Recruitment dynamics, estimated vital rates, and population modelling of a Wood Turtle (*Glyptemys insculpta*) population in northeastern Minnesota

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Abstract

Wood Turtles (*Glyptemys insculpta*) are medium-sized, semi-aquatic, freshwater turtles that are classified as endangered by the International Union for Conservation of Nature (IUCN) due to declines in populations across their distribution in the Great Lakes region and eastern North America. Threats to Wood Turtle populations vary across their range, with recruitment failure due to nest predation considered a major threat in northern Minnesota.

In Chapter 1, we determine Wood Turtle nest predator species, nest predator visitation rates, and nest predation rates in northeastern Minnesota. We monitored 20 new nesting areas (NNAs) and 15 established nesting areas (ENAs) with camera traps for 1 to 4 summers (2015–2018). Turtle nests at some locations were individually caged, and an electric fence was installed at one ENA. We used camera traps to estimate predator visitation rates and to identify potential and observed nest predators. American badgers (*Taxidea taxus*) accounted for 55% and 4% of potential predator visitation events at ENAs and NNAs, respectively. All nests found were at ENAs, with 85% of depredation events by badgers. Mean hatching success was 62% and 6% at caged and uncaged nests, respectively. Most nest failures at both caged and uncaged nests were due to predation. Our study indicates that nest depredation rates are high in northeastern Minnesota, and that protecting nests from predation can be an effective management tool for increasing nest success.

In Chapter 2, we use reconstruction and simulation models to estimate population vital rates and sensitivity of the population to changes in recruitment and survival. Since 1990, 1,117 unique Wood Turtles have been captured, aged, and marked in the northeastern Minnesota population. We used 2,774 recaptures of these marked turtles to estimate abundance changes through time using a population reconstruction approach. The population model tracks age classes from birth until death (up to 60 years of age). The reconstructed population was compared with an age-class structured population model to estimate survival rates and evaluate population sensitivity to changes in survival of different age classes. Nest hatching rates and survival to 1 year were estimated with sensitivity analysis. In order to match the reconstructed population, annual survival of adults >14 years needed to be >95% and average annual survival for juveniles (1–14 years) needed to be approximately 86%. Nest/hatchling survival was estimated to be between 10% and 14% to be consistent with the reconstructed population over the past 30 years. Population reconstruction and modelling support a stable population historically, but recent high mortality rates of adults are cause for concern. Continued monitoring, marking, and recapturing of turtles in this population is critical to estimate population trends and identify management actions that will help maintain this population in the future.

Table of Contents

List of Tables

List of Figures

Chapter 1

Nesting success and nest predation of a Wood Turtle (*Glyptemys insculpta*) population in northeastern Minnesota

Introduction

Turtles are one of the most vulnerable taxonomic groups worldwide, with 43% of species classified as endangered or threatened (IUCN 2017). Ultimate factors that are driving declines in turtle populations include habitat loss and degradation, climate change, and pollution (Gibbs & Shriver 2002, IUCN 2017, Levell 2000, Saumure 2007). One proximate factor that is affecting many turtle populations is nest predation (Browne & Hecnar 2007, Geller 2012a, Holcomb & Carr 2013, Horne et al. 2003, Quinn et al. 2015). The predation rate on turtle nests can be greater than 90% (Horne et al. 2003, Limpus 2008, Marchand et al. 2002, Geller 2012a). Increased predation on turtle nests is in part the result of habitat fragmentation and increases in edge habitat used by many turtle nest predators (Temple 1987). Low recruitment can greatly affect population viability. For example, simulations assuming 90% nest predation and a juvenile survival rate of 80% for a population of Yellow Blotched Map Turtles (*Graptemys flavimaculata*) resulted in a declining population (Horne et al. 2003). In Illinois, two Spotted Turtle (*Clemmys guttata*) populations declined when nest predation was about 65% and juvenile survival varied between 65% and 80% (Feng et al. 2019).

The Wood Turtle is a species of conservation concern that is affected by high rates of nest predation. Wood Turtles are medium-sized, semi-aquatic, freshwater turtles that are classified as endangered by the International Union for Conservation of Nature (IUCN) due to declines in populations across their range around the Great Lakes and Eastern North America (IUCN 2017). After mating in fall and/or early spring, Wood Turtles typically nest once per year along sandy banks of rivers in early June (Compton 1999, Ernst & Lovich 2009). Predators learn the locations of nest areas because turtles often return to the same nest areas each year (Freedberg et al. 2005, Rowe et al. 2005). Documented Wood Turtle nest predators include American badger (*Taxidea taxus*), coyote (*Canis latrans*), common snapping turtle (*Chelydra serpentina*), Common Raven (*Corvus corax*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*) (Cochrane et al. 2015, Harding & Bloomer 1979, Geller 2012a). However, other carnivore species that are present where Wood Turtles exist may also be potential nest predators. For example, black bears (*Ursus americanus*) are documented nest predators of several turtle species, including Loggerhead Sea Turtles (*Caretta caretta*), Common Snapping Turtles, Western Pond Turtles (*Actinemys marmorata*), Peninsula Cooters (*Pseudemys peninsularis*), Florida Softshell Turtles (*Apalone ferox*), and Agassiz's Desert Tortoises (*Gopherus agassizii*) (Ernst & Lovich 2009, Lovich et al. 2014).

Wood Turtles were listed as a threatened species by the state of Minnesota in 1984 (MNDNR 2018), which is as the most western edge of the wood turtle's range. Wood Turtle nest depredation is high in this Northeastern Minnesota population (Cochrane et al. 2015, Berkeland et al. 2019). Conservation methods that have been used for the study population in Northeastern Minnesota include the construction and maintenance of new nest areas, fencing individual nests, and fencing around nest areas (Cochrane et al. 2017, Berkeland et al. 2019, MNDNR 2018).

Turtle nests can be protected from predation by fencing individual nests or by fencing an entire nest area. Electric fences or electrified nest boxes can be constructed around larger nesting areas where the land is not too steeply sloped or likely to erode. For a population of Diamondback Terrapin (*Malaclemys terrapin*) in Georgia, only one of 27 nests protected with electrified wire was depredated, while all nests without an electric wire were depredated (Quinn et al. 2015). Small cages can be placed over individual nests, although this is logistically difficult because it requires observing a nesting site to identify nest locations (Cochrane et al. 2017, Lapin et al. 2016, WIDNR 2016). Electric fencing at nest areas and individual nest cages can increase hatching rates in areas with high rates of nest predation (Levell 2000, Lapin et al. 2016, Quinn et al. 2015, WIDNR 2016).

Constructing and maintaining new nest areas is one technique that can reduce nest predation. Nest areas are created by adding sandy soil to a potential nesting area or by removing vegetation from a potential nesting area and disturbing the soil prior to the nesting season (Paterson et al. 2013, Grosse et al. 2015, Buhlman & Osborn 2011, Kiviat et al. 2000). Several species of turtles have been documented using new nest areas, including Painted Turtles (*Chrysemys picta*) (Paterson et al. 2013), Common Snapping Turtles (Paterson et al. 2013), Diamondback Terrapins (Grosse et al. 2015), Spotted Turtles (Beaudry et al. 2010), and Blanding's turtles (*Emydoidea blandingii*) (Kiviat et al. 2000, Paterson et al. 2013). Wood Turtles have also used new nesting areas (Buhlmann & Osborn 2011, Cochrane et al. 2017, Berkeland et al. 2019). Intuitively, new nest areas would have lower predation rates if they were not discovered by predators. Predator visitation rates to new nesting areas have not been compared to established nesting areas in previous studies, but nest success was thought to be higher at some of the new nesting areas compared to established nesting areas.

Identifying nest predator species visitation rates and predation rates at Wood Turtle nesting areas in northeastern Minnesota would help to evaluate the effectiveness of management actions for increasing nest success. We used camera traps to measure visitation rates of potential and known nest predators. We assessed use of new nest areas, compared hatching success of caged and uncaged nests, and compared hatching success of unfenced sites and a site with an electric fence around the nesting mound. We predicted that Wood Turtles, non-predators, and predators would visit new nesting areas less than established nesting areas. We also hypothesized that Wood Turtle and predator events would occur more often during the nesting season and would not vary from year to year.

Study Area

We studied Wood Turtle nest areas along a 15-km stretch of a river in northeastern Minnesota from 2015 to 2018. Specific locations are withheld in compliance with state of Minnesota data practices law. The river and tributaries are located within the Laurentian Mixed Forest ecological province (MNDNR 1999). Over 90% of the surrounding land is forested, with the remaining land in non-forest or aquatic habitat classes (Brown et al. 2016). Around 75% of the area is in public ownership. Fire dependent forests comprise 80% of the area. Aspen (*Populus* spp.), balsam fir (*Abies* *balsamea*), and paper birch (*Betula papyrifera*) dominate the forest cover. Pine cover types (*Pinus* spp.) are less common in the surrounding landscape due to past forest harvest, but they are present in sandy soils adjacent to some nest areas at river cutbanks. Black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*) comprise over 90% of hydric forest types in the surrounding area. Non-forest vegetation consists of lowland alder (*Alnus* spp.) and grass/forb openings. Oxbow lakes and other non-flowing water features also occur in the study area (Cochrane et al. 2017).

Methods

In 2015, the Minnesota Department of Natural Resources created 21 new nesting areas and restored a nesting mound created in 1990 (Cochrane 2017). Sites were grouped by forest stand and proximity to one another. New nesting areas (NNAs) were created in four different forest stands, identified by A, B, C, and D (Table 1.1). Group NNA-A includes three new nesting scrapes on south-facing, steep hillsides in brushy habitat about 50 m from a creek that is connected to the main river. Group NNA-B contains eight new nesting scrapes about 75 m from the river in a forested area with many young pine trees. Group NNA-C contains four new nesting scrapes about 100 m from the NNA-A creek. Group NNA-C new nesting scrapes are on south-facing slopes in a clear cut. Group NNA-D contains six new nesting scrapes in a clear cut along the edge of steep forested riverbanks about 25 m from the river.

Established nesting area (ENA) sites were made up of groups ENA-E, ENA-F, ENA-G, ENA-H, ENA-I, ENA-J, and ENA-K (Table 1.1). Group ENA-E contains three natural nest areas along a short stretch of river that the only major road in the area runs across, two nest areas are high sandy areas and one nest area is on a large cliff bank. Group ENA-E nest areas are adjacent to the edge of the river. Group ENA-F contains five nest areas that are relatively less accessible to people, three of the nest areas are natural, with two of these being high cliff banks and one a high sandy area across from the high cliffs. The remaining nest area in Group ENA-F is along a high bank where a bridge used to cross the river, but are currently the dead ends of minimum maintenance roads. Group ENA-F nest areas are adjacent to the edge of the river. Group ENA-G is composed of a nesting mound created in 1990, denuded of vegetation in 2015, and electrified in 2017, and a nearby nest area along a road. Group ENA-G nest areas are 2 m from the edge of the river. Group ENA-H has three nest areas along or near an old railroad grade where a bridge has been removed. Group ENA-H nest areas are adjacent to the edge of the river. Group ENA-I contains three nest areas in a privately owned gravel pit, and is about 120 m from the edge of the river. Although ENA-I is further from the river than other nest sites, there is a series of ponds that connect the nest site and the river.

Groups ENA-J and ENA-K were not monitored with cameras, but were surveyed as roadside sites throughout each nesting season from 2015 to 2018. ENA-J incorporates two roadside nest areas; one along the side of a 50 m stretch of a gravel road about 15 m from the edge of the river and the other along the same road, where a pond that is 90 m from the river intersects with the road. ENA-K incorporates four nest areas; all along roads or railroads and within 20 m of the water. One site is along the main river where a railroad track crosses. Three sites are along smaller tributaries (< 5 m) that flow into the main river, and are above where the tributary passes under a road by bridge or culvert. Two of these sites are more than 5 km away from the other ENA sites.

Bushnell Advantage and Bushnell Aggressor cameras were deployed to monitor Wood Turtle nesting and presence of predators at NNA and at ENA from 2015 through 2018 (Table 1.2). Cameras were deployed from May to September. The number of cameras deployed at a given time varied as cameras were moved among sites over time. Cameras were set to motion detection in 2015 and 2016, and to time-lapse and motion detection in 2017 and 2018. Photos were downloaded monthly.

