Is Genetics a Cure for Reproductive Loss?

L. B. Hansen
Department of Animal Science
University of Minnesota, St. Paul

Take Home Messages

- Genetic evaluations for daughter pregnancy rate (DPR) are published by USDA and can be used by dairy producers to improve the genetic potential for reproduction of cows in their herds. Introduced in February 2003, DPR is not yet included in the Net Merit index published by USDA. However, DPR will be included in Net Merit soon.
- Reproduction is a large component of productive life (PL) of dairy cows. Cows must become pregnant to stay in herds. However, there are other contributing factors to PL, including level of milk production, functional type traits, and disease resistance.
- The dairy industry's continual selection for cows with more dairy character ("sharpness") in addition to selection for milk production might be negatively impacting the reproduction of cows. Adequate body condition aids reproduction.
- Evidence is mounting that cows that are more moderate in size (due to genetics, not poor growth) have advantages for reproduction and PL compared to cows that are very large in size. Genetically, Holstein cows become larger each year.
- Inbreeding depression might be a contributing factor to poorer reproduction and decreased PL in some situations if pedigrees aren't inspected at the time of mating A.I. sires to individual cows. Pedigrees of cows must be compared to pedigrees of alternative bulls when mating.
- Some dairy producers are turning to crossbreeding to improve reproduction of cows. Crossbreeding research is underway to document consequences of crossbreeding using domestic dairy breeds as well as several European dairy breeds.

What is the Situation?

Length of herd life of dairy cows in the U.S. has not changed much during modern history. Over the years, the typical cow has completed about two and one-half lactations. Cows often have the functional ability to stay in herds longer than two or three lactations, but given the opportunity, dairy producers like to cull low producing cows from their herds. Supply of replacement heifers plays a role in the decision of whether to keep an older cow. Older cows are more predisposed to health problems than are young cows; therefore, dairy producers often freshen most of their replacement heifers to get higher average milk production in a more trouble-free fashion.

Good data is hard to get on cow longevity; however, there is general agreement that the ability of cows to survive in dairy herds has diminished during the 1990s and early 2000s. Evidence suggests that the number of lactations completed by cows has decreased in the U.S. in recent years, and some evidence suggests that the death rate of dairy cows has increased in recent years. Furthermore, the reproductive performance of cows seems to be declining and the incidence of stillborn calves appears to be increasing. Some reports suggest that age at disposal of cows has actually increased during the past couple of years. So, cows might be actually living as long as they have traditionally, but they might not be calving as many times during their lifetimes. Evidence suggests that percentage of cows culled involuntarily is increasing, so there is less opportunity for voluntary culling of cows for low milk production.

Genetic Evaluation for Productive Life

Productive Life (PL) is the trait published by the Animal Improvement Programs Laboratory (AIPL) of USDA, and it predicts the longevity of dairy cows. The trait PL is different than absolute longevity, because it measures only the days that a cow is milking during her lifetime with a maximum of 84 months (7 years) of age. The PL of a cow begins when she calves the first time and ends when she leaves the herd; however, cows are allowed only 305 days in milk for each lactation, so cows with long calving intervals are not rewarded. Predicted transmitting ability (PTA) for PL is reported in months.

The highest PTA for PL of a Holstein sire from the February 2003 genetic evaluations of USDA was +5.5 months. Among active A.I. sires, only three Holsteins had a PL greater than 3.2 months. Among sires that received their first proofs since February 1995, the average PTA for PL is +0.2 months and the range of PTA for PL is –4.6 months to +5.5 months -- a range of 9 months. This is almost a full lactation!

A problem with the trait PL is that we don't have a highly accurate PTA of sires until a large number of daughters have had an opportunity to stay in herds for long periods of time. Furthermore, the heritability of PL is low at 8.5%, which means that factors other than genetics (mostly dairy herd management) explain 91.5% of the differences in PL of cows. Yet, the 9-month range of PTA for PL is real and represents actual differences for herd life of daughters.

