

## GENETICS AND BREEDING

### Accounting for Inbreeding and Crossbreeding in Genetic Evaluation of Large Populations

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#### ABSTRACT

Inbreeding coefficients for 9.3 million registered Holsteins were computed by constructing a small relationship matrix for each animal and its ancestors instead of one large matrix for the whole population. Recent cows averaged 2.0% inbreeding if each pedigree path was extended to the most recent ancestor born before 1960. Inbreeding was underestimated because some pedigrees included unknown ancestors more recent than the defined base year. Alternative estimates of inbreeding can be derived by assigning mean relationship and inbreeding of known ancestors to unknown ancestors of the same period. Animals of different breeds are less related than animals of the same breed. Relationships and inbreeding within and across populations can be measured back to the common base population from which the breeds arose by treating earliest known ancestors within each breed as related and inbred. Increased heterozygosity and heterosis of crossbred animals are then predicted from their lower inbreeding coefficients. Relationship matrices that include related and inbred unknown-parent groups treated as random or fixed effects can be constructed and inverted quickly.

(**Key words:** inbreeding, genetic evaluation, crossbreeding, heterosis)

**Abbreviation key:** CPU = central processing unit, %<sub>a</sub> = percentage of inbreeding measured to across-breed base, %<sub>w</sub> = percentage of inbreeding measured to within-breed base.

#### INTRODUCTION

Relationship, inbreeding, and heterosis coefficients measure similarity or dissimilarity of genes (5, 6, 16). Genetic evaluations now account for covariances among animals with similar genes by including inverses of relationship matrices in mixed model equations (7). Effects of inbreeding and heterosis usually have not been included because of the difficulty of computing inbreeding coefficients and the extra parameters required to model specific heterosis among several breeds. Similarity of genes eventually might be quantified by direct analysis of DNA. For now, genetic similarity is measured by probabilities that genes are identical by descent, and these probabilities are computed from pedigrees.

Pedigrees of registered animals may be recorded fairly accurately over many generations, but genetic evaluations also include grade animals with pedigrees that may trace back only one or two generations. Ancestry information is difficult to obtain even for some registered animals because 1) one or more paths of their pedigrees may trace to or through foreign herdbooks and 2) early ancestry information may not be recorded electronically. Recent research (8, 10) often has ignored these problems and assumed that animals are not inbred and are unrelated if ancestry is unavailable.

Crossbred animals have been excluded from evaluations, and data sets for different breeds have been kept separate because of difficulty of accounting properly for heterosis. When data are combined, effects of either general heterosis among all breeds or specific heterosis for each pair of breeds usually are included, but breed crosses usually are assigned no more genetic variance than purebreds (3). Crossbred progeny must be more heterozygous than their purebred parents, and animals of the same breed must be related more to each other than to animals of different breeds; however, models have not included these two basic as-

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sumptions. Base populations have differed widely in studies of inbreeding. Some researchers have traced pedigrees back only a few years (10), but others have extended them for nearly 100 yr (18). Breeds of today diverged from some common base population hundreds, or even thousands, of years ago, but researchers have not tried to extrapolate beyond available pedigree files to this earlier base population when they analyze mixed breed data. Measures of relationship may be inaccurate if individual ancestry is not recorded back to a common base population. Inbreeding accumulates slowly in most livestock populations (9, 10, 18), but average relationships within breeds recently are becoming higher because the best sires have many descendants (18). New reproductive techniques and breeding programs likely will produce faster increases in inbreeding and more related animals.

Previous algorithms to compute inbreeding coefficients were inefficient for very large populations. Although required central processing unit (CPU) time (11), memory (8), or both (4) increase proportionally to the square of the number of animals, these requirements can be reduced by avoiding calculation of unneeded elements (13). Researchers (17, 18) have studied inbreeding in large populations by tracing two random paths among each animal's ancestors, but this technique estimates only mean inbreeding for the population rather than individual inbreeding coefficients (17). Exact calculation of inbreeding requires tracing all ancestors of each animal back to the defined base population.

