

Genotype by Environment Interaction in Nordic Dairy Cattle Studied by Use of Reaction Norms

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Abstract

Our objective was to detect and describe genotype by environment interaction on Nordic dairy cattle using a reaction norm model. This model also indicates a possibility to predict breeding values across countries, avoiding the problem with weak genetic ties between countries. Reaction norms were predicted for young sires of the Ayrshire breed group. A linear random regression model was used, regressing phenotypic observations of daughters within sire, on herd environment. The phenotypic measures were 305 days protein production and days open. The environmental value was the herd-year average of protein production or days open. The correlation between the level and the slope of reaction norms was high when the phenotypic observations were regressed on the herd-year average of the same trait. Crossing of reaction norms occurred, showing that genotype by environment interaction exists in the Nordic dairy cattle population. The heritabilities as functions of the environment were higher in herds with high protein yield and long period of days open. The most important result was that reaction norms could be estimated from Nordic field data, resulting in joint predicted breeding values across countries and environments.

1. Introduction

Adaptedness to local environments can cause a variation in how individuals respond to different environments, i.e. showing genotype by environment interaction (GxE). Genotype by environment interaction can be described by inclusion of an interaction term in the traditional quantitative genetic model, or by defining the phenotypic expression in various environments as separate traits and estimate the genetic correlation between those traits. Another approach is to model the reaction norm, describing the phenotype expressed by a genotype as a function of the environment.

From the farmer's point of view, the ideal reaction norm of a production trait has a high level and a flat slope. An animal with this reaction norm would be able to produce well even if the environment changes. However, such animals may be difficult to find. During many generations of selection in dairy cattle, the environment has been continuously improving. The improvement favours genotypes with steep

reaction norms, because these genotypes benefit the most from the improved conditions.

International genetic evaluations are often hampered by the lack of genetic ties between countries. We will show that the suggested reaction norm model circumvents this problem, but perhaps replaces it with another, namely how to define the environmental values.

Our objective was to describe the amount and pattern of GxE in Nordic dairy cattle, by use of a reaction norm model. A random regression model was applied to predict reaction norms of young bulls and to estimate genetic parameters of these reaction norms, from data available from Nordic milk recording schemes. The results can be used to give joint predicted breeding values for Nordic test bulls.

2. Material and Methods

Random regression models have been used in test day models, modelling the lactation curves

of individual cows. The test day model includes two sets of regressions: a fix regression common to all cows and a random regression specific for each cow (e.g. Schaeffer & Dekkers 1994). Here a random regression model has been applied to model the reaction norms of individual genotypes, in our case individual bulls. Phenotypic observations of daughters were regressed within sire on herd environment, by a linear random regression model.

2.1. Data

Production (305-day protein yield), fertility (days open, calving to last insemination) and pedigree information was collected for Finnish Ayrshire, Norwegian Dairy Cattle, and Swedish Red and White Breed from the national milk recording services in Finland, Norway and Sweden. Data were edited to include only observations on daughters of bulls having a minimum of 50 daughters. Only first lactation data for cows having their first calving during 1987-1995 and having at least one herd-mate in the same herd-year were included. After editing, the Finnish, Norwegian and Swedish data sets contained 491 088, 584 823 and 412 942 records, respectively. The national data sets were merged to form a joint Nordic data set, containing 1 488 853 records. The international identification used by Interbull was used to identify bulls in the joint data set. Data were pre-adjusted for calving age, calving month, and their interaction.

2.2. Reaction norm model

Variance-covariance components were estimated and breeding values were predicted for the intercept and coefficient of the reaction norm of each bull. The DMU package developed by Jensen & Madsen (1994), extended to handle random regressions was utilised. The model was defined as:

$$y_{ij} = \mu + b_F X_{ij} + s_{a_i} + s_{b_i} X_{ij} + e_{ij} \quad [1]$$

where

y_{ij} is 305 days kg protein production or days open of daughter j of sire i ,

μ is the overall mean (or the intercept for the fixed regression),
 b_F is the fixed coefficient of a regression of y on X_{ij} ,
 s_{a_i} is the random intercept of the reaction norm of sire i , also called *level*,
 s_{b_i} is the random linear coefficient of a random regression of y on X_{ij} , also called *slope*,
 X_{ij} is a the herd environment that daughter j of sire i encountered, and
 e_{ij} is the random residual associated with daughter j of sire i .

The random effects s_a and s_b were assumed to be normally distributed with expectations zero, variances $\sigma_{s_a}^2$ and $\sigma_{s_b}^2$, respectively, and covariance $\sigma_{s_{a,b}}$. The relationship matrix based on sire and maternal grandsire of sire was included.

