Swedish University of Agricultural Sciences
Faculty of Veterinary Medicine and Animal Science

Characterization of the global Brown Swiss cattle population structure

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Examensarbete / Swedish University of Agricultural Sciences,
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Contents

Abstract

The global Brown Swiss population was studied to estimate population genetic parameters, measure genetic variation and identify most influential animals. The population was found to have 3.30 mean equivalent complete generations. The mean inbreeding coefficient was 0.77% for the pedigree population. There was, in most cases, periodic and generational increase of mean inbreeding coefficient. Results showed that there was 0.40% increase in inbreeding by equivalent complete generations. Increase in average generation per period was also noted from the study. The pedigree population had 1.1% mean average relatedness. Effective population size for the equivalent complete generations was a mere 125.97, which could be considered as a small size considering the number of individuals in the population under study. There was big variation between average generation intervals for the four parental pathways. The highest average generation interval was seen in the sire-son path way, having a value of 8.73. The average generation interval for the whole population, which was 6.53, was also high. The pedigree population had 0.55% mean coancestry between its individuals. The French Brown Swiss subpopulation had the highest mean coancestry among its individuals. The French and the Austrian subpopulations had the highest mean coancestry between their subpopulations. The Italian subpopulation had the highest equivalent complete generation. The lowest genetic distance was recorded between the Italian and the US subpopulation, implying they had the highest genetic similarity. Most of the genetically influential individuals were sires. The highest contributing founder was a sire with 3.22% contribution. The highest contributing dam had 1.75% contribution. The effective number of founders and effective number of ancestors were 141 and 88, respectively.

1. INTRODUCTION

Pedigree information plays essential role in genetic analysis and is used in the evaluation of genetic variation in cattle populations. Analysis of well recorded pedigree enables description of genetic variability and evolution through generations (Gutierrez et al., 2003).

Inbreeding trend, effective number of founders, effective number of ancestors and effective population size are some measures of genetic variation evaluated based on pedigree information (Boichard et al., 1997). In this study the aforementioned measures of genetic variation have been calculated.

Pedigree analysis can be carried out using computer programs like ENDOG. ENDOG is a population genetics computer program that performs genetic analysis based on pedigree information. It can be used to compute functions like individual inbreeding (F), increase in inbreeding (ΔF), effective population size (N_e), effective number of founders (f_e), effective number of ancestors (f_a) ,average relatedness (AR) and other functions (Gutierrez and Goyache, 2005).

This study is focused on the pedigree analysis of Brown Swiss cattle populations from 22 countries from around the world. These populations have been joined to form a common reference population for a global genomic evaluation of dairy characters in this breed. The computer program was used to make the genetic and demographic analysis for this study.

In characterizing the global Brown Swiss population, this study attempts to perform genetic analysis on the pedigree information available and calculate functions like effective number of founders, effective number of ancestors, effective population size, individual inbreeding coefficient, average relatedness, F-statistics and other genetic functions.

The aims of this study are:

1) to estimate population genetic parameters,
2) to identify the most genetically important individuals for genotyping and
3) to evaluate genetic variation in Brown Swiss populations.

2. LITERATURE REVIEW

2.1. Brown Swiss

The world's Brown Swiss cattle population is about 7 million. It is ranked in the top two of world's dairy cattle population. It is one of the oldest cattle breeds originating from the valleys and mountain slopes of Switzerland and is now mainly found in Europe and America (Brown Swiss association, 2006).

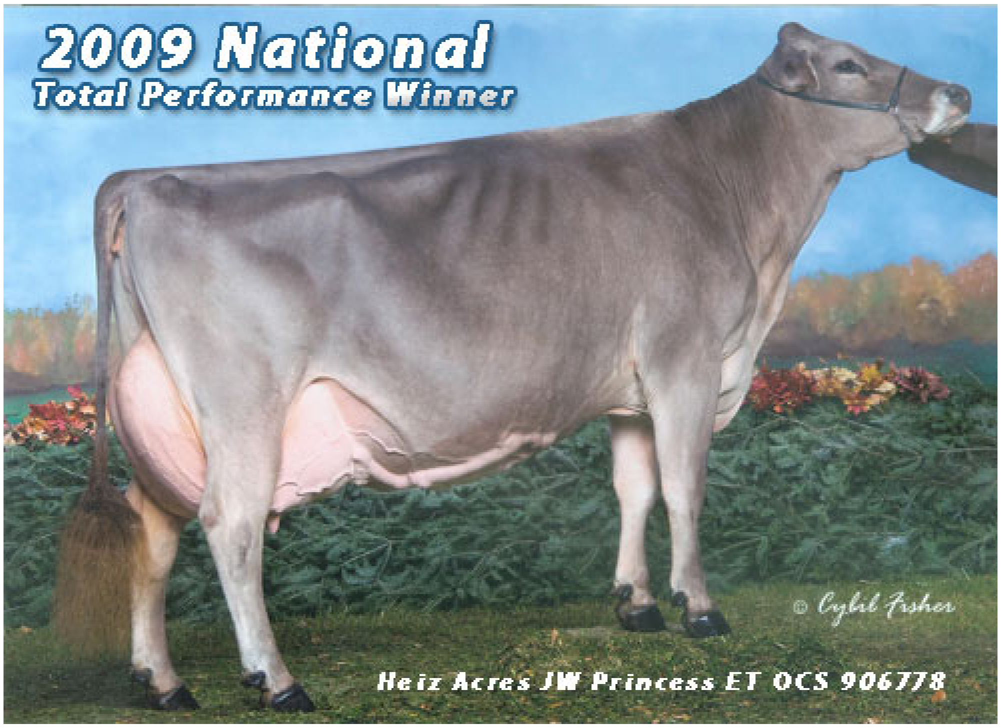


Figure 1. Brown Swiss. Photo courtesy of http://www.brownswissusa.com/history.asp

Brown Swiss are famous for production of good milk, butter fat and protein. They also have the one of the lowest counts of cell counts averages compared with other dairy breeds (Brown Swiss association, 2006).

2.2. Pedigree Analysis

Analysis of the probabilities of gene origin can be used to evaluate the genetic variability of a population (Boichard et al., 1997). The proportion of alleles in a pedigreed population derived from any ancestor is estimated after pedigrees of all individuals are traced and the proportion genetic contribution of each ancestor for each individual is calculated as fraction of pedigree lines tracing back to each specific ancestor (James, 1972).

Analyzing the probabilities of gene origin also determines effective number of founders (founder equivalents) and effective number of ancestors. Founders are defined as individuals whose only known genetic relationship is to their descendants (Boichard et al., 1997). In other words, founders are ancestors with no available parentage information. Effective number of founders or founder equivalents refers to number of founders that would give rise to a population having the same genetic diversity as the current population under study if all founders where to contribute equally (Lacy, 1989). This measurement does not account for genetic drift and bottlenecks. In real life situations, unequal founder contribution leads to lower effective number of founders than number of founders (Lacy 1989). Effective number of ancestors can be defined as the minimum number of equally contributing ancestors (not necessarily founders) that would produce the genetic diversity of the current population (Boichard et al., 1997). This measurement accounts for genetic bottleneck and effective number of ancestors is mostly smaller than effective number of founders.

Good pedigree information enables calculation of maximum number of generations traced, number of complete traced generations and equivalent complete generations. The number of generations between an individual and its furthermost traced ancestor is defined as maximum generation (Gutierrez and Goyache, 2005). Complete generation refers to number of generations (full generations) traced back from an individual with all ancestors known (Gutierrez and Goyache, 2005). Equivalent complete ancestors can be calculated as the sum of $(1/2)^n$ where n refers to number generations going back to the known ancestor of each individual (Gutierrez and Goyache, 2005; Maignel et al., 1996).

Inbreeding level, average relatedness and coancestry of individuals tell us about the level of genetic relationship among individuals in a population and can be calculated based on pedigree information (Frankham et al., 2002; Dunner et al., 1998) Inbreeding is a consequence of mating of relatives and inheritance of alleles that are identical by descent (Mc Parland et al., 2006). Inbreeding can be expressed using inbreeding coefficient (F). Inbreeding coefficient of an individual is defined as the probability that two alleles of a gene are identical by descent (Wright, 1931). Meanwhile, average inbreeding coefficient of a certain population can be used to measure autozygosity of a population. Average relatedness coefficient of an individual is the probability that a randomly picked allele from the entire population is identical by descent to an allele carried by a given individual (Gutierrez and Goyache, 2005). Coancestry between two individuals is equal to inbreeding coefficients of their offspring if the individuals were mated (Falconer and Mackay, 1996).

Calculation of effective population size is important in characterizing a population. Effective population size describes the level of inbreeding, fitness and random genetic drift which leads to loss of genetic variation (Gutierrez et al., 2008). The definition of effective population size is the number of individuals that would result in the actual increase in inbreeding given that they contributed equally to the next generation (Gutierrez and Goyache, 2005). Different ways of computing the effective population size address one or more of real life situations like overlapping generations, fluctuating population size and unequal number of mating male and female individuals (Harris and Allendorf, 1989).

Rate of genetic change in a population is also affected by generation interval. Generation interval specifies the age of the parents when offspring are born. Low generation interval results in maximum rate of genetic change (Marquez and Garrick, 2007).

Genetic diversity distribution among subpopulations can by calculated by Wright's (1969) F-statistics parameters (F_{IS} , F_{ST} and F_{IT}). F_{IS} is the average inbreeding coefficient for individuals of all subpopulations (Frankham et al., 2002). F_{ST} measures the loss of heterozygosity in a subpopulation as a result of random drift and F_{IT} refers to loss of heterozygosity as a result of non-random mating and population division in relation to the overall population (Wright, 1969). The equation

$$(1 - F_{IT}) = (1 - F_{IS})(1 - F_{ST})$$

relates the F-statistics parameters (Falconer and Mackey, 1996).

3. MATERIAL AND METHODS

3.1. Data

In this study, pedigree information of 181,094 Brown Swiss cattle was used. 71,497 were male and 109,597 were female. The pedigree data was gathered from more than 20 countries and sent to Interbull Center in Uppsala, Sweden. The contributing countries were mainly from Europe and North America.

The pedigree information included Animal ID, Sire ID, Dam ID, Sex and Birthdates. The individuals in the pedigree were born between the years 1906 and 2009. 36,895 individuals were missing birthdates so birthdates were constructed by looking at the birthdates of their parents and offspring. A crude method was used to construct birthdates and it resulted in replacement of reported birthdates by constructed birthdates for few hundred individuals.

Some of the individuals had offspring in different countries possibly because of semen export between countries.

While the data has been gathered from 22 countries, the table below (Table1) shows only 7 countries as the contribution of the other countries is considerably low. The three most contributing countries were Germany (103,476), Switzerland (29,476) and Austria (28,997).

