

**Home Range, Activity, Movement, and Habitat Selection of the Flattened Musk Turtle
(*Sternotherus depressus*) in the Bankhead National Forest, Alabama**

by

Arthur Joseph Jenkins

A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
August 3, 2019

Keywords: Flattened Musk Turtle, *Sternotherus depressus*, Habitat Selection, Home Range,
Movement, Activity

Copyright 2019 by Arthur Joseph Jenkins

Approved by

Daniel Warner, Chair, Assistant Professor of Biological Sciences
John Feminella, Professor of Biological Sciences
David Steen, Research Ecologist, Georgia Sea Turtle Center
Todd Steury, Associate Professor of Forestry and Wildlife Sciences

Abstract

The Flattened Musk Turtle, *Sternotherus depressus*, is an imperiled aquatic species endemic to the Upper Black Warrior watershed in Alabama. As one of the most understudied turtles in the United States, little is known about its habits. This is especially true of their spatial ecology, one of the most important fields of ecological knowledge to inform management and conservation practices. To fill this information gap, this study employs radio telemetry, trapping, habitat, and wading (visual encounter) surveys to explore aspects of *S. depressus* spatial ecology in Bankhead National Forest (BNF) by describing home range and areas of core use, identifying factors that affect activity and movement, and modeling habitat selection on multiple levels (second-order, or population level; third-order, or patch level; and fourth-order, or microhabitat level).

Home ranges, quantified as stream length inhabited, of 21 individuals averaged 332 m, ranging from 22 to 957 m. Areas of core stream use were also quantified as stream length by kernel density estimation using the Sheather-Jones plug-in method for individual bandwidth selection. Average 95 and 50 % kernel lengths of core use for 14 individuals were 185 (varying from 43 to 772 m) and 46 m (varying from 9 to 201 m), respectively. Activity, defined as a turtle being exposed instead of under refuge cover, increased with precipitation, but not with temperature, and peaked late in the evening. Movements increased with precipitation and temperature and were greater during breeding/nesting season (April to July) as compared to postnesting season (August to October). Overall, availability of bedrock and detached rock

substrate/cover were the most important factors positively affecting habitat selection across scales. Snail availability was only a significant factor at patch-scale selection. Stream width and depth were identified in top models as having a positive affect on population- and habitat-patch-scale selection, respectively, but effects were not significant.

These data help to inform management questions such as what length of stream is needed to maintain a viable population, how and when is best to survey for *S. depressus*, and what are the features of suitable habitat? As concern for this species among agencies and organizations rises with continued declines across its historic range, our results offer key information to better advise future conservation efforts.

Acknowledgments

I must begin by recognizing the displaced First Nations on whose stolen land my research took place: the Alibamu, the Coushatta, the Choctaw, the Chickasaw, and likely others lost to history and genocide. Removed from a home of lush abundance and banished to arid lands in the west, may they one day receive the liberty and justice that they deserve and that the country that so wronged them claims to support but continues to deny them.

It will be impossible for me to mention everyone who has contributed over the past seven years to my field work, thesis, and, most of all, growth as a young scientist. I'll be forever grateful to Craig Guyer for so much positive encouragement over the years and opening my world up to the possibility of following my passions and Jim Godwin for providing the opportunities for me to do so. I'd like to thank Dave Steen for taking me on as a graduate student, all the help with writing this thesis, and mentoring my conservation efforts. To all my committee members, whose edits and advice have been invaluable. I'm especially indebted to Dan Warner for graciously adopting me into his lab and helping me navigate the department, to Alison Cochran and the US Forest Service at Bankhead National Forest for accommodations and funding for this project, to Hannah Gerke and Evan Cedrone for each suffering a grueling Alabama summer while helping me in the field, and to Sara Piccolomini, Eric Wittig, Taylor Donelson, Taylor McKee, Mitch Grisham, Genny Jenkins, Maggie Jenkins, Dan Self, Birmingham Zoo, David Brothers, Zoo Atlanta, and countless others who have assisted me with fieldwork at one time or another. I cannot express how thankful I am to Teresa Palmer and

Warren Kelsoe for their loving hearts, taking in and feeding a smelly, tick-infested stray graduate student as one of their own.

Lastly, I would like to acknowledge my friend and mentor, the late Bob Mount and his family, who laid the groundwork for myself and so many other Alabama herpetologists. Thank you for passing on your knowledge and inspiration.

Table of Contents

Abstract.....	ii
Acknowledgments.....	iv
List of Tables	viii
List of Figures.....	xii
List of Abbreviations	xiii
Chapter 1. Describing Home Ranges and Exploring Activity and Movement Patterns of Flattened Musk Turtles (<i>Sternotherus depressus</i>)	1
Abstract.....	1
Introduction.....	2
Methods.....	6
Results.....	11
Discussion.....	14
Tables.....	17
Figures.....	27
Chapter 2. Multiscale Habitat Selection of an Imperiled Aquatic Endemic: the Flattened Musk Turtle (<i>Sternotherus depressus</i>).....	29
Abstract.....	29
Introduction.....	30
Methods.....	35
Results.....	44

Discussion.....	48
Tables.....	52
Figures.....	65
References	71

List of Tables

Chapter 1

- Table 1. Description of seasonal activity periods for *Sternotherus depressus* across the year. These periods are based on published natural history information (Dodd, 2008) 7
- Table 2. Stream length home range (SLHR), time elapsed from first to last observation, and total telemetry observations for 21 *Sternotherus depressus* in Brushy Creek and Sipsey Fork in Bankhead National Forest, Alabama. Data were collected via radio telemetry from June 2013 to March 2015 9
- Table 3. Two-dimensional Gaussian kernel density estimates (Silverman, 1986; Worton, 1989) for 95% and 50% core-use stream lengths for 14 individual *Sternotherus depressus*, each with at least 30 telemetry observations. Bandwidth was calculated via the Sheather-Jones plug-in method (SJPI; Sheather and Jones, 1991; Jones et al., 1996). Data were collected with radio telemetry from June 2013 to March 2015 in Brushy Creek and Sipsey Fork of Bankhead National Forest, Alabama and include time elapsed from first to last observation and total observations 11
- Table 4. Sample size (n), mean (\bar{x}), and standard deviation (σ), for female, male, Brushy Creek, and Sipsey Fork datasets of stream length home ranges (SLHR), 95%, and 50% two-dimensional Gaussian kernel density estimates (KDE, Silverman, 1986; Worton, 1989) using Sheather-Jones plug-in method (Sheather and Jones, 1991; Jones et al., 1996) for bandwidth. Mean and standard deviation units are meters. Females and males do not differ significantly from each other in any of the space use estimates, and neither do Brushy Creek turtles from Sipsey Fork Individuals 21
- Table 5. Correlation matrix with variance inflation factors (VIF) for parameters utilized in activity analysis. Parameters are not strongly correlated, $VIF > 4.0$. Time of day is adjusted to begin at 5:00 am local standard time. Precipitation is daily precipitation averaged between two weather stations near the study sites in Bankhead National Forest, AL (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temperature is the relative water temperature from the US Geological Survey's water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) 41
- Table 6. Top mixed-effects logistic regression models predicting activity of *Sternotherus depressus*. Turtle activity data was recorded during radio telemetry studies as either concealed (inactive) or exposed (active). For these models, cumulative AIC_c weight is 0.95. None of these models can be considered "best" as $\Delta AIC_c < 2.00$. DayTime is time of day adjusted to begin at 5:00 am local standard time. Precip is daily precipitation (mm) averaged between two weather stations near the study sites in Bankhead National Forest,

AL (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL)..... 48

Table 7. Model-averaged parameters from top mixed-effects logistic regression models for activity. Model-averaged parameter weights (w_p), model-averaged estimates, unconditional standard errors, and 95% unconditional confidence limits for each parameter. Time of day and daily precipitation explain significant variability. Time of day is adjusted to begin at 5:00 am local standard time. Daily precipitation (mm) is averaged between two weather stations near the study sites in Bankhead National Forest, AL (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Inactive season (November to March) is the reference for breeding/nesting (April to July) and postnesting (August to October) seasons..... 50

Table 8. Correlation matrix with variance inflation factors (VIF) for parameters utilized in movement analysis. Strong collinearity, $VIF > 4.0$ was not detected among any variables. Days Elapsed is the number of days between radio telemetry locations for an individual turtle. Precipitation is the average daily precipitation across the time elapsed, using an average of precipitation data between two nearby weather stations (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temperature is the relative water temperature from the US Geological Survey’s water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) averaged across the time elapsed between locations of an individual 41

Table 9. Model set utilizing generalized linear mixed regression to predict distance moved ranked by AIC_c . Sex is considered an uninformative parameter as models that include sex as a variable perform better without it. Therefore, \sim Days Elapsed + Precip + Temp + Season + (1|Turtle) is considered best model. DaysElapsed is the number of days between radio telemetry locations for an individual turtle. Precip is the average daily precipitation (mm) across the time elapsed, using an average of precipitation data between two nearby weather stations (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temp is the relative water temperature ($^{\circ}C$) from the US Geological Survey’s water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) averaged across the time elapsed between locations of an individual 48

Table 10. Estimates of effect, standard errors, z values, and levels of significance for the variables included in the top generalized linear mixed regression model describing movement by *Sternotherus depressus*. Days elapsed is the number of days between radio telemetry locations for an individual turtle. Precipitation is the average daily precipitation (mm) across the time elapsed, using an average of precipitation data between two nearby weather stations (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temperature is the relative water temperature ($^{\circ}C$) from the United States Geological Survey’s water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) averaged across the time elapsed between locations of an individual. Breeding/nesting season (April to July) is the reference for postnesting season (August to October) 50

Table 1. Substrate categories, their descriptions, and coinciding turtle refuge cover classification utilized in habitat selection analyses.....	7
Table 2. Proposed site covariates for modeling occupancy and the method used to sample the covariates	9
Table 3. Descriptions and measurement values of independent variables proposed for conditional logistic regression models of third-order (patch) and fourth-order (microhabitat) resource selection. Depth and width were not included in fourth-order analyses. In addition, proposed variables for third-order habitat selection also include cover from transect data as proportions for debris cover, log cover, crevice cover, rock cover, crevice or rock cover, and sand/silt cover.....	11
Table 4. Variance inflation factors between considered occupancy covariates. Variables beginning with “Z” are substrate variables calculated from stream habitat data taken every 5 m on zigzag transects. Variables beginning with “So” are stream substrate variables calculated from side scan sonar habitat mapping.....	21
Table 5. Models with sampling covariates to explain detection of <i>Sternotherus depressus</i> at stream reach sites in Bankhead National Forest. The only top model, $\Delta AIC_c \leq 2.0$, considered survey method alone as a sample covariate. Survey methods consisted of day wading surveys, night wading surveys, and trapping surveys.....	41
Table 6. Estimates of detection from the top model of sampling covariates, $\Psi(\cdot)$, $p(\text{Method})$, explaining detection patterns of <i>Sternotherus depressus</i> . Untransformed values are in parentheses. Day wading survey method represents the intercept for detection in this model.....	48
Table 7. Top models, $\Delta AIC_c \leq 2.0$, explaining occupancy of <i>Sternotherus depressus</i> at 24 stream reach sites in Bankhead National Forest. <i>Corbicula</i> was determined to be an uninformative parameter. Therefore, the $\Psi(\text{Width}+\text{Corbic})$, $p(\cdot)$ was removed from consideration as a top model. ZBed is bedrock substrate proportions obtained from zig-zag habitat transects. SoBed is bedrock substrate proportions obtained from side scan sonar habitat mapping.....	50
Table 8. Model results for occupancy analyses of <i>Sternotherus depressus</i> at 24 stream reach sites in Bankhead National Forest. Untransformed estimates of coefficients (β) and standard errors (SE) are included for each covariate. Variables beginning with “So” are substrate data from sonar mapping. Variables beginning with “Z” are substrate data from zig-zag transects.....	41
Table 9. Variance inflation factors (VIF) between independent variables being considered in third-order habitat selection. Variables included stream width and average depth in addition to proportions of sample plots with snails, <i>Corbicula</i> , bedrock substrate, detached rock substrate, sand/silt substrate, crevice cover, rock cover, and debris cover. None of the parameters were strongly collinear, $VIF > 4$	48

Table 10. Likelihood estimates, standard errors, and 95% confidence intervals (CI) of parameters included in the selected model for third-order habitat selection analyses for 10 m stream patch habitat by *Sternotherus depressus*. This model was built with full stepwise procedures using AIC_c and includes proportion of snail presence, crevice cover, debris cover, detached rock substrate, and average stream depth as independent variables. Strength of significance is denoted by asterisks 50

Table 11. Likelihood estimates, standard errors, and 95% confidence intervals (CL) of microhabitat use by concealed *Sternotherus depressus* for substrates categories relative to sand/silt substrate. Strength of significance is denoted by asterisks..... 51

Table 12. Likelihood effect sizes and statistical significance between substrate categories for microhabitat selection of *Sternotherus depressus* when conceal under refugia. The reference substrate is represented by columns and the substrate estimate by rows. The likelihoods of use for substrates that had a significantly different ($p < 0.05$) likelihood of use compared to the reference substrate are bold and underlined 52

List of Figures

Chapter 1

Figure 1. Telemetry study sites for *Sternotherus depressus* in Bankhead National Forest, Alabama. Three sites on Sipsey Fork and one site on Brushy Creek were included in this study. All sites had relatively pristine habitat and healthy populations of *S. depressus*... 7

Figure 2. Adult *Sternotherus depressus* with radio transmitters attached by cement putty. Transmitters were positioned on either side of the back of the carapace so not to increase the height profile of the carapace or interfere with breeding..... 9

Chapter 2

Figure 1. Study sites for four radio telemetry and 25 stream reach (250 m) surveys for *Sternotherus depressus* in Bankhead National Forest, Alabama. Thirty-three turtles were included in our telemetry study. Stream reach surveys at each of the 25 sites included two day-wading, two night-wading, and two 20 trap-night trapping surveys, each covering 250 m of stream length 21

Figure 2. Adult *Sternotherus depressus* with transmitters for radio telemetry attached using cement putty. Transmitters were positioned on either side of the back of the carapace so not to increase the height profile of the carapace or interfere with breeding 41

Figure 3. A 31x31 cm PVC square used as a sampling quadrat for collecting habitat data utilized to model habitat selection on multiple scales..... 48

Figure 4. Available habitat data at telemetry sites were recorded every 1 m, perpendicular to the stream bank, on transects that were spaced 10 m apart at radio telemetry sites. Depth, substrate type, available cover type, snail presence, and *Corbicula* presence data were collected at each point..... 50

Figure 5. Example of habitat sampling methods for 250 m stream reaches. Habitat points were every 5 m on zig-zag transects oriented 45° from the bank using a compass to sight direction. Substrate type, snail presence, and corbicula presence data were collected at each point 50

Figure 6. Example of substrate polygons, delineated from side scan sonar imagery, used in population-scale (second-order) modeling of habitat selection 50

List of Abbreviations

AIC	Akaike Information Criterion
BNF	Bankhead National Forest
CL	Confidence Limits
IUCN/SSC	International Union for the Conservation of Nature/Species Survival Commission
KDE	Kernel Density Estimates
LST	Local Standard Time
SJPI	Sheather-Jones Plug-In
USFWS	United States Fish and Wildlife Service
USGS	United States Geological Survey
VIF	Variance Inflation Factor

Chapter 1

Describing Home Ranges and Exploring Activity and Movement Patterns of Flattened Musk Turtles (*Sternotherus depressus*)

Abstract

Spatial and temporal ecology form the foundational knowledge for species conservation, informing aspects of wildlife management from population modeling and monitoring techniques to land protection and restoration. In turn, the spatial and temporal ecology of a species is generally considered to be driven by feeding and reproduction. Without knowledge of basic aspects of a species' spatial ecology such as home range, core areas of use, and movement, or temporal ecology such as how daily and seasonal activity are influenced, it is not possible to understand the basic needs of the species. In this study, we quantified home ranges and core use areas to describe space use of the imperiled Flattened Musk Turtle (*Sternotherus depressus*) in two large streams within Bankhead National Forest. Using radio telemetry to track 33 adult turtles from June 2013 to March 2015, home ranges were calculated for 21 individuals, averaging 332 m in stream length, while 95% and 50% kernel density stream lengths of core use for 14 individuals averaged 185 m and 86 m, respectively. We also built models to explain activity and movement patterns of tracked turtles using variables drawn from previous studies on *S. depressus* and similar species. Turtles were significantly more active later in the day and at night. Activity was also found to increase with precipitation. Water temperature did not significantly affect turtle activity during warm months. Turtle movements increased with daily average precipitation and average water temperature. Movements were also greater during the breeding/nesting season (April to July) compared to the postnesting season (August to October).

Home range size, core use stream lengths, activity patterns, and movement patterns did not differ significantly between males and females. Our study is the first to rigorously model activity and movement patterns of *S. depressus* and to quantify long-term home ranges and core areas of space use, filling important gaps in our knowledge of the spatial ecology of this imperiled species.

