Climate Change and Predator-Prey Interactions

Evelyn Nkanga, Hannah Mei, Sunny Chan, Sadhvi Surendhran, Matthew Spaargaren

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Abstract

The rising global temperature and its effects on the environment is common knowledge. However, in this paper, we study the effects of climate change on the traditional Lotka-Volterra predator-prey model. By introducing new variables relating to carrying capacity, temperature Allee effects, and applying these models to a specific case study involving spiders and fruit flies, we develop a framework to analyse the impact of climate change on interactions between species. When Allee effects were added to predator-prey systems it was found that they acted as destabilizers in the system leading to unstable fixed points. Moreover it was also found that when temperature is increased at a constant rate over time, it negatively affected predator-prey interactions. We observed this using an experiment conducted by Rall, Vucic-Pestic, Ehnes, Emmerson, and Brose [10] which studies the ingestion rate and metabolism rate of predatorial arthropods such as spiders and beetle and their dependence on temperature. Finally we obtained a system with both Allee and temperature effects. This system showed us that Allee effects on either the predator or the prey did not result in the other population thriving, both predators and prey experienced a population decline.

1 Introduction

Animals are facing new challenges within their ecosystems because of climate change. Warmer temperature, higher sea levels, frequent heat waves, and unpredictable weather are forcing animals to adapt to their environment. Gretchko, Marley, and Tyson [4] explore the dynamics of predators and preys by using a variable territory model with the Allee effect. They interpreted their climate function as "good" years and "bad" years, where good years represent the time where the climate has a positive influence on the species' population and vice versa for bad years. Their model shows that extinction of a species occurs when there is a low prey density and a climate function of bad years happening at the same time.

In this paper, we are exploring the Lotka-Volterra predator prey model involving climate change variables. The Lotka-Volterra model incorporates Alfred J. Lotka's and Volt Volterra's theories together about predator-prey interactions. Lotka originally created a system of equations for chemistry to illustrate the oscillations of chemical concentrations in a chemical reaction. However, his interest swayed to the application of mathematics in biology. He noticed that the interaction between herbivores and plants also resulted in oscillations for their populations. Eventually, his studies advanced to analyzing the competitive interactions between two predator species that are fighting for the same food resources.

Volterra was studying fish species when he was developing his model. He compared the proportions of big predatory fishes to smaller prey fishes from data sets given by Umberto D'Ancona. D'Ancona inferred that the increase of predatory fishes in the market resulted from fewer fishing activities during World War 1. Volterra proposed a differential equation model to explain the change in population for predatory and prey fishes. Later on, he extended the model to generalize the interaction between predators and preys. Thus, this model came to be known as the Lotka-Volterra model, even though Lotka and Volterra worked on the model independently from each other.

2 The Base Lotka-Volterra Model

The Lokta-Volterra model is a system of differential equations that describes a simple interaction between predators and preys. Many assumptions are made to simplify and isolate the model from extraneous variables.

1. Environment is constant
2. No genetic adaption for predator and prey
3. No food shortage for prey population
4. Predators will continuously and always eat only prey
5. The rate of change of the population is directly proportional to the size of the population

Before we incorporate our climate variables into the model, it is important to first discuss the traditional Lotka-Volterra Model, and to analyse its dynamics.

The dynamical system is defined as follows:

$$\begin{cases} \dot{R} = \alpha R - \beta RF \\ \dot{F} = c\beta RF - \delta F \end{cases}$$

With R denoting the number of rabbits, F denoting the number of foxes, and α, β, c, and δ being parameters related to the relationship between the rabbits and foxes. But what do these parameters actually denote?

Imagine if there were no foxes, that is $F = 0$. Then we would have the following:

$$\begin{cases} \dot{R} = \alpha R \end{cases}$$

Where α is the birth rate of new rabbits. Without any foxes, we would expect the number of rabbits to grow theoretically large, and so it is reasonable to expect that $\alpha \geq 0$. Similarly, δ would denote the death rate of foxes without any rabbits present, and so we would expect that $\delta \geq 0$.

