Genotype by environment interaction for yield traits in Holstein cattle in Slovenia using reaction norms

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SUMMARY

The objective of the study was to evaluate genotype by environment interaction for yield traits in Holstein cattle in Slovenia using the reaction norm approach. A total of 85515 first to third lactation records of 49947 daughters of 179 sires were included in the data. A linear random regression model with heterogeneous environmental variances and regression of phenotypic daughter observations within sire on herd environment was used. The phenotypic measures were the 305 days milk, fat and protein yield. The environmental value based on herd-year average deviation from the overall average of each trait. The estimated correlation between the level and slope of reaction norms were 0.65, 0.72 and 0.67 for milk, protein and fat yield, respectively. Residual variances increased approximately linearly with the increasing value of the herd environment. Heritabilities as a function of the production environment ranged from 0.20 to 0.25. The lowest heritability was found in the environments one standard deviation below the average of environmental variables analyzed. Distinctive crossing of sires' reaction norms for protein and fat production occurred. That is in agreement with the estimated rank correlations between the predicted offspring performances in average and deviating environments (higher than 0.89). The crossing of reaction norms for milk yield was less distinctive.

INTRODUCTION

Genotypes differ in the ability of organisms to respond to the environmental changes. So called phenotypic plasticity or environmental sensitivity may result in genotype by environment interaction (GxEI) (Falconer and Mackay, 1996). When phenotypes change gradually and continuously over a continuous environmental gradient, a reaction norm approach is useful for the evaluation of GxEI (De Jong, 1995). In the reaction norm model, the phenotypic expression of genotype in different environments is described as a linear function (reaction norm) of environmental gradient usually defined as the mean performance in the environment (Strandberg et al., 2000b). Kolmodin et al. (2002) applied such approach when testing for possible GxEI in dairy cattle. Genetic variation in a slope of linear reaction norm indicates the existence of GxEI (Kolmodin et al., 2002) and is useful in animal breeding programs to produce genetic material for a range of production environments (de Jong and Bijma, 2002). In addition, heterogeneous residual variances rather than constant residual variance over all environments would be preferable in the reaction norm approach (Kolmodin et al., 2002; Strandberg, 2006).

Holstein is a prevalent dairy breed on larger Slovenian dairy farms (Sadar et al., 2006). However, there are also some Holstein cows on smaller farms mixed with dual purpose breeds. Mainly, the same breeding bulls are used in the whole population while feeding and management conditions on those farms are more suitable for dual purpose needs and could be a factor causing GxEI, which might lead to re-ranking of bulls in different environments and have consequences for selection of breeding stock. Differences between sires in genetic ability of their daughters to perform in different environments may result from GxEI. At present, no information is available on the existence of GxEI in the Slovenian Holstein population.

Objective of the study was to evaluate the potential GxEI for dairy traits in Slovenian Holstein cattle using reaction norm approach.

MATERIAL AND METHODS

Milk production records and pedigree information were collected for Holstein breed from the database of Slovenian cattle recording scheme (Logar et al., 2005). Milk (MILK), protein (PROT), and fat (FAT) yield in standard lactation (305-days) were studied. To get sufficient number of observation per sire, the first, second and third lactations starting from 1990 to 2004 were included. Criteria for the inclusion of records were the first lactation known, at least 60 kg protein yield, age at first calving within 17-48 months, age at calving within 17-78 months. At least 50 daughter lactations per sire and at least five observations per herd-year of calving were required. The variables used to characterize the environment of each cow (herd environment) were the herd-year averages of each trait expressed as deviation from the overall average. Pedigree data included two generations of ancestors for each sire with daughter records. Descriptive statistics of observations and environmental variables on original scales are presented in Table 1. After editing 85515 records on 49947 daughters of 179 sires were jointly included in the study. The observations were spread over 9568 herd-year seasons.

