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A Deterministic Model to Evaluate the Breeding Schemes for Dairy Cattle Population with Overlapping Generations

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List of abbreviations.

c	Subscript to represent the youngest age class
DS	Dams to breed sires
DC	Dams to breed cows
$d(K)$	Difference between calculated and given proportion in converging the nonlinear equation
$e(K)$	Difference of given and calculated standardized selection differential
$e'(K_n)$	Rate of change in I at K_n
Δg	Genetic superiorities of selected animals within age class
G	Average genetic selection differential of selected parents for each path of gene transmission
$GMNB$	Genetic merit of new born animals, males or females
gsd	Genetic standard deviation
I^*	Given standardized selection differential
I	Calculated standardized selection differential
i_a	Selection intensity adjusted for small numbers
$K(k)$	Truncation point (deviation from mean)
L_{xy}	Generation length for the path XY
m	Population or subpopulation means before selection
ms	Mean genetic merit of selected animals from an age class
M	Average gnetic merit of overall selected parents for each path (sires or dams)
N	Population size (candidates) within age class
n	Number of selected animals within age class
P	Overall selected proportion
p	Proportion selected from an age class
q	Proportion of candidates in an age class
r	Accuracy of selection
SC	Sires to breed cows
SE	Standard error
SS	Sires to breed sires
SS_n	Selection scheme, n denotes the scheme number
vs	Versus
x	Truncation point on standardized normal distribution

CHAPTER I

INTRODUCTION (Historical review)

1. Population structure

Domestic livestock population structure is essentially hierarchical and pyramidal in nature as shown in the structure analyses of different breeds and species of domestic livestock[102]. ROBERTSON and ASKER[75] were the first to show the movement of animals between herds within breeds. This movement was so great as to preclude the possibility of local genetic differentiation. ROBERTSON and ASKER[76] showed that this movement of animals, especially bulls, was not at random. Rather it was a directional process due to the existence of the fashionable herds and breed structures. The hierarchical structures for a number of British breeds of dairy cattle, beef cattle, pigs and goats were reported by ROBERTSON[74]. The number of herds having any permanent genetic effect on the breed was less than 30. The genetic consequences of these structures were clearly recognized: only a small fraction of differences between herds in average performance could be of genetic origin[78]. The genetic improvement is made in the small group of animals 'nucleus' which are on the top of the pyramid system and genetic structure, and improvement of the breed depends on the breeding policy in that nucleus, which dominate the breed. Next to the top group (pedigree breeders) is a second group of breeders whose essential function is to multiply the genes from the top group of herds and pass them on to other herds. This function is fulfilled through buying and using the bulls or semen in their herds and selling sons to other herds. The non-pedigree herds of a given breed constitute a further layer below the pedigree layers. This flow of genes has important consequences since genetic change in the whole population is determined by a small group of nucleus. BICHARD[4] reported a detailed theoretical analysis for the flow of genes in terms of genetic improvement lags (the extent to which each tier is genetically behind the previous one is termed as ' improvement lags' by BICHARD[4]) between different layers of pyramidal structures of livestock populations. It is an important concept surprising to most practical breeders, if they are not on the top of the hierarchy, their selection efforts affect the distance of their livestock lag behind the upper level, but not the rate of genetic change in their population. Similar results were reported by GUY and SMITH[36]. The connection between the two, top and lower, will usually be maintained through the transfer of males or females. Some herds may adopt an intermediate function and multiply stocks from the nucleus in order to support a larger number of commercial herds with males or with both males and females. This, with 3 tiers, resembles the naturally occurring pyramidal structure revealed by herd and flock book analyses in many pedigree breeds of livestock[74]. This pyramidal structure initiated the utilization of the 'nucleus' concept in different aspects of breeding plan. SMITH[91], HILL[39] and BICHARD[4] dealt with such centralized breeding schemes while HINKS[47] described the most common features of progeny testing being operated and practiced world wide:

i) Batch mating of young bulls to a small milk recorded population to produce a small number of test daughters in each of many herds.
ii) The removal of bulls from service for several years until progeny test proofs are available.
iii) The selection, reintroduction and heavy usage of proven bulls, for many years, to breed daughters for herd replacement and son for progeny testing.

To increase the reproductive rates of females, Multiple Ovulation and Embryo Transfer (MOET) was reported by LAND and HILL[64] suggesting the possibility to increase the improvement rate for traits measurable to both sexes prior to puberty. These results were confirmed by SMITH[84] and were immediately applicable to beef cattle but not to dairy cattle in which the trait of interest, milk production, is sex limited and cannot be measured prior to puberty. The potential use of MOET in a small dairy herd was extended by NICHOLAS[70] and NICHOLAS and SMITH[71]. There after several studies indicated the possible uses of MOET to increase the genetic response[6,12,14,15,33,79,103]. Reproductive technologies such as frozen semen and embryo transfer make the generations overlap in dairy cattle populations. Moreover, in less developed countries the dairy population still faces the problem of low reproduction rate in females which dictates the necessity to keep the females for several breeding seasons and/or years. Thus after several years of selection some females may be from foundation stocks, some younger animals may be from the third generation and some animals may not have gone through the process of selection as reported by Hill[40]. Consequently, both in developed and less developed countries the generations in a dairy population overlap and genetic differences exist among age classes as a strong relationship between age and genetic merit of an animal. During 1960's and early 1970's, models were developed to take into account this type of population structures and prediction of short term responses. Two implicit assumptions often and commonly made in the derivation of these models were:

i) the records and additive genetic values follow multivariate normal distributions,
ii) genetic variation and normality are maintained through several generations of selection.

A brief description of these models will be given in this chapter at appropriate places while describing the general framework of selection theory.

2. Basic determinants for predicting the genetic responses

Annual rate of genetic improvement in an artificially selected population is determined by four basic factors:

1) accuracy of selection (r), 2) the genetic standard deviation (σa), 3) intensity of selection (i) and 4) generation interval (L). The role of a scientific animal

breeder in the design of breeding program is to develop strategies with respect to selection, mating and population and/or age structures that optimize the relationship among these four factors to maximize the genetic improvement. These four factors can be combined in three different genetic equations as a basis for predicting either short- or long-term genetic gain. Parts of these equations can be altered by the mode of reproduction and therefore these equations allow comparison of various breeding schemes.

A brief description of three basic genetic equations and possible ways to modify these equations to maximize the genetic response from a breeding program is given below:

1) Superiority of selected animals

The expected genetic superiority (Δg) in additive genetic values of selected males (m) and females (f) above that of those available for selection in generation t for a quantitative trait is given by

$$g_f(t) = i_f r_f(t) \sigma_a \qquad [1.1a],$$

$$g_m(t) = i_m r_m(t) \sigma_a \qquad [1.1b].$$

The superiority of selected animals can be enhanced by increasing the selection differential, decreasing the selected proportion to a limit which is determined by reproductive rate of the male and female. Reproductive technologies of artificial insemination (AI) and freezing semen have, for the last 45 years, played a major role in enhancing the male reproductive rates and currently the MOET[71] is in use to increase the female reproductive rates. These increased rates of reproduction both for males and females would enhance the selection intensity. Accuracy of selection can be increased by controlling the environment, reducing the measurement errors, using good design of testing and mating schemes, incorporating the information on relevant traits and fitting a model as good as possible. The use of information from relatives and computational power to fit appropriately large statistical models are ways in which Best Linear Unbiased Prediction (BLUP) and individual animal models will help the speed of genetic progress. However, increasing gain in accuracy cannot be viewed in isolation: for example accuracy on females can be increased by recording more lactation records before making the selection decision which in turn increase the generation interval and, consequently, dwindle the genetic progress. This issue will be addressed in detail in later parts of this dissertation. WOOLLIAMS[105] reported that selection progress can be increased with increasing the genetic variation in offspring employing positive assortative mating by introducing the positive covariance between the expected breeding values of the mates. By analogy the progress will be lower if covariance is negative, negative assortative mating.

2) Yearly genetic gain in discrete and overlapping generations

When all adult animals have a single limited period of reproduction and then all are replaced by their offspring, the generations will remain quite distinct in the population. Selection response can be described and predicted adequately by the mean performance of the group of animals born in the current generations (or time period since this can be taken as equal to generation interval). The difference between means of two successive generations will be the response to selection while the yearly gain will be obtained by dividing this response with generation interval. The response to selection for such a population could be predicted by [1.1a,b]. However, where reproduction in one or both sexes continues for a long period relative to the age at first calving then the generations will no longer be discrete but will overlap where it is necessary to describe the performance of all age groups present in the population at any time. For this purpose DICKERSON and HAZEL21) described the first classical relationship between age structures and rate of response in a population with overlapping generations. This was an attempt to incorporate then new AI technology which inspired animal geneticists to explore more details of this analysis. ROBERTSON and RENDEL77) envisaged the advantages of AI by calculating a theoretical progeny test scheme in a dairy cattle population and RENDEL and ROBERTSON73) developed the same using dairy data and framed the following more familiar equation to calculate the annual genetic gain(ΔG).

$$\Delta G = \frac{\Delta g_{SS} + \Delta g_{SD} + \Delta g_{SD} + \Delta g_{DD}}{L_{SS} + L_{SD} + L_{DS} + L_{DD}} \qquad [1.2]$$

where Δg refers to the genetic superiority, *SS* refers to sires to breed sons, *SD* refers to sires to breed daughters, *DS* refers to dams to breed sons and *DD* to dams to breed daughters and *L* to the generation interval of a particular group of animals. This implies that the rate of response in a continuing program equaled the ratio of mean selection differentials to the mean age of the parents when their selected progeny was born. Thus the generation interval is another factor determined by the breeding system. Yearly genetic gain in males and females in generation t can be predicted by using the appropriate portions of equation [1.2]. This equation has been used to predict and discriminate among breeding programs to fetch the highest genetic responses. Various modifications of [1.2] have been developed by BICHARD4), BICHARD *et al.*5) BRASCAMP7,8,10), DUCROCQ and QUAAS23), HILL40), HUNT *et al.*54), MEUWISSEN68), MORLEY69), SEARLE84), SHIMIZU and GHAFFAR88), SKJERVOLD89), SKJERVOLD and LAuGHOLZ90), SPECHT and McGILLIARD96) and VAN VLECK99) to balance the conflicting pressure for greater selection intensity, more accurate estimation of breeding values and shorter generation intervals or sometimes in a different contexts.

3) Superiority of new born progeny

A third equation can be used to predict short-term gain which appears from the fact that new born progeny will receive a sample one-half of genes from both parents. Thus the expected superiority from selected parents above that of randomly mating at particular generation (*t*) is

$$g(t+1)=\frac{\Delta g_m(t)+\Delta g_f(t)}{2} \qquad [1.3]$$

where, Δg_m and Δg_f is computed from [1.1a] and [1.1b], respectively. If actual predicted genetic values of the sires and dams are available then those can be substituted into the above equation to predict genetic merits of the progeny.

3. Truncation selection across age classes

One of the difficulties in selecting animals in a population with overlapping generations is in comparing the progeny from different parental age classes. If the population is improving, the younger animals (the results of several selections) are expected to be superior and, consequently, the progeny from the parents with younger ages would be superior to those from older. This is true on an average, however, individual progeny may be found better or worse from parents both of older or younger ages due to Mendelian inheritance. The superiority depends on the genetic gain being made in the population. Therefore, computation of genetic selection differential is not as straight forward in the overlapping generation model as is often assumed. BICHARD *et al.*[5] have shown that younger parents in the population are the results of more years of selection and thus are expected to have higher breeding values. So if the optimum selection scheme is being practiced the parental age distribution may depart considerably from that based on assumption of genetically homogenous parental age groups, an assumption made in deriving above three expressions. BICHARD *et al.*[5] reported that assumption to derive [1.2] was 'the different parents within each age class and sex group have equal opportunity to produce offspring' but, in fact, they assumed that parents of each age group leave equal proportions of selected offspring. HILL[40] commented that classical theory (equations [1.1a, b] and [1.2]) enables prediction of the rate of genetic response when the same selection scheme is practiced for many generations. However, when generations overlap the genetic improvement in the selected group of animals in one year is not immediately passed through the population as it is if the generations are discrete. He quoted an example that in a dairy cattle population selected bulls may only be used for a year or two, yet some of their progeny live for 10 years or more. Thus the effect of single cycle of selection on the performance of following generations is erratic for many years after the selection practiced as HILL[39] and HINKS[43] pointed out. Therefore, the rate of response predicted by the classical theory is reached only asymptotically. Alternative methods of computing the progress each year as a result of selection in a population with overlapping generations have been given by HILL[39,40,41], HINKS[42,43,44,45], SEARLE[84] and Van VLECK[99]. HILL[40,41] presented a formal method using simple matrix operation to predict the selection response with overlapping generations which has several applications. His method gives an insight into the genetic structure of a population with overlapping generations and enables prediction of short- and long-term response. The method relates the long term responses to asymptotic rate and provides a simple method to compute the genetic lag[4,36)] of improvement from nucleus to commercial stock. It also allows the computation of monetary returns from different breeding strategies. However, this method essentially does not account for the selection among parental age classes. OLLIVIER[72)] formalized a method to compute the optimum replacement rates and concluded that the more prolific the species, the more rapidly the generation should be turned over and this turn over should be faster in males.

JAMES[57)] and MEUWISSEN[68)] criticized that HILL's gene flow model[40)] is not suitable for predicting the responses to selection with optimal age structure of parents, because the age structure is a fixed input parameter of this model. This leads to the necessity to investigate and present a simple algorithm to optimize the selection across the age classes which could be used for genetic appraisal of different breeding systems. Moreover, in all previously known methods, the truncation was at common point across the age classes. There is no published report indicating the consequences of truncation at each age-specific point with same average genetic superiorities of selected animals across the age classes.

4. Objectives

The main aim of this investigation was to establish an algorithm to evaluate the optimized alternative breeding systems for short- and long-term genetic improvement.

The subobjectives include i) to explore the consequences of truncation selection across the age classes at same average genetic superiority of selected animals, ii) to compare this new algorithm with the existing algorithms to optimize selection across the age classes and/or populations.

The plan of this study was as follows:

1) investigation of the biases in age structures due to non-optimum selection across the age classes in a population with overlapping generations,
2) development of an algorithm to optimize the age and/or population structures and genetic responses,
3) verification of the developed algorithm by computer simulation,
4) implications of the developed algorithm and
5) comparison of the developed algorithm with gene flow model devised by HILL[40,41)] and BRASCAMP[10)].

CHAPTER II

Prediction of possible biases in parental age structures ascribed to non-optimized across-age classes selection in a population with overlapping generations

A. INTRODUCTION

In planning and evaluating breeding schemes, the comparison of predicted genetic responses to different selection procedures constitutes a compulsory approach. The asymptotic genetic progress achieved through selection is inversely proportional to the generation interval[73]. The generation interval can be optimized by selecting animals with highest breeding values irrespective of their ages and accuracy of selection[41,58,68]. The genes from a specified breeding stock are transmitted to later generations through the stock selected as parents of the next generation and not through the candidates or merely the census numbers. This leads to the expectation that there should be some differences in gene flow between those based on the age structure of parents at mating time and on the number of their progeny actually contributing to the next generation, when an age structure of parents is far from an optimum.

The objective of this chapter was to estimate the bias explicitly between assumed (at mating) and actual (number of progeny selected to be parents of the next generation) parental age structure by computer simulation. The influence of various factors such as genetic trends, accuracy of selection, selection intensity and population size on the bias in parental age structure (generation interval) were also investigated.

B. MATERIALS AND METHODS

1. Assumptions

The four pathways of inheritance of genes from generation to generation in a cattle population are sires to breed bulls, sires to breed cows, dams to breed bulls and dams to breed cows[73] as shown in Fig. 2.1. The selection was performed in the first 3 paths, nevertheless, maternal grand dams of bulls were also selected. The 6 paths of selection were settled to ponder the selection of parents and progeny as:

(1) paternal grandsires of bulls : pathways in two consecutive generations as illustrated in Fig. 2.1 termed as 1 to 1,
(2) paternal grandsires of cows : pathways in two consecutive generations as illustrated in Fig. 2.1 termed as 1 to 2,
(3) maternal grand sires of bulls: pathways in two consecutive generations as illustrated in Fig. 2.1 termed as 2 to 3,

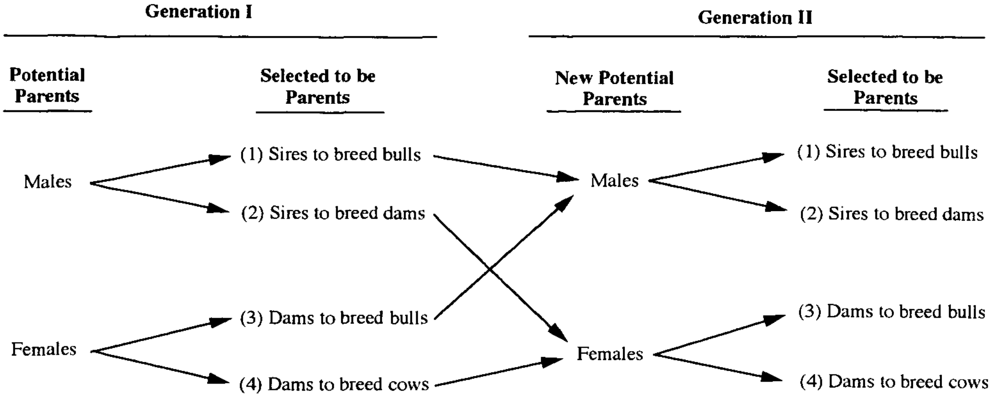


Fig. 2.1. Illustration of four pathways of gene transmission from one generation to the next generation.

(4) paternal grand dams of bulls : pathways in two consecutive generations as illustrated in Fig. 2.1 termed as 3 to 1,
(5) paternal grand dams of cows : pathways in two consecutive generations as illustrated in Fig. 2.1 termed as 3 to 2,
(6) maternal grand dams of bulls : pathways in two consecutive generations as illustrated in Fig. 2.1 termed as 4 to 3.

The age of proven bulls was assumed to be 5 years and the germ-plasm of all tested bulls were then stocked for two years. The stayability of cows among age classes was assumed to be 0.8. The breeding stock were selected among contemporary mates only once and the proportions of parents among age classes at mating were evenly distributed for sires and decreased for dams according to their survival probabilities, defined as the assumed age structure. The breeding stock were used for two [selection path numbers; (1), (2), (3)] and three [(4), (5)] or six [(6)] years as sires and dams, respectively. Two hundred young bulls were produced by mating the best 6 bulls with 1,000 selected dams, and out of these 200 young bulls the 3 best tested bulls were selected as sires of bulls and the 30 best bulls for AI service, to produce the female replacements every year. The total number of candidates across age classes for dams of bulls aged 4 to 9 years, were assumed to be 8,000 tested cows. One thousand cows were selected from these candidates to be mated to produce 200 young bulls (five cows for one young bull). It was, therefore, necessary for the 2,168 candidates and 271 selected dams of bulls every year to be kept till the age of 4 year.

The main factors affecting the bias considered were accuracy of selection (r), (4 levels; 0.3, 0.5, 0.7, 0.9) and genetic differences among age classes (7 levels; 0.0, 0.05, 0.10, 0.15, 0.20, 0.25, 0.30 genetic standard deviation units). The effects of sizes of candidates (5 levels; 6,504, 4,336, 2,168, 1,088 and 544 heads keeping the selected proportion 0.125) and the rate of selection (4 levels; 0.1, 0.125, 0.25, 0.50 keeping the base population 2,168 heads) on the bias were also investigated on the path of maternal granddams of bulls [(6)] with genetic difference of 0.20 and selection accuracy of 0.5.

2. Generation of base population and selection

The population of parents within age classes and the progeny produced from each age class of parents were generated by the following model:

$$X_{ij}=m_i+a_{ij}+e_{ij},$$

where X_{ij} refers to the performance of jth parent in ith age class or jth progeny from ith parental age, m_i to the average genetic merits of ith age class (the means of progeny from the ith parental age class were defined as half of the averaged genetic merits of parents selected from ith age class), a_{ij} to breeding value within the age class and it is assumed to be normally distributed with N(0, 1.0), and e_{ij} to environmental deviation and normally distributed with N(0, $(1-r^2)/r^2$).

The generated parents were ranked and selected according to their performance within the age classes. The proportions of selected parents were identical to their distribution in the base population. The generated offspring from these selected parents were ranked according to their performance and the top most offspring, irrespective of their parental ages, were selected as parents of next generation. The selected animals were classified according to their parental ages and the selected proportions across the ages were used to calculate actual age structure (generation interval). The differences between the assumed and actual age structures for each path were considered as the bias in their respective paths.

The records of both parents and progeny performance for each path with combination of all factors were simulated 20 times and averages and their variances over the replicates were calculated. The multiple linear regression analyses, including the standard error of estimates, for all considered paths were carried out to investigate the relative importance of variable factors on the variation of actual average age of parents.

