

Sire \times stud interaction for body measurement traits in Spanish Purebred horses¹

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ABSTRACT: The mating policy for Spanish Purebred horses encourages the same or closely related stallions to be used for reproduction across studs differing in environments. Stallions may perform differently across studs, and if so, adjustment for the sire \times stud (ss) interaction is recommended. However, there are no studies available that analyzed the influence of ss interaction on estimation of genetic parameters in horses. This research is aimed at assessing the implications of including ss interaction in models fitted for the estimation of genetic parameters for traits under selection using 8 body measurements in Spanish Purebred (Andalusian) horses: height at withers, height at chest, leg length, body length, width of chest, heart girth circumference, knee perimeter, and cannon bone circumference. Body measurements were available for 11,894 horses. Genetic parameters and EBV were estimated using animal models by REML. The inclusion of the ss interaction gives reduced estimates of heritability. Generally, the genetic correlations estimated using the

models including the ss interaction were greater than those obtained using the simpler model. Estimates for the ss variance as a proportion of the total phenotypic variance ranged from 0.02 (height at withers) to 0.11 (width of chest). Estimates between the ss interaction correlations associated with each body measurement were positive, significant, and from moderate to low. The range of EBV estimated using the model including the ss interaction decreased with respect to those estimated using the simpler model, and the EBV ranking order was affected. The models including ss interaction fitted significantly better. Therefore, the genetic parameters estimated using the ss interaction may be more realistic, and the obtained (co)variances may be assumed to be closer to the true population parameters. This interaction may result from selective decisions or preferential management practices causing greater similarity between the progeny of a sire in the same stud. It is therefore advisable to include it in genetic models used in horse breeding schemes.

Key words: genetic parameter, genotype \times environment interaction, horse breeding, zoometry

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INTRODUCTION

The Spanish Purebred (SPB) horse, also called the Andalusian horse, is the most recognized horse breed in Spain (Valera et al., 2005). The SPB horse Breeders Association has recently implemented a breeding

program including conformation (Molina et al., 1999; Gomez et al., 2008), reproductive (Valera et al., 2006), and functional traits (Miró et al., 2006; Molina et al., 2008; Valera et al., 2008). Mating policy encourages the same or closely related stallions to be used across studs differing in environments. It is possible that sires may perform differently across studs, thus requiring the inclusion of the sire \times stud (ss) interaction in evaluation models to minimize any bias from preferential mating and to avoid overestimating the accuracy of sire evaluation, particularly for sires that are used only in a limited number of studs (Meyer, 1987).

The influence of an environmental effect linked to sire groups on estimates of genetic parameters for traits under selection has been widely studied in other species such as beef cattle (Robinson, 1996a,b, 2007; Gutiérrez et al., 2006). Spurious sire \times contemporary group interaction can be caused by nonrandom mating among

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herds (Notter et al., 1992), management effects within contemporary groups not recorded or not fitted in the model (Meyer, 1987; Berweger-Baschnagel et al., 1999), or misidentification of the animals (Lee and Pollak, 1997a,b; Senneke et al., 2004).

We present here estimates of the variance due to the ss interaction in breeding evaluation models fitted to body measurements in SPB horses. These estimates are used to investigate the influence of the ss interaction on EBV and estimated genetic parameters (heritability and genetic correlation). By including the ss interaction, some of the nongenetic variance inflating the estimates of genetic parameters was removed, and thus, the reliability of EBV was improved.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database (Spanish Military Cavalry services of the Spanish Ministry of Defense).

In the studbook of the SPB horse, foals are identified and are subject to a paternity test before they can be registered. Paternity tests have been required in the breed since 1984, thus giving confidence in the registered genealogies. Breeders select their horses in the studs (usually following breed standard and body development). Horses have to pass a morphological assessment test in their stud before they are registered in the studbook as reproductive horses. Horses can be assessed at any time after they are 3 yr old. During the assessment, horses (both stallions and mares) are evaluated for breed quality, conformation, and movements. Additionally, 8 body measurements are obtained and included in the breeding program.

