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Seasonal Patterns in Activity and Occupancy Dynamics of the Imperiled Spotted Turtle
(*Clemmys guttata*)

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

by

Ellery V. Lassiter
Longwood University
Bachelor of Science in Biology, 2013

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This dissertation is approved for recommendation to the Graduate Council.

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ABSTRACT

Wetland ecosystems are often spatially patchy across a landscape and exhibit seasonal patterns in water levels, resulting in the need for aquatic wildlife to use several different wetland patches across a season. The ecology of semi-aquatic freshwater turtles is especially complex because individuals often move among a variety of habitats to meet life history needs and these habitat requirements often differ across a season. Understanding the temporal and spatial scale in which turtles move and distribute across the landscape is vital for effective management, especially in the face of continued habitat fragmentation and climate change. Thus, we sought to understand the spatio-temporal variation in activity, movement, and occupancy dynamics of an imperiled freshwater turtle, the spotted turtle (*Clemmys guttata*), in a dynamic wetland ecosystem.

In Chapter I, I used near-continuous automated radiotelemetry to quantify diel activity patterns of spotted turtles over 19 months across different seasons. I also examined how season, turtle characteristics (age and sex), and climatic conditions influenced diel activity patterns and nocturnal behaviors. Diel activity of spotted turtles remained constant across the year, but there was seasonal variation in total activity and nocturnal behaviors. As expected, adult spotted turtles were more active than juveniles, though there was no difference between adult male or females. Nocturnal activity was best predicted by recent climatic conditions. I consider automated radiotelemetry to be effective at documenting fine-scale activity patterns of spotted turtles and recommend widespread adoption of continuous monitoring methods to better understand how widespread nocturnal behavior is among turtles and identify the mechanisms driving nocturnal activity.

In Chapter II, I used VHF radio-transmitters to radio-locate adult and juvenile turtles and estimate movement and space-use during their active and aestivation seasons (March - August). I then explored how movement and space-use varied based on intrinsic turtle characteristics (sex and age class) and extrinsic wetland and climatic features. I demonstrated that spotted turtle movement is influenced by season, as well as climatic conditions and wetland characteristics. Spotted turtle movement peaked in late spring. Across this time, adult spotted turtles moved farther than juvenile turtles and occupied larger home-ranges, though there was no difference in movement or space-use between adult males and females. Turtle response to variation in season and wetland configuration highlight the need for complex and dynamic landscapes that are required to sustain this species.

In Chapter III, I conducted repeated surveys across three spring seasons (March – June) to determine the spatio-temporal occupancy dynamics and habitat associations of spotted turtle across wetland complexes. We then explored how wetland characteristics influenced occupancy and abundance, and how climatic conditions influenced detection of spotted turtles. Occupancy and abundance varied across the spring sampling season, with a peak in the number of occupied wetlands and abundance estimates in the middle of the season. There was a seasonal trend in occupancy based on wetland size, but not habitat type across the season. Abundance estimates were best predicted by presence of prey availability and wetland configuration. These results help to provide more accurate predictions of dynamic distributions and population persistence.

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EPIGRAPH

An excerpt from the poem, “The First Spotted Turtle Awakens” by Jacqueline D. Litzgus:

I watch and ponder

the pinpoints of light are dazzling

complementing your distinctive yellow spots

interrupting the black continuum

like stars in an impenetrable night sky.

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LIST OF PUBLISHED PAPERS

- Lassiter, E. V., Sperry, J. H., Ward, M. P., and DeGregorio, B. A. Using automated telemetry to quantify diel activity patterns and nocturnal behaviors of the spotted turtle (*Clemmys guttata*). *Canadian Journal of Zoology*. *Submitted for review*. (CHAPTER I)
- Lassiter, E. V., Sperry, J. H., and DeGregorio, B. A. Movement ecology of adult and juvenile spotted turtles (*Clemmys guttata*) in a seasonally dynamic environment. *Wildlife Research*. *In review*. (CHAPTER II)
- Lassiter, E. V., Sperry, J. H., and DeGregorio, B. A. Seasonal occupancy and abundance dynamics of the imperiled spotted turtle (*Clemmys guttata*). *Journal of Herpetology*. *Submitted for review*. (CHAPTER III)

INTRODUCTION

Wetland ecosystems are often spatially patchy across a landscape and exhibit seasonal patterns in water levels, resulting in the need for aquatic wildlife to use several different wetland patches across a season (Joyal et al. 2001, Naugel et al. 2001, Roe et al. 2009). Individuals within a population may occupy an array of wetland patches, rather than a single wetland to respond to variation in resource availability (Harrison 1991, Gibbs 2000, Marsh and Trenham 2001, Roe et al. 2009). Wildlife that inhabit wetland systems are therefore equally dependent on aquatic environments and terrestrial corridors between wetland patches (Marsh and Trenham 2001, Gibbons 2003). For these species, inter-patch movement is vital for maintaining population stability, and therefore characteristics such as wetland availability, quality, and connectivity are likely to influence demographic processes (Marsh and Trenham 2001, Gibbs 2000). Understanding the temporal and spatial scale at which wildlife occupy certain patches and move between those patches is vital, particularly for ecosystems that rely on multiple wetland patches and connectivity for population stability (Roe et al. 2009).

Due to their reliance on multiple wetlands, and therefore connectivity between these wetlands, semi-aquatic species are particularly vulnerable to habitat fragmentation (Cosentino and Schooley 2018). The ecology of semi-aquatic freshwater turtles is especially complex because individuals often make long distance movements among a variety of habitats for mating, foraging, basking, aestivating, and overwintering purposes (Buhlmann and Gibbons 2001, Bowne et al. 2006, Beaudry et al. 2009). These habitat requirements often differ across a season, in response to variation in resource availability, wetland hydroperiod, precipitation, and temperature (Bodie and Semlitsch 2000, Litzgus and Brooks 2000, Cosentino et al. 2010). Fragmentation may reduce access to wetlands necessary for population stability through habitat destruction, habitat degradation, and/or creation of barriers to movement (Prugh et al. 2008,

Cosentino and Schooley 2018). While movement and habitat use of many freshwater species has generally been well studied (e.g., Litzgus and Brooks 2000, Buhlmann and Gibbons 2001, Gibbs and Shriver 2002, Marchand and Litvaitis 2004, Bowne et al. 2006, Howell and Seigel 2012), many important questions or data gaps in movement, activity, and occupancy (habitat use) in fragmented landscapes remain (McKinney 2008, Roe et al. 2009, McDonnell et al. 2018, Hjort et al. 2021). Thus, we sought to understand the spatio-temporal variation in activity, movement, and occupancy dynamics of an imperiled freshwater turtle, the spotted turtle (*Clemmys guttata*), in a dynamic wetland ecosystem.

Understanding a species' activity pattern provides important insight into life history and behavior (Helm et al. 2017, Gaston 2019, Levy et al. 2019). Many organisms have the ability to be active during either diurnal or nocturnal periods (Kronfeld-Schor and Dayan 2003, Hut et al. 2012, Levy et al. 2019), and may even demonstrate seasonal switches or seasonal temporal plasticity in diel patterns in response to changes in temperature, food availability, and/or water availability (Fraser et al. 1993, Kronfeld-Schor and Dayan 2003, Boal and Giovanni 2007, Sperry et al. 2013, Davimes et al 2017). Freshwater turtles are one of such species that exhibit seasonal patterns in diel activity (Smith and Iverson 2004, Ennen et al. 2008, Tucker et al. 2015), though drivers of diel activity, especially that of nocturnal behaviors, in turtles is not well understood. This is in part due to the difficulty of monitoring efforts which is subject to technological limitations of remote observation (e.g., ectotherms do not reliably trigger passive infrared sensor cameras, organisms are too small for GPS transmitter attachment; Welbourne 2014) or relies on intensive trapping and VHF telemetry methods (Smith and Iverson 2004, Ennen et al. 2008, Rowe and Dalgarn 2009, Glorioso et al. 2012). Here (Chapter I), I use near-continuous automated radiotelemetry to characterize the diel activity of spotted turtles at our site.

I compared differences in diel activity patterns of turtles based on sex, age, and interaction of each turtle characteristic between seasons. I then correlated nocturnal activity with climatic factors to understand how nocturnal activity was influenced by temperature or precipitation. Chapter I was formatted with the intent of publication in the *Canadian Journal of Zoology* with Jinelle H. Sperry, Michael P. Ward, and Brett A. DeGregorio.

Understanding the temporal and spatial scale at which wildlife move is vital for conserving and managing wildlife, particularly for semi-aquatic species that rely on connectivity between distinct wetland patches (Trenham et al. 2001, Petranka et al. 2004, Roe and Georges 2007). When movement between patches occur, it can vary across time, frequency, and distance based on intrinsic values of the individual (e.g., sex, age, size) (Swingland and Greenwood 1983) and extrinsic values of the landscape (e.g., matrix resistance, resource quality) (Taylor et al. 1993, Bowne et al. 2006). Thus, to conserve populations that occupy dynamic wetland ecosystems, it's important to understand the frequency in which inter-patch movements occur, the spatial and temporal scales that movement occurs, and the (intrinsic and extrinsic) drivers of inter-patch movements (Joyal et al. 2001, Roe et al. 2009, Cosentino et al. 2010). For example, it has been shown that inter-wetland movements of a variety of semi-aquatic species can be influenced by extrinsic factors such as weather, season, and distribution of resources (Bennett et al. 1970, Plummer et al. 1997, McIntyre and Wiens 1999, Roe and Georges 2007). Additionally, intrinsic factors such as sex, size, sexual maturity, and physiological and behavioral traits (Morreale et al. 1984, Gibbons et al. 1990, Litzgus and Mousseau 2004, Roe and Georges 2007) have also been shown to influence movement and space-use (i.e., home-range). In this study (Chapter II), I sought to understand how intrinsic turtle characteristics (sex and age class) and extrinsic wetland and climatic features influenced spotted turtle movement and space-use in the

under-studied central portion of its range. Chapter II was submitted to *Wildlife Research* with co-authors Jinelle H. Sperry and Brett A. DeGregorio. It was recently accepted, pending revisions.

For species that occupy dynamic wetland ecosystems, habitat requirements often differ across a season in response to variation in wetland hydroperiod, resource quality and availability, precipitation, and temperature (Bodie and Semlitisch 2000, Litzgus and Brooks 2000, Cosentino et al. 2010). Species must therefore occupy multiple different wetland patches across the year to accommodate their resource needs (Harrison 1991; Gibbs 2000; Marsh and Trenham 2001; Roe et al. 2009). Thus understanding observed, short-term occupancy dynamics can be important for making predictions of long-term population persistence (Hanski 1998, Sunderland et al. 2014). Dynamic occupancy models can inform both occupancy and turnover dynamics of patchy populations in which habitat quality varies (MacKenzie et al. 2003, Kery et al. 2003). Dynamic occupancy models have been applied to a number of different taxa occupying dynamic wetlands, which have improved our understanding of the behavioral and environmental drivers of dynamic species distribution, and refined our estimates of spatio-temporal occupancy patterns to better predict population persistence (Schooley and Branch 2011, Lamy et al. 2013, Sutherland et al. 2014, Ahlers et al. 2015, Chandler et al. 2015). Additionally, occupancy models address imperfect detection, which is critical for monitoring rare or cryptic species, such as most freshwater turtles (Grant and Doherty 2007, Marsh 2009, Durso et al. 2011, Refsnider et al. 2011, Crump and Forstner 2019). While single-season occupancy approaches have been increasingly utilized for turtle monitoring and management (e.g., Zylstra et al. 2010, Guzy et al. 2014, Stokeld et al. 2014, Buchanan et al. 2018, Markle et al. 2018, Chandler et al. 2020, Paterson et al. 2021), the use of dynamic occupancy models has rarely been applied (Cosentino et al. 2010, Scott and Rissler 2015, Cassel et al. 2019). Here (Chapter III), I use dynamic

occupancy models (MacKenzie et al. 2003) and N-mixture abundance models to (Royal 2004, Dail and Madsen 2011) to understand the spatio-temporal occupancy dynamics and habitat associations of the spotted turtle. My objective was to investigate the seasonal trends in occupancy and abundance patterns of this species to better understand how their habitat associations vary seasonally and how local wetland characteristics influenced occupancy and abundance. Chapter III was formatted with the intent of publication in the *Journal of Herpetology* with Jinelle H. Sperry and Brett A. DeGregorio.

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CHAPTER I

USING AUTOMATED TELEMETRY TO QUANTIFY DIEL ACTIVITY PATTERNS AND NOCTURNAL BEHAVIORS OF THE SPOTTED TURTLE (*CLEMMYS GUTTATA*)

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ABSTRACT

Diel activity patterns are a critical aspect of a species' biology, yet diel activity of some species, especially nocturnal behaviors, are often poorly described and difficult to study. This is particularly true for herpetofauna due to their cryptic nature and technological limitations of nighttime observation. We used near-continuous automated radiotelemetry to quantify the diel activity patterns of the imperiled spotted turtle (*Clemmys guttata*) in Virginia. We then explored how season, turtle characteristics (age and sex), and climatic conditions influenced diel activity patterns and nocturnal behaviors. Overall patterns of diel activity indicate a unimodal peak around noon or early afternoon with little variation between seasons. Detections of activity were predominately diurnal (81%), with some nocturnal activity (16%) and limited crepuscular activity (3%). Spotted turtles exhibited some nocturnal behavior throughout the entire year, although nocturnal activity was greatest during summer and fall corresponding to the warmest night temperatures. Adults were more active at night than juveniles, but there was no difference between adult males and adult females. Nocturnal activity was greatest following precipitation events when temperatures were greater than 25 °C. Our study demonstrates fine-scale diel activity patterns in spotted turtles and confirms recent reports that spotted turtles may be more nocturnally active than previously thought. Improved understanding of diel activity has important management and conservation implications, including predicting behavioral responses to rising temperatures from climate change.

INTRODUCTION

Understanding a species' activity pattern provides important insight into life history and behavior (Helm et al. 2017, Gaston 2019, Levy et al. 2019). These activity patterns are often characterized as being diurnal (daylight), nocturnal (darkness), crepuscular (twilight), or cathemeral (neither strictly diurnal nor nocturnal; Bennie et al. 2014). While some species may be adapted for specific diel periods (e.g., Healy and Guilford 1990, Cooper 1999, Pohlmann et al. 2004, Hall and Ross 2006, Seneviratne and Jones 2010, Land and Nilsson 2012), many species have the ability to be active during either diurnal or nocturnal periods (Kronfeld-Schor and Dayan 2003, Hut et al. 2012, Levy et al. 2019). Changes between diel periods can be adaptations to reduce predation risk (Suselbeek et al. 2014, Pavey et al. 2016, Velo-Aton and Cordero-Rivera 2017), avoid thermally stressful periods (Willmer 1983, Weatherhead et al. 2012), avoid human activity (Gaynor et al. 2018, DeGregorio et al. 2021), or maximize access to resources (Levy et al. 2016, Davimes et al 2017). Yet the diel activity patterns of some species, especially nocturnal behaviors, are still not well understood (Gaston et al. 2019). This is particularly true for herpetofauna due to their cryptic nature and technological limitations of nighttime observation (e.g., ectotherms do not reliably trigger passive infrared sensor cameras, organisms are too small for GPS transmitter attachment; Welbourne 2014). Here, we use near-continuous automated radiotelemetry to quantify the diel activity patterns of an imperiled species of freshwater turtle and explore the relationship between nocturnal activity and climatic and turtle characteristics.

Freshwater turtles are ectotherms; thus body temperature is largely dependent on environmental conditions and is controlled by physiological and behavioral processes (Huey 1982, Peterson et al 1993). Behavioral thermoregulation in turtles is primarily seen through

aerial basking (Sajwaj and Lang 2000, Clavijo-Baquet and Magnone 2017), aquatic basking (King et al 1998), and thermoconforming to water temperatures (Brown et al. 1990, Manning and Grigg 1997). Therefore, access to solar radiation influences diel activity patterns in turtles (Peterson et al. 2003, Rowe and Dalgarn 2009). As such, most species of freshwater turtle are characterized as diurnal (Smith and Iverson 2004, but see: Wade and Gifford 1965, Rowe and Moll 1991, Ernst et al 1994, Lindeman 2000, Rowe 2003). Though for some species which bask less frequently, crepuscular diel activity has been noted (Smith and Iverson 2004, but see: Wade and Gifford 1965, Vermersch 1992, Minton 2001, Glorioso and Cobb 2011). It was previously accepted that nocturnal activity was predominately limited to female nesting habits (Congdon et al. 1983, Congdon et al. 1987, Spencer 2002, Spencer and Thompson 2003, Frye et al. 2017), however, evidence of nocturnal activity not associated with nest laying continues to grow (Bancroft et al 1983, Rowe 2003, Smith and Iverson 2004, Ennen and Scott 2008, Rowe et al. 2009, Nordberg and McKnight 2020, Hjort et al. 2021). Little is known about the temporal, climatic, or turtle characteristics driving nocturnal behavior in freshwater turtles (Ennen et al. 2008, Nordberg and McKnight 2020, Hjort et al. 2021). This knowledge gap is largely due to technological constraints of observing turtles at night.

Studies of diel activity patterns in freshwater turtles have traditionally relied on intensive trapping (Graham and Hutchison 1979, Bancroft et al. 1983, Smith and Iverson 2004, Glorioso et al. 2012) or VHF telemetry (Rowe 2003, Rowe and Dalgarn 2009, Rowe et al. 2009, Ennen et al. 2008). However, recent advances in continuous monitoring methods (e.g., GPS telemetry or automated telemetry) have become available and expanded our ability to quantify around-the-clock activity in turtles. While most studies using continuous monitoring methods have primarily focused on movement and habitat use (Christensen and Chow-Fraser 2014, Thompson et al.

2018, Cochrane et al. 2019), a small number of studies focused on activity patterns have reported nocturnal behaviors and provided insight into the life history of focal species (Tucker et al. 2014, 2015; Hjort et al. 2021). For instance, Tucker et al. (2014) demonstrated that female ornate box turtles (*Terrapene ornata*) were more active at night, but that these nocturnal movements were associated with nesting. Hjort et al. (2021) used GPS telemetry to reveal that spotted turtles (*Clemmys guttata*) were active both day and night whereas co-occurring Blanding's turtles (*Emydoidiea blandingii*) were primarily diurnal. Continuous monitoring of individual turtles is a critical tool in understanding diel activity patterns and further elucidating the reasons why some turtle species engage in nocturnal activity.

The spotted turtle is a relatively small, semi-aquatic freshwater species that inhabit freshwater wetland ecosystems along the East Coast and Great Lakes regions of the United States and Canada. Spotted turtles use ephemeral wetland habitats, which are temporally and spatially dynamic (Milam and Melvin 2001; Litzgus and Mousseau 2004; Beaudry et al. 2010). Thus, spotted turtle activity and habitat use often differs across seasons in response to variation in resource availability, wetland hydroperiod, precipitation, and temperature (Litzgus and Brooks 2000; Joyal et al. 2001; Rowe et al. 2013). The exact timing of spotted turtle activity patterns varies across the range, with activity constrained to spring and early summer at the northern extent of the range (Litzgus and Brooks 2000) contrasted to year-long activity at the southern extent of the range (Chandler et al. 2019). Additionally, spotted turtle activity is considered primarily diurnal, with nocturnal activity limited to female nesting behaviors (Ernst and Lovich 2009). However, a recent study at the northern extent of the species range observed that 17% of turtle movements occurred at night and that this behavior was unrelated to nesting activity or thermoregulation (Hjort et al. 2021).

Here, we investigated the diel activity patterns of the imperiled spotted turtle in the central portion of its east coast range. Based on increasing evidence of chelonian nocturnal activity (Rowe et al. 2009; Nordberg and McKnight 2020; Toms et al. 2021; Hjort et al. 2022), we expected to observe some degree of nocturnal activity. Our first objective was to use near-continuous automated radiotelemetry to characterize the diel activity patterns of turtles at our site over 19 months during different seasons. We also compared differences in the diel activity patterns of turtles based on sex and age (adult vs juvenile). We predicted that nocturnal activity would be most pronounced during the late spring and summer seasons of the year because turtles are most active during these seasons (Litzgus and Mousseau 2004; Beaudry et al. 2009) and nighttime temperatures are warmer. We also predicted that juvenile turtles would display the least amount of nocturnal activity, because this age class is likely at the greatest risk of predation from nocturnal mammalian mesopredators (Congdon et al. 1993; Bowne et al. 2006). We predicted no difference between sexes as there is not a strong difference in movement and activity between male and female spotted turtles (Haxton and Berrill 1999; Litzgus and Mousseau 2004; Rasmussen and Litzgus 2010; O'Bryan et al 2016). Our final objective was to correlate nocturnal activity with climatic factors to understand how nocturnal activity was influenced by temperature or precipitation. We predicted that most nocturnal movements would occur during prolonged periods of warm temperatures and following precipitation events.

METHODS

Study Site

We studied spotted turtle activity patterns on a U.S. military installation in Virginia, U.S.A. from 2018-2019. The installation is 3,237 ha and has been partitioned for a number of uses, including urban infrastructure (e.g., offices, housing, etc.) and natural areas set aside for

training and wildlife conservation. The natural areas contained a continuum of habitat types from floodplain wetlands (dominated by *Carex spp.*, *Cephalanthus occidentalis*) to upland mixed pine-hardwood forests (dominated by *Pinus spp.*, *Quercus spp.*, *Fagus spp.*). Our study site was centered on a wetland complex, which included two large, emergent wetlands at the center and numerous surrounding ephemeral pools. The ephemeral wetlands were predominately forested and included a mix of natural vernal pools and anthropogenic depressions from ditches and other military activities.

