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Til Fødevarestyrelsen

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Levering på bestillingen "Højere overlevelse for pattegrise og smågrise fra dag 5 indtil slagtning gennem kvantitativ avl".

Fødevarestyrelsen har i en bestilling sendt den 30. april 2020, bedt DCA – Nationalt Center for Fødevarer og Jordbrug – om at afdække, hvorvidt det er muligt at avle for bedre overlevelse for pattegrise og smågrise fra dag 5 indtil slagtning. Fokus vil være på avlsmæssige muligheder for højere overlevelse for pattegrise og smågrise efter dag 5, da dette vil det være en genetisk parameter for grisenes overlevelsesevne frem til slagtning. Formålet er at skabe genetiske modeller for overlevelsesdata efter dag 5.

Besvarelsen i form af vedlagte rapport, er udarbejdet af Seniorforsker Guosheng Su, Akademisk medarbejder Johanna Höglund, Seniorforsker Ole Fredslund Christensen og Professor Mogens Sandø Lund fra Center for Kvantitativ Genetik og Genomforskning ved Aarhus Universitet. Professor Lene Juul Pedersen fra Institut for Husdyrvidenskab ved Aarhus Universitet og Professor Just Jensen fra Institut for Molekylærbiologi og Genetik ved Aarhus Universitet, har været fagfællebedømmere, og rapporten er revideret i lyset af deres kommentarer.

Som en del af denne opgave er der indsamlet og behandlet nye data, og rapporten præsenterer resultater, som ikke ved rapportens udgivelse har været i eksternt peer review eller er publiceret andre steder. Ved en evt. senere publicering i tidsskrifter med eksternt peer review vil der derfor kunne forekomme ændringer.

Besvarelsen er udarbejdet som led i "Rammeaftale om forskningsbaseret myndighedsbetjening mellem Miljø- og Fødevareministeriet og Aarhus Universitet" under ID 1.02 i "Ydelsesaftale Husdyrproduktion 2020-2023".

Venlig hilsen

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Possibilities for genetic improvement of pig survival until slaughter

Rapport fra DCA - Nationalt Center for Fødevarer og Jordbrug

Dato: 18.12.2020

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Sammendrag

Høj dødelighed i moderne svineproduktion er en stor velfærdsmæssig og økonomisk udfordring. I øjeblikket inkluderer avlsmålet i de to største danske avlsselskaber kuldstørrelse fem dage efter faring (LG5), som er en kombination af antallet af fødte smågrise og overlevelse i de første fem dage efter fødsel. Imidlertid er grisens overlevelse fra dag 5 til de skal slagtes ikke direkte inkluderet i de danske avlsprogrammer. I øjeblikket er overlevelsesraterne hos de danske grise ikke tilfredsstillende, og derfor ønsker Fødevarestyrelsen en udredning af mulighederne for at avle for højere overlevelse af grisene fra dag 5 indtil slagtning. Indtil videre er der ikke meget viden om mulighederne for at forbedre overlevelse ved avl, især for overlevelse efter fravænning. Formålet med denne rapport er at undersøge, om det er muligt at avle for forbedret overlevelse indtil slagtning. Rapportens mål er at: 1) give en litteraturoversigt over arvelighed af overlevelse/dødelighed, 2) undersøge kvaliteten af overlevelsesdata til genetisk evaluering, 3) Undersøge dødelighedsmønsteret i forhold til grisens alder, soens paritet og sammenhængen til LG5, 4) Beregne genetiske parametre og graderne af arvelighed i de forskellige perioder indtil slagtning, 5) vurdere nøjagtigheden af selektion og forventet genetisk gevinst ved selektion mod dødelighed.

I litteraturen er der benyttet to typer af fremgangsmåder til at analysere sådanne overlevelsesdata, enten at analysere overlevelse på kuld-niveau, eller at analysere overlevelse for den enkelte gris. I det sidste tilfælde har man benyttet to typer modeller, enten en lineær model (LM) på den observerede skala (f.eks., 0=overlevet, 1=død), eller en liability-threshold model (LTM) som bedre kan håndtere den binære natur (overlevet eller død) af overlevelse ved at analysere på en underliggende kontinuert skala (dvs. liability/tilbøjelighed til at dø). Generelt viser resultaterne fra litteraturen at overlevelse er en arvelig egenskab med lav grad af arvelighed for alle de forskellige perioder frem til slagtning, selvom der kun er få studier om arvelighed af overlevelse fra fravænning til slagtning.

Data benyttet i dette studie blev udleveret af Seges Svineproduktion som havde lavet en aftale med Danbred avlsbesætninger om at der for alle levendefødte hungrise i disse besætninger skulle registreres alle hændelser indtil de forlod systemet. Ingen synlige fejl blev fundet i de modtagne data. Vi observerede at ca. 10 % af grisene forlod systemet i live før slagtealder. De faktiske årsager til dette er ukendte, men avlsbesætninger har ret til at sælge nogle af grisene inden slagtealder. Til sidst, selv om data i dette studie omfatter mange målinger, så dækker det kun 1,3 generationer, og denne mangel på flere generationer gjorde det umuligt at inkludere en maternel genetiske effekt i dataanalysen. Generelt, var datakvaliteten tilstrækkelig til avlsværdivurdering af dødeligheds-egenskaber, men datakvaliteten kan dog forbedres på flere områder.

I dette studie var dødelighed kodet som 0 for værende i live og 1 for død, og dødelighedsraten i en periode var beregnet som antal døde grise i perioden divideret med antal grise i live ved periodens start. Gris levende eller død ved fødsel var defineret som levende eller død ved første inspektion efter faring. Dødelighed blev analyseret i forskellige perioder, dvs. Mort5: dødeligheden fra fødsel (første inspektion efter faring) til dag 5, Mort5w: fra dag 5 til fravænning, Mortg1: i fravænningsperioden (dag 21 til dag 70 for Duroc, dag 21 til dag 77 for Landrace og Yorkshire), Mortg2: i slagtesvinsperioden (dag 70 til dag 140 for Duroc, dag 77 til dag 150 for Landrace og Yorkshire), og Mortall: fra fødsel til slagtningsalder (dag 140 for Duroc og dag 150 for Landrace og Yorkshire). Baseret på de analyserede data, der omfatter hungrise, født fra oktober 2018 til august 2020, i besætninger med Duroc,

Landrace og Yorkshire, var dødeligheden 10,2 % for Mort5, 6,8 % for Mort5w, 4,8 % for Mortg1 og 3,8 % for Mortg2, i gennemsnit over de tre racer. Dødeligheden fra dag 5 til slagtning (Mort5g2) var 15,9 % for Duroc, 12,9 % for Landrace og 16,9 % for Yorkshire. Den samlede dødelighed fra fødsel til slagtning (Mortall) var henholdsvis 27,3 % for Duroc, 21,7 % for Landrace og 23,8 % for Yorkshire.

Da flertallet af søer var relativt unge i dette studie, var de aktuelle data ikke velegnede til at påvise en sammenhæng mellem grisedødelighed og soens alder eller soens paritet. Men det blev observeret, at grise fra den første paritet havde lidt højere dødelighed fra dag 5 til fravænning (Mort5w), og at der var en tendens til, at grise fra den anden paritet havde en lidt lavere dødelighed i de fleste perioder sammenlignet med grise fra andre pariteter. De aktuelle data viste også for alle racer, at når LG5 steg, så faldt Mort5 dramatisk, og Mort5w faldt svagt.

Genetiske parametre for de seks dødelighedsegenskaber (Mort5, Mort5w, Mortg1, Mortg2, Mort5g2 og Mortall) blev beregnet ved hjælp af en lineær model (LM) og en "liability-threshold" model (LTM) baseret på grisens individuelle overlevelse. På den observerede skala (0, 1) ved anvendelse af LM varierede graden af arvelighed fra 0,001 til 0,022, og estimater af graden af arvelighed på den underliggende skala ved hjælp af LTM varierede fra 0,018 til 0,089 for dødelighed i forskellige perioder og racer. For Mort5g2 var grader af arvelighed på den observerede skala 0,012, 0,015 og 0,021, og grader af arvelighed på den underliggende (liability/tilbøjeligheds) skala var 0,038, 0,040 og 0,044 i henholdsvis Duroc, Landrace og Yorkshire. For Mortall var grader af arvelighed på observeret skala 0,020, 0,021 og 0,022, og grader af arvelighed på underliggende skala var 0,046, 0,044 og 0,041 i henholdsvis Duroc, Landrace og Yorkshire. Ved en tilnærmet transformation var graderne af arvelighed, der blev beregnet fra de to modeller, meget ens.

De beregnede avlsværdier (EBV) på den observerede skala fra LM-model og på den underliggende skala fra LTM-model var meget ens. Korrelationskoefficienterne mellem de to sæt EBVer var højere end 0,98 for alle dødeligheds egenskaber og racer med en undtagelse af 0,95 for Mortg2 i Landrace. Sikkerhed af EBV (defineret som korrelationen mellem sand avlsværdi og beregnet avlsværdi) afhænger generelt set af graden af arvelighed og af antallet af registreringer på beslægtede dyr. For dødelighedsegenskaberne undersøgt her, var graderne af arvelighed på den ene side lave, men på den anden side var der målinger på mange helsøskende og halvsøskende, hvilket samlet set gav en sikkerhed som var acceptabel til avlsmæssig brug. For Mort5g2 og Mortall, var de forventede sikkerheder (sikkerheder beregnet ud fra modellen) på den observerede skala henholdsvis 0,319 og 0,367 i gennemsnit over de tre racer, og på den underliggende skala var de henholdsvis 0,341 og 0,380. Valideringssikkerheder (realiserede sikkerheder) som ikke afhænger af korrektheden af modellen, blev også beregnet som en kontrol, og disse sikkerheder svarede til de forventede sikkerheder.

Baseret på beregnede genetiske parametre og forventet sikkerhed af EBV blev den forventede genetiske gevinst i reduktion af dødelighed pr. generation beregnet. Den forventede genetiske gevinst afhænger af selektions-intensiteten, som vi ikke kender, da selektion i praksis er for et vægtet totalindeks af flere egenskaber som man ønsker at forbedre via avl. Et ekstremt scenarie er selektion udelukkende for reduktion af dødelighed og med en selektions-intensitet på 1. En selektions-intensitet på 1 er en anelse mindre end den faktiske selektionsintensitet på totalindeks i den danske svineavl, og svarer til at selektere de 38 % bedste dyr til avl. I et sådant ekstremt scenarie, varierede de

forventede genetiske reduktioner blandt dødelighedsegenskaber i forskellige perioder og i forskellige racer med et gennemsnit på 1,11 procentpoint pr. generation. For Mort5g2, gennemsnit over forskellige modeller og målemetoder, var de forventede reduktioner 1,40, 1,31 og 2,02 procentpoint i henholdsvis Duroc, Landrace og Yorkshire efter en generation. For Mortall var de forventede reduktioner 2,43, 2,09 og 2,43 procentpoint i henholdsvis Duroc, Landrace og Yorkshire. Men selektion udelukkende for reduktion af dødelighed er ikke realistisk, da et avlsmål for et svineavlsprogram indeholder en række egenskaber der skal forbedres. Den faktiske selektionsintensitet på reduktion af dødelighed ved at inkludere dødelighed i avlsmålet afhænger af vægten på dødelighed og sammenhængen mellem dødelighed og andre egenskaber i totalindeks. Sikkerheden af EBV og dermed genetisk gevinst ved selektion kan øges ved forbedret datakvalitet, yderligere registreringer af data, herunder registreringer over hangrise, mere sofistikerede statistiske modeller og inkludering af genomisk information.

