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Pedigree analysis of 5 swine breeds in the United States and the implications for genetic conservation[1]

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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. Although contractions of genetic diversity have been documented at the breed level, little within breed documentation has occurred. This situation is no different for US swine breeds. Therefore, the objective of this study was to establish an inbreeding baseline for 5 pig breeds via pedigree records extracted from purebred registrations to each breed association for Berkshire (n = 116,758), Duroc (n = 878,480), Hampshire (n = 744,270), Landrace (n = 126,566), and Yorkshire (n = 727,268). For all breeds the number of registrations peaked after 1990 and declined since that time. The breeder structure was analyzed for Berkshire and Duroc; the average breeder registered pigs for 4.0 yr for both breeds. Breeders were grouped by longevity and herd size, and the inbreeding levels for the current population (pigs born 2006 and later) were evaluated. Presently, more than 99% of all pigs are inbred with the majority having inbreeding less than 10%. The range for percentage of animals that are more than 25% inbred ranged from 1.16% for Yorkshire to 6.09% for Berkshire. The greatest inbreeding for all animals within a breed ranged from 51% for Landrace and 65% for Yorkshire. Sires were grouped into 10 percentiles based on number of great-grandprogeny (GGP) produced; for all breeds, the top 10 percentile accounted for more than 75% of all GGP. Sixty percent of all sires produced less than 1% of all GGP, indicating few males are contributing to future generations. 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 (the most generations computed across breeds), rate of inbreeding 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 2 breeds with fewest registrations, Berkshire and Landrace, had greater inbreeding rates and smaller effective population sizes, suggesting a need for more immediate conservation efforts. This analysis provides a basis for future monitoring of the genetic diversity of pig breeds and serves as a basis for planning conservation activities.

Key words: genetic conservation, genetic diversity, inbreeding, swine

INTRODUCTION

Globally and within the United States there has been a contraction in animal genetic resources (Blackburn et al., 2003; FAO, 2007). To address the contraction and potential loss of animal genetic resources, the USDA established the National Animal Germplasm Program to conserve livestock genetic resources (Blackburn, 2004, 2009). Ideally, genetic conservation efforts would capture all available alleles and their combinations in a population; collecting and cryopreserving germplasm samples allows these alleles to be made available for future use.

Evaluating the genetic diversity within a breed is also a requisite for genetic conservation. Fortunately, many breeds have pedigree information to serve as the basis for such an analysis. Breed-wide reports on levels of inbreeding for beef and dairy have been published. For example, Cleveland et al. (2005) reported inbreeding levels for Hereford cattle, the most complete analy-

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sis of that breed in the United States since the 1930s (Willham, 1937), and Wiggans et al. (1995) published inbreeding levels for Ayrshire, Brown Swiss, Guernsey, Holstein, Jersey, and Milking Shorthorn cattle. To date, no such breed-wide analysis has been performed for US Berkshire, Duroc, Hampshire, Landrace, and Yorkshire breeds. Partial analyses for these breeds have been performed in the US and Canada, but they lacked a long-term perspective and did not evaluate the status of the entire breed (Highfill et al., 1982; Hubbard et al., 1990). Rathje (2000) points out that 4 of the study breeds are used by breeding companies to form composite populations, underscoring their importance in supporting genetic progress and therefore a need to understand the level of genetic diversity. Therefore the objective of this study was to fill this information void by establishing a baseline for 5 major pig breeds. Specifically, to derive measures of inbreeding, trends in registration, breeder structure, generation intervals, and effective population size.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the study did not utilize any live animals. Pedigree records were obtained from the National Swine Registry 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). The stack_ped option in the ABTK was used to generate a list of animals that appear as both a sire and dam in the pedigree and animals that appear as their own parent. Inbreeding coefficients (**F**) were computed using the ABTK and serve as the primary basis for the evaluation.

Founder animals, defined as having both parents unknown, 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 with mean inbreeding, percentage of inbred animals, and number of years of registrations to determine any associations or trends.

Regression procedures were performed using SAS (Cary, NC). Increases in inbreeding per generation (**ΔF**) were calculated by regressing individual inbreeding coefficients on generation number (MacKinnon, 2003). Contrast statements were used to test for differences in ΔF among breeds. 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). Contrast statements were used to test breeds for differences in generation intervals. To determine if inbreeding levels were influenced by declining number of registrations, the rate of change of inbreeding was compared with the rate of change of number of registrations per year, and correlations were computed for each breed.

To obtain a current assessment of inbreeding levels for each breed, the inbreeding frequencies were calculated for animals born 2006 and later (using the relationships from the entire pedigree). Coefficient of relationship between boars provides an assessment of future inbreeding. The boars that are producing the majority of the offspring are driving changes in genetic diversity and the inbreeding levels for each population. Therefore, the approach by VanRaden and Smith (1999) was used to compute the coefficient of relationships between the top 10% of boars, as defined by number of progeny registered, for 2006 and later. The top 10% of boars included 90, 160, 114, 40, and 199 Berskshire, Duroc, Hampshire, Landrace, and Yorkshire males, respectively. To further assess the genetic relationship within each breed, influential males were determined by computing the number of great-grandprogeny (**GGP**) registered in the entire pedigree and were grouped into 10 percentiles; each percentile included 675, 2,662, 2,321, 737, and 4,046 males for Berkshire, Duroc, Hampshire, Landrace, and Yorkshire, respectively.

