Mathematical Modeling in Ecology: Simulating the Reintroduction of the Extinct Passenger Pigeon (*Ectopistes migratorius*)

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Abstract

The Passenger Pigeon (*Ectopistes migratorius*) was an iconic species of bird in eastern North America that comprised 25-40% of North American avifauna. Passenger Pigeons went extinct in 1914 due to excessive hunting over the previous 50 years. Current research aims to de-extinct the Passenger Pigeon and someday release the species into its historic range. To determine under which conditions a Passenger Pigeon could survive a reintroduction into a natural habitat, we used two types of models. First, we used a system of delay differential equations to explore the relationship between the young pigeon, adult pigeon, nest predator, and raptor populations. The model incorporates logistic population growth, an Allee effect, and a Holling Type III functional response. Next, we developed a spatially explicit, agent-based model to simulate the population dynamics of the Passenger Pigeon in a number of present-day forest environments. The model incorporates the following stochastic processes: varying availability of food sources, reproduction, and natural death of the Passenger Pigeon. Bio-energetics, tree distributions, and other ecological values were obtained from literature. Results from our simulations suggest that the Passenger Pigeon could survive a reintroduction into a natural environment.

Contents

1 Introduction

The Passenger Pigeon (*Ectopistes migratorius*) was an iconic bird species native to eastern North America. Before its extinction, the Passenger Pigeon accounted for approximately 25-40% of the entire North American avifauna. The Passenger Pigeon was a migratory species and was known to travel in flocks numbering in the billions. Accounts describe Passenger Pigeon flocks eclipsing the sun for hours, or even days, at a time [13].

However, humans hunted the Passenger Pigeon unsustainably throughout the 1800s. Every stage of the Passenger Pigeon's life cycle was interrupted. The trapping and shooting of pigeons and the disruption of the nesting sites resulted in rapid population decline [4].

Along with excessive hunting, deforestation in eastern North American played a key role in the Passenger Pigeon's extinction. As settlement into the area increased, the land was transformed from dense forests to cropland. This land transformation resulted in fragmented habitats and reduced food availability for the Passenger Pigeon. The lack of nesting grounds and food sources combined with overhunting led to a severe population reduction.

During the deterioration of the Passenger Pigeon population, a group of pigeons was taken into captivity and studied in an attempt to preserve the species. The last surviving Passenger Pigeon, named Martha, was a member of this group. The species officially went extinct in 1914 when she died in the Cincinnati Zoo [13].

In 2003, the Great Comeback became one of the first de-extinction projects in the world. The goal of this movement is to restore the Passenger Pigeon and someday release it back into the wild [17]. DNA was recently obtained from a Passenger Pigeon and sequenced. From the sequence, geneticists have identified the Band-tailed Pigeon *(Patagioenas fasciata)* as the Passenger Pigeon's closest living relative [11]. Through future scientific advancements combined with current genetic information, it is possible to engineer a viable Passenger Pigeon and release it into a natural habitat.

The de-extinction of the Passenger Pigeon could have many ecological benefits on the environment. The Passenger Pigeon was once a keynote species in eastern North America. Not only would de-extinction increase biodiversity by returning a once prominent species into its native habitat, but it could also be a stepping stone for other de-extinction projects. The Passenger Pigeon is the perfect candidate to raise extinction awareness and demonstrate the effects humans can have on an ecosystem. Human interference led to the Passenger Pigeon's extinction, and de-extinction is a way to remedy the damage done to both this species and the environment as a whole. The Great Comeback serves to not only bring back an iconic figure in nature, but also to advance awareness of extinction prevention in an effort to preserve biodiversity in the future.

The de-extinction process is both expensive and time-consuming. As of April 15, 2015, scientists are now just beginning to engineer Passenger Pigeon mutations into living pigeons. Through the use of mathematical modeling, researchers can begin to understand how the Passenger Pigeon may interact with a present-day environment before the pigeon has been created. Initially, we used a system of differential equations to model Passenger Pigeon dynamics. However, agent-based models are better suited to examine the success of a Passenger Pigeon reintroduction under varying environmental conditions.

Agent-based models have been used extensively in ecology to study population dynamics and species relationships [5] To simulate a Passenger Pigeon reintroduction, we constructed a spatially explicit, stochastic, agent-based model using the software NetLogo. Agent-based modeling is a technique that considers the components of a system and displays emergent properties from the interactions within the system [9]. Each component in the model has individual objectives that allow it to interact with and respond to the changing environment. In this paper, we present our modeling methods and the results obtained from this model.

2 Differential Equations Modeling

2.1 ODE

We used the Lotka-Volterra model as a foundation for our future set of ordinary differential equations in order to capture predator-prey dynamics between the Passenger Pigeon and its predators. The classic Lotka-Volterra DE model is

$$\frac{dP_1}{dt} = \alpha P_1 - \beta P_2 \tag{1a}$$

$$\frac{dP_2}{dt} = -\gamma P_2 + \upsilon P_1 P_2. \tag{1b}$$

Here, $P_1(t)$ is the population of Passenger Pigeons at time t and $P_2(t)$ is the number of predators at time t.

Next, we incorporated logistic growth into this model for both Passenger Pigeons and Predators in order to simulate more realistic population growth:

$$\frac{dP_1}{dt} = \alpha P_1 \left(1 - \frac{P_1}{K_1}\right) - \beta P_2 \tag{2a}$$

$$\frac{dP_2}{dt} = -\gamma P_2 + \upsilon P_1 P_2 \left(1 - \frac{P_2}{K_2}\right) \tag{2b}$$

where K_1 is the carrying capacity of the prey population and K_2 is the carrying capacity of the predator population.