Goals of this research were 1) to produce inbreeding coefficients for large populations, 2) to estimate inbreeding if some pedigree information is missing, 3) to extend the concepts of relationship and inbreeding to include animals of different breeds and heterosis, 4) to examine inverses of these relationship matrices for use in mixed model equations, and 5) to discuss adjustment of breeding values for inbreeding depression.

## MATERIALS AND METHODS

### Inbreeding

Inbreeding coefficients for large populations can be computed efficiently by constructing

many small relationship matrices instead of one large matrix for the whole population. For each animal, a list of its ancestors is formed, repetitions of ancestors are excluded, and the tabular method (4) is applied to this short list. Computing times increase linearly with size of population but quadratically with number of ancestors. Thus, costs are low unless pedigrees extend many generations. Memory required in this approach is also small: three vectors to store animal and parent identification and one square matrix with dimension equal to maximum number of ancestors of an individual.

Less memory is required if pedigrees are traced from direct access disk files, such as breed association databases. Calculation of inbreeding coefficients would then be practical for individual animals when registered or for potential matings as requested. Times required to process many animals would be reduced if at least the most popular ancestor lines were held in memory. Separate calculation of inbreeding for ancestors can be avoided by processing youngest animals first and storing their ancestors' inbreeding coefficients as well as their own. Processing times might be reduced within the tabular method by including only ancestors on paths connecting an animal's sire and dam through any of their common ancestors.

Actual time and memory required by the algorithm with all pedigree data in memory were tested for the US registered Holstein population. The 8,534,077 animals born 1960 to 1986, the 387,246 animals born before 1960 that had two or more offspring born after 1960, and the 361,304 females born in 1987 were included for a total of about 9.3 million animals. Identical edits were applied to the US registered Ayrshire population and resulted in 294,318 animals included.

A base population should be defined before calculating inbreeding coefficients (16). The editing procedures used here established an approximate 1960 inbreeding base with 1) animals born before 1960 treated as unrelated and not inbred, 2) the first generation after 1960 related but not inbred, and 3) second and later generations after 1960 increasingly related and inbred. With such a base definition, inbreeding in the second generation occurs only through close matings such as sire-daughter and full or half sibs; in more distant

generations, more distant mating types also contribute.

#### Incomplete Pedigrees

Incomplete pedigrees may cause underestimation of inbreeding and relationship because potential contributions of unknown ancestors are ignored. More accurate estimates, especially for grade animals, might combine actual relationships of known ancestors with assumed relationships of unknown ancestors derived from mean inbreeding of animals with full pedigrees. Inbreeding of animals with one or more unknown foreign ancestors also could be adjusted upward, except that mean relationship and inbreeding levels of foreign and domestic ancestors might differ. Domestic ancestors might be related more to each other than they are to unknown foreign ancestors (1) unless genetic exchange across the countries has been great.

Unknown-parent groups are used in animal model evaluations to account for changing genetic means across time (12, 14, 15). Genetic variation also may change across time because of selection, mating systems, or inbreeding. Variances and covariances of unknown parents might be set equal to corresponding parameters for known parents. Unknown-parent groups can be inserted in the tabular method and in the relationship inverse to account for these altered variances. Then genetic variance of descendants of these unknown parents will be specified automatically.

Inbreeding coefficients of unknown parents can be assumed to equal mean inbreeding of known parents of the same period to account for rising inbreeding and relationship levels across time. Unknown parents should be assumed to be related to all other parents by twice the mean inbreeding level of the period. Mean inbreeding of progeny, which equals half the mean relationship of parents, is then the same for animals with complete or incomplete pedigrees. Different inbreeding and relationship levels for foreign and domestic unknown ancestors could be established, but a better solution might be to obtain the foreign pedigree files so that the foreign ancestors would be known.

#### Crossbreeding

Crossbreeding and inbreeding are to some degree opposites (2, 5). Their effects can be modeled on the same scale by assuming that heterosis is simply the removal of accumulated inbreeding depression within each breed. Breeds of livestock originated from a common ancestral population that existed hundreds of years ago. Because breeds usually are closed populations, relationships and inbreeding accumulate within but not across breeds. The sire and dam of a purebred animal usually have a common ancestor a few generations back in the pedigree, whereas the sire and dam of a crossbred animal may share no common ancestors for hundreds of years back. Thus, crossbreds are less inbred than purebreds.

