

POPULATION VIABILITY OF REDDISH EGRETS (*EGRETTA RUFESCENS*) IN
TEXAS: A SYSTEM DYNAMICS APPROACH TO CONSERVATION AND
MANAGEMENT OF NORTH AMERICA'S RAREST HERON

by

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ABSTRACT

Reddish egrets (*Egretta rufescens*) are a threatened waterbird species that inhabit coastal areas of North, Central, and South America, including Cuba and the Bahamas. An estimated one-third to one-half of the global *E. rufescens* population occurs in the United States, with Texas having approximately 75% of the breeding pairs. The plume trade of the late 1800's drastically reduced global population numbers so that by the 20th century the species was decimated and possibly extirpated in many parts of its range. While population numbers may be increasing throughout portions of the range, many factors continue to threaten the persistence of the species in Texas. Population viability analyses (PVAs) are a common method of predicting a species' persistence into some future time. The purpose of developing a population viability analysis for *E. rufescens* is to identify possible factors impeding growth of the Texas population. By assessing the relative threat of each contributing factor and identifying vulnerable life stages, a robust PVA can estimate how different management actions may affect population demographics. I created a dynamic population demographic model of Texas reddish egrets based on difference equations, with stochastic variables drawn from normal distributions. I simulated the Texas *E. rufescens* population to 50 years and evaluated my model by comparing my results with current population trend and parameter estimates reported in the literature. Using a quasi-extinction criterion of ≤ 50 individuals, probability of persistence to 50 years was 98.2% (766 of 780 simulations) for the breeding population. I found four-year-old female survivorship to be the most influential model parameter, which is consistent with similar studies of long-lived avian species that mature late and lay relatively few eggs. Additionally, I found that while the breeding population is projected to remain stable ($\lambda \sim 1.0$) over the next 50 years there is only around a 5% probability of achieving the breeding population goal. These findings suggest that management actions focusing on increasing adult survivorship, such as habitat protection, would be most beneficial to population growth and persistence of reddish egrets in Texas.

I. INTRODUCTION

Extinction is a natural process and the inevitable fate of every species (Soulé 1987), however, current extinction rates are an estimated 1,000 times higher than background rates of extinction. Projections of future extinction rates are estimated to be 10,000 times higher than background extinction rates (Ceballos *et al.* 2015). The aim of biological conservation is to slow the rate of human-induced extinction through sound scientific decision-making. Conservation biologists attempt to quantitatively answer questions about threatened and endangered species to guide management decisions (Drechsler and Burgman 2004; Morris and Doak 2002). How many individuals remain in the population? What are the main factors influencing population growth? What management actions are appropriate to improve depressed vital rates? These questions can often be answered by one of the most important tools in conservation biology, a population viability analysis (Beissinger and McCullough 2002).

Population viability analyses (PVAs) are a set of methods used to project population trends into some future time in an effort to evaluate population persistence and feasible conservation management actions (Drechsler and Burgman 2004). Population viability analyses provide a means to examine how stochasticity influences population viability over time. Stochastic events within the system can create large fluctuations in the population size if the effects are cumulative (Beissinger and McCullough 2002). Often certain vital rates or age classes are disproportionately influenced by this stochasticity and therefore it is imperative to understand which of these parameters are most influential to population growth and decline (Morris *et al.* 1999). This can be accomplished through the construction of a dynamic model that acts as a substitute for the natural system being studied (Ford

1999). Models are often used in biological systems when the real system is too complex to study in nature (Hannon and Ruth 2001). A model that is dynamic helps us understand how the system of interest changes over time given growth, decay, and oscillations. Examining why and how these patterns occur is often referred to as system dynamics (Ford 1999). System dynamics can provide a window into how patterns of growth, decay, and oscillation affect the viability of threatened or endangered species.

It is currently estimated that around 13% of all bird species are threatened or endangered with extinction (Baillie *et al.* 2010). Population viability analyses have been used in a myriad of ways to help understand the threats to avian populations and examine feasible management actions (Akçakaya *et al.* 2004). Viability has been studied in populations of threatened and endangered island-nesting waterbird species such as the Laysan albatross (*Phoebastria immutabilis*) in the Hawaiian Archipelago and the Eurasian Oystercatcher (*Haematopus ostralegus*) in the Wadden Sea and has demonstrated the importance of targeted management actions to waterbird conservation (Finkelstein *et al.* 2009; van de Pol 2010). As avian biodiversity continues to decline it is imperative that high-quality habitat for key bioindicators species such as waterbirds is protected (Kushlan 1993; Sæther *et al.* 1996).

Reddish egrets (*Egretta rufescens*) are a state threatened waterbird species in Texas that inhabit the Gulf Coast of the U.S. and Mexico, as well as the Bahamas, Cuba, the Mexican Pacific Coast, and the Yucatan peninsula (Figure 1). The plume trade of the late 1800's drastically reduced *E. rufescens* population numbers so that by the 20th century, populations in many areas had been decimated and possibly extirpated. Although much of the historical range has been recolonized, *E. rufescens* remains one of North America's

least abundant heron species (Lowther and Paul 2002). The global population of *E. rufescens* is estimated at approximately 5,000 to 7,000 individual birds while the effective population size is estimated at 3,500 to 4,250 pairs (Wilson *et al.* 2012). An estimated one-third to one-half of the global *E. rufescens* population occurs in the United States, with Texas having approximately 75% of the breeding pairs. The Laguna Madre of South Texas accounts for around 45-65% of the entire Texas population (Paul 1991, Wilson *et al.* 2012). Although population numbers may be stable in some portions of the range, factors such as habitat loss and degradation continue to threaten the persistence of the species (BirdLife International 2012; Wilson *et al.* 2012). Due to continued threats to the population the Reddish Egret Working Group along with the Gulf Coast Joint Venture Monitoring, Evaluation, and Research Team Waterbird Working Group have set a breeding population goal for Texas at around 2,000 breeding pairs (Vermillion and Wilson 2009; Wilson *et al.* 2012).

Research Objectives

My research objectives were:

- 1) To build a stochastic, age- and sex- specific population model for *E. rufescens* on the Texas coast;
- 2) Use the model to identify the vital rate(s) that most influence population growth and the probability of population persistence for *E. rufescens* on the Texas coast; and
- 3) Evaluate management action impact on the Texas population goal of 2,000 breeding pairs set out by the Reddish Egret Working Group and the Gulf

Coast Joint Venture Monitoring, Evaluation, and Research Team (MERT) Waterbird Working Group (Wilson *et al.* 2012; Vermillion and Wilson 2009).

II. METHODS

Study Area

The Texas Gulf Coast, at 12.8 million acres, is one of the most biodiverse regions in the state. The coastline is separated into three distinct regions: the upper, mid, and lower coasts. The upper coast stretches from the Texas-Louisiana border southwest to Galveston Bay and is typified by marshes, coastal prairies, hardwood bottomlands, and interfluvial-forested wetlands. The mid-coast region extends from Galveston Bay south to Corpus Christi and is distinguished by the presence of barrier islands, bays, lagoons, and estuaries. The lower coast extends from Corpus Christi down to the Laguna Madre region of Texas and Mexico and has many of the same features as the mid-coast, except for a lack of freshwater inflow. Hypersaline wind tidal and salt flats characterize this region of the Texas coast (Moulton 1997). The estuaries and shallow tidal flats present along the entire Texas coast serve as essential foraging areas for *E. rufescens* (Lowther and Paul 2002).

The Gulf of Mexico predominantly determines the seasonal temperatures and precipitation along the extensive coast of Texas. Temperature tends to increase with decreasing latitudes, with average annual temperatures ranging from 15.6°C (60°F) along the northern coast to 20°C (68°F) along the southern coast. Precipitation typically increases with increasing latitude, with average annual precipitation ranging from 63.5 cm (25 inches) along the southern coast to 152.4 cm (60 inches) along the upper/mid coast. Due

to its geographic location at the convergence of seasonal air masses, however, hurricanes and tropical storms are a common disturbance in this area (Vaughan *et al.* 2012). Despite the risks adverse weather may impose, the coastal human population of Texas continues to grow. The 2010 United States census estimated the coastal population of Texas at 6,087,133 people, accounting for nearly 25% of the total state population. Population projections for the Texas Gulf Coast in the year 2050 range from 7,440,144 to 14,416,642 people (Texas Population Estimates and Projections Program 2014). With increasing populations along the Western Gulf Coast Plains there has been a subsequent increase in the amount of developed land. This region experienced a 1.2% increase in developed land from 1973 to 2000. Additionally, nearly 70% of industry and commerce takes place within 160 km of the coastline, including the production of over half of the petroleum in the United States (Taylor *et al.* 2015). Continued development and construction of structures such as seawalls, jetties, and groins not only destroy and degrade current reddish egret habitat, but also limit future habitat given current sea level rise projections (Gittman *et al.* 2015).

Reddish Egret Population Demographics

The model parameter estimates were derived from published and unpublished literature on *E. rufescens* in Texas including radio telemetry mark-recapture studies (see Appendix Section). The majority of parameter estimates come from the Laguna Madre region as around half of the Texas *E. rufescens* population reside in this area (Paul 1991). I used breeding pair survey data collected from 1973-2015 by the Texas Colonial Waterbird Society to calculate the number of birds starting out in each age class.

Nesting and Breeding

On average, *E. rufescens* reach sexual maturity at about 4 years of age (Paul 1991) and lay 3.29 eggs ($SD \pm 0.696$, $n=194$; Holderby *et al.* 2012). In Texas, the breeding season begins as early as March and can last as late as September (Koczur *et al.* 2017) with incubation lasting about 27 days (Holderby *et al.* 2012). Nesting success in the Laguna Madre region of the Texas Coast has been estimated at 0.851 ($SD \pm 0.58$, $n= 117$; Holderby *et al.* 2012). I assumed a sex ratio of 1:1 for males and females as sex ratio at hatch has been estimated at ~1:1 (Hill and Green 2016).

Survival

Nest surveys conducted in the Laguna Madre region estimate chick survival for both males and females at 0.25 ($SD \pm 1.75$, $n = 628$; unpublished data). Studies using satellite transmitters have estimated fledging survival at 0.76 ($SD \pm 0.083$; $n=25$), as well as first-year female and male breeding and non-breeding season survival at 0.53 ($SD \pm 0.113$; $n = 25$; Geary *et al.* 2015). Similarly, Koczur *et al.* (2017) estimated breeding season survival for second year and older females and males at 0.945 ($SD \pm 0.66$, $n = 591$) while non-breeding season survival for second year and older females and males was 0.7697 ($SD \pm 1.39$, $n = 591$). I used the same value, 0.7697 ($SD \pm 1.39$, $n = 591$), for migration survival as adult survivorship of migratory birds during the non-breeding season has not been found to be different than survivorship of non-migratory birds during the same time period (Koczur *et al.* 2017).

Density Dependence

Density dependence was incorporated into the model through a user defined graphical function $y = 0.8809936 + (1 - 0.8809936)/(1 + (x/2726.416)^{102.737})$. This function allowed me to limit the breeding population as it neared 3,000 breeding individuals and was based on a density dependence factor of maximum number of nests. I choose to use a value of 3,000 breeding individuals as this reflects the historical Texas population of no more than 1,500 breeding individuals (Paul 1991).

Dispersal and Migration

Geary *et al.* (2015) estimated female fledging dispersal rate at 0.04 (SD \pm 0.04; n = 25) and male fledgling dispersal rate at 0.08 (SD \pm 0.04; n = 25). The fall migration rate of adult female birds of was estimated at 0.125 (SD \pm 0.063, n = 16) and 0.2857 (SD \pm 0.071, n = 14). For the purposes of this model I assumed that the birds that migrate and survive the non-breeding season will return the following breeding season, so the spring migration rate was set to 1.0 (Koczur 2017).

Model Overview

My main objective was to create a model that would, as accurately as possible given the available data, simulate the population dynamics for the Texas population of *E. rufescens*. The Stella Professional v1.4.3 (ISEE Systems, Incorporated, Lebanon, NH) software package was chosen for this project as it allows for the creation of a visual model representing the dynamics of the real system. The model represents survival and reproduction, as well as dispersal and migration of *E. rufescens* in Texas (Figure 3). The

model was based on difference equations with each time step representing either the breeding (season=1) or non-breeding (season=2) seasons. Chicks produced during the breeding season were separated into male and female population segments. One model simulation represents 100 seasons total, or 50 years.

For the purposes of this model, I made the following assumptions:

- 1) Birds begin breeding at the age of 4.
 - a. While birds may begin breeding as early as the age of 3, birds typically don't begin breeding until the age of 4 (Lowther and Paul 2002).
- 2) Survival and mortality vital rate estimates are representative of the entire Texas population of *E. rufescens*.
 - a. Studies from the Laguna Madre region of Texas have shown no differences in vital rates within the largest portion of the Texas population (Bates *et al.* 2009; Koczur *et al.* 2017).
- 3) The population is open, so birds can both enter and leave the system (i.e. Texas; Geary *et al.* 2015; Koczur *et al.* 2017)
- 4) There exist no differences in the parameter estimates for the two color morphs.
 - a. Studies have shown no differences between the color morphs for the parameters used (Geary *et al.* 2015; Holderby *et al.* 2012; Koczur *et al.* 2017).

Variable Distributions to Invoke Stochasticity

Stochastic models should have variables randomly drawn from their probability distribution functions, however, probability distribution functions are often not available from empirical data for modeling purposes and are assumed to be normally distributed (Guthery *et al.* 2000). Because my model had few sources for the demographic parameters I was unable to estimate probability distributions due to the small number of samples. Therefore, I assumed all demographic parameters in the model to be normally distributed. Parameters such as survival and mortality were bounded between 0 and 1. STELLA® software draws a random number for each stochastic simulation iteration from a normal distribution based on the parameter mean (x) and standard deviation (SD) in the following formula:

NORMAL(x, SD), (STELLA® 9.0.2).

Therefore, survival would be calculated as

Survival = (NORMAL(x, SD))

Baseline Simulations

When simulating stochastic conditions, one must first determine how many simulations to run in order to detect a desired amount of change (Grant *et al.* 1998). My goal for this model was to be able to detect 10% change in the breeding population. This translates to an absolute change of 95 breeding pairs within the Texas population.

First, I ran 50 preliminary stochastic simulations and calculated the variance for the ending breeding populations value after 50 simulations of 100 seasons. The breeding

population standard deviation was estimated at 1,337.19 and was used to solve the equation below from Grant *et al.* (1998).

$$n \geq 2 \left(\frac{\sigma}{\delta}\right)^2 [t_{\alpha,\gamma} + t_{2(1-P),\gamma}]^2$$

where n represents the number of samples ($n=50$), σ represents the standard deviation ($\sigma = 1,337.19$), δ represents the desired detection difference ($\delta = 190$), γ represents the degrees of freedom ($\gamma = \infty$), α represents the significance level ($\alpha = 0.05$), P represents the probability that a difference will be found if it exists ($P = 0.80$), and $t_{\alpha,\gamma}$ and $t_{2(1-P),\gamma}$ represent values from a two-tailed t-table ($t_{\alpha,\gamma} = 1.96$, $t_{2(1-P),\gamma} = 0.842$). I determined that in order to detect a $\geq 10\%$ change in the breeding population if it exists I would need to run a total of 780 stochastic simulations.

