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Differential demographic responses of two sympatric turtle species to anthropogenic disturbance

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Differential demographic responses of two sympatric turtle species to anthropogenic disturbance

by

Sarah M. Mitchell

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Ecology and Evolutionary Biology

Program of Study Committee:
Fredric J. Janzen, Major Professor
Robert Klaver
Stephen J. Dinsmore

Iowa State University

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DEDICATION

This work is dedicated to Hayley Madland, Morgan Pearson, Monica Pearson, and Riley Glenn, without whose support and encouragement this work would not have been possible.

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ABSTRACT

Species extinction is a major crisis facing the biological world today. Conservation biologists are striving to determine what factors contribute to species declines. Many of these factors are anthropogenic, with issues such as climate change, invasive species, pollution, and habitat alteration and destruction concurrently affecting populations. Turtles have proven to be particularly vulnerable; among the vertebrate taxa, turtles are the most endangered. These studies seek to determine the effects of anthropogenic habitat alteration on two sympatric species of turtles: the painted turtle (*Chrysemys picta*) and the ornate box turtle (*Terrapene ornata*) using fecundity, survival estimates, and/or capture-mark-recapture data from long-term research sites. The first study examines how fecundity and survival rates vary across age classes for a riverine, anthropogenically-affected population of *C. picta* compared to previously studied smaller, more remote systems. The second study examines how different amounts of human development affect survivorship of adult *T. ornata*.

According to the results of the first study, *C. picta* appear to be resilient across age classes to the effects of human presence. This was somewhat surprising, given observations of road mortality and injuries to adult turtles, as well as increased amount of disturbance while turtles were nesting. Juvenile survivorship was very low, though this could be due to methodological issues or biological causes. More research into juvenile survivorship is needed.

The second study found that the survivorship of adult female *T. ornata* decreased in a developed area compared to a refuge site. This implies that construction of cottages and the management of vegetation associated with development was a deleterious effect on survivorship. However, the same pattern was not seen with the construction of a bike path through the refuge

site, although this could be due to a lack of time for effects to manifest in this long-lived population. Continued monitoring will be necessary to determine with confidence the long-term effects of bike path construction.

Overall, these studies present a mixed view on the effects of habitat alterations on turtles. One species, *C. picta*, appeared resilient to human presence; the other, *T. ornata*, did not appear to be resilient to human development. These results demonstrate that different types of human disturbance are likely to have different effects (e.g., human presence vs. human development), and that different species may demonstrate different levels of resilience.

CHAPTER 1. INTRODUCTION

Biological systems are facing unprecedented threats due to anthropogenic activity (Ernst & Lovich 2009; IPCC 2014). These dangers include climate change, pollution, invasive species, unsustainable harvest, and habitat alteration and destruction; together, these anthropogenic impacts are causing a global extinction crisis (Barnosky et al. 2011; Brook et al. 2008; Gurevitch & Padilla 2004). As societies have begun to recognize the dangers associated with the breakdown of natural ecosystems, a burgeoning professional community has evolved; this diverse community includes biofuel experts, climatologists, agriculturalists, politicians, sociologists, and biologists. These professionals tackle a wide variety of issues and questions surrounding the collapse of biological systems. One well-recognized issue caused by anthropogenic impacts is the growing number of species recognized as extinct, endangered, or threatened (IUCN 2015). Many of these species have cultural, economic, or ecological importance, and their conservation is of great concern (Chapin III et al. 2000; Gamfeldt et al. 2008). To this end, some conservation biologists are concerned with the following questions (Caughley 1994):

- Which species or populations are in danger?
- What factors are causing distress to those species or populations?
- How can limited resources be used to the greatest conservation effect?

This introductory chapter briefly illuminates some key methodologies of the field. Then, I discuss more specific issues in conservation biology as they relate to reptilian systems; specifically, how conservation biology can be used to combat threats specific to turtle species (looking in detail at the painted turtle (*Chrysemys picta*) and the ornate box turtle (*Terrapene*

ornata)). Finally, I outline important aspects of painted and ornate box turtles' biology and give a brief overview of the following data chapters.

In order to determine which species or populations are in danger, biologists must determine whether population sizes are increasing or decreasing. Population growth rate (r) is dependent upon four rates; births (b) and immigration (i), which add individuals to the population, and death (d) and emigration (e), which remove individuals (Whelpton 1936). This relationship is summarized in the following equation:

$$\textbf{Equation 1: } r = (b+i) - (d+e)$$

As demonstrated by **Eq. 1**, estimates of population growth rates require accurate information about birth, immigration, and emigration rates; these data are often summarized in a life table (Deevey 1947). Estimates of birth and death rates can be obtained in a variety of ways, the most popular of which is capture-mark-recapture methodology (Pradel 1996).

Capture-mark-recapture methodology relies on the capture and release of marked individuals into a population and their subsequent recapture. The ratio of marked to unmarked individuals can then be used to calculate population size (Bailey 1951; Seber 1986). Alternatively, the likelihood a marked individual is recaptured in the next sampling occasion can be described by **Eq. 2**:

$$\textbf{Equation 2: } \Phi_{i_x} p_{(x+1)}$$

Where Φ_{i_x} is probability that an individual survives and remains in the study area at time x and p_{x+1} is the likelihood of being recaptured at time $x+1$. Over time, capture histories can be compiled for multiple individuals of different stages, allowing researchers to determine survival and recapture rates for the population of interest at multiple stages (Caswell & Fujiwara 2004; Schwarz & Seber 1999).

While these methods are widely used, they can be difficult to apply to long-lived and cryptic species. Due to the necessity of tracking individuals over very long periods of time, from years to decades, capture-mark-recapture methods can be prohibitively expensive and time-consuming for many species of interest (Williams et al. 2002). In addition, high recapture rates are preferred for accurate estimation of parameters; this is difficult to achieve in cryptic species (Krebs & Boonstra 1984). Thus, long-term data sets are difficult to obtain for many species.

Even with these data, further research is necessary for understanding the interplay of anthropogenic and natural sources. One of the best tools to disentangle natural from human-caused influences on populations is comparative studies between natural and altered systems (Graumlich 2000). However, ‘matched’ habitats (habitats that are similar in most regards except in the amount of human influence in the system) are not always available. Only limited conclusions about anthropogenic effects can be drawn from comparative studies in unmatched habitats, as any differences found may be attributable to habitat traits unrelated to human activity.

When matched habitats are available, valuable data can be gathered detailing the influence of human disturbance on population demographic rates (Graumlich 2000). For example, birth and death rates can be compared between habitats, and the effects of human disturbance determined (Ticktin et al. 2012). This information is vital to understanding how humans impact natural systems, and what conservation efforts are needed to protect the population from deleterious effects (Schlaepfer et al. 2005).

