EXPLORING DEMOGRAPHIC PATTERNS IN YELLOW MUD TURTLES:
TRADE-OFFS BETWEEN SURVIVAL AND REPRODUCTION

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A Thesis Submitted in Partial Fulfillment

Of the Requirements for the Degree

MASTER OF SCIENCE

Major Subject: Biology

West Texas A&M University

Canyon, Texas

May 2021

ABSTRACT

Understanding demography is integral to understanding the ecology of any population. Given global concerns over declining turtle populations, having a better understanding of demography could have significant implications for the management and conservation of at-risk populations. Although demographic research has been increasing amongst turtles, we still lack an understanding of variation in demographic parameters amongst most turtle species. Without such an understanding, it becomes difficult to evaluate if a management strategy developed for one population or species could or should be applied to other populations or species. I explored patterns in survival and reproduction for yellow mud turtles (*Kinosternon flavescens*) by examining 6 populations in Texas from 2007-2018. I used age-structured regression from 3,132 captures of 1,973 individuals across the sites to produce survival estimates for each population and used x-rays to determine average clutch size and estimated both egg volume and clutch volume for each site. Annual survival varied from 62.2% to 87.6% across the 6 populations. Across 5 sites, clutch size ranged from 3.4 to 5.0, egg volume ranged from 3716 mm^3 to 4388 mm^3, and clutch volume ranged from 13991 mm^3 to 17667 mm^3. Variation in survival and reproduction did not appear to be related to a clinal gradient across the populations I examined. I detected no significant relationships between survival and reproduction within my populations. For both variables, within-site

differences in habitat might be more significant drivers of demography than among-site differences, and the observed variation suggests this species has adopted a bet-hedging strategy rather than a more traditional K-selected strategy. Continued data collection in these and other populations should help clarify these relationships. With the anticipated effects of climate change in the southwestern United States, continuation of this study could provide an interesting opportunity to explore adaptive shifts in demography in response to increased climate variability.

ACKNOWLEDGEMENTS

There are many, many people that I wish to thank for their help conducting this project without whom I would never have made it this far. First, I would like to express my appreciation and admiration for my thesis advisor, Dr. Richard Kazmaier, for taking me on and allowing me to continue this research. His support, guidance, mentorship, and seemingly boundless patience have been essential to my success and I am deeply grateful for them. I'd also like to extend my gratitude to Mark Lange, whose efforts with his own master's thesis laid the groundwork for this research and without whom "The Turtle Project" may not have begun. I would also like to thank the large number of individuals that have contributed to this study through allowing me access to various properties and providing logistical support: Chip Ruthven III, James Baker, Matthew Poole, Caroline Ellison, Trudi Cooke, Travis Smith with the Wildlife Division of Texas Parks and Wildlife Department, as well as Kristen Warren with the U.S. Forest Service and the Ramp family of Canadian, Texas. I thank my other committee members, Dr. Peter Scott, Dr. David Sissom, and Dr. Bradley Johnson, for their support, encouragement, and advice throughout this experience. I would like to extend my sincerest appreciation for the numerous helping hands that assisted me with fieldwork and data collection – there are simply too many to name them all, but I would particularly like to single out Trevor McVay, Lindsay Stroup, Logan Ediger, and Erin Stiede for their assistance, support (both

logistical and personal), and companionship throughout the entire process: I couldn't

have done this without you.

Last, but certainly not least, I must thank my husband, Cliff McCormick-Zenor,

for being so incredibly patient, supportive, and loving during this process: without you I

would not even be here.

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INTRODUCTION

Turtles are a unique group of organisms that arose over 200 million years ago,

predating birds and mammals (Ernst and Lovich 2009). Since that time, they have spread

across the globe, inhabiting all but the coldest regions of the earth from the hottest deserts

to the open ocean. They are on every continent except Antarctica and found in nearly all

waters except those near the poles. As a result of their presence in such a wide array of

environments, they have evolved a surprising diversity of size and form from the 7 cm

padloper tortoise (*Homopus* spp.) to the massive 2 m leatherback sea turtle (*Dermochelys*

coriacea). Regardless of the species or where you find them, turtles are crucial figures in

the ecosystems they inhabit, with several species occupying the role of keystone species

which profoundly impact their associated systems at a fundamental level. They are

important prey items to many organisms, are predators of others, and many are also

grazers. They contribute significantly to the total biomass of their associated systems, and

can play a significant role in mineral cycling, soil processes, seed dispersal, and

germination enhancement (Ernst and Lovich 2009). The loss of a turtle species from its

native ecosystem can be a significant blow to the health of said system.

Across all vertebrate taxa, herpetofaunal species are currently of the highest conservation concern with numbers in each major group falling at an alarming rate worldwide (Gibbons et al. 2000, Stanford et al. 2020). Among these groups, turtles are arguably the most threatened, with an estimated 61% of their 356 species considered to be either threatened or extinct as of 2017 (Lovich et al. 2018). Despite this, turtles remain, with few exceptions, one of the least studied taxonomic groups, with most attention being paid to only a handful of species (Lovich and Ennen 2013). To combat this decline, Gibbons et al. (2000) argued that proactive population monitoring may provide vital information about at-risk populations or species and the reasons for their decline. Such monitoring programs could facilitate the development of management programs that have the conservation of these species as their goal.

Demographic vital rates, such as annual survival, reproductive output, juvenile recruitment, etc. are essential to the assessment of a population's status. Survival is especially important for the conservation of a species because an understanding of the demographic, ecological, environmental, and genetic factors that influence a population's survival can allow us to track a population's success and to make predictions on future trends for that population (Murray and Patterson 2006). While tracking individual survival from birth to death is useful, annual survival of populations is more commonly estimated given the difficulty of tracking individuals throughout their entire lives (Skalski et al. 2005). Most interest in estimating annual survival has focused on birds and mammals, particularly game species, but studies examining survival in reptile populations are becoming more common (Stanford and King 2004, Converse et al. 2005).

Annual survival can be estimated in a number of ways, including the use of known-fate survival estimation via radiotelemetry data analyses, open population capture-mark-recapture (CMR) models, and life table analyses (Silvy 2012, Skalski et al. 2005, Murray Patterson 2006). Of these, both the radiotelemetry and CMR methods can be particularly intensive with regard to time, labor, and money. For instance, CMR relies on maximizing the proportion of recaptured individuals in a given population, and the monetary costs associated with radiotelemetry may be prohibitive (Silvy 2012). Additionally, while radiotelemetry may provide a way to characterize individual variation in survival probability, its conclusions are difficult or impossible to extrapolate beyond the tracked cohort (Murray and Patterson 2006). Estimating annual survival using life table analysis may alleviate some of these issues. One form of life table analysis is catch-curve analysis, a method of estimating survival which has seemingly not been used extensively to study turtle populations, but which is well established in the fields of wildlife and fisheries management (Edser 1908, Chapman and Robson 1960).

Life table analyses typically require the collection of age-structured data (Seber 1992). The method for collecting age data to be used in these analyses can vary depending upon the logistics of one's study or the organism in question. For many species, a useful strategy for such collection involves the analysis of annuli. Annuli are growth rings which are deposited in bones, scales, teeth and other body parts after periods of halted growth as a result of periods of inactivity or resource scarcity, typically during winter. For turtles, annuli deposited in the scutes of the shell can be used to gain an estimate of age (Germano and Bury 1998, Zug 1991). The utility of this technique has

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met some opposition, primarily as a result of the lack of studies supporting a strong relationship between age and the number of annuli (Wilson et al. 2003). However, this technique has demonstrated its validity in turtle research. Annuli analysis was used to estimate survival of Texas tortoises (*Gopherus berlandieri*) in a population located within the Rio Grande Plains ecoregion of Texas (Hellgren et al. 2000). Iverson (1991) also attested to the efficacy of the technique for a Nebraska population of the yellow mud turtle (*Kinosternon flavescens*) despite cautioning that age could be underestimated when unusually harsh conditions encourage the development of multiple annuli that could be interpreted as a single annulus. However, when compared to one another, survival calculated via both annuli analysis and more widely accepted CMR methods have generated virtually identical estimates (Zhao et al. 2019).

An ideal model for studies using annuli analysis is the yellow mud turtle (*Kinosternon flavescens*), a relatively small (maximum straight-line carapace length 16.8 cm) kinosternid turtle native to large portions of the south-central United States including much of the Great Plains (Ernst and Lovich 2009). It is characterized by a carapace which lacks a keel and is generally yellow to brown in coloration. Eleven pairs of marginal scutes are present, with the 9th and 10th scutes toward the posterior portion of the carapace extending past the adjacent marginals (Ernst and Lovich 2009). This species typically inhabits semi-permanent pools with soft substrates, with an apparent preference for burying in loess type soils (Webster 1986). They exhibit one of the shortest active feeding periods of any North American turtle (Christiansen et al. 1985), and much of the year is spent in terrestrial hibernation or estivation, an adaptation to evolving in a

seasonally fluctuating environment (Long 1985). This extensive dormancy is facilitated by the high lipid index of the species (Long 1985), but individuals have been documented consuming earthworms underground (Moll 1979). This species is easily sampled using aquatic net gear, often inhabits pools at high densities, and deposits readily recognizable annuli on its plastron, making it an excellent model for the evaluation of the age-structured regression method for calculating survival.

In 2006, research began at West Texas A&M University with the aim of monitoring yellow mud turtle populations in Texas using annuli analysis and age-structured regression to estimate survival for multiple populations of the species (Lange 2011). Since that time, annual survival estimates for 9 sites across the state of Texas have appeared to vary greatly (McVay 2017). Given that turtles are primarily ectothermic, one could assume that such variation might come as the result of climate, with populations in warmer areas exhibiting higher survival because of the potential for an extended season of activity. However, the variation in survival of these populations does not appear to be the result of a clinal climate effect (McVay 2017). Such conclusions hint that the yellow mud turtle does not exhibit a fixed annual survival rate across its range, which is supported by at least one study (Iverson 1991a). However, an overall lack of peer-reviewed literature examining regional variation in demographic strategies in turtles, particularly with regard to survival and reproduction, also led Iverson (1991a) to suggest that research continue on more populations of this species to help quantify such regional variation. This led me to question which factors are potentially responsible for driving the observed variation in survival of this species.

One such factor that has the potential to impact survival is reproduction. Reproduction can be a risky process requiring significant external and internal resources and which can potentially lead to increased mortality either directly or indirectly. Optimal egg theory suggests that selection should favor the production of more eggs of an optimal size than fewer eggs of a larger size, as investing in an additional offspring grants a greater benefit to maternal fitness than investing in already-existing offspring (Iverson 1992). However, life history theory suggests that a trade-off exists between the number of offspring and their size and that selection should therefore favor either large clutches of smaller offspring or smaller clutches of larger offspring (Stearns 1976, Congdon and Gibbons 1990). Given that demographic parameters such as annual survival and reproduction may be interconnected, it seems logical that a trade-off may also exist between reproductive effort and survival wherein an increase in reproductive effort comes at the cost of survival, or vice-versa. If such a trade-off existed, then an organism must also find a way to maximize its evolutionary fitness by minimizing potential trade-offs between these two demographic parameters. Studies on reproduction in turtles have concentrated primarily on individual reproductive effort, but comparatively little has been done to examine regional differences in reproductive effort or how such differences affect other population-level phenomena such as survival. In order to help fill in some of the gaps in our understanding of regional variation in demography for this species and its relatives, my objectives in this study were to examine potential trade-offs between survival and reproduction and to evaluate reproductive effort as a factor influencing the observed variation in survival for yellow mud turtles in Texas.

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STUDY AREA

Geographic Range

The yellow mud turtle is found throughout much of the south-central portion of the United States and is found primarily in the semi-arid portions of the region. The northern limit of its range lies in a disjunct population in western Nebraska (Iverson 1979). It continues in the southern portion of that state and stretches southward to the Mexican state of Veracruz. From east to west its range runs from a few threatened and disjunct populations in Missouri, Illinois, and Iowa westward to Arizona and Sonora, Mexico. Although the range of habitat conditions found throughout this large area is highly variable, this species is thought to prefer those regions with sandy soils, arid climate conditions, and ephemeral water (Iverson 1979;1991, Ernst and Lovich 2009). Its range in Texas includes most of the state, particularly the western portions, and excludes only the far eastern portions of the state (Figure 1, Ernst and Lovich 2009).

Ecoregions of Texas

The state of Texas spans about 68,391,873 ha (Gould 1960). Within this massive area, Gould (1960) describes 10 major vegetative regions or ecoregions, but some authorities put the number higher at 14 (Landers 1987). The geographic range of the yellow mud turtle extends throughout the majority of Texas and encompasses at least 5 of the ecoregions Gould describes, ranging from the High Plains in the north to the Rio Grande Plains in the south, and from the Trans-Pecos in the west to the eastern edge of the Edwards Plateau ecoregion. Given the large size of this geographic area, these ecoregions differ dramatically with regard to climate, soils, aquatic habitat, vegetation,

and other biotic or abiotic factors. I used 9 sites for sampling yellow mud turtles in 3 of Texas' ecoregions. Habitat variation between sites was considerable, but within-site variation in available aquatic habitat, vegetation, and soil type was also pronounced.

High Plains – The High Plains ecoregion lies in the northern portion of the state and makes up much of the region commonly referred to as the Panhandle. It is a high (915 to 1370-m elevation) plateau that abuts the Rolling Plains ecoregion to the east, with the Caprock Escarpment serving as the borderline between the two (Correll and Johnston 1979). Additionally, it is split by the Canadian River which runs west to east through the Panhandle, dissecting the High Plains with a band of Rolling Plains that follows the river. Covering an area of about 80,937 km^2, much of the region has been converted to rangeland for cattle and other agricultural uses, with deep aquifers providing supplemental water for crop irrigation and cattle consumption. The region is relatively arid, with average precipitation ranging from 38 – 53 cm. Soils are underlain by a bed of limestone or caliche and tend to be clayey and shallow in the north but deeper and sandier in the south. The dominant terrestrial vegetation is short and medium grasses, chiefly blue gramma (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*) on clay soils. Little bluestem (*Andropogon scoparius*), western wheatgrass (*Agropyron smithii*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) are the dominant grasses in sandier soils (Correll and Johnston 1979). Woody vegetation is uncommon in the region, but sites with sandy soils often contain Shinnery oak (*Quercus havardii*) and sand sagebrush (*Artemisia filifolia*). With fire suppression and poor grazing management, encroachment by species such as eastern red cedar (*Juniperus virginiana*) and honey

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mesquite (*Prosopis glandulosa*) is now relatively common throughout the region as well (Correll and Johnston 1979).

The relatively flat High Plains landscape is pockmarked with playa lakes: shallow, ephemeral water bodies that regularly dry up and refill with large rain events (Bolen et al. 1989). They average 6.3 ha in size, and although they occur in many arid regions of the world, they are particularly numerous and dense in the High Plains (Bolen et al.1989). Playas are also a critical component of the High Plains system, with many species relying on them for water, habitat, nesting or breeding, or foraging, and the regular cycling of wet and dry periods immensely increases the heterogeneity of plant communities (Polley and Wallace 1986). Playa communities are thus diverse, but commonly include species such as cattail (*Typha angustifolia*), bulrush (*Scirpus* spp.), western water clover (*Marsilea vestita*), pondweed (*Potamogeton* spp.), smartweeds (*Polygonum* spp.) and arrowhead (*Sagittaria* spp.; Rowell Jr. 1971). In addition to being excellent habitat for the yellow mud turtle, they are critical habitat (particularly for reproduction) for other Plains herpetofauna, including the barred tiger salamander (*Ambystoma mavortium*), plains leopard frogs (*Rana blairi),* bufonid toads (*Bufo* spp.), spadefoot toads (*Scaphiopus* spp. and *Spea* spp.), and the Plains narrowmouth toad (*Gastrophryne olivacea*; Bolen et al. 1989).

In addition to playa lakes, agricultural activity throughout the region has also provided additional aquatic turtle habitat in the form of windmill overflow ponds. These are artificial water bodies that are fed through the pumping of groundwater via wind or solar mills, a process which generates excess water which flows into a nearby shallow

depression. Conditions within these ponds varied considerably both across and within my study sites.

