Relevance of test information in horse breeding

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Abstract

The aims of this study were 1) to determine the role of test results of young horses in selection for sport performance, 2) to assess the genetic diversity of a closed horse breed and 3) the consequences of inbreeding for male reproduction. The study was performed using existing databases containing records collected on young horses during inspections, which were linked to databases containing records on sport performance. Multivariate animal models were applied in estimation of genetic parameters. Heritability estimates of movement and free-jumping traits collected at Studbook Entry and at First Stallion Inspection were moderate to high. Free-jumping traits collected at both inspections showed high to very high positive genetic correlations to show-jumping in competition. Movement traits collected at both inspections showed favourably genetic correlations to dressage in competition.

Subsequently, the effect of limb and foot conformation, in particular the trait uneven feet, as assessed at Studbook Entry Inspection on performance and length of sport career have been analysed. Limb and foot conformation had only weak to moderate genetic correlation to sport performance. Some foot conformation traits could be identified as risk factors for early retirement from sports; e.g. occurrence of uneven feet shortened the competitive life at elite level of jumping.

The development of genetic diversity in a closed breed have been studied using the pedigree structure of the Friesian horse breed. Considerable loss of genetic diversity have taken place during the history of the studbook, corresponding to an average inbreeding rate of 1.3% per generation. Loss of genetic diversity was mainly due to drift from small effective population size during several generations. In a subsequent analysis the relation of inbreeding with semen quality of young Friesian stallions was investigated. It was concluded that low semen quality in Friesian stallions could not be attributed to inbreeding. Heritability estimates for semen quality traits were moderate to high and had substantial variation. Selection can be used to improve semen quality.

Finally, opportunities for improvement of the breeding program have been discussed. Selection potentials are calculated to gain insight in the relative importance of each of the young horse tests to the breeding program. Additional opportunities to increase selection response have been discussed.

Contents

1

General Introduction

General Introduction

The horse was domesticated about 6000 years ago somewhere in what we now know as southern Russia, Kazakhstan, Ukraine and Romania. Since then, horses have played an important role in the history of human societies due to their impact on e.g. warfare, transportation and agriculture. In most countries, agricultural mechanization led to a rapid decline in the number of horses shortly after the Second World War. Due to the popularity of using horses for sports and leisure their numbers have increased dramatically in recent years. At present in the Netherlands 885,000 people are active in equestrian sports, which makes it the 2nd largest sport activity. The economic turnover of the horse sector in The Netherlands is estimated to amount 1,5 billion Euro (Rijksen et al., 2005) which is about the same order of magnitude as the poultry sector.

Horses are kept for a large variety of purposes, ranging from simple companionship to highly intensive performance in top sport. The demands of the owner with respect to the characteristics of the horse will vary accordingly, which might lead to preference for a particular breed. Breeding goals might also vary widely between breeds: for some breeds there might be more emphasis on preservation of the breed whereas for others conformation and functionality are more important. For sport horses the breeding goal comprises performance in dressage or show jumping at a high level in competition. The intensification of equestrian sports demands a constant improvement of athletic ability of modern sport horses and breeding is one of the options to improve the ability of horses.

Predicting sports performance

Selective breeding of horses has a number of characteristics which clearly distinguish it from breeding in other livestock species. Most importantly the trait of interest is the result of the ability of the horse in combination with years of intensive training. In breeding interest is in the genetic ability of the horse and therefore “nature and nurture” need to be disentangled. The majority of the horses are kept in small studs of one or a few horses and there is large variation in rearing and training among studs. The owner decides, depending upon his ambition and professionalism, what level of management and training a horse will receive during its rearing. Training of sport horses is very expensive and therefore only a fraction of the young horses, which are according to the owners’ expertise most promising, will be selected to undergo such an intensive training program. The consequence for breeding evaluation is that the traits are realised under highly variable conditions and “nature and nurture” are hard to disentangle or sometimes completely confounded. Therefore, breeding values cannot be estimated very accurately solely based on the sport career of the selection candidate. Based on the performance measured on a large number of progeny, accurate estimates of breeding values can be obtained. However, progeny testing all potential breeding stallions would require a far too large testing population. Therefore, a multi stage selection program is commonly used in which stallions are preselected based on traits that are related to the breeding goal. In the stallion breeding program of the Dutch Warmblood Riding Horse Association (KWPN) the Station Performance Test is such a selection stage. Huizinga (1989) indicated that traits measured during the Station Performance Test have a genetic basis and are genetically related to traits in the breeding goal. Therefore, this selection stage will contribute to the genetic progress of the breeding program (Huizinga, 1990). Station Performance Tests are very expensive and alternative traits might provide information about breeding goal traits at lower cost.

Early predictor of longevity

A successful sport career does not only concern top level performance, but also the duration of the sport career. Early retirement from sport will not only reduce returns on the investments but it often has also emotional consequences. The complexity of information available for estimating breeding values is even more profound when selection is for a long sport career. In that respect availability of traits measured early in life related to longevity would be extremely valuable, both with respect to deciding whether a horse will enrol in a training program, as well as with respect to breeding for longevity.

Genetic diversity

Most sport horses belong to the warmblood breed with one or more studbooks represented in a country. Worldwide, the majority of warmblood studbooks are concentrated in Europe. Breeding programs are conducted within warmblood studbooks, but under certain conditions exchange of genetic material among certified studbooks is allowed. Warmblood studbooks are therefore considered to have an open structure, as opposed to the strictly closed status of distinct horse breeds like the Friesian horse.

All Friesian horses are registered in one central studbook which is also responsible for the breeding program of the breed. The studbook has been closed for many generations, resulting in a horse with unique characteristics. On the other hand the closed status has inevitably led to accumulation of inbreeding. We can learn about the current inbreeding status of the Friesian horse breed, how it came about, and what are the main factors. Based on this information we can learn lessons for the future: how to genetically manage the population such that inbreeding is restricted and thus the loss of genetic diversity.

Aim and outline of the thesis

The objective of this study is to determine the role of traits measured on young horses in breeding sport horses, describe the genetic diversity of a closed horse breed, identify factors contributing to the loss of genetic diversity and the consequences thereof for reproductive characteristics.

Breeding programs for sports horses might benefit from including information collected at a young age. In Chapter 2 and 3 a genetic analysis is performed for traits collected during the First Stallion Inspection and the Studbook Entry Inspection.

Chapter 4 describes the relationship of limb conformation and feet conformation with sport performance, and in chapter 5 it is determined whether feet and limb conformation scores are risk factors for early retirement from sport.

The genetic diversity of the closed Friesian horse is described in chapter 6. Whether inbreeding is related to semen quality in the Friesian horse is described chapter 7.
Finally the opportunities for improving the breeding scheme for sports horses is dealt with in the General Discussion]

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2

Genetic relations of movement and free-jumping traits with dressage and show-jumping performance in competition of dutch warmblood horses

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Abstract

Genetic parameters for traits evaluated at the studbook entry inspection and genetic correlations with dressage and show-jumping performance in competition were estimated. Data comprised 36,649 Warmblood horses that entered the studbook between 1992-2002. The genetic analyses were performed using univariate and bivariate animal models. Heritabilities of the studbook entry traits were estimated in the range 0.15-0.40. The movement traits showed moderate to strong mutual genetic correlations, whereas the genetic correlations of movement traits with free-jumping traits were weak to moderate. The free-jumping traits showed strong to very strong mutual genetic correlations.

Competition results of 33,459 horses with performance in dressage and 30,474 horse with performance in show-jumping were linked to the studbook entry data to estimate the genetic relationship with performance in competition. Heritability estimates for dressage and show-jumping were 0.14. Genetic correlations of the movement traits with dressage were moderate to strong, and with show-jumping weak to moderate. Genetic correlations of the free jumping traits with dressage were weak to moderate and unfavourable. The free jumping traits were genetically strongly to very strongly correlated to show-jumping. It was concluded that a selection of the traits evaluated at the studbook entry inspection will favourably contribute to estimation of breeding values for sport performance.

Key words: Horse, Heritability, Movement, Free jumping, Dressage

2.1 Introduction

Many breeding organisations for sport horses want to improve performance in dressage and show-jumping competition by genetic selection (Koenen et al., 2004). Direct selection for performance using only highest results in regular competition is not efficient, for several reasons. First, results in high-level competitions can be recorded only at older ages (>8 years), which prolongs the generation interval. Second, heritabilities of high-level competition traits are generally low, ranging from 0.10 to 0.25 (Ricard et al., 2000), partly due to influence of rider (Brockmann and Bruns, 2000). A low heritability means that breeding values become reliable only if large numbers of offspring are tested.

Instead of using competition results at older ages, many breeding organisations use test results of young horses as predictors of the genetic ability to perform in sport competition. These tests concern either age-class competitions, specifically meant to collect performance data of young horses, or performance tests. Compared to regular competitions, the genetic parameters of young horse competitions are considerably higher (Brockmann and Bruns, 2000; Lührs-Behnke et al., 2006) and Brockmann and Bruns (2000) also concluded that advanced competitions could be used in breeding program. Performance tests of young horses generally can be divided into station performance tests and field performance tests. Station tests consist of uniform testing and training of the horses with intermediate and final judging by a trainer and a rider. Station tests usually last about 1 to 3 months, whereas field tests usually last one day and are one-time judgments of the horse. The traits that are judged at both station and field tests concern conformation, basic gaits, and riding and jumping ability. A recent review (Thorén Hellsten et al., 2006) showed that traits recorded at young horse competitions or performance tests, have moderate heritabilities and high genetic correlations with results at regular competitions, which makes them valuable information sources for indirect selection. The relevance of testing young horses in a breeding programme is maximised if large proportions of unselected young horses are routinely tested. In practice, however, the high cost of testing young horses limits the testing capacity.

In particular, the intensive station tests for stallions contain only a small proportion of highly- selected, candidate breeding stallions. The information provided by testing young horses to estimate breeding values of their parents, therefore, is limited.

In the breeding programme of the Royal Dutch Warmblood Studbook (KWPN) a large proportion of young horses is routinely inspected at studbook entry. Eligibility for entry into the studbook is, amongst others, based on judgement of conformation and movement. For judgement a number of traits, related to conformation and movement, are scored and since 1989, a descriptive system has been used. The inspection results from the studbook entry may serve as genetic predictors for later performance, as the young horse tests are used. The efficiency of indirect selection on studbook-entry traits depends on the genetic variation of these traits and on their genetic correlations with performance in competition. A first analysis (Koenen et al., 1995) showed that heritabilities of studbook-entry traits were moderate but most genetic correlations of conformation with performance were low. With the increasing interest in sport performance, KWPN has extended the studbook entry inspection with free-jumping and movement traits that may have a stronger relation with sport performance. It is not known to what extent movement and free-jumping traits can efficiently be used as genetic predictors of later performance. The objectives of this study were to estimate the heritabilities of movement and free-jumping traits recorded at the studbook entry and to estimate genetic correlations of these traits with performance in dressage and show jumping competition.

2.2 Material and Methods

Data of studbook entry

At studbook entry, two different types of traits are recorded: descriptive and subjective (Table 2.1). Descriptive traits are scored on a scale (1 to 40) that reflects the biological range in the population. For a specific trait, the scale compares a horse relative to the population extremes, irrespective of what is desired. The score of 20 reflects the average of the population. For most descriptive traits, the scale is defined such that a score below 20 is favourable, although extreme values are undesired.

Table 2.1 The descriptive and subjective traits of the studbook entry with definition of the extremes of the scoring scale.

	score -40	**score -1**
Descriptive traits		
Walk[a]		
- Correctness	toed out	toed in
- Stride (length)	short	long
- Elasticity	stiff	supple
Trot[a]		
- Stride (length)	short	long
- Elasticity	stiff	supple
- Impulsion	weak	powerful
- Carriage[b]	on forehand	carrying
Canter[c]		
- Stride (length)	short	long
- Impulsion	weak	powerful
- Carriage	on forehand	carrying
Free-Jumping[d]		
- Take-off: direction	forwards	upwards
- Take-off: speed	slow	fast
- Technique: foreleg	stretched	bend
- Technique: back	hollow	rounded
- Technique: haunches	tight	open
- Scope	little	much
- Elasticity	stiff	supple
- Care	reckless	careful
Subjective Traits[e]	**score 40**	**score 100**
Conformation	bad	good
Movement	bad	good
Jumping[f]	bad	good

[a] n = 36,110, except for walk which has not been scored after 1995
[b] The trait carriage of trot was introduced in 1996 (n = 21,499)
[c] n = 12,804; scored since 1998
[d] n = 8,378; scored since 1998
[e] n = 33,251
[f] n = 8,809; scored since 1998

Descriptive scores were multiplied by -1 to facilitate the interpretation of correlations.

Subjective traits are scored on a scale (40=very bad to 100=excellent, by 1), for which the maximum reflects the ideal level for that trait. The subjective traits movement, conformation and free-jumping are scored on a subjective scale. Free jumping is judged during jumping over three fences in an indoor arena.

Competition data

For a horse in sport competition, results are recorded by the equestrian sport organisation as the highest classification ever achieved by the horse. The organisation uses codes to represent the level at which the horse is performing, in either dressage or show-jumping, and to represent the total “winning points” the horse has gained at that level. In dressage, a horse will gain 3 winning points when the score by the jury of the trial is more than 70% (of 100%), 2 winning points when the score is 65-70%, and 1 winning point when the score is 60–65%. Promotion to the next level of competition is permitted with 10 winning points and is compulsory with 30 winning points. In show-jumping, a horse will gain 2 winning points when it has performed faultless and 1 winning point when not more than one fault has been made in a jumping track. Promotion to the next level of competition is permitted with 10 winning points and is compulsory with 20 winning points.

For analysis, the classification scores were transformed to linear scores (Huizinga and Van der Meij, 1989), using square-root transformation to achieve a more normally distributed error term. This procedure is in accordance with the protocol used in the routine breeding value estimation.

Data collection

The dataset contained the studbook entries held from 1992 through 2002. Scores on 39,649 horses were recorded, in combination with information about their age, classifier, date and place of classification, pedigree, percentage of thoroughbred and sex. When a horse was judged more than once (780 cases), only the first record was taken. The age at judging was from 3 through 7 years, which resulted in exclusion of 2,439 records.

Table 2.2 Number of studbook-entry records by year, and (from 1998 onwards) number of records with free-jumping records.

year	records	year	records	records with free jumping
1992	3435	1998	3000	1864
1993	3505	1999	3096	1597
1994	3467	2000	3175	1980
1995	3743	2001	3209	1946
1996	4127	2002	2281	1419
1997	3303			

A total of 292 records were excluded from the analysis because either classifier was unknown or had inspected fewer than 50 horses or fewer than 10 records were recorded at that location.

Records were also deleted when birth date was unknown (28 cases).The final dataset contained 36,110 horses descending from 1310 sires. Canter and jumping traits have been scored since 1998 and fewer records were available from these traits (Table 2.1). Inspection of jumping traits was not compulsory and the owner of the horse decided on participation. Number of horses participating each complete year ranged between 3000 and 4127, while the year 2002 contained fewer observations because not all records were collected at the supply of the data (Table 2.2). The majority of the participating horses were female (more than 80%).

Competition results were available on 33,459 horses that participated in dressage and on 30,474 horses that participated in show jumping from 1981 through 2002. Of all horses judged at studbook entry, about 33% had participated in dressage competition and about 24% in show-jumping. Of all horses scored for free-jumping, about 20% had participated in dressage competition and about 24% in show-jumping (Table 2.3).

Genetic analysis

To account for heterogeneous variation among classifiers and years, descriptive scores were standardised to a standard deviation of 4 within classifier and year groups. Subjective traits were standardised to a standard deviation of 6 within classifier and year groups.

Table 2.3 Number of horses with studbook entry records (without or with free-jumping) that participated in competition (dressage or show-jumping).

		Competition	
	n	Dressage	Show-jumping
without free-jumping	27,301	11,916	8,666
with free-jumping	8,809	1,676	2,011
studbook entry	36,110	13,592	10,677

The age of the horse is believed to affect the score, because young horses are not fully grown and possibly lack the power and balance of older horses. This age effect might differ with sex and therefore a combined effect of age and sex is included into the models.

Genetic parameters of the traits recorded at the studbook entry were estimated using the model:

$$Y_{ijkm} = \mu + agesex_i + classifier_j + placedate_k + animal_m + e_{ijkm}$$

where Y_{ijkm} is the observed score for each subjective (conformation, movement and free jumping) and descriptive trait (walk-stride,…,care) for the ith animal; μ is the population mean; $agesex_i$ is the fixed effect of the ith combination of age (3 to 7 years) and sex (mares, stallions, geldings) (i = 1,..,15); $classifier_j$ is the fixed effect of the jth classifier (j=1,…,21); $placedate_k$ is the fixed effect of the kth combination of place (23 places) and date (j = 1,…,1117) of the animal tested; $animal_m$ is the random effect of the mth animal ~ N(0, $A\sigma^2a$); and e_{ijkm} is the random ~N(0, $I\sigma^2e$) residual term.

