Math 410(510) Notes (1)
Modeling Population Growth
Part 1: single species

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The growth of a population depends on many factors, and often depends on the way that one population interacts with other populations. For example, a sophisticated model may include predator-prey interaction, parasitic interactions, mutualistic interactions, and more. In this module, however, we will focus on simpler models of a population.

Intuitively, the rate at which a population changes depends on at least three factors. Here we assume a specific mathematical form for these factors. For a real-life model, the way that a population depends on each factor would need to be determined by field observations and detailed knowledge of the population's social and reproductive characteristics. The factors we will consider in this module are:

Net Birth Rate for the Population

We assume that a population changes linearly in proportion to the current value of the population. The constant of proportionality represents the net birth rate for the population, and must account for a variety of factors such as

- The proportion of the population that will mate;

- The number of offspring for each mating pair;

- The proportion of the population that will die during the next period of time.

Overcrowding and Scarcity of Resources

We assume that a population is limited in size by resources such as the availability of food and land. We lump all of these factors into a single overcrowding term that will serve to decrease the population when it grows too large to be supported by the available resources.

Harvesting

The removal of a constant number of individuals from a population during each time period is known as harvesting (or sometimes fishing). As its name implies, this harvesting is often accomplished by humans. Advocates of harvesting point to stable populations of deer, fish, and other game animals, as evidence that harvesting can be used to reduce the number of animals who needlessly die from starvation or other natural causes. On the other hand, unregulated harvesting can lead a population to the brink of extinction, as is evidenced by well-known examples such as the North American Bison (Bison bison) and several populations of whales.

We will build up our understanding and intuition about each of these factors by considering them in turn. We will first consider population models that change according to the net birth rate of the current population, and will find that this leads to exponential growth or decay of the population. We then introduce an overcrowding term, and discover that the population may stabilize at a certain number of animals. We then study the effect of harvesting on populations. Along the way, we will learn new geometric techniques to help us qualitatively analyze solutions of differential equations.

Unbounded Populations

The very first differential equation that one typically encounters is the equation that models the change of a population as being proportional to the number of individuals in the population. In symbols, if $P(t)$

represents the number of individuals in a population at time t, then the so-called exponential growth model is

$$\frac{dP}{dt} = kP \qquad (1)$$

Recall that the general solution of this differential equation is of the form $C exp(kt)$ where C is the population at the time that we first consider it, and where "exp" is just another way to write "ee-to-the" Recall also that in order to get a particular solution, we must have some sort of experimental observations that tell us (1) the initial population, and (2) the net birth rate.

The sign of k determines whether the population will grow without limit, or whether it will become extinct. This exponential growth model was first proposed by Malthus in 1798.

Limits on Growth

No population grows without bounds, so we need to modify our population model to predict the fact that many populations have a so-called limiting population that is determined by the carrying capacity of their environment.

The easiest way to model a limiting population is to introduce a new term into our population model. This term is called an overcrowding term and the coefficient of this term is called the coefficient of overcrowding. The simplest overcrowding term is proportional to the square of the current population. In other words:

$$\frac{dP}{dt} = kP - AP^2 = P(k - AP). \text{ or } \frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right). \qquad (2)$$

Assuming that $A > 0$, the negative sign in the second term indicates that this term decreases the population. In the second form, N is called the carrying capacity. This population model is called the logistic model.

Logistic equation was first introduced by Verhulst in 1838. The algebraic form of the model is not to be taken literally. The model should be regarded as a metaphor for populations that have a tendency to grow from zero up to some carrying capacity N. Originally a much stricter interpretation was proposed, and the model was argued to be a universal law of growth (Pearl 1927). The logistic equation was tested in laboratory experiments in which colonies of bacteria, yeast or other simple organisms were grown in conditions of constant climate, food supply, and the absence of predators. These experiments often yielded sigmoid (S-shaped) growth curves, in some senses with an impressive match to the logistic equation.

On the other hand, the agreement was much worse for fruit flies, flour beetles, and other organisms that have complex life cycles, involving eggs, larvae, pupae, and adults. In these organisms, the predicted asymptotic approach to a steady carrying capacity was never observed—instead the populations exhibited large, persistent fluctuations after an initial period of logistic growth. See (Krebs 1972) for the discussions on that direction.

Harvesting

The removal of a constant number of populations during each time period is known as harvesting or fishing. Ever since primitive humans began hunting and fishing thousands of years ago, there has been a need to know how killing a certain number of animals will affect the population at large. The fact that there are over 750 plants and animals on the endangered species list indicates that humans are not always cognizant of how their actions will affect plants and animals.

