

# Breeding for component traits of litter size at day 5 increases piglet survival while maintaining litter size at day 5

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## Abstract

We tested the hypothesis that selection for component traits of live piglets at day 5 (LP5) realises more genetic gain ( $\Delta G$ ) for piglet survival than selection for LP5 while maintaining  $\Delta G$  for LP5. We tested this premise by stochastic simulation of the breeding scheme for Danbred's Landrace pigs. We estimated  $\Delta G$  for LP5 and piglet survival realised by selection for (i) an index for LP5 and (ii) an index for TNB and piglet survival at 1% rate of inbreeding. Selection for index TNB and survival realised about 30% more  $\Delta G$  for piglet survival than selection for the LP5 index while realising the same  $\Delta G$  for LP5. Clearly, it is worthwhile separating LP5 into its component traits: it realises more  $\Delta G$  for piglet survival while maintaining  $\Delta G$  for LP5.

## Introduction

Number of live piglets in a litter on day 5 after farrowing (LP5) is a key trait of DanBred's pig breeding program in Denmark (Su et al., 2020). LP5 is considered a trait that is expressed by the sow of each litter. It is a composite of total number of piglets born (TNB) and survival of individual piglets within litters until day 5 after farrowing (piglet survival). Breeding for increased LP5 has been remarkably successful in DanBred's two maternal breeds: Landrace and Yorkshire (Nielsen et al., 2013; Su et al., 2020). Breeding has realised genetic gain ( $\Delta G$ ) for LP5 by allocating selection pressure to TNB and piglet survival. The drawback is that breeding for LP5 does not allow breeders to control the amount of selection pressure allocated to TNB and piglet survival. Both TNB and piglet survival are economically important because they contribute to LP5. However, there is good reason to allocate more selection pressure to piglet survival: piglet survival is also a proxy for animal welfare and consumer acceptance. One way that we could breed for LP5 while allocating more selection pressure to piglet survival is to separate LP5 into its component traits and select for an index of these components. We could shift selection pressure from TNB to piglet survival by increasing the index weight for piglet survival. This led us to hypothesise that selection for component traits of LP5 realises more  $\Delta G$  for piglet survival than selection for LP5 while maintaining  $\Delta G$  for LP5. We tested this hypothesis by stochastic simulation of the breeding scheme for Danbred's Landrace pigs.

## Materials & Methods

**Procedure.** We used stochastic simulation of the breeding scheme for Danbred's Landrace pigs to estimate  $\Delta G$  for LP5 and piglet survival realised by selection for an index for LP5 – referred to as  $I_{LP5}$  – and an index for TNB and piglet survival ( $I_{TNB+S}$ ) at 1% rate of inbreeding. Selection index  $I_{TNB+S}$  was tested with different relative index weights for TNB and piglet survival. We also selected for TNB ( $I_{TNB}$ ) and piglet survival ( $I_S$ ) as extreme indices of  $I_{TNB+S}$ . The simulations were carried out by (i) sampling unobserved underlying liabilities for TNB and piglet survival; (ii) expressing and phenotyping LP5, TNB, and piglet survival on their observed scales based on the liabilities; (iii) predicting EBV for LP5, TNB, and piglet survival by fitting animal models to the phenotypes on the observed scales; (iv) using the EBV to construct

selection indices; and (v) selecting breeding animals by optimum-contribution selection (OCS) with the index values as estimates of genetic merit. All animals were phenotyped for piglet survival before EBV prediction and selection. Surviving animals were candidates for selection. Dams that were selected in each generation were phenotyped for LP5 and TNB after selection. Breeding schemes were run for 16 discrete generations ( $t = 1 \dots 16$ ) and replicated 300 times. Selection for the indices was carried out in generations  $t = 12 \dots 16$ . The first 11 generations were used to establish a pedigreed population with phenotypes.

