

Genetic parameters for canalization analysis of morphological traits in the Pura Raza Español horse

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Abstract

Measurements from 13 different morphological traits of importance in the Pura Raza Español (PRE) horse were used to estimate genetic and environmental parameters following a heteroscedastic model in which data were assigned to stallions. Data sets used ranged from 20,610 (*height at withers*) to 48,486 measurements (*length of shoulder*), and the number of animals analysed in the pedigrees varied from 17,662 (*height at withers*) to 23,962 (*dorsal–sternal diameter*). Results of heritabilities of the traits varied from 0.09 (*width of chest* and *upper neck line*) to 0.30 (*muscular development*). Further, genetic correlations between traits and their environmental variability were estimated, obtaining values from -0.56 (*muscular development*) to 0.69 (*height at withers*). Also, predicted breeding values for the mean and for the environmental variability were obtained for all horses in the pedigrees, providing individual information about not only the expected phenotypic value of their offspring but also the expected heterogeneity among them. Results proved the possibility of improving morphological traits and reducing the heterogeneity of offspring at a time by the selection of animals and levels of systematic effects.

KEYWORDS

body conformation, environmental variability, equine

1 | INTRODUCTION

Selection objectives for domestic animals are constantly adapting to major changes in production, the market and society. While some have historically focused on increased production (prolificacy, milk production, birthweight, etc.), others are oriented towards improving functional characteristics. Further, selection programmes also seek to integrate other objectives such as robustness, which is defined as the ability to maintain production potential under a wide variety of environmental conditions, or resilience, which is the maintenance of, or rapid return to, the initial state of performance despite environmental perturbations (Bodin et al., 2010; Lung et al., 2020). The possibility of increasing the robustness of

a phenotype against genetic or environmental disturbance is known as canalization (Bodin et al., 2010). Several papers have demonstrated that environmental variability can be controlled in species such as mice (Formoso-Rafferty et al., 2016, 2017), rabbit (Garreau et al., 2008) and sheep (SanCristobal-Gaudy et al., 2001) and mainly in production variables, as in the case of birthweight or litter size. Some of these studies involved divergent selection experiments or simulations (Tatliyer et al., 2019). However, studies of canalization in conformation traits are not very numerous and the bibliography only includes works on fish and cattle (Marjanovic et al., 2016; Neves et al., 2011). In fact, studies in species with long generational intervals are very scarce. In horses, there is one very recent work that addresses the

reduction in the variability of horses' rank position in endurance races (Cervantes et al., 2020).

Assuming that genetic heterogeneity of residual variance underlies differences in phenotypic stability and that a low variance indicates stable performance across environmental factors, residual variance estimates can be employed as an index trait to improve breeding goal uniformity (Jung et al., 2020). The presence of genetic heterogeneity of residual variance suggests that selection can be used to change residual variance based on pedigree information (Sancristobal-Gaudy et al., 1998; Sonesson et al., 2013).

The Pura Raza Español (PRE) horse Studbook comprises around 200,000 individuals in more than 65 countries from all continents (Solé et al., 2018). This makes it the most important Spanish horse breed and a very important breed in livestock production in economic terms. Furthermore, PRE is one of the hallmarks of Spanish culture and traditions and is the forerunner of other horse breeds (Anaya et al., 2017).

Since its approval in 2004, the PRE breeding programme has aimed both at improving functionality in horse sports, mainly dressage, and at conformation for sport performance, as the morphology of the horse's body is closely related to performance, and its movements and gaits depend on it (Solé et al., 2013). It has been demonstrated that morphological traits are genetically correlated with certain biokinematic variables at trot and that body conformation is related to a greater or lesser predisposition to dressage ability, allowing the indirect selection of animals for this discipline (Sánchez-Guerrero, Molina, et al., 2016). The body conformation of PRE horses is currently evaluated objectively, through a linear scoring system or quantitative zoometric measurements (Sánchez-Guerrero, Gómez, Molina, et al., 2013).

Due to the great importance that horse morphology presents for PRE breeders, matings are usually planned in order to maintain or improve body conformation, as well as to follow the breed and stud standards. In addition, it is highly desirable for breeders to obtain offspring that present very similar characteristics to their parents and to each other. Hence, the aim of this work was to assess the possibility of using selection to reduce the environmental variability of 13 morphological traits in the PRE horse by selecting the environmental variability genes attributed to the stallions. For this purpose, the genetic parameters and breeding values of the morphological traits were estimated using a canalization model that assumes heterogeneity of the residual variance for the first time.