Genetic parameters of competition data were estimated using the model of Ducro et al. (2002):

$$Y_{ij} = \mu + agesex_i + animal_j + e_{ij}$$

where Y_{ij} is the observed competition performance (dressage, show jumping) on the jth animal; μ is the population mean; $agesex_i$ is the fixed effect of the ith combination of age (4 yr,…, ≥10 yr) and sex (mares, stallions, geldings); $animal_j$ is the random effect of the jth animal ~ N(0, $A\sigma^2a$) and e_{ij} is the random residual term ~N(0, $I\sigma^2e$).

Genetic parameters and their standard errors were estimated using the ASReml software package (Gilmour et al., 2002). Estimated heritabilities were derived from univariate analyses. Genetic and phenotypic correlations were estimated in bivariate analyses using starting values for the variances from the univariate analyses. The pedigree of each horse with an observation was traced back three generations. In total, the pedigree comprised 132,429 individuals. Genetic groups were included in the pedigree to adjust for the percentage of thoroughbred.

Correlations with performance traits were estimated in bivariate analyses including one studbook entry trait and one performance trait (dressage or show-jumping).

2.3 Results

Means and heritabilities

Means and standard deviations of descriptive and subjective traits are in table 2.4. Means ranged from -22.1 to -19.6 for descriptive traits and from 62.2 to 67.5 for subjective traits. The fixed effects (agesex, classifier and placedate) included in the model were significant for all traits. The range in effects of agesex varied with trait; of descriptive traits canter and free-jumping traits had ranges of 2 and more. The ranges of trot and walk traits were below 2, except for elasticity of walk. The subjective traits conformation and movement had lower ranges, relative to the mean score for these traits, than the descriptive traits. The subjective trait of jumping showed a relative larger range of the agesex effect.

Heritability estimates of most descriptive traits varied from 0.19 (carriage of canter) to 0.32 (care of free-jumping and stride of trot) (Table 2.4). Heritability estimates for stride and elasticity of walk were below this range, whereas the estimate for scope of free-jumping was slightly above this range. The subjective traits conformation and movement showed similar heritability estimates; about 0.33, and the estimate for free-jumping was 0.40.

Table 2.4. Mean of the traits of the studbook entry, the maximum difference between levels of the agesex effect (mdiff_agesex) and the genetic standard deviation (σ_a) and heritability (h^2) estimates after standardisation.

Traits	mean	Mdiff agesex	σ_a	h^2
Walk				
Correctness	-19.6	1.76	1.97	0.25[a)]
Stride	-19.6	1.62	1.55	0.16
Elasticity	-20.2	3.01	1.51	0.15
Trot				
Stride	-20.1	1.55	2.18	0.32
Elasticity	-21.1	1.93	2.09	0.29
Impulsion	-21.9	1.49	2.02	0.27
Carriage	-21.8	1.94	2.01	0.28
Canter				
Stride	-20.7	2.69	1.90	0.25
Impulsion	-21.1	2.39	1.67	0.20
Carriage	-22.1	3.16	1.68	0.19
Free-Jumping				
Take-off: direction	-21.3	2.35	2.07	0.30
Take-off: speed	-20.3	2.41	1.80	0.22
Technique: foreleg	-20.6	2.30	1.81	0.22
Technique: back	-21.3	2.79	2.10	0.31
Technique: haunches	-21.3	3.25	1.97	0.27
Scope	-20.4	2.30	2.30	0.37
Elasticity	-21.9	3.37	1.86	0.24
Care	-19.6	2.29	2.13	0.32
Subjective Traits				
Conformation	67.5	3.77	3.32	0.33
Movement	66.9	2.64	3.39	0.34
Jumping	62.2	6.21	3.63	0.40

a) Standard errors of the heritability estimates were all below 0.04.

Table 2.5. Genetic (below diagonal) and phenotypic (above diagonal) correlations of descriptive traits related to free jumping at studbook entry.

		Take-off		Technique			Overall		
		scope	speed	Haun-ches	Fore-leg	back	impulse	Elasti-city	care
Take-off	scope	--	0.53[a]	0.48	0.38	0.52	0.52	0.48	0.60
	speed	0.66	--	0.33	0.44	0.30	0.30	0.51	0.51
Technique	haunches	0.84	0.57	--	0.33	0.54	0.63	0.65	0.47
	foreleg	0.76	0.75	0.66	--	0.36	0.26	0.44	0.45
	back	0.76	0.45	0.81	0.69	--	0.43	0.53	0.43
Overall	impulsion	0.84	0.57	0.92	0.66	0.72	--	0.53	0.48
	elasticity	0.79	0.78	0.82	0.78	0.82	0.72	--	0.57
	care	0.93	0.83	0.82	0.88	0.73	0.81	0.90	--

[a] Standard errors ranged from 0.03-0.09 for the genetic correlations and 0.01-0.04 for the phenotypic correlations.

Genetic correlations among the studbook entry traits

Detail traits of free-jumping all showed favourable genetic correlations (table 2.5). Genetic correlations between descriptive and subjective traits are in table 2.6. Descriptive traits of walk, trot and canter all had a favourable genetic correlation (higher than 0.63) to subjective traits of movement and conformation, except for correctness of walk. In particular, trot traits were highly correlated with movement. Correctness of walk was poorly related to any other trait of the studbook entry. Genetic correlations of the descriptive traits of trot and walk with jumping were near zero. Canter traits, however, showed moderate genetic correlations with jumping.

Descriptive traits of free-jumping showed low correlations with the subjective traits conformation and movement; most were near zero (Table 2.6). Elasticity of free-jumping was an exception, about 0.22. Genetic correlations of free-jumping traits with the subjective trait of jumping were strong to very strong correlated (correlations higher than 0.73, Table 2.6). Free-jumping traits were favourably correlated to each other; about 0.77

Table 2.6. Phenotypic (r_p) and genetic correlations (r_g) between descriptive traits of movement and the subjective traits.

Traits	Conformation		Movement		Jumping	
	r_g[a]	r_p	r_g	r_p	r_g	r_p
Walk						
Correctness	-0.04	-0.02	-0.06	-0.01	-0.02	-0.01
Stride	0.63	0.28	0.67	0.35	-0.09	0.03
Elasticity	0.77	0.38	0.82	0.49	0.01	-0.01
Trot						
Stride	0.71	0.40	0.93	0.63	-0.07	0.07
Elasticity	0.78	0.45	0.97	0.77	-0.00	0.15
Impulsion	0.73	0.46	0.96	0.67	0.05	0.14
Carriage	0.76	0.49	0.96	0.70	-0.10	0.11
Canter						
Stride	0.68	0.39	0.72	0.56	0.23	0.18
Impulsion	0.64	0.43	0.77	0.66	0.39	0.26
Carriage	0.75	0.43	0.85	0.65	0.16	0.21
Free-Jumping						
Take-off: direction	0.04	0.10	-0.02	0.14	0.92	0.61
Take-off: speed	-0.01	0.11	-0.00	0.19	0.73	0.46
Technique: foreleg	0.09	0.10	-0.01	0.12	0.84	0.47
Technique: back	0.17	0.12	0.07	0.11	0.77	0.56
Technique: haunches	0.07	0.08	0.04	0.14	0.91	0.61
Scope	0.09	0.15	0.04	0.20	0.92	0.60
Elasticity	0.23	0.20	0.21	0.28	0.84	0.61
Care	0.13	0.11	0.01	0.16	0.93	0.61
Subjective Traits						
Conformation	--	--	0.82	0.59	0.13	0.17
Movement			--	--	0.02	0.20
Jumping					--	--

[a] standard errors of the genetic correlations were below 0.10.

Among subjective traits of the studbook entry, the genetic correlation between movement and conformation was 0.82, whereas jumping only showed low correlations of 0.13 with conformation and 0.02 with movement.

Table 2.7. Genetic (r_g) and phenotypic (r_p) correlations of descriptive and subjective traits of studbook entry with dressage and show-jumping.

	Dressage		Show-Jumping	
	r_g [a)]	r_p	r_g	r_p
Walk				
- Correctness	0.05	0.00	0.06	-0.00
- Stride	0.53	0.12	0.04	-0.00
- Elasticity	0.50	0.12	0.14	0.01
Trot				
- Stride	0.65	0.19	0.11	0.02
- Elasticity	0.67	0.18	0.13	0.02
- Impulsion	0.59	0.18	0.11	0.02
- Carriage	0.65	0.19	0.14	0.01
Canter				
- Stride	0.49	0.14	0.33	0.05
- Impulsion	0.40	0.13	0.43	0.07
- Carriage	0.50	0.14	0.28	0.03
Free-Jumping				
- Take-off: direction	-0.34	-0.03	0.88	0.16
- Take-off: speed	-0.27	-0.02	0.53	0.10
- Technique: foreleg	-0.20	0.02	0.67	0.11
- Technique: back	-0.19	0.02	0.52	0.11
- Technique: haunches	-0.27	0.05	0.80	0.13
- Scope	-0.24	-0.03	0.82	0.14
- Elasticity	-0.09	0.01	0.64	0.11
- Care	-0.29	-0.00	0.80	0.14
Subjective Traits				
- Conformation	0.67	0.19	0.29	0.04
- Movement	0.69	0.21	0.23	0.03
- Jumping	-0.24	-0.01	0.87	0.16

a) Standard errors ranged from 0.03-0.09 for the genetic correlations and 0.01-0.04 for the phenotypic correlations.

Genetic correlations with sport

The estimated heritabilities of the sport traits dressage and show-jumping were 0.14 with a standard error of 0.02.

Genetic correlations of the descriptive traits (walk, trot and canter) with dressage were favourable, ranging generally from 0.40 for impulsion of canter to 0.67 for elasticity of trot (Table 2.7), except for the genetic correlation of the correctness of walk with dressage (0.05). The descriptive traits of the gaits were also favourably correlated with show-jumping: correlations of the canter traits were moderate and of the other gaits were low.

Genetic correlations of free-jumping traits with dressage were (about -0.24) moderate and unfavourable in most cases. Genetic correlations of free-jumping traits with show-jumping were strong: all estimates exceeded 0.52, and four traits had estimates of 0.80 and above.

The subjective traits conformation and movement showed high correlations to performance in dressage (about 0.68) and moderate correlations (about 0.26) to performance in show-jumping. The subjective trait jumping was highly correlated with show-jumping (0.87), but was moderate and unfavourable with dressage (-0.24).

2.4 Discussion

Heritabilities

The heritabilities for descriptive traits of walk and trot were higher than those reported by Koenen et al. (1995). Ducro et al. (2002) estimated heritabilities on similar jumping and movement traits from the First Stallion Inspection (FSI), a one-day field test for stallions. The estimates from the current study were slightly lower, but still in good agreement with the results of that study. The higher values of the FSI could be due to a lower environmental variance in the traits, since the FSI test is conducted at one location and by one team of judges, whereas the studbook entry inspections were conducted at different locations and judged by different teams of judges.

Comparing the subjective traits to the traits recorded at young horse tests (Thorén Hellsten et al., 2006), heritabilities from the studbook entry were generally at the lower end of the range. Wallin et al. (2003) studied field performance tests for mares and their analysis resulted in similar heritabilities for conformation. Their heritabilities for gaits, canter and trot were lower than our heritabilities, canter and trot.

Free-jumping, as analysed in our study, showed a heritability (0.40) similar to several German studies (Bösch et al., 2000 Brockmann, 1998) and was higher than jumping under rider in field performance test (Wallin et al., 2003) or in competition. The effect of training and rider probably causes the disturbance and can not be adjusted for.

Heritabilities for sport traits were moderately low and in the range found in literature (Ricard et al., 2000; Schade, 1996). As indicated by several studies, high estimates from regular competitions should not be expected, because effect of the rider on performance of the horse can hardly be accounted for.

Correlations of studbook entry traits for jumping

The genetic correlations of descriptive free-jumping traits with the subjective trait jumping were high to very high (Table 2.6). In particular the traits direction at take-off, technique of haunches, scope and care appeared to be genetically similar to the subjective trait jumping. Inclusion of these traits into breeding seems to be questionable. Schade (1996) also reported high genetic correlation between traits of the free-jumping complex and suggested to use only the overall free-jumping score.

Correlations of studbook entry traits with dressage

The subjective traits conformation and movement showed high favourable correlations with performance in dressage (about 0.68) and moderate with performance in show-jumping (about 0.26). The correlation of movement with show-jumping is mainly due to the favourable contribution of the canter traits, since trot and walk had low (-0.14 to -0.04) correlations to show-jumping. Low genetic correlations of trot and walk to show-jumping were found by Uphaus (1993) and Lührs-Behnke et al. (2006). The genetic correlations of walk and trot with performance in dressage agree with estimates of Wallin (2003) and of Lührs-Behnke et al. (2006), except for correctness of walk. Correctness of walk, although heritable, apparently has no linear relationship to performance in sport. The correlations of walk and trot traits with dressage as estimated by Koenen et al. (1995) were much lower, although their heritabilities were comparable to the results of the current study.

Correlations of studbook entry traits with show-jumping

Jumping traits of studbook entry had strong to very strong favourable genetic correlations to show-jumping. Strong genetic correlations were found also in other studies (Van Veldhuizen, 1997; Wallin et al. 2003)

Jumping traits of studbook entry had unfavourable genetic correlations with dressage in competition. Correlations of movement traits with show-jumping, however, were favourable. In literature, correlations between gaits recorded at performance tests and show-jumping varied from negative (Huizinga et al., 1990) or zero (Uphaus, 1993) to positive (Wallin et al., 2003). Perhaps an unfavourable genetic correlation between jumping and dressage can not be estimated when traits are inspected under rider. Then the horse is already specifically trained in dressage or jumping performance.

Implications

Because estimates of heritabilities and genetic correlations are now available, traits recorded at studbook-entry can be used efficiently to estimate breeding values for dressage and show-jumping. In particular selection for jumping can benefit from these results, because of the high heritability (0.40) and the high genetic correlation (0.87) with show jumping. Selection on jumping traits of the studbook entry, however, will reduce the genetic progress in dressage, because of the unfavourable correlations. The size of the correlations, nevertheless, indicate that a combined selection for dressage and show-jumping is possible.

Another important advantage of using the results of the studbook entry inspection in estimating breeding values, has to do with the large number of horses participating in this inspection. Each year, approximately 3,500 horses attend the studbook entry. As a consequence, results of studbook entry inspection are less affected by preselection than results of field or station tests, in which about 500 mares and stallions are being tested. The advantages of field performance tests over station tests as mentioned by Thorén Hellsten et al. (2006) are therefore also relevant to inspections: inspections allow more horses to be tested, reduce testing costs, and lead to higher accuracies of estimated breeding values. Data from studbook entries cannot entirely replace information from performance tests, however, because other important aspects of horses such as character, willingness to learn and endurance also can be achieved from these tests. It is recommended, therefore, that practical genetic evaluations should consider various sources of information simultaneously.

2.5 Conclusions

The objective was to estimate the genetic parameters of movement and free-jumping traits recorded at studbook entry inspection and to estimate genetic correlations of these traits with performance in dressage and show-jumping competition. The traits had moderate to high heritabilities. Genetic correlations of gaits with performance in dressage were favourable. Gaits were also favourably correlated with show-jumping, though to a lesser degree. The jumping traits recorded at studbook entry were favourably correlated with show-jumping, but unfavourably correlated with performance in dressage.

The current genetic evaluation for sport performance is based on performance data only. Inclusion of a set of the traits recorded at studbook entry is expected to increase the quality of the procedures for genetic evaluation.

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3

Genetic relations of First Stallion Inspection traits with dressage and show jumping performance in competition of Dutch warmblood horses

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Abstract

Genetic parameters for traits evaluated at the First Stallion Inspection (FSI) and genetic correlations with dressage and show-jumping performance in competition were estimated. Data comprised 2,361 stallions with FSI-observations from 1994 through 1999. Genetic analyses were performed using univariate and bivariate animal models. Heritability estimates of the FSI-traits ranged from 0.25 to 0.61. FSI-traits related to gaits showed strong genetic correlations (above 0.70) and FSI-traits related to free jumping had correlations close to unity.

Competition results of 23,897 horses with performance in dressage and 22,811 horses with performance in show-jumping were linked to the FSI data to estimate the genetic relationship with performance in competition. Heritability estimates for dressage and show-jumping were 0.14. Genetic correlation between FSI-gaits and dressage in competition were positive, ranging from 0.37 to 0.72. Genetic correlation between FSI-jumping traits and show-jumping were all above 0.80. FSI-jumping traits showed negative correlations with dressage (about -0.48). FSI-gait traits showed negative correlations with show jumping, except for canter. It is concluded that selection at First Stallion Inspection comprises an important component of the stallion selection program, because FSI-traits have good genetic relationships with performance in competition and, due to the number of animals involved, relative high selection intensities can be achieved.

