

**Sport horses: breeding specialist from a single
breeding programme?**

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Sport horses: breeding specialist from a single breeding programme?

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Abstract

The general goal of this thesis was to provide information useful for the breeding programme of the Royal Dutch Warmblood Studbook (KWPN) in relation with the ongoing specialisation of the population. Data provided by KWPN consisted of records from studbook-first inspection, competition performance on dressage and show-jumping, and pedigree information. Firstly, the effect of specialisation was studied on the connectedness between the subpopulations of dressage and show-jumping horses, using the pedigree information. Results indicated that relatedness between horses in the two subpopulations has been reduced to a low level, while relatedness within both subpopulations has been increasing consistently. A reduction in the number of influential ancestors in both subpopulations was observed. Secondly, it was analysed whether the specialisation for either dressage or show jumping has affected genetic parameters of traits recorded in the two subpopulations. Traits recorded at studbook-entry inspection were defined as a dressage trait or a show-jumping trait according to the type of horse that received the inspection. Bivariate analyses were performed to estimate the genetic correlation between the two traits. Results indicated that the specialisation process has resulted in a difference in mean trait values between dressage and show-jumping horses. However, differences in heritabilities for traits defined as dressage or show-jumping did not differ significantly, and the genetic correlations between them were not different from one considering their posterior standard deviation. Thirdly, the model to analyse performance in competition of dressage and show-jumping was studied. Results showed that performance in competition for dressage and show-jumping is a heritable trait ($h^2 \sim 0.11-0.13$), and that it is important to account for the effect of rider in the genetic analysis. Fourthly, it was estimated the genetic correlation between the performance of horses in dressage and show-jumping competition, and the genetic correlations between traits measured early in life and performance in competition in each of the disciplines. Results showed that the genetic correlation between performance of horses in dressage and show-jumping was slightly unfavourable (-0.12). The genetic correlation between dressage and show-jumping tended to become more unfavourable over time, but this trend was not reflected in changes in the correlations between competition traits and traits recorded in the studbook-entry inspection. From this study it can be concluded that no extra benefit is to be expected from definition of a combined breeding goal. However, entirely separated breeding programmes for both disciplines are therefore not advisable. Constructing separate selection indexes would allow for optimal weighting of information sources such as studbook-entry inspection traits in accordance to the breeding goal of each sports discipline.

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1

General Introduction

Introduction

Horses and equestrian sports are part of the common heritage of Europe. With an increasing number of horse riders and more than six million horses, the equestrian sector has a significant social and economic impact in many European countries (The European Horse Network 2013).

With the increasing mechanisation during the second half of the twentieth century, the role of the horses in the society shifted from the traditional activities related to warfare, agriculture and transport to sport and leisure related activities. The horse populations that became popular to fulfil the new needs were the Warmblood breeds.

Warmbloods originated in Europe from older local breeds used in agriculture and cavalry. They were derived from breeding between hotblood horses (Thoroughbreds and Arabs) and coldblood horses (draft horses). The different breeds are defined by the studbooks, that have unique and varied histories, and most were established from breeding between local mares and either imported warmblood sires from other breeds or Thoroughbred sires (Hamann and Distl 2008). Warmblood breeds are an open breeding population due to the contribution of different specific breeds (e.g. Thoroughbred, Trakehner) and the genetic exchange among Warmblood studbooks. This genetic exchange between studbooks has increased over the last decades due to more importation of sires or semen, facilitated by the availability and uptake of artificial insemination (Thorén Hellsten *et al.* 2008; Ruhlmann *et al.* 2009).

The general goal of the Warmblood breeders is to breed riding horses that mainly are used as sport horses. Warmblood horses are popular in the Olympics disciplines, i.e. dressage, show-jumping and eventing. In any case, studbooks have different emphases in their breeding goals. Some of them focus on one sport discipline (e.g. the Irish Sport Horse and Holstein studbooks focus on show jumping, Trakehner focus on dressage), but the majority of the breeder organisations aim to breed horses to compete at professional levels in dressage and show-jumping (Koenen *et al.* 2004; Stock *et al.* 2015). However, contrary to other livestock species, there is no precise determination of the weight of different traits in the breeding goal (Koenen *et al.* 2004).

1. General Introduction

The breeding goal of the Royal Dutch Warmblood Studbook (KWPN) is focused on performance at the highest level in dressage and show-jumping (KWPN 2015). In the breeding programme, the studbook focuses mainly on selection of stallions while the selection decisions on mares are mostly taken by the breeders. KWPN follows a multistage selection process to select the stallions. The first stage is the entry inspection where the stallions are assessed on conformation, movement and free jumping. The best horses from studbook inspections are selected to participate in the stallion performance test. The horses which approve the performance test are available for breeding. The breeding stallions are finally selected when records from their progeny are available (Ducro 2011; KWPN 2015).

Including young horse information into the selection programme is justified because of the favourable genetic correlations between traits recorded in the young horse performance tests and performance in competition (Thorén Hellsten *et al.* 2006). Specifically for the KWPN population, Huizinga *et al.*(1991), Koenen *et al.*(1995) and Ducro *et al.*(2007) showed that some traits recorded at the young horse inspections were genetically and phenotypically correlated with performance in competition. Therefore, selecting based on inspection traits gives the highest response to selection (Ducro 2011). This has made selection easier, although the weight of the most important traits in breeding goals is not always clear.

Historically, sport horses were bred to perform in both dressage and show jumping. However, during the last decades, equestrian sports have become more intensive and competitive demanding improvement of athletic abilities related to each specific discipline. Consequently, rearing and training became more and more directed to only one of the disciplines, and breeders have increasingly considered only one of the disciplines in their breeding and mating decisions (Ducro 2010).

From the studbook perspective, it is not clear if it is possible to breed horses to perform at professional level in both disciplines from the same genetic base. In other words, is it possible to have the same breeding goal and selection scheme aiming at a composite genotype for both dressage and jumping traits? Alternatively, the population could be divided in two groups where in each group the breeding is aimed at only one of the disciplines.

Genetic gain for a given discipline would be faster if the breeding goal consists only of that discipline. When the breeding goal consists of more traits, the response to selection for each of the traits depends on breeding goal (weights assigned to each trait) and the magnitude and direction of genetic correlations between the traits. When traits have unfavourable genetic correlations then genetic gain in both traits is slower, whereas for a favourable correlation, genetic gain in both traits is faster. The genetic correlation between the two disciplines is thus a key-parameter in the discussion on specialisation.

In literature, little is known about the genetic correlation between show-jumping and dressage. Some studies suggest weak positive correlations (Árnason and Van Vleck 2000) while others suggest weak negative correlations (Bruns 1981; Huizinga and van der Meij 1989). Most information is available on correlations between traits recorded at young horse tests. In young horse tests, dressage and show-jumping related traits are weakly and sometimes negatively correlated (Thorén Hellsten *et al.* 2006). In eventing, where the performance in competition is measured by the combined result of dressage, show-jumping and cross-country, low positive or close to zero correlations are reported between the dressage and show-jumping (Kearsley *et al.* 2008; Stewart *et al.* 2012). These contradictions in genetic correlations makes it difficult for breeding organisations to decide the best strategy to breed horses to perform at professional level of dressage and show-jumping.

Therefore, for optimisation of a multi-stage breeding programme considering specialisation, knowledge about the genetic correlation between disciplines is required at the level of the breeding goal traits (competition traits) as well as at the level of the additional selection traits (young horse traits). Depending on these correlations, including these traits can significantly change the response to selection of breeding goals traits (Ducro 2011). However, when the genetic merit of a horse is depending on its purpose, i.e. dressage or show-jumping, it can be regarded as genotype by environment (GxE) interaction (Falconer and Mackay 1996). Horses that perform best in a dressage “environment” may not perform best in a show-jumping “environment” causing a re-ranking of genotypes.

GxE has been studied in many livestock species, e.g. milk yield of dairy cows in different environments (e.g. Weigel *et al.* 2001), production performance of pigs in

nucleus or in commercial farms (e.g. Merks and Hanenberg 1998) and egg production of laying hens in different housing systems (Besbes and Gibson 1999). In most of these studies, the same trait was measured in different environments and the degree of GxE was derived as the genetic correlation between traits measured in the two environments. Genetic correlations reported in the literature cited previously range from 0.3 to 1. Functional traits measured in more contrasting environments tend to present the lowest values.

With little GxE (i.e. high genetic correlation) a single breeding programme across different environments may take advantages of selecting sires and dams from a bigger population, resulting in a higher selection intensity and genetic gain (Banos and Smith 1991; Smith and Banos 1991). Furthermore, Mulder and Bijma (2006) showed that the genetic correlation is the more relevant parameter to define if cooperation between breeding programmes is beneficial from a genetic point of view in presence of GxE. With low genetic correlations in the range of 0.4 to 0.6, progeny testing in different environments is crucial from a genetic point of view.

The effect of GxE has not been studied in horse breeding programmes. However, the framework used to optimise breeding programmes for other livestock species in presence of GxE (Mulder *et al.* 2006), can be used in the analysis to determine the optimum strategy to breed specialists for the two equestrian disciplines from a single population.

Currently, there is a tendency among practical breeders to specialise towards one of the disciplines. On the other hand, some breeders still aim at breeding a so-called dual purpose horse. As a consequence, the genetic base of studbook might become stratified to a certain degree. For organisations that include more than one discipline in their breeding goal, it is very important to analyse the consequences of the specialisation practice for the system of genetic evaluation (Thorén Hellsten *et al.* 2006).

Aim and outline of the thesis

The general goal of this thesis was to analyse the consequences of the ongoing specialisation in the population of the Royal Dutch Warmblood Studbook (KWPN) in order to support the design of an optimum breeding programme.

Chapter 2 describes the effect of specialisation on the connectedness between the subpopulations of dressage and show-jumping horses in the total population of horses registered by KWPN.

Chapter 3 analyses whether the specialisation for either dressage or show jumping has affected the heritabilities and the genetic correlations between traits observed in the two subpopulations.

Chapter 4 discusses the statistical model for analysing competition data in dressage and show-jumping. Particularly, the impact of considering the effect of the rider on genetic variance is addressed.

Chapter 5 presents the estimates of genetic correlations between performance in competition in dressage and show-jumping and between both disciplines and traits recorded for both disciplines in the studbook-entry inspections.

The General Discussion comprises two sections. The first section discusses the challenges related to the analyses of the current competition data. In the second section, the results obtained in this thesis are put in the context of the specialisation process and the opportunities for improving the breeding programme conducted by KWPN are discussed.

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2

Genetic connections between dressage and show-jumping horses in Dutch Warmblood horses

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Abstract

During the last decades, the breeding practice within the Dutch Warmblood studbook (KWPN) has resulted in an increasing specialisation of horses into show-jumping (JH) and dressage (DH). The objective of this study was to describe the effect of the specialisation on the connectedness between the subpopulations of JH and DH horses registered by KWPN. The subpopulations comprised 23,800 JH horses and 18,125 DH horses, born between 1995 and 2009. Genetic similarity (GS), genetic pool in common (GC_x) based on the marginal genetic contribution of common ancestors and coefficient of relationship (r) between and within subpopulations were analysed in three periods of time to describe changes in genetic connectedness between subpopulations. A decline in GS (0.97–0.45), $GC_{0.5}$ (0.69–0.13) and r (0.018–0.014) in the recent years was observed. Both subpopulations have a common genetic pool; however, if the specialisation process continues, it will result in two unrelated (genetic) groups.

Key words: Genetic connectedness, genetic similarity, sport horse.

2.1 Introduction

Horses and equestrian sports are part of the common heritage of Europe. With an increasing number of horse riders and a population of more than six million horses, the equestrian sector has a significant social and economic impact on many European countries (The European Horse Network 2013). In the Netherlands, with around 400,000 horses and 500,000 active practitioners, equestrian activities rank as one of the most popular sports in the country (Ducro 2011; KNHS 2013).

Sport horses belong mainly to Warmblood breeds which can be considered an open breeding population due to the contributions from other breeds, like Thoroughbred, and the genetic exchange among Warmblood studbooks. Many studbooks apply breeding programmes to improve performance in equestrian sports. Important performance traits are show-jumping (JH) and dressage (DH). These traits are extensively considered by most breeding organisations and are included in their breeding goals (Koenen *et al.* 2004). The Royal Dutch Warmblood Studbook (KWPN) is an organisation based in the Netherlands specialising in the breeding of JH and DH horses (KWPN 2013). The breeding goal of KWPN is focused on performance at the highest level in DH and JH. The KWPN is recognised as one of the most competitive studbooks in JH and DH, leading the ranking of the International Federation for Equestrian Sports in both disciplines, in recent years (FEI 2013).

During the last decades, the increasing intensification of equestrian activities has required a constant improvement of the athletic abilities of the horse to be able to achieve the highest level of competition. Consequently, rearing and training became more and more directed to only one of the disciplines, and similarly breeders considered in their breeding and mating decisions only one of the disciplines (Ducro 2010, 2011). Usually, this focus on one of the discipline is referred to as the specialisation process. The studbook took notice of the specialisation in the population and extended the studbook entry inspections in 1998 with an additional set of traits specifically for the jumping abilities of horses. Additionally, starting in 2006, the breeders have to opt for one discipline, JH or DH, when the foals were registered, and no longer as just a “riding” horse, which was a general category commonly used before. The specialisation process is recognised at the breeders’ level; but it is still under discussion how the specialisation should be

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considered on the studbook's breeding programme (Ducro 2010). At the research level, genetic correlations between DH and JH traits have been investigated in several studies (Huizinga *et al.* 1991; Ducro *et al.* 2007; Viklund *et al.* 2008), and it is unclear what would be an optimal breeding strategy for studbooks that consider both disciplines in their breeding goals. However, there is no study that describes how this process has been affecting the structure of the population and, consequently, how it may have an impact on the current breeding strategies followed by the studbook.

The objective of this study was to describe the effect of specialisation on the connectedness between the subpopulations of JH and DH horses in the population of horses registered by KWPN.

2.2 Materials and Methods

2.2.1 Data

Data files for the present study were provided by KWPN and consist of a pedigree file with 506,078 horses and a data file with 68,126 records of the studbook inspections from the period 1989 through 2012. The horses in the data file were assigned to one of the two subpopulations, JH and DH horses, based on the fact that the horse received an overall evaluation as a JH or DH, in its first studbook inspection in the period from 1998 through 2012 (Table 2.1). The subpopulations of JH and DH comprised 23,800 and 18,125 animals, born between 1995 and 2009, respectively. The JH subpopulation presented a larger percentage of males (25%) than the DH subpopulation (16%). The number of offspring by stallion and mare was similar in both groups. In the case of stallions, in both subpopulations ~10% of the stallions had more than 50 offspring and ~5% more than 100 offspring. The total number of stallions identified in the whole population studied was 1495, and 599 (40%) of them had offspring in both subpopulations. Considering the mares, 22,919 of them were identified in the whole population studied from which 3708 (16%) had offspring in both subpopulations (Table 2.2). The pedigree of animals from both subpopulations was traced back as far as possible to construct a common pedigree file that comprised 96,869 animals.

2.2.2 Characterisation of the subpopulations

Several demography parameters were calculated to describe the differences between JH and DH subpopulations. The pedigree completeness index (Maccluer *et al.* 1983) after three (PCI3) and five generations (PCI5) and the average number of equivalent discrete generation (EqG; Maignel *et al.* 1996) were calculated to compare the quality and depth of the pedigrees for the JH and DH subpopulations. The genetic background of JH and DH subpopulations was described through the number of founders (f), founder equivalent (f_e), genome equivalent (N_g) (Lacy 1989) and the effective number of ancestors (f_a ; Boichard *et al.* 1997). The average inbreeding coefficient (F) and the expected inbreeding under random mating for each subpopulation were computed with the EVA software (Berget *et al.* 2006) which uses the algorithm proposed by Meuwissen and Luo (1992). The generation interval for JH and DH was calculated as the average age of the parents at the birth of their offspring.

2.2.3 Genetic connectedness between subpopulations

Several parameters were calculated to describe the genetic connectedness between JH and DH subpopulations. Some of them, such as the number of stallions in common (SC) or genetic similarity (GS), were used in previous researches and permitted to compare the level of connectedness with other populations studied. In the case of parameters such as founders in common (f_c) and ancestors in common (f_{ac}), they were used to investigate if both subpopulations come from the same genetic pool.

Stallions in common. The number of SC between JH and DH is an intuitive and basic measure of genetic connectedness of the two populations, and shows the number of stallions with progenies in both subpopulations. This number was also expressed as a percentage of the total number of sires used in both subpopulations.

Genetic similarity. GS, as defined by Rekaya *et al.* (1999), was calculated as the ratio between the number of progenies of common stallions in two subpopulations and the total number of progenies of all stallions, i.e.:

$$GS_{JH,DH} = \frac{\sum_{k=1}^{N_{SC}} (n_{JHk} + n_{DHk})}{\sum_{k=1}^{N_{JH}} n_{JHk} + \sum_{k=1}^{N_{DH}} n_{DHk}}, \quad [1]$$

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where $GS_{JH,DH}$ is the GS between the subpopulation of JH and DH; N_{SC} is the number of stallions with progenies in the subpopulation of JH and DH; N_{JH} and N_{DH} are the number of stallions in the subpopulation of JH and DH, and n_{JHk} and n_{DHk} are the number of progenies of stallion k in the subpopulation of JH and DH, respectively.

Table 2.1 Number of foals registered by KWPN by type and year of birth from 1995 through 2012, and how many of them were presented to be judged in the first inspection for jumping and dressage.

Year Birth	Foals Registered				First inspection	
	Riding	Jumping	Dressage	Total	Jumping	Dressage
1995	11618	63	34	11715	1610	1485
1996	11046	84	52	11182	1818	1259
1997	10384	86	77	10547	1897	1142
1998	9916	134	117	10167	1841	1185
1999	10457	184	196	10837	1936	1125
2000	10887	245	291	11423	1919	1240
2001	11533	390	447	12370	1915	1183
2002	11218	645	723	12586	1912	1059
2003	10829	1427	1256	13512	1639	1460
2004	10059	1527	1477	13063	1376	1421
2005	10027	1453	1390	12870	1302	1329
2006	170	7608	4931	12709	1261	1194
2007	107	8051	5147	13305	1313	1142
2008	15	8435	5477	13927	1095	1038
2009	6	8247	5339	13592	966 ⁽¹⁾	863 ⁽¹⁾
2010	47	7309	4636	11992	n.a. ⁽²⁾	n.a. ⁽²⁾
2011	1	6686	4308	10995	n.a. ⁽²⁾	n.a. ⁽²⁾
2012 ⁽¹⁾	1	5503	3685	9189	n.a. ⁽²⁾	n.a. ⁽²⁾

⁽¹⁾ Records available until September 2012.

⁽²⁾ n.a.= not available. Horses born after 2009 will receive first inspection in 2013 onwards.

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The contribution of each subpopulation to the GS was calculated following Thorén Hellsten *et al.* (2008). With the same notation as that used in Equation [1], the contribution of JH to GS in percentage was defined as:

$$\text{Contribution of JH to GS in \%} = \frac{\sum_{k=1}^{N_{sc}} n_{JHk}}{\sum_{k=1}^{N_{sc}} (n_{JHk} + n_{DHk})} * 100, \quad [2]$$

The contribution of DH to GS was calculated with an analogous formula, summing both contributions 100%.

Table 2.2 Descriptive statistics of the Show-jumping (JH) and Dressage (DH) subpopulations studied.

	JH Subpopulation	DH Subpopulation
Number of horses	23,800	18,125
Sex		
Male	5881 (25%)	2889 (16%)
Female	17,006 (71%)	14,591 (80%)
Castrated	913 (4%)	645 (4%)
Stallions	1161	933
Median (offspring/stallion)	4	3
3 rd Percentile (offspring/stallion)	17	13
Max(offspring/stallion)	791	781
With 50 offspring or more	121	81
With 100 offspring or more	55	45
Mares	14,916	11,711
Median (offspring/mare)	1	1
3 rd Percentile (offspring/mare)	2	2
Max(offspring/mare)	9	10

Founders in common. Founders are animals with unknown parents that are ancestors of a population. The genetic contributions of the founders sum to one. Analogous to the definition of SC, the number of f_c between JH and DH was calculated. The proportion of f_c , in relation to the total number of ancestors in both subpopulations, and their genetic contribution indicate the importance of a common genetic origin of both subpopulations. The common genetic origin of the two subpopulations also measures the (expected) proportion of ancestral alleles

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shared by the two subpopulations. The proportion of the original genetic pool that is shared between two subpopulations was defined as the proportion of the original genetic pool that was provided by the genetic contributions of the f_c :

$$CGO_{JH,DH} = \frac{\sum_{k=1}^{f_c} (q_{JH} + q_{DH})}{2}, \quad [3]$$

where $CGO_{JH,DH}$ is the common genetic origin of subpopulations JH and DH; f_c are founders in common in the subpopulations of JH and DH; q_{JH} and q_{DH} are the genetic contributions of the f_c in the populations of JH and DH, respectively.

Ancestors in common. Despite that the two subpopulations originated from a common genetic pool, a differential selection aiming to improve different disciplines could lead to different contributions of ancestors in each subpopulation. The concept of the effective number of ancestors (founders or not) was suggested by Boichard *et al.* (1997) to account for bottlenecks in the population, which could be caused by the intense use of few stallions. The individual marginal genetic contribution expresses the importance of an ancestor for the genetic pool of the population in question. The populations' genetic variability could be expressed as the number of ancestors with the largest marginal genetic contributions that jointly accounted for the given fraction x of the genetic pool. Based on an ordered (descending) list of marginal genetic contribution, the set of important ancestors could be defined as:

$$A_x = \{A_{(1)}, \dots, A_{JH(k)}\}; \sum_{i=1}^k p_{(i)} = x \quad [4]$$

where, x is the proportion of the genetic pool explained, $p_{(i)}$ is the marginal genetic contribution of the ancestor i and k is the number of ancestors needed to reach the sum x . Following Equation 4, it could be defined a list of important ancestors that explained x proportion of the genetic pool of the JH and DH subpopulations, A_{JH} and A_{DH} , respectively. The list of important ancestors in common (fac_x) between JH and DH which explain x proportion of the genetic pool of both subpopulations is:

$$fac_x = A_{JH} \cap A_{DH}, \quad [5]$$

and the number of important ancestors in common ($nfac_x$) is:

$$nfac_x = \# (A_{JH} \cap A_{DH}), \quad [6]$$

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and the proportion of the important ancestors ($pfac_x$) is:

$$pfac_x = \# (A_{JH} \cap A_{DH}) / (\#A_{JH} + \#A_{DH} - \# (A_{JH} \cap A_{DH})), \quad [7]$$

where, A_{JH} and A_{DH} are the list of important ancestors for subpopulations JH and DH, respectively, and $\#$ is a counting function.

The marginal genetic contribution from important fac would indicate how important the common genetic pool is between two populations, considering the selection process to which they have been subjected. Analogous to the definition of GS and CGO, the genetic pool in common between JH and DH, given a proportion x of the total genetic pool of the subpopulations, was defined as:

$$GC_x = \frac{\sum_{i=1}^{nfac_x} (p_{JHi} + p_{DH(i)})}{2x}, \quad [8]$$

where GC_x is the genetic pool in common between JH and DH, given the x proportion of the genetic pool considered; $p_{JH(i)}$ is the marginal genetic contribution of the common ancestor i in JH and $p_{DH(i)}$ is the marginal genetic contributions of the ancestor i in DH. In this study, $x = 0.5$ was defined. The marginal genetic contribution of the ancestors and the number of effective ancestors were calculated using the PEDIG software (program prob_orig.f) (Boichard 2007) and were computed for a set of 1000 ancestors which was allowed to estimate the number of effective ancestors for the JH and DH subpopulations with an accuracy of 0.1.

