

# Analysis of genetic diversity in four Canadian swine breeds using pedigree data

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Melka, M. G. and Schenkel, F. 2010. **Analysis of genetic diversity in four Canadian swine breeds using pedigree data.** *Can. J. Anim. Sci.* **90**: 331–340. Conservation of animal genetic resources entails judicious assessment of genetic diversity as a first step. The objective of this study was to analyze the trend of within-breed genetic diversity and identify major causes of loss of genetic diversity in four swine breeds based on pedigree data. Pedigree files from Duroc (DC), Hampshire (HP), Lacombe (LC) and Landrace (LR) containing 480 191, 114 871, 51 397 and 1 080 144 records, respectively, were analyzed. Pedigree completeness, quality and depth were determined. Several parameters derived from the in-depth pedigree analyses were used to measure trends and current levels of genetic diversity. Pedigree completeness indexes of the four breeds were 90.4, 52.7, 89.6 and 96.1%, respectively. The estimated percentage of genetic diversity lost within each breed over the last three decades was approximately 3, 22, 12 and 2%, respectively. The relative proportion of genetic diversity lost due to random genetic drift in DC, HP, LC and LR was 74.5, 63.6, 72.9 and 60.0%, respectively. The estimated current effective population size for DC, HP, LC and LR was 72, 14, 36 and 125, respectively. Therefore, HP and LC have been found to have lost considerable genetic diversity, demanding priority for conservation.

**Key words:** Genetic drift, effective population size

Melka, M. G. and Schenkel, F. 2010. **Analyse de la diversité génétique de quatre races de porc canadiennes à partir des données généalogiques.** *Can. J. Anim. Sci.* **90**: 331–340. La préservation des ressources génétiques animales suppose avant tout une évaluation judicieuse de la diversité génétique. L'étude devait analyser les tendances de la diversité génétique au sein de la race et identifier les principales raisons pour lesquelles cette diversité s'amointrait chez quatre races de porc, d'après les données généalogiques. À cette fin, les auteurs ont analysé l'ascendance des races Duroc (DC), Hampshire (HP), Lacombe (LC) et Landrace (LR) grâce aux dossiers contenant respectivement 480 191, 114 871, 51 397 et 1 080 144 entrées. Ils ont déterminé la complétude, la qualité et l'étendue de la généalogie. Plusieurs paramètres dérivés de ces analyses approfondies ont permis de mesurer les tendances et le degré actuel de diversité génétique. L'indice de complétude pour chacune des quatre race s'établissait respectivement à 90,4, 52,7, 89,6 et 96,1%. Le pourcentage de diversité génétique qu'on estime avoir perdu au sein de chaque race au cours des trois dernières décennies se chiffrait respectivement à environ 3, 22, 12 et 2%. La proportion relative de la diversité génétique perdue attribuable à la dérive génétique due au hasard chez les porcs DC, HP, LC et LR s'établissait respectivement à 74,5, 63,6, 72,9 et 60,0%. La taille efficace actuelle de la population de porcs DC, HP, LC et LR a été estimée à 72, 14, 36 et 125, respectivement. Par conséquent, ce sont les porcs HP et LC qui ont perdu la plus grande diversité et ces races devraient être jugées prioritaires sur le plan de la conservation.

**Mots clés:** Dérive génétique, taille efficace de la population

The development of appropriate genetic conservation strategies entails, as an initial step, careful assessment of existing genetic diversity. Genetic diversity in livestock species can be divided into within-breed and between-breed genetic diversity. This study will focus on within-breed genetic diversity. The future genetic improvement of Canadian swine breeds is dependent upon the availability of sufficient genetic variation, which has tremendous benefits. Genetic diversity is required to meet current production needs in various environments, to allow sustained economically important genetic improvement (Reist-Marti et al. 2003), and to facilitate rapid adaptation to changing breeding objectives, changes in market preferences and environmental

conditions, including resistance to various diseases (Notter 1999). For example, higher genetic diversity

**Abbreviations:** DC, Duroc;  $f$ , founders;  $f_e$ , effective number of founders;  $f_{ge}$ , founder genome equivalents;  $\Delta F$ , rate of inbreeding; GD, genetic diversity accounting for loss due to drift and unequal founder contribution; GD\*, genetic diversity accounting for the loss due only to unequal founder contribution; HP, Hampshire;  $L_a$ , average generation interval; LC, Lacombe; LR, Landrace;  $N_e$ , effective population size;  $N_{enf}$ , effective number of non-founders; PCI, Pedigree completeness index

was long ago associated with increased superiority in performance in swine crosses (England and Laurence 1953).