2 | MATERIALS AND METHODS

The initial morphological data set analysed in this study comprised records from a total of 111,876 different PRE horses (43,554 males and 68,322 females). Data were obtained from the Asociación Nacional de Criadores de

Caballos de Pura Raza Española (ANCCE). Each of these animals had at least one morphological trait measurement collected between 2009 and 2018 in Spain. The number of available records per variable ranged from 20,610 to 48,486. The morphological traits studied included both zoometric measurements and linear scored variables. These traits were selected for being traditionally gathered in basic aptitude tests due to their correlation with dressage traits (Sánchez-Guerrero et al., 2017).

A total of 11 different zoometric measurements were evaluated: *height at withers* (HaW), *width of chest* (WoC), *dorsal–sternal diameter* (DsD), *buttock–stifle distance* (BsD), *scapular–ischial length* (SiL), *length of shoulder* (LoS), *length of croup* (LoC), *length of gaskin* (LoG), *perimeter of anterior cannon bone* (PoACB), *perimeter of knee* (PoK) and *thoracic perimeter* (TP). These variables were measured in centimetres. In addition, two linear scored variables evaluated in nine classes were studied: *upper neck line* (UNL), ranging from class 1 (very poorly marked) to class 9 (very marked); and *muscular development* (MD), which ranged from class 1 (very little) to class 9 (well developed). All the morphological traits were previously described in works by Sánchez, Gómez, Molina, et al. (2013) and Sánchez-Guerrero, Molina, et al. (2016). The morphological traits are defined in Figure S1.

The total number of individuals included in the pedigrees analysed (built from the stallions' generation) ranged from 17,662 (height at withers) to 23,962 (dorsal–sternal diameter), depending on the trait analysed. Pedigrees included all data of an animal model: animal (male or female), father and mother. All the generations available were considered (not less than 14 generations). The average number of offspring per stallion with available data that contributed to the estimation was 4.78. Table 1 shows the description of the data set used. Basic statistics were performed using the Statistica software 8.0 (Statsoft & Inc., 2007).

In this study, a heteroscedastic (HE) model developed by Sancristobal-Gaudy et al. (1998) was used. As almost all horses are measured only once on their lives and models require repeated measures per animal, data were assigned to stallions. Theoretically, measurements data could have been assigned equally to dams, but in practice, databases would have to be cut, as far fewer broodmares have a sizeable number of offspring. This model assumed that the residual variance is heterogeneous and partially under genetic control. It also assumed that the sampling distribution of data y is Gaussian, as follows:

$$y_i = \mathbf{x}_i \mathbf{b} + \mathbf{z}_i \mathbf{s} + e^{1/2 (\mathbf{x}_i \mathbf{b}^* + \mathbf{z}_i \mathbf{s}^*)} \varepsilon_i$$

where y_i is the measurement of the individual, * indicates the parameters associated with environmental variance, \mathbf{b} and \mathbf{b}^* are vectors that contain systematic effects, and \mathbf{s} and \mathbf{s}^* are the

TABLE 1 Descriptive statistics of data set

Zoometrical measurements	Number of stallions	Mean \pm SEM	C.V. (%)	Number of records ^a	Mean ^a \pm SEM	C.V. (%)		
HaW	5,297	163.97 \pm 0.06	2.87	20,610	161.03 \pm 0.03	3.03		
WoC	7,880	43.00 \pm 0.05	10.41	42,203	41.39 \pm 0.02	9.64		
DsD	7,807	74.72 \pm 0.05	5.85	41,759	73.82 \pm 0.02	5.63		
BsD	5,834	52.68 \pm 0.03	4.78	23,782	51.11 \pm 0.02	5.54		
SiL	7,815	161.47 \pm 0.06	3.35	41,862	159.94 \pm 0.03	3.41		
LoS	8,411	62.28 \pm 0.04	5.71	48,486	66.65 \pm 0.02	5.83		
LoC	5,849	54.36 \pm 0.04	5.57	23,823	52.83 \pm 0.02	5.85		
LoG	5,845	55.28 \pm 0.06	7.70	23,790	52.20 \pm 0.03	8.38		
PoACB	7,871	21.24 \pm 0.01	6.24	42,250	20.30 \pm 0.01	6.52		
PoK	7,818	34.21 \pm 0.02	6.36	41,864	32.19 \pm 0.01	6.75		
TP	7,803	190.53 \pm 0.10	4.41	41,743	189.94 \pm 0.05	4.92		
Linear scored variables	Number of stallions	Range	Quartile range	C.V. (%)	Number of records ^a	Range	Quartile range	C.V. (%)
UNL	5,854	3–9	2.00	19.83	23,818	1–9	2.00	24.00
MD	5,852	2–8	1.00	19.80	23,829	1–9	1.00	23.37

Note: Number of stallions and records, mean values and standard error of mean (SEM) and coefficient of variation (CV) of their zoometrical measurements, and number of stallions and records, range, quartile range and CV of their linear scored variables.

