

Controlling Inbreeding in Modern Dairy Breeding Programs

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■ Take Home Messages

- ▶ Inbreeding is a natural consequence of selection, and therefore inbreeding levels are increasing in virtually all major dairy cattle populations.
- ▶ Inbreeding depression can cause economic losses through reduced milk production, impaired fertility, and shortened productive life.
- ▶ Inbreeding can be managed rather easily through the use of computerized mate selection programs.
- ▶ Programs that use an objective function based on expected net lifetime profit of potential offspring, after adjustment for inbreeding depression, are most effective.
- ▶ Inbreeding cannot be managed if pedigrees are not recorded accurately and completely!

■ Introduction

Inbreeding is an increasing concern in dairy cattle breeding. Modern genetic selection programs accurately identify families with superior genetic potential, and reproductive technologies are used to disperse these genotypes throughout the population. Inbreeding decreases heterozygosity, thereby reducing phenotypic performance and viability. This phenomenon, known as inbreeding depression, causes a decrease in dairy farm profitability.

Wiggans et al. (1995) found mean inbreeding coefficients of 2.6% and 3.3%, respectively, for sire identified US Holstein cows born in 1990. However, many of these cows had incomplete pedigree information, and the level of inbreeding may have been underestimated. Inbreeding depression caused estimated losses per 1% inbreeding of 29.6 kg of milk, 1.1 kg of fat and 1.0 kg

of protein per lactation. Wiggans et al. (1995) also reported that inbreeding was increasing at an increasing rate. Smith et al. (1998) reported that inbreeding in registered US Holstein cows depressed lifetime net income by \$24.43 per 1% inbreeding in a fluid milk market and \$21.78 per 1% inbreeding in a cheese yield market. This depression in lifetime net income was primarily due to a decrease in productive life of 13.1 d and decreases in lactation milk, fat, and protein yield of 37.2, 1.2, and 1.2 kg, respectively, per 1% inbreeding. In addition, age at first calving increased by 0.4 d, and calving interval increased by 0.3 d per 1% inbreeding. Effects of inbreeding on somatic cell score (SCS) and type traits were minimal. Smith et al. (1998) reported a mean inbreeding coefficient of 1.7% for registered cows. Most cows in this study were born between 1980 and 1990, and current estimates of inbreeding in Holsteins are generally higher.

Estimated inbreeding coefficients and estimates of inbreeding depression were lower for grade cows, presumably due to incomplete pedigree information. Short and Lawlor (1992) reported decreases in lactation yield of 22.6 kg milk, 0.8 kg fat and 0.9 kg protein per 1% inbreeding in registered US Holstein cows. Miglior et al. (1992, 1995) reported an increase in SCS of .012 per 1% inbreeding in Canadian Holsteins and a decrease in lactation milk and fat yield of 9.8 kg and 0.6 kg, respectively, per 1% inbreeding in Canadian Jerseys. Young and Seykora (1996) reported a mean inbreeding coefficient of 5.1% in a random sample of US registered Holstein cows born in 1990. In this study, pedigrees were manually traced back to 1884. This procedure resulted in higher estimates than other studies that used pedigree data back to 1960 (e.g., Short and Lawlor, 1992; Smith et al., 1998; Wiggans et al., 1995), the earliest date at which such data were stored on a computer. Young and Seykora (1996) also reported that the mean relationship within the Holstein population has increased faster than the mean inbreeding coefficient, indicating a narrowing of the genetic base, and they predicted that avoidance of inbreeding will be more difficult in the future.

Farmers have traditionally tried to control inbreeding by avoiding matings of genetically related animals. However, as relationships within the breed increase it becomes difficult to avoid such matings without the aid of a computer. Many bulls and cows that appear to be unrelated based on one or two generations of pedigree data are in fact closely related due to common ancestors in earlier generations. Therefore, computerized mate selection programs, which have traditionally been used for corrective mating of conformation traits, may have potential as a tool for controlling inbreeding. Boswerger et al. (1994) found that selecting mating pairs of Holstein cattle based on sire predicted transmitting ability (PTA) milk and expected inbreeding of progeny resulted in a 1.3% decrease in mean inbreeding coefficient as compared with random mating. Although some existing mating programs consider inbreeding, this may not be done in an optimal manner. For example, some programs enforce an arbitrary maximum value for

inbreeding of proposed matings, but there is little scientific evidence with regard to the choice of an acceptable level of inbreeding. In addition, some commercial mating programs use pedigree data from only the most recent generations, and this can lead to underestimation of inbreeding.