C. RESULTS

The tendency and variation in deviation of actual average ages of parents from assumed values ascribed to the selection of their progeny is presented in Figs. 2.2 through 2.7 by paths of selection. It is obvious from Figs. 2.2 through 2.7 and negative coefficients of partial regression (Table 2.1) that the downward bias became larger on augmenting the genetic differences among age classes. The accuracy of selection was less important in affecting the bias estimation. Nevertheless, the magnitude of deviation was within the ranges of sampling error

Table 2.1. Partial and standardized linear regression coefficients of generation interval (Y) on genetic trend (X1) and accuracy of selection (X2) in different pathways of genetic improvement including the standard error (SE) of Y.

Path numbers	Regression	by1.2	SE	by2.1	SE
(1)	Partial	−0.180	0.450	0.046	0.201
	Standard	−0.080	0.199	0.045	0.199
(2)	Partial	−0.077	0.199	−0.053	0.089
	Standard	−0.077	0.198	−0.118	0.198
(3)	Partial	−0.058	0.172	−0.051	0.077
	Standard	−0.067	0.198	−0.132	0.198
(4)	Partial	−0.382	0.612	−0.029	0.274
	Standard	−0.124	0.198	−0.021	0.198
(5)	Partial	−0.370	0.274	−0.043	0.123
	Standard	−0.260	0.193	−0.068	0.193
(6)	Partial	−1.375**	0.544	−0.551*	0.237
	Standard	−0.415	0.164	−0.382	0.164

by1.2 Partial regression coefficient of Y on X1 for fixed X2.
by2.1 Partial regression coefficient of Y on X2 for fixed X1.
* Significant $P < 0.05$.
** Significant $P < 0.01$.

except for the path (6) (Fig. 2.7), therefore, the bias on paths (1) through (5) (Figs. 2.2 through 2.6) need not be pondered strictly.

Path (2) had smaller sampling variation in the average ages of selected parents (Fig. 2.3) compared to path (1) (Fig. 2.2), ascribed to the higher number of selected progeny in the former path than in the latter (30 vs 6) in spite of the same parents. Comparing the trends between path (2) and path (5) (Figs. 2.3 and 2.6), it was revealed that a downward trend of bias in path (5) was more obvious than that in path (2), though the reduction in both paths was statistically non-significant. The variation between these two paths attributed to higher number of the selected dams compared to sires (200 vs 30). The biases in paths (3) and (4) were similar to path (2) and path (1), respectively, as shown in Fig. 2.4 and Fig. 2. 5.

A dwindling trend on the selection path (6) in the actual average ages was manifested by augmenting the genetic differences among age classes and increasing the accuracy of selection with additive effects (Fig. 2.7). While the deviation was less than double standard error at the low accuracy of selection, 0.3, the actual average ages dwindled more significantly at the modicum genetic differences with augmenting the accuracy of selection.

Consequent to the significant downward bias in path (6), the age structure for dams to breed cows path should be perceived in two sub-paths considering two consecutive generations:

i) dams to breed cows (maternal granddams to breed dams) in the first

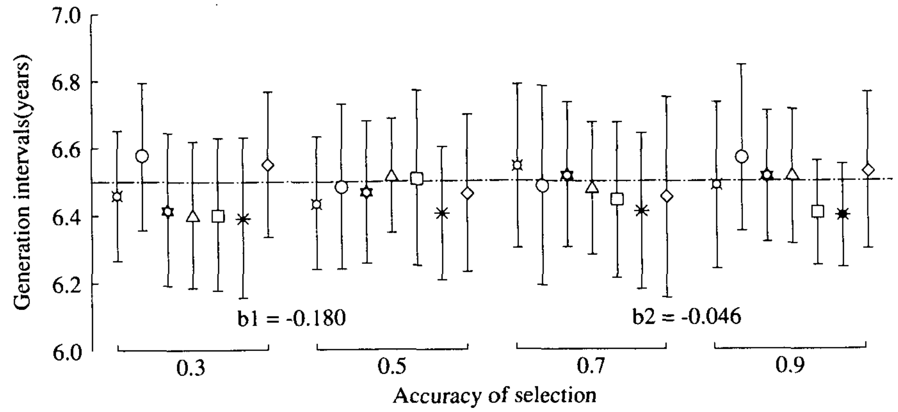


Fig. 2.2. Bias in parental average age structures for paternal grand sires of bulls. Assumed genetic differences : ¤ ; 0.0, ; ○ ; 0.05, ✡ ; 0.10, △ ; 0.15, □ ; 0.20, ✱ ; 0.25, ◇ ; 0.30.
Assumed average ages of parents : —— · ——
bl : Partial regression coefficient of generation interval on genetic differences. b2 : Partial regression coefficient of generation interval on accuracy of selection.

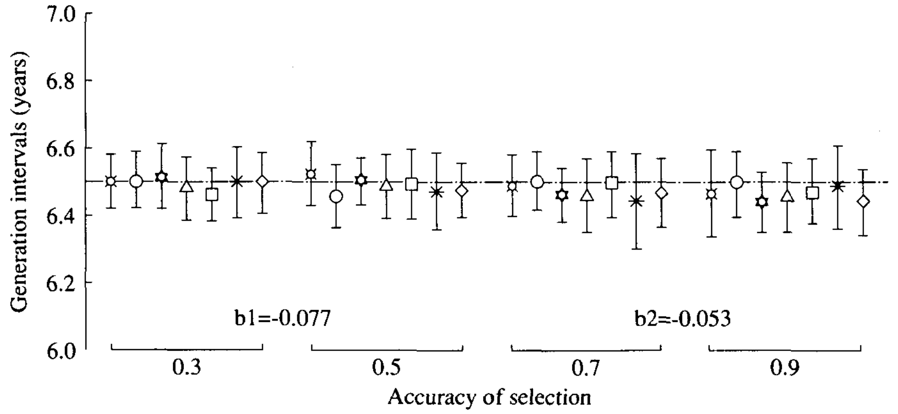


Fig. 2.3. Bias in parental average age structures for paternal grand sires of cows. Assumed genetic differences : ¤ ; 0.0, ○ ; 0.05, ✡ ; 0.10, △ ; 0.15, □ ; 0.20, ✱ ; 0.25, ◇ ; 0.30.
Assumed average ages of parents : —— · ——
bl : Partial regression coefficient of generation interval on genetic differences. b2 : Partial regression coefficient of generation interval on accuracy of selection.

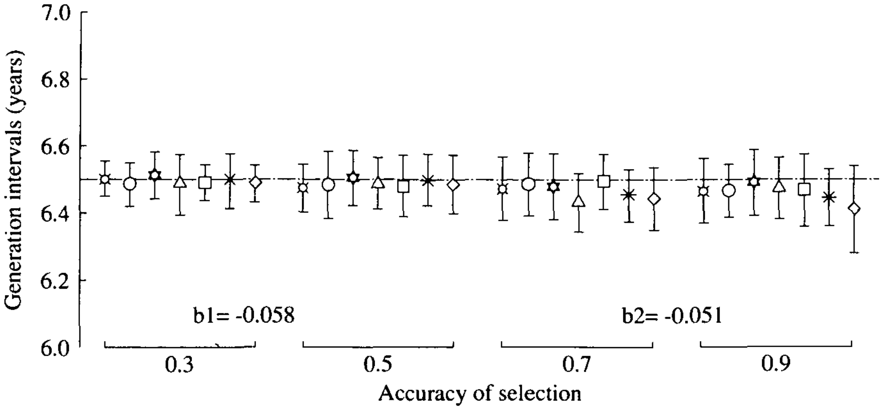


Fig. 2.4. Bias in parental average age structures for maternal grand sires of bulles. Assumed genetic differences : ¤ ; 0.0, ○ ; 0.05, ✡ ; 0.10, △ ; 0.15, □ ; 0.20, ✱ ; 0.25, ◇ ; 0.30.
Assumed average ages of parents : —— · ——
bl : Partial regression coefficient of generation interval on genetic differences. b2 : Partial regression coefficient of generation interval on accuracy of selection.

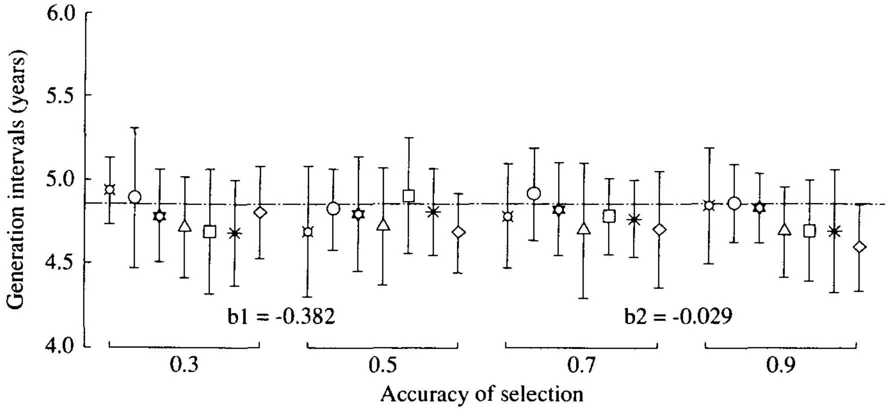


Fig. 2.5. Bias in parental average age structures for paternal grand dams of bulles. Assumed genetic differences : ¤ ; 0.0, ○ ; 0.05, ✡ ; 0.10, △ ; 0.15, □ ; 0.20, ✱ ; 0.25, ◇ ; 0.30.
Assumed average ages of parents : —— · ——
bl : Partial regression coefficient of generation interval on genetic differences. b2 : Partial regression coefficient of generation interval on accuracy of selection.

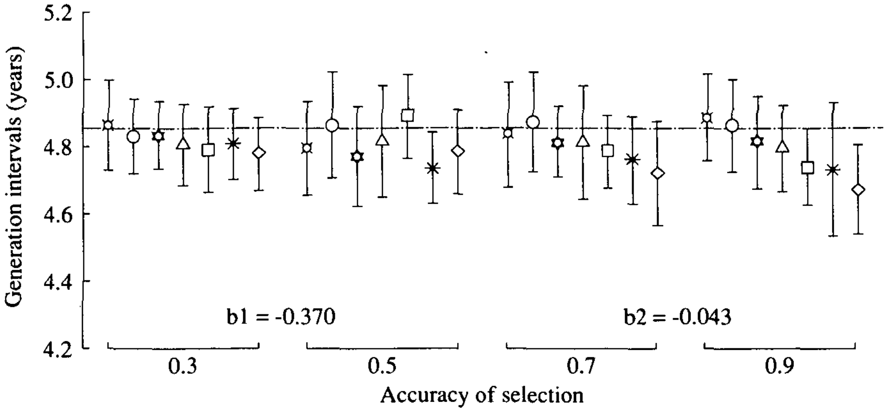


Fig. 2.6. Bias in parental average age structures for paternal grand dams of cows. Assumed genetic differences : ¤ ; 0.0, ○ ; 0.05, ✡ ; 0.10, △ ; 0.15, □ ; 0.20, ✳ ; 0.25, ◇ ; 0.30.
Assumed average ages of parents : —— · ——
b1 : Partial regression coefficient of generation interval on genetic differences. b2 : Partial regression coefficient of generation interval on accuracy of selection.

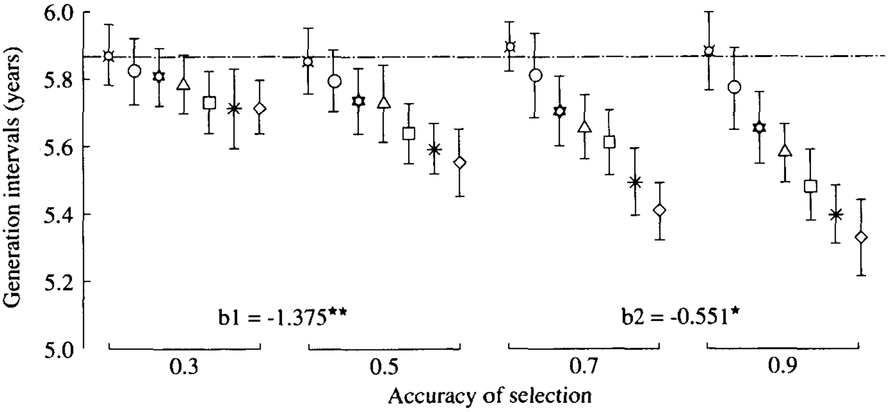


Fig. 2.7. Bias in parental average age structures for maternal grand dams of bulles. Assumed genetic differences : ¤ ; 0.0, ○ ; 0.05, ✡ ; 0.10, △ ; 0.15, □ ; 0.20, ✳ ; 0.25, ◇ ; 0.30.
Assumed average ages of parents : —— · ——
b1 : Partial regression coefficient of generation interval on genetic differences. b2 : Partial regression coefficient of generation interval on accuracy of selection.
$^{**}P<0.01$. $^{*}P<0.05$.

generation (4 to 4 in Fig. 2.1) and

ii) dams to breed cows or dams to breed bulls in the second generation (4 to 4 or 4 to 3 in Fig. 2.1, respectively).

For the first sub-path, (4 to 4), maternal granddams to breed daughters, the replacement heifers (daughters) at the second generation are randomly sampled among age classes or selected with very low selection intensity, hence, the bias in parental age structure would be negligible. For the second sub-path (4 to 3 in Fig. 2.1), maternal granddams to breed sons, the dams of bulls at the second generation would be selected with comparatively higher selection intensity among age classes, hence, the bias in age structure for this sub-path would be manifested as shown in Fig. 2.7 if the selection in first generation is not optimal among multiple age classes of parents.

The multiple linear regression analyses was carried out to estimate the effect of genetic gain and accuracy of selection on the age structures of the parents (generation interval). The partial regression coefficients were standardized to compare the relative importance of two independent variables, genetic trend and accuracy of selection. The results suggested that genetic differences among age classes in paths (1), (2), and (3) were 1.78, 0.65 and 0.51 times more important in reducing the generation interval than accuracy of selection, respectively, when candidate bulls were equally distributed among age classes. On the path numbers (4), (5), and (6) the genetic differences were 5.99, 3.82 and 1.09 times more important in reducing the generation intervals than accuracy of selection, respectively. The multiple correlation coefficient for the path (6) was 0.572, statistically significant at the probability of 0.05 indicating the combined effect of independent variables in influencing the generation interval. This was the only path revealing the bias in parental age structures (Fig. 2.7). For the path numbers (1), (2), (3), (4) and (5) the multiple correlation coefficients, respectively, were 0.092, 0.141, 0.148, 0.126, 0.269. All these correlations were non-significant which indicated the non-significant combined association of independent variables in affecting the generation intervals. The partial regression coefficients computed for each pathway of gene transmission considered in this study envisaged non-significant trends of biases on these paths with increasing the both variables except the path (6).

The difference in the size of candidates (544 to 6,504) had no significant systematic effects on the deviation from parental generation interval. The decreasing rate of selection (0.50 to 0.10) tended to cause the deviation to be large but its effect was statistically non-significant (Table 2.2). However, smaller size of candidates and intensive selection resulted in larger error of estimate associated with the small number of selected animals.

It was concluded that when the candidates were less in number as two hundreds and the selected animals were also few as tens, the bias in parental age structure would be unimportant. Nevertheless, when the number of candidates

Table 2.2. Effect of size of candidates and rate of selection (fraction selected) on the average ages of selected parents on the path of maternal grand dams considering genetic differences 0.20 and accuracy of selection 0.50.

Total number		Average ages (Years)			Percent decrease
Candidates	Selected	Assumed	Actual	SE	
A) Sizes of candidates (keeping the fraction selected 0.125)					
6,504	813	5.87	5.663	0.029	3.49
4,336	542	5.87	5.634	0.033	3.99
2,168	271	5.87	5.641	0.053	3.88
1,088	136	5.87	6.677	0.084	3.26
544	68	5.87	5.679	0.110	3.22
B) Rate of selection (keeping sizes of candidates 2,168)					
2,168	217	5.87	5.673	0.042	3.32
2,168	271	5.87	5.650	0.061	3.72
2,168	542	5.87	5.699	0.051	2.88
2,168	1,084	5.87	5.760	0.028	1.85

and selected animals are in thousands (maternal granddams of bulls) the bias would be important in breeding schemes.

D. DISCUSSION

Hill[40)] and Elsen and Mocquot[25)] independently developed the formal method, based on the probability transition matrix theory, to predict the genetic responses and discounted returns from improvement in a population with overlapping generations with fixed age structures of parents. Meuwissen[68)] criticized that the gene flow model was not suitable for predicting the responses to selection with optimal age structure of parents, because the age structure is a fixed input parameter of this model. This model is useful to compare the breeding schemes with fixed generation interval. Jeon and Smith[59)] used this model with optimal age structure. In this chapter the bias between fixed (assumed) and optimal (actual) age structures of parents has been considered through computer simulation. The animals were selected once among the contemporary groups to be the parents of next generation. The genetic differences among the two successive parental age classes were assumed to be constant, where as in the practical animal breeding this rarely occurs since the different proportions of different age classes are allowed to leave the progeny in the population. This fact was ignored for simplicity.

Assuming an average milk yield, the coefficient of variation and heritability of milk yield, respectively, to be 7,500 kg, 0.20, and 0.25, the genetic standard deviation accrue 750 kg. Tsuruta *et al.*[98)] reported that the genetic improvement of milk yield in Hokkaido dairy cow population was 88.1 kg (0.12 genetic standard deviation, a quantity where the bias in age structure was more than double standard error at the accuracy of 0.7 or a higher value) per year from 1981 through 1986. When the cows' genetic abilities are evaluated merely on their first lactation records the bias in their parental age structure would not be important. Nevertheless, when the cows' genetic abilities are evaluated through animal model (BLUP) with all available information, the accuracy of selection would be increased[83] and consequently, the yearly genetic improvement would be enhanced. In such situations the bias in parental age structure may introduce significant differences in the expected genetic improvement based on the non-optimized parental age structure.

The highest bias was observed in the path where a comparatively larger number of offspring were selected to be the parents of the next generation and the service length was more than 3 years.

Generation interval in selection programs can be optimized by selecting the animals with the highest breeding values, neglecting their ages[41,51,58]. When the age structure of parents is not optimal, the expected gene flow could be different from the actual gene flow because of differences in the number of progeny selected to be parents of the next generation from each parent as shown in this computer simulation.

E. SUMMARY

Computer simulation was carried out to investigate the bias in prediction of generation interval in the gene flow model. Three pathways of genetic improvement sires to breed bulls, sires to breed cows, dams to breed bulls were considered. The effects of 7 levels (0.0 to 0.30 by 0.05 genetic standard deviation units) of genetic differences among age classes, 4 levels (0.3, 0.5, 0.7, 0.9) of accuracy of selection, 4 levels of population sizes and 4 levels of rate of selection were studied. Simulation was performed 20 times for each combination of parameters. The actual generation interval was shortened on the sires' path, but this was within the ranges of standard error dictating the non-significance of the biases. On dams' path the bias was significant at $P<0.01$ when the genetic difference among age classes increases from 0.05 genetic standard deviation units and accuracy was higher than 0.5. The partial regression coefficients were standardized to envisage the relative importance of genetic differences across the age classes and accuracy of selection, two independent variables. The results suggested that genetic differences among age classes on paths (1), (2), and (3) were, respectively, 1.78, 0.65 and 0.51 times more important in reducing the generation interval than accuracy of selection, when candidate bulls were equally distributed among age classes. On the path numbers (6), (5), and (4) this relative importance was 1.09, 3.82 and 5.99 times, respectively, at the stayability of 0.80 across the age classes. Population size at fixed rate of selection had no direct effect on bias estimation,

while rate of selection had an effect on the bias of generation interval but within the ranges of double standard error.

CHAPTER III

Theoretical and mathematical development to optimize selection across age classes in a population with overlapping generations

A. INTRODUCTION

In a livestock population with overlapping generations, the optimum breeding policy is based on the best combination of selected proportions within and/or across age classes. Selection between age classes affects the age structure of parents which determines the generation interval and reflects on the rate of genetic improvement. HILL[40,41] and Elsen and MOCQUOT[25] developed independently a formal matrix method to predict and compare the genetic responses to selection for the short and long term improvement breeding plans with fixed age structure of parents in a population with overlapping generations and sub-groups. HOPKINS and JAMES[51,53] demonstrated the recurrence relationship to relate the breeding values of age-sex classes from different time periods which imply the effect of age structure, initial genetic differences between age groups. It has been pointed out that the methods are not suitable for predicting the response to selection with optimal generation intervals[68] since the generation interval is a fixed input parameter of these models. An optimum age structure is required to construct an optimum breeding plan. Bichard *et al.*[5] considered the fact that when genetic gains are being made in a population where generations overlap, progeny of younger parents will on an average be genetically superior to progeny of older parents. Further, the rate of gain can be increased by making allowance for genetic effects of parental age. They concluded this while comparing the following three selection criteria: 1) selection on the deviation from the means of each parental age class, 2) common truncation point on phenotypic values, and 3) the truncation point at same predicted breeding value. They found the truncation point(s) by trial and error using the Table of Probits[29]. However, they did not present the systematic methodology which could be combined in a computing program. DUCROCQ and QUAAS[23] presented an algorithm for determining the common truncation point on the distributions of genetic evaluations of candidates following the optimal rule proposed by BICHARD *et al.*[5] using the Newton's method of iteration[18].

