# Breeding for uniformity by exploiting genetic differences in environmental variance with an application to carcass weight in pigs.

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**Abstract:** Genetic variation in environmental variance may be utilized to improve uniformity in livestock populations by selection. The objective of this study was to investigate effects of genetic parameters and breeding goal on selection responses in mean and variance when applying index selection. Both means and environmental variances were treated as heritable traits. Economic values for mean and variance were derived when profit is based on thresholds with an intermediate optimum. Carcass weight in pigs was used as an illustration, where the highest price is paid for pigs between 80 and 98 kg carcass weight. The ability to change the variance in the desired direction depended on the genetic correlation between the breeding values for mean and environmental variance and on the economic values in the breeding goal. After one generation of selection, the proportion of pigs in the optimum range increased from 80% to 82 – 86%, depending on the heritability of environmental variance. Consequently, profit increased by € 0.19 to € 0.83 per pig. It is concluded that genetic variation in environmental variance can be exploited to select for increased uniformity in pigs, resulting in higher profit.

## INTRODUCTION

Uniformity of livestock is of economic interest in many cases. For example, some meat quality traits, such as pH in pigs, are preferably in a narrow range (Hovenier et al., 1993). Another example is carcass weight in pigs: farmers get premiums when they deliver animals in the preferred range and penalties for animals outside it (Kanis et al., 2006). Different strategies can be used to reduce variability, e.g. management, mating systems and genetic selection (Hohenboken, 1985), but selection can be effective only when there are genetic differences among animals in phenotypic variability.

There is some empirical evidence for the presence of genetic variance in environmental variance, so-called genetic heterogeneity of environmental variance. Sorensen and Waagepetersen (2003) found substantial genetic variance in environmental variance in analysis of litter size in pigs. Rowe et al. (2006) found large differences between sires in phenotypic variance within progeny groups in analysis of body weight in broilers. Based on a number of studies with results of different species, heritabilities of environmental variance tend to be low (0.02 – 0.05), but the genetic standard deviations are high relative to the population average environmental variance (25-60%) (reviewed by Mulder et al., 2007a). This indicates that there are opportunities to reduce variability, i.e. to improve uniformity, by selection. It is unknown, however, how large selection responses in uniformity and profit can be, when applying index selection to change simultaneously the mean and the variance of traits in breeding programs.

The aim of this study is to quantify selection responses in variance and profit by using the framework developed by Mulder et al. (2007a). The economic values of the mean and the variance of a trait are derived in the case of a payment system with differential pricing levels. The theory is illustrated with carcass weight in pigs.

## MATERIAL AND METHODS

### Genetic model

In this study, it is assumed that selection is for only carcass weight in the presence of genetic differences in environmental variance. Both the mean and the environmental variance are partly under genetic control according to the genetic model (Hill and Zhang, 2004; Mulder et al., 2007a):

$$P = \mu + A_m + \chi\sqrt{\sigma_E^2 + A_v} \tag{1}$$

where $P$ is phenotype, $\mu$ and $\sigma_E^2$ are, respectively, the mean trait value and the mean environmental variance of the population, $A_m$ and $A_v$ are, respectively, the breeding value for the mean and environmental variance and $\chi$ is a standard normal deviate for the environmental effect. It is assumed that $A_m$ and $A_v$ follow a multivariate normal distribution $N\left(\begin{pmatrix}0\\0\end{pmatrix}, \mathbf{C}\otimes\mathbf{A}\right)$, where $\mathbf{A}$ is the additive genetic relationship matrix, $\mathbf{C} = \begin{bmatrix}\sigma_{A_m}^2 & cov_{A_{mv}}\\ cov_{A_{mv}} & \sigma_{A_v}^2\end{bmatrix}$, $\sigma_{A_m}^2$ and $\sigma_{A_v}^2$ are the additive genetic variances in $A_v$ and $A_m$, respectively, $cov_{A_{mv}} = \mathrm{cov}(A_m, A_v) = r_A\sigma_{A_m}\sigma_{A_v}$, and $r_A$ is the additive genetic correlation between $A_m$ and $A_v$. The term $\chi$ is scaled by $\sqrt{\sigma_E^2 + A_v}$ to obtain the environmental effect. The mean phenotypic variance of the population ($\sigma_P^2$) is the sum of $\sigma_{A_m}^2$ and $\sigma_E^2$. The heritability of the mean is defined as $h_m^2 = \sigma_{A_m}^2 / \sigma_P^2$ and the heritability of environmental variance is defined as $h_v^2 = \sigma_{A_v}^2 / (2\sigma_P^4 + 3\sigma_{A_v}^2)$ (Mulder et al., 2007a).