However, a considerable amount of genetic diversity is thought to have already been lost in swine breeds. Over the past 50 yr, because of rapid changes in production systems, market forces, and indiscriminate crossing with exotic breeds, animal genetic resources available throughout the world have been in a state of dramatic decline (FAO 2000; Barker 2001). Several authors (e.g., Nomura et al. 2001; Carolino and Gama 2008; Vicente et al. 2008) have reported loss of diversity in livestock breeds. For example, Vicente et al. (2008) reported that the level of inbreeding was a major concern in native Portuguese swine breeds.

The reduction in genetic diversity is associated with various adverse incidents, such as inbreeding depression in fitness-related traits, and an increased fluctuation in selection response (Falconer and Mackay 1996).

In closed populations, inbreeding increases at a higher rate, leading to loss of alleles, which is impossible to counterbalance without migration (Wooliams 2007). Even in the absence of selection, alleles present in one generation may, by chance, become more or less frequent, or even "extinct," in subsequent generations due to the fact that genetic drift can eliminate alleles, but only mutation or immigration can restore lost variants (Lacy 1989).

Conservation programs have basically two major targets: first, to reduce inbreeding and its subsequent effects on fitness and other traits; and, second, to maintain a high level of genetic diversity (Lacy 1995; Barker 2001; Fernandez et al. 2001). In order to maintain the highest possible level of diversity within a given population, the first step should be to assess the trend in genetic diversity within the population. The assessment of genetic diversity is especially important in highly specialized livestock breeds because the use of assisted reproduction techniques, such as artificial insemination and embryo transfer technologies, can potentially rapidly reduce the genetic diversity of a population (Vasconcellos et al. 2003).

Detailed knowledge of population structure among and within breeds of livestock is essential to establish conservation priorities and strategies (Caballero and Toro 2002). It will, therefore, be appropriate to assess the genetic diversity within the Canadian swine breeds. Pedigree information has been used in monitoring and evaluating genetic diversity of breeds based on effective population size and the probabilities of gene origin (e.g., Honda et al. 2004; Sørensen et al. 2005). The objectives of this study were to analyze the trend of genetic diversity within four Canadian swine breeds in Canada and to determine the major cause of loss of genetic diversity based on pedigree data.

## MATERIALS AND METHODS

### Characterization of the Pedigree Information

Four Canadian swine breeds were investigated: Duroc, Hampshire, Lacombe and Landrace. Pedigree data were provided by the Canadian Centre for Swine Improvement (Ottawa, Ontario, Canada) and included all pedigree records available for each breed up to 2008. For each breed, a reference population was defined as the piglets born from the years 2006 to 2008. This period was selected as a reference population because the average generation interval for each breed was close to 2 yr and, hence, it comprises the last generation of data evaluated in each breed. For HP, there has been not been sufficient registration for the most recent generation (Rare Breeds of Canada 2009). Therefore, the reference population size is the smallest of all the breeds in this study.

The parameters were calculated for the reference population in each breed. The number of animals analyzed in the entire pedigree and in the reference population in each breed is shown in Table 1. Pedigree files from DC, HP, LC, and LR containing 480 191, 114 871, 51 397 and 1 080 144, records, respectively, were analyzed. Data used in this study came from pigs cared for following the management practices of commercial swine production in Canada.

The pedigree completeness level of the reference populations (Animals born from 2006 to 2008) was evaluated by using four parameters: (1) the maximum number of generations traced back, (2) the number of equivalent complete generations, (3) the percentage of known ancestors per generation, and (4) the pedigree completeness index. The number of generations between an individual and its earliest ancestor was taken as the maximum number of generations traced back in each breed. PEDIG software (Boichard 2002) was used to

**Table 1. Number of animals in the whole pedigree file and in the reference population (2006–2008), pedigree completeness index, maximum generations traced and average complete generation equivalents of animals in the reference population and percentage of known ancestors in a given generation**

Breed <sup>z</sup>	DC	HP	LC	LR
Whole pedigree	480 191	114 871	51 397	1 080 144
Size of reference population	46 779	98	1 420	78 228
Pedigree completeness index (%)	90.4	52.7	89.6	96.1
Maximum generations traced	33	21	30	29
Complete generation equivalent	13	5.5	17.5	11
% known ancestors in:				
1st generation	100	100	100	100
3rd generation	84.7	67.8	63.4	81.7
5th generation	72.2	61.9	61.3	64.8
7th generation	59.4	57.7	60.0	48.5

