

ORNATE BOX TURTLE (*TERRAPENE ORNATA*)  
DEMOGRAPHY IN NORTHERN ILLINOIS

BY

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THESIS

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## ABSTRACT

Demographic studies of wildlife populations are needed to guide management decisions for threatened species. Without data on population vital rates, decisions are often speculative and based on general information about a species rather than at the population level. The Ornate Box Turtle (*Terrapene ornata*) is a threatened species in Illinois and lacks essential demographic data. Over the last two centuries, nearly all Illinois prairie has been converted to agriculture, and consequently, Ornate Box Turtles are now confined to small isolated habitat fragments. Despite their threatened status and patchy Illinois distribution, we understand little about the demography of remaining populations. I collected population vital rates and projected persistence for two Ornate Box Turtle populations in northern Illinois. I estimated reproductive output by radiographing female turtles, and of the 70 females radiographed, 28 had visible eggs. Clutch size ranged from 1 to 6 eggs, with a mean of 2.53 at Ayers Sand Prairie and 4.20 at Nachusa Grasslands. To estimate annual survival, I conducted capture-mark-recapture surveys. Annual apparent survival was 0.970 at Ayers Sand Prairie and 0.860 at Nachusa Grasslands. Matrix population models showed the Ayers Sand Prairie population as stable, whereas the Nachusa Grasslands population was in decline. Population growth was most sensitive to adult survival. My results highlight the importance of long-term demographic studies for threatened species and show protecting adult female Ornate Box Turtles is critical for ensuring populations continue to persist in Illinois.

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## TABLE OF CONTENTS

|                                                                   |    |
|-------------------------------------------------------------------|----|
| CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW.....                | 1  |
| CHAPTER 2: REPRODUCTIVE OUTPUT.....                               | 10 |
| CHAPTER 3: STAGE-BASED DEMOGRAPHIC ANALYSIS .....                 | 33 |
| CHAPTER 4: SUMMARY AND CONSERVATION IMPLICATIONS .....            | 58 |
| REFERENCES .....                                                  | 64 |
| APPENDIX A: RADIOGRAPH DATA .....                                 | 85 |
| APPENDIX B: REPORTED DEMOGRAPHIC TRAITS IN THE LITERATURE.....    | 87 |
| APPENDIX C: JUSTIFICATION OF PARAMETERS USED IN PROJECTIONS ..... | 89 |

## **CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW**

Wildlife populations are declining at alarming rates, with conservative estimates suggesting nearly a third of terrestrial vertebrate species are decreasing in abundance and range (Dirzo et al. 2014; Ceballos et al. 2017). Causes of decline are synergistic and include habitat loss, overexploitation, invasive species, disease emergence, pollution, and climate change (Brook et al. 2008). Addressing threats to prevent extinction requires intensified conservation efforts, not only protecting habitat and restoring ecosystems but also focused at the species level (Brooks et al. 2004; Sutherland et al. 2009). Of equal importance to preventing species extinction is reversing population declines and ensuring high population diversity within species (Hughes et al. 1997). Conservation action is urgently needed to address declining wildlife populations and preserve Earth's vital ecological systems.

Planning species recovery and enacting effective conservation action requires knowledge of the demographic traits shaping wildlife populations (Morris et al. 2002). Birth and death rates, sex ratio, fecundity, and abundance are the fundamental demographic characteristics determining the trajectory of wildlife populations. Abundance, an estimate of how many individuals there are in a population, is at the core of making conservation decisions for threatened species (Mills 2006). Tracking abundance through time provides estimates of population growth needed for determining if wildlife populations are stable, growing, or declining (Garber and Burger 1995). Such information is crucial to enacting conservation programs in time to reverse negative population growth before extirpation and eventual species extinction.

Although abundance is the primary metric wildlife managers are interested in, conducting a census to directly measure the number of individuals can be impossible. Instead, researchers and wildlife managers use vital rates such as birth and death rates to calculate abundance and

estimate population growth (Resit Akçakaya et al. 1999). The change in a population size equals the number of births and immigrants minus the number of deaths and emigrants (Mills 2006). Fecundity is used for birth rate, calculated by taking the number of surviving offspring produced in a discrete period and dividing it by the number of potential reproductive females in the population. Mortality is used for death rate, but instead of attempting to determine which individuals die in a population, the reciprocal of mortality, survival, is more easily collected in the field and better used for calculating abundance (Mills 2006). More realistic (and complex) estimates of abundance consider immigration and emigration rates.

However, vital rates are not often available because they are labor intensive and logistically challenging to collect. For instance, estimating annual survival through capture-mark-recapture methods requires at least three years (and often more to improve precision) of sampling (Beissinger et al. 1998; Schmidt et al. 2002). Further, estimating population growth from vital rates to detect declines can require field studies lasting decades, especially for long-lived species with low recruitment (Coulson et al. 2001; East et al. 2013). Natural fluctuations in population size are easily mistaken for positive or negative growth rates when researchers conduct studies over shorter terms (Meyer et al. 1998). Additionally, fecundity and survival rates for wildlife populations vary with age or life stage, though sampling all life stages adequately is often difficult. Despite these challenges, monitoring fecundity and survival is often the only way to observe population trends and project population persistence.

Demographic studies of turtles and tortoises are sorely needed because chelonians are one of the most highly threatened vertebrate groups (Lovich et al. 2018). More than half of all turtle and tortoise species face extinction, with overexploitation and habitat loss heralded as the greatest threats (Todd et al. 2010; Mittermeier et al. 2015). Successful conservation requires

quality data on population vital rates to assess the impacts of management scenarios and evaluate proposed actions. For example, demographic analyses have shown commonly used turtle conservation measures such as head-starting may not be effective when adult survival is suppressed (Frazer 1992; Heppell and Crowder 1996). Without adequate demographic data, it is impossible to conduct analyses to guide conservation decisions for declining turtle populations.

While there is a pressing need for studying turtle demography, age- or stage-specific vital rates are only available for a small portion of the more than 300 turtle and tortoise species. Previous studies have identified adult survival as the vital rate managers should target to stabilize declining turtle populations (Congdon et al. 1994; Heppell 1998), but general recommendations may not fit the life history pattern of all turtle species or demography of all populations. Additionally, there is variation in vital rates within species between populations (Frederiksen et al. 2005), so using estimates of survival or fecundity from one site as surrogates for another can misinform conservation.

The Ornate Box Turtle (*Terrapene ornata*) is a species in need of increased conservation attention. It is a member of the pond turtle family Emydidae and one of four species in the genus *Terrapene* (Minx 1996; Spinks et al. 2016). Three of four *Terrapene* species are polytypic and recent molecular work suggests several subspecies constitute a genetically distinct fifth species (Martin et al. 2013), though scholars continue to debate its validity (Fritz and Havaš 2014; Martin et al. 2014). All box turtles can close their shell into a well-sealed box when threatened, hence their common name (Dodd 2001). There are two morphologically distinct *T. ornata* subspecies. The Desert Box Turtle, *T. o. luteola*, has at least nine lines radiating from the center of carapacial scutes, whereas the Ornate Box Turtle, *T. o. ornata*, usually has between five and nine (Dodd 2001; Fig. 1.1). Despite the differences in pattern, there is no evidence to support a

phylogenetic distinction between *T. o. ornata* and *T. o. luteola* (Herrmann and Rosen 2009; Martin et al. 2013). Only *T. o. ornata* occurs in Illinois, though it hybridizes with the Eastern Box Turtle (*T. c. carolina*) at several sites in the state (Smith 1955).

Legler (1960) provides the most comprehensive account of Ornate Box Turtle natural history, noting the prairies of Nebraska, Kansas, Oklahoma, and Texas as optimum habitat. The species has a wide distribution beyond its core range in the Great Plains, with populations extending northeast into Wisconsin and Indiana, south to Louisiana, and west to Arizona and Sonora, Mexico (Fig. 1.2). In Illinois, Ornate Box Turtles have a patchy distribution, occurring in northern sand prairies but also at sites in the southern till plains and west along the Illinois River (Fig. 1.3). Their disjunct distribution has been called “one of the most peculiar distributional patterns of all Illinois reptiles” (Smith 1961).

Despite historical records throughout Illinois, presently there are few sites where you can readily encounter Ornate Box Turtles. Some Illinois populations likely now consist of a very few old individuals with low to no recruitment rather than viable populations. Such populations are an example of delayed extinction, where there is a time lag in the disappearance of a species following rapid environmental change due to the life history traits of the species (Kuussaari et al. 2009). In the case of Ornate Box Turtles, their long lifespan and lengthy generation time could result in old adults persisting on the landscape at sites with inadequate or no recruitment, giving the false impression of viable populations (Redder et al. 2006).

There have been several notable conservation efforts and research projects directed toward Ornate Box Turtles in Illinois. Populations in the Upper Mississippi River National Wildlife and Fish Refuge in the northwest part of the state have received the most attention. There, Lincoln Park Zoo, Niabi Zoo, and the U.S. Fish and Wildlife Service collaborated on a

head-starting program to reinforce a declining population on a decommissioned military base (Sievers 2015; Strickland et al. 2018). The military base, along with nearby remnant prairies within the larger wildlife refuge, has also served for research on Ornate Box Turtle reproduction (Tucker et al. 2014; 2017), activity and home range (Refsnider et al. 2012; Tucker et al. 2015), genetic diversity (Kuo and Janzen 2004), and the effects of habitat alteration (Mitchell et al. 2016). Two valuable studies have also examined Ornate Box Turtle demography within the refuge (Bowen et al. 2004; Refsnider et al. 2011). Only a single published study has been carried out elsewhere in Illinois, focusing on hibernation (Milanovich et al. 2017). Given their threatened status together with the lack of demographic data on most Illinois populations, there is a pressing need for conducting demographic studies to learn the status of other populations.

Two of the best-known Illinois sites still supporting populations of Ornate Box Turtles are Ayers Sand Prairie in Carroll County and Nachusa Grasslands in Lee and Ogle Counties. Ayers Sand Prairie is 44 ha of original sand prairie and blowout habitat managed by the Illinois Nature Preserves Commission. Nachusa Grasslands consists of more than 1,200 ha of restored and remnant prairie, woodlands, and wetlands managed by The Nature Conservancy (Fig. 1.4). Both sites are known for their Ornate Box Turtles, but until now, researchers have not conducted demographic studies to assess the status of each population. Herein, I provide results from a demographic study on Ornate Box Turtle populations at Ayers Sand Prairie and Nachusa Grasslands, along with baseline data from five additional sites throughout Illinois.

## Figures

Fig. 1.1. Ornate Box Turtles (*Terrapene ornata ornata*) are characterized by a pattern of five to nine yellow lines radiating from each carapical scute. There is individual variation within populations, and the turtles below exemplify the intrapopulation variability.



Fig. 1.2. Distribution of the Ornate Box Turtle adapted from Dodd 2001, Redder et al. 2006, and Martin et al. 2013.



Fig. 1.3. Confirmed records of Ornate Box Turtles in Illinois. Dots represent vouchered specimens in the Illinois Natural History Survey database. Gray dots are records before the year 2000, and black dots are between 2000 and 2018.

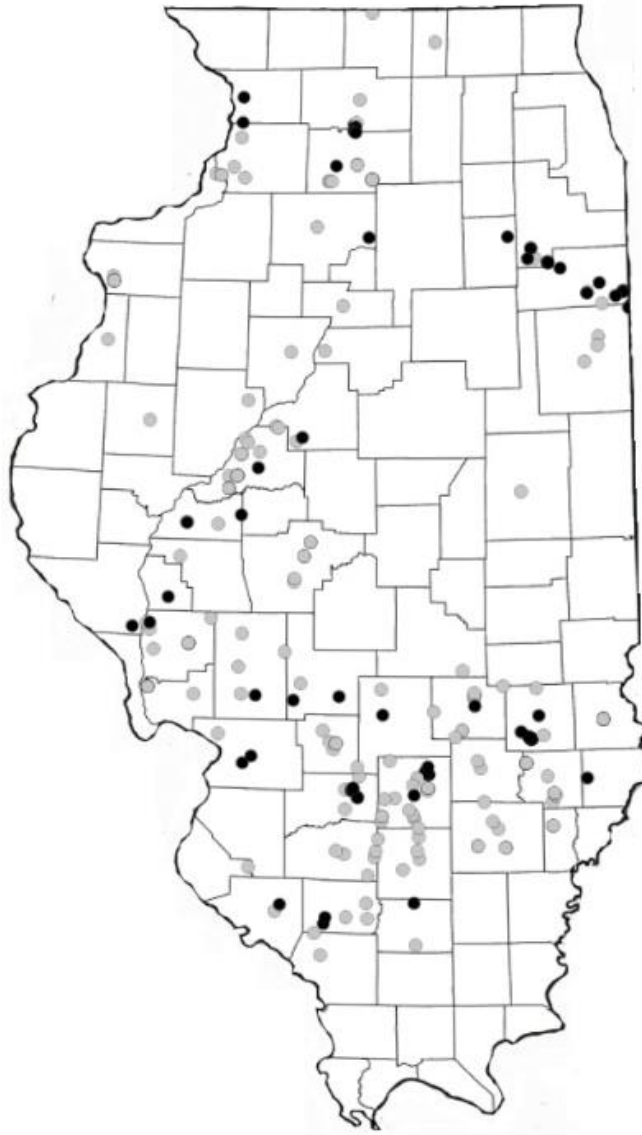


Fig. 1.4. Typical Ornate Box Turtle habitat at Nachusa Grasslands, which was one of two focal sites for the research project.



## CHAPTER 2: REPRODUCTIVE OUTPUT

### Introduction

Over half of all turtle and tortoise species are threatened with extinction, making chelonians one of the most threatened vertebrate groups (Lovich et al. 2018). Enacting conservation measures to address threats and prevent extinction often requires information about a species' reproductive biology (Cree 1994; Hamann et al. 2010), yet our knowledge of reproduction in most turtle and tortoise species is incomplete. Even in species where basic reproductive information exists, clutch size and frequency can vary clinally, making population-level data valuable (*e.g.*, Tinkle 1961; Christiansen and Moll 1973; Litzgus and Mousseau 2006; Hedrick et al. 2018). Without estimates of reproductive output, it is impossible to project population persistence under varying management scenarios to inform conservation decisions.

Fecundity is a measure of the number of offspring produced per individual in a discrete period (Mills 2006). For chelonians, calculating fecundity involves clutch size as well as frequency, which are determined from the proportion of gravid females in the population and number of clutches produced each breeding season (Gibbons et al. 1982; Frazer 1984). Nest success, adult female survival, and sex ratio at birth also factor into calculating the average number of female offspring an adult female contributes to a population. Researchers then use fecundity with survival estimates to examine population growth. For most turtles and tortoises, however, we lack crucial data on population vital rates like fecundity (Ernst and Lovich 2009).

When female turtles invest resources in producing eggs, less energy is available for growth. For organisms like reptiles with indeterminate growth, investing energy in reproduction could be costly when fecundity is positively associated with clutch size (Reznick 1985). One

way to study the tradeoff between growth and reproduction in chelonians is by focusing on the relationship between body size and clutch size. The body size/clutch size relationship can explain why larger female turtles produce more eggs in some populations and not others, revealing life history constraints shaping selection patterns. However, the relationship between body size and clutch size can differ between species and populations (Shine and Greer 1991; Iverson et al. 2019) or can be absent altogether (Broderick et al. 2003; Litzgus and Mousseau 2006). There are also latitudinal effects on growth and reproduction. Notably, clutch size increases while breeding frequency decreases at higher latitudes due to shorter nesting seasons and fewer available resources (Iverson 1992).

Reproductive output increases with female body size in most turtle species studied (Iverson et al. 2019). The greater internal volume of larger shells is thought to allow for a greater number of eggs (Dodd 1997). Absent data on internal shell volume, researchers traditionally use other morphometric traits such as carapace and plastron length as proxies (*e.g.*, Gibbons et al. 1982; Ryan and Lindeman 2007; Naimi et al. 2012), but other estimates could be more suitable. For example, by using carapace length, height, and width, the volume of the shell can be approximated with a modified formula for the volume of an ellipsoid (Loehr et al. 2004; Zuffi and Foschi 2015). Alternatively, King (2000) outlines the advantages of using the allometric coefficient from log-transformed data, especially because it allows for interspecific comparisons. Multivariate statistical approaches are also well suited for approximating the size and shape of chelonians (Jolicoeur and Mosimann 1960; Somers 1986; Lutterschmidt et al. 2007), but until now, they have not been used to investigate a relationship to clutch size.

