Homework 2

ESM 211

Due 1/31/2020

For this assignment you will analyze a model for controlling an invasive species through hunting. An example might be wild pigs on Santa Cruz Island.

The general model is

$$\frac{dN}{dt} = (\text{intrinsic population growth rate}) - (\text{harvest rate}). \tag{1}$$

We will assume that, in that absence of control, the species grows logistically, and that the harvest rate is proportional to the number of hunters active at the same time, which we will call P:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - Pf(N). \tag{2}$$

The last term, $f(N)$, is the per-hunter harvest rate. If this were a predator–prey model, so that P was the number of predators, $f(N)$ would be called the "functional response." The main difference between this model and the predator–prey models with which you are familiar, such as the Lotka-Volterra or Rosenzweig-MacArthur models, is that the number of "predators" (hunters) does not depend on the abundance of the prey, but rather is set by the manager. For example, the number of recreational hunters can be limited by the number of permits issued; and if the number of recreational hunters is too low, they can be supplemented by hiring professional hunters.

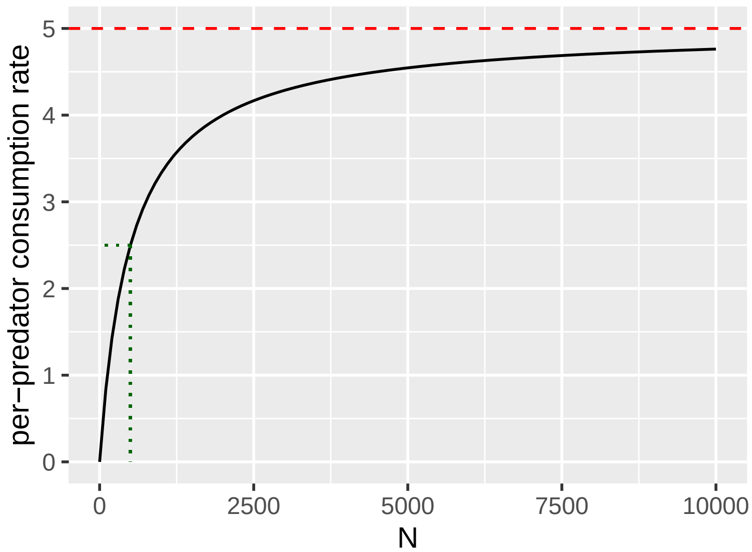
In the predator–prey models you studied in ESM 201, the functional response was linear: $f(N) = aN$, where a is the per-prey attack rate. Note that this means that, as the prey population gets large, each predator individual consumes more and more without limit. This is unrealistic, for two reasons: after killing the prey, the predator will require time to actually eat it (unless prey are so small they can be swallowed whole); and the predator's digestive tract may fill up, requiring time to pass before the next prey can be consumed. These both contribute to something called "handling time," which is the time that must pass between the successful capture of a prey and the when the predator is ready to start hunting again. For human hunters, the handling time could be related to the time required to carry the pig out of the control site, either for later consumption or because leaving carcasses in place would attract undesireable scavengers.

The ecologist C.S. Holling proposed the following functional response to account for this:

$$f(N) = \frac{aN}{1 + ahN}, \tag{3}$$

where h is the handling time. This form is supported by both behavioral experiments and observational studies. The function saturates to the value $1/h$ when N gets large: basically that means that the predator is spending all its time handling its prey; the prey are so abundant that as soon as the predator is done with one item, it turns around and captures the next. The shape of this function is shown in the following figure, with $a = 0.01$ and $h = 0.2$ (this might make sense if time were measured in days). The red dashed line shows the asymptote at $f(N) = 1/h$. The green dotted lines show how to find the so-called "half saturation constant," given by $N = 1/(ah)$, which is the prey abundance at which the consumption rate is one half its maximum value (you will sometimes see this functional response parameterized with a half-saturation constant rather than a handling time).

In his original paper, Holling called this the "type II" functional response (he also defined two others, called "type I" and "type III"); it is still referred to by that arbitrary name.



So, assuming that we want the hunters to remove the carcasses from the site, the full model becomes

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - P\frac{aN}{1 + ahN}. \tag{4}$$

It is time to start analyzing the model.

1. Make a graph of dN/dt vs. N, for particular values of the parameters. Use $r = 0.05$, $K = 2000$, $P = 4$, $a = 0.01$, and $h = 0.2$.

R TIP

To plot a function in gplot, use `stat_function`. For example, here is how you might plot the logistic growth equation with $r = 0.5$ and $K = 10$:

```
r <- 0.5
K <- 10
f <- function(N) r * N * (1 - N/K) # Here is where you define the function
ggplot(data.frame(N = 0:12), aes(x = N)) +
  stat_function(fun = f, color = "red") +
  geom_hline(yintercept = 0) +
  ylab("dN/dt")
```

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2. Based on this graph, how many equilibria are there? Which ones are stable?

3. Returning to the full model with arbitrary parameter values, is there an equilibrium at $N = 0$ for all plausible parameter values? For what values of hunter number (P), expressed in terms of the other parameters of the model, is the zero equilibrium locally stable? If your goal is to eliminate the insvasive species, what does this tell you about how many hunters you need?

4. Write down the equation you would need to solve in order to find the value of any non-zero equilibria. If you enjoy doing algebra, you may use the quadratic formula to find the values of N that satisfy this equation, but that is entirely optional (the result is a rather complicated expression!).

5. Because the algebra is tedious, and the result is so complex that it doesn't give a lot of insight, it's useful to do some more graphical analysis. In particular, we break the equation into its two component parts, the intrinsic population growth ($rN\left(1 - \frac{N}{K}\right)$) and the hunting ($P\frac{aN}{1+ahN}$).

a. Using the same parameters as before, graph both the intrinsic growth rate and hunting rate as functions of N on the same graph.
b. What do you expect will happen to the population when the hunting rate is greater than the intrinsic growth rate? When it is less? When they are equal?
c. How do the patterns you see on this graph relate to the ones in problem 1?

6. Now make two similar graphs, keeping all the parameters the same but setting $P = 1$ in one graph and $P = 6$ in the other. How many equilbria are there in each case, and which are stable?

7. The situation in problem 5 is an example of *bistability*, like in the strong Allee effect. It has important management implications.

   a. What is the domain of attraction of the zero equlibrium (approximately—you can estimate it from the graph) b, What is the domain of attraction of the largest equibrium?
   b. If you noticed the arrival of the species soon after it arrived, and initiated control activities when it had reached $N = 100$ individuals, would you be able to extirpate it with 4 hunters?
   c. What about if the population was already at carrying capacity when you initiated control activities?

8. It can be instructive to see how the equilibrium values depend on the number of hunters. Here you will make plots of this, using the same parameter values as above. You already know the formula for the zero equilibrium, N_0^*; the formulas for the other two are:

$$N_1^* = \frac{1}{2}\left[(K-d) - \sqrt{(K-d)^2 + \frac{4Kd}{r}(r-aP)}\right] \tag{5}$$

$$N_2^* = \frac{1}{2}\left[(K-d) + \sqrt{(K-d)^2 + \frac{4Kd}{r}(r-aP)}\right], \tag{6}$$

   where $d = 1/(ah)$ is the half-saturation constant.

   a. Plot each of the three equilbria as a function of P, for values of P ranging between 0 and 7.
   b. Draw a vertical dotted line where the zero equilbrium changes from locally stable to locally unstable. What else happens at this value of P?
   c. What else can you learn from this graph? What confuses or concerns you about this graph?

All questions worth one point, except 5 and 8, which are worth two.