Should I Stay or Should I Go? Spatial Ecology of Western Chicken Turtles (*Deirochelys reticularia miaria*)

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Abstract.—Though its distribution within Texas is widespread, the spatial resource requirements of the Western Chicken Turtle (*Deirochelys reticularia miaria*) are poorly understood. Formal protection is lacking for the subspecies and its habitat, and past research suggests that its remaining habitat in Texas is under threat from increasing urbanization. For these reasons, the U.S. Fish and Wildlife Service issued a 90-day finding that states listing the subspecies as Threatened or Endangered may be warranted. Here, we present analyses of telemetry data using a variety of methods to understand annual home range, core activity area, and movements. We evaluate the applicability of Minimum Convex Polygons, Kernel Density Estimators, and Autocorrelated Kernel Density Estimators to a species that migrates between isolated wetlands, spending most of the year aestivating underground. To improve model fit, we applied each method to datasets with all positions included, repeated consecutive coordinates excluded, and with only aquatic positions included. The 95% Kernel Density Estimators provided the most consistent estimates of annual home range. Traditional 50% core activity area estimators had questionable utility, and we observed better geographic fit for core activity areas in 95% Kernel Density Estimates using the least-squares cross validation on the aquatic dataset. When making habitat conservation decisions, managers should consider how extensive periods at rest affects home range estimates, how periods of drought affect movement, and how the longevity of the species, the potential to make long migrations over land, and the landscape characteristics of the site could affect spatial resource requirements.

Key Words.—aestivation; emigration; home range; movement; wetland mosaic

Introduction

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 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: long-term movements including seasonal migrations, annual movements, or displacement, and 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 body size, sex, age, or resource needs of an individual, 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, 1943; Börger et al. 2008). Understanding the size and shape of the home range of an animal 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; Ross et al. 2019). Minimum Convex Polygons (MCP) 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 what are considered normal activities of resource acquisition and reproduction throughout its lifetime (Burt 1943), and later broadened to include movements within and among several core activity areas (Rose 1982).

For some taxa, these definitions elicit 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 less time active than aestivating at rest, how does that alter the method selection process used to determine home range and core activity 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 Model and temporal autocorrelation via the Ornstein-Uhlenbeck Foraging 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 be considered when studying the movements of Chicken Turtles (*Deirochelys reticularia*), a turtle species that spends much of its time at rest (Buhlmann 1995; McKnight et al. 2015; Bowers 2020). *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 *D. reticularia* populations in the Florida peninsula may be active year-round, north of the peninsula they aestivate or hibernate for at least part of the year (Ernst and Lovich 2009), and both sexes periodically migrate across upland areas between wetland habitats (Gibbons 1986). *Deirochelys reticularia* is the lone extant species in the genus, and three subspecies are recognized: Florida Chicken Turtles (*D. r. chrysea*) in peninsular Florida, Eastern Chicken Turtles (*D. r. reticularia*) along the Atlantic and Gulf coastal plains from Virginia to the Mississippi River, and Western Chicken Turtles (*D. r. miaria*) west of the Mississippi River in Louisiana, Texas, Arkansas, Oklahoma, and Missouri (Schwartz 1956). Though phylogenetic comparisons suggest a deep split between *D. r. miaria* and the other two subspecies (Walker and Avise 1998; Hilzinger 2009), their aquatic habitats and foraging behaviors are functionally similar (Ernst and Lovich 2009). In Oklahoma and Texas, *D. r. miaria* are in aquatic habitat from late winter to early summer and underground the remainder of the year (McKnight et al. 2015; Bowers 2020). 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). 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 which states that listing the western subspecies as Threatened or Endangered under the U.S. Endangered Species Act may be warranted (USFWS 2011).

Studies on the spatial ecology of *D. reticularia* have been relatively sparse, but prior publications reported home range sizes up to 101,000 m^2 (Buhlmann 1995), individual seasonal movements up to 635 m (Marchand 1945: Buhlmann 1995), use of wetland mosaics between one and nine wetlands (Buhlmann 1995), and inter-wetland movements between 300 and 830 m (Dodd 1992; Dodd and Cade 1998; McKnight et al. 2012). In Oklahoma, individuals migrated up to 225 m from water to aestivation sites (McKnight and Ligon 2019). The objectives of our study were 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 the above 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

affects annual home range size; (5) investigating demographic differences in movement patterns; and (6) examining the effects of extreme drought on movement behavior. Our recommendations 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.—The Katy Prairie Conservancy (KPC) is a 7,284-ha site in the Gulf Coast Prairies and Marshes ecoregion of Texas, USA. We collected movement data on *D. r. miaria* at two sites managed by the KPC. Site A was 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 was 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 was interrupted by livestock ponds, ephemeral wetlands, and ephemeral irrigation ditches. Site B was 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 was 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 two metapopulations or possibly one population, though we did not observe movement between the two sites during the 2018–2020 period. A third site sampled during this study (Site C) was approximately 200 km northeast of sites A and B on a Wildlife Management Area (WMA) 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 WMA was a 5.2 km² mosaic of ephemeral wetland cells, levees, herbaceous uplands, and forested uplands. It was 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.—We captured *D. r. miaria* between 2018 and 2020 for a long-term capture-mark-recapture 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 Bowers (2020). We 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. We determined the sex and maturity stage of each individual as described in Bowers (2020).

