Assessment of inbreeding depression for body measurements in Spanish Purebred (Andalusian) horses

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ABSTRACT

Our aim was to ascertain inbreeding depression in the Spanish Purebred horses for eight body measurements. A total of 16,472 individuals were measured for height at withers, height at chest, leg length, body length, width of chest, heart girth circumference, knee perimeter and cannon bone circumference. Three different multivariate animal models including, respectively, no measure of inbreeding, individual inbreeding coefficients (F_i) or individual increase in inbreeding coefficients (ΔF_i) as linear covariates were used. Significant inbreeding depression was assessed. Even though the models including measures of inbreeding fitted better with data, no effect on estimates of genetic parameters was assessed. However, the inclusion of inbreeding measures affected the ranking order according to the Expected Breeding Values (EBV). Due to the better fit with data and nice properties (the adjustment of individual inbreeding coefficients with the pedigree depth and linear behaviour) the use of ΔF_i in the evaluation models can be recommended for morphological traits in horses.

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1. Introduction

The inbreeding coefficient (F) of an animal is the average probability that two genes at any given locus are identical by descent (Falconer and MacKay, 1996), and results from mating individuals related by common ancestors. Historically, inbreeding has been used in livestock breeding to "purify" the breed, to "concentrate" the good genes, and to increase uniformity of the offspring. Moreover, breeding practices that make selection programs effective in generating genetic gain also contribute to increase F and to reduce mean phenotypic values for some traits. This fact, the so called inbreeding depression, results both from the expression of partially recessive deleterious alleles and from the loss of heterozygosity (Charlesworth and Charlesworth, 1987; Lynch, 1991; Hansson and Westerberg, 2002; Norberg and Sorensen, 2007).

Inbreeding depression is more likely to occur for traits related to reproduction and fitness (Hansson and Westerberg, 2002) whilst production or morphological traits, such as body measurements, typically show little or no change (Fioretti et al., 2002; Sierszchulski et al., 2005; Van Eldik et al., 2006; Van Wyk et al., 2006). This topic is of particular interest for populations under selection for morphological traits. However, the number of studies testing this on real populations of domestic animals is scarce (Curik et al., 2003).

The Spanish Purebred (SPB; Andalusian) horse is the most recognised horse breed in the Iberian Peninsula (Valera et al., 2005). At present, the SPB Stud-Book includes 66% of the registered Spanish horse population. In 2003, the Breeders' Associations of the SPB horse have initiated the development of a breeding program including conformational (Molina et al., 1999), functional (Castejón et al., 1994; Molina et al., 2007; Valera et al., 2006b, 2007) and reproduction traits (Valera et al., 2006a). Moreover, genealogical analyses have shown that a limited number of founders of the breed besides selection for type traits have caused significant inbreeding levels in this population (Valera et al., 2005).

No clear evidence on detrimental effects of inbreeding on horse performance is available both at the reproduction (Dusék,

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1980; Barreiros and Barata, 1982; Mahon and Cunningham, 1982; Klemetsdal and Johnson, 1989; Cothran et al., 1984; Van Eldik et al., 2006) and at the morphological level (Curik et al., 2003; Van Eldik et al., 2006). This lack of evidence on detrimental effects of inbreeding on horse performance can be partially explained by the fact that the individual inbreeding coefficients are non-linearly dependent on the pedigree depth of each individual (Falconer and MacKay, 1996). Recently, González-Recio et al. (2007) proposed the use of the individual increase in inbreeding coefficients (ΔF_i) as a useful approach to overcome this problem, but also for describing the effect of inbreeding depression on productive and reproductive traits, since this accounts for the depth of the known pedigree over generations.

In horse breeding, conformation is more important than in other species (Preisinger et al., 1991). Estimated relative economic values of selection criteria for riding horses, based on sale prices, indicate that conformation and moving ability are the most important traits in horse breeding (Bruns et al., 1978; Schwark et al., 1988) to achieve high prices. Such traits have particular importance in SPB breeding (Molina et al., 1999; Valera et al., 2006b). The aim of this research was to ascertain the existence of inbreeding depression for body measurements in the SPB horse, by testing the usefulness of ΔF_i as a predictor of inbreeding depression, and quantify it from body measurements and from genetic parameters and breeding values. Recommendations on the inclusion of inbreeding coefficients (F_i and ΔF_i) in the evaluation models for body measurements in SPB horse are discussed.

2. Material and methods

Data were obtained by the Spanish Military Cavalry services (FESCCR) through the Spanish Ministry of Agricul-ture. Body measurements of 16,472 SPB individuals (40.25% stallions and 59.75% mares) belonging to 537 different studs were gathered between 2004 and 2005 during the obligatory assessment for horse registration in the definitive register of the SPB Stud-Book. At the time of registration, animals were, on average, 3.94 ± 0.01 years old.

Eight body measurements were recorded: 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). They were directly obtained from the left side of the individual, using Lydthin stick and tape measure; animals were put on a level and hard floor and led by personnel of the respective stud during this process (see Fig. 1). Although live weight is probably the most important trait to describe the size of an animal, it was not studied because this trait is not registered in leisure horses, like SPB.