β and c describe similar relationships between the rabbits and the foxes, namely the effects of the predation of rabbits by the foxes. We can think of β as the 'rate of attack' of the predators, that is the average rate of rabbits attacked and consumed by the foxes. Then c can be thought of as the efficiency of the foxes at turning rabbits into new offspring. So we are left with the following system:

$$\begin{cases} \dot{R} = \alpha R - \beta RF \\ \dot{F} = c\beta RF - \delta F \end{cases}$$

With $\alpha, \beta, \delta, c \geq 0$. Linearising this system produces the following Jacobian matrix:

$$J^* = \begin{bmatrix} \alpha - \beta F & -\beta R \\ c\beta F & c\beta R - \delta \end{bmatrix}$$

With $Trace = \alpha - \beta[cR + F] - \delta$ and $\Delta = \beta[\alpha cR + \delta F] - \alpha\delta$

We will need to find our fixed points, namely where $\dot{R} = \dot{F} = 0$. Trivially, $R = F = 0$ will produce a fixed point. Factoring that out, we are left to solve

$$\begin{cases} \alpha - \beta F = 0 \\ c\beta R - \delta = 0 \end{cases}$$

Which leads to

$$\begin{cases} F = \frac{\alpha}{\beta} \\ R = \frac{\delta}{c\beta} \end{cases}$$

$$J^*(0,0) = \begin{bmatrix} \alpha & 0 \\ 0 & -\delta \end{bmatrix}$$

With $Trace = \alpha - \delta$ and $\Delta = -\alpha\delta$

$$J^*(\frac{\delta}{c\beta}, \frac{\alpha}{\beta}) = \begin{bmatrix} 0 & -\frac{\delta}{c} \\ c\alpha & 0 \end{bmatrix}$$

With $Trace = 0$ and $\Delta = \alpha\delta$

So, interestingly, the stability of these fixed points is solely determined based on the birth and death rates of the rabbits and foxes, and not at all by their interaction with one another. For the fixed point $(0, 0)$, the fixed point is always a saddle, since $\Delta < 0$, $\forall \alpha, \delta > 0$. Similarly, the fixed point $(\frac{\alpha}{\beta}, \frac{\delta}{c\beta})$ is never a saddle point for a similar reason. Because Trace $= 0$, we can say that this fixed point is a center and its eigenvalues are imaginary. Thus, the model for both populations will contain oscillations.

In the rest of this paper, we will quickly simplify and write that $\gamma = c\beta$.

2.1 Numerical Model

The base Lotka-Volterra model can be solved analytically using the initial values of the predator and prey populations. However, as we add more parameters to the model, a numerical approximation for this nonlinear model is more practical. The Runge-Kutta Method is chosen for its high accuracy and simplicity. With chosen starting values for the population of prey and predators as 10 and 2 respectively, the variation of population for each species with time is shown below.

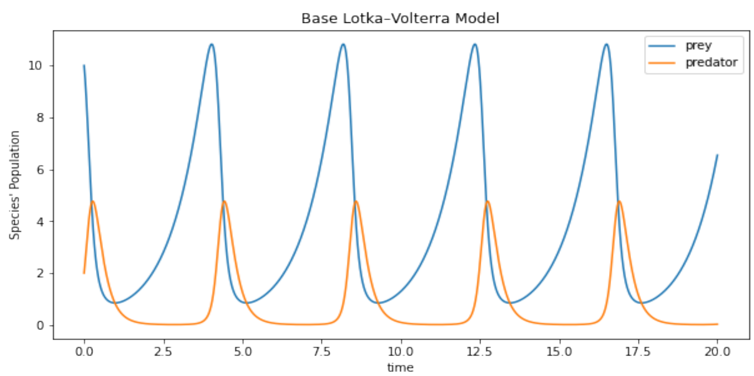


Figure 1: Runge-Kutta Approximation of Lotka–Volterra Model over time

As shown in both the discretized numerical model and the phase plane, the Lotka-Volterra system of equations oscillates. These oscillations reflect the cycle of attack on prey by predators leading to decreased population of prey, decreased population of predators as a result, then, increased population of prey due to lack of predators.

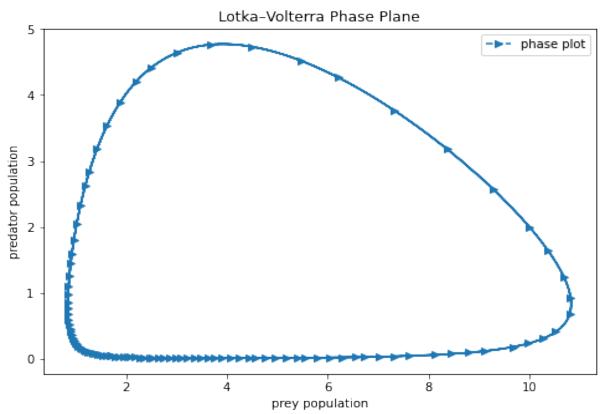


Figure 2: Phase Plane of Predator/Prey Populations

2.2 Carrying Capacity

The carrying capacity is defined as the maximum size of a population that an environment can support sustainably. The basic logistic growth model with carrying capacity is:

$$\dot{N} = rN(1 - \frac{N}{K})$$

With $\dot{N}$ denoting the rate of change of the population, r denoting the growth rate, N denoting the population size, and K denoting the carrying capacity.

