Optimizing the Spatial Distribution of Fruiting Agave on Bat-Friendly Tequila Plantations

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Abstract

Bat-friendly tequila plantations aim to feed pollinating bats like the Mexican Long-nosed Bat (*Leptonycteris nivalis*) by allowing a portion of their crop to flower at the expense of the final harvest size. We seek to determine if the spatial distribution of flowering agave has any impact on the number of bats a plantation could support, so that farmers interested in preserving nectarivorous bats could do so more efficiently. We created an agent-based model, a type of computer simulation, to study the interaction of *L. nivalis* bats and *Agave tequilana*. The model is informed by phenology and empirical parameters from the literature such as energetics. We compared four different spatial arrangements of flowering agave and determined spatial distribution does impact bat populations, with the most efficient arrangements yielding population estimates consistent with conservationist predictions, validating our model. Finally, the emergent bat carrying capacity of a plantation is directly proportional to the amount of flowering agave meaning that farmers need not worry about diminishing returns from their conservation efforts.

Keywords: agent-based-modeling, NetLogo, *Leptonycteris nivalis*, *Agave tequilana*, optimization, bat-friendly, conservation

Contents

1 Introduction

The Mexican Long-nosed bat (*Leptonycteris nivalis*) is a migratory and nectarivorous species found across central Mexico and the southwestern United States. In 2016, *L. nivalis* was declared endangered according to the International Union for Conservation of Nature (IUCN). *L. nivalis* continues to hold a spot on the IUCN Red List of threatened species as population levels have remained low (Medellín 2016).

L.nivalis plays a crucial ecological role as a pollinator. The reproduction and survival of many agave species in Mexico depend on *Leptonycteris* bats. Each night, as these bats visit agave flowers to feed, they transfer pollen between plants. This mutualistic relationship allows bats to sustain their high energy requirements, while also supporting agave reproduction, genetic diversity and long-term viability (Trejo-Salazar et al. 2016). Ultimately, these bats play a significant role in maintaining agave biodiversity and sustainability of both natural sources of agave and sources used for industrial purposes such as tequila production.

The tequila industry is both economically viable and physically expansive. In 2019, 141,123 hectares of land were utilized to cultivate agave for tequila production and 34,187 hectares of agave were harvested (Honorato et al. 2021). Tequila exports to the US were worth 4.9 billion USD in 2019 alone(Russell and Kenner 2023). While there is an abundance of agave plants in Mexico to support the tequila industry, these plants are not allowed to flower, limiting food sources for nectarivorous bats such as *L. nivalis* (Alducin-Martínez et al. 2022).

A nectarivorous species feeds primarily on nectar from flowers and other nectar-bearing plants. *L. nivalis* specifically relies on the nectar of agave species as one of their main food sources (Region 2022). Some of the most notable threats to *L. nivalis* populations include the loss of food sources due to agriculture and human exploitation of agave, and the impact of human disturbances on roosting sites (Fish and Service 2018).

Agave are a monocarpic species, meaning they can only flower and reproduce once in their life(Gómez-Ruiz and Lacher 2016). On average, it takes an agave plant at least 8 years to reach maturation and be able to flower (Monja-Mio et al. 2019). This is also the age at which agave would be harvested for tequila production. Both processes take place when sugar levels in the piña (plant's core) are highest and utilize the sugars stored in the plant, thus, agave plants cannot be used for both tequila production and conservation efforts to support nectarivorous bats.

Bat conservationists have suggested the promotion of a bat-friendly tequila concept to support bat populations. Through this initiative, by allowing just 5% of agave in tequila fields to flower, one hectare of land would provide food for 89 bats. If extended all throughout Mexico, *Agave tequilana* would provide food for over nine million bats alone. Not only would this help bat populations, it would also help agave plantations be less susceptible to disease from monoculture practices (Trejo-Salazar et al. 2016).

The survival of *L. nivalis* depends heavily on healthy and flowering populations of agave.

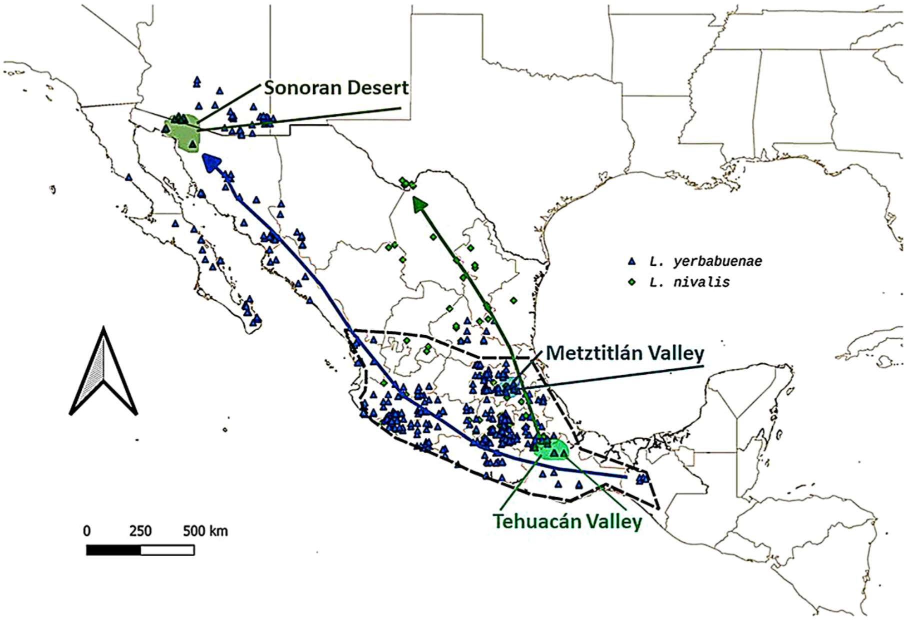

Figure 1: Migration routes of *L. nivalis* in green, with bats residing year round within the boxed region Trejo-Salazar et al. 2023.

Both their migratory and reproductive behaviors heavily align with the location of agave sources and peak flowering season (Moreno-Valdez et al. 2004).

For instance, the annual long-distance migration, which is carried out primarily by pregnant females, follows "nectar corridors" on the eastern side of Mexico from southern-central Mexico to the southwestern United States, specifically Texas and New Mexico (1). These "nectar corridors" are a sequential path of flowering agave that provide critical energy during migration and are essential for sustaining the bats' high metabolic demands, particularly for pregnant or lactating females (Santiago Arizaga 2000).

Both female and male bats live in the same region (southern and central Mexico) during the fall and winter months, and mating occurs between them from December to February (Fish and Service 2018). The pregnant female bats follow the nectar corridors to migrate north as agave are in full bloom, having less competition from their male counterparts for nectar (Santiago Arizaga 2000). Most agave species have a four-month flowering window that overlaps with the bats' northward journey. The migration north happens as early as March. Females then give birth in June and July in northern caves. Each female gives birth to one pup, and then begins migration South in September, arriving in far southern roosts in October (Moreno-Valdez et al. 2000). Figure 2 summarizes this cycle.

