

Phenotypic and genetic analysis of reproductive traits in horse populations with different breeding purposes

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(Received 11 July 2019; Accepted 6 January 2020; First published online 6 February 2020)

Reproductive traits have a major influence on the economic effectiveness of horse breeding. However, there is little information available. We evaluated the use of reproductive traits as selection criteria in official breeding programs to increase the reproductive efficiency of breeding studs, analysing 696 690 records from the pedigree data of eight Spanish horse populations, with different breeding purposes. The reproductive parameters studied in both sexes were age at first foaling (AFF), age at last foaling, average reproductive life and generational interval. In the females, the average interval between foaling (AIF) and interval between first and second foaling were also studied. There were clear differences between sexes and breeds, which may be due to management practices, breeding purposes and the status of the populations, rather than to differences in actual physiological conditions. Riding mares were the most precocious (AFF, 1937.64 to 2255.69 days) and had a more intensive reproductive use (AIF, 625.83 to 760.07 days), whereas sires used for meat production were the most precocious males (AFF, 1789.93 to 1999.75 days), although they had a shorter reproductive life (1564.34 to 1797.32 days). Heritabilities (0.02 to 0.42 in females and 0.04 to 0.28 in males) evidenced the genetic component of the reproductive traits, with Sport Horses having the higher average values. These results support the selection by AFF to improve reproductive aspects because of its medium–high heritability and its positive correlations with other important reproductive traits. The inclusion of the AIF is also recommended in sport populations, because this determines the length of the breaks between foaling and conditions the reproductive performance of the dams, as well as their selective intensity, genetic gain and genetic improvement. It is therefore an important economic parameter in breeding studs.

Keywords: equine, heritability, pedigree, reproduction, selection

Implications

Reproductive traits have a major influence on the economical effectiveness of breeding studs. However, limited information is available concerning demographics and production data, and there are also very few estimations of genetic parameters of reproductive traits in equines. The possibility of including reproductive traits as selection criteria in the breeding programs of different horse populations has been evaluated in order to contribute to solving possible reproductive problems and improving reproductive efficiency. We suggest the inclusion of age at first foaling and average interval between foaling, which can be estimated (easily and cheaply) from the pedigree data and which has shown suitable heritability levels.

Introduction

Reproductive traits are crucial for the survival of the species not only in natural populations but also in livestock, since they have a major influence on the economic effectiveness of breeders and farms (Wolc *et al.*, 2009). This is particularly important in horses, where fertility disorders can have serious economic implications, considering that broodmares are expensive to keep, leading to economic losses if they do not produce one foal per year. Despite this importance, fertility traits are often considered less important than performance traits in most official breeding programs (Morris and Allen, 2002; Sairanen *et al.*, 2009; Wolc *et al.*, 2009).

Reproductive efficiency in horses has been reported to be low in comparison with other domesticated species. The

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generational interval (GI) in other Spanish populations of mammals is 2.97 years on average in sheep (Goyache *et al.*, 2003), 4 to 5 years in goats (Cervantes *et al.*, 2011a) and 3.70 to 6.08 years in reference populations of beef cattle breeds (Gutiérrez *et al.*, 2003). This could be due to certain limitations existent in the natural and assisted reproductive techniques employed, although these have improved in the last few years. The low-reproductive efficiency has also been partially attributed to the fact that broodmares have been traditionally selected for their war, draft and sporting abilities rather than on fertility traits. Nowadays, however, all over the world, horses are selected by a combination of pedigree, performance results and several morphological traits, and the physiological, environmental and managerial factors that might affect reproductive performance are generally overlooked (Dubois and Ricard, 2007; Sharma *et al.*, 2010). Thus, the reproductive management of individuals (Morris and Allen, 2002) as well as the environmental conditions in which they are bred (Schmidt *et al.*, 2017) have become key factors for increasing their reproductive efficiency and for contributing to the success of mares in carrying a pregnancy to term. According to Cilek (2009), the fertility of mares can be affected by many genetic and environmental factors, some of which can be measurable (age, breeding season, etc.) while others not (infectious diseases, parasitic infestations, etc.). We need to act on both kinds of factors in order to increase reproductive performance.

The veterinary literature on equine reproductive function and physiology is extensive (Madill, 2002; Scoggin, 2015). However, there is very little information available concerning demographic and production data in the breeding industry, including horses bred for different purposes, and what exists is mainly focused on thoroughbred horses (Allen *et al.*, 2007; Bosh *et al.*, 2009). For this reason, the estimation of genetic parameters for reproductive traits is limited (Campos *et al.*, 2007; Taveira and Silveira da Mota, 2007; Sairanen *et al.*, 2009; Wolc *et al.*, 2009;

Solé *et al.*, 2016). In addition, this lack of data is also heightened by the fact that the reproductive parameters should be analysed by taking the influence of productive management for each population into consideration.

We have therefore estimated the main reproductive parameters and their reproductive efficiency in eight Spanish horse populations using pedigree information. The heritability levels for the five largest populations have also been estimated in order to evaluate their inclusion as selection criteria in official breeding programs, considering that genetic selection can help to solve possible reproductive problems and to improve reproductive efficiency in breeding studs.

Material and methods

The official pedigree data of eight Spanish horse populations selected for different breeding purposes were analysed. In total, 696 690 records were obtained from 8 Breeders' Associations responsible for managing the official studbooks of these populations in Spain. The analysis included three pure breeds bred in Spain mainly used for riding: Pura Raza Español (PRE, $n = 307\ 831$), Arab Horse (AH, $n = 24\ 529$) and Purebred Menorca Horse (PRMe, $n = 4363$); three Spanish populations bred for sporting performance: Spanish Sport Horse (also recognized as Caballo de Deporte Español - CDE-) (SSH, $n = 296\ 168$), Anglo-AH (AAH, $n = 22\ 918$) and Spanish Trotter Horse (STH, $n = 23\ 752$); and two Spanish pure breeds used for meat production in extensive conditions: Jaca Navarra (JN, $n = 2315$) and Burguete (BUR, $n = 14\ 814$). A description of the pedigree records used in each population is shown in Table 1.

