

*Dynamics of a Predator-Prey-Vegetation Model***Introduction***Construction of a Model for Deer Population*

Using the Stella Professional software, a model for the dynamics of a deer population was constructed, including birth and death as mechanisms for changing the population based on a rate that was linear with the deer population. This initial model corresponds to the simple differential equation $\frac{dD}{dt} = \alpha D - \beta D$, where α and β are the birth and death rates per deer, respectively. Thus, the net growth rate of the deer population is simply dependent on the difference between the two individual rates, and may then be used to determine whether the population will grow indefinitely or shrink to zero.

Addition of Vegetation as a Food Source

In order to investigate the effects of food source levels on the dynamics of the deer population, a vegetation population was introduced. The vegetation population increases via regeneration, which occurs at a fixed rate per member of the population. The consumption rate, however, is dependent not on the vegetation population, but rather on the deer population, which consume the plants at a fixed amount per time period per individual. Conversely, the death rate of the deer was then modified by the presence of the food source. Known data for the death rate per deer was included in a graphical representation of the death rate, which began with an initial death rate of 1.000 without the presence of food and rapidly decayed, approaching the natural death rate (taken to be 0.020), as the population of vegetation increased to a sufficient amount to keep the deer population fed. This addition changes the model to a system of differential equations for the deer and vegetation dynamics, taking the form: $\frac{dD}{dt} = \alpha D - \beta(V)D$ and $\frac{dV}{dt} = \gamma V - \delta D$, in which α is the deer birth rate per individual, β is the deer death rate per individual and is a function of the vegetation population, V , γ is the vegetation regeneration rate per individual, and δ is the amount of plants eaten per deer per year (or per time point, in general).

Addition of Predators of the Deer Population

The final interaction to be investigated was that of the predator-deer relationship, and thus a predator population (e.g. wolves) was introduced to the model. For the purposes of the model, it is assumed that the predators and vegetation do not interact directly (i.e. the predators are carnivorous, or at least do not share the same plant consumption as that of the deer). A linear birth rate was also assumed for the predators, in the same way that it was utilized for the other two populations. The deer death rate was modified by the introduction of the effects of the predators by adding a second term to the expression for overall death. The new term is of the same form as that of the effects of the deer population on the vegetation, assuming a linear relationship of predator population and effect on the deer with a proportionality constant of the

amount of deer eaten by a single predator per year. The final addition to the model is the effect of deer population on the predator death rate. It was assumed that the overall form of the dependence of the predator death rate on the deer population was identical to that of the dependence of the deer death rate on the vegetation. Thus, the same values were used, ranging from 1.000 to 0.020 in a graphical fit, but the domain of the x-axis was changed to more accurately fit the deer population numbers, as they are approximately an order of magnitude less to begin with and do not approach that of the vegetation throughout the time course of the model. Now, the system of equations contains three variables, resulting in three interdependent equations. The vegetation equation has not changed: $\frac{dV}{dt} = \gamma V - \delta D$. The predator equation is analogous to the previous form of the deer equation: $\frac{dP}{dt} = \varepsilon P - \zeta(D)P$, in which ε is the predator birth rate per individual and ζ is the predator death rate per individual, dependent on the deer population. The deer equation has become more complex, as a result of the addition of interactions with the predator population. Now, $\frac{dD}{dt} = \alpha D - \beta(V)D - \eta(P)D$. Thus, the deer equation still contains the same birth rate and vegetation-dependent death rate as before, but also has a new predator-dependent death rate due to consumption.