Predator exclusion

During the 2015 and 2016 field seasons, we opportunistically covered 29 Wood Turtle nests with individual nest cages. Cages were constructed with 1.3 x 1.3 cm mesh wire fencing. Individual nest cages were 41 x 41 cm wide and 18 cm tall. Nest cages were open on the bottom. Each cage was placed over a single Wood Turtle nest and secured on all four corners with 15 cm metal tent spikes. Camera traps were set at caged nests to evaluate the effectiveness of the cages (Cochrane et al. 2017).

An electric fence exclosure was constructed around the nest mound at site ENA-G in spring 2017. The river-facing side of the 15 m x 7.5 m exclosure consists of a three-stranded, solar-powered electric fence over a grounded wire mesh (Geller 2012b). The other three sides have wire mesh and two electrified strands of wire along the top of the fence. Camera traps were placed on the nesting mound in 2017 and in 2018 to evaluate the effectiveness of the electric fence.

Camera trap data

An event was defined as one or more pictures of an animal passing in front of the camera. If pictures were taken of the same species of animal within a five minute interval, those photos were considered the same event. We classified events to species when possible, and grouped events as Wood Turtles, predators, and non-predators for analysis. Predators included members of the order Carnivora, the Common Snapping Turtle, the American Crow (*Corvus brachyrynchos*), and the Common Raven (Ernst 2009, WIDNR 2016). If a predator was present in pictures without evidence of digging or consuming eggs, the event was classified as presence of a predator. If a predator was observed digging at a nest area or consuming eggs, the event was classified as nest predation. All other events were classified as non-predator events.

Statistical analyses

The number of events were standardized to events per 100 camera days because the number of days that cameras were deployed at a site varied. We used NNAs as one treatment group and ENAs as the other treatment group. The number of events at NNAs and ENAs was compared using a one-tailed Welch two-sample t-test or a two-sample t-test. A Kruskal-Wallis rank sum test was used to test if Wood Turtle, non-predator, and predator event frequencies varied by month or across years. Differences between months and between years were tested using a Dunn (1964) Kruskal-Wallis multiple comparison post-hoc test, with p-values adjusted using the Holm method.

Normality was assessed using the Shapiro-Wilk test and examining a histogram. If a dataset was not normally distributed, square root, cube root and log transformations were tested. Equal variance was assessed using the Bartlett test and examination of a boxplot. If variance was equal, parametric tests were used, otherwise the robust Welch's t-test or the non-parametric Kruskal-Wallis rank sum test was used. The threshold of significance was set at $\alpha = 0.05$.

All analyses were carried out in R (version 3.5.2) (R Core Team 2013). Packages used included ggplot2 (Wickham 2016), car (Fox & Weisberg 2019), FSA (Ogle et al. 2020), and readxl (Wickham et al. 2019).

Results

Camera traps recorded 7,808 events over 6,040 camera days. Project personnel, people, cars, and domestic dogs accounted for 1,652 events. There were 1,105 insect events, 741 events that could not be identified, and 4,310 events by mammals, birds, and reptiles. Of these 4,310 events, there were 3,040 events over 3,822 camera days at NNAs and 1,270 events over 2,218 camera days at ENAs. By camera deployment, there were 54.7 ± 23.4 events per 100 camera days at ENAs and 93.6 ± 25.0 events per 100 camera days at NNAs by all species (Table 1.3). There were 13.9 ± 4.4 predator presence events per 100 camera days at ENAs, and 3.7 ± 1.2 predator presence events per 100 camera days at NNAs (Table 1.4).

There are many differences between the species found at ENAs compared to NNAs. Wood Turtles and badgers had the most extreme contrast between ENAs and

NNAs, with over 82 and 23 times more events at ENAs than at NNAs, respectively (Table 1.3, Fig. 1.1). Bird, cervid, and lagomorph events were 50% of events at ENAs and 91% of events at NNAs (Fig. 1.1). Known Wood Turtle predators were more common at ENAs, with skunks and snapping turtles only present at ENAs (Table 1.3, Fig. 1.1).

Non-predator events were more similar between ENAs and NNAs. About 25% of events at both NNAs and ENAs were birds. Cervids and lagomorphs also accounted for more than 10% of events at ENAs and NNAs, with 3-5 times more events at NNAs than at ENAs.

Predators

Badgers accounted for 55% of 301 predator presence events at ENAs, compared to only 4% of 117 predator presence events at NNAs (Fig. 1.2). Badgers were detected at four of the 20 NNAs and at 13 of 15 ENAs (Table 1.4). All nests and all depredation events were at ENAs (Table 1.5), with 85% of the 66 depredation events by badgers. Raccoons, red fox, ravens, and striped skunks each accounted for 3-5% of depredation events (Fig. 1.3).

Most badger events occurred in July (Table 1.6). Badger events per 100 camera days at NNAs and ENAs from 2015 to 2018 were normally distributed (Shapiro-Wilk test NNA: $W = 0.830$, $p = 0.167$; ENA: $W = 0.916$, $p = 0.222$). Assumptions of equal variance were not met (Bartlett's test, $df = 1$, $K^2_1 = 17.613$, $p < 0.001$). Badger events occurred more often at ENAs than NNAs (Welch two sample t-test, $t_{12.0} = 4.125$, $p = 0.0014$).

Predator presence events per 100 camera days at NNAs and ENAs from 2015 to 2018 were normally distributed (Shapiro-Wilk test, NNA: W = 0.912, p-value = 0.070; ENA: W = 0.883, p = 0.053), with variance higher at ENAs than at NNAs (Bartlett's test, df = 1, $K^2_1 = 351.9$, $p < 0.001$). Predator presence events occurred more often at ENAs than at NNAs (Welch two sample t-test, $t_{14.5} = -3.67$, p = 0.002), with about 8 predator presence events / 100 camera days at ENAs compared to 2 predator presence events / 100 camera days at NNAs (Table 1.6).

Predator presence events per 100 camera days did not vary among NNA sites between years or among ENA sites between years (Kruskal-Wallis rank sum test, NNA: df = 3, $\chi2$=2.358, p = 0.501; ENA: df = 3, $\chi2$= 5.195, p = 0.158) (Table 1.5). Most predator presence events occurred in June and July (Table 1.6), but predator presence events did not vary significantly between the months of May through August (Kruskal-Wallis rank sum test, df = 3, $\chi2$= 7.694, p = 0.052, Dunn Kruskal-Wallis multiple comparison, p-values adjusted with the Holm method). June and July is when most badger events occurred.

Non-predators

Non-predator events per 100 camera days at NNAs and ENAs from 2015 to 2018 were normally distributed (Shapiro-Wilk test NNA: W = 0.970, p = 0.745; ENA: W =0.903, p = 0.146), with higher variance at NNAs (Bartlett's test, df = 1, $K^2_1 = 4.836$, p = 0.0279). Non-predator events occurred more often at NNAs than ENAs (Two sample t-test, $t_{31} = 3.999$, p = 0.00037), with about 20 non-predator events / 100 camera days at ENAs compared to 64 non-predator events / 100 camera days at NNAs (Table 1.6). Non-predator events per 100 camera days varied among NNA sites between years and ENA sites between years (Table 1.4). Most non-predator events at NNAs occurred in June, while most non-predator events at ENAs occurred in September (Table 1.6).

Wood Turtles

There were 182 Wood Turtle events at ENAs, and only 4 Wood Turtle events at NNAs. Wood Turtles were detected at 12 of 15 ENAs with almost 10 events per 100 camera days, and at 3 of 20 NNAs with 0.1 events per 100 camera days (Table 1.5). Wood Turtle events per 100 camera days at NNAs and ENAs from 2015 to 2018 were normally distributed after a cube root transformation (Shapiro-Wilk test, NNA: $W = 0.999$, $p = 0.945$; ENA: $W = 0.911$, $p = 0.219$), with lower variance at NNAs because there were so few events (Bartlett's test, $df = 1$, $K_{21} = 10.963$, $p < 0.001$). Wood Turtle events occurred more often at ENAs than at NNAs (Welch two sample t-test, $t_{12.72} = -4.03$, $p = 0.0015$).

Wood Turtle events per 100 camera days did not vary among NNA sites across years or among ENA sites across years (Kruskal-Wallis rank sum test, NNA: $df = 3$, $\chi 2=4.972$, $p = 0.174$; ENA: $df = 3$, $\chi 2= 7.119$, $p = 0.0682$) (Table 1.5). June, the month when most nesting occurs in this population, had more Wood Turtle activity than all other months (Table 1.6, Kruskal-Wallis rank sum test, $df = 4$, $\chi 2= 39.52$, $p < 0.001$, Dunn Kruskal-Wallis multiple comparison, p-values adjusted with the Holm method).

Wood Turtle Nesting Success

Overall success of uncaged nests was 6% (Table 1.7). In 2015, only one of 90 uncaged nests that were monitored hatched across 15 sites. In 2016, 5 of 15 uncaged nests hatched, with all five hatching at the restored nesting mound site ENA-G. Predation was the cause of nest failure at the other 10 uncaged nests at five other sites. Fewer nests were found in 2017 and 2018 because nest areas were monitored opportunistically or with cameras. Of the 16 nests found in 2017 and 6 nests found in 2018, 11 were discovered after depredation events.

Protecting nests with cages increased hatching success. None of the six nests caged in 2015 were depredated (Table 1.7). In 2016, three of 23 caged nests were depredated by badgers. Five of the 23 caged nests had been moved to the restored nesting mound, and four of these nests hatched. In 2017 and 2018, all 10 nests found at the nesting mound protected by an electric fence hatched. Nest success in 2015 and 2016 at this nesting mound before the fence was installed was 54%. Overall, about 62% of caged or fenced nests hatched, compared to about 6% of uncaged nests (Table 1.7). Additionally, 14% of nests did not hatch due to flooding or other factors (Table 1.8).

Discussion

Nest predation appears to be a major factor affecting reproductive success in this northeast Minnesota Wood Turtle population. Most nest failures were due to predation by badgers, which were identified as Wood Turtle nest predators in northeast Minnesota (Cochrane et al. 2015) and Wisconsin (Vraniak et al. 2017). Nest predation is a significant source of egg mortality for many freshwater turtle species (Dawson et al. 2016, Holcomb & Carr 2013), and primary nest predators vary geographically. The raccoon is the most common predator of Wood Turtles across much of the Wood Turtle's distribution (Saumure & Bider 1998, Harding 2008, Ernst & Lovich 2009, Buhlmann & Osborn 2011, Parren 2013). Raccoons are considered a subsidized predator, a native species able to survive and expand in range due to resources provided by humans (Mitchell & Klemens 2000). Raccoon events were much less common than badger events in our study area. The low human population density in the study area may prevent the raccoon population from increasing as it does in areas where the human population density is higher. Other predators including bobcat, non-badger mustelids, bear, wolves, and coyotes were detected, but these predators did not detect or depredate nests.

The nest success rate was about 62% when nests were covered with cages or surrounded with an electric fence. This suggests that many of the Wood Turtle eggs in nests would hatch if nest predation were prevented. Camera traps showed American badger, red fox, common raven, raccoon, and striped skunk depredating Wood Turtle nests. These predators were much more common at ENAs than NNAs and may have targeted ENAs because freshwater turtles often exhibit nest-site fidelity (Freedberg et al. 2005, Rowe et al. 2005). Predators can learn nest area locations to return to year after year and use rivers as natural corridors to walk and search along. For example, badgers were detected at nearly all ENAs, and returned to many of the ENAs every year. For a few ENAs, badgers were not detected in every year that cameras were present, potentially due to individual badgers dying, dispersing, or alternative food sources being available in certain years.

