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An Evaluation of Western Chicken Turtle (*Deirochelys reticularia miaria*) Survey and Capture Protocols

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Abstract.—**The behaviors and activity season of *Deirochelys reticularia miaria* (Western Chicken Turtle) are poorly understood in Texas. Though distribution of *D. r. miaria* in the eastern portion of the state is widespread, turtle assemblage studies conducted within the range of the species in Texas have seldom documented its presence. There is a lack of formal protection for this subspecies and their habitat, and past research suggests that remaining habitat within the state is under threat from increasing urbanization. Therefore, the US Fish and Wildlife Service issued a 90-day finding that states listing the subspecies as threatened or endangered may be warranted. To provide survey recommendations for the western subspecies, we review species-wide capture techniques from the literature, recommend a survey season for *D. r. miaria* in Texas, and evaluate the efficacy and potential demographic biases of capture protocols implemented during field studies in the state in 2018 and 2019. We compared road surveys, dipnet surveys, seine surveys, night wading surveys, and two types of unbaited fyke net trap. Fyke nets were effective in every study that deployed them and captured *D. r. miaria* in this study at a rate of 0.25 captures per trap night. Dipnet surveys had the highest capture rate among active survey methods, but body size biases between methods were apparent. In Texas, road surveys yielded significantly lower capture rates than all other survey types. The best survey method selection will vary depending on research questions, budget, and time constraints. Utilizing proper survey protocols and understanding the activity season are crucial for performing effective studies on this species.**

Deirochelys reticularia are emydid turtles that inhabit the shallow, lentic waters of ephemeral wetlands throughout the southeastern United States (Carr, 1952; 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 estivate 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), literature on capture protocols of all three subspecies are considered here because their aquatic habitats and foraging behaviors are functionally similar (Ernst and Lovich, 2009).

There have been no range-wide status surveys for *D. reticularia* (Buhlmann et al., 2008), and the habitat of the western subspecies in Texas is under increasing threat because of urbanization (Ryberg et al., 2017). Though their distribution within the eastern portion of the state is widespread (54 counties; Dixon, 2013; Hibbitts and Hibbitts, 2016), turtle assemblage studies and herpetological site inventories within the range of *D. r. miaria* in its Texas range have seldom documented presence (Ryberg et al., 2004; Adams and Saenz, 2011; Fitzgerald and Nelson, 2011; Riedle, 2014; Crump et al., 2016; 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 US Fish and Wildlife Service (USFWS) issued a 90-day finding that states listing the western subspecies as threatened or endangered under the US Endangered Species Act may be warranted (USFWS, 2011). The objectives of our study 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.—We included existing studies in our capture method evaluation if a publication met the following criteria: 1) either the primary research target was *D. reticularia* or a majority of the research activity was within areas where *D. reticularia* presence has been documented, and 2) capture methods were documented. For each qualifying study, we inventoried all capture methods attempted, categorized them based on whether or not they were used successfully to capture *D. reticularia*, and recorded the capture rate per unit of effort (if reported).

Field Study Sites.—The Katy Prairie Conservancy is a 7,284-ha 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 (TJH, pers.

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obs.), making this the only Texas site we were aware of in 2018 with multiple recent *D. r. miaria* captures. We also collected demographic data, morphological measurements, and capture methods used for *D. r. miaria* at an additional site in the East Texas Pineywoods ecoregion. The site included portions of the Alazan Bayou Wildlife Management Area and the Stephen F. Austin (SFA) State University Experimental Forest, where *D. r. miaria* had been observed recently (Adams and Saenz, 2011).

Software.—We performed all statistical analyses in R version 3.6.1 (R Core Team, 2019) using the integrated development environment RStudio version 1.2.1335 (RStudio Team, 2018). We created figures using either base plot or package ggplot2 (Wickham, 2016).

Statistical Comparisons of Trap and Survey Success Rates.—Because trap and survey success rates are incidence rates (total number of detections per total number of time units) without any measurable distribution, we used statistical comparisons of rates as in Poisson probability law problems (Haight, 1967; Baldi and Moore, 2012). We implemented a comparison of Poisson rates using the function poisson.test in R, using the standard workflow:

```
poisson.test(c(A, C), c(B, D)),
```

where A is the number of individuals captured using the first method, B is the number of individuals captured using the second method, C is the number of time units (person-hours or trap-nights) spent employing the first method (or effort), and D is the number of time units spent employing the second method (effort). A, B, C, and D are scalars. We did not compare trap success rates to active survey success rates because the units of time (trap nights and person hours) were not comparable.