The next level of complexity added to the model describes different types of predators. We separate the predator populations to account for their differing behavior. Predators such as weasels, raccoons, and minks prey upon eggs and squabs (young pigeons), and birds of prey target adult pigeons. [13]

Separating the pigeon population into young and adult subpopulations requires considering the maturation of the young pigeons into adult pigeons. The ODE system now contains four equations:

$$\frac{dY}{dt} = \alpha_1 Y \left(1 - \frac{Y}{K_1}\right) - \mu Y - \beta_1 N \tag{3a}$$

$$\frac{dA}{dt} = \alpha_2 A \left(1 - \frac{A}{K_2}\right) + \mu Y - \beta_2 R \tag{3b}$$

$$\frac{dN}{dt} = -\gamma_1 N + \upsilon_1 Y N \left(1 - \frac{N}{K_3}\right) \tag{3c}$$

$$\frac{dR}{dt} = -\gamma_2 R + \upsilon_2 A R \left(1 - \frac{R}{K_4}\right). \tag{3d}$$

In this system, the nesting predators (N) attack the young pigeon population (Y) and the raptors (R) attack the adult pigeon population (A). This system is not independent since maturation of the young population is included.

The next modification to our model accounts for the Allee effect, which had a substantial impact on the population of the the Passenger Pigeon. The

Allee effect is the phenomenon in which small populations or populations with low densities suffer from negative growth [6]. Many factors play a role in determining the Allee parameter,or the population threshold at which the population will eventually reach extinction[7]. Examples of factors considered when determining the Allee parameter include ability to locate food sources, vulnerability to predators, and difficulty finding a mate.

The following system takes into account the Allee effect:

$$\frac{dY}{dt} = \alpha_1 Y \left(1 - \frac{Y}{K_1}\right)\left(\frac{Y}{\epsilon} - 1\right) - \mu Y - \beta_1 N \tag{4a}$$

$$\frac{dA}{dt} = \alpha_2 A \left(1 - \frac{A}{K_2}\right) + \mu Y - \beta_2 R \tag{4b}$$

$$\frac{dN}{dt} = -\gamma_1 N + \upsilon_1 Y N \left(1 - \frac{N}{K_3}\right) \tag{4c}$$

$$\frac{dR}{dt} = -\gamma_2 R + \upsilon_2 A R \left(1 - \frac{R}{K_4}\right) \tag{4d}$$

where ϵ is the Allee parameter.

The final factor we take into account for our system of ordinary differential equations is the Holling type for predation. We decided to use a Holling Type III functional response to describe predation upon the young and adult pigeons. Type III is used to simulate organisms with learning behavior and who will not utilize their prey below a threshold density [22].

When we include this in our system,our final ODE model is as follows:

$$\frac{dY}{dt} = \alpha A\left(1-\frac{A}{K_1}\right)\left(\frac{A}{\epsilon}-1\right) - \mu Y - N\left(\frac{\beta_1 Y^2}{1+\beta_1\psi_1 Y^2}\right) - \pi_1 Y \tag{5a}$$

$$\frac{dA}{dt} = \mu Y - R\left(\frac{\beta_2 A^2}{1+\beta_2\psi_2 A^2}\right) - \pi_2 A \tag{5b}$$

$$\frac{dN}{dt} = \lambda_1 N\left(1-\frac{N}{K_2}\right) + \gamma_1 Y N \tag{5c}$$

$$\frac{dR}{dt} = \lambda_2 R\left(1-\frac{R}{K_3}\right) + \gamma_2 R A. \tag{5d}$$

2.2 DDE

A delay differential equation (DDE) is similar to an ODE, but includes a time delay parameter. When modeling population dynamics, a time delay parameter can be used as gestational delay [19]. We consider the incubation period to be comparable to the gestational delay.

Our final model is a system of delay differential equations which takes into account the incubation period, τ. The system is as follows:

$$\frac{dY}{dt} = \alpha A\left(1-\frac{A}{K_1}\right)\left(\frac{A}{\epsilon}-1\right) - \mu Y(t-\tau) - N\left(\frac{\beta_1 Y^2}{1+\beta_1\psi_1 Y^2}\right) - \pi_1 Y \tag{6a}$$

$$\frac{dA}{dt} = \mu Y(t-\tau) - R\left(\frac{\beta_2 A^2}{1+\beta_2\psi_2 A^2}\right) - \pi_2 A \tag{6b}$$

$$\frac{dN}{dt} = \lambda_1 N\left(1-\frac{N}{K_2}\right) + \gamma_1 Y N \tag{6c}$$

$$\frac{dR}{dt} = \lambda_2 R\left(1-\frac{R}{K_3}\right) + \gamma_2 R A. \tag{6d}$$

The benefits to modeling with ODE and DDE systems are that interactions between populations are relatively easy to model, and qualitative analysis for population stability is accessible through numerical solutions. However, the system is deterministic, and we lack the data necessary to determine appropriate parameter values. Since we are modeling a reintroduction, it is important to include stochastic variability in order to better identify successful reintroduction scenarios.

2.3 Results

We used `MATLAB` to numerically solve our system of ODEs and DDEs. For the ODE system, we used the `ode45` solver. A plot of the output for one set of parameters and initial conditions is included in figure 1.

