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Fecundity, Female Maturation, and Nesting Season of Western Chicken Turtles (*Deirochelys reticularia miaria*) in Texas

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Abstract. – **The reproductive lifespans of turtles are consistently long, but reproductive cycles are under environmental control and thus can vary within species, populations, and individuals over time and space. Knowledge of turtle species' reproductive traits and their associated variances over time and space are critical to understanding the dynamics of turtle populations, especially those requiring management or conservation. *Deirochelys reticularia* is a species being considered for protection by the US Fish and Wildlife Service and contains 3 subspecies with some differences in reproductive characteristics of nesting season, annual nesting frequency, and egg retention. We collected ultrasound and x-radiograph data in Texas to identify the maturation size, nesting season, annual nesting frequency, and clutch size of female *D. r. miaria* in Texas. We observed no reproductive activity in individuals from 101 to 146 mm in plastron length (PL) and detected either unshelled eggs, shelled eggs, or both in individuals from 150 to 197 mm PL. Maturation sizes were similar to those in other regions and for other subspecies. We observed shelled clutches or nesting events from April to July, confirming a spring–summer nesting season in Texas consistent with other *D. r. miaria* sites and supporting the paradigm that the western subspecies does not follow the autumn–winter nesting season of the other subspecies. We found no evidence that individuals retain shelled eggs while aestivating or overwintering. Individuals nested up to 3 times/yr in Texas. Individuals laid 7–11 eggs and the mean clutch size was 9.2 eggs, similar to other regions and other subspecies. Nesting phenology is regionally variable, so management plans and policies for the species will need to consider that variation and potentially recognize management differences among *D. reticularia* subspecies.**

Key Words. – **oviparity; fecundity; clutch size; phenology; aestivation; activity patterns; maturation**

The life history of turtles consists of a long lifespan, delayed reproductive maturity, high and stochastic egg and hatchling mortality rates, and low adult mortality rates (Shine and Iverson 1995). An extended reproductive lifespan is key to turtle species' persistence because seasonal fluctuations in the environment result in some periods being more favorable than others for egg and hatchling survival (Congdon et al. 1993). Indeed, the success of a turtle species regionally depends on how well constituent populations adjust the timing of reproductive cycles to match seasonal environmental variability throughout the species' range (Heatwole and Taylor 1987, Miller and Dinkelacker 2007). However, extended reproductive lifespans also compromise our ability to assess turtle population stability from simple population density measures, because individuals, whether successfully reproducing or not, remain in the population for long periods and can create time lags between true population declines and our ability to detect the declines (Heatwole and Taylor 1987). Knowledge of turtle species' reproductive traits (e.g., vital rates) and their associated variances over time and space can reduce such time lags by helping us better understand the dynamics of turtle populations (Miller and Dinkelacker 2007). Here, we aim to better understand the reproductive biology of chicken turtles (*Deirochelys reticularia*), which can be difficult to study because of temporary emigrations, the inconsistent seasonal availability of individuals (Bowers et al. 2021a, in press), and population declines in parts of their range (Ryberg et al. 2017).

Deirochelys reticularia is a turtle in the family Emydidae that inhabits the shallow, lentic waters of ephemeral wetlands throughout the southeastern United States (Carr 1952; Buhlmann 1995; Buhlmann et al. 2008;

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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. 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). Although 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 in surrounding uplands the remainder of the year (McKnight et al. 2015; Bowers et al. 2021a, in press). There have been no range-wide status assessments for *D. reticularia* (Buhlmann et al. 2008) and the western subspecies is under potential threat in Texas as result of impacts from increasing urbanization and land management practices (Ryberg et al. 2017; Bowers et al. 2021b). In Missouri, the subspecies is listed as locally endangered because 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-d finding that states that listing the species as Threatened or Endangered under the US Endangered Species Act may be warranted (USFWS 2011).