The carrying capacity can be applied to the Lotka-Volterra Model for prey. Assuming in this model, if rabbits were to overpopulate, their food resources will not be sufficient enough to supply their entire population, thus a carrying capacity is necessary. For predators, they are unable to reproduce without preys in this model. Since the rate of new offsprings for predators is dependent on the population size of preys, carrying capacity for predators is not necessary.

The Lotka-Volterra Model with carrying capacity:

$$\begin{cases} \dot{R} = \alpha R(1 - \frac{R}{K}) - \beta RF \\ \dot{F} = \gamma RF - \delta F \end{cases}$$

yielding stable non-trivial $(R^*, F^*) = (\frac{\delta}{\gamma}, \frac{\alpha}{\beta}(1 - \frac{\delta}{\gamma K}))$.

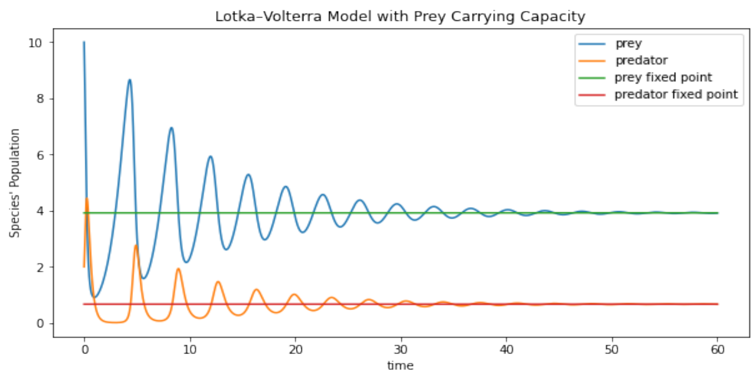


Figure 3: Approximation of Model with Prey Carrying Capacity

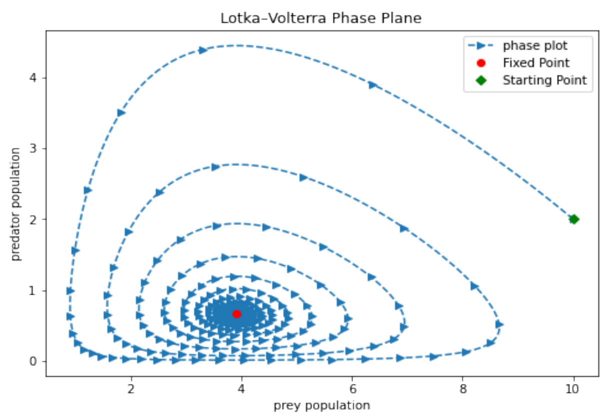
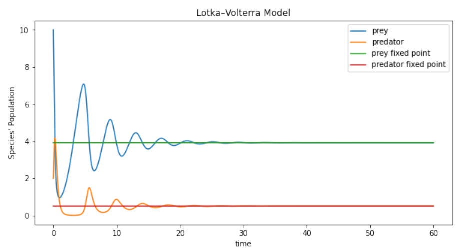
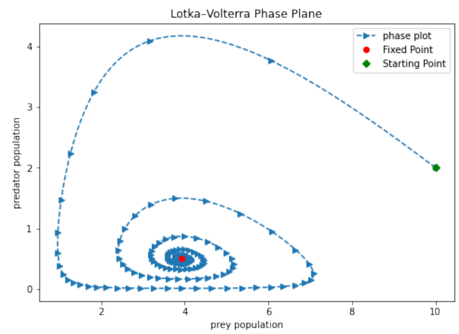


Figure 4: Phase Plane of System Populations with Carrying Capacity

Above are the populations model over time and the phase plane with prey carrying capacity $K = 20$. In both species, we see that over time their populations approach their respective equilibria due to the added restricted growth of prey from its carrying capacity. In the phase plane, the system experiences decaying oscillations towards the fixed point (a stable spiral node). Shown below, we see that if the carrying capacity decreases, the time to which the populations reach their respective stable points is decreased.