We used VHF radio transmitters (various models; Advanced Telemetry Systems, Isanti, Minnesota, USA) at all three sites. We used GPS loggers (model PP-120; Lotek Wireless, Seattle, Washington, USA) on some individuals at the KPC sites until battery recharge life had decayed significantly. Initially, we attached all equipment to the posterior margin of the carapace, but early in the study some individuals lost the equipment due to the natural shedding of the carapacial laminae and subsequent tangling in vegetation. We 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 then threading an aluminum wire through the holes. We then encased the equipment bundle in waterproof epoxy putty (J-B Weld 8277; J-B Weld Company, Sulphur Springs, Texas, USA). Each equipment bundle (VHF transmitter, epoxy putty, aluminum wire, and GPS logger if used) weighed < 5% of the body mass of the individual. At the KPC sites, we tracked individuals 2–4 times per week until aestivation, then once every one to two weeks during aestivation. At each position, we recorded the GPS coordinates, the activity status (active or aestivating), and whether or not research activities (such as transmitter replacement) may have induced additional movement.

To avoid detecting movement when it did not occur, we 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, we tracked individuals once per week while they were aquatic, then once every two weeks when individuals left the water to aestivate. At Site C, we did not use flagging tape to mark aestivation sites but used photographs to verify repeated positions at the same site. We tracked individuals at the KPC sites for varying durations between March 2018 and July 2020. At Site C, we 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, we recorded the coordinates but excluded the position from movement and annual home range analyses. We set observation times from captures and recaptures in traps to 1200 on the day of retrieval, as there was no way to determine when the individual entered the trap.

Movements.—For each individual with one or more relocations via either telemetry or recapture, we recorded the number of days monitored and the number of days to the last position with unique coordinates. We used the sp package (Pebesma and Bivand 2005) to calculate total distance traveled, mean step length, mean daily distance (total distance traveled/number of days between

the initial capture and the last unique position, including periods of inactivity), and total net displacement. To calculate total distance traveled, we summed the straight-line distances between all temporally consecutive positions. 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). We did not use mean step length in comparisons because the time between tracking sessions varied by season. To calculate total net displacement, we measured the straight-line distance between the point of initial capture and last position recorded for the individual. For total net displacement, we included individuals with at least 350 d between first and last relocations or captures to include at least one complete season. When assumptions of normality and homoscedasticity were met, we 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, we used the mean of the log-transformed values. If assumptions were still not met, we used Mann-Whitney U-tests. We used a low alpha value ($\alpha = 0.01$) to prevent Type I error because we performed multiple tests.

Annual home range.—We 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). We 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) to account for some of the annual movement variation we observed. We then plotted 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. We 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 Least-squares Cross Validation (LSCV). On datasets with repeated consecutive coordinates removed, we removed all tracking events where an individual remained underground at the exact same position as the prior tracking; only unique coordinates were included. When possible, we 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, we 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. We 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, we also estimated 50% MCP, 50% KDE (using both the reference bandwidth and LSCV), and 50% AKDE polygons using both datasets. Because *D. r. miaria* are inactive when aestivating, we 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 core activity areas. We made statistical comparisons for core activity area estimates among sites and demographics as described for movement statistics and annual home range estimates above.

Landscape characteristics.—To decipher the relationships between annual home range size and the spatial characteristics of the landscape, we measured three variables for each qualifying individual in the annual home range dataset: (1) the number of wetlands visited by the individual, (2) the total summed area of wetlands visited (SWA), and (3) the mean pairwise distance (MPD) between all wetlands used by the individual (a surrogate for the level of spatial isolation within the wetland mosaic). We considered any inundated area visited by an individual to be a wetland for the purposes of this study. We did not differentiate between ephemeral wetlands, perennial ponds, and low-elevation upland areas that were inundated too temporarily to be considered wetlands. The dataset did not meet the homoscedasticity assumptions of Linear Regression analysis. We implemented a less assumptive multivariate process called Classification and Regression Tree (CART) analysis, which is a form of recursive partitioning (Brieman et al. 1984). Using the package rpart in R (Therneau and Atkinson 2019), we created regression trees assigning 95% KDE areas and 100% MCP areas as response variables and the three landscape characteristics as predictor variables. Regression Tree analyses partitioned the entire data set into successive subsets of data called nodes based on decision rules that considered all possible binary splits of the variables and bifurcated the data set wherever the sum of squared differences between observed and predicted responses, or deviance, was smallest. By repeating this process recursively, a branching tree was produced with binary splits that corresponded to one or more explanatory variables. To prevent over-fitting

from such recursive procedures, we 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. We 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). We created additional figures using either base plot or package ggplot2 (http://ggplot2.tidyverse.org.).

RESULTS

Telemetry.—We tracked 47 individuals during the study, including 15 at Site A, 28 at Site B, and four at Site C. Most of the individuals were initially captured in unbaited fyke nets (Bowers 2020). Unfortunately, 13 individuals shed their radios in late May of 2018 and were not relocated. After switching to anterior radio placement, no radios detached. GPS loggers did not capture positions during aquatic activity. We did not include logger data in movement or home range analyses because they added few positions to the dataset and had variable GPS error. At KPC, two individuals (one mature female and one juvenile) were preyed upon during the activity season before accumulating 25 relocations and one mature male was preyed upon during the 2019 activity season. We were not able to identify the predator species involved, but the juvenile and mature female were both in water, shells crushed, indicating possible pig or otter predators. The mature male was in water, shell intact, but the head had been removed, possibly indicating an avian predator.