Rolling Plains – The Rolling Plains ecoregion is characterized by a landscape of hills and canyonlands (Correll and Johnston 1979). Sitting adjacent to the High Plains ecoregion, and together forming the Texas Panhandle, it spans about 9,712,000 ha with an elevation ranging from 244 to 914 m. It is somewhat less arid than the High Plains, with average annual precipitation ranging from 56 to 76 cm and many small streams running throughout; however, summer dry periods with high temperatures and evaporation rates are typical (Correll and Johnston 1979).

The soils of the region trend toward sandy types with some tight red clays and shales, and in riparian areas coarser sands dominate (Gould 1960). Although there is much similarity in the plant community between the two ecoregions of the Texas Panhandle, some noticeable differences arise. Species that favor sandier soils, such as sand dropseed (*Sporobolus cryptandrus*), sandbur (*Cenchrus* spp.), sand sage (*Artemisia filifolia*), and shinnery oak (*Quercus havardii*) are common in the Rolling Plains ecoregion. The dominant plant species once trended toward prairie grasses and forbs, but heavy grazing and fire suppression have allowed native woody species such as shinnery oak, sand sage, eastern red cedar, and honey mesquite to became invasive throughout the region (Correll and Johnston 1979). In riparian areas, exotic saltcedar (*Tamarix* spp.) are a considerable threat to native waterways.

Given that large portions of the Rolling Plains region are used as rangeland, much of the available habitat for yellow mud turtles exists in the form of windmill overflow

ponds. As in the High Plains, these artificial water bodies are semi-permanent and vary considerably in their plant and soil characteristics. However, acceptable habitat is also found in the creeks and rivers of the region, particularly in those places where waterflow is decreased, resulting in muddier substrates and higher quantities of aquatic vegetation.

Trans-Pecos – This large ecoregion encompasses all of the land that lies west of the Pecos River, with the exception of the Stockton area which is often grouped within the Edwards Plateau region (Landers 1987). Overall, the region exhibits considerable diversity in its characteristics and is difficult to summarize as a single geological or vegetational unit. Variation in elevation is considerable (762 to 2,590 m) as the landscape ranges from low desert valleys to mountain slopes that support conifer forests. While precipitation is higher in the mountainous areas, overall the region is quite arid with average annual rainfall typically less than 30 cm (Correll and Johnston 1979).

The soils of the region are similarly varied, formed from erosion of the surrounding mountains, and this drives the considerable variation in plant communities exhibited throughout the region (Landers 1987). Correll and Johnston (1979) list the most notable vegetation communities as being creosote-tarbush desert shrub, grama grassland, yucca and juniper savannahs, piñon pine and oak forests, and ponderosa pine forest. Of these, the creosote-tarbush desert shrub and yucca-juniper savannahs most closely characterize the areas used in my study. Rocky, calcareous soils with little rainfall support communities characterized by the presence of species such as lechuguilla (*Agave lechuguilla*), creosote (*Larrea tridentata*), ocotillo (*Fouqueria splendens*), cenizo

(*Leucophyllum frutescens*), numerous species of *Yucca* and cacti, and multiple species of arid-adapted grasses and forbs.

Study Sites

I used 6 specific study sites for sampling yellow mud turtles in Texas, spanning a north-south gradient of 940 km. These 6 sites represented 3 ecoregions: the High Plains, the Rolling Plains, and the Trans-Pecos (Figure I.1). The Edwards Plateau and Rio Grande Plains regions were not represented in this study.

Black Gap Wildlife Management Area (WMA) – At about 41,600 ha, Black Gap WMA is the largest WMA in Texas. It is managed as a research and demonstration site for the Trans-Pecos region by the Wildlife Division of Texas Parks and Wildlife Department. The area lies 82 km southeast of Marathon, Texas, and abuts both Big Bend National Park and the Rio Grande River. Overall, it can be characterized as roughlands with considerable topographic relief and a wide range of habitats including rocky plateaus and uplands, limestone drainages, creosote flats, and even riparian areas. It is extremely arid with average annual rainfall being approximately 41 cm. The plant community is diverse and can change considerably within different portions of the site. Notable plant species include ocotillo, lechuguilla, creosote, candelilla (*Euphorbia antisyphlitica*), sotol (*Dasylirion leiophyllum),* several species of *Yucca*, and multiple genera of cacti. In the limestone drainages that cross the landscape, woody species such as little walnut (*Juglans microcarpa*) and Texas persimmon (*Diospyros texana*) become more common (personal observation). Bufflegrass (*Cenchrus ciliaris*), an invasive exotic, is also common in certain areas (personal observation).

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Available aquatic habitat at Black Gap WMA is restricted almost entirely to a small series of artificially constructed ponds or "tanks" that were constructed to control runoff water (Axtell 1959). Unlike the ponds at many of my sites, these ponds, although manmade, are filled primarily through rainwater during monsoonal events. They are thus quite ephemeral and do not always hold water year-round (personal observation). The substrate at the bottom of the bottom is quite soft, but the surrounding terrain is mostly limestone rock and gravel. The area lacks the sandy soils typically favored by this species leading me to suspect that the turtles aestivate in the mud of the pools when they dry up. Aquatic vegetation within the pond is quite sparse and is comprised primarily of stoneworts (*Chara* sp.), pondweeds (*Potamogeton* spp.), and a few species of sedges (*Cyperus* spp.). This property is not grazed, and as such these ponds lack the cattle disturbance and fecal load typical at my other properties. The tanks usually lack fish (although I did capture several small decorative koi (*Cyprinus carpio*) on one trip which were not captured the next year), and insect life appears to be diverse (personal observation). Tadpoles and adults of Couch's spadefoot (*Scaphiopus couchii*), red-spotted toad (*Bufo punctatus*), green toad (*Bufo debilis*), Rio Grande leopard frog (*Rana sphenocephala*), and Plains narrowmouth (*Gastrophryne olivacea*) are commonly encountered in and around the tanks (Axtell 1959), and blackneck garter snakes (*Thamnophis cyrtopsis*) and western diamondback rattlesnakes (*Crotalus atrox*) were often found at their banks (personal observation).

Gene Howe Wildlife Management Area – Gene Howe WMA is a 2,382 ha property located just 2 km north of the town of Canadian in Hemphill County, Texas

(Rowell 1957). It is maintained as a research and demonstration area by the Wildlife Division of Texas Parks and Wildlife, providing a site for wildlife research and a source of recreation for the local community. It sits along the Canadian River in the Rolling Plains ecoregion of Texas and can be roughly divided up into 2 habitat types. In the northern upland portion of the WMA, the habitat can be characterized as rolling sand sage prairie with deep, sandy soils. Notable plant species include sand sagebrush, sand plum (*Prunus angustifolia*), fragrant sumac (*Rhus aromatica*), little bluestem, sand dropseed, mat sandbur (*Cenchrus longispinus*), blue grama, hairy grama (*Bouteloua hirsuta*), and side-oats grama (*Bouteloua curtipendula*). In the lowland portion of the WMA, notable plants also include western cottonwood (*Populus deltoides*), Russian olive (*Elaeagnus angustifolia*), western soapberry (*Sapindus drummondii*), Siberian elm (*Ulmus pumila*), big bluestem (*Andropogon gerardi*), switchgrass, Indiangrass, and alkali sacaton (*Sporobolus airoides*; Rowell 1957).

Available aquatic habitat at Gene Howe WMA is somewhat diverse. In the upland areas of the WMA, most aquatic habitat is in the form of windmill overflow ponds maintained for use by cattle and wildlife (personal observation). Given their intended use and the often prolonged periods which they hold water, the substrate of these ponds tends to be thick and soupy, often with a high concentration of cow manure. While it is not uncommon for them to lack plants, some do support marginal and submergent aquatics such as arrowhead, bulrush, cattail, stoneworts, pondweed, and duckweed (*Lemna* sp.). The uplands also have shallow ephemeral pools and ditches that are temporarily available habitat in years that receive sufficient rainfall. In the lowland portions of the WMA, most

aquatic habitat for yellow mud turtles is in the form of sloughs of the Canadian River and natural catchments. Most of these bodies of water are larger, more ephemeral, appear to be less heavily utilized by cattle, and support more diverse plant and animal communities. While yellow mud turtles can be found at high densities in the upland windmill overflow ponds, their density in the lowland sloughs is comparatively very low (personal observation). In addition to yellow mud turtles, common snapping turtles (*Chelydra serpentina*), spiny softshell turtles (*Apalone spinifera*), and sliders (*Trachemys scripta*) were commonly captured on this property, and ornate box turtles (*Terrepene ornata*) were commonly found on the roads.

Matador Wildlife Management Area – Matador WMA is comprised of 11,410 ha located in Cottle County, Texas, about 10 km north of Paducah, Texas. Managed by the Wildlife Division of Texas Parks and Wildlife Department, it was purchased for wildlife research and management in addition to public use. Located in the Rolling Plains ecoregion of Texas, the property is comprised of rolling to rocky grassland savannahs, riparian areas, and shinnery oak rangeland. In the canyon breaks of the property, redberry juniper (*Juniperus pinchotii*) and honey mesquite are the dominant woody plants, and significant effort has been exerted on the property to prevent or reverse their encroachment onto adjacent grasslands. In said grasslands, portions still remain heavily encroached upon by such woody vegetation, but effective management techniques have been utilized to revert much of them back to open tall- and mixed-grass savannahs dominated by species such as sand dropseed, sideoats gramma, Arizona cottontop (*Digitaria californica*), purple three-awn (*Aristida purpurea*), and little bluestem. Forb

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communities on the property can be quite variable, but species such as western ragweed (*Ambrosia psilostachya*), common sunflower (*Helianthus annuus*), buffalo gourd (*Cucurbita foetidissima*), and Texas bullnettle (*Cnidoscolus texanus*) are common (personal observation).

Aquatic habitat at Matador WMA is quite variable, with available turtle habitat consisting of a mixture of small ponds and portions of the Middle Pease River which runs through the property. The ponds, most of which are windmill overflows, are considerably variable with some maintaining water year-round while others are noticeably ephemeral. As the property is grazed by cattle, several of the windmill overflow ponds receive frequent visitation and are thus heavily disturbed areas with a considerable amount of fecal matter present. Vegetation in the more heavily utilized ponds is minimal. Other ponds on the property are less frequently utilized by cattle and thus support more diverse aquatic communities. Aquatic vegetation is comprised mostly of bulrush, cattail, stoneworts, pondweed, and duckweed. The largest two ponds I sampled also support fish communities comprised mostly of green sunfish (*Lepomis cyanellus*) and mosquitofish (*Gambusia affinis*). Along the river, invasive salt cedar and the occasional patch of cottonwoods (*Populus deltoides*) can be found. The river seldom flows except during periods of increased rainfall, and for much of the year consists of intermittent pools of varying size. Aquatic vegetation can be variable but consists mostly of bulrush and cattail. In addition to yellow mud turtles, sliders, common snapping turtles and spiny softshells are commonly captured in the river, along with sunfish (*Lepomis* spp.) and gizzard shad (*Dorosoma cepedianum*).

Ramp Ranch – Ramp Ranch is a 3,800-ha property that is privately owned and managed by the Ramp family in Hemphill County, Texas. As it is only 14 km south of the Gene Howe WMA, this property is very similar to the upland portions of the WMA with rolling sandsage prairie dominating the property. Soils are deep and sandy, and the plant community overlaps significantly with the Gene Howe WMA. This property is also highly fragmented, with many oil pads spotting the landscape and multiple roads that experience frequent traffic. Available aquatic habitat for mud turtles on this site is mostly in the form of windmill overflow ponds maintained for cattle. These ponds are quite variable in size and character. The largest, from which most of my turtles were captured, was heavily utilized by cattle and had no apparent vegetation. Despite this, I observed yellow mud turtles, sliders, and barred tiger salamander larvae living in this pond in surprising densities. By contrast, most of the other ponds were much smaller, seemingly less utilized, and supported common aquatic plants including cattails, bulrush, arrowhead, and pondweed. The Washita River flows through a section of this property and was trapped a few times in 2017, however no mud turtles were captured in the river proper.

Rita Blanca National Grasslands – This area is a 37,631-ha property maintained by the United States Forest Service for public uses which include hunting, livestock production, and recreation such as camping and fishing (Hazlett et al. 2009). It is unlike the other properties included in this study as it is not a continuous piece of protected land but is instead a series of small blocks of land interspersed with private properties. Located in Dallam County, Texas, it lies within the High Plains ecoregion of Texas, displaying many of the features of the region. It is classified as semi-arid shortgrass

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steppe with shallow clay to sandy soils. The topography of the area is extremely flat with few hills or depressions in the landscape. Vegetation on the property consists almost entirely of shortgrasses and prairie forbs, with very little woody vegetation. Common terrestrial species include sideoats grama, buffalo grass, snakeweed (*Gutierrezia sarothrae*), soapweed yucca (*Yucca glauca*), and the occasional tree cholla (*Opuntia imbricata*). In disturbed areas, notably along roadways, ragweeds (*Ambrosia* sp.), sweet clover (*Melilotus offinalis*), goat's head (*Tribulus terrestris*), and common sunflower (*Helianthus annuus*) were common. Although woody vegetation is not naturally common to the area, some areas support the growth of trees such as Siberian elm (*Ulmus pumila*) and honey locust (*Gleditsia triacanthos*), although these are largely planted (Hazlett et al. 2009). Other commonly observed herpetofaunal species on the property included ornate box turtles, western barred tiger salamanders, Great Plains toads (*Bufo cognatus*), Woodhouse's toads (*B. woodhousii*), and prairie rattlesnakes (*Crotalus viridis*).

Aquatic habitat on this property is restricted to windmill overflow ponds maintained for use by cattle, although some small depressions exist that likely fill up with water following significant rainfall (personal observation). As is the case on many of my properties, these ponds are typically shallow, often lack vegetation, and are extremely high in nutrient load from the steady addition of cow manure. The bottoms of these ponds are comprised of a deep, soft clay mixed with considerable amounts of decayed plant matter. The water conditions are variable as well, with the more heavily disturbed ponds having very little to no water clarity and less disturbed ponds having greater water clarity and greater variety of vegetation present (personal observation). Vegetation both in and

around the ponds themselves can be considerably variable. Wetland plants common to the area include the common High Plains riparian genera: cattail, bulrushes, spikerushes, and sedges are common marginals (Hazlett et al. 2009). Most of the sampled ponds contained little or no submergent vegetation, but in those that did pondweeds, stoneworts, and duckweed were the only commonly observed inhabitants (personal observation).

Yoakum Dunes Wildlife Management Area – This area is a 13,800-ha property maintained by the Wildlife Division of TPWD primarily for maintaining and improving habitat for the state-threatened lesser prairie chicken (*Tympanuchus pallidicinctus*). It lies about 15 km west-southeast of Sundown, Texas, and is situated within the High Plains ecoregion, although it has some characteristics more similar to the Rolling Plains ecoregion. The soils on this area are typically quite deep and sandy, with much of the property being covered in the sand dunes that lend the property its name. On the dunes, shinnery oak is dominant, but throughout the property honey mesquite, sand sagebrush are also common. Aquatic habitat at this property is restricted entirely to windmill overflow ponds. The overflow ponds at Yoakum Dunes are maintained mostly year-round for wildlife use, and several of them are heavily vegetated with bulrush, stonewort, and hair algae. Aside from yellow mud turtles, other herpetofaunal species encountered at this property included ornate box turtles, prairie rattlesnakes, bufonid toads, and long-nosed snakes (*Rhinocheilus lecontei*).

METHODS

Sampling Gear and Protocol

To answer the questions posed in this study, there was a need to maximize capture success at each site while obtaining a representative sample of each site's age structure. To do this, turtles were sampled using a variety of trap types placed in multiple aquatic habitats within each property. Such aquatic habitats included ephemeral ditches, playa lakes, both man-made and natural ephemeral ponds, and windmill overflow ponds. At two properties, Matador and Gene Howe WMAs, stretches of the Middle Pease River and sloughs of the Canadian River, respectively, were also trapped. Given the history of land use at most of my study sites, windmill overflow ponds maintained for the use of cattle were the most commonly available habitat for this species. Sampling occurred through the months of May to July for most sites, with the exception of Black Gap WMA, where sampling was typically conducted during the month of September. Sampling at some sites began in 2007 and continued through 2019 (Table 1).