In general, the number of breeders producing breeding stock within any breed has decreased. Evaluating the number of breeders and the length of time a breeder has registered animals provides insight into potential losses of genetic diversity. To make such an assessment, breeder summary statistics were computed for the breed with the fewest registrations (Berkshire) and the most registrations (Duroc) to evaluate how breeder structure influences the genetic diversity of the breed.

Breeder statistics included number of breeders, geographic location, and years they registered pigs of a particular breed. Breeders were grouped into longevity groups of 1 to 3, 4 to 6, 7 to 9, 10 to 12, and 13 and more years of registering pigs as described by Maiwashe and Blackburn (2003) and were evaluated using contrast statements in SAS for differences in inbreeding levels. Average herd size for birth years 2006 to 2008 was computed and grouped into 1 to 5, 6 to 20, 21 to 50, and more than 50 pigs registered per year, and differences in inbreeding levels were evaluated using contrast statements in SAS.

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), coefficient of relationship between sires, 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[1]	6,748	26,615	23,206	7,370	40,458
Unique dams[1]	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
Coef. of relationship[2]	0.135 (90)	0.083 (160)	0.122 (114)	0.129 (40)	0.116 (119)
Boars in repository, n	29	50	33	29	91

[a-e]Within a row, values without a common superscript differ ($P < 0.0001$).

[1]Unique sires and dams include any boar or sow that produced any number of progeny.

[2]Coefficient of relationship between top 10% of sires producing the most progeny born 2006 and later, number boars in parentheses.

RESULTS AND DISCUSSION

Population Status

Summary statistics for each breed are shown in Table 1. In general, records started being stored in electronic format for each breed registry around 1980. Number of registrations peaked in 1990 for all breeds, except Berkshire, which peaked in 2000. From 2001 to the present, registration numbers have declined for all breeds. Comparing peak year registrations with registrations in 2007 showed a decline of 59.8, 92.8, 95.2, 73.0, and 58.6% for Berkshire, Duroc, Hampshire, Landrace, and Yorkshire, respectively. Duroc registrations, the most populous breed, declined from 176,621 in 1990 to 12,787 in 2007. This decline in registrations is indicative of the shift of the swine industry from reliance on purebred populations to large breeding companies that primarily develop and market composite populations.

Number of dams outnumbered number of sires by approximately 4 to 1. The most offspring registered for a single sire for lifetime production by breed was 481, 3,797, 1,624, 949, and 1,417, whereas the single dam lifetime 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, showing how influential individual boars are within a breed.

The Food and Agriculture Organization of the United Nations (**FAO**, 2000) suggested the N_e for a breed be maintained above 50; however, Meuwissen and Woolliams (1994) suggested a minimum range for N_e of 31 to 250 to maintain population fitness. By both benchmarks, Duroc, Hampshire, and Yorkshire have relatively robust N_e levels. The N_e values for Berkshire and Landrace are smaller and therefore may warrant additional attention. Inbreeding rate is another criterion for measuring population health, and Nicholas (1989) has recommended a ΔF rate of <0.005, whereas the

FAO (2000) suggested a ΔF rate of <0.01 as a goal. All breeds meet the FAO goal, but Berkshire and Landrace are greater than the rate suggested by Nicholas (1989). 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 yr for Berkshire to 2.21 yr for Yorkshire. Generation intervals (Table 1) were significantly different among breeds ($P < 0.0001$); however, this difference was just over 6 mo between the longest and shortest GI.

With the increase in AI in the swine industry (Blackburn, 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 (e.g., Meuwissen, 1997).

