Bhutan Journal of Animal Science (BJAS)
Volume 6, Issue 1, Page 12-21, March 2022

INBREEDING EFFECTS ON REPRODUCTIVE TRAITS OF PURE-LINE COLORED PIG BREEDS IN GOVERNMENT PIG FARM IN BHUTAN

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ABSTRACT: Inbreeding in most cases reduces the performance of animals referred to as inbreeding depression. The objectives of the study were (i) to investigate the increase of inbreeding over time and (ii) to estimate the effects of inbreeding on seven reproductive traits in three pure-line colored pigs at National Piggery Research and Development Centre (NPiRDC) in Bhutan. Farrowing records of 3073 from 694 sows were used to estimate the effects of dam inbreeding, sire inbreeding and litter inbreeding on reproductive traits using a linear mixed model. The inbreeding rate per generation was 2.59% for Duroc, 1.14% for Large Black and 1.06% for Saddleback population. The sire inbreeding showed a significant (p<0.05) effect on gestation length (GL). The litter inbreeding significantly reduced number weaned (NW) by 0.015 piglets and increased pre-weaning mortality (PWM) by 0.174% per 1% increase in litter inbreeding. The linear model of dam inbreeding did not show significant effects on any of the traits analyzed. However, the quadratic model showed a significant (p<0.05) effect of dam inbreeding on PWM, suggesting that the effect of dam inbreeding depend on level of dam inbreeding. The interaction of dam inbreeding and breed was significant (p<0.001) for PWM, suggesting the effect of dam inbreeding differ between breeds on PWM. The effects of dam inbreeding were -0.315% (SE=0.081) in Duroc, 0.390% (SE=0.139) in Large Black and 0.614% (SE=0.124) in Saddleback. Although unfavorable effects of inbreeding were detected on most of the analyzed traits, the inbreeding depressions were not drastic at present. Relatively, the litter inbreeding had stronger effect than dam and sire inbreeding on the traits analyzed. In the future, investigating effects of inbreeding on other traits that were not covered under this study might be useful to understand more on the effects of inbreeding at the farm.

Keywords: Colored pig breeds; effects of inbreeding; inbreeding coefficients; pedigree; reproductive traits

1. INTRODUCTION

Livestock breeding programs mostly take place with closed populations which makes inbreeding an important issue (Lopes et al. 2019). Inbreeding is the probability that the alleles are identical by descent (IBD) as they are inherited from a common ancestor (Curie-Cohen 1982; Wakchaure and Ganguly 2015) from mating between relatives (McParland et al. 2007; Pooley et al. 2014). Inbreeding mainly result due to a small population size (Yadav et al. 2019), and keeping inbreeding per generation at an acceptable level is imperative to avoid deleterious consequences (Croquet et al. 2006). It is recommended to maintain rate of inbreeding below 1% per generation as a general thump rule (Meuwissen and Woolliams 1994; FAO 1998; Wakchaure and Ganguly 2015).

Detrimental effects of inbreeding are called inbreeding depression and is characterized with a reduction of the mean phenotypic value and premature death in the extreme case of deleterious alleles (Doekes et al. 2019; Vígh et al. 2007). Inbreeding depression is closely related to fitness of inbred individuals (Keller and Waller 2002;

Mattey et al. 2013). It may affect fitness in two ways; reduction of fitness in inbred individuals themselves and then outbred individuals may also suffer a reduction in fitness when they depend on care from inbred parents (Mattey et al. 2013). Inbreeding is reported to reduce the immune system functions (Yadav et al. 2019), increase susceptibility to infectious diseases (Acevedo-Whitehouse et al. 2003), reduce fertility (Fitzpatrick and Evans 2009; Hauser et al. 1952; Wakchaure and Ganguly 2015) and tolerance to extreme environmental conditions (Dahlgaard et al. 1995; Shikano et al. 2001). In addition, it also affects genetic variance (Keller et al. 1990). In a closed population, inbreeding accumulates and genetic variance reduces over generations reducing rate of response to selection (De Roo 1988; Gama and Smith 1993).