Turtles are excellent examples of these population sampling issues. With the life span of some species ranging up to 190 years, following a single cohort through time would require multiple generations of scientists. In addition, many species are highly vagile, cryptic, or aquatic,

making high rates of recapture difficult to attain and demographic parameters difficult to estimate precisely (Gibbons et al. 2000). Finally, although anthropogenic influences have strong effects on turtle populations, the strength of these effects vary between species and populations (Dodd & Dreslik 2008; Rees et al. 2009). Turtles occupy a diversity of habitats, including the ocean, deserts, freshwater, and prairies. This range of habitats means that threats to population maintenance vary widely between species, and specific data pertaining to anthropogenic effects on each population is necessary to inform management decisions (Johnson et al. 2010).

Data are nevertheless vital to the conservation of these organisms. Much like other taxa, turtles have high cultural, economic, and ecological importance (Butler et al. 2012; Iverson 1982). With more than 50% of the species of turtles endangered globally, accurate estimation of demographic parameters is a priority of conservation efforts (IUCN 2015). Here, I estimate demographic rates of a human-impacted population of the painted turtle (*Chrysemys picta*), and determine the effects of anthropogenic habitat alterations on the locally threatened ornate box turtle (*Terrapene ornata*).

These species exhibit many differences in habitat, lifestyle, and type of human impact. *C. picta* is a highly aquatic generalist that ranges from northern Mexico to southern Canada. Due to its generalist nature, *C. picta* can be found in a wide array of habitats, from big rivers to small ponds and highly populated areas to remote regions (Ernst and Lovich 2009). Thus, high variability in demographic rates may be present between populations. Currently, only one life table has been published for the species (Wilbur 1975); however, data on survival and fecundity rates have been published in a piecemeal manner for a variety of populations. The second chapter of this thesis details demographic rates of an anthropogenically-impacted population of *C. picta*

living in the Mississippi River. These data are put in the context of other studies, and anthropogenic effects on survival and fecundity rates are discussed.

In contrast, *T. ornata* is terrestrial and has more stringent habitat requirements than *C. picta*; it is distributed mostly in the Great Plains area, and prefers arid to semiarid habitats including sand hills, prairies, and desert grasslands (Ernst & Lovich 2009). Populations of *T. ornata* are declining in many locations (IUCN 2015), and they are listed as threatened by the Illinois Endangered Species Protection Board (2015). The third chapter of this thesis compares survival rates in two microhabitats of a population living in Thomson, Illinois; the habitat of one area has been heavily altered by humans, while the other remains relatively undisturbed. Using capture-mark-recapture methodology, survival rates at the two regions are compared, and management implications addressed. Finally, the fourth chapter discusses the implications found in the prior chapters, and illuminates future directions necessary to our understanding of the systems.

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CHAPTER 2. DEMOGRAPHICS OF A HUMAN-IMPACTED RIVERINE PAINTED
TURTLE (*CHRYSEMYS PICTA*) POPULATION

A manuscript for submission to *Ecological Applications*

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Co-authors contributed to the collection of data and preparation of this manuscript

Abstract

Population monitoring of long-lived organisms is a difficult but necessary goal of conservation biologists. Though logistically challenging, these studies provide vital insight into the biology of many endangered taxa. Life tables are one of the basic tools of population ecology; however, these tables can be difficult to construct for long-lived and cryptic species such as turtles. Here, a life table is constructed for an anthropogenically-impacted population of riverine painted turtles (*Chrysemys picta*) and compared to demographic data of other populations. Overall, estimates reflected general trends for other populations except for juvenile apparent survivorship, which was comparatively low. The results suggest that anthropogenic effects do not have a strongly deleterious effect on most painted turtle life stages, with the possible exception of juvenile turtles.

Introduction

Adequate population monitoring of long-lived organisms has been a persistent challenge for biologists (Clutton-Brock & Sheldon 2010). One of the basic tools of population ecology, the life table, is often difficult to construct due to the long-lived, cryptic nature of many endangered

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taxa. Life tables are composed of vital population parameters, such as fecundity estimates and survival rates (Chiang 1984; Cutler & Ederer 1958). These values are critical to conservation efforts, and can guide managers seeking to use limited resources to the greatest effect. However, these important estimates of fecundity and survival can be difficult to determine, as intensive field research can be time-consuming and expensive, and can take decades to attain necessary sample sizes and data.

Turtles are a prominent example of this trend. Despite being disproportionately imperiled compared to other taxa, population data are restricted to relatively few species (Gibbons et al. 2000). Turtles are important members of ecological communities, representing a high proportion of the biodiversity in some systems (Iverson 1982). However, despite their ecological importance and conservation concern, the body of knowledge on population dynamics is biased toward a limited number of species (Schlaepfer et al. 2005). Even within species, population dynamics can vary enormously between populations and regions (Ricklefs & Wikelski 2002).

Surprisingly, a full life table exists for just a single population of one of the most studied freshwater turtles, the painted turtle (*Chrysemys picta*) (Wilbur 1975). The painted turtle may be of particular interest in this regard due to differences in its life history from other turtle species. For instance, it is relatively short-lived compared to other well-studied turtles, with an average life span of about 15-20 years (Janzen, pers. obs.), though life spans in the wild may range up to 30-40 years (Ernst & Lovich 2009). Moreover, due to its broad distribution and ability to exploit diverse habitats, different populations of *C. picta* are likely to vary demographically. For instance, predator diversity and intensity may be very different in a pond system than in a big river habitat such as the Mississippi River. In addition, varying levels of human impact between sites may play a significant role in altering population parameters, and with the broad

distribution of *C. picta* in developed and undeveloped areas, comparisons between populations should reveal these effects. For these reasons, it is possible that *C. picta* populations display different demographic patterns than are commonly expected in other turtle species.

During the past 27 years, various reproduction and capture-mark-recapture data have been collected for a population of *C. picta* in the Mississippi River near Thomson, Illinois (Schwanz et al. 2010). This population is notable in its large size, placement in a big river system, and the degree to which it experiences human impacts (Bowen & Janzen 2008). These characteristics set it apart from many previously studied populations, and make it more likely that atypical demographics may be discovered in this system (Spencer & Janzen 2010). For instance, increased mortality to adults due to collisions with cars and boats may alter demographic rates compared to more remote systems. In addition, increased human presence may deter nesting females, reducing fecundity rates. To that end, we compiled fecundity and survivorship estimates necessary to create a life table for this population and compare these findings to demographic information gleaned from other *C. picta* populations.