The original database included 16,472 measured animals. All of them were obtained from the data sets of the Spanish Military Cavalry services of the Spanish Ministry of Defense. Genetic connectedness between animals and studs was tested following the methodologies proposed by Rekaya et al. (1999), Nakaoka et al. (2008), and Thoren et al. (2008), among others. Our results have shown that there are no disconnected studs in the sample. Nevertheless, an increased level of genetic connectedness between studs must be ensured for the estimation of ss interaction. So, the connectedness level of the sample with all of the generations was directly calculated estimating the coancestry coefficient between all of the animals included in this analysis. It was calculated using the Endog package (Gutiérrez and Goyache, 2005). Then, mean coancestry between animals for each pair of studs was estimated (537×537 studs). The mean coancestry of the animals belonging to each stud with the rest of population was 0.066, ranging between 0.034 and 0.100. The coancestry between animals belonging to a stud and the animals belonging to other studs included in the sample has a minimum value of 0.007, with an average value of 0.067 and a maximum of 0.434. Although the genetic

connectedness between studs was adequate, to ensure the greatest genetic connectedness between them, the studs with a mean coancestry value with the others less than 0.05 were excluded. Sire × stud combinations with less than 5 measured animals were also excluded. The final database included body measurements of 11,894 SPB horses (40.9% males and 59.1% females). They represented 56.14% of the animals eligible for evaluation during the analyzed years. Data were collected during morphological assessment of the horses in 2004 and 2005. The horses were on average 3.9 yr old, ranging between 3 and 11 yr. The number of times in which the sires born in a herd acted as fathers in other herds averaged 24.3, and the ratio of foreign father/foals averaged 19.93. The mean value of the genetic similarity was 15.97% [similar to that reported by Thoren et al. (2008) in European Sport horses].

Eight body measurements were recorded by trained inspectors from the studbook (Figure 1): height at withers (**HW**), height at chest (**HC**), leg length (**LL**), body length (**BL**), width of chest (**WC**), heart girth circumference (**HGC**), knee perimeter (**KP**), and cannon bone circumference (**CBC**). The measurements were obtained directly from the left side of the horse using a Lydthin stick and tape measure; the horses were put on a level and hard floor and led by personnel from the respective studs during this process (Figure 1).

The pedigree file used in the genetic analysis included at least 4 generations for each measured horse. The total number of horses in the pedigree was 30,753 (4,476 sires and 14,393 mares). A total of 2,627 sires and 9,516 mares had progeny in the data set. The number of sires and dams with their own record was 2 and 11, respectively, and the average number of progeny records per sire was 4.53. A total of 481 sires were connective animals (with progeny in more than 1 stud), with a mean number of progeny of 11.88. The animals were born in 498 studs with an average number of progeny of 19.9.

Genetic parameters (heritability and genetic correlations) and EBV were estimated using animal models by REML using the VCE software v.5.0 (Kovac et al., 2002). Preliminary statistical analyses were carried out using SAS/STAT (results not included; SAS Inst. Inc., Cary, NC) and showed that, consistent with Molina et al. (1999), the year of scoring did not have significant influence on the data. As a consequence, all of the models fitted here included the following fixed effects: sex of horse (2 levels: male and female), age group (5 levels: 3, 4, 5, 6, and ≥ 7 yr old), and stud (498 levels). Two models were considered:

Model 1: Multivariate animal model that included the additive genetic effect, the covariance between trait additive genetic effects, and the residual as random effects:

$$y = \mu + \text{sex} + \text{age-group} + \text{stud} + \text{additive genetic effect} + \text{covariance between trait additive genetic effects} + \text{residual error.}$$

