FACTORS AFFECTING AGE STRUCTURES AND GENETIC RESPONSES TO TRUNCATION SELECTION SCHEMES IN A POPULATION WITH OVERLAPPING GENERATIONS

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Summary

Four truncation selection schemes (SSs) were framed to predict and compare the age structures and genetic responses under the influence of various factor employing the scheme-specific algorithms. 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 precision of evaluation, 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, and 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 candidates' distribution) revealed longest generation lengths and lowest yearly genetic responses. The average ages were youngest and yearly genetic responses were highest in SS4 (selection at each age-specific truncation point with the same average genetic superiority of selected parents across the ages) and followed by SS3 (selection at each ages-pecific truncation point with same predicted genetic values) and SS2 (selection at common truncation point on phenotypic values) in a population with overlapping generations. The results revealed the importance of choosing suitable selection scheme to acquire maximum yearly genetic responses especially when the genetic differences among age classes are large and the precision of evaluation is relatively low.

(Key Words: Truncation Selection, Age Structures, Genetic Responses)

Introduction

When generations overlap, the potential candidates for selection at a time are progeny from parents of different ages and the parents themselves are expected to be of different genetic merits as a consequence of the strong relationship between the genetic merit and age of the parents. Consequently the parents belongs to different distributions with different means and variance. Therefore it is reasonable to expect that the genetic merits of potential candidates are not belonging to an unique distribution. Consequently, if normal truncation selection across the distributions is applied by 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. Shimizu and Ghaffar (1992) proposed algorithms for computing the normal truncation points on phenotypic values 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.

The objectives of this investigation are to determine the influence of several variable factors on the variation in average ages (generation length) and genetic responses to 4 different selection schemes and their differences among schemes, and to find best theoretical selection scheme within the stated assumptions.

Materials and Methods

Assumed variable factors

Assumptions and variable factors considered

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Received February 5, 1993
Accepted July 10, 1993

in this study are presented in table 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 (Van Vleck, 1977). The third path, involving sires, sires to breed cows was taken into account by changing the selection intensity on the path of bulls' sires. Genetic differences among age classes (5 levels) with constant differences among ages, precision of evaluation (correlation of breeding values with the criterion of evaluation, r; 4 levels) with the same values across the age classes, 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 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 every year and out of these progeny tested bulls the 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 same and the number of selected bulls were changed.

TABLE 1. ASSUMED PARAMETERS AND VARIABLE FACTORS SETTED IN THE STUDY

Assumed variable factors	Values
Genetic parameters	
Genetic variance (constant across the age classes)	1.0
Genetic differences among age classes: 5 levels (genetic standard deviation unit)	0.0, 0.05, 0.10, 0.15, 0.20
Precision of evaluation (r): 4 levels	0.3, 0.5, 0.7, 0.9
Paths of selection	
Sires to breed bulls	
Number of candidates	200 young bulls
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 the age classes	0.50 or 0.25
Proportions selected: 4 levels	0.02, 0.04, 0.05, 0.10
Dams to breed bulls	
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

Selection schemes

Four selection schemes (SSs), 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 of candidates' distribution across the age classes: SS1 (Method I in previous paper (Shimizu and Ghaffar, 1992)),

2) selection at the common truncation point based on phenotypic values across the age classes: SS2 (Method II),

3) selection at each age-specific truncation points on the same predicted genetic values across the age classes: SS3 (Method III), and

4) selection at each age-specific truncation points with the same average genetic values of selected parents across the age classes: SS4

(Method IV).

The detailed algorithms for operating these selection schemes are presented by Shimizu and Ghaffar (1992), 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 is given in table 2.

TABLE 2. NUMERICAL ILLUSTRATION FOR DISTINCTION 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 0.60, PRECISION OF EVALUATION 0.05, 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	460	276	165	99
Proportions selected among age classes				
SS1	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
Truncation points[a,d]				
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
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
Genetic selection differentials[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

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

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 includes age distribution of candidates, genetic means of each age class of candidates, precision of evaluation, numbers in the base population and numbers to be selected. The generation length (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 highest genetic means. It is useful for asymptotic results to measure the genetic superiority of selected animals as the deviation from the youngest age class means instead of population means (Ducrocq and Quaas, 1988). The average yearly genetic responses were

computed by dividing the weighted means of the genetic superiority by generation length of parents. Since actual population size was finite hence the selection intensities were corrected for finite numbers of sampled animals according to the method proposed by Burrows (1972).

