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Inavelseffekter på kullegenskaper hos Hampshiresuggor

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Abstract

In Swedish pig production, the use of three breed crosses is the most common and Hampshire is one of the most common breeds to use as the father breed. Hampshire are bred for its meat quality, feed conversion ratio and high growth rate, but the Swedish purebred population is quite small, and inbreeding could be a problem. However, inbreeding is believed to affect traits connected to fitness, such as litter size and health traits. Therefore, the aim of this study is to analyse how the total number of piglets born (TNB), the number of piglets born alive (NBA) and the percent of stillborn piglets (SB) are affected by dam and litter inbreeding in the Hampshire breed. The results show that all the analysed traits are negatively affected by inbreeding. The dam inbreeding had an effect of -0.173 for TNB and -0.028 for NBA while the litter inbreeding had an effect of -0.417 for TNB and -0.286 for NBA. This is for each 10 % increase in inbreeding. Although, the SB showed a decreasing trend, meaning the percent of stillborn piglets are lower with increasing trend of inbreeding but the only significant factor for this trait was the nucleus herd. This could mean that the management of the animals have a larger impact on this trait than inbreeding has. The inbreeding level has also been increasing the last 10 years in the Hampshire breed and if it continues to increase this could have a negatively impact on the reproductive traits and maybe, in the end, also the meat quality traits.

Sammanfattning

I svensk grisproduktion är tre-raskorningar vanligast att använda och Hampshire rasen är en av de vanligaste raserna att använda som faderras. Hampshire är främst avlad för köttegenskaper, foderomvandlingsförmåga och tillväxt men inte kullstorlek. Den svenska renrasiga populationen är ganska liten och inavel kan därför bli ett problem. Inavel tros påverka egenskaper som är kopplade till överlevnad, som kullstorlek och hälsa. Syftet med denna studie var att undersöka hur kullstorlek: totalt antal födda kultingar (TNB), antalet levande födda kultingar (NBA) och procenten av dödfödda kultingar (SB) påverkas av inavel i Hampshire rasen. Resultaten visar att de analyserade egenskaperna påverkas negativt av inavel. Effekten av suggans inavel var -0.173 för TNB och -0.028 för NBA medan kullens inavelseffekt var -0.417 för TNB och -0286 för NBA. Detta för varje 10 % inavelsökning. Fastän SB visade en minskande trend, alltså att procenten av dödfödda kultingar blir lägre men den enda signifikanta faktorn för denna egenskap var avelsbesättningen. Detta kan betyda att skötseln av djuren har en större påverkan på just denna egenskap än vad inavel har. Inavelsnivån har också ökat de senaste 10 åren i Hampshire rasen och om detta fortsätter kan det ha en negativ påverkan på de reproduktionsegenskaperna och kanske, i slutändan, även ha en påverkan på produktionsegenskaperna.

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1 Introduction

In Sweden there were in 2017, 1 272 pig farms (Grönvall, 2017) and a total of 2.5 million pigs were slaughtered (Fransson, 2018). The pig production uses different systems, for example, a farmer can either have only slaughter pigs (multiplier herd), and buys pigs weighing 30 kg from specialized piglet producers and raise them for slaughter. A farmer can also have only sows (sow pod) and others can then "borrow" the sows when they are pregnant and when the sows have farrowed, and the piglets are weaned, the sows are sent back again (Simonsson *et al*. 1997). Pig production uses cross-breeding system meaning that two or more breeds are crossed to get heterosis and the best qualities from every breed. The most common crossing is the three-breed crossing between Landrace, Yorkshire (motherbreed) and Hampshire or Duroc (fatherbreed) (Svenskt Kött, 2018). Hampshire is the only pig breed bred in Sweden today and around 70 % of the slaughter pigs in Sweden has Hampshire as father (Eriksson, 2018).

One could divide the breeding into various parts, described by a pyramid. At the top are the nucleus herds that breed the pure breeds such as Hampshire. The nucleus herds are not that large and can have quite small populations of pigs (Kyriazakis & Whittemore, 2006). Small populations are at a higher risk of inbreeding and high inbreeding can have negative effects on the production and fitness of animals. Recessive deleterious genes have a higher chance of getting expressed when the inbreeding level increases (Falconer & Mackay, 1996).

The Hampshire population in Sweden is not large and have therefore a considerable risk of getting inbred. Nordic Genetics is the company responsible for the Hampshire breeding in Sweden. There are three nucleus herds in Sweden and one in Norway (Nordic Genetics). In total there are 536 females on these four herds (Eriksson, 2018). *Svenska Köttföretagen* (Swedish meat company) has two semen stations in Sweden with about 250 males (Nordic Genetics). The aim of this study was to analyse the inbreeding effects on litter size in purebred Swedish Hampshire dams.

2 Literature study

2.1 Inbreeding and its effects

When two related individuals are mated, inbreeding occurs (Hinrichs & Thaller, 2011). Small populations are often at a higher risk of getting inbred than a large population. An important consequence of inbreeding is that an individual can get a higher number of homozygous alleles. Two individuals with a common ancestor might carry replicates of the same allele and if they mate, they can pass these replicates to their offspring. Meaning that the offspring may carry two copies of the same allele that, in a previous generation, were one copy in one individual. (Falconer & Mackay, 1996). This is one effect of inbreeding and other effects can be for example, inbreeding depression, genetic drift and reduction of genetic diversity (Hinrichs & Thaller, 2011).

Inbreeding depression is defined as "the reduction of the mean phenotypic value shown by characters connected with reproductive capacity or physiological efficiency" (Falconer & Mackay, 1996). Even though the genetic basis of inbreeding depression is still unclear (Curik *et al*, 2017) it is believed to be caused by at least two components, partial dominance and overdominance (Charlesworth & Charlesworth, 1987; Höglund, 2009). When inbreeding increases, homozygosity increases as well, making it a higher chance for recessive, deleterious alleles to be expressed. This is what happens at the partial dominance. Overdominance, however, declines when the inbreeding level increases. Heterozygous genotypes are considered to be better over homozygous genotypes. But when inbreeding increases it may cause a decrease in proportion of overdominance and in turn cause inbreeding depression. One major difference between partial dominance and overdominance is that natural selection can remove the alleles causing inbreeding depression due to partial dominance while it cannot do so for overdominance (Höglund, 2009).

