Optimal Effective Population Size for the Global Population of Black and White Dairy Cattle

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ABSTRACT

The replacement of other black and white cattle strains by the North American Holstein breed, which itself is dominated by a small number of elite sires, has reduced the genetic diversity of the global population. Intense selection on a global basis leads to rapid genetic improvement but reduces effective population size.

The optimal global effective population size was chosen to maximize the net present value of all future benefits from the breeding program. Two separate discount rates were used to reflect concerns about the long-term costs of small effective population size. This led to a higher optimal number of bull-sires than in past analyses. The optimum was sensitive to the magnitude of inbreeding depression and to the discount rates, but not to the variance caused by new mutations and the size of the world population.

The genetic correlation between the breeding objectives of different AI studs controls the extent to which they all select the same sires of sons and, hence, affects the global effective population size. The prediction is made that different countries will select partially different sires, but genetically isolated strains will not reemerge. A better global breeding program is likely when selection of sires takes account of inbreeding depression and small genotype by environment interactions.

(Key words: effective population size, world, black and white cattle, population, inbreeding depression, EBV = estimated breeding values, G × E = genotype by environment interaction, MOET = multiple ovulation and embryo transfer, Ne = effective population size, NPV = net present value of all future genetic gains.)

INTRODUCTION

Prior to 1970, several distinct strains of black and white dairy cattle existed around the world. The increased international trade in semen, cattle, and embryos has converted these into a single global population. Comparisons of the black and white strains found that the North American Holstein was superior for milk production (20). Consequently, nearly all other strains of black and white cattle are being replaced by Holsteins. This process has been accelerated in recent years by the export of large numbers of Holstein embryos from North American to become AI bulls in other countries. Consequently, bulls with almost identical pedigrees are being progeny tested simultaneously in several countries.

A consequence of this process is a substantial loss of genetic diversity, which is viewed with concern by some people. Intense selection within the AI bull breeding sector means that a few "super sires" dominate the breed worldwide. Likely improvements in reproductive technology could lead to equally intense selection on cows and to a decline in generation interval, causing a further increase in the rate of inbreeding (ΔF) and the relatedness of all black and white cattle worldwide. Therefore, it seems important to consider the optimal balance between selection intensity and effective population size (Ne) for the world black and white breeding program, and this is the first aim of this paper.

However, the world black and white breeding program is not managed by a single person with power to implement an optimal design. The world breeding program is the result of the collective decisions taken by a number of
AI studs, which are in competition with one another. Therefore, the second aim of this paper is to make a prediction of what will happen in the future as a result of this collective decision-making process.

**BENEFITS AND DISADVANTAGES OF A GLOBAL BREEDING PROGRAM**

The first advantage of selection from a global population is the opportunity for between-strain selection, which is precisely what has led to the replacement of many black and white strains with Holsteins. Consequently, the opportunities for between-strain selection in the future are greatly reduced.

The second advantage is that larger populations can make faster genetic gains than smaller populations (7, 17), although this conventional wisdom has been challenged by Franklin (4). This advantage derives largely from the more intense selection of sires of sons that is possible when more bulls are progeny tested. In theory, there is little advantage for a larger population in selection of sires of commercial cows because, although more bulls are tested, more proven sires are needed. However, in practice, dairy farmers vary in their selection objectives and criteria. This means that more bulls than needed are selected to cover a variety of market niches. In a large population, it should be possible to cover all market niches with widely used bulls.

To gain these benefits, each country must be able to select from among the world population those bulls that best meet local breeding objectives. To do this, it is necessary to compare all available bulls for traits in the local breeding objective either by equations that convert foreign genetic evaluations to the local scale (5, 19) or by a joint analysis of data from two or more countries (1). In either case, it is important to allow for small genotype × environmental (G × E) interactions, which cause a reranking of sires between countries. This is frequently done in calculating conversion equations but has not yet been done in combined analyses.

The disadvantage of intense selection from a global population is reduced \( N_e \). The effects of small \( N_e \) are inbreeding depression (D), loss of genetic variance, and a degree of random drift in the mean merit of the population. Because intense selection inevitably reduces \( N_e \), a compromise is needed.

**DESIGN OF A GLOBAL BREEDING PROGRAM**

**Selection**

Many studies have investigated the optimal design for dairy breeding programs using conventional progeny testing (7, 17) and multiple ovulation and embryo transfer (MOET) schemes (12, 13). These studies usually assumed a closed population, and it is doubtful that their authors intended the conclusions to apply to the world population of the major dairy breed. Intuition suggests that more attention be given to the disadvantages of small \( N_e \) when considering the world population. This section interprets this intuition in a rational, quantitative manner.