**Breeding scheme.** Each replicate was initiated by sampling a unique base population of 100 sires and 1000 dams. One-hundred sires and 1000 dams were randomly selected and mated in generations  $t = 1 \dots 11$ . In generations  $t = 12 \dots 16$ , 1000 matings were allocated to selection candidates by OCS. The number of matings allocated to each male varied from 0, 1, 2 ... to 50 matings. One thousand females were allocated a single mating. The 1000 sire and dam matings were paired randomly. Litter size of each mating (dam) was the dam's phenotype for TNB on the observed scale. Offspring were assigned as males or females with probability 0.5.

**Sampling underlying liabilities.** Unobserved underlying liabilities for TNB and piglet survival ( $\ell_T$  and  $\ell_S$ ) were sampled as:

$$\begin{bmatrix} \ell_T \\ \ell_S \end{bmatrix} = \begin{bmatrix} \mathbf{1} & \mathbf{0} \\ \mathbf{0} & \mathbf{1} \end{bmatrix} \begin{bmatrix} \mu_T \\ \mu_S \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a_d} & \mathbf{Z}_{a_s} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{a_{id}} & \mathbf{Z}_{a_m} \end{bmatrix} \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_s \\ \mathbf{a}_{id} \\ \mathbf{a}_m \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_s & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix} \begin{bmatrix} \mathbf{s} \\ \mathbf{0} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_l & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{l_s} \end{bmatrix} \begin{bmatrix} \mathbf{l} \\ \mathbf{l}_s \end{bmatrix} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_e \end{bmatrix} \begin{bmatrix} \mathbf{0} \\ \mathbf{e} \end{bmatrix} \quad (1)$$

where  $\mu_T=15.3$  and  $\mu_S=0$  are mean liabilities for TNB and piglet survival,  $\mathbf{a}_d$  and  $\mathbf{a}_s$  are vectors of true genetic sow and service-sire effects for TNB,  $\mathbf{a}_{id}$  and  $\mathbf{a}_m$  are vectors of true direct-genetic effects and maternal-genetic effects for piglet survival,  $\mathbf{s}$  is a vector of non-genetic service-sire effects for TNB,  $\mathbf{l}$  is a vector of litter effects for TNB that can also be interpreted as a vector of residuals,  $\mathbf{l}_s$  is a vector of litter effects for survival,  $\mathbf{e}$  is the vector of residuals for piglet survival,  $\mathbf{1}$  are vectors of 1's,  $\mathbf{0}$  are vectors and matrices of 0's, and  $\mathbf{Z}_{a_d}$ ,  $\mathbf{Z}_{a_s}$ ,  $\mathbf{Z}_{a_{id}}$ ,  $\mathbf{Z}_{a_m}$ ,  $\mathbf{Z}_s$ ,  $\mathbf{Z}_l$ ,  $\mathbf{Z}_{l_s}$ , and  $\mathbf{Z}_e$  are design matrices. Effects for animals in the base populations were sampled as:

$$\mathbf{a} = \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_s \\ \mathbf{a}_{id} \\ \mathbf{a}_m \end{bmatrix} \sim N \left( \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \mathbf{G} = \begin{bmatrix} 1.367 & 0.231 & -0.036 & -0.094 \\ 0.231 & 0.508 & -0.078 & 0.066 \\ -0.036 & -0.078 & 0.003 & -0.008 \\ -0.094 & 0.066 & -0.008 & 0.003 \end{bmatrix} \right), \quad s \sim N(0, 0.63),$$

$\begin{bmatrix} \mathbf{l} \\ \mathbf{l}_s \end{bmatrix} \sim N \left( \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 14.98 & -0.58 \\ -0.58 & 0.14 \end{bmatrix} \right)$ , and  $\mathbf{e} \sim N(0, 0.78)$ . True genetic effects of animals in subsequent generations were sampled as  $\mathbf{a}_i \sim N(\frac{1}{2} \cdot (\mathbf{a}_{sirei} + \mathbf{a}_{dami}), \frac{1}{2} \cdot (1 - \bar{F}_i) \cdot \mathbf{G})$ , where  $\mathbf{a}_{sirei}$  and  $\mathbf{a}_{dami}$  are additive-genetic values of the sire and dam of animal  $i$  and  $\bar{F}_i$  is the average inbreeding coefficient of the sire and dam.