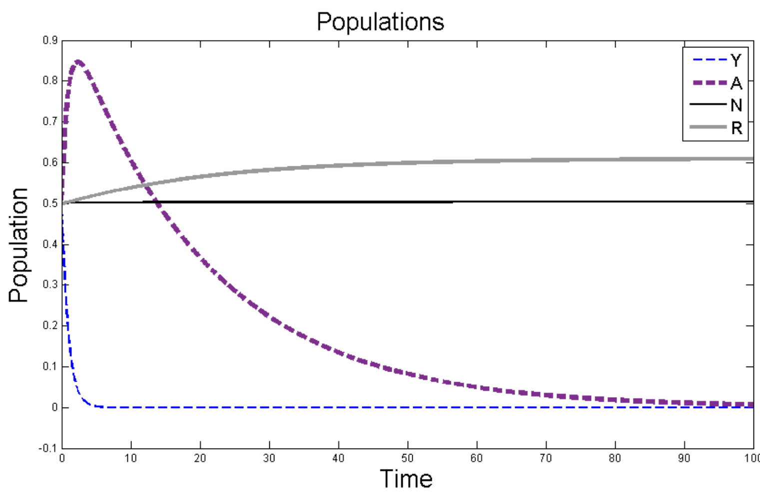

Figure 1: Plot describing numerical solutions to the ODE model described in section. Population is described in billions and time is described in days.

In this scenario, the young pigeon population decreases rapidly while the adult population has a spike due to the maturation of the young pigeons. The remaining adult pigeons start to die off without recovery as time continues. Both predator populations level out at their carrying capacities.

For the DDE system, we planned to use the `dde23` solver. However, since this form of modeling was not the proper tool for our project goals, we did not further pursue numerical solutions for our system of DDEs.

3 Agent-based Modeling

We outlined our explanation of the agent-based model using the Overview, Design concepts, and Details (ODD) protocol. This method is recommended for the discussion of agent-based models [9].

3.1 Purpose

The purpose of this agent-based model is to simulate the reintroduction of the extinct Passenger Pigeon into its natural habitat. We did this by considering the factors known about the Passenger Pigeon, its phylogenic relatives, and the current landscape. From the simulation results, we are able to determine the ideal conditions for a successful Passenger Pigeon reintroduction into a present-day environment.

3.2 State Variables and Scales

The Passenger Pigeon agent-based model (ABM) is comprised of two main components: 1) pigeon agents characterized by gender, age, and movement and 2) a landscape representation of eastern North American forests with varying tree species and densities. These agents correspond to the agents in the NetLogo program.

The individual pigeon agents in the model are characterized by gender,

Parameter	Description
Y	number of young pigeons
A	number of adult pigeons
N	number of nest predators
R	number of raptors; predators that attack adult pigeons
α	birth of new pigeons
μ	maturation of young pigeons to adult pigeons
π_1	death of young pigeons
π_2	death of adult pigeons
λ_1	growth of nest predators
λ_2	growth of raptors
β_1	Holling Type parameter for the first independent system: the young pigeons and the nest predators
β_2	Holling Type parameter for the second independent system: the adult pigeons and the raptors
f	growth of adult pigeons
γ_1	predation for the nest predators
γ_2	predation for the raptor predators
ψ_1	handling type for the young pigeons
ψ_2	handling type for the adult pigeons
K_1	carrying capacity for the young pigeons
K_2	carrying capacity for the nest predators
K_3	carrying capacity for the raptors,
ϵ	Allee parameter for the adult pigeons.

Table 1: A glossary of the parameters for the DE models 5 and 6.

age, and their ability to move and reproduce. Female pigeons are given an extra variable to determine when they lay an egg during the breeding season. All the pigeons in the model are considered to be members of the same population and have no specific social ranking within the model. Because the Passenger Pigeon was a migratory species, we assume that they do not have specific territories and are able to move freely in the simulation.

There are two different forest distributions represented in the model: oak-hickory and oak-pine. The oak-hickory forest displayed in our model is a forest distribution found in the Mashomack Reserve in Long Island, New York. We determined the values for the tree distribution by averaging five forest distributions found in this area [3]. The Oak-Pine forest tree distribution displays a forest from the Fredericksburg and Spotsylvania National Military Park in eastern Virginia [18]. Both of these forests are within the Passenger Pigeon's historic range and represent two potential locations for a Passenger Pigeon reintroduction. The environment state variables include the percentage of land covered by each species of tree, the corresponding time of year, and food availability. The forests represented in the model are 1,600 km^2, and each patch of trees is 1 km^2. To simplify the model, each patch contains only one type of tree.

3.3 Process Overview and Scheduling

The model proceeds in daily time steps. Within each day, every agent in the simulation assess their unique state and chooses an action that best meets their needs based on a pre-set decision making process.

For every patch of trees in the environment, five phases are implemented in the following order: assess agent state, grow nuts, spawn insects, increase

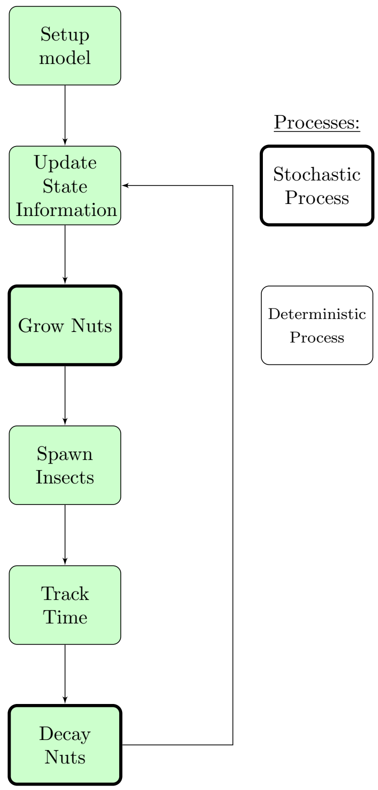

Figure 2: The decision tree of the environment for each time step in the model throughout a simulation.

time, and decay nuts. See Figure 2.