The types of traps used can be classified as either active or passive, with the majority of the turtles captured for this study being captured with passive trap gear. Passive trapping was conducted by placing traps in suitable habitat during the afternoon or evening, leaving them overnight, and checking them the next day. Traps were staked in place with rebar to maintain their position and prevent movement or interference from factors such as predators. To reduce the chance of turtle mortality from drowning, each trap was placed with a significant air space. Traps were baited primarily with canned cat food. For the summer of 2016, however, canned sardines, raw chicken, and raw chicken

coated with buffalo sauce were also utilized, but choice of bait did not appear to affect capture success (McCormick-Zenor, unpublished data). Six basic trap designs were used, some of which come in differing sizes. All were essentially derivations of a traditional minnow or funnel trap.

Eel, Crawfish, Flounder and Turtle Traps – This trap type (Promar, Gardena, CA, USA) was designed for capturing primarily benthic organisms such as eel, crawfish, flounder, and turtles. It was rectangular in shape, comprised of a set of square frames that support the netting and keep it taught. The frames connect at a central point and are collapsible, providing simple storage. These traps are excellent for "bottom-walking" species such as the yellow mud turtle, as the frame lies flat on the substrate and the flexible slit funnels allow multiple animals to enter with little resistance. The traps have two horizontal slit-funnels, one on each end that run the width of the trap, that also allow for some flexibility of placement. These were placed either with both funnels running parallel to some structure or vegetation, or with one funnel pointed out toward open water. Because of their low profile, these were utilized mostly in very shallow water, but were useful for capturing individuals from a wide range of age classes.

This trap came in two sizes, with the larger being more commonly used because of its capacity to hold larger numbers of animals. The large flounder trap measured 80 cm by 60 cm by 28 cm, with a square mesh size of 10 mm. The small flounder trap measured 59 cm by 43 cm by 22 cm, with a square mesh size of 12 mm. Both sizes were purchased from Memphis Net and Twine (Memphis, Tennessee, USA).

Collapsible Seabass/Porgy/Crab Traps – These were designed for fish such as sea bass as well as crabs and crayfish (Promar, Gardena, CA, USA) and were similar to the to the flounder traps. They are comprised of a collapsible metal frame that when expanded supports a taught mesh, but the frame is D-shaped and the funnels are rounded and inflexible. Their greater height makes them suitable for trapping deeper water, but their greater mesh size makes them less suitable for capturing younger age classes and the restrictive funnels potentially prevent extremely large individuals from entering. Another trap design with two funnels, these were also typically placed either along some edge in the habitat formed by vegetation or structure, or with one of the funnels placed toward open water.

The larger version of this trap measured roughly 96 cm by 64 cm by 61 cm when erected, with a square mesh size of 25 mm. The smaller trap measured about 79 cm by 48 cm by 35 cm and had a square mesh of 10 mm. The mouths of the larger trap measured about 15 cm in diameter, and those of the smaller trap measured about 12 cm. As with flounder traps, the larger of the two sizes available was more commonly used because of its better capture success despite its potential bias toward larger individuals.

Hoop Nets – These are elongated traps comprised of a series of either metal or wooden hoops connected by mesh. The hoops support at least one funnel which leads to an area at one of the trap where captured individuals are held, termed the "cod end". The two sizes used were extremely similar in overall design but have some noticeable differences.

Large hoop nets (Sterling Net and Twine, Montclair, New Jersey, USA) were made from 3 hoops measuring 88 cm in diameter. The diameter of the funnel leading to the cod end measured 31 cm and the overall length of the trap is 245 cm. The square mesh size for this trap is 25 mm. These traps are widely used for turtle sampling across many taxa and are considered to be the default "turtle trap". However, because of their large size and limited utility in shallow water coupled with their relatively low capture success, they were seldom used for this study.

Catfish hoop nets (Memphis Net and Twine, Memphis, Tennessee, USA) were comprised of a series of 4 fiberglass hoops which measured 47 cm in diameter. This trap design featured 2 funnels leading to the cod end, each with a mouth opening of 27 cm. The overall length of the trap was 155 cm and the mesh size was 25 mm. A piece of rebar was required at each end to expand the trap and keep it anchored. They were designed for catfish, but during this study were found to be particularly useful for capturing mud turtles. Their collapsible nature and light weight made them easy to transport, and they can be utilized in a variety of habitat conditions. They were useful for both deep and relatively shallow water, as well as bare-bottomed or heavily vegetated water bodies. Most often, they were set with the opening directed toward deeper water but can also be placed along some sort of edge. Most importantly, they were useful for capturing a wide range of age classes.

"D-hoop" Nets – The so-called "D-hoop" traps were comprised of 3 half-circle frames arranged in a configuration similar to the hoop nets described above. A piece of rebar was also required at each end to expand and support the trap. Each frame measured

78 cm in diameter, and whole trap measured about 130 cm in length by 52 cm in height. The D-shaped frames supported a 35 mm square mesh with a relatively large slit-shaped funnel in the middle that measured 54 cm across. The wide, loose slit funnel and flat frame likely contributed to this trap's capture success, but its large mesh seemed to bias it toward larger individuals. These traps were handmade and did not come from a commercial source.

As with hoop nets, these had wide utility as they can be set at varying depths and conditions. They were typically placed with the opening faced toward open water but could also be placed along a vegetative or structural edge within the pond.

Crayfish Traps – Crayfish traps or "extra-mini hoops" (Promar, Gardena, CA, USA) were, as the name implies, primarily produced for capturing crayfish. These were small cylindrical traps with a small funnel at each end supported by a collapsible, coiled, spring-shaped frame. They measured roughly 59 cm in length with a diameter of 30 cm. The square mesh size was 10 mm. Given their collapsible nature and small size, they were highly portable: over a dozen could be easily transported in a standard 5-gallon bucket. Their small mesh size made them ideal for capturing juvenile turtles all the way down to hatchling size, but their small size also restricted their use to very shallow water. Most often, these were placed along some vegetative or structural edge within a pond, although they were occasionally placed with a single funnel faced toward open water.

Modified Fyke Nets – Modified fyke nets (Christiansen's Nets, Duluth, Minnesota, USA) were the largest trap type used for this study. As with hoop nets, the 2 sizes used are essentially identical in design with a few differences. Both were comprised

of a series of rectangular and circular frames connected by a square mesh. A series of funnels within led backward toward the cod end of the trap where captured individuals are held. At the front of each trap was a mesh lead that acted as a drift fence, directing animals toward the mouth of the trap. The trap was erected and held taught with the use of rebar, and the lead was equipped with floats at its top edge and lead weights at its bottom edge to keep the lead erect.

The large modified fyke nets had a lead which measured 14.5 m by 88 cm. The body of the trap measured 4.5 m in length. At the front of the trap were 2 rectangular frames that measure 88 cm in height by 120 cm in width. Each rectangular frame had a vertical slit-shaped funnel the full height of the frame. Towards the back of the trap were 5 circular hoops that supported 3 regular-shaped funnels. The square mesh size for this trap was 10 mm. Typically, this trap was set with the lead reaching out into open water, but the trap could also sometimes be angled to follow an edge or to block off movement through a channel. Despite its usefulness for capturing large number of individuals across many age classes, its large size restricted its use to larger, deeper bodies of water.

Small modified fyke nets had a lead which measured 7.4 m by 67 cm. The body of the trap measured 3.3 m and the mesh size was also 10 mm. The rectangular frames measured 67 cm tall by 95 cm wide. The trap design was virtually identical to the larger fyke net. The small fyke, however, had 4 rings toward the back that supported 2 funnels. They were set the same way as large fyke nets and had many of the same pros and cons, but the smaller, squatter stature of this trap made them somewhat more useful for bodies of water not suitable for placing large fykes.

Active Sampling Methods – Whenever possible, a number of active sampling methods were used to help maximize captures at each site. Chief among these was the use of a bag seine (Sterling Net and Twine, Montclair, New Jersey, USA). This was comprised of a 9.1 m portion of netting with a square mesh size of 2.5 mm supported on either end by a pole or braille. The bottom of the net had lead weights and the top had floats, both of which kept the net taught in deeper water. As the seine was pulled through the water, the bag positioned at the center of the net expands and animals are directed into it. Seining was conducted at various times of the day and was primarily used as a method of quickly sampling a small water body with little structure or vegetation. If seining proved successful, it was often followed by setting appropriate passive gear.

Capturing individuals by hand was also utilized. This typically occurred during the process of either setting or removing traps, and very occasionally individuals were captured on land. In shallower ponds, particularly those with a high density of turtles, feeling for turtles in the mud or water with one's feet or hands ("noodling") often bore success. In clearer water, turtles could often by spotted in the shallows, and these would be captured by hand if possible. As these turtles appear to be quite active at night, wading through clear water at night and using a spotlight to detect turtles was also utilized. Remains from predation events were also somewhat commonly found, and these were also utilized as much as possible.

Marking and Measuring

After capture, turtles were placed into tubs or buckets and transported to an on-site location for marking and measuring. As this species has exhibited quite high fidelity

to particular water bodies, with individuals captured in the same water body from year-to-year, each tub or bucket was labeled with fluorescent flagging tape marked with the location where those individuals were captured. This was done to ensure they could be returned to the same water in which they were trapped.

Processing began with taking a series of standardized morphometric measurements. This was done not only to track growth of individuals across time, but also exhibited utility in troubleshooting later in the process should individuals somehow become confused with one another. Mass in grams was measured using an electronic balance. Straight-line carapace length, straight-line plastron length, total width (measured at the front hinge of the plastron, located between the pectoral and abdominal scutes), and total height (also measured at the front hinge of the plastron) were measured using a set of dial calipers. Individuals were also identified as either male or female based on a concordance of sex characteristics. This species is quite sexually dimorphic, with a number of useful characters aiding in the identification of sex, including tail shape and length, location of the cloaca, and shape and concavity of the plastron (Ernst and Lovich 2009). Male yellow mud turtles reach larger maximum sizes (carapace length, 16.8 cm) and have longer, more robust tails tipped with a pronounced spine. The cloaca in males is situated fairly far along the length of the tail, its position lying well past the posterior edge of the carapace. On the inner surface of the hind legs in males lie two patches of rough scales. The plastron is concave. Females, by contrast, are smaller (carapace length, maximum 12.8 cm), with shorter tails, a cloaca that lies at or within the posterior edge of the carapace, a flat plastron, and no rough patches of scales on the inner thighs (Ernst and

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Lovich 2009). It should be noted that much literature on this species states that females

lack tail spines. Most females captured during the course of my study, however, exhibited

tail spines, albeit less robust than those found in males. Individuals that were too small to

be sexed were recorded as juveniles.

To ensure that individuals were used only once in our analyses and to track

recaptures over time, every individual was given a unique mark. For all sites, individual

turtles were administered a code of notches cut into the marginal scutes of the carapace

using a Dremel® tool (Robert Bosch Tool Corporation, Mount Prospect, Illinois, USA)

fitted with a breakable cutoff wheel. For populations which were new to the study or

which were unlikely to be resampled in the future, the notch code given to each turtle was

unique. These codes comprised of 1 or more notches applied to the marginal scutes, each

of which is assigned an alphanumeric code (Cagle 1939). Additionally, for some

populations a passive integrated transponder (PIT) tag was also inserted into each

individual, assigning a unique alphanumeric code to each turtle. After cleaning the

injection site, the PIT tag is inserted into the abdominal cavity via the rear leg opening of

the shell using a specialized syringe and the wound is sealed with super glue. Because of

their relatively high cost, PIT tags were only utilized for populations that are likely to be

resampled in the foreseeable future. Individuals receiving a PIT tag were given a

secondary mark either as a unique notch code (typically recaptured individuals from

previous iterations of this study) or with a cohort notch code of *2R* (second marginal

scute on the right anterior margin of the carapace).

Lines of Arrested Growth

As the first step in estimating survival for each population, annuli on the plastral scutes of each turtle were examined to estimate the age of each individual. To do this, I used impressions taken of the plastron of each individual turtle. After marking, the plastron of each turtle was examined for the presence of algae or detritus and was cleaned with a sponge if necessary. Dental alginate, a substance used in dentistry for creating molds of human teeth, was mixed and applied to the plastron (Germano and Bury 1998). After it set, it was wrapped in a moistened paper towel and placed into a plastic bag to protect it from damage or warping until the next step in the process. To ensure that the impression could be tied to the individual from which it was taken, the bag was labeled with that turtle's identifying information.

Positive impressions were crafted from the alginate negatives by forming a clay mold around each impression and filling it with dental stone (GC America, Alsip, Illinois, USA), an extremely hard and durable plaster-like substance also used in dentistry. Once dry, these positives were then labeled and boxed until such time as they could be aged, usually shortly after the trapping season had ended. To reduce bias as much as possible, aging was done in tandem with my advisor with the assistance of a magnifying lamp. Each of us developed our own independent estimate for each turtle and then compared them. When we disagreed, the impression was examined further until an agreement was reached. Because of differential wear, each scute on the plastron was examined and the number of annuli was counted for as many scutes as possible. The mode of all annuli counts was taken and used to estimate the age of each turtle.

Analyses

Age-structured regression was used to estimate annual survival rate for each site (Hellgren et al. 2000). To do this, age data derived from aged impressions was compiled into a histogram by plotting age class (expressed as the number of annuli) against frequency. For individuals that were captured more than once, the age used was selected randomly from the list of ages estimated for that turtle. As younger age classes were underrepresented in our data and there was often a maximum age for each site beyond which aging individuals was difficult or impossible, those age classes were excluded from my analysis. Thus, the survival estimate for each site represents a range of ages for which survival could be estimated. Once compiled into a histogram, I regressed age against the log-transformed frequency of each age class using a linear regression. Taking the antilog of the slope of the resultant line yields the annual survival estimate for that site and age range (Hellgren et al. 2000). I repeated this process for each property.

I tested the strength of my survival estimates by comparing them to annual survival estimated using a Jolly-Seber CMR model as both CMR models and age-structured regression carry the assumption that a marked sample of the population is representative of the whole (Chapman and Robson 1960, Robson and Chapman 1961, Hellgren et al. 2000, Skalski et al. 2005, Silvy 2012). These Jolly-Seber analyses were conducted using Program MARK (White and Burnham 1999) for the 3 of my sites which possessed the most robust capture histories: Black Gap WMA, Gene Howe WMA, and Matador WMA.

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Indices of reproductive output were developed by examining x-ray films taken from each site. To do this, I used a handheld x-ray system designed for use in dentistry (NOMAD; Aribex Inc., Orem, UT, USA). Female turtles were placed upside-down on plates containing pieces of x-ray film with identifying information for each female (site, date, notch code, and PIT tag number if applicable) etched into lead tape and placed in a readable location, allowing for each female's identifying information to appear on the x-ray film itself. Given the intended use of the NOMAD®, its cone of exposure is quite narrow, making it difficult to x-ray multiple turtles simultaneously. To solve this problem, I used a homemade frame constructed of a single piece of plywood to hold the x-ray plates in place at the feet of a ladder. This kept the plates in the same place and, with some practice, allowed to me to aim for the plate at roughly the same angle for each x-ray. From the top of the ladder, the cone of exposure was thus widened enough to capture an entire plate of turtles at once.

To estimate average clutch size, females were examined for the presence of eggs and the number of eggs per female were counted (Congdon and Tinkle 1982, Germano 2014, Hellgren et al. 2000). For both average clutch volume and average egg volume, the length and width of each egg were measured on the x-ray film using a ruler and volume was calculated using a formula for an oblate spheroid ($v = \frac{4}{3}\pi \cdot (\frac{length}{2})^2 \cdot (\frac{width}{2})$). For average clutch volume, the total volume of each clutch was estimated by adding the volumes for all eggs in the clutch and then the average volume of all clutches was calculated. In some cases, the same female was x-rayed multiple times while gravid. In these instances, such multiple clutches were randomized to a single clutch to maintain

independence. The 3 indices of reproductive output (mean clutch size, mean egg volume, mean clutch volume) were then regressed against the independent variable of survival using linear regression with study site used as the experimental unit.

RESULTS

I analyzed data from 3,662 captures of 2,076 individuals. Captures of yellow mud turtles used for this study began in 2006 and continued until 2019, with sampling effort varying across sites and years (Table 1). Although every effort was made to visit all sites as often as possible during the activity period, it was not possible to visit each site every year and thus some sites were not visited in certain years. This variance was mostly caused by logistical constraints on planning collection trips in combination with unpredictable weather patterns across sites. For much of this study, the state of Texas was going through an extreme drought, and this affected sampling effort. The ephemeral nature of the water bodies that this species favors also meant that at times there was little to no water available to sample at some sites.