2.2.4 Effect of specialisation on genetic connectedness between subpopulations

The effect of specialisation on the genetic connectedness between JH and DH was described through the following procedures:

Marginal contribution of ancestors. The changes of the $fac_{0.5}$, $pfac_{0.5}$ and $GC_{0.5}$ over times (years) are measures of change in the common genetic pool between JH and DH across time and, consequently, measures of the changes in connectedness between the two subpopulations. The change of the parameters were analysed over three periods of time defined according to classes of year of birth: 1995–1999, 2000–2005 and 2005–2009.

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Average relatedness. Wright's coefficient of relationship between two animals (r) is the correlation coefficient between their additive breeding values (Wright 1922). The coefficient of relationship is a parameter which clearly indicates the magnitude of the relatedness between two individuals or populations. Moreover, it is also a parameter directly related to the prediction of breeding values for any trait of interest, in the current genetic evaluations. The change across time of the average relationship coefficient within and between JH and DH horses was calculated by year of birth. Under the hypothesis that the specialisation process has been affecting the connectedness between both subpopulations, a decrease in the mean of the coefficient of relationship between both groups over years is expected. The software package CFC (Sargolzaei *et al.* 2006) was used to compute the average relationships between and within groups of animals.

2.3 Results

2.3.1 Characterisation of the subpopulations

The JH and DH subpopulations have a similar level of pedigree deepness, and a similar generation interval and inbreeding coefficient (Table 2.3). The completeness of the pedigree is high for both JH and DH subpopulations; the average of the pedigree completeness index after five generations (PCI5) was 0.96 in JH and 0.97 in DH, expressed in terms of EqG, 8.4 generations in JH and 8.8 in DH. In both subpopulations, PCI5 and EqG were higher for the later year of birth. In JH, PCI5 increased from 0.93 in horses born in 1995 to 0.98 in the cohort born in 2009. In DH, PCI5 changed from 0.93 to 0.99 in the same years. Measured in terms of EqG, the depth of the pedigree increased in JH from 8.0 to 8.9 generations and in DH from 8.1 to 9.6 generations.

The generation interval (L) for the animals traced was 10.1 years for JH and 9.5 years for DH. In JH, the generation interval of stallions was one year longer than in mares (10.6 vs. 9.6 years) while, in DH, the generation interval was similar in stallions (9.3 years) and mares (9.7 years). The proportion of inbred animals increases in JH and DH from 0.89 in animals born in 1995 to 0.99 in animals born in 2009. The average inbreeding coefficient changed from 0.007 to 0.014 in JH and from 0.008 to 0.011 in DH for animals born in 1995 and 2009, respectively. However, in both subpopulations the average inbreeding coefficient (i.e. realised inbreeding) was lower than the inbreeding coefficient expected under random

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mating, showing certain policy to avoid inbred mating (Figure 2.1). Considering the genetic background, JH presented a bigger number of founders but DH had maintained a more balanced representation of them in their genetic pool, expressed by a bigger number of effective founders (589 vs. 442) and effective genomes (44.0 vs. 40.4). Additionally, the number of effective ancestors was larger in DH (80.5) than in JH (68.5), which could indicate a more moderate use of outstanding animals as parents. In contrast, when different periods were analysed, the reduction of the genetic diversity was stronger in DH than in JH, and for animals born between 2005 and 2009, both subpopulations presented similar values (Tables 2.3 and 2.4).

Table 2.3. Pedigree completeness index for three (PIC3) and five generations (PIC5), Equivalent generation coefficient (EqC), generation interval (L), number of founders (f), effective founders (f_e), effective founder genomes (N_g), effective ancestors (f_a) and average coefficient of inbreeding (F).

Subpopulation	Pedigree Completeness				Genetic Background				
	PIC3	PIC5	EqG	L	f	f_e	N_g	f_a	F
JH	0.99	0.96	8.8	10.1	7707	442	40.4	68.5	0.009
DH	0.99	0.97	8.4	9.5	6958	589	44.0	80.5	0.009

2.3.2 Measures of connectedness

Stallions in common. Considering both JH and DH subpopulations, 1495 different stallions were used, and 599 (40%) of them had offspring in both subpopulations. Observed by year (Table 2.4), the number of SC used in both subpopulations decreased strongly from 191 (60%) in 1995 to 8(3%) in the cohort born in 2009.

Genetic similarity. The GS between JH and DH was 0.83 and the Contribution to GS was 57.9% from JH and 42.1% from DH. Following the decreasing trend of SC across year of birth (Table 2.4), the GS decreased strongly from the cohorts born in the 1990s (~0.9) to the cohorts born after 2005 (~0.1). However, the contribution of each subpopulation to the GS remained stable with similar contribution from both of them.

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Table 2.4 Number of stallions in common (SC) between JH and DH, number of stallions in JH and DH (Sire JH and Sire DH), genetic similarity (GS) and contribution to genetic similarity of JH (% JH) and DH (% DH) in percentage, according with year of birth of horses.

Year	SC	Sire JH	Sire DH	GS	% JH	%DH
1995	191	260	251	0.92	52	48
1996	188	283	245	0.92	59	41
1997	179	285	243	0.90	62	38
1998	175	281	237	0.91	60	40
1999	167	292	224	0.89	62	38
2000	156	265	217	0.89	59	41
2001	141	281	190	0.82	57	43
2002	105	281	161	0.71	55	45
2003	56	229	175	0.38	49	51
2004	46	229	174	0.29	58	42
2005	46	228	161	0.29	36	64
2006	35	243	149	0.14	64	36
2007	22	218	137	0.10	60	40
2008	21	207	144	0.12	49	51
2009	8	183	121	0.03	25	75

Founders in common. Considering the whole population analysed, 9217 different founders were identified, from which 5448 (59%) were f_c contributing to both JH and DH. The genetic contribution of f_c , defined in this work as the common genetic origin ($CGO_{JH,DH}$), was 0.99 in JH and 0.98 in DH. This result confirms that both subpopulations were originated from a common genetic pool, and they share, practically, the same ancestral alleles.

Ancestors in common. When the ancestors (founders or not) with more important genetic contributions were analysed, 27 ancestors were identified in JH that explained 50% of the current genetic pool, while in the case of DH, 31 ancestors were identified which marginal genetic contributions (p) explained 50% of the genetic pool of the subpopulation. In total, there were 45 ancestors in both subpopulations from which 13 (29%) ancestors were in common among the

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ancestors with major p in both subpopulations and their $GC_{0.5}$ was 0.49, with a larger contribution from JH than DH (55% vs. 45%).

Table 2.5 Ancestors in JH ($nfa_{JH0.5}$) and in DH ($nfa_{DH0.5}$), number and proportion of common ancestors ($nfac_{0.5}/pfac_{0.5}$), genetic pool in common ($GC_{0.5}$) and contribution to the $GC_{0.5}$ from JH (% JH) and from DH (% DH) in three periods of time.

Period*	GS	%JH	%DH	$Nfa_{JH0.5}$	$nfac$	$nfac_{0.5}/pfac_{0.5}$	$GC_{0.5}$	%JH	%DH
1	0.97	60	40	31	36	20 / 0.43	0.69	55	45
2	0.91	58	42	26	28	11 / 0.26	0.45	58	42
3	0.45	64	36	21	21	3 / 0.08	0.13	46	54

* 1: 1995-1999; 2:2000-2004; 3:2005-2009

2.3.3 Effect of specialisation on genetic connectedness

Marginal contribution of ancestors. When the connectedness between JH and DH is expressed in the three periods of time defined, two trends are observed (Table 2.5). First, there is a reduction in the number of ancestors that explain 50% of the total genetic pool ($fa_{0.5}$) for both subpopulations. Second, from such ancestors that explain 50% of the total genetic pool ($fa_{0.5}$), the number of ancestors in common ($nfac_{0.5}$) between JH and DH and the proportion of them in relation with the total ($pfac_{0.5}$) decrease more markedly than the reduction in the number of ancestors in each subpopulation. Moreover, the reduction of the genetic contribution of these $nfac_{0.5}$ ($GC_{0.5}$) between JH and DH was even more important. The contribution of each subpopulations to the $GC_{0.5}$ had a small imbalance; the contribution of JH was bigger than DH (~55% vs. 45%), except for the last period when the contribution of DH to the $GC_{0.5}$ was bigger than JH.

Average relationship. Figure 2.2 shows the evolution of the coefficient of relationship (r) within and between horses of the JH and DH subpopulations. From 1995 to 2000, r was similar within and between different subpopulations. For horses born in 1995, the average r was 0.021 in JH, 0.019 in DH and 0.018 between JH and DH. However, after birth year 2000, r increased steadily to 0.038 in JH and 0.050 in DH, and decreased to 0.014 between JH and DH, for horses born in 2009. Furthermore, the standard deviation of r between JH and DH horses decreased

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from the cohort born in 1995 to the ones born in 2009, indicating that r between JH and DH is homogeneously decreasing along the last 15 years (Table 2.6).

Table 2.6 Descriptive statistics of coefficient of relationship (r) between horses in JH, DH and between both groups (JH-DH) for cohorts born in 1995 and 2009.

Cohort	Group	1 st Q ¹	Mean	3 rd Q ²	SD ³
1995	JH	0.004	0.021	0.023	0.04
	DH	0.004	0.019	0.019	0.03
	JH-DH	0.004	0.018	0.019	0.03
2009	JH	0.017	0.038	0.044	0.04
	DH	0.012	0.050	0.071	0.06
	JH-DH	0.008	0.014	0.018	0.01

¹1st Quartile, ²3rd Quartile, ³ Standard deviation

2.4 Discussion

2.4.1 Characterisation of the subpopulations

The present study aimed to describe the effects of the specialisation process on the structure of the population, based on the analysis of the pedigree information. The measures of the completeness of the pedigree registered ensured that the number of founders, ancestors known and connections do not reflect only differences in the depths of the pedigrees. Even when JH and DH presented similar and higher levels of pedigree completeness, at the end of the period, horses in DH presented a bigger average of EqG. The completeness of the pedigree of JH and DH was similar to the German sport horses (PCI3 =0.99; Schöpke *et al.* 2013), Hanoverian (PCI5 =0.98 and 8.43 EqG; Hamann and Distl 2008) and Selle Français (EqG = 7.29; Pirault *et al.* 2013). It was more complete than the Swedish Warmblood population (average PCI5 = 0.85 and PCI5 = 0.91 for stallions with more progenies; Thorén Hellsten *et al.* 2009), Norwegian Warmblood population (PCI5 = 0.47; Furre *et al.* 2013) and Spanish sport horses (4.29 EqG; Bartolomé *et al.* 2011). Generation intervals (L) were longer in JH than in DH (10.1 vs. 9.5 years) and in JH stallions L was one year longer than for the mares (10.6 vs. 9.6 years), while in DH the difference between sexes was imperceptible (stallion 9.3 vs. mares 9.7 years). These values are in the ranges of values presented for other riding horse populations: Selle Français 11.7 years (Moureaux *et al.* 1996), Hanoverian 10.0

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years (Hamann and Distl 2008), Spanish sport horse 10.8 years (Bartolomé *et al.* 2011).

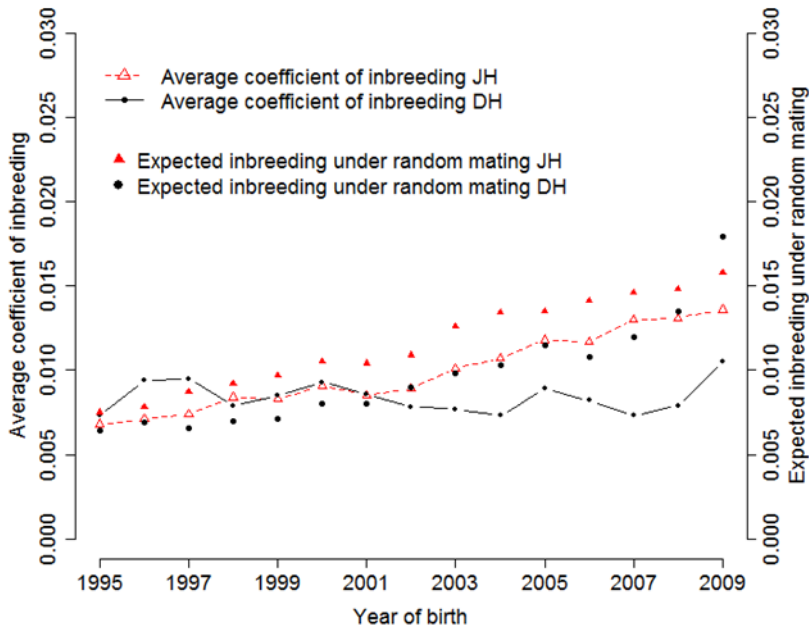


Figure 2.1 Evolution of the average realized inbreeding coefficient and the average expected inbreeding coefficient of Show-jumping (JH) and Dressage subpopulations (DH) according to year of birth of horses.

The parameters in Table 2.3 show that both subpopulations have a diverse origin expressed in a large number of founders compared with the results presented in other populations of horses (Hamann and Distl 2008; Janssens *et al.* 2010; Bartolomé *et al.* 2011; Schurink *et al.* 2012). The number of founders represented a similar proportion of each subpopulation, 0.32 in JH and 0.38 in DH. However, the larger number of effective founders and effective genomes for DH indicate that the variability of the founders was more preserved than in JH. The number of effective ancestors was also larger in DH than in JH, expressed in a larger number of effective founders (589 vs. 442) and effective genomes (44.0 vs. 40.4). Both subpopulations have a larger number of effective founders than that found in other horse riding

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populations; for example, for Selle Français, Moureaux *et al.* (1996) estimated 333 f_e for animals born in 1992, while Hamman and Distl (2008) calculated an f_e of 224.9 in Hanoverian horses born between 1980 and 2000. Compared with the whole population of Spanish sport horses, the number of f_e was smaller and also the number of founder genome equivalent; but the values were similar if compared with the subpopulation of animals with both Spanish parents (Bartolomé *et al.* 2011). Compared with the Hanoverian population, JH and DH had more f_e , but for N_g the difference was smaller (~40 vs ~35). The level of inbreeding in JH and DH was small as in other populations of riding horses with similar deepness of pedigree registered, like for Selle Français (1.34%; Pirault *et al.* 2013) and Hanoverian (1.33%; Hamman and Distl 2008).

2.4.2 Genetic connectedness

The SC and the GS between JH and DH were considerably higher than the values found in the literature reviewed. There are some limitations by comparing SC between studies because it is a parameter that depends on the size of population compared. Nevertheless, in a similar study in German sport horses, the two more related subpopulations had 267 SC, which represented 50.3% and 44.8% of the sires used in each region. These two regions, Berlin-Brandenburg and Saxony-Anhalt, also presented the highest GS (0.67), followed by the GS (0.61) between the regions of Saxony and Thuringia, even when the SC were fewer than in between other regions (Schöpke *et al.* 2013).

Several studies on genetic connectedness in sport horses have been performed with the aim to evaluate the feasibility of common genetic evaluations of two or more different studbooks or populations. Compared with these studies, JH and DH presented a larger proportion of SC and GS. The biggest value of GS found in this kind of studies was 0.32 between the Netherlands (KWPN) and Germany (several studbooks) (Ruhlmann *et al.* 2009). Thorén-Hellsten *et al.* (2008), analysing the genetic connectedness among five European sport horse populations, reported values of GS of 0.31 between KWPN and Holstein studbook, 0.20 between Danish Warmblood and Holstein and 0.18 between Danish and Swedish Warmblood studbooks. In a similar study, Furre *et al.* (2013) reported GS to be 0.31 between Norwegian and Swedish Warmblood. Although several values of GS were similar in magnitude, there were important differences in the balance of the contribution to GS. In the case of the German sport horses, the contribution to GS was balanced in

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all the cases, varied from equal contribution (50:50) to an imbalance of 41:59 between Saxony and Thuringia regions. This is similar to what was obtained for JH and DH. Referring to the studies that involved populations from different countries or studbooks, a wide range of values was observed. Extreme grade of imbalance was reported for Norwegian and Swedish Warmblood (2:98; Furre *et al.* 2013), but also important imbalances were reported in the case of the GS between KWPN and Holstein (7:93; Thorén-Hellsten *et al.* 2008) and the Netherlands and Germany (20:80; Ruhlmann *et al.* 2009). More balanced contributions of KWPN were with the Danish Warmblood (34:66) and with Swedish Warmblood (64:36), but in both cases with small GS (Thorén-Hellsten *et al.* 2008).

2.4.3 Evolution of the connectedness

Thorén-Hellsten *et al.* (2008) analysed the evolution of the connectedness among five European sport horse populations across three periods of time (1952–1974, 1975–1984 and 1985–1997). The general average of the GS increased among studbooks in more recent years (from 0.13 to 0.18), but there was not a unique pattern in the evolution of GS among all the studbooks considered over years. For example, the GS between Holstein and KWPN decreased to the most recent years from 0.50 to 0.27 and between Hanoverian and KWPN from 0.18 to 0.07. Conversely, the GS increased for Danish Warmblood-Holstein (from 0.05 to 0.25) and Danish Warmblood-Swedish Warmblood (from 0.09 to 0.29). In the present study, the GS between JH and DH was very high (more than 0.9) until the cohorts born in 2003. After that, the GS decreased to 0.45, considering horses born in the period 2005–2009. Despite the decreasing trend in the GS the values are still high compared with the literature reviewed. However, given that the pedigree of the subpopulations is available, analysis based on the marginal contribution of ancestors and on the change in the coefficient of relationship was considered to be a more precise and informative measure of the genetic connectedness between JH and DH. The results from different measures of connectedness were congruent indicating that the connectedness between JH and DH was decreasing in more recent years and that the trend has been more intense after year 2003. Particularly of interest is it to observe the change in the dynamic of both subpopulations, in both there is a decrease in the number of stallions used but this reduction is proportionally more intense in DH than in JH. Similarly, the number of ancestor that explained 50% of the genetic pool decreased in both subpopulations from ~30 to ~20 in 15 years. In the period 1995–1999, 31 and 36 ancestors explained the

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50% of the genetic pool of JH and DH, respectively, while in the period 2005–2009, the number of important ancestors dropped to 21 in both groups. Concerning the objective of this study, this reduction in number of relevant ancestors was followed by an important reduction of the ancestors in common and in the marginal genetic contribution of them in JH and DH.

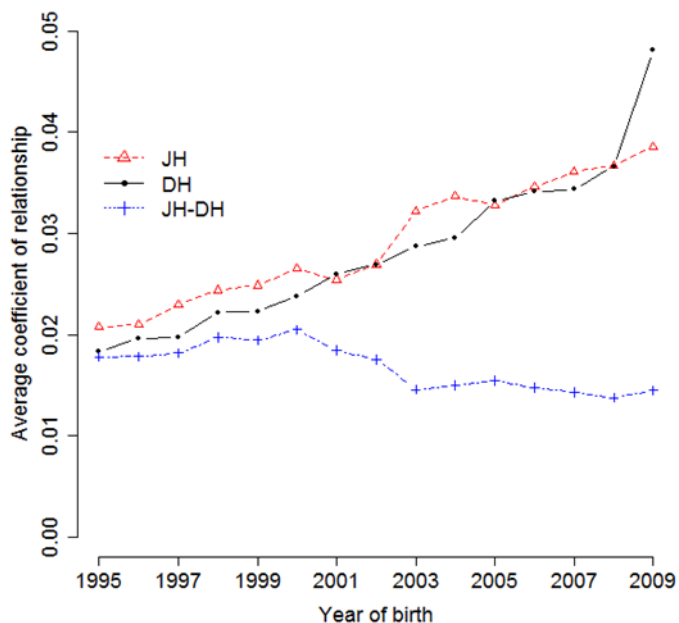


Figure 2.2 Evolution of the average coefficient of relationship within JH subpopulation (JH), DH subpopulation (DH) and between both subpopulations (JH-DH) according year of birth of horses.

2.5 Conclusions

The JH and DH subpopulations originate from essentially the same genetic pool based on the fact that the contribution of the common ancestors explained 98% and 99% of the total genetic pool of JH and DH. JH and DH still maintain an important level of genetic connection based on the number of SC before 2000, which represented more than 50% of the sires used in each subpopulation. From 2006, JH and DH subpopulations start to lose genetic links between them markedly.

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Meanwhile, the relatedness within both subpopulations has been increasing consistently; the relatedness between horses in the two subpopulations has been reduced to a very low level. Despite the systematic increase of the relatedness within JH and DH subpopulations, the average coefficient of realised inbreeding is still low. Considering that the values of realised inbreeding resulted lower than the average coefficient of expected inbreeding under random mating, it could be concluded that certain policy to avoid inbred mating is implemented. However, given the strong reduction in the number of relevant ancestors in both subpopulations, it is important to optimise the genetic contribution of relevant stallions to avoid the loss of genetic diversity in both subpopulations.

The trend in the reduction of the relatedness between both subpopulations is expected to continue or maintain in a very low level, and in consequence JH and DH subpopulations are becoming weakly genetic connected populations. This reduction in genetic connection will limit the value of using phenotypic data from one group to predict genetic values to the other group. The consequences of the specialisation process on genetic parameters and genetic correlations of traits measured in both subpopulations will be analysed in a later paper.

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3

Effect of specialisation on genetic parameters of studbook–entry inspection in Dutch Warmblood horses

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Abstract

Recent studies on data from the Dutch Warmblood Studbook (KWPN) have shown that the ongoing specialisation of horses for either dressage (DH) or show jumping (JH) has led to a decreasing genetic relationship between the two subpopulations. The aim of this study was to analyse the effect of the specialisation process on the genetic parameters of traits measured in the studbook–entry inspection of KWPN during the last fifteen years. Data from 18,125 DH and 23,800 JH recorded from 1998 until 2013 were used to analyse 13 traits scored in both DH and JH. Analyses were performed in a Bayesian framework. Firstly, variance components were estimated based on the whole data set. Secondly, genetic correlations between traits measured in DH or JH were estimated using bivariate analyses. Thirdly, three time periods were defined and genetic correlations between subpopulations were estimated within each period. Heritability was moderate (0.17–0.39) for both DH and JH. Genetic correlations between traits measured in DH or JH were not different from one considering the posterior standard deviation of the estimation; however, in most of the traits, a clear trend in reduction of the genetic correlation for traits expressed in DH and JH and an increase in their posterior standard deviation for recent years was observed. These results suggest that specialization could lead to differences in traits measured in DH and JH in the recent years.

Key words: Dressage, genetic correlation, show jumping, sport horse

3.1 Introduction

Most warmblood horse studbooks aim to improve the performance in dressage and show jumping (Koenen *et al.* 2004). In the case of the Dutch Royal Warmblood Studbook (KWPN) the breeding goal includes performance in dressage (DH) and show jumping (JH) at the highest level of competition. Competing at advanced level requires an intense preparation and specific training of the horses, which implies that they can participate in only one of the disciplines. To meet these requirements at high competition level, individual breeders have started to focus on breeding horses for one of the two disciplines. The breeding programme conducted by KWPN has evolved in the same direction, and from 2006 onwards, specific objectives were defined for DH and JH (KWPN 2014). In the breeding programme, the studbook focuses more on the selection of stallions while the selection decisions on mares are mostly taken by the breeders. KWPN follows a multistage selection process to select the stallions. The first stage of selection of stallions is the entry inspection and the first stallion inspection where the stallions are assessed on conformation, movement and free jumping. The best horses are selected to participate in the stallion performance test and the stallions that approve the performance test are allowed to breed. The final selection takes place when records of progeny are available (Ducro 2011; KWPN 2014).