There are regional differences in female reproductive traits among and within the 3 *D. reticularia* subspecies. In South Carolina, *D. r. reticularia* followed an autumn–winter nesting season and produced up to 2 clutches/yr (Gibbons and Greene 1978; Congdon et al. 1983; Buhlmann et al. 1995; Buhlmann 1998; Buhlmann and Gibbons 2001). During one South Carolina study, all mature females reproduced each year, and 60% of mature females produced second clutches within years (Buhlmann et al. 2009). Some individuals produce autumn clutches with development arrested in the gastrula stage during a diapause period through the winter and eggs then developing during warmer periods (Ewert 1985). Some females retain viable shelled eggs within the body cavity through the winter (Cagle and Tihen 1948; Congdon et al. 1983; Buhlmann et al. 1995; Ernst and Lovich 2009). Fewer females nested during drought years than in nondrought years in South Carolina (Gibbons et al. 1983). In Virginia, observations of females with shelled eggs on 12 March, 20 May, and 13 June suggest that the nesting season for *D. r. reticularia* may extend into summer in that region (Buhlmann 1995). In Florida, females nested from autumn through early spring but produced up to 4 clutches/yr (Carr 1952, Jackson 1988; Ewert et al. 2006). Neither the autumn–winter nesting season, the requirement of developmental diapause for successful incubation, nor the retention of shelled eggs through the winter has been observed in *D. r. miaria*. In Louisiana, 3 nesting events were observed in May and June, 2 gravid females were found walking on land in May, and 1 individual dissected in late January contained 2 size classes of ovarian follicles (Carr and Tolson 2017). In Arkansas, *D. r. miaria* eggs obtained via induced oviposition did not require a diapause period for successful incubation (Dinkelacker and Hilzinger 2014). During an Oklahoma study, 3 individuals monitored via ultrasound for 1–2 yrs developed follicles from March through July, contained shelled eggs from May through July, nested up to 3 times/yr, and did not retain eggs during aestivation periods (McKnight et al. 2015, 2018). In Texas, the reproductive season has not been studied, but one observation in the literature occurred on 11 May (David 1975).

Although there are regional differences in nesting season and reproductive frequency, documented female maturation sizes are similar across the range of *D. reticularia*. Although age is more relevant than size when modeling population dynamics, there are several reasons to use size as a surrogate in this species. Determining the age of individuals by counting growth rings on the plastral scutes can be difficult on mature individuals (Dinkelacker and Hilzinger 2014). Additionally, there have been drought years in Texas with no aquatic foraging activity at some sites and we do not know how that affects the growth of individuals or the addition of new rings on the plastral scutes (Bowers et al. 2021a). The smallest mature females documented in South Carolina had plastron lengths (PL) $>$ 140 mm (Gibbons 1969; Gibbons and Greene 1978; Buhlmann et al. 2008, 2009). The smallest mature females in Florida were 145–147 mm PL (Jackson 1988, Ewert et al. 2006). In Arkansas, the smallest female with palpable eggs was 150.5 mm PL, but researchers noted a general lack of females in the 130–150 mm PL range among captures during the study (Dinkelacker and Hilzinger 2014). An absence of enlarged follicles in several females $>$ 180 mm PL in South Carolina prompted a hypothesis of reproductive senescence, but the individuals were observed outside the period in the local reproductive cycle when enlarged follicles would be expected (Gibbons 1969; Ernst and Lovich 2009).

Egg sizes and clutch sizes are also similar across the range of *D. reticularia*. The relationship between body size, clutch size, and egg size has been studied at several sites. One study in South Carolina found clutch size to be weakly correlated with body size (Congdon et al. 1983). Another South Carolina study found both clutch sizes and egg sizes to be positively correlated with plastron length (Buhlmann et al. 2009). A study of *D. r. miaria* combining data from Louisiana and Oklahoma found clutch size to be

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positively correlated with plastron length and that *D. r. miaria* eggs were not significantly larger than eggs of *D. r. reticularia* (McKnight et al. 2018). Two early studies in South Carolina documented relatively low mean clutch sizes of 7.2–8.0 eggs (Gibbons et al. 1982; Congdon and Gibbons 1985) in comparison with later studies in South Carolina, Florida, Oklahoma, Louisiana, and Arkansas, which documented mean clutch sizes ranging from 9.5 to 10.9 eggs (Iverson 1977; Jackson 1988; Ewert et al. 2006; Buhlmann et al. 2009; Dinkelacker and Hilzinger 2014; Carr and Tolson 2017; McKnight et al. 2018). The females in the former studies were smaller on average (159–160 mm mean PL) than in the latter studies (174.8–186.1 mm mean PL), which may be reflected in the smaller mean clutch sizes. It is unknown whether females at those sites are genuinely smaller or whether the capture methods employed during those studies were biased toward smaller individuals, as has been documented in some capture methods for *D. reticularia* (Bowers et al., in press).

