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POPULATION STATUS OF MAJOR U.S. SWINE BREEDS

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ABSTRACT: Globally, genetic diversity of livestock populations is contracting. Knowing the true extent of the contraction is needed to develop effective conservation strategies. To accomplish this goal, pedigree records were obtained for: Duroc (n = 878,480), Hampshire (n = 744,270), Landrace (n = 126,566), and Yorkshire (n = 727,268) from NSR, and Berkshire (n = 116,758 American Berkshire Association). Number of registrations peaked in 1990 for all breeds except Berkshire and all have been declining in the current decade. Presently, more than 99% of all pigs are inbred with the majority having inbreeding less than 10%. The range for percent of animals that are more than 25% inbred ranged from 1.16% for Yorkshire to 6.09% for Berkshire. The highest inbreeding for all animals within a breed ranged from 51% for Landrace and 65% for Yorkshire. Sires were grouped into ten percentiles based on number of great-grandprogeny (GGP); the top percentile for all breeds accounted for more than 75% of all GGP. Sixty percent of all sires produced less than 1% of all GGP, indicating few males are responsible for the majority of future generations, thus narrowing the genetic base. Generation numbers were computed with the founders defined as having unknown parents, assigned as generation zero. Generations ranged from 17 to 19 per breed with a generation interval ranging from 1.65 yr for Berkshire to 2.21 yr for Yorkshire. Mean inbreeding (%) at generation 17, inbreeding rate of increase per generation, and effective population size were 12.3, 0.0065, and 77 for Berkshire, 11.8, 0.0044, and 113 for Duroc, 6.8, 0.0046, and 109 for Hampshire, 17.9, 0.0067, and 74 for Landrace, and 8.0, 0.0044, and 113 for Yorkshire, respectively. The two breeds with fewest registrations, Berkshire and Landrace, have a higher inbreeding rate and lower effective population sizes; these breeds need more aggressive conservation in order to maintain genetic diversity. This analysis provides a basis for future monitoring of the genetic diversity of pig breeds.

Key Words: Genetic diversity, Swine, Inbreeding

Introduction

Approximately 20% of the world's breeds are reported to be at risk of extinction (FAO, 2007). Blackburn et al. (2003) detailed the contraction of animal genetic resources (AnGR) in the U.S. To address the contraction and potential loss of AnGR, the USDA established the National Animal Germplasm Program (NAGP) to conserve livestock and aquatic genetic resources (Blackburn, 2004, 2009). Ideally, genetic conservation efforts would capture all available alleles and their combinations in a population. The U.S. swine industry is highly structured and competitive. As a result, breeders employ high selection

intensities for economically relevant traits. As a result of selection pressure and associated inbreeding, allele frequencies can be dramatically changed and there is potential for losing alleles that under the present selection and marketing strategies are not important (Falconer and Mackay, 1996). However, by collecting and cryopreserving germplasm samples, alleles and their various combinations can be made available for future use.

In order for the NAGP genebank to capture the genetic diversity available for each species, the genetic diversity and population status of each species and breed must first be established. Measures to establish the population status include inbreeding levels, registration trends, generation intervals, and effective population size. The objective of this study was to establish a baseline for five major U.S. pig breeds.

Materials and Methods

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database. Pedigree records were obtained from the National Swine Registry (NSR) for Duroc, Hampshire, Landrace, and Yorkshire; Berkshire records were obtained with approval from the American Berkshire Association.

For each breed, a complete pedigree was built until all ancestors were unknown using the Animal Breeders Tool-Kit (ABTK; Golden et al., 1992) and the AWK programming language (Aho et al., 1988). The ABTK generates a list of animals that appear as both a sire and dam in the pedigree and animals that appear as their own parent. Data corrections were made; if parentage could not be determined, it was converted to unknown. Inbreeding coefficients (F) were computed.

Founder animals, defined as having unknown parents, were assigned a generation number of zero. Then, subsequent generation numbers (g) were calculated iteratively as:

$$g = 1/2 (g_s + g_d) + 1,$$

where g_s is the generation number of the sire and g_d is the generation number of the dam (MacKinnon, 2003). Generation number was compared to mean inbreeding, percent of inbred animals, and number of years of registrations.

Regression procedures were performed using SAS (SAS Inst., Cary, NC). Increases in inbreeding per generation (ΔF) were calculated by regressing individual inbreeding coefficients on generation number (MacKinnon, 2003).

Effective population size (N_e), defined as the number of individuals that would generate the current level of inbreeding, was computed as:

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

(Falconer and Mackay, 1996). Generation intervals (**GI**) were computed by regressing generation number on birth year (MacKinnon, 2003).