The inclusion of harvesting into our mathematical model is easy: during each time period we assume that a constant number, h, of individuals are removed from the population, therefore the differential equation that models the population becomes

$$\frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right) - h. \qquad (3)$$

This is an extremely simple model for a fishery. In the absence of fishing, the population is assumed to grow logistically. The effect of fishing are modelled by the term $-h$, which says that fish are caught or harvested at a constant rate $h > 0$, independent of their population P. (This assumes that the fishermen aren't worried about fishing the population dry—they simply catch the same number of fish every day.) There's something silly about this model—the population can become negative! A better model would have an equilibrium at zero for all values of h.

A refinement of the model is

$$\text{(4)} \qquad \frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right) - h\frac{P}{A + P},$$

where $h > 0$ and $A > 0$. This model is more realistic in two aspects: it has an equilibrium at $P = 0$ for all parameters, and the rate at which fish are caught decreases with P. This is plausible—when fewer fish are available, it is harder to find them and so the daily catch drops. On the other hand, when there are sufficiently many fish, (when P is large), then $\lim_{P \to \infty} \frac{hP}{A + P} = h$, the fishing level is close to h. This model was first proposed by (Holling 1959).

Our next example of the harvesting model is for the sudden outbreak of an insect called the spruce budworm. This insect is a serious pest in eastern Canada and northern Minnesota, where it attacks the leaves of the balsam fir tree. When an outbreak occurs, the budworms can defoliate and kill most of the fir trees in the forest in about four years. (Ludwig, Jones and Holling 1978) proposed and analyzed an elegant model of the interaction between budworms and the forest. They simplified the problem by exploiting a separation of time scales: the budworm population evolves on a fast time scale (they can increase their density fivefold in a year, so their have a characteristic time scale of months), whereas the trees grow and die on a slow time scale (they can completely replace their foliage in about 7-10 years, and their life span in the absence of budworms is 100-150 years.) Thus, as far as the budworm dynamics are concerned, the forest variables may be treated as constants. The proposed model for the budworm population is

$$\text{(5)} \qquad \frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right) - h\frac{P^2}{A^2 + P^2},$$

where $h > 0$ and $A > 0$. Again, in the absence of the predators, the budworm population is assumed to grow logistically. The term $h\frac{P^2}{A^2 + P^2}$ represents the death rate of budworm due to predation, chiefly by birds. The function $h\frac{P^2}{A^2 + P^2}$ can be interpretated this way: there is almost no predation when budworms are scarce; the birds seek food elsewhere. However, once the population exceeds a certain level $P = A$, the predation turns on sharply and then saturates (the birds are eating as fast as they can.)

Finally we remark that the harvesting is often periodic in time variable t. We can add a simple periodic harvesting term $hP(1 - \cos t)$ to the logistic equation, where $h > 0$ is a parameter measuring the harvesting rate. For fixed time t, we assume the harvesting is proportional to the size of the population. The periodic function $(1 - \cos t)$ is non-negative with period 2π; when $t = 2m\pi$, the harvesting is at lowest point (like winter), and when $t = (2m + 1)\pi$, the harvesting is at highest point (like summer). (m here is an integer.) Then we have

$$\text{(6)} \qquad \frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right) - hP(1 - \cos t).$$

Other single species population models

Most equations which we considered so far (except (3)), take a form

$$\text{(7)} \qquad \frac{dP}{dt} = P \cdot g(P),$$

where $g(P)$ is a continuous function. That means dP/dt has to equals to zero when $P = 0$. The function $g(P)$ is called the per capita growth rate, or the intrinsic growth rate. By writing the equation this way, we emphasize that the intrinsic growth rate may depend on the size of the population. When $g(P)$ is independent of P, as in (1), we have the exponential growth. But when the intrinsic growth rate is density dependent, we have various population growth models. We can examine the intrinsic growth rates of all models we have introduced so far.

The intrinsic growth rate is a horizontal straight line when $g(P) = k$, a constant; and it is a decreasing straight line when $g(P) = k(1 - P/N)$, the logistic model. There are a few models which take other forms of $g(P)$:

<u>Allee Effect</u>: This was introduced by (Allee 1938) for asocial population. The intrinsic growth rate is negative at small densities due either to a paucity of reproductive opportunity or other causes, and it is again negative at large densities due to over-crowding just same as logistic equation. For example, we can have

$$(8) \qquad \frac{dP}{dt} = kP\left(1 - \frac{P}{N}\right)\left(\frac{P}{M} - 1\right),$$

where $k > 0$ and $N > 0$ are the same as logistic equation, and $M > 0$ is called sparsity constant. Apparently $N > M$. Another example of Allee effect is that the intrinsic growth rate is only small (but positive) at small densities, and still negative at large densities. (see Edelstein-Keshet, page 215) An example is

$$(9) \qquad \frac{dP}{dt} = kP[1 - a(P - b)^2],$$

where $k, a, b > 0$.

<u>Gompertz Growth in Tumors</u>: This equation is mentioned in Edelstein-Keshet, page 217:

$$(10) \qquad \frac{dP}{dt} = -kP\ln(aP),$$

where $k, a > 0$.

References

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