THE USE OF POPULATION GENERATION MATRIX IN DAIRY HERDS

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1. Introduction

In many animal breeding programmes the strength of the herd in terms of young ones and adult animals is kept at more or less a constant level. This is achieved by introducing a proper scheme of culling the inferior animals on the basis of economically important characters. However, the herd is also subject to several natural forces such as mortality, fertility, sex-ratio, abnormalities etc. Knowledge of the pattern of the growth of the herd under these factors is essential for deciding on a suitable selection scheme for effecting genetic improvement. If we fix a schedule of scheme of selection and assume that age-specific mortality and involuntary cullings for reasons of contagious disease, debility or injury, fertility rate, extent of abnormal calvings, sex-ratio etc. vary very little around given values, it is possible to work out the pattern of the growth of population at periodic intervals for a given composition of the initial population. Leslie (1945) advocated the use of population generation matrix in solving a similar problem in human populations. Leslie's model, however, assumed age groups of equal lengths and the unit of time the same as that of age. Lefkovitch (1965) extended Leslie's model to the case where the age groups are of unequal lengths. In the present paper explicit formulae for working out the elements of the generation matrices for any given schedule of vital characteristics with respect to dairy herds have been worked out. Further it has been shown how the herd strength can be maintained at a stable level. The method has been illustrated with the help of actual data on vital statistics from five different Indian dairy herds.

2. THE METHOD OF POPULATION GENERATION MATRIX

We assume that the female stock can be grouped in the following s distinct stage groups, where l, g and m are the lactation length, gestation period and calving interval in months respectively.

	Stage Group	*Duration in months*
1.	Youngstock between 0 to 12 months of age	12
2.	Youngstock between 12 to 24 months of age	12
3.	Youngstock between the ages 24 to $24+k$ months *i.e.* till the females conceive	k
4.	Heifer-cum-first calvers till the completion of their lactation	$g+l$
$p \geqslant 5$.	Females either dry $(p-4)$th time or in their $(p-3)$th lactation.	m

Let, there be $n_{i,t}$ individuals in stage group i (1, 2, ..., s) at time t so that the total number at time t is given by

$$\sum_i n_{i,t} = N_t$$

the numbers in the i-th stage group at time $t+1$ can be obtained deterministically by taking a linear function of those in all other stages at time t i.e.

$$n_{i,t+1} = \sum_{j=1}^{s} n_{jt}\, a_{ij} \qquad \ldots(1)$$

where a_{ij}'s ($j=1, 2, \ldots, s$) are the elements representing the biological dependence of the i-th stage at time $t+1$ upon the j-th stage at time t. Some of these constants would be zero but none can be negative since this would imply a negative number of individuals.

The series of equations obtained in this way for all the stages at time t and $t+1$ can be expressed in matrix notation as

$$\begin{bmatrix} n_{1,t+1} \\ n_{2,t+1} \\ \cdot \\ \cdot \\ \cdot \\ n_{s,t+1} \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} & \cdots & a_{1s} \\ a_{21} & a_{22} & \cdots & a_{2s} \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ a_{s1} & a_{s2} & \cdots & a_{ss} \end{bmatrix} \begin{bmatrix} n_{1t} \\ n_{2t} \\ \cdot \\ \cdot \\ \cdot \\ n_{st} \end{bmatrix}$$

or $\mathbf{n}_{t+1}=F\mathbf{n}_t$

where $\mathbf{n}_t$ and $\mathbf{n}_{t+1}$ are column vectors representing the composition of the population with N_t and N_{t+1} as the total numbers at time t and $t+1$ respectively. F is an $s\times s$ matrix of the coefficients a_{ij}'s. Using this relation repeatedly and assuming that the coefficients do not change with time, we get

$$\mathbf{n}_t=F^t\mathbf{n}_0$$

where $\mathbf{n}_0$ is the column vector representing the composition of the population at the start.

Thus the composition of the stock at a future time can be obtained by successive multiplication by the matrix F. The matrix F is the population generation matrix. The pattern of the growth of the herd depends on the properties of this matrix. The characteristic equation of the matrix F is given by

$$|\ \mathbf{F}-\omega\mathbf{I}\ |=0 \qquad \ldots(2)$$

Suppose the s roots of this equation are $\omega_1, \omega_2, \ldots, \omega_s$ with ω_1 as the largest root. The corresponding solutions of

$$F\,\mathbf{l}=\omega\ \mathbf{l}$$

are say $l_1, l_2, \ldots$ and l_s, the right hand eigenvectors. Given any initial age distribution $\mathbf{n}_0$, we can then write

$$n_t=F^t\mathbf{n}_0=C_1\omega_1{}^t\mathbf{l}_1, \text{ approximately for } t \text{ large}$$

Thus

$$n_{it}=C_1l_{1i}\omega_1{}^t, \qquad i=1, 2, \ldots, s$$

C_1 can be determined from the initial conditions. That is,

$$N_0=\sum_i n_{i0}=C_1(\sum_i l_{1i})$$

Hence $\sum\limits_i n_{it}=N_0\omega_1{}^t$ for age-stable population. The population has a stationary age distribution with individuals of stage groups 1, 2, 3, ... and s in the ratio of $l_{11} : l_{12} : l_{13} : \ldots : l_{1s}$. The population changes in total size at a rate ω_1. When ω_1 is greater than 1, the population is increasing ; when it is less than 1, the population is decreasing ; when $\omega_1=1$, the population is stable in size.

Often it is desirable to maintain the female stock at its existing level so that the herd strength fluctuates only between narrow limits from year to year. Any steady increase in the number from year to year would be a strain on the resources. Any steady decrease would ultimately leave only a very small herd of the females in the programme. Such a stability in size could be achieved either (*a*) by suitably modifying the voluntary rate of culling at various stages or (*b*) for a fixed rate of voluntary culling, by augmenting/culling the herd by a fixed number of females at periodic intervals.

