An agent-based model determining a successful reintroduction of the extinct passenger pigeon

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Abstract
The passenger pigeon (Ectopistes migratorius) was an iconic species in eastern North America that was one of the most numerous birds in the world at the time of European colonization. Passenger pigeons went extinct in 1914 due to excessive hunting. 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 colony could survive a reintroduction into a natural habitat, we developed an 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: resource distribution, reproduction, and natural death. Bioenergetics, forest composition, and other ecological values were obtained from literature. Our simulation results suggest that passenger pigeons could survive a reintroduction into a modern natural environment, but their survival can be optimized with certain release dates, sex ratios, and forest composition.
Recommendations for Resource Managers

Genome engineering advancements suggest that the de-extinction of passenger pigeons is feasible; however, the ability for passenger pigeons to live in the modern forest composition of their old habitat remains unexplored. Our model suggests the following regarding reintroduction strategies:

- A successful reintroduction of passenger pigeons is plausible, but sensitive to the strategy selected. Moderate deviations from optimal reintroduction strategies can greatly diminish the probability of a successful reintroduction.
- The optimal successful reintroduction strategy has an equal number of male and female passenger pigeons released in a dense oak-hickory forest at the peak of the forest’s masting cycle.
- Beyond persistence, the population growth of passenger pigeons within 10 years is at best, limited. Efforts to monitor and protect passenger pigeons during the transient phase of their reintroduction is critical.

KEYWORDS
agent-based model, bioenergetics, de-extinction, passenger pigeon, population dynamics

1 | INTRODUCTION

Biodiversity loss is a significant obstacle of the Anthropocene. The rate of loss has increased over the last four decades (Butchart et al., 2010). One of the tools our society could use in the fight against biodiversity loss is de-extinction of extinct species via genome engineering (Shapiro, 2015b). A primary candidate species for such a de-extinction project is the passenger pigeon (Ectopistes migratorius).

The passenger pigeon was an iconic bird species native to eastern North America. Before its extinction, the passenger pigeon accounted for approximately 20%–40% of the entire North American avifauna (Greenberg, 2014; Schorger, 1955). It was a nomadic species that would follow the availability of forest mast (Novak et al., 2018) 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 (Blockstein, 2002; Greenberg, 2014).

However, humans hunted the passenger pigeon unsustainably throughout the 1800s. The trapping and shooting of pigeons and the disruption of the nesting sites resulted in rapid population decline (Bucher, 1992). Along with excessive hunting, deforestation in eastern North
America 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 population collapse and the species was declared extinct in 1914 (Blockstein, 2002; Greenberg, 2014).

In 2003, The Great Passenger Pigeon Comeback became one of the first de-extinction projects in the world. One of the goals of this movement is to restore the passenger pigeon and someday release it back into the wild (Novak, 2018b). DNA was obtained from a passenger pigeon and sequenced. From the sequence, Johnson et al. identified the band-tailed pigeon (Patagioenas fasciata) as the passenger pigeon's closest living relative (Fulton et al., 2012; Johnson et al., 2010). Through future scientific advancements combined with current genetic information, it will likely be possible to genomically engineer a viable passenger pigeon and release it into a natural habitat (Shapiro, 2015a).

The de-extinction of the passenger pigeon could have many ecological benefits on the environment. The passenger pigeon once acted as an ecosystem engineer in eastern North America (Greenberg et al., 2016; Novak, 2016). Not only would its 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. Because of the rapidity with which passenger pigeons went from a population of billions to zero, the passenger pigeon is the perfect candidate species 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 may be a way to remedy some of the damage done to both this species and the ecosystem 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. Feasibility studies were conducted from 2017 to 2019 on the genetic engineering process in rock doves (Columba livia; Murray et al., 2017; Novak, 2018a) and will presumably eventually lead to engineering passenger pigeon genes into living pigeons. Also, the historical range of the passenger pigeon has changed substantially in the intervening century. In addition to human development, the ecosystem composition has changed. For example, the American chestnut tree (Castanea dentata), which served as a food source for the pigeons (Greenberg, 2014), was ravaged by the chestnut blight from 1904 to 1940 when 3–4 billion American chestnut trees were lost, nearly eliminating the species (Freinkel, 2007). The chestnut tree has been making a small recovery from its near extinction, but the current upward trend is likely extremely slow (Gustafson et al., 2017), or merely a transient trend (DavelosBaines et al., 2014). This difference, among other resource changes, poses a serious question of whether or not the passenger pigeon could survive in the modern landscape of its historic range.

We acknowledge that there are concerns about the ethics of de-extinction (Kasperbauer, 2017) and the science of whether such an organism could even be referred to as a passenger pigeon (Blockstein, 2017), yet our study will focus on whether it is feasible for a de-extincted passenger pigeon colony to be able to survive in a modern environment.

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 engineered and released. We employed an agent-based model (ABM) to examine the probability and degree of success of a passenger pigeon reintroduction under varying environmental conditions. ABMs have been used extensively in ecology to study population dynamics and species relationships (DeAngelis & Mooij, 2005; McLane et al., 2011). To simulate a passenger
pigeon reintroduction, we constructed a spatial, stochastic ABM using the software NetLogo v. 6.1.1 (Wilensky, 1999). Agent-based modeling is a technique that considers the components of a system and displays emergent properties from the interactions within the system (Grimm et al., 2010). Each component in the model has individual objectives that allow it to interact with and respond to the changing environment. We simulated a variation of food types and seasonal availability while monitoring the bioenergetics and reproduction of the birds to assess their survival under different reintroduction strategies.