Relationships and inbreeding within and across breeds should be extended back to the common base population from which the breeds of interest arose. If pedigrees also could be extended back to when the breeds diverged, animals of different pure breeds still would share no common ancestors and would be unrelated, whereas animals of the same breed all would share many common ancestors. Thus, only crossbreds can have an inbreeding coefficient of 0, and, by comparison, purebreds are all inbred and related within breed. Also, crossbreds are more heterozygous than purebreds because the crossbred receives a mixture of genes from unrelated populations, whereas the purebred receives similar genes from both parents.

More distant crosses, such as *Bos indicus* with *Bos taurus*, would require even earlier base definitions to keep inbreeding coefficients positive. Then all *B. taurus* animals would appear to be related to each other and inbred if compared with *B. indicus* by *B. taurus* crosses. Coefficients of relationship could be extended to even wider crosses and back even further to measure similarity of genes across the evolutionary scale. These more distant relationships might be quantified by analyzing DNA instead of searching for common ancestors in ancient pedigrees.

Relationship matrices should be traced back to a single, intermating base population, but pedigree recording and herdbook societies often started many generations after breeds were formed or populations became isolated. With a few assumptions regarding average relationship and inbreeding of earliest known

ancestors, coefficients measured relative to separate, recent bases can be adjusted to the common, older base. Figure 1 provides an example of the assumptions required. Inbreeding scales within and across breed could be aligned by actually measuring homozygosity of purebreds and crossbreds. Alternatively, scales can be aligned by equating effects of inbreeding and heterosis.

Inbreeding measured within breeds might be converted to an across-breed scale as follows. Suppose crossbreds exhibit heterosis of 375 kg of milk and regression on inbreeding within pure breeds is  $-25 \text{ kg}/1\%_w$ , where  $\%_w$  denotes the percentage of inbreeding measured to the within-breed base. The effect of heterosis is equivalent to the effect of a  $-15\%_w$  inbreeding coefficient, which is calculated as  $375 \text{ kg}/(-25 \text{ kg}/1\%_w)$ . To keep coefficients positive, an earlier base is chosen, so that crossbreds have inbreeding coefficients of  $0\%_a$ , where  $\%_a$  denotes the percentage of inbreeding across breeds.

On this across-breed base, a purebred with  $0\%_w$  now is credited with inbreeding of  $13\%_a$ , which is calculated as  $15\%_w(100\%_a)/(100\%_w + 15\%_w)$ . Units are larger on the across-breed scale because  $100\%_a$  now represents a wider range of heterozygosity ( $100\%_w + 15\%_w$ ). Consequently, the regression on inbreeding is larger:  $-28.8 \text{ kg}/1\%_a$ , which is calculated as  $-25 \text{ kg}/[1\%_w(100\%_a)/(100\%_w + 15\%_w)]$ . Also, genetic variance in the base population is 15% larger because a purebred base population is less genetically diverse by comparison.

The tabular method (4) can be adapted to calculate relationships on the across-breed base. Breed effects for all breeds present in the pedigree should precede the oldest ancestors in the list. The corresponding upper left submatrix of the relationship table then equals the breed effect (co)variance matrix divided by  $\sigma_a^2$ , where  $\sigma_a^2$  denotes additive genetic variance in the across-breed base population. Other elements of the table are calculated by the usual rules: off-diagonal elements are means of parent elements, and diagonals equal 1 plus half of the parents' relationship. Breed effects act as parents of the oldest known ancestors.