(*a*) *Control of population size through modification of voluntary culling rates* :

The characteristic equation given by (2) can be expanded as

$$\sum_{i=0}^{s} \omega^{s-i} (-1)^i tr_i F = 0 \qquad \ldots(3)$$

where $tr_i\, F$ is the sum of principal minors of order i of $|F|$.
For a constant herd strength $\omega_1 = 1$, which gives

$$\sum_{i=1}^{s} (-1)^{i+1}\, tr_i\, F = 1 \qquad \ldots(4)$$

For fixed rates of mortality, fertility, involuntary culling etc. the left hand side of equation (4) will be a function of the voluntary rates of culling at various stages. The voluntary culling rates can then be chosen so as to satisfy the relation given by equation (4).

(*b*) *Control of population size through augmentation/culling by a fixed number of females* :

Let us assume that a population vector proportional to the actual population vector is added or subtracted according as $\omega_1 < 1$ or $\omega_1 > 1$ to the population every unit of time i.e.

$$\mathbf{n}_{t+1} = (F + \alpha I)\mathbf{n}_t$$

α is to be so chosen as to ensure stable in size distribution.

From the theory of matrices, it is known that the matrix $(F + \alpha I)$ has the same latent vector as F and has a dominant latent root $(\omega_1 + \alpha)$. Thus α has to be equal to $1 - \omega_1$ for ensuring constant herd strength.

3. Derivation of the Elements of Population Generation Matrix

3.1. *Assumptions*

In the development of the expressions for a_{ij}'s, we shall, for convenience, take time in units of '*m*' months *i.e.* one calving interval and make the following assumptions :

(*i*) The females in a particular stage group at time t are uniformly distributed over the group interval. For example, in group 5, n_{5t} females are evenly distributed over its calving interval, of m months. That is to say, there are n_{5t}/m females which calved $(l-1)$ months earlier, an equal number which calved $(l-2)$ months earlier, and so on. Further, there are $\frac{l}{m}\, n_{5t}$ females in milk and $[(m-l)/m]n_{5t}$ females dry. Thus the n_{5t} females in group 5 may be conceived of as the aggregation of m 'sets' of n_{5t}/m females each. The oldest set in the group will be referred to as the first set and the youngest as the last set of that group.

(*ii*) A female not conceiving during its lactation period of l months is considered infertile and removed from the herd.

(*iii*) Multiple births are negligible.

(*iv*) Births and deaths are independent.

(*v*) No female is kept in the post-reproductive age group.

3.2. *Limitations*

The deterministic approach, considered here, suffers from certain limitations and to that extent the results can be taken as broadly indicative of the real situation. The limitations are :

(*i*) Individual variation in the durations of different stage groups is assumed negligible and hence ignored.

(*ii*) The range of various parameters is restricted as follows :

$$0 \leqslant k \leqslant m \; ; \; 9 \leqslant g \leqslant 10 \text{ and } 12 \leqslant m \leqslant l+g \leqslant 21.$$

The range of parametric values considered is based on the results of ten important Indian dairy herds as reported by Amble *et. al.* (1967 and 1970) and Amble and Jain (1967). These restrictions cover the situations where heifers mature at an age varying between 24 to $24+m$ months, with a gestation period of 9 to 10 months and a lactation period of not more than 12 months. The last condition implies that as a rule the females are bred while in lactation but not before they have completed first three months of their lactation.

3.3. *Notations*

μ_i monthly mortality rate in the i-th stage group, for $i=1, 2, 3$.

λ_i the corresponding involuntary culling rate.

μ'_i mortality rate over the entire duration of i-th stage group, for $i=1, 2, 3$.

λ'_i the corresponding involuntary culling rate.

μ monthly mortality rate in the stage groups 4 to s.

λ the corresponding involuntary culling rate.

μ' annual adult mortality rate.

λ' the corresponding annual involuntary culling rate among adult females (including heifers).

f infertility rate.

v rate of abnormal calvings including abortion, still births and premature calvings.

r proportion of female births.

s_n proportion of females culled after the completion of their n-th lactation among those which were retained after $(n-1)$-th lactation.

3.4. *Lemmas*

We prove the following lemmas :

Lemma 1 :

(*a*) If N be the number of individuals alive at the beginning of a particular stage group of duration $\geqslant m$ and μ be the monthly rate of mortality, then the average number alive at any point in this stage group during one calving interval of m months is given by $N\left(1-\frac{m}{2}\mu\right)$.

(*b*) Further, if μ' is the annual mortality rate, the two rates are connected by the relation : $e^{-12\mu}=1-\mu'$.

Proof :

(*a*) Since μ is the monthly mortality rate, the number expected to be alive in successive months will be $(1-\mu)$ times the number alive in the immediately preceding month. Therefore, the number alive at any time during this stage group will be the simple average of numbers alive at 'm' discrete points. This average can be computed in two ways : (*i*) when the numbers are counted at the beginning of each month, and (*ii*) when the numbers are counted at the end of each month. The former procedure overestimates whereas the latter underestimates the numbers alive at any time. The average of these two averages may be taken as the number alive at any point during one calving interval.

$$\bar{N}_1=\frac{N}{m}\,[1+(1-\mu)+(1-\mu)^2+\ldots+(1-\mu)^{m-1}]$$

$$=N\left[1-\frac{m-1}{2}\mu\right],$$ neglecting terms of order μ^2 and higher

$$\overline{N_2} = \frac{N}{m}\left[(1-\mu)+(1-\mu)^2+\ldots+(1-\mu)^m\right]$$

$$= N\left[1-\frac{m+1}{2}\mu\right], \text{ neglecting terms of order } \mu^2 \text{ and higher}$$

$$\overline{N} = (\overline{N}_1+\overline{N}_2)/2 = N\left(1-\frac{m}{2}\mu\right).$$

(*b*) With yearly mortality rate as μ', the number alive at the end of the year is $N(1-\mu')$, whereas that on the basis of monthly rates is $N(1-\mu)^{12}$. The latter can easily be seen to be equal to $Ne^{-12\mu}$ for small values of μ. Thus $e^{-12\mu} \doteq 1-\mu'$.