For sires with only young "first-crop" daughters from progeny testing programs, pedigree information from the sire and dam of the bull is used. Also, the PTAs of other traits are used to help predict the PTA for PL for these sires with only "first-crop" daughters. To assist in the prediction of PTA for PL of sires with limited numbers of young daughters, the PTAs for milk, fat, protein, SCS (all four of these traits are from USDA), udder, feet & legs, and body size (all three of these are "composite" traits from the Holstein Association USA) are used. The genetic relationships (on a +1.0 to –1.0 scale) of PL with these other traits are:

PL and Milk	+0.13
PL and Fat	+0.12
PL and Protein	+0.15
PL and SCS	–0.35 (lower SCS gives longer PL)
PL and Udder	+0.30 (better udders gives longer PL)
PL and Body Size	–0.04 (smaller body size gives longer PL)
PL and Feet & Legs	+0.19 (better feet & legs gives longer PL)

The genetic relationships of PL and the production traits have fallen substantially during the past few years. Earlier, the genetic relationships between PL and the production traits were about +0.30. So, non-production factors are explaining a higher percentage of the differences between sires for PL.

A New Trait to Select for Improved Reproduction

Daughter pregnancy rate (DPR) is a new trait (February 2003) published by USDA for dairy producers to use for sire selection. With cow reproduction expressed as pregnancy rate, each 1% of DPR equals 4 days open. The heritability (percentages of differences that are due to genetics) of DPR is 3.7%, about one half of the heritability of PL. We have suspected that DPR explains a large portion of the differences of sires for daughter PL, and the genetic relationship of PL and DPR (on a +1 to –1 scale) is +0.59.

The correlation of PTA for DPR with PTA for other traits:

DPR and Milk	–0.22 (higher milk hinders reproduction)
DPR and Body Size	–0.22 (bigger size hinders reproduction)
DPR and Dairy Form	–0.46 (sharpness hinders reproduction)

These correlations are very informative. The assumption of many might be that the deterioration of cow fertility is almost completely a correlated response to selection for increased milk production. However, the correlations suggest that continued selection for increased body size and, especially, the continued selection for more "sharpness" might be contributing as much, if not more, to the deterioration of cow fertility.

Examples of PTA for high-reliability sires are in Table 1. One sire was selected for each birth year from 1981 to 1989. For seven of the nine years, the sire listed had the largest number of sons among sires of sons born that year. All had a large number of sons sampled and are high-impact sires on the Holstein breed. All but one has a negative PTA for DPR and six of the nine have negative evaluations for PL.

In Table 2, sires of comparatively fewer sons are listed for the same birth years of sires of sons that were listed in Table 1. The sires in Table 2 probably should have had more sons and the sires in Table 1 probably should have had fewer sons. All of the sires of sons in Table 2 have positive PTA for DPR and PL. Hindsight is always better than foresight. However, do some things jump out about the two groups of sires of sons in Tables 1 and 2? Yes. The sires in Table 1 tend to rate highly for dairy form ("sharpness") and the sires in Table 2 tend to rate poorly for dairy form. Also, there is a tendency for the sires in Table 1 to transmit larger body size than the sires in Table 2. There is a slight difference for udder composite, favoring the sires in Table 1 (but no advantage for SCS), but a much larger difference in final score for type. The daughters of sires in Table 2 would be rated lower for final score for type because they are not as large or as “sharp”.

The sires in Table 2 rate higher for PTAs for DPR, PL, and Net Merit. Comparing Tables 1 and 2, it seems like there might be a contradiction between the type of cow that is desired by registered Holstein breeders (large and "sharp" cows) versus the type of cow that is optimum for commercial milk production. With near-perfect hindsight, it is a shame that so many sons were sampled of the sires in Table 1 and so few sons were sampled of the sires in Table 2.

Many of the major sires of sons and grandsons of the current active A.I. Holstein sires tend to have negative PTA for DPR, so the negative phenotypic and genetic trend for cow fertility in the Holstein breed should be expected. Perhaps we will need to learn to appreciate a dairy cow that is moderate in size and maintains some body condition during lactation so that she will be able to reproduce.

A History of Increasing Cow Size

Holsteins in North America have been selected for increased body size for many years. Likely reasons for selection for larger body size include: 1) scoring of type traits by the Holstein Association USA continues to place more favorable ratings on cows with larger body size, 2) some dairy producers believe that larger cows have more body capacity to consume more feed, which in turn might allow cows to produce greater volumes of milk, and 3) dissatisfaction with body size of heifers at first calving because of poor heifer growth leads some dairy producers to attempt to compensate for substandard heifer management by selecting for increased genetic potential for mature body size.

