39
Figure 14 Pooled AKDEs for Minnesota wood turtles throughout 2015 .....	40
Figure 15 Pooled speed estimates for Minnesota wood turtles throughout 2015 .....	41
Figure 16 AKDEs for Minnesota wood turtles throughout 2015 pooled by sex .....	42
Figure 17 Speed estimates for Minnesota wood turtles throughout 2015 pooled by sex .	43
Figure 18 Pooled AKDEs for wood turtles.....	44
Figure 19 Pooled speed estimates for wood turtles .....	45
Figure 20 Pooled AKDEs for females before, during, and after nesting.....	55
Figure 21 Pooled average speeds for females before, during, and after nesting .....	56
Figure 22 Average speeds for M304 and M703 .....	62

## LIST OF ABBREVIATIONS AND/OR SYMBOLS

95% Kernel Density Estimate .....	95KDE
95% Minimum Convex Polygon .....	95MCP
Aikake Information Criterion .....	AIC
Autocorrelated Kernel Density Estimate .....	AKDE
Bayesian Information Criterion .....	BIC
Brownian Motion .....	BM
Confidence Interval .....	CI
Continuous-Time Movement Modeling .....	CTMM
Continuous-time Stochastic Process .....	CTSP
Cumulative Median Daily Displacement .....	CMDD
Degrees of Freedom .....	DOF
Dynamic Brownian Bridge Movement Models .....	dBMM
Expectation-maximization .....	EM
Global Positioning System .....	GPS
Home Range .....	HR
Independent and Identically Distributed .....	IID
Integrated Ornstein-Uhlenbeck .....	IOU
Kernel Density Estimate .....	KDE
Minimum Convex Polygon .....	MCP
Ornstein-Uhlenbeck .....	OU
Ornstein-Uhlenbeck Foraging .....	OUF
Polymerizing Vinyl Chloride .....	PVC
Smithsonian High Performance Cluster .....	SI/HPC
Straight Line Distance .....	SLD
User Equivalent Range Error .....	UERE
Utilization Distribution .....	UD
Very High Frequency .....	VHF

## ABSTRACT

### FINE-SCALE MOVEMENT ECOLOGY OF WOOD TURTLES (*GLYPTHEMYS INSCULPTA*) BASED ON GPS TAG DATA AND MOVEMENT MODELING

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Little is known about long-distance dispersal movements in freshwater turtles, despite the probable importance of such movements for gene flow between populations. There is a pressing need to better understand these movements, especially within the context of an increasingly fragmented landscape. This study aimed to look at these and other long-distance movements by tracking wood turtles (*Glyptemys insculpta*) using miniaturized GPS units attached to their shells. The data were also used to estimate home range sizes and movement speeds, as well as to analyze the shift in these metrics throughout an active season. In total, 61 wood turtles (38 females, 23 males) were tracked for one to three years each, with hourly or sub-hourly locational fixes recorded for the duration of the active seasons. Two datasets, one from Minnesota (n=25) and one from Virginia (n=36), were combined for a total of over 140,000 GPS locations. Our results show that traditional measures of home range significantly underestimate actual home range sizes

for wood turtles. In Virginia, home range area and movement speed both increased significantly and peaked for females during the nesting season, while male movement was more consistent throughout the year. Movement speed for females peaked during the nesting season. These trends were not observed in the Minnesota population. We captured numerous long-distance nesting movements, two long-distance relocation movements following flood displacement events, and two long-range dispersal events by younger male turtles. Our data demonstrate the magnitude ( $>13$  km) and the danger of dispersal movements. It also indicates the potential of modern GPS technology for studying turtle movement and points toward the need for further studies with more individuals over longer timeframes.



## CHAPTER I: INTRODUCTION

### Background and Rationale

#### *Natural History*

Wood turtles (*Glyptemys insculpta*) are a semiaquatic freshwater species native to northeastern North America, occurring from northern Virginia to Nova Scotia, west across the Great Lakes basin, and into northern Iowa (Ernst and Lovich 2009). A mid-sized Emydid, wood turtles reach lengths of up to 230 mm, with striking orange coloration on their limbs and neck. They are an omnivorous species, commonly eating leaves, berries, fungi, and invertebrates, but also known to eat amphibian egg masses, fish remains, and carrion (Ernst and Lovich 2009).

Many studies have demonstrated declining wood turtle populations for the past 35 years across the species' range (e.g. Kaufmann 1992, Saumure and Bider 1998, Arvisais et al. 2004, Garber and Burger 1995, Daigle and Jutras 2005, Willoughby et al. 2013), primarily attributed to human impacts such as habitat loss, habitat fragmentation, road mortality, death from agricultural equipment, increased predation of nests and hatchlings by subsidized predators such as Raccoon (*Procyon lotor*) and Striped Skunk (*Mephitis mephitis*), and illegal poaching for the pet trade (van Dijk and Harding 2011, Akre and Ruther 2015, Arvisais et al. 2004, Saumure and Bider 1998, Parren 2013, Curtis and Vila 2015). As a result, they are currently classified as an endangered species by IUCN's

redlist (van Dijk and Harding 2011). In Canada, wood turtles are listed as a threatened species in Schedule 1 of the *Species at Risk Act* of 2010, while in the United States they are considered endangered, threatened, or a species of concern in every state within their distribution excluding Maryland (Brown et al. 2017). In Virginia they are state threatened and a tier one species in need of conservation (Akre and Ruther 2015).

Although other species may persist or even thrive with similar threats, what truly endanger wood turtles are the interactions between these threats and the nature of the species natural history and reproductive ecology. Longevity for wood turtles has been demonstrated to reach at least fifty-five years in the wild (Brown et al. unpublished data) but this is generally seen as a conservative number resulting from a lack of long-term studies (see Jones 2009). They are also slow to develop, requiring between fourteen and eighteen years to reach sexual maturity. This results in a generation time between thirty-six and forty-seven years. Due to their long generation times and delayed sexual maturity, which means wood turtles have a very low intrinsic rate of increase, meaning populations are particularly sensitive to disturbance. Additionally, wood turtles typically only lay between eight and eleven eggs per year (full range 3 – 20; van Dijk and Harding 2011). Adults do not exhibit reproductive senescence (Jones 2009, Congdon et al. 2001) and old adults have been shown to have annual survival rates twice as high as younger adult turtles (Jones 2009). This means populations rely on the continued survival and reproduction of adult individuals – particularly females – to maintain viable populations (see Heppell 1998).

### ***Movement Ecology***

Effective conservation action for imperiled species across taxa relies on detailed and accurate assessments of movement patterns, space use, and meta-population connectivity models. To properly address movement patterns, a number of findings and points are relevant. Wood turtles are a riverine species, spending colder months of the year in aquatic hibernacula where ambient water temperatures are warmer and more stable than air temperatures (Greaves and Litzgus 2008). Although generally remaining near flowing water throughout the year (Arvisais et al. 2002, Brown et al. 2016), they are terrestrial during warmer months from late spring into early fall (Kaufmann 1992, Compton et al. 2002). During this active season, male turtles make more use of agricultural fields where available for thermoregulation (Tingley et al. 2009) but generally remain near the streams, while females make more use of upland habitats and wander farther away from streams than male turtles (Kaufmann 1992, Tuttle and Carroll 1997, Compton et al. 2002, Parren 2013, Brown et al. 2016). Older adult turtles have also been shown to venture farther from water than young adult turtles (Jones 2009). Female wood turtles have been shown to display nesting site philopatry, often returning to their same nesting location in subsequent years (Akre and Ruther 2015, Walde et al. 2007). Some of these nesting movements can cover distances of several kilometers in a single direction (Akre and Ruther 2015).

In assessing space requirements, studies on wood turtles have reported individual home range sizes of from 0.2 ha to 1242.7 ha (Jones 2009; see also Quinn and Tate 1991, Foscariini 1994, Kaufmann 1995, Arvisais et al. 2002, Remsburg et al. 2006). The vast

majority of previously reported home ranges have been calculated using relocations from radio telemetry (but see Thompson et al. 2018). Larger ranges may be explained, in some cases, by relocation movement following flooding events and in others by movement of disperser individuals that were not truly range-resident. Exclusion of such movements would likely lead to more narrowly defined home ranges. On the other hand, many lower estimates are likely biased by sampling duration or frequency. Nonetheless, the average home range sizes across the species' range suggest large home ranges across annual cycles and even larger ranges across lifetimes.

Meta-population connectivity modeling is another key aspect of species conservation. Although no research has focused explicitly on this topic in wood turtle populations, studies of other non-marine North American turtles are informative. For instance, Shoemaker and Gibbs (2013) found that *Glyptemys muhlenbergii* rely on interconnected and adjacent habitat patches in order to properly disperse. Protection of such habitat is proposed as an effective conservation tool. Research has also shown that dispersal behavior in *Malaclemys terrapin* is sex-biased toward male turtles (Sheridan et al 2010). Although these two studies and others like them in different taxa are typically done through genetic analyses, such as first-generation migrant detection (Piry et al. 2004), connectivity models can also be informed by resistance surface parameterization using the recorded movement paths of individual dispersers (Elliot et al. 2014).

Based on unpublished data and survey results, we are increasingly aware of wood turtle movements across the landscape at scales that have never been demonstrated or considered for conservation implications (Akre and Ruther 2015). Therefore,

conservation going forward will also require a better understanding of how this species disperses across the landscape—both within and between populations—in terms of the prevalence, distance, and demography of such movements, as well as what corridors are likely to be used.

Most previous movement and home range studies, as mentioned, have relied on relocation via radio-telemetry and have therefore been limited to relatively small and coarsely sampled datasets when compared to modern data collected by GPS tracking units for many larger taxa. There is no published study on the topic of connectivity and modeling in wood turtles.

Recently, the technology for GPS units has advanced sufficiently for them to be miniaturized for use on smaller organisms, such as wood turtles. At the same time, new and powerful statistical techniques for analyzing finely sampled datasets have been developed, (e.g. Continuous-time Movement Modeling (CTMM)) (Fleming et al. 2015, Fleming et al. 2016, Calabrese et al. 2016). It is our aim to make use of the opportunities these two advancements afford to gain a more detailed understanding of wood turtle movement than previously possible. Additionally, we hoped to capture dispersal and other long-distance movements of individuals in greater detail than previously possible, as such data could be used to inform future connectivity models that could prove vital for conserving species in a modern, fragmented landscape.

## Study Areas

### *Virginia*

The southern study area was located within approximately the George Washington National Forest in Shenandoah and Frederick Counties, Virginia. The exact location is withheld here due to the threat of illegal poaching (Compton et al. 2002). This site was chosen because previous work at the site (Akre and Ruther 2015, Akre and Ernst 2006), including long-term annual stream surveys, provided a baseline familiarity with the population demographic, female nesting movement patterns, and hibernacula locations. It is approximately eight kilometers in length (ca. 1800 ha) and contains two first-order streams which join at approximately the halfway point and then flow out of the site. A U.S. Forest Service gravel road runs through the site parallel to both streams. Other anthropogenic features include a powerline right-of-way that bisects the site and six clearing units that are used for intermittent logging.

Streams at this site lack the sandy banks typically used by nesting wood turtles in other populations (Buhlmann and Osborn 2011, Hughes et al. 2009), meaning females must find other nesting habitats. Over the course of a five-year nesting study (Akre et al. unpublished), 55% of nesting sites discovered were along roadside banks, another 41% were found in other human-disturbed areas, and 4% were along stream banks.

The forest at the Virginia site is predominately hardwood and composed largely of oak (*Quercus* spp.) and maple (*Acer* spp.) species along with several species of pine (*Pinus* spp.) Sub-canopy species include dogwood (*Cornus florida*), hophornbeam (*Ostrya virginiana*), shadbush (*Amelanchier* spp.), and witch-hazel (*Hamamelis*

*virginiana*). Understory species include blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), huckleberry (*Gaylussacia* spp.), lyonia (*Lyonia* spp.), mountain-laurel (*Kalmia latifolia*), spicebush (*Lindera benzoin*), Vaccinium (*Vaccinium* spp.), viburnum (*Viburnum* spp.), Virginia creeper (*Parthenocissus quinquefolia*), and winterberry (*Llex verticillata*).

An additional study area with similar habitat was located in West Virginia, also within the George Washington National Forest. This site was used to track one Wood Turtle (M60) that had relocated there from our Virginia study site in 2015 and was therefore of particular interest. In 2018, two male turtles left the Virginia study site and dispersed into WV.

### ***Minnesota***

The northern study area encompassed 40km of river in northeastern Minnesota. Specific locations are again withheld. The site is over 90% forested, with 80% of the area being composed of mesic forests consisting predominately of aspen (*Populus* spp.), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*). Pine forests are present on sandy soils within the study area but are less common. Hydric forests at the site are dominated by black spruce (*Picea mariana*), balsam fir, northern white cedar (*Thuja occidentalis*) and tamarack (*Larix laricina*). Lowland alder (*Alnus* spp.) comprises much of the non-forest woody vegetation. Other habitat types within the area include grass openings and oxbow lakes, as well as other non-flowing water features (Cochrane et al. 2019).

## **Objectives**

### **I. To calculate the home range sizes and movement speeds of wood turtles in a southern (Virginia) and northern (Minnesota) population.**

Using robust statistical techniques, home range size and movement speeds for turtles were calculated. Comparisons were made between sexes as well as between populations. Home range estimates calculated in this way were also be compared with more traditional estimates of home range size for comparison with past research.

### **II. Analyze shifts in home range size or movement speed throughout the year.**

By temporally splitting the data and repeating home range and speed calculations, we looked for patterns in space use and movement speeds throughout the course of a year in both populations.

### **III. Describe and analyze the movement metrics of long-distance movements, such as relocation following flood displacement, nesting movements, and dispersing individuals.**

Long-distance movements—such as nesting, relocation following flood displacement, and dispersal movements—were isolated and compared to more range-resident behavior.



## **Methodology**

### ***Virginia***

*Active Season* – Turtle locations were sampled during the active season, defined as the period of the year in which Wood Turtles might be out of the water (the period in which turtles are active underwater was not sampled as GPS signal cannot penetrate liquid water). This varied from year to year with temperature variation but was generally from the start of April through mid-November.

*Individual selection* – Turtles from four adjacent hibernacula were selected for tracking in 2018. These hibernacula were surveyed extensively in November 2017 and February and March 2018 visually using view buckets and nets as well as by muddling in leaf packs and under banks. This sample was made up of 14 females and 10 males. An additional female from this area was also tracked in 2016. Together, these 25 individuals were considered our randomly selected Virginia turtles.

Other individuals selected for study were those known to make long-distance movements either to nesting banks or between streams, as well as others suspected of making similar movements, such as males that had never before been seen at the site prior to this study. These individuals were found by systematic visual encounter surveys spanning the entire site in Fall 2015, Spring 2016, and Fall 2016. This sample was made up of 4 females and 7 males.

All individuals were identified by marginal scute notches using a modified version of Cagle's (1939) method. Turtles were measured, weighed, and processed using the survey methodology of Akre and Ernst (2006) once per field season.

Overall, 36 turtles were tracked in Virginia and West Virginia from spring of 2016 to fall of 2018 (19 females and 17 males). The majority of turtles (n=30) were tracked during the 2018 season. For a detailed breakdown of turtles tracked per year and sampling schedules, see Appendix A, Table 3.

*Radio-telemetry* – Radio-transmitters (R1860, Advanced Telemetry Systems, Inc.) were attached to the posterior end of the turtles' carapaces by fast-drying gel epoxy (Figure 1). Turtles were then located periodically by radio-telemetry (R410n 164-168 MHz radio receiver, Advanced Telemetry Systems, Inc.). A signal was obtained for each turtle at least once a week for turtles in Virginia and at least every two weeks for M60 in WV to keep track of their general locations. Researchers located every individual at least once every two weeks to ensure the well-being of the animals and the secure attachment of all electronics while minimizing disturbances to the animals' behavior.

