

ABSTRACT

GARNER, LINDSEY AMANDA. Population Status of the American Alligator (*Alligator mississippiensis*) in North Carolina. (Under the direction of Drs. Christopher E. Moorman and David T. Cobb).

American alligators (*Alligator mississippiensis*) occur throughout the southeastern United States; however, little is known about the current distribution of alligators at the northern extent of their range. To determine the relative abundance and distribution of alligators in North Carolina, we conducted night spot light counts using a 2-phase sampling approach. We focused occupancy surveys over a broad area in 2012, and focused subsequent abundance surveys in areas of high predicted occupancy probability the following year. We fit a series of binomial N-mixture models to estimate site-specific abundance while accounting for imperfect detection of alligators. Null occupancy probability was 0.28 (SE \pm 0.05) while null abundance was 0.3025 (SE \pm 0.025) alligators/km. Alligator occurrence increased in southern and eastern portions of the study area, and decreased as water salinity increased. Increasing abundance of alligators was related to a decrease in water salinity. Overall, alligators occurred at very low densities or were not present throughout large areas in eastern North Carolina. Their distribution was clumped where individuals were protected due to restricted human access, which was similar to the distribution described from surveys conducted 30 years prior. Changes in population size and structure may occur over decades, and we recommend long-term monitoring to determine population and distribution changes.

In North Carolina, there is an increased interest in developing an alligator harvest season, but the potential impact of a harvest on northern populations is unknown. We developed a female-specific stage-structured matrix model of alligator life history at the northern extent of its range to determine the population growth rate (λ). We conducted

sensitivity and elasticity analyses to identify the contribution each vital rate made to λ , followed by a life-stage simulation analysis to account for vital rate variance in our model by using hypothesized variation in parameter probability densities. Finally, we assessed the relative sensitivities of λ to various theoretical harvest scenarios on a population of adult and sub-adult female alligators in eastern North Carolina. We determined a population growth rate of 1.0156. Adult female survival had the highest sensitivity and elasticity values, while hatchling survival had the least influence on λ . Because adult female alligator survival has the greatest impact on the population, only minimal total adult alligator population harvest (3%) with a minimal likelihood of adult females taken within that harvest (5%) resulted in a scenario with a median λ greater than 1. Additional data could improve the accuracy and precision of these models, but current available data coupled with harvest data from other states suggests harvest of alligators in North Carolina is not sustainable.

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Population Status of the American Alligator (*Alligator mississippiensis*) in North Carolina

by
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DEDICATION

To my parents, for their unwavering support

BIOGRAPHY

Lindsey Garner was born and raised in Roanoke Rapids, North Carolina. She spent her weekends exploring the vast wildernesses of Halifax County in search of largemouth bass, fence lizards, arrowheads, and fossils with her dad. On these adventures she developed a deep appreciation and understanding of all things wild. After the devastation of Hurricane Fran in 1996, Lindsey and her family rescued and raised an orphaned grey squirrel; the tangible experience was a surprisingly profound catalyst for her growing interest in wildlife ecology and animal behavior. Lindsey attended North Carolina State University and received her Bachelors of Science in Zoology in 2009. During this time, she was able to participate in a pivotal internship in the back swamps of Roanoke River National Wildlife Refuge, opening her eyes to a future career in wildlife biology. Afterwards, she worked several seasonal positions in North Carolina, South Carolina, and Florida, where she developed a specific interest in wetland ecology. In 2011, she returned to North Carolina State University to pursue her master's degree in Fisheries, Wildlife, and Conservation Biology. Currently, Lindsey is project coordinator of University of Florida's long-term wading bird monitoring project throughout the Greater Everglades.

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CHAPTER 1

Factors affecting occupancy and relative abundance of the American alligator at the northern extent of its range

ABSTRACT

American alligators (*Alligator mississippiensis*) occur throughout the southeastern United States; however, little is known about the current distribution of alligators at the northern extent of their range. To determine the relative abundance and distribution of alligators in North Carolina, we conducted night spot light counts using a 2-phase sampling approach. We focused occupancy surveys over a broad area in 2012, and focused subsequent abundance surveys in areas of high predicted occupancy probability the following year. We fit a series of binomial N-mixture models to estimate site-specific abundance while accounting for imperfect detection of alligators. Null occupancy probability was 0.28 (SE \pm 0.05) while null abundance was 0.3025 (SE \pm 0.025) alligators/km. Alligators were more likely to occur as water salinity decreased, and alligator occurrence increased in southern and eastern portions of the study area. Increasing abundance of alligators was related to a decrease in water salinity. Overall, alligators occurred at very low densities or were not present throughout large areas in eastern North Carolina. Their distribution was clumped where individuals were protected due to restricted human access, and the distribution was similar to that described from surveys conducted 30 years prior. Changes in population size and structure may occur over decades, and we recommend long-term monitoring to determine population and distribution changes.

INTRODUCTION

Historically, unregulated harvest and habitat loss led to a decrease in American alligator (*Alligator mississippiensis*) abundance throughout its range, resulting in federal protection. Following population recovery, many states have since established population monitoring programs, regulated harvest seasons, farming industries, and nuisance control (Owen et al. 2010). Many believe populations of alligators are more bountiful at present now than historically (Hines 1979, Barrow 2009, Lutterschmidt and Wasko 2006, Irwin and Wooding 2002), and the present range of alligators probably is close to their historical range (McKerrow et al. 2006). However, human encroachment resulting in a reduction of quality and availability of habitat could threaten alligator populations in the future (Guillete et al. 1994, Lutterschmidt and Wasko 2006, Fujisaki et al. 2007, Mazzoti 2009,).

Slow growth rates and relatively long life-spans of alligators makes determining long-term population trends difficult, because changes in population size and structure can occur over decades (Brandt 1991). At Par Pond in South Carolina, the status of alligators was compared to previous studies conducted in the 1970's to determine change in population. The comparison showed that the number of alligators more than doubled over a 14-year span (Brandt 1989). Coastal North Carolina represents the northern extent of the alligator's range in the U.S., but little is known about the current population abundance and distribution within the state. With federal protection, and projected recovery, population changes comparable to Par Pond could be expected in protected regions of North Carolina; however, habitat loss and poaching may have had adverse effects in non-protected areas.

The ecological status and distribution of the then-endangered American alligator in North Carolina was documented through extensive field research during 1978-1983 (Doerr and Hair 1983). Researchers outlined the significant life history differences between alligators in North Carolina versus those in more southern areas (Fuller 1981, Klause 1984). The relatively short growing season in North Carolina may restrict breeding, nesting, and hatching, especially in years with colder temperatures (Klause 1984). This decreased reproductive capacity may result in increased risk of local extinctions and therefore necessitates updated management strategies in North Carolina.

In addition to these studies focused on demographics and life history traits, a state-wide census of alligator distribution was completed through night spotlight counts. Our study expands on this previous research that suggested alligators occur in the coastal counties of North Carolina as patchily distributed populations (Doerr and Hair 1983, O'Brien and Doerr 1986). From 1979-1980, overall alligator density was relatively low and the distribution of alligators was clumped. The large number of surveys with no alligator sightings suggested that alligators did not occur or occurred at extremely low densities in significant portions of coastal counties. The clumping appeared to be related to areas of protection, including federal, state, and private lands. Seventy-five percent of alligators were located on 25% of the total routes; these routes were located in protected areas such as military bases, national forests, and private property with restricted access. Most alligators were observed in the southern Cape Fear watershed with the greatest overall density of 0.3 alligators/km (O'Brien and Doerr 1986). With continued protection, O'Brien (1983) predicted that the population of alligators in coastal North Carolina would remain stable and possibly increase in the future;

however, a follow-up assessment never was completed. Our objectives were to determine the current relative abundance and distribution of alligators in North Carolina to provide important information concerning the recovery of the portion of the population within the state.

To achieve our research objectives, we designed a two-phase adaptive sampling approach by replicating surveys spatially and temporally across the range of alligators in North Carolina (Conroy et al. 2008, Mathewson et al. 2012). This sampling design is frequently applied to obtain reliable population parameter estimates for rare or elusive species (Thompson 2004) and allowed us to accurately estimate alligator abundance despite their predicted rarity. Using this approach, we developed a predictive model based on several parameters, measured at both local and landscape scales, to estimate patch-level occupancy of alligators across their range in North Carolina and to focus subsequent survey effort to estimate relative abundance. We followed the survey protocol used by Obrien (1983) to qualitatively determine any long term population trends.

METHODS

Study Area

We conducted our research throughout an expansive area comprised of 25 coastal counties in eastern North Carolina where previous research suggested alligators occur (O'Brien 1983). Coastal counties were: Beaufort, Bertie, Bladen, Brunswick, Camden, Carteret, Chowan, Columbus, Craven, Currituck, Dare, Gates, Hertford, Hyde, Jones, Lenoir, Martin, New Hanover, Onslow, Pamlico, Pasquotank, Pender, Perquimans, Tyrrell, and Washington counties (Figure 1). The study area included portions of 8 watersheds; the

Chowan, Roanoke, Pasquotank, Tar-Pamlico and Neuse Rivers flow into the Albemarle-Pamlico estuarine systems, while the Cape Fear River and White Oak Rivers flow directly into the Atlantic Ocean. The Lumber River is part of the Pee Dee watershed, and flows from North Carolina, eventually into Winyah Bay in South Carolina (Street et al. 2005).

The study area included >40,000 km² of federal, state, and private lands. Public lands included Bladen Lakes State Forest, Croatan National Forest, numerous national wildlife refuges, military lands, state parks, and state-owned game lands. Surveys were stratified into three habitat types: rivers, lakes, and estuaries. Rivers were described as slow-flowing black and brown water streams with vegetation consisting almost entirely of forests of wetland trees. Bottomland hardwood forest and swamps were dominated by bald cypress (*Taxodium distichum*), water tupelo (*Nyssa biflora*), and various oaks (*Quercus* spp.) (Natureserv 2007). Lakes included man-made reservoirs, small millponds, and naturally occurring Carolina bay lakes. Reservoirs and millponds were highly variable, but bay lakes were characterized by shallow, acidic water with poor drainage. Thick layers of peat covering sandy soils were surrounded by dense shrubs, pond pine (*Pinus serotina*), and loblolly pine (*Pinus taeda*). Lake vegetation consisted of open water, with scattered pond cypress (*Taxodium ascendens*), or floating peat mats of vegetation (Sharitz 2003). Estuaries included areas of open water, tidal flats, freshwater, brackish, and saltwater marshes, and submerged plant beds with wind and lunar tidal influences. Vegetation varied but was dominated by large graminoids, and floating or submerged aquatics (Rader and Babcock 1989, Natureserv 2007).

Data Collection

We initiated a 2-phase sampling approach (Conroy et al. 2008, Pacifici et al. 2012) that focused occupancy surveys over a broad area in the first year and abundance surveys that focused on areas of high predicted occupancy probability in the second year, to determine distribution and landscape factors influencing alligator occupancy.

Phase I-Occupancy Surveys

In 2012, we used a stratified random sampling design to select 110 night spotlight survey routes on rivers, lakes, and estuaries in the coastal counties of North Carolina (Figure 1). All river and estuary survey routes were 16 km in length, and divided into 4-km spatial replicates. Due to variable sizes, the entire perimeter of each lake was surveyed and divided into as many 4-km spatial replicates as possible. Some survey routes were shortened or removed from sampling because of limited navigability or restricted access. Of the initial 110 routes, we were able to complete 103 survey routes. Route selection did not include any bias from known current alligator occurrence.

Night count data collection began on 2 June, 2012 and ended on 31 June, 2012. Detectability of alligators is seasonal and the highest counts usually occur in June when all size classes are most visible, and adult alligators move to more open waters (Woodward and Marion 1978, Fuller 1981, Lutterschmidt and Wasko 2006). Trained field biologists followed a strict protocol to minimize observer and detectability bias. Survey teams, comprised of one observer and one navigator per boat, began each 16-km survey 30 minutes after sunset when alligators are most active, and followed predetermined transects recorded in GPS units. The observer employed a 200,000 candlepower Q-beam spotlight, directly

plugged in to a constant power source to minimize battery strength variability. Observers swept the surface of the water with the beam to detect distinct red alligator eye-shine. For each spatial replicate, the raw counts of alligator eye shine detections were recorded.

For each survey, we recorded the date, time of day, location (latitude and longitude), water conditions, and habitat type. Using standardized protocol and measuring devices, we recorded water temperature, air temperature, water salinity, wind speed, and percent cloud cover, at the start of each survey replicate. Surveys were not conducted on nights with heavy winds or rain to reduce outside sources of variability in our data collection (Woodward and Marion 1978, Wood et al. 1985, Moore 1994, Webb et al. 2009, Fujisaki et al. 2011).

Phase-II Abundance Surveys

Using results from the initial occupancy survey in 2012, we focused phase-II efforts to estimate abundance in areas with the greatest occupancy probability in North Carolina. Survey routes surpassing a 35% threshold of probability of occupancy were selected for sampling in June, 2013. A total of 45 survey routes from the original 103 routes were above the threshold (Figure 2). Three temporal replicate counts were conducted for each survey route in June, 2013. Replicates were conducted on consecutive nights to ensure a closed population and by the same observer to reduce observer and detectability bias. Each 4-km section of the 2013 surveys was designated as an individual sample site to reduce site-level variability within the survey route. The standardized sampling protocol from 2012 was followed in 2013 for the abundance surveys, with the addition of recording vegetation. During surveys in 2012, we realized detection and occupancy probabilities could be influenced by aquatic and shoreline vegetation. In 2013, we recorded the average amount of

vegetation present for each 4-km site. We created an index of aquatic or overhanging vegetation present using a categorical measure. Vegetation was indexed on a scale of 1 to 4, indicating an increasing amount of vegetation present along the shoreline. Level 1 denoted a clear or visible shoreline with no overhanging vegetation; all alligators present should be detected. Subsequent levels described increments of increasing vegetation. Level 4 was described as having overhanging and aquatic vegetation present, with the shoreline not visible. The observer visually estimated the amount of vegetation present.

Analyses

Phase I

We used a single season, single-species occupancy modeling framework that relies on presence/absence data to account for imperfect detection probability (p) and examine how factors influence occupancy probability (ψ) (Royle 2004). We conducted all occupancy analyses in R using a logit-link function to model effects of covariates on variation among sites for both occupancy and detection. All continuous covariates were normalized prior to analysis. Using the package ‘unmarked’ (Fiske and Chandler 2011) in R, we fit a set of single-season, single-species occupancy models using data from our 2012 occupancy surveys. We assigned a zero to the survey replicate if no alligators were detected, and we assigned a one if at least one alligator was detected on the replicate. We assumed the population was closed, no heterogeneity occurred, other than measured covariate induced heterogeneity, and the detection process was independent at each site.

We anticipated weather and water conditions would impact detection, and thus included the observation covariates of wind speed, air temperature, cloud cover, and water

temperature. We included Julian date of each survey as a covariate to determine any temporal trends in detection. We also included habitat type as an observational covariate due to the differences in vegetation and water levels among the three habitat categories.

We used habitat type as a site covariate for occupancy because we expected habitat type would influence prey availability and cover, thus influencing alligator habitat selection. In addition, we included latitude and longitude as site covariates because North Carolina is the northern extent of the alligator's range, and we expected alligators to occur in southern and eastern portions of NC where average temperatures are slightly warmer. Previous research has shown that alligators prefer fresh to slightly brackish water, due to their low level of salt water tolerance (Laurén 1985); therefore, we also included water salinity as a site covariate. Julian date was included to determine if alligators were more available as the breeding season progressed. Also, we fit a model including quadratic relationship with Julian date to determine if alligator occupancy of open water suddenly decreased due to the onset of nesting season for females (Joanen and Chabreck 1979, Klause 1984). However, the model was not improved.

Using a multi-modal inference, we conducted initial analyses using the package 'MuMIn' in R to generate a set of models with all combinations of covariates within the global model to determine site specific occupancy while correcting for imperfect detection. We fit all possible models (Barton 2009) with all possible combinations of covariates on detection and occupancy and selected the best model according to the lowest AIC on covariates. To account for model uncertainty (Burnham and Anderson, 2002), we averaged the parameter estimates and their corresponding standard errors for those models within 2

Δ AIC from the top model. We predicted the probability of occupancy for each site based on the model averaged parameter estimates. We selected all surveys that surpassed a 35% occupancy threshold to resample in 2013.

