

Genotype by environment interactions in productive traits in a local cattle breed due to breeding area, farming systems and feeding strategies

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Summary

Genotype by environment interactions (GxE) may occur when individuals show different adaptation to local environment. Due to their typically great adeptness to environment local breeds may be reared in a variety of geographical areas and farming conditions, suggesting to investigate the occurrence of GxE for genetic improvement. Considering the local cattle breed Rendena, this study aimed to investigate GxE for traits of interest in a number of environmental conditions including the geographical area (plain, hill or mountain), the type of housing (tie-stall or loose housing), the feeding system (traditional or total mixed ration) and the occurrence of summer pasture. Following the reaction norm model approach, milk yield, fat and protein yield and percentage, and SCS were analysed via Bayesian inference. The solutions for the herd-test day (HTD) effect firstly obtained via animal model as estimates of environmental effect, were then used in a random regression model as environmental covariate for sire effect to obtain the intercept and the slope for target traits across different HTD levels. As result, GxE interactions explained a certain quote of phenotypic variance (about the 20% on average), even greater than G in milk, protein yield and SCS. Some differences in genetic variances were observed between estimates for HTD ascribable to different environmental conditions. A greater genetic component was observed for milk, fat and protein yield in plain farms, without summer pasture, under loose housing, and with a total mixed ration as feed. This may be explained by the fact that better conditions for individuals or for production could enhance the expression of individual performance. This study confirms the importance to detect GxE in local breeds reared in various environments.

Keywords: GxE, genotype by environment, Reaction norm model, local breed, cattle

Introduction

Variability may occur in individual adaptation to local environments, implying that different genotypes will respond differently to environmental changes. Genotype by environment interaction (GxE) may cause re-ranking of animal performances in different environments (Falconer, 1990). The reaction norm model approach (Kirkpatrick *et al.*, 1990) suggests to express phenotype as a function of environmental descriptors (e.g., temperature,

humidity, geographical position, farming management), allowing to detect environmental variations on a continuous scale (Bohmanova *et al.*, 2008).

Genotype by environment interaction has been found in dairy cattle productive traits, but current genetic improvement does not consider this component (Tiezzi *et al.*, 2017). GxE may be relevant in local breeds, often showing a variety in breeding areas, herd sizes, farming systems, feeding strategies, due their adaptability to environment. Genetic improvement of local breeds should account for GxE, as suggested by the heterogeneous variances estimated in different environments (e.g., Fuerst-Waltl *et al.*, 2013).

Focusing on the local Rendena cattle, this study applied a reaction norm model approach to investigate the effects of genotype, environment, and their interaction on dairy productive traits and somatic cells under a variety of environments.

Material and Methods

Study subject, datasets and traits

Rendena breed is a small local cattle (~4,000 cows) reared in the North East Italian Alps and in the close plains. The breed shows appreciable levels of fertility and longevity, and the ability to adapt to marginal areas and to graze during summer in high Alpine pastures. Rendena is mainly bred for milk improvement (65% of selection index) as well as for meat (Sartori *et al.*, 2017).

Test day data for milk yield traits (milk yield, **MY**, kg; fat yield, **FY**, kg; fat percentage, **F%**; protein yield, **PY**, kg; protein percentage, **P%**) and somatic cells (somatic cell score, **SCS**) routinely collected between 2003 and 2014 were provided by the Italian Animal Breeders Association. An amount of 163,859 test day records belonging to 9,986 cows, daughters of 553 sires and referring to 16,602 animals in pedigree, was considered. To investigate GxE, some environmental categories were defined (Table 1): geographical area (Plain vs. Hill vs. Mountain); Type of housing (Tie-stall vs. Loose housing); Feeding system (Traditional vs. Total Mixed Ration, **TMR**); Summer pasture (Yes vs. No).

