Controlling Inbreeding by Constraining the Average Relationship Between Parents of Young Bulls Entering AI Progeny Test Programs

K. A. Weigel* and S. W. Lin†

*Department of Dairy Science
University of Wisconsin, Madison 53706

†Department of Industrial Engineering
University of Wisconsin, Madison 53706

ABSTRACT

Inbreeding is known to impair the health, fertility, and productivity of dairy cattle and other livestock species. Mating programs can address inbreeding concerns on the farm, at least in the short term, but long-term control of inbreeding in a dairy population requires consideration of relationships between young bulls entering AI progeny test programs. The present study discusses an application of optimal contribution methodology to selection of young AI bulls in the five major US dairy breeds. Elite cows and active AI sires from the Ayrshire, Brown Swiss, Guernsey, Holstein, and Jersey breeds were considered as potential bull parents. Genetic merit of selected sires and dams was maximized subject to various constraints on the mean additive genetic relationship within the selected group. Relationships between selected parents can be reduced substantially relative to current levels, but the corresponding reduction in genetic merit may be large. This loss in genetic merit occurs due to lower selection intensity, although it is mainly a reflection of a larger number of bull parents (with progeny more evenly distributed among these parents), rather than selection of genetically inferior “outcross” parents that wouldn’t otherwise have been considered. Selected parents were generally older and slightly less inbred than those that would have been chosen had inbreeding been ignored. Although severe restrictions on relationships can be costly, in terms of lost genetic progress, it appears that moderate constraints can keep relationships at a manageable level without a significant loss in genetic merit. Cooperation between breed associations and several competing AI companies may be required to facilitate implementation of this methodology in dispersed populations, but if this can be accomplished, prospects for

achieving a balance between inbreeding and selection seem positive.

(**Key words:** inbreeding, dairy cattle, progeny testing)

INTRODUCTION

Inbreeding is a growing concern in livestock breeding programs. Advances in statistical methods for breeding value estimation, such as animal model BLUP, have increased the accuracy of sire and cow PTA, but the probability of coselection of related animals has also increased. Similarly, advances in reproductive technology, such as AI and embryo transfer have increased the reproductive capacity of individual sires and dams. Inbreeding depression can reduce farm profitability via reductions in the health, fertility, and performance of inbred animals relative to their contemporaries. Smith et al. (1998) reported that a 1% increase in inbreeding of US Holstein cows led to decreases of 37 kg of milk, 1.2 kg of fat, and 1.2 kg of protein per lactation, increases of 0.4 d in age at first calving and 0.3 d in calving interval, and a decrease of 13.1 d in length of productive life. Furthermore, Wilk and McDaniel (1995) noted that offspring of Danish Jersey sires and US Jersey dams had a 12.4% higher rate of survival to first calving than offspring of US Jersey sires and US Jersey dams in the same experimental herd. This advantage was attributed to a reduction of inbreeding depression in the former group.

A comprehensive review of methods to control inbreeding in livestock breeding programs was given by Weigel (2001). Numerous strategies were considered, including restricting family size, creating sublines, modifying BLUP evaluations, using computerized mating programs, and applying optimal contribution theory. The latter two alternatives appear most promising for short-term control of inbreeding on the farm and long-term control of inbreeding in the population, respectively. Weigel and Lin (2000) showed that a well-designed computerized sire selection and mating program could reduce inbreeding levels in the next generation of replacement heifers by 1.8% in Holsteins and

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Corresponding author: K. A. Weigel; e-mail: weigel@calshp.cals.wisc.edu.

2.8% in Jerseys. Corresponding increases in lifetime net income per animal were \$37 and \$60 in Holsteins and Jerseys, respectively. The authors noted that, although mate selection programs can help control inbreeding in the next generation, such programs offer little benefit with respect to long-term maintenance of genetic variation in the population. Mating programs simply make the best available use of the AI sires that are currently available, and if there is little genetic diversity present among these sires, mating programs will be less effective. Because AI plays such an important role in dairy cattle breeding programs, success in controlling inbreeding over the long term will depend on our ability to limit genetic relationships between young bulls in AI progeny test programs.