Leptonycteris bats have rigid daily energy requirements, especially during migration and reproduction. Nonreproductive individuals require approximately 40 kJ of energy per day, while lactating female require 60–80 kJ. Of this daily energy budget, 44% is spent on flight,

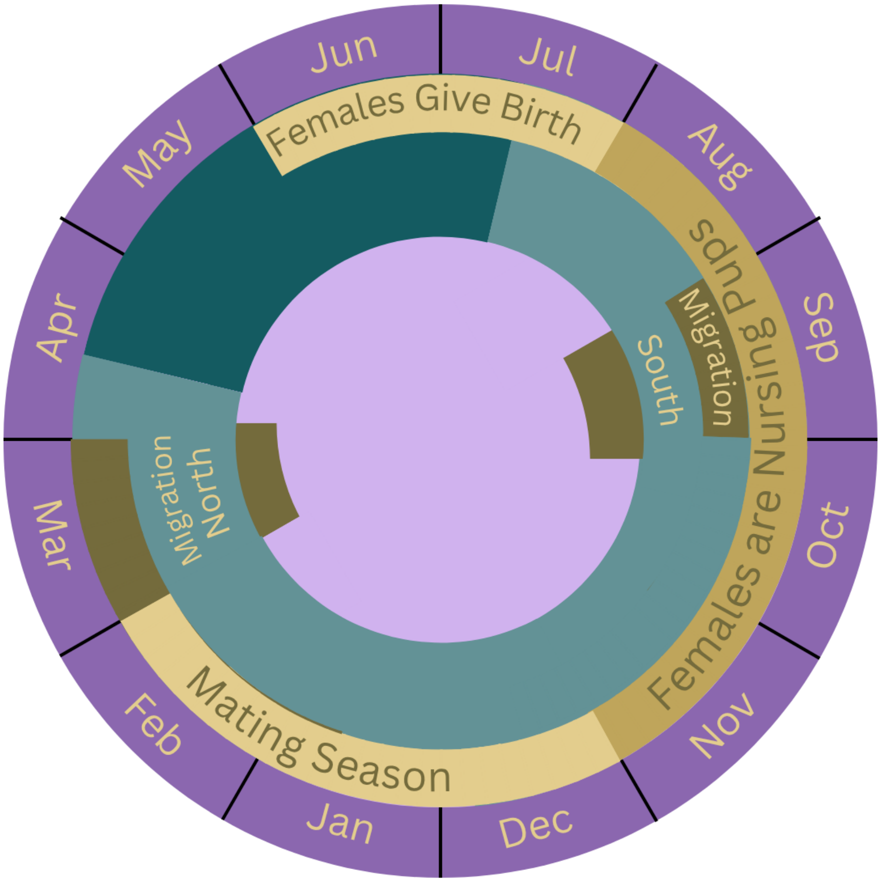

Figure 2: Phenology wheel summarizing the seasonal behaviors of *L. nivalis*.

despite the fact flight takes up only 21% of their time. In contrast, day roosting occupies 75% of their time but consumes only 50% of their energy (Cole and Wilson 2006). Furthermore, nectar-feeding bats have very limited internal energy reserves and are highly dependent on constant food intake. As much as 95% of their daily energy needs are met by direct sugar intake from their diet, rather than from stored reserves. After just 18 hours of fasting, *Glossophaga soricina* have severe implications, and individuals cannot survive 24 hours without food (Amaral et al. 2018). These strict energy requirements emphasize the importance of both abundant nectar sources and undisturbed roosting sites for bat survival.

To maintain their daily energy demands, *Leptonycteris* bats make roughly 80–100 visits to nectar-bearing plants throughout the night (Cole and Wilson 2006). Nectar production in agave peaks at night, which aligns with bat foraging as bats are a nocturnal species (Rocha et al. 2005).The bats are attracted to the agave plants based on the stage of the reprouctive cycle the plants are in, the height of the inflorescence, and the smell of the nectar that is produced in the flowers (Lear et al. 2024).

In an effort to model these biological behaviors of both of the bats and agave, we chose to use an Agent-Based model to capture the individual behavior, interactions, and emergent properties that come from the relationship between bats and agave. In the model we program the bats to have these biological characteristics in terms of their energy, age, reproduction, and foraging properties. We also program the agave to include such characteristics as their age, nectar concentration, and nectar production. In simulating these behaviors and interactions we are able to analyze different features that may have an effect on bat populations.

Given the species' endangered status, we look to find an optimal distribution of flowering agave on plantations that will lead to the highest increase in bat populations, following the idea of bat-friendly plantations. Perhaps there is a way to maximize bat populations beyond simply increasing flowering percentages, maybe the spatial distributions of flowering agave has an impact as well. In the model, we analyze the emergent properties, such as carrying capacity, to see if there is an optimal distribution, testing flowering agave randomly placed throughout the plantation, concentrated in a set corner, in rows, and along the perimeter.

2 Materials and Methods

The model description is structured according to the Overview, Design Concepts, and Details (ODD) protocol for agent-based models (Grimm et al. 2020). The model was implemented in NetLogo version 6.4.0 (Wilensky, U 2023).

2.1 Purpose and Patterns

This agent-based model (ABM) was developed to simulate foraging behavior of *L. nivalis* on agave plantations under varying flowering distributions to determine the effect on survival rates and population growth of nectar-feeding bats. The model aims to inform agave farming practices by incorporating considerations for the conservation of migratory pollinators. The model is based on agave cultivation on artisanal plantations in south-central Mexico, which this bat species inhabits year round (Fish and Service 2018).

2.2 Entities, State Variables, and Scheduling

Our model has two entities: bats (both male and female) and agave. All state variables characterizing these entities are listed in Table 1 (agents) and Table 2 (patches).

Both female and male bats are mobile agents having attributes represented as state variables in the model. These include age, energy, memory, and migrating. Female bats have an additional attribute represented as a state variable called reproductive-success.

Variable	**Description**	**Default Value**	**Range**	**Source?**
bat-population	Number of bats initially hatched during setup	100 bats	0–1000 bats	
age	Age of the bat in days	N/A	[0, 3650] days	(Clarke n.d.)
sensing-radius	Radius bats can sense flowering agave	10 patches	0–57 patches	
distance-from-roost	Distance between roost and farm that bats are assumed to travel each night to and from the roost	25 km	0–50 km	(Region 2022)
energy	Current energy level of a bat	$N(40, 2)$ kJ	$[0, \infty)$ kJ	(Cole and Wilson 2006)
daily-energy-use	Energy used for day roosting and digestion each day	$N(20, 1.5)$ kJ	$N(20, 1.5)$ kJ	(Cole and Wilson 2006)
feeding-times	Visits of an individual bat to a plant in an hour	$N(15, 2)$ flower visits/hour	80–100 visits to flowers per night	(Cole and Wilson 2006)

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Variable	**Description**	**Default Value**	**Range**	**Source?**
memory	List of previously visited flowering patches with nectar available	List of patch agents	N/A	
memory?	Whether the bat remembers where visited flowering patches with nectar available are	true	true/false	(Lear et al. 2024)
births	Counter for bats that are born	0	$[0, \infty)$	
migrating?	Whether the bat is currently migrating	false	true/false	
migrate-south	Determines whether a female bat survives migration	0.07424	N/A	(Cole and Wilson 2006)
reproductive-success	Determines whether a female bat returning from migration has a pup and the sex of the pup	N/A	$[0, 1)$	(Adams 2015)
random-deaths	Counter for bats that die due to random causes or old age	0	$[0, \infty)$	
random-death	Percent chance a bat will die each day due to random causes	0.02314% (juvenile), 0.03161% (adult)	N/A	(Adams 2015)
energy-deaths	Counter for bats that die due to starvation/energy depletion	0	$[0, \infty)$	

Table 1: Agent variables used in model

Variable	**Description**	**Default Value**	**Range**	**Source?**
flowering-distribution	Spatial distribution of flowering agave	N/A	"uniform-random" "corner' "rows" "perimeter"	
flower-percentage	Proportion of agave set to flower	0.05	0-1	
flowering?	Whether the patch is currently flowering	false	true/false	
nectar	Amount of sucrose available on a patch currently	0	$[0, \infty)$	
nectar-concentration	Sugar concentration of the nectar a plant produces	$N(22, 2)$	$[18, 26]$	(Trejo-Salazar et al. 2016)
set-nectar	Assigns a nectar value to flowering patches	$4.406 \cdot$ nectar-concentration	N/A	(Mielenz et al. 2015)
roost-patch	Randomized patch location of the central roost	1 patch agent	3 outermost rows and columns	

Table 2: Patch variables used in model

Grid cells (ie: patches) are representative of land cover and each patch represents the same amount of land. State variables storing information for grid cells include flowering?, nectar, and roost patch.

Grid cells can consist of agave (flowering or not flowering), a central roost, or be included in the boundary of the plantation (representative of land outside the plantation and present for increased variation when placing the roosting site).

The model operates on an hourly time step, simulating nocturnal bat behavior over a 24-hour daily cycle. Each day consists of a roosting period (daytime hours) and an active foraging period (11:00 p.m. – 05:00 a.m.). State variables also exist to keep track of what year, month, and day it is, and month and day both reset to zero after reaching 12 and 30, respectively. Within each hour, bats have the opportunity to forage and wander the plantation, assuming they are not migrating. The month state variable is useful for determining if bats are migrating or not, and thus if they are around to perform the daily wandering and foraging subroutines at the plantation.

