Elisabeth Kerns & Timothy Graven
Professor Stuart Jones
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Dynamic Modeling: Lotka-Volterra Report

The Lotka-Volterra model of predator-prey dynamics allows investigation into a number of variables that affect both predator and prey populations in an ecosystem. The power of the model comes through its relative simplicity when compared with others of its kind. The key assumptions that allow for this simplicity are as follows: The only limiting factor on prey population growth is the predator population, and that the only limiting factor on predator population growth is the prey population. With these key assumptions in mind, the Lotka-Volterra model allows for simulation of an ecosystem holding two organisms, one predator and one prey, and the likely fluctuations of population over time. The equations utilized to run a Lotka-Volterra simulation are listed below:

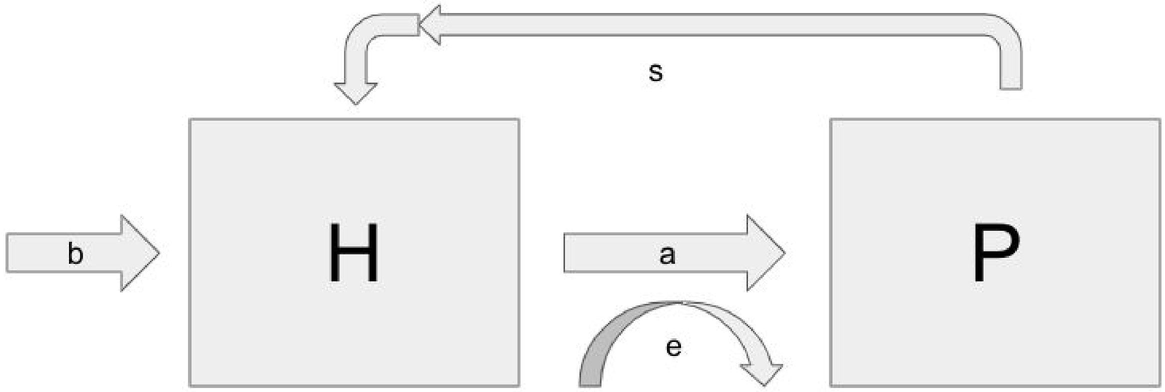
$$\frac{dH}{dt} = bH - aPH \tag{1}$$

$$\frac{dP}{dt} = eaPH - sP \tag{2}$$

In these equations, the capital H and P represent initial prey and predator population, respectively. These are the state variables, which are modified by b, a, e, and s. These four variables represent prey birth rate, predator attack rate, conversion efficiency of prey to predators, and predator death rate, respectively. The goal of this report is to investigate the effect of each parameter on the length of the predator-prey cycle, and also to determine the role of predators in a Lotka-Volterra simulation.

The conceptual model below provides a visual representation of the effect of each variable on the other.

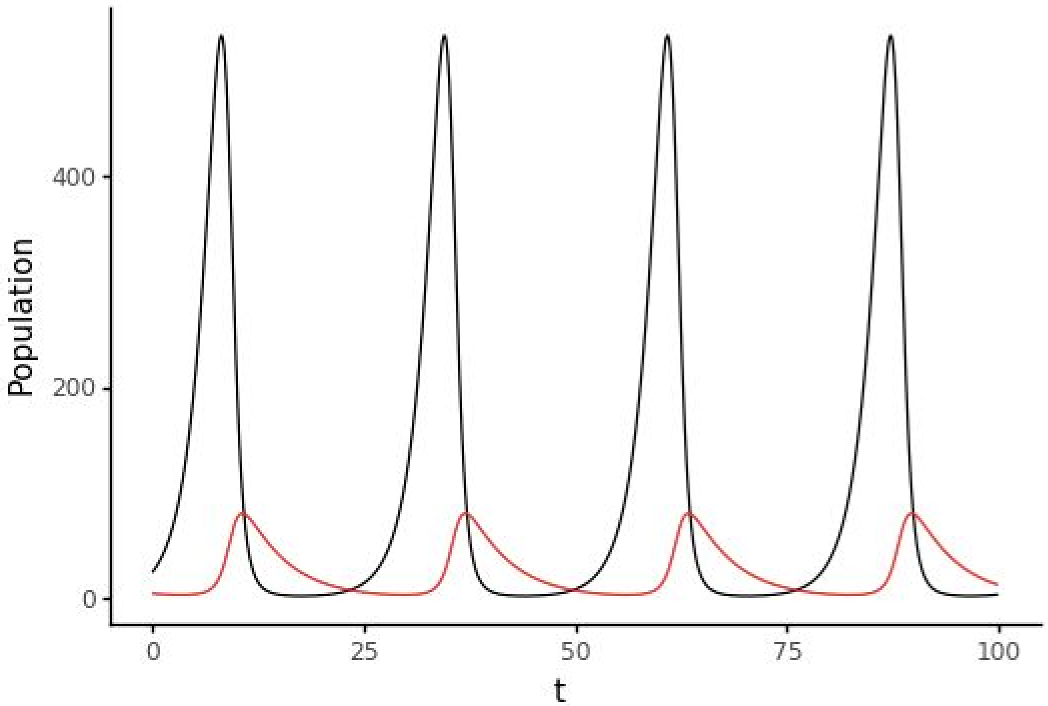
Conceptual Model



b - Prey Birth Rate
a - Predator Attack Rate
e - Conversion Efficiency of Prey to Predators
s - Predator Death Rate
H - Prey Population
P - Predator Population

Initial Plot

Note that predator population appears in red, and prey population in black



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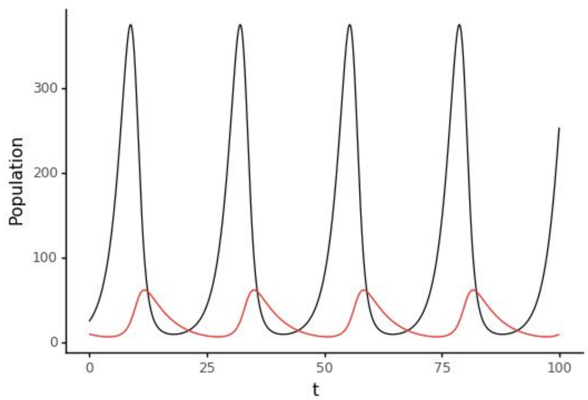
Original Parameters

This image represents the Lotka-Volterra simulation run with the original parameters: b=0.5, a=0.02, e=0.1, s=0.2, H_0=25, P_0=5. Predator-prey cycle length sits at roughly 25 units of time. This simulation was used as a baseline by which the modifications below were evaluated.