The mean F for each breed is reported in Table 1; however, because most of those animals are no longer actively contributing genes to the future generations, reporting the mean F values as representing the entire breed underestimate the inbreeding present in the current population, although this value is routinely reported. For Canadian pigs, Hubbard et al. (1990) reported average inbreeding levels of 0.75, 0.66, 0.53, and 0.70% for 10 yr for Duroc, Hampshire, Landrace, and Yorkshire, respectively; they assumed all ancestors before the 10-yr period were unrelated, while acknowledging this was unlikely. Clearly, the inbreeding levels of the US population exceed those of the Canadian population, although the Canadian numbers are likely underestimated. Knowing the status of the current population is crucial for conservation activities. Figure 1 shows the percentage of animals, born 2006 or later, with various inbreeding levels for the 5 breeds. Berkshire (44.7%) and Landrace (39.9%) had the greatest percentages of animals with F > 0.10 compared with the other breeds. In contrast, Duroc had 64% of the current population with F $\leq$ 0.05 and 88% with F $\leq$ 0.10.
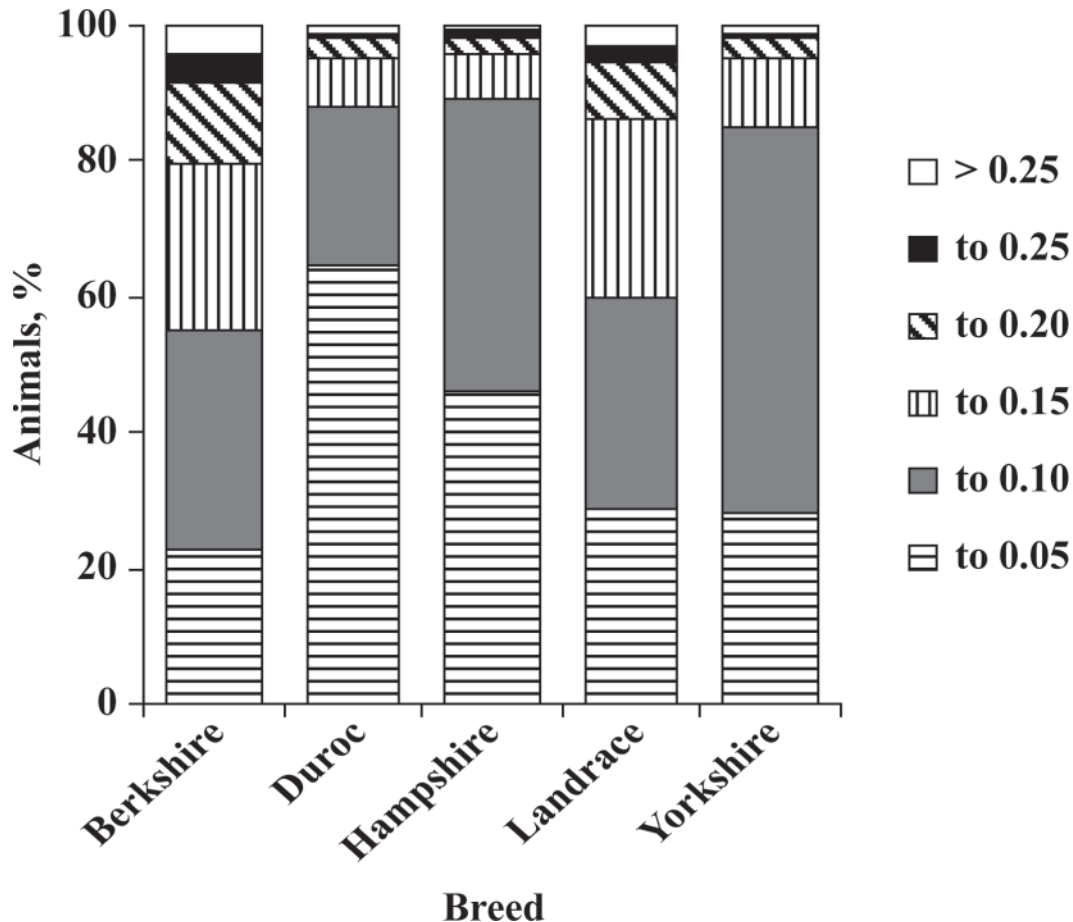
Figure 1. Inbreeding coefficient frequencies by breed for animals born 2006 and later.

The coefficient of relationships between the top 10% of sires producing the most progeny born 2006 and later are shown in Table 1. With the exception of Duroc, on average the most popular boars for the remaining 4 breeds had a relationship as close as first cousins.

After 17 generations (the most generations computed to allow for comparison across all breeds) Landrace had the greatest mean F of 17.9% (Figure 2). That is every animal being, on average, somewhere between half-siblings (12.5%) and full-siblings (25%). As a breed, Hampshires had the least F (6.8%). Whereas inbreeding tends to be less for this breed, the average relationship of Hampshires is greater than first cousins, suggesting even the breed with the least inbreeding is at risk for losing genetic diversity.

The progression of inbreeding for Berkshires is note-worthy (Figure 2); of particular interest is the decrease in inbreeding after 10 generations. Generations 10 through 12 generally correspond to the years 1993 to 2000. The decrease in inbreeding may be attributable to a change in breeding strategies to facilitate the marketing of Berkshire pork in US and Japanese markets, which began in 1994. The Berkshire Gold Program, started in 1994, and the Royal Berkshire Program, started in 1998, were eventually replaced by the 100% Berkshire Program, which markets Berkshire pork from certified herds to Japan and the United States for a

premium. This program guarantees the animals marketed are 100% Berkshire, traceable to source farms, and from herds that meet the National Pork Board's Pork Quality Assurance Level III guidelines (McMullen, 2006). Berkshire registrations were steady throughout the late 1980s and early 1990s, but began to increase steadily in 1995 until the peak in 2000. The increased value of Berkshire pigs brought about by specialized marketing programs further suggests that mating decisions changed for this breed, resulting in a decline of inbreeding. This is a similar situation to that observed in Hereford cattle by Cleveland et al. (2005).