Nest cages greatly improved nest success in 2015 and 2016. Individual nest cages, while successful, were time consuming to deploy and monitor. Nest areas had to be observed during the nesting season in order to identify where nests were laid and nest predation would often occur soon after the eggs were laid and before a cage could be placed over the nest. Another potential problem with individual nest cages is that badgers dug under cages to retrieve eggs during the summer of 2016, which means that a better nest cage design is needed. Badgers are olfactory predators that rely on their sense of smell to locate food resources (Conover 2007). Olfactory, visual, or tactile cues associated with soil disturbance are the primary indicator for nest location by raccoon, North American river otter (*Lontra canadensis*), and American mink (*Neovision vision*) (Rutherford et al. 2016). Skunks and foxes also rely on olfaction in addition to visual cues to locate prey (Conover 2007). Ravens rely on visual cues for finding nests (Conover et al. 2010). Nest monitoring protocols used for placing nest cages should be designed to avoid potentially increasing predation pressures from invasive techniques such as digging up potential nests to confirm presence and species identity.

One alternative to individual nest cages is to use an electric fence around a larger nesting area, as we did in 2017 and 2018 at the nesting mound built in 1990. No signs of predation were found inside the electric fence at the nesting mound in 2017 or 2018, but this location only had three visits from badgers, all in 2015. There were only 1.9 predator presence events per 100 camera days at the site from 2015-2018, with no predators detected inside the fence and 1.4 predator presence events per 100 camera days detected outside the fence from 2017-2018. In contrast, other ENAs had more than 30 predator events per 100 camera days. This may be due to the habitat around the nesting mound being very different from many of the other established nesting areas. While most of the nesting areas are along high, sandy banks connected to upland habitat, the nesting mound is a large mound of sand surrounded by wet swamp on three sides and the river on the fourth side. It may be that 2015 was a dry year when badgers were able to get out to the mound, and the following summers were too wet for them to visit the mound.

Although this may not have been a complete test of the electric fence as a deterrent due to few predator visits outside of the fence, the electric fence was effective and efficient, as found in other studies that have placed electric fences around individual nests (Quinn et al. 2015) or entire nesting areas (Geller 2012b). While effective, there are increased costs for the materials and labor to build and maintain an electric fence. Fences that are not electrified reduce maintenance costs but provide less of a deterrent for predators. In the U.K., researchers tried to exclude badgers using nonelectric and electric fences. Non-electric fences were not effective while the effectiveness of the electrified fences increased with increasing voltage (Poole et al. 2004).

Wood Turtles rarely visited NNAs. This may be due to the low likelihood of turtles discovering NNAs while foraging and then choosing to nest there. The NNAs created in 2015 are further on average from the river than the ENAs. The nesting mound established in 1990, which was used by Wood Turtles every year from 2015 to 2018, is within 2 m of the river, and visible from the river because the mound is about 2.5 m tall. All but 3 ENAs are also less than 20 m from river, while the minimum distance to the river for NNAs is 25 m. Turtles might begin nesting on new nest areas if they were closer to the river than the existing NNAs. However, nest site fidelity is a significant predictor of nesting location for many freshwater turtle species (Freedberg et al. 2005, Rowe et al. 2005). Gravid females, eggs, or hatchlings may have to be moved to a new nesting area before turtles start nesting there.

Simulation modelling for this population of Wood Turtles (chapter 2), indicates survival from egg to age one must be ≥8% to have the current minimum population numbers. From 2015 through 2018, only 6% of unprotected nests survived, and it is unlikely that most hatchlings are surviving over winter. Most current estimates for Wood Turtle hatchling survival to overwinter are between 7% and 37% (Dragon 2014, Jones et al. 2015, Paterson et al. 2012,) with one estimate of 88.8% (J. Tamplin, University of Northern Iowa, unpublished data). Predator control measures, such as trapping for badger, raccoon, skunk, and fox near the established nesting areas could be an effective strategy to increase nest success. Nest survival and recruitment of Yellow Mud Turtles (*Kinosternon flavescens)* at the Big Sand Mound study area in Iowa increased in 1979 and 1980 following the removal of raccoons from the nest areas in 1979 (Christiansen and Gallaway 1984). More intensive management techniques may be needed if the population is declining. A possible management action is headstarting, which involves raising turtles in captivity from egg stage to hatchling stage or later (typically for 1 or 2 years). This process is time and cost intensive as the turtles require care if they are head started beyond the hatchling stage. Head starting has been successful for Wood Turtles when used in conjunction with management actions that maintain high adult and juvenile survival (Mullin 2019, Mullin et al. 2020).

The results of this study will inform future efforts for increasing hatching success and may help managers decide which conservation strategies should be implemented. Very little use of NNAs occurred by Wood Turtles or predators, indicating that maintenance and protection of ENAs may be a more effective strategy for increasing productivity than expending resources creating NNAs. Both individual nest caging and electric fencing have been used within the study area, but both methods have associated costs and benefits and may be easily implementable for certain sites. In either case, the use of these predator exclusion methods is a viable way to increase hatching success within the study area. It may be that a combination of these conservation methods could be the most effective way to stop or prevent population decline now or in the future.

Figures & Tables

Table 1.1 Number of new nesting areas (NNAs) and established nesting areas (ENA) grouped by habitat type, location, and distance to the river. Most groups were monitored using camera traps from 2015 to 2018 while ENA-J and ENA-K were monitored by roadside surveys.

Group	Habitat type	Average Distance to River	Number of Nest Areas
NNA-A	Brush	50 m	3
NNA-B	Pine Forest	75 m	8
NNA-C	Clear Cut	100 m	4
NNA-D	Clear Cut	25 m	6
ENA-E	Mixed Forest	0 m	3
ENA-F	Mixed Forest/Brush	0 m	4
ENA-G	Brush	2 m	2
ENA-H	Brush	0 m	3
ENA-I	Open Pit	120 m	3
ENA-J	Mixed Forest	50 m	2
ENA-K	Open Railroad/Roadside	5 m	4

Table 1.2 Number of cameras deployed at new nesting areas and established nesting areas from 2015-2018. The total number of nest areas is less than the number of cameras because multiple cameras were deployed at the same site or, in some cases, a camera failed and was either replaced by a different camera or the nest area was excluded from the final numbers of monitored nest areas.

Year	Cameras Deployed	New Nest Areas	Established Nest Areas
2015	24	11	10
2016	24	9	6
2017	27	18	1
2018	26	15	9

Table 1.3 Total events per 100 camera days (CD) at camera traps by species or family at new nesting areas (NNA) and established nesting areas (ENA).The ENA:NNA ratio is calculated as appropriate, and the percent of events made up by each species at ENAs and NNAs is also calculated.

	Events / 100 CD		**ENA:NNA Ratio**	**Percent**	
Event Type	**ENA**	**NNA**		**ENA**	**NNA**
Wood Turtle	11.7±8.4	0.1±0.2	82.5	14.3	0.1
Snapping Turtle	0.5±0.7	0	-	0.6	0
Unknown Turtle	5.0±8.1	0.03±0.07	144.1	2.6	0.1
Mammalian Predators					
Badger	5.5±3.9	0.2±0.3	23.9	13.1	0.1
Raccoon	1.1±1.0	0.1±0.1	15.7	2.4	0.1
Striped Skunk	0.7±0.6	0	-	1.5	0
Canidae	0.4±0.5	1.8±0.9	0.2	1.3	2
Mustelidae[1]	0.2±0.4	0.01±0.02	20.5	0.3	0
Bobcat	0.4±0.7	0.1±0.1	5.7	0.9	0.1
Black Bear	0.9±1.0	1.2±1.0	0.8	2	1.1
Avian Predators					
American Crow	0.4±0.4	0.2±0.2	1.7	0.6	0.3
Common Raven	0.4±0.8	0.3±0.6	1.4	1.2	0.2
Non Predators					
Birds	11.1±5.8	24.6±8.6	0.5	26.5	25.2
Cervidae	8.4±4.4	47.7±21.6	0.2	13.8	44.1
Lagomorpha	3.2±4.3	10.7±9.1	0.3	10.2	21.5
Rodentia	8.2±15.6	13.4±16.7	0.6	3	1.6
Snake	0.02±0.03	0.02±0.05	0.7	0.1	0.1
Unknown Mammal	2.5±4.1	3.0±4.6	0.8	5.9	3.6
Total Average	54.7±23.4	93.6±25.0	0.6	100	100

[1] Mustelidae except for badger

Table 1.4 Non-predator, predator, badger, and turtle events per 100 camera days at established nesting areas (ENAs) and new nesting areas (NNAs) within the NE Minnesota study area in each year from 2015 to 2018.

	Non-predator		**Predator**		**Badger**		**Wood Turtle**	
Year (± SD)	**ENA**	**NNA**	**ENA**	**NNA**	**ENA**	**NNA**	**ENA**	**NNA**
2015	34.5 ± 25.8	78.9 ± 49.9	16.4 ± 16.1	3.9 ± 3.3	8.0 ± 8.7	0.1 ± 0.3	4.1 ± 6.7	0.0
2016	44.4 ± 21.1	114.9 ± 74.1	16.5 ± 15.6	5.3 ± 4.7	8.5 ± 11.5	0.6 ± 1.5	23.7 ± 30.5	0.0
2017	-	70.4 ± 53.0	-	2.3 ± 2.3	-	0.1 ± 0.3	-	0.1 ± 0.3
2018	20.7 ± 16.1	72.2 ± 44.1	8.7 ± 12.0	3.4 ± 4.1	5.2 ± 8.8	0.0	7.5 ± 20.4	0.4 ± 1.5
Mean	**33.2± 11.9**	**84.1 ± 20.9**	**13.9 ± 4.4**	**3.7 ± 1.2**	**7.2± 1.8**	**0.3 ± 0.3**	**11.8 ± 10.4**	**0.1 ± 0.2**

Table 1.5 Predator, depredation, badger, and Wood Turtle events per 100 camera days at 35 camera trap locations within the NE Minnesota study area from 2015 to 2018. Locations are classified as new nesting areas (NNAs) and established nesting areas (ENAs).

Site Type	Site	Predator	Depredation	Badger	Wood Turtle
NNA	A1	0.8	-	0.0	0.0
	A2	7.5	-	0.0	0.0
	A3	4.2	-	0.3	0.0
	B1	1.3	-	0.0	0.0
	B2	3.9	-	0.0	0.0
	B3	4.9	-	0.0	0.0
	B4	1.9	-	0.0	0.0
	B5	2.4	-	0.0	0.0
	B6	1.6	-	0.0	0.0
	B7	3.4	-	0.0	0.5
	B8	2.3	-	0.0	0.0
	C1	7.6	-	0.3	0.0
	C1	3.5	-	0.7	0.0
	C3	2.9	-	0.0	0.0
	C4	4.2	-	0.0	0.0
	D1	0.4	-	0.0	0.0
	D2	3.9	-	0.6	1.3
	D3	0.8	-	0.0	0.8
	D4	0.5	-	0.0	0.0
	D5	0.7	-	0.0	0.0
Mean ± SD		2.9 ± 2.1	-	0.1 ± 0.2	0.1 ± 0.3
ENA	E1	18.5	11.8	16.9	12.3
	E2	8.8	2.9	2.9	0.0
	E3	2.5	0.0	0.0	0.8
	F1	28.3	4.3	22.8	2.2
	F2	18.3	8.8	11.7	6.3
	F3	4.5	0.0	1.1	2.3
	F4	7.8	1.9	2.9	6.8
	G1	1.9	0.4	0.6	5.2
	G2	13.4	0.0	4.9	21.1
	H1	3.1	0.0	0.0	58.3
	H2	36.4	3.3	15.2	3.3
	H3	23.0	2.6	10.9	1.9
	I1	41.4	3.4	27.6	24.1
	I2	14.0	0.0	7.0	0.0
	I3	11.5	0.0	7.7	0.0
Mean ± SD		15.6 ± 11.8	2.6 ± 3.4	8.8 ± 8.3	9.6 ± 14.9

Table 1.6 Non-predator, predator, badger, and turtle events per 100 camera days at established nesting areas (ENAs) and new nesting areas (NNAs) within the NE Minnesota study area in each month across all study years.