I studied female Ornate Box Turtles (*Terrapene ornata ornata*) in Illinois to (1) learn the average clutch size and proportion of gravid females; (2) determine the relationship between

clutch size and body size; and (3) find the metric of body size best explaining clutch size. I also compiled clutch size data on *T. ornata* from literature and investigated latitudinal effects on reproductive output. As a threatened species in Illinois (Illinois Endangered Species Protection Board 2015), population-level data about reproductive output is valuable for conservation managers because they can be used to determine the viability of remaining isolated populations. Although clutch size is known for populations in Kansas (Brumwell 1940; Legler 1960), Nebraska (Converse 1999; Converse et al. 2002), New Mexico (Nieuwolt-Dacanay 1997; Germano 2014), South Dakota (Quinn et al. 2014), and Wisconsin (Doroff and Keith 1990), there are no published data for populations in Illinois. My results provide the first estimates of reproductive output for Ornate Box Turtles at the northeastern edge of their distribution, a part of their range where the species is declining.

## **Materials and Methods**

### *Study Sites*

I studied Ornate Box Turtles intensively at Ayers Sand Prairie and Nachusa Grasslands in northern Illinois. Surveys took place May–June 2018 and 2019. In 2019, I also collected data on turtles from five additional sites in the state where site managers had females with attached radio-transmitters, resulting in seven study sites of remnant prairie throughout five counties in northwest and east-central Illinois (Fig. 2.1).

## *Surveys and Morphological Data*

I located turtles using visual encounter surveys, wildlife detector dogs, and radio-telemetry. Wildlife detector dogs are highly effective at locating box turtles (Kapfer et al. 2012; Boers et al. 2017) but were not available for use at all sites during the limited window between egg calcification and nesting. For this reason, I attached radio-transmitters from Holohil Systems to 18 females located by dogs in early May 2019 and then relocated them at the end of the month when eggs were more likely to be calcified. I also surveyed sites visually during the last two weeks of May and first week of June. I carried out visual encounter surveys during May and June based on Tucker et al. (2014), who noted Ornate Box Turtles nesting in northern Illinois between 8 June and 20 June.

When I located a turtle, I recorded the location with GPS and then held it overnight in a plastic box for either radiography the following day or to attach a radio-transmitter for future location. I assigned each turtle a unique ID by marking marginal scutes as outlined by Cagle (1939) and then measured carapace length, carapace width, and shell height to the nearest mm using forestry calipers. I measured the left pectoral scute height along the midline to the nearest 0.1 mm with digital calipers. Lastly, I calculated plastron length by summing anterior plastral lobe length and posterior plastral lobe length measured to the nearest 0.1 mm.

## *Radiography*

I brought turtles to local veterinary clinics near study sites for radiographs, which is a safe method to determine clutch size in chelonians (Gibbons and Greene 1979; Hinton et al. 1997). I placed turtles with plastron facing up to help immobilize them while radiographing up to

five per plate. I noted the locations of individuals on the plate and recorded ID's of each turtle before each radiograph. Veterinarians exposed turtles at 150 mA for 1/20 to 1/10 of a second at 62–65 kV. I examined digital images of radiographs to determine if females were gravid and, if so, their clutch sizes (Fig. 2.2).

### *Statistical Analyses*

To assess the accuracy of clutch size estimates, I randomly sampled with replacement (bootstrapped) the dataset from the largest site-specific sample (Ayers Sand Prairie). I used 1000 bootstrap replicates for each sample size, beginning with two in increments of one until maximum  $n = 17$  and calculated 95% confidence intervals around the bootstrapped estimate. I then compared the relationship between sample size and the bootstrapped estimate by calculating summary statistics of clutch size for each site and comparing the bootstrap estimate to the mean clutch size from Ayers Sand Prairie.

I used linear regression to assess the effect of body size on clutch size. Various morphometrics are commonly used as an approximation for turtle body size in such analyses. Therefore, to determine the best model explaining clutch size I used an information theoretic approach, comparing models with various morphometric traits. To do so, I performed a principal component analysis (PCA) using measurements from 164 female Ornate Box Turtles from the study sites. The measurements used in the PCA were carapace length, carapace width, shell height, anterior plastron length, posterior plastron length, and left pectoral scute height. The Kaiser-Meyer-Olkin test of sampling adequacy and Bartlett's test of sphericity suggested a PCA was appropriate for the morphometric data ( $KMO = 0.90$ ;  $\chi^2 = 993.38$ ,  $df = 15$ ,  $P < 0.001$ ). Using PCA, I identified a single multivariate approximation of size (PC1), explaining 78% of the

variation (Table 2.1). I then developed a set of candidate linear models explaining clutch size in 25 gravid individuals using the explanatory variables of either PC1, individual and additive morphometrics, or shell volume estimated as half the volume of an ellipsoid:

$$Shell\ Volume = \left( \frac{4}{3} * \pi * CL * CW * SH \right) / 2$$

I centered and scaled morphometric data before analysis. Homoscedasticity was assessed by examining plots of residuals versus fitted values and the assumption of normality with QQ plots. Log-transformation, as proposed by King (2000), did not improve model fit. However, to allow the results to be comparable to other species and populations, I also log-transformed data for carapace and plastron length models and report the allometric coefficient. I used Akaike's information criterion adjusted for small sample size ( $AIC_c$ ) to determine the most parsimonious model in the set with package `AICcmodavg` (Mazerolle and Linden 2019). All statistical analyses were performed in R (R Core Team 2019).

To investigate the relationship between latitude and clutch size, I used linear regression. First, I compiled clutch size data from all published accounts for *T. ornata* and then recorded latitude in decimal degrees of study locations (Table 2.2). The relationship did not appear linear so I log-transformed both variables. Additionally, one of the study sites (Ayers Sand Prairie) appeared to be an outlier, and so I performed regression both with and without the site. I then back-transformed model predictions for interpretation and plotting, providing estimates of clutch size throughout the latitudinal range of the species.

## Results

### *Clutch Size and Proportion Gravid*

Mean clutch size at Ayers Sand Prairie was 2.53 (95% CI: 2.08–2.98; range, 1–4;  $n = 17$ ) and at Nachusa Grasslands was 4.20 (95% CI: 2.58–5.82; range, 3–6;  $n = 5$ ; Table 2.3). Two individuals at Lost Mound were gravid with 3 eggs each, one individual from Green River was gravid with 2 eggs, and one individual at Kankakee Sands was gravid with 4 eggs (Table 2.3). No individuals sampled from Prairie Ridge or the Richardson Wildlife Foundation were gravid. The bootstrap estimates from Ayers Sand Prairie show accuracy increasing only slightly with sample size (Fig. 2.3). Across sites and years, I found 40.0% (28 of 70) of the females were gravid. At Ayers Sand Prairie, 63.3% (19 of 30) were gravid compared to 25% (5 of 20) at Nachusa Grasslands. In 2018, 54.5% (12 of 22) were gravid compared to 33.3% (16 of 48) in 2019. Two gravid females radiographed twice in 2018 laid eggs between the radiograph sessions, so the true proportion of gravidity is higher.

### *Body Size Clutch Size Relationship*

I found evidence of a fecundity advantage where larger females produced larger clutches (Fig. 2.4–2.6). The top model showed clutch sizes depended on the multivariate body size component with clutch size increasing at less than the isometric rate with the body size component (Table 2.4). Models with shell volume and univariate components all ranked better than the null. Adjusted  $r^2$  showed no model accounted for more than 29% of clutch size variation. For the top model,  $\beta_{PC1}$  was 0.29 (95% CI: 0.12–0.47) and  $\beta_{Intercept}$  was 2.90 (95% CI: 2.53–3.27). The allometric coefficient from log-transformed regression was 2.54 for carapace

length and 2.57 for plastron length, suggesting clutch size increases as a cubic function of length. The smallest gravid female (1 egg) had a carapace length of 96 mm, and the largest gravid female (6 eggs) had a carapace length of 126 mm.

### *Latitudinal Variation in Clutch Size*

Linear regression showed Ornate Box Turtles at northern latitudes produced larger clutches (Fig. 2.7). Although the relationship was weak when including all sites in analysis ( $r^2=0.05$ ), after removing Ayers Sand Prairie where clutch size is unusually small for a population at such a high latitude (discussed below), the  $r^2=0.37$ . Across the species range, the predicted average clutch size of populations at 28° latitude was 2.1 eggs (95% CI: 1.2–4.1), and at 44° latitude was 4.2 eggs (95% CI: 3.3–5.3).

## **Discussion**

Reproductive output is influenced by somatic growth because of the positive relationship between body size and clutch size (Congdon and van Loben Sels 1991). Larger clutches at Nachusa Grasslands suggest turtles are either on average older and consequently larger or, more likely, growth patterns differ between sites. For example, turtles at Ayers Sand Prairie may grow more slowly or for a shorter duration and thus mature at smaller sizes, resulting in smaller clutches. Such growth patterns causing variation in size at maturity are known in other chelonians (*e.g.*, Congdon and Gibbons 1983; Rowe 1997; Willemsen and Hailey 1999). Disentangling the relationship between clutch size and growth will require additional research, for example by studying how food resources differ between sites, especially for juveniles when

growth rate is fastest. Additionally, because somatic growth in turtles appears density-dependent (Bjorndal et al. 2000), small body size and clutch size at Ayers Sand Prairie could reflect a population near carrying capacity.

Iverson (1992) showed clutch frequency in turtles has an inverse relationship with latitude. Latitudinal patterns of clutch frequency are due to a restricted nesting season in colder climates (Gibbons 1983). Because Illinois spans a large latitudinal gradient, populations could exhibit a similar pattern across the state. Although Ornate Box Turtles can produce two clutches per year in Kansas and Nebraska (Legler 1960; Converse 1999), double clutches have not been observed further north in Wisconsin (Doroff and Keith 1990). I did not radiograph females later than 11 June and consequently was unable to detect if multiple clutches occurred. However, I expect lower clutch frequency than populations in Nebraska or Kansas because of the reduced activity period in Illinois. Still, it would be useful to repeatedly radiograph a sample of females throughout the summer in Illinois to determine if double clutches are possible and, if so, the frequency females double clutch, especially for southern populations.

While clutch frequency decreases at higher latitudes, the opposite is true of clutch size (Iverson et al. 1993). Indeed, I identified clutch size increasing with latitude in Ornate Box Turtles, with latitude explaining 37% of the variation in mean clutch sizes reported in literature. That said, latitude accounted for only 5% of variation in clutch size when including an apparent outlier, Ayers Sand Prairie, in the regression. The Ayers Sand Prairie population is likely an extreme case where resource acquisition abnormally affects growth and reproduction. The mean clutch size is 2.5 eggs at Ayers Sand Prairie, which is smaller than all other *T. o. ornata* populations studied thus far. Only a population of the western subspecies *T. o. luteola* in New Mexico produces comparably small clutches (Nieuwolt-Dacanay 1997; Germano 2014). I

recommend continued research at Ayers Sand Prairie to determine the underlying mechanisms driving the small clutch size there.

My estimate of the proportion of gravid females should be interpreted with the caveat that it is the minimum. In 2018, two gravid females had eggs when initially radiographed but not when radiographed one week later, therefore turtles were nesting as early as 24–31 May 2018. As a result, in 2019, I chose to radiograph turtles earlier; however, eggs may not have been calcified and visible on the earliest radiographs. Tucker et al. (2014) found 66.7% of monitored females (12 of 18) nested at a site in northwest Illinois. In Wisconsin, 50–63% of females were gravid (Doroff and Keith 1990) and in South Dakota, 64% were gravid (Quinn et al. 2014). For *T. o. luteola* in New Mexico, 31.3–44.4% (Germano 2014), and 58.1% of females were gravid (Nieuwolt-Dacanay 1997). My results show at least 33.3–54.5% of females were gravid in Illinois, but the true proportion of gravid females is likely higher.

Although linear models showed larger turtles produce larger clutches, body size explained only part of clutch size variance. The results agree with Nieuwolt-Dacanay (1997) and Germano (2014), who also found a weak positive relationship between body size and clutch size in *T. o. luteola*. Although body size explained more variation than in some populations of the Eastern Box Turtle (*T. c. carolina*), where there appears to be no relationship (Congdon and Gibbons 1985; Burke and Capitano 2011), it is not strong enough to suggest a large growth-reproduction tradeoff. Such a tradeoff may be absent if clutch size is only weakly explained by female body size. What factors contributed to the observed but unaccounted for variance in clutch size? For example, how does clutch size vary with habitat use or quality? Clutch size depends not only on body size but also on abiotic conditions (Wilkinson and Gibbons 2005). Similarly, does body condition relate to clutch size? Spotted turtles (*Clemmys guttata*) with high

energy reserves produce larger eggs, though not larger clutches (Litzgus et al. 2008). Given that body size is only one factor affecting clutch size, further work is needed to parse out how abiotic and energetic factors relate to reproductive output.

Researchers use various size measurements to explore the relationship between body size and clutch size in chelonians. Often carapace length and plastron length are analyzed, and my results show both are adequate for approximating clutch size in Ornate Box Turtles. However, other approximations of body size may perform better. For a population of Eastern Box Turtles in Virginia, carapace width and shell height explained clutch size, whereas carapace length did not (Wilson and Ernst 2005). In European Pond Turtles, shell height was a better predictor of clutch size than either carapace length or width (Zuffi et al. 1999). The top model in my study showed the multivariate size component PC1 as the best explanatory variable, which was composed of carapace length, carapace width, shell height, plastron length, and left pectoral scute height. When reducing morphometric variables to principal components, PC1 typically represents body size, and PC2 represents body shape and random variation (Somers 1986). Measuring shell angles or other aspects of shell shape could produce a PC2 useful for analyses of body size, growth, and reproductive output. Future studies of growth and reproduction in chelonians should use multivariate approximations of body size when ample morphometric data are available.

I determined Ornate Box Turtle reproductive output in Illinois varied between populations and discovered evidence of a body size/clutch size relationship. Wildlife managers can use the data presented here on clutch size and frequency to calculate fecundity and, along with estimates of survival, project population persistence and viability. I also demonstrated that larger female Ornate Box Turtles produce larger clutches and clutch size increases with latitude,

both of which are common features in turtle populations (Christiansen and Moll 1973; Iverson et al. 1993; 2019). Because body size only accounted for part of observed clutch size variance, there is little support for a growth-reproduction tradeoff in Ornate Box Turtles. Still, considering the disparity in mean clutch size and body size of populations in this study, results warrant further research into the relationship between growth and reproduction.