For every pigeon agent in the model, six subroutines are implemented in the following order: starvation check, parental status, fertility, time stationary, eat nuts, eat insects, forage, starvation check, and random death. See Figure3

3.4 Design Concepts

The following concepts are considered in our model:

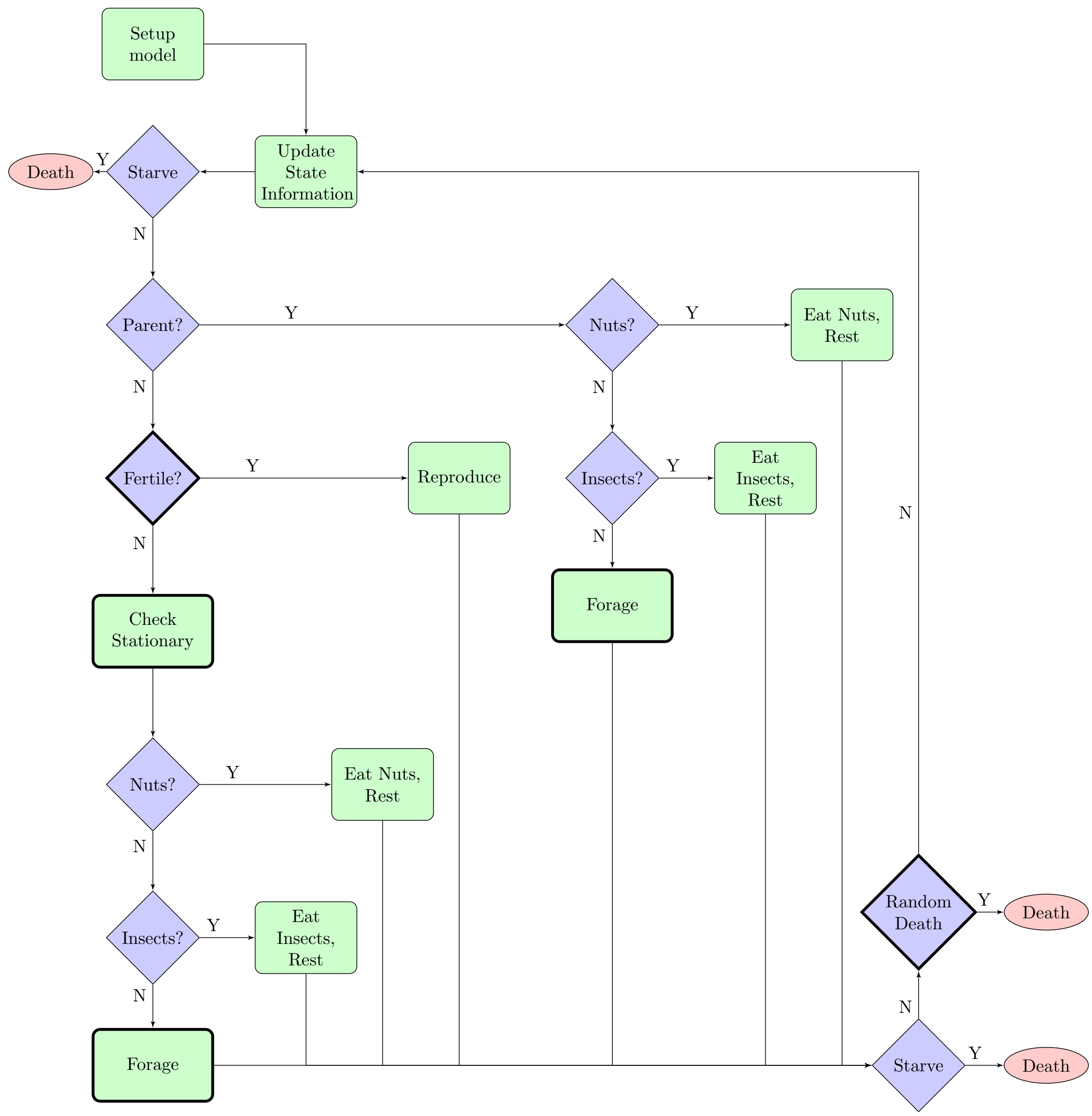

Figure 3: The decision tree for the pigeons at each time step in the model throughout a simulation.

Emergence: Population dynamics, such as a carrying capacity, emerge from the behavior of the individuals and their interaction with the environment. Pigeon behavior and movement is explicitly defined in the model and follows a specific set of rules outlined in the decision tree. However, in figure 3, the bolded blocks represent subroutines with some degree of stochasticity.

Fitness: The pigeon's objectives are explicitly modeled in the reintroduction simulations. The pigeon's goal is to expend as little energy as possible to maximize their efficiency in the model. This is accomplished through the pigeon decision tree. Priority is given to eating and resting, while foraging and movement are a lower priority. A pigeon's available energy is measured in calories.

Sensing: The pigeon agents are assumed to know the location of all other pigeons in the environment and the available food resources. Pigeons acting as a parent have a movement radius of 5 km. All other pigeons have a movement radius of 20 km [16]. Pigeons are aware of the available food and energy values on the patches within their radii. They are also aware of their own energy values, age, and gender.

Stochasticity: The stochastic aspects of the environment include the location of the species of trees, the number of nuts produced each year, and the number of nuts decayed each day. The stochastic aspects for the pigeon population include the time of pigeon reproduction, the gender of the pigeon, the probability of movement in stationary pigeons, and the chance of random death.

Observation: The data being recorded from the agent-based model was exported and analyzed using `MATLAB`. For each simulation, we recorded the pigeon population, rate of extinction, and age of the pigeons at death.

3.5 Initialization

At the start of each simulation, the forest distribution, the initial number of male and female pigeons, and the percentage of tree coverage is set by the observer. The location of each tree species is randomly assigned. We ran realizations for tree densities of 0% to 100% by increments of 10%. Initial pigeon populations consisted of 5 males and 5 females. Each run was 100,000 simulated days long, corresponding to approximately 274 years.