2.1.1 Effects of inbreeding in cattle and horse

To create various breeds in livestock species, inbreeding was one way to uniform the animals and to concentrate the good genes in a certain species (Gómez *et al*. 2009). In general, inbreeding often has a negative effect on different traits in various species. Studies have been made on the effects of inbreeding in several species, for example cattle (Thompson *et al*. 2000, Hinrichs & Thaller, 2011), horse (Klemetsdal, 1998, Gómez *et al*. 2009) and sheep (Lamberson *et al*., 1982, Norberg & Sørensen, 2007).

Thompson *et al*. (2000) studied the effects of inbreeding in American Holsteins and showed that milk production decreased as inbreeding increased. When the inbreeding coefficient was 0.02 to 0.06 the production per lactation decreased with 35 kg per percentage of inbreeding. When the inbreeding was between 7 and 10 % the decrease per lactation was 55 kg per percentage increased inbreeding. The largest losses in production occurred early in life and lactation. In animals with low inbreeding level, some traits showed a positive result of inbreeding but if the inbreeding level was too high it would have a negative effect on the traits. Though the results from their study also showed that even low levels of inbreeding can have a negative effect (Thompson *et al*. 2000).

Racing performance in Norwegian cold-blooded trotters has also been shown to be negatively affected by inbreeding. Klemetsdal (1998) studied how the variable ATSE (a racing performance variable) was affected by inbreeding. ATSE was combined with four different age-classes (3, 3-4, 3-5 and 3-6 years of age), giving four different ATSE variables. Also, for each of these four ATSE variables the effect for two (F2), three (F3), four (F4) and five (F5) generations were analysed. Also, a variable FTOT which was an inbreeding level given that all ancestors were known for at least five generations. The results from the study showed that racing performance decreases by inbreeding and the linear regression coefficients for ATSE ranged from -0.64 to -1.94 depending on age class and generation (F2 to FTOT) (Klemetsdal, 1998).

It is believed that fitness traits as litter size or lactation tend to be affected more by inbreeding than other traits (Falconer & Mackay, 1996). Conformation is not a fitness related trait but a very important trait in horse breeding. Gómez *et al*. (2009) studied the effects of inbreeding on eight different body measurements in Spanish Purebred horses and found that inbreeding had a significant effect on the measurements. The studied population had an average inbreeding coefficient of 8.2 % and one of the body measurements studied were height at withers, which decreased with 0.858 metres. The conclusion of the study was that inbreeding depression was clearly present in the breed and affected both body measurements and the ranking according to breeding value for each individual (Gómez *et al*. 2009).

2.2 Measuring inbreeding

2.2.1 Inbreeding coefficient

There are several ways of measuring inbreeding or the risk for inbreeding. One way is to use the pedigree of the animals to calculate an inbreeding coefficient for each of them. Based on that, the average inbreeding coefficient for all individuals in a population can be calculated. The inbreeding coefficient is defined as the probability that both alleles at random loci are ‘identical by descent’. When calculating the individual inbreeding coefficient, one need to trace back the pedigree to common ancestors of the parents and calculate the probabilities at each segregation (Falconer & Mackay, 1996). Another way to measure inbreeding is with the effective population size or with runs of homozygosity.

2.2.2 Effective population size

One common method is to measure the effective population size (Leroy *et al*. 2013). The effective population size (N_e) could be explained as the number of individuals that would give rise to the calculated variance in an idealized population (Falconer & Mackay, 1996). If a population of 100 animals have an effective population size of 50, this means that the genetic diversity in that population corresponds to as if there are 50 individuals (both sexes). Sørensen *et al*. (2005) estimated that the N_e was 49 for Danish Holstein, 53 for Jersey and 47 for Danish Red. The N_e value should not get lower than 50 to prevent inbreeding depression and to prevent the decrease of genetic diversity the value should not be lower than 500 (Kantanen *et al.* 1999). In Swedish Gute sheep the estimated N_e is 155.4 (Rochus & Johansson, 2017) and in Finnish Yorkshire and Landrace pigs the estimated value is 61 and 91 respectively (Uimari & Tapio, 2011).

2.2.3 Runs of homozygosity

Inbreeding coefficients that are calculated from pedigree data might not show the "true" value of inbreeding since it depends much on the depths and completeness of the pedigree. An incomplete pedigree might show a misleading (high) inbreeding coefficient (Marras *et al*. 2014). That is why runs of homozygosity (ROH) can be a more reliable source when calculating inbreeding coefficients since it is derived from genomic data and can be calculated as the proportion of genome covered by ROH (Zhang *et al*. 2015a). This method is defined as contiguous stretches of homozygous genotypes in a genome due to "transmission of identical haplotypes from parents to offspring" (McQuillan *et al*. 2008; Zhang *et al*. 2015b). Long ROHs are connected to recent inbreeding while short ROHs reflect more old inbreeding. Single Nucleotide Polymorphism (SNP) can be used to analyse ROHs but whole genome sequencing is preferable since it give an even more accurate result. The length of ROHs are often depended on the density of the SNP (Zhang *et al*. 2015a). For example, Marras *et al*. (2014) put a minimum length at 1 Mb while Zhang *et al*. (2015b) separated the ROHs into three sizes, small, medium and large, were small were 10 kpb to 100kpb and the large was higher than 3Mbp. McQuillan *et al*. (2008) had a minimum length set at 500 kb.

2.3 Pig breeding

Organized Swedish pig breeding started in the 1920'ies with Yorkshire and Landrace as the only breeds. At that time, crossbreeding was not accepted. In the 1960s, crossbreeding was implemented. During the 1970s, the terminal sire breeds Hampshire and Duroc was introduced and during the 1980s, the use of artificial insemination (AI) started. It was also during the 1980s that the Swedish pig breeding was taken over by a cooperative group and a private group after a subvention from the government was ceased. In Sweden the cooperative group, today known as Nordic Genetics, continued breeding Swedish Landrace, Yorkshire and Hampshire. The private group were breeding Landrace, Yorkshire and Duroc and bought genes from Norsvin. In 2005 started Nordic Genetics and Norsvin a cooperation on the Landrace (Norsvin) and Yorkshire (Nordic Genetics) breeds which led to the Swedish Landrace breeding ending. In 2012 this cooperation broke up and Norsvin started a cooperation with Topigs in the Netherlands instead. Sweden use the mother breeds from this cooperation and today the only pig breeding remaining in Sweden is that of Hampshire (Lundeheim, 2017).