Including young horse information into the selection programme is justified because of the substantial genetic correlations found in various studies between traits recorded in the young horse performance tests and performance in competition (Thorén Hellsten *et al.* 2006). Specifically for KWPN population, Huizinga *et al.* (1991); Koenen *et al.* (1995) and Ducro *et al.* (2007) showed that some traits recorded at the young horse inspections were genetically and phenotypically correlated with competition despite differences in magnitude and sometimes in direction between the estimates reported.

The breeding practice has resulted in an increasing specialisation of the horses. As a consequence, there has been a reduction in the relationship between horses belonging to the DH and JH subpopulations in recent years and the riding horse population of KWPN has started to become two more clearly demarked subpopulations (Rovere *et al.* 2014). A more intense directional selection for either dressage or show jumping could lead to changes in not only the means but also (co)variances of the selection traits. It is not known whether genetic parameters of selection traits have changed as a result of specialisation.

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The objective of this study was to analyse whether the specialisation for either dressage or show jumping has affected the heritabilities and the genetic correlations between traits observed in the two subpopulations.

3.2 Materials and Methods

3.2.1 Data

Data for this study were provided by KWPN and consisted of a pedigree file including 506,078 horses and 68,126 studbook–entry inspections from the year 1989 until 2013. All horses were assigned to one of two subpopulations: JH or DH, based on the overall evaluation as a JH or DH in its studbook–entry inspection (Table 3.1). The subpopulations comprised 23,800 JH and 18,125 DH born between 1995 and 2009. In the studbook–entry inspections, a KWPN jury assigns a score to evaluate the horses in several conformation and movement characteristics that provide a detailed description of the horse. The traits recorded are divided in two groups named descriptive and subjective traits (Ducro *et al.* 2007). For the descriptive traits, every individual horse is compared with the population’s mean on each trait. Currently, a scale from 1 to 9 is used to evaluate the horses for the descriptive traits. In this scale, values of 4–6 represent a trait as it appears in the average horse. Values from 1 to 3 and 7 to 9 represent to what extent and direction the expression of the trait is deviating from the population’s mean. For most descriptive traits, smaller values are considered favourable, although extreme values are undesired (Ducro *et al.* 2007; KWPN 2014). In the subjective traits, the juries express an overall opinion about the conformation, movement and jumping characteristics of the horse. The juries used a scale from 40 (very bad) to 100 (excellent), marked in five-point increments, to evaluate the qualification of the horses in these traits (KWPN 2014). A detailed description of the traits judged in the studbook inspections and their genetic parameters can be found in Koenen *et al.* (1995) and Ducro *et al.* (2007).

Only the first record of horses between 2 and 7 years old at the moment of their first inspection was included in this study. Records from classifiers who evaluated less than 50 horses, locations with less than 10 records and single tests (location-date) where less than 2 horses had been inspected were omitted. After editing, data comprised information of 40,712 horses from which 23,800 received a first inspection as show jumping horses and 18,125 horses as dressage horses. The horses were born between 1995 and 2009, and all animals included in the data file

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were traced back as far as possible to construct a pedigree file that comprised 96,869 animals.

Table 3.1 Number of observations, phenotypic means and phenotypic standard deviations of traits for the whole population and for DH and JH subpopulations.

Trait	Data analysed			Phenotypic Mean <small>standard deviation</small>		
	Overall	DH	JH	Overall	DH	JH
Descriptive traits						
Walk: stride	39414	16943	22471	4.85 _{0.99}	4.76 _{1.06}	4.92 _{0.92}
Walk: correctness	40573	17363	23210	4.85 _{1.02}	4.86 _{1.07}	4.84 _{0.99}
Trot: stride	40480	17293	23187	4.70 _{1.13}	4.46 _{1.15}	4.88 _{1.08}
Trot: elasticity	40495	17296	23199	5.04 _{1.20}	4.90 _{1.29}	5.15 _{1.13}
Trot: impulsion	40489	17293	23196	5.10 _{1.21}	4.99 _{1.30}	5.19 _{1.12}
Trot: balance	40471	17286	23185	5.36 _{1.16}	5.21 _{1.26}	5.47 _{1.07}
Canter: stride	37262	15143	22119	4.91 _{1.13}	4.93 _{1.19}	4.90 _{1.08}
Canter: impulsion	37324	15144	22180	4.96 _{1.13}	5.02 _{1.21}	4.92 _{1.07}
Canter: balance	37309	15139	22170	5.31 _{1.15}	5.39 _{1.24}	5.25 _{1.08}
Subjective traits						
Conformation	40536	17377	23159	67.33 _{5.94}	67.21 _{6.39}	67.43 _{5.57}
Movement	30750	17374	13376	67.70 _{5.87}	68.34 _{6.58}	66.88 _{4.68}
Walk	23492	10911	12581	66.94 _{6.80}	68.48 _{7.29}	65.59 _{6.03}
Trot	23501	10912	12589	67.53 _{7.75}	69.91 _{7.97}	65.46 _{6.92}
Canter	23437	10844	12593	68.45 _{7.21}	67.99 _{7.58}	68.84 _{6.84}

3.2.2 Traits analysed

The studbook inspections have been modified through the time to improve the judgment of the horses in traits which are considered related to performance in competition later in life. In 1998, KWPN extended the studbook inspections with free jumping and movement traits which are genetically correlated with sport performance as shown in a previous study Ducro *et al.* (2007). In 2006, a group of traits were incorporated in the subjective traits which describe the components of movement, and the scale used to evaluate the descriptive traits changed from a scale ranging from 1 to 40 to the current scale ranging from 1 to 9. To account for the change in the scale, the data recorded before 2006 were transformed to a scale of nine points (1 to 9) following the distribution of records in the former scale of 40 points.

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For this study, the traits analysed were nine descriptive traits and five subjective traits, all of them recorded in both DH and JH. Table 3.1 shows the number of records, phenotypic mean and phenotypic standard deviation for the traits analysed in this study. For the traits that were measured during the whole period, in average 34% of the records were recorded in the period 1998–2002, 36% in 2003–07 and 30% in 2008–12. The proportion of data that come from DH was approximately 0.4 and 0.6 from JH. Three subjective traits started to be recorded first in 2006: Walk, Trot and Canter. For those, the proportion of data provided by DH and JH was similar to the other traits and approximately 50% of the records analysed came from each period of time (around 11,700 records per period). The subjective trait Movement was recorded for both subpopulations until 2007 and then only for DH. Forty-five percent of the records were recorded in the period 1998–2002, 35% in 2003–07 and 20% in 2008–12. The proportion of records that belong to DH was 0.40 in 1998–2002, 0.57 in 2003–07 and 1 in 2008–12 and 0.6, 0.43 and 0 was the proportion of JH records in the same time periods, respectively.

The traits were analysed in three different frameworks. Firstly, univariate analyses for the whole data set were performed to estimate the variance components for each trait. Secondly, each trait was defined as a DH trait or a JH trait according to the type of the horse that received the inspection. Bivariate analyses were then carried out to estimate the genetic correlation between the two traits. Thirdly, three periods of time of 5 years each were defined. The genetic correlation between the traits measured in DH or JH was estimated using bivariate analysis for each time period.

3.2.3 Statistical methods and models

The full model used for all the traits was defined as follows:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{c} + \mathbf{e}, \quad [1]$$

where \mathbf{y} is the record of the animal, \mathbf{b} is the vector of systematic effects, \mathbf{a} is the vector of the animal direct genetic effects, \mathbf{c} is the vector of the environmental location-date effects and \mathbf{e} is the vector of random residual effects; \mathbf{X} , \mathbf{Z}_1 and \mathbf{Z}_2 are the incidence matrices relating the respective effects to \mathbf{y} .

The random effects were assumed to follow a multivariate normal distribution. The variance and covariance structure for the random effects were $\text{var}(\mathbf{a}) = \mathbf{A}\sigma_a^2$, $\text{var}(\mathbf{c}) = \mathbf{I}\sigma_c^2$, and $\text{var}(\mathbf{e}) = \mathbf{I}\sigma_e^2$; where \mathbf{A} is the numerator relationship matrix, \mathbf{I} is an

identity matrix, σ_a^2 the additive genetic variance, σ_c^2 the variance of the environmental location date effects and σ_e^2 the residual variance. The systematic effects are the classifier (32 levels), sex (3 levels: stallion, mare, gelding), age of the horse at the inspection (6 levels: 2, . . ., 7 years old), year of inspection (15 levels: 1998, . . ., 2012), proportion of thoroughbred expressed in eighths (6 levels: 0, 1, . . ., ≥ 5) and type of horse (2 levels: DH, JH).

For the bivariate analyses, the same linear model was used, removing the effect of type of horse because the traits were defined for DH and JH. In the bivariate analyses, the random effects of the location date of each trait were considered independent, and the residuals between the traits were uncorrelated.

All traits were analysed in a Bayesian framework using the RJMC module of the DMU software version 6 release 5.2 (Madsen and Jensen 2013). Uninformative prior (Flat) was used for systematic effects. Prior distribution for dispersion parameters were scaled inverse Wishart. The Gibbs sampler was run as a single chain of 600,000 samples after discard the first 40,000 samples and the sampling interval was 100, leaving 6000 samples to estimate the features of the posterior distributions. Convergence diagnostic and statistical and graphical analysis of the Markov chain Monte Carlo sampling output was performed with the BOA package (Smith 2007) of the R language/environment (R Core Team 2014).

3.3 Results

Descriptive statistics of the data are presented in Table 3.1 Phenotypic means of descriptive traits were similar for DH and JH, with a small difference in favour of DH for traits related to Trot and a small difference in favour of JH for traits related to Canter. However, DH presented systematically a larger phenotypic standard deviation than JH. For the subjective traits, DH presented a higher phenotypic means in Movement, Walk and Trot, and for Canter, the phenotypic mean was higher in JH. Also in the subjective traits, DH showed a larger phenotypic standard deviation. From the univariate analyses performed for the whole data set, the effect of type of horse (DH and JH) was significant in some traits, based on its posterior standard deviations, indicating that some of the phenotypic differences between each subpopulation could be genetic.

Posterior means and standard deviations for heritabilities obtained from a joint analysis across the subpopulations as well as a separate analysis for DH and JH are

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presented in Table 3.2. Although the heritabilities for DH and JH were not equal, the differences between the two subpopulations were not significant based on their posterior standard deviations. Neither did the heritabilities of the subpopulations significantly differ from the heritability of the whole population, which tended to be an intermediate value between DH and JH. The posterior means for genetic correlations between the traits defined as a DH or JH trait are presented in Table 3.2 as well. The genetic correlations were not significantly different from one between any of the traits measured in both DH and JH based on their posterior standard deviations. The lowest posterior means for genetic correlation between the two subpopulations were for the descriptive trait Walk-correctness (0.93) and the subjective trait Walk (0.93).

Table 3.2 Posterior mean and standard deviation (SD) of heritability of traits for the whole population and for DH and JH subpopulations and posterior mean and standard deviation (SD) of genetic correlation (GC) between the traits measured in DH and JH.

Trait	Heritability (Mean _{SD})			GC
	Overall	DH	JH	Mean _{SD}
Descriptive traits				
Walk: stride	0.19 _{0.01}	0.20 _{0.02}	0.17 _{0.02}	0.98 _{0.02}
Walk: correctness	0.30 _{0.01}	0.32 _{0.02}	0.30 _{0.02}	0.93 _{0.03}
Trot: stride	0.30 _{0.01}	0.30 _{0.02}	0.28 _{0.02}	0.98 _{0.02}
Trot: elasticity	0.27 _{0.01}	0.28 _{0.02}	0.26 _{0.02}	0.98 _{0.01}
Trot: impulsion	0.26 _{0.01}	0.28 _{0.02}	0.24 _{0.02}	0.99 _{0.01}
Trot: balance	0.23 _{0.01}	0.26 _{0.02}	0.22 _{0.01}	0.98 _{0.02}
Canter: stride	0.23 _{0.01}	0.27 _{0.02}	0.22 _{0.02}	0.97 _{0.02}
Canter: impulsion	0.21 _{0.01}	0.24 _{0.02}	0.19 _{0.01}	0.97 _{0.02}
Canter: balance	0.17 _{0.01}	0.20 _{0.02}	0.15 _{0.01}	0.98 _{0.02}
Subjective traits				
Conformation	0.30 _{0.01}	0.32 _{0.02}	0.29 _{0.02}	0.98 _{0.01}
Movement	0.31 _{0.01}	0.32 _{0.02}	0.33 _{0.02}	0.98 _{0.01}
Walk	0.25 _{0.02}	0.26 _{0.03}	0.21 _{0.02}	0.93 _{0.06}
Trot	0.39 _{0.02}	0.37 _{0.03}	0.39 _{0.03}	0.96 _{0.02}
Canter	0.28 _{0.02}	0.30 _{0.03}	0.28 _{0.02}	0.99 _{0.02}

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In Table 3.3, the results obtained from the analysis by time period for the descriptive traits are shown. Most of the descriptive traits had lower average scores towards the third period (more recent years) indicating some favourable change in the means, as lower values are considered favourable. The descriptive traits showed a smaller phenotypic variation in the first period. These results are considered a consequence of the change in the scale used to evaluate the descriptive traits; the use of the new scale may express more variation among animals. For heritabilities, the values by time period were mainly in the range of values from the analysis performed on the whole period of time. This holds for the joint analysis and the analysis by subpopulation. Nevertheless, heritabilities for the first time period tended to be lower than in the later periods in both subpopulations.

Similarly to the estimates from the whole period, in most of the cases, significant differences between DH and JH were not observed. The largest differences between posterior means were for heritabilities of Walk-length of stride and Canter-balance, showing higher values for DH in the three periods analysed. The genetic correlations decreased in the later period for all traits except for Walk-correctness, where the second period of time presented the lowest genetic correlation between the trait defined as DH or JH. The results obtained from the analysis by time period for the subjective traits are shown in Table 3.4. For these traits, different results were observed. For Conformation, the mean did not change across the time period and this was similar for both groups. Posterior means for heritabilities of Conformation ranged 0.27–0.37 and the genetic correlation between subpopulations in the three time periods varied from 0.90 to 0.93; both heritabilities and genetic correlations did not follow any clear trend towards any subpopulation or time period. The score for Movement increased towards the more recent period for DH but not for JH although the latter was not scored in the last period. Posterior means for heritabilities and genetic correlations were similar between time periods and subpopulation. For Walk, Trot and Canter which have been recorded since 2006, heritabilities were similar for time period and subpopulations with the exception of Walk in the first time period when the parameter was higher in DH than in JH. In the three traits, the genetic correlation dropped in the last period of time. For both the descriptive and subjective traits, the standard deviation of the posterior mean of the genetic correlation increased two to five times compared to the standard deviation of previous periods.

3. Effect of specialisation on genetic parameters

Table 3.3 Phenotypic mean and standard deviations (SD), posterior mean and standard deviation (SD) of heritability and posterior mean and standard deviation (SD) of genetic correlation (GC) of Descriptive traits measured in DH and JH, in three periods of time: (1) 1998-2002, (2) 2003-2007 and (3) 2008-2012.

Trait	Period	Phenotypic Mean _{SD}		Heritability _{SD}		GC _{SD}
		DH	JH	DH	JH	
Walk: length stride	(1)	5.00 _{0.58}	5.01 _{0.57}	0.10 _{0.02}	0.12 _{0.02}	0.88 _{0.06}
	(2)	4.70 _{1.20}	4.94 _{1.07}	0.27 _{0.04}	0.19 _{0.03}	0.93 _{0.05}
	(3)	4.59 _{1.22}	4.76 _{1.08}	0.23 _{0.04}	0.18 _{0.03}	0.76 _{0.15}
Walk: Correctness	(1)	4.88 _{0.63}	4.87 _{0.59}	0.24 _{0.03}	0.21 _{0.03}	0.95 _{0.04}
	(2)	4.81 _{1.19}	4.81 _{1.12}	0.36 _{0.04}	0.32 _{0.03}	0.85 _{0.07}
	(3)	4.91 _{1.23}	4.82 _{1.23}	0.37 _{0.04}	0.34 _{0.03}	0.92 _{0.09}
Trot: Length	(1)	4.92 _{0.78}	4.97 _{0.74}	0.23 _{0.03}	0.27 _{0.03}	0.95 _{0.04}
	(2)	4.36 _{1.21}	4.93 _{1.22}	0.29 _{0.04}	0.29 _{0.03}	0.91 _{0.06}
	(3)	4.14 _{1.23}	4.71 _{1.25}	0.28 _{0.04}	0.23 _{0.03}	0.81 _{0.14}
Trot: Elasticity	(1)	5.18 _{0.82}	5.19 _{0.77}	0.23 _{0.03}	0.26 _{0.03}	0.98 _{0.02}
	(2)	4.90 _{1.42}	5.26 _{1.28}	0.28 _{0.04}	0.26 _{0.03}	0.92 _{0.05}
	(3)	4.63 _{1.43}	4.94 _{1.30}	0.28 _{0.04}	0.25 _{0.03}	0.67 _{0.17}
Trot: Impulsion	(1)	5.27 _{0.85}	5.21 _{0.78}	0.19 _{0.03}	0.20 _{0.02}	0.95 _{0.04}
	(2)	4.91 _{1.43}	5.25 _{1.26}	0.32 _{0.04}	0.25 _{0.03}	0.93 _{0.04}
	(3)	4.81 _{1.46}	5.08 _{1.31}	0.28 _{0.04}	0.23 _{0.04}	0.69 _{0.22}
Trot: Balance	(1)	5.28 _{0.81}	5.28 _{0.74}	0.21 _{0.03}	0.21 _{0.03}	0.91 _{0.04}
	(2)	5.19 _{1.36}	5.62 _{1.16}	0.27 _{0.04}	0.22 _{0.03}	0.92 _{0.06}
	(3)	5.18 _{1.49}	5.53 _{1.28}	0.28 _{0.04}	0.21 _{0.04}	0.77 _{0.18}
Canter: Length	(1)	5.16 _{0.72}	5.04 _{0.68}	0.20 _{0.04}	0.21 _{0.03}	0.88 _{0.06}
	(2)	5.05 _{1.24}	5.05 _{1.17}	0.31 _{0.04}	0.24 _{0.03}	0.94 _{0.05}
	(3)	4.65 _{1.30}	4.51 _{1.25}	0.27 _{0.04}	0.20 _{0.03}	0.71 _{0.19}
Canter: Impulsion	(1)	5.28 _{0.73}	5.13 _{0.72}	0.24 _{0.04}	0.20 _{0.03}	0.90 _{0.05}
	(2)	5.06 _{1.30}	4.98 _{1.18}	0.29 _{0.04}	0.23 _{0.03}	0.95 _{0.04}
	(3)	4.83 _{1.31}	4.57 _{1.20}	0.24 _{0.04}	0.21 _{0.03}	0.71 _{0.15}
Canter: Balance	(1)	5.32 _{0.69}	5.38 _{0.71}	0.22 _{0.05}	0.19 _{0.03}	0.88 _{0.07}
	(2)	5.45 _{1.30}	5.36 _{1.15}	0.25 _{0.03}	0.19 _{0.02}	0.94 _{0.05}
	(3)	5.33 _{1.42}	5.01 _{1.32}	0.20 _{0.03}	0.17 _{0.03}	0.72 _{0.16}

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Table 3.4 Phenotypic means and standard deviations (SD), posterior mean and standard deviation (SD) of heritability and posterior mean and standard deviation (SD) of genetic correlation of Subjective traits measured in DH and JH, in three periods of time: (1) 1998-2002, (2) 2003-2007 and (3) 2008-2012.

Trait ⁽¹⁾ / Period	Phenotypic Mean _{SD}		Heritability _{SD}		Genetic Correlation _{SD}	
	DH	JH	DH	JH		
1	(1)	67.52 _{4.85}	67.88 _{4.14}	0.37 _{0.04}	0.35 _{0.03}	0.93 _{0.03}
	(2)	66.80 _{6.91}	66.64 _{5.57}	0.34 _{0.04}	0.27 _{0.03}	0.90 _{0.04}
	(3)	67.34 _{7.06}	67.83 _{7.03}	0.28 _{0.04}	0.36 _{0.04}	0.91 _{0.09}
2	(1)	66.99 _{5.42}	67.05 _{4.73}	0.32 _{0.04}	0.34 _{0.03}	0.95 _{0.04}
	(2)	68.12 _{6.71}	66.52 _{4.58}	0.37 _{0.04}	0.34 _{0.04}	0.98 _{0.02}
	(3)	69.85 _{7.12}		Recorded only in DH		
3	(1)			Not recorded		
	(2)	68.13 _{6.87}	65.49 _{6.03}	0.35 _{0.05}	0.22 _{0.03}	0.93 _{0.05}
	(3)	68.80 _{7.64}	65.71 _{6.02}	0.28 _{0.04}	0.30 _{0.04}	0.80 _{0.11}
4	(1)			Not recorded		
	(2)	69.20 _{7.97}	64.97 _{6.95}	0.37 _{0.04}	0.36 _{0.04}	0.95 _{0.03}
	(3)	70.55 _{7.92}	65.98 _{6.85}	0.33 _{0.04}	0.36 _{0.04}	0.89 _{0.08}
5	(1)			Not recorded		
	(2)	67.26 _{7.27}	67.44 _{6.57}	0.39 _{0.05}	0.33 _{0.04}	0.98 _{0.03}
	(3)	68.63 _{7.80}	70.35 _{6.81}	0.30 _{0.04}	0.30 _{0.04}	0.80 _{0.11}

⁽¹⁾ 1 Conformation; 2 Movement; 3 Walk; 4 Trot; 5 Canter

3.4 Discussion

The results obtained from the analyses on the whole population revealed that effect of discipline (DH and JH) had a significant effect on the mean of the trait, except for the descriptive trait Walk-length of stride. The results obtained by time period and subpopulation showed an improvement in the phenotypic mean of the traits over time, but the rate of change was different for DH and JH. These results suggest that the specialisation process has resulted in a difference in mean trait values between DH and JH.

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3.4.1 Genetic parameters

Heritability

The heritabilities estimated in this study were similar to those obtained in previous studies which partly used the same data (Koenen *et al.* 1995; Ducro *et al.* 2007). The estimates obtained by Koenen *et al.* (1995) were lower than those presented by Ducro *et al.* (2007) and those obtained in the present study (Table 3.5). However, traits related to Walk, especially Walk-length of stride, showed the lowest heritabilities in all three studies. For traits, like Walk and Trot at hand in young horses in field performance test, the results obtained in other studies were in the range of our results. This is the case of studies of Furre *et al.* (2013), for Norwegian and Swedish Warmblood populations; Becker *et al.* (2012) and Schöpke *et al.* (2013) for German Warmblood and German sport horses; and Viklund *et al.* (2008) for Swedish Warmblood population. For some descriptive traits, for example canter related traits, the heritabilities tended to be higher for DH than for JH. However, the differences in heritabilities for DH and JH did not differ significantly based on their posterior standard deviations in both group of traits.

Table 3.5 Estimates of heritabilities of Descriptive traits of the first inspection of KWPN obtained in three different studies.

	Koenen <i>et al.</i> (1995) ¹ h ²	Ducro <i>et al.</i> (2007) ² h ²	This study ³ h ²
Walk: length stride	0.12	0.16	0.19
Walk: correctness	0.21	0.25	0.30
Trot: length	0.22	0.32	0.30
Trot: elasticity	0.20	0.29	0.27
Trot: impulsion	0.20	0.27	0.26
Canter: stride	Not available	0.25	0.23
Canter: impulsion	Not available	0.20	0.21
Canter: balance	Not available	0.19	0.17

¹ Standard error between 0.02-0.03 (Koenen *et al.* 1995); ² Standard error between 0.02-0.03 (Ducro *et al.* 2007); ³ Posterior standard deviation 0.01 (Table 3.2).

