Analysis of Inbreeding and Its Relationship with Functional Longevity in Canadian Dairy Cattle

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Abstract

The aim of this study was to assess the level of inbreeding and its relationship to the functional survival of Canadian dairy breeds by using a Weibull proportional hazard model. Data consisted of records from 72,385 cows in 1,505 herds from 2,499 sires for Jerseys, 112,723 cows in 1,482 herds from 2,926 sires for Ayrshires, and 1,977,311 cows in 17,182 herds from 8,261 sires for Holsteins. Longevity was defined as the number of days from first calving to culling, death, or censoring. Inbreeding coefficients (F) were grouped into 7 classes ($F = 0$, $0 < F < 3.125$, $3.125 \leq F < 6.25$, $6.25 \leq F < 12.5$, $12.5 \leq F < 18.25$, $18.25 \leq F < 25.0$, and $F \geq 25.0\%$). The statistical model included the effects of stage of lactation, season of production, the annual change in herd size, type of milk recording supervision, age at first calving, effects of milk, fat, and protein yields calculated as within herd-year-parity deviations, herd-year-season of calving, inbreeding, and sire. The relative culling rate was calculated for animals in each class after accounting for the above-mentioned effects. A trend toward increased risk of culling among more inbred animals was observed for all breeds. Little difference in survival was observed for cows with $0 < F < 12.5\%$. The relative risk ratios (relative to $F = 0$) for cows with inbreeding coefficients up to 12.5% were 1.19, 1.16, and 1.14 for Jersey, Ayrshire, and Holstein cows, respectively. Greater effects of inbreeding were seen, however, when F increased beyond 12.5%.

Key words: functional longevity, inbreeding level, inbreeding depression

INTRODUCTION

The inbreeding coefficient of an animal is the average probability that 2 genes at any given locus are identical by descent (Falconer and Mackay, 1996). Numerous studies have shown an unfavorable association between

inbreeding and performance for production traits (Miglior et al., 1995b; Smith et al., 1998; Thompson et al., 2000) and nonproduction traits (Miglior et al., 1995a; Smith et al., 1998; Cassell et al., 2003; Wall et al., 2003). Inbreeding decreases the frequency of heterozygous individuals relative to the defined base population and, therefore, decreases mean performance for traits for which directional dominance exists. This loss in performance is called inbreeding depression. The rate of change in mean performance of a trait associated with inbreeding depends on the frequency of genes with effects of dominance and the size of these effects. The theoretical value for regression coefficients for inbreeding is a function of the dominance deviation for heterozygous loci. Increased inbreeding decreases the potential for genetic gain by decreasing genetic variance (Falconer and Mackay, 1996). Furthermore, an increased rate of inbreeding also means an increased risk to the breeding program in terms of the variance of genetic gain (Meuwissen, 1991), and a reduced additive genetic variance is expected. For these reasons, inbreeding is an important parameter to monitor and control in a breeding program.

Little information is available, however, on the effect of inbreeding on longevity of cows (Thompson et al., 2000; Caraviello et al., 2003). The extent of inbreeding depression seems to vary between different populations. The effect depends not only on the actual level of inbreeding but also on the rate at which inbreeding is increasing. A rapid rise results in greater inbreeding depression than a gradual rise (Falconer and Mackay, 1996).

When evaluating the effect of a given factor on longevity, survival analysis using a Weibull proportional hazards model can offer better fit than many simple linear models, due to its ability to properly account for censored records. The model also accounts for the typically skewed distribution of survival data. Furthermore, time-dependent variables can be used for the survival analysis to model accurately the effects of environment (Ducrocq and Solkner, 1998; Vukasinovic, 1999; Ducrocq, 2002).

The objectives of this study were to determine the current level and rates of inbreeding and to use survival

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Figure 1. Average percentage of animals with complete pedigree information for each ancestral generation (animals born from 1980 to 2004).

analysis with a proportional hazards model to assess the potential impact of inbreeding on functional longevity of Canadian dairy cows.

MATERIALS AND METHODS

Level of inbreeding and effect of inbreeding on survival were studied in 3 Canadian dairy breeds. Data consisted of records from 1,977,311 cows in 17,182 herds and 8,261 sires for Holsteins, 72,385 cows in 1,505 herds from 2,499 sires for Jerseys, and 112,723 cows in 1,482 herds from 2,926 sires for Ayrshires. Data were obtained from lactation records extracted for the May 2005 genetic evaluation of the Holstein, Jersey, and Ayrshires breeds. All cows were registered in official breed herdbooks. The inbreeding coefficients were calculated using pedigree data that dated back to 1942 and included 8,075,912 animals for Holstein, 368,518 for Jersey, and 512,681 for Ayrshires. Inbreeding coefficients for each animal were calculated using the algorithm of Meuwissen and Luo (1992). Mean inbreeding was calculated per year based on the year of birth of the animals. The average percentage of animals that had complete pedigree for 5 ancestral generations is shown in Figure 1 for animals born from 1980 to 2004.

