

Selection and Mating Considering Expected Inbreeding of Future Progeny

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ABSTRACT

Animals most related or least related to current members of their breed were revealed by calculating the expected inbreeding of their future progeny. A sample of potential mates was chosen by randomly selecting 600 females from a recent birth year (1995). Relationships among the sample were computed by the tabular method. Relationships of other animals to the sample population were computed quickly from the relationships of their parents or ancestors. To-Mar Blackstar-ET and Round Oak Rag Apple Elevation were most related to the Holstein breed with expected inbreeding of 7.9 and 7.7%, respectively. Corresponding Jersey bulls were Highland Magic Duncan and Soldierboy Boomer Sooner of CJF with expected inbreeding of 10.9 and 9.5%, respectively. The highest expected inbreeding was 11.1% for Selwood Bettys Commander, 8.6% for Forest Lawn Simon Jetway, 10.1% for Dutch Mill Telestars Fayette, and 7.4% for Korncrest Pacesetter for Ayrshire, Brown Swiss, Guernsey, and Milking Shorthorn breeds, respectively. Regression on inbreeding in the genetic evaluation model removed effects of past inbreeding. Future inbreeding effects could be included for each potential mating or by adjusting breeding values for average inbreeding expected with random mating. The correlation between Holstein breeding values unadjusted and adjusted for inbreeding was 0.9976. The estimated genetic trend was 6% lower with future inbreeding included.

(Key words: inbreeding, relationship matrix, mating programs)

Abbreviation key: AJCA = American Jersey Cattle Association, BV = breeding value, BV_0 = breeding value adjusted to zero inbreeding, BV_A = breeding value adjusted for average inbreeding, R = regression coefficient.

INTRODUCTION

Interest and concern regarding inbreeding continue to grow as breeders search for ways to avoid the eco-

nomic losses associated with inbreeding depression and slower progress resulting from homozygosity. The best way to do this while still making maximum genetic progress and maintaining genetic diversity involves identification of evaluated bulls that are least related to the cow or heifer being bred. Many different methods to obtain this goal have been proposed.

In 1922, Wright (14) defined the inbreeding of an individual and the relationship among individuals. Many methods to compute inbreeding and relationship coefficients have been developed since then. Examples of algorithms that reduce time or memory requirements are provided by Quaas (7), Hudson et al. (5), and Tier (8). In 1983, Boyce (1) reviewed available methods and concluded that although it was possible to calculate inbreeding coefficients from extensive, 30-generation pedigrees, it was neither computationally nor economically feasible to calculate the relationship between numerous individuals. Recently, VanRaden (9) and Wiggans et al. (10) demonstrated the calculation of inbreeding coefficients for populations of 10 million or more animals. They defined a base year of 1960 so that inbreeding coefficients could be more easily interpreted and compared but offered no method for determining average relationships.

Young and colleagues (15, 16) reported several studies of the trend in inbreeding and relationships of registered Holsteins. They identified those bulls and cows occurring most often in random samples of two-line pedigrees. The estimated relationship of these influential individuals to the breed was the ratio of the number of times the animal occurred in the sample pedigrees to the number of possible occurrences. The relationship between two random individuals was estimated as the ratio of common ancestors to the number possible.

Breed associations have also taken an active part in maintaining genetic diversity. Since 1988, Holstein Association USA has published a table in its Sire Summary (4) that identifies influential sires occurring in pedigrees of active AI bulls (bulls that have semen readily available through AI marketing systems), the number of occurrences, and an estimation of the percentage of genes each sire has in common with the list of active AI bulls. This table serves to inform readers

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of the direct impact of certain ancestors but does not provide an easy way to measure relationships for new bulls with few descendants or for cows. In 1997, the American Jersey Cattle Association (AJCA) (12, 13) began calculating and publishing kinship values (K values) that measured average relationships between young bulls and influential bulls. A predetermined base group of 32 sires with the most registered progeny born since 1993 was chosen to represent the breed. The AJCA now offers economic incentives in an effort to encourage use of bulls with low relationship to the breed, thus preserving genetic diversity and minimizing inbreeding.

