Age-specific population growth: Sustainable harvesting

Consider a (female) population which grows according to the Leslie model. We examine the effects of harvesting from such a population. We confine ourselves to *sustainable harvesting*, a harvesting policy in which an animal population is periodically harvested so that the yield of each harvest is the same and the age distribution of the population after each harvest remains the same. Thus, the animal population is not decreased; only the excess population is removed.

We start with a (female) population having a particular age distribution. This population grows according to the Leslie model over a period also called the growth period. At the end of the growth period, a certain fraction of each age class is harvested. The harvest duration is so short that population growth during the harvest period can be neglected. Finally, the population left after harvesting has the same age-class distribution as the original population. This cycle repeats after each harvest, and thus, the yield is sustainable.

Let

$$\boldsymbol{x} = \begin{pmatrix} x_1 \\ x_2 \\ \cdots \\ x_n \end{pmatrix}$$

be the age distribution at the beginning of the growth period. Here, x_i is the number of females in the age class i left unharvested. As in the Leslie model, the duration of each age class equals the growth period. For example, if the population is harvested every six months, then the duration of each age class is also six months. If $\mathcal{L}$ is the Leslie matrix describing the growth of the population, then $\mathcal{L}\boldsymbol{x}$ is the population at the end of the growth period just before the harvest. Let h_i $(i = 1, 2, \cdots, n)$ be the fraction of the females of the age class i that are harvested. We define the harvesting matrix $\mathcal{H} = \text{diag}(h_1, h_2, \cdots, h_n)$. By definition, $0 \leq h_i \leq 1$ for $i = 1, 2, \cdots, n$. Thus, we may harvest none for $h_i = 0$, all for $h_i = 1$, or some proper fraction for $0 < h_i < 1$. The number of females of the age class i at the end of the growth period (i.e., just before harvesting) is $\big(\mathcal{L}\boldsymbol{x}\big)_i$, which is the i-th component of $\mathcal{L}\boldsymbol{x}$. The distribution of the females just before harvesting is thus

$$\mathcal{L}\boldsymbol{x} = \begin{pmatrix} \big(\mathcal{L}\boldsymbol{x}\big)_1 \\ \big(\mathcal{L}\boldsymbol{x}\big)_2 \\ \vdots \\ \big(\mathcal{L}\boldsymbol{x}\big)_n \end{pmatrix}$$

Now the number of females harvested from the age class i is $h_i\big(\mathcal{L}\boldsymbol{x}\big)_i$ and hence the distribution

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of the age classes in the harvested population is

$$\begin{pmatrix} h_1\big(\mathcal{L}\boldsymbol{x}\big)_1 \\ h_2\big(\mathcal{L}\boldsymbol{x}\big)_2 \\ \vdots \\ h_n\big(\mathcal{L}\boldsymbol{x}\big)_n \end{pmatrix} = H\mathcal{L}\boldsymbol{x}$$

From the definition of a sustainable harvesting policy, we have

age class distribution at the end of the growth period	–	harvest	=	age class distribution at the beginning of the growth period

Equivalently

$$\mathcal{L}\boldsymbol{x} - \mathcal{H}\mathcal{L}\boldsymbol{x} = \boldsymbol{x} \implies \big(\mathcal{I} - \mathcal{H}\big)\mathcal{L}\boldsymbol{x} = \boldsymbol{x}$$

This relation implies that $\boldsymbol{x}$ is an eigenvector of the matrix $\big(\mathcal{I} - \mathcal{H}\big)\mathcal{L}$ with eigenvalue unity. We show that this places certain restrictions on h_is and $\boldsymbol{x}$. We assume the usual form of Leslie matrix $\mathcal{L}$ and thus

$$\big(\mathcal{I} - \mathcal{H}\big)\mathcal{L} = \begin{pmatrix} (1-h_1)a_1 & (1-h_1)a_2 & (1-h_1)a_3 & \cdots & (1-h_1)a_{n-1} & (1-h_1)a_n \\ (1-h_2)b_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & (1-h_3)b_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdot & (1-h_n)b_{n-1} & 0 \end{pmatrix}$$

Hence, $\big(\mathcal{I} - \mathcal{H}\big)\mathcal{L}$ *has the same mathematical form as that of the Leslie matrix* $\mathcal{L}$ *provided* $0 \leq h_i < 1$ *for all* i. Our analysis from now onwards also assumes that $0 \leq h_i < 1$. We know that a Leslie matrix has a nonzero eigenvalue λ when $q(\lambda) = 1$. Using the same, we find that $\big(\mathcal{I} - \mathcal{H}\big)\mathcal{L}$ has an eigenvalue $\lambda_1 = 1$ when

$$(1-h_1)\Big[a_1+a_2b_1(1-h_2)+a_3b_1b_2(1-h_2)(1-h_3)+\cdots+a_nb_1b_2\cdots b_{n-1}(1-h_2)(1-h_3)\cdots(1-h_n)\Big] = 1$$

