

Stochastic simulation of breeding schemes for total merit in dairy cattle

M.K. Sørensen^{*1}, P. Berg¹, J. Jensen¹ and L.G. Christensen²

¹ Danish Institute of Agricultural Sciences, Department of Animal Breeding and Genetics, P.O. Box 50, DK-8830 Tjele, Denmark.

² Department of Animal Science and Animal Health, The Royal Veterinary and Agricultural University, Groennegaardsvej 3, DK-1870 Frederiksberg C, Denmark.

Abstract

Total economic merit of dairy cattle depends on several traits. Despite of this, most studies of dairy cattle breeding schemes have assumed a single-trait breeding goal, i.e. milk production. In this paper, dairy cattle breeding schemes assuming a multi-trait breeding goal were studied using stochastic simulation. The breeding schemes studied consisted of a nucleus with 1500 females and a breeding population of 18 500 females. Bulls were assumed to be tested in a production population, which were not simulated. However, progeny test results of bulls were generated by simulating daughter yield deviations. All 10 traits in the current Danish breeding goal were simulated. The schemes studied included open vs. closed nuclei, selection for total merit vs. milk production, use of early predictors for milk production and different daughter group sizes. All simulations covered a 25-year period. Genetic gains were from 14 to 25 EURO per cow per year. Highest gains were obtained when selection was for total merit and early predictors were used. Higher daughter group sizes resulted in slightly higher economic gain, and the distribution of the gain were changed so the genetic gain for milk production were lowered and the genetic gain for cost reducing traits increased. For different schemes inbreeding increased from 0.98% up to 1.50% per year. On average genetic variance of the breeding goal were reduced by 30-39% in year 25.

1. Introduction

More than 15 years ago, breeding programs for dairy cattle in Denmark and other Nordic countries have introduced a total merit index with economic weights on milk production traits, beef production traits, female fertility, calving ease, conformation, milking speed, temperament, mastitis resistance, and in some of the countries also general health (Andersen *et al.*, 1993). The economic weights on the different traits differ from country to country. This is in agreement with Groen *et al.* (1997) who state that economic weights differ from country to country depending on production circumstances. In recent years more and more countries have moved towards a total economic breeding goal (Anonymous, 1996). Despite this, most studies of dairy cattle breeding schemes

have assumed a single-trait breeding goal, i.e. milk production. The very few simulations (e.g., Bovenhuis *et al.*, 1989; Pedersen and Christensen, 1993; Christensen and Pedersen, 1997) which include more traits were all carried out using deterministic simulation approaches, which did not take inbreeding into account. In this paper, dairy cattle breeding schemes assuming a multi-trait breeding goal were studied using stochastic simulation.

2. Material and methods

2.1. Traits

The traits in the present Danish breeding goal for dairy cattle listed in Table 1 were simulated. When selection was on total merit an average of the

economic weights used within Danish Holstein and Danish Red Cattle were used in the selection criteria (Anonymous, 1997). The same values were used in defining the true breeding goal. The early predictors simulated were physiological indicator traits reported by Løvendahl and Jensen (1997).

2.2. Genetic and environmental parameters

When simulating breeding schemes with several traits included knowledge about genetic and environmental parameters for the simulated traits are needed. In the work by Sørensen (1999) a comprehensive review over genetic and phenotypic parameters for the traits in the Danish breeding goal for dairy cattle in Denmark was carried out. Parameters from this review were used in the present simulations. The parameters used are shown in Table 2.