The main objectives of this chapter are (i) to generalize their algorithm which could be used to calculate the common truncation point and/or each age-specific point at the same predicted genetic values on the distribution of phenotypic values of candidates for selection among multiple age classes and (ii) to suggest a new algorithm for truncation selection across the age classes. This new algorithm takes into account the distribution of selected parents from various age classes.

B. MATERIALS AND METHODS

1. Methods of selection

Four selection schemes (SSs), differentiated by the base of truncation selection point(s), on phenotypic values, among age classes, were settled including the three methods of BICHARD *et al.*(5) as:

(1) selection within each age class at same proportions as the distribution of candidates across the age classes: SS1,
(2) selection at the common truncation point based on phenotypic values across the age classes: SS2,
(3) selection at each age-specific truncation point with the same predicted genetic values across the age classes: SS3, and
(4) selection at each age-specific truncation point with the same average predicted genetic values of selected parents across the age classes: SS4.

2. General assumptions, formulae and definitions

A very common assumption is that the records and genetic values follow a multivariate normal distribution. This assumption allows use of normal theory in predicting genetic gain from selection. Another, although less tenable assumption, is that both genetic variation and normality are maintained through several generations.

Average genetic superiority of the selected parents over the candidates for selection is expressed as:

$$\varDelta g = I.\ r.\ \sigma_a \qquad [3.1],$$

where r refers to accuracy of selection, σ_a to genetic standard deviation and I to selection intensity. Under the assumption of normal distribution (N(0, σ^2))

$$I = f(k)/F(k) \qquad [3.2],$$

where, $f(k)$ refers to the density function of k in a normal distribution:

$$f(k) = \exp[-k^2/2\sigma^2)]/(\sqrt{2\pi}\sigma) \qquad [3.3].$$

$F(k)$ refers to cumulative distribution function in a normal distribution:

$$F(k) = \int_k^{\infty} f(k)dx \qquad [3.4].$$

The equations [3.2] through [3.4] can be converted to standard normal distribution by dividing with the appropriate standard deviation of the distribution to be considered in numerical analysis.

m_i is the mean genetic merit of ith age group of candidates.

P is the overall selected proportion of all potential parents. This is computed by dividing total number selected as parents by total number of the candidates. This is an input parameter.

p_i is the proportion of animals selected from ith age group. This is used to calculate the weighted averages of selection differentials and average ages of selected animals. This describes the age structure of parents. The generation length for a particular path (e.g. sires to breed cows, SC) of gene transmission computed as:

$$L_{SC}=\sum_i (i+1).\ p_i \qquad [3.5].$$

G is the average within-group (genetic) selection differentials of selected parents

$$G=\sum_i p_i.\ \Delta g_i \qquad [3.6].$$

q_i is the relative size of candidates of ith age group. This is a fraction and describes age distribution of candidates. This sums up to unity. This accounts for the change in size of candidate groups over time e.g. mortality and whether or not animals of ith age group can be parents. This is also dependent on when selection decision is taken. qi is considered at the time of selection of animals and, consequently, the generation lengths were computed by adding one year to their calculated weighted average ages using [3.5]. This is an input parameter.

r_i is the accuracy of selection in ith age group. This is assumed to be same for all animals in an age group. This is an input parameter.

K_i is the truncation point to select the top out of candidates within age group. This may be common across the age classes or different among age classes depending upon the aggregate genotype. Calculation of K_i is the first step to apply the truncation selection across or within the age groups.

3. Computing the truncation point(s) and genetic superiorities

If a genetic trend exists in the population with overlapping generations and the accuracy of selection increases as a candidate gets older, animals of different age classes come from the distribution with different means and variances. Culling of animals from one year to the next year is not allowed except for the accidental reasons, to assure the normal distribution. Selection is usually performed by truncation (selection performed by keeping only those animals whose values are above a given threshold) within or across age classes. Truncation point(s) may be unique over all age classes or different among age classes depending upon the selection policy. The unit of measurements, genetic standard deviation, was assumed to be constant over all age classes. Additive genetic values, their selection index predictors and phenotypic values are normally distributed with N(m_i, 1), N(m_i, r_i^2) and N(m_i, $1/r_i^2$) in the i-th age class, respectively.

1) Selection scheme 1

For SS1, the proportions of selected parents were identical to the distribution of candidates among age classes hence the truncation is within the age classes with the given proportion to be selected. Consequently, the truncation point for the ith age class, K_i, given p_i can be found by the formula given in the mathematical handbook edited by ABRAMOVITZ and SEGUN[1)] and in the Statistical Tables with Computer Applications[2)]. The approximation for percentage points of the normal distribution described by HASTINGS *et al.*[37)] is used as function program. According to HASTINGS *et al.*[37)]

$$U(Q) = \frac{C_0 + C_1^z + C_2^{z^2}}{1 + d_1^z + d_2^{z^2} + d_3^{z^3}}, \ (0 < Q \leq 0.5),$$

where,

$U(Q)$ = percentage point of normal distribution at a given proportion Q

Z = square root of the natural log of the reciprocal of squared Q, given proportion,

$$Z = \sqrt{\ln(1/Q^2)},$$

$C_0 = 2.515517$ $\quad d_1 = 1.432788$

$C_1 = 0.802853$ $\quad d_2 = 0.189269$

$C_2 = 0.010328$ $\quad d_3 = 0.001308.$

The absolute error in this approximation is less than 0.00045. Selection intensity was adjusted for small numbers according to BURROWS[11)] as follows:

$$I_a = I_\infty - \frac{(N-n)}{2n(N+1)I_\infty}$$

where I_a, N and n, respectively, refers to the adjusted intensity of selection, population size (candidates) and number of selected animals within age class. The genetic superiority of selected animals within age class was computed by [3.1] and then deviated from the youngest age class. The average ages and average selection differential for each pathway were computed using [3.5] and [3.6], respectively.

2) Selection scheme 2

When parents are selected at the common truncation point K, on phenotypic values, the overall selected proportion (P) is

$$P = \sum_i q_i F[(K - m_i)r_i] \qquad [3.7].$$

DUCROCQ and QUAAS[23)] solved this nonlinear equation iteratively for K using the Newton's method[18] of iteration as described below using my own terminology. The deviation of calculated proportion from a given proportion (P^*) is

$$d(K) = P - P^* \qquad [3.8].$$

To get K such that $d(K) = 0$, start with some prior value K_0, e.g. K_0 = means of the youngest age class, and iterate on:

$$K_{n+1} = K_n - d(K_n)/d'(K_n) \qquad [3.9],$$

where

$$d'(K_n) = -\sum_i g_i r_i f[K_n - m_i r_i] \qquad [3.10].$$

Once K is obtained, other relevant quantities are calculated subsequently. The proportion of the parents selected from the i-th age class (p_i) to the overall total number of selected parents is

$$p_i = (q_i/p^*) F[(K - m_i) r_i] \qquad [3.11].$$

Average genetic superiority of the parents (Δg) selected across age classes as the deviation from the mean of the youngest age (m_c: subscript c refer to the youngest age class, to keep similarity to calculus where c means current estimate of a derivative) is

$$\Delta g = \sum_i p_i \{r_i f[(K - m_i) r_i]/F[(K - m_i) r_i] + m_i - m_c\} \qquad [3.12].$$

In this case, truncation point is common to all ageclasses. The average ages and average selection differential for each pathway are computed using [3.5] and [3.6], respectively.

3) Selection scheme 3

Assuming the highest genetic means for the youngest age class and the truncation point for this class as Kc on phenotypic values (Fig. 3.1), then, to equate the genetic values of animals in the youngest age class with the genetic values at the truncation point (K_i) in the i-th age class, we must add genetic gap $[(K_c - m_i) r_i^2]$ to the ith age class mean. The truncation point (K_i) where animals in the ith age class should have the same genetic values as animals at K_c in the youngest age is

$$K_i = [(m_c - m_i) + (K_c - m_c) r_c^2 + m_i r_i^2]/r_i \qquad [3.13]$$

When the accuracy of selection is same among age classes ($r_c = r_i$) marginal deviation ($K_i - K_c$) at the same predicted genetic values is

$$K_c - K_i = (m_i - m_c)(1 - r_c^2)/r_c^2$$

which coincided with equation (2) of BICHARD *et al.*[5].

The equations [3.7] through [3.12] are modified by transferring K to the truncation point for each age class (K_i) as:

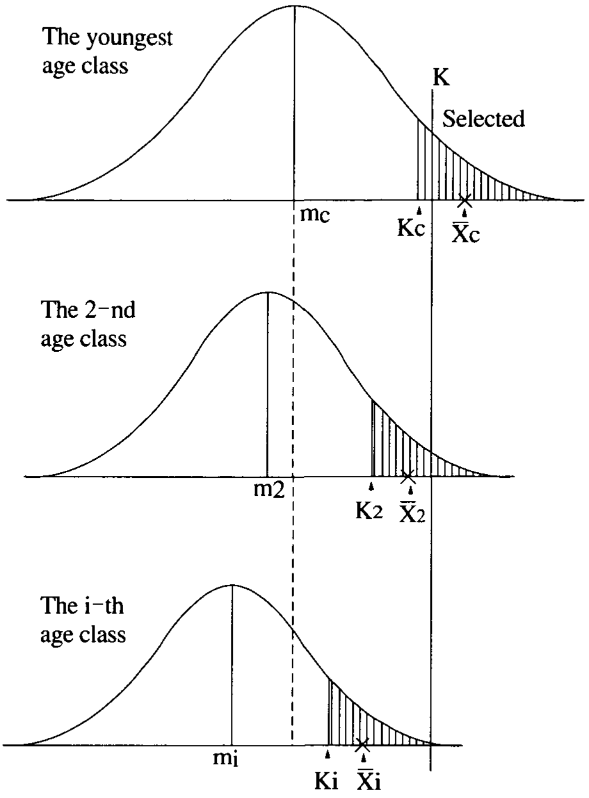


Fig. 3.1. Illustration of the symbols and distribution of different parental age classes with overlapping generations. m = genetic means, K = truncation point, x = means of selected parent.

$$P = \sum_i q_i F[(K_i - m_i) r_i] \qquad [3.7.1]$$

$$h(K) = P - P^* \qquad [3.8.1]$$

To get K_c such that $h(K)=0$, start with some priorvalue $K_{c,0}$, $K_{c.0}$=means of the youngest age class, and iterate on:

$$K_{c.n+1} = K_{c.n} - h(K_n)/h'(K_n) \qquad [3.9.1]$$

$$h'(K_n) = -\Sigma q_i r_i f[(K_{i.n} - m_i) r_i] \qquad [3.10.1]$$

$$p_i = (q_i/P^*) F[(K_i - m_i) r_i] \qquad [3.11.1].$$

$$\Delta g = \sum_i p_i \{ r_i f[(K_i - m_i)]/F[(K_i - m_i) r_i] + m_i - m_c] \qquad [3.12.1].$$

At the outset of iterations, allocate mean of the youngest age class to Kc in equation [3.13]. Use this in combination with equations [3.8.1] through [3.10.1] to compute K_c such that $h(K)=0$, {the difference between the given and selected proportion (computed using [3.7.1]) across the age classes is zero}. Therefore, K_i is computed using [3.13]. The average ages and average selection differential can be computed for each pathway using [3.5] and [3.6], respectively.

For SS3 the truncation is on the distribution of phenotypic values with the condition of same estimated breeding value at each age-specific truncation point in [3.13]. If selection index predictors are available and their distributions are normal with mean m_i and variances r_i^2 then

$$K'_i = K'_c = K'$$

thus

$$P = \sum_i q_i F[K' - m_i)/r_i] \qquad [3.7.2]$$

$$h'(K'_n) = -\sum_i q_i f[(K'_n - m_i)/r_i]/r_i \qquad [3.10.2]$$

$$p_i = (q_i/P_*)\, F[(K' - m_i)/r_i] \qquad [3.11.2]$$

$$\Delta g = \sum_i p_i r_i f[(K' - m_i/r_i]/F[(K' - m_i)/r_i] + m_i - m_c\} \qquad [3.12.2].$$

These equations are the same as [3.7], [3.10], [3.11], [3.12],respectively, if ri is replaced with $1/r_i$. The equations [3.7.2], [3.10.2], [3.11.2] and [3.12.2] are coincident with DUCROCQ and QUAAS's[23] equations for 'A', [8], [11], and[12], respectively.

4) Selection scheme 4

Again when the truncation point of selection for the youngest age class is K_c, the selection intensity (I_c) is calculated from equation [3.2]. The standardized selection differential (selection intensity (I_i*)) in which the average genetic value of selected parents in the ith age class is on the matching level of the average genetic value in the youngest age class, is

$$I_i^* = (m_c - m_i + r_c I_c)/r_i \qquad [3.14].$$

Tuncation point (K) with a given I^* can be computed using Newton's Method[18] of iteration. From equation [3.2],

$$I = f[(K - m)r]/F[(K - m)r] \qquad [3.15].$$

The deviation of calculated I from a given I^* is,

$$e(K) = I - I^* \qquad [3.16].$$

To get K such that $e(K) = 0$, start with some prior value K_0, e.g. $K_0 = 0$, and iterate on:

$$K_{n+1} = K_n - e(K_n)/e'(K_n) \qquad [3.17]$$

where,

$$e'(K_n) = I_n[I_n - (K_n - m)r], \qquad [3.18]$$

$e'(K_n)$ is the rate of change in I at K_n. The $e'(K_n)$ can be obtained by differentiating the equation [3.15] with a given K_n. Thus, the truncation point for each age class (K_i) for a given I_i^* based on K_c can be obtained such that $e(K)=0$ on a standard normal distribution. This calculated truncation point on unit standard deviation is transformed back to its original scale value of standard deviation by multiplying the standard deviation of the distribution under consideration. This is the outcome of inner iterations. Then this outcome of inner iteration is linked with the outer iterations to compute the optimum proportions across the age classes. These computations are performed by combining the equations [3.13] through [3.17] with [3.8.1] through [3.10.1] and asymptotically approximating K_c to the optimum value with the condition of equation [3.14], optimal truncation point for each age class can be obtained iteratively. Then the proportion selected across the age classes (p_i) and genetic superiority of selected animals are computed using [3.11.1] and [3.12.1], respectively.

If the truncation is on estimated breeding values or on selection index predictor and their distributions are normal with means m and variances r^2 then [3.15] and [3.18] should be modified as:

$$I=f[(K-m)/r]F(K-m)/r] \qquad [3.15.1]$$

$$e'(K_n)=I_n[I_n-(K_n-m)/r] \qquad [3.18.1]$$

The equations [3.14], [3.16] and [3.17], could be used without any alteration. Then with linking these equations with [3.7.2] through [3.12.2], the required quantities could be computed. The average ages and average selection differential for each pathway are computed using [3.5] and [3.6], respectively.

Two additional selection schemes SS5 and SS6 were considered to collate the selection schemes truncated on phenotypic values and estimated breeding values (or selection index predictors). Selection schemes 5 and 6 (SS5, SS6) were same as SS3 and SS4, respectively, but the truncation was on estimated breeding values instead of phenotypic values. For SS5 the truncation point and other relevant quantities were obtained using [3.7.2] through [3.12.2]. For SS6 the equations [3.15.1] and [3.18.1] along with [3.16] and [3.17] were combined with [3.7.2] through [3.12.2] to compute the truncation points and genetic superiorities for each pathway. The other quantities such as average ages and average genetic superiorities of selected parents from a group were computed in the same way as for SS3 and SS4 using [3.5] and [3.6], respectively.

Since the size of actual animal population is not infinite, actual selection intensity (I) in equations [3.12] and [3.12.1] or [3.12.2] should be recalculated according to BURROWS[11].

C. RESULTS

Since the path of dams of bulls has many age classes and older cows have higher accuracy of selection, the algorithms proposed were applied to this path to illustrate the goodness of its application. The main parameters used in this theoretical simulation are means of age classes before selection, accuracy of selection, total number of candidates and their distribution across the age classes as listed in the upper 4 lines of Table 3.1. A unique trait of interest for selection was assumed to be milk production. The genetic differences between consecutive age classes were assumed to be 0.1 genetic standard deviation (75 kg), based on the actual yearly improvement in dairy cattle population in Hokkaido for the path of dams of bulls[98)], considering phenotypic standard deviation of 1,500 kg and heritability of 0.25. The accuracy of selection was the rounded value based on an increase in a number of lactation records with older cows. The rate of selection was 500 cows from 2,500 candidates. The assumed proportions of candidates among the age classes were relative proportions assuming their stayability to be 0.80.

The comparison of calculated age structures, truncation points and genetic selection differentials with 4 selection schemes, is presented in Table 3.1. When parents were selected according to SS2, the generation interval was the shortest of four methods ascribed to the higher proportion of selection from younger parents, followed by SS3 and SS4. However, the average genetic superiorities were the highest for SS3 followed by SS4 and SS2, though the differences among three schemes were very small. Age structures of parents (e.g. generation interval) and estimated genetic superiorities depend on the selection scheme applied. These quantities would also be affected by the number of age classes, genetic difference among age classes and the accuracy of selection. More work would be needed to determine an optimal selection scheme among those examined in this study with combinations of different genetic and population parameters.

Theoretical results including previously described four selection schemes and two additional schemes SS5 and SS6 are presented in Table 3.2. Selection schemes 5 and 6 (SS5, SS6) were the same as SS3 and SS4, respectively, but the truncation was on estimated breeding values. The selected proportions across age classes and genetic superiorities of selected animals using SS3 and SS4 were identical to SS5 and SS6, respectively. The differences lie on the values of truncation points. For SS3 the truncation points, on phenotypic values, were different among age classes but estimated genetic values at the age-specific points were same, by the definition of SS3, where as in SS5 the truncation points and estimated breeding values were the same, and the genetic values for SS3 and SS5 were also the same which confirmed the identity of results in respective schemes. The differences in values of truncation points between SS3 and SS5, and, between SS4 and SS6 were due to the differences of distributions considered. This proves

Table 3.1. Comparison of different selection schemes on age structure, truncation point(s) of selection and genetic superiorities.

		Age classes (years)					
		3	4	5	6	7	8
Means of age classes (m_i)[a]		0.500	0.400	0.300	0.200	0.100	0.000
Accuracy of selection (r_i)[f]		0.500	0.600	0.645	0.670	0.690	0.710
Proportions among age classes		0.271	0.217	0.173	0.139	0.111	0.089
Number of candidates (total 2,500)		678	542	434	347	277	222
Percent selected across age classes							
SS1[b]	5.87[c]	27.1	21.7	17.4	13.9	11.1	8.9
SS2	5.43	37.1	23.6	15.9	10.9	7.5	5.0
SS3	5.51	33.2	24.9	17.3	11.7	7.8	5.2
SS4	5.60	29.3	26.0	18.6	12.5	8.2	5.4
Truncation points[a,d]							
SS1		1.68	1.30	1.10	0.96	0.82	0.69
SS2		1.20	1.20	1.20	1.20	1.20	1.20
SS3		1.38	1.14	1.11	1.14	1.16	1.18
SS4		1.57	1.08	1.03	1.07	1.12	1.14
Genetic merits[a,d] at truncation points							
SS1		0.621	0.405	0.343	0.264	0.181	0.097
SS2		0.300	0.369	0.383	0.374	0.363	0.358
SS3		0.345	0.345	0.345	0.345	0.345	0.345
SS4		0.392	0.324	0.310	0.315	0.322	0.327
Genetic superiorities[a,d]							
SS1	0.665[e]	0.699	0.738	0.701	0.635	0.563	0.490
SS2	0.676	0.607	0.710	0.732	0.722	0.706	0.695
SS3	0.677	0.641	0.692	0.702	0.699	0.692	0.685
SS4	0.676	0.677	0.676	0.676	0.675	0.673	0.671

a Genetic standard deviation units.
b Selection schemes, refer to text.
c Average generation intervals.
d Deviation from the means of age class 3.
e Average genetic superiorities corrected for small numbers and deviated from the means of age class 3.
f $\sqrt{nh^2/[1+(n-1)r]}$; where,
n = number of lactation records,
h^2 = heritability in narrow sense,
r = repeatability of milk yield

Table 3.2. Numerical illustration for the distinctions in selection schemes in terms of truncation point(s), genetic values at truncation point(s) and average genetic values of selected animals on the path of dams of bulls with 4 age classes, stayability 0.60, accuracy of selection 0. 50, genetic differences among ages 0.10 and overall selected proportion 0.10.

