

Genotype × country interaction for weaning weight in the Angus populations of Brazil and Uruguay¹

Ana Carolina Espasandin², Jorge Ignacio Urioste², Leonardo Talavera Campos³, Maurício Mello de Alencar⁴

- ¹ Convenio PEC-PG, Capes-CNPq-MEC.
- ² Depto. Produccion Animal y Pasturas, Facultad de Agronomia EEMAC UDELAR Uruguay.
- ³ PROMEBO, Universidade Federal de Pelotas, RS, Brazil.
- ⁴ Embrapa Pecuária Sudeste, São Carlos, SP, Brazil.

ABSTRACT - It was analyzed the existence of genotype × environment interaction for weaning weight in populations of Angus from Brazil and Uruguay by using records of 73,205 animals (10,257 from Uruguay and 62,948 from Brazil) belonging to 33 and 161 farms and 13 and 34 regions in Uruguay and Brazil, respectively. It was used the one- and two-trait animal model analyses considering weight at weaning of each country as different characters. Coefficients of direct and maternal additive-genetic correlation estimated by two statistical models (including or not bull × country effect) Models included the fixed effects of contemporary group (herd-year and month of birth), sex of the calf, the covariates age of dam at calving (years) and age of calf at weaning (days), and the random effects genetic-additive maternal and direct, maternal permanent environment and residual. Herdabilidades (of direct effect) were similar in both countries and with moderate magnitude (0.35 and 0.15, respectively). Coefficients of correlation among maternal and direct genetic effects between Brazil and Uruguay were 0.77 and 0.13, respectively, and comparison among models (with and without bull × country effect) showed significant differences. Correlations among classifications (ranking of genetic values) of bulls with progenie in both countries ranged from 0.35 to 0.41 for estimations in one- and two-trait models, respectively. The results suggest the existence of genotype × environment interaction for weight at weaning of Angus populations between Brazil and Uruguay. There is a need of considering interaction in further international genetic evaluations of the breed.

 $Key\ Words:\ beef\ cattle,\ genetic\ correlation,\ genotype\ \times\ environment\ interaction,\ international\ evaluation$

Interação genótipo × país para peso à desmama das populações Angus do Brasil e Uruguai

RESUMO - Foi analisada a existência da interação genótipo × ambiente para o peso à desmama nas populações da raça Angus do Brasil e do Uruguai usando os registros de 73.205 animais (10.257 do Uruguai e 62948 do Brasil) provenientes de 33 e 161 fazendas e 13 e 34 localidades do Uruguai e do Brasil, respectivamente. Utilizou-se modelo animal em análises, uni e bicaráter, considerando o peso à desmama de cada país como caracteres diferentes. Como indicadores da interação, foram utilizados os coeficientes de correlação genético-aditiva diretos e maternos estimados mediante dois modelos estatísticos (incluindo ou não efeito touro × país). Os modelos incluíram os efeitos fixos de grupo de contemporâneos (rodeio, ano e mês de nascimento), sexo do bezerro; as covariáveis idade da mãe ao parto (anos) e do bezerro à desmama (dias); e os efeitos aleatórios genético-aditivos direto e materno, de ambiente permanente da mãe e residual. As herdabilidades (dos efeitos diretos) foram semelhantes em ambos os países e de magnitudes moderadas (0,33 e 0,15, respectivamente). Os coeficientes de correlação entre os efeitos genéticos diretos e maternos entre Brasil e Uruguai foram de 0,77 e 0,13, respectivamente, e a comparação dos modelos (com e sem efeito touro × país) apresentou diferenças significativas. As correlações entre as classificações (*rankings* dos valores genéticos) dos touros com progênie em ambos os países variaram entre 0,35 e 0,41 para as estimações em modelos uni e bi caráter, respectivamente. Os resultados sugerem a existência de interação genótipo × ambiente para o peso à desmama das populações Angus entre Brasil e Uruguai. Há necessidade de se considerar a interação nas futuras avaliações genéticas internacionais da raça.

Palavras-chave: avaliação internacional, correlação genética, gado de corte, interação genétipo \times ambiente

Introduction

The knowledge on the genetic merit of sires in different countries or regions would contribute to increase genetic progress of animal populations, and adjust market prices to breeding values. This information is readily available for a number of dairy breeds. The Interbull Centre in Uppsala, Sweden, centralises the information of country members in a common data set, and genetic evaluations are made by using the MACE (Multiple Across Country Evaluation) procedures (Schaeffer, 1994). Data adjusted from each country by regression of breeding values are newly evaluated and genetic merit of animals are obtained for each country in the test. MACE considers the existence of genotype × environment interaction through genetic correlation between countries, and specific parameters of each country.