Breed and unknown-parent group effects represent mean breeding values of particular

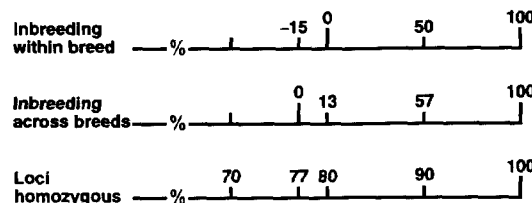


Figure 1. Example of corresponding scales to measure inbreeding.

populations. Variances of breed effects are twice the breed's inbreeding coefficient times  $\sigma_a^2$  if breeds differ only because of random genetic drift (5). Thus, diagonals of the relationship matrix would equal .26 for a breed in which the base animals are assumed to have  $13\%_a$  inbreeding. Off-diagonals of the relationship matrix are 0 for breeds that separated at the time of the original base population and positive for breeds that separated later. A general heterosis effect for all breeds might be modeled by assuming equal genetic distances between the breeds. If breeds are "unrelated" and have equal genetic variances, the breed covariance matrix is an identity matrix (I) times the variance of breed effects, or  $I\sigma_b^2$ . Let vector  $\mathbf{b}_i$  represent the fraction of genes each breed contributed to animal  $i$ . Elements of  $\mathbf{b}_i$  are calculated automatically when breed effects are included in the tabular method. Each animal's breed composition is the mean of its parents' breed compositions, or  $\mathbf{b}_i = .5(\mathbf{b}_s + \mathbf{b}_d)$ , where subscripts  $s$  and  $d$  refer to sire and dam. Elements of  $\mathbf{b}_i$  multiplied by  $\sigma_b^2/\sigma_a^2$  are the off-diagonal elements of the relationship table corresponding to animal  $i$  and breed effects. The fraction of heterosis expressed by animal  $i$  is  $1 - \mathbf{b}'_i \mathbf{b}_i$ .

Specific heterosis can be modeled by assuming that some breeds are related more closely than others. For example, North American Holsteins and European Friesians must be related to each other more than either is to Jerseys. Less heterosis (and a smaller gain in heterozygosity) would be expected from matings of Friesians with Holsteins than from matings of less related breeds. Breed relationships might be calculated from heterosis esti-

mates, from DNA differences, or from estimated time of separation. Relationships among breeds then are transferred to descendants by the tabular method and combined with relationships caused by common ancestors in the pedigree to calculate similarity of each animal's genes, regardless of breed.

Use of an across-breed base for inbreeding coefficients simplifies genetic evaluation models. General heterosis, specific heterosis, and inbreeding depression might all be accounted for with just one regression coefficient. Such a regression accounts for lower mean performance of animals with fewer heterozygous loci, either because parents were of the same breed or were related within breed. Higher Mendelian sampling variances in progeny of crossbred than of purebred parents and lower Mendelian sampling variances in progeny of inbred parents also are accounted for if such inbreeding coefficients are used in constructing inverses of variance matrices.

#### Inverse Relationship Matrices

Additive genetic covariance matrices have sparse inverses that are easy to construct if the known ancestors that cause ties among descendants are included and if inbreeding arises only from known ancestors (7). If unknown ancestors are related and inbred, inverses of relationship matrices may not have simple structure unless effects of genes common to the unknown ancestors are included. Assumptions about unknown ancestors determine the relationships among known animals through the recursive formulas of the tabular method. Some of these assumptions may lead to more accurate relationships or to simpler inverses than others.

An identity matrix is the simplest assumption regarding relationship of unknown parents, but this assumes that none is inbred and each is unrelated to the animal's other known and unknown ancestors. This may be true for early unknown ancestors, but more recent unknown parents may be inbred and related to others. Inbreeding and relationship of unknown parents may be set equal to mean inbreeding and relationship of known parents of corresponding periods. Fewer parameters are required when relationships of unknown parents are functions of their estimated inbreeding

coefficients. Relationships might be estimated as twice the inbreeding coefficient of the older unknown parent, twice the inbreeding of the younger, or twice the harmonic mean of the two. Estimating inbreeding as twice the inbreeding coefficient of the older unknown parent provided the most reasonable estimates and was used in the Ayrshire analysis. Inverses are constructed by linking progeny to their parents and by linking progeny of unknown parents to unknown-parent group effects as in work by Westell et al. (14). Inclusion of these unknown-parent group or breed effects results in sparser inverses because a descendant effect is linked to just one group effect instead of all animals possessing these same genes. Group effects now are treated as random instead of fixed, because variances of group effects are assumed to be known. Thus, a final step is to add the inverse of the group (co)variance matrix divided by  $\sigma_a^2$  to the group by group portion of the relationship inverse.