Vores generelle konklusioner var som følger: Graderne af arvelighed af dødelighed for grise rapporteret i litteraturen, var lave. Datakvaliteten i dette studie var generelt tilstrækkeligt til genetisk evaluering af dødeligheds egenskaber, men vil kunne forbedres på nogle områder. Dødeligheden faldt med stigende alder af grise, og dødeligheden før fravænning faldt med stigende LG5. Graderne af arvelighed var lave for dødelighed i alle perioder, helt på linje med de fleste tidligere undersøgelser. Selvom graderne af arvelighed var lave, så var sikkerhederne af EBV acceptable til selektion, og genetisk forbedring af overlevelse indtil slagtning er derfor mulig. Den genetiske gevinst for overlevelse ved avl afhænger i høj grad af den faktiske selektionsintensitet for overlevelse i et avlsprogram. Vi anbefaler: 1) fortsæt med at registrere dødelighed, 2) registrer dødelighed for hangrise som tilføjelse til registreringen af hungrise, 3) foretag yderligere undersøgelser for at optimere et avlsprogram til både genetisk reduktion af dødelighed og genetisk fremgang for de nuværende egenskaber i avlsmålet, 4) inkluder dødelighed i avlsmål for danske svineavlsprogrammer.

Summary

High mortality in modern pig production is a big welfare and economic challenge. Currently, the breeding goal in the two main Danish breeding companies includes litter size at five days after farrowing (LG5), which is a combination of number of piglets born and survival in the first five days. However, survival of the pig from day 5 to slaughter is not directly included in Danish pig breeding programs. Currently, survival rates in Danish pig populations are not desirable, and therefore the Danish Veterinary and Food Administration need an overview of the possibilities for improving pig survival from day 5 until slaughter. So far, there is not much knowledge about possibilities for improving survival by breeding, especially for survival after weaning. The purpose of this report is to evaluate whether it is possible to breed for higher pig survival until slaughter. The detailed objectives of this report are to: 1) provide a literature summary of heritability of pig survival/mortality, 2) examine the quality of survival data for genetic evaluation, 3) investigate mortality patterns with age of pig, dam parity and the relationship with LG5, 4) estimate genetic parameters and the resulting heritability in different periods until slaughter, 5) assess accuracy of selection and expected genetic gain by selection against mortality.

In the literature, two types of approaches have been used for analyzing such survival data, either analyzing survival at the litter level, or analyzing survival at the pig individual level. In the latter case, two types of models have been used, either a linear model (LM) on the observed scale (e.g., 0=survived, 1=dead) or a more sophisticated liability-threshold model (LTM) that better takes the binary nature (survived or died) of survival into account by analyzing on an underlying continuous scale (i.e., liability to die). In general, results from the literature shows that survival is a heritable trait with low heritability in all different periods until slaughter, although there are only few studies about heritability of survival from weaning to slaughter.

The data used in this study were provided by Seges Svineproduktion which had made an agreement with DanBred breeding herds that all female pigs alive at birth in these herds should be registered for all events until they leave the system. No visible errors were found in the data we received. We noticed that 10 % of pigs left the system alive before slaughter age and had no further record. The actual reasons for this are unknown, but breeding herds have been allowed to sell some of the pigs before finishing the test. Finally, although the data set in this study contained a large number of records, it covered only about 1.3 generations, and this lack of more generations made it impossible to include a maternal genetic effect in the analysis. Data quality was in general sufficient for genetic evaluation for mortality traits, but it can be improved in some aspects.

In this study, mortality trait was coded as 0 for alive and 1 for dead, and mortality rate in a period was calculated as number of pigs dead during the period divided by the number of

pigs alive at the start of the period. Pig alive or dead at birth was defined as alive or dead at the time of first visit after birth. Mortality was analyzed in different periods, i.e., Mort5: mortality in the period from birth (first visit after farrowing) to day 5, Mort5w: from day5 to weaning, Mortg1: in nursery period (day 21 to day 70 for Duroc, day 21 to day 77 for Landrace and Yorkshire), Mortg2: in finishing period (day 70 to day 140 for Duroc, day 77 to day 150 for Landrace and Yorkshire), Mort5g2: from day 5 to the end of finishing period, and Mortall: from birth to the end of finishing period. Slaughter age was defined as the age at the end of finishing period. Based on the data analyzed, comprising female pigs born from October 2018 to August 2020 in Duroc, Landrace and Yorkshire herds, mortality rates were 10.2 % for Mort5, 6.8 % for Mort5w, 4.8 % for Mortg1, 3.8 % for Mortg2, averaged over three breeds. Mortality rates from day 5 to slaughter (Mort5g2) were 15.9 % for Duroc, 12.9 % for Landrace and 16.9% for Yorkshire. Total mortality rates from birth to slaughter (Mortall) were 27.3 % for Duroc, 21.7 % for Landrace and 23.8 % for Yorkshire, respectively.

Since majority of sows were relatively young, the information in current data was not well-suited to detect a relationship between pig mortality and age of dam or parity. But it was observed that pigs from the first parity had slightly higher Mort5w, and there was a trend that pigs from the second parity had a slightly lower mortality in most periods, compared to pigs from other parities. The current data also showed that for all three breeds, when LG5 increased, Mort5 decreased dramatically, and Mort5w decreased slightly.

Genetic parameters for the six mortality traits (Mort5, Mort5w, Mortg1, Mortg2, Mort5g2 and Mortall) were estimated using a linear mixed model (LM) and a liability-threshold model (LTM) at pig individual level. Estimates of heritability on observed scale (0, 1) using LM ranged from 0.001 to 0.022, and estimates of heritability in underlying liability scale using LTM ranged from 0.018 to 0.089, for mortality in different periods and breeds. For Mort5g2, heritabilities on observed scale were 0.012, 0.015 and 0.021, and heritabilities on liability scale were 0.038, 0.040 and 0.044 in Duroc, Landrace, and Yorkshire, respectively. For Mortall, heritabilities on observed scale were 0.020, 0.021 and 0.022, and heritabilities on liability scale were 0.046, 0.044 and 0.041 in Duroc, Landrace, and Yorkshire, respectively. By an approximate transformation, the heritabilities estimated from the two models were highly consistent.

Estimated breeding value (EBV) on observed scale from LM model and EBV on liability scale from LTM model were very similar. The correlation coefficients between the two sets of EBV were higher than 0.98 for all mortality traits and breeds, with one exception of 0.95 for Mortg2 in Landrace. Accuracy of EBV (defined as the correlation between true and estimated breeding value) depends in general on heritability and number of records on relatives. For mortality traits investigated here, heritabilities were on the one hand low, but on the other hand, records were available on a number of full-siblings and half-siblings, resulting in an accuracy that is acceptable for breeding. For Mort5g2 and Mortall, the expected

accuracies (accuracy calculated from model information) of EBV on observed scale were 0.319 and 0.367 when averaged over the three breeds, respectively, and on liability scale they were respectively, 0.341 and 0.380. Validation accuracies (realized accuracies) that do not depend on the correctness of the model, were additionally computed as a control, and these accuracies were comparable to the expected ones.

Based on estimates of genetic parameters and expected accuracies of EBV, the expected genetic reductions of pig mortality per generation were calculated. The expected genetic reduction depends on selection intensity, which we don't know, since in practice selection is on a weighted total selection index of several traits of interest for breeding. An extreme situation is selection only for reduced mortality and selection intensity of 1.0. Selection intensity of 1.0 is a bit less than the realized selection intensity for total selection index in Danish pig breeding program and corresponds to select top 38 % animals as breeding animals. In such extreme situation, the expected genetic changes differed among mortality traits in different periods and in different breeds with an average reduction of mortality rate of 1.11 percentage point per generation. For Mort5g2, averaged over different models and measure methods, the expected reductions were 1.40, 1.31, and 2.02 percentage points in Duroc, Landrace, and Yorkshire, respectively, by one generation of selection. For Mortall, the expected reductions were 2.43, 2.09, and 2.43 percentage points in Duroc, Landrace, and Yorkshire, respectively. However, selection only on mortality is not realistic, since breeding goal of a pig breeding program includes a number of traits to be improved. The realized reduction of mortality due to including mortality in breeding goal will depend on the weight on mortality and the relationship between mortality and other traits in the selection index. Accuracy of EBV and thus genetic gain by selection may be increased by better data quality, further accumulation of data, including records of male pigs, more sophisticated statistical model, and using genomic information.

Our general conclusions were as follows: Heritabilities of pig mortality reported in the literature were low. Data quality in this study was in general sufficient for genetic evaluation for mortality traits, but can be improved in some aspects. Mortality decreased with increasing age of pigs, and pre-weaning mortality decreased with increasing LG5. Heritabilities were low for mortalities in all periods, in line with most previous studies. Although heritabilities were low, accuracies of EBV were acceptable for selection, and genetic improvement of pig survival until slaughter is therefore possible. The realized genetic gain of pig survival by breeding will greatly depend on actual selection intensity on pig survival in a breeding program. We recommend: 1) continue to register mortality, 2) register mortality of male pigs in addition to female pigs, 3) carry out further investigations to optimize a breeding program for both genetic reduction of mortality and genetic gain for the traits in current breeding goal. 4) include pig mortality in breading goals of Danish breeding programs.

Introduction

Pig mortality is a major economic and welfare issue in modern pig production. Currently, the two main Danish pig breeding companies, Danbred and Danish Genetics, breed for number of piglets alive at day 5. Litter size at day 5 (LG5) is equal to total number of piglets born minus number of deaths (including still born) before day 5. The inclusion of LG5 in the selection index implies that there is breeding for survival at birth and over the first five days. This is a simple way to genetically improve both litter size and piglet survival before day 5 using the information of a single trait. However, to reduce mortality, directly including mortality in the selection index could be a better alternative. Moreover, so far there is limited knowledge about possibilities for breeding to improve pig survival after day 5, in particular breeding for survival after weaning. Before initiating a breeding program for improving pig survival until slaughter, many relevant issues need to be explored.

- Experience with collecting survival data suggests that it is difficult to collect reliable data, which is crucial for efficient implementation in a breeding program. Therefore, as the first step in the development of a breeding program for genetic improvement of pig survival, it is necessary to examine the quality of survival data to make sure that the data are good enough to be used for genetic evaluation.
- The possibilities for genetic improvement of pig survival depends on how heritable pig survival is. Previous studies have shown a variation in estimates of heritabilities but in general the estimates are low, and studies of genetic variation in post-weaning mortality are very rare. It requires an investigation on mortality pattern along the time until slaughter, and an estimation of genetic variation and heritability of mortality in different periods in current Danish pig populations.
- Efficiency of genetic improvement also depends on the accuracy of selection, which is influenced by the heritability and genetic variation of the trait as well as the amount of records on the selection candidates and their relatives. Although heritability for pig mortality reported in the literature is low in general, it can be hypothesized that accuracy of selection may be acceptable in a breeding program for improving pig survival, since breeding values can be estimated from large amount of information including records of the individual itself and a large group of sibs. It is important to assess selection accuracy in the Danish breeding populations.

Therefore, the purpose of the current study is to evaluate whether it is possible to breed for better pig survival until slaughter by investigating the followings: 1) Literature summary of heritability of pig survival (or mortality); 2) Examine the quality of a survival data set from Seges Svineproduktion to make sure that such data are suitable to be used for genetic evaluation; 3) Investigate mortality pattern with the age of pig, dam parity and the relationship with LG5 which is the trait in the current breeding goal; 4) Estimate variance components and the resulting heritability of mortality in different periods until slaughter; 5) Assess accuracy of selection and expected genetic progress when selecting against mortality.

Litterature summary

Here we provide a short summary of scientific literature presenting heritability estimates on different pig survival/mortality traits. The purpose of this section is twofold. The first is to introduce the different survival/mortality traits and how they can be analyzed, and the second is to show information about heritability estimates in the literature.

Pig survival can be improved in various ways. Genetic improvement would be an important approach, since this improvement can be permanent and cumulative. The efficiency of genetic improvement depends on the genetic variation in pig survival or the equivalent trait, mortality. Genetic variation and heritability of pig survival/mortality before weaning have been investigated in a number of studies. Some studies treat pig mortality as the trait of sow and analyze mortality rate at litter level, and others treat pig mortality as the trait of the pig and analyze mortality at a pig individual level. Some studies estimate variance components and heritability on an observed scale (binary observation, 0 or 1 corresponding to alive or dead), and others in an underlying liability scale.

