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Genetic variability in pigs assessed by pedigree analysis: the case of Belgian Landrace NN and Pietrain in Flanders.

S. Janssens[1], J. Depuydt[2], S. Serlet[2], Vandepitte W.[1]*

[1]*Centre for Animal Genetics and Selection, Department of Biosystems, K.U.Leuven, Kasteelpark Arenberg 30, 3001 Leuven, Belgium, E-mail : steven.janssens@biw.kuleuven.be*
[2] *Vlaams Varkensstamboek, Van Thorenburghlaan 20, 9860 Scheldewindeke, Belgium*

Abstract

Pure breeding of pigs by independent, pig book breeders is under increasing pressure in Flanders. As a consequence, populations of pure breeds are decreasing which will eventually lead to a loss of genetic diversity and high rates of inbreeding. The homozygous stress-resistant Belgian Landrace (BL-NN) is considered most at risk and its current genetic variability was evaluated by pedigree analysis. The Belgian Pietrain (P), used as a terminal sire, was included as the second breed.

The variance of family size of sires was markedly different between P and BL-NN, and the high variance reduces the effective population size to approx. 80 in the BL-NN. The rate of inbreeding is increasing in the BL-NN whereas it remains stable in Pietrain.

Genetic variability measured by ancestors, effective founders and founder genomes in the BL-NN is about half of the value computed for Pietrain. However, compared to larger foreign populations, levels of genetic variability are still satisfactory.

Inbreeding control at farm level was introduced using an inbreeding matrix between all available boars in the population and the sows in each herd. At breed level, a maximum number of pure breed matings per boar was set to reduce the variance in family size.

Introduction

Pure breeding of pigs by independent, pig book breeders is under increasing pressure in Flanders. This is especially so for the Belgian Landrace. Initially, the Belgian Landrace was bred as a sire line but later developed into a stress resistant sow-line. The objective was to breed a fertile sow line while retaining good carcass conformation. This conformation should distinguish the Belgian Landrace from other European Landraces. Strong competition on the sow market, aggravated by a shrinking sow sector has increased the pressure on the breed and numbers are steadily decreasing. The current status of the breed, in terms of genetic diversity, is unknown but the impression is that the breed should be considered at risk of endangerment (Pauwels and Vettenburg, 2002a). The Pietrain is the predominant terminal sire breed in Belgium and it is known for its high lean meat content and its muscularity. Although numbers are also declining, the general belief is that genetic variability of the breed is not an issue but the true state of affairs is unknown (Pauwels and Vettenburg, 2002b).

In small populations, there is a higher risk of genetic drift and consequently potentially interesting alleles could be lost. Also genetic variability decreases and this could compromise future genetic progress. Genetic variability in different Belgian pig breeds has been assessed before by computing the level of heterozygosity using microsatellite markers (Van Zeeveren et al., 1995). Although this approach conveyed important information, it is not suited to generate information on individual animals. Information on an individual basis is required in breeding programs and this can be generated through the analysis of pedigree data. Pedigree analysis has been used to monitor genetic variability and it can provide clues on which animals to use for breeding to maintain genetic variability (Goyache et al., 2003; Verrier et al., 2005)

The inbreeding rate of individuals affects mainly fitness traits such as number born alive, litter weight at 21 days and, to a lesser extent, also production traits. Reductions in the number of piglets by -0.20 to -0.23 piglets and -3.35 kg in litter weight at 21 days per 10% inbreeding of the dam have been reported (Johnson, 1990; Culbertson et al., 1998). So, rapid increases in inbreeding depress productivity and information should be provided to breeders to avoid this. The change in inbreeding rate can be used to measure genetic variability and to assess effective population size. However, some drawbacks and limitations of this approach have been mentioned. Livestock populations are finite and due to selection decisions, not in steady state. Effects of selection decisions on inbreeding rates will be observed only in later generations. Secondly, in selected populations, the average inbreeding of a given generation is not purely the reflection of the genetic drift because of the mating policy and thirdly, inbreeding coefficients are sensitive to pedigree depth and completeness (Boichard et al.,1997). Therefore, additional measures have been proposed to monitor the amount of genetic diversity in a population. These methods measure aspects of the probability of gene origin. Lacy (1989) introduced the concepts of the number of effective founders and the number of effective founder genomes and Boichard et al.(1997) added to this the concept of the number of effective ancestors. For selection of breeding animals, the use of the average co-ancestry of reproductive animals seems to be advocated when pedigrees are complete (Caballero and Toro, 2000).

