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Author: Daniel Z. Caraviello¹

Inbreeding

Inbreeding is defined as half of the genetic relationship between an animal's parents. For example, the offspring from a mating of animals A and B, which have the same father, will have 12.5 percent inbreeding, because the genetic relationship between A and B is 25 percent.

Statistical methods to select the best sires of each generation have been developed, making it feasible to achieve any possible selection goal within a herd. When focusing on only one or few traits, the probability of selecting animals that are related increases [20], generating higher levels of inbreeding.

Reporting mean inbreeding coefficient for several breeds from 1965 to 1999, Norman et al. [10] noted that inbreeding levels increased more rapidly after 1980, especially in Jerseys. They also showed that the mean inbreeding coefficient of bulls entering AI progeny test programs ranged from

Table 1: Average inbreeding (F) of registered Holsteins and Jerseys freshening by year

Year	Holsteins		Jerseys	
	F	No. Observations	F	No. Observations
1970	0.011	110,608	0.008	10,037
1971	0.011	328,883	0.008	9355
1972	0.011	416,891	0.008	8610
1973	0.011	458,459	0.009	8023
1974	0.011	508,022	0.009	8242
1975	0.011	550,708	0.010	8534
1976	0.012	569,289	0.010	8763
1977	0.012	726,802	0.011	11,418
1978	0.013	549,460	0.011	13,140
1979	0.013	890,534	0.012	14,809
1980	0.014	938,720	0.013	16,392
1981	0.015	993,385	0.013	17,982
1982	0.015	1,031,741	0.014	18,821
1983	0.016	1,073,083	0.013	19,634
1984	0.016	1,062,259	0.014	20,474
1985	0.017	1,078,655	0.015	22,905
1986	0.018	1,063,500	0.017	22,514
1987	0.019	1,093,107	0.018	29,063
1988	0.023	1,461,593	0.020	30,326
1989	0.024	1,637,271	0.022	30,712
1990	0.026	1,872,512	0.025	48,333
1991	0.028	2,094,578	0.027	57,841
1992	0.030	2,293,983	0.030	58,294
1993	0.032	2,404,302	0.033	63,252
1994	0.035	2,718,844	0.036	65,183
1995	0.038	2,706,433	0.039	67,044
1996	0.040	2,766,567	0.042	69,234
1997	0.041	3,132,523	0.044	68,729
1998	0.042	1,532,303	0.046	35,110

3.8 percent in Brown Swiss to 6.4 percent in Jerseys.

Reporting (Table 1) the increase in inbreeding in Jersey and Holstein cows

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¹ Daniel Caraviello is a Graduate Research Assistant in the Department of Dairy Science at the University of Wisconsin-Madison.

Technical assistance provided by Kent Weigel, Assistant Professor, Dairy Science Department, University of Wisconsin-Madison

from 1970 to 1998, Thompson et al. [15], noted the need for the dairy industry to increase the population of males used as parents (i.e. reducing the relationship of the selected sires to the breed, and among themselves).

Hansen [7] presented (Table 2) relationships, expected inbreeding, and realized inbreeding per decade in US Holsteins, and we can see the dramatic increase during the last decade. Expected inbreeding increased from 2.7 percent in 1970 to 6.8 percent in 2000, and didn't depart greatly from realized inbreeding. Through artificial insemination (AI), relatively few sires have an enormous impact on the breed. For the same reason, finding an "outcross" sire is not very helpful, because it will be rapidly overused, (not being an outcross anymore). Under random mating, expected inbreeding increases if relationships increase. Mating individual cows to unrelated sires within a breed requires knowledge of pedigrees, but as relationships increase it becomes more difficult

Table 2: Relationship and inbreeding of US Holsteins¹

Year	Relationship	Expected	Realized
		Inbreeding	Inbreeding
		%	
1970	5.2	2.7	4.7
1976	7.3	3.8	3.8
1982	9.8	5.1	4.3
1990	10.2	5.4	5.1
2000 (Predicted)	12.7	6.8	...
2010 (Predicted)	15.2	8.2	...
2020 (Predicted)	17.7	9.7	...