The whole SPB Stud-Book included a total of 140,629 individuals from its foundation in the 19th century until now. Genealogical analyses were horses out with this whole pedigree, including all SPB Horses registered in the Stud-Book, using the program ENDOG v4.3 (Gutiérrez and Goyache, 2005). The following parameters were computed:

- The individual inbreeding coefficients (F_i), defined as the probability that an individual has two genes identical by descent (Malécot, 1948). The program ENDOG uses the algorithm described by Meuwissen and Luo (1992) to compute F_i.
- The number of equivalent to discrete generations (t) for each individual in the pedigree. This parameter is the sum overall known ancestors of the term $(1/2)^n$, where n is the
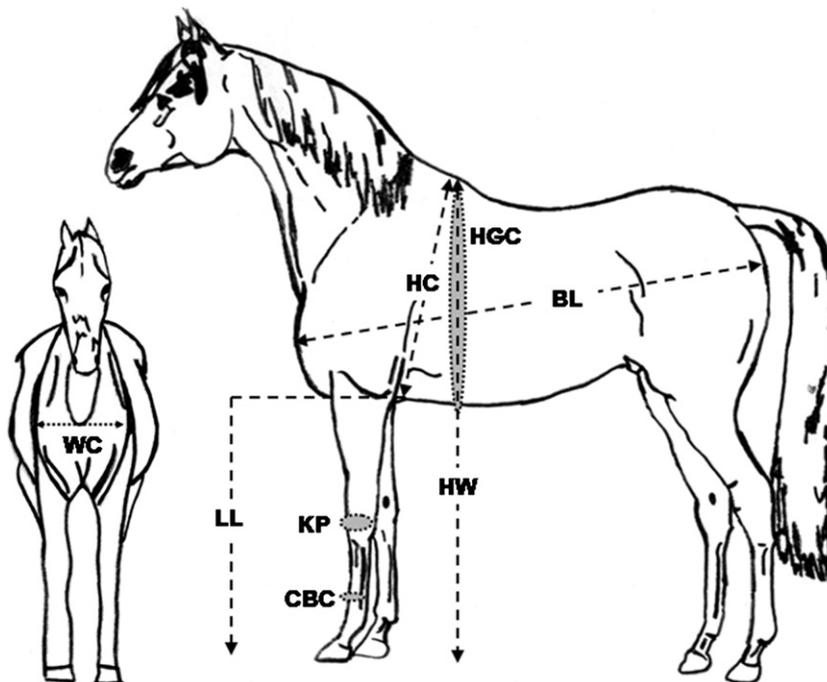
Fig. 1. Representation of the eight analysed body measurements in SPB horses. Where: HW is height at withers, HC is height at chest, LL is leg length, BL is body length, WC is width of chest, HGC is heart girth circumference, KP is knee perimeter and CBC is cannon bone circumference.

number of generations between the individual and the ancestor i (Maignel et al., 1996).

- The individual increase in inbreeding coefficients (ΔF_i), computed as $\Delta F_i = 1 - \sqrt[t]{1 - F_i}$. González-Recio et al. (2007) and Gutiérrez et al. (2008) suggested the use of ΔF_i as an alternative measure of inbreeding adjusted for the pedigree depth of the individual, making it possible to distinguish between two animals with the same inbreeding coefficient but differences in the number of generations in which this level of inbreeding has appeared. The ΔF_i coefficients share the well-known properties of ΔF (Falconer and MacKay, 1996) and, contrary to the F_i values, the individual increase in inbreeding coefficients are expected to have a linear behaviour over generations.

Multivariate mixed animal models were used to estimate genetic parameters, using the VCE software package v.5.0 (Kovac et al., 2002). This software includes inbreeding in the construction of the numerator relationship matrix thus avoiding confusions in the model. However, some previous analyses were carried out to make sure that inbreeding was not influencing the results (results not shown). Three different models were run:

- Model 1: Including the sex of animal (with 2 levels: male and female), age group (with 5 levels: 3, 4, 5, 6 and ≥ 7 years old), and stud (with 537 levels) as fixed effects, the animal additive genetic effect and the residual as random effects. This model was equivalent to that used previously by Molina et al. (1999) for the estimation of genetic parameters of morpho-functional traits in the same breed.
- Model 2: Similar to model 1, but including individual inbreeding coefficients (F_i) as a linear covariate.
- Model 3: Similar to model 1, but including individual increase in inbreeding coefficients (ΔF_i) as a linear covariate.

Torzyński et al. (2005) suggested that the maternal genetic effect should be included in the genetic evaluation of horses. However, preliminary analyses (not shown) carried out on our data showed that the influence of this effect was negligible for all variables. As a consequence the maternal genetic effect was not included in the fitted models. Moreover, following González-Recio et al. (2007), a quadratic term was tested for F_i and ΔF_i in models 2 and 3, but these terms did not show statistically significant influence on data and were not included in the models fitted.