The objective of this study was to examine the potential of several alternative mate selection strategies for the purpose of maximizing net profit and minimizing inbreeding in Holstein and Jersey cattle.

■ Data

Data from a random sample of 25 large Holstein herds and 25 large Jersey herds located in California and Minnesota were used in the present study. Only registered cows were included in the study, because complete pedigree information was required for all animals. All cows that had a reported breeding in the current lactation to a US AI sire with a valid National Association of Animal Breeders code number were included. Pedigrees of cows, service sires, currently available Holstein and Jersey AI sires, and their ancestors were traced back to 1960. Animals born prior to 1960 were considered as unrelated.

■ Mate Pair Allocation using Actual Service Sires

The first phase of the project considered only selection of mating pairs, after the service sires and number of matings per sire had already been determined. Three methods of mate pair selection were compared: actual matings, random matings, and matings that minimized inbreeding. First, the mean inbreeding coefficient was calculated for all of the actual matings that had been reported to DHIA technicians. Second, service sires were reallocated to different cows in the same herd randomly, with the number of matings per service sire held constant, and the mean inbreeding coefficient for these matings was calculated. Whether some of these farms already use a commercial mating program or practice some other type of inbreeding avoidance is unknown. Comparison of inbreeding from actual matings and random matings allowed an assessment of the effectiveness of their current programs for management of inbreeding. Third, expected inbreeding coefficients were calculated for hypothetical progeny resulting from a mating of each cow to each service sire that had been used within the herd. A linear programming algorithm was then used to minimize the mean inbreeding level for each herd, while holding the service sires and number of matings per sire constant. Linear programming has been previously suggested as a potential method to select mating pairs while optimizing some function of genetic merit or expected profit, possibly subject to various constraints. Extension of this

procedure to minimization of inbreeding was straightforward. Mean inbreeding coefficients were calculated for the recommended matings in each herd. In this manner, it was possible to determine the gain that would have been possible had each farmer used a mate selection program to minimize inbreeding. Mean genetic merit was held constant, because the service sires and number of matings per sire were constrained to be the same as in the actual matings.

■ Sire Selection and Mate Pair Allocation using Active AI Sires

In phase two, selection of service sires, determination of the usage level of each service sire, and selection of mating pairs were considered jointly. For each herd, a random sample of potential service sires was chosen from the top 50% of sires on the active AI list ranked by the USDA Net Merit index (NM\$; expressed in US currency). Twenty possible service sires were chosen for each Jersey herd, and 40 possible service sires were chosen for each Holstein herd (due to a greater number of available AI bulls in the Holstein breed). A constraint was imposed such that no service sire could be mated to more than 15% of the herd. Three alternative strategies were considered for selection of service sires and allocation of mating pairs. First, service sires were randomly chosen and mated to cows within each herd; this represented the control. Second, the mean NM\$ of service sires (weighted by the number of matings per sire) was maximized, subject to the constraint that no individual sire by cow mating could exceed a fixed threshold level of inbreeding. Threshold values were 5%, 6%, and 7% for Holsteins and 8%, 9%, and 10% for Jerseys. In addition, mean NM\$ was maximized with no constraint on inbreeding, and this represented an additional control. Third, the following profit function was calculated for each possible sire by cow mating in each herd:

$$\text{Expected Profit} = (\text{Expected lifetime merit}) - (\text{Expected inbreeding}) \times (\text{Inbreeding depression})$$