Herd environment, X_{ij} , was defined as the herd-year averages of protein production or days open, deviated from the across country average. The dependence of the environmental gradient on the observations was relaxed by including daughters of young and proven bulls in the herd-year averages, but only daughters of young bulls (born after 1982) in the estimation of (co)variance components and prediction of reaction norms.

In the reaction norm model the predicted breeding value, or the predicted offspring performance (POP), is depending on the environment that the daughter will produce in. Thus the predicted offspring performance for bull i is calculated as:

$$POP_{i|X} = \hat{\mu} + \hat{b}_F X + \hat{s}_{a_i} + \hat{s}_{b_i} X \quad [2]$$

In the same way that POP varies with the environment the offspring encounters, the heritability varies because the environmental measure will be included in the additive genetic variance, i.e. the variance of [2]: $\hat{\sigma}_s^2 = \hat{\sigma}_{s_a}^2 + X^2 \hat{\sigma}_{s_b}^2 + 2X \hat{\sigma}_{s_{a,b}}$. Estimated heritability was calculated as $4\hat{\sigma}_s^2 / (\hat{\sigma}_s^2 + \hat{\sigma}_e^2)$.

3. Results

Reaction norms were predicted for 3 279 young sires. Estimates of genetic (co)variances and correlations together with residual variance

estimates from the reaction norm model are shown in Table 1. As can be seen from standard errors, the genetic variance components of level and slope of reaction norms are significantly different from zero.

Table 1

Estimates of genetic (co)variances and correlations for effects of the level (s_a) and slope (s_b) of the reaction norms for 305-day protein yield or days open (SE shown as subscript of estimate)

Analysis ¹	Parameter estimate				
	$\sigma_{s_a}^2$	$\sigma_{s_{a,b}}$	$\sigma_{s_b}^2$	$r_{g_{a,b}}$	σ_e^2
PROT/prot	22.47 _{.47}	.161 _{.0052}	.0019 _{.000088}	.789 _{.015}	518.50 _{.57}
DOP/dop	15.84 _{.47}	.363 _{.011}	.00907 _{.00036}	.958 _{.0077}	1839.9 _{2.01}
DOP/prot	37.59 _{1.02}	-.0634 _{.013}	.00475 _{.00034}	-.150 _{.032}	2640.4 _{2.89}

¹PROT/prot represents the regression of 305 days kg protein production on herd production environment, DOP/dop the regression of days open on herd fertility environment and DOP/prot the regression of days open on herd production environment.

Heritabilities as functions of herd environment are shown in Fig. 1. For protein yield heritability increased continuously with increased production level. For days open in varying fertility environments, heritability increased with increasing average number of days open, at herd levels higher than -1.5 SD. The production environment influences heritability of days open less than does the fertility environment.

Rank correlation between POP predicted in average or deviating environments are shown in Fig. 2. For protein production the rank correlation between average and higher production environments were high. For low production environments the rank correlation declined.

For days open, rank correlation was high between average and bad fertility environments. Between average and very good fertility environments almost complete reranking was found. This can be explained by the fact that almost all reaction norms crossed at -1.5 SD and that the heritability was almost zero at -1.5 SD, indicating that in this environment all sires have the same breeding value. It should be remembered that days open has a skewed distribution, such that few herds have average days open below -1.5 SD (70 days). The extreme reranking that occurs in the graph would therefore seldom occur in reality.

When days open was regressed on production environment, the rank correlation decreased in both low and high production herds, but more in the latter.

4. Discussion

The herd-year average as measure of environmental value was chosen because it is easily available from milk recording data and it is a general measure of a complex of environmental factors. As the herd-year average includes the environmental and the genetic level of the herd, the environmental value will be biased upwards in herds having a high genetic level. Pre-adjustment of data for the genetic level could be partly achieved by including an effect of sire in the model used for calculation of herd-year averages. In an across-country evaluation, it might also be necessary to account for the difference in average genetic level between countries, even though this difference would be of smaller magnitude than the difference between low and high production herds.

An alternative measure of environmental value could be an index composed of herd averages of more than one trait. Another possibility could be to use information on management factors, e.g. feeding intensity, if such data were available, as the environmental gradient or as components of an environmental index.

Even though the main aim of this study was to detect and quantify GxE, the method used also has implications for a joint across-country genetic evaluation. If a common measure of the environmental level can be agreed upon, the reaction norm model could be used for international evaluations. Unique rankings could be presented for each environmental level. Each herd would have an environmental value, telling the farmer which ranking list to consult. Because the herd environment is measured on a single continuous scale across countries, grouping of observations is avoided and thereby also the problem of genetic connectedness between groups or countries.

We will continue our work by including heterogeneous environmental variances and to study multiple-trait reaction norms. For parts of the data we will also try to apply an animal reaction norm model.

