I flubbed the model that I intended to finish in today's class, so let me take this opportunity to lay it all out more carefully while I fix that final portion!

Let's try both a concrete example and the general case. Suppose we start off with 1000 sheep on an island where the sheep happily double in population every three years, until they get really crowded; the island can support only 100,000 sheep and so when the population approaches that level, the per-sheep growth rate will drop off linearly with the population level. Let us further assume that a bunch of wolves are dropped onto the island and they consume 100 sheep per year. What will happen to the sheep population over time?

The Malthusian model for population growth, $dP/dt = a\,P$, leads to an exponential growth rate, $P = P_0 e^{at}$. The fact that the population naturally doubles in three years means that $P(3) = 2 \cdot P(0)$, which in turn forces $a = \ln(2)/3 \approx 0.23$. (I'm assuming t measures the time in years after that moment which I called "start".)

Next, our assumption on the per-sheep growth rate, $(dP/dt)/P$, is that $P(t)$ will follow a logistic growth curve which solves the differential equation $dP/dt = a\,P - b\,P^2$ for some b. We have already noted in class that the carrying capacity of the island would in these terms be a/b, so the given data make $b = a/100,000 = 2.3 \times 10^{-6}$. I have noted that the general solution to this differential equation may be written either as

$$P(t) = \frac{a}{b + Ke^{-at}} \qquad \text{for some constant } K$$

or

$$P(t) = \frac{a/b}{1 + e^{-a(t-t_0)}} \qquad \text{for some constant } t_0$$

but really that's a little imprecise. If you solve the separable differential equation carefully, you need to compute some anti-derivatives of the form $\int du/u$ and that integral is not $1/u$ but rather $1/|u|$ (plus any constant of course); if you allow for the possibility that certain expressions inside an absolute value sign are negative, then the second solution I presented above should have a $\pm$ sign before the exponential, that is, $P(t)$ may be either as shown or may equal

$$P(t) = \frac{a/b}{1 - e^{-a(t-t_0)}} \qquad \text{for some constant } t_0$$

The previous form applies whenever we start with a value of P smaller than the carrying capacity, and this other variant applies if we start with a population which exceeds carrying capacity.

I will leave it to you to check the algebra behind the following claims: if the population follows the equation

$$P(t) = \frac{a/b}{1 + e^{-a(t-t_0)}} \qquad \text{for some constant } t_0$$

then for all times t the population will be less than the carrying capacity a/b but will approach that carrying capacity as $t \to \infty$. Note that when $t = t_0$, the population will reach exactly half the carrying capacity of the land (and the graph of the population will have reached its sole inflection point). It can be convenient to reset the calendar so that this moment is called "year zero", and then t stands for the number of years before or after this moment. In that case the population "at time t" is simply $P(t) = \frac{a/b}{1+e^{-at}}$

The value of t_0 may be computed from the initial data; you can deduce for yourself that we need $t_0 = (1/a)\ln\left(\frac{a/b}{P(0)} - 1\right)$, which in our case is $t_0 = 19.89$; thus if we do "reset the calendar" then the population is exactly 1000 at time $t = -19.89$.

We discussed in class the possibility of scaling both P (as a new dimensionless variable x times carrying capacity) and t (as a new dimensionless variable τ times $1/a$); allowing ourselves also to reset the calendar as above, we can see that *every* population which follows the logistics growth pattern will have a population represented by the single formula

$$x(\tau) = \frac{1}{1+e^{-\tau}}$$

(The graph of this function is called the *logistics curve.*) Our specific population starts off with only 1% of its eventual number of sheep, i.e. with $x = 0.01$. And we start in a time before "year zero": it will be 19.89 years before the sheep population reaches 50,000, so we start at time $t = -19.89$ years, i.e. at $\tau = -4.595$.

Now let's incorporate predation by wolves. The differential equation regulating the population of sheep is now

$$dP/dt = a\,P - b\,P^2 - c = (-b)(P - P_1)(P - P_2), \quad \text{say,}$$

where a and b are as before but $c = 100$. There are two stable populations, found by setting the right side of this ODE to zero: $P_1 = 99565.302$ and $P_2 = 434.698$. These can be interpreted as follows: populations at these levels are just enough to supply 100 new sheep per year to be wolf-food; when $P = P_2$ the supply is low because there are few sheep, and when $P = P_1$ the supply is low because (due to over-crowding) there are only a few more sheep being born than there are sheep dying due to non-wolf-related causes. Between these two extremes, the sheep population should grow over time.

