Virginia Cooperative Extension

PUBLICATION 404-080

INBREEDING

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Introduction

The mating of related individuals is called inbreeding. New dairy animals created by AI or natural service inherit a random sampling of the genetic makeup of each parent. If the parents are related, some of the genes transmitted to offspring by each parent will be copies of the same genes found in the common ancestor(s) which caused the parents to be related. As the genetic relationship between parents increases, the likelihood that pairs of genes in offspring are copies of a single gene in an ancestor generations back increases. Such genes are said to be "identical by descent."

The most extreme form of inbreeding is selfing, that is, the mating of an individual to itself. This process is possible in many plant species because each individual produces both male and female germ cells. Suppose a plant has genotype Bb for some part of its chromosome structure. Since germ cells contain a sample half of the plant's genetic material, half of all germ cells would carry B and half would carry b for both male and female cells. If the plant were "selfed," offspring would be BB, Bb, or bb in ratios of 1:2:1. BB individuals are called "homozygous" for the B allele, while bb individuals are homozygous for the b allele. Bb individuals are called "heterozygous" as they carry both B and b in their genetic material. If offspring of the selfed plant were also selfed, only BB offspring would result from the BB individuals and bb offspring from the bb individuals. The Bb individuals would again produce BB, Bb, and bb offspring in ratios of 1:2:1. The process, continued over several generations, would continue to increase the frequency of BB and bb (homozygous) individuals and reduce by half in each generation the number of Bb individuals. Selfing is not possible in mammals such as dairy cattle, but the same process of increased homozygosity and decreased heterozygosity occurs with inbreeding in all species.

Inbreeding does not change gene frequency, that is the total number of B or b genes in a population. It only changes the arrangement of those genes in pairs of BB, Bb, or bb. If some of those combinations are non-fertile, a selection process will occur which will change gene frequency.

Performance of inbred dairy cattle

Inbred animals become homozygous at more chromosome locations than non-inbreds. The positive aspect of inbreeding is that the genotypes of sperm or egg cells from inbred individuals are more predictable than for outbreds. BB or bb individuals can only produce B or b sperm and egg cells. The heterozygote, Bb, can produce either B or b sperm or egg cells. If the inbred animal were superior and transmitted its superiority with regularity, the advantages would be obvious. Inbreeding can also be used to "purge" a line of cattle of undesirable recessive genes.

Unfortunately, inbreeding produces many undesirable side effects as well. When undesirable recessive genes appear in the homozygous state (bb), the condition is often fatal. The fatality may occur very early in embryonic development and look like a failed conception to a dairy producer. If the genes are semi-lethal, and the individual does survive, it may be totally unprofitable. Most animal species (including dairy cattle and humans) carry low frequencies of lethal or semi-lethal genes hidden in the heterozygous state (Bb). Inbreeding, by increasing the frequency of homozygous individuals (BB or bb), removes the protective cover of the non-lethal, dominant gene (B), exposing more offspring to the lethal combination of genes (bb). For dairy cattle, inbreeding reduces the profitability of individual animals which is unacceptable for most producers.

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Produced by Communications and Marketing, College of Agriculture and Life Sciences,
Virginia Polytechnic Institute and State University, 2009

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The effects of inbreeding have been so much more negative than positive in animal breeding that the term “inbreeding depression” was coined. Table 1 shows inbreeding depression for lifetime and individual lactation traits of Holsteins from a recent study by Smith, et al. at Virginia Tech. The changes are expressed “per 1% increase in inbreeding.” This means that the lifetime economic loss for a mating producing 6.25% inbreeding would be $24 X 6.25 = $150 expected loss from such a mating. Notice that, with the exception of somatic cell score where inbreeding has no apparent effect, all consequences of inbreeding in Table 1 are undesirable. Age at first freshening goes up, length of productive life goes down, all production traits are reduced, and first calving interval is lengthened as inbreeding increases.