The Role of Each Parameter

<u>Predator Population, P</u>



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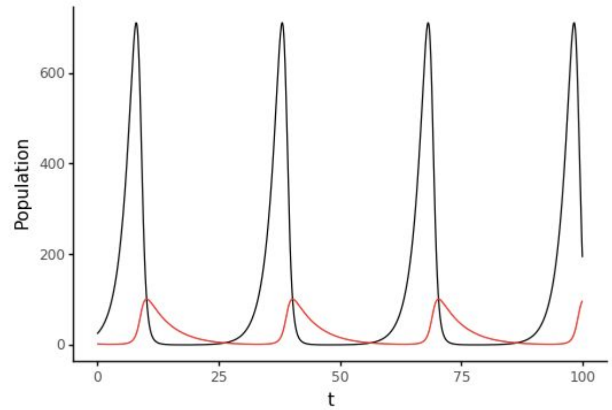
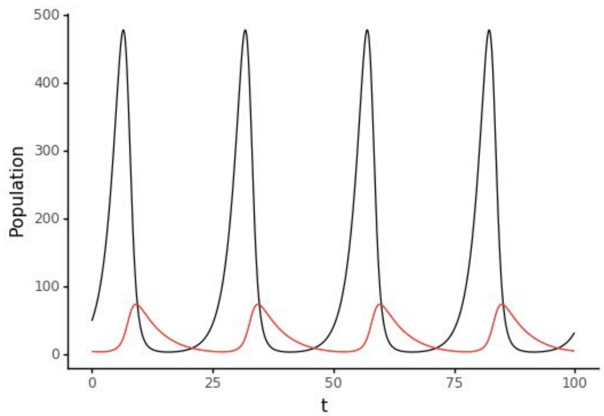
P Doubled



<ggplot: (7532430385)>
P Halved

These two images represent the effect of doubling and halving the predator population P, respectively. Doubling the initial predator population shortens the length of the predator-prey cycle, while halving it increases the length of the cycle. Prey population appears to be directly linearly affected by predator population, as the prey population reaches just under 400 with predator attack rate doubled, and just under 700 with predator attack rate halved.

<u>Prey Population, H</u>



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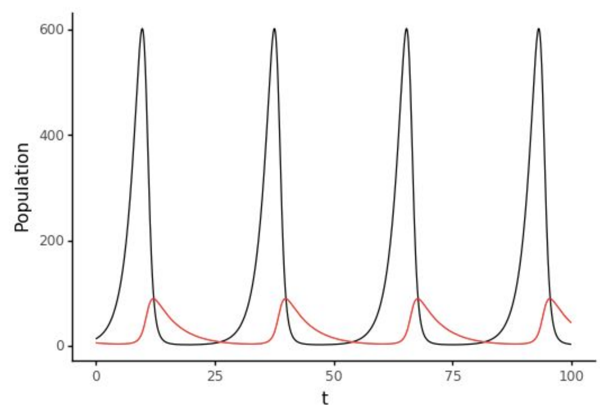
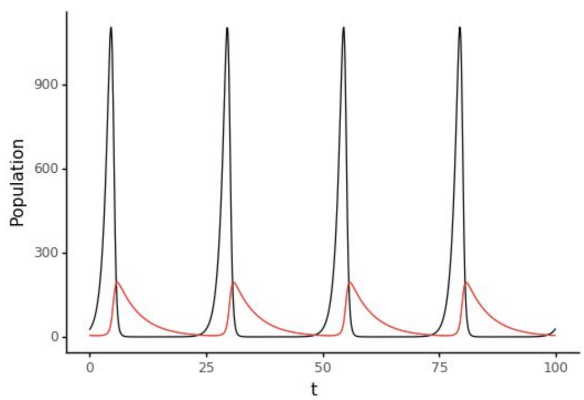
H Doubled



<ggplot: (7532389117)>
H Halved

The above two images represent the effect of doubling and halving prey population H, respectively. Doubling the prey population H shortens the predator-prey cycle marginally, while halving it appears to lengthen the predator-prey cycle marginally. Interestingly, halving initial prey population increases their maximum population.

<u>Prey Birth Rate, b</u>



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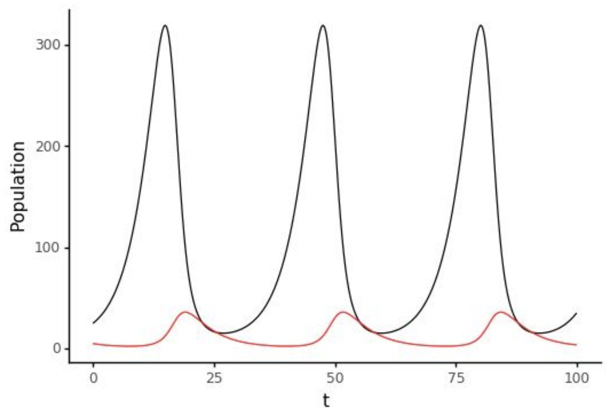
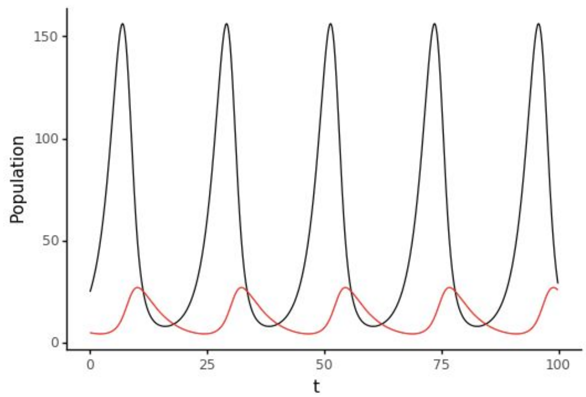
b Doubled