In beef cattle, Phocas et al. (2005) estimated genetic parameters and compared different strategies for an international genetic evaluation on Limousin breed. Venot et al. (2007) implemented a genetic evaluation for weaning weight on the same breed among France, Ireland and United Kingdom. In the Americas, de Mattos et al. (2000) and Lee & Bertrand (2002), by using the Hereford breed, concluded that it is possible to perform a joint genetic evaluation for Uruguay, Argentina, Canada and the United States by joining data set, because observed genetic correlations for growth traits among countries were close to 1.0.

Panamerican genetic evaluation was published in 2009. However, in Brazil and Uruguay, genotype × environment interaction was observed for growth traits (Mattos et al., 1997; Cardellino et al., 1997; Souza et al., 1998; Eler et al., 2000; Mercadante et al., 2000; Alencar et al., 2005; Mascioli et al., 2006). Studies comparing populations bred in temperate, subtropical and tropical regions are not common in the literature.

The objective of this study was to assess, by means of different methods, the existence of genotype × environment interaction for weaning weight in the Angus populations of Brazil and Uruguay.

Material and Methods

Data were from the data bases belonging to the National Associations of the Angus breed of Brazil and Uruguay, centralized by PROMEBO (Programa de Melhoramento de Bovinos de Corte) and from the Universidad de la Republica, Uruguay (Facultad de Agronomia). A joint data set with 73,802 animals was created, 10,475 animals from Uruguay

and 63,327 from Brazil. The data set was tested for conectability among contemporary groups (CG, defined by herd-year-month of birth containing at least five animals), using the MILC software developed by Fries & Roso (1997). Not connected contemporary groups, 25 in Uruguay (218 animals) and 76 in Brazil (3,799 animals), were deleted (Table 1). Common bulls with progeny in both countries came from USA, Canada and Argentina. After editing, 43 common bulls with, on average, 90 calves born in Brazil and 19 born in Uruguay, were kept for the analyses. Body weight of calves from Uruguay and Brazil were 34 \pm 3 kg and 32 \pm 2 kg at birth, and 168 \pm 32 kg and 173 \pm 32 kg at weaning performed at 6.3 and 7 months of age, respectively. Seven months were used as average weaning age, adjusting the data by linear regression.

The farms of Brazilian Angus herds belonged to the State of Rio Grande do Sul and were distributed across the whole territory (Figure 1). A similar distribution was observed for the Uruguayan herds, which were representative of the country, from a territorial point of view.

Table 1 - Description of joint data set of Brazil and Uruguay

Item	Uruguay	Brazil	Joint
Local ¹	13	34	47
Herd	33	161	194
Contemporary group	218	867	1,085
Animal	10,257	62,948	73,205
Sire	500	1,926	2,426*
Dams	6,246	36,211	42,457

¹ Localities: Municipalities from the State of Rio Grande do Sul, Brazil, and Departments (Provinces) of Uruguay.

^{* 43} common sires. Total number of calves from common bulls were 3,870 in Brazil and 817 Uruguay.



Figure 1 - Farm location of Angus breeders from Rio Grande do Sul State (Brazil) and Uruguay.

The genotype \times country interaction for weaning weight was studied by using three methods: a) estimation of additive genetic correlations (direct and maternal) between countries (M1); b) study of ranking correlation of common sires in both countries (M2); and c) comparison of univariate models including or not including the random effect of bull-country (M3).

In the first method (M1), also called character model method (Kolmodin et al., 2002), the genetic correlation between weaning weight in both countries, considered as different traits, was estimated through a two-trait analysis. The statistical model included the fixed effect of contemporary group (herd-year and month of birth), sex of the calf and the covariates age of dam at calving (years) and age of calf at weaning (days), plus the additive direct, additive maternal, and the maternal permanent environmental random effects. In this analysis, the covariance between the residuals of the two countries was considered equal to zero. According to Robertson (1959), a genetic correlation less than 0.80 indicates the existence of genotype × environment interaction; for Falconer (1952), the interaction exists when the value of this correlation is less than 1.0.

In M2, the Spearman correlation between rankings of breeding values (conditional to the parameters estimated in M1) for sires common to both countries was calculated with the CORR procedure of SAS (2000). A low correlation indicates that the classification of sires changes from one country to the other, suggesting the existence of genotype × environment interaction.