Of the 19 individuals that were relocated > 25 times, four individuals (three mature females and one mature male) used only one wetland each during both seasons, and five individuals (one mature female, two mature males, and two immature females) used only one wetland but were only monitored for one season. Five individuals (one mature female, one mature male, and three 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 (two mature females and one 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 considering that the species may live > 15 y (Gibbons 1987; Ewert et al. 2006). One on-site emigration was between wetlands over 800 m apart. Two individuals (both mature males) used six 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 activity 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 for us to lose the signal. The second potential emigrant used two wetlands during the 2018 season, used the same two wetlands from 2 March 2019 to 19 April 2019, then made five wetland-to-wetland migrations between 19 April 2019 and 24 May 2019 before moving so far off-site that we lost the signal. 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, we lost signal for unknown reasons to five juveniles (sex not determined) in 2018 and two mature males in 2019. It is possible that these individuals migrated off-site. Among 24 monitored individuals at KPC sites that we did not relocate at least 25 times, five individuals used 2–4 wetlands each, and 19 used only one wetland during their limited monitoring periods.

At Site C, we monitored four individuals (two mature males, one mature female, and one unsexed juvenile) from the 2019 activity season through aestivation to November 2019. 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 20-m-wide moist-soil management levee. The juvenile was found preyed upon during the 2019 aestivation season.

At KPC, we stopped tracking most individuals in December of 2019 and have only included data recorded before that time in analyses for this study. We did, however, continue tracking eight individuals every two weeks through July of 2020 and observed almost no movement, even during the usual activity season (Bowers 2020). 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. We tracked only one of the eight monitored individuals to aquatic habitat in 2020 (on 5 June 2020) and we found it aestivating underground two weeks before and two weeks after. 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, but not as severe, drought conditions occurred during the 2020 trapping sessions at Site C. Many individual turtles were active, but the inundated portion of the wetland was much smaller than during the 2019 season. The portions of Site C at which we trapped in 2019 were completely dry in 2020.

Table 1. Movement values for individuals with 25 or more relocations at Sites A and B of the Katy Prairie Conservancy, Texas, USA, and all monitored Western Chicken Turtles (*Deirochelys reticularia miaria*) at Site C of the Alazan Bayou Wildlife Management Area, Texas, USA. The abbreviation SD = standard deviation.

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

Movements.—The mean daily distance traveled ranged from 3.3 m to 18.5 m (mean = 9.5 ± 4.4 m standard deviation, n = 14) among individuals monitored two seasons at KPC sites (Table 1), and the total distance traveled ranged from 1,661 m to 7,025 m (mean = 4,102 ± 1,783 m, n = 14). Total net displacement ranged from 62 m to 2,250 m among individuals monitored two seasons (mean = 577 ± 673 m, n = 14). We found no significant movement parameter differences between Sites A and B (Table 2) or between adults and juveniles, but the only qualifying juveniles were immature females that were larger than mature male size (Table 3). We found no significant differences between the movement parameters of mature males and mature females, but males consistently had higher mean values (Table 4).

Annual home range.—Best annual home range model choice varied depending on the space use of the individual (Appendix Table). For eight of the nine 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 five individuals that used wetland complexes, the 100% MCP appeared reasonable for only one individual, including large areas unused in either state by the other four 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 the number of relocations during aestivation and whether or not repeated consecutive coordinates were included. We did not include the 95% MCP area estimates in tables because they were very similar to the 100% MCP estimates. 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. For that individual (2254), a potential emigrant, the 95% KDE polygon placed a large, over smoothed buffer on the entire area used by this individual until it began its migration off-
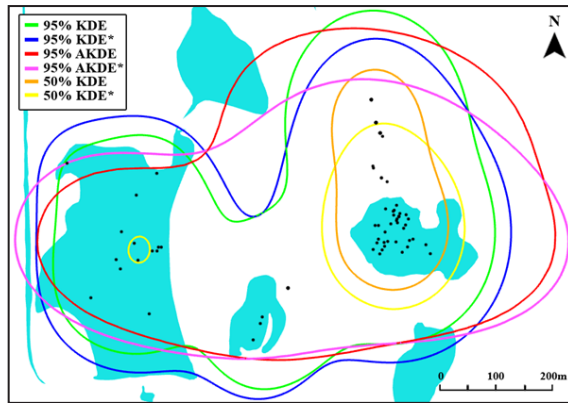
Figure 1. Map of wetlands occupied by Western Chicken Turtles (*Deirochelys reticularia miaria*) from the Katy Prairie Conservancy, Texas, USA, displaying four annual home range estimates and two core activity area estimates for a single mature male (2230). An asterisk (*) indicates that repeated consecutive coordinates were removed. The 95% Kernel Density Estimate (KDE) polygons provide better exclusion of unused area, while 95% Autocorrelated Kernel Density Estimate (AKDE) polygons implement better smoothing parameters. Both of the 50% KDE core activity area estimators are questionable, as *D. r. miaria* forage and mate in the water. Blue areas indicate surface water on the landscape.

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 (Fig. 1).