We hope that our simulations, which compare different target forest compositions and densities, as well as released sex ratios of pigeons and date of release, will provide wildlife managers working to de-extinct the passenger pigeon some assistance towards a successful reintroduction.

2 | METHODS

Our agent-based model is structured around the interactions of the sole agent, passenger pigeons, between one another and their environment. The standardized presentation of an ABM is the overview, design concepts, and details (ODD) protocol as outlined by Grimm et al. (2010). Our model is outlined in seven subsections: (a) purpose, (b) state variables, and scales, (c) process overview and scheduling, (d) design concepts, (e) initialization, (f) input, and (g) submodels.

2.1 | Purpose

The purpose of this model is to simulate the reintroduction of passenger pigeons into a modern natural habitat. In particular, this model is constructed to evaluate a variety of reintroduction strategies in two facets, (a) the probability of an initial colony of passenger pigeons surviving for 10 years, and (b) the average number of passenger pigeons that are alive 10 years after reintroduction. We limit the scope of our model to the early stages of the reintroduction process due to a simplifying assumption we make that the landscape is composed of a single forest; however, success of reintroducing passenger pigeons likely hinges on the eventual re-establishment of nomadic patterns to multiple masting forests.

2.2 | State variables, and scales

The sole agent of the model is passenger pigeons, and the sole habitat unit is a forest patch. Passenger pigeons have seven associated state variables with them: (a) sex (male or female), (b) energy (measured in kilocalories), (c) a distance of potential movement for each day (measured in kilometers), (d) parental status (a counter to record the temporal duration of parental behaviors), (e) the number of fruits that the passenger pigeon consumes in a day, (f) stationary status (a counter to record the temporal duration of which the passenger pigeon has remained in the same patch), and if they are a female, (g) a random day within the breeding cycle to attempt laying eggs.

The single forest is composed of forest patches. The single forest is constructed to be representative of either a modern oak-hickory or modern oak-pine forest. We discretize the landscape so that each patch represents a cluster of trees of the same species, including a “null” species option that represents an empty space. Each tree species has an associated triangular distribution (with minimum, maximum, and mean) to describe the number of fruits that a tree
produces each year, and has a corresponding masting length that dictates the number of days on which those fruits are distributed uniformly.

The temporal resolution of the model is measured in ticks, where one tick equates to 1 day. The spatial resolution of the model is measured in patches, where one patch is of area 1 km². The forest is constructed on a 41 × 41 patch grid, thus, the entire forest is of size 1,681 km². Each nonempty patch is assumed to be occupied by 15 trees (Abrams & Scheibel, 2013; Orwig & Abrams, 1994).

2.3 | Process overview and scheduling

The model initiates on January 1st of the first year, denoted Day 1. The model then proceeds in single day time steps, where each year ends on December 31st, representing the 365th day of that year.

The model begins by executing a full masting cycle (6-year period) before passenger pigeons are released. Each day during this initialization period, the nonempty patches execute the “Grow Mast” submodel, in which fruits are produced, and then the “Decay fruits” submodel, in which some amount of fruits are removed from the environment.

Once the first full masting cycle has passed, the number of ticks is reset. Passenger pigeons are released (as in their actions begin) on a user-specified day during the second masting cycle (Day 1 through Day 2190). The model proceeds in single day time steps until 10 years have passed since the day the passenger pigeons were released. Throughout this 10-year period, the following order of actions are executed by each passenger pigeon each day (where a randomly selected passenger pigeon completes all daily actions, followed by the next passenger pigeon, etc.). The passenger pigeons execute the submodels (a) “Starve” to remove any individuals with nonpositive energy, (b) “Reproduce” to attempt a nesting if the season is appropriate, (c) “Move” to move to a favorable location, (d) “Forage” to obtain energy, and (e) “Random death” to check for random instances of death in the population. After the passenger pigeons complete their actions, the nonempty patches execute the same two routines as before. If at anytime during the 10-year period the number of male or female passenger pigeons is zero, an extinction is recorded and the model terminates.

2.4 | Design concepts

2.4.1 | Basic principles

The focus of this study is to construct a model to assess the capacity of reintroduction strategies to keep a colony of passenger pigeons alive for 10 years. A major component in this reintroduction process is determining the optimal time (within the masting cycle) to release passenger pigeons into the forest.