**Observed phenotypes.** TNB and piglet survival were expressed and phenotyped on their observed scales. TNB was transformed from the unobserved underlying liability scale to the observed scale by rounding elements of  $\ell_T$  to the closest integer. Piglet survival was assumed to follow a threshold-liability model. Animal  $i$  survived ( $y_{Si}=1$ ) if its liability,  $\ell_{Si} > k$ , and died ( $y_{Si}=0$ ) if  $\ell_{Si} \leq k$ , where  $k=-0.82$  is a fixed threshold derived from the mean probability of piglet survival 0.79 for DanBred Landrace. LP5 were expressed for each litter as  $LP5_j = \sum_{i=1}^{TNB_j} y_{Sij}$ , where  $y_{Sij}$  refers to piglet  $i$  in litter  $j$ .

**Prediction.** Animal models were fitted to the observed phenotypes to estimate (co)variances and predict EBV. The models were (i) LP5:  $\mathbf{y}_{LP5} = \mathbf{1}v_{LP5} + \mathbf{Z}_{a_d}\mathbf{a}_d + \mathbf{Z}_s\mathbf{s} + \mathbf{e}$ ; (ii) TNB and

$$\text{survival: } \begin{bmatrix} \mathbf{y}_T \\ \mathbf{y}_S \end{bmatrix} = \begin{bmatrix} \mathbf{1} & \mathbf{0} \\ \mathbf{0} & \mathbf{1} \end{bmatrix} \begin{bmatrix} v_T \\ v_S \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a_d} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{z}_{a_{id}} & \mathbf{z}_{a_m} \end{bmatrix} \begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_{id} \\ \mathbf{a}_m \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_s & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix} \mathbf{s} + \begin{bmatrix} \mathbf{Z}_l & \mathbf{0} \\ \mathbf{0} & \mathbf{z}_{l_s} \end{bmatrix} \begin{bmatrix} \mathbf{1} \\ \mathbf{l}_s \end{bmatrix} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{z}_e \end{bmatrix} \begin{bmatrix} \mathbf{0} \\ \mathbf{e} \end{bmatrix}; \quad (\text{iii})$$

TNB:  $\mathbf{y}_T = \mathbf{1}v_T + \mathbf{Z}_{a_d}\mathbf{a}_d + \mathbf{Z}_s\mathbf{s} + \mathbf{e}$ ; and (iv) Survival:  $\mathbf{y}_S = \mathbf{1}v_S + \mathbf{Z}_{a_{id}}\mathbf{a}_{id} + \mathbf{Z}_{a_m}\mathbf{a}_m + \mathbf{Z}_{l_s}\mathbf{l}_s + \mathbf{e}$ , where  $\mathbf{y}_{LP5}$ ,  $\mathbf{y}_T$ , and  $\mathbf{y}_S$  are vectors of observed phenotypes for LP5, TNB, and piglet survival,  $\hat{v}_{LP5}$ ,  $\hat{v}_T$ , and  $\hat{v}_S$  are means for LP5, TNB, and piglet survival,  $\mathbf{e}$  are residuals, and all other effects are as defined for equation (1).