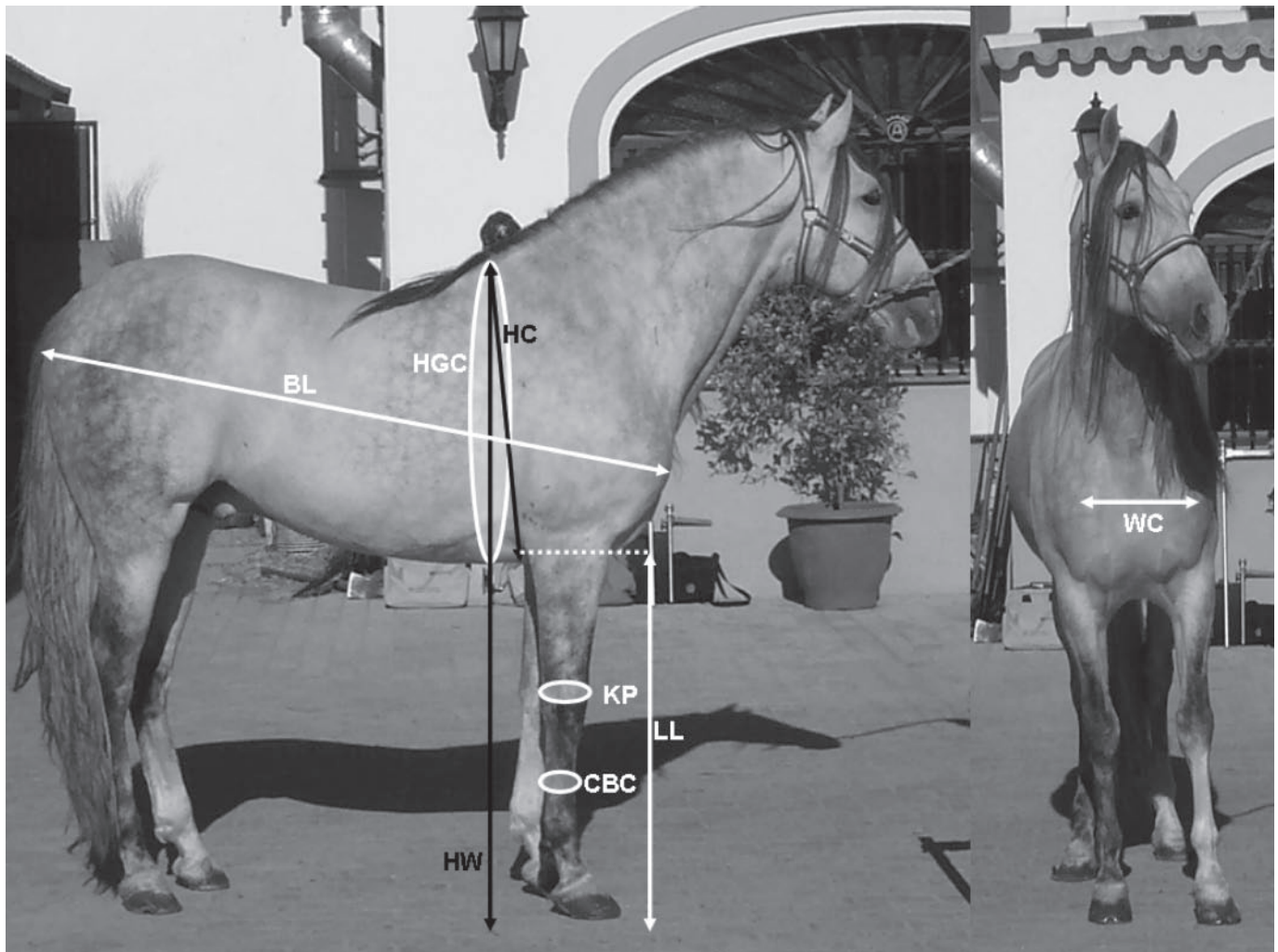


Figure 1. Representation of the 8 analyzed body measurements in Spanish Purebred horses. HW is height at withers, HC is height at chest, LL is leg length, BL is body length, WC is width of chest, HGC is heart girth circumference, KP is knee perimeter, and CBC is cannon bone circumference.

Model 2: Similar to model 1 adding the ss interaction and the ss covariance as other random environmental effects independent of the additive relationship matrix.