Table1. List of contributing countries and number of individuals from each country

Country	Number of Individuals
Austria	28,997
France	746
Italy	8,064
Germany	103,464
Slovenia	863
Switzerland	29,476
USA	9,033
Others	451
Total	181,094

Individuals from the seven major countries where treated as subpopulations and functions like coancestry, F-statistics and genetic distances were calculated in this study.

3.2. Pedigree Content

3.2.1 Maximum, Complete and Equivalent Generations

Available pedigree information was used to calculate maximum, complete and equivalent generations.

-Maximum generation was calculated counting the number of generations between an individual and its farthest available ancestor in the pedigree.

-Complete generation, meanwhile, was calculated by counting generations that can be traced back from an individual with all ancestors known.

- Equivalent complete generation is the sum over all known ancestors and was calculated by summing $(1/2)^n$ where n refers number of generations between an individual and each known ancestor (Gutierrez and Goyache 2005; Maignel et al., 1996).

Once the individual values were calculated, the mean maximum generations, mean complete generations and mean equivalent generations were calculated.

3.2.2 Pedigree Completeness

Pedigree information of good quality is important for calculating inbreeding trend in a population. Inbreeding can be looked at as a function of index of pedigree completeness to learn how the extent of increase in inbreeding through time depends on completeness of pedigree (MacCluer et al., 1983). Index of pedigree completeness expresses how complete the pedigree of a whole population is based on the proportion of known ancestors of each individual in the pedigree. The index of pedigree completeness was calculated based on the formula proposed by MacCluer et al. (1983)

$$PEC_{animal} = 2C_{sire}C_{dam} / C_{sire} + C_{dam},$$

where C_{sire} is contribution from paternal line and C_{dam} is contribution from maternal line (Sorensen et al.,2005). Contribution was calculated by

$$C = 1/d \sum_{i=1}^{d} g_i ,$$

where g_i represents the proportion of known ancestors in generation *i* and *d* stands for the depth of pedigree (number of generations).

In this study, mean pedigree completeness indices for the 23 maximum generations and the values are given in the result section.

3.2.3 Ancestral Contribution

The contribution of each ancestor to the fifth parental generation (sires and dams being the first parental generation) in a pedigree were calculated. The calculations made gave separated trees that show the male and female paths of each contributing ancestor in the pedigree. In this calculation the program calculated the genetic contribution made by the first paternal generation and maternal generation. The calculation continued for the subsequent parental generations and the tree kept on dividing to the male and female ancestral paths until the fifth parental generation.

3.3. Offspring Analysis

Offspring analysis calculated number of sires, number of dams, average number of offspring of sires, average number of offspring of dams and effective population size for year or period year of birth of reproductive individuals. The computer program used rounded the average generation interval to fit it to period of birth.

-For each period of birth, the number of sires and number of dams are counted.

-Average number of offspring of sires per birth period was calculated by dividing the number of offspring of the sires by the number of sires for each period of birth.

-Calculation of average of offspring of dams per birth period was made by dividing number offspring of the dams by the number of dams in each period of birth.

-To ascertain any possible bottlenecks in the pedigree population N_e was estimated for each birth period (and also for each year). N_e was estimated according to family size variance per period of time (Gutierrez, 2009).

3.4. Inbreeding and Average Relatedness

- Inbreeding coefficient of an individual (F) is the probability that two alleles from the same gene are inherited from a common ancestor, i.e., they are identical by descent (Wright, 1931). It is calculated by using Meuwissen and Luo (1992) algorithm.

- Mean inbreeding coefficient was calculated for each maximum generation, complete generation, certain periodic years and for the entire pedigree population in this study.
- Rate of inbreeding (ΔF) is the relative increase in inbreeding coefficient of individuals per generation. As proposed by Wright (1931), it was calculated as:

$$\Delta F = (F_t - F_{t-1}) / (1 - F_{t-1}),$$

where F_t is mean inbreeding coefficient at generation t and F_{t-1} is mean inbreeding coefficient at generation t-1.

- According to Dunner et al. (1998), average relatedness (AR) can be defined as the probability that an allele chosen randomly from a pedigree population belongs to a certain individual. Average relatedness coefficients could be calculated by:

$$c' = (1/n)1'A ,$$

where c' is a row vector and c_i is described as the average of AR coefficients in the row for individual i. A is a numerator relationship matrix and n is its dimension.

3.5. Effective Population Size

Effective population size (N_e) refers to the size of an ideal population that would have the same rate of inbreeding per generation as the real population (Sölkner et al., 1998). N_e was calculated as:

$$N_e = 1/ 2\Delta F,$$

where ΔF is the rate of inbreeding.

As described by Gutierrez and Goyache (2005), ENDOG gave three more N_e values by using the coefficient of regression (b) of individual inbreeding coefficients. b was calculated as the regression coefficient of the increase in inbreeding from generation to generation. The mathematical formula was given as:

$$b = F_t - F_{t-1} \quad .$$

Meanwhile, 1- F_t is assumed to be equal to 1.

N_e for maximum number of generations, complete number of generations and equivalent number of generations was calculated by:

$$N_e = 1/ 2b.$$

3.6. Generation Interval

Gutierrez et al., (2003) defined generation interval (L) as the average age of parents when their offspring, upon becoming parents themselves, are born. The average generation intervals for the whole population and for each of the four ancestral paths (Sire_son, Sire_daughther, Dam_son and Dam-daughter) were calculated.

Average age of parents at the birth of their offspring (which may or may not become parents themselves) was also calculated. This calculation was also made for the whole population and for the four ancestral paths.

3.7. Coancestry

Coancestry or kinship of two individuals is defined as the probability that two randomly taken alleles, one from each individual, are identical by descent (Frankham et al., 2002). In this study, mean of coancestry between individuals was calculated within subpopulations and for the entire metapopulation as calculated by Caballero and Toro (2002).

Mean coancestry within subpopulations was calculated by:

$$\tilde{f} = \sum_{i=1}^{n} f_{ii} N_i / N_T \ ,$$

where f_{ii} is average coancestry of subpopulation i, N_i is the number of individuals in subpopulation i, and N_T is the number of individuals in the total population.

Mean coancestry over the entire metapopulation was calculated by:

$$\bar{f} = \sum_{i,j=1}^{n} f_{ij} N_i N_j / N_T^2 \ ,$$

where f_{ij} is average coancestry over subpopulations i and j, N_i is the number of individuals in subpopulation i, Nj is the number of individuals in subpopulation j and N_T is the number of individuals in the total population.

Self coancestry of an individual is defined as the inbreeding coefficient of offspring which is produced by self-mating of an individual (Falconer and Mackay, 1996). According to Caballero and Toro (2002), mean self coancestry ($\tilde{S}$) for the entire population was calculated as:

$$\tilde{s} = \sum_{i=1}^{n} s_i N_i / N_T \ ,$$

where s_i is average self coancestry in subpopulation i, N_i is the number of individuals in subpopulation i, and N_T is the number of individuals in the total population.

3.8. Distance between Subpopulations

Caballero and Toro (2000, 2002) calculated average distance between individuals of two subpopulations i and j (D_{ij}) as:

$$D_{ij} = [(s_i + s_j)/2] - f_{ij},$$

where s_i is the average self coancestry of individuals in subpopulation i, s_j is the average self coancestry of individuals in subpopulation j and f_{ij} is the average coancestry in subpopulations i and j.

The most common way to measure genetic differentiation among populations is to use Nei's genetic distance. Nei's minimum distance (Nei,1987) between subpopulations i and j was calculated by:

$$D_{ij} = [(f_{ii} + f_{jj})/2] - f_{ij},$$

where f_{ii} is the average coancestry in subpopulation i, f_{jj} is the average coancestry in subpopulation j and f_{ij} is the average coancestry subpopulations i and j (Caballero and Toro, 2002).

The mean Nei's minimum distance ($\bar{D}$) over entire metapopulation was calculated as:

$$\bar{D} = \sum_{i,j=1}^{n} D_{ij} N_i N_j / N_T^2,$$

where D_{ij} is genetic distance between subpopulations i and j, N_i is the number of individuals in subpopulation i, and N_T is the number of individuals in the total population (Caballero and Toro, 2002).

3.9. F-statistics

Inbreeding coefficients were used by Sewall Wright to measure genetic diversity within and between fragments of population. Wright's (1969) F-statistics calculated F_{IS}, F_{ST} and F_{IT} .

- F_{IS} is the average inbreeding coefficient of individuals across their subpopulation and was calculated by :

$$F_{IS} = \tilde{F} - \tilde{f} / 1 - \tilde{f},$$

where $\tilde{f}$ is mean coancestry within subpopulations and $\tilde{F}$ mean inbreeding coefficient of subpopulations (Caballero and Toro, 2002).

- F_{ST}, also called fixation index, measures the effect population subdivision on inbreeding. It was calculated by:

$$F_{ST} = \tilde{f} - \bar{f} / 1 - \bar{f} \text{ ,}$$

where $\tilde{f}$ mean coancestry within subpopulations and $\bar{f}$ is mean coancestry over the entire metapopulation (Caballero and Toro, 2002).

- F_{IT} measures reduction in heterozygosity due to non-random mating and population sub-division. F_{IT} was calculated by:

$$F_{IT} = \tilde{F} - \bar{f} / 1 - \bar{f} \text{ ,}$$

where $\tilde{F}$ mean inbreeding coefficient of subpopulations and $\bar{f}$ is mean coancestry over the entire metapopulation (Caballero and Toro, 2002).

3.10. Effective Number of Founders and Ancestors

It is possible to analyze the probabilities of gene origin in a pedigree (Dickson and Lush 1933; James, 1972; Vu Tien Khang, 1983). The idea behind this approach is to calculate the genetic contributions of founders to the current population.

According to Lacy (1989), the effective number of founders (f_e) is the number of equally contributing founders that would give rise to the same genetic diversity as in the reference population under study. It was calculated as:

$$f_e = 1 / \sum_{k=1}^{f} q_k^2 \text{ , where } q_k \text{ is the expected contribution of founder k.}$$

The effective number of ancestors (f_a) is defined as the minimum number of ancestors (founders or not) that explain the complete genetic diversity in a reference population (Sölkner et al., 1998). It was calculated by:

$$f_a = 1 / \sum_{k=1}^{f} p_k^2 \text{ .}$$

p_k is the marginal contribution of an ancestor, which is the contribution yet to be explained by other ancestors (Boichard et al., 1997).

AR of a founder individual designates the percentage in which the founder can be regarded as the origin of the reference population (Gutierrez and Goyache, 2005). So founder contribution of a founder individual was calculated as its AR.