	Non-predator		**Predator**		**Badger**		**Wood Turtle**	
Month (± SD)	**ENA**	**NNA**	**ENA**	**NNA**	**ENA**	**NNA**	**ENA**	**NNA**
May	24.3 ± 32.8	83.0 ± 92.4	5.6 ± 12.1	2.5 ± 5.5	2.2 ± 8.6	0.1 ± 0.6	8.9 ± 34.4	0.0
June	29.4 ± 25.2	114.1 ± 81.9	13.9 ± 17.2	3.8 ± 3.7	5.7 ± 8.7	0.2 ± 0.5	19.6 ± 32.3	0.3 ± 1.0
July	19.9 ± 22.7	57.9 ± 39.6	14.9 ± 17.3	3.9 ± 4.1	10.1 ± 14.9	0.0	0.2 ± 0.8	0.2 ± 0.7
Aug	18.1 ± 15.0	52.9 ± 52.5	12.2 ± 14.3	1.9 ± 2.5	7.9 ± 10.7	0.0	0.2 ± 0.8	0.0
Sept	21.3 ± 32.0	46.0 ± 55.9	0.7 ± 1.9	0.2 ± 0.7	0.2 ± 0.9	0.2 ± 0.7	2.7 ± 8.9	0.0
Oct	4.4 ± 13.2	27.5 ± 68.3	0.0	0.0	0.0	0.0	10.0 ± 38.7	0.0
Mean	**19.6 ± 8.4**	**63.6 ± 30.6**	**7.9 ± 6.7**	**2.0 ± 2.1**	**4.3 ± 4.2**	**0.1 ± 0.1**	**6.9 ± 7.5**	**0.1 ± 0.1**

Table 1.7 Total number of nests found, number of nests that hatched, and percent success of unprotected nests and protected nests in each year from 2015 to 2018 and across all years.

Unprotected	**Year**	**Nests**	**Hatch**	**% Success**
	2015	90	1	1
	2016	15	5	33
	2017	11	1	9
	2018	1	0	0
	All years	117	7	6
Protected	2015	6	3	50
	2016	23	11	48
	2017	5	5	100
	2018	5	5	100
	All years	39	24	62

Table 1.8 Total number of protected and unprotected nests found at different nesting areas from 2015 to 2018 within the NE Minnesota study area. Predation indicates the number of nests that were depredated, Fail indicates that nests could not be confirmed to have been depredated, were flooded, or did not hatch for unknown reasons, and Hatch indicates the known number of nests that hatched at each established nesting area (ENA) group.

	Protected Nests					**Unprotected Nests**				
Group	**N**	**Predation**	**Fail**	**Hatch**	**Predation (%)**	**N**	**Predation**	**Fail**	**Hatch**	**Predation (%)**
E	11	2	7	2	18	5	4	1	0	80
F	3	1	0	2	33	15	13	2	0	87
G	22	0	3	19	0	25	13	7	5	52
H	3	2	0	1	67	7	5	2	0	71
I	0	-	-	-	-	21	20	0	1	95
J	0	-	-	-	-	14	13	0	1	93
K	0	-	-	-	-	30	30	0	0	100
TOTAL	**39**	**5**	**10**	**24**	**13**	**117**	**97**	**13**	**7**	**83**

Figure 1.1 Percent of camera trap events per 100 camera days by event type at established nesting areas (ENAs) and new nesting areas (NNAs) within the NE Minnesota study area from 2015 to 2018.

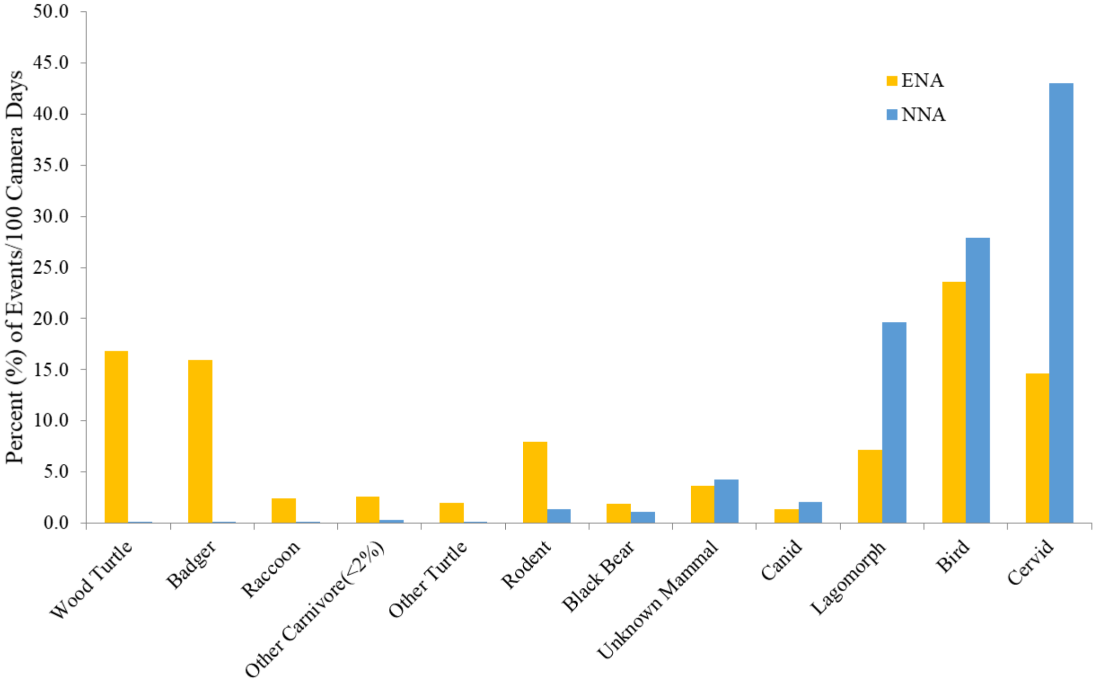


Figure 1.2 Predator events (%) per 100 camera days by potential predator species or group at established nesting areas (ENAs) and new nesting areas (NNAs) from 2015 to 2018.

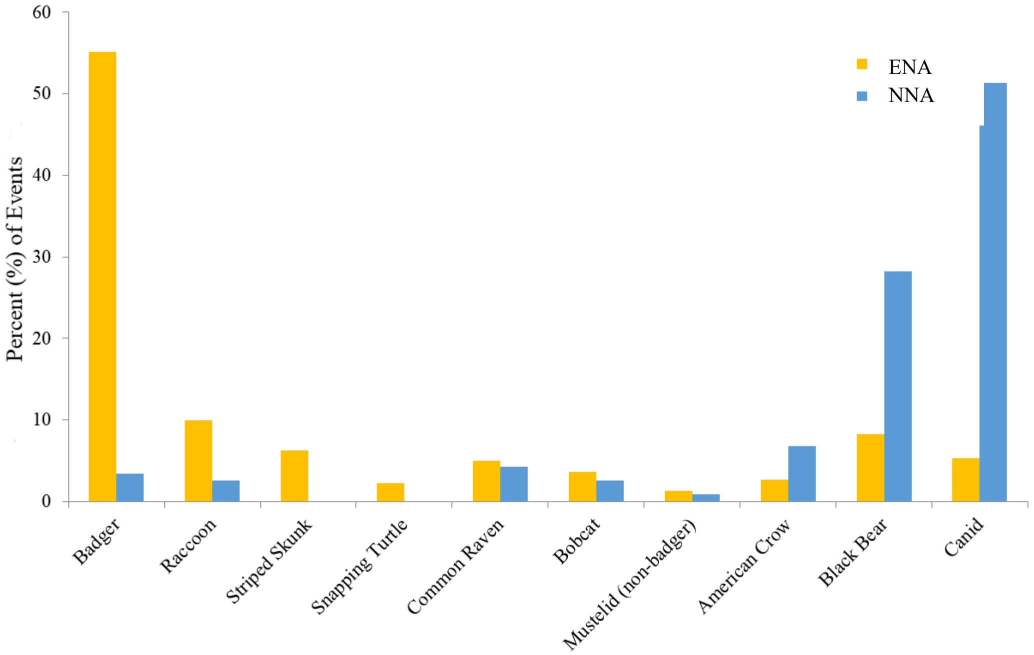
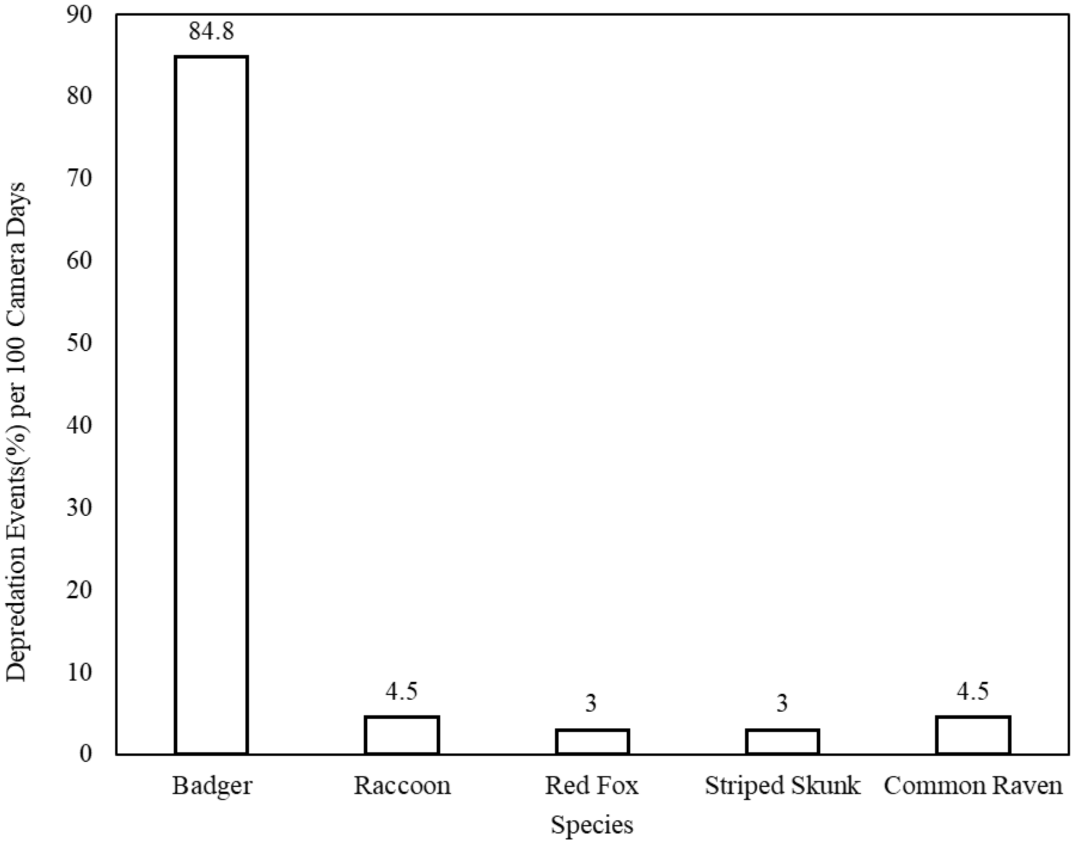


Figure 1.3 Depredation events (%) per 100 camera days by taxa recorded by camera traps at established nesting areas (ENA) within the NE Minnesota study area from 2015 to 2018. The number of depredation events is shown above each bar.



Chapter 2

Estimated vital rates and population modelling of a Wood Turtle (*Glyptemys insculpta*) population in northeastern Minnesota

Introduction

Declining populations are leading to an increasing need for long-term research to determine demographic parameters of animal species of concern such as turtles. Many turtle life history traits associated with longevity reduce the adaptive abilities of turtle populations to change and ultimately to persist (Congdon et al. 1993, Gibbons 1987). Slow growth and delayed sexual maturity are two examples of these life history traits that can impact the continued persistence of turtle populations. Turtle life stages include egg, hatchling, juvenile, and adult, with each stage susceptible to different causes of mortality. The lack of data on demographics of turtle populations, especially for the intermediate life stages, limits the effectiveness of conservation management for these populations.

Population monitoring or assessments track population trends and are used to evaluate the effectiveness of management decisions. Random or systematic sampling is typically needed to estimate population sizes, while population indices based on animal “sign” can be used to estimate relative population density. Monitoring techniques vary by species with age-at-harvest data typically used for game species, point-counts used for passerine birds, and mark-recapture or mark-resight methods often used for non-game species (Gove et al. 2002, Ruetz et al. 2015). Much like banding birds, marking captured turtles is useful for monitoring.