Initial Parameters of the Predator-Deer-Vegetation Model

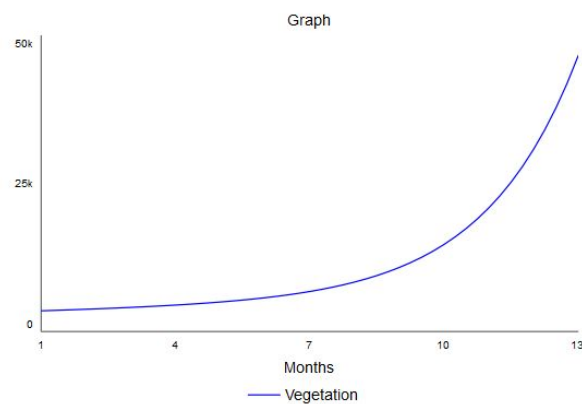
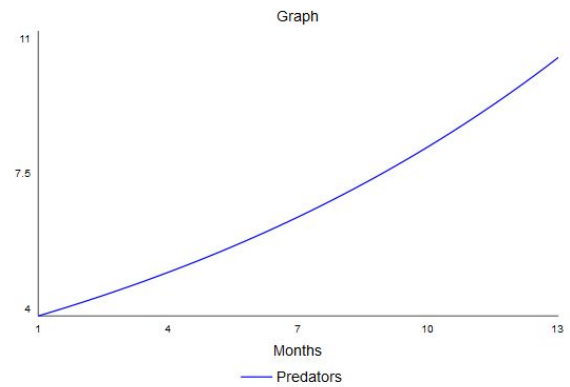
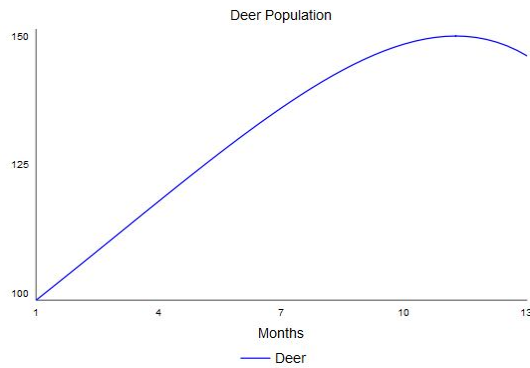
The addition of a third stock to the model further increases the total number of parameters that must be specified, and thus, the total number of variations that may be investigated. The vegetation rates were initially specified as 15 consumed/time per deer, 0.5 regeneration/plant, and an initial population of 3500. The deer population began with an initial value of 100, a birth rate per individual of 0.2, a predator-dependent death rate of 3 deer per predator, and a death rate dependent on the vegetation population as described in Table 1:

| | | | | | | | | | | | |
|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Veg. | 0 | 100 | 200 | 300 | 400 | 500 | 600 | 700 | 800 | 900 | 1000 |
| Rate | 1.000 | 0.815 | 0.610 | 0.480 | 0.360 | 0.260 | 0.165 | 0.110 | 0.055 | 0.030 | 0.020 |

This table depicts the initial form of the predator death rate dependence on the deer population as well, though the population limits were initially changed to range from 0 to 25. Note that the ratio of the upper bound of this plot to the initial population size is comparable (25/100 to 1000/3500). The predators were assumed to have an initial population of 4 individuals, and a birth rate per individual of 0.1.

The dynamics of this initial trial do not show collapse of any population over the range of time tested, but the data suggest that a collapse will occur outside of this range. The vegetation appears to grow exponentially throughout the time course of the trial. The predator population is nearly linear with slight upward curvature. The deer population, however, reaches a maximum at about 11.5 months, after which it begins to decrease. It is possible that this decrease will be

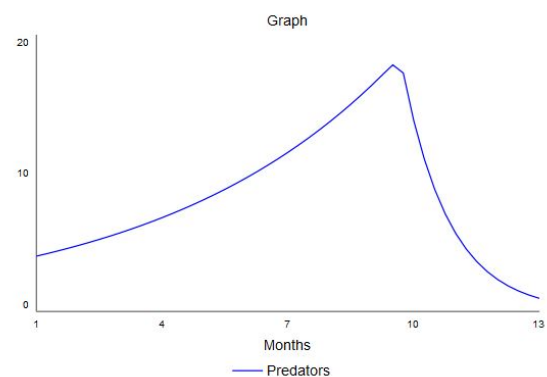
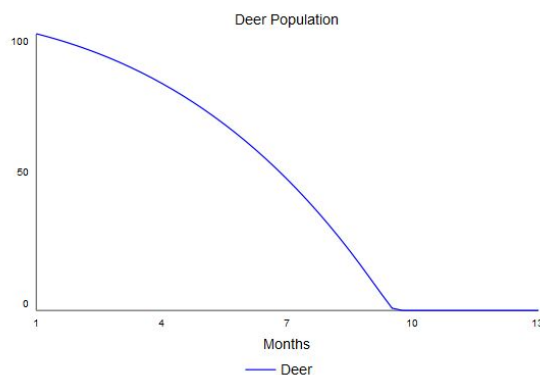
rapid, as the range terminates shortly after this, thus resulting in a sharp decline to zero in the deer population, after which the predator population will also be eliminated. As the vegetation's effect on the deer population has long since been removed by the high population size (well above 1000, at which the deer death rate returns to its natural value), the effects of the vegetation on preventing the collapse of the deer population will be limited.