4. RESULTS AND DISCUSSION

4.1. Pedigree Content

4.1.1 Maximum, Complete and Equivalent Generations

The number of maximum generations of the pedigree analyzed in this study was calculated to be 23 plus a base population (considered as generation 0).The distribution of the number of individuals in these maximum generations was not uniform, as shown in Figure 2.Though not indicated in Figure 2, generation 0 had 27,894 individuals which could be considered as base population for the 23 generations.

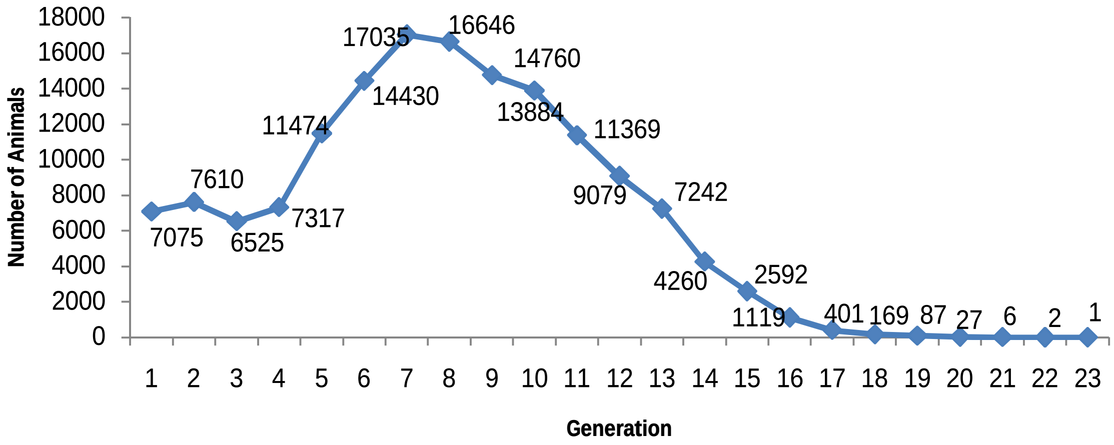


Figure 2.Number of individuals per maximum generation.

The number of complete generations was 8, considering generation 0 as a base population. The base population had 42929 individuals and the 8 complete generations consisted of 138,165 individuals. Figure 3 shows the distribution of the number of individuals through the 8 complete generations.

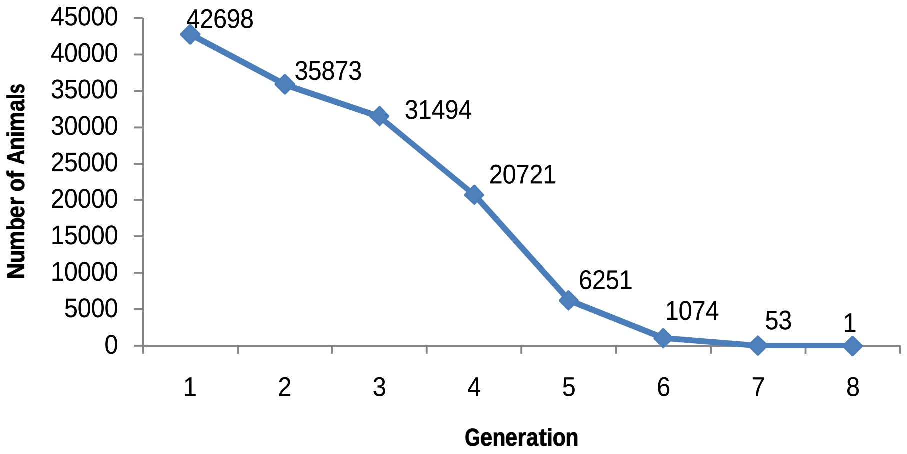


Figure 3.Number of individuals per complete generation.

The mean values of maximum, complete and equivalent generations were relatively lower and showed that the average number of generations in the pedigree were few. The mean of maximum generations was 6.60. Mean complete generations was calculated to be 1.82. Mean equivalent complete generation was 3.30

4.1.2. Pedigree Completeness

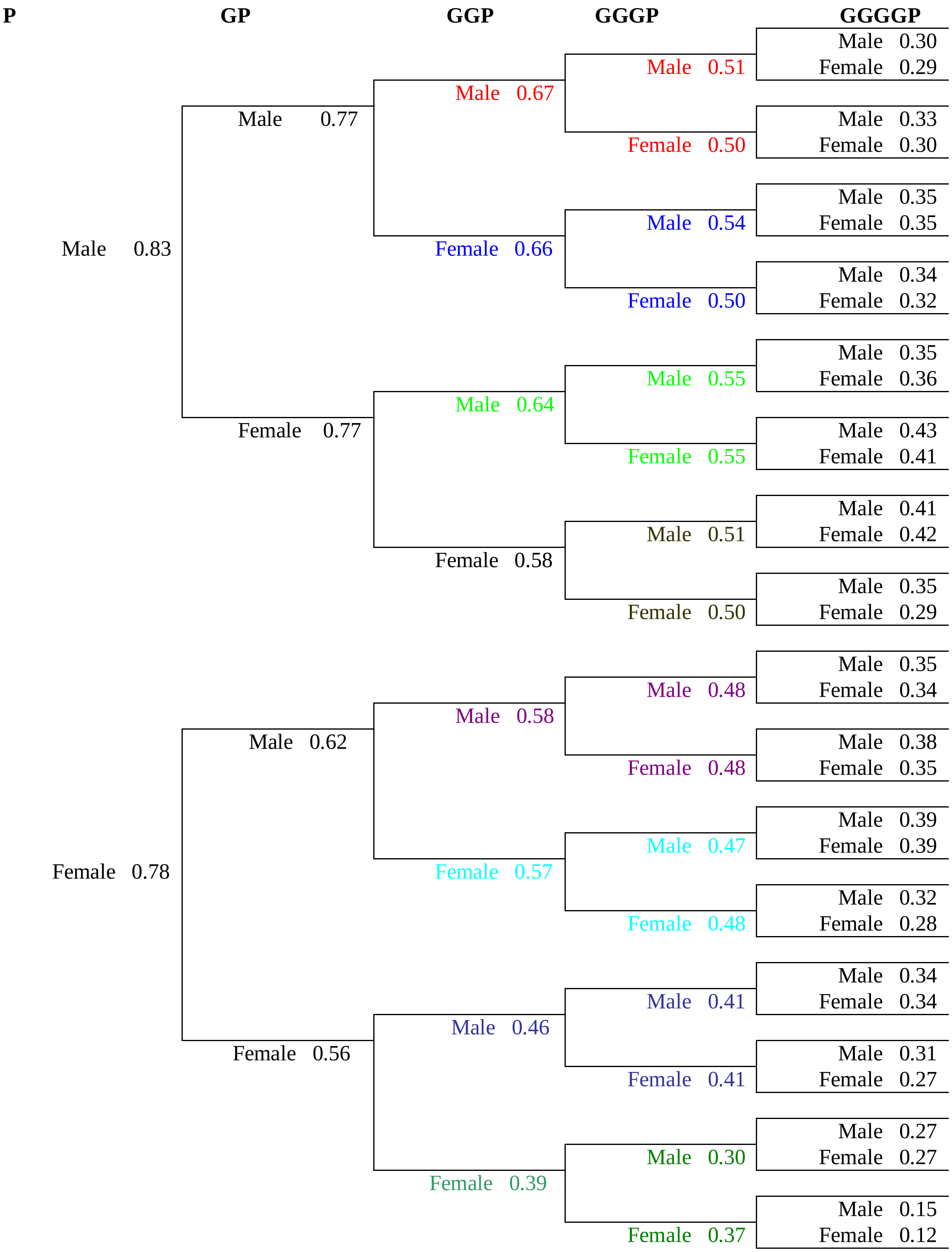
The index of pedigree completeness was calculated for the whole data set. The first generation (parents' generation) showed the highest index while generation 23 (the highest number of generations traced back) showed the lowest index. As it can be seen from Table 2, the index of pedigree completeness decreased with increasing maximum generation.

Table 2.Index of Pedigree completeness for maximum generations

Generation	Completeness
1	0.80
2	0.68
3	0.57
4	0.46
5	0.34
6	0.22
7	0.13
8	0.06
9	0.03
10	0.01
11	3.21E-03
12	9.21E-04
13	2.34E-04
14	5.5E-05
15	1.21E-05
16	2.4E-06
17	4.15E-07
18	6.18E-08
19	9.1E-09
20	1.19E-09
21	1.11E-10
22	1.32E-11
23	1.32E-12

4.1.3. Ancestral Contribution

The frequency of contribution of each ancestor in the pedigree to the 5th parental generation is given in Figure 4. The frequency of ancestral contribution can be used as an indication of pedigree completeness. As Figure 4 shows, the paternal side of the pedigree is more complete than the maternal side.



GP stands for grandparents
GGP stands for great grandparents
GGGP stands for great great grandparents
GGGGP stands for great great great grandparents

Figure 4.Contribution of ancestors in a five-generation pedigree.

4.2 Offspring Analysis

The result from offspring analysis of the pedigree showed that the average number of offspring per sire declined dramatically since the 1940s. Meanwhile, the average number of offspring per dam was always less than 2 indicating that very few dams gave birth to more than one calf during their reproductive years.

Table 3 shows the number of dams and sires born per 7 year period and the average number of offspring per sire and dam in every 7 year period.

Table 3.Table showing number of parents and offspring per 7 year period

Period	Sires	Average Off. Males	Dams	Average Off. Females	Ne
*1906- 1912	4	4.00	4	1.50	2.17
1913- 1919	14	11.29	20	1.95	1.26
1920- 1926	28	13.43	35	1.46	0.88
1927- 1933	22	26.50	25	1.72	0.07
1934- 1940	109	28.17	122	1.18	0.09
1941- 1947	525	2.94	572	1.13	17.43
1948- 1954	1505	2.04	2574	1.12	1500.95
1955- 1961	3373	3.34	6182	1.18	488.83
1962- 1968	4917	5.04	13902	1.18	270.92
1969- 1975	3692	5.57	19623	1.16	490.51
1976- 1982	2725	7.13	17806	1.15	301.28
1983- 1989	2141	5.41	12251	1.15	334.05
1990- 1996	1526	3.53	6273	1.17	863.91
1997- 2003	315	1.38	781	1.12	1306.96

* The limited number of individuals in this period could be because of constructed birthdates.

Effective population size calculated based on family size variance reached highest size for the period between the year 1948 and 1954, though the number of parents during this period was not the highest.

4.3. Inbreeding

The mean inbreeding coefficient calculated for the whole pedigree population was 0.77%. Mean inbreeding coefficient per five years period, calculated from 1950 till 2004, showed increase for every period, as shown in Figure 5.