<ggplot: (7532432285)>
b Halved

These two images represent the effects of doubling and halving prey birth rate, b. Doubling prey birth rate leads to a much more significant prey population of nearly 1200, and halving it leads to a population just over 300. The length of the predator-prey cycle is slightly decreased when b is doubled, and increased when b is halved. The shape of the curve is drastically affected by b. Doubling b leads to sharp increases and decreases in population, and halving b leads to relatively smoother increases and decreases. The length of time at which the population remains at its maximum and minimum is also noteworthy. For an increased b, the population remains at its maximum for a short time, and remains at minimum, which appears to be zero on the graph, for an extended length of time. For a decreased b, the maximum is maintained for a relatively extended period of time, and the population never reaches a near-zero point. The maximum value for population is significantly increased by doubling b, and significantly decreased by halving b.

Predator Attack Rate, a



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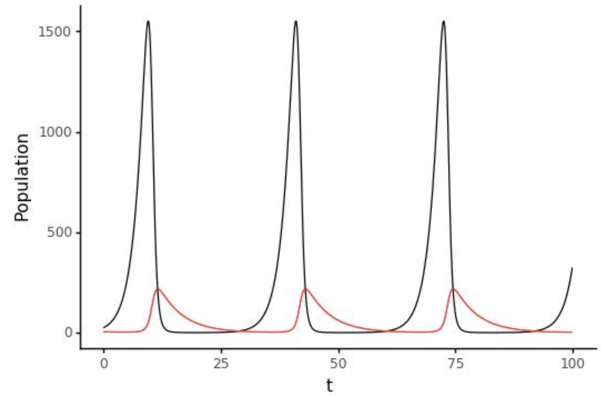
a Doubled



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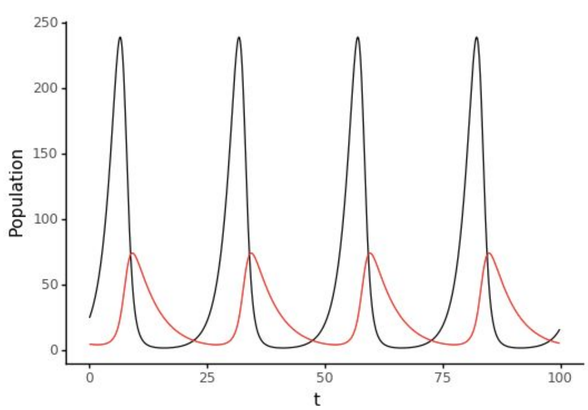
a Halved

The above graphs represent doubled and halved predator attack rate a, respectively. Doubling predator attack rate decreases the length of the predator-prey cycle, and produces curves that appear marginally smoother than the original parameters. Halving predator attack rate produces a longer predator-prey cycle, with comparatively sharper curves and a much more significant period of time at which population of prey is at an apparent zero.

Conversion Efficiency of Prey to Predators, e



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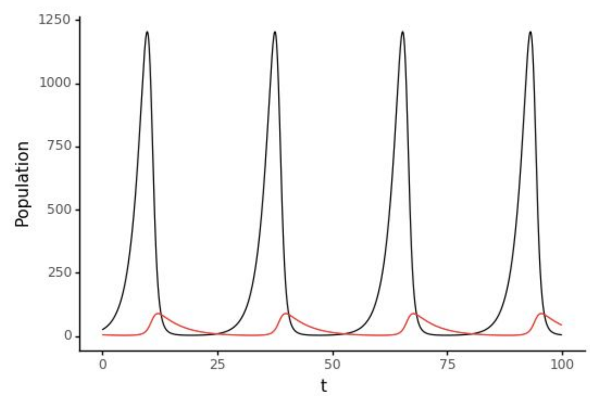
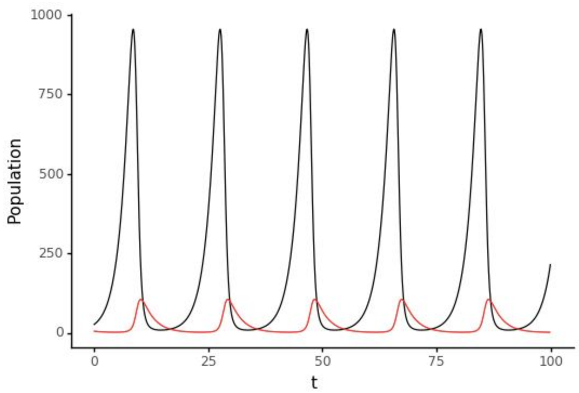
e Doubled



<ggplot: (283372669)>
e Halved

The above images represent doubled and halved conversion efficiency of prey to predators e, respectively. Modifying e by a factor of two in either direction does not appear to affect the maximum value of predator population significantly, but rather affects the ratio of predator-to-prey populations. Doubling e leads to a predator-to-prey ratio of roughly 2:7, while halving it leads to a predator-to-prey ratio of 1:16. Compared to an original ratio of about 1:6, the differences are remarkable. The length of the predator-prey cycle is marginally affected, and doubling e leads to a shorter cycle while halving it leads to a longer cycle.