Lemma 2 :

Let N be the number of individuals at the beginning of a particular stage group and λ be the monthly involuntary culling rate for this group, then the average number in this group at any time during one calving interval of m months is given by

$$N\left(1-\frac{m}{2}\lambda\right).$$

Proof :

Same as for Lemma 1.

Lemma 3 :

Let N be the number of individuals at the beginning of a particular stage group and μ and λ, the respective monthly mortality and involuntary culling rates, then the average number in this stage group at any time during one calving interval of m-months will be given by

$$N\left(1-\frac{m}{2}\mu\right)\left(1-\frac{m}{2}\lambda\right).$$

Proof :

The direct application of the first two lemmas under the assumption that the two forces of mortality and culling operates independently of each other gives the stated result.

Lemma 4 :

Let n_{1t} and n_{2t} be the respective number of young stock at time t in stage groups 1 and 2, each of 12 months duration. Further, let μ_1, μ_2 and μ_3 be the monthly mortality rates in groups 1, 2 and 3 respectively and μ'_2 be the annual mortality rate in group 2, then the average number of individuals in group 3, of k months duration, after one calving interval of m months will be given by

$$n_{3,\,t+1}=\begin{cases} n_{1t}\left(\frac{m-12}{12}\right)(1-\mu'_2)\left(1-\frac{m-12}{2}\mu_1\right)\left(1-\frac{m-12}{2}\mu_3\right) \\ +n_{2t}\left(\frac{12+k-m}{12}\right)\left(1-\frac{m+12-k}{2}\mu_2\right)\left(1-\frac{m+k-12}{2}\mu_3\right), \quad \text{for } k\geqslant m-12 \\ \text{and} \\ n_{1t}\left(\frac{k}{12}\right)(1-\mu'_2)\left(1-\frac{2m-k-24}{2}\mu_1\right)\left(1-\frac{k}{2}\mu_3\right), \quad \text{for } k<m-12 \end{cases}$$

Proof :

(*a*) *When* $k\geqslant m-12$

$n_{3,\,t+1}$ will comprise survivors of first $\overline{m-12}$ sets of individuals in stage group 1 and last $(k+12-m)$ sets in stage group 2 at time t. By using Lemma 1, the number of individuals in the first $\overline{m-12}$ sets in stage group 1 at time t will be

$$\left(\frac{m-12}{12}\right)n_{1t}\left(1-\frac{m-12}{2}\mu_1\right).$$

And by the same argument as employed in Lemma 1, the number of individuals in the last $(k+12-m)$ sets in stage group 2 at time t will be given by

$$\left(\frac{12+k-m}{12}\right)n_{2t}\left(1-\frac{m+12-k}{2}\right)\mu_2$$

Thus,

$$\begin{aligned} n_{3,\,t+1}=&\left(\frac{m-12}{12}\right)n_{1t}\left(1-\frac{m-12}{2}\mu_1\right)(1-\mu'_2) \\ &\times\frac{1}{2(m-12)}\left[(1-\mu_3)^\circ+(1-\mu_3)+\ldots+\overline{m-12}\text{ terms}\right. \\ &\left.+(1-\mu_3)+(1-\mu_3)^2+\ldots+\overline{m-12}\text{ terms}\right] \\ &+\left(\frac{12+k-m}{12}\right)n_{2t}\left(1-\frac{m+12-k}{2}\mu_2\right) \\ &\times\frac{1}{2(12+k-m)}\left[(1-\mu_3)^k+(1-\mu_3)^{k-1}+\ldots+\overline{12+k-m}\text{ terms}\right. \\ &\left.+(1-\mu_3)^{k-1}+(1-\mu_3)^{k-2}+\ldots+\overline{12+k-m}\text{ terms}\right] \\ =&\,n_{1t}\left(\frac{m-12}{12}\right)\left(1-\frac{m-12}{2}\mu_1\right)(1-\mu'_2)\left(1-\frac{m-12}{2}\mu_3\right) \\ &+n_{2t}\left(\frac{12+k-m}{12}\right)\left(1-\frac{m+12-k}{2}\mu_2\right)\left(1-\frac{m+k-12}{2}\mu_3\right) \end{aligned}$$

(*b*) *When* $k<m-12$

$n_{3,\ t+1}$ will comprise survivors of first k sets of individuals in stage group 1 at time t. Thus

$$n_{3,\ t+1}=\frac{n_{1t}}{12}(1-\mu'_2)[(1-\mu_1)^{m-12}(1-\mu_3)^0+(1-\mu_1)^{m-13}(1-\mu_3)+\ldots+k \text{ terms}$$

$$+(1-\mu_1)^{m-13}(1-\mu_3)+(1-\mu_1)^{m-14}(1-\mu_3)^2+\ldots+k \text{ terms}]$$

$$=n_{1t}\left(\frac{k}{12}\right)(1-\mu'_2)\left(1-\frac{2m-k-24}{2}\mu_1\right)\left(1-\frac{k}{2}\mu_3\right)$$

Lemma 5 :

The average number of female calves born every month during $(t, t+1)$ of m-months after allowing for mortality, infertility, abnormal calvings and involuntary cullings in different stages is given by

$$\bar{Q}=p_a\left[\frac{n_{4t}}{l+g}+\sum_{i=5}^{s}\frac{n_{it}}{m}\right],$$

where, $p_a=\left(1-\frac{m}{2}\mu\right)\left(1-\frac{m}{2}\lambda\right)(1-f)(1-\nu)r$

Proof :

Self explanatory.

3.5 *Expressions for matrix elements*

In order to derive a_{ij}'s, the elements of F, we work out $n_{i,\ t+1}$ from first considerations and express it as a linear function of $n_{1,t}$, $n_{2,t}$ ..., $n_{s,t}$ in accordance with relation (1). The coefficients of $n_{i,t}$'s give the elements of the martix.