Some of the changes shown in Table 1 are larger than other estimates in the literature. Wiggans, et al. reported slightly smaller milk yield losses in Holsteins of 65 lbs. per 1% increase in inbreeding. His work also showed that first lactation milk losses of 67 lbs./1% increase in inbreeding for Ayrshire, 43 lbs. for Guernsey, 47 lbs. for Jersey, and 54 lbs. for Brown Swiss.

Inbreeding in today’s dairy populations

Selection for higher production and improved type of dairy cattle has reduced genetic diversity. The diversity eliminated included undesirable genes for the traits we have selected to improve which was, of course, our purpose. Today, a limited number of animals in each breed serve as parents of highly influential sires in each generation. Wiggans, et al. found average inbreeding of 4.7% in Ayrshire cows, 3.0% in Guernsey, 2.6% in Holstein, 3.3% in Jersey, and 3.0% in the Brown Swiss breed. Are these numbers alarming? The critical issue is whether inbred dairy cows are functional under today’s management conditions and whether that functionality is compromised by less genetic diversity in the population. Cattle today are more inbred than their ancestors, but they are also much more productive. It would not be accurate to say that current levels of inbreeding are alarming.

A 1996 study by Young and Seykora looked at inbreeding changes in Holsteins throughout the 20th Century. Holstein cows were first imported to the United States in 1884. Young and Seykora’s work showed that today’s Holstein cow was about 5% inbred relative to that original importation date. The average relationship (percent of genes in common between any two animals) increased from about 3.4% in 1928 to approximately 10% (twice the average inbreeding value of 5%) in 1990. This increased relationship indicates the effects of selection for more productive, functional cattle and reflects a narrowing of the genetic base. Young and Seykora reported that Pawnee Farm Arlinda Chief and Round Oak Rag Apple Elevation accounted for nearly one fourth of all genes segregating in Holstein cattle in 1990. Holstein pedigrees without one of these two patriarchs in the first six or eight generations would often be a product of unusual breeding decisions.

Table 1. Effect of inbreeding on lifetime and individual lactation performance in registered Holstein cows.

Trait	Inbreeding depression per 1% increase in inbreeding
Lifetime net income ($)	-24
Age at first freshening (days)	+.36
Days of productive life	-13
Lifetime total milk production (lbs.)	-790
Lifetime total fat production (lbs.)	-29
Lifetime total protein production (lbs.)	-25
First lactation milk production (lbs.)	-82
First lactation fat production (lbs.)	-3
First lactation protein production (lbs.)	-3
First lactation average somatic cell score	-.004
First calving interval (days)	+.26

Consequences of inbreeding

Table 2 presents the results of three specific matings which could be made in dairy cattle. Most dairy farmers would avoid mating a sire to his own daughter and many would recognize that a selected AI bull should not be mated to daughters of his sire. However, the mating of a bull to a daughter of a half brother would be more difficult to recognize. In Holsteins, for instance, mating daughters of Mattie to another son of Mascot such as Javlin would produce the 6.25% inbreeding indicated in Table 2. Dairy farmers might make such matings because they did not recognize the relationship between Mattie and Javlin. NAAB short names don't reveal much about pedigrees!

We would expect a calf by Javlin out of a Mattie daughter (6.25% inbred) to lose over $150 lifetime net income compared to a non-inbred calf of otherwise equal merit. Should such a mating ever be made? As with all breeding decisions, the answer involves alternatives. **Can an outcross bull be found whose genetic merit is high enough for progeny to perform better than progeny of an inbred mating?** If we make the comparison on PTA milk instead of lifetime net income, the example may be clearer. A mating to Javlin would depress first lactation milk production by over 500 lbs. That means that an alternate sire could be about 500 lbs. lower for PTA milk than Javlin and be equally useful as a mate to Mattie daughters, provided he produced no inbreeding in the mating. On the Spring 1998 proofs, Javlin was +2374 for milk. A bull unrelated to a Mattie daughter could be as low as +1861 on PTA milk and be equal to Javlin as an improver of first lactation milk. If the only unrelated sires are lower for production than that, then avoiding inbreeding entirely would cost more in lost genetic improvement than would be lost from inbreeding depression. The search for an optimum mate should not be restricted to unrelated bulls. High ranking bulls to which the cow is related should also be considered.