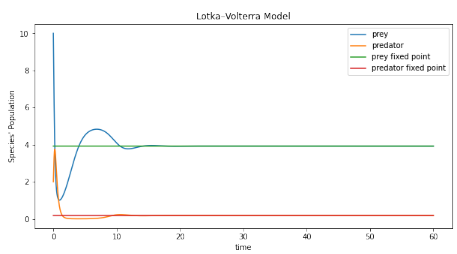


(a) Populations Model

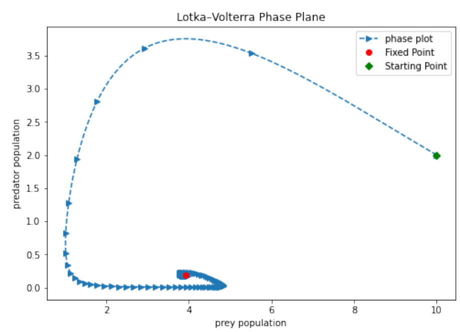


(b) Phase Plane

Figure 5: $K = 10$



(a) Populations Model



(b) Phase Plane

Figure 6: $K = 5$

3 Introducing Allee Effect

Before introducing the climate effect variables, we would like to explore more complex population dynamics between the two species by adding the Allee effect. The Allee effect is defined as a biological phenomenon characterized by a positive correlation between population size or density and the mean individual fitness of a species. In a constant environment an individual is more likely to survive and reproduce with a higher population density of its same kind. It is usually presented as the growth rate per capita. Here we express it using $\frac{R}{R+A}$ for prey and $\frac{F}{F+B}$ for predator.

Thus, we obtain new system of ODEs when applying the Allee effect on prey:

$$\begin{cases} \dot{R} = \alpha R(1 - \frac{R}{K}) \left(\frac{R}{R+A} \right) - \beta RF \\ \dot{F} = \gamma RF - \delta F \end{cases}$$

And a new system of ODEs when we apply the Allee effect on predator:

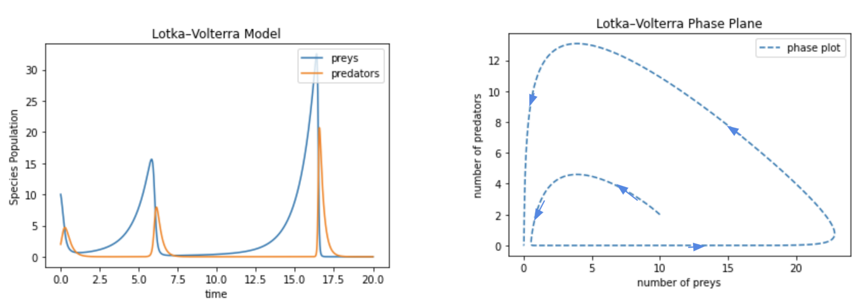
$$\begin{cases} \dot{R} = \alpha R(1 - \frac{R}{K}) - \beta RF \\ \dot{F} = \gamma RF\left(\frac{F}{F+B}\right) - \delta F \end{cases}$$

Here we assume A $>$ 0 and B $>$ 0, where they can be interpreted as the strength of the Allee effect on the respective population. For predators, the bigger B is, the slower they reproduce, especially when F is small, since now the growth rate per capita has been reduced from γR to $\frac{\gamma RF}{F+B}$. We see similar effect on prey where birth rate has been reduced from αR to $\frac{\alpha R}{R+A}$.

Thus, the larger the values of A and B, the larger the corresponding population must be in order to escape the Allee effect, which means the Allee effect can be seen as a destabilizer in our Lotka-Volterra Model. While we have a neutral oscillating fix points in the original model it becomes unstable when added Allee effect. When the population of either predator or prey is below certain threshold the species will become extinct and the system will therefore, collapse.

There are two cases we need to consider while adding the Allee effect, one upon prey and one upon predator. We have left out the scenario where both species are subjected to Allee effect since adding the effect on both species at the same time might cause interactions that is still unclear to the model and will lead to futile solutions.

Below are some plot examples of the dynamical system under different strength of Allee effect. Figure 7 describes the dynamical system with Allee effect at 0.75 on prey. We see the neutral oscillating fix points in the original model has become unstable. Looking at the phase plane, instead of being a perfectly closed cycle, it is spiraling out which means the dynamic is not fixed at a constant level anymore.

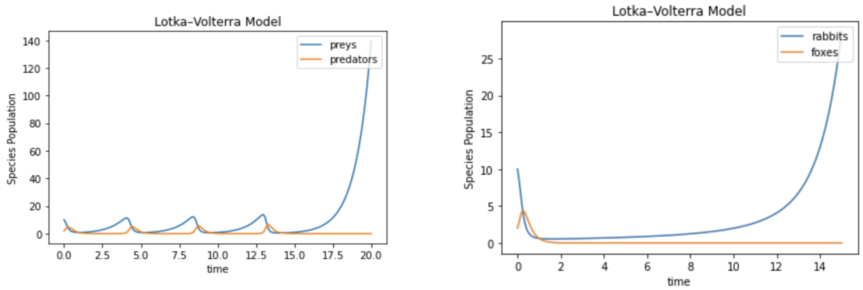


(a) Dynamical System

(b) Phase Plane

Figure 7: Allee effect on prey: A= 0.75

Moreover, we can see in Figure 8, when the Allee effect increases on prey from 0.75 to 2, the oscillations becomes weaker and weaker and when the effect is 5 the system collapsed where the predator dies out and prey grows to infinity. However, this is not exactly accurate since the prey shouldn't grow exponentially even when the predator has die out.

