Melina Wettstein
Q SCI 454
November 19, 2021

Project 2: Predator and Prey Relationships

Introduction

Predator-prey interactions are ubiquitous in nature, yet are a unique type of ecological interactions whose properties require further understanding. The most notable aspect of these interactions are that prey are beneficial for predator populations while predator populations are harmful for prey. Because of the co-dependence of these species, and the asymmetry in the direction of each population's effect on each other, it is possible for them to be unstable. This instability arises because predation should deplete prey populations, which in turn reduces predator production and abundance, leading to enhanced prey populations.

Identifying the ecological conditions under which this process is stable is well suited for ecological modeling. Unlike in real world situations, models can be used to directly measure inherent stability of equilibrium conditions. Further, modeling allows us to sequentially add or remove ecological interactions to models determine whether they stabilize or destabilize predator-prey systems.

Here I develop a series of models to evaluate effect of common ecological processes on the stability of predator-prey interactions. Specifically, I develop a simple discrete-time Lotka-Volterra model (the "base" model) that serves as a reference model to judge model stability. I then evaluate the stabilizing effects of density dependence and prey handling time, as well as the interactive effect of the two. I interpret the results of these simple models with respect to real world predator prey systems by extrapolating my understanding of mathematical models to what each implies about actual predator-prey interactions.

Base Model

The base model, as described above is the discrete time Lotka-Volterra model. The recursive equation for the prey population is $N_{t+1} = N_t + aN_t - bN_tP_t$ where Nt is the population at time t, Pt is the predator population at time t, a is the reproductive rate of the prey, and b is the per-capita attack rate of predators on prey. Similarly, the recursive equation for the predator population is $P_{t+1} = P_t + cbN_tP_t - dP_t$ where c is the conversion constant that relates prey consumption to reproduction of predators, and d is the predator death rate. The rate of change for the populations are $\frac{\Delta N}{\Delta t} = aN_t - bN_t P_t$ and $\frac{\Delta P}{\Delta t} = cbN_t P_t - dP_t$. These equations are used to find the isoclines, by setting them each equal to zero. The prey isoclines are determined by setting the $\frac{\Delta N}{\Delta t}$ equation equal to zero, and similarly for the predator isoclines. The prey isoclines are $N_t = 0$ and $P_t = \frac{a}{b}$. The predator isoclines are $P_t = 0$ and $N_t = \frac{d}{cb}$. When considering the equilibrium points, we must consider when both of the rate of changes are equal to zero. This occurs at two points, $(0,0)$ and $(\frac{d}{cb}, \frac{a}{b})$. The Jacobian, used to determine behavior of the model mathematically, was evaluated at the equilibrium point:

$$\begin{bmatrix} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{bmatrix} = \begin{bmatrix} 1 + a - bP^* & -bN^* \\ cbP^* & 1 + cbN^* - d \end{bmatrix} where\ (N^*, P^*) = (\frac{d}{cb}, \frac{a}{b})$$

From this, the eigenvalues and eigenvalue magnitude were determined which predict the trajectory of the population.

For this model, we assumed the parameters to be *a*=0.2, *b*=0.15, *c*=0.3, and *d*=0.15. Figure 1 shows the population of both the predator and prey oscillating as time goes on. Figure 2 shows the plot of predator vs prey populations with the isoclines, the equilibrium points, and the trajectory over time. The start time is the larger black dot, which occurs at 10% above the equilibrium, and the trajectory oscillates out as time passes. Using the model parameters, we get that the Jacobian is $\begin{bmatrix} 1 & -0.5 \\ 0.06 & 1 \end{bmatrix}$ which has eigenvalues 1+0.173*i* and 1-0.173*i*. When the eigenvalue magnitude is calculated, we get 1.0149. Since the eigenvalues are complex and the magnitude is greater than 1, this indicates the population oscillates away from equilibrium. This is consistent with the trajectory in figure 2.

For the parameters provided, the eigenvalues and the trajectory plot show the equilibrium is unstable. If the prey and predator population started directly on the equilibrium point, they would stay there, but even a slight nudge causes an oscillation away. This behavior can be explained thinking about the model ecologically. The starting point of the trajectory has high levels of predators and prey. This means that the predator population will increase because there is plenty of food and the prey will decrease because they are being eaten. When the prey population falls enough, the predator population will decrease because there is not enough food. Once the predator population is low, the prey population begins to increase. As it increases, there is more prey available for the predators and their population grows again. This is a cycle that repeats. With these model equations written in the base model, each oscillation has higher and lower populations for both predators and prey. This is seen in figure 1. The difference between oscillations get larger because without the predators (or for very low predator values), the prey can increase exponentially.