Data Collection and Processing

Starting in March each year, we attached VHF radio-transmitters to adult and juvenile spotted turtles. Turtles were captured using collapsible hoop-net traps (ProMar TR-502 36" x 12") or by hand during visual encounter studies. Transmitters (RI-2B, 6 or 10 g from Holohil Systems Ltd) were attached to adult turtles weighing at least 120 g with approximately 3 g of Devcon 5 min epoxy gel for a total package weight of 9-13 g (max% of body weight = 7%). Smaller transmitters (PD-2, 3.5 g from Holohil Systems Ltd) were attached to juvenile turtles weighing at least 80 g with approximately 1 g of Devcon 5 min epoxy gel for a total package weight of 4.5 g (max% of body weight = 7%). We orientated transmitters so that the antenna trailed behind the turtle as it moved to reduce likelihood of the transmitter tangling in the environment, and on the posterior pleural scute to reduce stress on the marginal scutes. We removed transmitters from the turtles at the end of the transmitter's life, at twelve and six months, respectively. Seven percent of the body weight is below the standard for turtles (10%) that has suggested by the American Society of Ichthyologists and Herpetologists (ASIH 2004). All work was conducted under the Institutional Animal Care and Use Committee (IACUC) protocol #20048.

We monitored turtle activity using automated receiving units (ARU; *JDJC Corp. Fisher, Illinois*). Each ARU consisted of a 5 m tall radio tower topped with a circular array of six 4-element yagi antennas. Antennas were arranged 60° apart to give 360° coverage around the tower. Three ARUs were arranged in an isosceles triangle formation in which towers were 450 m, 450 m, and 250 m apart and positioned at the center of the study site. The ARUs were set to scan the radio frequencies of the turtle VHF transmitters every 3 minutes and record signal strength (dB), electromagnetic noise (dB), pulse width (how long a transmitter emits a signal), and pulse frequency (interval between pulses). We removed any detection that had a signal strength below -125 dB, noise level greater than -130 dB, and pulse width greater than 10 (Smetzer et al. 2022). If an individual was detected by multiple ARUs at a given sampling time, we used the detection with strongest signal strength (Sperry et al. 2013).

In previous studies using ARUs (Kays et al. 2011; Sperry et al. 2013; Ward et al. 2013, Schofield et al. 2018), animal activity was determined by comparing the signal strength and bearing of consecutive detections. When a radiotagged individual moved, the orientation of its transmitter's antenna to the ARU changed, resulting in a subsequent change in the signal strength and bearing (Kays et al. 2011; Sperry et al. 2013; Ward et al. 2013). However, signal strength is measured on a log scale, thus the signal strength of individuals closer or farther from an ARU is not linearly distributed. Therefore, we used methods from a recent study (Smetzer et al. 2022) to help account for distance bias. First, we determined the magnitude of change in signal strength between consecutive detections. To do this, we used a rolling average of signal strengths around each set of consecutive detections (window size = 6). We then log-transformed the signal strength difference values. For each turtle, we used the 95th quantile of the log-transformed signal strength differences during diurnal and nocturnal periods, respectively, as a threshold to

classify whether a detection was inactive or active. We chose this conservative threshold to reduce the likelihood false positives. All detections of activity were classified as dawn (between nautical dawn and sunrise), diurnal (between sunrise and sunset), dusk (between sunset and nautical dusk), or nocturnal (between nautical dusk and nautical dawn), and then used for subsequent analyses. We classified activity times in R (R Core Team 2022) using the “suncalc” package (Thieurmel and Elmarhraoui 2019).

Statistical Analyses

We examined diel patterns of spotted turtles using the “overlap” package (Ridout and Linkie 2009). We first converted time of each individual’s detection of activity to radians to account for circular nature of time. We then calculated non-parametric kernels around activity times to quantify diel patterns (Ridout and Linkie 2009). Activity plots were generated for males, females, and juveniles, as well as season (including data from all individuals). In general, five activity seasons have been described for spotted turtles, including a) early spring: emergence from hibernation with basking, foraging, and mating; b) late spring/early summer: foraging and nesting; c) late summer: reduced activity and/or aestivation; d) fall: limited foraging and basking, movements to hibernacula; and e) winter: hibernation (Litzgus and Brooks 2000; Litzgus and Mousseau 2004; Beaudry et al. 2009). Here, we delineated season as a) early spring: March – April; b) late spring: May – June; c) summer: July – August; d) fall: September – October; and e) winter: November – February.

For sex and age comparisons of diel patterns, we calculated the area under the kernel curve that overlapped between each pair, which was quantified using a 0-1 index (Δ) (Schmid and Schmidt 2006; Ridout and Linkie 2009). We generated confidence intervals around each overlap index from bootstrap samples (1000 iterations). To determine if there was a sex, age, or

seasonal effect on frequency of activity overall or nocturnal activity we fit generalized linear mixed models (glmm) using the “lme4” package (Bates et al. 2015). For overall activity, we used counts of activity per turtle per season as the response variable in a Poisson glmm with turtle ID as the random effect to address pseudoreplication. For nocturnal activity, we used proportion of activity that was nocturnal per turtle per season as the response variable in a Binomial glmm with turtle ID as the random effect. For both models, we tested for differences in activity among age, sex, and season, and age*season and sex*season interactions. We compared each fitted model to a null model using parametric bootstrapping (1000 iterations) using the package “pbkrtest” (Halekoh and Hojsgaard 2014).

We obtained climatic data from a weather station located 30 km from our study site. We used these data to quantify several variables predicted to explain spotted turtle nocturnal activity patterns. For each activity detection, we calculated mean temperature during the previous three hours, mean temperature during the previous twelve hours, mean precipitation during the previous three hours, and mean precipitation during the previous 12 hours. These time intervals were chosen to represent ‘recent and ‘cumulative’ climatic conditions, respectively. We then used these variables to examine the relationship between climatic features and whether a turtle exhibited nocturnal activity. This was evaluated using a generalized linear mixed model with a binomial response variable (0 = no nocturnal activity, 1 = nocturnal activity). The fixed effects included the aforementioned climatic variables, and the random effect was turtle ID. Before model fitting, we checked collinearity by performing Spearman’s rank correlation; temperature-3hrs and temperature-12hrs were correlated. Covariates were then standardized by centering on the mean and scaling by standard deviation. Candidate models included two global models, including all non-correlated covariates, 2-way additive and interactive combinations, and single

covariate models. Model selection was conducted using Akaike's Information Criterion (AIC) approach (Burnham and Anderson 2002) and candidate models were considered competitive if within 2 Δ AIC. We used the package "AICcmodavg" (Mazerolle 2020) for model selection procedures. Model goodness of fit for our global models and top models were assessed using residual plots and checked for over-dispersion. Additionally, if the top model(s) included an interactive effect, visualization of the relationship was facilitated by binning one of the covariates into low, medium, and high categories as determined by the covariate's quartiles

RESULTS

We monitored spotted turtle activity starting in March 2018 through December 2019. Transmitters were primarily equipped during March and April each year ($n = 18$), though some transmitters were equipped as late as May or early June ($n = 6$). This was primarily due to the low detectability of juvenile turtles; thus more time was required to capture and equip those individuals. In 2018, we monitored 4 males, 5 females, and 5 juvenile turtles. Six adults were monitored from early spring through the following year, three adults were monitored through late fall due to transmitter failure, and one adult was only monitored through late spring because the turtle died. Juveniles were monitored through November, upon which time transmitters were removed due to shorter battery life. In 2019, we monitored 6 males, 6 females, and 9 juvenile turtles. Adults were monitored from early spring through December and juveniles were monitored early spring through November. Of these individuals, 10 individuals were monitored during both years, either continuously from the previous year ($n = 6$) or re-equipped with new transmitters in early spring ($n = 4$). Overall, we monitored 25 individual spotted turtles, including 14 adults (6M & 8F) and 11 juvenile turtles.

After processing the ARU data, we acquired a total of 1,039,925 detections (mean per turtle = 41,597; range = 3,601 – 106,587 observations per turtle) (Supp. Table 1). The mean number of days that a turtle was consecutively monitored was 139.72 days (range = 27 – 343 days per turtle). ARUs were set to monitor turtles every three minutes, however the average number of detections per day was far lower, 11.87 (range = 5 – 100), due to our conservative filtering thresholds, turtles moving far from ARUs, and/or the behavior of turtles. Detections of activity were predominately diurnal ($n = 28,592$; 81%) with some nocturnal activity ($n = 5,805$; 16%) and limited crepuscular activity ($n = 831$ dawn; 2%; $n = 243$ dusk; 0.6%).

Overall patterns of diel activity indicated that spotted turtle activity peaked around noon (Fig. 1) but shifted to later in the afternoon during colder seasons such as winter and early spring (Supp. Fig 1). There was substantial overlap of diel activity between age ($\Delta_4 = 0.95$, 95% CI = 0.94-0.96) and sex ($\Delta_4 = 0.98$, 95% CI = 0.97-0.99) classes (Fig. 1), as well as when age/sex comparisons were divided into season categories (Supp. Fig. 2). Additionally, there was no effect of age ($\chi^2 = 0.001$, $df = 1$, $P = 0.974$) or sex ($\chi^2 = 0.011$, $df = 1$, $P = 0.915$) classes on frequency of activity (total activity). There was a significant effect of season ($\chi^2 = 17192$, $df = 4$, $P = 0.020$) on total activity, as well as the interactive effect of season*age and season*sex. To ensure the season*age interaction term was significant, the model was compared to the null model ($\chi^2 = 17420$, $df = 9$, $P = <0.001$) and model with season as the fixed effect ($\chi^2 = 227.320$, $df = 5$, $P = <0.001$). The season*sex interaction was similarly compared to the null ($\chi^2 = 12000$, $df = 9$, $P = <0.001$) and season fixed effect model ($\chi^2 = 185.420$, $df = 5$, $P = <0.001$). Overall, activity was greatest during early spring and decreased through the subsequent seasons (Fig. 2). Adult turtles were significantly more active than juveniles during the spring seasons, though there was no difference during the remaining seasons (Fig. 2). Males were significantly more

active than females during early spring and this effect was reversed during late spring (Fig. 2). Similar to age effects, there was no significant difference in total activity between sexes during the remaining seasons.

There was no significant difference in age ($\chi^2 = 0.992$, $df = 1$, $P = 0.319$) or sex ($\chi^2 = 1.245$, $df = 1$, $P = 0.264$) on proportion of nocturnal activity. There was an effect of season ($\chi^2 = 870.110$, $df = 4$, $P = <0.001$), including the interaction between season and age (compared to null: $\chi^2 = 922.190$, $df = 9$, $P = 0.030$; compared to season: $\chi^2 = 52.073$, $df = 5$, $P = 0.020$). The interaction between season and sex was not significant ($\chi^2 = 719.590$, $df = 9$, $P = 0.142$). The proportion of nocturnal activity was low (<20%) in early and late spring, then increased during summer (25%) and fall (30-40%) (Fig. 3). There was little nocturnal activity during the winter season (5%). Adult nocturnal activity was greater than that of juveniles during early spring and fall but overlapped during the remaining months (Fig. 3). Probability of nocturnal activity was best predicted by the interaction between temperature during the previous 3 hours and precipitation during the previous 3 hours (Table 1). The probability of nocturnal activity increased with temperature but more rapidly during heavy rainfall events (Fig. 4). Similarly, probability of nocturnal activity increased with recent precipitation, however, only at high temperatures (>25°C).

DISCUSSION

Until recently, spotted turtles were considered to be almost exclusively diurnal and this study corroborates those recent findings (Hjort et al. 2021) that while spotted turtles may be primarily active during the day, nocturnal activity does occur. Indeed, we documented nocturnal activity across the entire year (although nocturnal activity in the winter was extremely rare) and by both juvenile and adult turtles. There was a seasonal pattern in both frequency of overall

activity and nocturnal activity, including an interaction with turtle age and sex class. Nocturnal activity was also positively related to temperature and recent precipitation events.

Spotted turtle diel activity peaked around noon or early afternoon with little variation between seasons (Supp. Fig. 1). Additionally, there was significant overlap in diel activity between both age and sex classes. This likely reflects that thermoregulatory behavior (e.g., morning basking) is a relatively consistent requirement over time and across turtle characteristics. Unimodal activity is common among many species of freshwater turtle (Smith and Iverson 2004, Edwards and Blouin-Demers 2007, Rowe and Dalgarn 2009, Tucker et al. 2015). However, there was a significant difference in the total frequency of activity among age and sex classes. Adult turtles were more active than juveniles during early and late spring months. During the spring, adult spotted turtles form mating aggregates (Litzgus and Brooks 2000, Litzgus and Mousseau 2004), and were therefore more active than juvenile turtles. Differences in reproductive activity is also likely responsible for differences in activity between male and female turtles. Males are often more active in early spring to increase mating opportunities (Litzgus and Brooks 2000, Litzgus and Mousseau 2004), while females are more active in late spring during nesting activities (Litzgus and Mousseau 2004, Litzgus and Mousseau 2006). Additionally, the overall seasonal pattern in total activity observed here supports previously described seasonality in movement and activity in spotted turtles (Litzgus and Brooks 2000, Joyal et al. 2001, Beaudry et al. 2009, Rowe et al. 2013).

Until a recent report to the contrary (Hjort et al. 2021), spotted turtle nocturnal activity was thought to be limited to female nesting activity (Ernst and Lovich 2009). In this study, we documented nocturnal activity during every month of the year, though it was most prominent during the summer and fall seasons (Fig. 3), when nighttime temperatures were at their highest.

Similar trends can be seen in other freshwater turtle species, in which thermal constraints of nocturnal activity are lessened during summer months (Ennen et al. 2008, Tucker et al. 2015) or at lower latitudes (Smith and Iverson 2004). Indeed, seasonal switches or seasonal temporal plasticity can be seen across taxa in response to changes in temperature, food availability, and/or water availability (Fraser et al. 1993, Kronfeld-Schor and Dayan 2003, Boal and Giovanni 2007, Sperry et al. 2013, Davimes et al 2017).

Unsurprisingly, there were few detections of nocturnal activity during the winter season. Some nocturnal activity continued through early November ($n = 18$) as turtles finished locating suitable hibernacula, but we only recorded three occurrences of nocturnal activity from late November through the end of February. During each occasion, nocturnal activity occurred just past sunset and during above-average temperatures ($>10^{\circ}\text{C}$). Spotted turtles are relatively cold tolerant and have been observed foraging at temperatures as low as 7.7°C (Rasmussen et al. 2009). Activity, including nocturnal activity, is likely possible during winter months under proper weather conditions. However, without direct observation or additional data, it is unclear whether the detections of activity we recorded corresponded to small adjustments within hibernacula or larger movements. Pairing manual radiotelemetry with automated radiotelemetry should help elucidate the magnitude of winter movements.

Nocturnal activity was greater for adults in early spring and fall, and generally equivalent during the other seasons (Fig. 3). In early spring, nocturnal activity may provide additional mating opportunities for adults, while juveniles do not need to risk suboptimal thermal conditions or predation (Riley and Litzgus 2014). Age effects on diel patterns have not been studied in freshwater turtles, but there are examples in other taxa in which juveniles have different diel patterns associated with predator avoidance (McDonough and Loughry 1997, Imre

and Boisclair 2004, Hertel et al. 2017). For some species of freshwater turtle, nocturnal activity is restricted to nesting behaviors by females (Ernst and Lovich 2009, Christensen and Chow-Fraser, 2014, Tucker et al. 2014, Hjort et al. 2021). However, we saw no effect of sex, with both males and females exhibiting similar levels of nocturnal behavior across each season. This indicates that for the spotted turtle, and others, nocturnal activity serves a purpose beyond just nesting behaviors and deserves further investigation (Rowe 2003, Ennen et al. 2008, Rowe et al. 2009, Glorioso and Cobb 2012, Hjort et al. 2021).

Nocturnal activity was also predicted by temperature and precipitation (Fig. 4). Nocturnal activity was positively related to temperature and during large precipitation events this relationship was stronger. Precipitation events alone was not sufficient to prompt nocturnal activity; it was only during warm temperatures ($> 25^{\circ}\text{C}$) that precipitation triggered nocturnal activity. Additionally, recent weather conditions (temp./precip. during previous 3-hrs) better predicted nocturnal activity compared to cumulative conditions (temp./precip. during previous 12-hrs). This is unsurprising for rainfall events, because turtle activity and movement often increase during rainfall events due to lower risk of evaporative heat loss (Ernst 1968, Stone and Iverson 1999, Wilson et al 1999). The relationship between warm temperatures, precipitation, and nocturnal activity may provide a glimpse into how this species may respond to climate change with an increase in nocturnal activity to avoid thermally stressful conditions. Additional studies of freshwater turtles are needed to quantify the extent and drivers of nocturnal activity, and to better understand the potential implications of increased nocturnal activity in response to climate change or other anthropogenic pressures.

As with previous studies using ARUs, our methods allowed us to compare relative activity profiles across covariates of interest, but is not capable of quantifying absolute activity

rates or describing types of activity (e.g., foraging, mating, etc.) (Schofield et al. 2018). Nevertheless, even with conservative estimates of activity, we were able to quantify the extent, timing, and meteorological correlates of nocturnal activity. A more widespread adoption of continuous monitoring methods should help better understand how widespread this behavior is amongst turtles and to begin to understand how turtles benefit from nocturnal activity. More accurate and more detailed understanding of diel activity can help guide timing of sampling (Waltert et al. 2006), identify critical habitat use (Austin et al. 2016), and predict potential responses to climate change (Levy et al. 2019).

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TABLES

Table 1. Model selection statistics for probability of nocturnal activity of spotted turtles (*Clemmys guttata*) in Virginia from 2018-2019. Covariates of nocturnal activity included mean temperature during the previous 3 hours, mean temperature during the previous 12 hours, mean precipitation during the previous 3 hours, and mean precipitation during the previous 12 hours. Models were ranked using Akaike’s Information Criterion (AIC) and included with each model is the number of parameters (K), difference from best model (Δ AIC), model weight (AICwt) and log-likelihood estimate (LL).

Model	K	AIC	Δ AIC	AICwt	LL
Temp3hrs*Precip3hrs	5	31913.67	0.00	0.98	-15951.84
Temp3hrs + Precip3hrs	4	31922.57	8.90	0.01	-15957.28
Temp3hrs + Precip3hrs + Precip12hrs	5	31924.31	10.64	0.00	-15957.15
Temp3hrs*Precip12hrs	5	31947.52	33.85	0.00	-15968.76
Temp3hrs + Precip12hrs	4	31957.44	43.77	0.00	-15974.72
Temp3hrs	3	31963.93	50.26	0.00	-15978.97

Table 1 (Cont.)

Temp12hrs*Precip3hrs	5	32049.88	136.21	0.00	-16019.94
Temp12hrs + Precip3hrs + Precip12hrs	5	32065.70	152.02	0.00	-16027.85
Temp12hrs + Precip3hrs	4	32067.08	153.40	0.00	-16029.54
Temp12hrs*precip12hrs	5	32093.37	179.69	0.00	-16041.68
Temp12hrs	3	32099.46	185.79	0.00	-16046.73
Temp12hrs + Precip12hrs	4	32099.55	185.88	0.00	-16045.77
Precip3hrs	3	33344.70	1431.03	0.00	-16669.35
Null	2	33367.13	1453.46	0.00	-16681.56
Precip12hrs	3	33369.12	1455.44	0.00	-16681.56

FIGURES

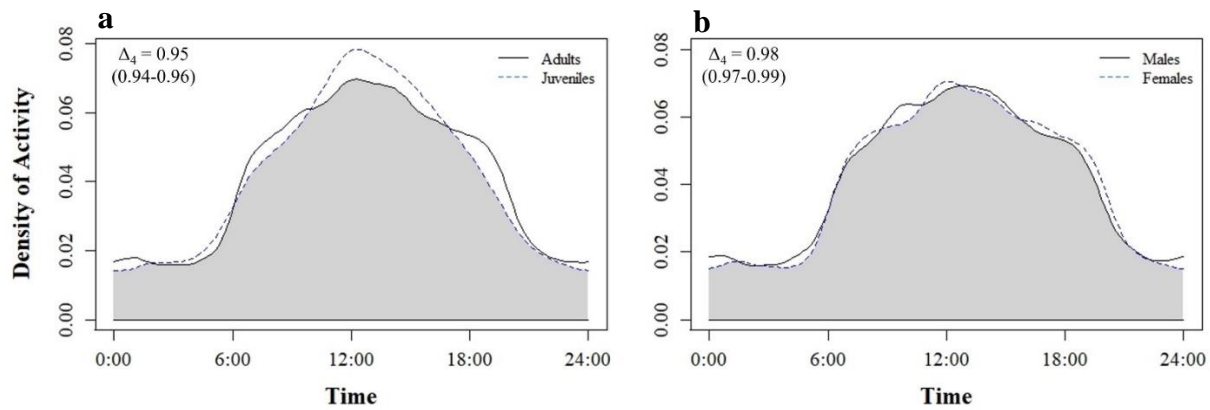


Figure 1. Density estimates of daily activity patterns of spotted turtles (*Clemmys guttata*) monitored using automated telemetry in Virginia from 2018 - 2019. a) solid lines are the kernel density estimates for adults and dashed lines are for juveniles. b) solid lines are the kernel density estimates for males and dashed lines are for females. The overlap coefficient is represented by the shaded area and as an index (Δ) with corresponding 95% confidence intervals.