<u>Predator Death Rate, s</u>



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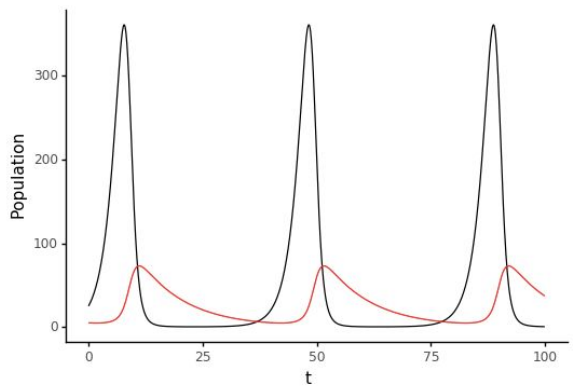
s Doubled



<ggplot: (7544602809)>
s Halved

These final graphs represent the effects of doubling and halving predator death rate s, respectively. The most significant difference caused by these modifications is observed in the length of the predator-prey cycle. Doubling s leads to a significantly shorter predator-prey cycle, while halving s leads to a significantly longer predator-prey cycle when compared to the original parameters. This parameter also affects the ratio of predators to prey, as doubling s leads to a larger difference between predator and prey populations, while halving it reduces the difference.

Role of Predators

Predators in the L-V model serve as a limiting factor for prey population, and determine both growth rate and maximum size of the prey population. Predators also determine the length of the predator-prey cycle more significantly than the prey population. A higher population of predators naturally requires a higher rate of prey deaths, leading to a faster predator-prey cycle. The predator-prey cycle relies on an inhibitory relationship between the two populations. As soon as one population rises to a threshold level based on parameters, the other population will change to modify the initial population. For example, if prey population grows too large, predator population will grow large in response, causing the prey population to decrease. This, in turn, will cause the predator population to decrease. In a sense, the two populations are in a constant battle with one another for equilibrium, but neither is ever allowed to achieve a steady equilibrium. What results is a sort of cyclical equilibrium that relies on both predator and prey to maintain itself over time.

Parameters vs. Predator-Prey Cycle Length

The apparent effect of each parameter on predator-prey cycle length is detailed in the below table, along with the evidence that suggests the relationship.

Parameter	Relationship to Pred-Prey Cycle Length	Evidence for Relationship
P	Negative, linear relationship	Doubling p shortens length, halving p increases length
H	Negative, linear relationship	Doubling H shortens length marginally, halving H increases length marginally
b	Negative, linear relationship	Doubling b shortens length, halving b increases length
a	Negative, linear relationship	Doubling a shortens length, halving a increases length
e	Negative, linear relationship	Doubling e marginally shortens length, halving e marginally increases length
s	Negative, linear relationship	Doubling s shortens length, halving s increases length

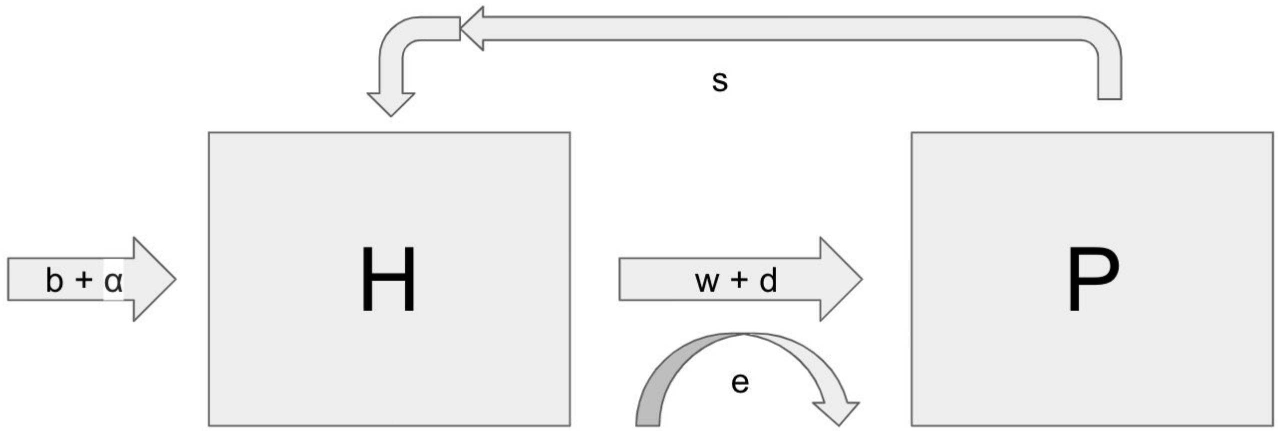
Modeling Project: Rosenzweig-MacArthur Report

In order to study the relationship between population dynamics, the interactions between the lynx and snowshoe hare were studied. Scientists first used the Lotka-Volterra model in order to simplify the interaction. This model relied on the assumption that predators are the only factor that affect prey population, and vice versa. However, scientists realized that this model fell short of reality. First, without predators, prey would self-limit their own population. In addition, external factors in the environment, such as the availability of resources, should also affect both predator and prey population. The Rosenzweig-MacArthur Model represents an extension of the Lotka-Volterra Model, with the addition of two parameters. Equation 1 and 2 listed below represent the Rosenzweig-MacArthur model.

$$\frac{dH}{dt} = bH(1 - \alpha H) - w\frac{H}{d+H}P \tag{1}$$

$$\frac{dP}{dt} = ew\frac{H}{d+H}P - sP \tag{2}$$

Several of the parameters were carried over from the Lotka-Volterra model. The variables are defined as followed. H represents the herbivore prey population, while P represents the predator population. The variable b indicates the prey birth rate. The variable e indicates the conversion efficiency of prey to predators, which refers to how many prey must be eaten to produce a new predator. The parameter s represents the predator death rate. In order to develop the Rosenzweig-MacArthur model, two additional parameters were added. The parameter d indicates handling time of predator per prey. Thus, d also determines the maximum number of prey that any one predator can catch. In addition, w refers to the maximum predator attack rate. The parameter α refers to the intra-specific competition coefficient, or the inverse of the carrying capacity of the population. Carrying capacity refers to the number of individuals that the population can support.



b - Prey Birth Rate
α - Intra-Specific Competition Coefficient (1/Carrying Capacity)
e - Conversion Efficiency of Prey to Predators
s - Predator Death Rate
H - Prey Population
P - Predator Population
w - Maximum Predator Attack Rate
d - Handling time of predator per prey - Time spent per kill

The above conceptual model provides a visual representation of the dynamics at work in the Rosenzweig-MacArthur model.