For M3, the genotype \times environment interaction was evaluated by comparing two one-trait models, a complete and a reduced one, by means of the likelihood ratio test. Additionally to additive direct, additive maternal, and permanent environmental effects, the complete model included a bull-country random effect, while the reduced model did not. A significant difference between the models suggests the existence of genotype \times environment interaction.

(Co)variance components were estimated by using the Restricted Maximum Likelihood Method, with the MTDFREML software (Boldman et al., 1995).

Results and Discussion

Direct additive variance components were similar for both Uruguay ($210.06 \, \mathrm{kg^2}$) and Brazil ($204.65 \, \mathrm{kg^2}$), whereas the maternal additive variance estimate was larger for the Uruguayan ($201.92 \, \mathrm{kg^2}$) Angus population than for Brazilian population ($92.47 \, \mathrm{kg^2}$) (Table 2).

Previous estimates of heritability for direct and maternal additive effects for the Angus population of Uruguay were published by Espasandin et al. (2002), who worked with a subset of the database used in this study. The values obtained by these authors varied from 0.38 to 0.49 and from 0.27 to 0.33 for direct and maternal genetic effects, respectively, using REML methods and Gibbs sampling.

Direct heritability was moderate and similar for the two countries (0.35 and 0.34). Maternal heritabilities were lower, with values of 0.33 for Uruguay and 0.15 for Brazil. The heritability estimates obtained for the Brazilian Angus population were superior for direct effects (0.34) and lower for maternal effects (0.15) to the published values estimated by Everling et al. (2001) (0.23 and 0.29, for direct and maternal effects, respectively) for an Angus – Nellore population in Brazil.

Previous studies carried out in Brazil showed evidences of genotype × environment interaction among some regions of the country in different beef cattle breeds. Simonelli (2004), when analyzing weaning weight of Nellore calves of five regions in the State of Mato Grosso do Sul, observed homogeneity for the direct and maternal additive variances and for direct and maternal heritabilities among some of the regions, but heterogeneity for others. Toral et al. (2004), also working with weaning weight of Nellore calves of some regions of the State of Mato Grosso do Sul, observed that the direct additive and the residual components of variance

Table 2 - Variance (diagonal) and covariance (above diagonal) components, heritability (diagonal, within parenthesis) and genetic correlation (below diagonal) for weaning weight estimated by Method 1

Effect	Effect			
	Direct additive genetic effect in Uruguay	Direct additive genetic effect in Brazil	Maternal additive genetic effect in Uruguay	Maternal additive genetic effect in Brazil
Direct additive genetic effect in Uruguay	210.06(0.35)	158.66	-108.85	-71.83
Direct additive genetic effect in Brazil	0.77	204.65(0.34)	20.31	-96.66
Maternal additive genetic effect in Uruguay	-0.53	0.10	201.92(0.33)	17.71
Maternal additive genetic effect in Brazil	-0.52	-0.70	0.13	92.47(0.15)

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were different among regions and, consequently, direct heritability varied from 0.36 to 0.59.

The estimated genetic correlation for the direct additive genetic effect for weaning weight between the countries was 0.77, and that for the maternal effects was 0.13. These values suggest the existence of genotype × country interaction for this trait, for both direct and maternal additive effects. This finding differs from the results obtained by De Mattos et al. (2000) and Lee & Bertrand (2002) for the Hereford populations of Uruguay, Argentina, Canada and the United States, and by Donoghue & Bertrand (2004) for the Charolais populations of Australia, Canada, New Zealand and the United States. These studies. which did not include data from Brazil, found high genetic correlations for weaning weight among countries, suggesting the absence of genotype × country interaction. However, Simonelli (2004) observed genetic correlations varying from 0.04 to 0.14 for direct effect and from 0.01 to 0.09 for maternal genetic effect, for weaning weight of Nellore calves of five regions of the State of Mato Grosso do Sul, Brazil, indicating the existence of genotype × environment interaction. Toral et al. (2004) estimated Pearson's correlation of weaning weight breeding values of Nellore animals from several regions of the State of Mato Grosso do Sul, Brazil; these breeding values were estimated for each region of birth separately and for all regions together. The correlations varied from 0.29 to 0.46 for all pairs of regions, from 0.85 to 0.89 for each region with all regions together, showing also evidences of genotype × environment interaction. In this study, the low values of Pearson's correlation between breeding values of the two countries suggest that weaning weight of Angus cattle of Brazil and Uruguay is affected by the interaction.