Treating mortality as a trait of the sow is based on the assumption that mortality at birth and in early life is mostly influenced by the ability of the mother to perform farrowing-related activities, provide a good environment for the piglets and nurse the piglets. From a computational perspective it reduces the size of data by summarizing pig individual records into one record on the sow. From a practical breeding perspective it also offers the advantage of being able to combine breeding for improved survival (reduced mortality) with breeding for fertility. An example of this is breeding for number of piglets alive at day 5 which is currently done by DanBred and Danish Genetics. When treating piglet mortality as a trait of the sow and analyzing litter mortality rate, in most studies the models include effect of service sire, but the possible effect of cross-fostering is ignored. By considering piglet mortality as a trait of sow, Damgaard et al. (2003) estimated heritability at litter level to be 0.13 for stillbirth, and 0.06 for pre-weaning mortality of live-born piglets, based on data from a Yorkshire population in Sweden. Based on data from Danish breeding herds, Su et al. (2007) showed that the heritability of survival rate was 0.11 at farrowing, 0.09 during the period from birth to day 5, and 0.02 during the period from day 5 to weaning as an average over Landrace and Yorkshire populations. Nielsen et al. (2013) and Guo et al. (2015) reported that heritabilities of mortality before day 5 (including stillbirth) ranged from 0.09 to 0.10 for Danish Landrace and Yorkshire populations in the two studies.

Treating survival/mortality as a trait of the pig is in principle more appropriate than treating it as a trait on the sow, but it adds complexity to the data analysis for two reasons. First, survival of an individual pig is influenced by two genetic effects, an effect of the pig itself to better survive, and an effect from the mother to provide an environment for the pig to better survive. The latter is particularly important for survival at birth and in early life. We will refer

to these two effects in genetics as direct and maternal genetic effects, respectively, and both of them are important for breeding for increased survival. Second, individual records on pigs are binary (0 or 1), and the question is whether it is appropriate to analyze them using a standard linear mixed model on this observed scale, or a more sophisticated model that incorporates this binary feature by analyzing on an underlying liability scale (further details on this can be found in the appendix). Similar to when analyzing litter mortality rate as a trait of the sow, in most studies cross-fostering is ignored when analyzing pig individual mortality as a trait of the pig.

By considering piglet survival as the trait of the piglet, Su et al. (2008) studied Danish Landrace and Yorkshire populations, and reported that direct heritabilities on the liability scale ranged from 0.012 to 0.056, and the maternal heritabilities ranged from 0.017 to 0.057 for survival at birth, survival from birth to day 5 and survival from day 5 to weaning, respectively. In a study on Yorkshire, Landrace and Pietrain pigs by Ibáñez-Escriche (2009), direct heritabilities were 0.02, 0.06, 0.10, and maternal heritabilities were 0.05, 0.13, and 0.06 on the liability scale, for the three breeds respectively. In a study on three Iberian lines by Muñoz (2017), direct heritabilities were 0.010, 0.004, 0.003, and maternal heritabilities were 0.034, 0.011, and 0.014 on the liability scale, for the three lines respectively. Strange (2013) obtained high estimates of direct heritability (0.08) and maternal heritability (0.24) on the liability scale for stillbirth, based on data from commercial production herds.

Direct and maternal genetic effect can also be estimated using records at litter level. Lund et al (2002) reported direct heritabilities ranging from 0.01 to 0.05, and maternal heritabilities ranged from 0.01 to 0.08 for survival rates at farrowing and from farrowing to weaning in Finish Landrace and Yorkshire populations.

Many studies analyzing pig individual mortality as a trait of the pig focused on direct additive genetic effect. In such analysis, litter effect or overall sow effect was included in the model to account for the effects other than direct additive genetic effect. Using such analysis, Grandinson et al. (2002) reported that the heritability on the observed scale (0,1) was 0.04 for stillbirth and 0.03 for total pre-weaning mortality, and on the underlying liability scale the estimate was 0.15 for stillbirth and 0.05 for pre-weaning mortality, in a Swedish Yorkshire population. Hellebugge et al. (2008) studied German Landrace pigs and Dufrasne et al (2013) studied commercial production pigs in US, and reported that heritability for pre-weaning mortality was 0.03 and 0.02 on the liability scale, respectively. Cecchinato (2010) estimated pre-weaning survival in a crossbred population and obtained a heritability of 0.04 on the liability scale.

Estimates of genetic parameters for post-weaning mortality are very rare in the literature. Harper et al. (2019) reported a heritability on the observed scale of 0.02 for pig mortality in the nursery phase of commercial production pigs. Cheng et al. (2020) reported a heritability

on the observed scale of 0.07 for mortality in a disease challenge nursery and 0.04 for pig mortality in finishing phase of Landrace×Yorkshire pigs.

In summary, estimates of the heritability for pig mortality are low in nearly all previous studies. However, non-zero heritabilities indicate that pig mortality traits are heritable and therefore breeding for these traits have the potential to reduce pig mortality. On the other hand, low heritability would limit the efficiency of genetic improvement in general, but a low heritability trait with large genetic variance can still be genetically improved efficiently.

Pig mortality in Danish pig breeding populations

Populations and data

The data used in this study were provided by Seges Svineproduktion which made an agreement with DanBred breeding herds that all female pigs alive at birth in nucleus herds should be registered for all events until they leave the system. The recording started from Ist October, 2018. The data we received contained the following variables: animal ID, sire, dam, breed, herd, birthdate, date in, date off, code off (73 codes indicating the reason of leaving), type off (death or alive at the time of leaving). For code off, the herd managers made their own definitions on the codes and these could be inconsistent among different herds, and thus the information was not used in the current study. Data of total number born and LG5 for the litters that the pig belonged to, and pedigree traced back for 7 generations were also provided by Seges Svineproduktion. Based on birth date of a pig, and the date of changing its status (i.e., death, moving to gilt development unit or sow unit, moving to another herd, etc.), it was possible to trace for each female pig whether it was dead or alive in different periods. The raw data contained 284,669 records from 211,462 pure female pigs of Duroc, Landrace and Yorkshire, and covered the period from birth date 2018-10-01 to 2020-08-26. Most individuals had only one record, but some individuals had more than one record since they were moved one or more times (e.g., from a growth unit to a gilt development unit or sow unit, from one herd to another).

The data were inspected for potential errors by checking the starting and end time of a status and the connection between adjacent statuses, e.g., whether there were animals that had further records after being recorded as dead. No such cases were found. When an animal had more than one record, the starting time of the later record was consistent with the ending time of the former status. Therefore, no visible errors were found in the data we received. This suggests that the data are under good quality control in the database.

Since the aim of this study was to investigate pig survival until slaughter, a data set was constructed with one record for each animal containing information about the last event before slaughter age. Thus each animal kept only the last record before slaughter age (defined as 150 days for Landrace and Yorkshire, and 140 days for Duroc). There were 67 animals from

five dams which did not have birth date and parent information, five animals had no record of being dead or alive when leaving the herd, and 69 animals came from two herds which had less than 100 pigs in the data. These animals were removed from the data. There were 21,742 (10%) pigs which left the system alive before slaughter age and had no further record. The reason for this was unknown, but breeding herds were allowed to sell pigs before finishing the test with a restriction of less than 1/7 being sold or moved out during the test period (i.e., finishing period). Due to the large number of such records, and the fact that they did provide information about animals being alive until a certain time at least, we could not remove these records; see below on how these records were incorporated. In total, the number of pigs in the analysis were 26,633 from 7,311 litters for Duroc, 67,025 from 9,665 litters for Landrace, 117,767 from 16,112 litters for Yorkshire.

To investigate mortality in different periods, a number of traits were defined. A feature of survival data is the animals that died before a specific time period do not provide information about survival in that period. In addition, an issue of such data is how to handle the fact that a number of animals were still in the system at the last day of data collection but younger than the ending age of the period, e.g. an animal that is 8 days old at this day had only partial information about survival until slaughter time. These issues were taken into consideration in the analysis of the data. The mortality traits were coded as 0 for survival and 1 for death. Mortality at farrowing (i.e., still born) was not calculated, because the data included only live-born female pigs, where being live-born was determined at the first inspection of the litter after farrowing.

The following mortality traits were analyzed in this study:

Mort5: Mortality from birth to day 5 for the live-born animals. For animals still alive at the end of data recording, if the age was less than 5 days, Mort5 was defined as missing (for example, a piglet born on 2020-08-23 was 3 days old at the end of data recording (2020-08-26), and if the piglet was still alive, the record for this piglet was treated as missing).

Mort5w: Mortality during the period from day 5 to weaning (21 days), given the pig was alive at day 5. Mort5w was missing for the pigs which died before or at day 5, and also defined to be missing for the pigs alive at the end of data recording but younger than 21 days.

Mortg1: Mortality during nursery period (nursery period could differ a bit between breeds, and was here defined to be day 21 to day 70 for Duroc, and day 21 to day 77 for Landrace and Yorkshire), given the pig was alive at day 21. Mortg1 was missing for pigs which died before or at day 21, and was defined to be missing for pigs still alive at the end of data recording and younger than the ending age of the nursery period (day 70/77).

Mortg2: Mortality during finishing period (finishing period could also differ between breeds, and was here defined to be day 70 to day 140 for Duroc, day 77 to day 150 for Landrace and Yorkshire), given the pig was alive at the beginning of the period (day 70/77). Mortg2 was missing for pigs which died in the nursery period or earlier, and defined to be missing for pigs still alive at the end of data recording and younger than the ending age of the finishing period (day 140/150).

Mort5g2: Mortality during the period from day 5 to the end of finishing period (slaughter age). Mort5g2 was missing for pigs which died before or at day 5, and defined to be missing for pigs still alive at the end of data recording and younger than the ending age of the finishing period (day 140/150).
Mortall: Mortality during the period from birth to the end of finishing period for live-born animals. Mortall was defined to be missing for pigs still alive at the end of data recording and younger than the ending age of the finishing period (day 140/150).

Concerning the 21,742 (10%) pigs which left the system alive before slaughter age and had no further record, records for these pigs (censored records) were treated such that if the pig left later than the midpoint of a particular period, the pig was assumed to survive over the period, otherwise the record for the period was assumed missing. For example, a Landrace pig which left the system at an age of 138 days (the midpoint in finishing period was 77+ (150-77)/2=113 days), the pig was assumed to survive over 150 days. Another example, a Landrace pig left system at an age of 40 days (the midpoint in nursery periods was 49 days), the pig was assumed having no information of survival over nursery period, and the records of the pig were treated as missing for Mortg1, Mortg2, Mort5g2, and Mortall. Censored records is a challenge in analysis of mortality. In our data, there are two types of censoring: animals still alive at the end of data recording, and animals which left the system alive before slaughter age. Survival models are statistical models that allow to distinguish censored and uncensored records in the analysis, and many different survival models have been proposed (Bewick et al., 2004; Qin, 2017). Since the use of survival models generally involves many assumptions, parameter settings and technical details, it requires an additional intensive study in order to determine a desired survival model for prediction of breeding values. Therefore survival models are not considered in the current study.

Mortality in relation to age of pigs

Percentage of deaths in each day during sucking period for the three breeds are plotted in Figure 1. For all three breeds, percentage of deaths in day 1 was lower than day 2. One reason for this could be that some sows farrowed in afternoon or evening and therefore the time period for registering deaths in day 1 was shorter than one day, i.e. shorter than other days. Another possible reason for this could be that there was a delay in recording mortality at farrowing, since the farmer might not visit the new born piglets immediately after the sow finished farrowing. Thus, some piglets that were live-born but died before the farmer's first

visit, might be registered as stillbirth, instead of death in day 1. From day 2 and onwards, percentage of deaths decreased with increasing age of piglets, being highest during the first week after farrowing, especially during the first four days. The three breeds had different patterns of mortality in relation to the age of the piglets. During the first four days after farrowing, Duroc had the highest and Yorkshire had the lowest mortality rate, with Landrace in-between. After one week, Yorkshire had higher mortality than Duroc and Landrace.