## Tables and Figures

Table 2.1. Results of a principal component analysis on Ornate Box Turtle (*Terrapene ornata*) morphometric traits. Only PC1 had an eigenvalue > 1 and so I used it for further analyses comparing models explaining clutch size by body size.

|                                | PC1         | PC2   | PC3                  | PC4   | PC5   | PC6   |
|--------------------------------|-------------|-------|----------------------|-------|-------|-------|
| Eigenvalue                     | 4.685       | 0.522 | 0.334                | 0.253 | 0.132 | 0.074 |
| Standard deviation             | 2.164       | 0.722 | 0.578                | 0.503 | 0.363 | 0.272 |
| Proportion of variance         | 0.781       | 0.087 | 0.056                | 0.042 | 0.022 | 0.012 |
| Cumulative proportion variance | 0.781       | 0.868 | 0.923                | 0.966 | 0.988 | 1.000 |
| Variable                       | PC1 Loading |       | PC1 Varimax rotation |       |       |       |
| Carapace length                | 0.437       |       | 0.431                |       |       |       |
| Posterior plastron length      | 0.431       |       | -0.188               |       |       |       |
| Anterior plastron length       | 0.436       |       | -0.071               |       |       |       |
| Shell height                   | 0.396       |       | -0.427               |       |       |       |
| Left pectoral scute height     | 0.347       |       | 0.575                |       |       |       |
| Carapace width                 | 0.395       |       | 0.511                |       |       |       |

Table 2.2. Clutch sizes for *Terrapene ornata* populations reported in literature. All refer to *T. o. ornata* except for studies carried out in New Mexico, which refer to *T. o. luteola*. *n* is the number of turtles sampled in the study.

| Location     | Mean | Range   | <i>n</i> | Latitude | Source                |
|--------------|------|---------|----------|----------|-----------------------|
| New Mexico   | 2.7  | 1–4     | 77       | 34.3     | Nieuwolt-Dacanay 1997 |
| New Mexico   | 2.9  | 1–5     | 39       | 34.3     | Germano 2014          |
| Kansas       | 4.7  | 2–8     | 23       | 39.1     | Legler 1960           |
| Nebraska     | 2.6  | 2–4     | 5        | 41.8     | Converse et al. 2002  |
| Nebraska     | 3.4  | 2–6     | 35       | 41.8     | Converse 1999         |
| Illinois     | 4.2  | 3–6     | 5        | 41.9     | Present study         |
| Illinois     | 2.5  | 1–4     | 17       | 42.1     | Present study         |
| Wisconsin    | 3.5  | Max = 7 | 21       | 43.2     | Doroff and Keith 1990 |
| South Dakota | 4.3  | 2–5     | 7        | 43.6     | Quinn et al. 2014     |

Table 2.3. Number of gravid and sampled female Ornate Box Turtles (*Terrapene ornata*) by site, year, and Illinois county. The percent gravid is a minimum because in 2018 at least one individual laid eggs during the sampling period and in 2019 eggs may not have been calcified in all turtles and fully visible in radiographs. Note 19 individuals were gravid at Ayers across both years but only 17 were included in further analyses because one individual did not have morphometric data, and another was gravid both years with 3 eggs (see Appendix A).

| Site          | County   | Year | # Sampled | # Gravid | Min. % Gravid |
|---------------|----------|------|-----------|----------|---------------|
| Ayers         | Carroll  | 2018 | 20        | 12       | 60%           |
| Ayers         | Carroll  | 2019 | 10        | 7        | 70%           |
| Green River   | Lee      | 2019 | 3         | 1        | 33%           |
| Kankakee      | Iroquois | 2019 | 5         | 1        | 20%           |
| Lost Mound    | Carroll  | 2019 | 6         | 2        | 33%           |
| Nachusa       | Ogle     | 2018 | 2         | 0        | 0%            |
| Nachusa       | Ogle     | 2019 | 18        | 5        | 28%           |
| Prairie Ridge | Jasper   | 2019 | 4         | 0        | 0%            |
| Richardson    | Lee      | 2019 | 2         | 0        | 0%            |
| Total         |          |      | 70        | 28       | 40%           |

Table 2.4. AIC<sub>c</sub> table of linear models explaining *Terrapene ornata* clutch size by body size. Results are sorted by  $\Delta\text{AIC}_c$ .  $K$  = number of parameters. PC1 = Principal Component 1, which is a multivariate body size component. CL = carapace length. PL = plastron length. CW = carapace width. SH = shell height.

| Model         | $K$ | AIC <sub>c</sub> | $\Delta\text{AIC}_c$ | $-2\ln(L)$ | Weight | $r^2$ |
|---------------|-----|------------------|----------------------|------------|--------|-------|
| Eggs~PC1      | 3   | 73.50            | 0.00                 | 66.36      | 0.37   | 0.29  |
| Eggs~Volume   | 3   | 75.53            | 2.03                 | 68.38      | 0.13   | 0.23  |
| Eggs~CL       | 3   | 75.57            | 2.07                 | 68.42      | 0.13   | 0.23  |
| Eggs~PL       | 3   | 75.96            | 2.46                 | 68.82      | 0.11   | 0.22  |
| Eggs~CW       | 3   | 76.70            | 3.19                 | 69.56      | 0.07   | 0.19  |
| Eggs~SH       | 3   | 77.00            | 3.50                 | 69.86      | 0.06   | 0.18  |
| Eggs~CL+SH    | 4   | 78.05            | 4.55                 | 68.06      | 0.04   | 0.21  |
| Eggs~PL+SH    | 4   | 78.41            | 4.91                 | 68.42      | 0.03   | 0.20  |
| Eggs~CW+SH    | 4   | 78.68            | 5.18                 | 68.68      | 0.03   | 0.19  |
| Null          | 2   | 80.58            | 7.07                 | 76.04      | 0.01   | -     |
| Eggs~CW+SH+CL | 5   | 81.21            | 7.70                 | 68.06      | 0.01   | 0.17  |
| Global        | 7   | 84.72            | 11.21                | 68.06      | 0.00   | 0.12  |

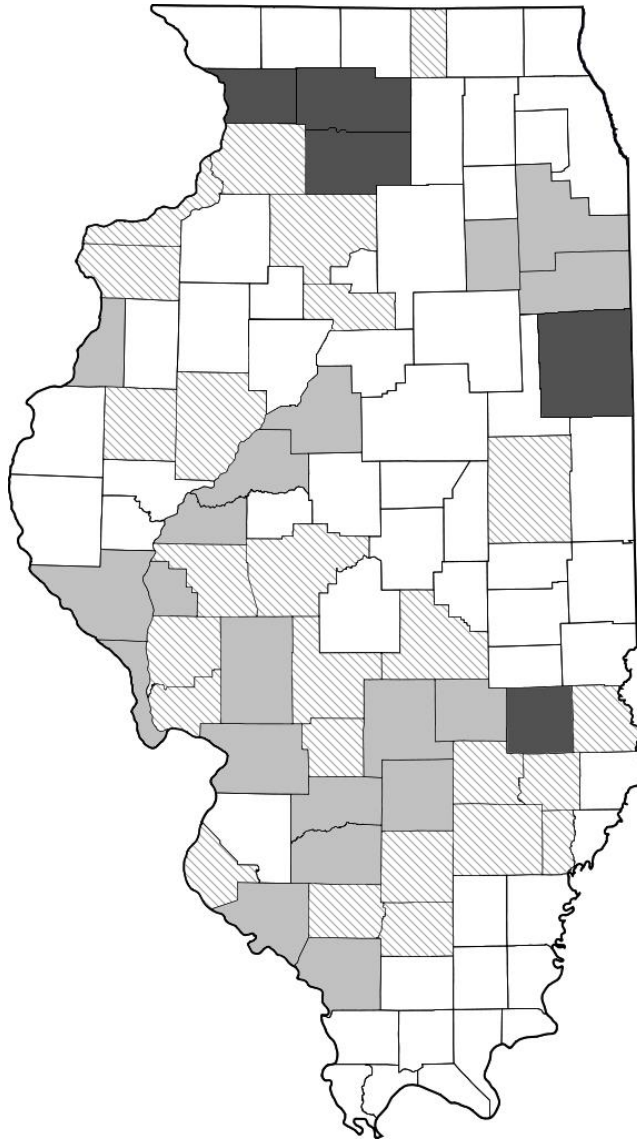


Fig 2.1. Ornate Box Turtle (*Terrapene ornata*) distribution in Illinois. Dark gray counties were sampled for the study. Light gray counties have records of occurrence after 1980. Hashed counties only have records pre-1980. Map adapted from the Illinois Natural History Survey (Available from [https://www.inhs.illinois.edu/collections/herps/data/ilspecies/te\\_ornata/](https://www.inhs.illinois.edu/collections/herps/data/ilspecies/te_ornata/). [Accessed 29 July 2019]).

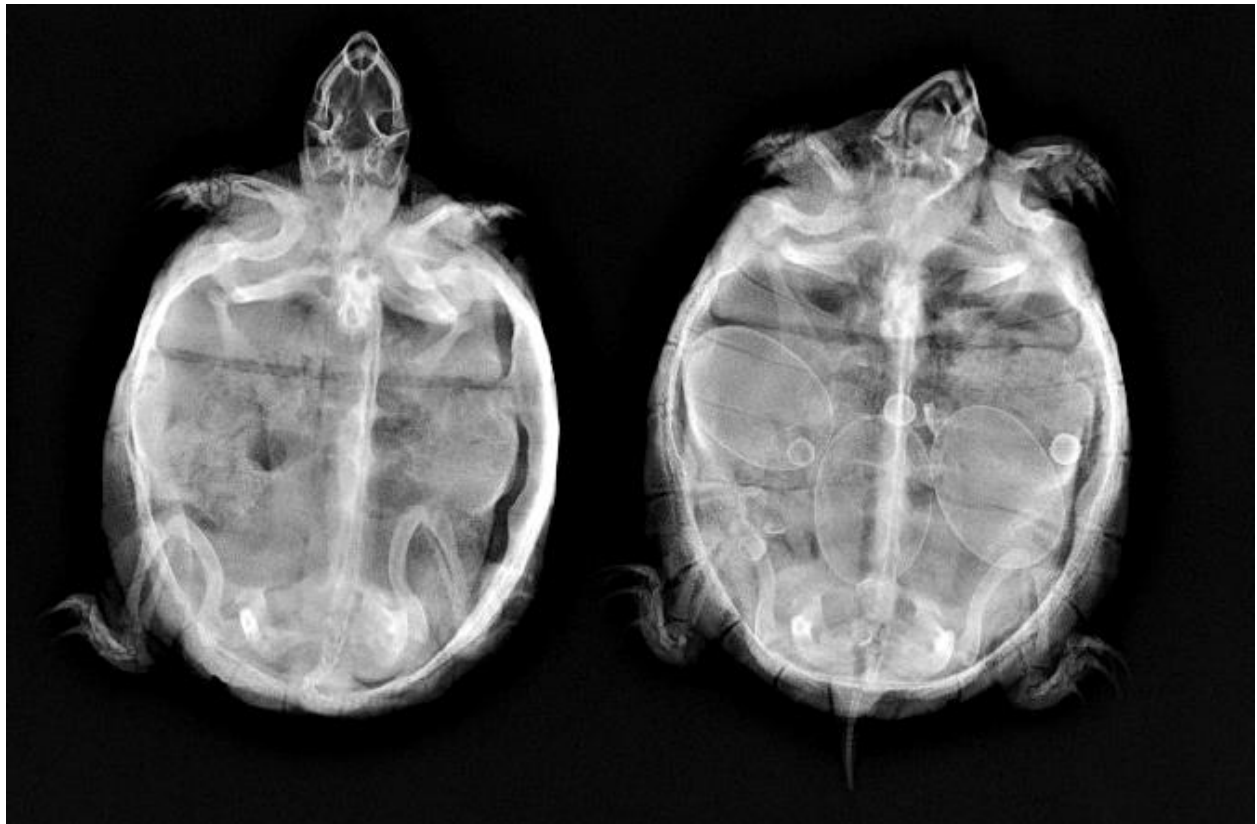


Fig. 2.2. Radiograph of Ornate Box Turtles (*Terrapene ornata*) from Ayers Sand Prairie, Illinois. The individual on the right is gravid with three eggs.

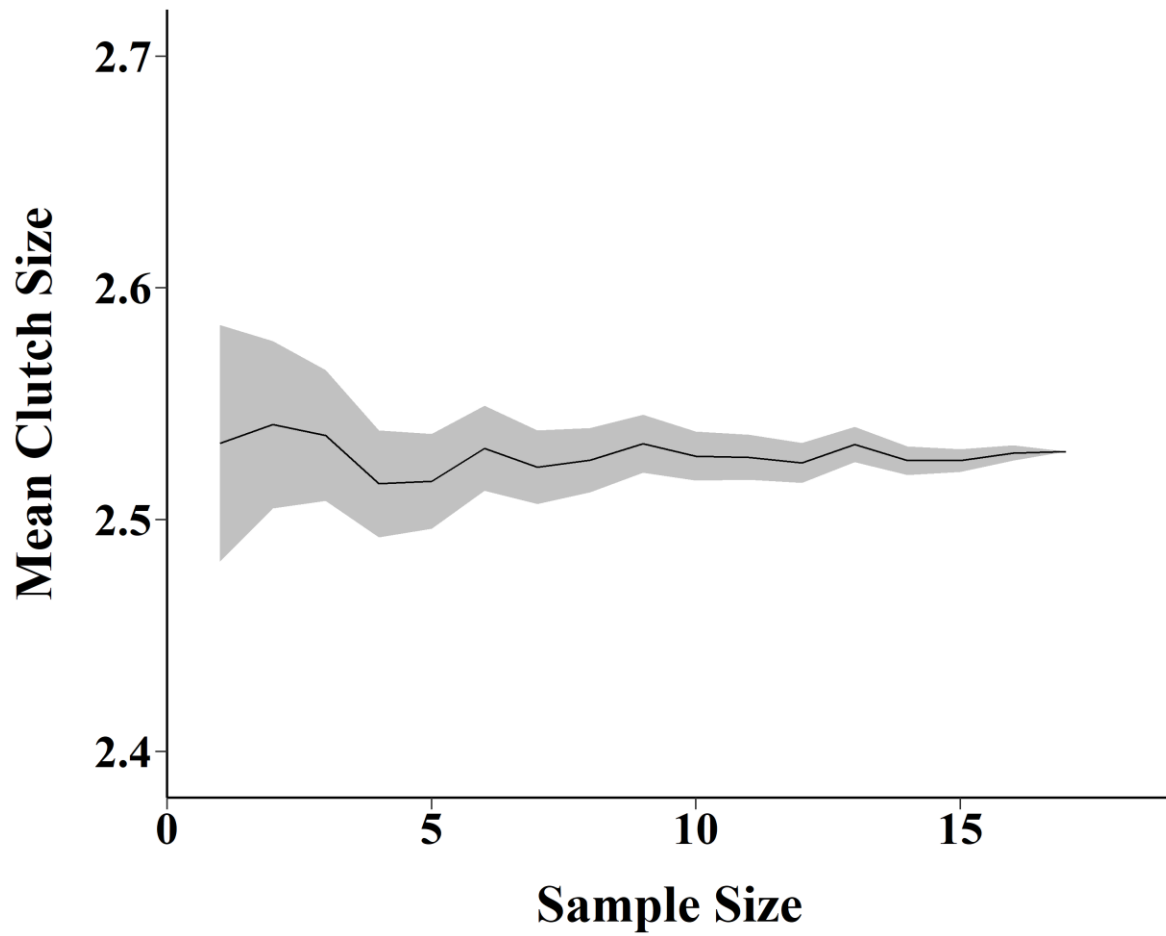


Fig 2.3. Bootstrap estimates of Ornate Box Turtle (*Terrapene ornata*) clutch size from Ayers Sand Prairie at different levels of  $n$  ranging from  $n = 2$  to  $n = 17$ . Shaded areas are 95% confidence intervals. Bootstrap replicates = 1000.

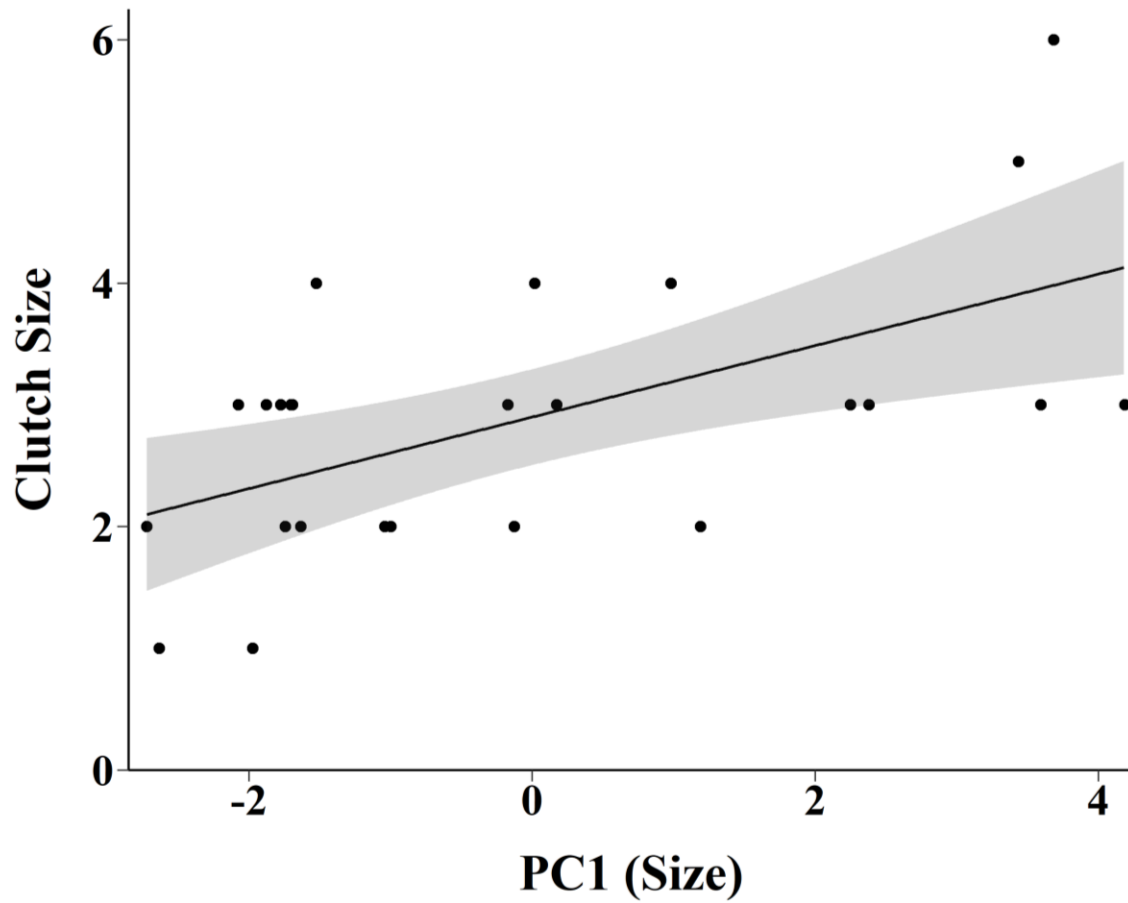


Fig 2.4. Top model showing positive relationship between female body size and clutch size in Ornate Box Turtles (*Terrapene ornata*) in Illinois. Gray areas are 95% confidence intervals of predicted values. Points are raw data. PC1 = Principal Component 1, a multivariate size component from a PCA using carapace length, carapace width, shell height, plastron length, and left pectoral scute height along midline.