Data were typically collected during the turtles' active period of late April through July; however, the active period for this species appears to vary across populations. For most sites, emergence appeared to be tied to rainfall that occurred in late spring, around late April or early May. Activity appeared to stay relatively stable through June, and then began to decrease in the middle of July. Females were the first to disappear for the season, reducing in number dramatically by the end of June or early July. Juveniles and males appeared to stay active through July, with capture success waning later in the summer (personal observation). Notably, populations at 2 of my sites,

Black Gap WMA and Yoakum Dunes WMA, had significant capture success in later months. At Yoakum Dunes WMA, turtles remained active well into August, and at Black Gap WMA they displayed a pronounced spike in activity in the month of September. For all other sites, sampling in these later months was largely unsuccessful.

Yellow mud turtles were sampled at Black Gap WMA in the years 2007, 2010, 2015-2019 (Table 1) resulting in 735 captures of 541 individuals. Average male carapace length was 110.2 mm (n = 192) and average female carapace length was 102.1 mm (n = 190). Adult sex ratio (M:F) was 1.3:1. Juveniles made up 29% of individuals. I made 804 age assessments from 480 individuals, resulting in an age distribution that ranged from 1 to 12 years of age (Figure 2). Annual survival as determined by age-structured regression of ages 2-12 (Figure 8) produced a survival estimate of 85.3% (Table 2). I detected 14 clutches from 33 radiographs. Radiographs were taken during a single sampling trip in 2019 and thus no double clutching was detected. Clutch size ranged from 1-5 and averaged 3.6 (Table 4).

Turtles were sampled at Gene Howe WMA in the years 2007-2014, 2016-2018 (Table 1) resulting in 853 captures of 410 individuals. Average male carapace length was 104.5 mm (n = 109) and average female carapace length was 93.7 mm (n = 131). Adult sex ratio (M:F) was 1.2:1. Juveniles made up 39% of individuals. I made 831 age assessments from 410 individuals, resulting in an age distribution that ranged from 0 to 11 years of age (Figure 3). Annual survival as determined by age-structured regression of ages 3-11 (Figure 9), produced a survival estimate of 80.2% (Table 2). I detected 31

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clutches from 214 radiographs resulting in 1 instance of double clutching. Clutch size ranged from 1-6 and averaged 4.1 (Table 4).

Turtles were sampled at Matador WMA in the years 2006- 2010, 2012-2018 (Table 1) resulting in 511 captures of 283 individuals. Average male carapace length was 111.8 mm (n = 92) and average female carapace length was 96.7 mm (n = 96). Adult sex ratio (M:F) was 1.1:1. Juveniles made up 34% of individuals. I made 475 age assessments from 282 individuals, resulting in an age distribution that ranged from 0-14 years of age (Figure 4). Annual survival as determined by age-structured regression of ages 3-14 (Figure 10), producing a survival estimate of 71.6% (Table 2). I detected 32 clutches from 131 radiographs resulting in 1 instance of double clutching. Clutch size ranged from 1-6 and averaged 3.4 (Table 4).

Turtles were sampled at Ramp Ranch in the years 2016-2018 (Table 1) resulting in 873 captures of 396 individuals. Average male carapace length was 109.2 mm (n = 121) and average female carapace length was 96.9 mm (n = 145). Adult sex ratio (M:F) was 1:1.2. Juveniles made up 32% of individuals. I made 859 age assessments from 396 individuals, resulting in an age distribution that ranged from 0-16 years of age (Figure 5). Annual survival as determined by age-structured regression of ages 4-16 (Figure 11), producing a survival estimate of 69.1% (Table 2). I detected 28 clutches from 235 radiographs resulting in 1 instance of double clutching. Clutch size ranged from 2-7 and averaged 4.1 (Table 4).

Turtles were sampled at Rita Blanca NG in the year 2016 (Table 1) resulting in 292 captures of 211 individuals. Average male carapace length was 106.7 mm (n = 51)

and average female carapace length was 100.4 mm (n = 96). Adult sex ratio (M:F) was 1:1.9. Juveniles made up 30% of individuals. I made 292 age assessments from 205 individuals, resulting in an age distribution that ranged from 1-14 years of age (Figure 6). Annual survival as determined by age-structured regression of ages 3-14 (Figure 12), producing a survival estimate of 76.9% (Table 2). No radiographs were taken at this property.

Turtles were sampled at Yoakum Dunes WMA in the years 2015-2018 (Table 1) resulting in 425 captures of 283 individuals. Average male carapace length was 1036.6 mm (n = 71) and average female carapace length was 98.5 mm (n = 143). Adult sex ratio (M:F) was 1:2. Juveniles made up 24% of individuals. I made 425 age assessments from 283 individuals, resulting in an age distribution that ranged from 0-14 years of age (Figure 7). Annual survival as determined by age-structured regression of ages 4-16 (Figure 13), producing a survival estimate of 62.2% (Table 2). I detected 13 clutches from 131 radiographs. No double clutching was detected. Clutch size ranged from 2-5 and averaged 3.9 (Table 4).

Survival

I used age data collected from 2,056 individuals across 6 sites to produce survival estimates for each population. The youngest age assigned to a turtle was 0, and the oldest was estimated at age class 16. The age class 0 was applied to hatchling turtles either found in the early season without any annuli present or late in the season following their emergence from nests. The absence of any annuli suggests that those individuals captured early in the season had overwintered in the nest after hatching, a phenomenon

documented in other populations of this species (Long 1986b). For each site, I found a

maximum age beyond which individuals were difficult or impossible to age with any

certainty because of annuli becoming too close to one another to read. The difficulty in

capturing juveniles and the presence of a maximum age meant that the age range for

which survival could be calculated was quite variable across sites (Table 2). Annual

survival for the 6 properties included in my study varied significantly, ranging from

62.2% at Yoakum Dunes WMA to 87.6% at Black Gap WMA (Table 2; Figures 8-13).

For the 3 sites which I was able to estimate survival using CMR, those estimates were

nearly identical to the ones obtained through age structured regression (Table 3).

As expected, the variation exhibited across my 6 sites did not appear to conform

to a climate gradient. Three of my sites within the Texas Panhandle (Matador WMA,

Ramp Ranch, and Yoakum Dunes WMA) were not significantly different from one

another, but significantly differed from my southern-most site, Black Gap WMA, which

exhibited the highest estimated annual survival (Figure 14). However, Gene Howe WMA

also exhibited a high annual survival rate similar to that of Black Gap, while differing

significantly from nearby Ramp Ranch.

Reproductive Output

X-rays were taken in the years 2017 to 2019, during which I detected clutches at 5

of the 6 sites for which survival was estimated. Additionally, x-rays from previous years

(Table 1) were also utilized for this study. 461 radiographs of 266 individual females

were taken across these 5 sites, with a total of 118 clutches detected (Table 4). For Rita

Blanca NG, logistical difficulties prevented sampling in 2017 and 2018 and no x-rays

were taken of females in previous years. I was thus unable to include this property in my comparisons of survival to reproductive effort.

Clutches were usually detected in the months of May and June when females appeared to be most active. After reproduction took place in late May through June, the number of females captured dropped precipitously. For Black Gap and Yoakum Dunes WMAs, however, capture success was still significant into August-September provided sufficient rainfall had occurred to keep the ponds full. No reproduction was detected in these later months, however. The earliest clutch I detected was on 11 May at Matador WMA and the latest was on 30 June at Gene Howe. The average clutch sizes for the 5 properties ranged from 3.41 at Matador WMA (n = 32) to 4.05 at Ramp Ranch (n = 28), (Table 4). Average egg volumes ranged from 3,716 mm^3 at Ramp Ranch to 4387.60 mm^3 at Yoakum Dunes WMA (Table 5). Average total clutch volumes ranged from 13,990 mm^3 at Matador WMA to 17248 mm^3 at Yoakum Dunes WMA (Table 6). While most females at my sites were only documented to lay a single clutch per season, 3 females across 3 of my sites (Gene Howe WMA, Matador WMA, and Ramp Ranch) were documented to lay multiple clutches. Those few females were captured once and found to be gravid, without any eggs on the second capture, and then gravid on the third.

Comparisons

I did not detect any significant relationship between survival and average clutch size ($F_4 = 0.582$, p = 0.501; Figure 15). I did not detect any significant relationship between survival and average egg volume ($F_4 = 0.315$, p = 0.613; Figure 16). I did not

detect any significant relationship between survival and average clutch volume (F_4 = 1.935, p = 0.258; Figure 17).

DISCUSSION

Survival

Variation in annual survival was considerable across my sites, and such variation continued to exhibit a lack of any apparent pattern related to gradients of climate or geography as found in previous iterations of this study (Lange 2011, McVay 2017). Gene Howe WMA and Ramp Ranch, for instance, have significantly different survival rates despite being only 18 kilometers apart and sharing multiple similarities in habitat and climate, whereas Gene Howe was not significantly different from Black Gap WMA, a property that lies hundreds of miles away in a completely different ecoregion of Texas. This suggests that yellow mud turtles exhibit variable annual survival across its range, a conclusion supported by other studies on this species (Iverson 1991a, Lange 2011, McVay 2017). McVay (2017) in particular examined the variation in survival rates for the same populations as myself and did not find evidence to support the idea that survival is affected by climate or annual rainfall even when correcting for low sample size. As such, there is a need to continue exploring potential influences on annual survival for yellow mud turtles.

Aside from variation in reproduction, there are other potential drivers of variation in survival which I suspect could have significant implications for the management of this species. One such potential factor is predation. Several species are known to prey on yellow mud turtles, with documented predators including hognose snakes (*Heterodon*

sp.)*, raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and coyotes (*Canis latrans*, Ernst and Lovich 2009, Iverson 1991a, Tuma 2006). Raccoons are especially well-documented predators of both adult turtles and their nests (Seigel 1980, Christiansen and Gallaway 1984, Karson et al 2018). Yellow mud turtles are thought to avoid waters with fish populations as large predatory fish such as bass (*Micropterus* sp.) are known predators of hatchlings (Ernst and Lovich 2009, Iverson 1991a, Tuma 2006). Female yellow mud turtles have been documented staying buried with their nests for up to a month, seemingly in an effort to increase nest success by deterring predators (Iverson 1990). This could at least partially explain the lower densities of turtles I observed when trapping in sloughs of the Canadian River at Gene Howe WMA and portions of the Middle Pease River at Matador WMA, since adult turtles could be selecting for smaller, more ephemeral bodies of water that lack large predatory fish.

Additionally, during the process of trap-setting, the perimeter of most water bodies was examined for turtle remains, and at some properties, such remains were a fairly common find. At the 2 properties for which I estimated the lowest annual survival (Ramp Ranch with 69.1% and Yoakum Dunes with 61.8%), turtle remains were commonly found at the water's edge or not far from it. Conversely, at the 2 properties for which I estimated the highest annual survival (Black Gap WMA with 85.6% and Gene Howe WMA with 79.5%), I did not find mud turtle remains. This is interesting, since at first glance Black Gap and Gene Howe share few similarities, and once again Ramp Ranch appears to differ considerably in estimated annual survival from its neighboring property, Gene Howe WMA. While admittedly anecdotal, this does lead me to suspect

that relative predator abundance could have a significant effect on the annual survival of yellow mud turtle populations. Mahmoud (1969) noted that yellow mud turtles travel long distances compared to other species within the same family, and such terrestrial movement could be an increased predation risk for populations where water bodies are more ephemeral and necessitate movement. Predation could thus play a significant role in influencing the complex series of trade-offs that must occur to maximize nest success, hatchling survival, and adult survival. Thus, the development of some index of predator abundance at my sites could be illuminating, especially if paired with an examination of site-specific habitat variables such as ephemerality of aquatic habitat.

The efficacy of aging turtles using scute annuli is somewhat contested (Germano and Bury 1998, Wilson et al 2003). While several researchers have found scute annuli to be a useful method for estimating the age of individual turtles (Gibbons 1987, Germano 1988, Castanet 1994, Zug 1991, Hellgren 2000), still others have doubted or qualified its use (Galbraith and Brooks 1987, Cox et al. 1991, Tracy and Tracy 1995, Brooks et al. 1997). For those who disagree with the method, the primary objection appears to revolve around the question of whether or not an individual annulus represents 1 year of growth. Iverson (1978) found that annuli counts were difficult to obtain for the loggerhead musk turtle (*Sternotherus minor*), a species within the same family as the yellow mud turtle but which exhibits a very different ecology. Germano (1988), however, evaluated the technique for a population of known-age tortoises and found that either the number of annuli matched the age of the turtle or led to an underestimation of age by only 1 or 2 years. Thus, I believe that the efficacy of this technique or its ease of use may well

depend on the species for which it is used and its usefulness should be evaluated on a case-by-case basis.

Additionally, age-structured regression, also known as catch curve analysis, assumes a constant survival rate from year to year (Robson and Chapman 1961). Turtles have been described as exhibiting such a curve with mortality rate staying fairly constant throughout life (Gibbons and Semlitsch 1982). While Iverson (1991b) suggests that turtles are better described as exhibiting a pattern in which survival is inversely related to age, data from my own sites do indeed suggest that, at least for adults, the survival rate in yellow mud turtle populations appears to remain constant across age classes. Given these assumptions and the remarkable concordance between my survival estimates derived from age-structured regression and CMR analyses, I believe that age-structured regression is a suitable method of estimating annual survival in turtles.

Were this study to continue, I would recommend increasing the sampling effort at certain sites in addition to expanding its scope to include other properties and, ideally, other states. Access to more sites across a wider range may help us begin to tease apart the underlying causes driving such extreme variation in survival. Annual survival may be influenced by a number of interacting environmental or ecological factors, and a better understanding of these factors and how they work together will be needed to effectively manage this species, particularly in regions where it is threatened.

Reproductive Output

Clutch data collected during my study seemed to generally coincide with those presented by other publications on this species, although they do differ somewhat.

Iverson (1991a) lists values for mean clutch size and mean egg size from several populations in Nebraska (Iverson), Iowa (Christiansen et al. 1984), Oklahoma (Mahmoud and Klicka 1972), Texas (Long 1986), and New Mexico (Iverson, unpublished data). Mean clutch sizes presented by these authors are larger than those measured in my own study, although mean egg lengths and widths were similar to my own. It should be noted, however, that aside from Iverson (1991a), most clutch data for this data appear to come from small sample sizes. For example, Christiansen et al. (1984) presents data for only 4 clutches for their study in eastern Iowa, and Long (1986) presents data for 14 clutches in my own state of Texas. Thus, it is unclear to what degree these figures can be considered representative of the species across its range, especially in light of the considerable variation that yellow mud turtles exhibit in their life history traits.

The smallest female I detected with eggs had a carapace length of only 78.02 mm, significantly smaller than figures presented by other researchers (Long 1986, Iverson 1991a). Christiansen and Dunham (1972) reported a minimum carapace length (CL) at maturity of 90 mm for a population in New Mexico, Long (1986) reported a minimum CL of 95 mm for a population in Texas, and Iverson (1991a) provided a range of 88.3-92.7 mm for his populations in the Nebraska Sandhills. For my populations, only one gravid female measured less than 80 mm and only 5 measured between 80 and 90 mm. The rest had a carapace length of >90 mm – in line with the minimum sizes at maturity provided by these researchers (Christiansen and Dunham 1972, Long 1986, Iverson 1991a).

Yellow mud turtles are typically thought to only lay one clutch per year (Christiansen and Dunham 1972, Mahmoud and Klicka 1972, Iverson 1991a), although they have been documented to split clutches across multiple nests (Tuma 1993, Lange 2011). However, I was able to detect multiple clutching at 3 of my study sites (Gene Howe WMA, Matador WMA, and Ramp Ranch) by occasionally capturing the same female multiple times in a season. Those few females were captured once and found to be gravid, without any eggs on the second capture, and then gravid on third. Multiple annual clutches have also been documented for several other turtle species (Congdon and Tinkle 1982, Gibbons et al. 1982, Meshaka et al., 2017). Additionally, throughout the length of this study and its previous iterations, some reproductive females captured in recurring years were not documented to reproduce each year. Of the 728 females radiographed from 2008 to 2019, 118 were gravid (16.2%). While it is possible that reproductive bouts were missed as a result of the timing of trapping effort, it is also possible that females in my populations do not reproduce every year, which is supported by research conducted on other populations of this species (Iverson 1991a). Bull and Shine (1979) suggest that skipping reproduction in alternating years may be widespread in a number of herpetofaunal species, particularly those with moderate to large clutch/litter sizes and/or asynchronous reproduction. Such a strategy could at least partially explain the seemingly low percentage of females I captured that were gravid at a given time if a certain proportion of females in a population are not reproducing every year.