The models fitted were compared using the likelihood ratio test (**LRT**; Swalve, 1993). The LRT is a statistical test of the goodness-of-fit between 2 models, where a complex model is compared with a simpler submodel to see if the complex model fits significantly better. The LRT was computed as $LRT = 2(\ln L_1 - \ln L_2)$, where L_1 is the likelihood value for the simpler submodel and L_2 is the likelihood value for the complex model. The LRT approximately follows a chi-square distribution, with the number of additional parameters in the complex model as degrees of freedom.

The EBV were estimated using the models described above. Spearman correlations between the best 100 EBV in the ranking estimated from model 1 and EBV from the same horses estimated with model 2 were computed. Spearman correlations were also computed between the worst 100 EBV with model 1 and the EBV of the same animals with model 2 in the ranking. Statistica

for Windows (Statsoft Inc., Tulsa, OK) was used. The EBV estimated using model 1 were established as the basis of the comparisons. Mean values and variations were also computed for the EBV of the best 100 and worst 100 ranked horses within each model and body measurement.

RESULTS

All of the body measurements analyzed showed moderate to low deviations, with WC showing the greatest CV and HW the least (Table 1). The ss variance as a proportion of the total phenotypic variance from model 2 (Table 2) ranged from 0.02 (HW) to 0.11 (WC). The LRT showed that model 2 fitted significantly better than model 1 ($P < 0.01$) regardless of the body measurement analyzed. The estimates of heritability obtained using model 1 (Table 2) ranged from 0.31 (LL) to 0.58 (HW). The estimates of heritability obtained using model 2 ranged from 0.18 (WC) to 0.53 (HW). So, by fitting additional terms in the model, the total observed variation is partitioned over the previous terms (including

Table 1. Mean ± SEM and CV of 8 body measurements (cm) in female and male Spanish Purebred horses

Trait ¹	Females ²		Males ²	
	\bar{x} ± SEM	CV, %	\bar{x} ± SEM	CV, %
HW	1.57 ± 0.0005	2.62	1.59 ± 0.0006	2.60
HC	0.74 ± 0.0004	4.65	0.73 ± 0.0005	4.94
LL	0.83 ± 0.0004	4.44	0.85 ± 0.0006	4.53
BL	1.59 ± 0.0006	3.23	1.59 ± 0.0007	3.20
WC	0.43 ± 0.0004	7.80	0.44 ± 0.0004	6.98
HGC	1.92 ± 0.0011	4.73	1.89 ± 0.0011	3.94
KP	0.31 ± 0.0002	4.16	0.33 ± 0.0002	4.39
CBC	0.20 ± 0.0001	5.35	0.21 ± 0.0002	5.48

¹Trait names are as follows: HW is height at withers, HC is height at chest, LL is leg length, BL is body length, WC is width of chest, HGC is heart girth circumference, KP is knee perimeter, and CBC is cannon bone circumference.

²n = 7,029 females and 4,865 males.

residual) and also the additional terms. Genetic correlations estimated using model 1 ranged between 0.07 (HC-LL) and 0.82 (HW-BL), whereas those estimated using model 2 varied between 0.30 (WC-LL) and 0.92 (CBC-KP).

Correlations estimated between the ss effects associated with each body measurement analyzed (model 2; Table 3) were positive, significant, and from moderate to low, varying between 0.18 (HC-WC) and 0.63 (HC-LL and WC-KP). However, the correlations related to LL were negative and low, ranging from -0.63 (HC-LL) to 0.36 (HW-LL).

A decrease in the variation of the EBV estimated using model 2 was assessed with respect to those estimated using model 1 (Table 4). The largest decrease in the variation was found for HC, WC, and HGC. Most Spearman correlations between the EBV of the 100 best horses and the correlations between the EBV of the 100 worst ones were less than 0.95, varying from 0.60 for WC in the 100 worst set to 0.94 for HW in the 100 best set.

DISCUSSION

Although selection within most horse breeds is based mainly on their performance, conformation and gaits still have considerable economic importance and play an important role in judging horses for registration in the Studbook (Bowling and Ruvinsky, 2000). The importance of conformation traits in SPB horses is still greater than in sport horse breeds because SPB horses are also selected for their breed quality. Nowadays, the genetic parameters and EBV estimated for the body measurements are being used to develop and control the linear assessment (similar to those used in dairy cattle), following Janssens et al. (2004).