Quantitative Model Description

The Texas *E. rufescens* demographic population model consists of 19 state variables which include the number of chicks (*chicks*), female fledglings (*FF*), male fledglings (*MF*), first-year females (*FY1*), first-year males (*MY1*), first-year females that migrate (*FY1 Mig*), first-year males that migrate (*MY1 Mig*), second-year females (*FY2*), second-year males (*MY2*), second-year females that migrate (*FY2 Mig*), second-year males that migrate (*MY2 Mig*), third-year females (*FY3*), third-year males (*MY3*), third-year females that migrate (*FY3 Mig*), third-year males that migrate (*MY3 Mig*), fourth-year and older females (*FY4+*), fourth-year and older males (*MY4+*), fourth-year and older females that migrate (*FY4+ Mig*), and fourth-year and older males that migrate (*MY4+ Mig*). Each state variable connects with inflows, outflows, and converters in the model to represent

system dynamics. Initial stock values for first-year and older birds were calculated using vital rates reported in the literature and an initial breeding population of 950 breeding pairs.

Prior to the first model inflow breeding density dependence, breeding population demographics, and vital rates are defined within the system. Throughout the model *Season* is defined as the annual life-cycle of reddish egrets broken into two time steps, where 1=breeding season (March-September) and 2=non-breeding season (October-February). *Nest Success* is defined as the number of nests that successfully fledged young out of the total number of nests laid at the beginning of each breeding season time step and was estimated at 0.851 (SD \pm 0.58, n= 117; Holderby *et al.* 2012). I define *Prop female nest* as the proportion of 4-year-old and older females that are breeding during the breeding season time step and used an estimate of 0.95 to account for environmental and behavioral factors that may impact the proportion of females within a colony that nest (Minias and Kaczmarek 2013). Density dependent nest success was incorporated into the model using *Max_Number_Nests*, which is defined as the sum of the average number of nests. While the exact causes behind density dependence within the population are unknown, it has been shown that density dependence does impact the Texas population of *E. rufescens* (Bates 2011). I used the estimate for breeding pairs in Texas, 950, as a proxy for the maximum number of nests. *Breeding_DD* is the density dependent factor based on breeding population size and was used to limit population growth as the total population neared 3,000 individuals. This limit was based on the maximum number of breeding pairs that are estimated to have historically populated Texas (Paul 1991). *Nesting Females* represents the number of 4-year-old and older females nesting during the breeding season time step. If breeding season (season = 1), then the value of four-year-old females (*FY4+*) multiplied

by the proportion of females nesting (*Prop_female_nest*) is given. If non-breeding season, a value of 0 is given as there are no nesting females present during the non-breeding season.

This is defined in the model as:

$$IF \text{ Season}=1 \text{ THEN } (FY4+ * Prop_female_nest) \text{ ELSE } 0$$

where *FY4+* is a stock holding four-year-old and older females and will be formally defined later in the quantitative model description.

Actual_Nesting_Females represents the actual number of females nesting during breeding season. If, during the breeding season (season = 1), the number of potentially nesting females (*Potential_Nesting_Females*) is greater than the maximum number of nests (*Max_Number_Nests*) then the equation returns the value of the maximum number of nests. If, however, *Potential_Nesting_Females* is not greater than *Max_Number_Nests* then the equation returns the value of ($0.95 * Potential_Nesting_Females$). This equation is defined in the model as:

$$IF (Prop_Females_Nesting > Max_Number_Nests) \text{ THEN } Max_Number_Nests \\ ELSE Prop_Females_Nesting$$

The initial model inflow *Chicks_Being_Produced* transfers the number of chicks produced during the breeding season to the stock *Chicks*, which is defined as the number of chicks produced during the breeding season time step. If breeding season (season =1), then the equation returns the product of *Actual_Nesting_Females*, *Clutch_Size*, *Nest_Success*, and *Breeding_DD*. *Nest_Success* represents the number of nests that successfully fledged young out of the total number of nests laid at the beginning of each time step and is randomly drawn from a normal distribution with a mean of 0.851 (SD \pm 0.58, n = 117) while *Clutch_Size* represents the number of eggs laid per breeding female

per season and is drawn randomly from a normal distribution with a mean of 3.29 (SD \pm 0.696). This inflow is defined in the model as:

*IF Season=1 THEN (Actual_Nesting_Females * Clutch_Size * Nest_Success * Breeding_DD) ELSE 0*

I used an initial value of 0 for this stock as there are no chicks present at the beginning of the breeding season. Chicks at time t is determined by the number of chicks in the previous timestep ($t-dt$) plus the difference between inflows and outflows where:

*Chicks(t) = Chicks(t - Δt) + (Chicks_Being_Produced - Male_Juv_Prod - Female_Juv_Prod - Chick_Mort) * Δt*

Chicks leave the stock in one of three ways. *Chick Mort* represents the number of chicks dying during the breeding season with *Chick_Surv* representing the number of chicks surviving to become juveniles and is randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.25 (SD \pm 1.75, n = 628) and is defined in the model as:

IF Season=1 THEN Chicks(1-Chick_Surv) ELSE 0*

Female_Juv_Prod and *Male_Juv_Prod* transfer the number of female and male juveniles being produced during the breeding season to the stock variables *FF* and *MF* respectively. *FF* and *MF* represent the number of female and male fledglings at the beginning of each time step. If breeding season (season=1), this outflow transfers the value for female and male juveniles produced to the *FF* and *MF* stocks. If non-breeding season, the outflow transfers a value of 0. This equation is defined in the model as:

IF Season=1 THEN Chicks ELSE 0

The initial value used for both female and male fledglings was 0 as no fledglings are present at the beginning of breeding season. The number of female fledglings and male fledglings at time $t+1$ is determined by the number of fledglings at the previous time step plus the difference between inflows and outflows where:

$$FF(t) = FF(t - dt) + (Female_Juv_Prod - FF_Stay - FF_Mort - FF_Disperse) * dt$$

and

$$MF(t) = MF(t - dt) + (Male_Juv_Prod - MF_Stay - MF_Mort - MF_Disperse) * dt$$

Fledglings leave the FF or MF stock in one of three ways. FF Stay and MF Stay transfer the number of surviving fledglings that do not disperse out of the population to the stocks FYI and MYI respectively. FYI and MYI represent the number of surviving female and male fledglings in the population at the end of the breeding season. If breeding season (season = 1) then the equation returns the value of the FF or MF stock. If non-breeding season (season = 2) then the equation returns a value of zero as no fledglings are present during the non-breeding season. This equation is defined as:

$$IF\ Season=1\ THEN\ FF\ ELSE\ 0$$

and

$$IF\ Season=1\ THEN\ MF\ ELSE\ 0$$

Fledglings may also exit the FF and MF stocks via mortality. FF Mort and MF Mort are defined as the number of female or male fledglings dying during the breeding season. If breeding season (season = 1), then the equation returns $(FF * (1 - FF_Surv))$ for females and $(MF * (1 - MF_Surv))$ for males, where FF Surv and MF Surv are defined as

the survival rate of female and male fledglings respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.76 (SD \pm 0.83, n = 25). If non-breeding season (season = 2) then the equation returns a value of 0 as no fledglings are present during the non-breeding season. This model equation is defined as:

$$IF \text{ Season}=1 \text{ THEN } FF*(1-FF_Surv) \text{ ELSE } 0$$

and

$$IF \text{ Season}=1 \text{ THEN } MF*(1-MF_Surv) \text{ ELSE } 0$$

The final way in which fledglings exit the *FF* and *MF* stocks is dispersal. *FF Disperse* and *MF Disperse* represent the number of female fledglings and male fledglings that disperse out of the population. If breeding season (season = 1) then the equation returns (*FF* * *FF_Dispersal_Rate*) for females and (*MF* * *MF_Dispersal_Rate*) for males, where *FF_Dispersal_Rate* and *MF_Dispersal_Rate* represent the dispersal rate of female and male fledglings out of the population and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.04 (SD \pm 0.04, n = 25) and 0.08 (SD \pm 0.04, n = 25) respectively. This equation is defined in the model as:

$$IF \text{ Season}=1 \text{ THEN } FF*FF_Dispersal_Rate \text{ ELSE } 0$$

and

$$IF \text{ Season}=1 \text{ THEN } MF*MF_Dispersal_Rate \text{ ELSE } 0$$

FF Stay and *MF Stay* become inflows, transferring the number of surviving fledglings that do not disperse out of the population to the stocks *FYI* and *MYI* respectively. *FYI* and *MYI* represent the number of surviving female and male fledglings in the population that go on to become first-year birds. I used an initial value of 242 for females and 232 for males. The number of first-year birds at time *t* is calculated by taking

the number of first-year birds in the previous time step ($t-dt$) and adding the difference between the equation inflows and outflows where:

$$\mathbf{FY1(t) = FY1(t - dt) + (FF_Stay - FY1_Survival - FY1_Mort - FY1_Fall_Migration) * dt}$$

and

$$\mathbf{MY1(t) = MY1(t - dt) + (MF_Stay - MY1_Survival - MY1_Mort - MY1_Fall_Migration) * dt}$$

First-year females and males leave the *FYI* and *MYI* stocks in one of three ways. *FYI Survival* and *MYI Survival* transfer the number of surviving first-year birds at the end of the breeding season to the stocks *FY2* and *MY2* respectively. If breeding season (season = 1) then the equation gives the value of the first-year stocks (*FYI* or *MYI*). If non-breeding season (season = 2) then the equation gives a value of 0. This outflow is modeled by the equation:

$$IF\ Season=1\ THEN\ FYI\ ELSE\ 0$$

and

$$IF\ Season=1\ THEN\ MYI\ ELSE\ 0$$

First-year birds can also exit the *FYI* or *MYI* stocks via mortality. *FYI Mort* and *MYI Mort* represent the number of first-year birds dying at the end of the breeding season. If breeding season (season = 1) then the equation returns ($FYI * (1 - FYI_Breed_Surv)$) for females and ($MYI * (1 - MYI_Breed_Surv)$) for males, where *FYI_Breed_Surv* and *MYI_Breed_Surv* represent the breeding season survival rate of first-year female and male juveniles respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.53 (SD \pm 0.113, n = 25). If non-breeding season

(season = 2) then the equation returns ($FYI * (1 - FYI_NB_Surv)$) for females and ($MYI * (1 - MYI_NB_Surv)$) for males where FYI_NB_Surv and MYI_NB_Surv represent the survival rate of first-year females and males during the non-breeding season and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.53 (SD \pm 0.113, n = 25). This process is defined by the equation:

IF Season=1 THEN FYI(1-FYI_Breed_Surv) ELSE IF Season=2 THEN FYI*(1-FYI_NB_Surv) ELSE 0*

and

IF Season=1 THEN MYI(1-MYI_Breed_Surv) ELSE IF Season=2 THEN MYI*(1-FYI_NB_Surv) ELSE 0*

Finally, first-year birds can exit the *FYI* and *MYI* stocks via fall migration. *FYI Fall Migration* and *MYI Fall Migration* transfer the number of first-year birds that migrate south in the fall to the stocks *FYI Mig* and *MYI Mig* respectively. *FYI Mig* and *MYI Mig* represent the number of first-year female and male migrants. If non-breeding season (season = 2), then the equation returns ($FYI * FYI_FM_Rate$) for females and ($MYI * MYI_FM_Rate$) for males, where FYI_FM_Rate and MYI_FM_Rate represent the fall migration rate of first-year females and males and are randomly drawn from a normal distribution with a mean of 0.125 (SD \pm 0.063, n = 16) and 0.2857 (SD \pm 0.071, n = 14) respectively. If breeding season (season = 1) then the equation returns a value of 0. This model equation is defined as:

*IF Season=2 THEN (FYI*FYI_FM_Rate) ELSE 0*

and

*IF Season=2 THEN (MYI*MYI_FM_Rate) ELSE 0*

FY1 Fall Migration and *MY1 Fall Migration* become inflows transferring the number of first-year birds that migrate south in the fall to the stocks *FY1_Mig* and *MY1_Mig* respectively. *FY1_Mig* and *MY1_Mig* represent the number of first-year females and males that migrate. I used an initial value of 30 for the females and 66 for the males. The number of first-year migrants at time t is determined by the number of first-year migrants at the previous time step ($t-dt$) plus the differences between inflows and outflows, where:

$$\mathbf{FY1_Mig(t)} = \mathbf{FY1_Mig(t - dt)} + (\mathbf{FY1_Fall_Migration} - \mathbf{FY1_Spring_Migration} - \mathbf{FY1_Mig_Mort}) * \mathbf{dt}$$

and

$$\mathbf{MY1_Mig(t)} = \mathbf{MY1_Mig(t - dt)} + (\mathbf{MY1_Fall_Migration} - \mathbf{MY1_Spring_Migration} - \mathbf{MY1_Mig_Mort}) * \mathbf{dt}$$

First-year birds that migrate can exit the *FY1_Mig* and *MY1_Mig* stocks in two different ways. *FY1 Spring Migration* and *MY1 Spring Migration* transfer the number of first-year birds that immigrate to the *FY2* and *MY2* stocks respectively. *FY2* and *MY2* represents the number of second year females and males at the beginning of each time step. If breeding season (season = 1) then the equation returns (*FY1_Mig* * *FY1_SM_Rate*) for females and (*MY1_Mig* * *MY1_SM_Rate*) for males, where *FY1_SM_Rate* and *MY1_SM_Rate* represent the spring migration rate of first-year females and males respectively and were set at a value of 1.0. If non-breeding season (season = 2) then the equation returns a value of 0. This outflow is defined as:

$$\mathbf{IF\ Season=1\ THEN\ (FY1_Mig*FY1_SM_Rate)\ ELSE\ 0}$$

and

$$IF \text{ Season}=1 \text{ THEN } (MY1_Mig * MY1_SM_Rate) \text{ ELSE } 0$$

First-year birds can also exit the *FY1_Mig* and *MY1_Mig* stocks through mortality during migration. *FY1 Mig Mort* and *MY1 Mig Mort* represent the number of first-year females and males dying during migration respectively. If non-breeding season (season=2) then the equation returns (*FY1_Mig* * (1- *FY1_Mig_Surv*)) for females and (*MY1_Mig* * (1 - *MY1_Mig_Surv*)) for males where *FY1 Mig Surv* and *MY1 Mig Surv* represent the survival rate of first-year female and male migrants respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.7697 (SD \pm 1.39, n = 591). If breeding season (season = 1) then the equation returns a value of 0. This outflow is defined as:

$$IF \text{ Season}=2 \text{ THEN } (FY1_Mig * (1 - FY1_Mig_Surv)) \text{ ELSE } 0$$

and

$$IF \text{ Season}=2 \text{ THEN } (MY1_Mig * (1 - MY1_Mig_Surv)) \text{ ELSE } 0$$