Results

Effect of variable factors on age structures

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 (figures 1, 2 and 3). The average ages of selected animals in SS1 were unchanged for any level of genetic differences among age classes, precision of evaluation and proportions selected. The average ages of selected animals in SS2, SS3, SS4 were reduced by augmenting the genetic differences among age classes (figure 1). However, an increase in the precision of evaluation results in reduction in average ages in SS2 and an increase in SS3 and SS4. Consequently the differences in average ages among the schemes reduced at higher precision except for SS1. The elucidation of this tendency among these selection schemes is given in Appendix. Consequently the differences in average ages among the schemes reduced at higher precision except for SS1. Overall, the average ages were youngest in SS4 followed by SS3 and SS2 for incorporating each of the assumed variable factors (figures 1, 2 and 3). When the proportions selected are increased from 0.05 to 0.25 the average ages are increased in all schemes except SS1. This reduces the differences between SS1 and SS2, and increases the differences between SS3 and SS4 (figure 1.a vs 1.b).

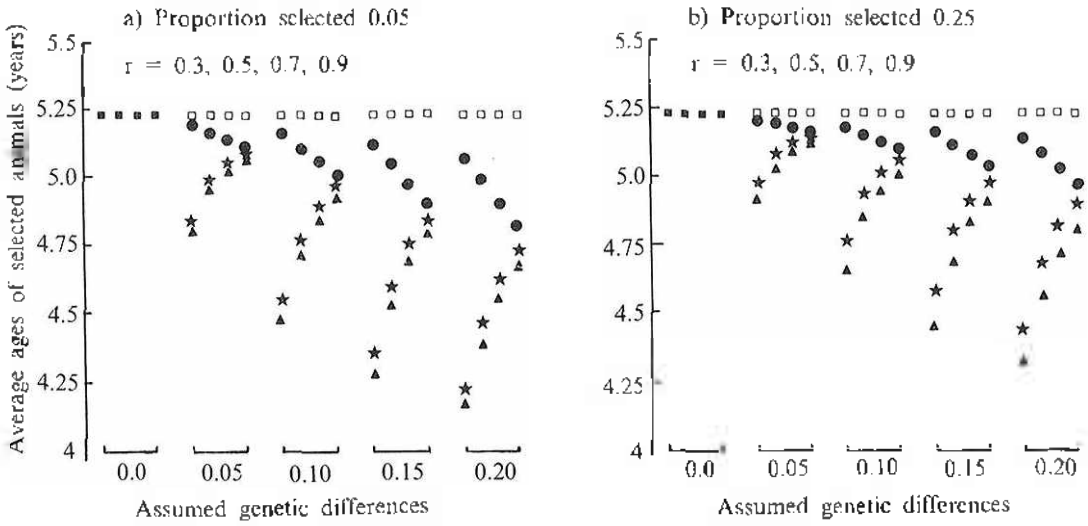

Figure 1. Effect of proportions selected on average ages through four selection schemes at different levels of genetic differences and precision of evaluation (r) on the path of bulls' dams with 4 age classes and stayability 0.80. SS1 ○ ; SS2 ● ; SS3 ★ ; SS4 ▲ .

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 (figure 1.a vs 2.a). 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 (figure 2.a vs 2.b) due to higher proportions of younger ages in the total population. On the path of bulls' sires the pattern was the same as on the bulls' dams. However, when the number of age classes were two and the selected proportion was 0.2, the average ages of selected animals

among schemes 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 (figure 3.a). Increasing the selected proportions from 0.02 to 0.10 on this path cleared this tendency (figure 3.b). The similar results were found with four age classes on bulls' sires path which were omitted for brevity.