Several authors, including Woolliams and Meuwissen (1993), Wray and Goddard (1994), Brisbane and Gibson (1995), Meuwissen and Goddard (1997), and Meuwissen (1997) have suggested strategies in which genetic merit of the selected group is maximized subject to a constraint or penalty on the average relationship within the selected group. In this manner, the potential contribution of each animal to the genetic merit of the selected group and to the average relationship within the selected group is determined, and animals that make an "optimal contribution" to future generations are chosen. The present paper follows the approach of Meuwissen (1997), in which average genetic merit of the selected group, $\mathbf{c'u}$, is maximized, subject to a constraint on the average relationship within this group, $\mathbf{c'A c} \leq (\mathbf{R} + 2\Delta\mathbf{F})$, where $\mathbf{c}$ is a vector of optimum contributions of each selection candidate, $\mathbf{u}$ is a vector of EBV of selection candidates, $\mathbf{A}$ is a relationship matrix between selection candidates, $\mathbf{R}$ is the mean additive genetic relationship in the current generation, and $\Delta\mathbf{F}$ is the acceptable (predefined) rate of increase in inbreeding. Additional constraints can be placed on the reproductive capacity of male or female selection candidates. These authors showed via simulation that this method could achieve genetic gains 21 to 60% greater than selection on BLUP EBV after responses were standardized to a constant level of inbreeding. Later studies by Grundy et al. (1998), Meuwissen and Sonesson (1998), Grundy et al. (2000), and Sonesson et al. (2000) have considered modifications of the method of Meuwissen (1997) to accommodate overlapping generations.

The objective of the present study was to apply the optimal contribution procedure of Meuwissen (1997) to selection of young AI sires in the five major US dairy breeds. Of particular interest were parameters of the selected group of bull parents (according to the specified level of inbreeding), such as the number of sires and dams, and their average age, inbreeding coefficient, and genetic merit.

MATERIALS AND METHODS

Data

Data for the present study were provided by the USDA Animal Improvement Programs Laboratory. These data consisted of Lifetime Net Merit PTA of elite (top 1% of) cows in the Ayrshire, Brown Swiss, Guernsey, Holstein, and Jersey breeds in February 2001, as well as the active AI sires in each of these breeds. Because of computational limitations, data for the Holstein breed were limited to the top 25% of active AI bulls, according to Lifetime Net Merit, and a random sample of 20% of the elite cows. Pedigrees were traced back to 1960 for all selection candidates. Holstein and Jersey animals were required to have at least four generations of known parentage, while three generations were required for the Ayrshire, Brown Swiss, and Guernsey breeds.

Methodology

For each breed, the relationship matrix, $\mathbf{A}$, between all selection candidates (i.e., elite cows and active AI sires) was calculated. Similarly, a vector of estimated breeding values, $\mathbf{u}$, was constructed for each breed; this vector contained the Lifetime Net Merit PTA of each selection candidate. Average genetic merit, $\mathbf{c'u}$, of the selected group was maximized, subject to the constraint $\mathbf{c'A c} \leq \mathbf{x}$, where the average additive genetic relationship in the selected group, $\mathbf{x}$, was varied from 8, 10, 12, . . . , 26%. In this analysis, we assumed that genetic relationships among selected parents in the current generation (8, 10, 12, . . . , 26%) will correspond approximately to inbreeding levels of 4, 5, 6, . . . , 13% in the next generation. The highest level of inbreeding (13%) could be thought of as an experimental control, because there was essentially no attempt to control inbreeding in this case. The optimal contribution vector, $\mathbf{c}$, contains the proportion offspring (young bulls) that should be provided by each sire or dam. The number of young bulls required in the Ayrshire, Brown Swiss, Guernsey, Holstein, and Jersey breeds was assumed to be 15, 25, 20, 1300, and 135, respectively (approximately the number of AI young sires of each breed tested annually in the United States). Initially, the reproductive capacities of males and females were left unconstrained. In a subsequent analysis, the reproductive capacity of females was constrained such that each dam could have no more than five progeny.

Several attributes of the optimal contribution vector, $\mathbf{c}$, were examined, including the number of sires and dams, their inbreeding coefficients, the expected inbreeding coefficients of their future progeny (sires only), and their average Lifetime Net Merit before and after

Table 1. Summary of the data used in the present study.

Breed	Young bulls Needed	Elite cows				Active AI bulls				M-F Rel. ³
		No.	Net merit	F ¹	Rel. ²	No.	Net merit	F	Rel.	
Ayrshire	15	162	\$352	4.6	12.8	20	\$222	4.1	12.1	12.8
Brown Swiss	25	350	\$461	3.5	11.8	48	\$302	2.6	13.2	12.2
Guernsey	20	207	\$349	3.8	12.7	19	\$280	3.2	12.2	12.2
Holstein	1300	1433	\$477	4.2	10.6	141	\$457	4.4	11.5	10.9
Jersey	135	1139	\$421	4.8	16.3	90	\$289	4.4	17.1	16.4

¹F = Average inbreeding coefficient of animals in the group.