Until now, most genetic evaluations have predicted the additive value of the genes of an animal and have ignored the inbreeding depression that occurs for most traits when related parents are mated. Regression on inbreeding in the model can remove the effects of past inbreeding, but no corresponding method was available to include the effects of future inbreeding. The true worth of an animal should include additive value and also an adjustment for mean relationship to the population of potential mates (6, 9). If average relationships can be calculated, the regression on inbreeding could be used both to remove past effects of inbreeding and to predict future effects. Average relationships would also be useful for identifying outcross animals.

The purposes of this research were 1) to calculate the average relationship of any animal to its respective breed using a random sample of recent animals to represent the breed, 2) to express that relationship as the expected inbreeding of the future progeny of that animal, 3) to identify influential ancestors in each breed and current individuals with the highest relationship to the breed, and 4) to compare genetic evaluations with and without inbreeding adjustment.

MATERIALS AND METHODS

Inbreeding equals half of the relationship of the parents (14). Similarly, the expected inbreeding with random mating equals half of the mean relationship of the animal to its potential mates. These two identities are true for inbred parents only if numerator relationships of Henderson (3) are used instead of coefficients of Wright (14) that include the square root of 1 plus inbreeding of each parent in the denominator. The covariance matrix of Henderson (3) is also needed instead of the correlation matrix of Wright (14) for use in mixed model equations. Exact calculation of average relationship might be possible if the population of potential mates is small. For large populations, a sample of potential mates can be chosen to represent the population.

An initial sample of 400 females and 400 males from the most recent birth year (1996) were chosen to represent each breed. Smaller subsets of 100 or 200 animals of each sex from the same birth year were used to investigate whether sample size was important. In later analyses and for routine processing, a sample of 600 females born in 1995 was chosen, and results of those analyses are presented. The advantages of using a somewhat smaller, older, all-female sample were that 1) young bulls may be sired by just a few sires, 2) pedigrees of grade heifers are not available until they freshen, and 3) large samples might exceed computer limits as pedigrees lengthen over time. Larger samples were not analyzed because the half-stored matrix required for computing relationships among the 800 sample animals and their ancestors occupied nearly all of the 2 Gbytes of memory available. The average relationship of each animal to the sample was calculated from this matrix and stored. The average relationships of these known animals to animals in the unknown parent groups were also stored. Unknown animals were assumed to be as inbred on average as known animals of the same age (9).

For any animal not represented in this initial large matrix, the average relationship to the sample population can be computed rapidly. By definition, such animals were not members of the sample and had no descendants in the sample. Thus, relationships with the sample population occurred only through the parents of the animal. The average relationship of the animal equalled the mean of the average relationships of its parents with the sample.

If a parent of an animal was represented in the initial matrix, the average relationship of the animal was available and could be substituted into the formula. If not the average relationships of its grandparents to the sample may be available. All common ancestors shared by an animal and the sample will be accounted for if this procedure is repeated until each pedigree path ends in either an unknown ancestor or an ancestor whose average relationship is known. These calculations are very affordable and can be done at the same time that inbreeding coefficients are calculated.

The computations can be displayed in algebra as follows. Let a_{ij} be an element of the numerator relationship matrix A , and let a_i be the average relationship of individual i with the r members of the random sample. Thus,

$$a_i = \sum_{j=1}^r a_{ij}/r$$

This formula also holds when i represents an unknown parent group. For individuals that are only related to

sample animals through their common ancestors, the formula simplifies to

$$a_i = (a_s + a_d)/2$$

where a_s and a_d are average relationships for the sire and dam of an individual to the sample population. This formula was repeated beginning from oldest ancestors to youngest, calculating the parent average of each ancestor and replacing these averages with those of the ancestor, a_i , if available.

An a_i of an individual was greater than the average of a_s and a_d only if the individual was a member of the breed sample or had descendants in the sample. For each descendant, the parents of the individual increased their relationships to the sample by only half as much as the individual. If the individual was inbred, a_s and a_d may be less than half of a_i .

The inbreeding (F.) that would occur if the sample animals were randomly mated to each other equals half their average relationship or

$$F. = 0.5 \sum_{i=1}^r \sum_{j=1}^r a_{ij}/r^2.$$

Selection and mating programs that ignore relationships among animals lead to higher inbreeding depression and lower long-term progress than ideal. Breeders should select animals that are less related to the population of potential mates and also less related to each other (2). Selection on breeding values adjusted for expected inbreeding achieves the first goal. The second goal can be achieved by examining a_{ij} among the selected animals. For populations of 10,000 or more (including ancestors), sampling may be needed instead of exact calculation.