(*a*) *Elements of the first row*

Since $n_{1,\ t+1}$ represents the number of females born during the last $m-12$ to m months and alive in stage group 1 at time $t+1$, we have using lemmas 1 and 5

$$n_{1,\ t+1}=12\bar{Q}(1-6\mu_1)(1-6\lambda_1)$$

$$=\sum_i n_{it}\, a_{1i}$$

with

$$a_{1i}=0 \ (i\leqslant 3)$$

$$a_{14}=\frac{12}{l+g}(1-6\mu_1)(1-6\lambda_1)p_a$$

$$a_{1i}=\frac{12}{m}(1-6\mu_1)(1-6\lambda_1)p_a \ (i\geqslant 5)$$

(*b*) *Elements of the second row*

The number in the second stage group at time $t+1$, will comprise females after allowing for mortality and culling during $(t, t+1)$ among those born during first $\overline{m-12}$ months plus the females of last $\overline{m-12}$ to 12th sets in stage group 1 at time t. Using lemma 4, this gives

$$n_{2,\ t+1}=(m-12)\bar{Q}(1-\mu'_1)(1-\lambda'_1)\left(1-\frac{m-12}{2}\mu_2\right)\left(1-\frac{m-12}{2}\lambda_2\right)$$
$$+\left(\frac{24-m}{12}\right)n_{1t}\left(1-\frac{m}{2}\mu_1\right)\left(1-\frac{m}{2}\lambda_1\right)\left(1-\frac{m}{2}\mu_2\right)\left(1-\frac{m}{2}\lambda_2\right)$$
$$=\sum_i n_{it}a_{2i}$$

with

$$a_{21}=\left(\frac{24-m}{12}\right)\left(1-\frac{m}{2}\mu_1\right)\left(1-\frac{m}{2}\lambda_1\right)\left(1-\frac{m}{2}\mu_2\right)\left(1-\frac{m}{2}\lambda_2\right)$$
$$a_{2i}=0\ (i=2,\ 3)$$
$$a_{24}=\left(\frac{m-12}{l+g}\right)(1-\mu'_1)(1-\lambda'_1)\left(1-\frac{m-12}{2}\mu_2\right)\left(1-\frac{m-12}{2}\lambda_2\right)p_a$$
$$a_{2i}=\left(\frac{m-12}{m}\right)(1-\mu'_1)(1-\lambda'_1)\left(1-\frac{m-12}{2}\mu_2\right)\left(1-\frac{m-12}{2}\lambda_2\right)p_a \qquad (i\geqslant 5)$$

(*c*) *Elements of the third row*

The numbers in stage group 3 at time $t+1$ depend upon whether $k\geqslant m-12$ or $k<m-12$.

(*i*) $k\geqslant m-12$

The number in this stage group will comprise females after allowing for mortality and culling during $(t, t+1)$ among the first $\overline{m-12}$ sets of females in stage group 1 and last $(k+12-m)$ sets in stage group 2 at time t, *i.e.*

$$n_{3,\ t+1}=\left(\frac{m-12}{12}\right)n_{1t}\left(1-\frac{m-12}{2}\mu_1\right)\left(1-\frac{m-12}{2}\lambda_1\right)\times$$
$$\left(1-\mu'_2\right)\left(1-\lambda'_2\right)\left(1-\frac{m-12}{2}\mu_3\right)\left(1-\frac{m-12}{2}\lambda_3\right)$$
$$+\left(\frac{12+k-m}{12}\right)n_{2t}\left(1-\frac{12+m-k}{2}\mu_2\right)\left(1-\frac{12+m-k}{2}\lambda_2\right)\times$$
$$\left(1-\frac{m+k-12}{2}\mu_3\right)\left(1-\frac{m+k-12}{2}\lambda_3\right)$$
$$=\sum_i n_{it}a_{3i}$$

$$\text{with, } a_{31} = \left(\frac{m-12}{12}\right)\left(1 - \frac{m-12}{2}\mu_1\right)\left(1 - \frac{m-12}{2}\lambda_1\right)\left(1 - \mu'_2\right) \times$$
$$\left(1 - \lambda'_2\right)\left(1 - \frac{m-12}{2}\mu_3\right)\left(1 - \frac{m-12}{2}\lambda_3\right)$$
$$a_{32} = \left(\frac{12+k-m}{12}\right)\left(1 - \frac{12+m-k}{2}\mu_2\right)\left(1 - \frac{12+m-k}{2}\lambda_2\right)\times$$
$$\left(1 - \frac{m+k-12}{2}\mu_3\right)\left(1 - \frac{m+k-12}{2}\lambda_3\right)$$
$$a_{3i} = 0 \quad (i \geqslant 3)$$

(*ii*) $k < m-12$

With this restriction, the number will comprise individuals belonging to $\overline{m-12-k}$ to $\overline{m-12}$th sets of females of stage group 1 at time t after allowing for mortality and culling, *i.e.*

$$n_{3,t+1} = \left(\frac{k}{12}\right)n_{1t}\left(1 - \frac{2m-k-24}{2}\mu_1\right)\left(1 - \frac{2m-k-24}{2}\lambda_1\right)\times$$
$$\left(1 - \mu'_2\right)\left(1 - \lambda'_2\right)\left(1 - \frac{k}{2}\mu_3\right)\left(1 - \frac{k}{2}\lambda_3\right)$$

$$\text{Thus, } a_{31} = \left(\frac{k}{12}\right)\left(1 - \frac{2m-k-24}{2}\mu_1\right)\left(1 - \frac{2m-k-24}{2}\lambda_1\right)\times$$
$$\left(1 - \mu'_2\right)\left(1 - \lambda'_2\right)\left(1 - \frac{k}{2}\mu_3\right)\left(1 - \frac{k}{2}\lambda_3\right)$$
$$a_{3i} = 0 \quad (i \geqslant 2)$$

(*d*) *Elements of the fourth row*

The numbers in stage group 4 at time $t+1$ will depend upon whether (*i*) $k \geqslant m-12$, and $m-k \geqslant g$ (*ii*) $k \geqslant m-12$, and $m-k < g$ or (*iii*) $k < m-12$, and $m-k \geqslant g$.