To gather data on extinction rates, we ran 100 simulations with tree densities ranging from 5% to 25%, increasing by 5% increments. We set the maximum time of the simulations to 50,000 simulated days (approximately 137 years). If the population survived for at least 50,000 simulated days, we assumed the population had reached an equilibrium value and was unlikely to go extinct. For those that did end in extinction, we recorded the time of extinction.

3.6 Input

Every species of tree in the model has unique properties associated with it, including the amount of food produced per year and the calories each type of food provides. The main food source provided by eastern North American deciduous forests is mast, or the aggregate fruits and nuts produced by any tree in the forest. In the past, the Passenger Pigeon's main food sources were beechnuts, acorns, and chestnuts [4]. However, forest composition has changed since the time of the Passenger Pigeon. The American chestnut tree is now nearly extinct in the wild [10], and different trees play a more dominant role than they have in the past [1]. Since our ABM is modeling a reintroduction of the Passenger Pigeon into a present-day environment, our simulations only take into account current forest conditions.

Many trees go through a cycle in which they have mast years or mast seeding. Mast seeding is the intermittent production of large seed crops by a population of plants [14]. While mast seeding has been heavily researched, it is still difficult to determine what exactly causes a mast year and how trees will cycle through mast years and non-mast years [15]. Most oak and pine species display a normal masting cycle; they seed most years, but have years with very high seed production [14]. To simplify mast production in our model, we divided our oak trees into two types: one-year and two-year species [15]. One-year species can produce mature acorns every year and two-year species require two years to produce mature acorns. One-year species include white oaks (*Quercus alba*), chestnut oaks (*Quercus prinus*), and post oaks (*Quercus stellata*). Two-year species include red oaks (*Quercus rubra*), black oaks (*Quercus velutina*), and scarlet oaks (*Quercus coccinea*). The one-year species typically have mast years every three to five years, while the two-year species will typically alternate between mast and non-mast years. Hickory trees behave similarly to one-year oak trees in our model because they also mature nuts every year [24]

Another important aspect of mast years is that they are synchronous [25]. This means that trees of the same species within a forest will all have a mast year during the same year.

Using this knowledge of mast seeding, we constructed a six year sequence for our ABM. Hickory trees and white, post and chestnut oaks have a mast year every three years while red, black, and scarlet oaks have a mast year every two years. To determine the number of nuts available in 1 km^2 by a species of tree, we averaged the literature values obtained from five forests in New York [3]. Because this article had no information on the acorn production of scarlet oaks, we used data gathered from five different forests in North Carolina [12]. From these data sets, we found the maximum, minimum, and average amount of nuts produced by each species of tree in both mast and non-mast years. We distributed this data triangularly, which allows each patch to produce a random number of nuts depending on the tree species and type of year (mast or non-mast). See figure 4 for a picture representation of the calories produced per tree species in the six year cycle. See table 2 for a list of the numbers used in the triangular distribution in our model.

Tree Species	Mast Year	Non-Mast Year
Hickory (*Carya spp.*)	210 36,040 7,702	0 3,960 259
Black Oak (*Quercus velutina*)	2,790 57,250 12,943	0 5,40 439
White Oak (*Quercus alba*)	170 18,380 10,910	0 2,750 350
Red Oak (*Quercus rubra*)	9,330 19,040 12,170	0 420 190
Scarlet Oak (*Quercus coccinea*)	1000 18,000 5,000	0 3,000 429
Chestnut Oak (*Quercus prinus*)	130 9,330 3,502	0 140 263
Post Oak (*Quercus stellata*)	710 12,920 6,815	0 710 355
Red Maple (*Acer rubrum*)	12,000 91,000 51,000	Same Values
Black Cherry (*Prunus serotina*)	6,800 17,900 10,600	Same Values

Table 2: Minimum, Maximum, and Average Number of Nuts Produced by Each Tree Species in 1 Square Kilometer

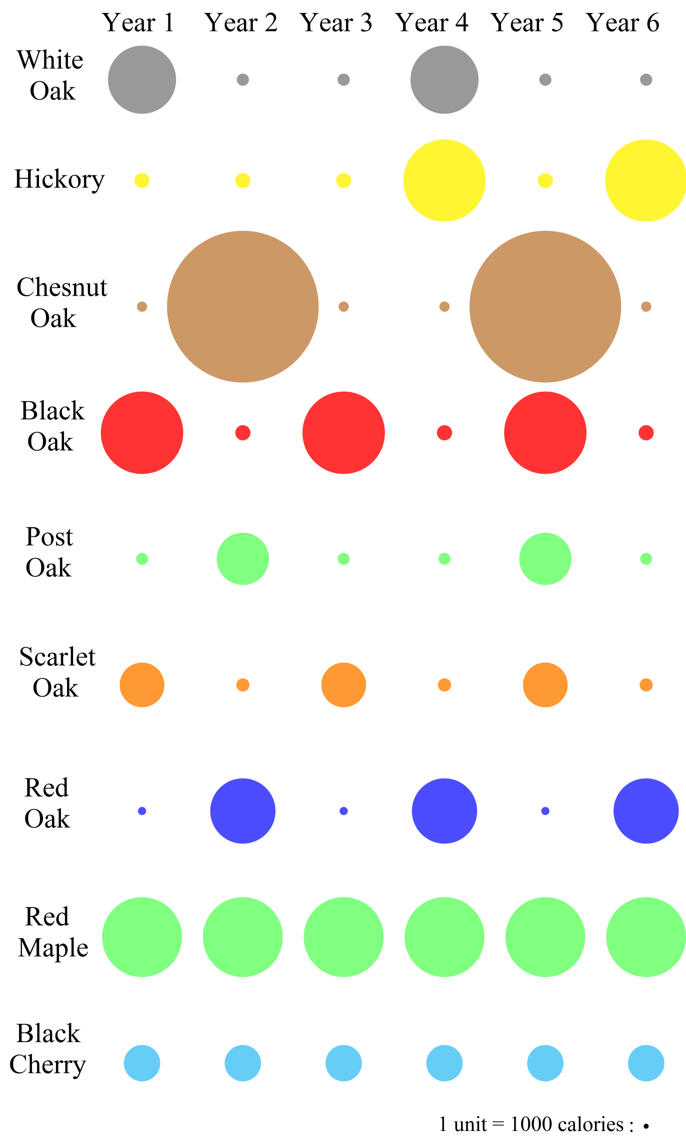

Figure 4: Mast produced by each species of tree per year of a six year cycle. One unit = 1 kcal.