Key words: riding horse, heritability, stallion inspection, dressage, show jumping

3.1 Introduction

In the Royal Dutch Warmblood Riding Horse Studbook (KWPN), selection of stallions for breeding consists of several stages (Figure 3.1), starting with the decision of the owner to submit his young horse to the stallion inspection. During this inspection young stallions are assessed on correctness, conformation, movement and free jumping. After the inspection, the best stallions are selected to participate in the stallion performance test. Stallions that pass the performance test are allowed to breed and the final selection takes place when records of progeny become available.

The significance of the stallion performance test in the selection procedure has been demonstrated by Huizinga et al. (1991). However, the impact of selection during the stallion inspection, which is preceding the performance test, has often been neglected in the evaluation of breeding schemes. In terms of selection intensities, stallion inspection is more important than performance tests because many more animals participate in particular in the first phase of the stallion inspection (FSI), which is a one-day event (Figure 3.1). The inspection can contribute substantially to the efficiency of the breeding program, provided that traits measured at stallion inspection have a good genetic relationship with the traits in the breeding goal.

The objectives of this study were (1) to estimate heritabilities and correlations for traits scored during first stallion inspection and (2) to estimate correlations of these traits with performance in dressage and show-jumping competition. These parameters are important to determine the relative importance of first stallion inspection in the breeding program for riding horses. This study is complementing the study of by Ducro et al. (2006) on similar traits measured at studbook entry of collateral relatives, because the candidate breeding stallions in this study comprise a selected sample of the population.

3.2 Material and Methods

Data from the First Stallion Inspection

The First Stallion Inspection of the Dutch Warmblood riding horses (KWPN) is held once a year at one location. Stallions are submitted for presentation mostly when they are between 2 and 3 years old. The stallions are inspected on seven traits. The basic gaits walk and trot are judged both in hand and during free moving in an indoor arena. Canter is judged only during free moving. The free-jumping traits takeoff, technique and power are judged

Table 3.1 Definitions of the 7 traits scored during the First Stallion Inspection (FSI).

Trait	Definition
Walk	Primarily a score for purity and correctness of movement, also suppleness and length of stride are of importance.
Trot	Scored as walk, but also impulsion and suspension of hind legs and posture are scored.
Canter	Scored as walk, but also impulsion and suspension of hind legs and posture are scored.
Balance	Ability to stay in balance and keep correctness in all gaits.
Takeoff	Ability to jump up and speed as the horse gets off the ground.
Technique	Technique of front and hind legs and of the back.
Power	Ability to jump with power in upward and forward direction.

during jumping over three fences in the indoor arena. The trait balance reflects the general view on way of movement (Table 3.1).

The stallions are judged by a team consisting of three people and the composition changes slightly over years. Scores are on a 1 to 10 scale with an increment of 0.5. Scores are given by the whole judging team at once, so only one score per trait is available. For this study a dataset was available, comprising 2,361 stallions with first stallion inspection observations from 1994 through 1999. Because of practical problems almost all records on walk were not available from 1995 through 1998, leaving 827 records available for analysis. The evaluated stallions descended from 373 sires, of which 27 have been evaluated for FSI themselves.

Competition data

Competition results were available on 23,897 horses that participated in dressage and on 22,811 horses that participated in show-jumping from 1981 through 2000. A total of 4,777 horses had results in both dressage and show-jumping. The system is described in more detail by Ducro et al. (2006). Of all stallions with FSI, 380 had participated in dressage competition and 520 stallions in show-jumping.

Analyses of variance

Genetic parameters of the traits scored during FSI were estimated using the model:

$$Y_{ijkl} = \mu + \text{year}_i + \text{age}_j + \text{tho}_k + \text{animal}_l + e_{ijkl}$$

where Y_{ijkl} is the observed score for the FSI trait (walk, trot, canter, balance, takeoff, technique, power) of the l^{th} animal; μ is the population mean; year_i

is the fixed effect of i^{th} year of inspection (i = 1994,…,1999); age_j is the fixed effect of the j^{th} age (j < 3 yr., ≥ 3 yr.); tho_k is the fixed effect of the k^{th} class of thoroughbred percentage (k = 0%, 12½, 25, 37½,≥ 50); $animal_l$ is the random effect of the l^{th} animal ~ N(0, $\mathbf{A}\sigma^2_a$); e_{ijkl} is the residual term ~N(0, $\mathbf{I}\sigma^2_e$). A thoroughbred effect has been included to account for a possible inflation of the genetic variance estimation in case of a breed difference for the trait under study.

Genetic parameters of the competition data were estimated using an animal model, identical to the model used by Ducro et al. (2006). Heritabilities were estimated in univariate analyses and genetic and phenotypic correlations of FSI traits and of competition traits were estimated in bivariate analyses, using the ASReml software package (Gilmour *et al*., 2002). The pedigree of each horse with an observation was traced back three generations. In total, the pedigree comprised 76,458 animals.

3.3 Results and Discussion

Heritabilities of FSI

Heritability estimates for FSI gaits varied from 0.25 (canter) to 0.50 (trot) (Table 3.2) and agreed well with the range of estimates as reviewed by Thorén Hellsten et al. (2006). Heritability for canter was slightly lower compared to the other gaits, probably due to the stress of a one-day test as suggested by the judging team. Heritabilities for free jumping traits were in the high end of the range for free jumping reported by Thorén Hellsten et al. (2006), and agreed well with the estimates of Bruns et al. (1985). The use of 3 different traits to score jumping might facilitate a more specified score for each of the aspects which could explain the relatively high heritability estimates. The young stallions were scored in order of their sire, rather than in random order. The scoring in order of the sires could have caused an overestimation of heritabilities, if judges were biased by being aware of the performance of the sire. The studbook is advised to score stallions in a random order to ensure an unbiased genetic evaluation.

Genetic correlations of FSI-traits

Movement traits showed positive correlations with genetic correlations of 0.70 and higher, and this agreed well with the results of Schade (1996) and

Table 3.2 Estimated additive genetic standard deviations, heritabilities, genetic correlations (under the diagonal) and phenotypic correlations (above the diagonal) of the traits scored at FSI

	σ_A	Walk	Trot	Canter	Balance	Takeoff	Technique	Power
Walk	0.50	**0.35**[a)]	0.58	0.56	0.57	0.13	0.14	0.16
Trot	0.67	0.86	**0.50**	0.69	0.82	0.13	0.07	0.11
Canter	0.45	0.70	0.75	**0.25**	0.87	0.29	0.26	0.27
Balance	0.54	0.79	0.88	0.94	**0.37**	0.24	0.20	0.21
Takeoff	0.66	-0.45	-0.32	0.08	-0.06	**0.45**	0.79	0.82
Technique	0.77	-0.43	-0.33	0.10	-0.09	0.96	**0.56**	0.81
Power	0.80	-0.42	-0.28	0.17	-0.02	0.97	0.97	**0.61**

[a)] Standard errors for heritability estimates were less than 0.06, except for standard error for walk was 0.11.

Brockmann (1998). The correlations found by Huizinga et al. (1991) were higher, probably due to a smaller number of animals. The genetic correlations among the 3 jumping traits were close to unity, indicating that the different aspects of free jumping were genetically the same traits, which was also found by Ducro et al. (2006) for some of the jumping traits.

The FSI-gaits walk and trot showed moderate negative correlations to the three jumping traits, ranging from -0.28 to -0.42, and were in agreement with the results of Schade (1996). However, Brockmann (1998) and Huizinga et al. (1991) found correlations close to zero and Gerber Olsson et al. (2000) found slightly positive genetic correlations. The negative relation found by Schade (1996) and in our study could be the result of simultaneous selection on two traits which will push the genetic correlation slightly downward (Falconer and MacKay, 1996). Additionally, there is a tendency for specialisation in the studbook population, with the result that matings are more frequently performed within each discipline. Specialisation accelerates the development of a negative correlation and with a further separation of the two disciplines, the existence of a common base population should be questioned. The development of a negative correlation between selection traits could also have affected the analysis of the Hanoverian studbook by Schade (1996). Brockmann (1998) considered in his analysis stallions from all German warmblood studbooks, including some less specialised studbooks. Ducro et al. (2006) did not find antagonistic relations in data from the studbook entry data, although the material was collected from collateral relatives. The stallions in the current study comprised, however, a selected sample from those generations consisting of animals with the potential of

Table 3.3 Estimated genetic (r_g) and phenotypic (r_p) correlations of FSI traits with dressage and show- jumping.

	Dressage		Show-jumping	
	r_g	r_p	r_g	r_p
Walk	0.72	0.03	-0.45	0.02
Trot	0.58	0.16	-0.36	0.02
Canter	0.37	0.11	0.06	0.06
Balance	0.53	0.18	-0.14	0.04
Take-off	-0.48	-0.04	0.92	0.26
Technique	-0.46	-0.04	0.81	0.26
Power	-0.48	-0.04	0.85	0.23

Standard errors for genetic correlations were less than 0.15

becoming breeding stallions and thus merely representing in part the genetic level of the generation ahead. Additionally, the stallions are more or less prepared by the owner for presentation during the FSI. A stallion with a jumping pedigree has probably more trained for jumping in its preparation than a stallion with a dressage pedigree and vice versa.

Genetic correlations with competition traits

The estimated heritabilities of dressage and show jumping in competition were 0.14 with a standard error of 0.02, and were in agreement with earlier results (Huizinga and Van der Meij, 1989; Koenen *et al,*. 1995).

The gait traits had moderate to high positive correlations to dressage (Table 3.3). From the overview of Thorén Hellsten (2006) the correlation of walk to dressage in competition ranged from 0.20 to 0.47, whereas our estimate was 0.72.

All genetic correlations between FSI-jumping traits and show jumping were higher than 0.80. The results agreed with literature and support the conclusion of Gerber Olsson et al. (2000) that these traits are suitable for selection purposes. In contrast, jumping traits of FSI showed substantial negative correlations with dressage (about -0.48). Unfavourable genetic correlations were also found between the gait traits of FSI and show-jumping, except for canter, which showed a correlation close to zero. This supports the antagonistic relation between the competition disciplines as suggested by Schade (1996) and Kühl (1991) and the results were in line with the correlations found between FSI-gaits and FSI-jumping. The

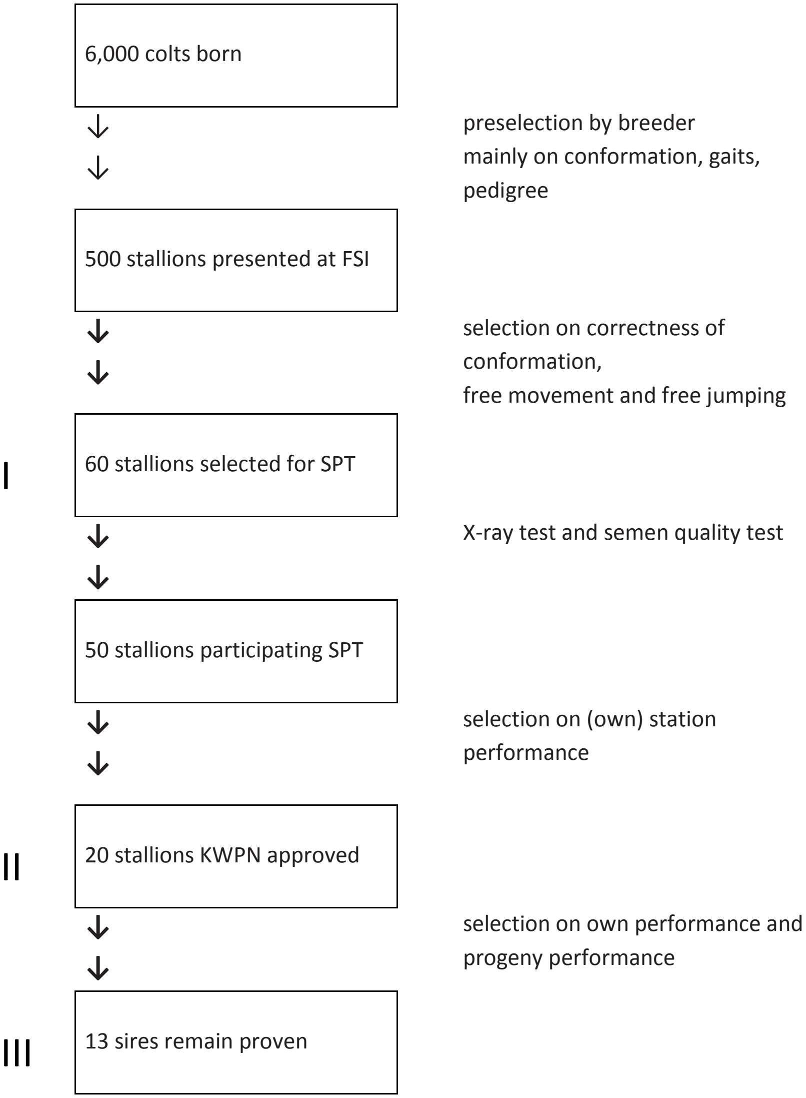

Figure 3.1 Approximate number of stallions selected at the selection stages after First Stallion Inspection (FSI) (I), after Stallion Performance Test (SPT) (II), and after progeny performance (III).

discussion about the development of a negative correlation between the disciplines is also relevant to the relation between FSI-traits and competition traits.

Implications

The final approval of a breeding stallion by KWPN is based on progeny performance, which becomes available when stallions are 11 years of age. Performance testing of young stallions facilitates the preliminary selection of stallions at an early age. As a consequence of limited number of stallions participating in the performance test, selection intensity is low at stage II (20 selected out of 50; Figure 3.1), as well as at the subsequent stage of selection on progeny performance (13 sires out of 20; Figure 3.1, stage III). Selection intensity achieved at FSI, which is preceding the performance test, is higher (60 stallions out of 500 submitted; Figure 3.1, stage I). The traits scored during First Stallion Inspection have high genetic correlations with the breeding objective traits dressage and show jumping. This implies that there are good opportunities to use FSI to improve the efficiency of the breeding programme. The value of FSI can be further improved by increasing the number of animals subject to FSI. In that case the selection intensity after FSI can be improved as well, and bias on parameter estimates, as a consequence of preselection, will be smaller. Extending the number of stallions participating in the FSI is relatively cheap because it is a one day-event and the animals do not have to follow a training programme. If the correlations between traits of the successive selection stages are known then the three-stage selection program, as performed by the KWPN studbook can further be optimized with regard to number of stallions tested at each stage. Alternatively, it can be calculated to what extent preselection prior to FSI can be allowed for with minor loss of selection response. Studies on optimizing multi-stage selection programs in horse breeding also emphasize the importance of the first stage of selection (Hugason et al., 1987).

Traits of FSI showed moderate to high heritability and genetic correlations with traits of the breeding goal and therefore the genetic progress that can be achieved is substantial. Therefore accurate selection at FSI has a determining impact on the subsequent genetic progress.

3.4 Conclusions

Heritabilities of traits scored at First Stallion Inspection are moderate to high and can therefore be used to select breeding stallions. The genetic correlations of the gaits of FSI with dressage in competition are high and favourable. The jumping traits of FSI had very strong genetic correlations with show-jumping in competition. The genetic correlations of trot and walk with show-jumping were negative and the jumping traits of FSI also had negative correlations to dressage in competition. Selection at First Stallion Inspection comprises an important component of the stallion selection program, because FSI-traits have good genetic relationships with performance in competition and, due to the number of animals involved, relatively high selection intensities can be achieved.

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4

Heritability of foot conformation and its relation to sports performance in a Dutch warmblood horse population

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Abstract

Reasons for performing study: Warmblood horse studbooks aim to breed horses with a conformation that will enable elite future performance, but reduce the risk of injuries and lameness. Negative conformational traits, such as asymmetrical or “uneven” forefeet would possibly diminish performance in sports.

Objectives: To assess the prevalence and heritability of uneven feet and its genetic relationship to other conformation traits as well as to sporting performance later in life in warmblood riding horses.

Materials and methods: The databases of the Royal Dutch Warmblood Studbook (KWPN, n=44,840 horses) and Royal Dutch Equestrian Sports Federation (KNHS, n=33,459 horses in dressage and n=30,474 horses in showjumping) were linked through the unique number of each registered horse. Therefore, heritabilities, and genetic and phenotypic correlations could be estimated from the scores of the jury at studbook admission and the sports performance of that population in dressage and jumping over the period 1990-2002.

Results: The prevalence of uneven feet was 5.3% on average, and the prevalence showed an increase from under 4.5% during the first 3 years of recording to over 8% in the years from 2000 onwards. Heritability estimates of foot conformation traits were moderate and ranged from 0.16 for heel height to 0.27 for hoof shape. The genetic correlation between the trait of uneven feet and performance in competition was negative but weak: -0.09 with dressage and -0.12 with show jumping.

Conclusions: Predisposition to uneven feet can be reduced by selection. Because of weak genetic correlations, the increased prevalence of uneven feet is not directly associated with selection for better sports performance (dressage or jumping) or higher conformation grade.

If the trait ‘uneven feet’ arises from a disproportionate relation between height at the withers and neck length, then selection on conformation grade might result in a situation prone to development of uneven feet. In general, limb conformation has a moderate genetic relationship to conformation grade and foot conformation traits have a genetic relation to sporting performance.