Genetic evaluations can adjust for inbreeding depression by removing the effects of past inbreeding and including the expected effect of future inbreeding.

Breeding values were adjusted to an inbreeding level of zero (BV_0) by subtracting the regression (R) multiplied by the inbreeding coefficient of a cow from her record (y). Often the regression was negative, which created a positive adjustment for inbred animals. The adjusted record (y^*) was then

$$y^* = y - R(a_{ii} - 1)0.5.$$

Future inbreeding could be included by using 1) the inbreeding coefficient ($0.5a_{ij}$) for each particular mating or 2) the average inbreeding coefficient ($0.5 a_i$), assuming that mating was random. For individual matings, the predicted value of progeny of sire s and dam d (P_{sd}) could be obtained from the BV_0 of sire and dam and their relationship as

$$P_{sd} = 0.5(BV_s + BV_d) + 0.5Ra_{sd}$$

For a random mating, a breeding value adjusted for the average expected inbreeding (BV_A) was estimated for any individual as

$$BV_A = BV_0 + Ra_i.$$

If the model of evaluation made no adjustment for inbreeding, prediction of individual matings was less precise because breeding values of each parent included an unknown effect of inbreeding from their own records or from past matings.

RESULTS

Little time was needed to calculate a relationship matrix for the sample population. The total number of ancestors for the Holstein sample of 600 animals was 122,841, but many of these ancestors were duplicates. Only 14,084 animals and ancestors remained after duplicates were excluded. About 5 min were required to

TABLE 1. Top 10 Ayrshire bulls with more than 1000 daughters and currently active bulls, ranked by expected inbreeding (%) of future progeny (Future). Also shown is the inbreeding (%) of past daughters (Past) and the inbreeding (%) of the bull (Bull).

No.	More than 1000 daughters			Active AI list				
	Name	Bull	Past	Future	Name	Bull	Past	Future
1	Selwood Betty's Commander	0.0	0.5	11.1	Covey-Farms Rebate	4.4	5.9	7.0
2	Mar-ral Hi Kick	0.0	3.4	8.1	Palmyra Luv's Regiment	6.9	6.8	6.9
3	Covey-Farms Vitality Reliable	4.3	5.3	7.7	Burr-Ayr-Farms Wel Vincent	12.8	7.3	6.9
4	Granbyenne Royal Command	0.6	3.5	6.9	Ardrossan EV Kates Trident	3.0	4.4	6.9
5	Des Peupliers Rebel	2.7	3.6	6.9	Covey-Farms Reno	7.9	4.8	6.8
6	Mar-ral Madge's Boy	0.0	4.0	6.4	Bonnie Brae Heligo	1.0	4.6	6.8
7	Donholm Commander Jack's Choice	0.0	2.9	6.3	Wilshore Spectacular	7.8	6.2	6.5
8	Mar-ral Commander's Pride	0.0	3.1	6.1	Palmyra Sailor	5.5	5.8	6.4
9	Donholm Commander's Victory	0.0	3.3	6.0	Maple-Dell Soldier	3.5	5.0	6.3
10	Oak-Ridge Flashy Klondike	0.0	0.4	4.6	Palmyra Sailor's Loverboy	7.9	6.4	6.3

TABLE 2. Top 10 Brown Swiss bulls with more than 1000 daughters and currently active bulls, ranked by expected inbreeding (%) of future progeny (Future). Also shown is the inbreeding (%) of past daughters (Past) and the inbreeding (%) of the bull (Bull).