Phase II

We continued using the package ‘unmarked’, in R, to fit a series of binomial N-mixture models (Royle, 2004) to estimate site-specific alligator abundance (λ) while accounting for imperfect detection (ρ) using the 2013 temporally replicated alligator counts. We included all covariates from the previous occupancy analysis, with the addition of survey start time on detection and vegetation index on both detection and abundance. Vegetation indices were placed into two bins representing low and high vegetation. The survey counts appeared to be over-dispersed, thus we fit the global model using three distributions to determine which best fit the data: negative binomial, Poisson, and zero-inflated Poisson distributions. Using the package ‘MuMIn’ in R, we fit all possible models (Barton 2009) with all possible combinations of covariates on detection and abundance and selected the best model according to the lowest AIC on covariates. To account for model uncertainty (Burnham and Anderson, 2002), we averaged the parameter estimates and their corresponding standard errors for those models within 2 Δ AIC from the top model.

RESULTS

In 2012, we surveyed 1,331 km of shoreline. We detected at least one alligator on 26 of the 103 surveys completed, or 25.2 % of surveys, with 117 individual observations of alligators. Across all survey routes, naïve detection probability was 0.46 (SE \pm 0.06). The detection of alligators increased as air temperature increased, but detection was less likely in

estuaries. The top averaged models also included a decrease in detection of alligators in rivers and during higher wind speeds, but these factors were not significant ($p > 0.05$). Null occupancy probability was 0.28 ($SE \pm 0.05$) across all surveys. The top ranked occupancy model included an increase of alligator presence in more southern and eastern portions of North Carolina and increased later in the season. Additionally, the likelihood of alligator presence decreased as water salinity increased (Table 1).

In 2013, 43 routes were surveyed for a total of 152 4-km sites. In total, 115 alligators were observed across all survey routes on the first temporal replicate, 116 on the second, and 110 on the third. Alligators were detected on 55.8% of the surveys. The minimum counts for all three site replicates were 0, and maximum counts for each site replicate were 27 for the first, 27 for the second, and 22 for the third.

Null abundance in the 43 selected survey routes was 0.3025 ($SE \pm 0.025$) alligators/km; naïve detection probability was 0.57 ($SE \pm 0.03$). While an increase in wind speed was the only significant predictor ($p < 0.05$) of a decrease in detection, the top models ranked by AIC also included other covariates. A decrease in detection in rivers and estuaries compared to lakes, and a decrease in detection in relation to an increase of aquatic vegetation and air temperature were included but not statistically significant.

While a decrease in salinity was the only significant predictor of increased alligator abundance, the top model also included higher abundance in lakes and estuaries than in rivers and in sites with more aquatic vegetation. Additionally, the top model included latitude and longitude, suggesting alligator abundance increased in southern and eastern portions of the study area (Table 2).

DISCUSSION

We conducted a wide-range two-phase adaptive sampling approach to provide insight into American alligator relative abundance and distribution at the northern edge of their range. Site characteristics coupled with our analyses indicated that several covariates affect alligator occupancy in North Carolina. Northern and western survey sites were less likely to be occupied by alligators. Alligators in North Carolina are most likely limited by temperature at the northern extent of their distribution. Alligators were less abundant or not observed in several lakes located in northern latitudes, despite the presence and availability of seemingly suitable conditions. Although American alligators are the northernmost occurring species of crocodilian and have behavioral adaptations to freezes (Hagan et al 1983), their distribution limits are most likely driven by cold temperatures (Brisbin et al. 1982). When ambient temperatures remain below 38° F for extended periods of time, alligators may die of hypothermia or become extremely cold stressed, reducing their overall fitness. Other research has shown that smaller alligators are more susceptible to cold temperatures than larger ones (Smith and Adams 1978), and cold stress can adversely affect reproductive physiology by reducing egg viability or nesting frequency (Klauser 1984). Alligators in northern and western portions of coastal North Carolina may experience more frequent or prolonged cold weather events, limiting their distribution in these areas, and further restricting size class distribution.

Furthermore, we observed a decrease in both alligator abundance and occurrence as water salinity increased. Salinity is considered to be one of the strongest abiotic factors limiting the distribution of alligators in estuaries throughout their range (Dunson and Mazzotti 1989). Alligators usually do not occur in high saline environments (adults < 15 ppt,

juveniles < 10 ppt), and long-term exposure is known to cause dehydration and potential death (Taplin et al. 1982, Lauren 1984). Unlike the American crocodile, alligators do not have salt glands used for osmoregulation, and therefore cannot remove excess salt from their bodies (McIlheney 1935, Joanen and McNease 1972, Dunson and Mazzotti 1989). However, behavioral osmoregulation has been observed in North Carolina when estuarine alligators followed a diverted flow of fresh water while still feeding in a highly productive estuary (Birkhead and Bennett 1981). Although alligators were more likely to occur in coastal areas, their intolerance for salt water was evident, limiting their abundance and distribution in these areas where other biotic factors may have been favorable.

Alligator occurrence and abundance did not vary statistically among habitat types, but pockets of highest alligator density occurred in a few small and relatively undisturbed southern bay lakes. These lakes, including Orton Pond, Lake Ellis Simon, and Great Lake, may provide ideal alligator habitat due to water quality characteristics, such as lower acidity, and less turbidity. High densities in lentic habitat types such as lakes and ponds are not uncommon in more southern populations. For example, alligator densities in a lake in Florida have exceeded 29 alligators/km (Woodward and Moore 1990). Lentic habitat types may provide alligators with fairly stable water levels (Fujisaki 2009), food sources, and vegetation for nesting and hiding cover (Webb et al 2009). Lower densities of alligators in riverine systems also have been observed in other states; comparable low densities occurred in South Carolina (0.25-1 alligator/km) (Murphy and Coker 1983), Mississippi (0.82 alligators/km) (Duran 2000), and Arkansas (0.6 alligators/km) (Irwin and Wooding 2002).

Overall, our results show that alligators occur at very low densities or are not present throughout large areas in eastern North Carolina. Alligator distribution appears to be clumped, suggesting a metapopulation structure, and is relatively similar to the distribution described by O'Brien (1983) 30 years prior (Figure 3). Alligator densities decreased from south to north, and no alligators were detected north of the Albemarle Sound, supporting the conclusion that this remains the northern limit of the range. However, alligators were detected farthest north in Merchant's Millpond State Park, as they were 30 years prior; it isn't clear whether this is a natural or introduced population. Additionally, comparisons of raw indices from four lakes surveyed in the early 1980's indicate the population has nearly doubled in these patches of highest density. In lake Ellis Simon, a raw maximum count of 33 alligators in 1980 increased to a maximum count of 53 alligators in 2013. Counts in Orton Pond, believed to have the highest density of alligators in North Carolina, increased from 40 in 1980 to 79 in 2013. This roughly suggests an annual population growth rate of 1.01 to 1.02.

In addition, areas of high alligator abundance appear to be clumped where alligators are somewhat protected, such as military bases, national forests, and private property with restricted access. This is consistent with distribution patterns documented by O'Brien (1983). Although the protection status does not guarantee that alligators will not be harmed or harassed, it does reduce chances for alligator/human interactions and increases the likelihood that interactions that do occur will be passive. The control of human harassment in North Carolina is beneficial to alligator populations as alligators frequently are poached, and become wary of humans (O'Brien 1983, Woodward and Moore 1990).

MANAGEMENT IMPLICATIONS

Overall, the alligator population in North Carolina appears to be stable or slightly increasing. However, the patchy distribution and extremely low densities of alligators in eastern North Carolina means that maintaining current strongholds of alligator habitat are crucial to alligator persistence at the northern edge of their range. Other research shows from 1994 to 2001, 1.95 % of wetland areas in the 20 coastal counties of North Carolina were converted to dry upland or open water (Carle 2011). Although estuaries are relatively protected, North Carolina has continued to lose non-tidal freshwater wetland resources to upland development, despite state and federal laws regulating wetland impact. These same freshwater wetland resources boast some of the highest alligator densities in the state. Changes in population size and structure may occur over decades, and we recommend long term monitoring to determine population and distribution changes. Our 2-phase sampling technique proved ideal to obtain initial population indices on established routes and could be used as a tool to maintain monitoring over the long term. Additionally, it is necessary to include modeling techniques that incorporate imperfect detection of alligators to estimate site-specific occupancy and abundance during long-term monitoring.

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Table 1. Model averaged beta coefficients (β), standard errors, P values, and relative variable importance for parameter estimates of occupancy (ψ) and detection (ρ) for our top ranked occupancy model of American alligators in eastern North Carolina, USA, 2013.

Covariate ^a	β	SE	Significance	Relative Variable Importance ^c
<i>Occupancy</i>(ψ)				
Intercept	-3.4668	1.1803	0.0033	
date	0.1557	0.0640	0.0150	1.0
latitude	-3.9047	1.0845	0.0032	1.0
longitude	-2.3335	0.8011	0.0036	1.0
salinity	-1.8427	0.6141	0.0027	1.0
<i>Detection</i>(ρ)				
Intercept	0.5899	0.4682	NS ^b	
air temp	0.8675	0.3155	0.0060	1.0
habitat B	-0.8619	0.6039	NS	1.0
habitat C	-2.3130	0.7113	0.0011	1.0
wind speed	-0.2492	0.3273	NS	0.51

^aHabitat A B or C=categorical variable, lake river, or estuary, date=Julian date, NS^b=Not significant, Relative Variable Importance^c=the frequency of occurrence of each covariate in the top two averaged models.

Table 2. Model averaged beta coefficients (β), standard errors, P values, and relative variable importance for parameter estimates of abundance (λ) and detection (p) for our 43 top-ranked abundance models of American alligators in eastern North Carolina, USA, 2012.

Covariate ^a	β	SE	Significance	Relative Variable Importance ^b
<i>Abundance(λ)</i>				
intercept	0.9286	0.6807	NS ^b	
habitat B	-0.9867	0.8218	NS	0.74
habitat C	0.5825	1.0630	NS	0.74
latitude	-0.5768	0.4508	NS	0.85
longitude	-0.3854	0.4799	NS	0.53
salinity	-0.7730	0.2403	0.0013	1.00
vegetation B	0.7572	0.6670	NS	0.78
<i>Detection(p)</i>				
intercept	-0.9956	0.7512	NS	
habitat B	-0.3666	0.9602	NS	0.74
habitat C	-1.3013	1.1990	NS	0.74
vegetation B	-0.2768	0.6047	NS	0.24
weather	0.0535	0.0723	NS	0.51
wind speed	-0.4124	0.1600	$p < 0.001$	1.00
water temp	0.0361	0.1021	NS	0.16
air temp	-0.0020	0.0229	NS	0.02

^aHabitat A B or C=categorical variable, lake river, or estuary, vegetation A or B=categorical variable, low or high vegetation abundance, weather=percent cloud cover. NS^b=Not significant. Relative Variable Importance^c=the frequency of occurrence of each covariate in the top six averaged models.

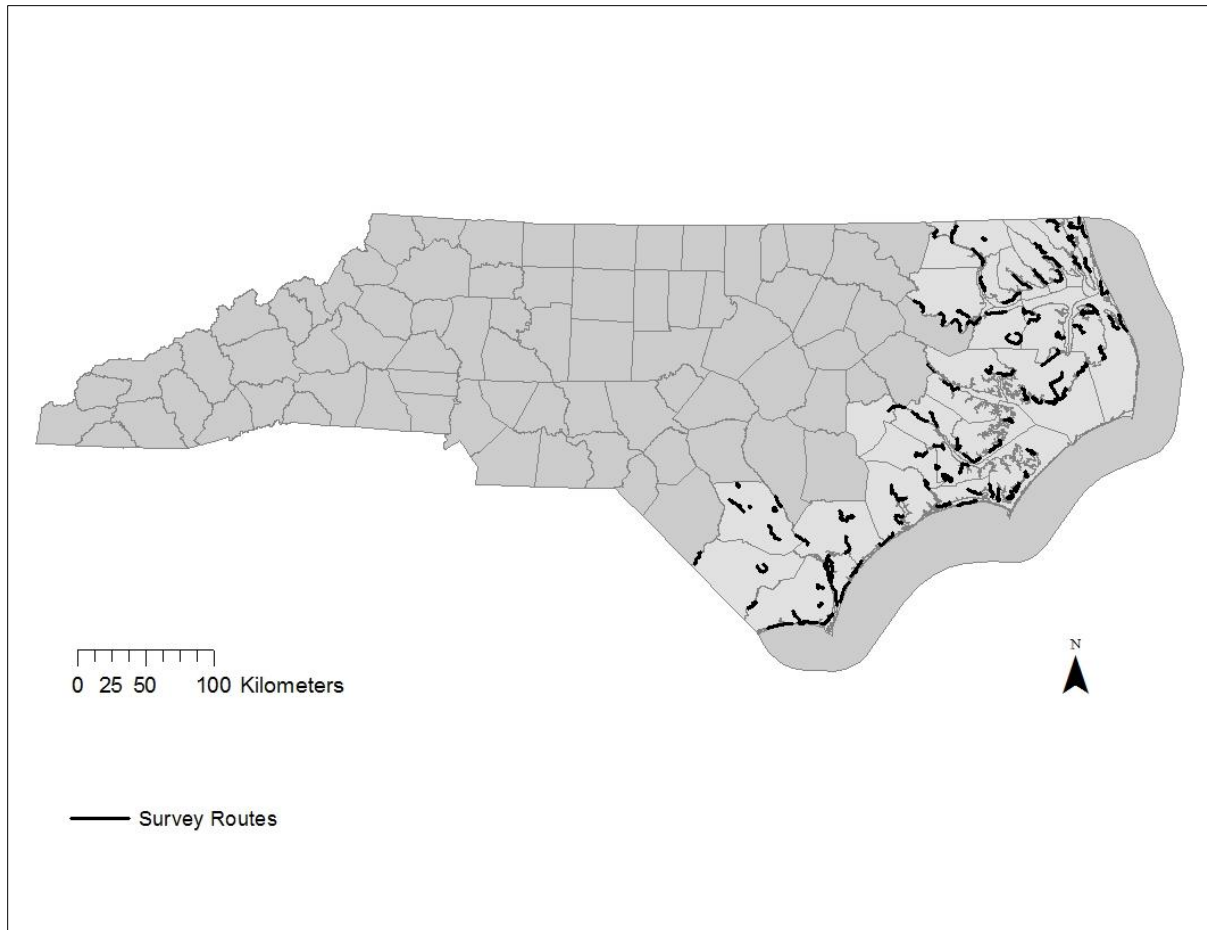


Figure 1. Locations of occupancy survey sites on rivers, lakes, and estuaries, for American alligators in 25 counties in North Carolina, USA (June 2012).

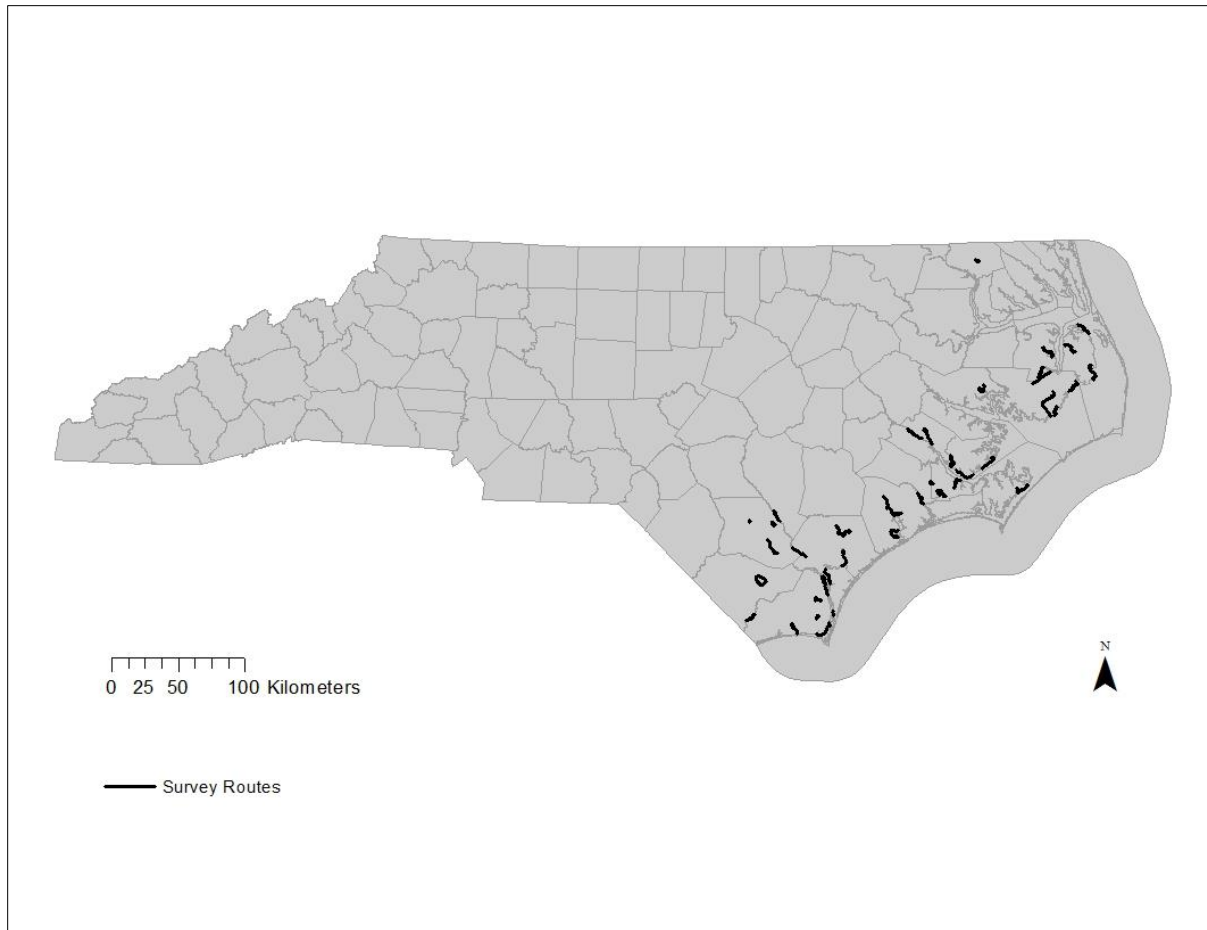


Figure 2. Locations of abundance survey sites surpassing a 35% likelihood of occupancy threshold by American alligators in eastern North Carolina, USA (June 2013).