Potential relevance: This study provides evidence that selection for better sport performance is not causing the increased prevalence of uneven feet. The other way around, reducing occurrence of uneven feet by selection is possible, without limiting progress in sport performance. Selection for conformation grade might induce a disproportional relation between height at withers and neck length, which indirectly would induce horses to be more sensitive to uneven feet. Breeders should be instructed to pay special attention to this risk in their selection procedures.

Key words: rinding horse, heritablilities, foot conformation, linear scoring

Figure 4.1 Typical posture for a foal to develop uneven feet (Van Heel *et al.* 2006).

4.1 Introduction

It is widely accepted that there is a relationship between limb conformation and predisposition to lameness (Balch et al. 1995, Kane et al. 1998, Stashak et al. 2002, Ross and Dyson 2003, Anderson et al. 2004, Weller et al. 2006). Distal limb injuries are still the main reason for early retirement and lowered performance in equine sports (Kaneene et al. 1997, Wallin et al. 2000, 2001). Considerable time and money is invested in (future) sport horses before they can reach their full performance potential. Therefore, a veterinarian often examines horses in order to check if there are any contra-indications for a sporting career (Holmström 2001). A commonly encountered fault at these checks is the occurrence of two differently shaped and sized front feet, the so-called “uneven” feet (Kroekenstoel et al. 2006, Van Heel et al. 2006). The clinical significance of uneven feet is unclear, but the condition appears to be more prevalent in lame horses than in sound horses (Ross and Dyson 2003).

At studbook admissions, attention is also paid to limb, and more specifically, to foot conformation, because of its relation to sport performance (Holmström 2001). Whether foot conformation is genetically determined is not known. To evaluate whether selection is possible, it is necessary to estimate the genetic variation in foot conformation traits and to determine whether these traits correlate genetically with other traits in the breeding goal. Uneven feet might develop as a consequence of persistent, lateral behaviour (Figure 4.1), and is supposed to be enhanced by a high juvenile growth rate and a relatively short neck length (Van Heel et al. 2006).

The aims of this study were to assess the prevalence and heritability of uneven feet, and to estimate the genetic relationship of this trait to other conformation traits in young warmblood riding horses, and also to investigate the significance of foot conformation for success in a sporting career later in life.

4.2 Materials and Methods

Studbook admission data

The inspection at the Royal Dutch Warmblood Studbook (KWPN) admission consists of assessments of three different types of traits:

1) Descriptive traits are specific characteristics regarding conformation, gaits and jumping which are linearly scored (Ducro et al. 2007). A score of 20 (on

a scale of 1 to 40) reflects the average of the population, and a score below 20 is desired, although extreme values are undesirable. Nevertheless, for this study descriptive scores were multiplied by -1 to facilitate interpretation of the correlations.

2) Grading traits are conformation, movement and jumping and these traits receive marks on a scale of 40 (=worst) to 100 (=best).

3) Undesired traits, such as uneven feet visible on the horse, and if so, this is scored on the admission form.

In this study, a selection of the descriptive traits (Table 4.1) regarding foot and limb conformation were analysed, together with measured height at the withers (HW), scored neck length (NL), conformation grade (CG) and the undesired trait uneven feet (UF). In this study, the status 0 refers to the absence of uneven feet and 1 refers to the presence of uneven feet.

Competition data

For a horse in a sporting competition (dressage or showjumping), the results are recorded by the equestrian sport organisation (KNHS) as the highest classification ever achieved by that horse (Ducro et al. 2007). The classification scores were transformed to linear scores (Huizinga and Van der Meij 1989), using a square-root transformation to achieve a more normally distributed error term. This procedure is in accordance with the protocol used in the routine breeding value estimation.

Data editing

The analysis was performed on a dataset containing foot and limb conformation records of horses subjected to studbook inspection during period 1990-2002. The final dataset included 44,840 records after data screening. Competition results were available for 33,459 horses that participated in dressage (‘dressage’) and 30,474 horses that participated in showjumping (‘jumping’) from 1981 through to 2002. Of all the horses with a score for uneven feet, about 25% had participated in dressage competition and about 18% in showjumping.

Tabel 4.1 Means and description of lower and upper value of traits scored at studbook entry (n=44,480) and graded in sports (n=33,459 in dressage, n=30,474 in jumping).

	Lower value		Upper value		Mean
	Value	Description	Value	Description	
Score at studbook entry					
Neck Length	-40	Short	-0	Long	-19.0
Forelimb Conformation	-40	Calf kneed	-0	Buck kneed	-18.5
Pastern Angle	-40	Upright	-0	Weak	-20.5
Hoof Shape	-40	Narrow	-0	Broad	-19.9
Heel Height	-40	Low	-0	High	-19.1
Limb Quality	-40	Blurred	-0	Dry	-19.8
Bone Circumference	-40	Light	-0	Heavy	-19.4
Conformation Grade	40	Bad	100	Good	67.5
Uneven Feet (no/yes)	0	Absent	1	Present	0.05
Height at Withers (cm)	158.3		178.2		164.8
Grade in sports					
Dressage Ranking[1]	0	Bad	200	Good	52.5
Jumping Ranking	0	Bad	200	Good	43.0

[1] original marks, before analysis square root transformed

Genetic analysis

Heritability (h^2) expresses to which extent differences between animals for a trait are due to genetic differences. The h^2 ranges from 0 (no genetics involved, differences are entirely environmental) to 1 (entirely determined by genes) (Falconer and Mackay 1996). Heritabilities and genetic correlations were estimated using the ASReml software package (Gilmour et al. 2002) with a linear animal model, as described by Ducro et al. (2007). The pedigree of each horse with an observation was traced back three generations. In total, the pedigree comprised of 132,429 individuals. Genetic groups were included in the pedigree to adjust for the percentage of Thoroughbreds.

Heritability estimate for the binary trait uneven feet is transformed to an estimate at the underlying liability scale according to Dempster and Lerner (1950). In the results section the heritability estimate of the liability will be presented.

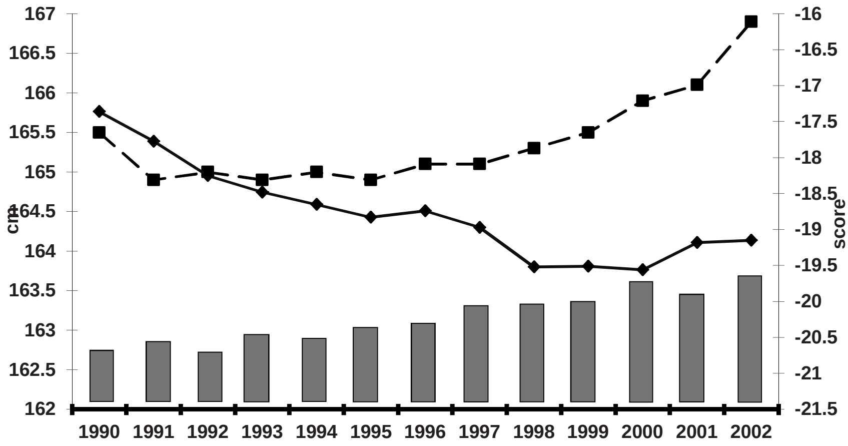

Figure 4.2 Least Square Means by year of height at withers (■--■, in cm) of neck length (♦━♦, score) and prevalence of uneven feet (bars, with percent prevalence on top) (n=44,480).

4.3 Results

Means and prevalence

The means of descriptive and subjective traits are shown in Table 4.1. The means presented are adjusted for effect of unequal number of data in each factor, such as year, sex, age group etc., and are therefore called least square means (LSmeans). The means ranged from -20.5 to -18.5 for descriptive traits. The prevalence of uneven feet (UF) was 5.3% on average, and the prevalence showed an increase from under 4.5% during the first 3 years of recording to over 8.0% in the years from 2000 onwards (Figure 4.2). The least square means of the measured height at withers (HW) was around 165.0 cm during most of the years up to 1997, except for 1990, which had a value of 165.5 cm. From 1998 to 2002, the height at withers increased further from 165.3 to 166.9 cm (Figure 4.2).

The prevalence of uneven feet (UF) showed an increase with age, both in males and females (see also: www.evj.uk/suppinfo). For the descriptive conformation traits, less negative (i.e., closer to zero) scores are desirable. Neck length was scored more negatively (and thus less desirable) throughout the years (Figure 4.2), indicating that necks were considered to become shorter.

Table 4.2 Heritabilities (diagonal, bold and underlined) and genetic (below diagonal) and phenotypic (above diagonal) correlations between traits scored at studbook entry (n=44,480) and graded in sports (n=33,459 dressage, n=30,474 jumping).

	HW[1)]	NL	UF	FC	PA	HS	HH	LQ	BC	CG	Jum	Dre
Height at W.	**.67**	-.12	.01	.04	-.05	.19	.03	-.17	.12	.19	-.02	.14
Neck Length	-.44	**.23**	-.01	-.12	.08	-.03	.04	.10	-.01	-.30	.02	.04
Uneven Feet	-.03	.10	**.12**	-.01	-.06	-.17	.05	-.03	.04	-.06	-.01	-.01
Forelimb Conf.	-.06	.16	-.05	**.16**	.0	-.04	.01	.10	.0	.08	-.01	-.08
Pastern Angle	-.03	.01	-.30	.21	**.17**	.13	-.16	.10	-.04	-.04	-.12	-.04
Hoof Shape	.28	.01	-.49	-.12	.27	**.27**	.07	.0	.25	.03	.09	-.07
Heel Height	-.01	.15	.47	-.19	-.42	-.41	**.16**	.08	.06	.15	.20	.04
Limb Quality	-.29	.22	-.12	.22	.22	.04	-.01	**.19**	-.25	.33	.04	.05
Bone Circ.	.35	.02	.20	-.17	-.16	.50	.18	-.58	**.24**	-.13	.09	.03
Conf. Grade	.35	-.59	-.04	.25	.15	.08	.28	.67	-.23	**.30**	.04	.19
Jum	.01	.14	-.12	.07	.01	.11	.19	.20	-.09	.29	**.14**	ne[2)]
Dre	.33	.32	-.09	-.01	.07	-.01	.15	.36	-.13	.67	ne[2)]	**.14**

[1)] HW= Height at Withers, NL=Neck Length, UF=Uneven Feet (%)FC=Forelimb Conformation, PA=Pastern Angle, HS=Hoof Shape, HH=Heel Height, LQ=Limb Quality, CG=Conformation Grade, Jum=Jumping Ranking, Dre=Dressage Ranking; standard errors of estimates were below 0.03; [2)] ne=not estimated

Heritability

The heritability estimates of descriptive conformation traits varied from 0.16 (forelimb conformation FC) to 0.27 (hoof shape HS) (Table 4.2). The heritability estimate of the subjective trait conformation grade (CG) was 0.33, and for measured height at withers (HW), the heritability was 0.67. The heritability of the liability of uneven feet (UF) was 0.12. The prevalence of uneven feet (UF) varied with sire group from 0% to 35% (Figure 4.3). Of the 576 sires, about 60 did not have progeny with uneven feet, whereas 6 sires had a prevalence of 25% or more in their progeny.

Genetic correlations

In general, traits of foot conformation were moderately correlated with each other (Table 4.2). Heel height (HH) had high negative correlations with pastern angle (PA: -0.42) and hoof shape (HS: -0.41), meaning that high heels are associated with narrow hoof shapes and more upright pasterns. Thus, pastern angle (PA) is correlated with hoof shape (HS: 0.27), but also with forelimb conformation (FC: 0.21), meaning that more upright pasterns (PA) are related to a calf kneed conformation (FC).

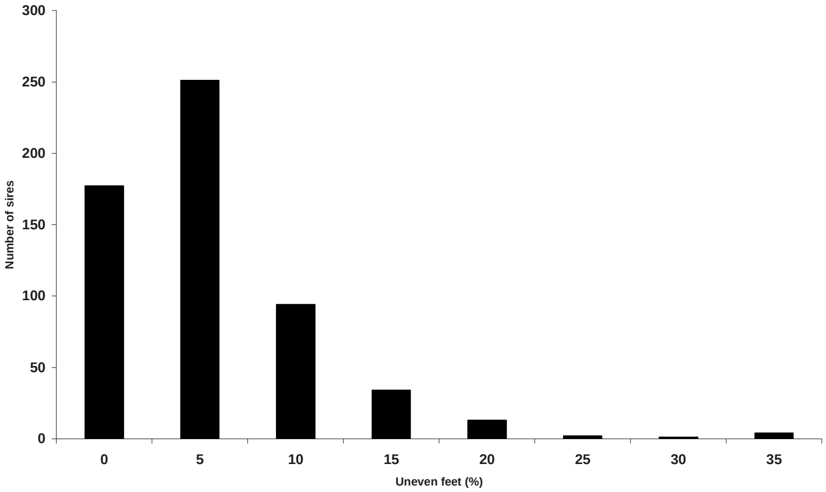

Figure 4.3 Mean prevalence of uneven feet in offspring related to number of sires (n=44,480 horses from n=630 sires).

Similarly, the bone circumference (BC) was moderately positively correlated with hoof shape (HS: 0.50), and moderately negatively correlated with limb quality (LQ: -0.58), meaning that a larger bone circumference (BC) was associated with a broader hoof shape (HS) and a more blurred limb quality (LQ).

The subjective trait conformation grade (CG) was moderately positively related to height at withers (HW: 0.35), forelimb conformation (FC: 0.25), heel height (HH: 0.28), limb quality (LQ: 0.67), but negatively related to neck length (NL: -0.59) and bone circumference (BC: -0.23), meaning that horses considered to have a better conformation for a sporting career are taller, have a less calf kneed conformation, higher heels and dryer, lighter limbs but concomitantly shorter necks. Uneven feet (UF) were moderately negatively correlated with pastern angle (PA: -0.30) and hoof shape (HS: -0.49), and positively related to heel height (HH: 0.47); when scoring positively on uneven feet judges apparently are relying on the limb with a more upright pastern and a narrow, high heeled foot. The sports traits dressage ranking and jumping ranking showed moderate correlations with heel height (HH: 0.15 and 0.19) and limb quality (LQ: 0.20 and 0.36), whereas correlations with other foot conformation traits were low, with absolute values below 0.13. For dressage ranking height at withers (HW: 0.33), neck length (NL: 0.32) and mainly conformation grade (CG 0.67) were positively correlated too, meaning that higher ranked horses in dressage were taller, had longer necks, dryer limbs, and a better conformation already at studbook admission. The genetic correlation between the trait uneven feet (UF) and the performance in competition was negative but weak, with values of -0.09 for dressage and -0.12 for jumping.

4.4 Discussion

The aim of this study was to assess the prevalence and heritability of uneven feet, and its genetic relationship to limb conformation traits and to sporting performance later in life in a population of warmblood riding horses. The role of height at the withers and neck length in sports performance was studied as well, to test the hypothesis that imbalance between height at withers and neck length would predispose to the development of uneven feet (Van Heel et al. 2006).

Each year, about 3,500 horses attend the studbook entry out of about 12,000 foals that are born annually. Compared to other opportunities for inspection, such as the annual stallion or mare performance tests, studbook entry serves as a good opportunity to inspect a large and rather unselected sample of the population at low costs, allowing a proper genetic analysis to be carried out (Koenen et al. 1995, Ducro et al. 2007).

Prevalence and fixed effects

The prevalence of the conformation trait of uneven feet was 5.3% based upon scoring 44,840 horses at studbook entry (Table 4.1). There may be a certain degree of underestimation in this prevalence estimation, due to an owner's choice not to send in their horse with a severe degree of uneven feet. In addition, mild cases of uneven feet may have been temporarily masked by adequate hoof trimming and shoeing. However, underestimation is probably limited because uneven feet are not a reason for rejection at studbook entry.

Over the years that were recorded, the prevalence of uneven feet tended to increase (Figure 4.2). The increase could be due to a more stringent judgment by the inspectors, perhaps after incidental negative experiences with final approval of horses with uneven feet, and possibly after uneven feet were redefined. The height at the withers also slightly increased (Figure 4.2), which has been previously reported to propagate uneven feet (Van Heel et al. 2006).

Heritability estimates of foot conformation

Heritability estimates of foot conformation traits were moderate, but significant, and ranged from 0.16 for heel height to 0.27 for hoof shape (Table 4.2). The liability for uneven feet revealed a heritability estimate of only 0.12, which is similar to the heritability for sporting traits of 0.14 for both jumping and dressage. Therefore, the prevalence of the conformation trait uneven feet could be reduced by selection, but, given this heritability, selection on own performance (i.e. removal of individual horses when they are positive for this trait, irrespective of information about this trait from relatives) will not be efficient, thus information from the progeny in the selection programme is required.

Genetic correlations of foot conformation

The genetic correlations of height at withers, neck length and limb quality with dressage ranking ranged between 0.32 and 0.36, indicating that selection for taller horses with longer necks and a better limb quality at studbook entry will improve dressage ranking. This selection will have much smaller effect for jumping ranking and no effect of selection on height at withers.