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 two individuals that migrated off-site, two of the on-site individuals that changed wetlands permanently, and one individual that used multiple wetlands spread across an elongate north-south gradient. The larger the cluster of relocations for an individual, 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 home range area into 2–10 polygons. For the six individuals that only used one wetland or a complex of nearby wetlands, the polygons presented reasonable home range estimates. For 14 of the 16 individuals where AKDE estimates were possible, the Ornstein-Uhlenbeck 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 Ornstein-Uhlenbeck Foraging 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
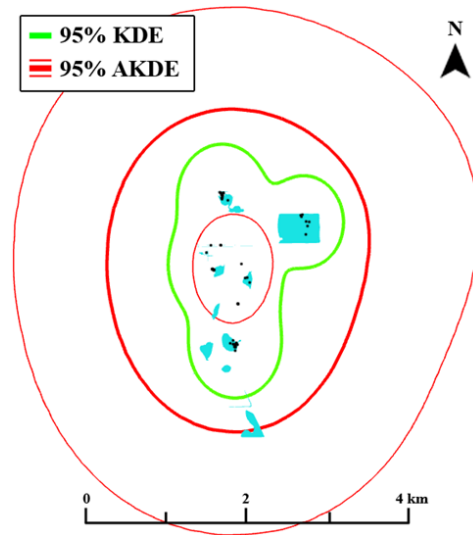
Figure 2. Map of wetlands occupied by Western Chicken Turtles (*Deirochelys reticularia miaria*) from the Katy Prairie Conservancy, Texas, USA, displaying the 95% Kernel Density Estimate (KDE; green boundary) and 95% Autocorrelated Kernel Density Estimates (AKDE; thick red boundary) with 95% confidence intervals (thin red boundaries) for a single mature male (2229). Although the Ornstein-Uhlenbeck Foraging model had the best ΔAIC, accommodated the sequential order of spatial positions, and visually fit the variogram for this individual, the resulting estimate appears over smoothed in comparison to the more widely used 95% KDE using the reference bandwidth. Blue areas indicate surface water on the landscape.

correction. 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 three individuals.

For 13 individuals where AKDE estimates were possible, the polygons represented reasonable annual home ranges (Fig. 1). 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 three 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 home range estimates, and had very wide confidence intervals (Fig. 2).

We found no significant differences in annual home range area estimates between Sites A and B (Table 2) or between adults and juveniles, but the only qualifying juveniles were immature females that were larger than mature male size (Table 3). We 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 4). We

TABLE 2. Comparisons between mature Western Chicken Turtle (*Deirochelys reticularia miaria*) movement statistics (m), annual home range estimates (m²), and core activity area estimates (m², below line) at Sites A and B (α = 0.01) of the Katy Prairie Conservancy, Texas, USA. NRCC indicates that repeated consecutive coordinates were removed. An asterisk (*) indicates that non-transformed values were used; all others were log-transformed for comparison. Two asterisks (**) indicates that we performed a Mann-Whitney U-test. All mean values are displayed non-transformed. The abbreviation SD = standard deviation.

	Site A		Site B		*t*-value or *W*-statistic	*P*-value
	n	Mean ± SD	n	Mean ± SD		
Total Distance Traveled*	5	3,612 ± 1,567	9	4,375 ± 1,924	-0.80	0.44
Mean Daily Distance Traveled*	5	7.94 ± 3.59	9	10.43 ± 4.78	-1.10	0.30
Total Net Displacement	5	466 ± 751	9	638 ± 665	-0.97	0.36
100% MCP	5	340,000 ± 590,000	9	200,000 ± 280,000	-0.31	0.77
95% KDE	5	1,030,000 ± 2,010,000	9	380,000 ± 430,000	-0.32	0.76
95% KDE NRCC	5	1,180,000 ± 2,260,000	9	440,000 ± 600,000	-0.29	0.78
95% AKDE**	5	2,130,000 ± 4,570,000	9	490,000 ± 530,000	$W = 10$	0.11
95% AKDE NRCC**	5	1,980,000 ± 4,210,000	9	580,000 ± 780,000	$W = 12$	0.19
50% MCP	5	80,000 ± 160,000	9	20,000 ± 20,000	-0.26	0.80
50% KDE**	5	280,000 ± 570,000	9	70,000 ± 60,000	$W = 15$	0.36
50% KDE NRCC**	5	330,000 ± 680,000	9	70,000 ± 80,000	$W = 15$	0.36
95% KDE (LSCV) - aquatic positions only**	5	60,000 ± 80,000	9	40,000 ± 30,000	$W = 26$	0.70

calculated mean and standard deviations for population annual home range size across all methods using all qualifying individuals at Sites A and B (Table 5). The number of relocations required to observe an asymptotic relationship with annual home range size varied (Fig. 3). For eight of the 14 qualifying individuals, fewer 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 in area during wetland-to-wetland migrations. We also plotted 100% MCP areas for a more direct visual representation of this phenomenon (Fig. 3). The 95% KDE areas for the two potential

TABLE 3. Comparisons (α = 0.01) between adult and juvenile Western Chicken Turtle (*Deirochelys reticularia miaria*) movement statistics (m), annual home range estimates (m²), and core activity area estimates (m², below line) at the Katy Prairie Conservancy, Texas, USA. NRCC indicates that repeated consecutive coordinates were removed. An asterisk (*) indicates that non-transformed values were used; all others were log-transformed for comparison. Two asterisks (**) indicates that we performed a Mann-Whitney U-test. All mean values are displayed non-transformed. The abbreviation SD = standard deviation.