Age classes (years)	3	4	5	6
Means of age classes[a]	0.300	0.200	0.100	0.000
Proportions of candidates among ages	0.460	0.276	0.165	0.099
Number of candidates within age classes	4600	2760	1650	990
Proportions selected among age classes				
SS1[d]	0.460	0.276	0.165	0.099
SS2	0.496	0.273	0.149	0.082
SS3	0.598	0.255	0.105	0.042
SS4	0.623	0.247	0.095	0.035
SS5	0.598	0.255	0.105	0.042
SS6	0.623	0.247	0.095	0.035
Truncation points[a,b]				
SS1	2.654	2.464	2.364	2.264
SS2	2.476	2.476	2.476	2.476
SS3	2.252	2.552	2.852	3.152
SS4	2.201	2.586	2.958	3.320
SS5	0.563	0.563	0.563	0.563
SS6	0.550	0.571	0.589	0.605
Genetic values at truncation points[a,b]				
SS1	0.641	0.541	0.441	0.341
SS2	0.619	0.544	0.469	0.394
SS3	0.563	0.563	0.563	0.563
SS4	0.550	0.571	0.589	0.605
SS5	0.563	0.563	0.563	0.563
SS6	0.550	0.571	0.589	0.605
Average genetic superiorities[a,b,c]				
SS1	0.877	0.777	0.677	0.577
SS2	0.859	0.780	0.701	0.622
SS3	0.813	0.796	0.780	0.766
SS4	0.803	0.803	0.803	0.803
SS5	0.813	0.796	0.780	0.766
SS6	0.803	0.803	0.803	0.803

[a] Genetic standard deviation units.

[b] Deviated from means of the youngest age class.

[c] For infinite population.

[d] Selection schemes, refer to text.

that algorithm used in SS3 and described by DUCROCQ and QUASS[23)] accrues the identical results. This was also proved mathematically in the previous section. For SS4 the truncation points, on phenotypic values, as well as genetic values at truncation points were different but the average genetic superiorities of selected animals in the infinite population were exactly same across the age classes, (the definition of SS4). The results of SS6, truncation at same genetic superiorities of selected animals on predicted genetic value, in terms of average ages, genetic values and genetic superiorities of selected animals were identical to SS4.

D. DISCUSSION

Several styles of selection in animal breeding have the objective of directional change in quantitative traits of economic importance such as milk, fat and protein production in dairy cattle. Projection of consequences of such selection involves three main factors: the selection differential, accuracy of selection and some measure of variation in response variable prior to selection as stated in Chapter I. The last two must be considered to specific selection procedures and their formulations are largely a matter of appropriate model structures. In contrast, the genetic selection differentials ($Ir\sigma_a$) may be treated more generally being functions of population size, number selected and the distribution of the trait being selected for improvement. In animal breeding, up to date, no attempt was made to look at selection response after truncation on equal genetic selection differential across age classes. Hence the main objective of this study was to present a generalized algorithm for truncation selection within and across the age classes, including the across age selection with equal genetic selection differential.

Initial point of selection ($K_{c.0}$) was settled on the means of the youngest age class. The convergence conditions were relatively severe to obtain good convergence. The limited deviation of truncation points ($d(K)$, $h(K)$) and selection intensity ($e(K)$) at their convergence were fixed to be 10^{-5} in equations [3.8], [3.8.1] and [3.16] respectively.

Under these conditions, the truncation point with a given selection intensity (SS4) was obtained in less than4 cycles. When the deviation of selected proportion converged to the limited threshold range, the number of iterations were 3 for SS2 and 9 for both SS3 and SS4. When there were some differences in accuracy of selection among age classes, as in numerical example, the number of cycles required for the convergence increased. Cows not selected as parents, in this model, were never used for breeding but were kept from one year to another for possible future use. In practice, a breeder would be reluctant to pursue such a policy as already described by JAMES[58)] and HILL[41)]. The results achieved here have some similarity with COCHRAN[13)] and HOPKINS and JAMES[52,53)]. The distribution of actual dairy population of each age class would be skew due to earlier culling of low producers. In principle, the methods described with the implicit assumptions of normal distributions of each age class would not be suitable for application to such a skewed population. However, this adjustment is cumbersome so currently it is an easy way to assume normality of distribution in each age class.

The algorithm used to compute the truncation point in SS3 is equivalent to the algorithm proposed by DUCROCQ and QUAAS[23]. They considered selection index predictor, g, (Best Linear Prediction, BLP, commonly called index selection) of g (an animal's genetic merit) and computed the common truncation point on the distribution of selection index predictor. The differences lie on the consideration of distributions. While they explicitly explained the truncation on the distribution of estimated breeding values, we in SS3 explicitly considered the distribution of phenotypic values of different age classes and corrected for the genetic gaps among the age classes when computing the age-specific truncation points on the same estimated breeding values as in the youngest age class at k_c. If one considers the distribution of estimated genetic values, the algorithm accrues more simple due to truncation on common point (as in SS2) which is determined for young age class and then truncate on the same point across the age classes. When considering the distribution of estimated genetic values the standard deviation will be r provided the standard deviation of genetic values is 1.0. The algorithm used for SS2 can be used to compute the similar results as of SS3 but in this case the standard deviation will be r instead of $1/r$ so the differences lie on the standardization for numerical analysis. This has been proved mathematically in [3.7.2 through 3.12.2]. Theoretical results including six selection schemes (Table 3.2) confirmed that the algorithm could be used for phenotypic values as well as on estimated breeding values because the selected proportions across age classes and genetic superiorities of selected animals using SS3 and SS4 are identical to SS5 and SS6, respectively. For SS3 the truncation points are different among age classes on phenotypic values but estimated genetic values at the age-specific point(s) are the same whereas in SS5 the truncation point(s) and estimated breeding values both are identical. This is due to different variances of distributions considered for SS3 and SS5. This proved that algorithm used in SS3 and described by DUCROCQ and QUAAS[23], which was used in SS5, coincided. The new proposed algorithm can be applied on the distributions of phenotypic values as well as on estimated breeding values.

E. SUMMARY

Simple procedures for computing the truncation selection points, on the distribution of phenotypic values, such as: (1) predicted genetic values at truncation points and (2) average genetic values of selected parents should be on the same level for each age class of parents in a population with overlapping generations, were presented. The new proposed algorithm [SS4 in the text or (2) in this SUMMARY] took into account the distribution of selected parents from different age groups. To illustrate these procedures, the path of bulls' dams in a dairy cattle population was taken as a choice for a numerical example. The optimal proportions of bull's dams that should be selected from different age groups were determined. The results in respect of optimization of age structure and prediction of genetic response to truncation selection were compared with two other selection schemes: (3) selection of fixed proportions within parental age classes and (4) selection on common truncation point on phenotypic values for a single generation. The procedures can also be applied to decide an optimal proportion of parents to be introduced from an exotic population. The algorithm developed for predicting the genetic response and optimizing the age structure on the distribution of phenotypic values was also extended to use on the distributions of estimated breeding values. These procedures with some modifications can also be applied to more complex situations such as independent culling levels, selection on correlated traits and selection in a multiple tier breeding structure.

CHAPTER IV

Numerical verification on the selection theory with overlapping generations by computer simulation

A. INTRODUCTION

The age structures (generation length) and genetic responses can easily be calculated when the selection has already occurred from the recorded data. However, to predict the age structure and genetic response at planning stage has been the subject of interest among animal breeders. DICKERSON and HAZEL[21] described the relationship between age structure and rate of response while their expression was put into its more familiar form by RENDEL and ROBERTSON[73]. BICHARD *et al.*[5] reported the genetic superiority of progeny from younger parents over older parents and described the theory in detail of how to select larger proportions of younger animals in a population with overlapping generations. GHAFFAR and SHIMIZU[30] revealed, by computer simulation, some possible biases in the parental age structures due to selection of the progeny from different parents belonging to different age classes using two generation methods, from grand parents to grand progeny.

The offspring which are potential candidates for selection as a parents of next generation are the progeny from parents of different ages in the population where generations overlap. The potential candidates for selection are expected to be of different average genetic merits if genetic trend exists as a result of the selection process. BICHARD *et al.*[5] computed the truncation point(s) by trial and error from Table of Probits[29]. Recently, DUCROCQ and QUAAS[23] presented an algorithm for computing the common truncation point across the cohorts for selection on selection index predictor and demonstrated the interdependence of selection differentials and average ages in the four pathways of selection. In Chapter II biases in parental age structures were ascribed to non-optimized selection across the age classes which have different means and variances. In Chapter III, the algorithm of DUCROCQ and QUAAS[23] was used in more general form, applicable to distributions of both phenotypic and predictor values to optimize the selection across age classes. The algorithm used to truncate at the same average genetic superiorities of selected parents across age classes was new (SS4 *in Chapter III*). The objective of this computer simulation study was to verify the extended and newly developed theoretical algorithms and assess their application for selecting the breeding stock with overlapping generations.

B. MATERIALS AND METHODS

1. Assumed parameters and variables

Genetic and population parameters used in the simulation are presented in Table 4.1. The genetic differences among age classes and accuracy of selection (r), respectively, were assumed to be 4 levels with constant differences among age classes and 3 levels with same values across age classes. Two pathways of selection, bulls' sires (bulls to breed young bulls path) and bulls' dams (cows to breed young bulls path), were pondered to examine the effects of the number of candidates and the number selected on the verification of proposed algorithms. The theoretical selected proportions across age classes (Table 4.2) computed employing the scheme-specific algorithm, described in Chapter III, were used as an input in this computer simulation for numerical verification of the algorithm. The parameters used to compute these proportions were the same as those used in this study (Table 4.1). On the path of sires of bulls the same theoretical selected proportions across age classes for SS1 through SS4 (Table 4.2) could be attributed due to few bulls' sires selected and only two age classes assumed. Moreover, potential candidates for selection in this path were equally distributed across the age classes.

2. Generation of population

The performance records were generated according to the same following model as in Chapter II:

$$X_{ij} = m_i + a_{ij} + e_{ij},$$

where X_{ij} refers to the performance of candidate j from parental age class i, m_i to the average genetic merits of parental age class i, a_{ij} to additive genetic values of candidate j in age class i and is normally and independently distributed with

Table 4.1. Input parameters used in the computer simulation.

Variables	Values
Genetic parameters	
Genetic variance	1.0
Accuracy of selection (r) : 3 levels	0.5, 0.7, 0.9
Genetic differences (genetic standard deviation units) among age classes : 4 levels	0.05, 0.10, 0.15, 0.20
Population parameters	
Phenotypic variance	$1/r^2$
Environmental variance	$(1-r^2)/r^2$
Bulls' sires pathway	
Ages of candidates (2 age classes)	5 through 6 years
and their proportion across age classes	0.5, 0.5
Selection pressure (number of selected/candidates)	4/200
Usage period	2 years
Bulls' dams pathway	
Selection pressure (number of selected/candidates)	200/1,600
Ages of candidates (8 age classes)	3 through 10 years
Stayability from a year to the next year	0.80

$N(0, 1)$, and e_{ij} to environmental deviation with $N(0,(1-r_i^2)/r_i^2)$.

3. Selection schemes

Seven truncation selection schemes (SSs) were framed to explore the theoretical and practical aspects of algorithms as follows:

(1) selection within each age class at same proportions as the distribution of candidates across the age classes; SS1,

(2) selection of theoretical proportions within each age class so as to select at the common truncation point on phenotypic values across the age classes; SS2,

(3) selection of theoretical proportions within each age class at age-specific truncation point so as to select on the same predicted genetic values across the age classes; SS3,

(4) selection of theoretical proportions within each age class at age-specific truncation point so as to select on same average predicted genetic values of selected parents across the age classes; SS4,

(5) selection on the generated phenotypic values across the age classes; SS5,

(6) selection on the estimated (from generated phenotypic values) genetic values across the age classes; SS6,

(7) selection on the generated true breeding values across the age classes; SS7.

The theoretical average ages and theoretical average genetic values of selected animals for the first four (SS1 through SS4) and the last one (SS7) were computed through the procedures described in Chapter III. However, for ready reference the general equation for predicting the theoretical genetic values (g) is given

Table 4.2. Theoretical optimal proportions (percentages) to be selected across age classes computed using the scheme-specific algorithm and used in the simulation as an input for SS1 through SS4 and SS7.

Parameters			Age classes							
Schemes	r[a]	g[b]	3	4	5	6	7	8	9	10
Bulls' dams pathway, selection pressure 200/1600										
SS1	.5	.05	24.0	19.0	15.5	12.5	10.0	8.0	6.0	5.0
SS2	〃	〃	26.5	20.5	15.5	12.0	9.0	7.0	7.0	5.5
SS3	〃	〃	33.5	23.0	16.0	10.5	7.0	5.0	3.0	2.0
SS4	〃	〃	35.5	23.5	15.5	10.0	6.5	4.5	2.5	2.0
SS7	1.0	〃	29.0	21.5	15.5	11.5	8.5	6.0	4.5	3.5
SS1	.9	〃	24.0	19.0	15.5	12.5	10.0	8.0	6.0	5.0
SS2	〃	〃	28.5	21.0	15.5	11.5	8.5	6.5	5.0	3.5
SS3	〃	〃	29.5	21.5	15.5	11.5	8.5	6.0	4.5	3.0
SS4	〃	〃	30.5	22.5	15.5	11.5	8.0	5.5	4.0	3.0
SS7	1.0	〃	29.0	21.5	15.5	11.5	8.5	6.0	4.5	3.5
SS1	.9	.10	24.0	19.0	15.5	12.5	10.0	8.0	6.0	5.0
SS2	〃	〃	32.5	22.5	15.5	11.0	7.5	5.0	3.5	2.5
SS3	〃	〃	34.5	23.5	15.5	10.5	7.0	4.5	3.0	1.5
SS4	〃	〃	37.0	24.0	15.5	9.5	6.0	4.0	2.5	1.5
SS7	1.0	〃	33.5	23.0	16.0	10.5	7.0	5.0	3.0	2.0
Bulls' sires pathway, selection pressure 4/200										
SS1	.5	.05			50.0	50.0				
SS2	〃	〃			50.0	50.0				
SS3	〃	〃			50.0	50.0				
SS4	〃	〃			50.0	50.0				
SS7	1.0	〃			50.0	50.0				
SS1	.5	.10			50.0	50.0				
SS2	〃	〃			50.0	50.0				
SS3	〃	〃			50.0	50.0				
SS4	〃	〃			75.0	25.0				
SS7	1.0	〃			50.0	50.0				
SS1	.9	〃			50.0	50.0				
SS2	〃	〃			50.0	50.0				
SS3	〃	〃			50.0	50.0				
SS4	〃	〃			50.0	50.0				
SS7	1.0	〃			50.0	50.0				

a = Accuracy of selection.
b = Genetic differences among age classes in genetic standard deviation units.

below,

$$g = \sum_i p_i[I_i r_i + m_i - m_c]$$

where, p_i, I_i, r_i and m_i, respectively, refer to the across-age proportions of selected animals, selection intensity, accuracy of selection and average genetic means before selection in the ith age class and subscript c refers to the youngest age class. Simulated average genetic values of selected animals were computed from their generated additive genetic values.

Selection was based on the generated phenotypic values within (SS1 and SS2) or across (SS5) the age classes; on the estimated genetic values within (SS3 and SS4) or across (SS6) the age classes and on the generated true genetic values (SS7) across the age classes. The generated candidates were ranked according to their individual performance within or across the age classes depending on the selection schemes.

Three statistics: proportions of selected animals among parental ages (average ages of parents), average genetic values of selected animals and their respective standard errors were computed through 20 runs of simulation incorporating all assumed variable factors for all seven selection schemes. To verify the algorithms for all the schemes, the realized (simulated) values were compared with theoretical values specifically SS2 and SS3 with SS5 and SS6, the realizations of SS2 and SS3, respectively.

C. RESULTS

1. Age structures

The average ages of selected animals through seven truncation selection schemes for both pathways of bulls' sires and bulls' dams are shown in Figs. 4.1 and 4.2, respectively. Double hatched bars, SS5 and SS6, are realizations for SS2 and SS3. Selection in SS1 through SS4 was carried out within age classes on the theoretical proportions computed by their respective algorithms described in Chapter III, so average ages of selected animals did not oscillate among the replicates. Consequently, these average ages should be considered as serving theoretical and simulated values for themselves. The average ages in SS2 and SS3 were also theoretical values for SS5 and SS6, respectively. On the path of bulls' dams where the number of potential candidates and selected animals were comparatively large, the average ages of selected animals (bulls' dams) in SS2 and SS3 were in good agreement with those of selected in SS5 and SS6, respectively, for each factor pondered in this study (Fig. 4.1). However, on the path of bulls' sires where the number of potential candidates and selected animals were relatively small, the differences in the average ages of selected animals between SS2 and SS5, and SS3 and SS6 were relatively large but within the ranges of standard error (Fig. 4.2). The average ages for SS2 and SS3 coincided with SS5 and SS6,

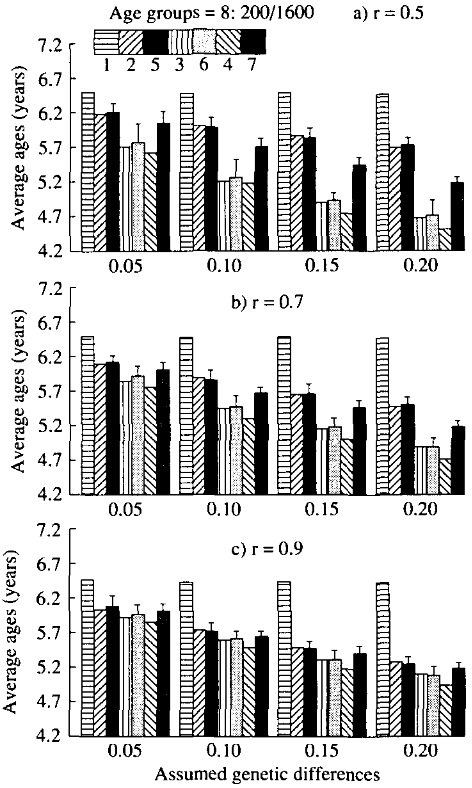


Fig. 4.1. Average ages of selected animals as dams of bulls through seven selection schemee.

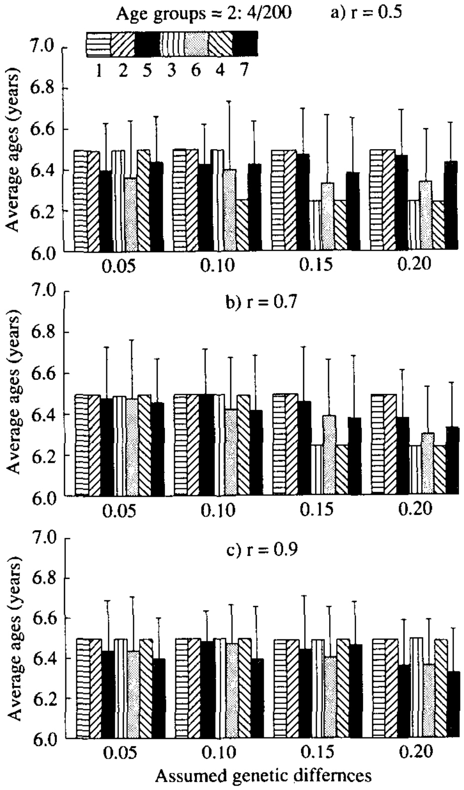


Fig. 4.2. Average ages of selected animals as dams of bulls through seven selection schemes.

respectively, on both paths of selection, which confirmed their respective algorithms.

The average ages on path of bulls' dams became younger with the expansion of genetic differences among age classes through all schemes except SS1, due to its framed definition, for any value of accuracy of selection. The increase in the accuracy of selection decreased the average ages of selected animals in SS2 or SS5 and increased in SS3, SS4 and SS6 (Fig. 4.1 a, b, c) for any level of genetic differences among age classes. The average ages on the path of bulls' sires also exhibited similar tendency: the increase in accuracy of selection decreased the average ages in SS5 and increased in SS6 (Fig. 4.2 a, b, c). However, the variation in average ages was large as reflected in standard errors ascribed to only few animals (only 4 in this simulation) to be selected. Augmenting the genetic differences accrues in the decrease in average ages on both paths of selection, though the tendency at low accuracy of selection ($r = 0.5$) was not very clear on the path of bulls' sires.

