

# Comparison of Selection Methods at the Same Level of Inbreeding<sup>1</sup>

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**ABSTRACT:** Animal geneticists predict higher genetic responses to selection by increasing the accuracy of selection using BLUP with information on relatives. Comparison of different selection methods is usually made with the same total number tested and with the same number of parents and mating structure so as to give some acceptable (low) level of inbreeding. Use of family information by BLUP results in the individuals selected being more closely related, and the levels of inbreeding are increased, thereby breaking the original restriction on inbreeding. An alternative is to compare methods at the same level of inbreeding. This would allow more intense selection (fewer males selected) with the less accurate

methods. Stochastic simulation shows that, at the same level of inbreeding, differences between the methods are much smaller than if inbreeding is unrestricted. If low to moderate inbreeding levels are targeted, as in a closed line of limited size, then selection on phenotype can yield higher genetic responses than selection on BLUP. Extra responses by BLUP are at the expense of extra inbreeding. The results derived here show that selection on BLUP of breeding values may not be optimal in all cases. Thus, current theory and teaching on selection methods are queried. Revision of the methodology and a reappraisal of the optimization results of selection theory are required.

Key Words: Selection, Inbreeding, Best Linear Unbiased Prediction

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## Introduction

Animal geneticists usually design and compare breeding programs using a given total number of animals tested per year. It is usual to choose a fixed number of males as sires and often a fixed mating ratio (number of females per male) so as to give some acceptable (low) level of inbreeding per year. This has generally been the case in comparing schemes, such as selection on phenotype (mass selection) and on BLUP (Henderson, 1984) of breeding value (Belonsky and Kennedy, 1988). However, BLUP selection tends to select members of the same families. This increases the rate of inbreeding, thus breaking the original restriction on inbreeding. The same applies to schemes that

generate greater genetic response per year by reducing the generation interval (Nicholas and Smith, 1983; Smith, 1985, 1988) and thereby increase the rate of inbreeding per year. An alternative would be to compare selection methods at the same level of inbreeding, as suggested by Goddard (1987) and Wray and Simm (1990). This would allow a higher selection intensity in males in phenotypic selection to offset the extra accuracy in BLUP selection. The objective here is to compare genetic responses with mass selection and BLUP at the same level of inbreeding. This was achieved using stochastic computer simulation, estimating genetic responses for a range of numbers of sires selected, deriving the genetic response and inbreeding obtained in each case, and comparing the results.

## Materials and Methods

A single trait (economic merit) was modeled stochastically using a model with infinitesimal gene effects. For convenience, the trait was consid-

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Table 1. Comparison of cumulative average simulated genetic response (G) (in SD units) and inbreeding (F) (percentage) and their standard deviations ( $S_G$  and  $S_F$  in 100 replicates) from 10 generations of selection on phenotype and on best linear unbiased prediction (BLUP), using a fixed number (10) of males selected as sires (heritability = .25<sup>a</sup>)

No. of generations	Phenotypic selection				BLUP selection			
	G	$S_G$	F	$S_F$	G	$S_G$	F	$S_F$
1	.16	.08	0	0	.16	.08	0	0
2	.46	.11	2	.8	.53	.11	3	.8
3	.74	.13	3	.9	.86	.14	6	1.3
4	1.01	.16	5	.9	1.18	.18	9	2.0
5	1.27	.18	7	1.1	1.47	.21	11	2.7
6	1.52	.19	8	1.1	1.77	.22	14	3.0
7	1.77	.21	10	1.3	2.06	.24	17	3.0
8	2.03	.22	11	1.2	2.35	.26	20	3.5
9	2.28	.23	13	1.3	2.61	.28	22	3.8
10	2.53	.25	14	1.4	2.87	.29	25	3.8

<sup>a</sup>Males 10/100 selected; females 50/100 selected.