	Adult		Juvenile		*t*-value or *W*-statistic	*P*-value
	n	Mean ± SD	n	Mean ± SD		
Total Distance Traveled*	10	3,393 ± 1,779	4	4,374 ± 2,035	-0.33	0.76
Mean Daily Distance Traveled*	10	9.21 ± 4.67	4	10.37 ± 4.24	-0.45	0.67
Total Net Displacement	10	630 ± 754	4	300 ± 223	0.58	0.58
100% MCP	10	310,000 ± 470,000	4	100,000 ± 40,000	0.45	0.66
95% KDE	10	750,000 ± 1,430,000	4	260,000 ± 130,000	-0.11	0.91
95% KDE NRCC	10	890,000 ± 1,620,000	4	220,000 ± 110,000	0.42	0.68
95% AKDE**	10	1,380,000 ± 3,180,000	4	310,000 ± 90,000	$W = 18$	0.84
95% AKDE NRCC	10	210,000 ± 180,000	4	300,000 ± 150,000	0.10	0.92
50% MCP	9	50,000 ± 120,000	4	30,000 ± 20,000	-1.33	0.21
50% KDE	10	180,000 ± 400,000	4	60,000 ± 30,000	-0.52	0.62
50% KDE NRCC	10	210,000 ± 470,000	4	50,000 ± 30,000	0.31	0.76
95% KDE (LSCV) - aquatic positions only	10	50,000 ± 60,000	4	40,000 ± 30,000	0.11	0.92

TABLE 4. Comparisons (α = 0.01) between mature female and mature male Western Chicken Turtle (*Deirochelys reticularia miaria*) movement statistics (m), annual home range estimates (m^2), and core activity area estimates (m^2, below line) at the Katy Prairie Conservancy, Texas, USA. NRCC indicates that repeated consecutive coordinates were removed. An asterisk (*) indicates that non-transformed values were used; all others were log-transformed for comparison. All mean values are displayed non-transformed. The abbreviation SD = standard deviation.

	Female		Male			
	n	Mean ± SD	n	Mean ± SD	t-value	P-value
Total Distance Traveled*	6	3,508 ± 1,467	4	4,722 ± 2,174	-0.98	0.37
Mean Daily Distance Traveled*	6	7.45 ± 3.47	4	11.84 ± 5.49	-1.42	0.22
Total Net Displacement	6	343 ± 324	4	1,204 ± 1,003	-1.06	0.35
100% MCP	6	8,000 ± 8,000	4	650,000 ± 630,000	-1.49	0.21
95% KDE	6	150,000 ± 140,000	4	1,640,000 ± 2,080,000	-1.62	0.18
95% KDE NRCC	6	210,000 ± 210,000	4	1,920,000 ± 2,350,000	-1.39	0.24
95% AKDE	6	190,000 ± 160,000	4	3,180,000 ± 4,810,000	-1.55	0.20
95% AKDE NRCC	6	220,000 ± 180,000	4	3,160,000 ± 4,380,000	-1.38	0.24
50% MCP	5	6,000 ± 6,000	4	110,000 ± 180,000	-2.29	0.07
50% KDE	6	30,000 ± 20,000	4	410,000 ± 610,000	-1.82	0.15
50% KDE NRCC	6	40,000 ± 30,000	4	480,000 ± 720,000	-1.50	0.21
95% KDE (LSCV) - aquatic positions only	6	20,000 ± 7,000	4	90,000 ± 80,000	-2.95	0.04

emigrants were still increasing when they migrated out of signal range after we collected about 50 relocations (Fig. 3, gray lines).

Core activity area.—For most individuals, the 50% MCP provided the poorest representation of the core activity area (Fig. 4). For individuals that used one wetland, the 50% MCP often excluded large portions of the wetland if the active positions were evenly distributed throughout the wetland area. For individuals that used multiple wetlands, the 50% MCP 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 we recorded more than 50% of the relocations at individual 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 activity area estimates but these methods included much upland area when individuals used more than one wetland. For individuals that used only one wetland, the 50% MCP from the aquatic dataset excluded portions of the wetland that were frequently used if the positions were evenly distributed. For individuals that used multiple wetlands, the 50% MCP from the aquatic dataset left
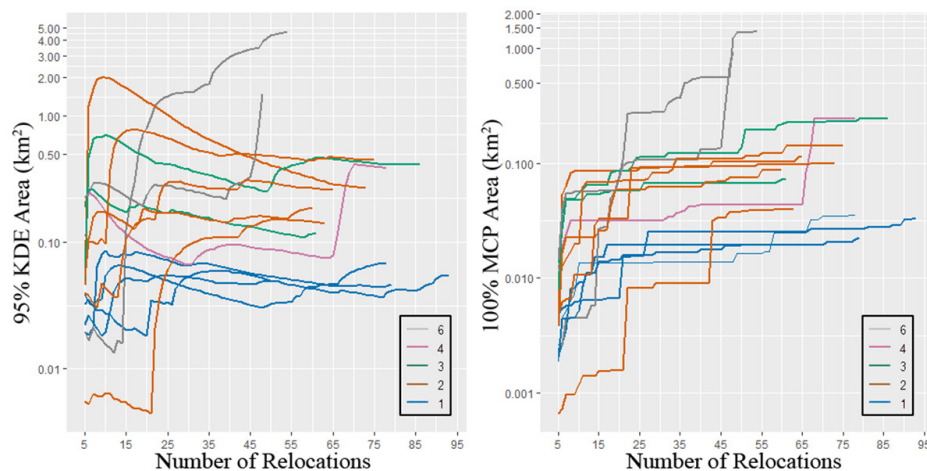

FIGURE 3. Plot of home range areas of Western Chicken Turtles (*Deirochelys reticularia miaria*) from the Katy Prairie Conservancy, Texas, USA, by the number of relocations included in the analysis. Line color indicates the number of wetlands visited by the individual. (A) plot of 95% Kernel Density Estimate areas; (B) plot of 100% Minimum Convex Polygon areas.