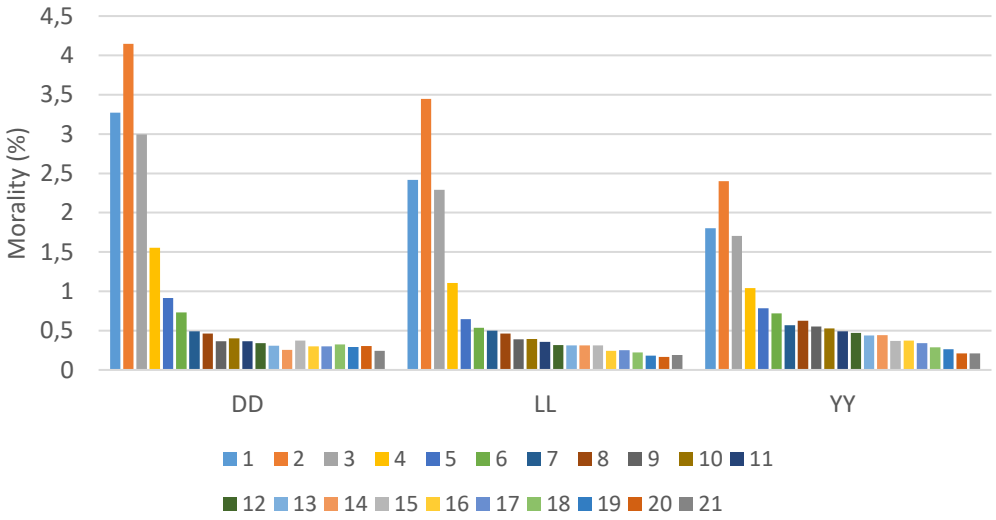

Figure 1. Percentage of deaths in each day during the period from day 1 to day 21 after birth in Duroc (DD), Landrace (LL), and Yorkshire (YY). Percentage of deaths in a day was calculated as the number of dead piglets in the day divided by number of piglets alive at the time of first inspection after farrowing.

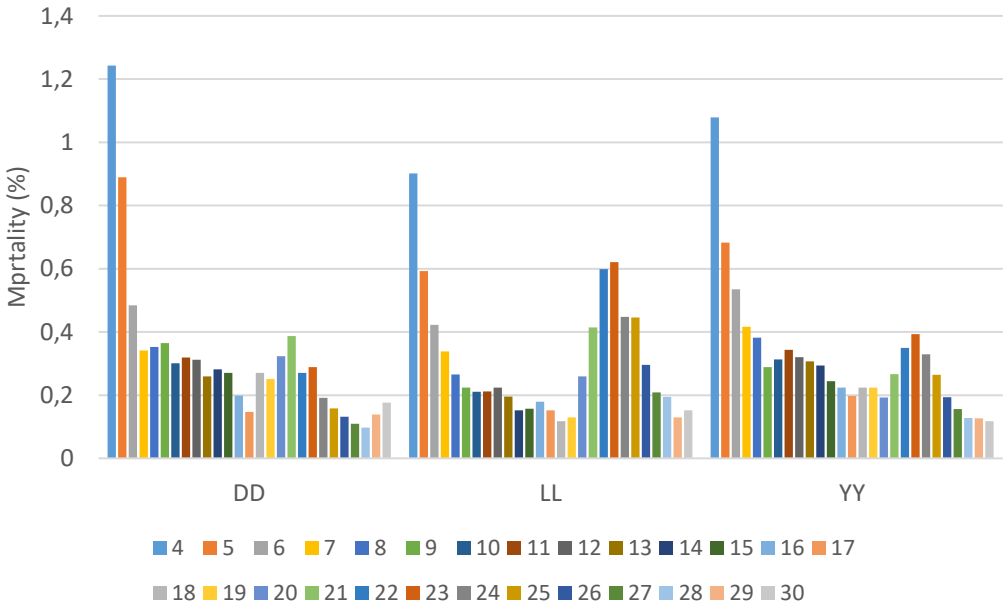

Figure 2. Percentage of deaths in each week during the period from week 4 to week 30 in Duroc (DD), Landrace (LL), and Yorkshire (YY). Percentage of deaths in a week was calculated as the number of dead piglets in the week divided by number of pigs alive at the time of first inspection after farrowing.

Figure 2 presents the percentage of deaths in each week during the period from week 4 to week 30 for the three breeds. Age at slaughter is about 20 weeks Duroc and 21.5 weeks for Landrace and Yorkshire, but here we presented a bit longer time period in order to show the tendency of mortality in a few weeks after slaughter age. Percentage of deaths decreased quickly during the first three weeks (week 4 to week 6) after weaning, and then decreased gradually with the age of the pigs until week 17 for Duroc pigs and week 19 for Landrace and Yorkshire pigs. Following that, percentage of deaths increased until week 20 for Duroc pigs, and until week 22 for Landrace and Yorkshire pigs, and then decreased again. The small peak in percentage of deaths happened around slaughter age, with the highest peak in Landrace. It was not clear whether the higher percentage of deaths around slaughter age was real or just due to recording errors.

Mortality rates in different life stages are shown in Table 1. To be consistent with the definitions of Mort5, Mort5w, Mortg1, Mortg2, and Mortall, mortality in these periods was measured as mortality rate instead of percentage of deaths, i.e., calculated as number of dead pigs divided by the number alive at the start of the period. As shown in Table 1, mortality rate during the first 5 days after farrowing was 10.2% on average over the three breeds, highest for Duroc and lowest for Yorkshire. Average mortality rate during the period from day 5 to weaning was 6.8%, highest for Yorkshire and lowest for Landrace. Average mortality rate was 4.8% during the nursery period, and 3.9% during the finishing period. In these two periods, Duroc and Yorkshire had similar mortality rates and Landrace had lower mortality rate. It should be noted that Duroc had seven days less in the nursery period and three days less in the finishing period than Landrace and Yorkshire, according to the definition of the mortality traits in this study. Total mortality rate from birth to slaughter age was 27.3% for Duroc, 21.7% for Landrace, 23.8% for Yorkshire, and 24.3% on average.

Since mortality rate in a given period is the number of dead pigs divided by the number alive at the start of the period, the sum of the mortality rates in the different time periods should not equal the total mortality. In principle the total mortality rate should equal 1- (1-Mort5) (1-Mort5w) (1-Mortg1) (1-Mortg2), but this equality does not hold exactly for the mortality rates in Table 1. The reason for this is the way we have handled partial information on the animals still being alive at the end of the data recording, i.e., the young pigs which did not reach slaughter age were not included for calculating mortality in later periods, but in earlier periods. The mortality rates were slightly higher than those on crossbred pigs in the reports of Seges Svineproduktion (Hansen, 2019; 2020). However, it should be kept in mind that the current data included only females from relatively young sows (62% as first parity), In addition, mortality might differ between purebred and crossbred pigs. Finally, quality of mortality records might also differ, since production herds might not have the same incentive as breeding herds to record precisely.

Table 1. Mortality rate (%) during first five days after farrowing (Mort5), from day 5 to weaning (Mort5w), nursery period (Mortg1), finishing period (Mortg2), from day 5 to slaughter age (Mort5g2), and total mortality rate (Mortall).

Trait	Duroc		Landrace		Yorkshire	
	N*	Mortality	N*	Mortality	N*	Mortality
Mort5	26488	12.9	66660	9.9	116909	7.8
Mort5w	22455	6.9	58479	5.8	104853	7.7
Mortg1	19358	5.2	49671	4.0	87321	5.2
Mortg2	15608	4.1	40466	3.5	69215	4.2
Mort5g2	17791	15.9	44851	12.9	79873	16.9
Mortall	20580	27.3	49908	21.7	87015	23.8

* The number of pigs in the table was the sum of deaths in the period and the pigs still in the system at the end of the data recording with age larger than or equal to the days of the end of the period.

Mortality of pigs in relation to parity

As shown in Figure 3, the peaks of number of pigs born (live-born female piglets in this study) appeared when dam age was about 12 months, 17 months, 22 months and 27 months. These peaks represented the popular dam age at farrowing in the first, second, and third parity. Correspondingly, the troughs appeared as dam age was about 15 months, 20 months, and 25 months. Most mothers in the data were young with 91% less than 18 months old. This is because the data come from breeding herds where sows are replaced at an early age in order to make use of genetic gain from breeding program.

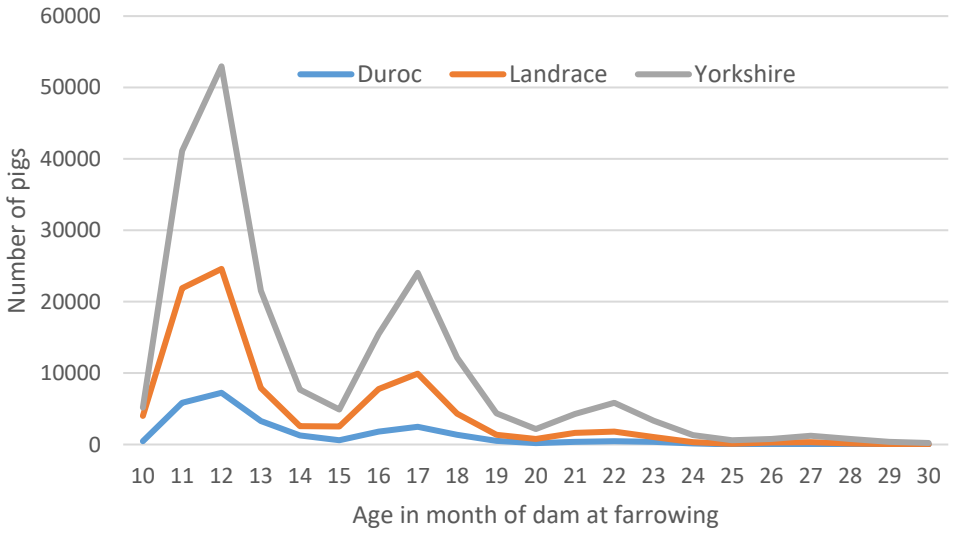

Figure 3. Number of pigs born in relation to age of dam at farrowing.

Accordingly, in this study, variables representing parities of a sow were defined as:

Parity 1: age at farrowing < 435 days,

Parity 2: 435 days <= age at farrowing < 584 days,

Parity 3: 585 days <= age at farrowing < 734 days,

Parity 4: age at farrowing >=735 days.

As shown in Figure 4, Mortality of pigs from the first parity had slightly higher Mort5w. There was also a trend that pigs from the second parity had a slightly lower mortality in all periods.

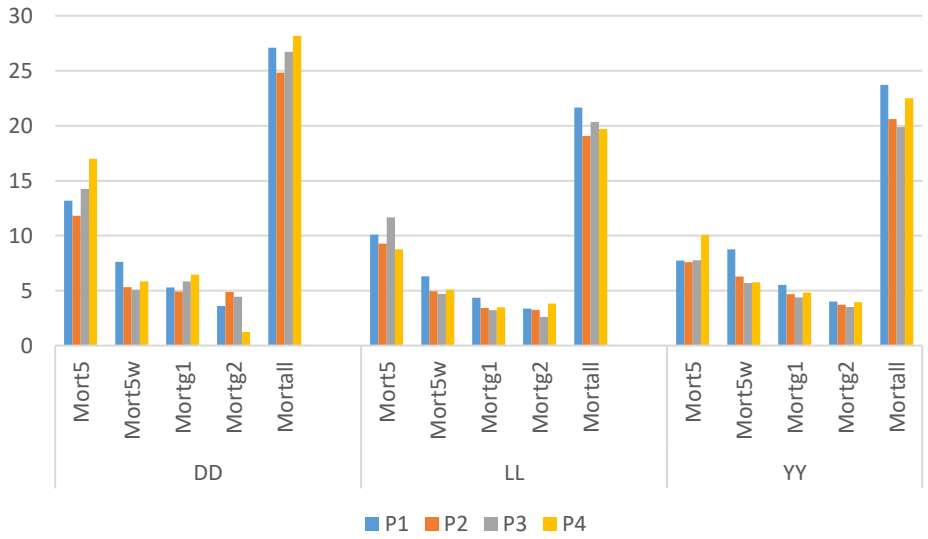

Figure 4. Mortality rates of pigs in different parities (P1 – P4: parity 1 - 4) in Duroc (DD), Landrace (LL), and Yorkshire (YY).