Overally, the average ages were youngest in SS4 followed by SS3 or SS6, and

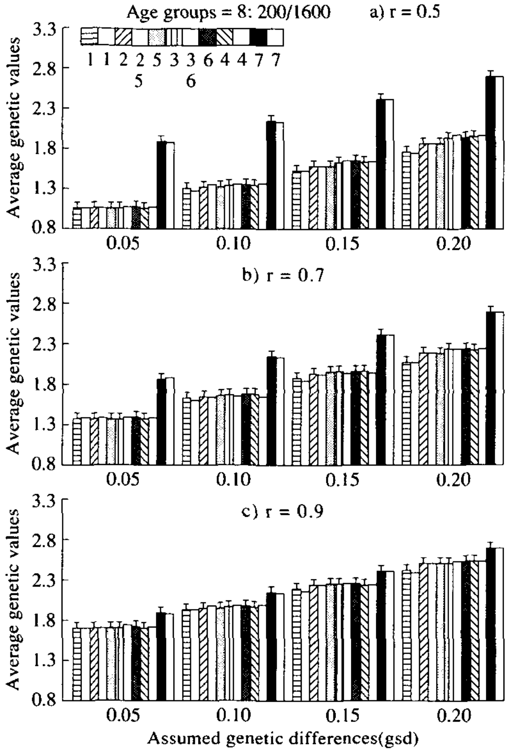


Fig. 4.3. Theoretical and simulated average genetic values of animals selected as dams of bulls through seven selection schemes.

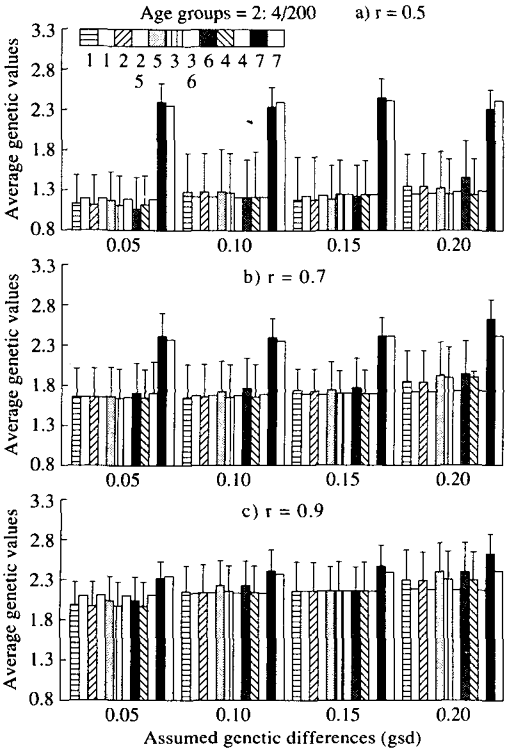


Fig. 4.4. Theoretical and simulated average genetic values of animals selected as sires of bulls through seven selection schemes.

SS2 or SS5 and SS1 on both path of selection for any combination of variable factors. The average ages in SS7 were in between SS2 or SS5 and SS3 or SS6. The differences among schemes became apparently large as increasing the genetic differences among age classes and decreasing the accuracy of selection, however, unlike to bulls' dams, large standard errors were observed on the path of bulls' sires.

2. Genetic values of selected animals

The theoretical and simulated average genetic values of selected animals employing 7 selection schemes for the path of bulls' dams and bulls' sires are presented in Figs. 4.3 and 4.4, respectively. Rectangles without hatching, in these figures, are the theoretical values for the earmarked selection schemes. Double hatched rectangles, SS5 and SS6, are realizations for SS2 and SS3. On the path of bulls' dams where the number of potential candidates and selected animals were comparatively large, simulated genetic values coincided with the theoretical genetic values in all schemes. Realized average genetic values in SS5 and SS6 were also in good agreement with those of SS2 and SS3, respectively. On the path of bulls' sire where the number of potential candidates and selected animals were comparatively small, some deviations in realized average genetic values from theoretical values were found within the ranges of standard error over the repetition of simulation. These good agreements within the wide ranges of assumed parameters used in this study, confirmed the proposed algorithms.

The simulated and theoretical average genetic values of selected animals differed more among schemes with expanded genetic differences among age classes. On the contrary, an increase in the accuracy of selection decreased the differences among selection schemes for both paths of selection.

Average genetic values in SS3, SS6 and SS4 were always higher compared with others (SS1 and SS2 or SS5) except for SS7 over any combination of variable factors, but the differences between SS3 or SS6 and SS4 were very small. This tendency was clearly exhibited at large genetic differences (0.15-0.20) among age classes and low accuracy of selection ($r=0.5$) on the path of bulls' dams (Fig. 4. 3a). However, on the path of bulls' sires, some deviations from this tendency were found (Fig. 4.4 a) due to larger sampling errors. The theoretical and simulated mean genetic values either coincided or showed a slight variation in all schemes on both paths of selection.

The standard error of simulated average genetic values ranges from 0.03 to 0.07 on the path of bulls' dams in all schemes (Fig. 4.3). However, the standard error of simulated genetic values on the path of bulls' sires were large, hardly less than 0.25 for all schemes except SS7 where these values were not greater than 0. 25 (Fig. 4.4).

D. DISCUSSION

The main objective of this study was to verify whether the previously proposed algorithms for predicting the age structures and genetic values of selected animals could be used in truncation selection schemes. It is clear from the results that the theoretical and numerical values for average ages and genetic values of selected animals were in good agreement within the wide ranges of assumptions. This reality confirmed the proposed algorithms concerning the selection within or across the age classes in a population with overlapping generations.

TSURUTA *et al.*[98] reported that the yearly genetic improvement in milk yield in Hokkaido dairy cattle population was 88.1 kg from 1981 through 1986. This gain is equal to 0.12 genetic standard deviation units assuming genetic standard deviation to be 750 kg. This value of genetic gain is within the ranges of assumed constant genetic differences among age classes. The variation in genetic response to selection in the early years of the breeding program has been reported by some authors[40,41,53]. This early variation was ignored assuming the breeding program in an asymptote. When the genetic abilities of cows are evaluated through BLUP procedures[38] with animal model using all available information and considering the h^2 to be 0.25, the accuracy of selection would be higher than 0.5 for youngest age class of cows having only one lactation record and the increment in the accuracy of selection will be decreased with the aging of cows. The selection of bulls' dams based on estimated breeding values is equivalent to SS3 or SS6 in this study. This revealed that increasing the accuracy of selection, constant among age classes, causes the average ages of selected animals to be older in SS3 or SS6 and SS4 and younger in SS2 or SS5. These findings lead to the suspicion of under prediction of the average ages in SS3 and SS4. However, apparent differences between SS1 and other schemes even when the accuracy of selection was taken as 0.9 (Fig. 4.1) suggested that the described algorithms would be useful to predict the average ages especially on the path of bulls' dams in the respective schemes. On the path of bulls' sires where only 2 age classes were considered with a few selected animals the sampling error dominated over the differences among the schemes (Fig. 4.2). The average ages in SS7 were in between SS5 and SS6, an agreement with the results of BICHARD *et al.*[5].

The average ages of parents at the birth of their selected progeny were taken as generation length, hence, the effect of selection across age classes would be placed in generation length and not in the genetic values as described by JAMES[56]. This heuristic argument elucidate why the genetic values among the schemes did not differ significantly. Another possible explanation could be that average ages of selected animals would deviate from each other among SS1, SS2 or SS5, and SS3 or SS6 by more than the double standard error and the average genetic values would not significantly differ among schemes.

The average ages were younger in the schemes operated on predicted breeding values (SS3 or SS6 and SS4) and consequently, the yearly genetic improvement would be higher in these schemes. The conclusion that selection on predicted breeding value manifested younger average ages is in agreement with that of BICHARD *et al.*[5] and JAMES[58]. Moreover, SS4, newly proposed algorithm revealed more promising results in terms of higher yearly genetic improvement owing to youngest ages, though the differences in average genetic values among SS3 or SS6 and SS4 were small.

E. SUMMARY

A Monte Carlo simulation study was performed to verify the algorithms described to select the animals within and/or across the age classes to reduce the average ages of selected parents and to maximize the genetic responses to truncation selection. Seven selection schemes (SSs) on two pathways (bulls' sires and bulls' dams) were framed to verify and assess the implications of previously proposed (SS3 and SS4, Chapter III) theoretical algorithms. Three statistics: average ages, genetic values of selected animals and their respective standard errors, were used as a criteria for numerical verification of the algorithms.

Theoretical and numerical values for average ages of selected animals and genetic responses were in good agreement in their respective schemes which confirmed the proposed algorithms. The average ages and yearly genetic responses were youngest and highest, respectively, in SS4 followed by SS3 or SS6 and SS2 or SS5. The algorithms were found satisfactory within different ranges of accuracy of selection and genetic differences among age classes. The differences among schemes became more obvious at higher genetic differences among cohorts, lower accuracy of selection and larger number of age classes.

The average ages increased in SS3, SS4 and SS6, and decreased in SS2 with an increase in accuracy of selection. This necessitates to develop mathematical elucidation for this tendency. The average ages in SS7 were independent of accuracy of selection but do depend on genetic differences across the age classes.

CHAPTER V

Implications of the developed selection theory on the prediction of age structures and genetic superiorities in a population with overlapping generations

A. INTRODUCTION

A relationship exists between the age of parents and their average genetic merits in a population with overlapping generations such as cattle. If the potential candidates for selection at a time are the progeny from the parents of different ages and the parents themselves are expected to come from various distributions of genetic values with different means and variances, the genetic merits of potential candidates for selection cannot be considered as belonging to a unique distribution. Consequently, when normal truncation selection across the distributions is applied at a common truncation point on phenotypic values or even on estimated genetic values, the average genetic superiorities of selected animals across different age classes of parents are no longer similar. The algorithms for computing the normal truncation points for each age class separately to hold predicted genetic values at truncation points or average predicted genetic values of selected animals unique among age classes were proposed in Chapter III and verified in Chapter IV.

The objectives of this chapter are i) to determine the influence of several variable factors on the variation in average ages (generation length) and genetic responses to four truncation selection schemes, as in Chapter III, and ii) to find the best theoretical selection scheme within the stated assumptions.

B. MATERIALS AND METHODS

1. Assumed variable factors

Assumptions and variable factors considered in this study are presented in Table 5.1. Two paths of selection, sires to breed young bulls (bulls' sires) and dams to breed young bulls (bulls' dams) were considered, because 95 percent or more of total improvement is contributed through selection on these paths involving bulls[100]. The third path, involving sires, sires to breed cows was taken into account by altering the selection intensity on the path of bulls' sires. Genetic differences among age classes (5 levels) with constant differences among ages, accuracy of selection (correlation of breeding values with the criterion of evaluation, *r*; 4 levels) with the same values across the age classes and proportions selected (4 levels) were assumed. On the path of bulls' dams 4 or 8 age classes with each of 0.80 and 0.60 stayability (the probability of a cow remaining in the herd to a specific age, in this case from a year to the next year, when given the opportunity to reach that age) across age classes were considered. Sires were used for two or four consecutive years on the path of bulls' sires. Two hundred young bulls were progeny tested in every year and out of these progeny tested bulls the

Table 5.1. Assumed parameters and variable factors set in the study.

Assumed variable factors	Values
Genetic parameters	
Genetic variance (constant across the age classes)	1.0
Genetic differences (gsd[a]) among age classes : 5 levels	0.0, 0.05, 0.10, 0.15, 0.20
Accuracy of selection (r) 4 levels	0.3, 0.5, 0.7, 0.9
Pathways of selection	
Sires to breed bulls	
Total number of candidates	200 young bulls
Total number of selected bulls	4, 8, 10, 20
Number of age classes : 2 levels	2 or 4
Ages at selection for 2 or 4 age classes	5 through 6 or 5 through 8 years
Distribution across age classes	0.50 or 0.25
Proportions selected : 4 levels	0.02, 0.04, 0.05, 0.10
Dams to breed bulls	
Total number of candidates : 4 levels	20,000, 10,000, 8,000, 4,000
Total number of selected dams	1,000 dams
Number of age classes : 2 levels	4 or 8
Ages at selection for 4 or 8 age classes	3 through 6 or 3 through 10 years
Stayability across the age classes : 2 levels	0.80 or 0.60
Proportions selected : 4 levels	0.05, 0.10, 0.125, 0.25

a Genetic standard deviation unit

assumed numbers were selected as sires to breed young bulls. One thousand bulls' dams were selected to produce 200 candidate young bulls. The proportions selected on path of bulls' dams were changed by altering the base population while on the path of bulls' sires the base population was the same and the number of selected bulls were changed.

2. Selection schemes

Same four selection schemes (SSs) as in Chapter III, each of them differentiated by the conditions associated with truncation selection point(s) on phenotypic values, were constituted as:

(1) selection within each age class at same proportions as the distribution of candidates across the age classes; SS1,
(2) selection at the common truncation point based on phenotypic values across the age classes; SS2,
(3) selection at each age specific truncation point with the same predicted genetic values across the age classes: SS3, and
(4) selection at each agespecific truncation point with the same average predicted genetic values of selected parents across the age classes; SS4.

The detailed algorithms for operating these theoretical selection schemes are presented in Chapter III, however, numerical illustration of these selection schemes in terms of truncation point(s), genetic values at truncation points and average genetic values of selected animals on the path of bulls' dams with four parental age classes, stayability 0.8, accuracy of selection 0.7 and overall fraction selected 0.125 are presented in Table 5.2.

3. Prediction of genetic responses and generation lengths

A computer program was written in FORTRAN 77 to determine scheme-specific truncation point(s) and to predict genetic responses and average ages of selected animals. The input parameters included age distribution of candidates, genetic means of each age class of candidates, accuracy of selection, numbers in base populations and numbers to be selected. The relative sizes (proportions) of candidates among age classes depends on the time when selection is actually performed. In this study, the relative sizes of age classes were considered at the time of selection of parents, consequently, the generation lengths (average ages) were predicted by adding one year (an allowance for gestation length and service period) to weighted average ages of selected animals. The youngest age class was assumed to have the highest genetic means, and average genetic superiority of selected animals from each age group was measured as the deviation from the youngest age class means instead of the population means[23]. The average yearly genetic superiorities were computed by dividing the weighted means of the genetic superiority by average ages of parents. Since actual population size was finite, the selection intensities were corrected for finite numbers of sampled

Table 5.2. Numerical illustration for the distinctions in selection schemes in terms of truncation point (s), genetic values at truncation point (s) and average genetic values of selected animals on the path of bulls' dams with 4 age classes, stayability 0.80, accuracy of selection 0.7, genetic differences among ages 0.10 and overall selected proportion 0.125.

Age classes (years)	3	4	5	6
Genetic means of age classes[a]	0.300	0.200	0.100	0.000
Proportions of candidates among age classes	0.339	0.271	0.217	0.173
Total number of candidates within age classes	2710	2168	1734	1387
Proportions selected among age classes				
SS1	0.339	0.271	0.217	0.173
SS2	0.387	0.276	0.197	0.140
SS3	0.437	0.279	0.176	0.108
SS4	0.459	0.278	0.166	0.097
Truncation points[a,b,c]				
SS1	1.644	1.544	1.444	1.344
SS2	1.526	1.526	1.526	1.526
SS3	1.413	1.517	1.622	1.726
SS4	1.367	1.520	1.667	1.810
Genetic values at truncation points[a,b]				
SS1	0.805	0.705	0.605	0.505
SS2	0.747	0.696	0.646	0.595
SS3	0.693	0.693	0.693	0.693
SS4	0.670	0.694	0.715	0.734
Genetic superiorities of selected parents[a,b,d]				
SS1	1.153	1.053	0.953	0.853
SS2	1.106	1.046	0.986	0.926
SS3	1.062	1.042	1.025	1.008
SS4	1.043	1.043	1.043	1.043

a In genetic standard deviation units.
b Deviated from yougest age class.
c On the distribution of phenotypic values.
d For infinite population.

animals according to the method proposed by BURROWS[11].

C. RESULTS

1. Implication on the prediction of age structures

The effects of various variable factors on the prediction of age structures are depicted in Figs. 5.1 through 5.4. Four levels of accuracy of selection are included in these graphs with the increase in value from left to right within the each level of genetic differences among age classes on abscissa. When genetic differences among age classes does not exist in the dairy population, the selection of animals through any selection scheme incorporating all assumed variable factors results in the same average ages of selected animals. The average ages of selected animals in SS1 were unchanged for any level of genetic differences among age classes, accuracy of selection and proportions selected (Figs. 5.1 through 5.4). The average ages of selected animals in SS2, SS3 and SS4 were reduced with augmenting the genetic differences among age classes (Fig. 5.1). However, an increase in accuracy of selection results in differential variation in average ages among schemes: reduction in SS2 and an increase in SS3 and SS4. The elucidation and mathematical proof of this tendency is given in a later section of this chapter. Consequently, the differences among the schemes reduced at higher precision except for SS1. Overally, the average ages were the youngest in SS4 followed by SS3 and SS2 for incorporating each of the assumed variable factors (Figs. 5.1 through 5.4). The higher proportions selected causes to increase in the average ages in all schemes except SS1. Increasing the proportions selected reduces the differences between SS1 and SS2, and increases

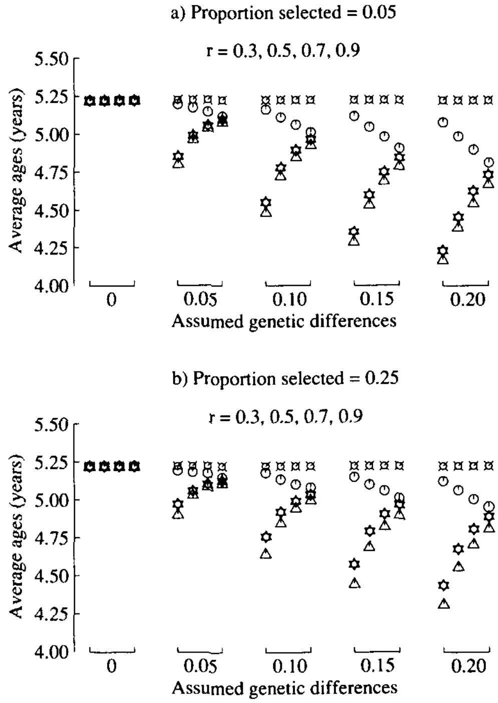


Fig. 5.1. Effect of proportions selected on average ages through four selection schemes at various levels of genetic differences and accuracy of selection (r) on the path of dams of bulls with four age classes and 0.8 stayability. SS1 ; ⊠, SS2 ; ⊖, SS3 ; ✡, SS4 ; △.

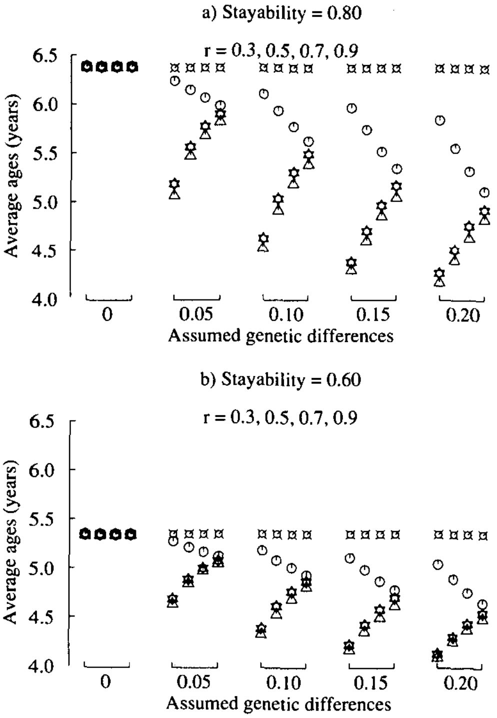
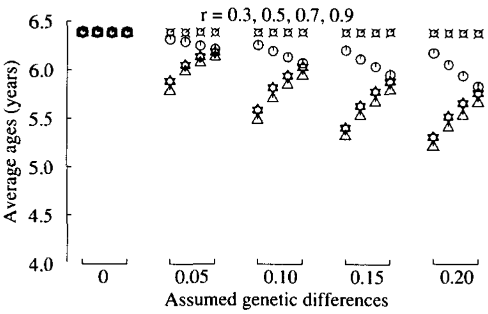


Fig. 5.2. Effect of stayability on average ages four selection schemes at various levels og genetic differences and accuracy of selection (r) on the path of dams of bulls with eight age classes and proportion selected 0.05.
SS1 ; ⊠, SS2 ; ⊖, SS3 ; ✡, SS4 ; △.

the differences between SS3 and SS4 (Fig. 5.1a vs 5.1b).