<sup>z</sup>DC = Duroc; HP = Hampshire; LC = Lacombe; LR = Landrace.

compute the first three parameters. As proposed by MacCluer et al. (1983), the pedigree completeness index (PCI) of the four Canadian swine breeds was calculated using the software package developed by Berg (2003), using the following formula:

$$PCI = 4C_{\text{sire}}C_{\text{dam}}/(C_{\text{sire}} + C_{\text{dam}}).$$

Where  $C_{\text{sire}}$  and  $C_{\text{dam}}$  are contributions from the paternal and maternal lines, respectively, and

$$C = \frac{1}{g \sum_{i=1}^g a_i}$$

Where  $a_i$  is the proportion of known ancestors in generation  $i$ , and  $g$  is the number of generations considered in this study ( $g = 4$ ).

### Demographic Parameters

Generation interval was computed for the four possible selection pathways (sire–son, sire–daughter, dam–son, and dam–daughter) as the average age of the parents when all their offspring were born.

### Parameters Used to Measure Genetic Diversity

To describe the genetic diversity of the four swine breeds, inbreeding coefficient, effective population size and parameters based on the probability of gene origin (effective number of founders, non-founders and founder genomes) were used.

#### Inbreeding Coefficient

The software package EVA-Inbred by Berg (2003) was used to calculate both observed and expected inbreeding coefficients for each individual animal. In this software the individual observed inbreeding coefficients are calculated using the algorithm of Meuwissen and Luo (1992), while the expected inbreeding coefficients are calculated as the coancestry of the breeding animals assuming random mating (Falconer and Mackay 1996). The average coancestry within birth cohorts is calculated using the algorithm of Colleau (2002).

#### Effective Population Size ( $N_e$ )

Following the standard calculation, the effective population size was computed based on the rate of inbreeding between 2006 and 2008 (the most recent generation interval with records available) ( $\Delta F$ ) for each breed:

$$N_e = 1/(2\Delta F).$$

#### Effective Number of Founders ( $f_e$ )

Founders were defined as animals with both parents unknown. The  $f_e$  was calculated as the number of equally contributing founders that would be expected to generate the same level of genetic diversity as in the

population under study (Lacy 1989), using the following formula:

$$f_e = \left[ \sum_{i=1}^f qi^2 \right]^{-1}$$

where  $qi$  is the genetic contribution of the  $i$ th founder to the reference population and  $f$  is the total number of founders. If all founders were to contribute equally, the total number of founders would be the same as the  $f_e$ . Nevertheless, the  $f_e$  is usually lower than  $f$  indicating unequal contributions of founders due to selection. However,  $f_e$  alone may not be a useful parameter for assessing genetic diversity, because the genetic contributions of founders would converge after a number of generations (Bijma and Woolliams 1999), and hence, the  $f_e$  would remain constant after that.

#### Founder Genome Equivalent ( $f_{ge}$ )

Founder genome equivalent was defined as the number of equally contributing founders with no random loss of founder alleles that would be expected to give the same level of genetic diversity observed in the population under study (Lacy 1989), and it was computed as:

$$f_{ge} = 1/(2 \times f_g)$$

where  $f_g$  is the average co-ancestry for the group considered, as illustrated by (Caballero and Toro 2000).

#### Effective Number of Non-founders ( $N_{enf}$ )

It accounts only for the effect of random genetic drift in the non-founder generations. According to Caballero and Toro (2000),  $N_{enf}$  was computed from the following relationship:

$$1/f_{ge} = 1/f_e + 1/N_{enf}.$$

Measures of the loss of genetic diversity can be derived from the effective number of founders, effective number of founder genomes and effective number of non-founders. The amount of genetic diversity (GD) in the reference population accounting for loss of diversity due to genetic drift and unequal founder contribution was calculated as (Lacy 1995):

$$GD = 1 - \frac{1}{2f_{ge}}.$$

When expressed as  $1 - GD$ , the value obtained is the measure of genetic diversity lost in the population since the founder generation due to bottlenecks and genetic drift. It is assumed that the number of founders in the base population is large enough so that GD in the base population is close to 1.

The amount of genetic diversity in the reference population accounting for loss of diversity due to

unequal founder contribution ( $GD^*$ ) was calculated as (Lacy 1995):

$$GD^* = 1 - \frac{1}{2f_e}$$

Similarly,  $1 - GD^*$  represents the loss of genetic diversity due to unequal founders' contributions to the population (Caballero and Toro 2000). The difference between  $GD^*$  and  $GD$  estimates the loss of diversity by genetic drift accumulated over non-founders generations and was calculated as the inverse of  $2N_{enf}$  (Caballero and Toro 2000; Honda et al. 2004).