Many previous studies have shown that there is a higher mortality rate at farrowing in the litters of high parity or from old sows (Roehe and Kalm, 2000; Lucia et al., 2002; Borges et al., 2005; Canario et al., 2006; Vanderhaeghe et al., 2010). In the current study it was not possible to confirm this finding, because no records of mortality at farrowing was in the data. In addition, the current data were collected from breeding herds where there was a high replacement rate of sows. Thus, the sows were relatively young and very few were older than two years of age, and only the sows having good performance in previous parity was used to produce in the next parity. Therefore, the information in the current data was not well-suited to detect a relationship between pig mortality and age of dam or parity. Furthermore, the lack of data from later parities implies that estimates of maternal effect on offspring mortality rely mostly on information from first few parities, and only little on information from later parities which are common in production herds. For this reason, genetic progress of maternal ability by selection in breeding herds may be not fully realized in production herds if correlation of maternal ability between parities are less than one.

Mortality of pigs in relation to litter size at day 5

Liter size at day 5 (LG5) ranged from 0 to 16 with an average of 6.5 for Duroc, from 0 to 25 with an average of 12.7 for Landrace, and from 0 to 27 with an average of 14.1 for Yorkshire. Average LG5 in parity 1 to parity 4 were 6.4, 6.8, 7.0 and 6.4 for Duroc, 12.0, 14.2, 14.3 and 14.6 for Landrace, and 13.2, 15.4, 16.1 and 15.3 for Yorkshire, respectively, where averages of LG5 for parity 4 were based on small number of litters as shown in Figure 3. The relationship between LG5 and mortality rate of pigs is shown in Figure 5a, 5b, and 5c for Duroc, Landrace and Yorkshire, respectively. There was a clear trend that Mort5 decreased with increasing LG5 in all three breeds. Moreover, it was seen that Mort5w decreased slightly with increasing LG5 for all three breeds, and Mortg1 decreased slightly with increasing LG5 for Landrace and Yorkshire. On the other hand, there was not a clear relationship between LG5 and Mortg2. On the whole, larger LG5 tended to decrease the total mortality in all three breeds, since there was an autocorrelation between total mortality and mortalities in different periods, especially Mort5. The patterns of mortality rates in relation to LG5 were consistent with the genetic and phenotypic correlation between LG5 and Mort5 and between LG5 and Mort5w in the study by Su et al. (2007), and in line with the observations by Nielsen et al. (2013).

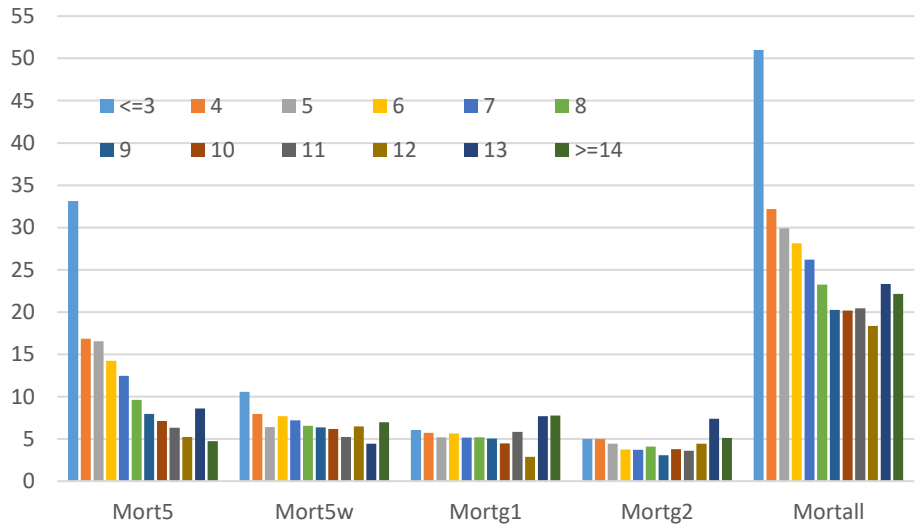

Figure 5a. Mortality rate in relation to litter size at day 5 in Duroc.

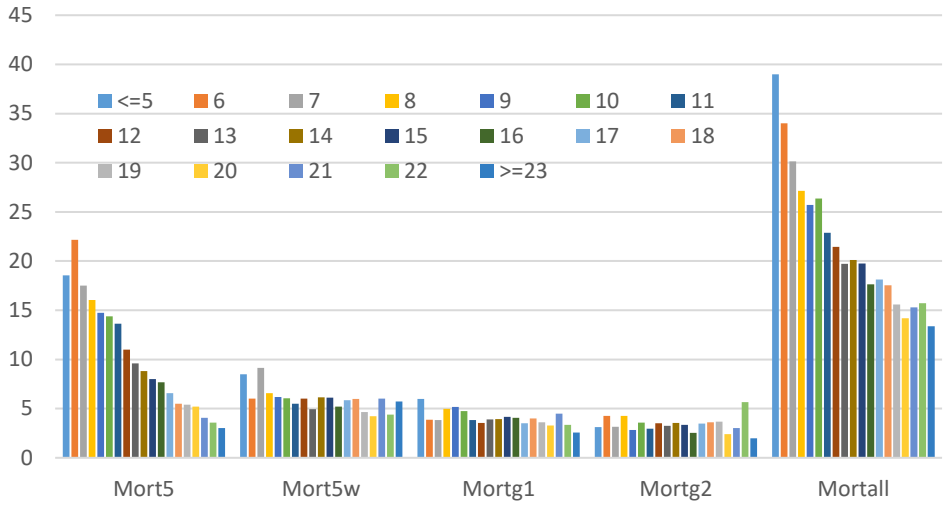

Figure 5b. Mortality rate in relation to litter size at day 5 in Landrace.

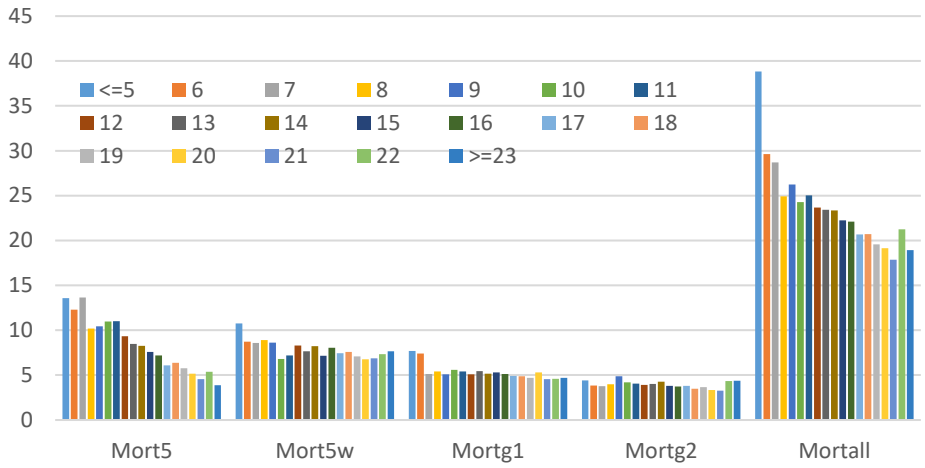

Figure 5c. Mortality rate in relation to litter size at day 5 in Yorkshire.

Variance components and genetic parameters of mortality traits

Statistical models

To explore the feasibility to improve pig survival by breeding, variance components and breeding values (EBV) for mortality in different periods were estimated using two statistical models, one was a linear mixed model on an observed scale (0 or 1) and the other was a liability threshold model on an unobserved underlying liability scale (details can be seen in Appendix A1).

The linear mixed model (LM) used to estimate variance components and breeding values was,

LM: y = parity effect + herd effect + year_month effect + herd_year_month effect + litter effect + additive genetic effect (i.e., breeding value of the pig) + residual

In the model, y was a binary variable with 0 as alive and 1 as dead for a mortality trait (i.e., mortality in a given period). Parity, herd, and year_month were treated as fixed effects. The other effects were treated as random effects and assumed to follow respective normal distributions. The purpose of having parity effect, and effect of shared environments (herd, year_month, herd_year_month and litter effects) in the model is to correct for such non-genetic effects in the analysis.

For a trait with binary observations, the assumption of the random effects in the model following a normal distribution is violated. More sophisticated models for analysis of the traits with binary observations may be desirable. Therefore, in this study, in addition to LM model, a liability threshold model (**LTM**), also called probit model, was used to estimate variance components and breeding values of the mortality traits. The LTM model in this study has the same form as the LM model.

LTM: *l* = parity effect + herd effect + year_month effect + herd_year_month effect + litter effect + additive genetic effect (i.e., breeding value) + residual

where *l* is the underlying liability to die. The LTM model assumes that the observed outcome is determined by whether the underlying liability is smaller or larger than a threshold, and the underlying liability is affected by many factors. The details of the LTM model, heritability on the underlying liability scale, and the relationship between heritability on liability and heritability on the observed scale are presented in Appendix A1.

Using the LM and the LTM models, phenotypic variance was calculated as the sum of additive genetic variance, litter variance and residual variance. Thus, heritability was $h^2 = \frac{Additive\ genetic\ variance}{phenotypic\ variance}$, and the ratio of litter variance was $Lit^2 = \frac{litter\ effect\ variance}{phenotypic\ variance}$.

A LM model and a LTM model including maternal additive genetic effect were also used to analyze the data in order to explore pig´s direct additive genetic effect and maternal additive genetic effect on pig survival respectively, thus providing the probability of genetic improvement on both a pig´s own performance and maternal performance. However, the data covered only about 1.3 generations for survival to slaughter and the information was not sufficient to distinguish these two additive genetic effects, and thus not presented in this report.

Estimation of variance components using the LM model was performed using average information restricted maximum likelihood (AI-REML) approach (Jensen et al., 1997) and the prediction of breeding values was performed using best linear unbiased prediction (BLUP) approach (Henderson, 1975). Estimation of variance components and prediction of breeding values using the LMT model was performed using Bayesian Markov chain Monte Carlo

(MCMC) approach with Gibbs sampling method (Sorensen et al., 1994). All these analyses were carried out using the DMU package (Madsen et al., 2010).

Variance components and heritabilities estimated from linear mixed model and liability threshold model

Variance components estimated from the LM model and the LTM model are shown in Table 2. Heritabilities on observed scale (h^2_o) estimated from the LM model ranged from 0.003 to 0.022 for the six mortality traits in the three breeds. There was a trend that the heritability on the observed scale increased with increasing mortality rate, in line with the general characteristics of heritability on the observed scale for a binary trait (Tenesa and Haley, 2013; Ge et al., 2017). Averaged over three breeds, this heritability was 0.021 for Mortall, 0.016 for Mort5g2, 0.0137 for Mort5, 0.008 for Mort5w, 0.009 for Mortg1 and 0.004 for Mortg2.

Heritabilities on the liability scale(h^2_l) estimated from the LTM model were less different between mortality traits and between breeds, compared with the heritability on observed scale, since heritability on the liability scale is independent of mortality rate (Dempster and Lerner, 1950). Heritabilities on the liability scale ranged from 0.023 to 0.060 with an exception of 0.089 for Mortg1 in Duroc. Averaged over three breeds, the heritability was 0.044 for Mortall, 0.041 for Mort5g2, 0.043 for Mort5, 0.036 for Mort5w, 0.043 for Mortg1 and 0.025 for Mortg2. Due to different scales, the estimates of heritability on the liability scale were much higher than the estimates of heritabilities on the observed scale from the LM model. However, as shown in Table 2, heritabilities on the observed scale ($^*h^2_o$) transformed from those on the liability scale were highly consistent with those on the observed scale estimated from LM model; see details in appendix about this transformation.

Compared with heritability, litter effects were relatively large. It is usually assumed that litter effect will be small after weaning. However, litter effect on Mortg1 and Mortg2 did not decrease much compared to earlier periods. It could be argued that the litter effect on mortality after weaning included not only maternal effects and common environmental effects in the suckling period, but also other components. Firstly, maternal effect and common environmental effect on mortality during suckling period might lead to a permanent effect on mortality in later periods. Secondly, litter effect might include environmental effects common for litter mates after weaning. In other words, the pigs from the same litter might still share common environment during the nursery and finishing period, such as being reared in the same unit and even in the same pen, which were not considered in the model. In addition, non-additive genetic effects also would tend to be included in the litter variance components. Therefore, litter effect might catch many sub-components of effects common on litter mates that could not be accounted for in the currently used models and data.