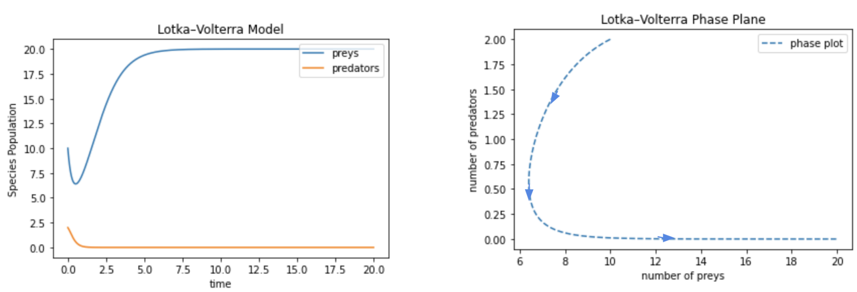


(a) Allee effect on predator: A= 2

(b) Allee effect on predator: A= 5

Figure 8: Different levels of Allee effect on Predator

Thus, we add back the carrying capacity to the system and now in Figure 9 when the predator dies out around 1.5 unit of time, the prey kept growing till 20 which is the carrying capacity and then level off which is a more reasonable result.

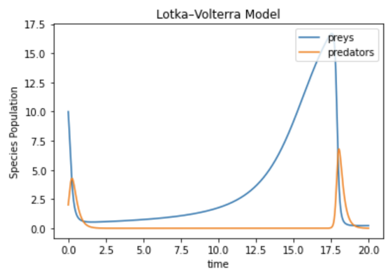


(a) Dynamical System

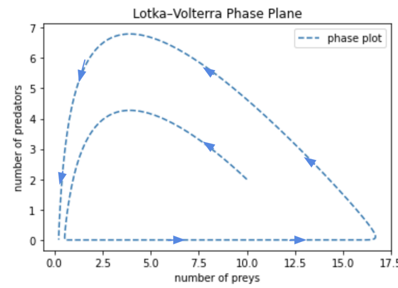
(b) Phase Plane

Figure 9: Allee effect on predator: A= 5 with carrying capacity K= 20

Lastly, we see an overall effect of both carrying capacity and Allee effect on prey in Figure 10. Now, instead of going through two cycles of oscillation like the dynamical system graph in Figure 7 (a), the system only goes through one cycle since now the birth rate of prey has been reduced and the cycle has been prolonged.



(a) Dynamical System



(b) Phase Plane

Figure 10: Allee effect on prey: B= 5 with carrying capacity K= 20

4 Climate Effect : Temperature

Changes in temperature as a result of climate change can impact predator-prey interactions. One way this impact can be considered is by studying changes in predator metabolic and ingestion rates at different temperatures (Rall, Vucic-Pestic, Ehnes, Emmerson, Brose, 2010). The experiment conducted by Rall, Vucic-Pestic, Ehnes, Emmerson, and Brose, with terrestrial arthropods like beetles and spiders yields equations showing the dependence of the metabolic and ingestion rates of predators on temperature. The ingestion rate can be thought of as the rate of gain of energy gained by the predator, whereas, the metabolic rate is the rate of energy loss.

$$I = i_0 m^{b_I} e^{\frac{-E_I}{kT}}$$

$$M = m_0 m^{b_M} e^{\frac{-E_M}{kT}}$$

In the equations above, I and M are the ingestion and metabolic rates of the predator in Joules per second (J/s) respectively, i_0 and m_0 are normalization constants, m is the body mass of the predator, b_I and b_M are allometric exponents which are scaling factors used in body mass dependent systems (Degen, 1997), k is Boltzmann's constant ($k = 8.62 \times 10^{-5} eVK^{-1}$), E_I and E_M are activation energies (eV), and T is temperature in Kelvin (K). Activation energy is the minimum amount of energy needed for a chemical reaction to occur. In this case, it is the energy needed to facilitate the energy gain and energy loss that occurs within the predator.