The objective of this study was to determine the genetic variability in two Belgian pig breeds by means of pedigree analysis. This information is urgently needed to 1) asses the status of the breeds in terms of viability and danger of extinction and 2) make recommendations about the selection strategy and breeding policy.

Keywords : pedigree analysis , pig , genetic variability, Belgian Landrace, Pietrain

Material and methods

Breeds

The origin of the Belgian Landrace is situated in the early 1930's when the "improved Landrace" (Veredeld Landvarken, Pauwels and Vettenburg, 2002a) was created by crossing local white pigs with German and Dutch Landrace. As a consequence of higher prices for lean meat, the breed developed then into a meaty boar line and in 1961 it was attributed the official name of Belgian Landrace. Since 1985, selection against stress-susceptibility (halothane-test) was practiced and resulted in the development of the stress resistant Belgian Landrace. In 1999 the breed was renamed to Belgian Landrace, homozygous stress-resistant (abbreviated to BL-NN).

The Pietrain-breed is named after the village Pietrain in which surroundings the breed was said to originate somewhere around 1920. A pig book was formed in 1953 and in the following five years, the popularity of the breed increased rapidly (Camerlynck and Brankaer, 1958). Since then, exports have been made worldwide and the breed is extensively used as a terminal sire for the production of lean carcasses.

Data

Pedigree data for BL-NN and for Pietrain were obtained from the Flemish Pig Breeding Association (Vlaams Varkensstamboek or VVS). Data included the animal identification number, the breed code, the sire and dam identification number, the date of birth and the date of culling and the herd identification of the owner. Animals born since 1980 and all available ancestors were selected from the database. Some parameters were computed only for animals born in the period 2000 to 2004 and genetic variability was assessed for a reference population of animals born in 2002, 2003 and 2004. Family size was determined by counting animals by sire and by dam.

Methods

Pedigree completeness was assessed by tracing back the pedigree of each individual as far as possible and by expressing the number of known ancestors in a given generation as a percentage of the expected number. From this information, the number of equivalent generations could be computed, which represents the number of complete generations equivalent to the actual situation. The number of known ancestors was computed for every individual.

Generation intervals, defined as the age of the parents at the time when selected progeny was born, were computed along 4 pathway's, namely from sire to son, sire to daughter, dam to daughter and dam to son. Differences between the different pathways can point to breeders' strategies in the selection.

The genetic variability that is still present in the reference population was assessed by evaluating the number and the contribution of founders and ancestors. Founders (*f*) are ancestors without further pedigree information and they are the origin of the genes of the (reference) population. The sum of the contribution of founders equals 1. The effective number of founders is computed assuming an equal contribution of all founders resulting in the same amount of genetic variability. The effective number of founders (f_e) measures the (im)balance of founder contributions to the current population.

$$f_e = \frac{1}{\sum_{k=1}^{f} p_k^2} \tag{0.1}$$

p_k is the contribution of each founder. When contributions are equal among founders $p_k = 1/f$ and $f_e = f$.

$$f_e = \frac{1}{f\left(\frac{1}{f}\right)^2} = f \tag{0.2}$$

A related measure is the number of ancestors and the effective number of ancestors (f_a). Ancestors are not necessarily founders. The effective number of ancestors values the contribution of important ancestors, independently of them being founder or not. This measure is less affected by pedigree depth than the effective number of founders. A high number indicates little "bottlenecks" and less prominent individuals in the pedigree.

The computation of the effective number of ancestors involves the computation of the marginal contribution of the n most important ancestors. It is possible that ancestors are related to each other and the overall sum of the contributions might exceed 1. Therefore, any redundancies have to be removed. An exact computation of the effective number of ancestors is difficult but it suffices to compute an upper and lower bound for this number (Boichard et al., 1997).