After 12 generations, for all breeds, all animals had an F > 0 (Figure 3). All breeds followed a similar rate of increase in the proportion of inbred animals. A steady increase in the proportion of inbred animals was also reported by Hubbard et al. (1990).

Figure 4 shows how the average generation number increased with number of registration years. The steepest ascent was observed for Berkshire, which also had the shortest GI. Yorkshire generation number plateaued during registration yr 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
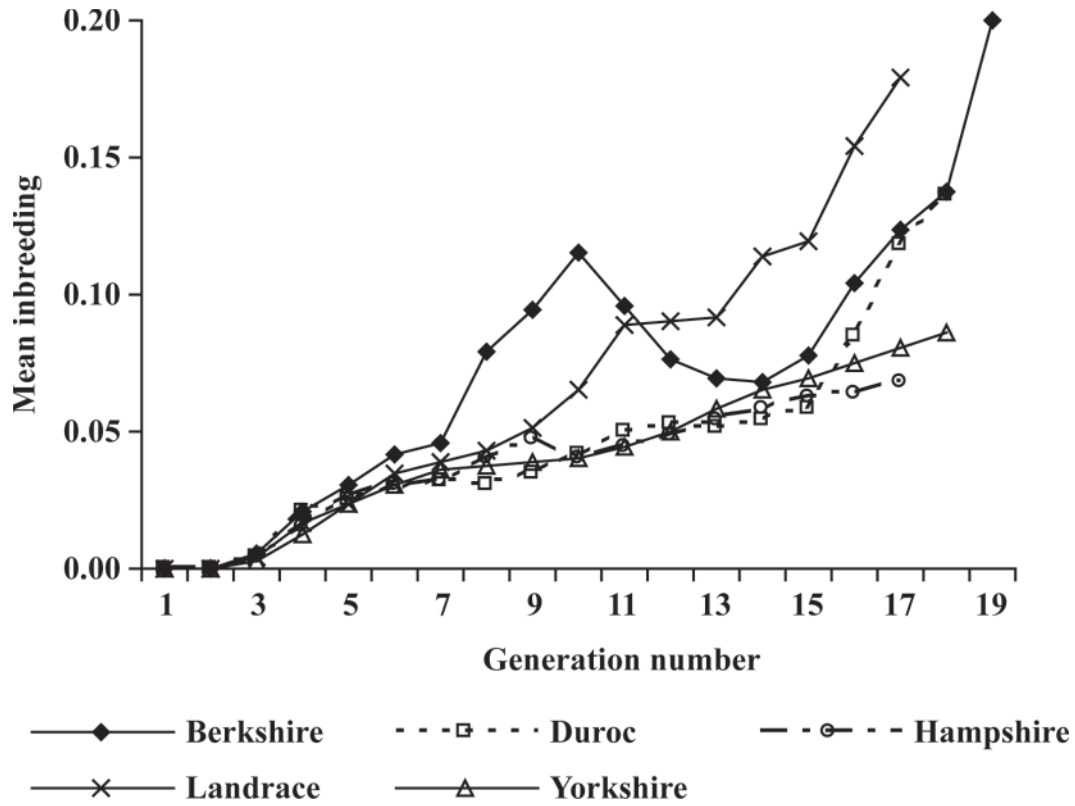
Figure 2. Inbreeding by generation number for all breeds.

were assigned the average generation number for their birth year, and the generation numbers of the population were recalculated. The slope of the curve increased (Figure 5), showing how influential a few heavily used imported males were for the Yorkshire breed. The influence of imports was also observed by Cleveland et al. (2005) in Hereford cattle and Hubbard et al. (1990) in Duroc and Hampshire pigs.
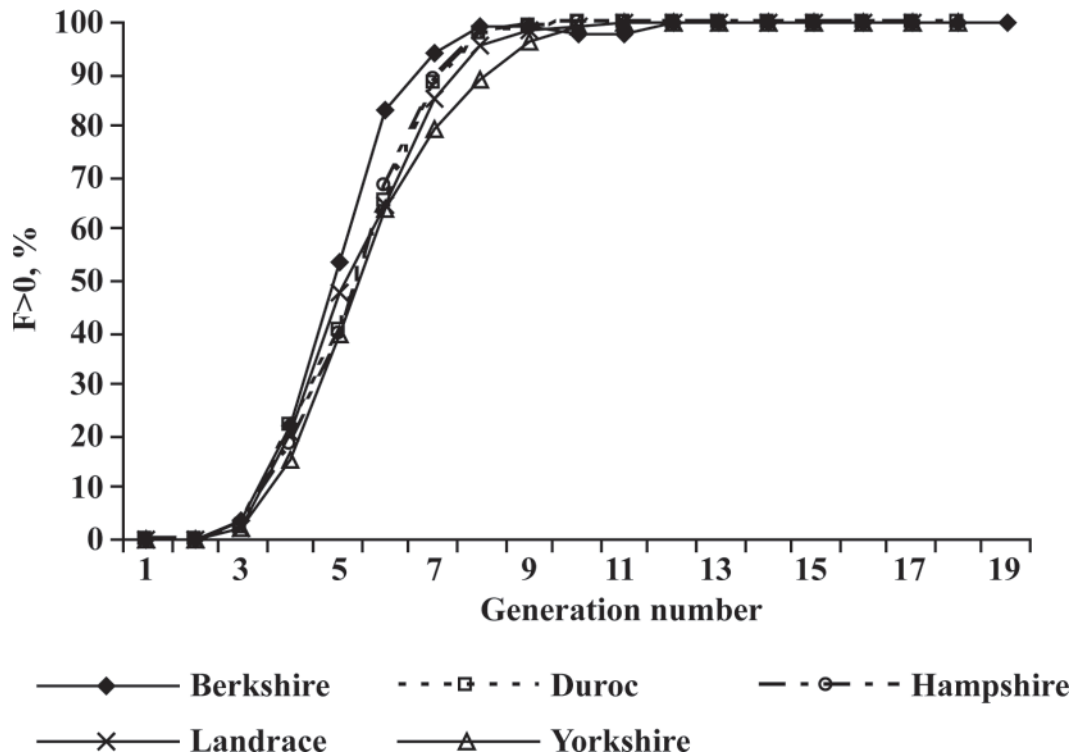

