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Genetic study of gestation length in andalusian and arabian mares

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Abstract

The length of gestation in Andalusian, or Spanish Purebred (SPB) and Arabian (AB) mares reared in Spain was analysed, based on 766 spontaneous full-term deliveries appertaining to 141 mares of SPB breed and 72 mares of AB breed in 31 breeding seasons. The data were obtained from the Yeguada Militar de Jerez de la Frontera stud farm in Cádiz, Spain. The mean length of gestation was of 336.8 ± 0.48 days in the SPB mares and 340.3 ± 0.63 days in AB mares. To assess the accurate prediction of time of birth the potential effect of a number of factors was investigated. The influences of the breed, mare, month and year of mating, age of the mother, number of births and sex of the foal were statistically significant. The factor have the greatest influence over the gestation length was the mare itself, with a correlation among consecutive births of around 0.4. The effect of inbreeding, both of the mare and foal, was negligible. Gestation length shortened as the breeding season progressed: in both breeds, a delay of 1 month in mating corresponded to a decrease of 3 days in the gestation length. According to our results, gestation length decrease as the mare gets older, with the shortest gestation periods when the mare is 10–12 years old, and from this point on, it slowly increases. The gestation period shortens as the 4th or 5th birth approaches, and then gets progressively longer. The range of variation in gestation length due to the number of births to the mare is of 2.9 days for the AB mares, and 2.2 days for SPB mares. The heritability for the gestation length for AB and the SPB breeds was 0.2, with a repeatability of 0.36 and 0.37, for SPB and AB breeds, respectively. With the data from both breeds, and using a classical approach, the response to selection was estimated if mares with extreme gestation lengths were culled, i.e. lengths which are under 310 days, or over 360 days. According to our results, in the case of

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SPB, a decrease of 14–45% would occur in the number of extreme gestation lengths, while in the AB breed, this value would decrease from 2 to 39%.

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1. Introduction

The length of gestation is a physiological variable of economical importance in most domestic species. The length of full-term pregnancies varies within a short range of days, even though a certain variability can be appreciated and justified genetically as much as by environmental factors. In horses, the range of variability of the gestation length is larger than in other domestic species (Bos and Van Der Mey, 1980), probably due to the fact that their long gestation period is influenced by physiological factors that do not influence the gestation lengths of other species (for instance, embryonic diapause, reported by Lofstedt, 1992). A number of studies have confirmed these wide variations in gestation length for various breeds of horses (Pérez et al., 2003).

Additionally, the variation in physical signs of imminent parturition makes the prediction of parturition in the mare particularly difficult. The management of high-value stock demands the precise prediction of parturition. Even though in the equine the gestational length is insufficient to determine foetal readiness for birth (Lofstedt, 1992), since, to a certain extent, the mare can regulate the size of the foal (Allen et al., 2002), the knowledge of the gestation length and the possibility of predicting the date of birth can be important to a successful management of the pregnant mare. The inability to accurately predict the timing of parturition is incurred in extra labour and veterinary costs, as well as higher risks to both mare and foal (Davies-Morel et al., 2002). Furthermore, to coordinate deliveries in a given period of time, mares can be grouped according to their predicted gestation lengths. On the other hand, this enables the culling of mares with very long gestation periods that result in very large foals, which can, under some conditions, cause dystocic labours, as well as of mares with very short gestation periods that produce very light-weight foals. Therefore, any factors that may be used to help determine the moment of parturition are of considerable interest to the industry.

Gestation lengths from 310 to 380 days (Rossdale et al., 1984) have reportedly resulted in viable foals, although generally gestation lengths of 320–360 days are considered acceptable (Panchal et al., 1995). This large variability of time in which viable foals can be born, indicates that gestation length in the mare may be highly susceptible to both genetic and environmental factors.

According to published studies, the main environmental factors influencing gestation period in a certain breed are related to age of mother, number of foalings, nutrition, sex of the foal, year and month of conception, season of conception and photoperiodic influence (Howell and Rollins, 1951; Pozo-Lora, 1954; Flade and Frederich, 1963; Hevia et al., 1994; Panchal et al., 1995; Davies-Morel et al., 2002; Vassilev et al., 2002). Nevertheless, other factors have been analysed, like hair colour (Dring et al., 1981; Blesa et al., 1999) or moon cycle phase (Blesa et al., 1999), even though the results obtained were not significant.

From a genetic point of view, the studies that have been conducted up till now show values of heritability high enough to expect a significant response to selection (Vassilev et al., 2002). In this sense, to determine the best selection method and to estimate the genetic progress in a

specific breed, it is essential to estimate genetic parameters and define the genetic structure and environmental breeding conditions in this breed.

The aim of this study was to analyse the main environmental and genetic factors influencing gestation length and to estimate the heritability and repeatability of the gestation lengths in the Spanish population of Spanish Purebred (SPB) and Arabian (AB) breeds. The final objective was to test whether selection would result in a corresponding decrease in the percentage of animals with short or prolonged gestation lengths in the next generation.

2. Material and methods

Reproductive records were taken from the populations of Spanish Purebred and Arab horses, belonging to the Yeguada Militar de Jerez de la Frontera, Cadiz, stud farm, situated at latitude 36°41′N and longitude 06°09′W. Throughout its history, this stud farm has strongly influenced the SPB breed. In it were born several stallions that were among the most influential on the breed (Valera et al., 2005). It is a breeding farm and, simultaneously, a stallion deposit, with both SPB and AB stallions available to breed in stud farms that requested them. As such, it has maintained individuals that represent most genetic lines from both breeds (Valera et al., 2003). Yeguada Militar de Jerez de la Frontera can, therefore, be considered as a good representative of the existing variability, for both SPB and AB, in Spain. Furthermore, its breeding management control is superior to most Spanish stud farms.

The reported analysed data represents 31 breeding years and were grouped in 20 classes (<1980, 1980–1998). Mating was by natural mount. Until 1980, gestation lengths were calculated as the time from mating to parturition. This was assumed to be equivalent to ovulation to parturition, even though sperm may survive for up to several days within the mare's tract and still achieve fertilization (Newcombe, 1994). From this year on, in all gestations, the moment of ovulation was determined using ultrasound scanning. The mares were covered within the imminent ovulation period, considering the time of ovulation coincident with that of fertilization (Davies-Morel et al., 2002). The advent of ultrasonic scanning in Spain began in this stud farm and so, from 1980 onwards, the accurate timing of ovulation and, hence, the precise calculation of gestation length, could be made.