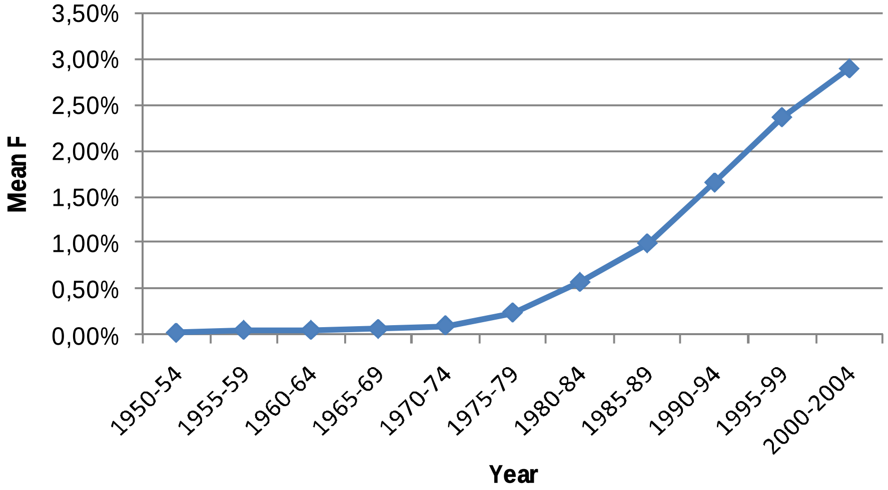


Figure 5.Mean inbreeding coefficient per 5 years period.

The mean inbreeding coefficient per maximum generation presented in Figure 6 is only for the first 16 maximum generations traced back because the number of individuals from generation 17 on dropped drastically (well below 500, as shown in Figure 2) compared with the other maximum generations. The mean inbreeding coefficient showed increase from 0.00% in generation 1 to 3.38% in generation 16.

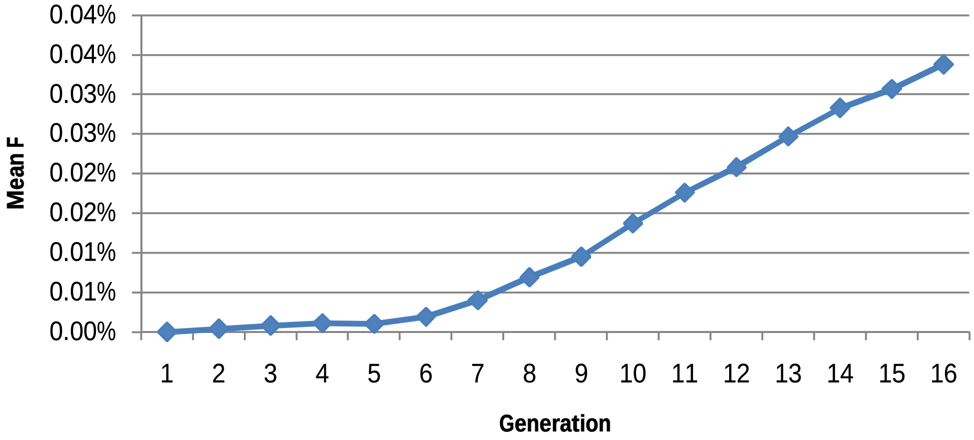


Figure 6.Mean inbreeding coefficient per maximum generation.

Mean inbreeding coefficient increased continuously as the number of complete generations traced backed increased. Figure 7 did not include generation 7 and 8 because of very low number of individuals in these generations (see Figure 3).

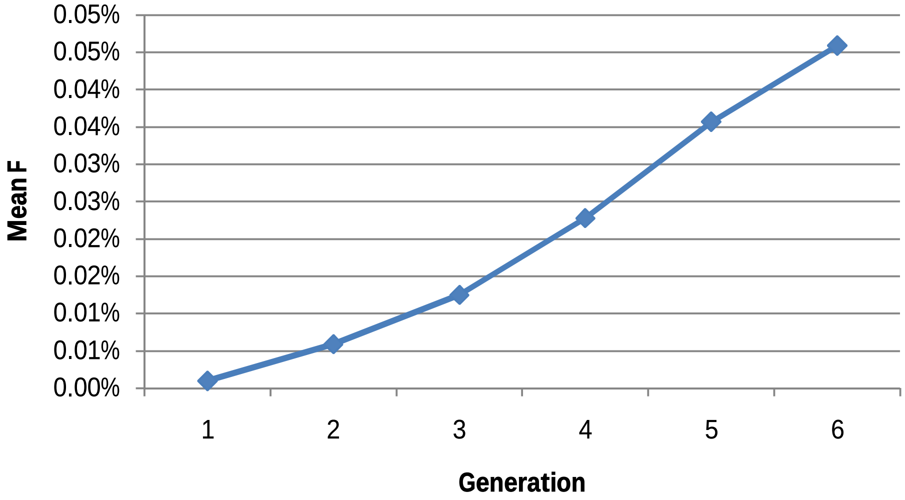


Figure 7.Mean inbreeding coefficient per complete generation.

Increase in inbreeding by complete generation was higher than increase by maximum generation and by equivalent generation. Inbreeding showed increase of 0.61% by complete generation. Increase in inbreeding by maximum generation was the least with a value of 0.18%. Results also showed 0.40% increase in inbreeding by equivalent complete generation.

4.4. Average Relatedness

The mean average relatedness calculated in the total pedigree population was 1.10%.

The periodic (period of 5 years) mean average relatedness calculated showed increase for every period until it decreased in individuals born between 1985 and 1989, but there was again increase for individuals born since 1990 (see Figure 8).

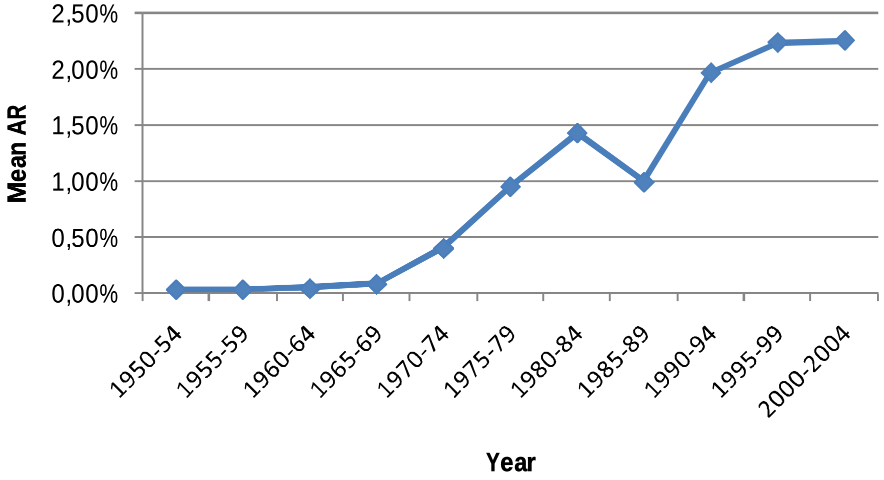


Figure 8.Mean average relatedness per five years period.

The mean average relatedness between the 4th and 12th maximum generation increased promptly before levelling off in the next generations (see Figure 9). Just as the case with mean inbreeding coefficient, the study only considered the first 16 maximum generations to calculate mean average relatedness per generation.

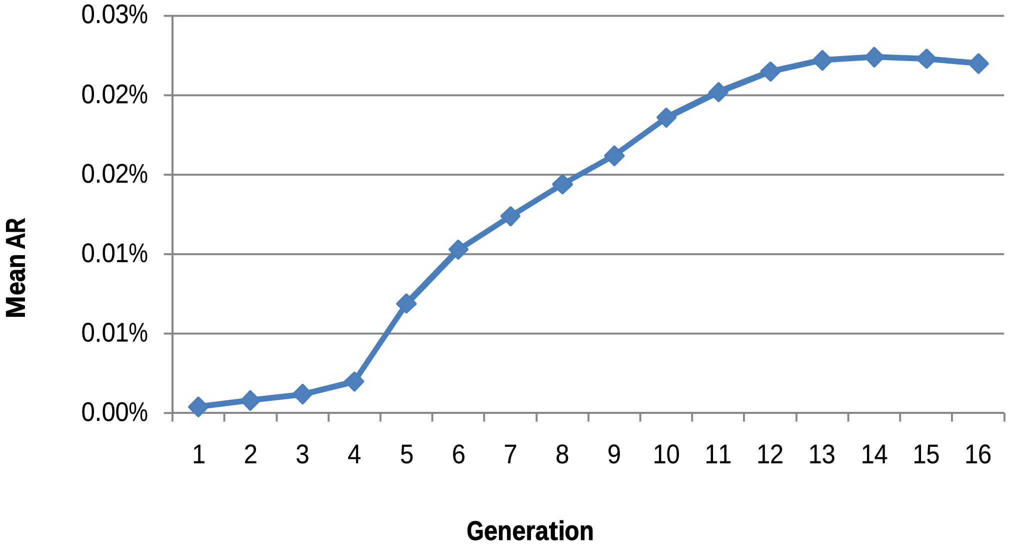


Figure 9.Mean Average relatedness per maximum generation.

Figure 10 shows that mean average relatedness increased through the first 5 complete generations traced back before it decreased from 2.41% in generation 5 to 2.14% in generation 6.

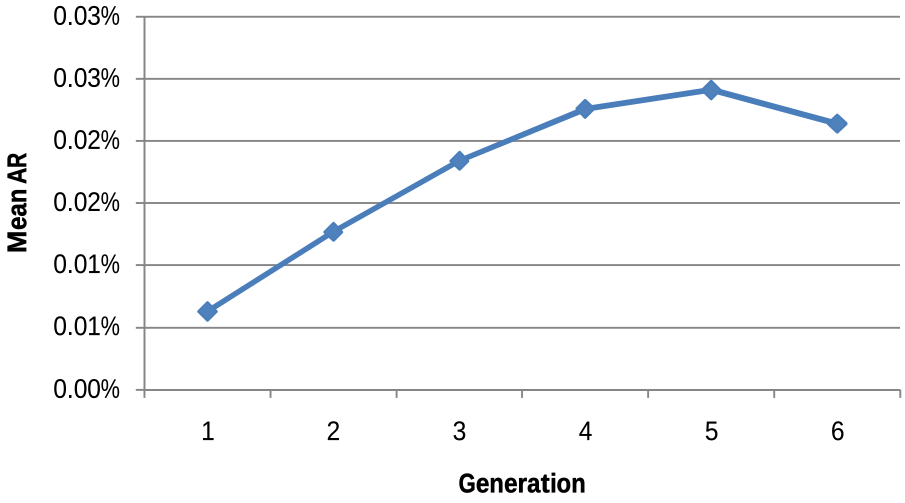


Figure 10.Mean average relatedness per complete generation.