To determine the optimal design, the objective must first be defined. For instance, when the aim is to maximize the total response achieved when a selection plateau is reached, Robertson (15) concluded that the best half of the animals tested should be selected. Similarly, when the objective is to conserve genetic resources or to minimize genetic abnormalities or the probability that a desirable allele is lost, a low selection intensity is optimal. These objectives all emphasize long-term effects that, in cattle, may take many years to eventuate and that lead to recommendation of low selection intensity. Others may wish to emphasize short-term gains by, for instance, maximizing the annual selection response (\( 4G \)), which leads to very intense selection. This should at least be adjusted for the expected D. On an annual basis, this is \( A - \Delta F \) per year and \( D_1 \) per unit of inbreeding. Goddard and Smith (7) called this quantity “net genetic gain”.

To compare long- and short-term gains, it is conventional to use discounting to assign an equivalent present value to future benefits. Therefore, the objective should be the net present value (NPV) of all future genetic gains from the breeding program. This includes both long- and short-term objectives discussed here. This is the appropriate strategy for the world community, although it is not necessarily one that would be adopted by competing AI studs.

To calculate NPV, a discount rate must be chosen. This should be the real rate of return.
(i.e., adjusted for inflation) on alternative, secure investments. Traditionally, this has been 2 to 5%/yr. However, the price of milk to the farmer has not kept pace with inflation and is unlikely to do so in the future. Therefore, the decline in the real price of milk must be added to the discount rate. In Australia, this has been approximately 2%/yr. The need to allow for the declining real price of milk applies from the viewpoint of both consumers and farmers. Because the real price of milk is dropping, the benefit of a further proportional drop in price, caused by genetic improvement, is also falling. There is also a risk that the expected genetic gain in profitability will not occur. If this risk increases approximately exponentially with time, it can be accommodated by increasing the discount rate (3).

One risk is that selection objectives will change such that the value of present genetic improvements is reduced. For instance, past selection for milk fat yield is of less value when milk price is based on protein content; similarly, the value of selection to increase mastitis resistance would be greatly reduced if an effective vaccine were released. This risk might add up to 5% to the discount rate, assuming that the value of a present genetic gain declines by less than 5%/yr.

However, future selection decisions will be directed at the selection objectives appropriate at that time. Therefore, this loss of 5%/yr does not apply until the selection decisions have been made. Although selection objectives change, genetic variance is always valuable because improvement is always desirable for some traits.

Despite changes in selection objectives, D will continue to be detrimental. Inbreeding depression reduces milk production, fertility, survival, and general hardiness. These effects clearly are always a cost to the dairy farmer and should not be discounted by the additional 5%/yr.

These arguments dictate the use of two discount rates: a base rate of approximately 4 to 7% (real return plus declining real milk price) and a higher rate (e.g., 10%) that includes risk. The value of genetic improvement from prior selection decisions is discounted at the higher rate, but the value of future selection decisions and D is discounted at the lower rate.

An individual company deciding on its optimal breeding program might include several other sources of risk, e.g., the risk that a more successful competitor may force it out of business. These risks do not apply to the world black and white cattle population. The main additional risk from this global perspective is that the world dairy industry would decline in importance. However, an increase in importance with the increasing world population is also possible.

For any specified breeding program, the genetic merit of commercial dairy cows in all future years can be predicted, the discount rates chosen can be applied, and an NPV for that program can be calculated. By using a few simplifying assumptions, relatively simple expressions for NPV can be derived.

Derivation of an Expression for NPV

Let \((1 - a)/a = 1 - a = \text{base discount rate,}\) \((1 - b)/b = 1 - b = \text{risk discount rate, and} \) \(\Delta G_j = \text{genetic response in dollars because of selection in year } j\). Then \(a\Delta G_j = \text{NPV of this gain in year } j\), and \(\sum_{k=0}^{\infty} a^k \Delta G_j (ab)^k = \text{NPV of this gain in all future years} = a\Delta G_j/(1 - ab)\). (For simplicity, this ignores the lag between selection decisions and genetic improvement.) The NPV of all future gains is then

\[
\sum_{j=0}^{\infty} a^j \Delta G_j \frac{1}{1 - ab}.
\]

Now \(\Delta G_j\) depends on the genetic variance \(V_{gj}\) present in year \(j\). Assume that

\[
\Delta G_j = \Delta G_0 \frac{V_{gj}}{V_{go}}.
\]

(This underestimates the response to selection in future years.) The genetic variance declines because of inbreeding but increases because of mutation, which have long-term importance (9).