CHAPTER 2

Estimating Population Dynamics and Harvest Potential for the American Alligator Population in North Carolina

ABSTRACT

Harvest of wild American alligators (*Alligator mississippiensis*) has been a sustainable-use success throughout most of the species' range. In North Carolina, there is growing interest in developing an alligator harvest season, but the impact of a harvest on northern populations is unknown. We developed a female-specific stage-structured matrix model of alligator life history at the northern extent of its range to determine the population growth rate (λ). We conducted sensitivity and elasticity analyses to identify the contribution each vital rate made to λ , followed by a life-stage simulation analysis to account for vital rate variance using hypothesized variation in parameter probability densities. Finally, we assessed the relative sensitivities of λ to various theoretical harvest scenarios on a population of adult and sub-adult female alligators in eastern North Carolina. We estimated a population growth rate of 1.02. Adult female survival had the highest sensitivity and elasticity values, while hatchling survival had the least influence on λ . Because adult survival has the greatest impact on population change, only minimum harvest of adult females resulted in a median λ greater than 1. Additional data could improve the accuracy and precision of these models, but current available data coupled with harvest data from other states suggests harvest of alligators in North Carolina is not sustainable.

INTRODUCTION

The American alligator (*Alligator mississippiensis*) is an economically and culturally important species that occurs throughout the southeastern United States from Texas, eastward to Florida and northward to North Carolina. The species' wide distribution and popularity among trappers and hunters make it a valuable commodity; however, alligator numbers declined substantially in the 19th century as a result of overharvest and habitat destruction (McIlhenny 1935). Populations have since recovered, but the alligator's historical decline led to heightened concern over the species' population status, making it a management priority. Annually, thousands of wild alligators are harvested for meat, hides, and as trophies in several southern states including Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, South Carolina, and Texas. However, the majority of population monitoring and research has occurred in Florida, South Carolina, and Louisiana, and restoration projects are underway to conserve habitat for alligators in these same areas (Dutton et al. 2002, Butfiloski 2013, Louisiana Department of Wildlife and Fisheries 2013).

Due to limitations of studying large-bodied and long-lived apex predators, many details of the American alligator's life history are poorly known. Additionally, alligator's life history is spatially and temporally variable throughout its range; habitat use, activity, and movement vary according to gender, age class, season, and geographic location (Chabreck 1965, Joanen and McNease 1970, Goodwin and Marion 1979, Taylor 1984, Rootes and Chabreck 1993). Although many characteristics of alligator ecology have been well-researched in southern populations, less is known about alligators at the northern range limit. Growth rates and survivorship in some stages are based on estimates from southern

populations; thus, modeling the potential effects of hunter harvest for northern populations of alligators is an exercise fraught with uncertainty.

Yet, there is increased interest in creating a season for trapping and hunting alligators in North Carolina where alligators are still protected. As human development within alligator habitat continues at a high rate along the coasts of North and South Carolina, an increase in the occurrence of nuisance alligators is projected. Hence, a proposed alligator harvest season in North Carolina could manage perceived growing populations and potential nuisance alligators, offer a unique hunting opportunity to sportsmen, and provide revenue from permit sales to further monitor alligator populations (Owen et al. 2010).

Wild animal harvest (i.e., hunting and trapping) is an effective management strategy to reduce populations of overabundant wildlife and reduce negative human-wildlife interactions while providing economic incentives to stakeholders (Bradshaw et al. 2006). Yet, sustainable harvest management has proved to be a complex and difficult challenge, requiring a suite of current ecological and demographic information of the harvested population (Tucker 1995). Uncontrolled variation in harvest rates, randomly fluctuating environmental conditions, unapprised assumptions about population response to harvest, and management policies with short-term population projections have led to resource collapse (Ludwig et al. 1993, Hutchings and Myers 1994, Landres et al. 1999).

The use of matrix population models allows managers to explore and assess population status, diagnosing causes of decline, projecting population size, and prescribing management tactics such as harvest strategies and regulations (Caswell 2001). Analyses of population projection matrices have been applied widely to assess alternative population

management strategies (e. g. Crouse et al. 1987, Brault and Caswell 1993, Doak et al. 1994).

The life-stage simulation analysis (LSA) is a simulation-based method under plausible or hypothesized variation and uncertainty in vital rates for a given population. Through population simulation and sensitivity analyses, long-term effects of alternative harvest strategies can be evaluated. Additionally, inconsistencies in available data and deficiencies of current information are determined, allowing research needs to be identified. Such models can aid decision making when a species' ecology is poorly known, where research budgets are limited, or if the cost-to-benefit ratios of the management alternatives are unknown (Tucker 2000).

Stage-structured matrix models have been constructed for several crocodilian species to explore parameters influencing population growth and inform management priorities (Tucker 2000, Richards 2003, Dunham et al. 2014). A similar exercise for the North Carolina alligator population will provide a better understanding of future population change and the potential impact of a regulated harvest. Because conservation efforts are most likely to succeed when they focus on increasing vital rates that most strongly influence population growth (*i.e.*, the vital rates with the highest sensitivities or elasticities), our objectives were to assess the relative importance of stage-specific vital rates of alligator populations in North Carolina using an LSA framework with published alligator vital rates. Additionally, we presented several harvest scenarios to demonstrate their potential to impact alligator population estimates via underlying changes in vital rates.

METHODS

Parameter Estimation

We used a variety of published sources to collect vital rates of American alligators at the northern extent of their range to be used in a matrix model specific to alligators in North Carolina (Table 1.) The life history traits of interest were stage class, growth rate, durations in a stage, survival rate for each stage, and fecundity (i.e., clutch size and nesting effort). Through research conducted at Lake Ellis Simon and surrounding areas from 1978-1983 (Doerr and Hair 1983), researchers outlined the significant life history differences (e.g., growth and reproductive rates) between a population of alligators in North Carolina and those in more southern areas (Fuller 1981, Klause 1984). The alligator population at Lake Ellis Simon represents one of the highest concentrations of alligators in North Carolina. Lake Ellis Simon lies approximately 130 km south of Albemarle Sound, which is still regarded as the present northern limit of the species' natural occurrence (Doerr and Hair 1983, Garner unpub.).

Growth rates from North Carolina were recorded by Fuller (1981) for alligators in Lake Ellis Simon, using Fabens's growth curve. We used these growth rates to calculate residence time in a stage, which we then used to calculate retention and transition rates for our matrix model. Fecundity parameters, including mean clutch size, percentage of eggs hatching, nest success, and frequency of nesting alligators in North Carolina, were reported by Klause (1984). We replaced missing vital rates for alligators in North Carolina, such as hatchling sex ratios and stage-specific survivorship, with estimates from other states. Data

from across the range of alligators suggests that the sex ratio of hatchlings may vary temporally and spatially, dependent on local climatic and microclimate conditions, as well as individual nest characteristics (Rhodes and Lang 1996, Lance et al. 2000). For example, researchers in South Carolina found substantial clutch-dependent variability in sex ratios. Additionally, hatchling sex ratios were likely to vary from year to year within the same habitat (Rhodes and Land 1996). For simplicity in our model, we chose a 1:1 sex ratio of alligator hatchlings. Only generalized adult survival rates from a short-term, 2-year mark recapture study (Fuller 1981) were available for alligators in North Carolina. Therefore, we used annual hatchling survival rates reported by Woodward et al. (1987) in a lake in central Florida, with similar habitat conditions to Lake Ellis Simon. We used monthly-recorded survival rates of female alligators reported in Louisiana to determine yearly survival rates for the remaining stage classes in the model (Nichols et al. 1976). Because North Carolina's average monthly temperatures reduce the growing season by one month, we adjusted survivorship of each stage class to reflect the assumed lack of predation that occurs during the dormant season (Nichols 1976).

Model development

We developed a female-specific stage-structured matrix model for alligators at the northern extent of the species' range to determine population growth and compare the relative importance of different vital rates. We assumed the population was not male-limited, which allowed us to accurately assess dynamics from only females. Due to different survival probabilities for males and females, many researchers have determined adult alligator

populations often are skewed toward a greater male-to-female ratio (Lance et al. 2000). Also, females may breed with multiple males and with subdominant males when dominant males are not available (Lance et al. 2009). Because males outnumber females and do not limit reproduction, our model only included data for female alligators. We calculated the annual asymptotic growth rate (λ) as the dominant eigenvalue of the matrix, while making several simplifying assumptions about the alligator population in North Carolina (Caswell 2001). We assumed there were no effects from migration, density-dependence, or environmental stochasticity. The assumption of geographic closure was made, which is reasonable because female alligators often display nest site and mate fidelity (Lance et al. 2009, Wilkinson 1984) and because alligators in North Carolina are patchily distributed. In addition, females on average travel less and have smaller home ranges than males (Joanen & McNease 1972). We assumed density-independence due to the low densities reported (O'Brien 1983, Garner 2016) compared to other states (Wood 1985, Brandt 1991*b*). Alligators in North Carolina are relatively undisturbed from hunting and management, so we assumed the population represented a natural stable stage distribution. Finally, we assumed homogeneity for each stage (i.e., all individuals in each stage had the same parameters; Nichols et al. 1976), though some research suggests larger female alligators have larger clutch sizes (Lance et al. 2009). Because our primary purpose was to determine population growth and demonstrate a range of possible effects for several management strategies, examining population dynamics under simple conditions was necessary (Merrill et al. 2003).

Model Structure

To calculate the population growth rate, reproductive values, and stable stage distribution, we partitioned alligator size classes into stage elements in a female stage-based matrix as follows:

$$\mathbf{n}_{t+1} = \mathbf{A} \cdot \mathbf{n}_t$$

where \mathbf{n}_t was a vector of abundances for each stage in the population at time t and \mathbf{A} was the population projection matrix. Our model consisted of 5 stages (Table 1), corresponding to hatchlings (H), small juveniles (sj), large juveniles (lj), sub adults (sa), and adults (A; ≥ 6 feet). The projection interval (from t to $t + 1$) was 1 year, with the following structure:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 0 & F_A \\ G_H & P_{sj} & 0 & 0 & 0 \\ 0 & G_{sj} & P_{lj} & 0 & 0 \\ 0 & 0 & G_{lj} & P_{sa} & 0 \\ 0 & 0 & 0 & G_{sa} & P_A \end{bmatrix}$$

Where P_i is the retention rate-probability of surviving and remaining in the same stage (i), G_i is the transition rate-probability of surviving and advancing to the next stage, and F_i is the fecundity of each stage. G_i is calculated as:

$$G_i = p_i \times c_i$$

where p_i is the stage-specific annual survival rate and c_i is the probability of advancing to the next stage (Caswell 2001). Fecundity, or average reproductive contribution for adults, was calculated as follows:

$$F_i = \text{mean clutch size} \times \text{percent hatching} \times \text{nest success} \times \text{sex ratio} \\ \times \text{percent breeding}$$

Or:

$$F_i = 35.5 \times 0.70 \times 0.88 \times 0.5 \times 0.5$$

We assumed the hatchling, juvenile, and sub-adult classes did not reproduce, so we did not include a fecundity value for those stages. We executed the matrix model in the R package “popbio” (Stubben and Milligan 2007) to determine λ and to project population sizes for 50 years. Additionally, we conducted an eigen analysis to determine stable stage distribution (SSD), stage-specific reproductive values, sensitivities, and elasticities (Table 3.)

Model Validation and Parameter Adjustments

Results from our initial matrix model “Matrix 1” showed the alligator population in North Carolina was declining rapidly ($\lambda=0.91$). Other recent research using assumed and published vital rates for North and South Carolina also suggested that alligator populations were declining (Dunham et al. 2014). Yet, these modeling exercises do not match anecdotal field observations from trappers, landowners, and biologists in eastern North Carolina (Garner 2016, personal observation). Hence, we attempted to validate the initial model predictions using comparisons of actual alligator indices over time in known locations within North Carolina. We compared indices of alligator populations recorded 30 years apart at two known locations with similar habitat and protection in North Carolina to obtain a geometric growth rate over the 30-year span (Mills 2007). Indices were included from Lake Ellis Simon

and Orton Pond, which are comprised of private and protected lentic lake habitat. These sites support higher alligator density relative to overall alligator populations in coastal North Carolina and most likely exhibit a natural stable stage distribution. We used the abundance of a population (N) over a total of T time steps in the formula:

$$\lambda = \sqrt[T]{\frac{N_T}{N_0}} = \left(\frac{N_T}{N_0}\right)^{1/T}.$$

From this exercise, we estimated the yearly geometric growth rate in North Carolina was between $\lambda=1.01$ and $\lambda=1.02$. This suggested the demographic parameters in the initial matrix model were not correct; therefore, we thoughtfully constructed a new matrix “Matrix 2” using adjusted vital rates to explore other parameterizations. We carefully adjusted vital rate parameters within the matrix to reflect more realistic estimates of the species within the northern limit of its range.

We expanded our literature review that parameterized Matrix 1 and now reviewed studies on alligator survival, growth, and reproduction across the species’ range to determine which parameters in the initial model were most likely biologically accurate, and what landscape factors influenced them. Based on the review, we shortened the duration of time that alligators spent in each stage class by assuming a more rapid annual growth rate. Growth rates of American alligators vary widely across their range, and are influenced not only by temperature, but also density, food availability, and habitat conditions (Hines et al. 1968, Chabreck 1971, Chabreck and Joanen 1979, Dietz 1979, Jacobsen and Kushlan 1989, Brandt 1991a, Rootes et al. 1991, Wilkinson and Rhodes 1997, and Saalfeld et al. 2008). Annual

growth rates of alligators reported in North Carolina are slower than in southeastern populations and researchers suggest this is due to a shorter annual period of growth (Fuller 1981, Klause 1984). Although alligators in North Carolina are active for only one month less than alligators in Louisiana, their reported annual growth rate is almost half as slow. Therefore, we suspected that the growth rate may actually be higher than reported and we subsequently decreased the time during which alligators remained in each stage class to reflect a faster growth rate than suggested previously.