Despite the emphasis on larger body size in selection programs, especially by registered breeders, no research has documented that large cows have functional or economic advantages over small cows on a genetic basis. Previous studies have indicated that small cows are more feed efficient than are large cows (Yerex et al., 1988) and that small cows have fewer health problems, especially for digestive disorders than large cows (Mahoney et al., 1986). The major justification for including type traits in selection programs is to improve the PL of cows; however, no evidence exists to support continued selection for larger body size of cows.

Research Herd of Cows

An experimental herd of Holstein cows at the Northwest Research and Outreach Center, Crookston, of the University of Minnesota has been selected since 1966 for large versus small body size. Holstein cows in an existing herd were paired by sire and/or producing ability and randomly assigned to one of two genetic lines -- large or small. Progeny were assigned to the same genetic line as their dams. Except for sire selection, animals have been housed and managed alike. Milking cows are housed in a tie-stall barn.

Service sires have been selected from among the top 50% of active A.I. sires available in the U.S. for PTA for production. The actual production traits changed over the years of the study and, in time order, were 1) milk (lb), 2) milk-fat dollar value, and 3) fat (lb) plus protein (lb). All other selection was based on body size of daughters, either large or small. Sires were selected on standardized PTA with the body size index: 0.5(stature) + 0.25(strength) + 0.25(body depth). The three most extreme sires for transmitting large and small body size were selected once each year from the summer genetic evaluations of USDA for production and the Holstein Association USA for body size. Repeatability of PTA was required to be at least 70% prior to the adoption of Animal Model methodology and 80% thereafter. Cows within line were randomly mated to sires, except inbreeding coefficients were not allowed to surpass 6.25% (or minimized if none of the three sires permitted an inbreeding coefficient less than 6.25%).

Cows used for this study were born from January 1, 1983 to April 30, 1991. Measures of PL for this study were reported in days, and days in milk were summed across lactations similar to the methods used by USDA, except that days in milk were summed only to 72 months (6 years) of age. All cows were weighed immediately after calving, as were their calves. Body dimensions were recorded one month after calving.

Direct Response to Selection for Body Size

Table 3 has the numbers and ranges of observations for body weights at calving. The ranges of observations in Table 3 indicate that there was considerable overlap across the two genetic lines. Table 4 has the averages for body weight and dimensions and the differences for the genetic lines. Cows in the small line had average body weight of 1230 lb immediately after calving. Most dairy producers probably would not regard this average weight as very small. On the other hand, cows in the large line had average body weight of 1342 lb after first calving, which would be regarded as quite large by most dairy producers, especially with an average age of first calving of only 25.5 months.

Cows in both lines increased in body weight with lactation number; however, the difference of body weight became more pronounced with increased lactation number. In other words, the cows that were bred to be large continued to grow more after first calving than the cow that were bred to be small. Immediately after third calving, cows in the small line had average body weight of 1413 lb, which is a good-sized cow. In comparison, cows in the large line had average body weight of 1587 lb after third calving. At time of dry off, cows in both size lines weighed much more than they did immediately after calving; in fact, some cows in the large line surpassed 2000 lb at the time of dry off. Once dairy cows reach an acceptable body size, continued growth beyond that body size might not be desirable economically.

The magnitude of difference (lb and inches) in average body size in Table 4 might seem fairly small. However, the greater body weight of cows in the large line -- 9% (1st lactation), 11% (2nd lactation), and 12% (3rd lactation) -- seemed considerable based on eyeball inspection. Although the increase in stature (height at the withers) was less pronounced than body weight on a percentage basis (5% to 6%), the difference of about 3 inches also seemed to be magnified on casual observation. For this study, consistent use for over 25 years of the most extreme sires for transmitting small size resulted in cows that would be considered of adequate size by most dairy producers.

Across years of this study, body weights did not change with year for cows in the small line, but body weights had a significant increase with year for the large line. Because of the continued emphasis on larger body size of Holsteins, the cows in the small line in this study have not changed in body size with time; however, cows in the large line have continued to become larger. The continued emphasis on larger cow size began in the late 1960s. The ideal model cow of the Holstein Association USA was altered markedly in 1977, especially by increasing her body size. The small genetic line in this study might reflect the body size of the earlier ideal Holstein, which was developed in 1922. The genetic base for all traits is changed every five years, and the base changes for stature, strength, and body depth in 2000 indicate that the U.S. Holstein cow will continue to become larger into the future.