### Software Used

The parameters and trends in genetic diversity in the swine breeds were computed using three software packages. Founder equivalents, effective number of non-founders and founder genome equivalents were obtained using CFC (Sargolzaei et al. 2006), percentages of known ancestors in each generation, the proportion of gene pool explained by certain number of ancestors, and cumulated marginal contributions of ancestors were obtained using PEDIG (Boichard 2002). The software package EVA (Berg 2003) was used to compute pedigree completeness indices, number of complete generation equivalents, and average co-ancestry. The average observed inbreeding coefficients, expected inbreeding coefficients under random mating and the departure from randomness in actual matings were also computed using EVA.

## RESULTS

### Pedigree Completeness

The PCI of animals in the reference population in DC, LC and LR was above 89%, but it was 52.7% in the HP breed (Fig. 1, Table 1). Therefore, the measure of genetic diversity should be compared with caution among breeds with substantially different PCI. The higher the similarity of the PCI among breeds the

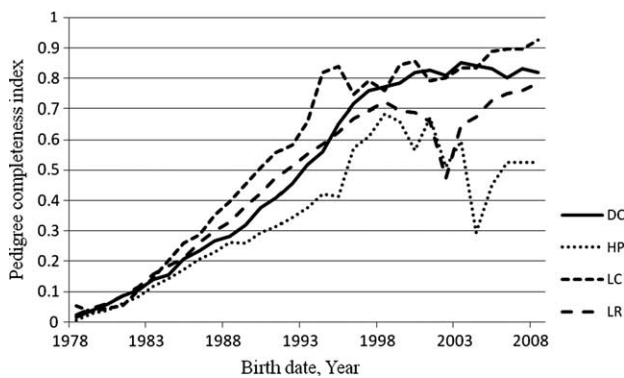


Fig. 1. Pedigree completeness index of the four swine breeds (DC = Duroc, HP = Hampshire, LC = Lacombe, LR = Landrace).

more reliable will be the comparisons. Results of the maximum number of traced generations, complete generation equivalents, and percentage of known ancestors for the first, third, fifth and seventh generation for the reference populations in each breed are shown in Table 1. All ancestors were known in each breed in the first generation. With respect to the depth of the pedigree LC and LR showed the highest (60.0) and lowest (48.5) percentage of known ancestors in the seventh generation, respectively. The complete generation equivalent for the reference population was the least in HP (5.5) and the highest in LC (17.5), while DC and LR showed similar intermediate values.

### Demographic Parameters

The longest and shortest generation intervals were observed in HP (2.07) and DC (1.60), respectively. The average generation interval across breeds was about 1.8 yr (Table 2). In general, generation intervals were slightly shorter for males than for females, except for the DC breed, which showed equal generation intervals for both genders.

### Probabilities of Gene Origin

Results of the probabilities of gene origin are shown in Table 3. The lowest total number of founders was observed in LC (158) followed by HP (257), while the highest number was observed in DC (1803) followed by LR (1621). The  $f_{ge}/f_e$  ratio was lower in LR and HP than in DC and LC. This might indicate the presence of relatively higher selection intensity in LR and HP. The knowledge of the production system over the past years justify higher selection intensity for traits such as backfat, slaughter age, litter size, etc., as well as aggregate selection index for both breeds. However, in DC some imported genetics was also used that might be under lower selection intensity than in the Canadian population. On the other hand, DC and LC showed the lowest and equal  $f_{ge}/f_e$  ratio (0.07) indicating substantial effect of random genetic drift in both populations, compared with HP and LR (0.36 and 0.33, respectively). However, the effect of random genetic drift in HP seems to be underestimated because of lower pedigree completeness in this breed.

Table 2. Effective population sizes ( $N_e$ ), rate of inbreeding in the last generation ( $\Delta F_L$ ), % of inbred animals in the last generation, generation intervals (L) of male and female genetic pathways and the average generation interval in years, in four Canadian swine breeds

Breed <sup>z</sup>	$N_e$	$\Delta F_L$ (%)	Inbred animals (%)	L by pathway (yr)		
				Male	Female	$L_a$
DC	72	0.69	95.1	1.60	1.60	1.60
HP	14	3.6	85.7	1.97	2.16	2.07
LC	36	1.4	99.7	1.54	1.92	1.73
LR	125	0.40	97.3	1.54	1.77	1.65

<sup>z</sup>DC = Duroc; HP = Hampshire; LC = Lacombe; LR = Landrace.