*GPS* – Global Positioning System (GPS) units (Telemetry Solutions and Lotek PinPoint 240) were similarly attached to the posterior end of carapaces for the entirety of the field seasons (see Table 3, Appendix A for a breakdown of when each model was used). Telemetry Solutions units (~20 g) were attached directly to the carapace by fast-drying liquid epoxy. They were programmed to record three location and temperature fixes per day: one at 09:00, one at 13:00, and one at 17:00. Their timeout was set to 90 seconds with an additional fix time of 45 seconds. Data were downloaded onto computers

in the field via wireless VHF signals. These units were replaced twice within each season due to battery life limitations.

Custom-made PVC sheaths (~10g) were made to accommodate placement of Lotek PinPoint 240 GPS units (~10 g). Sheaths were cut to 50mm and held in boiling water until pliable. They were then clamped shut on one end, flattened, and allowed to cool until rigid. Two sets of 2mm holes were then drilled in each end of the sheath and they were painted a light brown color and cross-hatched with black Sharpie® marker as camouflage. Sheaths were placed on the posterior end of carapaces by fast-drying gel epoxy with the clamped end toward the anterior. The drill-holes at this end provided extra hold for the epoxy (Figure 1).

PinPoint-240 units then placed inside the sheath with their antennas sticking out for proper reception (Figure 1). They were held in place by crossing two zip-ties threaded through the posterior drill-holes. Units were programmed to record a location and temperature fix once every hour and were removed and replaced once every two weeks with a fully charged PinPoint GPS unit. Removed units were downloaded manually and recharged for re-deployment. By staggering deployment of PinPoint units, only forty-five units were needed at any given time to track 30 turtles in 2018. The combined mass of radio-transmitter, GPS unit, PVC sheath, and epoxy did not exceed 5% of any individual Wood Turtle's weight.



**Figure 1 A wood turtle in Virginia with equipment attached. Advanced Telemetry Solutions R1860 VHF unit (left) and Lotek Pinpoint-240 GPS unit zip-tied into a PVC sheath (right).**

### ***Minnesota***

29 individual wood turtles were tracked during 2015 and 2016 (19 females, 10 males), but four were excluded from this study due to limited data (n=25, 19 females, 6 males) (see Appendix A, Table 4 for turtle sampling schedules). Turtles were tracked using plated VHF units (R1680, Advanced Telemetry Systems, Inc.) and G10 UltraLITE GPS receivers were attached to the VHF metal plate with nuts. These units recorded location fixes every 10 minutes. Turtles were located approximately every 30 days to

download data and replace GPS units. All equipment attached to Minnesota turtles did not exceed 5% body mass in any case. For more detailed information on this study area and sampling methods see Cochrane et al. 2019.

## **CHAPTER II: WOOD TURTLE HOME RANGE SIZES AND MOVEMENT SPEEDS IN A MINNESOTA AND A VIRGINIA POPULATION**

### **Introduction:**

When developing and initiating conservation actions for an endangered species, a key aspect of planning is accurate knowledge of the species' space use and movement patterns. By calculating home range sizes, the amount of space that an individual within a population requires can be taken into account when selecting sites and populations for protection. In turtles, this can be especially important when considering the proximity of infrastructure such as agriculture and roads which pose an existential threat to individuals traversing the landscape. In this regard, it would also be helpful to know how much, or how quickly, individual turtles are moving within their home ranges. Average movement speed serves as a useful proxy for such information.

Over the past half-century, wood turtle home ranges have been calculated a number of times (e.g. Ernst 1968, Harding and Bloomer 1979, Kaufmann 1995, Quinn and Tate 1991, Strang 1983, Ross et al. 1991, Arvisais et al. 2002, Remsberg et al. 2006, Curtis and Vila 2015, McCoard et al. 2016, Thompson et al. 2018). See Table 1 in Remsberg et al. (2006) for a summary of previous research. In these studies, as with studies on other taxa, the most common estimates of home range size have been minimum convex polygons (MCP) and kernel density estimates (KDE). These are often

reported at various levels, such as 50%, 95%, and 100% MCP or KDE, indicating the percentage of most central locations that were used to calculate the home range area. In this way, outliers can be filtered and “core area” can be looked at separately.

While these measures have certainly been instrumental in our understanding of wood turtle space use and helpful in conservation efforts for this species as well as many others, estimates such as MCPs and KDEs have a number of drawbacks (briefly explored here, but see Fleming et al. 2015 for a more thorough exploration). One major issue is their lack of confidence intervals. For each of these estimates, only a point estimate is given, leaving only the sample size as a poor proxy for the degrees of freedom.

Secondly, both measurements make the statistical assumption that all locations are independent and identically distributed. This means that they are only valid if the data are sampled coarsely enough in time that there is no autocorrelation between subsequent points. If an individual is found in one place at one time, the next time it is found it should be possible for it to be at any other point within its home range. This assumption was likely met for many past studies that relied on radio-telemetry for location data and therefore may only have collected one or two points per week. With the shift toward GPS units in modern movement datasets, however, location data is often collected on much finer temporal scales. This shift has been delayed in research on smaller taxa but is beginning to accelerate with the development of miniaturized GPS technologies (Kays et al. 2015).

Similarly, estimates of speed are historically simple and unreliable in movement ecology studies, often relying on sums of straight-line-distances (SLD). As with home

range estimates, SLDs are also point estimates, meaning they come without confidence intervals and are heavily scale-dependent. Because of the finer temporal resolution of modern GPS datasets, SLD estimates are often artificially inflated by telemetry error (Ranacher et al. 2015, Noonan et al. 2019). This is only made worse in smaller and slower taxa, such as turtles, where movement between subsequent location fixes is more likely to be less than the error of the GPS unit itself (Noonan et al. 2019) (For a demonstration of this in practice using data collected by this study, see Noonan et al. 2019). This scale-dependent inflation of SLD movement estimates in wood turtles can clearly be seen in Thompson et al. 2018 Fig. 1, where the authors compare yearly SLD movement for male and female wood turtles calculated using both fine-scale GPS unit measurements as well as coarser-scaled radio-telemetry locations.

Because of the downsides of traditional measurements of movement metrics such as home range size and movement speed, and with the aid of modern computing power and software availability, more sophisticated statistical techniques have recently been developed. The only study on wood turtles to date that has made use of such statistics is Thompson et al. 2018, in which researchers collected fine-scale GPS data and used it to calculate probabilistic utilization distributions (UD) using dynamic Brownian bridge movement models (dBBMM). These UD, however, are not a proper estimate of home range size, as they collapse to the movement paths of individuals as error and temporal intervals between measurements approach zero (Fleming et al 2015). To account for this difference, Thompson et al. 2018 also reported 95% MCP (95MCP) estimates.



One recent development for movement modeling, and our choice for this study, is the CTMM (Continuous-time Movement Modeling) package available in R (Fleming and Calabrese 2019). In brief, CTMM provides a platform for easily working with continuous-time stochastic process (CTSP) models for movement, as well as integrated visualizations and AIC-based model selection. CTMM attempts to fit movement data to all single-component CTSP models currently in use in the literature. These include, from most simple to most complex, the independent and identically distributed (IID) process, Brownian motion (BM), the Ornstein-Uhlenbeck (OU) process, the integrated Ornstein-Uhlenbeck (IOU) process, and the Ornstein-Uhlenbeck foraging (OUF) process. OUF models are those which are able to produce estimates of both home range area and average speed, as the data are sampled finely enough to produce autocorrelation in velocities as well as long enough to demonstrate range-residency. As such, they are the preferred models for producing movement metrics (Calabrese et al. 2016).

With the opportunity of recent statistical advancements and the relative paucity of studies making use of them, particularly in herpetofauna and specifically in wood turtles, our aim in this study was to address this gap in the literature by collecting fine-scale movement data and analyzing it with rigorous and statistically defensible methods. We predict that previous home range estimations have generally been both underestimated due to limited VHF relocation data and outdated home range estimators, as well as occasionally overestimated due to inclusion of non-range resident movement patterns such as flooding events and dispersal behavior. There is, however, an argument to be made that such movements may constitute a relatively frequent enough pattern, at least in

some demographics, when considered in the span of such a long-lived species that they could be included in the classic definition of a home range as defined by Burt (1943). For this reason, more longitudinal research is needed on the relative frequencies of such movement patterns in wood turtles and many other turtle species.

### **Methodology:**

As described in chapter I, our location data came from two distinct wood turtle populations: one in northern Virginia at the southern extent of the species' range and another in northeastern Minnesota, a more northern population near the western extent of the species' range. Turtles originally selected in the Virginia population due to foreknowledge of their previous long-distance movements were excluded from this analysis to provide a true random sample. In total, data from 26 turtles (15 females, 11 males) tracked at the Virginia site and 25 turtles (19 females, 6 males) tracked at the Minnesota site were included, for a total of 51 turtles (34 females, 17 males). All individuals were equipped with GPS units. In Virginia, GPS units attempted to record, at minimum, three points per day and more often at every hour (see Table 3, Appendix A), while in Minnesota, GPS units took points every 10 minutes. After filtering of outliers, these location fixes summed to a total of 141,200 points.

To estimate home range sizes, as well as movement speeds, we used the CTMM (Continuous Time Movement-modeling; Calabrese et al. 2016, Fleming and Calabrese 2019) package in R (R Core Team 2019). This allowed us to calculate both an auto-

correlated kernel density estimate (AKDE) (Fleming et al. 2015) as well as a scale-free estimate of movement speed (Noonan et al. 2019) that properly accounted for the high levels of temporal autocorrelation inherent in our sampling schedules. Many of our computationally-intensive analyses were conducted on the Smithsonian High Performance Cluster (SI/HPC).

With movement data in general, but particularly for data coming from smaller and slower species such as turtles, error calibration is an important step in the modeling process. This is because not calibrating for locational error could cause the model to conflate error with actual movement. For each of the three different GPS unit models that were attached to wood turtles for this study, multiple units were placed in wooded environments at fixed locations for extended periods of time to collect calibration data. In this way, points taken were similar to the environment that turtles were expected to be found in the majority of the time. These data were then input into CTMM to calculate each model's user equivalent range error (UERE).

Once a UERE value had been calculated for a GPS model, the calibration data collected using that model were then filtered in CTMM using the outlier function in conjunction with the UERE value. Points that had an estimated velocity of  $> 0.03$  m/s were excluded from the data. Based on observed movements, we believed it was unlikely that turtles would sustain a velocity of greater than 0.03 m/s for an extended period of time, so these points were deemed to be inaccurate. Once these outliers had been removed from the calibration data, new UERE values were calculated for each model. When reading the turtle movement data into CTMM, points were filtered in the same way

as the calibration data and then assigned the appropriate UERE values. In this way, CTMM modelled the error before modeling the movement.

Once the data had been appropriately filtered and input into CTMM, movement models were estimated and selected. We then used non-parametric bootstraps in order to reduce bias in model estimates. Bootstraps were first attempted with a relative threshold of 0.01 for six days, then at 0.05 for another six days. In the end, 34 of 36 Virginian turtles' models were successfully bootstrapped at a relative error threshold of 0.01 while the remaining two were unable to be bootstrapped at either level. These two individuals were, unsurprisingly, the two dispersing individuals. For Minnesotan turtles, 21 of 25 were able to be bootstrapped at an error of 0.01, one was bootstrapped at an error of 0.05, and the remaining three were unable to be bootstrapped at either level.

These models were then used to calculate auto-correlated kernel density estimates (AKDEs) as well as average speeds within CTMM. Home range estimates used optimally weighted AKDEs when possible ( $n = 49$ ) but relied on normal AKDE estimates when calculation time exceeded six days ( $n = 2$ ). Sampling distribution of speed estimates for each individual were summarized using median instead of mean values. This was helpful in resolving speeds for some models in cases where velocity could barely be resolved without these robust estimates.

Each AKDE home range area estimate and speed estimate from CTMM comes with its own degrees of freedom and variance estimates. This means that the variances cannot be expected to be equal and are often quite dissimilar. Because of this, random-effects meta-analyses were used to pool output metrics using the R package metafor

(Viechtbauer 2010). Two male turtles that displayed non-range resident dispersal behavior in 2018 and therefore had extremely high AKDEs and area variances were removed from all random-effects meta-analyses as the models were unable to account for such drastically different variances between individuals. Additionally, speeds were unable to be estimated for these two dispersers and a third male Virginian turtle.

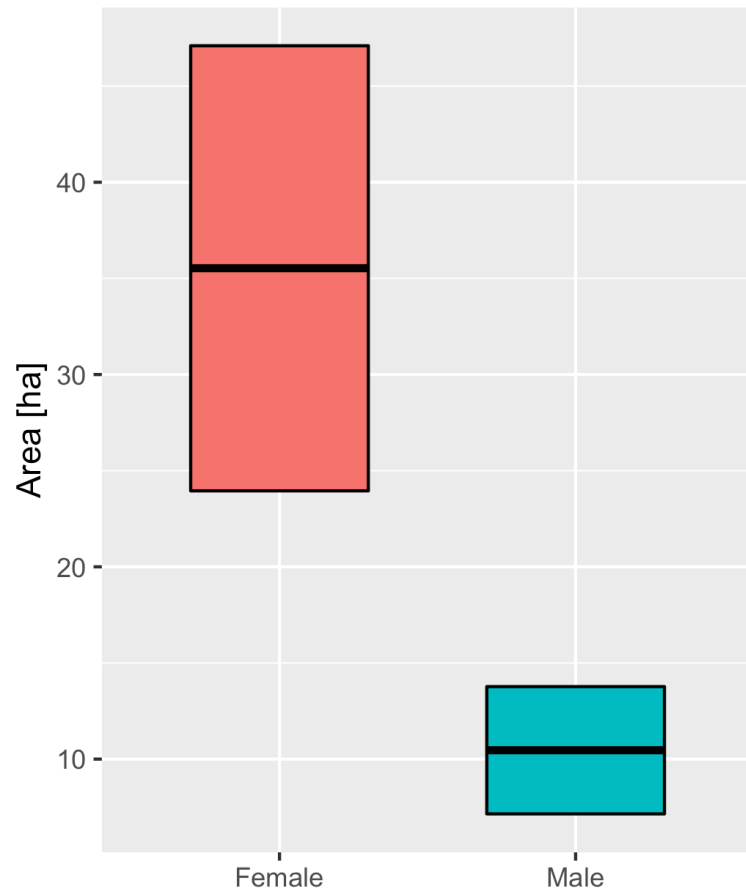
In order to compare AKDEs for wood turtles to more traditionally common home range estimators we also used our data to calculate 95% MCPs (95MCP) and 95% KDEs (95%) using the R package *adehabitatHR* (Calenge 2006). Mean and median values for all estimates, as well as mean and median percent differences between AKDE and other methods were calculated. This step was completed with all turtles tracked during the study (n=61, 38 females, 23 males) as well as with only randomly selected, non-disperser individuals (n=49, 34 females, 15 males).