The effective number of founder genomes is the inverse of the average relationship coefficient connecting all animals of a population. It measures the pool of founder genes that is still present in the reference population. The effective number of founder genomes is the expected number of founders that would be required to provide the genetic diversity in the population if the founders were equally represented and had lost no alleles (Caballero and Toro, 2000). This parameter is directly related to 1) genetic diversity, defined as the expected frequency of heterozygotes by descent and 2) to group-co-ancestory (the average pairwise co-ancestory of a given group of individuals) with the pedigree.

$$N_g = \frac{1}{2 * co_{avg}} = \frac{1}{2 * inb_{pro}} \tag{0.3}$$

co_{avg} is the average co-ancestry between animals which is equal to inb_{pro} the average inbreeding of progeny of a pair of animals (Maignel et al., 1998; Zechner et al., 2002). The effective number of founder genomes is also equal to half of the number of founder genes.

$$N_g = \frac{N_a}{2} \tag{0.4}$$

This quantity is computed using Monte Carlo techniques. A number of $2 * founders$ is generated and their genes are passed from parent to offspring. The gene frequencies in the reference population are computed and the effective number of founder genomes is computed as

$$N_g = \frac{N_a}{2} = \frac{1}{2\sum_{k=1}^{2f} f_k^2} \tag{0.5}$$

Effective population size is usually derived from the change in the average degree of inbreeding between generations (Falconer and Mackay, 1996; Boichard et al., 1997).

$$\frac{1}{N_e} = 2 * \frac{\overline{F}_{t+1} - \overline{F}_t}{1 - \overline{F}_t} \tag{0.6}$$

which can, for relatively low levels of inbreeding, be simplified to

$$N_e = \frac{I}{2\Delta F}$$
$$and \tag{0.7}$$
$$\Delta F = \frac{1}{2N_e}$$

Realized (effective) size of a population can thus be computed by evaluating the change in inbreeding levels from one generation to the other. This method reflects mainly long term selection choices and is sensitive to pedigree completeness (Boichard et al., 1997). In populations with shallow pedigrees, Ne is usually overestimated by formula (0.6) and other measures have been proposed (Gutierrez and Goyache, 2003).

Variance of family size was computed for sires and dams of active animals. In an ideal population, family size can be closely approximated by a Poisson distribution with mean and variance equal to 2 (Falconer and Mackay, 1996). Non random deviations in family size will increase the variance and this will lead to unequal contributions and lower effective size according to the following formula.

$$N_e = \frac{8N}{(V_{km} + V_{kf} + 4)} \tag{0.8}$$

The programs PEDIG (Boichard, 2002) and ENDOG (Gutierrez and Goyache, 2003) were used to compute measures of genetic variability from the pedigree data.

Results

Population and family size

The number of active breeding animals of BL-NN and Pietrain, (Table 1) has declined over the period 1998-2004. The reduction is proportionally most significant in Pietrain because the population size in 2004 is only 49% of the 1998 figure. In BL-NN, the population in 2004 is 63% of the numbers counted in 1998.

Table 1 : Number of active breeding animals of the BL-NN and Pietrain breed

	BL-NN		PIETRAIN	
	BOAR	SOW	BOAR	SOW
1998	127	1225	845	3960
1999	139	1167	957	3483
2000	138	1304	1043	3158
2001	163	1215	1033	2845
2002	127	1140	834	2643
2003	102	1106	794	2397
2004	62	797	605	1759

The active animals in 2004 originated from 140 sires and 463 dams in BL-NN and 711 sires and 1500 dams in P. Mean, variance and the maximum of family size are given in Table 2.