To complete the pedigree for the calculation of the inverse of the relationship matrix, the Stud-Book of the SPB horse was used, and all the ancestors of the measured animals were added, until the fourth generation, giving a total of 40,449 horses. All the measured animals had a 100% known pedigree until the fourth generation.

Regression coefficients estimated using models 2 and 3 were used to compute the phenotypic values of each trait for $F = 0$ and for $F = 0.25$ in order to check for statistical significance of inbreeding depression assessed on each trait by computing the parameter δ (Fox et al., 2007) as $\delta = \frac{(\text{Meaninbred} - \text{Meanoutbred})}{\text{Meanoutbred}}$, where Meaninbred and Meanoutbred are the phenotypic values for each analysed for $F = 0$ and for $F = 0.25$, respectively. So, the numerator was $b*0.25$ and the denominator the global mean of the population. The

same parameter was computed for each trait according to the ΔF_i values corresponding to $F = 0$ and $F = 0.25$ assuming t as the average t of the analysed population. Parameter δ can be defined as the proportional decrease in body measurements in inbred individuals compared with outbreds and are expected to be 0 when there is no inbreeding depression, and negative or positive values depending on whether inbred individuals have lower or higher performance than outbreds, respectively.

Spearman correlation coefficients were computed between the Expected Breeding Values (EBVs) estimated for the 100 best and 100 worst ranked animals for each model. The EBVs estimated using the model that included neither F_i nor ΔF_i coefficients as linear covariate were the basis of the comparisons.

The fitted models were compared using the Likelihood Ratio Test (LRT) (Torzyński et al., 2005). The LRT is a statistical test of the goodness-of-fit between two models, where a more complex model is compared to a simpler model to see if it fits a particular dataset significantly better. LRT was computed as $\text{LRT} = 2(\text{Ln}L_1 - \text{Ln}L_2)$, where L_1 is the likelihood value for the simpler model and L_2 is the likelihood value for the more complex model. The LRT approximately follows a Chi-square distribution. So, in order to determine if the difference in likelihood scores between two given models is statistically significant, we had to compare the obtained value with the Chi-squared value with k degrees of freedom, with k being the number of additional parameters in the more complex model. Univariate models were used for LRT estimation in order to give more information for each analysed trait.

3. Results

Descriptive statistics of the eight analysed body measurements in stallions and mares are given in Table 1.

In general, males had higher average values than females for all the analysed body traits except for height at chest, with the same value for both sexes, and heart girth circumference, which was wider in females, as previously reported (Molina et al., 1999). In general, coefficients of variation were from moderate to low (2.63 to 6.99 in males and 2.63 to 7.75 in females), characterising a highly homogeneous population.

Table 2 gives descriptive statistics of the genealogical parameters computed from the whole pedigree of the SPB

Table 1

Descriptive statistics of the eight body measurements analysed in SPB females ($N = 9,842$) and males ($N = 6630$).

Trait[a]	Females				Males			
	Mean ± S.E.	Min.	Max.	CV	Mean ± S.E.	Min.	Max.	CV
HW	1.56 ± 0.0004	1.42	1.79	2.63	1.59 ± 0.0005	1.44	1.77	2.63
HC	0.73 ± 0.0003	0.55	0.90	4.69	0.73 ± 0.0004	0.51	0.90	4.97
LL	0.83 ± 0.0004	0.57	0.95	4.48	0.85 ± 0.0005	0.55	0.95	4.50
BL	1.58 ± 0.0005	1.33	2.01	3.26	1.59 ± 0.0006	1.36	1.89	3.27
WC	0.43 ± 0.0003	0.30	0.59	7.75	0.44 ± 0.0004	0.32	0.58	6.99
HGC	1.92 ± 0.0009	1.50	2.30	4.73	1.89 ± 0.0009	1.53	2.20	3.92
KP	0.31 ± 0.0001	0.27	0.39	4.22	0.33 ± 0.0002	0.27	0.40	4.43
CBC	0.20 ± 0.0001	0.17	0.30	5.38	0.21 ± 0.0001	0.17	0.30	5.52

[a] 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. CV is the coefficient of variation (%). Traits were measured in metres.

Table 2
Descriptive statistics of individual inbreeding coefficients (F_i), individual increase in inbreeding (ΔF_i) and equivalent to discrete generations for the whole SPB population (g) ($N = 140{,}629$) and the measured subpopulation (t) ($N = 16{,}472$).