### Derivation of economic values with pricing systems based on thresholds

The pricing system for carcass weight in pigs is based on thresholds with an intermediate optimum. The highest price per kg carcass weight is paid for pigs in the range of 80 to 98 kg, whereas a lower price is paid for pigs outside this range.

In the general case with an optimum range between thresholds, we may assume that animals with a phenotype between the lower threshold ($T_l$) and higher threshold ($T_u$) have a profit $M_{T_l<P<T_u}$ and animals with a phenotype outside these thresholds have a profit $M_{P<T_l}$ and $M_{P>T_u}$. The average profit $\overline{M}$ of the population is:

$$\overline{M} = M_{P<T_l}\int_{-\infty}^{T_l} f(P)dP + M_{T_l<P<T_u}\int_{T_l}^{T_u} f(P)dP + M_{P>T_u}\int_{T_u}^{\infty} f(P)dP \tag{2}$$

where $f(P)$ is the probability density function of phenotype. When we would assume that $M_{P<T_l}$ and $M_{P>T_u}$ are equal, profit can be increased by increasing the proportion of animals in the optimum range and is a function of the difference in profit between optimum range and outside the optimum range ($\Delta M$). Therefore, when looking at marginal profit ($mM$), we can simplify Equation 2 to:

$$mM = \Delta M \int_{T_l}^{T_u} f(P)dP \tag{3}$$

The economic values of the mean and the variance can be obtained by taking the first derivatives of Equation 3 with respect to $\mu$ and $\sigma_P^2$, respectively:

$$v_{A_m} = \frac{\mathrm{d}mM}{\mathrm{d}\mu} = \Delta M \frac{z_l - z_u}{\sigma_P} \tag{4a}$$

$$v_{A_v} = \frac{\mathrm{d}mM}{\mathrm{d}\sigma_P^2} = \Delta M \frac{\frac{1}{2}(z_l t_l - z_u t_u)}{\sigma_P^2} \tag{4b}$$

where $z_l$ and $z_u$ are, respectively, the ordinate of the standard normal distribution at the standardized lower and upper thresholds $t_l = (T_l - \mu)/\sigma_P$ and $t_u = (T_u - \mu)/\sigma_P$. In the case of carcass weight the thresholds are at $\pm 1.29\sigma_P$ of the optimum at 89 kg.

**Breeding scheme and prediction of genetic gain**

Selection is for carcass weight and the breeding goal comprises both its mean and variance $H = v_{A_m} A_m + v_{A_v} A_v = \mathbf{v'a}$, where $H$ is the aggregate genotype, $v_{A_m}$ and $v_{A_v}$ are respectively the economic values for $A_m$ and $A_v$, $\mathbf{v}' = \begin{bmatrix} v_{A_m} & v_{A_v} \end{bmatrix}$ and $\mathbf{a}' = \begin{bmatrix} A_m & A_v \end{bmatrix}$. The breeding scheme is based on a sib testing scheme with 100 half-sibs per sire assuming one progeny/dam to keep the selection index relatively simple, although sows have about 10 piglets per litter. The available phenotypic information is: own phenotype $P$, own phenotype squared $P^2$, mean phenotype of half-sibs $\overline{P}$, mean phenotype of half-sibs squared $(\overline{P})^2$ and the within-family variance of half-sibs $varW$. Generations are discrete. Each generation 20% of the dams and 5% of the sires are selected by truncation on an index $I = \mathbf{b'x}$, where $\mathbf{b} = \mathbf{P}^{-1}\mathbf{Gv}$, $\mathbf{x}$ is the vector with phenotypic information, expressed as deviations from the expectations, $\mathbf{P} = \mathrm{cov}(\mathbf{x},\mathbf{x})$ and $\mathbf{G} = \mathrm{cov}(\mathbf{x},\mathbf{a})$. Details of the $\mathbf{P}$- and $\mathbf{G}$-matrices and the calculation of genetic gain are given by Mulder et al. (2007a,b).

