

SURVEY PROTOCOLS AND SPATIAL ECOLOGY OF THE WESTERN CHICKEN

TURTLE (*Deirochelys reticularia miaria*)

A Thesis

by

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ABSTRACT

The behaviors, activity season, and spatial ecology of *Deirochelys reticularia miaria* (Western Chicken Turtle) are poorly understood in Texas. Though its distribution within the state is widespread, turtle assemblage studies conducted within its range in Texas have seldom documented presence. Formal protection is lacking for the subspecies, and past research suggests that its remaining habitat within the state is threatened by increasing urbanization. The U.S. Fish and Wildlife Service issued a 90-day finding that listing the subspecies as threatened or endangered may be warranted. I designed two studies to meet two primary objectives: (1) standardize survey protocols and (2) assess the turtles' spatial ecology and examine how its prolonged aestivation period affects model fit when selecting an annual home range estimation method. For the first objective, I reviewed capture techniques from the literature, identified an activity season and period of highest capture success within that season for *D. r. miaria* in Texas, and evaluated the efficacy and biases of capture methods. I compared capture methods consisting of both active (i.e., road surveys, dipnet surveys, seine surveys, night wading surveys) and passive techniques (i.e., two types of unbaited fyke net). Among passive capture techniques, fyke nets were effective in every study that deployed them and had the highest number of captures in the Texas field study. Dipnet surveys had the highest capture rate among active survey methods. Body size biases were apparent among all methods with enough captures to compare. For the second objective, I analyzed telemetry data to understand annual home range, core area, and movements, or

collectively the spatial ecology of the species at two Texas sites. I evaluated the applicability of several home range estimators. The 95% kernel density estimators provided the most consistent estimates of annual home range. Traditional 50% core activity area estimators had questionable utility because they either excluded aquatic areas that were frequently used or included aestivation sites. Managers should consider how extensive aestivation affects home range estimates, how periods of drought affect movement, and how the longevity of the species, the potential to make long migrations, and landscape characteristics could affect spatial resource requirements.

DEDICATION

This thesis is dedicated to S. Joseph Polka. After 23 years of service in the United States Air Force, Joe Polka spent seven years as a docent at the Kansas City Zoo then logged over 14,000 volunteer hours for the Missouri Department of Conservation. He is still the only person to achieve that milestone. He has contributed to countless educational programs introducing his lifelong fascination with animal behavior to many people, often championing species that are not traditionally charismatic. He was the 2012 Missouri Volunteer Interpreter of the year. His name has become synonymous with the Burr Oak Woods Conservation Area, and the waves of wildlife books spilling from the doors and windows of his home eventually end up in their nature center. He taught me that it is perfectly fine to be a grown adult with books stacked to the ceiling of your house.

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NOMENCLATURE

ABWMA	Alazan Bayou Wildlife Management Area
AKDE	Autocorrelated Kernel Density Estimator
CART	Classification and Regression Tree
CL	Carapace Length
KDE	Kernel Density Estimator
KPC	Katy Prairie Conservancy
LSCV	Least-squares Cross Validation
MCP	Minimum Convex Polygon
MISE	Mean Integrated Standard Error
MPD	Mean Pairwise Distance
OU	Ornstein-Uhlenbeck Model
OUF	Ornstein-Uhlenbeck Foraging Model
PL	Plastron Length
SFAEF	Stephen F. Austin State University Experimental Forest
SWA	Summed Wetland Area
USFWS	United States Fish and Wildlife Service
WMA	Wildlife Management Area

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CHAPTER I

INTRODUCTION

Prior to the Anthropocene period, turtles (Order Testudines) boasted proportional biomass levels among the highest reported for animal taxa, a numerical dominance that granted them substantial influence on ecological communities, but turtles currently represent one of the most imperiled vertebrate clades, with over 60% of global turtle species threatened or already extinct (Lovich et al. 2018). Conservation efforts to preserve biodiversity hotspots may neglect some turtle taxa, as turtle biodiversity tends to be concentrated in lowlands and in extratropical latitudes such as the southeastern United States and southern Asia (Ennen et al. 2020). Many turtle species are long-lived and exhibit delayed maturity, making continued harvest for consumption or the pet trade unsustainable (Turtle Taxonomy Working Group 2017). The body of knowledge on turtles has been growing at an exponential rate, but that does not necessarily translate to conservation success, so study designs that specifically address the needs of species and build upon long term conservation plans are essential to recovery (Lovich and Ennen 2013).

Deirochelys reticularia is a turtle in the Family Emydidae that inhabits the shallow, lentic waters of ephemeral wetlands throughout the southeastern U.S. (Buhlmann 1995; Buhlmann et al. 2008; Ernst and Lovich 2009). Although some populations in the Florida peninsula may be active year-round, *D. reticularia* north of the peninsula aestivate or hibernate for at least part of the year (Ernst and Lovich 2009),

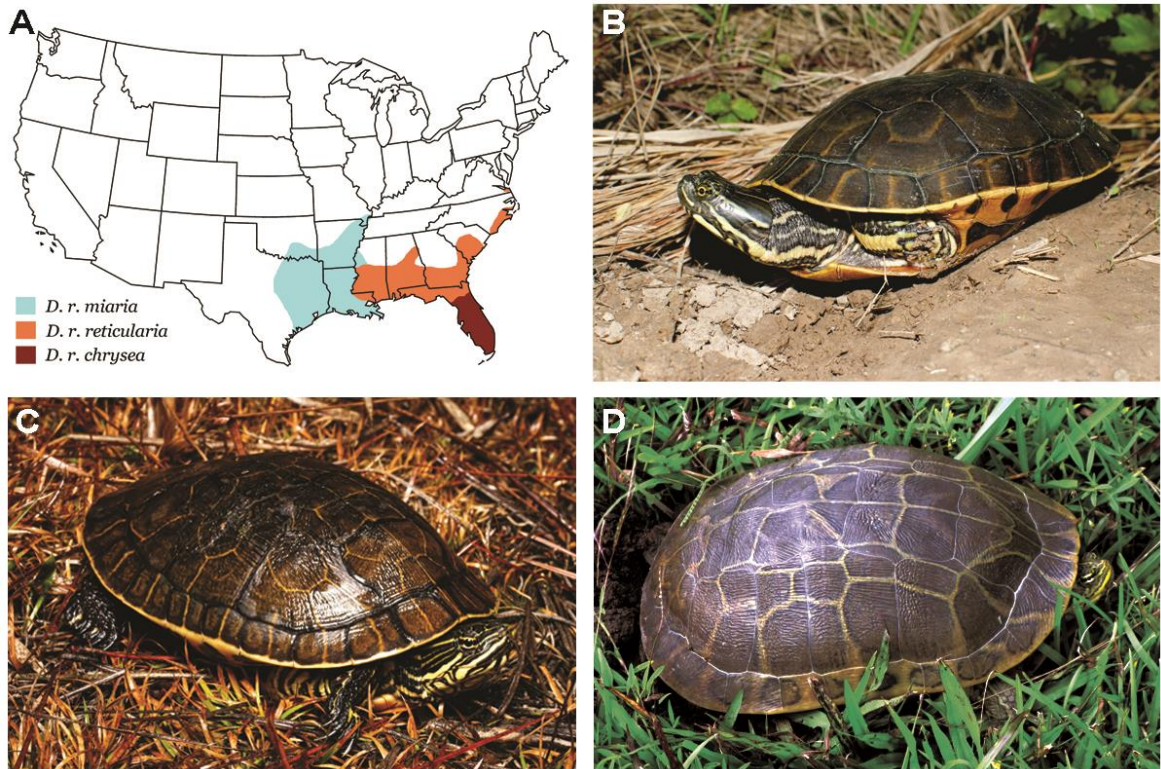


Figure 1. A range map (A) for the three subspecies of *D. reticularia* and photos of each subspecies: (B) *D. r. miaria* photo by author; (C) *D. r. reticularia* photo by Jonathon Bolton; and (D) *D. r. chrysea* photo by Scott D. Beazley.

and both sexes periodically migrate across upland areas between wetland habitats (Gibbons 1986). *Deirochelys reticularia* (Figure 1A) is the lone extant species in the genus, and three subspecies are recognized : Western Chicken Turtles (*D. r. miaria*) west of the Mississippi River in Louisiana, Texas, Arkansas, Oklahoma, and Missouri (Figure 1B), Eastern Chicken Turtles (*D. r. reticularia*) along the Atlantic and Gulf coastal plains from Virginia to the Mississippi River (Figure 1C), and Florida Chicken Turtles (*D. r. chrysea*) in peninsular Florida (Figure 1D). (Schwartz 1956). There have been no range-wide status assessments for *D. reticularia* (Buhlmann et al. 2008), and the habitat of the western subspecies in Texas is under increasing threat due to urbanization

(Ryberg et al. 2017). Phylogenetic comparisons suggest a deep split between *D. r. miaria* and the other two subspecies (Walker and Avise 1998; Hilzinger 2009), and the U.S. Fish and Wildlife Service (USFWS) has issued a 90-day finding that states that listing the western subspecies as threatened or endangered under the U.S. Endangered Species Act may be warranted (USFWS 2011). In order to approximate gaps in our understanding of the ecology of the western subspecies, I have considered literature on all three subspecies here, as their aquatic habitats and foraging behaviors are functionally similar (Ernst and Lovich 2009).

In order to study a taxon, we must first be able to readily observe that taxon. An evaluation of detection methods, an inventory of the demographic biases of those methods, and a standardization of survey protocols are essential first steps to collecting useful data on any species (Davis 1982; Fellers et al. 1988; Corn and Bury 1990). Similarly, understanding emigration and landscape use is essential to future evaluations of local population status for a species that is prone to wandering on land between distinct aquatic activity areas. To inform conservation decisions regarding *D. r. miaria* and guide future research, I have implemented two studies that provide foundational knowledge in these areas. The objectives of the first study, outlined in Chapter II, were to establish survey protocols that optimize *D. r. miaria* sampling efforts by: (1) evaluating existing literature on species-wide *D. reticularia* capture protocols; (2) comparing efficacies of various survey and trapping methods in the field; (3) inventorying potential demographic biases among capture methods; (4) identifying mean aquatic activity depths among monitored individuals and potential demographic bias in

depth; and (5) identifying aquatic trapping and road survey seasons for *D. r. miaria* in Texas. The recommendations in Chapter II provide a refined guide for designing *D. r. miaria* research and management programs that increase detection, reduce field labor costs, and minimize sampling bias. The objective of the second study, outlined in Chapter III, was to establish a preliminary understanding of *D. r. miaria* spatial ecology by: (1) evaluating home range estimation method selection for a species that spends most of the year at rest and migrates between isolated wetlands; (2) determining whether or not models incorporating temporal information from sequential telemetry positions provide a good fit for movement data given those behaviors; (3) relating the tracking duration and resolution (data collection frequency) to the asymptotic relationship between the number of relocations of an individual and its annual home range size; (4) deciphering whether wetland quantity, size, or isolation affect annual home range size; (5) investigating demographic differences in movement patterns; and (6) examining the effects of extreme drought on movement behavior. Finally, the recommendations in Chapter III provide a foundational structure guiding future research on *D. r. miaria* spatial ecology that will assist in model selection for studies on home range and movement in other regions.

CHAPTER II

SURVEY AND CAPTURE PROTOCOLS

Though its distribution within the state is widespread (Dixon 2013; Hibbitts and Hibbitts 2016), turtle assemblage studies and herpetological site inventories within the range of *Deirochelys reticularia miaria* in its Texas range have seldom documented presence (Ryberg et al. 2004; Adams and Saenz 2011; Fitzgerald 2011; Riedle 2014; Crump et al. 2016; Ryberg et al. 2017). Its habitat in Texas is under considerable threat due to urbanization (Ryberg et al. 2017). In Missouri, the subspecies is listed as locally endangered, as no specimens were reported from 1962 to 1995 (Anderson 1965; Buhlmann and Johnson 1995), and the species may be extremely rare in Arkansas (Buhlmann et al. 2008). For these reasons, the U.S. Fish and Wildlife Service (USFWS) issued a 90-day finding that states listing the western subspecies as threatened or endangered under the U.S. Endangered Species Act may be warranted (USFWS 2011). Existing studies on *D. reticularia* have employed several different survey methods and survey protocols have not been standardized.

My study objectives on survey protocols were to optimize *D.r.miaria* sampling efforts by: (1) evaluating existing literature on species-wide *D. reticularia* capture protocols; (2) comparing efficacies of various survey and trapping methods in the field; (3) inventorying potential demographic biases among capture methods; (4) identifying mean aquatic activity depths among radio-tracked individuals and potential demographic bias in depth; and (5) identifying aquatic trapping and road survey seasons for *D. r.*

miaria in Texas. The recommendations in this study provide a refined guide for designing *D. r. miaria* research and management programs that increase detection, reduce field labor costs, and minimize sampling bias.

Materials and Methods

Literature Review of Prior Protocols

I included existing studies in the capture method evaluation if the publication met the following criteria: (1) either the primary research target was *D. reticularia* or a majority of the research activity was within documented *D. reticularia* habitat; and (2) capture methods were documented. For each qualifying study, I inventoried all capture methods attempted, categorized them based on whether or not they were successfully used to capture *D. reticularia*, and recorded the capture rate per unit of effort (if published).

Field Study Sites

The Katy Prairie Conservancy (KPC) is a 7,284-hectare site in the Gulf Coast Prairies and Marshes ecoregion of Texas. Two individuals were detected there in 2015 (Ryberg et al. 2017), and two more on a herpetology class trip in 2016 (Hibbitts, pers. comm.), making this the only site I was aware of in 2018 with multiple recent *D. r. miaria* captures. I also collected demographic data, morphological measurements, and capture methods used for *D. r. miaria* at an additional site in the East Texas Pineywoods ecoregion. This site included portions of the Alazan Bayou Wildlife Management Area

(ABWMA) and the Stephen F. Austin State University Experimental Forest (SFAEF), where *D. r. miaria* had been recently observed (Adams and Saenz 2011).

Animal Use

All field research for this thesis was conducted under Texas A&M University animal care permit number IACUC 2018-0026.

Software

I performed all statistical analyses in R version 3.6.1 (R Core Team 2013) using the integrated development environment RStudio version 1.2.1335 (RStudio Team 2018). I created figures using either base plot or package ggplot2 (Wickham 2016).

Trap Type Comparisons

I calculated capture rates (number of *D. r. miaria* captures per night of trap deployment) for trapping sessions using two types of unbaited fyke nets, a style of trap where an underwater drift fence is installed within aquatic habitat to direct turtles into funnel traps (Figure 2; Vogt 1980). I constructed large fyke nets consisting of two round funnel traps 91 cm in diameter with 5 cm mesh netting. I spread a 6.1 m by 1.2 m seine net between the two funnel trap openings as an underwater drift fence. I attached the seine at the bottom-center and top-center of the funnel trap ring, with enough vertical slack to allow a slight curvature in the net to direct turtles into the funnel, but not enough slack to send turtles below the outer ring. I buried the seine weights and the bottom of each funnel ring in the substrate at each trap deployment. I also designed a smaller fyke apparatus to trap in shallower waters. I constructed the small fyke nets using two round, collapsible



Figure 2. A fyke net trap consisting of two hoop net turtle traps at the ends of a minnow seine. The seine serves as an aquatic drift fence.

crawfish traps 30 cm in diameter with two 3 m lengths of nylon rope joining the top-center and bottom-center of the ring at each funnel entrance. I folded a 3 m by 1.2 m sheet of flexible plastic over the top rope, then attached the plastic with zip ties to the bottom rope. I buried the 30 cm of excess plastic in the substrate at each deployment to prevent turtles from crawling under the fence. I used a comparison of Poisson rates to determine whether capture rates were significantly different between the traditional fyke trap and the smaller design.

Trap Check Frequency and Deployment Duration

Due to concerns that trap retrieval activities may deter subsequent captures by disturbing aquatic vegetation, I intentionally checked some traps every two nights, while I checked others nightly unless delayed by thunderstorms or research activities. To determine how often traps should be checked, I used a comparison of Poisson rates to compare capture rates between traps checked every two nights and traps checked more frequently. To

determine how long traps should be deployed at one location, I divided trap data into two categories: data from the first two nights at each deployment location and data from after the second night at each location (2–6 additional nights). I used a comparison of Poisson rates to determine if capture rates during the first two nights and after the second night were significantly different.