Yellow mud turtles have also adopted a strategy for follicle development wherein up to 3 sets of ovarian follicles at different size classes are progressively developed at any

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given time, allowing females to develop multiple clutches simultaneously (Christiansen and Dunham 1972, Christiansen et al. 1984, Long 1986, Iverson 1991a). In chelonians that exhibit this strategy, these differing size classes can undergo successive ovulation and deposition across multiple clutches within a single season, or across multiple seasons (Long 1986). Given this, I believe the follicular development and alternation of reproductive years exhibited by this species to be a form of bet-hedging which enables the females of the species to capitalize on bountiful resources in good years while simultaneously preparing for the next season.

The use of clutch or egg size and volume as I measured them may therefore be insufficient indices of reproductive effort for a population of female yellow mud turtles as they do not account for reproductive effort being spread out across multiple clutches or years. If reproduction in this species is variable, as it appears to be, then a comprehensive examination of reproductive parameters which accounts for the phenology of this species' reproduction is warranted.

Comparisons

No significant relationships were detected between annual survival and the measures of reproductive output I used in this study. One possible explanation for this is simply low statistical power. I was only able to conduct my analyses for 5 sites and for most sites the number of clutches I was able to detect was lower than anticipated. Low sample size spread across a small number of experimental units could negatively affect my ability to make any strong conclusions about the relationship between survival and

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reproduction in yellow mud turtles. Despite this, however, it still seems plausible that such a relationship exists and warrants further exploration.

This relationship between reproduction and survival is likely complex, as life history traits are coevolved in response to various ecological influences that directly affect population parameters (Stearns 1976, Congdon and Gibbons 1990). As an example of this complexity related to my own study, previous analyses by Lange (2011) suggest that within-site differences in habitat may be more significant drivers of variation in annual survival than across-site differences. When separating females into the two broad categories of aquatic habitat found at Gene Howe WMA (windmill overflow pond vs. slough), Lange (2011) found that females captured within sloughs exhibited significantly higher rates of gravidity and larger clutch sizes than those females captured in windmill overflow ponds (Lange 2011). Differences in resource availability and turtle density between these two habitat types may be releasing those females inhabiting sloughs from intraspecific competition, allowing for increased reproductive effort in addition to increased chances of predation. Thus, rather than directly influencing survival, reproduction for these populations may exist as part of a tapestry of life history traits evolved by this species as adaptation to the variability of ecological conditions within its range. If such a pattern were to hold true for other populations, it could potentially complicate the management of the species, as wildlife managers may be required to develop separate approaches for sub-populations existing in different types of habitat on the same property.

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In the previous section of my discussion, I mentioned that I believe this species to be exhibiting a bet-hedging strategy wherein multiple size classes of ovarian follicles are developed simultaneously, essentially allowing a female to "prepare" for multiple reproductive bouts (Christiansen and Dunham 1972, Long 1986). According to Christiansen and Dunham (1972), roughly 50% of female yellow mud turtles in their study retained their enlarged ovarian follicles through August. They suggest that this represents a delay in ovulation until the next year, since they did not find evidence to suggest that individuals in their population laid multiple clutches per season. In a few of my own populations, however, multiple clutches were detected. Given this discrepancy, I believe that this strategy of follicle development may enable female mud turtles to maximize reproduction by granting them the flexibility to increase reproductive output in years where conditions are favorable while also minimizing their risk of reproductive loss by enabling them to forgo reproduction in unfavorable years.

That the yellow mud turtle is a bet-hedging species is an excellent alternative hypothesis that potentially explains the lack of a relationship between annual survival and reproduction presented in this study. I originally expected such a relationship under the assumption that turtles utilized a typical K-selection strategy, exhibiting long-life expectancy, iteroparity, late maturity, large body size, and a Type II survivorship curve characterized by consistent mortality rates (Tinkle et al. 1981, Gibbons and Semlitsch 1982, Mitchell 1988). Under this assumption, one might expect a decrease in survival to be a suitable trade-off for increased reproductive output. Iverson (1991b), however, suggests that freshwater turtles are better described as possessing a Type III survivorship

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curve characterized by high juvenile mortality and high adult survival. At all of my sites, juveniles were indeed seldom captured, and nest predation by raccoons and hognose snakes is well documented for this species (Christiansen and Gallaway 1984, Iverson 1991a). At first glance, the shape of my survival curves and the lack of data available for hatchling and juvenile turtles also seem to support the Type III survivorship pattern hypothesis. However, adult turtles are seemingly abundant at all my properties and are readily captured at ages as young as 2 or 3. If hatchling or juvenile mortality were particularly high, then it would follow that fewer individuals would survive to age classes 3 and beyond. As this species appears to have a relatively low recruitment rate (with small clutches laid irregularly across seasons), it seems likely that high hatchling and juvenile mortality would be reflected in the shape of my survival curves. This is not the case, however, as individuals from age classes 3 and beyond are regularly captured at high numbers, and survival across these older age classes appears constant. Given this, I believe that Iverson (1991b) is likely incorrect to suggest that hatchling and juvenile mortality is high enough for this species to justify the assertion that a Type III survivorship curve better describes the survival pattern for yellow mud turtles. Instead, I believe it is more likely that it is the cryptid and elusive nature of hatchlings, combined with the difficulties in capturing such small individuals, which contributes to their lack of representation in my survival estimates.

Under the r/K selection paradigm, turtles should theoretically compensate for lower survival rates by increasing reproductive output in some way, but this is only favorable in stable environments, where increased reproductive output can more reliably

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guarantee an increase in reproductive fitness. In variable and unpredictable environments, as in this case, reproductive output is likely to vary considerably between years, as the risks of nest predation, predation on females, and hatchling mortality make large clutch sizes particularly risky for the long-term fitness of populations. In such situations, a smaller reproductive output of fewer young per clutch should theoretically be favored (Stearns 1976) as it would maximize long-term reproductive success in unpredictable conditions with high juvenile survivorship (Congdon et al. 1982). Such a strategy, known as bet-hedging, increases reproductive success over time by lowering the variance in its reproductive output in the short-term to minimize losses and increase success over the long-term (Philippi and Seger 1989, Olofsson et al. 2009, Lovich et al. 2015, Macip-Rios et al. 2017). By producing relatively small clutches of small eggs combined with an ability to prepare for multiple future clutches simultaneously and forego reproduction in unfavorable conditions, I believe female yellow mud turtles are potentially maximizing their long-term reproductive success whilst simultaneously minimizing their loss in the case of poor environmental conditions or nest/hatchling predation. Essentially, yellow mud turtles could be deshackling the presumed connection between reproductive output and annual survival by adopting a strategy that enables them to forego reproduction (and thus, reallocate those resources toward food acquisition and fat deposition while simultaneously reducing exposure to predation).

The importance of understanding the factors that drive variation in annual survival and reproduction within and across populations increases when the effects of anthropogenic climate change are taken into consideration. As global temperatures and

climate variability continue to increase, so does the need to understand how organisms are likely to respond to such changes if the effects on their populations are to be mitigated. For bet-hedging species such as yellow mud turtle, the precise effect of increased climate unpredictability is not yet clear. It is possible that it could adversely affect them as bet-hedgers tend to rely on occasional "good years" for successful reproduction. Thus, increasing variability in climatic conditions could negatively affect populations of the species if the conditions favorable for successful reproduction become increasingly rare. Additionally, as this species appears to rely on certain environmental triggers, namely spring rain, to regulate its activity patterns (Christiansen et al. 1985, Iverson 1990), and since these triggers are likely to become increasingly unpredictable as our climate changes, the shifting of rainfall patterns is potentially threatening to the survival and reproduction of the species. Alternatively, it is also possible that by utilizing a bet-hedging strategy, yellow mud turtles are well-suited to an environment prone to rapid change, and thus, further investigation of climate's impact on their demography is warranted.

For species with temperature-dependent sex determination, including the yellow mud turtle (Vogt et al. 1982, Ewert et al. 2004), extreme variation in temperature with a trend towards warming also threatens the potential demographic collapse of populations as sex ratios become increasingly skewed in one direction (Valenzuela et al. 2019). Although populations of this species do not currently appear to be threatened in Texas, it is protected in Iowa, Illinois, and Missouri (Christiansen et al. 2012). As climatic conditions continue to become increasingly unpredictable, any findings that aid in the

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management of this species could potentially have implications for these at-risk populations, as well as for related species.

Future Directions

All my sites are naturally quite different from one another, representing different ecoregions with distinct plant and animal communities, habitat types and availability, weather patterns, and even management strategies. Were this study to continue, there are a few factors that I believe are worth evaluating as potential influences on the variation in survival and reproduction I observed in this species.

At some of my properties, turtle remains were a common find but were seldom discovered at others. Given the range of conditions found at each property, including anthropogenic factors like habitat fragmentation, predator diversity and abundance likely vary across my sites. Therefore, I hypothesize that such variation in predator communities would in turn impact the life history traits of yellow mud turtles and I would recommend the development of a metric for predation to aid in exploring its potential impact on demographic variation in the species.

Additionally, differing management practices and natural conditions at my properties appear to result in a fair degree of variation in the habitats occupied by this species. Some properties are grazed more than others, some exhibit a greater diversity of habitat types and their associated communities, and some exhibit more extreme variation in weather patterns. Thus, I suspect that site-specific and even habitat-specific variation has an impact on survival and reproduction. In particular, I would recommend an

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exploration of the impacts of land use, water ephemerality, type of aquatic habitat, and the diversity of associated insect and plant communities as potential influences of variation in life history traits at these properties.

To further test the hypothesis that yellow mud turtles are bet-hedgers, more robust, site-specific data on variation in reproduction are needed. I suspect that clutch size, egg volume, and clutch volume provide an incomplete picture of reproductive effort for yellow mud turtles. As such, I recommend using other indices of reproductive output aside from those used in my study, such as clutching frequency, number of clutches per year, and a ratio of egg size and number to female mass to more fully complete the picture of how much effort this species puts into reproduction. Were such data to be obtained, it could be compared with previously mentioned environmental or habitat variables such as rainfall, ephemerality of aquatic habitat, or predator abundance to determine if any patterns exist between variation in environmental variables and reproductive output. However, such a thorough analysis would likely be beyond the scope of a single long-term study, as it would be logistically difficult for a single researcher to study multiple populations in this way over a long period of time.

In summation, my results suggest that the influence of variation in survival on reproduction (and vice versa) in this species is indirect and likely represents a mere snapshot of the larger tapestry of life history traits interacting to influence the ecology of yellow mud turtles. In order to more fully understand this tapestry and how these life history traits interact, I believe that expanding the scope of this study to include more sites as well as indices of predation, reproductive effort, and habitat variation is needed.

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Table 1. Total number of individuals captured and total number of captures of yellow mud turtles sampled from 6 sites in Texas, 2006-2019. Years in which each site was sampled are indicated with the number of individuals captured at each site for that year. Within each year, number of individuals captured is indicated.

			Years Sampled					
Site	Total Captures	Total Individuals	2006	2007	2008	2009	2010	2011
Gene Howe WMA	826	367		96	186	144	1	2
Black Gap WMA	735	541		220			129	
Rita Blanca NG	292	211						
Matador WMA	513	283	4	85	48	31	4	
Ramp Ranch	873	393						
Yoakum Dunes WMA	424	281						
Total	3,662	2,076	4	401	234	175	134	2

Table 1. Con't. Total number of individuals captured and total number of captures of yellow mud turtles sampled from 6 sites in Texas, 2006-2019. Years in which each site was sampled are indicated with the number of captures made at each site for that year. Within each year, numbers of individuals captured is indicated.

Site	Years Sampled							
	2012	2013	2014	2015	2016	2017	2018	2019
Gene Howe WMA	200	103	16		39	28	9	
Black Gap WMA				23	137	98	11	117
Rita Blanca NG					292			
Matador WMA	40	58	44	14	359	43	75	
Ramp Ranch					146	288	439	
Yoakum Dunes WMA				103	54	151	117	
Total	240	161	60	140	1027	608	651	117

Table 2. Number (n) and age range of yellow mud turtles used to calculate annual survival using age-structured regression for 6 populations in Texas, 2006-2019. Upper and lower 95% confidence intervals are asymmetrical because of the ln-transformation of age data to calculate the survival estimates. Coefficients of determination (r^2) and P-values describe the strength of the regression used to calculate survival.

Site	n	Age Range	Survival	Lower 95% CI	Upper 95% CI	r^2	P-value
Black Gap WMA	541	2-12	0.853	0.825	0.881	0.931	<0.001
Gene Howe WMA	410	3-11	0.795	0.759	0.848	0.927	<0.001
Matador WMA	283	3-14	0.755	0.684	0.749	0.964	<0.001
Ramp Ranch	396	4-16	0.676	0.671	0.712	0.986	<0.001
Rita Blanca NG	211	3-14	0.769	0.688	0.859	0.738	<0.001
Yoakum Dunes WMA	283	4-16	0.622	0.536	0.712	0.903	<0.001

Table 3. Comparison between survival estimates obtained via age-structure regression and capture-mark-recapture (CMR) method for yellow mud turtles from 2003 to 2006.

| | Age-Structured Survival | Jolly-Seber CMR | |
		Survival	SE
Gene Howe WMA	79.5%	79.7%	0.031
Black Gap WMA	85.6%	86.7%	0.034
Matador WMA	75.5%	75.1%	0.034

Table 4. Comparisons between annual survival and average clutch size for yellow mud turtles from 5 sites in Texas, 2006-2019.

Site	Survival (%)	Clutch Size			
		$\overline{x}$	Range	Std. Dev.	n
Black Gap WMA	85.6	3.64	1 – 5	1.22	14
Gene Howe WMA	79.5	4.03	1 – 7	1.51	31
Matador WMA	75.5	3.41	1 - 8	1.52	32
Ramp Ranch	67.6	4.05	2 - 6	1.05	28
Yoakum Dunes	62.2	3.92	2 - 5	0.95	13

Table 5. Comparisons between annual survival and mean egg volume for yellow mud turtles from 5 sites in Texas, 2006-2019.

Site	Survival (%)	Egg Volume (mm^3)			
		$\bar{\text{x}}$	Range	Std. Dev.	n
Black Gap WMA	85.6	4,015	1,642 – 6,049	860	51
Gene Howe WMA	79.5	3,961	2,279 - 5,293	668	129
Matador WMA	75.5	4,107	2,413 – 5,259	625	109
Ramp Ranch	67.6	3,790	2,710 - 5,104	589	89
Yoakum Dunes	62.2	4,397	2,875 – 5,407	618	51

Table 6. Comparisons between annual survival and mean clutch volume for yellow mud turtles from 5 sites in Texas, 2006-2019.