FY1 Spring Migration, *FY1 Survival*, *MY1 Spring Migration*, and *MY1 Survival* become inflows transferring the number of first-year birds that immigrate and the number of surviving first-year birds at the end of the breeding season to the *FY2* and *MY2* stocks. I used an initial value of 136 female birds and 139 male birds. The number of second-year birds at time *t* is calculated using the number of second-year birds during the previous time step (*t-dt*) plus the difference between inflows and outflows, where:

$$FY2(t) = FY2(t - dt) + (FY1_Survival + FY1_Spring_Migration - FY2_Survival - FY2_Mort - FY2_Fall_Migration) * dt$$

and

$$\text{MY2}(t) = \text{MY2}(t - dt) + (\text{MY1_Survival} + \text{MY1_Spring_Migration} - \text{MY2_Survival} - \text{MY2_Mort} - \text{MY2_Fall_Migration}) * dt$$

Second year birds leave the *FY2* or *MY2* stock in one of three ways. *FY2 Survival* and *MY2 Survival* transfer the surviving second-year birds to the *FY3* and *MY2* stocks respectively. *FY3* and *MY3* represent the number of third year females and males at the beginning of each time step. If breeding season (season =1), then the equation returns the value of the *FY2* or *MY2* stock. If non-breeding season (season =2), then the equation returns a value of zero. This outflow is defined as:

IF Season=1 THEN FY2 ELSE 0

and

IF Season=1 THEN MY2 ELSE 0

Second year birds may exit the *FY2* or *MY2* stock through mortality. *FY2 Mort* and *MY2 Mort* represents the number of second year females and males dying during the breeding and non-breeding seasons. If breeding season (season = 1) then the equation returns (*FY2* * (1 - *FY2_Breed_Surv*)) for females and (*MY2* * (1 - *MY2_Breed_Surv*)) for males, where *FY2_Breed_Surv* and *MY2_Breed_Surv* represent the breeding season survival rate of second year females and males respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.945 (SD ± 0.66, n = 591). If non-breeding season (season = 2) then the equation returns (*FY2* * (1 - *FY2_NB_Surv*)) for females and (*MY2* * (1 - *MY2_NB_Surv*)) for males where *FY2_NB_Surv* and *MY2_NB_Surv* represent the survival rate of second-year females and males during the non-breeding season and are randomly drawn from a normal distribution

truncated between 0.0 and 1.0 with a mean of 0.7697 (SD \pm 1.39, n = 591). This outflow is defined in the model as:

IF Season=1 THEN FY2(1-FY2_Breed_Surv) ELSE IF Season=2 THEN FY2*(1-FY2_NB_Surv) ELSE 0*

and

IF Season=1 THEN MY2(1-MY2_Breed_Surv) ELSE IF Season=2 THEN MY2*(1-MY2_NB_Surv) ELSE 0*

The third and final way in which second year birds exit the *FY2* or *MY3* stock is through fall migration. *FY2 Fall Migration* and *MY2 Fall Migration* transfer the number of second-year birds that migrate south in the fall to the stock *FY2 Mig* and *MY2 Mig* respectively. *FY2 Mig* and *MY2 Mig* represent the number of second-year females and males that migrate. If non-breeding season (season = 2) then the equation returns (*FY2 * FY2_FM_Rate*) for females and (*MY2 * MY2_FM_Rate*) for males where *FY2_FM_Rate* and *MY2_FM_Rate* represents the fall migration rate of second-year females and males and are randomly drawn from a normal distribution with a mean of 0.125 (SD \pm 0.063, n = 16) and 0.2857 (SD \pm 0.071, n= 14) respectively. If breeding season (season = 1) then the equation returns a value of zero. This model outflow is defined as:

IF Season=2 THEN (FY2 FY2_FM_Rate) ELSE 0*

and

IF Season=2 THEN (MY2 MY2_FM_Rate) ELSE 0*

FY2 Fall Migration and *MY2 Fall Migration* become inflows transferring the number of second-year birds that migrate south in the fall to the stock *FY2 Mig* and *MY2 Mig* respectively. *FY2 Mig* and *MY2 Mig* represent the number of second-year female and

male migrants. I used an initial value of 17 for females and 40 for males. The number of second-year migrants at time t is determined by the number of second-year migrants at the previous time step ($t-dt$) plus the differences between inflows and outflows, where:

$$FY2_Mig(t) = FY2_Mig(t - dt) + (FY2_Fall_Migration - FY2_Spring_Migration - FY2_Mig_Mort) * dt$$

and

$$MY2_Mig(t) = MY2_Mig(t - dt) + (MY2_Fall_Migration - MY2_Spring_Migration - MY2_Mig_Mort) * dt$$

Second-year birds that migrate can exit the *FY2_Mig* and *MY2_Mig* stocks in two different ways. *FY2 Spring Migration* and *MY2 Spring Migration* transfer the number of second-year birds that immigrate to the stock *FY3* and *MY3* respectively. *FY3* and *MY3* represent the number of third-year females and males at the beginning of each time step. If breeding season (season = 1) then the equation returns ($FY2_Mig * FY2_SM_Rate$) for females and ($MY2_Mig * MY2_SM_Rate$), where *FY2_SM_Rate* and *MY2_SM_Rate* represent the spring migration rate of second-year females and males respectively and was set at a value of 1.0. If non-breeding season (season = 2) then the equation returns a value of 0. This outflow is defined as:

$$IF\ Season=1\ THEN\ (FY2_Mig*FY2_SM_Rate)\ ELSE\ 0$$

and

$$IF\ Season=1\ THEN\ (MY2_Mig*MY2_SM_Rate)\ ELSE\ 0$$

Second year birds can also exit the *FY2_Mig* and *MY2_Mig* stocks through mortality during migration. *FY2 Mig Mort* and *MY2 Mig Mort* represent the number of second-year females and males that die during migration. If non-breeding season (season

= 2) then the equation returns ($FY2_Mig * (1 - FY2_Mig_Surv)$) for females and ($MY2_Mig * (1 - MY2_Mig_Surv)$) for males where $FY2_Mig_Surv$ and $MY2_Mig_Surv$ represent the survival rate of second-year female and male migrants respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.7697 (SD \pm 1.39, n = 591). If breeding season (season = 1) then the equation returns a value of 0. This outflow is defined as:

IF Season=2 THEN (FY2_Mig(1-FY2_Mig_Surv)) ELSE 0*

and

IF Season=2 THEN (MY2_Mig(1-MY2_Mig_Surv)) ELSE 0*

FY2 Spring Migration, *FY2 Survival*, *MY2 Spring Migration*, and *MY2 Survival* become inflows transferring the number of second-year birds that immigrate and the number of surviving second-year birds at the end of the breeding season to the stocks *FY3* and *MY3*. I used an initial value of 100 female and 103 male birds for these stocks. The number of third-year birds at time t is calculated using the number of third-year birds during the previous time step ($t-dt$) plus the difference between inflows and outflows, where:

$$FY3(t) = FY3(t - dt) + (FY2_Survival + FY2_Spring_Migration - FY3_Survival - FY3_Mort - FY3_Fall_Migration) * dt$$

and

$$MY3(t) = MY3(t - dt) + (MY2_Survival + MY2_Spring_Migration - MY3_Survival - MY3_Mort - MY3_Fall_Migration) * dt$$

Third-year birds can leave the *FY3* and *MY3* stocks in one of three ways. *FY3 Survival* and *MY3 Survival* transfer the surviving third-year birds to the *FY4+* and *MY4+* stocks respectively. *FY4+* and *MY4+* represent the number of fourth-year and older

females and males at the beginning of each time step. If breeding season (season =1), then the equation returns the value of the *FY3* or *MY3* stock. If non-breeding season (season =2), then the equation returns a value of 0. This outflow is defined as:

IF Season=1 THEN FY3 ELSE 0

and

IF Season=1 THEN MY3 ELSE 0

Third year birds may also exit the *FY3* or *MY3* stocks through mortality. *FY3 Mort* and *MY3 Mort* represent the number of third-year females and males dying during the breeding and non-breeding seasons. If breeding season (season = 1) then the equation returns (*FY3* * (1 – *FY3_Breed_Surv*)) for females and (*MY3* * (1 – *MY3_Breed_Surv*)) for males, where *FY3_Breed_Surv* and *MY3_Breed_Surv* represent the survival rate of third-year females and males during the breeding season and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.945 (SD ± 0.66, n = 591). If non-breeding season (season = 2) then the equation returns (*FY3* * (1 – *FY3_NB_Surv*)) for females and (*MY3* * (1 – *MY3_NB_Surv*)) where *FY3_NB_Surv* and *MY3_NB_Surv* represent the survival rate of third-year females and males during the non-breeding season and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.7697 (SD ± 1.39, n = 591). This outflow is defined in the model as:

IF Season=1 THEN FY3(1-FY3_Breed_Surv) ELSE IF Season=2 THEN FY3*(1-FY3_NB_Surv) ELSE 0*

and

IF Season=1 THEN MY3(1-MY3_Breed_Surv) ELSE IF Season=2 THEN MY3*(1-MY3_NB_Surv) ELSE 0*

The third and final way in which third-year birds exit the *FY3* and *MY3* stocks is through fall migration. *FY3 Fall Migration* and *MY3 Fall Migration* transfer the number of third-year birds that migrate in the fall to the stocks *FY3 Mig* and *MY3 Mig* respectively. *FY3 Mig* and *MY3 Mig* represent the number of third-year females and males that migrate. If non-breeding season (season = 2) then the equation returns (*FY3 * FY3_FM_Rate*) for females and (*MY3 * MY3_FM_Rate*) for males where *FY3_FM_Rate* and *MY3_FM_Rate* represent the fall migration rate of third-year females and males and are randomly drawn from a normal distribution with a mean of 0.125 (SD \pm 0.063, n = 16) and 0.2857 (SD \pm 0.071, n = 14) respectively. If breeding season (season = 1) then the equation returns a value of zero. This model outflow is defined as:

IF Season=2 THEN (FY3 FY3_FM_Rate) ELSE 0*

and

IF Season=2 THEN (MY3 MY3_FM_Rate) ELSE 0*

FY3 Fall Migration and *MY3 Fall Migration* become inflows transferring the number of third-year birds that migrate in the fall to the stocks *FY3 Mig* and *MY3 Mig* respectively. *FY3 Mig* and *MY3 Mig* represent the number of third-year female and male migrants. I used an initial value of 12 females and 29 males. The number of third year migrants at time *t* is determined by the number of third-year migrants at the previous time step (*t - dt*) plus the differences between inflows and outflows, where:

$$FY3_Mig(t) = FY3_Mig(t - dt) + (FY3_Fall_Migration - FY3_Spring_Migration - FY3_Mig_Mort) * dt$$

and

$$MY3_Mig(t) = MY3_Mig(t - dt) + (MY3_Fall_Migration - MY3_Spring_Migration - MY3_Mig_Mort) * dt$$

Third-year birds that migrate can exit the *FY3_Mig* and *MY3_Mig* stocks in two different ways. *FY3 Spring Migration* and *MY3 Spring Migration* transfer the number of third-year birds that immigrate to the stocks *FY4+* and *MY4+* respectively. If breeding season (season = 1) then the equation returns (*FY3_Mig* * *FY3_SM_Rate*) for females and (*MY3_Mig* * *MY3_SM_Rate*) for males, where *FY3_SM_Rate* and *MY3_SM_Rate* represent the spring migration rate of third year females and males respectively and was set to a value of 1.0. If non-breeding season (season = 2) then the equation returns a value of 0. This outflow is defined as:

$$IF\ Season=1\ THEN\ (FY3_Mig * FY3_SM_Rate)\ ELSE\ 0$$

and

$$IF\ Season=1\ THEN\ (MY3_Mig * MY3_SM_Rate)\ ELSE\ 0$$

Third year birds can also exit the *FY3_Mig* and *MY3_Mig* stocks through mortality during migration. *FY3 Mig Mort* and *MY3 Mig Mort* represent the number of third-year females and males dying during migration. If non-breeding season (season = 1) then the equation returns (*FY3_Mig* * (1 - *FY3_Mig_Surv*)) for females and (*MY3_Mig* * (1 - *MY3_Mig_Surv*)) for males where *FY3 Mig Surv* and *MY3 Mig Surv* represent the survival rate of third-year female and male migrants respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.7697 (SD ± 1.39, n = 591). If breeding season (season = 2) then the equation returns a value of 0. This outflow is defined as:

IF Season=2 THEN (FY3_Mig(1-FY3_Mig_Surv)) ELSE 0*

and

IF Season=2 THEN (MY3_Mig(1-MY3_Mig_Surv)) ELSE 0*

FY3 Survival, FY3 Spring Migration, FY4+ Spring Migration, MY3 Survival, MY3 Spring Migration, and MY4+ Spring Migration are inflows to the *FY4+* and *MY4+* stocks. The inflows *FY4+ Spring Migration* and *MY4+ Spring Migration* transfer the number of fourth-year and older birds that immigrate to the *FY4+* and *MY4+* stocks respectively. I used an initial value of 950 birds for *FY4+* and *MY4+*, representing an initial breeding population of 1,900 birds. The number of birds that are four-year old and older birds at time t is calculated by using the number of four-year old and older birds at the previous time step ($t-dt$) plus the differences between inflows and outflows, where

$$FY4+(t) = FY4+(t - dt) + (FY3_Survival + FY3_Spring_Migration + FY4+_Spring_Migration - FY4+_Mort - FY4+_Fall_Migration) * dt$$

and

$$MY4+(t) = MY4+(t - dt) + (MY3_Survival + MY3_Spring_Migration + MY4+_Spring_Migration - MY4+_Mort - MY4+_Fall_Migration) * dt$$

Fourth-year and older birds may leave the *FY4+* and *MY4+* stocks in one of two ways. *FY4+ Mort* and *MY4+ Mort* represent the number of fourth-year and older females and males dying during the breeding and non-breeding seasons. If breeding season (season = 1) then the outflow returns ($FY4+ * (1 - FY4+_Breed_Surv)$) for females and ($MY4+ * (1 - MY4+_Breed_Surv)$) for males where *FY4+_Breed_Surv* and *MY4+_Breed_Surv* represent the breeding season survival rate of fourth-year and older females and males respectively and are randomly drawn from a normal distribution truncated between 0.0 and

1.0 with a mean of 0.945 (SD \pm 0.66, n = 591). If non-breeding season (season =2) then the model outflow returns ($FY4+ * (1-FY4+_{NB_Surv})$) for females and ($MY4+ * (1-MY4+_{NB_Surv})$) for males where $FY4+_{NB_Surv}$ and $MY4+_{NB_Surv}$ represent the non-breeding season survival rate of fourth-year and older females and males respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 with a mean of 0.7697 (SD \pm 1.39, n = 591). The model outflow is defined as:

*IF Season=1 THEN $FY4+ * (1-FY4+_{Breed_Surv})$ ELSE IF Season=2 THEN $FY4+ * (1-FY4+_{NB_Surv})$ ELSE 0*

and

*IF Season=1 THEN $MY4+ * (1-MY4+_{Breed_Surv})$ ELSE IF Season=2 THEN $MY4+ * (1-MY4+_{NB_Surv})$ ELSE 0*