ered to be standardized, so the initial phenotypic variance is unity. Phenotypes of individuals in the base population (50 males and 50 females) were generated as the sum of a normally distributed genetic value and a normally distributed environmental effect,  $v\sigma_a + w\sigma_e$ , where  $v$  and  $w$  are random normal deviates,  $\sigma_a$  is the square root of the genetic variance (equal to the heritability  $h^2$ ), and  $\sigma_e = \sqrt{1 - h^2}$ . An individual's phenotype in subsequent generations was given by  $.5g_s + .5g_d + v\sigma_a\sqrt{(1 - F)/2} + w\sigma_e$ , where  $g_s$  and  $g_d$  are the genetic values of the sire and dam, respectively, and  $F$  is the average inbreeding coefficient of the sire and dam derived from the additive relationship matrix (Quaas, 1976). The third term generates the Mendelian sampling effect. The same base population was used in each simulation replicate in comparing different selection methods and logistical variables, such as the number of sires selected (see below).

Inbreeding causes a reduction in the genetic variance and in the genetic response rate. This is automatically taken into account by the simulation. Inbreeding may also lead to inbreeding depression, but this is not allowed for in estimating response rates.

The population modeled was an idealized one, with nonoverlapping generations and selection of males and females on records available before reproductive age. In the standard case, 50 females were selected and each produced two male and two female offspring, giving 100 males and 100 females available for selection. The number ( $S$ ) of males selected as sires was varied, from 1 to 2 and then by intervals of 2 up to 40. This gave a range of genetic responses with the corresponding inbreeding levels. Selection was either on phenotype (individual or mass selection) or on BLUP using

the animal model, and included information on all the relatives available (Henderson, 1984). Selection on a conventional selection index (Hazel, 1943) including the individual, full sibs, and half-sibs was also used, but the results were very similar to BLUP, so are not reported in detail. There were no restrictions imposed on the number of sires (or dams) selected from any one sibship or family, and matings were at random. Any effect of inbreeding depression on phenotypic performance was not included in the simulations. One hundred replicates were run for each case to obtain a reliable result. Variation in genetic response, in inbreeding, and in other output variables was calculated. Selection was carried out for 20 generations.

The simulation was performed for each of four levels of heritability (.05, .1, .25, and .5). To study the effects of population size, the standard case of 50 dams and 200 offspring was increased to 100 dams and 400 offspring per generation. To study the effect of female reproductive rate, 50 dams and 400 offspring were used.

The number of selection lines simulated was large. The standard case involved three selection methods (phenotypic, BLUP, and index), four levels of heritability, 100 replicates, and 21 cases for the number of males selected, giving 25,200 selection lines simulated.

## Results

Results for a conventional comparison of phenotypic and BLUP selection using a fixed number of sires are given in Table 1. The predicted genetic responses accumulate over the generations, along with the inbreeding levels. Selection, using BLUP with its higher accuracy, gives higher rates of

response for the same number of sires selected, but the inbreeding incurred is also higher than for phenotypic selection. Standard deviations of response and of inbreeding are higher for BLUP than for phenotypic selection. This is expected from selecting related individuals from fewer families, rather than selecting individuals on their own phenotypic merit. Standard errors of the averages, from 100 replicates, are one-tenth of the standard deviations listed, showing that the responses and inbreeding levels are well estimated. This is also shown by the smoothness of the graphs in Figure 1.

The main results of the paper are illustrated in Figure 1, and the details are given in Table 2. Figure 1 shows the average simulated cumulated response over 10 generations of selection (heritability .25, 50/100 females selected, and S/100 males selected; S:1 to 40), relative to the cumulated inbreeding. As shown in Table 1, for a given number of sires selected, BLUP selection always gives the highest response. Selection using BLUP

also gives the highest maximum response. However, this is achieved with rather small numbers of sires selected, and so with high levels of inbreeding. These high levels reduce genetic variance and subsequent selection response and impose more inbreeding depression on economic merit (see below).