Abbreviations: BsD, buttock–stifle distance; DsD, dorsal–sternal diameter; HaW, Height at withers; LoC, length of croup; LoG, length of gaskin; LoS, length of shoulder; MD, muscular development; PoACB, perimeter of anterior cannon bone; PoK, perimeter of knee; SiL, scapular–ischial length; TP, thoracic perimeter; UNL, upper neck line; WoC, width of chest.

^aRecords correspond to measurements of stallions' offspring.

stallion genetic effects; x_i and z_i are the incidence vectors for systematic and additive genetic effects, respectively; and finally, $\varepsilon_i \sim N(0, 1)$. It must be noted that as defined, the direct genetic effects s and s^* are paternal effects that include half of the direct genetic effect of the offspring.

The genetic effects s and s^* are distributed together and are assumed to be Gaussian:

$$\begin{pmatrix} s \\ s^* \end{pmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_s^2 & \rho\sigma_s\sigma_{s^*} \\ \rho\sigma_s\sigma_{s^*} & \sigma_{s^*}^2 \end{bmatrix} \otimes \mathbf{A} \right)$$

where \mathbf{A} is the additive genetic relationship matrix; σ_s^2 is the additive genetic variance of the trait; $\sigma_{s^*}^2$ is the additive genetic variance affecting the environmental variance of the trait; ρ is the coefficient of genetic correlation, and \otimes denotes the Kronecker product.

The model applied included offspring sex, with two levels (male or female); age, with eight levels (level 1: ≥ 3 – < 4 years old, level 2: ≥ 4 – < 5 years old, level 3: ≥ 5 – < 6 years old, level 4: ≥ 6 – < 7 years old, level 5: ≥ 7 – < 8 years old, level 6: ≥ 8 – < 9 years old, level 7: ≥ 9 – < 10 years old and level 8: ≥ 10 years old); and the effect of the interaction between the year–geographical area–season in which the data were recorded, as systematic effects (\mathbf{b} and \mathbf{b}^*), with 338 (HaW) to 543 (LoS) levels.

The model was resolved using the GSEVM programme (Ibáñez-Escriche et al., 2010). The variance components were obtained by running 500,000 iterations, sampling 1 in each of the 100 iterations and discarding the first 50,000 as burn-in. This software allows us to define the genetic parameters for mean and environmental variability while providing their correspondent breeding values following this model.

The global heritability (h^2) of each of the traits was considered as the mean of the solutions for each of the systematic effects affecting the residual variability. Besides, the heterogeneity of the residual variances also allowed us to obtain specific heritabilities for the different levels of each systematic effect within the variables, by adding to the specific solution for a level the mean of the solutions for each of the rest of the systematic effects affecting the residual variability (Formoso-Rafferty et al., 2017).

The genetic coefficient of variation of environmental variability (GCV) was computed as the mean value of the root square of each of the iterations of the posterior distribution of $\sigma_{s^*}^2$ (Hill & Mulder, 2010).

3 | RESULTS

Table 1 shows the number of stallions and records and the mean value of the morphological variables studied in this

TABLE 2 Additive genetic variances of the mean (σ_s^2) and of the residual variance ($\sigma_{s^*}^2$) of the traits, global heritability estimates of the systematic effects affecting the traits (h^2), coefficient of genetic correlation (ρ_{s,s^*}), genetic coefficient of variation (GCV) estimates and corresponding *SD* from posterior marginal distributions

Trait	σ_s^2 (SD)	$\sigma_{s^*}^2$ (SD)	h^2 (SD)	ρ_{s,s^*} (SD)	GCV (SD)
HaW	6.74 (0.24)	0.58 (0.03)	0.28 (0.04)	0.69 (0.02)	0.76 (0.02)
WoC	1.47 (0.05)	0.20 (0.01)	0.09 (0.01)	-0.11 (0.04)	0.45 (0.02)
DsD	1.51 (0.07)	0.35 (0.02)	0.14 (0.02)	0.14 (0.03)	0.59 (0.02)
BsD	0.54 (0.04)	0.20 (0.02)	0.11 (0.01)	0.18 (0.06)	0.45 (0.02)
SiL	5.87 (0.17)	0.06 (0.01)	0.25 (0.01)	0.54 (0.04)	0.24 (0.01)
LoS	1.72 (0.08)	0.12 (0.01)	0.19 (0.02)	0.11 (0.04)	0.34 (0.01)
LoC	1.13 (0.06)	0.10 (0.02)	0.18 (0.02)	0.37 (0.05)	0.32 (0.02)
LoG	1.26 (0.04)	0.19 (0.02)	0.17 (0.02)	0.19 (0.05)	0.44 (0.02)
PoACB	0.20 (0.01)	0.38 (0.04)	0.17 (0.03)	0.51 (0.03)	0.61 (0.02)
PoK	0.51 (0.02)	0.29 (0.02)	0.21 (0.02)	0.22 (0.03)	0.54 (0.01)
TP	14.65 (0.62)	0.05 (0.01)	0.21 (0.01)	0.71 (0.05)	0.23 (0.02)
UNL (class)	0.10 (0.01)	0.06 (0.01)	0.09 (0.01)	0.25 (0.08)	0.24 (0.02)
MD (class)	0.04 (0.00)	0.29 (0.02)	0.30 (0.19)	-0.56 (0.03)	0.54 (0.02)