In conclusion, we have shown that it is possible to estimate reaction norms of sires across countries and we found some evidence

of genotype by environment interaction both for protein and days open.

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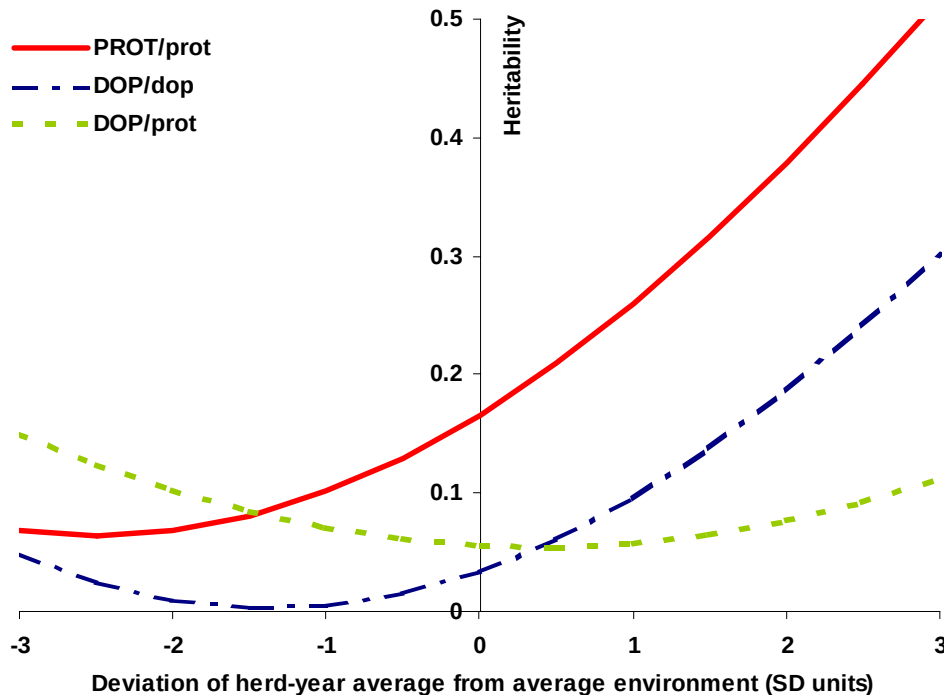


Fig. 1. Heritabilities as functions of the environment. Labels as in Table 1.

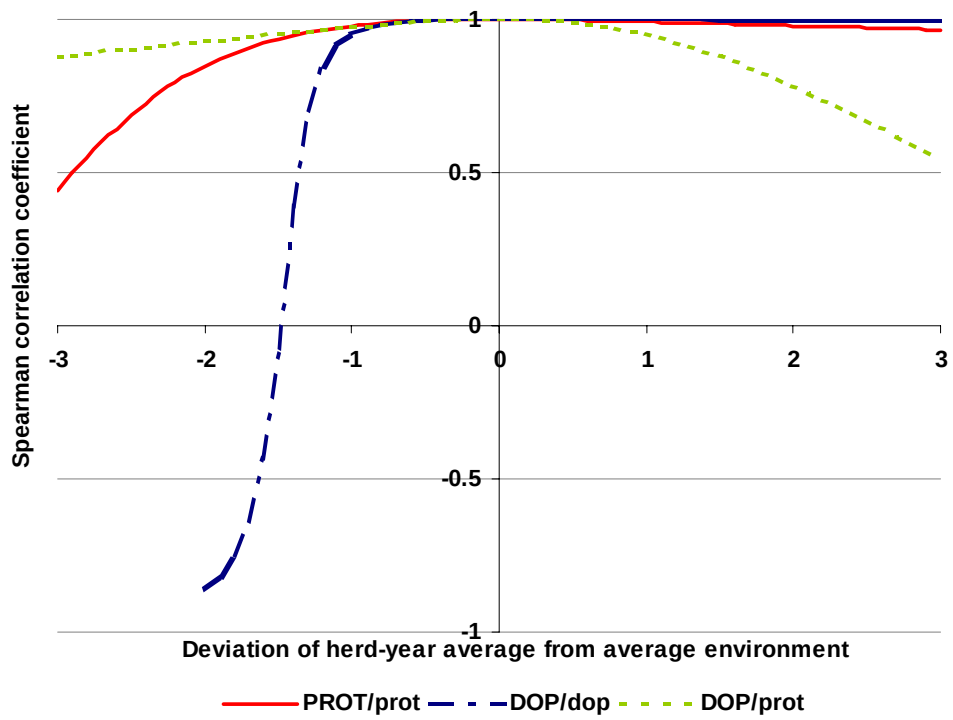


Fig. 2. Rank correlations between predicted offspring performance in different environments. Labels as in Table 1.