INTRODUCTION

Home range size and behavioral activity are key aspects of species life history and play a fundamental role in understanding of species ecology (Swingland and Greenwood, 1984). Studying home range sizes of individuals informs how a population spatially utilizes its environment and is necessary for management of species of concern (Litzgus and Mousseau, 2004). Likewise, studies examining activity and movement patterns inform how individuals utilize their environment temporally and spatially. Home range, activity, and movement patterns are considered to be regulated by feeding and reproduction (Huey and Pianka, 1981; Rusak, 1981; Rose, 1982; Doody et al., 2002). Biotic and abiotic influences on activity and movement of animals include seasonal patterns in weather and reproduction, daily weather, diel cycle, and dissimilar reproductive strategies between males and females (Mahmoud, 1969; Ashby, 1972; Rusak, 1981; Rose, 1982; Haxton and Berrill, 2001; Brown and Shine, 2002; Doody et al., 2002; Litzgus and Mousseau, 2004).

In riverine systems, water temperature is an additional, important factor that affects behavior in aquatic species (Mahmoud, 1969; Haxton and Berrill, 2001). Activity of aquatic ectotherms is especially governed by water temperature as their ability to thermoregulate is limited (Mahmoud, 1969) compared to terrestrial ectotherms which generally have a greater

variety of temperatures across their habitat to select from. Being aquatic ectotherms, yet dependent on air for respiration and land for nesting, turtles are influenced by factors in aquatic and terrestrial environments, which are ultimately influenced by atmospheric conditions. In freshwater turtles, studies have found water temperature (Mahmoud, 1969; Haxton and Berrill, 2001; Litzgus and Mousseau, 2004), seasonal patterns (Jones, 1996; Litzgus and Mousseau, 2004), daily weather conditions (Mahmoud, 1969; Rowe and Dalgarn, 2010), diel cycle (Mahmoud, 1969; Rowe and Dalgarn, 2010), and sex (Jones, 1996; Doody et al., 2002; Litzgus and Mousseau, 2004) to influence activity and/or movement.

A recent study by the IUCN/SSC Turtle Taxonomy Working Group reported that at least 50% of turtle species worldwide are imperiled (van Dijk et al., 2014). Turtle declines have been largely attributed to habitat degradation and over-exploitation (Moll and Moll, 2004). Riverine species are especially susceptible to habitat degradation from pollution, impoundments, and associated changes in land use that are common in major river systems throughout the world. As habitat structure changes, turtles will attempt to meet their reproductive and metabolic functions by adjusting their spatial ecology (Ernst, 1986; Marchand and Litvaitis, 2004; Moll and Moll, 2004; Rees et al., 2009). Examples included shifting home ranges in response to pond draining (Ernst, 1986) and increased movements during drought by turtles in disturbed habitats (Rees et al., 2009). Furthermore, climate change is already influencing activity of species (Parmesan and Yohe, 2003) and will continue to do so in the future. Therefore, it is important to study the activity and movement patterns of imperiled species so that we may better understand their ecological requirements for the purpose of improving current and future management practices for the conservation of those species (Litzgus and Mousseau, 2004; Pressey et al., 2007).

Sternotherus depressus (Testudines, Kinosternidae) is a small turtle endemic to the Black Warrior River Drainage above the Fall Line in Alabama that feeds predominantly on small, aquatic mollusks such as bivalves and gastropods. Both in its extensive use of rock refuges and degree of population declines, *S. depressus* is unique among its congeners (Jackson, 1988). Since the 1960s, *S. depressus* has declined severely throughout its range and many populations have been extirpated or remain as old, non-recruiting relic populations (Dodd et al., 1988; Ernst et al., 1989; Dodd, 1990; Bailey and Guyer, 1998; Dodd, 2008; Scott and Rissler, 2015). In response, the species was listed as threatened under the Endangered Species Act by the US Fish and Wildlife Service in 1987 (USFWS, 1987). Declines have largely been attributed to siltation and decreased water quality from extensive coal mining, agriculture, deforestation, and impoundment (Dodd et al., 1988; Dodd, 2008). Human landscape development in recent years has significantly increased siltation and sediment deposition in streams, having detrimental effects on natural biotic assemblages (Wood and Armitage, 1997). Despite continued declines and increasing threats to *S. depressus* habitat, there have been relatively few studies exploring basic aspects of its ecology and is one of the least-studied turtle species in the United States (Lovich and Ennen, 2013).

Home range size of *S. depressus* is virtually unknown as the only published estimates are from a single adult male tracked every day across 40 days in Sipsey Fork (Dodd, 1988). Dodd (1982) calculated a minimum convex polygon home range of 77 m² with inhabited stream length of ~35 m, a 95% ellipse area of concentrated use (Anderson, 1982) of 123 m² or ~20 m core stream length, and a 50% fourier transformation area of concentrated use (Anderson, 1982) of 88 m² or ~15 m core stream length. Studies of common musk turtles, *Sternotherus odoratus*, found

larger home ranges and areas of core use with average areas varying from 600 m² to 2.8 ha (Mahmoud, 1969; Rowe et al., 2009).

Current knowledge of activity and movement patterns of *S. depressus* is limited to anecdotal observations (Mount, 1981; Dodd, 2008) and a short term, 4-40 day, radio-telemetry study conducted in the summer of 1985 that noted greater movement in males compared to females (Dodd, 1988). Seasonal activity may peak in late spring and early summer as adults breed in April and May, and females lay one or two clutches of two eggs during June and July on sand banks (Dodd, 2008). Flooding and predation are known sources of mortality (A.J., pers. obs.). Turtles may decrease the risk of these threats by taking refuge during times of elevated risk, such as heavy precipitation events and daylight hours. One study found that congener, *S. odoratus*, were more active on cloudy/rainy days and at crepuscular times during summer, speculating that this may be driven by turtle preference for warm water temperatures while also avoiding the intense heat and sunlight of summer, mid-day, sun (Mahmoud, 1969).

Information pertaining to the spatial ecology of *S. depressus*—that which is necessary to inform conservation strategies (Pressey et al., 2007)—is insufficient. In this study, we describe home range and explore factors that potentially influence the activity and movement of adult *S. depressus* on multiple spatial and temporal scales. Ideally, this information will help us predict their sensitivity to future environmental changes while informing management efforts. Our objectives are to determine size of home ranges and core spatial use areas of *S. depressus* and to identify and model factors that affect their activity and movement under natural conditions in the relatively pristine stream habitats of Bankhead National Forest. We hypothesize that activity and movement of *S. depressus* will...

1. differ between males and females because of differential reproductive activities.

2. be greatest during late spring and early summer months because that is when breeding and nesting occur.
3. decrease with heavy precipitation (> 3 cm) because turtles will seek shelter to prevent injury and downstream displacement; and/or increase with light precipitation (< 3 cm) as turtles take advantage of favorable water temperatures and decreased visibility for predators.
4. decrease with water temperature due to the ectothermic physiology of turtles.
5. be greatest later in the day and at night due to environmental advantages such as decreased risk of predation and more favorable water temperatures in the summer.

METHODS

Study Sites

This study was conducted at four sites on two fourth-order streams in Bankhead National Forest (BNF) in Winston County, Alabama (Figure 1). Three of the sites were on Sipsey Fork at AL Hwy 33, the end of FSR 1000, and the end of Caney Creek Rd. The fourth site was on Brushy Creek at Hickory Grove Rd. Sipsey Fork and Brushy Creek are characterized as shallow, mixed bottom streams (clay, sand, small rock, slab rock, bedrock) that run through steep sandstone canyons. These sites were selected because they are of the few accessible locations with healthy populations that continue to maintain moderate-to-high densities of *S. depressus* (Dodd et al., 1988; Bailey and Guyer, 1998; Scott and Rissler, 2015). Being largely within BNF, upstream land cover is chiefly mixed hardwood and pine forest, and riparian vegetation has remained relatively intact compared to areas outside of BNF.

Radio Telemetry

Radio telemetry was used to track turtles to determine home range, movement, and activity patterns of *S. depressus*. Thirty-three adult turtles were captured via trapping and wading surveys in 2013 and 2014. Our methods conformed to USFWS regulations and guidelines (USFWS Permit No: TE32397A-2; IACUC Protocol No. 2016-2833; ADCNR Permit No. 2017118163068680). Turtles were fitted with radio transmitters (Model SB-2, 5 gram, Holohil Systems) on the posterior side of the carapace using cement putty (Fix-It™ Stick Epoxy Putty, Oatey; Figure 2). Transmitters were carefully positioned on the carapace so as not to increase the height profile of the shell, which could prevent turtles from entering previously accessible crevices and rock refuges. Transmitter and putty attachments weighed 10 g, equivalent to 25% or less ($\bar{x} = 12\%$) of the mass of the turtle they were attached to. Although this transmitter mass is greater than the widely recommended limit of 10% for reptiles and amphibians (Beaupre et al., 2004), water displacement decreases this increase in weight carried by ~25%. To check our assumption that transmitters are not significantly hindering movements and space use by smaller individuals, we calculated the Pearson's correlation coefficient to test for a significant correlative relationship between transmitter mass as a percentage of individual body mass and home range size and kernel density space use. Turtles were released at the location of capture and tracked using a receiver (Model R-1000, 148 – 154 MHz, Communications Specialists) and yagi antennae. Turtles were tracked until transmitters were removed or fell off, battery death, or turtle death. From June 2013 to March 2015, turtles were tracked one to three times a week during the months of May to August and once or twice a month during the rest of the season. For ease of access and researcher safety, tracking was usually conducted during daytime hours.

When located, individual, time, date, location, and concealment were recorded. A turtle was considered active if it was out in the open and inactive if it was concealed under some cover

type that was considered a refuge. Dates were split into three seasons: breeding/nesting, post nesting, and inactive (Table 1). In addition, daily precipitation records from two nearby weather stations (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL) were averaged to get precipitation for each day. Hourly records of water temperature from the U.S. Geological Survey's (USGS) water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) were utilized as values for relative water temperature.

Statistical Analyses

We quantified home range and space use for individual turtles via three values: stream length home range (SLHR), two-dimensional 95% kernel density estimate, and two-dimensional 50% kernel density estimate. The SLHR signifies total home range utilized by individuals, while kernel density estimates represent areas of core use. These core use areas are necessary for understanding space use by turtles because individuals usually establish a familiar area, within a home range, where they spend most of their time (Mahmoud, 1969; Rowe and Dalgarn, 2010). Together, these values help to portray the space use habits of individual turtles. Stream length home ranges were calculated from the total stream length inhabited for individuals with at least 20 telemetry observations to decrease bias from individuals with fewer observations. Two-dimensional Gaussian kernel density estimates (KDE; Silverman, 1986; Worton, 1989) with Sheather-Jones plug-in bandwidth selection (SJPI; Sheather and Jones, 1991; Jones et al., 1996) were calculated for individuals with at least 30 telemetry observations to decrease bias from individuals with fewer observations (Girard et al., 2002). Telemetry locations for individual turtles were mapped in ArcGIS (ESRI, 2015) and snapped to lines representing the stream's mid-channel. ArcGIS was used to calculate the location of telemetry points along each stream-length.

Program R (R Foundation for Statistical Computing, 2018) was used to calculate the SLHR. The package stats (R Core Team, 2018) was used to calculate SJPI for each turtle, and the package hdr kde (Hyndman, 2018) was used to calculate 95% and 50% KDE, applying the SJPI for bandwidth smoothing.

We quantified activity via concealment at the instant of telemetry observation. Exposed turtles were considered active, while concealed turtles were considered inactive. Data were culled if they involved murky water conditions, turtles with fewer than two locations, sick individuals (Turtle 300), or chronic land use, which is indicative of disease (Fonnesbeck and Dodd, 2006). Mixed-effects logistic regression and AIC_c (Burnham and Anderson, 2002) were utilized to evaluate competing models for concealment. Statistical analyses were conducted in program R (R Foundation for Statistical Computing, 2018) using the package lme4 (Bates et al., 2015) for modeling and the package AICcmodavg (Mazerolle, 2019) for model averaging. Independent variables included time of day, daily precipitation (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL), relative water temperature (USGS stream gauge no. 02450250; USGS, 2017), seasonal activity period (Table 1), and sex. Time of day was calculated as hours past 5:00 AM local standard time (LST). We calculated variance inflation factors (VIF) using the package car (Fox and Weisberg, 2011) to check for collinearity, VIF > 4, among independent variables. A model set featuring all subsets of the independent variables was analyzed with individual applied as a random effect for all models.

Movement was quantified as the linear stream-distance between consecutive telemetry observations. In addition to data culling for the situations listed above in the activity analyses, movement data points that were influenced by a major flood on 3-6 July 2013 were also culled as some turtles were washed downstream by the flood, movement not as the result of their own

volition. Distance moved was modeled by generalized linear mixed regression using the package “lme4” (Bates et al., 2015) in program R (R Foundation for Statistical Computing, 2018). Our models utilized poisson distribution to account for non-normal distribution of movement data. Independent variables included sex and averages across the time elapsed between telemetry observations for daily precipitation (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL), relative water temperature (USGS stream gauge no. 02450250; USGS, 2017), and seasonal activity period (Table 1). We calculated VIF between model parameters to check for collinearity. We built a model set with all model subsets of these independent variables with individual random effect included in all models. To control and account for greater distances moved as a function of individuals having had more time to move, all models also included the independent variable of days elapsed between telemetry locations, and movements with more than five days elapsed were removed from the dataset. Competing models were evaluated with AIC_c (Burnham and Anderson, 2002) using the package `AICcmodavg` (Mazerolle, 2019).

For the activity and movement analyses, models were compared using AIC_c (Burnham and Anderson, 2002). After checking for and removing uninformative parameters (Arnold, 2010), we utilized multi-model inference, calculating model-averaged parameter weights (w_p) for each parameter in the top model set (Burnham and Anderson, 2002). The models with the greatest support and had a cumulative AIC_c weight of at least 0.95 were considered to be the top model set. For each parameter in the top models, we calculated model-averaged estimates of effect, unconditional standard errors, and 95% unconditional confidence intervals. We considered a parameter to be a significant predictor of variability if $w_p > 0.70$ and if its 95% unconditional confidence intervals do not include zero (Burnham and Anderson, 2002).

RESULTS

During June 2013 to March 2015, 33 *S. depressus* were fitted with radio transmitters and tracked by radio telemetry, yielding 921 telemetry locations of which there were 715 instances of individuals being inactive, denoted as concealed under refugia, and 83 observations of active, or exposed, turtles. Individuals were observed on land 27 times, although a third of those observations were of an injured turtle (turtle 300) that did not move for weeks and eventually died on land. There were 123 locations when streams were too murky, due to recent rains, to determine status of individuals. Ten individuals in Brushy Creek were tracked for a total of 267 location points, and 23 Sipse Fork individuals were tracked for 654 points.

Pearson's correlation coefficient was calculated between transmitter percentage mass to turtle body mass and SLHR ($n = 21, r = 0.11, p = 0.64$), 95% KDE ($n = 14, r = 0.29, p = 0.31$), and 50% KDE ($n = 14, r = 0.32, p = 0.27$), exhibiting no statistically significant support for a correlative relationship between transmitter mass as a percentage individual body mass and home range size or core range size. Thus, our assumption that transmitters were not so massive as to significantly affect the spatial ecology of smaller *S. depressus* compared to larger individuals stands. For individuals with 20 or more telemetry observations, SLHR varied between 22 and 957 m, averaging 332 m ($n = 21, \sigma = 322$, Table 2). These individuals were tracked 20 to 64 times, averaging 37 times, and with time elapsed varying between 29 and 636 days with an average of 296 days. For individuals with 30 or more observations, 95% KDE stream lengths ranged from 43 to 772 m, averaging 185 m ($n = 14, \sigma = 208$, Table 3), and 50% KDE stream lengths ranged from 9 to 201 m, averaging 46 m ($n = 14, \sigma = 53$, Table 3). These individuals were tracked 30 to 64 times, averaging 44 times, and with time elapsed varying between 117 and

636 days with an average of 354 days. There was no statistically significant difference between male and female home ranges or between turtles in Brushy Creek and Sipsey Fork, although sample sizes were relatively low for Brushy Creek and males (Table 4). There were no statistically significant, $p < 0.05$, correlative relationships between SLHR or KDE data and days elapsed or number of telemetry observations, indicating that our 20-observation minimum for SLHR and 30-observation minimum for KDE calculations were sufficient at limiting bias due to time elapsed and number of observations.

The original set of models formed from all subsets of independent variables for the activity analysis resulted in 32 models. Parameters utilized in these models for activity did not exhibit strong collinearity, $VIF > 4$ (Table 5). However, after comparing models using AIC_c , relative water temperature was identified as an uninformative parameter as it does not perform better than the null model and models with relative water temperature consistently rank lower than the same models without relative water temperature (Arnold, 2010). The removal of models with relative water temperature results in a winnowed set of 16 models. Of these models, six are top models, used for model-averaging parameters, with an AIC_c cumulative weight of 0.95 (Table 6). We found that the highest-ranked model included time of day, precipitation, and season variables, with the second-ranked model having the same variables as the highest-ranked model in addition to sex (Table 6). The AIC_c weights for highest and second-ranked models are 0.243 and 0.236, respectively. This means that there is a 24.3% chance that the highest-ranked model is the best model out of all models tested. The AIC_c weights of the parameters are 1.000 for time of day, 0.707 for precipitation, 0.722 for season, and 0.497 for sex. This means that there is a 100% chance that time of day is in the best model.