Three-breed crosses between Yorkshire, Landrace and Hampshire or Duroc are the most common to use in Sweden. By combining different breeds, one can get pigs with good qualities (Svensk Kött). Cross-breeding leads to heterosis, which is the opposite of inbreeding depression (Falconer & Mackay, 1996).

The Hampshire pig is popular to use as a father breed due to its good meat qualities, high growth rate and feed conversion ability (Nordic Genetics, 2015). The breeding began in 1976 and today there are three breeding herds in Sweden, one in Norway and one in the United Kingdom (Svenska Köttföretagen). The Hampshire nucleus herds in Sweden produce 900 purebred litters per year. In the Hampshire breed the focus is on the production and meat quality traits, for example, days at 100 kg, feed conversion rate and meat percentage but not on litter size (Nordic Genetics, 2015).

2.4 Previous studies about inbreeding effects in pigs

Due to Hampshire not being bred for their reproductive traits, the results from the following studies are from other maternal breeds such as Landrace and Large White. Farkas *et al*. (2007) reported in their study on Hungarian Landrace and Large White that the number of piglets born alive (NBA) was negatively affected by both inbreeding level of the litter and of the dam. They also studied the inbreeding effect on gestation length and found that inbreeding of the litter increased gestation length, but the increase was negligible. Dam inbreeding level had no effect on the gestation length (Farkas *et al*. 2007). The effects on total number born (TNB), NBA and number of weaned (NW) can be seen in table 1.

Table 1: Published effects of inbreeding in Landrace and Large White. Results from Farkas et al. 2007 and Köck et al. 2009

	Austrian Landrace		**Hungarian Landrace**		**Austrian Large White**		**Hungarian Large White**	
	Dam	Litter	Dam	Litter	Dam	Litter	Dam	Litter
TNB	-0.16	-0.26	-	-	-0.21	-0.05	-	-
NBA	-0.12	-0.25	-0.122	-0.105	-0.19	-0.10	-0.197	-0.164
NW	-0.21	-0.29	-	-	-0.16	-0.19	-	-

The effects of inbreeding in Austrian Landrace and Large White (Köck *et al*. 2009) and Hungarian Landrace and Large White (Farkas *et al*. 2007) on total number of piglets born (TNB), number of piglets born alive (NBA) and the number weaned piglets (NW) per 10% inbreeding.

In Austrian Large White pigs, the dam inbreeding decreased the NBA with 0.19 piglets per 10% inbreeding. In Austrian Landrace the decrease was 0.12 piglets per 10 % inbreeding, but this result showed a weaker significance level (P<0.05) than for Large White (P<0.001). A strong significant result (P<0.001) for both Landrace and Large White showed that litter inbreeding decreased NW with 0.29 and 0.19 piglets per 10 % inbreeding respectively (Köck *et al*, 2009). The NBA in Hungarian Landrace dams showed a decrease of -0.122 piglets per 10 % inbreeding and litter inbreeding decreased NBA with 0.105 piglets per 10 % inbreeding. In Hungarian Large White the result of dam and litter inbreeding was a bit lower, with a decrease of 0.197 and 0.164 piglets per 10% inbreeding respectively (Farkas *et al*. 2007) (Table 1). However, the effects of sire inbreeding in Austrian Landrace showed a significant positive result on TNB, NBA and NW. A positive effect of inbreeding is rare, and this was explained by possible better sperm quality in the inbred sires (Köck *et al*, 2009).

In Austrian Landrace the mean inbreeding coefficients for dam and litter were somewhat higher compared to the Hungarian Landrace. Austrian Large White had also a higher mean dam and litter inbreeding coefficients compared to Hungarian Large White dam and litter, which has the lowest mean inbreeding coefficients between the two breeds (table 2).

Table 2: The mean inbreeding coefficients, %

	Austrian Landrace			**Hungarian Landrace**		**Austrian Large White**			**Hungarian Large White**	
Mean inbreeding coefficient	Dam	Litter	Sire	Dam	Litter	Dam	Litter	Sire	Dam	Litter
	0.93	1.24	0.67	0.798	0.887	2.02	2.23	1.59	0.537	0.496

The mean inbreeding coefficients for Austrian and Hungarian Landrace and Large White, Farkas *et al* (2007) did not analyse the sire inbreeding as Köck *et al* (2009).

The methods in the studies differ somewhat, Farkas *et al*. (2007) did a Bayesian approach while Köck *et al* (2009) did not but both used the SAS software and a software called PEDIG. Another difference between the studies was that Köck *et al*. (2007) also divided the inbreeding into new and old, with the new inbreeding being defined as the period of the first five generations. This division between old and new inbreeding showed that between 45 % and 53 % of the total inbreeding coefficient in Austrian Large White came from the new inbreeding. In Austrian Landrace a higher proportion of the total inbreeding coefficient came from new inbreeding (72 % to 80 %). In general, there was a higher inbreeding level in Austrian Large White, but a larger part of the inbreeding came from the first five generations in Austrian Landrace (Köck *et al*, 2009). Another difference between the two studies are that Farkas *et al* (2007) only analysed the litter and dam inbreeding and its effects on NBA and gestation length while Köck *et al* (2009) looked on the effects on TNB, NBA and number of weaned in dam, litter and sire.

Culbertson *et al*. (1998) studied the effects of inbreeding in Yorkshire and it showed similar results on NBA as Hungarian Large White and Austrian Large White. The inbreeding effects on NBA and 21-d litter weaning weight (LWT). The NBA decreased with 0.23 per 10 % inbreeding piglets and the LWT decreased with 0.52 per 10 % inbreeding (Culbertson *et al*. 1998). Yorkshire is also called Large White (Kyriazakis & Whittemore, 2006).

Studies of other breeds have also been performed. One was made on two closed Iberian pig lines, Torbiscal and Gamito, where there were two lines of the Torbiscal breed, Torbiscal and Torbiscal-S. The Iberian breeds were related (Silió *et al*. 2016). Another study was made on purebred Pampa Rocha, Duroc and crosses between these two breeds (Bell *et al*. 2015).

The inbreeding coefficients for the Gamito, Torbiscal and Torbiscal-S breed were 0.271, 0.115 and 0.176 % respectively. The TNB in the Torbiscal breed decreased with -0.165 per 10 % inbreeding. In the Gamito breed the effect on TNB was -0.177 per 10 % inbreeding (Silió *et al*. 2016). Bell *et al*. (2015) divided their observations into three classes according to the inbreeding level, where over 90 % were classed as low inbreeding level and only 2.6 % were classed as high inbreeding level. This resulted in that they could not find any significant effect of inbreeding on the traits analysed.