Different types of population models have been developed to approximate population structure from monitoring data by estimating abundance, age and sex composition, survival rates, and recruitment into a population (Gove et al. 2002). Available data determine the most appropriate population model. Population reconstruction models have been used for several wildlife species including rock ptarmigan (*Lagopus muta*) (Sturludottir et al. 2018), elk (*Cervus canadensis*) (Gove et al. 2002), American marten (*Martes americana*) (Skalski et al. 2013), and moose (*Alces alces*) (Peterson & Vucetich 2017, Hoy et al. 2019). A population can be reconstructed if ages of animals are known. For example, if an animal is 20 years old in 2019, it would be added to the reconstructed population as a 1-year old in 2000, and would be part of the reconstructed population through 2019. Datasets used for reconstruction must be relatively long in order to ensure accuracy and to allow time for capture or recovery of a significant portion of the population (Gove et al. 2002, Davis et al. 2007). Lower population size at the beginning and end of a study period is common due to a tapering bias present in population reconstruction models. (Pocock et al. 2004). Annuli are used to estimate the age of turtles and thus assign presence before capture. Population reconstruction can then determine the minimum number of live turtles within the population assuming immigration and emigration are negligible.

The Wood Turtle (*Glyptemys insculpta*) is classified as endangered by the IUCN because of declining populations across the species range, which includes the Eastern United States, Eastern Canada, and the Great Lakes Region (IUCN 2017). Wood Turtles are classified as threatened by the state of Minnesota and the Committee on the Status of Endangered Wildlife in Canada (MNDNR 2018, COSEWIC 2007), and the species is currently under review for listing under the Endangered Species Act in the U.S. (U.S. Fish and Wildlife Service 2018). Population modelling has been used for one population of Wood Turtles in Michigan. Eighteen years of capture-mark-recapture data were used, with 260 different turtles marked (Schneider et al. 2018). Adult survival was estimated to be 97%, and over the 18-year study the population grew by 50%.

We use a population reconstruction approach for a Wood Turtle population based on captures that spanned 30 years, and created an age-structured population model to test whether field-measured recruitment and survival are consistent with the reconstructed population and to evaluate effects of changes in demographic parameters on population growth rate. We varied the survival of each life stage in order to identify the Wood Turtle life stages that most impact the population growth rate. This research uses population models to estimate vital rates of turtle age/stage classes that are difficult to study and will help guide managers to effective conservation actions by focusing on age classes of concern.

Study Area

Wood Turtles were captured along a 40 km stretch of a river and associated tributaries in a sparsely populated section of Northeastern Minnesota. Specific locations are withheld in compliance with state of Minnesota data practices law. Some of the capture sites were intensively studied in 1990 (Buech et al. 1990). Around 75% of the land in the area is publicly owned, with the river and tributaries located within the Laurentian Mixed Forest ecological province (MNDNR 1999). Over 90% of the surrounding land is forested, with fire-dependent forests comprising 80% of the area, and the remaining land in non-forest or aquatic habitat National Land Cover Database classes (Brown et al. 2016). Aspen (*Populus* spp.*),* balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*) dominate the forest cover while pine cover types (*Pinus* spp.) are less common in the surrounding landscape due to historical forest harvest. Black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*) comprise over 90% of hydric forest types in the area. Non-forest vegetation consists of lowland alder (*Alnus* spp.*)* and grass/forb openings with Oxbow lakes and other non-flowing water features also occurring in the study area (Cochrane et al. 2017).

Methods

Field captures and marking

The study population has been monitored since 1990 by surveys that have included aging and carapace notching of captured turtles, allowing the individual turtles to be tracked over time (Cagle 1939). Measurements taken on captured turtles included straightline carapace length (SCL) and width, straightline plastron length and width, and weight (Buech et al. 1990, Cochrane et al. 2017, Moen et al. 2017). Additional data recorded included sex, gravidity for females, plastron annuli counts once per year, and photographs once per year. Capture locations were marked on aerial photographs in the early 1990s (Buech et al. 1997, Brown et al. 2016). Other capture locations were usually recorded using a handheld GPS (Cochrane 2017). We classified individuals as juveniles when SCL was ≤ 170 mm (Harding and Bloomer 1979).

From 1990 to 2018, 1,117 individual Wood Turtles were marked. There were 2,774 recaptures of 442 of those individuals as of 2018 (Moen et al. 2017, Cochrane et al. 2018). Recapture identities were confirmed from scute notches and in some cases matching plastron photos with Wild.ID software (TEAM Network 2017). Wood Turtles were captured and marked opportunistically at nesting sites and roads from 1997 through 2014. Intensive surveys were conducted from 2015 to 2018 (Cochrane et al. 2018) along some of the same sections of river surveyed from 1990 to 1993 (Buech et al. 1990, Brown et al. 2017), with the intent of finding previously marked turtles, thus enabling population reconstruction.

Population reconstruction

The capture dataset was checked for duplicate records, to make sure that all marked turtles were included, and to check for misreading of turtle identification numbers. Identification number, sex, and age of marked turtles was verified through plastron and carapace photos and field notes for discrepancies or missing records, when possible. The age at first capture of turtles was evaluated because Wood Turtles are reliably aged with annuli only to approximately 20 years of age (Lovich 1990). The age recorded on the datasheet was used except when shells were listed as too worn to age or listed with a + after the estimated age (e.g. Age: 24+). Photographs for these exceptions were checked to see if they could be aged. The age was estimated from the photograph if annuli were clearly visible. If annuli were not visible on the photograph, or if no photograph was available, the age recorded on the data sheet was used (e.g., 24+ was converted to 24). If the data sheet indicated the shells were too worn to age from annuli, individuals were assigned age 29, and thus were assumed to have been alive in 1990.

The minimum number of Wood Turtles in the northeastern Minnesota study population was reconstructed from 1990–2018. The reconstructed population in year *x* included turtles caught in year *x*, turtles that were caught in future years that would have been alive in year *x*, and turtles that had been caught before year *x* but had not been recaptured. For these unknown fate individuals that had not been recaptured, we tested a range of annual survival rates between 89% and 97% after their last capture event to estimate the number of turtles that we assumed were still alive in year *x*. For the unknown fate individuals, we used a binomial probability distribution to estimate the number of survivors in each subsequent year using survival probabilities of 89% and 97%, respectively. The estimated survival rate for adult turtles in this population through telemetry was 89% (Lapin et al. 2019) and the estimated survival rate for adult turtles in the Michigan population was 97% (Schneider et al. 2018). We replicated the analyses 1,000 times and used the mean of the replications as the lower and upper bound for number of unknown fate individuals assumed to be alive during each year of the reconstruction. The assumed alive category is likely a slight over-estimate because about 20% of the unknown fate turtles were juveniles at last capture but were projected forward using adult survival probabilities.

We also assumed that immigration and emigration was low because we recaptured many turtles near or at the same sites. We witnessed Wood Turtles returning to the same nesting sites year after year, as many turtle species do (Freedberg et al. 2005, Rowe et al. 2005). If a turtle immigrated, it would be counted as being present for the duration of the reconstruction.

Population modelling

We developed an age-class structured simulation model in Microsoft Excel. The model used an annual time step. The population model included age classes from 1 to 60 years old. Input parameters for the model were obtained from data collected on this Wood Turtle population, and from the literature (Table 2.1). Survival rates found in the literature, within the study site, and through personal communications were used to bracket the survival for each of the different age classes (Table 2.1). The baseline parameter values were then evaluated for consistency with the MNA reconstruction, with adult, juvenile, and nest/hatchling survival rates adjusted for sensitivity analysis.

The population model incorporates the variables listed in Table 2.1. The population was initialized in 1975 to allow enough time for hatchlings in year one to start entering the adult stage. The stages of age classes used in the model include nest and hatchling survival to age one, juveniles from age 1 through 14, and adults from age 15 to 60. The simulated population should be equal to or greater than the reconstructed population, because the reconstructed population is a minimum estimate.

Population Model Structure

The first age class of the model incorporated nest success and hatchling survival to age one (Feng et al. 2019). The number of eggs laid per year (E_t) was calculated assuming a 1:1 sex ratio (Table 2.1) in the adult population (N_a) with a fraction of adult females nesting per year (F_n) and each nest containing E_n eggs:

$$E_t = 0.5N_aF_n * E_n \qquad \text{Eq. 1}$$

The total number of eggs hatching per year (H_t) is equal to the number of eggs laid multiplied by the egg hatching rate (E_h) and nest success (S_n):

$$H_t = E_t * E_h * S_n \qquad \text{Eq. 2}$$

Egg hatching rate was assumed to be 0.94 using the number of hatchlings produced per nest in the field (8.5 hatchlings/nest, with 9 eggs/nest [Berkeland et al. 2019, Greaves and Litzgus 2009]). Nest success rates in the literature vary from 0% to 83% success per year (Table 2.1). Finally, hatchling survival (H_s) was incorporated into the year one age class to calculate the number of hatchlings that survive their first year (H_1):

$$H_1 = H_t * H_s \qquad \text{Eq. 3}$$

Baseline nest/hatchling survival was estimated to be 6% using the values from existing literature for nest success and survival of known fate hatchlings to overwinter or to one year (Table 2.1).

The second age class of the model included juveniles surviving from age 1 through 14. We calculated annual survival from the Michigan estimate combining nest predation and juvenile survival until age 14.7 into a single survival rate of 5.8% (Schneider et al. 2018). Our model required annual age classes, therefore we used a constant 83% annual survival rate that was consistent with the Schneider et al. (2018) estimate as our base estimate for juvenile survival. An improvement to the juvenile survival calculations would be to use an age-specific survival rate, with younger juveniles having a lower annual survival rate than older juveniles.

The third age class of the model included adults surviving from age 15 to 60. Annual survival from age 15 to age 60 was set at 89% in the base model, consistent with the telemetry estimate (Lapin et al. 2019). The oldest turtle captured in the study area was at least 55 years old at the time of capture (Brown et al. 2014). We assumed that turtles would not live past the age of 60 (only a small proportion of turtles in the model or in the field survive to this age).

Sensitivity analysis

A sensitivity analysis was conducted in which age-specific survival was varied to determine which age class was most influential in affecting lambda (λ), the finite rate of increase of the population over time, and which combinations of survival are not consistent with the reconstructed population. The initial model was deterministic and used for testing scenarios with changes in survival rates for individual age classes (Table 2.2). Nest/hatchling survival combines nest success and hatchling survival to age 1 into a single variable. Simulations created for sensitivity analysis were compared graphically.

The population model was then used to examine population trends over the past three decades. Stochasticity was introduced with the sensitivity analysis and predictive modelling, with annual survival randomized for the different age classes. The base survival value for each age class (S_b) was altered every year ± 1%, 3%, and 5% (Table 2.3) in order to determine the effect of parameter uncertainty on model results. A random value, V_r, was drawn from a uniform distribution between the variation threshold values of ± 1%, 3%, or 5%, and was added to the base survival value, S_b.

$$S = S_b + V_r \qquad 0 \leq S < 1 \qquad \text{Eq. 4}$$

If $S_b + V_r$ exceeded 1.00, the survival rate was set at 0.9999. If $S_b + V_r$ was less than 0.00, the survival rate was set at 0. Each age class was varied using each of the different variation thresholds (± 1%, 3%, or 5%) while other age classes were held at the base value. The predicted population size was compared to predicted population size of other sensitivity analysis simulations and to the reconstructed population size.

Results

Reconstruction

The Minimum Number Alive (MNA) population reconstruction resulted in a population that was relatively stable through 2014 (Fig. 2.1). With 97% survival for turtles that had not been recaptured, the reconstructed population peaked at 949 individuals in 2003 and decreased by 105 to 844 individuals in 2018. If survival is only 89%, then the reconstructed population peaked at 813 individuals in 2003 and decreased by 280 to 533 individuals in 2018.