¹ Estimates for 1970 to 1990 are from Young and Seykora (13).

Table 3: Genetic composition of US Holsteins

Year	Direct Relationship ¹		Relationship ²
	1982	1990	1996
Ivanhoe (1952)	10.2	8.3	8.8
Chief(1962)	6.8	12.3	14.0
Valiant (1973)	...	9.6	12.8
Elevation (1965)	10.1	12.2	12.2
Mark (1978)	...	...	12.2
Blackstar (1983)	...	...	12.0
Rotate (1975)	...	...	11.2
Southwind (1964)	...	...	10.6
Bell (1974)	...	5.6	10.2
Cleitus (1981)	...	...	10.2
Leadman (1985)	...	...	10.0

¹ Young and Seykora (13).

² USDA Animal Improvement Programs Laboratory

to avoid matings to related animals. In Table 3, we see the relationship of influential sires with the Holstein breed. Notice that Chief has a 14 percent relationship to the breed. Before 1982, no sires surpassed a 10 percent relationship with the breed. Now, several do, and the number is increasing alarmingly. Hansen [7] reported that, when his study was performed, almost all of the top 25 sires for Type and Production Index and Net Merit, had $\geq 9\%$ of relationship with the breed.

In a study by Weigel and Lin [20], the average relationship between a pool of 141 high-ranking Holstein sires and 1433 elite Holstein cows was 10.9 percent. For Jerseys, the mean relationship between 135 sires and 1139 elite cows was 16.4 percent. These results show that inbreeding is a problem for all breeds, especially Jerseys.

Increased inbreeding, and consequently decreased heterozygosity, results in impaired survival, health, vigor, and reproductive efficiency [15, 16], and generates increased frequency of animals affected by genetic defects.

Smith et al. [12] showed that an increase of one percent in inbreeding costs 23.11 per animal in lifetime net income, or 37 kg of milk, 1.2 kg of fat, and 1.2 kg of protein per lactation, and 13.1 days of productive life. These results are not considering direct costs due to reduced reproductive performance. This study also reported an increase in calving interval of 0.26 days per one percent increase in inbreeding. Caraviello et al. [2] evaluating 268,008 US Jersey cows, reported a slight increase in the risk of culling for cows with inbreeding coefficients >10 percent, (as compared to cows with coefficients <5 percent).

Thompson et al. [15], evaluating the effects of inbreeding on production in 265,905 Jersey cows, showed (Table 4) a reduction in yield of inbred animals, when compared with non-inbred animals. Noting that inbred animals have reduced yield, early in lactation and at younger

Table 4: Effect of inbreeding on test-day milk, fat, protein productions (kg) and linear SCS in registered Jerseys

F	Milk	SE	Fat	Protein	SCS	No. Observations
Test-day production						
0.00	0.000	0.000	0.000	0.000	0.000	1,520,868
0.01	-0.060	0.007	-0.012	-0.005	0.001	647,157
0.02	-0.064	0.007	-0.013	-0.006	-0.008	749,238
0.03	-0.054	0.007	-0.014	-0.007	-0.002	679,193
0.04	-0.082	0.008	-0.016	-0.008	-0.007	593,413
0.05	-0.171	0.008	-0.017	-0.011	0.006	441,339
0.06	-0.278	0.010	-0.020	-0.015	-0.010	295,512
0.07	-0.405	0.011	-0.023	-0.018	-0.020	185,989
0.08	-0.524	0.015	-0.026	-0.024	-0.024	114,891
0.03	-0.537	0.017	-0.029	-0.027	-0.018	79,851
0.10	-0.581	0.021	-0.028	-0.028	0.011	52,656
0.13	-0.748	0.015	-0.043	-0.037	0.000	102,693
0.17	-1.071	0.032	-0.062	-0.047	0.004	21,791
0.26	-0.976	0.054	-0.054	-0.040	-0.048	7252
305-d Lactation production						
0.01	-18.4		-3.59	-1.52		
0.02	-19.3		-4.01	-1.79		
0.03	-16.4		-4.15	-2.07		
0.04	-25.0		-4.84	-2.49		
0.05	-52.1		-5.11	-3.32		
0.06	-84.8		-5.94	-4.70		
0.07	-123.5		-7.05	-6.22		
0.08	-159.7		-8.02	-7.33		
0.09	-163.6		-8.99	-8.16		
0.10	-177.4		-8.57	-8.71		
0.13	-228.1		-13.14	-11.20		
0.17	-326.7		-18.95	-14.38		
0.26	-297.5		-16.46	-12.17		