To represent the current population, F frequencies were calculated for animals born 2006 and later. Coefficient of relationships were computed between the top 10% of boars that sired progeny born 2006 and later (VanRaden and Smith, 1999).

Influential males were determined by computing the number of great-grandprogeny (**GGP**) registered and were grouped into ten percentiles.

Results and Discussion

Summary statistics for each breed are shown in Table 1. The year when records started being stored in electronic format for each breed registry varies, but generally started with animals born in 1980. Number of registrations peaked in 1990 for all breeds, except Berkshire, which peaked in 2000. All breeds have declining registration numbers in the current decade.

Number of dams outnumbered number of sires by approximately 4 to 1. The sire count for the highest number of offspring registered for each breed was 481, 3,797, 1,624, 949, and 1,417 while the dam count was 80, 99, 96, 84, and 142 for Berkshire, Duroc, Hampshire, Landrace, and Yorkshire, respectively. The most prolific Duroc male registered more than 38 times more offspring than the most prolific Duroc female.

The Food and Agriculture Organization of the United Nations (FAO; 2000) established an N_e of 50 animals as the critical number to be above; however, Meuwissen and Woolliams (1994) suggested a minimum N_e range of 31 to 250 to maintain population fitness. Duroc, Hampshire, and Yorkshire have relatively robust N_e levels. Berkshire and Landrace are lower and therefore may warrant additional attention. Nicolas (1989) recommended a ΔF rate of < 0.005 as satisfactory, while the FAO (2000) recommended a ΔF rate of < 0.01 as a goal. All breeds meet the FAO goal, but Berkshire and Landrace are above the Nicolas suggested rate ($P < 0.0001$). All breeds had a ΔF that was significantly different from each other ($P < 0.0001$). A rapid turnover of generations for all breeds was found, ranging from 1.65 to 2.21 yrs ($P < 0.0001$). The breeds had significantly different GI ($P < 0.0001$).

The mean F for each breed is reported in Table 1; however, since most of those animals are no longer contributing genes to the future generations, this information is of limited use. Knowing the status of the current population is crucial for conservation activities; Figure 1 shows the F frequencies for animals born 2006 and later. Berkshire (44.7%) and Landrace (39.9%) have a higher percentage of animals with $F > 0.10$ than the other

breeds. In contrast, Duroc has 64% of current animals with $F \leq 0.05$ and 88% with $F \leq 0.10$.

The coefficient of relationships between the top 10% of sires producing progeny born 2006 and later were 0.135, 0.083, 0.122, 0.129, and 0.116 for Berkshire, Duroc, Hampshire, Landrace, and Yorkshire, respectively. With the exception of Duroc, the most popular boars for the remaining 4 breeds are, on average, as closely related as cousins.

After 17 generations, the most generations computed to allow for comparison across all breeds, Landrace has the highest mean F of 17.9% (Figure 2). That is every animal being, on average, somewhere between half-siblings and full-siblings. Hampshire has the lowest F (6.8%). After 12

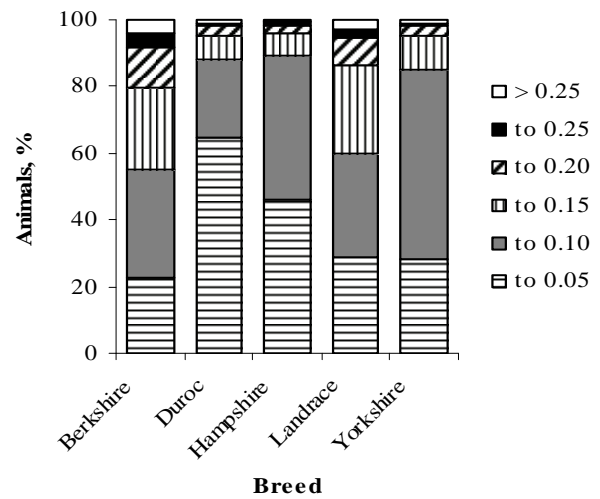


Figure 1. Inbreeding coefficient frequencies by breed for animals born 2006 and later

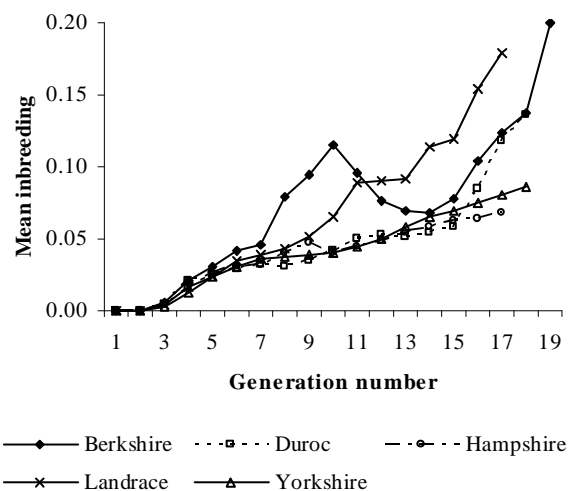


Figure 2. Inbreeding by generation number for all breeds

generations, for all breeds, all animals have an $F > 0$ (Figure 3). All breeds follow a similar rate of increase in the proportion of inbred animals.