Population Modelling

When adult survival was 89%, juvenile survival was 83%, and nest/hatchling survival was 6%, the modelled population was much lower than the MNA population (Fig. 2.2). In order for the modelled population to be similar to the MNA population, nest/hatchling survival had to be above 6% regardless of juvenile and adult survival. As nest/hatchling survival was increased from 9% to 12%, changes in either juvenile or adult survival could result in a modelled population that was similar to the MNA population. With adult survival increased to 97%, juvenile survival at 86%, and nest/hatchling survival at 10%, the modelled population was similar to the MNA population (Fig. 2.2). This provided a baseline to compare to changes in the survival of different age classes.

Sensitivity Analysis

The sensitivity analysis on adult survival indicated adult survival has to approach 99% in order for lambda to be close to 1.00 if nest/hatchling survival is 8% and juvenile survival is 86% (Fig. 2.3). Simulation model results show that adult survival rates as high as 0.97 have a declining population trend ($\lambda < 1.00$) if nest/hatchling survival is 8%. When nest/hatchling survival is increased to 10% and adult survival is > 95%, lambda is ≥ 1.00 (Fig. 2.4). Adult survival ≥ 95% is consistent with the MNA population, and as adult survival declines the model becomes less consistent with the MNA trend. When nest/hatchling survival is increased to 12%, the simulated population is higher than the MNA population at adult survival rates > 95% (Fig. 2.5). This provides support for the nest/hatchling survival being < 12% in this turtle population, if adult survival rates are > 95%.

The simulations in Figs. 2.3 – 2.5 were created using a deterministic version of the population model. When random variation was introduced to nest/hatchling survival, the 95% confidence interval around predicted population size was about 5% with 10 replications (Fig. 2.6). When comparing the same amount of variation in both juvenile and adult survival, the 95% confidence intervals are slightly smaller (Figs. 2.8 & 2.9). This is due to the proportional change in survival for each of these variables. For example, increasing nest/hatchling survival from 6% to 11% nearly doubles the number of surviving hatchings (11/6 = 1.83) while increasing adult survival from 95% to 100% only increases the number of adults surviving by a small fraction (100/95 = 1.05).

The juvenile and nest/hatchling stages can have a greater effect on the population because there is the potential for more individuals to survive than at the adult stage. Increasing juvenile survival by 1% from 1990 to 2018 increases the simulated juvenile and adult population size in 2018 by 96.7±23.2, whereas increasing nest/hatchling survival by 1% from 1990 to 2018 would add 94.7±12.4 individuals to the juvenile and adult population in 2018, and increasing adult survival by 1% from 1990 to 2005 would add 60.6±21.2 individuals to the juvenile and adult population (Table 2.4).

Discussion

Changing juvenile or nest/hatchling survival had a greater effect on predicted population size than increasing adult survival. This effect occurred even though juvenile turtles have to survive to reach the adult stage before they start reproducing. When adult and juvenile survival is high, which the literature and our simulations suggest, the population size can be maintained even if the nest/hatchling stages have low survival (Congdon et al. 1993, Congdon et al. 1994, Pike & Siegel 2006). In many populations, changes in survival rates of the juvenile or adult stages have the most effect (Congdon et al. 1993, Congdon et al. 1994, Feng et al. 2019, Limpus 2008). However, if adult survival is high and a population is still declining, management focusing on juvenile and nest/hatchling survival may be necessary (Feng et al. 2019).

Although it takes several years for juveniles to become adults, increasing the number of hatchlings that survive to the juvenile age class would increase the breeding population. Most individuals die either from nest predation or during the first year of life, and if survival to 1 year of age is increased, these individuals are carried through the juvenile age class. Once the juveniles enter the adult population and begin reproducing, the effect of higher nest/hatchling survival will be more pronounced.

Increasing survival of the nest/hatchling age class would also be easier because of the higher survival of juveniles and adults. For example, it would probably be more difficult to raise adult survival from 97% to 99% and increase juvenile survival above 86% than it would be to increase nest/hatchling survival, which is below 10% (see Chapter 1). Adult survival could increase at most by 3%, juvenile survival could be increased by 14%, while nest/hatchling survival could be increased by over 90%. Of course, 100% survival at the nest/hatchling stage is highly unlikely, but there is much more room to increase nest/hatchling age class survival. Nest/hatchling survival could be increased by protecting nesting sites and the areas around them or using targeted predator control near nesting sites where there are high predation rates (Chapter 1, Christiansen & Gallaway 1984). An additional benefit of targeted predator control could be a reduction of predation on juvenile and adult turtles in those same areas.

We found that adult survival needed to be greater than or equal to 95% to be consistent with the MNA population. We expected high survival of adults because the adult survival rates of other Wood Turtle populations range from 88% in Massachusetts, New Hampshire and Virginia (Jones 2009, Akre and Ernst 2006) to 97% in Michigan (Schneider et al. 2018) and 96 – 100% in Maine (Compton 1999). Wood Turtle telemetry data indicated adult survival of 87% in Wisconsin, 86% in Iowa, and 89% for this northeastern Minnesota population (Lapin et al. 2019). The 26 turtles monitored in this population were radiocollared in 2015 and 2016 (Cochrane et al. 2019). The adult survival rates for Wisconsin, Iowa, and northeast Minnesota are low relative to the estimates from most other populations and are unsustainable according to our results.

Based on the population reconstruction, the population appears to be relatively stable from 1990 to 2014. The decline beginning after 2014 occurs at least in part because there are juvenile and adult turtles that have not been caught. As these turtles are caught in future years (2020 to 2040) more of the turtles that are alive from 2014 to 2019 will be filled in and the tapering bias from 2014 to 2019 will be reduced. However, there are signs that adult survival may have declined recently in the study population. The lower survival rate for adults in Lapin et al. (2019) is also supported by recent field work—68 dead turtles were found from 2016 to 2018, 62 of which were adults. Of the 68 dead turtles, 52 were found in 2016 and 2017 (Cochrane et al. 2018) and 16 were found in 2018 (pers. observation). In 2017, maximum adult survival was estimated to be 87% based on the number of dead adult turtles found at eight monitoring sites and the estimated number of adult turtles at those eight monitoring sites (Cochrane et al. 2018). Furthermore, it is highly unlikely that all of the adult mortalities in the study area were found. According to our simulation results, an annual adult survival rate of either 87% or 89% in the NE Minnesota study area would result in lambda being less than 1.00 when nest/hatchling survival is 12%. This suggests that from 1990 to 2018, average annual adult survival had to be higher than 89% estimated from telemetry.

In order for lambda to be close to 1, juvenile survival needs to be approximately 86% with the estimated adult and nest/hatchling survival rates (Tables 2.1, 2.2, & 2.3). For the stochastic model simulation, a juvenile survival rate of 86% was consistent with the MNA reconstruction. When juvenile survival was reduced to 83% in stochastic simulations, the population declined and was much lower than the MNA population reconstruction (Fig. 2.8). Juvenile survival less than 86% would require increasing either adult survival or nest/hatchling survival in order to be consistent with the MNA. This juvenile survival rate is higher than the annual survival rate of 83% to age 14.7 for a Wood Turtle population in Michigan (Schneider et al. 2018) and within the range of Wood Turtle juvenile and adult combined survivorship between 80% and 92% in Virginia (Akre and Ernst 2006). While we used the same survival rate for the entire juvenile age class, it is likely that survival increases as turtles age and juveniles increase in size. As an average for the juvenile life stage, juvenile survival is probably between 83% and the estimated adult survival rate of 95% to 97%.

Given our estimates of expected juvenile and adult survival rates, the combination of nest success and hatchling survival to one year should be at least 9%. This can result from high nest success and low hatchling survival, or from low nest success and high hatchling survival. There is also a temporal aspect, because nest success is extremely variable from year to year for turtles, in large part because of nest predation (Chapter 1, Horne et al. 2003, Limpus 2008, Marchand et al. 2002, Geller 2012a). Yearly nest success ranges from 0-84% for Wood Turtles and other species of long-lived turtles in the Midwest (Berkeland et al. 2019, Bougie et al. 2019, Congdon et al. 1993, Congdon et al. 1994).

Hatchling survival must be at least 35% on average in order for nest/hatchling combined survival to be at least 10% when nest success is 30%. Wood Turtle hatchling survival estimates range from 7-89% to overwinter (Dragon 2014, Jones et al. 2015, Paterson et al. 2012, , J. Tamplin, University of Northern Iowa, personal communication), while the only hatchling survival estimate to one year is 10% (T. Bougie, University of Wisconsin-Madison, personal communication). If the hatchling survival rate is only 10%, then the nest success rate would need to be 100% for nest/hatchling survival to be 10%, the minimum long term survival needed to have as many juveniles and adults as estimated by the MNA reconstruction. Because the nest success rate is < 100%, model results suggest that average hatchling survival is likely higher than has been measured in field studies.

Given the high predicted population size with nest/hatchling survival of 14%, and the documented low nest survival rate of 4% in one year (Table 2.1), it is unlikely that average nest/hatchling survival is as high as 14% in this river system. Stochastic simulations also provide support for nest/hatchling survival being near 10%, with the 6% nest/hatchling survival simulation showing a decline in the population that is inconsistent with the MNA reconstruction. Model results suggest that nest/hatchling survival (i.e., egg to one year) is most likely between 10% and 14%.

Sensitivity analysis showed that increasing the survival of any life stages would increase the population over time. Managers could consider techniques that can have a positive impact for multiple age classes. Additionally, continued monitoring of this population is needed to investigate the turtle mortalities as well as for modelling the population into the future. Specifically, monitoring of hatchlings and juveniles through VHF telemetry or GPS telemetry in order to develop age-specific survival rates would be one way to better inform future modelling efforts. Wood Turtle populations in Minnesota face impacts from recreation (Lenhart et al. 2013, MNDNR 2018), which can lead to increases in threats such as habitat loss, nest predation, and road mortality (Garber &

Burger 1995). Modelling efforts should also consider the potential impact of changes in human recreation activities, geography, habitat, and presence of predators on survival rates of each age class.

Figures & Tables

Table 2.1 Variables used in the population model. Variable name listed along with symbol if used in equations (see Population Model Structure). The value column contains the value that was used for each variable in the base population model. The notes column provides the values found in the literature and unpublished data. Data sources for the values are listed in the citations column.

Variable	Symbol	Value	Notes	Citations
Sex Ratio		1:1	Equal number of males and females	Greaves and Litzgus 2009
Eggs/nest	E_n	9	9.2 (± 2.2 SD, n= 16) 8.5 (± 2.0 SD, n = 15, range = 6 – 11)	Greaves and Litzgus 2009 Berkeland et al. 2019
Egg hatching rate	E_h	94%	8.5 (± 2.0 SD, n = 15, range = 6 – 11) 8.5 hatch / 9 eggs = 94%	Berkeland et al. 2019
Females nesting/year	F_n	75%	54%–88% (mean = 75% , n = 76) Minimum of 64% gravid (n = 62) Estimated 75% nested Estimated 33% nested	Jones 2009 Walde et al. 2007 Jones et al. 2015 (Brooks unpub.) Foscarini 1994
Clutches/year		1	Wood Turtles rarely lay multiple clutches	Harding and Bloomer 1979 Farrell and Graham 1991
Age of first reproduction		15	15 years old	Greaves and Litzgus 2009
Nest Success	S_n	30%	0-33% in 4 years for unprotected nests 22% over 5 years for unprotected nests 0-63% in 16 years for unprotected nests 0-64% in 17 years for unprotected nests	Berkeland et al. 2019 Bougie et al. 2019 Congdon et al. 1993 Congdon et al. 1994

Table 2.1 Continued.

0 to 1	H_s	21%	11% survived to overwinter (n = 45)	Paterson et al. 2012
			12.5% survived to overwinter (n = 8)	Jones et al. 2015 (Wicklow unpub.)
			7-37% surviving to overwinter in 2 years (n=68)	Dragon 2014
			89% surviving to overwinter in 1 year (n = 9)	Tamplin (personal communication)
			10% surviving to one year in 1 year (n = 20)	Bougie (personal communication)
1 to 14		83%	Survival to age 15 of 0.058 ±0.019 SD, corresponds to constant annual survival of 83%	Schneider et al. 2018
15 to 59		89%	Radiotelemetry - 89% adult survival	Lapin et al. 2019
			Adult survival (0.97 ± 0.016 SD)	Schneider et al. 2018
Maximum Age		60	55 year old Wood Turtle, assumed to live 5 years after capture	Brown et al. 2014

Table 2.2 Survival rate simulations by age class for deterministic sensitivity analysis. Altering the survival rates from the base survival rate enabled comparison to the reconstructed population.