where expected lifetime merit of each mating was calculated as: ((lactation NM\$ of cow + lactation NM\$ of service sire) / 2) x (expected number of lactations). The expected number of lactations was 2.62 for Holsteins and 2.83 for Jerseys; these values were calculated from phenotypic means for cows in USDA productive life evaluations (26.2 mo and 28.3 mo, respectively, for Holsteins and Jerseys) assuming that 10 months of productive life represents one 305 d lactation. Because NM\$ values were unavailable for some cows, breed averages (\$64.00 for Holsteins and \$58.00 for Jerseys) were substituted for all cows. Conclusions were not affected by this substitution, because the group of cows to be mated within each herd was constant (i.e., no cow selection was practiced). Expected inbreeding was

equal to the inbreeding coefficient for a hypothetical offspring of each possible sire by cow mating, expressed as a deviation from the mean inbreeding for that breed. An inbreeding depression value of -\$23.11 in lifetime net profit per 1% inbreeding was used, based on an average of the inbreeding depression estimates for fluid and manufacturing markets in the study of Smith et al. (1998). A linear programming algorithm was used to maximize the mean of the expected profit function for each herd, subject to the constraint that no service sire was allowed to mate more than 15% of the cows in a given herd. Means of inbreeding coefficients, NM\$ and expected lifetime profit were calculated for each mate selection scheme.

Lastly, the impact of incomplete pedigree information was assessed. Inbreeding coefficients were recalculated using pedigrees of cows and sires that traced back to 1985, rather than 1960. Means and correlations of inbreeding coefficients with differing amounts of historical pedigree data were examined.

■ Discussion

A summary of the data is shown in Table 1. After editing, the mean herd size was 257 for Holsteins and 437 for Jerseys. Actual size of the Holstein herds was generally greater than for Jerseys, but many of the large Holstein herds had a high proportion of unregistered cattle. The mean number of service sires per herd was 51 for Holsteins and 38 for Jerseys; this number was large because cows and service sires were examined at a fixed point in time. Many service sires had only one or two matings per herd, and the actual number of service sires represented in each semen purchase is probably much smaller than the values shown in Table 1.

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

	<u>Holstein</u>	<u>Jersey</u>
No. herds	25	25
Mean no. cows / herd	257	437
Minimum	123	151
Maximum	586	1154
Mean no. service sires / herd	51	38
Minimum	21	14
Maximum	156	75

Table 2 shows the mean inbreeding coefficients for actual matings, random matings, and matings that minimized inbreeding. For the latter two mating scenarios, service sires and number of matings per sire were constrained to be the same as in actual matings. For Holsteins, the mean inbreeding

coefficient for actual matings was 4.9%, and means for the lowest and highest herds were 4.3% and 5.9%, respectively. Inbreeding was higher in Jerseys, with mean actual inbreeding of 6.5% and herd means ranging from 5.2% to 7.3%. For random matings, mean inbreeding coefficients were 5.1% for Holsteins and 7.1% for Jerseys. The range in herd means was the same as with actual matings for Holsteins but was slightly higher than with actual matings for Jerseys. Comparison of inbreeding coefficients from actual and random matings provides a measure of the effectiveness of current programs for inbreeding control in these herds; many herd owners may already attempt to avoid inbreeding by examining sire pedigrees or by using a commercial mating program. Because mean inbreeding for actual matings was only slightly less than mean inbreeding for random matings, it appears that current programs for inbreeding avoidance in these herds are rather ineffective. When inbreeding was minimized via linear programming, mean inbreeding coefficients were 3.3% for Holsteins and 4.6% for Jerseys. Thus, mean inbreeding was reduced by 1.6% or 1.8% compared with actual or random mating, respectively for Holsteins and by 1.9% or 2.5% compared with actual or random mating, respectively, for Jerseys. Assuming a decrease in lifetime profit of approximately \$23.11 per 1% inbreeding (Smith et al., 1998), the mate selection algorithm provided a financial benefit of \$36.98 or \$41.60 relative to actual or random matings for Holsteins, respectively, and a benefit of \$43.91 or \$57.78 relative to actual or random matings for Jerseys, respectively. For large commercial herds, such as those in this study, this represents a substantial economic benefit.