In general, the estimates of genetic parameters reported in the present study for the body measurements analyzed in SPB horses are consistent with those reported in the literature for the same breed (Molina et

al., 1999) and for other riding populations (Torzynski and Szwaczkowski, 1999; Zechner et al., 2001; Dario et al., 2006).

The existence of genotype × environment interaction in a population indicates that different genotypes respond to environmental change in different ways. Although still largely undocumented, a clear pattern seems to exist supporting that selection in more than one environment is ineffective at improving performance in any of the environments. The ss interaction occurs when the difference in progeny performance among sires is dependent upon some factor of the environment under which the progeny were compared. Therefore, where a sire is used in a variety of studs, ss interactions will need to be included in an animal evaluation model as indicated by Naser et al. (1995) for Bonsmara cattle. Estimates of ss interaction are obtained by comparing the relative performance of some sires in different studs. Thus, the extent and nature of sire connections among studs may influence the precision of estimates of ss interaction from field data. Genetic connectedness between animals and studs were analyzed (results not shown) and was shown to be adequate for this type of analysis.

No other study has estimated the effect of the ss interaction on genetic parameters and EBV for traits under selection in a horse population. We used a population including horses with records for all of the body measurements analyzed and full genealogies known and proven via paternity tests up to 4 generations back. The available data give us confidence that misidentification is not the cause, or at least not the major cause, of the identified ss interaction. Moreover, nonrandom mating among studs or other selection decisions reported as possible causes of ss interaction (Notter et al., 1992) do probably arise when breeders select horses to act as parents within a stud. In the SPB horse, selected horses must be morphologically assessed by the breeders associations before being considered as possible parents in the studbook.

Table 2. Genetic parameters (heritabilities and genetic correlations for model 1, above diagonal and model 2, below diagonal), sire \times stud variance as a proportion of phenotypic variance (s^2), and likelihood ratio test (LRT), estimated with multivariate animal models in Spanish Purebred horses

Trait ¹	Model		s^2	LRT	HW	HC	LL	BL	WC	HGC	KP	CBC
	1	2										
HW	0.58 \pm 0.024	0.53 \pm 0.029	0.02 \pm 0.007	19.25**		0.69 \pm 0.026	0.77 \pm 0.020	0.82 \pm 0.018	0.40 \pm 0.035	0.55 \pm 0.029	0.79 \pm 0.020	0.52 \pm 0.028
HC	0.36 \pm 0.020	0.23 \pm 0.022	0.07 \pm 0.008	128.11***	0.78 \pm 0.033		0.07 \pm 0.050	0.57 \pm 0.033	0.40 \pm 0.039	0.56 \pm 0.033	0.58 \pm 0.033	0.31 \pm 0.036
LL	0.31 \pm 0.021	0.22 \pm 0.021	0.05 \pm 0.007	55.15***	0.85 \pm 0.024	0.33 \pm 0.078		0.58 \pm 0.038	0.30 \pm 0.089	0.25 \pm 0.044	0.56 \pm 0.033	0.42 \pm 0.041
BL	0.45 \pm 0.019	0.36 \pm 0.025	0.04 \pm 0.008	56.05***	0.87 \pm 0.020	0.63 \pm 0.047	0.75 \pm 0.047		0.50 \pm 0.034	0.53 \pm 0.032	0.79 \pm 0.022	0.63 \pm 0.032
WC	0.41 \pm 0.021	0.18 \pm 0.024	0.11 \pm 0.009	197.87***	0.54 \pm 0.065	0.58 \pm 0.068	0.30 \pm 0.089	0.63 \pm 0.062		0.72 \pm 0.025	0.55 \pm 0.034	0.60 \pm 0.032
HGC	0.45 \pm 0.020	0.28 \pm 0.023	0.09 \pm 0.008	195.47***	0.61 \pm 0.042	0.71 \pm 0.053	0.32 \pm 0.067	0.61 \pm 0.046	0.84 \pm 0.042		0.63 \pm 0.089	0.57 \pm 0.031
KP	0.43 \pm 0.020	0.33 \pm 0.023	0.03 \pm 0.007	66.90***	0.84 \pm 0.024	0.67 \pm 0.045	0.72 \pm 0.047	0.82 \pm 0.027	0.69 \pm 0.062	0.66 \pm 0.042		0.81 \pm 0.022
CBC	0.46 \pm 0.019	0.31 \pm 0.025	0.07 \pm 0.008	147.66***	0.65 \pm 0.041	0.44 \pm 0.061	0.69 \pm 0.054	0.78 \pm 0.039	0.74 \pm 0.048	0.67 \pm 0.046	0.92 \pm 0.024	