²Rel. = Average relationship between animals in the group.

³M-F Rel. = Average relationship between elite cows and active AI bulls.

adjusting to zero inbreeding (using a penalty of \$23 in lifetime net income per 1% inbreeding). All means were weighted according to the suggested proportion of progeny from each sire or dam (i.e., the corresponding element of the optimal contribution vector, *c*).

RESULTS AND DISCUSSION

A summary of the selection candidates is shown in Table 1. The number of potential bull dams ranged from 162 Ayrshires to 1433 Holsteins, while the number of potential bull sires ranged from 19 Guernseys to 141 Holsteins. The mean inbreeding coefficient of elite Brown Swiss cows was lowest at 3.5% and the inbreeding coefficient of elite Jersey cows was highest at 4.8%. The mean inbreeding coefficient of Brown Swiss AI sires was lowest at 2.6%, while the corresponding parameters for Holstein and Jersey AI sires were highest at 4.4%. The mean relationship between elite cows ranged from 10.6% for Holsteins to 16.3% for Jerseys, while the mean relationship between active AI sires ranged from 11.5% for Holsteins to 17.1% for Jerseys. The mean relationship between elite cows and active AI sires ranged from 10.9% in Holsteins to 16.4% in Jerseys.

The optimal number of bull sires at each level of the inbreeding constraint is shown in Table 2. The lowest

achievable levels of inbreeding in the next generation were 6% for Ayrshires and Guernseys, 5% for Brown Swiss, and 4% for Holsteins and Jerseys. The optimal number of bull sires at the minimum inbreeding constraint ranged from 15 for Ayrshires to 55 (58) for Holsteins without (with) a constraint of five progeny per bull dam. At the maximum inbreeding constraint (13%), on the other hand, the optimal number of bull sires ranged from 2 in the Guernsey breed (with a constraint of the female reproductive rate) to 10 in the Brown Swiss breed (without the reproductive constraint). In general, the optimal number of bull sires decreased rapidly as the inbreeding constraint increased, particularly at low levels of inbreeding. The optimal number of bull sires was typically lower when the female reproductive rate was constrained, because more bull dams were chosen. However, the reproductive constraint had little effect on the number of sires and dams chosen in the numerically small breeds, because relatively few young sires (and hence few bull dams) were needed. The optimal number of bull dams at each level of the inbreeding constraint is shown in Table 3. This number varied widely, from three Holstein bull dams at 13% inbreeding (without a reproductive constraint), to 289 Holstein bull dams at 4% inbreeding (with a reproductive constraint). As expected, the optimal number of

Table 2. Optimal number of bull sires, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							55	58	28	28
5			23	23			47	36	20	21
6	15	15	19	19	15	15	35	34	15	15
7	12	12	15	14	12	12	18	7	14	14
8	8	8	14	13	9	9	11	6	13	12
9	7	7	12	10	8	7	10	5	13	9
10	5	5	11	9	6	6	7	3	11	9
11	4	4	11	8	5	4	7	3	10	5
12	4	4	10	5	4	3	6	3	10	4
13	4	4	10	3	4	2	6	3	9	4

Table 3. Optimal number of bull dams, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							59	289	51	60
5			25	25			31	280	36	44
6	15	15	18	18	20	20	20	269	29	35
7	15	15	12	12	20	20	15	263	21	31
8	15	15	10	9	18	18	9	262	15	29
9	15	13	9	6	14	14	6	261	13	32
10	12	12	6	6	13	13	5	261	11	20
11	11	10	6	7	12	11	3	261	10	28
12	10	7	5	6	10	10	3	261	7	28
13	6	5	5	6	9	8	3	261	6	28

bull dams decreased rapidly as the inbreeding constraint was relaxed, and more bull dams were selected when a constraint was placed on their reproductive capacity, particularly for the numerically large breeds.

