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STUDENT VERSION
Plants Versus Herbivores

Mary Vanderschoot
Department of Mathematics and Computer Science
Wheaton College
Wheaton IL USA

STATEMENT

In a recent study [5] of a plant-herbivore ecosystem on an island in the North Sea, ecologists made a surprising observation: Instead of more vegetation resulting in more grazers, more vegetation resulted in fewer grazers. The ecologists hypothesized that, as the vegetation grew more dense, it became increasingly difficult for the herbivores to reach and/or to digest the vegetation. Eventually, the vegetation might grow so dense that it became unsuitable for the herbivores altogether. In this modeling scenario, you will apply techniques for studying nonlinear systems to analyze plant-herbivore models, including the two models used in the North Sea study.

Submission Version

1 Background

In the 1970s [1] ecologists began to apply the predator-prey model used in differential equations to model plant ('prey') and herbivore ('predator') interactions. Let P represent the plant biomass (usually measured in kg/m^2) and let H represent the herbivore density (usually measured in number of herbivores or number of droppings per unit of area). We first consider a simpler case of the standard plant-herbivore model, in which the herbivores are granivores. Granivores, such as kangaroo rats, feed primarily on dropped leaves or dropped seeds; they do not subtract biomass from the plant itself. The plant-granivore model is based on the following assumptions:

- The plant biomass exhibits logistic growth with intrinsic growth rate r and carrying capacity K.

- The seed loss is proportional to the plant biomass (i.e. seed loss is fP for some $f > 0$.)
- The herbivore density grows at a rate γ proportional to the seed loss.
- The herbivore density decreases at a rate m proportional to its current value.

These assumptions give the following plant-granivore model:

$$\frac{dP}{dt} = rP(1 - P/K) - fP\,, \tag{1}$$

$$\frac{dH}{dt} = \gamma fP - mH. \tag{2}$$

1. Understanding the model:
   (a) Explain why it makes sense to use logistic growth for plant biomass. (What are some of the limitations to plant growth?)
   (b) In using fP for seed loss, what assumptions are being made about the plant?
   (c) In your own words, what does γ represent for the herbivores? What does m represent?
2. Consider the differential equation (1) for the plant biomass:
   (a) Explain why (1) does not depend on H. What is the biological meaning?
   (b) Find the equilibrium points and sketch the phase line.
   (c) Using the phase line, what will be the plant density in the long-run?
3. Suppose the plant-granivore model, (1) and (2), is applied to a population of granivorous kangaroo rats in a desert where $r = 0.25, K = 10, f = 0.05, \gamma = 2$, and $m = 0.5$.
   (a) Sketch the nullclines and determine the equilibrium points of the system.
   (b) Use the Jacobian to classify the equilibrium points.
   (c) Use all of this information to sketch the phase portrait. Based on the phase portrait, what does this model predict about the plant and herbivore densities in the long-run?

In most plant-herbivore ecosystems, the herbivores consume more than just dropped leaves and/or dropped seeds. The rate at which an herbivore consumes plant biomass has been found to depend primarily on the amount of available vegetation. (Intuitively, we expect more grazing when there is more grass growth.) Thus, a simplifying assumption in many plant-herbivore models is that the herbivore consumption rate can be represented by a function of P.

Let $c(P)$ be the herbivore per-capita consumption rate. The function $c(P)$ is called the *functional response*. The total herbivore consumption rate is found by multiplying $c(P)$ by H. The plant-herbivore model is obtained by replacing the seed loss in the plant-granivore model with the total herbivore consumption rate:

$$\frac{dP}{dt} = rP(1 - P/K) - c(P)H\,, \tag{3}$$

$$\frac{dH}{dt} = n(P)H\,, \tag{4}$$

where $n(P) = (\gamma c(P) - m)$. The function $n(P)$ is called the *numerical response*, which is the herbivore per-capita growth rate.

The remaining exercises in this activity require use of a technology for plotting phase portraits. The phase portraits in this scenario were created using pplane, a free MATLAB application written and developed by John C. Polking [4]. The most recent version of pplane (pplane8) can be found on the MathWorks File Exchange. (See [2].) After downloading pplane8.m, place it in a special folder, open the .m file, and then press run. A setup screen will appear for entering the system of differential equations and the parameters. In addition to generating the vector field, pplane8 can be used to sketch trajectories and nullclines as well as to find and classify equilibrium points as saddles, spiral sinks, etc. (See [3] for additional directions on downloading and using pplane8.)

4. Suppose that (3) and (4), with $c(P) = \frac{aP}{b+P}$, is used to model a population of snowshoe hares in a boreal forrest where $K = 18$, $r = 1$, $a = 1$, $\gamma = 0.4$, $b = 10$, and $m = 0.1$.

   (a) Sketch the graph of $c(P)$. What is the maximum consumption rate (also called the saturation constant)? What is the biological meaning of b?

   (b) Sketch the graph of $n(P)$. Explain why $n(P)$ is negative for small values of P. What is the biological meaning of this negativity?

   (c) Note that $(0, 0)$ and $(18, 0)$ are equilibrium points. Use technology to find the third equilibrium point.

   (d) Use technology to sketch the phase portrait. Observe that solution curves approach a periodic orbit. Is the direction of this orbit clockwise or counterclockwise? Based on the phase portrait, what does this model predict about the plant and herbivore densities in the long-run?

Note: The functional response in Exercise 4 is said to be *saturating* because it satisfies the assumption that the foraging ability of the herbivore increases as more plant biomass becomes available, but it levels off as the herbivore reaches satiation.