Survey Comparisons

I calculated capture rates for four types of survey: dipnet surveys, night wading surveys, two-person seine surveys, and road surveys. I included data from road surveys performed during a prior study in 2015 (Ryberg et al. 2017) and this study in 2018 for comparison if conducted on roads adjacent to or bisecting the KPC properties. I did not conduct road surveys at ABWMA or the SFAEF. Dipnet surveys employed the use of a modified steel HDD2 dipnet (Memphis Net and Twine Company). The dipnet opening was 53.3 cm wide, 44.5 cm tall, and attached to a 61 cm bag made of 3 mm mesh. At each wetland, I pulled the dipnet's drag bar along the bottom through aquatic vegetation as many times as was necessary to survey the entire habitat area. I performed wading surveys by walking slowly through vegetated waters between dusk and midnight with a headlamp. During wading surveys, I detected *D. r. miaria* either visually or by bumping feet into turtles hidden in the vegetation. If water was too turbid to see the bottom with the aid of a headlamp, I did not perform wading surveys. I did not perform wading surveys at ABWMA or the SFAEF. To determine the significance of differences between capture rates among survey types, I compared each rate to the next highest rate using a comparison of Poisson rates.

Demographic Bias Among Capture Methods

Since most capture-mark-recapture procedures assume equal catchability among individuals in a population (Carothers 1979; Hwang and Chao 1995), I inventoried potential demographic biases that may be caused by method choice. To determine sex, I used the ratio of preanal tail length to plastron length (PL) because the species is sexually dimorphic in preanal tail length, with males having proportionally longer tails (Gibbons 1969). I assumed individuals were male if the preanal tail length was greater than or approximately equal to the horizontal distance between the posterior margin of the plastron and the posterior margin of the carapace. Because *D. reticularia* are also sexually dimorphic in body size (Schwartz 1956), I used body size to distinguish between juveniles and adults after I determined the sex of each individual. Though size at maturity has not been determined for males of the western subspecies (Dinkelacker and Hilzinger 2014), male *D. reticularia* in South Carolina exhibited divergent preanal tail lengths upon reaching plastron lengths of 7.5–8.5 cm (Gibbons 1969). For the purposes of this study, I assumed males with plastron lengths longer than 8.0 cm were mature. I assumed females with carapace lengths (CL) above 16.5 cm were mature, as is consistent with the literature and data collected for a reproductive study at the same site (Gibbons 1969; Ewert et al. 2006; Dinkelacker and Hilzinger 2014; Bowers et al., unpubl. data). To graphically represent potential bias, I plotted the capture proportions of three demographic groups (adult females, adult males, and juveniles) by each capture method. To calculate significance of *D. r. miaria* size bias across capture methods, I performed a one-way ANOVA and Kruskal-Wallis Rank Sum test on log-transformed

carapace lengths of *D. r. miaria* captured using each method, followed by a post-hoc Tukey Honest Significant Differences test.

Potential Bias from Trap and Survey Deployment Depth

I used telemetry data collected at the KPC in conjunction with a study on the habitat, annual home range, and movements of the species to determine optimum survey and trapping depths. Determining an average activity depth is important because dipnet and seine surveys can be performed at depths ranging from a few centimeters to more than a meter, and because the physical characteristics of several kinds of turtle traps allow them to be deployed at a variety of water depths. I recorded aquatic observation depths using a tape measure lowered to the substrate within one meter of the turtle's position. In cases where my presence may have caused the turtle to evade and obscure the exact telemetry position, I did not record the water depth.

Optimizing Deployment Depth

To determine whether fyke nets have been deployed at appropriate water depths, I collected data for each *D. r. miaria* captured in a fyke net by measuring the water depth in the center of the seine wall. I used a Mann-Whitney U-test to determine whether mean capture depths among fyke captures and mean telemetry observation depths were significantly different.

Demographic Bias in Aquatic Activity Depth

I also evaluated whether surveying or trapping at certain depths would create a demographic collection bias. To assess potential age and sex bias in aquatic activity

depth, I categorized radio-tracked individuals with more than ten depth observations as juvenile, mature male, or mature female for comparison. I employed both Welch's Two-sample T-tests and Mann-Whitney U-tests on log-transformed observation depths to compare adults to juveniles and to compare adult females to adult males. I used nested analyses of variance (ANOVA) to evaluate the effect of individual activity on depth comparison results.

Aquatic Trapping Season

To identify a trapping season, I grouped session data into two-week periods. If I deployed a trap during nights included in two periods, I categorized it in the period during which most deployment nights had occurred. Since telemetry efforts at these sites indicate that most *D. r. miaria* are underground in terrestrial habitats between late June and early March, I did not attempt to trap during that period. I calculated success rates for each period. To control for site variation, I only included KPC sessions, as I only trapped the other sites in 2019. To control for trap type variation, I only included large fyke nets, as I did not design the smaller fyke apparatus until 2019.

Terrestrial Survey Season

As trail and roadside surveys may be necessary to inventory areas with limited access, a time and season for above-ground terrestrial activity must be identified. I used telemetry data to inventory dates of terrestrial migration at the KPC sites. I employed two methods to determine start-times for terrestrial migrations. I attached Lotek brand pp-120 GPS loggers to turtles and programmed them to record positions every two hours. I selected

this two-hour increment in the interest of collecting behavioral information throughout each day and night while also preserving battery life. I recharged batteries every fifty days in loggers set to record positions every two hours. Occasionally, I programmed loggers to collect data more frequently to document nesting behavior. For the purposes of this study, I have divided migration start times into two-hour increments. I collected some start times by installing automated Hyperfire HC500 (Reconyx) wildlife cameras above aestivating or hibernating *D. r. miaria*. I programmed cameras to fire every minute, providing documentation of exact migration start times.

Results

Literature Review of Prior Protocols

I included 13 studies at six study sites from prior literature in the evaluation, including two sites in Arkansas and singular sites in South Carolina, Virginia, Oklahoma, and Texas. Published studies that met inclusion criteria used five methods to capture *D. reticularia* (Table 1). Eight out of the 13 studies presented data collected by wholly or partially enclosing known *D. reticularia* aquatic habitats with terrestrial drift fences, with individuals falling into pitfall buckets buried along the fences as they migrate over upland habitats (Gibbons 1969; Gibbons and Nelson 1978; Gibbons et al. 1982; Congdon et al. 1983; Buhlmann et al. 1995; Buhlmann et al. 2009; Patton and Wood 2009; McKnight et al. 2014). Of these studies, only Patton and Wood (2009) were unsuccessful at capturing *D. reticularia* with this method, but turtles were not the primary target of terrestrial drift fences in that study. The same is true of a later

herpetological inventory study at the same site (McKnight 2014), during which only one individual *D. r. miaria* was captured using this method. I did not use terrestrial drift fences in the Texas field study because of restrictions on the study areas, the presence of livestock that need access to the wetlands, and the fact that I was not aware of which wetlands within the mosaic contained substantial *D. r. miaria* densities prior to this study.

Several aquatic trap types have been used in prior studies. Wire mesh swim-in traps (Gibbons 1968) were used successfully in South Carolina (Gibbons 1969) but failed to capture *D. reticularia* in Virginia (Buhlmann 1995). Two studies employed baited collapsible crawfish traps. In Oklahoma, *D. r. miaria* were captured in baited crawfish traps with a capture rate of 0.003 individuals per trap night (McKnight 2014). In Texas, baited crawfish traps did not capture *D. r. miaria* (Ryberg et al. 2017). Seven studies employed baited hoop nets. Three studies at the Savannah River Site in South Carolina reported *D. reticularia* in baited hoop nets (Congdon et al. 1983; Buhlmann et al. 1995; Demuth and Buhlmann 1997). Two studies in Oklahoma employed baited hoop nets (Patton and Wood 2009; McKnight 2014) reporting 11 captures in 338 trap nights (0.033 captures / trap night) and 75 captures at a rate of 0.007 captures per trap night, respectively, but the latter study combined captures in baited hoop nets with captures in fyke nets, so it is unclear which method captured more *D. reticularia*. Baited hoop nets were used at a fish hatchery in Arkansas but captures at that site were also combined with fyke net captures (Sachse 2014). All seven studies employing fyke nets successfully

Table 1. Literature review of *D. reticularia* capture methods, 2020. Symbol “X” indicates that the method captured *D. reticularia* during the study. Symbol “o” indicates that the method was used during the study but did not capture *D. reticularia*. Symbol “*” indicates that both baited hoop nets and fyke nets were used, but method was not recorded for each capture.

Author	Year	Location	Upland Drift Fences	Baited Wire Mesh Trap	Baited Crawfish Trap	Baited Hoop Net	Fyke Net	Seine Surveys	Dipnet Surveys	Wading Surveys	Road Surveys
Gibbons	1969	SC: Savannah River Site	X	X							
Gibbons and Nelson	1978	SC: Savannah River Site	X								
Gibbons et al.	1982	SC: Savannah River Site	X								
Congdon et al.	1983	SC: Savannah River Site	X			X					
Buhlmann et al.	1995	SC: Savannah River Site	X			X					
Buhlmann	1995	VA: Seashore S.P.		o			X				
Demuth and Buhlmann	1997	SC: Savannah River Site				X	X				
Hilzinger	2009	AR: Holland Site					X				
Buhlmann et al.	2009	SC: Savannah River Site	X				X				
Patton and Wood	2009	OK: Boehler Seeps and Sandhills	o			X					
McKnight	2014	OK: Boehler Seeps and Sandhills	X		X	X*	X*				
Sachse	2014	AR: Joe Hogan State Fish Hatchery				X*	X*				
Ryberg et al.	2017	TX: Katy Prairie			o	o	X				X
This study	2018	TX: Katy Prairie					X	X	X	X	o

captured *D. reticularia* in them (Buhlmann 1995; Demuth and Buhlmann 1997; Hilzinger 2009; Buhlmann et al. 2009; McKnight 2014; Sachse 2014; Ryberg et al. 2017).

Two research efforts did not meet inclusion criteria but are worth mention. In a Florida study, 24 out of 25 *D. reticularia* collected between 1974 and 1977 were located on roads or in upland habitats incidentally (Jackson 1996). In Louisiana, six *D. r. miaria* collected between 1999 and 2003 were collected incidentally on roads or in upland habitats during other research activities (Carr and Tolson 2017).

Texas Field Study Results

Survey and trap sessions at Texas sites resulted in 140 captures of 96 individual *D. r. miaria*, including 129 captures of 86 individuals at KPC and 11 captures of 10 individuals at the ABWMA. For the purposes of this study, captures and recaptures have been combined. No *D. r. miaria* were captured and then recaptured on the same date. The largest adult female at KPC was 23.2 cm in carapace length (CL) and the largest adult male was 16.8 cm CL. The largest adult female at the ABWMA was 21.1 cm CL and the largest male was 15.3 cm CL. Comparisons between capture methods, season, and depth are outlined below.

Trap Type Comparisons

A total of 380 trap nights employed the use of the traditional large fyke nets. A total of 153 trap nights employed the use of the smaller fyke apparatuses. Traditional fyke nets had significantly higher capture rates than the smaller plastic design (comparison of Poisson rates, $P < 0.001$). I captured 95 *D. r. miaria* in fyke nets over 380 trap nights

(0.25 captures/trap night). I captured five *D. r. miaria* in plastic fyke traps over 153 trap nights (0.033 captures/night).

Trap Check Frequency and Deployment Duration

I captured 57 *D. r. miaria* in traps checked every two days over 376 nights of deployment (0.152 captures/ trap night), and 43 *D. r. miaria* in traps checked more frequently over 157 nights of deployment (0.274 captures/trap night). Waiting longer periods between checking traps did not increase capture rates. The capture rate was actually significantly lower when checking at longer intervals (comparison of Poisson rates, $P = 0.005$). I captured 62 *D. r. miaria* during checks within the first two nights (260 nights of deployment, 0.238 captures/night), and 36 *D. r. miaria* during checks performed after the second night (273 nights of deployment, 0.132 captures/ night). Success rates decreased with trap session duration, as capture rates during the first two nights of deployment were significantly higher than rates after the second night (comparison of Poisson rates, $P = 0.005$).

Survey Type Comparisons

Dipnet surveys captured *D. r. miaria* at the highest rate, followed by wading surveys, seine surveys, and road surveys (Table 2). To determine if the difference between capture rates among trap types was significant, I compared each rate to the next highest rate using a comparison of Poisson rates. Capture rate during dipnet surveys was not significantly higher than the rate during wading surveys ($P = 0.2$). Rate of capture during wading surveys was not significantly higher than that of seine surveys ($P = 0.5$), but the

Table 2. Survey effort and capture rates for *D r. miaria* using dipnet, seine, and wading surveys during the 2018 - 2019 trapping season and road surveys in 2015 (Ryberg et al. 2017) and 2018 (this study). *Road survey recovered a traffic mortality specimen; not a live individual.

Survey Type	Captures	Survey Effort (Person-Hours)	Capture Rate
Dipnet	10	30.4	0.329
Wading	4	27.4	0.146
Seine	12	108.7	0.110
Road	1*	102.2	0.010

dipnet survey capture rate was significantly higher than the seine survey capture rate ($P = 0.02$), and both the seine survey rate and wading survey rate were significantly higher than the road survey capture rate ($P = 0.004$ and $P = 0.009$, respectively).

Demographic Bias Among Capture Methods

Demographic proportions of captures by traditional fyke net ($n = 99$), dipnet ($n = 9$), hand during wading surveys or incidentally while checking traps ($n = 13$), seine ($n = 11$), and plastic fyke trap ($n = 5$) indicated that there were demographic and body size biases among capture methods (Figure 3). I captured no adult females via seine surveys or plastic fyke traps.

The mean carapace lengths among different capture methods (Figure 4) were significantly different (one-way ANOVA, $F_{4,132} = 11$, $P < 0.001$; Kruskal-Wallis rank

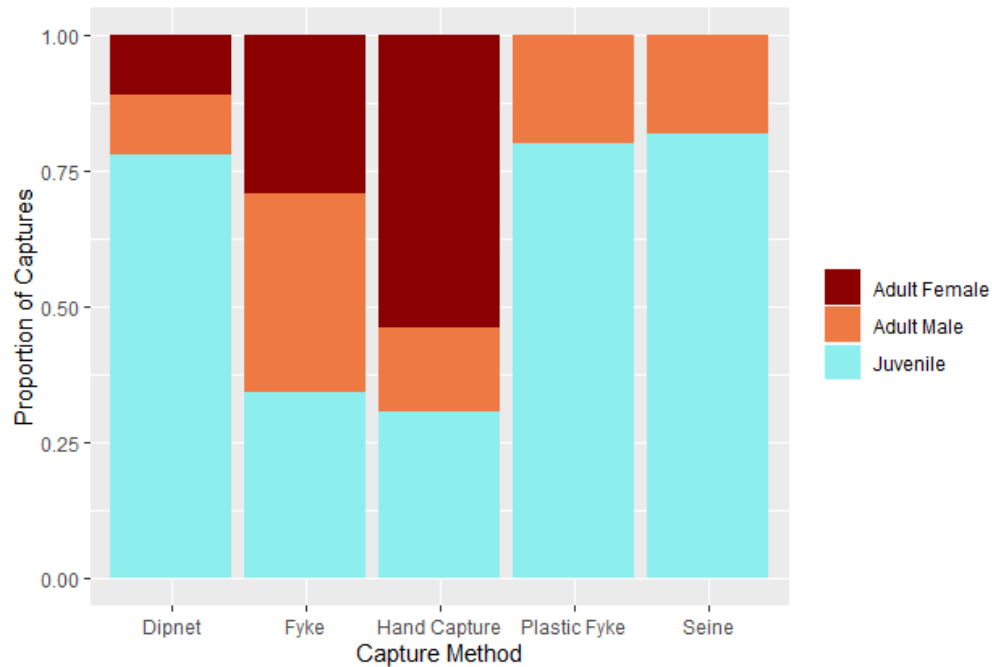


Figure 3. Proportion of juvenile, adult male, and adult female *D. r. miaria* collected by capture method, including recaptures. I included individuals captured by dipnet, fyke trap, plastic fyke trap, seine net, and by hand during wading surveys or incidentally while checking traps. I did not include road survey data because I was unable to determine the sex or age class of road mortality specimens.

sum test, $H=24.4$, 4 d.f., $P < 0.001$). A Tukey Honest Significant Differences test indicated that *D. r. miaria* captured via dipnet were significantly smaller than individuals captured via fyke nets ($P < 0.001$) and wading surveys ($P < 0.001$), and that individuals captured via seine were significantly smaller than individuals captured via fyke nets ($P = 0.006$).