Figure 4 shows how the average generation number increases with number of years of registrations. The

steepest ascent was observed for Berkshire, which also has the shortest GI. Yorkshire plateaus during years 20 to 24, which corresponds to 1992 to 1996. Upon investigation, it was determined there were 13 imported animals, or sons of imported animals, that were contributing between 216 and 1,019 offspring per boar during this time period. To verify if these animals were reducing the slope of the curve, they were assigned the average generation number for their birth year, and the population's generation numbers were recalculated. The slope of the curve increased (Figure 5), showing how influential a few heavily used imported males were for the Yorkshire breed.

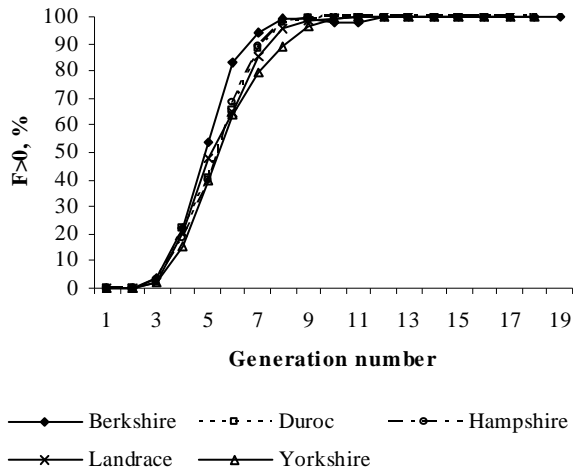


Figure 3. Percent of animals with $F > 0$ by generation number for all breeds

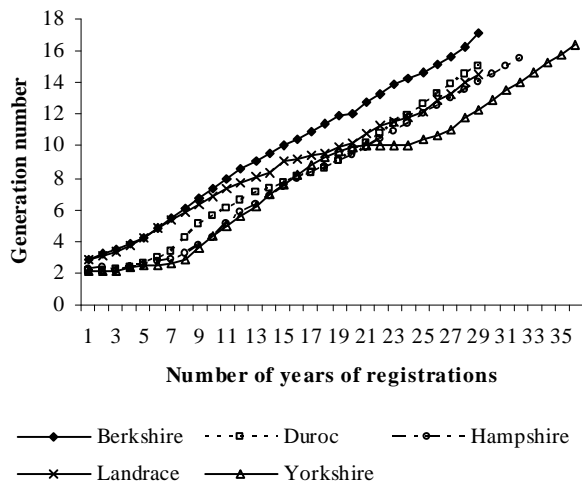


Figure 4. Generation number by number of years of registrations for all breeds

The top 10% of males produced more than 75% of all GGP for all breeds; in Duroc and Hampshire this was more pronounced (85 and 87%, respectively). The bottom 60% of sires produced less than 1% of GGP across breeds. Considering how few males are selected to become sires, and even fewer of those selected males are producing the vast majority of GGP, demonstrates how quickly the genetic base can narrow in a few generations.

With the increase in AI in the swine industry (Blackburn et al., 2003), it will be important to ensure inbreeding levels do not increase more rapidly than they currently are; therefore, the swine industry may wish to incorporate approaches into their genetic evaluation programs that minimize the rate of inbreeding (Meuwissen, 1997).

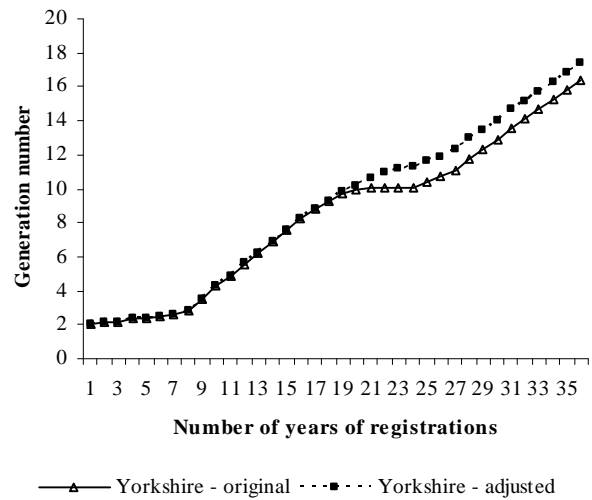


Figure 5. Generation number by number of years of registrations for Yorkshire and for Yorkshire adjusted for 13 sires

Implications

This study serves as a baseline for these five pig breeds in the U.S. Having estimated effective population size, inbreeding levels, and inbreeding rates provides NAGP with greater insight about the genetic diversity of these breeds and how to pursue conservation strategies. While the inbreeding levels are useful genetic diversity indicators, the depth of the pedigrees is relatively shallow given the length of time since these breeds were imported into the U.S. Due to the pedigree depth, it might be safely assumed the reported inbreeding levels are underestimates. Analysis using DNA markers might further elucidate within breed genetic diversity and the genetic differences among the breeds presented in this study (Vicente et al., 2008).