Table 2. Phenotypic variance (σ_p^2), ratio of litter variance (lit^2) to phenotypic variance, heritability on observed scale (h^2_o) and on liability scale (h^2_l) estimated from LM model and LTM model.

Breed	Trait	LM			LTM			
		σ_p^2	lit^2	h^2_o	σ_p^2	lit^2	h^2_l	$^*h^2_o$
Duroc	Mort5	0.111	0.089	0.015	1.307	0.191	0.044	0.017
	Mort5w	0.063	0.062	0.004	1.259	0.183	0.023	0.006
	Mortg1	0.049	0.026	0.017	1.231	0.098	0.089	0.021
	Mortg2	0.038	0.029	0.001	1.177	0.124	0.027	0.005
	Mort5g2	0.129	0.048	0.012	1.160	0.100	0.038	0.017
	Mortall	0.193	0.079	0.020	1.221	0.136	0.046	0.025
Landrace	Mort5	0.089	0.060	0.019	1.255	0.143	0.060	0.021
	Mort5w	0.054	0.078	0.011	1.330	0.197	0.051	0.013
	Mortg1	0.038	0.027	0.003	1.141	0.106	0.018	0.003
	Mortg2	0.032	0.064	0.004	1.244	0.175	0.021	0.004
	Mort5g2	0.110	0.067	0.015	1.209	0.133	0.040	0.016
	Mortall	0.167	0.076	0.021	1.218	0.134	0.044	0.023
Yorkshire	Mort5	0.071	0.049	0.007	1.187	0.132	0.025	0.007
	Mort5w	0.070	0.070	0.010	1.251	0.166	0.035	0.010
	Mortg1	0.049	0.028	0.006	1.129	0.091	0.023	0.005
	Mortg2	0.039	0.039	0.006	1.174	0.120	0.028	0.006
	Mort5g2	0.138	0.058	0.021	1.181	0.109	0.044	0.020
	Mortall	0.178	0.068	0.022	1.190	0.119	0.041	0.021

* Heritability on observed scale obtained by a transformation from heritability on the liability scale (h^2_l).

In some previous studies, piglet mortality was treated as a trait of sow and heritability of piglet mortality was estimated at litter level. To be able to compare with the results from these previous studies, the heritabilities of mortality at pig individual level were transformed to heritabilities at litter level. The transformation was performed using the following formula (Falconer and Mackay, 1996) $h_f^2 = h^2 \frac{1+(n-1)r}{1+(n-1)t}$,

where h_f^2 is the heritability of litter mortality rate, h^2 is the heritability of mortality at individual level, n is the number of litter mates, r is the genetic relationship between litter mates (full sibs) which is 0.5, and t is the phenotypic correlation between litter mates which is $0.5h^2+lit^2$. Since the current data only included female pigs, we did not use the number of female pigs as litter size for the calculation, but assumed litter size to be 12 for Landrace and Yorkshire, and 6 for Duroc, for all traits. The transformed heritability at litter level from LM model (observed scale) and from LTM model (liability scale) are shown in Table 3.

Table 3. Heritabilities at litter level (heritabilities of family mean, on observed scale from LM and on liability scale from LTM), given litter size 6 for Duroc, 12 for Landrace and Yorkshire

Trait	Duroc		Landrace		Yorkshire	
	LM	LTM	LM	LTM	LM	LTM
Mort5	0.034	0.074	0.068	0.135	0.029	0.063
Mort5w	0.012	0.040	0.037	0.096	0.037	0.075
Mortg1	0.051	0.183	0.013	0.051	0.028	0.071
Mortg2	0.004	0.055	0.013	0.046	0.027	0.073
Mort5g2	0.034	0.083	0.052	0.097	0.079	0.117
Mortall	0.048	0.089	0.071	0.106	0.076	0.104

Table 4. Genetic (upper diagonal) and phenotypic (lower diagonal) correlation between mortality traits, estimated using LM model

Breed	Trait	Mort5	Mort5w	Mortg1	Mortg2	Mort5g2	Mortall
Duroc	Mort5		0.752	0.770	0.355	0.761	0.941
	Mort5w	na		0.809	0.671	0.909	0.896
	Mortg1	na	na		0.858	0.983	0.948
	Mortg2	na	na	na		na	na
	Mort5g2	na	0.634	0.580	na		na
	Mortall	0.643	0.475	0.461	na	na	
Land-race	Mort5		0.458	0.095	-0.208	0.262	0.817
	Mort5w	na		0.311	0.469	0.860	0.845
	Mortg1	na	na		0.762	0.801	0.706
	Mortg2	na	na	na		na	na
	Mort5g2	na	0.650	0.594	na		na
	Mortall	0.640	0.516	0.501	na	na	
York-shire							
	Mort5		0.595	0.544	0.283	0.543	0.760
	Mort5w	na		0.880	0.639	0.952	0.945
	Mortg1	na	na		0.732	0.911	0.943
	Mortg2	na	na	na		na	na
	Mort5g2	na	0.656	0.431	na		na
	Mortall	0.537	0.557	0.528	na	na	

Genetic correlations between mortalities in different periods

Covariances between mortality traits were estimated using the multiple-trait LM model only, because of convergence problems with the multiple-trait LTM model. Covariances between some pairs of traits were not estimable due to certain features of the data (see Appendix A2). As shown in Table 4, genetic correlations between mortality in different periods were positive, except for the correlation between Mort5 and Mortg2 in Landrace which was negative but not significantly different from zero. The positive genetic correlations indicated that the pigs having higher genetic potential to survive in a particular period also had higher genetic potential to survive in another period. In general, the correlations were higher between mortalities in adjacent periods. Mortall had strong genetic correlation with its component traits of Mort5, Mort5w and Mortg1, and Mort5g2 had strong correlation with its compo-

nent traits of Mort5w and Mortg1. For the three breeds, genetic correlations between mortality traits were highest for Duroc, and lowest for Landrace. Phenotypic correlations were similar for the three breeds.

Accuracy of estimated breeding values and expected genetic gain of survival by breeding

Expected accuracy of estimated breeding value from the LM and LTM models

Table 5 presents the expected accuracies (see the calculation in Appendix A3) of EBV from the LM and LTM models for the individuals born after 2019-03-31 and survived to slaughter age, which is a group of potential selection candidates. Although heritabilities were low, accuracies of EBV were not low. This was attributed to large number of full-sibs and half-sibs which contributed large amount of phenotypic information to estimate breeding value of an individual. Model expected accuracies of EBV from LTM were slightly higher than those from LM for most traits, except for Mortg1 in Duroc, Mort5 in Landrace, and Mortg2 in Yorkshire. Although heritabilities on liability scale from the LTM model were much higher than those on observed scale, accuracy of EBV on liability scale from the LTM model were only slightly higher than those for EBV on observed scale from LM model. It could be due to the fact that underlying liabilities are unknown and have to be estimated from the binary observations and that estimation of prediction error variance are slightly different between the two models (see Appendix A3).

For the three breeds, in general, Yorkshire had the highest accuracy of EBV, and Landrace and Duroc had similar accuracy. There was a trend that accuracies of EBV in decreasing order were Mortall, Mort5g2 and Mort5, Mort5w, finally Mortg1 and Mortg2. Averaged over three breeds, the accuracies were 0.340 for Mort5, 0.263 for Mort5w, 0.234 for Mortg1, 0.127 for Mortg2, 0.330 for Mort5g2, and 0.367 for Mortall, when using the LM model, and the accuracies were 0.349 for Mort5, 0.309 for Mort5w, 0.258 for Mortg1, 0.192 for Mortg2, 0.342 for Mort5g2, and 0.379 for Mortall, when using the LTM model.

Table 5. Expected accuracy of EBV for the individuals born after 2019-03-31 and survived to slaughter age.

Trait	Duroc		Landrace		Yorkshire	
	LM	LTM	LM	LTM	LM	LTM
Mort5	0.332	0.372	0.367	0.291	0.321	0.383
Mort5w	0.163	0.222	0.285	0.331	0.341	0.374
Mortg1	0.340	0.309	0.067	0.091	0.295	0.375
Mortg2	0.012	0.169	0.097	0.162	0.271	0.244
Mort5g2	0.287	0.306	0.306	0.311	0.395	0.408
Mortall	0.349	0.361	0.354	0.362	0.399	0.416

Validation on accuracy of estimated breeding value from the LM and LTM models

In previous paragraph, accuracies were computed internally in the model, and that measure of accuracy depends on how well the model fits to the data, i.e. if for some reason the model is very wrong, then model-based accuracies are also very wrong. To obtain a measure of accuracy that is less dependent on the model, accuracy of EBV was also assessed using a validation procedure which measures "realized" accuracy. In the validation procedure, the full data were divided into training and test datasets. The test data comprised about one quarter of litters which were farrowed most recently and the mothers had their own survival records in the training data, and the rest of the full data were used as training data. Breeding values of the mothers of the test pigs and breeding values for the test pigs were predicted using the training data. Since the phenotypes of the pigs in the test data were not used to estimate their breeding values, the EBV of these pigs were actually the parent average (PA) or pedigree index. Two validation accuracies were calculated. One was accuracy of dam EBV (r_{EBV_dam}) calculated by comparing mother EBV and the performance of its offspring in test data. This was the accuracy of mother's EBV validated by offspring's performance. The other was accuracy of EBV (r_{EBV_pig}) for pigs in test data calculated by comparing pig EBV and its performance. This was the accuracy of parent average EBV validated by offspring's performance. Both accuracies reflected the accuracy of selecting pigs to be parents of next generation. See details about the calculation of validation accuracy in Appendix A4.

Table 6 presents validation accuracy of EBV for Mort5g2 and Mortall. Accuracies of EBV from validation on mothers were not exactly the same as those on pigs since the two validation accuracies were calculated using different sets of EBV and phenotypic variables and there also existed a random sampling error. However, averaged over the traits, models and breeds, the two validation accuracies were similar (0.295 for r_{EBV_dam} and 0.310 for r_{EBV_pig}). Moreover, they had a similar pattern, i.e., higher for the two traits in Yorkshire and Mort5g2 in Duroc, and lower for the two traits in Landrace and Mortall in Duroc. It was observed that the correlation coefficients for measuring validation accuracies had a large uncertainty in validation on mothers in Duroc and Landrace, indicating these were less reliable. Within the same validation animals, the two prediction models (LM and LTM) led to similar validation accuracy, except for Mort5g2 in Landrace when validating mothers. Validation accuracies of the two traits in Yorkshire were similar to the corresponding model expected accuracies, Mort5g2 in Duroc had a little higher validation accuracy, while the two traits in Landrace and Mortall in Duroc had lower validation accuracies. On average over validation scenarios, the validation accuracies were 0.374, 0.276, 0.357 for Mort5g2, and 0.196, 0.256 and 0.356 for Mortall, in Duroc, Landrace and Yorkshire, respectively.

It should be noted that the model expected accuracy for the EBV was obtained from full data, while validation accuracy was for the EBV obtained from test data (i.e., reduced data). The differences between validation accuracy and expected accuracy could be mainly due

to random sampling error and size of data. As the whole, validation accuracy was generally in agreement with expected accuracy.

Table 6. Validation accuracy of EBV of mother and EBV of pigs in test data, based on correlation between EBV and corrected phenotype.

Breed	Trait	Valid-pig		Valid-mother	
		LM	LTM	LM	LTM
Duroc	Mort5g2	0.451	0.443	0.306	0.296
	Mortall	0.264	0.254	0.140	0.127
Landrace	Mort5g2	0.285	0.299	0.230	0.289
	Mortall	0.253	0.256	0.253	0.260
Yorkshire	Mort5g2	0.313	0.315	0.399	0.399
	Mortall	0.289	0.295	0.422	0.417

Correlation between estimated breeding value from LM and LTM

EBV from LM was for mortality on observed scale, and EBV from LTM was for mortality on underlying liability scale. Although on different scales, the Pearson product-moment correlations between the two EBVs (Table 9) ranged from 0.979 to 0.997, except for Mortg2 in Landrace for which the correlation was around 0.953. Average over all traits, the correlation was 0.989. Spearman rank correlations were also calculated, and the results were the same as Pearson product-moment correlations. The correlations indicate the EBV from the two models were highly consistent and the BLUP method with the LM model was robust to the violation of the normality assumption in predicting breeding value of binary traits.