In this study, we also grouped the populations, according to studbook management, as open, in which the inclusion of animals belonging to other authorized breeds or populations as breeding stock is allowed (SSH, AAH and STH) and closed, in which only animals of the same breed or population as breeding stock (PRE, AH, PRMe, JN and BUR) can be used.

Table 1 Description of pedigree information and structure of dataset available for each Spanish horse population analysed

Population	Use – Type of breeding							
	Riding – Close			Sport – Open			Meat – Close	
	PRE	AH	PRMe	SSH	AAH	STH	JN	BUR
N pedigree	307 831	24 529	4363	296 168	22 918	23 752	2315	14 814
N reference population	265 319	6958	2346	39 127	6798	10 101	1492	7681
Males	148 836	11 590	2272	132 690	13 652	9270	542	4077
Females	158 995	12 883	2091	163 478	9266	14 482	1773	10 737
Sires	71 450	2175	407	27 701	5232	3558	85	649
Dams	22 540	5660	824	82 706	10 488	9965	774	4415
Studbook foundation	1912	1847	1988	1999	1884	1979	2001	1999
Number of registered studs	17 475	2443	755	3979	2450	1812	51	265

PRE = Pura Raza Español; AH = Arab Horse; PRMe = Pura Raza Menorquina; SSH = Spanish Sport Horse; AAH = Anglo-AH; STH = Spanish Trotter Horse; JN = Jaca Navarra; BUR = Burguete.

In the case of open populations, SSH is a recent composite population created in 2002, as multipurpose individuals with a first-rate performance at any of the Olympic equestrian disciplines (dressage, showjumping and eventing). As a result, all individuals which fulfill these sporting requirements are accepted for the breeding of SSH animals. Furthermore, immigration (introducing outside breeds into the SSH) is a key part of the original concept of the population (Bartolomé *et al.*, 2011). Similarly, STH is a composite population that allows the inclusion of any individual participating in trotting competitions registered in the different studbooks of trotter horses all around the world (Gómez *et al.*, 2010). For AAH, individuals could be registered if they were bred as the result of mating between AH, thoroughbred and AAH. Additionally, three of the breeds analysed (PRMe, JN and BUR) were catalogued as endangered populations according to the Official Catalog of Breeds of Spain.

Pedigree completeness and structure analysis

The pedigree completeness level was computed using all the available information from the parental studbooks, as the proportion of ancestors known per generation. The number of equivalent to discrete generations (t) for each individual in a pedigree was computed as the sum of $(\frac{1}{2})^n$, where n is the number of generations separating the individual to each known ancestor, following Boichard *et al.* (1997). The inbreeding coefficient (F), defined as the probability that two alleles at a randomly chosen locus are identical by descent (Malécot, 1948), and the average relatedness coefficient (AR), defined as the probability that an allele randomly chosen from the whole population belongs to a given animal (Gutiérrez *et al.*, 2003) were also computed. Finally, the effective population size was computed for the last GI using both the individual increase in inbreeding (NeF) (Gutiérrez *et al.*, 2009) and the increase in pairwise coancestry (NeC) (Cervantes *et al.*, 2011b).

Reproductive analysis

A total of six reproductive parameters were estimated for each population using the studbook information as follows:

- Age at first foaling (**AFF**), defined as the average age of the sire or dam at birth of first registered offspring (days).
- Age at last foaling (**ALF**), defined as the average age of the sire or dam at birth of last registered offspring (days).
- Average interval between foaling (**AIF**), defined as the average time between the birth of the different offspring of the same dam (days).
- Interval between first and second foaling (**I12F**), defined as the time between the first and the second birth of offspring of the same dam (days).
- Average reproductive life (**ARL**), defined as the average time between the first and last birth of the offspring of the same sire or dam (days).
- The GIs of sire-son (**GIs-s**), sire-daughter (**GIs-d**), dam-son (**GId-s**) and dam-daughter (**GId-d**), defined as the average age of parents at the birth of their offspring used for reproduction (years).

It is important to note that, in order to prune for animals that are still reproductively active, only animals with at least 2 years since the last registered foaling were included in the ALF and ARL analysis.

These parameters were estimated using the ENDOG program v4.8 (Gutiérrez and Goyache, 2005) and self-made scripts implemented in visual basic. The statistical analysis was performed using Statistica for Windows v12.0 (StatSoft, 2014) and the PROC GLM from SAS v9.3 (SAS, 2011) to estimate the influence of the population on the reproductive parameters. The least square means and their corresponding standard errors were obtained for every trait at population level. A multiple comparison Tukey's test was applied to study the differences between populations.

The heritability levels of five (AFF, ALF, ARL, AIF and I12F) and three (AFF, ALF and ARL) reproductive parameters were estimated in mares and sires, respectively, within each population, using a univariate animal model (which assumed normally distributed errors) with VCE v6.0 (Kovac *et al.*, 2010). The model included month of birth (12 classes in all the populations, only for AFF and ALF) and the year (with 43 to 121 classes) as fixed effects, and the year-breeder interaction (651 to 20 953 classes), with animal and error as random effects. The same model was used for all the populations in order to compare the obtained results, because genetic parameter estimates are specific to a trait and a population, and they are heavily determined by the structure of the model used for their estimation (Wilson, 2008).