That is,

\[
V_{gj} = V_{gj-1} (1 - \Delta F) + V_m = (V_{go} - V_m/\Delta F)(1 - \Delta F)^j + \frac{V_m}{\Delta F}
\]

where \(V_m = \text{mutational variance per year.}\)

\[
\sum_{j=0}^{\infty} \frac{a^j}{1 - ab} \frac{\Delta G_o}{V_{go}}
\]

\[
= \frac{1}{1 - ab} \frac{\Delta G_o}{V_{go}}\left[\frac{V_{go} - V_{m}/\Delta F}{1 - a(1 - \Delta F)} + \frac{V_{m}/\Delta F}{1 - a}\right]
\]

where \( V_m^* = V_m/V_{go} \).

From this must be subtracted the cost of \( D \). If in year \( j \) the inbreeding coefficient is

\( F_j = 1 - (1 - \Delta F)^j \),

the cost of \( D \) is

\( D(1 - (1 - \Delta F)^j) \),

and the discounted value of this is

\( a^jD[1 - (1 - \Delta F)^j] \).

The sum of these losses over all years is

\[
\sum_{j=0}^{\infty} a^jD[1 - (1 - \Delta F)^j]
\]

\[
= \frac{D}{1 - a} - \frac{D}{1 - a(1 - \Delta F)}.
\]

The NPV of all genetic gains is Equation [4] minus Equation [5].

For any particular breeding program, equilibrium values of \( \Delta G \) and \( \Delta F \) can be calculated and substituted into Equation [4] minus Equation [5].

**Optimal Selection Intensity**

When bull-dams are selected on estimated breeding values (EBV), they are often the daughters of the bull-sires of the previous generation. Thus, the bull breeding part of the population tends to become a dispersed nucleus; the same elite sires are used to breed sons and daughters, as discussed by Goddard and Smith (7). In this case, \( \Delta F \) is

\[
\Delta F = 1/(8N_mL^2)
\]

where

\( N_m = \) effective number of new bulls per year used in the nucleus,

\( L = \) generation length, and

\[
\Delta G = i_m\sigma_g^m + i_f\sigma_g^f
\]

where \( i = \) standardized selection differential, \( r = \) accuracy of selection, \( L_m = \) generation length, and subscripts refer to male (m) or female (f).

The standard parameters used in evaluating NPV, \( \Delta F \) and \( \Delta G \), were \( r_m = .85, r_f = .5, L_m = 6 \) yr, \( L_f = 3.5 \) yr, \( \sigma_g = 7\% \), \( D = .5, V_m = .004V_{go} \) and \( 1 - a = .03, \) and \( 1 - b = .07 \).
The effect of discount rates on optimal number of bulls to select to maximize net present value.

<table>
<thead>
<tr>
<th>Base discount rate</th>
<th>Risk discount rate</th>
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<tbody>
<tr>
<td>.20</td>
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<tr>
<td>.10</td>
<td>.07</td>
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<tr>
<td>.03</td>
<td>.004</td>
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<table>
<thead>
<tr>
<th>Mutation variance</th>
<th>Inbreeding depression²</th>
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<tbody>
<tr>
<td>0</td>
<td>.50</td>
</tr>
<tr>
<td>.004</td>
<td>1.50</td>
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1Mutation variance as a proportion of initial genetic variance.

2Decline in objective per unit inbreeding coefficient.

Typical estimates of mutation variance are approximately .001 Vₚ per generation (11) where Vₚ = environmental variance. For a trait with heritability of .25, this is .003 Vₚ per generation. If generation length is 5 yr, Vₚ = .0006 Vₑ. Table 2 shows that even a value of Vₚ more than six times this level has a negligible effect on the optimal number of bulls to select.

As an alternative to conventional progeny testing, a juvenile MOET breeding program was briefly examined. The purpose was not to predict the genetic gain accurately from such a scheme but, rather, to examine the effect of the NPV criterion on the optimal selection intensity. For simplicity, 1000 yearling males and females were assumed to be available for selection with accuracy r = .5 in both sexes. The family structure of this population was ignored, and reproductive technology was assumed to allow an unlimited number of offspring per cow.