3 Materials and methods

3.1 Data and data editing

The primary dataset contained 8 002 records on purebred Hampshire dams' reproduction performance in the period 2008 to 2017, provided by the breeding organisation Nordic Genetics. The records were from three nucleus herds in Sweden that had records for all 10 years. The primary records included the information presented in table 3. In addition, inbreeding level (%) was calculated for each dam, sire and litter in the data. Base generation was for this calculation set to parents of animals born in 2002. The inbreeding levels were calculated by and received from Nils Lundeheim. Based on the primary variables and factors, several secondary factors were created, such as: percentage of stillborn piglets of total born piglets (SB) and year-month combination for farrowing. Also, inbreeding levels were grouped as shown further down.

Table 3. Primary information in the dataset

Variable	Description
damID	Unique identity number of the sow
birthdate	The birth date for the sow
litterID	Unique identity number for the litter
parity	The parity number
sireID	Unique identity number for the boar
TNB	Total number of piglets born
NBA	Number born alive
frdate	Farrowing date
herd	Nucleus herd, A, B or C

Several tests were made to decide which factors the final model should include. Since only about 58 % of the dams had a 2nd parity, the statistical were restricted to first parity litters. In the preliminary analyses, the sire inbreeding gave no significant effect and were therefore not included in the analysis, but the effect of sire was still included in the models. After editing the dataset, the information from 4 015 dams first parity litters remained for analysis.

3.1.1 Inbreeding classes

The inbreeding level of the dam, sire and litter was grouped into classes to estimate the effect TNB, NBA and SB between the inbreeding classes. The classes are presented in table 4. The pigs with inbreeding levels between 0 and 0.9 % were assigned to class 0 and etcetera. The pigs with inbreeding level 7 or higher were assigned class 7, mainly to have a good number of observations for each group. A mean inbreeding value was calculated for each class (table 4).

Table 4. Grouping of inbreeding level, and mean inbreeding level for each class

Inbreeding class	**Inbreeding level, %**	**Mean inbreeding, %**
0	0-0.9	0.39
1	1-1.9	1.45
2	2-2.9	2.44
3	3-3.9	3.44
4	4-4.9	4.43
5	5-5.9	5.40
6	6-6.9	6.44
7	7 and higher	8.17

3.2 Statistical analysis

The statistical analysis was performed using the Statistical Analysis Software SAS version 9.4 (SAS Institute, 2012). The procedures used were PROC FREQ, PROC MEANS, PROC MIXED and PROC GLM. PROC FREQ and MEANS were mainly used to perform descriptive statistics while PROC MIXED and GLM (analysis of variance) were used to analyse how inbreeding affect the reproductive performance. Least squares means (lsmeans) were calculated to show the influence of inbreeding and other fixed factors included in the statistical model.

3.3 Statistical models

The statistical model used for analysing the influence of inbreeding on TNB, NBA and SB were:

$$Y = \mu + yr + d_{cl} + l_{cl} + herd + sire + frtime(herd) + e$$

Y is the observed value (TNB, NBA or SB), μ is the mean value, yr is the fixed effect of year of farrowing, d_{cl} is the fixed effect of dam inbreeding (8 classes), l_{cl} is the fixed effect of litter inbreeding (8 classes), herd is the fixed effect of nucleus herd (n=3), sire is the random effect of boar (father of the litter) and frtime is the random effect of the combination of year and month of farrowing nested within nucleus herd and e is the random residual effect.

The reason for using the percent of stillborn piglets and not number of stillborn piglets is that this takes the total number of piglets born alive into consideration.

4 Results

4.1 Descriptive statistics

The mean of total born, born alive and percent of stillborn in parity number 1 are presented in table 5.

Table 5. Mean values and standard deviation (SD) and min-max for total born, born alive and the percent of stillborn

Variable	Mean	SD	Minimum	Maximum
TNB, number	8.79	2.41	2	18
NBA, number	7.91	2.36	1	16
SB, %	9.76	12.76	0	88.89

The number of dams, boars and litters in each inbreeding class are presented in figure 1. There are higher number of animals in the lowest inbreeding classes and then it decreases for each class. Except for the litter where the number of animals increase for each class up until inbreeding class 2, then it decreases again. The number of boars have a peak at inbreeding class 3 and decreases thereafter.

Figure 1. The frequency of how many animals there are in each inbreeding class for dam, boar and litter

The mean values for TNB, NBA and percent of stillborn for each nucleus herd are presented in table 6. Herd A had the highest mean value of TNB and NBA and a lower percent of stillborn piglets compared to the other two nucleus herds. Herd C had the smallest litters with a mean of 8.74 TNB and 7.57 NBA. This herd also has the highest percent of stillborn piglets: 13.31%. However, this herd had a large range of TNB (2 to 18 piglets), which is higher compared to the other two herds.

Table 6. Mean values and SD for each nucleus herd, 2008-2017

Variable	Herd A n=1 291			Herd B n=1 347			Herd C n=1 377		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
TNB	9.02	2.43	2-16	8.63	2.26	5-17	8.74	2.51	2-18
NBA	8.31	2.41	1-15	7.87	2.08	5-15	7.57	2.50	1-16
SB	7.76	10.99	0-72.73	8.06	10.77	0-58.33	13.31	15.14	0-88.89

The mean values for TNB (total number born), NBA (number born alive) and the percent of stillborn in parity one for each nucleus herd. SD = standard deviation. Range is the minimum and maximum number of piglets in each litter.

The mean inbreeding levels from 2008 to 2017 has increased for dam, litter and boar (figure 2). The litter have a slightly higher inbreeding level than the dams and boars and seems to reach a more stable level between the years 2016 and 2017 compared to the dams and boars which seem to still be increasing after 2017. The mean regression coefficient for the increasing inbreeding level is 0.56 and is the mean value for dam litter and boar together.