Our model represents an artisinal plantation, assumed to be 8.5 hectares. It is assumed that agave plants are planted in fields organized by the age of the plant, such that all plants in one field would be harvested at the same time. Our model looks at one field per year, the field that is ready to be harvested. On average, agave takes seven to ten years to flower (Lopez Romero et al. 2017). We are assuming the agave will uniformly reach maturity at 8.5 years to simplify the model. Additionally, we are assuming farmers use a planting method in which all plants in one area of the field are of the same age and maturity level. This way, we can cycle through different sections of the plantation when it reaches the flowering season in sequential years. Within the model, each patch is scaled to correspond to two agave plants, simplifying the tracking of flowering status, harvestability, and maturity, and enabling the model to evaluate how the spatial distribution of flowering agaves affects foraging behavior, mortality, and energy dynamics in bat populations.

Each year, five percent of the mature agave in the plantation (2/17th of the plantation) is designated to flower, providing a nectar source for *L. nivalis* pollinators. Agave will either flower in a uniform random, row, corner, or perimeter distribution. The remaining mature agaves are harvested for tequila production, as this typically occurs just before the plants would naturally flower (Honorato et al. 2021). After the flowering and harvesting season ends, this section of the plantation would be replanted and the model would move on to the next oldest section of the plantation.

At the start of the next flowering season, the next section of the plantation would flower following the same distribution (uniform random, row, corner, or perimeter). The same procedures would be followed in this section, flowering and harvesting, then the replanting of new agave plants. The cycle then advances to the next oldest section. This rotational replanting system ensures a continuous annual supply of flowering agave to support bat populations, without interrupting the harvest needed for tequila production.

2.3 Design Concepts

2.3.1 Basic Principles

Nectarivorous bats have low body energy reserves and cannot consistently survive fasting for 24 hours (Amaral et al. 2018). It is estimated that bats consume, on average, 15 milliliters of nectar a night (Trejo-Salazar et al. 2016), the bats' daily energy budget is 40 kJ, and that bats make between 80-100 visits to flowers each night (Horner et al. 1998). We have programmed the bats to forage between the hours of 11 pm and 5 am, and eat on average 15 times per hour if they find a flowering agave plant to model this natural pattern. Our bats are assumed to feed from the hours of 11:00 p.m. to 5:00 a.m., which coincides with maximal nectar production in many *Agave* species (Rocha et al. 2005). It has been suggested that flowering times and nectar production impact bat behavior patterns, so it is prudent to assume that agave-feeding bats will be active when agave nectar production is maximal (Bogan et al. 2017).

2.3.2 Emergence

The key emergence in our model is the carrying capacity of our plantation. Through our experiments, we have determined that flower-percentage, sensing-radius, memory, and flowering-distribution all have significant influence on the carrying capacity. Another emergent behavior that depends heavily on the presence of memory in the model is the method by which bats disperse through the plantation.

2.3.3 Adaptation

Bats exhibit adaptive behavior when determining where to forage through the night. All bats have a sensing radius, and will prioritize travel towards any agave with nectar within this radius, mimicking bats' usage of their olfactory senses in the real world. Bats have memory where they store the locations of agave with nectar. If there are no flowering agave plants with nectar within their sensing radius, then when they go to forage they will move towards agave plants stored in their memory. Finally, if there is both no agave in their sensing radius or memory, they will move randomly. This behavior is indirect objective-seeking, as bats in the model do not evaluate their options using some measure of success, but rather behave as observed in the wild, where they travel to the nearest agave with nectar, and if there are no agave with nectar near, return to a known location, and if no known locations have nectar, wander until they find a new plant to forage from.

2.3.4 Sensing

Bats have highly developed olfactory senses, which they use to navigate and identify flowering agave (Gonzalez-Terrazas et al. 2016). The bats' sensing radius is a user-defined variable and bats will be able to sense all flowering agave with nectar in the area within their sensing radius. Bats are assumed to accurately know if a plant has nectar or not, as they primarily use their olfactory senses when seeking out fruiting plants.

2.3.5 Interaction

Bats have mediated interactions with other bats, as all bats are competing for a common food source, nectar. Bats compete nightly: as the evening continues, the concentration of nectar within the agave is depleted as it is consumed. Bats need to forage enough nectar each night to cover flight costs both within and to the plantation, and as nectarivorous animals, bats have significant energetic requirements. Bats consistently forage for nectar when nectar concentration is the highest, but as the night continues, nectar resources become more scarce. Bats typically do not drain plants completely of nectar, rather they tend to spread out feedings amongst multiple plants in an area (Horner et al. 1998). However, a large population of bats will quickly use up limited nectar resources, leading to energy-related deaths.

2.3.6 Stochasticity

Stochastic processes are used to initialize this model. Bat age is set to a random number no larger than 3650 in an exponential distribution with a mean of 1095, or three years. Bat energy is set to a random number in a normal distribution with a mean of 40 and a standard deviation of 2. The layout of the farm also relies on random processes, after selecting the farm layout type and the flowering percentage, random patches in the layout are set to flower until the desired percentage of flowering agave has been reached. Each patch is initialized with a nectar-concentration, a random number pulled from a normal distribution with a mean of 22 and a standard deviation of 2. The number of feedings a bat participates in each timestep is also determined with a random number pulled from a normal distribution with a mean of 15 and a standard deviation of 2. Bat energy, number of feedings, and nectar-concentration are randomized using known mean values to introduce variability into a bat's nightly routine (Horner et al. 1998). When bats perform the wander subroutine because there is no flowering agave in their sensing radius or memory, they move in a random direction to find agave. These stochastic processes ensure that subroutines have some sort of variation to account for any number of natural phenomena like windspeed, daylight hours, and rainfall that may affect foraging success and nectar concentrations within agave plants.

2.3.7 Observation

The model has many different reporters, including number of random-deaths, number of energy-deaths, the time, the total population, and the number of male and female bats specifically. This data was collected through Behavior Space, with the reporters' values being recorded at the beginning of each month.

2.4 Initialization

The model is initialized with the to setup function. The model starts on January 1, year 1, and the environment is a square with a side length of 46. The landscape of the model is determined by user input. The user determines the percentages of agave left to flower and chooses between four flowering methods: uniform-random, which selects the chosen number of random agave plants across the world to let flower, random-perimeter, which selects the chosen number of random agave plants on the perimeter of the farm, random-rows, which selects the chosen number of agave plants from the same random row or column, and corner-cluster, which selects the chosen number of agave plants from a specific corner. Patches have their nectar-concentration set randomly based on a normal distribution with a mean of 22 and a standard deviation of 2. Patches that have flowered then have their nectar set to their nectar-concentration * 2.203 * 2, representing the available nectar in their flowers. The entire environment is the farm, except for a 3 cell wide border around the outside of the world. Any cell in the border region has a random chance of being chosen as the bat cave. Bats are placed in the bat cave upon its creation. Equal numbers of male and female bats are created. Their migrating status is set to false, their energy is set randomly based on a normal distribution with a mean of 40 and a standard deviation of 2, their age is set randomly based on an exponential distribution with a mean of 1095 days, with a hard cut-off at 3650 days (the end of a bat's natural lifespan), and their memory is empty.

2.5 Input Data

The model does not use input data to represent time-varying processes.

2.6 Submodels

Forage. This procedure is executed by non-migrating male and female bats from the hours of 11:00 p.m. to 5:00 a.m (hours ≥ 23 or ≤ 5). Each bat can only forage once per hour, but they have three chances to find available nectar as bats are mobile and fly around at night. During each attempt, a bat scans within the sensing-radius for patches that are both flowering and have available nectar (denoted by patch variables flowering? and nectar). If such patches exist, the bat randomly selects one and moves to it, expending energy proportional to the distance traveled ($0.0005 \cdot$ distance, explained in daily-energy-use). At the flowering patch with available nectar, the bat consumes nectar a random number of times drawn from a normal distribution with a mean of 15 and a standard deviation of 2 because bats feed 80-100 times per night (see intro). For each feeding, the bat gains 0.444 energy, while the patch's nectar is reduced by 1.289 units per feeding. If no suitable patches are found within the sensing radius, the bat instead initiates a wander subroutine to search for nectar elsewhere.

