

ESTIMATES OF EFFECTIVE POPULATION SIZE AND INBREEDING LEVEL FOR THREE AUSTRALIAN PIG BREEDS

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SUMMARY

Selective breeding may result in higher inbreeding levels which can lead to inbreeding depression and limit future genetic gain. This study quantified inbreeding levels and evaluated effective population sizes for Large White (LW), Landrace (LR) and Duroc (DU) populations in Australia. Pedigree data from 1994 to 2015 representing about 12 generations on average were explored with the software package PopRep by Groeneveld *et al.* (2009) which provides multiple population parameters. Pedigree completeness was highest in 2004 and 2005 when it reached about 95% and 80% in the third and sixth generation. Average inbreeding levels were highest for these years with averages of 0.031, 0.034 and 0.050 in LW, LR and DU, respectively. Two herds joined the across-herd genetic evaluations at that time and pedigree completeness varied from 80 to 90% and from 60 to 70% in the third and sixth generation in subsequent years leading to lower estimates of inbreeding levels. Estimates of effective population size varied from 64 to 98 in LW, from 52 to 108 in LR and from 42 to 61 in DU over time. These estimates of effective population size are imprecise and an underestimate of true effective population sizes given the limited time period considered and the extent of missing pedigree.

INTRODUCTION

Selective breeding may result in higher inbreeding levels leading to inbreeding depression, which is a decrease of the population fitness, because of the accumulation of deleterious recessive alleles (Falconer & Mackay 1996; Ouborg *et al.* 2010). Higher inbreeding levels may also limit future genetic gain because of a lack of genetic variation between individuals. It is therefore important to be able to quantify inbreeding levels in order to estimate population structure and avoid these problems. Moreover, if very few sires (compared to dams) are used for artificial insemination, the effective population size (N_e) is lowered, which increases inbreeding. According to Kimura and Crow (1963), "the effective population size is defined as the size of an idealized population that would have the same amount of inbreeding or of gene frequency drift as the population under consideration." The aim of this study was to estimate inbreeding levels and to evaluate effective population size of 3 Australian pig populations.

MATERIALS AND METHODS

Pedigree for the Large White (LW), Landrace (LR) and Duroc (DU) breeds were extracted from the National Pig Improvement Program database (<http://npip.une.edu.au>). Data were recorded from January 1994 to September 2015 for LW, and from January 1995 to September 2015 for LR and DU (Table 1). The pedigree of these 3 breeds were explored using the software package PopRep by Groeneveld *et al.* (2009).

Pedigree Completeness. The pedigree completeness statistically quantifies the percentage of missing animals over generations. It is important to quantify completeness of pedigree because estimates of inbreeding levels and effective population sizes are affected by this parameter. If there are too many missing animals, the results will be biased because the inbreeding coefficients will be

underestimated. This will also affect estimates of effective population size as they depend on the rate of inbreeding per generation. Pedigree completeness was computed with the following formula:

$$I_{dk} = \frac{1}{d} \sum_{i=1}^d a_i$$

where d is the number of generations considered, k represents the paternal or maternal line of the individual I , and a_i is the proportion of known ancestors in the generation i (MacCluer *et al.* 1983). Pedigree completeness ranges from 0 to 1 and increases for later generations as more pedigree information becomes available over time. For the first generation, pedigree completeness is often 100% because pedigree of parents is known.