## **Results:**

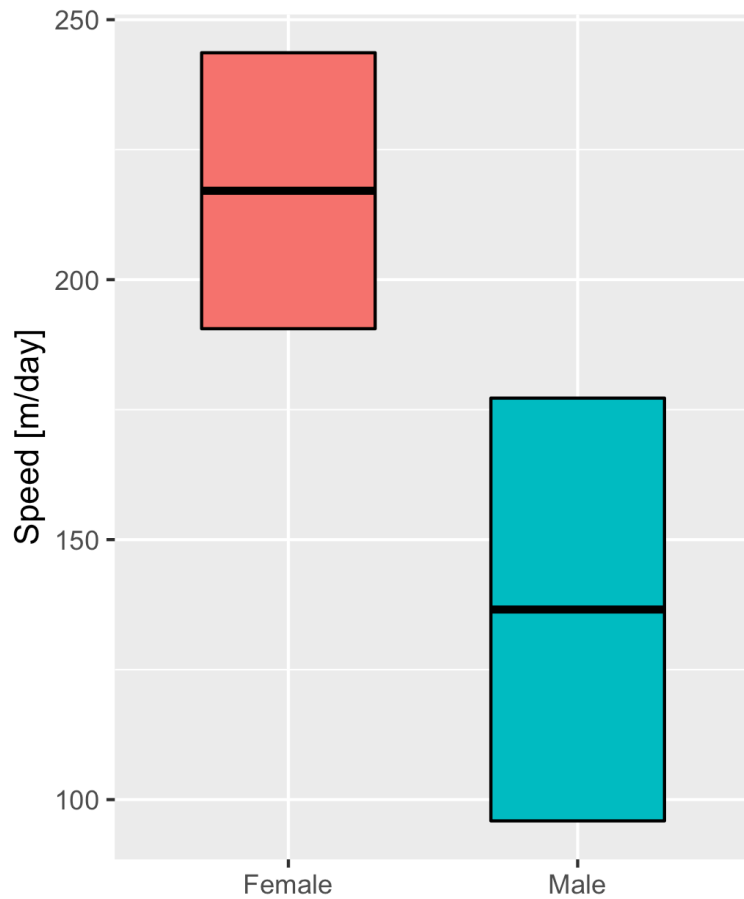
All home range estimates can be found in Appendix B, Table 5 and Table 6. All speed estimates can be found in Appendix C, Table 7 and Table 8. Pooled estimates are reported along with 95% confidence intervals (CIs) as well as k values, indicating the number of individuals that were pooled for each estimate.

Individual AKDE home range estimates for range-resident, randomly selected turtles in our study ranged from 3.45 ha to 1244.76 ha, 95% CIs [2.59, 4.42] and [261.01, 2982.04], respectively. For models with speed DOF estimates above 5, average speed ranged from 44.32 m/day to 419.70 m/day, 95% CIs [39.71, 49.27] and [371.86, 460.37], respectively.

The pooled estimate for home range area was 20.90 ha (95% CI [15.70, 26.10],  $k = 49$ ) and for speed was 193.65 m/day (95% CI [168.46, 218.85],  $k=48$ ). For males, home range area was estimated at 10.46 ha (95% CI [7.15, 13.77],  $k = 15$ ) and for females it was 35.53 (95% CI [23.95, 47.1],  $k = 34$ ) (Figure 2). Male speed was estimated at 136.56 m/day (95% CI [95.91, 177.22],  $k = 14$ ) and female speed was estimated at 217.1 m/day (95% CI [190.57, 243.64],  $k = 34$ ) (Figure 3).



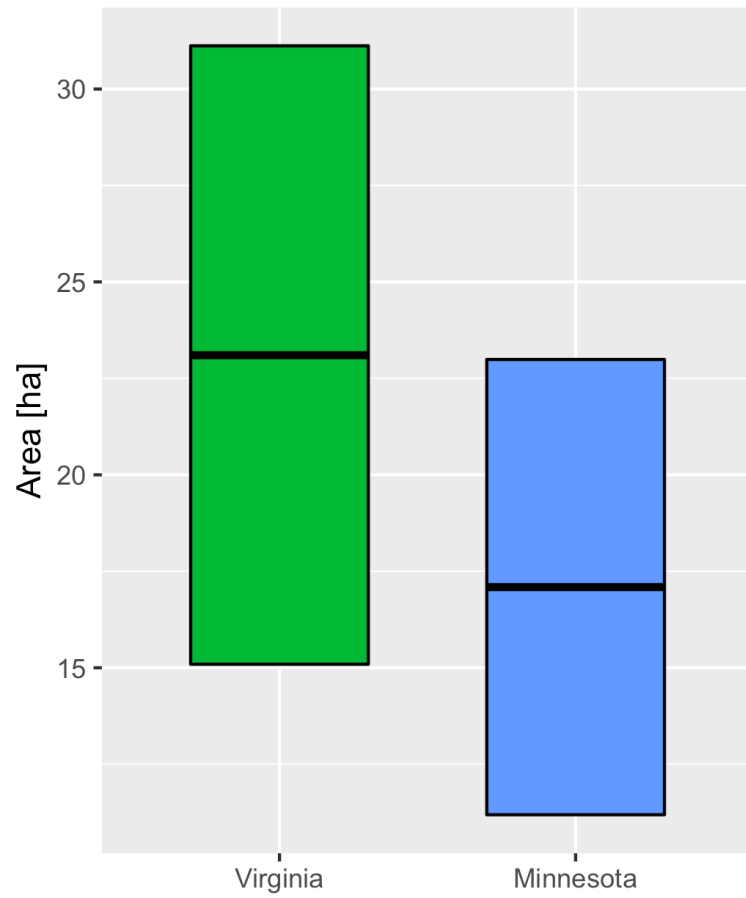
**Figure 2 AKDEs pooled by sex. Intervals represent point estimates and 95% confidence intervals.**



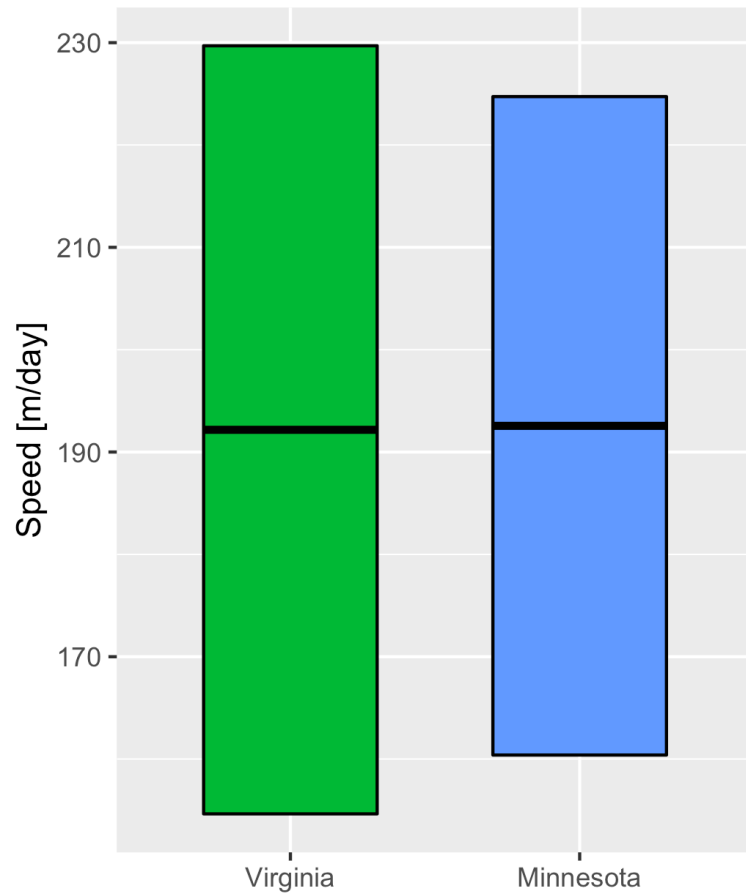
**Figure 3 Average speed pooled by sex. Intervals represent point estimates and 95% confidence intervals.**

The pooled estimate for home range size of Virginia turtles was 23.1 ha (95% CI [15.09, 31.12],  $k = 24$ ) and for Minnesota turtles was 17.09 ha (95% CI [11.19, 22.99],  $k = 25$ ) (Figure 4). The pooled speed estimate for Virginia turtles was 192.17 m/day (95% CI [154.64, 229.70],  $k = 23$ ) and for Minnesota turtles was 192.56 m/day (95% CI [160.39, 224.73],  $k = 25$ ) (Figure 5).





**Figure 4 AKDEs pooled by state. Intervals represent point estimates and 95% confidence intervals.**

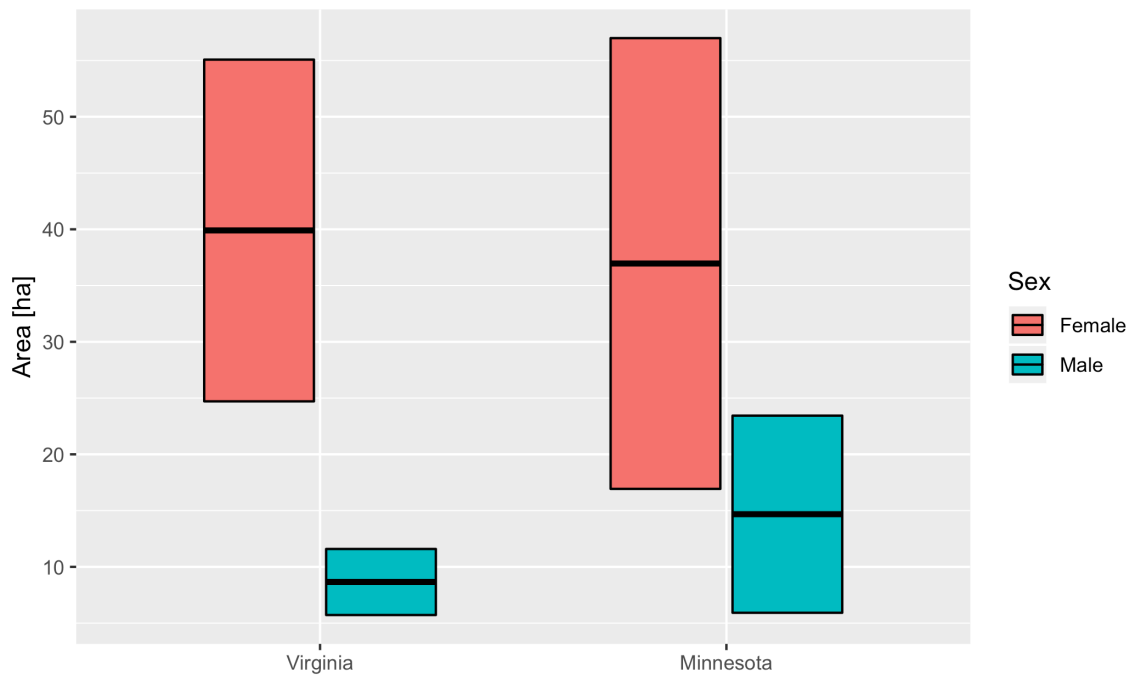


**Figure 5 Average speeds pooled by state. Intervals represent point estimates and 95% confidence intervals.**

Pooled turtle area estimates by sex and state are summarized in Table 1 and Figure 6. Pooled turtle speed estimates by sex and state are summarized in Table 2 and Figure 7.

**Table 1 AKDEs pooled by sex and state. K represents the number of individuals used in each analysis. Bounds represent 95% confidence intervals. See Figure 6.**

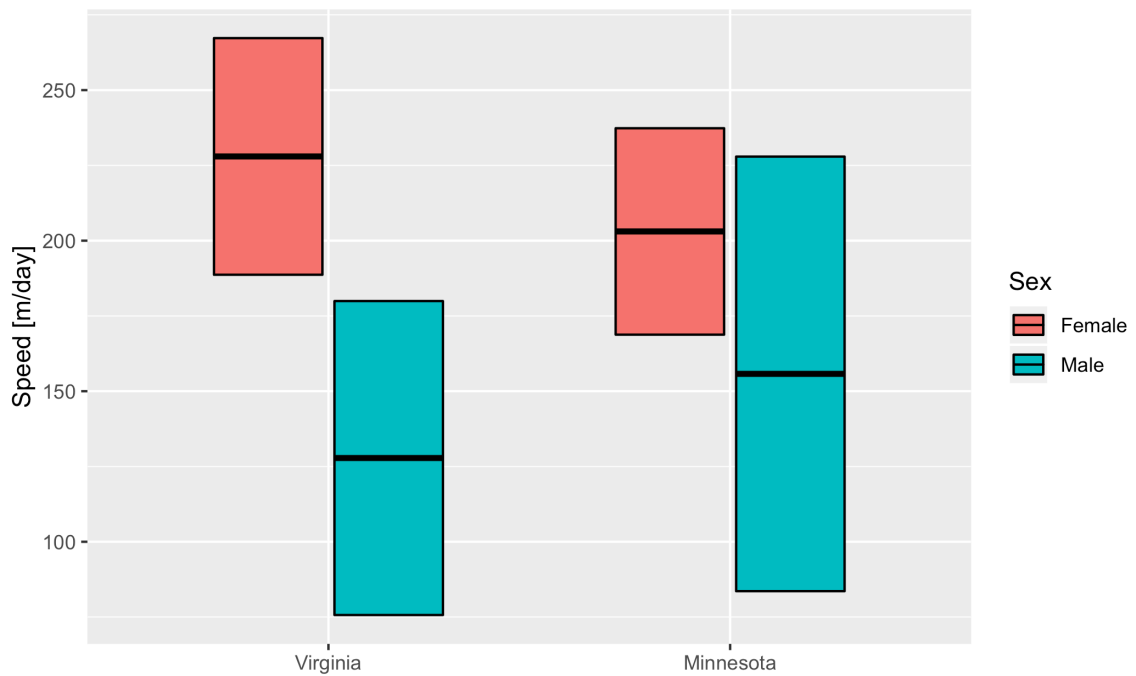
State	Sex	Area [Ha]	Lower bound	Upper bound	K
VA	F	39.9	24.71	55.08	15
VA	M	8.66	5.72	11.59	9
MN	F	36.96	16.93	56.99	19
MN	M	14.68	5.92	23.44	6



**Figure 6 AKDEs pooled by sex and state. Intervals represent point estimates and 95% confidence intervals. See Table 1.**

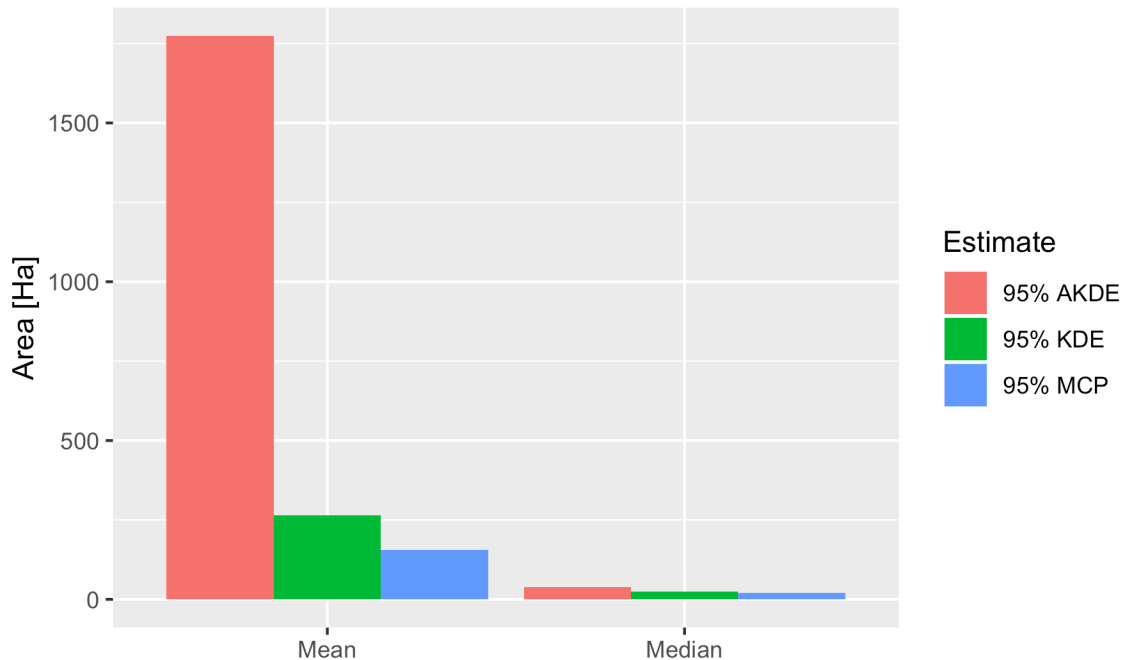
**Table 2** Speed estimates pooled by sex and state. **K** represents the number of individuals used in each analysis. Bounds represent 95% confidence intervals. See Figure 7.