Figure 3. Percentage of animals with inbreeding coefficient (F) >0 by generation number for all breeds.
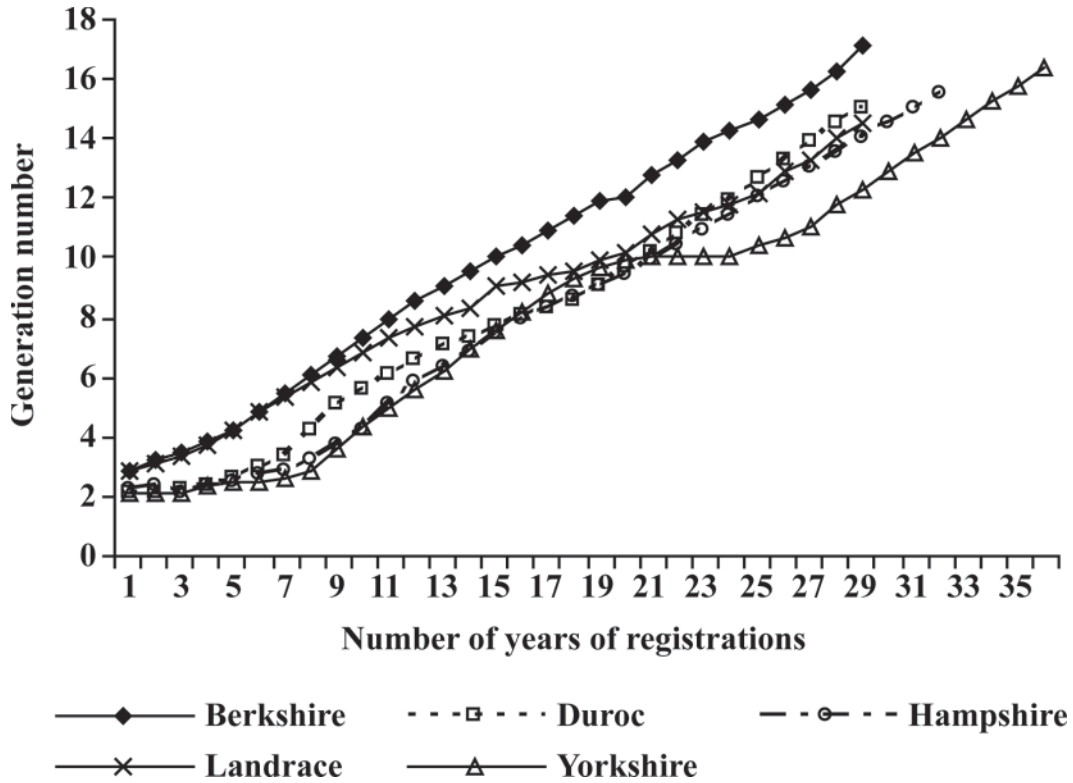
Figure 4. Generation number by number of years of registrations for all breeds.