Assuming a bat feeds 90 times per night (center point of 80-100) to acquire 40 kJ of energy (Cole and Wilson 2006), each feed results in an average gain of .444 kJ. Hence, to calculate energy gained while foraging, the randomized number of feeds that hour is multiplied by 0.444. Furthermore, if 2.48 *Agave angustifolia* inflorescence are needed to sustain one bat assuming a 26% sucrose concentration and an average of 180 μL of nectar per inflorescence (Trejo-Salazar et al. 2016), this means a bat requires 116 μL of sucrose $\left(\frac{180\mu\text{L nectar}}{\text{inflorescence}} \cdot \frac{2.48 \text{ inflorescence}}{\text{bat}} \cdot \frac{.26\mu\text{L sucrose}}{\mu\text{L nectar}}\right)$ to obtain their energy requirements. This equates to an average of 1.289 μL of sucrose consumed per feeding, assuming 90 feeds per night.

If memory is enabled (memory? = true), whenever a bat visits a flowering agave patch with available nectar, the patch is added to the bat's memory. This patch will remain in the bat's memory until it runs out of nectar.

Despite having three attempts to forage, a bat can only forage once per hour. If the bat forages, foraged-this-hour? is set to true and the bat cannot do anything until the next time step. Then the foraged-this-hour? tracker is set to false at the beginning of each hour. Throughout the night, the bat will repeat this same procedure after successful foraging attempts or after running through the wander subroutine. The following hour after a successful foraging attempt, the bat repeats the same procedure outlined above. Similarly, if the bat was sent to wander the previous hour, it scans to see if there is available nectar at its new location. If the bat visits a new patch with available nectar, the patch is added to the bat's memory. Similarly, if and only if there is no nectar available in the sensing radius, the bat performs the wander subroutine.

Wander. If a bat cannot find flowering agave with available nectar in its sensing radius, the bat is called to execute the wander subroutine. This can occur anywhere on the plantation, whether there are no flowering plants in the bat's sensing radius, or if a flowering plant runs out of nectar and there are no other flowering plants with nectar near the bat. This subroutine can be performed by all non-migrating bats.

If the bat is called to wander at 11:00 p.m., from the roost facing the center of the plantation, the bat rotates a random angle up to 45° in either direction, then travels 10 units in that direction. The bat loses energy proportional to the distance it flew while wandering. From 12:00 a.m. to 5:00 a.m., if the bat is called to perform the wander subroutine, the bat rotates a random angle up to 90° in either direction, then travels 10 units, still losing energy proportional to the distance it flew while wandering. Bat movement was limited to a 45° rotation while facing the center of the plantation at 11:00 p.m. to direct the agents to the plantation. *L. nivalis* has strong olfactory senses that would guide them to the plantation (Gonzalez-Terrazas et al. 2016), thus the model assumes the bats can make it to the plantation. However, after 11:00 p.m., bats can rotate more freely, up to 90° in either direction, to allow for a more random wandering of the plantation. This restricted movement increases the likelihood the agents will stay in the plantation area searching for agave, rather than randomly flying around beyond the edge of the plantation.

If the bat successfully foraged in previous nights and memory? is set to true, these agave plants have been added to the bat's memory. On following nights, the bat agents can travel directly to the successful flowering plants, losing energy proportional to the distance they have to fly to reach the plants. If a plant runs out of nectar, it is removed from the bat's memory. To be re-added to the bat's memory, the bat must rediscover the plant when it has regenerated nectar.

Check-death. Check death is executed every hour by all bats and can result in bat death by one of two methods. Bats can either die from energy depletion or due to random causes. To account for energy related deaths, any time there is energy expenditure, energy levels are checked. If a bat has an energy level of or below zero, that bat dies and the death is recorded as an energy related death.

To die due to random causes, a bat can do one of two things. First, at 10:00 p.m. (hour = 22), a random float is generated and if the float is less than 0.0002314 for juvenile bats (bats less than a year old) or 0.0003161 for adult bats, the bat dies. In a given year, juvenile bats have a 91.86% chance of making it through the year while adult bats have an 85.07% chance of surviving to the next year (Adams 2015), leading to a daily survival rate of 0.02314% and 0.03161% for juvenile and adult bats, respectively. This is representative of common mortality factors like predation, human disturbance, and dying of natural causes (Medellín 2016). The second way to die a random death is dying of old age. If the bat's age is greater than 3650, or ten years, the bat dies and the death is recorded with random-deaths.

Daily-energy-use. This subroutine updates each bat's overall energy expenditure after day roosting, reflecting the constant metabolic cost of survival regardless of activity. Of a bat's daily energy budget, 17.6 kJ are used for flight and 20 kJ are used while day roosting

(Cole and Wilson 2006). This subroutine reduces a bats energy by approximately 20 kJ ($N(20, 1.5)$ and occurs in one timestep (hour = 22) to simplify the model.

While not a part of the daily-energy-use subroutine, the bat also loses energy proportional to its journey from the roost to the plantation in the same timestep (as well as hour = 6 when the bat returns to the roost in the morning). Since a bat can fly up to 50 km to a food source in a given night, we divided 17.6 kJ by 100 km (roundtrip), equating to 0.176 kJ/km. However, since 50 km is as far as bats can fly to a food source, we rounded to 0.2 kJ of energy needed to fly one km. Therefore, when flying to or from the roost, a bat loses 0.2 kJ of energy per kilometer. This also translates to 0.0002 kJ of energy per meter, and with each patch in netlogo being 2.5 meters X 2.5 meters, bats lose 0.0005 (2.5 m $\cdot$ 0.0002 kJ/m kJ of energy per patch they fly during foraging and wander subroutines.

Check-migration. Check-migration is executed by bats every hour. In it, the bats check the time to ensure that female bats migrate north in March and return south in October, to fit with known patterns of female bat presence in northern roosting sites (Moreno-Valdez et al. 2004). On hour 10 of the first day of March, all female bats execute the migrate-north function. On hour 10 of the first day of October, the female bats who had migrated north execute the migrate-south function. At every other timestep, nothing happens.

Migrate-north. Migrate-north is executed by all female bats. It sets their migrating? variable to true, preventing them from performing wander, forage, or check death, and moves them to the roost, where they expend no energy. This simulates migration away from the farm.

Migrate-south. Migrate-south is executed by any bats with migrating set to true during October. It asks 7.424% of the migrators to die, simulating death in migration. Then it assigns each female bat a number between 0 and 1 called reproductive-success. Female bats with a number above 0.9186, which is 1 minus the rate of infant mortality for *L. nivalis*, do not hatch a new bat. Female bats with a number between 0.9186 and 0.5 * 0.9186 hatch a male bat. Female bats with a number less than 0.5 * 0.9186 hatch a female bat. All newly hatched bats have migrating? set to false, age set to zero, energy randomized using a normal distribution with a mean of 40 and a standard deviation of 2, and their memory is emptied. The birth counter is increased by one for each bat born. Finally, all migrating bats have migrating? Set to false.

Let-flower. Let-flower. The let-flower subroutine is executed when the model is initialized and anytime the field is rotated during a new flowering season. First, the number of agave allowed to flower is calculated by multiplying flower-percentage and the number of agave patches (1600). Then, based on the selected flowering arrangement, agave is set to flower, up until the number of flowering agave and calculated number are equivalent.

The four different spatial distributions include uniform-random, corner-triangle, random,rows, and random-perimeter. A "uniform-random" distribution selects a random subset of agave patches across the plantation, "corner-triangle" selects a triangular cluster of patches in the bottom left corner of the grid, “random-rows” selects agave in identified rows or columns; and “random-perimeter” restricts flowering to patches along the plantation’s outer edge. Patches selected to flower are set to flowering? = true and passed to the set-nectar routine to initialize nectar levels.

Set-nectar. The set-nectar subroutine assigns an initial amount of nectar to all agave patches marked as flowering and is performed after the let-flower subroutine when initializing the model or when rotating the field. The amount of nectar assigned to each patch is proportional to the nectar-concentration randomly assigned to the patch. *A. angustifolia* averages 18% - 26% sucrose concentration in its nectar (Trejo-Salazar et al. 2016).