(*i*) $k \geqslant m-12$, *and* $m-k \geqslant g$

The number in this stage group at $(t+1)$ will comprise females of first $\overline{m-k}$ sets of stage group 2 (composed of last g sets among $\overline{m-k}$ sets which are still carrying and the rest $\overline{m-k-g}$ sets which have calved at time $t+1$), all the k sets of stage group 3 and the last $(l+g-m)$ sets of stage group 4 at time t after allowing for mortality, culling and infertility during $(t, t+1)$, *i.e.*

$$n_{4,t+1} = \left(\frac{g}{12}\right)n_{2t}\left(1 - \frac{2m-g-2k}{2}\mu_2\right)\left(1 - \frac{2m-g-2k}{2}\lambda_2\right)\times$$
$$\left(1 - \mu'_3\right)\left(1 - \lambda'_3\right)\left(1 - \frac{g}{2}\mu\right)\left(1 - \frac{g}{2}\lambda\right)$$
$$+\left(\frac{m-k-g}{12}\right)n_{2t}\left(1 - \frac{m-g-k}{2}\mu_2\right)\left(1 - \frac{m-g-k}{2}\lambda_2\right)\times$$

$$\left(1-f\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)\left(1-\frac{m+g-k}{2}\mu\right)\times$$
$$\left(1-\frac{m+g-k}{2}\lambda\right)$$
$$+n_{3t}\left(1-\frac{k}{2}\mu_3\right)\left(1-f\right)\left(1-\frac{2m-k}{2}\mu\right)\left(1-\frac{2m-k}{2}\lambda\right)$$
$$+\left(\frac{l+g-m}{l+g}\right)n_{4t}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)\left(1-f\right)$$
$$=\sum_i n_{it}\,a_{4i}$$

with $a_{42}=\left(\frac{g}{12}\right)\left(1-\frac{g}{2}\mu\right)\left(1-\frac{g}{2}\lambda\right)\left(1-\frac{2m-g-2k}{2}\mu_2\right)\times$

$$\left(1-\frac{2m-g-2k}{2}\lambda_2\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)$$
$$+\left(\frac{m-k-g}{12}\right)\left(1-f\right)\left(1-\frac{m+g-k}{2}\mu\right)\left(1-\frac{m+g-k}{2}\lambda\right)\times$$
$$\left(1-\frac{m-g-k}{2}\mu_2\right)\left(1-\frac{m-g-k}{2}\lambda_2\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)$$

$$a_{43}=\left(1-f\right)\left(1-\frac{2m-k}{2}\mu\right)\left(1-\frac{2m-k}{2}\lambda\right)\left(1-\frac{k}{2}\mu_3\right)\times$$
$$\left(1-\frac{k}{2}\lambda_3\right)$$

$$a_{44}=\left(\frac{l+g-m}{l+g}\right)\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)\left(1-f\right)$$

$$a_{4i}=0 \quad (i\neq 2, 3, 4)$$

(ii) $k\geqslant m-12$, *and* $m-k<g$

The number in this stage group at time $(t+1)$ will comprise females of first $m-k$ sets of stage group 2 (all of them will be carrying at time $t+1$), all the k sets of stage group 3 (composed of last $g+k-m$ sets which are still carrying and the rest $m-g$ sets which have calved at time $t+1$) and the last $(l+g-m)$ sets of stage group 4 at time t after allowing for mortality, culling and infertility during $(t, t+1)$, *i.e.*

$$n_{4,\,t+1}=\left(\frac{m-k}{12}\right)n_{2t}\left(1-\frac{m-k}{2}\mu_2\right)\left(1-\frac{m-k}{2}\lambda_2\right)\left(1-\mu'_3\right)\times$$
$$\left(1-\lambda'_3\right)\left(1-\frac{m-k}{2}\mu\right)\left(1-\frac{m-k}{2}\lambda\right)+\left(\frac{g+k-m}{k}\right)n_{3t}\times$$
$$\left(1-\frac{m-g+k}{2}\mu_3\right)\left(1-\frac{m-g+k}{2}\lambda_3\right)\left(1-\frac{g+m-k}{2}\mu\right)\times$$

$$\left(1-\frac{g+m-k}{2}\lambda\right)+\left(\frac{m-g}{k}\right)n_{3t}\left(1-\frac{m-g}{2}\mu_3\right)\times$$
$$\left(1-\frac{m-g}{2}\lambda_3\right)\left(1-f\right)\left(1-\frac{m+g}{2}\mu\right)\left(1-\frac{m+g}{2}\lambda\right)$$
$$+\left(\frac{l+g-m}{l+g}\right)n_{4t}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)\left(1-f\right)$$
$$=\sum_i n_{it}a_{4i}$$

with

$$a_{42}=\left(\frac{m-k}{12}\right)\left(1-\frac{m-k}{2}\mu\right)\left(1-\frac{m-k}{2}\lambda\right)\left(1-\frac{m-k}{2}\mu_2\right)\times$$
$$\left(1-\frac{m-k}{2}\lambda_2\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)$$

$$a_{43}=\left(\frac{g+k-m}{k}\right)\left(1-\frac{g+m-k}{2}\mu\right)\left(1-\frac{g+m-k}{2}\lambda\right)\times$$
$$\left(1-\frac{m-g+k}{2}\mu_3\right)\left(1-\frac{m-g+k}{2}\lambda_3\right)+\left(\frac{m-g}{k}\right)\left(1-f\right)\times$$
$$\left(1-\frac{m+g}{2}\mu\right)\left(1-\frac{m+g}{2}\lambda\right)\left(1-\frac{m-g}{2}\mu_3\right)\left(1-\frac{m-g}{2}\lambda_3\right)$$

$$a_{44}=\left(\frac{l+g-m}{l+g}\right)\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)\left(1-f\right), \text{ and}$$