No.	More than 1000 daughters				Active AI list			
	Name	Bull	Past	Future	Name	Bull	Past	Future
1	White Cloud Jason's Elegant	0.0	0.6	7.4	Forest Lawn Simon Jetway	0.0	4.1	8.6
2	K Top Acres Dotson	0.4	3.9	7.2	Top Acres Dotson Prophet	5.1	3.9	7.9
3	Top Acres Elegant Simon	0.0	2.2	7.2	Top Acres Dotson Proto	5.1	3.5	6.8
4	Norvic Telstar	0.0	1.3	6.9	Top Acres Pyramid	3.6	4.3	6.7
5	Bridge View Elegant Jade	0.0	3.5	6.7	Bridge View Elegant Jade	0.0	3.5	6.7
6	Victory Acres Jubilation Emory	0.4	2.8	6.4	Top Acres Peerless	1.1	3.8	6.6
7	West Lawn Stretch Improver	0.0	2.1	6.2	Forest Lawn Simon Jupiter	0.0	3.5	6.6
8	Trout Run Distinct Blend	0.0	2.7	5.4	Top Acres Emory Perot	1.6	4.6	6.6
9	Johann Pete Rose	1.8	2.5	5.0	Victory Acres Jubilation Emory	0.4	2.8	6.4
10	E E Beautician King	0.0	2.1	4.5	Forest Lawn Simon Star	0.0	2.6	6.3

set up and fill out this $14,084 \times 14,084$ matrix on an IBM RS/6000 workstation (IBM, Armonk, NY). For the remaining 29 million Holsteins, about 9 h were required to calculate inbreeding by repeated application of the tabular method (9). With the additional steps to calculate the relationships of each animal to the sample population, time increased to 13 h.

Tables 1 through 6 contain results for the six breeds, including the top ten bulls in each of two categories. The more than 1000 daughters category was intended to represent the top 10 most influential bulls of the breed and the active list represented bulls in current use with highest estimated relationship to the breed.

Breed Results

Ayrshire. Selwood Betty's Commander, born in 1953, had the highest relationship to the current members of the Ayrshire breed. No other dairy bull was as highly related to its breed as Selwood Betty's Commander is to the Ayrshire breed. If he were progeny tested again today, the resulting progeny would be inbred by an average of 11.1% as shown in Table 1. This bull already appears several times in the pedigrees of most Ayrshires. This breed, while having a smaller overall popula-

tion, also exhibits the highest mean and standard deviation for expected inbreeding for All Bulls of the breed and in the more than 1000 daughters category (Table 7).

Brown Swiss. Table 2 contains results for the Brown Swiss breed. The top bull with over 1000 daughters was White Cloud Jason's Elegant with an expected inbreeding of 7.4%. The bull with the highest expected inbreeding in the breed was Forest Lawn Simon Jetway. This bull, born in 1988 and still on the active AI list, had a higher expected inbreeding than any of the older bulls with many daughters. Victory Acres Jubilation Emory is on both the active (#9) and more than 1000 daughters lists (#6). He is an example of a bull that is highly related to the breed (expected inbreeding = 6.4%), has already produced over 1000 daughters, and is still available to the producer.

Guernsey. The high bull in the more than 1000 daughters list was Dutch Mills Telestars Fayette with an expected inbreeding of 10.1%. High active bull was Nells Glow Perfecto Flint (7.8%), who had only 35 producing daughters at the time of this research. Table 7 shows that Guernseys have the lowest mean expected inbreeding for the all bulls category (1.1%) but an intermediate mean expected inbreeding for active bulls, probably because of a declining population over time.

TABLE 3. Top 10 Guernsey bulls with more than 1000 daughters and currently active bulls, ranked by expected inbreeding (%) of future progeny (Future). Also shown is the inbreeding (%) of past daughters (Past) and the inbreeding (%) of the bull (Bull).

No.	More than 1000 daughters				Active AI list			
	Name	Bull	Past	Future	Name	Bull	Past	Future
1	Dutch Mill Telestars Fayette	0.0	3.0	10.1	Nells Glow Perfecto Flint	12.4	5.8	7.8
2	Maurana Wis Telestar	0.0	1.6	9.1	Trotacre Ideal Logic	7.1	6.0	7.3
3	Lily Lane Penny Perfecto	2.7	5.5	9.1	Myrtledales Smokey Hornet	6.3	6.1	6.7
4	Nells Glow Admiral Magic	0.7	3.3	7.9	Marodore Ideal Luke	4.7	5.5	6.4
5	Wampanoag Fayette Smokey	1.2	4.6	7.8	Jimco Pansys Billy	8.1	4.9	6.4
6	Kellogg Minnies Choice	0.0	1.0	7.3	Coulee Crest Smokey Garwood	4.3	5.2	6.2
7	Lincrest Telestar Buttermost	1.6	4.7	7.2	Lantz Farm Smoking Putter	5.6	5.2	6.1
8	Welcome Choice Admiral	0.8	1.8	7.2	Tamaracks Perfectos Valiant	2.3	5.4	6.0
9	Bettsward Telestar Victory	0.0	2.8	6.5	Myrtledales Magic Hot Shot	7.1	4.3	6.0
10	Kellogg E. Choice Pender	1.6	2.4	5.3	Trotacre Mercury Lorry	0.8	5.0	6.0