The second and final way in which fourth-year and older birds leave the $FY4+$ and $MY4+$ stocks is through fall migration. $FY4+$ *Fall Migration* and $MY4+$ *Fall Migration* transfer the number of fourth-year and older birds that emigrate to the stock $FY4+$ *Mig* and $MY4+$ *Mig* respectively. $FY4+$ *Mig* and $MY4+$ *Mig* represent the number of fourth-year and older females and males that migrate. If non-breeding season (season =2) then the outflow returns ($FY4+ * FY4+_{FM_Rate}$) for females and ($MY4+ * MY4+_{FM_Rate}$) for males where $FY4+_{FM_Rate}$ and $MY4+_{FM_Rate}$ represent the fall migration rate of fourth-year and older females and males and are randomly drawn from a normal distribution with a mean of 0.125 (SD \pm 0.063, n = 16) and 0.2857 (SD \pm 0.071, n = 14) respectively. If breeding season (season =1) then the outflow returns a value of 0. The model outflow is defined as:

*IF Season=2 THEN $(FY4+ * FY4+_{FM_Rate})$ ELSE 0*

and

IF Season=2 THEN (MY4+ MY4+_FM_Rate) ELSE 0*

Fall migration becomes the final model inflow with *FY4+ Fall Migration* and *MY4+ Fall Migration* transferring the number of fourth-year and older birds that emigrate to the stock *FY4+ Mig* and *MY4+ Mig* respectively. I used an initial value of 120 females and 270 males for these stocks. The number of fourth-year and older birds that migrate at time t is determined by the number of fourth-year and older birds that migrated in the previous time step ($t-dt$) plus the difference between model inflows and outflows, where:

$$FY4_Mig(t) = FY4_Mig(t - dt) + (FY4_Fall_Migration - FY4_Spring_Migration - FY4_Mig_Mort) * dt$$

and

$$MY4_Mig(t) = MY4_Mig(t - dt) + (MY4_Fall_Migration - MY4_Spring_Migration - MY4_Mig_Mort) * dt$$

Fourth-year and older migrants leave the *FY4+ Mig* and *MY4+ Mig* stock in one of two ways. *FY4+ Mig Mort* and *MY4+ Mig Mort* represent the number of fourth-year and older female and male migrants dying. If non-breeding season (season = 2) then the outflow returns ($FY4_Mig * (1 - FY4_Mig_Surv)$) for females and ($MY4_Mig * (1 - MY4_Mig_Surv)$) for males where *FY4+ Mig Surv* and *MY4+ Mig Surv* represent the survival rate of fourth-year and older female and male migrants respectively and are randomly drawn from a normal distribution truncated between 0.0 and 1.0 normal with a mean of 0.7697 (SD ± 1.39 , $n = 591$). The model outflow is defined as:

IF Season=2 THEN (FY4+_Mig(1-FY4+_Mig_Surv)) ELSE 0*

and

IF Season=2 THEN (MY4+_Mig(1-MY4+_Mig_Surv)) ELSE 0*

Finally, fourth-year and older migrants may leave the *FY4+_Mig* and *MY4+_Mig* stocks through spring migration. *FY4+ Spring Migration* and *MY4+ Spring Migration* transfer the number of fourth-year and older birds that immigrate back to the stocks *FY4+* and *MY4+* respectively. If breeding season (season = 1) then the model outflow returns (*FY4+_Mig * FY4+_SM_Rate*) for females and (*MY4+_Mig * MY4+_SM_Rate*) for males where *FY4+ SM Rate* and *MY4+ SM Rate* are defined as the spring migration rate of fourth-year and older females and males respectively and was set to a value of 1.0. If non-breeding season (season = 2) then the outflow returns a value of 0. The outflow is defined in the model by:

*IF Season=1 THEN (FY4+_Mig * FY4+_SM_Rate) ELSE 0*

and

*IF Season=1 THEN (MY4+_Mig * MY4+_SM_Rate) ELSE 0*

Model Testing and Verification

To test and verify the model, I solved the model equations to 1 time step and compared my calculations to those of the model to ensure that various mathematical equations in the model functioned as intended. Similar results indicated the model was performing properly. Once I verified the model calculations, I evaluated model performance in 3 steps:

1) I visually evaluated population trends of model output for population fluctuations characteristic of the species previously reported,

2) I compared the population trend and slope of our simulation model results to an independent population index, Texas Colonial Waterbird Society breeding pair counts, using linear regression, and

3) I compared model predictions of fledglings/adult I obtained from 780 replicate-stochastic simulations to estimates reported in the literature.

Sensitivity Analysis

Sensitivity analyses are a set of analytical and simulation-based methods that examine how changes in demographic parameters within the model may impact population growth (Mills and Lindberg 2002). In order to examine how sensitive the model output was to each demographic parameter I first converted my stochastic model to a deterministic one by replacing the normal distributions with the mean parameter estimates. I then varied each model parameter individually by +/- 15%, representing the average variance in the parameters and examined the change in the baseline breeding population to quantify which parameters impacted the population the most. As little information exists to suggest which vital rates may be most impactful to *E. rufescens* population growth in Texas, I varied all parameters in the model that had a value of less than one. These parameters included *Chick Surv*, *Clutch Size*, *FF Dispersal Rate*, *FF Surv*, *FY1 Breed Surv*, *FY1 FM Rate*, *FY1 Mig Surv*, *FY1 NB Surv*, *FY2 Breed Surv*, *FY2 FM Rate*, *FY2 Mig Surv*, *FY2 NB Surv*, *FY3 Breed Surv*, *FY3 FM Rate*, *FY3 Mig Surv*, *FY3 NB Surv*, *FY4+ Breed Surv*, *FY4+ FM Rate*, *FY4+ Mig Surv*, *FY4+ NB Surv*, *MF Dispersal Rate*, *MF Surv*, *MY1 Breed Surv*, *MY1 FM Rate*, *MY1 Mig Surv*, *MY1 NB Surv*, *MY2 Breed Surv*, *MY2 FM Rate*, *MY2 Mig Surv*, *MY2 NB Surv*, *MY3 Breed Surv*, *MY3 FM Rate*, *MY3 Mig Surv*, *MY3 NB Surv*, *MY4+*

Breed Surv, *MY4+ FM Rate*, *MY4+ Mig Surv*, *MY4+ NB Surv*, and *Nest Success*. I did not vary *FY1 SM Rate*, *FY2 SM Rate*, *FY3 SM Rate*, *FY4+ SM Rate*, *MY1 SM Rate*, *MY2 SM Rate*, *MY3 SM Rate*, or *MY4+ SM Rate* as they were all set at 1.0. I then examined which demographic parameters impacted the baseline breeding population by $\geq 10\%$.

Population Persistence

While there exists no standard threshold that defines a viable population, a time interval from 50 to 200 years and extinction rates of less than 5% are commonly used to evaluate population persistence (Beissinger and Westphal 1998). After executing the primary 780 stochastic simulations I calculated the stochastic growth rate (λ_s), mean simulation outcome and 95% confidence intervals. These estimates were then used to test and recommend feasible management actions. Additionally, using a quasi-extinction threshold of ≤ 50 and ≤ 25 breeding birds I examined the probability of population persistence by quantifying the number of stochastic simulations that fell at or below this amount. Finally, I quantified the number of simulations that achieved the breeding population goal of 2,000 breeding pairs, or 4,000 breeding individuals.

III. RESULTS

Model Testing and Validation

The linear trendline of the five random stochastic simulations was estimated $y = 3.5651x + 1206.2$ ($R^2 = 0.0061$, 95% CI -0.411673 7.541808) with a stochastic growth rate (λ_s) of 0.966 (Figure 3) which was found to be similar to that of the TCWS survey data ($y = -7.7424x + 2814.5$; $R^2 = 0.0128$; 95% CI -29.17321 to 13.68846) with a growth

rate (λ) of 0.998 (Figure 4). The mean simulated fledglings per adult ($n=780$) was estimated at 1.96 ($SD \pm 2.00$) which was similar to and found to overlap with values reported by Holderby *et al.* (2012; Table 2) The model results appear to agree with current population trends and parameter estimates for the Texas population of *E. rufescens* (Vermillion and Wilson 2009; Wilson *et al.* 2012) and are therefore, I believe, appropriate to use for model validation.

Sensitivity Analysis

I found that nine out of the thirty-nine model parameters varied impacted the baseline breeding population by $\geq 10\%$. In decreasing order of impact, the model parameters identified were *FY4+ NB Surv*, *FY4+ Breed Surv*, *Clutch Size*, *Nest Success*, *FY3 NB Surv*, *FY2 NB Surv*, *FY1 NB Surv*, *MY4+ NB Surv*, and *FY4+ FM Rate* (Table 1). The parameters identified as having $> 0\%$ but $< 10\%$ impact, in decreasing order of impact were *MY2 NB Surv*, *MY1 NB Surv*, *MY3 NB Surv*, *MY4+ Breed Surv*, *MY4+ FM Rate*, *MY2 FM Rate*, *FY3 Breed Surv*, *FY2 FM Rate*, and *FY2 Breed Surv*. All other parameters examined had no impact on the baseline breeding population.

Population Persistence

The mean simulation outcome ($n = 780$) was calculated at 1,579 breeding individuals ($SD \pm 1,238$; 95% CI = 0 to 3,939; Figure 5) and, using the median simulation outcome, I estimated the stochastic growth rate (λ_s) at 0.996. I found that 14 out of the 780 (1.80%) stochastic simulations fell at or below the quasi-extinction threshold of ≤ 50 breeding individuals while only 7 (0.90%) simulations fell at or below

the quasi-extinction threshold of ≤ 25 breeding individuals. Additionally, I found that 743 out of the 780 (95.3%) stochastic simulations did not achieve the population goal of 2,000 breeding pairs (Figure 6).

IV. DISCUSSION

Model testing and verification

Both the simulated and TCWS survey data show similar stable population trends. While there is no reliable dataset to directly test and validate the model output, it appears to be a suitable model of the Texas population of *E. rufescens* based on current population trend estimates suggesting the Texas population is stable or declining (Kushlan *et al.* 2002; Vermillion and Wilson 2009; Wilson *et al.* 2012). Additionally, the simulated parameter estimate for the number of fledglings per adult was consistent with values reported in the literature for *E. rufescens* in Texas (Holderby *et al.* 2012).

Sensitivity analysis

FY4+ NB Surv was the most sensitive parameter in the model with a 15% decrease in survival of four-year-old and older females yielding ~98% decrease in the breeding population and a 15% increase exhibiting ~440% increase in the breeding population. *FY4+ Breed Surv* was the second most sensitive parameter in the model with similar results to non-breeding survival. A 15% decrease in breeding survival led to ~90% decrease in the breeding population whereas a 15% increase exhibited ~150% increase in the breeding population. It is reasonable to conclude that changes in adult survivorship (breeding or non-breeding) may have the greatest impact on *E. rufescens* as they are a long-lived species

that matures late (Geary *et al.* 2015, Koczur *et al.* 2017). Individuals that have survived to become adult have endured the most difficult life stages and face few threats to survivorship, other than senescence, as breeding adults (Koczur *et al.* 2017).

The *Nest Success* and *Clutch Size* parameters impacted the breeding population by the same amount. A 15% decrease in *Nest Success* and *Clutch Size* yielded a ~60% decrease in breeding population whereas a 15% increase in these parameters would have a >120% increase in the breeding population. In many long-lived species that lay small clutches, such as seabirds, it is reasonable to see a marked change in population with changes in nest success or clutch size. In reddish egrets that have 10+ year lifespans and lay medium sized clutches relative to seabirds, it is not surprising that the effects are less dramatic than adult survival. Nest success within colonies is usually high in the absence of predation or human disturbance (Holderby *et al.* 2012) which can be detrimental to population growth, underscoring the importance of colony protection.

My results are similar to other sensitivity analyses performed on waterbird populations. In other long-lived avian species, adult survivorship has been found to be the most influential parameter to population growth while fecundity plays a somewhat limited role (Lebreton and Clobert 1991). Saether and Bakke (2000) examined demographic data from 49 bird species and found that adult survivorship was the most influential parameter in species that mature late and lay relatively few eggs. Similarly, adult survivorship was found to be the most influential vital rate in other long-lived waterbird species that also reach sexual maturity at 3+ years such as black terns (*Chlidonias niger*), Hutton's shearwaters (*Puffinus huttoni*), and red-tailed tropicbirds (*Phaethon rubricauda*; Cuthbert 2001; Doherty *et al.* 2004; Servello 2000).

Population Persistence

The stochastic model simulations predict a stable breeding population over the next 50 years with a stochastic growth rate of ~ 1.0 . With current breeding population estimates in Texas at around 950 breeding pairs (TCWS, unpublished data), I believe these model results are in agreement with current population estimates that have found the Texas population of *E. rufescens* to be stable or declining (Kushlan *et al.* 2002; Vermillion and Wilson 2009; Wilson *et al.* 2012). While I found that there is a high probability of the breeding population persisting above a quasi-extinction threshold over the next 50 years, I found only about a 6% probability of achieving the population goal of 2,000 breeding pairs set out by the Reddish Egret Working Group and Gulf Coast Joint Venture Monitoring, Evaluation, and Research Team Waterbird Working Group without additional management of the population.

Management implications

When creating a conservation plan for endangered or threatened species it is necessary to find out how demographic parameters could be influenced by management actions (Green and Hirons 1991). The results of a PVA can be used alongside cost-efficiency analysis in order to determine the best available management actions given limited money, resources, and time (Sebastián-González *et al.* 2011). This allows wildlife managers to focus on the vital rates that are most influential to population growth and avoid focusing on those that may not have a noticeable impact. The Reddish Egret Conservation Action Plan suggests focusing research efforts on adult habitat use and mortality during

the non-breeding season as this period appears to be limiting for survival (Wilson *et al.* 2012). Bates (2011) examined differences in breeding season and non-breeding season foraging habitat for reddish egrets in the Laguna Madre region of Texas and found that only a fraction of the foraging habitat available during the breeding season is also available during the non-breeding season due to fluctuating water levels. Water-level fluctuations have been found to impact adult survivorship in the Everglade Kite (*Rostrhamus sociabilis plumbeus*), and Hawaiian stilt (*Himantopus mexicanus knudseni*), endangered species for which adult survivorship is also limiting (Nichols *et al.* 1980; Reed *et al.* 1997). Sæther *et al.* (1998) found that in long-lived species that lay relatively few eggs, the annual variation in habitat tends to be greater compared to the habitat of similar species such as seabirds that only lay one egg. My study results only underscore the importance of understanding and maintaining the complex relationship that exists between *E. rufescens* and the habitat upon which they rely.

Management actions identified as being needed now or within the next 5 to 10 years by Vermillion *et al.* (2009) all address increasing the breeding population and should be used as a guide for conservation action on the ground. Specific management actions that could increase breeding adult survival would include the protection, restoration, or creation of additional habitat along with erosion control. A recent study of Texas colonial waterbird rookery islands estimated that 25% of the islands examined are at risk of disappearing completely within 50 years (Hackney *et al.* 2016). Additionally, it is predicted that with \geq 1.5-meter sea level rise, the majority of breeding sites currently used by the species would be permanently inundated (Wilson *et al.* 2012). With sea levels predicted to rise anywhere from 0.2 to 2.0 meters by the year 2100 (Melillo *et al.* 2014) *E. rufescens* nesting and

foraging habitat continues to be threatened. Assuming habitat management actions focused on increasing the non-breeding survival rate of four-year-old and older females also increase the non-breeding survival rate of all adult birds by the same amount, then when simulating management actions that aim to increase these vital rates by 10%, the breeding population is projected to surpass the goal of 2,000 breeding pairs within the next 50 years given continued management (Figure 7). These management simulations only highlight the need for continued habitat conservation measures to ensure the availability of high-quality habitat.