**Selection indices.** The selection indices were (i) LP5:  $\mathbf{I}_{LP5} = \hat{\mathbf{a}}_d$ ; (ii) TNB and survival:  $\mathbf{I}_{TNB+S} = \hat{\mathbf{a}}_d + \omega \cdot (\frac{1}{2} \cdot \hat{\mathbf{a}}_{id} + \hat{\mathbf{a}}_m)$ ,  $\omega=10, 15, 16, 18, 20, 25, 30, 40$ ; (iii) TNB:  $\mathbf{I}_{TNB} = \hat{\mathbf{a}}_d$ ; and (iv) Survival:  $\mathbf{I}_S = \frac{1}{2} \cdot \hat{\mathbf{a}}_{id} + \hat{\mathbf{a}}_m$ . EBV used in indices (i)-(iv) were predicted by corresponding animal models (i)-(iv). We use the circumflex “^” to denote EBV predicted by the models. The effects and weights in the selection indices reflected Landrace’s genetic contribution to Duroc x (Landrace x Yorkshire) pigs that are used in production.

**Optimum-contribution selection.** OCS solved  $U_t(\mathbf{c}) = \max\{\mathbf{c}'\mathbf{I}_j|\mathbf{c}'\mathbf{A}\mathbf{c} \leq C_{t+1}\}$  with respect to  $\mathbf{c}$ , where  $\mathbf{c}$  is a vector of genetic contributions to the next generation,  $\mathbf{I}_j$  is a vector of index values ( $\mathbf{I}_j=\mathbf{I}_{LP5}, \mathbf{I}_{TNB+S}, \mathbf{I}_{TNB}, \mathbf{I}_S$ ),  $\mathbf{A}$  is a numerator-relationship matrix, and  $C_{t+1}$  is the pre-defined average relationship in generation  $t+1$  (Meuwissen, 1997).  $C_{t+1}$  was a function of average relationship in generation  $t$  and the pre-defined 1% rate of inbreeding.

**Genetic gain and rate of inbreeding.** We plotted  $\Delta G$  for LP5 against  $\Delta G$  for piglet survival for the four selection indices based on Landrace’s genetic contribution to production pigs.  $\Delta G$  for LP5 and piglet survival were calculated as the linear regression of  $LP5_t$  and  $S_t$  on  $t$ , where  $LP5_t$  and  $S_t$  are the average true breeding values for LP5 and piglet survival of animals born at generation  $t = 12 \dots 16$ . The true breeding values for LP5 and piglet survival of animal  $i$  born at generation  $t$  were estimated as  $LP5_i = (\mu_T + a_{di}) \cdot S_i$  and  $S_i = 1 - \Phi(k = -0.82, \text{mean} = \frac{1}{2} \cdot a_{id_i} + a_{mi}, \text{sd} = 1)$ , where  $a_{di}$ ,  $a_{id_i}$ , and  $a_{mi}$  are the  $i$ th elements of  $\mathbf{a}_d$ ,  $\mathbf{a}_{id}$ , and  $\mathbf{a}_m$ , and  $\Phi(\cdot)$  is the cumulative standard-normal distribution. Rate of inbreeding was calculated as  $1 - \exp(\beta)$ , where  $\beta$  is the linear regression of  $\ln(1-F_t)$  on  $t$  and  $F_t$  is the average coefficient of pedigree inbreeding for animals born at times  $t = 12 \dots 16$ .