An alternative, assuming inbreeding is a limiting factor in the choice of breeding programs, is to compare the two methods at the same level of inbreeding. This has the advantage that the reduction of genetic variance and the inbreeding depression will then be the same for the two methods. A lower level of inbreeding per generation may be sought, say 1% per generation. At this level in the simulation, (Figure 1, Table 2,  $h^2 = .25$ , 10 generations), the number of sires selected per generation with phenotypic selection is 16, whereas for BLUP it is 32. This reflects the fact that with family information there is an increased chance that more members from fewer families will be selected by BLUP. The result is that, for lower levels of inbreeding, at the same inbreeding the genetic response is greater with phenotypic selection. The extra information in BLUP incurs proportionally more inbreeding, and the predicted extra gains are lost at a fixed low level of inbreeding. For comparison at the same level of inbreeding, phenotypic selection exceeds BLUP selection until an inbreeding of 1.7% per generation is reached, when 8 and 16 sires are selected, respectively, in the two methods. The graphs cross eventually, because the maximum response by phenotypic selection is less than that for BLUP selection.

Results for the same basic set of parameters in Figure 1 at Generation 10 are also given for Generations 5 and 20 in Table 2. The maximum responses by phenotypic and BLUP selection are each achieved with four sires at Generation 5, four and six sires at Generation 10, and six and eight sires at Generation 20, respectively. The crossover points (in graphs similar to Figure 1) are at 1.8, 1.7, and 1.4% inbreeding per generation, at 5, 10, and 20 generations, with 6 and 14, 8 and 16, and 9 and 20 selected sires, respectively, for phenotypic and for BLUP selection. These trends all reflect the increasing effect of inbreeding in decreasing the genetic variation as inbreeding accumulates over time. Thus, phenotypic selection can give higher rates of response than BLUP over a range in time spans for low to moderate rates of inbreeding.

The results for differences in the heritability of the selected trait (economic merit) for 10 generations of selection are given in Table 3. Maximum responses (at very high inbreeding rates) for phenotypic and for BLUP selection, respectively, at the four levels of heritability (.05, .1, .25, and .5)

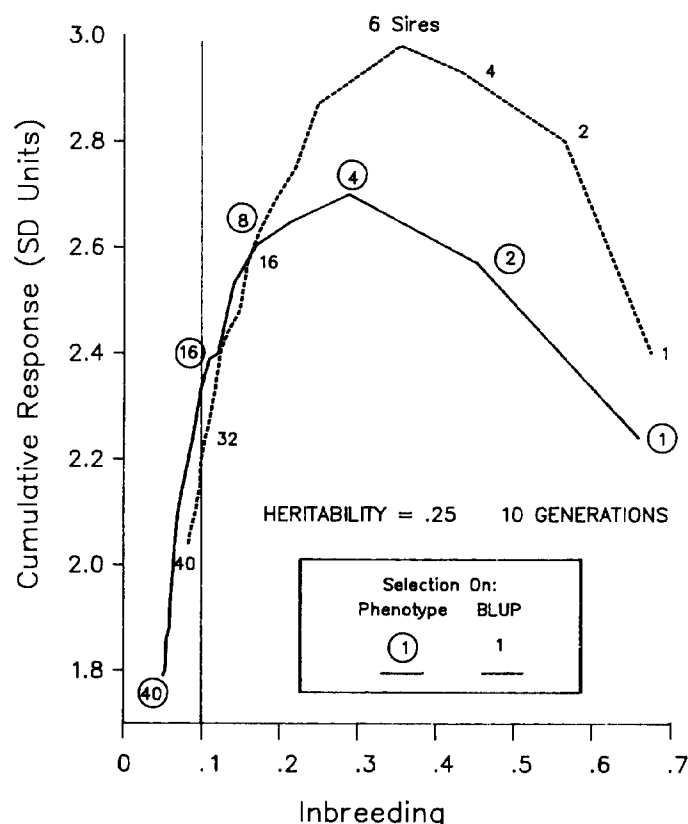


Figure 1. The average (100 replicates) simulated cumulative genetic response and inbreeding after 10 generations of phenotypic and best linear unbiased prediction (BLUP) selection for a range (1 to 40) in the number (S) of sires selected (heritability .25, S/100 males selected, 50/100 females selected). Numerical results are given in Table 2.

were for 8 and 10, 5 and 4, 4 and 6, and 4 and 4 sires selected, respectively. The crossover points were at lower levels of inbreeding with lower heritability, 1.0, 1.1, 1.7, and 2.2% per generation, respectively. The numbers of sires selected by the two methods at the crossover points were 14 and 40, 14 and 36, 8 and 16, and 6 and 10 for the four levels of heritability. It required very mild selection (many sires selected) to achieve low inbreeding rates with BLUP, when heritability is low, and this may be a restriction on the method.