Using the six top models predicting activity for model-averaging parameters, we found that for each 1 hour increase in time past 5:00 am LST, *S. depressus* were 1.166 (1.091 - 1.245, 95% CL) times as likely to be active ($p < 0.001$). For each 1 cm increase in precipitation, turtles were 1.644 (1.041 - 2.570, 95% CL) times as likely to be active ($p = 0.04$). During breeding/nesting season, turtles were 5.298 (0.717 - 39.154, 95% CL) times as likely to be active compared to the inactive season ($p > 0.10$). However, this result is not statistically significant. During postnesting season, turtles were 3.128 (0.394 - 24.811, 95% CL) times as likely to be active compared to the inactive season ($p > 0.10$), though this result is not statistically significant. Female turtles were 1.653 (0.829 - 3.300, 95% CL) times as likely to be active as male turtles ($p > 0.10$). However, this result is not statistically significant.

Limiting movement data to a maximum of 5 days elapsed between telemetry locations eliminated all data during the inactive season, removing that category from our analysis. Collinearity between parameters for movement was not detected (Table 8). An all model subsets list resulted in 16 models created from the independent variables. There were two top models for movement patterns: \sim Days Elapsed + Average Precipitation + Average Temperature + Season + (1|Turtle) and the global model, \sim Days Elapsed + Average Precipitation + Average Temperature + Sex + Season + (1|Turtle). However, sex is an uninformative parameter as sex alone does not perform better than the null model and models with sex rank lower than the same models without sex (Table 9; Arnold, 2010). Therefore, we disregard the global model in favor of the single top model, \sim Days Elapsed + Average Precipitation + Average Temperature + Season + (1|Turtle), in which all independent variables are significant predictors of movement (Table 10). For each 1 day increase in elapsed time, turtles moved 1.099 (1.083 - 1.115, 95% CL) times further ($p < 2e^{-16}$). For each 1 cm increase in average daily precipitation, turtles moved 1.128 (1.093 - 1.164,

95% CL) times further ($p = 6.59e^{-14}$). For each 1 °C increase in average water temperature, turtles moved 1.045 (1.033 - 1.058, 95% CL) times further ($p = 1.04e^{-12}$). During the breeding/nesting season, turtles moved 1.210 (1.137 - 1.288, 95% CL) times further than in the postnesting season ($p = 2.19e^{-9}$).

DISCUSSION

Our study described home ranges, identified model parameters predicting activity and movement, and revealed how those parameters influence activity and movement of *S. depressus* in relatively pristine habitat and population conditions, filling gaps in the natural history knowledge of this imperiled species. Prior information about home range, activity, and movement of *S. depressus* are sparse, consisting of anecdotes and a single short-term telemetry study across 40 days during the summer of 1985 (Dodd, 1988).

Although calculations differ somewhat from our study, the only previously calculated home range as well as 95% and 50% core use areas of an adult *S. depressus* (Dodd, 1988) concur with our results when considering the difference in time scales between the two studies. Home ranges for *S. depressus* are less than 1 km in stream length, averaging a few hundred meters, 95% core use stream lengths tend to be a couple hundred meters of stream or less, and 50% core use stream lengths are usually less than 100 meters. These values did not differ between sex or stream.

Our methods were not sufficient at collecting activity and movement data during periods of heavy precipitation as adverse field conditions coinciding with heavy rains often prevented researchers from tracking turtles. Therefore, few data points with heavy rain, > 30 mm/day, exist in our activity and movement data. However, precipitation was still included in our analyses to

explore the possibility of light precipitation having a relationship with activity and movement as observed by Mahmoud (1969) in *S. odoratus*. We found time of day and daily precipitation to be significantly informative of activity, while time elapsed, average daily precipitation, average temperature, and season were significantly informative of movement. As in a previous study on a related species, *S. odoratus* (Mahmoud, 1969), precipitation was determined to have a positive relationship with activity and movement. The increase in activity and movement around days with precipitation could be explained by turtles moving to secure refuges before storms and/or exploiting rainy and overcast conditions to forage and make movements during a time in which visibility is decreased for predators and temperatures are more favorable. Although water temperature was identified to be an uninformative parameter in activity analyses, average water temperature was found to be strongly informative for movement, partially supporting our hypothesis for a positive relationship with water temperature. As surveys were often conducted during the day, and movements typically occur at night, it isn't surprising that relative water temperature is not informative for instantaneous activity data that was usually taken during the day, while water temperature averaged across the intervening time for movement data is informative.

The breeding/nesting season had a positive effect on activity and movement compared to postnesting and inactive seasons. Although the effect of breeding/nesting season compared to postnesting season was only significantly informative for movement, not activity, season appeared in top models for activity. Thus, our hypothesis of activity and movement peaking during the breeding/nesting season is partially supported. Sex was determined to be an uninformative parameter for movement and was not a strong indicator of variability for activity, failing to support our hypothesis of differential reproductive activities between sexes having an

influence on activity and movement. This result is unexpected given a previous small-scale radio telemetry study conducted in the summer of 1985 on Sipsey Fork which found that the seven male *S. depressus* moved more often and greater distances than the six females that were tracked (Dodd, 1988). However, studies of *S. odoratus* have also failed to detect significant differences between male and female activity and movements (Mahmoud, 1969; Rowe et al., 2009).

As plans for species conservation arise, management efforts must be informed by scientific studies of how those species utilize their habitat in both a spatial and temporal sense. Without these ecological studies, the proper size and placement of management areas and best times for management activities such as surveys are not known. In this study, we determined that the extent of home ranges and core use areas for individuals of healthy *S. depressus* populations can range up to 1 km, but typically consist of a few hundred meters of stream length or less. We also modeled activity and movement of *S. depressus*, showing that activity is positively influenced by time of day and low to moderate amounts precipitation, while movement has a positive relationship with water temperature, low to moderate precipitation, and the breeding/nesting season. Our findings indicate that, while *S. depressus* typically maintain relatively small home ranges, they sometimes make large movements that greatly expand their home ranges, thus they require large sections of intact stream habitat to thrive. In addition, our activity and movement models indicate that precipitation, water temperature, time of day, and season are important factors to consider when planning management actions or surveying for *S. depressus*.

Table 1. Description of seasonal activity periods for *Sternotherus depressus* across the year. These periods are based on published natural history information (Dodd, 2008).

Season	Months	Description
Inactive	November - March	The period when turtles enter brumation and significant movements cease.
Breeding/nesting	April-July	The period when turtles emerge from brumation, breed, and nest.
Post nesting	August - October	The period between nesting until activity slows and brumation begins.

Table 2. Stream length home range (SLHR), time elapsed from first to last observation, and total telemetry observations for 21 *Sternotherus depressus* in Brushy Creek and Sipsey Fork in Bankhead National Forest, Alabama. Data were collected via radio telemetry from June 2013 to March 2015.

Turtle	Stream	Sex	Time Elapsed (days)	Observations	SLHR (m)
2	Brushy	M	306	30	957
21	Brushy	F	560	49	767
22	Brushy	F	560	61	201
100	Brushy	M	97	23	22
1100	Brushy	M	375	46	766
4900	Brushy	F	162	21	62
3	Sipsey	M	144	39	74
4	Sipsey	F	229	47	604
5	Sipsey	F	29	20	193
6	Sipsey	M	144	40	88
7	Sipsey	F	393	60	368
8	Sipsey	M	279	44	329
17	Sipsey	F	117	36	103
18	Sipsey	F	636	64	72
19	Sipsey	F	282	34	938
20	Sipsey	F	392	33	759
23	Sipsey	M	535	36	86
30	Sipsey	F	300	25	227
36	Sipsey	F	292	23	248
50	Sipsey	F	161	20	22
220	Sipsey	F	220	21	94

Table 3. Two-dimensional Gaussian kernel density estimates (Silverman, 1986; Worton, 1989) for 95% and 50% core-use stream lengths for 14 individual *Sternotherus depressus*, each with at least 30 telemetry observations. Bandwidth was calculated via the Sheather-Jones plug-in method (SJPI; Sheather and Jones, 1991; Jones et al., 1996). Data were collected with radio telemetry from June 2013 to March 2015 in Brushy Creek and Sipsey Fork of Bankhead National Forest, Alabama and include time elapsed from first to last observation and total observations.

Turtle	Stream	Sex	Time Elapsed (days)	Observations	SJPI Bandwidth	95% Length (m)	50% Length (m)
2	Brushy	M	306	30	76.4	772	201
21	Brushy	F	560	49	60.7	503	123
22	Brushy	F	560	61	7.9	129	26
1100	Brushy	M	375	46	3.6	73	9
3	Sipsey	M	144	39	6.1	59	20
4	Sipsey	F	229	47	7.8	117	24
6	Sipsey	M	144	40	9.1	86	27
7	Sipsey	F	393	60	9.5	142	30
8	Sipsey	M	279	44	20.8	172	41
17	Sipsey	F	117	36	8.6	85	25
18	Sipsey	F	636	64	3.4	58	12
19	Sipsey	F	282	34	30.9	278	60
20	Sipsey	F	392	33	4.5	43	12
23	Sipsey	M	535	36	11.1	78	30

Table 4. Sample size (n), mean (\bar{x}), and standard deviation (σ), for female, male, Brushy Creek, and Sipsy Fork datasets of stream length home ranges (SLHR), 95%, and 50% two-dimensional Gaussian kernel density estimates (KDE, Silverman, 1986; Worton, 1989) using Sheather-Jones plug-in method (Sheather and Jones, 1991; Jones et al., 1996) for bandwidth. Mean and standard deviation units are meters. Females and males do not differ significantly from each other in any of the space use estimates, and neither do Brushy Creek turtles from Sipsy Fork Individuals.

	SLHR			95% KDE			50% KDE		
	n	\bar{x}	σ	n	\bar{x}	σ	n	\bar{x}	σ
Female	14	333	306	8	169	153	8	39	37
Male	7	332	379	6	207	280	6	55	72
Brushy Creek	6	462	413	4	369	329	4	90	90
Sipsy Fork	15	280	278	10	112	71	10	28	14

Table 5. Correlation matrix with variance inflation factors (VIF) for parameters utilized in activity analysis. Parameters are not strongly correlated, VIF > 4.0. Time of day is adjusted to begin at 5:00 am local standard time. Precipitation is daily precipitation averaged between two weather stations near the study sites in Bankhead National Forest, AL (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temperature is the relative water temperature from the US Geological Survey’s water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017).

	Time of Day	Precipitation	Temperature	Nesting Season	Postnesting Season	Sex
Time of Day	Inf	1.002	1.049	1.003	1.002	1.004
Precipitation	1.002	Inf	1.009	1.026	1.014	1.000
Temperature	1.049	1.009	Inf	1.390	1.019	1.000
Nesting Season	1.003	1.026	1.390	Inf	3.342	1.000
Postnesting Season	1.002	1.014	1.019	3.342	Inf	1.001
Sex	1.004	1.000	1.000	1.000	1.001	Inf

Table 6. Top mixed-effects logistic regression models predicting activity of *Sternotherus depressus*. Turtle activity data was recorded during radio telemetry studies as either concealed (inactive) or exposed (active). For these models, cumulative AIC_c weight is 0.95. None of these models can be considered “best” as $\Delta\text{AIC}_c < 2.00$. DayTime is time of day adjusted to begin at 5:00 am local standard time. Precip is daily precipitation (mm) averaged between two weather stations near the study sites in Bankhead National Forest, AL (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL).

Model	<i>K</i>	AIC _c	ΔAIC_c	AIC _c Wt
DayTime+Precip+Season+(1 Turtle)	6	434.42	0	0.24
DayTime+Precip+Season+Sex+(1 Turtle)	7	434.48	0.06	0.24
DayTime+Season+Sex+(1 Turtle)	6	435.70	1.28	0.13
DayTime+Precip+(1 Turtle)	4	435.84	1.41	0.12
DayTime+Season+(1 Turtle)	5	435.91	1.49	0.12
DayTime+Precip+Sex+(1 Turtle)	5	436.04	1.62	0.11

Table 7. Model-averaged parameters from top mixed-effects logistic regression models for activity. Model-averaged parameter weights (w_p), model-averaged estimates, unconditional standard errors, and 95% unconditional confidence limits for each parameter. Time of day and daily precipitation explain significant variability. Time of day is adjusted to begin at 5:00 am local standard time. Daily precipitation (mm) is averaged between two weather stations near the study sites in Bankhead National Forest, AL (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Inactive season (November to March) is the reference for breeding/nesting (April to July) and postnesting (August to October) seasons.

Parameter	w_p	Mod-Avg Estimate	exp(Mod-Avg Estimate)	Uncond Std Error	Uncond 95% CL	exp(Uncond 95% CL)
Time of Day*	0.950	0.1534	1.166	0.0337	(0.0873, 0.2195)	1.091 - 1.245
Precipitation*	0.707	0.0495	1.051	0.0230	(0.0043, 0.0947)	1.004 - 1.099
Nesting Season	0.722	1.6673	5.298	1.0205	(-0.3328, 3.6675)	0.717 - 39.154
Postnesting Season	0.722	1.1404	3.128	1.0566	(-0.9305, 3.2113)	0.394 - 24.811
Male	0.472	-0.5032	0.605	0.3526	(-1.1943, 0.1879)	0.303 - 1.207

*Considered to be a significant predictor of activity: $w_p > 0.70$ and unconditional 95% confidence limits don't overlap zero.

Table 8. Correlation matrix with variance inflation factors (VIF) for parameters utilized in movement analysis. Strong collinearity, VIF > 4.0 was not detected among any variables. Days Elapsed is the number of days between radio telemetry locations for an individual turtle. Precipitation is the average daily precipitation across the time elapsed, using an average of precipitation data between two nearby weather stations (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temperature is the relative water temperature from the US Geological Survey’s water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) averaged across the time elapsed between locations of an individual.

	Days Elapsed	Season	Sex	Temperature	Precipitation
Days Elapsed	Inf	1.005	1.007	1.000	1.005
Season	1.005	Inf	1.002	1.037	1.000
Sex	1.007	1.002	Inf	1.001	1.001
Temperature	1.000	1.037	1.001	Inf	1.022
Precipitation	1.005	1.000	1.001	1.022	Inf

Table 9. Model set utilizing generalized linear mixed regression to predict distance moved ranked by AIC_c . Sex is considered an uninformative parameter as models that include sex as a variable perform better without it. Therefore, \sim Days Elapsed + Precip + Temp + Season + (1|Turtle) is considered best model. DaysElapsed is the number of days between radio telemetry locations for an individual turtle. Precip is the average daily precipitation (mm) across the time elapsed, using an average of precipitation data between two nearby weather stations (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temp is the relative water temperature ($^{\circ}$ C) from the US Geological Survey’s water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) averaged across the time elapsed between locations of an individual.

Model	K	AIC_c	ΔAIC_c	$AIC_c Wt$
\sim DaysElapsed+Precip+Temp+Season+(1 Turtle)	6	16454.30	0	0.72
\sim DaysElapsed+Precip+Temp+Sex+Season+(1 Turtle)	7	16456.23	1.92	0.28
\sim DaysElapsed+Precip+Temp+(1 Turtle)	5	16489.60	35.30	0.00
\sim DaysElapsed+Precip+Temp+Sex+(1 Turtle)	6	16491.50	37.20	0.00
\sim DaysElapsed+Precip+Season+(1 Turtle)	5	16503.96	49.66	0.00
\sim DaysElapsed+Temp+Season+(1 Turtle)	5	16504.57	50.27	0.00
\sim DaysElapsed+Precip+Season+Sex+(1 Turtle)	6	16505.86	51.56	0.00
\sim DaysElapsed+Temp+Season+Sex+(1 Turtle)	6	16506.47	52.17	0.00
\sim DaysElapsed+Season+(1 Turtle)	4	16537.71	83.40	0.00
\sim DaysElapsed+Season+Sex+(1 Turtle)	5	16539.59	85.28	0.00
\sim DaysElapsed+Temp+(1 Turtle)	4	16540.62	86.32	0.00
\sim DaysElapsed+Temp+Sex+(1 Turtle)	5	16542.50	88.20	0.00
\sim DaysElapsed+Precip+(1 Turtle)	4	16550.74	96.44	0.00
\sim DaysElapsed+Precip+Sex+(1 Turtle)	5	16552.62	98.31	0.00
\sim DaysElapsed+(1 Turtle)	3	16584.10	129.80	0.00
\sim DaysElapsed+Sex+(1 Turtle)	4	16585.95	131.64	0.00

Table 10. Estimates of effect, standard errors, z values, and levels of significance for the variables included in the top generalized linear mixed regression model describing movement by *Sternotherus depressus*. Days elapsed is the number of days between radio telemetry locations for an individual turtle. Precipitation is the average daily precipitation (mm) across the time elapsed, using an average of precipitation data between two nearby weather stations (station: US1ALWN0001, Double Springs, AL; station: USC00010063, Addison, AL). Temperature is the relative water temperature (°C) from the United States Geological Survey’s water gauge on Sipsey Fork (USGS stream gauge no. 02450250; USGS, 2017) averaged across the time elapsed between locations of an individual. Breeding/nesting season (April to July) is the reference for postnesting season (August to October).