We also used higher hatchling and juvenile survival rates in the adjusted model. Other researchers reported that juvenile mortality, followed by hatchling mortality, is most influenced by cannibalism, and individuals remained vulnerable until they reached 140 cm total length (Delany et al. 2001). However, the rate of cannibalism is a topic of frequent debate and most likely varies widely both temporally and spatially; cannibalism has been estimated to range from 22-42% reported in Louisiana (Rootes and Chabreck 1993), 6-7% in Florida (Delaney et al. 2011), and 2-6% additionally in Florida (Nichols et al. 1976), and is usually considered a function of density and water depth (Nichols et al. 1976). At 21.4 individuals/km, the population of alligators at Orange Lake Florida is considerably denser than the estimated density at Lake Ellis Simon of 3.78-6.08 individuals/km (Wood et al. 1985). Therefore, we postulated that cannibalism is less prevalent in North Carolina than in more southerly populations where densities are much greater and not additive to mortality rates for hatchlings and juveniles. Additionally, small alligators may be less vulnerable to overall predation for two reasons. First, alligators are much less common in North Carolina, so they are not viewed as a common/steady food source by predators. Second, alligators are

dormant for an extra month compared to populations in more southern locations, and during this period they are rarely depredated. We used the adjusted vital rates (Table 2) in the new Matrix 2 to determine a stable stage distribution, stage-specific reproductive values, and a population growth rate more representative of the true geometric λ (Table 3).

Next, we created a Life-stage Simulation Analysis (LSA) using the vital rates incorporated into matrix models 1 and 2 to demonstrate the variation of λ over a 50-year population projection (Figures 1 and 2). The LSA is a simulation-based method under plausible or hypothesized variation, covariation, and uncertainty in vital rates for a given population (Wisdom et al. 2000, Mills 2007). To further maximize our ability to recommend efficient management actions, we analyzed Matrix 1 and the adjusted vital rates of Matrix 2 using several different sensitivity matrices within the LSA framework across 1,000 replicate matrices over 100 years. We calculated mean sensitivities and elasticities for each vital rate across the simulated matrices to identify the contribution each vital rate made to the population growth rate.

To create an LSA, vital rates were drawn randomly from a specified probability distribution that reflected the spatial variation and covariation of interest. Each set of randomly selected vital rates for the population was used to construct a time invariant matrix population model. One-thousand matrix replicates were generated through resampling of the probability distribution of each vital rate for each replicate. Data were analyzed across replicates to determine probability of potential effects of each vital rate on λ , the finite rate of increase (Wisdom et al. 2000).

To account for parametric uncertainty, we built matrices with random draws of each of the vital rates from an appropriate probability distribution (Figure 3). We used beta distributions for each of the survival and transition rates because they are naturally bound between 0 and 1, and we used a gamma distribution for the fecundity because it naturally is greater than 0. We used the known vital rates to define the mean of each distribution, and we allowed for a reasonable amount of variance to reflect current uncertainty.

For the beta distributions, we defined the α and β parameters as follows:

$$\alpha = 100 \times est.$$

$$\alpha + \beta = 100$$

Therefore:

$$\beta = 100 - \alpha$$

$$\mu = \frac{\alpha}{\alpha + \beta} = \frac{100 \times est.}{\alpha + (100 - \alpha)} = est.$$

$$\sigma^2 = \frac{\alpha\beta}{(\alpha + \beta)^2(\alpha + \beta + 1)}$$

Increasing the magnitude of the α and β parameters decreases the variance, which is why we constrained $\alpha + \beta = 100$.

For the gamma distribution, we used the α and β parameterization. We defined them as follows:

$$\alpha = est.$$

$$\beta = 1$$

Therefore:

$$\mu = \frac{\alpha}{\beta}$$
$$\sigma^2 = \frac{\alpha}{\beta^2}$$

We chose 1,000 random draws for each parameter and ran the simulation for a population projection over 100 years. We were also able to determine the sensitivities, elasticities, reproductive value frequencies, and 95% CI's for our matrices.

The LSA was used to account for uncertainty in the estimates of survival and fecundity due to process variance. While sensitivities of each life stage were relatively the same in Matrix 1 and Matrix 2, the population growth rate estimate ($\lambda=1.016$) from Matrix 2 was much closer to the calculated geometric growth rate from population indices ($1.01 \leq \lambda \leq 1.02$). Therefore, we chose the adjusted Matrix 2 as the foundation to create scenarios of different female alligator harvest rates.

Potential Management Strategies

Using the adjusted vital rates of Matrix 2, we assessed the relative sensitivities of the population growth rate to various theoretical harvest scenarios on a population of alligators in eastern North Carolina to evaluate possible impacts of alternative management strategies. We simulated these harvests by altering the model variables directly. We used the adjusted stage-structured matrix model to explore the potential impacts of harvest on λ , and evaluated the population growth projections based on a goal of a sustainable population. If the population

size at year 100 was less than the starting population size resulting in a geometric mean $\lambda < 1$, we concluded the population was not sustainable. We used the stable age distribution and a theoretical but likely population estimate of 100 female alligators for an area considered to be of high alligator density and optimum habitat in North Carolina. We based all modeling outcomes over a 100-year projection period, and we excluded density-dependent effects. We ran the 100-year simulation 1,000 times. We included scenarios which only accounted for parametric uncertainty, followed by scenarios incorporating demographic stochasticity within the models to highlight the variability. We created population projections following likely harvest scenarios based on other states. These scenarios included 3, 6, and 10% of the total population of adult male and female alligators harvested annually. These are standard alligator harvest quotas in Florida based on night count survey indices (L. Brandt, National Wildlife Service, personal communication). Because alligator populations are not male-limited, and greater percentages of males are normally harvested due to their large sizes and behavioral differences, the take of adult females could be minimized but not eliminated by taking advantage of these attributes. Therefore, we treated adult female harvest as bycatch and with a 1:1 sex ratio for model simplicity. By including varying amounts of total adult male and female alligator harvest (i. e., values between 3 and 10%) and using random draws from a binomial distribution to represent varying amounts of adult female bycatch within the total harvest (i.e., values between 5 and 50%), this represented the yearly demographic stochasticity and can demonstrate variable harvest sex ratios reported in other states. We also examined population growth under given proportions of sub-adult harvest as sub-adult

female alligators have lower reproductive values. The resulting 14 scenarios of different harvest rates are included in Table 7.

RESULTS

We calculated a geometric λ of 1.01-1.02 using alligator population indices at the same two sites over a 30-year span. In the stage-structured population matrix, we estimated λ as 0.91 (declining population) in the Matrix 1 model and 1.012 (stable or slightly increasing population) in Matrix 2. The λ derived from Matrix 2 was more accurate according to the trend analysis and predicted a slightly increasing population. We used vital rates from both matrices for subsequent analyses. We conducted an LSA with the vital rates in Matrices 1 and 2 and obtained mean elasticity and sensitivity values for each vital rate within the matrix. Adult female survival had the highest sensitivity and elasticity values for both matrices, while hatchling survival had the least influence on λ for both matrices (Tables 4, 5 and 6). Stable stage distributions predicted an alligator population consisting mostly of hatchlings and juveniles with 40% hatchlings, 36% juveniles, 18% sub-adults, and only 7% adults (Table 3). Adult females had significantly higher reproductive values (Table 3). We also reported the frequencies of highest parameters for both sensitivity and elasticity (Table 4).

Population projections of various harvest scenarios focused on removal of adult and sub-adult female alligators while including the effects of demographic stochasticity (Table 7). Two of the 14 harvest scenarios produced a mean λ greater than 1 (Figures 4-17). Only minimal harvest (3%) of the total population coupled with the minimal bycatch (5%) of adult female alligators and no harvest of sub-adult females resulted in a steady to slightly

increasing median λ with large uncertainty. Additionally, this same scenario with demographic stochasticity included within the model had a slightly increasing median λ . This suggests in a theoretical population of 100 alligators, only 0.13 adult female alligators could be harvested annually. No scenario of sub-adult female harvest had a median λ greater than 1, while every harvest scenario had a wide range of uncertainty. The uncertainty of the null matrix model (Figure 2) lent credibility to the decline in λ for 12 of the 14 harvest models (Figures 4-17).

DISCUSSION

A key result of our analysis is that the elasticity of λ was highest for adult survival, followed by the transition of sub-adults to adults for both matrices. This indicates that a given reduction in mean adult survival would have the greatest proportional change in λ and is more likely to lead to population declines than the same magnitude of reduction in other vital rates. The overall proportional change in λ was least affected by a change in juvenile survival and transitions. These sensitivity results are similar to that of Dunham et al. (2014) and Tucker (2000), where adult crocodilian survival was most important. These two studies showed that American alligators and Australian freshwater crocodiles (*Crocodylus johnstoni*) exploited the bet-hedging strategy through overcoming low early stage survival by long life and high adult survival. Furthermore, the Australian freshwater crocodile is a slow-growing crocodilian, reaching maturity at 19 years, similar to that of American alligator at the northern extent of its range. However, Tucker (2000) showed that spectacled caiman (*Caiman crocodylus*) reached maturation much quicker and juvenile survival was more vital to overall population growth than for other crocodilian species. Spectacled caiman reached

sexual maturity at 4-7 years of age, not unlike alligators in more southern populations such as Louisiana and Florida.

Because adult survival has the greatest impact on population change for both matrices, only extremely modest harvest rates of adult females were sustainable in the harvest scenarios. This is a realistic problem due to the nature of alligator harvest and the inability to determine the sex of alligators before a take (Dutton et al. 2002, Louisiana Department of Wildlife and Fisheries 2013, Butfiloski 2013). Although sub-adult survival had a much lower influence on λ , when sub-adult and adult survival were reduced simultaneously, the cumulative reduction in λ still did not yield a sustainable population. However, transient dynamics showed a brief increase in population for some scenarios, followed by a steep decline, outlining the importance of projecting the population over a long period. Predicting long-term effects of sustained hunter harvest is especially difficult. A large reduction in a smaller size class, which may be more prone to stochastic events like severe winters, can also affect λ greatly (Raithel et al. 2005).

Additional field studies are needed to determine processes affecting vital rates including environmental stochasticity, density-dependence, and population momentum. Across their range, alligators are susceptible to environmental stochasticity, including fluctuating water levels (Fujisaki et al. 2009), freezes (Brisbin et al. 1982, Hagan et al. 1983), environmental degradation (Guillette et al. 1994), and hurricanes (Hall 1991, Elsey and Kinler 2006, Elsey and Aldrich 2009). For example, Hall (1991) stated that the early arrival of 1985 hurricanes in Louisiana resulted in the loss of about 80-90% of the coastal alligator egg crop due to flooding. Alligators in North Carolina may be more vulnerable to

catastrophic events, including harsh winters and frequent hurricanes. Additionally, density dependence is ultimately a necessity for all populations and would stop the population from growing exponentially, potentially narrowing the upper bounds of our population projections (Caswell 2001). However, researchers have suggested that the selective take of larger nesting adult female alligators may result in a population increase from higher nesting densities of smaller subordinate females (Hall 1991).

MANAGEMENT IMPLICATIONS

Population growth estimates based on published demographic parameters for alligators in North Carolina suggest a declining population (Dunham et al. 2014). However, anecdotal evidence and recent population surveys suggest the North Carolina alligator population is stable or increasing. These inconsistencies lead to uncertainties in population projection trajectories and reinforce the need for more comprehensive research on alligator natural history and demographic rates in North Carolina. Because the life history traits of alligators are not well known at the northern extent of their range in North Carolina, modeling of the potential effects of harvest on population trends should be interpreted with caution. Further, if the demographic rates used by Dunham et al. (2014) are more accurate than the corrected rates we used, removals via a hunting season could cause even more substantial population declines.

Due to the extreme importance of adult female alligator survival to population growth, coupled with a relatively low λ , we advise against a general recreational harvest of alligators in North Carolina until further field research needs are met to improve to accuracy of harvest models. It is impossible to determine sex of alligators under 10 feet in length

before harvest, and thus female bycatch is likely. If harvest is pursued by managers, potential solutions may include novel harvest methods to minimize adult female mortality. These alternatives may include live capture and subsequent sexing of alligators before harvest, the use of licensed guides to oversee and regulate capture and sexing of alligators, strict trophy-only hunting of alligators over 10 feet in length, and harvest only late in the summer to encourage the take of adult males only.

As a decision-making tool, we demonstrated that incorporating a simulation modeling approach into the management planning process is of great value, especially for a long-lived and difficult-to-study species like the American alligator. However, as Tucker (2000) suggested, a model framework is a tool to begin studying many alternative hypotheses; hence, this initial model can be modified to explore various combinations of vital rates that promote a sustainable harvest. A key value of our simulation model allows managers to detect strategies which may have catastrophic consequences such as the additive mortality due to harvest. Furthermore, our simulations highlight the risk of an adaptive-harvest management plan for alligators in North Carolina.

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Table 1. Five-stage life history parameters for American alligators in North Carolina included in “Matrix 1.”

Stage	Description	Stage duration (d_i)(yrs)	Annual survivorship (p_i)	Annual fecundity (F)
Clutch	Eggs	0	0.7	0
1	Hatchlings	1	0.41	0
2	Small juveniles	2	0.407	0
3	Large juveniles	3	0.647	0
4	Sub-adults	14	0.818	0
5	Adults	>20	0.891	5.44

Table 2. Five-stage life history parameters for American alligators in North Carolina modified to reflect an increase in growth rate and juvenile survival. Parameters included in “Matrix 2.”

Stage	Description	Stage duration (di) (yrs)	Annual survivorship (pi)	Annual fecundity (F)
Clutch	Eggs	0	0.7	0
1	Hatchlings	1	0.51	0
2	Small juveniles	1.5	0.507	0
3	Large juveniles	1.5	0.747	0
4	Sub-adults	7.5	0.818	0
5	Adults	>35	0.891	5.44

Table 3. Stable-stage distribution and reproductive values for the American alligator population matrices 1 and 2 using 5-stage life history parameters shown in Tables 1 and 2. Table 2 and the resulting Matrix 2 reflect an increase in juvenile alligator survivorship and growth rate parameters.

Stage	Description	Stable Stage Distribution		Reproductive Value	
		Matrix 1	Matrix 2	Matrix 1	Matrix 2
1	Hatchlings	0.432	0.395	1.0	1.0
2	Small juveniles	0.287	0.255	2.21	2.00
3	Large juveniles	0.089	0.098	11.36	5.65
4	Sub-adults	0.119	0.179	33.80	8.98
5	Adults	0.079	0.074	326.67	45.04

Table 4. Frequency of highest survival (G) and transition (P) parameter values of each stage class (hatchlings (h), small juveniles (sj), large juveniles (lj), sub adults (sa), adults (a), and fecundity (f) of sensitivity and elasticity within the LSA models for American alligators in North Carolina, after 1000 matrix iterations.

Stage	Sensitivity		Elasticity	
	Matrix 1	Matrix 2	Matrix 1	Matrix 2
G_h	0	0	0	0
P_{sj}	0	0	0	0
G_{sj}	0	0	0	0
P_{lj}	0	0	0	0
G_{lj}	0	0	0	0
P_{sa}	0	0	47	7
G_{sa}	709	983	0	0
F	0	0	0	0
P_a	291	17	953	993

Table 5. Sensitivity values, or the effect on λ when small changes in vital rates occur while other vital rates are held constant for the American alligator population given in “Matrix 1” and “Matrix 2.” Vital rates include survival (G), transition (P), and fecundity (F) for each stage in the matrices.

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & F_A \\ G_H & P_{sj} & 0 & 0 & 0 \\ 0 & G_{sj} & P_{lj} & 0 & 0 \\ 0 & 0 & G_{lj} & P_{sa} & 0 \\ 0 & 0 & 0 & G_{sa} & P_A \end{bmatrix}$$

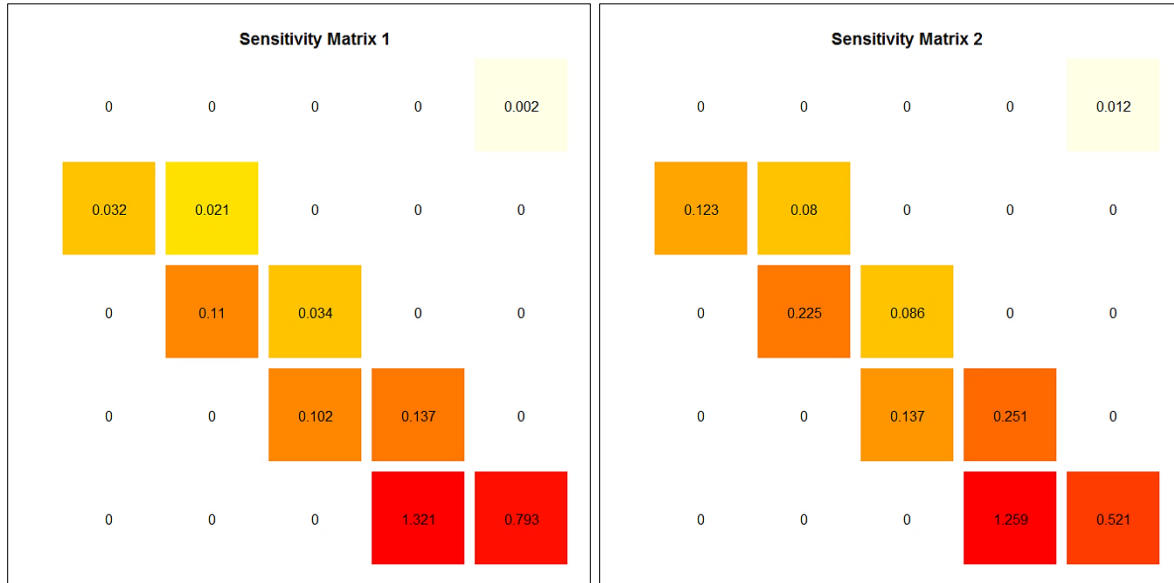


Table 6. Elasticity values, or the effect of a proportional change in the vital rates on λ for the American alligator population “Matrix 1” and Matrix 2.” Vital rates include survival (G), transition (P), and fecundity (F) for each stage in the matrices.