Table 4 shows the weighted mean age of bull sires according to the level of inbreeding constraint. Mean age of bull sires ranged from 74 mo in Jerseys to 95 mo in Ayrshires at the minimum inbreeding constraint. At the maximum inbreeding constraint, mean age of bull sires ranged from 68 mo in Jerseys to 96 mo in Brown Swiss. Mean age of bull sires decreased substantially in Ayrshires, Guernseys, Holsteins, and Jerseys as the acceptable inbreeding level increased. However, the opposite trend was found in Brown Swiss, where somewhat older bulls were chosen at the higher rates of inbreeding. Table 5 shows the weighted mean age of bull dams according to the level of inbreeding constraint. Mean age of bull dams at the minimum inbreeding constraint ranged from 52 mo in Holsteins to 84 mo in Ayrshires. At the maximum inbreeding constraint, mean age ranged from 56 mo in Holsteins (with the reproductive constraint) to 107 mo in Brown Swiss. With the exception of the Guernsey breed, age of bull dams increased as the allowable inbreeding level in-

creased, if the female reproductive rate was unconstrained. With the reproductive rate constrained, however, there was no clear trend in age of bull dams across inbreeding levels.

Table 6 shows the weighted mean inbreeding coefficient of bull sires, according to the level of inbreeding constraint. Mean inbreeding coefficients varied widely, from 1.1% in Brown Swiss sires at the 13% inbreeding constraint, to 7.5% in Jersey sires at the 11% inbreeding constraint (in both cases the female reproductive capacity was constrained). In Ayrshires, there was no clear trend in sires' inbreeding coefficients as the inbreeding constraint was modified. In Brown Swiss and Guernseys, bull sires were slightly less inbred at higher levels of the inbreeding constraint, but in Holsteins and Jerseys the trend was in the opposite direction. Restricting the female reproductive capacity did not have a consistent impact on inbreeding coefficients of bull sires.

Table 7 shows the weighted mean inbreeding coefficient of bull dams, according to the level of inbreeding constraint. Brown Swiss dams had the lowest inbreeding coefficients, 2.2%, at the 12 or 13% levels of the inbreeding constraint (with reproductive capacity unconstrained). On the other hand, Jersey bull dams con-

Table 4. Weighted mean age of the selected bull sires (in months), according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							84	88	74	74
5			93	93			79	75	71	71
6	95	95	91	91	88	88	74	70	70	70
7	92	92	90	91	85	85	71	69	70	70
8	89	89	90	93	82	82	70	69	69	70
9	87	87	91	95	80	80	70	69	69	70
10	85	85	92	100	79	79	69	70	69	69
11	84	84	93	104	78	76	69	70	69	64
12	84	84	94	109	76	73	69	71	68	64
13	84	84	96	115	75	72	69	71	68	64

Table 5. Weighted mean age of the selected bull dams (in months), according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							52	56	56	56
5			81	81			55	55	62	63
6	84	84	86	85	74	74	57	55	65	63
7	88	88	90	89	73	73	60	56	68	63
8	90	90	95	93	72	72	62	56	68	64
9	89	89	98	94	71	71	64	56	67	64
10	90	90	100	95	70	71	67	56	67	65
11	91	87	103	94	69	69	71	56	68	65
12	92	83	105	91	68	69	73	56	69	67
13	92	80	107	91	67	65	74	56	70	65

sistently had the highest inbreeding coefficients, and these were as high as 5.8% at the maximum level of the inbreeding constraint (with reproductive capacity constrained). Raising the inbreeding constraint led to more inbred bull dams in the Guernsey, Holstein, and Jersey breeds, but this trend was not observed in the Ayrshire and Brown Swiss breeds. Constraining the female reproductive capacity did not consistently lead to selection of more or less inbred bull dams. Note that the inbreeding coefficients of selected parents are peculiar to the population structure of each breed, and we cannot make a general conclusion based on the data presented in these tables.

Table 8 shows the mean expected inbreeding coefficient of future progeny which, as measured by the USDA Animal Improvement Programs Laboratory, reflects the mean relationship of each sire to a random sample of 600 females from its respective breed. This measure is typically used to classify a given sire as “highly related to the breed” or as “an outcross.” As shown in the table, relaxing the inbreeding constraint led to selection of Holstein sires that were more highly related to the breed. However, only a slight trend was observed for Jersey sires, and no trend was observed

in the other three breeds. In other words, the selected sires at the maximum inbreeding constraint were no more related to the breed than the selected sires at the minimum inbreeding constraint. Although this seems counterintuitive, the main effect of the inbreeding constraint was to encourage selection of more sires, and a more uniform number of progeny from each sire, rather than to identify a few “outcross” sires that could subsequently be used heavily within the population. In general, we feel that the long-term rates of inbreeding in the major dairy breeds are more likely to depend on relationships between selected parents (i.e., sires and dams of young AI bulls), rather than relationships between available AI sires and the remainder of the population.