**Parameter values**

The heritability of mean carcass weight ($h_m^2$) is assumed to be 0.3 and the phenotypic standard deviation is 7 kg. It is assumed that the mean carcass weight is 89 kg, which is equal to the optimum, or that the mean carcass weight is 85.5 or 88.5 kg, just below the optimum. The price per kg carcass weight is € 1.25 within the optimal range between 80 and 98 kg and € 1.10 outside the range ($\Delta M$ = € 13.35) (Knol, personal communication). The costs are assumed to be constant per animal. The heritability of environmental variance ($h_v^2$) is varied between 0.01 and 0.05, in the range as found in the literature (reviewed by Mulder et al., 2007a). The genetic correlation between $A_m$ and $A_v$ is varied between -0.5 and 0.5, reflecting the range in the literature (Sorensen and Waagepetersen, 2003; Ros et al., 2004; Rowe et al., 2006).

## RESULTS

Table 1 shows the predicted genetic gain in $A_v$, phenotypic standard deviation, proportion of pigs in the optimum range of 80 – 98 kg and the increase in ‘profit’ per slaughter pig, when selecting solely to reduce environmental variance. The reduction in phenotypic standard deviation increases with increasing heritability of environmental variance due to a higher genetic variation in environmental variance and a higher accuracy of selection. Selection increases the proportion of animals in the optimum range from 80% to 82 – 86% depending on $h_v^2$. The profit increases by € 0.19 – € 0.83 per pig.

Table 2 shows predicted genetic gain in mean and phenotypic variance of body weight when the population mean is 3.5 and 0.5 kg below the optimum of 89 kg, such that selection is practiced to change both traits. Reductions in phenotypic variance are smaller than in Table 1. When the genetic correlation is positive, phenotypic variance may increase as an unfavorable correlated response to selection on the mean. The table shows that simultaneous improvement of mean carcass weight and its phenotypic variance is possible, but the ability to change the variance in the desired direction depends on $r_A$ and the economic values in the breeding goal.

Table 1. Predicted genetic gain in $A_v$, phenotypic standard deviation ($\sigma_P$), proportion of pigs in the optimum range of 80 – 98 kg ($p_{optimal}$) and the increase in profit due to increased uniformity in €/pig after one generation of selection on uniformity of carcass weight for different values of the heritability of the environmental variance $h_v^2$ [1].

| $h_v^2$ | $\Delta A_v$ (kg$^2$) | $\sigma_P$ (kg) | $p_{optimal}$ | $\Delta profit$ (€/pig) |
|---|---|---|---|---|
| Generation 0 | | 7.00 | 0.80 | |
| | | After 1 generation of selection | | |
| 0.01 | -3.10 | 6.77 | 0.82 | 0.19 |
| 0.03 | -8.13 | 6.39 | 0.84 | 0.53 |
| 0.05 | -12.48 | 6.04 | 0.86 | 0.83 |

[1] $h_m^2 = 0.3$, $\sigma_P = 7$ kg, $r_A = 0$, 100 half-sibs per sire, selected proportion sires = 0.05; selected proportion dams = 0.20.