Site	Survival (%)	Clutch Volume (mm^3)			
		$\overline{x}$	Range	Std. Dev.	n
Black Gap WMA	85.6	14,627	4,388 – 25,897	5,975	14
Gene Howe WMA	79.5	15,967	3,563 – 27,896	6,402	31
Matador WMA	75.5	13,991	3,619 – 30,869	6,235	32
Ramp Ranch	67.6	15,330	6,296 – 28,009	5,521	28
Yoakum Dunes	62.2	17,248	8,474 – 23,343	4,590	13

Figure 1. Properties used as study sites to explore variation in demography for yellow mud turtles in Texas. The different color sections correspond to the ecoregions each site lies in. Properties included: Gene Howe WMA (1), Ramp Ranch (2), Matador WMA (3), Yoakum Dunes WMA (4), Black Gap WMA (5), and Rita Blanca NG (6).
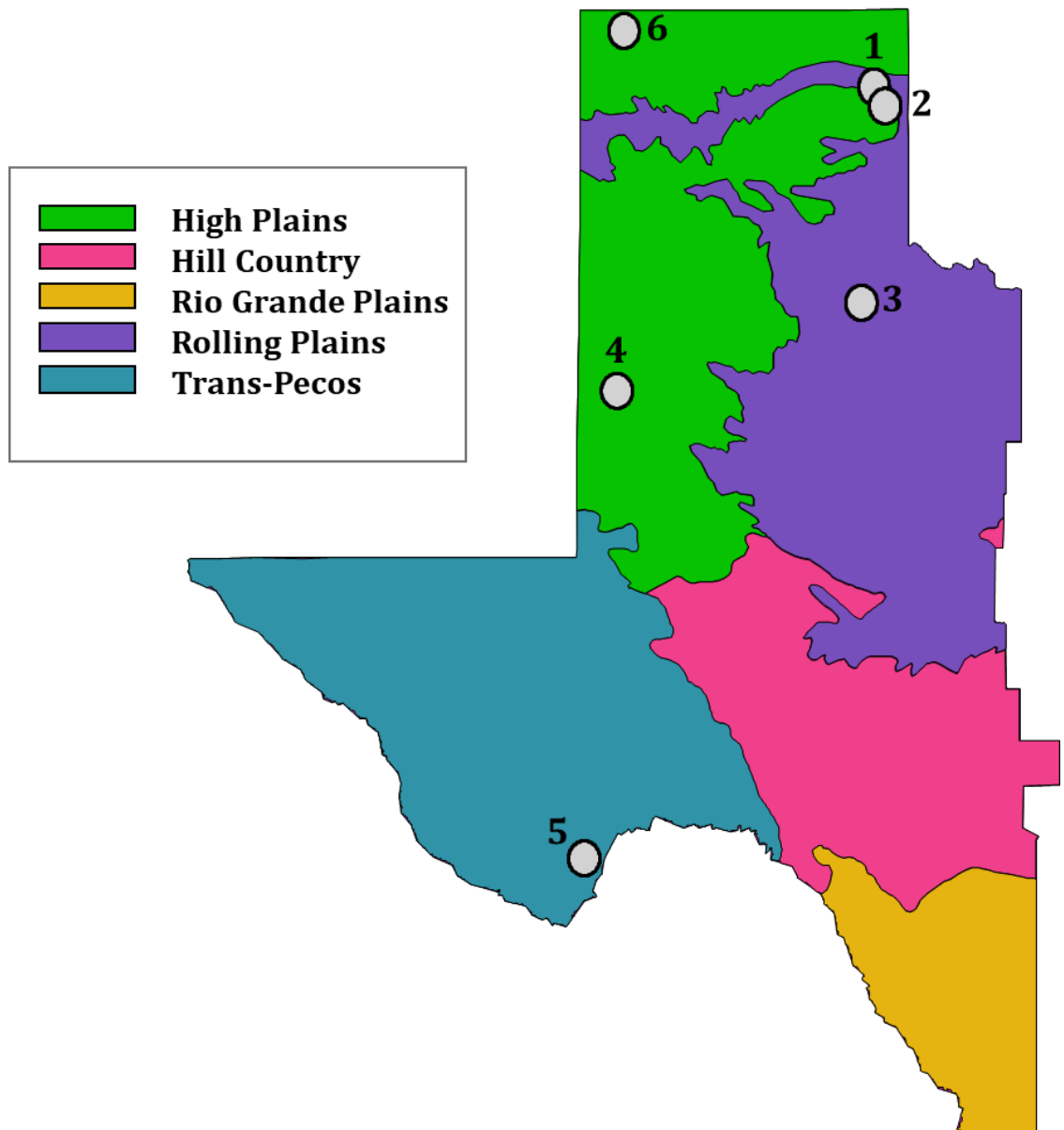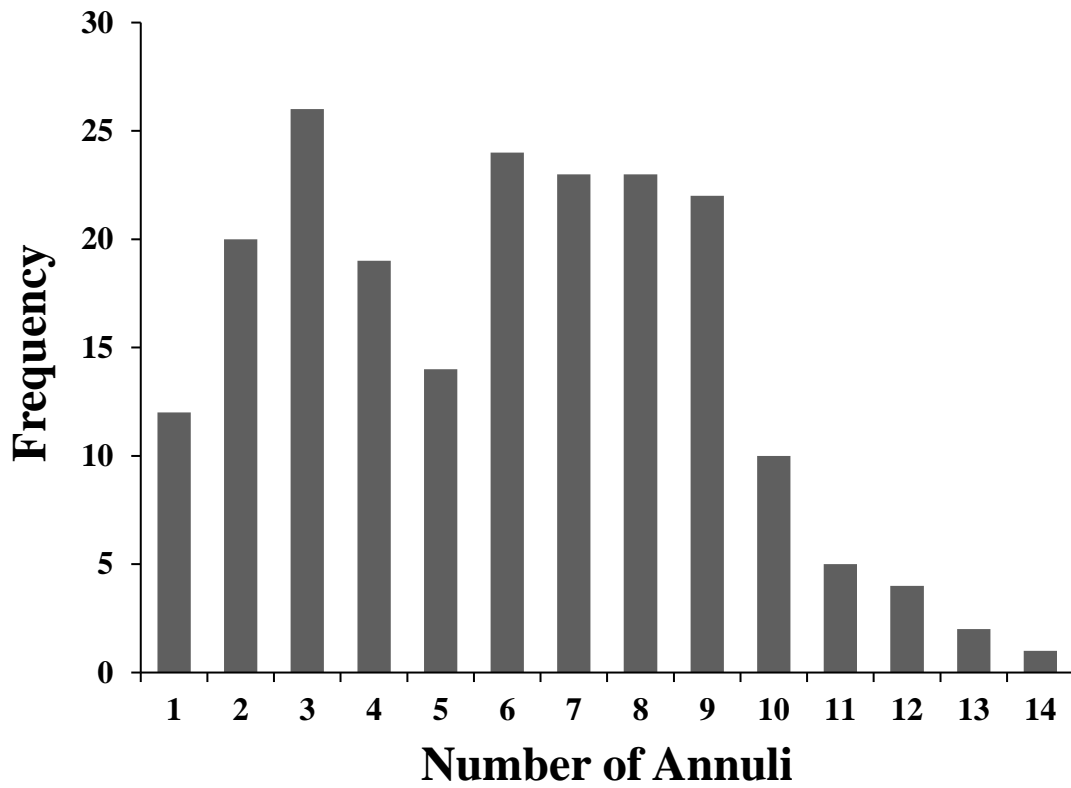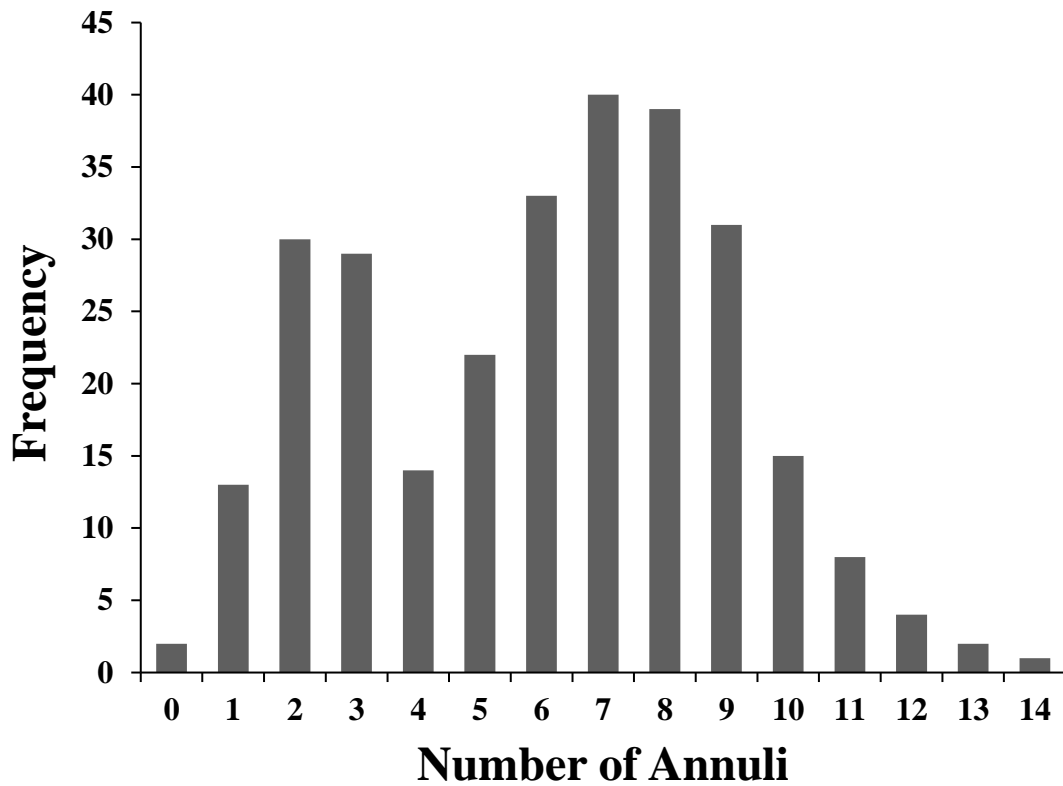
Figure 2. Age distribution for yellow mud turtles at Black Gap Wildlife Management