The optimal designs to maximize NPV and ΔG = DΔF are in Table 3. Although not intended to be accurate, the rates of genetic gain calculated are comparable with those of Kinhorn et al. (10) for a similar scheme. As expected from the assumptions, the same number of bulls and cows is selected. When NPV is maximized, ΔF is higher than for progeny
testing programs but, perhaps, still acceptable. When $\Delta G - \Delta F$ is maximized, $\Delta F$ of 1%/yr appears to be dangerously high.

### Expected Future $N_e$

The future world breeding program will not be planned by a single individual or institution but will result from the collective decisions of the AI studs. As competing commercial organizations, AI studs are likely to give more emphasis to short-term returns than has been advocated as optimal from a global perspective. For instance, if AI studs maximized $\Delta G - \Delta F$, they would select far fewer bulls (Figure 1 and Table 3) than needed to maximize NPV. If they all select the same bulls, the world black and white population will be genetically less diverse than is desirable.

However, if they have different selection objectives, they will not select exactly the same bulls; hence, the total number of sires used will increase. If the commercial herds served by an AI stud are considered as an “environment”, then different selection objectives can be considered as a $G \times E$ for profitability; i.e., the bulls do not rank in the same order for profitability in all environments.

A $G \times E$ for profitability can occur for two reasons. First, there may be different selection objectives in different environments. For instance, some countries pay farmers for milk on the basis of volume, but other countries pay for milk fat and protein but penalize milk volume. In Norway, but not in most countries, a large economic weight is given to mastitis resistance (18). Second, a $G \times E$ may exist for individual traits. For instance, bulls rank differently for milk production in Canada and New Zealand (14), probably because of the marked difference in feeding systems in the two countries. Small changes of ranking probably also occur between other countries, but they are usually not large (6).

The degree of reranking for profitability can be expressed as a genetic correlation between profitability in the two environments. Because milk production traits are important everywhere and generally show only minor $G \times E$, the genetic correlation for profitability will be high, although less than 1.0, between most environments.

If the genetic correlation between profitability in country A and profitability in the rest of the world is sufficiently low, then country A will make more genetic progress by closing its population and not selecting from the global population. In this way, separate strains of black and white might reemerge in different countries, although the global population would have passed through a bottleneck as other countries converted to American Holsteins.

Will isolated strains reemerge? The net genetic gain in an isolated strain is $\Delta G_a - \Delta F_a$ where $\Delta G_a - \Delta F_a$ is optimized for the number of bulls progeny tested in that country. Genetic isolation will be better than some continued importation if $\Delta G_a - \Delta F_a$ is greater than $r_g \Delta G_r$, where $\Delta G_r$ is the genetic progress in the rest of the world, and $r_g$ is the general correlation between profitability in country A and in the rest of the world. No $\Delta F_r$ term is included because, when country A is almost isolated, bulls from other countries will not be increasing in their relatedness to country A cows; i.e., they have an advantage over country A bulls because they produce calves with a lower average inbreeding coefficient.

Figure 2 shows the value of genetic correlation at which $\Delta G_a - \Delta F_a = r_g \Delta G_r$ assuming that 2000 bulls are progeny tested per year in the rest of the world. As the number of bulls progeny tested per year in country A increases, the breakeven value of the genetic correlation increases. For situations below the curve in Figure 2, country A would benefit from eventually stopping the import of genes from the rest of the world. This need not be a deliberate policy. As a result of selection based on appropriate EBV, all of the best bulls will eventually be in country A. Although no formal analysis has been done, the situation in most countries will probably lie above the curve in Figure 2, and some continued importation will be desirable. Therefore, most local black and white populations will probably not become isolated from the global population.

Even if all countries continue to import genes from the global population, this does not imply that they all select exactly the same bulls. Again, the degree of overlap in their selections depends on the genetic correlation between the objectives. Consider two countries that each progeny tested 1000 bulls of equal
genetic merit per year. Both countries select the best two as bull-sires from the complete 2000 bulls tested. Will they select the same two bulls?

Two situations can be distinguished. In the first situation, economic weights differ between the two countries, but there is no $G \times E$ for individual traits, and all bulls are evaluated with equal accuracy for all traits. This means that selection for the objective of country A is equally accurate, regardless of the country in which a bull was progeny tested. In the second situation, the economic weights are the same, but there is a $G \times E$ for the individual traits. This means that an EBV based on a progeny test in country A must be "regressed toward the mean" when it is converted to an EBV in country B (i.e., $EBV_B = r_g \cdot EBV_A$). The true situation is likely to lie between these extremes and is due in part to traits evaluated only in the country that includes them in its objective.