Many tree species perform cyclic patterns in seeding, where peak seeding years are referred to as mast years or mast seeding (Kelly, 1994). While mast seeding is well studied, the cause and prediction of masting is under development (Koenig & Knops, 2000). However, most oak and pine species display a predictable masting cycle; seeding most years, but have years with high seed production (Kelly, 1994). Mast years are assumed to be synchronous (Sork, 1993), meaning that trees of the same species within a forest will all have a mast together. While the many tree species in our model produce mast of various types, for example, nuts, fruits, acorns, we will refer to all masting units as fruit for simplicity.
To incorporate masting dynamics into our model we simplify mast production by dividing oak trees into two types: 1-year and 2-year species (Koenig & Knops, 2000). One-year species produce mature fruits every year and 2-year species produce mature acorns every-other year. One-year species typically have mast years every 3–5 years, while the 2-year species will alternate between mast and nonmast years in a species-dependent cycle. Hickory trees are assumed to produce mature fruits every year (Sork, 1983). Red maple and black cherry trees are assumed to produce their fruits annually. See Figure 1 for a visual representation of the kilocalories produced per tree species during the masting cycle.

2.4.2 | Emergence

The model is constructed to evaluate the plausibility of a successful reintroduction of passenger pigeons. Therefore, the only emergent properties tracked are (a) if the passenger pigeons reintroduced are able to form a persistent population (for at least 10 years), and further, (b) the number of passenger pigeons alive at 10 years after reintroduction.

**FIGURE 1** Mast produced by each species of tree per year of a 6-year cycle. One unit of area (as seen in the legend) represents one kcal.
2.4.3 | Adaptation

Passenger pigeons are assumed to interact with one another and their environment in a way to keep their own energy value above zero. Passenger pigeons primarily maximize their fitness through both their reproduction and movement choices. In regard to reproduction, passenger pigeons refrain from reproducing if their individual energy is below a minimum energy threshold for reproducing, $E_r$, which reflects the amount of energy required to both construct a nest and produce an egg. In regard to movement, passenger pigeons can move (with a nonzero probability) to a new patch if they (a) are forced to through implicit predation pressures, or, (b) if they determine a nearby patch has more fruit.

2.4.4 | Sensing

Passenger pigeons are assumed to be aware of the following: the day of the year, their sex, if they are currently parenting an offspring, how long they have remained in their current patch, the maximum amount of energy they can have, their current energy value, the energy cost of reproducing, the number of fruits they have consumed, and the number of fruits in each patch that is within a radius $r$ of the pigeon’s current patch.

2.4.5 | Interaction

Passenger pigeons are assumed to interact with other species only through implicit ecological pressures. To include the effects of predation, each passenger pigeon checks to see how many days it has spent in the current patch. A random process then determines if the passenger pigeon is forced to move to a new patch, where the probability of this occurring increases each day of being stationary. We also include pressures that reduce the amount of available fruit in a patch, such as (a) competition pressures from coexisting species with similar dietary preferences, and (b) the natural decaying processes of unconsumed fruits. To do so, we assume that all fruits available in each patch decay at a constant rate $\lambda$.

Passenger pigeons only interact with one another explicitly through the mating process. During this process, females with sufficient energy for reproduction are assumed to form a monogamous bond with a single male (Blockstein & Westmoreland, 1993; Westmoreland et al., 1986). Both parents are assumed to take part in parental care (Westmoreland et al., 1986) in which each parent’s movement radius is reduced from $r$ to $r_p$.

Passenger pigeons interact explicitly with the landscape primarily through foraging. Each passenger pigeon is able to consume a daily, patch independent, fixed number of fruits $n$, which directly reduces the number of fruits in that patch. Pigeons also consume alternative food sources within their environment (e.g., earthworms; Bendire, 1892; Pokagon, 1895), where the population of such food sources are assumed to remain abundant (Bucher, 1992). Passenger pigeons are permitted to consume additional food sources up to some upper bound in the case there is not $n$ fruits in the patch they are currently in. Passenger pigeons that have reached a maximum energy level of $E_m$ are assumed to not forage until their energy levels have been reduced to incorporate the opportunity cost of foraging behavior.
2.4.6 | Stochasticity

The number of patches representing each tree type in the environment is assigned in a stochastic fashion that is based on current Eastern North American forests described in Abrams and Scheibel (2013) and Orwig and Abrams (1994).

The number of fruits produced by a patch of trees is simulated by a species-dependent, year-dependent, triangular distribution. These distributions were derived from literature-based mean, maximum, and minimum number of fruits produced per year (Abrams & Scheibel, 2013; Greenberg, 2000).

Passenger pigeon breeding is modeled where each reproductive female is assigned a uniformly distributed nesting date within the breeding season where she will lay a singular egg (Wilson, 1812) and randomly selects an available mate.

Passenger pigeons choose to leave their current patch with a probability dependent on the ratio of the maximum number of fruits on a single patch within their detectable range to the number of fruits in their current patch. Further, each day in which a passenger pigeon remains in a patch, a probability representing various other ecological pressures, which force the pigeon to move, increases to avoid stationary behavior.

The final stochastic process for passenger pigeons is the chance of random death. We assumed the probability that a pigeon dies from nonstarvation causes to be a constant probability at each time step, resulting in the lifespan of pigeons to be distributed exponentially. The fixed probability of natural death $d$, then was derived from the fixed natural mortality rate $\mu$, which can be found using the average lifespan of a wild rock dove (Centre, 2015), as the average lifespan of a wild passenger pigeon is unknown (Blockstein, 2002).

2.4.7 | Observation

At each time step the number of male and female passenger pigeons are recorded.