2 More Grass, Fewer Grazers

The herbivores in [5] consisted of geese, hares, and rabbits, which grazed on a standing crop of vegetation in an island salt marsh. From field observations (using herbivore droppings to measure herbivore density), the ecologists found that the maximum foraging pressure was not at a maximum level of the crop, but at an intermediate level of the crop. They hypothesized that as the vegetation became taller and/or more dense, it became more difficult for smaller herbivores to digest and/or to reach. In this section you will analyze two models from this study. The parameters for the study are $r = 1$, $a = 1$, $\gamma = 0.4$, $b = 10$, and $m = 0.1$.

The following system of differential equations was used by van der Koppel *et al.* to model reduced digestion efficiency:

$$\frac{dP}{dt} = rP(1 - P/K) - \frac{aP}{b+P}H\,, \tag{5}$$

$$\frac{dH}{dt} = \left(\gamma\frac{aP}{b+P}e^{-.065P} - m\right)H. \tag{6}$$

Note that this is the standard plant-herbivore model given by (3) and (4), with $c(P) = \frac{aP}{b+P}$ and $n(P) = (\gamma\frac{aP}{b+P}e^{-.065P} - m)$.

5. Sketch the graph of $n(P)$. Observe that $n(P)$ is negative for small and large values of P. Explain what this means biologically. How does this differ from the numerical response in Exercise 4? (The parameter values are the same as those in Exercise 4, only the numerical response is different.)

As in Exercise 4, we can use technology to generate phase portraits for various values of K. Figure 1 shows the phase portrait (including nullclines) for $K = 18$. Observe that the P and H nullclines intersect at four points (the equilibrium points). Here $(0,0)$ is a source, $(18,0)$ is a sink, $(5.6, 10.7)$ is a spiral sink, and $(12, 7.3)$ is a saddle. From Figure 1 we observe that solution curves with initial conditions on one side of the saddle's stable separatrix approach the spiral sink, while those on the other side approach $(18,0)$.

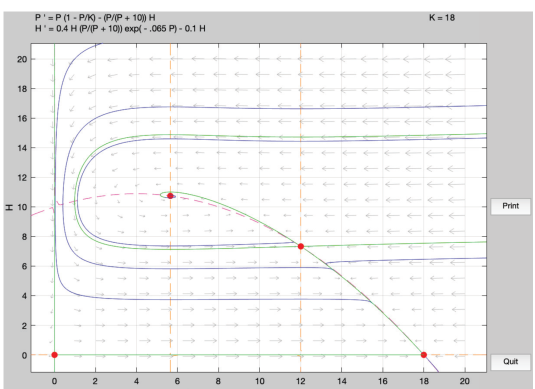

Figure 1. Phase portrait for K=18.

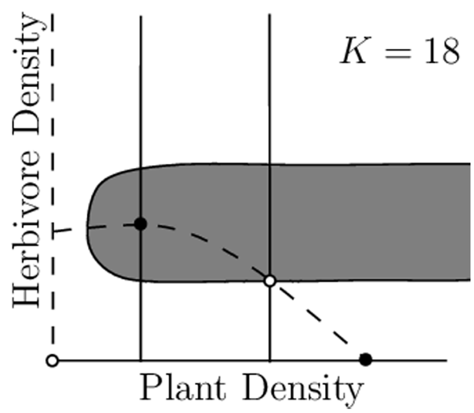

Figure 2. Phase representation for K=18.

The sketch shown in Figure 2 (called a phase representation) provides a summary of all the possible long-term outcomes. This sketch includes the nullclines (the P nullclines are dashed and the H nullclines are solid) and the equilibrium points. Equilibrium points are indicated by filled circles for sinks or open circles for sources or saddles. If the initial plant and herbivore populations, $(P(0), H(0))$, is in the interior of the shaded region then $(P(t), H(t))$ approaches the sink $(5.6, 10.7)$ as $t \to \infty$. If $(P(0), H(0))$ is not in the shaded region then the solution curve $(P(t), H(t))$ will approach $(18, 0)$, which means that the vegetation becomes too dense for the herbivores to graze.

Ecologists call the shaded region the *domain of attraction* of the plant-herbivore equilibrium and the unshaded region the domain of attraction of the plant equilibrium.

6. Use technology to sketch phase representations for (5) and (6) (as in Figure 2) for $K = 5, 10, 14, 22$ and 24. (In some cases you will find that solutions in the shaded region approach a periodic orbit in the region.) At what value of K are the herbivores no longer able to keep the vegetation in check? That is, at this level of K, the vegetation will become so dense that it is no longer suitable for grazing, regardless of the initial number of herbivores.

The second model in [5] was also designed to incorporate the assumption of reduced consumption efficiency:

$$\frac{dP}{dt} = rP(1 - P/K) - \frac{aP}{b+P}e^{-0.065P}H\,, \tag{7}$$

$$\frac{dH}{dt} = \left(\gamma\frac{aP}{b+P}e^{-.065P} - m\right)H. \tag{8}$$

7. Sketch the functional response for this model and estimate the value of P for which $c(P)$ is maximum. Is this functional response saturating? Explain what this means biologically in terms of herbivore consumption efficiency.
8. Use technology to sketch phase representations as in Figure 2 for $K = 5, 10, 18$, and 22. How do the results compare with those in Exercise 6 (the reduced digestion efficiency model)?

REFERENCES

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