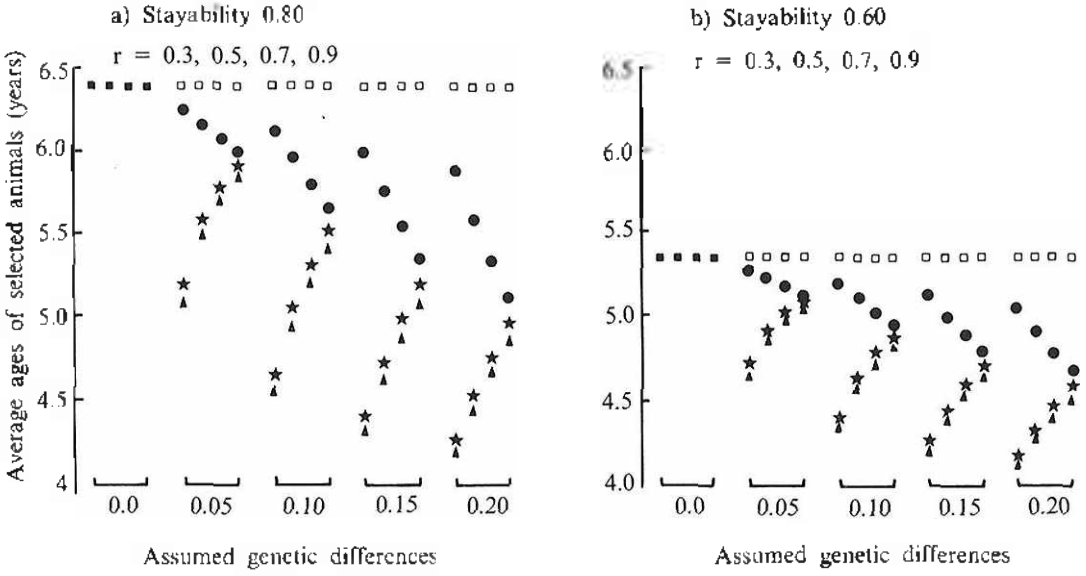

Figure 2. Effect of stayability on average ages through four selection schemes at different levels of genetic differences and precision of evaluation (r) on the path of bulls' dams with 8 age classes and proportions selected 0.05. SS1 □ ; SS2 ● ; SS3 ★ ; SS4 ▲ .

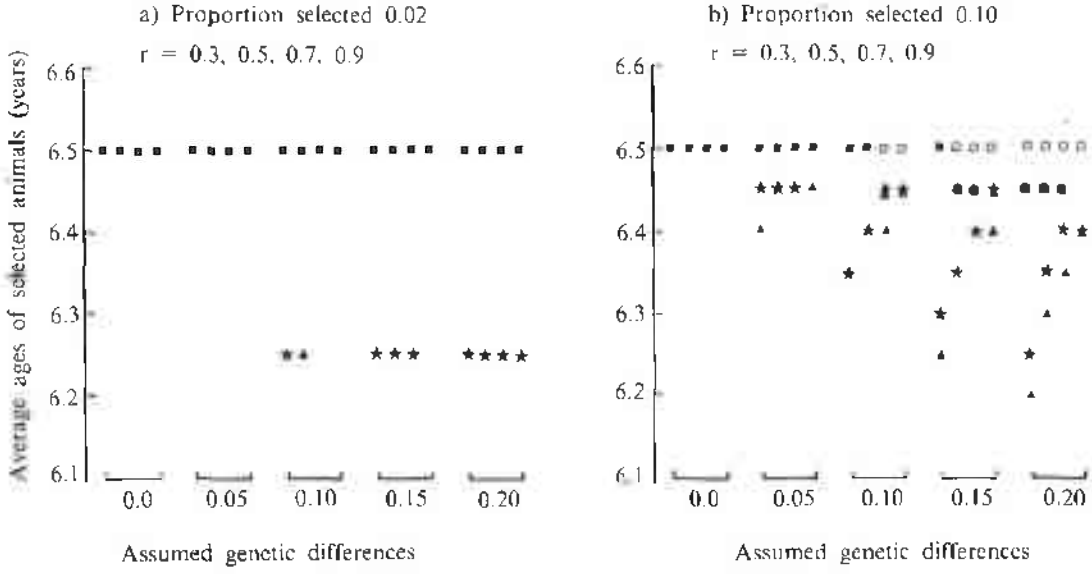

Figure 3. Effect of proportions selected on average ages through four selection schemes at different levels of genetic differences and precision of evaluation (r) on the path of bulls' sires with 2 age classes. SS1 □ ; SS2 ● ; SS3 ★ ; SS4 ▲ .