Abbreviations: BsD, buttock–stifle distance; DsD, dorsal–sternal diameter; HaW, Height at withers; LoC, length of croup; LoG, length of gaskin; LoS, length of shoulder; MD, muscular development; PoACB, perimeter of anterior cannon bone; PoK, perimeter of knee; SiL, scapular–ischial length; TP, thoracic perimeter; UNL, upper neck line; WoC, width of chest.

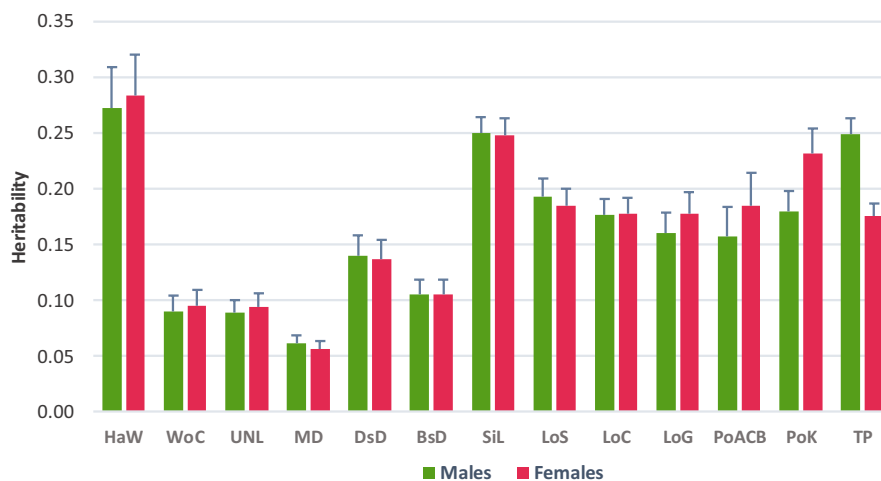


FIGURE 1 Heritabilities for morphological traits according to sex (male or female) and standard deviation. BsD, buttock–stifle distance; DsD, dorsal–sternal diameter; HaW, height at withers; LoC, Length of croup; LoG, Length of gaskin; LoS, length of shoulder; MD, muscular development; PoACB, perimeter of anterior cannon bone; PoK, perimeter of knee; SiL, scapular–ischial length; TP, thoracic perimeter; UNL, upper neck line; WoC, width of chest [Colour figure can be viewed at wileyonlinelibrary.com]

work. According to the coefficient of variation, WoC was the zoometric measurement that presented the highest variability (10.41% in stallions and 9.64% in offspring), while HaW displayed the lowest CV (2.87% and 3.03%, respectively). Meanwhile, the two linear scored variables (UNL and MD) showed a very similar CV in stallions and offspring (19.83% and 19.80% in the case of UNL vs. 24.00% and 23.37% in MD).

The variance components and genetic parameters estimated are shown in Table 2. The genetic variances for the variability

ranged between 0.05 (TP) and 0.58 (HaW). The coefficients of genetic correlation between the traits and their corresponding environmental variability were mainly positive, although they presented a wide range of values: from high and negative (-0.56) in the case of MD, to high and positive (0.71) in the case of TP. Genetic coefficient of variation estimates are also shown in this table. The lowest GCV value was for TP (0.23), while HaW produced the highest value (0.76).

Global heritabilities of the traits, estimated for an average scenario of fixed effects, ranged from 0.09 (WoC and