The ingestion rate I is related to the attack rate β by a correction factor, C_f [R s $day^{-1}J^{-1}$], that converts the ingestion rate to the number of prey per day from J/s. So,

$$\beta = C_f I$$

Similarly, the metabolic rate, M, is related to the death rate of the predators δ by a correction factor, C_r [F s $day^{-1}J^{-1}$], that converts the metabolic rate from J/s to number of predators per day.

$$\delta = C_r M$$

When considering this new β and δ in the Lotka-Volterra model with carrying capacity, K, we get the following system of ODEs, where α is the birth rate of predators and $\gamma = c\beta$.

$$\begin{cases} \dot{R} = \alpha R\left(1 - \frac{R}{K}\right) - C_f i_0 m^{b_I} e^{\frac{-E_I}{kT}} RF \\ \dot{F} = \gamma RF - C_r m_0 m^{b_M} e^{\frac{-E_M}{kT}} F \end{cases}$$

Moreover, the study also describes a dependence of the birth rate of prey, α, and the carrying capacity, K, on environmental temperature, T (Rall, Vucic-Pestic, Ehnes, Emmerson, Brose, 2010). In the following equation describing the birth rate of prey, α_0 is a normalization constant, D is the body mass of the prey, b_α is a constant exponent, k is Boltzmann's constant, E_α is the activation energy and T is environmental temperature.

$$\alpha = \alpha_0 D^{b_\alpha} e^{\frac{E_\alpha}{kT}}$$

The following equation describes the carrying capacity, K, in which, K_0 is a normalization constant, b_k is a constant exponent, E_k is the activation energy, σ is the annual primary productivity of the habitat, z is constant exponent, tl_0 is a constant and tl is the trophic level. The trophic level is the position a species occupies on the food web.

$$K = K_0 D^{b_k} e^{\frac{E_k}{kT}} \sigma^z e^{tl_0(tl-1)}$$

where σ can described using the following equation in which, σ_0 is the net primary productivity at the temperature, T_0, and E_σ is the activation energy.

$$\sigma = \sigma_0 e^{\frac{E_\sigma(T_0 - T)}{kTT_0}}$$

The National Oceanic and Atmospheric Administration's 2020 Annual Climate Report states that the average rate of increase of global temperature since 1981 is $0.18°C$ per decade (Lindsey and Dahlman, 2021). So this means that the average rate of change of global temperature in K/decade is,

$$\dot{T} = 0.18$$

Thus we now obtain a 3-dimensional system. Since we focus only on two species interacting in this paper, $m =$ average mass of predator individual and D is the average mass of prey individual.

Letting $n = C_f i_0 m^{b_I}$ and $l = C_r m_0 m^{b_M}$,

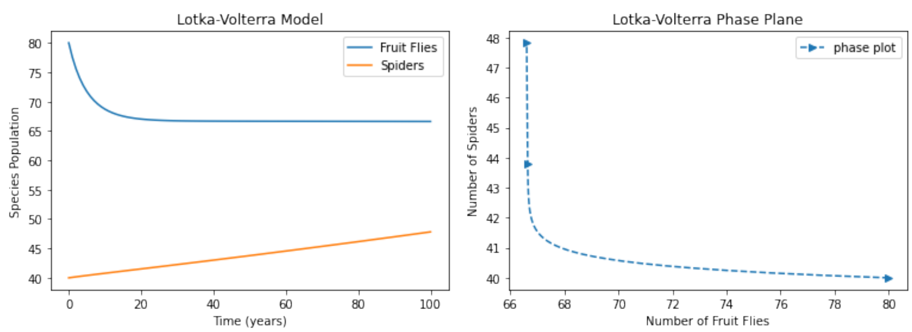
$$\begin{cases} \dot{R} = \alpha R\left(1 - \frac{R}{K}\right) - n e^{\frac{-E_I}{kT}} RF \\ \dot{F} = \gamma RF - l e^{\frac{-E_M}{kT}} F \\ \dot{T} = 0.18 \end{cases}$$

It is important to note that both α and K are also variables dependent on temperature, however, they were not expanded in the equation above to avoid overcrowding of variables in the equation.

5 The Spider and the Fruit Fly

Considering predator-prey interactions between two species of arthropods, spiders and fruit flies,and using the constants outlined in Table 1, the following figures show how the population of spiders and fruit flies are affected with changes in temperature.

In the following analysis we assume initial population of fruit flies to be 80 and initial population of spiders to be 40. In order to provide a comparison between constant climate conditions and climate change, Figure 11 represents the change in the spider and fruit fly populations when temperature remains constant at 282.65 K (9.5 $^{\circ}C$) over time of 100 years for the same temperature dependent parameters outlined in this section. In Figures 12 and 13, however, there is a temperature change of 0.18 K per decade being considered. The initial temperature in Figure 10 is 282.65 K (9.5 $^{\circ}C$) and in Figure 13, it is taken to be 290 K (17 $^{\circ}C$).