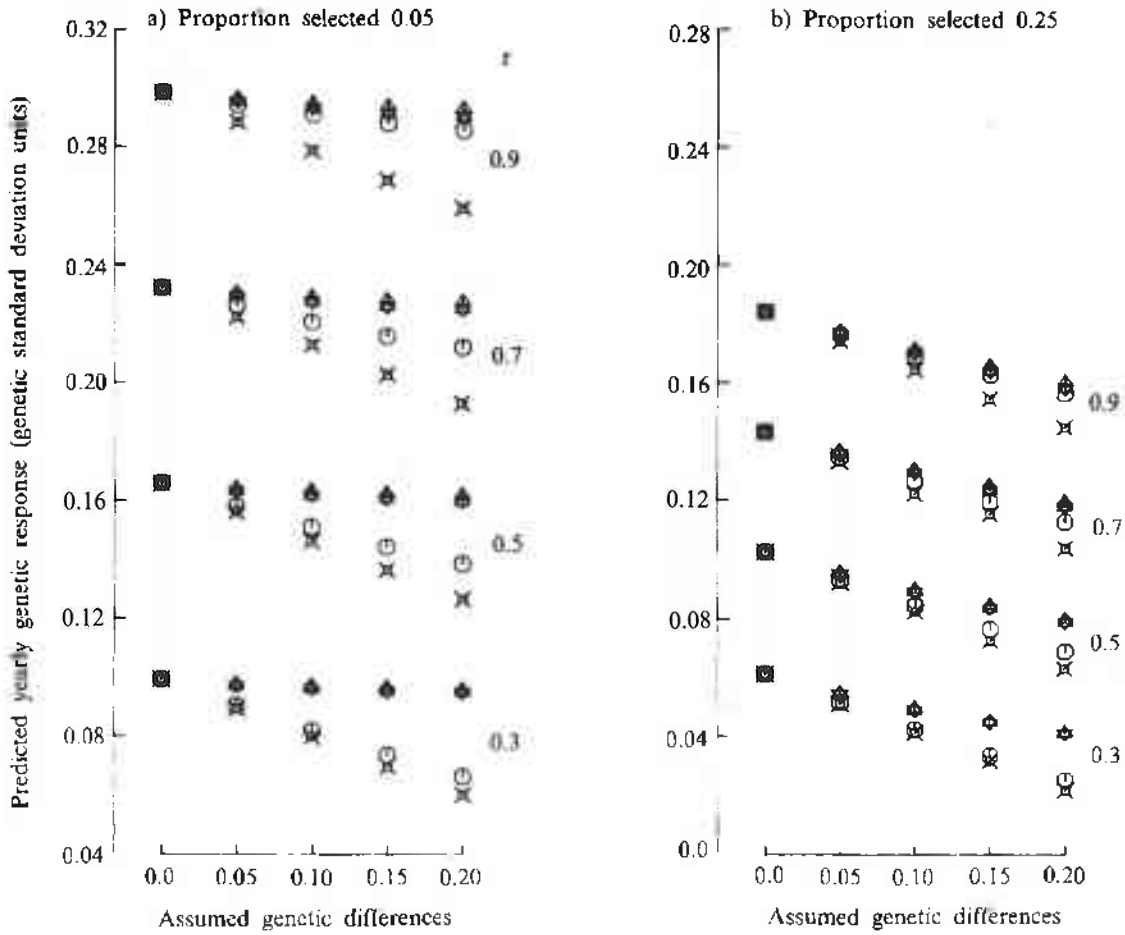

Figure 4. Comparison of yearly genetic responses through four selection schemes at different levels of genetic differences and precision of evaluation (r) on the path of bulls' dams with 4 age classes as affected by proportions selected at stayability 0.80. SS1 ✖ ; SS2 ⊙ ; SS3 ✿ ; SS4 ▲ .