To better understand the association between the rates of change in inbreeding and number of registrations per year, within breed correlations were performed. The correlations were 0.24, 0.38, 0.31, 0.58, and 0.20 for Berkshire, Duroc, Hampshire, Landrace, and Yorkshire, respectively, indicating a modest, but
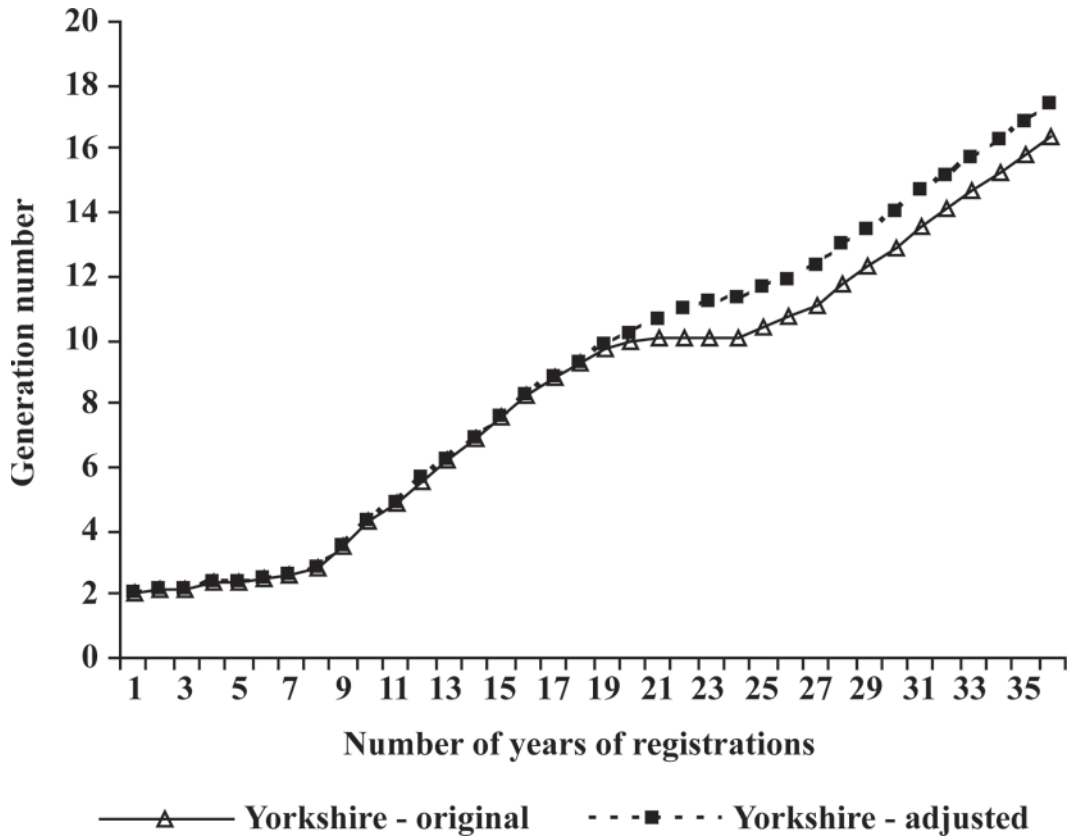

Figure 5. Generation number by number of years of registrations for Yorkshire and for Yorkshire adjusted for 13 sires.
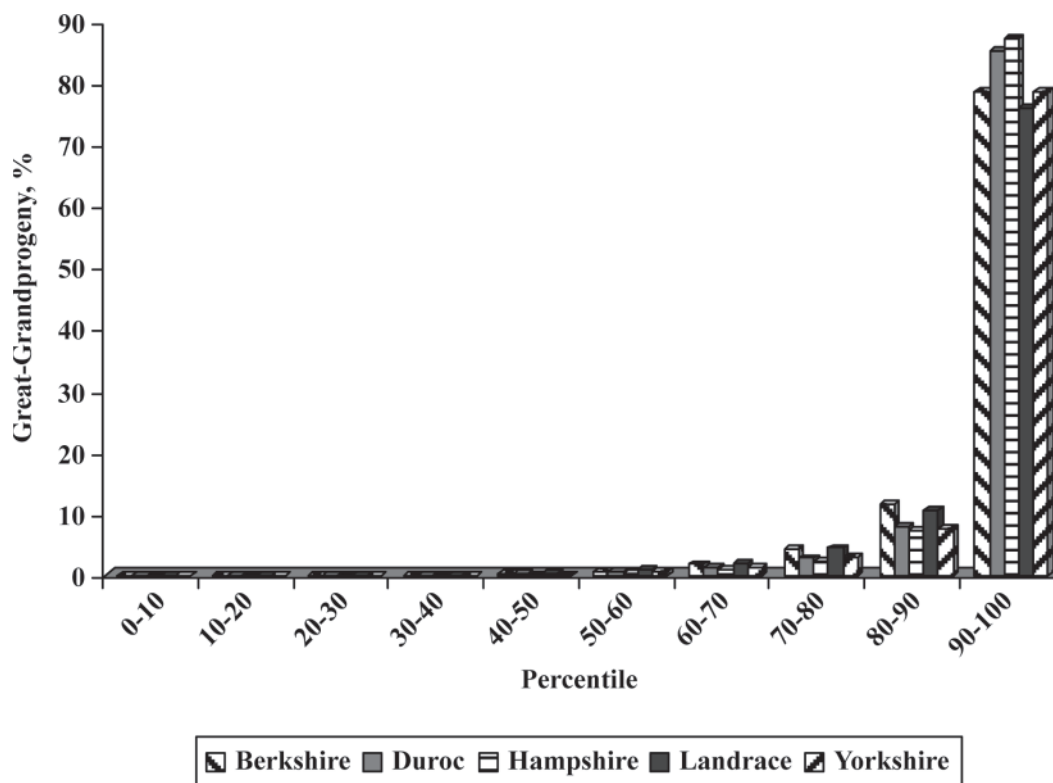
Figure 6. Influential males grouped into 10 percentiles by number of great-grandprogeny registered for all breeds.

nonsignificant ($P > 0.05$), association between the rates of change in inbreeding and number registered. This result suggests that other factors influenced inbreeding besides population size; otherwise the correlations would have been closer to unity. One factor expected to influence inbreeding levels is the popularity of particular boars, regardless of the population size.