2.5 | Initialization

The model begins with six years (the length of one masting cycle) in absence of pigeons to generate a pre-existing supply of fruits. After the first masting cycle ends, the ticks are reset to one, and the second masting cycle begins. A user-specified initial number of male and female passenger pigeons are released at a user-specified date and year in the second masting cycle $t_0 \in [1, 2190]$. All pigeons are initialized to have maximum possible energy $E_m$, and have parental status set to 0 (meaning nonparental); thus, they have a movement radius of $r$.

The environment is constructed with a forest type as either oak-hickory or oak-pine, and with a forest density $\rho \in [0, 100]$, both of which are specified by the user. Each patch in the landscape is first set to either inhabited or null by generating a random number $R_1 \in U[0, 100]$, where if $R_1 \leq \rho$, the patch is said to be inhabited; otherwise it is set to null. Next, all inhabited patches are assigned a tree species that occupies that forest type. To do so, the interval $[0, 100]$ is partitioned into subintervals corresponding to each species in that forest type, where the size of the subinterval is relative to the percentage that species composes in the assigned forest type. Then, each inhabited patch is assigned a random number
Table 1. The kilocalories per fruit for each tree species, and their relative abundance in each forest type.

| Tree species          | Kilocalories per fruit (kcal) | Relative abundance |
|-----------------------|-------------------------------|--------------------|
|                       | Oak-hickory forest (%)        | Oak-pine forest (%)|
| Hickory (Carya spp)   | 35                            | 21                 | 13                 |
| Black Oak (Quercus velutina) | 21                         | 20                 | 4                  |
| Other, nonfood producing | 0                           | 18                 | 42                 |
| White Oak (Quercus alba) | 17                          | 12                 | 33                 |
| Red Oak (Quercus rubra)  | 14                           | 7                  | -                  |
| Chestnut Oak (Quercus prinus) | 16                        | 6                  | -                  |
| Red Maple (Acer rubrum)         | 5                            | 6                  | 1                  |
| Scarlet Oak (Quercus coccinea) | 16                        | 6                  | -                  |
| Black Cherry (Prunus serotina)    | 5                            | 3                  | -                  |
| Post Oak (Quercus stellata)      | 16                           | 1                  | -                  |

\(R_2 \in \mathcal{U}[0, 100]\), which is contained in one of the species subintervals, and now the trees in that inhabited patch are said to be that of the corresponding species to that subinterval. Table 1 displays the relative abundance of each tree species for both forest types, oak-hickory and oak-pine. The oak-hickory forest is representative of 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 (Abrams & Scheibel, 2013). The oak-pine forest tree distribution is representative of a forest from the Fredericksburg and Spotsylvania National Military Park in eastern Virginia (Orwig & Abrams, 1994). Both of these forests are within the passenger pigeon's historic range (AOU, 1998) and represent two potential locations for a passenger pigeon reintroduction.

Following the landscape construction, each patch is assigned a color and a number of kilocalories per fruit corresponding to the tree species occupying that patch. Values for the amount of energy obtained per fruit were calculated by using values for kilocalories per gram of fruit from that species (Abrams & Nowacki, 2008) and the mass of a fruit from that species (Dunham, 2009). To fill in the missing caloric values and fruit masses, we obtained as much information as possible for the average fruit size and kilocalories for a general acorn, hickory nut, cherry, and samara (found by SELF Nutrition Data SELFNutritionData, 2015), yet these values are roughly estimated in our model. The number of kilocalories per fruit for each species of tree in our model is also provided in Table 1.

2.6 | Input

The user specifies the forest type, the forest density \(\rho\), the release day \(t_0\), the number of initial females and number of initial males.
2.7 | **Submodels**

The model operates each day by having the patches perform the subroutines: grow mast, and decay fruits, followed by the passenger pigeons performing the subroutines: starve, reproduce, movement, forage, and random death.

2.7.1 | **Grow mast**

Each patch is classified by species using color. Next, if $t$ is within the masting cycle, then the number of new fruits that become available to passenger pigeons is calculated by drawing a number from a triangular distribution (with parameters as specified by Table 2), and then dividing that number of fruits by the number of days in the masting date range. Then, the number of fruits in the patch is increased from its existing fruits in the patch by adding the number of new fruits available.

To determine masting date ranges, we considered that oak trees typically drop their fruits at the beginning of autumn, which we defined in our model as the beginning of August (Pons & Pausas, 2007), while hickories drop their fruits in September (Sork, 1983). 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 (USDA, 2015), and are summarized in Table 2.

2.7.2 | **Decay fruits**

To simulate the effects of removing fruits from the environment due to factors other than passenger pigeon consumption, such as consumption from other species or natural decaying processes, we assume the lifespan of a fruit is exponentially distributed. However, we were unable to determine any literature-supported ranges for the average lifespan of a fruit in a forest environment; thus, we used a wide range of feasible values in simulations. Regardless, the fruits are determined to decay at a rate of $\lambda$, with average fruit lifespan $\lambda^{-1}$, and the probability of decay of a fruit is $1 - e^{-\lambda}$. For efficiency, we use a Poisson approximation of the binomial distribution to calculate the number of fruits a patch will lose, where the number of fruits in a given patch is the trial number. The number of fruits to be decayed are removed from the patch, and if the Poisson approximation results in a negative quantity of fruits to remain in the patch, the patch is deemed to have zero fruits.