In this work, we only considered gestations with normal parturition and viable newborn. The 766 analysed births represent a population of 213 mares (141 SPB and 72 AB). These births resulted in 49.1% males and 50.9% females. The age of the mares at delivery ranged from 2 to 23 years (mean 7.6, 95% boundaries between 3 and 16). The mean number of births was of 3.8 per SPB mare and 3.3 per AB mare. As for stallions, the mean was of 5.6 foals per SPB stallion and 5.4 foals per AB stallion.

2.1. Analysis of factors influencing gestation length and statistical procedures used

With this information, we have studied the descriptive statistics of the gestation length variable for the global population, as well as for each breed.

To analyse the possible influence of the different environmental factors on gestation length of the mares, we carried out an ANOVA factorial model, which included as factors the age of the mother (13 classes: under 4 years old, 4, 5 and up to 14 years old and over 14 years old), the month (7 classes: December–June) and year of conception (20 classes: <1980 and yearly from 1980 to 1998), and the sex of the foal, as well as different interactions between these factors. A previous model (data not shown) included the number of births as a factor, instead of the age of

the mare. Because of both factors are so highly correlated (r = 0.85, 0.90 to AB and 0.82 to SPB), and also because of the higher coefficient of determination of the model that includes the age of the mare, we chose to include the latter in the definitive model.

Those factors that were found to be significant were submitted to a variance component estimate for the quantification of the variance of gestation length explained by each factor.

To understand to what extent the foaling length of a mare could be used to estimate the length of her next foaling, a regression analysis was carried out on the length of a gestation over the length of the previous one. This kind of analysis is a classical method to estimate the repeatability of a certain character. Weighted correlations between adjacent records of the same mare were also computed, another classic method of estimating repeatability (Bliss, 1967). This was accomplished by estimating the correlation coefficient between the length of the first and the length of the second foaling, and also the correlation coefficient between the lengths of two consecutive foalings of the same mare.

We also studied the possible influence of the inbreeding coefficient of the mare and the foal over the gestation length, through the analysis of the correlation between gestation length and inbreeding coefficients of both mare and foal. An ANOVA test was used to compare the mean gestation lengths of different inbreeding levels for both mare and foal: low F being under 6.25%, moderate F between 6.25 and 12.5% and high F over 12.5%. For the individual inbreeding coefficient estimation (Wright, 1931), genealogical trees were reconstructed to the last known generation using the studbooks of both breeds. They were then entered into a database with 8439 records (5823 for SPB, and 2616 for AB).

Finally, we analysed the predisposition of the mares that presented at least one gestation length over or under the 95% limits to have longer or shorter gestation periods. For this, we estimated the mean gestation length for those mares, removing all records above and under those limits.

The statistical analyses were achieved using the Corr, Glm, Means, Tabulate and Varcomp procedures of the Statistical Analysis System (SAS) package, Version 6.0.

2.2. Genetic parameters estimation

To estimate of heritability and repeatability parameters, we designed a best linear unbiased predictor (BLUP) univariate animal model, in which we considered the length of gestation as a character of the mare, and, as fixed environmental factors, the year of conception, the delivery season and the sex of the foal. In this case, the age of the mare was considered a co-variable (linear and quadratic). The random factor included in the model was the additive genetic effect of the animal itself (the mare), and the permanent environment effect of the mare as uncorrelated random effect.

To obtain the relationship matrix, we expanded the genealogical trees up to the third known generation (great grandparents), through the data gathered from the SPB and AB studbooks, creating a database with a total of 1253 genealogic entries (841 belonging to SPB and 412 belonging to AB).

To estimate of heritability and repeatability parameters, we used Groeneveld (1998) VCE program, Version 4.0, which follows a REML iterative procedure.

Finally, and using these parameters and the statistical values that characterize the frequency distribution (mean and standard deviation) of both breeds, with a classical approach (see Falconer and Mackay, 1996; Roff, 1997; Lynch and Walsh, 1998), we estimated the genetic progress (mean and variance) that would be obtained if we eliminated mares with gestation lengths under the inferior limit of the frequency distribution (premise a), or with gestation lengths outside the 310–360 days

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Breed	N	Mean \pm S.E.M.	Median	95% Populations boundaries	Coefficient of variation (%)
SPB	532	336.75 ± 0.480	337	311–358	3.29
AB	234	340.27 ± 0.632	341	313-357	2.84

Table 1
Descriptive statistics of the gestation length in Spanish Purebred (SPB) and Arabian (AB) mares

boundaries (premise b). Having estimated the progress in the following generation, we calculated the percentage of animals with gestation lengths standing outside of these boundaries.

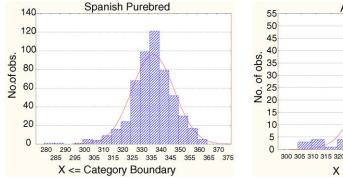
3. Results

We have obtained a mean gestation length of 336.8 days for SPB mares and 340.3 days for AB mares (Table 1). A wider range was found among the SPB mares, with boundaries at 95% of 47 days, and a difference of 79 days between extreme values, when compared to the 44 days found in the AB breed with 54 days between extreme values.

In both breeds, the greatest frequency was found in the 335–340 modal class, with 23% of the gestations (Fig. 1). In both breeds, the coefficients of variation were very small, indicating the low variability of this reproductive parameter, much lower than for other reproductive parameters in the horse (Langlois, 1973).

3.1. Analysis of the main factors influencing gestation length

Table 2 gives the significance levels of the multifactor ANOVA models of those factors that significantly affected the length of the gestation period. According to our results, the pregnant mare itself is the most influential factor in gestation length. Thus, globally, the mare's influence represents 25.8% (Table 2) of this variable's variability, which means over 50% of the variability taken up by the analysed model, 47.8% of the gestation length variability. If this same analysis is done separately to each of the breeds, we will find that the mare explains 25.7% of the variability, i.e. 56% of the variability taken up by the model, in the SPB, while in the AB, it accounts for 26.4% of the variability, i.e. 59% of the variability taken up by the model.



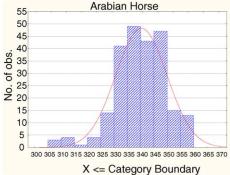


Fig. 1. Histogram of gestation length for Spanish Purebred (SPB) and Arab breed (AB).