Effect of variable factors on genetic responses

In the absence of genetic differences among age classes the population, the average yearly genetic responses obtained employing four selection schemes were similar for a particular level of precision of evaluation (figures 4, 5 and 6). With the increase of genetic differences among age classes the differences in responses among the schemes were increased. The lowest genetic responses in SS1 may be 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 increased with augmenting the genetic differences and these relative differences reduced with greater proportions selected (figure 4.a vs 4.b). The differences between SS2 and SS3 or SS4 diminished with enhancing the precision of evaluation (figure 4). The SS4 showed maximum annual genetic responses and was followed by SS3, SS2 and SS1 (figure 4). When the number of age classes were increased from 4 to 8 on the path of bulls' dams, the differences among the schemes increased (figure 4.a vs 5.a). Decreasing stayability from 0.80 to 0.60 results in reduction in relative differences between SS2 and SS3 or SS4 and, indeed, the absolute values of responses were increased for all schemes (figure 5) due to younger average ages. On the path of bulls' sires, there were no differences in yearly genetic responses among the schemes till the genetic differences augmented to 0.1 genetic standard

deviation (figure 6.a). 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 (figure 6.a vs 6.b).

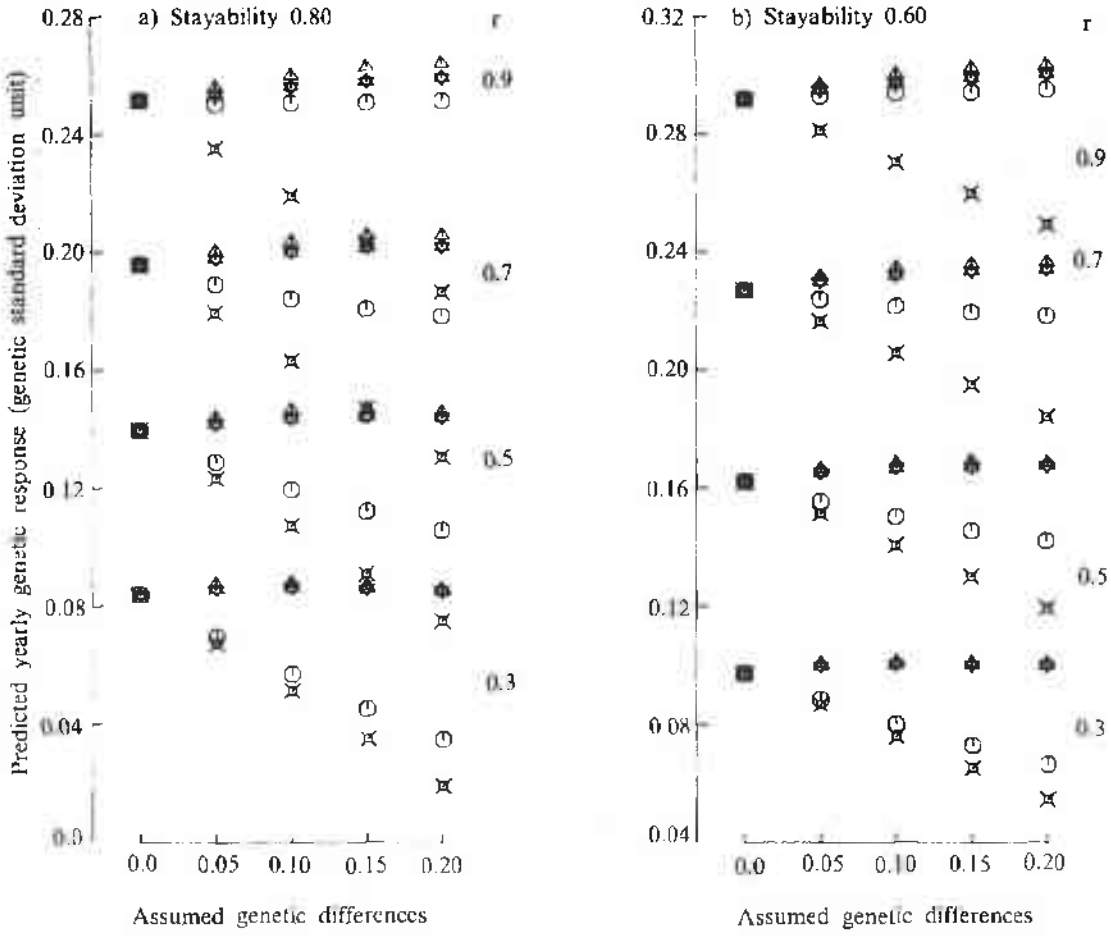

Figure 5. Comparison of yearly genetic responses through four selection schemes at different levels of genetic differences and precision of evaluation (r) on the path of bulls' dams with 8 age classes as affected by stayability at proportions selected 0.05. SS1 ⌘ ; SS2 ◷ ; SS3 ✿ ; SS4 ▲ .