Table 2. Genetic gain in mean and phenotypic variance of carcass weight in pigs when the current population mean is 3.5 and 0.5 kg below the optimum value for different values of the genetic correlation between $A_m$ and $A_v$ [1].

| | Relative emphasis[2] | | | | | |
|---|---|---|---|---|---|---|
| $\mu_0$ (kg) | $A_m$ | $A_v$ | $r_A$ | $\Delta A_m$ (kg) | $\Delta A_v$ (kg$^2$) | $\sigma_{P,1}$ (kg) |
| 86.5 | 0.62 | 0.38 | -0.50 | 4.19 | -8.31 | 6.38 |
| 86.5 | 0.62 | 0.38 | 0.00 | 4.04 | -2.74 | 6.80 |
| 86.5 | 0.62 | 0.38 | 0.50 | 3.96 | 4.09 | 7.29 |
| | | | | | | |
| 88.5 | 0.23 | 0.77 | -0.50 | 3.73 | -9.37 | 6.30 |
| 88.5 | 0.23 | 0.77 | 0.00 | 2.00 | -7.19 | 6.47 |
| 88.5 | 0.23 | 0.77 | 0.50 | -1.70 | -8.76 | 6.34 |

[1] $h_m^2 = 0.3$, $h_v^2 = 0.03$, $\sigma_P = 7$ kg, 100 half-sibs per sire, selected proportion sires = 0.05; selected proportion dams = 0.20.

[2] Relative emphasis $A_m$ = $v_{A_m}\sigma_{A_m} / (v_{A_m}\sigma_{A_m} + v_{Av}\sigma_{A_v})$; Relative emphasis $A_v$ = $v_{Av}\sigma_{A_v} / (v_{A_m}\sigma_{A_m} + v_{Av}\sigma_{A_v})$.

## DISCUSSION

In this study, possibilities were explored to improve uniformity of carcass weight in pigs by selection in the presence of genetic differences in environmental variance. Furthermore, the increase in profit was quantified in a simplified situation with two price thresholds. A more precise economic evaluation of uniformity of carcass weight would involve more thresholds, costs and the economic merit of growth rate. The present study shows that selection for increased uniformity of carcass weight increases profit of meat pigs, but requires genetic variation in environmental variance.

Selection for increased uniformity is not only of importance for carcass weight, but is also of relevance for meat quality traits, for example pH (Hovenier et al., 1993). Von Rohr et al. (1999) showed that profit of meat quality traits is based on multiple thresholds. Most of these traits have an intermediate optimum. To deal with multiple thresholds, Equations 2 and 3 can easily be extended.

When genetic differences in environmental variance are present and selection for uniformity is expected to increase profit, it can be worthwhile to exploit these genetic differences in breeding programs. Due to the low heritability of environmental variance, EBV for environmental variance would heavily rely on family information. Large family group sizes (e.g. 100 progeny per sire) are necessary to estimate $EBV_v$ with sufficient accuracy (Mulder et al., 2007a). An additional complexity in pigs is the environmental correlation between full-sibs due to a common maternal environment, which may further increase the required number of progeny per sire. Furthermore, breeding programs may need to be optimized when including environmental variance in the breeding goal and in the index. For example, Mulder et al. (2007b) shows that progeny testing schemes are more efficient in reducing environmental variance than sib testing schemes. Therefore, when reducing variance is a major goal, progeny testing schemes may be better than sib testing schemes even at the cost of a longer generation interval.

## CONCLUSIONS

This study shows that it is possible to change simultaneously the mean and the variance of carcass weight in pig breeding programs if there are genetic differences in environmental variance. The ability to change the variance in the desired direction depends on the genetic correlation between the breeding values for mean and environmental variance and on the economic values in the breeding goal. After one generation of selection the proportion of animals in the optimum range can be increased from 80% to 82 – 86% depending on the heritability of environmental variance. Consequently the profit per pig increases with € 0.19 – € 0.83 per pig. It can be concluded that genetic variation in environmental variance can be exploited to select for increased uniformity in pigs.

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