State	Sex	Speed [m/day]	Lower bound	Upper bound	K
VA	F	227.97	188.68	267.27	15
VA	M	127.81	75.67	179.94	8
MN	F	203.06	168.78	237.34	19
MN	M	155.76	83.59	227.92	6

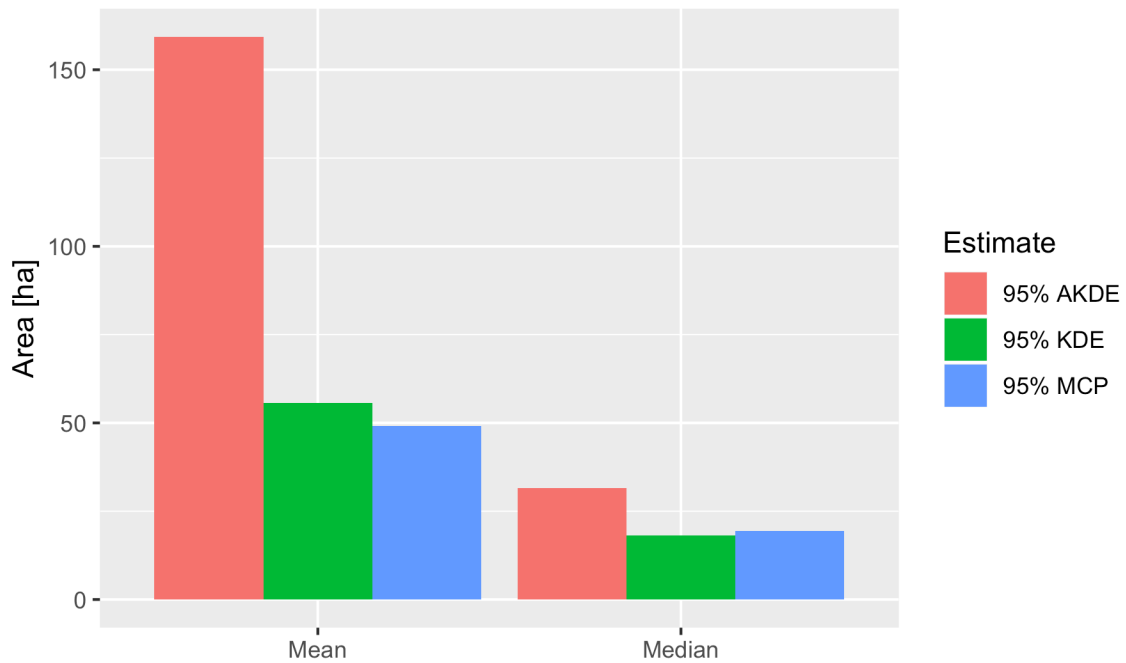


**Figure 7** Speed estimates pooled by sex and state. Intervals represent point estimates and 95% confidence intervals. See Table 2.

Using AKDEs, the mean home range when including all turtles (n=61, 38 females, 23 males) was 1774.33 ha and median was 38.57 ha. For 95% KDEs, the mean was 264.49 ha and the median was 23.61 ha. For 95% MCP estimates, the mean was 156.55 ha and the median was 20.63 ha (Figure 8). The mean percent increase from 95% KDEs to AKDEs was 175.00% and the median was 85.19%. The mean percent increase from 95% MCP estimates to AKDEs was 230.57% and the median was 81.22%.



**Figure 8 Mean and median home range area estimates for all turtles (n = 61) calculated using auto-correlated kernel density estimates (AKDE), 95% kernel density estimates (95KDE), and 95% minimum convex polygons (95MCP).**



**Figure 9 Mean and median home range area estimates for all randomly selected, non-dispersing turtles (n = 49) calculated using auto-correlated kernel density estimates (AKDE), 95% kernel density estimates (95KDE), and 95% minimum convex polygons (95MCP).**

When limiting the sample to only randomly selected, non-dispersing individuals (n=49, 34 females, 15 males), the mean AKDE was 159.35 ha and the median was 31.54 ha (SD = 293.42). The mean 95% KDE was 55.64 ha and the median was 18.07 ha (SD = 106.53). The mean 95% MCP estimate was 49.05 ha and the median was 19.35 ha (SD = 89.52) (Figure 9). The mean percent increase from 95% KDEs to AKDEs was 157.15% and the median was 74.83%. The mean percent increase from 95% MCP estimates to AKDEs was 189.48% and the median was 60.43%. One-sided, paired t-tests indicate that

AKDEs were significantly greater than both 95% KDEs and 95% MCP estimates ( $p < 0.001$ ).

### **Discussion:**

Our results indicate that wood turtle home ranges have traditionally been significantly underestimated. AKDEs in our study were, on average, over 150% greater than both 95% KDE and 95% MCP estimates (Figure 8, Figure 9). This finding should be taken into account when interpreting any past or future study making use of these estimators, and any conservation actions based on home range size and already in place for this species should be re-evaluated.

Our study is also the first to find a significant difference in home range size between sexes, with females having significantly larger home ranges than males (Figure 2). This is likely due to female nesting movements, as many individuals nest outside of the area in which they spend the rest of the year. Interestingly, when split by state, this relationship held true in Virginia but was not significant in Minnesota (Table 1, Figure 6). We hypothesize that this may be due to a difference in nesting habitats between the two populations. At the Virginia site, suitable nesting locations are largely limited to road-cut banks and a single power-line right-of-way, meaning that females may need to travel further on average to nest, increasing the size of their home ranges. If true, this would indicate that home range sizes for females may be related to the relative locations and availability of nesting habitat, meaning that quantifying these aspects of populations may be an important step in delineating conservation area buffers. Further research in a variety of populations is required to further explore this issue.

Female wood turtles were also found to have significantly greater average speeds than male turtles (Figure 3). As with home range area, this trend held true in Virginia but was not significant in Minnesota (Table 2, Figure 7). We believe that this is also likely due to female nesting movements and supports the hypothesis that female turtles in Virginia travel farther on average to reach nest sites.

There was no significant difference found in either home range size or speed between states in this study (Figure 4, Figure 5). This held true when comparing estimates for each sex across states (Table 1, Table 2, Figure 6, Figure 7).

Home range size was found to be highly variable between individuals, with a raw SD of 293.42 ha for AKDE point estimates of range-resident, randomly selected turtles. This means that mean and median home range sizes should not be considered representative of all individuals within population. Given the importance of adult turtle survivorship—reproductive females in particular—to the long-term success of wood turtle populations (Heppell 1998), conservation actions should instead incorporate maximum home range size. Our findings indicate that home ranges for non-dispersing wood turtles over the course of two years can exceed 12 km<sup>2</sup>. Furthermore, considering the longevity of this species, all home ranges calculated in this and other studies should be considered underestimates of true, life-long home range sizes. Longitudinal studies following individuals throughout their life are needed.



## **CHAPTER III: A TEMPORAL MOVING WINDOW ANALYSIS OF WOOD TURTLE MOVEMENT THROUGHOUT AN ACTIVE SEASON**

### **Introduction**

Modern GPS units enable the collection of movement data on scales never before possible. Without the constraint of radiotracking individuals for each relocation, modern movement datasets are typically on much finer temporal scales (Kays et al. 2015). Although this does present statistical challenges for analysis associated with temporal autocorrelation, it also presents an opportunity to investigate movements over smaller temporal windows, enabling a better understanding of how movement fluctuates over time.

This understanding has conservation applications, as it enables researchers to identify seasonal periods in which animals may be more active as well as periods in which they may move over larger areas and longer distances. Since these are the periods during which individuals are at the highest risk, it is these movement patterns that should be taken into consideration when considering conservation actions such as buffer sizes or restricted access to protected areas. This is especially true for long-lived, slow-reproducing species such as wood turtles, as their populations can be more dramatically affected by the removal of a few individuals (Heppell 1998).

## Methods

For this part of the study, the movement data of all randomly selected Virginia turtles from 2018 ( $n = 24$ , 14 females, 10 males) and all Minnesota turtles from 2015 ( $n = 22$ , 17 females, 5 males) were used. Data were limited to single years in order to avoid climatic and random effects between years and specific years were chosen for having more data. All data were cleaned and calibrated as explained in chapter II.

Data were then temporally split into continuous 30-day periods for each turtle. Twenty-seven periods were defined in total, with the first starting on April 1 and the last starting on September 30. The beginning of each period was separated from the prior by seven days. In this way, all locations from April 1 to October 30 were included in the overall analysis. This included 99.71% of all Virginia locations and 100% of all Minnesota locations.

Movement models, AKDEs, and speed estimates were then calculated for each turtle within each period using CTMM. For movement models, bootstraps were attempted for 12 hours at an error of 0.05. If this did not succeed, the normal model was used. In some cases, no model was fit due to a lack of sufficient data. This was especially true in Minnesota turtles, where the colder climate restricts the active season. Furthermore, not all models were sufficient to calculate AKDEs or speed estimates. All AKDEs based on models with an area DOF estimate  $< 1$  and all speed estimates based on models with a speed DOF estimate  $< 1$  were removed.

For Virginia data, out of the 648 attempted models, 578 were successfully fit and 530 of these were successfully bootstrapped. Out of 578 attempted AKDEs, 542 were

successful and had area DOF estimates  $> 1$ . Out of 578 attempted speed estimates, 274 were successful and had speed DOF estimates  $> 1$ .

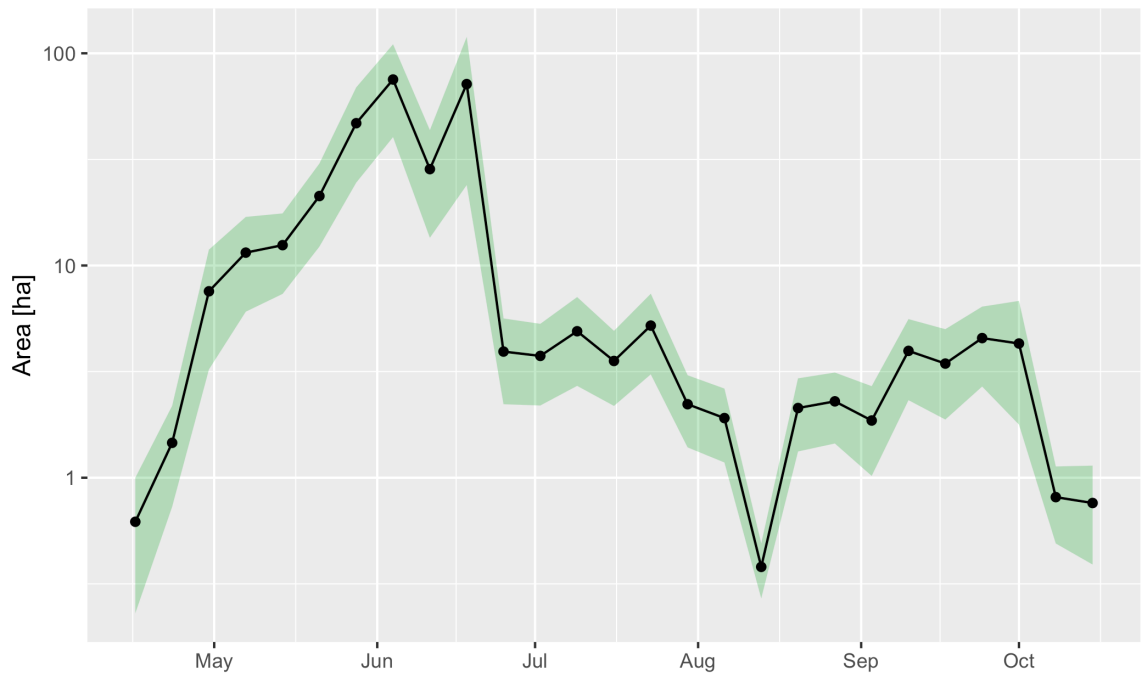
For Minnesota data, out of the 594 attempted Minnesota models, 310 were successfully fit and 252 of these were successfully bootstrapped. Out of 310 attempted AKDEs, 301 were successful and had area DOF estimates  $> 1$ . Out of 310 attempted speed estimates, 137 were successful and had speed DOF estimates  $> 1$ .

Resulting values were pooled using random-effects meta-analyses.

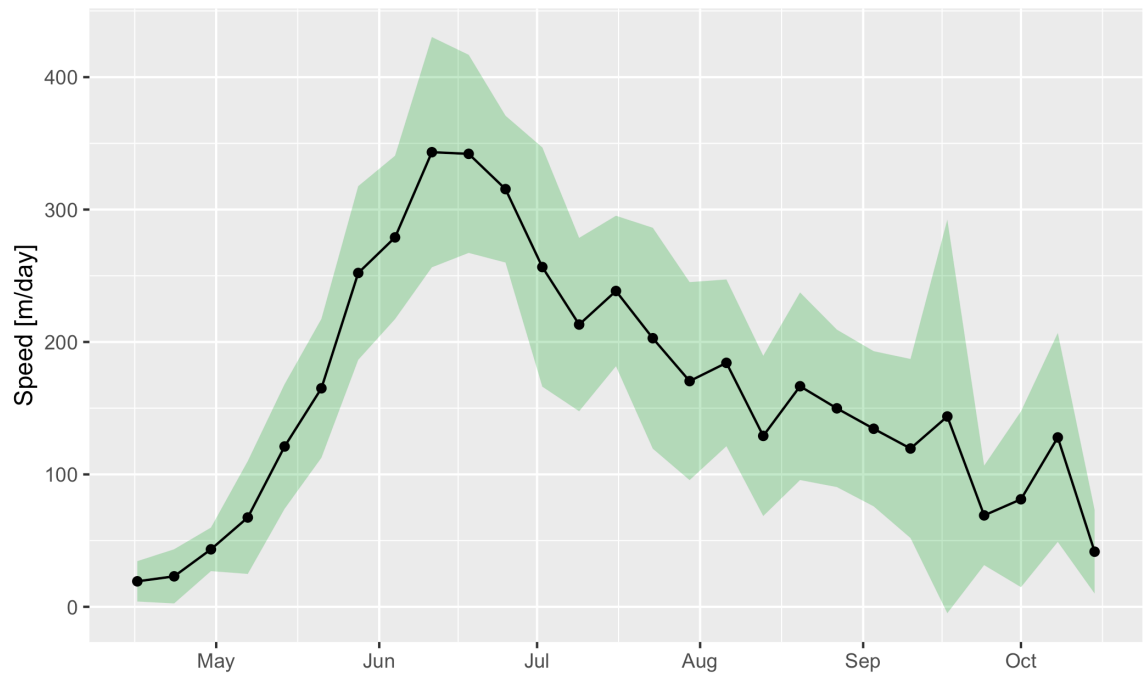
## **Results**

All results are presented as figures here and as tables in appendix D. Dates represent the mid-point of each analyzed 30-day period.

Virginia AKDEs are shown in Figure 10. Virginia speed estimates are shown in Figure 11.