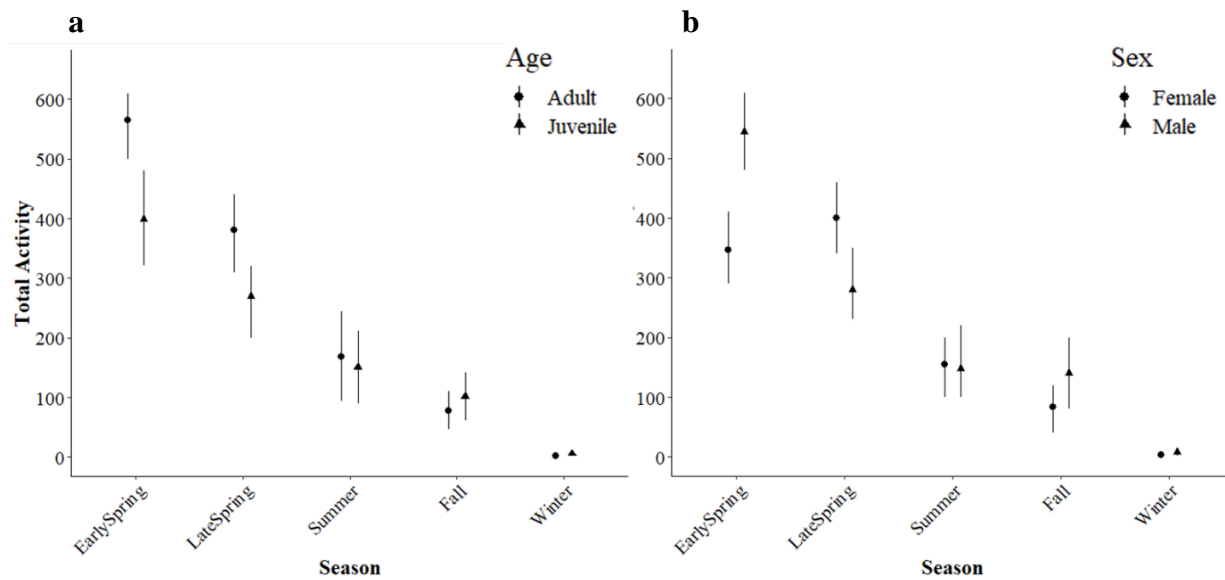


Figure 2. Influence of age and season interactions (a) and sex and season interactions (b) on spotted turtle (*Clemmys guttata*) activity. 95% confidence intervals are presented using black bars. Total activity is estimated by detections of activity using automated telemetry data collected in Virginia from 2018-2019.

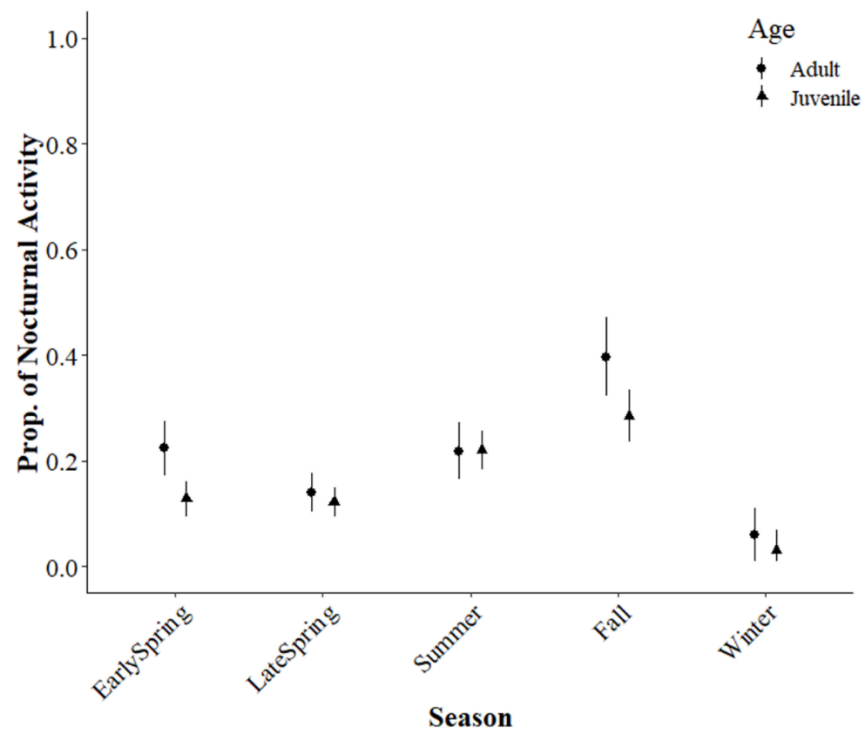


Figure 3. Influence of age and season interactions on spotted turtle (*Clemmys guttata*) nocturnal activity. 95% confidence intervals are presented using black bars. Proportion of nocturnal activity is estimated by detections of activity using automated telemetry data collected in Virginia from 2018-2019.

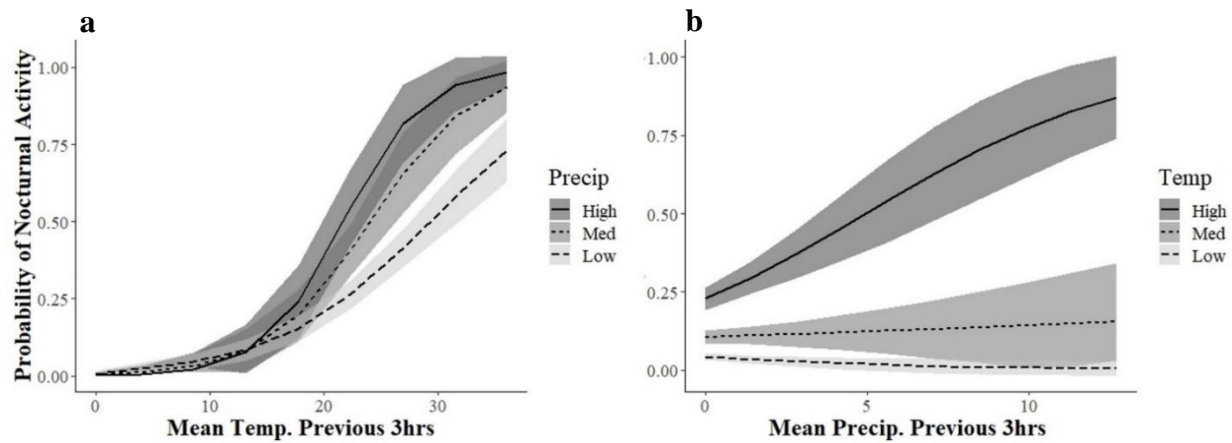


Figure 4. The interactive effects of mean temperature (C°) during the previous three hours and mean precipitation (cm) during the previous three hours on probability of nocturnal activity by spotted turtles (*Clemmys guttata*) monitored using automated telemetry in Virginia from 2018-2019. Each respective covariate was binned around its quartiles for ease of visualization: a) precipitation bin and b) temperature bin. 95% confidence intervals are presented using a gray band.

SUPPLEMENTARY INFORMATION

Table S1. Summary table of automated telemetry detections of spotted turtles (*Clemmys guttata*) collected in Virginia from 2018-2019. For individual turtles, intrinsic information about ID, age category, and sex category are included. “Monitor duration” refers to how long a turtle was monitored for, including entire study period from early spring 2018 through December 2019 (continuous), two study seasons with data collected early spring through November/December each respective year (2-years), or one study season from early spring through November/December that year (1 year). Summary statistics about the number of detections overall (Total # Detect), number of days with detections (# Days), number of detections per day (Mean, Min, and Max Det./Day), and number of detections in which a turtle was active (Total # Active) are also summarized.

ID	Age	Sex	Monitor Duration	Total # Detect.	# Days	Mean Det./Day	Min Det./Day	Max Det./Day	Total # Active
4	A	M	Continuous	106587	343	11.075	5	45	3699
7	A	F	Continuous	67974	193	13.08	5	47	3027
9	A	M	Continuous	93733	246	13.93	5	100	3371
37	J	J	2-years	66542	200	10.59	5	71	2076
42	A	F	Continuous	101544	299	12.83	5	64	3843
101	A	M	Continuous	55582	230	12.97	5	34	1240
102	A	F	1-year	9935	55	10.69	5	42	252
123	A	M	Continuous	56367	253	9.505	5	41	2134
142	A	F	1-year	25602	96	8.66	5	69	832

Table S1 (Cont.)

162	J	J	2-years	28915	138	11.195	5	43	922
180	J	J	1-year	14148	54	12.22	5	36	471
181	A	M	1-year	11780	37	14.7	5	26	174
233	A	F	1-year	7616	76	13.22	5	29	345
234	J	J	1-year	23433	102	9.56	5	65	652
239	A	F	1-year	58303	159	13.77	5	45	2190
242	J	J	1-year	33492	160	9.5	5	67	1201
252	A	F	1-year	14155	81	10.12	5	26	333
298	J	J	2-years	14336	89	9.21	5	56	564
300	A	F	2-years	40816	177	12.255	5	46	1405
313	J	J	1-year	50424	90	13.9	5	48	1251
361	J	J	1-year	3601	27	11.18	7	44	302
363	J	J	1-year	40367	99	15.12	5	59	1497
365	J	J	1-year	5854	48	9.88	5	31	331
377	J	J	1-year	46228	99	13.29	5	58	1316
7020	A	M	1-year	62591	142	14.4	5	58	2045

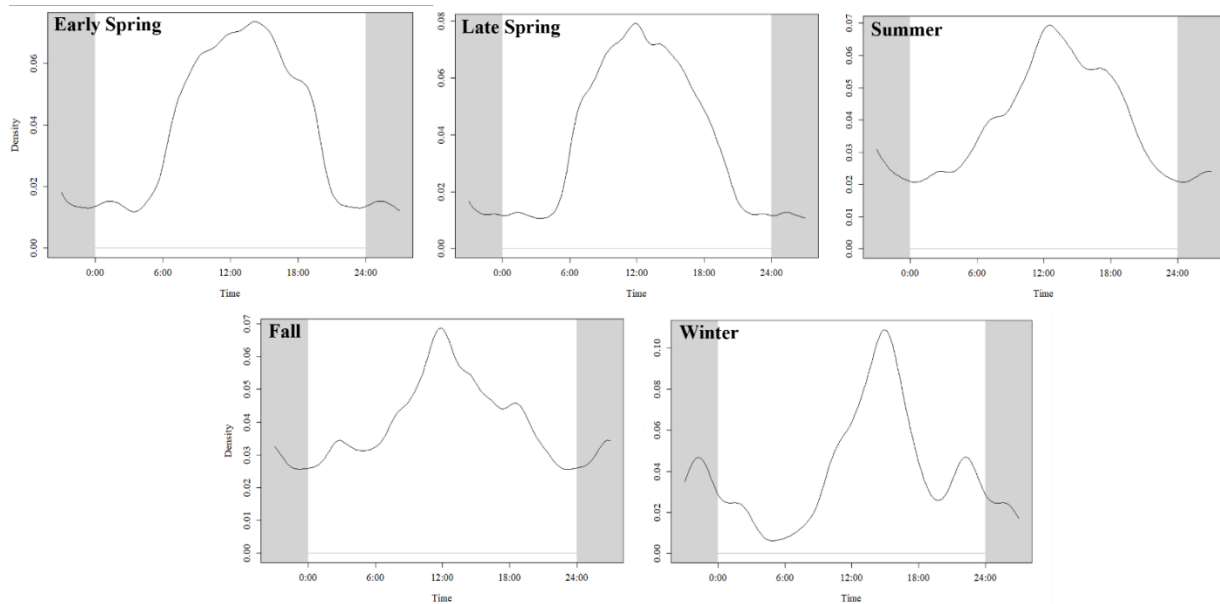


Figure S1. Estimates of daily activity patterns per season of spotted turtles (*Clemmys guttata*) monitored using automated telemetry in Virginia during 2018 and 2019. Solid lines are the kernel density estimates. Seasons are broken into the following categories: early spring: March-April, late spring = May-June, summer = July-August, fall = September-October, and winter = November-February.

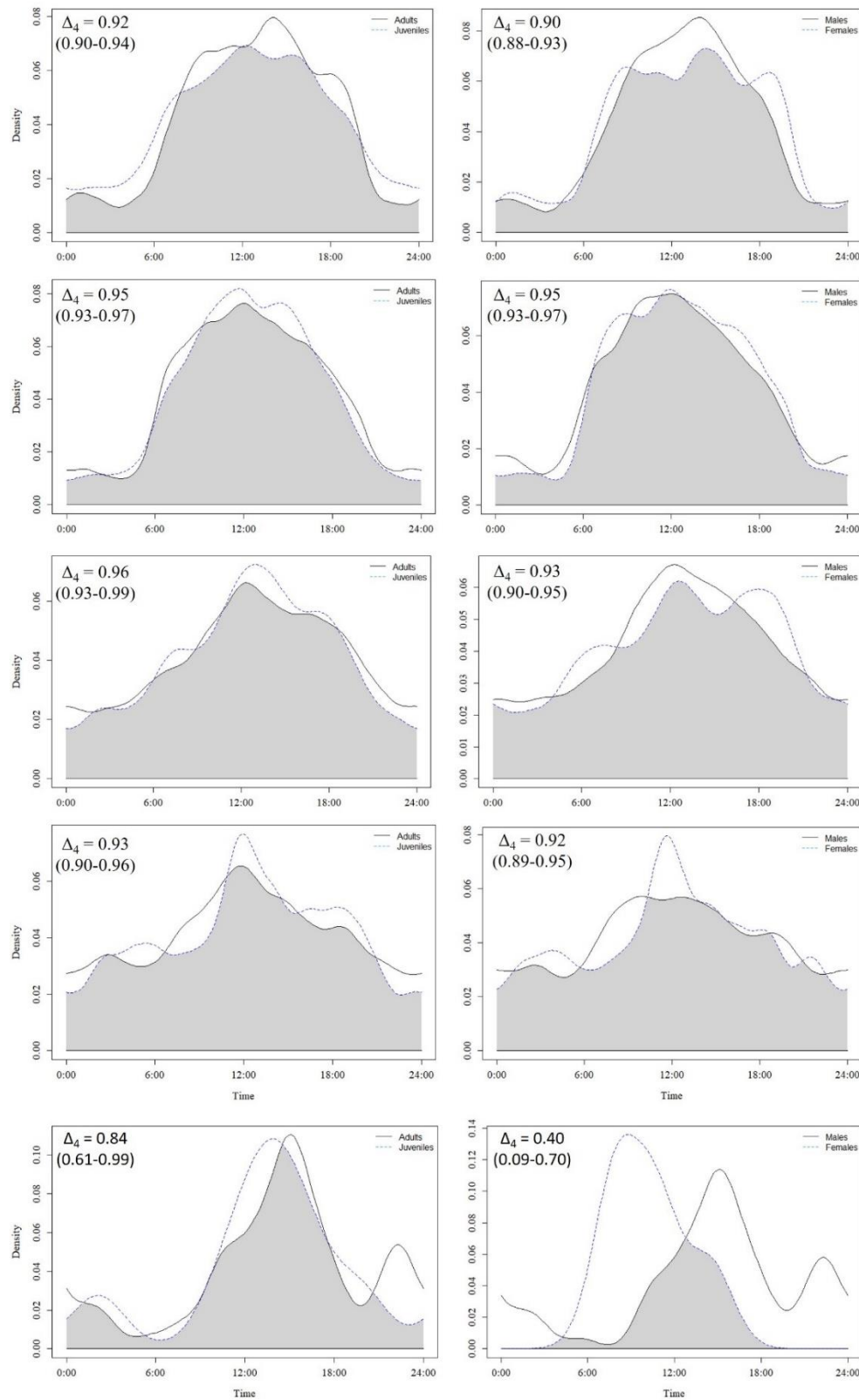


Figure S2. Density estimates of daily activity patterns per season of spotted turtles (*Clemmys guttata*) monitored using automated telemetry in Virginia during 2018 and 2019. On the left,

solid lines are the kernel density estimates for adults and dashed lines are for juveniles. On the right, solid lines are the kernel density estimates for males and dashed lines are for females. The overlap coefficient is represented by the shaded area and as an index (Δ) with corresponding 95% confidence intervals. Seasons are broken into the following categories, starting from the top: early spring: March-April, late spring = May-June, summer = July-August, fall = September-October, and winter = November-February.

CHAPTER II

MOVEMENT ECOLOGY OF ADULT AD JUVENILE SPOTTED TURTLES (*CLEMMYS* *GUTTATA*) IN A SEASONALLY DYNAMIC ENVIRONMENT

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ABSTRACT

Context. Understanding the temporal and spatial scale at which wildlife move is vital for conservation and management. This is especially important for semi-aquatic species which make frequent inter-wetland movements to fulfill life-history requirements.

Aims. We investigate the drivers of movement and space-use of the imperiled spotted turtle (*Clemmys guttata*), an ephemeral wetland specialist, in three large, isolated wetland complexes in Virginia, U.S.A.

Methods. We use VHF radio-transmitters to radio-locate adult and juvenile turtles and estimate movement and space-use during their active and aestivation seasons (March - August). We then use generalized linear mixed models to examine how movement and space-use varied based on intrinsic turtle characteristics and extrinsic wetland and climatic features.

Key results. We showed that on average individual spotted turtles used 5 wetlands per year (range 3 – 13) and that their inter-wetland movement and daily movement distance varied seasonally in accordance with wetland availability and breeding phenology. Spotted turtle movement and space-use was influenced by the arrangement and size of the wetland complexes, with turtles moving farther and occupying larger home-ranges as size and distance between wetlands increased. Inter-wetland movement was not influenced by intrinsic turtle characteristics, but larger adult turtles moved farther, used more wetlands, and had larger home-ranges than smaller turtles.

Conclusions. Turtle response to variation in season and wetland configuration highlight the need for complex and dynamic landscapes that are required to sustain this species.

Implications. This study has important management implications showing that spotted turtles rely on a large number of diverse wetlands as well as upland habitat to fulfill their resource needs and that these habitat associations vary seasonally. And more broadly, results from our study can aid in the understanding of the spatial and temporal variation in patch characteristics (e.g., quality and extent) and inter-patch movement by organisms, which is critical for the conservation and management of semi-aquatic species and other species that occupy patchy or fragmented landscapes.

INTRODUCTION

Vital rates of populations inhabiting fragmented landscapes are in part constrained by movement patterns between patches (Fahrig and Merriam 1994; Hanski et al. 2000). Landscape connectivity, the degree to which the landscape facilitates or impedes movement between patches (Taylor et al. 1993), therefore influences population demographic parameters. While fragmentation is often induced by human activities, some habitats naturally exist in discrete habitat patches. For example, individual wetlands rarely harbor independent populations of semi-aquatic organisms, and instead, individuals often move among wetlands to exploit spatially distinct but critical resources. Therefore, the patchy occurrence of wetlands within a terrestrial matrix creates an environment in which individual organisms must make inter-wetland movements to fulfill their life history requirements. Thus, understanding the patterns in these movements provides important insights into the ecology and resource requirements of populations (Gibbs 2000; Gibbons 2003; Semlitsch and Bodie 2003).

Understanding the temporal and spatial scale at which wildlife move is vital for conserving and managing wildlife, particularly for semi-aquatic species that rely on connectivity between distinct wetland patches (Trenham et al. 2001; Petranka et al. 2004; Roe and Georges

2007). For example, it has been shown that inter-wetland movements of a variety of semi-aquatic species can be influenced by extrinsic factors such as weather, season, and distribution of resources (Bennett et al. 1970; McIntyre and Wiens 1999; Plummer et al. 1997; Roe and Georges 2007). Additionally, intrinsic factors such as sex, size, sexual maturity, and physiological and behavioral traits (Morreale et al. 1984; Gibbons et al. 1990; Litzgus and Mousseau 2004; Roe and Georges 2007) have also been shown to influence movement and space-use (i.e., home-range). Thus, understanding which factors drive inter-wetland movement in a given system or focal species can help managers predict when and where movement might occur and where management intervention could be most effective to facilitate safe dispersal.

The ecology of semi-aquatic freshwater turtles is especially complex because individuals often make long distance movements among a variety of habitats for nesting, mating, foraging, basking, aestivating, and overwintering purposes (Buhlmann and Gibbons 2001; Bowne et al. 2006; Beaudry et al. 2009). These habitat requirements often differ across seasons and, in response to variation in resource availability, wetland hydroperiod, precipitation, and temperature (Bodie and Semlitisch 2000; Litzgus and Brooks 2000; Cosentino et al. 2010). Fragmentation may reduce access to wetlands necessary for population stability through habitat destruction, habitat degradation, and/or creation of barriers to movement (Prugh et al. 2008; Cosentino and Schooley 2018). Additionally, long-distance movements across fragmented landscapes can be risky, primarily due to road mortality (Gibbs and Shriver 2002; Marchand and Litvaitis 2004; Howell and Seigel 2012), predation (Smith and Engeman 2002), or human collection (Steen and Gibbs 2004). This potential mortality can be particularly influential for turtle populations because studies on the life history traits of long-lived freshwater turtles

indicate that adult survivorship is the most important factor contributing to population stability (Congdon et al 1993; Congdon et al. 1994; Heppell 1998).