Here, the dynamics of the Rosenzweig-MacArthur Model were studied in comparison to the Lotka-Volterra results. The plots below represent the results of those simulations. For each trial, the y axis shows population over the x axis, time The black line indicates prey population, while the blue line indicates predator population at a given time.

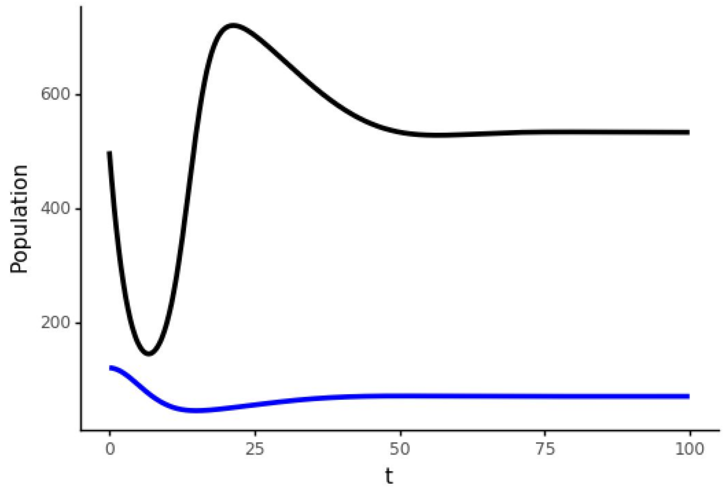


Figure 1. Simulation with standard parameters

When the simulation was ran with the starting parameters, the population of prey significantly outnumbered the population of predators. In this standard model, the prey experiences a dip in population at earlier times, as the predators consume significant prey. Then, the prey population booms based on overconsumption by the predators. After some time, both the predator and prey populations reach an asymptote, as the system reaches an equilibrium. At this point, the rate at which predators consume prey equals the rate at which prey are born.

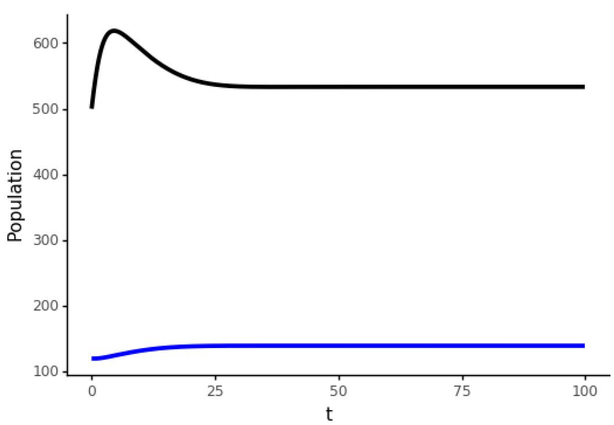


Figure 2. Simulation using a doubled prey birth rate, b.

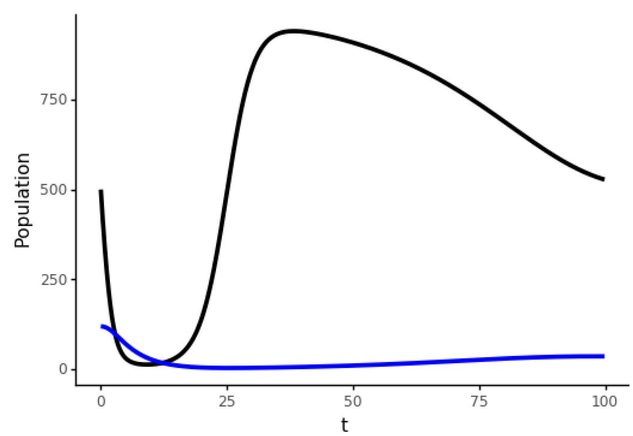


Figure 3. Simulation using a halved prey birth rate, b.

To study the relationship of various factors to predator-prey dynamics, the rates of various parameters were changed. First, the model was simulated with a doubled prey birth rate. In contrast to the standard model, the prey population experiences an initial increase in population. Then, prey reach an equilibrium population of about 500, while predators reach an equilibrium population of about 125. Figure 2 shows the results of this simulation.

Then, the simulation was ran with a birth rate half of that in the standard simulation. Here, the prey population experiences an initial sharp decline, temporarily dropping below the prey population. This decline in prey population cuts off the food supply to the predator population and also causes a decline in predator population. This leads to a significant shift in the equilibrium populations, and a large spike in prey population.

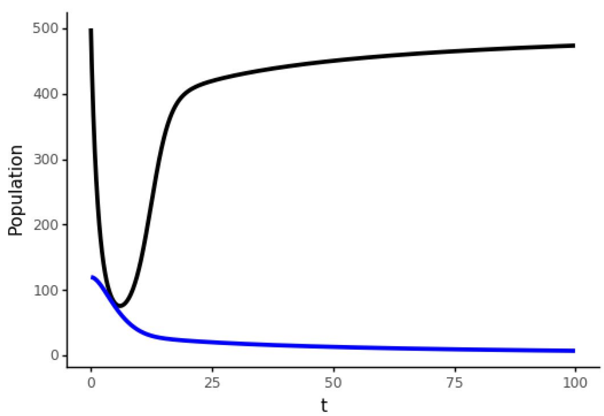


Figure 4. Simulation using tripled competition coefficient, α.