Statistical analysis

GxE interaction was evaluated via reaction norm model in a two-steps analysis (Silva *et al.*, 2014; Tiezzi *et al.*, 2017). In the first step, the following single trait test day repeatability animal model, slightly modified from the one used for routinely genetic evaluations, was run:

$$y_{ijklmn} = \text{HTD}_i + \text{fixed}_{jkl} + a_m + \text{Pe}_n + e_{ijklmn} \quad (1)$$

where y_{ijklmn} is the test-day record of MY, FY, F%, PY, P%, SCS of the cow n ; HTD_i is the fixed effect of the herd test day, or **HTD** i ; fixed_{jkl} includes the overall mean and the fixed effects of the days of gestation class j (18 classes), AP-LN $_k$ is the fixed effect of age at parity k within lactation (42 classes); MP-LN l is the fixed effect of the month of parity l within lactation (36 classes). Fourth order Legendre polynomials described the shape of lactation curve for AP-LN and MP-LN. Random effects included were the additive genetic effect a_m , the permanent environmental component Pe_n , and the error term e_{ijklmn} . The software GIBBS3f90 (Misztal, 2008) applying a Gibbs sampling algorithm was used to run the analysis. The algorithm performed 220,000 iterations, 20,000 of which were discarded as burn-in, and posterior estimates of variances were obtained running the POSTGIBBSf90 software and considering a thinning interval of 2,000 iterations.

In the second step a sire model (2) derived from (1) was run. This model included the same effects as in (1) apart the HTD_i and the a_n . The sires of cows were considered (863 individuals in pedigree) as genetic term. The GxE was assessed by introducing the solutions of the HTD effect (12,204 levels), expressed as Legendre polynomials of order 0 and 1 (i.e., 1 and x term), both as fixed covariate and as random covariate for sire. Model (2) was therefore:

$$y_{klnop} = fixed_{ijkl} + \sum_{k=0,1} \phi_o + \sum_{k=0,1} \phi_o s_p + P e_n + e_{ijklnop} \quad (2)$$

where $\sum_{k=0,1} \phi_o$ terms are the Legendre polynomials, and s_p the sire effect. Considering GxE, the $\sum_{k=0,1} \phi_o$ term represented E, $\sum_{k=0} \phi_o s_p$ was G (the intercept), and $\sum_{k=1} \phi_o s_p$ the GxE (the slope). The heterogeneity in residual variance was considered by assuming 5 classes for $\sum_{k=0,1} \phi_o$ as quantiles of the HTD solutions (Silva *et al.*, 2014). After ensured the convergence of posterior estimates in preliminary analysis, Gibbs sampling estimates were obtained by running 70,000 iterations with a burn-in of 20,000 and a thinning of 50. An additional model (3), equal to (2) but including the sire effect instead of $\sum_{k=0,1} \phi_o s_p$, was run to compare estimates obtained with or without GxE term. The heterogeneity of variance in different environments (Table 1) was obtained for $\sum_{k=0,1} \phi_o s_p$ term as $\mathbf{Z}'\mathbf{G}\mathbf{Z}$, where \mathbf{Z} is an incidence matrix for Legendre polynomials for HTD solutions and \mathbf{G} the genetic (co)variance matrix.

Results

Descriptive statistics of the target traits by environmental category were reported in Table 1. In a number of cases (e.g., MY, FY, PY) the same trait has different phenotypic means, suggesting a possible effect of environmental conditions on productive traits.

Table 2 shows heritability calculated from variance components estimated via animal model (1). It is possible to note that values are close to previous findings in Rendena cattle (Guzzo *et al.*, 2009). Similar estimates have been also found in other dairy and dual purpose breeds, e.g. Aosta Red Pied (Mazza *et al.*, 2016), Italian Simmental (Frigo *et al.*, 2013). The protein percentage in milk is the most heritable trait, whereas SCS is the less variable.

Results of the second step are shown in Figure 1. Here, the proportion of the phenotypic variance due to G term (the intercept for $\sum_{k=0,1} \phi_o s_p$) and GxE effects (the slope) obtained by model (2) is reported and compared with the G component estimated by excluding GxE (3). When GxE was not considered, variance component for G resulted higher for all traits apart fat percentage. In MY and PY, in particular, when the GxE component was introduced, G lowered of about a 25% (~5% of phenotypic variance). A consistent GxE effect was estimated for most of traits excluding P%, resulting even greater than G for MY, PY, SCS.