Trap Type Comparisons.—We calculated capture rates (number of *D. r. miaria* captures per night of trap deployment) for trapping sessions using two types of unbaited fyke net, a style of trap where an underwater drift fence is installed within aquatic habitat to direct turtles into funnel traps (Vogt, 1980). We constructed large fyke nets consisting of two round funnel traps 91 cm in diameter with 5-cm mesh netting and spread a 6.1×1.2-m seine net between the two funnel trap openings as an underwater drift fence. We 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. We buried the seine weights and the bottom of each funnel ring in the substrate at each trap deployment. We also designed a smaller fyke apparatus to trap in shallower waters. We constructed small fyke nets using two round, collapsible 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. We folded a 3×1.2-m sheet of flexible plastic over the top rope, then attached the plastic with zip ties to the bottom rope. The 30 cm of excess plastic was buried in the substrate at each deployment to prevent turtles from crawling under the fence. The plastic sheet, once folded and buried, served as a 3×30-cm drift fence between the two funnel traps. We used a comparison of Poisson rates to determine whether capture rates were significantly different between the large 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, we intentionally checked some traps every 2 nights, while we checked others nightly unless delayed by thunderstorms or other research activities. To determine how often traps should be checked, we used a comparison of Poisson rates to compare capture rates between traps checked every 2 nights and traps checked more frequently. To determine how long traps should be deployed at one location, we divided trap data into two categories: data from the first 2 nights at each deployment location and data from after the second night at each location (2–6 additional nights). We used a comparison of Poisson rates to determine if capture rates during the first 2 nights and after the second night were significantly different.

Survey Comparisons.—We calculated capture rates for four types of survey: dipnet, night wading, two-person seine, and road. We included data from road surveys performed during a prior study in 2015 (Ryberg et al., 2017) and this study in 2018 for comparison when conducted on roads adjacent to or bisecting the Katy Prairie Conservancy properties. We did not conduct road surveys at the Alazan Bayou site or the SFA Experimental Forest. 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, we pulled the dipnet's drag bar along the bottom through aquatic vegetation as many times as was necessary to survey the entire habitat area. We performed wading surveys by walking slowly through vegetated waters between dusk and midnight with a headlamp. During wading surveys, we 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, we did not perform wading surveys. We did not perform wading surveys at the Alazan Bayou site or the SFA Experimental Forest. To determine the significance of differences between capture rates among survey types, we compared each rate to the next highest rate using a comparison of Poisson rates with sequential P-value corrections for multiple comparisons using the Holm method within the function p.adjust() in R.

Demographic Bias among Capture Methods.—Because most capture–mark–recapture procedures assume equal catchability among individuals in a population, we inventoried potential demographic biases that may be caused by method choice. To determine sex, we 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). We 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), we used body size to distinguish between juveniles and adults after we 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 a PL of 7.5–8.5 cm (Gibbons, 1969). For the purposes of this study, we assumed males with PL $>$ 8.0 cm were mature. We assumed females with carapace lengths 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; Buhlmann et el., 2009; Dinkelacker and Hilzinger, 2014; BCB et al., unpubl. data). To graphically represent potential bias, we 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, we performed a Kruskal-Wallis rank sum test on carapace lengths of *D. r. miaria* captured using each method followed by a post hoc Dunn test with Bonferroni corrections using the function dunnTest() in the package Fisheries Stock Analysis (FSA; Ogle et al., 2021).

Potential Bias from Trap and Survey Deployment Depth.—We used telemetry data collected at the Katy Prairie Conservancy in conjunction with a study on the habitat, 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 trap allowed them to be deployed at a variety of water depths. At each aquatic telemetry position, we recorded aquatic observation depths using a tape measure lowered to the substrate within 1 m of the turtle's position. In cases where the presence of a researcher may have caused the turtle to evade and obscure the exact telemetry position, we did not record the water depth.

Optimizing Deployment Depth.—Mark and recapture efforts for *D. r. miaria* at Texas study sites rely heavily on fyke net trapping. To determine whether fyke nets have been deployed at appropriate water depths, we collected data for each *D. r. miaria* captured in a fyke net by measuring the water depth in the center of the seine wall. We 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.—We 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, we included radio-tracked individuals with more than 10 depth observations. We used two nested analyses of variance (ANOVA) on log-transformed observation depths to compare adults (both sexes combined) to juveniles (both sexes combined) and then to compare adult females to adult males, while also evaluating the effect of variation in individual activity on depth comparison results.

