

11. Optimal Harvesting

You are harvesting from a wild or domestic population. What population parameters determine the maximum sustainable harvesting rate, and how does that rate depend on these parameters?

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The biomass of a population can be characterized by two rate constants—a gross loss or outflow rate, D , and a gross inflow rate, F . D is the sum of the death rate, the excretory and metabolic rates, and the emigration rate. F is the sum of all the rates at which biomass is added to the population by ingestion and immigration. The net growth rate, G , is given by

$$G = F - D. \quad (1)$$

The rate of change of the population's biomass, X , is

$$\frac{dX}{dt} = G. \quad (2)$$

Consider a preharvested population with the steady-state biomass X , characterized by a specified value of F and D , with $F = D$. An optimal, sustainable strategy would appear to be attained if the population could be harvested at a rate equal to the natural loss rate, D , so that the harvesting simply replaced the natural loss. Such a scheme appears sustainable because the harvested biomass is no greater than what would have exited the population anyway at the same rate had no harvesting occurred. It appears to be the maximum sustainable rate because if the harvest rate were to exceed D it would exceed F as well, rendering the net rate negative and sending the population into a decline.

However, there are several gaps in this reasoning. First, harvesting individuals just before they die naturally or emigrate and harvesting biomass equivalent to metabolic and excretory losses are highly impractical endeavors. If the population is harvested at the rate, D , some natural losses will occur anyway and the population will decline. Second, the gross rates, F and D , will generally depend on the population biomass, X . If X is harvested temporarily below its original steady-state value, then feedback effects will occur that will change the values of F and D . One such feedback effect might be the alleviation of overcrowding, leading to a decrease in the natural death rate and an increase in X . On the other hand, individuals in the less dense population might have trouble finding mates, and the species might drift toward extinction. Such effects could make our putative

optimal rate less than or greater than optimal. With corrections leading in both directions, a model is needed to help sort out the situation.

Returning to the natural, unharvested population, let D be represented by two types of terms. One is a linear loss rate, αX , corresponding to a loss rate per unit of biomass, $\alpha X/X = \alpha$, independent of the size of the population. For some populations, such a population-independent per-unit-biomass rate is a very good approximation. For example, if the human population in your city or country is growing, the total death rate is also growing; but the population growth probably will not lead to an increase in the per capita death rate. This means that more people will die each year when the population is larger, but any individual's chances of dying in a given year remain unchanged. In a very crowded city, however, the per capita death rate might, in fact, increase as the city gets more crowded; diseases spread more effectively under crowded conditions, and murder and automobile accident rates might increase faster-than-linearly with population size.

In wild populations, the pressure of limited resources, including territory for breeding and food supply, can cause such a nonlinear effect, described by a second type of term in D . An individual's opportunity to obtain needed resources is diminished by large numbers of neighbors, and therefore the per capita death rate depends on population size.

This type of non-linear crowding effect is often represented mathematically by replacing $D = \alpha X$ with

$$D = \alpha X + \gamma X^2. \quad (3)$$

The αX term describes death and other losses by linear processes, and the γX^2 term corresponds to a loss rate per unit biomass of $\gamma X^2/X = \gamma X$. In the ecological literature the latter is called a density-dependent effect. The specific density-dependent behavior in Eq. 3 is called the Verhulst effect.

The gross growth rate, F , is most simply taken to be proportional to X , corresponding to a constant gross growth rate per unit of biomass:

$$F = \sigma X. \quad (4)$$

A modification that is sometimes made replaces this term with

$$F = \frac{\sigma X^2}{X_0 + X}, \quad (5)$$

where X_0 represents a critical level of biomass. When X is very large compared to X_0 , this expression behaves the way Eq. 4 does, for in that case

$$F \approx \frac{\sigma X^2}{X} = \sigma X. \quad (6)$$

But when X is small compared to X_0 , the F in Eq. 4 goes to zero faster than the F in Eq. 5. A type of density-dependent behavior called the Allee effect is described in Eq. 5, which represents mathematically the feedback mechanism that can cause a depressed population to drift toward extinction because of reproductive difficulties. We will use the simpler expression in Eq. 4 here, but see Exercise 3.