Length of productive life was defined as time (in days) from one calving to the next calving, death, or culling. Records from cows being sold for dairy purposes, ex-

ported, leased to another herd, or still in the herd at the time of the study were censored. A lifetime record was considered complete (uncensored) if the cow received a termination code, indicating that the cow was removed for any reason. Records associated with missing sire identification, incorrect calving dates, and age at first calving outside the range of 18 to 40 mo were excluded from the analysis. Inbreeding coefficients (F) were grouped into 7 classes ($F = 0$, $0 < F < 3.125$, $3.125 \leq F < 6.25$, $6.25 \leq F < 12.5$, $12.5 \leq F < 18.25$, $18.25 \leq F < 25.0$, and $F \geq 25.0\%$).

The following model was used to analyze the impact of inbreeding on survival:

$$\lambda(t) = \lambda_{0,s}(t) \exp\{x'_m(t)\beta z'_m u\}$$

where $\lambda(t)$ is the hazard of a cow; i.e., her probability of being culled at time t given she is alive just before t ; $\lambda_{0,s}(t) = \lambda\rho(\lambda t)\rho^{-1}$ is the Weibull baseline hazard function with scale parameter λ and shape parameter ρ , and t is the time in days from one calving to the next calving or date of culling or censoring for each stratum; β contains the fixed (and possibly time-dependent) covariates affecting the hazard, with $x'_m(t)$ being the corresponding design vectors, and u is a vector of random variables with associated incidence vector $z'_m(t)$.

The fixed covariates included in the model were as follows: time-dependent effect of stage of lactation in

days (1 = 0 to 80; 2 = 81 to 235; 3 > 235); effect of year and season of calving (years of calving were from 1985 to 2003 and seasons of calving were January to March, April to June, July to September, and October to December); effect of season of production with the same definition as seasons of calving; effect of the annual change in herd size with 3 classes (decreasing = for a decrease in herd size of >5%, nearly unchanged = no appreciable change, and increasing = for an increase in herd size of >10%); effect of the type of milk recording supervision with 3 classes (unsupervised, supervised, and unknown; i.e., records that do not fulfill the minimum criteria set by the milk recording agency); effect of age at first calving in months; and effects of milk, fat, and protein yields. The latter effects were calculated as within herd-year-parity deviations with 3 classes for each, low = for cows producing more than 0.4 SD below the herd-year-parity average, average = for cows producing between 0.4 SD below and 0.6 SD above the herd-year-parity average, and high = for cows producing above 0.6 SD of the herd-year-parity average. Inbreeding was included as a covariate on the model and the significance of the effect of inbreeding on functional survival was assessed using the likelihood ratio test.

The random effects included were the effect of herd-year-season class, which was assumed to follow a log gamma distribution, and the genetic effect of the cow's sire, which was assumed to follow a multivariate normal distribution with mean zero and variance $A\sigma_s^2$, where σ_s^2 is the variance among sires and A is the relationship matrix. Sire variances of 0.046, 0.039, and 0.040 for Holstein, Ayrshire, and Jersey, respectively, were used in the analyses, based on prior work by Sewalem et al. (2005).

The analyses, using a Weibull proportional hazards model, were performed using the Survival Kit Version 5.1 (Ducrocq and Solkner, 1998). The analyses were stratified, with a different baseline hazard function $\lambda_{0,s}(t)$ for each lactation (subscript s designates different strata). Detailed descriptions of the model and survival analysis of longevity data in dairy cattle on a lactation basis have been published by Ducrocq (2002), Roxstrom et al. (2003), and Sewalem et al. (2005).