Aquatic Trapping Season.—To identify a trapping season, we grouped session data into 2-wk periods. If we deployed a trap during nights included in two periods, we categorized it in the period during which most deployment nights had occurred. Because telemetry efforts at these sites indicate that most *D. r. miaria* are underground in terrestrial habitats between late June and early March, we did not attempt to trap during that period. We calculated success rates for each period. To control for site variation, we only included Katy Prairie sessions because we only trapped the other sites in 2019. To control for trap type variation, we only included large fyke nets, as we 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. We used telemetry data to inventory dates of terrestrial migration at the Katy Prairie sites. We employed two methods to determine start times for terrestrial migrations. We attached Lotek brand pp-120 global position system (GPS) loggers to turtles and programmed them to record positions every 2 h. We selected this 2-h increment in the interest of collecting behavioral information throughout each day and night while also preserving battery life. We recharged batteries every 50 days in loggers set to record positions every 2 h. Occasionally, we programmed loggers to collect data more frequently to document nesting behavior. For the purposes of this study, we divided migration start times into 2-h increments. We collected some start times by installing automated Hyperfire HC500 (Reconyx) wildlife cameras above estivating or hibernating *D. r. miaria*. We programmed cameras to fire every minute, providing documentation of exact migration start times.

Results

Literature Review.—We included 13 studies at 6 study sites from prior literature in our evaluation, including 2 sites in Arkansas and singular sites in South Carolina, Virginia, Oklahoma, and Texas. Studies that met inclusion criteria used five methods to capture *D. reticularia* (Table 1). Eight of the 13 studies presented data collected by wholly or partially enclosing known *D. reticularia* aquatic habitats with terrestrial drift fences, with individuals crawling into funnel traps placed along the fences, falling into pitfall buckets buried along the fences, or captured by hand along the fences as they migrate over upland habitats (Gibbons, 1969; Gibbons and Nelson, 1978; Gibbons et al., 1982; Congdon et al., 1983; Buhlmann and Johnson, 1995; Buhlmann et al., 2009; Buhlmann and Gibbons, 2001; Patton and Wood, 2009; McKnight et al., 2015a). 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 et al., 2015a), during which only one individual *D. r. miaria* was captured using drift fences. We did not use terrestrial drift fences in our field study because of restrictions at the study sites, the presence of livestock that needed access to the wetlands, and the fact that we were 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 et al., 2015a) reporting 11 captures in 338 trap nights (0.033 captures/night) and 75 captures at a rate of 0.007 captures per 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 captured *D. reticularia* (Buhlmann, 1995; Demuth and Buhlmann, 1997; Hilzinger, 2009; Buhlmann et al., 2009; Sachse, 2014; McKnight et al., 2015a; 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*,

TABLE 1. Literature review of *D. reticularia* capture methods. × Indicates that the method captured *D. reticularia* during the study. † Indicates that the method was used during the study but did not capture *D. reticularia*. * Indicates that both baited hoop nets and fyke nets were used but method was not reported for each capture. SC = South Carolina; VA = Virginia; AR = Arkansas; OK = Oklahoma; TX = Texas.

Author(s)	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	×	×							
Gibbons and Nelson	1978	SC: Savannah River Site	×								
Gibbons et al.	1982	SC: Savannah River Site	×								
Congdon et al.	1983	SC: Savannah River Site	×			×					
Buhlmann et al.	1995	SC: Savannah River Site	×			×					
Buhlmann	1995	VA: Seashore S.P.		†			×				
Demuth and Buhlmann	1997	SC: Savannah River Site				×	×				
Hilzinger	2009	AR: Holland Site					×				
Buhlmann et al.	2009	SC: Savannah River Site	×				×				
Patton and Wood	2009	OK: Boehler Seeps and Sandhills Preserve	†			×					
McKnight	2014	OK: Boehler Seeps and Sandhills Preserve	×		×	×*	×*				
Sachse	2014	AR: Joe Hogan State Fish Hatchery				×*	×*				
Ryberg et al.	2017	TX: Katy Prairie			†	†	×				×
This study	2018	TX: Katy Prairie					×	×	×	×	†

including 129 captures of 86 individuals at the Katy Prairie Conservancy and 11 captures of 10 individuals at the Alazan Bayou Wildlife Management Area. 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 the Katy Prairie Conservancy was 23.2 cm in carapace length (CL) and the largest adult male was 16.8 cm CL. The largest adult female at the Alazan Bayou Wildlife Management Area 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 large fyke nets. A total of 153 trap nights employed the smaller fyke apparatuses. Large fyke nets had significantly higher capture rates than did the smaller design (comparison of Poisson rates: $P < 0.001$). We captured 95 *D. r. miaria* in fyke nets over 380 trap nights (0.25 captures/night). We captured five *D. r. miaria* in small fyke traps over 153 trap nights (0.033 captures/night).

Trap Check Frequency and Deployment Duration.—We captured 57 *D. r. miaria* in traps checked every 2 days over 376 nights of deployment (0.152 captures/night) and 43 *D. r. miaria* in traps checked more frequently over 157 nights of deployment (0.274 captures/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: $P = 0.005$). We captured 62 *D. r. miaria* during checks within the first 2 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 2 nights of deployment were significantly higher than rates after the second night (comparison of Poisson rates: $P = 0.005$).