Table 1. Descriptive statistics for the dependent and environmental variables milk yield (MILK), protein yield (PROT), and fat yield (FAT)

Dependent variable	No. of observations	Mean	SD	Min	Max	No. of cows
MILK, kg	85515	6771.4	1513.9	1901	15740	49947
PROT, kg		220.2	51.2	62.1	506.7	
FAT, kg		274.6	66.6	73	685	
Herd environment						
MILK, kg	9568	0.0	1084.9	-4141	4716	
PROT, kg		0.0	39.6	-142.0	169.0	
FAT, kg		0.0	49.4	-188.0	268.0	

VCE-5 package, Version 5.1.2 (Kovač et al., 2002) where random regression methodology was applied was used to estimate variance and covariance components and other parameters of the reaction norm model. The following model was used for the reaction norm approach:

$$y_{ijlmn} = \mu + C_i + A_j + \mathrm{HY}_l + s_{am} + s_{bm}\, x_{mn} + e_{ijlmn} \qquad [1]$$

where

y_{ijlmn} = 305-days milk, protein or fat yield record of n-th daughter of sire m with calving in herd year l, calving age class j and parity i;
μ = overall mean;
C_i = fixed effect of parity i;
A_j = fixed effect of calving age j (in months);
HY_l = fixed effect of herd year l;
s_{am} = random intercept (level) of the reaction norm for sire m;
s_{bm} = random linear coefficient (slope) of the random regression of y on x_{mn} for sire m;
x_{mn} = herd environment (expressed as deviation of herd-year average from the overall average) which daughter n of sire m produced in;
e_{ijlmn} = random residual.

The intercept (s_a) and regression coefficient (s_b) are level and slope of the linear reaction norm of each sire and are treated as random being normally distributed with mean zero and the variance-covariance structure:

$$var\begin{bmatrix}\mathbf{s}_a \\ \mathbf{s}_b\end{bmatrix} = \begin{bmatrix}\sigma^2_{s_a} & \sigma_{s_{ab}} \\ \sigma_{s_{ab}} & \sigma^2_{s_b}\end{bmatrix} \otimes \mathbf{A} = \mathbf{S} \otimes \mathbf{A} = \frac{1}{4}\begin{bmatrix}\sigma^2_{a_a} & \sigma_{a_{ab}} \\ \sigma_{a_{ab}} & \sigma^2_{a_b}\end{bmatrix} \otimes \mathbf{A} \qquad [2]$$

In the equation 2, the direct additive genetic variance is composed into three components: variance for level ($\sigma^2_{a_a}$), variance for slope ($\sigma^2_{a_b}$) and covariance between level and slope ($\sigma_{a_{ab}}$). Matrix **A** is the additive relationship matrix and the matrix **S** is equal to one quarter of the genetic variance matrix for the level and slope.

Heterogeneity of residual variance was assumed. The herd-year averages were grouped into seven classes and the variances of residuals were calculated within each class. The observations were assigned to classes by their herd environment value. The lowest values formed first class, the next lowest second class, and so on, up to the class with the highest value. The classes had the same range of environmental values in each except the border classes. The residuals were assumed to be independently distributed with mean zero and variance $\sigma^2_{e_c}$, homogenous within an environmental class c.

In the reaction norm models, the standard breeding value is divided into level and slope. Predicted breeding values in the reaction norm models or predicted offspring performance (POP) depend on the environment the offspring will be producing in (Equation 3). The predicted daughter performance of sire m given environment x is calculated as:

$$\mathrm{POP}_{\mathrm{m|x}} = s_{am} + s_{bm}\,x \qquad [3]$$

In the same way, the predicted breeding value changes through the environments, the heritability varies, too. The additive genetic variance including environmental value can be calculated as:

$$\sigma^2_{s|x} = \sigma^2_{s_a} + x^2\sigma^2_{s_b} + 2x\sigma_{s_{ab}} \text{ and the heritability estimate becomes: } h^2|x = \frac{4\sigma^2_{s|x}}{\sigma^2_{s|x} + \sigma^2_e} \qquad [4]$$

Spearman correlation coefficients were calculated between POP in the average and deviating herd environments, to illustrate the potential re-ranking of sires between environments. In order to have more accurate correlation curves, calculations were based only on sires with daughters in the data set.

RESULTS AND DISCUSSION

The variables used to characterize the environment of each daughter were defined as deviation of the herd-year averages from overall herd-year mean of MILK, PROT and FAT. These were assumed to apply for cows with the first, second and third calving in particular herd-year. The herd environment represents a combination of many environmental components influencing dairy production, has a reasonable variation within the country, is easily available from milk recording data, and have been shown to cause GxEI for milk yield traits in several studies (Cromie et al., 1998; Strandberg et al., 2000a; Kolmodin et al., 2002; Petersson et al., 2005; Carlén et al., 2005).