2.7.3 | **Starve**

If the amount of energy a passenger pigeon has is nonpositive, it is removed from the population and is said to have died.

2.7.4 | **Reproduce**

For each passenger pigeon that is acting as a parent, the number of days until their parental behavior ends is reduced by one. If the passenger pigeon reaches a parental count of zero, their
| Tree species                  | Masting year cycle (year) | Masting date   | Mast year fruit production | Nonmast year fruit production |
|-------------------------------|---------------------------|----------------|-----------------------------|-------------------------------|
|                               |                           |                | Min | Mean | Max | Min | Mean | Max |
| Hickory (Carya spp)           | 4, 6                      | Sept 1–Jan 1   | 210 | 7,702 | 36,040 | 0   | 259 | 3,960 |
| Black Oak (Quercus velutina)  | 1, 3, 5                   | Aug 1–Dec 1    | 2,790 | 12,943 | 57,250 | 0   | 439 | 5,040 |
| Other, nonfood producing      | –                         | –              | 0   | 0    | 0    | 0   | 0    | 0    |
| White Oak (Quercus alba)      | 1, 4                      | Aug 1–Dec 1    | 170 | 10,910 | 18,380 | 0   | 350 | 2,750 |
| Red Oak (Quercus rubra)       | 2, 4, 6                   | Aug 1–Dec 1    | 9,330 | 12,170 | 19,040 | 0   | 190 | 420 |
| Chestnut Oak (Quercus prinus) | 2, 5                      | Aug 1–Dec 1    | 130 | 3,502 | 9,330 | 0   | 140 | 263 |
| Red Maple (Acer rubrum)       | 1, 2, 3, 4, 5, 6          | Apr 1–Aug 1    | –   | –    | –    | 12,000 | 51,000 | 91,000 |
| Scarlet Oak (Quercus coccinea)| 1, 3, 5                   | Aug 1–Dec 1    | 1,000 | 5,000 | 18,000 | 0   | 429 | 3,000 |
| Black Cherry (Prunus serotina)| 1, 2, 3, 4, 5, 6          | June 1–Oct 1   | –   | –    | –    | 6,800 | 10,600 | 17,900 |
| Post Oak (Quercus stellata)   | 2, 5                      | Aug 1–Dec 1    | 710 | 6,815 | 12,920 | 0   | 355 | 710  |
movement radius is reset to be $r$. If the passenger pigeon is female and the current date is April 1st, the start of the breeding season (Schorger, 1955), the female is assigned a random nesting date using the discrete uniform distribution, between April 1st and April 14th. If the current tick corresponds to the female's nesting date, and there is an available male, that is, a male with a parental counter that is zero, and the female has a sufficient amount of energy to reproduce $E_r$, the female and male are both assigned a parental counter of 28 (14 days of egg incubation and 14 days of raising the squab to fledgling age), both movement radii are set to $r_p$, and the female's energy is reduced by an amount $E_r$. When the parental counter for a female reaches 14 (Schorger, 1955), a chick is hatched, which is assigned a random sex, the maximum possible energy $E_m$, and a temporary reduced movement radius equal to its parents $r_p$, by artificially assigning a parental counter to the juvenile.

### 2.7.5 Movement

Nonparenting passenger pigeons begin their movement with a check for how long they have remained stationary in a patch. Passenger pigeons are allowed a maximum of $S$ days to remain in a patch, where the probability of a pigeon being forced to move out of a patch due to their stationary behavior increases by increments of $1/S$ each day. Pigeons that are forced to move simply select a patch within their movement radius $r$, that has a positive number of fruits, and their stationary counter is reset. In the event that no patch in their movement radius has fruits, a stationary pigeon will select a random patch in their movement radius and move there. If the pigeon moves to a new patch, their stationary counter returns to zero.

Parenting pigeons, along with those pigeons that are not forced to move due to a stationary check, will only consider the possibility of relocating if there is another patch in their movement radius with a positive number of fruits. In this case, the pigeon is able to identify the patch with the most fruits and has a probability of moving to that new patch, which is the complement of the ratio of the number of fruits in the current patch to the number of fruits in that new patch. If the pigeon decides to relocate to the new patch, then the pigeon has its stationary counter set to zero.

Regardless of the pigeons movement options, if a pigeon moves to a new patch, it is assessed an energy cost corresponding to the field metabolic rate (FMR), where the FMR is dependent on if the passenger pigeon is a parent or not. If a pigeon elects to stay in the current patch, it is assessed an energy cost corresponding to the basal metabolic rate (BMR), where the BMR is dependent on if the passenger pigeon is a parent or not. The values for FMR and BMR are discussed in the electronic supplementary material (ESM).