Table 2. Mean, minimum and maximum inbreeding coefficients (%) for Holstein and Jersey herds resulting from actual matings, random matings, or matings that minimized inbreeding while keeping service sires and the number of matings per sire the same as for actual matings.

<u>Mate Selection Scheme</u>	<u>Holstein</u>	<u>Jersey</u>
Actual		
Mean	4.9	6.5
Minimum herd mean	4.3	5.2
Maximum herd mean	5.9	7.3
Random		
Mean	5.1	7.1
Minimum herd mean	4.3	5.6
Maximum herd mean	5.9	8.6
Minimize inbreeding		
Mean	3.3	4.6
Minimum herd mean	2.8	3.4
Maximum herd mean	3.8	5.2

Table 3 shows the effects of using a mate selection algorithm for sire selection and allocation of mating pairs in the Holstein herds. Random mating to a sample of 40 service sires from the top 50% of the active AI list resulted in means of 4.7% inbreeding, \$184.54 NM\$, and \$330.67 estimated lifetime profit. Maximization of NM\$ regardless of inbreeding also resulted in 4.7% inbreeding, indicating that the cows in this study were not more closely related to high NM\$ sires than to average NM\$ sires. Therefore, selection of the highest NM\$ bulls available will increase productivity without causing any additional inbreeding. Mean NM\$ and estimated lifetime profit were \$225.43 and \$383.99, respectively. Commercial mating programs typically invoke a restriction on the maximum inbreeding of recommended matings. Several possible threshold values for inbreeding were considered, and results are shown for 5%, 6%, and 7% levels. Restricting inbreeding to $\leq 5\%$ reduced mean inbreeding by 0.9% with no change in mean NM\$. However, estimated lifetime profit was \$20.71 higher than when inbreeding was ignored, because of a substantial reduction in inbreeding depression. Restricting inbreeding to 6% or 7% gave slightly higher mean inbreeding with no gain in NM\$, so estimated lifetime profit was reduced. Again, it is important to emphasize that allowing more inbreeding did not lead to higher genetic merit of selected service sires. Although enforcing a maximum level of inbreeding effectively decreased inbreeding and increased lifetime profit, this method has limitations. First, the optimum choice of inbreeding threshold is not obvious, and this value can differ across populations. Second, any mating that results in inbreeding less than the predetermined threshold is accepted, but other matings with lower inbreeding may exist. In this sense, inbreeding is not minimized. A more efficient method is to jointly maximize NM\$ and minimize inbreeding or, equivalently, to maximize a function of NM\$ minus inbreeding depression. The results of this method are also shown in Table 3. When the objective function was maximum expected lifetime profit (i.e., lifetime merit minus inbreeding depression), mean inbreeding level was 2.9%, a reduction of 1.8% relative to the methods that ignore inbreeding. Inbreeding was also 0.9%, 1.2% and 1.4% lower than when NM\$ was maximized with limits of 5%, 6%, and 7% inbreeding, respectively. Estimated lifetime profit was \$421.36; this represented an economic benefit per mating of \$16.66 relative to use of a 5% inbreeding threshold and \$37.37 relative to maximization of NM\$ regardless of inbreeding.

Table 3. Mean inbreeding coefficients (F), Net Merit (NM\$), and expected lifetime profit for Holstein herds resulting from random matings to a sample of 40 current active AI sires, matings that maximized Net Merit with a constraint inbreeding, or matings that maximized expected lifetime profit adjusted for inbreeding depression.

<u>Mate Selection Scheme</u>	<u>Inbreeding</u>	<u>Net Merit</u>	<u>Lifetime</u>
<u>Profit</u>			
Random mating	4.7	\$184.54	\$330.67
Maximize NM\$	4.7	\$225.44	\$383.99
Maximize NM\$ with $\leq 5\%$ F	3.8	\$225.43	\$404.70
Maximize NM\$ with $\leq 6\%$ F	4.1	\$225.44	\$398.14
Maximize NM\$ with $\leq 7\%$ F	4.3	\$225.44	\$393.29
Maximize (NM\$ - \$23.11 x F)	2.9	\$222.44	\$421.36