Table 2 : Number of sires and dams of active breeding animals in 2004 of the BL-NN and Pietrain breed Mean, variance and largest family size of sires and dams

	BL-NN		PIETRAIN	
	SIRES	DAMS	SIRES	DAMS
NUMBER	140	463	711	1500
MEAN NUMBER OF PROGENY	6.13	1.9	3.32	1.58
VARIANCE OF NUMBER OF PROGENY	63.0	2.14	22.7	1.03
MAXIMUM OF NUMBER OF PROGENY	49	10	44	11

Pedigree quality

Pedigrees of BL-NN and Pietrain had a maximum depth of 18 generations. The average pedigree completeness is shown for individuals born in respectively 2000 and 2004. Comparison of animals born in 2000 with the most recent generation (born in 2004) showed an increase in pedigree completeness. This was most pronounced in the BL-NN breed where about 90% of the pedigree is known up to generation 9. In the Pietrain, the improvement was less marked.

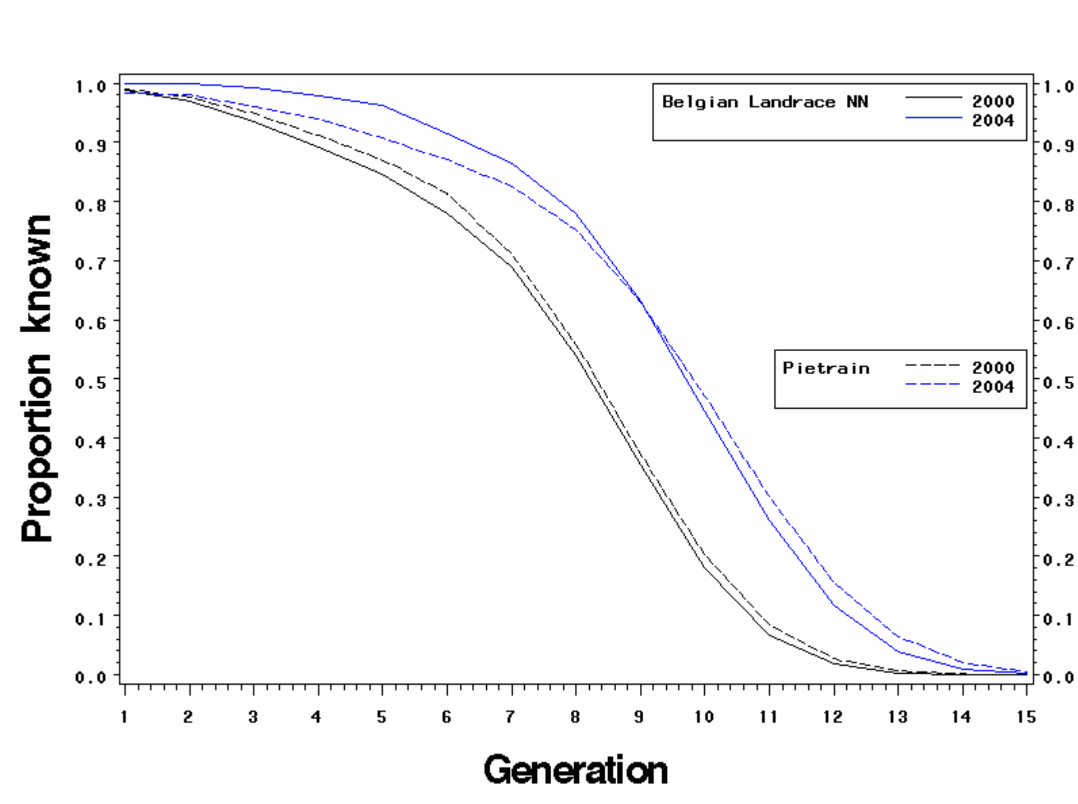

Figure 1 : The proportion of known ancestors of Belgian Landrace-NN and Pietrain boars, born in 2000 and 2004

The equivalent number of generations of animals born in 2004 was approximately 9 in BL-NN and 8.8 in Pietrain, and respectively 2780 and 3543 ancestors are known on average. This also shows that in Pietrain, completeness in recent generations was less than in BL-NN but in remote generations the reverse was true.