Response for Milk Production, Number of Services, and PL

The 305-2X-ME production of the two body size lines differed only for cows during their first lactations. Cows in the small line averaged 24,279 lb and cows in the large line averaged 22,663 lb, for a difference of 1616 lb favoring the small line. Herd average production throughout the years of the study has tended to favor the small line, but differences have usually not been significantly different.

Table 5 has averages for number of services. Although differences were statistically different only for first lactations, all differences in the genetic lines for number of services favored the small line.

Cows in the small size line had 88 days longer PL than cows in the large size line. Small line cows (n = 157) averaged 658.3 days and large line cows (n = 119) averaged 570.6 days. Typically, advocates for placing emphasis on type traits in selection programs have argued that type traits are important for increasing the longevity of cows. The results of this study suggest that selection for increased body size of Holsteins results in decreased longevity.

Dairy producers should not attempt to overcome deficiencies in heifer growth by selecting sires for larger mature body size. If most heifers grown by a dairy producer lack adequate body size, then factors other than genetics almost certainly are the cause. Cows that are bred to be larger continue to grow more after first calving than cows that are bred to be somewhat smaller. Once a cow reaches an acceptable size, continued growth beyond that size likely is not economically desirable. Over the long haul, selection for traits with documented positive impact on profitability should result in cows of near optimum size.

Inbreeding

Inbreeding can rob dairy producers of income by reducing fertility, increasing stillbirths, hampering growth rates, and reducing disease resistance. Most of these consequences are masked and not readily noticed. With increased relationships among Holsteins, inspection of pedigrees is necessary when mating individual cows to individual bulls. Relationships continue to mount within the Holstein breed as expected with our highly effective selection methods. As relationships between individuals continue to increase, it becomes more and more likely that cows and bulls that are mated to each other will be closely related.

Table 6 has the relationship to the Holstein breed in 2003 of individual sires with high impact. These relationships are estimated by USDA and trace pedigrees to only 1960, so relationships prior to that year are not considered. Two bulls born in the 1960s -- Elevation and Chief -- together make up about 30% of the Holstein breed today. All of the other bulls in Table 6 are descendants of at least one of these two stalwarts of the breed. Table 6 should demonstrate how relationships within the Holstein breed are creeping upward. Blackstar is a relatively "young" ancestor with a birth year of 1983, yet he already has a relationship of 14.8% to the Holstein breed. Many of Blackstar's sons (especially Duster and Emory) and grandsons (such as Mtoto and Decision) are just beginning to have their impact on the breed. To date, no bull has surpassed 16% for relationship to the Holstein breed, but Blackstar could easily be the first bull to surpass 18% relationship to the breed.

The standard recommendation is that inbreeding coefficients should not surpass 6.25% for commercial milk production. What does the 6.25% mean? Cows have two genes at every location on their chromosomes -- one from each parent. The inbreeding coefficient measures the percentage of those two genes (across all chromosomes) that are identical because they trace to the same ancestor. As the inbreeding coefficient goes up, the likelihood of doubling up on genetic recessives (most of them of minor consequence) becomes greater.

Table 7 has the average inbreeding coefficient of Holsteins recorded through DHI by birth year. These estimates are conservative, because many cows in DHI lack parts of their pedigree and because the pedigrees are taken back to only 1960. The increases in inbreeding are constant at about 0.2% per year. At this rate, the average inbreeding of the Holstein breed should reach 6.25% by 2010. Furthermore, the "background" relationships prior to 1960 suggest that 2% should be added to all current estimates of inbreeding using the 1960 base for pedigrees. Therefore, the average inbreeding coefficient for Holsteins today with complete pedigrees would be something like 7% -- beyond the 6.25% recommended for commercial milk production.

With an average estimate of 4.9% for 2002 with the 1960 base, many cows have probably surpassed the maximum recommended level of inbreeding (6.25%). Most dairy producers are probably unaware that they have individual cows in their herd that have inbreeding coefficients higher than what is recommended. Unintentional inbreeding could be a silent contributor to reduced fertility and shortened PL of dairy cows.

The corrective mating programs offered by A.I. organizations can assist in the avoidance of individual matings of A.I. sires and cows that will result in unacceptable levels of inbreeding. However, pedigrees of cows must be provided to the programs, and the programs must go deeply into pedigrees to pick up bulls like Elevation and Chief, which often appear many times far back in the pedigrees of individual bulls and cows.