The spotted turtle (*Clemmys guttata*) is a relatively small (< 120 mm), semi-aquatic freshwater species, and like many other emydid species, are long-lived (up to 110 years) (Litzgus 2006), have delayed sexual maturity (up to 12 years) (Litzgus and Mousseau 2006), and relatively low reproductive output (3-6 eggs/clutch, may not nest annually) (Rasmussen and Litzgus 2010b). The species inhabits ephemeral or dynamic wetland ecosystems, such as wet meadows, vernal pools, flooded hayfields, marshes, swamps, springs, and bogs (Ernst and Lovich 2009), and make frequent use of the surrounding upland habitat (Beaudry et al. 2010; Litzgus and Mousseau 2004; Milam and Melvin 2001). Spotted turtles rely on wetlands for overwintering, mating, foraging, and thermoregulating purposes (Milam and Melvin 2001; Ernst and Lovich 2009). Individual spotted turtles occupy numerous wetlands across a season and often make large movements between wetlands in response to changes in habitat quality and availability (Milam and Melvin 2001; Beaudry et al. 2009; Litzgus and Mousseau 2004). Due to the fluctuating nature of ephemeral wetland systems, spotted turtles have evolved flexible behavioral and physiological responses that allow them to hibernate, estivate, or disperse, potentially up to 1.5 km among different habitats (Joyal et al. 2001; Rowe et al. 2013), to sustain ecological needs. Yet, they depend on stable aquatic environments for hibernation and often exhibit fidelity to wetland patches (Litzgus et al. 1999; Beaudry et al. 2009; Ernst and Lovich 2009). While many studies of spotted turtle movement ecology have occurred in the southern and northernmost regions of the species range (e.g., Joyal et al. 2001; Milam and Melvin 2001; Litzgus and Mousseau 2004; Rasmussen and Litzgus 2010a; Chandler et al. 2019), only one study (Ernst 1970) has been conducted in the central region. Additionally, studies of juvenile

freshwater turtles is rare (Brewster et al. 1991; Carstairs et al. 2019; McCourd et al. 2019) and no study to date has radio-located juvenile spotted turtles, which are a critical life-stage for population growth (Congdon et al. 1993; Congdon et al. 1994; Heppell 1998).

Here, we investigated the drivers of movement and space-use of the imperiled spotted turtle in an isolated spotted turtle population in Virginia, USA. Specifically, we examined how movement and space-use varied based on intrinsic turtle characteristics and extrinsic wetland and climatic features. We predicted movements would be largest and most frequent early in the spring, when spotted turtles are most active (Litzgus and Mousseau 2004; Beaudry et al. 2009). We expected climatic signals, such as increased precipitation or decreasing water availability in wetlands, would result in increased turtle movement. We expected turtles to move more between seasonal wetlands than permanent wetlands (Milam and Melvin 2001; Litzgus and Mousseau 2004; Beaudry et al. 2009) and that home-ranges would contain many, adjacent seasonal wetlands. Lastly, we expected to see differences in movement and space-use between adult and juvenile turtles, because juvenile turtles are constrained by size and predator avoidance (Congdon et al. 1993; Bowne et al. 2006), but not male and female adult turtles (Rasmussen and Litzgus 2010a; Buchanan et al. 2017; Chandler et al. 2020).

METHODS

Study site

We studied spotted turtle movement patterns on a U.S. military installation in Virginia, U.S.A. The installation is 8,000 acres and has been partitioned for a number of uses, including urban infrastructure (e.g., offices, housing, etc.) and natural areas set aside for training and wildlife conservation. The natural areas contained a continuum of habitat types from floodplain wetlands

to upland mixed pine-hardwood forests. We studied spotted turtles in three natural areas on the installation. Each of these sites had numerous wetlands occupied by spotted turtles, and although turtles were able to disperse among the sites, dispersal events were expected to be rare due to the distance among sites and the intervening upland habitat. Site 1 was predominantly managed as a wetland reserve, with a large, emergent wetland in the center, surrounding by two beaver-maintained, emergent wetlands and numerous small, ephemeral wetlands. The ephemeral wetlands were predominately forested and included a mix of natural vernal pools and anthropogenic depressions from ditches and other military activities. Site 2 was centered around a public-use area, including many paved and dirt walking paths. The site included several, large emergent wetlands, each with expansive floodplain, as well as numerous natural and anthropogenic ephemeral pools. Site 3 consisted of a large tract of contiguous hardwood and pine forest. The wetland complex included two large, emergent wetlands at the center and was surrounded by numerous forested natural and anthropogenic ephemeral pools. Sites 2 and 3 were connected by upland forest and adjacent bay and were approximately 1.5 km apart (straight-line distance). Site 1 was isolated from the other sites (~3 km apart), with a hostile intervening matrix of urban development and roads. The installation was surrounded by roads and urban development, with the only possibilities for emigration through a shared border with county parks at site 1 and site 3, respectively. These parks too were surrounded by roads and urban development, thus the army installation and two adjacent parks served as an island of remaining forested habitat. Specific locations of study sites are withheld throughout due to risk of illegal wildlife poaching.

Data Collection

Starting in May in 2016 and March 2017-2019, we attached VHF radio-transmitters to adult and juvenile spotted turtles in each of the three sites. Turtles were captured using collapsible hoop-net traps (ProMar TR-502 36" x 12") or by hand during visual encounter studies. Transmitters (RI-2B, 6 or 10 g from Holohil Systems Ltd) were attached to adult turtles weighing at least 120 g with approximately 3 g of Devcon 5 min epoxy gel for a total package weight of 9-13 g (max% of body weight = 7%). Smaller transmitters (PD-2, 3.5 g from Holohil Systems Ltd) were attached to juvenile turtles weighing at least 80 g with approximately 1 g of Devcon 5 min epoxy gel for a total package weight of 4.5 g (max% of body weight = 7%). We orientated transmitters so that the antenna trailed behind the turtle as it moved to reduce likelihood of the transmitter tangling in the environment, and on the posterior pleural scute to reduce stress on the marginal scutes. We removed transmitters from the turtles at the end of the transmitter's life, at twelve and six months, respectively. Seven percent of the body weight is below the standard for turtles (10%) that has suggested by the American Society of Ichthyologists and Herpetologists (ASIH 2004).

Upon initial capture, we assigned all turtles a unique ID code by notching the marginals with a triangular metal file (modified Ernst 1976). We categorised all turtles with a carapace length less than 100 mm as juveniles. For turtles greater than 100 mm, we determined their sex by examining the plastron curvature. For each initial capture or first recapture in a given year, we measured straight-line carapace and plastron lengths (mm) using calipers (Haglof Mantax Blue Calipers) and mass (g) using a pesola spring scale. All work was conducted under the Institutional Animal Care and Use Committee (IACUC) protocol #20048.

In 2016, we radio-located turtles two times a week from May through November. In 2017-2019, turtles were radio-located every 48 hours from March through August. Hibernation locations were later confirmed in November. We tracked turtles using a yagi antenna and a receiver (R-1000, Telonics). Each time we tracked turtles, we recorded their location using a global positioning system unit (GPS, Garmin eTrex), and we recorded a general description of the turtle's position, behavior, and habitat characteristics. For habitat measurements, within 1 meter of the turtle location we characterised habitat type (aquatic or terrestrial), wetland type (e.g., emergent wetland, seasonal forest pond, etc.), depth (m) of the turtle in the water and depth of the wetland (m) using a meter stick. We delineated wetland size by walking the perimeter of each wetland using a Trimble (R-1000, Telonics) with 1m resolution. We then plotted the wetlands on ArcGIS (ArcGIS Pro, ESRI Inc) to determine size (ha) and distance (m) to the next nearest wetland. Lastly, for each turtle location event, we calculated the number of days since last precipitation event using publicly available meteorological data for this site provided by NOAA (<http://www.noaa.gov/>).

Movement

We calculated two indices of spotted turtle movement. For each individual turtle, we first calculated the number of inter-wetland movements that turtle made during each year of monitoring. Daily movement distance was calculated by dividing the total distance moved by the number of days between tracking events. For movement and space-use indices, we only calculated these metrics for turtles tracked a minimum of 2 months (i.e. 30 tracking locations). For inter-wetland movement, we excluded data from 2016 because we tracked turtles infrequently and may have missed inter-wetland movements.

Space-use

We also calculated two indices of spotted turtle space-use. We first summed the number of discrete wetland patches used by individual turtles in a given year. For each individual, we calculated home-range sizes using autocorrelated kernel density estimates (AKDE) (Fleming et al. 2014), which addresses inherent autocorrelation in movement data. More specifically, we estimated 95% bivariate kernels using a maximum likelihood approach to fit a variogram to address the exact structuring of the underlying autocorrelation (Fleming et al. 2014, 2015; Fleming and Calabrese 2017). We also calculated the percent overlap of all home-ranges for each site and for individuals with multiple tracking years. Additionally, to allow for comparisons with a wider range of previous and future studies, we also calculated home-range size using 95% minimum convex polygons and 95% kernel density, which are included as supplementary material (Table S1). Home-range was estimated for each turtle for each year using data from 2016-2017. Individuals with fewer than 30 locations were removed from the analysis.

Statistical analyses

To assess patterns in spotted turtle movement and space-use, we used generalized linear mixed effects models to investigate the effects of intrinsic and extrinsic variables on movement and space-use. To quantify variation in movement, we used inter-wetland movement and movement distance. For variation in space-use, we used number of wetlands occupied in a year and home-range size.

Inter-wetland movement, or the probability a turtle would move from one discrete wetland to another, was assessed by creating a binomial response variable (0 = no move, 1 = moved). Fixed effects included wetland type (seasonal or permanent), wetland size (ha), distance

to nearest wetland (m), month, and number of days since last precipitation event, with turtle ID as the random effect. The daily movement distance models were fit using the gamma distribution with a log-link function to address normality violations and included the same fixed and random effects as the inter-wetland movement models. Additionally, non-movements were excluded from the data to better fit the assumptions of the model. Intrinsic turtle effects, sex, age, and size (plastron length), were fit in separate models, using predicted mean inter-wetland movement probability and mean movement distance per turtle per year, respectively, as response variables.

The number of wetlands occupied models were fit using a Poisson distribution. We used mean wetland size (ha), mean distance to nearest wetland (m), month, and year as fixed effects, and turtle ID as the random effect. The home-range models, using AKDE estimate, were fit using a gamma distribution with a log-link function. We used the same fixed and random effect as movement distance.

For the above, our candidate model set included every permutation of the applicable covariate set. We performed all model fitting in R (R Core Team 2022) with the “lme4” package (Bates et al. 2015). Model selection was conducted using Akaike’s Information Criterion (AIC) approach (Burnham and Anderson 2002). To improve clarity in presenting model selection tables, we only display models that were competitive within 4 Δ AIC. Similarly, when applicable, parameter estimates were derived by model averaging all models within 4 Δ AIC (Burnham and Anderson 2002). Model goodness of fit for our top models was assessed using residual plots.

RESULTS

In 2016, we tracked 6 turtles (4 M and 2 F) evenly distributed across each of the three sites. We collected 181 observations of the 6 turtles (min-max: 30-42). In 2017, we radio-tracked 21 turtles

(12 M and 9 F) across sites 1 and 3, including one male previously tracked in 2016. We collected 1364 observations of the 21 turtles (min-max: 40-73). In 2018, we tracked 29 turtles (9 M, 10 F, and 10 J) across sites 1 and 2, including 7 adult turtles previously tracked in 2017. We collected 1191 observations of the 29 turtles (min-max: 30-61). In 2019, we radio-tracked 21 turtles (6 M, 6 F, and 9 J) at site 1, including 7 adult and 3 juvenile turtles that were radio-tracked in the previous year(s). We collected 1005 observations of the 21 turtles (min-max: 30-65). In total, we radio-tracked 21 males, 21 females, and 16 juveniles between 2016-2019. Of the 58 turtles, we radio-tracked 43 individuals for one year, 7 individuals for two years, 4 individuals for three years, and 1 individual for all four years.

Across the four-year study period, four radio-equipped adult turtles (n=42) were found dead. In July 2016, one female was found dead to suspected avian predation. Across the winter of 2017-2018, one male and one female hibernated terrestrially. The male was found deceased in its hibernation location in March 2018, while the female forwent reproduction that year and was later found dead in June. Lastly, one female was found deceased (unknown causes) following emergence from hibernation in March 2019. Only one radio-equipped juvenile was found dead in November 2018, likely due to mesopredator predation between August and November radiolocation.

Movement

Spotted turtles used all wetland types at the three sites and inter-wetland movement between these wetlands was common. Inter-wetland movement probability was best predicted by month, number of days since last precipitation event ($\beta = -0.18 \pm 0.05$), percent change in wetland depth ($\beta = -0.15 \pm 0.04$), type of wetland, and size of wetland ($\beta = 0.22 \pm 0.23$) (Table 1). There was no influence of intrinsic turtle characteristics on inter-wetland movement probability. There was a

strong seasonal effect on turtle inter-wetland movement, where turtles increased in movement probability through the spring and then drastically decreased movement into the summer months (Figure 1). Turtle inter-wetland movement probability decreased with number of days since the last precipitation event with the highest movement probability (~ 0.40) during the day of the precipitation event. There was also a negative relationship between inter-wetland movement probability and percent change in wetland depth, in which turtles made inter-wetland movements in response to wetland drying (Figure 2). Turtle inter-wetland movement probability was higher in seasonal wetlands (0.25 , $CI=0.22-0.28$) than permanent wetlands (0.17 , $CI=0.14-0.20$), while movement probability increased as wetland size increased, regardless of type.

Daily movement distance by turtles was best predicted by month, number of days since last precipitation event ($\beta = -0.15 \pm 0.04$), type of wetland, size of wetland ($\beta = -0.11 \pm 0.03$), and distance to nearest wetland ($\beta = -0.11 \pm 0.03$) (Table 1). Additionally, there was an effect of age class ($\beta = -0.22 \pm 0.09$), but not sex class, on movement distance. There was a similar seasonal effect on distance moved by turtles (Figure 1), but with large variance around August movements. Additionally, as with inter-wetland movement, there was a negative relationship between daily movement distance and number of days since last precipitation event; however, the confidence intervals were much wider for distance moved than inter-wetland movement. Contrary to inter-wetland movement, movement distance by turtles was higher in permanent wetlands (24.44 , $CI=21.23-27.64$) than seasonal wetlands (18.54 , $CI=17.90-19.18$) or upland habitat (27.64 , $CI=11.02-117.91$), though, there was a positive relationship between movement distance and wetland size, again, regardless of location type. As expected, movement distance by turtles increased as distance between wetlands increased. And though adult and juvenile turtles

make inter-wetland movements at the same rate, the daily movement distance of adults (20.22, CI=18.90-21.54) was almost twice as far as juvenile movement (12.27, CI=10.44-14.11).

Space-use

Collectively, spotted turtles used 92 unique seasonal wetlands and 24 permanent wetlands. Individual turtles annually used a mean of 5 wetlands (range 3 – 13 wetlands). For extrinsic effects, number of wetlands occupied by turtles in a given season was best predicted by mean distance between wetlands ($\beta = -0.09 \pm 0.06$) (Table 2). For intrinsic turtle effects, number of wetlands occupied was influenced by turtle size ($\beta = 0.18 \pm 0.06$) and age (Table 2). There was a positive relationship between mean distance between wetlands and number of wetlands occupied, with the greatest number of wetlands occupied when wetlands were an average of ~40 m apart. Despite no effect of turtle size on inter-wetland movement or daily movement distance, larger turtles tended to occupy more wetlands (Figure 3). Similarly, adult turtles (6.64, CI=6.01-7.23) occupied almost twice as many wetlands as juveniles (3.73, CI=2.96-4.5).

Spotted turtle home-ranges were generally small (less than 10 ha). Male (4.64, CI=2.65-6.65) and female (5.59, CI=2.89-7.29) turtles had similar mean home-range size however, adult home-range size (5.06, CI=3.56-6.56) was larger than juvenile home range (1.86, CI=0.97-2.75). Home-range size was best predicted by mean distance between wetlands ($\beta = 0.67 \pm 0.20$) and mean wetland size ($\beta = 0.69 \pm 0.20$), as well as turtle age class and size ($\beta = 0.38 \pm 0.15$) (Table 2). Similar to number of wetlands occupied, home-range size increased as distance between wetlands increased and as wetland size increased. Additionally, larger individuals tended to have larger home ranges (Figure 3). We observed significant overlap in turtle home-ranges (Figure S1), with some individuals home ranges completely encompassed by the home-range of other individuals. Mean home-range overlap was 45%. Inspection of individual home-ranges and

home-range overlap per site denoted clearly defined areas where turtles congregated. Turtles also exhibited fidelity to their home-range centers between years, with temporal home-range overlap estimated at 85% (Figure 4).

There were two outlier movements that were removed from the home-range dataset based on variogram inspection. In 2016, one male turtle moved 3425 m during June – August. The turtle moved from one site to another through a combination of upland movements and forays into an adjacent bay, and ultimately settled at the new site (for at least the following 2 years of the study). In 2018, one male turtle moved 2340 m during June – July. The turtle also moved from one site to another and used a small river to avoid a major highway along its movement path. This male also remained at this new site for the remaining year of the study. If these movements are included a sex effect on home-range size is evident between male (28.73, CI=12.24-55.26) and female (5.59, CI=3.12-9.58) turtles, however the confidence intervals around male movement were very large.

DISCUSSION

Understanding the extrinsic and intrinsic drivers of movement and space-use provide insight into the temporal and spatial dynamics of populations and the resources upon which the organism depends. Our results demonstrate that individual spotted turtles use and depend on a large number of wetlands to meet their annual resource needs (mean = 5 wetlands per turtle: range 3-13) and that the movement patterns of spotted turtles are influenced by turtle age as well as wetland characteristics, weather, and season. These specific patterns and their causes are explored in turn.

Movement

Spotted turtle inter-wetland movement and movement distance was strongly seasonal (Figure 1) and coincides with seasonality in activity documented across the species range (Litzgus and Brooks 2000; Litzgus and Mousseau 2004; Beaudry et al. 2009). In general, five activity seasons have been identified for spotted turtles, including a) early spring: emergence from hibernation with basking, foraging, and mating; b) late spring/early summer: foraging and nesting; c) late summer: reduced activity and/or aestivation; d) fall: limited foraging and basking, movements to hibernacula; and e) winter: hibernation (Litzgus and Brooks 2000; Litzgus and Mousseau 2004; Beaudry et al. 2009). Though, the exact timing of these differs across the species range, and for southernmost populations, turtles may forgo both aestivation and hibernation and retain low activity levels across the entire year (Litzgus and Mousseau 2004; Stevenson et al. 2015; Chandler et al. 2019). In our study, following hibernation emergence, turtle movement was mostly restricted within wetlands, with limited inter-wetland movements from male turtles presumably looking for additional mating opportunities (Litzgus and Mousseau 2004). Turtle inter-wetland movement and movement distance increased sharply across the spring, with turtles making frequent inter-wetland movements primarily between seasonal wetlands, where we documented turtles eating amphibian egg masses and aquatic vegetation, and basking. Female turtles began nesting movements in mid-May, deposited nests late May – early June, and then returned to spring activity centers. Exact nest locations were not documented for this study, but females were palpated biweekly to determine timing of reproduction. Starting in June, movement began to decrease precipitously. And as wetlands dried in late June and early July, inter-wetland movements became infrequent, and most turtles exhibited aestivation behavior in upland habitats. Interestingly, inter-wetland movement and movement distance across the late summer

period varied highly between individual turtles. During large summer rain events (> 5 cm), some individuals would move from their terrestrial aestivation location to a newly filled wetland, while others remained in their aestivation habitat. Additionally, some individual females made large movements (~50-100m) in mid-July, moving from one summer activity center to another, which has also been observed in other southern populations (Litzgus and Mousseau 2004).

In addition to seasonal effects, spotted turtle inter-wetland movement and daily movement distance was also associated with precipitation and changes in wetland depth. Inter-wetland movement probability was highest on the day of a precipitation event and had a negative relationship with number of days since the last precipitation event. After precipitation events, turtles were seen in wetlands and shallow depressions that were recently inundated by the rising water levels. This is potentially explained by foraging on recently submerged vegetation and invertebrates (Chandler et al. 2019). Additionally, movement during precipitation events likely reduces the risk of terrestrial movement due to lower risk of evaporative water loss (Ernst 1968; Stone and Iverson 1999), especially for juvenile turtles (Costanzo et al. 2001). However, for daily movement distance, the confidence intervals were wide, thus precipitation can be considered an influential but not a limiting factor of long-distance movements. Inter-wetland movement was associated with decrease in wetland depth (Figure 2), in which both adult and juvenile spotted turtles responded similarly to changes in habitat availability across the season. Though long-distance movements were made solely by adult turtles. Due to the fluctuating nature of ephemeral wetland systems, spotted turtles have evolved flexible behavioral and physiological responses to dynamic habitat and resource quality and availability (Joyal et al. 2001; Rowe et al. 2013). Adult and juvenile turtles demonstrated similar responses to environmental changes across the season (e.g., inter-wetland movements, aestivation, etc.),

however, adult turtles were able to move farther and occupy more space than juveniles, likely due to increased physiological costs and predator avoidance by juveniles (Congdon et al. 1993; Bowne et al. 2006).

Inter-wetland movement and daily movement distance were also influenced by wetland characteristics, including type, size, and positioning across the landscape. There were a greater number of turtle inter-wetland movements between seasonal wetlands than permanent wetlands, as seasonal wetlands were characterised by more dynamic hydroperiods and resource availability; though we acknowledge this relationship also reflects habitat availability (80% of wetlands were seasonal) as opposed to habitat quality. Inter-wetland movement probability also increased with size of the wetland, regardless of wetland type. When wetlands were saturated, turtles shuttled between wetlands in response to resource availability. However, as wetland depth decreased, turtles had to shift to larger, deeper wetlands that maintained water availability. Thus, there was diffusion of inter-wetland movement among small and large wetlands when all wetlands have water, but a congregation of turtles into larger wetlands when water was limited. Similarly, we saw a positive relationship between wetland size and movement distance. We suspect two potential causes: 1) within wetland movement: turtles are able to move farther in larger wetlands than smaller wetlands; and 2) between wetland movement: larger wetlands draw a disproportionate number of turtles as smaller wetlands dry, thus turtles may have to move farther distance to reach these limited habitats. This also supports why we saw greater inter-wetland movements between seasonal wetlands, but greater movement distances in permanent wetlands. Lastly, probability of inter-wetland movement and movement distance decreased with increased distance between wetlands, however, emigration across relatively large distances is possible.