Study site

We conducted our research at the Thomson Causeway Recreation Area (TCRA) in Thomson, Illinois (41°57'N, 90°7'W). The TCRA is an island situated on the eastern bank of the Mississippi River, and measures 450 x 900m. The campground portion is heavily used during the summer season, with more than 10,000 people and 5,000 recreational vehicles visiting between the months of April and November each year (Spencer & Janzen 2010). In addition, numerous fishermen and boaters use the adjacent waters nearby for recreational use. We conducted nesting surveys in the South Potter's Marsh campground (1.5 ha), which is surrounded by a backwater slough to the east, another campground to the north, and forests to the south and west. Available

nesting areas included loam, sand, and gravel, and were mowed weekly by Army Corps of Engineers personnel. Roughly 150-300 turtles nest in the area each year. The backwater slough was the site of aquatic trapping efforts (**Fig. 1**).

Methods

Field methods

We monitored nesting activity from mid-May to the end of June every year from 1990-2015. We conducted hourly transects for nesting turtles from 0500 to 2100, or until nesting activity ceased (whichever was later). When a nesting turtle was found, we observed it until nest construction was complete and the mother stepped off the nest. We then captured the female and give it unique marks using notches on marginal scutes (Cagle 1939), then released it. For recaptured individuals, we recorded the identification mark. We remarked turtles if shells had been damaged to the point where marks were indistinguishable with a new unique mark. Subsequently, we numbered, excavated, and counted the clutch size for each nest, then monitored it for predation or nest failure. During the third Saturday of each September, we excavated all intact nests, and counted the number of surviving hatchlings.

Additionally, we set aquatic traps between mid-May to the end of June yearly from 1996-2015. We deployed an assortment of hoop traps, fyke nets, and box nets for two to five weeks each year, and checked them daily. We assigned captured turtles unique marks and noted subsequent recaptures as described above.

Analyses

We assigned turtles to the following age classes: egg (assigned to the period of time between oviposition and retrieval by researchers in mid-September), hatchling (defined as the period between mid-September and emergence from the nest or release by researchers the

following May), juvenile (beginning at emergence from the nest and ending at 6 years, the typical age of sexual maturity for females in this population (Schwanz et al. 2010)), and adult (assigned to turtles older than 6 years). Since turtles do not show sex-specific characteristics until age 4 (for males) or 6 (for females), sex is unknown for many juveniles. Juveniles recaptured as adults were reclassified as males or females. Mean life span for individuals in this population is approximately 15 years (Janzen, pers. obs.).

We determined annual fecundity by multiplying the average number of eggs laid per year per female by the proportion of female eggs produced (as presented in Schwanz et al. (2010)). We calculated survivorship of the eggs by multiplying the percent of successful nests by the proportion of eggs that hatched within surviving nests. We used the mean survivorship for overwintering hatchlings described in Weisrock & Janzen (1999) as an overall estimate for hatchling survivorship.

Using live-recaptures-only Cormack-Jolly-Seber analyses (Cormack 1964; Jolly 1965; Seber 1965) in program MARK population software, we estimated juvenile and adult apparent survivorship using a logit link function to constrain parameter estimates between 1 and 0 (White & Burnham 1999). Cormack-Jolly-Seber analysis is able to use individual capture histories to disentangle apparent survival probability (combined probability of a turtle remaining alive between time periods and remaining in the study area) from recapture rates (rate that a turtle alive and in the study area is recaptured). We compared a series of models using capture histories generated from aquatic trapping (19 years) and nesting (25 years) records.

Previous studies have indicated an effect of stage on survival and recapture rates, so we included these factors in our models (Crouse et al. 1987). Additionally, we generated models including an omnibus year factor to determine if annual environmental fluctuations affected

survival and recapture rates. We also considered that rising global temperatures may place stress on these ectothermic animals due to increased energetic demands, and ran models including a trend of survival over the course of the study. Recapture rates may have been affected by additional factors, such as trapping effort (number of days traps were deployed per year) and nesting activity (number of nests laid per year), thus these factors were included in the model selection process. Finally, an individual covariate denoted the first source of capture (nesting or aquatic trap) to determine if capture source had an impact on subsequent recapture rates. To summarize, we ran biologically relevant models including stage, year, and trend effects on apparent survival rates and stage, year, trend, trapping effort, nesting activity, and capture source effects on recapture rates.

Using Program RELEASE in MARK (White et al. 2001), we ran goodness-of-fit tests, and determined the best model based on the quasi-likelihood corrected form of the Akaike Information Criterion (QAICc) (Anderson et al. 1998; Burnham et al. 1995; White et al. 2001). For the best model, we used MCMC estimation to define estimates more precisely. We report parameter estimates and their 95% credibility intervals for the best model only.

Although this approach is effective in most cases, careful interpretation of results is required to distinguish biologically meaningful models from overparameterized models that overfit the data. Some models, for example, may be competitive in terms of QAICc ranking, but lack the data necessary to distinguish the effect size from zero. Therefore, attention is required to avoid including uninformative parameters and for correct interpretation of model selection results (Arnold 2010). We eliminated models with uninformative parameters. Finally, using the popbio program (Stubben & Milligan 2007) in program R (R development core team 2007),

survival and fecundity estimates were input into a population projection matrix and the finite rate of increase (λ) was determined.

Reproduction & nest survival model

For this population, 87% of adult females lay at least one nest per year (Spencer & Janzen 2010). Of the turtles that lay at least one nest, 25% lay two clutches in a year (Schwanz & Janzen 2008), creating an average of 1.0875 clutches per female turtle per year. Average clutch size between 1990 and 2015 was 10.22 eggs (number of clutches=4,459), generating an average annual production of 11.12 eggs per female per year. Hatchling sex ratio for this population is estimated to be 37% female (Schwanz et al. 2010); thus, an average individual female produced 4.1134 female eggs per year. Mean nest survival rate from 1990 to 2015 was 0.33 (number of clutches=5503). Common causes of nest failure were depredation, flooding, and fungal or ant infestation.

Results

Survivorship

During the course of 23 years, we captured 1,579 unique non-male turtles (1,467 females, 112 juveniles). Model selection showed the most support for the effect of stage on apparent survival rates and year on recapture rates (**Table 1**). Apparent survivorship of juveniles was estimated to be 0.058 (95% credibility intervals 0 to 0.173) and adult female was estimated as 0.857 (95% credibility intervals 0.847 to .866). Models with effects of trapping effort, nesting activity, trend, and capture source were not competitive or were non-informative parameters (betas overlapped zero).

Life table analyses

A summary of fecundity and survival estimates can be found in **Table 2**. Using parameter values estimated in the previous analyses, λ was estimated at 0.41, and generation time was estimated at 14.28 years.

Discussion

Reptiles remain understudied despite their ecological importance and need for conservation efforts (Gibbons et al. 2000). Turtles are indicative of this trend; despite being heavily endangered (IUCN 2015) and important members of their ecological communities (Iverson 1982), baseline population data are lacking for many species (Schlaepfer et al. 2005). Our results show that even for species with documented demographic data, population persistence predictions, survival probabilities, and fecundities may vary widely between locations.