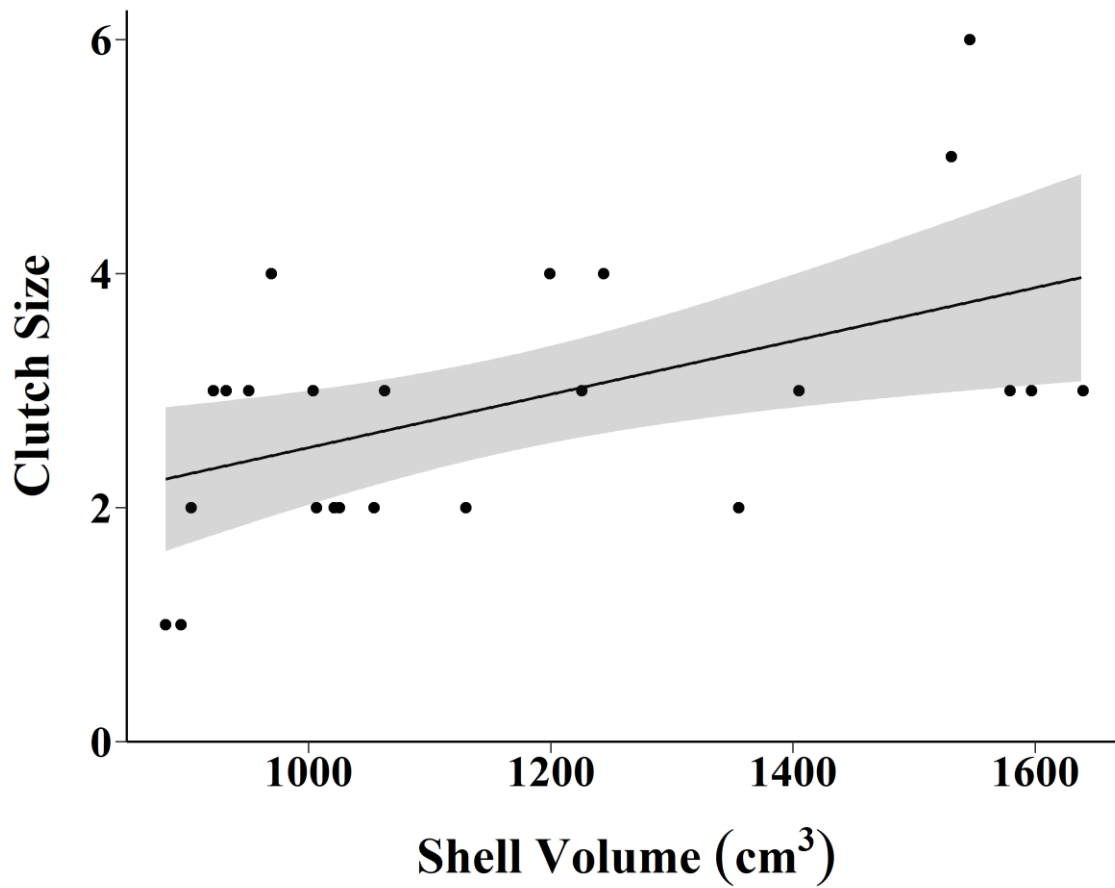


Fig 2.5. Positive relationship between shell volume and clutch size in Ornate Box Turtles (*Terrapene ornata*) in Illinois. Gray areas are 95% confidence intervals of predicted values. Points are raw data. Shell volume was estimated as half the volume of an ellipsoid using carapace length, width, and height.

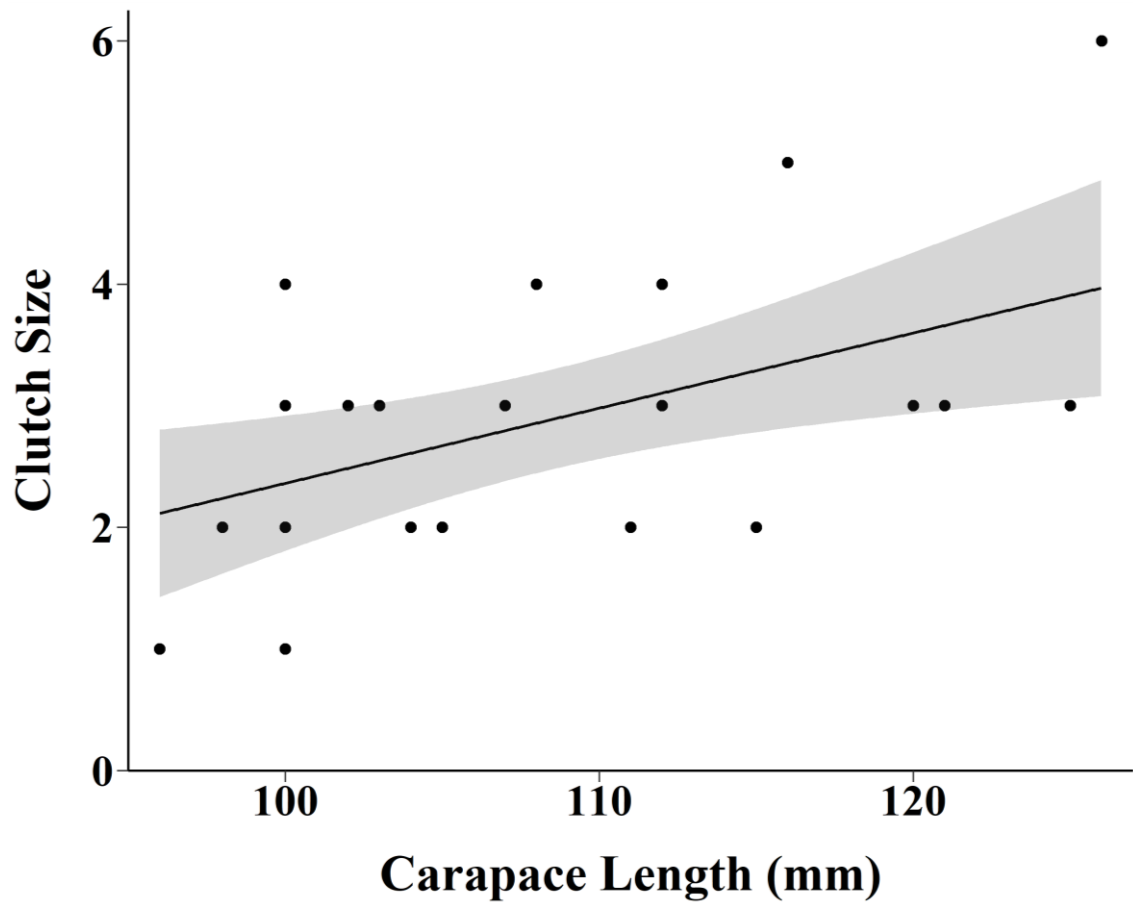


Fig 2.6. Positive relationship between carapace length and clutch size in Ornate Box Turtles (*Terrapene ornata*) in Illinois. Gray areas are 95% confidence intervals of predicted values. Points are raw data.

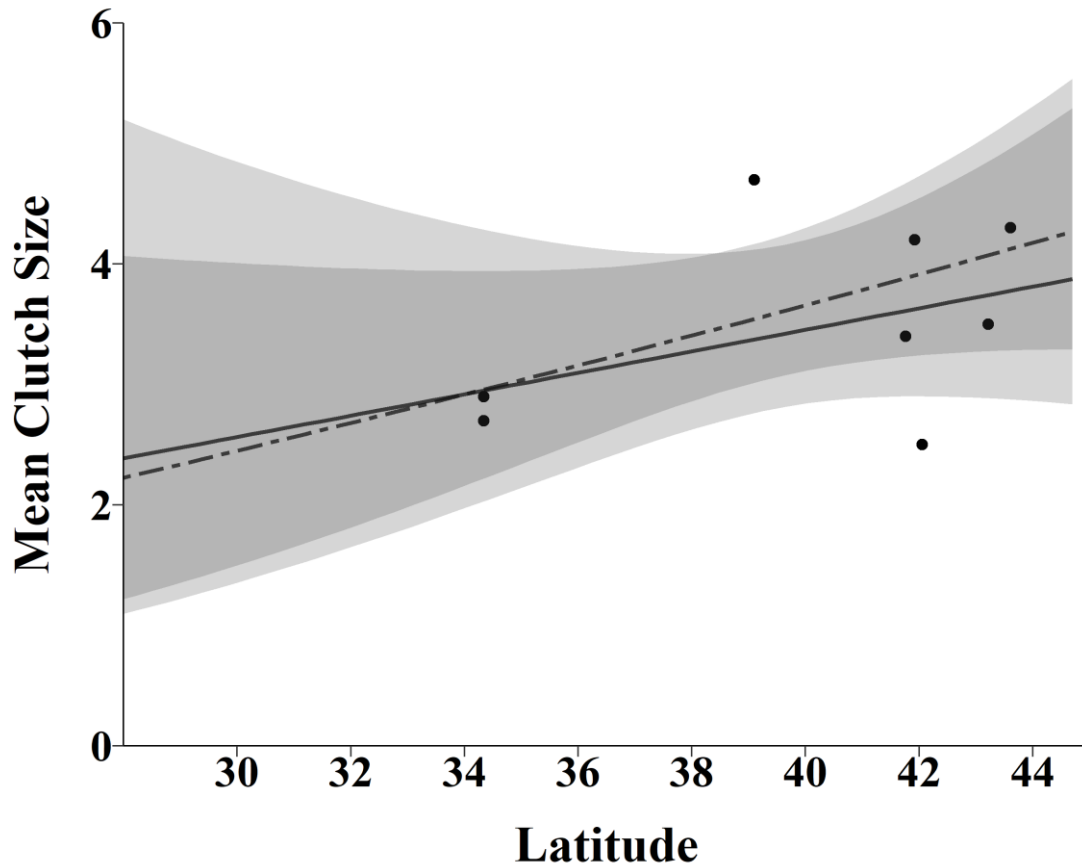


Fig 2.7. Positive relationship between latitude and clutch size in the Ornate Box Turtle (*Terrapene ornata*). Points are reported mean clutch sizes published in literature (see Table 2.1). The solid line is the regression including all sites ( $r^2=0.05$ ), while the dotted line is the regression when the outlier site Ayers Sand Prairie is removed ( $r^2=0.37$ ). Shaded areas are 95% confidence intervals of predicted values.

## **CHAPTER 3: STAGE-BASED DEMOGRAPHIC ANALYSIS**

### **Introduction**

Turtle life histories consist of delayed sexual maturity, a long lifespan, and high adult survival (Iverson 1991a; Shine and Iverson 1995), all of which put populations at risk of decline from chronic environmental perturbations (Congdon et al. 1993). For instance, population growth is disproportionately affected by adult survival when compared to other vital rates (Heppell 1998). Decreasing adult survival by as little as 2-3% a year, which in small populations may equate to additional losses of one to two turtles annually, can trigger a viable population to decline (Gibbs and Shriver 2002; Spencer et al. 2017). Additionally, due to their long lifespan and generation time, old adults can persist in non-viable populations, giving the perception that conservation actions are unnecessary (Hylander and Ehrlén 2013; Lovich et al. 2018; Howell et al. 2019). In such situations, population declines, and eventual extinction may go unnoticed (Kuussaari et al. 2009). Given the constraints posed by turtle life histories and with the threatened status of over half of described chelonian species, there is a pressing need to increase monitoring efforts of remaining small populations to assess the likelihood of extirpation and identify the suppressed vital rates responsible (Lovich et al. 2018).

Matrix population models are widely used to project population persistence for threatened species under varying conditions and management scenarios (Enneson and Litzgus 2008; Feng et al. 2019). Projection matrices provide estimates of how a population will fair in the future by using initial abundances and vital rates, which, in turn, inform conservation decisions (Sandercock 2006). Although researchers can use age-specific vital rates to construct matrices (Leslie 1945), demography for many species depends more on size or life stage (Caswell 1989). For instance, survival may be lower for smaller turtles regardless of age due to

increased predation risk (Janzen et al. 2000). Additionally, estimating turtle age with precision can be challenging or impossible (Litzgus and Brooks 1998; Wilson et al. 2003). As a result, stage-based matrix models (Lefkovitch 1965), using population vital rates for size classes or life stages, are well suited for turtles.

Although matrix population models are a useful tool, modeling turtle population persistence is challenging because of the logistics involved in collecting data on vital rates (Crouse et al. 1987; Jackson et al. 2008). Estimating annual survival for multiple life stages can take decades of capture-mark-recapture surveys. Although they are ideal for demographic studies (Wilbur 1975), most turtle species and populations lack demographic data, especially for younger life stages. Consequently, wildlife managers are often left to make decisions impacting turtles based on generalized models which tend to have inadequate site-specific, species-specific, and population-level data.

Ornate Box Turtles (*Terrapene ornata*) are declining over much of their range and need conservation attention, especially at the edges of their distribution (Redder et al. 2006). Habitat loss is the greatest threat they face considering most grasslands formerly covering middle North America have undergone agricultural conversion (Samson and Knopf 1994). Mortality from vehicles and the collection of animals for the pet trade also contribute to declines (Doroff and Keith 1990; Converse et al. 2005). Consequently, many Ornate Box Turtle populations persisting on the landscape are remnants, heavily impacted by the loss of adults from anthropogenic mortality, and at risk from reduced genetic diversity (Kuo and Janzen 2004; Howell and Seigel 2019). Given such threats, coupled with a disjunct distribution at the northeast edge of their range, Ornate Box Turtles are listed as endangered in Indiana and Wisconsin and threatened in

Illinois and Iowa (Iowa DNR 2009; Wisconsin DNR 2015; Illinois Endangered Species Protection Board 2015; Indiana DNR 2019).

Despite being a species of high conservation concern, we know little about the demography of Ornate Box Turtle populations. Doroff and Keith (1990) provided one of the most thorough demographic accounts for the species, focusing on a population in south-central Wisconsin. In the 1980s, the population was in decline and now is likely extirpated (R. Hay, pers. comm.). More recent demographic studies have focused on a site in northwest Illinois, where longstanding development reduced adult survival (Bowen et al. 2004; Mitchell et al. 2016). However, for most of the remnant Ornate Box Turtle populations in Illinois, it is unclear if populations are stable, growing, or declining. Here, I use population vital rates collected from two populations in northern Illinois to investigate Ornate Box Turtle demography and project population persistence within a stage-based matrix population model framework. I then discuss conservation actions and species management implications based on my results.

## **Materials and Methods**

### *Study Sites*

I studied Ornate Box Turtles at two isolated sites in northern Illinois, both circumscribed by row crop agriculture and urbanization. Ayers Sand Prairie is 44 ha of remnant dry prairie, blowouts, and sand dunes located near the Mississippi River. It is one of the few sand prairie fragments left in Illinois never converted to agriculture. The second site, Nachusa Grasslands, is located 60 km southeast of Ayers Sand Prairie. Nachusa Grasslands is separated from Ayers

Sand Prairie by a gridwork of development, agriculture, and roads. Within Nachusa Grasslands, I focused on the Orland Prairie Unit consisting of 142 ha historically used for cattle grazing.