Table 1 Simulated traits and their economic values

Trait	EURO per genetic standard deviation unit
Milk production	71.1
Fertility	21.2
Calving ease	12.8
Body capacity	0
Feet and legs	17.3
Udder	25.0
Milking speed	9.9
Temperament	2.7
Somatic cell count	0
Mastitis	38.0
General health	13.4
Beef production	10.6
Early predictor	0

2.3. Population structure

The females in the population were divided into three groups: Nucleus cows, breeding cows and production cows. The nucleus cows and the breeding cows were individually simulated. The nucleus consisted of 1500 lactating cows, which

were kept under stable environmental conditions. Therefore higher heritabilities for milk production and somatic cell count were assumed in the nucleus. Heritability for milk production was set to 0.42 and for somatic cell count to 0.20. In the nucleus the best cows were flushed, and the number of live-born calves per cow were Poisson distributed with an average of five. Cows were kept in the nucleus until genetically better replacement heifers were available, or until they were randomly involuntary culled, or they reached the end of second lactation.

The breeding population consisted of 18 500 cows distributed in 185 herds each with a herd size of 100 cows. In the breeding population the only reproduction strategy available were AI. Cows were kept in the herd until they were randomly involuntary culled, or until better replacement heifers were available, or they reached the end of sixth lactation.

The cows in the production population were not simulated individually, since they in relation to the breeding program only were used as a test population. The size of the production population was 270 000 cows. In the simulations we assumed that 30% of the calves born in the production population had a young test bull as sire. This means that 30 000 first lactation daughters per year were available for young bull testing.

In closed nucleus breeding schemes only cows in the nucleus were simulated. In open nucleus breeding schemes both cows in the nucleus and the breeding population were simulated. In open schemes the best heifers across both sub-populations were selected to enter the nucleus. Consequently the nucleus always consisted of the animals with the highest predicted breeding values. Cows discarded from the nucleus were randomly distributed to herds in the breeding population.

Table 2. Heritabilities (on diagonal) genetic correlations (below diagonal) and phenotypic correlations (above diagonals) for traits in the simulations

	Milk production	Fertility	Calving ease	Body capacity	Feet and legs	Udder	Milking speed	Temperament	Somatic cell count	Mastitis	General health	Beef production	Early predictor
Milk production	0.28	-0.10	0	0.05	0	0	0.05	0	0.08	0.03	0	0	0
Fertility	-0.35	0.03	0	0	0	0	0	0	0	0	0	0	0
Calving ease	0	0.20	0.11	0	0	0	0	0	0	0	0	0	0
Body capacity	0.15	0	0	0.30	-0.10	0.10	0	0.05	0	0	0	0	0
Feet and legs	0	0	0.10	-0.20	0.18	0	0	0	0	0	0	0	0
Udder	-0.10	0	0	0.20	0	0.32	0.05	0	0.08	0.04	0	0	0
Milking speed	0.05	0	0	0	0	0.10	0.26	0.20	-0.05	0	0	0	0
Temperament	0	0	0	0.20	0	0.15	0.30	0.15	0	0	0	0	0
Somatic cell count	-0.10	0.30	0.10	-0.05	0	0.25	-0.15	0	0.13	0.20	0	0	0
Mastitis	-0.35	0.20	0.20	-0.10	0	0.20	0.10	0	0.60	0.04	0	0	0
General health	-0.25	0.30	0	0	0	0	0	0	0	0.26	0.02	0	0
Beef production	0	0	0	0	0	0	0	0	0	0	0	0.20	0
Early predictor	0.42	0	0	0	0	0	0	0	0	0	0	0	0.30

The young bulls used for test insemination were selected from the nucleus in closed schemes, and across the nucleus and the breeding population in the open schemes. The progeny tests were based on daughter group sizes of 80 or 160. With a fixed test capacity of 30 000 daughters this corresponds to testing either 350 or 187 bulls per year. All test bulls less than ten years old were available for AI in both the nucleus and the breeding population, whether they had daughter proofs or not. Sire-daughter matings and full- and half-sib matings were not allowed, and a single bull was at most the sire of 25% of the life-born calves per year.