Prey Density Dependence

In this model, we now assume that there is a density dependence in the prey population. Unlike the base model, which assumes that without predators, the prey grows exponentially, we now have a carrying capacity *K* which regulates the growth of the prey population in the absence of predators. This model is represented by the following population equations:

$$N_{t+1} = N_t + aN_t(1-\frac{N_t}{K}) - bN_tP_t$$
$$P_{t+1} = P_t + cbN_tP_t - dP_t$$

The prey isoclines, found in similar way as the base model, are $N_t = 0$ and $P_t = \frac{a(1-\frac{N_t}{K})}{b}$. The predator isoclines remain unchanged because the predator population equation remains the same. These isoclines are $P_t = 0$ and $N_t = \frac{d}{cb}$. The equilibrium points were found similar to above, by setting both rates of change equal to zero. Three equilibriums were found, $(0,0)$, $(K,0)$, and $(\frac{d}{cb}, \frac{acbK-ad}{cb^2K})$. The Jacobian evaluated at the equilibrium point was determined to be

$$\begin{bmatrix} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{bmatrix} = \begin{bmatrix} 1+a-\frac{2aN^*}{K}-bP^* & -bN^* \\ cbP^* & 1+cbN^*-d \end{bmatrix} where\ (N^*, P^*) = (\frac{d}{cb}, \frac{acbK-ad}{cb^2K})$$

The parameters were assumed to be the same as for the base model (*a*=0.2, *b*=0.15, *c*=0.3, and *d*=0.15) and the carrying capacity *K* was assumed to be 15. Figure 3 shows the predator and prey populations over time. Unlike the base model, these clearly stabilize. This is further illustrated in figure 4, where the two populations are compared, with their isoclines, equilibrium points, and the trajectory over time. The trajectory clearly goes from the ‘nudge point,’ 10% above the equilibrium value, to the equilibrium. When the Jacobian was calculated, the matrix was $\begin{bmatrix} 0.8666 & -1.5 \\ 0.00666 & 1 \end{bmatrix}$, the eigenvalues were 0.9333+0.0745*i* and 0.9333-0.0745*i*, and the magnitude was 0.9363. Since the eigenvalues are complex and the magnitude is less than 0, this indicates the population oscillates towards equilibrium, which supports the trajectory in figure 4.

For the parameters provided, the prey density dependent model oscillated towards equilibrium rather than away from it. That is, with the same parameters of the base model, the introduction of a carrying capacity changed the equilibrium with both populations present from unstable to stable, though the population still oscillates around that point before converging. Given a slight nudge off this equilibrium point, the population will return to it after some time. The population undergoes a similar oscilliation to the base model, where the increase in prey leads to an increase in predators, then a decrease in prey which leads to a decrease in predators. This is the same mechanic as described above. However, because a carrying capacity was implemented for the prey, the population cannot get larger the same way it did under the base model. Instead, the difference in oscillations gets smaller and returns to equilibrium.

Predator Handling Time

Another real world aspect of population dynamics ignored in the above models is the constraints on feeding rate of predators. The equations are below where *h* is the time required to subdue the prey that is consumed. The maximum rate they can feed, when prey is not a limiting factor, is 1/*h*. The new model equations are

$$N_{t+1} = N_t + aN_t(1-\frac{N_t}{K}) - \frac{bN_tP_t}{1+bhN_t}$$

$$P_{t+1} = P_t + \frac{cbN_tP_t}{1+bhN_t} - dP_t$$

The predator and prey isoclines are both different for this model when compared to the base model. The prey isoclines are $N_t = 0$ and $P_t = \frac{a(1-\frac{N_t}{K})(1+bhN_t)}{b}$ and the predator isoclines are $P_t = 0$ and $N_t = \frac{d}{cb-dbh}$. The equilibrium points are $(0,0)$, $(K,0)$, and

$\left(\frac{d}{cb-dbh}, \frac{ad}{cb-dbh}(1-\frac{d}{(cb-dbh)K})\right)$. The Jacobian was evaluated at the third equilibrium point, where both populations are present and was determined to be

$$\begin{bmatrix} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{bmatrix} = \begin{bmatrix} 1-\frac{bP^*}{(1+bhN^*)^2} & \frac{-bN^*}{1+bhN^*} \\ \frac{cbP^*}{(1+bhN^*)^2} & 1+\frac{cbN^*}{1+bhN^*}-d \end{bmatrix}$$