One hectare of *A. angustifolia* has a biomass of 22 tons/hm^2 while *A. tequilana* has a biomass of 28 tons/hm^2 (Mielenz et al. 2015). Thus we assumed a *A tequilana* plant is 1.273 (28/22) times as large as a *A. angustifolia* plant. Furthermore, since a *A. angustifolia* plant with a 26% sucrose concentration produces 45 μL of sucrose per night (Trejo-Salazar et al. 2016), the plant produces 1.7303 μL of sucrose per sucrose percentage per night (45/26). When scaled to *A tequilana*, this equates to 2.203 μL of sucrose per sucrose percentage per night (45/26*1.273).

Since each patch represents two agave plants, when setting the nectar in the patch, nectar is equal to 2, the number of plants per patch, times 2.203, the μL of sucrose per sucrose percentage, times nectar-concentration, the concentration of sucrose in the nectar randomly assigned to the agave patch.

Regenerate-nectar. The regenerate-nectar subroutine restores nectar to flowering agave patches at the beginning of each new night, simulating the natural overnight regeneration of nectar. It is called once per night, immediately before bats begin their nightly foraging behavior. For patches with flowering? = true, it resets the nectar value to the same value defined in set-nectar. This ensures that nectar-depleted plants can become viable again in subsequent nights, while also not allowing patches to store infinite nectar as nectar is only good for so long. Patches that are not currently flowering do not receive regenerated nectar.

Rotate-field. Rotate-field represents the end of each harvesting year, where the field is tilled and emptied for a new crop of agave. During this time, another field on the plantation comes to maturity and begins to flower and be prepared for harvest. To simulate this, all plantation patches are cleared and their nectar is set to zero to clear the bats’ memories, and then the field is replanted.

2.7 Experimental Design and Execution

We ran several experiments and began sensitivity analysis on our model. Our experiments were conducted through Behavior Space in NetLogo. We used Behavior Space’s table output when collecting our data. Modeling, along with Statistical and Graphical analysis, was done using MatLab.

In our first experiment, we tested varied initial populations and flowering distributions to identify mean final populations and carrying capacities for each of the scenarios. We had memory on, distance-from-roost set to 25 km, flowering-percentage set to 5%, and sensing radius set to 10. We ran the model for 10 years with an initial population of 100, 20 years with an initial population of 10, and 20 years with an initial population of 250. We ran the model longer for initial populations of 10 and 250 to give the model time to approach a steady state. We ran each scenario 100 times, for a total of 1200 runs. We hypothesized the carrying capacity of our model to be 89, since (Trejo-Salazar et al. 2016) suggested that one hectare of plantation that allowed 5% of their agave to flower could support 89 bats.

In our second experiment, we tested the impact of memory on final bat populations and carrying capacities for each flowering distribution. We ran the model for 10 years with memory off and an initial population of 100, with the same initial conditions as the model run for 10 years with memory on, and we ran each scenario 100 times, for a total of 400 runs.

In our third experiment, along with flowering-distribution, we varied flower-percentage from 0% to 25% by 1 percentage point to determine if final bat population was proportional to flowering percentage. We had memory on, initial population was set to 100, sensing radius was set to 10, and distance from roost was set to 25 km. Each run lasted 10 years and we ran each scenario 10 times for a total of 1040 runs, 260 with each flowering-distribution. We recorded final population only.

In our fourth experiment, we varied sensing-radius along with flowering-distribution. Since our plantation is represented by a 40x40 patch grid, a bat at the far corner of the plantation would be able to sense the entire plantation with a sensing-radius of 57, so we varied sensing-radius from 1 to 57 patches by 1 patch. True bat sensing radius is not known, so we wanted to see if this model parameter had a significant impact on the data. We had memory on, initial population set to 100, distance from roost set to 25 km, and flowering percentage set to 5%. Each run lasted 10 years and we ran each scenario 10 times for a total of 2280 runs, 570 per flowering distribution. We recorded final population only.

3 Results

3.1 Emergent Carrying Capacity

To investigate emergent carrying capacity, we ran 100 simulations for each spatial distribution across different initial bat populations: 10 and 250 bats over 20 years, and 100 bats over 10 years. We then fit the logistic population growth model,

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right),$$

to the simulation data using MatLab. From each run, we calculated the mean final population, carrying capacity K, and growth rate r. Table 3 summarizes the mean values across all repetitions.

(Figure 3a) shows a representative logistic fit for an initial population of 10 bats for one of the repetitions. All spatial distributions reached a carrying capacity, though the size varied. Uniform-random and corner distributions yielded the highest final populations and K values (mean K = 101.64 and 172.35, respectively). Rows and perimeter had lower mean final populations (69.00 and 62.55) and corresponding K values.

With an initial population of 100 bats (Figure 3b), populations stabilized more quickly. The mean K values aligned more closely with the final populations, as expected with initial populations near carrying capacity allowing the model to reach an equilibrium faster. Growth rates r were significantly higher, particularly for the uniform-random distribution ($r = 1.0681$). Uniform-random and corner distributions again had higher mean K and final population values compared to rows and perimeter.

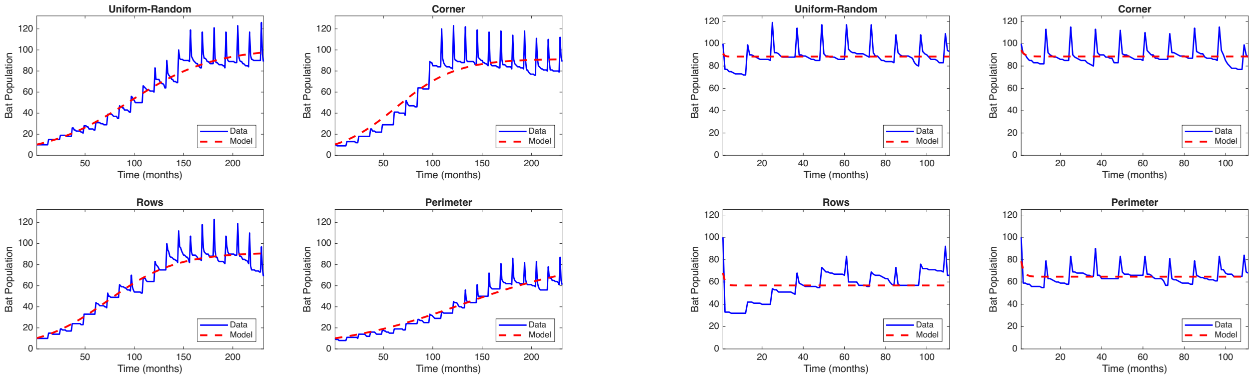
Simulations with an initial population of 250 bats (Figure 3c) also showed logistic dynamics. All spatial distributions again reached a carrying capacity, with uniform-random and corner producing final populations around 85, and rows and perimeter again lower (70.30 and 62.58, respectively).

We also examined the role of memory by disabling it for the initial population of 100 bats (Figure 3d). The uniform-random distribution performed similarly to the memory-enabled case. However, the corner distribution experienced a sharp drop in performance (mean $K = 17.78$), likely due to increased energy deaths when bats could not remember nectar locations. As seen in the singular repetition from (Figure 3d), the bat population dies out quickly, though this doesn't happen in all repetitions depending on the location of the roost in respect to the corner of flowering agave. The chance of a bat finding nectar is now random each day and if the roost is spawned far away from the corner, it takes too long for the bats to reach the nectar as they disperse throughout the plantation wandering instead of heading straight towards the nectar. In addition, the rows and perimeter performed better showing an increase K and final population value. With no memory and more dispersal through the plantation, the bats are able to find other sources of nectar besides the sources closest to the roost or only within the sensing radius of previously found nectar.

Notably, in the cases with an initial population of 10 especially, the mean K values are not as consistent with the final mean populations. For corner and uniform-random, the mean K values often exceeded final populations. Some of the simulations out of the 100 repetitions were not able to reach an equilibrium within 20 years. These results skewed the data and therefore resulted in a K value significantly higher than the final populations that the data might suggest. (Figure 4) reveals wide variability in K values. Because of this, we have chosen to disregard the K values as a primary metric when comparing the optimal spatial distributions bat-friendly plantations should use.