In managing a breeding program, be aware of the effects of inbreeding, but keep in mind that the degree of inbreeding determines its effect on an animal's performance. Further, inbreeding only depresses additive genetic merit. Lack of inbreeding does not add to genetic merit. Breeders should not avoid the use of the best sons of a particular bull simply because the bull has female offspring in their herd. Some combinations of bulls with cows in a herd may produce more inbreeding that you find acceptable. Avoid the matings that produce unacceptable amounts of inbreeding rather than eliminating the bull from a breeding program.

Identification is essential

Inbreeding cannot be avoided unless the pedigree of the cow to be inseminated is known in depth. Extremely close matings can occur when identity is unknown, but much of the loss from inbreeding comes from common ancestors three or more generations back in a pedigree. Many producers are unaware that the animals affected are inbred at all. More than one common ancestor can affect overall inbreeding as well. This means that complete pedigree information for four or five generations back is needed to do a good job of managing inbreeding. It may well be that one of the most valuable assets of a registered cow in years to come will be the ability to assign mates for her with optimum control of inbreeding. Grade animals, particularly the increasing number of such animals from very large dairy herds, frequently don't have complete pedigree data for several generations back. Even if a complete pedigree on a grade animal could be developed through use of historic DHI records, the information is not of much use unless it is available in a form that allows computerized mating programs to use it.

Table 2. Expected change in lifetime economic merit and individual lactation performance from matings producing inbred offspring.

Mating of a bull to	Percent inbreeding	Expected change in		
	income	Lifetime net milk (lbs)	First lactation protein (lbs)	First lactation
His own daughter	25%	$600	2,050	75
His own half sister	12.5%	$300	1,025	38
A daughter of a half brother	6.25%	$150	513	19

We saw how important complete pedigree information was in the inbreeding study by Smith, et al. mentioned earlier. In this work, we estimated effects of inbreeding separately for cows from entirely registered and entirely grade herds. Inbreeding depression cost over $24 per 1% increase in inbreeding in registered herds, but less than $10 per 1% increase in grade animals. For first lactation milk production, registered cows had 82 lbs. inbreeding depression compared to just 35 lbs. in grade cattle. Do genes in grade cows work differently than they do in registered cows? I doubt it. Inbreeding in grade cattle is likely larger than calculated because of missing ancestors in the known pedigree. The estimated inbreeding coefficients were three times higher in registered than in grade cows. If we can't estimate inbreeding in a mating because of limited pedigree data, we cannot avoid inbreeding or estimate its costs.

Summary

Inbreeding will become more difficult to avoid as relationships between animals in the various dairy breeds increase. Increased relationships are a natural consequence of using only a few sires in an AI breeding program. Inbreeding can be avoided, but not without sacrifice of progress toward improved productivity. The bulls to which carefully bred cattle should be mated were selected for the same reasons as the cows themselves, and can only be expected to have many of the same genes. Optimum methods to control inbreeding will choose the sire with highest genetic merit adjusted for inbreeding in a specific mating rather than avoiding some maximum level in inbreeding. Complete, accurate pedigree data for cows to be mated and sires used as mates will be a necessary part of such mating decisions.

References

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Wiggans, G.R., P.M. VanRaden, and J. Zuurbier. 1997. Calculation and use of inbreeding coefficients for genetic evaluation of United States dairy cattle. J. Dairy Sci. 78:1584-1590.

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APPENDIX

Calculation of Inbreeding Coefficients

We must know details of the relationship between two prospective parents to determine the degree of inbreeding of any progeny they might produce. To assist us, we calculate the coefficient of relationship, R_{XY}, between two individuals, X and Y. The formula for R_{XY} appears in equation [1] shown later. R_{XY} is defined as the expected fraction of genes which X and Y share as a result of common ancestry. A base population must be chosen for calculation of R_{XY} and only common ancestors identified in the generations between X and Y and the base population are used in calculations. Inbreeding depends on a part of the equation to calculate relationships between parents and is also relative to a base population that is assumed to consist of non-inbred and unrelated individuals.