Uneven feet had moderate correlations with traits of the distal limb (pastern angle, hoof shape and heel height), and low correlations with traits relating to the entire leg (forelimb conformation, limb quality and bone circumference). The genetic ability to develop uneven feet is associated with the genetic value of more upright pasterns, narrower hoof shape and higher heels. This also implies that scoring feet as being uneven is mainly based upon the recognition of a unilateral more upright distal limb conformation.

However, the genetic correlations of foot conformation with ranking in dressage and in jumping are only low to moderate. Selection for sporting traits will mostly improve foot conformation traits for heel height (0.19 jumping and 0.15 dressage), but will not increase the prevalence of uneven feet at all, and is therefore not responsible for the observed increased prevalence of uneven feet in the population (Table 4.2).

The genetic correlations of uneven feet with withers height and neck length are rather weak, thus giving little evidence that fast growing horses with short necks would be more sensitive to uneven feet. However, the negative genetic correlation between withers height and neck length (HW-NL: -0.44) suggests that an imbalance between height at withers and neck length will arise when selecting for height at withers. This imbalance would indirectly make horses more sensitive to the development of uneven feet, as this discrepancy would propagate this trait at foal age (Van Heel et al. 2006). This imbalance might be induced by selection on conformation grade, because of its positive correlation to height at withers (0.35) and its negative correlation to neck length (-0.59). Conformation grade serves as an important selection trait because, due to its moderate heritability (0.30) and its high genetic correlation with dressage ranking (0.67), it can serve as an early predictor for the selection of dressage horses.

In conclusion, prevalence of uneven feet as recorded at studbook entry was on average 5% and was increasing in the period of study. Heritability of liability for uneven feet was 0.12 and genetic correlations to selection traits conformation grade, jumping and dressage ranking were only low and unfavourable. Therefore, it is unlikely that selection for sports performance has directly contributed to the observed increase in uneven feet. Selection on conformation grade however, might have contributed indirectly to an increase in prevalence of uneven feet by inducing a disproportionate ratio between height at withers and neck length.

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Supplementary info on line (www.evj.uk/suppinfo) to:

Heritability of foot conformation and its relation to sports performance in a Dutch warmblood horse population

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Results

The prevalence of uneven feet (UF) was 5.3% on average, and the prevalence showed an increase from under 4.5% during the first 3 years of recording to over 8.0% in the years from 2000 onwards (Table 4.3). The prevalence of uneven feet (UF) showed an increase with age, both in males and females (Table 4.4).

Males received better scores for neck length (NL) than females, since in all of the age groups, the males had scores above -18.41, and the females had scores below -18.64 (Table 4.2). Similarly, males had better scores for forelimb conformation (FC), hoof shape (HS) and heel height (HH). In general, males had longer necks, a smaller hoof shape and higher heel depth than females.

With increasing age, the mean score for pastern angle (PA) became more negative both in males (from -19.86 in age group 3, to -21.22 in age group 5) and females (-19.98 to -20.77), therefore as animals aged, the pasterns were more upright. Similarly, mean scores became more negative with increasing age in both sexes for the traits of neck length (NL) and limb quality (LQ).

Uneven feet were seen more frequently in older horses of both sexes (Table 4.4: M5 and F5). It is possible that the higher bodyweight of mature horses is likely to more severely load the lower angled, weaker developed foot, and this may be exacerbated by a longer shoeing interval (Moleman et al. 2006).

Table 4.3 Least square means by year of traits scored at studbook entry (n=44,480).

	UF[1)]	HW	NL	FC	PA	HS	HH	LQ	CG[2)]
1990	3.81	165.5	-17.36	-20.55	-20.48	-18.94	-19.86	-19.49	-
1991	4.47	164.9	-17.77	-20.06	-20.68	-19.09	-19.78	-20.08	-
1992	3.66	165.0	-18.25	-20.07	-20.64	-18.91	-20.09	-19.53	66.71
1993	5.02	164.9	-18.48	-20.18	-20.51	-18.71	-19.38	-19.39	66.19
1994	4.72	165.0	-18.65	-20.05	-20.28	-18.83	-19.55	-19.44	66.29
1995	5.53	164.9	-18.83	-19.87	-20.31	-19.08	-19.80	-19.33	65.62
1996	5.87	165.1	-18.74	-20.18	-20.19	-19.05	-19.60	-18.97	66.70
1997	7.20	165.1	-18.97	-19.97	-20.19	-19.35	-19.62	-19.54	63.66
1998	7.28	165.3	-19.52	-20.16	-20.44	-19.42	-19.75	-20.02	69.11
1999	7.48	165.5	-19.51	-19.84	-20.12	-19.39	-19.78	-20.23	68.34
2000	9.02	165.9	-19.56	-20.16	-20.48	-19.00	-19.87	-20.41	67.51
2001	8.05	166.1	-19.18	-20.54	-20.69	-19.15	-19.83	-20.52	67.36
2002	9.39	166.9	-19.15	-20.63	-20.67	-18.83	-20.46	-20.49	66.97
LSD[b]	0.12	1.24	0.22	0.22	0.22	0.23	0.23	0.23	0.42

[1)] UF=Uneven Feet (%), HW=Height at Withers, NL=Neck Length, FC=Forelimb Conformation, PA=Pastern Angle, HS=Hoof Shape, HH=Heel Height, LQ=Limb Quality, CG=Conformation Grade; [b] Least Significant Difference; [2)] Conformation was not recorded in the years 1990 and 1991.

Table 4.4 Least square means of sexage groups of males (M) and females (F) at the age of 3, 4 and more than 4 years of age (M5, F5) for traits scored at studbook entry (n=44,480).

	UF[1)]	HW	NL	FC	PA	HS	HH	LQ	CG
M3	4.04	165.8	-18.29	-19.88	-19.86	-19.33	-19.56	-19.21	65.75
M4	6.85	166.8	-18.27	-19.92	-20.94	-18.74	-19.20	-20.17	67.50
M5	7.94	166.9	-18.41	-19.66	-21.22	-18.43	-19.17	-20.90	66.52
F3	5.32	164.9	-18.64	-20.52	-19.98	-19.43	-20.28	-18.79	68.90
F4	6.35	164.3	-19.27	-20.63	-20.17	-19.32	-20.51	-19.49	66.84
F5	8.04	164.3	-19.57	-20.44	-20.77	-19.28	-20.43	-20.25	65.09
LSD[2)]	0.16	1.42	0.29	0.28	0.28	0.29	0.29	0.29	0.56

[1)] UF=Uneven Feet (%), HW=Height at Withers, NL=Neck Length, FC=Forelimb Conformation, PA=Pastern Angle, HS=Hoof Shape, HH=Heel Height, LQ=Limb Quality, CG=Conformation Grade; [2)] Least Significant Difference.

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5

Influence of foot conformation on length of competitive life in a Dutch warmblood horse population

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Abstract

Reasons for performing study: Warmblood horse studbooks aim to breed horses with a conformation that will enable elite future sports performance, but reduce the risk of early retirement due to lameness. Negative conformational traits, such as asymmetrical or “uneven” forefeet would possibly shorten the career of sporthorses.

Objectives: To investigate the significance of foot conformation at young age for length of the career of sporthorses.

Materials and methods: Databases of the Royal Dutch Warmblood Studbook (KWPN) and of the Royal Dutch Equestrian Sports Federation (KNHS) were matched and resulted in a dataset comprising 23,116 records of horses for which their conformation scores and length of their sports career was available. Survival analysis was used to determine which of the conformation traits had a significant effect on duration of sports career in dressage and jumping at basic and elite level.

Results: Length of competitive life was shorter for jumping than for dressage. A different set of risk factors was found for each level and discipline: e.g. height at withers was a risk factor at basic level in dressage and jumping, while pastern angle was a risk factor at the elite level of jumping and dressage. The trait ‘uneven feet’ tended to shorten the competitive life in dressage, but was a significant risk factor at the elite level of jumping.

Conclusions: Limb conformation, and in particular, the conformation of the distal limb, are important for length of competitive life. From the prevalence of uneven feet in sports disciplines, it may be concluded that this is an undesirable trait, particularly at the elite level of jumping, since uneven feet have a detrimental effect on the length of competitive life in a sporthorse population.

Potential relevance: This study provided evidence that the conformation trait uneven feet has a negative effect on warmblood jumping performance, and therefore breeders should be instructed to possibly prevent this phenomenon already at foal age.

Key words: Foot Conformation, Competitive life span, riding horse, linear score.

5.1 Introduction

Considerable time and money is invested in sport horses before they can reach their performance potential later in life. Early retirement due to injuries has therefore substantial economic consequences and should be prevented. Reasons of early retirement are hardly recorded or available, but musculoskeletal injuries are likely one of the most prevalent reasons (Ricard and Fournet-Hanocq 1997). Wallin et al. (2001) demonstrated indeed that limb conformation measured in young horses had a significant influence on lifespan in Swedish Warmblood horses.

At studbook admissions, attention is paid to that conformation, and more specifically, to limb and foot conformation. Also, several undesirable traits such as uneven feet are scored at studbook admission. The clinical significance of uneven feet is unclear, but appears to be more prevalent in lame horses than in sound horses (Ross and Dyson 2003). A previous study showed that limb conformation traits had moderate genetic relations to performance in competition, in particular in dressage (Ducro et al. 2008), but uneven feet had only weak correlations to sports performance.

Since musculoskeletal injury is the most significant cause of early retirement in sports horses and a relationship is assumed between conformation and predisposition to lameness, we hypothesize that length of competitive life is influenced by conformation as measured in young horses at studbook admission.

The aims of this study are to investigate the significance of foot conformation at young age for length of sports career in dressage or jumping later in life.

5.2 Materials and Methods

Horses

From the database of the equestrian sport organisation (KNHS), records on horses were retrieved for which date at first start in competition (dressage or showjumping) were available. Most records older than 1996 did not include date at first start and were therefore removed. Level of performance is divided into basic level, mainly suited for novice and recreational sports, and elite level, which is intended for advanced and professional competing (Ducro et al. 2007).

Tabel 5.1 Means and description of lower and upper value of traits scored at studbook entry (n=44,480) and graded in sports (n=33,459 in dressage, n=30,474 in jumping).

	Lower value		Upper value		Mean
	Value	Description	Value	Description	
Score at studbook entry					
Neck Length	-40	Short	-0	Long	-19.0
Forelimb Conformation	-40	Calf kneed	-0	Buck kneed	-18.5
Pastern Angle	-40	Upright	-0	Weak	-20.5
Hoof Shape	-40	Narrow	-0	Broad	-19.9
Heel Height	-40	Low	-0	High	-19.1
Limb Quality	-40	Blurred	-0	Dry	-19.8
Bone Circumference	-40	Light	-0	Heavy	-19.4
Conformation Grade	40	Bad	100	Good	67.5
Uneven Feet (no/yes)	0	Absent	1	Present	0.05
Height at Withers (cm)	158.3		178.2		164.8
Grade in sports					
Dressage Ranking[1]	0	Bad	200	Good	52.5
Jumping Ranking	0	Bad	200	Good	43.0

[1] original marks, before analysis square root transformed

Data on sports results were matched with the studbook admission database of the Dutch Warmblood Studbook (KWPN) to link scores on conformation traits to the competition results. This resulted in a set of 13,622 records of horses that been admitted to studbook inspection and that participated in dressage, and a set of 9,494 horses that been admitted to studbook inspection and that participated in jumping.

Traits

In this study, a selection of the descriptive traits (Table 5.1) regarding foot and limb conformation were analysed, together with measured height at the withers (HW), scored neck length (NL), conformation grade (CG) and the undesired trait uneven feet (UF). In this study, the status 0 refers to the absence of uneven feet and 1 refers to the presence of uneven feet.

Further details on studbook admission procedure can be found in Ducro et al. (2007).

Survival analysis

Length of competitive life of a horse is calculated as the period between date at first and date at last start in competition. For horses still in competition at the end of data collection the true length is not known and these data are called censored. To exclude these records from the analysis or to consider them as the true length of competitive life would lead to biased results. Survival analysis properly combines information from retired (uncensored) horses and horses that are still active in sports (censored) to statistically analyse the significance of limb conformation on the length of competitive life.

A proportional hazard model was fitted using PROC PHREG and PROC TPHREG in SAS (v9.0) to carry out a survival analysis. The four disciplines (basic and elite level in both dressage and jumping) were analysed separately, and for each discipline, a stepwise selection procedure was performed to determine which combination of conformation traits (uneven feet, withers height, hoof shape) best explained the survival pattern and thus gave the best fit. Goodness of fit was based on a likelihood ratio test.

Prior to the survival analysis, all conformation traits were corrected for effects of event, age and classifier using PROC GLM in SAS. To account for possible curvilinear relationships with the length of competitive life, conformation traits were classified into four quartiles; quartile 1 consisted of the 25% of horses with the lowest score for that conformation trait, and quartile 4 consisted of the 25% of horses with highest score for that conformation trait.

Three correction factors were always included in the models, because it was believed that they had a systematic influence on the length of competitive life: sex (males and females), class of starting year (before 2000 (=’<2000’) and 1999 (=’ ≥2000’)), and class of starting age (quartile 1+2, quartile 3 and quartile 4). The class of the starting year was included in accordance with a study by Wallin et al. (2000), in which a positive trend was found between time and length of life. The class of the starting age was included in accordance with other studies (Ricard and Fournet-Hanocq 1997), in which a negative trend was found between competitive life and a higher starting age. The starting age was classified into quartiles, and the 1st and 2nd quartiles were combined; therefore quartile 1+2 comprised the younger 50% of the horses, and quartile 4 comprised the 25% oldest horses in the specific sports discipline. For ease of interpretation, the effect of a particular score for a limb conformation trait, on length of sports life is expressed as risk ratio. This is the risk of being culled due to that score relative to the risk of being culled due to a base score for that trait. The base score is arbitrarily assigned to one of the values of the trait and is set to one. As an example, if risk ratio of group A over B is 1.6 then the risk of being culled of group A is 60% higher compared to group B. A risk ratio is considered significantly deviating from the reference if the confidence interval does not contain the value 1.

5.3 Results

Table 5.2 presents the least square means of studbook entry traits split into the four discipline groups (basic dressage, basic jumping, elite dressage, and elite jumping). Prevalence of uneven feet did not significantly differ between groups. Horses participating at the elite level had received in general less negative (i.e., closer to zero) scores at studbook entry; meaning that at elite level horses had longer necks, higher heels, drier legs. Horses at elite level had also a higher score for conformation grade and elite dressage had the highest score (69.27). The elite dressage group was significantly taller than the other groups (166.1 vs. 165.6). In addition, hoof shape was important for jumping, but not for dressage.

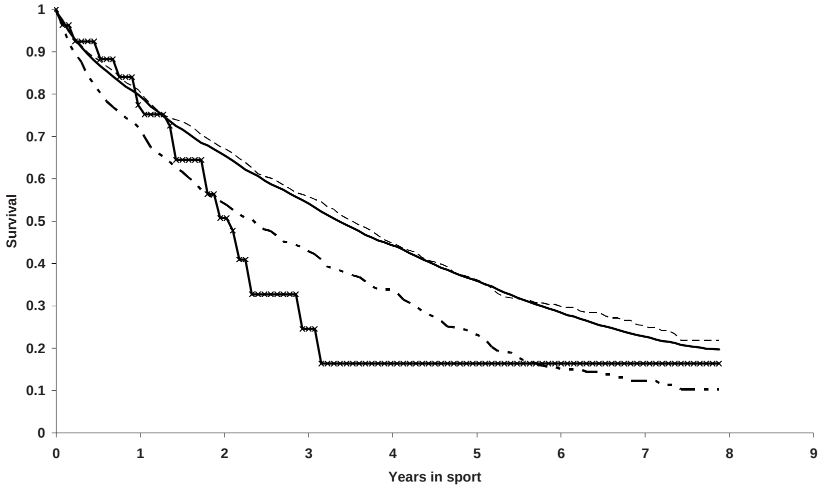
Table 5.2. Least square means of traits scored at studbook entry for level (basic and elite) and for sports discipline (n=33,459 dressage, n=30,474 jumping).