Genetic correlation

In this study, the genetic correlation between the traits measured in DH or JH was adopted as an indicator of the effect of the specialisation on the traits. Therefore, genetic correlations of one indicate that the traits measured in DH or JH are the same while genetic correlations different from one would indicate that traits

measured under two different breeding goals (DH or JH) would be genetically different. For descriptive traits, genetic correlation is expected that horses were scored with respect to the population's mean, independently of being DH or JH. Based on that, genetic correlations of one are expected between the traits measured in DH or JH although the subpopulations would have different means for them. In contrast, subjective traits are scored considering the discipline in which the horse is evaluated (DH or JH). Thus, it is possible that traits measured in DH or JH have started to differentiate, and, consequently, genetic correlations lower than one could be expected. Considering the whole time period, the posterior means for genetic correlations indicate that traits measured in DH and JH can be considered the same traits (Table 3.2). However, the genetic correlations obtained from the analyses by period of time indicate a clear reduction of the genetic correlation in the last time period in all the descriptive traits (Table 3.3). For the subjective traits (Table 3.4), Walk, Trot and Canter showed a reduction in the genetic correlation like in the descriptive traits.

In all the cases, it is hardly possible to affirm that the genetic correlations are different from one considering the posterior standard deviation of the estimation. In any case, the genetic correlations estimated in this study are higher than the genetic correlation presented in the literature between traits recorded by two different but related studbooks as Norway and Sweden Warmblood studbooks (Furre *et al.* 2013). Similar conclusion was found when the results were compared with the results obtained in studies that estimate genetic correlations between similar traits tested in different moments of the life of the horse, for example foal inspection and brood mare inspections (Schöpke *et al.* 2013) and different tests in different countries and studbooks (Thorén Hellsten *et al.* 2006). The results obtained in this study showed equal or higher correlation than the results presented for similar traits in studies realised with the objective to compare information from different countries and studbooks in international genetic evaluations (Árnason *et al.* 2006; Ruhlmann *et al.* 2009; Thorén Hellsten *et al.* 2009). The genetic correlations between traits defined as DH or JH were equal or higher than those presented by (Viklund *et al.* 2008) for the same trait measured in different periods of time. Different to these studies, the present study focused on analysing the same trait under two different breeding goals. In this sense, the present study is innovative and the results provide a first insight into the effect of specialisation on the genetic parameters of traits under selection. In this respect, it is interesting to note that the results indicate a clear trend in reduction of the genetic correlation for traits expressed in DH and JH for the most recent time

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period, when the genetic connections between the subpopulations are reduced (Rovere *et al.* 2014). The reduction in genetic correlation could be a consequence of different selection emphasis for the DH and JH subpopulations, and the decreasing genetic connectedness between the two subpopulations leads to less information for estimation of genetic correlation, which is reflected in the increase in the posterior standard deviation for the genetic correlations in all traits analysed.

3.5 Conclusions

The results of this study indicate that the specialization process has resulted in a difference in mean trait values between DH and JH. The differences in heritabilities for DH and JH did not differ significantly based on their posterior standard deviations, in both descriptive and subjective traits. Similarly, the genetic correlations between traits measured as DH or JH were not different from one considering their posterior standard deviation. However, the results showed lower values of the posterior mean of the genetic correlation for traits expressed in DH and JH for recent years and an increase in their posterior standard deviation. This reduced genetic correlations and their increased posterior standard deviation could be a consequence of the specialisation process.

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4

Analysis of competition performance in dressage and show-jumping of Dutch Warmblood horses

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Submitted

Abstract

Most warmblood horse studbooks aim to improve the performance in dressage and show jumping. To evaluate genetic ability of performance the Dutch Royal Warmblood Studbook (KWPN) includes the highest score achieved in competition by a horse. However, the records collected during competition are associated with some aspects that might affect the quality of the genetic evaluation based on these records. These aspects include the influence of rider, censoring and pre-selection of the data. The aim of this study was to quantify the impact of rider effect, censoring and pre-selection on the genetic analysis of competition data of dressage and show-jumping of KWPN. Different models including rider effect were evaluated. To assess the impact of censoring, genetic parameters were estimated in data sets that differed in the degree of censoring. The effect of pre-selection on variance components was analysed by defining a binary trait (sport-status) depending on whether the horse has a competition record or not. This trait was included in a bivariate model with the competition trait and used all horses registered by KWPN since 1984. Results showed that performance in competition for dressage and show-jumping is a heritable trait ($h^2 \sim 0.11-0.13$), and that it is important to account for the effect of rider in the genetic analysis. Censoring had a small effect on the genetic parameter for highest performance achieved by the horse. A moderate heritability obtained for sport-status indicate that pre-selection have a genetic basis, but the effect on genetic parameters was relatively small.

Key words: Genetic evaluation, rider effect, pre-selection, censoring, sport horse

4.1 Introduction

Breeding programmes of sport horses are run with the aim to breed horses which can compete successfully at the highest levels of competition in dressage and show-jumping. For that purpose, genetic evaluations are conducted and information on the genetic ability of the horses allows breeders to make the right selection decisions. For genetic evaluation of horses, information collected early in life at studbook inspections and in performance tests can be used as these traits have a relation to the breeding goal (Ducro *et al.* 2007). In addition, information collected for horses that participated in competitions can be used as they are directly related with the breeding goal. Ranks, earnings and scores are the most common expression used for performance in competition (Koenen and Aldridge 2002). The Royal Dutch Warmblood studbook (KWPN) uses in their breeding evaluation a combination of young horse tests and competition results. For competition results, the highest score of a horse in competition is used (KWPN 2015). Performance of horses in competition results from an interaction between rider and horse. A well-balanced communication between rider and horse is important for a good performance of the horse (Peham *et al.* 2004; Schöllhorn *et al.* 2006). For that reason, it is important to consider the rider effect in the genetic evaluations of horses (Bartolomé *et al.* 2013; Sánchez Guerrero *et al.* 2014). However, many riders only ride a limited number of horses and many horses are ridden by only one rider in competition. This creates difficulties to disentangle the effects of the horse and the rider with an obvious risk of having confounding effects (Albertsdóttir *et al.* 2007).

The performance in competition is expressed as the highest score achieved by a horse. Therefore older horses have an advantage over younger animals because they have had more time to get a higher score. Carriquiry *et al.* (1987) showed that this type of censoring can bias estimates of genetic parameters and breeding values. Little is known, however, about the impact of censoring when using the highest score achieved in competition and opportunities to overcome this potential problem. In addition to censoring, many horses do not have a chance to compete for many reasons such as lack of interest of the owner or lack of ability of the horse. Therefore, they do not have any competition scores. When horses do not compete because they performed poorly for traits related to the breeding goal (pre-selection) then not including them in the analysis may bias breeding values (Klemetsdal 1994; Árnason 1999). Research has demonstrated the existence of pre-

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selection in sport horses (Bugislaus *et al.* 2005; Albertsdóttir *et al.* 2011; Árnason *et al.* 2012). Ducro (2010) showed that pre-selection in dressage horses decreased the estimate of heritability for dressage competition and biased estimation of breeding values.

In conclusion, performance in competition is an important breeding goal for many horse breeding organisations, but rider, censoring and pre-selection decrease the reliability of the genetic evaluation based on these records. There is currently limited information about how to overcome these problems. Therefore, objective of this paper was to quantify the impact of the rider effect, censoring and pre-selection on the genetic analysis of competition data of dressage and show-jumping horses of the Royal Dutch Warmblood studbook.

4.2 Material and Methods

4.2.1 Data

Performances in competition are recorded by the Royal Dutch National Equestrian Federation (KNHS). The KNHS defines the level of competition for a horse based on the number of points gained by that horse. In dressage, the jury decides how many points the horse gets for each trial. If the jury assigns a score higher than 70% for the performance, the horse receives 3 points, if the score is between 65-70% the horse receives 2 points and if the jury's score is between 60-65% the horse receives 1 point. Starting in the base level, 10 points allows the horse to be promoted to a higher level, and with 30 points it is compulsory to move to a higher level. For show-jumping, the horse gets 2 points if it has a faultless performance and 1 point if it has no more than one fault in the jumping track. Ten points are required to be promoted to a higher level and with 20 points promotion to a higher level is compulsory (Ducro *et al.* 2007). There are twelve competition levels in dressage and ten in show-jumping. The level of performance and points gained at that level are converted into a linear score defined by KWPN. For this study, data was provided by KWPN, consisting of 87,920 competition records for dressage and 66,591 competition records for show jumping. A competition record consisted of the highest score and the age of the horse when it received the highest score. After edition, the performance of 82,694 horses in dressage and 62,072 horses in show-jumping were analysed. To make the data more normal distributed, the linear scores were transformed using a square-root transformation (Huizinga and van der Meij 1989). The square-root transformation is also applied in the routine genetic evaluation performed by KWPN (KWPN 2015). The competition records were

collected from the period 1993 – 2012 on horses between 4 and 20 years old (year of birth between 1974 and 2009). For dressage, about 48% of the records were from mares, 23% from stallions and 29% from geldings. For show jumping, 48% of the records were from mares, 26% from stallions and 26% from geldings. The number of riders in dressage was 42,062 (average ~1.97 horses per rider, max. number of horses per rider =61) and in show-jumping was 15,277 (average ~ 4.06 horses per rider, max. number of horses per rider =206). The pedigree file was constructed tracing back five generations for animals with records and comprised 189,959 horses. Table 4.1 shows the descriptive statistics of transformed linear score for dressage and show-jumping.

Table 4.1 Descriptive statistics of transformed linear score for dressage and show-jumping.

	Minimum	1st Quantile	Mean	3 rd Quantile	Maximum
Dressage	1	3.46	5.68	5.75	15.33
Show-jumping	1	3.16	4.57	5.48	13.78

4.2.2 Statistical analyses

Fixed effects were identified using a preliminary analyses of variance of linear scores using the function `glm()` from `stat` package and `lsmeans()` from `lsmeans` package (Lenth and Hervé 2015) in the R language/environment (R Core Team 2015). Sex, percentage of thoroughbred, age at the highest performance, year of the performance and interaction between these two latter effects were statistically significant in both show-jumping and dressage ($P < 0.001$). Additionally stallions and geldings performed similarly and statistically better than mares in both disciplines. The performance showed a quadratic response on age with a linear increase until 10 years, followed by a plateau for later ages in both disciplines. Horses with 12.5 to 50% of thoroughbred had the best performance in both disciplines.

Impact of the rider effect

To estimate the impact of the rider effect on genetic parameters, three different univariate animal models were tested for both disciplines. No rider effect was included in model [1], a random effect for each rider was included in model [2], and a fixed effect for class of rider was included in model [3]:

$$y_{ijkl} = \mu + \text{yearage}_i + \text{sex}_j + \text{thor}_k + a_l + e_{ijkl}, \quad [1]$$

$$y_{ijklm} = \mu + \text{yearage}_i + \text{sex}_j + \text{thor}_k + a_l + r_m + e_{ijklm}, \quad [2]$$

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$$y_{ijklm} = \mu + yearage_i + sex_j + thor_k + a_l + rl_m + e_{ijklm} , \quad [3]$$

where y_{ijkl} (y_{ijklm}) is the linear score for dressage or show-jumping of the l^{th} animal; μ is the population mean; $yearage_i$, is the fixed effect of the i^{th} class of the combined effect (120 classes) of the year of highest performance (20 levels: 1993,...,2012) and the age of the horse (6 levels: ≤ 5 , 6,..., ≥ 10 yr) at the highest performance; sex_j is the fixed effect of the j^{th} sex of the horse (2 classes: stallion and gelding, mare); $thor_k$ is the fixed effect of the k^{th} class of the thoroughbred percentage (6 classes: 0%, 12.5%, 25%, 37.5%, 50%, $\geq 62.5\%$); a_l is the random additive effect of the l^{th} animal $\sim N(0, A\sigma_a^2)$; r_m is the random effect of the m^{th} rider $\sim N(0, I\sigma_r^2)$ in model [2]; rl_m is the fixed effect of the m^{th} class of the level of the rider (6 classes: 1,...,6) in model [3] and e_{ijkl} (e_{ijklm}) is the residual random term associated with each observation $\sim N(0, I\sigma_e^2)$.

The class of rider was defined as the highest level achieved by the rider before riding the horse that produced the record included in the analysis. In both disciplines six levels were defined. For the first performance of the rider in the data analysed, the class of the rider was set to the lowest class. By modelling the effect of rider as the best level achieved, information on several horses and riders is used to estimate the effect, and this approach allows the effect of a rider to improve over time. Estimation of (co)variance components was performed using the Average Information Restricted Maximum Likelihood (AI-REML) implemented in the DMUAI module of DMU software version 6 release 5.2 (Madsen and Jensen 2013).

Effect of censoring

Performance records in the last years from young horses are likely to be right censored. Young horses that compete first time in the recent years have a limited opportunity to express their full potential. The highest performance is recorded on these young horses but it is not possible to distinguish between horses that have reached their highest potential and those that will improve further in the future. To test the impact of this censoring of data, additional analyses were performed for data sets including records until 2009 and until 2007. For all horses in each data set it is known that they have not improved their performance up to end of 2012, i.e. the endpoint of data recording in the full data. Horses that improved their performance in the last three (data_2009) or five years (data_2007) were not

included in the truncated data sets because only the highest performance is recorded.

Effect of pre-selection

The significance of the pre-selection on the genetic parameters estimated was assessed by considering all horses registered to be available for participation in competition. A binary trait (0,1), sport-status, was defined indicating whether a horse had competed or not. As foals have been registered as either dressage or show-jumping in the studbook only since 2006, it was not possible to identify separate populations of potential competitors for each discipline, based on this criterion. Consequently, it was decided to use for both disciplines all horses registered as a riding horse in the period 1984-2004, which is the period when the competing horses considered in the analysis were born. The data file considered was data_2009 to avoid the possible censoring effect in the analysis. Thus, the data for dressage comprised a total of 208,045 horses from which 58,184 horses had competition records (28%). The data for show jumping comprised a total of 190,075 horses from which 44,929 horses had competition records (24%). The pedigree files tracing back five generations of ancestors included 355,080 horses for dressage and 313,373 for show-jumping. First, a genetic variance components were estimated to determine whether the (0,1) trait of sport status is heritable. For estimating variance components for sport status, two models were used: a linear model and a threshold (probit) model. The linear model used was:

$$y_{ijk} = \text{year}_i + \text{sex}_j + a_k + e_{ijk}, \quad [4]$$

where, y_{ijk} is the observed sport-status on the k horse; year_i is the fixed effect of the i^{th} class of year of birth (classes: 1984,...,2007); sex_j is the fixed effect of the j^{th} class of sex (3 classes: stallion, gelding, mare); a_k is the random effect of the k^{th} horse $\sim N(0, A\sigma_a^2)$; e_{ijk} is the random residual term $\sim N(0, I\sigma_e^2)$.

The threshold (probit) model used was:

$$\Pr(y_{ijk} = 1 | \text{year}_i, \text{sex}_j, a_k) = \Phi(\text{year}_i + \text{sex}_j + a_k), \quad [5]$$

where, $\Phi(\cdot)$ is the standard cumulative standard normal distribution function, and the other parameters are as described above.

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Second, the impact of including sport-status in the analysis on genetic parameters for competition was evaluated using a bivariate model. In the bivariate analyses, sport-status was included using either the single linear model [4] or the probit model [5], while competition traits were analysed under model [3]. In all analyses, the residual covariance between sport performance (show-jumping and dressage) and sport-status was assumed zero.

For analysis involving the probit model, variance components were estimated by Gibbs sampling using the RJMC module of DMU software version 6 release 5.2 (Madsen and Jensen 2013). Uninformative priors were used for systematic effects. The Gibbs sampler was run in two independent chains of 500,000 samples after discarding the first 50,000 samples. Sampling interval was 50, leaving 10,000 samples to estimate the features of the posterior distributions. Convergence diagnostics and analysis of the Markov chain Monte Carlo sampling output were done with the BOA package (Smith 2007) of the R language/environment (R Core Team 2014).

Model Comparison

Models were compared based on goodness of fit to the data, predictive ability and unbiasedness of the predictions. The goodness of fit of each of the models was evaluated by computing the mean-squared error statistic (MSE),

$$\text{MSE} = n^{-1} \sum (y - \hat{y})^2, \quad [6]$$

where, y is the vector of observed phenotypes, \hat{y} is the vector of predicted phenotypes obtained from the solutions provided by each model, and n is the number of horses with phenotypes included in the analysis. In addition, the Pearson's correlation ($r_{y,\hat{y}}$), between y and \hat{y} was calculated to evaluate goodness of fit.

The predictive ability of the models was evaluated based on mean-squared predictive error obtained using a three-fold cross-validation. Three random disjoint folds (f) were defined and phenotypes of the horses included in each of the folds were predicted based on the solutions for fixed and random effects obtained using the model on the other two folds. The mean-squared predictive error (MSPE) for each model was calculated as:

$$MSPE = n^{-1} \sum_f \sum (y - \hat{y}^{-f})^2 \quad \forall f = \{1,2,3\}, \quad [7]$$

where, \hat{y}^{-f} is the vector of predicted phenotypes obtained when the data in fold f was excluded from the analyses.

The unbiasedness of the models' predictions was studied by estimating breeding values (EBV) on full data and EBV from a data set where records from the last registration year were deleted. EBV from full data and reduced data was computed using variance components obtained from the full data for the actual model (1-3). EBV of horses with their own performance removed are basically parent average in the reduced data set. The regression coefficient of EBV predicted on full data on EBV predicted on reduced data ($b_{ebv,pa}$) was estimated within the group of horses with deleted own performance for each model. A regression coefficient of one is expected if the model predicts without bias (Reverter *et al.* 1994). Spearman rank correlations were calculated between the solutions for all the animals with records and for stallions with 10 or more offspring with records, in each discipline.

4.3 Results

Table 4.2 shows the characteristics of the three data sets analysed in this study. The full data (2012) for dressage consisted of records on 82,694 horses and 42,064 riders and for show jumping it consisted of records on 62,072 horses and 15,277 riders. For dressage, 30% of the riders in the full data had only a single record and for show-jumping only 13% of the riders had a single record. The largest proportion of records was on horses in age class 4-5 years (Table 4.2). The number of records per year (data not shown) was twice as high for 2012 as for the previous years. The higher number of records in the last year can be explained by the inclusion of horses which had their highest performance in 2012 but which are expected to achieve higher levels of competition in future years. The distribution over age classes was very similar for the different data sets.

Impact of rider effect

Genetic parameters were estimated with three models that differed in the way the rider effect was included. The results from the models in both disciplines are presented in Table 4.3. Not including rider (model [1]) resulted in the highest estimates of genetic variance and heritability in both disciplines. The estimates of the additive genetic variance estimated in model [2] and [3] were less than one

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third of the estimates from model [1]. The estimate for heritability was roughly halved when including the effect of rider (model [2] and [3]). In model [2], the variance explained by the random effect of the rider was four to five times larger than the variance explained by animal effect. The heritability estimates from model [2] and model [3] hardly differed for both disciplines. However, for both disciplines the estimate of the additive genetic variance from model [3] was roughly one-third smaller than the estimate from model [2].

Table 4.2 Characteristics of the three data sets defined by the last year of performance records included for dressage and show-jumping competitions: 2012 represents the full data set and 2009 (2007) is the data set in which performance records up to 2009 (2007) were included.

	Horses	Riders	H/R ⁽¹⁾	H/R=1 ⁽²⁾	Age classes (years) ⁽³⁾					
					4-5	6	7	8	9	>=10
Dressage										
2012	82,694	42,062	1-61	30	21	14	13	12	10	30
2009	60,870	33,341	1-44	34	21	14	13	12	10	30
2007	52,928	29,850	1-42	36	22	14	13	12	10	29
Show-jumping										
2012	62,072	15,277	1-206	13	28	21	17	12	8	14
2009	48,079	12,819	1-189	15	28	21	16	12	8	15
2007	41,399	11,631	1-164	16	29	21	16	12	8	14

⁽¹⁾ Minimum and Maximum number of horses per rider; ⁽²⁾ Percentage (%) of riders with one performance; ⁽³⁾ Percentage (%) of records by age class at highest performance.

Effect of censoring

Cases where horses only had a limited or no time to receive their highest lifetime performance, such as horses with their highest performance in 2012, is referred to as censoring. This effect is expected to be largest in the data_2012. In data_2009 and data_2007 only records on horses that did not improve their performance in the subsequent 3 or 5 years are included. The latter two subsets are considered uncensored. The estimated genetic parameters for both disciplines from all models are presented in Table 4.4. The genetic variance estimated was higher in the full data set than in the two truncated subsets. Only small differences were found between data_2009 and data_2007. Therefore, only the results for data_2009 are shown in Table 4.3 and discussed. For the model without rider effect (model [1]), the differences in estimates between the datasets were very small for both disciplines (Table 4.3). For the models with rider effects included, the heritability

estimated from data_2009 was lower than from data_2012. The heritability for dressage was reduced by 21% for model [2] and 44% for model [3] whereas the heritability for show-jumping was reduced by 22% for model [2] and 9% for model [3].

Table 4.3 Variance components⁽¹⁾ and heritability (h^2) estimates by different models tested on complete (data_2012) and truncated data sets (data_2009⁽²⁾) for dressage and show-jumping.

Model	Data set	Variance components			h^2 ⁽³⁾
		Genetic	Rider	Residual	
<i>Dressage</i>					
[1] No rider	2012	1.57		4.81	0.25
	2009	1.64		4.82	0.25
[2] Random rider	2012	0.63	2.78	2.43	0.11
	2009	0.50	2.91	2.47	0.09
[3] Rider class (fixed)	2012	0.40		2.72	0.13
	2009	0.21		2.72	0.07
<i>Show-jumping</i>					
[1] No rider	2012	0.98		2.47	0.28
	2009	0.85		2.41	0.26
[2] Random rider	2012	0.34	1.18	1.64	0.11
	2009	0.25	1.09	1.63	0.08
[3] Rider class (fixed)	2012	0.23		1.87	0.11
	2009	0.20		1.80	0.10

⁽¹⁾ Additive genetic variance (Genetic), rider variance (Rider), residual variance (Residual)

⁽²⁾ Results of data_2007 not presented as they were similar to data_2009

⁽³⁾ Standard error of h^2 ranged from 0.006 to 0.013

Effect of pre-selection

To investigate the potential role of pre-selection, a genetic analysis was performed including sport-status, a trait describing whether or not a horse entered into competition. The heritability for sport-status estimated with univariate linear animal model was 0.16 for dressage and 0.19 for show-jumping (Table 4.4). Heritability estimates from probit models were higher, as expected based on the literature (e.g., Dempster and Lerner 1950; Gianola 1982). The bivariate analyses did not change the genetic parameters for dressage or show jumping regardless of the model used for sport-status. For the linear model analysis, the estimated genetic correlation between sport-status and dressage was 0.73 and between

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sport-status and show-jumping 0.82. The genetic correlation estimated using the probit model was 0.66 for dressage and 0.76 for show-jumping. The correlation between breeding values for horses with a record predicted by univariate and bivariate models was 0.95 for dressage and 0.94 for show-jumping.