2.4. Simulation of breeding values and phenotypic observations

The Cholesky decomposition \mathbf{L}' of the genetic (co)variance matrix and the Cholesky decomposition \mathbf{C}' of the environmental (co)variance matrix were

calculated from the parameters given in Table 2. For animals in the base population a vector of breeding values (\mathbf{bv}_i) were calculated as:

$$\mathbf{bv}_i = \mathbf{L}' * \mathbf{r}_1 \quad (1)$$

For females a vector of observations (\mathbf{obs}_i) for the simulated traits for each animal were calculated as:

$$\mathbf{obs}_i = \mathbf{bv}_i + \mathbf{C}' * \mathbf{r}_2 \quad (2)$$

where \mathbf{r}_1 and \mathbf{r}_2 were vectors of random numbers from a standardised normal distribution. For bulls, own records for early predictors were simulated in the same way. For the remaining traits, twice the daughter group deviations were simulated to represent progeny testing results. Therefore \mathbf{obs}_i on males were simulated as:

$$\mathbf{obs}_i = \mathbf{bv}_i + 2 * (\sqrt{0,75} * \mathbf{L}' * \mathbf{r}_1 + \mathbf{C}' * \mathbf{r}_2) * \mathbf{Diag}(\mathbf{n}_i)^{-1/2} \quad (3)$$

where \mathbf{n}_i is a vector with the numbers of daughters with registrations for each of the traits.

Simulated observations were only used if they were realised before the animal was culled. For the traits fertility, calving ease, mastitis, general health and beef production only progeny testing results were used in prediction of breeding values.

In later generations breeding values (\mathbf{bv}_i) were simulated as:

$$\mathbf{bv}_i = 1/2 * (\mathbf{bv}_i(\text{sire}) + \mathbf{bv}_i(\text{dam})) + \sqrt{1/2 * (1 - (F_{i(\text{sire})} + F_{i(\text{dam})})/2)} * \mathbf{m}_i \quad (4)$$

where \mathbf{m}_i was the Mendelian sampling deviation:

$$\mathbf{m}_i = \mathbf{L}' * \mathbf{r}_1 \quad (5)$$

Breeding value estimation was carried out using the DMU package (Jensen and Madsen, 1996). Breeding values were for all traits, except milk production and mastitis, predicted using single trait animal model, and subsequently combined into a total merit index according to the economic weights. For milk production a multitrait model including milk production in both first and second lactation plus early predictor were used. For mastitis a model including both somatic cell count and mastitis registrations were used.

2.5 Simulated breeding schemes

Since simulation of breeding schemes using this program is very compute intensive only a few breeding schemes have been investigated until now. In the present investigation four factors have been varied, and each factor had two levels. All combinations were investigated. Below is given an overview over the factors investigated:

Nucleus strategy

- I. Closed nucleus
- II. Open nucleus

Selection strategy

- I. Selection for milk production
- II. Selection for total merit

Early predictors

- I. No early predictors (-EP)
- II. Use of early predictors (+EP)

Daughter group size

- I. 80 daughters per bull
- II. 160 daughters per bull

All combinations were simulated with at least five replicates each. Within each replicate breeding values and the realised observations for all animals were stored. From these data the average genetic merit, the average inbreeding rate and the average genetic variance for animals born within year were calculated. Yearly results from the simulation model were analysed in a model taking account of the four main factors investigated as well as all interactions. Correlations among time series were modelled assuming a Toeplitz structure. Analyses were carried out using proc mixed in SAS (Littell *et al.*, 1996). Only data from year 6 to year 25 were used in the analyses of genetic gain and inbreeding.

3. Results

3.1. Genetic gain

Analyses of the data showed that the four factor interaction were significant at 10% level, as well as the year*selection strategy effect. The total genetic gain in the 16 different breeding schemes is therefore given in Table 3. Results are given as genetic gain in EURO per cow per year. Due to the small number of replicates per simulated breeding scheme differences between estimates of the total genetic gain per cow per year had to be above 2.1 EURO to be significant at 10% level.