4.5. Effective Population Size

The effective population size of the whole pedigree population calculated for mean maximum generations was 273.02. This number could be considered as the maximum estimate for effective population size.

The effective population size changed for every maximum generation dropping to as low as 124.2 in generation 13. Figure 11 below shows portion of the whole trend.

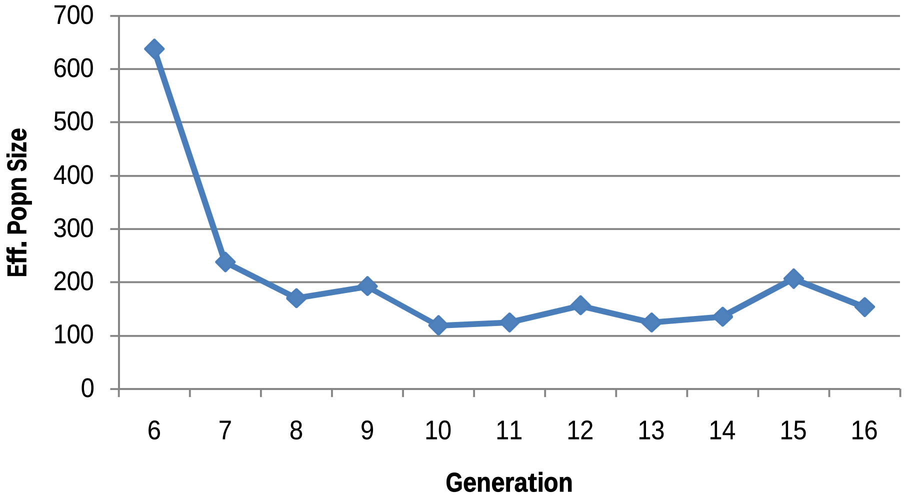


Figure 11.Effective population size per maximum generation.

The effective population size for mean complete generations, which shows the minimum estimate for effective population size for the whole population, was calculated to be 82.16. Meanwhile, every complete generation had different effective population as shown in Figure 12.

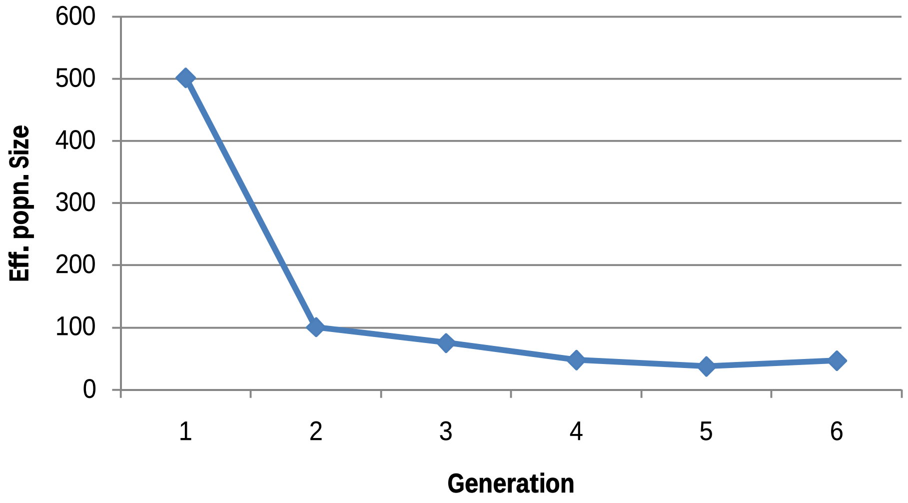


Figure 12.Effective population size per complete generation.

The effective population size per year increased from 63 (in year 1995) to 203 (in year 2004). The change in the effective population size per year can be seen in Figure 13.

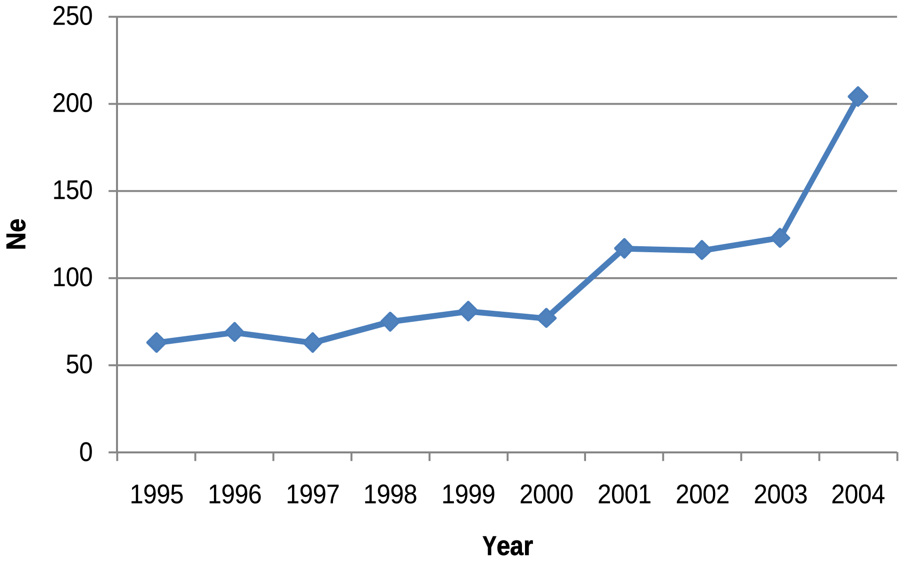


Figure 13.Effective population size per year.

For mean equivalent complete generations, the effective population size was 125.97. Thus, the best estimate of ideal population showing the same level of inbreeding as the actual pedigree population was 125.97.

4.6. Generation Interval

Generation interval calculated for the four ancestral paths is shown in Table 4. The generation interval was calculated as the age of parents when their offspring, which become parents themselves, were born. On average, dams gave birth to their offspring at a younger age than sires.

Table 4.Average generation Interval for the four ancestral pathways

	Generation	Interval	
Type of Path	Number of Individuals	INTERVAL	STDEV
Sire-Son	18784	8.73	9.73
Sire-Dau	83503	7.81	8.13
Dam-Son	18689	5.26	3.04
Dam-Dau	74499	4.93	2.36
Total	195475	6.56	6.53

Table 5 shows the average age of parents when the offspring, which may or may not become parents themselves, were born. In this case, the average age of parents when their offspring were born was slightly higher than average generation interval.

Table 5.Average age of parents at the birth of offspring for the four ancestral pathways

	Mean Age	of Parents	
Type of Path	Number of Individuals	INTERVAL	STDEV
Sire-Son	66304	9.15	8.81
Sire-Dau	83763	7.82	8.15
Dam-Son	66521	5.70	2.65
Dam-Dau	74687	4.94	2.37
Total	291275	6.90	6.52

4.7. Coancestry

Mean values of coancestry within subpopulations and the entire metapopulation are shown Table 6. Self coancestry for the entire population is also shown in the same table.

Table 6.Population Average of coancestry

Population Average of	**Values**
Mean Coancestry of Subpopulations ($\tilde{f}$)	0.006767
Self coancestry for the entire population ($\tilde{s}$)	0.503842
Mean Coancestry over the Metapopulation ($\bar{f}$)	0.005470

Table 7 shows mean coancestry calculated in each subpopulation and within paired subpopulations. The highest mean coancestry in a single subpopulation was calculated within in the French subpopulation. The highest coancestry between subpopulations was calculated between Austrian and French subpopulations.

The diagonal values on table 7 are mean coancestry values for each subpopulation while the other values indicate mean coancestry within paired subpopulations.

Table 7.Mean coancestry within and between subpopulations (values multiplied by 100)

fij	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	0.85						
2	0.43	0.35					
3	0.58	0.30	0.72				
4	0.76	0.40	0.59	1.23			
5	0.61	0.33	0.48	0.68	0.58		
6	0.63	0.35	0.46	0.69	0.52	0.63	
7	0.49	0.27	0.42	0.50	0.40	0.40	0.61

1= Austria 2 = Switzerland 3 = Germany 4 = France 5 = Italy
6 =USA 7 = Slovenia

4.8. Equivalent Complete Generations for Subpopulations

Of the seven major subpopulations in this study, Italy had the highest mean equivalent generations. The American subpopulation, meanwhile, had the lowest mean equivalent generations.

Table 8.Mean equivalent complete generations in each subpopulation

Subpopulations	**Mean Equivalent Complete Generations**
Austria	3.30
Switzerland	3.18
Germany	3.37
France	3.17
Italy	3.48
Slovenia	2.86
USA	2.73

4.9. Distance between subpopulations

The diagonal elements of Table 9 show average distance between individuals of the same subpopulation. Table 9 also shows average distance between individuals of paired subpopulations.

Table 9.Average distance between individuals of subpopulations

Distance	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	0.4961						
2	0.4996	0.4996					
3	0.4983	0.5004	0.4964				
4	0.4971	0.4999	0.4984	0.4926			
5	0.4986	0.5005	0.4993	0.4980	0.4988		
6	0.4988	0.5009	0.5001	0.4983	0.4999	0.4995	
7	0.4983	0.4998	0.4986	0.4984	0.4992	0.4997	0.4958

1= Austria 2 = Switzerland 3 = Germany 4 = France 5 = Italy
6 =USA 7 = Slovenia

The Nei genetic distance calculated across the whole pedigree population was 0.0013.
Nei’s genetic distance is given between paired populations in Table 10.

Table 10.Nei distance (values were multiplied by 100)

Nei	1	2	3	4	5	6	7
1	0						
2	0.17	0					
3	0.21	0.24	0				
4	0.28	0.38	0.39	0			
5	0.11	0.14	0.17	0.23	0		
6	0.10	0.14	0.21	0.23	0.08	0	
7	0.24	0.21	0.25	0.42	0.20	0.21	0

1= Austria 2 = Switzerland 3 = Germany 4 = France 5 = Italy
6 =USA 7 = Slovenia

4.10. F-statistics

The F-statistics parameters for the pedigree population are shown in Table 11.

Table 11.Wright's F parameters

Wright F Parameters	Values
F_{IS}	0.000922
F_{ST}	0.001304
F_{IT}	0.002225

Table 12 illustrates F_{STs} for paired subpopulations. In this case, the paired subpopulations of France and Slovenia had the highest value of F_{STs}.

Table 12.Paired Fsts (values were multiplied by 100)

F_{STs}	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1							
2	0.0858						
3	0.0709	0.0823					
4	0.0137	0.0186	0.0056				
5	0.0382	0.0458	0.0232	0.0354			
6	0.0377	0.0488	0.0317	0.0333	0.0406		
7	0.0153	0.0133	0.0047	0.2073	0.0383	0.0375	

1= Austria 2 = Switzerland 3 = Germany 4 = France 5 = Italy 6 =USA 7 = Slovenia

The American Brown Swiss cattle subpopulation had the highest reduction of heterozygosity due to non-random mating, as shown in table 13. The negative F_{IS} suggest the mean coancestry is greater than mean inbreeding for the subpopulation.