Again, the parameters for the base model were used (a=0.2, b=0.15, c=0.3, and d=0.15). the maximum feeding rate h was assumed to be 0.5. The carrying capacity varied because its value changed the output of the model. First, assume the carrying capacity K is 10. Figure 5a shows the predator and prey populations over time and figure 6a shows the predator and prey trajectory and isoclines. The start of this trajectory is 10% higher than the equilibrium point. The populations begin oscillating slightly but settle into a stable state. The trajectory graph shows this by showing some oscillation to equilibrium, rather than going straight there, but shows that the population does settle into that stable equilibrium value. The Jacobian matrix was $\begin{bmatrix} 0.9388 & -0.5 \\ 0.025 & 1 \end{bmatrix}$, the eigenvalues were 0.9694+0.1075i and 0.9694-0.1075i, and the eigenvalue magnitude was 0.9754. Since the eigenvalues are complex and the magnitude is less than 1, this indicates the population oscillates towards a stable equilibrium. This is supported by the trajectory map in figure 6a. Now consider the carrying capacity K=25. The predator and prey populations over time and plotted against one another with a trajectory are in figures 5b and 6b respectively. With the higher carrying capacity, the oscillations are much larger as seen in figure 5, and they do not get smaller to approach a stable value. Instead, they continue to get bigger. The trajectory in figure 6b shows the population values oscillating away from equilibrium and never reaching a stable point. The Jacobian matrix is $\begin{bmatrix} 1.0056 & -0.5 \\ 0.037 & 1 \end{bmatrix}$, the eigenvalues were 1.0028+0.13598i and 1.0028-0.13598i. The eigenvalue magnitude was 1.012. Since the values are complex and the magnitude is greater than 1, the population oscillates away from equilibrium. This is consistent with the trajectory in figure 6b.

The model behavior depends on the carrying capacity. Though both behaviors oscillate due to the same population movements as described before, whether they approach a stable equilibrium or go away from an unstable equilibrium depends on the value of K. This is because the prey handling term h changes the way the prey population decreases. Since $bN_tP_t > \frac{bN_tP_t}{1+bhN_t}$, the prey population decreases less. This means that the carrying capacity is more important in determining how much the prey population increases and when the carrying capacity is too high, the prey population can grow too much to go back to the same equilibrium point, like in the base model. When the carrying capacity is lower, it is sufficient to control population sizes and return to equilibrium, like in the second model.

Discussion

The base model was the simplest, though it included the fewest adjustments to account for real world properties of the populations. Under this model, there was no stable coexistence between prey and predator. Realistically, this is not correct because there are clearly populations with predators and prey coexisting. Another issue with this model is that if the predator species goes extinct, the prey population growth is exponential.

The prey density dependent model has a slightly more complex equation for prey and the same equation for predators. Under this model, there is always stable coexistence. This seems to be more accurate because we know that there are predator and prey populations that coexist. However, the third model accounts for the most biologically relevant processes.

The predator handling time model accounts for the amount of time it may take a predator to subdue the prey. Under this model, the carrying capacity determines stability. For the lower carrying capacity the model oscillates towards a stable equilibrium, but for the larger carrying capacity, the model oscillates away, meaning there isn't a stable equilibrium. When the carrying capacity is low, the model behaves like the prey density dependent model and when the carrying capacity is high, it behaves more like the base model, without a carrying capacity. Without a carrying capacity, the predator handling model very quickly oscillates away from equilibrium, but the density dependence is the key to having some population interaction that goes towards equilibrium.

The predator handling model contains most real biological systems, though it is the most complicated so may not be necessary in all situations. If the carrying capacity of a system is known to be sufficiently small, the behavior is the same as the density dependent model, so it may be simplified. However, if the carrying capacity is higher, it is essential to consider the feeding rate of the predator in the model. The base model assumes exponential growth in the absence of the predator and is the least biologically relevant. Since there is no way to get an oscillation towards equilibrium, this model appears too simple to give accurate data.

All of these models assume that the predator is the main cause of death for the prey. If the prey have a significant cause of death unassociated with the predator, like environmental factors or food scarcity, this would need to be added. The model is also assuming that every age of prey is equally likely to be eater, and likewise for the predators hunting habits at all ages. If there are large differences in behavior by age or stage in these populations, including stage based equations may be necessary. Finally, though I don't think it impacted this model or parameters specifically, if prey are significantly more abundant than predators, the predators would display an exponential growth because they do not have a density dependent relationship with birth rate. It may be necessary to add a carrying capacity for the predator population as well. However, if that were the case, then the predator and prey interactions in this model may not be relevant anyways.

Figures

Figure 1. Predator and prey population over time under the base model.