Table 1: Data structure for the Large White (LW), Landrace (LR) and Duroc (DU) breeds

	Number of animals	Number of males	Number of females	Number of sires	Number of dams	Number of herds	Period of recording
LW	264,296	133,020	131,276	2,287	13,206	11	1994-2015
LR	147,160	74,727	72,433	1,351	6,995	8	1995-2015
DU	53,931	27,511	26,420	643	2,445	8	1995-2015

Effective population size and inbreeding level. PopRep uses 6 different methods to compute inbreeding levels within population, leading in turn to 6 estimates of effective population size (N_e). The standard method (Falconer and Mackay, 1996) to calculate N_e is $N_e = 1/(2\Delta F)$, where ΔF is the rate of inbreeding per generation. In order to decide which method is the best to use, PopRep computes 2 side conditions which have to be met for the method to be reliable. These 2 side conditions require positive estimates of N_e for at least 4 years and impose a limit on the variation of estimates of N_e over time. Based on these conditions, the method by Gutiérrez *et al.* (2009) was the only one to be reliable for the 3 breeds based on the 2 side conditions (data not shown). This method provided most consistent estimates of N_e over time because it considered the complete pedigree length.

RESULTS AND DISCUSSION

The amount of pedigree data available affects maximum levels of inbreeding and subsequently effective population size. The current study was based on data from 20 years. Given the average generation interval of 1.8 in LW and LR and 1.7 in DU, these data represent about 12 generations on average. A longer time period of 35 years was considered by Welsh *et al.* (2010) who reported results for 19 generations equivalent of an average generation interval of 1.8 years. In comparison, Krupa *et al.* (2015) used pedigree data over 25 years from 1988 to 2013 and the maximum number of generations traced varied from 20 to 25 between breeds. These differences in number of generations should be taken into account when comparing inbreeding levels.

Pedigree Completeness. Pedigree information was complete (100%) for the first generation in 12 (LW), 13 (LR) and 10 (DU) years of the 20 years from 1995 to 2014. In the first year when data were available (1994 for LW and 1995 for LR and DU), pedigree completeness started with 33% for the third generation and then increased linearly for about 6 years as fewer generations were censored (Figure 1). Similarly, pedigree completeness started with 17% for the sixth generation and increased linearly for the following 10 years of pedigree recording. Maximum pedigree completeness plateaued at about 95% in the third generation for DU and LR and decreased to a range of 80 to 90%

in subsequent years. In comparison, maximum pedigree completeness was about 80% in the sixth generation and decreased to a range of 60 to 70% afterwards. The trend in pedigree completeness over time was slightly different for LW in comparison to LR and DU. Pedigree completeness was initially lower and reached its highest value at a later point while pedigree completeness was slightly higher in later years. Animals with unknown pedigree were introduced in 2004 and 2006 when 2 new herds joined the scheme and some importation of unknown animals continued over time. These importations of unknown animals reduced pedigree completeness in the Australian populations. Specific time points for importation of unknown animals into Czech pig breeds were also visible in the trends for pedigree completeness shown by Krupa *et al.* (2015). These importations occurred in the early 1990s and until 2013, pedigree completeness converged to nearly 100% for all 6 generations in LW and LR populations. Czech DU and Pietrain had further importations over time and in 2013, pedigree completeness varied from 75 to 90% in the third to sixth generation in these 2 breeds. Overall, these trends demonstrate the extent of missing pedigree observed in pig breeding populations.

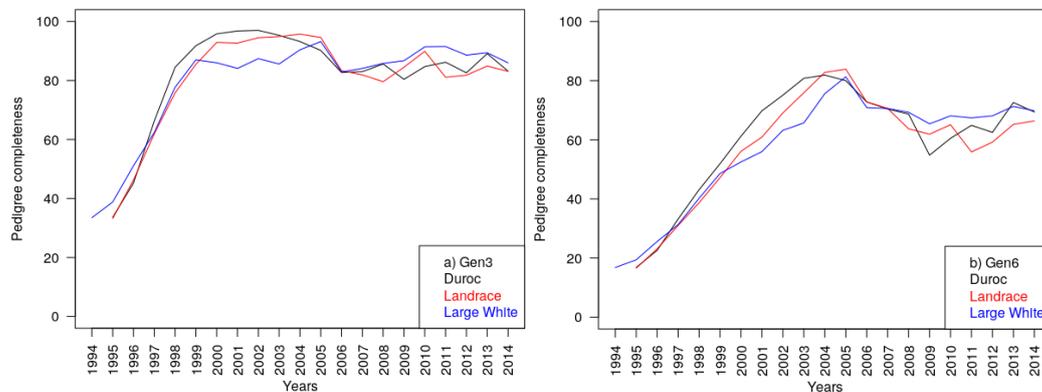


Figure 1. Pedigree completeness for the 3 breeds in the a) third and b) sixth generation.