Table 4.4 Additive-genetic variance (σ_a^2), residual variance (σ_r^2) and heritability (h^2) for sport-status and highest score achieved for dressage and show-jumping estimated in univariate and bivariate analyses with linear and probit model for sport-status, and correlation between breeding values for competition obtained in univariate and bivariate analysis ($r_{a1,a2}$) on truncated dataset (data_2009).

		Sport-status			Competition			$r_{a1,a2}$
		σ_a^2	σ_r^2	h^2	σ_a^2	σ_r^2	h^2	
<i>Dressage</i>								
Univariate	Linear	0.03	0.14	0.16	0.23	2.73	0.08	
	Probit	0.49	1	0.33				
Bivariate	Linear	0.03	0.14	0.15	0.22	2.75	0.07	0.73
	Probit	0.49	1	0.33	0.23	2.74	0.08	0.66
<i>Show-Jumping</i>								
Univariate	Linear	0.03	0.13	0.19	0.21	1.78	0.10	
	Probit	0.66	1	0.40				
Bivariate	Linear	0.03	0.13	0.19	0.19	1.80	0.10	0.82
	Probit	0.65	1	0.39	0.18	1.81	0.09	0.73

Model Comparison

Goodness of fit and predictability capacity of the models.

For both disciplines, model [2] had the best goodness of fit criteria, mean-squared error (MSE) and correlation between observed and predicted phenotype ($r_{y,\hat{y}}$) (Table 4.5). Model [3] showed intermediate values for goodness of fit with the exception of $r_{y,\hat{y}}$ for show jumping. The predictive ability was measured by mean-squared prediction error (MSPE) estimated using three-fold cross validation. Model [3] had the lowest predictive ability in both disciplines (Table 4.5). Model [1] had a substantial higher MSPE than model [3], while model [2] gave intermediate values in both disciplines. The relative differences in MSPE between models were larger in dressage than in show-jumping. The regression coefficient on parent average ($b_{ebv,pa}$) revealed that model [1] and [2] tended to underestimate breeding values in

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the complete data. For model [3] on data_2012 and for all models on data_2009, regression coefficients were close to one.

Table 4.5 Mean-squared error (MSE), correlation between observed and estimated performance ($r_{y,\hat{y}}$), mean-squared error of prediction (MSEP) from cross-validation analysis and regression coefficient of estimated breeding values on estimated parent average ($b_{ebv,pa}$) for models [1], [2] and [3] in data_2012 (2012) and data_2009 (2009) for both disciplines⁽¹⁾.

Model	Data	Dressage				Show-jumping			
		MSE	$r_{y,\hat{y}}$	MSEP	$b_{ebv,pa}$	MSE	$r_{y,\hat{y}}$	MSEP	$b_{ebv,pa}$
[1]	2012	3.93	0.76	5.92	0.89	1.94	0.77	3.15	0.86
	2009	3.91	0.76	5.99	1.03	1.93	0.75	3.00	1.04
[2]	2012	1.44	0.92	4.45	0.94	1.24	0.85	2.19	0.88
	2009	1.46	0.92	4.57	1.02	1.27	0.84	2.14	1.01
[3]	2012	2.45	0.85	2.60	1.04	1.71	0.78	1.73	1.04
	2009	2.57	0.83	2.52	1.00	1.65	0.77	1.70	1.00

⁽¹⁾ Results of data_2007 not presented as they were similar to data_2009

Table 4.6 Spearman rank correlations between predicted breeding values for animals with records (above diagonal) and sires with more than 10 offspring (below diagonal) from models [1], [2] and [3] in data_2012 for both disciplines⁽¹⁾.

Model	Show-jumping			Dressage		
	[1]	[2]	[3]	[1]	[2]	[3]
[1] No rider	1	0.95	0.96	1	0.89	0.93
[2] Random rider	0.93	1	0.98	0.85	1	0.96
[3] Rider class (fixed)	0.95	0.97	1	0.91	0.95	1

⁽¹⁾ Number of sires was 1,943 for dressage and 590 for show-jumping. Number of animals with observations was 60,870 for dressage and 48,079 for show-jumping.

Correlation of breeding values from different models

The Spearman rank correlation between breeding values estimated by the different models tested was high in both disciplines (Table 4.6). In all the cases, the correlation between solutions provided by model [2] and [3] were the highest, ranging from 0.95 to 0.98. The correlations between solutions from model [2] and [3] with model [1] were lowest ranging from 0.85 to 0.96. The lowest values for a given combination of models and largest differences between models were found for breeding values of animals with records for dressage.

4.4 Discussion

Competition results are the breeding goals traits for genetic evaluation of sport horses and are routinely recorded on many horses. However, several aspects are recognized to limit usefulness of competition results as they might lead to biased breeding values. The aim of this research was therefore to assess impact of rider, censoring and pre-selection on competition results of Dutch Warmblood horses and to propose methods to reduce negative impact. The main non-genetic effects included in the statistical models used for genetic evaluation of competition traits are age and sex (Koenen and Aldridge 2002). This was confirmed by results obtained in the present study. It was found that performance in competition on average increase with age, and stallions and geldings have on average a higher performance than mares. This is in agreement with earlier analyses reported by Koenen and Aldridge (2002).

Impact of rider effect

This study was the first to investigate the effect of the rider on genetic parameters for competition records of the Dutch sport horses. Models used in previous studies on the same population included the effect of sex and age and their interaction (Huizinga and van der Meij 1989; Koenen *et al.* 1995; Ducro *et al.* 2007), and percentage of thoroughbred was considered as a genetic group in the pedigree file (Ducro *et al.* 2007). The analysis revealed that ignoring rider leads to a higher estimation of genetic parameters for performance in competition. This is in line with earlier findings in literature (e.g., Bartolomé *et al.* 2013; Sánchez Guerrero *et al.* 2014) which concluded that ignoring a rider effect overestimated the genetic parameters. Disentangling the effects of the horse and the rider depends on the structure of the data. Unlike other studies, in this study, horses' performance is linked with one rider but many riders only rode one horse making it difficult to disentangle the rider effect from the horse effect. This difference in data structure makes it difficult to make a direct comparison between studies on the partition of the variance and the relative importance of the effect of the rider. However, the effect of the rider in literature represented a significant part of the total phenotypic variance. Testing different models on eventing, competition records showed that the rider effect accounted for 22%-34% of the total variance in dressage phase (heritabilities 0.08-0.09) and 8% -14% in show-jumping phase (heritabilities 0.10-0.25) (Stewart *et al.* 2012). Results obtained in this study from model [2] showed that the rider component explained ~50% of the total variance in dressage, and

~37% in show-jumping. The higher proportion of riders with a single record in dressage could explain a higher overestimation of the rider variance in dressage than in show-jumping when rider was considered as a random effect. Model [3] was included in the study as an option to reduce the confounding between rider and horse. Model [3] used a systematic effect that represented different levels of rider skills, defined based on results obtained by the rider before riding the horse that produced the record. This approach is similar to that used by Jönsson *et al.* (2014) for Danish Warmblood horses for dressage competitions. Genetic parameters for both disciplines from model [1] were higher in this work than in previous studies on the same population using a similar model (Huizinga and van der Meij 1989; Koenen *et al.* 1995; Ducro *et al.* 2007). The heritabilities estimated with Models [2] and [3] were between 0.07 and 0.13. These values are in the lower range of heritabilities compared to the estimates by Huizinga and van der Meij (1989) (0.10 dressage, and 0.20 show-jumping), and were lower than the results obtained by Koenen *et al.* (1995) (0.17 dressage and 0.19 show-jumping), and by Ducro *et al.* (2007) (0.14 for both disciplines). The heritabilities estimated by model [2] and [3] did not differ very much, but for dressage, model [3] estimated a lower additive genetic variance. The higher proportion of riders with only one performance in dressage compared to show-jumping could explain the bigger difference observed between model [2] and [3]. However, when considering the predictive ability of the model, model [3] performed better than model [2] (Table 4.5). Model [3] also resulted in the most unbiased predictions. These results suggest that for genetic evaluations based on competition results it is justified to incorporate a fixed effect representing the level and experience of the rider.

Effect of censoring

Studies on censored data in horses have been done for longevity and lifetime performance (e.g., Wallin *et al.* 2003; Ricard and Blouin 2011). No studies on censoring related to competition traits were found in literature. This study revealed that genetic variance was reduced in data_2009 compared to data_2012 when using models accounting for the rider effect. This reduction is due to reduction of censoring. The heritability estimates were only slightly reduced due to elimination of censoring. This small effect of censoring on heritability is in line with results from a simulation study by Burns *et al.* (2006) where censoring affected random animals, it was not related with the selection criterion and sample bias was minimised. When data_2009 was created from data_2012, animals were removed which had an improved performance in 2010-2012. The animals that were removed had not reached their highest performance. In the case of youngest ages, all animals were

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removed and no selection was applied. However, by this process we would introduce an effect of selection on other age classes, i.e. only animals from a given age class which had reached their highest performance before the end of 2009 were kept and others were removed. For the analysis, we only had data on the highest performance ever of a horse. We were, therefore, not able to investigate the effects of censoring and selection in more detail. We recommend sport associations and breeding organisations to not only collect the highest performance ever but also the highest performance and/or points earned by year. This would allow for a more detailed genetic analysis of competition results which could increase the accuracy of genetic evaluations for dressage and show-jumping.

Effect of pre-selection

The moderate heritabilities estimated for sport-status showed that participation in competition can be partly explained by the genetic background of the horse. In show-jumping the proportion of horses entering into competition was smaller compared to dressage, indicating more pre-selection. The heritability of sport-status was very similar in both disciplines. In dressage, the proportion of horses entering into competition in this data set was slightly higher (27%) than in the set analysed by Ducro (2010) (~23%). The heritability of sport-status estimated with a linear model in the present study was slightly lower (~0.15 vs 0.23) than found by Ducro (2010). The present study included mares, stallions and geldings, and horses registered in the pedigree as riding horses were considered the population available for competition. The previous study of Ducro (2010) was on mares only, and mares inspected at studbook-entry inspection were considered as the population available for competition rather than all foals registered.

The genetic parameters estimated for competition traits did not change in the analyses performed with a bivariate model including sport-status (Table 4.4). This does not agree with findings in earlier studies (Ducro 2010; Albertsdóttir *et al.* 2011). The genetic correlation between sport-status and dressage (0.73) and show-jumping (0.82) showed that horses which competed in dressage and show-jumping have higher genetic ability to compete compared with horses that never competed, and this trend is strongest in show-jumping. However, the genetic correlation was lower than the 0.89 reported by Ducro (2010) between sport status and dressage. On the other hand, the (Spearman) correlation between the breeding values with and without including sport-status ranged from 0.93-0.95. These values are substantially higher than the 0.69 reported by Ducro (2010), and close to the 0.98 reported by Bugislaus *et al.* (2005) in race horses for racing time per km. These

results indicate that little re-ranking of horses based on breeding values is expected by considering sport-status in the analysis of performance in both disciplines. Sport-status is a trait derived from the competition results. Traits measured on all young horses that are correlated to performance in competition might be a better option to account for pre-selection in genetic analysis.

4.5 Conclusions

Highest performance in competition for dressage and show-jumping is a heritable trait which can be improved by selection. This heritability is affected by rider with breeding values most accurate when rider is included as a fixed effect that represents the level and experience of riders. Censoring had a small effect on the genetic parameters for dressage and show-jumping. It is suggested that important insights on the performance of the horses could be gained analysing repeated records of competition. Whether or not a horse entered into competition, referred to as sport-status, was heritable but did not affect the genetic parameters estimated for competition traits. In conclusion, horse breeding organisations should as a priority include rider as a fixed effect when estimating breeding values for show-jumping and dressage.

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5

Genetic correlations between dressage, show-jumping and studbook-entry inspection traits in a process of specialisation in Dutch Warmblood horses

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Abstract

To compete at professional levels in equestrian sports the athletic abilities of the horse needs to be improved. Dressage and show-jumping are two important traits in the breeding goals of many equestrian studbooks. Currently, there is limited information about the genetic correlation between performance for jumping and dressage and between traits measured early in life and performance in competition in these disciplines. These correlations are required to determine the optimum selection scheme for jumping and dressage. This study estimated these genetic correlations to support decision making on specialisation of breeding horses for dressage and show-jumping for warmblood horses registered by the Royal Dutch Warmblood Studbook (KWPN). Genetic correlation between the performance of horses in dressage and show-jumping was estimated as well as the genetic correlation between traits recorded during studbook-entry inspections and performance in dressage and show-jumping competition. Records from 1993-2012 were used for performance from 82,694 horses for dressage and 62,072 horses for show-jumping with 26,056 recorded for both disciplines. Records recorded at studbook-entry inspections were used from 62,628 horses, recorded in the period 1992-2013. Genetic correlations between the disciplines and between the disciplines and traits recorded in the studbook-entry inspection were estimated using bivariate genetic analyses. To see if these genetic correlations have changed over time, three periods of time were defined by birth year of the horse and genetic correlations for each period were estimated using bivariate analyses. The genetic correlation between performance of horses in dressage and show-jumping was slightly unfavourable (-0.12). The genetic correlation between dressage and show-jumping tended to become more unfavourable over time. The increasingly negative correlation between disciplines was not reflected in changes in the correlations between competitions traits and the traits recorded in the studbook-first inspection.

Key words: Genetic parameter, competition trait, rider effect, sport horse

5.1 Introduction

During the last decades, equestrian sport has received increasing attention, both at the amateur level and at the professional level. Three disciplines are represented at the Olympics, being dressage, show-jumping and eventing. Success at the highest level of competition requires an intensive preparation and specific training of the horse and horses compete more and more in only one discipline to maximize the chance of reaching the highest level. This specialisation does not only affects rearing and training of the horses, but also breeding of sport horses. Breeders increasingly specialise into one specific discipline in their breeding and mating decisions (Rovere *et al.* 2014).

The Royal Dutch Warmblood Studbook (KWPN) is breeding horses that can perform at the highest level of dressage or show-jumping (KWPN 2015). The studbook noticed changes in the breeding practices by individual breeders and implemented in 1998 an additional set of traits for jumping abilities of horses in the studbook-entry inspections. This was the first step of the specialisation process at the studbook level. Rovere *et al.* (2014) showed that subpopulations of dressage and show-jumping horses of the KWPN have become less connected genetically over time. Currently, there is limited information about the genetic correlation between performance for jumping and dressage and between traits measured early in life and performance in competition in these disciplines. These correlations are required to determine the optimum selection scheme for jumping and dressage.

Previous studies have shown that the traits recorded during the studbook-entry inspections of KWPN are heritable. Koenen *et al.* (1995) reported a low genetic correlation between conformation traits measured during studbook-entry inspections and performance in competition. Further, they found only small differences between the conformation of a good dressage and a good show-jumping horse. For movement traits, previous studies reported that gaits were favourably correlated with dressage and to a smaller degree with show-jumping; while free-jumping traits were favourably correlated with show-jumping, but unfavourably correlated with performance in dressage (Ducro *et al.* 2007). Early studies on German horses and Dutch Warmblood horses concluded that the genetic correlation between breeding values estimated for dressage and show-jumping were close to zero (Bruns 1981; Huizinga and van der Meij 1989). More recently, a moderate positive genetic correlation was found between dressage and

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show-jumping measured in the Riding Horse Quality Test for Swedish Warmblood horses (Viklund *et al.* 2008). Based on these results, the authors concluded that there is no conflict in breeding horses for the two disciplines for this population.

This study aimed to estimate genetic parameters to support decision making on specialisation of breeding horses for dressage and show-jumping. First, we estimated the genetic correlation between the performance of horses in dressage and show-jumping. Additionally, the genetic correlation was estimated between functional traits recorded during studbook-entry inspections and performance in dressage and show-jumping competition.

5.2 Material and Methods

5.2.1 Data

Data was provided by KWPN. Competition records from 82,694 horses in dressage and 62,072 horses in show-jumping were recorded in the period 1993-2012 (year of birth between 1974 and 2009). For 26,056 horses information was available for both dressage and show-jumping. For each horse highest performance in competition in a discipline and age at highest performance was recorded. Highest performance refers to the highest class the horse has performed at and the total number of points it gained in this class (Ducro *et al.* 2007). The highest classification score is transformed to a linear score for further analysis using a square-root transformation to make a more normally distributed error term. The transformation is used routinely in the genetic evaluation of KWPN (KWPN 2015). Competition results of horses older than 20 years of age were not considered. A detailed description of the competition traits can be found in Ducro *et al.* (2007).

Records from 62,628 horses on traits recorded at studbook-entry inspections in the period 1992-2013 were analysed. Horses included in the analysis were between 3 and 7 years old at the time of inspection. In 1989 a new linear scoring system was implemented in the studbook-entry inspections and number of traits considered at inspection increased over the years. In 1998 a set of traits on jumping ability was added, and in 2006 the scoring system was extended to include traits related to movement. Additionally, since 2006 breeders have to choose one discipline, dressage or show-jumping, when registering their foals with the studbook. The studbook entry traits can be divided into two groups; Descriptive and Subjective traits. For the Descriptive traits, every individual horse is compared with the population's mean on each trait on a scale which currently ranges from 1 to 9. For

most Descriptive traits, smaller values are considered favourable, although extreme values are undesired (Ducro *et al.* 2007; Rovere *et al.* 2015b). For the Subjective traits, the jury express an overall opinion about conformation, movement and jumping characteristics of the horse. The jury use a scale from 40 (very bad) to 100 (excellent), marked in five-point increments, to evaluate the qualification of the horses in these traits. The traits recorded in the studbook-entry inspection will be referred to as inspection traits in this paper.

5.2.2 Statistical methods and models

Estimation of genetic correlation between dressage and show-jumping

To estimate the genetic correlation between dressage and show-jumping a bivariate analysis was used on both competition traits using the following model:

$$y_{ijklm} = \mu + yearage_i + sex_j + thor_k + a_l + rl_m + e_{ijklm} , \quad [1]$$

where y_{ijklm} is the linear score for dressage or show-jumping of the l^{th} animal; μ is the population mean; $yearage_i$ is the fixed effect of the i^{th} class (120 classes) of the combined effect of the year of highest performance (20 levels: 1993,...,2012) and the age of the horse (6 levels: ≤ 5 , 6,..., ≥ 10 yr) at the highest performance; sex_j is the fixed effect of the j^{th} sex of the horse (2 classes: stallion and gelding or mare); $thor_k$ is the fixed effect of k^{th} class of the thoroughbred percentage (6 classes: 0%, 12.5%, 25%, 37.5%, 50%, $\geq 62.5\%$); a_l is the random additive genetic effect of the l^{th} animal $\sim N(0, A\sigma_a^2)$; rl_m is the fixed effect of the m^{th} class of the level of the rider (6 classes: 1,...,6) and e_{ijklm} is the residual random term associated with each observation $\sim N(0, I\sigma_e^2)$.

The level of the rider was defined as the highest level which had been achieved by the rider before riding the horse that produced the record. In both disciplines six levels of rider were defined following the linear scale used by KWPN. For the first performance of the rider, the level of the rider was set to the lowest class. With this definition, the effect of a particular rider may vary between horses reflecting improvements in the rider's experience, and it may differ between disciplines.

To compare with previous studies and with results estimated with the model currently used in the genetic evaluation, additional bivariate analyses using models without the fixed effect of the level of rider were used. Most horses had records in one discipline only, but some of the horses had records in both disciplines. To

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investigate the impact of this group of dual-competitors, genetic correlations between disciplines was also estimated in (1) a dataset with only dual-competitors, and (2) a dataset with only single-competitors.

Estimation of genetic correlations between dressage and show-jumping over time

To study if the genetic correlation has changed over time, three periods of time were defined by year of birth. Period 1 considered records from animals born before 1995; period 2 included horses born between 1995 and 2002, and period 3 included horses born after 2002. Two different analyses were performed. Firstly, it was investigated whether performance in competition (show-jumping or dressage) in the different periods genetically is the same trait. To address this question, genetic correlations of competition results in the three periods were estimated using a tri-variate analysis within discipline. Secondly, it was investigated whether the genetic correlation between the two disciplines changed over time. To address this question, bivariate analyses were carried out on competition results in each period. These analyses were performed on the complete data and on data excluding dual-competitors.

Estimation of genetic correlation between inspection and competition traits

Genetic correlations between competition traits and the traits recorded at studbook-entry inspections were estimated using bivariate models. Model [1] was used for competition results from dressage and show-jumping, and model [2] was used for inspection traits. Model [2] is taken from Rovere *et al.* (2015b):

$$y_{ijklmno} = \mu + classifier_i + age_j + sex_k + year_l + thor_m + a_n + locdat_o + e_{ijklmno}, [2]$$

where $y_{ijklmno}$ is the record for the inspection trait analysed of the n^{th} animal; μ is the population mean; $classifier_i$ is the fixed effect of the i^{th} classifier (32 classes); age_j is the effect of the j^{th} class of age of the horse at inspection (6 classes: $\leq 2, \dots, 7$ yr); sex_k is the fixed effect of the k^{th} class of sex of the horse (3 classes: stallion, mare, gelding); $year_l$ is the effect of the l^{th} class of the year of inspection (15 classes: 1998, ..., 2012); $thor_m$ is the fixed effect of m^{th} class of the thoroughbred percentage (6 classes: 0%, 12.5%, 25%, 37.5%, 50%, $\geq 62.5\%$); a_n is the random additive genetics effect of the n^{th} animal $\sim N(0, A\sigma_a^2)$; $locdat_o$ is the random environmental effect of the location and date of inspection $\sim N(0, I\sigma_{locdat}^2)$, and $e_{ijklmno}$ is the residual random term associated with each observation $\sim N(0, I\sigma_e^2)$.

Estimation of genetic correlation between inspection and competition traits over time

Bivariate analyses were used to see if the genetic correlations between inspection and competition traits for each discipline have changed over time. The three periods of time described in the previous section were used. In all the analyses, model [1] was used for traits recorded during competition and model [2] for inspection traits.

Genetic parameters were estimated using the Average Information Restricted Maximum Likelihood (AI-REML) implemented in the DMUAI module of DMU software version 6 release 5.2. (Madsen and Jensen 2013).

5.3 Results

Total number of records and number of records per period for competition traits and for a set of inspection traits considered in this study are shown in Table 5.1.

Table 5.1 Number of records analysed for the whole period and by time period for different traits considered.

<i>Competition Traits</i>	<i>Periods⁽¹⁾</i>			<i>Total</i>
	<i>P1</i>	<i>P2</i>	<i>P3</i>	
Dressage	37,696	28,955	16,043	82,694
Show-jumping	24,994	23,379	13,699	62,072
Dual competitors ⁽²⁾	13,973	8,805	3,278	26,056
<i>Inspection Traits</i>				
Movement	20,304	22,081	9,075 ⁽³⁾	42,385
Free-jumping	n.a.	13,475	10,027	23,502
Conformation	20,296	23,140	19,084	62,520

⁽¹⁾ P1 included all birth year before 1995, P2 birth years between 1995-2002, P3 birth years after 2002. ⁽²⁾ Horses with records in both disciplines. ⁽³⁾ After 2006 only foals registered as dressage horse is evaluated in this trait.