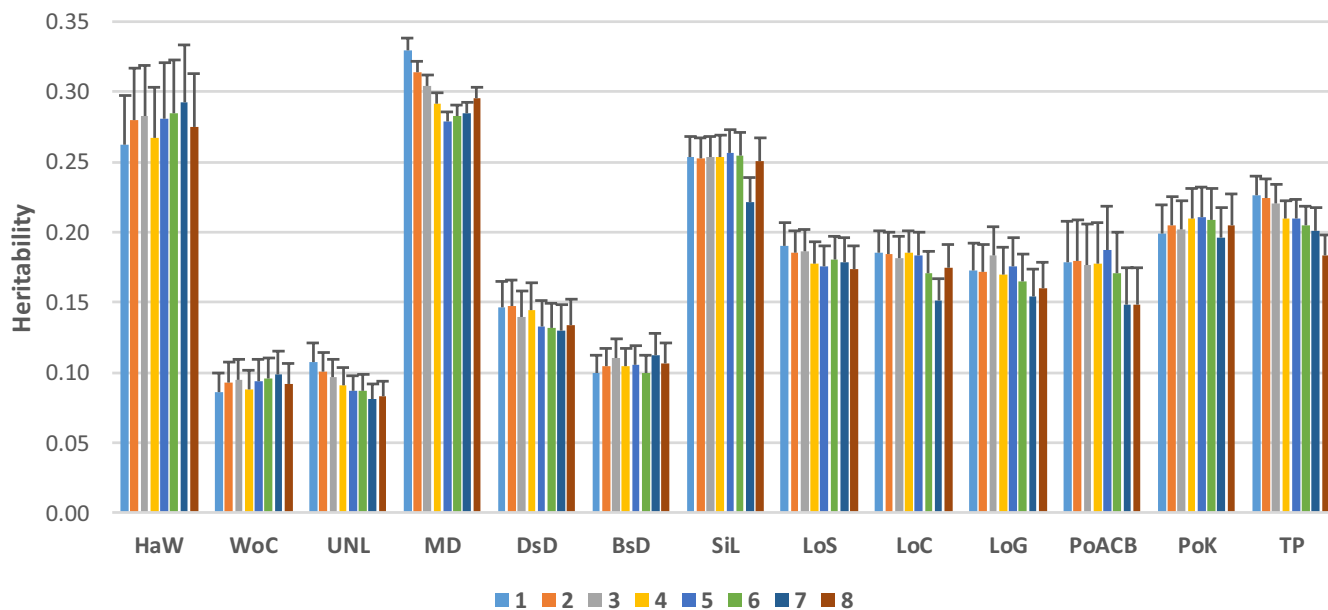


FIGURE 2 Heritabilities for morphological traits according to age levels. BsD, buttock–stifle distance; DsD, dorsal–sternal diameter; HaW, height at withers; LoC, length of croup; LoG, length of gaskin; LoS, length of shoulder; MD, muscular development; PoACB, perimeter of anterior cannon bone; PoK, perimeter of knee; SiL, scapular–ischial length; TP, thoracic perimeter; UNL, upper neck line; WoC, width of chest. 1: ≥ 3 – < 4 years old; 2: ≥ 4 – < 5 years old; 3: ≥ 5 – < 6 years old; 4: ≥ 6 – < 7 years old; 5: ≥ 7 – < 8 years old; 6: ≥ 8 – < 9 years old; 7: ≥ 9 – < 10 years old; and 8: ≥ 10 years old [Colour figure can be viewed at wileyonlinelibrary.com]

UNL) to 0.30 (MD). Heritabilities for the morphological traits in study according to the systematic effect of sex are shown in Figure 1. In all variables, the differences between the effect of gender within the same trait do not surpass 0.08. Nonetheless, it is possible to observe striking discrepancies of heritabilities between genders in some variables. This is the case of PoK and TP, which show differences of 0.05 and 0.07 between males and females, respectively.

Heritabilities for the morphological traits as systematic effects according to the 8 levels of age are displayed in Figure 2. All of the variables show a fairly stable heritability throughout the life of the animal. However, many of them show the greatest heritabilities in the early stages of life, such as UNL, MD, LoS, LoC and TP in level 1 and DsD in level 2. Conversely, HaW, WoC and BsD have a greater heritability in level 7, which corresponds to the 9–10 years old age group. The rest of the traits present the highest values of heritability at level 3 (LoG) and level 5 (SiL, PoACB and PoK). Finally, heritabilities according to the interaction year–geographical area–season (results not shown) present an average value of 0.20, with the 50% of them ranging between 0.01 and 0.18.

The evolution of mean predicted breeding values (PBV) for the traits and for their variability through years of birth of individuals is shown in Figure 3. The general trend of both PBV is similar, with an initial rise in values followed by a more accentuated increase from 1991 until the last years of birth.