		Whole population			Measured subpopulation		
		F_i	ΔF_i	g	F_i	ΔF_i	t
Females	Mean	0.081	0.010	8.932	0.084	0.009	9.882
	S.E.	0.000	0.000	0.008	0.001	0.000	0.009
	Min.	0.000	0.000	0.000	0.000	0.000	4.646
	Max.	0.540	0.206	11.749	0.454	0.060	11.398
Males	Mean	0.083	0.010	9.164	0.083	0.009	9.874
	S.E.	0.000	0.000	0.006	0.001	0.000	0.009
	Min.	0.000	0.000	0.000	0.009	0.001	7.436
	Max.	0.540	0.206	11.760	0.371	0.050	11.760
Totals	Mean	0.082	0.010	9.044	0.084	0.090	9.879
	S.E.	0.000	0.000	0.005	0.000	0.000	0.007
	Min.	0.000	0.000	0.000	0.000	0.000	4.646
	Max.	0.540	0.206	11.760	0.454	0.060	11.760

horses and the whole pedigree of the measured horses. The average F_i value for the whole population was 8.2% (8.1% for females and 8.3% for males) varying, at the individual level, from 0 to 54%; whereas it was 8.4% for the measured females and 8.3% for the measured males, ranged from 0 to 45%. The average increase in inbreeding (ΔF_i) was similar in females and males for the whole population and the measured animals (1% and 0.9%, respectively). The average number of equivalent complete generations for the whole population (g) was 9.04, which was slightly higher for the measured animals ($t = 9.88$).

The evolution of the mean values of F_i and ΔF_i in the SPB horse Stud-Book by year of birth of the individuals is shown in Fig. 2. The F_i of the whole registered SPB horses increased quickly to reach a maximum in 1950s. As previously reported by Valera et al. (2005) a gradual decrease of the F_i was observed during the 1990s. As a parameter corrected for pedigree depth, the ΔF_i values anticipated markedly the behaviour of F_i; average ΔF_i decreased since the 1960s and then stayed stable up to the present day.

Regression coefficients, δ values and LRTs for each model and trait are given in Table 3. All computed regression
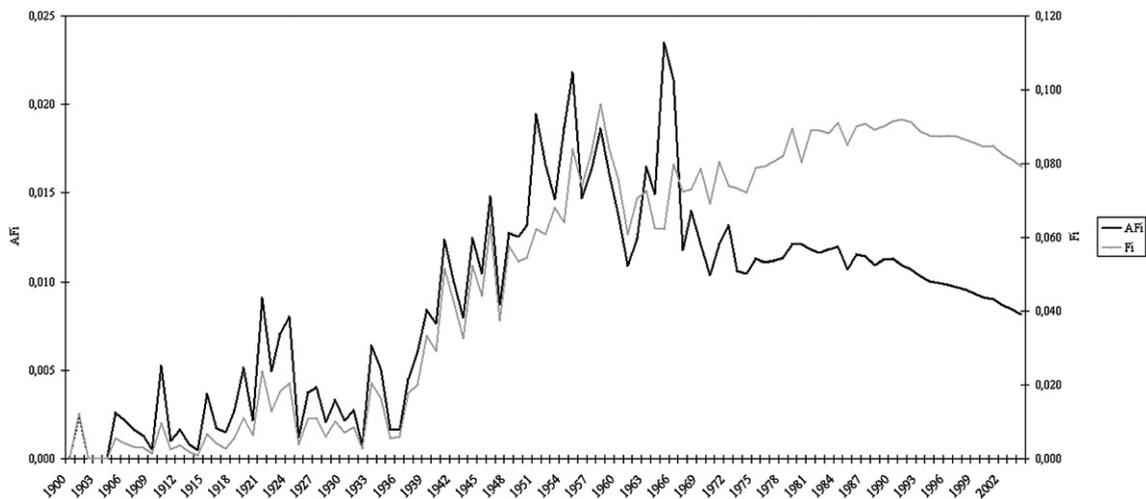
Table 3
Regression coefficients for the analysed traits, predicted change in the body measurements (δ), Likelihood Ratio Test (LRT) comparing univariate models 1 vs 2 and models 1 vs 3.

Trait	Regression coefficients		δ		LRT	
	F_i	ΔF_i	F_i	ΔF_i	1–2	1–3
Height at withers	−0.858	−8.801	−0.136[*]	−0.181[*]	292.56	296.10
Height at chest	−0.455	−4.071	−0.155[*]	−0.180[*]	375.36	382.02
Leg length	−0.440	−6.182	−0.131[*]	−0.239[*]	289.49	302.64
Body length	−0.948	−9.999	−0.149[*]	−0.204[*]	390.69	394.77
Width of chest	−0.546	−6.639	−0.315[*]	−0.498[*]	325.99	336.84
Heart girth circumference	−0.495	−5.420	−0.065[*]	−0.092[*]	371.96	380.66
Knee perimeter	−0.030	−1.281	−0.023	−0.129[*]	130.05	140.53
Cannon bone circumference	−0.586	−6.567	−0.073[*]	−0.106[*]	296.74	305.47

Regression coefficients are in metres.
[*] As superscript means statistical significance for $p < 0.01$.

coefficients were negative and significant, and those for F_i around 10 times higher than those for ΔF_i. The parameter δ was also negative and significant ($p < 0.05$), except for KP with F_i, characterising inbreeding depression. They ranged between 0.023 for KP and 0.315 for WC for model 2, and between 0.092 for HGC and 0.498 for WC for model 3. The values obtained in the LRT using univariate models 2 and 3 shows that complex models fitted data better than univariate model 1.