Crossbreeding

An easy way to prevent inbreeding is to crossbreed. Milk pricing has changed over time to place more emphasis on the solids in milk rather than the fluid carrier, which places the Holstein breed at less of a competitive advantage compared to other breeds. All dairy breeds in the world likely have fewer problems than the Holstein breed for the direct and maternal effects of calving difficulty. Furthermore, cow fertility has gained in interest among dairy producers at the same time that concerns about inbreeding have arisen. For all or some of these reasons, many dairy producers have implemented or have expressed interest in crossbreeding systems.

The effects of crossbreeding are the opposite of inbreeding. The two genes at each location on the chromosomes are much less likely to be alike with crossbreeding than with same-breed matings. Therefore, genetic recessives of major and minor consequence are not as likely to be expressed. Old research has indicated that hybrid vigor from crossbreeding is greatest for traits related to fertility, survival, and health. Routine crossbreeding of Holsteins and Jerseys in New Zealand has resulted in a 7-month advantage in PL compared to purebreds.

Crossbreeding should be of the most benefit when environments are limited and when dairy producers are resistant or unable to keep reliable records on parentage of cows in their herds. New research is underway to help uncover the potential value of crossbreeding for commercial milk production in the U.S. At the University of Minnesota, we are crossing portions of two herds of Holstein cows with Jersey and Montbeliarde sires to gauge the consequences of crossbreeding. Furthermore, we are receiving and analyzing the data for production, calving ease, fertility, and survival of seven herds in California that are crossbreeding using the breeds of Holstein, Jersey, Brown Swiss, Normande, Montbeliarde, and Scandinavian Red. The commercial pig and beef cattle industries have relied on crossbreeding to improve reproduction, growth rates, and disease resistance for about half a century.

References

Dechow, C. D., G. W. Rogers, L. Klei, and T. J. Lawlor. 2002. Heritabilities and correlations among body condition score, dairy form, and selected linear type traits. J. Dairy Sci. 85: In press.

Hansen, L. B., J. B. Cole, G. D. Marx, and A. J. Seykora. 1999. Productive life and reasons for disposal of Holstein cows selected for large versus small body size. J. Dairy Sci. 82:795-801.

Mahoney, C. B., L. B. Hansen, C. W. Young, G. D. Marx, and J. K. Reneau. 1986. Health care of Holsteins selected for large or small body size. J. Dairy Sci. 69:3131.

VanRaden, P., Sanders, A., Tooker, M., Miller, B., and D. Norman. 2002. Daughter pregnancy rate evaluation of cow fertility. USDA-AIPL Research Report DPR1(11-02). http://aipl.arsusda.gove/reference/fertility/DPR_rpt.htm

Yerex, R. P., C. W. Young, J. D. Donker, and G. D. Marx. 1988. Effects of selection for body size on feed efficiency and size of Holsteins. J. Dairy Sci. 71:1355.

Table 1. PTAs for daughter fertility (pregnancy rate) and other traits of A.I. sires (by birth year) with a large number of sons sampled.

Birth Year	Name	Sons	**DPR**[1]	**Dairy Form**	**Body Size**	PL	Udder	Type	SCS	Net Merit
1981	Cleitus	402	**-0.2**	**+1.20**	**-0.83**	+1.2	-0.51	-0.41	3.36	105
1982	Melwood	209	**-2.0**	**+0.97**	**+1.73**	-2.1	-0.69	+0.36	2.90	115
1983	Elton	227	**-0.6**	**+1.71**	**-0.62**	+0.3	+0.56	+0.57	3.32	298
1984	Southwind	211	**-0.7**	**+0.84**	**+0.63**	-0.7	+0.17	+0.70	3.19	128
1985	Leadman	683	**-0.1**	**-0.08**	**-0.23**	+1.1	+0.25	+0.13	3.01	201
1986	Mascot	387	**-0.8**	**+0.40**	**+0.11**	-2.9	+0.56	+0.20	3.32	29
1987	Jed	109	**-1.6**	**+1.89**	**+1.40**	-0.7	+1.29	+1.60	3.33	33
1988	Luke	209	**-2.4**	**+0.58**	**+0.63**	-1.8	+0.52	+0.65	3.27	132
1989	Bellwood	361	**+0.2**	**+2.06**	**+1.38**	-0.5	-1.03	+0.20	3.01	356
Average			**-0.9**	**+1.06**	**+0.47**	-0.7	+0.12	+0.44	3.19	155

[1] Daughter pregnancy rate.