The correlation between maternal and direct genetic effects within each country, with values of -0.53 and -0.70 for Uruguay and Brazil, respectively, showed similar trends to those (-0.74 to -0.30) observed by Donoghue & Bertrand (2004).

A practical visualization of the genotype \times environment interaction can be seen through the Spearman's rank correlation between the breeding values of bulls common to both countries, estimated with the two-trait model. The value obtained in this study (0.48) indicates relevant changes in the classifications of the bulls from one country to the other.

There are some consequences in ranking and breeding value change when using separate, national evaluations (one-trait model) for each country, or a two-trait analysis considering weaning weight in each country as a different trait, using a sub sample of bulls common to both countries (Table 3).

Spearman correlations were 0.94 in Brazil (rankings 1 and 3), but only 0.35 in Uruguay (rankings 2 and 4), showing that for Brazil, the rankings of the bulls are the same regardless to the type of analysis (one-trait for each country separately or two-trait considering weaning weight as different traits in each country), whereas for Uruguay the rankings were different. Probably, the differences were due to the higher number of observations in Brazil (86% of the total amount of data) contributing to the two-trait analysis.

Despite the high correlation between the rankings of the bulls in Brazil, based on their breeding values obtained in both analyses, only 36% of the bulls of the sub sample with progenies in both countries kept their place. In Uruguay, all bulls changed position when rankings obtained in the one-trait separated analysis and the two-trait analysis, were compared. Examples of drastic changes

Table 3 - Breeding values (kg) and rankings (within parentheses) of bulls common to Uruguay and Brazil, in one and two-trait analysis

	One-trait analysis		Two-trait analysis		
Bull	Ranking 1- Brazil	Ranking 2 - Uruguay	Ranking 3 - Brazil	Ranking 4 - Uruguay	
A	26.2 (1)	12.1 (5)	27.2 (1)	17.7 (3)	
В	22.7 (2)	14.2 (4)	22,9 (2)	18.4 (2)	
C	13.5 (3)	2.4 (11)	13.6 (4)	11.8 (4)	
D	13.4 (4)	15.7 (3)	14.6 (3)	21.2 (1)	
E	9.8 (5)	22.6 (1)	9.9 (5)	7.7 (8)	
F	7.5 (6)	6.4 (7)	7.5 (7)	5.9 (10)	
G	6.6 (7)	4.0 (9)	8.8 (6)	8.7 (5)	
Н	4.9 (8)	1.6 (13)	4.9 (9)	3.7 (12)	
I	4.6 (9)	18.5 (2)	4.8 (10)	4.1 (11)	
J	3.0 (10)	5.0 (8)	2.8 (13)	1.8 (14)	
K	2.9 (11)	1.6 (12)	6.7 (8)	2.8 (13)	
L	2.1 (12)	2.9 (10)	3.9 (12)	8.1 (7)	
M	-0.5 (13)	1.2 (14)	4.2 (11)	8.7 (6)	
N	-6.2 (14)	11.9 (6)	-0.99 (14)	6.1 (9)	

can be seen for bulls E and I, which moved from the first and second places, respectively, in the Uruguayan evaluation, to positions 8 and 12 in the two-trait analysis. Toral et al. (2004), working with the Nellore breed in the State of Mato Grosso do Sul also verified changes in the rankings of bulls according to their breeding values for weaning weight, when the evaluations were made for all the regions together or in each region separately.

The correlation between rankings 1 (Brazil) and 2 (Uruguay) was 0.43, showing different rankings of bulls in Brazil and Uruguay when the analysis was for each country separately.

In Brazil, negative breeding values were observed in both two-trait and one-trait separate analyses, but with more emphasis in the two-trait analysis. The observed range of breeding values for all of the sires (common and non common) was different between countries, with values ranging from –13.4 to +10.5 kg in Brazil and +2.2 to +21.4 kg in Uruguay (joint analysis).

The common bulls displayed superior breeding values in Uruguay when compared to those estimated for Brazil. While for the latter country the average breeding values were negative (-4.1 kg) or close to zero (+0.6 kg) for the maternal and the direct effects, respectively, in Uruguay the estimates were positive and clearly different from the "Brazilian" values (+7.7 kg and +9.4 kg, respectively), suggesting effects of genotype × environment interactions.