The influence of the inclusion of F_i and ΔF_i on the estimation of the genetic parameters was also tested. In Table 4 are given the value of the heritabilities and genetic correlations between the analysed traits estimated using, respectively, models 1, 2 (including F_i as a linear covariate) and 3 (with ΔF_i as a linear covariate).

The estimates of heritability for the analysed body measurements were from moderate to high, ranging between 0.32 and 0.60 for model 1 (Table 4). Particularly, height at

Fig. 2. Evolution of the average inbreeding value (F_i) and the individual increase in inbreeding (ΔF_i) in the Spanish Purebred horse Stud-Book by year of birth on the animals computed for the whole SPB population.

Table 4
Estimates (± standard errors) of heritability (on diagonal) and genetic correlations between the eight analysed body traits (below diagonal) obtained using models 1, 2 and 3.

Model	Trait[a]	HW	HC	LL	BL	WC	HGC	KP	CBC
1	HW	0.60 ± 0.017							
2		0.61 ± 0.019							
3		0.61 ± 0.019							
1	HC	0.69 ± 0.020	0.38 ± 0.016						
2		0.68 ± 0.020	0.38 ± 0.019						
3		0.68 ± 0.022	0.37 ± 0.019						
1	LL	0.78 ± 0.016	0.12 ± 0.039	0.32 ± 0.016					
2		0.79 ± 0.015	0.10 ± 0.038	0.31 ± 0.017					
3		0.80 ± 0.015	0.10 ± 0.039	0.31 ± 0.017					
1	BL	0.79 ± 0.014	0.60 ± 0.026	0.53 ± 0.029	0.49 ± 0.019				
2		0.78 ± 0.014	0.59 ± 0.026	0.54 ± 0.029	0.49 ± 0.017				
3		0.79 ± 0.014	0.59 ± 0.026	0.53 ± 0.029	0.49 ± 0.017				
1	WC	0.38 ± 0.026	0.32 ± 0.031	0.16 ± 0.036	0.43 ± 0.028	0.42 ± 0.017			
2		0.38 ± 0.028	0.30 ± 0.033	0.16 ± 0.036	0.42 ± 0.028	0.41 ± 0.017			
3		0.37 ± 0.028	0.30 ± 0.033	0.16 ± 0.036	0.42 ± 0.027	0.41 ± 0.017			
1	HGC	0.56 ± 0.022	0.56 ± 0.025	0.26 ± 0.035	0.53 ± 0.024	0.70 ± 0.021	0.47 ± 0.017		
2		0.56 ± 0.022	0.56 ± 0.025	0.25 ± 0.034	0.54 ± 0.023	0.68 ± 0.022	0.47 ± 0.017		
3		0.56 ± 0.022	0.56 ± 0.025	0.25 ± 0.034	0.53 ± 0.024	0.68 ± 0.022	0.47 ± 0.017		
1	KP	0.76 ± 0.015	0.58 ± 0.025	0.56 ± 0.028	0.78 ± 0.017	0.51 ± 0.027	0.66 ± 0.022	0.49 ± 0.017	
2		0.76 ± 0.015	0.58 ± 0.026	0.56 ± 0.028	0.78 ± 0.016	0.49 ± 0.028	0.66 ± 0.022	0.49 ± 0.018	
3		0.76 ± 0.015	0.58 ± 0.026	0.56 ± 0.028	0.78 ± 0.016	0.49 ± 0.028	0.66 ± 0.022	0.49 ± 0.018	
1	CBC	0.49 ± 0.022	0.31 ± 0.030	0.39 ± 0.031	0.57 ± 0.023	0.60 ± 0.025	0.64 ± 0.023	0.76 ± 0.016	0.51 ± 0.017
2		0.49 ± 0.022	0.30 ± 0.030	0.39 ± 0.031	0.57 ± 0.024	0.60 ± 0.026	0.64 ± 0.023	0.76 ± 0.016	0.51 ± 0.017
3		0.49 ± 0.022	0.30 ± 0.030	0.39 ± 0.031	0.57 ± 0.023	0.60 ± 0.026	0.64 ± 0.023	0.76 ± 0.016	0.51 ± 0.017

[a] 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.

withers showed the highest value and leg length the lowest one. The genetic correlations also varied from moderate to high, ranging from 0.12 (HC-LL) to 0.79 (HW-BL). These parameters were very slightly affected by the introduction of the individual inbreeding coefficients (F_i) or the individual increase in inbreeding (ΔF_i) as linear covariates in the fitted models. These negligible changes were the consequence of those registered in the corresponding genetic and residual (co)variances.

Finally, the 100 best animals and the 100 worst ones according to their EBVs for each trait were compared using Spearman correlation coefficients considering the model without inbreeding effects as a reference (Table 5). Most Spearman correlation coefficients were lower than 0.95, varying from 0.98 for CBC in the 100 best set to 0.723 for WC in the 100 worst set. Spearman correlations between EBVs obtained with models 2 and 3 were also estimated; all of them were higher than 0.99 (results not shown).

4. Discussion

The inbreeding depression is a reduction of mean phenotypic values in animals that are inbred. We report here the existence of significant inbreeding depression for body measurements in SPB horses, which affects both performance and the EBVs ranking order.