Factors Significance level (P)Variance components % Of variance components Breed 6.789 5.40 < 0.001 Mare < 0.001 32,429 25.81 Age of mare < 0.001 2.402 1.41 Sex of foal < 0.05 0.546 0.43 Year of conception < 0.001 5.533 4.40 5.48 Month of conception < 0.001 6.888 Year × month of conception < 0.001 5.434 4.32

Table 2
Significance level of ANOVA factorial significant factors and explained proportion of variance of gestation length in Spanish Purebred and Arabian mares

From the remaining analysed effects, those with greater significance levels are the breed, which explains 5.4% of the variability, the year of conception, the month of conception and the interaction between both these factors. Globally, the factor month—year of conception accounts for 14.2% of the variability. The factors with lesser levels of significance are the age of mare (1.41%) and the sex of the foal (0.43%).

3.1.1. Mare

As shown in Table 2, if we consider the factors inherent to the mare itself (maturity, physiological status and so on) together with its age, we can account for 27.2% of the variability of the gestation length.

The regression of the length of a second gestation over a previous gestation had a moderate magnitude, but this was, statistically, highly significant (b = 0.359 in the global simple, 0.338 in SPB and 0.365 in AB). The correlation between the length of two consecutive gestation periods was of 0.383 (0.394 in SPB and 0.380 in AB).

Finally, we studied mares that presented at least one gestation period out of the 95% boundaries (Table 1) to analyse their predisposition to present longer or shorter gestation periods. We found a reduced number of mares (26), with a total of 96 births, so results should be considered with extreme caution (8 AB mares and 18 SPB mares). Of these 26 mares, 14 presented an extremely short gestation period (4 AB mares and 10 SPB mares), while 12 presented an extremely long gestation period (4 AB and 8 SPB).

We estimated the mean gestation lengths for these mares, excluding the extreme gestation periods. The mean gestation length for mares presenting an extremely short gestation period was of 336.9 for the SPB and 337.2 for the AB breed. In the case of mares presenting an extremely long gestation period, the mean was of 342.4 in SPB mares and 354.2 in AB mares. The differences between the means of this group and the general group were non-significant in the SPB, whereas in the AB the differences were significant to a 99% level. When both breeds are included, the means were also statistically different.

From our results, seven of the eight AB mares presented mean gestation periods above or below the breed mean values, as expected. In the case of SPB, however, only 10 of the 18 mares had means that fitted the expected values, although in the other cases, they were very near the breed mean values.

As regards the age of the mare, the greatest number of foalings occurred when the mare was between 4 and 9 years old in the case of SPB mares (66.9%), and between 4 and 7 years old for Arabian mares (55.3%). The lowest number of foalings happened in mares older than 14 in the SPB breed (6.6%) and older than 11 in the AB breed (15.2%).

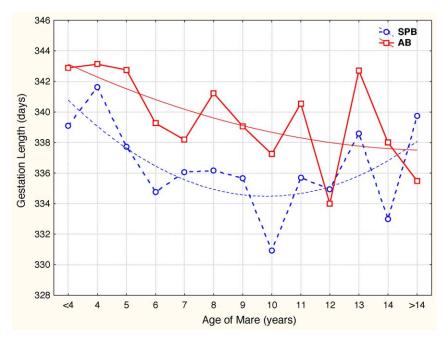


Fig. 2. Evolution of mean gestation length according to age of the mare in Spanish Purebred (SPB) and Arab breed (AB).

According to our results, the gestation length decrease as the mare gets older, with the shortest gestation periods when the mare is 10–12 years old; from this point on it slowly increases (Fig. 2). Differences of 10 days for the SPB and 9 days for the AB breed were found. Upper values were found when mares are 4 years old, presenting mean gestation lengths of 341.6 days for SPB and 343.1 days for AB. On the other hand, values for the shortest gestation periods were when mares are 10 and 12 years old for SNB and AB, respectively, with mean values of 330.9 and 334 days, respectively. These values adjust themselves to a second-degree polynomial equation.

The number of foalings is highly correlated with the age of the mare (r=0.85) in the global simple, 0.90 in AB and 0.82 in SPB). It was noticed that the gestation period shortens with the approach of the 4th or 5th birth, and then gets progressively longer. The range of variation undergone by the gestation length due to the number of births is 2.88 days for AB mares and 2.22 days for SPB mares.

As concerns the influence of inbreeding over the gestation length, negligible results were found in the correlations between both the mares' and the foals' inbreeding coefficients and the gestation length (-0.0002 and 0.0222, respectively).

The mean inbreeding coefficient for the 376 SPB mares that were inbred (71% of the animals) was 0.070 ± 0.0035 (with a maximum of 0.5). In the AB mare, the mean coefficient for the 211 inbred animals (90% of the whole sample) was of 0.083 ± 0.0032 (with a maximum of 0.5).

The mean inbreeding coefficient found the inbred AB foals (120 animals, representing 51% of the AB foals sample) was of 0.086 ± 0.0035 , with a maximum value of 0.252, whereas in the SPB breed, the mean value was of 0.073 ± 0.0036 , with a maximum of 0.316, for the 234 inbred foals, representing 44% of the SPB foals.

To determine whether the low correlation values found were due to a lack of association of the variables, or if the range of inbreeding coefficients was too low to show signs of

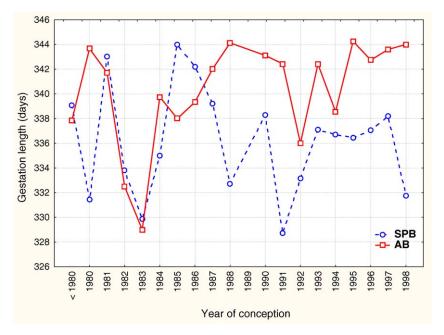


Fig. 3. Evolution of mean gestation length according to year of conception in Spanish Purebred (SPB) and Arabian mares (AB).

the inbreeding effect, a simple ANOVA test was performed to compare the mean gestation lengths of mares grouped under three levels of inbreeding coefficient: low (F < 6.25%), average ($6.25\% \le F \le 12.5\%$) and high ($F \ge 12.5\%$). Our results showed no significant differences (F(2, 272) = 2.0860, p = 0.06729). The same results were obtained when using the same test to analyse the influence of the foal's inbreeding coefficient (F(2, 272) = 1.8680, p = 0.15640).