Inbreeding in pig population has negative effects on most reproduction and production traits (Köck et al. 2009) such as the litter size (total number of piglets born, number born alive, number weaned) and weight (litter weight at birth, litter weight at wean) showing a larger inbreeding depression impact (Leroy 2014). Inbreeding is gaining economic importance due to losses resulted from inbreeding depression in production, growth, health and fertility (Weigel 2001). Do et al. (2015) also emphasized on the benefits to investigate and control inbreeding.

Pig breeding at the National Piggery Research & Development Centre (NPiRDC) started with relatively small founder populations following line breeding strategy for the last 16 years; as such, a high rate of inbreeding and inbreeding depression is expected at the farm. Several breeding animals at the farm had high inbreeding coefficients (~ 40%) which warrants studies to investigate effects of inbreeding. With a mandate of the farm to produce and distribute quality piglets to the farmers, an increase in the inbreeding rate at the farm would affect farm productivity and piggery development as a whole in the country. Therefore, this study was aimed to investigate the inbreeding rate of colored pig breeds reared in the government farm and to estimate the effects of inbreeding on seven reproductive traits of pigs, which would enable in making an informed policy decision on the future pig breeding strategy in the country.

2. MATERIALS AND METHODS

2.1 Data source

The data was provided by NPiRDC under the Department of Livestock (DOL), Ministry of Agriculture and Forests (MOAF) of Bhutan, in collaboration with Genetic Solutions Limited, New Zealand. The Breeding animals (sows and boars) on the farm were purebred Duroc, Large Black and Saddleback, which were imported from the British Pig Association (BPA), United Kingdom in 2003.

2.1.1 Production data

Data files containing information on the reproduction traits were extracted from the program EliteHerd© Plus (version 4.2.2.0), a software package that facilitates the management of the pig breeding and grower herd records at the farm. Initially, a total of 3,282 farrowing records were available between 2004 and 2019. After data cleaning, 3,073 farrowing records from 694 sows (139 Duroc with 487 records, 297 Large Black with 1445 records and 258 Saddleback with 1151 records) were used for the study. The seven reproductive traits included for this study were gestation length (GL), total number born (TNB), number born alive (NBA), litter weight at birth (LWB), number weaned (NW) and litter weight at weaning (LWW). GL was the interval between the last mating and farrowing dates. TNB included total piglets born including those born dead in each farrowing. LWB was a sum of piglet's birth weight in each litter. NW included piglets available alive from each farrowing (from each sow) at the time of weaning. Piglets were normally weaned at the farm between 35 to 42 days after farrowing. LWW is calculated as a sum of piglet's weights at weaning (from each sow). An additional trait, pre-weaning mortality (PWM) was generated by subtracting NW from NBA divided by NBA and multiplied by 100, to estimate the effects of inbreeding on mortality of piglets between birth and weaning.

2.1.2 Fixed effects

The breed, parity, farrowing year, farrowing month, farrowing season were available as fixed effects. Number of classes, number of observations per class, mean and standard deviation (SD) for each class of fixed effects were checked to determine if there are enough numbers of observations in each class and to adjust class levels. The parity of breeding sows in the farm ranged from parity 1 to parity 10 with declining numbers of observations for higher parities. Thus, these 10 classes of parity effects were combined into three new class levels - Parity 1, Parity 2 and Parity 3. All sows in parities higher than or equal to parity 3 were combined in Parity 3. Biologically, sows in parity 1 and Parity 2 are young and it is likely to have immature endocrine systems, and different reproductive performance (Vargas et al. 2009).

For farrowing-year-season (FYS), the 12 months of farrowing were first incorporated into two classes of April-September (warm and monsoon) and October-March (dry and moderate) based on climatic pattern records of the National Hydrology and Meteorology Report of Bhutan (NCHM 2018). Subsequently, 16 year-class and 2 season-class were concatenated to form 32 groups of FYS effects. All the fixed factors, with adjusted classes, were verified for their significance in the model using R v3.0 and then in ASReml 4.1.