Moreover, the inclusion of measures of inbreeding in the models fitted to estimate genetic parameters for body traits, significantly increases the goodness of the models even though the obtained estimates are not affected to a large extent. This happens regardless of the high inbreeding levels previously reported in the SPB population which have a remote basis, and linked to the abusive use of the descendants

of a little number of founder Carthusian stallions until the last quarter of the 20th century (Valera et al., 2005). Inbreeding depression has clearly appeared even though inbreeding levels and individual increase in inbreeding coefficients tended to decrease and to remain stable for the last few decades of the 20th century (see Fig. 2). Average F_i remained constant whereas ΔF_i tended to decrease in recent years as a consequence of the efforts made by breeders to control inbreeding rates by avoiding mating between close relatives (Valera et al., 2005).

Table 5
Spearman correlations for Expected Breeding Values for best 100 and worst 100 individuals for models including individual inbreeding and individual increase in inbreeding coefficients (models 2 and 3) with respect the rank obtained ignoring inbreeding estimates in the fitted model (model 1).

Trait[a]	Model	100 best set	100 worst set
HW	2	0.921	0.725
	3	0.926	0.752
HC	2	0.897	0.955
	3	0.900	0.959
LL	2	0.964	0.924
	3	0.959	0.924
BL	2	0.914	0.857
	3	0.923	0.865
WC	2	0.979	0.730
	3	0.981	0.726
HGC	2	0.913	0.931
	3	0.915	0.937
KP	2	0.981	0.944
	3	0.980	0.941
CBC	2	0.982	0.816
	3	0.983	0.821

[a] 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.

In real populations, in which the generation overlapping is the rule, it is not possible to assume that all individuals in a pedigree have approximately the same pedigree depth. In the measured population analysed here, the pedigree knowledge for each individual varied from 4.6 to 11.8 equivalent generations, thus making the standardization of inbreeding useful (ΔF_i; Table 2).

In an evaluated (historical) population, it would be expected that all animals have approximately the same depth of pedigree, therefore evaluation according F_i or ΔF_i should be similar. But as shown in Table 2, the range in the pedigree knowledge is wide thus making the standardization of inbreeding useful. The stabilization and decrease of both inbreeding measurements were insufficient to avoid inbreeding depression even though the average ΔF_i of the whole analysed population was 1% (Table 2). Van Wyk et al. (2006) suggested that slow inbreeding (1.53%/generation over 19 generations) allows natural selection to operate and to remove the less adapted animals; at any given level of F_i, less inbreeding depression would then be expected among the individuals who accumulated the inbreeding over a larger number of generations. In contrast, Norberg and Sorensen (2007) in Danish meet sheep populations reported inbreeding depression for production and reproduction traits with inbreeding cumulated at around 1%/generation.

Morpho-functional traits are basic for the breeding scheme of the SPB breed (Molina et al., 1999; Valera et al., 2006b, 2007) and accuracy of the EBVs are of major importance for the SPB breeders. Although the sample used here was independent and more than twice in size than that previously used by Molina et al. (1999), the estimates of genetic parameters obtained for the analysed body measurements are consistent with those reported by these authors regardless of the model fitted for the estimation. Because of the higher sampling size, the current estimates have lower standard errors. The estimates of heritability for most analysed traits (HC, BL, WL, HGC and KP) were lower than those reported by Molina et al. (1999), thus confirming the possible over-estimation suggested by these authors.

The assessment of the effect of inbreeding on estimates of genetic parameters and EBVs is usually carried out by including the individual inbreeding coefficient (F_i) as a covariate in models (Keller and Brinks, 1978; Fioretti et al., 2002; Van Eldik et al., 2006; Van Wyk et al., 2006). We have also included the coefficients of individual increase in inbreeding (ΔF_i) because this allows us to account for the depth of the known pedigree over generations (González-Recio et al., 2007; Gutiérrez et al., 2008). The LRT showed that models, which include measures of inbreeding (especially ΔF_i) fit better with data than the model excluding inbreeding (Table 3). Even though no noticeable effect was found by including F_i or ΔF_i in estimates of genetic parameters, the use of these additional parameters could be justified in terms of significant improvement of model goodness. Regarding F_i, ΔF_i relates individual inbreeding coefficients with the pedigree depth of the individuals, so the dependence of t was avoided. This property, besides having a more linear behaviour, has the advantage of ΔF_i when compared with F_i. Furthermore, the lack of influence of both F_i and ΔF_i in the estimated genetic parameters makes us confident on the reported results and in the fact that they do not come from statistical artefacts due to the nature of inbreeding coefficients.

Curik et al. (2003) reported in Lipizzan horses significant and negative regression coefficients of body measurements and morphological traits in individual inbreeding coefficients, whereas no differences in the estimated genetic parameters were found.