### 2.7.6 Forage

Pigeons who have an energy less than the maximum energy $E_m$, attempt to eat a constant number of fruits per day $n$ to reach their daily energy requirement $E_d$. However, if the patch has a number of fruits less than $n$, the pigeon consumes only the number of fruits in the patch. The number of fruits in the patch is then reduced by the number of fruits the pigeon consumed, and the energy of the pigeon increases according to the caloric value of the feeding, which depends
on the fruit variety. Finally, all nonsatiated pigeons consume alternative food sources, where the number of alternative food source units consumed are

\[ a(E_d, c, n) = \left( \frac{E_d}{c} \right) 0.05 - 0.1 \frac{(\# \text{ fruits eaten today})}{n} + 0.1 \left( \frac{E_d}{c} \right), \]  

(1)

where the derivation of the \( a \) function is provided in ESM. According to Equation (1), passenger pigeons are able to increase the number of alternative food units they consume (up to some bound) when fruits are limited and decrease the number of alternative food units when fruits are plentiful.

### 2.7.7 Random death

Each pigeon concludes its actions by a random death check. The pigeon dies with probability \( d = 1 - e^{-\mu} \), where \( \mu \) is the mortality rate.

### 2.7.8 Parameter table

A summary of all parameters in the model is provided in Table 3.

### 3 RESULTS

We conducted numerous simulations of the reintroduction of passenger pigeons to their historic range using various reintroduction plans. Throughout our results we attempted to optimize the probability that a colony of passenger pigeons would survive for at least 10 years and that their population in 10 years would be as large as possible. Model parameters were informed from the literature, or estimated when necessary.

Our study had two major aims.

1. To assess our model’s sensitivity to our literature-based and estimated values.
2. To evaluate the relative importance and find the optimal values for characteristics of a reintroduction plan, specifically release date, sex ratio, and forest density.

### 3.1 Sensitivity analysis

Any modeling of a real-world process contains a number of sources of uncertainty, yet our study is more prone to this circumstance due to our species of interest having been extinct for over a century and, thus, there are gaps in the scientific information available about it. These sources of uncertainty are primarily bioenergetic and movement restriction parameters and the mortality rate of pigeons. Additionally, our model includes the average fruit lifespan as a parameter, which is necessarily broad and encompasses many factors averaged across the plant species (e.g., natural decay rate of the fruit, uptake time from competing species, and dispersal) to keep the model parsimonious. To compensate for this uncertainty, we have varied our simulations
| Parameter | Units       | Definition                                      | Default value | Source                                      | LHS ranges     |
|-----------|-------------|-------------------------------------------------|---------------|---------------------------------------------|----------------|
| BMR       | kCal/day    | BMR of nonparental pigeons                      | 37.2          | Gavrilov and Dolnik (1985)                  | [33.5, 40.9]‡  |
|           |             |                                                 |               | Schleucher and Withers (2002)              |                |
| BMR<sup>†</sup> | kCal/day    | BMR of parental pigeons                        | b(BMR)        | Beissinger (1987)                          | –              |
| FMR       | kCal/day    | FMR of nonparental pigeons                      | 126.1         | Gessaman and Nagy (1988)                   | [108.7, 143.5] |
| FMR<sup>†</sup> | kCal/day    | FMR of parental pigeons                        | b(FMR)        | –                                           |                |
| E<sub>m</sub> | kCal       | Maximum pigeon energy                           | 872.3         | ESM                                         | [785.07, 959.53]‡ |
| E<sub>r</sub> | kCal       | Minimum energy needed to reproduce for females | 78            | ESM                                         | [70.2, 85.8]‡  |
| E<sub>d</sub> | kCal       | Daily energy requirement                        | 255           | ESM                                         | [229.5, 280.5]‡ |
| a<sup>†</sup> | Alt. food units | Number of alternative food units eaten per day | Eq. (1)       | Murton and Westwood (1966)                 | –              |
| b         | Unitless    | Additional energy multiplier for parents        | 1.263         | Beissinger (1987)                          |                |
| c<sup>†</sup> | kCal       | Kilocalories per alternative food unit          | 0.7           | ESM                                         |                |
| n<sup>†</sup> | fruits     | Max number of fruits eaten per day              | \(\frac{0.9%(E_d)}{16}\) | Murton and Westwood (1966) | – |
| S         | days        | Number of potential stationary days            | 4             | SELFNutritionData                          |                |
| λ<sup>−1</sup><sup>§</sup> | days     | Average fruit lifespan                          | 30            | [5, 60]                                    |
| μ         | days<sup>−1</sup> | Mortality rate of pigeons                     | \(\frac{1}{365.4}\) | Centre (2015)                             | [0.9 \(\frac{365.4}{365.4}\), 1.1 \(\frac{365.4}{365.4}\)] |

Note: Parameters marked with † indicate a parameter that is calculated as a function of other parameters. Parameters marked with ‡ indicate a parameter for which we could not determine literature supported ranges; hence, they are varied by 10% (or approximately if they require integer values) in the LHS. Parameters marked with § indicate a parameter for which we could not determine a literature supported value, nor a range, and are estimated with a wide range.

Abbreviations: BMR, basal metabolic rate; ESM, electronic supplementary material; FMR, field metabolic rate; LHS, Latin hypercube sampling.
across potential values for the average fruit lifespan and used Latin hypercube sampling (LHS) analysis for bioenergetic, movement restriction, and mortality rate parameters. The sensitivity analysis we performed provides insight into the robustness of our model to deviations from the default value selected for these uncertainties. The ranges of parameter values selected were informed by empirical studies with species-specific information when possible; however, some ranges were determined using similar species when necessary.