Population persistence

One of the most notable results from this study is the estimate of the net population growth rate ($\lambda=0.41$), which indicates that the population is shrinking over time ($\lambda<1$). This result is surprising, as nesting activity levels and personal observations do not indicate a decrease in population size. It is probable that methodological issues surrounding the recaptures of juveniles contributed to this discrepancy. Because λ depends on the number of individuals added to the population due to births and removed from the population due to mortality, the very low estimate of survival for juveniles would have a large negative influence on population growth rate. This effect is further enhanced by the length of the juvenile stage; since female turtles remain as juveniles for 5 years, the low mortality compounds over time. The methodological issues surrounding the low juvenile estimate are addressed in more detail below.

Fecundity

Overall, our estimates of fecundity were within the range of other published studies (**Table 3**). This finding suggests that human presence at the TCRA does not deter females from nesting (*sensu* Bowen & Janzen 2008). Notably, different estimates of average offspring sex ratio between Schwanz et al. (2010) and Spencer & Janzen (2010) generated substantially different fecundity estimates in the same population. This result would be expected, as different offspring sex ratios produce different numbers of female eggs; since fecundity is estimated as the average number of female eggs laid per female per year, this change alters the overall fecundity estimate.

Egg and hatchling survivorship

Egg survivorship, which was highly influenced by predation, was within the range reported by other studies (**Table 3**). Interestingly, the TCRA population examined here was more heavily influenced by humans than locations in previous studies; this result thus suggests that human development and presence does not deter predator behavior. This conclusion is further reinforced by observations made in previous studies at the TCRA (Strickland & Janzen 2010).

Overwinter survivorship of hatchlings in the TCRA population is lower than that reported in other populations (**Table 3**). However, the value used here may not be representative of the true mean for the population, as it was estimated only over one year. In addition, temperatures in the nest are significantly affected by overstory vegetation cover; thus, maternal nest site choice may play an important role in hatchling survival (*sensu* Weisrock & Janzen (1999)) and other aspects of fitness (Spencer & Janzen 2014).

Juvenile survivorship

Survivorship of juvenile turtles in this population is notably lower than that in other populations (**Table 3**). This outcome could be due to methodological or biological reasons. Some methodological concerns in this study include the ability of smaller turtles to escape from wide-meshed aquatic traps. In addition, juvenile turtles who were recaptured as adults were reclassified into the appropriate sex. This procedure artificially removed turtles from the juvenile data pool, further negatively biasing apparent survival estimates (Nichols et al. 2004). Finally, if apparent survivorship of juvenile males differs from that of females, this would bias the juvenile apparent survivorship estimate away from the true value for female juveniles.

Reasonable biological explanations also exist for the reduced apparent survival of juveniles in this population. The high level of human activity at the TCRA may adversely affect juvenile survival, either through harvest of young turtles (Mitchell, pers. obs.) by members of the public for pets, or through direct mortality due to collisions with vehicles or motorized boats. Alternatively, a big river system such as the Mississippi River may harbor predators that do not trouble juveniles at other sites (e.g. river otters). Finally, the large diversity of microhabitats available for the dispersal of juveniles may decrease apparent survival by increasing the emigration rate of juveniles from the study area. It is possible, for instance, that microhabitats that benefit adult recaptures are not preferred by juveniles; if so, any trapped juveniles that move to a more preferred microhabitat would be indistinguishable from a juvenile that died, and the apparent survivorship rate would decrease. Further research is necessary to disentangle the causes of the low apparent survival of juveniles at this location, and may generate a more accurate estimate of population growth rate.

Adult survivorship

Apparent survivorship of adults at the TCRA was within the range of estimates reported for other populations (**Table 3**). Although this value combines rates of emigration and true survival of the population, it is likely that the estimate is closely tied to true survivorship due to the high level of philopatry exhibited by adult females in this population (Janzen & Morjan 2001). This result suggests that the high level of human activity does not have a strongly deleterious effect on adult survivorship. This inference is further supported by a previous study, which found that nesting behavior and activity of *C. picta* at the TCRA was unrelated to levels of human activity (Bowen & Janzen 2008).

Summary

Despite large differences in habitat and human impacts, the *C. picta* population in Thomson, IL showed similar demographic trends to those previously reported for other populations. The major exception to this pattern was the survivorship of juveniles; further investigation will be required to identify the roots of this discrepancy. The estimated growth rate of the population suggests that the population is declining in numbers; however, this finding is contradicted by personal observations and trends in nesting activity. Thus, caution is required for interpretation of population trends.

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Tables & Figures

Figure 1: Satellite image of study site showing nesting area for *C. picta* (outlined in red) and aquatic trapping area (outlined in blue). This image is bordered on the left by the Mississippi River, which stretches 3 miles across at this location.

Table 1: Model selection results for *C. picta* population in Thomson, IL. Effects for survival (Phi) and recapture (p) are shown within parentheses for each model. The two most competitive models are shown. K denotes number of parameters.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	K	QDeviance
Phi(stage) p(time)	1651.71	0.00	0.99	1.00	24	1603.39
Phi(constant) p(stage*time)	1662.97	11.25	0.00	0.00	30	1602.46

Table 2: Life table for *C. picta* population in Thomson, IL. Estimates of survival and fecundity calculated from data collected from 1990-2015. Survival is denoted by $s(x)$, percent of cohort surviving at each age class is denoted by $l(x)$, and fecundity is denoted by $m(x)$.

age class	$s(x)$	$l(x)$	$m(x)$	$l(x)m(x)$
egg	0.2404	1.0000	0.0000	0.0000
hatchling	0.6888	0.2404	0.0000	0.0000
juvenile	0.0586	0.1656	0.0000	0.0000
juvenile	0.0586	0.0097	0.0000	0.0000
juvenile	0.0586	0.0006	0.0000	0.0000
juvenile	0.0586	3.33E-05	0.0000	0.0000
juvenile	0.0586	1.95E-06	0.0000	0.0000
adult	0.8568	1.14E-07	4.1134	4.71E-07
adult	0.8568	9.80E-08	4.1134	4.03E-07
adult	0.8568	8.40E-08	4.1134	3.46E-07
adult	0.8568	7.20E-08	4.1134	2.96E-07
adult	0.8568	6.17E-08	4.1134	2.54E-07
adult	0.8568	5.28E-08	4.1134	2.17E-07
adult	0.8568	4.53E-08	4.1134	1.86E-07
adult	0.8568	3.88E-08	4.1134	1.60E-07
adult	0.8568	3.32E-08	4.1134	1.37E-07
adult	0.8568	2.85E-08	4.1134	1.17E-07

Table 3: Comparison of fecundity and survivorship estimates between the current study and previously published *C. picta* research.