Average generation intervals (Table 3) varied from 2.06 to 3.92 according to year of birth and the pathway considered. Averaged over pathways and years, the generation length was 2.50 in BL-NN and 3.15 in Pietrain. Some variation in generation interval, according to years and pathways, was observed. In the BL-NN-breed, generation interval was increasing for animals born in 2000 compared to 2004. Such a trend could not be observed in Pietrain.

The BL-NN-breed could be characterized by long intervals for the pathways from offspring to dam. In Pietrain, the pathways involving the sire were longer than the intervals between offspring and dam.

Table 3 : Generation intervals (years) in Belgian Landrace NN and Pietrain pigs for different paths

	BOARS		SOW		
YEAR OF BIRTH	SIRE	DAM	SIRE	DAM	AVERAGE*
BL-NN					
2000	2.16	2.55	2.06	2.74	2.39
2001	2.46	2.64	2.32	2.57	2.48
2002	2.22	2.90	2.43	2.63	2.54
2003	2.25	2.83	2.32	2.78	2.55
2004	2.45	2.87	2.78	2.74	2.72
AVERAGE*	2.32	2.73	2.29	2.68	2.50
PIETRAIN					
2000	3.15	3.26	2.84	3.10	3.09
2001	2.89	3.14	2.58	2.74	2.90
2002	3.77	3.43	3.97	2.67	3.51
2003	2.79	2.52	4.02	3.92	3.19
2004	2.94	2.77	2.82	2.78	2.84
AVERAGE*	3.18	3.14	3.25	3.04	3.15

* weighted average based on the numbers of individuals for which the interval was computed

Concentration of gene origin

Measures of gene origin and gene concentration for individuals born in the years 2002 to 2004 are given in Table 4. The absolute number of founders in the BL-NN breed was approximately half of the number in the Pietrain. Due to imbalanced contributions, the effective number of founders was much lower than the total number of founders, namely 125 in BL-NN and 327 to 370 in Pietrain (depending on sex).

When looking at ancestors of animals in the reference population, only 43 to 52 effective ancestors were computed in BL-NN and 105 to 155 in Pietrain. Only 16 ancestors were needed to explain half of the genetic variability in the BL-NN-boars and the highest single contribution of one ancestor was 7.8%. The corresponding values in Pietrain were 39 ancestors tp explain 50% of the variability and a contribution of 4% from a single ancestor. Values for BL-NN females were comparable to the results obtained for the boars. In the Pietrain breed, more differentiation existed between sexes.

The effective remaining founder genomes in BL-NN were 17 and 20 in boars and sows respectively and in Pietrain the values were 45 and 65.

An interesting finding is that all measures of genetic variability are higher for males born in the reference period than for females.

Table 4 : Number of founders, ancestors and effective founder genomes in Belgian Landrace NN and in Pietrain according to sex (the reference population consisted of individuals born in 2002, 2003 and 2004)

	BL-NN		PIETRAIN	
	BOARS	SOWS	BOARS	SOWS
REFERENCE POPULATION	517	1258	4448	2487
TOTAL NUMBER OF FOUNDERS (*f*)	772	808	1622	1618
EFFECTIVE NUMBER OF FOUNDERS (f_e)	124.8	126.8	327	369.9
EFFECTIVE NUMBER OF ANCESTORS (f_a)	43.5	51.9	104	155.5
N OF ANCESTORS CONTRIBUTING 50% OF THE GENES	16	17	39	56
HIGHEST CONTRIBUTION OF A SINGLE ANCESTOR	7.8	5.2	4	2.3
EFFECTIVE NUMBER OF FOUNDER GENOMES (N_g)	17.3	19.8	44.8	64.78
f_e/f_a	2.86	2.44	2.32	2.37
N_g/f_e	0.14	0.16	0.14	0.18

Inbreeding

The average inbreeding coefficients are plotted in Figure 2 for animals born since 1991. These averages refer to all animals, inbred or not, and were computed using all available pedigree-information. The percentage of animals that is inbred has increased from 70% (1991) to approximately 100% percent in 2002 and later. Rates of change of inbreeding coefficients over the period (1991-2004) are very similar between breeds. The yearly increase is about 0.12% in

BL-NN and about 0.14% in Pietrain. However, periods of steeper increases or reductions in average inbreeding were observed.