4 | DISCUSSION

Horse conformation is of great importance in any breed and is therefore the result of generations of natural and artificial selection. Apart from aesthetic reasons, the relationship between morphology and biokinematics permits the early selection of individuals with a greater predisposition for dressage. This has led to the inclusion of morphological traits in the PRE breeding programme (Sánchez-Guerrero, Molina, et al., 2016). Mostly, breeders tend to select horses as breeding animals, especially stallions, due to their interest in obtaining foals with specific, desirable morphological characteristics and following the breed standards, which establish certain limits between which the variables must be included. Despite having genetic tools at their disposal for this purpose, as in the case of PBV, homogeneous offspring is not always possible to achieve. Apart from the distinct genetic breeding values of stallions, there are detectable differences in the variability of the offspring of a given father compared with others. In fact, some stallions present a high homogeneity among their offspring, while others of similar genetic value present offspring with greater variability. Consequently, selection for environmental variability is of special relevance in equine species (Cervantes et al., 2020). This work aimed to study for the first time the environmental variability in 13 morphological variables related to dressage using a heterogeneity model. Data were assigned to the stallion in order to obtain repeated records for one animal, since

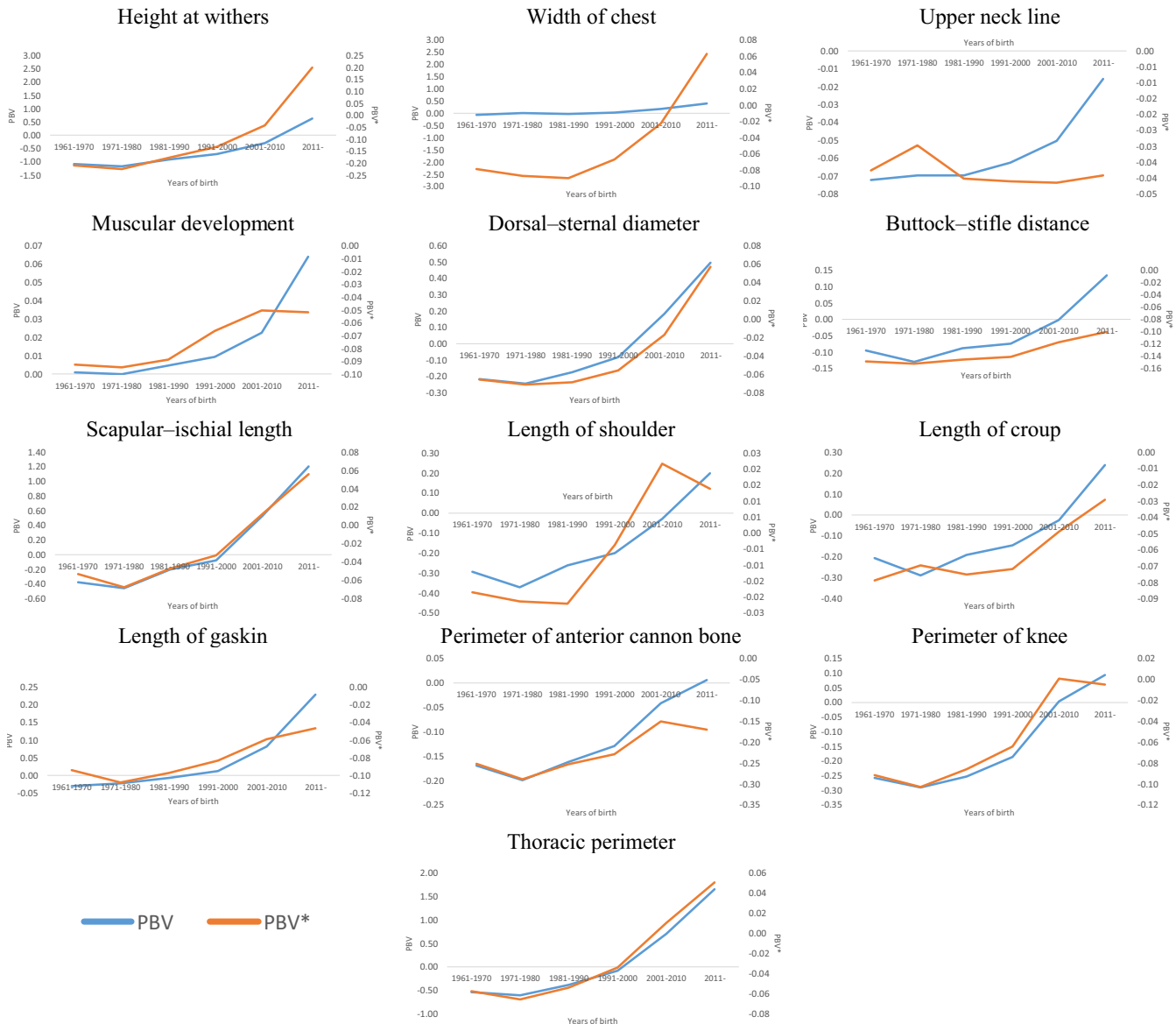


FIGURE 3 Mean predicted breeding values (PBV, primary axis) and mean predicted breeding values for variability of morphological traits in this study (PBV*, secondary axis) across years of birth (abscissa axis) [Colour figure can be viewed at wileyonlinelibrary.com]

it is only possible to select homogeneity when more than one record is collected per animal. Different previous works have demonstrated the suitability of this model (Formoso-Rafferty et al., 2017; Pun et al., 2013). The selection success under this model has already been reported after seven generations of selection (Formoso-Rafferty et al., 2016) and continues being successful after more than 20 generations (Formoso-Rafferty et al., 2020), in which the model is completely comparable to that used here in horses, with the birthweight and its variability assigned to the mother. An alternative to deal with heritability estimates could be considering the traits as different traits by sexes, but in this work, a different approach has been implemented. The morphological variables are not only exclusively paternal, but also maternal. The choice of attributing data to the stallions meets both the requirements

of the model and the fact that males have an average of 4.78 offspring versus 1.61 in females.