Aquatic Activity Depth

Population mean water depth among all *D. r. miaria* telemetry observations with depth data (501 observations of 27 individuals) at KPC was 35.3 cm (Figure 5). Population mean

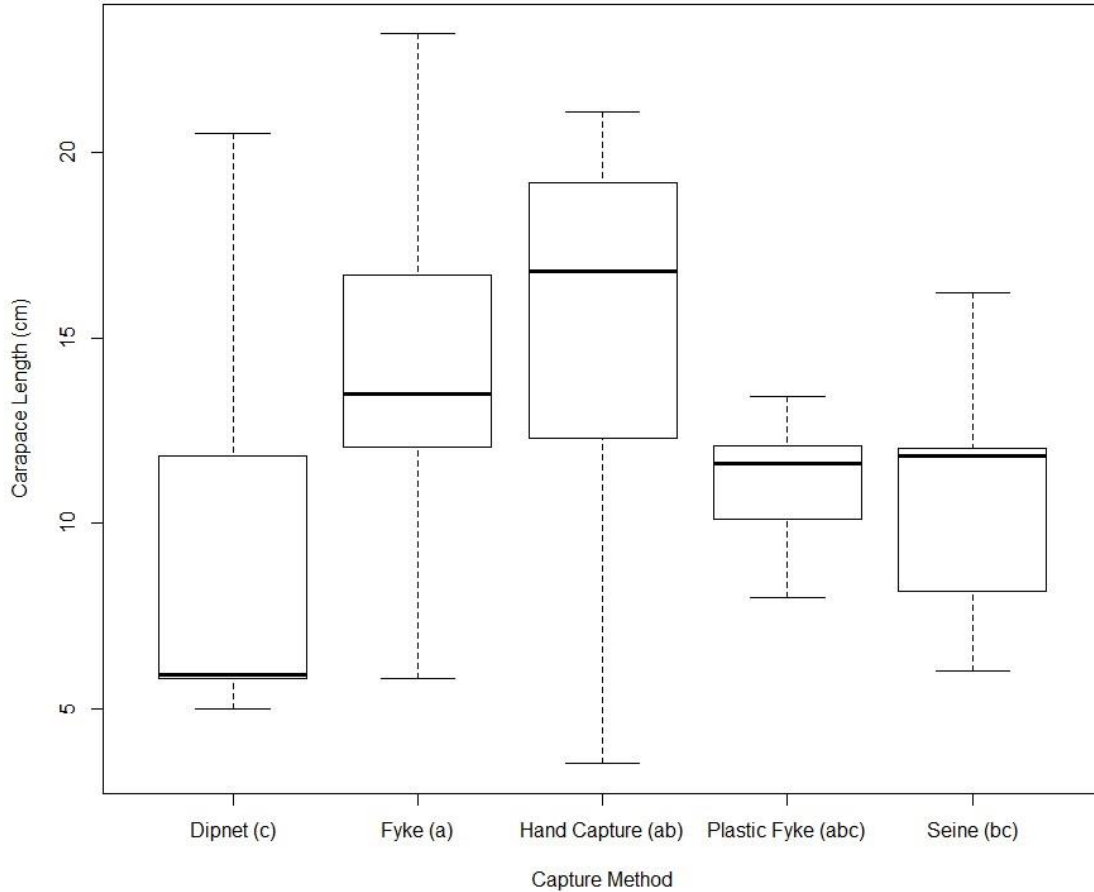


Figure 4. *Deirochelys r. miaria* sizes by capture method, including recaptures. Horizontal bars represent median, the bottom and top edges of the box represent 25th and 75th percentiles, and whiskers extend to the 5th and 95th percentiles. Values derived by measuring straight-line carapace length with calipers. Groups resulting from a Tukey Honest Significant Differences test are denoted in lower case letters ($\alpha = 0.05$).

activity depth was significantly shallower than mean capture depth using traditional fyke nets ($n = 58$, mean = 48.4 cm) when compared using a Mann-Whitney U-test ($U = 21710$, $P < 0.001$).

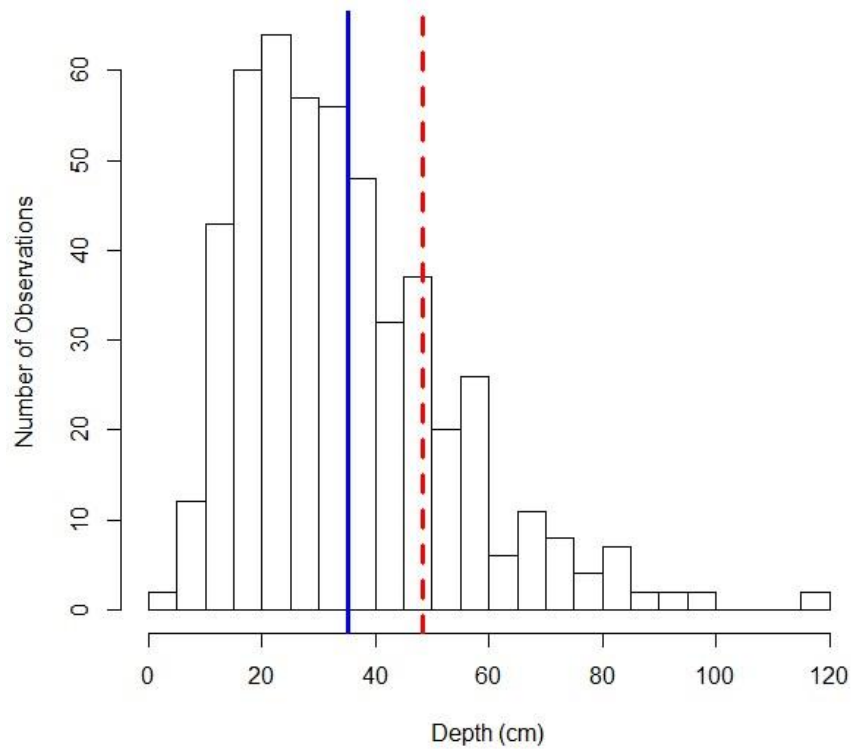


Figure 5. Observed water depths (501 observations of 27 monitored individuals) at *D. r. miaria* positions during radio telemetry monitoring. Solid blue line indicates mean activity depth (35.3 cm). Dashed red line indicates mean depth of capture among fyke net captures (48.4 cm).

Demographic Bias in Aquatic Activity Depth

When isolating only individuals with more than 10 depth observations for demographic comparisons, results included: 187 observations of 7 mature females; 174 observations of 8 mature males; and 114 observations of 4 immature individuals. Mean activity depth for the juvenile age class (mean = 34.7 cm) did not differ significantly from adult mean depth (mean = 36.0 cm) when using parametric or nonparametric tests on log-transformed depth observations (Welch's Two-sample T-test, $t = 0.97$, 178 d.f., $P = 0.3$; Mann-Whitney U-test, $U = 21716$, $P = 0.4$). The results of a nested ANOVA indicated

that there were not significant differences among individuals within age classes ($F_{2, 18} = 1.1, P = 0.3$) or among age classes ($F_{1, 2} = 1.0, P = 0.3$). Adult males were active in significantly shallower water (mean = 33.1 cm) than adult females (mean = 38.6 cm) when using both parametric and nonparametric tests on log-transformed depth observations (Welch's Two-sample T-test, $t = 2.8, 358$ d.f., $P = 0.006$; Mann-Whitney U-test, $U = 19130, P = 0.004$), but a nested ANOVA revealed that there were also significant differences among adults within both sexes ($F_{13, 14} = 6.5, P < 0.001$) and among sexes ($F_{1, 13} = 9.3, P = 0.003$). When examining the activity depths of monitored adults more closely (Figure 6), it becomes apparent that I observed one individual female (ID#2255) in much deeper water on average than the other monitored *D. r. miaria*. Upon removing this individual (ID#2255) from the analysis, the difference in mean activity depths between adult male (mean = 33.1 cm) and female (mean = 34.3 cm) *D. r. miaria* was no longer significant (Welch's Two-sample T-test, $t = 1.2, 339$ d.f., $P = 0.25$; Mann-Whitney U-test, $U = 15800, P = 0.16$).

Aquatic Trapping Season

The highest rate of capture occurred during late April of 2018 (0.60 captures per trap night; Table 3). The lowest rate of capture occurred during late March of 2019.

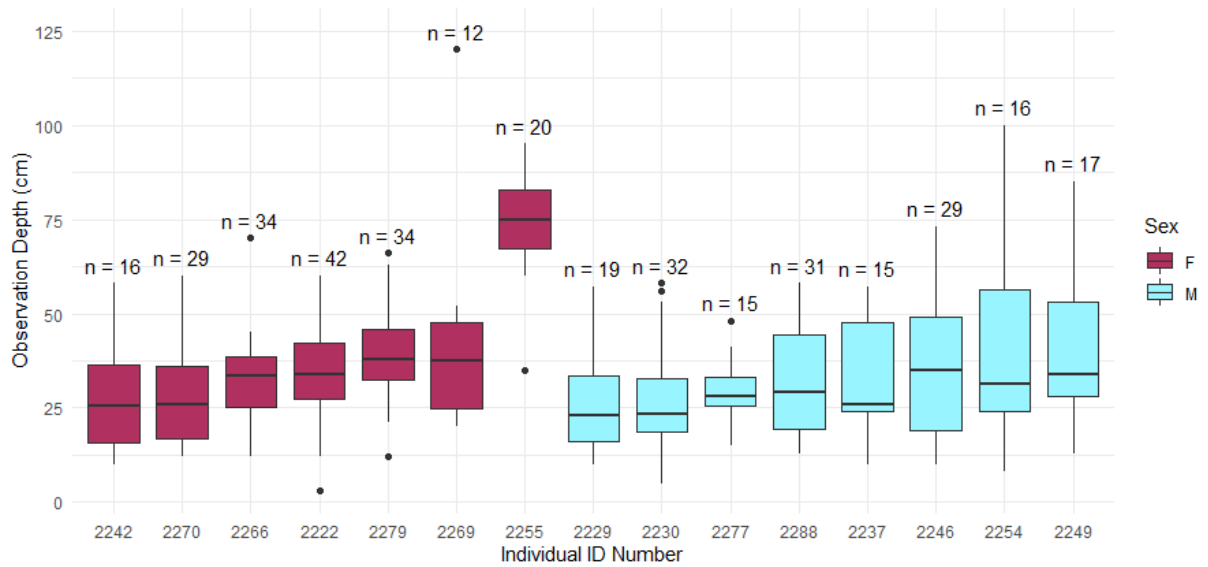


Figure 6. Observation depths of monitored *D. r. miaria* by individual turtle and sex.

Table 3. Large fyke trap success at KPC sites by seasonal period.

Year	Period	Number of Traps	Trap Nights	Captures	Success Rate (captures/night)
2018	Early April	2	15	2	0.13
	Late April	3	10	6	0.60
	Early May	8	44	19	0.43
	Late May	7	31	11	0.35
	Early June	20	80	16	0.20
2019	Late March	12	48	2	0.04
	Early April	24	96	30	0.31

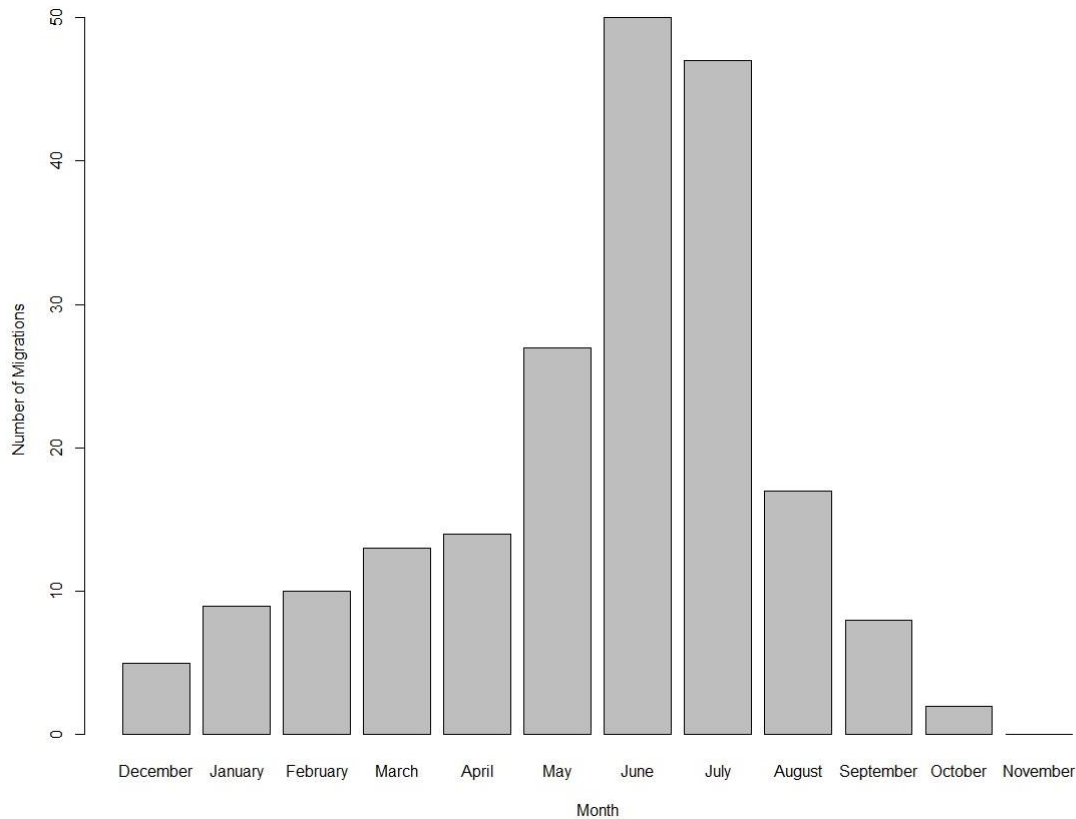


Figure 7. *Deirochelys r. miaria* terrestrial migration start dates observed via radio telemetry (202 migration start dates observed among 27 monitored individuals).

Terrestrial Survey Season

I observed 202 terrestrial migrations among 27 monitored individuals during the telemetry study at KPC (Figure 7). *Deirochelys r. miaria* were most terrestrially active during June and July. I documented 61 migration start times among 13 monitored individuals using GPS loggers and automated game cameras (Figure 8). Most terrestrial movements were diurnal and upland movement peaked around 1100 hrs.

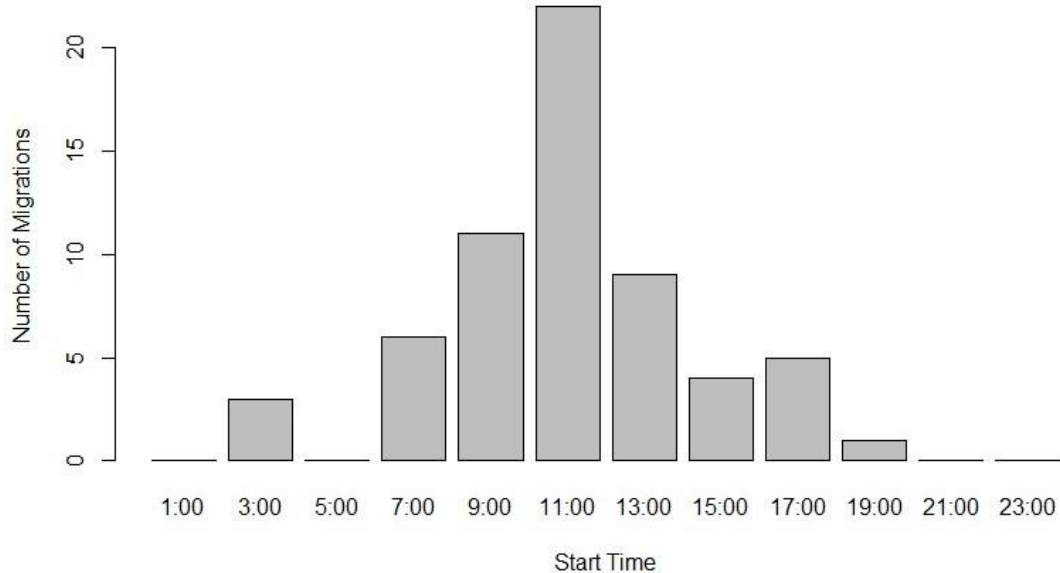


Figure 8. *Deirochelys r. miaria* terrestrial migration start times documented by GPS loggers and wildlife cameras (61 migration start times observed among 13 monitored individuals).