	Fecundity	Egg survivorship	hatchling survivorship	juvenile survivorship	adult survivorship
Current study	3.3	0.24	0.69	0.06	0.86
Wilbur (1975)	6.6	0.08	-	0.75	0.84
Tinkle et al. (1981)	2.8	0.67	-	0.76	0.76
Iverson & Smith (1993)	19.3	-	-	-	0.91
Frazer et al. (1991)	-	-	-	0.21-0.51	0.29-0.50
Gibbons (1968)	-	0.02	-	-	-
Mitchell (1988)	-	-	-	0.46	-
Zweifel (1989)	-	-	-	0.93	0.86-1.00
Eskew et al. (2010)	-	-	-	-	0.80-0.90
Nagle et al. (2000)	-	-	0.89	-	-
Breitenbach et al. (1984)	-	-	0.81	-	-
Spencer & Janzen (2010)	5.5	-	-	-	0.83

CHAPTER 3. EFFECTS OF HABITAT ALTERATION ON SURVIVAL RATES OF THE
ORNATE BOX TURTLE (*TERRAPENE ORNATA*)

A manuscript for submission to the *Journal of Wildlife Management*

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Co-authors contributed to data collection and the preparation of this manuscript

Abstract

Habitat destruction and modification may be the most prominent anthropogenic forces affecting extant biological systems. Although numerous species are subject to these forces, growing evidence suggests that turtles are especially vulnerable to many anthropogenic stressors. In this study, we evaluated the effects of habitat modification on survival rates of the threatened ornate box turtle (*Terrapene ornata*) using a 21-year mark-recapture dataset. Longstanding development (cottages and outbuildings along with associated landscape management) reduced the apparent survival of *T. ornata*. In contrast, smaller, more recent development (construction and paving of a bike path) did not have demonstrable negative effects. These diverse findings could indicate that the scale of development is important to consider and/or that adverse effects of anthropogenic development may require a considerable time frame to manifest in long-lived organisms.

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Introduction

Anthropogenic changes to the environment have produced a diverse array of pressures on natural populations. Habitat modification and destruction may be the most influential changes, contributing to the extirpation of numerous species across a variety of taxa (Burkey 1995; Fahrig 2002; Hokit & Branch 2003; Holland & Bennett 2010), and causing various sublethal responses (McCauley & Bjorndal 1999), including shifts in community composition (Perkin & Gido 2012). Anthropogenic influences, though problematic for many species, have been particularly detrimental for turtles (Order Testudines), of which 50% are considered endangered and an additional 25% are threatened (IUCN 2015). Turtles may be particularly vulnerable to the effects of habitat alteration and destruction due to their high levels of site fidelity (e.g. Avens et al. 2003), high population sensitivity to adult survival (e.g. Heppell 1998), and need for a diverse array of terrestrial and aquatic microhabitats (Steen et al. 2012). Thus, understanding the effects of habitat alteration on demographic parameters is necessary to best inform management practices (Böhm et al. 2013; Gibbons et al. 2000).

In turtles, adult survival rates are highly important to population growth rates (Brooks et al. 1991; Congdon et al. 1993; Congdon et al. 1994; Crouse et al. 1987; Heppell 1998). However, given the often cryptic nature and lengthy lifespans of many turtles, the amount of time and effort required to gather adequate mark-recapture data often precludes the estimation of these crucial parameters. Yet, management attempts are frequently hampered by the lack of these vital data (Gibbons et al. 2000), and environmental impact assessments require these data for accurate calculation of development risks to natural populations (Trewick 1996).

The effects of habitat alteration and destruction on turtle populations are still being determined. Although most studies report an adverse impact on demographic parameters such as

survival rates (Converse et al. 2005; Garber & Burger 1995; Marchand & Litvaitis 2004; Sirois 2011), the magnitude of these effects vary (Dodd & Dreslik 2008; Rees et al. 2009) and are not universal (Bowen et al. 2004; Cureton et al. 2014; Plummer et al. 2008). Thus, further studies are necessary to determine the intricacies of interactions between altered habitats and turtle survival.

In this study, apparent survival rates of ornate box turtles (*Terrapene ornata*) are compared between two sites with differing levels of long-term, persistent human development (i.e., cottages with maintained yards). In addition, we assessed the demographic impacts of more recent installation of a gravel, and later paved, bicycle path into and through *T. ornata* habitat previously inaccessible to vehicles. We anticipated that substantial long-term levels of development would reduce *T. ornata* survival rates due to altered microhabitat availability and possibly enhanced collecting, and that recent construction and paving of the bike path would yield higher rates of poaching, decreasing apparent survival of adult *T. ornata*.

Study Site

We performed seasonal surveys from 1996-2015 at three adjacent relict sand prairie sections located in northwestern Illinois. These sites are located in the Upper Mississippi River National Fish and Wildlife Refuge in Carroll and Whiteside Counties, Illinois. As described in more detail elsewhere (Bowen et al. 2004; Kolbe & Janzen 2002), sections were separated from each other by cottages or fences, and differed from each other primarily by the amount of human development found on each site. Two adjacent sections have been heavily developed since the 1940s, with cottages, yards, and sand driveways present; these sections were grouped together for all analyses and considered the “disturbed” site (**Fig. 1a**). In contrast, the third section (“refuge”) was undeveloped other than the introduction of a gravel bike path from 2000-2008, after which the path was paved (**Fig. 1b**). Radio telemetry data indicate that movement of turtles

between sites is possible but uncommon, with most turtles exhibiting high site fidelity (Refsnider et al. 2012, Jeramie Strickland, pers. comm.).

Methods

Study organism

The ornate box turtle, *Terrapene ornata*, is a terrestrial species distributed throughout much of the Great Plains, including portions of the southwest United States and northeast Mexico (Ernst & Lovich 2009; Lodato & Hulvershorn 2001). The species' distribution roughly covers the area of the Prairie Peninsula during the Pleistocene (Ernst & Lovich 2009). The ornate box turtle is found in arid and semiarid habitats, including sand hills, prairies, and desert grasslands that are primarily without tree cover and consisting of sandy soils with low laying vegetation (Ernst & Lovich 2009; Legler 1960). Their yellow-tan mottled coloration and often subterranean behavior renders them challenging to locate in the environment (Refsnider et al. 2011). *Terrapene ornata* is listed as threatened in Illinois (Illinois Endangered Species Protection Board 2015) and near threatened globally (IUCN 2015).