TABLE 2. Survey effort and capture rates (captures per person-hour) 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

Survey Type Comparisons.—Dipnet surveys captured *D. r. miaria* at the highest rate, followed by wading, seine, and road (Table 2). To determine if the difference between capture rates among survey types was significant, we compared each rate to the next highest rate using a comparison of Poisson rates, and then applied sequential *P*-value corrections using the Holm method. Capture rate during dipnet surveys was not significantly higher than during wading surveys ($P = 0.4$). Rate of capture during wading was not significantly higher than seine surveys ($P = 0.5$), but the dipnet capture rate was significantly higher than seine ($P < 0.05$). The dipnet, seine, and wading survey capture rates were each significantly higher than for road ($P < 0.001$, $P = 0.02$, and $P = 0.03$, respectively).

Demographic Bias among Capture Methods.—Demographic proportions of captures by large fyke net ($n = 99$), dipnet ($n = 9$), hand during wading surveys or incidentally ($n = 13$), seine ($n = 11$), and plastic fyke trap ($n = 5$) indicated that there were demographic and body size biases among capture methods (Fig. 1). We captured no adult females via seine surveys or plastic fyke traps. The mean carapace lengths among different capture methods (Fig. 2) were significantly heterogeneous (Kruskal-Wallis rank sum test: $H_4 = 24.4$, $P < 0.001$). A post hoc Dunn test with Bonferroni corrections indicated that *D. r. miaria* captured via dipnet were significantly smaller than individuals captured via fyke nets ($P = 0.009$) and wading surveys ($P = 0.01$). Individuals captured via seine were also significantly smaller than individuals captured via fyke nets ($P = 0.02$) and wading surveys ($P = 0.03$).

Aquatic Activity Depth.—Population mean water depth among all *D. r. miaria* telemetry observations with depth data (501 observations of 27 individuals) in the Katy Prairie was 35.3 cm (Fig. 3). Population mean activity depth was significantly shallower than mean capture depth using large fyke nets ($n =$

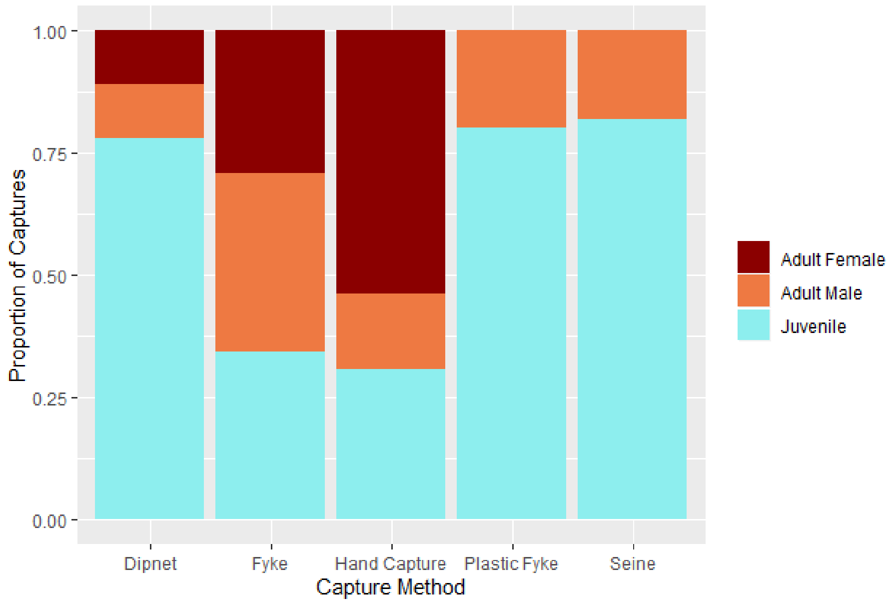

FIG. 1. Proportion of juvenile, adult male, and adult female *D. r. miaria* collected by capture method, including recaptures. We included individuals captured by dipnet, fyke trap, plastic fyke trap, seine net, and by hand during night wading surveys or incidentally while checking traps. We did not include road survey data because we were unable to determine the sex or age class of road mortality specimens.

58, mean = 48.4 cm) when compared using a Mann-Whitney U-test ($U = 21710$, $P < 0.001$).

Demographic Bias in Aquatic Activity Depth.—Individuals with more than 10 depth observations included, for demographic comparisons: 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); nested ANOVA indicated that there were not significant differences among individuals within ($F_{2,18} = 1.1$, $P = 0.3$) 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 were adult females (mean = 38.6 cm; $F_{1,13} = 9.3$, $P = 0.003$), and nested ANOVA revealed that there was significant variation among adult females ($F_{13,14} = 6.5$, $P < 0.001$). When examining activity depths of radio-tracked adults more closely (Fig. 4), it became apparent that we observed one individual female (ID 2255) in much deeper water on average than other radio-tracked *D. r. miaria*. Upon removing this outlying 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 ($F_{1,12} = 9.3$, $P = 0.24$).