RESULTS AND DISCUSSION

Mean Level of Inbreeding

Descriptive statistics for the F for Canadian Jersey, Ayrshire, and Holstein animals born from 1980 to 2004 are presented in Table 1. The F in the population was low until 1980, so the results reported here describe the population trends since 1980. As shown in Table 1, the overall mean F from 1980 to 2004 for Holstein was

Table 1. Average level of inbreeding (%) for the 3 breeds between 1980 and 2004

	Breed		
	Jersey	Ayrshire	Holstein
Average	3.60	3.99	3.20
Standard deviation	3.05	3.19	2.81
Minimum	0.00	0.00	0.00
Maximum	35.78	45.41	44.71

3.2% with a standard deviation of 2.81%. The corresponding figures for Jersey were 3.6 and 3.05% and for Ayrshire, 3.99 and 3.19%. The maximum F was 35.78% in Jerseys, 45.4% in Ayrshires, and 44.7% in Holsteins. The mean F for animals born in 2004 was 5.04% in Holsteins, 5.00% in Jerseys, and 6.04% in Ayrshires. Miglior et al. (1992) reported a mean F of 2.9% for Canadian Jerseys; Miglior and Burnside (1995) reported an average F of nearly 3.0% for Canadian Holsteins. Kearney et al. (2004) reported a mean F of 2.64% for females and 3.06% for males for the United Kingdom dairy population. Sørensen et al. (2005) reported a mean F of 4.7% for Danish Holsteins and Jerseys. In the United States, the current mean F of Holstein, Jersey, and Ayrshire cows are 5.1, 7.0, and 6.0%, respectively (AIPL, 2005).

Table 2 presents the numbers of animals, mean F, and the proportion of animals for each class of inbreeding. In 1980, more than 80% of the cows had F between 0 and 3.125%, but in 2004, over 90% had F between 3.125 and 12.5%. The trend of inbreeding has increased gradually over time. Normally, mating of progeny of half-sibs would result in 6.25% expected inbreeding (assuming the half-sibs were not inbred), but today the offspring would likely be closer to 12% inbred due to the accumulated relationships among animals. Kearney et al. (2004) reported that the number of inbred animals in the United Kingdom has increased significantly since 1990 and they showed that 98% of all males and 96% of all females were inbred in 2002 to some degree, compared with approximately 50% in 1990.

The trends in F for the 3 Canadian breeds are shown in Figure 2. The increase in F was linear for Ayrshires and Jerseys and nonlinear in Holsteins, as tested using quadratic regression. Five distinct periods were considered in terms of the rate change in F; the change in F across the different periods was assessed based on birth year of the animals (Table 3). In all breeds no appreciable differences in the rate of inbreeding were observed during the periods from 1980 to 1984 and 1985 to 1989. During this period, Ayrshires had the largest change in F among the 3 breeds. In Holsteins, the rate of change in F increased dramatically from 0.05%/yr in 1985 to 1989 to 0.29%/yr in 1990 to 1994. In Ayrshires, the

Table 2. Number of animals, average inbreeding level (F) by birth year, and percentage of animals in each class of inbreeding for Jersey, Ayrshire, and Holstein breeds

Breed	Birth year	No. of animals	Mean	Classes of inbreeding (%)						
				F = 0	0 < F < 3.125	3.125 ≤ F < 6.25	6.25 ≤ F < 12.5	12.5 ≤ F < 18.25	18.25 ≤ F < 25	F ≥ 25
Jersey	1980–1984	39,826	3.23	8.40	49.61	31.20	8.69	1.73	0.13	0.24
	1985–1989	41,327	3.30	5.62	51.91	31.07	9.69	1.46	0.07	0.19
	1990–1994	39,243	3.82	3.53	45.27	35.05	14.73	1.27	0.05	0.10
	1995–1999	35,090	4.32	2.35	37.03	41.21	17.79	1.43	0.11	0.08
	2000–2004	31,035	4.79	2.90	25.50	48.86	20.90	1.57	0.14	0.14
Ayrshire	1980–1984	73,933	3.36	18.89	32.13	35.16	12.08	1.38	0.16	0.21
	1985–1989	69,111	4.07	8.31	30.14	45.87	13.79	1.52	0.15	0.22
	1990–1994	55,766	4.66	5.04	20.90	54.26	18.02	1.38	0.16	0.23
	1995–1999	46,937	5.14	7.05	8.81	58.57	23.94	1.45	0.09	0.09
	2000–2004	37,997	5.41	6.54	7.19	55.71	28.97	1.41	0.11	0.07
Holstein	1980–1984	1,079,159	1.80	23.70	55.64	15.60	4.56	0.42	0.02	0.06
	1985–1989	1,180,099	2.04	11.29	66.16	17.68	4.41	0.40	0.01	0.05
	1990–1994	1,292,548	2.86	13.53	48.17	29.28	8.42	0.55	0.01	0.04
	1995–1999	1,298,484	4.22	11.77	23.98	43.64	19.66	0.86	0.03	0.04
	2000–2004	1,276,208	4.97	9.20	10.75	52.56	26.59	0.79	0.06	0.04