- 50% MCP
- 50% KDE.ref
- 50% AKDE
- 95% KDE.lscv.aq
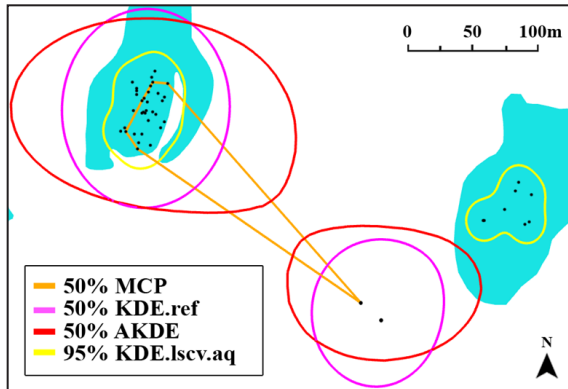
Figure 4. Map of wetlands occupied by a Western Chicken Turtle (*Deirochelys reticularia miaria*) at the Katy Prairie Conservancy, Texas, USA, displaying four core activity area estimates for one immature female (2241); 50% Minimum Convex Polygon, 50% Autocorrelated Kernel Density Estimate (AKDE), 50% Kernel Density Estimate (KDE) using the reference bandwidth, and 95% KDE using the least squares cross validation and only aquatic coordinates (KDE.lscv.aq). Blue areas indicate surface water on the landscape.

Table 5. Population mean and standard deviation values for all qualifying individual Western Chicken Turtles (*Deirochelys reticularia miaria*) for sites A and B (n = 14) at the Katy Prairie Conservancy, Texas, USA. Home range estimators are MCP = Minimum Convex Polygon, KDE = Kernel Density Estimate, and AKDE = Autocorrelation-corrected Kernel Density Estimate. One asterisk (*) indicates that repeated consecutive coordinates were removed from the dataset. Two asterisks (**) indicate that only aquatic positions were included in the dataset.

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

some wetlands out entirely, usually including only portions of the wetland where the individual had been tracked for the longest duration. The 50% KDE polygons using the reference bandwidth only projected a reasonable activity area for one of 19 individuals when we used the whole dataset and three of 19 individuals when we removed repeated consecutive coordinates. When using either dataset, the estimators either included aestivation sites, excluded entire wetlands (Fig. 4), or projected parcels that included no wetland area because the individual had more aestivation positions than active relocations.

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 activity area polygons for five of 19 individuals. For the other 14, the model provided reasonable core activity 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 we included only aquatic positions. The 95% KDE polygons using the LSCV and only aquatic positions (Fig. 4) provided good core activity 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 six individuals where the LSCV did not minimize the MISE, the polygons still provided the most reasonable core activity area estimates.

We found no significant differences between core activity area estimates at Sites A and B (Table 2) or between adults and juveniles (Table 3). We found no significant differences between core activity area estimates of mature females and mature males, but males consistently had higher mean values (Table 4, α = 0.01). We calculated mean and standard deviations for population core activity area size across all methods using all qualifying individuals at Sites A and B (Table 5).

Landscape characteristics.—Landscape parameters summed wetland area and mean pairwise wetland distance trended higher among individuals with larger annual home ranges sizes (Fig. 5), 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 6), so we plotted the cross-validated error by the corresponding number of splits for each tree 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 three and five, respectively (Figs. 6 and 7). The Regression Tree Analysis for 95% KDE areas included mean pairwise wetland distance and summed wetland area as predictor variables (Fig. 6). The analysis for 100% MCP areas included all three landscape predictor variables.

Discussion

Annual home range and core activity area estimates varied considerably depending on what estimation method was used. 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
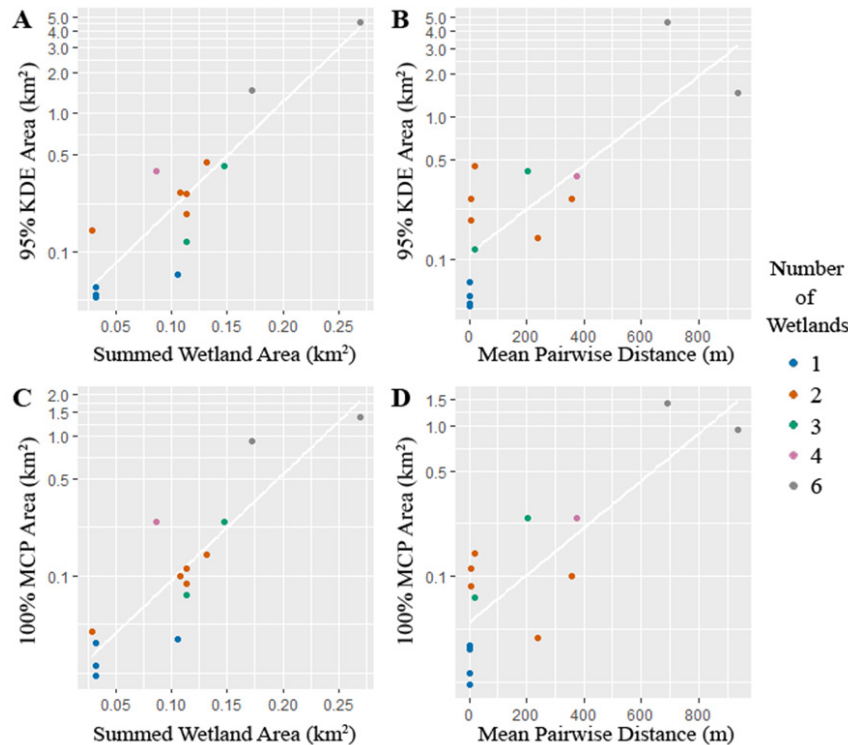
FIGURE 5. Plot of annual home range areas for Western Chicken Turtles (*Deirochelys reticularia miaria*) from the Katy Prairie Conservancy, Texas, USA by landscape parameter value. Dot color indicates the number of wetlands used by the individual. (A) 95% Kernel Density Estimate (KDE) areas by summed 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% Minimum Convex Polygon (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.