After the nuts are produced by the tree, they can be removed from the simulation through a random decay process. We modeled this using a Poisson distribution. We first attempted to model nut decay with a binomial distribution. However, this was very computationally heavy in NetLogo, so we instead approximated a binomial distribution using a Poisson distribution. We can use this technique in our model because our simulation has a very large number of nuts produced and a very small probability that they will decay on any given day. According to the National Institute of Standards and Technology, the general rule of thumb is that with an $n \geq 20$ and a $p \leq .05$, the Poisson approximation is appropriate. The trees in our simulation will likely produce greater than 20 nuts per year and the probability that a nut will decay is .00889. This value comes from the expected value of an exponentially distributed random variable when λ is the average lifespan of one nut. In our model, $\lambda = 112$ days (16 weeks). The probability that a nut will decay is therefore

$$p = 1 - e^{-\frac{1}{\lambda}}. \tag{7}$$

Other important food sources for the Passenger Pigeon were fruits. In our model, we have populations of black cherry trees (*Prunus serotina*) and red maple trees (*Acer rubrum*), which produce cherries and samara fruits, respectively.

To make our ABM as accurate as possible, we took into account the seasonality of all available food sources. Oak trees typically drop their nuts at the beginning of autumn, which we defined in our model as the beginning of August[21], while hickories drop their nuts in September [24]. Cherries are ripe in June and samaras are available in April. Estimates for fruit production and seasonality were made from information found on the USDA Northeastern Area Forestry Service website.

Insects are an alternative food source for the Passenger Pigeon [4].These insects provide a baseline amount of energy for the pigeons and are available year-round.

Each food source in our model provides a different number of calories. Values for the amount of energy obtained per nut were calculated by using values for calories per gram of nut [2] and the weight of a nut [8]. To fill in the missing caloric values and nut weights, we obtained as much information as possible for the average nut size and calories for a general acorn, hickory nut, cherry, and samara (found by SELF Nutrition Data), yet these values are roughly estimated in our model. See Table 3 for a list of all values used in our model.

3.7 Submodels

Throughout each simulation, the pigeon agents implement several submodels. These submodels take into account how much energy a pigeon has, whether or not it is a parent, if it is able to reproduce, how long it has been stationary, and if it has died due to natural causes (see figure 3).

Starve: To determine the energy of each pigeon agent, we first look at how each agent expends energy. Pigeons lose energy through resting, daily activities, and reproducing. While exact energy expenditure values for the Passenger Pigeon are unknown, we used allometric comparisons of closely related species to the Passenger Pigeon. The model uses the Rock Dove's basal metabolic rate as a substitution for the Passenger Pigeon's rate [23], and a calculated value for the amount of energy a pigeon takes to fly. There was a lack of this information in the literature. To determine this value, we used information on the amount of food required to raise Rock Doves [20]. The number of calories in a pigeon egg was used to determine reproduction energy expenditure. If a pigeon expends more energy that it has, it will die in the simulation. A pigeon can gain energy by eating nuts, fruits, and insects off of a patch in the model's landscape.

Parent: Next, the model checks to see if the pigeon is acting as a parent. If the pigeon is a parent, it is less likely to to forage. To incorporate this into the model, the simulation does not increase the probability that the agent will move as time stationary. The pigeon will only leave its patch if there is no food currently available on the patch. The model also reduces the pigeon's radius for foraging from 20 km to 5 km. The pigeon will act as a parent for 14 days after a new pigeon is produced.

Fertile: If the pigeon is not acting as a parent, then the model checks to see if the pigeon is ready to reproduce. To reproduce, the pigeon must be female, have an energy value of 300 kcal, and the time must correspond to the breeding season. Because the Passenger Pigeon was monogamous throughout the breeding season, there must be a male present for every reproducing female. If a pigeon is eligible for reproduction, it is assigned a random number between 1 and 30. This number decreases by one each time step in the simulation. When the counter reaches zero, a new pigeon is produced. The male and female pigeons then become parents.

Check Stationary: Because it is unlikely that a pigeon in the wild will stay on one patch for extended time periods, the model incorporates pigeon movement. Even if there is food available to the pigeon without it moving, the pigeon's likelihood of leaving the patch foraging increases with time.

Each day, chances of pigeon movement increase by 25%. If the pigeon has been stationary for four consecutive days, it will be forced to move.

Random Death: Finally, the model takes into account random death. In order to make our simulation more realistic, we included the probability that a pigeon dies from natural causes, such as old age or predation. To incorporate this into the model, we used an exponential probability distribution function to describe random death. Because the average lifespan of the Passenger Pigeon in the wild is unknown, the model uses literature values for the average lifespan of a wild Rock Dove *(Columba livia)*, which is approximately six years according to the Pigeon Control Resource Centre.

4 Results

We ran our simulation for various parameter values. Simulations ran for tree densities of 0% to 100% by increments of 10%. Initial pigeon populations consisted of 5 males and 5 females. Each run was 100,000 simulated days long.

After gathering data from the oak-hickory and oak-pine simulations, a logistic growth curve was fit to each realization to estimate the initial growth rate and carrying capacity. Data from ten simulations for each tree density was averaged to find resulting parameter estimates.