Although our study sites were thought to be largely independent, two individual male turtles emigrated from one site to another, demonstrating the incredible movement capability of this species (3425 and 2340 m, respectively). Long-distance movements for this species have been previously documented (1.1-1.3 km; Joyal et al. 2001; Milam and Melvin 2001; Beaudry et al. 2009), however, it is not known how common these movements are. Yet, even uncommon long-distance movements or dispersal events represent the potential for genetic dispersal, as even one individual per generation can reduce the potential for inbreeding depression and genetic drift (Mill and Allendorf 1996). Though long-distance dispersal can be vital for population stability, these movements may result in increased risk of mortality through vehicle collisions (Gibbs and Shriver 2002; Marchand and Litvaitis 2004; Howell and Seigel 2012), predation by mesopredators (Smith and Engeman 2002), and human collection (Steen and Gibbs 2004). Turtles may mitigate this risk through avoidance of high-risk habitats or areas. For example, the long-distance mover from site 2 traveled along intermittent streams and a river, avoiding multi-use trails and a major 6-lane highway. The long-distance mover from site 3 traveled along the edge of a large, deep bay, thereby reducing upland habitat movements and risk of predation by terrestrial meso-predators. This demonstrates the importance of isolated wetlands and other bodies of water that may serve as routes or stepping-stone habitats for large-scale movements of spotted turtles, highlighting the importance of the features for wetland connectivity at local (population-center) and landscape (meta-population) scales.

Space-use

Mean home-range sizes at our site (5.06 ha) were larger than mean home-range size for the species (3.7 ha), though within the range reported for this species, which varies substantially across the species' range from < 1 – 16 ha (e.g., Litzgus and Mousseau 2004; Rowe et al. 2013;

Chandler et al. 2020). There was no difference in home-range size between male and female turtles, a trend that also varies across the species range (e.g., Haxton and Berrill 1999; Litzgus and Mousseau 2004; Rasmussen and Litzgus 2010a; O'Bryan et al 2016). Unsurprisingly, number of wetlands occupied and home-range size was nearly twice as large for adult than juvenile turtles. While adult and juvenile turtles respond similarly to environmental cues, adults utilise more of the landscape as compared to their juvenile counterparts. More information is needed to determine whether population home-range size is correlated to wetland patch availability or if there are landscape or latitudinal effects across the species range. Nevertheless, these home-range sizes can help guide land managers to the amount of habitat needed to conserve a population of spotted turtles and identify whether key features (e.g., nesting habitat, roads) in the landscape may be encountered by turtles. Additionally, even across other emydid turtles, little is known regarding the movement of juvenile turtles. Therefore, in this study, we are helping to fill the knowledge gap of an understudied, cryptic life-stage for this species.

Spotted turtle space-use was also influenced by wetland size and arrangement on the landscape. As expected, home-range size increased as mean distance between wetlands increased. There was also a positive relationship between mean distance between wetlands and number of wetlands occupied, contrary to previous findings in the literature (Joyal et al. 2001; Milam and Melvin 2002; Beaudry 2009). This is potentially due to the arrangement of wetlands at our site, where wetlands < 10 m often had similar composition and hydrology, while wetlands slightly farther away (40 m) away were more heterogenous. Home-range size also increased with mean wetland size, though wetland size did not influence number of occupied wetlands by turtles. There was also an effect of turtle size on space-use, in which larger turtles occupied more wetlands and had larger home-ranges (Figure 3), though was unrelated to inter-wetland

movement or even daily movement distance. At each site, spotted turtles occupied wetland complexes with well-defined activity centers where turtles were clustered. Activity centers were generally located around wetlands where turtles congregated in March and April for courtship and mating (Litzgus and Mousseau 2004). Some individuals moved away from activity centers by early summer, however, many turtles' activity centers did not differ greatly between spring and summer activity. This can also be seen in the spatial overlap of spotted turtle home-ranges (mean 45% overlap), where clustering of individuals around certain habitat features was detected. Additionally, spotted turtle home-range overlapped considerably across years (85%) (Figure 4). This supports results from other studies, which have document spotted turtle fidelity to overwintering wetlands and spring breeding wetlands (Litzgus and Mousseau 2004). This has considerable implications for the persistence of this species in the future in the face of continued land use and climatic changes, which have the potential to disrupt hydroperiods of key wetland habitats.

Management recommendations

Spotted turtles in this study used numerous wetlands, including both ephemeral and permanent wetlands, with turtles using an average of 5 wetlands per year. Due to this species' reliance on numerous wetlands to meet their resource requirements, management for this species must entail protection of multiple connected wetlands with a safe upland matrix between them. Our turtles used a large number of small (> 0.08 ha) vernal pools or anthropogenic depressions (e.g., trench) and these types of wetlands often fail to get detected or meet criteria to be eligible for protection (e.g., "No Net Loss" criteria). Thus, the loss of small wetlands could result in a dramatic reduction in wetland availability and would also increase the isolation of remaining wetlands (Semlitsch and Brodie 1998; Joyal et al. 2001). We documented a high degree of inter-wetland

movement across each of the sites, which demonstrates the importance of wetland mosaics as the basis for managing spotted turtle populations. Spotted turtles would likely benefit from the protection of entire wetland complexes that include a mix of wetland types and sizes with minimal distance between wetlands, and with an upland matrix without threats and barriers such as road, agriculture, or development. Long-term persistence of spotted turtle populations likely rely on occasional long-distance movements (up to 1-2 km) between wetland complexes (Joyal et al. 2001). These long-distance movements would likely benefit from the presence of landscape features such as streams and road underpasses that facilitate movement.

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TABLES

Table 1. Model selection statistics for spotted turtle (*Clemmys guttata*) inter-wetland movement and daily movement distance. Only top candidate models, models within 4 Δ AIC, are presented. Covariates of movement include extrinsic wetland and climate covariates: month, number of days since last precipitation event (dslp), percent change in wetland depth (pchange), wetland type (type), wetland size (size), and intrinsic turtle covariates: sex, age, and size (PL; plastron length). Models were ranked using Akaike’s Information Criterion (AIC) and included with each model is the number of parameters (K), AIC difference between model of interest and model with lowest AIC (Δ AIC), model weight (AICwt), and log-likelihood estimate (LL). Data is derived from spotted turtle radio-telemetry conducted from 2016-2019 in Virginia.

Inter-Wetland Movement					
Model	K	AIC	ΔAIC	AICwt	LL
Extrinsic only					
month + dslp + pchange + type + size	11	2736.24	0.00	0.97	-1357.07
Intrinsic only (age)					
null	1	38.47	0.00	0.55	-18.20
Intrinsic only (sex)					
null	1	28.85	0.00	0.56	-13.39
Movement Distance					
Model	K	AIC	ΔAIC	AICwt	LL
Extrinsic only					
month + dslp + type + size + dist	12	17013.01	0.00	0.94	-8493.42
Intrinsic only (age)					
age	3	550.45	0.00	0.76	-272.06
age + PL	4	552.66	2.22	0.24	-273.32
PL	3	553.53	3.08	0.00	-272.55
Intrinsic only (sex)					
null	2	437.01	0.00	0.52	-216.40

Table 2. Model selection statistics for spotted turtle (*Clemmys guttata*) wetland occupancy (number of wetlands occupied by an individual turtle in a given year) and home-range (autocorrelated kernel density estimate; ha). Only top candidate models, models within 4 Δ AIC, are presented. Covariates of movement include extrinsic wetland and climate covariates: year, mean wetland size (size), mean distance to nearest wetland (m), and intrinsic turtle covariates: sex, age, and size (PL; plastron length). Models were ranked using Akaike's Information Criterion (AIC) and included with each model is the number of parameters (K), AIC difference between model of interest and model with lowest AIC (Δ AIC), model weight (AICwt), and log-likelihood estimate (LL). Data is derived from spotted turtle radio-telemetry conducted from 2016-2019 in Virginia.

Number of Wetlands Occupied					
Model	K	AIC	ΔAIC	AICwt	LL
Extrinsic only					
MeanDist + MeanSize + Year	4	320.58	0.00	0.31	-156.00
MeanDist + Year	3	320.65	0.06	0.30	-157.15
MeanDist	2	321.20	0.62	0.23	-158.52
Intrinsic only (age)					
age + PL	3	305.51	0.00	0.74	-149.64
Intrinsic only (sex)					
null	1	229.61	0.00	0.51	-113.77
Home-Range Size					
Model	K	AIC	ΔAIC	AICwt	LL
Extrinsic only					
MeanDist + MeanSize + year	7	399.59	0.00	0.82	-191.95
MeanDist + MeanSize	4	402.62	3.03	0.18	-197.02
Intrinsic only (age)					
age	3	344.25	0.00	0.71	-168.95
age + PL	4	346.24	1.99	0.26	-168.82
Intrinsic only (sex)					
null	2	277.49	0.00	0.49	-136.62

FIGURES

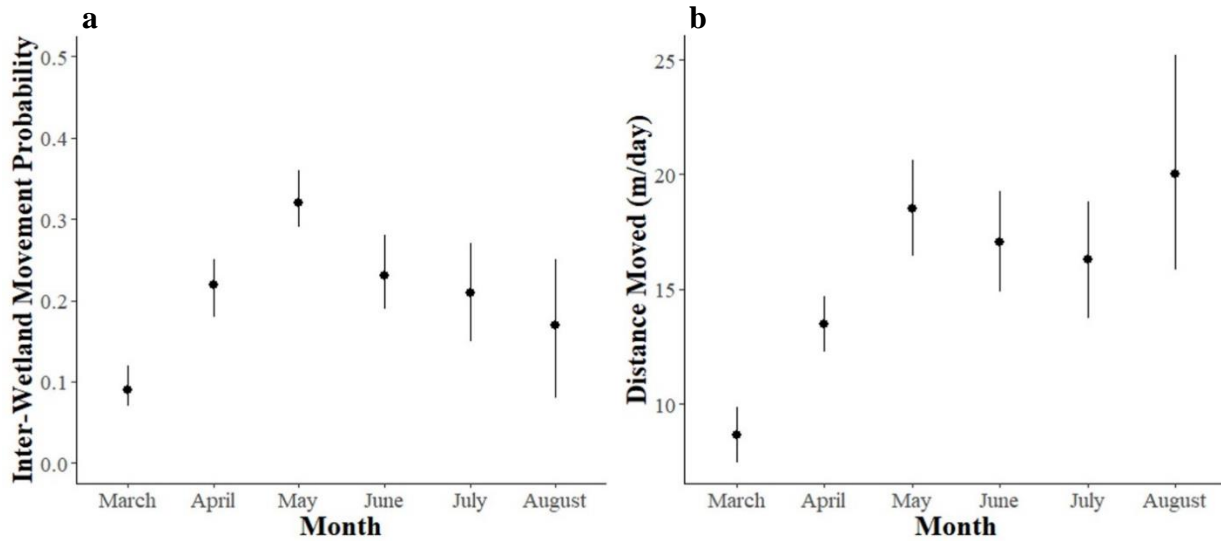


Figure 1. Influence of month on spotted turtle (*Clemmys guttata*) inter-wetland movement probability (a) and daily movement distance (b). 95% confidence intervals are presented using a gray band. Data is derived from spotted turtle radio-telemetry conducted from 2016-2019 in Virginia.

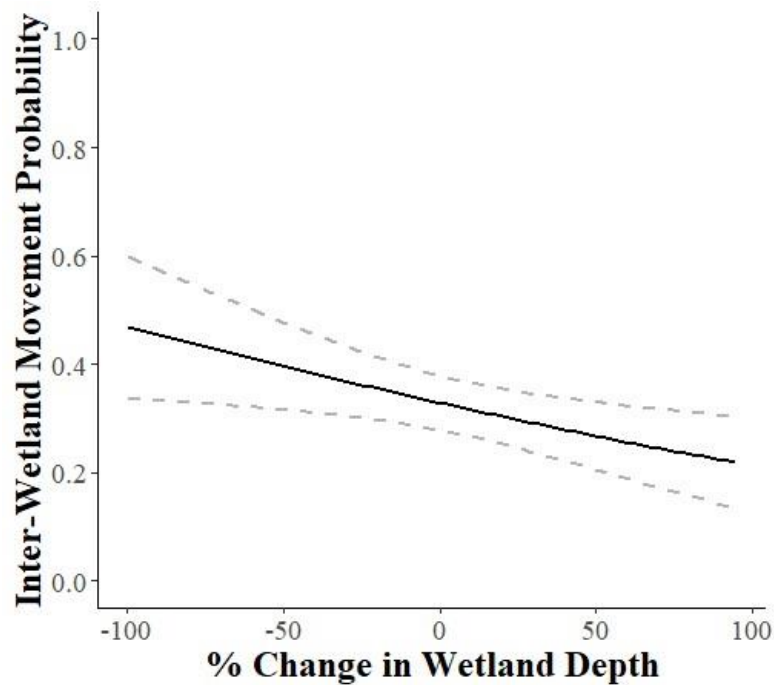


Figure 2. Influence of percent change in wetland depth on spotted turtle (*Clemmys guttata*) inter-wetland movement probability. 95% confidence intervals are presented using a gray band. Data is derived from spotted turtle radio-telemetry conducted from 2016-2019 in Virginia.

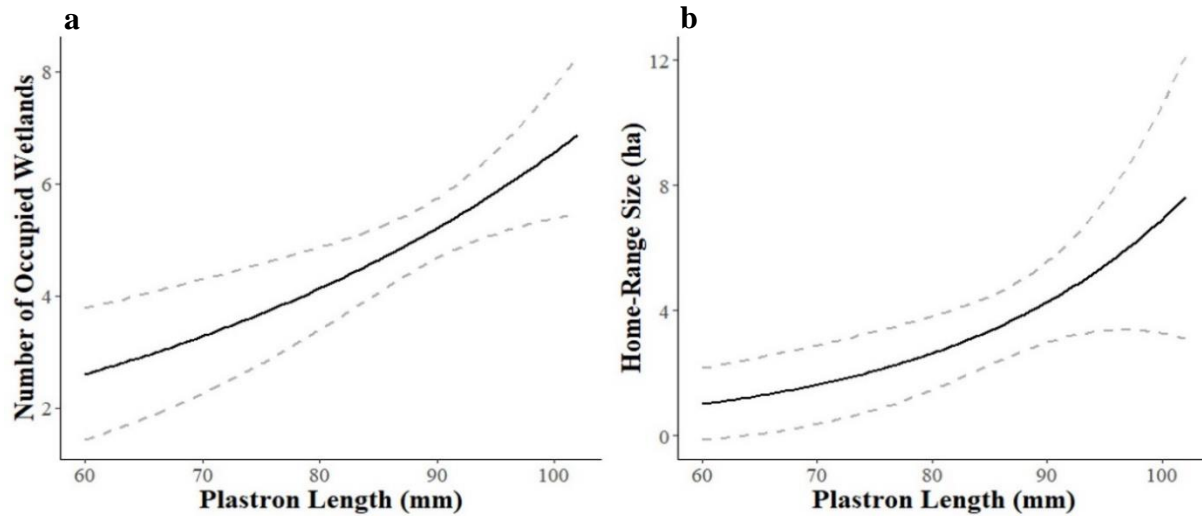


Figure 3. Influence of plastron length (mm) on spotted turtle (*Clemmys guttata*) wetland occupancy (number of wetlands occupied by an individual turtle in a given year) (a) and home-range size (autocorrelated kernel density estimate; ha) (b). 95% confidence intervals are presented using a gray band. Data is derived from spotted turtle radio-telemetry conducted from 2016-2019 in Virginia.

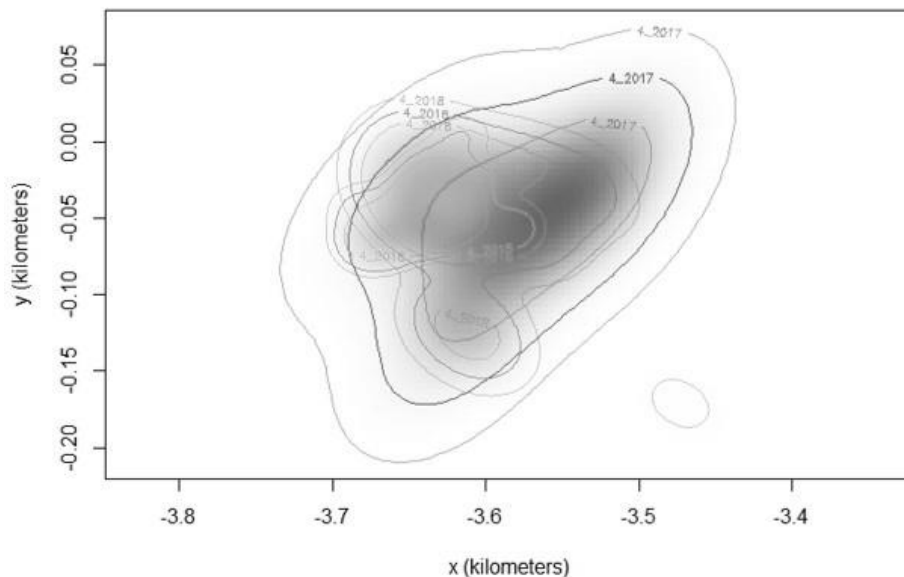


Figure 4. Temporal overlap of yearly home-range distribution (autocorrelated kernel density estimate) across four years for an individual spotted turtle (*Clemmys guttata*). Data is derived from spotted turtle radio-telemetry conducted from 2016-2019 in Virginia.

SUPPLEMENTARY INFORMATION

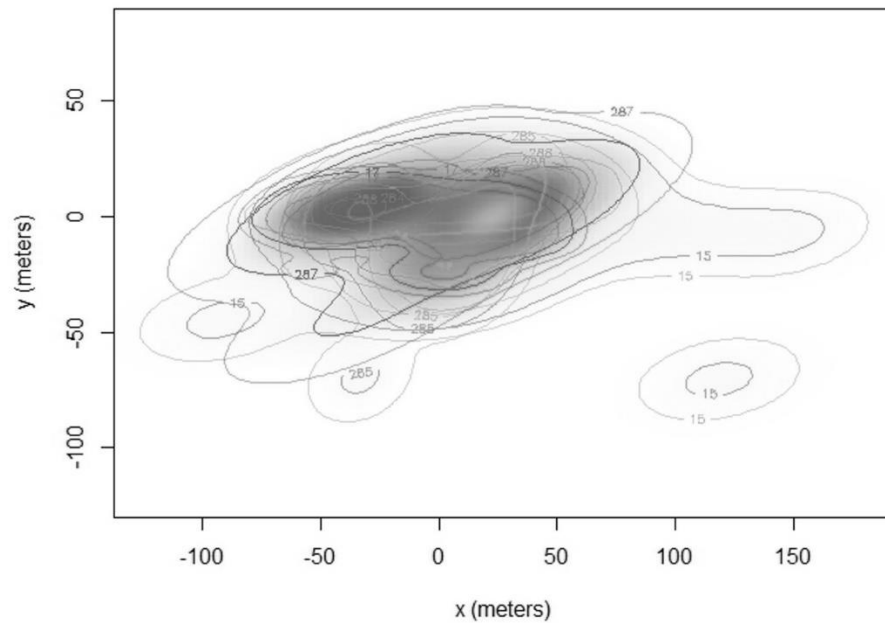


Figure S1. Spatial overlap of five individual spotted turtle (*Clemmys guttata*) home-range distributions (autocorrelated kernel density estimate) at a single site in a given year. Data is derived from spotted turtle radio-telemetry conducted from 2016-2019 in Virginia.

CHAPTER III

SEASONAL OCCUPANCY AND ABUNDANCE DYNAMICS OF THE IMPERILED SPOTTED TURTLE (*CLEMMYS GUTTATA*)

Ellery V. Lassiter, Jinelle H. Sperry, and Brett A. DeGregorio

ABSTRACT

Turtles are facing worldwide declines, in major part due to habitat loss and fragmentation. Turtles that inhabit wetland ecosystems are especially vulnerable due reliance on multiple wetlands and connectivity between those wetlands. Here we conducted repeated surveys across three spring seasons (2017-2019) to better understand the spatio-temporal occupancy dynamics and habitat associations of the imperiled spotted turtle (*Clemmys guttata*). We then explored how wetland characteristics influenced occupancy and abundance, and how climatic conditions influenced detection of spotted turtles. We detected spotted turtles in 65% of available wetlands at our site, in which turtles predominantly (73%) occupied forested ephemeral pools. Occupancy and abundance varied across the spring sampling season, with a peak in the number of occupied wetlands and abundance estimates in the middle of the season. Occupancy probability was relatively high (65%) and was positively related to wetland size. There was a seasonal trend in wetland size use in which turtle occupancy and abundance in smaller wetlands decreased across the season but increased in larger wetlands. Abundance estimates from N-mixture models at our site were relatively high (418 – 464), and abundance was best predicted by the number of amphibian egg masses, but also had a positive relationship with wetland size and negative relationship with distance to nearest wetland. Overall, our results corroborate findings that spotted turtles rely on numerous wetlands and that wetland use varies across the season. We also demonstrate the utility of dynamic occupancy monitoring for better understanding the resource requirements of freshwater turtles inhabiting dynamic ecosystems, which is less field intensive than other approaches and provides better predictions of dynamic distributions and population persistence.