Computer simulation was used to calculate the total number of bulls selected, assuming that each country selects the best two for its own objective out of the 2000 tested (Figure 3). Naturally, when their objectives are the same ($r_g = 1.0$), both countries select the same bulls, and the total number selected is 2. As the correlation between their objectives fall, they tend to select different bulls, and, when $r_g = .6$, the total number selected approaches 4 (the maximum possible under these assumptions). The results for the two situations just described differ, but not greatly.

Simulations were also carried out for more than two countries. In this case, the total number of bulls tested was assumed to be 2000, divided equally among the countries, and the correlation between the objectives of any pair of countries was assumed to be .9. The mean breeding value of bulls tested in each country was assumed to be the same. Figure 4 shows that, as the number of countries increases, the total number of bulls selected increases. If there is a $G \times E$ for individual traits (the second situation), the number of bulls selected reaches a maximum of 5. To understand this, consider two countries, A and B, out of 10 countries that each test 200 bulls. For the objective of country A, the bulls tested in country A are evaluated more accurately than other bulls and so are more likely to be selected. On average, .47 bulls are selected from country A and 1.53 from all other countries. Any bulls from country B will also be selected for use there, and the majority of bulls, which come from neither A nor B, will rank in the same order in both countries, so the same ones will be selected. As the number of countries increases, the proportion of all bulls tested in country A decreases, and fewer country A bulls are selected. This balances the...
Figure 4. The total number of bulls selected from 2000 bulls tested. The best two for each objective area selected. The genetic correlation between any pair of objectives is .9. Situation 1, all bulls evaluated for all objectives (---); situation 2, bulls only evaluated for local objective (—).
markers to the same decisions as would be made by implementation of an optimal design. Because of its importance in determining the optimum, this is most likely to happen if individual decision markers consider D in their decisions. Goddard and Smith (8) suggested that farmers select AI sires to maximize EBV – DF of the resulting calf (where F is the inbreeding coefficient of the calf). If farmers do this, then AI studs will have to consider the relatedness of their bulls to one another and to the cow population. Goddard and Smith (8) suggested that AI studs choose their young and proven bull teams to maximize EBV – DR/2, where EBV is the mean EBV of the team, and R is the mean relatedness of the bulls.

Farmers and AI studs already consider relatedness of bulls and cows in making decisions. Advisers should show how this can be done in a systematic way. In doing this, a higher rather than lower D value would benefit the individual because a higher D value acknowledges the discount rate arguments used to derive NPV and because it allows for a weighting for drift.

Avoiding inbreeding may also have noneconomic benefits. Recessive genes for genetic abnormalities are individually rare, but, when all abnormalities are combined, recessive genes are quite common. Avoiding known genetic abnormalities is given far greater weight than their economic value justifies. The most effective way to avoid abnormal homozygote calves is to avoid inbreeding.

Use of a high D value will also be of benefit to the industry as a whole because it will cause the outcome of collective decisions to approach the optimal design more closely.

Even when D is taken into account by individual decision makers, they will likely put more emphasis on short-term gains and low N<sub>r</sub> than desirable for the world black and white population. However, Figures 3 and 4 show that, if selection objectives differ, the world N<sub>r</sub> will increase. Genuine difference in objectives will be recognized by considering all traits, not just milk production, and by allowing for even small G × E. As Figure 4 shows, even a genetic correlation between environments of .9 causes different bulls to be selected in different places and the total N<sub>r</sub> to increase. Thus, formulas to convert EBV between countries and joint analyses of data from several countries should recognize these G × E.

If the genetic correlations between objectives in different countries were sufficiently low, all of the best bulls in a country would eventually be progeny tested locally, and a genetically isolated progeny tested would reemerge. Banos and Smith (2) investigated the time course of this process in two populations that each tested 1000 bulls per generation. They (2) found that, if the genetic correlation between their objectives was .7, each country stopped selecting bulls from the other country after three generations. However, inbreeding effects and the large size of the world population work to prevent complete isolation. A possible future course is one in which, following a bottleneck, some differences between local population reemerge, but these local populations continue to exchange genes and do not become isolated strains.

REFERENCES