The inclusion of the maternal effect in the models was tested, but it resulted in a lack of convergence in most of the analysed populations and unsatisfactory results obtained in others. The maternal effect was therefore not included in the genetic models for the following reasons: (1) in animal breeding, this effect is included in traits when the animal is young, but a mare or a stallion is an adult when they have a descendant, (2) none of the works related to the estimation of genetic parameters for reproductive traits published to date have included it, (3) the inclusion of the maternal effect should be as a random effect in the model and even in the genetic analysis, thus increasing the memory needed, and also, in most of the analysed populations, there is a lack of convergence and (4) according to Heydarpour *et al.* (2008) and Meyer (1992), the estimation of variance components with maternal genetic effects is influenced by population structure. Heydarpour *et al.* (2008) stated that the proportion of dams without records and the correlation between direct and maternal effects had the strongest effects on the bias of estimates. In their simulations, the greatest biases were obtained when the proportion of dams without records was high, the correlation between direct and maternal effects was positive and the direct variance was greater than the maternal variance, which is the normal situation for most growth traits in livestock.

Pearson correlations between the estimated breeding values (**EBVs**), with their standard errors within and between

sexes for dams and sires weighted by the number of animals with breeding values per breed, were estimated, as an indirect measure of relatedness between the reproductive parameters analysed, using Statistica for Windows v12.0 (StatSoft, 2014).

Results and discussion

Pedigree completeness and genetic variability parameters

The percentage of known ancestors per generation and pedigree completeness, as well as the genetic variability parameters per population, is shown in Figure 1 and Table 2, respectively.

As was expected, the longest pedigrees belonged to PRE and AH purebreds, with more than 10 average

maximum known generations in the whole studbook (16.58 and 10.40, respectively). Similarly, the percentage of known ancestors was over 60% until the 9th and 6th generations, depicting the robustness and reliability of the pedigree. Additionally, the same populations also showed the highest F (>6%) and AR (\approx 10%) values. These results show a decrease in both parameters in comparison with the values reported in the same populations (Valera *et al.*, 2005; Cervantes *et al.*, 2008b). The decrease in the F value observed could be partially explained by management decisions suggested by Breeders' Associations, since the establishment of official breeding programs, with their recommendations to avoid high levels of inbreeding in mating.

Similar results were also obtained in the pedigree analysis of SSH and STH, which also showed considerable

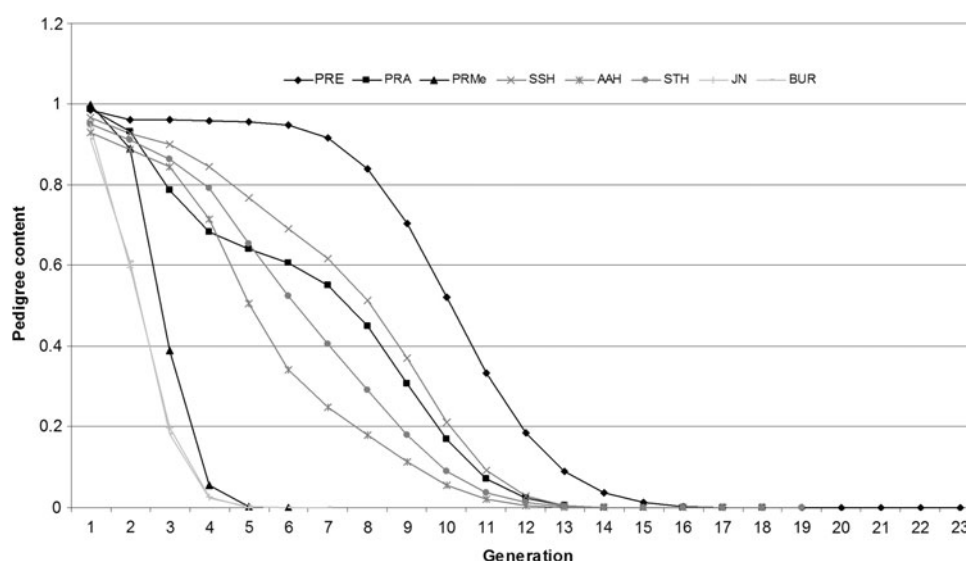


Figure 1 Percentage of ancestors known per generation in the eight Spanish horse populations analysed, with parental generation 1 corresponding to parents, 2 corresponding to grandparents, etc. PRE = Pura Raza Español; AH = Arab Horse; PRMe = Pura Raza Menorquina; SSH = Spanish Sport Horse; AAH = Anglo-AH; STH = Spanish Trotter Horse; JN = Jaca Navarra; BUR = Burguete.

Table 2 Descriptive parameters of pedigree information available for each Spanish horse population analysed

Parameter/ Population	PRE	AH	PRMe	SSH	AAH	STH	JN	BUR
F (%) ¹	6.44	6.10	1.15	4.62	1.28	2.21	1.07	0.57
NeF ¹	68.43 ± 6.531	55.56 ± 7.518	53.91 ± 20.578	63.94 ± 10.031	175.14 ± 35.019	130.65 ± 12.814	36.92 ± 17.614	60.91 ± 30.301
NeC ¹	93.34 ± 0.421	80.49 ± 1.177	80.22 ± 2.557	149.41 ± 1.413	333.84 ± 3.404	141.76 ± 1.241	82.05 ± 3.609	399.24 ± 7.816
AR ¹	10.38	8.70	1.77	3.47	0.98	2.07	1.69	0.24
AEG ¹	9.38	6.22	2.33	6.94	4.85	5.72	1.76	1.73
AEG ²	9.08	5.50	1.71	5.31	2.99	3.87	1.57	1.43
AMG ²	16.58	10.40	2.17	9.05	5.61	8.38	2.10	1.95
ACG ²	5.35	3.10	1.40	3.15	1.81	2.02	1.21	1.14

PRE = Pura Raza Español; AH = Arab Horse; PRMe = Pura Raza Menorquina; SSH = Spanish Sport Horse; AAH = Anglo-AH; STH = Spanish Trotter Horse; JN = Jaca Navarra; BUR = Burguete; F = average inbreeding; NeF = effective population size based on individual increase in inbreeding; NeC = effective number of population size based on individual increase in coancestry; AR = average relatedness coefficient; AEG = average number of equivalent generations; AMG = average maximum number of known generations; ACG = average number of completed generations.