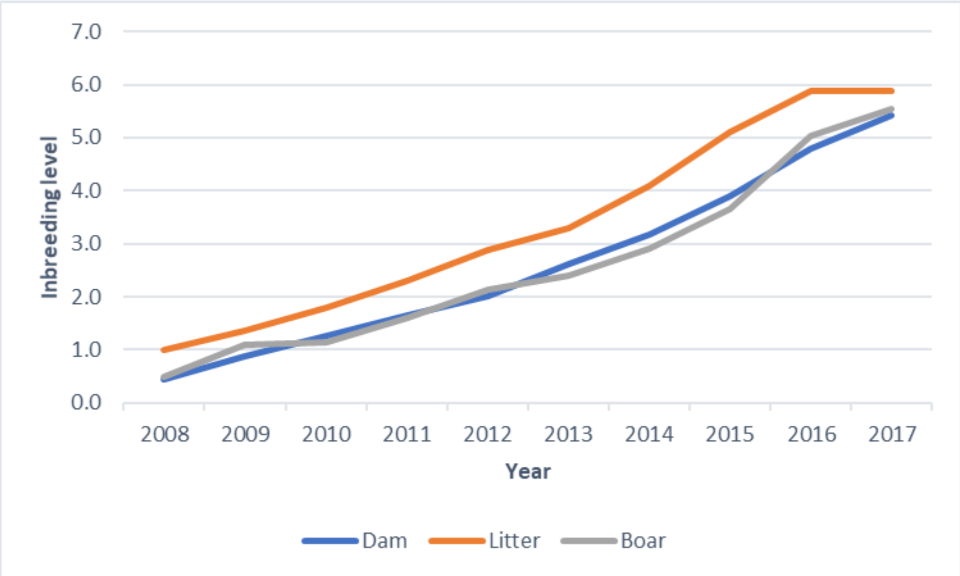

Figure 2. The mean inbreeding levels between 2008 to 2017

The mean inbreeding coefficients (%) for dam, litter and sire are presented in table 7. The sires have the lowest average inbreeding coefficient and the lowest range of these estimates. Litter has the highest inbreeding coefficient and the highest range.

Table 7. The mean inbreeding levels, %, for dam, litter and sire in the dataset

N= 4 015	Dam			Litter			Sire		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Mean inbreeding coefficient	2.71	2.09	0-16.4	3.43	2.21	0-17.2	2.51	2.07	0-10.9

Mean inbreeding level, %, SD = standard deviation and Range is the maximum and minimum inbreeding level

4.2 The effects of inbreeding on the reproductive traits

Only the effect of litter inbreeding, but not the dam inbreeding, and herd were significant except for SB where only the herd was significant as presented in table 8. The year of farrowing and the dams inbreeding level had non-significant effect on all three variables analysed.

Table 8. The levels of significance for the fixed effects in the models

Factor	TNB	NBA	SB
yr	n.s.	n.s.	n.s.
d_{cl}	n.s.	n.s.	n.s.
l_{cl}	**	**	n.s.
herd	**	***	***

**P≤0.01 ***P≤0.001 n.s.= non-significant

Since the mean inbreeding value for inbreeding class 7 was 8.17 (table 4) for dam and litter, values on the x-axis in figures 3 to 8 are placed on the value 8. This is due to get a better estimate of the trendlines.

4.2.1 Effects of inbreeding on total number of piglets born

The effects of dam and litter inbreeding on TNB are presented in figure 2 and 3. The highest TNB were in inbreeding class 0 for dam and class 4 for litter. In general, for the dams the number of piglets decreases with higher inbreeding but increases for class 7 (position 8). While for the litter inbreeding, it decreases with about 0.43 piglets between class 1 and 2 before it increases again to class 4 where it reaches its highest peak before decreasing again. The trendline shows a decrease for each percentage increased inbreeding and the estimated regression coefficient were calculated for increase of 10 % inbreeding. These estimates for TNB were -0.17 and -0.42 per 10 % inbreeding for dam and litter respectively (table 9).

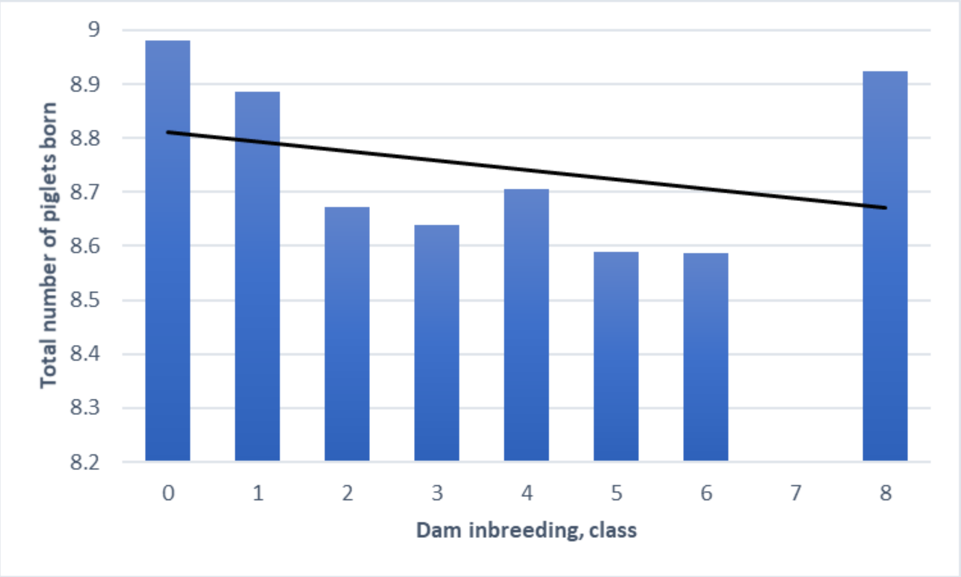

Figure 3. The dam inbreeding effect on the total number of piglets born, with the trendline