The effects of increasing population size and of increasing the reproduction rate are studied in Table 4. With 400 rather than 200 progeny tested (from 100 vs 50 breeding females), the level of inbreeding at the crossover point fell appreciably (.9 vs 1.7% inbreeding per generation) and the number of sires then needed for phenotypic and BLUP selection consequently increased (8 and 16 to 16 and 32, respectively). With larger populations, intensity of selection in males is reduced less by selecting more males, and this improves the relative response from BLUP compared with phenotypic selection at the same level of inbreeding. On the other hand, increasing the reproductive rate of females (from four to eight progeny) does the reverse, raising the crossover point (from 1.7 to 2.2% inbreeding per generation, with 8 and 16 vs 8 and 28 sires for phenotypic and BLUP selection, respectively). This is probably due to

more sibs giving more accurate family information, and to the increased opportunity of selecting the sires from fewer sibships, because no restrictions were made on the number of sires selected per sibship. These effects will be more pronounced with lower heritability.

## Discussion

A cornerstone of animal breeding theory has been that the accuracy of selection can be increased by use of information on relatives (Lush, 1947; Falconer, 1989), and, hence, the rate of genetic response can be increased. The selection index (Hazel, 1943) was used to combine the information in an optimal way. More recently, BLUP has been shown by Henderson (1984) to be optimal if a complete relationship matrix is used. Best linear unbiased prediction takes account of fixed effects, all family information and relationships, genetic merit of mates, genetic trend, and overlapping generations. These may be important factors in practice that may justify BLUP estimation of fixed effects.

For any given breeding scheme (fixed number of males and females), the predicted genetic responses have always been shown to be higher with BLUP than with phenotypic selection (e.g., Belonsky and Kennedy, 1988; Wray and Hill, 1989).

Table 2. The average (100 replicates) simulated cumulative genetic response and inbreeding after 5, 10, and 20 generations of phenotypic and best linear unbiased prediction (BLUP) selection for a range (1 to 40) in the number (S) of sires selected (heritability = .25, S/100 males selected, 50/100 females selection, as in Figure 1)

No. of sires selected (S)	Generation											
	5				10				20			
	P <sup>a</sup>		B <sup>a</sup>		P		B		P		B	
	G <sup>b</sup>	F <sup>b</sup>	G	F	G	F	G	F	G	F	G	F
1	1.38	39	1.48	40	2.25	66	2.40	68	3.00	90	3.22	91
2	1.43	24	1.60	30	2.57	45	2.81	56	4.01	72	4.17	84
4	1.44	14	1.61	22	2.70	29	2.94	43	4.70	51	4.83	71
6	1.39	10	1.60	17	2.65	21	2.99	35	4.83	39	5.10	62
8	1.34	8	1.52	13	2.60	17	2.91	29	4.82	32	5.17	53
10	1.27	7	1.47	11	2.53	14	2.87	25	4.77	27	5.15	47
12	1.22	5	1.41	10	2.40	12	2.75	22	4.61	24	5.10	42
14	1.19	5	1.37	9	2.39	11	2.69	19	4.61	21	5.05	38
16	1.15	4	1.33	8	2.33	10	2.63	17	4.54	19	4.95	34
18	1.13	4	1.30	7	2.28	9	2.58	16	4.43	18	4.90	32
20	1.09	4	1.24	6	2.20	8	2.48	15	4.32	17	4.78	29
24	1.04	3	1.20	6	2.12	7	2.41	12	4.19	14	4.66	25
28	.97	3	1.12	5	2.00	6	2.28	11	4.02	13	4.47	22
32	.92	3	1.07	5	1.91	6	2.21	10	3.84	12	4.34	20
36	.88	3	1.01	4	1.86	6	2.10	9	3.73	11	4.17	18
40	.85	2	.99	4	1.79	5	2.05	8	3.59	10	4.03	17

<sup>a</sup>P = selection on phenotype; B = selection on BLUP.