$$a_{4i}=0 \quad (i\neq 2, 3, 4)$$

(*iii*) $k<m-12$, *and* $m-k\geqslant g$

The number in this group at $(t+1)$ will comprise females of first $\overline{m-12-k}$ sets of stage group 1, all the 12 sets of stage group 2 (composed of last $\overline{g+12+k-m}$ sets which will still be carrying and the remaining $\overline{m-g-k}$ sets which have calved at time $t+1$), all the k sets of stage group 3 and the last $(l+g-m)$ sets of stage group 4 at time t, after allowing for mortality, culling and infertility during $t, t+1$, *i.e.*

$$n_{4,\ t+1}=\left(\frac{m-12-k}{12}\right)n_{1t}\left(1-\frac{m-k-12}{2}\mu_1\right)\left(1-\frac{m-k-12}{2}\lambda_1\right)\times$$
$$\left(1-\mu'_2\right)\left(1-\lambda'_2\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)\left(1-\frac{m-12-k}{2}\mu\right)\times$$
$$\left(1-\frac{m-12-k}{2}\lambda\right)+\left(\frac{g+12+k-m}{12}\right)n_{2t}\times$$
$$\left(1-\frac{12+m-k-g}{2}\mu_2\right)\left(1-\frac{12+m-k-g}{2}\lambda_2\right)\left(1-\mu'_3\right)\times$$
$$\left(1-\lambda'_3\right)\left(1-\frac{g+m-k-12}{2}\mu\right)\left(1-\frac{g+m-k-12}{2}\lambda\right)$$

$$+\left(\frac{m-g-k}{12}\right)n_{2t}\left(1-\frac{m-g-k}{2}\mu_2\right)\left(1-\frac{m-g-k}{2}\lambda_2\right)\times$$
$$\left(1-f\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)\left(1-\frac{m+g-k}{2}\mu\right)\times$$
$$\left(1-\frac{m+g-k}{2}\lambda\right)+n_{3t}\left(1-\frac{k}{2}\mu_3\right)\left(1-\frac{k}{2}\lambda_3\right)\times$$
$$\left(1-f\right)\left(1-\frac{2m-k}{2}\mu\right)\left(1-\frac{2m-k}{2}\lambda\right)+\left(\frac{l+g-m}{l+g}\right)n_{4t}\times$$
$$\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)\left(1-f\right)$$
$$=\sum_i n_{it}a_{4i}$$

with

$$a_{41}=\left(\frac{m-12-k}{12}\right)\left(1-\frac{m-12-k}{2}\mu\right)\left(1-\frac{m-12-k}{2}\lambda\right)\times$$
$$\left(1-\frac{m-12-k}{2}\mu_1\right)\left(1-\frac{m-12-k}{2}\lambda_1\right)\left(1-\mu'_2\right)\times$$
$$\left(1-\lambda'_2\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)$$

$$a_{42}=\left(\frac{g+12+k-m}{12}\right)\left(1-\frac{g+m-k-12}{2}\mu\right)\times$$
$$\left(1-\frac{g+m-k-12}{2}\lambda\right)\left(1-\frac{12+m-k-g}{2}\mu_2\right)\times$$
$$\left(1-\frac{12+m-k-g}{2}\lambda_2\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right)+\left(\frac{m-g-k}{12}\right)\times$$
$$\left(1-f\right)\left(1-\frac{m+g-k}{2}\mu\right)\left(1-\frac{m+g-k}{2}\lambda\right)\times$$
$$\left(1-\frac{m-g-k}{2}\mu_2\right)\left(1-\frac{m-g-k}{2}\lambda_2\right)\left(1-\mu'_3\right)\left(1-\lambda'_3\right).$$

$$a_{43}=(1-f)\left(1-\frac{2m-k}{2}\mu\right)\left(1-\frac{2m-k}{2}\lambda\right)\left(1-\frac{k}{2}\mu_3\right)\left(1-\frac{k}{2}\lambda_3\right)$$

$$a_{44}=\left(\frac{l+g-m}{l+g}\right)\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)(1-f), \text{ and}$$

$a_{4i}=0 \ (i\geqslant 5)$

(d) *Elements of the fifth row*

The number in this group at $t+1$ will comprise females of first m sets of stage group 4 at time t after allowing for mortality, infertility and voluntary and involuntary cullings during $(t, t+1)$, i.e.

$$n_{5,\,t+1}=\frac{m}{l+g}\left[\frac{l}{l+g}n_{4t}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)(1-f)(1-s_1)+\right.$$
$$\left.\frac{g}{l+g}n_{4t}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)(1-f)\right]$$

$$=\sum_i n_{it}\, a_{5i}$$

with

$$a_{54}=\frac{m}{l+g}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)(1-f)\left[1-\frac{ls_1}{l+g}\right], \text{ and}$$

$a_{5i}=0\ (i\neq 4)$.

(*f*) *Elements of the p-th row for* $p\geqslant 6$

The number in the p-th stage group at time $(t+1)$ will comprise all the m sets of females of stage group $(p-1)$ at time t after allowing for mortality, infertility, and voluntary and involuntary cullings during $(t, t+1)$, *i.e.*

$$n_{p,\,t+1}=\frac{l}{m}n_{p-1,t}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)(1-f)(1-s_{p-4})$$

$$+\frac{m-l}{m}\,n_{p-1,t}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)$$

$$=n_{p-1,\,t}\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)\left[1-\frac{l}{m}\left\{s_{p-4}+f(1-s_{p-4})\right\}\right]$$

$$=\sum_i n_{it}\, a_{pi}.$$

with

$$a_{p,\,p-1}=\left(1-\frac{m}{12}\mu'\right)\left(1-\frac{m}{12}\lambda'\right)\left[1-\frac{l}{m}\left\{s_{p-4}+f\,(1-s_{p-4})\right\}\right], \text{ and}$$

$a_{pi}=0\ (i\neq p-1)$.