We began by fixing all control parameters (the number of pigeons released, the sex ratio of the initial colony, their release date, the forest type, and forest density) and investigated the robustness of our model to the assumed parameter values. The number of pigeons released in each simulation was held constant at 10 to reflect (a) the large cost of such a de-extinction program, (b) to avoid extreme demographic stochastic effects of populations with lower numbers, and (c) to limit the already extensive exploration of control parameters. We varied nine parameters (indicated in Table 3) in 500 combinations, using a LHS method (McKay et al., 1979), with 100 realizations for each parameter combination. We then calculated partial rank correlation coefficients (PRCC) for each parameter according to two outputs: (a) the mean survival percentage (the percentage of runs where neither males nor female pigeons reach a population of zero across the 100 realizations), and (b) the mean number of pigeons alive 10 years after release.

Figure 2 shows a barchart for the PRCC values for each output. Against both outputs, the PRCC results suggest that our model is moderately robust to all parameters within their biological or estimated range, except two: the average fruit lifespan and the mortality rate. Mortality rates for passenger pigeons in the wild are unknown (Blockstein, 2002), so we used a comparable species, the rock dove, to estimate the mortality rate for passenger pigeons. We remark that we were unable to determine a scientific study that estimated the average lifespan of a fruit in forest conditions; as a result, we assigned it a large range. Therefore, for the rest of our results we fix all parameters except the average lifespan of a fruit and vary the control parameters.

### 3.2 Reintroduction plan characteristics

#### 3.2.1 Release date

We continued by examining the influence that the release date of the pigeon colony had on their survival for various forest densities, both forest types, and across possible average fruit lifespans. We randomly selected 10 release days in the 6-year masting cycle of the forests, and at each average fruit lifespan we simulated the model 100 times for each of the 10 release dates. Then, at every average fruit lifespan value, we record the mean and standard deviation in the mean survival percentage across the 10 release dates. The results in Figure 3 indicate that for average fruit lifespans less than 10 days, there exists no possible forest density nor release date that are sufficient for the pigeon colony to persist. However, with moderate average fruit lifespans, approximately 15 to 25 days, the persistence of the colony is plausible, and increases with forest density. Beyond average fruit lifespans of 25 days, the colony is nearly certain to survive. The influence of the release date is greatest for moderate average fruit lifespans, and that influence is greater when forest densities are lower, but this influence of release dates is reduced modestly when average fruit lifespans exceeds 25 days; however, the interaction effect of forest densities and average fruit lifespans dissipates. For further results, we will fix $\lambda^{-1}$ to a value where survival is neither implausible nor certain. The inflection point of the mean
survival percentage when forest density is approximately 75% is approximately \( \lambda^{-1} = 18 \), and the curve saturates near \( \lambda^{-1} = 21 \).

### 3.2.2 | Sex ratio

Next, we investigated the feasibility of a survival advantage by releasing more female or more male pigeons, while the total population released remained fixed. To do so, we fixed the average fruit lifespan, forest density, and the release date (which was optimized for the release of five male and five female pigeons) and recorded the survival percentage and mean number of pigeons alive.
at 10 years across 1,000 realizations of the model at each sex ratio. Figure 4 suggests that at lower $\lambda^{-1}$ the natural selective forces are greater than any disadvantage/advantage brought on by a disproportionate number of females. However, at moderate values of $\lambda^{-1}$, we find that a disproportionate number of females reduces the survival percentage and reduces the average 10-year population.

3.2.3 | Forest density

Finally, we varied forest density while fixing all other control parameters, while measuring the survival percentage and 10-year population, with 500 realizations per forest density tested. Figure 5 results indicate that there exists a minimum forest density at which survival becomes feasible. For moderate forest densities, when $\lambda^{-1}$ is low, there does not exist a threshold forest density at which survival becomes substantially more likely; however, there exists such thresholds when $\lambda^{-1}$ is moderate. The two forest types performed similarly for low forest densities, although, at moderate and large forest densities the oak-hickory forest had higher survival probability and mean number of pigeons alive at 10 years.
4 | DISCUSSION

The numerous ethical concerns and extraordinary costs of genetically de-extincting the passenger pigeons warrant a study to determine the feasibility of such a project succeeding from a resource landscape perspective. Our mathematical model is a tool that allows us to vary re-introduction strategies in silico before enacting a plan in situ, thus, giving the initial colony the highest probability of survival. Due to our assumptions on the ecological framework, our model is limited in application to an early transient phase of the re-introduction process. We also make a number of assumptions about parameter values; for example, we used the mortality rate for rock doves as a proxy for the passenger pigeon’s, which may have differed greatly due to their
Despite these approximations, we demonstrate that our model is relatively robust to deviations from our default parameter values. Before assessing reintroduction strategies, we determined our model's robustness to the numerous known, derived, and estimated biological values. Figure 2 suggested that our model was only sensitive to one unknown parameter value, the average fruit lifespan, to which it is highly sensitive. Our results indicate the successful reintroduction of passenger pigeons is controlled by a threshold value for the average fruit lifespan. When average fruit lifespan is less than 17 days, any reintroduction plan is unlikely to succeed. When average fruit lifespan nears a threshold value of 18 days, the probability of a successful reintroduction increases significantly and saturates near 21 days. Though we were unable to locate a study in which fruit lifespans were relative abundance. Despite these approximations, we demonstrate that our model is relatively robust to deviations from our default parameter values.