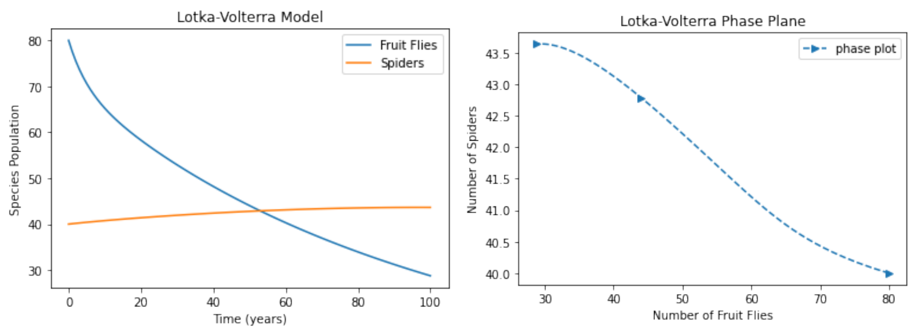


(a) Dynamical System

(b) Phase Plane

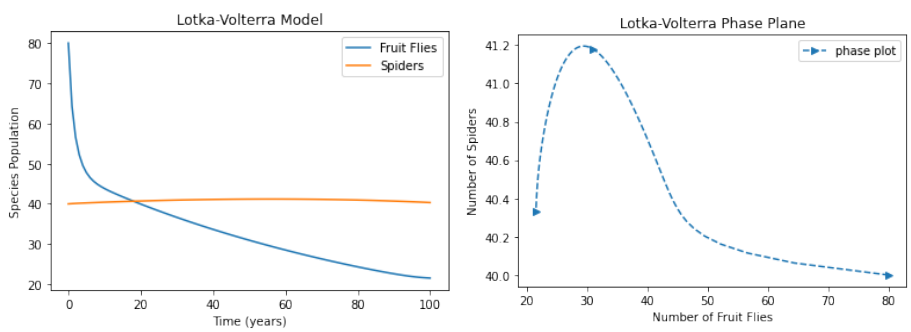
Figure 11: When Temperature is Constant over time, T = 282.65 K

From the dynamical system in Figure 11(a), it is observed that over time, the fruit fly population reaches a carrying capacity while the spider population is thriving. The phase plane shows a more dramatic increase in spider populations once the fruit fly population reaches it carrying capacity.



(a) Dynamical System (b) Phase Plane

Figure 12: With Temperature Change, Initial Temperature = 282.65 K



(a) Dynamical System (b) Phase Plane

Figure 13: With Temperature Change, Initial Temperature = 290 K

In Figures 12 and 13, there is a significant decrease in the fruit fly population which continues to diminish over time. Moreover, the growth of the spider population has also slowed down in comparison to Figure 11. The phase planes in Figure 12(b) represents the gradual decrease in the growth rate of the spider population as fruit fly population also decreases. Figure 13(b) is a more dramatic representation as it also shows the decline in spider population.

Table 1 is a detailed list of all the constants used to compute the graphical representations of the changes experienced by the spider and fruit fly populations. These constants were derived by Rall, Vucic-Pestic, Ehnes, Emmerson, and Brose in their study.

Table 1: Constants Used

m	1 g	Mass of predator
k	8.62×10^{-5} eV/K	Boltzmann Constant
C_f	1	Correction factor
i_0	$e^{-14.34}$	Normalization constant
b_I	-0.63	Allometric exponent
E_I	-0.09 eV	Activation energy
C_r	1	Correction factor
m_0	$e^{23.62}$	Normalization constant
b_m	0.46	Allometric exponent
E_M	0.8 eV	Activation energy
α_0	$e^{32.39}$	Normalization constant
D	0.2615 mg	Mass of prey
b_α	-0.25	Constant exponent
E_α	-0.84 eV	Activation energy
K_0	$e^{-31.15}$	Normalization constant
b_K	-0.72	Constant exponent
E_K	0.71 eV	Activation energy
tl_0	-2.68	Constant exponent
z	1.03	Constant exponent
tl	1.5	Trophic level of prey
σ_0	$600gm^{-2}yr^{-2}$	Net primary productivity
T_0	282.65 K	Temperature for σ_0
E_σ	-0.35 eV	Activation energy

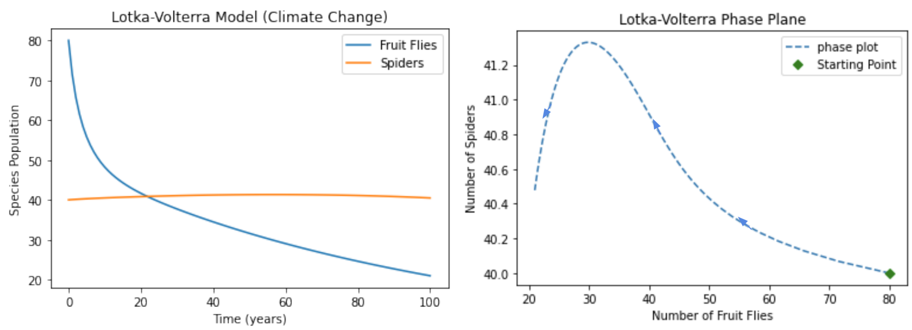
6 Allee Effect and Climate Change

So far, this paper has discussed how predator-prey populations change with differing Allee effects and changing temperature. Now, considering both Allee effects and the effect of temperature on predator-prey interactions, a new system of equations are defined below.