Genetic correlation between dressage and show-jumping

The estimated heritability was 0.13 for dressage and 0.15 for show-jumping (Table 5.2). The estimated genetic correlation between dressage and show-jumping was -0.28 (Table 2). When level of rider was excluded from the analysis, heritability estimates increased from 0.13 to 0.25 for dressage and from 0.15 to 0.28 for show-jumping, while the genetic correlation changed from -0.28 to -0.09. In all cases

5. Genetic correlation between dressage and show-jumping

variance components and heritabilities obtained from bivariate analyses were similar to those from univariate analyses (results not shown). The average competition score of the 26,056 dual-competitor horses, (i.e. horses with competition results for dressage and show-jumping), was lower than the mean of the single-performance horses in both disciplines (dressage 4.92 vs 6.03 and show-jumping 3.96 vs 5.01). Also, the phenotypic variance of competition scores in both disciplines was lower in dual-competitors (variance was 2.60 vs 3.00 for dressage and 1.75 vs 2.18 for show-jumping). When the dual-competitors were excluded from the analysis, the genetic correlation changed from -0.28 to -0.12. The genetic correlation estimated in the data set with dual-competitors only was more negative (-0.44), whereas the heritability estimates for competition traits from the entire dataset were comparable to the estimates from the subsets investigated (data not shown).

Table 5.2 Additive genetic (σ_a^2) and residual (σ_r^2) variances, heritability (h^2), and genetic (r_a) and residual (r_r) correlations between dressage and show-jumping.

	Dressage			Show-jumping			Correlation	
	σ_a^2	σ_r^2	$h^{2(1)}$	σ_a^2	σ_r^2	h^2	$r_a^{(1)}$	$r_r^{(1)}$
Level rider ⁽²⁾	0.65	4.19	0.13	0.36	2.09	0.15	-0.28	0.12
No rider ⁽³⁾	1.62	4.79	0.25	0.96	2.45	0.28	-0.09	0.19
No dual-competitors ⁽⁴⁾	0.66	4.39	0.13	0.28	2.14	0.11	-0.12	0.00
Dual-competitors ⁽⁵⁾	0.58	3.66	0.14	0.21	1.79	0.11	-0.44	0.08

⁽¹⁾Standard errors of: h^2 0.01; r_a 0.03-0.07; r_r 0.01; ⁽²⁾ Refer to model [1]; ⁽³⁾ Refer to model [1] without the effect of level of rider; ⁽⁴⁾ Model [1] on data without dual-competitors; ⁽⁵⁾ Model [1] on dual-competitors (26,056 horses).

Genetic correlation between dressage and show-jumping over time

For dressage, the genetic correlation between the different periods ranged from 0.95 to 0.98 and the correlation was lowest between period 1 and 2. For show-jumping, the genetic correlation ranged from 0.91 to 0.97 and the correlation was lowest between period 1 and 3. Table 5.3 shows the genetic correlation between show-jumping and dressage for each period. The genetic correlation between show-jumping and dressage became more unfavourable over time. When dual-competitors were excluded from the analysis, the genetic correlation was smaller but the trend over time was very similar (Table 5.4).

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Table 5.3 Additive genetic (σ_a^2) and residual (σ_r^2) variances, heritability (h^2), and genetic (r_a) and residual (r_r) correlations between dressage and show-jumping in three time periods(P). Genetic correlation of competition traits between different time periods, above diagonal dressage and below diagonal show-jumping (Period Correlation).

P	Dressage			Show-jumping			Correlation		Period correlation		
	σ_a^2	σ_r^2	h^2	σ_a^2	σ_r^2	h^2	r_a	r_r	1	2	3
1	0.79	4.77	0.14	0.41	2.19	0.16	-0.24	0.12	1	0.95	0.98
2	0.66	3.88	0.14	0.44	2.12	0.17	-0.53	0.15	0.97	1	0.98
3	0.58	2.90	0.17	0.35	1.57	0.18	-0.59	0.25	0.91	0.96	1

Standard errors of: h^2 0.01-0.02; r_a 0.06-0.08; r_r 0.01-0.03; Period Correlation 0.02-0.04

Table 5.4 Number of records analysed, additive genetic (σ_a^2) and residual (σ_r^2) variances, heritability (h^2), and genetic (r_a) and residual (r_r) correlations between dressage and show-jumping over time for a set of data without dual-competitors.

Period	N	Dressage			Show-jumping			Correlation	
		σ_a^2	σ_r^2	h^2	N	σ_a^2	σ_r^2	h^2	r_a
1	23,723	0.79	5.19	0.13	11,021	0.40	2.42	0.14	-0.01
2	20,750	0.67	4.08	0.14	14,574	0.27	2.19	0.11	-0.29
3	12,765	0.65	2.91	0.18	10,421	0.16	1.62	0.09	-0.38

Standard errors of: h^2 0.01-0.02; r_a 0.10-0.15

Genetic correlation between competition and inspection traits

Genetic correlations between inspection traits and competition traits for Descriptive traits are presented in Table 5.5 and results for Subjective traits are presented in Table 5.6. In the tables, results are given for models with and without rider effect but in this section only results from the model with rider are addressed. Heritabilities and variance components estimated by a bivariate analysis for Descriptive traits and competition traits did not differ from the estimates obtained from the univariate analyses (results not shown). Moderately favourable genetic correlations were found between dressage in competition and Descriptive traits related to movement, except for Walk_correctness (Table 5.5). These genetic correlations with dressage ranged from -0.32 for Canter_balance to -0.61 for Trot_length. Lower values are preferred for the Descriptive traits. Therefore, negative genetic correlations between the competition and Descriptive trait are favourable. Descriptive traits on movement showed a non-existing or low favourable genetic correlation with show-jumping. These genetic correlations with show-jumping ranged from -0.03 for Walk_correctness to -0.41 for Canter_length.

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The highest genetic correlations for dressage were with trot traits and for show-jumping were with canter. Free-jumping traits had high favourable genetic correlation with show-jumping and moderately unfavourable with dressage.

The genetic correlations between the Subjective traits Conformation and Movement were favourable for dressage and show-jumping and largest for dressage (Table 5.6). Similar to the Descriptive traits, the genetic correlation for the Subjective trait Jumping was highly favourable correlated with show-jumping and moderately and unfavourably correlated with dressage in competition. The recently introduced traits Walk and Trot had a medium-high favourable genetic correlation with dressage and no correlation with show-jumping and Canter had a favourable correlation with both disciplines but more so with show-jumping.

Table 5.5 Heritability (h^2) of descriptive traits and genetic (r_a) correlations with dressage and show-jumping estimated with models without and with a fixed effect for class of rider.

<i>Descriptive traits</i>	h^2	Dressage		Show-jumping	
		No rider	Rider	No rider	Rider
<i>Movement</i>		r_a	r_a	r_a	r_a
Walk: length stride	0.18	-0.50	-0.46	-0.03	0.05
Walk: correctness	0.27	0.05	0.04	0.01	-0.03
Trot: length	0.27	-0.61	-0.54	-0.03	0.04
Trot: elasticity	0.24	-0.54	-0.47	-0.10	-0.06
Trot: impulsion	0.25	-0.50	-0.42	-0.15	-0.11
Trot: balance	0.22	-0.51	-0.46	-0.13	-0.10
Canter: length	0.22	-0.40	-0.32	-0.25	-0.20
Canter: impulsion	0.20	-0.33	-0.26	-0.38	-0.39
Canter: balance	0.16	-0.32	-0.24	-0.40	-0.41
<i>Free-jumping</i>					
Take off: direction	0.17	0.37	0.46	-0.73	-0.73
Take off: speed	0.14	0.38	0.43	-0.49	-0.52
Technique: foreleg	0.17	0.29	0.37	-0.51	-0.52
Technique: back	0.22	0.34	0.43	-0.56	-0.53
Technique: haunches	0.17	0.41	0.51	-0.69	-0.68
Scope	0.22	0.32	0.43	-0.75	-0.73
Elasticity	0.21	0.20	0.27	-0.61	-0.60
Care	0.14	0.40	0.50	-0.81	-0.79

Standard errors of: h^2 0.01; r_a 0.03-0.06

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Table 5.6 Heritability (h^2) of subjective traits and genetic (r_a) correlations with dressage and show-jumping estimated with models without and with a fixed effect for class of rider.

Subjective traits	h^2	Dressage		Show-jumping	
		No rider	Rider	No rider	Rider
Conformation	0.29	0.52	0.47	0.16	0.23
Movement	0.32	0.61	0.54	0.19	0.16
Jumping	0.33	-0.31	-0.39	0.81	0.79
Walk	0.24	0.59	0.51	0.03	-0.07
Trot	0.39	0.50	0.43	0.07	0.03
Canter	0.28	0.29	0.20	0.42	0.41

Standard errors of: h^2 0.01-0.02; r_a 0.02-0.06

Genetic correlation between inspection and competition traits over time

The estimated correlations between inspection and competition results in the different periods are presented in Appendix 5.1. The heritabilities for the Descriptive traits related to movement increased over time. No changes over time were found for the genetic correlations with dressage, except for the correlation between Trot_balance and Canter_balance. For both traits, the genetic correlation dropped in the last time period. For show-jumping, however, the genetic correlation with Canter_balance was more favourable in the last period. The genetic correlations between show-jumping and traits related to Trot became less favourable or even slightly unfavourable over time. Descriptive traits related to Free-jumping did not show any significant change over time for any of the disciplines.

The genetic correlation between conformation and dressage or show-jumping fluctuated over time. No trends were observed in the correlations between competition traits and Subjective traits.

5.4 Discussion

Genetic correlation between dressage and show-jumping

In this study results showed a low but unfavourable genetic correlation between dressage and show-jumping. Dressage and show-jumping are two important traits in the breeding goals of many studbooks (Koenen *et al.* 2004). The genetic

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correlation has a major impact on the opportunities to combine selection for both disciplines in a breeding programme. It is, therefore, surprising that literature on the genetic correlation between dressage and show jumping is scarce. Some estimates of the genetic correlation between disciplines are available in studies on eventing competitions where horses perform in three phases; show-jumping, dressage and cross-country and the result is a combined score for all three disciplines. For eventing, low positive and close to zero genetic correlations between dressage and show jumping were found (Kearsley *et al.* 2008; Stewart *et al.* 2012). However, because of the combined scores, horses can compensate for a suboptimal performance in one discipline with an outstanding performance in the other. This compensation is not possible for competitions in a single discipline such as the current study. Therefore, considering each discipline separately may contribute to the negative correlation from this study compared to eventing.

Other research that considered single disciplines from the German equestrian federation (Bruns 1981) and Dutch warmblood horses (Huizinga and van der Meij 1989) found no genetic correlation between dressage and show-jumping. During the time of these studies, it was common that horses performed in both disciplines. Currently breeding, rearing and training is focused on performance in a single discipline. Therefore, selection for horses for either dressage or show-jumping may have also contributed to the negative correlation between show-jumping and dressage.

This study revealed a moderately negative (-0.28) genetic correlation between both disciplines when a model with a rider effect was used. When the effect of rider was ignored in the model, the genetic correlation was close to zero. However, in a previous study (Rovere *et al.* 2015a) has shown that accounting for rider results in better predictability and less bias of genetic evaluations.

In the data analysed, a considerable number of horses had competed in both disciplines. These horses were referred to as dual-competitors. For the dual-competitor, the age at the highest performance differed for the two disciplines. This suggests that the preferred discipline for the horse was chosen based on the performance in both disciplines at a younger age. This makes dual-competitor horses different from the single performance horses. This could also explain the differences in genetic correlations in the different datasets. When horses that had competed in both disciplines were excluded from the analysis, the genetic correlation was close to zero. Additionally, the genetic correlation in the data set

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with dual-competitor horses only was more negative than in full data. These results indicate that including dual-competitors leads to a more negative genetic correlation. The more negative genetic correlation in the dual-competitors could be due to the choice of specialisation based on early performance in competition. This leads to dual-competitors having a high performance in one discipline and a lower performance for the other. That lower performance, however, is due to the decision of the owner to stop competing in this discipline. The performance could have been higher if the horse had continued competing in this discipline. In conclusion, to support the design of breeding programme for both disciplines, the genetic correlation should be used from the dataset excluding dual-competitors as that reflects the target population better.

Genetic correlation between dressage and show-jumping by time period

There is a trend for horses to perform in one discipline only because the number of dual-competitors has reduced in recent years (Table 5.1). It is therefore likely that breeding, rearing and training is also aimed at performance in one discipline. Estimation of the genetic correlation between both disciplines is relying on genetic connections between the horses of the two disciplines. In a previous study Rovere *et al.* (2014) showed that the dressage and show-jumping subpopulations of KWPN descend from the same genetic pool, but the original tight genetic connections have weakened in recent years. Creating subpopulations on different but related selection traits might change the genetic correlation between selection traits (a.o. Villanueva and Kennedy (1992)). Therefore, the genetic correlation between the two disciplines was investigated in subsequent time periods. The genetic correlation between disciplines was almost zero in period 1 and increased to -0.38 in period 3. The estimate in period 1 corresponds closely to estimates found by Huizinga and van der Meij (1989) and Bruns (1981). Alternatively, genetic correlations between periods within discipline hardly changed in the period studied.

Correlation between competition and inspection traits

The genetic correlations between inspection and competition traits were similar with estimates reported previously on the same population (Koenen *et al.* 1995; Ducro *et al.* 2007), with stronger correlations within disciplines (e.g. jumping related inspection traits to show-jumping) and weaker correlations to the opposite discipline. Similar to previous studies, results from this study indicate that measures in young horses are genetically correlated with performance in competition later in life. Movement traits related to gaits are more related with

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dressage than with show-jumping, and traits related to free-jumping present a high genetic correlation with show-jumping and, in general, are not or unfavourably correlated with dressage (Thorén Hellsten *et al.* 2006; Olsson *et al.* 2008; Viklund *et al.* 2010; Becker *et al.* 2011; Schöpke *et al.* 2013).

Correlation between competition and inspection traits over time

Heritability estimates for inspection traits appeared to increase over time. The lower heritabilities in first time period might be caused by poor uniformity or inconsistency in applying the new linear scoring system in the early years after introduction. The genetic correlations across time period did not change for the main part of the Descriptive traits. Changes observed in traits related to Movement were in the same direction as changes of the phenotypic means of the two subpopulations (Rovere *et al.* 2015b). Subjective traits summarize the overall opinion on the quality of a horse with respect to the breeding goal. Changes over time in the genetic correlation between Subjective traits and competition traits somewhat reflects the different weight that judges put on the traits for dressage or show-jumping horses in different periods. In that respect, the gaits trot and walk are more important to dressage, whereas canter is the most important gait for show-jumping.

5.5 Conclusions

The genetic correlation between performance of horses in dressage and show-jumping is slightly unfavourable (-0.12). The magnitude of the genetic correlation is reduced towards zero when horses that performed in both disciplines are excluded from the analysis.

The genetic correlation between dressage and show-jumping tended to become more unfavourable over time. The increasingly negative correlation between disciplines is not reflected in changes in the correlations between competitions traits and the traits recorded in the studbook-first inspection.

Moderate to high genetic correlations between competition and traits recorded in the studbook-entry inspections were found which is in line with earlier studies. The traits related to free-jumping are strongly correlated with show-jumping and unfavourably correlated with dressage. The traits related to movement are favourably correlated with dressage and tend to be uncorrelated with show-jumping except for the ones related with canter.

This study provides useful information to support the design of breeding programmes for horses and the opportunities for specialisation of breeding for dressage and show-jumping.

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Annexe5.1

Table 5.1.1 Heritability (h^2) of descriptive traits related with Movement and genetic correlations (r_a) with dressage and show-jumping estimated in three time periods.

<i>Descriptive traits</i>	<i>Movement</i>	Period	h^2	Dressage	Jumping
				r_a	r_a
Walk: length stride		(1)	0.12	-0.49	-0.11
		(2)	0.14	-0.52	0.22
		(3)	0.22	-0.41	0.09
Walk: correctness		(1)	0.15	0.10	-0.04
		(2)	0.24	0.10	-0.07
		(3)	0.37	0.16	0.02
Trot: length		(1)	0.22	-0.57	-0.17
		(2)	0.26	-0.61	0.22
		(3)	0.33	-0.50	0.18
Trot: elasticity		(1)	0.24	-0.57	-0.20
		(2)	0.23	-0.47	0.12
		(3)	0.30	-0.34	0.02
Trot: impulsion		(1)	0.23	-0.46	-0.26
		(2)	0.22	-0.46	0.02
		(3)	0.29	-0.41	-0.01
Trot: balance		(1)	0.21	-0.59	-0.12
		(2)	0.19	-0.59	0.16
		(3)	0.27	-0.37	-0.03
Canter: length		(1)		n.a.	
		(2)	0.23	-0.29	-0.21
		(3)	0.23	-0.23	-0.15
Canter: impulsion		(1)		n.a.	
		(2)	0.20	-0.21	-0.39
		(3)	0.22	-0.19	-0.36
Canter: balance		(1)		n.a.	
		(2)	0.16	-0.28	-0.24
		(3)	0.19	-0.12	-0.46

n.a.= trait not recorded in this period

Standard errors of: h^2 0.01-0.02; r_a 0.05-0.09

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Table 5.1.2 Heritability (h^2) of descriptive traits related with Free- Jumping and genetic correlations (r_a) with dressage and show-jumping estimated in three time periods.

<i>Descriptive traits</i>			Dressage	Jumping
<i>Free-Jumping</i>	Period	h^2	r_a	r_a
Take off: direction	(1)		n.a.	
	(2)	0.22	0.57	-0.78
	(3)	0.21	0.54	-0.78
Take off: speed	(1)		n.a.	
	(2)	0.16	0.39	-0.63
	(3)	0.15	0.51	-0.60
Technique: foreleg	(1)		n.a.	
	(2)	0.19	0.40	-0.65
	(3)	0.18	0.42	-0.54
Technique: back	(1)		n.a.	
	(2)	0.23	0.54	-0.67
	(3)	0.26	0.55	-0.53
Technique: haunches	(1)		n.a.	
	(2)	0.19	0.70	-0.80
	(3)	0.22	0.49	-0.71
Scope	(1)		n.a.	
	(2)	0.26	0.58	-0.81
	(3)	0.29	0.50	-0.68
Elasticity	(1)		n.a.	
	(2)	0.22	0.45	-0.66
	(3)	0.24	0.49	-0.71
Care	(1)		n.a.	
	(2)	0.19	0.57	-0.84
	(3)	0.15	0.64	-0.82

n.a.= trait not recorded in this period

Standard errors of: h^2 0.02-0.03; r_a 0.04-0.11

5. Genetic correlation between dressage and show-jumping

Table 5.1.3 Heritability (h^2) of subjective traits and genetic correlations (r_a) with dressage and show-jumping estimated in three time periods.

<i>Subjective traits</i>	Period	h^2	Dressage	Jumping
			r_a	r_a
Conformation	(1)	0.31	0.55	0.27
	(2)	0.32	0.41	0.13
	(3)	0.32	0.22	0.35
Movement	(1)	0.33	0.56	0.23
	(2)	0.36	0.56	0.07
	(3)	0.35	0.55	0.00
Jumping	(1)		n.a.	
	(2)	0.40	-0.58	0.85
	(3)	0.35	-0.48	0.71
Walk	(1)		n.a.	
	(2)	0.20	0.57	-0.26
	(3)	0.23	0.58	-0.24
Trot	(1)		n.a.	
	(2)	0.28	0.69	-0.27
	(3)	0.39	0.52	-0.14
Canter	(1)		n.a.	
	(2)	0.25	0.18	0.38
	(3)	0.29	0.14	0.36

n.a.= trait not recorded in this period

Standard errors of: h^2 0.02-0.03; r_a 0.03-0.13

6

General Discussion

6.1 Introduction

The general goal of this thesis was to provide information related to the ongoing specialisation in the population of the Royal Dutch Warmblood Studbook (KWPN) which is useful for optimization of their breeding programme.

The specialisation process in this context is defined as the changes in the breeding practices related to producing horses that will perform in only one of the sports disciplines, dressage or show-jumping. Specialisation has been occurring during the last decades in the population of KWPN. Knowledge on the effect of specialisation both on the genetic composition of the population and on the genetic parameters of selection traits is required to design optimal breeding programmes.

In this thesis different aspects of specialisation were studied in the population of KWPN. Firstly, it was shown that the population of the studbook started to show a degree of stratification into two subpopulations, corresponding to the disciplines dressage and show-jumping. Over time these two subpopulations became genetically less connected. Secondly, it was analysed if inspection traits measured early in life of the horse were different whether they were measured in dressage or in show-jumping horses. In chapter 4 a statistical model was developed which accounted for effect of rider on competition results. This model was used to estimate the genetic correlations between competition results for dressage and show-jumping as well as genetic correlations of inspection traits and these two competition traits. This chapter comprises two sections. In the first section, the challenges in the analyses of competition data as it is currently available will be discussed and the opportunities that can be explored by considering more information from competitions will be discussed. In the second section, the results obtained in this thesis and literature are put in the context of the specialisation process and opportunities are discussed for improving the breeding programme conducted by KWPN.

6.2 Analyses of performance in competition

6.2.1 Performance in competition phenotype

Dressage and show-jumping are two important traits in the breeding goals of many studbooks (Koenen et al., 2004). The definition and measurement of the traits are important for its application as selection criterion. However, there is no objective scale to measure performance in competition. In the case of dressage, a jury

6. General Discussion

determines the quality of the performance. Show-jumping can be more objectively measured because the score is determined by time and number of faults committed during the event. In both disciplines, horses compete at different levels being difficult to compare the performances between levels and disciplines.

Results of events are mostly recorded by national equestrian federations. The most usual expressions of performance in competition are earnings, scores, number of placings and rankings (Hintz 1980; Bruns 1981; Koenen and Aldridge 2002). An intrinsic problem of competition data is that only a small proportion of the horses participates in competitions (Árnason 1999; Ducro 2010a; Chapter 4). Further, often only horses are recorded that finish in first places or those that earn money or points. All other participants are not recorded or they are all recorded with the same performance. In some cases, the number of placings is expressed in relation to the number of starts of the horse to consider the variation in the number of events in which the horse participated, i.e. the number of opportunities the horse had to demonstrate its ability. A comparison of any measure of performance in competition is further complicated by the differences in the level of difficulty of the events, i.e. the technical difficulty of the event and the quality of the competitors (Brunns 1981; Tavernier 1990). The competition results do not follow a normal distribution but are skewed. For genetic analysis a mathematical transformation of competition results is usually carried out to achieve a normal distribution. Logarithmic functions, inverse normal distribution and square-root transformations are usually used for ranks, earnings and scores (Brunns 1981; Huizinga and van der Meij 1989; Aldridge *et al.* 2000).

6.2.2 The highest score achieved as a competition phenotype

In The Netherlands, performances in competition are recorded by the Royal Dutch National Equestrian Federation (KNHS). The KNHS defines the highest performance in competition for a horse based on the number of points gained by that horse. In dressage, the number of points achieved is based on the judgment of the jury of the trial. If the jury assigns a score higher than 70% for the performance, the horse receives 3 points, 2 points if the score assigned is 65-70% and 1 point if the jury's score is 60-65%, if the jury's score is less than 60% the horse does not receive any points. In principle, each horse starts competing at base level. When the horse has gained 10 points, the horse can be promoted to a higher level of competition, and with 30 points it is compulsory to compete at a higher level. In the case of show-jumping, the horse gains 2 points if it has a faultless performance and 1 point if it has no more than one fault. Ten points are required to be promoted to a higher

level and with 20 points promotion to a higher level is compulsory (Ducro *et al.* 2007). Highest performance refers to the highest level the horse has performed at and the total number of points it had gained at that level. For breeding value estimation, the Royal Dutch Warmblood Studbook (KWPN) uses information from studbook-entry inspections, young performance tests and competition data (KWPN 2015). The highest performance achieved during the lifetime of the horse is used as the competition information. The information provided by KNHS (ordinal scale, level + points) is transformed into a linear scale by KWPN based on the experience of the practitioners (Ducro 2011).