Parameters estimated in the study, variance components for the level and slope along environments, genetic correlations between reaction norm parameters and residual variances estimated in the analyses are shown in Table 2. Estimated genetic correlations between level and slope were 0.65, 0.72 and 0.67 for MILK, PROT and FAT, respectively, which is an indication of potential scaling and re-ranking. The estimated variances of the slope were small, similar to those in a simulation study of Calus et al. (2004), where the variance for the low heritable traits became very small. In the reaction norm approach, the variation of parameters indicates GxEI. As long as the variance of the reaction norm slope is greater than zero, the genetic correlation between environments is smaller than one, which confirms the existence of GxEI (de Jong and Bijma, 2002). Using linear reaction norm, GxEI is indicated by the variation of the slope (Kolmodin et al., 2002). Genetic correlation between the reaction norm level and the slope far from plus one will cause re-ranking of animals in different environments (Su et al., 2006).

After the preliminary analysis with constant residual variance over all environments, adjustment for heterogeneity of residual variance was performed. The estimated residual variances (Table 4) increased progressively with increasing value of the herd environment for MILK, PROT and FAT.

Table 2. Genetic variances for the effect of level (*S_a*) and slope (*S_b*) of the reaction norm, genetic correlation between level and slope ($r_{g_{ab}}$) and residual variances by residual classes for milk (MILK), protein (PROT), and fat yield (FAT)

Trait	$\sigma^2_{S_a}$	$\sigma^2_{S_b}$	$r_{g_{ab}}$	$\sigma^2_{e_1}$	$\sigma^2_{e_2}$	$\sigma^2_{e_3}$	$\sigma^2_{e_4}$	$\sigma^2_{e_5}$	$\sigma^2_{e_6}$	$\sigma^2_{e_7}$
MILK	63228	0.0028	0.65	476375	566786	745514	947694	1201312	1474845	1709865
PROT	57.1	0.0018	0.72	392.9	451.6	618.0	847.5	1128.6	1379.5	1687.1
FAT	113.2	0.0024	0.67	815.1	946.4	1279.5	1636.3	2009.4	2872.5	3518.1

For each sire, the level and slope of linear reaction norm were estimated for the herd environments based on herd-year averages for MILK, PROT and FAT. POPs were calculated in a range of ±3 standard deviations (SD) for the herd environments and reaction norms for random sample of 36 sires are shown in figures 1, 2, 3 for MILK, PROT and FAT, respectively. The crossing of reaction norms is an indication of GxEI. Thus, re-ranking between sires is evident for PROT and FAT (Figures 2, 3) and is less pronounced for MILK yield (Figure 1).

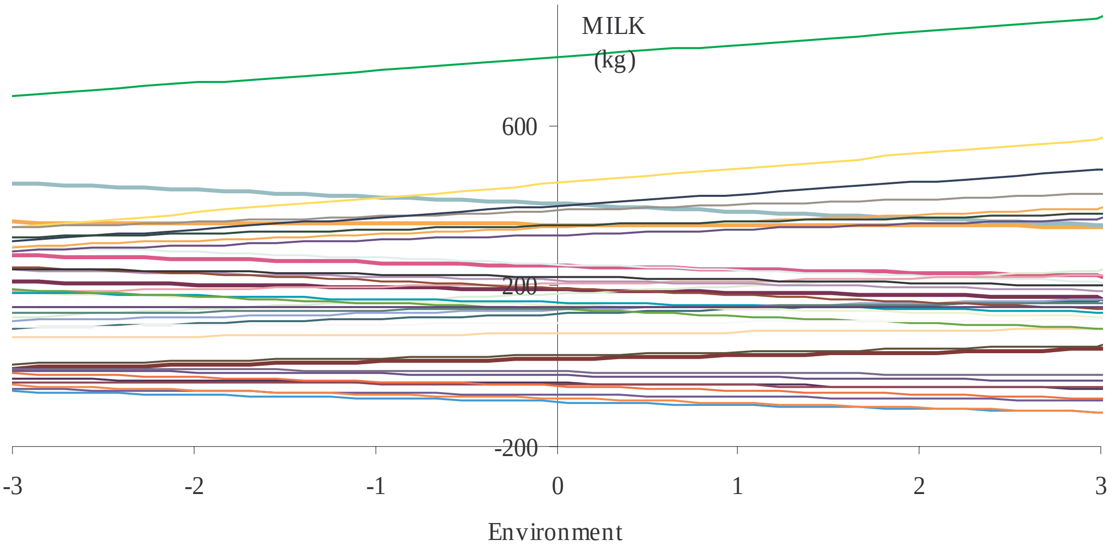


Figure 1. Reaction norms for random sample of 36 sires for milk yield (MILK in kg) in different herd environments (x-axe shows deviation from average environment in SD units of herd-year average)