<sup>b</sup>G = cumulative genetic change (in SD units); F = cumulative inbreeding (percentage).

Table 3. The average (100 replicates) simulated cumulative genetic response and inbreeding after 10 generations of phenotypic and best linear unbiased prediction (BLUP) selection for a range (1 to 40) in the number of sires selected for three levels of heritability (S/100 males selected, 50/100 females selected, as in Figure 1)

No. of sires selected (S)	Heritability											
	.05				.10				.50			
	P <sup>a</sup>		B		P		B		P		B	
	G <sup>b</sup>	F	G	F	G	F	G	F	G	F	G	F
1	.43	66	.49	68	.83	66	1.00	68	4.53	66	4.70	67
2	.56	44	.67	60	1.06	45	1.23	59	5.03	46	5.20	52
4	.54	26	.76	49	1.12	27	1.41	48	5.12	30	5.29	37
6	.56	19	.75	41	1.12	20	1.39	40	5.05	22	5.15	30
8	.57	15	.74	36	1.07	15	1.37	33	4.92	18	5.06	24
10	.55	12	.78	32	1.07	13	1.34	29	4.79	15	4.95	20
12	.53	11	.72	27	1.03	11	1.29	25	4.64	13	4.81	18
14	.52	10	.72	25	.99	10	1.28	23	4.49	12	4.66	16
16	.50	9	.72	22	.98	9	1.25	20	4.39	10	4.57	14
18	.48	8	.68	20	.96	8	1.23	19	4.30	10	4.49	13
20	.48	7	.66	19	.94	8	1.18	17	4.22	9	4.36	12
24	.46	6	.62	16	.90	7	1.14	15	3.99	7	4.17	10
28	.42	6	.6	14	.83	6	1.09	13	3.82	7	4.01	9
32	.41	5	.56	13	.82	5	1.05	12	3.66	6	3.81	8
36	.40	5	.55	12	.80	5	.99	11	3.47	6	3.65	8
40	.39	5	.54	10	.76	5	.97	10	3.36	5	3.49	7

<sup>a</sup>P = selection on phenotype; B = selection on BLUP.

<sup>b</sup>G = cumulative genetic change (in SD units); F = cumulative inbreeding (percentage).

These predictions are confirmed by the present simulation. The simulation also showed, for the simple situation studied here, without the complicating factors in practice as mentioned above, that the genetic responses and inbreeding with index selection are almost identical to BLUP selection, so the results and discussion apply to both. Some of the gains achieved by BLUP, compared with phenotypic selection, may be reduced if the genetic parameters used in BLUP are not well estimated (Sales and Hill, 1976), if there are pedigree errors (Long et al., 1990), or if there are time delays in obtaining the BLUP evaluations (Smith and Burnside, 1990). None of these factors affects phenotypic selection.

The simulation results show another feature less often studied, namely, that the maximum possible response, allowing the breeding structure to change, is also obtained with BLUP. These maximum responses have been of less interest because of the high rates of inbreeding they create. Yet, if inbreeding is not important, or no attention is paid to it, these BLUP schemes are the breeding schemes that would be recommended. Note also that even with large test facilities, maximum response will be obtained with few males selected and sufficient females selected to regenerate the test population. So the effective size of the breeding population will always be limited, and inbreeding will accumulate. Then schemes that obtain maximum response in the

short term may not be viable in the long run.

The infinitesimal additive model is widely used in simulation work on selection methods. However, it does not allow for dominance effects and so for inbreeding depression. Yet, inbreeding depression on performance traits is well established. Falconer (1989) reported inbreeding depression to be from approximately 3 to 6% of the mean per 10% increase in inbreeding for several performance traits in farm livestock. The effect would likely be larger for economic merit because it involves fitness traits that are more adversely affected by inbreeding.