Before assessing reintroduction strategies, we determined our model's robustness to the numerous known, derived, and estimated biological values. Figure 2 suggested that our model was only sensitive to one unknown parameter value, the average fruit lifespan, to which it is highly sensitive.

Our results indicate the successful reintroduction of passenger pigeons is controlled by a threshold value for the average fruit lifespan. When average fruit lifespan is less than 17 days, any reintroduction plan is unlikely to succeed. When average fruit lifespan nears a threshold value of 18 days, the probability of a successful reintroduction increases significantly and saturates near 21 days. Though we were unable to locate a study in which fruit lifespans were
estimated in actual forest conditions, the lower bound we found for the average fruit lifespans is unlikely to have changed drastically from the value that once sustained passenger pigeons, even though forest composition and density has. This logical conclusion is supported by a limited number of studies that do suggest that fruits such as acorns can exist in consumable states for at least 35 days (Novak et al., 2018). This means that, while survivability looks bleak for simulations below this threshold, we are optimistic that realistic values of average fruit lifespan are not in the extinction range.

Reintroduction plans for passenger pigeons require several specifications, of which, can drastically alter their survival probability and their population at 10 years. We analyzed four key characteristics of reintroduction plans: (a) release dates, (b) sex ratio, (c) forest density, and (d) forest type.

The influence of release date was highly correlated with the average fruit lifespan, where the effect is negligible when average fruit lifespan is below the threshold value, is greatest at the threshold value, and dissipates to a nontrivial level beyond that threshold (see Figure 3). Intuitively, this relationship arises as the average fruit lifespan dictates how many temporal gaps there are without any available fruits, causing unstable reproduction patterns and extinctions due to demographic stochastic effects or overpopulation.

Next, it’s plausible that a reintroduction plan could benefit from deviating from a symmetric sex ratio due to the uneven energy costs of reproduction between the sexes. While fixing the number of total passenger pigeons released, we were unable to detect any advantage by allowing additional male or female passenger pigeons. In fact, we found that as the average fruit lifespan increased, the cost of altering the sex ratio away from symmetry was harmful. This observation could be explained by noting that the natural selective forces are greater than any disadvantage or advantage brought on by a disproportionate number of females when survivability is unlikely due to environmental conditions, but when natural selective forces are weakened, the consequences of a disproportionate number of females is amplified (see Figure 4).

We also determine that forest density is highly influential on reintroduction success. When the average fruit lifespan is low, there exists a minimum forest density for survivability to be plausible and beyond this threshold the increase in survivability is nearly linear. However, as environmental conditions become more favorable, an inflection point at which survivability increased substantially appears, suggesting that forest densities as low as 40 or 50% result in persistence in at least half of the realizations (see Figure 5). This nonlinear relationship seems predictable, since, as the forest density increases, the compounding effect of extended fruit lifespan acts non-linearly, and so too does the survival probability.

The final reintroduction characteristic we analyzed was the forest type selected for the colony. Our model’s sensitivity was not significantly altered in different forest environments; however, the relative importance of the other reintroduction characteristics did change. In particular, the importance of the release date was reduced in oak-pine forests, and guaranteed persistence of the colony required slightly higher average fruit lifespans (Figure 3c,d). Consequently, due to lower survivability, the influence of nonsymmetric sex ratios was reduced in oak-pine forests (Figure 4). Finally, differences in the influence of forest density on survivability were amplified as forest density increased (Figure 5), and in particular, oak-hickory forests seem to pose an advantage in comparing the number of pigeons alive 10 years after release.

Our model acts as a base model with numerous assumptions about the landscape and passenger pigeon dynamics that can be relaxed in future adaptations. Examples of such extensions include (a) simulating the passenger pigeon reintroduction program on a longer time scale by allowing multiple forest systems and travel between them, (b) including forest...
compositions beyond oak-hickory and oak-pine, and (c) including flocking dynamics to magnify the effects of spatially-dense forging behavior.

Although our model indicates the reintroduction of passenger pigeons into their historic range could be successful, there exist several ways that success can be optimized. Our model suggests the highest chance for success is to release a colony of an equal number of males and females into an oak-hickory forest with at least 50% density on an optimized release date (which, in this case, would be at or around the spring equinox of Year 3 in the 6-year cycle). Despite optimal conditions, it’s important to note that even by 10 years after release, it’s unlikely that that the passenger pigeon population could triple (Figure 5b), suggesting that careful monitoring and protection would be a key element of any reintroduction plan.

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AUTHOR CONTRIBUTION
A. C. conceived the idea, design, experiment. D. E., E. B., J. C., and A. R. performed the experiments. D. E., E. B., J. C., A. R., and A. C. wrote the paper. D. E. and A.C. developed or designed method. D. E. and A. C. analyzed the data. A. C. contributed substantial materials, resources, or funding.

CONFLICT OF INTERESTS
The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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