### *Data Collection and Organization*

I surveyed sites in May and June using a combination of visual encounter surveys and wildlife detector dogs (Kapfer et al. 2012; Boers et al. 2017). I used data from Ayers Sand Prairie collected in 1999, 2010, 2018, and 2019, and at Nachusa Grasslands annually 2016–2019. Sampling with dogs lasted 1–4 days. In most years, I conducted several additional days of visual encounter surveys up to a month following initial canine surveys. In the earliest year at Ayers Sand Prairie (1999), surveyors used only visual encounter surveys. Additionally, turtles were marked at Ayers Sand Prairie as early as 1988, allowing me to examine longevity for the oldest recaptures in most recent survey years. However, I was unable to use the earliest marked turtles for further demographic analyses because I was missing data on sex, size, and life stage.

When I located a turtle, I recorded the location with GPS and assigned a unique ID by notching marginal scutes following Cagle (1939). I measured straight carapace length, carapace width, and shell height to the nearest mm with forestry calipers. I used digital calipers to measure the left pectoral scute height along the midline to the nearest 0.1 mm, as well as anterior and posterior plastron lobe length, which I summed to record plastron length.

I determined sex based on secondary sexual characteristics, including iris color, precloacal tail length, and degree of curvature of the first toe on hindlegs (Dodd 2001; Ernst and Lovich 2009). I used a binomial test to decide if the sex ratio differed from 1:1. I classified turtles into life stages post-survey by examining histograms of carapace length. To determine

how many stages to include in the model, I compared unimodal through quadrimodal carapace length distributions using package *AdaptGauss* in program R (Thrun et al. 2019). I then staged turtles based on where the weighted distributions overlapped (Bayes boundary) for each site.

### *Vital Rate and Abundance Estimation*

I calculated fecundity using estimates of site-specific clutch size, sex ratio, and survival together with data from the literature on nest success and breeding frequency (Table 3.1; see Chapter 2). Specifically, I calculated annual fecundity ( $F_i$ ) as:

$$F_i = \text{clutch size} * \text{breeding frequency} * \text{female survival} * \\ \text{nest survival} * \text{sex ratio at birth}$$

where maximum annual clutches per female is assumed to be 1, and breeding frequency is the proportion of gravid females in a year. Although Ornate Box Turtles are known to double-clutch in Nebraska and Kansas (Legler 1960; Converse 1999), double-clutches have not been observed where there is a reduced activity period further north in Illinois. The annual fecundity used for further analyses was 0.342 (95% CI: 0.235–0.484) offspring per female for Ayers Sand Prairie and 0.499 (95% CI: 0.203–0.907) offspring per female for Nachusa Grasslands.

To estimate apparent annual survival, I created individual capture histories and used Cormack-Jolly-Seber (CJS) models in package *RMark* (Lebreton et al. 1992; Laake 2013). Using Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ), I evaluated 13 candidate CJS models to test whether survival ( $\phi$ ) and/or capture probability ( $p$ ) depended on stage, sex, and/or time (Tables 3.2 and 3.3). I considered the best model(s) as having a  $\Delta AIC_c$  less than 2.

To estimate abundance, I used the POPAN parameterization of the Jolly-Seber model (Schwarz and Seber 1999), using an identical covariate structure as the top CJS model for each site.

Abundance ( $\hat{N}$ ) and 95% confidence intervals were calculated from the top POPAN model for each population. Analyses were performed in R version 3.6.1 (R Core Team 2019).

### *Stage-based Demographic Model*

I created female-only deterministic matrix models using hatchling, juvenile, and adult vital rates under three scenarios with average, minimum, and maximum estimates, and projected populations into the future for the length of two average cohort generations. Cohort generation time ( $T_c$ ) was calculated following Caswell (2001), corresponding to the mean age of a female when it produces hatchlings provided there is a stable stage distribution. To examine the impact of vital rates on population growth, I calculated sensitivities and elasticities for both sites under all three scenarios. I used package *popbio* (Stubben and Milligan 2007) to build stage-based deterministic matrix models and perform analyses.

I calculated juvenile and adult female starting abundance for population projections from POPAN model estimates multiplied by the sex ratio and site-specific stage distribution. Additionally, I varied starting adult female abundance at each site based on the confidence intervals around the mean. Because I never located first-year hatchlings during surveys, I estimated starting female hatchling abundance as:

$$\hat{N}_{hatchling} = clutch\ size * breeding\ frequency * \\ nest\ survival * sex\ ratio * \hat{N}_{female}$$

where site-specific clutch size and breeding frequency were used with mean nest survival from Doroff and Keith (1990). Additionally, I used values for annual hatchling survival from the literature (Appendices B and C). Sosa and Perry (2015) radio-tracked 18 hatchlings and reported on mortality but did not calculate survival, so I used previously unpublished data on their fates to do so. Using known fate models in *RMark*, I estimated annual hatchling survival from their study as 0.194 (95% CI: 0.039–0.589). Additionally, Redder et al. (2006) reported the hatchling survival of Ornate Box Turtles as 0.309. For the matrix model, I took the harmonic mean (see Ferger 1931) of hatchling survival rates from Redder et al. (2006) and Sosa and Perry (2015), resulting in an annual apparent hatchling survival of 0.238. Finally, I calculated transition probabilities  $G_i$  and  $P_i$  following Crouse et al. (1987).  $G_i$  is the probability of surviving and transitioning to the next stage whereas  $P_i$  is the probability of surviving and remaining in the same stage.

## Results

### *Population Structure*

Over 20-years, there were 411 captures of 295 individuals at Ayers Sand Prairie. I found 44.1% male, 39.7% female, and 16.3% juvenile. At Nachusa Grasslands, there were 279 captures of 181 individuals over 4 years, with 44.2% male, 40.3% female, and 15.5% juvenile. I did not find evidence the adult sex ratio differed from 0.5 at either site (binomial test, Ayers 95% CI: 0.40–0.56,  $p = 0.63$ ; Nachusa 95% CI: 0.46–0.59,  $p = 0.442$ ). The most parsimonious Gaussian mixture model indicated a bimodal distribution for carapace length, representing two size classes (Table 3.4). The Bayes boundary for the Ayers Sand Prairie population was 94.0 mm (Fig. 3.1),

whereas for Nachusa Grasslands, the boundary was 99.3 mm (Fig. 3.2). Accordingly, I classified turtles above the size limit as adults and below as juveniles.

#### *Annual Survival, Population Size, and Longevity*

The annual apparent survival rate for Ayers Sand Prairie from the top model was 0.970 (95% CI: 0.945–0.983). The stage-dependent survival model showed an adult survival rate of 0.966 (95% CI: 0.942–0.981) and a juvenile survival rate of 0.913 (95% CI: 0.809–0.963; Fig. 3.3). At Nachusa Grasslands, the annual apparent survival rate from the top model was 0.860 (95% CI: 0.693–0.943; Fig. 3.3). There were too few recaptured juveniles from Nachusa Grasslands to estimate juvenile survival with a reasonable degree of precision.

I estimated population size at 429 (95% CI: 385–483) for Ayers Sand Prairie, providing a density of 9.8 (95% CI: 8.7–11.0) turtles per ha (Table 3.5). At Nachusa Grasslands, I estimated population size at 278 (95% CI: 238–328), corresponding to a density of 2.0 (95% CI: 1.7–2.3) turtles per ha (Table 3.5). I also recorded some of the oldest Ornate Box Turtles in a wild population to date. At Ayers Sand Prairie, I recaptured one male and one female in 2018 and one female in 2019 originally marked in 1988. Assuming the turtles were adults when marked, finding the three individuals alive suggests the lifespan of Ornate Box Turtles in the wild can approach >40 years.

#### *Population Growth*

Using mean demographic rates, I found the Ayers Sand Prairie population to be nearly stable, declining annually at <1% ( $\lambda=0.995$ ; Fig. 3.4). The most optimistic scenario using

maximum demographic rates shows the Ayers population growing at 3.0% ( $\lambda=1.034$ ) annually but declining at 5.4% ( $\lambda=0.946$ ) annually when using minimum demographic rates. Elasticity and sensitivity analyses for all scenarios revealed adult survival has the greatest proportional impact on population growth (Fig. 3.5; Table 3.6). Cohort generation time  $T_c$  was 28.8, 33.5, and 43.9 years using the maximum, mean, and minimum population vital rates.

At Nachusa Grasslands, mean demographic rates provided an estimated annual decline of 12.7% ( $\lambda=0.873$ , Fig. 3.4). Minimum estimates showed an annual decline of 23.6% ( $\lambda=0.764$ ), and even the most optimistic scenario using maximum demographic rates showed an annual decline of 3.1% ( $\lambda=0.969$ ). Elasticity and sensitivity analyses for scenarios using the mean and maximum demographic rates showed adult survival having the greatest impact on population growth. When using the minimum demographic rates, juvenile survival had the greatest impact on population growth (Fig. 3.5; Table 3.6); however, such results reflect the uncertainty in the estimate of adult survival and lack of juvenile survival data. Generation time  $T_c$  was 18.0, 20.3, and 27.0 years using the maximum, mean, and minimum population vital rates.

## **Discussion**

### *Comparison of demographic traits*

I estimated vital rates and projected population persistence for two Ornate Box Turtle populations at the edge of their range. The Ayers Sand Prairie population appears stable whereas the Nachusa Grasslands populations may be declining. Like other stable Ornate Box Turtle populations (*e.g.*, Bowen et al. 2004; Converse et al. 2005; Mitchell et al. 2016), I found high apparent annual survival at Ayers Sand Prairie. In contrast, annual survival at Nachusa

Grasslands was relatively low, though estimated with greater uncertainty. Nevertheless, survival at Nachusa Grasslands was higher than a declining Illinois population (0.66; Mitchell et al. 2016) and a now extirpated Wisconsin population (0.81; Doroff and Keith 1990). Further monitoring and proactive conservation efforts are warranted at Nachusa Grasslands to ensure annual survival remains high, preventing the population from meeting a similar fate as the Wisconsin population studied by Doroff and Keith (1990).

There was no evidence of an unequal sex ratio at either site even though Bowen et al. (2004) suggest a female-biased sex ratio may be typical for Ornate Box Turtle populations. Ornate Box Turtles have temperature-dependent sex determination (Ewert and Nelson 1991; St. Clair 1998), and so environmental factors or habitat features affecting nest site temperatures could explain varying sex ratios between sites (Janzen 1994). Sampling bias could also be a factor, considering males and females are not always equally active above ground (Nieuwolt 1996; Tucker et al. 2015). Further, survival can differ between sexes, skewing population sex ratios (Converse et al. 2005). Top models for both Ayers and Nachusa had survival constant but capture probability dependent on sex. I used an equal sex ratio to estimate vital rates for the deterministic matrix models because there was no evidence the sex ratio was unequal, however if the sex ratio was instead male-biased, the population projections would be overly pessimistic because females would be underrepresented in analyses.

I found Ayers Sand Prairie supports a population of Ornate Box Turtles almost double the size of the population at Nachusa Grasslands, even though Ayers Sand Prairie is less than half as large. Moreover, turtle density at Ayers Sand Prairie is the highest reported in literature outside of a Kansas population studied by Legler (1960) over 50 years ago (Table 3.5). Factors affecting turtle density include not only current carrying capacity and habitat quality but also demographic

history. Due to their long lifespan and generation time, low historic recruitment results in low observed turtle densities in the present day (Galbraith et al. 1988). Considering Nachusa Grasslands is recently restored prairie used for cattle grazing whereas Ayers Sand Prairie is remnant habitat, the high Ornate Box Turtle densities at Ayers Sand Prairie could be what was historically typical for the species in optimal conditions.

Notably, at Ayers Sand Prairie, I recaptured three individuals originally marked in 1988, representing some of the oldest Ornate Box Turtles known. While studies have documented the closely related Eastern box turtle (*T. carolina*) living >100 years (Kiestler and Willey 2015), the longevity of Ornate Box Turtles appears shorter. Legler (1960) suggested the longevity of Ornate Box Turtles might reach 50 years, though the oldest known individuals in literature are a captive animal of 42 years (Ernst and Lovich 2009) and a female from New Mexico also estimated to be > 40 years (Germano 2014). Elsewhere, in Texas, complete population turnover was found to occur every 32 years (Blair 1976), with a similar demographic pattern noted in a Kansas population (Metcalf and Metcalf 1985). The cohort generation time (*i.e.*, reproductive timing) for my study sites under varying demographic scenarios ranged 18.0–43.9 years, with  $T_c$  at Nachusa Grasslands shorter than Ayers Sand Prairie due to lower annual survival. Given such demographic traits, population responses to management improving vital rates may not be detectable for many years after implementation (Congdon et al. 1993).

### *Juvenile survival, the missing piece*

Juvenile survival is a challenging life history parameter to estimate because people seldom encounter young turtles once on surveys, much less multiple times to build an encounter history (Converse et al. 2005). I was unable to estimate juvenile survival after four years of

surveys at Nachusa Grasslands because I rarely captured and almost never recaptured juveniles. Although one explanation is high juvenile mortality, another is the difficulty in detecting juveniles because they occupy different habitats, are more cryptic, or rarely move (Congdon et al. 1993; Daigle and Jutras 2005; Pike et al. 2008). Most likely is juvenile Ornate Box Turtles have both lower survival than adults and are also challenging to detect.

Refining survival estimates is the first step toward better guiding conservation efforts at Nachusa Grasslands. The most pessimistic Nachusa scenario showed juvenile survival influencing population growth more than adult survival (Fig. 3.5; Table 3.6). Although juvenile survival is a fundamental life history parameter impacting  $\lambda$  (Iverson 1991b), such a scenario is counter to elasticities of other freshwater turtle species studied (Heppell 1998). Capture-mark-recapture studies spanning many years or decades may be needed to estimate survival with greater precision, over which time turtle populations can suffer severe declines (Garber and Burger 1995). Intensive monitoring using radio telemetry to record individual fates has been used to precisely estimate Eastern Box Turtle (*Terrapene carolina*) survival in a relatively short period of 2-years (Currylow et al. 2011), but the effort and resources necessary for such a study are greater than the annual visual encounter surveys I performed. Either continued long-term annual surveys or increased monitoring efforts are needed to develop juvenile survival estimates for Nachusa Grasslands.

Like my results from Ayers Sand Prairie, studies on Florida Box Turtles (*Terrapene carolina bauri*) found relatively high juvenile survival (Dodd et al. 2006). However, the juvenile stage describes a range of size classes before maturation. I considered turtles at Ayers Sand Prairie to be juveniles if their carapace length was less than 94.0 mm. Survival, though, is often more size-dependent than stage-dependent (Caswell 1989), and smaller juveniles should have

lower survival than larger juveniles. Further partitioning the juvenile stage into several size classes would improve matrix model projections, although obtaining data on small size classes for turtles requires considerable effort using multiple survey methods (Teschke and Hodges 2015). Alternatively, instead of matrix models, integral projection modeling, which does not require discrete life stages, is well suited to project population persistence (Easterling et al. 2000; Ellner and Rees 2006), although it has not been used yet for a chelonian to my knowledge.

### *Management implications*

My results show increasing fecundity, hatchling survival, and juvenile survival have a lesser impact on population growth than increasing adult survival. Nevertheless, conservation practitioners must consider not only which vital rate has the greatest effect on population growth, but also which vital rates management can meaningfully change (Sæther et al. 1996). For example, increasing juvenile survival or nest success can be beneficial for turtle populations when adult survival is near its maximum value (Cunnington and Brooks 1996). At Ayers Sand Prairie, where both juvenile and adult survival rates are relatively high, nest protection or head-starting programs might be feasible for increasing population growth even though younger life stages do not impact  $\lambda$  proportionately as much as adult survival does. Conversely, at Nachusa Grasslands there is greater potential to increase adult survival, so resources should focus on protecting existing adult females rather than boosting the survival of younger life stages or increasing fecundity.