ages. Losses from inbreeding levels >5 percent increased significantly, reaching 177 kg for F = 10 percent and 327 kg for F = 15 to 19 percent (per 305-day lactation). In that study, inbreeding showed no clear impact on SCS. Increased inbreeding reduces survival, where chances of survival to the next lactation are smaller in highly inbred animals.

Evaluating the effects of inbreeding in 1,805,773 Holstein cows and for each percent increase in inbreeding Thompson et al. [16] reported losses in milk production per lactation of 35 kg when inbreeding was one percent and 55 kg when inbreeding was seven to 10 percent (Table 5). Losses in fat and protein production were proportional to losses in milk production. The level of inbreeding did not affect somatic cell score. Thompson et al. [16] also noted that

age at first calving increased by up to 26 days, and lactation length decreased by two to eight days, when inbreeding levels were above 10 per-cent. Wiggans et al. [21] estimated reductions of 21.3 kg of milk, 1.03 kg of fat, and 0.88 kg of protein per lactation for each one percent increase in inbreeding in the Jersey breed.

Effective population size reflects the amount of variation present in an equivalent number of unrelated animals. Table 6 shows the effective population sizes of the five major US dairy breeds, where it is noted that the breed with greatest inbreeding problems is the Jersey, followed by the Holstein. For example, the genetic variation in the eight million or so US Holstein animals is equivalent to that of 39 totally unrelated animals. The fact that the Holstein and Jersey breeds have smaller

Table 5: Estimates of effect inbreeding (F) on test-day milk, fat, protein (kg) and linear SCS in registered Holsteins [SE=standard error for test-day milk (kg)]

F	Milk	SE	Fat	Protein	SCS	No. Observations
Test-day production						
0.000	0.000	0.0000	0.000	0.000	0.0000	6,807,799
0.010	-0.010	0.0036	0.000	0.001	0.0171	9,278,494
0.020	-0.118	0.0041	-0.005	-0.001	0.0074	6,436,869
0.030	-0.238	0.0045	-0.009	-0.004	-0.0059	4,727,350
0.040	-0.381	0.0045	-0.013	-0.009	-0.0242	4,136,228
0.050	-0.468	0.0054	-0.018	-0.012	-0.0228	2,672,763
0.060	-0.592	0.0063	-0.023	-0.014	-0.0184	1,558,343
0.070	-0.784	0.0072	-0.028	-0.021	-0.0119	1,163,684
0.080	-0.984	0.0086	-0.032	-0.025	-0.0066	699,017
0.090	-1.074	0.0117	-0.040	-0.028	-0.0103	361,286
0.100	-1.296	0.0158	-0.045	-0.035	-0.0250	192,247
0.128	-1.594	0.0117	-0.056	-0.044	-0.0153	353,865
0.169	-2.066	0.0294	-0.071	-0.058	-0.0274	53,121
0.264	-2.321	0.0440	-0.076	-0.065	0.0036	23,949
305-d Lactation production						
0.000	0.00		0.00	0.00		
0.010	-3.18		0.01	0.41		
0.020	-36.24		-1.56	-0.22		
0.030	-72.63		-2.90	-1.27		
0.040	-116.34		-4.21	-2.83		
0.050	-142.91		-5.47	-3.62		
0.060	-180.68		-7.13	-4.46		
0.070	-239.34		-8.64	-6.47		
0.080	-300.35		-10.00	-7.74		
0.090	-327.60		-12.27	-8.67		
0.100	-395.53		-13.83	-10.81		
0.128	-486.42		-17.36	-13.55		
0.169	-630.30		-21.54	-17.81		
-0.264	-707.78		-23.33	-19.93		

effective population size than the other breeds shows that selection intensity and rate of genetic progress are more important factors, with respect to inbreeding, than total population size.