A useful model of the unharvested population, from which we can then explore how harvesting strategies relate to population parameters, combines Eqs. 2, 3, and 4:

$$\begin{aligned} \frac{dX}{dt} &= \sigma X - \alpha X - \gamma X^2 \\ &= rX - \gamma X^2, \end{aligned} \quad (7)$$

where $r = \sigma - \alpha$. This is customarily written in the form

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K} \right), \quad (8)$$

where $K = r/\gamma$. Eq. 8 is sometimes referred to as the logistic equation.

K is called the carrying capacity; it is the maximum value of X that can occur without causing a population decline. It is a stable point in the sense that if X starts out below K , then dX/dt will be positive and the population will increase to K ; if X exceeds K , then $dX/dt < 0$ and the population will decline to the value of K . Note, for later reference, that the growth rate, dX/dt , is maximum where $X = K/2$ (see Figure III-10).

Now suppose that harvesting begins. The harvesting process must fall into one of two broad categories. Either the harvest rate is fixed at a constant value independent of the population size, or it can vary. If it can vary, it is most likely set proportional to the population size. In the first category, a fixed yield is established. Where each of a fixed number of hunters is allowed a quota of kills each year, for example, the total harvest rate is independent of the population size. To achieve their quotas in years when the prey population is depressed, the hunters may have to hunt many extra hours.

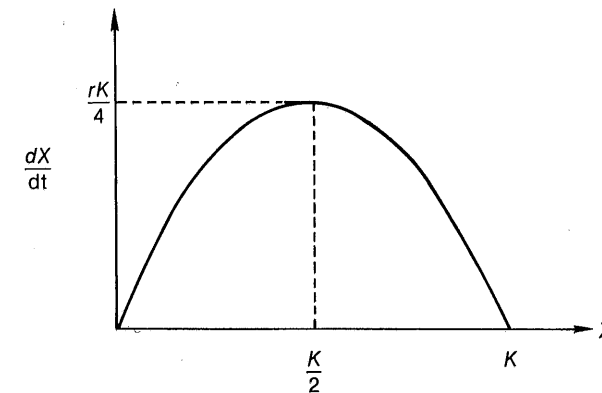


Figure III-10 The relation between the net growth rate of the population, dX/dt , and the size of the population, X , in a logistic-equation model of population growth. K is the carrying capacity and r is the linear growth rate constant.

The second category involves harvesting at a fixed effort. For example, if a fixed number of fishermen with specified equipment ply the ocean waters for a certain number of hours per year, then the catch is likely to depend on the population size. A reasonable first approximation assumes the harvest rate is linearly proportional to the population, with the proportionality constant equal to a measure of the harvesting effort. With these harvesting strategies in place, the population equation becomes

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K} \right) - h \quad (9)$$

in the first case, and

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K} \right) - EX \quad (10)$$

in the second. In Eq. 9, h is the fixed harvest rate, while in Eq. 10 E is the fixed effort expended in harvesting.

Consider Eq. 10. What level of effort, E , corresponds to the maximum sustainable yield? We will assume that the effort is constant rather than time-varying. In that case, the population eventually reaches a steady state, $X = \bar{X}$, and thus the harvest is indeed sustainable. The value of \bar{X} is given by setting $dX/dt = 0$, or

$$E\bar{X} = r\bar{X} \left(1 - \frac{\bar{X}}{K} \right). \quad (11)$$

Solving for \bar{X} ,

$$\bar{X} = \left(1 - \frac{E}{r}\right)K. \quad (12)$$

Hence the sustainable harvest rate is

$$E\bar{X} = E\left(1 - \frac{E}{r}\right)K. \quad (13)$$

The maximum sustainable yield will be obtained when $E\bar{X}$ is maximized. This occurs at a value $E = E_m$, given by