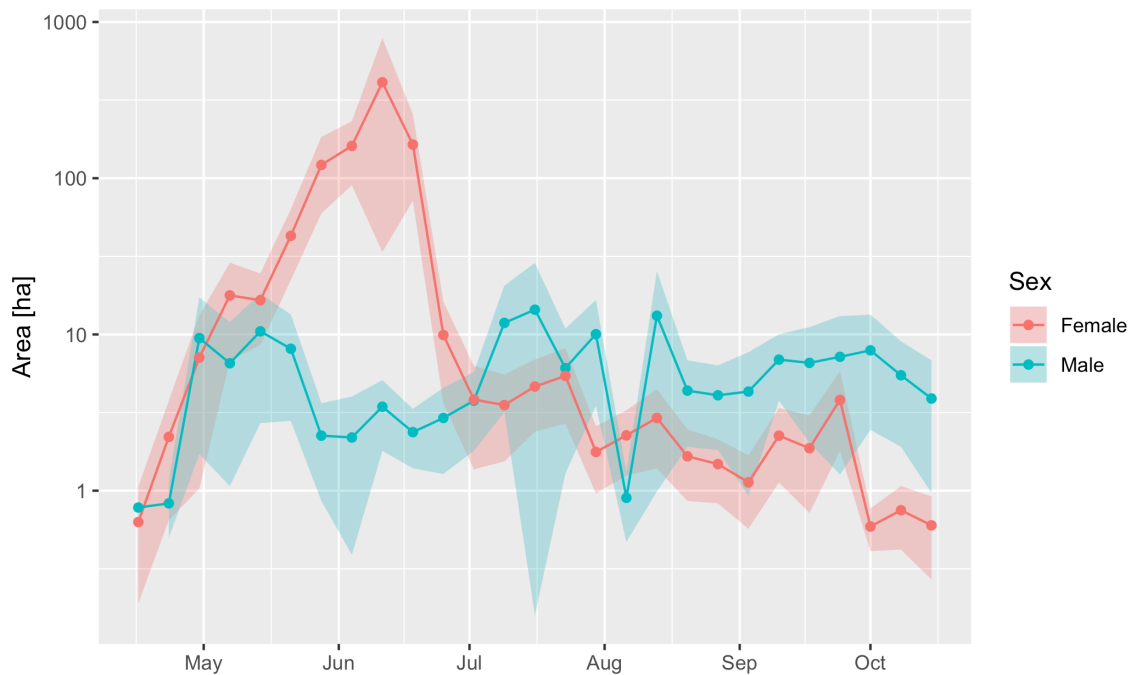


**Figure 10 Pooled AKDEs for Virginia wood turtles throughout 2018. The y-axis is Log10 transformed. Intervals represent 95% confidence intervals.**

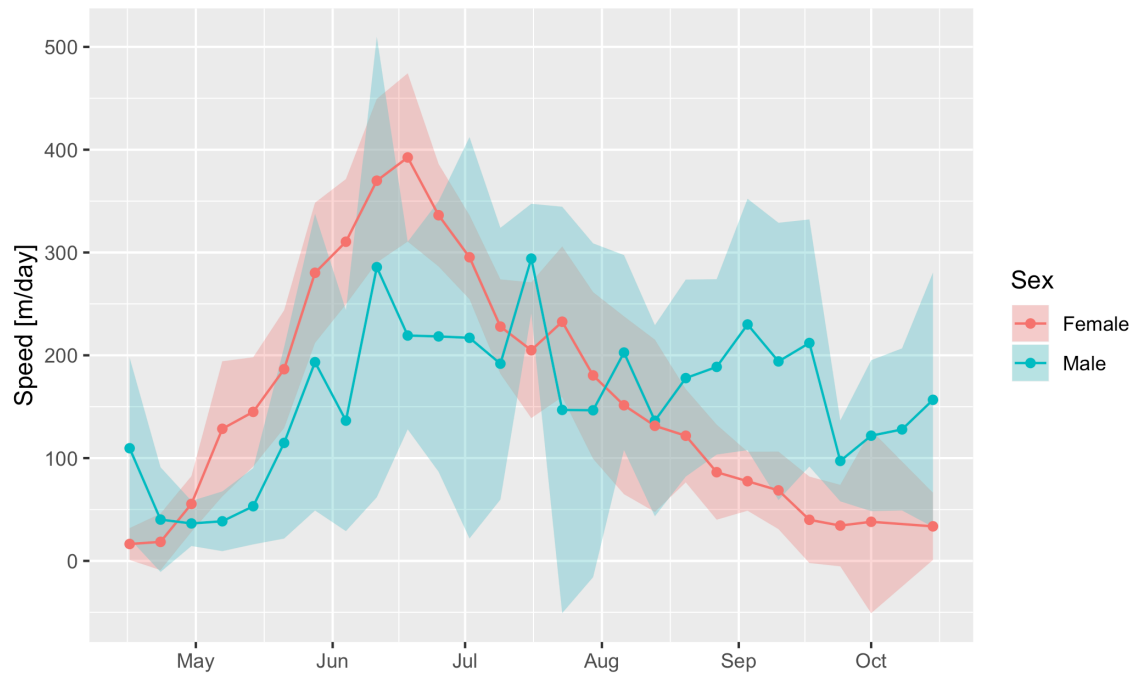


**Figure 11 Pooled speed estimates for Virginia wood turtles throughout 2018. Intervals represent 95% confidence intervals.**

Virginia AKDEs were pooled and graphed without the inclusion of M703, the randomly selected disperser. This was done because inclusion of M703 heavily skewed one 30-day period, making it difficult to visualize. These results are shown in Figure 12. Virginia speed estimates pooled by sex are shown in Figure 13.

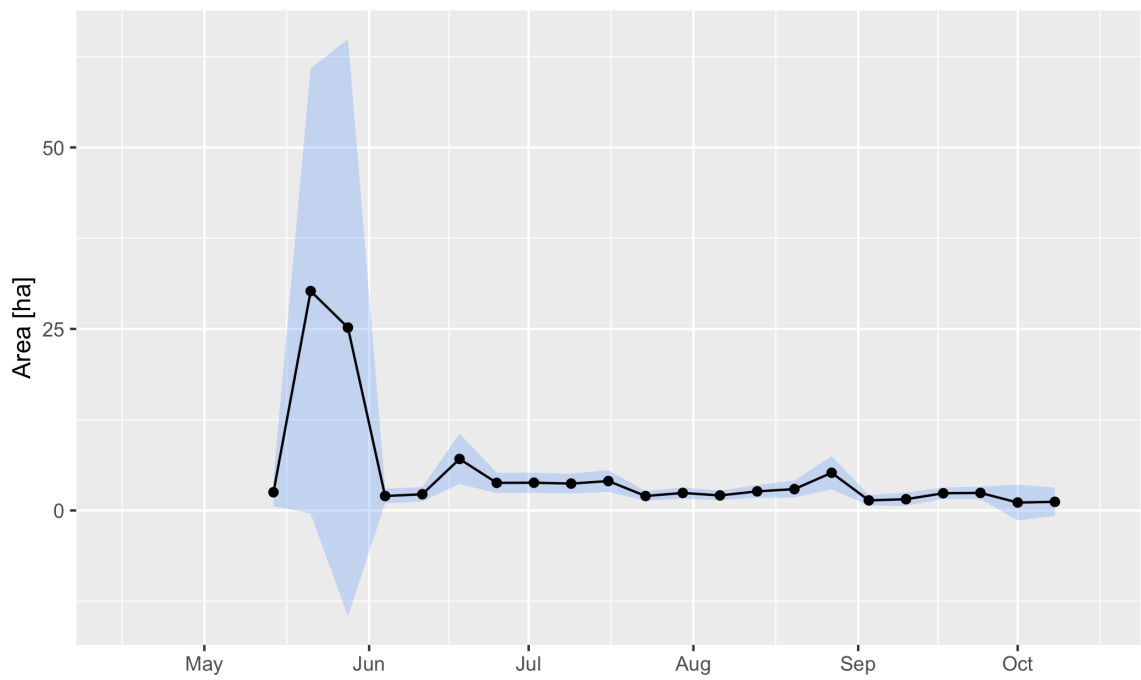


**Figure 12 AKDEs for Virginia wood turtles throughout 2018 pooled by sex, excluding M703. The Y-axis is Log10 transformed. Intervals represent 95% confidence intervals.**



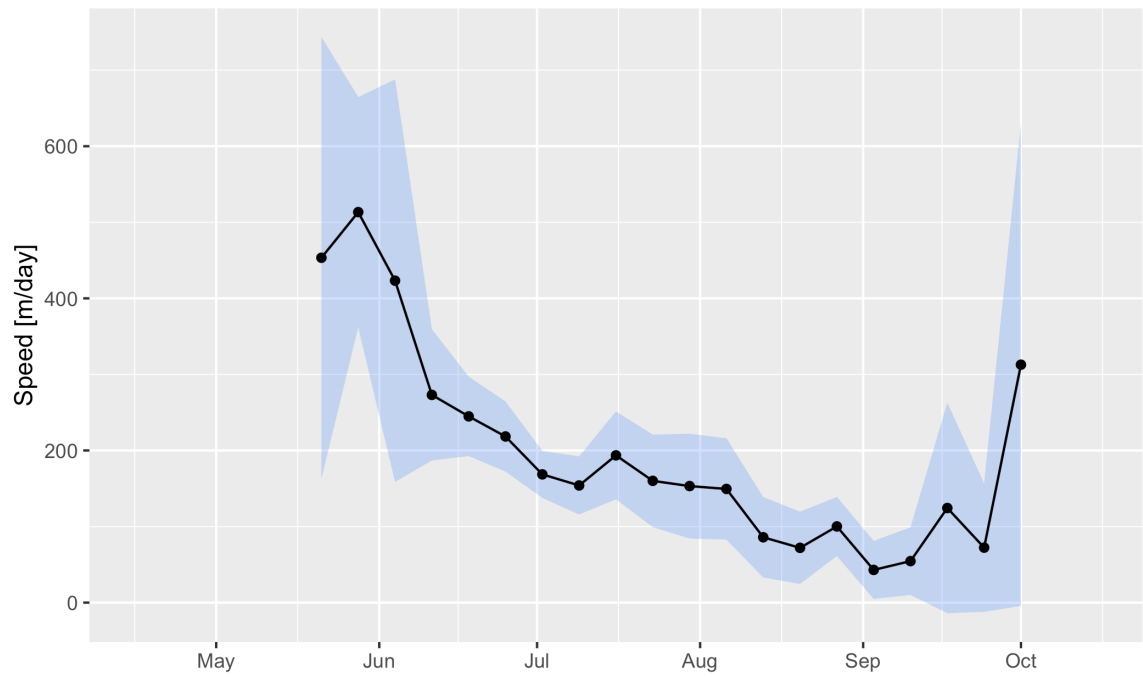
**Figure 13 Speed estimates for Virginia wood turtles throughout 2018 pooled by sex. Intervals represent 95% confidence intervals.**

Minnesota AKDEs are shown in Figure 14. Minnesota speed estimates are shown in Figure 15.



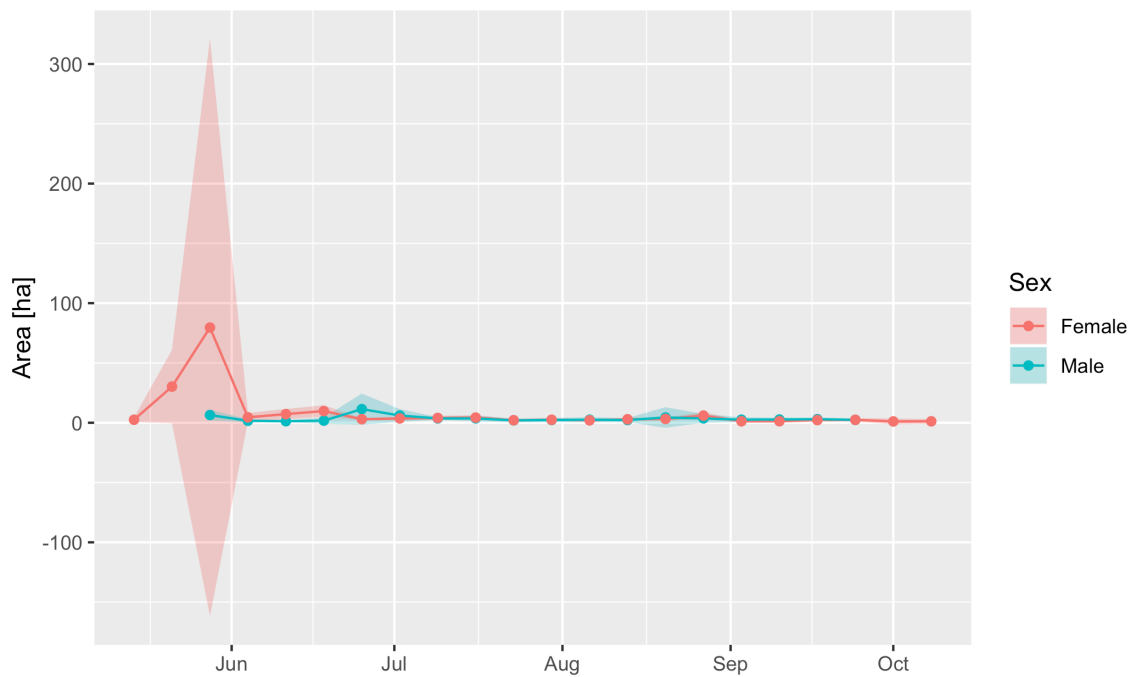
**Figure 14 Pooled AKDEs for Minnesota wood turtles throughout 2015. Intervals represent 95% confidence intervals.**



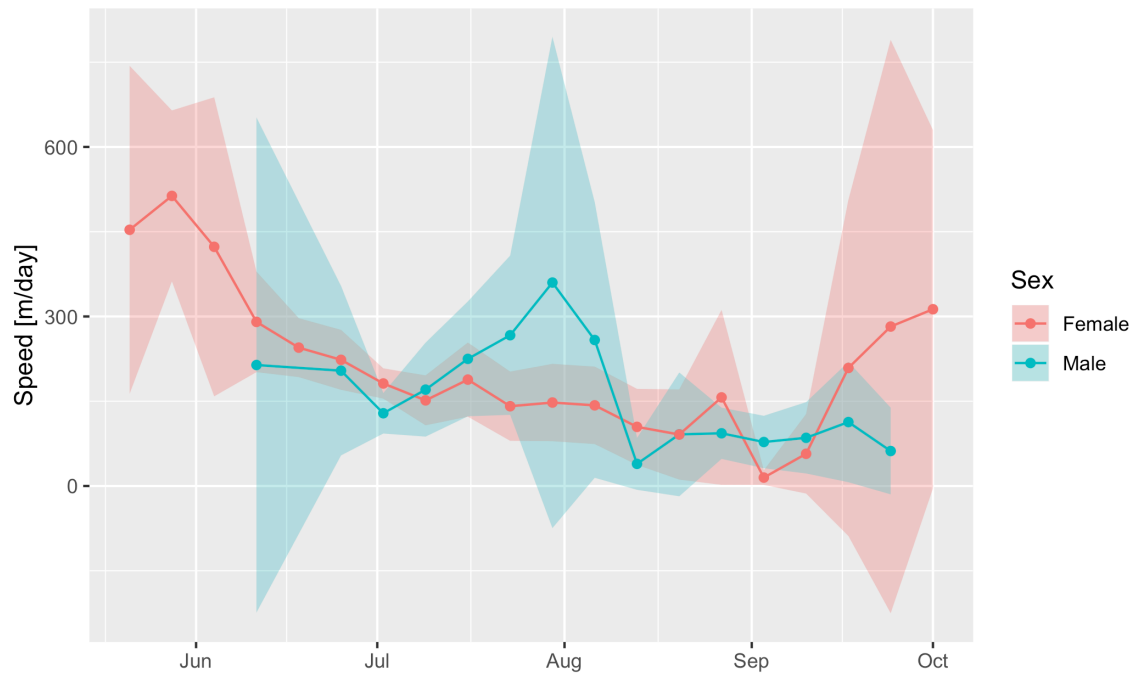


**Figure 15 Pooled speed estimates for Minnesota wood turtles throughout 2015. Intervals represent 95% confidence intervals.**

Minnesota AKDEs pooled by sex are shown in Figure 16. Minnesota speed estimates pooled by sex are shown in Figure 17.