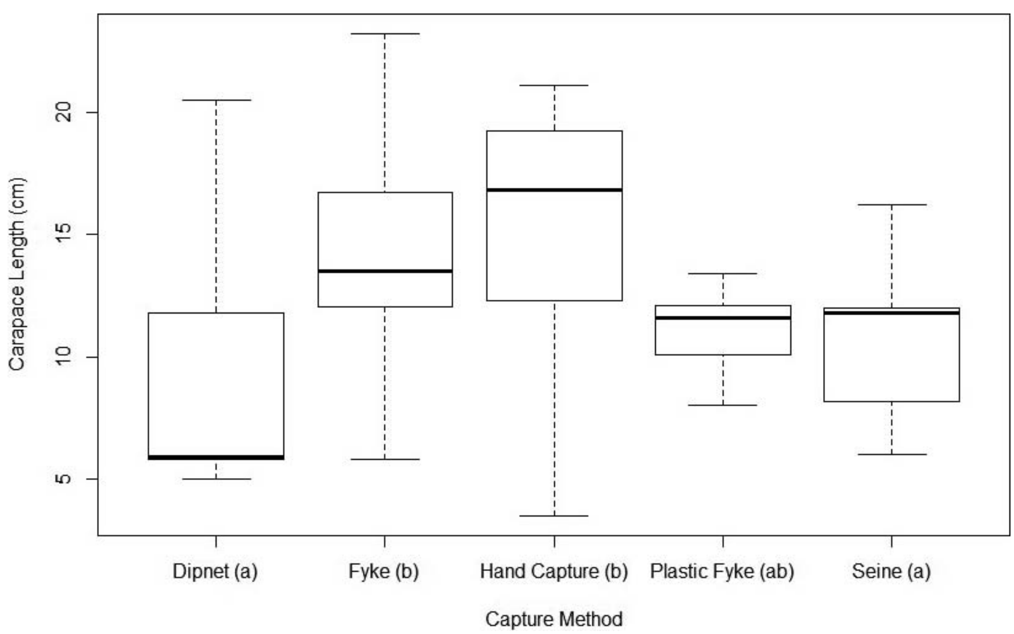

FIG. 2. *Deirochelys r. miaria* sizes by capture method, including recaptures. Horizontal bars represent median, the bottom and top edges of the box represent 25th and 75th percentiles, and whiskers extend to the 5th and 95th percentiles. Values were derived by measuring straight-line carapace length with calipers. Groups resulting from significant differences shown by a post hoc Dunn test are denoted in lower case letters ($\alpha = 0.05$).

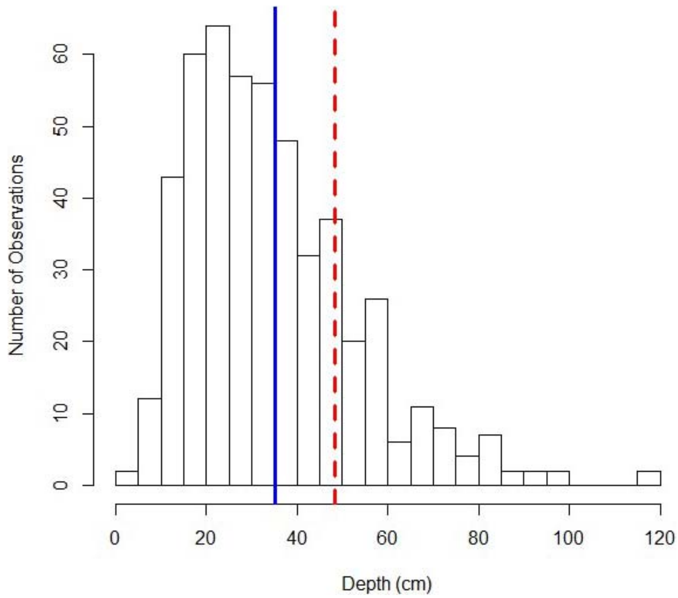

FIG. 3. Observed water depths (501 observations of 27 radio-tracked individuals) at *D. r. miaria* positions during radio telemetry monitoring. Solid blue line indicates mean activity depth (35.3 cm). Dashed red line indicates mean depth of capture among fyke net captures (48.4 cm).

Aquatic Trapping Season.—The lowest rates of capture occurred during the earliest sessions of each year, including late March of 2019 and early April of 2018 (0.04 and 0.13 captures per trap night, respectively; Table 3). The highest rate of capture occurred during late April of 2018 (0.60 captures per trap night), and capture rates dropped during each of the subsequent three periods.