Table 9 shows the weighted mean Lifetime Net Merit of the selected group (bull sires and bull dams combined), according to the level of inbreeding constraint. Results are not comparable across breeds, because PTA for each breed are expressed relative to a different genetic base. In Holsteins, for example, mean Lifetime Net Merit increased from \$573 at 4% inbreeding to \$794 at 13% inbreeding. The corresponding increase in Jerseys was from \$413 to \$615. This demonstrates that

Table 6. Weighted mean inbreeding level of the selected bull sires, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							4.1	3.9	6.0	5.9
5			3.3	3.3			4.4	4.6	6.1	6.1
6	5.5	5.5	3.3	3.3	3.8	3.8	4.5	4.6	6.1	6.1
7	5.6	5.6	3.3	3.2	3.9	3.9	4.6	4.7	6.1	6.2
8	5.8	5.8	3.1	3.0	4.0	4.0	4.6	4.6	6.1	6.4
9	5.9	5.9	3.1	2.6	4.0	4.0	4.7	4.6	6.2	6.9
10	5.9	5.9	2.9	2.2	3.7	3.6	4.8	4.6	6.3	7.2
11	5.9	5.8	2.8	2.0	3.4	3.1	4.7	4.7	6.4	7.5
12	5.7	5.6	2.8	1.7	3.2	2.7	4.6	4.8	6.5	6.9
13	5.6	5.4	2.7	1.1	2.9	2.5	4.5	4.8	6.7	6.5

Table 7. Weighted mean inbreeding level of the selected bull dams, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							3.9	3.9	5.3	5.3
5			3.0	3.0			4.0	3.9	5.0	5.2
6	4.2	4.2	2.6	2.6	3.3	3.3	4.1	4.2	5.0	5.2
7	4.0	4.0	2.5	2.5	3.7	3.7	4.0	4.3	5.1	5.6
8	3.8	3.8	2.4	2.6	3.8	3.8	4.2	4.3	5.2	5.6
9	3.8	3.8	2.4	2.6	3.9	3.7	4.4	4.3	5.3	5.5
10	3.7	3.7	2.3	2.6	3.9	3.7	4.4	4.4	5.4	5.6
11	3.7	3.9	2.3	2.7	3.9	3.8	4.4	4.4	5.4	5.7
12	3.6	4.1	2.2	2.8	4.0	3.8	4.4	4.4	5.4	5.7
13	3.5	4.2	2.2	2.8	4.1	4.0	4.4	4.4	5.4	5.8

there can be a significant cost in controlling inbreeding; the average genetic merit of the selected group will always be higher if we ignore inbreeding. As expected, however, the cost of controlling inbreeding is not linear. Large sacrifices in genetic merit may be necessary to achieve extremely low levels of inbreeding, but a moderate reduction in inbreeding is less costly. For example, the difference in genetic merit of Holstein bull parents at 4% inbreeding versus 8% inbreeding was \$182 (with no female reproductive constraint), but the corresponding difference between Holstein bull parents at 9% inbreeding versus 13% inbreeding was only \$25. Thus, it appears that the cost of controlling inbreeding will be manageable. Mean genetic merit was typically lower when a constraint was placed on female reproductive capacity, because more bull dams were needed (hence lower selection intensity).

Table 10 shows the weighted mean Lifetime Net Merit of the selected group, after adjustment to zero inbreeding using a cost factor of \$23 per 1% inbreeding (Smith et al., 1998). As shown in the table, the optimal level of inbreeding in the next generation appears to be intermediate for all five breeds. Without a constraint on female reproductive capacity, adjusted genetic merit

was maximized at 8% inbreeding in Ayrshires and 7% in Brown Swiss, Guernseys, Holsteins, and Jerseys. When female reproductive capacity was limited, this function was maximized at 8% in Ayrshires, 7% in Brown Swiss and Guernseys, and 6% in Holsteins and Jerseys. In general, selection for net lifetime profit adjusted for inbreeding depression seems to be an appropriate strategy, because it implies that higher rates of inbreeding are acceptable if the costs of inbreeding depression are small or if the costs of inbreeding depression are (more than) offset by economic returns from genetic progress.