When the number of age classes are increased from 4 to 8 on the path of bulls' dams, the differences in average ages between SS1 and SS2, SS3 or SS4 became larger (Fig. 5.3). The rate of reduction in average ages was higher with 8 age classes as compared to 4 age classes on this path. Stayability of candidates across the age classes influenced the average ages. Decreasing the stayability from 0.80 to 0.60 reduced the average ages of selected animals in all schemes (Fig. 5.2a vs b) due to selecting higher proportions from younger ages. On the path of bulls' sires the pattern was the same as that on the bulls' dams. However, when the number of age classes were two and the proportion selected was 0.02, the average ages of selected animals were identical at lower genetic differences (0.05) and then with the increase of genetic differences among age classes the differences between SS1 or SS2 and SS3 or SS4 became obvious (Fig. 5.4a). Increasing the proportions selected on this path cleared this tendency (Fig. 5.4b). Similar

a) Number of age classes = 8



b) Number of age classes = 4

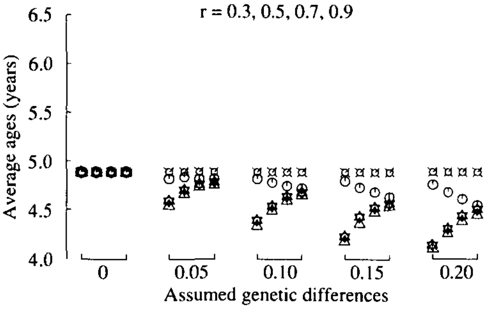
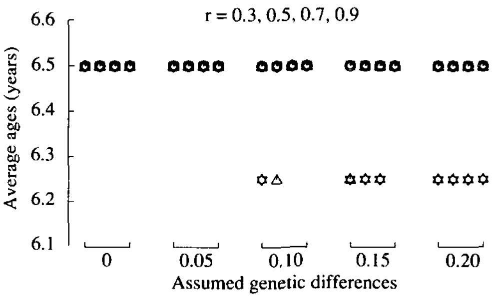


Fig. 5.3. Effect of number of age classes on average ages through four selection schemes at various levels of genetic differences and accuracy of selection (r) on the path of dams of bulls with stayability 0.6 and proportion selected 0.25. SS1 ; ¤, SS2 ; ○, SS3 ; ✡, SS4 ; △.

a) Proportion selected = 0.02



b) Proportion selected = 0.10

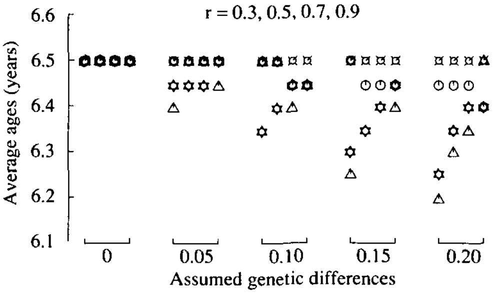


Fig. 5.4. Effect of proportions selected on average ages through four selection schemes at various levels of genetic differences and accuracy of selection (r) on the path of sires of bulls with two age classes. SS1 ; ¤, SS2 ; ○, SS3 ; ✡, SS4 ; △.

results were found with four age classes on bulls' sires path which have been omitted for brevity.

2. Implications on the prediction of yearly genetic superiorities

Figs. 5.5 through 5.8 unfold the effects of various variable factors on the yearly genetic superiorities. Four levels of accuracy of selection are placed on the right ordinates of these graphs and the value of accuracy increases from bottom to upwards for each level of genetic differences among age classes. In the absence of genetic differences among age classes in the population, the average yearly genetic superiorities obtained employing four selection schemes were similar for a particular level of accuracy of selection (Figs. 5.5 through 5.8). The differences in yearly genetic superiorities among the schemes were enhanced on the increase of genetic differences among age classes. The yearly genetic superiorities were reduced for SS1 and SS2 and increased in SS3 and SS4 with augmenting the genetic differences at higher selection intensity (Fig. 5.5a) and larger number of age classes (Fig. 5.7a). The lowest yearly genetic superiorities in SS1 were attributed to the selection of animals with lower genetic values from older age classes. The differences in yearly genetic responses between SS1 or SS2 and SS3 or SS4 were enhanced on the increase of genetic differences and these relative differences were reduced with larger proportions selected (Fig. 5.5a vs 5. 5b). The differences between SS2 and SS3 or SS4 diminished as enhancing the accuracy of selection (Fig. 5.5). The SS4 revealed maximum annual genetic response and was followed by SS3, SS2 and SS1 (Fig. 5.5). When the number of age classes were raised from 4 to 8 on the path of bulls' dams, the differences

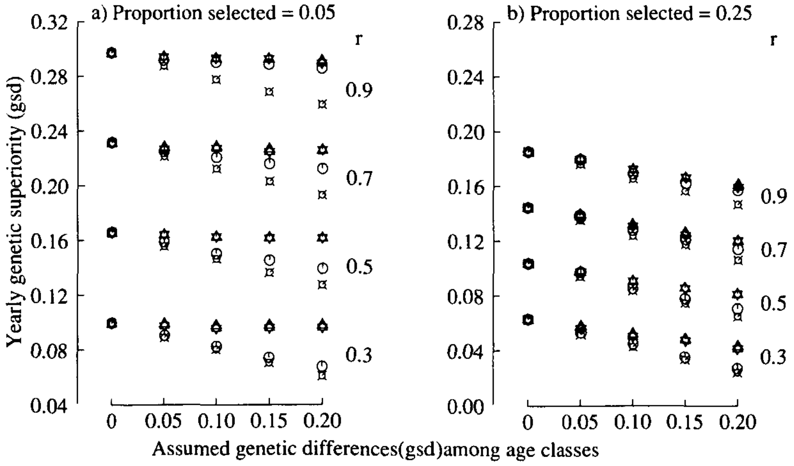


Fig. 5.5. Consequences of proportions selected on yearly genetic superiority through four selection schemes at various levels of genetic differences and accuracy of selection (r) on the path of dams of bulls with 4 age classes and 0.8 stayability.
SS1 ; ¤, SS2 ; ○, SS3 ; ✡, SS4 ; △.

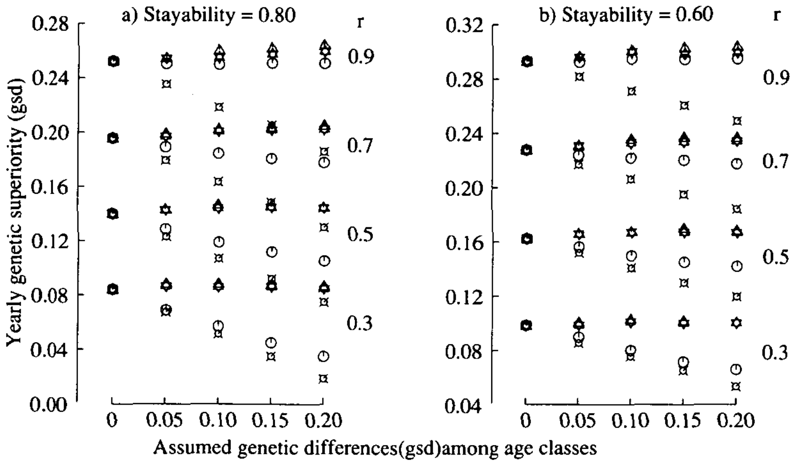


Fig. 5.6. Consequences of stayability on yearly genetic superiority through four selection schemes at various levels of genetic differences and accuracy of selection (r) on the path of dams of bulls with 8 age classes and proportion selected 0.05.
SS1 ; ¤, SS2 ; ⊖, SS3 ; ✡, SS4 ; △.

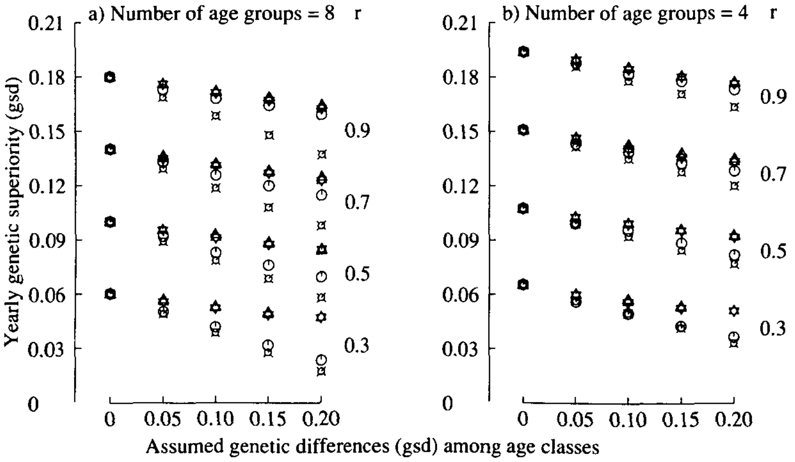


Fig. 5.7. Consequences of number of age calsses on yearly genetic superiority through 4 selection schemes at various levels of genetic differences and accuracy of selection (r) on the path of dams of bulls with stayability 0.6 age proportion selected 0.25.
SS1 ; ¤, SS2 ; ⊖, SS3 ; ✡, SS4 ; △.

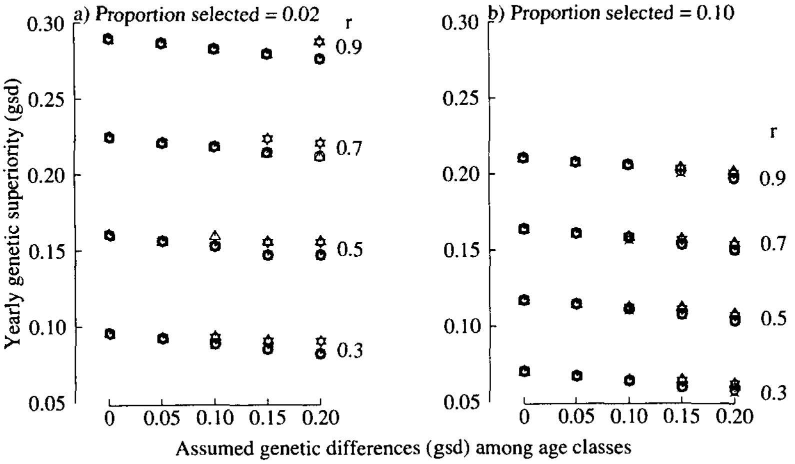


Fig. 5.8. Consequences of proportions selected on yearly genetic superiority through four selection schemes at various levels of genetic differences and accuracy of selection (r) on the path of sires of bulls with 2 age classes.
SS1 ; ¤, SS2 ; ○, SS3 ; ✡, SS4 ; △.

among the schemes increased (Fig. 5.7a vs 5.7b). Decreasing stayability from 0. 80 to 0.60 minimized the relative differences between SS2 and SS3 or SS4 and, indeed, the absolute values of responses were increased for all schemes (Fig. 5.6) due to younger average ages. On the path of bulls' sires with two age classes, there were no differences in yearly genetic responses among the schemes till the genetic differences augmented to 0.1 genetic standard deviation (Fig. 5.8a). When the number of selected animals increased from 4 to 20 the differences among the schemes were reduced as similar to the path of bulls' dams (Fig. 5.8b). Similar results were found for 4 age classes on this path which have been omitted for brevity.

3. Relationship between accuracy of selection and truncation points

Fig. 5.9 illustrates the distribution of candidates across the age classes. Let m_0, k_0 and x_0 be the phenotypic means, truncation selection point (as the deviation from means) on phenotypic values and truncation point on standardized normal distribution, respectively, in the youngest age class, and the corresponding values for ith age class are m_i, k_i and x_i. Assume the genetic variance 1.0 and phenotypic variance $1/r^2$ where, r is the accuracy of selection. Then

$$x_0 = k_0 r_0 \qquad [5.1]$$

and

$$x_i = k_i r_i \qquad [5.2].$$

1) Selection on phenotypic values.

When selection is applied on common truncation point at the same

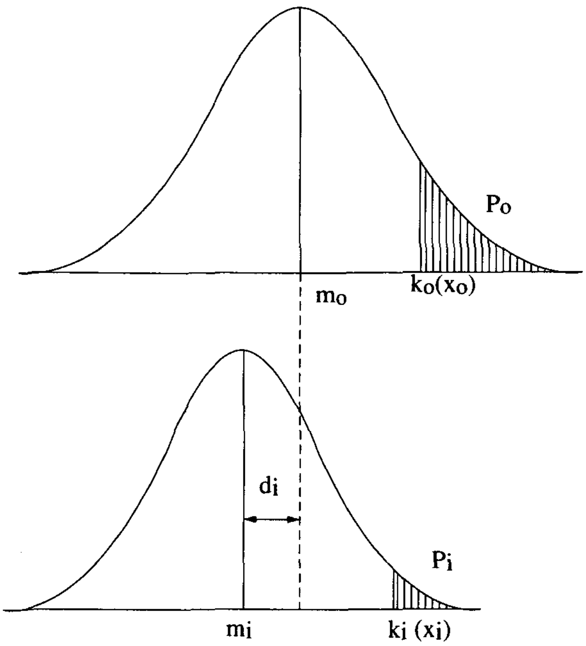


Fig. 5.9. Distribution of phenotypic values of candidates across ages. m = phenotypic means, k = truncation point and standardized normal distribution (x). Subscript o and i refers to the youngest and ith age class respecively.

phenotypic values across the age classes, the difference in means between the ith age class (m_i) and the youngest age (m_0) is d_i ($d_i = m_0 - m_i$), k_i with the same phenotypic values as in the youngest age class is $k_i = d_i + k_0$ and replacing the k_0 from [5.1]

$$k_i = d_i + x_0/r_0 \qquad [5.3].$$

Now from [5.3] and [5.2] the truncation point on standardized normal distribution (x_i) is

$$x_i = r_i d_i + x_0 r_i/r_0 \qquad [5.4].$$

When r increases to r', x_i changes to x_i' as

$$x_i' = r_i' d_i + x_0 r_i'/r_0'.$$

The differences in truncation points, $\Delta x = x_i' - x_i = d_i[r_i' - r_i + x_0(r_i'/r_0' - r_i/r_0)]$ could be found while the point in the youngest age class is fixed (proportion selected is constant).

If $r_i = r_0$, $r_i' = r_0'$ (as in this study) or $r_i'/r_0' = r_i/r_0$, then,

$$\Delta x = x_i' - x_i = (r_i' - r_i)d_i > 0 \qquad [5.5].$$

It is evident from [5.5] that x depends on the rate of change in r and d but independent from x_0. When r_i increases to r_i' then Δx is positive to change the truncation point to a larger level so the proportion (p) to be selected from the ith age class decreases. This implies that compared to younger age class the relative proportion from older age class becomes small as the accuracy (r) and/or genetic differences (d) increases and, consequently, the average ages are shortened.

2) Selection with same predicted genetic values across the age classes

When selection is practiced on truncation points with same predicted genetic values (SS3) the truncation point in the ith age class can be found by the relationship

$$x_0 r_0 + m_0 = x_i r_i + m_i$$

therefore,

$$x_i = d_i/r_i + x_0 r_0/r_i \qquad [5.6]$$

and

$$x_i' = d_i/r_i' + x_0 r_0'/r_i'$$

When accuracy of selection changes from r_i to r_i' the rate of change in the truncation point is

$$\Delta x = x_i' - x_i = d_i(1/r_i' - 1/r_i) + x_0[(r_0'/r_i') - (r_0/r_i)] \qquad [5.7].$$

If $r_i = r_0$, $r_i' = r_0'$ (as in this study) or $r_i'/r_0' = r_i/r_0$, then,

$$\Delta x = d_i(r_i - r_i')/r_i r_i' \qquad [5.8].$$

When r_i' is greater than r_i, Δx will be negative. Hence, the truncation point will be shifted to lower level and thus pi' is larger than pi, that is to say, a higher proportion to be selected from the ith age class with the increase in accuracy of selection and, subsequently, an increase in the average ages.

3) Selection on same average predicted genetic values of selected animals

When selection is practiced on the same predicted average genetic values of selected animals (SS4), standardized selection differentials (I_i) can be obtained as $I_i = (d_i + I_0 r_0)/r_i$ and similarly $I_i' = (d_i + I_0 r_0')/r_i'$, then,

$$\Delta I = I_i' - I_i = d_i(1/r_i' - 1/r_i) + I_0[(r_0'/r_i') - (r_0/r_i)] \qquad [5.9]$$

If $r_i = r_0$, $r_i' = r_0'$ (as in this study) or $r_i'/r_0' = r_i/r_0$, then

$$\Delta I = d_i(r_i - r_i')/r_i r_i' \qquad [5.10]$$

When r_i' is greater than r_i, ΔI is negative. Therefore,the truncation point will be moved to a lower level and, consequently increases the average ages of selected parents. The equations [5.10]and [5.8] are coincident with the identical results.

D. DISCUSSION

The genetic differences among age classes were assumed to be constant, where as yearly variation in genetic responses till the equilibrium is reached has been reported by HILL[41], Hopkins and JAMES[53] and JAMES[57]. Similarly accuracy of selection was assumed to be same across the age classes. Both these facts were ignored for simplicity and will definitely be considered in the next Chapter.

The selection scheme, SS4, truncation on phenotypic values with the condition of same predicted average genetic superiorities of selected animals has not yet been reported. It was shown in the results that selection on separate truncation points, at same predicted genetic values (SS3) or at same average predicted genetic values of selected animals (SS4), among age classes declined the proportions to be selected from older cows relatively at higher rate compared to SS2 and, consequently, the average ages decreased more in SS3 and SS4 as compared to SS2. JAMES[57] reported similar results in a somewhat different context. The reduction in average ages in SS2, SS3 and SS4 on the increase of the genetic differences among age classes is attributed to the selection of larger proportions from younger parents with high genetic merits as compared to proportions selected from older parents of low genetic merits. However, augmenting the assumed accuracy of selection results in differential variation in average ages among schemes, younger ages in SS2 and older ages in SS3 and SS4 at any fixed level of genetic differences. This differential variation was elucidated considering the movement of truncation points on standardized normal distributions and, consequently, the proportions selected. For SS2 decrease in average ages with the increase in accuracy of selection (r) could be attributed to a positive Δx and the independence of the change in truncation point from x_0, truncation point on standardized normal distribution for youngest age class, as proved in [5.5]. For SS3 and SS4 the rate of change in truncation points, Δx, with the increase of r is negative as shown in [5.8] and [5.10], respectively. This negative rate of change in the truncation points implies a larger proportion to be selected from the ith age class when r_i increases to r_i' which results in the longer generation intervals for these schemes.

The yearly genetic responses in SS1 were the lowest attributed to longer generation length due to selection of fixed proportions across the parental age classes. The results are in agreement to BICHARD *et al.*[5], HILL[40], and HOPKINS and JAMES[53]. Stayability (Fig. 5.7) and the number of age classes (Fig. 5.8) exhibited an inverse relationship with yearly genetic superiorities. When the number of age classes increased, the yearly genetic superiorities were predicted to be smaller due to longer generation lengths. The number of age classes could be artificially controlled which would be limited by the reproductive rate especially for dams. An application of MOET to produce potential candidates for selection could decrease the number of age classes, and, also, in an open nucleus breeding scheme, an introduction of breeding stock from commercial group would be useful for the enhancement of genetic improvement provided the genetic merits of those animals were higher. The replacement rate would also depend on the reproductive rates of selected animals.

When genetic differences among age classes and selection intensity increased, the differences in yearly genetic superiorities were expected to be larger between SS1 and SS2, SS3, or SS4 and also between SS2 and SS3 or SS4.

The results were in agreement with the expectation. At higher accuracy of selection the differences between SS1 and SS2, SS3, or SS4 increased but the differences between SS2 and SS3 or SS4 became smaller due to obvious reasons as expected. The differences in superiorities between SS3 and SS4 were enlarged with higher genetic differences and higher accuracy of selection. It can be concluded that in the population where large genetic differences among age classes exist and intensive selection, with either low or high precision, is required, the choice of selection scheme would be very important to obtain the maximum genetic responses.

Several authors have described the age structures and genetic responses in different contexts. HOPKINS and JAMES[51] compared parent and progeny selection strategies and concluded that parent selection strategies are superior to progeny selection strategies. HOPKINS[49] discussed the age structures in the context of open nucleus breeding systems and HOPKINS[50] considered the initial genetic differences among age classes but none of these studies compared the age structures and genetic responses as a function of the base of truncation selection points. GOFFINET and ELSEN[34], HILL[41], HOPKINS and JAMES[51], and JAMES[58] concluded that selection should be by truncation on expected breeding values as suggested in our SS3. Moreover, in this investigation SS4 gives more promising results in terms of short generation lengths and higher genetic superiorities per year.