I recommend wildlife managers working to recover declining Ornate Box Turtle populations focus efforts on reducing mortality related to three common prairie management

practices: prescribed burns, vegetation mowing, and vehicle use in turtle habitat. Prescribed burns should occur as early as possible to coincide with hibernation (Milanovich et al. 2017). Research examining factors influencing hibernation emergence is needed to inform the timing of prescribed burns. Vegetation mowing is another common cause of adult mortality (Metcalf and Metcalf 1985; Doroff and Keith 1990), so planning mowing to coincide with unfavorable environmental conditions and inactivity (*e.g.*, midday in hot weather or during cool temperatures below 6°C, see Tucker et al. 2015) should reduce mortality risks. Finally, vehicle use can significantly contribute to adult mortality (Blair 1976) and should be limited in Ornate Box Turtle habitat. At some sites, fencing roadways and installing underpasses may be a viable management action, especially if roads transect high-use areas (Aresco 2005; Boarman and Sazaki 2006). I also recommend continued prohibition of collection for the pet trade because the removal of even a small number of individuals from an otherwise stable population can lead to extinction (Dodd et al. 2016). Increasing or maintaining high adult survival rates is key to ensuring Ornate Box Turtle populations continue to persist along the edge of their range.

## Tables and Figures

Table 3.1. Demographic rates used to model population growth of Ornate Box Turtles (*Terrapene ornata*) at Ayers Sand Prairie and Nachusa Grasslands in northern Illinois. Mean, minimum, and maximum are parameters used in models representing average, worst, and best-case scenarios. The parameters with a superscript are from literature (see Appendix C). \* indicates the value from literature was used only for Nachusa Grasslands.

| Parameter                         | Ayers Sand Prairie |         |         | Nachusa Grasslands |         |         |
|-----------------------------------|--------------------|---------|---------|--------------------|---------|---------|
|                                   | Mean               | Minimum | Maximum | Mean               | Minimum | Maximum |
| Clutch size                       | 2.53               | 2.08    | 2.98    | 4.20               | 2.58    | 5.82    |
| Clutches per year                 | 1                  | 1       | 1       | 1                  | 1       | 1       |
| Breeding frequency <sup>a</sup>   | 0.57               | 0.57    | 0.57    | 0.57               | 0.57    | 0.57    |
| Sex ratio at birth                | 0.50               | 0.50    | 0.50    | 0.50               | 0.50    | 0.50    |
| Nest survival <sup>a</sup>        | 0.49               | 0.42    | 0.58    | 0.49               | 0.42    | 0.58    |
| Hatchling survival <sup>b,c</sup> | 0.238              | 0.238   | 0.238   | 0.238              | 0.238   | 0.238   |
| Juvenile survival <sup>f*</sup>   | 0.913              | 0.809   | 0.963   | 0.769*             | 0.769*  | 0.769*  |
| Adult survival                    | 0.970              | 0.945   | 0.983   | 0.860              | 0.693   | 0.943   |
| Years to maturity <sup>d,e</sup>  | 9.5                | 11      | 8       | 9.5                | 11      | 8       |
| Starting $\hat{N}_{hatch.female}$ | 45                 | 33      | 59      | 30                 | 14      | 48      |
| Starting $\hat{N}_{juv.female}$   | 35                 | 31      | 39      | 22                 | 18      | 25      |
| Starting $\hat{N}_{female}$       | 180                | 161     | 202     | 117                | 101     | 139     |
| Population growth ( $\lambda$ )   | 1.00               | 0.95    | 1.03    | 0.88               | 0.77    | 0.97    |

a. Doroff and Keith 1990; b. Redder et al. 2006; c. Sosa and Perry 2015; d. Blair 1976; e. Legler 1960; f. Converse 1999

Table 3.2. Cormack-Jolly-Seber models with covariates sex, stage, and time used to estimate Ornate Box Turtle (*Terrapene ornata*) survival at Ayers Sand Prairie, Carroll County, Illinois. The global model is bold.

| Model                                                                | $K$ | AIC <sub>c</sub> | $\Delta$ AIC <sub>c</sub> | weight |
|----------------------------------------------------------------------|-----|------------------|---------------------------|--------|
| $\varphi(.)p(sex)$                                                   | 4   | 426.90           | 0.00                      | 0.78   |
| $\varphi(sex)p(sex)$                                                 | 6   | 429.64           | 2.75                      | 0.20   |
| <b><math>\varphi(time + sex + stage)p(time + sex + stage)</math></b> | 12  | 434.91           | 8.01                      | 0.01   |
| $\varphi(time + sex)p(.)$                                            | 6   | 437.44           | 10.54                     | 0.00   |
| $\varphi(sex)p(.)$                                                   | 4   | 439.87           | 12.97                     | 0.00   |
| $\varphi(stage)p(stage)$                                             | 3   | 447.16           | 20.26                     | 0.00   |
| $\varphi(.)p(stage)$                                                 | 4   | 447.18           | 20.28                     | 0.00   |
| $\varphi(stage)p(.)$                                                 | 3   | 447.38           | 20.48                     | 0.00   |
| $\varphi(stage + time)p(.)$                                          | 5   | 447.98           | 21.08                     | 0.00   |
| $\varphi(.)p(time)$                                                  | 4   | 457.38           | 30.49                     | 0.00   |
| $\varphi(.)p(.)$                                                     | 2   | 457.73           | 30.83                     | 0.00   |
| $\varphi(time)p(time)$                                               | 6   | 460.75           | 33.86                     | 0.00   |
| $\varphi(time)p(.)$                                                  | 4   | 461.39           | 34.49                     | 0.00   |

$\varphi$  is survival.  $p$  is capture probability.  $K$  is the number of parameters.

Table 3.3. Cormack-Jolly-Seber models with covariates sex, stage, and time used to estimate Ornate Box Turtle (*Terrapene ornata*) survival at Nachusa Grasslands, Ogle County, Illinois. The global model is bold.

| Model                                                                | $K$ | AIC <sub>c</sub> | $\Delta$ AIC <sub>c</sub> | weight |
|----------------------------------------------------------------------|-----|------------------|---------------------------|--------|
| $\varphi(.)p(sex)$                                                   | 4   | 398.50           | 0.00                      | 0.84   |
| $\varphi(sex)p(sex)$                                                 | 6   | 402.23           | 3.73                      | 0.13   |
| $\varphi(sex)p(.)$                                                   | 4   | 406.75           | 8.25                      | 0.01   |
| $\varphi(time + sex)p(.)$                                            | 6   | 408.35           | 9.85                      | 0.01   |
| <b><math>\varphi(time + sex + stage)p(time + sex + stage)</math></b> | 12  | 409.80           | 11.30                     | 0.00   |
| $\varphi(.)p(stage)$                                                 | 3   | 411.16           | 12.66                     | 0.00   |
| $\varphi(stage)p(stage)$                                             | 4   | 412.83           | 14.33                     | 0.00   |
| $\varphi(stage + time)p(.)$                                          | 5   | 413.34           | 14.85                     | 0.00   |
| $\varphi(stage)p(.)$                                                 | 3   | 413.75           | 15.25                     | 0.00   |
| $\varphi(.)p(.)$                                                     | 2   | 415.35           | 16.85                     | 0.00   |
| $\varphi(time)p(.)$                                                  | 4   | 415.64           | 17.14                     | 0.00   |
| $\varphi(.)p(time)$                                                  | 4   | 418.73           | 20.24                     | 0.00   |
| $\varphi(time)p(time)$                                               | 6   | 419.47           | 20.98                     | 0.00   |

$\varphi$  is survival.  $p$  is capture probability.  $K$  is the number of parameters.

Table 3.4. Gaussian mixture models used to identify the number of modes present in carapace length data for Ornate Box Turtles (*Terrapene ornata*) at two sites in northern Illinois. The number of modes were subsequently used to stage turtles as either juvenile or adult.

| Model       | Ayers Sand Prairie |         |              |        | Nachusa Grasslands |              |        |
|-------------|--------------------|---------|--------------|--------|--------------------|--------------|--------|
|             | <i>K</i>           | AIC     | $\Delta$ AIC | weight | AIC                | $\Delta$ AIC | weight |
| Bimodal     | 6                  | 2378.74 | 0.00         | 0.84   | 1357.78            | 0.00         | 0.79   |
| Trimodal    | 9                  | 2382.67 | 3.93         | 0.11   | 1360.60            | 2.82         | 0.19   |
| Quadrимodal | 12                 | 2384.96 | 6.22         | 0.04   | 1365.61            | 7.82         | 0.02   |
| Unimodal    | 2                  | 2538.40 | 159.66       | 0.00   | 1433.96            | 76.18        | 0.00   |

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Table 3.5. Density as turtles per hectare of Ornate Box Turtles

(*Terrapene ornata*) reported in literature and present study.

| Location  | Density (turtles/ha) | Source                |
|-----------|----------------------|-----------------------|
| Texas     | 0.5–0.9              | Blair 1976            |
| Nebraska  | 1.7                  | Trail 1995            |
| Illinois  | 2.0                  | Present study         |
| Wisconsin | 2.9–5.0              | Doroff and Keith 1990 |
| Kansas    | 5.0                  | Rose 1978             |
| Iowa      | 5.1–6.4              | Bernstein et al. 2007 |
| Illinois  | 6.4                  | Refsnider et al. 2011 |
| Illinois  | 9.8                  | Present study         |
| Kansas    | 6.4–15.6             | Legler 1960           |

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Table 3.6. Sensitivity of Ornate Box Turtle (*Terrapene ornata*) population growth to varying vital rates under average, worst-, and best-case scenarios for Ayers Sand Prairie and Nachusa Grasslands, two isolated populations in northern Illinois.

| Scenario    | Vital Rate         | Ayers Sensitivity | Nachusa Sensitivity |
|-------------|--------------------|-------------------|---------------------|
| Optimistic  | Hatchling survival | 0.194             | 0.111               |
|             | Juvenile survival  | 0.262             | 0.114               |
|             | Adult survival     | 0.693             | 0.858               |
|             | Fecundity          | 0.095             | 0.029               |
| Average     | Hatchling survival | 0.117             | 0.075               |
|             | Juvenile survival  | 0.193             | 0.134               |
|             | Adult survival     | 0.778             | 0.845               |
|             | Fecundity          | 0.082             | 0.036               |
| Pessimistic | Hatchling survival | 0.031             | 0.042               |
|             | Juvenile survival  | 0.046             | 0.853               |
|             | Adult survival     | 0.946             | 0.134               |
|             | Fecundity          | 0.031             | 0.049               |

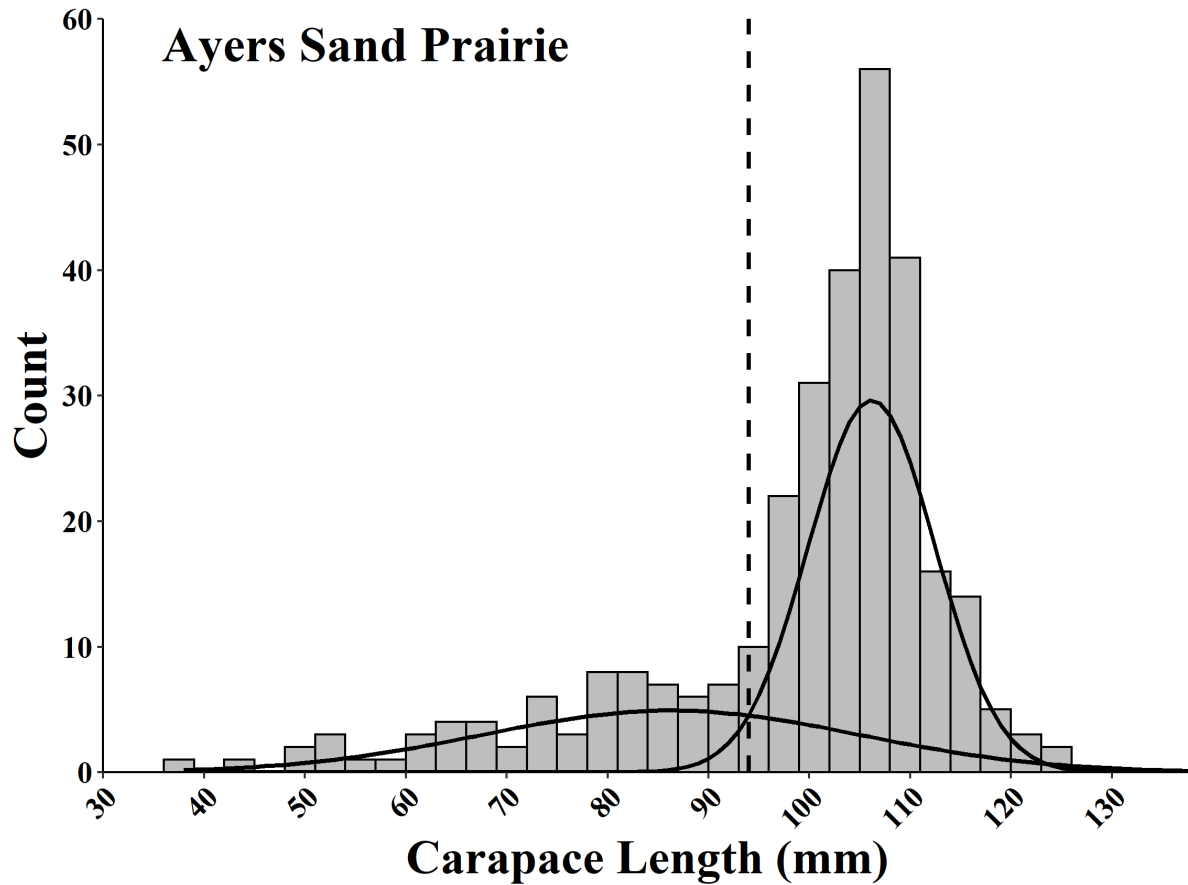


Fig. 3.1. Size frequency of Ornate Box Turtle (*Terrapene ornata*) carapace length at Ayers Sand Prairie overlaid with bimodal distribution from the top Gaussian mixture model. The dashed vertical line is the Bayes boundary (94.0 mm), indicating the threshold above which I staged turtles as an adult and below, juvenile.

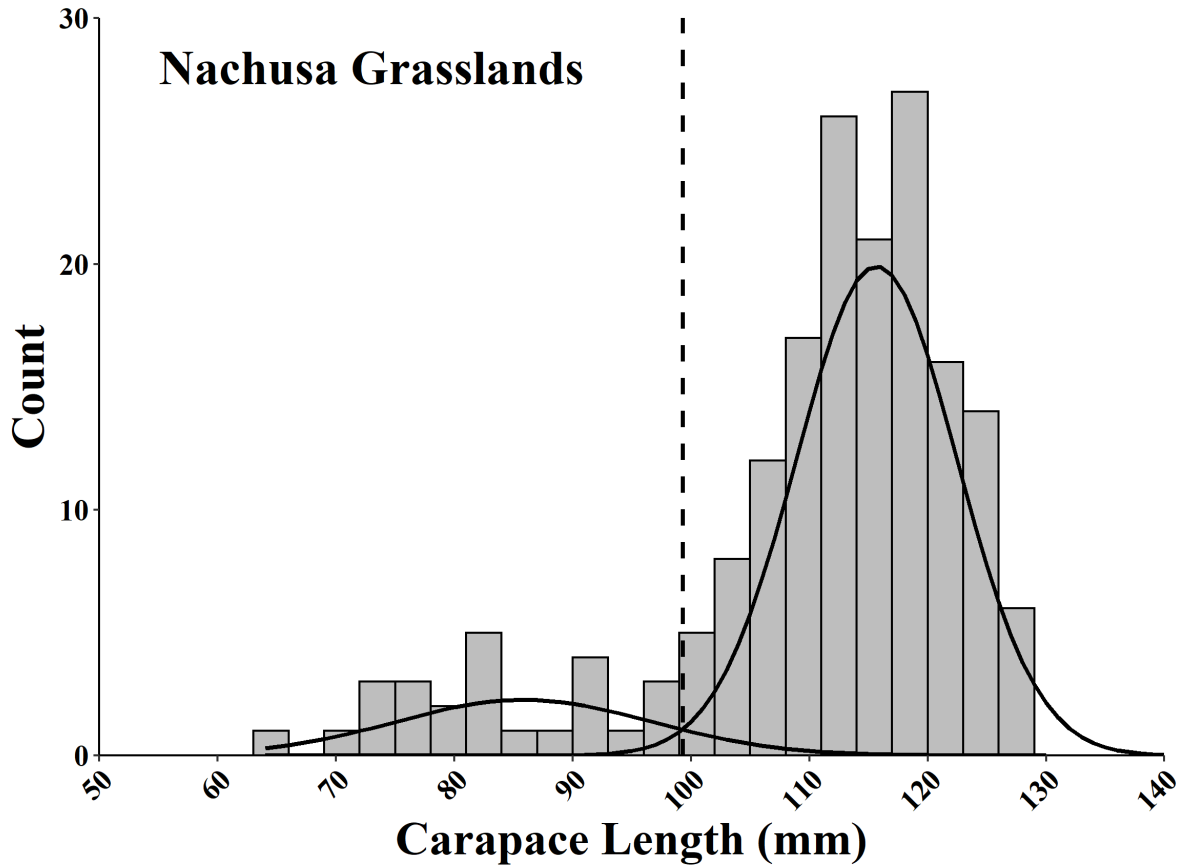


Fig. 3.2. Size frequency of Ornate Box Turtle (*Terrapene ornata*) carapace length at Nachusa Grasslands overlaid with bimodal distribution from the top Gaussian mixture model. The dashed vertical line is the Bayes boundary (99.3 mm), indicating the threshold above which I staged turtles as an adult and below, juvenile.