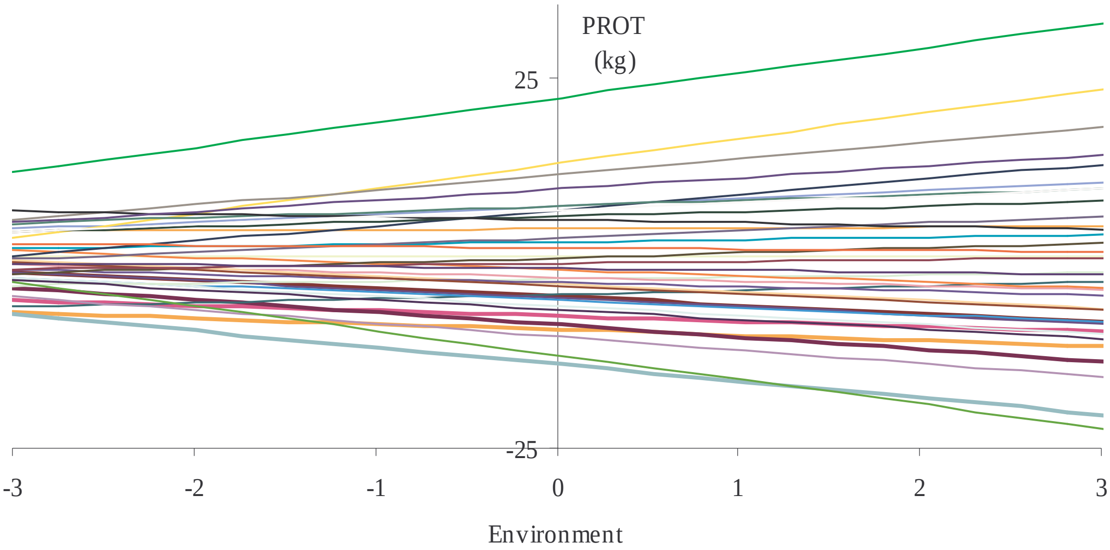


Figure 2. Reaction norms for random sample of 36 sires for protein yield (PROT in kg) in different herd environments (x-axe shows deviation from average environment in SD units of herd-year average)