Differences in variability were observed between the morphological traits in the coefficient of variation of the data set of this study (Table 1). For this parameter, the level of variation in the 11 zoometric measurements was low to medium, which is very similar to the CVs obtained in the work of Sánchez, Gómez, Peña, et al. (2013). The CV of the linear scored variables was very similar between them and also matches previous studies in this breed. In the traits with higher values of CV, it would be more urgent to use selection in order to reduce the variation, assuming genetic causes.

Additive genetic variance of the residual variance is also a dimensionless factor. The difference between the highest and lowest genetic variances of residual variances (HaW and TP)

is noticeable (11.60). We must remember that the additive genetic variance for the variability of a trait could be affected by a scale effect, due to the presence of the additive genetic variance (Tatliyer et al., 2019).

One key parameter obtained in this study is genetic correlation, which measures the reciprocity between the genetic variance of the traits and their environmental variability. These correlations determine responses in the mean or the variability when selecting by the additive variance (Tatliyer et al., 2019). Thus, high genetic correlations imply that it is not possible to canalize the traits without major changes in their mean values (Gutiérrez et al., 2006). The sign of the value of the genetic correlation determines the direct or indirect relationship between additive genetic variance and environmental variability so that a positive one implies that a selection in favour of the mean would be accompanied by a more environmental variability and thus a greater heterogeneity. For example, a very high positive coefficient of genetic correlation, as in the cases of TP and HaW (0.71 and 0.69, respectively), would imply that selecting stallions with high PBV values for these variables would also increase the variability and hence produce a more heterogeneous offspring. On the contrary, a negative and high correlation, which is the case of MD, implies the possibility of exerting a selection on the character while reducing the variability of its descendants. The majority of morphological traits present low positive values, in line with other studies of conformation characters in different species, such as fish or cattle (Marjanovic et al., 2016; Neves et al., 2011). The study by Tatliyer et al. (2019) showed that positive genetic correlations can be partially generated by a scale effect so that the modification of the mean of a trait would imply a modification in the same sense in the variability. In this way, intermediate values for the genetic correlations between the trait and its variability (0.11–0.69) would be attributed to the scale effect.

The GCV parameter can be interpreted as a measure of the evolvability (Hill & Mulder, 2010), and thus, high values indicate a good evolutionary adaptability of the traits. Our results indicated GCV estimates from 0.23 (TP) to 0.76 (HaW). All these values are within the range described in previous studies, except in the case of HaW. GCV values higher than 0.69 have been only described in simulation studies and were not considered relevant. Therefore, it can be suspected that the estimation of this variable is not very reliable. This may be due to the fact that measures of HaW follow an asymmetric distribution because of the existence of a greater number of horses dedicated to sports, where there is a greater demand for taller animals (Hill & Mulder, 2010; Tatliyer et al., 2019).

The global heritabilities of the traits mostly remain low, under 0.20, although in some traits they had a medium range of values. Most of the global heritabilities obtained in this study are lower than those previously reported in the

literature, although some are very similar (Sánchez, Gómez, Molina, et al., 2013; Sánchez-Guerrero, Molina, et al., 2016). The differences among models used could explain these dissimilarities in heritability, as HE models assume that records are balanced across the data set, whereas in the real data set, they are unbalanced (Cervantes et al., 2020).

Even though the influence of sex on heritabilities is different between morphological traits, in general, males and females (Figure 1) did not show noticeable differences in heritabilities. PoK and TP are the two traits that stand out of the rest and exhibit a higher heritability in females and males, respectively. PoK is a forelimb perimeter that is of great importance in dressage (Sánchez-Guerrero, Molina, et al., 2016), while TP measurements are influenced by pregnancy, as this perimeter grows as the foetus develops, which would explain the greater heritability and stability in stallions. As the selection response is proportional to the heritability, higher heritability results in a greater response (Formoso-Rafferty et al., 2017), and artificial selection for these traits would be more favourable in the gender with higher heritability, namely in mares in PoK and stallions in TP.