Dynamics of the Predator-Deer-Vegetation Model

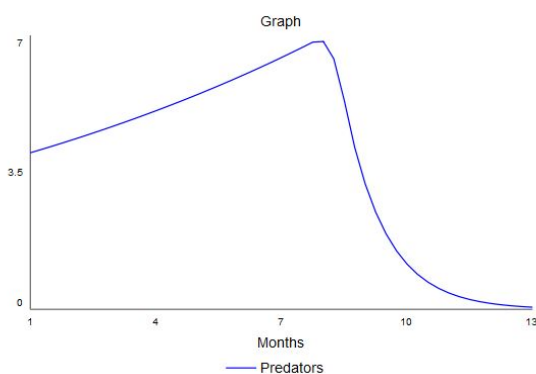
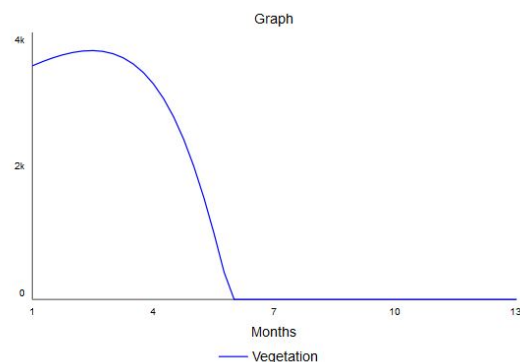
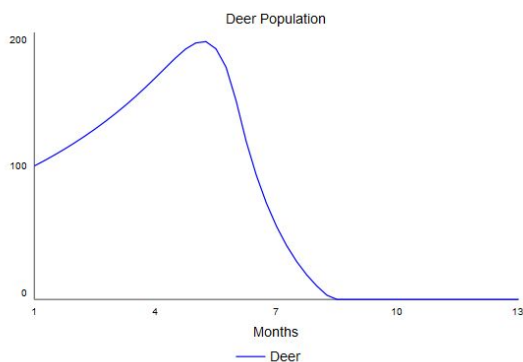
The discussions in this section will be limited primarily to adjusting initial population values, birth/regeneration rates, and death rates, both in the form of number of individuals eaten per year for deer and vegetation and in effects of consumption on the death rate of deer and predators by changing the population axis of the experimental data. It is assumed that the overall form of the death rate curve, however, is

constant, as it was experimentally obtained, and intuitively reflects how lack of food should alter population.



Increasing the predator birth rate from 0.1 to 0.2 or decreasing the deer birth rate from 0.2 to 0.1 has essentially the same effect: the predator population will grow too quickly until the deer population cannot sustain it. Ultimately, the deer population will decay to zero as they are all eaten, and the predator population will then collapse as they have eliminated their food source. The trend of the vegetation population (not pictured above) remains the same, but the scale is different, reaching a maximum value of almost 300,000 as opposed to 50,000, as the deer are no longer around to eat them. Intermediate values simply serve to change the time scale over which the deer population is extinguished and the predator population reaches the collapsing point.

In the above scenario, the growth of the predator population exceeded the growth of the deer population. In the opposite case, which arises from raising the deer birth rate (to 0.3) or reducing the predator birth rate (to 0.02), results in the deer-vegetation dynamics dominating. In this scenario, the deer population growth exceeds that of the vegetation, and thus the vegetation population is eliminated. This results in the deer population collapsing to zero without any food source, and the same happening to the predators afterwards.



The effects of the vegetation regeneration rate on these dynamics are as one would expect: increasing regeneration rate by, for example, using a different species, prolongs the time until the population decays to zero and may also result in the predator population eliminating the deer population first. Decreasing the regeneration rate by, for example, changing the species or the availability of nutrients and space, causes the

trend to go in the opposite direction, with the collapse of both other populations occurring more rapidly.

As can be predicted, altering the constant death rates of the different populations essentially has the opposite effect. For example, if deer were to only eat 10 plants instead of fifteen, the time until the deer population collapse would lengthen and depending on the dynamics of the predator population, may preferentially occur due to consumption by the

predators. Increasing the number of plants eaten by deer has the opposite effect, as does decreasing the number of deer eaten by predators. In both cases, the vegetation population is more rapidly consumed. Finally, increasing the number of deer consumed by predators will favor elimination of the deer population, allowing the vegetation to continue to grow and the predators to subsequently die out.