The genetic gains for milk production, cost reducing traits (fertility, calving ease, mastitis and general health), conformation (feet and legs, udder, milking speed and

temperament) and beef production are given in Table 4.

Table 3. Total economic gain in EURO per cow per year in different breeding schemes

	Selection for total merit				Selection for milk production			
	<i>Closed nucleus</i>		<i>Open nucleus</i>		<i>Closed nucleus</i>		<i>Open nucleus</i>	
	80 daughters	160 daughters	80 daughters	160 daughters	80 daughters	160 daughters	80 daughters	160 daughters
- EP	21.5	23.0	22.3	21.2	13.6	14.3	14.1	14.5
+ EP	21.5	24.2	23.0	24.8	15.3	16.8	18.3	14.0

Table 4. Genetic gain in EURO per cow per year for milk production, cost reducing traits, conformation and beef production in different breeding schemes (in parentheses are given genetic gain for milk production in genetic standard deviation units)

	Selection for total merit				Selection for milk production			
	<i>Closed nucleus</i>		<i>Open nucleus</i>		<i>Closed nucleus</i>		<i>Open nucleus</i>	
	80 daughters	160 daughters	80 daughters	160 daughters	80 daughters	160 daughters	80 daughters	160 daughters
- EP milk production	15.2 (0.21)	13.8 (0.19)	15.6 (0.22)	14.5 (0.21)	21.3 (0.30)	21.1 (0.30)	22.1 (0.31)	22.1 (0.31)
cost red. Traits	0.1	3.4	1.3	1.5	-7.0	-6.3	-7.4	-6.8
conformation	5.6	5.5	5.1	4.6	-1.1	-0.9	-0.9	-0.8
beef production	0.6	0.3	0.3	0.6	0.3	0.4	0.3	0.0
+ EP milk production	16.0 (0.23)	15.3 (0.22)	18.5 (0.26)	17.6 (0.25)	21.9 (0.31)	23.8 (0.33)	24.8 (0.35)	23.6 (0.33)
cost red. Traits	0.7	3.5	0.5	2.4	-6.7	-6.4	-6.7	-8.3
conformation	4.6	5.0	3.6	4.4	0.3	-0.8	-0.3	-1.3
beef production	0.2	0.4	0.4	0.4	-0.2	0.2	0.5	0.0

Table 5. Yearly increases in inbreeding in different breeding schemes

	Selection for total merit				Selection for milk production			
	<i>Closed nucleus</i>		<i>Open nucleus</i>		<i>Closed nucleus</i>		<i>Open nucleus</i>	
	80 daughters	160 daughters	80 daughters	160 daughters	80 daughters	160 daughters	80 daughters	160 daughters
- EP	1.17	1.15	0.98	1.00	1.45	1.48	1.25	1.28
+ EP	1.16	1.14	1.04	1.06	1.48	1.50	1.24	1.27

From Table 3 and Table 4 it is seen that both total genetic gain and genetic gain for single traits were very dependent on the selection strategy applied. On average total genetic gain were reduced by 7.5 EURO per cow per year when selection was on milk production compared to total merit selection. At the same time the composition of the total gain was substantially changed. Thus selection for milk production (of course) resulted in higher genetic gain for milk production, but at the same time resulted in big reductions for the other traits in the breeding goal.

On average no significant difference in total genetic gain between closed and open breeding schemes was found. For milk production alone the average effect was an increase of 6.9%, which was in agreement with Colleau (1986). Meuwissen and Woolliams (1994) found a small effect of opening the nucleus when the limit on the increase in inbreeding rate were low as in the present simulations.

The consequence of using early predictors for milk production in breeding schemes was from neutral to quite positive. On average the effect for total economic gain was 1.7 EURO per cow per year. The effect was highest for milk production; 2.0 EURO per year per cow. This is in agreement with results from deterministic simulations (Meuwissen and Woolliams, 1993), who found an increase for milk production of 11% when an early predictor with a correlation of 0.5 with milk production were introduced.