It is assumed here that inbreeding depression is a limiting factor. However, good estimates of the depression in economic merit are not currently available. Estimates may be obtained by mixed-model data analysis, regressing economic merit on inbreeding level. However, these estimates may not be reliable when depression also depends on dominance relationships. In the absence of good estimates of inbreeding depression, a range of possible values can be used to test the sensitivity of the response to the depression. This has been done for the standard simulation case (heritability .25, 10 generations of selection) in Table 5, with inbreeding depression of -.25, -.50, and -1.0 SD units per 10% increase in inbreeding. These correspond to 2.5, 5, and 10% depression per 10% inbreeding for a trait with a CV of 10%, and twice these values for a CV of 20%. As depression

increases the net (phenotypic) responses in Table 5 decrease. The response curve, for different numbers of sires, is flatter and the maximum net response is with more sires selected. With high inbreeding depression rates, the maximum response is higher with phenotypic selection than with BLUP in this case. The comparisons could also be made at different time horizons (Smith, 1967; Keller et al., 1990a,b) and could be discounted in perpetuity to their net present value (given the discount rate [Smith, 1978] and the generation interval). These alternatives again illustrate that comparing different breeding methods depends very much on the conditions of the comparison.

Another possible criterion for the balance of response and inbreeding is the ratio of response to inbreeding. It turns out that this is not a good criterion, because maximum ratios in the simulation were all obtained with low genetic response and low inbreeding.

The intended use of the stock also affects the levels of inbreeding deemed acceptable. Stocks to be used in crossing programs can be allowed higher inbreeding rates, because inbreeding depression in the purebred stock is then of less importance.

Comparison of responses at the same (moderate) levels of inbreeding per year gives a straightforward and useful comparison of breeding methods, as suggested by Wray and Simm (1990). In the simulation here, the genetic responses at the same moderate levels of inbreeding were usually larger for phenotypic selection than for BLUP, thus reversing conventional animal breeding results. Much of the literature in achieving higher rates of response have relied on reducing generation intervals (Nicholas and Smith, 1983; Smith, 1985, 1988) or on increasing accuracy of selection by using information on relatives (Belovsky and Kennedy, 1988). Both strategies tend to increase the rate of inbreeding per year. These comparisons need to be reevaluated with fixed testing resources per year and at the same inbreeding rate per year. The inbreeding rates tolerated per year will lead to different rates per generation for different generation lengths. An inbreeding rate of 1% per generation would be 1% per year for poultry and pigs but .5% per year for sheep with a generation interval of 2 yr and .25% per year for beef cattle with a generation interval of 4 yr. With the long generation intervals in dairy cattle, optimum inbreeding rates per generation may be quite high (Goddard and Smith, 1990a), but

Table 4. The average (100 replicates) simulated cumulative genetic response and inbreeding after 10 generations of phenotypic and best linear unbiased prediction (BLUP) selection for a range (1 to 40) in the number of sires selected, to compare with the standard case (S/100 males and 50/100 females), twice the population size (selecting S/200 males and 100/200 females), and twice the reproductive rate (selecting S/200 males and 50/200 females) (heritability = .25)

No. of sires selected (S)	Increased population size, four offspring/dam 100 dams				Increased reproductive rate, eight offspring/dam 50 dams			
	P <sup>a</sup>		B		P		B	
	G <sup>b</sup>	F	G	F	G	F	G	F
1	2.38	66	2.65	67	2.59	66	2.82	68
2	2.81	45	3.08	58	3.05	47	3.30	61
4	2.91	28	3.31	42	3.26	31	3.60	51
6	2.94	21	3.31	35	3.23	23	3.62	45
8	2.91	16	3.30	29	3.25	19	3.58	39
10	2.87	13	3.27	25	3.19	16	3.57	36
12	2.79	12	3.20	22	3.13	14	3.54	33
14	2.74	10	3.12	20	3.09	13	3.50	29
16	2.71	9	3.08	18	3.04	11	3.47	27
18	2.66	8	3.06	16	3.01	11	3.46	27
20	2.62	7	3.00	15	2.96	10	3.39	25
24	2.54	6	2.88	12	2.89	9	3.31	22
28	2.47	6	2.82	11	2.80	8	3.25	20
32	2.40	5	2.73	9	2.74	8	3.18	19
36	2.33	5	2.65	9	2.67	7	3.10	17
40	2.28	4	2.58	8	2.64	7	3.01	16

<sup>a</sup>P = selection on phenotype; B = selection on BLUP.