The influence of age as a fixed effect on heritabilities of the morphological traits (Figure 2) is not homogeneous either among the variables in study, although they present a similar magnitude. More interestingly, the results demonstrate that there are differences between levels of age within the same trait. Although a horse is considered adult at 4 years old, these differences can be attributed to the fact that zoometric measurements can change with the age of the horse if they are still growing or are affected by ageing (Wejer & Lewczuk, 2016).

Moreover, these results can be interpreted so that at ages where there exists a greater heritability of the trait, horses express more their genotype than the residual variance: in other words, they are less affected by the environment. This would explain the fact that zoometric measurements of relevant morphological lengths of the horse, such as HaW or WoC, show the highest heritabilities at later ages, as they may be influenced by different growth precocities, which may be stabilized over the years. In addition, the traits with higher heritability, which are therefore less influenced by the environment at early ages, are related to dressage and exercise (e.g. MD). It has been demonstrated that zoometric measurements and physical condition can vary according to the amount of exercise to which the animal is subjected (Sánchez-Guerrero et al., 2019). As most dressage horses begin training at around 3 or 4 years old and continue over a considerable number of years, their morphology at age level 1 is not affected by exercise as much as at older age levels. In addition, certain diseases affecting the morphology of the horse, such as osteochondrosis or cresty neck, are associated with ageing (Bourebaba et al., 2019; Sánchez-Guerrero, Azor, et al., 2016).

The work of Formoso-Rafferty et al., 2017, puts forward the possibility of modulating heritability of the traits by selecting the most convenient combination of levels of the systematic effects. Therefore, as the selection response is proportional to heritability, the selection of a morphological trait would be greater if the measurements are registered at the age level at which it presents higher heritabilities. Nowadays, the data for all morphological traits of PRE horses are collected at the same time for obvious practical and economic reasons, when the animals are 3 or more years old. Therefore, the choice of the most important variables for the selection objectives in the PRE Breeding Programme is of major significance in order to establish the ideal age for measuring and selecting the breeding animals. According to our results, for example, the linear conformation score should be carried out at an early age, at the same time as some zoometric measurements are currently taken.

The general trend for both PBVs in the population is initial stability or slight increase, followed by a clear increase in recent years. Horses born around the 2000s present higher average PBVs than older individuals. This can be explained by the fact that these generations encompass the years when the PRE breeding programme was started and a more effective breeding plan has been carried out since then, improving the breeding values of animals. Likewise, mean PBV*s have followed a similar path and variability has increased in turn, with parallel values in morphological traits with positive genetic correlations. The genetic trend in the variability of these traits depends on the genetic correlations with the mean trait and whether this has been selected or not. In addition, the assessment of some zoometric measurements has changed over the breed's history. As a consequence, the environmental variability of morphological traits could be affected by the way some variables are collected, such as in the two perimeters and the length of shoulder, whose variability has diminished over the last 20 years, when the way animals are measured has been standardized and breeders' interest in certain traits has changed. Finally, these results may be partly justified by a scale effect, which would explain the fact that the increase in the mean values of a trait leads to a rise in its environmental variability in the case of traits that show positive genetic correlations (Tatliyer et al., 2019). In the case of MD, a trait with a high negative genetic correlation, PBV*s tend to decrease as the PBVs rise, as the selection of animals with high genetic values for the mean provides a greater homogeneity in progeny.

In conclusion, we found statistical evidence that there is a genetic component for the residual variance, which suggests it would be possible to select for this component. However, not all of the studied traits could be modulated in the same way. If the correlation is positive and high, the morphological trait cannot be improved, while environmental sensitivity is lowered. On the contrary, negative correlations will provide the ideal scenario for simultaneously selecting for larger measurements and

obtaining a homogeneous offspring. The different heritabilities among the levels of the systematic effects, especially age in terms of practicality, can also provide ideas of how to record performance in order to improve the response to selection. In other words, it is essential to establish the specific age at which measurements should be taken, following the most important selection objectives. Moreover, in the future, the creation of a global index combining PBVs for the traits and for their variability could be used as a new tool for breeders.

ACKNOWLEDGEMENTS

The authors wish to thank the National Association of Pura Raza Española Horse Breeders (ANCCE) for providing the data used in this study.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT


The data that support the findings of this study are available from the Asociación Nacional de Criadores de Caballos de Pura Raza Española (ANCCE). Restrictions apply to the availability of these data, which were used under licence for this study. Data are available from the authors with the permission of ANCCE.

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SUPPORTING INFORMATION

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How to cite this article: Poyato-Bonilla J, Sánchez-Guerrero MJ, Cervantes I, Gutiérrez JP, Valera M. Genetic parameters for canalization analysis of morphological traits in the Pura Raza Español horse. *J Anim Breed Genet*. 2021;138:482–490. <https://doi.org/10.1111/jbg.12537>