The importance of complete pedigrees for inbreeding control and for inbreeding research was studied by Cassell et al. [3], where 441,096 registered Holstein, 772,379 grade Holstein, and 72,780 Jersey cows were evaluated. Grade Holsteins, Registered Holsteins and Jersey cows had 50, 98 and 90 percent complete pedigrees, respectively. Inbreeding depression generated a decline in peak milk yield of -0.12 to -0.06 kg/d per percent increase in inbreeding in Holsteins and -0.08 kg per percent increase in inbreeding in Jerseys. Inbreeding averaged 3.55 percent for

Jerseys, 2.67 percent for registered and 2.75 percent for grade Holsteins.

Cassell et al. [4] found one to two percent inbreeding depression in 70-days non-return rate when evaluating 50,613 Holstein and 47,673 Jersey cows with five generations of pedigree data, as well as three percent maternal inbreeding depression per 10 percent inbreeding. Maternal inbreeding depression means that cows with 10 percent inbreeding will

Table 6: Effective size of US dairy cattle populations

Ayrshire	161
Brown Swiss	61
Guernsey	65
Holstein	39
Jersey	36

Table 7: Weighted mean Lifetime Net Merit (in dollars) of the selected group, according to the level of inbreeding constraint, with (R) and without (U) a restriction of five progeny per dam (results are not comparable across breeds)

Inbreeding Constraint (%)	Ayrshire		Brown Swiss		Guernsey		Holstein		Jersey	
	U	R	U	R	U	R	U	R	U	R
4							573	485	413	408
5			532	532			653	569	475	470
6	373	373	587	587	377	377	701	599	512	504
7	419	419	620	618	411	411	733	611	538	525
8	448	448	641	635	432	432	755	616	559	238
9	470	470	656	646	445	445	769	619	575	546
10	486	486	669	654	454	453	780	621	588	551
11	499	498	679	659	460	458	786	621	599	555
12	509	508	688	663	466	462	791	622	607	556
13	518	515	696	667	470	464	794	622	615	557

have a three percent lower 70-day non-return rate than cows with zero percent inbreeding. Wilk and McDaniel [22] reported increased death losses in Jersey calves when inbreeding was above six percent, with linear increases as inbreeding increased. Calves of inbred dams also had increased death loss, suggesting maternal inbreeding depression. It is important to worry about inbreeding in the long-term, because inbreeding problems are not dramatic enough to compromise the cattle in one generation [2, 4]. However, farmers and AI companies generally don't want to compromise genetic gain in the next generation to avoid inbreeding in the future generations.

It is difficult to reduce inbreeding through mating unrelated animals, because they usually have common ancestors far back in their pedigrees (some of these common ancestors show up several times). Comp-uterized mating programs require several generations of pedigree data for each animal, but it is often unavailable.

Expected future inbreed-ing (EFI), released by the USDA, usually ranges from five to seven percent, and indicates inbreeding in the next generation if this sire were mated with 600 random cows and heifers from the US population. This value indicates which sires are "outcross" and is far more important than the sire's own inbreeding coefficient.

Inbreeding control is one of the main reasons a farmer should use a computerized mating program. In the Holstein breed, Weigel [18]

found that inbreeding of the current matings, in commercial dairy herds, was around 4.9%, versus 5.1% if matings had been done at random and 3.3% if computerized mating programs had been used. These gains were obtained without changing the cows, the number of sires, or the number of matings per sire, so average genetic merit of the matings did not change.