<sup>b</sup>G = cumulative genetic change (in SD units); F = cumulative inbreeding (percentage).

Table 5. The average (100 replicates) simulated cumulative genetic response net of inbreeding depression after 10 generations of phenotypic and best linear unbiased prediction (BLUP) selection for a range in the number of sires selected for four levels of inbreeding depression on performance (heritability .25, S/100 sires selected, 50/100 females selected)

No. of sires selected	Selection							
	Phenotypic inbreeding depression (SD per .01 F)				BLUP inbreeding depression (SD per .01 F)			
	0	.025	.05	.10	0	.025	.05	.10
1	2.25 <sup>a</sup>	.60	—	—	2.40 <sup>a</sup>	.70	—	—
2	2.57	1.45	.32	—	2.81	1.41	—	—
4	2.70	1.48	1.25	—	2.94	1.87	.79	—
6	2.65	2.13	1.60	.55	2.99	2.12	1.24	—
8	2.60	2.18	1.75	.90	2.91	2.19	1.46	—
10	2.53	2.18	1.83	1.13	2.87	2.25	1.62	.37
12	2.40	2.12	1.80	1.20	2.75	2.20	1.65	.55
14	2.39	2.10	1.84 <sup>b</sup>	1.29	2.69	2.22	1.74	.79
16	2.33	2.08	1.83	1.33	2.63	2.21	1.78	.93
18	2.26	2.04	1.81	1.36	2.58	2.18	1.78	.98
20	2.20	2.00	1.80	1.40	2.48	2.11	1.73	.98
24	2.12	1.95	1.77	1.42	2.41	2.11	1.81	1.21
28	2.00	1.85	1.70	1.40	2.28	2.01	1.73	1.18
32	1.91	1.76	1.61	1.31	2.21	1.96	1.71	1.21
36	1.86	1.71	1.56	1.29	2.10	1.88	1.65	1.20
40	1.79	1.67	1.54	1.24	2.05	1.85	1.65	1.25

<sup>a</sup>See Table 2.

<sup>b</sup>2.39 - 11 × .05 = 1.84.

they will be lower with multiple ovulation and embryo transfer schemes with shorter generation intervals.

To limit the rate of inbreeding, in theory and in practice, restrictions are often applied on the use of males, such as the use of only one male per full sibship (Nicholas and Smith, 1983), selection within sires or differential sire use (Toro and Perez-Enciso, 1990), or using males for a limited time span (Goddard, 1987). Such restrictions inevitably also reduce selection response. Toro and Nieto (1984) and Toro and Perez-Enciso (1990) have studied a variety of mating designs to sustain genetic response while reducing inbreeding rates (or to increase response at the same rate of inbreeding). An alternative might be to take account of an individual's prospective inbreeding impact on the line or stock in selection decisions on individuals, as suggested by Goddard and Smith (1990b).

It can be argued that with more information (from relatives) it would be anomalous to have less response. There should be a combination between individual and family information in selection that is optimal, given some criterion. The problem is to find the criterion and the optimum combination. Another strategy may be to go for maximum response, irrespective of inbreeding, in two or several subpopulations and to intercross the subpopulations periodically and start a new subset of subpopulations. The results here warrant a reap-

praisal of much of the work comparing breeding schemes and raise a new set of problems to solve in recommending improved breeding strategies.

## Implications

Considering inbreeding in selection changes the perspectives and the conclusions about the relative merit of different breeding selection systems in genetic improvement. Best linear unbiased prediction evaluation and unrestricted selection on estimated breeding values may not always be optimal. Thus, current theory and teaching on selection methods are queried. Revision of the methodology and a reappraisal of the results of selection theory and optimization of net genetic response rates are required.

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