In the light of foregoing values of a_{ij}'s, the generation matrix F of female herd strength takes the following form

$$F=\begin{bmatrix} 0 & 0 & 0 & a_{14} & a_{15} & \cdots & a_{1s} \\ a_{21} & 0 & 0 & a_{24} & a_{25} & \cdots & a_{2s} \\ a_{31} & a_{32} & 0 & 0 & 0 & \cdots & 0 \\ a_{41} & a_{42} & a_{43} & a_{44} & 0 & \cdots & 0 \\ 0 & 0 & 0 & a_{54} & 0 & \cdots & 0 \\ 0 & 0 & 0 & 0 & a_{65} & \cdots & 0 \\ 0 & 0 & 0 & 0 & 0 & a_{76} \cdots & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdots & \cdot \\ 0 & 0 & 0 & 0 & 0 & \cdots a_{s,\,s-1} & 0 \end{bmatrix}$$

4. Growth Of Female Population In Dairy Herds

The use of population generation matrix was made to study the growth obtainable in five leading Indian dairy herds—Red Sindhi and Kangayam herds of Hosur, Red Sindhi and Gir herds of Bangalore and Tharparkar herd of Patna. The breeding data of these herds have been analysed and reported by Amble *et. al.* (1967 a). The relevant results reported by them have been suitably utilised for developing appropriate parameters needed for the present study. Some of the pertinent and salient features of these herds are given in what follows.

The Red Sindhi herd at the Hosur Farm was started with a foundation stock of 40 cows and 4 bulls, purchased during 1921 to 1928. The herd grew in strength progressively and the strength of the adult females during the period 1946-52 averaged 117 cows.

The Sindhi herd at the Bangalore Farm was constituted in the year 1923 with the purchase of 19 cows and one bull and was augmented by 153 more cows and 16 bulls purchased from time to time till the year 1943. The herd increased in strength from inception to 1932 when a substantial reduction was effected by culling in order to make room for the Gir herd added to the Farm that year. From 1932 to 1948 there were irregular fluctuations in the herd strength. Since 1948 the herd strength gradually decreased. The adult female stock in April 1952, upto which the data were collected, consisted of 44 cows only.

The Kangayam herd at the Hosur Farm was reared from a foundation stock of 66 cows and 15 bulls purchased during 1922 to 1930. The herd registered a steady increase in its strength and the adult female stock during the period 1946-52 consisted on an average of 180 cows.

The Tharparkar herd at the Patna Farm was started in the year 1926 and 51 foundation cows were purchased during the period 1926-1934. The herd strength increased upto the year 1936 and thereafter it was more or less static. The strength of adult females in May 1956 was 154 cows.

The Gir herd at the Bangalore Farm was started in the year 1933 with the purchase of 15 cows and was augmented by 26 more cows purchased from time to time till 1940. The herd remained small throughout the period from 1933 to 1952, the adult female stock in April 1952 was 31 cows.

The mortality and culling rates as reported by Amble *et. al.* (1967) were for different age-classifications. Accordingly, these rates were appropriately converted so as to conform to the stage groupings considered here. The total number of stage groupings was 13 corresponding to ten completed lactations as hardly any female was retained on the farms beyond that stage. Of the total depletion on account of mortality and culling among adult stock, a uniform rate

TABLE 1

Vital Statistics and Culling Rates of Different Dairy Herds

Characteristic		*Red Sindhi Hosur*	*Red Sindhi Bangalore*	*Kangayam Hosur*	*Tharparkar Patna*	*Gir Bangalore*
		Mortality rate (%)				
Below 12 months	(μ_1')	9.5	16.5	7.3	9.7	10.1
12 to 24 months	(μ_2')	1.0	1.5	1.3	2.0	1.5
24 to 24+k months	(μ_3')	0.5	1.0	1.0	2.5	1.0
Annual rate among adult females	(μ')	1.0	1.0	1.0	2.0	1.0
		Involuntary culling rate (%)				
Below 12 months	(λ_1')	4.3	22.5	4.0	9.5	18.7
12 to 24 months	(λ_2')	7.2	8.2	11.5	15.2	8.7
24 to 24+k months	(λ_3')	5 2	6.2	10.4	20.0	10.2
Annual rate among adult females	(λ')	5.0	5.0	5.0	1.0	3.0
		Voluntary culling rate at the end of a lactation (%)				
I lactation	(s_1)	6.0	10.0	22.0	20.0	11.0
II ,,	(s_2)	3.0	2 0	5.0	1.0	2.0
III & IV ,, each	(s_3, s_4)	9.0	9.0	3.0	5.0	17.0
V & VI ,, each	(s_5, s_6)	9.0	15.0	9.0	8.0	19.0
VII & VIII ,, each	(s_7, s_8)	15.0	30.0	13.0	16.0	25.0
IX ,,	(s_9)	11.0	52,0	25.0	47.0	37.0
		Other statistics				
% abortion & still births	(v)	2.0	2.0	2.0	2.0	2.0
% infertility rate	(f)	5.0	5.0	5.0	5.0	5.0
Prop. female births	(r)	0.5	0.5	0.5	0.5	0.5
Lactation length	(l)	10.5	8.7	8.7	9.7	9.4
Calving interval	(m)	18.0	14.7	16.6	14.7	15.6
Gestation period	(g)	9.0	9.0	9.0	9.0	9.0
Duration of stage 3	(k)	9.0	9.0	11.0	14.0*	14.0

* Although a figure of 16.0 was obtained but in view of the restriction on the range of k it was taken as 14.0.

for mortality, infertility and involuntary culling was apportioned and the remainder suitably modified to represent voluntary cullings at the completion of a lactation. Since aged and debilitated animals are likely to be culled, the mortality rate can be taken to be uniform over different stage groups. Table 1 gives age-specific mortality and culling rates, infertility rate as obtained in the manner indicated above along with abnormal calvings, sex ratio, lactation length, gestation period, calving interval, duration of stage group 3 (calculated from age at first calving), etc.

The numerical values of the elements of generation matrices of different herds computed from the expressions derived in section 3.5 along with their dominant latent roots are given in Table 2. An examination of the values of dominant roots shows that all the herds will be increasing in size.