Effective population size. Pedigree data was not complete for 2015 and population estimates for that year are not shown because the computation of N_e may be incorrect. Similarly, not all herds were represented in the 1994 data for LW and the high N_e estimated for this year was likely an overestimate (Figure 2a.) From 1995 until 2014, estimates of N_e varied from 64 to 98 in LW, from 52 to 108 in LR and from 42 to 61 in DU. Effective population sizes varied from 30 to 225 across years and breeds in the study by Krupa *et al.* (2015). In 2012, population sizes were more stable and varied from 35 for DU to 83 in Pietrain, similar to the range observed in this study.

Inbreeding. Average inbreeding levels of all animals increased until 2004 and 2005 (Figure 2b). For these years average inbreeding levels were highest with averages of 0.031, 0.034 and 0.050 in LW, LR and DU, respectively. Since then, breeds were less stable with herds leaving or joining the recorded populations which is reflected in lower pedigree completeness and more variable estimates of average inbreeding coefficients over time. In comparison, mean inbreeding levels were about 0.045 for Yorkshire, Duroc and Hampshire, about 0.065 for Landrace and about 0.075 for Berkshire after 12 generations in a US study (Welsh *et al.*, 2010). Approximately 12 generations were considered in the current study and mean inbreeding levels continued to increase after 12 generations for the US pig populations. Considering a longer time period and more generations with more complete pedigree information is expected to result in higher estimates of mean inbreeding levels and lower estimates of effective population size.

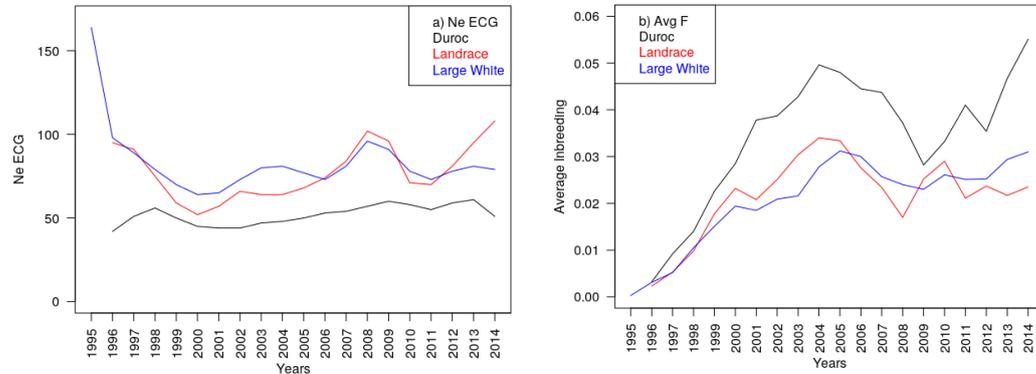


Figure 2. Evolution of a) effective population size and b) average inbreeding over years for the 3 breeds using the complete pedigree to estimate rate of inbreeding per generation.

CONCLUSION

Maximum estimates of inbreeding levels varied from 0.031 to 0.050 for the 3 breeds and effective population sizes varied from 42 to 108 over years for these breeds. These estimates were similar to estimates presented in other studies. However, pedigree was incomplete and estimates of inbreeding levels and subsequently effective population sizes are imprecise and an under-estimate of true population values. Pedigree data is often incomplete in livestock populations and estimates of effective population size based on pedigree information should only be regarded as ‘guestimates’. Further research should focus on evaluation of the benefits of using genomic information for estimating inbreeding levels more accurately and the impact of higher inbreeding levels on performance and fitness traits.

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