An animal's additive genetic merit is the mean of its parents' merits plus a residual, regardless of whether parents are not inbred or are inbred, purebred, or crossbred. The residual is Mendelian sampling ( $m$ ) and has mean 0 and variance that depends on heterozygosity of parents through the formula  $\text{Var}(m) = (.5 - .25F_s - .25F_d)\sigma_a^2$ , where  $F_s$  and  $F_d$  are inbreeding coefficients of sire and dam, whether known or unknown. If group effects replace unknown parents, the unknown parent's deviation from group adds to the residual an effect with variance  $.25(1 - F_s)\sigma_a^2$  or  $.25(1 - F_d)\sigma_a^2$ . Thus, each animal contributes the following coefficients to the inverse:

$$\begin{bmatrix} \text{animal} & \text{sire} & \text{dam} \\ 1 & -.5 & -.5 \\ -.5 & .25 & .25 \\ -.5 & .25 & .25 \end{bmatrix} \times \frac{4}{(1 + u_s)(1 - F_s) + (1 + u_d)(1 - F_d)}$$

where  $u_s$  ( $u_d$ ) takes values of 0 if sire (dam) is known and 1 if sire (dam) is unknown.

When sire or dam are unknown, coefficients are assigned to corresponding breed or group

effects. These coefficients are identical to those derived by Westell et al. (14) when  $F_s$  and  $F_d$  are 0. Resulting equations differ from those of Westell et al. (14) because coefficients are now adjusted for inbreeding, multiple breeds and breed crosses can be included, and genetic groups are considered to be random rather than fixed.

Breed and unknown-parent group effects are assumed to result only from random genetic drift. If selection has caused larger differences, fixed groups can be reimposed by avoiding addition of the group (co)variance inverse. Also, an unknown sire's (dam's) deviation from group might have reduced variance, e.g.,  $r(1 - F_s)\sigma_a^2$ , where  $r$  is the fraction of genetic variance remaining after selection. The appropriate denominator for the  $3 \times 3$  coefficient matrix is then  $(1 + u_s r)(1 - F_s) + (1 + u_d r)(1 - F_d)$ .

#### Animal Rankings

With inbreeding depression and populations containing harmful recessives, the value of an animal's genes depends on how frequently those same genes appear in the population of mates. Predicted transmitting abilities can be adjusted for the mean inbreeding that occurs if the animal is mated randomly to the current population; however, mean relationship to the population may be expensive and difficult to compute without faster algorithms. Rankings derived from randomized progeny tests with no adjustment for inbreeding may be sufficient. Alternatively, transmitting abilities may be corrected to zero inbreeding by inclusion of a regression on inbreeding. Users can then adjust such rankings for the inbreeding caused in the mating, herd, or population of interest.

Breeds and animals that are less related to the average current animal should be credited for contributing less inbreeding (more heterosis) if mated at random to the current population. Holsteins would contribute little heterosis because most potential mates are Holsteins. Other breeds would be rewarded much more for heterosis, but this assumes their genes actually would be combined with Holstein genes. If this assumption is inaccurate, transmitting abilities could be corrected to  $0\%_a$  inbreeding, and breeders could adjust downward for purebred and other matings not capturing the full benefits of heterosis.

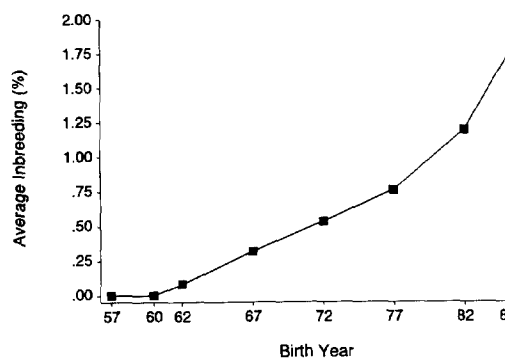


Figure 2. Holstein inbreeding by birth year.