3.1.2. Month and year of conception

Fig. 3 shows the gestation length evolution according to the year of conception in the analysed period. It can be seen that there is a great variability with maximum differences between 2-year periods, which range between 11 days in AB (between 1981 and 1982) and 12 days for SPB (between 1983 and 1984). In general, the range in variation of the gestation lengths among years was 5 days for SPB mares and 3.7 days for Arabian mares.

Fig. 4 shows the gestation length evolution according to the breeding season and month of conception. The greatest number of conceptions occurs between the months of February and May (84% in SPB and 88% in AB), the natural breeding season in Spain (Pérez et al., 2003), corresponding to births from January to April. Transitional period conceptions (from September to January) were only 13 and 9% for SPB and AB mares, respectively. Finally, the end of the breeding season (June and July) represented the remaining 3% of conceptions in both breeds.

It was found that the gestation lengths decrease as the months of conception progress, reaching their upper value when conception happens in the months of December and January, and the lower value when it happens in the months of May and June (Fig. 4). The comparison of means test for the three mating seasons resulted in highly significant statistical differences (F(2, 760) = 9.08, p = 0.00013; very significant in SPB, F(2, 529) = 5.88, p = 0.002107 and highly significant in AB (F(2, 231) = 7.64, p = 0.00061 or p < 0.001), with a 3-day difference between transitional period

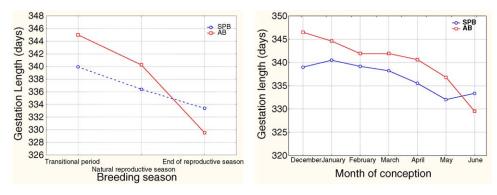


Fig. 4. Evolution of mean gestation length according to the breeding season and month of conception in Spanish Purebred (SPB) and Arabian mares (AB).

and natural breeding season in SPB mares and an equal difference between natural breeding season and the end of breeding season. These differences reach 5 and 10 days, respectively, in the AB breed.

The range of variation of gestation length, according to the conception month, is 8 days in SPB and 17 days in AB. So, when the SPB mares conceive in January, the gestation period increases up to 340 days, but when the mares conceive in May, this variable decreases to 332 days. When AB mares conceive in December, the gestation period increases to 346 days, and when they conceive in June, this variable decreases to 329 days. Finally, the average difference among the gestation periods, corresponding to two consecutive conception months, fluctuates around 3 days in both breeds.

3.1.3. Sex of the foal

In the populations of SPB and AB, 50.9 and 44.9% of gestations, respectively, resulted in a colt, while 49.1 and 55.1% resulted in a filly. Our results show (Table 3) larger gestation lengths for the colts (337.9 days and 341 days for SPB and AB, respectively) than for the fillies (335.5 and 339.6 days, respectively), resulting in a difference of 2.37 days between the gestation periods of both sexes in SPB, and 1.41 days in AB.

3.2. Genetic parameters of the gestation length in SPB and AB mares

The heritability obtained using a BLUP animal model for the gestation length parameter was 0.21 in both breeds (Table 4). Repeatability was of 0.36 for SPB and 0.37 for AB.

Table 3
Descriptive statistics of gestation length according to the sex of foal on Spanish Purebred (SPB) and Arab breed (AB)

Breed	Sex of foal	N	Mean \pm S.E.M.	95% Sample boundaries	Coefficient of variation (%)
SPB	Male	271	337.91 ± 0.674	310–359	3.28
	Female	261	335.54 ± 0.676	313–356	3.25
AB	Male	105	341.05 ± 0.956	313–359	2.87
	Female	129	339.64 ± 0.842	313–357	2.82

	SPB	AB
Genetic additive variance (days ²)	22.12	19.15
Permanent environmental variance (days ²)	15.36	13.74
Environmental variance (days ²)	68.32	56.66
Phenotypic variance (days ²)	105.80	89.55
Heritability	0.21 ± 0.013	0.21 ± 0.027
Reneatability	0.36 ± 0.048	0.37 ± 0.062

Table 4
Genetic parameters for gestation length in Spanish Purebred (SPB) and Arab breed (AB)

Table 5 shows the expected results of gestation length after a cycle of selection under the two premises that were analysed in both breeds.

It can be seen that the percentage of mares to cull would be under 1% for both breeds in premise A (culling of mares with gestation lengths under 310 days) and over 2% in premise B (culling of mares with gestation lengths under 310 and over 360 days). The response to selection has determined a very slight increase in the gestation period mean in both breeds under premise A, and a very slight decrease in this value for both breeds under premise B. As for the expected reduction in the phenotypic variance of this variable in the next generation, it varied from 0.9% (AB breed, premise A) to 17.8% (SPB breed, premise B). With both parameters (mean and phenotypic variance), in the next generation one can expect from 1.3% (AB breed, premise B) to 2.2% (SPB breed, premise B) of animals with gestation lengths outside these boundaries. When compared to animals with extreme gestation periods in the parental population (2.58% in SPB and 2.14% in AB), the expected response will be a decrease of 2–45% in extreme animals, depending on the considered breed and premise.

4. Discussion

A number of studies have confirmed wide variations in gestation length for different breeds of horses (Salerno and Montemurro, 1965b; Pérez et al., 2003). Hence, even though the mean gestation found in literature for different breeds is generally between 335 and 345 days (see Pérez et al., 2003, for a review), an equine gestation length between 320 and 360 days can be considered normal (Laing and Leech, 1975; Rossdale et al., 1984; Rossdale, 1993; Immegart, 1997). Gestations of less than 320 days are generally considered short and resulting foals may present, among other characteristics covered by the term 'prematurity', predisposition to illness, low birth weight and inability to stand. Gestations shorter than 300 days are not viable because vital foetal organs are not fully developed (Rossdale, 1976), even though 'full-term' gestations have been described lasting from 294 to 386 days. It should be pointed out that in the SPB breed, there were two foals coming from gestations under 300 days that survived normally, which seems to disagree with previously reports on foal viability and the classification of dysmature foals (Rossdale, 1976).

Likewise, a gestation period over 360 days is considered long or 'prolonged'. In such cases, the newborn foal is 'post mature' and might display weakness, large size with poor muscular development, among other abnormalities (Rossdale, 1993). Nevertheless, there are references of gestation periods over 400 days resulting in a live foal: 403 days (Braunton, 1990) or 419 days (West, 1994). In our sample, no gestation lasted over 360 days in the AB breed and only 5 did in the SPB breed (<1%). This value was slightly lower than that found by Pérez et al. (2003) in this same breed, but in the Carthusian lineage, that pointed to 1.10% of prolonged gestations.