¹Estimated for reference population, using animals included in the last generation interval for each population (8.5 years in JN, 9 years in BUR, 10 years in PRE, 11 years in AH and SSH, 12 years in PRMe).

²Estimated for whole population.

robustness (with approximately nine average maximum known generations in the whole pedigree in both cases), because the pedigree of foreign parental individuals was imported from the studbooks of origin during the registration of foals. The percentage of known ancestors per generation was also over 60% until the 7th and 5th generations, respectively (Figure 1). However, in contrast, the inbreeding values were lower since they are open populations (4.62% and 2.21%, respectively) as were their relatedness values, which were below 3.5. Our results show that the SSH population increased their F and AR values in comparison with a previous analysis (Bartolomé *et al.*, 2011). This could be explained by the increased use of other related PRE animals, in an attempt to improve the temperament of the descendants, which also increased the connection between individuals and the percentage of PRE influence in the population. In the STH, the F values registered were lower than SSH, which could be caused not only by the intensive use of artificial insemination (AI) with foreign sires (Gomez *et al.*, 2009) but also by the lower depth of pedigree available for this population. The F value in STH was close to that found in French Trotters (Moureaux *et al.*, 1996), one of the trotter populations with the highest influence on the pedigree of STH by the use of AI. The F values were higher in comparison with the previous analysis we performed 10 years ago (Gomez *et al.*, 2009). However, this could be attributed to the use of closely related French Trotter stallions, which also have a more robust pedigree, thus producing this contradictory phenomenon for an open population.

The shallowest pedigrees belonged to populations with most recent studbooks (PRMe, JN and BUR), with an average number of maximum generations close to 2 (2.17, 2.10 and 1.95, respectively), and an average F (1.15%, 1.07% and 0.57%, respectively) and AR close to 1% (1.77%, 1.69% and 0.24%, respectively). In this case, the low F values could be produced by low-pedigree completeness, since higher values should be expected in such small populations. This can also be expected in young studbooks, in which individuals with unknown origin are included at its creation. This fact is supported by the low percentage of known ancestors per generation after the second generation (Figure 1). In PRMe, F and AR values were lower compared with the results obtained by Solé *et al.* (2013) in the same breed, but this can be explained by the management rules included in its official breeding program over the last few years. Finally, AAH was the only case that showed low F and AR values (1.28% and 0.98%, respectively) with a respectable pedigree robustness (5.61 average maximum known generations). In this population, the use of stallions and broodmares belonging to two different breeds, which had a long, reliable pedigree (thoroughbred and AH), led to a decrease in both parameters among individuals. However, it would be expected that the reproductive use of AAH individuals would produce a gradual increase in those values over the following generations, since the use of AAH individuals as breeders has been on the rise over the last few years in the Spanish population.

The Ne values (estimated only with animals included in the last GI) are not influenced by pedigree completeness, as F, and the values can be compared across populations. However, the Ne values were still dependent on the shallowness of the analysed pedigree in small, young populations. According to Cervantes *et al.* (2008a), a minimum number of generations are needed to obtain reliable results in a given population. For this reason, the results obtained in PRMe, JN and BUR should be treated with caution. Moreover, as the number of individuals in the reference populations increases, a higher amount of pedigree is needed to attain reliable results.

The higher NeF values were observed in two open populations (AAH and STH; >100), while they were below 70 in the closed populations and SSH. In PRE and AH, this parameter was higher than those found by Cervantes *et al.* (2008a), probably because of a higher control in mating design over the previous years. On the other hand, for AAH and SSH, they were lower than previous reports in the populations (Cervantes *et al.*, 2008a; Bartolomé *et al.*, 2011).

NeC/NeF, a relation commonly employed to determine the existence of genetic lines within a population, was close to 2 in SSH and AAH (2.3 and 1.9, respectively). In both cases, individuals are bred to participate in sport competitions that require different abilities (dressage, showjumping or eventing). Langlois and Blouin (2004) reported no antagonism between selection trends for sport and numerical productivity (number of foals/year). However, the management of animals is different and such differences could be ascribed not only to zootechnical causes but also to genetic differences by lines. This fact was previously demonstrated in an SSH population, in which differences according to genetic lines were detected (Bartolomé *et al.*, 2011). High values were also obtained in meat breeds, which showed NeC/NeF ratios of 2.2 and 6.6 in JN and BUR, respectively. However, these results should be considered cautiously since their pedigrees were considerably weaker (Table 2). Conversely, the NeC/NeF ratios were lower in the closed riding populations (PRE and AH, 1.4; PRMe, 1.5), suggesting an increased homogeneity within populations. Finally, our results suggest that STH could be considered as a random mating population since its NeC/NeF ratio was close to 1. This population is well known for the intensive use of French AI. For this reason, the animals could be more closely related between them while maintaining lower levels of inbreeding and avoiding a subdivision of the population.