Specific management actions that have been identified to increase nest success include continued colony monitoring, continuation or implementation of predator control programs, and human disturbance mitigation (Vermillion and Wilson 2009). Mullin *et al.* (2010) found that management actions focusing on fecundity, such as predator control and limiting human disturbance, may be necessary to maintain the threatened western snowy plover (*Charadrius alexandrinus nivosus*) population in coastal northern California. However, even if nest success in the Texas population of *E. rufescens* could be increased to 1.0 through similar management actions, the breeding population is projected to remain below the population goal at around 1,340 breeding individuals (Figure 8). It is for this reason that management actions that focus on protecting and creating high-quality foraging habitat are projected to be most impactful on the population. These actions can be implemented on the ground while the model is further developed and tested.

Future Research

The next step in *E. rufescens* population model development is to incorporate spatial and habitat parameters pertinent to foraging such as bathymetry, hydrology, and vegetation. Foraging habitat parameters such as water depth and sea grass cover have been shown to be strong predictors of *E. rufescens* colony size and location (Bates 2011).

After foraging habitat parameters have been incorporated the model can then be parsed into breeding colony islands creating a metapopulation model for Texas. This will allow researchers to examine how population fluctuations at larger breeding colonies impact the population as a whole. Metapopulation model studies on species such as the wandering albatross (*Diomedea exulans chionoptera*) have found that dispersal of juveniles to other colony islands impacted metapopulation persistence the most (Inchausti and Weimerskirch 2004). Conversely, when examining metapopulations of Hawaiian stilts Reed *et al.* (1997) found that the degree of connectivity between island population had little impact on the metapopulation size and persistence. It was predicted that this was due to the presence of three large island populations that could drive the metapopulation dynamics and therefore persist independently (Reed *et al.* 1997). While there is known to be drastic differences in colony island size in Texas (Texas Colonial Waterbird Society, unpublished data), the population dynamics between these islands remains unknown. For example, Green island in the Laguna Madre region of Texas has been documented to hold the highest number of breeding pairs (Bates 2011) however the relative importance of this island to the Texas population is currently unknown. After partitioning the model, it should then be expanded to include areas outside of Texas that have been identified as important wintering or foraging habitat for Texas birds (Geary *et al.* 2015). The end goal for this model is a

spatially explicit range-wide metapopulation model in an effort to conserve and manage reddish egret populations holistically.

Table 1: Sensitivity analysis results showing model parameters impacts on the baseline breeding population for reddish egrets (*Egretta rufescens*) in Texas

Parameter	Estimate	Estimate Variation	Resulting Breeding Population	Difference from baseline	% Difference from Baseline
<i>FY4+ NB Surv</i>	0.7697	-0.15	10	-517	-98.10%
		15%	2856	2329	441.94
<i>FY4+Breed Surv</i>	0.945	-0.15	51	-476	-90.32%
		15%	1348	821	155.79%
<i>Clutch Size</i>	3.29	-0.15	213	-314	-59.58%
		15%	1175	648	122.96%
<i>Nest Success</i>	0.85	-0.15	213	-314	-59.58%
		15%	1175	648	122.96%
<i>FY3 NB Surv</i>	0.7697	-0.15	226	-301	-57.12%
		15%	1124	597	113.28%
<i>FY2 NB Surv</i>	0.7697	-0.15	228	-299	-56.74%
		15%	1115	588	111.57%
<i>FY1 NB Surv</i>	0.53	-0.15	232	-295	-55.98%
		15%	1096	569	107.97%
<i>MY4+ NB Surv</i>	0.7697	-0.15	408	-119	-22.58%
		15%	837	310	58.82%
<i>FY4+ FM Rate</i>	0.125	-0.15	613	86	16.32%
		15%	452	752	-14.23%

Table 2: Comparison of estimated fledglings per adult between simulated values and those reported in the literature for the Texas population of *E. rufescens*.

Parameter	Simulation			Literature			Source
	n	Mean	Min	Max	Min	Max	
Fledglings per adult	780	1.96	0	33.55	1.22	1.35	Holderby <i>et al.</i> 2012

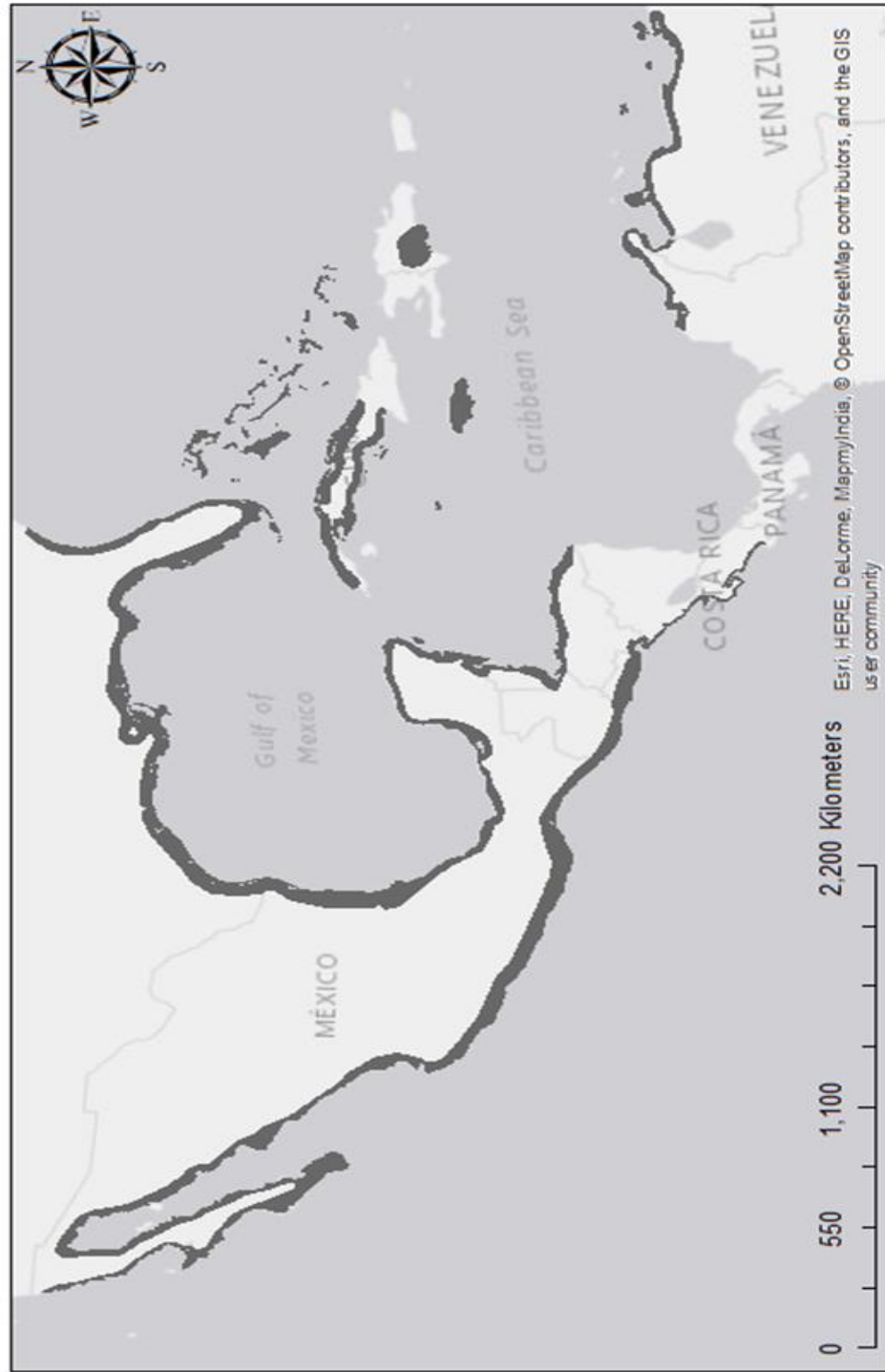


Figure 1: Geographic range of the reddish egret (*Egretta rufescens*)

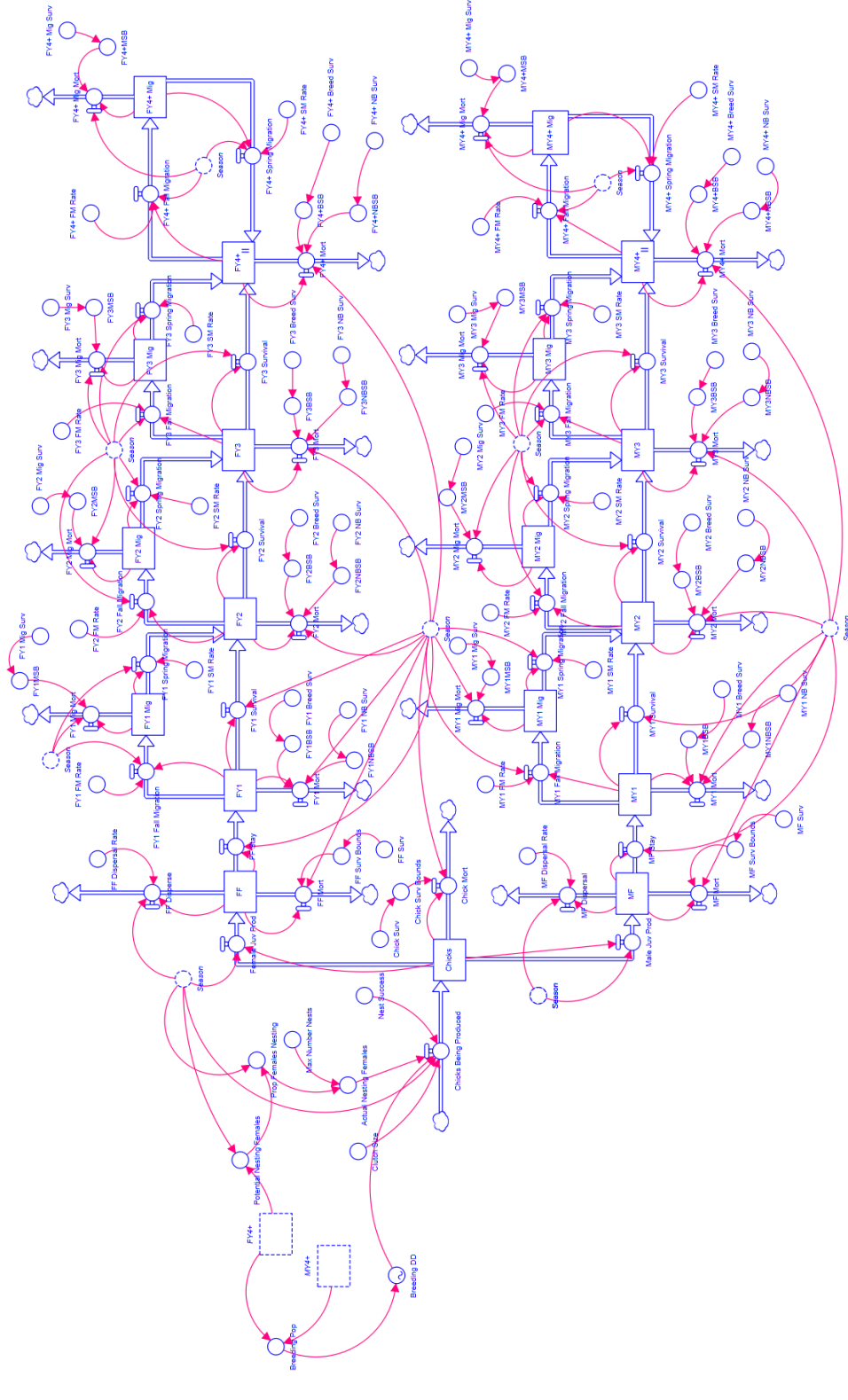


Figure 2: Stella® conceptual model diagram for the Texas *E. rufescens* population

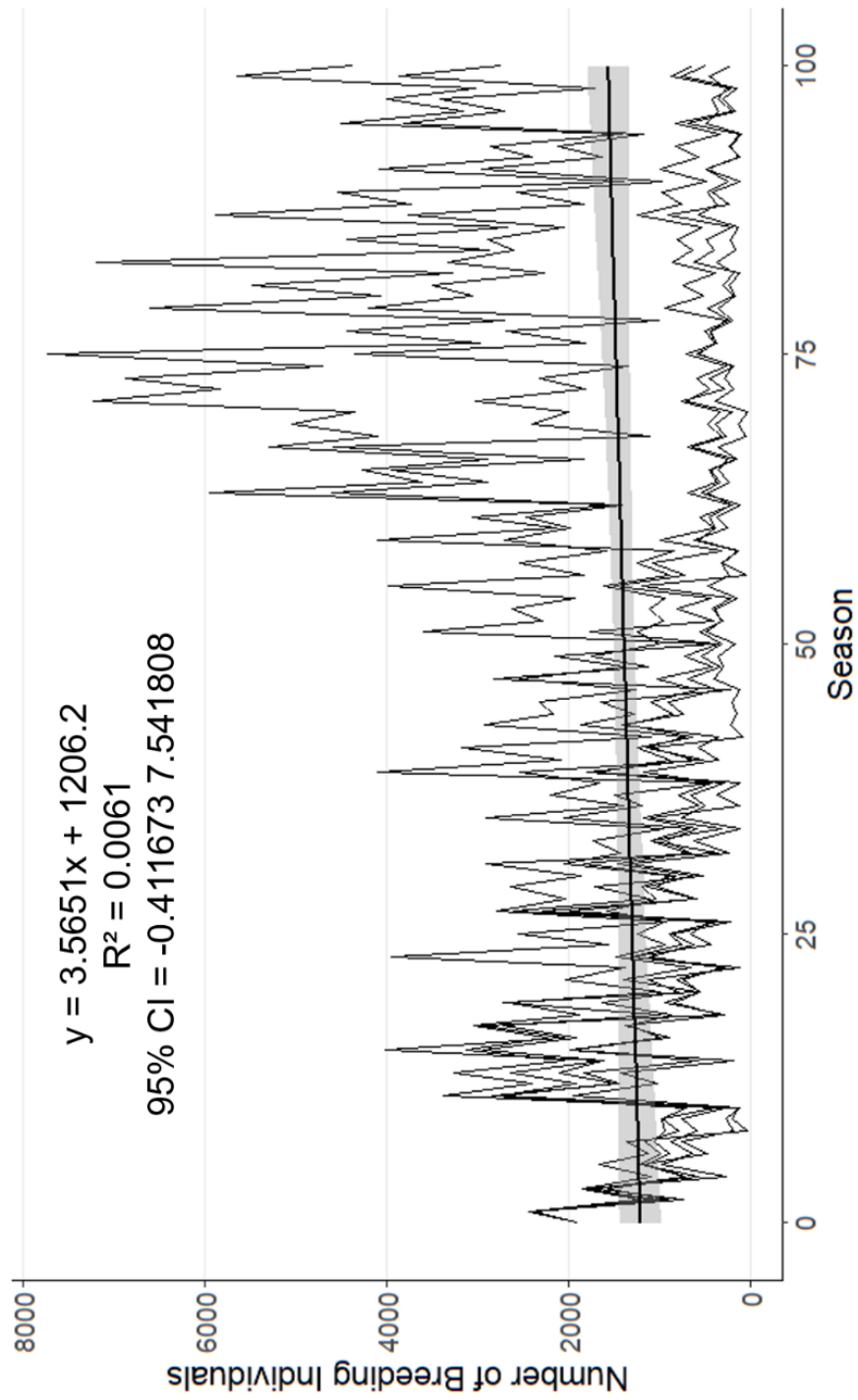


Figure 3: Population projections of 5 randomly selected Texas *E. rufescens* breeding population simulations of 100 seasons