Table 5
Expected response of selection to gestation length under different premises in Spanish Purebred (SPB) and Arab breed (AB)

	•	C	C			*		, ,		
Breed	Selection type	Animals to cull	% Animals to cull	i	R	G1 mean	% Variance reduction	$\sigma_{ m P}$	% Total animals (inferior; superior) out of boundaries	% Decrease ^a
SBP	Truncation	GL < 310 days	0.788	0.060	0.051	336.801	5.360	10.779	2.217 (0.646; 1.571)	14.129
	Stabilizing	GL<310 days GL>360 days	2.582 (0.788 + 1.794)	0.109	- 0.063	336.687	17.851	10.042	1.407 (0.394; 1.013)	45.515
AB	Truncation	GL < 310 days	0.086	0.060	0.007	340.277	0.941	9.614	2.095 (0.082; 2.013)	2.171
	Stabilizing	GL<310 days GL>360 days	2.142 (0.086+2.055)	0.109	- 0.099	340.171	15.456	8.882	1.313 (0.034; 1.280)	38.678

GL, gestation length; i, selection intensity; r_{AP} (precision of valuation method) = 0.458; R, expected response to selection; G1 mean, mean gestation length expected on the next generation; σ_P , phenotypic standard deviation expected on the next generation.

^a % Of decrease in mares with gestation periods out of the 310–360 days boundaries in the first generation, when compared to the parental population.

In our study, the range in gestation length was considerable, being of 71 days in the SPB breed, with gestations from 290 to 361 days, and 54 days (306–360) in the AB breed, yielding live foals. In the case of the Spanish Pure Bred horse, this value is similar to the frequently quoted value of 70 days (Immegart, 1997), and slightly lower than those obtained by other authors, such as Davies-Morel et al. (2002), for live foal births. In both breeds, the range is superior to the 40-day range considered acceptable by the industry, and likely to result in a viable foal (Rossdale, 1976). Nevertheless, the number of extreme length gestations is very low, with only 14 animals (9 SPB and 5 AB) having been found with gestation periods under 310 days and 5 animals (all SPB) with gestation periods over 360 days. Possibly, other gestation periods outside these boundaries could have occurred, but as they did not result in a viable foal, they were not included in our analysis.

In our analysis, it was found that, even considering the boundaries between which are found 95% of the population of SPB and AB (311–358 SPB and 313–357 AB, see Table 1), gestations lasting less than 320 days could not be found and, hence, beneath the generally considered normal limit. In fact, and considering that all the foals were viable, we found that 6.8% of SPB gestation lengths and 3% of AB were under 320 days. These values are higher than those of 1.65% obtained by Pérez et al. (2003) in the Carthusian lineage of the SPB horse.

Generally, we consider the wide range of gestation length in the mare to be due, among other causes, to the ability to prolong gestation by an embryonic diapause (Lofstedt, 1992; Vandeplassche, 1992), a feature not found in other domestic animals. This is one reason why gestational length, alone, is insufficient for determining foetal readiness for birth. Lofstedt (1992) mentions that a delayed embryonic development may be observed between days 20 and 40, which is associated with lower plasma progesterone levels.

The mean gestation length period obtained (Table 1) for the SPB (336.7 days) was lower than that found in SPB populations, by almost 7 days, to those obtained by Pozo-Lora (1954) and Rodero and Pozo-Lora (1960), and by 2 days to those obtained in the SPB Carthusian lineage by Pérez et al. (2003). However, our results were 3 days higher than those obtained by Pérez et al. (1997) in the Carthusian lineage of the SPB.

Comparing our results with results obtained in other genetically related breeds, we find that, in the Lusitano breed, the gestation periods are 1.1 and 7.2 days longer than ours, according to Vieira (1962) and Mario and Vidal (1986), respectively. In the Lippizaner horse, the mean gestation period is 3 days shorter than ours, according to Ilancic (1958).

Regarding the AB breed, we obtained a gestation period of 340.3 days, longer than that of 336.4 days found by Howell and Rollins (1951) and of 337.4 days found by Mauch (1937), but shorter than the values obtained by other authors who studied this breed in the Iberian Peninsula, such as Pozo-Lora (1954) in Spain (343 days) and Mario and Vidal (1986) in Portugal (348.3 days).

There is no doubt that the country or geographic area where breeds are kept can influence the differences observed within these breeds. We cannot compare gestation periods in a cold, rainy climate with few hours of sunlight (such as Holland or Germany), with a dry, hot climate with a much higher number of sunlight hours, such as Spain. In fact, Hammond (1938) showed that the amount of sunlight hours acts on the endocrine system of the mare, causing variations on the gestation length. Likewise, the physiological mechanisms of the mare and foal can suffer slight changes, to make sure that the moment of birth coincides with the environmental conditions most favourable to the foal's development. Consequently, mean temperature, humidity, etc. can, in some way, influence the moment of birth. Therefore, a possible explanation to the longer gestation periods found for the AB breed in the Iberian Peninsula may be due the much higher number of sunlight hours in Spain and the particular weather conditions of the area.

4.1. Analysis of the main factors influencing gestation length

Numerous studies have addressed the influence of genetic and environmental factors on gestation length. The main environmental factors influencing gestation period are related to age of the mother, nutrition, sex of the foal, year and month of conception, season of conception and photoperiod (Staffe, 1935; Mauch, 1937; Howell and Rollins, 1951; Pozo-Lora, 1954; Flade and Frederich, 1963; Hevia et al., 1994; Panchal et al., 1995; Davies-Morel et al., 2002; Vassilev et al., 2002). Nevertheless, other factors have been studied, such as the colour of coat (Dring et al., 1981; Blesa et al., 1999) or the influence of moon phase (Blesa et al., 1999), even though the results were not significant.

The main genetic factor, apart from breed, is the mare itself, although the foal and sire effects have also been analysed (Marteniuk et al., 1998).

According to our results, the factors that show the greatest influence over the gestation length in the SPB and AB breeds reared in Spain are, apart from the breed itself, the mare, the month—year of conception and the sex of the foal.

4.1.1. Influence of the mare

Each specific species has a genetically determined development rate, and birth occurs in response to a signal, given when the foetus attains an appropriate size and/or maturity (Jenkin and Young, 2004). Such a signal could be transduced by the mother (e.g. uterine volume), the foetus (e.g. nutrient restriction) or placenta (e.g. increased foetal demand for nutrients). In most domestic species, the role of the foetus is clear (Lye, 1996), since it is essential that the foetus is born at a time when it is capable of surviving in the extra-uterine environment, it is, therefore, appropriate that the foetus plays a major role in determining the timing of parturition.