Parameter	Estimate	exp(Estimate)	Std Error	exp(95% CL)	Pr(> z)	
(Intercept)	1.5421	4.674	0.1891	3.216 - 6.774	3.55E-16	***
Days Elapsed	0.0942	1.099	0.0073	1.083 - 1.115	< 2e-16	***
Precipitation	0.0120	1.012	0.0016	1.009 - 1.015	6.59E-14	***
Temperature	0.0443	1.045	0.0062	1.033 - 1.058	1.04E-12	***
Postnesting Season	-0.1903	0.827	0.0318	0.776 - 0.880	2.19E-09	***

***Considered to be a significant predictor of movement.

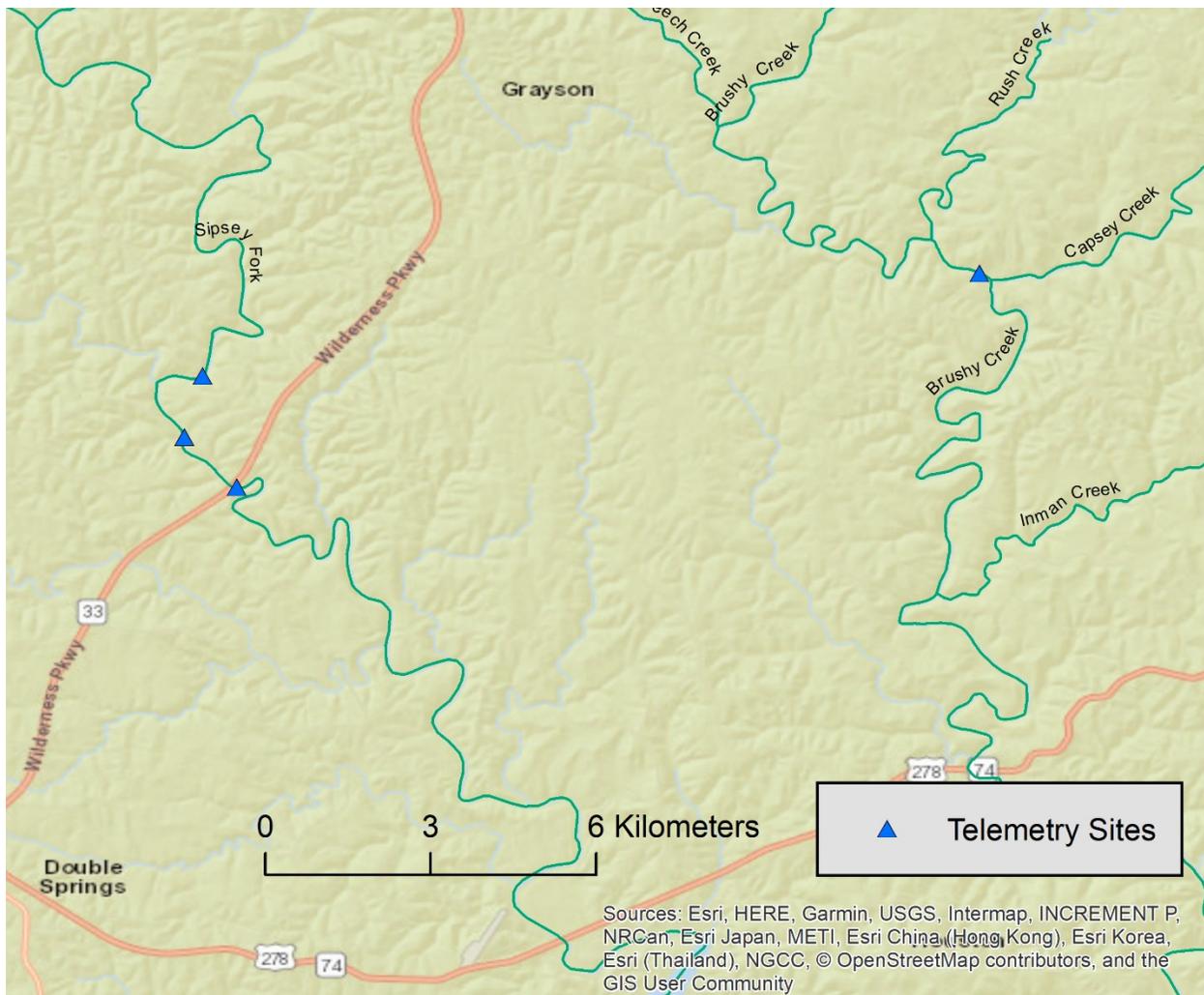


Figure 1. Telemetry study sites for *Sternotherus depressus* in Bankhead National Forest, Alabama. Three sites on Sipse Fork and one site on Brushy Creek were included in this study. All sites had relatively pristine habitat and healthy populations of *S. depressus*.



Figure 2. Adult *Sternotherus depressus* with radio transmitters attached by cement putty. Transmitters were positioned on either side of the back of the carapace so not to increase the height profile of the carapace or interfere with breeding.

Chapter 2

Multiscale Habitat Selection of an Imperiled Aquatic Endemic: the Flattened Musk Turtle (*Sternotherus depressus*)

Abstract

Habitat selection by flattened musk turtles, *Sternotherus depressus*, was modeled at three scales to determine how habitat features and resources effect habitat use. These included selection at the population-(second-order), patch-(third-order), and microhabitat-(fourth-order) scales of resource selection. Bedrock and rock substrates and cover influenced selection across all scales, while snail prey influenced selection only at the patch-scale. We also found some evidence for an effect of stream size on patch and population level selection. Trapping, wading, and habitat surveys at 250 m stream reaches conducted for second-order habitat selection (population level) analyses identified night wading surveys as the most effective method for turtle detection and indicated possible range contraction of *S. depressus* populations in BNF as compared to historic surveys. In addition, second-order habitat selection analyses utilized both traditional point-transect habitat surveys and side scan sonar mapping surveys for substrate, resulting in similar conclusions which demonstrates the efficacy of substituting side scan sonar for time-consuming point-transect surveys. As concern and action on behalf of this imperiled endemic increases, our results will help advise survey methods for *S. depressus* as well as inform conservation activities by allowing managers to identify areas with suitable habitat and prioritize those locations for surveys, restoration, population augmentation, or reintroduction of *S. depressus*.

INTRODUCTION

Habitat selection occurs on numerous scales from the microhabitat selected by an individual to the range selected by an entire species. Understanding resource selection at various scales helps inform proper habitat management for species of interest. Habitat selection has been defined at four levels, or orders (Johnson, 1980). First-order selection refers to selection on the scale of geographic range by a species (Johnson, 1980). Second-order selection is the selection of resources by a population that determines home ranges of individuals (Johnson, 1980). Third-order selection represents the use of habitat patches by an individual in its home range (Johnson, 1980). Fourth-order selection is the use of microhabitat components by an individual on a fine scale, such as food items or refuge (Johnson, 1980). Analyses for resource selection studies typically involve comparison of resource use to resource availability (Johnson, 1980). Describing habitat selection for imperiled species with narrow habitat requirements can be useful in advising conservation and management (Steen et al., 2014).

Anthropogenic habitat alteration is the leading cause of declines in wildlife worldwide (Wilcove et al., 1998; Sala et al., 2000; WWF 2016); this is perhaps particularly true for freshwater species, which are disproportionately affected by habitat change and are experiencing greater extinction rates compared to many other groups, including marine species (Wilcove et al., 1998; Ricciardi and Rasmussen, 1999; Sala et al., 2000; WWF, 2016). Multiple factors influence vulnerability of freshwater species to habitat change, including susceptibility to altered flow regimes by extensive hydroelectric infrastructure, increased pollutants and sedimentation from landscape development, and the limited geographic range and spatially limited habitat available to freshwater species (Postel et al., 1996; Richter et al., 1997; Dudgeon et al., 2006; WWF, 2016). Sedimentation is one of the most common forms of water pollution (Milliman and

Syvitski, 1992), and population declines due to sedimentation have been documented across many freshwater taxa (Richter et al., 1997; Wood and Armitage, 1997; Sutherland et al., 2002; Quinn et al., 2013). Increased erosion can inundate interstitial space in streams, decreasing habitat structure and creating a more homogenous streambed. This can disrupt aspects of the life histories of aquatic organisms and leave them vulnerable to predation and flooding (Wood and Armitage, 1997; Sutherland et al., 2002; Quinn et al., 2013). With ongoing changes to stream habitat structure, it is important to inform management plans with studies involving habitat utilization by imperiled freshwater species. One such imperiled species threatened by changes to habitat structure from sedimentation is the flattened musk turtle, *Sternotherus depressus*.

Sternotherus depressus (Testudines, Kinosternidae), is a small, aquatic turtle that only occurs in the portion of Black Warrior River Basin above the Fall Line in Alabama. The Upper Black Warrior River and its tributaries are historically characterized as having a heterogeneous substrate composition that includes stream reaches with bedrock crevices, medium to large detached rocks and boulders, submerged woody debris, sand, and silt. Bedrock crevices and large rocks may be particularly important for *S. depressus*, as they are used by *S. depressus* for over-wintering habitat and protection from predators, such as otters, and flooding (A.J. pers. obs.; Jackson 1988; Dodd, 2008). *Sternotherus depressus* feeds primarily on small, aquatic invertebrates, largely snails and *Corbicula*, nonnative Asian fingernail clams (Schnuelle, 1997; Dodd, 2008).

Having undergone significant declines across its range in the past few decades (Dodd et al., 1988; Ernst et al., 1989; Dodd, 1990; Bailey and Guyer, 1998; Scott and Rissler, 2015), *S. depressus* is considered critically endangered by IUCN Red List (van Dijk, 2011) and is protected under the Endangered Species Act (USFWS, 1987). Illness and poaching have played a

role in the decline of the species in localized areas (Guthrie, 1986; Dodd et al., 1988; Fonnesebeck and Dodd, 2003), but overall declines have been largely attributed to chemical pollution, sedimentation, and habitat alteration from coal mining, agriculture, hydroelectric dams, and deforestation and associated land development (Mount, 1981; Dodd et al., 1988; Ernst et al., 1989; Bailey and Guyer, 1998; Dodd, 2008). These impacts have occurred throughout the Black Warrior River Basin and have significantly eroded stream banks, converting large sections of stream from deeper bedrock and rock bottom substrates to more shallow sand and silt substrates (Mount, 1981; Dodd, 1990; Bailey and Guyer, 1998). Although studies have reported the relationship between increased sediment loads in stream habitats and declines in *S. depressus* (Mount, 1981; Dodd, 1990; Bailey and Guyer, 1998), finer-scale studies have not been conducted to model and describe habitat selection by *S. depressus* and understand the mechanisms behind these relationships and associated population declines. For example, the scales at which *S. depressus* selects habitat has yet to be quantified, and we know little about how other factors such as stream size or prey availability may factor into selection at those scales.

The Bankhead National Forest (BNF), which encompasses most of the Upper Sipsey Fork, represents a fraction of the historic range of *S. depressus*, but is considered the only area that contains relatively robust populations and intact habitat (Dodd, 1990; Bailey and Guyer, 1998; Scott and Rissler, 2015). Despite the importance of this population, there have not been any comprehensive surveys to determine the extent of their range in BNF. However, previous surveys have only documented *S. depressus* at five locations across three streams (Dodd, 1990; Bailey and Guyer, 1998), and they have not been found recently at two of those locations (Scott and Rissler, 2015). In addition, past population estimates at a site on Sipsey Fork in BNF

indicated population declines between the 1980s and 1990s (Bailey and Guyer, 1998). Although *S. depressus* populations in this area are generally considered stable, there is little quantitative evidence to support this assumption.

Recent changes to USFWS guidelines for trapping *S. depressus* no longer allow for trapping with traditional methods in which traps were set in the evening near rock ledges on the bottom of streams and checked at sunrise the next day. Due to concerns over drowning turtles, the new guidelines require that a portion of the trap be exposed to air to allow the turtle to breathe (USFWS, Permit No. TE32397A-2). While certainly safer for the turtle, this likely decreases trapping efficacy because traps must now be placed near banks where they are exposed to air. This may render trapping less effective at detecting turtles than other methods such as wading surveys, especially night wading surveys during the summer when turtles are most active. Surveys for *S. depressus* are often conducted by environmental consulting firms for bridges projects, mining, and other developments. Therefore, it is important that the most effective method for detecting *S. depressus* is determined and utilized during these surveys.

Techniques for quantifying habitat data have advanced in recent years with developments in sonar and GIS mapping technology. Transect surveys have traditionally been used to collect habitat data, and are still commonly used; however, they are time consuming. Sonar mapping of habitat is more time-efficient than transect surveys, and advancements in sonar technology have made sonar mapping more feasible in ecological studies (Kenny et al., 2003; Kaeser and Litts, 2010). This is especially true for technology associated with side scan sonar mapping of underwater habitat, which has been driven by demand from recreational fishermen. Although more commonly used in marine and lake settings, the use of side scan sonar for mapping habitat in freshwater streams is increasing (Kaeser and Litts, 2010). However, few studies have

implemented both habitat transects and side scan sonar mapping in streams and compared model results between the two methods. The ability of ecologists to quickly and efficiently gather accurate underwater habitat data has increased significantly with ongoing improvements in side scan sonar. However, only one published study using side scan sonar to map stream habitat has focused on a species of turtle (Sterrett et al., 2015), despite this group being among the most imperiled groups of organisms (van Dijk et al., 2014).

This study uses a combination of traditional techniques and modern technology to quantify *S. depressus* habitat selection on multiple scales for the first time. We developed models for second (home range-scale), third (patch-scale), and fourth-order (microhabitat/component-scale) habitat selection (Johnson, 1980) of *S. depressus* that involve variables of stream substrate, depth, width, available cover, and prey presence and abundance. We hypothesized that *S. depressus* selects for bedrock and/or rock substrate at all scales because, as a result of a lengthy evolutionary history with bedrock and rock substrates, they are thought to rely on these habitat features as refuge. Specifically, we hypothesized that *S. depressus* selects for cover, especially crevice and rock cover, at patch- and microhabitat-scales for secure refuge from threats such as predators and flooding. We hypothesized that *S. depressus* selects for deeper and wider habitat at population- and patch-scales because larger sections of stream, have a slower current, where it is easier to move than swiftly flowing sections and more habitat is available. We hypothesized that *S. depressus* selects for snails and *Corbicula* at all scales because *S. depressus* prey on them. Secondary goals of this study are to assess the current extent of *S. depressus* populations in BNF and to assess and compare the effectiveness of trapping, night wading, and day wading surveys at detecting *S. depressus*.

METHODS

Study Sites

Our study sites (Figure 1) were confined to Sipsey Fork, Brushy Creek, and their tributaries above Smith Lake in Bankhead National Forest (BNF), Alabama. Sipsey Fork and Brushy Creek were chosen because they are among the few remaining watersheds with sustaining populations of *S. depressus* (Dodd et al., 1988; Bailey and Guyer, 1998; Scott and Rissler, 2015). These streams represent the northwestern-most portion of the Upper Black Warrior River Basin. Streams throughout BNF flow through steep canyons with towering sandstone or limestone bluffs. These streams are characterized by a mosaic of substrates consisting of sandstone bedrock, boulders, rocks, sand, silt, and woody debris.

Four sites were selected for radio telemetry, based on their ease of access and local abundance of *S. depressus*. Three of the sites were on Sipsey Fork at AL Hwy 33, the end of FSR 1000, and the end of Caney Creek Rd. The fourth site was on Brushy Creek at Hickory Grove Rd. Twenty-five sites were selected for stream-reach surveys based on ease of access or proximity to public land. These stream reaches were 250 m in length. Ten stream reaches were evenly spaced between Winston Co. Rd. 60 and FSR 1000 on Sipsey Fork, and six were evenly spaced on Brushy Creek from Hickory Grove Rd. downstream to where Brushy Creek becomes inundated by Smith Lake, ~6 km upstream of US Hwy 278. The other nine reaches were near bridge crossings and represent smaller upstream portions and tributaries of Sipsey Fork and Brushy Creek.

Radio Telemetry

Radio telemetry was used to track turtles to explore third- and fourth-order habitat selection of habitat patches within home ranges and microhabitat by individual turtles. Thirty-three turtles were captured via trapping and wading surveys in 2013 and 2014. Adult turtles were fitted with radio transmitters (Model SB-2, 5 gram, Holohil Systems) using cement putty (Fix-It™ Stick Epoxy Putty, Oatey) on the posterior edge of the carapace (Figure 2). Transmitters were positioned so that the profile of the carapace was not increased and, the ability of turtles to enter refuges was not affected. The transmitter and putty attachments represented 12% of the individuals' mass, varying from 7 to 25% and weighed 10 g. This proportion of transmitter to turtle mass is greater than the recommended limit of 10% for reptiles (Beaupre et al., 2004). To determine whether there was evidence that exceeding this limit affected movement, we obtained the Pearson's correlation coefficient between the ratio of transmitter mass to turtle mass and home range as total stream length inhabited. Turtles were released at the location of capture and tracked with a receiver (Model R-1000, 148 – 154 MHz, Communications Specialists) and yagi antennae until transmitter removal, battery death, or turtle death. Telemetry studies were conducted from June 2013 to March 2015. Dependent upon weather, turtles were tracked one to three times a week from May to August and once or twice a month throughout the rest of the year. Tracking was usually conducted during daylight hours, although tracking times ranged throughout the day cycle. Once located, individual, time, date, location, concealment, cover (if concealed), substrate, and prey availability were documented. For concealed turtles, cover categories recorded were crevice, detached rock, sand/mud, roots/debris, and log (Table 1).