Discussion

One of the most vexing points of contention when designing a *D. reticularia* study is whether or not to employ baited traps. In Virginia, baited traps failed to capture *D. reticularia* in wetlands where they are known to be present (Buhlmann 1995). In Oklahoma, capture rates in baited traps were very low (Patton and Wood 2009; McKnight 2014). In a 2015 study in Texas (Ryberg et al. 2017), over half of the 1,068 trap nights at KPC used baited hoop nets and crawfish traps in wetlands now known to be occupied by *D. r. miaria* but no individuals were captured in baited hoop nets or crawfish traps. One possible explanation for the regional inconsistency in the success of baited traps is that *D. reticularia* diet may differ enough regionally for some populations

to be attracted to fish whereas others are not. Another is that low capture rates in baited traps at some sites indicate that *D. reticularia* occasionally wander into hoop nets on accident. *Deirochelys reticularia* may not be attracted to the bait itself, but to the live crawfish feeding on the bait (McKnight, pers. comm.). A review of the literature found no documented observations of *D. reticularia* feeding on carrion in the wild. If designing a study in an area where baited traps have not yet proven effective, unbaited fyke traps are recommended due to the regional inconsistencies in *D. reticularia* responses to baited traps.

When designing studies on *D. r. miaria*, different capture protocols may be implemented depending on research questions, budget, time constraints, and property access. Fyke nets provided a relatively even demographic distribution compared to other methods. Most capture-mark-recapture procedures assume equal catchability of individuals within a population and equal survey effort (Carothers 1979; Hwang and Chao 1995), so fyke traps or a combination of fyke traps and carefully standardized dipnet surveys are recommended to include all age cohorts within the population. If access time at a site is limited or traps are unavailable, dipnet surveys provide the quickest way to document presence (Table 2) but are less effective at capturing large individuals (Figures 3-4). For this reason, fyke trapping and hand capture during wading surveys are recommended in studies requiring reproductive females (Figure 3). Seine surveys are not recommended because they result in a significantly lower capture rate than dipnet surveys and have a similar size-bias against larger turtles (Table 2; Figure 4).

Road surveys are not recommended unless necessitated by a lack of property access. They resulted in significantly lower capture rates than all other survey types (Table 2).

A significant difference between mean fyke net capture depths and observed activity depths reveals that trap success could be improved by developing modifications that allow for shallower trap deployment. The plastic fyke net design introduced in this study allows for trapping in shallower water, but large *D. r. miaria* are unable to enter the funnel, and occasionally mud snakes (*Farancia abacura*) become tangled in the mesh and drown, a behavior also observed in Oklahoma with collapsible crawfish traps (McKnight 2014).

Although mean capture depth among monitored adult males was significantly shallower than that of adult females, the results of the nested ANOVA revealed that some of that variation is influenced by the behavior of individual *D. r. miaria*. When examining the activity depths of monitored adults more closely (Figure 6), it becomes apparent that I observed one individual female (ID#2255) in much deeper water on average than the other monitored *D. r. miaria*, and removing this individual from the analysis removed that significant difference in activity depth. This individual spent most of the 2018 and 2019 aquatic periods in a highly modified wetland that is different from typical habitat within the study area.

Though knowing a mean activity depth can optimize trap depth placement, further research into aquatic activity depths among *D. r. miaria* could also benefit the refinement of active survey procedures. In this study, I did not examine seasonal or temporal influences on activity depth. It could be helpful to know whether abiotic

components like temperature and precipitation as well as biotic components like the seasonal succession of annual plant species affect the seasonal water column use of *D. r. miaria* within wetlands. The effect of temporal behavioral differences in water depth during foraging or courting periods could also be studied. These components would assist researchers in choosing where to survey within the wetlands depending on the month or time of day that the survey is implemented.

Early in the 2018 aquatic activity season, I experimented with different survey methods so trapping effort was much lower than later 2018 periods and 2019 periods (Table 3). In 2019, I initiated trapping based on the return of monitored individuals to aquatic behaviors, and from late April of 2019 onward I trapped in other sites within the state and worked on other components of the project. Though this dearth of comparable data made analysis difficult, relatively low capture rates during early April of 2018 (0.13 captures per trap night) and late March of 2019 (0.04 captures per trap night) indicate that the return of individuals from dormancy does not necessarily indicate availability for capture using passive methods. It may be that even though these individuals have returned to the water, they are not active enough to frequently wander into fyke nets. Water temperature and precipitation are variables that could be investigated as additional variables affecting catchability.

Though the frequency of terrestrial migrations peaked in June (Figure 7), most *D. r. miaria* migrations over upland habitat were movements either from wetlands to aestivation sites after concluding aquatic activity, from aestivation sites to wetlands before resuming activity, or between consecutive aestivation sites. If road surveys are

not located between wetlands and upland aestivation sites (which are often near the wetlands themselves), detection is unlikely, which may explain the extremely low capture rate among road surveys (0.01 captures/person-hour; Table 2). If a lack of access to properties in the target area prohibits aquatic surveys or trapping and road surveys are the only option, conducting them during the peak diurnal activity period (Figure 8) may increase chances of detection.

Because of the functional similarities of the three *D. reticularia* subspecies, I believe these survey method suggestions could apply to the species throughout its range. However, activity seasons exhibit some variation among subspecies and may vary among Texas sites, so the activity and survey seasons outlined here are merely a starting point for designing studies on the western subspecies. Based on my literature review and field research, I believe the recommendations outlined in Chapter IV below will help guide the design of *D. r. miaria* research and management programs that increase detection, reduce field labor costs, and minimize sampling bias.

CHAPTER III

SPATIAL ECOLOGY

Understanding animal movement can guide decisions on a variety of conservation and management actions, but while the number of tracking studies has increased, the methods available to analyze the data generate different results depending on the temporal scale of their application (Nathan et al. 2008; Kays et al. 2015; Calabrese et al. 2016; Gurarie et al. 2016). Animal movement can be studied on at least two temporal scales: (1) long-term seasonal migrations, annual movements, or displacement, and (2) approaches that focus on daily activity (Kenward 2001). The latter can be used to denote behavioral activities such as mating or foraging, and the former may direct attention to seasonal activity patterns, migration, dispersal, or nomadic behavior (Ross et al. 2019). Movement can be initiated both by perceptual cues directing animals to specific resources and by memory (Mueller and Fagan 2008). The distance and duration of movements can vary by an individual's body size, sex, age, or resource needs, and can be affected by both seasonal and environmental factors (Burt 1943).

Our perception of the spatial ecology of an animal, information that can be an essential component of conservation planning, depends on our understanding of its movements and home range (Aarts et al. 2008; Millar and Blouin-Demers 2011). For most species, a home range is a defined area where most of its movements occur, typically in pursuit of resources required for survival and reproduction throughout its lifetime (Burt 1940; Burt 1943; Börger et al. 2008). Understanding the size and shape of

an animal's home range can guide conservation priorities and answer important questions about the ecology, dispersal, and metapopulation dynamics of the species, but no single home range estimation method can be applied to all species, and several methods are used in modern studies (Kenward 2001). Minimum convex polygons (MCP), though primitive and potentially obsolete, are still used to estimate home range in current studies for comparison with historical home range analyses (Jennrich and Turner 1969; Nilsen et al. 2008; Chandler et al. 2019; Hamernick et al. 2020). Fixed kernel density estimators (KDE) are now widely used to estimate the home ranges of reptiles, but their representation of ecologically meaningful information has been questioned, particularly when used for species that spend considerable time at rest (Row and Blouin-Demers 2006; Silva et al. 2020). Part of the problem with selecting a method lies in the definition of home range, at its origin described as the area an animal moves through during "normal" activities of resource acquisition and reproduction throughout its lifetime (Burt 1943), and later broadened to include movements within and among several core areas (Rose 1982).

For some taxa, these definitions prod several questions. Are prolonged periods of rest considered "normal" activities? Do movements in search of hibernation or aestivation sites qualify as resource acquisition? How does the duration of rest factor into the importance of hibernacula as a spatial resource? If an individual spends more time aestivating at rest than active, how does that alter the method selection process used to determine home range and core areas? Ross et al. (2019) noted that although areas used to migrate between core activity areas may function as important movement

corridors, they do not necessarily represent appropriate habitat for the species. They suggested that evaluating core activity areas and demographic spatial differences will require estimation methods that do not include large areas of unused space. While MCP and KDE methods neglect temporal information, autocorrelated kernel density estimators (AKDE) accommodate both spatial autocorrelation via the Ornstein-Uhlenbeck (OU) model and temporal autocorrelation via the Ornstein-Uhlenbeck Foraging (OUF) model, and have been successfully applied to modern datasets where sampling at finer scales using GPS loggers exposed velocity autocorrelation in the movement data (Calabrese et al. 2016). Silva et al. (2020) provided another recommendation for analyzing spatial data for species that are dormant for extended periods, in which repeated consecutive coordinates are removed from the dataset to avoid the overemphasis of single positions of rest by kernel density estimators.

A model with some consideration of the temporal sequence of telemetry positions should definitely be considered when studying the movements of *Deirochelys reticularia*, a turtle species that spends much of its time at rest. Studies on the spatial ecology of *D. reticularia* have been relatively sparse, and any discussion of home range has been limited to annual or seasonal home range estimates. Prior publications reported annual home range sizes up to 101,000 m² (Buhmann 1995), individual seasonal movements up to 635 m (Marchand 1945, Buhmann 1995), use of wetland mosaics between 1 and 9 wetlands (Buhmann 1995), and inter-wetland movements between 300 and 830 m (Dodd 1992; Dodd and Cade 1998; McKnight et al. 2012).

The objective of my spatial ecology study was to inform future research by: (1) evaluating annual home range estimation method selection for a species that spends most of the year at rest and migrates between isolated wetlands; (2) determining whether or not models incorporating temporal information from sequential telemetry positions provide a good fit for movement data given those behaviors; (3) relating the tracking duration and resolution (data collection frequency) to the asymptotic relationship between the number of relocations of an individual and its annual home range size; (4) deciphering whether wetland quantity, size, or isolation affect annual home range size; (5) investigating demographic differences in movement patterns; and (6) examining the effects of extreme drought on movement behavior. The recommendations in this study provide a foundational structure guiding future research on *D. r. miaria* spatial ecology that will assist in model selection for studies on home range and movement in other regions.

Materials and Methods

Study Sites

I collected movement data on *D. r. miaria* at two sites managed by KPC. Site A included a 4.1-km² parcel in Waller County characterized by a mosaic of restored prairie pothole wetlands and prairie uplands with little grazing. The site is bounded to the west and north by private farming properties, to the east by another KPC tract with heavier grazing, and to the south by fallow rice agriculture cells with moderate grazing. Each of the adjacent tracts is interrupted by livestock ponds, ephemeral wetlands, and ephemeral

irrigation ditches. Site B included a 6.3-km² portion of the KPC lands in Harris County characterized by a mosaic of natural and restored ephemeral wetlands, perennial livestock ponds, ephemeral irrigation canals, and prairie uplands. It is bounded to the north by private properties with similar vegetation and grazing regimes, to the south by a large hayfield with few wetlands or ponds, to the east by a large lake, and to the west by assorted private 1-km² homesteads. Sites A and B are approximately 9 km apart and may represent one population or possibly two metapopulations, though I did not observe movement between the two sites during the 2018-2020 period. Site C is approximately 200 km northeast of sites A and B on the Alazan Bayou Wildlife Management Area (ABWMA) in the Pineywoods ecoregion. It had been an isolated clearing for grazing until 1997, when it was converted to wetland cells for waterfowl management. This portion of the property is a 5.2 km² mosaic of ephemeral wetland cells, levees, herbaceous uplands, and forested uplands. It is bounded to the east and west by dense forest, to the south by floodplains of tributaries of the Angelina River, and to the north by private grazing lands.

Telemetry

I captured *D. r. miaria* between 2018 and 2020 for a long-term capture-mark-capture study using unbaited fyke net traps (Vogt 1980), seine surveys, dipnet surveys, by hand during night wading surveys, and incidentally while tracking or moving between traps. A complete description of capture methods is available in Chapter II. I marked individuals by either drilling holes or filing notches in the marginal scutes, using only the four scutes on either side of the nuchal scute and the eight posterior-most marginal

scutes. I determined the sex and maturity stage of each individual as described in Chapter II.

I used VHF radio transmitters (Advanced Telemetry Systems, various models) at all three sites. I used GPS loggers (Lotek Wireless, PP-120) on some individuals at the KPC sites until battery recharge life had decayed significantly. Initially, I attached all equipment to the posterior margin of the carapace, but early in the study some individuals lost the equipment after the natural shedding of the carapacial laminae and subsequent tangling in vegetation. I attached all future equipment to the anterior margin of the carapace by drilling a small hole in the two marginal scutes adjacent to the nuchal scute and threading an aluminum wire through the holes. I then encased the equipment bundle in waterproof epoxy putty. Each equipment bundle (VHF transmitter, epoxy putty, aluminum wire, and GPS logger if used) weighed less than 5% of the body mass of the individual. At the KPC sites, I tracked individuals two to four times per week until aestivation, then once every 1 to 2 weeks during aestivation. At each position, I recorded the GPS coordinates, the activity status (active or aestivating), and whether or not research activities (such as transmitter replacement) may induce additional movement. In order to avoid detecting movement when it did not occur, I also flagged aestivation sites and made note that the individual had not moved if it was in the same position as the prior tracking session. At Site C, I tracked individuals once per week while aquatic, then once every two weeks when individuals left the water to aestivate. I tracked individuals at the KPC sites for varying durations between March 2018 and July 2020. At Site C, I tracked individuals from April 2019 to November 2019, the approximate life of the

transmitter batteries deployed there. If a monitored individual had been preyed upon, I recorded the coordinates but excluded the position from movement and annual home range analyses. I set observation times from captures and recaptures in traps to 1200hrs on the day of retrieval, as there is no way to determine when the individual entered the trap. Some movement data from recaptures of monitored individuals at all sites are included here.

Movements

For each individual with one or more relocations via either telemetry or recapture, I recorded the number of days monitored and the number of days to the last position with unique coordinates. I used the `sp` package (Pebesma and Bivand 2005) to calculate total distance traveled, mean step length, mean daily distance (total distance traveled/days to last unique coordinates), and total net displacement. For total distance traveled and mean daily distance, individuals were only included in comparisons if they had been monitored for two seasons (minimum number of relocations > 46). I did not use mean step length in comparisons because the time between tracking sessions varied by season. For total net displacement, I included individuals with at least 350 days between first and last relocations or captures. When assumptions of normality and homoscedasticity were met, I used t-tests to compare mean values among movement statistics of mature males and females, adults and juveniles, and between sites A and B. If assumptions were not met, I used the mean of the log-transformed values. If assumptions were still not met, I used Mann-Whitney U-tests. I used a low alpha value ($\alpha = 0.01$) to prevent type I error because I performed multiple tests.

Annual Home Range

I generated 100% MCP, 95% MCP, and 95% KDE polygons using the `adehabitathr` package (Calenge 2006). Home range estimators are sensitive to the number of relocations included (Stone and Baird 2002). I have presented estimates here for each individual with 25 or more relocations, but only included individuals tracked from one aquatic season into the next in annual home range comparisons (minimum number of relocations > 46) in order to account for some of the annual movement variation I observed. I then plotted annual home range size estimates by number of relocations for each individual to determine whether this period was an adequate duration to observe asymptotic area estimates and make inferences about the migratory nature of the species. I estimated the annual home range size several times for each individual: once using all relocations, once without repeated consecutive coordinates, once using the reference bandwidth, and once using the least-squares cross validation (LSCV). When possible, I used the `ctmm` package (Fleming and Calabrese 2019) to estimate 95% AKDE polygons of the best fitting model for each individual using the standard workflow for `ctmm` described by Calabrese et al. (2016) on datasets that included and excluded repeated consecutive coordinates. For each individual, I visually compared all potential annual home range polygons to plotted relocations, recorded whether or not the LSCV succeeded in minimizing the mean integrated standard error (MISE), recorded notes on polygon separation and smoothing, and recorded notes on the visual fit of variograms for both datasets. I made statistical comparisons for annual home range estimates among sites and demographics as described for movement statistics above.