4.1 Time Series

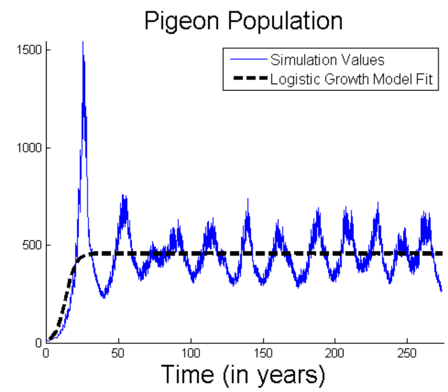

Figure 5: Time series of a pigeon population with tree density of 60% in an Oak-Hickory forest with a logistic curve fit to the data. The average carrying capacity for this environment is 462, pigeons and the average growth rate of the population is .30407.

4.2 Carrying Capacities

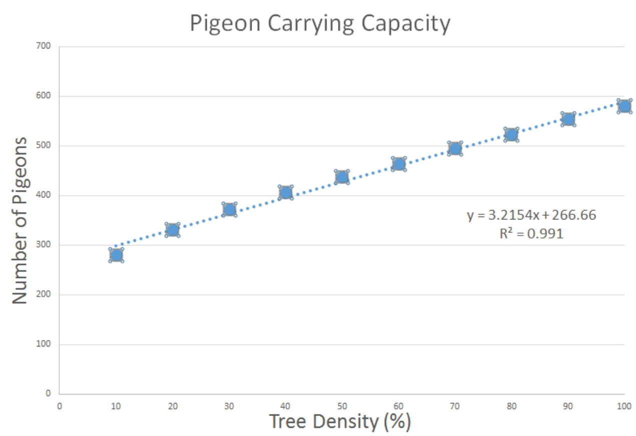

Figure 6: Plot describing the relationship between the average carrying capacity and tree density in an oak-hickory forest.

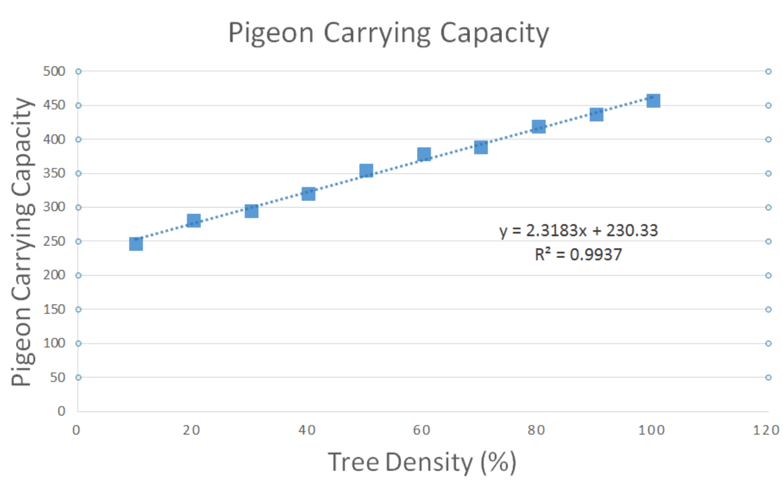

Figure 7: Plot describing the relationship between the average carrying capacity and tree density in an oak-pine forest.

4.3 Age Distribution

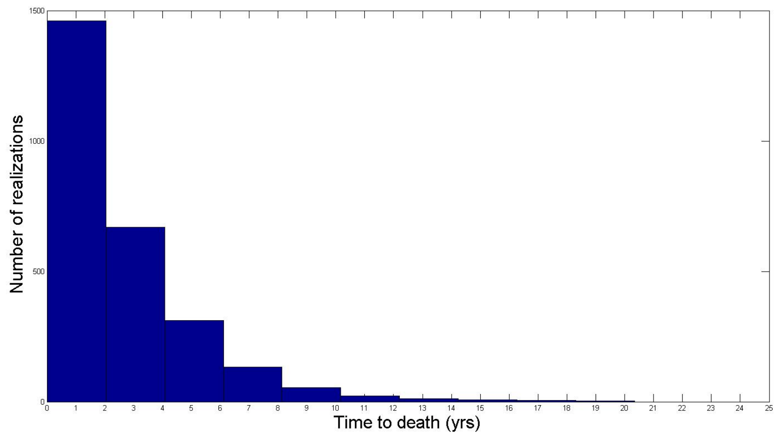

Figure 8: Histogram showing the age distribution of pigeon death in an oak-hickory forest at 50% tree coverage. Death can occur when a pigeon starves or dies due to natural causes. Death from natural causes is modeled using an exponential distribution.

4.4 Extinction Rates

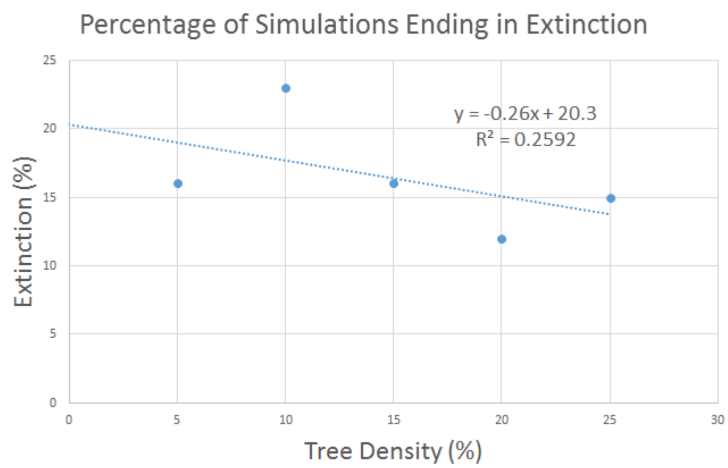

Figure 9: Plot showing the percentage of simulations resulting in extinction under varying tree densities in an oak-hickory forest.