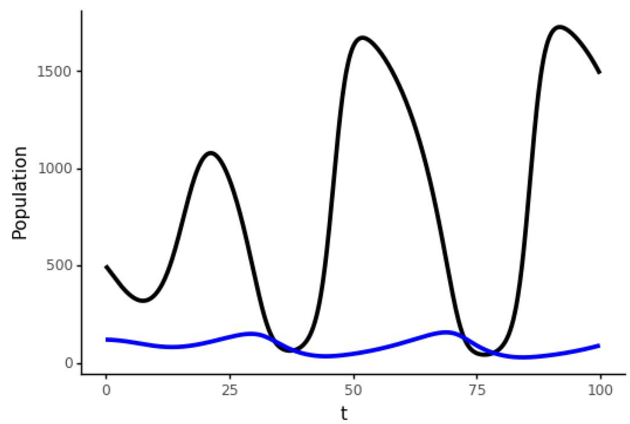


Figure 5. Simulation using halved competition coefficient, α.

Further, the effect of the competition coefficient, α, was tested. When α was tripled, prey population experiences an initial sharp decline, then reaches equilibrium. However, when α was halved, prey population oscillates from about 100 to 1600 in regular time cycles.

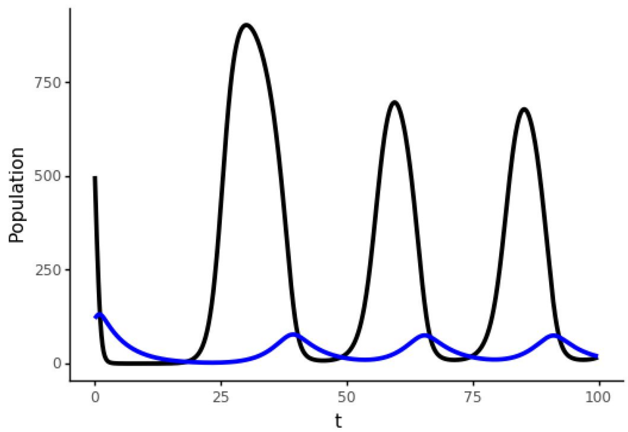


Figure 6. Simulation using doubled maximum predator attack rate, w.

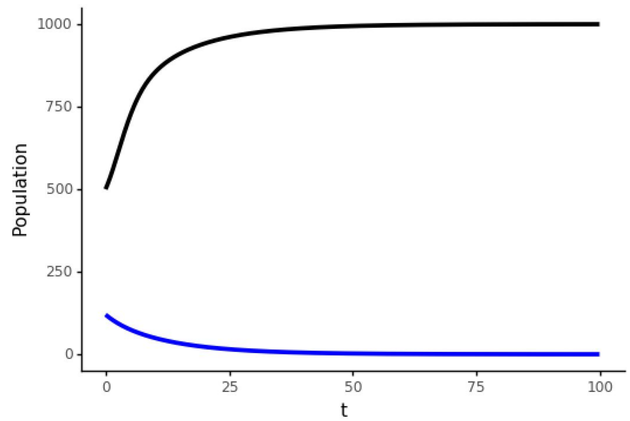


Figure 7. Simulation using halved maximum predator attack rate, w.

Next, the effect of predator attack rate, w, was tested on the population dynamics. When w was doubled, prey population initially declines sharply, then oscillates from 800 to close to 0. Predator population also oscillates, but at lower population levels. Effectively, when predators attack more often, prey population declines as more are killed. However, a lack of available prey leads to a decline in predator population. The oscillation cycles do not align perfectly, which makes sense given the delay of the predator-prey food cycle changes.

When predator attack rate is halved, the prey population increases, then reaches an equilibrium population of about 1000. In the standard parameter case, the equilibrium population is about 600. Thus, the prey population is allowed to grow to a higher level, but ultimately cannot continue to grow forever.

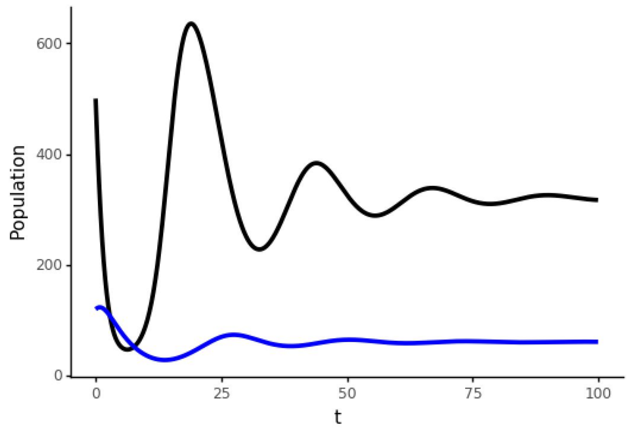


Figure 8. Simulation using doubled handling time predator per prey, d.

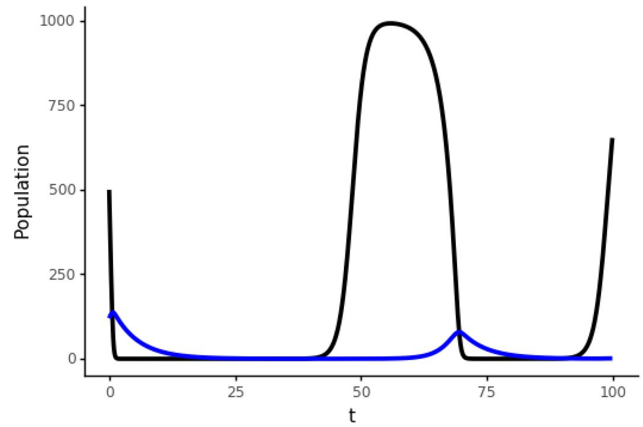


Figure 9. Simulation using halved handling time predator per prey, d.

The effect of d, the handling time of predator per prey, was simulated. When d is doubled, both predator and prey populations initially decline. However, as time progresses, the populations oscillate. The prey population reaches a lower equilibrium level than in the standard model.