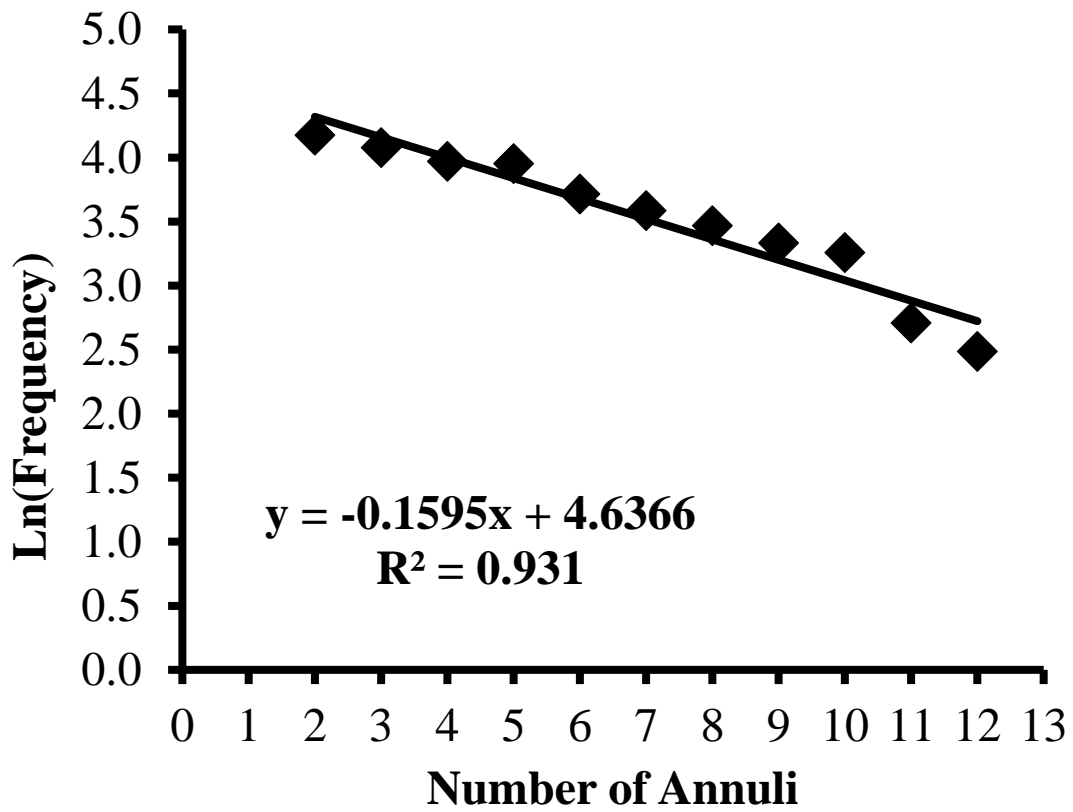Area in Brewster County, Texas, from 2007 to 2019 (n = 480).
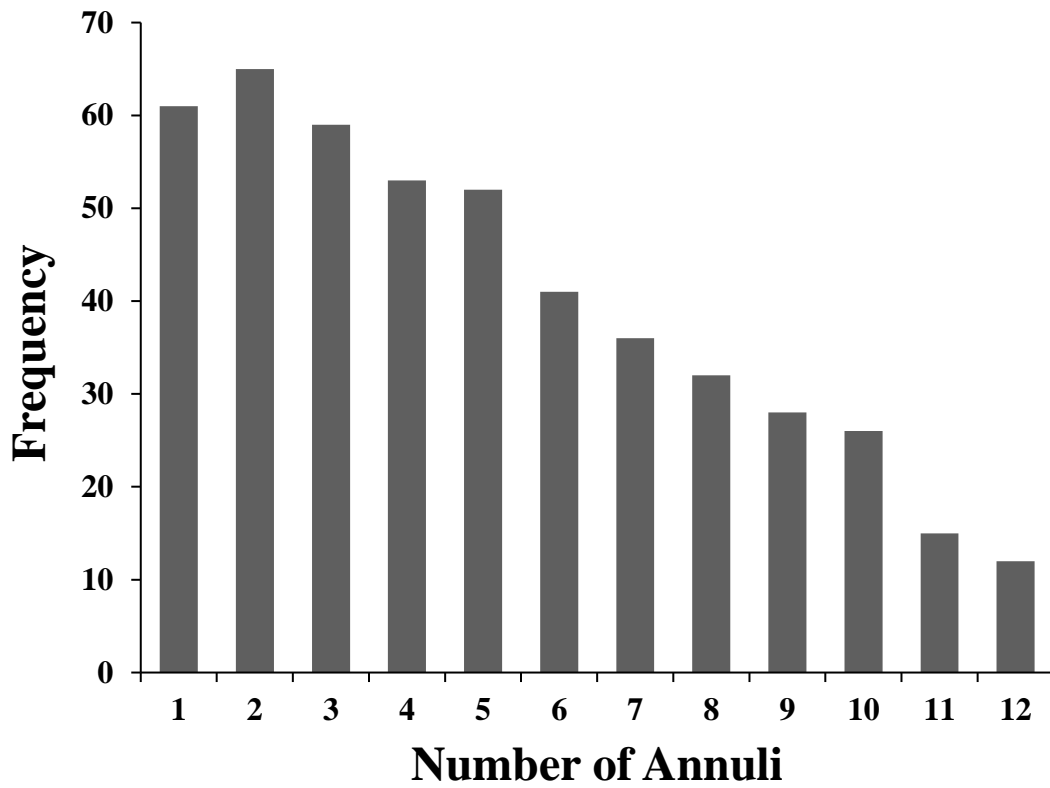
Figure 3. Age distribution for yellow mud turtles at Gene Howe Wildlife Management
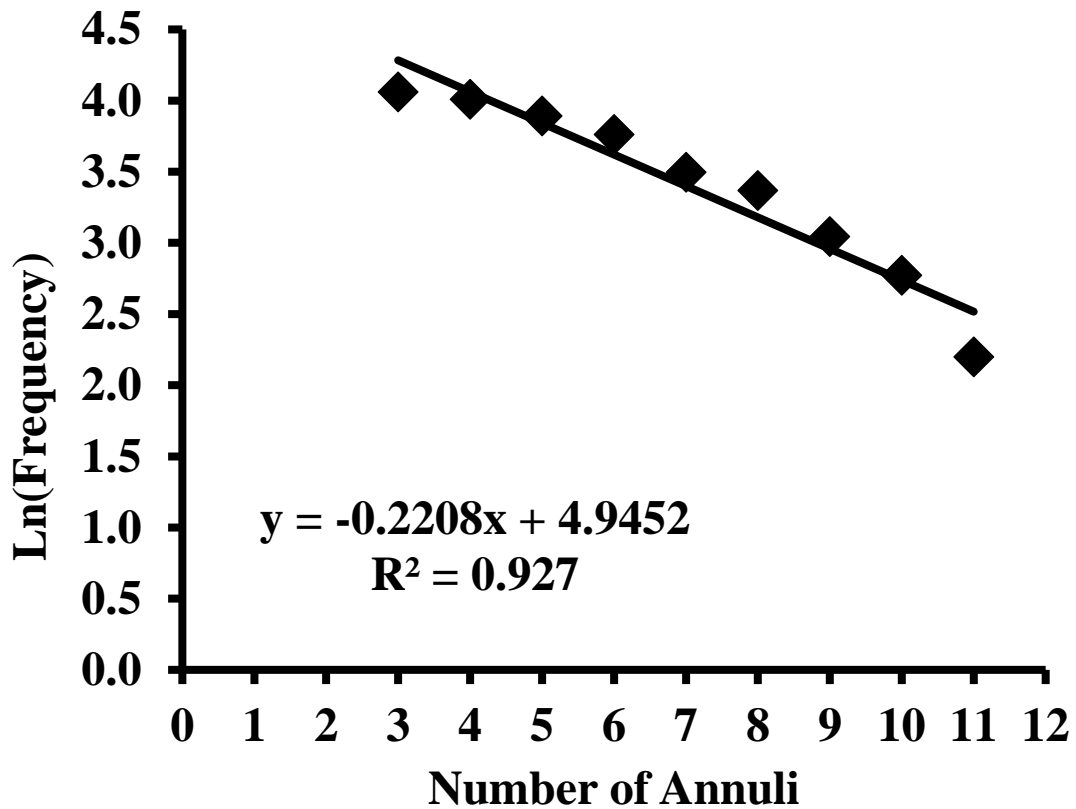
Area in Hemphill County, Texas, from 2007 to 2019 (n = 410).
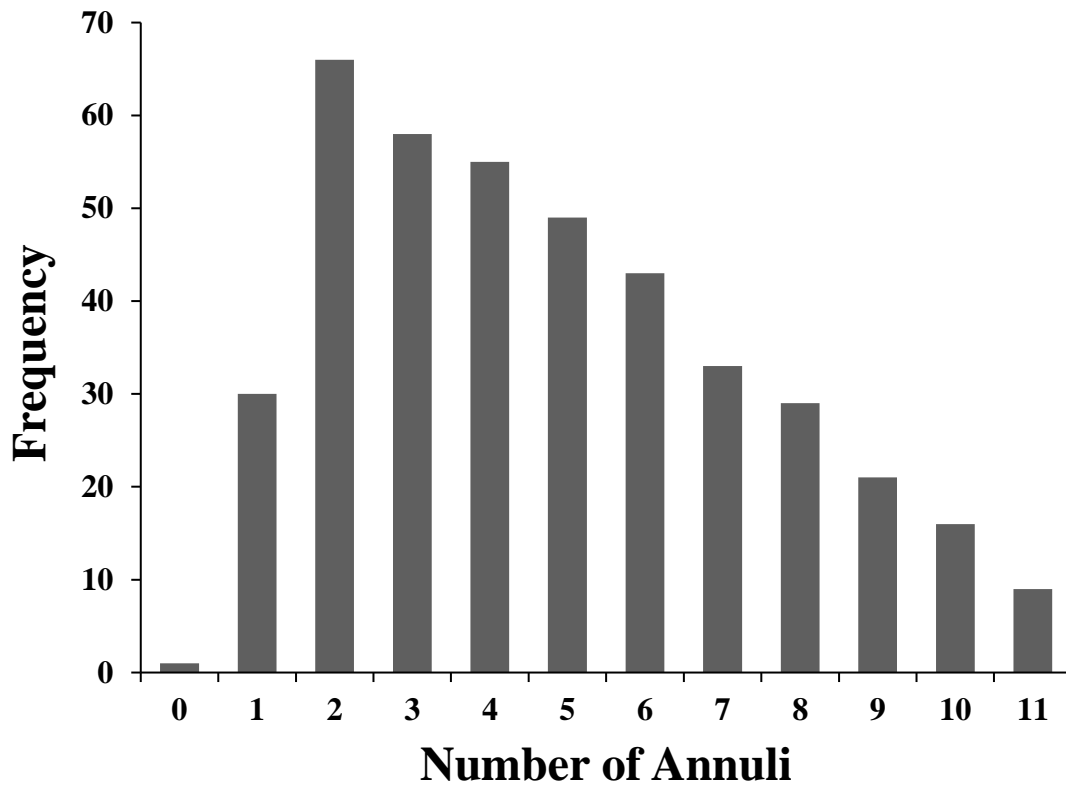
Figure 4. Age distribution for yellow mud turtles at Matador Wildlife Management Area in Cottle County, Texas, from 2006 to 2018 (n = 282).
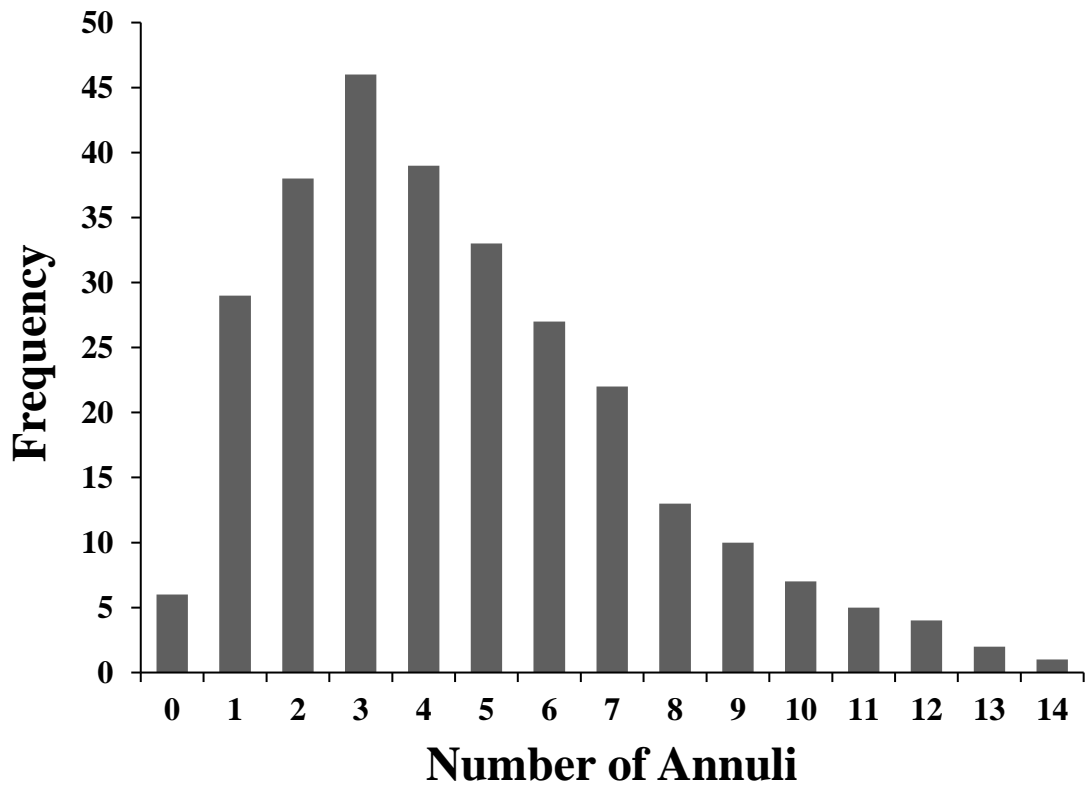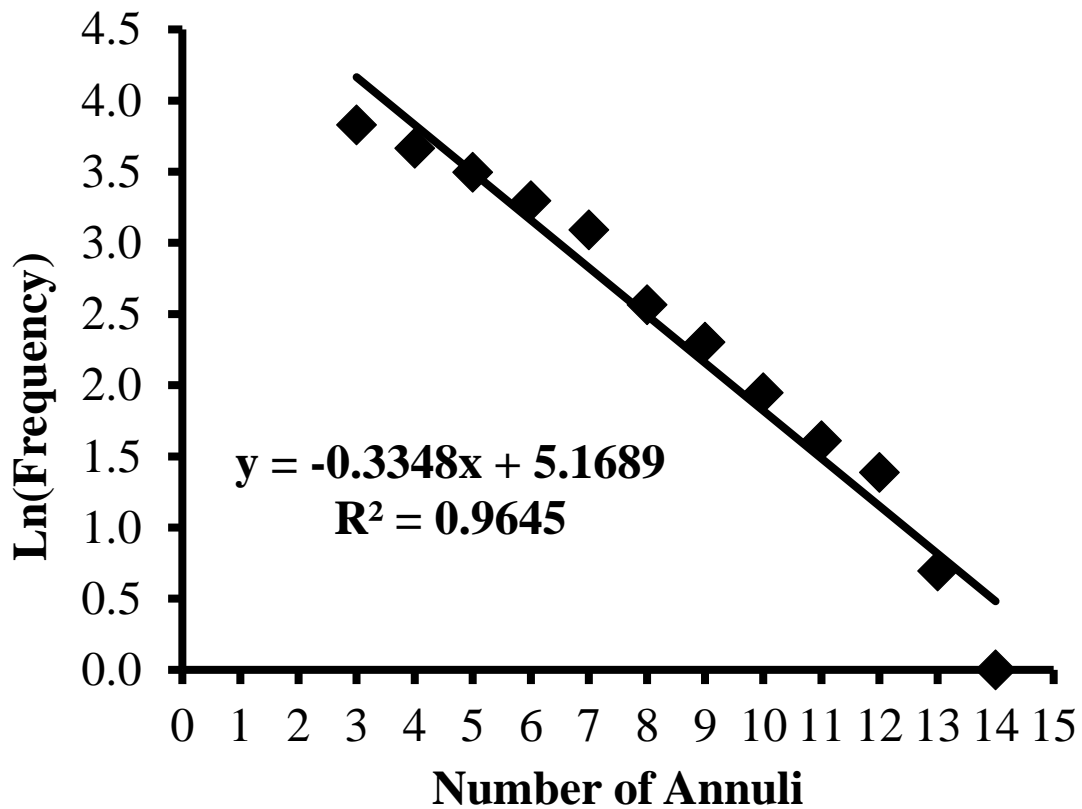
Figure 5. Age distribution for yellow mud turtles at Ramp Ranch in Hemphill County, Texas, from 2016 to 2018 (n = 396).
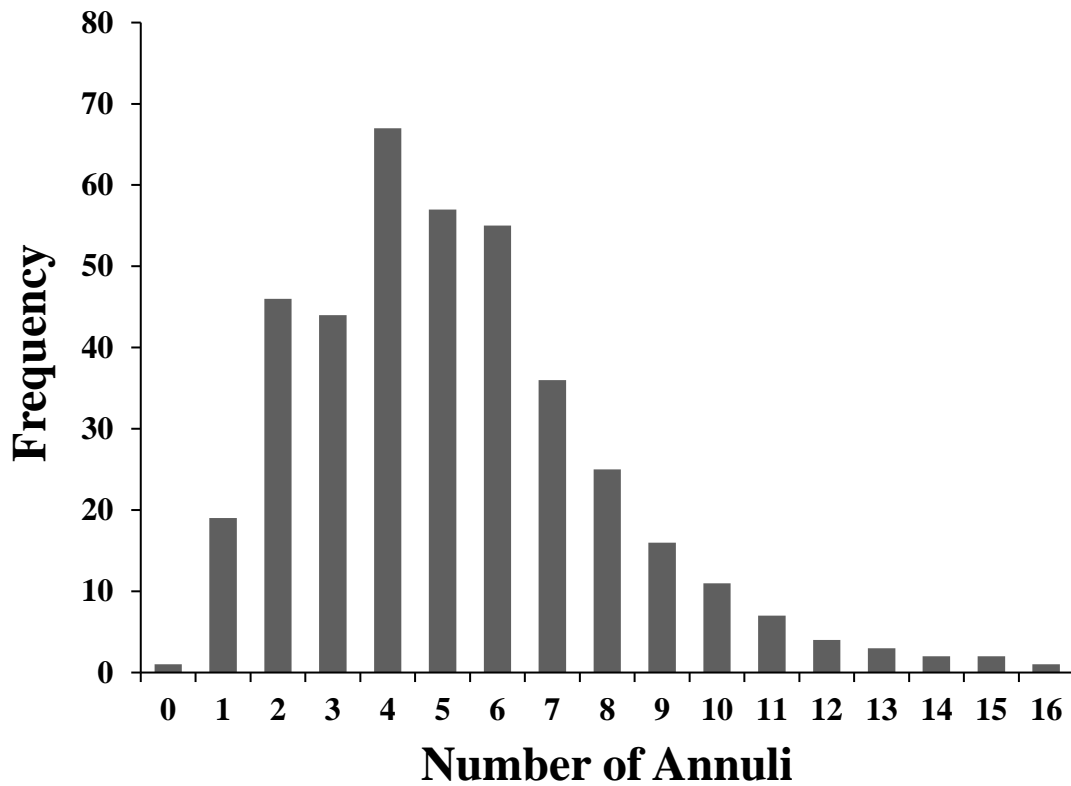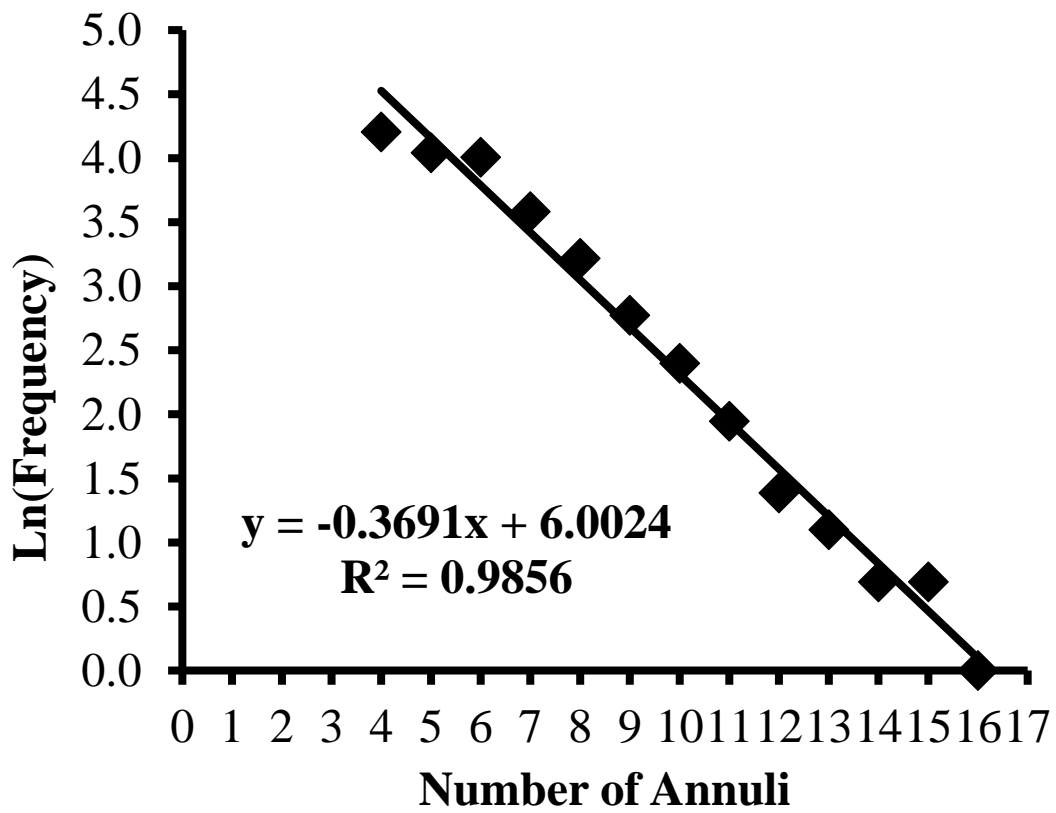
Figure 6. Age distribution for yellow mud turtles at Rita Blanca National Grasslands in
Dallam County, Texas, in 2016 (n = 205).

Figure 7. Age distribution for yellow mud turtles at Yoakum Dunes Wildlife

Management Area in Cochran County, Texas, from 2015 to 2018 (n = 283).

Figure 8. Age-structure regression of yellow mud turtles at Black Gap Wildlife

Management Area in Brewster County, Texas, from 2007 to 2019 (n = 480).