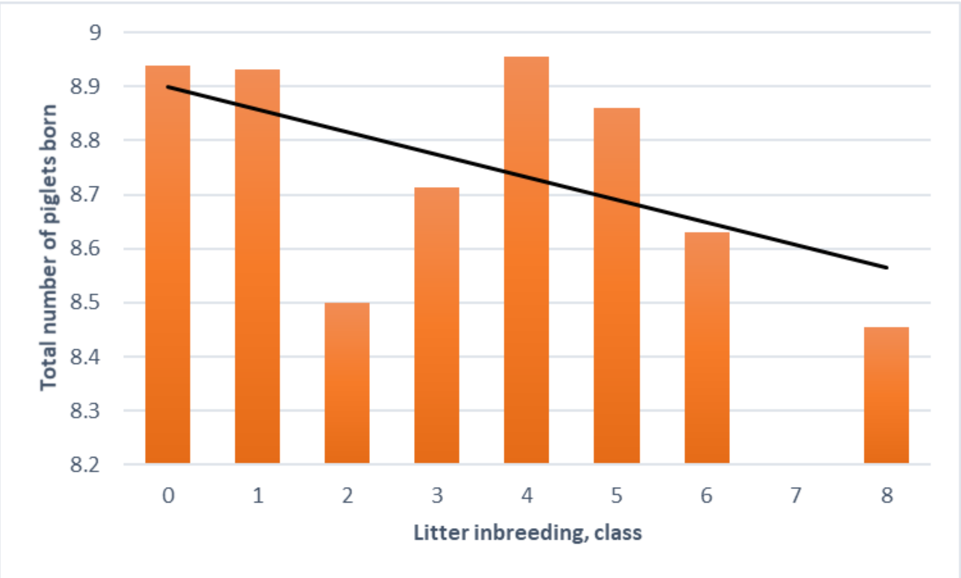

Figure 4. The litter inbreeding effect on the total number of piglets born, with the trendline

4.2.2 Effects of inbreeding on number of piglets born alive

The effect of dam inbreeding on NBA show a bit different result compared with TNB. NBA decreases from class 0 to 3 before it increases again up to class 7 (position 8) (figure 4). The effect of litter inbreeding on NBA showed similar results as for TNB were it decreases with about 0.46 piglets between class 1 and 2 before it increases again and reaches highest peak at class 4 before it decreases again until class 7 (position 8) (figure 5).

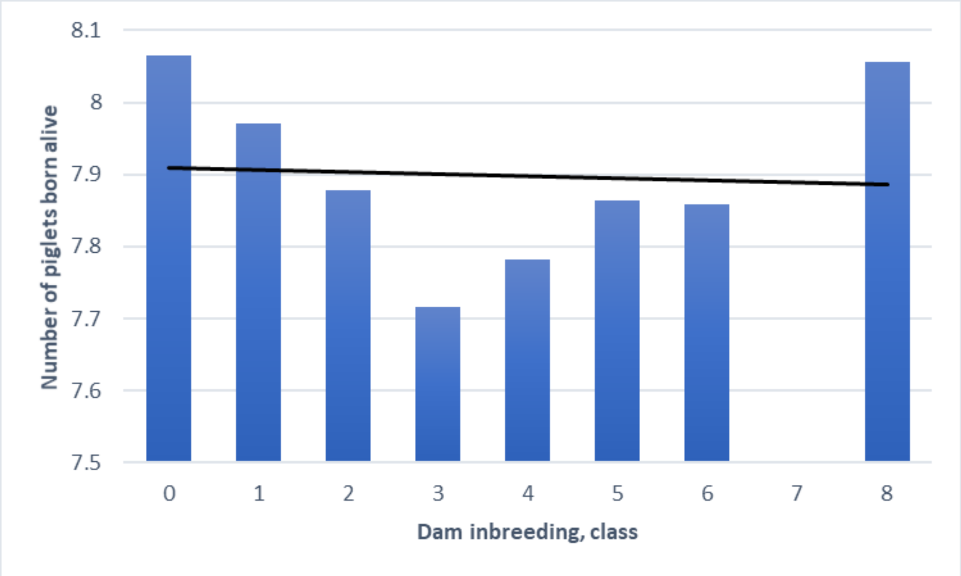

Figure 5. The dam inbreeding effect on the number of piglets born alive, with the trendline

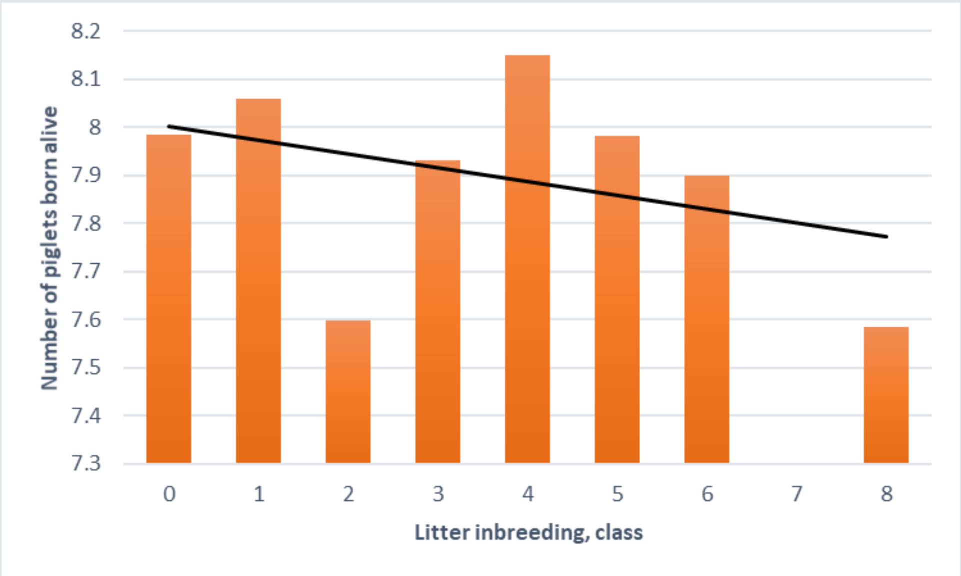

Figure 6. The litter inbreeding effect on the number of piglets born alive, with the trendline

4.2.3 Effects of inbreeding on the percent of stillborn piglets

The highest percentage of stillborn piglets, in relation to dam inbreeding, was found in class 3 and 4, and thereafter it decreased (figure 6). The lowest percentage of stillborn piglets was found in class 6. For the litter inbreeding, the highest percentage of stillborn piglets was found in class 0 and the lowest percent is also in class 6 (figure 7).