To evaluate the importance of the most popular boars, the number of GGP registered were computed and were grouped into 10 percentiles (Figure 6). 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). Heavier use of a small proportion of available boars implies a greater selection intensity, which might be expected for Duroc and Hampshire because they tend to be used as sire breeds. However, it is interesting that these breeds have smaller inbreeding levels (Figure 1). Perhaps, this smaller level may be due to larger populations. 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 majority of GGP, suggests the genetic base can contract in a few generations.

Breeder Dynamics

Breeder summary statistics are shown in Table 2. Berkshire breeders were found in 39 states, whereas Duroc breeders were in 47 states plus Puerto Rico. In addition, the Duroc is internationally important, being found in 93 countries (FAO, 2007). The top 5 states by number of Berkshire breeders were Oklahoma, Indiana, Illinois, Texas, and Iowa; breeders from these states accounted for 60.5% of all pigs registered. The greatest concentration of Berkshire pigs was in Iowa, Illinois, Indiana, Minnesota, and Wisconsin. Trends and rankings have changed over time; when looking at the current population of pigs born 2006 and later rather than the entire population, the most number of breeders were found in Indiana, Oklahoma, and Illinois, whereas the most pigs were in Iowa, Indiana, and Illinois. For Duroc, the top 5 states by number of breeders were Indiana, Oklahoma, Texas, Illinois, and Ohio, accounting for 46.5% of pig registrations. The most pigs were registered in Illinois, Indiana, Ohio, Iowa, and Nebraska. Reranking occurred in the current Duroc population; the most breeders of pigs born 2006 and later are located in Indiana, Texas, and Illinois, with the most pigs being concentrated in Indiana, Illinois, and Ohio.

The inbreeding levels for the current population (pigs born 2006 and later) were evaluated for differences by breeder longevity group, and the results are presented in Figure 7. Although some of the within breed groups were statistically different from one another ($P < 0.02$), there was no trend for either breed to conclude the results are biologically important. As with all breeds in the study, the Berkshire and Duroc fulfill different markets, and differences in breeder structure were expected to exist that would assist in identifying areas of opportunity to manage genetic diversity in each breed. Maiwashe and Blackburn (2004) discussed the poten-
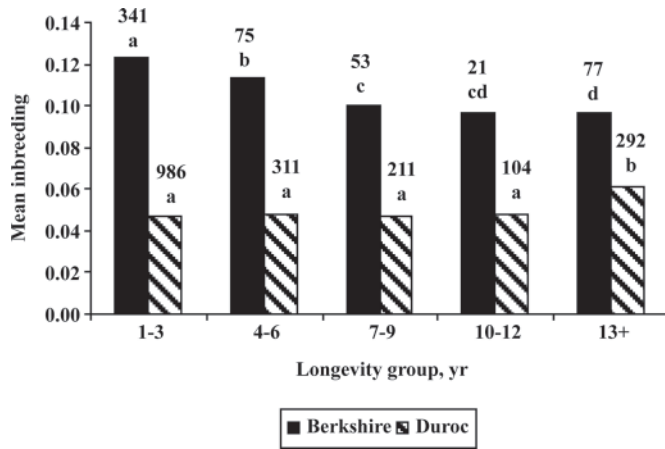
Figure 7. Inbreeding level by longevity group for Berkshire and Duroc pigs born 2006 and later. [a–d]Values are within breed, and those without a common letter differ ($P < 0.02$). Values above each bar are the number of breeders.
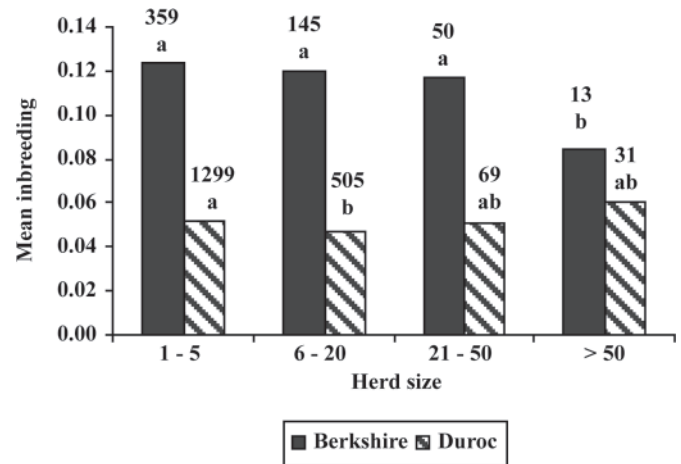