2.2 Calculation of inbreeding coefficients

The dam and sire inbreeding coefficients were calculated in the program EliteHerd© Plus 4.2.2.1 as the program was capable of calculating the inbreeding coefficients of individuals retained as breeding animals. The litter inbreeding coefficients were calculated using ASReml 4.1 as described by Gilmour et al. (2015). To do that, a unique litter identification number was assigned to one of the individuals from each farrowing and then added to the pedigree file which was extracted from EliteHerd© 4.2.2.1 (Gelephu herd). Subsequently, the inbreeding coefficient of litters were merged to the farrowing data file by their parents using R program.

3. Calculation of generation interval and inbreeding rate

The realized rate of inbreeding per year (ΔF) was calculated in retrospect from the average inbreeding in the current year (F_t) in comparison to that in the previous year (F_{t-1}) as illustrated in the formula below.

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

Generation interval (L) for each breed was computed with Retriever v1.0, an inbreeding monitor software as described by Windig (2021).

3.1 Statistical analyses

Effects of inbreeding on the traits analyzed were estimated by regressing phenotypes on inbreeding coefficients with single trait linear mixed model (Model 1). Inbreeding coefficients were defined as covariates. For simplicity, inbreeding coefficients of the dam, sire and litter were considered separately in the model to estimate their effects on traits.

$$y_{ijklm} = \mu + breed_i + parity_j + fys_k + \beta_1 (F)_{ijk} + Animal_l + PE_m + e_{ijklm} \quad (1)$$

Where y_{ijklm} is the individual observation of trait, μ is the overall mean of the trait, $breed_i$ is the i^{th} pig breed at the farm (i=1, 2, 3), $parity_j$ is the j^{th} adjusted new parity class (j=1, 2, 3), fys_k is the k^{th} farrowing-year-season of farrowing (k=1-32), β_1 the regression coefficients of inbreeding, F the inbreeding coefficients (i.e. F_d the dam inbreeding coefficient, F_s the sire inbreeding coefficient, F_l the litter inbreeding coefficient), $animal_l$ is random genetic effect for the l^{th} animal, PE_m is permanent environmental effect of m^{th} animal, and e_{ijklm} is the random residual error. Besides, effects of inbreeding coefficients were tested as non-linear covariates (quadratic and cubic). Only quadratic expression of dam inbreeding coefficients showed significant effect for PWM. Thus, the estimated effect of dam inbreeding on PWM was also obtained by including dam inbreeding coefficient as linear with quadratic term (Model 2).

$$y_{ijklm} = \mu + breed_i + parity_j + fys_k + \beta_1 (F_d)_{ijk} + \beta_2 (F_d)^2_{ijk} + Animal_l + PE_m + e_{ijklm} \quad (2)$$

Where y_{ijklm}, μ, $breed_i$, $parity_j$, fys_k, $animal_l$, PE_m, e_{ijklm}, are defined as described above, while β_1-β_2 are the regression coefficients for linear and quadratic term of the dam inbreeding Fd and F_d^2

the quadratic term of the dam inbreeding coefficient. Furthermore, a linear mixed model that included an interaction between breed and inbreeding coefficient of the dam, sire and litter were fitted for all traits (Model 3).

$$y_{ijklm} = \mu + breed_i + parity_j + fys_k + breed_i{*}\beta_1(F)_{ijk} + Animal_l + PE_m + e_{ijklm} \quad (3)$$

Where y_{ijklm}, μ, $breed_i$, $parity_j$, fys_k, β_1, β_2, $animal_l$, PE_m, e_{ijklm} are defined as described above, while $breed_i{*}\beta_1(F)_{ijk}$ the interaction of breed and the dam inbreeding coefficient.