The use of the highest score achieved, as an expression of the performance in competition, has some limitations that should be considered. The transformation of the ordinal scale (level+points) to a linear score takes in account the level of competition, but, as it was mentioned previously, the amount of points assigned to demarcate different levels has been determined based on a subjective opinion of practitioners. Literature shows, for example, that the type of transformation applied to correct by level of competition affects genetic evaluation of competition records (Peeters *et al.* 2010). Further, Kearsley *et al.* (2008) and Stewart *et al.* (2012) showed that genetic correlations between different levels of competition were different from one and were lower between low and high level of competitions. Ducro (2011) has already discussed this point and suggested using multivariate analysis considering the performance in different levels of competition as different traits.

Based on early studies it is assumed that the genetic correlation between performance at different ages are highly genetically correlated (Huizinga and van der Meij 1989). More recently, it was suggested the existence of age-genotype interaction (Bartolomé *et al.* 2013). Using repeated records of horses that participated in test events, the authors showed changes in the ranking of animals when breeding values were estimated at 4, 5, and 6 years old, and referred to this change in the genetic response at different age as environmental sensitivity. Different to other livestock where the effect of age on the performance could be due to the physiological development of the animal, in equestrian activities it could comprise additional factors like different ability to learn of the horses or to handle the stress associated with the competition and rider relationship (Wolff and Hausberger 1996; Schöllhorn *et al.* 2006; Hausberger *et al.* 2008). It takes a couple of years of training before a horse enters into competitions and it takes even longer before the horse can show its ability at a high level of competition. In this sense,

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the highest score achieved summarizes in one record the lifetime competition performance of the horse but it does not provide information for inferences about differences among horses in their competition career, e.g. age at the first competition, amount of competitions or amount of competitions without achieving points. Thus, some differences in performance might be merely due to a different amount of participations in competitions than a real genetic difference. However, from the current information available this effect cannot be accounted for.

Specifically, in Chapter 4 the effects of the pre-selection and censoring of the data were addressed, as well as the impact of inclusion of rider effect in the genetic analyses of the highest score. The effect of pre-selected data and the effect of the rider are topics commonly cited in studies on performance in competition for all disciplines. The presence of censored data is related with the kind of expression used for performance in competition. The highest score achieved from young horses in recent years might be affected by censoring given the constraint in time to compete at higher levels. Thus, the highest performance is recorded on these young horses but it is not possible to distinguish between horses that have reached their highest performance and those that might improve further in the future. The analysis in Chapter 4 revealed that estimation of genetic variances and heritabilities are affected by censoring of the data.

6.2.3 Age at the highest performance

In the genetic analysis of performance in competition (Chapters 4 and 5) age at highest performance was included as a fixed effect in the model of analysis. Accounting for age at highest performance in evaluation of competition data seems justified as younger horses lack training to show their full potential compared to older horses. However, the correction would not be justified if the horse indeed had the opportunity to compete at older ages but did not manage to achieve any better performance later in life. Comparison to contemporaries of the same age at highest performance might be wrong because horses that had the opportunity to increase their performance cannot be distinguished from horses that did not have the opportunity (because time was up). Perhaps a better comparison could be to horses of the same birth-year, they all had the same chance in time to show best performance. To test accounting for birth-year rather than age, age effect was replaced by the effect of birth-year in model [3] of Chapter 4. Results showed that accounting for birth-year instead of age resulted in heritability for highest score to 0.08 in dressage (Table 6.1), whereas the heritability remained the same in show-jumping. The lower values of heritability obtained in dressage is due to the reduced

estimate obtained of the additive genetic variance and slightly increase of the residual variance. In the case of show –jumping, the estimates obtained were very similar in both models.

Consequences of the different models for ranking of breeding stallions has been considered by computing rank correlations between the breeding values for each model in dressage and show-jumping. In show-jumping the rank correlation was very high when estimated on animals with an own record (0.98), and when estimated on sires with 10 or more offspring (0.97). In the case of dressage the rank correlation was lower, 0.94 for animals with an own record and 0.91 for sires with 10 or more offspring. These results suggest that the opportunities should be examined to change the effect of age by birth-year in the analysis of highest score in the case of dressage.

Table 6.1 Additive genetic variance (σ_a^2), residual variance (σ_r^2) and heritability (h^2) of highest score in dressage and show-jumping from models with age effect or birth-year (Data and model used based on Model [1] of Chapter 4).

Factor	Dressage ⁽¹⁾			Jumping ⁽¹⁾		
	σ_a^2	σ_r^2	h^2	σ_a^2	σ_r^2	h^2
Age	0.42	2.74	0.13	0.23	1.91	0.11
Birth-year	0.26	2.94	0.08	0.24	1.96	0.11

⁽¹⁾ Standard errors of h^2 0.006 – 0.009

Note: parameters were estimated using the Average Information Restricted Maximum Likelihood (AI-REML) implemented in the DMUAI module of DMU software version 6 release 5.2. (Madsen and Jensen 2013).

The genetic analyses in previous chapters were concentrated on highest performance in competition and corrected performances for age at highest performance. The highest score for a horse represents the lifetime cumulative number of points achieved by that horse. In this sense, the highest score resembles lifetime performance traits used in other livestock species (e.g. Strandberg 1992). On the other hand, age at highest performance could also be considered as a measure of performance itself. As the highest score resembles lifetime performance traits used in other livestock species, age at highest performance in horses resembles longevity or productive life in other livestock species (e.g. Strandberg 1992). Thus, rather than focussing on the highest score and correcting

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for age at the highest performance, the age at highest performance could also be considered as a selection criterion in itself. The underlying assumption is then that horses that are staying longer in competition are preferred as they better fit the ambitions of the rider. Early retirement in that case would be considered to be due to insufficient performance or due to any health problem affecting the horse.

The genetic basis of the age at the highest performance was investigated as well as the genetic correlation of age at highest performance with performance in competition. In this analysis, the data set analysed in Chapter 4 was used. The data comprised information on competition from 82,694 horses in dressage and 62,072 horses in show-jumping, recorded in the period 1993-2012 (year of birth between 1974 and 2009). Firstly, univariate models were performed for age at the highest performance in both disciplines. Secondly, univariate analysis of highest score for dressage and show-jumping were performed with and without adjustment for age at highest performance. Thirdly, the genetic correlation between highest score and age at highest performance was investigated in each of the disciplines. The model for the highest score was based on model [3] of Chapter 4, with and without the effect of age in the model included. Following the basic models used for highest score and age at highest performance:

$$y_{ijklmn} = \mu + year_i + age_j + sex_k + thor_l + a_m + rl_n + e_{ijklmn} , \quad [1]$$

$$y_{iklmn} = \mu + year_i + sex_k + thor_l + a_m + rl_n + e_{iklmn} , \quad [2]$$

where y_{ijklmn} is the highest score for either dressage or show-jumping of the m^{th} horse (model [1]) and y_{iklmn} is the age at highest score (model [2]); μ is the population mean; $year_i$, is the fixed effect of the i^{th} class of the year of highest score (20 levels: 1993,...,2012); age_j is the j^{th} class of the age of the horse (6 levels: ≤ 5 , 6,..., ≥ 10 yr) at the highest score; sex_k is the fixed effect of the k^{th} sex of the horse (2 classes: stallion and gelding, mare); $thor_l$ is the fixed effect of l^{th} class of the thoroughbred percentage (6 classes: 0%, 12.5%, 25%, 37.5%, 50%, $\geq 62.5\%$); a_m is the random additive effect of the m^{th} horse $\sim N(0, A\sigma_a^2)$; rl_n is the fixed effect of the n^{th} class of the level of the rider (6 classes: 1,...,6) and e_{ijklmn} and e_{iklmn} are the residual random terms associated with each observation $\sim N(0, I\sigma_e^2)$ in model [1] and model [2], respectively.

Genetic parameters obtained are shown in Table 6.2. Inclusion of age in the model reduced the heritability for highest score from 0.25 to 0.13 in dressage, whereas the heritability for highest score remained the same (0.11) in show-jumping. For both disciplines the genetic and phenotypic variance reduced to the same extent when including the age effect (Table 6.2).

Table 6.2 Additive genetic variance (σ_a^2), residual variance (σ_r^2) and heritability (h^2) of highest score in dressage and show-jumping from models with and without age effect. Additive genetic and residual variance, and heritability for age at highest score.

Trait	Factor	Dressage ⁽¹⁾			Jumping ⁽¹⁾		
		σ_a^2	σ_r^2	h^2	σ_a^2	σ_r^2	h^2
<i>Highest score</i>	With age	0.42	2.74	0.13	0.23	1.91	0.11
	No age	1.04	3.04	0.25	0.30	2.51	0.11
<i>Age at highest score</i>	-	5.19	2.72	0.66	2.56	2.77	0.48

⁽¹⁾ Standard errors of h^2 0.006 – 0.009

Note: parameters were estimated using the Average Information Restricted Maximum Likelihood (AI-REML) implemented in the DMUAI module of DMU software version 6 release 5.2. (Madsen and Jensen 2013).

For the age at highest performance (from now on referred to as just age) the estimated heritability was 0.66 for dressage and 0.48 for show-jumping (Table 6.2). The heritabilities estimated indicate that age has a clear genetic background. This means that age can be used as a selection trait. However, it also highlights that the justification of age correction in the genetic analysis of highest score needs to be revisited. The bivariate analyses revealed a moderately positive genetic correlation between age and highest score when the age effect is not considered in the model of highest score. The genetic correlation was 0.68 for dressage and 0.51 for show-jumping (Table 6.3). This high genetic correlation indicates that selection for either of them will improve the other trait as well. From the results it can be concluded that age is a trait with high heritability for dressage and medium-high for show-jumping. For dressage the effect of age is partially confounded with the additive genetic effect. This confounding is expressed in the higher genetic variance and heritability for highest score when the age effect was removed from the model. In show-jumping confounding effect between age and the additive genetic effect appeared to be much smaller with the consequence that the heritability was not

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affected. When neither the age effect nor birth-year was included in the model for the highest score, the genetic correlation was 0.68 for dressage and 0.51 for show-jumping (Table 6.3). This high genetic correlation indicates that selection for either of them will improve the other trait as well.

Table 6.3 Heritabilities (h^2) and genetic correlations (r_G) for highest score in dressage and show-jumping, and age at highest score from models with and without age effect (bivariate analysis).

Model [1]	Dressage ⁽¹⁾			Jumping ⁽¹⁾		
	h^2 score	h^2 age	r_G	h^2 score	h^2 age	r_G
<i>Highest score</i>						
With age	0.09	0.66	0.08	0.11	0.50	-0.54
No age	0.17	0.66	0.68	0.09	0.50	0.51

⁽¹⁾ Standard errors of h^2 0.006 – 0.008. Standard errors of r_G 0.01 - 0.03

Note: parameters were estimated using the Average Information Restricted Maximum Likelihood (AI-REML) implemented in the DMUAI module of DMU software version 6 release 5.2. (Madsen and Jensen 2013).

From the previous analyses, it appears that dressage and show-jumping behave differently. In the case of dressage, the additive effect of the highest score achieved by a horse is confounded with the age. The estimate of additive genetic variance of highest score achieved is reduced when the effect of age is considered in the model. Furthermore, in the bivariate analyses with age, the genetic variance (not shown) and heritability (Table 6.3) of the highest score is also reduced. The model currently used in the genetic evaluation by KWPN includes the effect of age in the analyses of the highest score achieved. The effect of the age removed differences in highest score due to different class of age what could be considered an environmental systematic effect. However, genetic differences associated with age classes are also removed which is not desirable. Omitting the effect of age in breeding value estimation will cause selection of highest score at high age, instead of highest score. In a separate section it will be discussed the opportunities to change the collection of records of performance in competition. However, for the analysis of highest score achieved in dressage, it can be suggested to use a bivariate analysis with highest score (model without the effect of age) and age, and develop an index with different weights defining explicitly the emphasis desirable on each trait.

In show-jumping, the confounding between the highest score and age is not as clear as in dressage. The exclusion of the effect of the age from the model incremented the estimate of the additive genetic variance of highest score achieved; however, the estimate of the heritability did not change because the residual variance increased proportionally, as well (Table 6.3). The estimates from bivariate analysis resulted in the same estimates of the additive genetic variance. As in dressage, the current model used in the genetic evaluation of KWPN for show-jumping includes the effect of age in the analyses of the highest score achieved. The distribution of the breeding values estimated by class of age obtained with this model, presented a kind of overcorrection of the youngest ages. This possible overcorrection can be seen in the distribution of the estimated breeding values (EBV) estimated with Model [1] (with fixed age effect) by age class (Figure 6.1). The negative genetic correlation obtained from the bivariate analyses between highest score achieved and the age can be related with this overcorrection. The correction by age probably should be revisited in the analysis of the highest score. Similar as it was suggested for dressage, a bivariate analysis of highest score (model without the age effect) and age can be an alternative analysis which permit the construction of a selection index with the combination of both traits to develop selection criterion which better can be controlled.

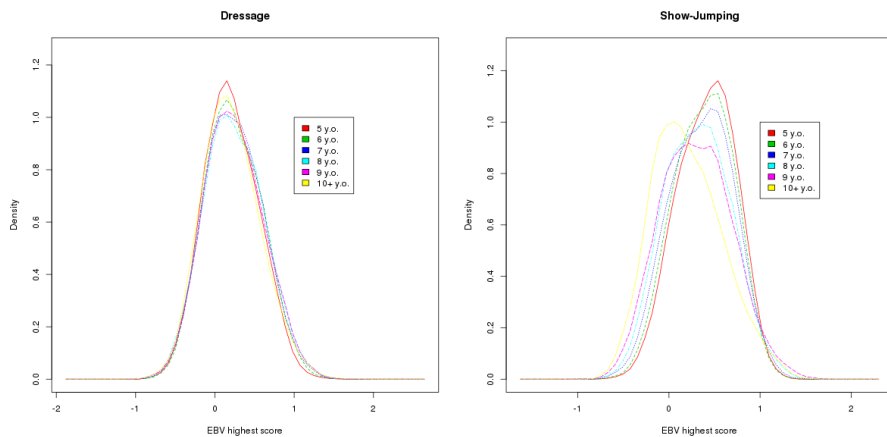


Figure 6.1 Distribution of estimated breeding values of highest score (EBV highest score) by six classes of age effect (5 y.o.,...,≥10 y.o) for dressage and show-jumping competition data.

6.2.4 Opportunities to improve utilisation of competition results in breeding

Performance in competition is directly related to the breeding goal and therefore an important source of information in genetic evaluation. Recording the sport performance as highest score is an efficient system of the equestrian sports federation to subtract only the information from each competition event that is relevant to keep track of the progress of horses. For this purpose the equestrian sports federation does not need to collect results of all horses that participate in an event, which would require much more data management and storage capacity. For breeding purposes availability of competition results of all horses participating in an event would allow for a better genetic evaluation as will be described in this section.

Data selection

When results from single competition events of all participating horses are available for genetic evaluation, then the issue of evaluation on selected data has been prevented. Selection in the competition data as it is currently applied in practise has two consequences. Firstly, only horses that achieved points are considered in the analyses. Secondly, from all events in which the horse participated, only the ones in which it achieved points are taken for its phenotypic record. The current phenotypic records do not contain information about the number of attempts that was used to achieve the final score. Further, it is not possible to distinguish between horses that did not participate in competition and those that participated in competition but did not achieve points.

Considering only horses that obtained points might lead to an underestimation of the genetic variance. Breeding value estimations could be biased since only better competitors are considered. Recording only the events in which the horse gained points might lead to unfair comparison between horses with different opportunities to compete. Currently, part of the difference among horses considered as genetic differences, actually can be also differences in the number of participations. An evaluation of the performance of all horses participating in a competition would avoid the problems related to selected data.

Effect of age and levels of competition

When results from single events are available then there are better opportunities to disentangle effect of age and level of competition. Kearsley *et al.* (2008) showed that genetic correlations between levels of competition were deviating from one,

and they were lower when levels were more distant. Defining levels of competition as different traits, a multi-trait model will permit to account for different genetic correlations between them. The use of a multi-trait model has an additional important advantage, as it accounts for the selection bias caused by the fact that only the better horses move to higher levels of competition. Additionally, multi-trait models will permit flexibility in the use of the breeding values estimated because they can be used individually or combined in an index with different weights defined in accordance with the breeding goal. In case of many levels of competitions, reaction norm models might be an option as these models have been applied successfully in other livestock species to account for GxE interactions when many levels of environment are present (Su *et al.* 2006, 2009).

The rider effect

In Chapter 4, the significant influence of the rider on the performance in competition was demonstrated. From the analysis it became clear that the rider effect could not be properly disentangled from the genetic effect because highest score is by definition linked with only one rider. The rider recorded is the one that rode the horse when it received the last points, and it is further assumed that the horse was always ridden by this rider. Additionally, the analysis in Chapter 4 revealed that ~30% of riders only rode one horse in dressage, limiting even more the possibilities to disentangle the genetic and the rider effect. If genetic evaluation is based on data from single events with proper rider recording, then fewer single rider-horse combinations might be expected in the dataset. However, in addition of the advantages mentioned in the previous paragraphs in having information from single events, the contribution of extra information for a better treatment of rider effect in the genetic analyses strongly support this point.

The analysis of competition records in equestrian activities has many challenges. The highest score achieved is an expression of performance in competition whose analysis added even more challenges. The results from this section and from Chapter 4 support the idea that there are many opportunities to improve the genetic evaluations of performance in competition by using more extensively the information generated in single events recorded by the equestrian federation. With more knowledge on the structure of data, different models should be analysed and validated looking for the most accurate breeding values estimations obtained by the simplest models (i.e. law of parsimony).

6.3 The Specialisation Process

Specialisation in livestock

Specialisation can be observed in the history of almost all livestock species and has resulted in a considerable number of subpopulations. The current state of these subpopulations, which are defined as different breeds, is the product of varying degree of geographical isolation, selection by their stakeholders and other evolutionary forces (Woolliams and Toro 2007). Selection has been leading some breeds to specialise in specific deliverables. In other cases, specialised strains within breeds were created. An example of the use of specialised lines in breeding is the poultry industry. The use of specialised lines in poultry breeding programmes dates from the fifties and by crossing them, complementary effects are exploited (Tixier-Boichard *et al.* 2012). In the broiler production once the negative genetic correlation between growth and fertility was verified, specialised lines were developed to produce chickens with the genetic potential for efficient meat production from parents with good reproductive performance (Tixier-Boichard *et al.* 2012). In the case of dairy cattle, the Holstein line can be considered as a specialised strain selected for high milk production from the traditional Friesian cattle population. In horses, the kind of specialisation that is occurring might be considered more similar to dairy cattle.

Breeding history of the sport horse

The modern version of sport horses started to be established as a special population of horses in Europe relatively recently. Since early fifties the horse population in Europe decreased steadily until the eighties. The technological change in agriculture with an increasing mechanization of the activities had a major impact on this demographic reduction (Staun *et al.* 1982). From mid- eighties, the number of horses in Europe has been relatively stable between ~ 3.5 to 4.0 million of horses (FAO 2015). However, when examining the demographic changes in the horse population in more detail, different trends can be observed. With the changing role of the horse in society, the number of the commonly called draught horses decreased constantly while the number of the so called blood horses, related with leisure activities constantly increased (Langlois *et al.* 1983; FAO 2015). The emphasis in breeding horses shifted from heavier working horses to lighter riding horses suitable for sport and recreation. Horses used in agriculture or in the cavalry and coach horses, in crosses mostly with English Thoroughbreds, were the background of the modern Warmblood (Edwards *et al.* 1994). Therefore, the

modern Warmblood horses might be considered as a population composed of a blend of breeds in which the Thoroughbred contribution is a common factor (Edwards *et al.* 1994). The Warmblood horse breeder organizations are characterized by open studbook policy and a studbook selection with the aim to breed sport horses. A sport horse, in this case, refers to horses bred for the Olympic equestrian disciplines of dressage, show-jumping or eventing, although harnessing is also considered in some studbooks.

The Royal Dutch Warmblood Studbook (KWPN) is the organisation that is responsible for the breeding program of the Dutch Warmblood horses. The KWPN is recognised as one of the most competitive studbooks in dressage and show-jumping, leading the ranking of the International Federation for Equestrian Sports in both disciplines, in recent years (FEI 2015). The Dutch Warmblood is a horse population that has roots in the old regional breeds, known as horses from Gelderland and Groningen, with contributions from other breeds like Oldenburger, Hanoverian, Holsteiner or Trakehner, and Thoroughbred (Edwards *et al.* 1994; KWPN-NA 2015).

Breeding goals in sport horses

The general goal of the Warmblood breeders is to breed riding horses that mainly are used as sport horses. Warmblood horses are popular in the Olympics disciplines, i.e. dressage, show-jumping and eventing. In 2004 a survey was held among the warmblood studbooks in Europe about the characteristics of their breeding program (Koenen *et al.* 2004). It appeared that main emphasis in all breeding organisations was on performance, although conformation and gaits received high weightings as well. Within the performance traits, many organisations put an equal weighting on show jumping and dressage. Several studbooks indicated that they encouraged specialisation in selection of stallions for either of the two disciplines. Furthermore, a few studbooks focus mainly on one trait in their breeding program. The Holstein, Selle Français and Irish Sport Horse studbooks clearly put more weighting on show jumping, whereas the Trakehner studbook puts significantly more weighting on dressage. Recently, a new survey has been held among the studbooks and, based on the first responses; it seems that specialisation seems to continue at the expense of all-rounder qualities (Stock *et al.* 2015).

The breeding goal of the Royal Dutch Warmblood Studbook (KWPN) is focused on performance at the highest level in dressage and show-jumping (KWPN 2015).

6. General Discussion

During the last decades an increasing professionalisation of the equestrian sport has been noted. Rearing and training became more and more directed to only one of the disciplines, and similarly breeders considered in their breeding and mating decisions only one of the disciplines (Ducro 2010b). In the case of the members of KWPN, the focus on one of the disciplines has been more intense from late eighties. The first indications of specialisation were expressed by the reduction in the proportion of matings between stallions and mares from different disciplines, i.e. dressage or show-jumping background, and concomitantly, a significant increment of matings within discipline (Ducro 2010). The studbook took notice of the specialisation in the population and in 1998 started to evaluate an additional set of traits for jumping abilities in the studbook-entry inspections.

Traits in the selection program

At the level of the studbook, initially, selection was mostly based on conformation, gaits and pedigree, and based on stationary tests (Huizinga *et al.* 1991). The judgement of conformation and gaits were based on subjective scoring methods. In 1989 the application of a descriptive linear system started in the judgment of traits related to conformation and movement in the routinely studbook-entry inspection. In 1998, an additional set of traits specifically for the jumping abilities of horses was included in the studbook-entry inspections.

In practise conformation and movement is commonly assessed by inspectors and recorded as scores on a scale, using a descriptive or an appreciating scale (Ducro 2011). The scoring system implemented by KWPN considers descriptive and subjective traits. When a trait is recorded using a descriptive scale; every individual horse is compared with the population's means which is placed at the centre of the scale. The subjective traits are recorded using an appreciating scale and depend on the breeding goal for which the horse is evaluated. A score on an appreciating scale is not informative about the level of the trait, e.g. a suboptimal score for rump length does not give information whether rump length is too short or too long (Ducro 2011; Duensing *et al.* 2014).

Descriptive scales have higher repeatability, show less inter-inspector variation, but require that the inspectors know the population's mean. An important advantage of descriptive scales is that the scoring is independent of the breeding goal, which means that data collection, as well as the genetic evaluation does not have to be adjusted when specialisation leads to separate breeding goals. Nowadays, most of

the warmblood studbooks are shifting to or have already adopted the descriptive scoring system for judgement of their horses (Duensing *et al.* 2014).