Field methods

Researchers conducted linear visual surveys via transects in our denoted habitats. These surveys occurred periodically from mid-May to early July, during the morning hours (0600-1200) when *T. ornata* are most likely to be active (Legler 1960). The amount of time spent conducting these surveys varied annually and person-hours were recorded for each year. Turtles were hand captured and handled in accordance with IACUC, Illinois DNR and U.S. Fish and Wildlife Service permits. Upon capture, an individual was identified as an adult or juvenile, depending on the presence or absence of secondary sexual characteristics and sex was noted if

identified as an adult. Each turtle received an individual mark as an identifier by notching the marginal scutes, and straight carapace length was measured (Cagle 1939).

Statistical analyses

We calculated apparent survival and recapture rates for the population using live-recapture-only Cormack-Jolly-Seber (CJS) analyses (Cormack 1964; Jolly 1965; Seber 1965) in Program MARK (White & Burnham 1999), with parameter estimates constrained between 1 and 0 using a logit link function (White & Burnham 1999). Model selection was based on corrected Akaike Information criterion modified for overdispersion (QAICc), with lower numbers showing greater parsimony (Anderson et al. 1998; Burnham et al. 1995). Using Program RELEASE in MARK, we conducted goodness-of-fit tests (White et al. 2001).

We sought to investigate the effect of anthropogenic structure development on survival rates; thus, we included a site effect on survival and recapture rates. In addition, female turtles may experience increased visibility associated with nesting, making them more vulnerable to predation and location by researchers, so sex effect on survival and recapture was included in the model. To determine if yearly environmental factors play a role in survival and recapture rates, we included year as an omnibus effect for survival and recapture estimates. Additionally, we theorized that size may have an effect on survival and recaptures if larger turtles are more visible to researchers and predators. For this reason, we included an effect of size on survival and recapture. Additionally, we compared models at the refuge site that estimated apparent survival rates based on the effects of path construction (years grouped into three periods: before path construction, after gravel path constructed, and after the path was paved). This effect was not estimated at the disturbed site, as no bike path was constructed in the area. Finally, we included search effort as a potential factor impacting recapture rates. To summarize, we generated

biologically relevant models for survival based on effects of year, sex, size, and site, while recapture rates were modeled based on effects of year, sex, size, site, and search effort. For the most competitive model, we used MCMC estimation to define estimates more precisely. For the most competitive model, we report parameter estimates and 95% credibility intervals.

CJS analyses incorporate individual capture histories to estimate apparent survival (ϕ) and recapture rates (p). Without detailed movement data, the probability that individuals move outside of the study area is difficult to estimate and permanent emigration from the study area is indistinguishable from mortality. Apparent survival combines both those probabilities. Apparent survival and recapture rates can be estimated using many individual capture histories, and models including relevant biological effects can be developed (White & Burnham 1999). These models can then be compared; the most competitive models will receive the most statistical support (lower AIC values).

While this analytical approach is generally effective, attention is required to distinguish models that truly represent the data from overparameterized models that ‘overfit’ the data. For instance, though overparameterized models may be statistically competitive in terms of QAICc ranking, further inspection of the underlying beta parameters may show that no effect is statistically supported (confidence intervals for effect size overlap zero). Thus, careful attention to both QAICc ranking and beta parameters is necessary to distinguish true effects from statistical abnormalities (Arnold 2010). In this study, we removed models with uninformative parameters from the model pool.

Results

During the course of the 21-year study, we captured 158 unique turtles, with 159 recaptures. Of these turtles, 89 were female (56%), 42 were male (27%), and 27 were juveniles of unknown sex (17%).

Two similar models contained all the model weight. These models differed only in the inclusion of a sex effect or path effect on survival; while the top model had a sex effect and the second-ranked model had a path effect, both models shared effects of site on survival, and site and year on recapture (**Table 1**). Beta estimates suggest path effect was an uninformative parameter ($\beta_{\text{before}}=-0.012$, $se=1.95$, 95% confidence interval -3.84 to 3.81, $\beta_{\text{gravel}}=1.67$, $se=2.15$, 95% confidence interval=-2.55 to 5.89). In addition, credibility intervals of survival estimates at different stages of path construction overlap (**Fig. 2**). Other effects were unimportant for survival and recapture estimates.

Estimates from the top model showed yearly recapture rates at the disturbed site varied from 0.06 to 0.56, and from 0.08 to 0.83 at the refuge location. Adult survival rates for females were significantly higher at the refuge site than at the disturbed location (0.97, credibility interval 0.94-0.99 and 0.66, credibility interval 0.50-0.80 respectively); this trend was reflected for adult males as well, although the difference was not quite statistically significant (0.91 refuge, credibility interval 0.85-0.97, 0.76 disturbed, credibility interval 0.63-0.88) (**Fig. 3**).

Discussion

Anthropogenic influences on habitat alteration and destruction have wide-ranging impacts on natural populations. In organisms such as turtles, where adult survival strongly predicts population persistence, the awareness of effects of habitat degradation on survival rates are vital to population management efforts (Crouse et al. 1987). This information is important to

estimate for more than just a few turtle species or populations, as growing evidence suggests that certain turtle populations can be resilient to particular anthropogenic impacts (Fordham et al. 2009; Jergenson et al. 2014; Spencer & Janzen 2010; Strickland & Janzen 2010; Wolak et al. 2010).

In this population, model selection strongly implies a detrimental effect of extensive human development on female box turtle survival. Specifically, the heavily disturbed areas yielded a 32% decrease in female apparent survival compared to the refuge site, although this effect was not estimated well (wide 95% credibility intervals). Trends in the data suggest similar but less striking pattern in males, although more data are required to assess this possibility with statistical confidence (95% credibility intervals overlap). These results add to a growing number of studies suggesting an unsurprising, but alarming, deleterious effect of habitat alteration on survival rates of turtles (Converse et al. 2005; Garber & Burger 1995; Marchand & Litvaitis 2004; Sirois 2011). This impact on survival may have major implications for population persistence, as many turtle populations exhibit a strong sensitivity to decreases in adult survivorship (Heppell 1998).

Previous research suggests that the decrease in apparent survival of turtles at the disturbed site may be due to alterations to available microhabitats (Refsnider et al. 2012). Alternatively, permanent human presence in the area could contribute to the decrease in apparent survival due to harvest of the turtles for the pet trade (Schlaepfer et al. 2005). Since this study began 50 years after construction of the cottages, the effects of disturbance on survival are likely to have been present long enough to manifest in the population.

Apparent survival estimates at the refuge site were comparable to those found for *T. ornata* populations in Nebraska (Converse et al. 2005), and higher than those found in south-

central Wisconsin (Doroff & Keith 1990). Additionally, and unsurprisingly, estimates were similar to those previously calculated for the same Illinois population (Bowen et al. 2004).