change in F per year decreased from 0.23 to 0.12% in the same period. From 1995 to 1999, the rate of inbreeding jumped from –0.05 to 0.20% in Jerseys, decreased in Ayrshires, but remained relatively constant in Holsteins. In the United Kingdom, the mean F was 2.64% for females and 3.06% for males and the rate of inbreeding was 0.17%/yr from 1992 to 2002, a significant increase compared with 0.03%/yr reported in previous years (1968 to 1991; Kearney et al., 2004). Moreover, Sørensen et al. (2005) showed that F has increased at a rate of 0.9 to 1.1% per generation for Danish dairy breeds in recent years. In the United States, the annual

rate of change in F was 0.14, 0.24, and 0.10% for Holsteins, Jerseys, and Ayrshires, respectively, for the period from 1994 to 2004 (AIPL, 2005).

Relative Risk of Culling

Inbreeding had a statistically significant ($P < 0.001$) association with functional longevity in Holsteins, Ayrshires, and Jerseys; this was determined by comparing the full model (with classes of F) to the reduced model (without F). The results are expressed in relative culling risk, defined as the ratio of the estimated risk of

Figure 2. Inbreeding trends in Canadian dairy breeds.

Table 3. Annual rate of change in inbreeding coefficient ($\pm$ SE) for the 3 breeds for each period

Birth year	Inbreeding coefficient (%)		
	Jersey	Ayrshire	Holstein
1980–1984	0.02 $\pm$ 0.011	0.18 $\pm$ 0.008	0.05 $\pm$ 0.002
1985–1989	0.04 $\pm$ 0.010	0.23 $\pm$ 0.006	0.05 $\pm$ 0.001
1990–1994	–0.05 $\pm$ 0.011	0.12 $\pm$ 0.009	0.29 $\pm$ 0.002
1995–1999	0.20 $\pm$ 0.011	–0.02 $\pm$ 0.010	0.27 $\pm$ 0.002
2000–2004	0.06 $\pm$ 0.012	0.26 $\pm$ 0.011	0.14 $\pm$ 0.001
Overall	0.08 $\pm$ 0.005	0.11 $\pm$ 0.004	0.17 $\pm$ 0.001

being culled under the influence of certain environmental factors relative to the average risk (or reference risk), observed for the class with $F = 0$. Values greater than 1 indicate increased culling risk. Following the approach by Larroque and Ducrocq (2001), if the relative culling risk for a given class is 2, a cow in that class has twice the risk of being culled compared with a cow in the reference class. Conversely, if the relative culling risk for a given class is 0.5, then a cow in that particular class has 50% less chance of being culled than a cow in the reference class.

Table 4 shows the relationship between F and the relative risk of involuntary culling for Jersey, Ayrshire, and Holstein breeds. In both breeds a slight trend toward higher risk of culling was observed among more inbred animals. The relative risk ratios for cows with F up to 6.25% were 1.17, 1.11, and 1.07 for Jerseys, Ayrshires, and Holsteins, respectively. Relative to the noninbred cows, there was minimal effect on the relative risk ratios for cows less than 12.5% inbred. The difference was greater when F increased beyond 12.5%. For instance, Holstein cows with $12.5\% \leq F < 18.25\%$ were 1.25 times more likely to be culled than noninbred cows. The corresponding ratios for Jerseys and Ayrshires were 1.28 and 1.36, respectively. Cows with $F > 25\%$ were 1.51, 1.58, and 1.31 times more likely to be culled for Holsteins, Ayrshires, and Jerseys, respectively. However, as shown in Table 2, the proportion of animals in these groups ($F \geq 12.5\%$) was very low compared with the other groups. Generally, as shown

Table 4. Relative risk of culling for the 3 breeds (relative risk of culling for inbreeding class $F = 0$ was set to 1)

Class of inbreeding (F %)	Relative risk of culling		
	Jersey	Ayrshire	Holstein
$F = 0$	1.00	1.00	1.00
$0 < F < 3.125$	1.12	1.10	1.02
$3.125 \leq F < 6.25$	1.17	1.11	1.07
$6.25 \leq F < 12.5$	1.19	1.16	1.14
$12.5 \leq F < 18.25$	1.28	1.36	1.25
$18.25 \leq F < 25.0$	1.41	1.33	1.42
$F \geq 25.0$	1.31	1.58	1.51

in Table 4, a slight trend toward higher relative risk of culling among more inbred animals was observed. The effect of inbreeding on functional survival of cows found in the present study corroborates the findings of Thompson et al. (2000) and Caraviello et al. (2003).