	Dressage			Jumping		
	Basic	Elite	Prob[a]	Basic	Elite	Prob[a]
Uneven Feet (%)	6.20	5.78	0.78	6.43	5.32	0.32
Height at Withers	165.6	166.1	<.0001	165.6	165.6	0.4
Neck Length	-18.36	-17.90	<.0001	-18.55	-18.00	<.0001
Forelimb Conformation	-20.02	-19.97	0.14	-19.91	-19.98	0.43
Pastern Angle	-20.71	-20.42	0.006	-20.61	-20.71	0.05
Hoof Shape	-18.99	-18.91	0.62	-18.97	-18.85	0.02
Heel Height	-19.38	-19.28	0.05	-19.47	-19.14	0.005
Limb Quality	-19.66	-19.10	<.0001	-19.62	-19.28	<.0001
Conformation Grade	67.62	69.27	<.0001	67.53	68.33	<.0001

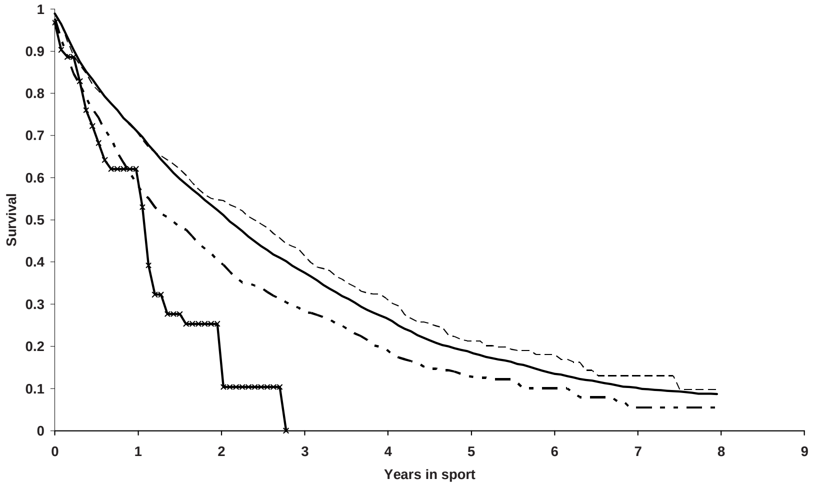
[a] Prob = Probability of equal means of basic and elite level in each discipline.

Figure 5.1. Survival curves for a) dressage (basic dressage n=12,776: Uneven Feet n=836 (---)// Even Feet n=11,940 (━━━); elite dressage n=684: UF n=27 (~~xxx~~)// EF n=657 (━--━)) and b) jumping performance (basic jumping n=8,738: UF n=517 (---)// EF n=8,221(━━━); elite jumping n=756: UF n=31 (~~xxx~~)// EF n=725 (━--━)) and the number of years horses were registered as being in competition.

a)



b)



Relation of conformation with length of competitive life

In Figure 5.1a, survival curves are presented for horses with even and uneven feet in the basic and elite levels of dressage. At the basic level, the median length of competitive life was not significantly different between horses with even feet and uneven feet (both 3.4 years). At the elite level in dressage, the median length of competitive life was shorter for uneven feet (1.9 years) compared to even feet (2.3 years), but this difference was not significant.

In Figure 5.1b, survival curves are presented for horses with even and uneven feet, both at the basic and elite levels in jumping. In general, the median length of competitive life in jumping was lower than the corresponding levels in dressage. At the basic level, no significant difference was found between the median length of competitive life for even feet (2.1 years) and uneven feet (2.4 years).

Table 5.3 Risk Ratio (95% confidence interval) Sex, Starting year and Starting age for basic dressage (n=12,776), elite dressage (n=684), basic jumping (n=8,738) and elite jumping (n=756).

	Dressage		Jumping	
Covariate	Basic	Elite	Basic	Elite
Sex				
Female	1.36 (1.26 – 1.46)	1.10 (0.79 – 1.51)	0.97 (0.89 – 1.05)	0.95 (0.70 – 1.28)
Male	1	1	1	1
Starting year				
Class<2000	1.23 (1.12 – 1.36)	2.01 (1.33 – 3.03)	1.51 (1.37 – 1.68)	2.05 (1.50 – 2.80)
Class≥2000	1	1	1	1
Starting age				
Quartile 1+2	0.67 (0.63 – 0.72)	0.54 (0.27 – 1.07)	0.63 (0.58 – 0.68)	0.66 (0.45 – 0.97)
Quartile 3	0.79 (0.73 – 0.86)	0.92 (0.45 – 1.88)	0.79 (0.73 – 0.86)	0.67 (0.44 – 1.03)
Quartile 4	1	1	1	1

At the elite level, a dramatic decrease in the survival probability of horses with uneven feet was observed, and none of the horses with uneven feet had a competitive life longer than 3 years. At the elite level, the median length of competitive life with uneven feet (1.1 years) was significantly lower than the length of competitive life with even feet (1.4 years).

In Table 5.3, the Risk Ratios of correction factors are shown for each of the four sports disciplines. In basic level dressage, the RR value of 1.36 indicates that females have a higher risk of being culled than males. The 95% confidence interval of the basic level of dressage ranged from 1.258 to 1.460, and does not contain the value 1, indicating that the risk is significantly different from males.

Table 5.4 shows the additional covariates selected in the survival analysis procedure, resulting in the best fit for records of the particular sports discipline, together with the systematic covariates sex, starting year and starting age. In basic level dressage, the covariate height at withers (HW) was selected. Height at withers had a significant effect on the length of sports career in this discipline, but smaller horses had a lower risk of being culled.

Table 5.4 Risk Ratios (RR[1]) and (95% confidence intervals) for the set of conformation traits (divided into quartiles) best describing survival pattern for basic dressage (n=12,776), elite dressage (n=684), basic jumping (n=8,738) and elite jumping (n=756).

		Dressage		Jumping	
Trait		Basic	Elite	Basic	Elite
Height at Withers	Q1	0.88		0.89	
		(0.78 – 0.98)		(0.78 – 1.01)	
	Q2	0.91		0.87	
		(0.84 – 0.99)		(0.78 – 0.96)	
	Q3	0.96		0.91	
		(0.88 – 1.05)		(0.82 – 1.01)	
Pastern Angle	Q1		0.83		0.66
			(0.42 – 1.63)		(0.35 – 1.24)
	Q2		0.92		0.59
			(0.53 – 1.60)		(0.38 – 0.93)
	Q3		0.96		0.61
			(0.32 – 0.97)		(0.39 – 0.95)
Forelimb Conformation	Q1			1.10	
				(0.93 – 1.28)	
	Q2			1.07	
				(0.98 – 1.17)	
	Q3			1.15	
				(1.03 – 1.29)	
Limb Quality	Q1			0.97	1.65
				(0.87 – 1.09)	(1.03 – 2.63)
	Q2			0.91	1.43
				(0.83 – 0.95)	(0.96 – 2.12)
	Q3			1.00	1.68
				(0.91 – 1.10)	(1.10 – 2.56)
Uneven Feet	Even				0.52
					(0.28 – 0.98)

[1] Risk ratios are relative to the fourth quartile, which is set to 1. Except for uneven feet, in which uneven is set to one.

5.4 Discussion

The aim of this study was to assess the significance of limb conformation traits for duration of sports career later in life in a similar manner to assessments in other breeds (Love et al. 2006). The role of height at the withers and neck length was also investigated, to test the hypothesis that imbalance between height at withers and neck length would predispose to the development of uneven feet (Van Heel et al. 2006).

The duration of sport career was analyzed using survival analysis. In a Swedish warmblood population, diseases of the musculoskeletal system were the predominant cause of death, accounting for about 55% of the dead horses, and almost 45% was due to degenerative joint diseases, and 10% of this percentage was due to navicular diseases (Wallin et al. 2000). Death due to musculoskeletal failure typically affected the age group of 7 to 10 years, at a time point when horses were building up their sports career (Wallin et al. 2000). The reasons for being culled also differ between the disciplines and levels of sport, as each of these sports requires different qualifications from a horse. In this respect, it may be expected that performing at an elite level requires a more sound conformation but will increase the risk for developing lameness and eventually becoming culled (Kaneene et al. 1997).

The duration of sports career differed for the sports discipline and level of sports. The risk of being culled was higher for jumping compared to dressage, and was higher at the elite level than at the basic level, although most horses participating at the elite level had passed the basic level and were obviously older. This possible difference in age has been accounted for by including the variable ‘starting age’ in the survival analysis for each of the four performance groups. The combined 1st and 2nd quartile (=25% + 25% of values) had lowest RR, indicating that, when horses start their sports career at an older age, they have a higher risk of being culled. A higher age at first race was also found to be a risk factor in racehorse fatility (Henley et al. 2006) and in jumping horses (Ricard and Fournet-Hanocq 1997). Females (RR=1.36) only had a higher risk of being culled than males in basic dressage. This was in contrast to the effects on RR reported from studies in Swedish riding horses, where males had a higher risk of being culled (Wallin et al. 2001).

Height at withers appeared to be a risk factor at the basic levels of both dressage and jumping (Table 5.4). Horses belonging to the highest quartile of height at withers at studbook entry appeared to have a higher risk of being culled in sports later in life. High growth rate is often supposed to be associated with less limb quality (e.g. osteochrondrosis). Selection on height at withers would indeed coincide with heavier bones and broader hooves, but diminish limb quality. The influence of height at withers on early retirement was larger for dressage than for jumping.

The role of height at withers in sport performance is contradictory, because larger horses are desirable for a higher ranking in dressage, as found by Ducro et al. 2008. However, apparently these oversized horses are also associated with early retirement in sports.

Pastern angle was also included in elite levels of both dressage and jumping. It appeared that the more upright angle, which is the score of the 1st quartile, had a lower risk of being culled. Apparently this trait is associated with protection against the intensive life at the elite level of sports. This is in accordance with the more upright pasterns in highly ranked jumping horses, but is in contrast to the weak pasterns seen in highly ranked dressage horses (Table 5.2). A weaker pastern seen in elite dressage may be interpreted as indicative of greater suppleness (Back et al. 1994), whereas a more upright pastern appeared to be favourable for jumping e.g. at take-off. Limb quality is a risk factor in jumping, both at the basic and elite levels, but it showed a curvilinear relationship with RR, since intermediate quartiles had the lowest risk of being culled. Uneven feet appeared to be a significant risk factor in elite jumping, as uneven feet almost doubled the risk of being culled.

In conclusion, limb conformation, and in particular, conformation of the distal limb, is important for sports performance. From the prevalence of uneven feet in the sports disciplines, it may be concluded that it is an undesirable trait, particularly at the elite level of jumping, since it has a detrimental effect on the length of competitive life in a sporthorse population.

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6

Genetic diversity in the Friesian Horse population using pedigree analysis

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To be Submitted

Abstract

The purpose of this study was to describe the impact of the breeding history on the genetic diversity in the Friesian Horse breed. The pedigree of the Friesian Horse comprising a total of 104,570 horses was analysed to ascertain the genetic history of the breed. The effective number of founders, effective number of ancestors, effective number of founder genomes and variance effective numbers were calculated for birth cohorts of 10 years from 1908 to 2008. To investigate whether inbreeding rate was affected by population subdivision a cluster analysis was performed on simulated gene probabilities, obtained from gene dropping, of individuals from the last year of the study. The results showed that the Friesian Horse breed has a high inbreeding level as a result of unequal founder contribution and genetic bottlenecks, but primarily due to drift from small effective population size during several generations since the foundation of the breed. Although 4 clusters could be identified, pairwise kinships showed that they were not very distinct from each other. From the decrease in kinship and the increased variance effective number it is expected that the rate of inbreeding will decrease in the future.

Key words: Genetic diversity, pedigree analysis, Friesian horse

6.1 Introduction

The Friesian horse is an old horse breed originating from the Netherlands with daughter studbooks in more than 30 countries. The Royal Friesian Horse Studbook has been registering horses since its foundation in 1879. The current size of the active breeding population is with about 100 stallions and 8 000 mares quite large. However, the history of the population shows several periods in which the active breeding population was much smaller (Osinga, 2000; Geurts, 1969). The breed has been closed over a long period of time and this has inevitably led to accumulation of inbreeding and decrease of genetic diversity. Besides the small population size during certain time periods and the closed status of the population, selection might have contributed to an increased level of inbreeding. These aspects combined lead to the Friesian breed being suspected to have high degree of inbreeding, which can cause inbreeding depression as well as high incidences for particular genetic defects. In several horse breeds increase in inbreeding was related to infertility and a high level of genetic defects (Cook, 1992). Sevinga et al. (2003) demonstrated that the high incidence of retained placenta in Friesian horses could be partly explained by inbreeding.

It is well documented that population subdivision might result in higher inbreeding rates (Falconer and Mackay, 1996). Population subdivision in the Friesian horse could result from insufficient exchange of genetic material between the different countries and differences in breeding goal between regions. Caballero and Toro (2000) showed that it is possible to ascertain the extent to which an inappropriate mating policy contributes to population subdivision. The degree of subdivision in the Friesian horse population is unknown.

The rate of inbreeding per generation (ΔF) can be calculated from pedigree information to evaluate the accumulation of inbreeding in a population (e.g. Boichard et al., 1997). The rate of inbreeding has certain shortcomings in practice, because its value depends on the completeness and the depth of the available pedigree. Additional descriptive measures derived by Lacy (1995) and Boichard et al. (1997) allow characterization of population dynamics, in terms of founder effects, genetic drift, and identification of the most influential ancestors.

Genetic diversity of the Friesian Horse population has never been described properly, but it is a prerequisite for the implementation of a sustainable breeding program. The Friesian Horse population is a closed population for many years which is known for its high quality of pedigree registration. This makes it an ideal population for the comparison of various measures of genetic diversity.

The aim of the study is to describe the impact of the breeding history on the genetic diversity in the Friesian Horse breed in terms of inbreeding and genetic representation.

6.2 Material and methods

Data

From its foundation in 1879 till November 2008, in total 104,570 horses were registered in the Friesian horse studbook. Each registration comprised parents, birth date and sex. Horses with missing parents were excluded from the analysis when they had less than 3 progeny and those progeny were not parents themselves. In other cases horses with missing parents were assumed to represent founder animals. Founder animals were supposed to introduce unique genomes to the population.

Missing birth dates of parents were arbitrarily set to 10 years before the average birth year of their progeny. The time interval of 10 years is approximately the generation interval in horses. An arbitrary birth year was set in records of 18 females.

The pedigree in this study included the registrations from the foundation of the studbook until the end of 2007. After editing the data consisted of 99,322 animals ,which descend from 24,879 dams and 887 sires. 18,000 dams had less than 4 progeny, and 159 dams had more than 15 progeny.

Quality of pedigree

Quality of the pedigree was assessed by calculating the proportion of ancestors known per ancestor generation for each individual animal.

Measures of genetic diversity

To identify factors influencing genetic diversity in time we defined birth-cohorts of 10 years from 1908 to 2007. A time span of 10 years was chosen as it corresponds to average length of generation interval in horses (Valera et al, 2005). Inbreeding (F) is computed following the method of Meuwissen and Luo (1992). The increase in inbreeding (ΔF) is obtained from the annual rate of inbreeding, multiplied by the generation interval. Mean kinship as proposed by Ballou and Lacy (1995) was calculated as the average of pairwise kinships between an individual and all reproductive individuals of a given population. For each cohort additional parameters characterizing the structure of the population were calculated. These parameters will be described in more detail.

Effective number of founders. Some founders have been used more intensely and therefore contribute more to the current population than other founders. The effective number of founders (f_e) (Lacy, 1989) has been developed to account for this phenomenon and it represents the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study. The effective number of founders is computed as $N_{ef} = 1/\sum_{k=1}^{N_f}(c_k/N)^2$ where c_k is the contribution the k^{th} founder and N_f is the number of real founders. All animals with both parents unknown are regarded as founders in this analysis. In addition, if one parent is unknown, then this parent is regarded as a founder. In case all founders contribute equally to the current generation, then the effective number of founders is equal to the real number of founders.

***Effective number of ancestors* (*f_a*).** The effective number of ancestors is the minimum number of ancestors (which may or may not be founders), required to explain the complete genetic diversity of the population under study (Boichard et al., 1997) . The parameter f_a does not fully account for account for gene loss by drift from the ancestors to the population under study but complements the information offered by the effective number of founders accounting for the unbalanced use of reproductive individuals producing bottlenecks. In computing f_a only the marginal contribution of an ancestor should be considered, which is the contribution made by an ancestor that is not explained by other ancestors chosen before. Boichard et al. (1997) has developed an algorithm to process a pedigree for identifying influential ancestors based on expected frequencies of alleles derived from founder k in the population under study.

According to long term genetic contribution theory (Bijma and Woolliams, 1999), it is expected that contributions of influential pedigree animals (founders or ancestors) will converge in about 5 to 7 generations. The ratio of effective number of founders to effective number of ancestors (f_e/ f_a) was therefore considered additionally, since it can be indicative for occurrence of genetic bottlenecks in the development of the population. If the ratio is close to unity, the population has been stable in terms of effectively contributing animals. If f_e is larger than f_a then the bottlenecks have played a role in the population formation (Sørensen et al., 2005).

Effective number of founder genomes **(f_g).** The effective number of founder genomes, f_g, accounts for both unequal contributions of founders, bottlenecks and random loss of alleles due to genetic drift (Lacy, 1989). It is defined in the same way as effective number of founders, but founder contributions are modified by the proportion of the founders' genes that are found in the reference population, r_i. As $(1-r_i)$ quantifies the proportion of alleles from the founder that are not expected to be present in the reference population, f_g takes account of random loss of alleles during bottlenecks. The effective number of founder genomes is calculated as

$f_g = 1/(\sum_{i=1}^{N} q_i^2 / r_i)$

where q_i is the contribution of the i^{th} founder and r_i is the proportion of genes of founder i that are found in the population.