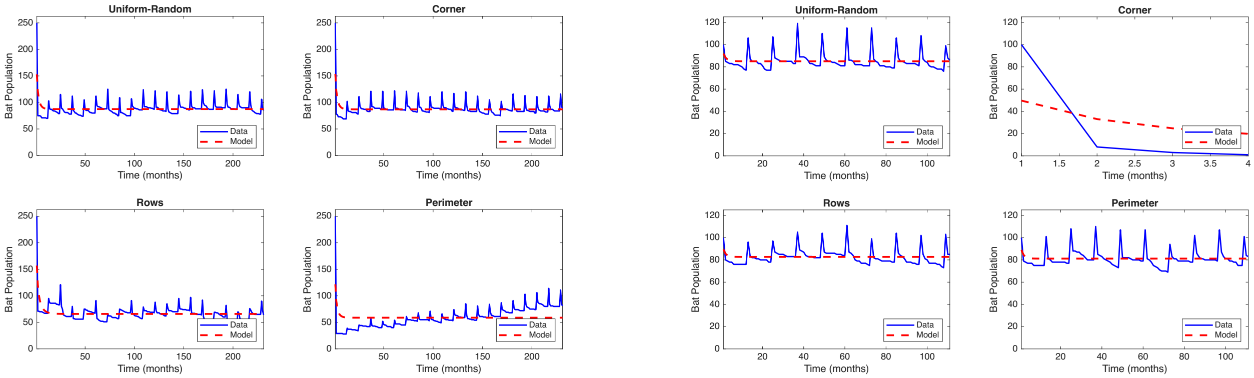
Instead, we focus on the final mean population size as a more stable and interpretable indicator of spatial distribution performance. Table 3 shows this data for each spatial distribution. Across all scenarios with memory enabled, the uniform-random and corner distributions consistently supports the largest final bat populations across a range of initial conditions.

We are also choosing the neglect the situation where memory?=false considering that bats are assumed to have memory of where available nectar is based on the fact that bats will scout areas to forage so that they can find feeding sites in advance Lear et al. 2024.



(a) Initial population of 10 bats

(b) Initial population of 100 bats



(c) Initial population of 250 bats

(d) Initial population of 100 bats, no memory

Figure 3: **Population variability across different initial conditions and memory settings.**

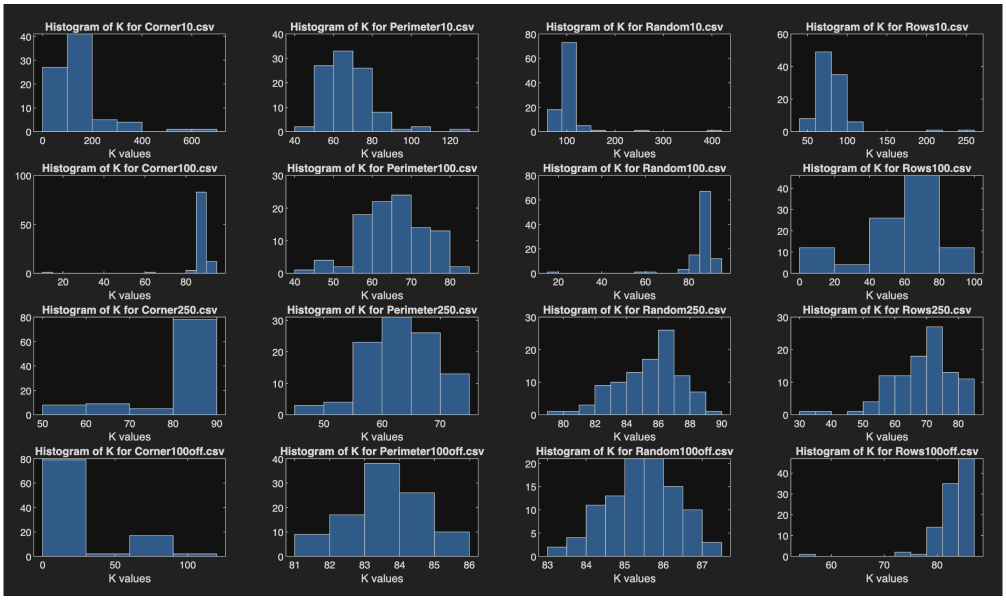


Figure 4: **Histograms of the carrying capacity (K) values for each spatial distribution.**

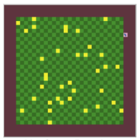
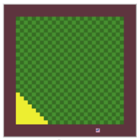
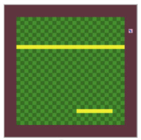
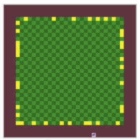
Spatial Distribution	Initial Condition	Final Mean Population	Mean K	Mean r
 Uniform-Random	$N_0 = 10$	83.24	101.64	0.0257
	$N_0 = 100$	86.61	85.75	1.0681
	$N_0 = 250$	84.70	85.41	0.3978
	memory = false	85.56	85.44	0.7114
 Corner	$N_0 = 10$	83.50	172.35	0.0203
	$N_0 = 100$	88.42	87.50	0.5544
	$N_0 = 250$	85.38	81.52	0.4006
	memory = false	75.91	17.78	0.1015
 Rows	$N_0 = 10$	69.00	82.08	0.0274
	$N_0 = 100$	72.43	57.97	0.6216
	$N_0 = 250$	70.30	68.60	0.3150
	memory = false	83.26	82.96	0.6893
 Perimeter	$N_0 = 10$	62.55	68.39	0.0251
	$N_0 = 100$	65.61	65.73	0.6240
	$N_0 = 250$	62.58	63.38	0.2638
	memory = false	83.71	83.59	0.7572

Table 3: **Final mean bat population, mean logistic carrying capacity (K), and mean growth rate (r) for each spatial distribution across varying initial population sizes and memory conditions.**

3.2 Vary Flower-Percentage

Next we investigated if bat population continued to grow with an increase of flowering percentage or if there was a maximum percentage when the bat population leveled off. To do this we ran 10-year-long simulations with 10 repetitions for each flowering percentage from 0% to 25% for each spatial distribution. After collecting the simulation data we fitted the linear regression model: $y = mx + b$ where y is the final bat population, m is the slope, x is the flowering percent, and b is the population when flower-percentage = 0%. This method allowed us to understand how closely the two variables are connected and whether one increases or decreases as the other changes.

The fitted curve provided estimates for the slope, which tells us the bat population each plantation can support per percent allowed to flower. We also include the goodness-of-fit metrics, such as the R^2 value and plots to assess how well the model captured the trends in the data.

The regression analysis revealed a strong positive relationship, supporting our hypothesis that increased flowering agave leads to higher bat population sizes. All four of the spatial distributions had R^2 values close to 1, meaning that the data is very linear and fits the model well.

The uniform-random and corner distributions had the highest R^2 values, being 0.9986 and 0.9991 respectively. There was more heteroskedasticity observed in the data for rows and perimeter which we thought was interesting. The variability in final bat populations became more uneven as the flowering percentage increased, some simulations led to much higher or lower populations than others, even at similar flowering levels, as seen in (Figure 5). Though the R^2 values for rows and perimeter were still very close to 1.

In terms of slope and the amount of bats each spatial distribution can sustain, uniform-random and corner also performed the best. Both of these distributions can sustain about 18 bats per percentage. This equates to about 90 bats if 5% of the plantation is allowed to flower which lines but with the conversationalists predicted bat populations for bat-friendly tequila plantations. Rows is estimated to support about 85 bats and perimeter supports about 70 bats for the allowed 5% of flowering agave. We also did not observe diminishing returns as the flowering percentage increased.