To find the non-constant solutions we solve

$$\left(\frac{1}{-b}\right)\int \frac{dP}{(P-P_1)(P-P_2)} = \int dt$$

We can recast the left integrand as

$$\frac{1}{P_1 - P_2}\left(\frac{1}{P-P_1} - \frac{1}{P-P_2}\right)$$

and then our differential equation has solutions

$$\ln\left(\left|\frac{P-P_2}{P-P_1}\right|\right) = b(P_1 - P_2)(t - t_1)$$

for arbitrary constants t_1. Then $P(t)$ can be expressed as being one of these (depending on the sign of $\frac{P-P_2}{P-P_1}$):

$$\frac{P_1 - P_2 e^{-b(P_1-P_2)(t-t_1)}}{1 - e^{-b(P_1-P_2)(t-t_1)}}$$

$$\frac{P_1 + P_2 e^{-b(P_1-P_2)(t-t_1)}}{1 + e^{-b(P_1-P_2)(t-t_1)}}$$

The latter formula applies if, as in our particular numerical example, we start with a population between P_2 and P_1. As in the previous model, we can change our calendar so that the moment $t = 0$ corresponds to the moment we pass through the inflection point; then in this calendar we may take $t_1 = 0$. We may scale time to the dimensionless quantity $\tau = a \cdot t$. The population will for all values of time lie between P_2 and P_1, so the best dimensionless variable is the percentage x of that interval that the population has achieved, that is, $P = P_2 + (P_1 - P_2)x$. (Note that $\tau = 0$ is now the moment at which $x = 0.5$, just as in the logistics model.) Finally the severity of the predation is already wrapped up into the parameter c, which affected the roots P_1 and P_2; thus it determines the dimensionless parameter $h = (P_1 - P_2)/(a/b)$, which shows the fraction by which the range of population levels has been reduced by predation. (It used to vary between 0 and the carrying capacity a/b of the land; now it varies only between P_2 and P_1.) In terms of these variables the differential equation is now

$$dx/d\tau = -h\, x(x - 1)$$

We can re-scale time by an additional factor of h and this equation will become identical to the logistic equation itself! Or we can keep the scalings as they are above and simply solve this differential equation to get

$$x(\tau) = \frac{1}{1 + e^{-h\tau}}$$

In other words, the effects of predation have been simply this: Compared to the situation without predation, the growth curve for the population of the sheep is following a curve which is of the same shape and has the same inflection point, but the range of values of the population is more constrained, and the actual population moves through that limited range more slowly than before.

Most of those conclusions sound plausible (it's harder for the sheep population to grow when the wolves are eating the sheep!) but I should say a few words about why the population can never be below P_1. In fact, P_1 is the limit of $P(t)$ as $t \to -\infty$, that is, we deduce that even far into the distant past, there were never fewer than P_1 sheep. That may seem counterintuitive (wolves cause more sheep?!) but in fact it's quite reasonable: the right way to say it is that if now there are more than P_1 sheep, then in the past there can never have been fewer than P_1 sheep, because if that had been the case, then the rate of predation would have exceeded the natural growth rate of the sheep population and the sheep could never have gotten to the point where they are today!

It is a separate situation to ask what happens if we DO start with fewer than P_1 sheep. In that case, the sheep will indeed die off, the populations will be negative, and we will discover that the model's assumptions cannot have been realistic. We discussed this in class: once P drops to zero, the differential equation can no longer apply. Algebraically, this solution can be spotted in the formulas for $P(t)$: if $P(t)$ is less than P_2 (or, for that matter, more than P_1) at any time t then $P(t)$ stays in that range for all times t, and we must use the alternative formula for $P(t)$ with the negative signs:

$$\frac{P_1 - P_2 e^{-b(P_1-P_2)(t-t_1)}}{1 - e^{-b(P_1-P_2)(t-t_1)}}$$

This solution simplifies under scaling, too: these correspond to the solutions to

$$x(\tau) = \frac{1}{1 - e^{-h\tau}}$$

that have $x < 0$ (or $x > 1$). Ordinarily solutions with $x < 0$ are of no interest in modeling populations, but recall that now a negative x does not mean a negative population but rather a population below P_1. We can continue to follow the graph until $x = -P_2/(P_1 - P_2)$, at which time the sheep population reaches zero and stays there (so obviously the wolves no longer eat 100 sheep per year any more!)