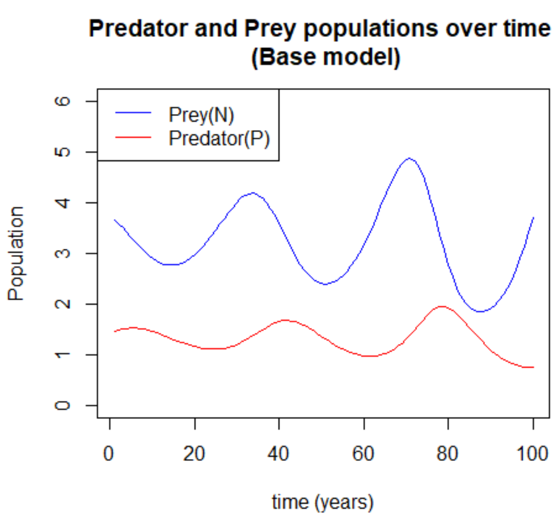

Figure 2. Predator vs prey population plot with isoclines, equilibrium points, and trajectory over time for the base model

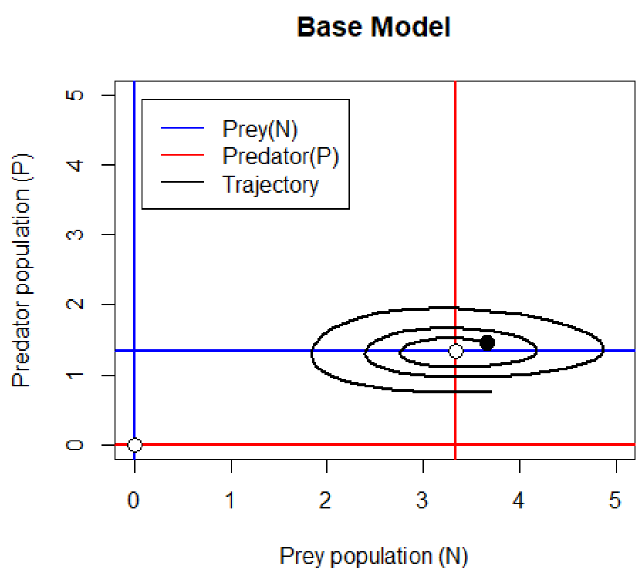

Figure 3. Predator and prey population over time under the prey density dependence model.

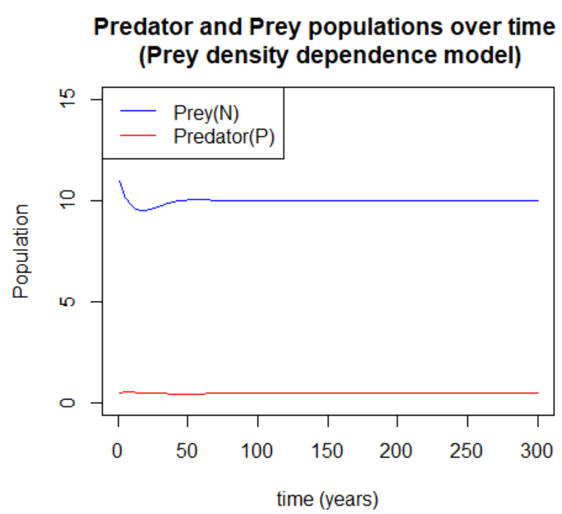

Figure 4. Predator vs prey population plot with isoclines, equilibrium points, and trajectory over time for the prey density dependence model; with zoomed in plot of trajectory towards the equilibrium point.