**Table 3. Parameters derived from the probability of gene origin in the most recent years (2006–2008) in each breed**

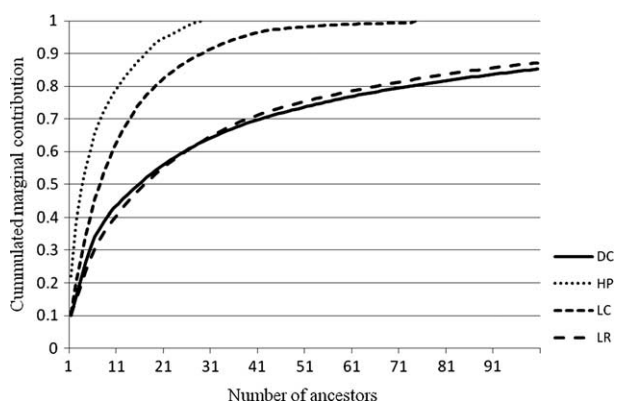
Breeds	DC	HP	LC	LR
Total number of founders, $f$	1803	257	158	1621
Effective number of founders, $f_e$	275	11	56	54
Founder genome equivalent, $f_{ge}$	19	4	4	18
$f_e/f$ ratio	0.15	0.04	0.35	0.03
$f_{ge}/f_e$ ratio	0.07	0.36	0.07	0.33
Number of ancestors to explain:				
50% of gene pool <sup>2</sup>	16	4	7	17
75% of gene pool	55	9	16	50
100% of gene pool	837	29	74	826

<sup>2</sup>Gene pool of the reference population (animals born from 2006 to 2008).

Four ancestors in HP and seven ancestors in LC contributed to 50% of the gene pool in the reference population (current gene pool), while in DC and LR more ancestors (16 and 17, respectively) were needed to explain half of the current gene pool (Table 3). The entire current gene pool was explained only by 29 and 74 ancestors in HP and LC, respectively. Higher numbers of ancestors (~800) were involved in explaining 100% of the current gene pool of DC and LR populations (Fig. 2). This implies that LR and DC currently have higher genetic diversity than HP and LC breeds based on the ancestral contributions. The highest marginal contributions of 10 major ancestors were observed in HP and LC. In HP and LC, only two major ancestors contributed 38.4 and 20.0%, to the gene pool, respectively. In DC and LR, the two major ancestors contributed 15.4 and 14.9% to the current gene pool (data not shown).

**Inbreeding and Genetic Diversity**

Lacombe was found to have the highest percentage of inbred animals (all individuals with  $F > 0$ ) followed by LR and DC, while HP had the least percentage of inbred animals, which should reflect the lower pedigree

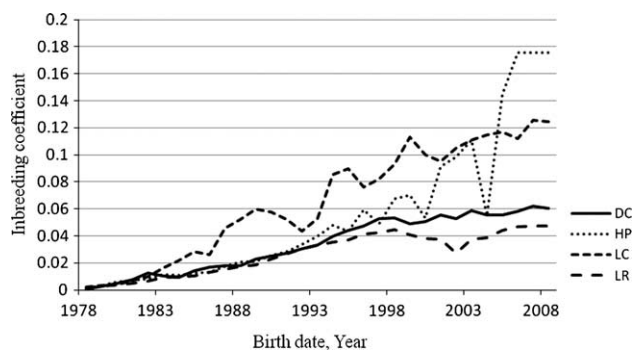


**Fig. 2.** Cumulated marginal contribution of 100 major ancestors in the Canadian swine breeds (DC = Duroc, HP = Hampshire, LC = Lacombe, LR = Landrace).