INTRODUCTION

Turtles are experiencing global population declines, with nearly 60% of species considered threatened, endangered, or extinct (Gibbons et al. 2000, Ernst and Lovich 2009, Hoffman et al. 2010). Turtle populations face numerous threats including unsustainable exploitation for food and commercial pet trade, climate change, and disease, however, the primary cause of turtle declines is due to habitat loss and fragmentation (Gibbons et al. 2000, Lovich et al. 2018, Spencer et al. 2018). Turtles that inhabit wetland ecosystems are especially vulnerable to habitat loss due to their reliance on multiple wetlands and therefore connectivity between those wetlands (Gibbs 2000, Marsh and Trenham 2001, Cosentino and Schooley 2018). Wetland ecosystems are often spatially patchy across the landscape and exhibit seasonal patterns in water levels and resource availability (Joyal et al. 2001, Naugel et al. 2001, Roe et al. 2009). Thus, turtles that inhabit such ecosystems often use a variety of different wetlands and other habitats for mating, foraging, thermoregulation, aestivating, and overwintering purposes (Buhlmann and Gibbons 2001, Bowne et al. 2006, Beaudry et al. 2009). These habitat requirements may differ across a season in response to variation in resource availability, wetland hydroperiod, precipitation, and temperature (Bodie and Semlitisch 2000, Litzgus and Brooks 2000, Cosentino et al. 2010). Understanding how habitat requirements of freshwater turtles vary across space and time is critical for effective monitoring and management of these species (Roe et al. 2009). Here, we conducted repeated surveys across three spring seasons to better understand the spatio-temporal occupancy dynamics and habitat associations of an imperiled freshwater turtle.

Effective monitoring of rare or cryptic species, such as most freshwater turtles, can be complicated by low or variable detection of focal organisms (Grant and Doherty 2007, Marsh

2009, Durso et al. 2011, Refsnider et al. 2011, Crump and Forstner 2019). Thus, analytical approaches that account for imperfect detection in surveys can greatly improve our ability to discern patterns in habitat associations and relative abundance within different habitats (Grant and Doherty 2007, Marsh 2009, Durso et al. 2011, Crump and Forstner 2019). Occupancy modeling (MacKenzie et al. 2006) has emerged as an invaluable framework for understanding distribution and habitat associations for many species of turtle (e.g., Zylstra et al. 2010, Guzy et al. 2014, Stokeld et al. 2014, Buchanan et al. 2018, Markle et al. 2018, Chandler et al. 2020, Paterson et al. 2021), and many variants exist to accommodate different parameter estimation (e.g. n-mixture abundance) (Royle 2004, Rizkalla and Swihart 2006, Smith et al. 2009, Erb et al. 2015, Horn and Gervais 2018) or sampling approaches (e.g., distance sampling) (Royle et al. 2004, Smith et al. 2009, Stober et al. 2010, Castellon et al. 2015).

Because many freshwater turtle species inhabit seasonally dynamic environments, they may be better studied through dynamic occupancy (MacKenzie et al. 2003) and open-population n-mixture (Royal 2004, Dail and Madsen 2011) models. These approaches can inform both occupancy and turnover dynamics of patchy populations in which habitat quality varies (Cosentino et al. 2010, Schooley and Branch 2011, Lamy et al. 2013, Sutherland et al. 2014, Ahlers et al. 2015). Population responses to temporal and spatial variation in habitat can be the result of behavioral responses and demographic processes (Marsh 2001, Cosentino et al. 2010), thus it's important to understand how these processes interact with patterns of distribution and turnover. For turtles, behavioral processes are especially important for estimating colonization and extinction dynamics, because individuals adjust habitat use and occupy multiple wetland patches in response to fluctuations in resource availability (Joyal et al. 2001, Bowne et al. 2006, Ennen and Litzgus 2009, Roe et al. 2009, Serrano et al. 2019). The use of dynamic occupancy

models has improved our understanding of the behavioral and environmental drivers of dynamic species distributions, which can refine our estimation of occupancy patterns across space and time and better predict colonization or extinction probabilities under biologically meaningful scenarios (Schooley and Branch 2011, Lamy et al. 2013, Sutherland et al. 2014, Ahlers et al. 2015, Chandler et al. 2015). However, these methods have rarely been applied to studies of turtles (Cosentino et al. 2010, Scott and Rissler 2015, Cassel et al. 2019).

Spotted turtles (*Clemmys guttata*) are a species of freshwater turtle that inhabit dynamic wetland systems (Ernst and Lovich 2009). Spotted turtles are a relatively small (to 120 mm), semi-aquatic freshwater species, with populations distributed continuously along the east coast from Florida to Maine, and in disjunct populations along the great lakes in the U.S. and Canada (Ernst and Zug 1994, Ernst and Lovich 2009). They inhabit ephemeral wetland ecosystems (Ernst and Lovich 2009) and seasonally use the surrounding upland habitat (Milam and Melvin 2001, Litzgus and Mousseau 2004, Beaudry et al. 2010). Spotted turtles rely on wetlands for overwintering, mating, foraging, and thermoregulating (Milam and Melvin 2001, Ernst and Lovich 2009), and often make large movements (up to 1.5 km; Joyal et al. 2001) between wetlands in response to changes in habitat quality and availability (Milam and Melvin 2001, Litzgus and Mousseau 2004, Beaudry et al. 2009). While seasonal patterns of spotted turtle movement and habitat use have been documented (Litzgus and Brooks 2000, Joyal et al. 2001, Rowe et al. 2013), no study has investigated seasonal trends in occupancy or abundance patterns for this species. This approach could be beneficial for improving sampling design (e.g., when to survey specific habitats) and could be applied to understand distribution and vital rates of spotted turtle populations on a landscape-scale.

Here, we investigate the occupancy and abundance patterns of spotted turtle population occurring on a relatively large, but isolated military installation. Our overall objective was to investigate the seasonal trends in occupancy and abundance patterns of this species to better understand how their habitat associations vary seasonally and to then explore local habitat drivers of occupancy and abundance. Based on seasonal patterns of movements (Litzgus and Brooks 2000, Joyal et al. 2001, Rowe et al. 2013), we predicted that there would be a seasonal pattern in spotted turtle occupancy and abundance patterns. More specifically, we predicted that turtles would shift association with small ephemeral wetlands to large semi-permanent wetlands later in the season to maintain access to aquatic resources. Additionally, because turtles frequently move between wetlands in response to changes in resource availability (Milam and Melvin 2001, Litzgus and Mousseau 2004, Beaudry et al. 2009), we expected occupancy and abundance to have a negative relationship with distance between wetlands, and for colonization and extinction probabilities to be consistently high throughout the study. Because habitat availability was limited at our site, we expected occupancy probability to be high, but for abundance patterns to be correlated with high quality wetland characteristics such as seasonal food availability in the form of amphibian egg masses as well as presence of structural complexity within wetlands. We also expected detection probability for both occupancy and abundance to be related positively to temperature, because turtle activity (and thus detectability) increases with temperature (Armstrong 2016, Buchanan et al. 2018, Cassel et al. 2019).

METHODS

Study site

We studied spotted turtle occupancy and abundance patterns on a U.S. military installation in Virginia, U.S.A. The installation is 3,237 km² and has been partitioned for a

number of uses, including urban infrastructure (e.g., offices, housing, etc.) and natural areas set aside for training and wildlife conservation. The natural areas contained a continuum of habitat types from floodplain wetlands (dominated by *Carex* spp., *Cephalanthus occidentalis*) to upland mixed pine-hardwood forests (dominated by *Pinus* spp., *Quercus* spp., *Fagus* spp.). We studied spotted turtles in three natural areas on the installation. Site 1 was predominantly managed as a wetland reserve, with a large, emergent wetland in the center, surrounding by two beaver-maintained, emergent wetlands and numerous small, ephemeral wetlands. The ephemeral wetlands included a mix of natural vernal pools and anthropogenic depressions from powerline right-of-way and other military activities. Site 2 was centered around a public-use area, including many paved and dirt walking paths. The site included several, large emergent wetlands, each surrounded by expansive floodplain, as well as numerous natural and anthropogenic ephemeral pools. Site 3 consisted of a large tract of contiguous hardwood and pine forest. The wetland complex included two large, emergent wetlands at the center and was surrounded by numerous forested natural and anthropogenic ephemeral pools. Specific locations of study sites are withheld throughout due to risk of illegal wildlife poaching.

Data Collection

In 2017 – 2019, we conducted aquatic trap surveys for spotted turtles from March through June while wetlands contained water. We based our trapping protocol by the Northeast Partners of Amphibian and Reptile Conservation “Spotted Turtle Working Group” but modified it to meet our objectives of inventorying every wetland. We used ProMar TR-502 91 cm x 30 cm collapsible hoop-net traps baited with sardines in soybean oil (whole can with holes punctured in the lid). We placed traps 20m apart around the perimeter of wetlands and at least 3m from the wetland edge. The perimeter of each wetland determined the number of traps deployed so that

density was generally standardized. For small ($< 400 \text{ m}^2$) and medium sized wetlands ($400\text{-}1000 \text{ m}^2$), mean trap density was 1 trap per 100 m^2 (± 2 traps) and for larger wetlands ($> 1000 \text{ m}^2$) mean trap density was 1 trap per 1000 m^2 (± 0.5 traps). We placed traps in areas such as in shallow channels between vegetation, at the edge of thick vegetation, near basking sites, and at sites with high solar exposure to maximize the chances of capturing turtles. Traps were firmly affixed to adjacent structure to prevent animals or flood waters from moving them. We equipped each trap with a foam flotation device (a pool noodle) to ensure that the entire trap was never completely submerged by rising water, and that turtles within trap were always able to surface and breathe. Traps were checked daily and left in place for three consecutive nights. During trap checks, we recorded the number of individual spotted turtles captured and then released captured individuals. This process was repeated three times across the season with four weeks in between each trapping session. Additionally, this procedure was repeated for two sampling years, such that every wetland was sampled for 18 total nights ($3 \text{ nights} * 3 \text{ weeks} * 2 \text{ years}$). All work was conducted under the Institutional Animal Care and Use Committee (IACUC) protocol #20048.

During trap checks, we measured wetland water depth (m). Additionally, for each trap day, we calculated minimum daily temperature using publicly available meteorological data for this site provided by NOAA (<http://www.noaa.gov/>). For each wetland, we characterized wetland type (emergent wetland, seasonal forest pond, early successional pool, anthropogenic ditch), noted presence of habitat structure (coarse woody debris, sedges, and leaf litter), and delineated wetland size by walking the perimeter using a Trimble (R-1000, Telonics) with 1m resolution. We then plotted the wetlands on ArcGIS (ArcGIS Pro, ESRI Inc) to determine size (m^2) and distance (m) to the next nearest wetland. We also recorded the number of amphibian egg masses in each wetland through visual inspection during 2018 and 2019, but only partially for 2017. In

early April and again in early May, we walked the perimeter of small wetlands or along haphazard transects in larger wetlands and recorded the number of amphibian egg masses detected. For wetlands missing data in 2017, we interpolated data by using the mean of the combined 2018 and 2019 data.

Statistical Analyses

We constructed dynamic occupancy models (MacKenzie et al. 2003, MacKenzie et al. 2006, Wier et al. 2009) to estimate the probability of spotted turtle occurrence and turnover in wetlands and to explore the influence of covariates on occupancy and detection probabilities. We defined site as each sampled wetland and data from all traps was summed within a wetland. The three trap nights within a sampling week were considered the secondary sampling period and the three sampling weeks within a year were considered the primary sampling period. Models were fit for each individual year instead of pooling data to avoid biased parameter estimates that would result from uneven sampling intervals between years. We used wetland characteristics as covariates of initial occupancy, including total number of amphibian egg masses, structure diversity (presence of each type of structural object), wetland type, wetland size, and distance to closest wetland. Trap density (# traps/wetland size) and minimum daily air temperature were used as covariates of detection. We used percent change in wetland depth as a covariate of extinction but included no covariates of colonization.

To avoid issues of model over-fitting, we used a multi-stage model fitting approach (Karanth et al. 2011, Fuller et al. 2016). First, we used model selection to identify the best extinction model with initial occupancy and detection models fixed to global parameterization. We then fixed the best extinction model for subsequent model selection of detection covariate models. From there, we fixed the best colonization-detection models for subsequent model

selection of initial occupancy covariate models. For each stage of model fitting, we considered all additive permutations of covariates. Before model fitting, we checked collinearity of covariates by performing Spearman's rank correlation (none were correlated). Covariates were then standardized by centering on the mean and scaling by standard deviation. We performed all model fitting in R (R Core Team 2020) with the unmarked package (Fiske and Chandler 2011). We used the Mackenzie and Bailey (2004) goodness-of-fit test with parametric bootstrapping (1000 iterations) to assess fit of the global model for each year. Model selection was conducted using Akaike's Information Criterion (AIC) approach (Burnham and Anderson 2002). To improve clarity in presenting model selection tables, we only display models that were competitive within 2 Δ AIC (Burnham and Anderson 2002). Similarly, when applicable, parameter estimates were derived by model averaging all models within 2 Δ AIC (Burnham and Anderson 2002). Additionally, if wetland size or wetland type were included in top candidate models, we used these covariates to generate parameter estimates for both sampling week and year. Wetland size was binned into four categories (small = <400 m², medium = 400-1000 m², large = 1000-2000 m², and expansive = 2000-12000 m²) to facilitate visualization.

Because occupancy probability of wetlands at this site was anticipated to be very high, we also constructed n-mixture models for open populations (Royal 2004, Dail and Madsen 2011, Hostetler and Chandler 2015) to provide a more nuanced estimate of spotted turtle abundance within wetlands and to explore the influence of covariates on abundance and detection probabilities. We used the same procedure as above, but removed percent change in water depth as a covariate and only used a 2-stage model fitting approach to fit detection and abundance model covariates.

RESULTS

During 2017-2019, we placed 224 traps (4032 trap nights) across 91 individual wetlands. We trapped in: 1) seasonal forested pools: ephemeral pool in closed-canopy, forested habitat (n=67); 2) early successional pools: ephemeral pool in early successional habitat and no canopy cover (n=7); 3) anthropogenic depressions: ephemeral pool in ditch or depression caused by human activity (n=9); and 4) emergent wetlands: large, semi-permanent wetland with emergent vegetation (n=7). We detected spotted turtles in 65% of wetlands (64 turtle captures; 20/31 wetlands) in 2017, 55% of wetlands (75 turtle captures; 34/65 wetlands) in 2018, and 45% of wetlands (53 turtle captures; 25/56 wetlands) in 2019. Overall, spotted turtles occupied 78% of available seasonal forested pools, 57% of early successional pools, 56% of anthropogenic depressions, and 71% of emergent wetlands.

There was a seasonal effect in initial occupancy probability, in which occupancy increased between sampling week one and two and then decreased between sampling week two and three (Fig. 1). Though, there was overlap in confidence intervals

between sampling weeks (Fig 1). In 2017, no covariates of extinction or detection were retained during the model selection process. Additionally, covariates included in occupancy top candidate models had little effect on initial occupancy probability (Table 1, Supp. Table S1). In 2018, no covariates of extinction or detection were retained. Initial occupancy probability was best predicted by wetland size ($\beta = 12.82$, $SE = 6.81$) (Table 1, Supp. Table S2). Occupancy probability increased with wetland size, but when estimated per sampling week, occupancy probability decreased over time for wetlands smaller than 1000 m and increased over time for wetlands greater than 1000 m (Fig. 2). In 2019, no covariate of extinction was retained, however, there was a positive relationship between temperature ($\beta = 0.86$, $SE = 0.21$) and detection

probability. However, occupancy covariates in top candidate models had little effect on probability of initial occupancy (Table 1, Supp. Table S3).

In all years, model averaged probabilities of initial occupancy were similar to respective naïve occupancies, and detection probabilities were relatively low. Probability of initial occupancy was 0.65 (95% CI = 0.03-0.94) in 2017, 0.61 (95% CI = 0.24-0.82) in 2018, and 0.56 (95% CI = 0.36-0.62) in 2019. Probability of detection was 0.44 (95% CI = 0.35-0.53) in 2017, 0.25 (95% CI = 0.17-0.36) in 2018, and 0.37 (95% CI = 0.26-0.48) in 2019. Probability of colonization was very low in all years, while probability of extinction was low during 2017 and 2018 but higher in 2019. Probability of colonization was 0.02 (95% CI = 0.01-0.34) in 2017, 0.05 (95% CI = 0.01-0.54) in 2018, and 0.06 (95% CI = 0.02-0.42) in 2019. Probability of extinction was 0.13 (95% CI = 0.05-0.33) in 2017, 0.21 (95% CI = 0.07-0.49) in 2018, and 0.46 (95% CI = 0.32-0.62) in 2019.

Similar to occupancy, there was a seasonal effect in estimated abundance (Fig. 1). Abundance estimates nearly doubled from the first sampling week to second, and then decreased to below initial values during the third sampling week. However, there was overlap in confidence intervals between weeks. For all years, there was a positive relationship between estimated abundance and number of amphibian egg masses (2017: $\beta = 0.44$, SE = 0.21; 2018: $\beta = 0.34$, SE = 0.17; 2019: $\beta = 0.39$, SE = 0.18) (Fig. 3). Additionally, in 2017 distance to nearest wetland ($\beta = -1.14$, SE = 0.24) was negatively related to estimated abundance (Fig. 4), and detection probability was best predicted by trap density ($\beta = 0.82$, SE = 0.20). In 2018, estimated abundance was also best predicted by wetland type (Fig. 4). Forested ($\beta = -1.64$, SE = 0.37) and early successional ($\beta = -2.47$, SE = 0.68) ephemeral pools had the lowest estimates of abundance, while emergent wetlands ($\beta = 6.82$, SE = 1.88) had the greatest (Fig. 4). However, there was no

difference in abundance per wetland type when estimated per sampling week. Detection probability was best predicted by temperature ($\beta = 0.41$, $SE = 0.10$). In 2019, estimated abundance was also positively related to wetland size ($\beta = 0.37$, $SE = 0.15$) (Fig. 4), and both temperature ($\beta = 0.41$, $SE = 0.12$) and trap density ($\beta = 0.43$, $SE = 0.11$) best predicted detection probability. Similar to that of occupancy, turtle abundance increased with wetland size, and when estimated per sampling week abundance decreased for wetlands smaller than 2000m and increased over time for wetlands greater than 2000 m (Fig. 2).

Model averaged spotted turtle abundance estimates varied slightly from year to year and probability of detection was very low. Estimated abundance was 14.32 turtles per wetland (95% CI = 8.46-21.00) in 2017, 5.11 (95% CI = 1.86-9.67) in 2018, and 9.49 (95% CI = 4.44-13.00) in 2019. Estimated abundance of all wetlands combined was 418 (95% CI = 279-602) in 2017, 464 (95% CI = 248-690) in 2018, and 448 (95% CI = 279-602) in 2019. Probability of detection was 0.07 (95% CI = 0.05-0.11) in 2017, 0.04 (95% CI = 0.02-0.10) in 2018, and 0.03 (95% CI = 0.01-0.07) in 2019. Estimated recruitment was also very low across all years, including 0.2 (95% CI = 0.001-3.19) in 2017, 1.47 (95% CI = 0.49-4.43) in 2018, and 0.02 (95% CI = 0.007-2.09) in 2019.

DISCUSSION

Our study indicated that spotted turtle occupancy probability and estimated abundance did vary across the sampling season, which mirrors the reported peak in activity and movement described by other investigators (Litzgus and Brooks 2000, Joyal et al. 2001, Beaudry et al. 2009, Rowe et al. 2013). As predicted, spotted turtle occupancy at our site was high with turtles utilizing most (> 50%) available wetlands. Amphibian egg masses were an important food source and potential driver for increased abundance during early spring. Additionally, habitat

characteristics including distance to nearest wetland, size of wetland, and type of wetland also influenced turtle abundance patterns. Temperature influenced detection rates for occupancy and abundance, though more support for this relationship was seen in estimates of abundance.

We saw a unimodal pattern in occupancy probabilities and abundance estimates across the sampling season. In early spring, spotted turtles form mating aggregations (Litzgus and Brooks 2000, Litzgus and Mousseau 2004), thus occupancy and abundance was concentrated into particular wetlands. Occupancy and abundance then increased across the season as spotted turtle activity increased and turtles occupied a greater number of wetlands, likely to utilize different resources spread across individual wetlands. During mid-late spring, spotted turtles have been documented using a variety of habitats for mating, foraging, and thermoregulation (Haxton and Berrill 1999, Litzgus and Brooks 2000, Milam and Melvin 2001, Litzgus and Mousseau 2004, Beaudry et al. 2009). This pattern has also been described in other freshwater turtle species that inhabit dynamic ecosystems (Joyal et al. 2001, Bowne et al. 2006, Ennen and Litzgus 2009, Roe et al. 2009, Serrano et al. 2019). Occupancy and abundance then decreased at the end of the sampling period as wetlands began to dry and spotted turtles shifted habitat use to larger wetlands or aestivated terrestrially. Wetland hydroperiod has been found to be an important driver of freshwater turtle occupancy dynamics (Roe and Georges 2007, Bowne 2008, Roe et al. 2009, Cosentino et al. 2010). The seasonal pattern in occupancy and abundance was supported by the relationship between both respective parameters and wetland size (Fig. 2), however we did not see an effect of wetland type across sampling weeks. Seasonal shifts in occupancy and habitat associations have been documented in other species of turtles (Roe and Georges 2007, Roe et al. 2009, Cosentino et al. 2010, Barley and Walker 2013). Our findings may have been limited by low habitat and wetland heterogeneity at our site, as the majority

(73%) of wetlands available were seasonal forested pools. While spotted turtles are often found occupying ephemeral pools, spotted turtle habitat use extends to vernal pools, bogs, swamps (e.g., cypress, red-maple), fens, flooded meadows, emergent wetlands, edges of large ponds or bays, and marshes (Litzgus and Brooks 2000, Ernst and Lovich 2009, Stevenson et al. 2015).