Age Class	Base Rate	Sensitivity analysis rates
Nest/hatchling	6%	8%, 10%, 12%, 14%
Juvenile	83%	84%, 86%, 88%
Adult	89%	91%, 93%, 95%, 97%, 99%

Table 2.3 Stochastic model survival rate simulations by age class. Individual or multiple age classes have random variation each year. Variation of ± 5% around each survival rate was tested. All age classes were altered individually, holding the other age class survival rates constant.

Age Class	Low	Middle	High
Nest/hatchling	6%	10%	14%
Juvenile	83%	86%	89%
Adult	89%	93%	97%

Table 2.4 Simulated change in the Wood Turtle population per 1% change in survival of nest/hatchling, juvenile, and adult life age classes. These population changes use the 2005 deterministic and stochastic modelled populations, with survival rates held constant from 1990 to 2018.

Life Age class	Deterministic	Stochastic
Nest/hatchling	94.7±12.4	87.8±20.4
Juvenile	96.7±23.2	108.1±32.3
Adult	60.6±21.2	70.3±36.1

Figure 2.1 Estimated minimum number of adult and juvenile Wood Turtles in a northeastern Minnesota population from 1990– 2018. Caught (white) bars represent individuals detected each year. Alive (black) bars include turtles that were detected in future years, but were not detected during a survey year. Assumed Alive (gray) bars represent turtles that were assumed to be alive after their final detection year. Turtles were assumed to have survival rates from 89% to 97% after their last recapture event. The red line represents the number of turtles that are assumed alive if survival is 89% and the blue line represents the number of turtles that are assumed alive if adult survival is 97%.

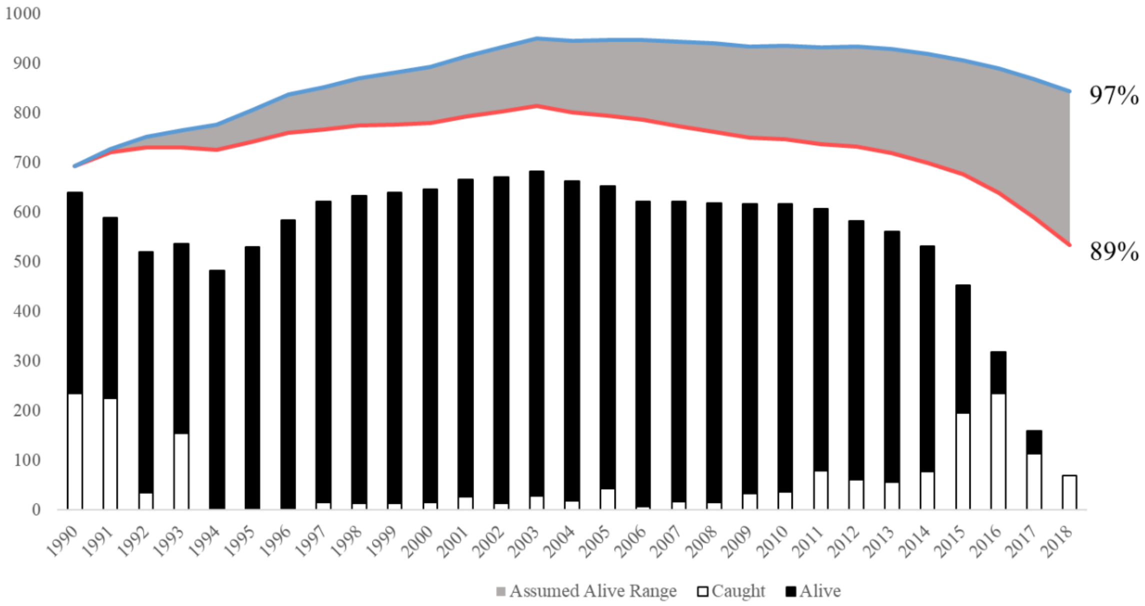


Figure 2.2 Population model results when adult survival is 89%, juvenile survival is 83%, and nest/hatchling survival is 6% compared to population reconstruction. These base survival rates are shown by the solid black line, while the colored and dashed lines correspond to combinations of survival consistent with the estimated population size from the reconstruction (Fig. 2.1), shown by the light gray band. The average lambda (λ) was calculated from 1990 to 2018 for each simulation.

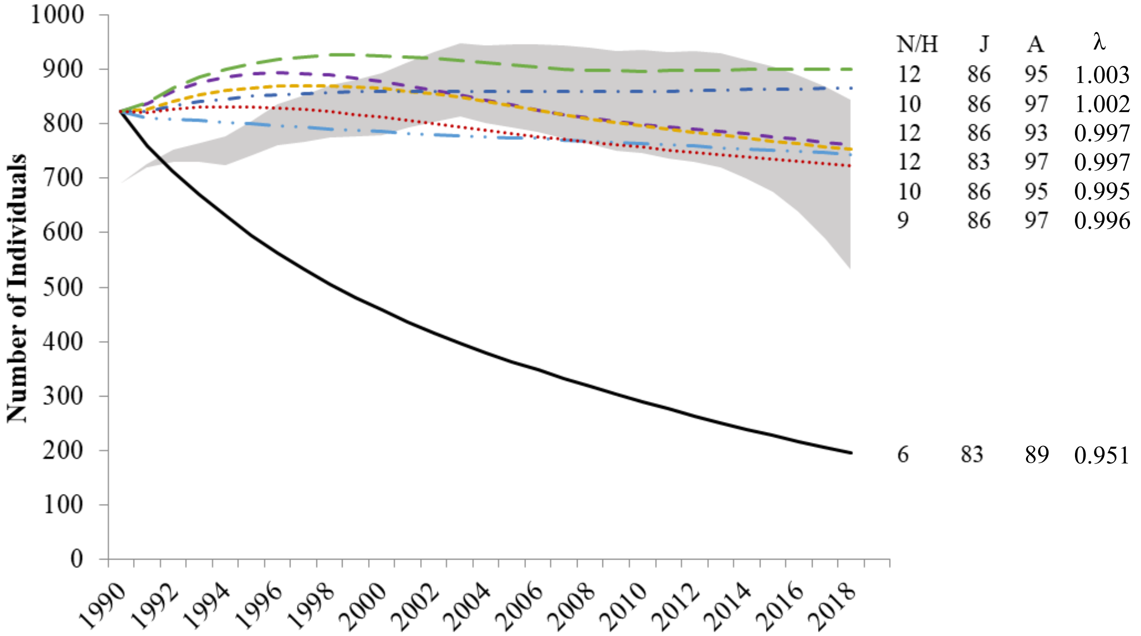


Figure 2.3 Predicted population size when adult survival is varied from 89% to 99%, juvenile survival is 86%, and nest/hatchling survival is 8%, compared to the population size from the population reconstruction. Lines correspond to adult survival. The projected population from the reconstruction is the number of adults and juveniles in the population, shown by the light gray band. The average lambda (λ) was calculated from 1990 to 2018 for each adult survival rate.

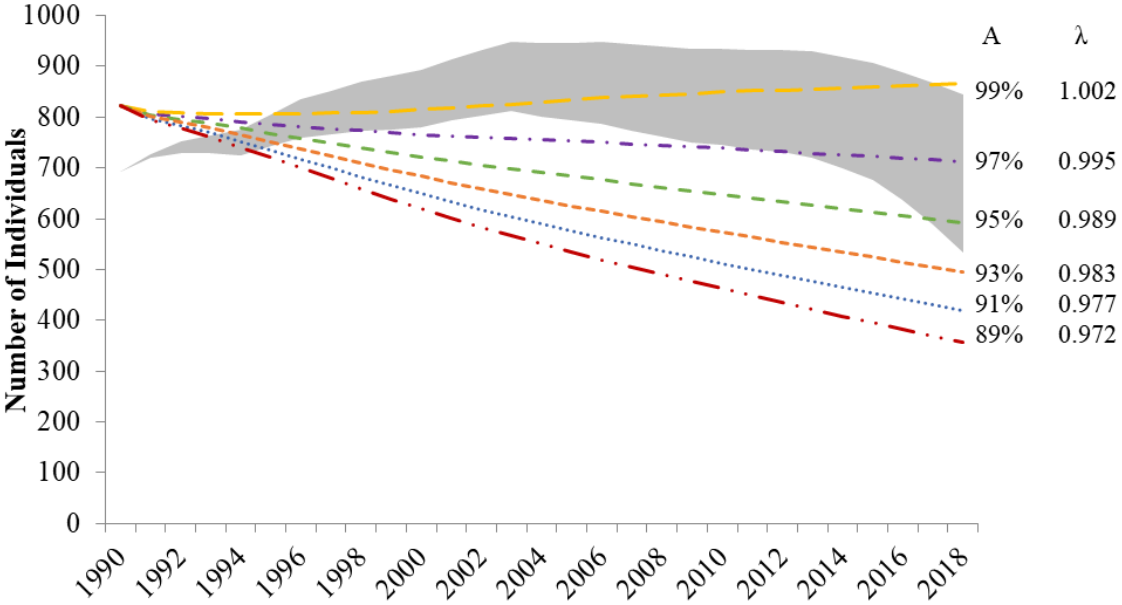


Figure 2.4 Predicted population size when adult survival is varied from 89% to 99%, juvenile survival is 86%, and nest/hatchling survival is 10%, compared to the population size from the population reconstruction. Lines correspond to adult survival. The projected population from the reconstruction is the number of adults and juveniles in the population, shown by the light gray band. The average lambda (λ) was calculated from 1990 to 2018 for each adult survival rate.

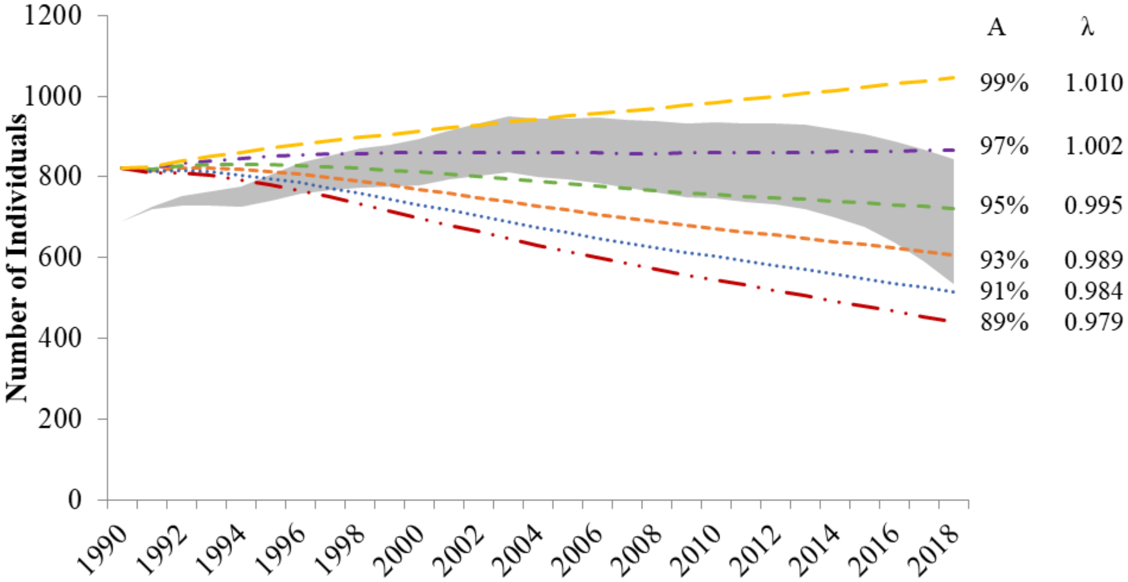


Figure 2.5 Predicted population size when adult survival is varied from 89% to 99%, juvenile survival is 86%, and nest/hatchling survival is 12%, compared to the population size from the population reconstruction. Lines correspond to adult survival. The projected population from the reconstruction is the number of adults and juveniles in the population shown by the light gray band. The average lambda (λ) was calculated from 1990 to 2018 for each adult survival rate.