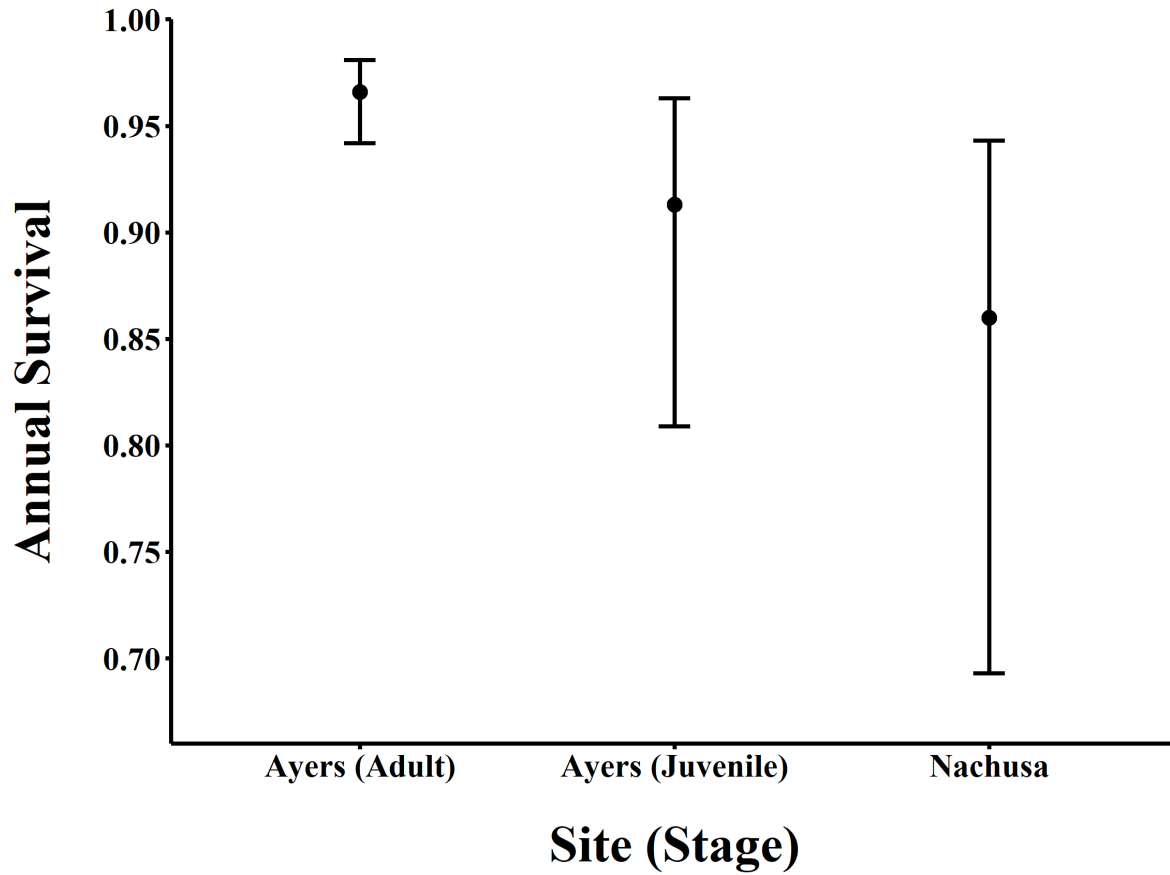


Fig. 3.3. Annual apparent survival estimates of Ornate Box Turtle (*Terrapene ornata*) populations at Ayers Sand Prairie and Nachusa Grasslands in northern Illinois. Error bars are 95% confidence intervals. Stage was not used as a covariate to estimate survival for Nachusa due to low sample size for juvenile turtles.

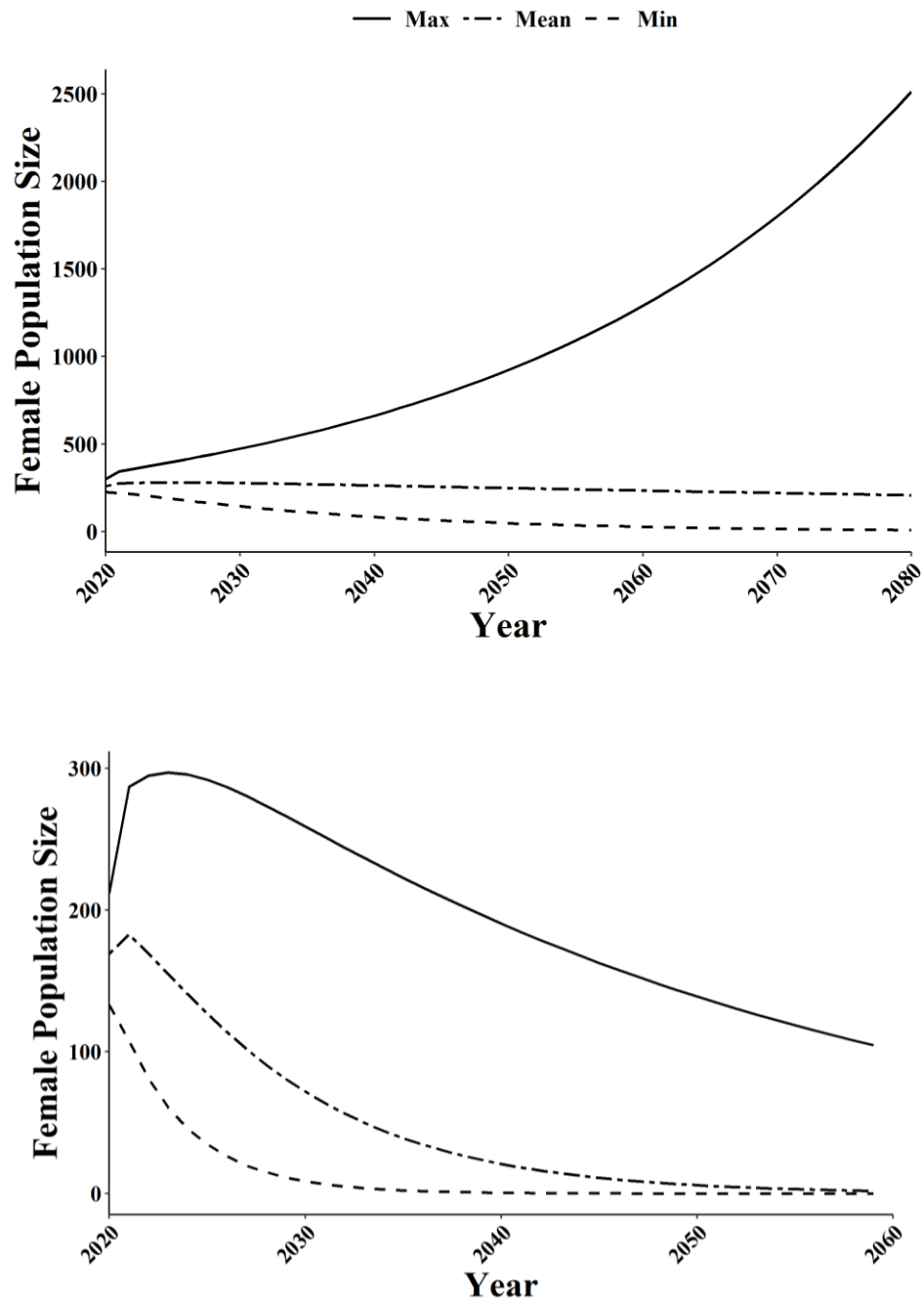


Fig. 3.4. Population projections from stage-based deterministic matrix models for female Ornate Box Turtles (*Terrapene ornata*) at Ayers Sand Prairie (top) and Nachusa Grasslands (bottom) in northern Illinois. Max, mean, and min represent optimistic, average, and pessimistic scenarios. I projected populations over two cohort generations under the average scenario.

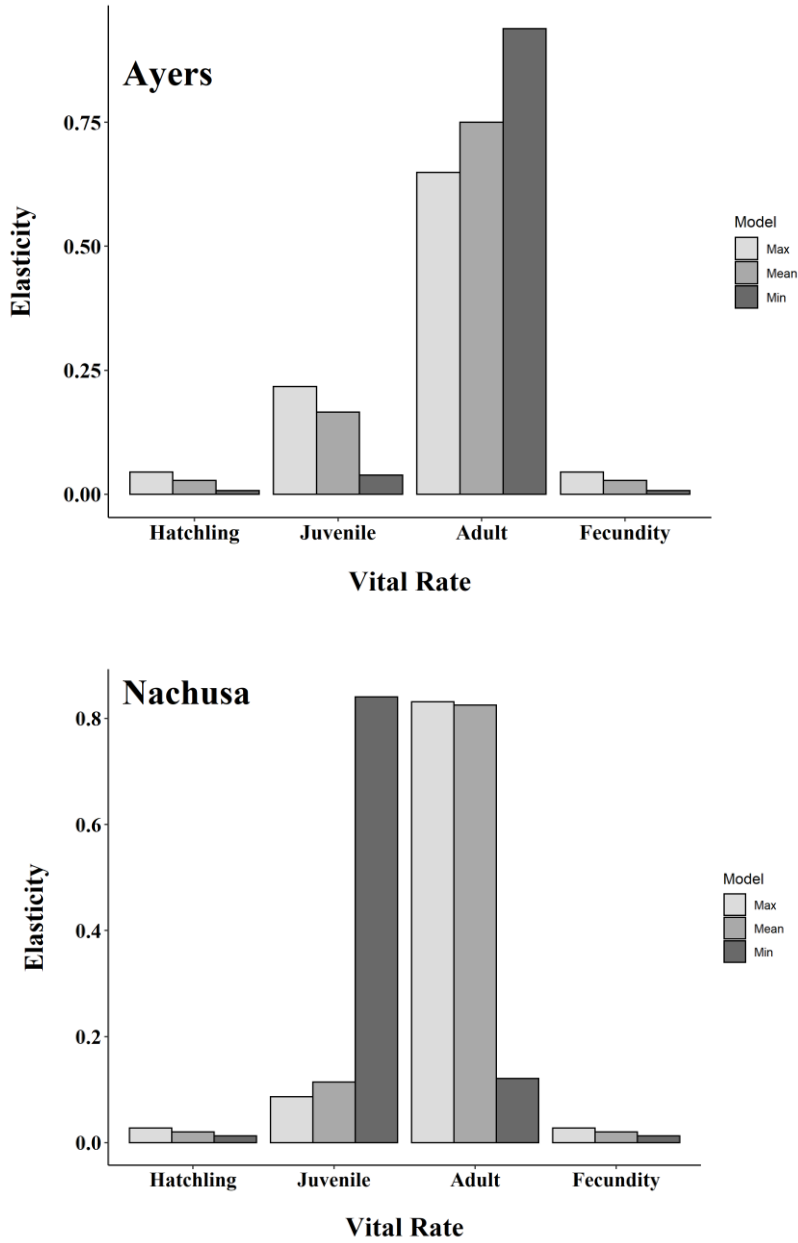


Fig. 3.5. Elasticity analyses for Ornate Box Turtle (*Terrapene ornata*) populations at Ayers Sand Prairie and Nachusa Grasslands in northern Illinois. Elasticity is the proportional change in population growth to percent change in vital rates. Hatchling, juvenile, and adult relate to annual survival rates while fecundity is reproductive output. The three models (max, mean, min) represent best, average, and worst-case scenarios given the range of estimated vital rates collected in the field or used from literature (Table 3.1).

## **CHAPTER 4: SUMMARY AND CONSERVATION IMPLICATIONS**

The objective of my research was to estimate vital rates for Ornate Box Turtle populations in Illinois and use the data to project population persistence. In Chapter 2, I examined clutch size and found variation across the state. There was a fecundity advantage in body size, whereby larger females produced more eggs. Examining clutch size reported in literature revealed populations at northern latitudes have greater mean clutch sizes than populations further south. In Chapter 3, I used reproductive data to calculate fecundity for populations at Ayers Sand Prairie and Nachusa Grasslands. Coupling fecundity and annual survival estimated from capture-mark-recapture surveys, I projected population persistence using stage-based matrix population models. My results showed the Ayers Sand Prairie population is stable, whereas the Nachusa Grasslands population may be declining.

The results highlight how the value of long-term demographic data increases with each additional survey year (Lebreton et al. 1992). Using data spanning 20 years and with a greater number of recaptured individuals, the Ayers Sand Prairie population annual survival estimates were more precise than survival estimated from surveys over 4 years at Nachusa Grasslands. Indeed, precise vital rate estimation requires many decades of intensive surveys in long-lived species (Lovich et al. 2014). Concurrently, species with a life history defined by a long lifespan and delayed sexual maturity are vulnerable to rapid environmental change (Congdon et al. 1994; Reynolds 2003). Such life history constraints, coupled with the extended timeframe needed to estimate vital rates precisely, make it a challenge to detect turtle population declines in time to prevent extirpation.

Limited funding, personnel, and equipment restrict the ability for wildlife managers to implement more intensive survey methods for rapidly estimating turtle population vital rates.

Capture-mark-recapture necessitates repeated site visits over a minimum of three years to calculate annual survival (Pollock et al. 1990). More than 100 person-hours may be needed to detect just 10% of individual Ornate Box Turtles in a population (Refsnider et al. 2011). A faster alternative to capture-mark-recapture is known-fate survival estimation using radio-telemetry, though the method is more demanding of resources (White and Garrott 1990; Murray 2006). Considering also how a lack of sustained support is a common reason monitoring programs fail (Field et al. 2007), funding agencies must provide substantial commitments over multiple generations if they wish to ensure a future for threatened species like the Ornate Box Turtle.

## **Management Implications**

### *Habitat Loss*

The greatest factor impacting Ornate Box Turtle populations in Illinois is habitat loss. Upwards of 99% of Illinois prairie has been destroyed and nearly 80% of what remains is unprotected (Bowles et al. 2003; Corbett 2004). Expanding habitat protection and increasing restoration efforts are crucial conservation actions to safeguard the remaining Ornate Box Turtle populations. At Ayers Sand Prairie, where the population appears stable and density is some of the highest reported in the literature, purchasing adjacent private land and restoring it to prairie should be a priority for management. Importantly, even though I estimated the Ayers Sand Prairie population to number >400 individuals, the population size is still below the threshold considered large enough to maintain ample genetic diversity for long-term persistence (Kuo and Janzen 2004). Assuming the Ayers Sand Prairie population is approaching carrying capacity, the best way to increase population size is to restore adjacent habitat and expand the relict sand

prairie fragment. Conversely, the Orland Tract of Nachusa Grasslands is nearly three times larger than Ayers Sand Prairie yet supports ~40% fewer turtles. Considering the lower density of turtles at Nachusa Grasslands and the negative population growth rate, the most pressing need at Nachusa is not to expand habitat but instead to address sources of adult mortality.

### *Vehicle-caused Mortality*

Road mortality is a well-documented cause of adult mortality in Ornate Box Turtles (Metcalf and Metcalf 1979; Converse et al. 2005; Sosa and Perry 2015). The remaining habitat in Illinois is heavily fragmented and divided by a gridwork of roadways. Mortality from vehicles can have devastating impacts on the demography of turtle populations (Gibbs and Shriver 2002; Steen et al. 2006; Shepard et al. 2008), and at sites where Ornate Box Turtles persist, including Nachusa Grasslands (Hellgren and Whiles 2014), adult turtles have been found dead on surrounding roads. One solution may be to fence roads bisecting Ornate Box Turtle habitat and divert turtle crossing to culverts. Such measures have increased survival in threatened tortoise populations (Guyot and Clobert 1997), though roadway fences can also unintentionally increase mortality, so management must carefully monitor populations after installation (Lovich et al. 2011; Baxter-Gilbert et al. 2015).