With this definition, the interpretation is the number of equally contributing founders with no loss of founder alleles that would be expected to produce the same amount of diversity as in the population under study (Lacy, 1995).

The concepts of effective number of founders, ancestors and founder genomes highlights different causes of loss of genetic diversity and can be related to genetic diversity through (Caballero and Toro, 2000):

GDc*= 1 − 1/2f*, where GDc is the genetic diversity in birth cohort c, calculated from effective number of founders ($f^*=f_e$), ancestors ($f^*= f_a$), or founder genomes ($f^*= f_g$). Total loss of genetic diversity equals thus to $1/2f_g$ and loss due to unequal founder contribution equals to $1/2f_e$, and $1/2f_a$ represents loss due to genetic bottlenecks.

Variance effective number (N_e)

In each cohort the variance effective number (N_e), i.e the effective population size in terms of variances of family size was calculated according to Hill (1979):

$$\frac{1}{N_e} = \frac{1}{16ML}\left[2+\sigma_{mm}^2 + 2\left(\frac{M}{F}\right)\mathrm{cov}(mm,mf) + \left(\frac{M}{F}\right)^2 \sigma_{mf}^2\right] +$$
$$\frac{1}{16FL}\left[2+\left(\frac{F}{M}\right)^2 \sigma_{fm}^2 + 2\left(\frac{F}{M}\right)\mathrm{cov}(fm,ff) + \sigma_{ff}^2\right]$$

where M and F represents number of males and females, L is the average generation interval,σ_{mm}^2 and σ_{mf}^2 are the variances of the male and female offspring of a male, σ_{fm}^2 and σ_{ff}^2 are the variances of the male and female offspring of a female, and cov(*mm,mf*) and cov(*fm,ff*) the respective covariances. Except for variance effective number, calculations were performed using the software package Pedig by Boichard (2002). The variance effective number was calculated using the Endog software (Gutiérrez et al., 2005).

Gene dropping simulation

The frequencies of founder alleles (c.) in the population were obtained by performing a gene-drop method as proposed by MacCluer et al. (1986). In this method founder alleles are successively dropped through a pedigree from the founders to the entire set of their descendants. By repeating the gene drop process 10,000 times the distribution of frequencies of alleles from each founder was estimated which corresponds to the genetic contribution of the founder (Lacy, 1989). From the estimated distribution, the probability of extinction of alleles that originated from a given founder was calculated as the proportion of replicates in which both alleles from the founder were not present in the last birth-cohort.

Population subdivision

A quantitative measure of population subdivision of animals in birth cohort 1998-2007 was obtained by a K-means clustering to identify clusters of descendants having maximal common ancestry. Clustering was performed on the vector of allele frequencies, obtained from the gene dropping, of each individual in the last birth year. For each cluster, the mean value for ancestor j is the proportion of descendants in the cluster having j as an ancestor. Strong population subdivision corresponds to widely separated mean values in different clusters, so that each cluster has a very different pattern of ancestry. Cluster analysis was performed using Proc Cluster of SAS (SAS Inst. Inc., Cary. NC).

6.3 Results

Population size

The data contained 86 horses that were born before the year of foundation of the studbook (1879), of which the oldest was born in 1863. During the first years after foundation the number of foals registered each year

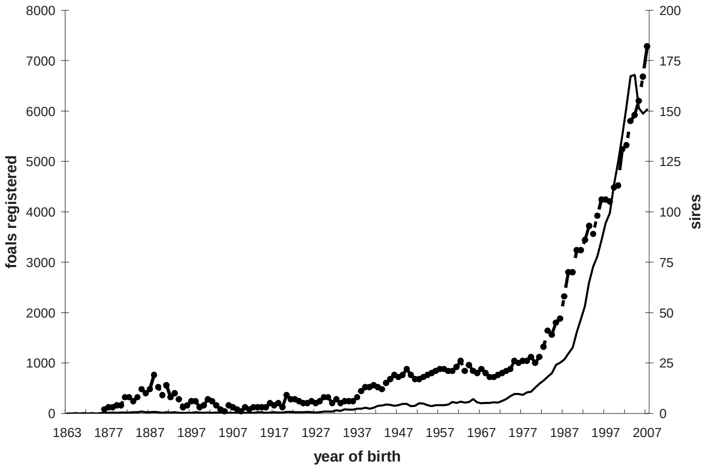

Figure 6.1 Number of foals registered per year (——)and number of sires with progeny per year (♦——♦).

remained small and came first above 50 foals in 1930. Until 1986 the number of foals yearly registered did not exceed 1 000 (Fig. 1). Since then there has been a considerable increase in population size and the number of yearly registered foals increased to a maximum of 6,719 in 2004 and remained approximately at 6,000 thereafter. The increase of population size

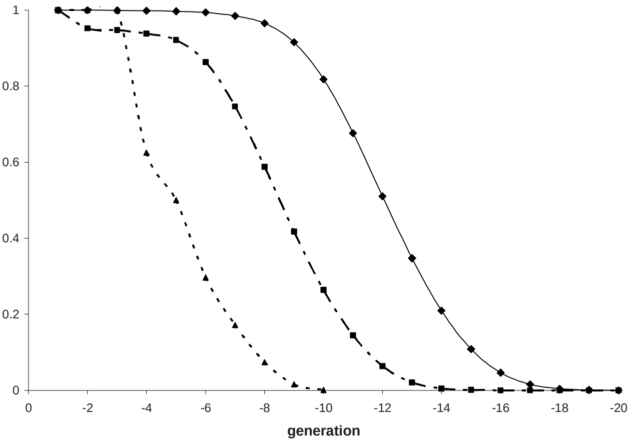

Figure 6.2 Proportion of ancestors known per generation back in time for cohort 1998-2007(♦——♦), cohort 1968-1977 (■– - – - ■) and cohort 1938-1947 (▲- - - ▲).

was accompanied by an increase in the number of breeding stallions and by an increase in the average number of progeny per sire. In 1986, 47 stallions were listed for breeding while in 2004 more than 140 stallions were listed for breeding. The average number of progeny per sire was 22 in 1986 and 45 in 2004.

Quality of pedigree data

The proportion of ancestors known per generation can be seen as a measure for the quality of pedigree registration. Figure 6.2 shows the average proportion of known parents in the first ancestral generation, of known grandparents in the second ancestral generation, of known great-grandparents in the third ancestral generation, and so on. This is shown for cohort 1998-2007, 1968-1977 and 1938-1947; each with a different registration length from the foundation of the studbook.

For cohort 1998-2007 the proportion of ancestors known was close to 100% up to the 6th generation and at least 90% of the ancestors were known up to the 9th generation. This means that at least 90% of the 1 022 ancestors were known (number of ancestors up to generation l is $2^{l+1} - 2$) . After the 9th generation the percentage of known ancestors decreased sharply and was 50% in the 12th generation and 10% in the 15th generation. For a few horses in the cohort 1998-2007 ancestors were known back to the 24th generation.

Earlier cohorts, e.g. cohort 1938-1947 and cohort 1968-1977 (Figure 6.2) had fewer generations known because registration started with the foundation of the studbook. The cohort 1968-1977 already had 5% missing parents in the 2nd generation and from 9th generation onwards proportion of known ancestors was less than 50%. Otherwise the pattern was very similar to the cohort 1998-2007. For the cohort 1938-1947 less than 50% of ancestors was known from generation 5 onwards, whereas the first 3 generations were almost complete.

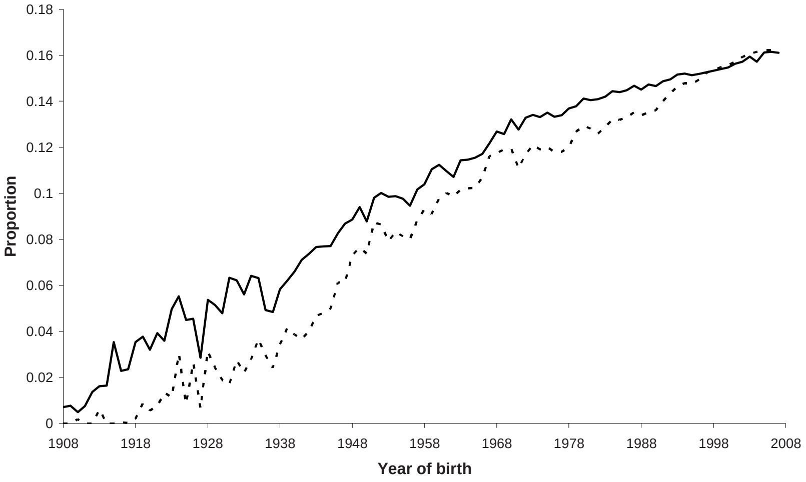

Figure 6.3 Average inbreeding coefficient (broken line) and kinship coefficient (straight line) per birthyear

Measures of population diversity

More than 90% of the horses in the population showed some degree of inbreeding and 20 horses had inbreeding coefficients between 0.35 and 0.38. These horses were all born in the last 3 cohorts of the study. Mean inbreeding coefficient per birth year increased from 0.02 in 1908 to 0.16 in 2007 with considerable fluctuations in the beginning (Figure 6.3). The value of 0.16 is higher than the level of inbreeding resulting from half-sib mating of unrelated parents (0.125). The rate of inbreeding amounted to 0.0015 per year. This corresponds to 0.015 per generation, when we assume a generation interval of 10 years in horses. Parameters on diversity are presented in Table 6.1 for birth cohorts between 1908 and 2007. All parameters showed a sharp decrease from first to second cohort. Number of founders showed further fluctuations in time, indicating that in later cohorts still animals with missing parents (i.e. founders) were present. The number of effective founders (f_e) showed much less fluctuations than the actual number of founders and became stable at 260 from the 8th cohort onwards. The effective number of ancestors (f_a) gradually decreased from 107 at the start to 9 in the last cohort and showed relative larger reductions in the 2nd and in the 5th cohort. Effective number of founder genomes (f_g), decreased from 67.6 to 3.0 during the period of analysis. Variance effective number was lowest in the second cohort and highest (124) in the two last cohorts of the study.

Table 6.1 Population size (N), number of founders (N_f), effective number of founders (f_e), effective number of ancestors (f_a), ratio of f_a and f_e (f_a/f_e), effective number founder genomes (f_g), and variance effective number (N_e), for birth cohorts from 1908 until 2007.

Cohort	Period	N	N_f	f_e	f_a	f_e/f_a	f_g	N_e
1	1908-1917	254	207	168	107	1.59	67.6	6.5
2	1918-1927	261	105	49	22	2.23	13.2	2.4
3	1928-1937	535	194	60	22	2.73	12.5	14.3
4	1938-1947	1431	396	55	20	2.75	9.0	25.3
5	1948-1957	1744	299	35	12	2.92	5.6	12.6
6	1958-1967	2144	282	31	11	2.73	4.7	7.7
7	1968-1977	2699	231	29	10	2.90	3.8	5.5
8	1978-1987	6488	260	28	10	2.80	3.5	32.5
9	1988-1997	21304	260	27	9	3.00	3.2	124
10	1998-2007	54417	260	26	9	2.89	3.0	124

Table 6.2 Sex, birth year and number of progeny of the 10 ancestors with the highest marginal contribution and the 10 founders with the highest full contribution to the last birth cohort.

	Sex	Yr of birth	contribution (%)	#prog
Ancestor-rank				
1	Male	1924	23.04	297
2	Male	1955	15.64	452
3	Male	1921	9.85	65
4	Male	1920	9.76	101
5	Female	1931	6.11	9
6	Female	1915	5.91	5
7	Male	1917	4.17	51
8	Female	1923	3.34	2
9	Male	1956	2.70	100
10	Male	1901	2.24	43
Founder-rank				
1	Male	1901	7.61	43
2	Female	1907	6.93	3
3	Male	1885	6.49	4
4	Female	1909	6.31	2
5	Male	1880	6.03	32
6	Female	1915	5.46	4
7	Male	1883	4.57	37
8	Male	1875	4.28	10
9	Male	1885	3.93	7
10	Female	1894	3.61	4

Influential ancestors

In table 6.2 details are presented about the 10 ancestors and 10 founders contributing the most to the last cohort (cohort 1998-2007). Largest marginal contribution was 23.04% and came from a male born in 1924, that had 297 progeny.

The youngest influential ancestors was born in 1956 and ranked 9 (Table 6.2). There were three females among the 10 most influential ancestors. The founder with the highest contribution was a male born in 1901 and had a contribution of 7.61%, which he descended to the population by 43 progeny. The youngest founder among the 10 most influential ones was a female born in 1915.

Cluster analysis

Figure 6.4 shows the dendrogram that resulted from the cluster analysis of the last birth year, divided in 10 clusters. The length of the branches reflect the distance between the average seeds of each cluster. When 10 clusters were allocated, distances between clusters were not significantly larger than distances within clusters. Significant differences between clusters were found when the number of clusters was reduced to 4. Figure 6.4 reveals that the increase from 4 to 10 clusters was almost entirely due to splitting of cluster I into 5 extra clusters.

Considering 4 clusters, almost 50% of the population belonged to cluster I, whereas cluster II comprised almost 30% of the population. These two clusters were also closest to each other and showed almost similar diversity measures (Table 6.3).

Cluster III and IV contained the remaining 20% of the animals. The average inbreeding coefficient in these clusters was slightly lower, whereas the average mean kinship between animals in the cluster was higher than in cluster I and II. The clusters III and IV were more isolated from the other two. Their average mean kinship indicated that a larger increase in inbreeding in coming generations might be expected when clusters are maintained.

6.4 Discussion

The aim of this study was to describe the impact of the breeding history on genetic diversity in the Friesian Horse. The Friesian Horse is a unique population with a long history of a closed population. Various measures of diversity were assessed in order to unravel the different processes that have contributed to the loss of diversity over time.

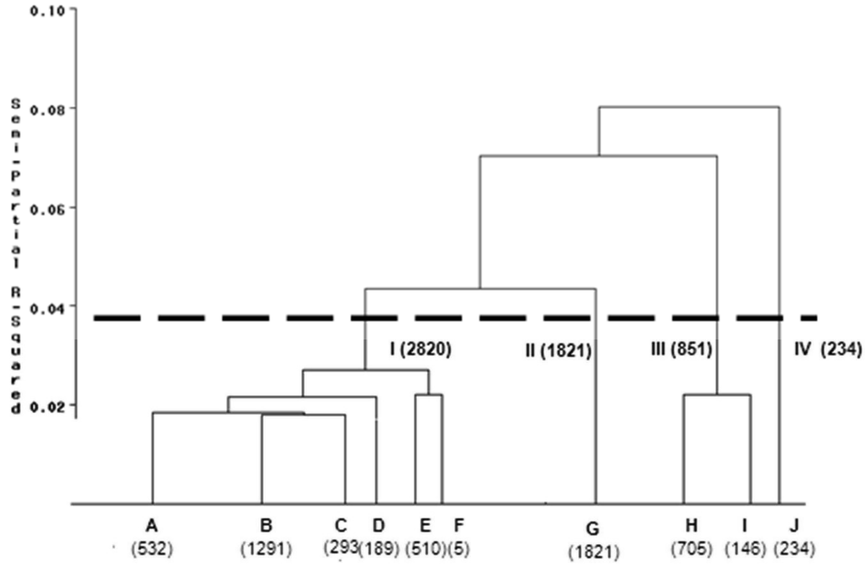

Figure 6.4 Dendogram of current generation divided in 10 clusters (A, .. J) with their sizes. The broken line represents the population divided in 4 significant clusters (I,..,IV). In brackets number of animals in each cluster.

Population size, completeness of pedigree

Since its foundation in 1879 the population size has increased from approximately 100 horses registered at foundation to more than 50 000 horses registered in the recent cohort. Almost three quarters of all registered horses were born in the last two cohorts.

Figure 6.1 shows that for the most recent cohort more than 90% of ancestors were known up to the 9th generation. Moureaux et al. (1996) investigated 5 different horse breeds in France and found that in these populations the proportion of known ancestors was less than 80% from the sixth generation onwards. From the eighth generation onwards, some breeds had less than 12% of ancestors known. For the Andalusian breed, Valera et al. (2005) found that 90% of ancestors were known for the first 5 generations, but it dropped to 33% in the tenth generation. For the Lipizzan breed, Zechner et al. (2002) found that 90% of the ancestors were known up to the ninth generation, after which the decline was slower than in the Friesian breed. This shows that the Friesian population like the Lipizzan population has been maintained as a closed population with a good pedigree recording for a long period of time.

Inbreeding and inbreeding rate

Average inbreeding coefficient in the recent cohort amounted to 0.16 and this is somewhat higher than in other breeds like values of 0.12 found in Andalusian (Valera et al., 2005), of 0.13 found in Thoroughbred (Cunningham et al., 2001), of 0.11 in Lipizzaner (Zechner et al., 2002) and values of 0.12 in the Scandinavian Doele and Nordland breeds (Saastamionen et al, 2005). However, it is well known that the average inbreeding coefficient is determined by the number of generations of ancestors and the completeness of the pedigree information (e.g. Caballero and Toro, 2000). The closed character of the Friesian population can explain the higher average inbreeding coefficient in the recent cohort. More important than the level of inbreeding is the rate of inbreeding which is surprisingly not mentioned in any of the studies. The rate of inbreeding in the most recent cohort of the Friesian population was 0.013.