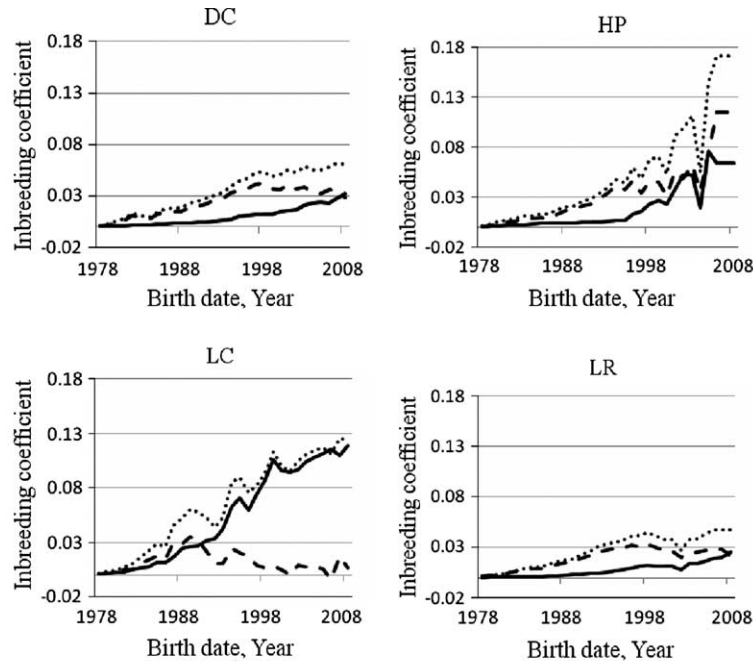
completeness in this breed. Hampshire had the highest rate of inbreeding per year in the last generation followed by LC, while DC and LR had lower rates of inbreeding (Table 2). Regarding the trend of inbreeding coefficient over the last three decades, LR showed the least average inbreeding coefficient of all the breeds, followed by DC, while LC had the highest average inbreeding coefficient for the same period; However, in recent years, it has been overtaken by the steep increase in inbreeding rates in HP breed (Fig. 3). Average inbreeding coefficient in LR and DC has never been above 6%. However, in LC and HP the average inbreeding coefficient has been above 6% since 1994 and 1998, respectively. The corresponding inbreeding coefficients of the two breeds in the most recent year (2008) was approximately 12 and 18%, respectively, which was also reflected by low effective population sizes in the reference population (36 and 14, respectively).

There has been considerable deviation of the actual inbreeding coefficient from expected inbreeding under random mating in each population in the past 20 yr with the actual inbreeding being higher than expected under random mating (Fig. 4). This likely implies that appropriate mating systems were not used for these breeds, so that related individuals were mated more often than under random matings. In addition, the trend in coancestry coefficients (Fig. 5) in each breed was, as expected, similar to their respective trends in inbreeding. Accordingly, DC and LR showed lower than 5% of coancestry, whereas LC and HP had increasing level of coancestry (13 and 21% in 2008, respectively).

The overall trend in the genetic diversity of the four swine breeds (Fig. 6) shows that each breed has been losing genetic diversity over the past two decades. The highest losses of diversity were observed in HP and LC (22 and 12%, respectively), whereas LR and DC showed much lower losses (2 and 3%, respectively). The relative proportion of genetic diversity lost due to random genetic drift in DC, HP, LC and LR was 74.5, 63.6, 72.9 and 60%, respectively, in what shows a much



**Fig. 3.** The trend in the coefficient of inbreeding over the past three decades in the Canadian swine breeds (DC = Duroc, HP = Hampshire, LC = Lacombe, LR = Landrace).



**Fig. 4.** Actual inbreeding (dotted line), the level of inbreeding expected under random mating (solid line) and the deviation between the actual and expected (broken line) in the four swine populations (DC = Duroc, HP = Hampshire, LC = Lacombe, LR = Landrace).

smaller role of the unequal founder contribution to loss of genetic diversity in all four breeds.

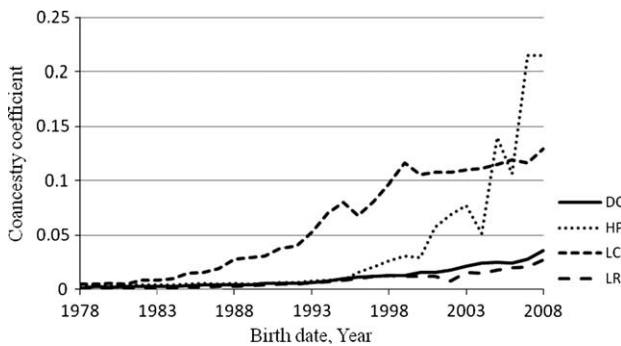
## DISCUSSION

In recent years, the genetic diversity and relationships of different pig populations have been investigated using microsatellite markers (e.g., Li et al. 2000; Fan et al. 2002) and mitochondrial DNA amplified polymorphism (e.g., Jiang et al. 2001; Alves et al. 2003) methods. This study, however, demonstrates an application of pedigree information to evaluate the status of genetic diversity and to identify major causes of the diversity loss in four swine breeds. In conservation programs, the rate of inbreeding is the most important parameter in monitoring