Spotted turtle occupancy probability was best explained by wetland size, and abundance estimates were best explained by number of amphibian egg masses, wetland type, distance to nearest wetland, and wetland size. When wetlands were saturated, turtles were able to occupy a variety of wetland habitats in response to resource availability. However, as wetland depth decreased across the season, turtles had to shift to larger, deeper wetlands that still had water. Thus, wetland occupancy was fairly high among small and large wetlands when all wetlands had water but was restricted to larger wetland when water was limited, which is a pattern seen in other dynamic wetland systems (Roe and Georges 2007, Bowne 2008, Roe et al. 2009, Cosentino et al. 2010). We likely saw a positive relationship between wetland size and occupancy because larger wetlands were occupied during every sampling week while smaller wetlands were primarily occupied earlier in the sampling period. Additionally, larger wetlands can support larger numbers of turtles (Rizkalla and Swihart 2006, Beaudry et al. 2009, Buchanan et al. 2019). Spotted turtle abundance was greater in emergent wetlands than forested or early successional ephemeral pools. This is likely related to size of the wetlands in each category more than habitat selection, as emergent wetlands were many times larger (mean = 8327 m²) than most ephemeral pools (mean = 487 m²). Additionally, spotted turtles were found to use most available wetlands regardless of wetland category. As expected, turtle abundance decreased with wetland isolation (measured as distance to nearest wetland). This corroborates findings from other studies demonstrating the importance of patch quality and connectivity in understanding the distribution

and habitat associations of species inhabiting patchy habitats (Bowne et al. 2006, Roe et al. 2009, Cosentino et al. 2010, Serrano et al. 2019).

Spotted turtle abundance was also positively related to the number of amphibian egg masses. Spotted turtles have previously been reported depredating wood frog (*Lithobates sylvaticus*) and ambystomatid egg masses (Fowle 2001, Hulse 2001, Ernst and Lovich 2009, Beaudry et al. 2009). For example, spotted turtle habitat use in spring was best predicted by basking habitat availability and wood frog egg masses for a population in Maine (Beaudry et al. 2009). Amphibian egg masses are one of the most abundant sources of animal protein in ephemeral wetlands on the east coast (Gibbons et al. 2006, Baldwin et al. 2006). Amphibian egg masses can also be used as indicators of vernal pool habitat (Calhoun and deMaynadier 2008), which are often favored by spotted turtles in the spring (Joyal et al. 2001, Milam and Melvin 2001, Beaudry et al. 2009). Though this relationship requires further investigation, as we did not address imperfect detection of amphibian egg masses. For example, we may have failed to detect egg masses that were very small (e.g., *hyla versicolor*) or laid in thick, emergent vegetation (e.g., *Rana clamitans*), thus failing to identify additional prey or habitat drivers of spotted turtle occupancy.

Our reported abundance estimates derived from n-mixture models of 418 - 464 were very high compared to other studies of spotted turtle abundance or population size. Previous studies of spotted turtle populations have documented population sizes ranging from 14.3-116, though these estimates were primarily derived from much smaller sites ($\leq 1 \text{ km}^2$) (Seburn 2003, Litzgus and Mousseau 2004, Reeves and Litzgus 2008, Jones et al. 2014, Feng et al. 2019a). Abundance estimates from our site support the importance of large, connected wetland complexes for preserving spotted turtle populations. Additionally, large abundance estimates can improve

detection probability and, in some cases, the relationship between occupancy and abundance is such that population demographic trends can be monitored using occupancy estimates alone (Gaston et al. 2002, Steenweg et al. 2018, Dallas et al. 2019). Improved estimates of abundance and population size may be used to better inform population viability estimates to understand long-term demographics and identify threats to population stability (Beaudry et al. 2008, Enneson and Litzgus 2008, Feng et al. 2019b, Howell and Siegel 2019). Colonization and extinction probabilities were lower than expected. These results may have been related to sample size limitations at our site (McKann et al. 2013) or because occupancy probability remained relatively high among sites even when factoring in seasonal perturbations.

We found that minimum daily temperature was positively related to detection probability for both occupancy and abundance. As temperature increases, turtle activity, basking thermoregulatory behaviors, and foraging increase (Grayson and Dorcas 2004, Litzgus and Mousseau 2004, Ernst and Lovich 2009), thus increasing likelihood of visual detection or trap capture (Dodd 2001, Scott and Rissler 2015, Armstrong 2016, Cassel et al. 2019, Buchanan et al. 2019, Harju and Camrbin 2019). Turtle monitoring should be conducted when climate conditions promote turtle activity, especially if sampling replicates are limited or using visual detection (Castellon et al. 2015, Armstrong 2016). Trap density was positively related to detection probability of turtle abundance, but not occupancy. While abundance was higher in larger wetlands, trap density in large wetlands was lower due to our sampling design. Trap density has been found to be influential in other studies (Cassel et al. 2019), thus to avoid bias in parameter estimates, trap density should be included as a detection covariate when trap density is not precisely standardized.

Our study indicated that spotted turtle occupancy probability and estimated abundance did vary across the sampling season. However, we failed to detect our predicted seasonal differences in habitat associations. Single-site or fine-scale patterns of occupancy are likely too coarse for spotted turtles. At the landscape scale or for multi-species analyses, spotted turtle habitat associations have been more clearly delineated (Buchanan et al. 2019, Compton et al. 2020). Nevertheless, our results highlight that spotted turtles rely on numerous wetlands across the spring season and management for this species must entail protection of wetland complexes with connectivity rather than single, isolated wetlands. Additionally, the use of dynamic occupancy monitoring allowed for a less intensive field approach than traditional methods (e.g., radio-telemetry) and by incorporating wetland turnover, provided a more detailed understanding of the spatio-temporal distribution of spotted turtles. Predictions of dynamic distributions and population persistence will be vital in the face of continued habitat fragmentation and climate stochasticity.

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TABLES

Table 1. Model selection statistics for probability of initial occupancy and abundance of spotted turtles (*Clemmys guttata*) in Virginia from 2018-2019. Covariates of occupancy (Ψ) and abundance (λ) included wetland type (“type”; forested pool, emergent wetland, etc.), wetland size (“size”), distance to nearest wetland (“dist”), number of amphibian egg masses (“egg”), and structure diversity (“diverse”; leaf litter, coarse woody debris, sedges) within the wetland. Covariates of detection (p) included minimum daily temperature (“temp”) and trap density (“density”; # traps/wetland size). No covariates of colonization (ϵ) and extinction (γ) or recruitment (ϵ) and apparent survival (Ω) were included. Models were ranked using Akaike’s Information Criterion (AIC) and included with each model is the number of parameters (K), difference from best model (Δ AIC), model weight (AICwt) and log-likelihood estimate (LL).

Occupancy					
Model	K	AIC	Δ AIC	AICwt	LL
2017					
$\Psi(\text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	11	266.80	0.00	0.33	-122.40
$\Psi(\text{size} + \text{diverse}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	10	267.54	0.74	0.23	-123.77
2018					
$\Psi(\text{size}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	6	407.15	0.00	0.23	-197.58
$\Psi(\text{size} + \text{egg}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	7	407.64	0.49	0.18	-196.82
$\Psi(\text{size} + \text{type}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	9	407.85	0.70	0.17	-194.92
$\Psi(\text{size} + \text{type} + \text{egg}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	10	408.53	1.38	0.12	-194.26
2019					
$\Psi(\text{diverse} + \text{dist} + \text{egg} + \text{type}), \gamma(\cdot), \epsilon(\cdot), p(\text{temp})$	16	273.83	0.00	0.58	-120.91
$\Psi(\text{diverse} + \text{dist} + \text{egg} + \text{size}), \gamma(\cdot), \epsilon(\cdot), p(\text{temp})$	14	275.44	1.61	0.26	-123.72

Table 1 (Cont.)

Abundance					
Model	K	AIC	Δ AIC	AICwt	LL
2017					
$\lambda(\text{dist} + \text{egg} + \text{type} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	15	580.22	0.00	0.40	-275.11
$\lambda(\text{dist} + \text{egg} + \text{type} + \text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	15	581.09	0.87	0.26	-274.54
2018					
$\lambda(\text{type} + \text{egg} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	15	725.20	0.00	0.38	-347.60
$\lambda(\text{type} + \text{egg} + \text{diverse} + \text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	16	727.11	1.91	0.15	-347.56
$\lambda(\text{type} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	14	727.13	1.93	0.14	-349.57
$\lambda(\text{type} + \text{egg} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	16	727.20	2.00	0.14	-347.60
2019					
$\lambda(\text{egg} + \text{size} + \text{type}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	16	550.12	0.00	0.49	-258.06
$\lambda(\text{egg} + \text{size} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	16	552.12	2.00	0.18	-258.06

FIGURES

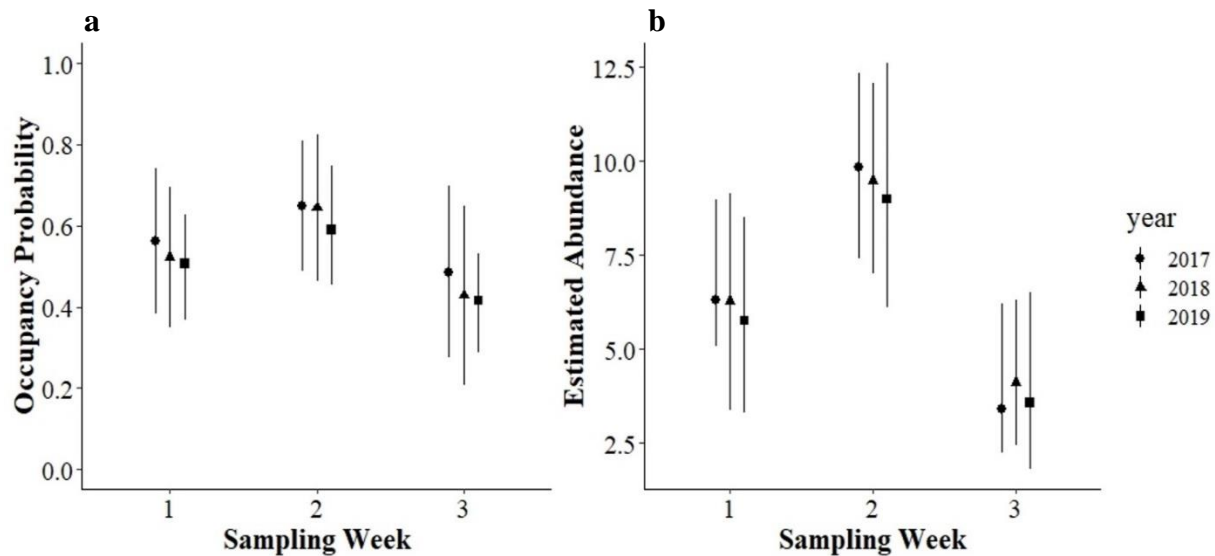


Figure 1. Spotted turtle (*Clemmys guttata*) initial occupancy probability (a) and abundance estimates (b) across sampling weeks in Virginia from 2017-2019, respectively. 95% confidence intervals are presented using a vertical black line.

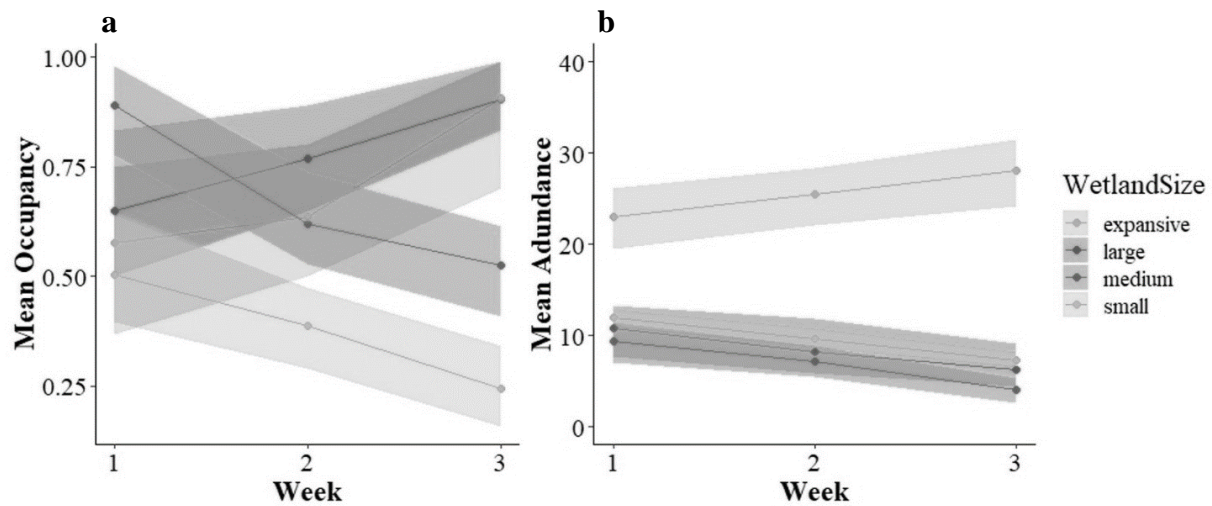


Figure 2. The effect of wetland size class (small = <400 m², medium = 400-1000 m², large = 1000-2000 m², and expansive = 2000-12000 m²) on estimated spotted turtle (*Clemmys guttata*) occupancy (a) and abundance (b) per sampling week in Virginia from 2017-2019. 95% confidence intervals are presented using a gray dotted line

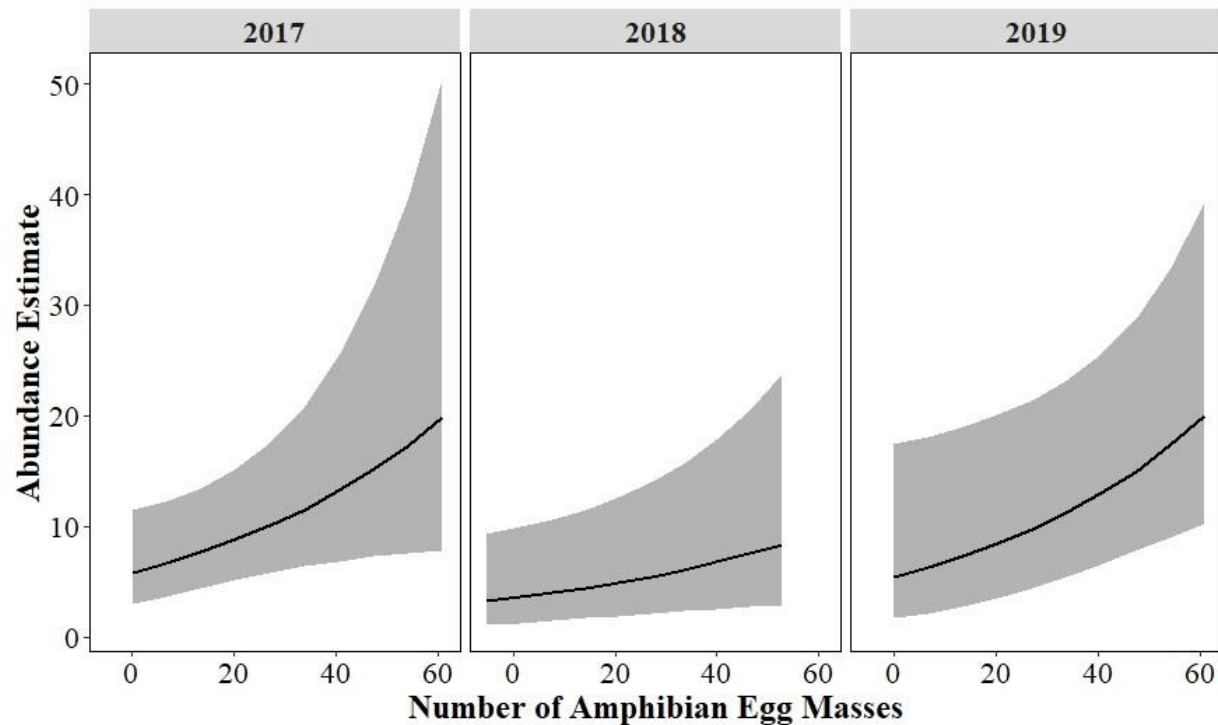


Figure 3. The effect of number of amphibian egg masses on estimated spotted turtle (*Clemmys guttata*) abundance in Virginia from 2017-2019. 95% confidence intervals are presented using a gray dotted line.

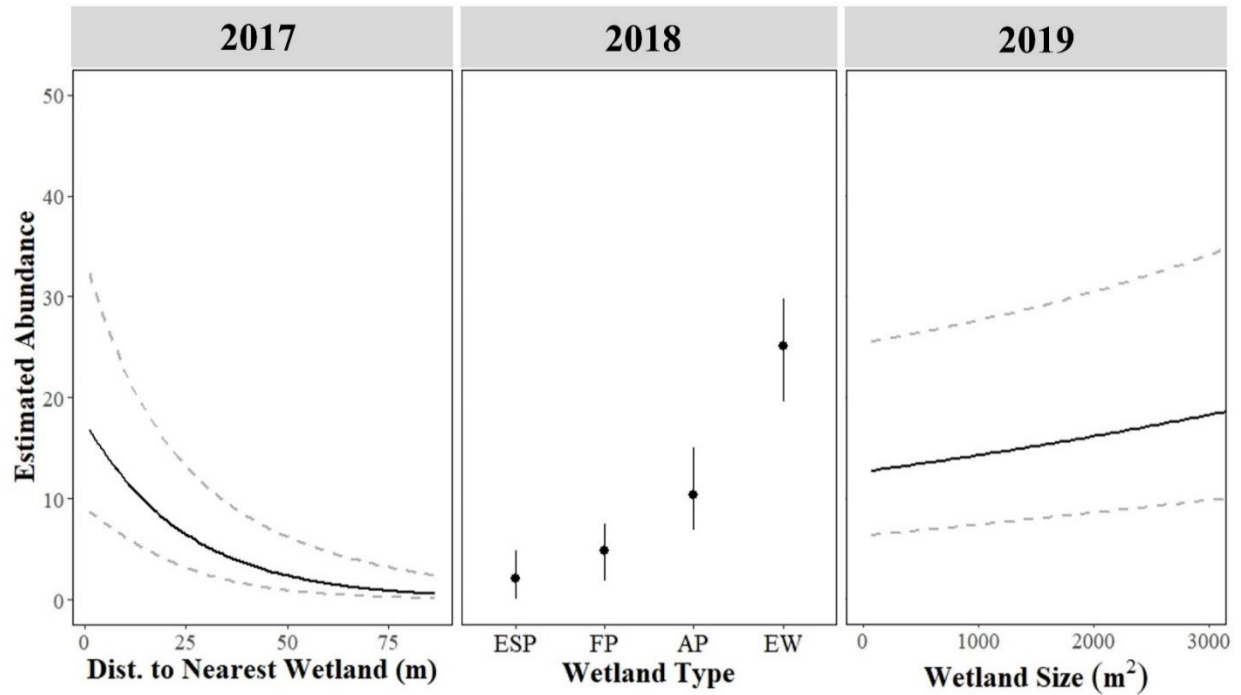


Figure 4. The effect of distance to nearest wetland, wetland type (early-successional pool, forested pool, anthropogenic depression, and emergent wetland), and wetland size on abundance estimates of spotted turtles (*Clemmys guttata*) across 2017-2019, respectively. 95% confidence intervals are presented using a gray dotted line.

SUPPLEMENTAL INFORMATION

Table S1. Model selection statistics for probability of initial occupancy and abundance of spotted turtles (*Clemmys guttata*) in Virginia during 2017. Covariates of occupancy (Ψ) and abundance (λ) included wetland type (“type”; forested pool, emergent wetland, etc.), wetland size (“size”), distance to nearest wetland (“dist”), number of amphibian egg masses (“egg”), and structure diversity (“diverse”; leaf litter, coarse woody debris, sedges) within the wetland. Covariates of detection (p) included minimum daily temperature (“temp”) and trap density (“density”; # traps/wetland size). No covariates of colonization (ϵ) and extinction (γ) or recruitment (ϵ) and apparent survival (Ω) were included. Models were ranked using Akaike’s Information Criterion (AIC) and included with each model is the number of parameters (K), difference from best model (Δ AIC), model weight (AICwt) and log-likelihood estimate (LL).

Model	K	AIC	Δ AIC	AICwt	LL
Occupancy					
$\Psi(\text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	11	266.80	0.00	0.33	-122.40
$\Psi(\text{size} + \text{diverse}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	10	267.54	0.74	0.23	-123.77
$\Psi(\text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	12	268.83	2.03	0.12	-122.41

Table S1 (Cont.)