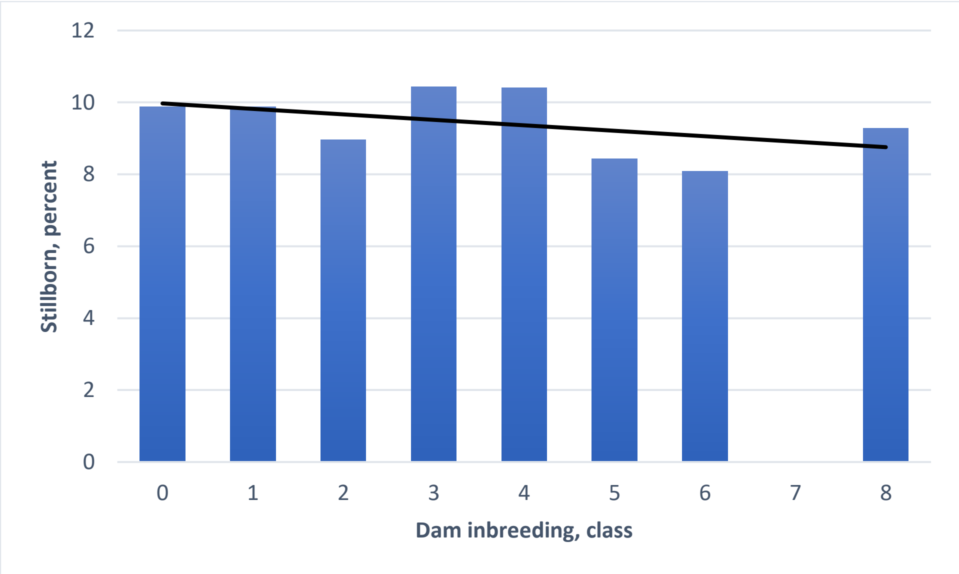

Figure 7. The dam inbreeding effect on the percent of stillborn piglets, with the trendline

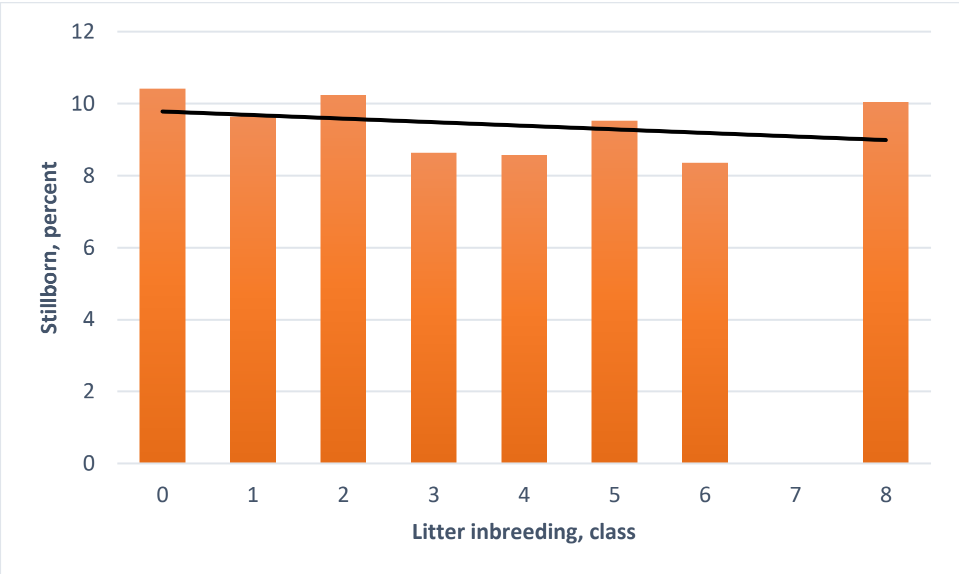

Figure 8. The litter inbreeding effect on the percent of stillborn piglets, with the trendline

From the histograms (figures 3 to 8) regression of litter size on inbreeding level was estimated in Microsoft Excel. The regression coefficient show the estimated decrease per 10 % increase in inbreeding level.

Table 9. The regression coefficients for dam and litter per 10 % inbreeding

	TNB		**NBA**		**SB**	
	Dam	Litter	Dam	Litter	Dam	Litter
Regression coefficient	-0.173	-0.417	-0.028	-0.286	-1.52	-0.993

5 Discussion

5.1 Effects of inbreeding on total number of piglets born

In Hampshire litters the TNB decreased with 0.17 piglets per 10 % increased inbreeding of the dam which agrees with the result from Köck *et al* (2009) who estimated -0.16 in Landrace. It also agrees with the results from Silió *et al*. (2016) who studied Iberian pig breeds and estimated -0.165 (Torbiscal) and -0.177 (Gamito) (table 10). For the Large White breed, the decrease was a little lower (-0.21) compared to the results from this study. However, the Hampshire litter inbreeding had a decrease of about 0.42 piglets per 10 % inbreeding which has a larger impact compared to Landrace (-0.26) and Large White (-0.05) (Köck *et al*. 2009). The differences in litter inbreeding could be due to the use of different factors in the models or some breed differences. Köck *et al*. (2009) also studied the effects of sire inbreeding on TNB and got significant positive results for Landrace but since there were non-significant results for the Hampshire sires that factor was not included in this study.

Table 10. Comparison of inbreeding effect between TNB in different breeds

Breed	Dam	Litter
Hampshire	-0.173	-0.417
Large White	-0.21	-0.05
Landrace	-0.16	-0.26
Torbiscal	-0.165	
Gamito	-0.177	

Large White and Landrace results from Köck *et al*. (2009)
Torbiscal and Gamito results from Silió *et al.* (2016)
Hampshire is the results from the current study

For inbreeding class 7 (position 8), TNB increases again for dam (the same effect could be seen in NBA). It is still unclear why the TNB would increase at such high inbreeding level. The number of dams with the highest inbreeding levels (>15%) are few (less than 10 dams) and a possibility is that these dams had good qualities or good body conformation. Maybe the keepers decided to continue using these dams in breeding despite the high inbreeding level due to their possibly good qualities.

5.2 Effects of inbreeding on number of piglets born alive

NBA in Hampshire decreased for dam inbreeding with 0.028 piglets per 10 % increasing inbreeding while the litter inbreeding effect was about -0.29 per 10 % increasing inbreeding. The results of litter inbreeding in this study was more in agreement with other studies than the dam inbreeding compared to previous studies (Culbertson *et al.* 1998, Farkas *et al*. 2007, Köck *et al.* 2009). The results that were most similar to the ones in this study were from Köck *et al*. (2009) (-0.25) and Culbertson *et al.* (1998) (-0.23). Farkas *et al*. (2007) got -0.164 (Large White) and -0.105 (Landrace) for litter inbreeding which is somewhat close to the Hampshire result in this study.

Table 11. Influence of inbreeding on NBA in different breeds

Breed	Dam		Litter	
Hampshire	-0.028		-0.286	
Large White	-0.197*	-0.19**	-0.164*	-0.10**
Landrace	-0.122*	-0.12**	-0.105*	-0.25**
Yorkshire	-0.23			

*Farkas *et al*. (2007) **Köck *et al*. (2009). Culbertson *et al*. (1998) (Yorkshire) had not divided the inbreeding into dam and litter as the other studies had. The results of Hampshire is from the current study.