Terrestrial Survey Season.—We observed 202 terrestrial migrations among 27 radio-tracked individuals during the telemetry study at Katy Prairie (Fig. 5). These migrations included transitions from wetlands to other wetlands, wetlands to estivation sites, estivation sites to other estivation sites, and estivation sites to wetlands. *Deirochelys r. miaria* were most terrestrially active during June and July. We documented 61 migration start times among 13 radio-tracked individuals using GPS loggers and automated game cameras (Fig. 6). Most terrestrial movements were diurnal and upland movement peaked around 1100 h.

TABLE 3. Large fyke trap success at Katy Prairie 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

DISCUSSION

Our literature review and field research showed that *D. reticularia* were captured with each of the trapping and survey methods investigated, but not all methods were successful across the entire species range (Table 1). In addition to this regional variation in trapping success, we found variation in trapping success over time and demographic bias in trapping and survey methods for *D. r. miaria* in Texas (Tables 2, 3; Figs. 1, 2). Our radiotelemetry results revealed the importance of trap location with respect to water depth for *D. r. miaria* (Figs. 3, 4), and the significance of terrestrial survey timing with respect to the frequency of terrestrial *D. r. miaria* movements (Figs. 5, 6). Together, our results suggest that *D. reticularia* trapping and survey success may be regionally specific (e.g., *D. r. miaria* in Texas) but ultimately knowable given careful foundational work on species' natural history in each region (McKnight et al., 2012, 2015a; McKnight, 2014). With this theme in mind, below we discuss our trapping and survey success in greater detail while drawing comparisons to results from other regions.

One of the most vexing points of contention when designing a *D. reticularia* study is whether or not to employ baited traps. Several *D. reticularia* studies (Table 1) have used baited traps successfully (Gibbons, 1969; Congdon et al., 1983; Buhlmann et al., 1995; Demuth and Buhlmann, 1997; Patton and Wood, 2009). In Virginia, baited traps failed to capture *D. reticularia* in

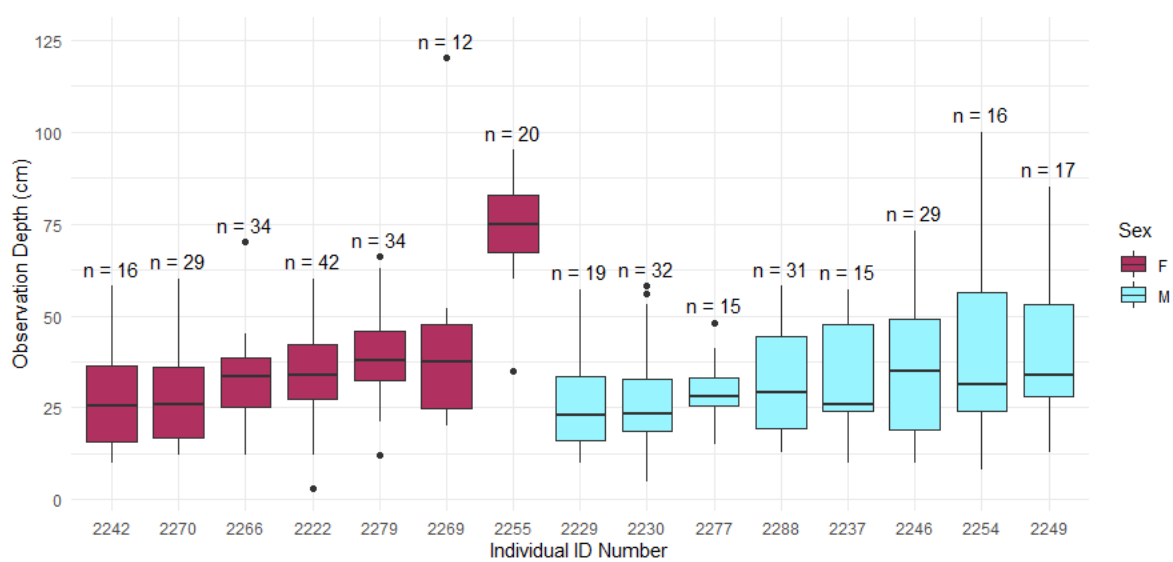

FIG. 4. Observation depths of radio-tracked *D. r. miaria* by individual turtle and sex.