TABLE 2

Values of the Elements of Population Generation Matrices and the Dominant Latent Root of Different Dairy Herds

Elements of matrix and dominant root	*Red Sindhi Hosur*	*Red Sindhi Bangalore*	*Kangayam Hosur*	*Tharparkar Patna*	*Gir Bangalore*
a_{14}	.2540	.2412	.2849	.2644	.2509
a_{1p} $(p \geqslant 5)$	.2752	.2904	.3038	.3363	.2960
a_{21}	.4190	.5462	.5151	.6057	.5253
a_{24}	.1159	.0437	.1004	.0528	.0638
a_{2p} $(p \geqslant 5)$	.1255	.0527	.1071	.0672	.0752
a_{31}	.4344	.1915	.3192	.1789	.2534
a_{32}	.2204	.4631	.4403	.7414	.7551
a_{42}	.6693	.4243	.3952	.0452	.1174
a_{43}	.8593	.8841	.8562	.8561	.8920
a_{44}	.0666	.1493	.0542	.1958	.1371
a_{54}	.7732	.6956	.7294	.6449	.7210
a_{65}	.8694	.8894	.8710	.9257	.9091
a_{76}	.8391	.8529	.8802	.9016	.8276
a_{87}	.8391	.8529	.8802	.9016	.8276
a_{98}	.8391	.8216	.8528	.8834	.8168
$a_{10, 9}$	.8391	.8216	.8528	.8834	.8168
$a_{11, 10}$	.8088	.7434	.8345	.8351	.7842
$a_{12, 11}$	.8088	.7434	.8345	.8351	.7842
$a_{13, 12}$	.8290	.6287	.7796	.6479	.7190
Dominant root	1.0852	1.0207	1.0658	1.0438	1.0393

Assuming the female foundation stock to consist of 100 females in stage group 4, the growth of female population at intervals of 5 calving interval units for the different herds are shown in Table 3. This table would also be useful in giving the distribution if the number to start with is other than 100, by suitably multiplying the numbers in the various stage groups. The growth was quite fast in the two herds maintained at Hosur viz. Red Sindhi and Kangayam and slow in Tharparkar and Gir herds whereas Red Sindhi herd of Bangalore was on the verge of equilibrium. The adult female stock of Red Sindhi and Kangayam herds of Hosur, doubled in strength over 18 and 22 years period respectively. The corresponding figures for the Tharparkar and Gir herds were 28 and 33 years respectively.

The total adult stock at periodic intervals as given in Table 3 is broadly in agreement with the one actually observed for all the herds. The comparison is only of broad nature and one cannot expect more closer results with a deterministic approach because of inherent limitations already mentioned in section 3.2. Moreover, the parameters derived for this study do not have a one-to-one correspondence with the actual situation. For example:

(*i*) the vital statistics and culling rates have been assumed to be constant over the entire period whereas in reality these are subject to wide fluctuations;

(*ii*) the female foundation stock has been assumed to consist of animals in stage group 4 only while actually the foundation stock may be distributed over the stage groups 4 to 7, if not beyond;

(*iii*) a uniform rate of abortion and still births at 2 per cent may not be reflecting the real situation; and

(*iv*) the parameters utilised for this study are those based on appropriately converted mortality and culling rates as obtained from the live data which may not be exact specially in view of the fact that the original figures were available according to age while converted figures pertained to different orders of lactation.

An important conclusion which has a bearing on the policy to be followed in these breeding farms would be regarding culling. The foundation stock is usually constituted with a much smaller number than the optimum which the farm can maintain. The herd strength in due course of time will increase beyond this limit. In order to maintain constant herd strength it is essential to continually appraise

TABLE 3

Growth of Female Population in Different Herds

Time (in m units)	*Nmnbers in different stage groups*													*Total adult stock*	*Total herd strength*
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*		
0	0	0	0	100	0	0	0	0	0	0	0	0	0	100	100
							1. *Red Sindhi, Hosur*								
5	28	23	16	28	21	18	5	3	40	0	0	0	0	115	182
10	45	37	25	45	32	25	19	15	11	9	7	2	1	166	273
15	65	54	37	67	47	37	30	23	18	14	10	7	6	259	415
20	97	82	56	101	72	58	44	34	27	20	15	12	9	392	627
							2. *Red Sindhi, Bangalore*								
5	24	16	12	20	14	9	2	7	37	0	0	0	0	89	141
10	27	20	14	24	16	14	11	9	8	6	3	1	2	94	155
15	29	21	15	25	17	15	13	11	9	7	5	4	2	108	173
20	33	23	17	28	19	17	14	12	9	7	5	4	3	118	191

							3. Kangayam, Hosur								
5	28	23	17	23	18	13	2	3	42	0	0	0	0	101	169
10	41	34	26	35	23	19	15	12	9	9	6	1	1	130	231
15	53	45	35	47	31	25	22	18	15	12	9	7	5	191	324
20	74	62	48	64	44	36	30	25	20	15	12	10	7	263	447
							4. Tharparkar, Patna								
5	28	21	20	22	13	5	2	10	43	0	0	0	0	95	164
10	37	29	27	29	17	15	12	11	10	8	3	1	3	109	202
15	44	35	32	33	20	19	17	15	12	10	8	6	4	144	255
20	55	43	40	42	26	23	20	17	14	12	10	8	5	177	315
							5. Gir, Bangalore								
5	24	18	19	23	16	8	1	6	37	0	0	0	0	91	152
10	31	24	25	27	19	16	12	10	8	7	3	0	2	104	184
15	37	28	30	32	22	20	16	13	10	8	6	4	3	134	229
20	45	34	36	40	27	24	19	15	12	9	7	6	4	163	278

the progress of the population and suitably modify the voluntary culling rates.

SUMMARY

The population generation matrix method has been used to study the growth of female population in Indian dairy herds. Explicit expressions for the elements of generation matrix in terms of the parameters defining the scheme of selection and vital characteristics of a dairy herd have been derived. Two different approaches for controlling the strength of a herd which is changing over time have been suggested. The theory developed has been illustrated with the help of actual data from five Indian dairy herds.

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