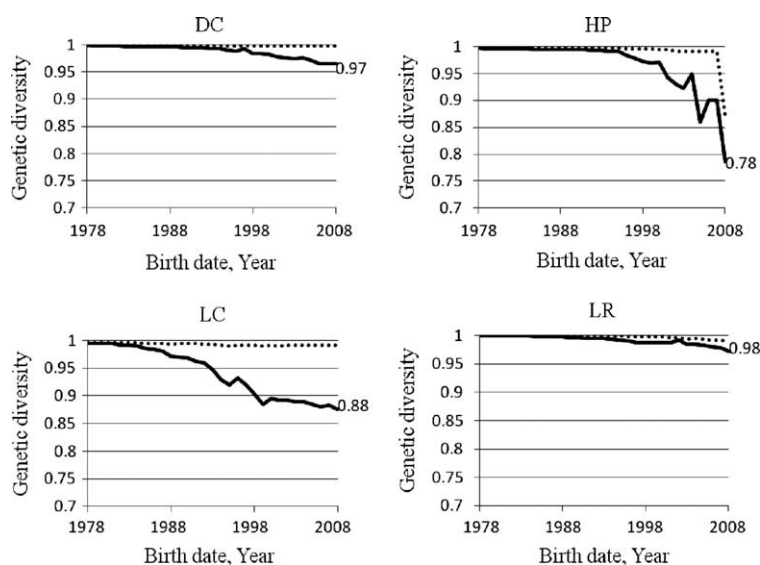
genetic diversity (FAO 2000). In this study, the rate of inbreeding per year in the last generation of available data ranged from 0.47% in DC to 1.80% in HP.

Although there are several criteria to prioritize breeds (Bennewitz and Meuwissen 2005) for conservation programs, the endangerment status of breeds is the most important criterion which can be indicated by the effective population size (Ruane 2000). In this study, the effective population sizes of Canadian swine breeds ranged from 14 in HP to 125 in LR.

An effective population size of 50 is required in order for a population to withstand the effects of inbreeding, while a size of 500 is essential to sustain the genetic diversity and evolutionary potential of the population for several generations (Frankham et al. 2002). However, HP and LC already showed fewer than the recommended population size, implying the immediate need for conservation practices. Small effective population size and an increasing inbreeding coefficient will lead to lower genetic diversity in the future. Maintaining within-breed genetic diversity in the long-term depends very much on the effort to increase effective population size, and balancing the contribution of ancestors (Woolliams and Thompson 1994) or avoiding mating of much-related animals and reducing genetic drift (Simianer 2005). Therefore, more effort should be directed towards increasing the effective population size of each breed by lowering the rate of inbreeding or by introducing genetically unrelated individuals.



**Fig. 5.** The trend of average coancestry in Duroc (DC), Hampshire (HP), Lacombe (LC) and Landrace (LR) over the past three decades.



**Fig. 6.** Genetic diversity accounting for loss of diversity due to unequal founder contribution and random genetic drift (solid line) and due only to unequal founder contribution (broken line) in DC = Duroc, HP = Hampshire, LC = Lacombe, and LR = Landrace.

The parameters derived from the probabilities of gene origin are useful tools in measuring genetic diversity within breeds even after only a small number of generations (Boichard et al. 1997). The  $f_e$  was one of those parameters that was used to assess whether or not there was a balanced contribution of founders, and, hence, to assess the loss of genetic diversity in each breed due to unequal contributions of founders (Lacy 1989). The departure from equal contributions of founders was highest in LR followed by HP, whereas the lowest departure was observed in LC followed by DC. This implies that the effect of selection has been considerable in LR and HP, as it is supported by the knowledge of the production system. Selection of parents of the next generation, so as to maintain higher genetic diversity (Lacy 1995), would be more important in LR than the other breeds. Overall, the comparison between the  $f_e$  and  $f$  demonstrates a decline in genetic diversity due to unequal contributions of founders, which could happen as a consequence of the excessive use of some animals as parents of subsequent generations.

The  $f_{ge}$  is a very important parameter for measuring genetic diversity aimed at the management of small populations (Lacy 1995). The  $f_{ge}$  accounts for the loss of genetic diversity due to unequal founder contribution and also random genetic drift. It is a more accurate description of diversity. All determinations of genetic loss are relative to the genetic diversity in the founder population. The analysis of allelic loss is, therefore, a determination of the probability that alleles present in the founder population still reside within the descendant population (Lacy 1989). The  $f_{ge}/f_e$  ratio measures the impact of genetic drift excluding the effect of founder contributions on genetic diversity, such that lower ratios

are associated with a higher impact of genetic drift. Accordingly, the effect of random genetic drift was higher in DC and LC than in HP and LR. This result was also reflected by a lower relative contribution of random genetic drift in HP and LR. However, it should be noted that the impact of random genetic drift in the HP breed might be underestimated because the pedigree information available for this study was incomplete.