Figure 8. Inbreeding level by average herd size for Berkshire and Duroc pigs born 2006 and later. [a,b]Values are within breed, and those without a common letter differ ($P < 0.05$). Values above each bar are the number of breeders.

tial impact of short-term ownership on Navajo Churro sheep genetic diversity, and the average ownership of Berkshire and Duroc pigs being only 4.0 yr suggests that those breeders with less time invested in either breed might tend to have a greater inbreeding level than more established breeders. The longest-term Berkshire breeders had a reduced inbreeding level (2.7%) than the shortest-term breeders ($P < 0.0001$). However, the longest-term Duroc breeders had a greater inbreeding level (1.4%) than the shortest-term breeders ($P < 0.0001$). The lack of a consistent trend for these 2 breeds may suggest that due to the relatively larger number of pig breeders (vs. Navajo Churro breeders), the effects of breeder dynamics are dampened.

Inbreeding levels were evaluated for differences by average herd size (Figure 8). Similar to the results for differences in longevity group, herd size showed no definitive trend despite some of the within-breed groups being statistically different from each other ($P < 0.05$). For Berkshire, herd sizes greater than 50 animals had a reduced inbreeding level than the other 3 groups ($P < 0.05$). For Duroc, herd sizes of 1 to 5 animals had a greater inbreeding level than herd sizes 6 to 20 animals ($P < 0.04$), with no other statistical differences among the other herd sizes. From a practical standpoint, herd size does not appear to influence inbreeding levels.

Conclusions

This study serves as a baseline for these 5 pig breeds in the United States. Having estimated effective population size, inbreeding levels, and inbreeding rates provides greater insight about the genetic diversity of these breeds which can be used in conservation strategies. Although the inbreeding levels are useful genetic diversity indicators, the depth of the pedigrees is relatively shallow given the initial import dates (1820 to 1830) into the US Berkshire, Duroc, Hampshire, and Yorkshire, and the 1930s for Landrace (McMullen, 2006; National Swine Registry, 2009). Due to the pedigree depth, it might be safely assumed the reported inbreeding levels are underestimates. However, the rate of change in inbreeding is likely not to be biased and is in fact an important indicator of how quickly genetic diversity may be contracting which can be utilized in genetic resource management. Analysis using DNA markers might further elucidate within breed genetic diversity and the genetic differences among the breeds presented in this study (e.g., Vicente et al., 2008).

Berkshire and Landrace are borderline for both effective population size and increase in inbreeding per generation, whereas Duroc, Hampshire, and Yorkshire are within acceptable levels. Berkshire and Landrace also had the fewest registrations, increasing the challenge

Table 2. Summary statistics for number of breeders, mean and range of number of years of registering animals, and peak number of active breeders for Berkshire and Duroc

Item	Berkshire	Duroc
Breeders, n	1,596	7,481
Mean years registering animals	4.0	4.0
Range of years registering animals	1 to 33	1 to 31
Peak active breeders, n (year)	361 (2007)	1,604 (1989)

breeders face making mating decisions that minimize long-term inbreeding and maximize performance.

Over the past 2 decades the swine breeding industry has been restructured toward corporate breeding companies developing proprietary composite lines that have replaced a significant portion of the purebred seedstock industry. The status of the rate of inbreeding for such composite populations is unknown and not formally part of this analysis. Furthermore, it is not clear how frequently and to what order of magnitude pigs from purebred breeders migrate into composite populations. Based upon Rathje (2000), Danish Landrace, Hampshire, and Duroc nucleus herds (which are part of a corporate breeding strategy) had levels of ΔF and GI that suggest a slightly faster contraction of genetic diversity than what was found in this report. We also know that breeding companies can and do set limits on the extent to which high performing boars are used and as a result are able to control ΔF among their populations. Whereas breeding companies may successfully control ΔF, the tendency for inbreeding to increase over time will still exist, and if for no other reason corporations will still depend upon various purebred populations as a source of lowly related breeding stock.

The current trends suggest level of inbreeding will continue to rise, if so and accompanied by artificial selection, the potential for changing allele frequencies or loss of alleles or both could be a concern. Such a situation can be managed at the in situ and ex-situ levels. For in situ purebred and composite populations, there is a need to incorporate mating strategies that control the rate of inbreeding (Meuwissen, 1997). As an alternative for some breeds or populations, the establishment of a set of rules that limit the impact of individual sires or dams by limiting the number of progeny utilized in future matings could be established (Rathje, 2000). However, for such procedures to function, a method of compensating a breeder for foregoing additional profits from a specific animal would have to be established.

Ex situ germplasm collections held by gene banks are also a source of genetic variability for industry to utilize. For such collections to have utility, they must contain a broad sampling of minimally related animals. In addition, the frequency of collection efforts must be such as to ensure the genetics contained in the collection are relevant to the industry. To date, the National Animal Germplasm Program has initiated germplasm collections on all 5 breeds (Table 1); however, additional collections are needed and planned to complete the process. 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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