The F values calculated using the algorithm of Meuwissen and Luo (1992) tend to be underestimated when some pedigree records are missing. An iterative approach presented by VanRaden and Hoeschele (1991) accounts for missing pedigree records by setting the F of animals with missing pedigree records equal to the mean F of animals born in the same year. To examine the consequences of using the 2 different algorithms, F for Holsteins were calculated using both approaches. Results presented in Figure 3 show that the F values calculated according to Meuwissen and Luo (1992) were on average 0.8% less than with the VanRaden and Hoeschele (1991) approach. However, yearly trends in F and relative risks of culling were similar for both approaches, so results using Meuwissen and Luo (1992) were reported and discussed.

Because the amount and depth of pedigree information increased over time, cows that were born later were predisposed to have a greater F , regardless of the true amount of inbreeding. Thus, to test the possible confounding effects of estimated F over time, the analyses were repeated with classes of F crossed within periods. The result of these analyses suggested no confounding effects of inbreeding over the time for Ayrshires and Jerseys. In Holsteins, however, significant associations between classes of inbreeding and time periods were observed, but with no clear trends for some of the classes of inbreeding. For inbreeding classes $0 < F < 3.125$, $3.125 \leq F < 6.25$, $6.25 \leq F < 12.5$, and $12.5 \leq F < 18.25$, a linear relationship between classes of F and periods was seen. For instance, animals born from 2000 to 2004 with inbreeding classes $0 < F < 3.125$, $3.125 \leq F < 6.25$, $6.25 \leq F < 12.5$, and $12.5 \leq F < 18.25$ were 0.73, 0.72, 0.77, and 0.88 times less likely, respectively, to be culled than were cows born during 1980 to 1984 with the same inbreeding classes. This may suggest that animals born more recently (2000 to 2004) have higher F in part due to the availability of deeper pedigree information than animals born in the period 1980 to 1984. No clear relationship was observed across periods for inbreeding classes $F = 0$, $18.25 \leq F < 25.0$, $F \geq 25.0\%$. This lack of a clear result may, however, have been due to few observations in each class of F .

The breeding strategies currently applied in dairy cattle breeding are effective in generating genetic gain. However, reproductive technologies such as AI and embryo transfer have increased the focus of selection on a few superior animals and their offspring, especially for a few superior bulls. Moreover, the advanced meth-

Figure 3. Comparison of mean inbreeding trends using the algorithms of Meuwissen and Luo (1992; —) and VanRaden and Hoeschele (1991; - - -) in Canadian Holsteins.

ods of breeding value estimation have increased the accuracy of prediction by using information on all available relatives. Both of these advancements in animal breeding will increase the probability of generating inbred animals (Verrier et al., 1993; de Boer and van Arendonk, 1994). This study has shown that nearly 96% of the registered dairy cow population in Canada was inbred to some degree, and the proportions of cows in the highest classes of F have increased markedly since 1990 (Table 2). If the trend continues, effects of inbreeding depression will become more pronounced. To avoid this consequence, the current rate of inbreeding should be controlled or reduced if further losses are to be avoided.

As shown in Table 2, the rate of increase in F decreased in Holstein and Jersey breeds from 2000 to 2004. The decreased rate of change in F the 2 breeds might be attributed to the growing awareness of farmers in Canada about the consequences of inbreeding brought on by publishing F for each animal and providing an inbreeding calculator on the Canadian Dairy Network (CDN) web site (CDN, 2005). More recently, CDN has started publishing relationship values (R -values) for every bull and cow in each dairy breed. This information indicates each animal's genetic relationship with the active female population for its breed, and helps identify outcross animals. From an industry perspective, genetic mating programs offered by AI organizations have recently become very popular and may have had an influence on the yearly change in F . These

programs consider minimum acceptable F when sires are recommended for mating.

CONCLUSIONS

Inbreeding levels in the Canadian dairy population have increased gradually and it appears that the current rise in inbreeding will likely continue. To counteract this trend, CDN has been providing services (online inbreeding calculator and relationship values) to farmers and producers to increase awareness about the effects of inbreeding. The survival analysis showed that there was a significant relationship between F and longevity of Canadian dairy breeds. However, the impact of inbreeding on survival of cows was small. The increase in inbreeding will lead to greater inbreeding depression and possibly increased prevalence of recessive genetic disorders in the population. Estimation of rates of change in F and inbreeding depression, especially for nonproduction traits, should be routinely performed to monitor levels and effects of inbreeding.

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