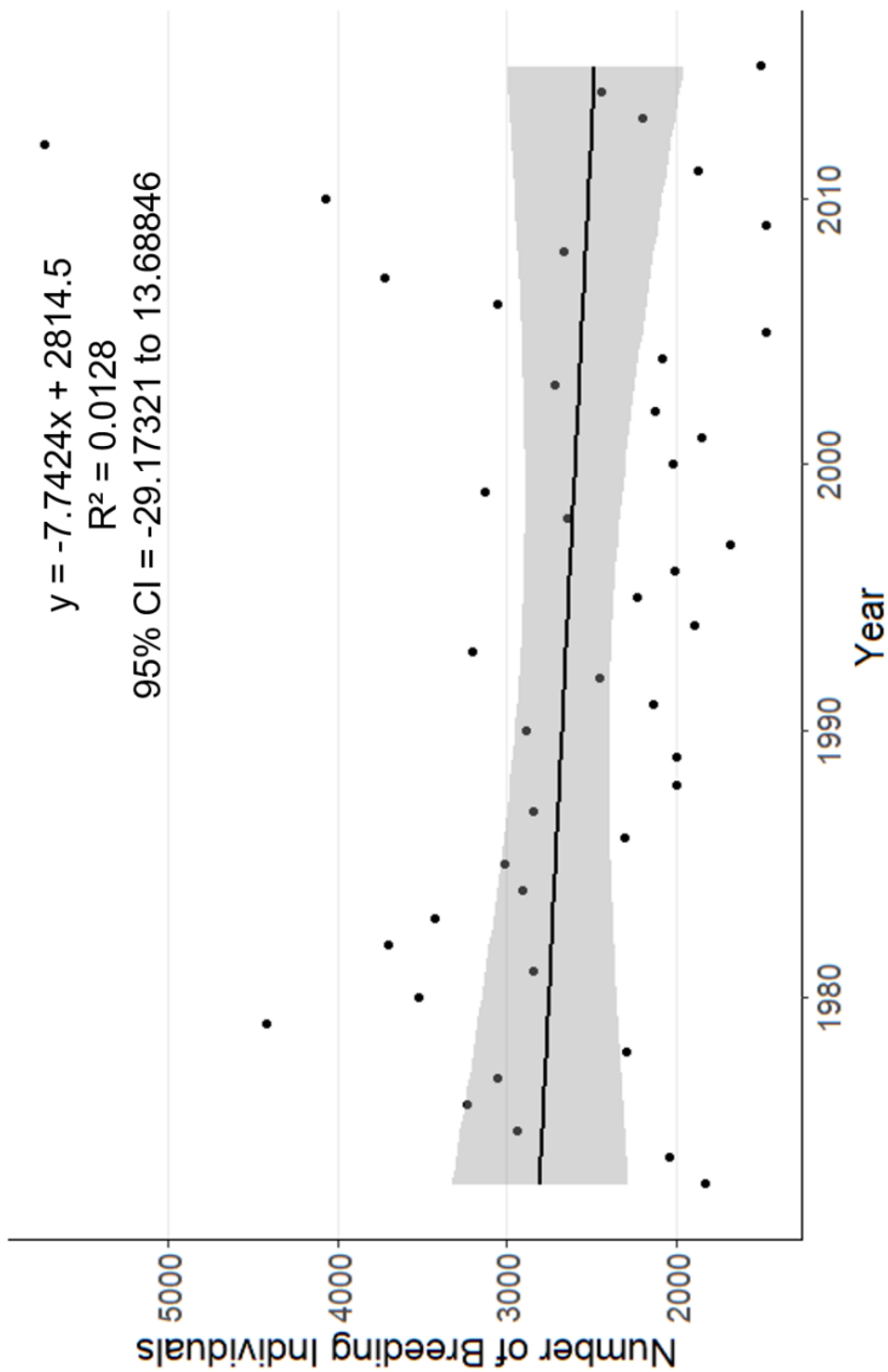


Figure 4: Breeding population trend for *E. rufescens* in Texas based on TCWS annual survey data (1973-2015)

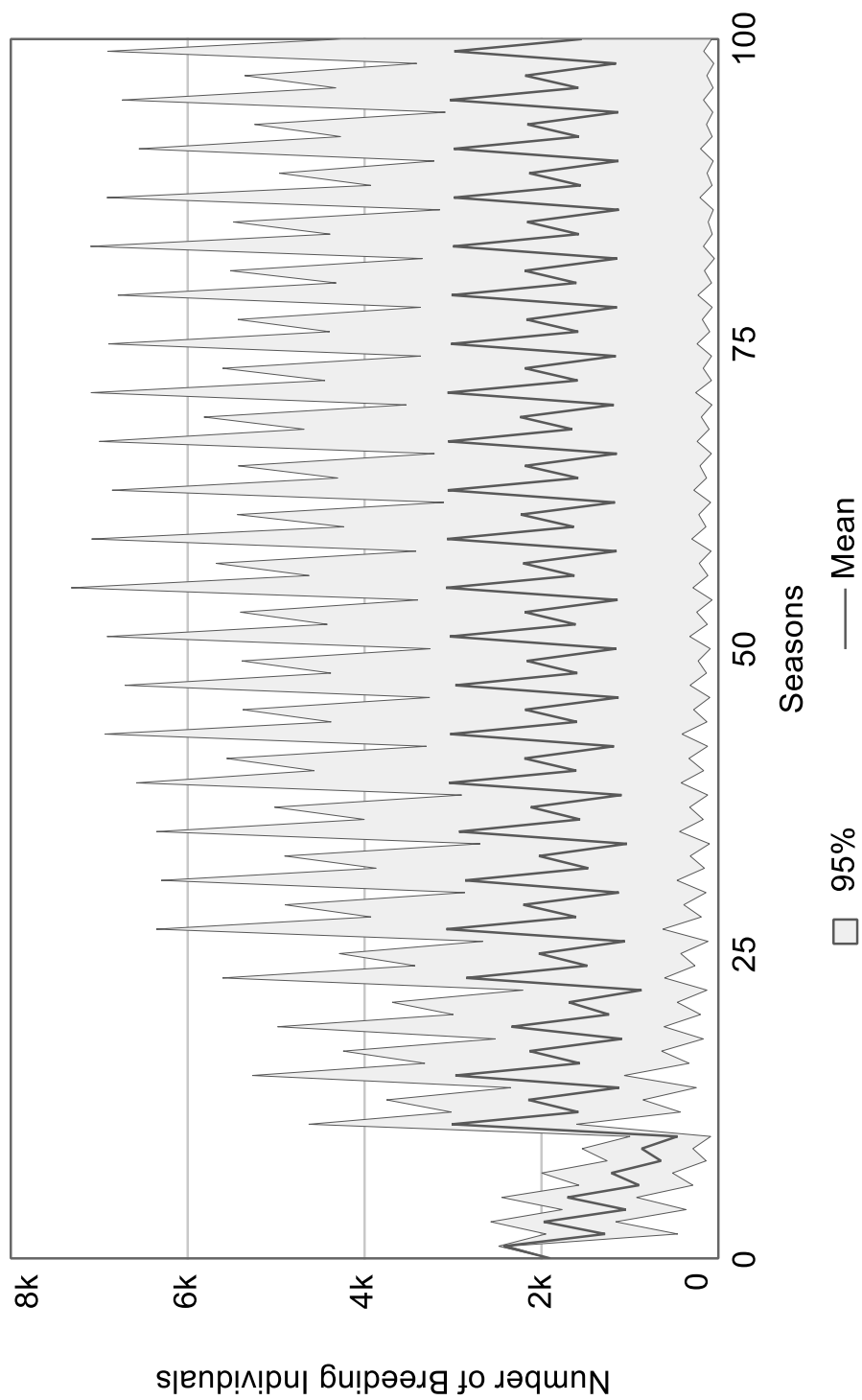


Figure 5: Mean projected population trend for the Texas population of *E. rufescens* over the next 50 years. Solid line represents the simulation mean outcome of 1,579 breeding individuals ($\pm 1,239$; 95% CI 0-3,393)

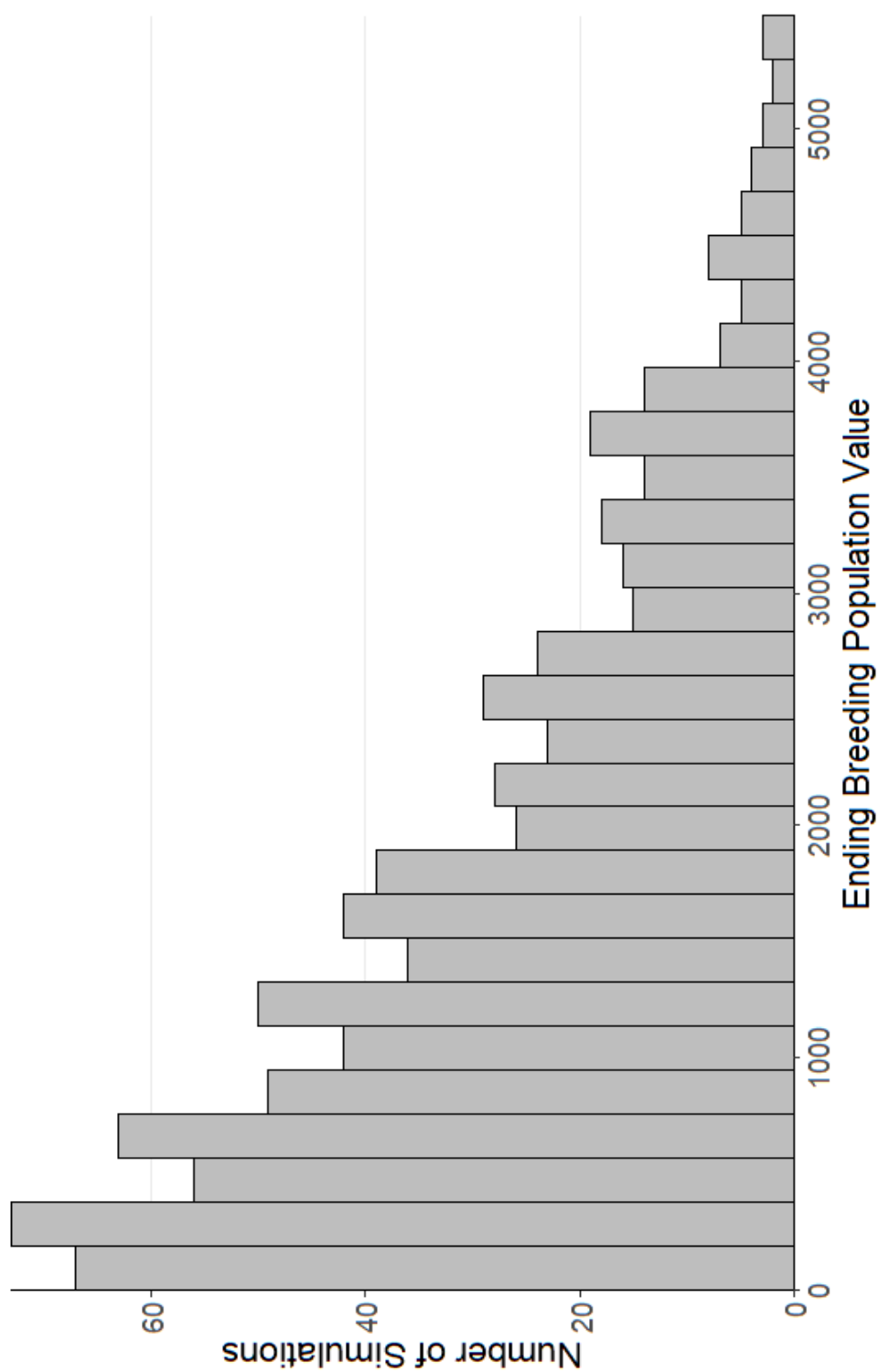


Figure 6: Distribution of simulated breeding population outcomes for the Texas population of *E. rufescens* (n = 780 simulations)

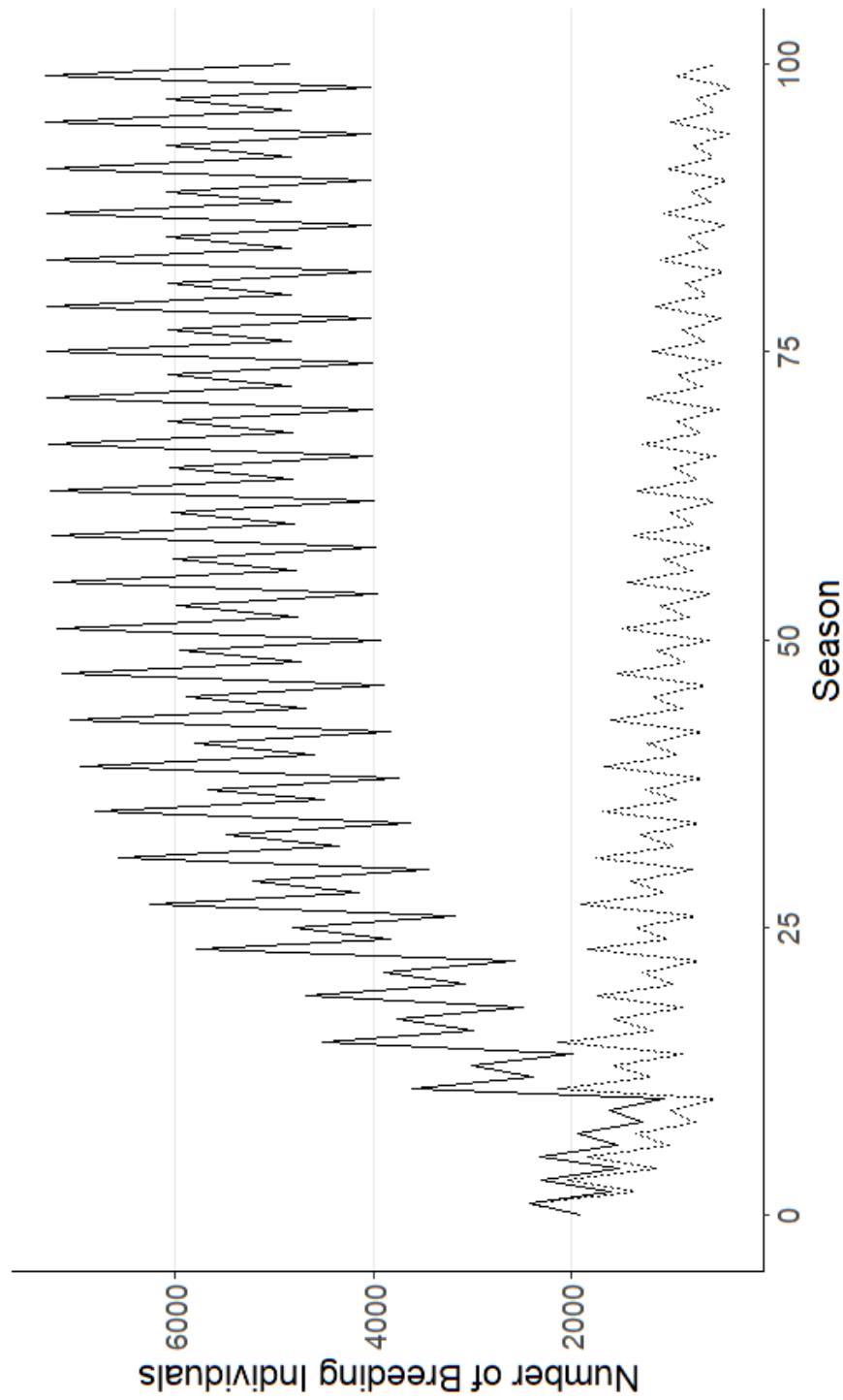


Figure 7: Projected Texas *E. rufescens* breeding population trend before and after simulated management actions focusing on increasing non-breeding survival. Solid line represents the projection after simulated management actions, dashed line represents the projection prior to management actions