Vehicle-caused mortality of Ornate Box Turtles is not limited to roadways but also occurs within habitat from mowers and farming equipment (Metcalf and Metcalf 1985; Doroff and Keith 1990). During surveys, I observed turtles with healed shell damage consistent with what I would expect from the impact of maintenance equipment. While it may be impossible to prevent Ornate Box Turtles from wandering into neighboring farmland, I recommend site

managers time mowing to coincide with conditions unfavorable to Ornate Box Turtles activity. For example, management could limit mowing to mid-day during hot weather when turtles are sedentary under shade trees rather than in the morning or late afternoon when turtles are more likely to be active (Nieuwolt 1996; Plummer 2003; Tucker et al. 2015). Additionally, when operating all-terrain vehicles for maintenance, drivers should stay on trails so that turtles can more easily be seen and avoided, and site staff should be made aware of the impact losing even one adult female turtle to a vehicle could have on a small population.

### *Timing Prescribed Burns*

Prescribed burns are a further source of adult turtle mortality related to site management. Although evolved to cope with frequent fires (Orenstein 2001), prescribed burns can pose a risk to box turtle populations (Platt et al. 2010). At both study sites, I recorded turtles with what appeared to be burn damage. Given the threatened status of the species, burn managers at Ayers Sand Prairie and Nachusa Grasslands factor Ornate Box Turtle activity into their burn schedule, burning as early as possible to avoid harming turtles. Milanovich et al. (2017) recommended burning no later than 10 April in Illinois to avoid incidental mortality, although I noted movement above ground during the last week of March in 2019. Further research is needed examining factors contributing to hibernation emergence, especially given accelerating effects of climate change. Guidelines about prescribed burn timing will need to be matched to environmental triggers of emergence, such as temperature or rainfall, as seasonal shifts occur less predictably.

### *Collection for the Pet Trade*

Although natural resource management agencies prohibit commercial collection throughout much of their range, overexploitation of Ornate Box Turtles for the pet trade is still a serious threat to remaining populations (Converse et al. 2005; Refsnider et al. 2012). Much of the demand for box turtles originates from pet markets abroad, especially in Asia, although domestic pet markets also regularly sell wild-caught Ornate Box Turtles (Cheung and Dudgeon 2006; Johns 2006). Obscuring site locations reported to the public can help prevent poachers from learning where populations of threatened species are located (Pimm et al. 2015). Additionally, the collection of individual turtles for personal pets could threaten Illinois populations near outdoor recreational areas, especially if populations are already small (Refsnider et al. 2012). My results showed the sensitivity of population growth to removal of adults, supporting continued prohibition of Ornate Box Turtle collection in Illinois, as well as increased monitoring efforts of the domestic and international pet trade.

### *Mesopredator Control*

Finally, several authors have cited increased mesopredator populations as a potential threat to Ornate Box Turtles (Temple 1987; Redder et al. 2006). Given the patchy distribution of remaining Illinois prairie and the high abundance of mesopredators in edge habitat, turtle nests may be more susceptible now than in times past to predation by raccoons, skunks, foxes, and other mesopredators (Bernstein et al. 2015). However, results from my sensitivity analyses showed fecundity at both Ayers Sand Prairie and Nachusa Grasslands had <10% of the impact on population growth than adult survival. Consequently, nest predation from mesopredators

would need to be many times inflated beyond historical levels to have the same impact on population growth as minor reductions in annual adult survival rates. Still, in Kansas, coyotes have been documented predating on adult Ornate Box Turtles (Legler 1960; Metcalf and Metcalf 1985), and so mesopredator control measures may be warranted in some situations, especially if there is evidence of predation on adult turtles.

### **Conclusion**

Globally, reptile populations are estimated to have declined by more than 50% since 1970 (Saha et al. 2018). Ornate Box Turtles are among the species declining, and in Illinois, at the edge of their distribution, populations are small and isolated. I projected population persistence for two well-known though understudied populations in the state, providing data on the demography of an Illinois threatened species. I found the Nachusa Grasslands population to be smaller than the population at Ayers Sand Prairie and possibly declining, but more precise survival estimates from long-term monitoring are needed to refine predictions. Importantly, although there is evidence of population decline, small turtle populations with as few as 15 adult females can have high probability of persistence on the landscape (Shoemaker et al. 2013). Therefore, even small remnant Ornate Box Turtle populations in Illinois are worth protecting and have conservation value.

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## APPENDIX A: RADIOGRAPH DATA

| Date      | Site        | Individual  | # Eggs | Notes                               |
|-----------|-------------|-------------|--------|-------------------------------------|
| 5/24/2018 | Ayers       | 01L-03L-09R | 2      |                                     |
| 5/24/2018 | Ayers       | 01L-08L-12L | 1      |                                     |
| 5/24/2018 | Ayers       | 02L-03L-03R | 1      |                                     |
| 5/24/2018 | Ayers       | 08L-09L-11R | 0      |                                     |
| 5/29/2018 | Ayers       | 01L-03L-11R | 0      |                                     |
| 5/29/2018 | Ayers       | 01L-08L-01R | 2      |                                     |
| 5/29/2018 | Ayers       | 01L-08L-02R | 0      |                                     |
| 5/29/2018 | Ayers       | 01L-08L-03R | 0      |                                     |
| 5/29/2018 | Ayers       | 02L-03L-03R | 0      | Duplicate. Radiographed on 5/24/18. |
| 5/29/2018 | Ayers       | 08L-10L-12L | 0      |                                     |
| 5/29/2018 | Ayers       | 11L-09R     | 3      |                                     |
| 5/30/2018 | Ayers       | 01L-02L     | 0      |                                     |
| 5/30/2018 | Ayers       | 01L-08L-10R | 2      |                                     |
| 5/30/2018 | Ayers       | 01L-09L-11L | 2      |                                     |
| 5/30/2018 | Ayers       | 12L-08R-10R | 3      |                                     |
| 5/31/2018 | Ayers       | 01L-08L-12L | 0      | Duplicate. Radiographed on 5/24/18. |
| 5/31/2018 | Ayers       | 01L-08L-12R | 0      |                                     |
| 5/31/2018 | Ayers       | 01L-09L-02R | 0      |                                     |
| 5/31/2018 | Ayers       | 01L-09L-03R | 2      |                                     |
| 5/31/2018 | Ayers       | 02L-08L-01R | 3      |                                     |
| 5/31/2018 | Ayers       | 08L-09L-03R | 2      | No morphometrics recorded           |
| 5/31/2018 | Ayers       | 10R-12R     | 4      |                                     |
| 5/31/2018 | Ayers       | 11L-09R     | 3      | Duplicate. Radiographed 5/29/18.    |
| 6/5/2019  | Ayers       | 01L-01R-09R | 0      |                                     |
| 6/5/2019  | Ayers       | 01L-03L-11R | 0      |                                     |
| 6/5/2019  | Ayers       | 01L-08L-12R | 4      |                                     |
| 6/5/2019  | Ayers       | 02L-10L-12R | 3      |                                     |
| 6/5/2019  | Ayers       | 02L-11L-03R | 0      |                                     |
| 6/5/2019  | Ayers       | 02L-11L-09R | 3      |                                     |
| 6/5/2019  | Ayers       | 02R-10R     | 3      |                                     |
| 6/5/2019  | Ayers       | 09L-10R     | 2      |                                     |
| 6/5/2019  | Ayers       | 11R         | 3      |                                     |
| 6/5/2019  | Ayers       | 12L-08R-10R | 3      |                                     |
| 5/29/2019 | Green River | L01R02      | 0      |                                     |
| 5/29/2019 | Green River | L10         | 2      |                                     |
| 5/29/2019 | Green River | L11         | 0      |                                     |
| 6/11/2019 | Kankakee    | None        | 0      |                                     |
| 6/11/2019 | Kankakee    | None        | 0      |                                     |

**Appendix A: Radiograph Data continued.**

| <b>Date</b> | <b>Site</b>   | <b>Individual</b> | <b># Eggs</b> | <b>Notes</b> |
|-------------|---------------|-------------------|---------------|--------------|
| 6/11/2019   | Kankakee      | None              | 0             |              |
| 6/11/2019   | Kankakee      | None              | 0             |              |
| 6/11/2019   | Kankakee      | None              | 4             |              |
| 6/5/2019    | Lost Mound    | 01L-02L-03R-10R   | 0             |              |
| 6/5/2019    | Lost Mound    | 01L-02L-09R-11R   | 3             |              |
| 6/5/2019    | Lost Mound    | 10L-10R           | 3             |              |
| 6/5/2019    | Lost Mound    | Morgan            | 0             |              |
| 6/5/2019    | Lost Mound    | None              | 0             |              |
| 6/5/2019    | Lost Mound    | None              | 0             |              |
| 5/23/2018   | Nachusa       | 02L-08L-10L       | 0             |              |
| 5/23/2018   | Nachusa       | 12L-09R           | 0             |              |
| 5/29/2019   | Nachusa       | 01L-03L-10L       | 0             |              |
| 5/29/2019   | Nachusa       | 01L-08R           | 6             |              |
| 5/29/2019   | Nachusa       | 02L-03L-10L       | 3             |              |
| 5/29/2019   | Nachusa       | 02L-03L-11R       | 0             |              |
| 5/29/2019   | Nachusa       | 02L-03L-12L       | 0             |              |
| 5/29/2019   | Nachusa       | 02L-08L-12L       | 0             |              |
| 5/29/2019   | Nachusa       | 02L-09L-11L       | 3             |              |
| 5/29/2019   | Nachusa       | 02L-09L-11L-01R   | 0             |              |
| 5/29/2019   | Nachusa       | 02L-09L-12L       | 0             |              |
| 5/29/2019   | Nachusa       | 02L-10L-11L       | 0             |              |
| 5/29/2019   | Nachusa       | 02L-10L-12L       | 0             |              |
| 5/29/2019   | Nachusa       | 02L-11L-12L       | 4             |              |
| 5/29/2019   | Nachusa       | 03L-08L-09L       | 0             |              |
| 5/29/2019   | Nachusa       | 03L-08L-10L       | 0             |              |
| 5/29/2019   | Nachusa       | 03L-08L-11L       | 0             |              |
| 5/29/2019   | Nachusa       | 03L-10R           | 0             |              |
| 5/29/2019   | Nachusa       | 08R-09R           | 0             |              |
| 5/29/2019   | Nachusa       | 09L-09R-10R       | 5             |              |
| 6/11/2019   | Prairie Ridge | 01L-02L           | 0             |              |
| 6/11/2019   | Prairie Ridge | 01L-03L           | 0             |              |
| 6/11/2019   | Prairie Ridge | 01L-08L           | 0             |              |
| 6/11/2019   | Prairie Ridge | 01R               | 0             |              |
| 5/29/2019   | Richardson    | L02R03            | 0             |              |
| 5/29/2019   | Richardson    | R01               | 0             |              |

## APPENDIX B: REPORTED DEMOGRAPHIC TRAITS IN THE LITERATURE

| Demographic trait          | Value           | Source                | Note                                      |
|----------------------------|-----------------|-----------------------|-------------------------------------------|
| Adult survival             | 0.81–0.96       | Blair 1976            | See Redder et al. 2006                    |
|                            | 0.97            | Bowen et al. 2004     |                                           |
|                            | 0.90–0.96       | Converse 1999         |                                           |
|                            | 0.883 (males)   | Converse et al. 2005  | Declining population                      |
|                            | 0.932 (females) | Converse et al. 2005  |                                           |
|                            | 0.81            | Doroff and Keith 1990 |                                           |
|                            | 0.97            | Mitchell et al. 2016  | Site with development                     |
|                            | 0.66            | Mitchell et al. 2016  |                                           |
|                            | 0.83            | Pike et al. 2008      |                                           |
| Juvenile survival          | 0.769           | Converse 1999         | Survival estimate for a stable population |
|                            | 0.71            | Mitchell et al. 2016  |                                           |
|                            | 0.78            | Pike et al. 2008      |                                           |
| Nest success <sup>a</sup>  | 0.67            | Converse et al. 2002  | For three turtle species                  |
|                            | 0.69            | Doroff and Keith 1990 |                                           |
|                            | 0.36            | Temple 1987           |                                           |
| Nest survival <sup>b</sup> | 0.49            | Doroff and Keith 1990 | Nests were caged to prevent predation     |
|                            | 0.83            | Tucker et al. 2017    |                                           |
| Clutches per year          | 0.50–0.53       | Doroff and Keith 1990 | 33% double-clutched                       |
|                            | 1.1             | Converse 1999         |                                           |
|                            | Max. 2          | Legler 1960           |                                           |
| % Breeding females         | 50–63%          | Doroff and Keith 1990 | 10–61.3% over 3 years                     |
|                            | 31.3–44.4%      | Germano 2014          |                                           |
|                            | 58.1%           | Nieuwolt-Dacanay 1997 |                                           |
|                            | 63.6%           | Quinn et al. 2014     |                                           |
|                            | 66.7%           | Tucker et al. 2017    |                                           |

**Appendix B: Reported Demographic Traits in the Literature continued.**

| Demographic trait      | Value                | Source                   | Note                   |
|------------------------|----------------------|--------------------------|------------------------|
| Age at sexual maturity | 7 years (male)       | Blair 1976               |                        |
|                        | 8 years (female)     | Blair 1976               |                        |
|                        | 14 years             | Converse 1999            |                        |
|                        | 8–9 years (male)     | Legler 1960              |                        |
|                        | 10–11 years (female) | Legler 1960              |                        |
|                        | 9 years              | Quinn et al. 2014        |                        |
|                        | 5 years (male)       | St. Clair 1998           |                        |
|                        | 8 years (female)     | St. Clair 1998           |                        |
| Longevity              | 32 years             | Blair 1976               |                        |
|                        | 42 years             | Ernst and Lovich 2009    | Captive animal         |
|                        | >40 years            | Germano 2014             |                        |
|                        | 50 years             | Legler 1960              | Estimate, not observed |
|                        | 28 years             | Metcalf and Metcalf 1985 |                        |

<sup>a</sup>Nest success defined as percent nests with at least 1 egg hatching

<sup>b</sup>Nest survival as percent eggs hatching in the nest

## APPENDIX C: JUSTIFICATION OF PARAMETERS USED IN PROJECTIONS

| Parameter (value)          | Source                | Justification                                                                                                                                                                                                                                                                                                                                                                                                 |
|----------------------------|-----------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Breeding frequency (0.57)  | Doroff and Keith 1990 | Table 1 in Doroff and Keith shows 57% as the mean percent of females laying eggs over two years. The value is comparable to other studies, which ranged from 42–64% females laying each year. I chose to use the value from Doroff and Keith rather than my own estimates from Chapter 2 because I radiographed females late in 2018 and early in 2019, so my estimate of 40% for breeding frequency was low. |
| Nest survival (0.42–0.58)  | Doroff and Keith 1990 | Table 1 in Doroff and Keith shows % eggs hatched, with a range of 42–58% and a weighted mean of 49%. The study is the only report of nest survival in the literature. I was unable to collect data on nesting myself.                                                                                                                                                                                         |
| Hatchling survival (0.309) | Redder et al. 2006    | The only reported hatchling survival in the literature is provided in a document for the U.S. Forest Service by Redder et al. The author's use the value 0.309 in their matrix population model. I averaged the value with that of Sosa and Perry (below) because it was not clear how Redder et al. developed their estimate of survival.                                                                    |
| Hatchling survival (0.194) | Sosa and Perry 2015   | Sosa and Perry radiotracked hatchling Ornate Box Turtles released from a rehabilitation center to examine habitat use and site fidelity. They reported mortality but not annual survival. I used their valuable data to estimate hatchling survival.                                                                                                                                                          |
| Juvenile survival (0.769)  | Converse 1999         | There are only three published estimates of juvenile survival in the literature. The estimate from Converse (1999) is between the other two. Although the value was estimated from very few individuals, it is comparable to juvenile survival in Pike et al. 2008 (0.78), which was estimated as the juvenile survival rate needed to maintain a stable population.                                          |
| Years to maturity (8)      | Blair 1976            | Over a 23-year capture-mark-recapture study, Blair found the youngest female observed copulating was 8 years. I therefore used 8 years as the age of sexual maturity in optimistic projections.                                                                                                                                                                                                               |
| Years to maturity (11)     | Legler 1960           | Analyzing the relationship between growth rate and age, Legler estimated females mature at 10–11 years. I used 11 years as the age of sexual maturity in pessimistic projections.                                                                                                                                                                                                                             |