Berkshire and Landrace are intermediate for both effective population size and increase in inbreeding per generation while Duroc, Hampshire, and Yorkshire are within acceptable levels. Inbreeding in the current population is high for Berkshire and Landrace. These two breeds have the fewest registrations, making an even greater challenge for breeders to make mating decisions that minimize long-term inbreeding and maximize performance.

The current trends suggest inbreeding will continue to increase, potentially resulting in loss of alleles from these populations. Broad sampling of lowly related animals within each breed by NAGP is vital to maximize genetic diversity for conservation activities. To date, germplasm collections have been initiated on all five breeds (Table 1); however, additional collections are needed and planned. With the completion of the germplasm collection for each of these breeds, a greater level of protection will be afforded the swine industry.

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Table 1. Summary statistics for pedigree file size, inbreeding (F), sires and dams, change in inbreeding per generation (ΔF), generation interval (GI), effective population size (N_e), and boars in repository for all breeds

Item	Berkshire	Duroc	Hampshire	Landrace	Yorkshire
Pedigree file size	116,758	878,480	744,270	126,566	727,268
Mean F	0.078	0.032	0.036	0.053	0.039
F range	0 to 0.61	0 to 0.58	0 to 0.59	0 to 0.51	0 to 0.65
Unknown sires, %	1.27	1.15	1.04	2.37	3.23
Unknown dams, %	1.26	1.13	1.02	2.38	3.44
Unique sires	6,748	26,615	23,206	7,370	40,458
Unique dams	27,487	126,289	100,246	28,827	175,985
ΔF	0.00647 ^a	0.00442 ^b	0.00458 ^c	0.00674 ^d	0.00443 ^e
GI, yr	1.65 ^a	1.92 ^b	2.06 ^c	1.83 ^d	2.21 ^e
N_e	77.28	113.12	109.17	74.18	112.87
Boars in repository, n	29	50	33	29	91

^{a-e}Within a row, values without a common superscript differ ($P < 0.0001$).

Table 1. Summary of data for analyses of mature cow weight (MWT, kg) and mature cow height (MHT, cm) for two samples of Angus cows

	Sample 1		Sample 2	
	MWT1	MHT1	MWT2	MHT2
No. Records	23,658	13,012	23,698	13,310
No. Cows	14,056	8,131	15,038	8,439
No. Cont. Groups	1,180	581	1,227	692
No. Pedigree	43,105	43,105	44,141	44,141
Means	596.6	135.7	588.3	134.3

Table 2. Estimates of genetic parameters (SD) for mature cow weight (MWT, kg) and mature cow height (MHT, cm) for two samples of Angus cows (single trait analyses)

Estimates	Sample 1		Sample 2	
	MWT1	MHT1	MWT2	MHT2
Heritability ^a	0.45 (0.012)	0.64 (0.018)	0.48 (0.011)	0.62 (0.018)
Repeatability ^a	0.64	0.77	0.66	0.70
Cont. Group ^b	0.50	0.52	0.52	0.46
Phenotypic Variance	5012.78	36.27	5332.92	33.02

^a fraction of phenotypic variance not including contemporary group variance.

^b fraction of phenotypic variance including contemporary group variance.

Table 3. Estimates of genetic parameters for mature cow weight (MWT, kg) and mature cow height (MHT, cm) for two samples of Angus cows (two trait analyses).

Estimates	Sample 1		Sample 2	
	MWT1	MHT1	MWT2	MHT2
Heritability ^a	0.44	0.62	0.47	0.62
Repeatibility ^a	0.64	0.76	0.66	0.70
Cont. Group ^b	0.50	0.53	0.52	0.46
Phenotypic Variance	5009.21	36.08	5285.49	32.65

^a fraction of phenotypic variance not including contemporary group variance.

^b fraction of phenotypic variance including contemporary group variance.

Table 4. Estimates of correlations between mature cow weight (MWT) and mature cow height (MHT).

Correlations	Sample 1		Sample 2	
	Genetic	Permanent Environmental	Genetic	Permanent environmental
	0.80	0.75	0.83	0.69