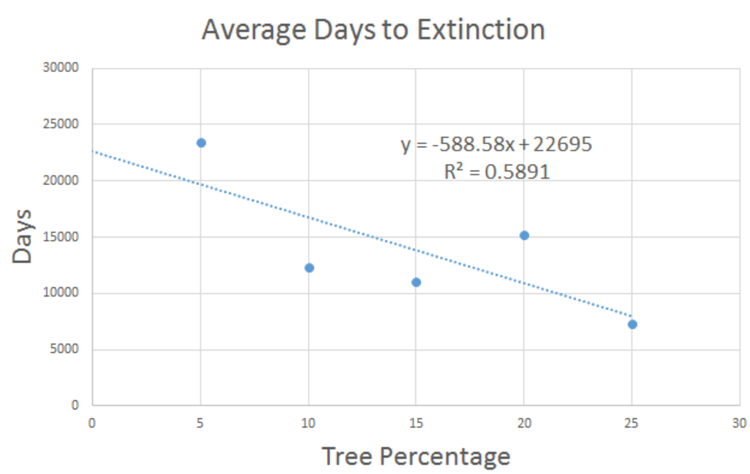

Figure 10: Plot showing the average time in days it took a simulation to reach extinction under varying tree densities in an oak-hickory forest.

5 Discussion

Agent-based modeling allows us to add stochasticity to the model, describe individual pigeon behavior, and set up the desired environment for the agents.

In order to determine the carrying capacity of each tree density, we fit a logistic growth model to each of the simulations. From this fit, we were able to approximate a growth rate and carrying capacity for the pigeon population at each tree density. Based on the data that we collected, there is a very strong positive correlation between tree density and pigeon carrying capacity for both the oak-hickory and oak-pine simulation sets (see figures 6 and 7). These results also show that the carrying capacity is an emergent property of the pigeon population. This is an intuitive result, as the more food resources available to the pigeons, the more pigeons the environment can sustain.

After examining the histogram for pigeon life expectancy, we can see that our exponentially distributed death probability was properly incorporated into the model. In our simulations, the average age of the pigeons in the wild was six years. Based on the properties of exponential distributions, approximately 63% of the pigeons in the simulation will have died by age six. This is supported by our model (see figure 8).

When examining the rate of simulation extinction for various tree densities, we see a slight negative trend (see figure 9). This implies that as tree density increases, fewer realizations resulted in extinction. It is important to note that we only ran 100 realizations for for five tree densities. With more simulations and smaller increments for the data points, a more obvious trend may arise.

When examining the time to extinction for each simulation for various tree densities, we also see a slightly negative trend (see figure 10). This result is less intuitive. We hypothesize that it is due to stochastic processes in our model. At higher tree densities, if the pigeon population reaches their carrying capacity, it is unlikely for the simulation to result in extinction, as the environment has enough food to sustain the population. Therefore, the only time when simulations at high tree coverage go extinct is at the beginning of the realization when the population is small. These extinctions are mostly due to stochastic processes. However, at low tree densities, even if the pigeon population survives for an extended period of time, the environment does not have enough available resources to sustain the population. This makes the environment less suited for the Passenger Pigeon and results in extinction at a later time in the model.

Based on our results, we found that a Passenger Pigeon reintroduction into either an oak-hickory or oak-pine forest would result in survival of the species.

6 Future Directions

In the future, we would like to scale our results for the carrying capacities to represent both present-day and historic eastern North American forest density. This would allow us to validate the model and predict a natural carrying capacity in the present landscape.

We would like to further analyze the relationship between extinction and forest coverage by running more simulations for both oak-hickory and oak-pine tree densities. By running more simulations at smaller density increments, we could better understand this relationship. This analysis would further describe the relationship between tree density, extinction probability, and extinction time.

We also would like to expand our model to other tree distributions within the pigeon's historic range. By gathering more data on specific locations within the eastern part of North America, we can most accurately pinpoint an ideal forest environment for a Passenger Pigeon reintroduction.

Table 3: This table displays all of the parameter values used in the agent-based model. O/H shows the tree distribution percentage in an oak-hickory forest. O/P shows the tree distribution percentage in an oak-pine forest. Seasonality is the time of the year when nuts are available for each tree. Mast Year in Cycle are the years when the species of tree has a mast year during the six year cycle. Calories/Nut is the number of calories a pigeon can gain by eating one nut in the simulation.

Tree Species	O/H (%)	O/P (%)	Seasonality	Mast Years in Cycle	Calories/Nut (kcal)
Hickory (*Carya spp.*)	21	13	Sept. 1 - Jan. 1	Year 4, 6	35
Black Oak (*Quercus velutina*)	20	4	Aug. 1 - Dec. 1	Year 1, 3, 5	21
White Oaks (*Quercus alba*)	12	33	Aug. 1 - Dec. 1	Year 1, 4	17
Red Oak (*Quercus rubra*)	7	7	Aug. 1 - Dec. 1	Year 2 ,4, 6	14
Scarlet Oak (*Quercus coccinea*)	6	-	Aug. 1 - Dec. 1	Year 1, 3, 5	16
Chestnut Oak (*Quercus prinus*)	6	-	Aug. 1 - Dec. 1	Year 2, 5	16
Post Oak (*Quercus stellata*)	1	-	Aug. 1 - Dec. 1	Year 2, 5	16
Red Maple (*Acer rubrum*)	6	1	April 1 - Aug. 1	Same All Years	5
Black Cherry (*Prunus serotina*)	3	-	June 1 - Oct. 1	Same All Years	5
Other (Non-food producing trees)	18	42	-	-	-

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