The magnitude of GxE interaction in different contexts can be appreciated by looking at Table 3, reporting the genetic variances in the environmental categories reported above (Table 1). Milk, FY and PY recorded at herds in plains showed a greater genetic variance than in hills and mountain herds. For the same traits, loose housing system was characterized by a greater variance than tie-stall housing. Milk and protein yield showed a greater variability when TMR was adopted. A greater variance for MY, FY and PY was found for herds that are not used to summer pasture. Conversely, F% and P% were almost pretty homogeneous in the different environments considered. Similar considerations may be done for SCS.

Discussion

Local breeds are often reared in a variety of environments, thanks to a greater adaptability

than specialized breeds, and valuable characteristics of longevity, fertility, and resistance both to the disease and to the stress (Biscarini *et al.*, 2015). Notwithstanding, the genetic improvement of local breeds (as for specialized breeds) needs to consider the context in which the breed is reared. Not accounting for the GxE incidence could lead to biased predictions of individual genetic merits, e.g. causing a re-ranking of bulls and a reduced genetic gain (Tiezzi *et al.*, 2017). A greater variability in milk, fat and protein yield variances was observed in the most efficient environmental contexts (e.g., breeding in plains areas without pasture), but also when improved conditions for animal management were adopted, e.g., when cows were kept in loose housing and when TMR was preferred to traditional ration. This could be explained by the better conditions for expressing individuals' genetic potentials that these environments may offer. Furthermore, the magnitude of GxE reported in Figure 1 suggests that introducing this component in genetic evaluation could effectively optimize genetic improvement in Rendena and, similarly, in other local breeds well adapted to a variety of environments.

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Table 1. Phenotypic means (SD in brackets) within environment for traits considered.

	Milk yield	Fat yield	Fat %	Protein y.	Protein %	SCS
<i>Geographical area</i>						
Plain	17.8 (5.93)	0.62 (0.22)	3.53 (0.56)	0.59 (0.19)	3.36 (0.35)	2.88 (1.82)
Hill	15.1 (4.77)	0.53 (0.17)	3.54 (0.60)	0.48 (0.15)	3.22 (0.34)	2.78 (1.77)
Mountain	16.4 (5.26)	0.58 (0.21)	3.52 (0.62)	0.54 (0.17)	3.32 (0.34)	2.65 (2.03)
<i>Type of housing</i>						
Tie-stall	16.5 (5.38)	0.57 (0.19)	3.52 (0.57)	0.54 (0.17)	3.32 (0.36)	2.87 (1.91)
Loose housing	18.9 (6.12)	0.67 (0.23)	3.54 (0.58)	0.64 (0.19)	3.40 (0.33)	2.68 (1.83)
<i>Feeding system</i>						
Traditional	16.7 (5.49)	0.58 (0.20)	3.50 (0.57)	0.55 (0.18)	3.31 (0.35)	2.78 (1.92)
TMR ¹	18.3 (6.08)	0.65 (0.23)	3.56 (0.59)	0.62 (0.19)	3.41 (0.37)	2.86 (1.82)
<i>Summer pasture</i>						
No	17.9 (5.86)	0.63 (0.22)	3.54 (0.55)	0.60 (0.18)	3.37 (0.35)	2.78 (1.84)
Yes	16.2 (5.41)	0.56 (0.21)	3.51 (0.61)	0.53 (0.17)	3.31 (0.35)	2.85 (1.95)

¹ Total Mixed Ration

Table 2. Heritability (SD in brackets) for target traits estimated via animal model analysis.

	Milk yield	Fat yield	Fat %	Protein yield	Protein %	SCS
Heritability	0.19 (0.01)	0.16 (0.01)	0.19 (0.01)	0.16 (0.01)	0.31 (0.01)	0.09 (0.01)

Table 3. Heterogeneity of variance in different environmental categories obtained for $\Sigma_{k=0,1}\Phi_{0Sp}$ as $Z'GZ$ (see definition in Materials and Methods).