The effects of a mate selection algorithm for sire selection and mate allocation in the Jersey herds are shown in Table 4. Random mating to a sample of 20 sires from the top 50% of the active AI list gave means of 7.1% inbreeding, \$168.01 NM\$, and \$305.26 estimated lifetime profit. Ignoring inbreeding while maximizing NM\$ resulted in 7.2% inbreeding, once again indicating that the difference between relationships with high NM\$ sires and average NM\$ sires is minimal. Mean NM\$ and estimated lifetime profit were \$186.39 and \$327.56, respectively, when inbreeding was ignored. Higher inbreeding thresholds were necessary for the Jersey breed. For example, many Jersey cows had progeny with inbreeding $> 7\%$ regardless of which service sire was chosen. No mating solution existed for one herd at 8% inbreeding, so the means shown for this level represent results from only 24 herds. Solutions were found for all herds at the 9% and 10% levels. This illustrates another limitation of mating algorithms based on threshold values for maximum inbreeding; such algorithms are limited by the most highly inbred animal. Restricting inbreeding to 8% reduced mean inbreeding by 1.4% relative to maximization of NM\$ ignoring inbreeding, and mean NM\$ decreased by only \$0.45. Therefore, estimated lifetime profit was \$32.91 higher when inbreeding was limited to 8%, due to a reduction in inbreeding depression. Maximum inbreeding levels of 9% or 10% level gave slightly higher mean inbreeding with a minimal gain in NM\$, so estimated lifetime profit was reduced. Maximization of estimated lifetime profit adjusted for inbreeding depression gave mean inbreeding of 4.4%, mean NM\$ of \$182.44, and mean lifetime profit of \$387.33. Although NM\$ was \$3.50 lower than when inbreeding was limited to 8%, lifetime profit was \$26.86 higher, and this was due to an additional 1.4% reduction in inbreeding. Therefore, mate selection algorithms effectively reduced inbreeding and increased expected lifetime profit in these Jersey herds, especially the algorithm based on maximizing expected profit minus inbreeding depression.

Table 4. Mean inbreeding coefficients (F), Net Merit (NM\$), and expected lifetime profit for Jersey herds resulting from random matings to a sample of 20 current active AI sires, matings that maximized Net Merit with a constraint inbreeding, or matings that maximized expected lifetime profit adjusted for inbreeding depression.

<u>Mate Selection Scheme</u>	<u>Inbreeding</u>	<u>Net Merit</u>	<u>Lifetime</u>
<u>Profit</u>			
Random mating	7.1	\$168.01	\$305.26
Maximize NM\$	7.2	\$186.39	\$327.56
Maximize NM\$ with $\leq 8\%$ F	5.8	\$185.94	\$360.47
Maximize NM\$ with $\leq 9\%$ F	6.1	\$186.39	\$354.04
Maximize NM\$ with $\leq 10\%$ F	6.4	\$186.39	\$347.98
Maximize (NM\$ - \$23.11 x F)	4.4	\$182.44	\$387.33

Table 5 shows the consequences of ignoring historical pedigree information. Tracing all pedigrees back to 1960 resulted in estimated inbreeding coefficients that were 4.2% and 5.5% higher for Holsteins and Jerseys, respectively, than coefficients estimated from pedigrees traced to 1985. A difference in the magnitude of estimated inbreeding coefficients is unimportant if relative differences in inbreeding between animals are maintained. This is not the case, however, because correlations between inbreeding coefficients from base years of 1960 and 1985 were only 0.25 to 0.59. For this reason, it is extremely important to have complete historical pedigree data for all animals. If pedigrees are incomplete, inbreeding coefficients will be erroneous, and mating recommendations will not be optimal. Obviously there are many (grade) cows in the US and in other countries for which pedigree data are incomplete. Mate selection programs can be used for such cows, but their effectiveness will be reduced. Many commercial mating programs consider only one or two recent generations of pedigree data. If more historical pedigree data exists, it should be used. Lastly, the importance of complete pedigree data is different between the sexes. Because the group of cows to be mated is typically fixed (i.e., no cow selection is being practiced), results will still be useful if pedigrees for some cows are incomplete. However, incomplete pedigrees for service sires can lead to ridiculous results. For example, if a foreign sire or a grade sire has incomplete pedigree data, estimated inbreeding coefficients for all of his future progeny will be underestimated, and this bull will be recommended for far too many matings. For this reason, it may be necessary to exclude or somehow penalize potential service sires that have incomplete historical pedigree data.