Genetic correlation at level of the breeding goal

To estimate the genetic correlation between dressage and show-jumping it is necessary that horses competing in each discipline are genetically connected. For the estimation of the genetic correlation between two traits it would be an advantage to have records on both traits from the same animals. At present the dataset for genetic evaluation has records from horses performing in one discipline and from horses that have performance in both disciplines, the so-called dual competitors. The impact of dual-competitors on estimation of the genetic correlation between dressage and show-jumping was investigated in Chapter 5. A low but unfavourable genetic correlation between dressage and show-jumping was found when the analysis was based on performance of single competitors only. Including dual-competitors resulted in a more negative genetic correlation. The negative correlation found in dual-competitors might indicate that participation in both disciplines is at different levels of intensity. For example, a horse has been tested in both disciplines and based on the initial results the rider decided to continue only in the discipline where the horse showed the best performance. The lower performance in the other discipline in that case is due to the decision of the owner to stop competing in this discipline. The final score in that discipline would most likely have been higher, if the horse had continued competing in that discipline. This could explain the stronger negative correlation estimated in the data including dual-competitors. For genetic evaluation, the genetic correlation estimated from the dataset excluding dual-competitors is preferred.

Genetic correlation over time

The genetic correlation within discipline over time was high indicating that performance in competition can be considered genetically the same trait during the years under study for both disciplines. In this context, i.e. no changes in the disciplines, the genetic correlation between dressage and show-jumping is increasingly unfavourable in the years under study. Genetic correlation between disciplines should be reconsidered at all the levels of competition when more detailed information on performance in competition is available.

The correlation between disciplines was close to zero when analysing horses born before 1995. This correlation might have been influenced by the selection and mating scheme in the population. Parents were selected based on the combination

6. General Discussion

of performance in both disciplines. In addition, corrective mating was commonly used in these years (Ducro 2010b). From quantitative genetic theory it is known that selection which includes specialisation can change the genetic correlation between selection traits (a.o. Villanueva and Kennedy (1992)). The focus on one discipline in each subpopulation can lead to a negative genetic correlation for traits that are genetically uncorrelated. The estimated genetic correlation between dressage and show-jumping was -0.12 (Chapter 5). The estimates obtained using different models and sets of data varied between zero and moderately negative values (Chapter 5).

Genetic correlation at level of selection traits

Results from Chapter 3 were not conclusive about differences between studbook-entry inspection traits measured in dressage and show-jumping horses that justify, for example, considering separate genetic evaluations. Genetic correlations between inspection traits defined as dressage or show-jumping traits were hardly different from unity in most of the cases (Chapter 3). Based on these results, to maintain a single genetic evaluation for both subpopulations is recommended. Furthermore, results from Chapter 5, showed that there are traits related with movement that are favourably correlated with both disciplines, e.g. the canter related traits. Inclusion of information from studbook-entry inspection traits from a common breeding evaluation would be beneficial for both breeding goals (competition in dressage or show-jumping). In addition, a common breeding programme for, e.g. health and competitive life time might be beneficial as well. The previous statements support the idea that despite selection for two different breeding goals can be recommended, there are arguments to maintain common measures, recording systems and breeding values estimations for traits that can be considered in the selection for both breeding goals.

Specialist from one population or two specialised subpopulations

With the emerging specialisation in breeding practise the question arises, should horses for both disciplines be taken from a single breeding programme paying attention to both disciplines or from two breeding programmes, one for each specialisation?. This question is similar to the situations studied by Mulder (2007). More specifically, how to generate improved genetic material for two different breeding goals from one single population? Mulder (2007) demonstrated that the genetic correlation between the breeding goals for the two specialisations is one of the key factors to determine the optimum breeding scheme. When the genetic correlation decreases, the advantages in terms of genetic gain in both populations

of specialised breeding programmes compared to a single breeding programme increases. Mulder (2007) calculated the break-even value of the genetic correlation between breeding goals to determine whether it is better to maintain one or two breeding programmes to breed for two different breeding goals.

To determine the optimum selection scheme for jumping and dressage, knowledge on the genetic correlation between both disciplines is crucial. Genetic correlations between disciplines should not only be known for the traits including in the breeding goal, but also between traits that are included in the breeding value estimation. In the case of multi-stage breeding programme, first stages of selection are based on traits measured on young horses. Moreover; breeding values estimated at later ages are based on multi-trait models that also consider young horse traits.

Largest genetic gain will be achieved when the breeding goal consist of a single trait. The largest advantage of specialisation is, therefore, that horses can be selected for a single purpose and no attention should be paid to other neutral or conflicting selection traits. A disadvantage of specialisation is that the population size will be reduced. The population size is reduced with 50% when both disciplines are given equal emphasis. Smaller population size impacts the selection intensity, and the amount of information collected and thereby on the accuracy of selection.

Ducro (2011) presented the breeding programme of KWPN in detail. From that description and results obtained in this thesis, it seems that specialisation can be implemented by developing two different selection indexes, one for each discipline, for the selection of stallions. However, it seems not advisable to split the population in two closed subpopulations. In contrast to other livestock species, the population of horses is relatively small. Around new 4,000 horses for dressage and 6,000 for show-jumping are registered annually with KPWN. Additional to the small population size, diversification of the breeding goal is likely to exist as a result of the large number of stakeholders owning the breeding material. The studbook has only influence on the selection of stallions whereas selection and mating decisions for mares are taken by the individual stakeholders. Based on the results obtained, specialised breeding goals seem an appropriate option as far as it concerns selection for sport performance at professional level.

Structure of population

The effect of the ongoing specialisation on the genetic structure of the population was analysed in Chapter 2. Until 1998 there was no distinction between horses competing in dressage or show-jumping. Horses born before 2000 mainly come from stallions with offspring in both disciplines, but this proportion decreased in favour of sires with progeny in one of the disciplines only. After 2002, the number of stallions with offspring in both subpopulations, dressage and show-jumping, decreased very significantly until the most recent years (Chapter 2). The study presented in Chapter 2 was done using the dataset from the studbook-entry inspection of KWPN. When the same analysis was performed on the dataset of Chapter 5, which consisted of horses with competition records, a similar trend was found; the proportion of stallions with offspring in both disciplines decreased from 54% to 27% during the last 20 years. This resulted in a reduction of genetic links between both subpopulations. Additionally, the number of sires used within each subpopulation has been reduced as well. As a consequence, the number of effective ancestors that explained 50% of the genetic pool in each subpopulation decreased from ~30 to ~20 ancestors in each subpopulation during the last 15 years (Table 2.5, Chapter 2). Considering the more intense selection for a single breeding objective within each subpopulation, it is relevant to pay increased attention to prevention of loss of genetic diversity in the subpopulations. The studbook is responsible for the selection programme of the stallions which is the most influential part in the genetic improvement but also most influential in maintaining genetic diversity in the population. In this sense, the studbook can implement procedures to avoid undesirable reduction of the genetic diversity within subpopulations. A reduction in genetic diversity will compromise the genetic response in the medium and long term. Constraining the loss of genetic diversity while maximizing genetic gain can be achieved using optimum-contribution selection (Woolliams *et al.* 2015). By using optimum-contribution selection, the reduction in genetic diversity can be prevented.

6.4 Conclusions

The genetic evaluation of performance in competition should account for rider effect. In the genetic analysis of the highest score achieved in competition, the rider effect is better accounted for when is considered as a fixed rather than a random effect. Utilization of competition data can be optimized for breeding value predictions by recording single events. The competition data should include the

information of rider and rider should be included in the models used in the genetic analysis of performance in competition.

The results obtained in this thesis suggest that performance in dressage and show-jumping competition are two genetically different traits which are unrelated or weakly unfavourable correlated. A common genetic evaluation across disciplines of studbook-entry inspections is possible and therefore will contribute to more accurate breeding values for sport performance in both disciplines.

Based on the findings from this study a breeding programme under specialisation is most effective when it comprises separate aggregate breeding goals for each of the disciplines, rather than one combined breeding goal. The accompanying selection index for each of the disciplines includes in part the same sources of information (e.g. traits of studbook-entry inspection) but weighted in accordance with the genetic relation to the breeding goal of the discipline. Intensification of selection for one single objective should be combined with constraints on the loss of genetic diversity.

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Summary

Summary

Horses and equestrian sports are part of the common heritage of Europe. Equestrian sports, in this case, refer to the Olympic equestrian disciplines of dressage, show-jumping and eventing. The modern version of sport horses started to be defined in Europe relatively recently. Since early fifties the role of the horse in the society shifted from heavier working horses to lighter riding horses suitable for sport and recreation. These horses, used for a general purpose in agricultural, coach horses or even in the cavalry, in crosses mostly with English Thoroughbreds were the background of the modern Warmblood. Sport horses belong mainly to Warmblood breeds and Warmblood horse breeder organisations are characterized by open studbook policy and a studbook selection with the aim to breed sport horses. The Royal Dutch Warmblood Studbook (KWPN) is the organisation that rules the breeding of the Dutch Warmblood horses. The breeding goal of KWPN is focused on performance at the highest level in dressage and show-jumping.

During the last decades an increasing professionalisation of the equestrian sport had been noted. Rearing and training became more directed to only one of the disciplines, and similarly breeders considered in their breeding and mating decisions only one of the disciplines. In this context, the shift in the breeders practice focusing in only one discipline is referred to as specialisation. This focus on one of the disciplines has been more intense from the late eighties. It is still under discussion how the specialisation should be considered in the studbook's breeding programme. It is unclear what would be an optimal breeding strategy for studbooks that consider both disciplines in their breeding goals. Therefore, the general goal of this thesis was to provide information useful for the breeding programme of the KWPN in relation with the ongoing specialisation of the population.

Firstly, the effect of specialisation was studied on the connectedness between the subpopulations of dressage and show-jumping horses registered by KWPN, using the pedigree information (Chapter 2). Genetic similarity (GS), genetic pool in common (GC_x) based on the marginal genetic contribution of common ancestors and coefficient of relationship (*r*) between and within subpopulations were analysed in three periods of time to describe changes in genetic connectedness between the subpopulations. The subpopulations comprised 18,125 dressage horses and 23,800 show-jumping horses, born between 1995 and 2009. A decline in GS (0.97–0.45), GC_{0.5} (0.69–0.13) and *r* (0.018–0.014) in the recent years was observed. These results indicate that the relatedness between the two subpopulations has been reduced, while the relatedness within both

subpopulations has been increased consistently. Additionally, a strong reduction in the number of influential ancestors in both subpopulations was observed.

Secondly, it was analysed whether specialisation for either dressage or show jumping has affected the heritabilities and the genetic correlations between traits observed in the two subpopulations (Chapter 3). Traits recorded at studbook-entry inspection, from 1998 and 2013, were defined as a dressage trait or a show-jumping trait according to the type of horse that received the inspection. Data from 18,125 dressage horses and 23,800 show-jumping horses were used to analyse 13 traits scored in both subpopulations. Analyses were performed in a Bayesian framework. Bivariate analyses were performed to estimate the genetic correlation between the two traits. Three time periods were defined and genetic correlations between subpopulations were estimated within each period. Results obtained indicated that heritabilities were moderate (0.17–0.39) for both subpopulations, and genetic correlations between traits, measured in dressage or show-jumping horses, were not different from one considering the posterior standard deviation of the estimation.

Thirdly, the model to analyse performance in competition of dressage and show-jumping was studied (Chapter 4). Performance of 82,694 horses in dressage and 62,072 horses in show-jumping, from the period 1993 – 2012, were analysed. For each horse only the highest performance in competition was available. In this study the impact of censoring in the data was quantified, as well as the impact of rider effect and the impact of the preselection of data on the genetic analysis of competition data of dressage and show-jumping. To assess the impact of censoring, genetic parameters were estimated in data sets that differed in the degree of censoring. To evaluate the impact of the rider effect, different models including rider were evaluated. The effect of preselection on variance components was analysed by defining a binary trait (sport-status) depending on whether the horse had a competition record or not, and a bivariate analysis with the competition trait was subsequently performed. Results showed that performance in competition for dressage and show-jumping is a heritable trait ($h^2 \sim 0.11-0.13$), and that it is important to account for the effect of rider in the genetic analysis. To account for the rider effect in genetic analysis, inclusion of a fixed effect that represents the level and experience of riders showed a better predictive ability than a random effect for each rider. Results revealed a small effect of censoring on the genetic parameter for highest performance achieved by the horse, and no changes on genetic parameters estimated were observed by including sport-status in the analyses to account for pre-selection.

Fourthly, it was estimated the genetic correlation between the performance of horses in dressage and show-jumping competition, and the genetic correlations between traits measured early in life and performance in competition in each of the disciplines (Chapter 5). The information on competition comprised the highest performance in competition of 82,694 horses in dressage and 62,072 horses in show-jumping, recorded in the period 1993-2012. For 26,056 horses information was available for both disciplines. The information on traits recorded at studbook-entry inspections comprised 62,628 horses, recorded in the period 1992-2013. To estimate the genetic correlation between the disciplines and between the disciplines and traits recorded in the studbook-entry inspection, bivariate genetic analyses were performed. To study if the genetic correlations have changed over time, three periods of time were defined by birth year of the horse and bivariate analyses were carried out in each period. The genetic correlation between performance of horses in dressage and show-jumping was slightly unfavourable (-0.12) when horses that performed in both disciplines were excluded from the analysis. The genetic correlation between dressage and show-jumping tended to become more unfavourable over time. However, the increasingly negative correlation between disciplines was not reflected in changes in the correlations between competitions traits and the traits recorded in the studbook-entry inspection.

Finally, in the general discussion two topics were addressed (Chapter 6). The first topic concerns the challenges in the analyses of competition data was discussed and the opportunities that can be explored by considering more information from competitions. In the second topic, the results obtained in this thesis and literature were put in the context of the specialisation process and the opportunities for improving the breeding program conducted by KWPN were discussed. From this study it can be concluded that, based on the estimate of the genetic correlation between the two sport disciplines, no extra benefit is to be expected from definition of a combined breeding goal. Genetic evaluations in both disciplines will be improved by inclusion of traits from studbook entry inspection because of favourable genetic correlations to both breeding goals. Genetic parameters of traits scored at the studbook entry inspection were similar in the two subpopulations and genetic evaluation of these traits can be performed simultaneously. Entirely separated breeding programmes for both disciplines are therefore not advisable. Constructing separate selection indexes would allow for optimal weighting of information sources such as studbook entry traits in accordance to the breeding goal of each sports discipline.

Sammendrag

Sammendrag

Formålet med denne afhandling er at belyse effekten af den specialisering hen mod dressur eller ridebanespringning der har pågået indenfor heste, samt fremskaffe viden for forbedring af det avlsarbejde, som gennemføres af KWPN (Royal Dutch Sport Horse), med hensyntagende til denne specialisering.

Materialet til afhandlingen er fra KWPN og består af afstammingsinformationer, resultater fra 1. kåring, hvor hestene er kåret enten for dressur eller spring, samt konkurrenceresultater fra enten dressur eller ridebanespringning. Første del belyser hvordan specialisering har påvirketslægtskabet mellem individer fra de to linjer. Resultaterne viser at slægtskabet mellem individer fra de to linjer reduceres over tid og er i de seneste år meget lav, mens der er en tydelig stigning i slægtskabet indenfor linjerne. Samtidig er der en markant reduktion i antallet af individer med mange efterkommere som har afkom i begge linjer. Anden del omfatter analyser af hvorvidt specialiseringen for enten dressur eller spring har påvirket genetiske parametre, så som heritabiliteter for og genetiske korrelationer mellem egenskaber registreret ved 1. kåring, hvor der i princippet er tale om samme egenskab, men hesten er tilmeldt kåringen som dressur- eller springhest. Analyserne blev gennemført ved hjælp af et antal bi-variate analyser, hvor samme egenskab bedømt ved kåring som dressurhest eller springhest, blev betragtet som forskellige egenskaber. Resultaterne indikerer at specialiseringen har medført ændringer i egenskabernes niveau for de to linjer, men de beregnede heritabiliteter var ikke signifikant forskellige mellem de to linjer, ligesom de genetiske korrelationer mellem samme kåringsegenskab ikke var signifikant forskellige fra 1.0. Tredje del omhandler vurdering af modeller til at analysere konkurrenceresultater fra dressur og ridebanespringning. Resultaterne viser at konkurrence præstationer indenfor dressur og ridebanespringning er arvbar ($h^2 \sim 0.11-0.13$) og at det er vigtigt at tage hensyn til effekten af rytter. Til sidst blev den genetiske sammenhæng mellem konkurrence præstationer hos dressur og springheste, samt egenskaber bedømt ved kåring tidligere i hestens liv beregnet. Resultaterne viste at sammenhængen mellem konkurrence resultater var ugunstig (-0.12). Analyse af udviklingen i den genetiske korrelation over tid viser en stadig øgning i den ugunstige genetiske korrelation. Den stigende negative genetiske korrelation mellem konkurrencedisciplinerne medfører ikke ændringer i de genetiske korrelationer mellem konkurrenceresultater og egenskaber registreret ved 1. kåring.

Sammendrag

Fra denne afhandling kan det konkluderes at der ikke kan forventes en ekstra fordel ved at definere et kombineret avlsmål. Dog er en strikt separering af avlsprogrammerne ikke tilrådelig. Separate selektionsindeks for de to discipliner vil tillade optimal vægtning af de ulige informationskilder, som f.eks. kåringsresultater, der understøtter avlsmålet for de to discipliner.

Samenvatting

Samenvatting

Het fokken van sportpaarden maakt de laatste decennia een verandering door van fokkerij van een veelzijdigheidspaar naar fokkerij van een paard specifiek voor springsport, dan wel voor dressuursport.

Doelstelling van dit proefschrift is beschrijving van de effecten van specialisatie en het verschaffen van de benodigde kennis om de fokkerij van sportpaarden, zoals uitgevoerd door KWPN (Koninklijk Warmbloed Paardenstamboek Nederland) te verbeteren.

Het materiaal is afkomstig van KWPN en bestaat uit keuringsresultaten van eerste bezichtigingen en stamboekopnames, alsmede competitiestanden van dressuur- en springpaarden.

In hoofdstuk 2 is de genetische relatie tussen beide selectierichtingen in de loop van de tijd geanalyseerd. De analyse is gebaseerd op de afstammingsgegevens van paarden die hebben deelgenomen aan de stamboekkeuringen. De resultaten wijzen uit dat de gemiddelde verwantschap tussen de twee selectielijnen gedaald gedurende de onderzochte periode, terwijl de gemiddelde verwantschap binnen de selectielijnen is toegenomen. Bovendien zijn het juist de vaders met veel nakomelingen in een selectierichting, die geen nakomelingen in de andere selectierichting hebben.

In hoofdstuk 3 is onderzocht in hoeverre specialisatie heeft geleid tot verandering in erfelijkheidsgraden van en genetische correlaties tussen kenmerken van stamboekkeuringen. In principe zijn het dezelfde kenmerken, maar gemeten aan paarden die als dressuur- of als springpaard zijn ingeschreven. Voor deze studie zijn een aantal bivariate analyses uitgevoerd, waarbij hetzelfde kenmerk bepaald aan een springpaard als een ander kenmerk wordt beschouwd dan gemeten aan een dressuurpaard. Uit de analyses is gebleken dat als gevolg van specialisatie het gemiddelde is gaan verschillen voor een deel van de kenmerken. De erfelijkheidsgraden verschilden echter niet en evenmin weken de genetische correlaties tussen de keuringskenmerk niet af van 1.

In hoofdstuk 4 zijn competitiestanden geanalyseerd om inzicht te verschaffen in hoeverre in de genetische evaluatierekening moet worden gehouden met ruitereffecten, met censoring van data en met voorselectie. De effecten van censoring van data en voorselectie waren gering op de genetische evaluatie. Resultaten lieten zien dat het van belang is om in de genetische evaluatie rekening te houden met effect van ruiter. Vervolgens zijn verschillende methodes van correctie voor ruitereffect bedacht en vergeleken op criteria als goodness-of-fit van het model en voorspellend vermogen. Een fixed effect waarbij de ruiter is

ingedeeld op basis van zijn of haar competitieniveau en het aantal gereden wedstrijden was de beste correctiemethode in genetische evaluatie van competitiestanden.

In hoofdstuk 5 zijn genetische correlaties geschat tussen competitiestanden van springen en dressuur, alsmede de genetische correlaties met kenmerken van stamboekkeuringen. De genetische correlatie tussen dressuur- en springcompetitie was zwak en ongunstig (-0.12). Verdere analyse naar het verloop van deze correlatie in de tijd toonde aan dat deze sterker ongunstig werd in de onderzochte periode. De ongunstige correlatie werd versterkt doorpaarden die in beide disciplines uitkwamen. Gedurende de onderzochte periode was er geen duidelijke verandering in de genetische correlaties tussen de competitiekenmerken en de kenmerken van de stamboekkeuringen.

Hoofdstuk 6 bevat de algemene discussie van het proefschrift. Het fokdoelkenmerk competitiestand is nader bediscussieerd en mogelijke verbeteringen zijn besproken. Voorts zijn de bevindingen van dit proefschrift in het licht van specialisatie bediscussieerd en zijn aanbevelingen voor een fokprogramma onder specialisatie gegeven.

List of publications

Peered reviewed papers

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Training and education

Training and education



The basic package (8 ECTS)

Welcome to the EGS-ABG (Ethics on animal breeding)	2011
WIAS Introduction Course	2012
Summer Research School EGS-ABG Aarhus/Denmark	2012
Summer Research School EGS-ABG ILRI/Ethiopia	2013

Scientific exposure (11 ECTS)

International conferences

62th EAAP Annual Meeting, Stanvanger, Norway	2011
63 th EAAP Annual Meeting, Bratislava, Slovak Republic	2012
64 th EAAP Annual Meeting, Nantes, France	2013
10 th WCGALP, Vancouver, Canada	2014

Seminars and workshops

Seminar: "Healthy as a (sport) horse"	2011
Wageningen Institute for Animal Science (WIAS) Science Day	2012-13
Opening Symposium of GENSAP (Denmark)	2013
2nd Annual Meeting of GENSAP (Denmark)	2014

Presentations

63 th EAAP Annual Meeting, Bratislava, Slovak Republic (poster)	2012
Opening Symposium of GENSAP (Denmark) (poster)	2013
64 th EAAP Annual Meeting, Nantes, France (poster)	2013
10 th WCGALP, Vancouver, Canada (oral)	2014

In-depth studies (19 ECTS)

Disciplinary and interdisciplinary courses

Statistical Learning Methods For DNA-based Prediction Of Complex Traits	2011
Genomic selection in livestock	2011
Advanced methods and algorithms in animal breeding with focus on genomic selection	2012
Breeding plans for sustainable animal breeding	2013

Training and education

Advanced statistics courses

Statistics for the Life Science 2012

PhD students' discussion groups

Quantitative genetics discussion group 2011-15

R users group 2011-12

Fortran user group 2011-12

MSc level courses

Genetic Improvement on Livestock 2011

Professional Skills Support Courses (6 ECTS)

Techniques for Writing and Presenting a Scientific Paper 2012

Project and time management 2012

Competence Assessment 2012

Academic English 2014

Research Skills Training (4 ECTS)

Introduction to R for statistical analysis 2011

Getting started in ASReml 2012

QGG Research Skills 2014

External training period: Aarhus University, Denmark 2013-14

Management Skills Training (1 ECTS)

Membership of boards and committees

Reviewer in Research Master Cluster 2011

Education and Training Total 48 ECTS

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Gabriel Rovere
Wageningen, February 2016

Colophon

Colophon

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