Table 2. PTAs for daughter fertility (pregnancy rate) and other traits of A.I. sires (by birth year) with a small number of sons sampled.

Birth Year	Name	Sons	**DPR**[1]	**Dairy Form**	**Body Size**	PL	Udder	Type	SCS	Net Merit
1981	Promise	54	**+1.6**	**-1.18**	**-2.50**	+2.2	-0.71	-1.58	3.19	195
1982	Bell Troy	104	**+2.3**	**-0.39**	**-0.97**	+0.2	-0.34	-1.01	3.26	109
1983	Laban	75	**+1.5**	**+0.13**	**-0.83**	+0.6	-0.08	-0.52	2.92	114
1984	Chair. Val.	25	**+2.4**	**+0.31**	**+1.06**	+1.0	+0.16	+0.38	3.12	36
1985	Vic Kai	34	**+0.7**	**-0.54**	**-1.23**	+1.2	-0.73	-1.24	3.08	246
1986	Mich	38	**+1.5**	**-1.94**	**-1.53**	+0.4	-1.49	-1.65	3.23	245
1987	Converse	75	**+1.2**	**-0.50**	**-0.66**	+1.9	+0.97	+0.55	3.02	330
1988	Top Gun	43	**+2.0**	**-0.21**	**-0.27**	+1.0	-0.26	-0.47	3.21	171
1989	Infinity	39	**+3.2**	**-1.49**	**-1.13**	+3.1	+0.93	-0.41	3.39	245
Average			**+1.8**	**-0.65**	**-0.90**	+1.3	-0.17	-0.66	3.16	188
Difference from Table 1			**+2.7**	**-1.71**	**-1.37**	+2.0	-0.29	+2.0	-0.03	+33

[1] Daughter pregnancy rate.

Table 3. Number and ranges of observations for direct response to selection for body size.

Trait	Lactation number	Small line			Large line		
		No.	Min.	Max.	No.	Min.	Max.
			-----(lb)-----			-----(lb)-----	
Body weight	1	217	917	1587	159	992	1812
	2	126	1076	1612	93	1133	1839
	3	70	1135	1728	53	1279	1951

Table 4. Average for response to selection for body size.

Trait	Lactation number	Small line	Large line	Difference
		------------------------(lb)------------------------		
Body weight	1	1230	1342	112
	2	1314	1464	150
	3	1413	1587	174
		------------------------(in)------------------------		
Wither height	1	50.8	53.5	2.8
	2	51.3	54.1	2.8
	3	51.5	54.6	3.0
Depth of chest	1	26.4	27.9	1.5
	2	26.9	28.6	1.7
	3	27.4	29.2	1.9
Chest circumference	1	73.3	76.8	3.5
	2	74.8	78.9	4.1
	3	76.4	81.0	4.6

Table 5. Averages for number of services, calving ease, and calf weight.

Trait	Lactation number	Small line		Large line		Difference
		No.	Average	No.	Average	
Number of services	Virgin heifer	233	1.54	164	1.67	0.13
	1	141	1.79	98	2.08	0.29*
	2	88	1.91	59	2.08	0.17
	3	48	2.02	25	2.24	0.22

*Difference is statistically significant.

Table 6. Relationships of individual sires to the Holstein breed.

Sire	Pedigree	Birth year	Relationship
			(%)
Elevation		1965	15.4
Chief		1962	15.2
Blackstar	Son of Chairman	1983	14.8
Valiant	Son of Chief	1973	14.6
Mark	Son of Chief	1978	13.6
Chairman	Grandson of Elevation and Chief	1976	13.4
Emory	Son of Blackstar	1989	12.4
Starbuck	Son of Elevation	1979	12.4
Leadman	Grandson of Elevation	1985	12.2
Duster	Son of Blackstar	1990	11.8

Table 7. Average inbreeding[1] of Holstein females[2].

Birth year	Inbreeding Coefficient
	(%)
1990	2.5
1992	3.0
1994	3.5
1996	3.9
1998	4.2
2000	4.5
2002	4.9

[1] Inbreeding is the percentage of times across the genome of an animal that the two genes at a single location on the two chromosomes are identical because they came from the same ancestor.

[2] Pedigrees all have a base of 1960, so a constant value of 2% should be added to all estimates to account for background relationships from 1880 to 1960.