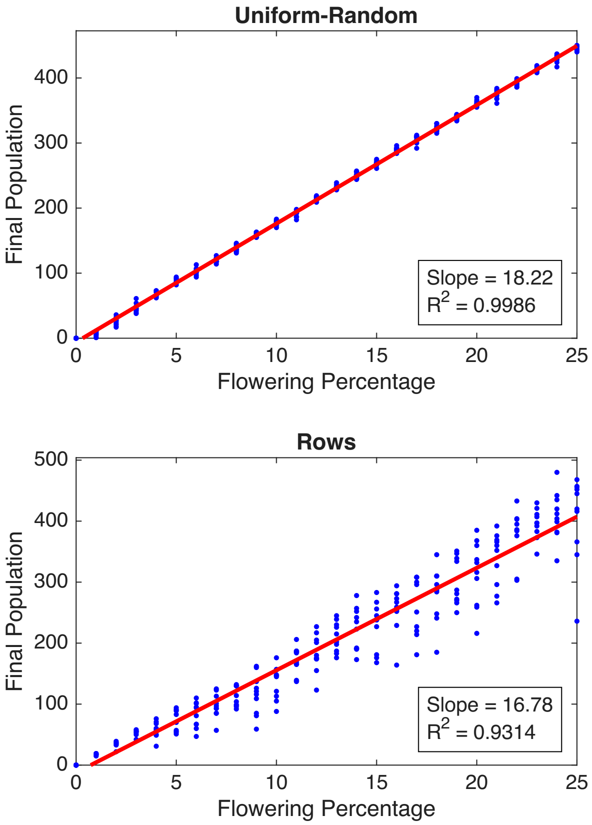


Figure 5: **Regression results for varying flower percentages.**

3.3 Vary Sensing-Radius

To investigate the effect sensing ability has on population outcomes, we ran simulations varying the sensing radius from 1 to 57 by increments of one for each spatial distribution (corner, perimeter, uniform-random, and rows). In each case, we initialized the population with 100 bats (50 male and 50 female), set flowering percentage to five percent, set the distance from the roost to the plantation as 25 km, and enabled bat memory. For each individual sensing radius for each spatial distribution, we ran 10 simulations lasting 10 years. We recorded final bat populations, births, and energy and random deaths for each simulation.

Once all 570 simulations were ran for each spatial arrangement of flowering agave, we used MatLab to fit multiple equations producing concave down curves to the data. These equations include the logistic growth model, the Gompertz function, logarithmic and transformed logarithmic equations, an exponential model, a power law, and a quadratic polynomial.

To identify the most parsimonious model, we use the second-order Akaike Information Criterion corrected for small sample sizes (AICc) (Akaike, 1974???) as our selection metric. The AICc is defined as:

$$\mathrm{AICc} = 2k - 2\ln L + \frac{2k(k+1)}{n-k-1}, \tag{1}$$

where k is the number of parameters, L is the maximum likelihood of the model, and n is the number of data points. Specifically, $k = p + 1$, where p is the number of estimated parameters in the model and the additional parameter accounts for the constant variance σ^2 of noise in the collected data. A lower AICc value represents a better fitting model, with ΔAICc being especially useful for comparing model fit.

Out of the seven equations, the logistic growth model, Gompertz function, and negative quadratic each fit at least one spatial distribution the best, with the lowest AICc value for the spatial distribution. The logistic growth model fits the perimeter and uniform random spatial distributions best, with AICc values of 2347.38 and 1807.26, respectively. The Gompertz function fit the corner distribution best (AICc = 1813.48), but the logistic model had a very similar AICc value. The row spatial arrangement was most accurately modeled using a quadratic equation (AICc = 2524.97). Figure 6 depicts these three models (logistic, Gompertz, and quadratic) fit to the data from each spatial arrangement.

From figure 6, one can see that increasing the sensing radius beyond a certain threshold does not lead to higher final bat populations. In the corner distribution, the final population plateaued once the sensing radius reached seven, with little variation in subsequent simulations. Similarly, the perimeter and uniform-random distributions leveled off at sensing radii of approximately 16 and 10, respectively. The rows distribution exhibited the most variability in final population size across all sensing radii. The highest final bat population occurred with a sensing radius of six, and there was significant fluctuation in final bat populations for sensing radii up to 26. Beyond that point, the mean final population for the rows arrangement appeared to stabilize, but there was more variation for final populations in individual simulation runs compared to for other spatial distributions once an optimal sensing radius was reached.

Despite a logistic model fitting two spatial arrangements the best, the Gompertz function consistently fit the data with a low AICc score compared to the other equations fit to the data, and hence was used to model the relationship between sensing radius and bat populations. Table 4 compares ΔAICc values for all modeled equations using the Gompertz function as a reference point.

The Gompertz model is a type of sigmoidal (S-curve) growth model commonly used to describe biological systems. This model differs from the logistic growth model as the Gompertz curve is asymmetric, capable of representing growth that is rapid at first but then slows as the upper asymptope is approached. The Gompertz function equation is as follows:

$$P(x) = a \cdot \exp\left(-b \cdot \exp(-k \cdot x)\right), \tag{2}$$

where $P(x)$ is the predicted final bat population at sensing radius x, a is the upper asymptote representing the maximum population size, b scales the displacement along the x-axis,and k controls the growth rate or steepness of the curve.

Figure 7 overlays the four Gompertz function equations fitted to each spatial arrangement. The uniform random, corner, perimeter, and row spatial distributions approach a values of 89.067, 88.898, 90.159, and 93.943 respectively. With a sensing radius in the 40's, all four spatial distributions appear to support roughly the same number of bats, approximately 89. These curves also show that increasing the sensing radius of bats comes with diminishing returns. Bat population growth slows as sensing radius increases.

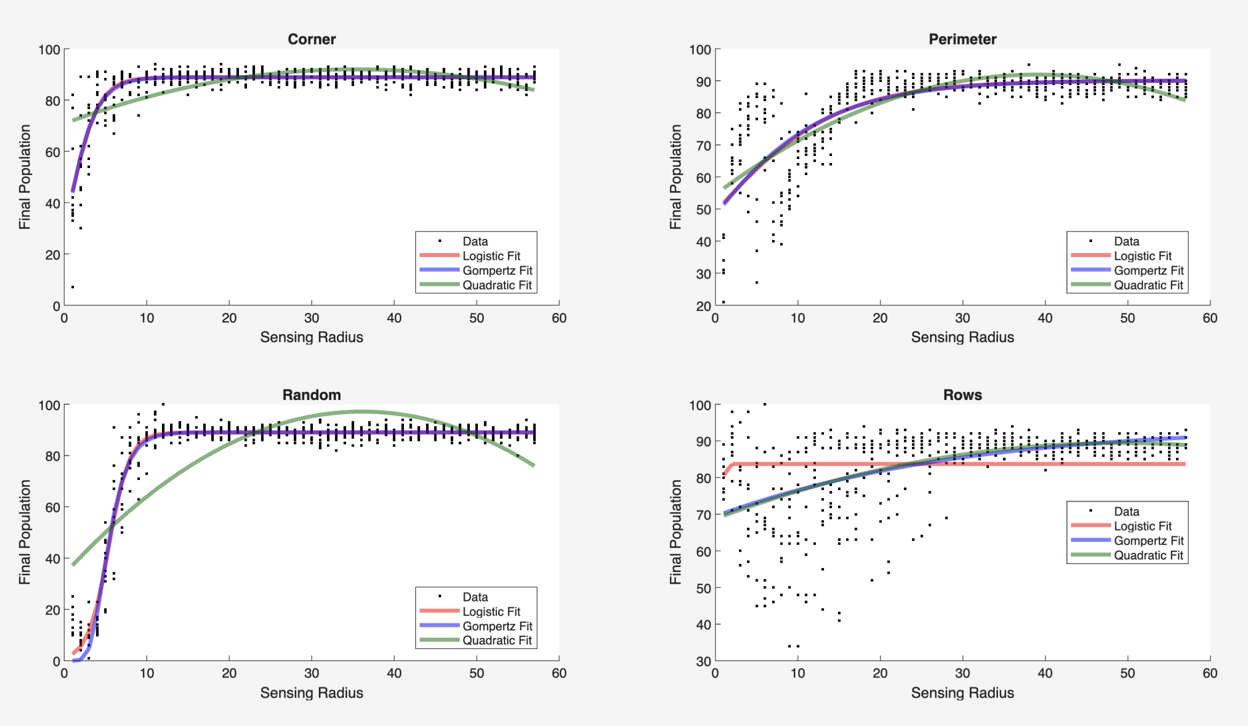


Figure 6: **Models best fitting data for varying sensing radius.**

Model Equation	**ΔAICc Values**			
	Corner	**Perimeter**	**Uniform Random**	**Rows**
Gompertz	0	0	0	0
Logarithmic	393.64	44.75	1044.75	53.23
Transformed Logarithmic	404.90	18.03	1007.16	9.40
Logistic	1.08	-5.18	-53.57	198.95
Power	397.50	48.53	1051.58	18.48
Rational	63.62	27.89	738.12	4.79
Exponential	616.29	291.88	1422.94	25.56
Quadratic	453.74	12.60	1088.80	-7.84
Reciprocal	621.93	279.54	1468.47	32.60