E. SUMMARY

Four truncation selection schemes (SSs) were framed to visualize the impact of the developed theory to predict age structures and genetic responses. Two paths of selection, sires(bulls' sires) and dams (bulls' dams) to breed young bulls were considered. Among variable factors, four levels (0.3, 0.5, 0.7, 0.9) of accu-

racy of selection, five levels (0.0, 0.05, 0.10, 0.15, 0.20 genetic standard deviation) of genetic differences among age classes and 4 levels of proportions selected (for bulls' sire, 0.05, 0.10, 0.125, 0.25, and, for bulls' dams 0.02, 0.04, 0.05, 0.10) contemplated on both paths of selection. The number of age classes for bulls' dams and bulls' sires were 4 or 8 and 2 or 4, respectively. The stayability across age classes for bulls' dams was assumed to be 0.80 or 0.60. The candidates for selection for bulls' sires were equally distributed (0.5 or 0.25) across the age classes. The SS1 (selection on same proportions as the distribution of candidates across the age classes) revealed the longest generation lengths and lowest yearly genetic responses. The average ages reduced and yearly genetic responses to truncation selection enhanced, in a given order, through SS2 (selection at common truncation point on phenotypic values), SS3 (selection at each age-specific truncation point with same predicted genetic values) and SS4 (selection at each age-specific truncation point with the same average genetic superiority of selected parents) in a population with overlapping generations within the wide ranges of assumed assumptions. The results revealed the importance of choosing a suitable selection scheme to acquire maximum yearly genetic responses especially when the genetic differences among age classes are large and the accuracy of selection is relatively low.

CHAPTER VI

Prediction of long-term genetic responses to truncation selection in a closed population with overlapping generations

A. INTRODUCTION

The comparison of predicted genetic responses to different selection strategies is an essential feature for determining an efficient breeding scheme. The rate of response is usually predicted using the classical theory of selection developed by DICKERSON and HAZEL[21)] and formalized by RENDEL and ROBERTSON[73)]. This theory normally holds only asymptotically. The selection among age classes affects the age structure of parents which determines the generation interval, and reflects on the rate of genetic improvement. Asymptotic genetic gain has been a very common criterion among animal breeders to evaluate the alternative breeding schemes. However, DUCROCQ and QUAAS[23)] revealed the limitations of this criterion in a dairy cattle population attributed solely to genetic reasons. The asymptotic genetic progress is inversely related to age structure (generation interval). Some possible biases in parental age structure were found using computer simulation carried out for two consecutive generations in Chapter II. These biases were attributed to the selection of progeny across the age classes from the parents of different means and accuracy of genetic evaluation without optimizing the selected proportions across the age classes. In Chapter III an algorithm was developed to optimize the proportions to be selected across the age classes and to compute the time dependent selection differentials for a single generation only. The aim of this Chapter is to extend the developed algorithm to predict evolution of genetic merits of new born animals for the desired period of length and compare the results with those of HILL[40,41] and BRASCAMP[7,8,9,10].

B. MATERIALS AND METHODS

1.Selection schemes

Four Selection schemes, the same as in Chapter III, were considered as follows:

(1) selection within each age class at the same proportions as the distribution of candidates across the age classes: SS1,
(2) selection at the common truncation point based on phenotypic values across the age classes: SS2,
(3) selection at each age-specific truncation point with the same predicted genetic values across the age classes: SS3, and
(4) selection at each age-specific truncation point with the same average predicted genetic values of selected parents across the age classes: SS4.

2. Definitions and general formulae for proposed and/or employed methods

The input parameters $q(i)$, $r(i)$, $m(i)$ and P used in the algorithm for single generation needs to be redefined. The scalars must be replaced by vectors and vectors must be replaced by matrices to extend the algorithm for multiple generations or years.

$q(i,t)$ is the relative size of candidates in the ith age class at time t. This is a fraction and describes age distribution of candidates. This sums up to unity for each time unit.

$r(i,t)$ is the accuracy of selection in the ith age class at time t. This is assumed to be the same at time t for all animals in a group.

$m(i,t)$ is the mean genetic merit of the ith age group of candidates in a year t and $\Delta g(i,t)$ is the (genetic) selection differential of animals selected as parents of the next generation from the ith age class at time t, then, the mean genetic merit of selected animals from the ith age class $[ms(i,t)]$ is

$$ms(i,t) = m(i,t) + \Delta g(i,t) \qquad [6.1].$$

The algorithm developed in Chapter III to compute $\Delta g(i,t)$ explicitly used the deviations from means of the youngest age class, equation numbers [3.11] and [3.11.1]. Therefore, to compute the mean genetic merits of selected animals from the ith age class at time t, the mean of the youngest age class must be added instead of their own age class mean, for this reason [6.1] must be rewritten as:

$$ms(i,t) = m(c,t) + \Delta g(i,t) \qquad [6.1.1]$$

where c refers to the youngest age class.

$P(t)$ is the overall selected proportion at time t. This is computed by dividing total numbers of selected animals by total number of candidates for a particular time t. This is an input parameter.

$K(i,t)$ is the truncation point for the ith age class at time t to select the required best animals out of all potential candidates. This would be computed for each scheme as described in Chapter III for each time t and age group for all paths considered in the breeding scheme by repeating the same procedure every time using new means of each age class as shown in flow chart (Fig. 6.1).

$p(i,t)$ is proportion selected from the ith age class at time t. This is used to calculate the weighted averages of selection differentials and average ages of selected animals for every year (time t) for each pathway of selection. This describes the age structure of parents. The generation length for a particular path (e.g. sires to breed cows, SC) of gene transmission is computed as

$$L_{sc} = \sum_i p \cdot (i+1) \qquad [6.2].$$

$G(t)$ is the average (genetic) selection differentials of selected parents for each path of gene transmission

$$G(t) = \sum_i p(i,t).\ \Delta g(i,t) \qquad [6.3].$$

$M(t)$ is the average genetic merit of selected parents (sires or dams) and it is computed as:

$$M(t) = \sum_i p(i,t) \cdot ms(i,t) \qquad [6.4]$$

then, the genetic merit of new born (*GMNB*) animals is half average genetic merit of their parents

$$GMNB(t+1) = 0.5 \sum M(t) \qquad [6.5].$$

The genetic merit of new born animals computed using[6.5] is placed in zero-year-old animals in the next year[$m(0,t+1)$] as shown in Fig. 6.1. The contribution of new born animals in genetic advances depends on their selection as parents of the next generation.

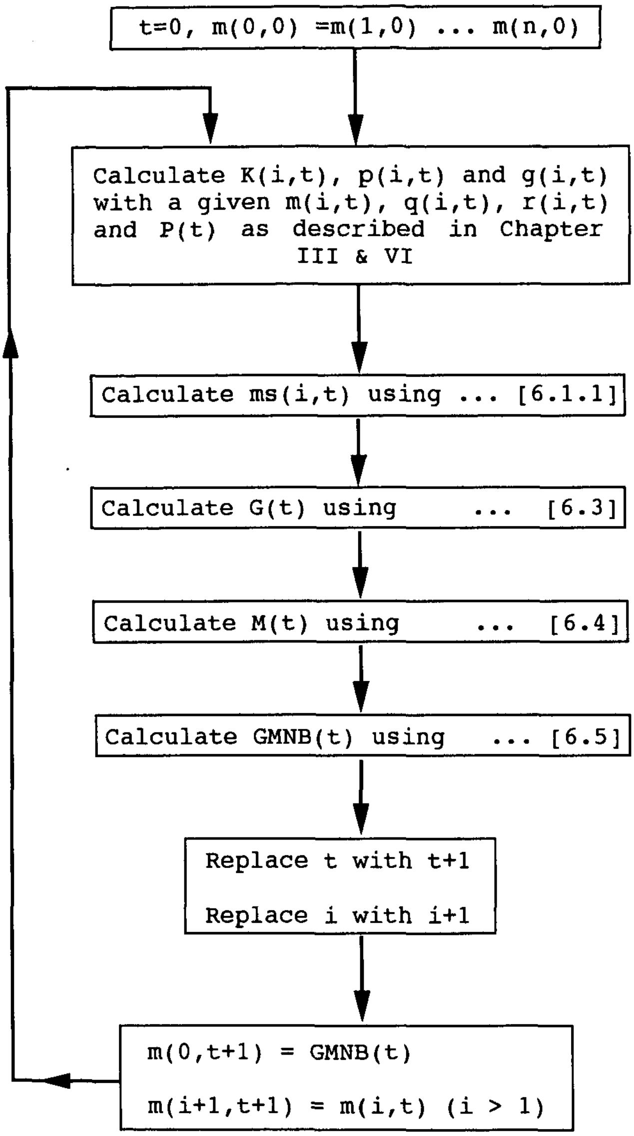


Fig. 6.1. Flow chart and pseudocode description of allocating the new born animals to zero-year-old age class.

3. Comparison with gene flow method

The gene flow method of HILL[40)] is theoretically based on the assumption that parental age distribution is unchanged (constant) among years and parents are usually selected once in their life (no selection across the age classes). This method would be equivalent to the first selection scheme (SS1) where the age structure of parents is fixed. The selection responses through gene flow method were computed using the GFLOW computer program written by BRASCAMP[10)] and partially modified by SHIMIZU *et al.*[87]. In this program the genetic make up of sexes and age classes, and the genetic superiority of selected parents in a year t, starting from the situation in year 0, $m(0)=[0, 0 \ldots.]$, is computed for each pathway of gene transmission from one generation to the next generation. This splitting of selection responses by paths of selection can be formalized by

$$n(t)=Q^t n(0) \qquad \text{(BRASCAMP}^{10)}\text{)}$$

$$m_j(t)=R_j n(t-1)+P m_j(t-1) \qquad \text{(BRASCAMP}^{10)}\text{)}$$

where, $m_j(t)$ represents the genetic make up of sexes and age classes in year t for path j. The first equation represents aging of the initial animals. Usually $n(0)$ contains zeroes except the age class 1 (zero-year-old) for a particular pathway representing that the animals in the age class 1 contain 100 percent of their own genes. This is the group of animals for a particular path for which the effect of selected animals (flow of genes) through the population is to be evaluated. The $n(0)$ vector was changed to take into account the immediate effect of selection of parents, at start of breeding plan, in new born animals. For this purpose 1.0 was placed in $n(0)$ vector at the level equal to the age at the first mating of the parents for a particular path, termed as GF1. Usually $n(0)$ contains zeroes except the age class 1 for a particular pathway. This implicitly implies that the breeding plan starts at the year when the candidates of the first generation are born. This usual procedure is termed as GF2.

4. Assumptions and breeding schemes

The assumed parameters and the description of different alternatives are presented in Table 6.1. Out of four, three pathways of gene transmission from one generation to the next generation: sires to breed bulls: SS, dams to breed bulls: DS, sires to breed cows: SC, were assumed to be selected while on the fourth path, dams to breed cows: DC, no selection was assumed. Among the genetic parameters the genetic variance was assumed to be 1.0 and, therefore, the unit of measurement was genetic standard deviation. Two levels of accuracy of selection for males (0.5, 0.85) and females (0.5 and 0.588) were assumed according to the number of information available. The value of 0.5 and 0.85 for males was based on 5 and 40 daughters records, all in different herds, respectively. The value 0. 5 and 0.588 for females was based on the first lactation record only and the first lactation record plus 40 paternal half-sibs as described by SCHMIDT *et al.*[82]. Sires to breed bulls and sires to breed cows were used for two or four and four years, respectively. The results were compared in two sets using different assumed parameters. In the first set of genetic responses, GF1, GF2 and other four schemes were compared using the same age structure (4 age groups) and selection intensity (4/200) for SS and SC. The accuracy of selection for males and females was assumed to be equal for the first set. However, for the second set of comparison involving only SS1, SS2, SS3 and SS4, the age structures as well as selection intensity on SS (2 age classes and 8/200, respectively) and SC (4 and

Table 6.1. Assumed parameters and variable factors fixed in the study.

Assumed variable factors	Values
Genetic parameters	
Genetic variance (same across the age classes in genetic standard deviation unit)	1.0
Accuracy of selection (r)	
Males : 2 levels	0.5, 0.850
Females : 2 levels	0.5, 0.588
Paths of selection	
Sires to breed sires	
Total number of candidates	200 young bulls
Number of age classes	2 or 4
Ages (Years) at selection for 2 or 4 age classes	5 through 6 or 5 through 8
Usage period	2 or 4 Years
Ages at birth of progeny for 2 or 4 age classes	6 through 7 or 6 through 9
Distribution across the age classes	0.50, or 0.25
Overall proportions selected : 2 levels	0.02, 0.04
Sires to breed cows	
Total number of candidates	200 young bulls
Number of age classes	4
Ages (Years) at selection	5 through 8
Usage period	4 years
Ages (Years) at birth of progeny	6 through 9
Distribution across the age classes	0.25
Overall proportions selected : 2 levels	0.02, 0.16
Dams to breed sires	
Total number of potential candidates	4000
Number of age classes : 2 levels	7 or 8
Ages (Years) at birth of progeny for 7 or 8 age classes	4 through 10 or 4 through 11
Stayability across the age classes	0.80
Overall proportion selected	0.05
Dams to breed cows	
No selection	
Distribution of cows	

Age at calving	Proportions (q (i, t)	Proportions ($\mathring{q}_{DS}$ (i, t)
2	0.224	0.0
3	0.179	0.0
4	0.143	0.253
5	0.115	0.203
6	0.092	0.162
7	0.073	0.130
8	0.059	0.104
9	0.047	0.083
10	0.038	0.066
11	0.030	0.0

32/200, respectively) paths were different. Accuracy of genetic evaluation for males (0.85) and females (0.588) was also different. Two hundred dams were selected out of 4,000 candidates. Dams to produce males were constituted on 8 age classes (4-11 years) for the comparison with gene flow and 7 age classes (4-10 years) for the comparison among the four schemes. The distribution of cows across the age classes were computed considering the stayability 0.8 from one year to the next year for both cases. This procedure is equivalent to ERERETT[28]. Age at first calving was assumed to be 2 years. On the path of dams to breed cows no selection was assumed. However, dams older than eleven years were not used for breeding the replacement heifers in both cases.

C. RESULTS

1. Comparison with gene flow

The comparisons of the genetic responses to selection employing gene flow and other four selection schemes are depicted in Figs. 6.2 and 6.3 for males and females, respectively, over a period of 40 years. The predictions of genetic responses to selection using gene flow for GF1 and GF2 show the same genetic trends for males and females. The total genetic improvement was higher in GF1 as compared to GF2 but both of them were inferior to SS1 as exhibited in Figs.

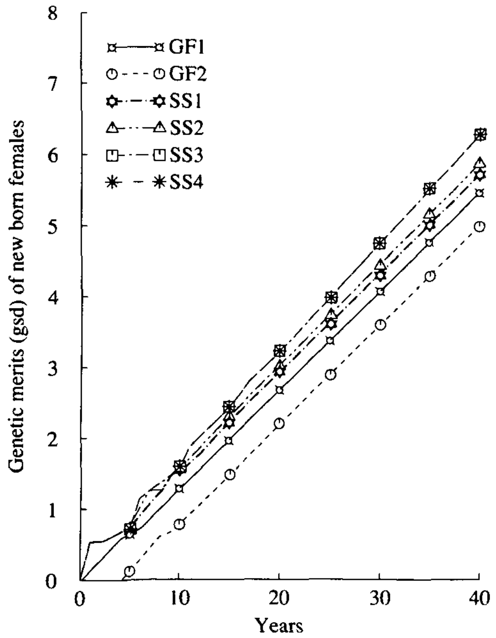


Fig. 6.2. Comparison of genetic merits of new born females using gene flow and other four selection schemes.

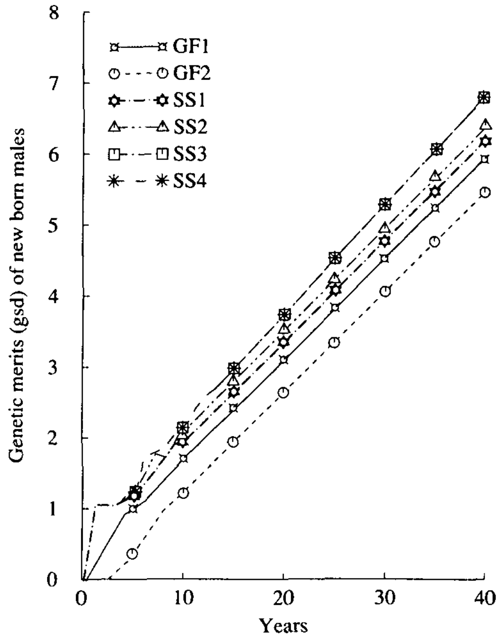


Fig. 6.3. Comparison of genetic merits of new born males using gene flow and other four selection schemes.

6.2 and 6.3. There were some differences in pattern of genetic improvement, especially, at the early stage among GF1, GF2 and SS1. However, in the later years, nearly straight lines for these schemes envisage the same asymptotic yearly genetic improvement. The differences between GF1 and GF2 in the early years were due to the placement of 1.0 in n vector at the outset. For example, for the path of SS the elements of initial n_0 for GF1, GF2 and SS1 were:

$n_0' = [0, 0, 0, 0, 1, 0, 0, 0]$; GF1
$n_0' = [1, 0, 0, 0, 0, 0, 0, 0]$; GF2
$ms(i,0) = [0, 0, 0, 0, \Delta g, \Delta g, \Delta g, \Delta g]$; SS1

The differences between SS1 and GF1 or GF2 are due to the contribution of multiple or single, age class in the first year of the breeding plan. These differences affected the genetic improvement in their respective schemes and exhibited the genetic improvement lag, genetic differences among different strata in a pyramidal structure of populations at a particular time[4]. Both the genetic superiority and accuracy of selection were the same for three selection schemes, therefore, the variation in response between GF1 or GF2 and SS1 reflects the differences in their respective algorithms.

The yearly variation in genetic improvement in SS1, GF1 and GF2 converged to an identical value while this converged value was higher in SS2 and SS3 or SS4 (Fig. 6.4). The responses to selection schemes SS3 and SS4 were same.

2. Genetic improvement from four selection schemes

The scheme-specific algorithm was employed to predict the genetic response

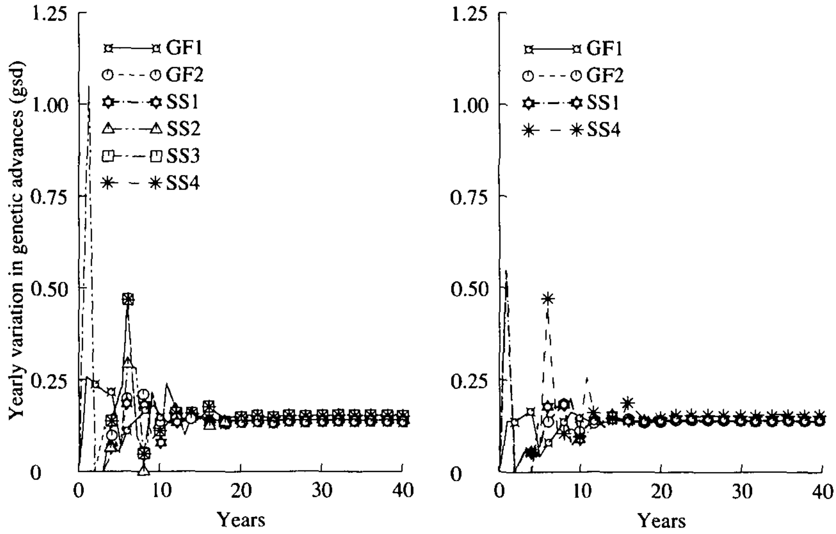


Fig. 6.4. Comparison of yearly variation in genetic advances of new born males (left) and females (right) using gene flow and other four selection schemes.

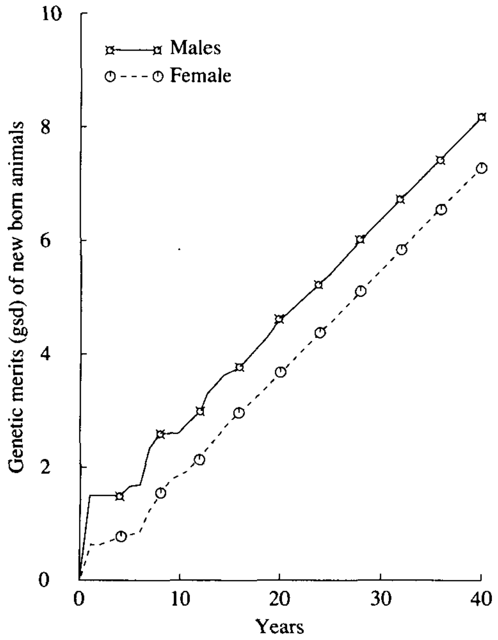


Fig. 6.5. Evolution of genetic merits of new born males and females employing selection scheme 4.

to four truncation selection schemes. Starting from a completely unselected homogenous population, dams and sires of young bulls were selected concurrently. Evolution of genetic merits of new born males and females, over 40 years, are depicted in Fig. 6.5 using only selection schemes SS4 to avoid overcrowding on the graph and also owing to the similar trends of genetic merits of males and females (Figs. 6.2 through 6.4) among four selection schemes. The genetic merits of new born males were higher than new born females due to concurrent selection of both sires and dams of males while for females the improvement was only through the sires to breed cows path and dams to breed cows were not selected (Table 6.1). The genetic merits of new born females reached a steady-state earlier compared to males because selection was performed for only one path (sire to breed cows) while for new born males selection was carried out for both (sires and dams to breed bulls) paths. Therefore, on the male side more years were required to reach a steady-state. However, after reaching the steady-state the yearly genetic improvement in males and females was similar.