On average there was no effect on total genetic gain of increasing the daughter group size from 80 to 160, but the composition of the total gain were substantially changed when selection were on total merit. Increased daughter group size gave lower genetic gain for milk production and higher (or less decrease) genetic gain for the cost reducing traits with low heritabilities.

3.2. Inbreeding

For inbreeding the four-factor interactions were not significant, but two of the three-factor interactions were. From these two effects the inbreeding rate in the 16 different breeding schemes were estimated.

From Table 5 it is seen that the increase in inbreeding was higher in breeding schemes where selection was on milk production compared to those where selection was on total merit. Since the heritability for most of the traits in the total merit selection goal was lower than the heritability for milk production this result was unexpected. The explanation is that the generation interval for bulls was shorter when selection was on milk production. If only progeny tested bulls had been used as sires then the simulations presumably would have resulted in the expected results and general lower yearly increases in inbreeding.

Closed nucleus breeding schemes had a higher increase in inbreeding than open nucleus breeding schemes, which should be expected due to the higher number of animals in open schemes. Daughter group size and use of early predictors had little effect on inbreeding.

In all breeding schemes simulated, very high inbreeding levels were seen in year 25. The accumulated inbreeding was in the interval from 0.19 to 0.32. These very high inbreeding levels together with the "Bulmer-effect" were the reasons for the quite large reduction in the genetic variance of the traits under selection.

3.3. Genetic variation

Figure 1 shows the change in genetic standard deviation of the true breeding goal. The change is given for groups of breeding schemes. It is seen that the genetic standard deviation was reduced dramatically within the first five years of the simulation. Reduction in that period

was purely due to “Bulmer-effect” since no inbreeding was seen in the breeding schemes before year five. The reduction due to “Bulmer-effect” was largest in the closed breeding schemes. This is a consequence of the higher heritability of milk production and somatic cell count in the nucleus. After year five an approximately constant reduction was seen. This reduction was primarily due to inbreeding, which increased in the same period. A larger reduction in genetic standard deviation was seen in the closed breeding schemes compared with the open breeding schemes, as a consequence of a higher inbreeding level in the closed breeding schemes. The genetic standard deviation of the true breeding goal was reduced from 82 EURO to app. 69 EURO in open nucleus breeding schemes and to app. 64 EURO in closed nucleus breeding schemes after 25 years of selection. This corresponds to a reduction of 30% and 39% in genetic variation. The reduction in genetic variation caused by “Bulmer effect” and inbreeding was the main reason for the effect of year on genetic gain. The total economic gain was on average reduced by 0.23 EURO per year in closed nucleus breeding schemes and with 0.19 EURO in open nucleus breeding.

3.4. Connection between genetic gain and inbreeding

Several studies have shown that there is a connection between genetic gain and inbreeding in different breeding schemes when selecting for a single trait (Quinton *et al.*, 1992; De Boer and Van Arendonk, 1994; Brisbane and Gibson, 1995; Quinton and Smidt, 1995; Meuwissen, 1997). This means that breeding schemes resulting in high genetic gain generally also result in large increases in inbreeding. In the present simulations similar connections between genetic gain for milk production and annual increase in inbreeding was observed. On contrary

there was no connection between total economic gain and inbreeding, which appears from Figure 2. The reason for this lacking connection is that the large numbers of traits in both breeding goal and selection criteria change generation intervals and accuracy of the indexes.

4. Conclusion

The present simulations showed that the simulation model constructed estimated reliable results for genetic gain for the traits in the breeding goal, for increase in inbreeding and for the change in genetic variation. The disadvantage is that the program is time consuming, since all breeding animals have to be simulated. This often gives difficulties with the differentiation between breeding schemes due to few replicates.