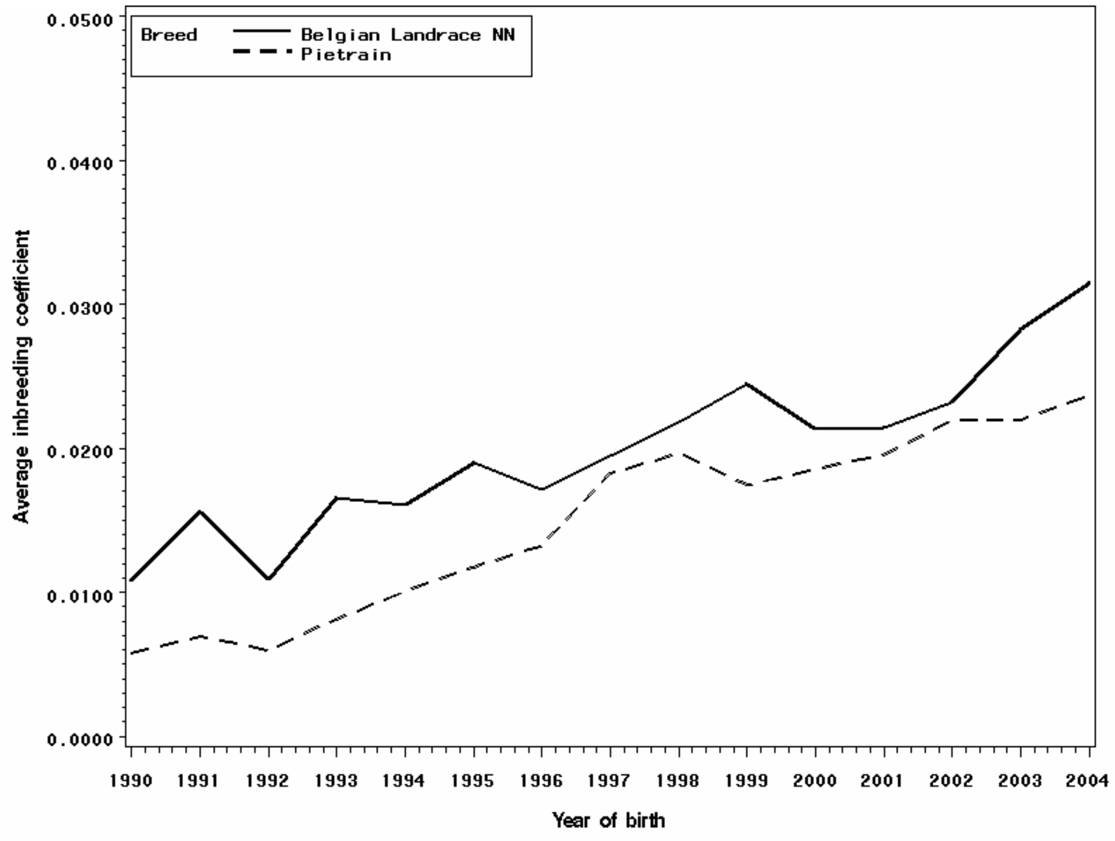

Figure 2 : The trend in average inbreeding rate in Belgian Landrace-NN and Pietrain

Average levels of inbreeding of animals, born in 2004, reach 3.15% in BL-NN and 2.36 % in Pietrain. Especially in BL-NN, an acceleration of the inbreeding rate is observed for the recent years of birth. In BL-NN, the increase in inbreeding is also due to common ancestors in the first 5 generations, whereas in Pietrain, the rise in inbreeding is mainly caused by distant relationships (see Table 5).