Although female reproduction has been studied in *D. reticularia,* regional differences in reproductive characteristics highlight the importance of studying reproductive traits and phenology throughout the range of the species. Here, we report on a study designed to better understand the female reproductive biology of *D. r. miaria* in Texas. Our objectives were to 1) identify the nesting season in Texas, 2) document clutch sizes and annual reproductive frequency, 3) determine size of sexual maturation, and 4) synthesize these data with prior observations in Texas and literature from studies in other states to summarize differences in reproductive biology informative to the status assessments and management plans of the USFWS for this species.

METHODS

Study Site. — The study site was an 18,000-acre private property managed by the Katy Prairie Conservancy 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 (T.J. Hibbitts, *pers. comm.*), making this the only Texas site we were aware of in 2018 with multiple recent *D. r. miaria* captures.

Female Maturation Size. — To identify the female maturation size of *D. r. miaria* in Texas, we opportunistically collected data on the reproductive condition of females in a range of body sizes during telemetry and monitoring studies aimed at optimizing survey protocols for the species (Bowers et al. in press). We scanned individuals via ultrasound (General Electric, Logiq S7) at a nearby veterinary clinic (Wellborn Road Veterinary Medical Center, College Station, TX). We recorded the straight-line carapace length (CL) and plastron length (PL) of each individual and classified individuals as having shelled eggs, enlarged follicles, both shelled eggs and enlarged follicles, or no apparent reproductive activity. To ensure that we were collecting data during the season when individuals were most likely to be reproductively active, we collected only data aimed at identifying maturation size between March and July of 2018 and 2019 and included only individuals captured during periods of aquatic activity.

Clutch Size, Reproductive Frequency, and Nesting Season. — We used the ultrasound methods described above to monitor the reproductive condition of 6 females larger than 140-mm PL once per month for 12 mo beginning on 14 January 2019 during a telemetry study on the spatial ecology of *D. r. miaria* in Texas (Bowers et al. 2021a). If shelled eggs were detected via ultrasound, we scanned the individual via X-radiography (Varian, Sound Smart DR) to count eggs and determine whether new clutches had been shelled by comparing the position and number of eggs with imagery of prior clutches. When individuals contained shelled eggs, we recorded the date to determine whether the nesting season at this site was consistent with the spring–summer nesting season documented in the literature for the western subspecies and whether individuals in this population shell multiple clutches per year. To supplement nesting season information, we also searched for citizen science observations of *D. r. miaria* nesting events within the state of Texas (iNaturalist 2022).

RESULTS

Female Maturation Size. — Between March and May of 2018 and 2019, we performed 14 ultrasounds on 11 individuals between 101- and 197-mm PL and between 113- and 232-mm CL (Table 1; Fig. 1A–B). We observed no reproductive activity in all individuals from 101- to 146-mm PL (113–165-mm CL) and detected either enlarged follicles, shelled eggs, or both in all individuals from 150- to 197-mm PL (166–232-mm CL). One individual (ID# 2252) was of immature size and nonreproductive when scanned on 10 May 2018 (118-mm PL) and again on 18 March 2019 (141-mm PL), but contained shelled eggs when scanned on 16 December 2019 (161-mm PL).

Nesting Season. — We performed monthly ultrasounds and X-radiographs on 6 mature females during 2019 (Figs. 1 and 2). We monitored 4 individuals from 14 January to 16 December 2019, 1 individual from 14 January to 14 August 2019, and 1 individual from 16 April to 16 December 2019. Some individuals contained enlarged follicles during all months of the study, but we only detected shelled eggs from April through June. However, one individual contained shelled eggs when found preyed upon during the maturation size study on 26 July 2018 (Table 1). Two incidental observations of nesting events also contributed to our understanding of the nesting season in Texas. On 14 June 2021, an individual (ID# 2999, not measured) laid eggs on a property adjacent to the study site. While tracking for a telemetry study at a

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Table 1. Reproductive condition, plastron length, and carapace length of 11 individual *Deirochelys reticularia miaria* opportunistically scanned via ultrasound in Texas. PL = plastron length; CL = carapace length.