The above effects are the same as those resulting from changing the scale of the domain of the population axis in the graphical death rate curves. Increasing the number of deer at which death rates for predators decay to natural values (0.02) makes it more likely that the predators will die, slowing their growth and prolonging the time until collapse. Similarly, increasing or decreasing the scale of the vegetation population for the deer death rate serves to reduce or lengthen the time to collapse of the deer population, respectively. It is worth noting that, with the present dynamics, altering this scale anywhere between 1 and 3500 has very little effect on the system dynamics, as the vegetation population is monotonically increasing from an initial value of 3500 and thus the deer death rate will be constant at 0.02 the entire time.

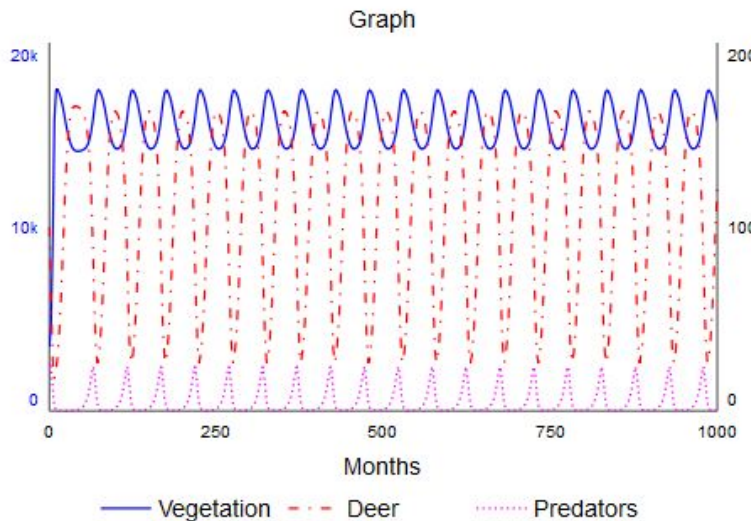
The final parameter that may be investigated is the initial values of the system. The effects of these changes fall into the categories discussed above as well. Increasing the predator population, for example, will promote collapse of the deer population and growth-collapse behavior for the predators, as will decreasing initial values of the deer. Increasing initial deer values, or decreasing predator values, will extend the time until this collapse occurs, unless the vegetation value cannot sustain the growth of the deer population. Similar effects result for the deer-vegetation dynamics.

Overall, the dynamics of this system follow one of two behaviors. If the vegetation population is sufficient to sustain deer growth, then the predator population will grow until all the deer are eaten, after which the predator will die out and the vegetation may grow exponentially. If the vegetation cannot sustain deer growth, then it will be the first population to die out, after which, the deer and predators will follow quickly. Changing system parameters and initial values serves to change the time scale of these dynamics and may cause a switch from one extinction mechanism to the other.

By varying each of the individual system parameters, a state at which all three populations stabilize was not found. However, it is possible that, at some specific combination of each death rate, birth rate, and initial population value, fixed points may exist that will be attractive, i.e. the system will trend toward these values, or repelling, i.e. a small perturbation will cause the system to collapse. Introducing more species makes finding a condition at which the birth rate and death rate of all three species equilibrate more difficult, though that is not to say that one cannot exist.

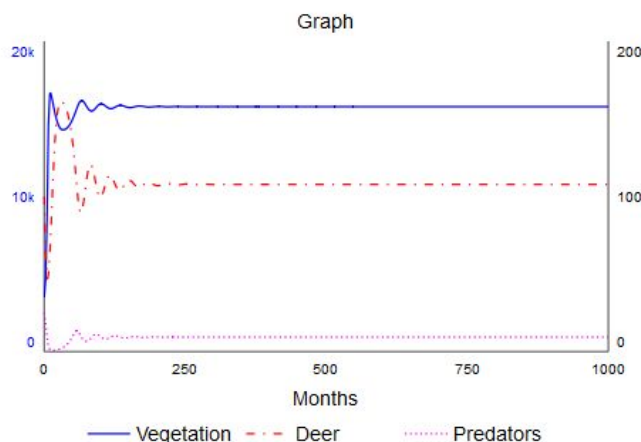
Carrying Capacity

In order to more accurately model the effects of environmental resource limits on populations, carrying capacities were introduced to both the deer and the vegetation death rates. These capacities were assumed to have the opposite functional form as the vegetation-dependent death rate for deer and deer-dependent death rate for predators. Thus, the carrying capacity death rate begins at 0.020 and increases to 1.000 as the population approaches the carrying capacity. It was assumed that the predator population was small enough to not experience environment-based constraints on its population, and that predator death would be dominated by reduced deer populations. The vegetation carrying capacity was taken as 25,000 and that for the deer was 400. Some of the predator constants were also adjusted: the birth rate was set to be 0.2, the deer population at which the natural (0.020) death rate is reached is 150, and it is assumed that each predator consumes one deer per time period. With these values, the following dynamics are observed. These results are consistent with observed Lotka-Volterra dynamics, in which