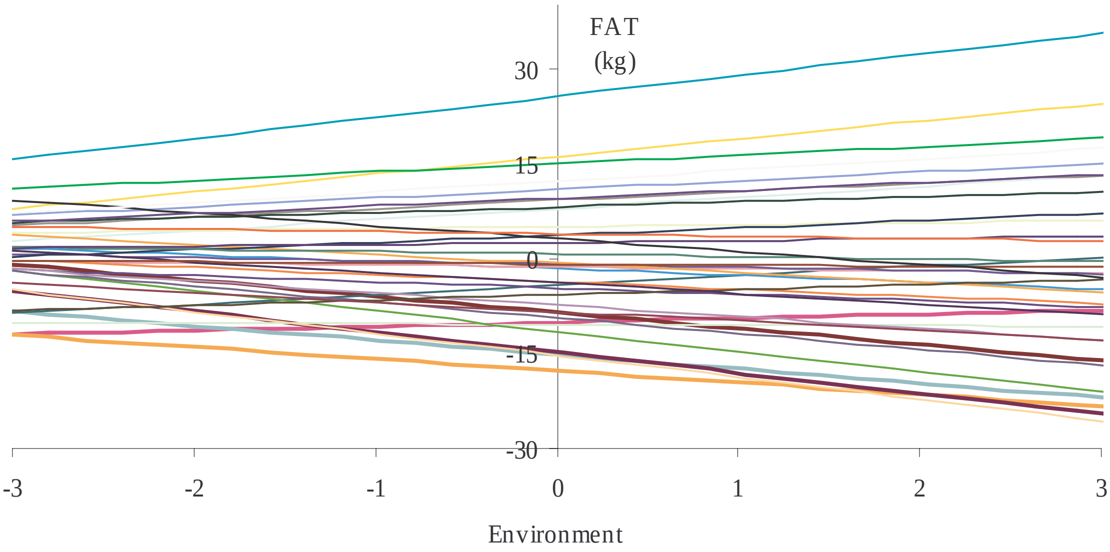
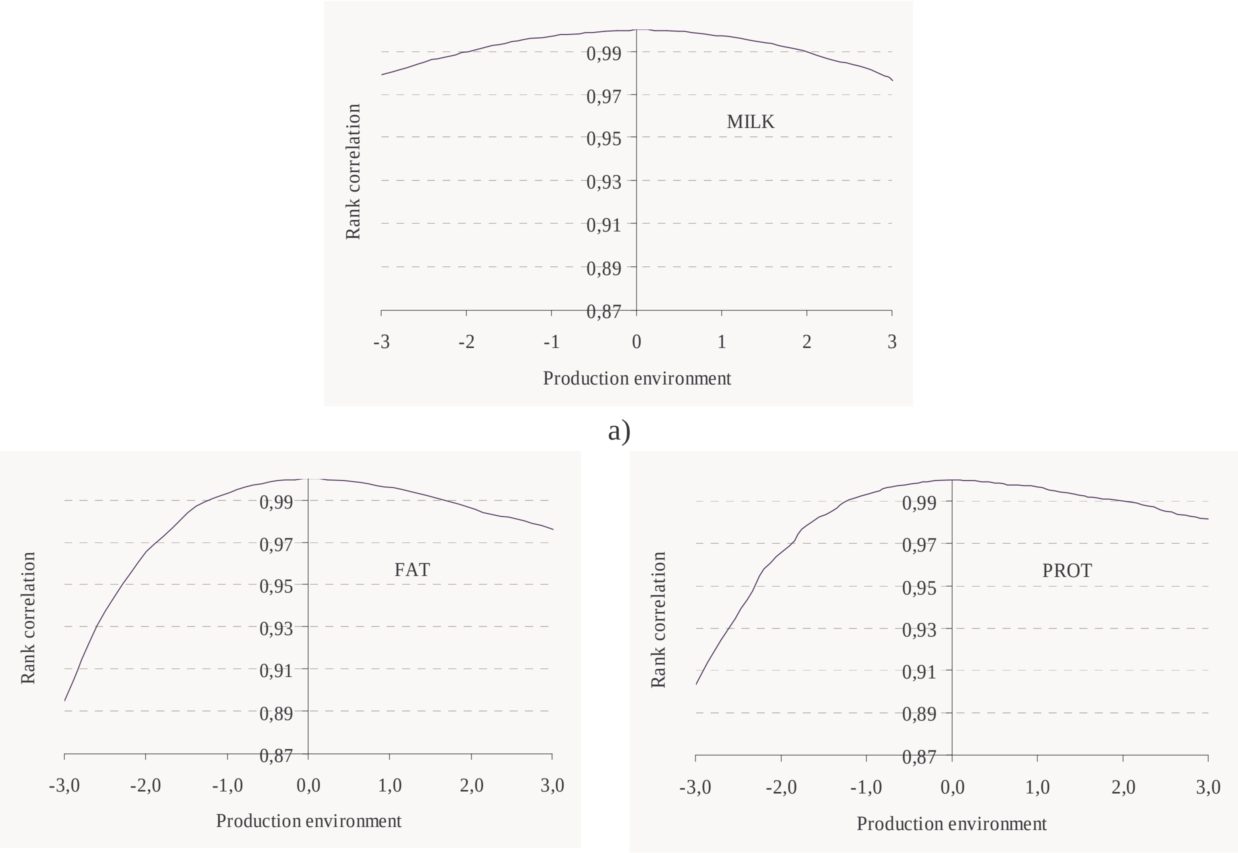


Figure 3. Reaction norms for random sample of 36 sires for fat yield (FAT in kg) in different herd environments (x-axe shows deviation from average environment in SD units of herd-year average)