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & F_A \\ G_H & P_{sj} & 0 & 0 & 0 \\ 0 & G_{sj} & P_{lj} & 0 & 0 \\ 0 & 0 & G_{lj} & P_{sa} & 0 \\ 0 & 0 & 0 & G_{sa} & P_A \end{bmatrix}$$

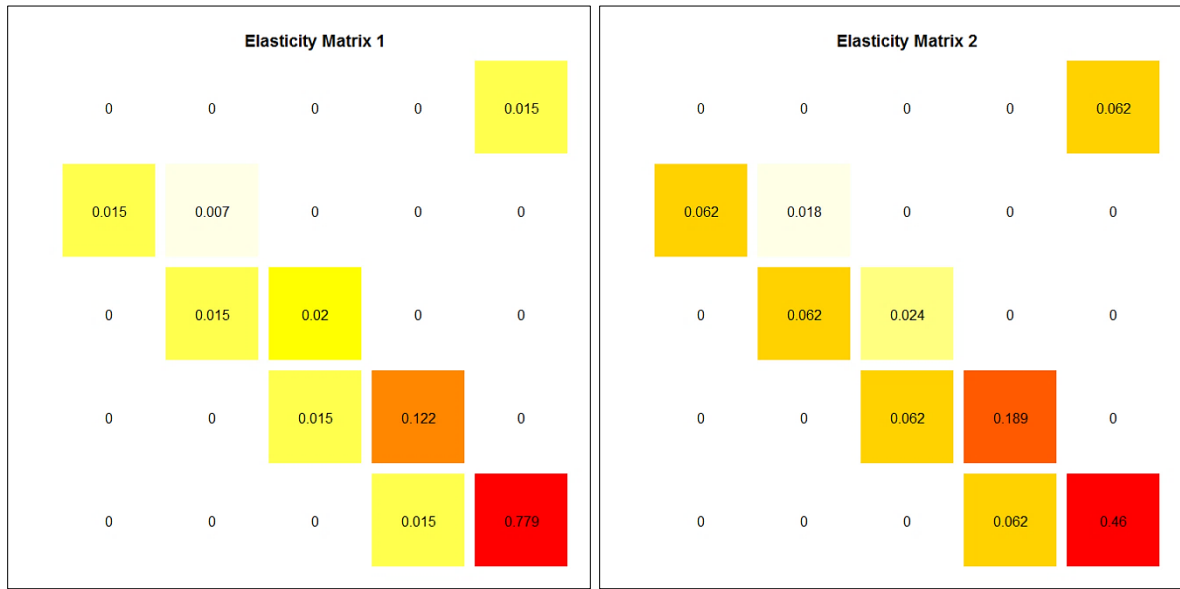
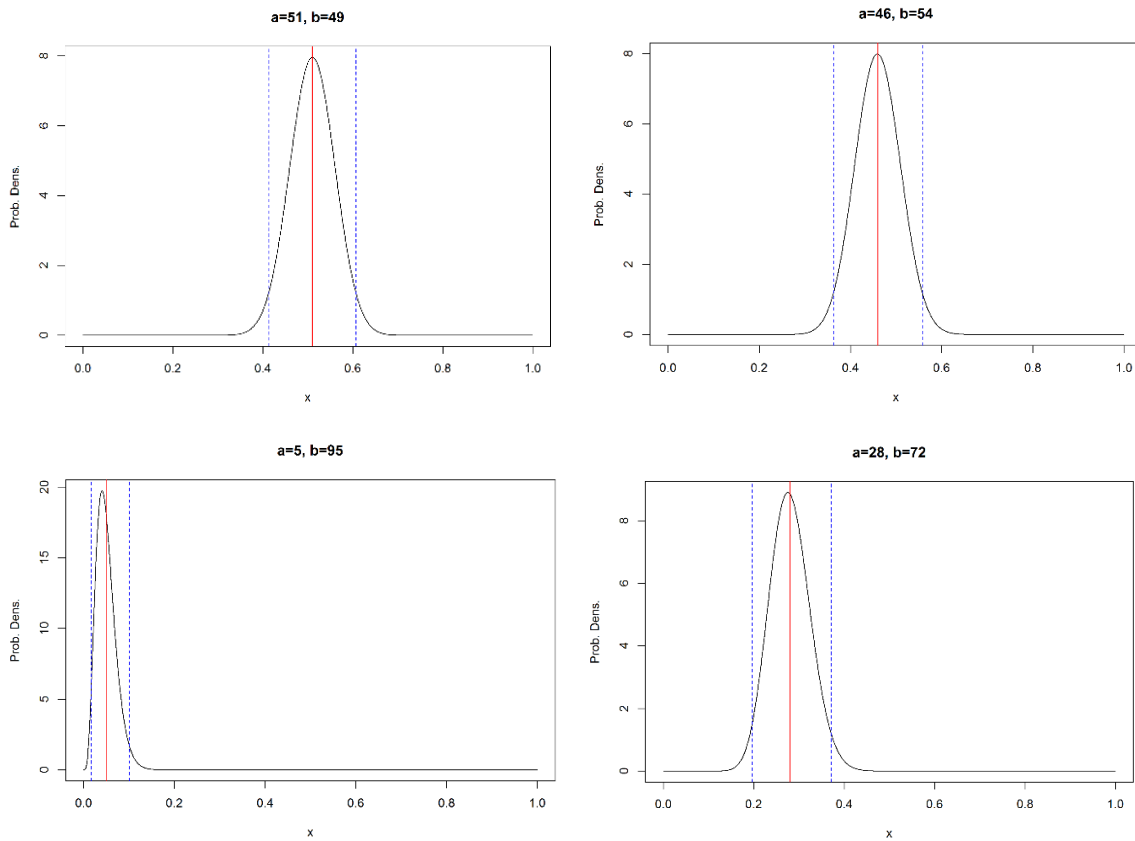


Table 7. Fourteen theoretical additive mortality harvest scenarios of female American alligators in North Carolina, projected over 100 years, using life history parameters included in “Matrix 2.” Each scenario is comprised of varying population harvest rates, percentage of adult and sub-adult females harvested, subsequent population growth rate (λ) and the inclusion of demographic stochasticity.

Harvest Scenario	Total Population Harvest Rate	% Female Harvest	% Sub-adult Harvest	Demographic Stochasticity included in Model?	Median $\lambda > 1$
1	3%	50%	0%	False	False
2	6%	50%	0%	False	False
3	10%	50%	0%	False	False
4	3%	20%	0%	False	False
5	3%	10%	0%	False	False
6	3%	5%	0%	False	True
7	3%	50%	0%	True	False
8	3%	20%	0%	True	False
9	3%	10%	0%	True	False
10	3%	5%	0%	True	True
11	3%	50%	50%	True	False
12	3%	20%	50%	True	False
13	3%	50%	20%	True	False
14	3%	20%	20%	True	False

Figure 1. Using a beta distribution with alpha (a) and beta (b) parameterization, we simulated parametric uncertainty within growth and transition parameters of the American alligator population models with parameter probability densities and 95% confidence intervals.



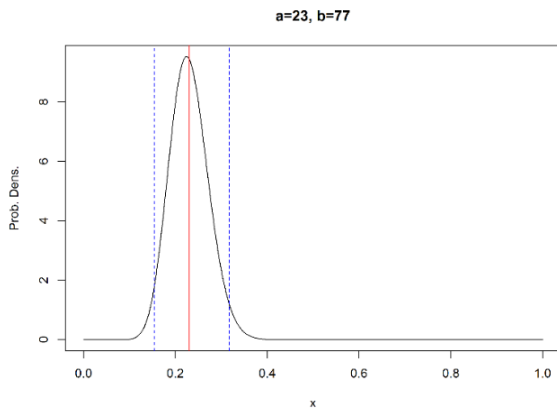
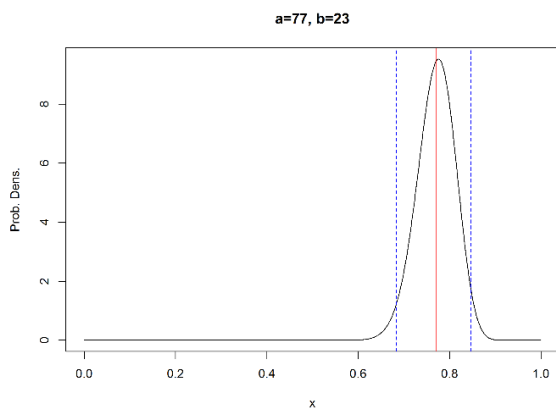
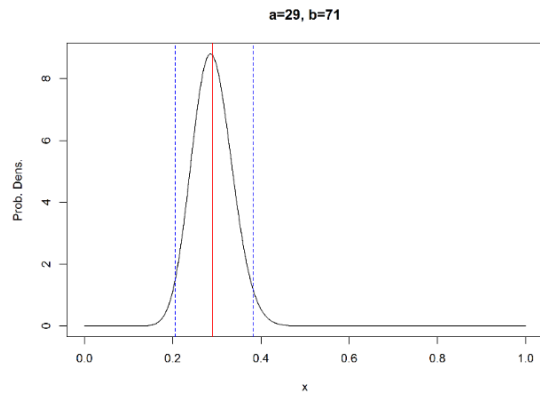
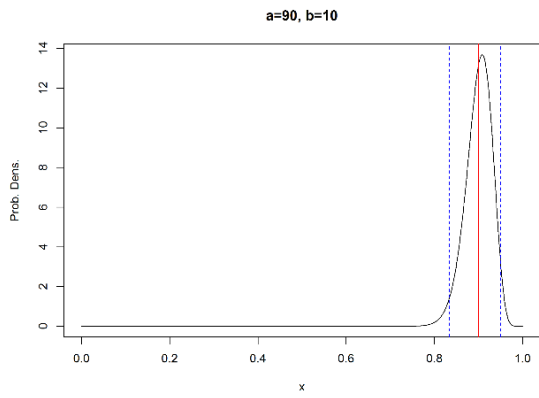


Figure 2. Fifty-year projection and 95% confidence intervals of a theoretical population of American alligators in optimal habitat within eastern North Carolina, similar to that of Lake Ellis Simon. The population projection is derived from “Matrix 1” where mean λ is less than one ($\lambda=0.91$).

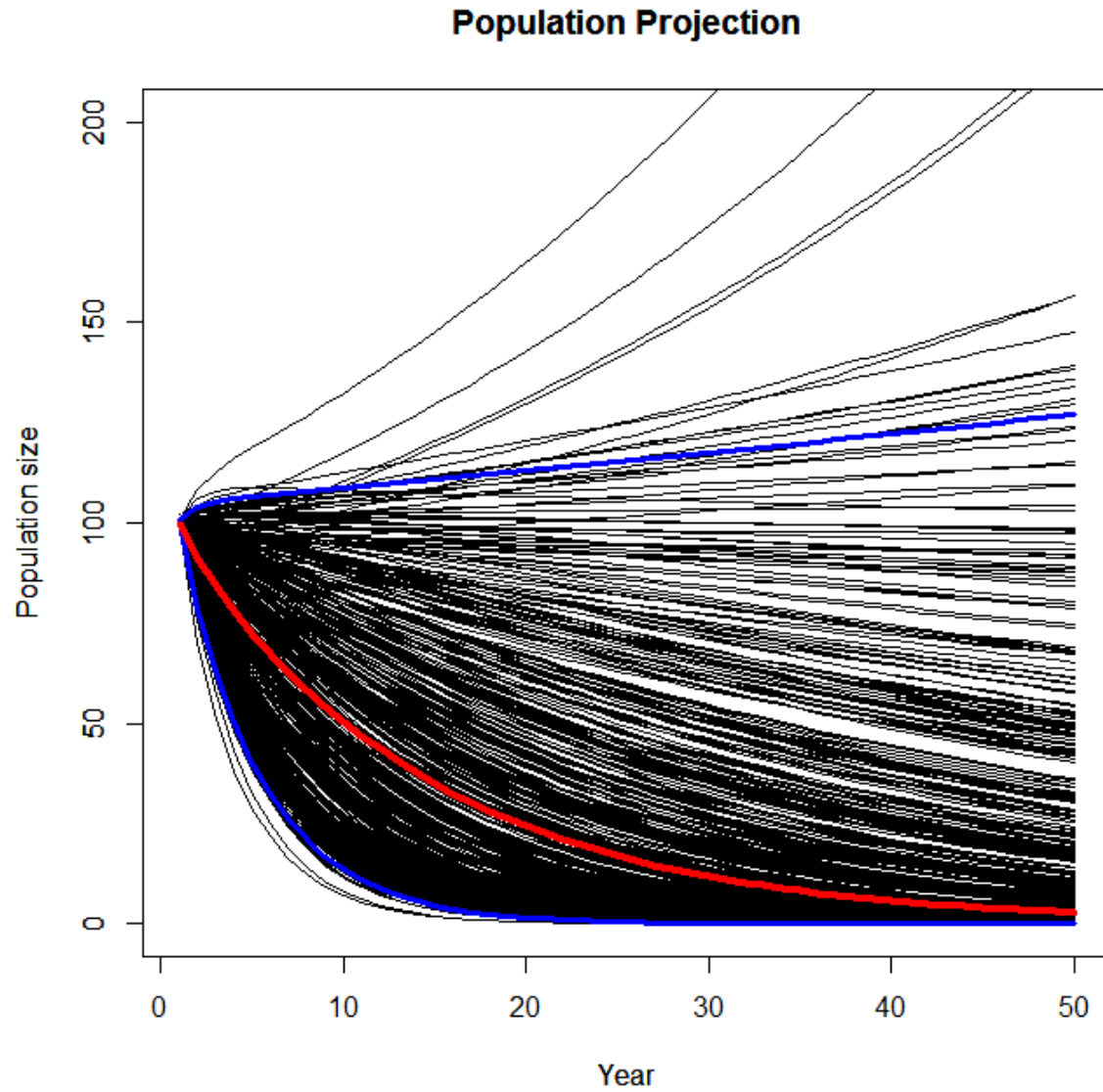


Figure 3. Fifty-year projection and 95% confidence intervals of a theoretical population of American alligators in eastern North Carolina within optimal habitat, similar to that of Lake Ellis Simon. The population projection is derived from “Matrix 2” where mean λ is greater than one ($\lambda=1.021$).