In the horse, there is no strong evidence in support of a major role of the foetus in initiating parturition (Liggins and Thorbum, 1994), even though Allen et al. (2002) showed significant effects of both maternal and foetal genome on the duration of gestation. They showed the interacting influences of maternal size and foetal genotype on placental and foetal development in the mare, by comparing conventional within-breed experimental foalings established by embryo transfer. The timely birth of a developmentally mature foetus, appropriate for the species, requires that some mechanism synchronizes foetal development and maturation with the maternal mechanisms that affect the birth. In some species, particularly ruminants, the synchronizing factor has clearly been shown to be glucocorticoid, secreted by the foetal adrenal cortex. In the horse, the foetal cortisol profile increases only in the last 48 h before delivery and maternally administered glucocorticoid does not induce labour, as it does in other domestic animals (Jenkin and Young, 2004).

Our results point to the mare being mainly responsible for the gestation length. Within the 'mare' effect one can include the direct effect of genes directly related to the gestation length (for instance, loci that are responsible for the production of occitocin when there is a repletion of the uterine mucosa), as well as the maternal environment that all foals from that mare have in common (called the permanent environmental effect).

Both effects can contribute to the high correlation between consecutive births in the same mare. Thus, the correlations among the phenotypic expressions of gestation length in different foalings of the same mare are due, at least partially, to the genotypes of mares, to the maternal environment and the similarity of the genotypes of the foals, given that a quarter of the genes of the foals are, on average, common to maternal siblings.

The values of regression of the length of a second gestation over a previous one, although highly significant, were of a moderate magnitude (between 0.34 and 0.36). This indicates that

the existence of other factors, not related to the mare, influencing this variable, agreeing with the results of the multifactorial ANOVA test. This estimate of regression is a classical method for the calculation of the repeatability of a character (Cunningham and Herdenson, 1965), such as the intra-class (intra-mare) correlation or the weighted mean of the correlations between adjacent records of the same mare (Bliss, 1967). Using this last method, our estimates were slightly higher than those obtained through regression (0.38–0.39).

The age of the mother is also considered an important factor by most authors, but there are discrepancies, since some authors have not found significant differences (Hintz et al., 1979b; Vivo et al., 1983; Pérez et al., 1997; Kurtz Filho et al., 1997; Sánchez et al., 1999; Davies-Morel et al., 2002).

In our study, the age of the mare is a statistically significant factor, although less influential than others. We observed longer gestation periods in both younger and older mares (Table 2). Similar results were obtained in most studies (Akkayan and Demirtel, 1974; Platt, 1979; Bos and Van Der Mey, 1980; Demirci, 1988). This was postulated to be due to a decrease in uterine/placental nutritional efficiency (Pashan and Allen, 1979) and/or the metabolic-hormonal drive to grow (Gluckman and Hanson, 2004), as a consequence of age and the multiparous state, slowing intrauterine growth and prolonging gestation. Alternatively, other authors concluded that primiparous mares had shorter gestation periods than other mares (Pjanovic, 1965; Schermerhorn et al., 1980).

The same occurs with the number of foalings, on which Pool-Anderson et al. (1994) report a 10-day longer duration in nulliparous versus multiparous Quarter Horse mares, although other researchers have failed to record significant differences (Arora et al., 1983; Sánchez, 1998). It can be considered that primiparous mothers (which are usually young mares) present longer gestation periods, since they are not as anatomically and physiologically prepared as older, multiparous mares. In contrast, the older mother can also present longer gestation periods, since it can present changes in the implantation of the placenta, with decrease in the nutrient supply (Hafez, 1987) and a decrease in the speed of foetal development.

The effects of inbreeding over different reproductive parameters have been thoroughly discussed in different equine populations (Mahon and Cunningham, 1982; Klemetsdal and Johnson, 1989; Cunningham, 1991). Nevertheless, the lack of association between gestation length and inbreeding coefficients of both mare and foal seems to agree more with an actual absence of influence than with low inbreeding levels in both populations, since previous work in the Carthusian lineage (Pérez et al., 1997), which has a considerably higher mean inbreeding coefficient, also did not find any significant differences. This is also consistent with the statements of Torres et al. (1977), who consider that the effect of inbreeding is patent in the zygotic phase or at the beginning of embryonic development, but find no data to sustain its influence in the more advanced stages of the uterine life.

4.1.2. Month and year of conception

The month and year of conception are two of factors that have also caused a greater variability in the gestation length parameter (nearly 10%).

In the first case, our results show that breeding season factors clearly affected gestation length, and that gestation length shortened as the breeding season progressed. The difference in the mean gestation length, for each month later in the breeding season a mare was mated, is the same as that obtained by Pérez et al. (2003) in the main SPB lineage (Carthusian), who found a decrease in gestation length of 2.75 days per month. In most studies, longer gestational periods are reported in mares bred early in the breeding season (Rophia et al., 1969; Hintz et al., 1979b; Arora et al.,

1983; Sánchez, 1998). In the SPB, Pérez et al. (2003) found that foalings of mares bred later in the breeding season were significantly shorter than those of mares bred in the transitional period or during the breeding season (334, 341 and 340 days, respectively). We found differences that are similar to these. Variation was greater when mares were bred out of season, as reported by Platt (1984) and Pérez et al. (2003).

These differences can be influenced by factors, such as feeding conditions or temperature. It has been suggested that nature attempts to bring the timing of parturition back to the ideal, i.e. early Spring, and that this may be achieved by shorter or longer gestations in late born and early born foals, respectively (Evans and Torbeck, 1998). Hence, favourable weather conditions affect the nutritional value of grasslands and, as a result, the mare can have a larger nutritional intake and the foal takes less time to reach the proper weight for birth (Davies-Morel et al., 2002). Langlois (1973) and Hafez (1987) indicated that well-nourished mares have shorter gestational lengths than mares on maintenance diets. Moreover, nutrition can accelerate or delay foetal growth and pre-birth maturity. As such, the balance between foetal and maternal nutritional requirements at the end of gestation may partly account for variations in gestation length in mares (Fowden et al., 1984). Moreover, as the temperature rises, the moment of delivery gets nearer to the months that have more favourable nourishing conditions (April and May).