TABLE 4. Top 10 Holstein bulls with more than 1000 daughters and currently active bulls, ranked by expected inbreeding (%) of future progeny (Future). Also shown is the inbreeding (%) of past daughters (Past) and the inbreeding (%) of the bull (Bull).

No.	More than 1000 daughters				Active AI list			
	Name	Bull	Past	Future	Name	Bull	Past	Future
1	To-Mar Blackstar	4.7	3.8	7.9	Rothrock Blackstar Loyal	5.0	3.3	7.1
2	Round Oak Rag Apple Elevation	0.0	1.2	7.7	Queens-Manor-G Rave	6.3	4.5	7.1
3	Pawnee Farm Arlinda Chief	0.0	0.3	7.6	Queens-Manor-G Raven	6.3	4.2	7.1
4	S-W-D Valiant	0.0	1.1	7.3	Hard-Le Darkstar	4.6	4.2	7.0
5	Hard-Le Darkstar	4.6	4.2	7.0	Holmes-View Mark Star	4.2	3.6	7.0
6	Cal-Clark Board Chairman	1.6	3.0	6.9	Langs-Twin-Elm Matrix	4.8	3.4	6.9
7	Mowry-E Valiant Elmer	7.0	3.8	6.9	Langs-Twin-Elm Much More	4.8	3.2	6.9
8	Walkway Chief Mark	0.0	2.6	6.8	Langs-Twin-Elm BS Bucky	4.8	3.6	6.9
9	Fustead Billijo	3.8	4.4	6.8	Langs-Twin-Elm Mitzer	4.8	3.0	6.9
10	Wa-Del RC Matt	4.5	5.0	6.8	Regancrest Blackcrest	4.2	3.3	6.9

Holstein. Table 4 shows the top bull in the more than 1000 daughters group was To-Mar Blackstar (Blackstar) with an expected inbreeding of 7.9%. Round Oak Rag Apple Elevation (Elevation) was second on this list, and Pawnee Farm Arlinda Chief (Chief) was third. The expected inbreeding for Elevation was 7.7% and, when multiplied by 2 (15.4%), could be compared with findings by Young et al. (16) in which the relationship of Elevation to the breed was estimated as 12.2%. Similar results were found for Pawnee Farm Arlinda Chief and S-W-D Valiant whose expected inbreeding values, (7.6% and 7.3%, respectively), when multiplied by two, were 15.2% and 14.6%. These values can be compared with 12.3% and 9.6% in Young et al. (16). Consistently higher results from this research could have been due to more recent information and addition of influential sires such as Walkway Chief Mark and To-Mar Blackstar. Table 7 shows that inbreeding levels were lower for the Holstein breed than for most other breeds.

The pedigree analysis table of the Holstein Association (4) provided similar rankings to those in Table 4 for bulls with more than 1000 daughters. Numerically, the percentage of genes in common displayed by Hol-

stein Association was greater than our expected future inbreeding but was lower than the mean relationship of the bull to potential mates. Reasons may be that 1) only direct descendants of a bull were counted, whereas we included relationships through any common ancestor; 2) their population of interest had been evaluated bulls, whereas ours was young calves; and 3) their pedigrees were traced five generations, whereas ours ended at the first ancestor born before 1960. Procedures of the Holstein Association (4) were not designed for use with cows or young stock.

Jersey. Highland Magic Duncan was the top more than 1000 daughters bull (Table 5) with expected inbreeding of 10.9%. Mason Boomer Sooner Berretta, #3 on this list at 9.2% was also #1 on the more than 1000 daughters list. This bull is another example of a currently active AI bull with high relationship to the breed, which has already produced more than 1000 daughters. Table 7 confirms this close relationship of active bulls to the breed by showing that this group of bulls had a greater mean relationship to the breed than did active bulls of any other breed.