Table 5. Effect of ignoring pedigree information prior to 1985 on mean inbreeding coefficient (%) from actual matings, random matings to actual service sires, and random matings to sires from the current active AI list.

	<u>Holstein</u>	<u>Jersey</u>
<u>Actual matings</u>		
Pedigree data since 1960	4.9	6.5
Pedigree data since 1985	0.7	1.0
Correlation (1960, 1985)	0.25	0.37
<u>Random matings with actual service sires</u>		
Pedigree data since 1960	5.1	7.1
Pedigree data since 1985	0.9	1.5
Correlation (1960, 1985)	0.41	0.58
<u>Random matings to current active AI sires</u>		
Pedigree data since 1960	5.1	7.1
Pedigree data since 1985	1.0	1.6
Correlation (1960, 1985)	0.32	0.59

■ Implications

This study clearly demonstrates the important role that computerized mate selection programs can play in reducing inbreeding and increasing farm profitability. Mate selection algorithms based on maximizing NM\$ subject to a fixed inbreeding threshold (5% in Holsteins and 8% in Jerseys) increased estimated lifetime profitability per mating by \$20.71 and \$32.91 in Holsteins and Jerseys, respectively, relative to programs that maximized NM\$ while ignoring inbreeding. Allowing higher levels of inbreeding reduced profits, because mean inbreeding coefficients increased but mean NM\$ did not. This occurred because genetic relationships with elite AI sires were no higher than genetic relationships with average AI sires. Algorithms based on maximizing expected lifetime profit adjusted for inbreeding depression provided an additional economic benefit of \$16.66 in Holsteins and \$26.86 in Jerseys relative to programs that enforced an (optimum) threshold for inbreeding. Thus, total gains in expected lifetime profit per mating due to the optimal mate selection program were \$37.37 in Holsteins and \$59.77 in Jerseys. Application of these mating programs to control inbreeding in large commercial dairy herds could be of tremendous economic benefit. Benefits were greater for Jerseys than for Holsteins, presumably due to higher inbreeding in the current cow population and fewer available sires. Mate selection programs were beneficial in sire selection and in mate pair allocation. Even in situations where service sires and matings per sire were fixed, inbreeding was reduced substantially by reallocation of mating pairs.

Optimal mate selection programs rely on calculation of expected inbreeding coefficients for all possible mating pairs. This can be a computationally demanding task, particularly if the number of potential service sires is large. However, widespread implementation of such programs is feasible, due to the availability of powerful, inexpensive computers and computationally efficient algorithms for extracting ancestor pedigrees and calculating inbreeding coefficients. An additional difficulty may be the lack of availability of complete international pedigree files for the breed of interest. Pedigrees of each cow and each potential service sire must be traced back to the original base population. Therefore, breeding companies that wish to apply these mate selection algorithms must routinely access a large herdbook file from the national evaluation center or breed association. Missing pedigree data for cows will substantially reduce the realized economic benefits of mate selection programs. Perhaps results of inbreeding studies such as this one can be used to motivate producers into improving the accuracy and completeness of identification data for their animals. Incomplete pedigree data for service sires is an even more serious problem, as this can bias mating recommendations in favor of bulls with missing ancestor data; such bulls must be eliminated or otherwise penalized by the mating program.

In summary, mate selection programs can successfully reduce inbreeding in the next generation and increase profitability of commercial dairy operations. However, mating programs cannot solve long-term inbreeding or genetic diversity problems at the population level. Such problems can only be addressed by breeding companies and pedigree breeders; these individuals must maintain genetic diversity in selected animals to which advanced reproductive technologies are applied

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