Nevertheless, it is believed that the main cause of this variation is photoperiod, through its effect on the maternal brain. The precise mechanisms involved remain unclear, even though Sharp (1988) suggested that melatonin might be involved. The works of Hodge et al. (1982) demonstrated that pregnant mares subjected to 16 h of light per day from December 1st onwards, anticipated the date of birth. This suggestion echoes the findings of Langlois (1973), who reports that the hormonal environment in pregnant mares may be altered by variations in circadian rhythm. Also, it has been suggested that variation in light may be a cause of considerable variation in equine gestation length, due to the modification of the foetal maturation rate as labour approaches (Pérez et al., 2003). The results obtained here suggest that the mare may be able to bring parturition forward when more daylight hours are detected, which could be interpreted as the end of the breeding season. This natural adaptation mechanism allows the newborn foal access to the best nutritive and environmental resources. In our work, when the photoperiod was maximum (May-June), the gestation length was minimum (no artificial light was used in barns to modify the natural photoperiod). An association between increasing day length, increasing environmental temperature and decreasing gestation length was previously reported (Astudillo et al., 1960).

Other works report that the routine use of artificial lights to 'advance' Spring, and so induce early reproductive activity, and the now common practice of observing foaling mares by CCTV under 24 h light, may well be a complicating factor, since these practices will results in shorter gestation lengths and births earlier in the year (Davies-Morel et al., 2002).

Our results are also consistent with those of other authors regarding the influence of the year of conception on the variability of the gestation length. Hintz et al. (1979a), working with thoroughbred mares, obtained mean differences of 6.8 days between years. Pérez et al. (1997) reached similar conclusions for the SPB breed.

Thus, dry years and high average temperatures have a negative effect on the gestation length. Our study confirmed, after studying Peguy's climate diagrams for the years 1980–1988, that the drier years or those with more extreme temperatures are simultaneously the years with gestation periods longer than the population mean. Likewise, the pluviometric year 1994–1995 was the last of a 5-year dry period, Spain's second longest such period in the last 60 years. This may have influenced the nutritional quality of feedstuffs, which might have become deficient and irregular

(Silver and Fowden, 1982) leading to an early end of gestation as a mechanism for adjusting to adverse climatic and nutritional conditions.

4.1.3. Sex of the foal

Our results show that this is significant factor with less influence over the gestation length, since it only accounts for 0.43% of the total variance of gestation length (Table 2). According to our results, the gestations of colts are longer (2 days) than those of fillies (Table 3). Influence of foal sex on gestation length in the SPB breed was also reported by Vivo et al. (1983) and Pérez et al. (2003) found that colts' gestation periods were around 2–3 days longer than females'. In the AB breed, Mauch (1937) also found longer gestations for colts.

Many other authors have studied the effect of sex of the foal on equine gestation length (Gerger, 1960; Matassino, 1962; Pjanovic, 1965; Kodagali, 1973; Akkayan and Demirtel, 1974; Hintz et al., 1979a; Schermerhorn et al., 1980; Hevia et al., 1994; Panchal et al., 1995; Davies-Morel et al., 2002), and found statistically significant differences, with colt gestations being from 1.7 to 7 days longer.

Though it is generally accepted that the male offspring of many species have longer gestations than the females, the reason is unclear. It is agreed that the male body development is greater than the female's and, therefore, as birth only occurs when the foetal development is complete, the colts' gestation period would be longer, even though Wilsher and Allen (2002) have shown that colts have a better developed placenta, and might, therefore, be expected to develop more quickly. The longer gestation period of colts has been justified as being due to androgen action (Zegher et al., 1999), to different endocrine functions of male and female foetuses interacting differently with the endocrine control of parturition (Jainudeen and Hafez, 2000) and to sex chromosome-linked effects (Pergament et al., 1994).

4.2. Genetic parameters

The values obtained for heritability in both breeds (0.21) are of middle values, especially when compare to values obtained for other reproductive parameters (such as fertility, age at first descendant, number of births, etc.), where the heritability is usually under 0.1 (Langlois, 1973).

The heritabilities obtained by others authors for this physiological variable in SPB and AB breeds were, in general, higher than those we obtained for both breeds. This was probably due to the estimation models used, mainly the maternal half-sibs and full sibs models and, as a consequence, to the contamination with other effects. Nevertheless, genetic parameters also depend of the genetic composition of the population and the environmental circumstances to which the animals are subjected. So, in the estimation of parameters, the environmental sources of variation of the trait must be previously identified and included in the correspondent model. In our case, this included, apart from the mare itself as a genetic effect, the month—year of conception, sex of the foal and the age of the mare as co-variable.

As for the estimation method, one should refer to the works of Howell and Rollins (1951) on the AB breed with a heritability value of 0.36 (using a paternal half-sibs model), of Rodero and Pozo-Lora (1960) for SPB with 0.97 (with a maternal half-sibs model) and, finally, of Hintz et al. (1979b) on the AB breed with values of 0.25 (paternal half-sibs model), 0.97 (maternal half-sibs model) and 0.60 (full sibs model). These classical methods offer no advantage over the BLUP method and usually overestimate heritability due to the inclusion of other genetic effects (dominance and epistatic effects), especially the maternal and full sibs models (Falconer and Mackay, 1996).

In other breeds, and also using the classical methods, heritabilities between 0.19 and 0.38 have been obtained. Sato et al. (1973) obtained values of 0.19 (paternal half-sibs model) and 0.30 (full sibs model) for the Tokachi breed, whereas Schermerhorn et al. (1980) obtained 0.38 on Standardbreds (paternal half-sibs model).

The results of Vassilev et al. (2002), using the same model we used (animal model) on the Pleven Warmblood horse, estimated a heritability of 0.21–0.30.

The BLUP animal model, based on Restricted Maximum Likelihood (REML) methodology, is considered as the model that presents less bias in the estimates, since it presents a better correction of environmental factors and is less sensitive to problems that are typical of equine estimates, such as directed couplings (Langlois et al., 1983; Tavernier, 1988).

Repeatability in this study, which includes the direct genetic effect plus the permanent environmental effect of the mare itself, was 0.36 in SPB and 0.37 in AB. This result is similar to that one obtained by Rodero and Pozo-Lora (1960) with the AB, and Vassilev et al. (2002) with the Pleven Warmblood horse, although our results are lower than those obtained for the SPB and Salernitaine breeds by Rodero and Pozo-Lora (1960) and Salerno and Montemurro (1965a), respectively, with a repeatability of 0.5.