Unexpectedly, *T. ornata* appear to be resilient to small amounts of human development. For example, the construction and paving of a bike path through the refuge site left no detectable impact on survival of the box turtles, despite markedly increasing the amount of humans crossing through the site (Janzen, pers. obs.), and thus the potential for poaching. However, it is possible that any deleterious effect on survival has simply not yet manifested in the population due to the long-lived nature of the species, and was therefore undetected in this analysis. Caution should be exercised before relying heavily on this apparent lack of anthropogenic impact. Consequently, this population warrants further monitoring to assess the ongoing time course of survival patterns of *T. ornata*.

Management Implications

Our results suggest that managers seeking to provide recreation opportunities for the public may not be forestalled from non-vehicular trail construction out of concern for ornate box turtle preservation, though it is possible that deleterious effects of trail construction may not have had time to manifest in the study population. However, heavier development, such as the construction of buildings and associated management regimes (for instance, the mowing of vegetation and suppression of fire management), should be avoided to minimize adverse impacts on ornate box turtles.

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Tables & Figures



Figure 1: Representative images of study sites for *Terrapene ornata* in Thomson Illinois. (a) Disturbed site, showing cottages, mowed yards, and trees. (b) Refuge site, showing sand prairie with blowout area.

Table 1: Table of model results for *Terrapene ornata* in Thomson, IL. Models show effects on apparent survival (ϕ) and recapture (p) rates, with K being the number of parameters estimated for each mode. The two most competitive models are shown.

Model	QAICc	Delta QAICc	AICc weights	Model Likelihood	K	QDeviance
Phi(site*sex) p(site*year)	823	0.00	0.86	1.00	42	722
Phi(site*path) p(site*year)	827	3.87	0.13	0.15	43	723

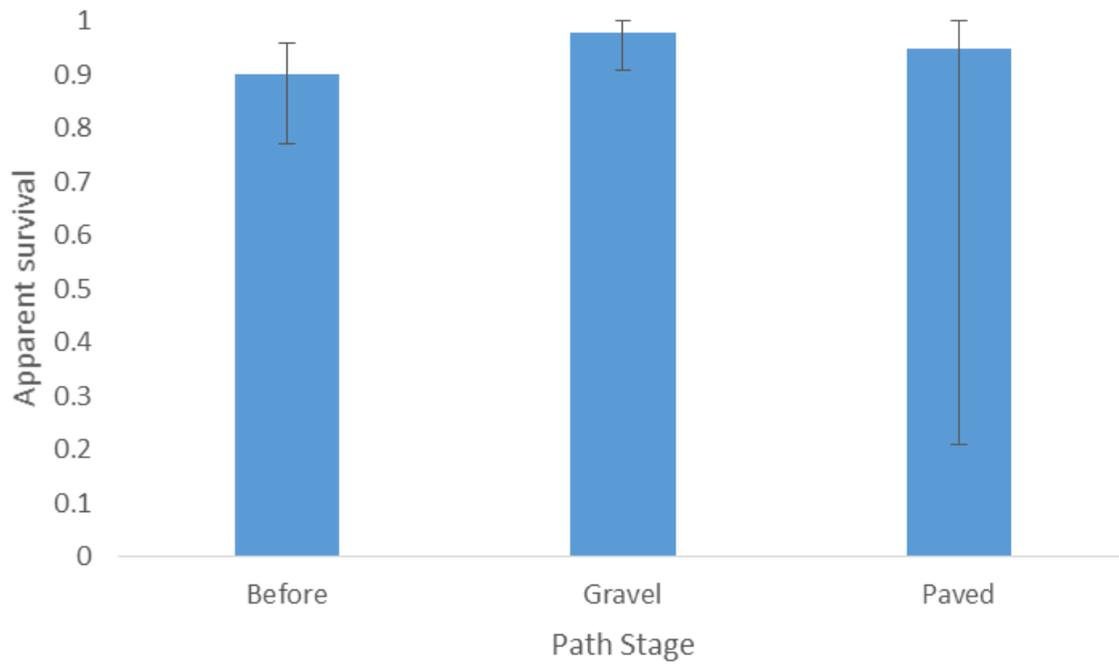


Figure 2: Comparison of apparent survival between stages of path construction. ‘Before’ denotes the time period before path construction (1996-1999). ‘Gravel’ denotes the time between path construction and paving (1999-2008). ‘Paved’ denotes the time after paving of the path (2009-2015). Bars show 95% credibility intervals around estimates.