$\Psi(\text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	11	269.34	2.54	0.09	-123.67
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	14	270.87	4.07	0.04	-121.43
$\Psi(\text{type} + \text{size} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	13	271.24	4.44	0.04	-122.62
$\Psi(\text{type} + \text{size}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	8	271.57	4.77	0.03	-127.79
$\Psi(\text{type} + \text{size} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9	271.93	5.14	0.03	-126.97
$\Psi(\text{type} + \text{size} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9	272.15	5.35	0.02	-127.08
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	15	272.50	5.71	0.02	-121.25
$\Psi(\text{type} + \text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	10	272.88	6.08	0.02	-126.44
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	14	273.22	6.43	0.01	-122.61
$\Psi(\text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	10	274.57	7.77	0.01	-127.28
$\Psi(\text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	11	275.14	8.34	0.01	-126.57
$\Psi(\text{type} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	13	275.94	9.14	0.00	-124.97
$\Psi(\text{type} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	14	276.65	9.85	0.00	-124.33
$\Psi(\text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9	277.34	10.54	0.00	-129.67
$\Psi(\text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	5	278.12	11.33	0.00	-134.06
$\Psi(\text{size} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	6	278.22	11.42	0.00	-133.11
$\Psi(\text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	10	278.36	11.56	0.00	-129.18
$\Psi(\text{size}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	5	278.40	11.61	0.00	-134.20
$\Psi(\text{type} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	12	278.58	11.79	0.00	-127.29
$\Psi(\text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	6	279.74	12.94	0.00	-133.87
$\Psi(\text{type} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	13	279.75	12.95	0.00	-126.87
$\Psi(\text{size} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	6	279.84	13.04	0.00	-133.92
$\Psi(\text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	7	279.92	13.12	0.00	-132.96
$\Psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	4	280.44	13.64	0.00	-136.22
$\Psi(\text{type} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	8	281.14	14.35	0.00	-132.57
$\Psi(\text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	5	281.69	14.89	0.00	-135.84
$\Psi(\text{type} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9	282.30	15.50	0.00	-132.15
$\Psi(\text{type}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	7	283.79	16.99	0.00	-134.89
$\Psi(\text{type} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	8	284.39	17.59	0.00	-134.20
Abundance					
$\lambda(\text{type} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	15	580.22	0.00	0.40	-275.11
$\lambda(\text{type} + \text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	11	581.09	0.87	0.26	-274.54
$\lambda(\text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	12	582.37	2.15	0.14	-279.18
$\lambda(\text{type} + \text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	15	582.66	2.44	0.12	-276.33
$\lambda(\text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	13	584.11	3.89	0.06	-279.05
$\lambda(\text{type} + \text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	16	586.51	6.29	0.02	-282.26
$\lambda(\text{type} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	10	588.96	8.74	0.01	-284.48
$\lambda(\text{type} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	14	590.18	9.96	0.00	-281.09
$\lambda(\text{type} + \text{size} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	10	594.58	14.35	0.00	-287.29

Table S1 (Cont.)

$\lambda(\text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	12	597.78	17.56	0.00	-286.89
$\lambda(\text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	11	603.50	23.28	0.00	-290.75
$\lambda(\text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	8	606.77	26.55	0.00	-295.38
$\lambda(\text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	7	610.51	30.29	0.00	-298.25
$\lambda(\text{size} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	7	615.10	34.88	0.00	-300.55
$\lambda(\text{type} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	9	618.35	38.13	0.00	-300.18
$\lambda(\text{type} + \text{size} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	14	619.79	39.56	0.00	-295.89
$\lambda(\text{type} + \text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	15	620.54	40.32	0.00	-295.27
$\lambda(\text{size} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	11	621.23	41.00	0.00	-299.61
$\lambda(\text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	12	623.20	42.98	0.00	-299.60
$\lambda(\text{type} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	14	624.51	44.29	0.00	-298.25
$\lambda(\text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	6	626.89	46.67	0.00	-307.45
$\lambda(\text{type} + \text{size} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	10	627.22	47.00	0.00	-303.61
$\lambda(\text{type} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	13	631.55	51.33	0.00	-302.77
$\lambda(\text{type} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	9	633.62	53.40	0.00	-307.81
$\lambda(\text{type} + \text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	9	639.28	59.06	0.00	-310.64
$\lambda(\text{size} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	7	640.75	60.53	0.00	-313.37
$\lambda(\text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	11	647.41	67.19	0.00	-312.71
$\lambda(\text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	10	648.28	68.05	0.00	-314.14
$\lambda(\text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	6	650.07	69.84	0.00	-319.03
$\lambda(\text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	6	662.09	81.87	0.00	-325.04
$\lambda(\text{type}), \gamma(\cdot), \Omega(\cdot), p(\text{density})$	8	668.14	87.91	0.00	-326.07
$\lambda(\cdot), \gamma(\cdot), \Omega(\cdot), p(\cdot)$	4	695.74	115.52	0.00	-343.87

Table S2. Model selection statistics for probability of initial occupancy and abundance of spotted turtles (*Clemmys guttata*) in Virginia during 2018. Covariates of occupancy (Ψ) and abundance (λ) included wetland type (“type”; forested pool, emergent wetland, etc.), wetland size (“size”), distance to nearest wetland (“dist”), number of amphibian egg masses (“egg”), and structure diversity (“diverse”; leaf litter, coarse woody debris, sedges) within the wetland. Covariates of detection (p) included minimum daily temperature (“temp”) and trap density (“density”; # traps/wetland size). No covariates of colonization (ϵ) and extinction (γ) or recruitment (ϵ) and apparent survival (Ω) were included. Models were ranked using Akaike’s Information Criterion (AIC) and included with each model is the number of parameters (K), difference from best model (ΔAIC), model weight (AICwt) and log-likelihood estimate (LL).

Model	K	AIC	ΔAIC	AICwt	LL
Occupancy					
$\Psi(\text{size}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	6	407.15	0.00	0.23	-197.58
$\Psi(\text{size} + \text{egg}), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	7	407.64	0.49	0.18	-196.82

Table S2 (Cont.)

$\Psi(\text{type} + \text{size}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9	407.85	0.70	0.17	-194.92
$\Psi(\text{type} + \text{size} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	10	408.53	1.38	0.12	-194.26
$\Psi(\text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	11	410.72	3.57	0.04	-194.36
$\Psi(\text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	12	411.04	3.89	0.03	-193.52
$\Psi(\text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	13	411.21	4.06	0.03	-192.60
$\Psi(\text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	13	411.76	4.60	0.02	-192.88
$\Psi(\text{type} + \text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	11	411.97	4.82	0.02	-194.98
$\Psi(\text{size} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	12	412.04	4.89	0.02	-194.02
$\Psi(\text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	12	412.19	5.04	0.02	-194.10
$\Psi(\text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	13	412.38	5.23	0.02	-193.19
$\Psi(\text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	14	412.91	5.75	0.01	-192.45
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	16	412.92	5.77	0.01	-190.46
$\Psi(\text{size} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	7	412.96	5.81	0.01	-199.48
$\Psi(\text{type} + \text{size} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	10	413.24	6.09	0.01	-196.62
$\Psi(\text{type} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	15	414.17	7.02	0.01	-192.08
$\Psi(\text{type} + \text{size} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	15	414.36	7.21	0.01	-192.18
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	17	414.84	7.69	0.01	-190.42
$\Psi(\text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	7	415.21	8.06	0.00	-200.61
$\Psi(\text{type} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	14	415.25	8.10	0.00	-193.63
$\Psi(\text{type} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	16	415.26	8.11	0.00	-191.63
$\Psi(\text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	6	415.68	8.53	0.00	-201.84
$\Psi(\text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	8	416.02	8.87	0.00	-200.01
$\Psi(\text{type} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	15	416.07	8.92	0.00	-193.04
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	16	416.11	8.96	0.00	-192.05
$\Psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	4	419.77	12.62	0.00	-205.89
$\Psi(\text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	6	419.77	12.62	0.00	-203.89
$\Psi(\text{type} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	10	419.97	12.82	0.00	-199.99
$\Psi(\text{type} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9	420.57	13.42	0.00	-201.29
$\Psi(\text{type} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	9	423.27	16.12	0.00	-202.63
$\Psi(\text{type}), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	8	424.95	17.80	0.00	-204.48
Model	K	AIC	ΔAIC	AICwt	LL
Abundance					
$\lambda(\text{type} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	15	725.20	0.00	0.38	-347.60
$\lambda(\text{type} + \text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	16	727.11	1.91	0.15	-347.56
$\lambda(\text{type} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	14	727.13	1.93	0.14	-349.57
$\lambda(\text{type} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	16	727.20	2.00	0.14	-347.60
$\lambda(\text{type} + \text{size} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	15	728.92	3.72	0.06	-349.46
$\lambda(\text{type} + \text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	17	729.09	3.89	0.05	-347.54
$\lambda(\text{type} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	15	729.09	3.90	0.05	-349.55

Table S2 (Cont.)

$\lambda(\text{type} + \text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	16	730.69	5.49	0.02	-349.35
$\lambda(\text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	11	744.70	19.51	0.00	-361.35
$\lambda(\text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	12	745.33	20.13	0.00	-360.66
$\lambda(\text{size} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	12	746.27	21.07	0.00	-361.14
$\lambda(\text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	12	746.48	21.28	0.00	-361.24
$\lambda(\text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	13	747.13	21.93	0.00	-360.56
$\lambda(\text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	13	747.28	22.08	0.00	-360.64
$\lambda(\text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	13	747.41	22.21	0.00	-360.71
$\lambda(\text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	14	748.84	23.64	0.00	-360.42
$\lambda(\text{type} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	9	793.73	68.53	0.00	-387.87
$\lambda(\text{type} + \text{size} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	10	794.88	69.68	0.00	-387.44
$\lambda(\text{type} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	10	795.41	70.21	0.00	-387.70
$\lambda(\text{type} + \text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	11	796.88	71.68	0.00	-387.44
$\lambda(\text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	6	797.00	71.81	0.00	-392.50
$\lambda(\text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	7	798.90	73.70	0.00	-392.45
$\lambda(\text{size} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	7	798.95	73.75	0.00	-392.48
$\lambda(\text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	8	800.89	75.69	0.00	-392.45
$\lambda(\text{type} + \text{size} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	10	807.01	81.81	0.00	-393.50
$\lambda(\text{type} + \text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	9	807.93	82.74	0.00	-394.97
$\lambda(\text{type}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	8	808.58	83.38	0.00	-396.29
$\lambda(\text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	6	810.41	85.21	0.00	-399.21
$\lambda(\text{type} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	9	810.55	85.35	0.00	-396.28
$\lambda(\text{size} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	7	811.53	86.33	0.00	-398.76
$\lambda(\text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{temp})$	6	814.31	89.11	0.00	-401.15
$\lambda(\cdot), \gamma(\cdot), \Omega(\cdot), p(\cdot)$	4	819.57	94.38	0.00	-405.79

Table S3. Model selection statistics for probability of initial occupancy and abundance of spotted turtles (*Clemmys guttata*) in Virginia during 2019. Covariates of occupancy (Ψ) and abundance (λ) included wetland type (“type”; forested pool, emergent wetland, etc.), wetland size (“size”), distance to nearest wetland (“dist”), number of amphibian egg masses (“egg”), and structure diversity (“diverse”; leaf litter, coarse woody debris, sedges) within the wetland. Covariates of detection (p) included minimum daily temperature (“temp”) and trap density (“density”; # traps/wetland size). No covariates of colonization (ϵ) and extinction (γ) or recruitment (ϵ) and apparent survival (Ω) were included. Models were ranked using Akaike’s Information Criterion (AIC) and included with each model is the number of parameters (K), difference from best model (ΔAIC), model weight (AICwt) and log-likelihood estimate (LL).

Model	K	AIC	Δ AIC	AICwt	LL
Occupancy					
$\Psi(\text{type} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	16	273.83	0.00	0.58	-120.91
$\Psi(\text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	14	275.44	1.61	0.26	-123.72
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	16	278.10	4.27	0.07	-123.05
$\Psi(\text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	13	278.43	4.60	0.06	-126.21
$\Psi(\text{type} + \text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	15	280.68	6.85	0.02	-125.34
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	17	281.70	7.87	0.01	-123.85
$\Psi(\text{size} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	12	290.51	16.68	0.00	-133.25
$\Psi(\text{type} + \text{size} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	10	291.29	17.46	0.00	-135.65
$\Psi(\text{type} + \text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	11	291.29	17.46	0.00	-134.65
$\Psi(\text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	13	292.50	18.67	0.00	-133.25
$\Psi(\text{type} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	14	293.28	19.45	0.00	-132.64
$\Psi(\text{type} + \text{size}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	9	293.32	19.49	0.00	-137.66
$\Psi(\text{type} + \text{size} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	10	293.88	20.05	0.00	-136.94
$\Psi(\text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	11	293.89	20.06	0.00	-135.94
$\Psi(\text{type} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	9	294.10	20.27	0.00	-138.05
$\Psi(\text{type}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	8	294.12	20.29	0.00	-139.06
$\Psi(\text{type} + \text{size} + \text{diverse}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	15	294.19	20.36	0.00	-132.09
$\Psi(\text{type} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	10	294.47	20.64	0.00	-137.23
$\Psi(\text{type} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	15	294.86	21.03	0.00	-132.43
$\Psi(\text{type} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	9	294.87	21.04	0.00	-138.43
$\Psi(\text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	12	295.75	21.92	0.00	-135.88
$\Psi(\text{type} + \text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	16	296.15	22.32	0.00	-132.07
$\Psi(\text{diverse} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	12	296.16	22.33	0.00	-136.08
$\Psi(\text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	13	296.17	22.34	0.00	-135.08
$\Psi(\text{size} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	7	296.59	22.76	0.00	-141.30
$\Psi(\text{size}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	6	297.21	23.38	0.00	-142.61
$\Psi(\text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	6	297.52	23.69	0.00	-142.76
$\Psi(\text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	6	297.67	23.84	0.00	-142.83
$\Psi(\text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	8	297.74	23.91	0.00	-140.87
$\Psi(\text{size} + \text{dist}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	7	299.09	25.26	0.00	-142.54
$\Psi(\text{dist} + \text{egg}), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	7	299.29	25.46	0.00	-142.65
$\Psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	4	308.71	34.89	0.00	-150.36
Model	K	AIC	ΔAIC	AICwt	LL
Abundance					
$\lambda(\text{type} + \text{size} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	11	550.12	0.00	0.49	-258.06
$\lambda(\text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	14	552.12	2.00	0.18	-258.06
$\lambda(\text{type} + \text{size} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	16	553.75	3.63	0.08	-260.88
$\lambda(\text{type} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	15	554.40	4.28	0.06	-262.20

Table S3 (Cont.)

$\lambda(\text{type} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	16	554.81	4.69	0.05	-261.41
$\lambda(\text{type} + \text{size} + \text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{dens} + \text{temp})$	17	555.39	5.27	0.04	-263.69
$\lambda(\text{type} + \text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{dens} + \text{temp})$	17	555.56	5.44	0.03	-260.78
$\lambda(\text{type} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	16	555.82	5.70	0.03	-261.91
$\lambda(\text{type} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{dens} + \text{temp})$	17	556.26	6.14	0.02	-261.13
$\lambda(\text{size} + \text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	15	557.03	6.91	0.02	-263.51
$\lambda(\text{size} + \text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	13	559.12	8.99	0.01	-266.56
$\lambda(\text{size} + \text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	14	561.11	10.99	0.00	-266.55
$\lambda(\text{diverse}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	12	570.43	20.31	0.00	-273.21
$\lambda(\text{diverse} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	13	571.84	21.72	0.00	-272.92
$\lambda(\text{diverse} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	13	572.39	22.27	0.00	-273.20
$\lambda(\text{diverse} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	14	573.80	23.68	0.00	-272.90
$\lambda(\text{type} + \text{size} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	11	578.10	27.98	0.00	-278.05
$\lambda(\text{type} + \text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	10	578.72	28.60	0.00	-279.36
$\lambda(\text{type} + \text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	12	579.67	29.55	0.00	-277.84
$\lambda(\text{type} + \text{size} + \text{div} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{dens} + \text{temp})$	18	580.06	29.93	0.00	-279.03
$\lambda(\text{type} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	10	581.33	31.21	0.00	-280.67
$\lambda(\text{type} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	11	583.04	32.92	0.00	-280.52
$\lambda(\text{type}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	9	584.08	33.96	0.00	-283.04
$\lambda(\text{type} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	10	585.59	35.47	0.00	-282.80
$\lambda(\text{size}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	7	587.53	37.41	0.00	-286.77
$\lambda(\text{size} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	8	589.22	39.10	0.00	-286.61
$\lambda(\text{size} + \text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	8	589.24	39.11	0.00	-286.62
$\lambda(\text{size} + \text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	9	591.02	40.90	0.00	-286.51
$\lambda(\text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	7	601.96	51.84	0.00	-293.98
$\lambda(\text{dist}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	7	602.46	52.34	0.00	-294.23
$\lambda(\text{dist} + \text{egg}), \gamma(\cdot), \Omega(\cdot), p(\text{density} + \text{temp})$	8	602.91	52.79	0.00	-293.45
$\lambda(\cdot), \gamma(\cdot), \Omega(\cdot), p(\cdot)$	4	627.99	77.87	0.00	-309.99

CONCLUSION

In this dissertation, I sought to understand the spatio-temporal variation in activity and occupancy dynamics of the spotted turtle in a dynamic wetland ecosystem. Indeed, I saw seasonal variation in patterns of activity, movement, occupancy, and abundance dynamics for this species. In Chapter I, I demonstrated that there was a seasonal pattern in total frequency of activity and nocturnal behaviors. Differences between adult and juvenile turtles and adult male and female turtles was best explained by reproductive activity (Litzgus and Brooks 2000, Litzgus and Mousseau 2004) and overall seasonal pattern in activity supports previously described seasonality in movement (Litzgus and Brooks 2000, Joyal et al. 2001, Beaudry et al. 2009, Rowe et al. 2013). Until recently, spotted turtles were considered almost exclusively diurnal and this study corroborates recent findings (Hjort et al. 2021) that spotted turtles exhibit non-reproductive related nocturnal behaviors. I was able to quantify the extent, timing, and meteorological correlates of nocturnal activity and recommend a more widespread adoption of continuous monitoring methods to better understand turtle nocturnal and the drivers influencing this behavior.

In Chapter II, I demonstrated seasonal variation in movement patterns, and that movement and space-use was dependent upon multiple wetland patches in a given season. Spotted turtle inter-wetland movement and movement distance peaked during late spring, which coincides with seasonality in movement and habitat use documented for this species (Litzgus and Brooks 2000, Joyal et al. 2001, Beaudry et al. 2009, Rowe et al. 2013). Inter-wetland movement was also related to climatic conditions and wetland hydroperiod with adults and juveniles responding similarly to variation in habitat quality and availability. Though adult turtles generally moved farther and occupied more wetlands and larger home-ranges than juveniles. Movement and space-use were also related to wetland size and configuration. Home-range sizes

are our site (5.06 ha) were greater than the mean home-range size for this species (3.7 ha), though within what has been reported, which varies substantially across the species range from < 1 – 16 ha (e.g., Litzgus and Mousseau 2004; Rowe et al. 2013; Chandler et al. 2020). Spotted turtles in this study used numerous wetlands across the season with a high degree of inter-wetland movement between the wetland patches. These results demonstrate spotted turtle rely on numerous wetlands to meet their resource requirements and that management for this species must entail protection of multiple connected wetlands with a safe upland matrix between them.

In Chapter III, I demonstrated seasonal effects in spotted turtle occupancy and abundance patterns. Spotted turtle occupancy probability and abundance estimates peaked in late spring, which again mirrors the reported spring activity patterns in movement and habitat use documented for this species (Litzgus and Brooks 2000, Joyal et al. 2001, Beaudry et al. 2009, Rowe et al. 2013). The seasonal pattern in spotted turtle occupancy and abundance was supported by the relationship between both respective parameters and wetland size, however I did not see an effect in wetland type across sampling weeks. Occupancy probability was relatively high across wetland patches and best predicted by wetland size. There was a more discerning influence of wetland characteristics on spotted turtle abundance estimates, with abundance positively related to amphibian egg masses and wetland quality and configuration. Abundance estimates at my site of 418-464 were far greater than what has been previously reported for this species (range: 14.3-116; Seburn 2003, Litzgus and Mousseau 2004, Reeves and Litzgus 2008, Jones et al. 2014, Feng et al. 2019). These estimates support the importance of large, connected wetland complexes for preserving spotted turtle populations. Additionally, detection of turtles was positively related to temperature for that of occupancy and abundance

estimates. By incorporating wetland turnover, I have provided a more detailed understanding of the spatio-temporal distribution of spotted turtles in a dynamic ecosystem.

Results from all chapters provide overwhelming evidence that spotted turtles rely on numerous wetlands across the spring season and management for this species must entail protection of wetland complexes with connectivity rather than single, isolated wetlands. Additionally, that the life history of this species is closely related to the temporal and spatial variation of the habitat in which it occupies, which is evident in seasonal patterns of activity, movement, and occupancy dynamics. Predictions of dynamic distributions and population persistence will be essential for this species in the face of continued habitat fragmentation and climate stochasticity. Data from this study will provide vital information to conservationists and land managers to help understand the spatial and temporal drivers of activity and occupancy dynamics of species inhabiting dynamic ecosystems.

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APPENDIX



UNIVERSITY OF
ARKANSAS

Office of Research Compliance

To: Brett DeGregorio
From: Jeff Wolchok
Date: December 16, 2019
Subject: IACUC Approval
Expiration Date: December 15, 2022

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol #20048, *Spotted Turtle (Clemmys guttata) Movement and Population Dynamics in an Isolated Population*.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond December 15, 2022 you must submit a new protocol. The IACUC may not approve a study for more than three years at a time.

The following individuals are approved to work on this study: Brett DeGregorio and Ellery Lassiter. Please submit personnel additions to this protocol via the modification form prior to their starting work.

The IACUC appreciates your cooperation in complying with University and federal guidelines involving the care and use of animals.

JCW/jgr

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