Table 1. F_{IS} *values for the major subpopulations (values were multiplied by 100)*

Subpopulation	F_{IS}
Austria	0.0770
Switzerland	0.2740
Germany	-0.0010
France	-0.2600
Italy	0.3350
USA	0.5250
Slovenia	-0.2400

4.11. Effective Number of Founders and Ancestors

The size base population, consisting of individuals with one or more unknown parents, was 42,929 individuals. As shown in Table 6, the effective number of founders was less than the effective number of ancestors.

Table 14.Measures of genetic variation

Genetic Variation Measures	**Value**
Total number of Individuals in the pedigree	181,094
Base Population	42,929
Reference Population	138,165
Number of Founders	41,011
Number of Ancestors	36,795
Effective Number of Founders	141
Effective Number of Ancestors	88
Effective Population Size of Founders	230.55
Number of Ancestors explaining 50% of Genetic Diversity	57

The twenty most contributing founders are shown in Table 7. The largest contributing founder was a sire with 3.22% genetic contribution. The top 20 founders contributed almost 23% of the genetic variation in the whole population.

Table 15.Genetic contribution of top 20 founders

Founder ID	%Contribution	Sex	Birth Date	Number of Offspring
50	3,22	SIRE	1922-10-29	88
7001	2,61	SIRE	1956-02-04	157
13	2,36	SIRE	1914-10-29	54
84	1,75	DAM	1926-10-29	6
49	1,72	SIRE	1922-10-29	98
117	1,58	DAM	1930-10-29	4
116	1,26	SIRE	1930-10-29	24
10726	1,06	SIRE	1959-02-22	57
3	0,98	SIRE	1910-10-29	3
5372	0,88	SIRE	1954-04-04	91
60	0,81	DAM	1922-10-29	2
9	0,77	SIRE	1914-10-29	7
48	0,64	SIRE	1922-10-29	30
82	0,62	SIRE	1926-10-29	27
8201	0,58	SIRE	1957-03-31	30
83	0,54	DAM	1926-10-29	1
1	0,49	SIRE	1906-10-29	1
2	0,49	DAM	1906-10-29	1
24	0,48	SIRE	1918-10-29	5
27	0.47	DAM	1918-10-29	1

5. GENERAL DISCUSSION

5.1. Pedigree Content

5.1.1. Maximum, Complete and Equivalent Generations

Maximum, complete and equivalent generations calculated tell us the deepness of the pedigree. The number of individuals in each maximum and complete generation shows the distribution of individuals across the different generations.

23 maximum generations were counted for the pedigree population of this study. This means the highest generation gap between a pedigree individual and its farthest ancestor recorded in this study was 23 generations. Only one individual had 23 generations between itself and its farthest ancestor, while the maximum generation for two individuals was 22. Compared with some other literature (Sölkner et al., 1998; D. Boichard et al., 1997) on different cattle breeds, 23 is a bigger number of maximum generations. For example, D. Boichard et al. (1997) found 13, 16 and 18 maximum generations in Abondance, Normande and Limousine breeds, respectively. Sölkner et al. (1998) were able to calculate 12 maximum generations in Braunvieh (the Austrian Brown Swiss), while Simmental and Pinzgauer had 10 maximum generations.

Generation 7 had the most number of individuals, with 17,035 individuals. For 7,075 individuals, the maximum number of generations between themselves and their farthest ancestors was 1. Almost 65% of the pedigree individuals had not more than 10 generations between themselves and their farthest ancestors. Only 5% of the individuals had 17 or more number of generations between themselves and their farthest ancestors. These results suggest that very few individuals had records of extended history of ancestry in this pedigree.

The mean maximum generation for the pedigree population was 6.60. This indicates the average number of generations between an offspring and its farthest ancestor was 6.60. Considering the pedigree population had individuals born between 1903 and 2009, the mean maximum generation is low.

The number of complete generations was 8. Only one individual had 8 generations traced back with all it own ancestors known. The first complete generation had the highest number of individuals (42,698). The number of individuals decreased as the complete generations increased indicating most individuals had few known ancestral generations.

42929 individuals had no parental generation that could be traced back, so they were included in the base population leaving 138,165 complete generations. 43% of the pedigree population had a maximum of 2 complete generations while less than 0.03% had at least 7 generations traced back with all their ancestors known.

Mean complete generation for the pedigree population was 1.82. This means, on average, the number of generations traced back from an offspring with all known ancestors was less than 2.

Mean equivalent complete generation of 3.30 suggests each individual on average was separated from its known ancestors by 3.30 generations. Compared with the works of Mc Parland et al. (2006), Sölkner et al. (1998), Bozzi et al. (2006) and D. Boicherd et al. (1997) on different cattle breeds, on average, the pedigree population under study did not have a deep pedigree. For example, Bozzi et al. (2006) calculated mean equivalent complete generations of 5.66, 4.54 and 4.95 in Chianina, Marchigiana and Romagnola (Italian beef cattles), respectively.

5.1.2. Pedigree Completeness

Generation 1 had, as expected, the highest index of pedigree completeness from the 23 maximum generations of the pedigree population. The index of pedigree completeness of 0.80 for generation 1, which comprises of individuals that can be traced back only just as far as their parents, suggests that first parental generations (the sires and dams) is about 80% complete.

There was marked decline in index of pedigree completeness as the number of parental generations increased. The first three maximum parental generations had at least 50% pedigree completeness while the last thirteen maximum parental generations had less than 1% pedigree completeness. This decline in pedigree completeness through parental generations can be explained as a result of the decrease in the proportion of known ancestors as the parental generation increases.

While looking at other papers, the pedigree completeness of the population under study is higher than some pedigrees and lower than others. The majority of breeds (Spanish beef cattle breeds) Gutierrez et al. (2003) investigated had pedigree completeness of lower than 80% for the first generation. Cassell et al. (2003) showed that the Holstein and Jersey breeds they studied had almost 90% or more pedigree completeness.

5.1.3. Ancestral Contribution

Calculating the frequency of contribution of each ancestor helps in analyzing the completeness of parental and maternal side. The results showed that the parental ancestry was more complete than the maternal ancestry. Sires had 0.83 frequency of contribution compared to 0.78 frequency of contribution of dams. This result shows the pedigree was 83% complete for sires and 78% complete for dams. The difference in completeness between the paternal and maternal paths shown in this study is higher compared with the findings of other people on other pedigree populations of different cattle breeds (Cassell et al., 2003; Gutierrez et al., 2003) so it is better to look at the results of this study with caution.

The frequency of ancestral contribution decreased as the parental generations increased with paternal ancestors having more contribution. Grandparents of the paternal line had 0.77 frequency of contribution while grandparents from the maternal line had a mere 0.59 frequency of contribution. Great grandparents from the paternal side had 0.64 frequency of contribution, which was 0.14 more than the frequency of contribution of great grandparents of the maternal side.

The fact that the paternal path of the pedigree showed higher completeness than the maternal path can be explained by the presence of more ancestors in the paternal side. The maternal path had a relatively lower number of known ancestors.

5.2. Offspring Analysis

The total number of sires born between 1906 and 2003 was 20,896 and the number of dams born between these years was 80,170.The 1960s and the 1970s saw the highest number of birth of parents than any other periods.

Sires born before the 1940s had unusually big number of offspring compared with sires of the other periods. The average number of offspring per sire reached as high as just over 28 for sires born between the years 1934 and 1940. The next periods showed marked decrease in the average number offspring per sire varying between 2.04 and 7.13. The last period (between 1997 and 2003) showed the lowest average number of offspring per sire, which was 1.38. This number, however, does not tell the whole story as there is a need to wait for some years as most of the sires born in that period could still produce more offspring in the coming years.

The high number of offspring per sire in the early periods of the pedigree population could suggest that bulls were more extensively used for producing offspring than present times. However, the number of sires in the pedigree born before the 1940s was so small (compared with the later periods) that giving emphasis to the early periods will not draw the real picture. Thus, emphasizing on sires born after 1940 is more complete. The sires born between 1941 and 2003 (which equals 95% sires used in the whole offspring analysis) had 4.13 offspring each on average. This is number is more reflective of the current situation.

The average number of offspring per sire in the pedigree population under study is very low when compared with the work of other people on different breeds. In the findings of Mc Parland et al. (2006), for example, sires born in the 90s had at least 27 offspring each on average.

The average number of offspring per dam never topped 2 in any period. The highest average number of offspring per dam, which was 1.95, was recorded for dams born between the years 1913 and 1919 (this period only represents 0.02% of the dams used in the total offspring analysis). 99% of the dams born between 1906 and 1997 on average had less than 1.20 offspring. This shows huge majority of dams only gave birth to one offspring during their life time.

5.3. Inbreeding

To see the level of inbreeding, mean inbreeding coefficient was calculated for the whole pedigree population, for five years periods, for maximum generation and for complete generations. The whole pedigree population under study had mean inbreeding coefficient (F) of 0.77%. But to have a deeper look at how the inbreeding level changed down the years, it is better to look at the mean inbreeding coefficient in different periods and generations. Looking at the rate of increase of average inbreeding coefficients can be used as a measure of genetic diversity (Quinton et al., 1992; Wang, 1997).

The results from the calculation of mean inbreeding coefficients per five years period show that there has been continuous increase in inbreeding. The mean inbreeding coefficient for individuals born between the years 1950 and 1954 was 0.02%. This number showed continuous increase in the next periods and reached almost 1% in the late 1980s, 1.65% in early 90s and 2.36% in late 90s. The highest mean inbreeding coefficient was recorded in individuals born between 2000 and 2004.These findings illustrate higher level of inbreeding (in the last periods) in the pedigree population under study than most other cattle populations in different part of the world. To mention some, Roughsedge et al. (1999) showed the British Holstein-Friesen population had mean inbreeding coefficients much less than 0.5% for individuals born in late 90s. All 8 Spanish cattle breeds studied by Gutierrez et al. (2003) showed less than 0.1% mean inbreeding coefficient in all periods even in the late 90s. However, there were literatures which showed cattle populations with much higher mean inbreeding coefficient than the population under study. For example, Hammami et al. (2007), reported mean inbreeding coefficients of 3.10% and 2.12% (for year 2000) in Holstein populations in Luxumberg and Tunisia, respectively.