These results show the importance of the use of a genetic base of reference in each country for the estimation of breeding values, as well as the contribution of the information from one country to the other in the multi-trait evaluations.

It should be noted that most common bulls come originally from US and Canada, arising a question on the consequences of using common genotypes produced (selected) under the conditions of Brazil and/or Uruguay instead of the imported bulls. At first, because of the results, it could be inferred that animals selected for the predominant conditions of their native countries (United States and Canada) seem to be less adapted to the environmental production conditions of Brazil.

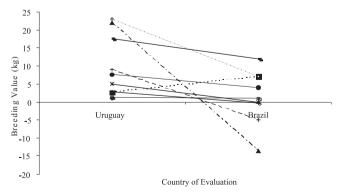
As reported by Espasandin (2005), some differences in climatic condition exist between Rio Grande do Sul and Uruguay, as for example the minimum winter temperature (13.5°C and 11°C in Brazil and Uruguay, respectively) or the accumulated annual precipitations (1,300 and 1,700 mm). These climatic differences may be expressed through different performance for the same genotypes, as observed in the available sample of animals. As previously mentioned, the differences can be observed when the common bulls are classified in relation to the total of bulls within each country.

Whereas in Uruguay 19% of the common bulls were within the superior 5% bulls for the direct breeding value, in Brazil only 2% of them were in this place.

Although these data represent a limited sample of the bulls used in the two countries, it is readily observed that the same genetic merit of the bull can differ according to the environment in which was evaluated. This trend agrees with the findings by Cardellino et al. (1997), in which 19% and 31% of the American bulls (Hereford and Angus, respectively) evaluated in Brazil presented negative EPD for weaning weight. According to these authors, the genetic progress achieved could have been superior if genotype × environment interaction had been considered.

It is possible that, in some cases, the genotypes adapted to the North American production systems are not suited to grazing systems in Brazilian tropical conditions. Therefore, higher genetic benefit would be obtained if sires selected under conditions similar to the conditions in which their progenies will be reared, are used. Nevertheless, in many countries it is necessary to improve the genetics of the herds by import of superior genetic material. In these cases, it is important to know the environmental conditions where the sires were selected, giving priority to the superior genotypes in production systems similar to those of the country or region where they will be mated. In many cases this information is not easily available, implying increased risks or low accuracy in the purchase of these animals. Variables as the stability of the bulls could offer orientation in the decision of importing new genetic materials.

Not all bulls behave in the same manner when exposed to two different environments (Figure 2). It is illustrated in Figure 2 the stability of breeding values for weaning weight across countries, using the ten common bulls with the highest number of progeny (average of 141 and 49 calves per sire in Brazil and Uruguay, respectively).



Filled lines = bulls with more variable breeding values; discontinuous trace lines = more steady bulls.

Figure 2 - Breeding values of the 10 common bulls with largest progeny groups, obtained by two-trait analysis.

There is a variability or dispersion observed in the behaviour of the progenies of common bulls in each country, showing once more the interaction of the genotypes with the environments of each country.

Stability is related to the variability of the genotypes throughout different environments. If the additive genetic correlations among different environments are high, the genotype will offer greater stability. Higher stability is synonymous of lower environmental sensibility of these genotypes. Lin & Togashi (2002) consider the study of the stability as a strategy to be developed when selecting bulls in the presence of genotype × environment interaction. Sires that generate more similar progeny in different environments are considered more stable, still under interaction. Higher stability means lower sensitivity of the genotypes to environmental influences. However, the steadiest genotypes do not necessarily imply better performance in all environments. Strategies that optimize the genetic improvement would have to consider the following elements: performance and stability of the genotypes evaluated in different environments.

The results in this study suggest that the existence of genotype × environment interaction at the country level should not be ignored when planning an international genetic evaluation for the Angus breed, involving Brazil and Uruguay. This is in contrast to Meyer (1995), who verified that the interaction could be disregarded in the joint evaluation of the Angus breed for Australia and New Zealand. For Brazil and Uruguay, the implementation of an evaluation assuming absence of interaction with the environment could bring severe consequences for the genetic improvement of the Angus population in the region.

The complete (with bull-country random effect) and the reduced (without the bull-country effect) models are different (P<0.001), indicating the existence of genotype \times environment interaction, for the studied trait.

Conclusions

Genotype × country interaction for weaning weight between the Angus populations of Brazil and Uruguay are identified. As a consequence, a prospective joint genetic evaluation needs to consider this interaction to increase the genetic progress of the breed in the two countries.

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