Core Activity Area

Using the process described above, I also estimated 50% MCP, 50% KDE (using both the reference bandwidth and LSCV), and 50% AKDE polygons using both datasets. Because *D. r. miaria* is inactive when aestivating, I also generated 100% MCP, 95% MCP, 50% MCP, 95% KDE, and 50% KDE polygons using a third dataset that only included aquatic positions to see if it provided better estimations of the core activity area. I made statistical comparisons for core area estimates among sites and demographics as described for movement statistics and annual home range estimates above.

Landscape Characteristics

In order to decipher the relationships between annual home range size and the spatial characteristics of the landscape, I measured three variables for each qualifying individual in the annual home range dataset: the number of wetlands visited by the individual, the total summed area of wetlands visited (SWA), and the mean pairwise distance (MPD) between all wetlands used by the individual (a surrogate for the level of spatial isolation within the wetland mosaic). I considered any inundated area visited by an individual to be a wetland for the purposes of this study. The dataset did not meet the homoscedasticity assumptions of linear regression analysis. I implemented a less assumptive multivariate process called classification and regression tree (CART) analysis, which is a form of recursive partitioning (Breiman et al. 1984). Using the package `rpart` (Therneau and Atkinson 2019), I created regression trees assigning 95% KDE areas and 100% MCP areas as response variables and the three landscape characteristics as predictor variables. I examined the risk level at complexity parameters

for each split, then pruned the trees to the number of splits that minimized the cross-validated error without overfitting the data.

Software

I performed all statistical analyses in R version 3.6.1 (R Core Team 2013) using the integrated development environment RStudio version 1.2.1335 (RStudio Team 2018). I created additional figures using either base plot or package `ggplot2` (Wickham 2016).

Results

Telemetry

I tracked 47 individuals during the study, including 15 at Site A, 28 at Site B, and 4 at Site C. Unfortunately, 13 individuals shed their radios in late May of 2018 and were not relocated after detachment. After switching to anterior radio placement, no radios detached. GPS loggers did not capture positions during aquatic activity. I did not include logger data in movement or annual home range analyses because they added few positions to the dataset and had variable GPS error. At KPC, 2 individuals (1 mature female and 1 juvenile) were preyed upon during the activity season before accumulating 25 relocations and one mature male was preyed upon during the 2019 activity season.

Of the 19 individuals that were relocated more than 25 times, 4 individuals (3 mature females and 1 mature male) used only one wetland each during both seasons, and 5 individuals (1 mature female, 2 mature males, and 2 immature females) used only one wetland but were only monitored for one season. Five individuals (1 mature female, 1

mature male, and 3 immature females) used a complex of 2-4 wetlands each (8-282 m apart in nearest wet season boundary distance), sometimes moving between multiple wetlands several times. Three individuals (2 mature females and 1 immature female) moved from one wetland to another during the first season and never returned to the first, but it is unclear whether that represents permanent emigration because the duration of the study was relatively short when compared to the lifespan of turtle species. One on-site emigration was between wetlands over 800 meters apart. Two individuals (both mature males) used 6 wetlands each, moved off-site, and may have been emigrating individuals. The first individual seemed to emigrate gradually, making several long upland migrations between aestivation sites and wetlands during the winter of 2018, and beginning the 2019 season in a wetland 1.6 km away from the wetland of initial capture. This individual made one more migration to a wetland over 600 m away before moving far enough off-site to lose signal. The second potential emigrant used two wetlands during the 2018 season, used the same two wetlands from March 2, 2019 to April 19, 2019, then made 5, wetland to wetland migrations between April 19 and May 24, 2019 before moving so far off-site that the signal was lost. Its final wetland before moving out of range was 1.8 km away from the wetland of initial capture. In addition to these two individuals, I lost signal for unknown reasons to 5 juveniles in 2018 and 2 mature males in 2019. It is possible that these individuals wandered off-site. Among 24 monitored individuals at KPC sites that were not relocated at least 25 times, 5 individuals used between 2 and 4 wetlands each, and 19 used only one wetland during their limited monitoring periods.

At Site C, I monitored 4 individuals (2 mature males, 1 mature female, and 1 unsexed juvenile) from the 2019 active season through aestivation to November. All four individuals used only one wetland while monitored, but one individual had been captured prior to the study in a wetland on the opposite side of a moist-soil management levee. The juvenile was preyed upon during the 2019 aestivation season.

At KPC, I stopped tracking most individuals in December of 2019 and have only included data recorded before that time in analyses for this study. I did, however, continue tracking 8 individuals through July of 2020 and observed almost no movement, even during the usual activity season described in Chapter II. Weather data collected by the KPC indicated that rainfall had been substantially lower than normal from July 2019 to December 2019, resulting in a severe drought during the 2020 season. Some wetlands occupied in 2018 and 2019 remained completely dry through the entire 2020 activity season. Only 1 of the 8 monitored individuals was tracked to aquatic habitat in 2020 and was aestivating underground during both the prior and following tracking sessions. Occasionally, aestivating individuals moved to new aestivation sites a few meters away during the spring of 2020. On one occasion, two individuals aestivating in a field that was disked to provide ground-nesting bird habitat moved to new aestivation sites in the nearest upland area that had not been disked. Similar drought conditions were observed but not as severe during the 2020 trapping sessions at Site C. Many individuals were active, but the inundated portion of the wetland was much smaller than during the 2019 season. The portions of Site C that were trapped in 2019 were completely dry in 2020.

Movements

The mean daily distance traveled ranged from 3.3 m to 18.5 m ($\mu = 9.5$ m, $N = 14$) among individuals monitored two seasons at KPC sites (Table 4), and the total distance traveled ranged from 1,661 m to 7,025 m ($\mu = 4,102$ m, $N = 14$). Total net displacement ranged from 62 m to 2,250 m among individuals monitored two seasons ($\mu = 577$ m, $N = 14$). I found no significant movement parameter differences between sites A and B (Table 5) or between adults and juveniles, but the only qualifying juveniles were immature females that were larger than mature male size (Table 6). I found no significant differences between the movement parameters of mature males and mature females, but males consistently had higher mean values (Table 7).

Annual Home Range

Best annual home range model choice varied depending on the space use of the individual (Table 8). For 8 of the 9 individuals that used only one wetland, the 100% MCP appeared to be a reasonable representation of the annual home range, although it included large areas not used in either state (i.e., active or aestivating) for one individual. For the 5 individuals that used wetland complexes, the 100% MCP appeared reasonable for only 1 individual, including large areas unused in either state by the other 4 individuals. The portion of unused area included was further amplified in individuals that permanently changed wetlands or migrated off-site. The 95% MCP had similar issues, but in individuals that used only one wetland the polygons excluded multiple aestivation sites, portions of the wetland that are frequently used, or both, depending on how many relocations had been in the dormant state and whether or not repeated

consecutive coordinates were included. All 95% KDE polygons using the reference bandwidth included some areas unused by the individual, but provided reasonable representation of the annual home range area nonetheless in all but one individual (2254), a potential emigrant, for which the method placed a large, oversmoothed buffer on the entire area used by this individual until it began its migration off-site. When repeated consecutive coordinates were removed, the 95% KDE polygons placed smaller buffers on aestivation sites (as expected) and seemed to display better polygon smoothing (Figure 9).

The LSCV failed to minimize the MISE for 18 of the 19 individuals when all relocations were included but succeeded in minimizing the MISE for 14 individuals when repeated consecutive coordinates were removed. Among the latter, the LSCV failed to minimize the MISE for the 2 individuals that migrated off-site, 2 of the on-site individuals that changed wetlands permanently, and 1 individual that used multiple wetlands spread across an elongate north-south gradient. The larger the individual's cluster of relocations was, the more likely the LSCV would fail. For 13 of the 19 individuals, the 95% KDE polygon using the LSCV without repeated consecutive coordinates appeared under-smoothed and separated the annual home range area into 2-10 polygons. For the 6 individuals that only used one wetland or a complex of nearby wetlands the polygons presented reasonable annual home range estimates. For 14 of the 16 individuals where AKDE estimates were possible, the OU anisotropic model provided the best fit. For one individual that stayed in the same wetland for two seasons the isotropic alternative performed better, and for one emigrating individual the OUF

Table 4. Movement values for individuals with 25 or more relocations at sites A and B, and all monitored *D. r. miaria* at Site C.

Site	ID	Sex	Life Stage	CL (cm)	Mass (g)	Relocations	Distance Traveled (m)	Mean Step Length (m)	SD Step Length (m)	Days Monitored	Days to Last Unique Position	Mean Daily Distance (m)	Total Net Displacement (m)
A	2222	F	A	20.1	1310	92	4557.3	49.5	48.7	598	570	8.0	148.6
	2242	F	A	17.3	933	78	2069.6	26.5	45.9	558	558	3.7	234.7
	2266	F	A	21.1	1500	77	4450.0	57.8	103.2	532	416	10.7	81.1
	2279	F	A	19.2	1191	44	1072.9	38.7	30.7	235	207	5.2	297.4
	2229	M	A	16.2	641	53	5195.3	98.0	174.8	426	426	12.2	1804.8
	2237	M	A	13.3	327	49	1785.7	36.4	35.7	350	350	5.1	62.3
	2288	M	A	16.8	636	41	1646.8	40.2	34.2	151	151	10.9	227.5
	2296	F	J	14.3	466	28	521.1	18.6	34.7	126	126	4.1	167.6
	2297	F	J	13.9	408	26	681.3	26.2	44.0	111	100	6.8	144.5
B	2255	F	A	16.5	681	60	5261.8	87.7	80.0	460	450	11.7	284.3
	2269	F	A	16.9	777	77	1661.2	21.6	41.2	531	503	3.3	331.7
	2270	F	A	17.5	925	72	3047.1	42.3	108.9	440	416	7.3	977.9
	2230	M	A	11.8	237	85	4881.6	57.4	93.6	510	424	11.5	697.3
	2254	M	A	16.1	626	47	7025.3	149.5	199.6	379	379	18.5	2250.0
	2246	M	A	11.6	215	39	2585.6	66.3	57.3	167	106	24.4	347.1
	2241	F	J	13.3	345	62	1789.5	28.9	55.4	382	382	4.7	33.8
	2252	F	J	13.2	403	74	5639.8	76.2	99.5	480	436	12.9	578.0
	2260	F	J	13.3	410	64	6312.1	98.6	89.1	455	445	14.2	280.4
2268	F	J	15.4	577	59	3753.5	63.6	60.3	440	388	9.7	307.7	
C	2000	F	A	20.5	1347	17	579.6	34.1	65.9	249	219	2.6	268.6
	0007	M	A	15.3	496	16	1489.1	93.1	104.0	204	174	8.6	406.9
	4000	M	A	15	460	17	1111.6	65.4	103.2	204	98	11.3	423.3
	0004	U	J	8.1	97	10	1064.2	106.4	67.2	115	115	9.3	89.2

Table 5. Comparisons between mature *D. r. miaria* movement statistics (m), annual home range estimates (m²), and core area estimates (m², below line) at Sites A and B ($\alpha = 0.01$). NRCC indicates that repeated consecutive coordinates were removed. * indicates that non-transformed values were used; all others were log-transformed for comparison. ** indicates that I performed a Mann-Whitney U-test. All mean values are displayed non-transformed.

	Site A		Site B		<i>t</i> -value or <i>W</i> -statistic	<i>p</i> -value
	<i>n</i>	Mean \pm SD	<i>n</i>	Mean \pm SD		
Total Distance Traveled*	5	3612 \pm 1567	9	4375 \pm 1924	-0.80	0.44
Mean Daily Distance Traveled*	5	7.94 \pm 3.59	9	10.43 \pm 4.78	-1.10	0.30
Total Net Displacement	5	466 \pm 751	9	638 \pm 665	-0.97	0.36
100% MCP	5	3.4 e5 \pm 5.9 e5	9	2.0 e5 \pm 2.8 e5	-0.31	0.77
95% KDE	5	10.3 e5 \pm 20.1 e5	9	3.8 e5 \pm 4.3 e5	-0.32	0.76
95% KDE NRCC	5	11.8 e5 \pm 22.6 e5	9	4.4 e5 \pm 6.0 e5	-0.29	0.78
95% AKDE**	5	21.3 e5 \pm 45.7 e5	9	4.9 e5 \pm 5.3 e5	<i>W</i> = 10	0.11
95% AKDE NRCC**	5	19.8 e5 \pm 42.1 e5	9	5.8 e5 \pm 7.8 e5	<i>W</i> = 12	0.19
50% MCP	5	0.8 e5 \pm 1.6 e5	9	0.2 e5 \pm 0.2 e5	-0.26	0.80
50% KDE**	5	2.8 e5 \pm 5.7 e5	9	0.7 e5 \pm 0.6 e5	<i>W</i> = 15	0.36
50% KDE NRCC**	5	3.3 e5 \pm 6.8 e5	9	0.7 e5 \pm 0.8 e5	<i>W</i> = 15	0.36
95% KDE (LSCV) - aquatic positions only**	5	0.6 e5 \pm 0.8 e5	9	0.4 e5 \pm 0.3 e5	<i>W</i> = 26	0.70

Table 6. Comparisons ($\alpha = 0.01$) between adult and juvenile *D. r. miaria* movement statistics (m), annual home range estimates (m²), and core area estimates (m², below line). NRCC indicates that repeated consecutive coordinates were removed. * indicates that non-transformed values were used; all others were log-transformed for comparison. ** indicates that I performed a Mann-Whitney U-test. All mean values are displayed non-transformed.

	Adult		Juvenile		<i>t</i> -value or <i>W</i> -statistic	<i>p</i> - value
	n	Mean \pm SD	n	Mean \pm SD		
Total Distance Traveled*	10	3393 \pm 1779	4	4374 \pm 2035	-0.33	0.76
Mean Daily Distance Traveled*	10	9.21 \pm 4.67	4	10.37 \pm 4.24	-0.45	0.67
Total Net Displacement	10	630 \pm 754	4	300 \pm 223	0.58	0.58
100% MCP	10	3.1 e5 \pm 4.7 e5	4	1.0 e5 \pm 0.4 e5	0.45	0.66
95% KDE	10	7.5 e5 \pm 14.3 e5	4	2.6 e5 \pm 1.3 e5	-0.11	0.91
95% KDE NRCC	10	8.9 e5 \pm 16.2 e5	4	2.2 e5 \pm 1.1 e5	0.42	0.68
95% AKDE**	10	13.8 e5 \pm 31.8 e5	4	3.1 e5 \pm 0.9 e5	<i>W</i> = 18	0.84
95% AKDE NRCC	10	2.1 e5 \pm 1.8 e5	4	3.0 e5 \pm 1.5 e5	0.10	0.92
50% MCP	9	0.5 e5 \pm 1.2 e5	4	0.3 e5 \pm 0.2 e5	-1.33	0.21
50% KDE	10	1.8 e5 \pm 4.0 e5	4	0.6 e5 \pm 0.3 e5	-0.52	0.62
50% KDE NRCC	10	2.1 e5 \pm 4.7 e5	4	0.5 e5 \pm 0.3 e5	0.31	0.76
95% KDE (LSCV) - aquatic positions only	10	0.5 e5 \pm 0.6 e5	4	0.4 e5 \pm 0.3 e5	0.11	0.92

Table 7. Comparisons ($\alpha = 0.01$) between mature female and mature male *D. r. miaria* movement statistics (m), annual home range estimates (m²), and core area estimates (m², below line). NRCC indicates that repeated consecutive coordinates were removed. * indicates that non-transformed values were used; all others were log-transformed for comparison. All mean values are displayed non-transformed.