$$\frac{d}{dE} \left[E\left(1 - \frac{E}{r}\right)K \right] = 0 \quad (14)$$

or

$$E_m = \frac{r}{2}. \quad (15)$$

Substituting Eq. 15 into Eqs. 12 and 13, we find the population under optimum harvesting, \bar{X}_m , to be

$$\bar{X}_m = \frac{K}{2}, \quad (16)$$

and the optimal harvesting rate is

$$E_m\bar{X}_m = \frac{rK}{4}. \quad (17)$$

Eqs. 16 and 17 can be interpreted as follows. In the absence of harvesting ($E = 0$), the net growth rate, dX/dt , is maximum when $X = K/2$ (see Figure III-10). At this value of X , $dX/dt = rK/4$. Thus, the optimal harvesting rate equals the maximum net growth rate of the unharvested population, and the size of the sustainable population under optimal harvesting equals the size of the population that yields that maximum net growth rate in the unharvested population. This is all quite reasonable. Less obvious is the fact that the optimal level of effort, E_m , which is the quantity of concern to the harvester, is equal to $r/2$ or half the linear growth rate of the unharvested population.

Let's now shift our perspective and explore some economic considerations. Suppose the harvested population is viewed as a commodity that fetches a certain price, p , per unit of yield. The gross rate of income, I , is then,

$$I = pEX, \quad (18)$$

where EX is, again, the harvest rate. Suppose, also, that the rate of expense, C , to the harvester is proportional to the effort, E , expended in harvesting. Thus

$$C = cE. \quad (19)$$

Then the total rate of net income or profit, Y , is

$$\begin{aligned} Y &= I - C \\ &= pEX - cE. \end{aligned} \quad (20)$$

Let us maximize the rate of net income, keeping the sustainability criterion that $dX/dt = 0$.

Since $dX/dt = 0$, we must still enforce Eq. 11. Therefore, $X = \bar{X} = (1 - E/r)K$, and

$$Y = E[p(1 - E/r)K - c]. \quad (21)$$

Maximizing Y with respect to E yields

$$\frac{dY}{dE} = pK - 2E\frac{pK}{r} - c = 0 \quad (22)$$

or

$$\begin{aligned} E_m &= \frac{rpK - cr}{2pK} \\ &= \frac{r}{2} - \frac{cr}{2pK}. \end{aligned} \quad (23)$$

The value of X at the level of maximum sustainable net income is now obtained by substituting Eq. 23 into Eq. 12:

$$\begin{aligned} \bar{X} &= K \left[1 - \frac{1}{r} \left(\frac{r}{2} - \frac{cr}{2pK} \right) \right] \\ &= \frac{K}{2} + \frac{c}{2p}. \end{aligned} \quad (24)$$

So we see that profit maximization results in a higher steady-state population (Eq. 24) than does yield maximization (Eq. 16). Comparing Eq. 23 with Eq. 15, we see that profit maximization results in a lower effort rate. How does the actual yield, $E_m\bar{X}_m$, compare in the two cases? Profit maximization gives

$$E_m \bar{X}_m = \left(\frac{r}{2} - \frac{cr}{2pK} \right) \left(\frac{K}{2} + \frac{c}{2p} \right) = \frac{rK}{4} - \frac{c^2 r}{4p^2 K}, \quad (25)$$

which is less than the value $rK/4$ obtained for the yield-maximization case.

The effect on the steady-state population of bringing in economic considerations in this manner is to optimize at a higher value of X . This is a good thing if one's interest is in species preservation. Larger wild populations can sustain higher genetic diversity than smaller ones. Because of this and because smaller populations are more vulnerable to inevitable fluctuations in their numbers, larger populations are usually less vulnerable to extinction if a sudden change in their habitat occurs, or if harvesting pressure increases rapidly.

