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STUDENT VERSION

How many sheep may safely graze?

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STATEMENT

One of the most well-known mathematical models in ecology is the Lotka-Volterra predator-prey system of differential equations. Though the model was originally intended for two animal populations, ecologists discovered that the model could also be used to describe plant ('prey') and herbivore ('predator') interactions. Imanuel Noy-Meir was one of the first ecologists to apply the predator-prey model to a type of plant-herbivore system called a grazing system [1]. In a grazing system (sheep in a pasture, for instance) the number of herbivores is controlled by humans. Of these systems Noy-Meir wrote, "...grazing systems are one of the type of ecosystems which are of greatest importance to man; if theoretical ecology could contribute to their understanding and to the solution of their practical management problems, this would be a very useful contribution indeed" [1]. In this scenario you'll use graphical analysis to analyze a mathematical model for a grazing system.

SUBMISSION VERSION

1 Grazing Model Design

In order to apply the predator-prey model to herbivore ('predator') and plant ('prey') interactions, ecologists needed to find a useful way to represent the 'plant population' using a single variable. This is often done by letting P represent the plant biomass (in kg/m^2). The quantity P can be thought of as the amount of vegetation that is available, both for consumption by the herbivore and for producing plant growth.

Suppose that a farmer places H_0 sheep to graze in a pasture with biomass P. What is the long-term impact that this level of grazing will have on the vitality of the pasture grass? The standard grazing model is based on the following assumptions about the rate of growth of the pasture grass and the consumption rate of the sheep:

- In the absence of sheep P exhibits logistic growth with intrinsic growth rate r and carrying capacity K. That is, P has growth rate $G = rP(1 - P/K)$.
- The per sheep consumption rate of grass, denoted $c(P)$, depends only on the quantity of available vegetation. The function $c(P)$ is called the *functional response*. Thus the total consumption rate of vegetation by the sheep population is $C = H_0 c(P)$.

The net change in plant biomass P is the growth G minus consumption C, that is,

$$\frac{dP}{dt} = G - C = G(P) - C(P),$$

or

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - H_0 c(P). \tag{1}$$

Ecologists have found a number of useful formulas for $c(P)$ to model the consumption rates of different herbivores. Functional responses that satisfy the following assumptions are called *saturation* functional responses: The herbivore's consumption rate is limited by foraging availability. The consumption rate increases as more edible plant biomass becomes available. But there is an upper limit (based on digestion) on the rate at which an herbivore can feed.

1. The following two saturation functional responses (where $a, b > 0$) are often used in plant-herbivore models:

$$c_1(P) = \left(\frac{aP}{b + P}\right) \tag{2}$$

$$c_2(P) = \left(\frac{aP^2}{b^2 + P^2}\right) \tag{3}$$

Sketch the graphs of c_1 and c_2 for $a = 1$ and $b = 10$ on one set of axes and include any horizontal asymptotes. Use your sketch to answer the following:

(a) Briefly explain why c_1 and c_2 are saturation functional responses.

(b) In each case, what is the "saturation constant", that is, what is the value of the maximum rate at which vegetation can be consumed? In your own words, explain what b signifies.

(c) For which functional response is the sheep more efficient at finding food at low vegetation densities? For which is the sheep more efficient at reaching satiation?

2 Analyzing a Model

Suppose that for a pasture with biomass P and H_0 grazing sheep, the following parameters were known: $r = 0.1$, $K = 100$, $a = 1$ and $b = 10$. And suppose that, in the long-run, the per sheep consumption rate must be at least 75% of the saturation constant. (Below this level the sheep risk malnourishment.) In the following exercises, you will use graphical analysis to analyze the grazing model in (1) with the functional responses in (2) and (3). Your task is to determine the maximum number of sheep that the pasture can support.

2. Suppose the farmer allows one sheep to graze in this pasture, that is, assume $H_0 = 1$. Sketch the growth rate $G(P)$ and the consumption rate $C_1(P) = H_0 c_1(P)$ as functions of P on the same set of axes. Use technology to determine the value(s) of P where the two curves intersect. Note that $\frac{dP}{dt}$ is zero at these values of P, that is, these values of P are the equilibrium solutions to (1). Sketch the corresponding phase line and briefly explain what the model predicts about the vegetation in the long-run and at what percent of the saturation constant the sheep will be grazing.
3. Repeat Exercise 2 for the values of $H_0 = 2, 3$ and 4.
4. Sketch a bifurcation diagram in the $H_0 - P$ plane that includes the phase lines for $H_0 = 0, 1, 2, 3$ and 4.
5. What does the model predict is the maximum number of sheep that can be placed in the pasture without the biomass of the pasture grass going to zero? What initial amount of plant biomass is necessary to maintain this level of grazing?
6. What number of sheep results in overexploitation of the vegetation, regardless of the initial plant biomass?
7. Repeat Exercises 2–6 with the function $c_2(P)$ as the functional response. What are the differences in the long-term predictions between the two models?

REFERENCES

[1] Noy-Meir, I. 1975. Stability of Grazing Systems: An Application of Predator-Prey Graphs. *Journal of Ecology*. 63: 459-579.

[2] Feng Z., DeAngelis. D. 2018. *Mathematical Models of Plant-Herbivore Interactions.* Boca Raton FL USA: CRC Press.