	Female		Male		<i>t</i> -value	<i>p</i> -value
	n	Mean \pm SD	n	Mean \pm SD		
Total Distance Traveled*	6	3508 \pm 1467	4	4722 \pm 2174	-0.98	0.37
Mean Daily Distance Traveled*	6	7.45 \pm 3.47	4	11.84 \pm 5.49	-1.42	0.22
Total Net Displacement	6	343 \pm 324	4	1204 \pm 1003	-1.06	0.35
100% MCP	6	0.8 e5 \pm 0.8 e5	4	6.5 e5 \pm 6.3 e5	-1.49	0.21
95% KDE	6	1.5 e5 \pm 1.4 e5	4	16.4 e5 \pm 20.8 e5	-1.62	0.18
95% KDE NRCC	6	2.1 e5 \pm 2.1 e5	4	19.2 e5 \pm 23.5 e5	-1.39	0.24
95% AKDE	6	1.9 e5 \pm 1.6 e5	4	31.8 e5 \pm 48.1 e5	-1.55	0.20
95% AKDE NRCC	6	2.2 e5 \pm 1.8 e5	4	31.6 e5 \pm 43.8 e5	-1.38	0.24
50% MCP	5	0.6 e4 \pm 0.6 e4	4	1.1 e5 \pm 1.8 e5	-2.29	0.07
50% KDE	6	0.3 e5 \pm 0.2 e5	4	4.1 e5 \pm 6.1 e5	-1.82	0.15
50% KDE NRCC	6	0.4 e5 \pm 0.3 e5	4	4.8 e5 \pm 7.2 e5	-1.50	0.21
95% KDE (LSCV) - aquatic positions only	6	0.2 e5 \pm 0.7 e4	4	0.9 e5 \pm 0.8 e5	-2.95	0.04

Table 8. Annual home range and core area estimates (m²) for *D. r. miaria* with over 25 relocations at KPC sites. * indicates that repeated consecutive coordinates were removed from the dataset. Individuals with a 50% MCP of 0 m² were located at aestivation sites at least 50% of the time.

Site	ID	Sex	Life Stage	CL (cm)	Relocations	100% MCP	95% KDE	95% KDE*	95% AKDE	95% AKDE*	50% MCP	50% KDE	50% KDE*	95% KDE (LSCV, aquatic)
A	2222	F	A	20.1	92	32531	54674	41462	59168	37332	4087	10749	6635	14865
	2242	F	A	17.3	78	22610	46950	67115	43135	53973	951	10007	17628	20622
	2266	F	A	21.1	77	244638	386780	542473	187482	268357	16301	60865	77394	27198
	2279	F	A	19.2	44	19606	43546	35800	165203	114570	1085	6805	5652	3521
	2229	M	A	16.2	53	1393961	4626344	5211595	10300190	9511380	371213	1311792	1543541	196904
	2237	M	A	13.3	49	19188	49067	41996	49370	39896	10075	13858	10464	27155
	2288	M	A	16.8	41	14324	32467	29659	29654	28816	2342	7128	5679	12568
B	2255	F	A	16.5	60	72601	117240	121881	374844	360504	6062	25210	25376	6916
	2269	F	A	16.9	77	35066	68700	98421	71408	96744	0	13145	21191	22046
	2270	F	A	17.5	72	99983	267953	387441	377304	479464	2733	46311	63022	14808
	2230	M	A	11.8	85	245286	413934	451697	493862	462935	12161	81273	81100	40787
	2254	M	A	16.1	47	936627	1478191	1987597	1869772	2631474	34432	218565	274510	104444
	2241	F	J	13.3	62	39359	141729	127013	195065	134171	8634	31896	20110	9457
	2252	F	J	13.2	74	142700	447308	378125	317007	326278	59549	111628	83446	72058
	2260	F	J	13.3	64	113588	262951	235047	415032	489661	30483	71082	56348	16036
2268	F	J	15.4	59	86675	188440	151727	296897	256060	32874	50348	32624	51050	

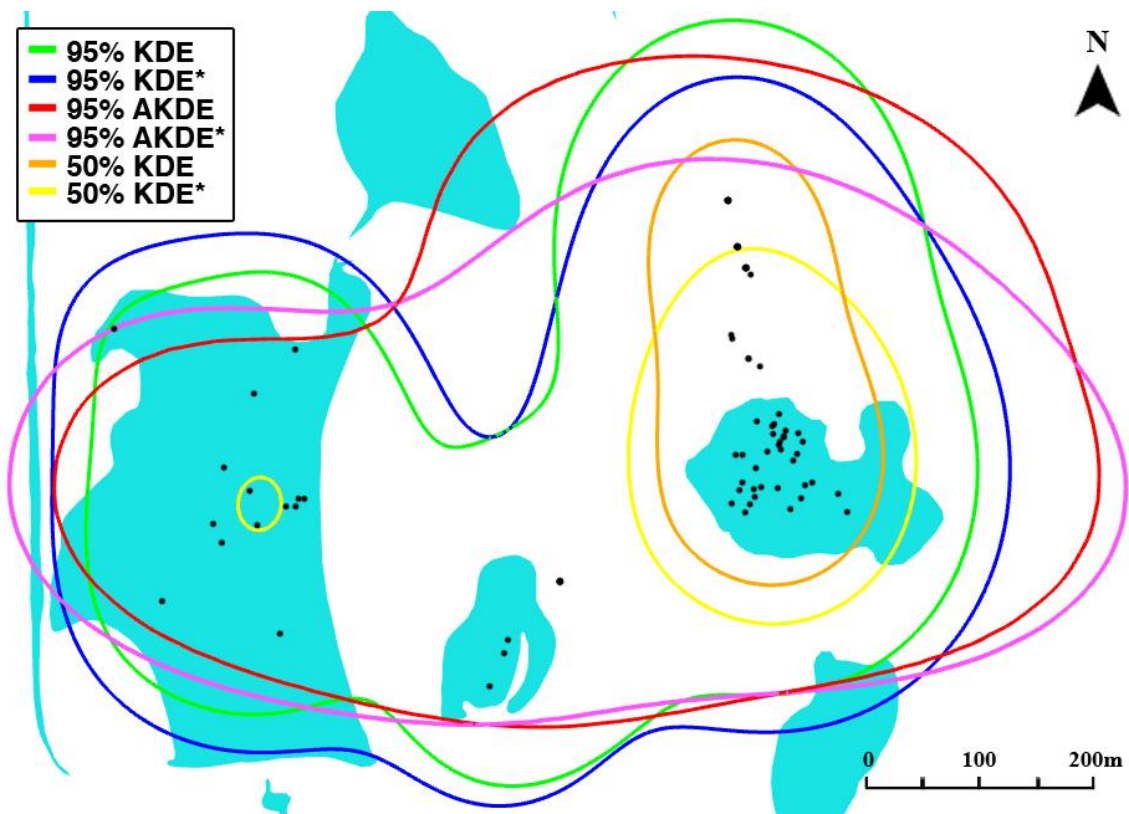


Figure 9. Map of wetlands occupied by *D. r. miaria* displaying 4 annual home range estimates and 2 core activity area estimates for 1 mature male (2230). Symbol “*” indicates that repeated consecutive coordinates were removed. The 95% KDE polygons provide better exclusion of unused area, while 95% AKDE polygons implement better smoothing parameters. Both of the core area estimators are questionable, as *D. r. miaria* only forage and mate in the water.

isotropic model, which corrects for temporal autocorrelation, provided the best fit. Upon inspection of the variograms, model fit among the recommended models seemed appropriate for 14 individuals, including the emigrating individual with temporal autocorrelation. Variograms appeared questionable for two individuals that spent considerable time in an eroded segment of an ephemeral irrigation canal. Removing repeated consecutive coordinates only improved the variogram fit for 3 individuals.

For 13 individuals where AKDE estimates were possible, the polygons represented reasonable annual home ranges (Figure 9). Removing repeated consecutive coordinates either improved smoothing of the AKDE polygons or excluded some of the aestivation area, but also widened confidence intervals if the individual had an elongate collection of relocations. For 3 individuals with relocation clusters elongated from north to south either through activity in the canal segment, emigration off-site, or permanent on-site emigration, both AKDE polygons seemed over-smoothed, provided very large annual home range estimates, and had very wide confidence intervals (Figure 10).

I found no significant differences in annual home range area estimates between sites A and B (Table 5) or between adults and juveniles, but the only qualifying juveniles were immature females that were larger than mature male size (Table 6). I found no significant differences between the annual home range area estimates of mature females and mature males, but males consistently had higher mean values (Table 7). I calculated mean and standard deviations for population annual home range size across all methods using all qualifying individuals at sites A and B (Table 9). The number of relocations required to observe an asymptotic relationship with annual home range size varied (Figure 11). For 8 of the 14 qualifying individuals, less than 20 relocations were necessary to estimate 95% KDE areas. For the others, the relationship between the number of relocations and annual home range size displayed a series of shelves during intermittent resting periods and sudden increases during wetland to wetland migrations. I also plotted 100% MCP areas for a more direct visual representation of this phenomenon (Figure 11B). The 95% KDE areas for the two potential emigrants were still increasing

when they migrated out of signal range after ~50 relocations had been collected (Figure 11A, gray lines).

Core Activity Area

For most individuals, the 50% MCP provided the poorest representation of the core activity area (Figure 12). For individuals that used one wetland, they often excluded large portions of the wetland if the active positions were evenly distributed throughout the wetland area. For individuals that used multiple wetlands, they often included large areas never used by the individual or excluded some frequently used wetlands entirely. For three individuals, the 50% MCP method did not generate a polygon when including all positions because more than 50% of the relocations were at recorded single aestivation sites. For individuals that only used one wetland, the 100% MCP and 95% MCP from datasets that only included aquatic positions provided reasonable core area estimates but included a lot of upland area when individuals used more than one wetland. The 50% MCP from that dataset either excluded portions of the wetland that were frequently used if the positions were evenly distributed or left some wetlands out entirely for individuals that used multiple wetlands. The 50% KDE polygons using the reference bandwidth only projected a reasonable activity area for 1 of 19 individuals when the whole dataset was used and 3 of 19 individuals when repeated consecutive coordinates were removed. When using either dataset, the estimators either included aestivation sites, excluded entire wetlands (Figure 12), or projected parcels that included no wetland area because the individual had more aestivation positions than active relocations.

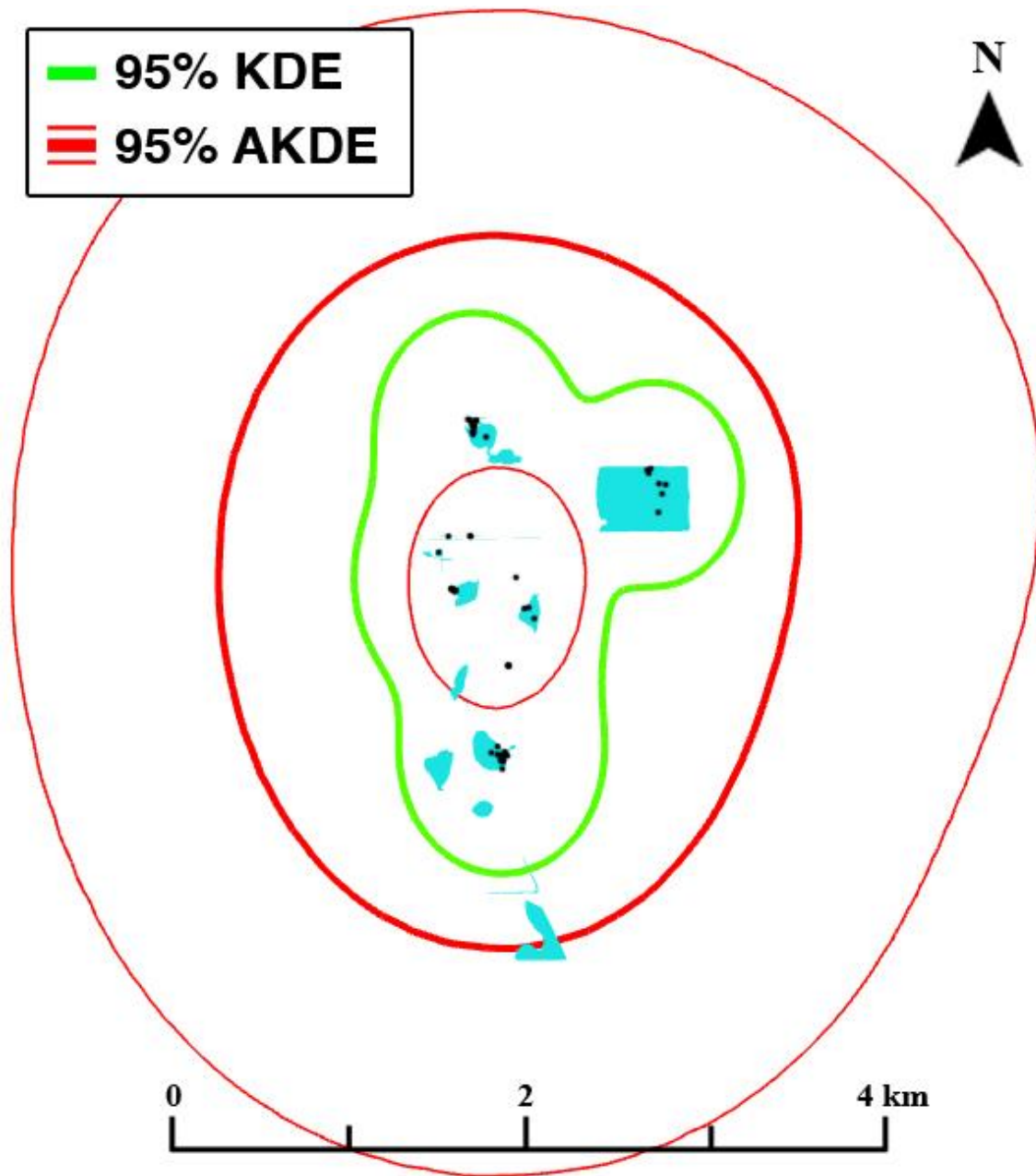


Figure 10. Map of wetlands occupied by *D. r. miaria* displaying the 95% KDE (green boundary) and 95% AKDE (thick red boundary) with 95% confidence intervals (thin red boundaries) for 1 mature male (2229). Although the OUF model had the best Δ AIC, accommodated the sequential order of spatial positions, and visually fit the variogram for this individual, the resulting estimate appears oversmoothed in comparison to the more widely utilized 95% KDE using the reference bandwidth.

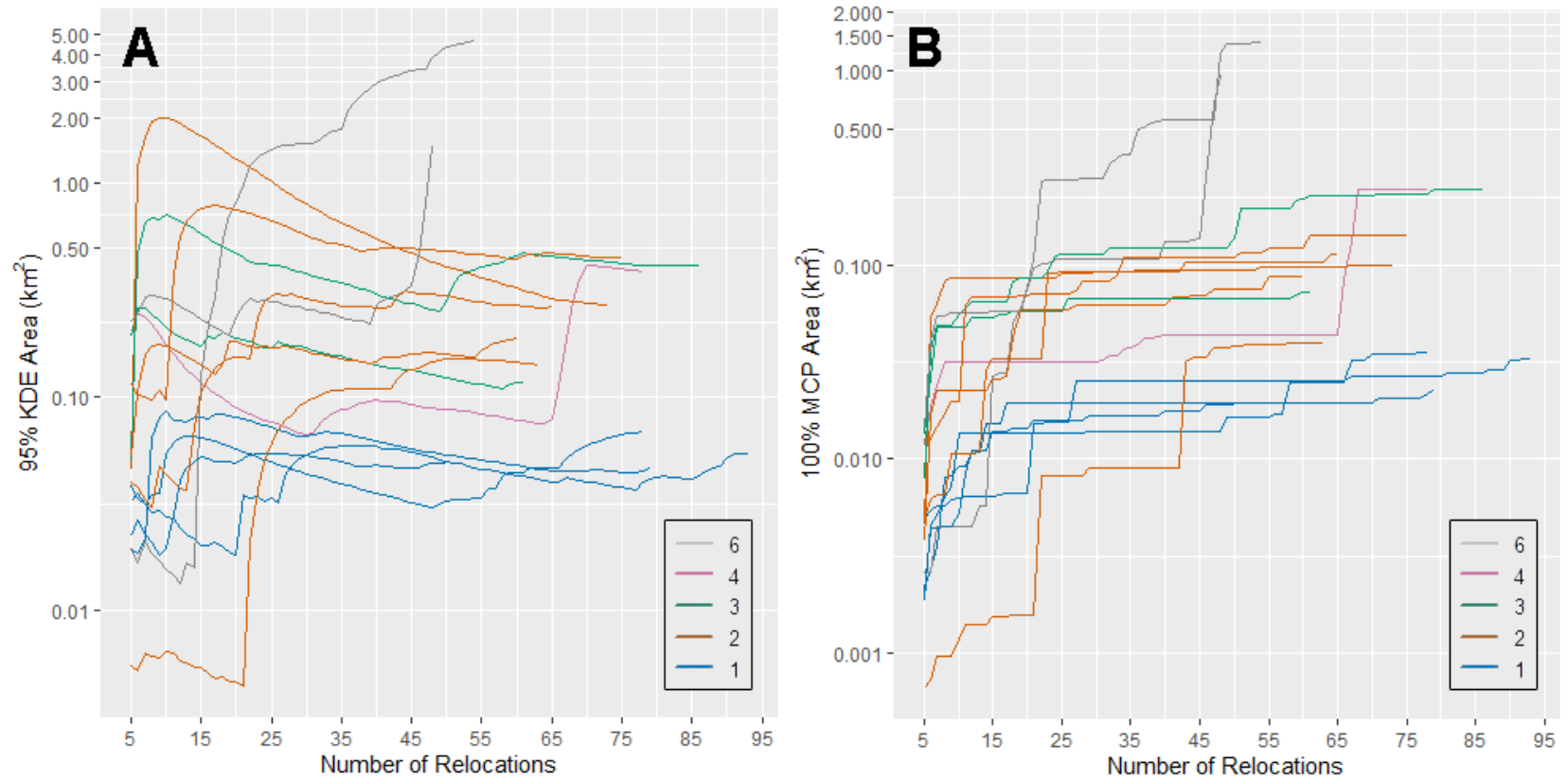


Figure 11. Plot of annual home range areas by the number of relocations included in the analysis. Line color indicates the number of wetlands visited by the individual: (A) plot of 95% KDE areas; (B) plot of 100% MCP areas.