Figure 9. Age-structure regression of yellow mud turtles at Gene Howe Wildlife Management Area in Hemphill County, Texas, from 2007 to 2018 (n = 410).

$$y = -0.2208x + 4.9452$$
$$R^2 = 0.927$$
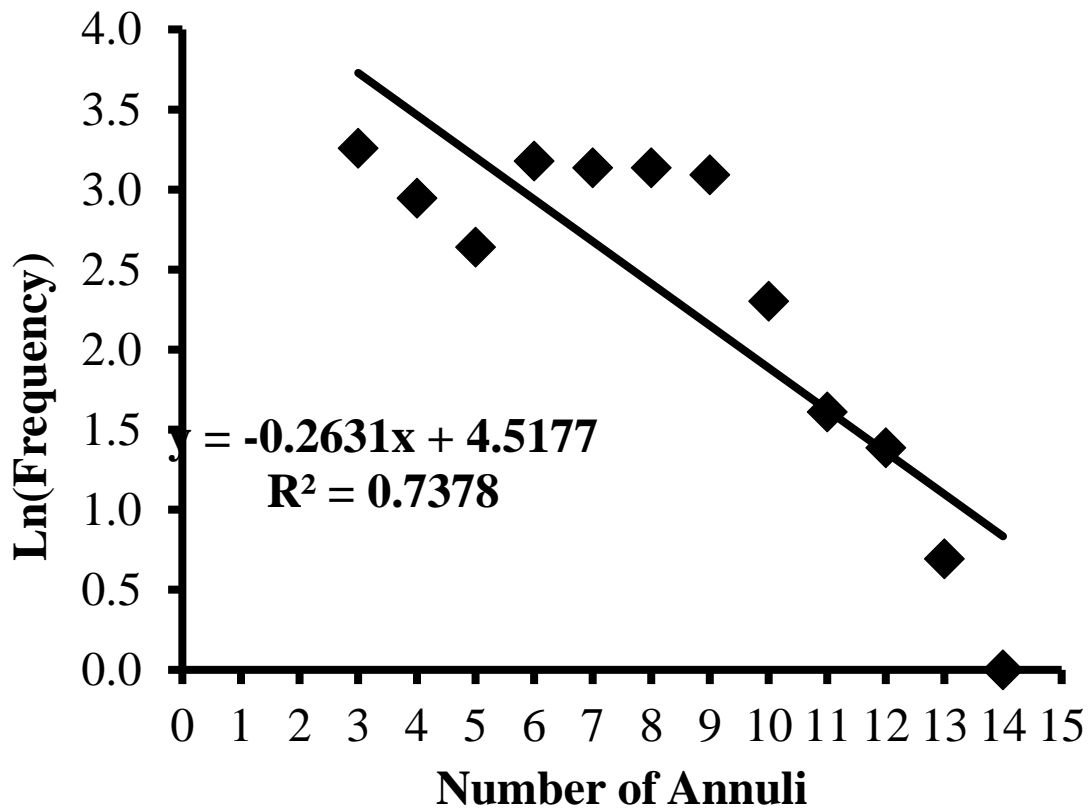
Figure 10. Age-structure regression of yellow mud turtles at Matador Wildlife

Management Area in Cottle County, Texas, from 2006 to 2018 (n = 282).

$y = -0.3348x + 5.1689$

$R^2 = 0.9645$

Figure 11. Age-structure regression of yellow mud turtles at Ramp Ranch in Hemphill County, Texas, from 2016 to 2018 (n = 396).

$y = -0.3691x + 6.0024$
$R^2 = 0.9856$

Figure 12. Age-structure regression of yellow mud turtles at Rita Blanca National
Grasslands in Dallam County, Texas, in 2016 (n = 205).

$y = -0.2631x + 4.5177$

$R^2 = 0.7378$

Figure 13. Age-structure regression of yellow mud turtles at Yoakum Dunes Wildlife

Management Area in Cochran County, Texas, from 2015 to 2018 (n = 283).

$y = -0.4814x + 7.1637$
$R^2 = 0.9025$

Ln(Frequency)

Number of Annuli
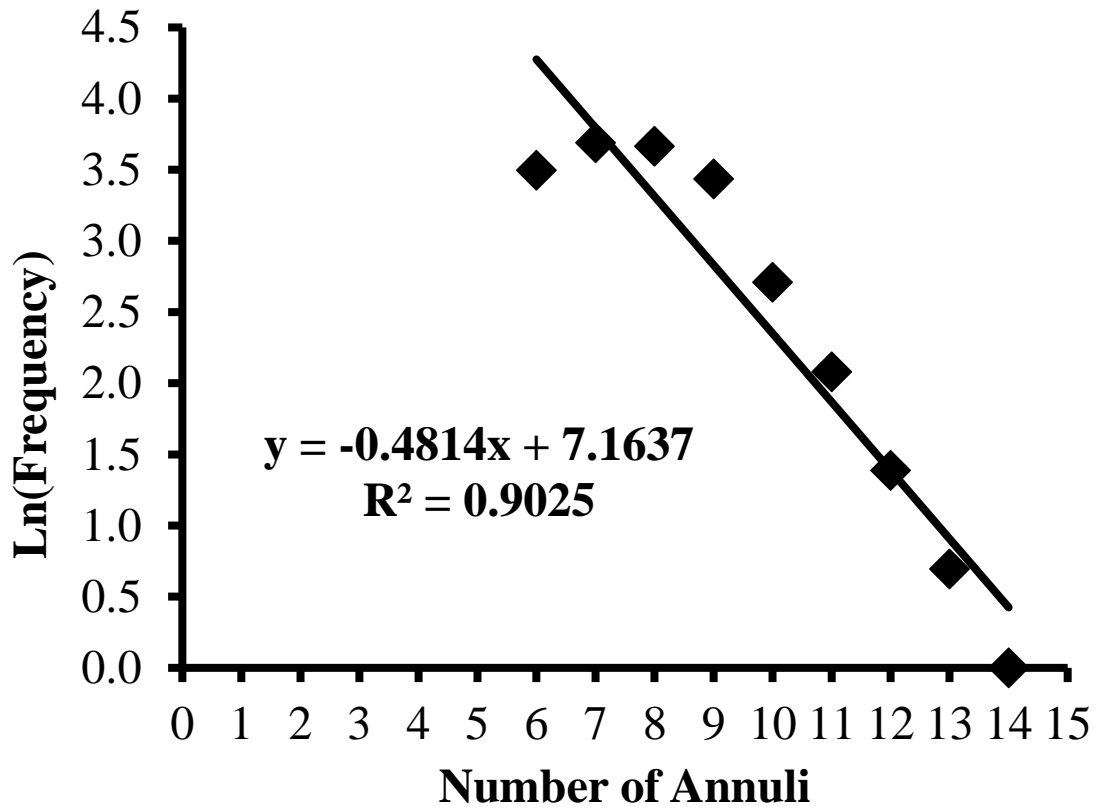
Figure 14. Comparison of annual survival for six sites used to explore demography of yellow mud turtles in Texas. Annual survival estimates labeled with the same letter are not significantly different from one another but are different from estimates labeled with another letter. Error bars indicate 95% confidence interval.
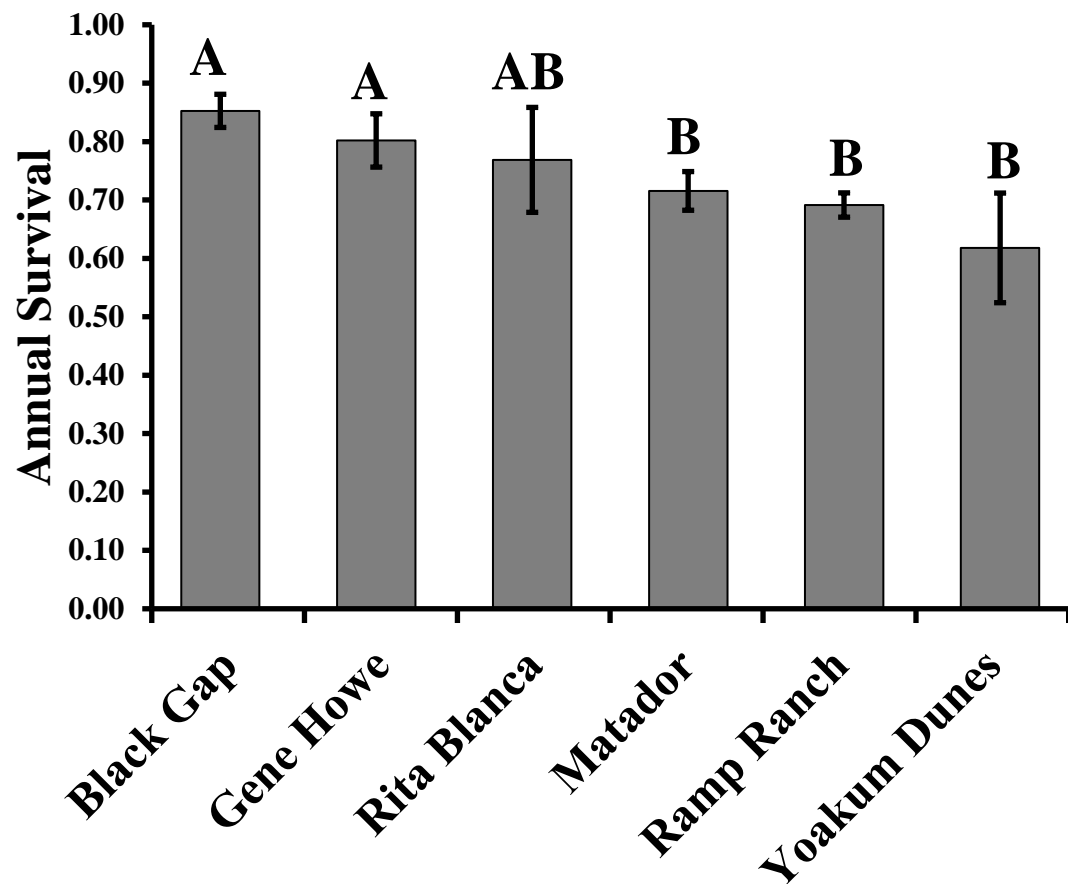
Figure 15. Relationship between clutch size and annual survival for 5 yellow mud turtle populations in Texas, 2006-2019 (n = 113; F_4 = 0.582; p = 0.501).
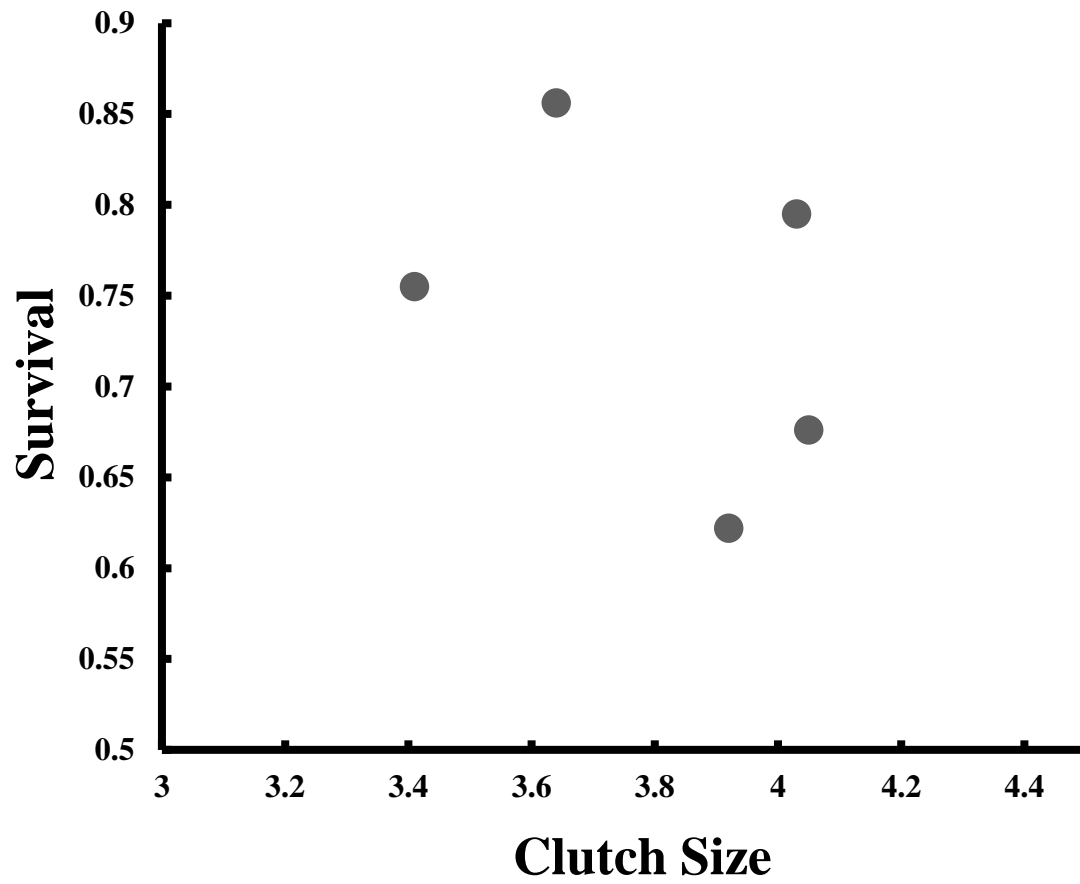
Figure 16. Relationship between egg volume and annual survival for 5 yellow mud turtle populations in Texas, 2006-2019 (n = 113; F_4 = 0.315; p = 0.614).
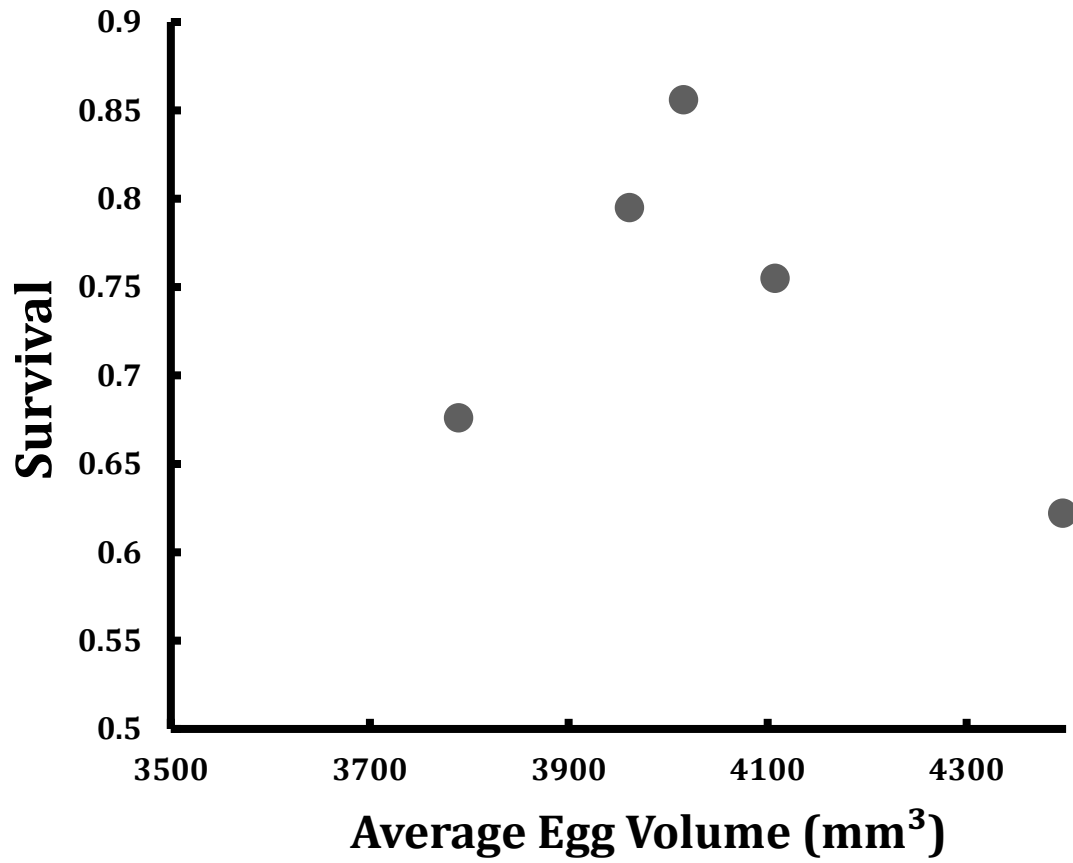
Figure 17. Relationship between clutch volume and annual survival for 5 yellow mud turtle populations in Texas, 2006-2019 (n = 113; F_4 = 1.935; p = 0.258).