Individual ID[a]	PL (mm)	CL (mm)	Reproductive condition[b]	Observation date
2240	101	113	—	24 Apr 2018
2239	113	127	—	24 Apr 2018
2252a	118	132	—	10 May 2018
2241	138	155	—	18 Mar 2019
2268	141	157	—	18 Mar 2019
2252b	141	153	—	18 Mar 2019
2255	146	165	—	10 May 2018
2256	150	166	U	10 May 2018
2242	156	173	U + S	3 May 2018
2252c	161	173	U	16 Dec 2019
2257	163	181	U + S	10 May 2018
2299	178	205	U + S	16 Apr 2019
2236a	197	232	U + S	18 Apr 2018
2236b	197	232	S*	26 Jul 2018

[a] Observations with letters following the ID number indicate individuals that were scanned multiple times during the maturation size study.
[b] — = no reproductive activity was observed. U = unshelled eggs were observed. S = shelled eggs were observed. S* = the individual contained shelled eggs when found after being preyed upon, but decay would have made the unshelled eggs undetectable.

second site in the East Texas Pineywoods Ecoregion, we observed an individual digging a nest on 29 May 2021, but it abandoned the nest, potentially startled by our presence. Texas observations contributed via citizen science include a nesting event in April 2018 and another in May 2020, both within the Coastal Prairie Ecoregion (iNaturalist 2022).

Reproductive Frequency. — Of the 4 individuals that shelled eggs during the monitoring period, 1 shelled 3 clutches, 2 shelled 2 clutches, and 1 shelled 1 clutch. However, one individual that had previously shelled 2 clutches during the season (ID# 2266) contained eggs on 11 June 2019 that were developed enough to be visible in X-radiographs but not clearly enough to be counted. We suspect that this individual laid 3 clutches during the study. Although not monitored monthly, an individual scanned during the maturation size study (ID# 2236; 197-mm PL, 232-mm CL) contained both shelled eggs and enlarged follicles when scanned on 18 April 2018 and contained crushed or desiccated shelled eggs when found preyed upon on 26 July 2018; thus, she had produced ≥ 2 clutches during that season. We were not able to determine whether unshelled follicles were present at the time of predation. Two individuals (ID#s 2242 and 2269) never contained shelled eggs during monthly ultrasounds in 2019. These two individuals were the smallest females included in monthly monitoring, but both individuals contained enlarged follicles in 2019 and one of them (ID# 2242) contained 8 shelled eggs 1 yr prior during the female maturation study on 3 May 2018. Both of these individuals had much shorter aquatic activity periods than did the other individuals monitored during the telemetry study in 2019. One individual (ID# 2269) was only active aquatically for 30 d during 2019 and another (ID# 2242) was only active for 58 d, compared with 103–150 d of activity for the 4 individuals that shelled eggs.

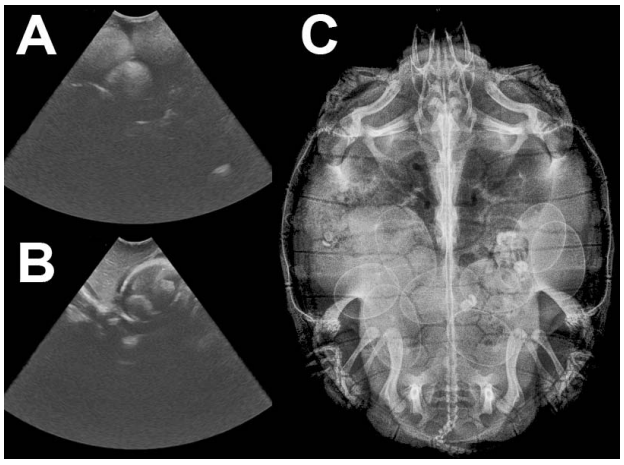

Figure 1. Veterinary imaging of reproductive female *Deirochelys reticularia miaria* in Texas, including (A) an ultrasound image of enlarged follicles, (B) an ultrasound image of a shelled egg, and (C) an X-radiograph image of 1 individual female containing 8 shelled eggs.