Path diagrams or charts of relationships between individuals in a pedigree are useful in calculating R_{XY}. The most basic relationship is between parent and offspring, for instance between cow Y and her sire, X.

$$\mathbf{Y} \xleftarrow{\quad 1/2 \quad} \mathbf{X}$$

Cow Y shares 50% of her genes with sire X because she inherits them from him at the time of her conception. R_{XY} is 1/2 in this case.

If Z were the parent of X, R_{ZY} would be (1/2) * (1/2) = 1/4, since the sample half of genes X inherited from Z would be halved again in the formation of the sperm cell that produced Y.

$$\mathbf{Y} \xleftarrow{\quad 1/2 \quad} \mathbf{X} \xleftarrow{\quad 1/2 \quad} \mathbf{Z}$$

Relationships between individuals become much more complicated than the above examples of direct descent. The formula for R_{XY}, the coefficient of relationship between X and Y can be generalized to fit even the most complex pedigrees.

Equation [1]

$$R_{XY}= \frac{\Sigma[(1/2^{n})(1+F_{A})]}{\sqrt{(1+F_{X})(1+F_{Y})}}$$

In this formula, the following definitions apply:

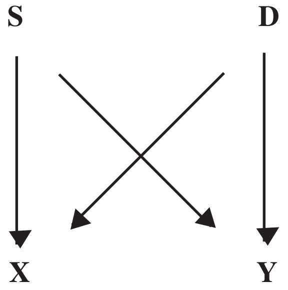
- Σ means to "sum over" all paths connecting X and Y through common ancestors. If there are several common ancestors, $1/2^n$ is calculated for each common ancestor. Also, more than one path can connect X and Y through a common ancestor. The value of $1/2^n$ must be determined for each path and n may or may not be the same for each such path. A pedigree chart is always helpful to see the common ancestors and various pathways connecting parents through them.
- *n* is the number of arrows (sample halves of genes) which connect X and Y through each common ancestor.
- F_A is the inbreeding coefficient of the common ancestor
- F_X and F_Y are the inbreeding coefficients for X and Y

The formula for the inbreeding coefficient (Equation 2) is one-half the <u>numerator</u> of R_{XY} where X and Y are the parents of individual Z. The Σ operator again means to "sum over" all paths connecting parents X and Y through common ancestors. F_A is the inbreeding coefficient of each common ancestor. If the common ancestor is inbred, inbreeding of progeny of the mating of X and Y is increased. <u>If the parents of Z have no common ancestors, Z is not inbred, even if the parents themselves are highly inbred</u>.

Equation [2]

$$F_{z}=\frac{\Sigma[(1/2^{n})(1+F_{A})]}{2}$$

We will apply Equation 1 using the following pedigree where X and Y are full sibs. R_{XY} depends on two paths, one through the sire (S), X-S-Y, and one through the dam (D), X-D-Y. When drawing a path diagram, list older animals at the top or one side of the diagram. Only enter each animal once. When counting paths, be careful not to pass through a given individual more than once for a given path. Different paths, however, may trace through the same individual.



Path	Value
X – S –Y	$(1/2)^2(1+F_S) = 1/4$ since $F_S = 0$
X – D – Y	$(1/2)^2(1+F_D) = 1/4$ since $F_D = 0$
Total for numerator of R_{XY}	1/2

R_{XY}, using Equation [1], is simply 1/2, because neither X nor Y are inbred based on information in the path diagram. How can we check to see if X or Y are inbred? Inspect the pedigree to see if their parents are related. The information available to us doesn't disclose any relationships between the parents of X and Y, though a more complete pedigree might disclose some inbreeding in X and Y.