Discussion

Among assumptions 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 many authors (e.g. Hill, 1977; Hopkins and James, 1979; James, 1979; Ducrocq and Quaas, 1988). Similarly precision of evaluation was assumed to be same across the age classes. These both facts were ignored for simplicity.

The selection scheme SS4, truncation on phenotypic values with the condition of same average genetic superiorities of selected animals has not been reported previously. It is shown in the results that selection at separate truncation points on phenotypic values at same predicted genetic values (SS3) or same average predicted genetic values of selected animals (SS4) declined the proportions to be selected from older cows relatively at higher rate compared to SS2 and consequently decreased the average ages more in SS3 and SS4 as compared to SS2. The reduction in average ages in SS2, SS3 and SS4 with augmenting the genetic differences among age classes is attributed to the selection of larger

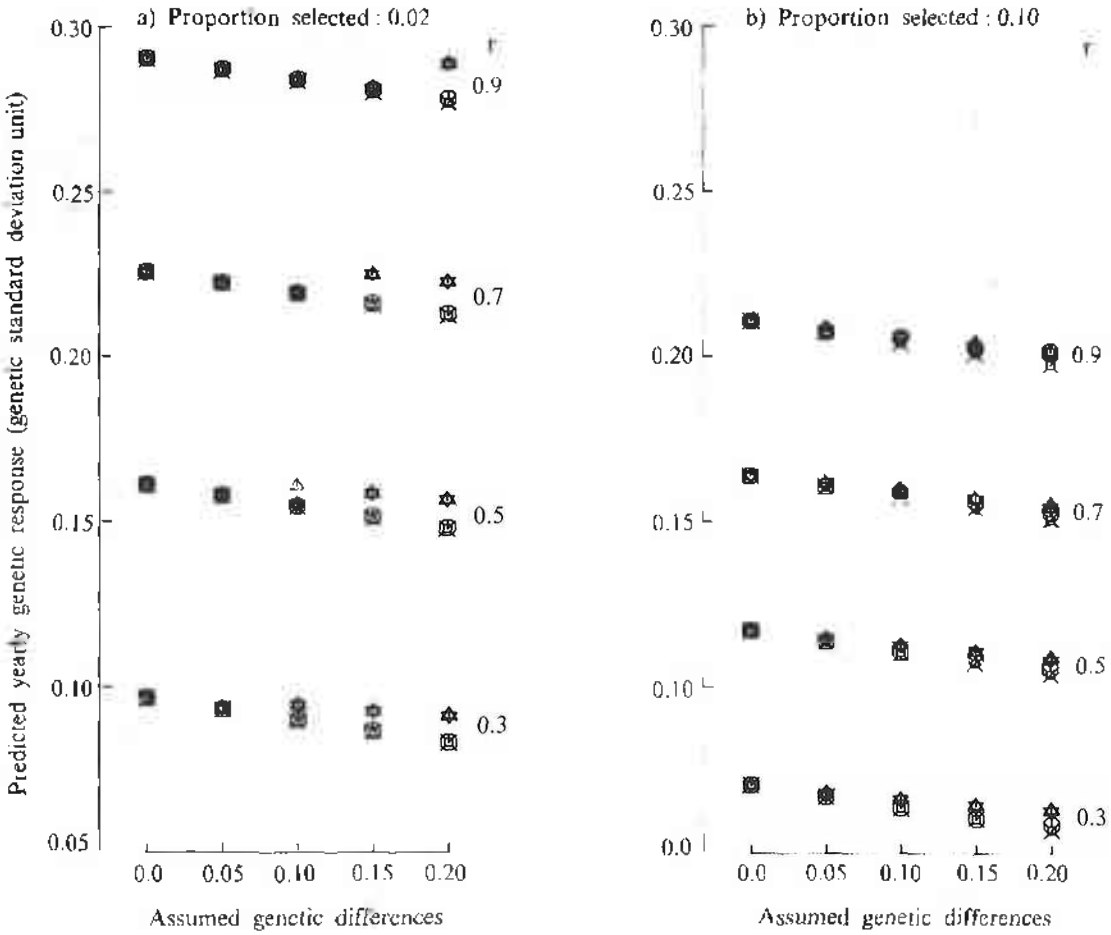

Figure 6. Comparison of yearly genetic responses through four selection schemes at different levels of genetic differences and precision of evaluation (r) in the path of bulls' sires with 2 age classes as affected by proportions selected. SS1 ⊠ : SS2 ⊙ : SS3 ✿ : SS4 △ .

proportions from younger parents with high genetic merits as compared to proportions selected from older parents of low genetic merits. However, augmenting the assumed precision of evaluation results in younger ages in SS2 and older ages in SS3 and SS4 at any level of genetic differences. The elucidation of this pattern is presented in Appendix in terms of rate of change of truncation points on standardized normal distributions and consequently the proportions selected across the age classes.

When selection is applied on common truncation point at the same phenotypic values across the age classes, the truncation point is from [A4] as

$x_1 = r_1 d_1 + x_0 r_1/r_0$

When r increases to r', x_1 changes to x_1' then the differences in truncation points ($\triangle x = x_1' - x_1$) could be found keeping the selected proportion from youngest age class constant (the point in the youngest age class is fixed).

If $r_1 = r_0$, $r_1' = r_0'$ (as in this study) or $r_1'/r_0' = r_1/r_0$ then

$\triangle x = (r_1' - r_1)\, d_1 > 0$

It is evident from above equation that $\triangle x$ depends on the rate of change in r and d but independent from x_0. When r_1 increase to r_1' then $\triangle x$ is positive to change the truncation point to a larger level so the proportion (p) to be selected from $_1$th age class decreases. This implies that the relative proportion from older age compared to younger age class becomes small as the accuracy (r) and/or genetic differences (d) increases and consequently the average ages are decreased.

When selection is practiced on truncation points with same predicted breeding values (SS3) the truncation point at the $_i$th age class can be found by [A5] and the rate of shift in x is found by [A7]