Prey availability was determined by placing a 31x31 cm quadrat (Figure 3) at the location of the turtle and exploring, by hand, the top 2 cm of substrate for the presence of aquatic snails and nonnative *Corbicula sp.* Native unionid mussels were not included as they were rarely found

in the top 2 cm of substrate in BNF. Substrate categories were bedrock, detached rock, sand/silt, roots/debris, and wood (Table 1). Substrate was recorded as being the substrate type that covered most of the area in the quadrat. In addition to the location of the turtle, habitat and prey availability data were collected at three points, upstream, downstream, and towards midstream, that were 1 m from the turtle location; these data were used for microhabitat selection analyses.

During May to October from 2014 to 2018, at the Hwy33 and FSR 1000 Sipsey Fork sites and the Brushy Creek site, we gathered data on available patch and microhabitat to compare to used habitat by walking transects across the streams, perpendicular to the stream banks, recording data every 1 m starting 0.5 m from a bank (Figure 4). We recorded depth, available cover, substrate, and presence of snails and *Corbicula* within the quadrat. Ninety-five habitat transects were spaced 10 m apart along the length of streams encompassing core telemetry areas.

Stream-Reach Surveys

To explore second-order habitat selection by *S. depressus* populations, turtle presence/absence and habitat surveys were conducted at the 25 stream-reach sites. During May to August in 2015, 2016, and 2017, a total of four, timed, visual-encounter surveys (VES), two trapping surveys, and one habitat survey were conducted at each stream reach. Surveys were conducted when streams were at base flow with clear visibility, not during or after heavy rains when water levels were elevated and visibility reduced. Timed VES consisted of one or two observers searching for turtles in the water while slowly wading upstream and/or downstream to visually cover the entire area of the stream reach. Two of the four wading surveys at each site were conducted during daylight hours and two were conducted during night hours. During day wading surveys, observers wore polarized sunglasses to reduce glare at the water's surface.

Waterproof headlamps with a brightness of at least 800 lumens were used for night wading surveys (Model ZLH600Fw Mk 2, ZebraLight). Date, start time, end time, and observers were recorded in addition to sex and age class of all turtles detected. Age class was recorded either as adult or juvenile based on midline carapace length (>75 mm for adult females, >65 mm for adult males; Close, 1982; Dodd, 1988). At the end of the survey, captured *S. depressus* were weighed and measured for shell dimensions (carapace midline length, carapace maximum length, carapace width between the 2nd and 3rd vertebral, shell height between the 2nd and 3rd vertebral, plastron length, and plastron width) on site and then released to the location of capture. Coinciding with the start time of each wading survey, water temperature from the U.S. Geological Survey (USGS) Sipsey Fork water gauge at the Winston Co. Rd. 60 bridge was recorded (USGS stream gauge no. 02450250; U.S. Geological Survey, 2017).

Collapsible box traps, 61 x 46 x 20 cm with 1.3 cm netting (Model Eel, Crawfish & Flounder Trap, 1/2 in. Sq. Mesh, 24 in. by 18 in. by 8 in., Memphis Net & Twine), were used for turtle trapping. Trapping methods complied with USFWS guidelines for trapping *S. depressus* (USFWS Permit No: TE32397A-2; IACUC Protocol No. 2016-2833; ADCNR Permit No. 2017118163068680). Canned sardines were used as bait by either putting the sardines in a perforated bait bottle or opening the can of sardines slightly and hanging it in the trap's bait bag. Traps were set in the evening along the stream bank but with a few centimeters of the top of the trap out of the water to prevent drowning. Traps were placed near submerged structures and in slow moving water when possible and checked the next morning. Two trapping surveys were conducted, each with 20 trap-nights. Twenty traps were set for one night at each stream reach for the first set of trapping surveys, and ten traps were set for two consecutive nights for the second set of trapping surveys for a total of 40 trap-nights and three nights of trapping per site. Date, set

time, check time, and number of traps set were recorded in addition to sex, age class, and species of any turtles caught. Trapped *S. depressus* were processed in the same manner as those caught during wading surveys. The midnight water temperature from the USGS Sipsey Fork water gauge at the Winston Co. Rd. 60 bridge was recorded as the relative water temperature for the trapping night (USGS stream gauge no. 02450250; USGS, 2017).

To quantify aspects of the habitat of each stream-reach site, surveys of the stream reaches were conducted by walking in a zigzag pattern from bank to bank, heading upstream at a 45° angle from the stream bank (Figure 5). A compass was used to determine the correct trajectory. Beginning with two steps from a bank at the downstream-most point of the stream reach, the same quadrat used for telemetry habitat sampling was placed at the toe of the observer so that opposite corners of the square pointed towards the direction of the sampling path. Presence of snails and *Corbicula sp.* were recorded in addition to substrate type in the quadrat as in the habitat collection procedures for the radio telemetry sites. Thereafter, the quadrat was placed and habitat data recorded every five steps until the observer traversed 250 m in the upstream direction. Steps were approximately 1 m in length.

Although we included Clear Creek in our data collectionsurveys, it was apparent that it may not be appropriate to include results from this site in analyses; most of the watershed is outside the protection of the national forest; consequently, it has been heavily impacted by deforestation and agriculture whereas the other 24 sites are in relatively pristine condition. Thus, the Clear Creek stream reach was removed from our dataset prior to statistical analyses.

Side Scan Sonar

In 2018-2019, we used a GPS-equipped side scan sonar (Model HELIX 9 CHIRP MEGA SI GPS G2N, Humminbird) to map the substrate, depth, and stream width for additional habitat availability data to include in our analyses for habitat selection at all stream-reach sites. Surveys were conducted during times of normal flows based on the USGS water gauge on Sipsey Fork at the Winston Co. Rd. 60 bridge (USGS stream gauge no. 02450250; U.S. Geological Survey, 2017). We considered normal flow to be when the water gauge reads a height of 1.0 to 1.4 m, as the average height for 2015 (the only year of our study for which there were complete averaged data from the water gauge) was 1.23 m (USGS stream gauge no. 02450250; USGS, 2017). Video recordings were taken from side scan sonar and processed in program SonarTRX (Leraand Engineering, 2017), which converts side scan video recordings into geo-referenced imagery. Incorporating substrate categories we described previously, we processed the sonar imagery in ArcGIS (ESRI, 2015) with the methods established by Kaeser and Litts (2008, 2010), creating habitat polygons based on our identified substrate categories (Figure 6) and determining depth and width every 10 m.

Statistical Analyses

Second-Order Habitat Selection

We implemented a Design I setup (Manly et al., 2002) to explore second-order selection, the selection of resources that determine individual home ranges within the available landscape (Johnson, 1980), by *S. depressus*. Habitat availability data for 24 stream reaches were collected using zigzag plot surveys and side scan sonar mapping and processed in ArcGIS (ESRI, 2015). Turtle wading surveys and trapping surveys were conducted to collect turtle presence data at the 24 stream reaches. Due to concerns about imperfect detection of turtles during surveys,

occupancy estimation methods were applied to model the use of the stream reaches by *S. depressus*. Habitat data and sample data were extracted from ArcGIS and utilized in program R (R Foundation for Statistical Computing, 2018) with the package unmarked (Fiske and Chandler, 2011), using turtle presence data to model detection probability and occupancy. Values for continuous variables were normalized by their standard score to aid with model convergence. We considered detection probability as a nuisance parameter in single-season models (MacKenzie et al., 2002) with sample covariates of detection probability being constant, varying by temperature, varying by survey method (day wading, night wading, and trapping), and varying by temperature and survey method. Akaike Information Criterion weighted for sample size, AIC_c (Burnham and Anderson, 2002), was used to determine the covariate(s) that best predicted detection probability. This sample covariate was included in subsequent competing single-season occupancy models involving habitat covariates of the stream reaches. Site covariates included variables relating to average stream dimensions, abundance of prey, and substrate data from both zigzag plot surveys and sonar mapping in the stream-reach sites (Table 2). Variance inflation factors (VIF) were calculated across site covariates using the package car (Fox and Weisberg, 2011) to check for collinearity. We considered stream reach site covariates with VIF > 4 to be correlated and removed covariates from our analyses as necessary to avoid collinearity. We built all possible subsets of models using site covariates under two limitations. We limited models to two site covariates or less due to our small site sample size of 24. In addition, we did not include substrate variables obtained via sonar surveys with those obtained via zigzag point surveys together in any models so as not to include variables measuring the same objective. These competing models and parameters were evaluated and ranked using AIC_c and AIC_c weight, AIC_cwt (Burnham and Anderson, 2002). Models with $\Delta AIC_c \leq 2.0$ were considered top models

(Burnham and Anderson, 2002) if they did not include an uninformative parameter (Arnold, 2010).

Third-Order Habitat Selection

We implemented a Design II setup (Manly et al., 2002) to explore third-order resource selection, the use of habitat patches by an individual *S. depressus* within its home range (Johnson, 1980). GPS coordinates of locations were collected via radio telemetry to determine the use of stream habitat patches by tracked turtles. Biased telemetry data such as those of sick and deceased turtles, flood-influenced locations, and the first locations for turtles were eliminated from our dataset. Point-transect data from three telemetry sites were utilized as habitat data. The point data for each transect were combined to create a single data point consisting of habitat variable averages and proportions for each transect. In ArcGIS (ESRI, 2015), these transect points were mapped along midstream and evenly spaced, with GPS coordinates for the upstream and downstream most transect points as references. Points were ~10 m apart, so each point represents a patch of stream from ~5 m upstream to ~5 m downstream of it. To check for collinearity among habitat variables, we calculated VIF using the package *car* (Fox and Weisberg, 2011) in program R (R Foundation for Statistical Computing, 2018). We considered site covariates with $VIF > 4$ to be collinear and removed covariates from our analyses as necessary. We utilized a matched design. For each turtle telemetry point, we randomly selected one habitat patch from the eight closest habitat patches, four upstream and four downstream, to create a paired dataset of used and unused habitat data. Movements of turtles between telemetry locations averaged 33 m ($n = 864$, $\sigma = 76$ m), averaging 11 m ($n = 864$, $\sigma = 28$ m) per day, and movements of 40 m or more over in a day are not uncommon for adult *S. depressus* (A.J., pers.

obs.). Therefore, we believe that this is a reasonable stream-distance in which to consider available patch-scale habitat for individuals. Only telemetry points that fell five habitat patches or more to the inside of the surveyed areas were included in this analysis. Modeling our data with conditional logistic regression, we used the package *survival* (Therneau, 2015) to model third-order habitat selection. Patch habitat analyses included independent variables pertaining to substrate proportions, cover proportions, prey availability, and stream dimensions (Table 3). Full stepwise procedures using AIC (Murtaugh, 2009) were utilized for model building instead of all subsets because running all model subsets is not feasible to do with large quantities of potential variables.

Fourth-Order Habitat Selection

We implemented a Design III setup (Manly et al., 2002) to explore fourth-order resource selection, the selection of microhabitat or specific component in a habitat patch (Johnson, 1980), for habitat use by concealed and exposed *S. depressus*. Microhabitat use and availability data were collected via radio telemetry of turtles and habitat transects at the four telemetry sites. Telemetry locations were included in our fourth-order selection analysis if they did not include deceased or sick individuals, land locations, or murky conditions that prevented collection of habitat data. For each turtle telemetry location, three unused habitat data points collected 1 m upstream, downstream, and towards midstream from each telemetry location were matched with each used habitat telemetry point. Separate analyses were conducted for locations in which turtles were exposed and those in which turtles were concealed. For exposed telemetry points, independent variables included substrate and prey presence (Table 3). For concealed telemetry points, only substrate was included as turtles were assumed not to be actively foraging and,

therefore, not selecting for prey. In program R (R Foundation for Statistical Computing, 2018), we used the package *survival* (Therneau, 2015) with the function *clogit* to model conditional logistic regression for used/unused models.

For each model set in our habitat selection analyses, models and parameters were evaluated and ranked using the package *AICcmodavg* (Mazerolle, 2019) to calculate AIC_c . For second- and fourth-order selection, model-averaged parameter weights (w_p ; Burnham and Anderson, 2002) were calculated for parameters in the top models. The best set of models with a cumulative AIC_{cwt} of at least 0.95 were considered top models (Burnham and Anderson, 2002), and checked for uninformative parameters (Arnold, 2010). We assessed model parameters as significantly explaining the dependent parameter if 95% confidence intervals of the untransformed estimates did not include zero and the cumulative AIC_{cwt} of the independent parameters in the top models were ≥ 0.70 (Burnham and Anderson, 2002).

RESULTS

Second-Order Habitat Selection

We conducted 150 surveys at 25 stream reach sites and detected turtles in 21 of these surveys at ten sites. Of models testing sample covariates, survey method model ($n = 24$) was the only model with $\Delta AIC_c \leq 2.0$, therefore best for describing probability of detection (Table 5). At sites occupied by *S. depressus*, this model estimates that night wading was the method most likely to detect individuals ($Pr = 0.663$, 0.413 - 0.846, 95% CL); trapping was less than half as effective at detecting *S. depressus* compared to night wading ($Pr = 0.284$, 0.130 - 0.513, 95% CL); and day wading was least likely to detect turtles ($Pr = 0.047$, 0.007 - 0.272, 95% CL) according to the model (Table 6). For day wading and night wading surveys, untransformed 95%

Confidence Limits (CL) estimates did not overlap zero, while trapping survey CL marginally overlapped zero (Table 6). Night wading surveys successfully detected turtles at all ten sites where turtles were found during surveys, including 67% of survey detections overall.

Because day wading and trapping surveys failed to identify any additional occupied sites beyond those identified by night wading surveys and to simplify our occupancy models, we removed day wading and trapping surveys from our occupancy analyses. We removed wood substrate from our analyses because of low occurrence, < 5 %. Correlation analyses revealed some collinearity ($VIF > 4$) between site covariates sand and bedrock + detached rock (Table 4). Therefore, we removed the bedrock + detached rock covariate from our analyses. Between sonar and zigzag sampling methods, bedrock variables are correlated (Table 4). However, they are still included in modeling as substrate variables between sonar and zigzag sampling methods are not modeled together. Thus, limiting model subsets to two site covariates yields 30 models for a total model set of 32 models when global models for sonar sampling and zigzag sampling are included.

Our occupancy analyses identified three top models ($\Delta AIC_c \leq 2.0$, Table 7): $\Psi(\text{Width} + \text{ZBed}), p(\cdot)$; $\Psi(\text{Width} + \text{Corbic}), p(\cdot)$; and $\Psi(\text{Width} + \text{SoBed}), p(\cdot)$. All three models had similar likelihoods of support with $AIC_c\text{wts}$ of 0.31 to 0.33 (Table 7). However, *Corbicula* appears to be an uninformative parameter (Arnold, 2010). When *Corbicula* is modeled as a lone parameter, it has a worse fit than the null model and the untransformed estimates of coefficients for *Corbicula* vary widely across models, from having a positive effect on occupancy to having a negative effect on occupancy. This is not the case for the other parameters in the top models: stream width, bedrock by zigzag, and bedrock by sonar, which have consistent positive estimates of

coefficients across models and perform relatively well in models by themselves (Table 8). Thus, we disregard the model $\Psi(\text{Width} + \text{Corbic}), p(\cdot)$.

When considering parameter weights, due to the remaining two top models containing the same substrate of bedrock measured by sonar in one and by zigzag surveys in the other, the models should be considered as if in separate subsets as they are essentially the same model. Taking this into account, stream width, bedrock by zigzag survey, and bedrock by sonar had strong parameter weights, $w_p > 0.90$. However, untransformed CL estimates for each of the three parameters overlap zero in the top models, and, therefore, were not statistically significant (Table 8).

Third-Order Habitat Selection

We tracked 33 *S. depressus* using radio telemetry from June 2013 to March 2015, during which we recorded 921 locations. Habitat transects covered 220 m, or 23 points, on Sipsey Fork at Hwy 33; 270 m, or 28 points, on Sipsey Fork at FSR 1000; and 430 m, or 44 points, on Brushy Creek at Hickory Grove Rd. After culling telemetry locations, there remained 429 telemetry location points with habitat patch use data, each paired with one unused habitat patch randomly selected within the four closest 10 m patches on either side of the telemetry point. Log cover, wood substrate, and debris substrate variables were removed because each represented < 0.05 of habitat samples. There was no strong collinearity, $VIF > 4$, detected between the remaining variables (Table 9). The variables included in the stepwise model building process were stream width, average depth, snails, *Corbicula*, bedrock substrate, rock substrate, sand substrate, crevice cover, rock cover, and debris cover.