As d is halved, prey population sharply drops to nearly 0, as predators can capture more prey in a given time. However, this starving of food supply also leads predator population to drop to nearly 0. Over time, predators and prey reach delayed cyclical population dynamics, which is also observed in several other parameter simulations.

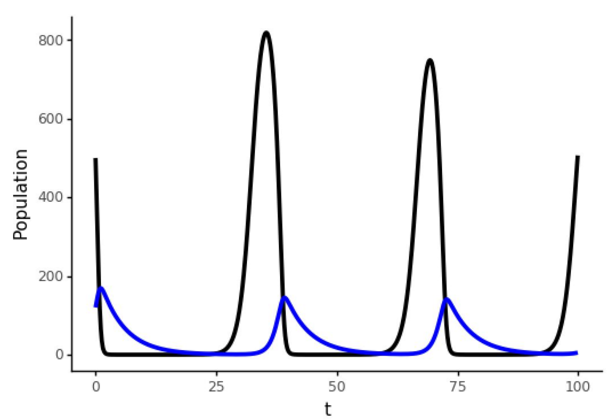


Figure 10. Simulation using doubled conversion efficiency, e.

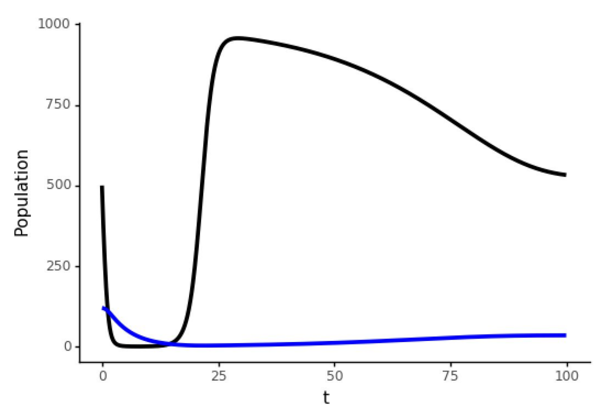


Figure 11. Simulation using halved conversion efficiency, e.

The effect of conversion efficiency, e, was simulated. Conversion efficiency refers to the number of prey which must be eaten to produce a new predator. As e is doubled, prey population sharply declines, then oscillates, while predator population experiences a delayed oscillation. Higher conversion efficiency means that more prey must be eaten to produce a new predator, so predator population would be lower. Thus, the predator population oscillates but ultimately reaches a lower value than in the standard model.

As e is halved, prey population also declines. The number of prey to produce new predators decreases, so new predators are born much faster. This leads to a sharp decrease in prey population, which cuts off food supply to predators. Thus, the equilibrium prey population is about 600, and the predator population about 75, which is smaller than in the standard model. Thus, the greater ease of producing new predators actually inhibits predator population in the long run.

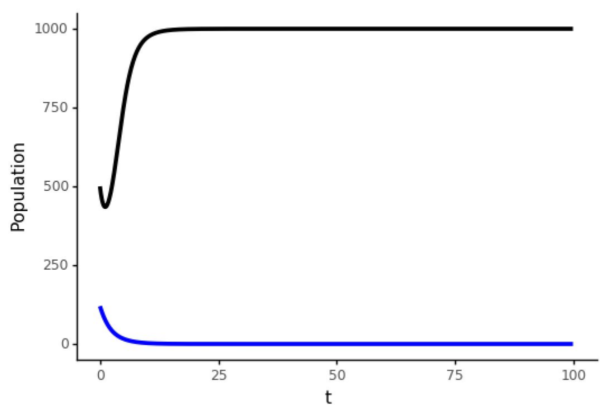


Figure 12. Simulation tripled predator death rate, s.

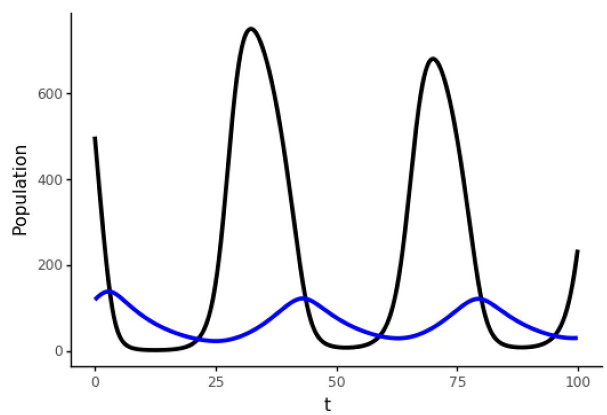


Figure 13. Simulation using halved predator death rate, s.

The effect of predator death rate, s, was also tested. As s was tripled, prey population sharply increases, and reaches an equilibrium level of about 1000, much higher than the level of 600 in the standard model. Predator population also declines, then reaches a lower equilibrium population than in the standard model.

As s was halved, prey population initially declined and predator population initially decreased. Over time, the populations demonstrate out of phase cyclical behavior. An increase in prey population leads to a delayed increase in predator population, as more prey provides food to increase the number of predators. However, the equilibrium level is slightly higher than in the standard model.

The following table describes the effect of each parameter on predator abundance. Increasing and decreasing each of these parameters often had sharp effects on predator and prey populations in the short term. However, the effect of predator abundance in the table refers to its effect on equilibrium population. Here, the equilibrium population is compared to the equilibrium populations in the standard model: about 575 individuals for prey and about 75 individuals for predators.

Parameter	Effect on Predator Abundance	Evidence for Effect
H	No effect	Populations, not parameters that can be changed
P	No effect	Populations, not parameters that can be changed
b	No long-term effect	Doubling b and halving b have little effect on equilibrium population of predators
α	Inverse relationship on long-term, equilibrium population	Tripling α leads to initial drop in prey population, reaches equilibrium; halving α leads to significant oscillations in prey population
e	Slight inverse relationship in long-term	Doubling e causes large oscillations in predator and prey populations; Halving e leads to overall decline in predator and prey populations
s	Slight inverse relationship in long-term	Tripling s leads to long-term decrease in predator population; halving s leads to long-term predator population oscillations, but overall greater than standard model
d	Linear relationship in long-term	Doubling d leads to slight increase in long-term predator population; halving d causes long-term predator population to be close to 0

Table 1. Table showing the effect of each parameter on equilibrium predator abundance.