Although, the effects of dam inbreeding were quite low (-0.028) compared to previous studies. Why there is such a difference between Hampshire, Large White and Landrace in this case could be due to breed differences. Since both Köck *et al*. (2009) and Farkas *et al*. (2007) analysed Large White and Landrace which are bred for higher number of piglets in each litter, while Hampshire is bred for its meat traits which will be discussed further down. Culbertson *et al*. (1998) did not separate the inbreeding effects in litter and dam so the result is probably for the whole breed of Yorkshire which is also called Large White. The estimated effect from Culbertson *et al*. (1998) is a little higher (-0.23) compared to Farkas *et al*. (2007) and Köck *et al*. (2009) but still somewhat similar and it could be due to the fact that they have analysed the same breed but in different geographical regions.

5.3 Effects of inbreeding on percent of stillborn piglets

No other study has analysed the influence on inbreeding on percent of stillborn piglets (SB) which means there is no other results to compare with but the results in this study were quite interesting. One could think that SB would increase with higher inbreeding, meaning more stillborn piglets with higher inbreeding level but the results from this study shows a different trend. The trendlines in figures 7 and 8 show a general decrease in SB. The percent gets lower for each inbreeding class and the reason for this is still unclear. It could be due to some statistical errors or that the definition of stillborn varies between the herds.

As mentioned before, Köck *et al* (2009) got a positive effect of sires inbreeding effect on TNB and NBA in Landrace, which was explained to be most likely due to better sperm quality of the inbred sires. Positive effects of inbreeding are rare but can happen and Shields (1982) cited by Köck *et al*. (2009) described this as inbreeding enhancement and could be due to fixation of favourable gene complexes or epistatic relationships (Tempelton, 1979 cited by Köck *et al*. 2009). Although, for this trait, no other factor than herd were significant which could also be a reason for it to show this positive trend. It could be that this trait relies more on the management of the pigs than the genetics of the dam or litter.

5.4 Differences and similarities between the breeds

The Hampshire breed is not bred for reproductive traits compared to the Landrace and Large White breeds and yet there were some similarities with previous studies in the effects of inbreeding. One could think that since the other breeds are highly selected for reproductive performance, the litter traits would be more affected by inbreeding than Hampshire, but the results are similar to previous studies especially for Landrace and Hampshire in this current study. Still, they are of the same species and maybe that is the reason for it to be similar. The Gamito and Torbiscal breeds showed similar results as Landrace and Hampshire which is also quite interesting since the Gamito and Torbiscal breeds studied were closed pig lines and probably not closely related to Hampshire or Landrace.

The inbreeding coefficients for the Hampshire in this study are over-all higher compared to previous studies (other breeds). The inbreeding coefficient for litter in Hampshire have the highest value compared to other studies (table 12). In almost every breed, litter has the highest inbreeding coefficient which is logical since the inbreeding level increases for each generation if the offspring has inbred parents. But the litter inbreeding for the Hungarian Large White is lower than for dam and sire and the reason could be that there are more non-inbred litters in their dataset compared to the number of inbred litters which lowers the mean value a bit. In the current study the Hampshire breed is a bit more inbred compared to previous studies of other breeds. Although, this could be affected by the number of generations used in this study compared to the previous studies. If the previous studies have calculated the inbreeding coefficient using a higher number of generations then it could lower the values.

Table 12. Comparison of the inbreeding coefficients (%)

Breed	**Dam**		**Litter**		**Sire**
Hampshire	2.71		3.43		2.51
Landrace	0.798*	0.93**	0.887*	1.24**	0.67**
Large White	0.537*	2.02**	0.496*	2.23**	1.59**
Gamito			0.271		
Torbiscal			0.115		

*Hungarian, Farkas *et al*. (2007) **Austrian, Köck *et al*. (2009). Gamito and Torbiscal, Silió *et al*. (2016) did not divide the coefficients in dam, litter and sire. The results of Hampshire are from the current study.

5.5 Inbreeding depression and pig production

The genetics behind inbreeding depression is still unclear despite having been researched for the last century (Curik *et al*. 2017) and this affect animals in different ways, in most cases negative. Even though there have been some results that show that at a certain level of inbreeding the effect is positive and sometimes better than non-inbred animals (Thompson *et al*. 2000), inbreeding is not something to strive for. The effect of dam inbreeding in this study show in inbreeding class 7 (position 8) a value almost as high as the non-inbred animals but the general trend is negative meaning that the higher inbreeding, the lower number of piglets will be born.

Positive effects of inbreeding are, as mentioned before, rare and is probably due to some fixation of favourable genes in the animal or better sperm qualities for the sires (Köck *et al*. 2009), and if breeding with close relatives continues, it is possible that deleterious genes gets expressed in the end. The results from this study shows that the Hampshire breed is affected negatively the higher inbreeding and the inbreeding level have increased from 2008 to 2017. The mean increase of inbreeding level is 0.56 per year. The increase itself is not that surprising considering that the population is smaller at nucleus level than production level. Crossbreeding is most common in pig production which means that inbreeding is not a problem on production level but might be a problem in nucleus herds, especially if the inbreeding level continues to increase.

Traits connected to fitness, such as litter size is believed to be more affected by inbreeding depression (Falconer & Mackay, 1996) but body measurements in Spanish Purebred horses has also been reported to be affected by inbreeding (Gómez *et al*. 2009). Hampshire pigs are bred for better meat quality, efficient feed conversion and leaner meat, if the inbreeding continues to increase in the breed, this may also affect these traits in the end. Also, if the inbreeding increases, the litter sizes might get smaller and that will lead to less animals for selection.

6 Conclusion

The aim of this study was to analyse the effects of inbreeding in the Hampshire breed and the results shows that the TNB, NBA and SB decreases with higher inbreeding level. The decrease of TNB and NBA are considered to be negative while the decrease of SB can be considered as positive since the percent of stillborn piglets gets lower. However, the only significant factor for SB was the herd, meaning the management in the herd could have a major effect on this and not inbreeding itself. The inbreeding levels have been increasing the last 10 years and if this continues to increase the litter size will get smaller and, in the end, it could affect the traits that Hampshire are bred and selected for.

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