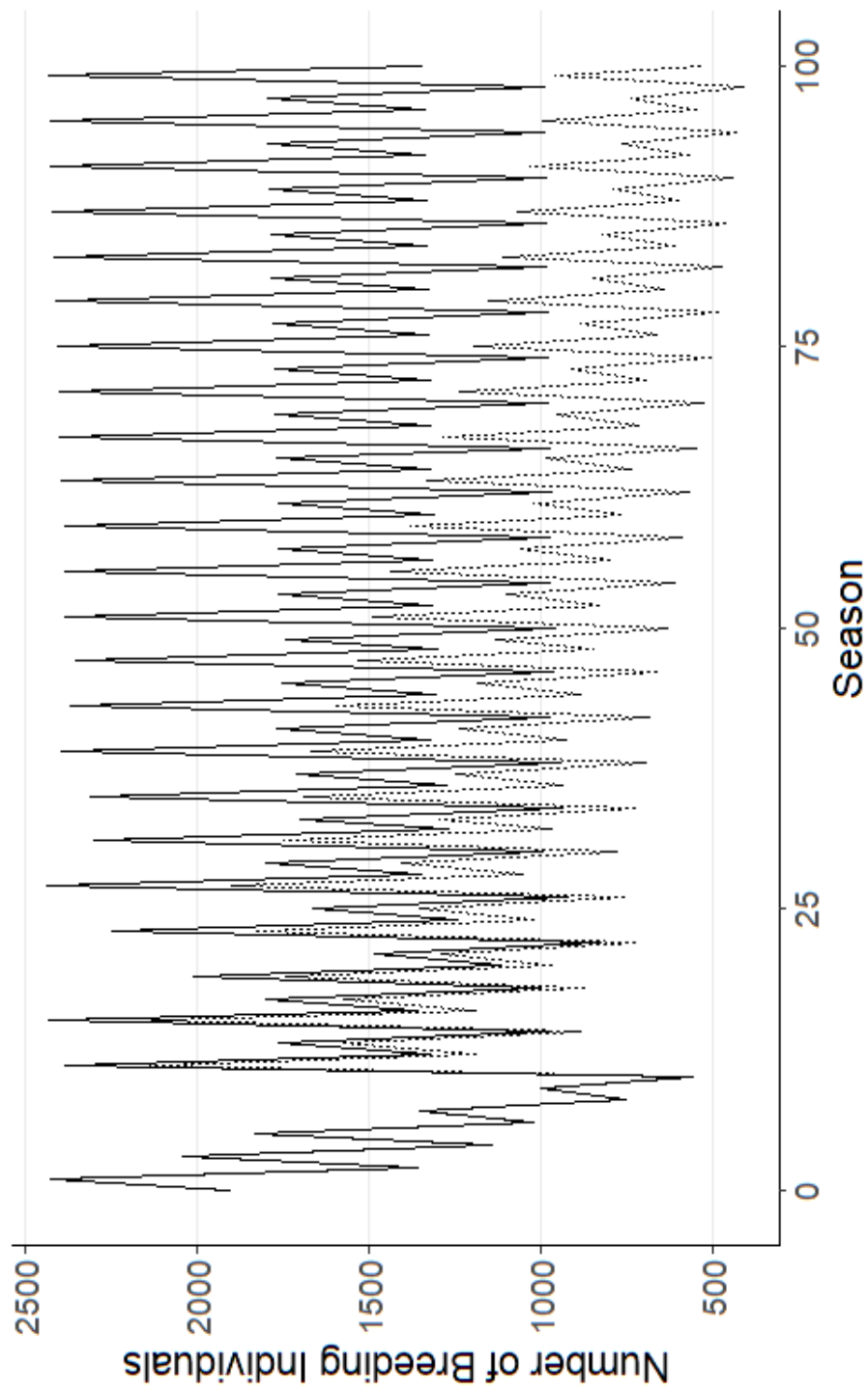


Figure 8: Projected Texas *E. rufescens* breeding population trend before and after simulated management actions focusing on increasing nest success. Solid line represents the projection after simulated management actions, dashed line represents the projection prior to management actions

APPENDIX

Parameter	Definition	Quantitative Model Definition	Source	Sample Size (n)
<i>Actual Nesting Females</i>	Actual number of females nesting during breeding season.	IF (Potential_Nesting_Females > Max_Number_Nests) THEN Max_Number_Nests ELSE Potential_Nesting_Females		
<i>Breeding DD</i>	Density dependent factor based on breeding population size.	$y = 0.8809936 + (1 - 0.8809936)/(1 + (x/2726.416)^{102.737})$		
<i>Breeding Pop</i>	Total number of breeding Y4+ birds	(FY4+) + (MY4+)		
<i>Chick Mort</i>	Number of chicks dying during the breeding season at each time step.	IF Season=1 THEN Chicks*(1-Chick_Surv) ELSE 0		
<i>Chick Surv</i>	Number of chicks surviving to become juveniles during each time step.	0.25 (SD \pm 1.75)	Unpublished data	628
<i>Chick Surv Bounds</i>	Bounds <i>Chick Surv</i> between 0.00 and 1.00	IF (Chick_Surv<0) THEN 0 ELSE IF (Chick_Surv>1) THEN 1 ELSE (Chick_Surv)		
<i>Chicks</i>	Number of chicks produced during the breeding season time step.	0		

<i>Chicks Being Produced</i>	Transfers the number of chicks produced during the breeding season to the stock variable "Chicks" at the beginning of the breeding season.	IF Season=1 THEN (Nesting_Females*Clutch_Size*Nest_Success) ELSE 0		
<i>Clutch Size</i>	Number of eggs laid per breeding female per season.	3.29 (SD \pm 0.696)	Holderby <i>et al.</i> 2012	194
<i>Female Juv Prod</i>	Transfers the number of female juveniles being produced during the breeding season to the stock variable <i>FF</i> .	IF Season=1 THEN Chicks ELSE 0		
<i>FF</i>	Number of female fledglings at the beginning of each time step.	0		
<i>FF Dispersal Rate</i>	Dispersal rate of female fledglings out of the population.	0.04 (SD \pm 0.04)	Geary <i>et al.</i> 2015	25
<i>FF Disperse</i>	Number of female fledglings that disperse out of the population.	IF Season=1 THEN (FF*FF_Dispersal_Rate) ELSE 0		

<i>FF Mort</i>	Number of female fledglings dying during the breeding season.	IF Season=1 THEN FF*(1-FF_Surv) ELSE 0		
<i>FF Stay</i>	Transfers the number of surviving female fledglings that do not disperse out of the population to the stock "FY1"	IF Season=1 THEN FF ELSE 0		
<i>FF Surv</i>	Survival rate of female fledglings.	0.76 (SD \pm 0.083)	Geary <i>et al.</i> 2015	25
<i>FF Surv Bounds</i>	Bounds <i>FF Surv</i> between 0.00 and 1.00	IF (FF_Surv <0) THEN 0 ELSE IF (FF_Surv >1) THEN 1 ELSE (FF_Surv)		
<i>FYI</i>	Number of surviving female fledglings (juveniles) in the population at the end of the breeding season.	242		
<i>FY1 Breed Surv</i>	Survival rate of first-year female juvenile during the breeding season.	0.53 (SD \pm 0.113)	Geary <i>et al.</i> 2015	25
<i>FY1BSB</i>	Bounds <i>FY1 Breed Surv</i> between 0.00 and 1.00	IF (FY1_Breed_Surv <0) THEN 0 ELSE IF (FY1_Breed_Surv>1) THEN 1 ELSE (FY1_Breed_Surv)		

<i>FY1 Fall Migration</i>	Transfers the number of first-year females that migrate south in the fall to the stock <i>FY1 Mig</i>	FY1*FY1_FM_Rate		
<i>FY1 FM Rate</i>	Fall migration rate of first-year females.	0.125 (SD \pm 0.063)	Koczur <i>et al.</i> 2017	16
<i>FY1 Mig</i>	Number of first-year female migrants.	30		
<i>FY1 Mig Mort</i>	Number of first-year female migrants dying.	IF Season=2 THEN (FY1_Mig*(1-FY1_Mig_Surv)) ELSE 0		
<i>FY1MSB</i>	Bounds <i>FY1 Mig Mort</i> between 0.00 and 1.00	IF (FY1_Mig_Surv <0) THEN 0 ELSE IF (FY1_Mig_Surv>1) THEN 1 ELSE (FY1_Mig_Surv)		
<i>FY1 Mig Surv</i>	Survival rate of first-year female migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
<i>FY1 Mort</i>	Number of first-year female juveniles dying at the end of the breeding season.	IF Season=1 THEN FY1*(1-FY1_Surv) ELSE 0		
<i>FY1 NB Surv</i>	Survival rate of first-year female juvenile during the non-breeding season.	0.53 (SD \pm 0.113)	Geary <i>et al.</i> 2015	25
<i>FY1NBSB</i>	Bounds <i>FY1 NB Surv</i> between 0.00 and 1.00	IF (FY1_NB_Surv <0) THEN 0 ELSE IF (FY1_NB_Surv >1) THEN 1 ELSE (FY1_NB_Surv)		

<i>FY1 SM Rate</i>	Spring migration rate of first-year females.	1		
<i>FY1 Spring Migration</i>	Transfers the number of first-year females that immigrate to the stock <i>FY2</i>	FY1_Mig*FY1_SM_Rate		
<i>FY1 Survival</i>	Transfers the number of surviving first-year female at the end of the breeding season to the stock <i>FY2</i> .	IF Season=1 THEN FY1 ELSE 0		
<i>FY2</i>	Number of second year females at the beginning of each time step.	136		
<i>FY2 Breed Surv</i>	Survival rate of second year females during the breeding season.	0.945 (SD \pm 0.66)	Koczur <i>et al.</i> 2017	591
<i>FY2BSB</i>	Bounds <i>FY2 Breed Surv</i> between 0.00 and 1.00	IF (FY2_Breed_Surv <0) THEN 0 ELSE IF (FY2_Breed_Surv>1) THEN 1 ELSE (FY2_Breed_Surv)		
<i>FY2 Fall Migration</i>	Transfers the number of second year females that migrate south in the fall to the stock <i>FY2 Mig</i>	FY2_FM_Rate*FY2		
<i>FY2 FM Rate</i>	Fall migration rate of	0.125 (SD \pm 0.063)	Koczur <i>et al.</i> 2017	16

	second year females.			
<i>FY2 Mig</i>	Number of second year females that migrate.	17		
<i>FY2 Mig Mort</i>	Number of second year female migrants dying.	$FY2_Mig * (1 - FY2_Mig_Surv)$		
<i>FY2 Mig Surv</i>	Survival rate of second year female migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
<i>FY2MSB</i>	Bounds <i>FY2 Mig Surv</i> between 0.00 and 1.00	IF (FY2_Mig_Surv < 0) THEN 0 ELSE IF (FY2_Mig_Surv > 1) THEN 1 ELSE (FY2_Mig_Surv)		
<i>FY2 Mort</i>	Number of second year females dying during the breeding and non-breeding seasons.	IF Season=1 THEN $FY2 * (1 - FY2_Breed_Surv)$ ELSE IF Season=2 THEN $FY2 * (1 - FY2_NB_Surv)$ ELSE 0		
<i>FY2 NB Surv</i>	Survival rate of second year females during the non-breeding season.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
<i>FY2NBSB</i>	Bounds <i>FY2 NB Surv</i> between 0.00 and 1.00	IF (FY2_NB_Surv < 0) THEN 0 ELSE IF (FY2_NB_Surv > 1) THEN 1 ELSE (FY2_NB_Surv)		
<i>FY2 SM Rate</i>	Spring migration rate of second year females.	1		

<i>FY2 Spring Migration</i>	Transfers the number of second year females that migrate north in the spring to the stock <i>FY3</i>	FY2_Mig*FY2_SM_Rate		
<i>FY2 Survival</i>	Transfers the surviving second year females to the stock <i>FY3</i>	IF Season=1 THEN FY2 ELSE 0		
<i>FY3</i>	Number of third year females at the beginning of each time step.	100		
<i>FY3 Breed Surv</i>	Survival rate of third year females during the breeding season.	0.945 (SD \pm 0.66)	Koczur <i>et al.</i> 2017	591
<i>FY3BSB</i>	Bounds <i>FY3 Breed Surv</i> between 0.00 and 1.00	IF (FY3_Breed_Surv <0) THEN 0 ELSE IF (FY3_Breed_Surv>1) THEN 1 ELSE (FY3_Breed_Surv)		
<i>FY3 Fall Migration</i>	Transfers the number of third year females that emigrate to the stock <i>FY3 Mig</i>	FY3*FY3_FM_Rate		
<i>FY3 FM Rate</i>	Fall migration rate of third year females.	0.125 (SD \pm 0.063)	Koczur <i>et al.</i> 2017	16
<i>FY3 Mig</i>	Number of third year females that migrate.	12		
<i>FY3 Mig Mort</i>	Number of third year female	FY3_Mig*(1-FY3_Mig_Surv)		

	migrants dying.			
<i>FY3 Mig Surv</i>	Survival rate of third year female migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
<i>FY3MSB</i>	Bounds <i>FY3 Mig Surv</i> between 0.00 and 1.00	IF (FY3_Mig_Surv<0) THEN 0 ELSE IF (FY3_Mig_Surv>1) THEN 1 ELSE (FY3_Mig_Surv)		
<i>FY3 Mort</i>	Number of third year females dying during the breeding and non- breeding seasons.	IF Season=1 THEN FY3*(1-FY3_Breed_Surv) ELSE IF Season=2 THEN FY3*(1-FY3_NB_Surv) ELSE 0		
<i>FY3 NB Surv</i>	Survival rate of third year females during the non- breeding season.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
<i>FY3NBSB</i>	Bounds <i>FY3 NB Surv</i> between 0.00 and 1.00	IF (FY3_NB_Surv<0) THEN 0 ELSE IF (FY3_NB_Surv>1) THEN 1 ELSE (FY3_NB_Surv)		
<i>FY3 SM Rate</i>	Spring migration rate of third year females.	1		
<i>FY3 Spring Migration</i>	Transfers the number of third year females that immigrate to the stock <i>FY4+</i>	FY3_SM_Rate*FY3_Mig		
<i>FY3 Survival</i>	Transfers the surviving third year females to the stock <i>FY4+</i>	IF Season=1 THEN FY3 ELSE 0		