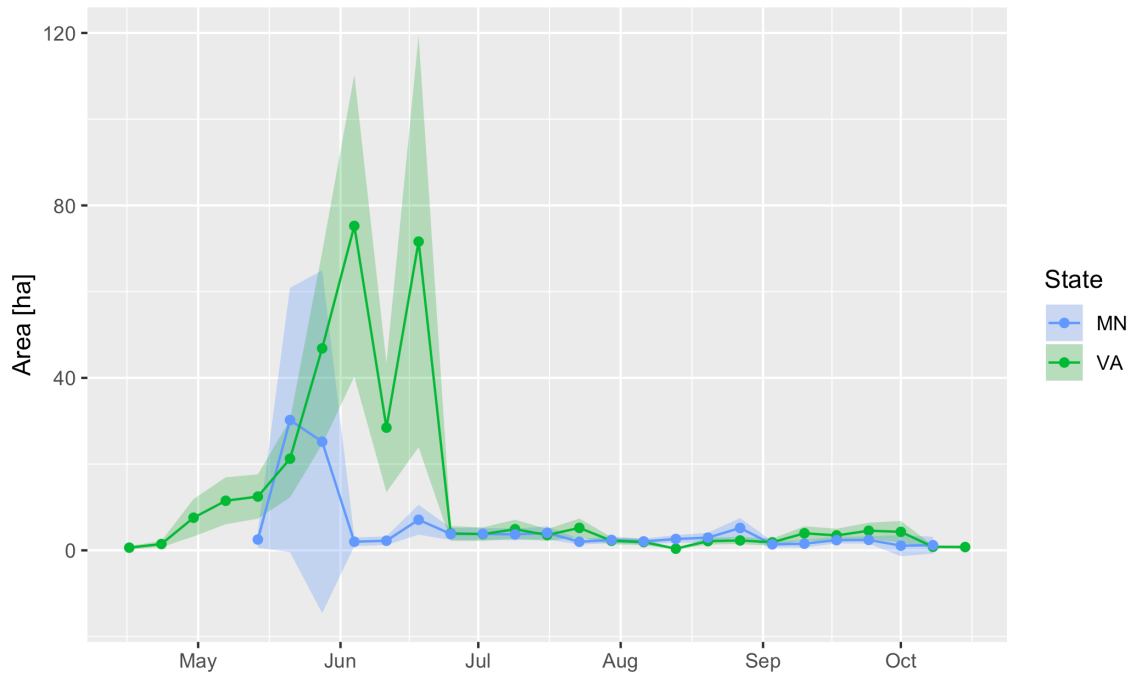


**Figure 16 AKDEs for Minnesota wood turtles throughout 2015 pooled by sex. Intervals represent 95% confidence intervals.**

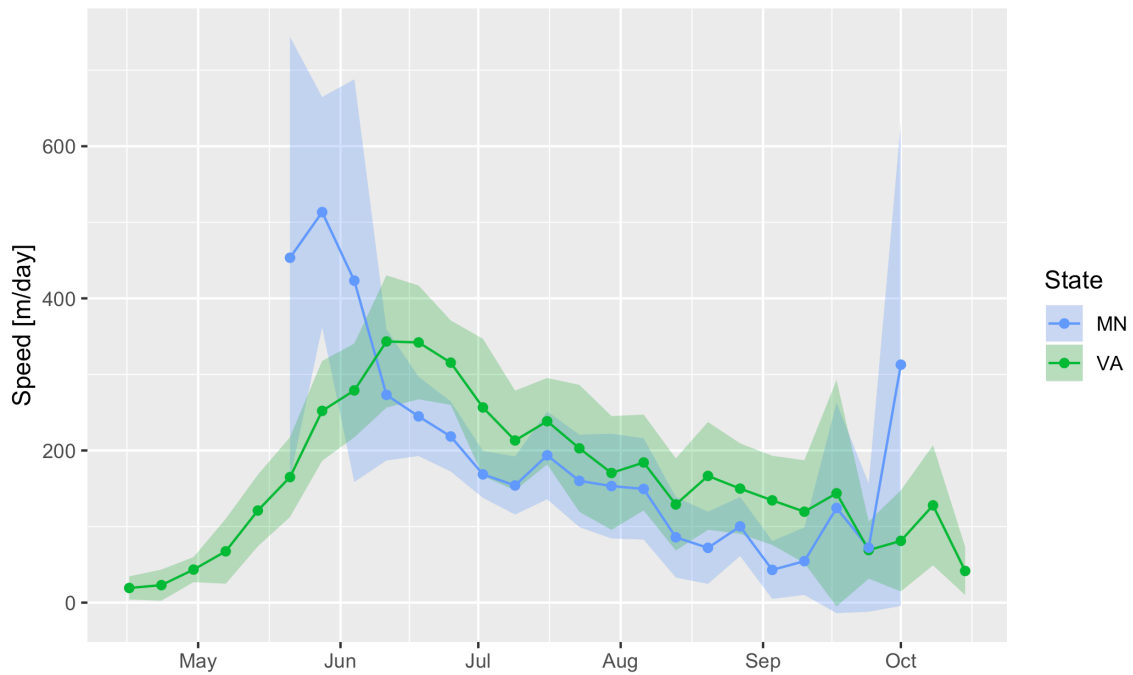


**Figure 17 Speed estimates for Minnesota wood turtles throughout 2015 pooled by sex. Intervals represent 95% confidence intervals.**

Pooled AKDEs (excluding M703) and speed estimates for each state in their respective years are shown together for comparison in Figure 18 and Figure 19, respectively.



**Figure 18 Pooled AKDEs for wood turtles in Virginia (2018; excluding M703) and Minnesota (2015). Intervals represent 95% confidence intervals.**



**Figure 19 Pooled speed estimates for wood turtles in Virginia (2018) and Minnesota (2015). Intervals represent 95% confidence intervals.**

## Discussion

Our results indicate that wood turtles utilize more area during late spring and early summer than at other times of year (Figure 10, Figure 14, Figure 18). They also show that this trend is driven largely by female individuals, while male home range area remains more consistent throughout the year (Figure 12, Figure 16). This is likely due to nesting movement during this time period, as some females travel long distances to nest (see Chapter IV).

A similar trend was observed for movement speed throughout the year, with faster speeds seen during late spring to early summer (Figure 11, Figure 15, Figure 19). Although females appear to peak at slightly higher speeds during this period, they also seem to decline more than males in the latter portion of the year (Figure 13, Figure 17).

Overall, our results show these trends more clearly in the Virginia population than in the Minnesota population. This is likely due in part to a longer active season in Virginia allowing for more models to be fit. Additionally, a smaller sample size of males in the Minnesota population likely obscured differences between the sexes in this case.

Both home range area and movement speed can be viewed as a proxy for risk of mortality within the context of a modern, fragmented landscape. As these metrics increase, individuals become more likely to come in contact with roads and agricultural areas. Our results therefore indicate that female wood turtles are at a greater risk of mortality during the nesting season (see Chapter IV for a more detailed exploration), consistent with research into road mortality rates in turtle populations (Steen et al. 2006, Gibbs and Steen 2005, Steen and Gibbs 2004). Male movement metrics do not peak at this time of year and remain more consistent throughout the season, but become higher than those of females later in the season (Figure 12, Figure 13). This is consistent with recent research into road mortality rates for a number of North American freshwater turtle species (Carstairs et al 2018).

As GPS technology continues to improve and miniaturize, more studies of fluctuations in fine-scale turtle movement patterns throughout the active season will be needed to verify and clarify these results.

## CHAPTER IV: LONG-DISTANCE MOVEMENTS OF WOOD TURTLES IN VIRGINIA

### Introduction:

Long-distance movements in non-marine turtles is a known occurrence, but evidence of these movements has to this point been more anecdotal than empirical, due largely to a general lack of large-scale tracking studies. Here, we break down long-distance movements into three categories: nesting, relocation following flood displacement, and dispersal.

Nesting movements for wood turtles are not necessarily long-distance movements. For some individuals, their selected nest site may be immediately adjacent to or even within the area they utilize for other activities throughout the year. Some females, however, do make long-distance movements of multiple kilometers both to and from nesting sites each year (Akre et al. unpublished data), a pattern also observed in *Malaclemys terrapin* (Gibbons et al. 2001, Butler et al. 2004).

These long-distance movements may occur for a few reasons, especially in such a long-lived species. One possibility is that female turtles displaying nest site fidelity shift their general home range area over time as the habitat changes, making it less suitable for activities such as foraging and thermoregulation. A second possibility is that females displaying home site philopatry shift their nesting site over time as it becomes unsuitable

for nesting due to, for example, increased vegetation, flooding, or an increase in local predator populations. Both nest-site fidelity (e.g. Freedberg et al. 2005, Bona et al. 2012, Rowe et al. 2005) and general home range philopatry (e.g. Bernstein et al. 2007, Andres and Chambers 2006, Sheridan et al. 2010) have been documented in freshwater turtle species and have been observed in wood turtles as well (Akre et al. unpublished data, Sweeten 2008).

Given the value of nesting females for the reproductive rate and therefore the long-term viability of wood turtle populations, long-distance nesting movements are in need of further research. Long-distance movements increase the likelihood of crossing roads and active agricultural fields, placing female turtles at a higher risk of mortality from both natural and anthropogenic causes during the nesting season. In fact, road mortality has been shown to put female freshwater turtles at a higher risk of mortality than males, resulting in male-biased sex ratios in many populations (Steen et al. 2006, Gibbs and Steen 2005, Steen and Gibbs 2004). Recent research, however, suggests that females are at a higher risk of road mortality only during the nesting season with male road mortalities being spread more evenly throughout the year. This results in no significant difference in road mortality between the sexes for most species (Carstairs et al 2018).

Relocation of wood turtles following displacement due to flood events is another reason wood turtles make long-distance movements. The first study into the homing abilities of wood turtles found that individuals are able to relocate to their previous home ranges when displaced by researchers, but that this ability was less effective for distances



greater than 2 km, leading the researchers to conclude that the species exhibits intermediate-ranged homing (Carroll and Ehrenfeld 1978).

More recently, researchers have studied the relocation of wood turtles following natural flood displacement events (Jones and Sievert 2009). Displacement distances ranged from 1.4 to 16.8 km and averaged 4.8 km (n=9). Of these individuals, three managed to relocate to their initial home range, travelling a maximum meandering distance of 3.7 km (2.5 km straight line distance). Researchers also noted that displaced individuals suffered higher mortality rates as well as lower mating and nesting rates in the year following displacement. Jones and Sievert (2009) believed that as much as 40% of the population at their study sites are displaced by flooding events each year.

Due to the increase in flooding events in the US due associated with climate change (Mallakpour and Villarini 2015), the proportion of wood turtles displaced by flooding events will likely continue to increase, putting populations at greater risk. For this reason, it is important to understand the prevalence of such events as well as their timing and the movement patterns of affected individuals.

A third reason for long-distance movement in wood turtles is dispersal behavior. This encompasses all intentional movement of individuals away from their conspecifics in search of breeding opportunities or habitat. This kind of dispersal has been implied by coarsely sampled recaptures of individual wood turtles (e.g. Akre, unpublished data, Sweeten 2008), but never explicitly shown. Therefore, many questions surrounding dispersal behavior in wood turtles remain unresolved. Further research is needed to quantify the proportion of turtles that are likely to disperse within their lifetime, how

many times or how long they are likely to disperse, how far they travel, and which demographics are most likely to disperse.

Dispersal behavior studies have been common in both mammals and birds. In these taxa, dispersal movements are generally linked to sex-specific philopatry based on mating systems; dispersal tends to be male-biased in mammals and female-biased in birds (Greenwood 1980, Handley and Perrin 2007). Studies into dispersal in reptiles in general and freshwater turtles in particular, have been much less common. Based on both a mark-recapture study and genetic analyses, Dubey et al. (2008) found evidence of male-biased dispersal in a snake species (*Stegonotus cucullatus*), while a study of juvenile loggerhead turtles (*Caretta caretta*) also found male-biased dispersal (Casale et al. 2002). For freshwater turtle species, evidence of male-biased dispersal has been found for both radiated tortoises (*Astrochelys radiata*; Paquette et al. 2010) and diamondback terrapins (*Malaclemys terrapin*; Sheridan et al. 2010).

We expect dispersal in wood turtles to be male-biased as well and mostly comprised of young adults and sub-adults. This is for several reasons. First, young individuals are less likely to have settled into an established home range. Second, adults are able to travel faster and over farther distances than juveniles, due to their physical size and available energy. Finally, adult females are likely to exhibit nest-site fidelity and invest energy in egg development. We also predict that dispersal is likely to occur most often through and parallel to stream networks but that individuals in populations located in first-order streams, such as the Virginia study area for this study, will not only disperse downstream, but also over ridges and into adjacent watersheds.

Additionally, photo-identification using Wild-ID at our Virginia study site and surrounding streams has shown seven cases of turtles moving between streams. All seven were male although not all appeared to be young individuals (unpublished report).

Capturing and detailing the dispersal movements of wood turtles is an important step in conservation actions. Similar to female nesting movements, dispersal behavior puts individuals at a much higher risk of mortality, as they are exposed to not only unfamiliar landscapes, but also roadways, agricultural fields, and urban areas. It is therefore important to know when such movements occur, how often they occur, what distances they cover, and what kinds of paths they follow.

These dispersal movement paths could be analyzed alongside stream and road network buffers as well as land cover class data to parameterize resistance surfaces. These, in conjunction with genetic data being collected and photo identification from several surrounding sites, could lay the groundwork for future connectivity models which would in turn focus conservation for this species at a larger, landscape-level scale.

## **Methods:**

### ***Nesting Movement***

To analyze nesting movements, 2018 data from 13 of the 14 randomly selected Virginian females were used. One female was excluded as she was fatally hit on the road on her way to her nesting site. All data were collected with an hourly GPS location schedule and cleaned as described in chapter II.

Data for each individual were then spatio-temporally clustered using the R package *mclust* (Scrucca et al. 2016). *Mclust* models are based on finite Gaussian mixture models, estimated using the expectation-maximization (EM) algorithm, and selected according to the Bayesian information criterion (BIC). The latitudes, longitudes, and timestamps for each dataset were used in the *Mclust* function and allowing for up to 30 unique clusters. These clusters were then used as a reference of potential behavioral change points for nesting movement. By looking at the movement data itself and with the *a priori* knowledge of the known nesting sites at the Virginia field site (based on Akre and Ruther 2015) clusters were determined to represent either pre-nesting, nesting, or post-nesting behavior.

Using these classifications, the data for each female were split into these categories for further analysis. Nesting was considered any point captured between the first point of the first nesting cluster and the last point of the final nesting cluster. Movement models were calculated using CTMM and bootstrapped if the area DOF estimate was below five in the initial model (possible in all but one case). AKDEs were calculated along with robust speed estimates. Random-effects meta-analyses were used to pool estimates.

### ***Flood Displacement***

From 2016 to 2018, we observed two definite flood displacement events as well as a potential, fatal third event. For the two known events, because both turtles successfully relocated, data were clustered and split using *mclust* into before flood,

relocation, and after relocation groups. These were fed through CTMM to estimate AKDE and speeds, but analyses were unsuccessful. Because the relocation movements were so directional, the resultant movement models were poorly defined. This meant that AKDEs had extremely high variances and speed estimates were unable to be calculated.

Therefore, speeds were estimated using a less robust approach. Median locations were calculated for each day and the distances between them were calculated, giving median daily displacements. These were then summed for each period to calculate total distance travelled as a cumulative median daily displacement (CMDD) and divided by the length of the period to calculate average speed. These estimations are, therefore, less accurate than CTMM speed estimates and likely underestimated. They also have no associated confidence intervals.

### ***Dispersal Movement***

Over the course of our tracking in Virginia, two dispersal events were observed, both during the summer of 2018. The data for these individuals were split into dispersal and non-dispersal periods using mclust, but CTMM models for dispersing behavior were unable to produce well defined AKDE and speed estimates in most cases. Speeds and distances were therefore calculated using median daily displacements.