If X and Y were mated, would an offspring, Z, be inbred? Since X and Y are related, the answer is yes. How much inbreeding would result? Use Equation [2]

$$F_{z}=\frac{\Sigma[(1/2^{n})(1+F_{A})]}{2}$$

$$=[(1/2^{2})(1+0)+(1/2^{2})(1+0)]/2$$

$$=(1/4 + 1/4)/2$$

$$= 1/4 \text{ or } .25$$

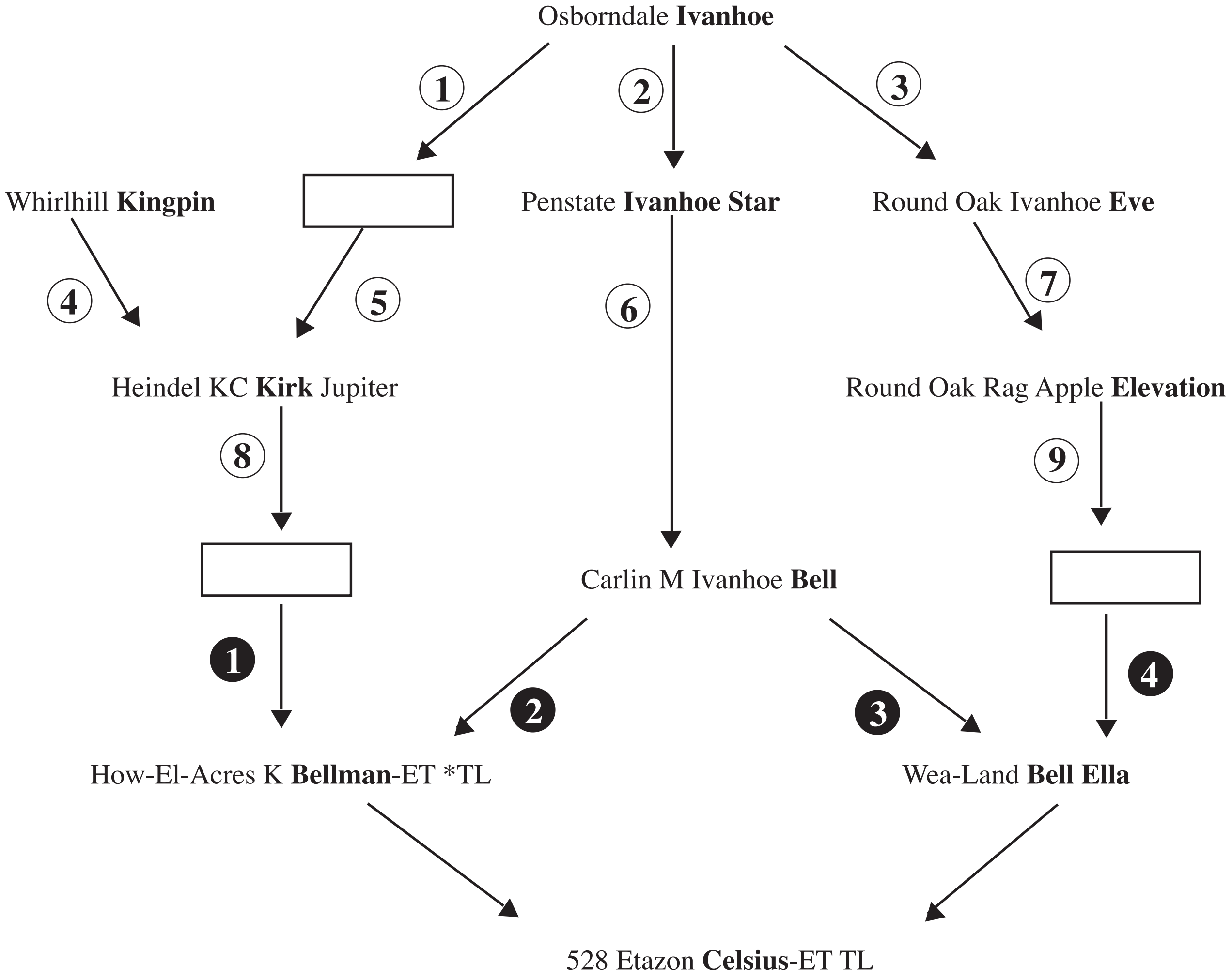
The offspring of a full sib mating would be at least 25% inbred. Why "at least" 25%? There may be common ancestors further back in the pedigree. In the above example, the only information available indicates that X and Y are simply full sibs.