All the analysis were performed with ASReml 4.1 as described by Gilmour et al. (2015). Estimated effects and corresponding standard errors (SE) for the dam, sire and litter inbreeding were obtained from the corresponding outputs. Besides, *p*-values of Wald F test obtained from output were used to check for significance of effects of the inbreeding on traits.

3 RESULTS AND DISCUSSIONS

3.1 Increase in the inbreeding coefficient over time

The inbreeding coefficients of young boars and gilts that were retained as breeding animals were averaged over year for each breed separately and presented in Figure 1.

The changes of average inbreeding over time showed increasing trends in all three pig populations, namely, Duroc, Large Black and Saddleback at the farm. The average inbreeding coefficients of the founder populations (in 2003) were zero in all three populations. The inbreeding coefficients of sows and boars ranged from 0-40.6% in Duroc, 0-29.9% in Large Black and 0-26.6% for Saddleback population. Inbreeding rate per year was 1.07% in Duroc, and 0.41% for Large Black and Saddleback populations. In the herd year 2019, the average inbreeding coefficient had reached 18.2% in Duroc and 6.9% each for Large Black and Saddleback populations. The L calculated with software Retriever 1.0 was 2.42 years for Duroc, 2.49 years for Large Black and 2.57 years for Saddleback population. Accordingly, the inbreeding rate per generation was 2.59% (1.07*2.42) for Duroc, 1.02% for Large Black and 1.05% for Saddleback population, which were above the commonly used acceptable limit for livestock populations. FAO recommended the acceptable inbreeding rate to be below 1%, preferably below 0.5% per generation.

The increase in inbreeding level did not differ much between the Duroc, Large Black and

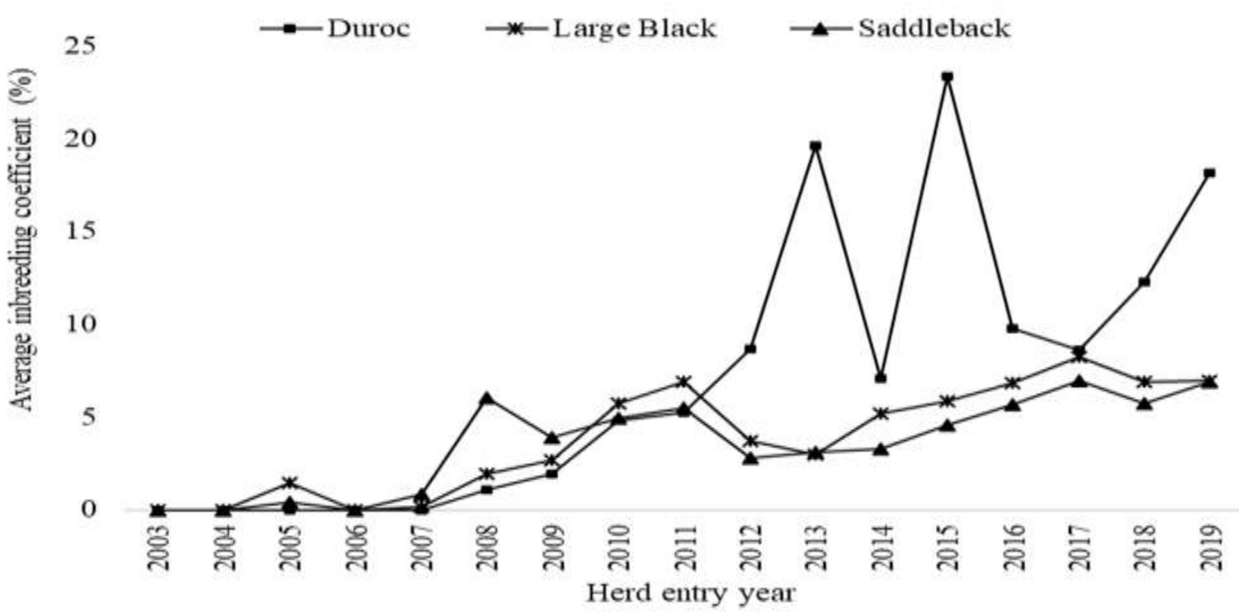

Figure 1: The trend in the average coefficient of inbreeding over the last 16 years in Duroc, Large Black and Saddleback population, based on the number of boars and gilts retained as parents