The simulations showed that selection for true breeding goal always was best. In most cases it was advantageous to use open nucleus breeding schemes compared to closed nucleus breeding schemes, since genetic gain tended to be larger and the inbreeding at a lower rate. With the assumptions used, early predictors are advantageous. Daughter group sizes around 160 have to be recommended compared to daughter-group sizes around 80 daughters, since it in most cases increase total genetic gain. Moreover the composition of the genetic gain is changed, genetic gain for cost reducing traits is increased without a corresponding reduction of the genetic gain for milk production.

References

- Andersen, B.B., Steine, T. and Pedersen, G.A. 1993. Economic consequences of including health and fertility traits in dairy cattle breeding. 44th meeting of the European Association for Animal Production. Denmark. 7 pp.
- Anonymous, 1996. Sire evaluation procedures for non-dairy-production traits practised in

- various countries . Interbull Bullitin no. 13. 199 pp.
- Anonymous, 1997. Årsstatistik, avl 1996-97 sektion for avlssystemer. Report no. 70 from Landsudvalget for Kvæg, Skejby, Denmark. 363 pp.
- Bovenhuis, H. Niebel, E. and Fewson, D. 1989. Implications of selection for secondary traits on MOET-nucleus cattle breeding programs for dairy and dual-purpose breeds. *Livest. Prod. Sci.* 22: 237-254.
- Brisbane, J.R. and Gibson, J.P. 1995. Balancing selection response and rate of inbreeding by including genetic relationship in selection decisions. *Theor Appl. Genet.* 91: 421-431.
- Christensen, L.G. and Pedersen, G.A. 1997. Fremtidens avlsplaner for kvæg. Internal report no. 95, Danish institute of Agricultural Sciences. 47 pp.
- Colleau, J.J. 1986. Genetic improvement by embryo transfer within an open selection nucleus in dairy cattle. *Proc. 3th World Congr. Genet. Appl. Livest. Prod.* , Lincoln 12:127-132.
- De Boer, I.J.M. and Van Arendonk, J.A.M. 1994. Additive response to selection adjusted for effects of inbreeding in a closed dairy cattle nucleus assuming a large number of gametes per female. *Anim. Prod.* 58: 173-180
- Groen, A.F., Steine, T., Colleau, J.J., Pedersen, J., Pribyl, J., Reinsch, N. 1997. Economic values in dairy cattle breeding, with special reference to functional traits. Report of an EAAP-working group. *Livest. Prod. Sci.*, 49:1-21.
- Jensen, J. and Madsen, P. 1996. A user's guide to DMU, a package for analysing multivariate mixed models. *Nat. Inst. of Anim. Sci.*, Tjele Denmark. 19 pp.
- Littell, R.C., Milliken, G.A., Stroup, W.W. and Wolfinger, R.D. 1996. SAS system for mixed models. 1. udgave. SAS institute Inc., SAS campus drive, Cary, North Carolina. 633 pp.
- Løvendahl, P. and Jensen, J. 1997. Physiological challenge tests. In Liboriussen, T. and Andersen, B.B. (ed.) Embryo transfer, physiological challenge test and nucleus breeding with dairy cattle. Report no. 737, Danish institute of Agricultural Sciences. Page 73-108.
- Meuwissen, T.H.E. 1997. Maximizing the response of selection with a predefined rate of inbreeding. *J. Anim. Sci.* 75:934-940
- Meuwissen, T.H.E. and Woolliams, J.A. 1993. Responses of multi-trait selection in open nucleus schemes for dairy cattle breeding. *Anim. Prod.* 56: 293-299.
- Meuwissen, T.H.E. and Woolliams, J.A. 1994. Maximizing genetic response in breeding schemes of dairy cattle with constraints on variance of response. *J. Dairy Sci.* 77: 1905-1916.
- Pedersen, G.A. and Christensen, L.G. 1993. Optimering af avlsplaner. Internal report no. 23, Danish institute of Agricultural Sciences. 43 pp.
- Quinton, M. and Smith, C. 1995. Comparison of evaluation-selection systems for maximizing genetic response at the same level of inbreeding. *J Anim. Sci.* 73:2208-2212.
- Quinton, M., Smith, C. and Goddard, M.E. 1992. Comparison of selection methods at the same level of inbreeding. *J. Anim. Sci.* 70:1060-1067.
- Sørensen, M. K. 1999. Stochastic simulation of breeding schemes for dairy cattle. Ph.D thesis. The Royal Veterinary and Agricultural University, Denmark and Danish institute of Agricultural Sciences . 226 pp.