Table 7. Pearson product-moment correlation between EBV from the LM and LTM models for the individuals born after 2019-03-31 and survived at slaughter age.

Trait	Duroc	Landrace	Yorkshire
Mort5	0.993	0.992	0.993
Mort5w	0.990	0.986	0.990
Mortg1	0.993	0.987	0.995
Mortg2	0.979	0.953	0.990
Mort5g2	0.996	0.991	0.995
Mortall	0.997	0.995	0.997

Expected genetic gain in reduction of mortality by selection

Genetic gain per generation by selection, i.e., response to selection per generation, can be expected as,

$$\Delta G = ir_{EBV}\sigma_a,$$

where i is selection intensity which is normal standardized selection differential in EBV, r_{EBV} is accuracy of EBV, and σ_a is square root of additive genetic variance. Since $r_{EBV}\sigma_a=\sigma_{EBV}$ where σ_{EBV} is standard deviation of EBV, genetic gain can also be calculated according to realized standard deviation of EBV, i.e., directly calculation from EBV (SD_{EBV}). In reality, only the animals alive at the time of selection can be used as breeding candidates. In the current study, expected genetic gains by selection against mortality in a particular period were calculated in two ways. First was based on expected accuracy and additive genetic variance, and second was based on directly calculated standard deviation of EBV, i.e.,

$$\Delta G_{r\sigma} = ir_{EBV}\sigma_a, \text{ and } \Delta G_{SD} = iSD_{EBV}$$

where r_{EBV} and the SD_{EBV} were obtained from the individuals which were born after 2019-03-31 and survived over the corresponding period, since these pigs are the potential selection candidates in the current generation. Genetic gain (ΔG) based on EBV estimated from the LM model with binary variables (0, 1) is the gain on observed scale, and thus it is a direct measure of the change in mortality rate. However, genetic gain based on EBV estimated from the LTM model is the gain on liability scale. To obtain genetic gain in mortality rate, a transformation from underlying liability to mortality rate was performed (see Appendix A5).

For computing expected genetic gain, what remains is to decide on the selection intensity. Nielsen (2013) inferred that selection intensity in Danish pig breeding program was about 1.5. Here, we decided to present result for selection intensity equal to 1, since this from formula above corresponds to expected gain of one standard deviation of EBV. We then would obtain result in units of selection intensity, and results for another intensity can easily be obtain by multiplying with that intensity. Moreover, the expected genetic gain was calculated without taking maternal additive genetic effect into consideration, since the current data set covering only about 1.3 generations did not contain enough generations for estimating a maternal genetic effect accurately. As shown in Table 8, genetic gains per generation under selection intensity of 1.0 using different parameters (SD_{EBV}, $r_{EBV}\sigma_a$) and different models (LM and LTM) were highly consistent. The expected reduction in mortality rate by one generation of selection ranged from 0.10 to 2.63 percentage points, except for Mortg2 in Duroc calculated based on $r_{EBV}\sigma_a$ from the LM model. On average, the reduction of mortality rate was 1.12 (ΔG_s) and 1.04 ($\Delta G_{r\sigma}$) percentage points for the LM model, 1.13 (ΔG_s) and 1.12 ($\Delta G_{r\sigma}$) percentage points for the LTM model.

Table 8. Expected genetic gain in percentage point reduction of mortality rate per generation under selection intensity of 1.0.

Breed	Trait	LM		LTM		Mean
		ΔG_{SD}	$\Delta G_{r\sigma}$	ΔG_{SD}	$\Delta G_{r\sigma}$	
Duroc	Mort5	1.32	1.34	1.34	1.57	1.39
	Mort5w	0.47	0.27	0.52	0.43	0.42
	Mortg1	0.93	0.98	0.93	0.92	0.94
	Mortg2	0.11	0.01	0.29	0.24	0.16
	Mort5g2	1.47	1.14	1.60	1.40	1.40
	Mortall	2.45	2.16	2.63	2.50	2.43
Landrace	Mort5	1.36	1.49	1.38	1.19	1.35
	Mort5w	0.90	0.69	0.89	0.82	0.82
	Mortg1	0.24	0.07	0.28	0.10	0.17
	Mortg2	0.25	0.10	0.25	0.18	0.20
	Mort5g2	1.39	1.22	1.35	1.27	1.31
	Mortall	2.05	2.11	2.02	2.18	2.09
Yorkshire	Mort5	0.76	0.72	0.76	0.85	0.77
	Mort5w	0.99	0.92	0.95	0.95	0.95
	Mortg1	0.54	0.50	0.50	0.59	0.53
	Mortg2	0.48	0.42	0.43	0.35	0.42
	Mort5g2	1.99	2.13	1.90	2.07	2.02
	Mortall	2.38	2.49	2.32	2.51	2.43

ΔG_{SD}: Expected genetic gain derived from SD_{EBV}.
$\Delta G_{r\sigma}$: Expected genetic gain derived from $r_{EBV}\sigma_a$.
Mean ΔG: Mean of ΔG_{SD} and $\Delta G_{r\sigma}$ over two models.

Since the genetic gains were measured in mortality rate (observed scale), the gains were consistent with heritabilities on observed scale and mortality rates in different periods and different populations. The amount of genetic gain was also associated with accuracy of EBV. Averaged over six mortality traits and the two models, the genetic gain in terms of reduction of mortality rate was 1.11 percentage points for Duroc, 0.99 percentage points for Landrace, and 1.19 percentage points for Yorkshire. Averaged over two models and three breeds, after one generation of selection with selection intensity of 1.0, the reduction of mortality rate was expected to be 1.58 percentage points for Mort5g2 and 2.32 percentage points for Mortall. The generation interval in Danish breeding program is only a little more than one year, therefore the genetic change per year would be close to the expected change per generation. The generic gain was calculated given selection intensity equal to 1.0 and selection only on survival. However, a pig breeding program includes many traits to be improved and selection is based on a total selection index with weights on different traits. When increasing the number of traits in a selection index, genetic gain for a single trait will reduce. Therefore, the

real selection intensity with regard to survival and thus the genetic gain by selection is dependent on weight on survival in the total selection index and the genetic correlations with other traits in the index. Multiplying numbers in Table 8 by a different selection intensity would give expected genetic gain for that intensity, i.e., $i \times 1.32$ would be the expected genetic gain for Mort5 in Duroc with selection intensity i.

As shown above, genetic correlations between mortalities in different periods were positive. This indicates that selection against one mortality trait can lead to a reduction of other mortality traits, i.e., correlated selection response. Correlated response for trait y by selection for trait x can be calculated as described in Appendix A6. Table 9 shows expected genetic gain in reduction of Mortall by direct selection against Mortall or selection against three earlier mortality traits, Mort5, Mort5w or Mortg1. The correlated genetic gains were calculated using the genetic correlations estimated from the multi-trait LM model and other parameters from the single-trait LM model. As shown in Table 9, the correlated genetic gain in proportion to the gain by direct selection against Mortall (CR/R) ranged from 0.28 to 0.92 with a large variation between selected traits and between breeds. Averaged over breeds, the proportion was 0.78 by selection against Mort5, 0.64 by selection against Mort5w and 0.58 by selection against Mortg1. Due to insufficient information in the data (covering only about 1.3 generations), it is difficult to estimate the genetic parameters that are needed for calculating correlated genetic gain in reduction of Mortall by selection for LG5. Similarly, information in the data is also insufficient for assessing the correlated genetic change in mortality by selection for the traits in the current selection index of the Danish pig breeding programs.

On the other hand, if breeding directly for reduced mortality is introduced in the breeding program, genetic gains for the traits in the current breeding goal will change. It will also lead to a correlated response for the traits which are not in the breeding goal, such as total number of piglets born and number of piglets at weaning. The correlated changes due to introducing mortality in the breeding program depend on the weight on mortality and the genetic correlations with the other traits of interest. Therefore, consequences of including mortality in the breeding program requires further investigations. Two important issues that should be considered are: first, which mortality trait should be included into total selection index, e.g., Mortall, Mort5g2 or a sub-index comprising Mort5, Mort5w, Morg1 and Mortg2 with different weights; second, the weight on mortality in the total selection index to optimize a breeding program for both genetic reduction of mortality and genetic gains for the traits in current breeding goal.

Table 9. Genetic gain (CR, percentage point) in reduction of mortality rate by direct selection against Mortall or by selection against Mort5, Mort5w or Mortg1.

Selected trait	DD		LL		YY		Mean
	CR	CR/R	CR	CR/R	CR	CR/R	CR/R
Mort5	1.93	0.90	1.78	0.85	1.52	0.61	0.78
Mort5w	0.90	0.42	1.43	0.68	2.01	0.81	0.64
Mortg1	1.99	0.92	0.28	0.13	1.73	0.70	0.58
Morrall	2.16	1.00	2.11	1.00	2.49	1.00	1.00

Transmission of genetic gain to production herds

The expected genetic gains presented above were the genetic gains in breeding herds. It could be more important to assess the generic gain in commercial production herds through selection in breeding herds. Since genetic gains calculated in this study were based on direct additive genetic effect, in the case that the genetic gains obtained in breeding herds can be completely transmitted to commercial production herds, the expected genetic gain in commercial production herds can be calculated as $\Delta Gc = 0.5*\Delta G_{Duroc} + 0.25*\Delta G_{Landrace} + 0.25*\Delta G_{Yorkshire}$. Under this assumption, according to the last column of Table 8, the expected reduction of mortality rate per generation in production herds would be 1.53 percentage points for Mort5g2, and 2.24 percentage points for Mortall.

However genetic gains obtained from breeding herds may not be completely transmitted to production herds, because the performance of a genotype may be somewhat different between breeding herds and production herds. The possible difference can be caused by many factors. The first is due to different genetic backgrounds between purebred and crossbred, i.e., genotype by genetic background interaction. The second is due to different production environments and managements, i.e., genotype by environment interaction. We have not been able to find the studies in the scientific literature about genetic correlation in survival performance between breeding herds and production herds.

Another issue with the transmission of genetic gain from breeding herds to production herds is the time lag of genetic improvement, i.e. the extra time it takes for genetic progress to reach the production herds compared to breeding herds. In Danish pig production system, the terminal sires of production population are directly from breeding herds. Therefore there is no genetic lag in this sire path. In other words, the genetic gain obtained in Duroc breeding herds is transmitted to production herds immediately. However, for dam paths, genetic gain from Landrace and Yorkshire breeding herds are transmitted to multiplier herds, then sow herds and finally commercial production herds. The genetic lag on dam side may take some years, depending on replace rate in multiplier herds and sow herds.

Approaches to increase genetic gain in survival by breeding

As shown above, even though heritabilities were low, the expected accuracies of EBV were 0.336 for Mort5g2, and 0.375 for Mortall, averaged over the two models and the three breeds. This indicates that increasing pig survival by breeding is possible. The accuracy and correspondingly the genetic gain by selection can be enhanced by several initiatives.

Amount of data

One important aspect to increase selection accuracy is amount of phenotypic data. In the current study, the data comprised the records of individuals born in the period from 2018-10-01 to 2020-08-26, and the individuals born after February 2020 did not have records of Mortall and Morr5g2 yet. Therefore, the data covered only a period of 15 months which corresponds to about 1.3 generations. Yang and Su (2016) have shown that the accuracy of EBV increases considerably by increasing the amount of data from one generation to two generations, and then continuously increase but with low rate when data cover more generations. It is expected that with a collection of several generations of mortality data, accuracy of EBV and thus response to selection will be higher than those presented above. Moreover, with the data covering two or more generations, both direct and maternal additive genetic effect can also be estimated accurately. This will make it possible to improve both maternal capacity for survival of piglet and individual pig capacity of survival, and thus increase genetic gain of pig survival by breeding.