Table 1: Estimated effects of dam, sire and litter inbreeding (per 1%) with standard error (SE) on all the traits evaluated

Trait	Dam (F_d)		Sire (F_s)		Litter (F_l)	
	Estimate	SE	Estimate	SE	Estimate	SE
GL (days)	-0.006	0.008	0.014*	0.007	0.016**	0.005
TNB (piglets)	-0.015	0.010	0.003	0.011	0.002	0.007
NBA (piglets)	-0.015	0.010	0.003	0.011	0.002	0.007
LWB (kg)	-0.013	0.011	-0.005	0.014	0.012	0.009
NW (piglets)	-0.014	0.010	0.000	0.011	-0.015*	0.007
LWW (kg)	-0.058	0.088	0.010	0.096	-0.081	0.063
PWM (%)	-0.062	0.060	0.053	0.076	0.174**	0.050

GL: gestation length; TNB: total number piglets born; NBA: number of piglets born alive; LWB: litter weight at birth; NW: number of piglets weaned; LWW: litter weight at weaning; PWM: pre-weaning piglet mortality; significant effects $p>0.05$; *$p<0.05$, **$p<0.001$.

Saddleback populations until 2011. Nevertheless, the increase in inbreeding was much higher in Duroc population from 2011 onwards compared to Large Black and Saddleback populations. The higher increase in inbreeding for Duroc population is likely due to small founder population (n=10) compared to Large Black (n=36) and Saddleback (n=35). In addition, it can be due to effective population size during the whole period as the increase in inbreeding depends on the effective population size (van der Werf and de Boer 1990). Relatively low numbers of young boars and gilts were retained annually as breeding animals for Duroc population compared to Large Black and Saddleback population. A study by De Roo (1988) found that number of boars used has a large effect on the level of inbreeding. For instance, chance of mating related individuals increases in a small population (Melka and Schenkel 2010; De Roo 1988). Thus, smaller population sizes generally represent the highest inbreeding coefficients (Krupa et al. 2015; Lopes et al. 2019), and the highest inbreeding coefficient in Duroc population in this study is in agreement with their findings. On the other hand, the trends in increase in inbreeding did not vary much between the Large Black and Saddleback population for entire breeding period (2003-2019).

The Large Black (n=36) and Saddleback (n=35) population started with almost same number of founders. Besides, the proportion of young boars and gilts retained as parents in each herd year were almost similar in these two populations.

3.2 Estimated effects of inbreeding

Estimates on the effects of dam, sire and litter inbreeding on all traits analyzed for all breeds simultaneously are presented in Table 1 (from Model 1). Generally, low inbreeding depression were present for each of the inbreeding coefficient.

3.2.1 Estimated effects of the dam inbreeding

The dam inbreeding showed non-significant ($p>0.05$) inbreeding depression in all trait means. The inbreeding depression in PWM was favorable because a 1% increase in dam inbreeding was associated with a decrease in death of 0.062% of piglets between birth and weaning. The estimated effect on GL of -0.006 days per 1% dam inbreeding was negligible. For litter size and weight traits, the dam inbreeding revealed unfavorable effects; however, the effects were not significant. The estimated effect of 1% increase in dam inbreeding was related with a reduction in TNB and NBA of 0.015 piglets each, and related with 0.014 piglets less weaned. A larger and significant dam inbreeding depression of 0.21 for TNB, 0.19 for NBA and 0.16 for NW per 10% dam inbreeding were estimated by Köck et al. (2009) in Large White population. The dam inbreeding caused a significant reduction in litter size of 0.53 piglets at birth and 0.96 piglets at 21 days (Dickerson et al. 1954). The inbred dams were inferior firstly in ovulation rate and pre-natal nourishment of fetus and later in mothering ability (Dickerson et al. 1954; Köck et al. 2009; Mattey et al. 2013). Thus, the negative effect of dam inbreeding on NW was likely due to reduced mothering abilities of inbred sows. A similar observation has been made in mice (Holt et al. 2005).