Estimation of reproductive parameters

Reproductive parameters in horses are complex traits which are greatly influenced by environmental and management issues, which usually makes it difficult to detect underlying factors directly linked to animals themselves (Sairanen *et al.*, 2009). For this reason, in order to provide breeders with objective information to utilize in mating decisions, we estimated six reproductive parameters which can affect the profitability of studs from a breeding perspective.

Age at first foaling is further considered an important trait in a mare's reproductive performance evaluation, with results in the whole horse breeding system (Taveira and Silveira da Mota, 2007), since it indicates the beginning of the reproductive life of individuals. In our study, the most precocious broodmares were bred for riding purposes (PRE = 1937.64 days, AH = 2255.69 days and PRMe = 2064.96 days; Table 3), showing similar results to other populations (Taveira and Silveira da Mota, 2007). In contrast, the less precocious dams were used for sport activities (SSH = 3103.33 days, AAH = 3330.51 days and STH = 3447.00 days). This agrees with the reports of Solé *et al.* (2017a), which demonstrated that the younger a horse is when it wins first prize in a competition, the longer its competitive career and, therefore, later it is used as a broodmare. However, in sporting populations, AFF, if genetic, may be genetically correlated with performance in competitions, although selecting with AFF would not necessarily in itself increase performance. A different trend was observed in sires, since the most precocious were used for meat production, with an early evaluation, according to productive criteria, around 3 years of age (JN = 1999.75 days and BUR = 1789.93 days; Table 4). In sport populations, stallions are tested by their functional performance in competitions before their use for reproductive purposes within studbooks (AAH = 3331.14 days and STH = 3744.76 days), thus delaying their first offspring. Our results also support the findings of Solé *et al.* (2017b), which affirmed that the relative risk of mares ending their sporting career was greater than that of stallions and geldings in STH, because mares withdrawn from training could be used for breeding purposes. However, it was also demonstrated that there is an incompatibility between the use of horses for sport and the development of gestation, which contributes to an increase in the variability of reproductive parameters, especially in mares, in populations where embryo transfer (ET) is not commonly used (Sairanen *et al.*, 2009). However, our results were higher than those previously obtained in the populations reviewed. Furthermore, they were higher in sires than in dams in all populations, excepting those used for meat production, because stallions are early tested to evaluate their quality as breeding stock and are culled if they do not meet certain quality standards.

Age at last foaling is a reproductive trait considered as the measurement of the end of the reproductive activity of individuals, thus showing the reproductive lifetime of the population. In our study, PRE broodmares finish their productive life earlier (3770.40 days), whereas PRMe, JN and AH mares were the most long-lived from a reproductive point of view, with over 4170 days on average. The first two breeds are classified as endangered and are usually bred with conservational criteria for amateur breeders, thus limiting the culling of individuals for selective reasons. Langlois and Blouin (2004) evidenced that the poor productivity results and the lack of improvement are due to this highly traditional breeding management, in spite of modern breeding technologies such as AI or ET, which are not commonly used. These minor populations are therefore expected to be

Table 3 Reproductive parameters (mean and standard error, SE) estimated in Spanish dams belonging to eight horse populations, and comparison between them

Population	PRE		AH		PRMe		SSH		AAH		STH		JN		BUR	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
AFF	1937.64	± 2.563 ^g	2255.69	± 13.782 ^e	2064.96	± 32.499 ^f	3103.33	± 19.616 ^c	3330.51	± 15.634 ^b	3447.00	± 13.503 ^a	2463.34	± 46.740 ^d	2511.74	± 17.326 ^d
ALF	3770.40	± 7.316 ^d	4206.18	± 29.721 ^a	4179.02	± 78.797 ^{ab}	4156.44	± 25.811 ^{abc}	4021.48	± 18.272 ^{bc}	4096.15	± 16.459 ^{bc}	4172.17	± 104.315 ^{bd}	3868.07	± 32.728 ^{cd}
AIF	625.83	± 1.497 ^e	760.07	± 8.010 ^f	630.40	± 15.100 ^e	833.69	± 11.566 ^c	1087.89	± 15.798 ^a	955.40	± 14.320 ^b	859.11	± 25.395 ^c	824.96	± 10.298 ^c
I12F	598.81	± 1.832 ^e	742.11	± 9.707 ^d	631.30	± 19.600 ^e	860.98	± 13.509 ^c	1096.44	± 17.355 ^a	1015.73	± 16.490 ^b	884.29	± 30.202 ^c	893.59	± 12.708 ^c
ARL	2438.84	± 7.919 ^b	2682.20	± 31.570 ^a	2493.35	± 76.611 ^{ab}	1899.35	± 24.787 ^d	2171.29	± 29.354 ^c	2163.07	± 26.604 ^c	1416.55	± 68.105 ^e	1255.78	± 23.838 ^e
Gid-s	9.42	± 0.039	10.34	± 0.111	9.69	± 0.270	10.78	± 0.058	9.60	± 0.110	10.51	± 0.097	9.14	± 0.624	8.99	± 0.180
Gid-d	9.29	± 0.024	10.02	± 0.067	9.44	± 0.177	11.09	± 0.038	9.85	± 0.071	10.77	± 0.065	9.49	± 0.190	8.95	± 0.072

PRE = Pura Raza Español; AH = Arab Horse; PRMe = Pura Raza Menorquina; SSH = Spanish Sport Horse; AAH = Anglo-Ah; STH = Spanish Trotter Horse; JN = Jaca Navarra; BUR = standard error; AFF = age at first foaling; ALF = age at last foaling; AIF = average interval between first and second foaling; I12F = interval between first and second foaling; ARL = average reproductive life; Gid-s = generational interval of dam-son (years); Gid-d = generational interval of dam-daughter (years).