Crossbred populations have not only higher means than the means of parents but also more genetic variation than exists within the parent breeds. Selection within pure breeds has been effective, but selection response should be greater within crossbred populations containing new combinations of unrelated genes. Genetic evaluations incorporating these assumptions should rank animals more accurately and should serve to remind breeders of basic genetic principles.

#### RESULTS

Calculation of inbreeding coefficients for 9.3 million Holsteins required only 3.4 CPU hours on an IBM 3090 (IBM Corp., Armonk, NY) and required 260 MB of memory. Maximum number of ancestors in an individual pedigree was 197. Mean inbreeding levels (Figure 2) were  $0\%_w$  in 1960,  $4\%_w$  in 1970,  $1.0\%_w$  in 1980, and  $2.0\%_w$  in 1987. Recent estimates of Young et al. (18) to a much older base did not indicate this trend. Hudson and Van Vleck (9) reported an increase of only  $.3\%_w$  from 1960 to 1979 for Holsteins in the northeastern US, but they included grades with less complete pedigrees and used approximate methods. Miglior et al. (10) reported a trend of less than  $.5\%_w$  from 1980 to 1987 for Canadian Holsteins, but pedigrees were incomplete, and a base year was not mentioned.

Among cows born in 1987, 84.7% had inbreeding coefficients greater than  $0\%_w$ . Other studies reported much smaller percentages; 44% of cows born in 1979 were reported posi-

tive by Hudson and Van Vleck (9), and only 15% of cows born in 1987 were reported positive by Miglior et al. (10). The maximum inbreeding coefficient of any animal was 32.8%<sub>w</sub>. Holstein results did not include unknown-parent groups to adjust for inbreeding from unknown parents, most of which were likely Canadian.

Ayrshire inbreeding coefficients calculated with and without unknown-parent grouping are in Table 1. Unknown parents initially were assigned inbreeding and relationship coefficients of 0. In subsequent rounds, values were assigned based on mean inbreeding from the previous round for animals of that year group. Mean inbreeding of cows born in 1987 rose from 3.7%<sub>w</sub> initially to 4.2%<sub>w</sub>; unknown parents were considered to be inbred and related. Rapid convergence occurred in this example because most pedigrees were complete.

Figure 3 provides an example of a Jersey (J)-Holstein (H) relationship matrix including breed effects (J0, H0), purebred animals (J1, J2, H1, H2), and a crossbred animal (J1 × H2). On the more recent within-breed bases, the purebreds were not inbred and were unrelated to each other. If measured on the across-breed base, the two Jerseys (J1, J2) were related to each other but not to the Holsteins (H1, H2). Only the crossbred was not inbred on the across-breed base. Inbreeding and relationship coefficients in Figure 3 were adjusted to the older, across-breed base by assigning .26 for variance of breed effects and by using rules of the tabular method to complete the relationship matrix.

Figure 4 provides the inverse of the relationship matrix in Figure 3. The inverse appears to be sparse and simple to construct. For example, the crossbred animal (J1 × H2) contributed coefficients

$$\begin{bmatrix} & J1 & H2 & J1 \times H2 \\ & .57 & .57 & -1.15 \\ & .57 & .57 & -1.15 \\ & -1.15 & -1.15 & 2.30 \end{bmatrix}$$

Its purebred parent J1 contributed coefficients

$$\begin{bmatrix} & J0 & J0 & J1 \\ & .29 & .29 & -.57 \\ & .29 & .29 & -.57 \\ & -.57 & -.57 & 1.15 \end{bmatrix}$$

Four of these coefficients sum to 1.15 on the diagonal for J0. Two other off-diagonal pairs sum to -1.15. Finally, the inverse of the breed (co)variance matrix contributes coefficients

$$\begin{bmatrix} & J0 & H0 \\ & 3.85 & .00 \\ & .00 & 3.85 \end{bmatrix}$$

Table 2 provides an example of breeding values adjusted to inbreeding of 0% or to mean

TABLE 1. Mean inbreeding coefficients for Ayrshires with and without unknown-parent grouping.