As it can be seen from correlation curves (Figure 4) the rank correlation between POPs in average and deviating environments were generally higher than 0.89 in the environmental range of ±3 SD of herd environments. For MILK, the rank correlation between POPs in average and unfavorable environments and between POPs in average and favorable ones was larger than 0.97. The rank correlations between average and extreme FAT environments were 0.89 for poor and 0.97 for rich environment, and for PROT were similar, only 0.01 higher than for FAT. The rank correlation for low production environments slightly declines, which causes more re-ranking. Re-ranking of sires were expected in larger extend for low environments for PROT and FAT (Figure 4). That is in agreement with the presented reaction norms (Figures 2, 3) where the greater part of reaction norms crossed in the environments below the average. In addition, potential re-ranking is in agreement with the results of bivariate GxEI analysis (Logar et al., 2007) where the genetic correlations between low and high production environment (low and high quartile) were 0.89 for PROT and 0.95 for FAT.



a)

b)

c)

Figure 4. Rank correlation between predicted offspring performance of milk (a, MILK), fat (b, FAT) and protein (c, PROT) production in average and deviating production environments (x-axis shows deviation from average environment in SD units of herd-year average)

The heritabilities for yield traits estimated as a function of production environment are presented in Figure 5. The range of environments in SD units of each environmental variable was ±3 SD. The heritabilities ranged from 0.20 to 0.25 for MILK, from 0.21 to 0.25 for PROT and from 0.20 to 0.24 for FAT. In the average environment, the heritabilities for all traits were rather similar, in range from 0.21 to 0.22. The lowest heritability was found in the environments 1 SD below the average of environmental variables analyzed. For all traits, the heritability was higher in the most deviating environments. The increase of heritability in favorable production environments was higher than in unfavorable ones. Generally, heritability did no differ much with the environment. The main reason was necessary adjustment for heterogeneity of residual variances, which highly increased with the environmental (residual) classes. When the heterogeneity of residual variances was omitted, the shape of heritability curves (not presented) was similar like in the study of Kolmodin et al. (2002) where heritability increased continuously with the production level. Likewise, after the adjustment for heterogeneity of residual variances increasing of heritability with production level was smaller in this study as well.

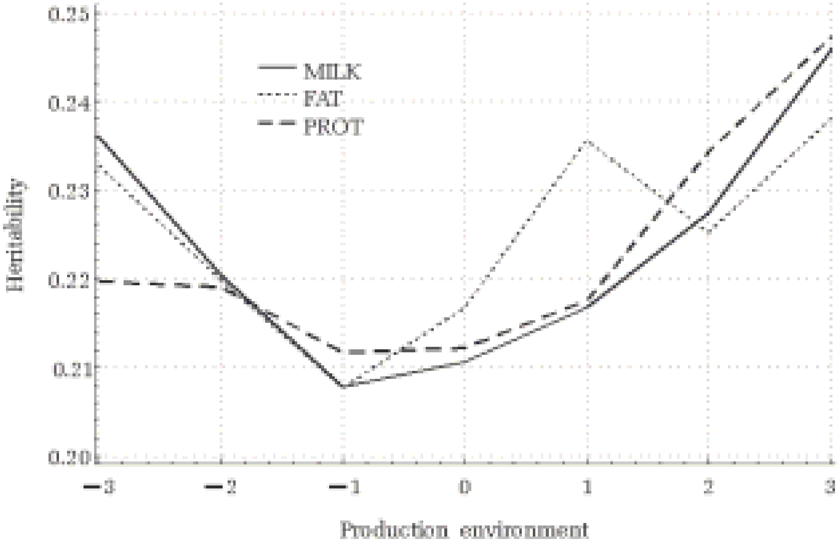


Figure 5. Heritability of milk (MILK), fat (FAT), and protein (PROT) production as a function of the production environment (x-axis shows deviation from average environment in SD units of herd-year averages)

CONCLUSIONS

The presence of genotype by environment interaction (GxEI) for yield traits in Holstein cattle in Slovenia was studied using the reaction norm approach. The herd-year average of each trait was used as the environmental value. The genetic correlations between level and slope of linear reaction norm ranged from 0.65 to 0.72, which is an indication of scaling and re-ranking of sires in different environments. From the reaction norms, re-rankings between sires are evident for protein and fat yield and less pronounced for milk yield. The greater part of reaction norms crossed in the environments below the average, suggesting re-ranking of sires is more evident in poor environments. The crossing of reaction norms is indicated from the correlation curves as well.