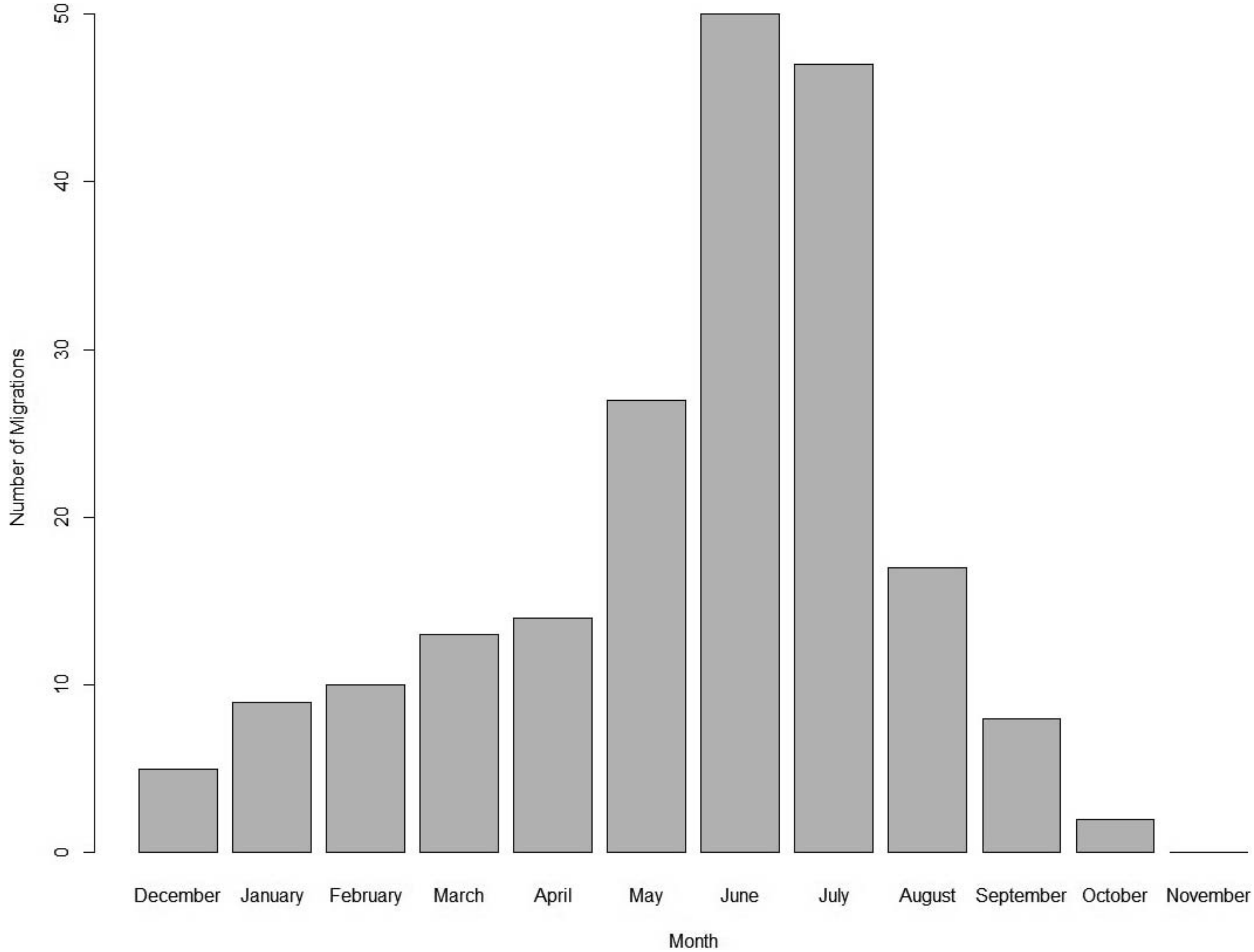

FIG. 5. *Deirochelys r. miaria* terrestrial migration start dates observed via radio telemetry (202 migration start dates observed among 27 radio-tracked individuals).

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 Katy Prairie 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