The final model included proportions of snails, crevice cover, debris cover, rock substrate, and average stream depth (Table 12). For every 0.1 increase in the proportion of sample plots with snails present, 10 m stream patches were 1.170 (1.042 – 1.314, 95% C.L.) times more likely to be selected (Table 12, $p = 0.008$). For every 0.1 increase in the proportion of sample plots with crevice cover, 10 m stream patches were 1.240 (1.090 – 1.410, 95% C.L.) times more likely to be selected (Table 10, $p = 0.001$). For every 0.1 increase in the proportion of sample plots with debris cover, 10 m stream patches were 1.150 (1.025 – 1.290, 95% C.L.) times more likely to be selected (Table 10, $p = 0.017$). For every 0.1 increase in the proportion of sample plots with rock substrate, 10 m stream patches were 1.187 (1.058 – 1.331, 95% C.L.) times more likely to be selected (Table 10, $p = 0.0034$). For every 10 cm increase in average stream depth, 10 m stream patches were 1.121 (0.995 – 1.268, 95% C.L.) times more likely to be selected, although this relationship is not statistically significant (Table 10, $p = 0.060$).

Fourth-Order Habitat Selection

After culling deceased, sick, land, and murky telemetry points in which habitat data were unable to be recorded or were considered biased, 526 telemetry locations were included in our fourth-order selection analysis, totaling 2104 habitat used/unused points. Of those telemetry locations, 45 were when a turtle was exposed, and 481 were when a turtle was concealed by cover. None of the models involving exposed turtle locations were better than the null model ($\Delta AIC_c < 2.0$). For concealed turtle locations, the substrate model was better than the null model ($\Delta AIC_c = 20.3$).

Sand/silt substrate was least likely to be used by concealed *S. depressus*, significantly less likely to be used than debris, bedrock, detached rock, and log substrates (Table 11, Table 12).

Log substrate was most likely to be used, 5.09 (2.57 – 10.08, 95% CL) times more likely to be used than sand/silt (Table 11, $p = 3.02e^{-6}$), and significantly more likely than bedrock, detached rock, and debris substrates (Table 12). Bedrock was 2.51 (1.53 – 4.10, 95% CL) times more likely to be used than sand/silt (Table 11, $p = 0.0002$). Detached rock was 2.30 (1.40 – 3.78, 95% CL) times more likely to be used than sand/silt (Table 11, $p = 0.001$). Debris was 1.98 (1.05 – 3.74, 95% CL) times more likely to be used than sand/silt (Table 11, $p = 0.034$). The likelihood estimates of use for bedrock, detached rock, and debris substrates were not significantly different from each other (Table 11, Table 12).

DISCUSSION

Our study evaluates habitat selection by *S. depressus* at three scales. At the population-scale (second-order) of selection (250 m stream lengths) our best models included bedrock proportion and stream width as variables, selecting for more bedrock and larger streams as we predicted. However, the effects of the variables were not significant, and snails didn't make any top models. At the patch-scale (third-order) of selection, the top model supported turtles selecting for more snails, crevice cover, debris cover, rock substrate, and greater stream depth. At the microhabitat-scale (fourth-order) of selection, concealed turtles selected for log, bedrock/crevice, rock, and debris substrates, but we found no evidence for the selection of prey or substrate habitat by exposed turtles. Our hypotheses that *S. depressus* select for bedrock and rock substrates as well as crevice and rock cover are largely supported. Our hypothesis for prey selection was only supported for selection of snails at the patch-scale. We also found partial support for our hypothesis that stream width and depth positively influence selection as width

was in our top models for population-scale and depth was in our top model for patch-scale, but their effects were not significant.

These results support previous findings that populations of *S. depressus* are reliant on mid to large-sized streams with abundant snails, bedrock, and crevice cover (Mount, 1981; Dodd, 1990; Bailey and Guyer, 1998). Our data lend evidence to the preeminent importance of bedrock habitat to *S. depressus* with support for the selection of bedrock occurring across levels of habitat selection. Furthermore, these data describe resource selection at various levels, providing greater resolution to our understanding of the habitat required by *S. depressus*. Our models allow us to assess other streams for suitable habitat in which to focus survey efforts or determine candidate areas for possible reintroductions. This may prove vitally important as *S. depressus* have experienced severe declines and are already extirpated from most of their range (Dodd, 1990; Scott and Rissler, 2015). Thus, future conservation efforts will likely entail locating relict populations outside BNF and determining the best areas for restoration and future reintroduction or augmentation programs.

Worryingly, our study indicates that even in the relatively pristine and protected Bankhead National Forest, the range of *S. depressus* appears to be contracting. Historic surveys located populations at smaller, upstream sites that we were unable to locate turtles such as Capsey Creek and the upper reaches of Sipsey Fork (Ernst et al., 1989; Bailey and Guyer, 1998). This range contraction may have been caused by the loss of bedrock habitat due to bank erosion from invasive wild hogs, past forestry practices, and/or increased hiking/camping impacts. For example, Ernst et al. (1989) noted the presence of deep pools and rock crevices in 1983 near our most upstream site on Sipsey Fork. Presently the area is largely filled in with sand and little bedrock remains exposed.

This study has important implications for conservation of *S. depressus*. The new USFWS guidelines (USFWS, Permit No. TE32397A-2) for trapping requiring trap placement that allows access to air. Although this is safer for turtles, it likely results in lower trap success as compared to historical trapping methods. This change has major implications as our study indicates that trapping by following the new guidelines in an area with 20 traps only produces a one in four chance of detection in a single night. To satisfy due diligence for projects impacting streams, this means that multiple nights of trapping are required to have a reasonable level of confidence that turtles are not present before the project begins. Our study offers a more reliable alternative to trapping. Night-wading surveys are over twice as effective at detecting turtles when compared to trapping with a two in three chance of detection. We recommend that future surveys for *S. depressus* incorporate night-wading surveys in some fashion if the goal is to effectively locate individuals. A minimum of four night-wading surveys is needed to be reasonably confident ($Pr = 0.99, 0.88 - 1.00, 95\% \text{ CL}$) that *S. depressus* are not present.

Second-order habitat selection analyses with substrate data from side scan sonar mapping presented the same conclusions as analyses with transect substrate data. In addition, substrate proportions between sonar mapping and transect surveys were correlated across 250 m stream reaches (Table 4). These results demonstrate the efficacy of replacing time-consuming point-transect surveys with side scan sonar mapping for analyses involving stream habitat.

Our study has established models for habitat selection, identified night wading surveys as a better alternative to trapping with the new USFWS guidelines, and determined the current extent of *S. depressus* range in BNF which appears to have contracted. This information will increase the efficacy of future surveys and advise management efforts in BNF and elsewhere. Using our models and side scan sonar mapping, we can estimate likelihood of occupancy for

sites outside this study. This can aid future conservation efforts by quickly identifying suitable areas for reintroduction projects and narrowing down locations where *S. depressus* may still occur to focus survey efforts. As *S. depressus* continues to decline throughout its range, these new tools and information will be important for efforts to recover the species.

Table 1. Substrate categories, their descriptions, and coinciding turtle refuge cover classification utilized in habitat selection analyses.

Substrate	Cover	Description
Bedrock	Crevice	continuous rock that is not obviously detached from the base bedrock or detached rock that is greater than 2 m across at its widest
Detached Rock	Rock	a rock that is detached from the bedrock and is less than 2 m and greater than 20 cm across at its widest
Sand/Silt	Sand/Mud	silt, sand, gravel, or rock that is less than 20 cm at its greatest width
Roots/Debris	Roots/debris	small to medium size organic matter such as algae mats, leaves, sticks, or roots
Wood	Log	logs with diameters greater than 10 cm

Table 2. Proposed site covariates for modeling occupancy and the method used to sample the covariates.

Site Covariate Name	Description	Sampling Method (Sonar/Zigzag Plots)
Depth	average midchannel depth (m) of stream reach	Sonar
Width	average width (m) of stream reach	Sonar
Snail	proportion of samples with snails present	Zigzag Plots
Corbic	proportion of samples with <i>Corbicula</i> present	Zigzag Plots
Bed	proportion of bedrock substrate in samples	Sonar/Zigzag Plots
BedRock	proportion of samples with bedrock or detached rock substrate	Sonar/Zigzag Plots
Log	proportion of log substrate in samples	Sonar/Zigzag Plots
Sand	proportion of samples with sand or silt substrate	Sonar/Zigzag Plots

Table 3. Descriptions and measurement values of independent variables proposed for conditional logistic regression models of third-order (patch) and fourth-order (microhabitat) resource selection. Depth and width were not included in fourth-order analyses. In addition, proposed variables for third-order habitat selection also include cover from transect data as proportions for debris cover, log cover, crevice cover, rock cover, crevice or rock cover, and sand/silt cover.

Variables	Description	Third-Order (Transect Value)	Fourth-Order (Point Value)
Depth	average stream depth across transect points	centimeters	---
Width	stream width (m) at transect, determined from total sample points in the transect	meters	---
Snail	snail presence	proportion	present/absent
Corbic	<i>Corbicula</i> presence	proportion	present/absent
Debris	organic debris such as leaves or roots	proportion	present/absent
Wood	logs	proportion	present/absent
Bed	bedrock substrate	proportion	present/absent
Rock	detached rock substrate	proportion	present/absent
Sand	sand or silt substrate	proportion	present/absent

Table 4. Variance inflation factors between considered occupancy covariates. Variables beginning with “Z” are substrate variables calculated from stream habitat data taken every 5 m on zigzag transects. Variables beginning with “So” are stream substrate variables calculated from side scan sonar habitat mapping.

	Width	Depth	Snail	Corbic	ZBed	ZBedRock	ZWood	ZSand	SoBed	SoBedRock	SoWood	SoSand
Width	Inf	1.93	1.07	1.25	1.01	1.01	1.01	1.01	1.05	1.01	1.00	1.01
Depth	1.93	Inf	1.01	1.05	1.00	1.05	1.10	1.03	1.00	1.01	1.03	1.01
Snail	1.07	1.01	Inf	1.08	1.02	1.01	1.00	1.01	1.04	1.06	1.26	1.04
Corbic	1.25	1.05	1.08	Inf	1.52	1.87	1.04	2.02	1.11	1.19	1.00	1.21
ZBed	1.01	1.00	1.02	1.52	Inf	1.96	1.32	1.90	5.51	2.67	1.02	2.76
ZBedRock	1.01	1.05	1.01	1.87	1.96	Inf	1.49	67.52	1.38	3.36	1.03	3.67
ZWood	1.01	1.10	1.00	1.04	1.32	1.49	Inf	1.29	1.28	1.54	1.06	1.54
ZSand	1.01	1.03	1.01	2.02	1.90	67.52	1.29	Inf	1.34	2.99	1.03	3.24
SoBed	1.05	1.00	1.04	1.11	5.51	1.38	1.28	1.34	Inf	2.24	1.05	2.22
SoBedRock	1.01	1.01	1.06	1.19	2.67	3.36	1.54	2.99	2.24	Inf	1.18	165.44
SoWood	1.00	1.03	1.26	1.00	1.02	1.03	1.06	1.03	1.05	1.18	Inf	1.12
SoSand	1.01	1.01	1.04	1.21	2.76	3.67	1.54	3.24	2.22	165.44	1.12	Inf

Table 5. Models with sampling covariates to explain detection of *Sternotherus depressus* at stream reach sites in Bankhead National Forest. The only top model, $\Delta AIC_c \leq 2.0$, considered survey method alone as a sample covariate. Survey methods consisted of day wading surveys, night wading surveys, and trapping surveys.

Model	Parameters	AIC _c	ΔAIC_c	AIC _c wt
$\Psi(\cdot), p(\text{Method})$	4	98.58	0.00	0.81
$\Psi(\cdot),$ $p(\text{Method}+\text{Temperature})$	5	101.55	2.96	0.19
$\Psi(\cdot), p(\cdot)$	2	113.02	14.44	0.00
$\Psi(\cdot), p(\text{Temperature})$	3	115.65	17.06	0.00

Table 6. Estimates of detection from the top model of sampling covariates, $\Psi(\cdot)$, $p(\text{Method})$, explaining detection patterns of *Sternotherus depressus*. Untransformed values are in parentheses. Day wading survey method represents the intercept for detection in this model.

Survey Method	Estimate	Std Error	95% CL	
			0.007 (-	0.272 (-
Day Wading	0.047 (-3.00)	0.046 (1.03)	5.01)	0.99)
Night Wading	0.663 (3.68)	0.117 (1.13)	0.413 (1.45)	0.846 (5.90)
			0.130 (-	
Trapping	0.284 (2.08)	0.101 (1.13)	0.14)	0.513 (4.30)

Table 7. Top models, $\Delta AIC_c \leq 2.0$, explaining occupancy of *Sternotherus depressus* at 24 stream reach sites in Bankhead National Forest. *Corbicula* was determined to be an uninformative parameter. Therefore, the $\Psi(\text{Width}+\text{Corbic})$, $p(\cdot)$ was removed from consideration as a top model. ZBed is bedrock substrate proportions obtained from zig-zag habitat transects. SoBed is bedrock substrate proportions obtained from side scan sonar habitat mapping.

Model	AIC _c	ΔAIC_c	AIC _c wt
$\Psi(\text{Width}+\text{ZBed})$, $p(\cdot)$	34.55	0.00	0.33
$\Psi(\text{Width}+\text{Corbic})$, $p(\cdot)$	34.56	0.01	0.33
$\Psi(\text{Width}+\text{SoBed})$, $p(\cdot)$	34.64	0.09	0.31

Table 8. Model results for occupancy analyses of *Sternotherus depressus* at 24 stream reach sites in Bankhead National Forest. Untransformed estimates of coefficients (β) and standard errors (SE) are included for each covariate. Variables beginning with “So” are substrate data from sonar mapping. Variables beginning with “Z” are substrate data from zig-zag transects.

Model	Width		Depth		Corbic		Snail	
	β	SE	β	SE	β	SE	β	SE
$\Psi(\text{Width}+\text{ZBed}), p(\cdot)$	28.58	71.29						
$\Psi(\text{Width}+\text{Corbic}), p(\cdot)$	126.96	226.10			-54.43	97.81		
$\Psi(\text{Width}+\text{SoBed}), p(\cdot)$	359.84	434.53						
$\Psi(\text{Width}+\text{ZSand}), p(\cdot)$	16.21	11.19						
$\Psi(\text{Width}+\text{SoSand}), p(\cdot)$	18.31	15.28						
$\Psi(\text{Corbic}+\text{ZBed}), p(\cdot)$					27.31	65.35		
$\Psi(\text{Depth}+\text{ZBed}), p(\cdot)$			20.18	35.34				
$\Psi(\text{Depth}+\text{SoBed}), p(\cdot)$			49.23	74.12				
$\Psi(\text{Width}), p(\cdot)$	5.28	3.40						
$\Psi(\text{Width}+\text{Snail}), p(\cdot)$	29.08	215.37					16.84	146.42
$\Psi(\text{ZBed}+\text{ZSand}), p(\cdot)$								
$\Psi(\text{SoBed}+\text{SoSand}), p(\cdot)$								
Sonar Global	29.42	193.31	3.03	85.08	-11.11	94.30	1.69	242.75
Zigzag Global	32.15	242.35	1.99	221.74	-5.65	428.54	-0.51	267.43
$\Psi(\text{ZBed}), p(\cdot)$								
$\Psi(\text{Depth}+\text{Width}), p(\cdot)$	18.54	60.43	26.72	70.93				
$\Psi(\text{SoBed}), p(\cdot)$								
$\Psi(\text{Depth}+\text{SoSand}), p(\cdot)$			1.81	0.99				
$\Psi(\text{Zbed}+\text{Snail}), p(\cdot)$							1.89	2.78
$\Psi(\text{Depth}), p(\cdot)$			6.08	5.38				
$\Psi(\text{Depth}+\text{ZSand}), p(\cdot)$			2.27	1.79				
$\Psi(\text{Corbic}+\text{SoBed}), p(\cdot)$					-0.13	1.16		
$\Psi(\text{Depth}+\text{Corbic}), p(\cdot)$			3.09	1.74	-1.01	0.98		
$\Psi(\text{Depth}+\text{Snail}), p(\cdot)$			3.21	2.52			1.18	1.55
$\Psi(\text{SoSand}), p(\cdot)$								
$\Psi(\text{ZSand}), p(\cdot)$								
$\Psi(\text{Corbic}+\text{ZSand}), p(\cdot)$					12.37	42.18		
Null								
$\Psi(\text{Corbic}+\text{SoSand}), p(\cdot)$					0.13	0.69		
$\Psi(\text{Snail}), p(\cdot)$							0.45	0.62
$\Psi(\text{Corbic}), p(\cdot)$					-0.36	0.56		
$\Psi(\text{Corbic}+\text{Snail}), p(\cdot)$					-0.52	0.61	0.61	0.69

Table 8. Continued.