$$\triangle x = d_i\ (r_i - r_i')/r_i\ r_i' \qquad [A7]$$

When r_i' is greater than r_i, $\triangle x$ is negative. Hence truncation point will be shifted to lower level and thus P_i' is greater than P_i resulting an increase in average ages due to selection relatively higher proportion from older age classes.

When selection is practiced on same average predicted genetic values of selected animals (SS4), change in standardized selection differentials (I_i) can be obtained from [A9]

$$\triangle I = d_i\ (r_i - r_i')/r_i\ r_i' \qquad [A9]$$

When r_i' is greater than r_i, $\triangle I$ is negative. Hence truncation point will be moved to lower level and thus P_i' become larger than P_i hence an increase in average ages. The equations [A9] and [A7] are coincident giving the similar results. These formulae elucidate the variation in pattern of average ages among schemes.

The yearly genetic responses in SS1 were lowest attributed to longer generation length due to selection of fix proportions across the age classes. The results are in agreement to Bichard, et al. 1973 and Ducrocq and Quaas, 1988. The response in SS2 was inferior to both SS3 and SS4 is in agreement to Bichard, et al. 1973; Hill, 1977; Hopkins and James, 1979. The number of age classes (figure 4.a vs 5.a) exhibited an inverse relationship with yearly genetic responses. When the number of age classes increased, the yearly genetic responses were predicted to be smaller due to longer generation lengths. The number of age classes can be controlled artificially which would be limited by the reproduction 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.

When genetic differences among age classes and selection intensity were increased, the differences in yearly genetic responses to selection 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 precision of evaluation the differences between SS1 and SS2, SS3, or SS4 increased but the differences between SS2 and SS3 or SS4 became smaller as per expectation. The differences in responses between SS3 and SS4 were enlarged with higher genetic differences and higher precision of evaluation. It can be concluded that in the population where large genetic differences among age classes exists 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 has described the age structures and genetic responses in different contexts. Hopkins and James (1977) and James (1979) compared parent and progeny selection strategies and concluded that parent selection strategies are superior to progeny selection strategies. Hopkins (1978) discussed the age structures in context of open nucleus breeding systems and Hopkins (1979) 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 conditions associated with truncation selection points on the phenotypic values. Hill (1977), Hopkins and James (1977), Goffinet and Elsen (1984) and James (1987) concluded that selection should be by truncation on estimated 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 responses per year.