The mean inbreeding coefficient per maximum generation also increased as the number of maximum generations traced back increased. The first maximum generation had 0.00% inbreeding. This implies that individuals (a total of 7,075 individuals) that had only their first parental generation had zero inbreeding because their parents were hardly related. This scenario, however, changed as the number of maximum generations traced back increased. For individuals which had 2 generations traced back, the mean inbreeding coefficient was 0.04%. This number continued to increase slightly for every maximum generation (except in generation 5) until it started to increase linearly from maximum generation 6 on. Maximum generations above 16 were not considered in mean inbreeding coefficient calculation as the number of individuals was very low in those generations.

The mean inbreeding coefficient for individuals with only one complete generation traced back was 0.10%. The mean inbreeding coefficient increased almost linearly with increasing complete generations. As it can be noted there are big differences in the value of mean inbreeding coefficients between corresponding complete and maximum generations. These differences are because of the differences in the individuals present the corresponding generations.

Increase in mean inbreeding coefficient by generation was evident in the pedigree population under study. The lowest increase of inbreeding was seen by maximum generations. The increase in inbreeding by maximum generation was 0.18%.This lower increase per maximum generation (compared with increase per complete and per equivalent complete generation) could be explained by the higher number of maximum generations unlike the other generation. Increase in inbreeding per equivalent complete generation was 0.40%. Increase in rate of inbreeding was the highest by complete generation with a value of 0.61%.

5.4. Average Relatedness

The average degree of relationship between the pedigree individuals increased periodically. The mean average relatedness calculated in the early 1950s was 0.03%. There was slight increase in mean average relatedness until the 1970s, as it was with mean inbreeding coefficient. Since 1970, mean average relatedness showed swift increase, except the decline between 1985 and 1989. There was only a marginal increase between 2000 and 2004. These results indicate that the relationship between newly born animals is increasing, though the rate increase is lower in the later periods.

The first 16 maximum generations were used to see the change in mean average relatedness. The results showed that the first four generation showed a slight increase (from 0.04% to 0.20%). The increase from the fourth generation to the twelfth generation was swifter (reaching 2.15%). The highest mean average relatedness, with a value of 2.24%, was seen in maximum generation 14. There was a marginal decrease in mean average relatedness between the fourteenth and sixteenth generations.

Mean average relatedness also increased as the number of complete generations traced back increased, except the decline in complete generation 6. Of the first 6 complete generations, complete generation 5 had the highest level of mean average relatedness (2.41%).

The whole pedigree population had mean average relatedness of 1.10%. This value suggests a bit higher average relatedness compared with some breeds (see Gutierrez et al., 2003). Meanwhile, Peixoto et al. (2010) reported 1.10% (similar to the value in population under study) average relatedness in Guzerat breed in Brazil. Generally, there was increase in mean average relatedness through maximum generations and complete generations. This shows degree of relationship between ancestors increases the further generations we trace back.

5.5. Effective Population Size

Effective population size over maximum number of generations traced back, complete number of generations traced back and equivalent complete generations were calculated. Effective population size calculated over maximum number of generations was 273.02. This number could be seen as the maximum estimate of the ideal population size that would give the actual increase in inbreeding. Effective population size calculated over complete generation had the size of 82.16. Equivalent complete generations had effective population size of 125.97. This size could be seen as the ‘real’ estimate of effective population size (Gutierrez and Goyache, 2005).

The ‘real’ estimate of effective population size of the population under study is above the recommended 50 -100 effective population size in animal breeding (FAO, 1998; Bijma, 2000, Sorensen et al., 2005). It should, however, be noted that this recommended number is based on the theoretical thought of natural selection cancelling out inbreeding depression (Sorensen et al., 2005). Franklin and Frankham (1998) suggested that effective population size of at least 500 is a requirement to maintain genetic variation in the long term.

The effective population size calculated per maximum generation was variable. This was because there was difference in the rate increase of inbreeding between maximum generations. Most of the maximum generations had effective population size between 100 and 200 (dropping as low as 118.9 in generation 10 and reaching as high as 237.8 in generation 7). Considering the number of individuals in the population under study, these numbers indicate a small effective population size.

The highest estimate of effective population size per complete generation was seen in generation one, which was 501.8. This is because the rate of increase in inbreeding from the base population (where mean inbreeding coefficient was zero) to generation was the lowest. The next complete generation had effective population size of 100.8. The effective population size continued to decrease in the subsequent generations indicating the increase in the degree of inbreeding.

The effective population size calculated per year ranged between 63 and 204. To maintain the genetic variation in this pedigree population this size should be increased to at least 500 (Franklin and Frankham, 1998)

5.6. Generation Interval

The average generation interval for the total pedigree population was 6.56, with a high standard deviation of 6.53. This interval is considerably higher when compared with average interval seen in other breeds. For example, the Danish Holstein, Jersey and Red population had generation intervals between 4.6 and 5.2 years (Sorensen et al., 2005). Gutierrez et al. (2003) also showed most of the Spanish beef breeds they analyzed had average generation intervals between 3.7 and 5.5 years. Bozzi et al., (2006) also reported generation intervals less than 5.35 in the three Italian breeds they studied.

The sire-offspring pathway had the highest average generation intervals. Both sire-offspring pathways had high standard deviations for the average generation intervals suggesting higher degree of variation between ages of sires when their offspring were born.

The average generation intervals in the dam-offspring pathways had lower values. For example, dam-daughter pathway had average generation interval of 4.93, which was the lowest average generation interval from the four parental pathways. This implicates dams were replaced earlier than sires.

The average age of parents calculated when their offspring, which may or may not become parents themselves, were born showed similar values with average generation intervals for sire-daughter and dam-daughter pathways; while there were slight differences with average generation for the sire-son and dam-son pathways.

5.7. Coancestry

The mean coancestry in the total population was calculated to be 0.0055.This value indicates that probability of picking two alleles that are identical by descent from two individuals (one from each individual) in the pedigree population under study is 0.55% (Frankham et al., 2002).

The French subpopulation had the highest mean coancestry with the value of 1.23%. The lowest mean coancestry was seen between individuals of the Swiss subpopulation.

When looking at the mean coancestry between subpopulations, the Austrian and French subpopulations had the highest mean coancestry between them suggesting lower level of variability between the subpopulations. The Slovenian and Swiss populations, in the other hand, had the lowest coancestry between subpopulations, which could mean higher variability.

It showed be noted that coancestry values show level of genetic variability and minimizing these coancestry values is useful to properly manage genetic variability in individual breeding (Wray and Goddard, 1994; Brisbane and Gibson, 1995; Caballero and Toro, 2000).

5.8. Equivalent Complete Generations for Subpopulations

Five of the seven subpopulations had more than 3.00 equivalent complete generations. The Italian subpopulation had the highest mean equivalent complete generation with 3.48 generations. The German subpopulation had 3.37 mean equivalent complete generations, which was the second highest.

The US and Slovenian subpopulations had the two lowest equivalent complete generations. The US subpopulation had 2.73 equivalent complete generations while the Slovenian subpopulation had 2.86 equivalent generations.

Generally, the subpopulations have shown low mean equivalent generations. Sölkner et al. (1998) showed Braunvieh (the Austrian Brown Swiss) in Austria had 4.16 mean equivalent generations. Other breeds they studied (in Austria) all had more than 4.00 mean equivalent complete generations. Italian breeds studied by Bozzi et al. (2006) also showed higher equivalent complete generations than all of the subpopulations in this study.

5.9. Distance between Subpopulations

The mean genetic distance (Nei's minimum distance, Nei 1987) between the subpopulations over the entire metapopulation was 0.0013. This genetic distance value is very low and shows that there is high genetic similarity between the subpopulations of the whole pedigree population under study.

The lowest genetic distance, which was 0.0008, was recorded between the Italian and the US subpopulations meaning they had the highest genetic similarity among all subpopulations. The highest genetic distance was recorded between the German and the French subpopulations. They had average genetic distance of 0.0039 between them. This shows the genetic similarity between these two subpopulations was the lowest.

The average distance between individuals of the Swiss and the US populations was the highest. Based on the equation given by Caballero and Toro (2002), high average distance results from high difference between average self coancestry and average coancestry between individuals within subpopulations. Individuals of the Austrian and the French subpopulations had the lowest average distance between them indicating their individuals had the lowest difference between their average self coancestry and average coancestry.

5.10. F-statistics

The F-statistics parameters for the pedigree population had small positive values. F_{IS} had a value of 0.000992, which is a small positive value. F_{IS} can be defined as the inbreeding coefficient of an individual when calculated relatively to its subpopulation (Falconer and Makay, 1996) and the low positive values of F_{IS} show that, on average, there was mating of related individuals in subpopulations a bit more frequently than expected under random mating.

F_{ST} had a value of 0.001304.This shows that there was slight reduction in the level of heterozygosity of the subpopulations as a result of random drift. F_{IT} of 0.002225 was recorded in the total population. This implies individuals, on average, had 0.22% reduction of heterozygosity relative to the total population.

While calculating F_{STs} of paired subpopulations, it was found that the French and Slovenian subpopulations had the highest value. These imply, when paired, the French and the Slovenian subpopulations show the highest reduction of heterozygosity. The lowest paired F_{STs} was seen between the French and the German subpopulations.

The F_{IS} calculated for each subpopulation showed that the French subpopulation had the largest negative F_{IS}. As the equation used by Caballero and Toro (2002) suggests, negative F_{IS} values result when mean coancestry is greater than mean inbreeding coefficient of a subpopulation. The large negative F_{IS} values could indicate that French subpopulation is an outbreed population but the relatively higher mean coancestry value among its individuals suggest otherwise.

5.11. Effective Number of Founders and Ancestors

The number of founders, referring to individuals in the base population that produced offspring, was counted to be 41,011 corresponding to 22.65% of the total pedigree population. The number of ancestors (founders or not) was 36,795, which was 20.32% of the whole population.

Effective of number of founders of the pedigree population was 141. According to Lacy (1989), this number indicates that equally contributing 141 founders would give rise to the same genetic diversity as in the reference population (which contained 138,165 individuals). Compared with the number of founders, the effective number of founders is very low. This suggests the vast majority of the founders had low and unequal contribution to the genetic variability of the reference population so there was loss due to unequal contribution of founders (Lacy, 1989).

The minimum number of ancestors (not necessarily founders) that would explain the whole genetic diversity of the reference population was 88. This number is lower than effective number founders, which is because effective number of ancestors accounts for genetic bottlenecks and loss as a result of unequal founder contribution (Boichard et al., 1997).

The analysis of the top contributing (genetic contribution) founders showed most genetically contributing founders were sires. 14 out of the 20 highest contributing founders were sires. This can be explained by the fact that the number of offspring produced per sire was much higher than the number of offspring per dam (as shown in this study).The highest contributing sire had 3.22% contribution while the highest contributing founder dam had 1.75% contribution. The overwhelming majority of the founders for the total reference population were from the US subpopulation.