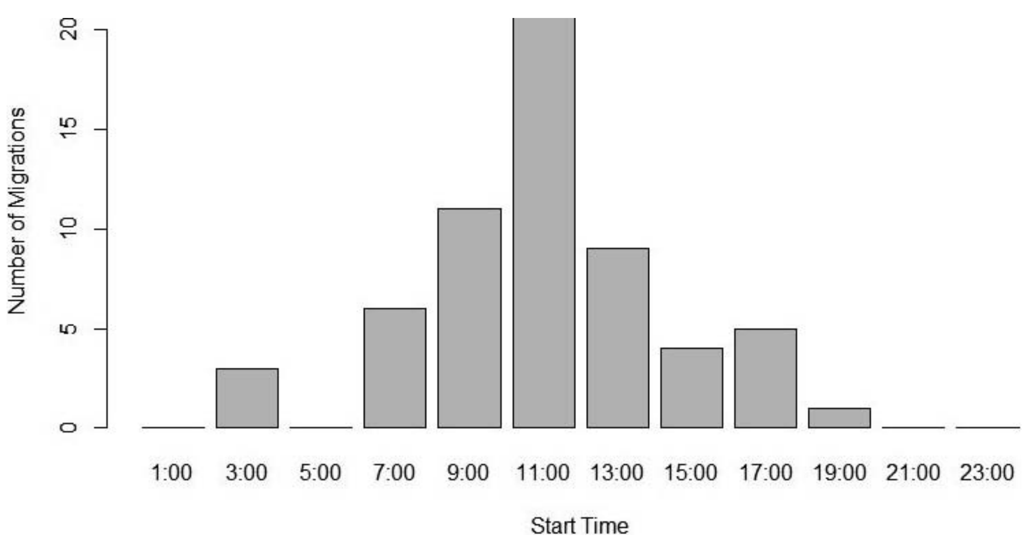

FIG. 6. *Deirochelys r. miaria* terrestrial migration start times documented by GPS loggers and wildlife cameras (61 migration start times observed among 13 radio-tracked individuals).

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 by accident. *Deirochelys reticularia* may not be attracted to the bait itself, but to the live crawfish feeding on the bait (McKnight, pers. com.). A review of the literature found no documented observations of *D. reticularia* feeding on carrion in the wild (Jackson, 1996; Demuth and Buhlmann, 1997; McKnight et al., 2015c). If designing a study in an area where baited traps have not yet proven effective, unbaited fyke traps are recommended because of the regional inconsistencies in *D. reticularia* responses to baited traps.

When using a comparison of Poisson rates via the poisson.test function, it is possible that certain capture protocols may violate Poisson process assumptions. If an individual being in a trap may deter others from entering the trap or make other individuals more likely to enter the trap, the incident rate may not represent a true Poisson process. In such cases, a comparison of Poisson rates may still be the most robust way to compare incidence rates in situations with variable levels of effort (total units of time). The same is true of surveys in which a detection during the survey prevents future detections.

When designing studies on *D. r. miaria*, different capture protocols may be implemented depending on research questions, budget, time constraints, and property access. Most capture–mark–recapture procedures assume equal catchability of individuals within a population and equal survey effort, 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 (Figs. 1, 2). For this reason, fyke trapping and hand capture during wading surveys are recommended in studies requiring reproductive females at sites that do not permit terrestrial drift fences (Fig. 1). 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; Fig. 2). 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 Western Mudsnakes (*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 radio-tracked adult males was significantly shallower than that of adult females, the results of the nested ANOVA revealed that some of that variation was influenced by the behavior of individual *D. r. miaria*. When examining the activity depths of radio-tracked adults more closely (Fig. 4), it becomes apparent that we observed one individual female (ID 2255) in much deeper water on average than the other radio-tracked *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, we did not examine seasonal or temporal influences on activity depth. It could be helpful to know whether abiotic components such as temperature and precipitation, as well as biotic components such as 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 we experimented with different survey methods, so trapping effort was much lower than later 2018 periods and 2019 periods (Table 3). In 2019 we initiated trapping based on the return of radio-tracked individuals to aquatic behaviors, and from late April of 2019 onward we trapped at other sites and worked on other components of the project. Though this dearth of comparable data made analysis difficult, relatively low fyke capture rates (Table 3) during early April 2018 (0.13 captures per trap night) and late March of 2019 (0.04 captures per trap night) indicate that the return of individuals to aquatic habitats does not necessarily indicate availability for capture using passive methods. During that time, most individuals monitored via telemetry had returned to the wetlands. It may be that although these individuals had returned to aquatic habitats, they were not active enough during that period to frequently wander into fyke nets. No individuals in the telemetry study remained in aquatic habitats during the late summer or fall of 2018 or 2019, a seasonal pattern also observed in prior studies on the western subspecies (Dinkelacker and Hilzinger, 2009; McKnight et al., 2015b). Water temperature and precipitation are variables that could be investigated as additional variables affecting catchability.

Though the frequency of terrestrial migrations peaked in June (Fig. 5), most *D. r. miaria* migrations over upland habitat were movements either from wetlands to estivation sites after concluding aquatic activity, from estivation sites to wetlands before resuming activity, or between consecutive estivation sites. If road surveys are not located between wetlands and upland estivation 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 (Fig. 6) may increase chances of detection.

Based on our literature review and field research, we 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 we 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 radio-tracked individuals indicate that traps should be deployed in waters as close as possible to 35 cm in depth.

(4) Traps should be checked daily. We 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 because of escaped individuals.

(5) Success rates were significantly higher during the first 2 days of trap deployment, potentially because of individuals becoming trap-shy with time. We recommend leaving traps at a site for 3 nights or less and then moving them.

(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, 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 radio-tracked individuals.

(8) Road and trail surveys are not recommended, as road surveys resulted in significantly lower capture rates than did other active survey methods. In studies where limited property access necessitates terrestrial surveys as a last resort, we recommend surveying roads in Texas during June and July when migrations over terrestrial habitats are most frequent. These surveys should be centered around 1100 hrs, the peak terrestrial activity period.

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