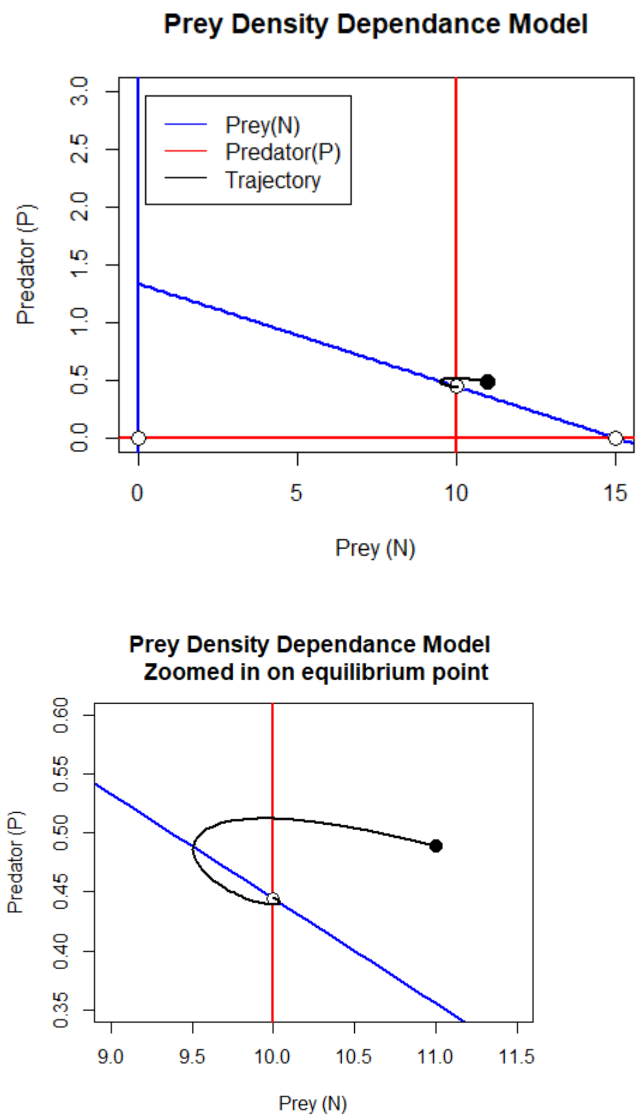

Figure 5. Predator and prey population over time under the Prey handling model. Each also assumes a different carrying capacity. A) K=10. B) K=25.

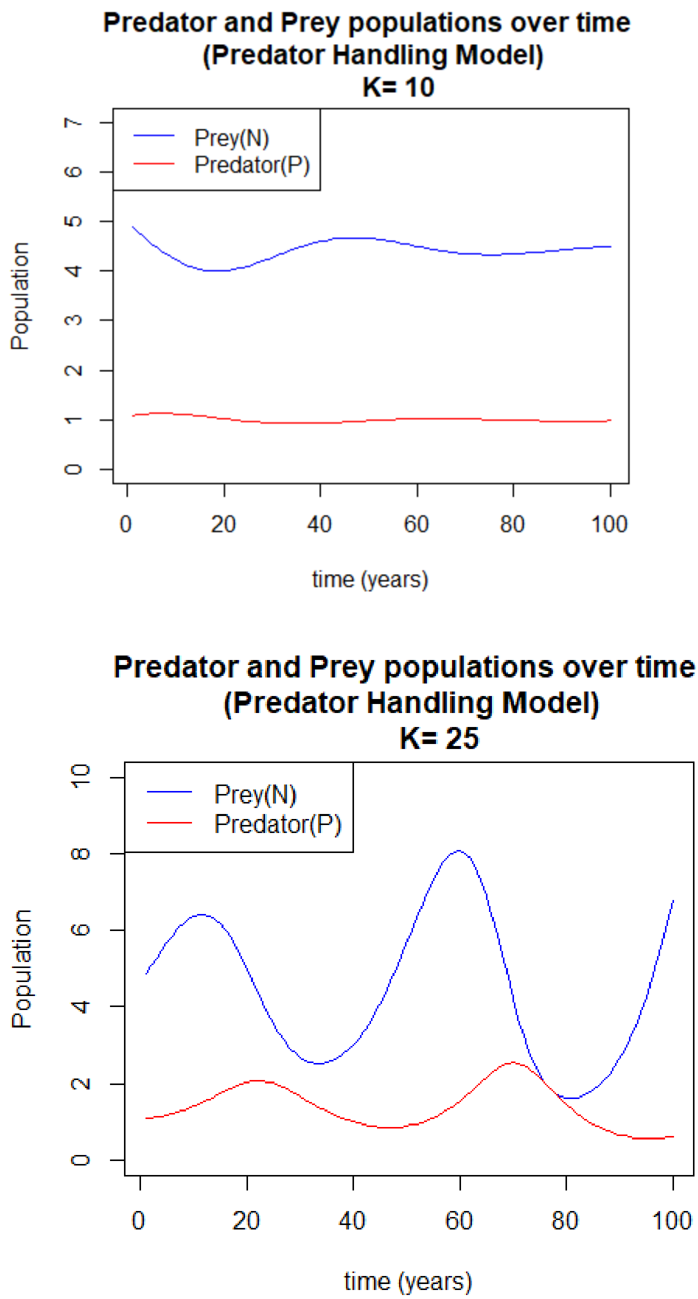

Figure 6. Predator vs prey population plot with isoclines, equilibrium points, and trajectory over time for the predator handling model, assuming different K values. For K=10, a zoomed in plot is included.