The deviation of the actual inbreeding coefficient from the expected inbreeding under random mating was substantial in HP followed by DC and LR, while the deviation in LC was small. The deviation of the actual inbreeding from the expected inbreeding under random mating could be due to the lack of appropriate mating strategies in the breeding programs for preventing mating of related individuals or, as Caballero and Toro (2002) demonstrated, by subdivision of the population into local populations, leading to increased inbreeding within subpopulations. Caballero (1994) stated that the subdivision of the population could be generated by using particular breeding systems in the different subsets of the population.

In all breeds, an increase in coancestry was observed over the past three decades, particularly for HP and LC. The coancestry coefficient of a population predicts the average inbreeding coefficient of the subsequent generation (Falconer and Mackay 1996). Various studies indicate that the average coancestry is a good measure of genetic diversity as it accounts for both founder effects and the effects of genetic drift (Lacy 1995; Caballero and Toro 2000). From the relationship between average coancestry and genetic diversity, Lacy (1995) demonstrated that choosing animals for breeding with the objective of minimizing coancestry in

the next generation would maximize genetic diversity. Therefore, application of minimum coancestry mating is desirable to increase future effective population size and increase genetic diversity in each breed. In particular, minimizing coancestry mating in LR and HP is essential due to the fact that unequal founder contribution has been playing a great role in both populations. As part of a conservation program, the use of older parents from previous generations could be considered to improve the genetic diversity of the current population which was alarmingly lower in the HP breed.

Fabuel et al. (2004) reported the observed heterozygosity by direct count and expected heterozygosity under Hardy-Weinberg equilibrium in DC to be, on average, 0.549 and 0.648, with an average level of inbreeding equal to 0.0451. Vicente et al. (2008) reported the effective number of alleles per locus and expected heterozygosity to be larger in LR than in DC. In the current study, greater genetic diversity and  $N_e$  were found in LR than in DC. Nucleotide diversity analysis suggests that genetic variability was greater in DC than in HP (Upholt 1977; Nei and Li 1979). Similarly, in the current study, DC showed higher  $N_e$  and genetic diversity than HP.

Overall, genetic diversity has been lost over the past three decades in all the breeds in this study. Moreover, the rate of loss of diversity is increasing over time as illustrated by rapid increase in coancestry level. This shows that relatively higher total loss of diversity will occur in the next three decades compared with the previous decades. One of the major causes of loss of genetic diversity in small populations is random genetic drift (Rochambeau et al. 2000). Similarly, several studies (e.g., Fernandez et al. 2005; Toro et al. 2006) suggested that genetic diversity within breeds is mainly lost by genetic drift, which leads to an increase in homozygosity and fixation of alleles. In this study, the proportion of genetic diversity lost due to random genetic drift was higher than that of unequal contribution of founders. However, the effect of unequal founder contribution was also substantial, which implies selection of breeding animals has impacted the diversity in the populations. Therefore, as a practical implication of the results, breeding strategies should be designed for each breed in such a way that  $N_e$  could be increased or the rate of inbreeding could be minimized. In addition, introduction of new genetic material or occasional immigrants into a managed population could be helpful to counter the effects of drift (Lacy 1987) and improve the level of genetic diversity. Practical approaches such as optimum contribution selection (e.g., Jean-Jacques et al. 2004; Hinrichs et al. 2006), minimizing inbreeding and maximizing diversity (e.g., Haile-Mariam et al. 2007) and balancing genetic merit and genetic diversity (e.g., Piyasatian and Kinghorn 2005) need to be considered in the management of the existing genetic diversity in the four Canadian swine populations.

## CONCLUSIONS

The four swine breeds analyzed were found to have lost considerable genetic diversity over the past three decades. Random genetic drift played a major role in the loss of genetic diversity in all the breeds, particularly in LC and DC. The role of random genetic drift in HP might have been underestimated due to lower pedigree completeness in this breed. Unequal contribution of founders showed a relatively higher impact on the loss of genetic diversity in LR and HP compared with DC and LC. The effective population sizes of HP and LC have become smaller than the recommended size required to prevent inbreeding depression. Therefore, the results demonstrate a pressing need for developing appropriate breeding strategies (e.g., application of optimum contribution selection) for each swine population, particularly for LC and DC. However, HP showed such a lower  $N_e$  that the introduction of genetically unrelated individuals of the same breed would be highly advisable to recover the genetic diversity in this population.

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