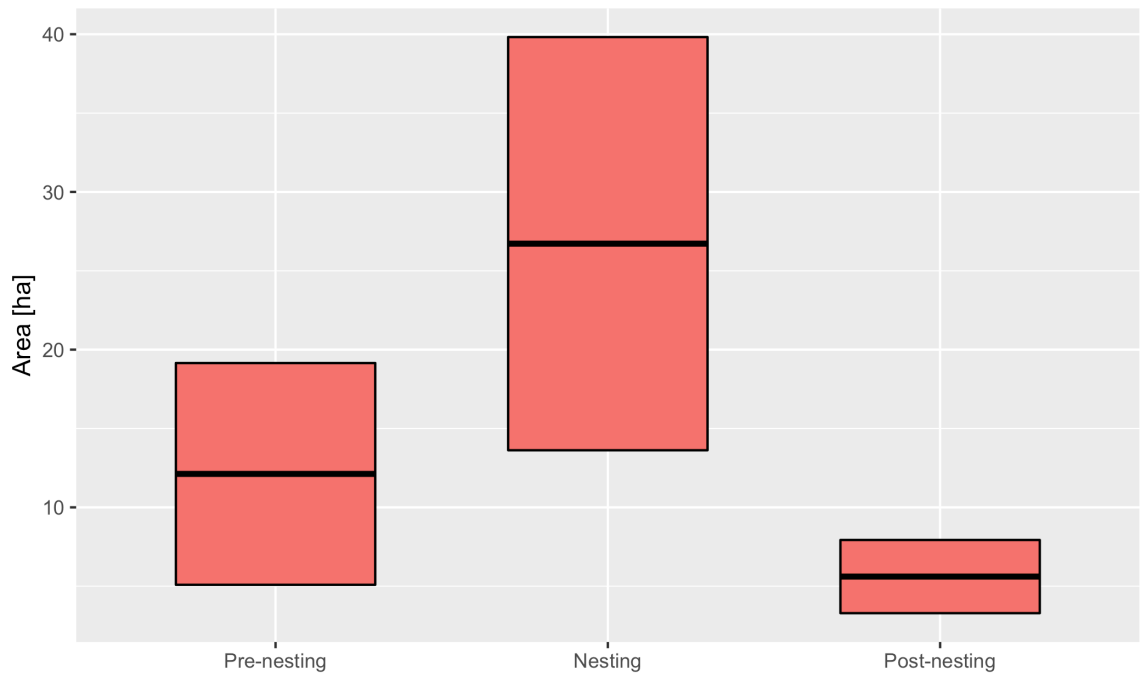
## Results:

### *Nesting Movement*

The average AKDEs for female turtles prior to nesting was 17.96 ha (range = 1.48 to 86.17, SD = 23.71). During nesting the average was 520.68 ha (range = 3.79 to 3,568.32, SD = 1020.84). After nesting the average was 20.97 ha (range = 1.21 to 171.14, SD = 45.56). One-sided, paired t-tests indicated that area estimates during nesting were marginally significantly larger than pre-nesting estimates ( $p = 0.051$ ) and were significantly larger than post-nesting estimates ( $p = 0.045$ ).

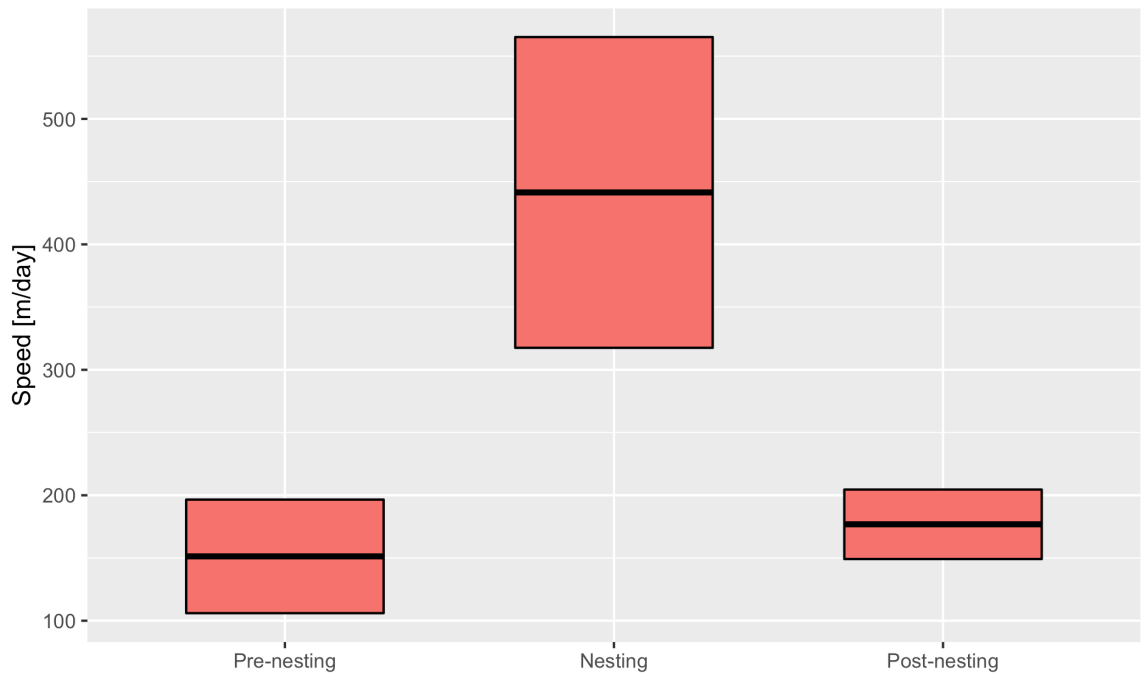
Average speed estimates for females prior to nesting was 135.87 m/day (range = 40.97 to 272.32, SD = 63.18). During nesting the average was 466.49 m/day (range = 202.74 to 926.94, SD = 222.55). After nesting the average was 266.65 m/day (range = 137.78 to 491.38, SD = 130.62). One-sided, paired t-tests indicated that speed estimates during nesting were significantly larger than both pre-nesting estimates ( $p < 0.001$ ) and post-nesting estimates ( $p < 0.022$ ).

The pooled AKDE home range area for pre-nesting female movement was 12.12 ha (95% CI [5.09, 19.15],  $k = 13$ ). For nesting movements, the pooled area estimate was 26.72 ha (95% CI [13.62, 39.82],  $k = 13$ ). For post-nesting movements, the pooled area estimate was 5.61 ha (95% CI [3.29, 7.93],  $k = 13$ ) (Figure 20).



**Figure 20 Pooled AKDEs for females before, during, and after nesting periods. Intervals represent point estimates and 95% confidence intervals.**

The pooled mean speed estimate for pre-nesting female movement was 151.30 m/day (95% CI [106.03, 196.56],  $k = 12$ ). For nesting movements, the pooled speed estimate was 441.38 m/day (95% CI [317.53, 565.23],  $k = 12$ ). For post-nesting movements, the pooled speed estimate was 176.86 m/day (95% CI [149.18, 204.55],  $k = 12$ ) (Figure 21).



**Figure 21 Pooled average speeds for females before, during, and after nesting periods. Intervals represent point estimates and 95% confidence intervals.**

### ***Flood Displacement***

Two definite flood displacement events were observed in Virginia during the course of our study. The first was M85 in the spring of 2016 and the second was M60 in the spring of 2017.

When first radio-tracking M85 in 2016, he was discovered on March 31 1.89 km downstream of his typical home range (1.62 km SLD). On May 3, a GPS unit was attached to his shell when he was radio-tracked 0.3 km upstream from his March 31 location (0.28 km SLD). By May 26, he made it back to his typical home range, where he



remained for the remainder of the year. Within the scope of our GPS data, M85's relocation lasted 23 days, during which time his cumulative median daily displacement (CMDD) was 1.10 km, indicating that he moved an average speed of 47.87 m/day. His movement path was close to the stream for most of his relocation movement, as he appeared to follow a streamside trail. Over the rest of the 163 days he was tracked that year, M85's cumulative CMDD was 6.03 km, giving him an average speed of 37.00 m/day.

Tracking data for our other displaced turtle, M60, in 2017 began on April 19. Sixteen days later, on May 5, his GPS unit showed him 2.10 km downstream (1.99 km SLD) of his previous home range for that year. The GPS unit had not recorded a point for the previous two days, likely indicating that it was submerged in the stream. Previous to this displacement, his CMDD was 1.07 km, giving him an average speed of 66.65 m/day. Over the following 40 days, M60 made his way back upstream. Interestingly, the majority of his movement path was in upland habitat, removed from the stream by greater than 300 m. When his relocation movement came to an end on June 14, M60 had returned to the stream 0.72 km upstream (0.68 km SLD) from his initial home range. During this relocation period, M60's CMDD was 4.80 km, giving him an average speed of 120.05 m/day. Over the remainder of the 146 days he was tracked that year, M60 split his time between his original and secondary activity areas. His CMDD was 11.24 km for this period, meaning his average speed was 76.96 m/day.

A third flood displacement event was suspected in 2018, when M4100 was discovered dead and plastron-up on the streambank approximately 120 m downstream (110 m SLD) from his nearest recorded locations that year.

### ***Dispersal Movement***

Over the course of three years of GPS tracking data in Virginia, two dispersal events were observed. In 2018, two young male turtles, M304 and M703, left our study site by travelling over a ridgeline and continuing considerable distances into an adjacent watershed.

M304 was first discovered at our Virginia field site on June 28, 2017. Because he had not been found during previous stream surveys and due to his location near the most downstream section of our site, it was suspected that he had wandered upstream into our site from a different population. A radio-transmitter was attached to him so that he could receive a GPS unit the following spring.

GPS tracking data for M304 began on April 14, 2018. He remained near his initial 2017 capture location until May 9. During this time period of 25 days, his CMDD was 0.34 km, giving him an average speed of 13.78 m/day for this time period. On May 9, he began travelling upstream, settling into range-resident behavior again on May 20. During this time period of 11 days, his CMDD was 0.69 km, bringing his average speed up to 63.14 m/day. He remained at this upstream location for 12 days, with a CMDD of 1.50 km and an average speed of 124.95 m/day.

On June 1, M304's dispersal movement began as his trajectory let directly away from the stream into upland habitat. After initially traveling uphill his movement paralleled the ridgeline for approximately 2.68 km as he remained 200-300 m from the top. He then turned uphill once again and reached the top of the ridge on June 21, climbing over 280 m in elevation from his starting location on the 1. From there, he travelled down the other side of the ridge until he reached another stream at the bottom on July 4, dropping over 400 m in elevation. During this initial 33 days of dispersal, his CMDD was 6.67 km, giving him an average speed of 202.08 m/day. Upon reaching the stream, M304 settled into range-resident behavior once again, staying in the general vicinity for 55 days before leaving it on August 28. During this residential period, his CMDD was 2.76 km, giving him an average speed of 50.27 m/day. To leave this stream, M304 crossed another, smaller ridge, climbing over 60 m to cross the ridgeline and descending over 110 m to a river on the far side. In doing so, he crossed Main St in a small town. From there, he continued moving, going down river for approximately 1.5 km before leaving the river to cross 1 km of open agricultural and farmland. He crossed another stream and eventually came back to it farther upstream, where he followed it a short way and settled into residential behavior once again on October 6. His CMDD for this dispersal period was 5.74 km, giving him an average speed of 147.07 m/day. M304 remained in the stream at this location for the remainder of the year. His tracking data extended until October 12, during which period his CMDD was 0.49 km, making his average speed 80.89 m/day.

Between his two large dispersal movements, M304's CMDD came to 12.4 km for a 72-day period, making his overall average displacement speed 172.28 m/day. From his initial location in April to his final location in October, his total SLD displacement was 9.46 km.

Unlike M304, our other disperser, M703, had been a known resident of our study site for a long time. He was first found in 2005 during a visual encounter survey. Based on annuli counts from that capture he was four years old at the time, putting his age when we began tracking him in 2018 at 17 years old. Between his initial capture in 2005 and receiving a GPS unit in 2018, M703 had been seen at our site 24 times in eight different years, making it highly likely that he was range-resident that entire time.

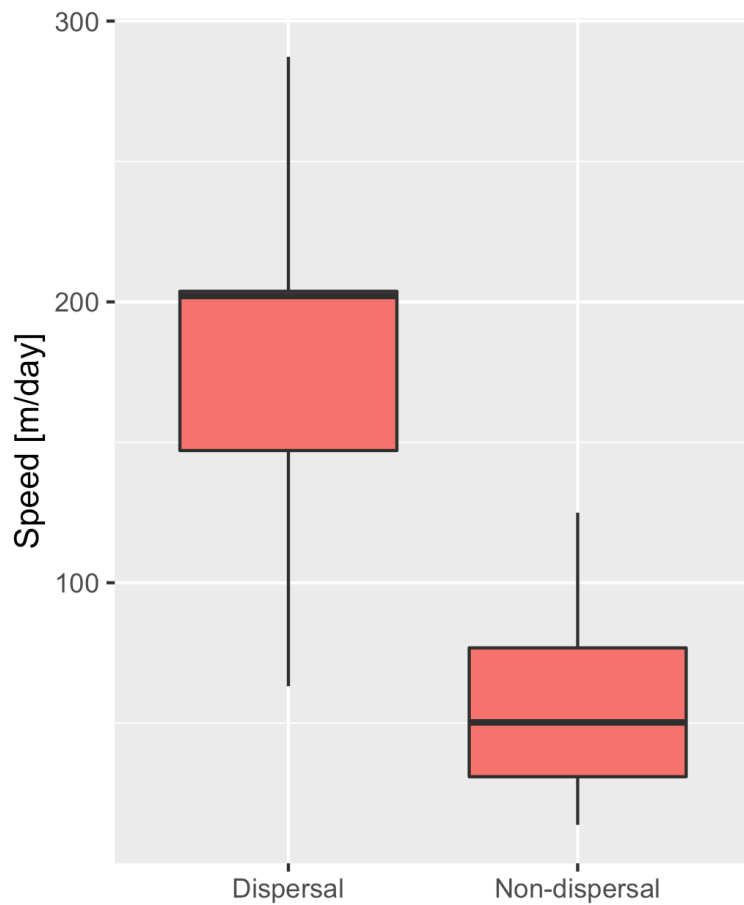
For the 61 days from April 3 to June 3 in 2018, M703 was range-resident. His CMDD for this time came to 1.38 km making his average speed 22.57 m/day. On June 3, he began his dispersal movement into the uplands, toward the same ridgeline that M304 had begun moving toward two days prior. He climbed over 240 m in elevation to reach the top of the ridge on June 9, and then continued down the other side. Although his path took him near a small stream, he appeared to travel largely by land until at least June 19, when he reached another stream where he became range-resident for a brief period. During this initial dispersal period, M703's CMDD was 4.88 km over a period of 17 days, making his average speed 287.29 m/day. M703 remained near this location until June 30, 10 days later. His CMDD for this period was 0.73 km and his average speed was 72.73 m/day.

The next location for M703 was two days later and 1.98 km away along the river into which the stream he had been at flows, making it likely that he travelled downstream by water most of this distance. This river was the same one M304 would arrive at 59 days later on August 30. From there, M703 travelled up-river and then upstream in a tributary stream—the same one M304 would cross and then end the year in. Unlike M304, M703 remained right along this streambed as he travelled, continuing his movement until August 30, at which point he remained residential for the remainder of the year. For this second phase of his dispersal, his CMDD was 12.43 km making his average speed 203.77 m/day. His residential period at the end of the year encompassed 80 days of GPS data, during which his CMDD came to 3.14 km and his average speed was 39.29 m/day.

Between his two dispersal movements, M304's CMDD came to 24.86 km for a 78-day period, making his overall average displacement speed 318.71 m/day. From his initial location in April to his final location in November, his total SLD displacement was 12.86 km.

In the course of tracking these two dispersers at their new locations near the end of the year, multiple other individual wood turtles were seen incidentally, indicating that they were able to successfully locate new wood turtle populations.

Speeds as calculated using CMDDs for both dispersal and non-dispersal movement are summarized in Figure 22.



**Figure 22 Average speeds for M304 and M703 during dispersal and non-dispersal periods calculated using cumulative median daily displacement (CMDD).**

## **Discussion:**

### ***Nesting Movement***

Our results indicate that female wood turtles use more area while making nesting movements than they do in the remainder of the year following nesting (Figure 9). We also found that females are moving at significantly greater average speeds during nesting

movements when compared to before or after such movements (Figure 20). This finding indicates that females are at a greater risk of mortality from threats such as cars and agricultural machinery during nesting season, as they are likely to be moving farther distances during that period. In fact, a motorist fatally struck one female in our study (F91) as she made her way to her usual nesting site. Considering the importance of reproductive female survivorship to a species with such a slow reproductive strategy (Heppell 1998), conservation actions should be planned with this particular demographic and time period in mind.