3.2.2 Estimated effects of the sire inbreeding

The effect of sire inbreeding on litter size trait and LWB was small and negligible. Inbreeding of sire showed to increase PWM, which was unfavorable, but the effect was not significant (p>0.05). The sire inbreeding significantly (p<0.05) increased GL, and it was associated with an increase in GL of 0.014 days per 1% sire inbreeding. The biology behind the effect of sire inbreeding on GL was not clear. Nevertheless, Garnett (1979) and Zhang et al. (2016) found a significant negative relationship between litter size and GL in sows of different breeds. This indicates that the inbreeding of the boar seemed to reduce sperm quality, which in turn reduces litter size in sows and might ultimately increase GL. A study on inbreeding depression by Hinkson and Poo (2020) found severely reduced sperm quality (in terms of motility, concentration and viability) in captive dusky gopher frog. Likewise, the reduced sperm quality due to inbreeding were reported in wild rabbits (Gage et al. 2006) and Mexican gray wolves (Asa et al. 2007). Conversely, non-significant correlation between sperm quality attributes and litter size in pigs was described by Tsakmakidis et al (2010). Although the effect was not significant (p>0.05), a 1% increase in sire inbreeding was associated with an increase in death of 0.053% between birth and weaning.

3.2.3 Estimated effects of the litter inbreeding

The litter inbreeding showed significant effects on GL (p<0.001), NW (p<0.05) and PWM (p<0.001). The estimated effect of 1% increase in litter inbreeding was related with an increase in GL of 0.016 days, an increase in PWM of 0.174% and a decrease in NW of 0.015 piglets. An increase in GL due to litter inbreeding was in agreement with Farkas et al. (2007), who studied effects of inbreeding in Hungarian Landrace and Large White populations. Farkas et al. (2007) estimated an increase in GL of 0.098 days in Hungarian Landrace and 0.077 days in Hungarian Large White population per 10% litter inbreeding, which were smaller than the estimated effects of litter inbreeding on GL in this study. The increased in GL due to litter inbreeding is likely due to a negative litter inbreeding effects on prenatal litter growth (Farkas et al. 2007). A longer GL was associated with smaller litter size on commercial pig farms (Sasaki and Koketsu 2007). Reduced litter size might be due to a higher embryonic death (inbred embryos) because higher embryonic death rate (22.3%) for inbred embryos was observed compared to outbred embryos (19.8%) in cattle by Ayalon (2004). A negative correlation between litter size and GL in dogs was described by Okkens et al. (1993). A larger effect of -0.83 pigs for NW per 10% increase in litter inbreeding were found by Dickerson et al. (1954). A significant negative effect of litter inbreeding on NW of -0.19 piglets (Austrian Large White) and -0.29 piglets (in Austrian Landrace) were estimated by Köck et al. (2009). The significant effect of litter inbreeding on PWM and NW were as expected because a major effect of a litter inbreeding on viability have been reported in the earlier studies. The performance of piglets were directly affected by litter inbreeding through genetic constitution whereas dam inbreeding affects only the maternal environment provided for piglets (Dickerson et al. 1954). According to Fahmy and Benard (1971), mortality of young pigs increased from 15.1% to 20.9% when litter inbreeding increased from less than 5% to above 25% in a Yorkshire population. The inbreeding of litter showed relatively larger effects compared to the dam inbreeding and sire inbreeding on the traits analyzed.