Clutch Size. — In total, we observed 11 *D. r. miaria* clutches with eggs that could be counted among 7 individual females (Table 2). During monthly monitoring, we observed 8 clutches in 4 individuals ranging from 7 to 11 eggs (Fig. 2). To add to our data set on clutch size, we performed opportunistic X-radiograph scans on 2 individuals during the female maturation size study (ID#s 2242 and 2299), resulting in clutch sizes of 8 and 11 eggs, respectively. Additionally, 1 individual laid 7 eggs on an adjacent property on 14 June 2021. The mean clutch size among the 11 clutches observed during this study was 9.2 eggs.

DISCUSSION

Female maturation sizes of individual *D. r. miaria* in Texas were similar to those observed in the literature in other regions and for other subspecies. We observed no reproductive activity in individuals smaller than 146-mm PL. We observed some reproductive activity in all females

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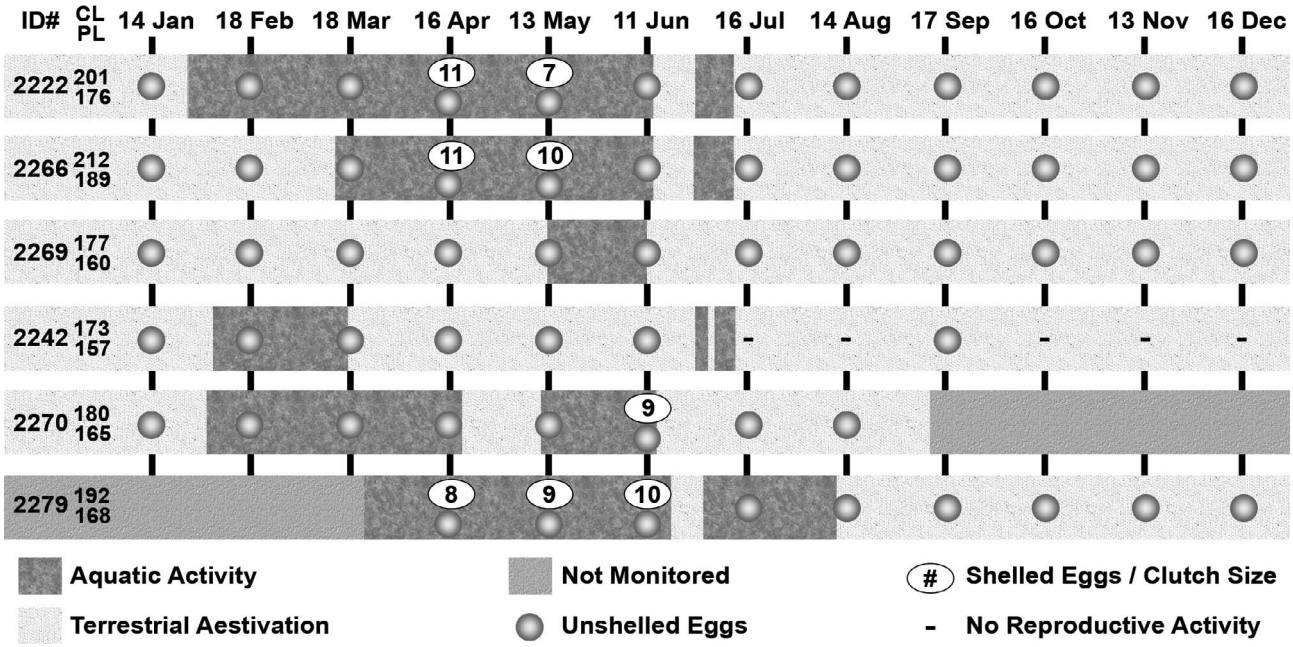

Figure 2. Monthly reproductive condition of 6 *Deirochelys reticularia miaria* in Texas during 2019. Carapace (CL) and plastron (PL) lengths are presented in mm.

above 150-mm PL and the largest female with data on reproductive condition was 197-mm PL and 232-mm CL. Individuals laid 7–11 eggs and mean clutch size was 9.2 eggs. Individuals nested up to 3 times annually and all nesting events and shelled clutches were observed during April–July.