Though the AJCA has released kinship values only for the very youngest bulls, some basic comparisons of

TABLE 5. Top 10 Jersey bulls with more than 1000 daughters and currently active bulls, ranked by expected inbreeding (%) of future progeny (Future). Also shown is the inbreeding (%) of past daughters (Past) and the inbreeding (%) of the bull (Bull).

No.	More than 1000 daughters				Active AI list			
	Name	Bull	Past	Future	Name	Bull	Past	Future
1	Highland Magic Duncan	1.6	4.0	10.9	Mason Boomer Sooner Berretta	2.2	3.8	9.2
2	Soldierboy Boomer Sooner of CJF	0.0	3.3	9.5	Greenwood Poseidon	5.5	5.9	9.2
3	Mason Boomer Sooner Berretta	2.2	3.8	9.2	Greenwood Sooner Khan	3.2	5.8	9.0
4	Observer Chocolate Soldier	0.0	0.2	8.8	Stonyrun Sooner Franco	4.0	5.9	8.9
5	Duncan Duke of Glenwood	5.8	6.3	8.7	WF/L&M Duncan Barber	7.6	5.2	8.9
6	Highland Duncan Dexter	6.3	5.9	8.6	Osbs Mister T	6.1	5.9	8.9
7	Avon Road Trader	4.5	6.2	8.3	Midnight Storm	5.1	5.4	8.8
8	A-Nine Top Brass	0.0	2.9	8.3	Stonyrun Sooner Freddy	4.0	5.6	8.8
9	Au Duncan Brass Carmel	5.9	5.3	8.2	Sooner Nina Earl	5.1	5.4	8.7
10	Highland Duncan Lester	2.5	4.6	8.2	Forest Glen Dexter Gemini	11.4	5.1	8.7

TABLE 6. Top 10 Milking Shorthorn bulls with more than 100 daughters and currently active bulls, ranked by expected inbreeding (%) of future progeny (Future). Also shown is the inbreeding (%) of past daughters (Past) and the inbreeding (%) of the bull (Bull).

No.	More than 100 daughters				Active AI list			
	Name	Bull	Past	Future	Name	Bull	Past	Future
1	Korncrest Pacesetter	0.4	3.2	7.4	Dusty Glen	1.3	3.7	4.7
2	Sunny View Princess' Promise	0.0	0.5	7.3	Wildwood Dusty K-Schie	1.3	3.7	4.6
3	Kingsdale Elegant P.S.	9.6	6.8	6.8	Red Cedar Valiant	2.4	5.0	4.4
4	Kingsdale Elegant Duke	9.6	5.8	6.6	Blaser Acres Pepper B2	2.7	3.0	4.2
5	Pinehurst Rebel 9th	4.2	4.2	5.6	Bar-D Broker	7.3	4.2	4.2
6	Clayside Prince Bicenten	3.1	3.1	5.3	Blissful Elegant Resolve	1.6	3.1	3.6
7	Elwood S. V. Promise	0.0	3.7	5.1	Meriville Peerless	19.5	2.4	3.4
8	Prairie-Pine Wr's Big Time	4.4	3.8	5.0	Idalee Central Theme	3.3	3.3	3.4
9	Innisfail Lady's Promise	0.0	1.0	4.9				
10	Kingsdale Enhancer	2.5	4.7	4.8				

the two procedures can be drawn. Seven of the top more than 1000 daughters bulls are on the AJCA list of 32 base sires. The three bulls not present in the AJCA list, Highland Magic Duncan (#1, 10.9%), Observer Chocolate Soldier (#4, 8.8%), and A-Nine Top Brass (#8, 8.3%) were born in 1980, 1962, and 1977, respectively. As AJCA selected their base sires on the highest number of registered female progeny born since 1993, the absence of these three highly related sires is most likely due to age and lack of recent usage, as no bull on the AJCA list was born before 1980.