The data used in the current study includes only female pigs, since the agreement between Seges Svineproduktion and breeding herds is only for female pigs. Breeding value of an individual can be estimated from not only the information of the individual's own record but also the relatives, especially the close relatives such as full-sibs and half-sibs. According to the theory of selection index, the contribution from information of relatives is more important for low heritability trait than high heritability traits. Therefore, information of relatives is very important for mortality traits which have a heritability less than 0.03 on observed scale and less than 0.1 on liability scale. When male pigs are also registered for mortality, number of full-sibs and half-sibs will be doubled, and accuracy of EBV and consequently genetic gain by selection will increase. Therefore, it is strongly recommended to register mortality for both female and male pigs.

Survival performance may be different between breeding herd and production herd due to difference in genetic background (purebred vs. crossbred), biological background (e.g., young sows in breeding herds vs. relatively old sows in sow herds), as well as production environments and managements. Selecting purebred animals for increased survival in production herds is expected to increase genetic gain for survival of pigs in production herds. However, this would require individual records of mortality together with pedigree for pigs in production herds, which is currently a challenge in practice.

Quality of data

In addition to amount of data, data quality is an important factor affecting accuracy of EBV. The data we received were inspected for potential errors. No wrong records in the data are detected. In addition, variance components estimated from this data set are comparable with previous studies. This indicates that data quality is sufficient for genetic evaluation for mortality traits. However, there may exist a number of inaccurate records in the data, as shown by some evidences. For example, the distribution of mortality rate in relation to age of pig shows a peak around slaughter age, which does not seems to have a biological basis. Moreover, the data lack information about cross-fostering. Thus the litter effect for mortality before weaning might not be appropriately accounted for in prediction of breeding values. Cross-fostering may have larger influence when maternal additive genetic effect is considered. In addition, about 10% pigs left the system alive before slaughter age without further information. To achieve accurate selection, attention should be paid to accurate registration of mortality events.

Statistical model

Statistical model used for predicting breeding value is also an important aspect for improving genetic gain by selection. In the current study, variance components and breeding values are estimated using both a linear mixed model (LM) and a liability threshold model (LTM). It has been expected that the LTM model would perform better than the LM model in which the normality hypothesis is violated. Contrary to the expectation, the EBV from the two models are highly consistent with a correlation over 0.98, indicating that for these data LM is robust to violation of normality hypothesis. However, LTM model still showed a slightly higher accuracy. Furthermore, both LM and LMT models have some limitations in analysis of mortality data and more appropriate statistic models might be advantageous. As shown above, many pigs (about 10%) have left the system before slaughter age at survival status, and many pigs have not reached slaughter age at the time of genetic evaluation. The information on these pigs (i.e., censored records) are useful for genetic evaluation of survival until slaughter for breeding candidates, though breeding candidates themselves usually reach slaughter age at the time of selection. These censored records are not efficiently used in the current study. In addition, in the current study, breeding value for mortality during the whole period from birth to slaughter (Mortall) or from day 5 to slaughter (Mort5g2) are estimated using a model treating mortality in different time periods as the same trait. This may not be a desirable approach because our results show that genetic correlations between mortalities in different periods are far from unity. More sophisticated models, such as proportional Hazard model (Cecchinato et al., 2010) and random regression model (Mrode, 2005), are expected to improve accuracy of selection, and thus genetic gain.

Genomic selection

Accuracies of EBV and expected genetic gains presented above are based on conventional selection. Genomic selection (Meuwissen et al., 2001), has been widely used in pig breeding, and Danish pig breeding was the first one to implement genomic prediction in pig in the world. Previous studies have shown that genomic prediction can increase accuracy by 10 – 50% (Christensen et al., 2012; Su et al., 2012; Guo et al., 2015). Knol et al. (2016) reported that genetic gain increased by 50% when changing conventional selection to genomic selection. Genomic information is especially valuable for low heritability traits (Meuwissen et al., 2001; Calus et al., 2008; Su et al., 2010), such as mortality traits considered here. It has been reported that for post-weaning mortality, genomic selection doubles accuracy of EBV, compared with conventional selection (Knol et al., 2016). Therefore, the accuracies of EBV will increase by using genomic evaluation.

Conclusion

Heritability of pig mortality reported in the literation is low. Although the data set in this study contain a large number of records, it covers only about 1.3 generations, which limit the analysis of maternal genetic effects. Data quality is in general sufficient for genetic evaluation for mortality traits but can be improved in some aspects. Based on the current data, averaged over three breeds, mortality rates are 10.2% in the period from birth to day 5, 6.8% from day 5 to weaning, 4.8 during nursery period and 3.8% in finishing period. Selection for LG5 reduces pre-weaning mortality. Estimates of heritability on observed scale (0, 1) using LM range from 0.001 to 0.022, and estimates of heritability in underlying liability scale using LTM ranged from 0.018 to 0.089. Breeding values estimated from the two models are highly consistent. Although heritability for mortality traits is low, accuracy of EBV is acceptable for selection. However, genetic gain for survival depends on the weight on survival in the total selection index. It requires further investigations to optimize a breeding program for both genetic improvement of survival and genetic gain for the traits in current breeding goal. In addition, low heritability of mortality indicates that improvements of environment and management are also important for increasing pig survival.
We recommend: 1) continue to register mortality, 2) register mortality of male pigs in addition to female pigs, 3) carry out further investigations to optimize a breeding program for both genetic reduction of mortality and genetic gain for the traits in current breeding goal. 4) include pig mortality in breading goal of Danish breeding programs,

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Appendix

The appendix contains more technical materials, which we believe is not of interest to the average reader, only to specialists in the field.

A1. Liability threshold model and heritability on underlying liability scale

A liability threshold model (LTM) assumes that the observed outcome is determined by whether an underlying unobservable liability is smaller or larger than a threshold, and the underlying liability is affected by many factors. The relationship between binary variable for mortality and underlying liability can be seen in Figure 6.

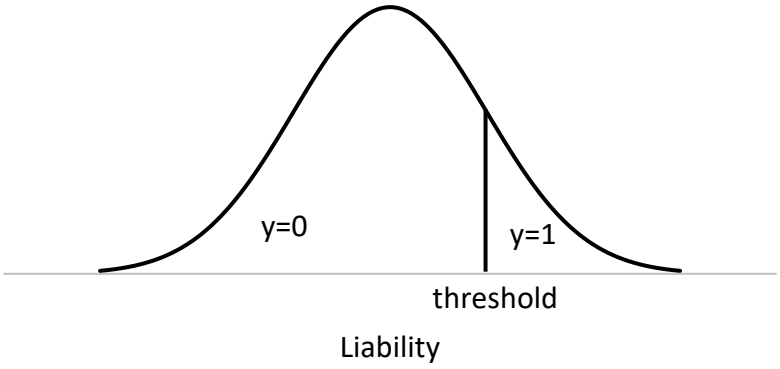

Figure 6. Illustration of underlying liability and observed mortality in a liability threshold model.

Variance components estimated from a linear mixed model (LM) for binary trait are on observed scale, which are dependent on incidence of the trait, while those estimated from LTM model for binary trait are in underlying liability scale, which are independent of incidence. However, heritabilities estimated from the two models can be transformed back and forth using an approximate formula. As presented by Dempster and Lerner (Dempster and Lerner, 1950), the relationship between the heritabilities for binary trait on observed scale (h_o^2) and on liability scale (h_l^2) is,

$$h_o^2 = \frac{h_l^2 z^2}{\pi(1-\pi)}$$

where z is the height of the normal distribution curve at the threshold, and π is the proportion for y = 1. According the formula, $h_o^2 < h_l^2$. When π=0.5, z=0.4, h_o^2 is most close to h_l^2.

A2. Non-estimable genetic and phenotypic correlations between some mortality traits

Covariances between Mortg2, Mort5g2 and Mortall were not estimable due to features of the data. Mort5g2 data comprised Mortg2 data and the records of animals which died during the period from day 5 to the end of nursery. Mortall data comprised Mortg2 data and the

records of animals which died before the end of nursery. In other words, for the animals that had records on Mortg2, these records were exactly the same as those in Mort5g2 and Mortall. Similarly, for the animals that had records in Mort5g2 data, these records were exactly the same as those in Mortall. Therefore, the variance and covariance components were not identifiable since the data available led to an autocorrelation of 1.

Phenotypic correlation between Mort5, Mort5w, Mortg1 and Mortg2 and between Mort5 and Mprt5g2 could not be estimated appropriately. This was due to the fact that only the pigs survived over the previous period had observation in the current period. In other words, for a pig having records for both trait, there existed a constant value (y=0) in one trait and a binary variable (y=0 or 1) in another trait. After adjusting for fixed effects, the observations could deviate from 0 and 1, otherwise the correlation between the two traits was undefined. Consequently, the correlations between a pair of the traits were close to zero for the effects other than additive genetic effect. On the other hand, genetic correlations could be appropriately estimated via pedigree relationships.

A3. Calculation of expected accuracy of estimated breeding value

Expected accuracy of EBV was approximately calculated as

$$r_{EBV} = \sqrt{1 - {PEV}/{\sigma_a^2}},$$

where PEV was prediction error variance, obtained from the inverse of coefficient matrix of the mixed model equation when using LM model, and from posterior distribution of EBV samples when using the LTM model. It should be noted that the measures of accuracy of EBV are not exactly the same in the two models. In particular, for the LM model, PEV is calculated assuming that the estimated variance components are the true values, whereas in the LTM, PEV includes extra inaccuracy due to estimation of variance components.

A4. Calculation of validation accuracy

Two validation accuracies (r_{EBV}) were calculated in this study. One was accuracy of mother EBV, calculated as

$$r_{EBV\_dam} = Cor(EBV_{dam}, PTD)/\overline{r_{PTD}}.$$

The other was accuracy of pig EBV (i.e., parent PA for validation animals), calculated as

$$r_{EBV\_pig} = Cor(EBV_{pig}, y_c)/\overline{r_{yc}}.$$

In the equations, PTD was progeny trait deviation of a mother, y_c was corrected phenotype of a pig, $\overline{r_{PTD}}$ was accuracy of PTD averaged over the validation mothers, and $\overline{r_{yc}}$ was accuracy of y_c averaged over the validation pigs. PTD was defined as mean of offspring's trait deviation (y_d), and y_d for individual i was $y_{di} = EBV_i - EBV_{sire} + \hat{e}_i$. Corrected phenotype for a pig was $y_{ci} = EBV_i + \hat{e}_i$. The EBVs and residuals ($\hat{e}_i$) were estimated from the full data using

the LM model described above. Accuracy of PTD was measured as $r_{PTD} = \sqrt{\frac{n_d}{n_d+\lambda}}$ and $\lambda = \frac{4-h^{2*}}{h^{2*}}$, where n_d was the number of progenies in the test data. Accuracy of y_c was measured as $r_{yc} = \sqrt{h^{2*}}$ which was the same for all pigs, and h^{2*} was heritability of y_c, defined as $h^{2*} = \frac{\sigma_a^2}{\sigma_a^2+\sigma_e^2}$. Here heritability is calculated based on phenotypic variance without litter variance, because y_c and PTD do not include litter effects.

A5. Calculation of expected genetic gain by selection on EBV from LTM model

Genetic gain (ΔG) based on EBV estimated from the LM model with binary variables (0, 1) is the gain on observed scale, and thus it is a direct measure of the change in mortality rate (i.e., probability of death). However, genetic gain based on EBV estimated from the LTM model is the gain on liability scale. To obtain genetic gain in mortality rate, a transformation from underlying liability to mortality rate can be performed in the following procedure. 1) Obtain threshold (t) in standard normal distribution based on mortality rate of the current population (i.e., $P_x(x>t)$). 2) Standardize underlying genetic gain (Δx) by dividing square root of phenotypic variance estimated from the LTM model. 3) Calculate the probability $P_x(x>t+\Delta x)$ in the standard normal distribution (i.e., the probability of death for the population after one generation of selection. 4) Finally, the genetic progress on observed scale is calculated as $\Delta G = P_x(x>t+\Delta x) - P_x(x>t)$.

A6. Correlated response to selection

The correlated response of trait y (CR_y) to selection for trait x can be calculated by the following formula (Falconer and Mackay, 1996).

$$CR_y = ih_x r_a \sigma_{ay}$$

where h_x is square root of heritability of trait x, r_a is genetic correlation between trait x and trait y, and σ_{ay} is square root of additive genetic variance of trait y.

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