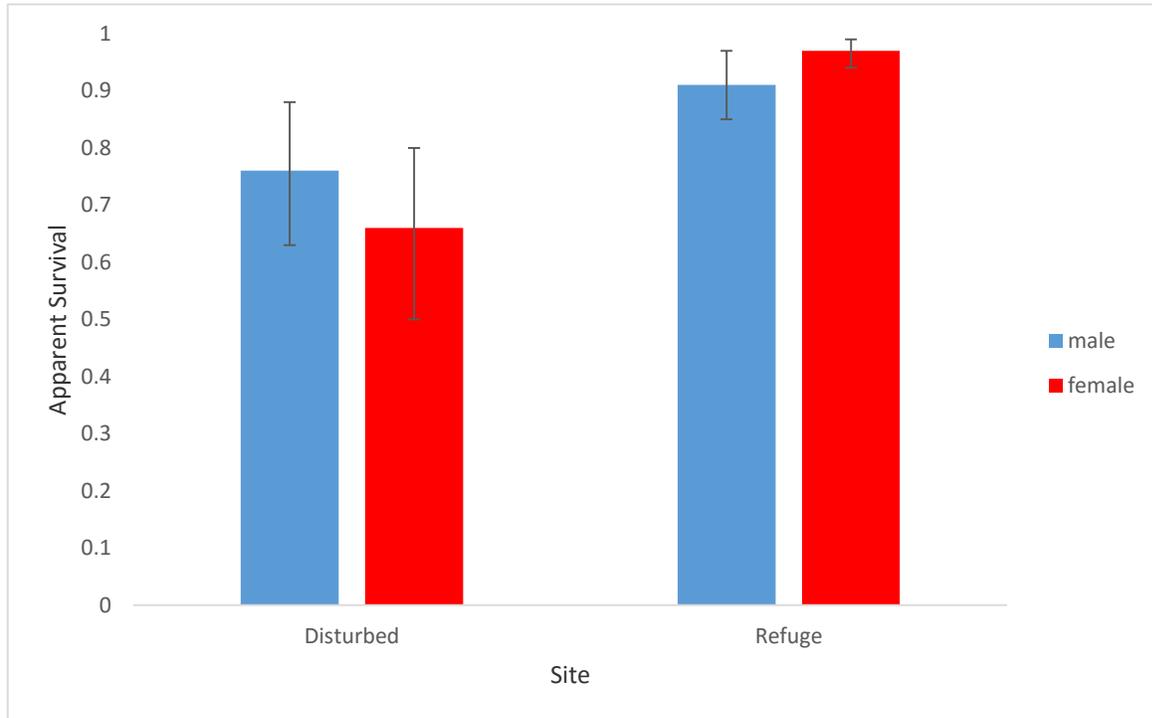
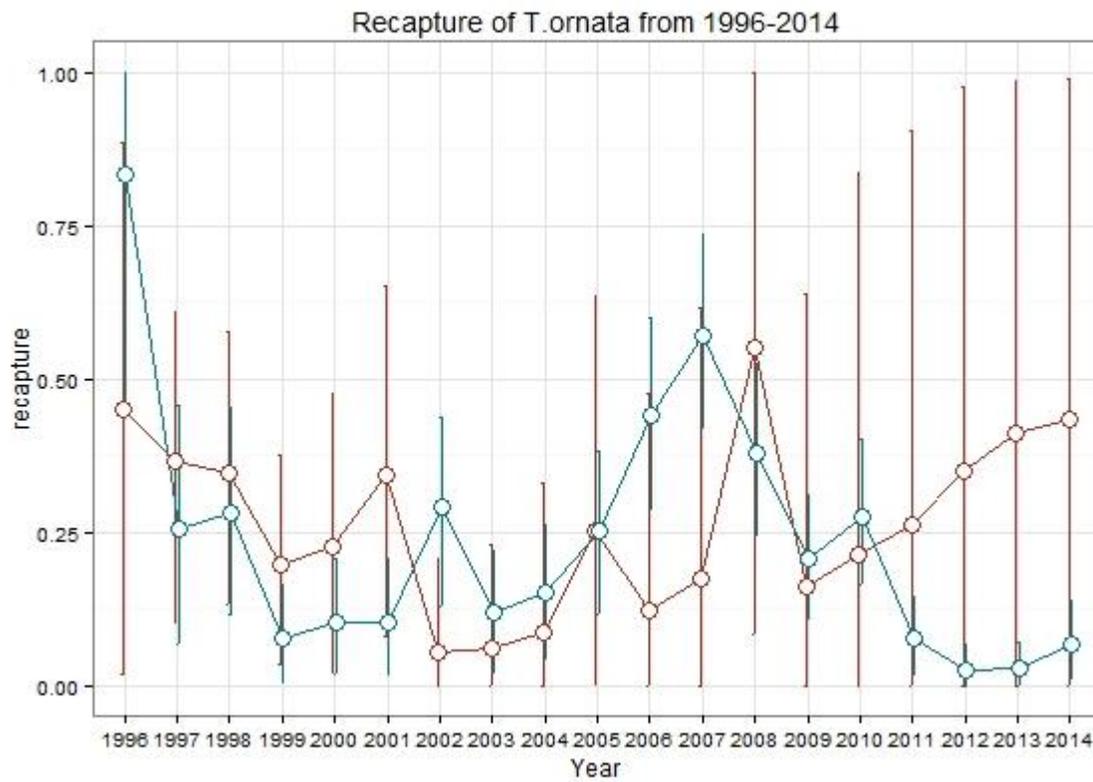


Figure 3: Comparison of apparent survival rates between sites and sexes for *T. ornata* adults in Thomson, IL. Bars show 95% credibility intervals around estimates.

Supplementary information



SI Figure 1: Recapture rates for *Terrapene ornata* by year at disturbed (red) and refuge (blue) site in Thomson, IL. Vertical bars are 95% credibility intervals around estimates.

CHAPTER 4. CONCLUSION

As societies recognize the importance of the contemporary global extinction crisis, conservation biologists are increasingly in demand to identify species of conservation concern, determine the factors causing their decline, and recommend the most efficient management practices to promote population persistence. Here, we examine these issues in light of one of the most endangered vertebrate taxa, turtles (IUCN 2015). Specifically, demographic parameters were estimated for populations of painted turtles (*Chrysemys picta*) and ornate box turtles (*Terrapene ornata*), both of which experience anthropogenic impacts despite living in very different habitats.

The effects of human development and presence seem to impact *C. picta* and *T. ornata* to varying degrees. In most data-rich estimates (including fecundity and adult survival), *C. picta* did not appear to be deleteriously affected by a large human presence in its habitat. In contrast, juvenile survival was much lower in this population compared to other estimates in the literature (Frazer et al. 1991; Mitchell 1988; Tinkle et al. 1981; Wilbur 1975; Zweifel 1989). Although this estimate is alarming, it is probable that methodological issues explain much of the discrepancy. Confidence intervals around the juvenile survivorship estimate are large, due to low recapture rates, and the estimate is likely biased downward due to a variety of methodological factors including reclassification of juveniles recaptured as adults into adult stages and the ability of juvenile turtles to escape from aquatic traps. Finally, nesting data and personal observations suggest that the population is not declining, lending more skepticism to our juvenile survivorship estimate. Thus, further research is required before

assuming that juvenile survivorship is reduced in this population. Most other estimates were in the range of those cited in other studies (Breitenbach et al. 1984; Eskew et al. 2010; Frazer et al. 1991; Gibbons 1968; Iverson & Smith 1993; Mitchell 1988; Nagle et al. 2000; Spencer & Janzen 2010; Tinkle et al. 1981; Wilbur 1975; Zweifel 1989); thus, little support is shown for a deleterious effect of anthropogenic presence on the persistence of this *C. picta* population. Before making broad conclusions about population persistence from the *C. picta* study, additional data on juvenile survival rates is necessary.

In contrast, anthropogenic habitat alteration was associated with significant decrease in the survival of adult female *T. ornata*. The microhabitat composed of cabins and associated structures and management regimes had lower survival rates for both adult females and adult males compared to the refuge site, though this distinction was only statistically significant for females. This difference between human-caused effects on *C. picta* and *T. ornata* emphasizes that effects of anthropogenic influence vary between species, and caution should be used before making generalizations.

In the future, an examination of the relative contribution of various demographic parameters to population growth rate would provide valuable information to wildlife managers. Specifically, determining elasticities and sensitivities of per capita population growth to specific demographic parameters would enable managers to identify the life stages most influential to long-term population persistence (Benton & Grant 1999). Although studies in other turtle species suggest that adult and juvenile survival play the most important role (Congdon et al. 1993; Congdon et al. 1994; Frazer et al. 1991; Heppell 1998) some research suggests that these trends may differ in shorter lived species (Spencer & Janzen 2010); therefore, further inquiry into these systems may lend beneficial insight.

In addition, continuing long-term monitoring of the *T. ornata* population in Thomson, IL would be helpful in determining the long-term effects of bike trail construction. Currently, survival rates appear to be unaffected; however, deleterious effects may just not have become apparent yet in this long-lived species. Additional years may bring additional information to light.

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