### ***Flood Displacement***

Our study was limited in its investigation of flood displacement due to our limited sample size of such events. One of 10 tracked turtles in 2016 was displaced a significant distance and one of 11 was displaced in 2017. In 2018, one suspected and fatal flood displacement occurred in our sample of 30 turtles. Jones and Sievert (2009) found rates of flood displacement much higher than this. These rates likely depend heavily on variables such as habitat structure, stream gradient, as well as flood size, frequency, and timing.

Our results, however, provide support for the homing ability of wood turtles over intermediate distances consistent with past research (Jones and Sievert 2009, Carroll and Ehrenfeld 1978, Barzilay 1980). These studies indicate that turtles displaced by flooding events travel at greater average speeds to return to their home range than they typically would. This likely increases stress on the individual, decreasing their overall fitness and

chance of survival. Additionally, our results provide an example of potential dangers of flood displacement, with such an event suspected to have contributed to the death of one of our turtles (M4100).

### ***Dispersal Movement***

This is the first study to capture freshwater turtle dispersal behavior at this scale and resolution. Although our sample size of two dispersal events is small, we believe there is important information to be gained from these as case studies.

When including all turtles tracked in this study across all three years, our rate of dispersal is 2 out of 36, or 5.56%. However, if limited to only male turtles, it becomes 2 out of 17, or 11.76%. Out of all randomly selected males, the rate comes to 1 out of 10, or 10%. Out of all turtles in our study, our one disperser, M703, is thought to be the youngest at 17 years old. If our hypothesis that young male turtles are more likely to disperse is correct, then rates of dispersal for this demographic may be much higher than 10-11.76%. Therefore, we recommend that future research into wood turtle dispersal behavior focus on tracking young adult male turtles for multiple years.

These case studies also confirm our hypothesis that individuals dispersing from headwater streams are not limited to following streams downstream but will also travel over land and over ridgelines to enter new watersheds. This may make the protection of land-based dispersal corridors more imperative in these habitats. At this point, however, it is unknown how common over-land dispersal movements are in higher-order waterways.



Due to the more directionally persistent nature of dispersal events, individuals are more likely to pass through dangerous areas. For instance, both of our tracked turtles travelled across wide expanses of active farmland and crossed multiple roads. Although some individuals, such as M703, may disperse largely along waterways, others may not, similar to M304. Our data also suggests that, similar to nesting females and turtles relocating following flood displacement events, dispersing individuals travel at greater average speeds than more range-resident individuals, which likely increases stress levels.

In terms of timing, both of our dispersing turtles left in the beginning of June, a week to two weeks after the onset of the nesting season in our population that year. The movements of both were characterized by two larger dispersal events interrupted by a period of range residency. In one, this period was only 10 days, but in the other it was 55 days long. Although one disperser ended his movement by the end of August, the other continued moving into October, around the time that all wood turtles in the region begin returning to streams for the winter.

It is also interesting to note the similarity in movement paths between our two observed dispersers. Both individuals began in the same population, separated by 2.64 km as of April 14. They began their dispersal movements within two days of each other, travelled over the same ridgeline, crossed the same river, and travelled up the same tributary to that river, where they eventually settled down for the winter. Despite this similarity, the differences in timing of their breaks in dispersal movement meant that they were never closer than 2.57 km from each other, based on median daily locations. In

addition, although they travelled over 12.4 and 24.86 km overall, at the end of both dispersal movements on October 12 they were only 5.71 km away from each other.

Although the landscape was unfamiliar to both turtles, they both ended up at another wood turtle population in the same stream system, even after crossing a river along the way known to have a population of wood turtles. This raises a number of questions. Were both turtles were following similar cues that made their movement paths similar? If so, are these cues olfactory, landscape, habitat, weather, or something else? With such a small sample, the similarity could be pure coincidence. Further research into dispersal behavior is needed to answer these questions.

Overall, these case studies demonstrate the occurrence and scale of wood turtle dispersal behavior, as well as the dangers inherent in them within the context of a modern landscape. These movements are likely important for the flow of genes between disparate populations, which itself is vital to the long-term survival of these populations. Therefore, conservation efforts cannot be focused on single populations, but must be refocused toward a landscape-level scale for protection of the species as a whole. Interconnected populations, as well as the corridors between them, need to be priority targets of conservation (e.g. Pittman and Dorcas 2009, Milam and Melvin 2001).

## APPENDIX A

### Virginia Sampling Schedules

**Table 3 Virginia turtle sampling schedules reported as GPS model used. Telemetry Solutions (TS) units were set to take 3 points per day at 0900, 1300, and 1700. Lotek Pinpoint-240 units were set to take a point at every hour mark. “Both” indicates that a turtle received both types of unit that year.**

<b>Turtle</b>	<b>Sex</b>	<b>2016</b>	<b>2017</b>	<b>2018</b>
13	F	TS		
40	F			Lotek
46	F			Lotek
47	F	TS	Lotek	Lotek
71	F			Lotek
91	F		TS	Lotek
94	F			Lotek
98	F		TS	Lotek
217	F			Lotek
220	F			Lotek
231	F	TS	Lotek	Lotek
235	F	TS		
242	F			Lotek
343	F			Lotek
403	F	TS		
406	F		Both	Lotek
702	F			Lotek
705	F			Lotek
816	F			Lotek
20	M			Lotek

60	M	TS	TS	
62	M			Lotek
85	M	TS		
87	M			Lotek
90	M			Lotek
221	M			Lotek
226	M			Lotek
236	M	TS	Both	Lotek
262	M		Both	Lotek
270	M	TS	Both	Lotek
271	M	TS		
304	M			Lotek
420	M		Both	Lotek
703	M			Lotek
4100	M		Both	Lotek
8218	M			Lotek

## Minnesota Sampling Schedules

**Table 4 Minnesota turtle sampling schedules with “X” indicating that a turtle was tracked that year. All turtles were sampled at 10-minute intervals.**

<b>Turtle</b>	<b>Sex</b>	<b>2015</b>	<b>2016</b>
310	F	X	
320	F	X	X
783	F	X	
1001	F	X	X
1230	F	X	X
1232	F	X	
1605	F	X	X
1615	F		X
2028	F	X	X
2035	F	X	X
2066	F	X	X
2111	F	X	X
2134	F		X
2139	F	X	X
3311	F	X	
3321	F	X	X
3322	F	X	X
3341	F	X	X
3351	F	X	X
1238	M	X	X
1292	M		X
1610	M	X	X
2123	M	X	X
2141	M	X	
3367	M	X	X

## APPENDIX B

### Virginia Home Range Estimates

**Table 5 Home Range estimates for Virginia turtles in hectares. Bounds on AKDEs represent 95% confidence intervals.**

Turtle	Sex	AKDE	Lower bound	Upper bound	DOF	95KDE	95MCP
13	F	106.30	48.15	187.08	8.82	42.99	15.13
40	F	23.54	13.58	36.20	16.47	15.24	19.79
46	F	271.98	92.87	545.61	5.37	68.78	62.28
47	F	13.18	10.62	16.01	91.67	12.70	13.39
71	F	14.59	9.62	20.58	27.09	10.71	17.91
91	F	533.16	256.46	909.40	10.07	201.28	294.22
94	F	140.43	53.08	269.53	6.30	46.48	28.66
98	F	737.29	324.06	1,317.46	8.29	283.39	220.26
217	F	21.84	12.56	33.66	16.29	35.58	25.05
220	F	68.49	36.64	110.15	13.16	39.18	43.13
231	F	67.46	46.55	92.20	33.39	36.22	31.41
235	F	884.16	380.48	1,596.56	7.95	321.83	172.68
242	F	21.61	14.84	29.63	32.62	14.50	11.92
343	F	31.54	9.73	65.93	4.67	18.07	20.63
403	F	7.01	2.98	12.73	7.78	1.04	1.23
406	F	55.68	28.21	92.33	11.41	26.23	23.88
702	F	24.12	11.25	41.83	9.38	8.81	19.35
705	F	69.51	34.91	115.81	11.17	25.10	35.68
816	F	229.43	62.73	502.21	4.02	32.55	24.61
20	M	17.34	11.58	24.26	28.57	20.66	23.64
60	M	201.97	144.57	268.81	40.44	184.86	279.81
62	M	36.43	16.84	63.44	9.22	27.38	16.13
85	M	485.48	184.60	929.28	6.36	202.06	116.79

87	M	5.21	4.00	6.58	62.31	4.78	4.11
90	M	7.62	4.91	10.91	24.64	5.98	6.60
221	M	6.19	3.87	9.03	21.92	5.58	4.22
226	M	36.08	18.81	58.89	12.28	27.77	19.09
236	M	85.61	63.51	110.95	49.87	23.61	29.23
262	M	4.50	3.26	5.93	43.15	3.69	4.07
270	M	38.57	29.46	48.89	60.38	30.28	20.48
271	M	200.06	78.88	376.64	6.76	66.34	59.52
304	M	32,962.55	1,194.77	115,484.20	1.13	3,766.02	2,482.06
420	M	8.10	6.06	10.42	53.01	10.28	8.30
703	M	66,219.59	2,295.57	233,564.30	1.11	9,024.70	4,060.59
4100	M	50.13	27.20	79.97	13.69	26.59	44.02
8218	M	9.18	5.96	13.09	25.31	11.59	10.10

## Minnesota Home Range Estimates

**Table 6 Home Range estimates for Minnesota turtles in hectares. Bounds on AKDEs represent 95% confidence intervals.**

Turtle	Sex	AKDE	Lower bound	Upper bound	DOF	95KDE	95MCP
310	F	64.13	20.69	131.69	4.96	8.57	10.66
320	F	712.08	358.27	1,185.36	11.22	459.08	471.1
783	F	208.03	85.2	384.72	7.24	30.22	31.05
1001	F	33.74	19.29	52.15	16.03	20.99	22.14
1230	F	6.51	4.12	9.42	22.98	4.21	5.15
1232	F	211.1	23.61	599.24	1.9	45.5	25.98
1605	F	125.08	50.72	232.43	7.11	67.35	57.75
1615	F	1,146.58	93.91	3,482.17	1.6	133.19	44.15
2028	F	160.19	96.9	239.14	19.32	27.27	99.85
2035	F	40.41	20.01	67.85	10.79	13.41	13.34
2066	F	153.09	74.7	259.12	10.42	39.14	67.21
2111	F	19.85	7.93	37.15	6.92	11.3	9.43
2134	F	1,244.76	261.01	2,982.04	3.05	463.58	277.92
2139	F	3.27	2.36	4.32	42.19	3.06	3.57
3311	F	13.85	6.33	24.25	9	7.48	8.84
3321	F	9.08	5.63	13.34	21.12	6.94	7.45
3322	F	14.99	9.12	22.31	19.69	6.24	7.72
3341	F	4.5	3.58	5.52	81.99	4.32	4.93
3351	F	13.23	7.06	21.31	13.09	7.16	9.3
1238	M	3.45	2.59	4.42	54.44	3.18	3.76
1292	M	17.24	8.68	28.68	11.24	14.09	9.81
1610	M	255.36	111.6	457.6	8.2	23.37	41.04
2123	M	13.64	8.4	20.12	20.61	9.55	10.92
2141	M	13.32	7.7	20.46	16.59	14.5	11.3
3367	M	50.64	25.88	83.57	11.67	27.32	25.33



## APPENDIX C

### Virginia Speed Estimates

**Table 7** Speed estimates for Virginia turtles. Bounds represent 95% confidence intervals.

<b>Turtle</b>	<b>Sex</b>	<b>Speed [m/day]</b>	<b>Lower bound</b>	<b>Upper bound</b>	<b>DOF</b>
13	F	1,114.11	34.74	9.24E+06	0.04
40	F	198.06	172.18	234.17	43.84
46	F	151.79	142.96	169.34	108.18
47	F	146.54	142.1	150.43	863.28
71	F	224.14	185.35	253.16	42.45
91	F	419.7	371.86	460.37	157.76
94	F	244.21	205.79	292.94	39.33
98	F	325.03	312.6	335.93	267.91
217	F	231.05	166.25	315.94	11.44
220	F	192.53	176.69	209.82	125
231	F	202.55	197.58	207.36	672.18
235	F	414.71	237.44	728.52	3.34
242	F	190.6	178.49	201.78	148.48
343	F	203.01	153.35	273.19	11.09
403	F	-	-	-	-
406	F	236.56	181.57	292.63	16.94
702	F	171.79	138.1	213.15	19.43
705	F	172.5	147.29	194.89	51.55
816	F	291.35	215.37	373.29	15.07
20	M	217.83	200.37	239.45	108.72
60	M	498.56	430.2	541.84	111.07
62	M	-	-	-	-
85	M	-	-	-	-
87	M	89.01	79.35	103.88	48.93

90	M	120.49	110.64	129.76	68.55
221	M	65.49	36.55	126.14	2.42
226	M	179.99	150.68	213.7	33.94
236	M	141.92	137.68	149.41	276.72
262	M	44.32	39.71	49.27	107.38
270	M	170.08	163.73	176.97	424.31
271	M	-	-	-	-
304	M	-	-	-	-
420	M	307.08	232.45	391.19	19.72
703	M	-	-	-	-
4100	M	374.71	282.23	474.12	18.61
8218	M	83.46	72.16	94.34	61.54

## Minnesota Speed Estimates

**Table 8** Speed estimates for Minnesota turtles. Bounds represent 95% confidence intervals.

<b>Turtle</b>	<b>Sex</b>	<b>Speed [m/day]</b>	<b>Lower bound</b>	<b>Upper bound</b>	<b>DOF</b>
310	F	368.46	262.17	475.43	13.34
320	F	239.49	229.91	253.96	149.78
783	F	326.06	252.09	387.97	22.91
1001	F	342.05	272.1	422.64	21.89
1230	F	303.25	176.29	512.08	3.14
1232	F	243.48	191.84	304.7	21.81
1605	F	209.1	193.1	221.08	240.78
1615	F	114.34	106.48	124.58	120.69
2028	F	133.21	128.05	137.8	299.72
2035	F	134.91	126.97	143.72	167.2
2066	F	169.45	163.78	175.46	183.57
2111	F	1,050.50	15.35	4.88E+09	0.01
2134	F	246.47	237.71	259.47	184.84
2139	F	409.22	140.92	1,266.73	0.82
3311	F	267.6	124.02	551.55	1.98
3321	F	404.68	57.41	2,852.25	0.25
3322	F	184.1	160.75	216.64	37.44
3341	F	213.99	182.91	256.14	41.41
3351	F	337.67	150.58	740	1.67
1238	M	358.49	160.17	781.72	1.57
1292	M	1,096.90	56.68	3.62E+06	0.07
1610	M	76.86	70.99	84.14	150.33
2123	M	222.45	174.3	276.16	20.3
2141	M	120.64	105.04	145.07	40.69
3367	M	221.74	192.95	248.6	56.09

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## **BIOGRAPHY**

Jonathan Drescher-Lehman has had a love of the natural world from a young age growing up in Richmond, Virginia, encouraged by his parents and cultivated through regular camping trips, backyard birdfeeders, and frequent visits to the local children's museum and Maymont. After moving to a house in the forest of southeastern Pennsylvania at age seven, this love of nature was immediately intensified. Long summer days were spent climbing trees, patrolling the creek banks for frogs and newts, kayaking through lily pads catching painted turtles, wading waist-deep in mud to catch stinkpots, and flipping every rock and log in search of salamanders and snakes. Occasionally, he even happened across a wood turtle wandering the woods or looking for place to lay her eggs. In 2011, he returned to Virginia to study biology at Eastern Mennonite University. At EMU, he had the opportunity to lead wood turtle surveys as part of a stream restoration research project, and following graduation in 2015, this experience carried over into an internship at the Smithsonian Conservation Biology Institute doing the same kind of work. A year later, in the fall of 2016, he began his M.S. education at George Mason University and the Smithsonian studying wood turtle movement ecology.