Table 5 : Average levels of inbreeding according to the number of generations in the pedigree of Belgian Landrace and Pietrain pigs born in 2000 and in 2004

BREED	BL-NN		PIETRAIN	
BIRTH YEAR	2000	2004	2000	2004
ALL GENERATIONS	2.14%	3.15%	1.85%	2.36%
10 GENERATIONS	2.07%	2.86%	1.80%	2.19%
5 GENERATIONS	1.77%	2.27%	1.33%	1.42%

Discussion

Maximal pedigree depth was found to be quite similar in BL-NN and Pietrain and amounts to 18 generations. This is somewhat lower than values reported for Large White and French Landrace but higher than for Pietrain in France (Maignel et al., 1998). Completeness of the pedigree for recently born animals on the other hand is relatively high. At generation 8 approximately 80% of the ancestors is still known which reduces the risk of severely underestimating the inbreeding rate (Lutaaya et al., 1999).

The differences in pedigree completeness between BL-NN and P were not expected. In Pietrain, pedigree completeness in recent generations was less than in BL-NN whereas in more distant generations the opposite was true. Also the evolution of the pedigree completeness between animals born in 2000 and those born in 2004 was different between the breeds. The reason for this was the presence of imported animals in the pedigree of recent breeding stock.

Generation intervals for animals born in the years 2000 to 2004 were longest in Pietrain with an average value of 3.15 years. In BL-NN, the average generation interval was 2.5 years. Compared to the breeds studied in France (Maignel et al., 1998), generation intervals in BL-NN and Pietrain are quite high and may reflect a rather conservative breeding strategy, especially in Pietrain. Theoretically optimal replacement rates for genetic improvement of reproduction traits in pigs were 96% for boars and 69% for sows (Ollivier, 1974). The generation intervals computed in BL-NN and Pietrain indicate much lower replacement rates and consequently genetic progress is below its maximum.

The generation intervals in BL-NN are steadily increasing (+0.33 years in the period studied) whereas in Pietrain some fluctuations were seen. The increase in length of the generation interval in BL-NN can be related to increasing lengths in the pathways involving the dam. A similar change in generation interval over time was also noticed in the three French pig breeds but this change was in the pathway involving the sire. In the BL-NN, breeders prefer breeding stock from older sows with "proven" maternal ability. The increase in generation interval could also result from less replacement sows coming in because the population is decreasing. In Pietrain, the pathway involving the sire is generally somewhat longer than the pathways involving the dam which is opposite to the situation in BL-NN and in the populations of pigs in France (Maignel et al., 1998). The situation in the Pietrain may reflect emphasis paid to the boar for breeding.

The number of founder animals amounts to approximately 800 in the BL-NN and 1620 in Pietrain which is relatively high compared to the number of animals in the reference population. However, when the effective number of founders is computed, numbers are reduced by a factor 6 in BL-NN and 5 in Pietrain. This indicates imbalanced contributions from the founders to the reference population and contributions are the least balanced in the BL-NN. Similar ratio's between founders/effective founders were found in French Pietrain (ratio of 5) and Landrace pigs (ratio of 6).

The large imbalance in contribution is also clear when looking at the number of ancestors explaining 50% of the variability. In BL-NN, this number is approximately 18, whereas in Pietrain, 44 (boar side) respectively 65 (female side) ancestors are needed to explain 50% of the variability. The highest contribution of a single ancestor amounts to 7.8% in BL-NN-boars which is almost the double of the corresponding value in Pietrain. However, the value found in French Landrace (single contribution of 7.5%) is comparable to the one in BL-NN.

The effective numbers of ancestors for the reference population were 43 (boars) and 52 (sows) in BL-NN and respectively 104 and 155 in Pietrain. The Landrace numbers resemble very closely the situation in the French Landrace whereas in Pietrain, the Flemish population (f_a = 104 and 155) represents more variability than present in the French Pietrain (f_a = 78).

Genetic concentration is strongest along the male side and this was seen in both breeds. Therefore, emphasis of the pig book in controlling genetic variability should be directed to the male side. The ratio f_e / f_a is informative for the occurrence of bottlenecks in the population. Values in BL-NN are higher than those obtained in Pietrain which indicates stronger historical bottlenecks in the former breed. However, compared to the values found in French Landrace (4.01) or French Large White (2.96), the situation is not too extreme.