3.2 Quadratic regression

Non-linear inbreeding effect was only observed for dam inbreeding on PWM (Table 4). Although the effect of dam inbreeding in linear model showed larger negative effect on PWM (-0.062 in Table 1), it was not significant. Non-linear effects of dam inbreeding on reproductive traits were also observed by Köck et al. (2009) in pigs. The quadratic regression indicated that the PWM per 1% increase in dam inbreeding first increased with the dam inbreeding coefficients and then decreased after 10% of dam inbreeding (Figure 2)

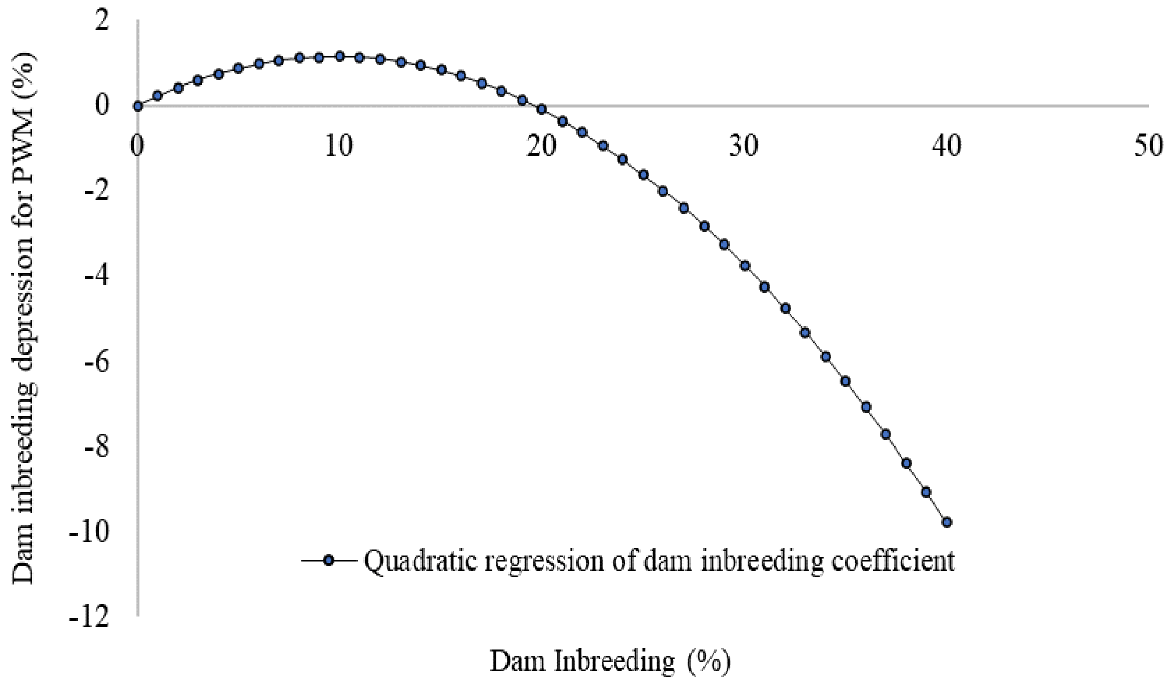

Figure 2: Dam inbreeding effect on PWM calculated by quadratic regression

3.4 Economic consequences of inbreeding depression

Sow performance is measured by the number of healthy piglets weaned per sow per year (Young et al. 2010). The inbreeding effects on litter size traits and pre-weaning mortality among others were already reported. As pointed out by Doekes et al. (2019), costs of inbreeding should be considered in the framework of a breeding program. For instance, in this study, the inbreeding level in Duroc population has increased from zero percent in 2003 to 18.2% in 2019, and the estimated effect on NW was -0.015 piglets per 1% increase in litter inbreeding. This would imply a mean loss of about 0.273 piglets (-0.015*18.2) at weaning due to litter inbreeding in Duroc population between 2003 and 2019. This inbreeding depression on PWM due to litter inbreeding seemed small when only this particular trait was considered. However, the overall impact of inbreeding depression is likely to be larger than for a single traits when such a small inbreeding depression on many other traits are considered (Doekes et al. 2019; Leroy 2014). Besides, it is important to realize that the other traits that were not covered in this study are likely to be affected by inbreeding. As per a review conducted by Yadav et al. (2019) on inbreeding and its impact in livestock, inbreeding reduced lifetime performance in many livestock species. Thus, controlling increase in inbreeding is important in the pig populations from an economic point of view as well (Do et al. 2015).