Milking Shorthorn. As the Milking Shorthorn breed had no bulls with greater than 1000 daughters, the cutoff was decreased to 100. The top bull in this category was Korncrest Pacesetter with an expected

inbreeding of 7.4% for future progeny. Table 7 shows that active bulls of the breed had nearly the same mean expected inbreeding as the more than 100 daughters group. This value was also lower than the expected inbreeding of active bulls of any other breed. The Milking Shorthorn population is small, but expected inbreeding was low because breeders have continued to outcross with Norwegian Red, Illawarra, and now even Red Holstein. This breed also contains the bull with the highest overall individual level of inbreeding, Meriville Peerless, with inbreeding of 19.5%.

Sample Size Results

The effect of sample size was examined, and results are in Table 8. Three of the top sires of each breed

TABLE 7. Means, standard deviations, minimums, and maximums for expected inbreeding of future daughters for all breeds for three different groups, All bulls, more than 1000 daughters, and active bulls.

Breed and group	N	\bar{X}	SD	Minimum	Maximum
Ayrshire					
All bulls	2212	2.6	2.3	0.0	11.1
More than 1000 daughters	21	4.6	2.8	0.6	11.1
Active bulls	22	6.0	0.9	3.5	7.0
Brown Swiss					
All bulls	2584	1.9	1.9	0.0	8.6
More than 1000 daughters	27	4.0	2.1	0.3	7.4
Active bulls	46	5.5	1.0	3.8	8.6
Guernsey					
All bulls	8301	1.1	1.6	0.0	10.1
More than 1000 daughters	64	2.8	2.7	0.1	10.1
Active bulls	25	5.7	1.0	3.3	7.8
Holstein					
All bulls	93,755	2.3	2.0	0.0	7.9
More than 1000 daughters	2214	2.4	2.0	0.0	7.9
Active bulls	597	4.9	1.0	1.3	7.1
Jersey					
All bulls	10,624	2.0	2.4	0.0	10.9
More than 1000 daughters	131	3.4	2.8	0.1	10.9
Active bulls	76	7.0	1.3	3.6	9.2
Milking Shorthorn					
All bulls	659	2.3	1.5	0.0	7.4
More than 100 daughters	38	3.9	1.7	1.3	7.4
Active bulls	8	4.0	.5	3.4	4.7

TABLE 8. Expected inbreeding values¹ for influential bulls when different numbers of sample animals were selected for the base population from which expected inbreeding was estimated.

Breed and bull	Expected inbreeding values (%)		
	n = 200	n = 400	n = 800
Ayrshire			
Selwood Betty's Commander	11.0	11.2	11.5
Covey-Farms Vitality Reliable	7.5	7.5	7.9
Mar-Ral High Kick	7.7	7.6	7.8
Brown Swiss			
White Cloud Jason's Elegant	7.3	7.4	7.2
Norvic Telestar	7.2	7.3	6.9
Top Acres Elegant Simon	6.9	7.1	6.6
Guernsey			
Dutch Mill Telestars Fayette	10.4	10.7	10.4
Lily Lane Penny Perfecto	9.9	10.3	9.6
Maurana Wis Telestar	8.6	8.7	8.7
Holstein			
Pawnee Farm Arlinda Chief	7.3	7.3	7.8
S-W-D Valiant	7.4	7.4	7.8
Round Oak Rag Apple Elevation	7.5	7.5	7.4
Jersey			
Highland Magic Duncan	10.3	11.2	11.1
Sooner Boomer Sooner of CJF	8.9	8.8	9.0
Duncan Duke of Glenwood	8.5	8.9	8.9
Milking Shorthorn			
Sunny View Princess' Promise	7.6	7.6	7.4
Korncrest Pacesetter	6.7	7.1	6.9
Kingsdale Elegant P.S.	6.1	6.6	6.5

¹Obtained from November 1997 evaluation results instead of August 1998.

are listed along with estimates of expected inbreeding calculated from the initial 200, 400, and 800 sample animals. Estimates changed very little as sample size increased from 200 to 800 animals. Simple correlations between estimates based on different sample sizes are located in Table 9 for the bulls listed. Correlations ranged from 0.98 to 0.99. Influential sires had stable estimates, but ancestors with fewer progeny could change more depending on whether their progeny were included in the sample.

Inbreeding Adjustment Results

Adjusted breeding values increased slightly for bulls whose previous daughters were the most inbred and decreased slightly for bulls most related to their potential mates. Table 10 contains simple statistical compar-

TABLE 9. Correlations between estimates of expected inbreeding for differing sizes of sample populations.