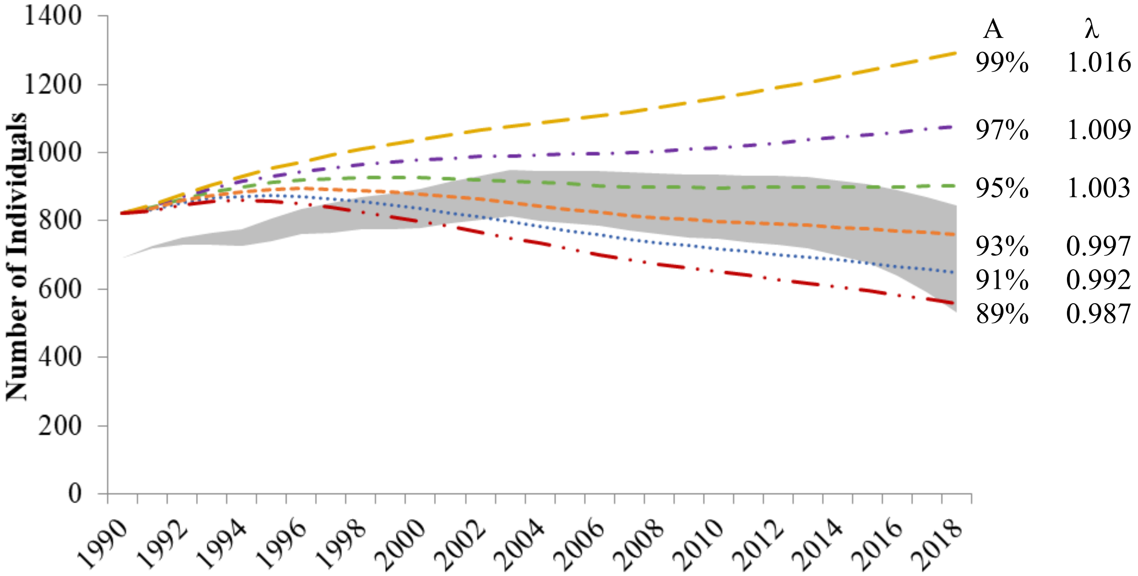


Figure 2.6 Population model results when adult survival is 97%, juvenile survival is 86%, and nest/hatchling survival has random variation each year compared to the population size from the population reconstruction, shown by the light gray band. Hatchling base survival rates used were 6%, 10%, and 14%, with variation of ± 5%. The 95% confidence intervals around mean population estimates are shown by the dark gray bars around each line. Simulations used 10 replicates each of the different survival scenarios.

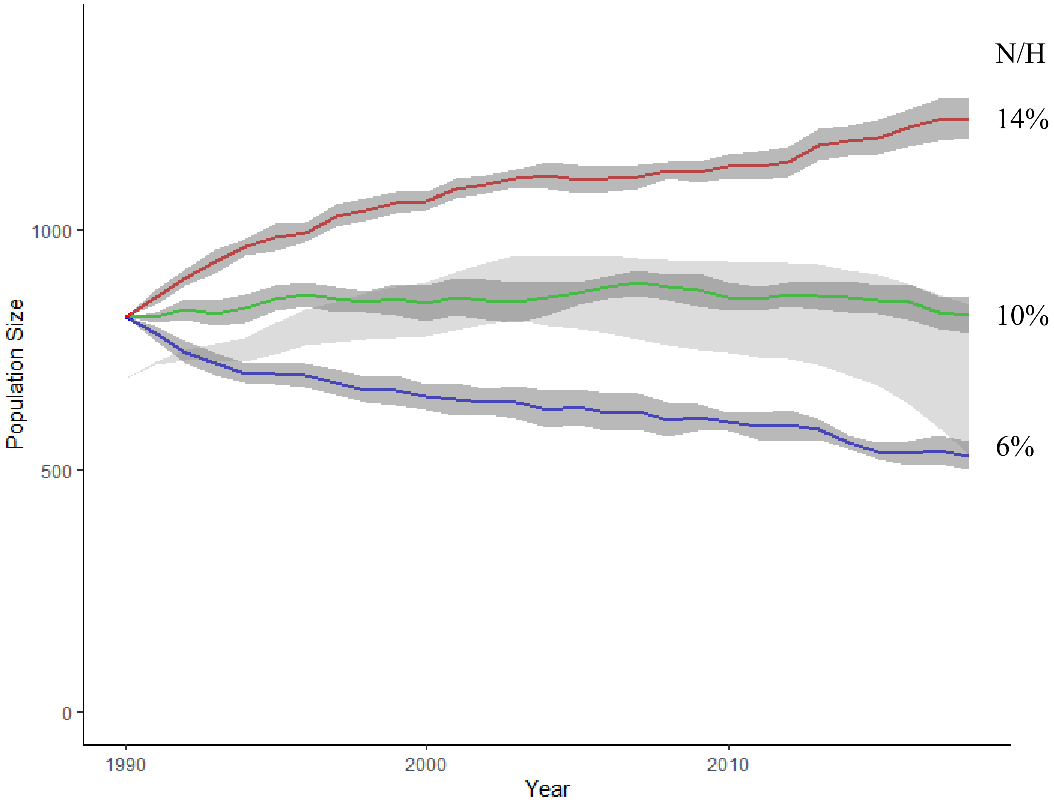


Figure 2.7 Population model results when adult survival is 97%, nest/hatchling survival is 10%, and Juvenile survival has random variation each year compared to the population size from the population reconstruction, shown by the light gray band. Juvenile base survival rates used were 83%, 86%, and 89%, with variation of ± 5%. The 95% confidence intervals around mean population estimates are show by the gray bars around each line. Simulations used 10 replicates each of the different survival scenarios.

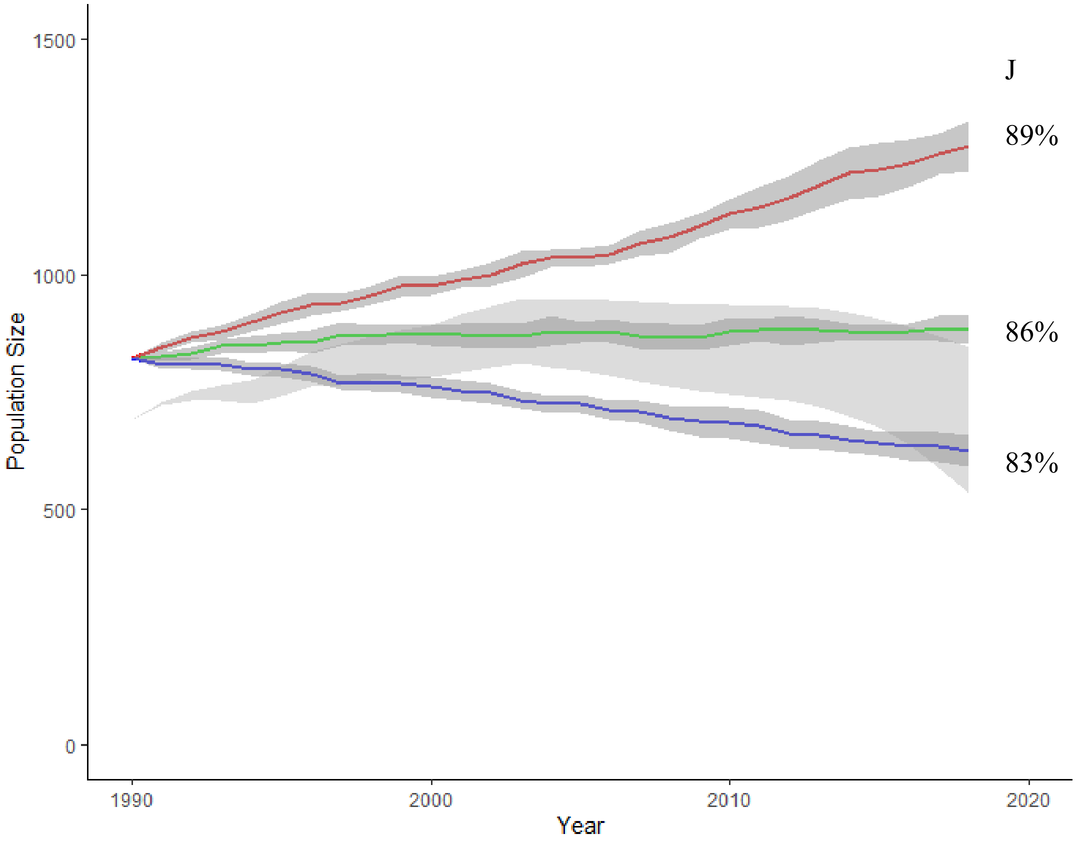
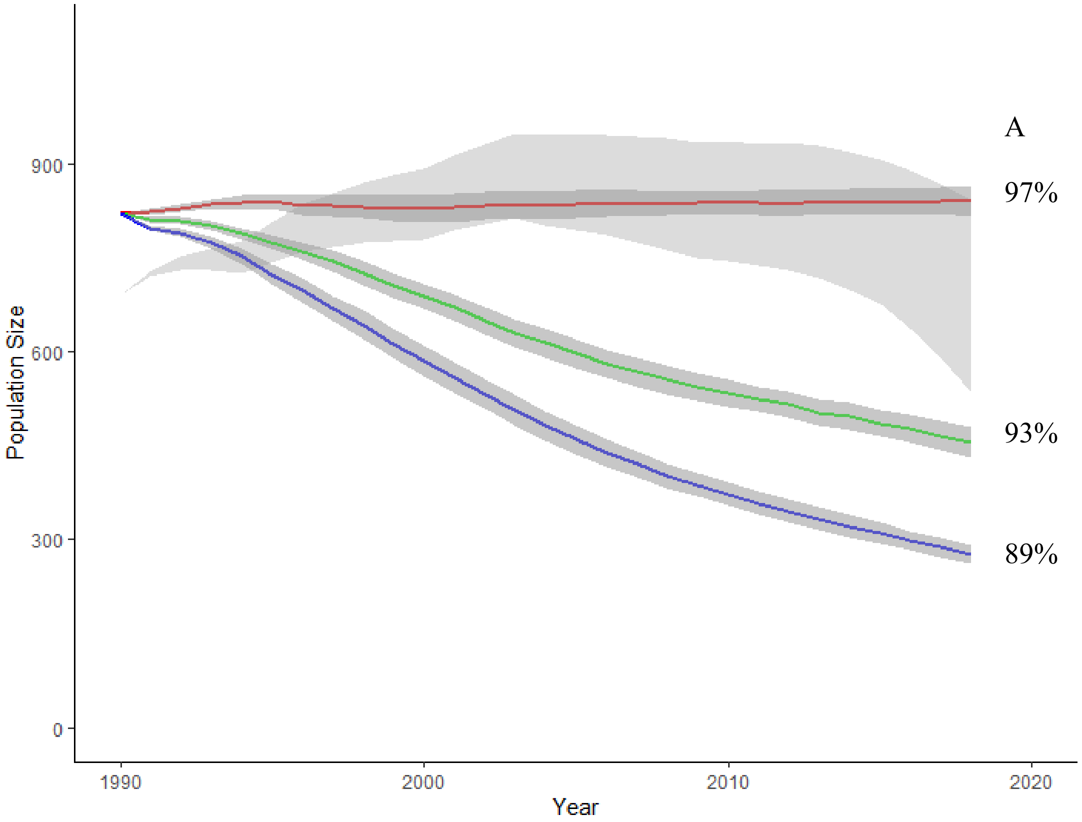


Figure 2.8 Population model results when juvenile survival is 86%, nest/hatchling survival is 10%, and adult survival has random variation each year compared to the population size from the population reconstruction, shown by the light gray band. Adult base survival rates used were 89%, 93%, and 99%, with variation of ± 5%. The 95% confidence intervals around mean population estimates are shown by the gray bars around each line. Simulations used 10 replicates each of the different survival scenarios.



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