¹Trait names are as follows: HW is height at withers, HC is height at chest, LL is leg length, BL is body length, WC is width of chest, HGC is heart girth circumference, KP is knee perimeter, and CBC is cannon bone circumference.
 ** $P < 0.01$ and *** $P < 0.001$.

Table 3. Estimates for the correlation between sire × stud for 8 analyzed body measurements in Spanish Purebred horses

Trait ^{1,2}	HC	LL	BL	WC	HGC	KP	CBC
HW	0.38 ± 0.12	0.36 ± 0.15	0.30 ± 0.13	0.26 ± 0.12NS	0.53 ± 0.11	0.34 ± 0.14	0.12 ± 0.12NS
HC		-0.63 ± 0.08	0.38 ± 0.09	0.18 ± 0.07	0.33 ± 0.06	0.30 ± 0.12	0.08 ± 0.07NS
LL			-0.12 ± 0.14NS	-0.05 ± 0.07NS	0.06 ± 0.08NS	-0.14 ± 0.15NS	-0.18 ± 0.10NS
BL				0.37 ± 0.08	0.32 ± 0.08	0.56 ± 0.12	0.19 ± 0.09
WC					0.54 ± 0.04	0.63 ± 0.09	0.31 ± 0.06
HGC						0.63 ± 0.09	0.35 ± 0.07
KP							0.43 ± 0.09

¹Trait names are as follows: HW is height at withers, HC is height at chest, LL is leg length, BL is body length, WC is width of chest, HGC is heart girth circumference, KP is knee perimeter, and CBC is cannon bone circumference.

²All of the estimates were significant, except those marked with NS (nonsignificant; $P > 0.05$).

Inclusion of the ss interaction in multivariate models, in general, reduces the estimates of heritability and increases correlations between the additive genetic effects of the different traits. The ss interaction was consistent for all of the body measurements analyzed. As expected, the decrease in heritability exceeds the portion of the phenotypic variances explained by the ss interaction. According to the results of the LRT, model 2, which included the ss interaction, performed significantly better than model 1, which did not include this interaction. Therefore, the genetic parameters estimated using model 2 may be more realistic and the (co)variance estimates may be assumed to be closer to the true population parameters than those obtained with model 1. If the ss interaction is not included in the model, additive genetic variance is inflated, but residual variance does not change substantially. This leads to overestimation of heritability and underestimation of genetic correlations between body measurements.

Inclusion of the ss interaction also affected substantially the estimates of EBV. The variation of estimated EBV was greater when the ss interaction was not included in the genetic analysis (model 1). The ranking order of EBV in SPB horses is also affected by the inclusion of the ss interaction. This could be partially caused by the change in the estimates of the genetic pa-

rameters, but also may be due to better environmental adjustment of the performance of the evaluated horses. Overall, the ss interaction cannot be considered negligible and should be taken into account in estimation models. The ss interaction should be used to minimize bias in preferential mating and to avoid overestimating the accuracy of sire evaluations, mainly for sires that are used in only a limited number of studs (Meyer, 1987). Therefore, ss interaction should be used until enough evidence is available that definitely identifies the environmental effects as the cause of the inflated estimates of additive variances.