23% of the genetic variation in the pedigree population was contributed by the top 20 founders. This result shows that the genetic variation in the pedigree population is explained by more number of founders than seen in other cattle populations (as an example, see Sölkner et al., 1998; Faria et al., 2009). The relatively higher effective number of founders and effective number of ancestors seen in this population explains the relatively low genetic contribution made by top founders and ancestors.

6. CONCLUSIONS

Based on the periodic values of mean inbreeding coefficient (F) and average relatedness (AR), it is possible to conclude that the level of inbreeding has been increasing in this pedigree population. This implies there has been decrease in the genetic variation of the pedigree population down the years. Breeders should be aware of this decrease in the genetic variation of the Brown Swiss population and better breeding methods should be designed to maintain the genetic variation.

The effective population size, which has also been increasing with increasing generations, needs to increase in the future to maintain the genetic variation in the pedigree population.

The study has also indicated that founder sires have been the most genetically influential sires in the pedigree population understudy. Most of these founder bulls were registered in USA.

The genetic contribution made by the top founders was not as high as seen in other populations.

The comparison between subpopulations has shown that the highest mean coancestry existed between the Austrian and the French subpopulations.

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APPENDICES

Appendix 1- Top 50 Founder dams

Founder	***Contr.%***	Country	ID	Constructed Birth date	Reported Birth date
84	***1.747***	USA	BSWUSAF000000357372	1926-10-29	1957-01-30
117	***1.577***	USA	BSWUSAF000000350995	1930-10-29	1956-09-19
60	***0.809***	USA	BSWUSAF000000363053	1922-10-29	1957-07-12
83	***0.541***	USA	BSWUSAF000000252231	1926-10-29	1951-01-01
2	***0.493***	USA	BSWUSAF000000028089	1906-10-29	1936-01-01
27	***0.471***	USA	BSWUSAF000000074522	1918-10-29	1946-01-01
57767	***0.364***	USA	BSWDEUF000922911871	1973-05-02	1973-05-02
9052	***0.354***	USA	BSWUSAF000000370830	1957-12-25	1957-12-25
32929	***0.326***	DEU	BSWDEUF000979056000	1967-08-12	1967-08-12
11943	***0.313***	USA	BSWUSAF000000397825	1959-11-24	1959-11-24
14	***0.294***	USA	BSWUSAF000000131796	1914-19-29	1945-01-01
53	***0.271***	USA	BSWUSAF000000172894	1922-10-29	1949-01-01
34352	***0.245***	DEU	BSWDEUF000923487906	1967-12-17	1967-12-17
9822	***0.240***	USA	BSWUSAF000000374758	1958-08-19	1958-08-19
623	***0.227***	USA	BSWUSAF000000056349	1944-01-01	1944-01-01
52	***0.212***	USA	BSWUSAF000000111105	1922-10-29	1944-01-01
55	***0.194***	USA	BSWUSAF000000218221	1922-10-29	1955-01-01
34193	***0.186***	DEU	BSWDEUF000923487816	1967-12-05	1967-12-05
4419	***0.185***	USA	BSWUSAF000000206959	1953-01-01	1953-01-01
5150	***0.185***	USA	BSWUSAF000000243043	1954-01-01	1954-01-01
29	***0.173***	USA	BSWUSAF000000186018	1918-10-29	1947-01-01
7798	***0.173***	USA	BSWUSAF000000342755	1956-12-02	1956-12-02
9280	***0.172***	USA	BSWUSAF000000371102	1958-02-14	1958-02-14
16673	***0.171***	DEU	BSWDEUF000805640569	1962-03-05	1962-03-05
2153	***0.166***	USA	BSWUSAF000000172279	1949-01-01	1949-01-01
5528	***0.164***	DEU	BSWDEUF000929983024	1954-07-21	
4579	***0.154***	DEU	BSWDEUF000929983155	1953-02-22	1953-02-22
34	***0.153***	USA	BSWUSAF000000215464	1918-10-29	1950-01-17
8577	***0.134***	DEU	BSWDEUF000978501205	1957-09-05	1957-09-05
13825	***0.134***	DEU	BSWDEUF000920022126	1960-11-24	1960-11-24
28081	***0.133***	DEU	BSWDEUF000979316305	1966-02-20	
17289	***0.131***	DEU	BSWDEUF000801013080	1962-07-07	
17	***0.127***	USA	BSWUSAF000000161999	1914-10-29	1951-01-10
6723	***0.124***	DEU	BSWDEUF000978457518	1955-11-22	1955-11-22

1896	***0.124***	DEU	BSWDEUF000929983053	1948-02-20	
1424	***0.124***	USA	BSWUSAF000000212767	1947-01-01	1951-01-01
26	***0.123***	USA	BSWUSAF000000057760	1918-10-29	1944-01-01
61	***0.123***	USA	BSWUSAF000000185909	1922-10-29	1947-08-23
16	***0.120***	USA	BSWUSAF000000190873	1914-10-29	1947-01-01
19319	***0.119***	DEU	BSWDEUF000801000663	1963-03-25	
57	***0.118***	USA	BSWUSAF000000220527	1922-10-29	1955-01-01
7375	***0.115***	USA	BSWUSAF000000344691	1956-08-15	1956-08-15
3125	***0.110***	USA	BSWUSAF000000163866	1951-01-01	1951-01-01
1799	***0.103***	USA	BSWUSAF000000175353	1948-01-01	1948-01-01
1378	***0.103***	USA	BSWUSAF000000184123	1947-01-01	1947-01-01
3068	***0.102***	DEU	BSWDEUF000929983222	1950-12-24	
5149	***0.101***	USA	BSWUSAF000000221344	1954-01-01	1954-01-01
2873	***0.101***	USA	BSWUSAF000000228066	1950-08-05	1950-08-05
8566	***0.099***	USA	BSWUSAF000000368743	1957-08-27	1957-08-27
6390	***0.099***	USA	BSWUSAF000000346972	1955-07-31	1955-07-31
Total	**13.128**				

Appendix 2- Top 50 Founder Sires

Founder	***Contr.%***	Country	ID	Constructed Birth date	Reported Birth date
50	***3.218***	USA	BSWUSAM000000131528	1922-10-29	1957-11-22
7001	***2.614***	USA	BSWUSAM000000125640	1956-02-04	1956-02-04
13	***2.358***	USA	BSWUSAM000000106902	1914-10-29	1950-07-16
49	***1.721***	USA	BSWUSAM000000124652	1922-10-29	1955-02-11
116	***1.257***	USA	BSWUSAM000000125472	1930-10-29	1955-10-27
10726	***1.062***	USA	BSWUSAM000000136140	1959-02-22	1959-02-22
3	***0.984***	USA	BSWUSAM000000067200	1910-10-29	1944-01-01
5372	***0.884***	USA	BSWUSAM000000121816	1954-04-04	1954-04-04
9	***0.769***	USA	BSWUSAM000000052728	1914-10-29	1945-01-01
48	***0.644***	USA	BSWUSAM000000109152	1922-10-29	1950-12-18
82	***0.615***	USA	BSWUSAM000000110327	1926-10-29	1951-08-08
8201	***0.580***	USA	BSWUSAM000000131096	1957-03-31	1957-03-31
1	***0.493***	USA	BSWUSAM000000029167	1906-10-29	1936-01-01
24	***0.478***	USA	BSWUSAM000000096076	1918-10-29	1947-01-01
466	***0.460***	USA	BSWUSAM000000055163	1942-01-01	1942-01-01
1013	***0.433***	USA	BSWUSAM000000069864	1947-01-01	1947-01-01
577	***0.403***	USA	BSWUSAM000000076059	1943-10-22	1948-01-01
21	***0.372***	USA	BSWUSAM000000071151	1918-10-29	1945-01-01
7494	***0.331***	USA	BSWUSAM000000128895	1956-10-03	1956-10-03
8603	***0.329***	USA	BSWUSAM000000130709	1957-09-27	1957-09-27
46	***0.271***	USA	BSWUSAM000000095956	1922-10-29	1948-01-01
4105	***0.255***	USA	BSWUSAM000000114123	1952-09-08	1952-09-08
80	***0.251***	USA	BSWUSAM000000086356	1926-10-29	1947-01-01
81	***0.250***	USA	BSWUSAM000000105449	1926-10-29	1951-02-12
1590	***0.244***	USA	BSWUSAM000000078152	1948-01-01	1948-01-01
45	***0.234***	USA	BSWUSAM000000059815	1922-10-29	1944-01-01
156	***0.227***	USA	BSWUSAM000000028594	1933-01-01	1944-01-01
999	***0.223***	USA	BSWUSAM000000065421	1947-01-01	1947-01-01
4624	***0.204***	USA	BSWUSAM000000119793	1953-03-25	1953-03-25
1647	***0.186***	USA	BSWUSAM000000098243	1948-01-01	1948-01-01
10	***0.184***	USA	BSWUSAM000000052728	1914-10-29	1945-01-01
22	***0.174***	USA	BSWUSAM000000077871	1918-10-29	1947-01-01
47	***0.168***	USA	BSWUSAM000000102073	1922-10-29	1950-07-10
7495	***0.163***	DEU	BSWDEUM000979268884	1956-10-03	1956-10-03
4578	***0.154***	DEU	BSWDEUM000929983145	1953-02-22	

9690	***0.141***	USA	BSWUSAM000000133783	1958-07-08	1958-07-08
12	***0.135***	USA	BSWUSAM000000090827	1914-10-29	1947-01-01
3503	***0.131***	DEU	BSWDEUM009002001105	1951-09-23	
1613	***0.130***	USA	BSWUSAM000000094392	1948-01-01	1948-01-01
11	***0.127***	USA	BSWUSAM000000092099	1914-10-29	1946-01-01
1083	***0.127***	USA	BSWUSAM000000084052	1947-01-01	1947-01-01
1895	***0.124***	DEU	BSWDEUM000929983046	1948-02-20	
18441	***0.116***	DEU	BSWDEUM000920031806	1962-12-09	1962-12-09
12577	***0.113***	DEU	BSWDEUM000979244124	1960-03-10	1960-03-10
16678	***0.110***	DEU	BSWDEUM000929983012	1962-03-06	1962-03-06
25	***0.107***	USA	BSWUSAM000000124122	1918-10-29	1955-01-14
1076	***0.106***	USA	BSWUSAM000000083411	1947-01-01	1947-01-01
1093	***0.104***	USA	BSWUSAM000000085350	1947-01-01	1947-01-01
969	***0.104***	USA	BSWUSAM000000052443	1947-01-01	1947-01-01
3067	***0.102***	DEU	BSWDEUM000929983219	1950-12-24	
Total	**24.971**				