With Allee effect on Prey

$$\begin{cases} \dot{R} = \alpha R(\frac{R}{R+A})\left(1 - \frac{R}{K}\right) - ne^{\frac{-E_I}{kT}}RF \\ \dot{F} = \gamma RF - le^{\frac{-E_M}{kT}}F \\ \dot{T} = 0.18 \end{cases}$$

With Allee effect at A=100, we can see in Figure 14 (a) that the population of fruit flies decreases more rapidly at the beginning due to a slower reproduction rate, while the population of spider increases faster to a higher maximum at around 41.5 before decreasing along with the decline of the fruit flies. We can see this more precisely by comparing Figure 13 (b) and Figure 14 (b).



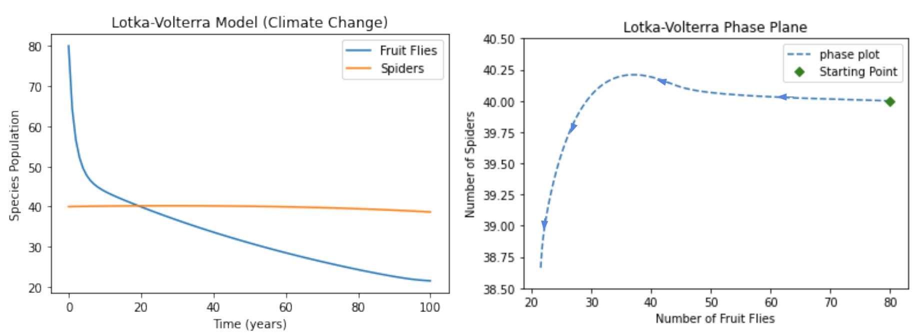
(a) Dynamical System

(b) Phase Plane

Figure 14: With Temperature Change, Initial Temperature = 290 K, A = 100

With Allee effect on Predator

$$\begin{cases} \dot{R} = \alpha R\left(1 - \frac{R}{K}\right) - ne^{\frac{-E_I}{kT}}RF \\ \dot{F} = \gamma(\frac{F}{F+B})RF - le^{\frac{-E_M}{kT}}F \\ \dot{T} = 0.18 \end{cases}$$



(a) Dynamical System

(b) Phase Plane

Figure 15: With Temperature Change, Initial Temperature = 290 K, B = 50

With Allee effect at B=50, even though in Figure 15 the overall trend of the dynamical system looks similar to the graphs above, the phase plane shows that the spider's population doesn't increase much due to a lower reproduction rate before it decreases, as in Figure 14. However, we still see a similar effect of increasing temperature on the dynamical system regardless of which species is being affected by the Allee effect and our original conclusion from Section 6 remains true.

7 Conclusion

After running the different models, we are able to make several conclusions about the enhanced predator-prey model and the effects of climate change on the model. First off, we find that introducing a carrying capacity for prey makes the system stabilise at the system's fixed points. When this carrying capacity is decreased, it takes less overall time for the system to stabilise. Second, introducing an Allee effect on both predator and prey causes the model to destabilise, leading to unstable fixed points and a potential collapse of the system.

Finally, once we add a linearly increasing temperature to the model, we can see that predator-prey interactions are affected negatively over time. In our case study of the spider and the fruit-fly, we saw that the population of fruit-flies decreased in a manner proportional to the starting temperature (meaning that the warmer it is, the more drastic the effect). This means that climate change could lead to a dramatic decrease in the population of fruit flies (and of prey in general), which could lead to an eventual extinction of species in general.

Our result aligns with the universal knowledge on climate change where increasing temperature negatively impacts ecosystems. Even though our model was a simple modification of the Lotka–Volterra Model with several assumptions, it nonetheless gives us some general insight on the impact of temperature on dynamical systems. While we have one case study regarding fruit flies and spiders, it could potentially be generalized to a larger variety of species using different empirical data, since the carrying capacity, Allee effect, and ingestion and metabolic rates are defined for all species in similar ways. Many more future studies could be done with more elaborate and robust methods yielding more precise results but we need to realize the seriousness of the impact of climate change on our ecosystem and protect more species from depopulation and potential extinction.

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