The comparison of evolution of genetic merits as affected by selection schemes for females and males is shown in Figs. 6.6 and 6.7, respectively. In the early years, the predicted genetic merits were identical among schemes due to the assumption of genetically homogenous population, no genetic differences among age classes, at the outset. After implementing the selection scheme described in

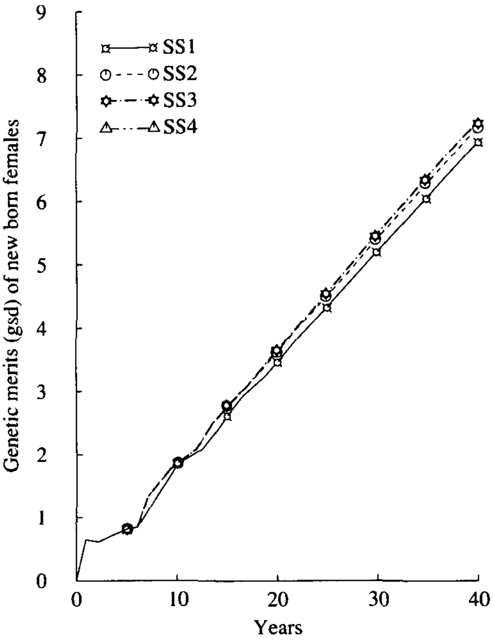


Fig. 6.6. Evolution of genetic merits of new born females employing selection schemes.

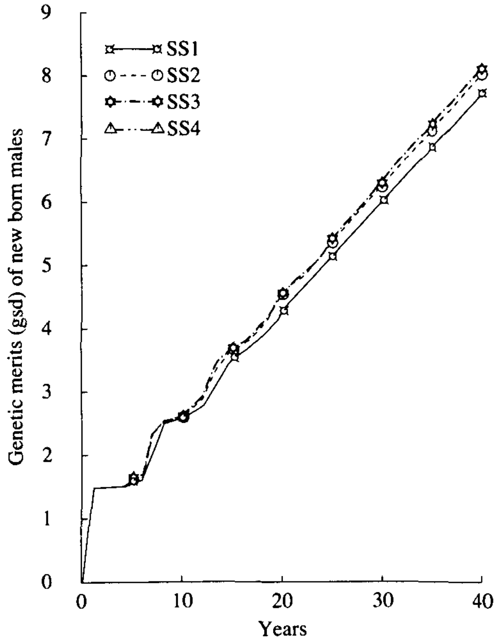


Fig. 6.7. Evolution of genetic merits of new born employing four selection schemes.

Table 6.1, the population diverges into different age groups having different genetic means, but same genetic variance, due to the presence of improvement time lags in the population and differential rates of replacements among age groups and sexes. The predicted genetic responses among selection schemes differed at that stage in both males and females. The selection schemes SS3 and SS4 predicted the identical genetic merits were ranked on the top while SS1 was at the lowest rank for predicting the genetic merits. The genetic improvement obtained by SS2 was lower than SS3 and SS4 but higher than SS1. The differences between SS2 and SS3 or SS4 were reduced with the increase in accuracy of selection as exhibited in Figs. 6.6 and 6.7 ($r=0.588$ for females and 0.85 for males) versus Figs. 6.2 and 6.3 ($r=0.5$ both for females and males), respectively.

3. Yearly variation in genetic responses

The comparison of yearly variation in genetic gain of new born males and females is presented in Figs. 6.8 and 6.9, respectively. The variation pattern in genetic gain was almost the same among the schemes. The magnitude of variation in genetic gain at the outset of breeding schemes was identical due to the assumption of a homogenous population. After the setup of genetic gaps between age classes, the yearly genetic gain varied among schemes and then it reaches a scheme-specific equilibrium. The time required to reach equilibrium

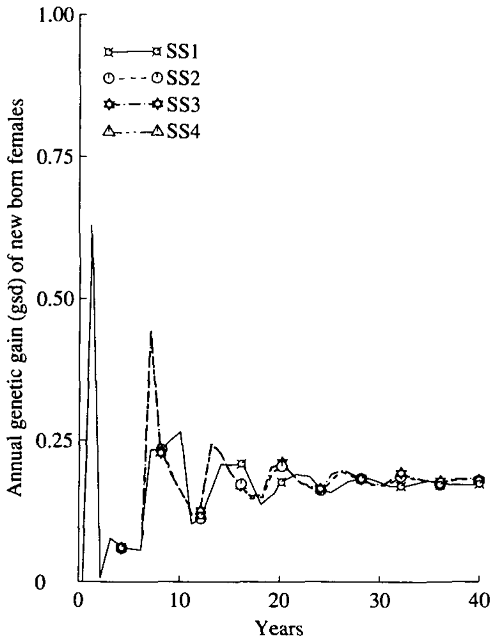


Fig. 6.8. Comparison of yearly variation in genetic gains of new born females using four selection schemes.

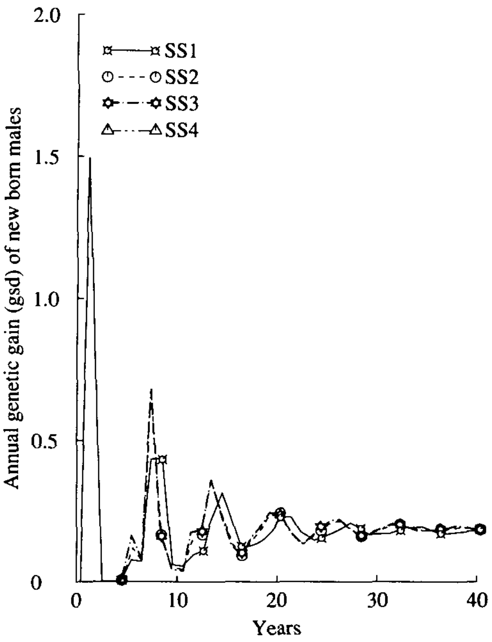


Fig. 6.9. Comparison of yearly variation in genetic gains of new born males using four selection schemes.

depend on the age structure of each path considered in the selection. The age structure (Table 6.1) of the SS and SC paths was identical in Fig. 6.4 where the scheme-specific equilibrium was attained after 18 years, however, age structures for the same paths were different in Figs. 6.8 and 6.9 where scheme-specific equilibrium was not attained even till 40th year after implementing the described selection scheme. Yearly gain was higher for SS3 and SS4 as compared to SS2 and SS1. Figs. 6.8 and 6.9 also stress the nonlinearity of the response to selection through four selection schemes as a strong relationship between age and genetic merit of an animal.

The yearly variation in average ages and genetic superiorities on the path of dams of sires are presented in Figs. 6.10 and 6.11, respectively. The average ages were younger in SS4 followed by SS3, SS2 and SS1. The average ages in SS1 were not influenced by any factor considered in this study for the selection of the same proportion within each age class. The genetic superiorities were higher or identical in SS4 and SS3, followed by SS2 and SS1.

4. Asymptotic responses

Asymptotic genetic gain was computed using [1.2]. The genetic superiorities and average ages for each path were computed using [6.3] and [6.2] every

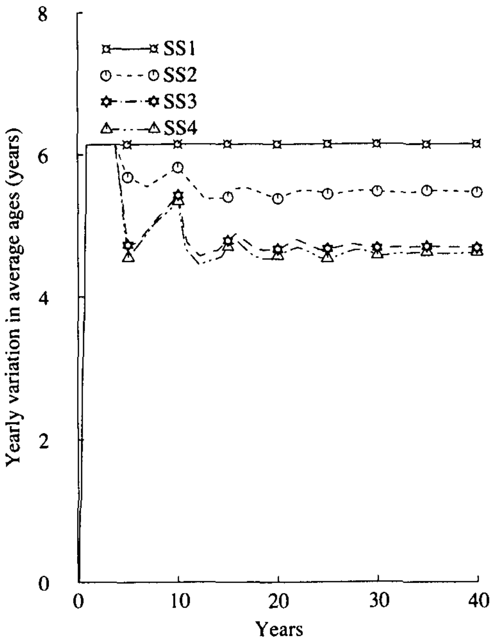


Fig. 6.10. Comparison of yearly variation in average ages on the path of dams of sires employing four selection schemes.

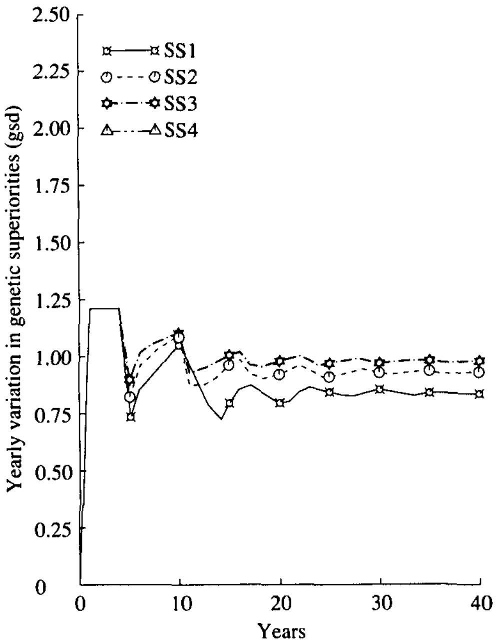


Fig. 6.11. Comparison of yearly variation in genetic superiorities on the path of dams of sires using four selection schemes.

Table 6.2. Generation intervals, genetic superiorities and asymptotic genetic gain computed through four selection schemes.

Schemes[a]	Generation intervals[b]					Genetic superiorities[c]					ΔG_a
	SS	DS	SC	DC	Avg	SS	DS	SC	DC	Avg	
SS1	6.50	6.15	7.50	4.60	6.19	1.69	0.83	0.99	0.0	0.88	0.142
SS2	6.38	5.47	7.19	4.60	5.91	1.71	0.93	1.03	0.0	0.92	0.155
SS3	6.38	4.70	7.09	4.60	5.69	1.71	0.98	1.03	0.0	0.93	0.163
SS4	6.38	4.62	7.03	4.60	5.66	1.71	0.98	1.03	0.0	0.93	0.164

Paths of transmission of genes from one generation to the next generation (SS : sires to sires ; DS : dams to sires ; SC : Sires to cows ; DC : dams to cows).

a Selection schemes, refer to text.

b In years.

c In genetic standard deviation units (gsd).

ΔG_a Asymptotic genetic gain.

year. After the initial oscillation, the values converged to a constant figure for each path. These respective constant values were used in [1.2] for each path of selection to obtain asymptotic yearly genetic gain. The asymptotic genetic gain for each selection scheme is presented in Table 6.2. The generation intervals and genetic superiorities for all selection schemes after reaching the equilibrium are also given in Table 6.2. SS1 leads in longer generation interval and lower genetic superiorities for each path compared to all other schemes. As compared to SS3 and SS2, SS4 manifested shorter generation intervals on DS and SC paths, which have either larger number of age classes or more number to be selected. The genetic superiorities were identical between SS4 and SS3 but higher than SS2 for these two paths. Asymptotic genetic gain was higher in SS4 followed by SS3 after the correction of genetic superiorities for small sample size of population as proposed by BURROWS11). The SS4 predicted 15.49, 5.81 and 0.61 percent higher asymptotic genetic gain as compared to SS1, SS2 and SS3, respectively.

D. DISCUSSION

Optimization of selection schemes involves various aspects of research in animal breeding such as defining the aggregate genotype, identification of different alternatives, estimation of biological (genetic) and economic parameters, construction of selection indices (computing estimated breeding values) and comparison of responses and costs associated with the application of alternative breeding schemes10). For the discrimination among the breeding schemes net returns are considered in terms of genetic gain and/or an economic value associated with the genetic improvement. After the initial work of DICKERSON and HAZEL21) and ROBERTSON and RENDEL77), the methodology was extended by Rendel and ROBERTSON73), SKJERVOLD and LANGHOLZ90) and LINDHE65). LINDHE65) introduced the variation in number of deep frozen semen doses and financial returns versus costs. Many studies were carried out especially for dual purpose cattle regarding the economic evaluation of breeding schemes after the initial work of LINDHE65). These studies were dealt with linear improvement at a stable state. McClintock and CUNNINGHAM66,67) and HILL40) developed the methodology to predict responses in early years and argued that ultimately, selection results in stable genetic gain after initial oscillation among years. The procedure involves the analyses of the gene flow of selected parents through a population, both in time and in different tiers usually referred to as 'gene flow method' and in economic analyses, future returns discounted usually back to the reference time is called 'discounted gene flow method'.

Population inventory approach first described, independently, by HILL40) and Elsen and MOCQUOT25) has been in use for predicting the genetic responses. This approach identifies groups of different ages and monitors their average genetic merit through time. This approach has been used for predicting the genetic gain19,23,40,41,88,99) as in this case, and for monitoring the average inbreeding coefficient in small populations20,62). The same approach has also been used for studying diffusion of Holstein genes in crossbred French Friesian population16). This is also extended to include complex hierarchical population24), inclusion of economic parameters for prediction of benefits from breeding programs.

Genetic and economic comparison of selection schemes based on this model have been reported for cattle [22,26], sheep[26], and swine [27]. Most of these authors assumed constant selection differentials. However, HILL[40] do noted that when the rule of BICHARD *et al.*[5] is applied the selection differentials are time-dependent and fluctuate in the early years substantially. The method described for the computation of time-dependent selection differential is directly applicable to the population inventory approach. Time dependent results can be obtained by repeatedly using [6.4].

The comparison of genetic responses among SS1, GF1 and GF2 coincided asymptotically but the initial differences among these three schemes were attributed to selection of parents which in SS1 occurs concurrently among age classes and in GF1 and GF2 only in one age class and then the replacement rates determined the age structures. The differences in GF1 and GF2 are solely the time consideration of the expression. In GF1 n vector is set to express the genetic responses in new born animals immediately after the breeding plan starts while in GF2 the responses are not expressed immediately. GF2 accounts for the time required for sexual maturity and then discounted expressions were expressed indicating the time lag in this scheme. The rate of improvement was not affected with this change as shown in Figs. 6.2 through 6.4. The decrease in generation intervals is usually accompanied with a decrease in selection intensity due to limitation of low reproductive rate. The genetic merits of new born animals are the function of both the genetic superiority and generation intervals of sires and dams. The decrease in generation interval in SS4 as compared to SS3 in the early years was little and, consequently, genetic merits of new born animals did not differ between SS3 and SS4 significantly. However, SS1 and SS2 manifested lower genetic improvements.

There is a great variety of breeding improvement systems in livestock selection and/or breeding schemes and their respective achievements[92]. SMITH and BANOS[95] presented an algorithm for selecting within or across populations by using the common truncation line over the distributions of estimated breeding values for different populations. The problem is similar tackled here in SS3 to select the best over a certain threshold. This truncation may be across the age classes or across the populations. Recently many authors have used the accuracy of selection in different contexts. GOMEZ-RAYA[35] has given an algebraic expression to predict the effect of different accuracies on the genotypic variance and KLIEVE *et al.*[63] investigated the impact of different ranges of accuracies of selection on genetic response and utility.

Truncation was based on the same genetic selection differential (average genetic superiorities of selected animals, $Ir\sigma_a$) among age classes for SS4. The selection differential is a function of proportion selected and accuracy of selection. The advantage of SS4 over SS3 was tied up with the number of age classes and proportion selected. The higher selection intensity at other fixed variables favors the SS4 which could be obtained through Multiple Ovulation and Embryo Transfer (MOET). MOET is usually considered as a means to shorten the generation length and increasing the selection intensity on dams path. Many authors have employed the MOET in the evaluation of breeding schemes such as BONDOC and SMITH[6)], COLLEAU[14)], DEKKERS[17)], JUGA and MAKI-TANILA[61)], NICHOLAS and SMITH[71)], RUANE[80)], RUANE and THOMPSON[81)] SMITH[94)] and WOOLLIAMS and WILMUT[104)].

E. SUMMARY

A simple procedure for predicting the long-term genetic merits of new born (males and females) was presented. Four selection schemes (SSs) were compared to appraise the effect of base of truncation across the age classes. SS1, truncation across the ages with given fixed proportions among age groups, was inferior among four schemes for any combination of parameters. SS2, truncation on phenotypic values, gave lower genetic values as compared to SS3 (truncation on predictor values) and SS4 (truncation on predictor values with the condition of same average predicted genetic values of selected animals across the age classes). Selection schemes SS3 and SS4 were competitive with each other. SS4 has a marginal edge over SS3 if the comparison is carried out on the asymptotic theory or if the number of age classes were large and selection intensity was higher. This marginal edge vanish with some other combinations leads to the conclusion that truncation on predictor values (SS3) will be preferred over all other schemes due to its easiness to apply on actual dairy data. Gene flow method devised by HILL[40)] and computer program GFLOW by BRASCAMP[10)] underestimates the genetic responses and the current use of optimal breeding schemes limits the utility of that method.

CHAPTER VII

CONCLUSIONS

When generations overlap in a dairy cattle population, the computation of the genetic selection differential is not as straight forward as considering the discrete generations (genetically homogenous parental age groups). For optimized breeding schemes the optimum generation intervals and optimum selection differentials are required. The generation intervals can be optimized by computing the optimum fractions to be selected across the age classes. The genetic selection differentials, in a population with overlapping generations, are time dependent particularly in the early years of breeding schemes. Till now, no study appears in the literature regarding the consequences of truncation based on same genetic selection differentials ($Ir\sigma_a$) across the age class. Keeping in view the importance of time dependent selection differentials and optimum generation intervals in the optimum breeding strategies, a series of theoretical and simulated studies were initiated to pave the way for developing a simple algorithm to evaluate alternative breeding schemes. The present study consists of five successive investigations performed consecutively. The two most common assumptions were:

i) multivariate normal distribution of records and genetic values,
ii) normality and genetic variation is maintained generation after generation in each age class.

The biases in generation intervals were studied in the first step (Chapter II) since MEUWISSEN[68] cited that the method of gene flow devised by HILL[40] was inappropriate to evaluate the breeding schemes due to fixed age structures without investigating the possible biases in age structures. Then, in the second study (Chapter III) the algorithm reported by DUCROCQ and QUAAS[23] was generalized and a new algorithm was developed to optimize the selection across the age classes. Four selection schemes, using a different algorithm in each scheme, were compared for predicting single generation response. The third study (Chapter IV) was conducted to verify the developed algorithm using Monte Carlo simulation. The implications of the proposed and other relevant available algorithms to predict generation intervals and annual genetic superiorities were visualized in the fourth study (Chapter V) using two pathways selection schemes. Lastly, in the fifth study (Chapter VI) the algorithms were extended to predict the time depended optimum selection differentials and optimum generation intervals and, consequently, the short and long term genetic responses. The newly developed algorithm was compared with the gene flow method of HILL[40] and BRASCAMP[10]. The conclusions drawn from these studies are summarized below.

1) If the selection is not optimized across the age classes, the assumed parental age structures based on genetically homogenous parental age groups may depart considerably from the actual age distribution of parents contributing to the next generation in a population with overlapping generations. This is particularly true for the pathways with a large number of age classes and relatively intense selection such as maternal granddams of sires.
2) A new algorithm was developed to evaluate the optimized breeding schemes. The new algorithm was presented in general form which could be applied to predict the genetic response to truncation selection across the age classes on the distribution of phenotypic values and selection index predictor after some relevant modifications for standardization of distribution in numerical analyses.
3) In this developed algorithm, the age-specific truncation selection points were computed with the same average predicted genetic merits of selected animals across the age classes.
4) Four selection schemes (SSs), each of them differentiated by the base of

truncation across the age classes, were framed and compared to assess the implications of the proposed algorithm to predict the genetic responses.

5) Truncation selection on equal intensity across parental age classes (SS1) was inferior to all other schemes. Selection on common truncation line on phenotypic values (SS2) was superior to SS1 but inferior to SS3 (selection on common truncation line on estimated breeding values) and SS4 (selection on age-specific truncation point with the same average predicted genetic merits of selected parents across the parental age classes).
6) The short-term genetic response to selection was higher using SS4 (new proposed algorithm) as compared to SS3, however, long-term response was same to SS3.
7) The newly developed algorithm was a superior gene flow method than that devised by HILL⁴⁰⁾ and BRASCAMP¹⁰⁾ for predicting the genetic response in the early years of the selection program.
8) The developed algorithm can easily be extended to capitalize new emerging reproduction technologies such as MOET and semen sexing since both add in accuracy of selection which is an input parameter of the model.

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