Acknowledgements

The authors are grateful to Inoue Foundation for Science, Japan for its partial financial support to present this contributory paper at 6th AAAP Animal Science Congress 1992 held in Bangkok, Thailand. The results of this theoretical study were computed at Hokkaido University Computing center.

Appendix

The objective of this appendix is to derive the expressions for the rate of change in the truncation points on standardized normal distribution as a function of accuracy of selection.

Figure 7 illustrates the distribution of phenotypic values 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 value and its standardized normal distribution respectively in the youngest age class and the corresponding values for $_i$th age class are m_i, k_i and x_i. Assume the genetic variance 1.0 and phenotypic variance $1/r^2$ where r_i is the precision of evaluation then

$x_0 = k_0 r_0$ and ..... [A1]

$x_i = k_i r_i$ ..... [A2]

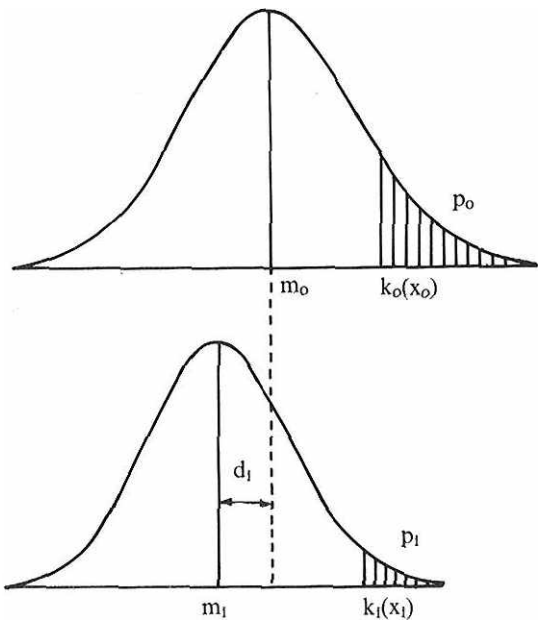

Figure 7. Distribution of phenotypic values of candidates across the ages. m = phenotypic means, k = truncation selection point and (x) = truncation point on standardized normal distribution. Subscript $_0$ and $_i$ refers to youngest and $_i$th age class respectively.

1) Selection on phenotypic values

When selection is applied on common truncation point at the same phenotypic values across the age classes, k_i with the same phenotypic value as in the youngest age class is

$k_i = d_i + k_0$, $(d_i = m_0 - m_i)$ and replacing the k_0 from [A1]

$k_i = d_i + x_0/r_0$ ..... [A3]

Now from [A3] and [A2] the truncation point on standardized normal distribution (x_i) is

$x_i = r_i d_i + x_0 r_i/r_0$ ..... [A4]

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

If selection is practiced on truncation points with same predicted breeding values (SS3) the truncation point at ith age class can be found by the relationship: $x_0 r_0 + m_0 = x_i r_i + m_i$ hence

$x_i = d_i/r_i + x_0 r_0/r_i$ ..... [A5]

when the accuracy changes from r_i to r_i' the rate of shift in the point is

$\triangle x = x_i' - x_i = d_i\ (1/r_i' - 1/r_i) + x_0\ [(r_0'/r_i') - (r_0/r_i)]$ ..... [A6]

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

$\triangle x = d_i\ (r_i - r_i')/r_i r_i'$ ..... [A7]

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

When selection is practiced on same average predicted genetic values of selected animals, standardized selection differentials (I_i) can be obtained as $I_i = (d_i + I_0 r_0)/r_i$ when the accuracy changes from r_i to r_i' the rate of change is

$\triangle I = I_i' - I_i = d_i\ (1/r_i' - 1/r_i) + I_0\ [(r_0'/r_i') - (r_0/r_i)]$ ..... [A8]

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

$I = d_i\ (r_i - r_i')/r_i r_i'$ ..... [A9]

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