Superscript letters are the results of the Tukey's test to study differences between populations.

Table 4 Reproductive parameters (mean and standard error, SE) estimated in Spanish sires belonging to eight horse populations, and comparison between them

Population	PRE		AH		PRMe		SSH		AAH		STH		JN		BUR	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
AFF	2400.60	± 7.618 ^e	2591.77	± 30.938 ^d	3149.95	± 78.667 ^b	2715.37	± 28.975 ^c	3331.14	± 23.510 ^b	3744.76	± 22.799 ^a	1999.75	± 101.373 ^{ef}	1789.93	± 32.833 ^f
ALF	3815.28	± 13.602 ^c	4200.82	± 53.150 ^b	4732.05	± 123.970 ^{ab}	4320.93	± 46.171 ^b	4361.43	± 30.014 ^b	4926.55	± 31.491 ^a	3861.61	± 278.188 ^{bc}	3395.32	± 88.623 ^c
ARL	1752.80	± 13.433 ^b	2094.18	± 52.715 ^a	1838.99	± 105.846 ^{ab}	2202.44	± 45.902 ^a	2150.22	± 39.195 ^a	2208.19	± 42.419 ^a	1797.32	± 225.225 ^{ab}	1564.34	± 70.649 ^b
Gls-s	10.18	± 0.043	10.97	± 0.124	12.55	± 0.335	11.84	± 0.055	11.17	± 0.082	13.01	± 0.116	9.53	± 0.728	8.01	± 0.171
Gls-d	10.27	± 0.025	10.95	± 0.076	12.10	± 0.205	11.76	± 0.033	11.13	± 0.058	13.26	± 0.063	9.29	± 0.168	7.96	± 0.069

PRE = Pura Raza Español; AH = Arab Horse; PRMe = Pura Raza Menorquina; SSH = Spanish Sport Horse; AAH = Anglo-AH; STH = Spanish Trotter Horse; JN = Jaca Navarra; BUR = Burguete; SE = standard error; AIF = age at first foaling; ALF = age at last foaling; ARL = average reproductive life; GlS-s = generational interval of sire-son (years); GlS-d = generational interval of sire-daughter (years). Superscript letters are the results of the Tukey's test to study differences between populations.

less efficient in terms of genetic improvement. Arab Horse have a longer lifespan and higher fertility in comparison with other populations, because they often maintain a good physical condition and reproductive abilities even after 20 years of age (Sabeva and Apostolov, 2011). On the other hand, PRE breeders are usually more professional (with greater knowledge about horse management) and breed their animals with clear economic objectives, which lead to an increased genetic turnover and the early replacement of mares by genetically superior individuals. A similar situation can be observed in BUR stallions, which showed the lowest values for ALF (3395.32 days), which suggests an increased genetic turnover towards meat production for sires. However, the highest values for this parameter were observed in STH stallions (4926.55 days), which could be also explained by the extended sporting performance, which prevents their use as breeding stock until they are older, thus retarding the selective process. Similar results were obtained in similar horse populations for both sires and dams (Langlois and Maheut, 1976; Klemetsdal, 1993).

In our study, AIF and I12F, which determine the length of the break between foaling and evidence the intensive use of these individuals as breeders, were lower in PRE, AH and PRMe, which suggests an increase in selective intensity and genetic improvement. These populations probably have the most professional management in terms of genetic selection and breeding in Spain. In contrast, we found the populations used for meat production (JN and BUR, usually bred in extensive systems with lower reproductive control of mares) and for intensive sports activities (SSH, AAH and STH, in which reproduction is not the priority use of the animals) showed higher values. This fact has already been demonstrated by Taveira and Silveira da Mota (2007), who affirmed that high I12F culminates in lower selective intensity, resulting in lower genetic gains and a delayed genetic improvement. The I12F values obtained are similar but higher than those obtained for AIF in most of the populations, as reported by Campos *et al.* (2007), although their values in Brazilian horses were lower than those obtained in all the populations included in this study. In the populations used for riding, such as PRE and AH, AIF is slightly higher than I12F. This suggests that the AIF deteriorates into successive foaling. However, PRMe showed similar values in both parameters (close to 630 days), suggesting that their reproductive ability is well conserved throughout their productive life. The results obtained for AIF and I12F in other horse populations (Singh *et al.*, 2002; Taveira and Silveira da Mota, 2007) are usually lower than those obtained in the Spanish populations analysed. This could be due to the nutritional and reproductive management of mares, professionalization of breeding studs, etc.

Average reproductive life evidences the length of the reproductive use of animals in different populations, expressed as the average of the sires and the dams included in the population. According to Wolc *et al.* (2009), a long herd life reduces replacement costs, increases selection intensity and allows mares to fully express their reproductive

potential, whereas a lower replacement rate slows down the genetic progress by increasing the GI. These authors recommended a herd life of about 7 years, which seems to be a good balance between the economic factors influencing replacement rate and the tendency to limit the GI to enhance the genetic gain. In this sense, the populations used for meat production presented the lowest ARL values (1416.55 and 1255.78 days in dams and 1797.32 and 1564.34 days in sires for JN and BUR, respectively) because the breeding stock is tested early and rejected if the productive results obtained in the descendants are not satisfactory. Both of these values are lower than those recommended by Wolc *et al.* (2009) to meet economic needs. The highest values were obtained for AH dams (2682.20 days), as these are recognized as one of the most long-lived populations (Sabeva and Apostolov, 2011) and SSH and STH sires (2202.44 and 2208.19 days, respectively) because of their sports use before reproduction (they also showed the highest values for AFF and ALF). These results are slightly lower than those obtained in other horse populations (Langlois and Maheut, 1976; Klemetsdal, 1993) but higher than those presented by Kuhl *et al.* (2015) for Warmblood mares and by Campos *et al.* (2007) in Brazilian horses.