intervals and did not improve model fit, even when repeated consecutive coordinates were included. Core activity area estimators were also problematic because of the tendency for monitored turtles 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. 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 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 activity area estimation methods (MCP and KDE) to a biologically meaningful understanding of *D. r. miaria* core activity areas in future studies. We caution, however, that when we used only 50% of the relocations of an individual, the resulting areas often excluded large wetland areas that were frequently
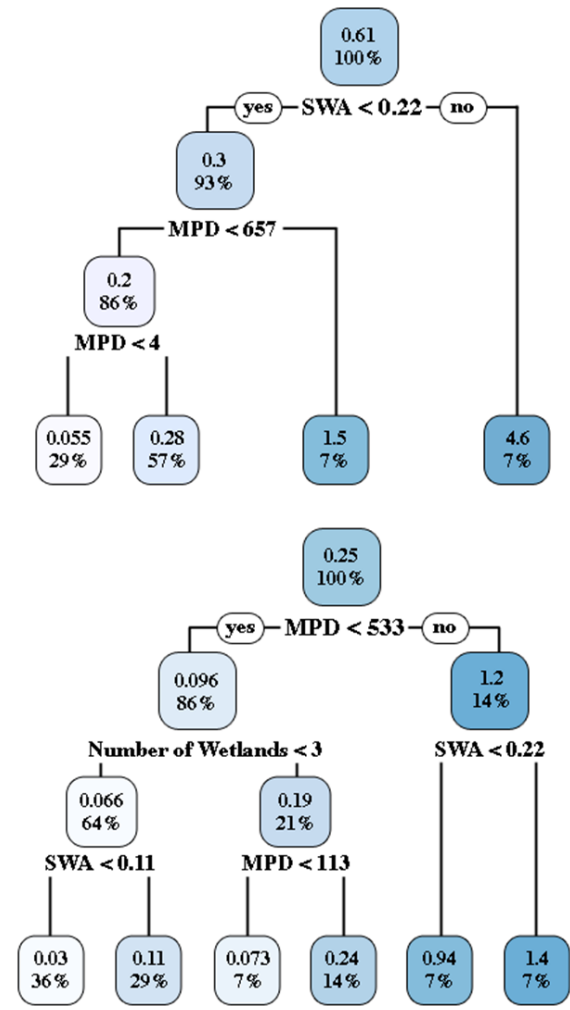
used by the individual, especially for individuals that had relocations scattered evenly within wetlands. If a clipping procedure is used for *D. r. miaria* core activity areas, we suggest clipping KDE shapefiles that include 95% of all aquatic positions to the surface inundation boundaries on the landscape.

Individuals in this study visited between one and six wetlands each, and the mean (248,915 m^2) and maximum (1,393,961 m^2) 100% MCP were 2.5 and 13.8 times the size of the largest recorded MCP area for the species in a study with similar tracking durations, respectively. In Virginia, individuals moved up to 635 m in a season, had annual home ranges up to 101,000 m^2, and used between one and nine wetlands each (Buhlmann 1995). In Florida, a marked individual moved 612 m in roughly 8 mo (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 (Stephen Dinkelacker and Nathaniel Hilzinger, unpubl. report). In our study, two individuals made movements

TABLE 6. Cross-validation table for two unpruned regression trees using classification and regression tree analyses of 95% Kernel Density Estimates (KDE) and 100% Minimum Convex Polygons (MCP) areas as response variables and summed wetland area, mean pairwise distance between all wetlands, and Number of Wetlands used as predictor variables. Summed Wetland Area and mean pairwise wetland distance 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. The abbreviations AHRE = Annual Home Range Estimator and SD = standard deviation.

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

FIGURE 6. Pruned regression trees with (Top) 95% Kernel Density Estimates and (Bottom) 100% Minimum Convex Polygon areas for Western Chicken Turtles (*Deirochelys reticularia miaria*) from the Katy Prairie Conservancy, Texas, USA, as response variables and landscape characteristics as predictor variables. Abbreviations are SWA = summed wetland areas and MPD = mean pairwise distance of wetlands.

off-site in excess of 1,500 m from their original point of capture and it is possible that the seven individuals for which we lost signal also moved too far off-site for us 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 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 that the species may live more than 15 y (Gibbons 1987; Ewert et al. 2006). Whether or not emigrating individuals 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 1 y (for long-lived animals) has been considered an indication of nomadic behavior (Bunnefeld et al. 2011). One possibility is that the species exhibits irruptive nomadism, in which long-distance movements are unpredictable in their timing and direction but may be interspersed by long periods of residency (Teitelbaum and Mueller 2019). Although most wetland-to-wetland migrations happened during the aquatic activity season at KPC sites, one of the potential emigrants in our study migrated off-site during the inactive season along a path that included several

aestivation sites and periods of dormancy. The other emigrating individual resided in two nearby (7 m) wetlands for the 2018 season then emigrated suddenly during the 2019 activity season. A 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, in which 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*), 39% of 83 females and 50% of 60 males maintained the same wetland of residence for more than 20 y (Congdon et al. 2011), indicating the possibility of partial nomadism. *Emydoidea blandingii* is a similar species to *D. r. miaria* that uses isolated wetlands, aestivates in uplands, and can make long-distance migrations over land. In another study on *E. blandingii,* multi-year (2–6 y) home range sizes were significantly larger than annual home range sizes (Schuler and Thiel 2008). In our study, four individual *D. r. miaria* used only one wetland for the duration of the study, and five individuals used complexes of wetlands that are < 300 m apart, sometimes returning to the same wetland multiple times. It is possible that these represent resident individuals, while others represent nomadic individuals, suggesting potential partial nomadism in this population. The only way to determine whether the species exhibits irruptive nomadism, partial nomadism, or simply large resident ranges is to design a longer study. The continued increases in 95% KDE area estimates after 2 y of tracking for some individuals indicates that relocation frequency may not be as important as study duration for our understanding of long-term *D. r. miaria* spatial ecology.