Model	SoBed		SoSand		Zbed		Zsand		k	AIC _c wt
	β	SE	β	SE	β	SE	β	SE		
$\Psi(\text{Width}+\text{ZBed}), p(\cdot)$					16.65	47.35			4	0.329
$\Psi(\text{Width}+\text{Corbic}), p(\cdot)$									4	0.327
$\Psi(\text{Width}+\text{SoBed}), p(\cdot)$	137.44	165.04							4	0.314
$\Psi(\text{Width}+\text{ZSand}), p(\cdot)$							-5.52	3.60	4	0.016
$\Psi(\text{Width}+\text{SoSand}), p(\cdot)$			-4.13	2.88					4	0.008
$\Psi(\text{Corbic}+\text{ZBed}), p(\cdot)$					89.39	183.66			4	0.001
$\Psi(\text{Depth}+\text{ZBed}), p(\cdot)$					63.05	107.17			4	0.001
$\Psi(\text{Depth}+\text{SoBed}), p(\cdot)$	230.72	344.71							4	0.001
$\Psi(\text{Width}), p(\cdot)$									3	0.001
$\Psi(\text{Width}+\text{Snail}), p(\cdot)$									4	0.000
$\Psi(\text{ZBed}+\text{ZSand}), p(\cdot)$					157.61	217.47	80.90	111.24	4	0.000
$\Psi(\text{SoBed}+\text{SoSand}), p(\cdot)$	256.43	259.05	114.15	114.74					4	0.000
Sonar Global	13.76	729.19	2.67	749.06					8	0.000
Zigzag Global					16.48	221.49	2.76	587.66	8	0.000
$\Psi(\text{ZBed}), p(\cdot)$					20.05	39.13			3	0.000
$\Psi(\text{Depth}+\text{Width}), p(\cdot)$									4	0.000
$\Psi(\text{SoBed}), p(\cdot)$	3.96	2.56							3	0.000
$\Psi(\text{Depth}+\text{SoSand}), p(\cdot)$			-1.43	0.77					4	0.000
$\Psi(\text{Zbed}+\text{Snail}), p(\cdot)$					5.89	5.65			4	0.000
$\Psi(\text{Depth}), p(\cdot)$									3	0.000
$\Psi(\text{Depth}+\text{ZSand}), p(\cdot)$							-1.20	0.75	4	0.000
$\Psi(\text{Corbic}+\text{SoBed}), p(\cdot)$	3.91	2.56							4	0.000
$\Psi(\text{Depth}+\text{Corbic}), p(\cdot)$									4	0.000
$\Psi(\text{Depth}+\text{Snail}), p(\cdot)$									4	0.000
$\Psi(\text{SoSand}), p(\cdot)$			-1.41	1.53					3	0.000
$\Psi(\text{ZSand}), p(\cdot)$							-3.21	2.89	3	0.000
$\Psi(\text{Corbic}+\text{ZSand}), p(\cdot)$							-		4	0.000
Null									2	0.000
$\Psi(\text{Corbic}+\text{SoSand}), p(\cdot)$			-1.44	1.47					4	0.000
$\Psi(\text{Snail}), p(\cdot)$									3	0.000
$\Psi(\text{Corbic}), p(\cdot)$									3	0.000
$\Psi(\text{Corbic}+\text{Snail}), p(\cdot)$									4	0.000

Table 9. Variance inflation factors (VIF) between independent variables being considered in third-order habitat selection. Variables included stream width and average depth in addition to proportions of sample plots with snails, *Corbicula*, bedrock substrate, detached rock substrate, sand/silt substrate, crevice cover, rock cover, and debris cover. None of the parameters were strongly collinear, $VIF > 4$.

	Width	Depth	Snail	Corbic	BedSub	RockSub	SandSub	CrevCov	RockCov	DebrisCov
Width	Inf	1.02	1.00	1.13	1.12	1.58	1.08	1.00	1.55	1.01
Depth	1.02	Inf	1.68	1.03	1.00	1.02	1.01	1.02	1.04	1.02
Snail	1.00	1.68	Inf	1.33	1.25	1.03	1.09	1.14	1.00	1.00
Corbic	1.13	1.03	1.33	Inf	1.09	1.13	1.01	1.00	1.05	1.00
BedSub	1.12	1.00	1.25	1.09	Inf	1.86	1.30	1.41	1.16	1.18
RockSub	1.58	1.02	1.03	1.13	1.86	Inf	1.08	1.02	2.36	1.07
SandSub	1.08	1.01	1.09	1.01	1.30	1.08	Inf	1.39	1.17	1.25
CrevCov	1.00	1.02	1.14	1.00	1.41	1.02	1.39	Inf	1.00	1.11
RockCov	1.55	1.04	1.00	1.05	1.16	2.36	1.17	1.00	Inf	1.04
DebrisCov	1.01	1.02	1.00	1.00	1.18	1.07	1.25	1.11	1.04	Inf

Table 10. Likelihood estimates, standard errors, and 95% confidence intervals (CI) of parameters included in the selected model for third-order habitat selection analyses for 10 m stream patch habitat by *Sternotherus depressus*. This model was built with full stepwise procedures using AIC_c and includes proportion of snail presence, crevice cover, debris cover, detached rock substrate, and average stream depth as independent variables. Strength of significance is denoted by asterisks.

	Estimate	Std. Error	Lower 95% CI	Upper 95% CI	$Pr(> z)$	
Snail	4.803	0.592	1.505	15.325	0.0080	**
CrevCov	8.599	0.657	2.374	31.152	0.0011	**
DebrisCov	4.044	0.586	1.284	12.742	0.0170	*
RockSub	5.554	0.586	1.762	17.513	0.0034	**
Depth	1.011	0.006	1.000	1.024	0.0600	

Table 11. Likelihood estimates, standard errors, and 95% confidence intervals (CL) of microhabitat use by concealed *Sternotherus depressus* for substrates categories relative to sand/silt substrate. Strength of significance is denoted by asterisks.

	Estimate	Std. Error	Lower 95% CL	Upper 95% CL	$Pr(> z)$	
Bedrock	2.511	0.250	1.537	4.101	0.0002	***
Rock	2.301	0.254	1.399	3.784	0.0010	**
Debris	1.984	0.324	1.052	3.742	0.0343	*
Log	5.091	0.349	2.571	10.079	3.02E-06	***

Table 12. Likelihood effect sizes and statistical significance between substrate categories for microhabitat selection of *Sternotherus depressus* when conceal under refugia. The reference substrate is represented by columns and the substrate estimate by rows. The likelihoods of use for substrates that had a significantly different ($p < 0.05$) likelihood of use compared to the reference substrate are bold and underlined.

	Reference Substrate				
	Sand	Bedrock	Rock	Debris	Log
Sand	---	<u>0.40</u>	<u>0.43</u>	<u>0.50</u>	<u>0.20</u>
Bedrock	<u>2.51</u>	---	1.09	1.27	<u>0.49</u>
Rock	<u>2.30</u>	0.92	---	1.16	<u>0.45</u>
Debris	<u>1.98</u>	0.79	0.86	---	<u>0.39</u>
Log	<u>5.09</u>	<u>2.03</u>	<u>2.21</u>	<u>2.57</u>	---

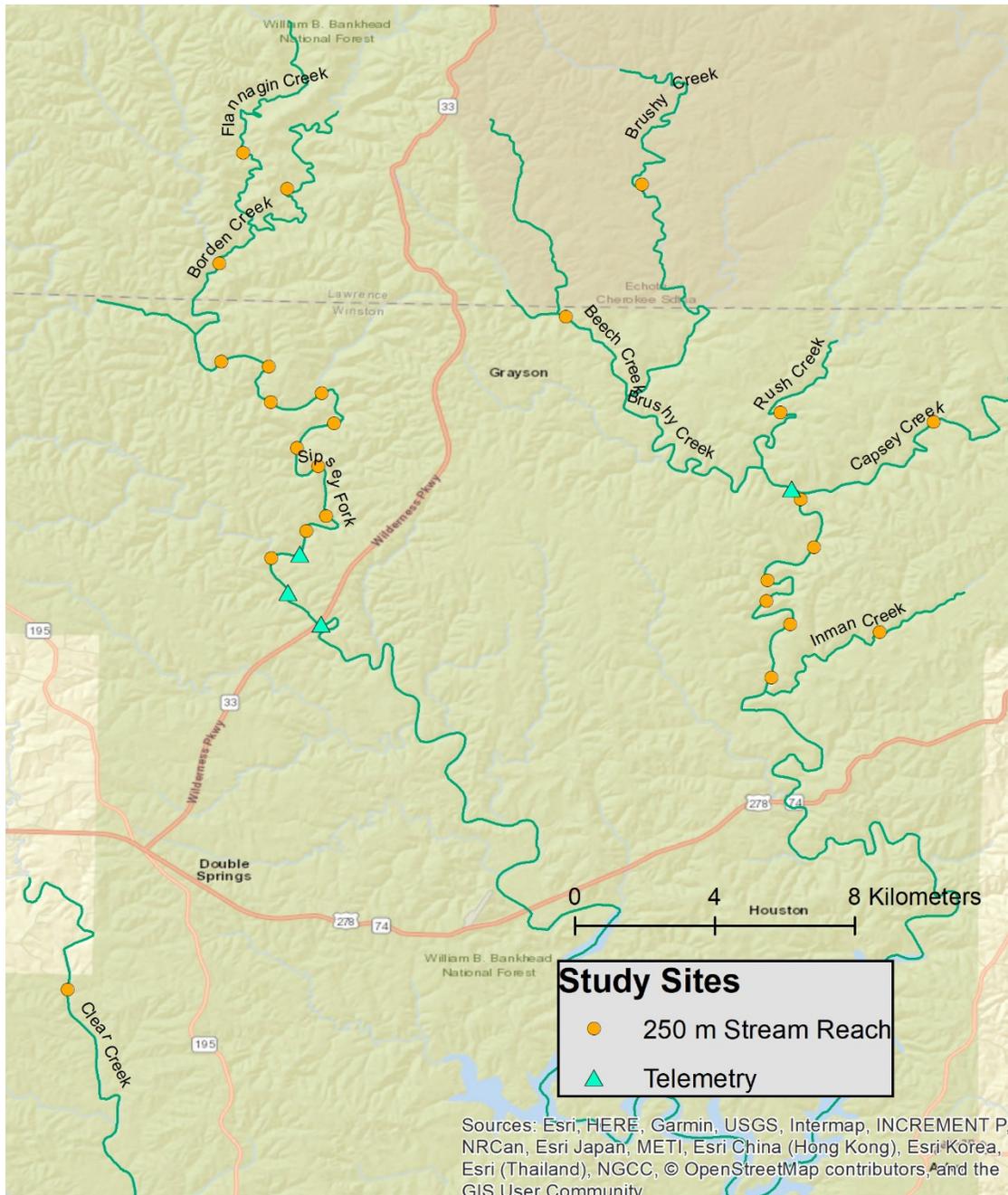


Figure 1. Study sites for four radio telemetry and 25 stream reach (250 m) surveys for *Sternotherus depressus* in Bankhead National Forest, Alabama. Thirty-three turtles were included in our telemetry study. Stream reach surveys at each of the 25 sites included two day-wading, two night-wading, and two 20 trap-night trapping surveys, each covering 250 m of stream length.



Figure 2. Adult *Sternotherus depressus* with transmitters for radio telemetry attached using cement putty. Transmitters were positioned on either side of the back of the carapace so not to increase the height profile of the carapace or interfere with breeding.



Figure 3. A 31x31 cm PVC square used as a sampling quadrat for collecting habitat data utilized to model habitat selection on multiple scales.

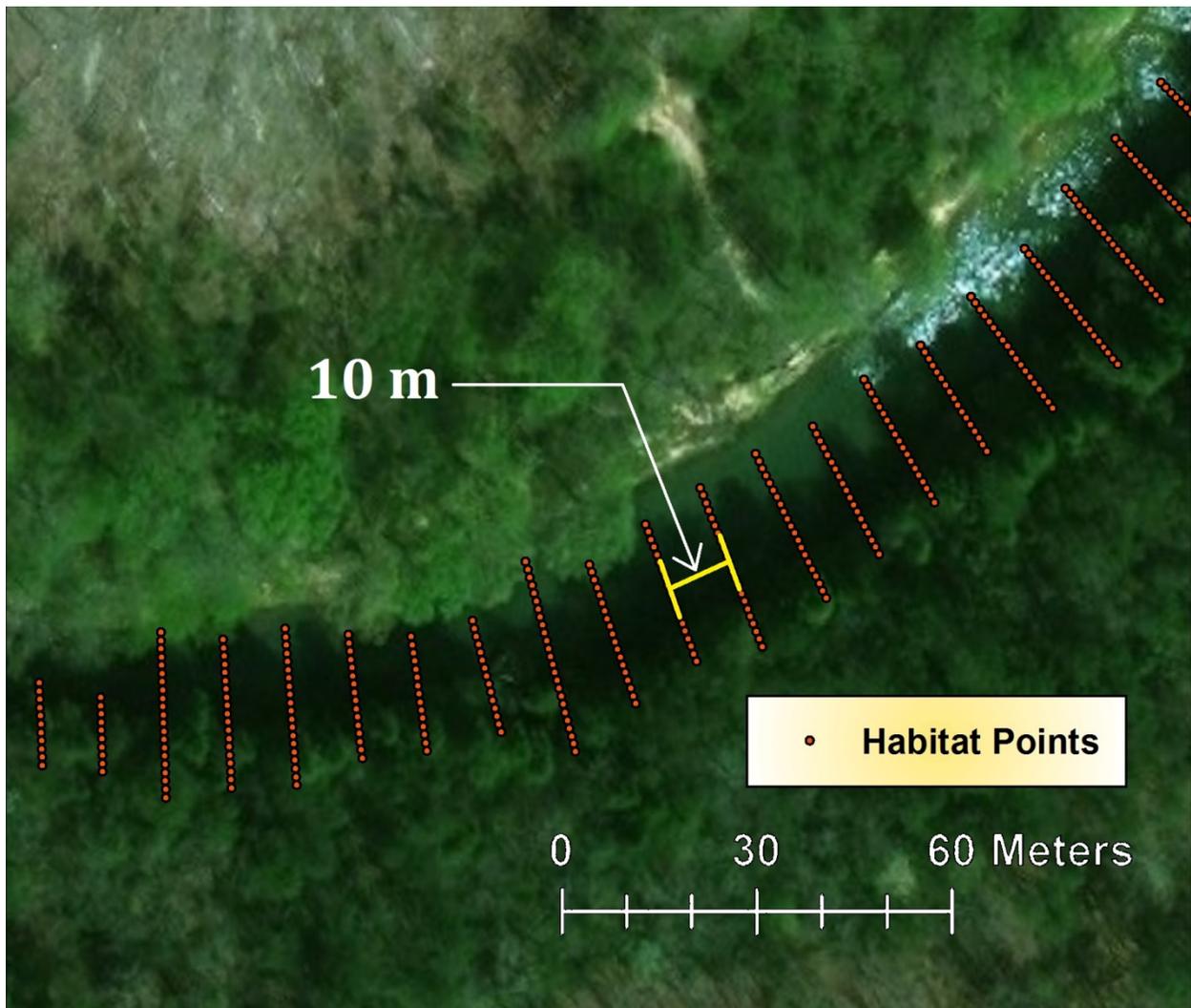


Figure 4. Available habitat data at telemetry sites were recorded every 1 m, perpendicular to the stream bank, on transects that were spaced 10 m apart at radio telemetry sites. Depth, substrate type, available cover type, snail presence, and *Corbicula* presence data were collected at each point.

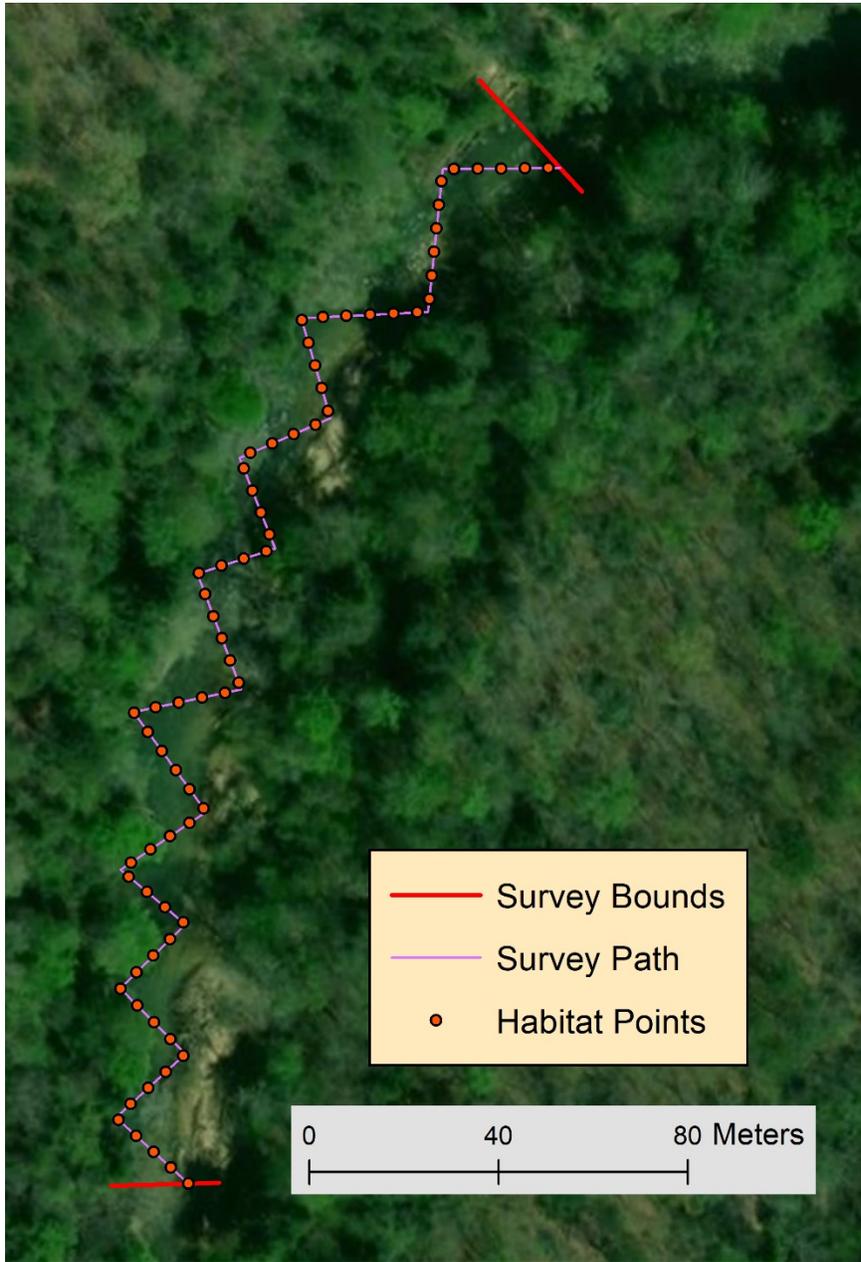


Figure 5. Example of habitat sampling methods for 250 m stream reaches. Habitat points were every 5 m on zig-zag transects oriented 45° from the bank using a compass to sight direction. Substrate type, snail presence, and *Corbicula* presence data were collected at each point.