Studies reporting significant influence of inbreeding on traits that are not related to fitness in horses are scarce. Inbreeding significantly influenced body measurements in Italian Haflinger horse (Gandini et al., 1992), Lusitano horses (Oom, 1992) and Arab mares (Sierszchulski et al., 2005). It also influenced racing performance in Norwegian cold-blooded trotters (Klemetsdal, 1998) and Polish Arabian horses (Radomska et al., 1984). Van Eldik et al. (2006) have reported that inbreeding affected semen quality in Shetland ponies but not body size measurements. Recent studies in other species have reported that inbreeding did not have important effects on estimates of variance components on reproduction and growth traits in Piedmontese cattle (Fioretti et al., 2002) and on production and reproduction traits in Elsenburg dormer sheeps (Van Wyk et al., 2006). EBVs' ranking order in SPB horses is affected to some extent by the inclusion of both F_i and ΔF_i in the evaluation models (see Table 5), probably, because models including measures of inbreeding can identify more accurately the 'real' additive variance regardless of whether it is affected, to a large extent, by inbreeding depression.

5. Conclusions

The aim of this work was to assess the effect of inbreeding depression on body measurements and on the estimates of the corresponding genetic parameters and EBVs in Spanish Purebred horses. Inbreeding depression has been clearly evidenced in body measurements in this breed. The inclusion of inbreeding measures in the evaluation models also affects the ranking order of the individuals according to their EBVs. The likelihood of the univariate models fitted including inbreeding measures to estimate genetic parameters for body measurements is significantly higher than that of the simpler model even though this does not have a major effect on the estimates. As a consequence the inclusion of inbreeding measures in the models fitted to estimate variance components and EBVs for body measurements in SPB horse can be advantageous. Due to the better fit with data and nice properties, which are basically the adjustment of individual inbreeding coefficients with the pedigree depth and a more linear behaviour, the use of the individual increase in inbreeding coefficient (ΔF_i) can be recommended instead of the individual inbreeding coefficient (F_i).

References

Barreiros, R., Barata, G., 1982. Efeito da consanguinidade em equinos. Rev. Port. Ciênc. Veter. 463, 167–177.

Bruns, E., Bierbaum, M., Frese, D., Haring, H.J., 1978. Die Entwicklung von Selektionskriterien fur die Reitpferdezucht. IV. Schatzung relativer okonomischer Gewichte anhand von Auktionsergebnissen. Zuchtungskunde 50, 93–100.

Castejón, F.M., Rubio, D., Tovar, P., Vinuesa, M., Riber, C., 1994. A comparative study of aeróbic capacity and fitness in three different horse breeds (Andalusian, Arabian and Anglo-arabian). J. Vet. Med. A 41, 645–652.

Charlesworth, D., Charlesworth, B., 1987. Inbreeding depression and its evolutionary consequences. Ann. Rev. Ecol. Syst. 18, 237–268.

Cothran, E.G., MacCluer, J.W., Weitkamp, L.R., Pfenning, D.W., Boyce, A.J., 1984. Inbreeding and reproductive performance in Standardbred horses. J. Hered. 75, 220–224.

Curik, I., Zechner, P., Sölkner, J., Achmann, R., Bodo, I., Dovc, P., Kavar, T., Marti, E., Brem, G., 2003. Inbreeding, microsatellite heterozygosity and morphological traits in Lipizzan horses. J. Hered. 94 (2), 125–132.

Dusék, J., 1980. The effect of inbreeding on some physiological traits of black Kladruby horses. Vet. Med. 25 (6), 349–358.

Falconer, D.S., MacKay, T.F., 1996. Introduction to Quantitative Genetics, 4th ed. Prentice Hall, Harlow, U.K.

Fioretti, M., Rosati, A., Pieramati, C., Van Vleck, L.D., 2002. Effect of including inbreeding coefficients for animal and dam on estimates of genetic parameters and prediction of breeding values for reproductive and growth traits of Piedmontese cattle. Livest. Prod. Sci. 74, 137–145.

Fox, C.W., Scheibly, K.L., Smith, B.P., Wallin, W.G., 2007. Inbreeding depression in two seed-feeding beetles, *Callosobruchus maculatus* and *Stator limbatus* (Coleoptera: Chrysomelidae). Bull. Entomol. Res. 97, 49–54.

Gandini, G., Bagnato, A., Miglior, F., Pagnacco, G., 1992. Inbreeding in the Italian Haflinger horse. J. Anim. Breed. Genet. 109, 433–443.

González-Recio, O., López de Maturana, E., Gutiérrez, J.P., 2007. Inbreeding depression on female fertility and calving ease in Spanish dairy cattle. J. Dairy Sci. 90, 5744–5752.

Gutiérrez, J.P., Goyache, F., 2005. A note on ENDOG: a computer program for analysing pedigree information. J. Anim. Breed. Genet. 122, 172–176.

Gutiérrez, J.P., Cervantes, I., Molina, A., Valera, M., Goyache, F., 2008. Individual increase in inbreeding allows estimating realised effective sizes from pedigrees. Genet. Sel. Evol. 40, 359–378.

Hansson, B., Westerberg, L., 2002. Invited review on the correlation between heterozygosity and fitness in natural populations. Mol. ecol. 11, 2467–2474.