Birth years	Percentage of unknown parents	Mean inbreeding coefficient		
		Traditional calculation	First iteration unknown-parent groups <sup>1</sup>	Second iteration unknown-parent groups <sup>2</sup>
1955 to 1959	100	0	0	0
1960 to 1964	30	.1	.1	.1
1965 to 1969	11	.5	.6	.6
1970 to 1974	4	1.2	1.3	1.4
1975 to 1979	2	2.4	2.6	2.7
1980 to 1984	2	3.2	3.5	3.5
1985 to 1986	1	3.3	3.8	3.9
1987	0	3.7	4.2	4.2

<sup>1</sup>Sets inbreeding of unknown parents equal to mean of traditionally calculated inbreeding coefficients in the same year group.

<sup>2</sup>Sets inbreeding of unknown parents equal to first iteration means.

	J0	H0	J1	J2	H1	H2	J1×H2
J0	.26	0	.26	.26	0	0	.13
H0		.26	0	0	.26	.26	.13
J1			1.13	.26	0	0	.565
J2				1.13	0	0	.13
H1					1.13	.26	.13
H2						1.13	.565
J1×H2							1.00

Figure 3. Example relationships between two Jerseys (J1 and J2), two Holsteins (H1 and H2), and a Jersey-Holstein crossbred (J1 × H2); breed effects are indicated by J0 and H0.

inbreeding expected from randomly mating each animal to the current population. Adjustment to 0% simply requires a regression on inbreeding in the model; adjustment to mean inbreeding then requires addition of the regression coefficient times the animal's mean inbreeding. Holsteins were assumed to be 90% of the population and thus caused more mean inbreeding. Holsteins had higher breeding values than Jerseys, but this advantage decreased somewhat when Holsteins were penalized for having higher mean relationships with the current dairy cattle population.

CONCLUSIONS

Inbreeding coefficients for a population of nearly 10 million animals with many of the pedigrees traced back five or more generations were computed in 3.4 h with a simple, new

	J0	H0	J1	J2	H1	H2	J1×H2
J0	6.15	0	-1.15	-1.15	0	0	0
H0		6.15	0	0	-1.15	-1.15	0
J1			1.72	0	0	.57	-1.15
J2				1.15	0	0	0
H1					1.15	0	0
H2						1.72	-1.15
J1×H2							2.30

Figure 4. Inverse of example relationships between two Jerseys (J1 and J2), two Holsteins (H1 and H2), and a Jersey-Holstein crossbred (J1 × H2); breed effects are indicated by J0 and H0.

TABLE 2. Hypothetical breeding values for protein yield for two Jerseys (J1, J2), two Holsteins (H1, H2), and a crossbred (J1 × H2) adjusted to inbreeding (F) of 0% or to mean F across breeds.

Animal	Mean F	Breeding value adjusted <sup>1</sup> to	
		0% F	Mean F
J1	1	-22	-23
J2	1	-63	-64
H1	15	-5	-20
H2	13	+34	+21
J1 × H2	7	+6	-1

<sup>1</sup>Regression on inbreeding assumed to be 1 kg of protein yield per 1% of F.

algorithm. Computing a small relationship matrix for each animal and its ancestors is more efficient than calculating one large matrix for the whole population. Average inbreeding of US Holsteins born in 1987 was 2.0% relative to a 1960 base. Inbreeding and relationship of animals with incomplete pedigrees can be estimated using an unknown-parent grouping strategy. Animals with genes most similar to those of the population or mate of interest should be penalized for the expected inbreeding depression.

Procedures to evaluate all breeds and crossbreds together are simplified by measuring relationships and inbreeding back to an ancestral population that existed before breeds separated. Inbreeding depression and heterosis effects then are united on the same scale; animals of the same breed are assumed to share common genes, and crossbreds are assumed to be more heterozygous than purebreds. If unknown ancestors are considered to be related and inbred, effects of their common genes can be included as separate effects in the relationship matrix to make its inverse simpler to construct and more sparse.

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