The effective number of founder genomes in Belgian Landrace is of the same order of magnitude as in the French Landrace (18 compared to 22, Maignel et al., 1998) but related to the effective number of founders, the risk of drift is lower in BL-NN than in the French Landrace. In Pietrain, the effective number of founder genomes is higher but the ratio's N_g / f_e , respectively 0.14 (boars) and 0.18 (sows), are comparable to the values found in BL-NN. The risk of gene loss seems to be very similar in the two breeds under study.

Inbreeding levels in BL-NN and Pietrain are relatively low. In the study by Maignel and co-workers (1998), inbreeding levels reached values of 3.5% in French Landrace and 2% in Pietrain and Large White in France. The yearly change in inbreeding rate attained 0.16%, 0.15% and 0.09% for respectively French Landrace, Pietrain and Large White. Hubbard et al. (1990) reported rates of increase in inbreeding per year between 0.10% and 0.13%. The yearly increase of inbreeding coefficient in BL-NN and Pietrain compares well with these values.

When we express the evolution of inbreeding rate per generation, the increase in our study is 0.30% in BL-NN and 0.44% in Pietrain. This is comparable to inbreeding rates in France expressed per generation, namely 0.20% (Large White), 0.30% (Pietrain) and 0.36% (French Landrace).

When the results in this study are compared with inbreeding levels of Belgian Landrace and Pietrain boars computed about 30 years ago (Hanset, 1973) inbreeding levels have not increased. An important reason for this is certainly the limitation of the current database (started in the early '80's). Zechner et al. (2002) extended the dataset on Lipizzaner horses retrospectively in order to improve pedigree depth. This possibility could be considered for our data too.

A small but maybe important difference between BL-NN and Pietrain lies in the proportion of distant and close inbreeding in the total inbreeding and its evolution over time. In BL-NN, the rise in inbreeding level can be attributed to a significant rise in the proportion of close inbreeding. In Pietrain, the increase in inbreeding level is caused by relationships that are more distant. Levels of inbreeding caused by pedigrees up to 5 generations remain fairly stable in Pietrain. This finding indicates a stronger gene concentration in the BL-NN in the last years, compared to the Pietrain.

The larger gene concentration and lower genetic variability in BL-NN is also apparent from the larger variance of family size of the boars. Widespread use of some individuals and their progeny has narrowed the genetic makeup. A similar phenomenon was seen in the French Large White, but there, it was due to the heavy use of some boars through AI.

Effective size of BL-NN and Pietrain based on variances of family size (formula (0.8)) yields values of respectively 76 and 686. Effective size computed from the increase in inbreeding rate between animals born in 2000 and 2004, according to (0.6), and taking into the average generation intervals of the breeds leads to N_e=88 in BL-NN and N_e=125 in P. The effective size in BL-NN is below the recommended value of 100 and according to the EAAP guidelines (EAAP, 2005) the breed should be classified as “potentially endangered”. However, the number of breeding animals and of breeding herds is declining which increases the class of endangerement. Therefore measures are needed to conserve genetic variability. Due to higher numbers of breeding animals and a more balanced use of boars, the situation in Pietrain is sufficiently good and no immediate action should be taken.

Along with zootechnical initiatives, efforts should be directed to finding specific market niches for the BL-NN. Verrier et al. (2005) have indicated that without a (new) market, conservation of a breed remains troublesome. Assets of the BL-NN are its conformation and leg quality and these should be exploited.

Implications

A rapid increase of the inbreeding coefficient has mostly negative effects and should be avoided. Therefore, breeders of BL-NN are now provided with a table showing the expected inbreeding rates of progeny resulting from (hypothetical) matings between all active boars and the sows in their herd.

As a measure to preserve genetic variability in BL-NN, a limit on the number of purebred matings per boar was proposed. This will restrict the variance of family size of the boars and at the same time shorten the generation interval. A short generation interval will contribute to a higher rate of genetic improvement. In the next step, other criteria (e.g. the average relationship) could be introduced to the breeders to refine the selection of boars and to balance inbreeding against selection as suggested by Meuwissen (1997).

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