Finally, the GI was analysed. The highest values suggest that new generations of individuals delay for longer their contribution to the breeding stock, thus slowing down the yearly genetic improvement. According to our results, the GI was lower in broodmares than in sires in most of the populations and was lower than those reported in Selle Français (Dubois and Ricard, 2007). In general, our results were in range and followed the trend of previous reports which included thoroughbred (Langlois and Maheut, 1976) and trotters (Klemetsdal, 1993), with the exception of JN and BUR. In mares, the lowest results were obtained in the meat breeds with a higher selection pressure of breeding stock (JN and BUR, ranging between 8.95 and 9.49 years, respectively), whereas the highest results were obtained in two sport populations (SSH and STH, 10.51 and 11.09 years, respectively), largely due to the previous evaluation of their sports performance before their use as breeding stock in the population. Similar results were obtained by Yamashita *et al.* (2010) in Japanese thoroughbred horses. This tendency was not observed in AAH, probably because it is an open

population which allows for the constant inclusion of tested AH and thoroughbred horses as breeding stock. In sires, the lowest results were also obtained in breeds used for meat production (between 7.96 and 9.53 years), probably due to the higher selection pressure, and the highest were obtained in the STH population (13.26 years) due to their intense sports use in trotter races which could both affect their fertility and delay their reproductive use as breeding stock for management reasons. The greatest differences between sexes were found in the PRMe and STH populations, in which the GI of sires is significantly higher than that of dams. This fact reflects how the selective pressure in dams is higher than in sires in both populations.

Our analysis showed that reproductive differences can be explained by the zootechnical management of populations, based more on their selection/conservation purposes and the status of the population than on the physiological reasons themselves. However, reproductive parameters in horses, related to fertility, are complex traits influenced by a wide variety of genetic, environmental and management factors, which makes it difficult to detect the underlying factors directly linked to the animals themselves (Sairanen *et al.*, 2009).

Estimation of genetic parameters

There are very few studies that determine the importance of the genetic component in reproductive parameters in horses (Campos *et al.*, 2007; Taveira and Silveira da Mota, 2007; Wolc *et al.*, 2009). This could be due to the low number of progeny per individual, to the long GI and/or issues related to the difficulty in modelling the reproductive characteristics of the species.

In this study, we measured the heritability levels of five reproductive parameters in mares (AFF, ALF, AIF, I12F and ARL; Table 5) and three reproductive parameters in sires (AFF, ALF and ARL; Table 6) using the five largest populations analysed (PRE, AH, SSH, AAH and STH). The heritability levels for the three smallest populations analysed (PRMe, JN and BUR) showed potential bias because of the scarce pedigree information available, and the results must be treated with caution (Supplementary Material Table S1).

In general, for the reproductive parameters analysed in both sexes, the highest values were obtained in AFF (ranging

Table 5 Heritability values (h^2) estimated for five reproductive parameters in dams of five Spanish horse populations

Population Parameter	PRE		AH		SSH		AAH		STH	
	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE
AFF	0.15	0.0008	0.20	0.0303	0.32	0.0311	0.16	0.0176	0.09	0.0135
ALF	0.08	0.0005	0.09	0.0215	0.25	0.0278	0.10	0.0139	0.09	0.0109
AIF	0.14	0.0102	0.05	0.0231	0.30	0.0343	0.27	0.0474	0.42	0.0551
I12F	0.04	0.0009	0.02	0.0149	0.30	0.0343	0.04	0.0540	0.22	0.0406
ARL	0.07	0.0005	0.07	0.0209	0.20	0.0328	0.17	0.0240	0.14	0.0286

PRE = Pura Raza Español; AH = Arab Horse; SSH = Spanish Sport Horse; AAH = Anglo-AH; STH = Spanish Trotter Horse; SE = standard error; AFF = age at first foaling; ALF = age at last foaling; AIF = average interval between foaling; I12F = interval between first and second foaling; ARL = average reproductive life.

Table 6 Heritability (h^2) values estimated for three reproductive parameters in sires of five Spanish horse populations

Population Parameter	PRE		AH		SSH		AAH		STH	
	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE
AFF	0.08	0.0010	0.07	0.0322	0.26	0.0614	0.16	0.0300	0.23	0.0474
ALF	0.06	0.0008	0.05	0.0301	0.28	0.0631	0.15	0.0234	0.15	0.0246
ARL	0.06	0.0007	0.04	0.0301	0.13	0.0566	0.11	0.0031	0.10	0.0255

PRE = Pura Raza Español; AH = Arab Horse; SSH = Spanish Sport Horse; AAH = Anglo-AH; STH = Spanish Trotter Horse; SE = standard error; AFF = age at first foaling; ALF = age at last foaling; ARL = average reproductive life.

between 0.09 and 0.32 in dams and between 0.07 and 0.26 in sires), while the lowest values were obtained in ARL (ranging from 0.07 to 0.20 in dams and 0.04 to 0.13 in sires). Differences observed between populations can be caused by the differences in the management of studbooks (open and closed populations) and the differences in the reproductive management of the populations (appropriate reproductive management in the stud, intensive use of AI, lack of interest for reproductive use, etc.) which could affect the residual variance and increase or decrease the heritability value. However, differences in the heritability value could also arise because of the genetic background of each population.