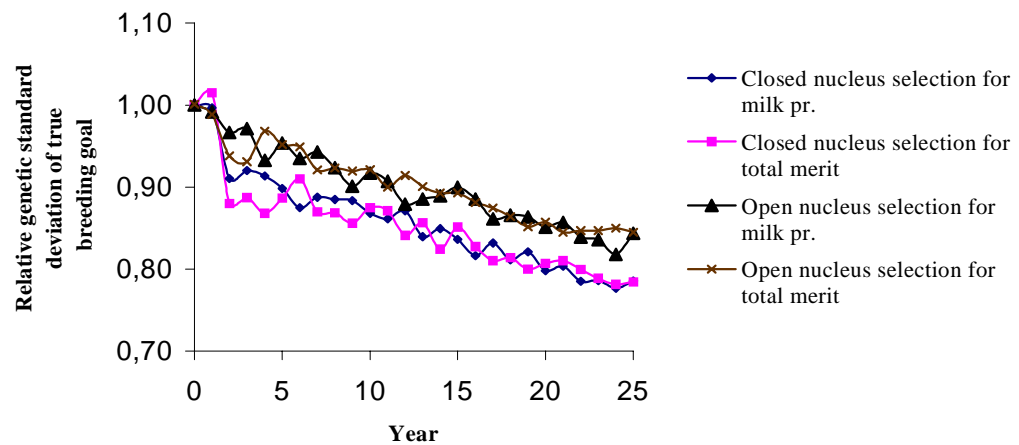


Figure 1. **Relative change in genetic standard deviation of the true breeding goal in different groups of breeding schemes.**

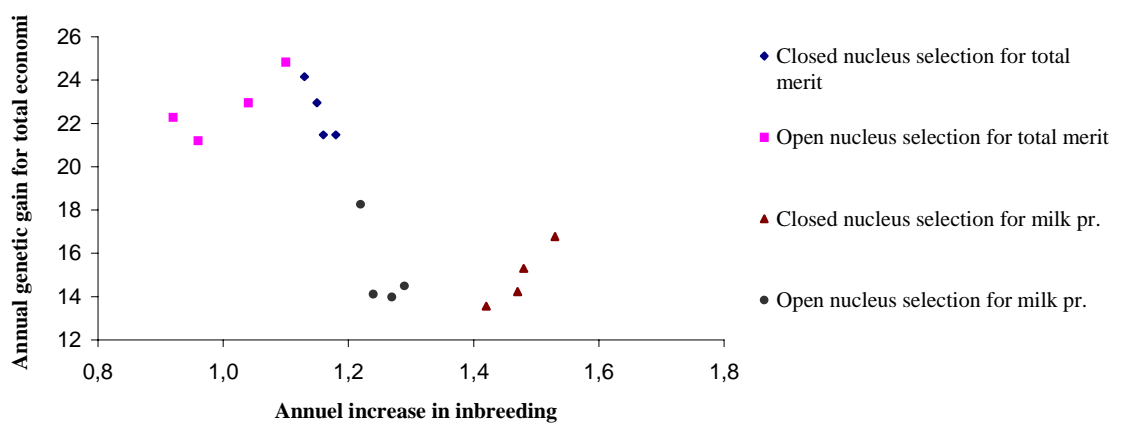


Figure 2. **Connection between total economic gain and annual increase in inbreeding in different breeding schemes**