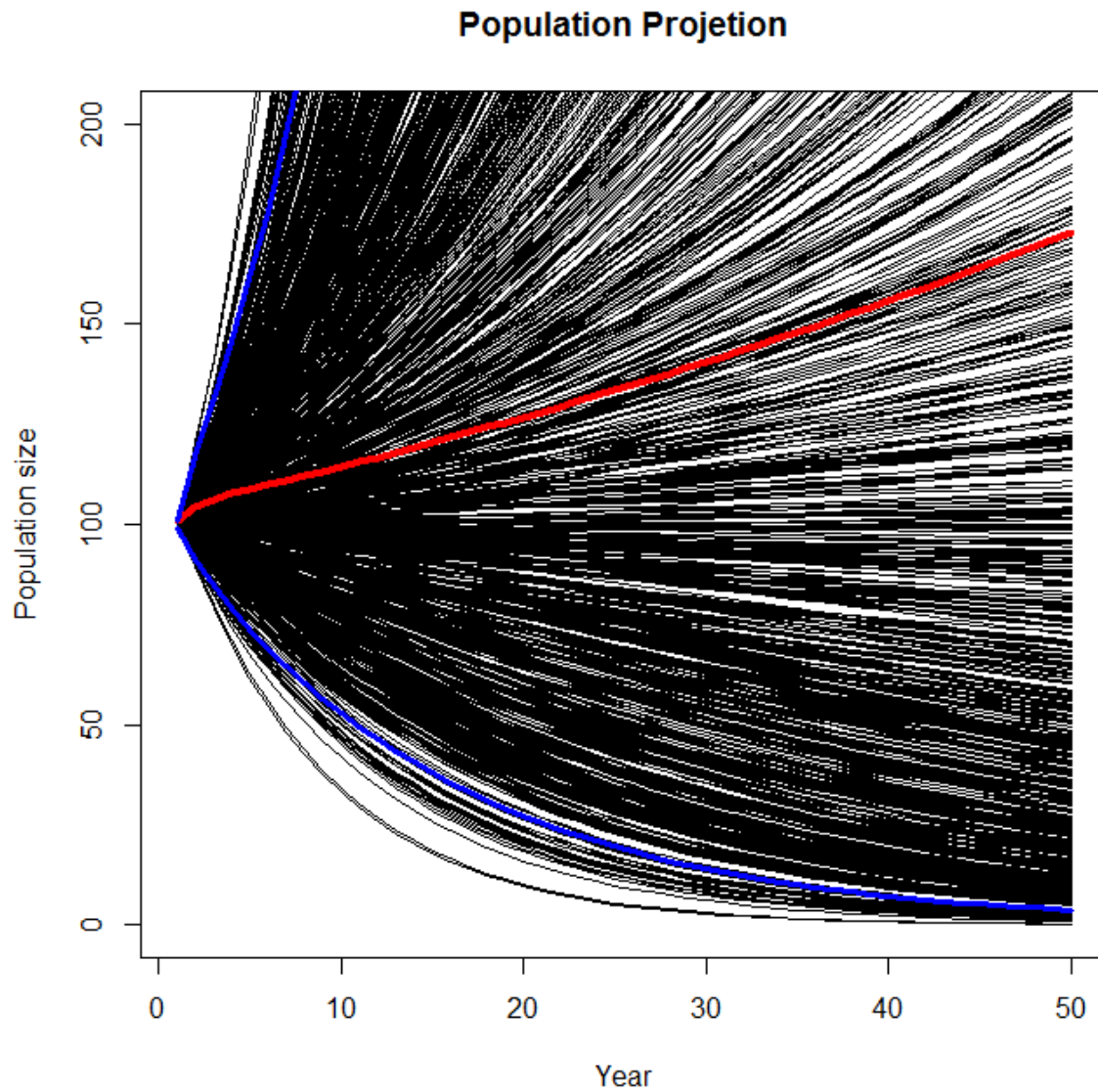


Figure 4. Theoretical additive mortality harvest scenario of female American alligators in North Carolina, projected over 100 years, using life history parameters included in “Matrix 2.” Harvest rates, median population growth (λ), and 95% confidence intervals are included.

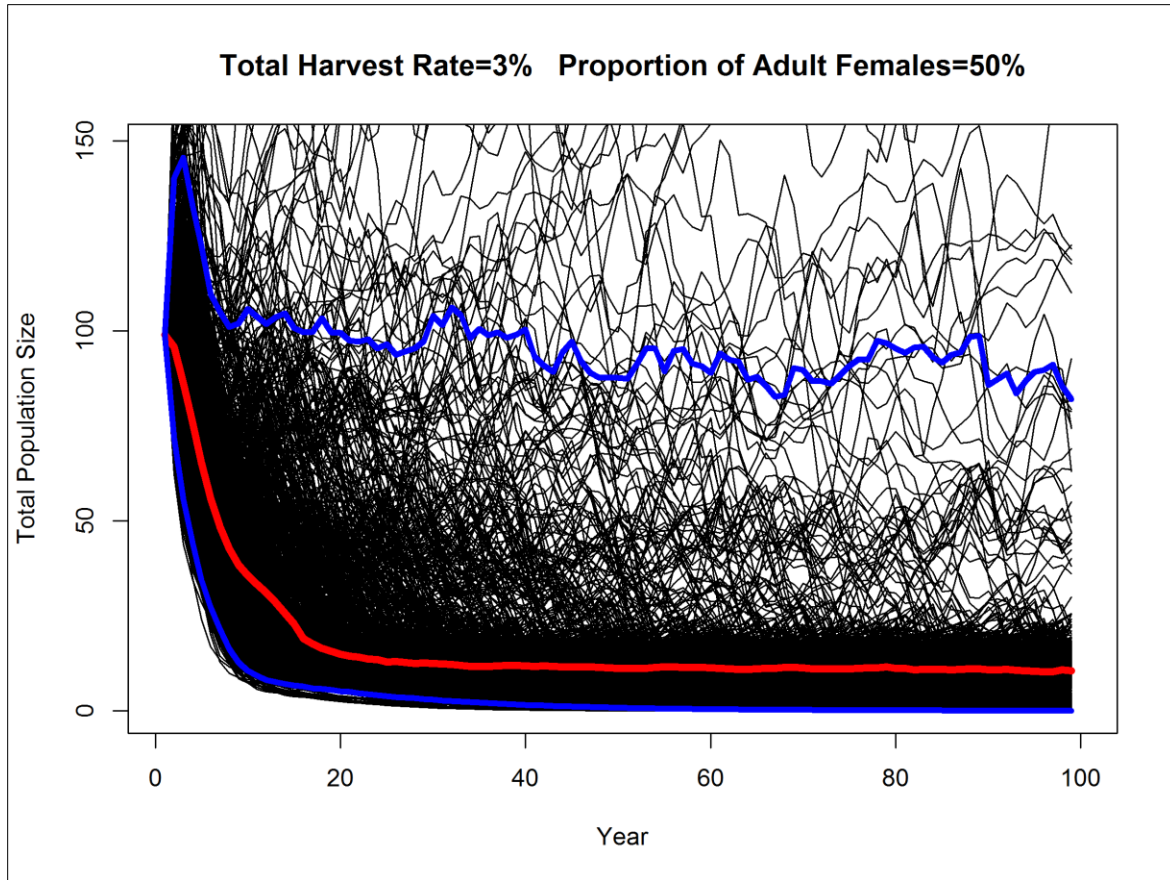


Figure 5. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, median population growth (λ), and 95% confidence intervals are included.

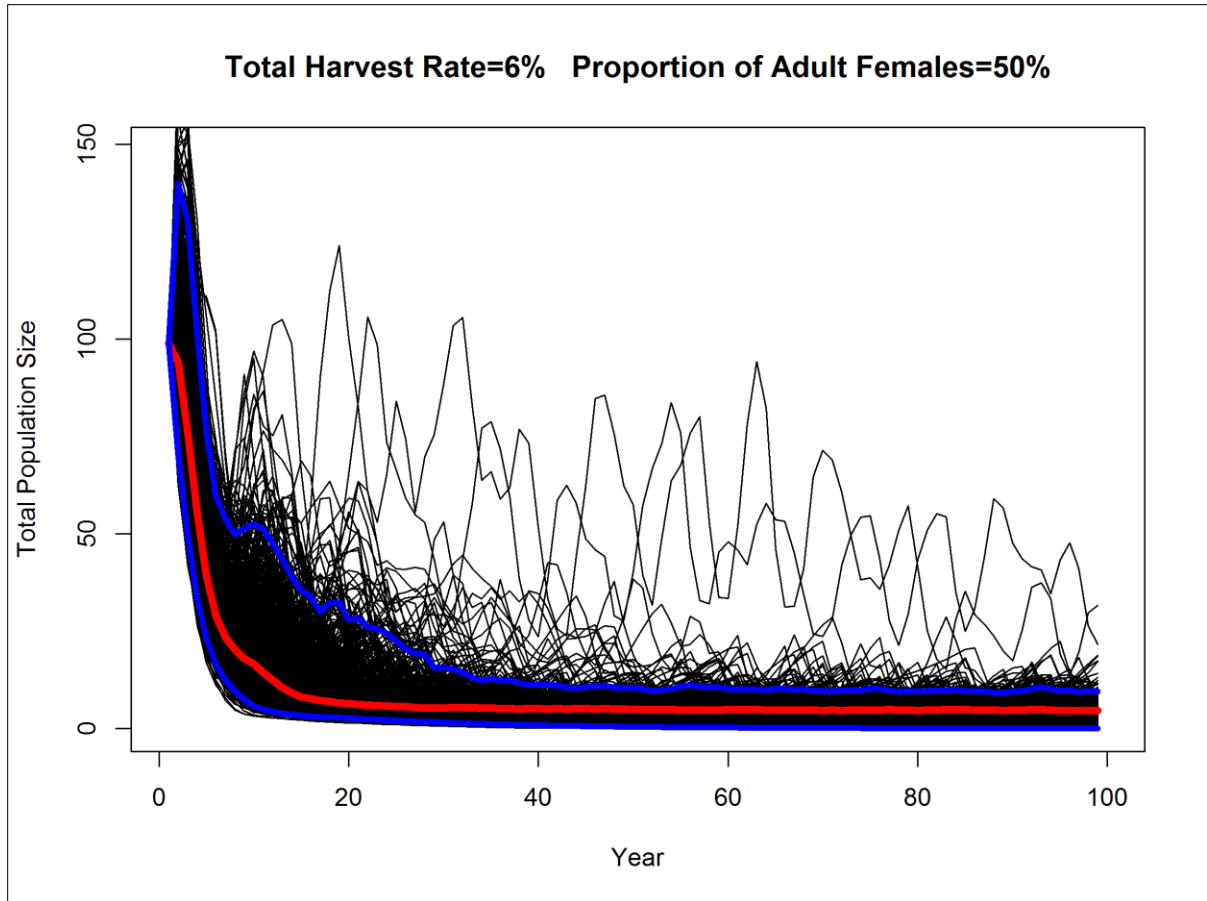


Figure 6. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, median population growth (λ), and 95% confidence intervals are included.

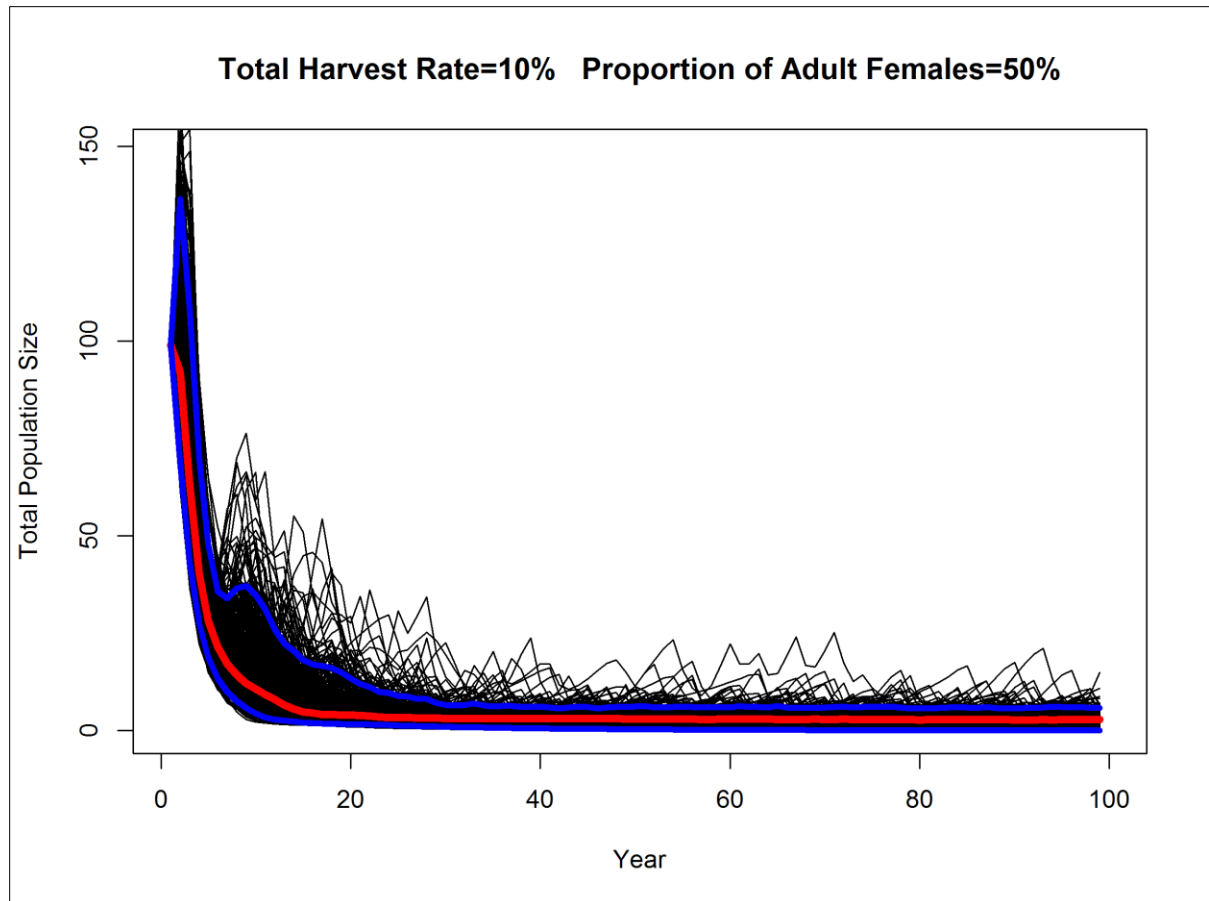


Figure 7. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, median population growth (λ), and 95% confidence intervals are included.

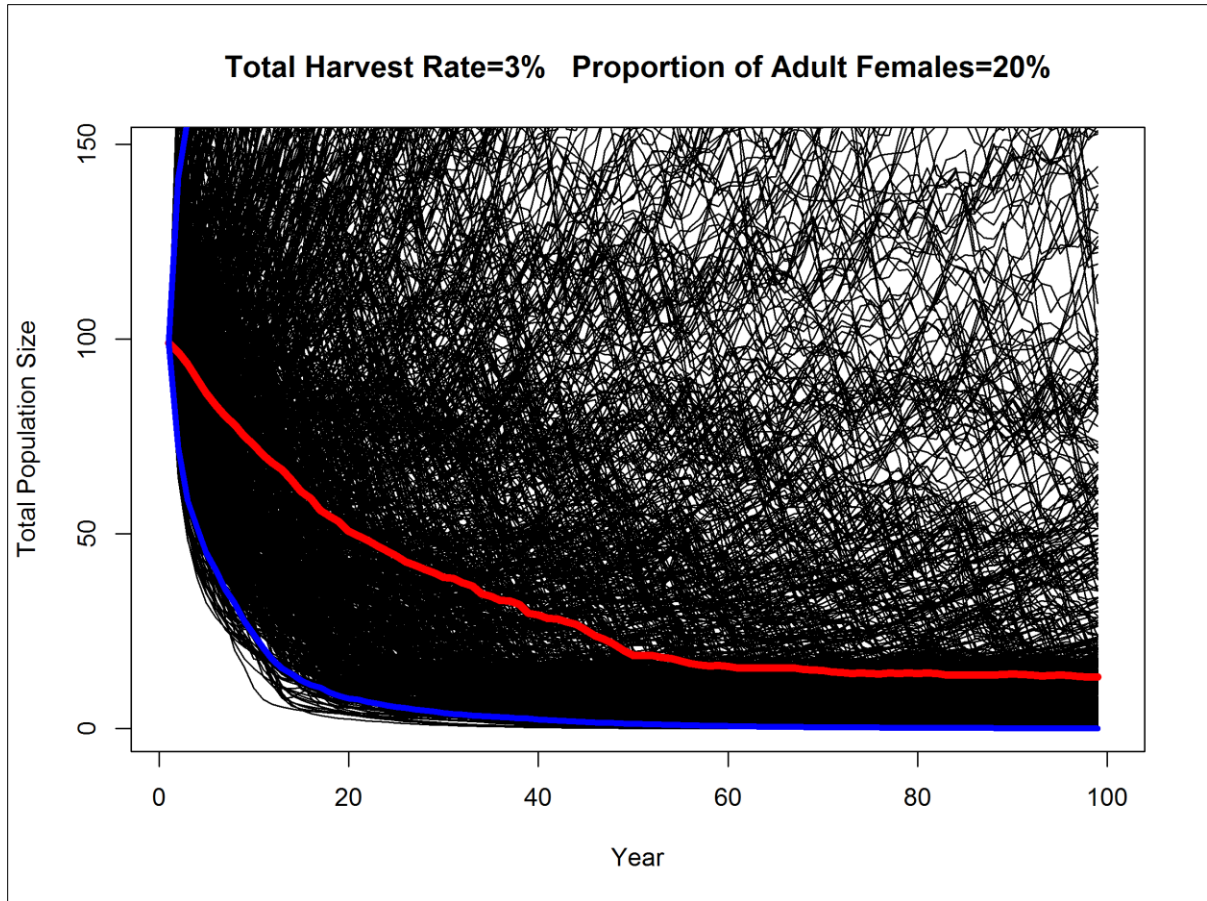


Figure 8. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, median population growth (λ), and 95% confidence intervals are included.