3.5 Breed differences in effects of inbreeding

A linear mixed model with an interaction term between breed and inbreeding were tested to investigate if effects of inbreeding on traits differ between breeds. The interaction was significant ($p<0.001$) only between dam inbreeding coefficient and breed, for PWM trait. The interaction effects on PWM were -0.315% (SE=0.081) in Duroc, 0.614% (SE=0.139) in Large Black and 0.391% (SE=0.124) in Saddleback. This suggests that the effect of dam inbreeding did differ between breeds for PWM trait.

The negative effect in Duroc indicates that higher inbred dams have lower PWM. In the Large Black and Saddleback, it was opposite. Dickerson et al. (1954) also found some breeds affected more by inbreeding than others. Effects of inbreeding might differ between lines if founders vary in the number of deleterious recessive genes (Miglior et al. 1994).

4 CONCLUSIONS & RECOMMENDATIONS

Inbreeding depression was observed for GL, PWM and NW in the pure-line colored pig breeds at Gelephu farm. Despites having several individuals in the herd with inbreeding coefficient as high as 40%, the inbreeding depression were not significant for majority of the traits analyzed. The litter inbreeding effect was stronger when compared to the dam inbreeding and sire inbreeding effects. It was probably because the traits analyzed in this study were more related to piglets. The PWM and GL seemed to be more affected by inbreeding than other analyzed traits. The effect of dam inbreeding on PWM differed between breeds. The inbreeding rate for all three pig breeds at the farm were greater than FAO recommended threshold of 1% per generation. Although the effects of inbreeding on the evaluated traits were not alarming at present, it might become substantial enough to cause significant effects in the future because the rate of inbreeding in all three pig populations were relatively high. Thus, unless approached carefully, inbreeding depression from the continued linebreeding would outweigh benefits. The farm should either plan for crossbreeding or mating decisions should be made carefully to keep the inbreeding at an acceptable level. The use of program EliteHerd© Plus 4.2.2.1 seemingly assisted to avoid frequent mating of more related individuals because the program directly computes individual inbreeding coefficient automatically once an animal is entered as breeding animal. This assisted to choose and mate less related individuals. Nevertheless, the program has not been able to maintain reasonably low rate of inbreeding probably due to smaller population size. This indicates that in the long run the program may not help to reduce inbreeding at the farm. Thus, the long-term solution to reduce the increase of inbreeding at the farm is to keep the population size of the herd large enough to facilitate the chances of mating between unrelated animals. The introduction of new genetic materials from outside could be another option to maintain inbreeding at acceptable level. In the future, investigating effects of inbreeding on other traits that were not covered under this study might be useful to understand more on the effects of inbreeding at the farm. One of the options requiring policy directives from the government could be to phase out the existing colored breeds and maintain white pig breeds with injection of new bloodline of the Duroc as terminal sire for sustainable development of piggery sector in the country.

Acknowledgements

We would like to acknowledge all the technical staff of the National Piggery Research and Development Centre (NPiRDC) Bhutan for providing clarification on data that I used for this study. I also owe my sincere thanks to Dr. Mariusz Skorupski (PhD), the Consultant Geneticist and Managing Director of Genetics Solutions Limited, New Zealand, for his technical assistance in extracting datasets from the EliteHerd© Plus 4.2.2.1 for this study. This research work was carried as a part of academic requirement under European Master in Animal Breeding and Genetics (EM-ABG) program. Authors therefore would like to thank the Erasmus Mundus Joint Master Degrees (EMJMD) and Erasmus+ program for funding studies to pursue EMABG.

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