Despite similar clutch sizes across the range of *D. reticularia,* care should be taken when incorporating fecundity estimates into fertility terms in studies on population dynamics because of regional differences in annual clutch frequency, annual duration of aquatic activity, and drought frequency, which undoubtedly influence reproductive potential. During a drought period at one Texas site in 2020, all individuals monitored via telemetry abstained from aquatic activity, remaining underground at aestivation sites for the entire year (Bowers et al. 2021a). We do not know whether individuals nested during 2020 at that site. Fewer females nested during drought years than during nondrought years in South Carolina (Gibbons et al. 1983). The observation that 2 individuals during our study did not contain shelled eggs during monthly ultrasounds in 2019 and had very short aquatic activity periods may indicate a relationship between activity period and fecundity even during nondrought years or the possibility that some *D. r. miaria* alternate nesting years in some regions. The relationship between aquatic activity duration and annual fecundity should be studied further, with future studies monitoring individuals for several years to determine whether all mature individuals nest annually.

We found no evidence that individuals retained shelled eggs while aestivating or overwintering. We observed shelled clutches or nesting events from April to July, confirming a spring–summer nesting season in Texas

Table 2. Clutch sizes, plastron lengths (PL), and carapace lengths (CL) for 7 individual *Deirochelys reticularia miaria* scanned via X-radiograph in Texas, arranged from smallest to largest clutch.

Individual ID[a]	Observation date	PL (mm)[b]	CL (mm) [b]	Clutch size
2222b	13 May 2019	175	201	7
2999	14 Jun 2021	NR	NR	7
2242	3 May 2018	156	173	8
2279a	16 Apr 2019	168	192	8
2270	11 Jun 2019	165	180	9
2279b	13 May 2019	168	192	9
2266b	13 May 2019	189	212	10
2279c	11 Jun 2019	168	192	10
2299	16 Apr 2019	178	205	11
2222a	16 Apr 2019	175	201	11
2266a	16 Apr 2019	189	212	11

[a] Observations with letters following the ID number indicate individuals with > 1 clutch.
[b] NR = not recorded.

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consistent with other *D. r. miaria* sites and supporting the paradigm that the western subspecies does not follow the autumn–winter nesting season of the other subspecies. Jackson (1988) suggested that an extended nesting period without a peak in *D. r. reticularia* may reduce nest predation. If *D. r. miaria* have a peak nesting period during the spring and early summer, then pressure from nest predators may have more impact on nests in the western subspecies. Nesting phenology is regionally variable, so management plans and policies for the species will need to consider that variation and potentially recognize management differences among *D. reticularia* subspecies.

Although our study was informative on the reproductive ecology of *D. reticularia* and fills an important gap in the geographic distribution of reproduction data on the species, there were some limitations to our approach. Monitoring more individuals could potentially have yielded sample sizes that were statistically comparable. The observation of one individual with eggs that were developed enough to detect via X-radiograph but not developed enough to count indicates that monitoring individuals more frequently may have identified additional shelled clutches. Monitoring individuals for several years could have answered questions on reproductive activity during drought years, the potential for mature individuals to skip nesting during nondrought years, and whether females nest during years with dry springs and wet autumns. At one Texas site in 2020, there was no aquatic activity among individuals monitored via telemetry for the entire year. However, at another Texas site there was no aquatic activity during spring of 2020, but individuals returned to wetlands after sudden rains in late September (Bowers et al. 2021a).

The reproductive traits of *D. reticularia* have been studied in several regions; however, questions remain and should be investigated to better understand the evolution of the species. Is regional divergence in *D. reticularia* reproductive phenology related to local differences in adult activity patterns, variation in seasonal availability of suitable nesting conditions, or a combination of the two? Do *D. r. miaria* females nest during wet autumns following occasional years with dry spring and summer periods? Do *D. r. miaria* females abstain from nesting during extended drought periods in Texas? Answering these questions could help us understand pressures that cause regional divergence in reproductive traits and inform studies on population dynamics by identifying stochastic variation in annual conditions that influences reproductive potential.

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