One question arising from these analyses is why does the ss interaction not affect all of the body measurements to the same extent? Management practices are responsible. Three body measurements related to body width (HC, WC, and HGC) showed the largest decrease in heritability. They have also the greatest variation for EBV. Nevertheless, the body measurement with the least decrease was HW, which was the most homogeneous trait in the sample analyzed ($CV = 2.6\%$). The breed standard for the SPB horse excludes horses smaller than 1.55 m for males and 1.53 m for females, and the selection for this body measurement is assumed to be the same for most SPB breeders. However, HW is not desirable if not accompanied by sufficient body de-

Table 4. Range of the EBV and Spearman correlations between the EBV estimated for 100 best and 100 worst horses in a model with (model 2) and without (model 1) the sire × stud interaction in Spanish Purebred horses

Trait ¹	Model 1		Model 2		Spearman correlation ²	
	100 best	100 worst	100 best	100 worst	100 best	100 worst
HW	6.94	-6.07	6.51	-5.73	0.94	0.93
HC	4.50	-4.32	3.12	-2.98	0.80	0.87
LL	3.10	-4.31	2.47	-3.42	0.80	0.90
BL	6.72	-8.05	5.48	-6.81	0.82	0.88
WC	4.20	-3.55	2.52	-2.40	0.80	0.60
HGC	12.10	-11.05	8.55	-8.21	0.72	0.73
KP	2.05	-1.93	1.74	-1.70	0.86	0.84
CBC	2.02	-1.55	1.53	-1.53	0.87	0.70

¹Trait names (cm) are as follows: HW is height at withers, HC is height at chest, LL is leg length, BL is body length, WC is width of chest, HGC is heart girth circumference, KP is knee perimeter, and CBC is cannon bone circumference.

²Model 1 was the basis of the comparison.

velopment, particularly body depth, and breeders seem to make their selection decisions by taking into account traits that characterize this. Moreover, correlations between the ss interactions affecting HC, WC, and HGC are not high (ranging between 0.18 and 0.54) except for the pair WC-HGC, suggesting that selective mating or preferential management practices carried out by the breeders are different for these body measurements.

Weaknesses in identification have been attributed as a source of spurious sire \times year interaction in beef cattle (Lee and Pollak, 1997a,b; Senneke et al., 2004). The horses analyzed here would not have identification or genealogical errors because of the paternity test before registration and individual electronic identification systems. Consistent with the scenario reported by Gutiérrez et al. (2006), if identification errors were the sole cause of the environmental effects linked to sire estimated here, the values of correlations found between the ss interaction estimated for each of the analyzed body measurements would be close to 1. The ss interaction estimated in this study ranged between 0.18 (HC-WC) and -0.63 (HC-LL); therefore, it is not the sole cause of the environmental effects linked to sire in the SPB horses. Robinson (1996a) suggested that a possible cause of such an environmental effect is the variation existing between sires of different genetic origins. This seems not to be important in most of the reviewed bibliography. Other explanations for the ss interaction are a possible unadjusted influence of both selective matings and preferential management practices within a contemporary group (Meyer, 1987; Notter et al., 1992; Berweger-Baschnagel et al., 1999). In the data available in this study, all of the studs and breeders may have planned to use some sires only on a given type of dam so as to obtain a given conformation. This may produce environmental covariance between the daughters of a given sire within a stud of SPB horses because of preferential treatment. It has been reported in dairy cattle as being possibly more important to cause a sire \times comparison-group interaction when some sires are used and evaluated in a small number of herds (Powell et al., 1994). This argument may be compatible with the usual SPB breeding practices, thus leading to a more intense effect of the environmental (co)variances existing among sires and studs, which affects the estimation of genetic parameters and EBV.

Our study provides evidence of environmental ss interaction affecting the estimation of genetic parameters and EBV for 8 body measurements in SPB horses. In this breed, the environmental ss interaction mainly affects those traits characterizing body width. Even though causes of this environmental effect remain unidentified, our results suggest that a selective decision process causes nonrandom mating among studs and preferential management practices, and they cause greater similarity between the progeny of a sire in the same stud. Therefore, the implementation of genetic models for body measurement must include the ss in-

teraction in a horse breeding scheme to correct for this effect in the genetic selection procedures.

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