Keller, D.G., Brinks, J.S., 1978. Inbreeding by environment interactions for weaning weight in Hereford cattle. J. Anim. Sci. 46, 48–53.

Klemetsdal, G., Johnson, M., 1989. Effects of inbreeding on fertility in Norwegian Trotter. Liv. Prod. Sci., 21 (3), 263–272.

Klemetsdal, G., 1998. The effect of inbreeding on racing performance in Norwegian cold-blooded trotters. Genet. Sel. Evol. 30, 351–366.

Kovac, M., Groeneveld, E., García-Cortez, L.A., 2002. VCE 5, a package for the estimation of dispersion parameters. 7th World Congress on Genetic Applied to Livestock Production, August 19–23, Montpellier, France.

Lynch, M., 1991. The genetic interpretation of inbreeding depression and outbreeding depression. Evolution, 45 (3), 622–629.

Maignel, L., Boichard, D., Verrier, E., 1996. Genetic variability of French dairy breeds estimated from pedigree information. Interbull Bull. 14, 49–54.

Mahon, G., Cunningham, E., 1982. Inbreeding and the inheritance of fertility in the Thoroughbred mare. Livest. Prod. Sci. 9, 743–754.

Malécot, G., 1948. Les mathematiques de l'Heredité. Ed. Masson et Cie., Paris.

Meuwissen, T.H.E., Luo, Z., 1992. Computing inbreeding coefficients in large populations. Genet. Sel. Evol. 24, 305–313.

Molina, A., Valera, M., Dos Santos, R., Rodero, A., 1999. Genetic parameters of morphofunctional traits in Andalusian horse. Livest. Prod. Sci. 60 (2–3), 295–303.

Molina, A., Valera, M., Galisteo, A.M., Vivo, J., Gómez, M.D., Rodero, A., Agüera, E., 2007. Genetic parameters of biokinematics variables at walk in the Spanish Purebred (Andalusian) Horse using experimental treadmill records. Livest. Sci. doi:10.1016/j.livsci.2007.09.021.

Norberg, E., Sorensen, A.C., 2007. Inbreeding trend and inbreeding depression in the Danish populations of Texel, Shropshire and Oxford Down. J. Anim. Sci. 85, 299–304.

Oom, M., 1992. O Cavalo Lusitano. Uma Raça em Recupeaçao. Tesis Doctoral. Universidad de Lisboa.

Preisinger, R., Wilkens, J., Kalm, E., 1991. Estimation of genetic parameters and breeding values for conformation traits for foals and mares in the Trakehner population and their practical implications. Livest. Prod. Sci. 29, 77–86.

Radomska, M., Burzynska, B., Fiszdon-Stecko, K., 1984. Effect of inbreeding on the performance of Polish Arabian Horses. 35th Annual Meeting of the EAAP. The Hague Netherlands.

Schwark, H.J., Petzold, P., Norengerg, I., 1988. Untersuchungen zur Auswahl von Selektionskriterien bei der Weiterentwicklung der Pferdezucht der DDR. Arch. Tierz., Berlin 31, 279–289.

Sierszchulski, J., Helak, M., Wolc, A., Szwaczkowski, T., Schlote, W., 2005. Inbreeding rate and its effects on three body conformation traits in Arab mares. Anim. Sci. Pap. Rep. 23 (1), 51–59.

Torzyński, G., Wolc, A., Szwaczkowski, T., 2005. Maternal effects on the conformation traits in half-bred horses. J. Anim. Feed Sci. 14 (4), 595–605.

Valera, M., Molina, A., Gutiérrez, J.P., Gómez, J., Goyache, F., 2005. Pedigree analysis in the Andalusian horse: population structure, genetic variability and influence of the Carthusian strain. Livest. Prod. Sci. 95, 57–66.

Valera, M., Blesa, F., Santos, R.D., Molina, A., 2006a. Genetic study of gestation length in andalusian and arabian mares. Anim. Reprod. Sci. 95 (1–2), 75–96.

Valera, M., Gómez, M.D., Cervantes, I., Molina, A., 2006b. Genetic evaluation of dressage performance in Spanish Purebred horses. 57th Annual Meeting of the European Association for Animal Production. Book of abstracts 12. Antalya, Turkey. 17–20 September.

Valera, M., Galisteo, A.M., Molina, A., Miró, F., Gómez, M.D., Cano, M.R., Agüera, E., 2007. Genetic parameters of biokinematic variables of the trot in Spanish Purebred horses under experimental treadmill conditions. Vet. J. doi:10.1016/j.tvjl.2007.07.031.

Van Eldik, P., van der Waaij, E.H., Ducro, B., Kooper, A.W., Stout, T.A.E., Colenbrander, B., 2006. Possible negative effects of inbreeding on semen quality in Shetland pony stallions. Theriogenology 65, 1159–1170.

Van Wyk, J.B., Fair, M.D., Cloete, S.W.P., 2006. Case study: the effect of inbreeding on the production and reproduction traits in the Elsenburg dormer sheep stud. Livestock Sci. doi:10.1016/j.livsci.2006.10.005.