Sample animals (no.)	200	400	600	800
200	1.0	0.99	0.99	0.98
400		1.0	0.98	0.98
600			1.0	0.98
800				1.0

TABLE 10. Means, standard deviations, minimums and maximums for inbreeding of current and future daughters, published milk breeding value (BV), unadjusted milk BV (BV₀), and adjusted milk BV (BV_A) and the absolute difference (Abs) between BV and BV_A for 584 currently active Holstein bulls.¹

	\bar{X}	SD	Minimum	Maximum
	(kg)			
Inbreeding				
Current daughters	3.4	0.5	1.8	5.9
Future daughters	4.9	1.0	1.3	7.1
BV	1373.6	509.7	-729.9	2836.5
BV ₀	1390.5	507.8	-754.0	2827.4
BV _A	1333.7	506.0	-736.8	2773.6
Abs(BV - BV _A)	43.1	31.5	0.8	609.6

¹Bulls active following the August 1998 evaluation.

sons of BV, BV₀, and BV_A for active Holstein bulls. The BV_A had a lower mean and standard deviation than BV. Correlations between BV, BV₀, and BV_A for the same bulls are in Table 11. The correlation between BV_A and BV (0.9976) was nearly the same as that between BV₀ and BV (0.9974). Correlations for other breeds were similar and are not shown.

Genetic Trend

Genetic trends for milk yield as measured by BV₀ were somewhat greater than were trends for published BV, whereas the trends for BV_A were always somewhat less. For Holsteins, average yearly progress across birth years 1980 to 1990 was 107.4 kg for BV₀, 104.4 for BV, and 98.2 for BV_A. The trend for BV_A was lower because the selected animals caused more inbreeding after becoming popular than they did in earlier years. The trend for BV₀ was higher because popular animals were assumed to cause zero inbreeding.

Trends for the other breeds were lower but followed similar patterns. For Jerseys, yearly progress for milk yield averaged 94.3 kg for BV₀, 90.5 for BV, and 82.0 for BV_A. Breeds with higher inbreeding had the larger changes in genetic trend, as expected. The trend for BV₀ included only additive genetic gain, whereas BV_A included additive gain plus the inbreeding depression that would result if the population were randomly mated. Future selection on BV_A will help breeders bal-

TABLE 11. Correlations between published breeding values (BV), unadjusted milk BV (BV₀), and adjusted milk BV (BV_A) for active Holstein bulls.¹

	BV	BV ₀	BV _A
BV	1.00	0.9974	0.9976
BV ₀		1.00	0.9976
BV _A			1.00

¹Bulls active following the August 1998 evaluation.

ance their goals of faster additive gains and slower inbreeding increase.

CONCLUSIONS

The average relationship of each animal to other animals can be computed quickly using a two-step procedure. First, a numerator relationship matrix is constructed for a sample of the potential mates with the ancestors of this sample included. Second, average relationship of any other animal to the sample population is calculated from average relationships of its ancestors to the sample. Random samples of several hundred animals gave acceptable rankings.

Over all breeds, the Ayrshire bull Selwood Betty's Commander, born in 1953, had the highest average relationship to his breed. Among 29 million Holsteins, greatest expected inbreeding of future progeny was for To-Mar Blackstar. For active AI bulls, inbreeding of previous daughters had correlation of 0.496 with expected inbreeding of future progeny. Expected inbreeding has a simpler definition, wider application, and requires no more computation than many previous measures of relationship within breeds (4, 13, 16).

Breeding values adjusted for inbreeding were highly correlated with unadjusted breeding values. Adjustments for inbreeding will cause slight rerankings for animals whose relationship to past mates differs from that expected for future mates. These adjustments are proposed to account for and to avoid inbreeding in situations in which animals are either not properly identified or where a mating is essentially random. Inbreeding can be further reduced by using mating programs. Proposed matings should be evaluated individually by combining breeding values of sires and dams adjusted to zero inbreeding and then including the inbreeding depression of the individual mating. Thus, BV_A are useful in selection, whereas BV_0 are needed in mating programs. Expected inbreeding of future progeny was dis-

tributed for all bulls beginning in February 1998 to help breeders find outcross bulls and avoid inbreeding.

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