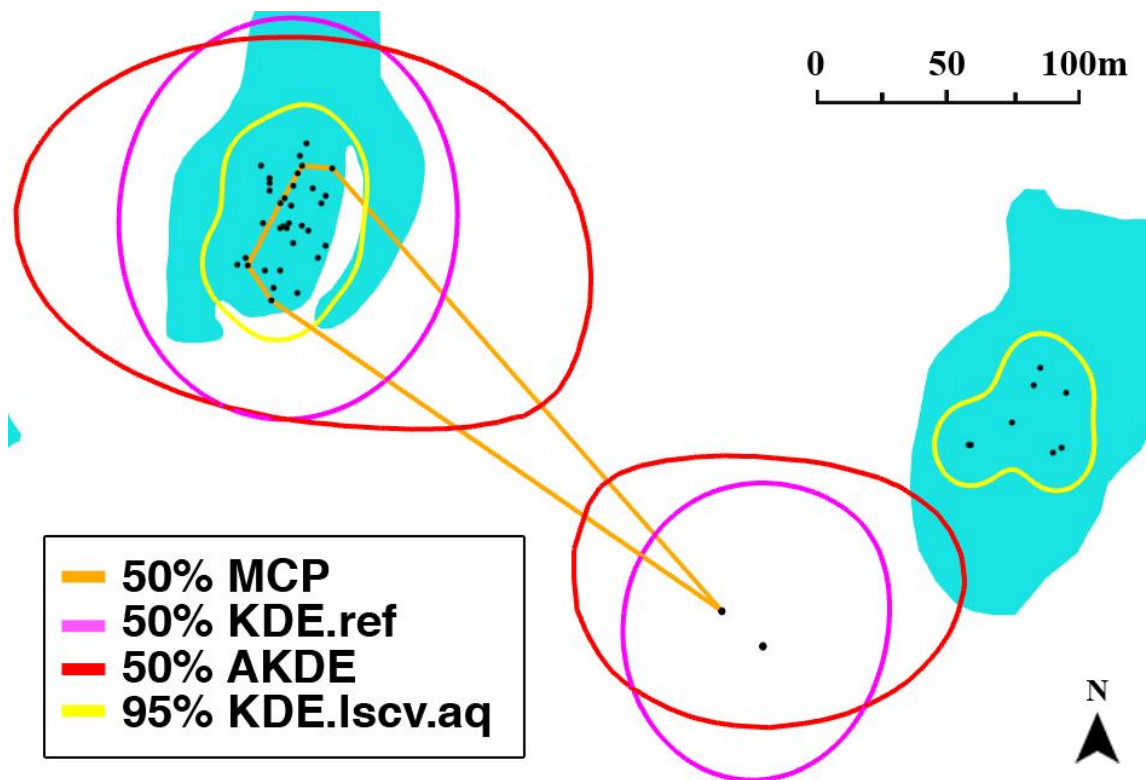


Figure 12. Map of wetlands occupied by *D. r. miaria* displaying 4 core area estimates for one immature female (2241). The 50% MCP, 50% AKDE, and 50% KDE using the reference bandwidth included upland areas not used for mating or foraging and neglected an entire wetland used by the individual. The 95% KDE using the LSCV and only aquatic coordinates provided a more reasonable core activity area for the individual.

The 50% AKDE polygons had similar issues, even when excluding repeated consecutive coordinates. The 50% KDE polygons using the LSCV and excluding repeated consecutive coordinates projected reasonable core area polygons for 5 individuals. For the other 14, the model provided reasonable core area polygons but also placed buffers around several aestivation sites, and a few estimates excluded wetlands used by the individual. The LSCV succeeded in minimizing the MISE for 13 individuals when only aquatic positions were included. The 95% KDE polygons using the LSCV

Table 9. Population mean and standard deviation values for all qualifying KPC individuals (Sites A and B, $N = 14$). * indicates that repeated consecutive coordinates were removed from the dataset. ** indicates that only aquatic positions were included in the dataset.

	Parameter	Mean \pm SD (m ²)
Annual Home Range	100% MCP	248,915 \pm 390,398
	95% KDE	610,733 \pm 1,168,326
	95% KDE*	703,114 \pm 1,339,201
	95% AKDE	1,075,038 \pm 2,596,479
	95% AKDE*	1,082,016 \pm 2,421,505
Core Area	50% MCP	42,111 \pm 92,723
	50% KDE	146,909 \pm 327,453
	50% KDE*	165,242 \pm 387,788
	95% KDE (LSCV**)	44,596 \pm 49,657

and only aquatic positions (Figure 12) provided good core use area estimates for 16 of 19 individuals and reasonable estimates for the other three, with the only apparent issues being under-smoothing and some upland inclusion because of the smoothing buffer. For the 6 individuals where the LSCV did not minimize the MISE, the polygons still provided the most reasonable core activity area estimates.

I found no significant differences between core area estimates of sites A and B (Table 5) or between adults and juveniles (Table 6). I found no significant differences between core area estimates of mature females and mature males, but males consistently had higher mean values (Table 7, $\alpha = 0.01$). I calculated mean and standard deviations for population core area size across all methods using all qualifying individuals at sites A and B (Table 9).

Landscape Characteristics

Landscape parameters SWA and MPD trended higher among individuals with larger annual home ranges sizes (Figure 13), but data did not meet the homoscedasticity assumptions of linear regressions. Both regression trees were overfit when pruned to the complexity parameters with the lowest cross-validated error (Table 10), so I plotted the cross-validated error by the corresponding number of splits for each tree (Figures 14 and 15), and concluded that the number of splits that minimized error risk without overfitting the pruned trees for 95% KDE area and 100% MCP area were 3 and 5, respectively (Figures 16 and 17). The regression tree analysis for 95% KDE areas included MPD and SWA as predictor variables (Figure 16). The analysis for 100% MCP areas included all three landscape predictor variables (Figure 17).

Discussion

Annual home range and core area estimates varied considerably depending on what estimation method was used (Table 8). The model of best fit was not the same for every individual, but the 95% KDE estimates with repeated consecutive coordinates removed provided the best fit for most individuals. Accounting for temporal autocorrelation yielded wide confidence intervals and did not improve model fit, even when repeated consecutive coordinates were included (Figure 10). Core activity area estimators were also problematic because of the tendency to migrate between wetlands. The 95% KDE polygons with LSCV smoothing provided the best estimates of core activity area when considering the inundation boundaries on the landscape (Figure 12).

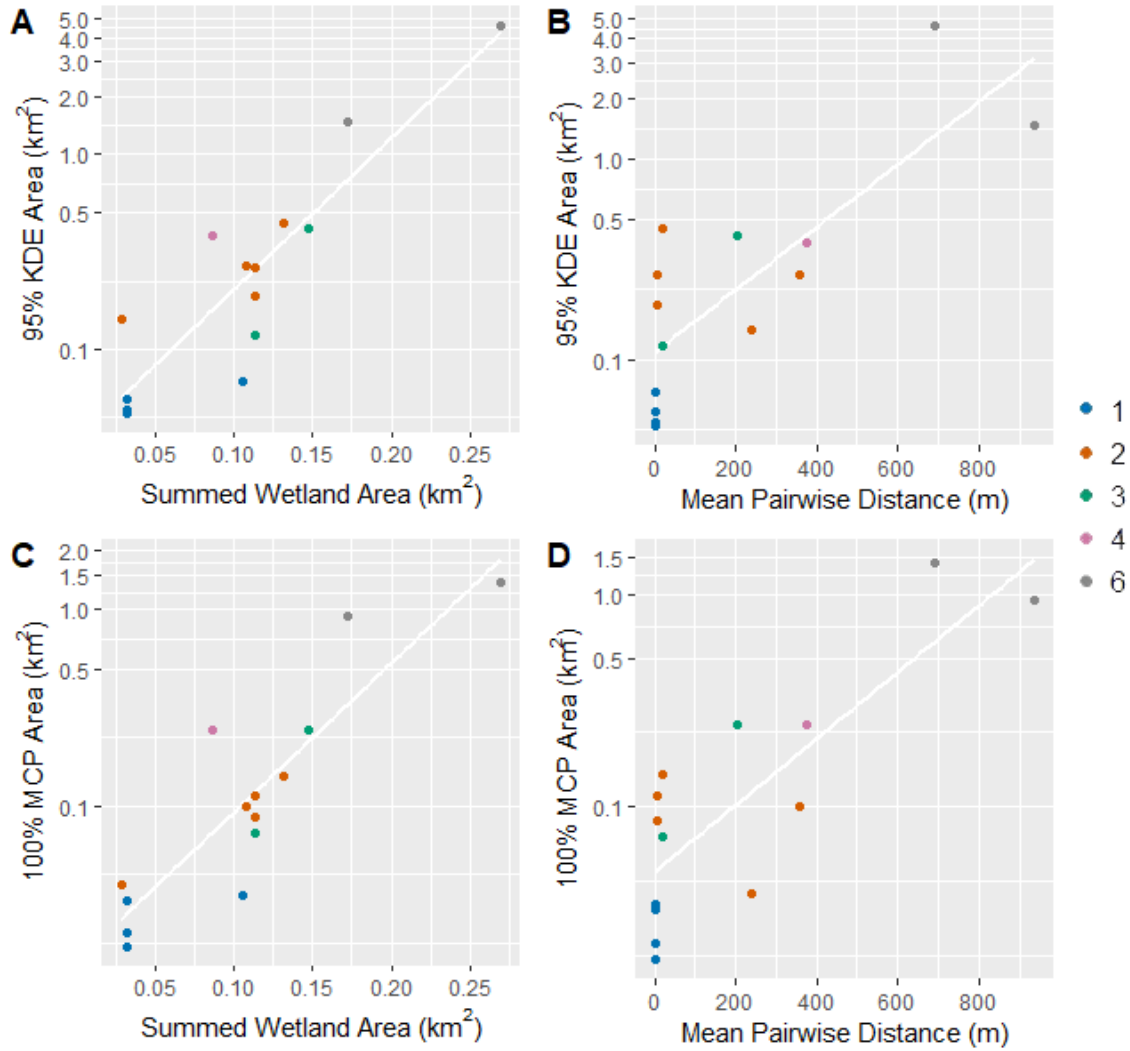


Figure 13. Plot of annual home range areas by landscape parameter value. Line color indicates the number of wetlands used by the individual: (A) 95% KDE areas by summed area of all wetlands used by the individual; (B) 95% KDE areas by mean pairwise distance between all wetlands used by the individual; (C) 100% MCP areas by summed area of all wetlands used by the individual; (D) 100% MCP areas by mean pairwise distance between all wetlands used by the individual.

Table 10. Cross-validation table for two unpruned regression trees using CART analyses of 95% KDE and 100% MCP areas as response variables and applying SWA, MPD, and Number of Wetlands used as predictor variables. SWA and MPD were used to construct the 95% KDE regression tree. All variables were used to construct the 100% MCP regression tree. Relative error values have been scaled so that trees with one node have an error value of 1.

Annual Home Range Estimator	Complexity Parameter	Number of Splits	Relative Error	Cross-validated Error Mean \pm SD
95% KDE	0.908723	0	1.000000	1.163 \pm 0.930
	0.078448	1	0.091277	1.518 \pm 1.031
	0.006967	2	0.012829	1.051 \pm 0.678
	0.003238	3	0.005862	1.052 \pm 0.677
	0.001593	4	0.002624	1.048 \pm 0.678
	0.000402	5	0.001031	1.049 \pm 0.678
	0.000377	6	0.000629	1.051 \pm 0.678
	0.000062	7	0.000252	1.051 \pm 0.678
	0.000029	8	0.000189	1.050 \pm 0.678
	0.000013	9	0.000160	1.050 \pm 0.678
	0.000000	10	0.000147	1.050 \pm 0.678
100% MCP	0.918298	0	1.000000	1.131 \pm 0.684
	0.049011	1	0.081702	0.621 \pm 0.386
	0.015634	2	0.032691	0.448 \pm 0.235
	0.009282	3	0.017057	0.477 \pm 0.232
	0.006831	4	0.007775	0.477 \pm 0.232
	0.000638	5	0.000945	0.464 \pm 0.234
	0.000054	6	0.000306	0.464 \pm 0.234
	0.000037	7	0.000252	0.462 \pm 0.234
	9.84x10 ⁻⁰⁸	8	0.000215	0.462 \pm 0.234
	6.89x10 ⁻⁰⁹	9	0.000215	0.462 \pm 0.234
	0.000000	10	0.000215	0.462 \pm 0.234

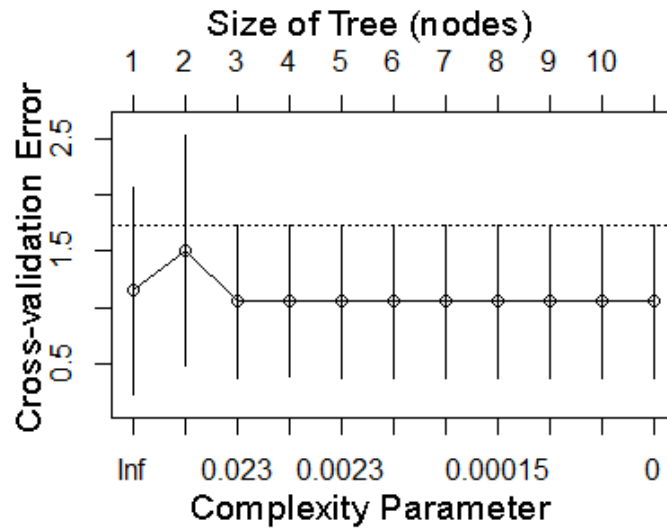


Figure 14. Plot of cross-validation error by regression tree complexity for 95% KDE areas.

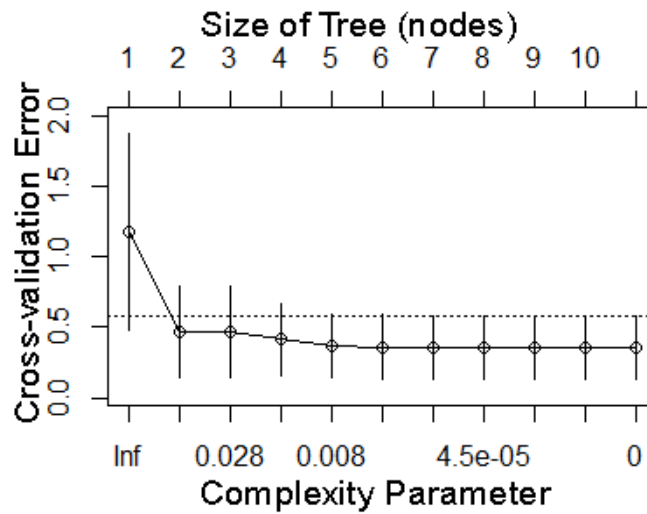


Figure 15. Plot of cross-validation error by regression tree complexity for 100% MCP areas.