Thus, only those values of $h_1, h_2, \cdots, h_n$, that satisfy this equation and lie in the interval $[0, 1)$ can produce a sustainable yield. The eigenvalue $\lambda_1 = 1$ is simple, and it has an eigenvector $\boldsymbol{v}_1$ of the following form (derived earlier):

$$\boldsymbol{v}_1 = \begin{pmatrix} 1 \\ b_1(1-h_2) \\ b_1b_2(1-h_2)(1-h_3) \\ b_1b_2b_3(1-h_2)(1-h_3)(1-h_3) \\ \vdots \\ b_1b_2b_3\cdots b_{n-1}(1-h_2)(1-h_3)(1-h_3)\cdots(1-h_n) \end{pmatrix}$$

Any other solution of $\big(\mathcal{I} - \mathcal{H}\big)\mathcal{L}\boldsymbol{x} = \boldsymbol{x}$ is a multiple of $\boldsymbol{v}_1$. The vector $\boldsymbol{v}_1$ thus determines the proportion of females in each age class after a harvest under a sustainable harvesting policy.

However, the total number of females in the population after harvest is unknown since we don't know the multiplicative factor. This depends on the ecological or economic constraints. For example, a harvester may be limited by a maximum population due to economic constraints, which in turn determines the multiplicative constant.

Uniform harvesting: With a large population, it is difficult to differentiate or catch animals of a specific age. In this case, the animals are caught at random, and we assume the same fraction of each class is harvested. We therefore set $h_i = h$ for $i = 1, 2, \cdots, n$. Now, the relation $\big(\mathcal{I} - \mathcal{H}\big)\mathcal{L}\boldsymbol{x} = \boldsymbol{x}$ becomes

$$\mathcal{L}\boldsymbol{x} = \frac{1}{1-h}\boldsymbol{x}$$

Hence, $\frac{1}{1-h}$ is the unique positive eigenvalue of the Leslie matrix $\mathcal{L}$. Thus,

$$\lambda_1 = \frac{1}{1-h} \implies h = 1 - \frac{1}{\lambda_1}$$

Hence, we find the uniform harvesting in terms of the dominant eigenvalue λ_1. Note that $\lambda_1 > 1$ in order for the harvesting fraction to lie in $(0, 1)$. In addition, the larger $\lambda_1 > 1$ is, the larger the fraction of animals we can harvest without depleting the population. Also, $\lambda_1 > 1$ is necessary for the population to increase in the growth period. The eigenvector corresponding to λ_1 is given by

$$\boldsymbol{v}_1 = \begin{pmatrix} 1 \\ \frac{b_1}{\lambda_1} \\ \frac{b_1 b_2}{\lambda_1^2} \\ \frac{b_1 b_2 b_3}{\lambda_1^3} \\ \vdots \\ \frac{b_1 b_2 b_3 \cdots b_{n-1}}{\lambda_1^{n-1}} \end{pmatrix}$$

Harvesting only the youngest age class: In some cases, only the youngest class has economic value. In this case, we set $h_1 = h$ and $h_i = 0$ for $i = 2, 3, \cdots, n$. Now the relation

$$(1-h_1)\Big[a_1+a_2b_1(1-h_2)+a_3b_1b_2(1-h_2)(1-h_3)+\cdots+a_nb_1b_2\cdots b_{n-1}(1-h_2)(1-h_3)\cdots(1-h_n)\Big] = 1$$

becomes

$$(1-h)\Big[a_1 + a_2b_1 + a_3b_1b_2 + \cdots + a_nb_1b_2\cdots b_{n-1}\Big] = 1 \quad \text{or} \quad (1-h)R = 1,$$

where

$$R = a_1 + a_2b_1 + a_3b_1b_2 + \cdots + a_nb_1b_2\cdots b_{n-1}$$

is called the *net reproduction rate per female* of the population [A female in age class 1 produces a_1 offspring, only b_1 fraction survives and hence offspring per one female in age class 1 produces a_2b_1 offspring in age class 2 and so on]. Solving for h leads to

$$h = 1 - \frac{1}{R}$$

We note that sustainable harvesting is possible only when $R > 1$, since only then is the population increasing. The age distribution vector after each harvest is proportional to

$$\boldsymbol{v}_1 = \begin{pmatrix} 1 \\ b_1 \\ b_1 b_2 \\ \cdots \\ b_1 b_2 \cdots b_{n-1} \end{pmatrix}$$

Optimal harvesting: We saw that a sustainable harvesting policy can be implemented by uniformly harvesting or by harvesting only the youngest age class. There are many other possible sustainable harvesting policies, and each will generally yield different amounts. One of the main interests is to find a sustainable harvesting policy that maximises yield. Such a policy is called an optimal sustainable harvesting policy, and the resulting yield is called the optimal sustainable yield. The following has been proved by J.R. Beddington and D.B. Taylor using linear programming theory ["Optimum age specific harvesting of a population," Biometrics, 29 (1973), pp. 801-809]:

An optimal sustainable harvesting policy is one in which either one or two age classes are harvested. If two age classes are harvested, then the older age class is completely harvested. This in effect reduces the age of the population.