<i>FY4+</i>	Number of fourth year and older females at the beginning of each time step.	950		
<i>FY4+ Breed Surv</i>	Survival rate of fourth year and older females during the breeding season.	0.945 (SD \pm 0.66)	Koczur <i>et al.</i> 2017	591
<i>FY4+BSB</i>	Bounds <i>FY4+ Breed Surv</i> between 0.00 and 1.00	IF (FY4+_Breed_Surv<0) THEN 0 ELSE IF (FY4+_Breed_Surv>1) THEN 1 ELSE (FY4+_Breed_Surv)		
<i>FY4+ Fall Migration</i>	Transfers the number of fourth year and older females that emigrate to the stock <i>FY4+ Mig</i>	FY4+_FM_Rate*FY4+		
<i>FY4+ FM Rate</i>	Fall migration rate of fourth year and older females.	0.125 (SD \pm 0.063)	Koczur <i>et al.</i> 2017	16
<i>FY4+ Mig</i>	Number of fourth year and older females that migrate.	120		
<i>FY4+ Mig Mort</i>	Number of fourth year and older female migrants dying.	FY4+_Mig*(1-FY4+_Mig_Surv)		
<i>FY4+ Mig Surv</i>	Survival rate of fourth year and older female migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591

<i>FY4+MSB</i>	Bounds <i>FY4+ Mig Surv</i> between 0.00 and 1.00	IF (FY4+_Mig_Surv<0) THEN 0 ELSE IF (FY4+_Mig_Surv>1) THEN 1 ELSE (FY4+_Mig_Surv)		
<i>FY4+ Mort</i>	Number of fourth year and older females dying during the breeding and non- breeding seasons.	IF Season=1 THEN FY4+*(1-FY4+_Breed_Surv) ELSE IF Season=2 THEN FY4+*(1-FY4+_NB_Surv) ELSE 0		
<i>FY4+ NB Surv</i>	Survival rate of fourth year and older females during the non- breeding season.	0.7697 (SD \pm 1.39)	Koczur <i>et</i> <i>al.</i> 2017	591
<i>FY4+NBSB</i>	Bounds <i>FY4+ NB Surv</i> between 0.00 and 1.00	IF (FY4+_NB_Surv<0) THEN 0 ELSE IF (FY4+_NB_Surv>1) THEN 1 ELSE (FY4+_NB_Surv)		
<i>FY4+ SM Rate</i>	Spring migration rate of fourth year and older females.	1		
<i>FY4+ Spring Migration</i>	Transfers the number of fourth year and older females that immigrate to the stock <i>FY4+</i>	<i>FY4+_SM_Rate*FY4+_Mig</i>		

<i>Male Juv Prod</i>	Transfers the number of male juveniles being produced during the breeding season to the stock variable <i>MF</i> .	IF Season=1 THEN <i>Chicks</i> ELSE 0		
<i>Max Number Nests</i>	Sum of average number of nests as density dependent factor for each colony.	950		
<i>MF</i>	Number of male fledglings at the beginning of each time step.	0		
<i>MF Dispersal Rate</i>	Dispersal rate of male fledglings out of the population.	0.08 (SD \pm 0.04)	Geary <i>et al.</i> 2015	25
<i>MF Disperse</i>	Number of male fledglings that disperse out of the population	IF Season=1 THEN (<i>MF</i> * <i>MF_Dispersal_Rate</i>) ELSE 0		
<i>MF Mort</i>	Number of male fledglings dying during the breeding season.	IF Season=1 THEN <i>MF</i> *(1- <i>MF_Surv</i>) ELSE 0		
<i>MF Stay</i>	Number of male fledglings that do not disperse out of the population.	IF Season=1 THEN <i>MF</i> ELSE 0		

<i>MF Surv</i>	Survival rate of male fledglings.	0.76 (SD \pm 0.083)	Geary <i>et al.</i> 2015	25
<i>MF_SurvBounds</i>	Bounds <i>MF Surv</i> between 0.00 and 1.00	IF (MF_Surv <0) THEN 0 ELSE IF (MF_Surv >1) THEN 1 ELSE (MF_Surv)		
<i>MYI</i>	Number of surviving male fledglings (juveniles) in the population at the end of the breeding season.	232		
<i>MYI Breed Surv</i>	Survival rate of first-year male juveniles during the breeding season.	0.53 (SD \pm 0.113)	Geary <i>et al.</i> 2015	25
<i>MYIBSB</i>	Bounds <i>MYI Breed Surv</i> between 0.00 and 1.00	IF (MY1_Breed_Surv <0) THEN 0 ELSE IF (MY1_Breed_Surv >1) THEN 1 ELSE (MY1_Breed_Surv)		
<i>MYI Fall Migration</i>	Transfers the number of first-year males that migrate south in the fall to the stock <i>MYI Mig</i>	<i>MYI</i> * <i>MYI_FM_Rate</i>		
<i>MYI FM Rate</i>	Fall migration rate of first-year males.	0.2857 (SD \pm 0.071)	Koczur <i>et al.</i> 2017	14
<i>MYI Mig</i>	Number of first-year males migrating.	66		
<i>MYI Mig Mort</i>	Number of first-year male migrants dying.	<i>MYI_Mig</i> * (1 - <i>MYI_Mig_Surv</i>)		

MY1 Mig Surv	Survival rate of first-year male migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
MY1MSB	Bounds <i>MY1 Mig Surv</i> between 0.00 and 1.00	IF (MY1_Mig_Surv <0) THEN 0 ELSE IF (MY1_Mig_Surv >1) THEN 1 ELSE (MY1_Mig_Surv)		
MY1 Mort	Number of first-year male juveniles dying at the end of the breeding season.	IF Season=1 THEN <i>MY1</i> *(1- <i>MY1_Surv</i>) ELSE 0		
MY1 NB Surv	Survival rate of first-year male juveniles during the breeding season.	0.53 (SD \pm 0.113)	Geary <i>et al.</i> 2015	25
MY1NBSB	Bounds <i>MY1 NB Surv</i> between 0.00 and 1.00	IF (MY1_NB_Surv <0) THEN 0 ELSE IF (MY1_NB_Surv >1) THEN 1 ELSE (MY1_NB_Surv)		
MY1 SM Rate	Spring migration rate of first-year males.	1		
MY1 Spring Migration	Transfers the number of first-year males that immigrate to the stock <i>MY2</i> .	<i>MY1_Mig</i> * <i>MY1_SM_Rate</i>		
MY1 Survival	Transfers the number of surviving male juveniles at the end of the breeding season to the stock <i>MY2</i> .	IF Season=1 THEN <i>MY1</i> ELSE 0		

MY2	Number of second year males at the beginning of each time step.	139		
MY2 Breed Surv	Survival rate of second year males during the breeding season.	0.945 (SD \pm 0.66)	Koczur <i>et al.</i> 2017	591
MY2BSB	Bounds <i>MY2 Breed Surv</i> between 0.00 and 1.00	IF (MY2_Breed_Surv<0) THEN 0 ELSE IF (MY2_Breed_Surv >1) THEN 1 ELSE (MY2_Breed_Surv)		
MY2 Fall Migration	Transfers the number of second year males that migrate south in the fall to the stock <i>MY2 Mig</i>	<i>MY2*MY2_FM_Rate</i>		
MY2 FM Rate	Fall migration rate of second year males.	0.2857 (SD \pm 0.071)	Koczur <i>et al.</i> 2017	14
MY2 Mig	Number of second year males that migrate.	40		
MY2 Mig Mort	Number of second year male migrants dying.	<i>MY2_Mig*(1-MY2_Mig_Surv)</i>		
MY2 Mig Surv	Survival rate of second year male migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
MY2MSB	Bounds <i>MY2 Mig Surv</i> between 0.00 and 1.00	IF (MY2_Mig_Surv<0) THEN 0 ELSE IF (MY2_Mig_Surv>1) THEN 1 ELSE (MY2_Mig_Surv)		

MY2 Mort	Number of second year males dying during the breeding and non-breeding seasons.	IF Season=1 THEN MY2*(1-MY2_Breed_Surv) ELSE IF Season=2 THEN MY2*(1-MY2_NB_Surv) ELSE 0		
MY2 NB Surv	Survival rate of second year males during the non-breeding season.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
MY2NBSB	Bounds MY2 NB Surv between 0.00 and 1.00	IF (MY2_NB_Surv<0) THEN 0 ELSE IF (MY2_NB_Surv>1) THEN 1 ELSE (MY2_NB_Surv)		
MY2 SM Rate	Spring migration rate of second year males.	1		
MY2 Spring Migration	Transfers the number of second year males that immigrate to the stock MY3.	MY2_SM_Rate*MY2_Mig		
MY2 Survival	Transfers the surviving second year males to the stock MY3	IF Season=1 THEN MY2 ELSE 0		
MY3	Number of third year males at the beginning of each time step.	103		
MY3 Breed Surv	Survival rate of third year males during the breeding season.	0.945 (SD \pm 0.66)	Koczur <i>et al.</i> 2017	591

MY3BSB	Bounds <i>MY3 Breed Surv</i> between 0.00 and 1.00	IF (MY3_Breed_Surv<0) THEN 0 ELSE IF (MY3_Breed_Surv>1) THEN 1 ELSE (MY3_Breed_Surv)		
MY3 Fall Migration	Transfers the number of third year males that emigrate to the stock <i>MY3 Mig</i>	<i>MY3_FM_Rate*MY3</i>		
MY3 FM Rate	Fall migration rate of third year males.	0.2857 (SD \pm 0.071)	Koczur <i>et al.</i> 2017	14
MY3 Mig	Number of third year males that migrate.	29		
MY3 Mig Mort	Number of third year male migrants dying.	<i>MY3_Mig*(1-MY3_Mig_Surv)</i>		
MY3 Mig Surv	Survival rate of third year male migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
MY3MSB	Bounds <i>MY3 Mig Surv</i> between 0.00 and 1.00	IF (MY3_Mig_Surv<0) THEN 0 ELSE IF (MY3_Mig_Surv>1) THEN 1 ELSE (MY3_Mig_Surv)		
MY3 Mort	Number of third year males dying during the breeding and non- breeding seasons.	IF Season=1 THEN <i>MY3*(1-MY3_Breed_Surv)</i> ELSE IF Season=2 THEN <i>MY3*(1-MY3_NB_Surv)</i> ELSE 0		
MY3 NB Surv	Survival rate of third year males during the non- breeding season.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591

MY3NBSB	Bounds <i>MY3 NB Surv</i> between 0.00 and 1.00	IF (MY3_NB_Surv<0) THEN 0 ELSE IF (MY3_NB_Surv>1) THEN 1 ELSE (MY3_NB_Surv)		
MY3 SM Rate	Spring Migration rate of third year males.	1		
MY3 Spring Migration	Transfers the number of third year males that immigrate to the stock <i>MY4+</i>	<i>MY3_SM_Rate*MY3_Mig</i>		
MY3 Survival	Transfers the surviving third year males to the stock <i>MY4+</i>	IF Season=1 THEN <i>MY3</i> ELSE 0		
MY4+	Number of fourth year and older males at the beginning of each time step.	950		
MY4+ Breed Surv	Survival rate of fourth year and older males during the breeding season.	0.945 (SD ± 0.66)	Koczur <i>et al.</i> 2017	591
MY4+BSB	Bounds <i>MY4+ Breed Surv</i> between 0.00 and 1.00	IF (MY4+_Breed_Surv<0) THEN 0 ELSE IF (MY4+_Breed_Surv>1) THEN 1 ELSE (MY4+_Breed_Surv)		
MY4+ Fall Migration	Transfers the number of fourth year and older males that emigrate to the stock <i>MY4+ Mig</i>	<i>MY4+_FM_Rate*MY4+</i>		

MY4+ FM Rate	Fall migration rate of fourth year and older males.	0.2857 (SD \pm 0.071)	Koczur <i>et al.</i> 2017	14
MY4+ Mig	Number of fourth year and older males that migrate.	270		
MY4+ Mig Mort	Number of fourth year and older male migrants dying.	$MY4+_{Mig} * (1 - MY4+_{Mig_Surv})$		
MY4+ Mig Surv	Survival rate of fourth year and older male migrants.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
MY4+MSB	Bounds $MY4+_{Mig_Surv}$ between 0.00 and 1.00	IF ($MY4+_{Mig_Surv} < 0$) THEN 0 ELSE IF ($MY4+_{Mig_Surv} > 1$) THEN 1 ELSE ($MY4+_{Mig_Surv}$)		
MY4+ Mort	Number of fourth year and older males dying during the breeding and non-breeding seasons.	IF Season=1 THEN $MY4+ * (1 - MY4+_{Breed_Surv})$ ELSE IF Season=2 THEN $MY4+ * (1 - MY4+_{NB_Surv})$ ELSE 0		
MY4+ NB Surv	Survival rate of fourth year and older males during the non-breeding season.	0.7697 (SD \pm 1.39)	Koczur <i>et al.</i> 2017	591
MY4+NBSB	Bounds $MY4+_{NB_Surv}$ between 0.00 and 1.00	IF ($MY4+_{NB_Surv} < 0$) THEN 0 ELSE IF ($MY4+_{NB_Surv} > 1$) THEN 1 ELSE ($MY4+_{NB_Surv}$)		

<i>MY4+ SM Rate</i>	Spring migration rate of fourth year and older males.	1		
<i>MY4+ Spring Migration</i>	Transfers the number of fourth year and older males that immigrate to the stock <i>MY4+</i>	$MY4+_{SM_Rate} * MY4+_{Mig}$		
<i>Nest Success</i>	Number of nests that successfully fledged young out of the total number of nests laid at the beginning of each time step.	0.851 (SD \pm 0.58)	Holderby <i>et al.</i> 2012	117
<i>Nesting Females</i>	Number of 4+ year old females nesting at each time step.	IF Season=1 THEN (<i>Female_Y4+*Prop_female_nest</i>) ELSE 0		
<i>Potential Nesting Females</i>	Number of females potentially nesting during breeding season.	IF Season=1 THEN <i>FY4+</i> ELSE 0		
<i>Prop female nest</i>	The proportion of 4+ year old females that are breeding at the beginning of each time step.	IF Season =1 THEN (0.95*Potential_Nesting_Females) ELSE 0		
<i>Season</i>	The annual life-cycle of reddish egrets	1=Breeding Season (March-August) and 2=Non-Breeding Season (September-April).		

broken into
two periods.

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