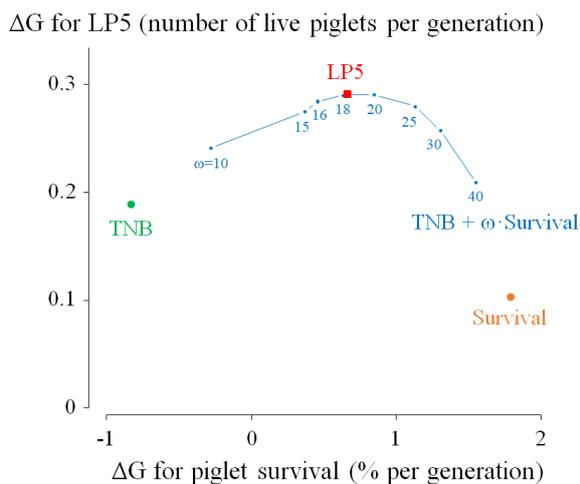
## Results

Selection for index TNB and survival,  $\mathbf{I}_{TNB+S}$ , with index weight  $\omega = 20$  applied to piglet survival realised about 30% more  $\Delta G$  for piglet survival than selection for index LP5,  $\mathbf{I}_{LP5}$ , while realising the same  $\Delta G$  for LP5 (Figure 1). Increasing the weight in  $\mathbf{I}_{TNB+S}$  to  $\omega = 25$  realised about 73% more  $\Delta G$  for piglet survival for only a 3.7% decrease in  $\Delta G$  for LP5. Selection for  $\mathbf{I}_{TNB+S}$  did not realise more  $\Delta G$  for LP5 than  $\mathbf{I}_{LP5}$  at the same  $\Delta G$  for piglet survival. Selection for the first of our extreme indices,  $\mathbf{I}_{TNB}$ , realised negative  $\Delta G$  for piglet survival and 36% less  $\Delta G$  for LP5 than selection for index  $\mathbf{I}_{LP5}$ . Selection for  $\mathbf{I}_S$  realised 174% more  $\Delta G$  for piglet survival than  $\mathbf{I}_{LP5}$ , but 65% less  $\Delta G$  for LP5.

## Discussion

Our findings supported our hypothesis that selection for component traits of LP5 realises more  $\Delta G$  for piglet survival than selection for LP5 while maintaining  $\Delta G$  for LP5. The additional 30%  $\Delta G$  for piglet survival that we simulated in Landrace pigs while maintaining  $\Delta G$  for LP5 makes it worthwhile separating LP5 into its component traits. We could realise even more  $\Delta G$  for piglet survival if we are prepared to accept a small decrease in  $\Delta G$  for LP5. Separating LP5 into its component traits and selecting for an index of these traits realised more  $\Delta G$  for piglet

survival because it shifted selection pressure from TNB to piglet survival. It must have shifted selection pressure, given that we realised more  $\Delta G$  for piglet survival while maintaining  $\Delta G$  for LP5. There will probably always be an incentive to increase  $\Delta G$  for piglet survival given that piglet survival is economically important and a proxy for animal welfare and consumer acceptance. However, separating LP5 into its component traits does come with challenges. It can increase the number of traits that need to be recorded, increase the dimension of multi-trait prediction models, and require reliable estimates of heritabilities and genetic and residual correlations between the component traits and all other traits included in these prediction models. These challenges could persuade some pig breeders to continue selecting for LP5. So, provided it does not burden breeding schemes, it makes perfect sense to separate LP5 into its component traits because it realises more  $\Delta G$  for piglet survival while maintaining  $\Delta G$  for LP5.



**Figure 1.  $\Delta G$  for LP5 against  $\Delta G$  for piglet survival realised by selection for four indices at 1% rate of inbreeding. Rates are means of 300 simulation replicates. SD between replicates ranged from 0.059-0.069 ( $\Delta G$  for LP5) and 0.27-0.46 ( $\Delta G$  for piglet survival).**

We were surprised to find that separating LP5 into its component traits did not realise more  $\Delta G$  for LP5 than selection for LP5 at the same  $\Delta G$  for piglet survival. Clearly, the animal model that we fitted to TNB and piglet survival did not provide additional benefits beyond allowing us to shift selection pressure to piglet survival. The model was designed to cater for differences in heritabilities of the traits and to differentiate between genetic and residual correlations. TNB and piglet survival have similar heritabilities in Landrace pigs when assessed as traits of the sow of the litters; and the genetic correlation between the traits is similar to their residual correlation. However, the model could still provide additional benefits in other pig breeds and animal species where heritabilities of component traits are different and genetic correlations differ from residual correlations. This leads us to speculate that separating composite traits into component traits realises more  $\Delta G$  for both component traits than selection for composite traits when the components differ for heritability and genetic and residual correlations.

## References

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