Inbred bulls in AI service

Several AI organizations sample inbred bulls. Such a practice offers advantages to dairy farmers because the risks of inbreeding depression from the practice are borne by the stud. Such bulls may be less prolific semen producers and may not survive as well to proven bull status, but, once proven, they are easier to use to avoid inbreeding in herds than non-inbred bulls. Inbred bulls have fewer different ancestors than outcross bulls. The pedigree of Etazon Celsius-ET below demonstrates this point. Celsius can be used on many cows with no Bell blood close up in their pedigrees. When relationships do exist, however, the degree of inbreeding from a given mating will likely be higher than for non-inbred AI bulls.

The above pedigree also gives us a chance to apply the principles outlined in this appendix. , 528 Etazon Celsius-ET TL, 2247437 was one of the first international Holstein bulls to gain popularity in the United States. He has an inbreeding coefficient of 16% according to Redbook Plus for Windows, May 1998, Holstein Association, Inc The evaluation of his pedigree as shown above will not reveal all of that 16%, but will show how inbreeding builds up through relationships with highly popular ancestors, both from recent times and in eras long gone.

The parents of Celsius were How-El-Acres K Bellman and Wea-Land Bell Ella. These two individuals share two common ancestors in this pedigree, Carlin M Ivanhoe Bell, a popular bull from the 1980's and Osborndale Ivanhoe, a bull that saw heavy use in the 1960's. The following table contains the intermediate steps necessary to calculate the inbreeding coefficient for Celsius.



The inbreeding coefficient for Celsius would be half of .2695 which is .1348 or 13.48% inbreeding. The estimate of 16% inbreeding from the Holstein Association Redbook computer program is based on more complete pedigree information. Whirlhill Kingpin and Osborndale Ivanhoe were related maternally. That relationship would add several long paths between the parents of Celsius. I did not have information on the maternal grandsire of Bell Ella which is another possible source of relationships with Bellman. Carlin M Ivanhoe Bell was out of a Burkgov Heilo Bell daughter. The Burke breeding in that line would provide connections through RORA Elevation, whose sire, Tidy Burke Elevation, was an inbred product of Burke breeding.

All these relationships, while numerous, were not the real source of inbreeding in this pedigree. Celsius is the product of a half sib mating, which by itself produces 12.5% inbreeding.

High levels of inbreeding are difficult to produce and are only maintained by deliberate crossing of highly related animals. Even if two completely inbred individuals were mated, their offspring would not be inbred unless the inbred individuals themselves were related. Thus, a single mating of two unrelated individuals would break down all inbreeding built up over generations of matings intentionally made to produce inbreeding.

Table 3. Steps in calculating the inbreeding coefficient for 528 Etazon Celsius-ET TL.

Paths connecting parents	**Common ancestor**	**Value**	**Contribution to total relationship**
❷–❸	Bell	$(1/2^2)\ (1 + F_{Bell})$	.25
❶–⑧–⑤–①–②–⑥–❸	Ivanhoe	$(1/2^7)\ (1 + F_{Ivanhoe})$	.0078
❷–⑥–②–③–⑦–⑨–❹	Ivanhoe	$(1/2^7)\ (1 + F_{Ivanhoe})$	.0078
❶–⑧–⑤–①–③–⑦–⑨–❹	Ivanhoe	$(1/2^8)\ (1 + F_{Ivanhoe})$	.0039
Numerator of the relationship between Bellman and Bell Ella			.2695