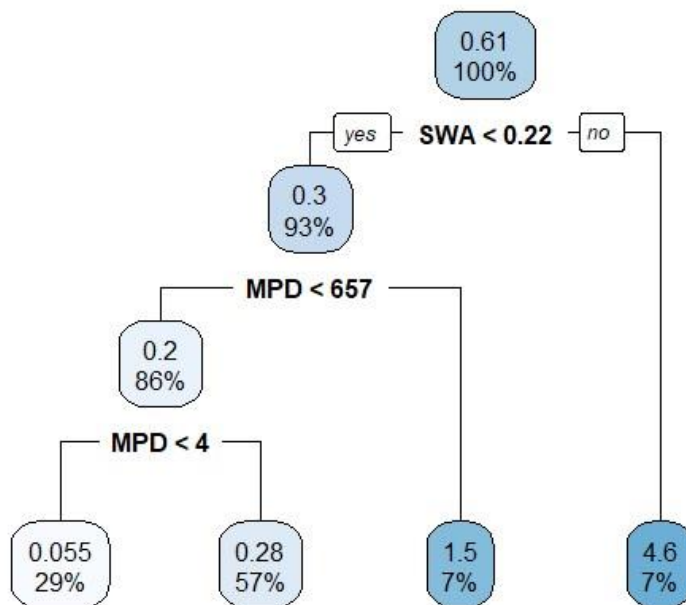


Figure 16. Pruned regression tree with 95% KDE areas as response variables and landscape characteristics as predictor variables.

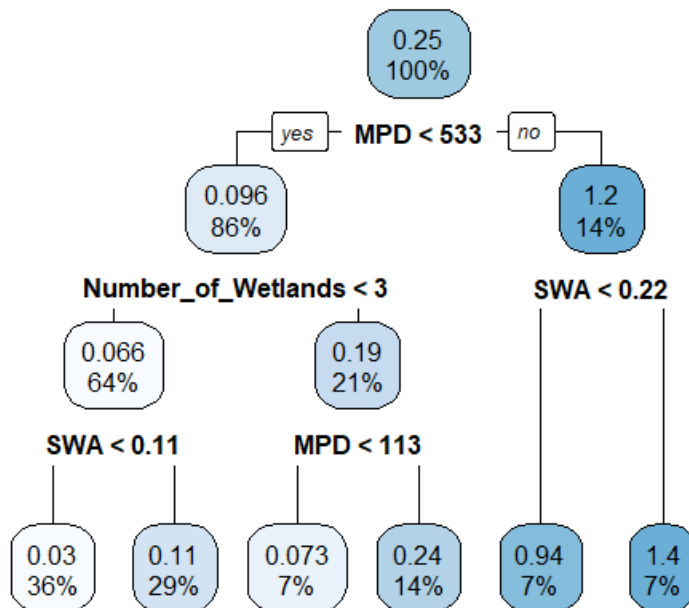


Figure 17. Pruned regression tree with 100% MCP areas as response variables and landscape characteristics as predictor variables.

In some species, the shape of a typical home range can dictate the method choice for researchers. For the Smooth Softshell Turtle (*Apalone mutica*), a riverine species, researchers clipped KDE areas to a shapefile of the river channel in order to exclude unused areas (Ross et al. 2019). For the white-lipped mud turtle (*Kinosternon leucostomum*), activity was restricted to a 2-3 m strip along the edge of a lake, leading researchers to define home range as “the linear distance between terminal observations along the shoreline of the lake” (Morales-Verdeja and Vogt 1997). It is possible that similar clipping procedures could allow for better application of traditional core area estimation methods (MCP and KDE) to a biologically meaningful understanding of *D. r. miaria* core activity areas in future studies. However, I caution that when only 50% of an individual’s relocations were used, the resulting shapefiles often excluded large wetland areas that were frequently used by the individual, especially with individuals that had relocations scattered evenly within the wetland areas. If a clipping procedure is used for *D. r. miaria*, I suggest clipping KDE shapefiles that include 95% of all aquatic positions to the surface inundation boundaries on the landscape.

Individuals in this study visited between 1 and 6 wetlands each, and the mean (248,915 m²; Table 9) and maximum (1,393,961 m²; Table 9) 100% MCP were 2.5 and 13.8 times, respectively, the size of the largest recorded MCP area for the species in a study with similar tracking durations. In Virginia, individuals moved up to 635 m in a season, had annual home ranges up to 101,000 m², and used between 1 and 9 wetlands each (Buhlmann 1995). In Florida, a marked individual moved 612 m in roughly 8 months (Marchand 1945). In another Florida study, some individuals occasionally

visited a very temporary wetland more than 300 m from a larger one (Dodd 1992; Dodd and Cade 1998). In Oklahoma, researchers documented some *D. r. miaria* movement between two wetlands that were 830 m apart (McKnight et al. 2012). In an Arkansas telemetry study, all *D. r. miaria* left the study site, were preyed upon, or shed the transmitters (Dinkelacker and Hilzinger 2009). In my study, two individuals made movements off-site in excess of 1,500 m from their original point of capture and it is possible that the 7 individuals I lost signal to also moved too far off-site to receive transmissions. The failure to continue monitoring the movements of those individuals may have resulted in either underestimated mean annual home range sizes due to exclusion of individuals with larger annual home ranges or an underestimation in the number of emigrating individuals. Sudden long-distance migrations over upland areas indicate potential for much larger lifetime home ranges when considering the longevity of turtles. Whether or not they eventually migrate back to the wetland complex of their origin remains unknown.

The variation in the number of relocations required to observe an asymptotic relationship with annual home range size may indicate that this species exhibits either irruptive or partial nomadism. The inability to reach asymptotic relationships in under one year (for long-lived animals) has been considered an indication of nomadic behavior (Bunnfeld et al. 2011). One possibility is that the species exhibits irruptive nomadism, defined by Teitelbaum and Mueller (2019) as “a form of nomadic movement where long-distance movement events are unpredictable in their timing and direction, but may be interspersed by long periods of residency”. Although most wetland-to-wetland

migrations happened during the aquatic activity season at KPC sites, one of the potential emigrants in my study migrated off-site during the inactive season along a path that included several aestivation sites and periods of dormancy. The other emigrating individual was resident in two nearby (7 m) wetlands for the 2018 season then emigrated suddenly during the 2019 activity season. The potential on-site emigrant made one wetland-to-wetland movement during the 2018 activity season, then aestivated nearby and remained in that wetland for the entire 2019 activity season. These periods of residency interrupted by long-distance migrations indicate the possibility of irruptive nomadism. Another possibility is that the species exhibits partial nomadism, defined as “a form of nomadic movement where some individuals in a population are nomadic and others are range residents or migratory” (Teitelbaum and Mueller 2019). In a study on Blanding’s Turtles (*Emydoidea blandingii*), a similar species that uses isolated wetlands, aestivates in uplands, and can make long-distance migrations over land, 39% of 83 females and 50% of 60 males maintained the same wetland of residence for more than 20 years (Congdon et al. 2011), indicating the possibility of partial nomadism. In another study on *E. blandingii*, multi-year (2-6 years) home range sizes were significantly larger than annual home range sizes (Schuler and Thiel 2008). In my study, 4 individual *D. r. miaria* used only one wetland for the duration of the study, and 5 individuals used complexes of wetlands that are less than 300 m apart, sometimes returning to the same wetland multiple times. It is possible that these represent resident individuals, while others represent nomadic individuals, indicating behaviors of partial nomadism. The only way to determine whether the species exhibits irruptive nomadism, partial

nomadism, or extremely large resident ranges is to design a longer study. The continued increases in 95% KDE area estimates after two years of tracking for some individuals (Figure 11) indicates that relocation frequency may not be as important as study duration for our understanding of long-term *D. r. miaria* spatial ecology.

Although I did not observe significant differences in movement and annual home range parameters between study sites (Table 5), the differences in movement observations among studies described above could indicate differences in movement patterns between populations, regions, or subspecies. The two sites that qualified for comparison were relatively close together (~9 km), were formerly connected via contiguous parcels of similar habitat, and could represent one population. In the 1940's, the prairie pothole wetland mosaic in the Katy Prairie between State Highway 290, Interstate Highway 10, and the Brazos River included 114,790 hectares of contiguous habitat similar in wetland density and isolation to Sites A and B, and may have included up to 50% more contiguous habitat if the highways were not barriers to dispersal at that time. Now, the boundaries are elevated 6-lane highways with concrete barricades and the original prairie pothole wetland mosaic in this area has been reduced to at least 8 fragments ranging from 316 to 7,530 hectares and summing to 15,421 total hectares (13% of the prior area). The remaining portions of the mosaic have been altered by residential development, plowing for agriculture, conversion of wetlands to perennial ranching ponds, construction of reservoirs, and forestation via the encroachment of Chinese Tallow (*Triadica sebifera*) and Yaupon (*Ilex vomitoria*). I do not know how this reduction in connectivity has affected the movement behaviors and metapopulation

dynamics of *D. r. miaria* in this system, but regression trees indicated that landscape parameters may have an influence on annual home range size (Figures 13, 16-17). For the Eastern Long-necked Turtle (*Chelodina longicollis*), an Australian obligate carnivore that migrates over land between ephemeral wetlands and aestivates in terrestrial refugia, landscape attributes had more influence on movements and use of space than body size or demographic group (Roe and Georges 2008). A comparative review using data on 64 turtle species found that energetic constraints relating to body size had less influence on annual home range size in turtles than the energetic cost of locomotion through different habitats (Slavenko et al. 2016).

It is highly probable that annual home range size and movement distances shrink substantially during periods of drought, due to reduced activity during severe droughts and a reduction in inundated surface area available during moderate droughts. Even though individuals were active at Site C in 2020, the inundated area available to them was much smaller than in the year prior. In South Carolina, Buhlmann et al. (2009) also observed that *D. r. reticularia* abstained from aquatic activity entirely during two consecutive years of drought. Data on *D. reticularia* movement from dry years should not be used in annual home range analyses that function to inform conservation decisions on habitat preservation or delineate geographic management units unless additional years are included with wetter conditions.

Some studies on *D. r. reticularia* have documented longer and more frequent movements in mature males than in mature females (Gibbons 1986; Buhlmann 1995). In my study, mean estimates for all movement, annual home range, and core activity areas

were also higher in mature males than in mature females (Table 7). All of the juveniles qualifying for comparison were female, and it is possible that with larger sample sizes and more even demographic distributions I would have detected more substantial differences between demographic groups.

In Chapter IV, I highlight several final recommendations that provide a foundational structure guiding future research on *D. r. miaria* spatial ecology that will assist in model selection for studies on annual home range and movement in other regions, or for other species that utilize wetland mosaics, estivate for extended periods, and make long-distance migrations over land.

CHAPTER IV
CONCLUSIONS AND RECOMMENDATIONS

Survey and Capture Protocols

I reviewed existing literature on species-wide *D. reticularia* capture protocols, compared efficacies of various survey and trapping methods on *D. r. miaria* in the field, identified mean aquatic activity depths among monitored individuals, inventoried potential biases among capture methods, and identified survey seasons for *D. r. miaria* in Texas. Below I highlight elements of those capture and survey protocols that should increase detection, reduce field labor costs, and minimize sampling bias in future research and monitoring programs on *D. r. miaria*.

Based on my literature review and field research, I believe the following recommendations will help guide the design of *D. r. miaria* research and management programs that increase detection, reduce field labor costs, and minimize sampling bias:

1. Published studies that met inclusion criteria used five methods to capture *D. reticularia*, including terrestrial drift fences, baited wire mesh traps, baited crawfish traps, baited hoop nets, and unbaited fyke traps. Most published *D. reticularia* studies successfully employed either terrestrial drift fences, unbaited fyke traps, baited hoop nets, or a combination of the three, but data on *D. reticularia* capture rates for each trap type are scarce within published literature.

2. Success rates using baited traps are regionally inconsistent in the literature, so I recommend using unbaited fyke traps in areas where baited traps have not yet proven effective, as fyke nets have been effective in all *D. reticularia* studies that deployed them.
3. Activity depths of monitored individuals indicate that traps should be deployed in waters as close to 35 cm in depth as possible.
4. Traps may be checked daily. I checked traps at longer intervals in some Texas trapping sessions to determine whether disturbing adjacent habitat while checking traps deters subsequent captures. Longer intervals between checking traps did not increase success, and actually resulted in a significantly lower capture rate in the Texas field study, possibly due to escaped individuals.
5. Success rates were significantly higher during the first two days of trap deployment, potentially due to individuals becoming trap-shy with time. I recommend leaving traps at a site for three nights or less and then moving the traps.
6. When designing a *D. r. miaria* study that requires active surveys, the best survey method choice varies depending on research questions, budget, and time constraints. Capture rates were highest using dipnet surveys, but individuals

captured during dipnet surveys were significantly smaller than those captured during wading surveys and fyke net sessions. Because most capture-mark-recapture study procedures assume equal catchability of individuals within a population (Carothers 1979; Hwang and Chao 1995), a combination of fyke net traps and dipnet surveys are recommended to encompass the range of *D. r. miaria* sizes, unless property access prohibits the deployment of traps. In such cases, a combination of wading surveys and dipnet surveys is recommended.

7. Aquatic survey and trap sessions in Texas should be performed between late April and early June to avoid periods when *D. r. miaria* may be underground in terrestrial habitats and periods where success rates have been relatively low in spite of documented aquatic behavior of monitored individuals.
8. Road and trail surveys are not recommended, as road surveys resulted in significantly lower capture rates than other active survey methods. In studies where limited property access necessitates terrestrial surveys, I recommend surveying roads in Texas during June and July when migrations over terrestrial habitats are most frequent. These surveys should be conducted as close to 11:00, the peak terrestrial activity period, as possible.

Spatial Ecology

The objective of my spatial ecology study was to inform future research by: (1) evaluating annual home range estimation method selection for a species that spends most of the year at rest and migrates between isolated wetlands; (2) determining whether or not models incorporating temporal information from sequential telemetry positions provide a good fit for movement data given those behaviors; (3) relating the tracking duration and resolution (data collection frequency) to the asymptotic relationship between the number of relocations of an individual and its annual home range size; (4) deciphering whether wetland quantity, size, or isolation affect annual home range size; (5) investigating demographic differences in movement patterns; and (6) examining the effects of extreme drought on movement behavior. Below I highlight several components that provide a foundational structure guiding future research on *D. r. miaria* spatial ecology that will assist in model selection for studies on annual home range and movement in other regions.

Based on my field research and subsequent analyses, I believe the following recommendations will help guide the design of future spatial ecology research on *D. r. miaria* or other species that utilize wetland mosaics, estivate for extended periods, and make long-distance migrations over land:

1. When working with aquatic foragers that use upland areas to migrate between wetlands or aestivate, care should be exercised when selecting an annual home range estimation method. AKDE estimators can be oversmoothed, can have wide

confidence intervals (Figure 10), and take considerable time to process. For species with clusters of positions in isolated wetlands, the LSCV can generate under-smoothed, severely fractured polygons when all positions are included. I recommend creating 95% KDE polygons using the reference bandwidth and removing repeated consecutive coordinates to improve boundary smoothing (Figure 9). When determining core activity area, if the species only forages and mates aquatically, I recommend creating 95% KDE polygons using the LSCV and only including aquatic positions to accommodate inundation boundaries on the landscape (Figure 12).

2. The long-distance movements interrupted by periods of residency could indicate several behavioral possibilities for this species, including irruptive nomadism, partial nomadism, or very large resident ranges. In order to determine which behavioral description is applicable and better understand the metapopulation dynamics of the species, future studies should prioritize study duration over relocation frequency. The escape of some individuals due to signal loss or migration off-site indicates that larger study sites and longer-range transmission technology could also benefit these studies.

3. Landscape characteristics have a relationship with movement behavior and annual home range size, and until the effect of landscape parameters can be studied in higher resolution, studies on *D. r. miaria* spatial ecology should be

designed to include multiple sites that represent multiple populations. I recommend occupied sites that have different landscape characteristics in order to observe the range of movement behaviors exhibited by the species.

4. When making decisions about conservation and habitat management for *D. r. miaria*, the longevity of the species and the ability to make long migrations over upland areas should be considered, as well as the area's hydrologic conditions. Over two seasons I estimated 95% KDE annual home ranges for *D. r. miaria* to be as high as 4,626,344 m² ($\mu = 610,733 \pm 1,168,326$ m²), but individual home ranges could be much larger over the course of a decade or much smaller during drought years.

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