The dynamics of the Rosenzweig-MacArthur model might be compared to the dynamics of the Lotka-Volterra model. The simulations run using the Lotka-Volterra model follow more predictable and simple cyclical patterns, while the graphs from Rosenzweig-MacArthur have more varied behavior.

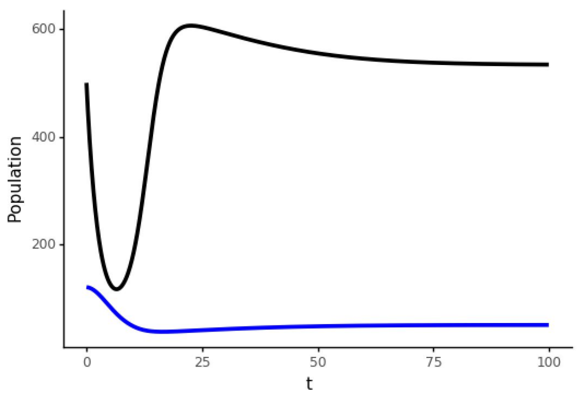
Thus, RM takes into account factors that LV does not consider. LV only looks at factors such as prey birth rate, predator attack rate, conversion efficiency, and predator death rate. For LV, only the relationships between prey and predators are considered. However, RM takes into account external factors that limit predator and prey population growth. RM includes d, the handling time of predator per prey. In LV, the assumption is that predator population growth is only limited by prey population growth. However, the addition of the d parameter asserts that predator population growth is also limited by the number of prey that each predator can handle.

In addition, the addition of the α term affects the dynamics of the models. The parameter α is the inverse of carrying capacity. So, the RM model includes the effect of available resources in the environment on populations. LV assumes that prey is the only factor affecting predator population and vice versa. However, RM asserts that the environment limits both predators and prey by the number of resources available. RM extends LV by including external factors on the system.

Paradox of Enrichment:

Further, the Paradox of Enrichment was simulated by varying α. The parameter α refers to the inverse of the carrying capacity of the population. Carrying capacity indicates numbers of individuals that the environment can handle. Thus, a larger α indicates that the population can handle fewer individuals.

The Paradox of Enrichment was simulated to determine the relationship between prey carrying capacity and predator population stability.



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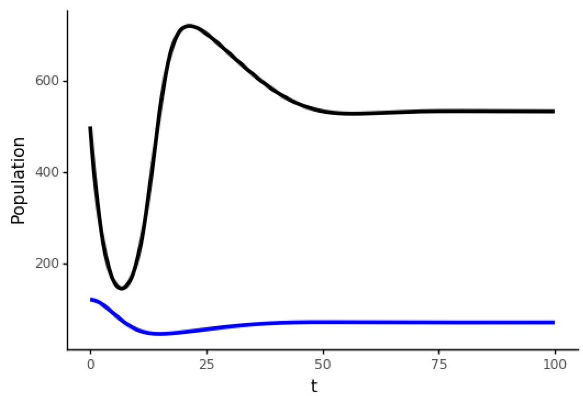

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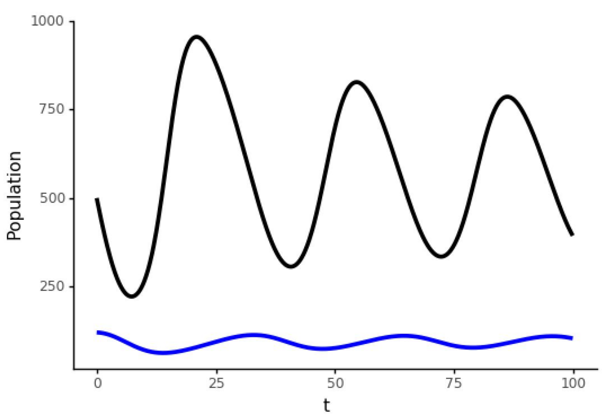
Figure 14. Simulation using competition coefficient α = 0.00125.

Figure 15. Simulation using competition coefficient α = 0.001.



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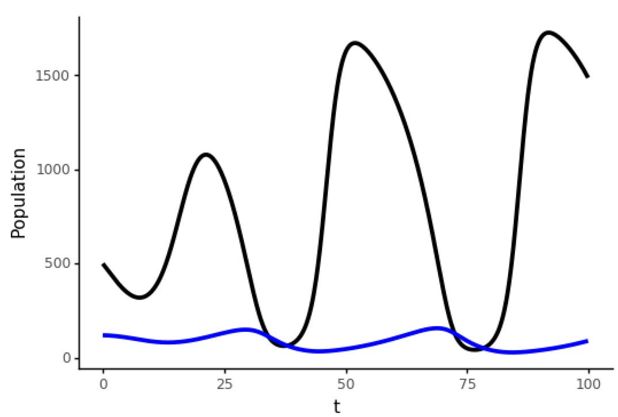

<ggplot: (7556959253)>

Figure 16. Simulation using competition coefficient α = 0.00067.

Figure 17. Simulation using competition coefficient α = 0.0005.

As α is increased, the carrying capacity of the system is decreased. In other words, the inverse relationship of α and carrying capacity leads to changes in population dynamics from changes in α. The decrease in α, which corresponds to an increase in carrying capacity, leads to an overall decline in predator population stability. This can be observed by the increasing oscillatory behavior in Figures 14-17 as carrying capacity increases.

Fundamentally, the Paradox of Enrichment occurs due to changes in resource availability. As carrying capacity increases, greater resources are available and more prey can be supported. The increase in prey allows for an increase in predator population. However, more predators can then consume more prey. This decreases the prey population, which leads to a decrease in predator population.