Adjustment for heterogeneity of residual variance was performed and the estimated residual variances increased progressively with increasing value of the environments. In the model with heterogeneous residual variance, heritability did not differ much through the environment and ranged from 0.20 to 0.25, for all traits studied.

Sufficient observation per sires is necessary for the reaction norm study. Less than two hundred sires had enough observations of daughters for inclusion in the analyses. To increase the amount of observation per sire, the first to third lactation data were included. Nevertheless, the results of this initial study provide some evidence for the existence of GxEI in the environments defined, especially in poor environment. GxEI signs were generally smaller for milk yield than for protein and fat yield. From the estimated genetic parameters, some re-ranking and scaling effect of GxEI are evident. The results indicated that it would be reasonable to take GxEI in Holstein cattle in Slovenia into account. For environments less suitable for intensive dairy production other breeds would be more appropriate.

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REFERENCES

Calus, M. P. L./Bijma, P./Veerkamp, R. F. Effects of data structure on the estimation of covariance functions to describe genotype by environment interactions in a reaction norm model. Genetics Selection Evolution 36(2004), 489-507.

Carlén, E./Jansson, K./Strandberg, E. Genotype by environment interaction for udder health traits in Swedish Holstein cattle. 56th Annual Meeting of European Association for Animal Production (2005).

Cromie, A. R./Kelleher, D. L./Gordon, F. J./Rath, M. Genotype by environment interaction for milk production traits in holstein friesian dairy cattle in Ireland. Proceedings of the 1998 Interbull meeting Rotorua 17(1998), 100-104.

de Jong, G. Phenotypic plasticity as a product of selection in a variable environment. The American Naturalist 145(1995), 493-512.

de Jong, G./Bijma, P. Selection and phenotypic plasticity in evolutionary biology and animal breeding. Livestock Production Science 78(2002), 195-214.

Falconer, D. S./Mackay, T. F. Introduction to Quantitative Genetics. Longmann & Co., London, (1996) 464 p.

Kolmodin, R./Strandberg, E./Madsen, P./Jensen J./Jorjani, H. Genotype by environment interaction in Nnordic dairy cattle studied using reaction norms. Acta Agriculturae Scandinavica 52(2002), 11-24.

Kovač, M./Groeneveld, E./García-Cortés, L. A. VCE-5, a package for the estimation of dispersion parameters. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. 28(2002).

Logar, B./Malovrh, Š./Kovač, M. Multiple trait analysis of genotype by environment interaction for milk yield traits in Slovenian cattle. Agriculture Scientific and Professional Review 12(2007), 8 p. (in press).

Logar, B./Podgoršek, P./Jeretina, J./Ivanovič, B./Perpar, T. Online-available milk-recording data for efficient support of farm management. In: A. Kuipers, M. Klopčič, and T. Cled (Eds.) Knowledge transfer in cattle husbandry : new management practices, attitudes and adaptation. Wageningen Academic Publishers, Wageningen (2005), 227-230.

Petersson, K.-J./Kolmodin, R./Strandberg, E. Genotype by environment interaction for length of productive life in Swedish Red and White dairy cattle. Acta Agriculturae Scandinavica 55(2005), 9-15.

Sadar, M./Podgoršek, P./Perpar, T./Logar, B./Ivanovič, B./Jeretina, J. Rezultati kontrole mleka in mesa 2005 - Results of animal recording, Slovenia 2005. Kmetijski inštitut Slovenije, Ljubljana 50(2006).

Strandberg, E. Analysis of genotype by environment interaction using random regression models. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production 25(2006).

Strandberg, E./Kolmodin, R./Madsen, P./Jensen, J./Jorjani, H. Genotype by environment interaction in Nordic dairy cattle studied by use of reaction norms. 51st Annual Meeting of European Association for Animal Production (2000a).

Strandberg, E./Kolmodin, R./Madsen, P./Jensen J./Jorjani, H. Genotype by environment interaction in Nordic dairy cattle studied by use of reaction norms. Proceedings of the 2000 Interbull meeting Bled. 25(2000b), 41-45.

Su, G./Madsen, P./Lund, M. S./Sorensen, D./Korsgaard, I. R./Jensen, J. Bayesian analysis of the linear reaction norm model with unknown covariates. Journal of Animal Science 84(2006), 1651-1657.