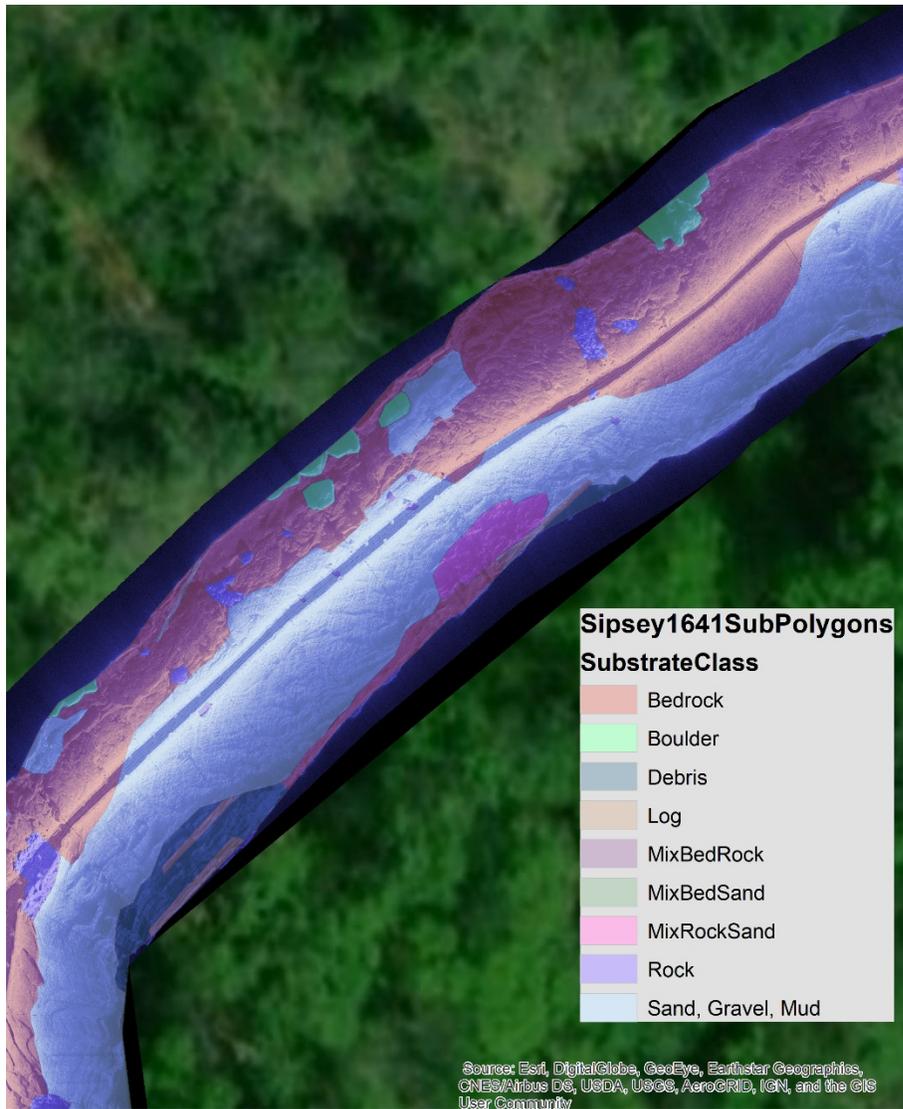


Figure 6. Example of substrate polygons, delineated from side scan sonar imagery, used in population-scale (second-order) modeling of habitat selection.

References

- Alabama Department of Conservation and Natural Resources (ADCNR). Federal and State Protected Collection Permit. Permit No. 2017118163068680.
- Anderson, D. J. (1982). The home range: a new nonparametric estimation technique. *Ecology* 63, 103-112.
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74, 1175-1178.
- Ashby, K. R. (1972). Patterns of daily activity in mammals. *Mammal Review* 1, 171-185.
- Bailey, K. A., & Guyer, C. (1998). Demography and population status of the flattened musk turtle, *Sternotherus depressus*, in the Black Warrior River Basin of Alabama. *Chelonian Conservation and Biology* 3, 77-83.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1-48.
- Beaupre, S. J., Jacobson, E. R., Lillywhite, H. B., & Zamudio, K. (2004). Guidelines for use of live amphibians and reptiles in field and laboratory research, Second Edition. Revised by the Herpetological Animal Care and Use Committee (HACC) of the American Society of Ichthyologists and Herpetologists.
- Brown, G. P., & Shine, R. (2002). Influence of weather conditions on activity of tropical snakes. *Austral Ecology* 27, 596-605.
- Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York.

- Close, D. K. (1982). The reproductive cycle of *Sternotherus minor depressus*. M.S. thesis. University of Alabama-Birmingham, Birmingham, Alabama.
- Communications Specialists. Model R-1000. 148 – 154 MHz. Communications Specialists Inc., Orange, California.
- Dodd, C. K. (1990). Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle, *Sternotherus depressus*. *Biological Conservation* 54, 33–45.
- Dodd, C. K. (2008). *Sternotherus depressus* Tinkle and Webb 1955 - flattened musk turtle. *Chelonian Research Monographs* 5, 013.1-013.7.
- Dodd, C. K., Enge, K. M., & Stuart, J. N. (1988). Aspects of the biology of the flattened musk turtle, *Sternotherus depressus*, in northern Alabama. *Bulletin of the Florida State Museum Biological Sciences* 34, 1–64.
- Doody, J. S., Young, J. E., & Georges, A. (2002). Sex differences in activity and movements in the pig-nosed turtle, *Carettochelys insculpta*, in the wet-dry tropics of Australia. *Copeia* 2002, 93–103.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, Robert J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81, 163.
- Ernst, C. H. (1986). Ecology of the turtle, *Sternotherus odoratus*, in Southeastern Pennsylvania. *Journal of Herpetology* 20, 341–352.
- Ernst, C. H., Cox, W. A., & Marion, K. R. (1989). The distribution and status of the flattened musk turtle, *Sternotherus depressus* (Testudines: Kinosternidae). *Tulane Studies in Zoology and Botany* 27, 1–20.

- ESRI. (2015). ArcGIS Desktop: Release 10.4.1. Environmental Systems Research Institute, Redlands, California.
- Fiske, I. and R. B. Chandler. (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1–23.
- Fonnesbeck, C. J., & Kenneth Dodd, C. (2003). Estimation of flattened musk turtle (*Sternotherus depressus*) survival, recapture, and recovery rate during and after a disease outbreak. *Journal of Herpetology* 37, 602–607.
- Fox, J. and Weisberg, S. (2011). An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. <<http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>>
- Girard, I., Ouellet, J.-P. P., Courtois, R., Dussault, C., & Breton, L. (2002). Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management* 66, 1290–1300.
- Guthrie, R. W. (1986). Derivation of a habitat quality predicting function for the flattened musk turtle. Report to U. S. Fish and Wildlife Service, Jackson, Mississippi.
- Haxton, T. & Berrill, M. (2001). Seasonal activity of spotted turtles (*Clemmys guttata*) at the northern limit of their range. *Journal of Herpetology* 35, 606–614.
- Holohil Systems. Model SB-2. 5 gram. Holohil Systems Ltd., Carp Ontario, Canada.
- Huey, R. B., & Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology* 62, 991–999.
- Huminbird. Model HELIX 9 CHIRP MEGA SI GPS G2N. Johnson Outdoors Inc., Racine, Wisconsin.
- Hyndman, R. J. (2018). hdrdce: Highest density regions and conditional density estimation. R package version 3.3, <<http://pkg.robjhyndman.com/hdrdce>>.

Institutional Animal Care and Use Committee (IACUC). Auburn University, Auburn, Alabama.
Protocol No. 2016-2833.

Jackson, J. F. (1988). Crevice occupation by musk turtles: taxonomic distribution and crevice attributes. *Animal Behaviour* 36, 793-801.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.

Jones, M. C., Marron, J. S., & Sheather, S. J. (1996). A brief survey of bandwidth selection for density estimation. *Journal of the American Statistical Association* 91, 401-407.

Jones, R. L. (1996). Home range and seasonal movements of the turtle *Graptemys flavimaculata*. *Journal of Herpetology* 30, 376–385.

Kaesler, A. J., & Litts, T. L. (2008). An assessment of deadhead logs and large woody debris using side scan sonar and field surveys in streams of Southwest Georgia. *Fisheries* 33, 589–597.

Kaesler, A. J., & Litts, T. L. (2010). A novel technique for mapping habitat in navigable streams using low-cost side scan sonar. *Fisheries* 35, 163–174.

Kenny, A. J., Cato, I., Desprez, M., Fader, G., Schüttenhelm, R. T. E., & Side, J. (2003). An overview of seabed-mapping technologies in the context of marine habitat classification. *ICES Journal of Marine Science* 60, 411–418.

Leraand Engineering. (2017). Model SonarTRX Pro x64 version 17.1. Leraand Engineering Inc., Honolulu, Hawaii.

Litzgus, J. D., & Mousseau, T. A. (2004). Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. *Copeia* 2004, 804–817.

- Lovich, J. E., & Ennen, J. R. (2013). A quantitative analysis of the state of knowledge of turtles of the United States and Canada. *Amphibia-Reptilia* 34, 11–23.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- Mahmoud, I. Y. (1969). Comparative ecology of the kinosternid turtles of Oklahoma. *The Southwestern Naturalist* 14, 31–66.
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media, Berlin, Germany.
- Marchand, M. N., & Litvaitis, J. A. (2004). Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conservation Biology* 18, 758–767.
- Marzluff, J. M., Millspaugh, J. J., Hurvitz, P., & Handcock, M. S. (2004). Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85, 1411–1427.
- Mazerolle, M. J. (2019). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.2-1.
- Memphis Net & Twine. Model Eel, Crawfish, & Flounder Trap, 1/2 in. sq. mesh, 24 in. by 18 in. by 8 in. Memphis Net & Twine Co. Inc., Memphis, Tennessee.
- Moll, D., & Moll, E. O. (2004). *The ecology, exploitation, and conservation of river turtles*. Oxford University Press, New York, New York.

- Mount, R. H. (1981). The status of the flattened musk turtle, *Sternotherus minor depressus*, Tinkle and Webb. Report. Submitted to the United States Fish and Wildlife Service.
- Murtaugh, P. A. (2009). Performance of several variable-selection methods applied to real ecological data. *Ecology Letters* 12, 1061–1068.
- Oatey. Fix-It™ Stick Epoxy Putty. Oatey Inc., Cleveland, Ohio.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.
- Postel, S. L., Daily, G. C., & Ehrlich, P. R. (1996). Human appropriation of renewable fresh water. *Science* 271, 785–788.
- Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology and Evolution* 22, 583-592.
- Quinn, S. A., Gibbs, J. P., Hall, M. H., & Petokas, P. J. (2013). Multiscale factors influencing distribution of the eastern hellbender salamander (*Cryptobranchus alleganiensis alleganiensis*) in the northern segment of its range. *Journal of Herpetology* 47, 78–84.
- R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.
- R Foundation for Statistical Computing. (2018). Program R version 3.4.4. R Foundation for Statistical Computing.
- Rees, M., Roe, J. H., & Georges, A. (2009). Life in the suburbs: Behavior and survival of a freshwater turtle in response to drought and urbanization. *Biological Conservation* 142, 3172–3181.
- Ricciardi, A., & Rasmussen, J. B. (1999). Extinction rates of North American freshwater fauna. *Conservation Biology* 13, 1220–1222.

- Richter, B. D., Braun, D. P., Mendelson, M. A., & Master, L. L. (1997). Threats to imperiled freshwater fauna. *Conservation Biology* 11, 1081–1093.
- Roe, J. H., & Georges, A. (2008). Maintenance of variable responses for coping with wetland drying in freshwater turtles. *Ecology* 89, 485–494.
- Rose, B. (1982). Lizard home ranges: methodology and functions. *Journal of Herpetology* 16, 253–269.
- Rowe, J. W., & Dalgarn, S. F. (2010). Home range size and daily movements of midland painted turtles (*Chrysemys picta marginata*) in relation to body size, sex, and weather patterns. *Herpetological Conservation and Biology* 5, 461–473.
- Rowe, J. W., Lehr, G. C., McCarthy, P. M., & Converse, P. M. (2009). Activity, movements and activity area size in stinkpot turtles (*Sternotherus odoratus*) in a southwestern Michigan lake. *The American Midland Naturalist* 162, 266–275.
- Rusak, B. (1981) Vertebrate Behavioral Rhythms. In: Aschoff, J. (eds) *Biological Rhythms*. Springer, Boston, Massachusetts.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L. R., Sykes, M. T., Walker, B. H., Walker, M., Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Schnuelle, K. A. (1997). Demography, diet, and prey availability of the flattened musk turtle, *Sternotherus depressus*. M.S. Thesis, Auburn University, Auburn, Alabama.
- Scott, P. A., & Rissler, L. J. (2015). Integrating dynamic occupancy modeling and genetics to infer the status of the imperiled flattened musk turtle. *Biological Conservation* 192, 294–303.

- Sheather, S. J., & Jones, M. C. (1991). A reliable data-based bandwidth selection method for kernel density estimation. *Journal of the Royal Statistical Society: Series B (Methodological)* 53, 683-690.
- Silverman, B. W. (1986). *Density estimation for statistics and data analysis*. Chapman and Hall, London, UK.
- Steen, D. A., Godwin, J. C., McClure, C. J. W., & Barbour, M. (2014). Informing management of endemic habitat specialists: Multiscale habitat selection by the Red Hills salamander. *Journal of Wildlife Management* 78, 463–470.
- Sterrett, S. C., Kaeser, A. J., Katz, R. A., Smith, L. L., Brock, J. C., & Maerz, J. C. (2015). Spatial ecology of female Barbour’s Map Turtles (*Graptemys barbouri*) in Ichawaynochaway Creek, Georgia. *Copeia* 2015, 263–271.
- Sutherland, A. B., Meyer, J. L., & Gardiner, E. P. (2002). Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology* 47, 1791–1805.
- Swingland, I. R., & Greenwood, P. J. (1984). *Ecology of Animal Movement*. Clarendon Press, Oxford, UK
- Therneau, T. (2015). A package for survival analysis in S. version 2.38. <URL: <https://CRAN.R-project.org/package=survival>>.
- United States Fish and Wildlife Service (USFWS). (1987). Determination of threatened status for the Flattened Musk Turtle (*Sternotherus depressus*). *Fed. Regist.* 52, 22418–22430.
- United States Fish and Wildlife Service (USFWS). Permit No. TE32397A-2. Date issued: November 2015.

- United States Geological Survey (USGS). (2017). USGS Water Data for the Nation. Accessed July 2017. <<http://waterdata.usgs.gov/nwis/>>
- van Dijk, P. P., Iverson, J. B., Rhodin, A. G. J., Shaffer, H. B., & Bour, R. (2014). Turtles of the World, 7th Edition: Annotated Checklist of Taxonomy, Synonymy, Distribution with Maps, and Conservation Status. In Turtle Taxonomy Working Group. IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Retrieved from http://www.iucn-tftsg.org/wp-content/uploads/file/Accounts/crm_5_000_checklist_v7_2014.pdf
- van Dijk, P.P. (2011). *Sternotherus depressus*. (errata version published in 2016) The IUCN Red List of Threatened Species 2011: e.T20824A97383753.
<http://dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T20824A9231032.en>. Downloaded on 12 July 2017.
- Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., & Losos, E. (1998). Quantifying threats to imperiled species in the United States. Assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. *BioScience* 48, 607–615.
- Wood, P. J., & Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management* 21, 203–217.
- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164-168.
- WWF. (2016). Living Planet Report 2016. Risk and resilience in a new era. WWF International, Gland, Switzerland.
- ZebraLight. Model ZLH600Fw Mk 2. ZebraLight Inc., Irving, Texas.