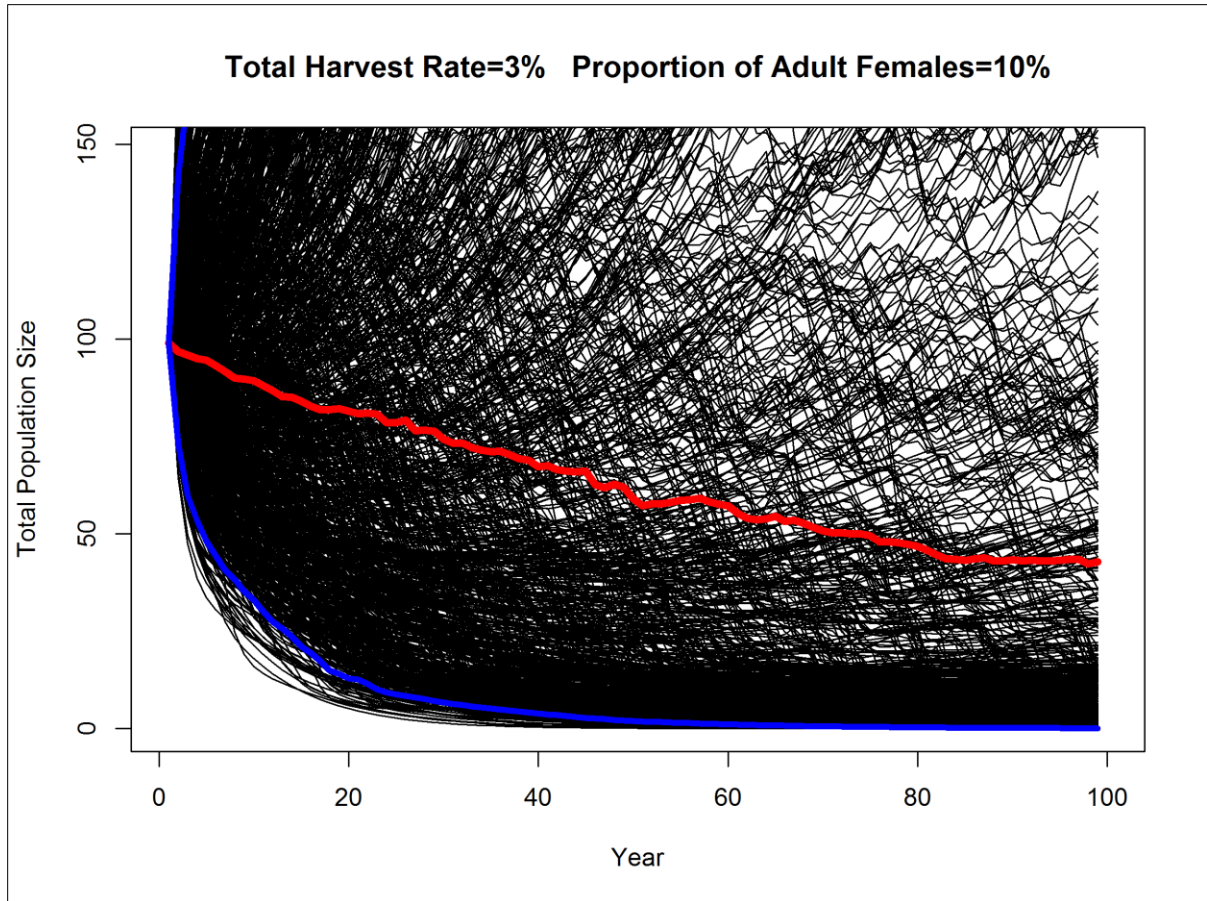


Figure 9. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, median population growth (λ), and 95% confidence intervals are included.