Although we did not observe significant differences in movement and annual home range parameters between study sites, 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 (about 9 km), were formerly connected via contiguous parcels of similar habitat, and could represent one population. In the 1940s, the prairie pothole wetland mosaic in the Katy Prairie between State Highway 290, Interstate Highway 10, and the Brazos River included 114,790 ha of contiguous habitat similar in wetland density and isolation to Sites A and B (Texas Natural Resources Information System [TNRIS] 2020) 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 six-lane highways

with concrete barricades and the original prairie pothole wetland mosaic in this area has been reduced to at least eight fragments ranging from 316 to 7,530 ha and summing to 15,421 ha (13% of the prior area; TNRIS 2020). 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*). We 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. 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) 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 our study, mean estimates for all movement, home range, and core activity areas were also higher in mature males than in mature females. It is possible that the lack of significant differences between mature males and mature females was an artifact of the small sample sizes (four males and six females). All of the juveniles qualifying for comparison were female, and it is possible that with larger sample sizes and more even demographic distributions, we would have detected more substantial differences between demographic groups. Future studies should prioritize inclusion of a larger number of individuals.

Conclusions and recommendations.—Based on our field research and subsequent analyses, we believe the following recommendations will help guide the design of future spatial ecology research on *D. reticularia* or other species that use wetland mosaics, aestivate 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, 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. We recommend creating 95% KDE polygons using the reference bandwidth and removing repeated consecutive coordinates to improve boundary smoothing. When determining core activity area, if the species only forages and mates aquatically, we recommend creating 95% KDE polygons using the LSCV and only including aquatic positions to accommodate inundation boundaries on the landscape.

(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. 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. We recommend occupied sites that have different landscape characteristics 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 hydrologic conditions of the area. Over two seasons, we estimated 95% KDE home ranges for *D. r. miaria* to be as high as 4,626,344 m^2 (mean = 610,733 ± 1,168,326 m^2), but individual home ranges could be much larger over the course of a decade or much smaller during drought years. Data that only includes dryer years should be avoided when estimating home range sizes for conservation or protection area purposes.

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APPENDIX TABLE. Annual home range and core activity area estimates (m²) for Western Chicken Turtles (*Deirochelys reticularia miaria*) with over 25 relocations at Sites A and B of the Katy Prairie Conservancy, Texas, USA. An asterisk (*) indicates that repeated consecutive coordinates were removed from the dataset. Individuals with a 50% Minimum Convex Polygon of 0 m² were located at aestivation sites at least 50% of the time. Home range estimators are MCP = Minimum Convex Polygon, KDE = Kernel Density Estimate, and AKDE = Autocorrelation-corrected Kernel Density Estimate. The abbreviations ID = identification and CL = carapace length.

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	32,531	54,674	41,462	59,168	37,332	4,087	10,749	6,635	14,865
	2242	F	A	17.3	78	22,610	46,950	67,115	43,135	53,973	951	10,007	17,628	20,622
	2266	F	A	21.1	77	244,638	386,780	542,473	187,482	268,357	16,301	60,865	77,394	27,198
	2279	F	A	19.2	44	19,606	43,546	35,800	165,203	114,570	1,085	6,805	5,652	3,521
	2229	M	A	16.2	53	1,393,961	4626,344	5,211,595	10,300,190	9,511,380	371,213	1,311,792	1,543,541	196,904
	2237	M	A	13.3	49	19,188	49,067	41,996	49,370	39,896	10,075	13,858	10,464	27,155
	2288	M	A	16.8	41	14,324	32,467	29,659	29,654	28,816	2,342	7,128	5,679	12,568
B	2255	F	A	16.5	60	72,601	117,240	121,881	374,844	360,504	6,062	25,210	25,376	6,916
	2269	F	A	16.9	77	35,066	68,700	98,421	71,408	96,744	0	13,145	21,191	22,046
	2270	F	A	17.5	72	99,983	267,953	387,441	377,304	479,464	2,733	46,311	63,022	14,808
	2230	M	A	11.8	85	245,286	413,934	451,697	493,862	462,935	12,161	81,273	81,100	40,787
	2254	M	A	16.1	47	936,627	1,478,191	1,987,597	1,869,772	2,631,474	34,432	218,565	274,510	104,444
	2241	F	J	13.3	62	39,359	141,729	127,013	195,065	134,171	8,634	31,896	20,110	9,457
	2252	F	J	13.2	74	142,700	447,308	378,125	317,007	326,278	59,549	111,628	83,446	72,058
	2260	F	J	13.3	64	113,588	262,951	235,047	415,032	489,661	30,483	71,082	56,348	16,036
	2268	F	J	15.4	59	86,675	188,440	151,727	296,897	256,060	32,874	50,348	32,624	51,050