The expected heritabilities for reproductive parameters are low because of the influence of environmental factors or management and the influence of dominance and epistasis (Falconer and McKay, 1996). The heritabilities of Spanish horse populations analysed were within the same range as those indicated for dams in the literature for AFF and ALF (Campos *et al.*, 2007; Taveira and Silveira da Mota, 2007; Wolc *et al.*, 2009) which were 0.01 to 0.38; they are also close to the values previously reported for AIF and ARL by Campos *et al.* (2007), which ranged between 0.00 and 0.64.

The riding populations (PRE and AH), which are closed populations, tended to show the lowest heritability values (ranging between 0.02 to 0.20 in dams and 0.04 to 0.08 in sires). This could be caused by differences in the population structure and in the reproductive management of the studs (e.g. studs with different sizes and with the influence of different external factors, such as tendencies in the use of different coat colours, genetic lines, etc.), which may condition the reproductive use of the sires and dams, according to the size of the stud or the breeding objectives. The heritability values obtained in the Spanish sporting populations analysed (SSH, AAH and STH) tended to be higher (less variety in the population structure and breeding objectives, higher number of geldings if animals are not of reproductive interest and increased use of AI). However, all of them are within the range of the reviewed bibliography (Campos *et al.*, 2007; Taveira and Silveira da Mota, 2007; Wolc *et al.*, 2009). The SSH is the sporting population with higher heritability levels both in dams and sires, and it is also the most open population; the AAH is the sporting population with the lowest heritability levels in both sexes, being the most closed population (because of the high percentage of Arab blood).

The STH is in the middle position. Heritability levels in the JN and BUR dams are acceptable for AFF and ARL, ranging between 0.11 to 0.69 and 0.12 to 0.40, respectively, although these results must be treated with caution.

These values could permit the use of genetic variation and direct selection in the breeding process, because selection for reproductive parameters offers the possibility of indirectly improving the reproductive performance of the animals and the profitability of breeding studs, thus increasing economic profitability.

There are clear differences in reproductive management caused by the difference in studbook management, the selection purposes and the status of the populations. However, the estimation of heritability levels also reveals a clear genetic component for these kind of traits.

Although it is essential to promote the control of environmental conditions in breeding studs to improve reproductive performance (suitable nutrition of mares, ultrasound control of mare's status, use of artificial reproductive techniques, etc.), the inclusion of reproductive parameters in the official breeding programs can contribute to an increase in the economic profitability of breeding studs by helping to increase their economic efficiency in the long-term.

Before suggesting the possible reproductive parameters to be included in the breeding programs for these populations, it is important to evaluate the relationships between them. In this context, Pearson correlations between EBVs within and between sexes for dams and sires, weighted by the number of animals with breeding values per breed, were estimated (Table 7). It is worth noting the medium and negative correlation between AFF and ARL in both sexes (-0.370 in dams and -0.440 in sires), which indicates that, in general, the younger a horse is when it starts its reproductive life, the shorter its reproductive life. In addition, as expected, the correlation between ALF and ARL was high (0.648 in dams and 0.708 in sires) because the older a horse is when it ends its reproductive life, the longer its reproductive life. The correlations between the EBVs for both sexes in homologous traits (Table 7) were positive and of a medium–low level (0.167 to 0.409). The selection of reproductive parameters in one sex is therefore expected to result in a positive response for the same trait in the other sex.

The results obtained support the inclusion of AFF in the official breeding programs of the Spanish horse populations in order to improve reproductive aspects, because of its

Table 7 Pearson correlations between the estimated breeding values (EBVs) for reproductive parameters analysed within and between sexes (*italics*) for dams (*grey*) and sires (*dark grey*), weighted by the number of animals with breeding values per each Spanish horse populations


Correlations EBVs	Dams/sires			Dams	
	AFF	ALF	ARL	I12F	AIF
Dams					
AFF	<i>0.167 ± 0.0044</i>	0.061 ± 0.0028	−0.370 ± 0.0026	0.116 ± 0.0028	0.194 ± 0.0028
ALF		<i>0.409 ± 0.0041</i>	0.648 ± 0.0021	−0.169 ± 0.0028	−0.239 ± 0.0027
ARL			<i>0.404 ± 0.0041</i>	0.036 ± 0.0028	0.030 ± 0.0028
I12F					<i>0.755 ± 0.0018</i>
Sires					
AFF	<i>0.167 ± 0.0044</i>	0.164 ± 0.0037	−0.440 ± 0.0033		
ALF		<i>0.409 ± 0.0041</i>	0.708 ± 0.0026		
ARL			<i>0.404 ± 0.0041</i>		

AFF = age at first foaling; ALF = age at last foaling; ARL = average reproductive life; I12F = interval between first and second foaling; AIF = average interval between foaling.

medium–high heritability and its positive correlations with other important reproductive traits. The inclusion of AIF is also recommended in sports populations, which showed the highest phenotypic values for this parameter, because it determines the length of the break between foaling and therefore conditions the reproductive performance of dams, selective intensity, genetic gain and genetic improvement. For this reason, it is a valuable economic parameter in breeding studs.

Acknowledgments

This study was financed by the AGL–2017–84217-P Research project from Ministerio de Economía, Industria y Competitividad of the Spanish Government. The authors wish to thank the Breeders' Association of Pura Raza Español Horse, Spanish Arab Horse, Menorca Horse, Caballo de Deporte Español, Anglo-Arab Horse, Spanish Trotter Horse, Jaca Navarra and Burguete for providing the pedigree data used in this study. S. Demyda-Peyrás is Universidad de Córdoba-PP-5.2.B fellowship.

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Declaration of interest

The authors have no conflict of interest to declare.

Ethics statement

No alive animals are used in this work.

Software and data repository resources

Pedigree data used in the analysis belong to the Breeders' Associations recognized for the management of the official studbooks of each population in Spain. The model was not deposited in an official repository.

Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S1751731120000087>

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