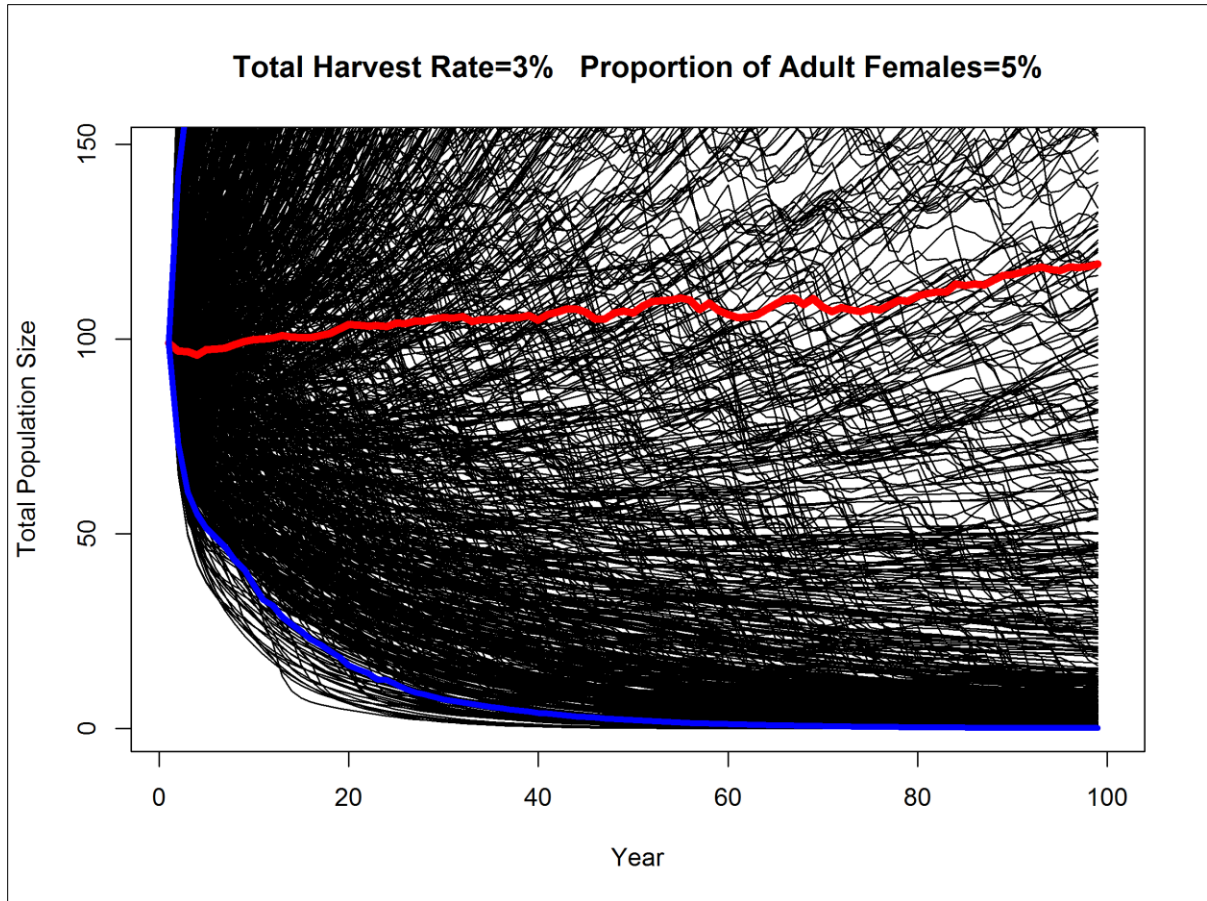


Figure 10. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

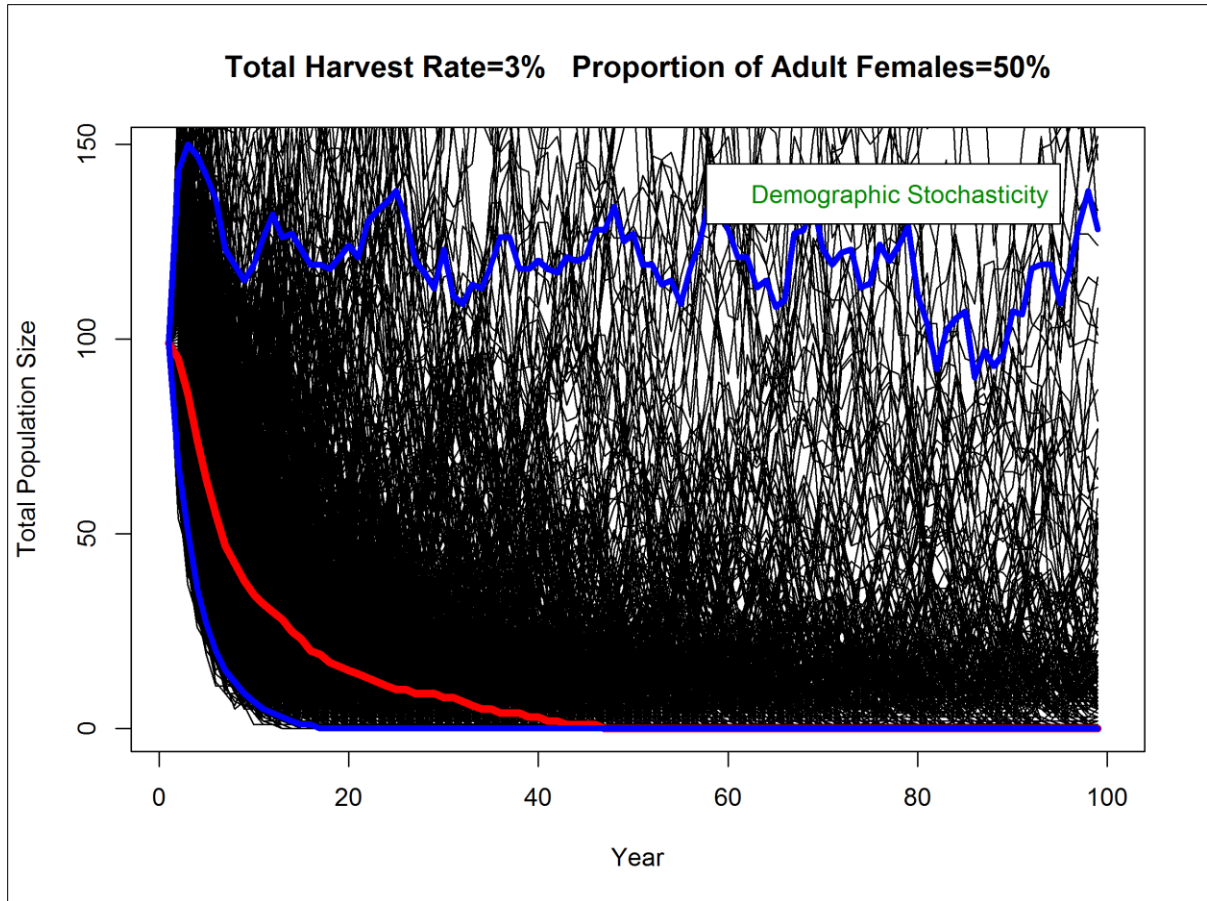


Figure 11. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

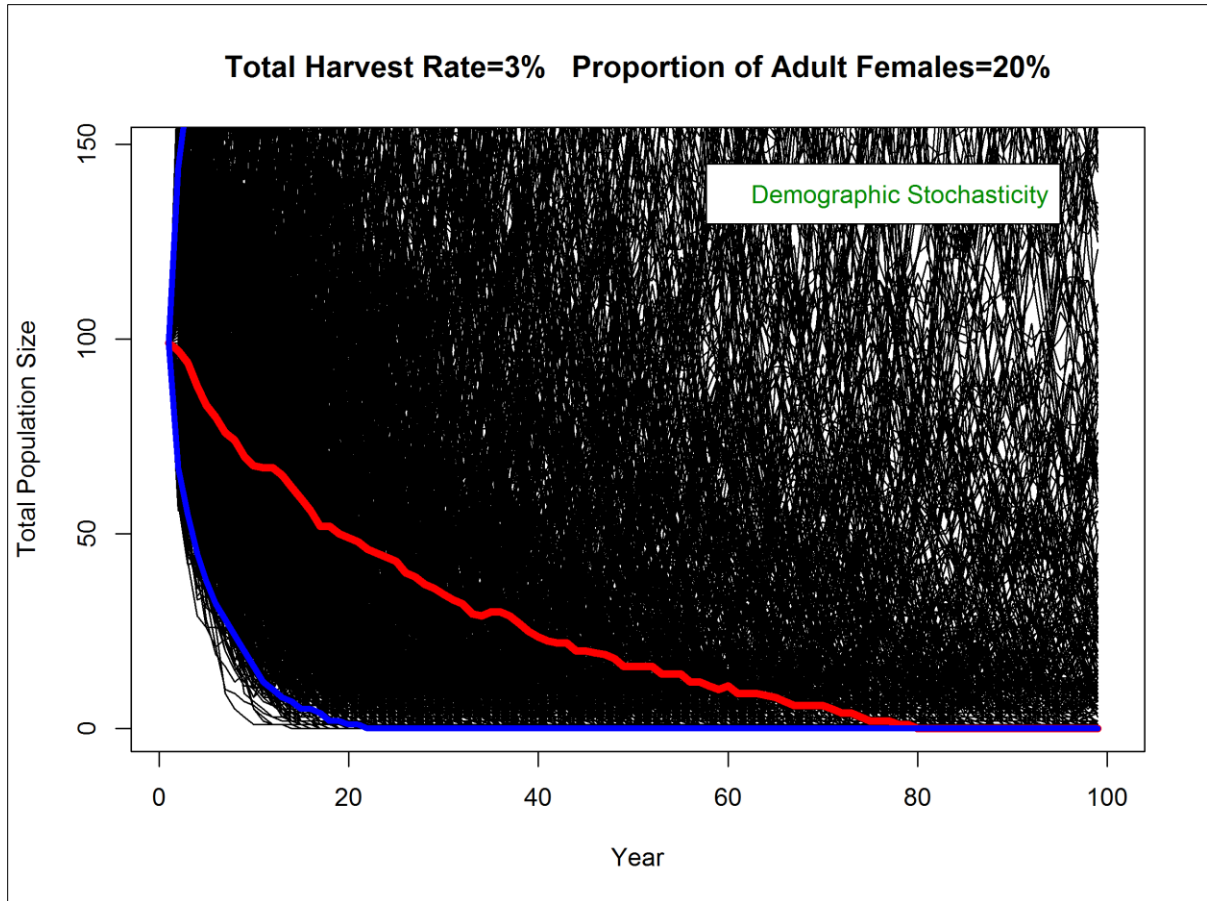


Figure 12. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

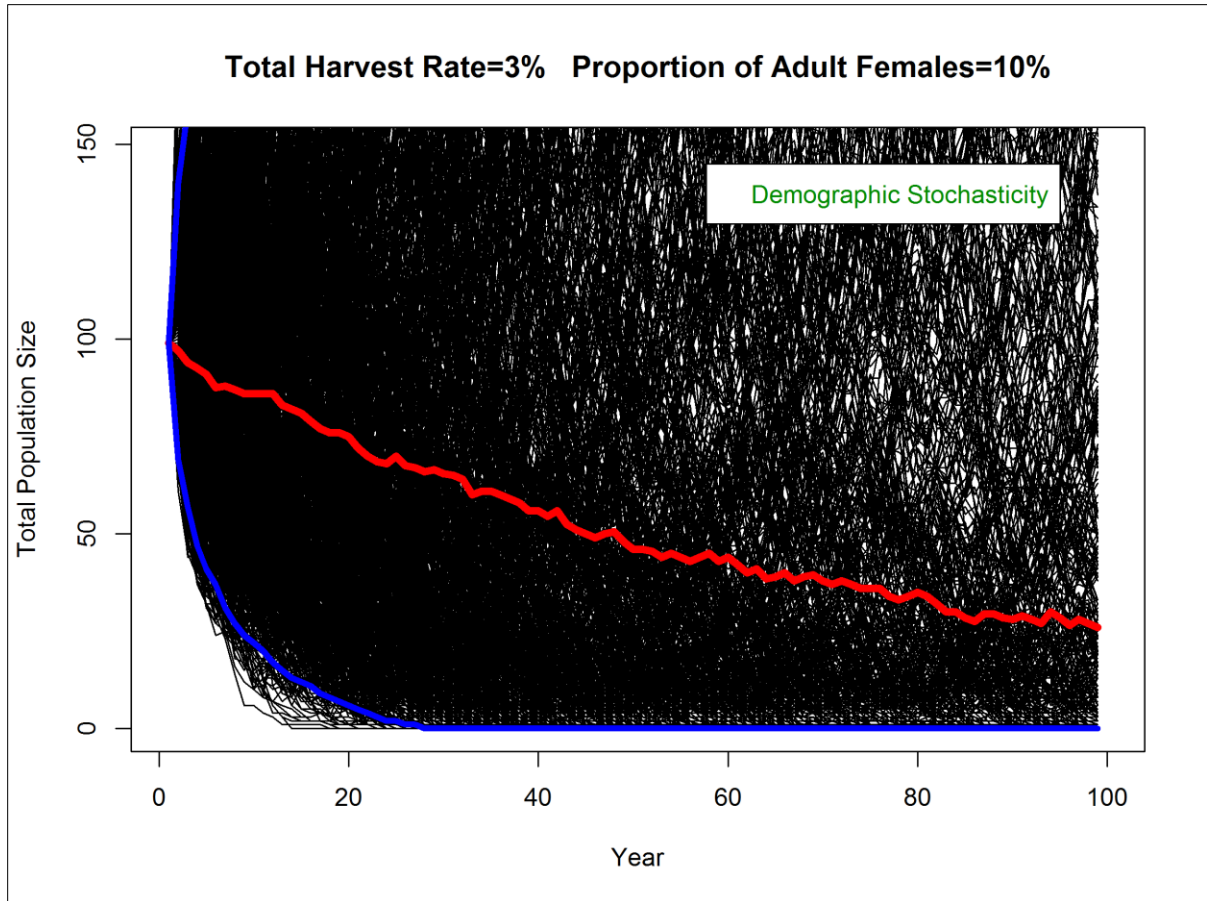


Figure 13. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

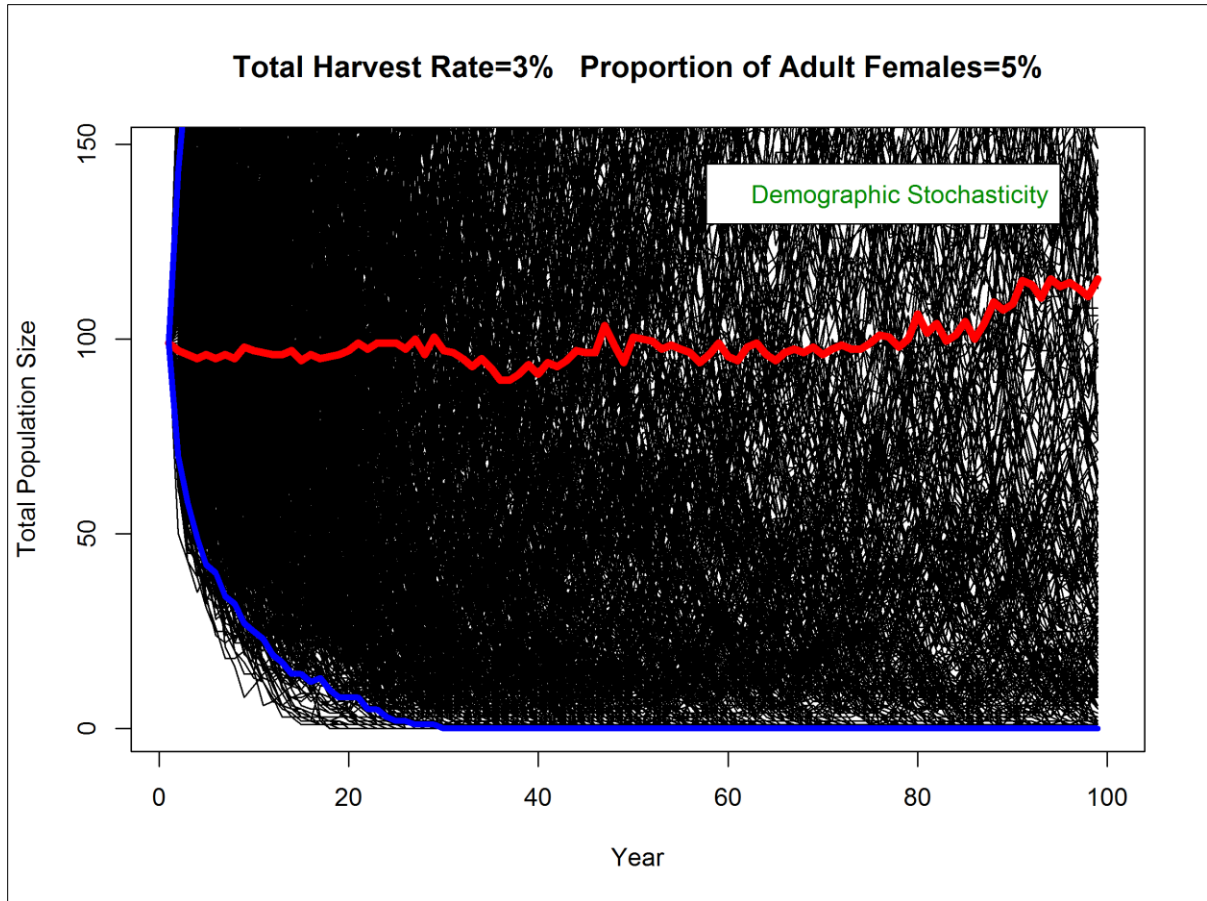


Figure 14. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

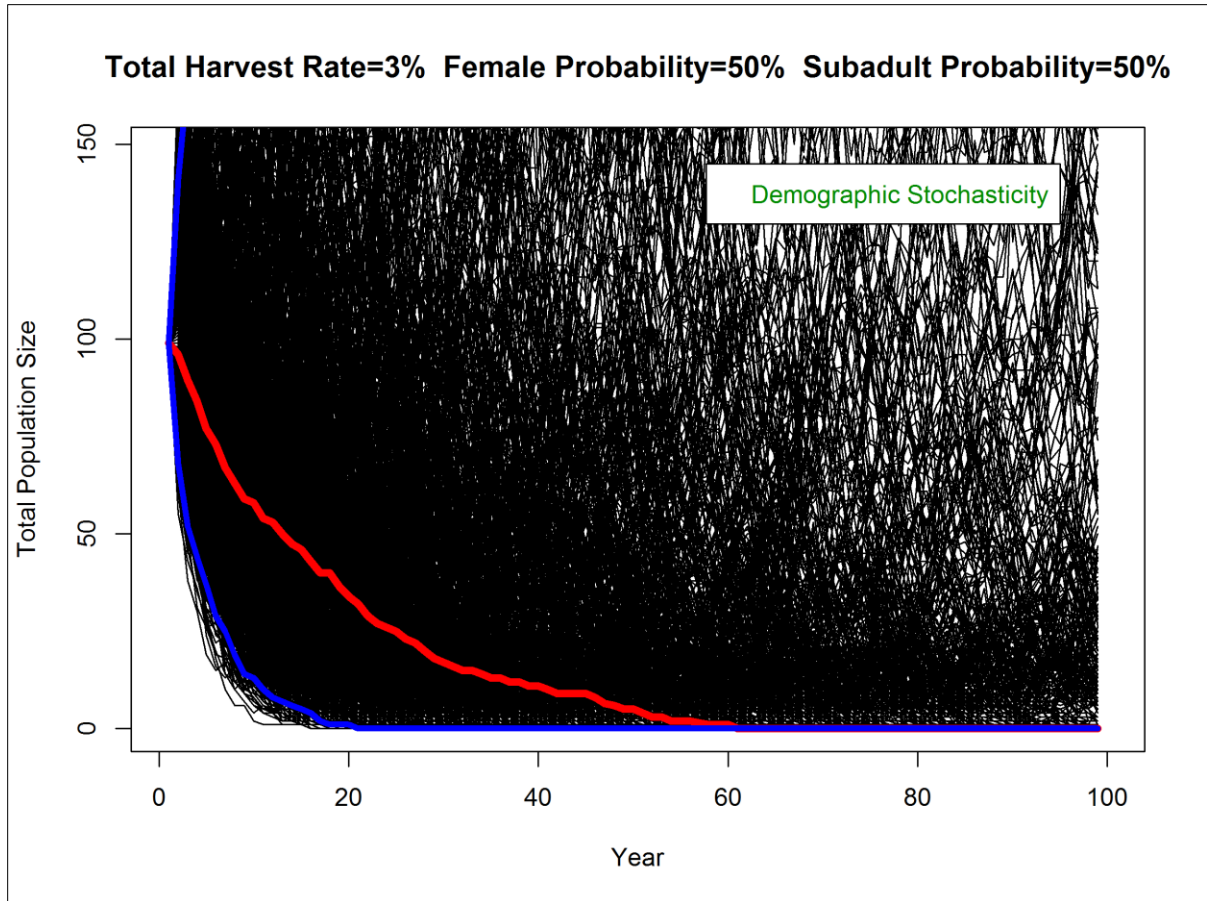


Figure 15. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

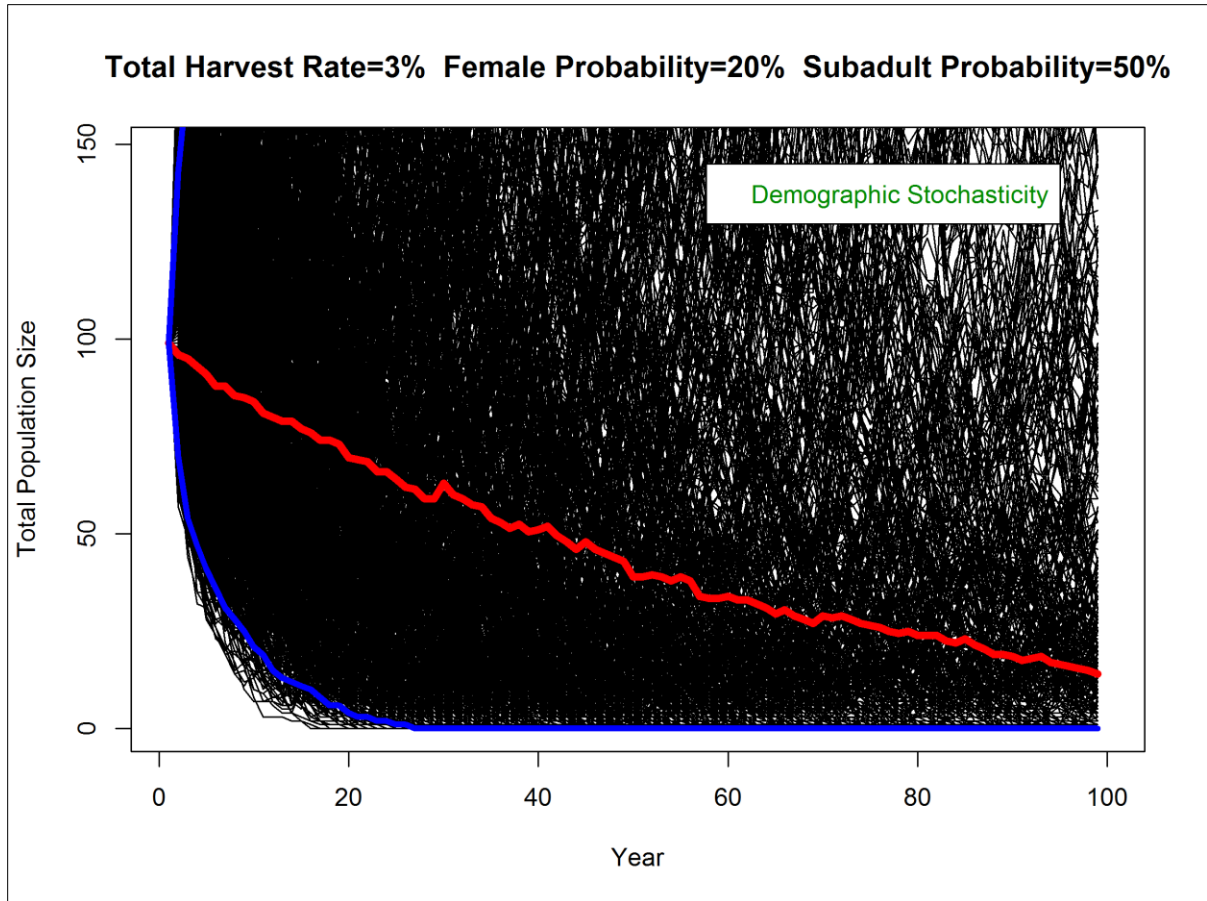


Figure 16. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

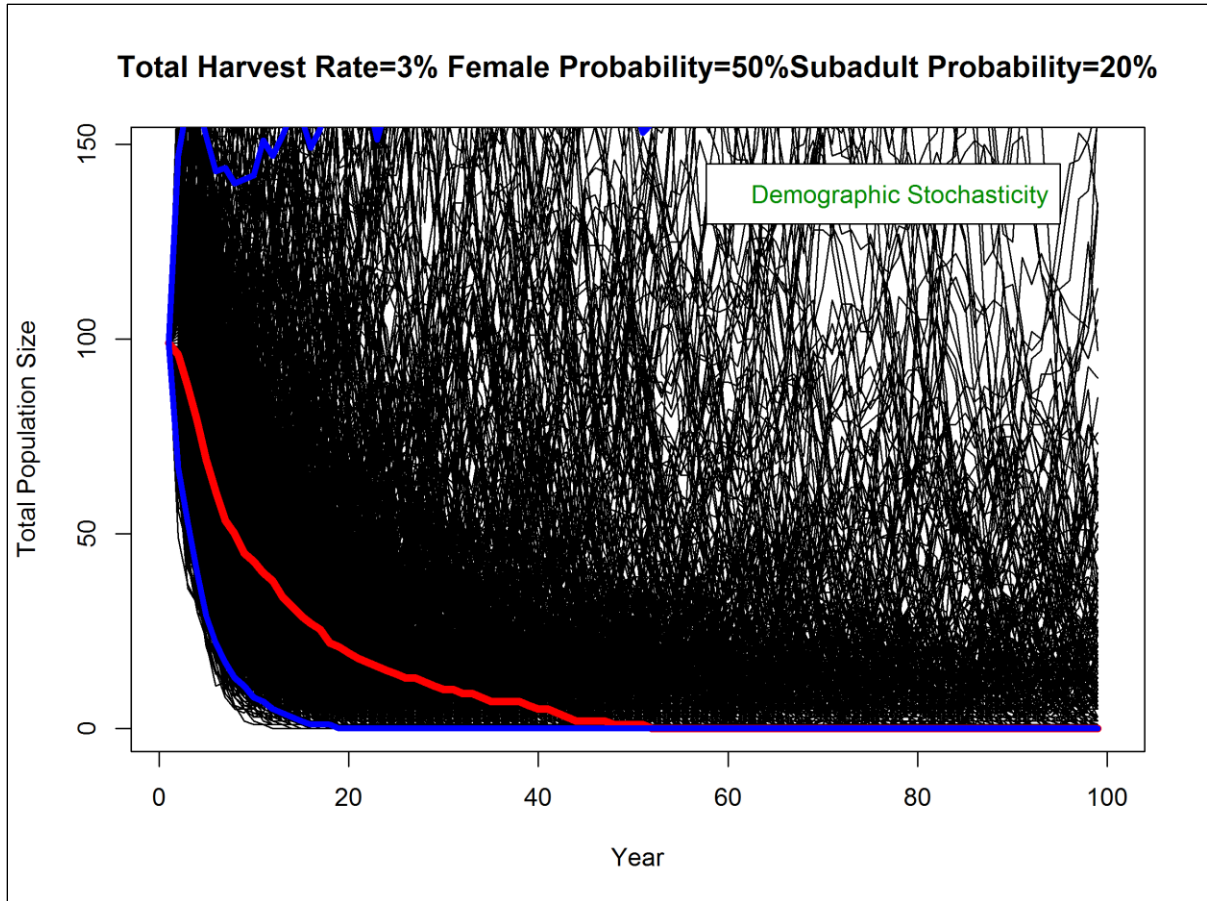


Figure 17. Theoretical additive mortality harvest scenario of female American alligators in North Carolina projected over 100 years using life history parameters included in “Matrix 2.” Harvest rates, demographic stochasticity, median population growth (λ), and 95% confidence intervals are included.