Z'GZ	n ¹	Milk yield	Fat yield ²	Fat % ²	Protein yield	Protein % ²	SCS
<i>Geographical area</i>							
Plain	6,432	1.27 (0.46)	0.14 (0.05)	1.04 (0.25)	1.22 (0.46)	0.51 (0.03)	0.08 (0.03)
Hill	902	1.11 (0.28)	0.12 (0.03)	1.06 (0.32)	1.05 (0.26)	0.51 (0.03)	0.08 (0.02)
Mountain	4,869	1.11 (0.30)	0.12 (0.04)	1.09 (0.5)	1.07 (0.3)	0.51 (0.03)	0.09 (0.04)
<i>Housing</i>							
Loose hou. ³	2,215	1.42 (0.55)	0.16 (0.05)	1.03 (0.25)	1.39 (0.57)	0.52 (0.04)	0.08 (0.03)
Tie-stall	9,988	1.15 (0.34)	0.13 (0.04)	1.07 (0.39)	1.10 (0.33)	0.51 (0.03)	0.09 (0.04)
<i>Feeding system</i>							
TMR ³	2,592	1.32 (0.49)	0.15 (0.05)	1.07 (0.26)	1.28 (0.49)	0.52 (0.04)	0.08 (0.02)
Traditional	9,611	1.16 (0.36)	0.13 (0.04)	1.06 (0.40)	1.11 (0.36)	0.51 (0.03)	0.09 (0.04)
<i>Summer pasture</i>							
No	6,246	1.28 (0.48)	0.15 (0.05)	1.06 (0.31)	1.23 (0.48)	0.52 (0.03)	0.08 (0.03)
Yes	5,957	1.11 (0.27)	0.12 (0.04)	1.06 (0.43)	1.06 (0.27)	0.51 (0.03)	0.09 (0.04)

¹ number of herd test days, HTD

² multiplied by 100

³ Loose housing; Total mixed ration

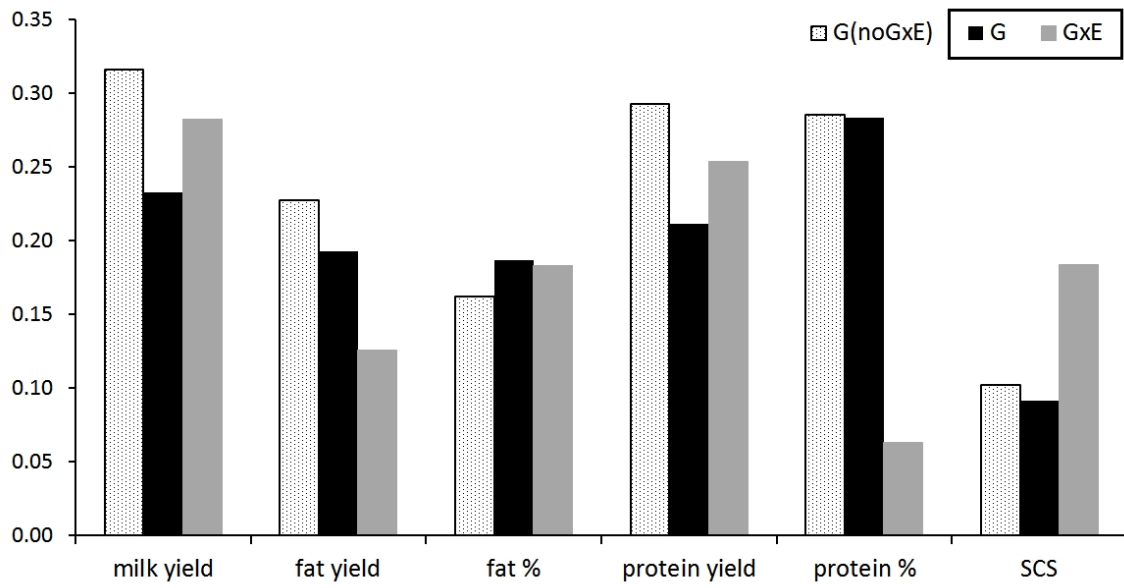


Figure 1. Proportion of phenotypic variance for G and GxE components obtained either including the random environmental covariate (filled G and GxE bars) or not (pointed G).