The obtained value is consistent with the importance of the mare effect over the gestation length, as was previously mentioned (Table 2), and the estimates obtained with classical methods of regression and correlation. Its mid-high value allows the estimation, within limits, of the range of gestation lengths of a certain mare based on the known value of one gestation period. This can be useful to the successful management of the pregnant mare, since it allows the culling of mares with very long gestation periods that result in very large foals, which can cause dystocic labours, as well as of mares with very short gestation periods that produce very light-weight foals. Also, mares can be grouped according to their predicted gestation lengths, to coincide deliveries in a determined period of time.

In improvement programmes, repeatability may be useful from different points of view. It indicates the increase in precision that can be obtained by repeated observations, enabling the prediction of future performance of the mare. It also reflects the mare's capacity at different ages and, as a consequence, improves the effectiveness of selection. With the obtained repeatability values, the increase in precision of the estimate obtained with two controls of length gestation over the estimate obtained with one control is only 18% (Falconer and Mackay, 1996), and the increase obtained with three controls over two is 5%. Obviously, the increase of precision is smaller as the number of controls increases. A repeatability of moderate magnitude, such as that found in this work, points to the need to collect data from two or three controls of gestation length per mare to obtain a reliable value without excessive time lost.

New schemes of genetic improvement aim to further adjust the decisions of selection to the demands and profitability of the breeding farms with a greater reproductive efficiency and a better use of all the available information resources. Although the selection of horses is primarily on the basic of non-reproductive parameters (speed, gait, etc.), nonetheless, the values obtained for heritability are large enough to allow a high response to selection for a shortened or a long gestation length in the two breeds studied in this work. Furthermore, effectively manipulating the timing of birth reduces perinatal loss and enhances productivity (Lye, 1996). Our results show a suitable response to selection either by culling mares with very short gestation lengths (directional selection) or culling mares with extreme gestation lengths (stabilizing selection).

The results of directional selection against short gestation length would be expected to show an effective decrease of very short gestations of 18% in SPB (from 0.788 to 0.646 %) and 5% in AB (from 0.086 to 0.082%) due to the different selection intensities used, the percentage of

gestations under 310 days is much smaller in the AB breed. This type of selection, in which we eliminate one tail of the frequency distribution, is usually known as *truncation selection* and it is, by far, the commonest form of artificial selection in animal breeding.

This type of selection would lead to a slight increase in the mean gestation length and a decrease in the phenotypic (and additive) variance of about 1% in the AB, and about 5% in the SPB due to the different selection intensities. Both these facts would also determine a decrease of gestation periods over 360 days, so, we would globally find a decrease in extreme gestation lengths (under 310 and over 360 days) of 2% for SPB and 14% for AB. This low magnitude is due to the low intensity of selection needed to cull animals with gestation periods less than 310 days.

Selection using double truncation, i.e. culling of animals with extreme gestation periods in both tails of the frequency distribution and maintaining animals with gestation periods between 310 and 360 days, would determine a kind of selection called *stabilizing selection*.

In contrast to the response seen in the case of directional selection, stabilizing selection is expected to influence more the variance than the mean in the selection against extreme individuals and pure stabilizing selection does not change the mean of the phenotype distribution. Stabilizing selection reduces variation and favours individuals with an average phenotype over the extremes (Lynch and Walsh, 1998). Hence, this mode of selection is often referred to as optimizing selection. In fact, there appears to be a fairly general acceptance of the idea that stabilizing selection is the cause of stasis, and that traits are maintained at local optima by stabilizing selection (Hansen and Houle, 2004).

Selection for an intermediate optimum will cause gametic disequilibrium or, in other words, reduce recombination in such a way as to reduce the amount of genetic variation (Hansen and Houle, 2004). Gametic-phase disequilibrium does not change the population mean. However, it affects the response to selection by introducing correlations between alleles at different loci, thereby, altering the additive genetic variance (Hansen and Houle, 2004).

In our case, we would expect a reduction in phenotypic variance superior to 15% in both breeds and a global reduction of extreme gestation lengths of about 40%, assuming a random mating population. The efficiency of this kind of selection is superior to the directional selection, even taking into account the difference in the applied intensity of selection, since the decrease in animals with short gestations is even greater, although it supposes culling a larger number of mares and of mares with prolonged gestations, which are usually considered less serious than shortened ones (Rossdale, 1976).

5. Conclusions

The mean gestation lengths found for the two breeds analysed in this study (336.7 ± 0.48) for SPB and 340.3 ± 0.63 for AB) are consistent with previous reports on these breeds under similar conditions, even though we found differences probably due to environmental conditions. The values considered normal in these breeds lay between 311 and 358 days in the SPB horse, and 313 and 357 days in the AB horse. This confirms the wide variation of this variable in the horse compared to other species. Nonetheless, the range in gestation lengths (290–361 days), all resulting in viable foals, is noteworthy and of clinical significance when considering foal dysmaturity.

According to our results, the mare itself is the main factor affecting gestation length. The correlation between different foalings of the same mare was moderate (0.38–0.40), but highly significant. Once several gestation lengths are known, predictions, with acceptable accuracy, can be made about the gestation length of that mare's following foalings. In contrast, we found no

influence of the inbreeding coefficients (neither the mare's, nor the foal's) over the gestation length, at least in the range of inbreeding values of the considered sample (mean 0.07 in the SPB and mean 0.83 in the AB).

Our data also pointed towards the significant influence of different environmental factors, such as year and month of conception, age of the mare and sex of foal. These results are also consistent with results found in other equine breeds, thus confirming the strong multifactorial influence of this variable.

Nevertheless, our data also showed values for heritability (0.21 for both breeds) and repeatability (over 0.35 for both breeds) that are high enough to enable to encourage suitable genetic progress should this variable be selected in a determined direction. Given the importance of this physiological variable, the most suitable selection method would be the stabilizing selection, in which animals with both very short and very long gestation periods are culled. The genetic response (both in mean and in variance) of the gestation length in the next generation ensures a clear decrease in extreme length gestations between 2 and 45%, depending on the breed and on the culling intensity. According to our results, the double-truncation selection would be more effective, even though it would mean the culling of a greater number of animals.

In improvement programmes, repeatability may be useful from different points of view. It indicates the increase in precision that can be obtained by repeated observations, and thus enabling the prediction of the future performance of the mare. This also reflects on the mare's capacity at different ages, thus improving the effectiveness of selection. Repeatability value obtained in this study, superior to 0.35 for both breeds, can be considered of moderate magnitude.

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