The consequences for a population's survival of the complex interplay of genetic diversity, changes in predation pressure, habitat alteration, and fluctuations in numbers are difficult to incorporate realistically in models. When working with simple models, like our Eq. 10, we should not lose sight of these complex effects. The optimal-profit and optimal-yield strategies both involve steady-state populations that theoretically should persist forever, in the narrow context of the model. Nonetheless, qualitative considerations inform us that the population is safer under an optimal-profit strategy.

A more complete analysis of economic factors influencing harvesting rate and optimal population size leads to a bleaker picture, however. Our analysis did not include a discount rate, which is a measure of the rate at which money can grow in real value (after inflation) if invested. People would rather get a dollar this year than next, and therefore from this narrow perspective an individual harvested from a population is worth more this year than next. With the discount factor incorporated into the analysis, it can turn out, in some cases,⁴² that $\bar{X}_m < K/2$. This can bode ill for the population being harvested.⁴³

EXERCISE 1: Show that in the optimal-yield case for the model described by Eq. 10, the natural loss rate, $\alpha X + \gamma X^2$, exceeds the optimal harvest rate.

EXERCISE 2: Repeat the analysis presented here that was based on Eq. 10, but assume a constant harvest rate, h , as in Eq. 9.

* **EXERCISE 3:** Repeat the analysis using a harvest rate, EX , as in Eq. 10, but with the Allee effect included in the population model.

42. This is discussed in an article by Clark (1977). The concepts and notation used here borrow heavily from Clark's treatment. Our treatment, here, of optimal harvesting is limited to the harvesting of a single species. For a discussion of harvesting strategies appropriate to multispecies fisheries, see May et al. (1979).

43. A lucid, highly knowledgeable treatment of the causes and consequences of species extinction can be found in Ehrlich and Ehrlich (1981).

12. Biomagnification of Trace Substances

How does biomagnification of a trace substance occur? Specifically, identify the critical ecological and chemical parameters determining bioconcentrations in a food chain. In terms of these parameters, derive a formula for the concentration of a trace substance in each link of a food chain.

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Imagine a young fish growing up in a lake and eating nothing but plankton. As the fish grows from, say, 10 g at birth to its average weight at death of 10^3 g, all of its newly acquired flesh and bone will be derived from the plankton it eats. To add on 990 g of tissue, it will have to eat far more than 990 g of plankton, because of excretory and metabolic losses. Excretory losses, in the sense used here, include the sloughing off of old tissue as it is replaced with new. The typical growing fish eats 10 g of plankton to grow by about 1 g of body weight. In the ecological literature this factor of 10% (the ratio of the weight it gains to the weight of the food it eats) is called an *incorporation efficiency*. The remaining 90% of the food the fish eats is excreted or metabolized.

Suppose, now, that the plankton contains a trace substance, such as DDT or mercury. If a greater proportion of the trace substance than of the plankton is retained in the fish rather than excreted and metabolized, then the concentration of the trace substance in the animal will build up to a level greater than that in the plankton. Similarly, if a population of osprey prey upon the fish, they too may preferentially retain the trace substance in their food; over the lifetime of the osprey, the concentration of the substance can build up to an even greater level than that in the fish. The fraction of ingested trace substance retained by an organism is called the retention factor.

From this qualitative discussion, the factors that determine the degree of concentration of a trace substance in an organism can be deduced:

(1) Preferential Retention of the Substance in the Body In the extreme case, the rate of bioconcentration is greatest when all the trace substance an animal ingests is stored in body tissue and none is metabolized⁴⁴ or excreted.

(2) Fraction of Ingested Food Incorporated into New Tissue If an animal is very inefficient in building new tissue out of its food source, it must consume a lot of food to grow by any specified amount. That

44. Some substances, such as alcohol, are metabolized so rapidly by many organisms that bioconcentration is not a problem.