CONCLUSIONS

In summary, the use of optimal contribution methodology to control relationships between young AI bulls while simultaneously maximizing genetic merit appears promising. A slight sacrifice in genetic gain may be required to achieve a desirable rate of accumulation of inbreeding, but this sacrifice should not be problematic unless severe constraints on inbreeding are imposed. If genetic gains are standardized to a common level of inbreeding, it is clear that balancing inbreeding

Table 8. Weighted mean expected future inbreeding of progeny of the selected bull sires, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							4.4	4.3	7.2	7.2
5			5.7	5.7			4.6	4.7	7.3	7.3
6	6.2	6.2	5.8	5.8	5.7	5.7	4.7	4.9	7.3	7.3
7	6.2	6.2	5.9	5.9	5.6	5.6	4.8	5.0	7.3	7.3
8	6.2	6.2	5.9	5.9	5.5	5.5	4.9	5.0	7.3	7.4
9	6.2	6.2	5.9	5.9	5.5	5.5	4.9	5.1	7.3	7.5
10	6.2	6.2	5.9	5.8	5.5	5.5	5.0	5.1	7.3	7.6
11	6.2	6.2	5.9	5.7	5.5	5.4	5.0	5.0	7.3	7.7
12	6.1	6.1	5.9	5.7	5.4	5.4	5.0	5.0	7.4	7.6
13	6.1	6.0	5.8	5.7	5.4	5.4	5.1	5.0	7.4	7.5

Table 9. Weighted mean Lifetime Net Merit (in dollars) of the selected group, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam (results are not comparable across breeds).

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							573	485	413	408
5			532	532			653	569	475	470
6	373	373	587	587	377	377	701	599	512	504
7	419	419	620	618	411	411	733	611	538	525
8	448	448	641	635	432	432	755	616	559	538
9	470	470	656	646	445	445	769	619	575	546
10	486	486	669	654	454	453	780	621	588	551
11	499	498	679	659	460	458	786	621	599	555
12	509	508	688	663	466	462	791	622	607	556
13	518	515	696	667	470	464	794	622	615	557

and selection is an economically viable exercise. Achieving such a balance will not require the identification of a few “outcross” sires for future use in the population. Instead, it will necessitate the use of a greater number of sires and dams, and it will require a more uniform number of progeny from each. In addition, slightly older animals may be chosen as parents. Constraints on the female reproductive capacity will be necessary due to biological limitations of potential dams, but such constraints should be used cautiously, because they can substantially alter the results. In the presence of inbreeding constraints, selection of sires and dams must be done simultaneously, because the usefulness of any individual sire or dam depends critically on its relationship to the sires and dams that have already been chosen. Conceptually this is not a problem, but bias in PTA of elite cows due to preferential treatment could lead to the overuse of certain cows (and perhaps the selection of too many bulls), unless the female reproductive rate is tightly constrained. Although optimal contribution methodology seems to provide a useful framework for balancing selection and inbreeding, implementation in

a dispersed population will clearly be more challenging than prior applications in closed nucleus populations. Cooperation between breed associations, pedigree breeders, and competing AI organizations will be necessary to ensure that a diverse group of young sires is sampled, and to ensure that individual families are not overused. Based on discussions with key industry leaders, it appears that such cooperate may be possible, particularly for the ‘colored’ breeds. Our intention is to focus on the Jersey breed first, because inbreeding is increasing most rapidly in this breed, and because pedigree breeders, sire analysts, and breed association staff have expressed interest in such a program. Future work should focus on determination of the optimal rate of accumulation of inbreeding, accommodation of overlapping generations, and characterization of the total cost of inbreeding effects on fertility, production, health, and survival. In practice, applications of this methodology will also need to consider the genetic composition of heifers, calves, and pregnancies (i.e., recent matings), because although these animals are not yet selection candidates, they may be highly related to certain bull

Table 10. Weighted mean adjusted Lifetime Net Merit (in dollars) of the selected group, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam (results are not comparable across breeds). Results are adjusted to zero inbreeding using a cost factor of \$23.00 in Lifetime Net Merit per 1% inbreeding.

Inbreeding constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							481	393	321	316
5			417	417			538	454	360	355
6	235	235	449	449	239	239	563	461	374	366
7	258	258	459	457	250	250	572	450	377	364
8	264	264	457	451	248	248	571	432	375	354
9	263	263	449	439	238	238	562	412	368	339
10	256	256	439	424	224	223	550	391	358	321
11	246	245	426	406	207	205	533	368	346	302
12	233	232	412	387	190	186	515	346	331	280
13	219	216	397	368	171	165	495	323	316	258

sires or dams. Given the availability of optimal contribution methodology for controlling relationships between young AI bulls, as well as the widespread use of computerized mating programs for controlling inbreeding on the farm, future prospects for achieving a suitable balance between selection and inbreeding seem positive.

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