Table 4: Caption

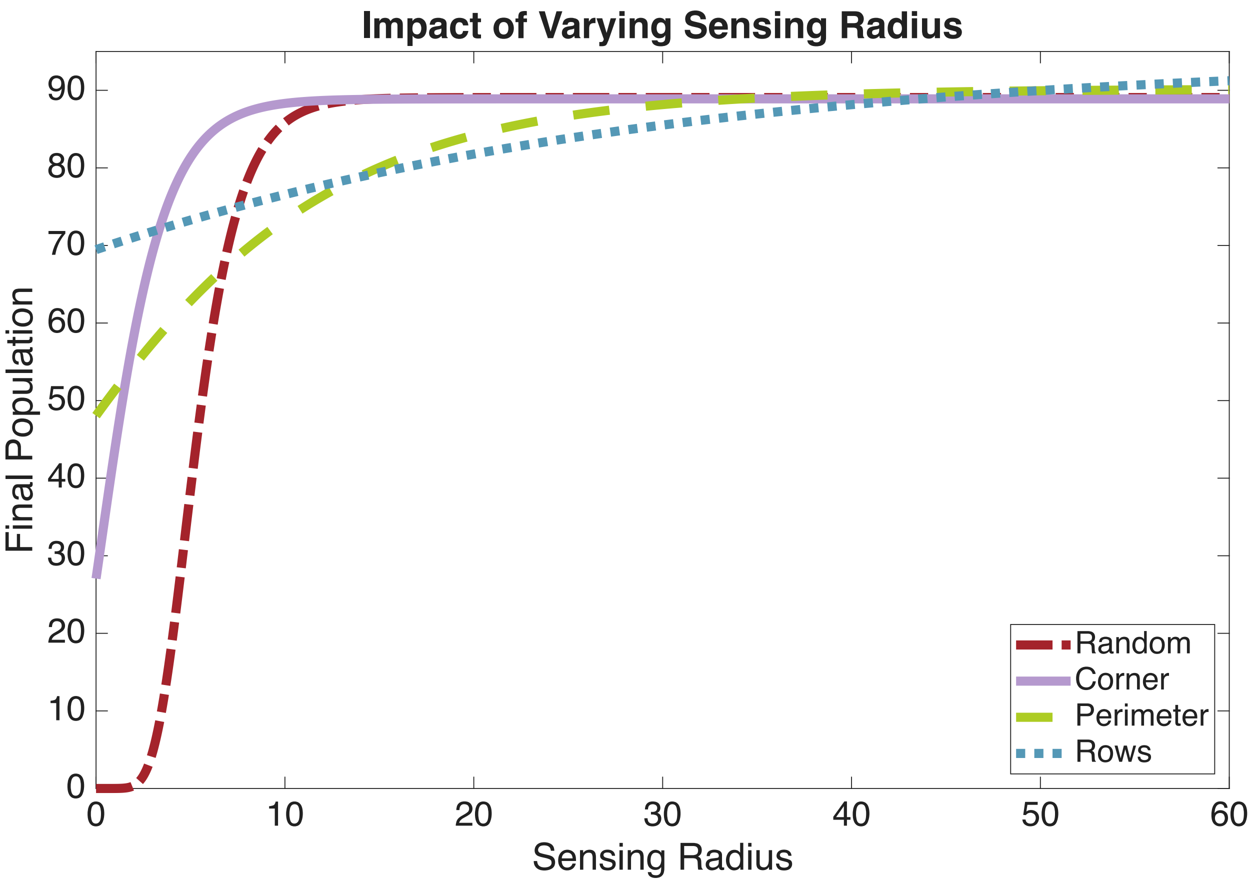


Figure 7: **Results for varying sensing radius.**

4 Discussion

When finding the emergent carrying capacities, we found that the bat population predicted by conservationists of 89 bats per 1 hectare of bat-friendly plantations with 5% flowering agave is supported by our model using the best spatial arrangements. This is determined using the final mean populations rather than looking at the K values. We recommend that plantations use either a uniform-random or corner distribution of flowering agave as both result in higher populations than Rows or Perimeter.

In our simulations, increasing the percentage of flowering agave consistently resulted in proportional increases in bat population size across all spatial arrangements. There were no diminishing returns as the flowering percentage increased. In many ecological systems, adding more of a beneficial resource leads to smaller and smaller gains—this is known as diminishing returns. This suggests that, within the tested range, each additional percent of flowering agave contributes roughly the same positive effect on bat population growth. This means that efforts to increase flowering agave, even beyond the minimum conservation thresholds, could continue to yield meaningful benefits for bat populations, without leveling off in effectiveness. So if plantations want to aid even more to conservation efforts to help bat populations increase, they can increase the percent allowed to flower as much as they want without bat populations plateauing.

In testing the impact of sensing radius on the effectiveness of each spatial distribution, we found that uniform-random and corner are only the optimal distributions up to a certain sensing radius. When fitting the Gompertz model to our data from the simulations, each curve intersected at a sensing radius of about 45. This information is really only valuable if the true sensing radius of a bat is known. However, with the species being endangered and limited knowledge on such characteristics of *L.nivalis*, we do not know how far they can actually sense nectar through smell or sight. This is something for future scientists or conversationalists to study further when looking into nectarivorous bat species. If it is found that the bats have a very large sensing radius then plantation owners can choose the easiest option in terms of harvesting and upkeep when it comes to selecting the plants that are allowed to flower.

Overall, the spatial arrangements that support the largest bat populations are the uniform-random and corner distributions. While both are effective ecologically, the corner arrangement may be more practical for farmers. Because flowering agave plants are concentrated in a specific area, they can be more easily avoided during the manual harvesting of non-flowering plants for tequila production. In contrast, a uniform-random distribution spreads flowering plants throughout the plantation, which could make them harder to identify without clear markers. However, since agave is harvested by hand (Davis and Long 2015), this challenge may be manageable, and the choice between layouts can ultimately be left to the discretion of the farmers based on what is most feasible for their operations.

5 Future Directions

In the future, for the conservation of these important pollinating bat species, it would be beneficial to study their behavior and characteristics further. The more that is known about the bats, the more can be done to protect their habitats and food sources. In particular for our model, testing how their sensing radius impacts their foraging and population dynamics may be beneficial. In the wild we may assume that they would forage on the closest plants to the one that they are currently feeding at. However, in our model the bats have the same likelihood of going to a plant that is further away than a plant that is directly next to the current one if they are both within the sensing radius. Perhaps the results may be different if we programmed the bats to have a larger sensing radius to find the initial plants with available nectar and then a smaller sensing radius during the next time step after a successful feeding at a plant. However more needs to learned about how these bats forage for food in greater depth.

Another factor to consider with this project besides just the impact on the bat populations is also the impact on the plantations themselves. It would be useful to perform some sort of ecological valuation to analyze the impact of allowing a certain percentage of agave to flower has on the plantation. Also to see the economic impact the plantations may face is worthwhile as agave is a prominent form of income for these plantation owners and Mexico. With limiting the amount of agave that may be used in tequila production, how does this effect the profit of the plantations and how much gain can there be made from advertising their product as bat-friendly. Currently there are some efforts to incentivize plantation owners to use bat-friendly practices such as these bat-friendly labels and for the general health and longevity of their agave with more biodiversity that comes from natural pollination Zapata-Morán et al. 2024.

Overall, the protection and research of these bat species are pertinent to the ecosystem and biodiversity of Mexico. There is always more that can be learned about the bats so that their populations can increase and more policy can be put into place. With more protective and bat-friendly policies for agave plantations and infrastructure in terms of protecting their food sources and habitats, *L.nivalis* populations can be conserved.

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