species oscillate out-of-phase with each other. Altering the constants from this point can still lead to collapse of the population. For example, increasing the consumption rate of deer by predators to 2 results in immediate eradication of the deer population, while increasing the deer carrying capacity to 500 causes overshoot and collapse of the predator population. Thus, this fixed

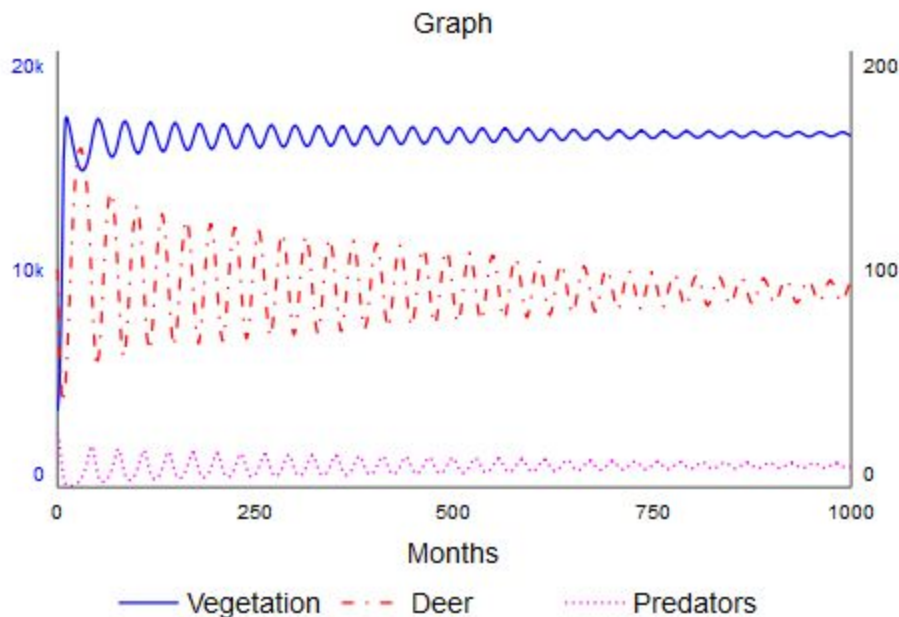
point still requires correct values for the model dynamics within a narrow range. Interestingly, keeping the predator birth rate at its initial value of 0.1 results in what appears to be a



non-oscillatory steady-state condition after approximately 200 months. It is likely that the oscillations are too small to be made out in this scenario, if they exist, as small perturbations from a steady-state condition will arise in reality.

Predator Carrying Capacity

To evaluate the above assumption that the predator carrying capacity is largely negligible for the above dynamics, a capacity was introduced of 100 individuals. As this is well above the values around which the predator population oscillates, the effects on the steady-state values for the birth rate = 0.1 condition are small. The system still oscillates initially, reaching stability around the 140-month mark, with values differing by less than ten individuals for the deer and less than one for the predator. Interestingly, changing the birth rate back to 0.2 for the predators reveals the following oscillatory behavior that converges to a steady-state solution over time. This elongated damped oscillatory region has not been seen in the other cases, and thus appears to be a unique case of all three populations having a carrying capacity. Increasing the capacity magnitude to 400 causes the dynamics to be consistent of that with no predator carrying capacity, as expected.



Final Considerations

One may suggest certain additions or modifications to this model that would make the scenario more realistic. Many of the considerations would simply be the addition of more species to various levels of the model, including different plant species that may be consumed more or less quickly by deer or predators, and may have different regeneration speeds, for example. Additionally, the overall form of the death rate-population may be different for different scenarios. Finally, due to the fairly large number of parameters that must be specified for the three-species system investigated here, specific combinations of parameters may result in dynamics that are not discussed above, such as stabilization of all three populations without a carrying capacity. This issue is exacerbated with the introduction of more species and environmental factors.