The reduction on inbreeding depression easily generates enough profit to justify the use of computerized mating programs, because this service is usually offered by breeding companies for a negligible cost. Weigel [18] reported a profit of 60 dollars per calf when inbreeding was reduced from 7.2 percent to 4.4 percent in the Jersey breed, and noted that sacrifices in genetic merit were minimal. Weigel and Lin [20] showed that mating programs, after correct sire selection, could reduce inbreeding by 1.8 and 2.8 percent on the next generation of Holsteins and Jerseys, respectively. This reduction would increase \$37 and \$60 in lifetime net income for Holsteins and Jerseys, respectively.

A limitation at farm level is usually lack of pedigree information, which leads to accounting for only one or two generations when avoiding inbreeding. Weigel and Lin [20] reported that controlling inbreeding in the short-term can be done in a farm level through mating programs, but long-term control depends on correctly selecting the young sires entering progeny test programs. Usually, when inbreeding is considered in a farm level, selected sires are

Table 8: Mean inbreeding coefficients, net merit, and expected lifetime profit for Jersey breeds resulting from random matings to a sample of 20 current active AI sires, matings that maximized net merit with a constraint on inbreeding, or matings that maximized expected lifetime profit adjusted for inbreeding depression

Mate Selection Scheme	Inbreeding	Net Merit	Lifetime Profit
Random mating	7.1	\$168.01	\$305.26
Maximize net merit regardless of inbreeding	7.2	\$186.39	\$327.56
Maximize net merit with <8% inbreeding	5.8	\$185.94	\$360.47
Maximize net merit with <9% inbreeding	6.1	\$186.39	\$354.04
Maximize net merit with <10% inbreeding	6.4	\$186.39	\$347.98
Maximize profit minus inbreeding depression	4.4	\$182.44	\$378.33

older and slightly less inbred than if inbreeding is ignored. This study shows that, when inbreeding is restrained to four percent, the bull sires used are much older than when inbreeding is restrained to 13 percent. Progeny of young bulls have consistently higher inbreeding levels than progeny of older bulls [1]. This difference in age of bull sires will certainly be reflected in genetic merit, thereby favoring the choice of younger bull sires. Table 7 shows the Net Merit that must be sacrificed to obtain different levels of inbreeding. “Optimal contribution” is another method for controlling inbreeding studied by [5, 6, 8, 9, 13, 20], in which the average genetic merit is maximized subjected to a constraint on average relationship within a group. In Holsteins, for example, mean Lifetime Net Merit increased from \$573 at four percent inbreeding to \$794 at 13 percent inbreeding, and the corresponding increase in Jerseys was from \$413 to \$615. The relationship is not linear, it requires a large compromise in genetic gain to obtain extremely low inbreeding level, but a moderate reduction in inbreeding is less costly. Weigel and Lin [20] also compared several combinations of restrictions on inbreeding (e.g. 8%, 9%, 10%...) with maximization of lifetime profit or net merit on Jersey cattle. The combination that provided the greater lifetime profit had 4.4 percent inbreeding and \$182 net merit as herd means (Table 8).

Weigel [17] reported that approximately 50 percent of the 5000 young Holstein sires

progeny tested every year globally are sons of the 10 most popular sires. Restricting the family size is one of the methodologies considered for controlling inbreeding, and it seems to work very well. Another important point is that traits with higher heritability lead to a lower chance of co-selection of relatives, because most of the weight in calculating EBV put on the individual’s performance, not on family information. On the other hand, much of the information for traits with low heritability comes from pedigree.

Regarding strategies in nucleus herds to control inbreeding, Weigel [17] concluded that several procedures (like external progeny testing, additional phenotypic records, and factorial mating designs) exist that may help to control inbreeding without leading to a significant reduction in selection response. But this increase in family size that comes from an increase in the number of parents may be lost in the subsequent generations if these extra parents have lower than average EBV.

Smith and Quinton [11] evaluated the creation of two sub-lines, and this led to lower genetic response at the same level of inbreeding than a single line. Another study [14] defends the use of sub-lines for controlling inbreeding (albeit a small loss in genetic response per year).

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