Genetic diversity measures

Additional parameters have been developed which give more details about the causes of loss of genetic diversity during the history of the population. The conclusions that can be drawn from these parameters will be discussed. Effective number of founder genomes (f_g) showed three substantial reductions during the history of the population (Table 6.1). The first and largest reduction in number of founder genomes already occurred from the 1st to the 2nd cohort. During this period reductions in other parameters can be observed as well, e.g. the actual number of founders halved, which might point to exclusion of specific founder lines from further breeding. This is supported by the small variance effective number (N_e) in this cohort.

A 2nd reduction in effective number of founder genomes occurred from the 3rd to the 4th cohort. In the 4th cohort many new founders entered the population, but this did not result in an increase in the effective number of founders or effective number of ancestors.

The 3rd reduction in effective number of founder genomes followed occurred from the 4th to the 5th cohort, and was accompanied by a sharp decrease in effective number of ancestors. Here, the ratio of effective number of founders to ancestors (f_e/f_a) showed that effective number of ancestors decreased more than the number of founders, indicating that a genetic bottleneck occurred in this cohort. This cohort was the first generation after WWII.

From the 6th cohort onwards effective number of founders, ancestors and founder genomes all showed small but steady decline and the constant ratio of effective number of founders to ancestors indicated that no further bottlenecks occurred after WWII. Loss of genetic diversity in that period as reflected by effective number of founder genomes from that point on, was mainly due to drift.

Interestingly, an additional bottleneck is suggested by low variance effective number (N_e), during the 6th and 7th cohort (Table 6.1). This bottleneck is referred to in literature (Osinga, 2000) and is associated with increased mechanization in agriculture at the expense of horses. From the other diversity measures it can be seen that this presumed bottleneck hardly had an effect on the diversity in the population. This shows that despite the low effective population, there was no large loss of genetic diversity in that cohort. This can be explained by the fact that the genetic contributions of influential ancestors had already reached their equilibrium values by that time.

In the early-eighties of the last century, artificial insemination was introduced in horse breeding. Artificial insemination reduces the number of stallions needed for the production of the next generation and could, therefore, affect genetic diversity. In our analysis (Table 6.1) we did not detect a reduction in genetic diversity. Introduction of artificial insemination coincided with the population expansion, which counteracted the effects of artificial insemination. Interestingly, loss of genetic diversity as a consequence of introduction of AI has not been mentioned in horses in literature.

The evolution of diversity parameters over the cohorts in the study revealed that loss of genetic diversity due to unequal founder contribution amounted to 2% and loss due to bottle necks amounted to 4%. The major loss of genetic diversity (10%), however, was caused by drift which resulted from the small effective population size during several generations since the foundation of the breed.

Influential ancestors

The effective number of founders to the recent cohort was estimated to be 26. We analysed the pedigree to determine founders and ancestors that made a major contribution to the recent cohort (Table 6.2). This analysis revealed that the 10 most influential founders explained 52% of the genetic diversity in the recent cohort. These founders were born between 1880 and 1915. The 10 most influential ancestors explained 83% of the genetic diversity of the recent cohort. These ancestors were born between 1901 and 1956. The ancestor with the largest marginal contribution (23%) was a stallion born in 1924.

Effective number of founders (f_e) is less influenced by the number of generations in the pedigree which facilitates a better comparison to other studies. The f_e found in the Friesian breed is lower than number of 40 found in Andalusian (Valera et al., 2005) and of 48 found in Lipizzaner (Zechner et al., 2002) , but comparable to the number of 28 found in Thoroughbred (Cunningham et al. 2001). The most influential founder contributed 8.2% in the Andalusian breed (Valera et al., 2005), whereas 7.6% in Thoroughbreds (Cunningham et al.,2001) and 6.7% in Lipizzaner (Zechner et al., 2002).

Only 4 ancestors are needed in the Friesian breed to explain 50% of the genetic diversity of which three were born before the first bottleneck i.e. in the first cohort. In the Andalusian breed 6 ancestors were needed to explain 50% of the genetic diversity (Valera et al., 2005) and in the Lipizzan breed 8 ancestors were needed (Zechner et al., 2002). The most influential ancestor contributed 23% to the gene pool in the Friesian breed, and this is considerably larger than 15.8% in the Andalusian (Valera et al., 2005) and 10.7% in the Lipizzan (Zechner et al., 2002).

The contribution of the most influential ancestor to all animals in the recent cohort was very similar, as is reflected by the standard deviation of 1.5%. This is in agreement with the theory of long term genetic contribution (Bijma and Woolliams, 1999 which states that after a number of generations the contribution of an ancestor has reached an equilibrium value.

Population subdivision

Compared to other breeds, the Friesian breed comprised a small number of influential ancestors with each having a large contribution. The Lipizzan and Andalusian breeds are characterized by division of the population into predefined strains which are located in different countries or regions. Population subdivision hampers the spread of genes throughout the population and could be the reason of smaller contributions of influential ancestors in the Lipizzan and the Andalusian breed. Population subdivision on the other hand may contribute to maintenance of genetic diversity at the breed level (Fernandez et al., 2008). Our study revealed some degree of population subdivision in the Friesian breed (Figure 6.4). The contributions of influential ancestors to the different clusters were very similar. The subpopulations were genetically not very distinct, as can be seen from the average pairwise kinships between individuals in the different clusters (Table 6.4). The subpopulations were geographically not very distinct and were spread equally over regions in the world. Breeding strategies aiming at overcoming the population subdivision will therefore not aid much to reduction of the rate of inbreeding.

Implications

In the entire period of study rate of inbreeding, was higher than 1% and thus above the recommended level (FAO,1998; Bijma 2000). In the current cohort the rate of inbreeding was 1.3%. Reduction of the rate of inbreeding in future generations is therefore necessary. Since 1979, the Friesian Horse Studbook is providing information to breeders on inbreeding coefficients for new offspring, and is advising against using sire-dam combinations that produce offspring with an expected inbreeding coefficient calculated over 5 generations that exceeds 5% (Sevinga et al., 2003). This measure is expected to result in delaying but not avoiding inbreeding. Further measures taken by the Studbook were imposing a maximum number of matings for breeding stallions since 1990 and since 2005 kinship percentages of breeding stallions have been published. The earlier measures have probably contributed to the reduction of the rate of kinship from 1980 onwards (Figure 6.1). However, it is important to realize that the sharp increase of the population size in recent years has contributed as well. In the last two cohorts the variance effective number has increased considerable (Table 6.1), indicating that variation in family size has been smaller. This is likely caused by imposing of mating quota. From the decrease in the rate of kinship in the recent generation, it is expected that the rate of inbreeding will decrease in the future.

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7

Genetic parameters and founder inbreeding depression on semen quality in Friesian horses

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To be submitted

Abstract

The Friesian horse breed has been a closed breed for many generations and, despite its current size, effectively it is a small population. Average semen quality is relatively low, possibly due to inbreeding depression. The objective of this study was to evaluate the importance of additive genetic factors and inbreeding, (both overall and partial inbreeding), on semen quality of Friesian horses. Semen quality was investigated for 1146 stallions submitted for breeding soundness examination. Inbreeding calculations were based on 8 generations of known pedigree. Heritabilities were moderate and varied between 0.16 (volume) and 0.27 (motility), except for percentages of normal cells and abnormal acrosomes with heritability estimates of 0.52 and 0.60. Most of the genetic correlations among semen quality traits were favourable. Inbreeding, both overall and partial inbreeding, did not have significant effects on semen quality traits. because of moderate to high heritabilities and substantial variation in semen quality traits, it can be concluded that semen quality of Friesian stallions can be improved by selection.

Key words: heritability, semen quality, Friesian horse, inbreeding depression, partial inbreeding

7.1 Introduction

Closed populations of limited size with skewed ratios of males to females might suffer from high inbreeding rates. High inbreeding rates are associated with a higher prevalence of genetic defects and a decline in performance, usually known as inbreeding depression (e.g., Falconer and Mackay, 1996). In domestic species, inbreeding depression has been demonstrated for various traits, including milk production in dairy cattle (Miglior et al., 1995), birth weight and litter size in sheep (Norberg et al., 2007), growth in pigs (Fernandez et al., 2002) and longevity in pigs (Casellas et al., 2009). Effects of inbreeding on reproductive performance in horses have been demonstrated by Cook (1992) who showed that inbreeding was related to infertility in several horse breeds. Inbreeding depression has also been reported to negatively influence male reproductive capacity (e.g. O’Brien et al., 2001). In Shetland ponies semen quality was negatively affected by inbreeding (van Eldik et al., 2006).

Severity of inbreeding depression might differ between breeds as a result of differences in recessive genetic load that a population carries. Uneven distribution of load among founder genomes can lead to between-founder heterogeneity in the extent to which inbreeding affects performance (Lynch, 1988) . If inbreeding depression is mainly due to alleles with large effects then considerable differences due to founder specific inbreeding might be expected. Some researchers have therefore proposed a way to account for inbreeding depression by modelling founder-specific partial inbreeding coefficients instead of analysing the overall inbreeding coefficients (Rodriganez et al., 1998; Gulisja et al., 2006). Application of this approach allows for a substantial heterogeneity of inbreeding depression effects in inbred descendants ranging from negative to even positive effects on litter size in swine (Rodriganez et al., 1998) and milk yield in dairy cattle (Gulisja et al., 2006).

The Friesian horse breed has been a closed breed for many years with a relatively high inbreeding rate (Ducro et al., submitted). Average semen quality in Friesian stallions is lower than in many other horse breeds (Van Buiten, 2005). Almost 50% of the Friesian stallions submitted for breeding soundness examination are excluded from breeding because of insufficient semen quality, whereas the semen quality criteria are lower than applied in other breeds. Improvement of semen quality is therefore desired to avoid any further loss of genetic diversity due to elimination of potential parents based on low reproduction. In order to improve semen quality through selective breeding it is important to know whether the trait is heritable. As shown by Ducro et al. (submitted), ancestral contributions to the genetic diversity are highly unbalanced with only a very few ancestors being responsible for the genetic make-up of the current generation. Bad semen quality could therefore be due to inbreeding on specific ancestors. This study aims to determine whether the degree of inbreeding affects semen quality in Friesian horse stallions, and whether semen quality is heritable and therefore amenable to improvement by selection.

7.2 MATERIALS AND METHODS

Animals

Semen quality of 1146 Friesian stallions was assessed in the months September, October and November of the years 1987-2002. The stallions were submitted to stallion inspection by their owners as being suitable for consideration as potential breeding stallion based on conformation, but had not been subjected to any other selection procedure. The age of the stallion at the time of semen evaluation ranged from 24 to 47 months.

The ‘founding’ population of the stallions was set to 8 generations back, because almost all stallions had a known pedigree to the 8th generation. This avoids potential bias due to differences in completeness of the pedigree. Two stallions could not meet the requirement of complete pedigree and these were discarded from further study.

Semen evaluation

Evaluation of semen quality was performed using standard techniques and parameters described previously for routing breeding soundness examinations of stallions (Colenbrander et al., 1992). The standard breeding soundness examination consisted of 2 ejaculates collected at an interval of approximately 1 hour.

For each ejaculate, gel-free volume, sperm concentration and the percentage of sperm displaying progressive motility were registered. In addition, a minimum of 200 spermatozoa including at least 100 live sperm were evaluated and categorized as being live or dead, and as being normal or having abnormalities of head, acrosome, mid-piece or tail (van Eldik et al., 2006). Finally, the total number of morphologically normal, progressively motile sperm per ejaculate (TNM) was calculated. TNM was calculated as a multiplication of the four traits gel-free volume, concentration, percentage progressively motile sperm and percentage morphologically normal sperm.

In the current study, only the second ejaculate of all stallions was analyzed. Because of sexual inexperience of most stallions, the first collection was in many cases the actually the first ejaculate produced, and therefore, the second ejaculate was considered to give a more reliable indication of semen quality than the first one.

Overall and partial inbreeding

The overall inbreeding coefficient reflects the probability that two alleles at a given locus are identical by descent (Malécot, 1948), irrespective of the founder the allele originated from. Partial inbreeding coefficients are the probabilities that an individual is homozygous for an allele descending from a specified founder. The sum of the partial inbreeding coefficients across all founders for an individual is equal to the inbreeding coefficient of that individual. A founder is an individual lacking genetic relationships to any other individuals in the pedigree, except to its descendants; the set of all such individuals represents the source of the gene pool of a population. Overall Inbreeding coefficients were calculated with the algorithm as proposed by Meuwissen and Luo (1992) implemented in the software package PEDIG (Boichard, 2002). Partial inbreeding coefficients have been calculated using the method of Lacy et al. (1996) for calculating inbreeding coefficients based on a modification of the matrix with additive genetic relationships.

Selecting influential founders

A set of 20 founders was selected, which had highest genetic contribution to the set of stallions under study. Together they explained about 80 % of the genetic diversity in the sample.

Since little variation in partial inbreeding coefficients will produce inaccurate estimates of regression coefficients with large errors, additional restrictions were imposed that a founder should have a partial inbreeding different from zero for at least 100 individuals in the current data observations and that at least 10 descendants had a partial inbreeding coefficient of at least 1% .

Statistical analysis

Six semen characteristics were investigated: gel-free ejaculate volume, sperm cell concentration, percentage progressively motile sperm, percentage morphologically normal sperm, TNM and the percentage abnormal acrosomes, which is part of morphology.Before analysis, sperm concentration and percentage abnormal acrosomes were log transformed and TNM was square-root transformed, to produce a closer approximation of a normal distribution.

The observations were analyzed using the following linear model:

$$Y_{ijkl} = \mu + \text{year}_i + \text{month}_j + \text{age}_k + \text{animal}_l + e_{ijkl}$$

Where:

Y = dependent variable (TNM, concentration, volume, motility, % normal sperm or % abnormal acrosomes)
μ = mean
year = fixed effect of year class i [1987-1989, 1990-1992, 1993, 1994, …, 2002]
month = fixed effect of month j [September, October, November]
age = fixed effect of age class k [2.5, 3.5]
animal = random animal effect, distributed as $N\left(0, A\sigma_a^2\right)$ where A is the additive genetic relationship matrix and σ_a^2 is the additive genetic variance
e = random error, distributed as $N\left(0, I\sigma_e^2\right)$ where I is the identity matrix and σ_e^2 is the residual variance

Because of low numbers of examined stallions per year from 1987 till 1992, these years were grouped in two classes, 1987-1989 and 1990-1992. Stallion age was grouped in two age classes: 24-35 months (<3 years) or 36-47 months (≥ 3 years) old. When a stallion appeared to have insufficient semen quality at the age of 2 years, it was sometimes resubmitted by the owner a year later, with the idea that semen quality improves when a stallion becomes more mature (Dowsett and Knott, 1996). In that case, only the last examination was analyzed. Of the 318 3-years-old animals, 132 had a second semen examination. In total, the last ejaculate of 1146 stallions were analyzed.

A random animal component was added to the model to account for genetic relations. Eight generations of the pedigree were included for setting up the additive genetic relationship matrix. Genetic analyses were performed using the ASReml package (Gilmour et al., 2002). Bivariate analyses were performed to obtain genetic and residual correlations

Partial inbreeding depression on semen quality was estimated by including linear regression coefficients for the founders selected into the analysis of variance. Due to the long period of data collection there is a risk that effects of inbreeding and year are (partly) confounded. It was therefore decided to exclude the observations from before 1997 from this analysis Number of observations reduced by 249 observations to 895. Additionally, the genetic variance was fixed at the estimate found in the complete analysis.

The observations were thus analyzed using the following linear model:

$$Y_{ijkl} = \mu + \mathrm{year}_i + \mathrm{month}_j + \mathrm{age}_k + b*\mathrm{Frmn}_l + \Sigma\, b_{fl}*\mathrm{Ffnd}_{fl} + \mathrm{animal}_l + e_{ijkl}$$

Where:

Y = dependent variable (TNM, concentration, volume, motility, % normal sperm or % abnormal acrosomes)

μ = mean

year = fixed effect of year class i [1997, …, 2002]

month = fixed effect of month j [September, October, November]

age = fixed effect of age class k [2.5, 3.5]

Frmn = remaining inbreeding coefficient

Ffnd_f = partial inbreeding coefficient of inbreeding on founder f (f=1..6)

b = regression coefficient

animal = random animal effect, distributed as $N\left(0, A\sigma_a^2\right)$ where A is the additive genetic relationship matrix and σ_a^2 is the additive genetic variance

e = random error, distributed as $N\left(0, I\sigma_e^2\right)$ where I is the identity matrix and σ_e^2 is the residual variance

Table 7.1. Mean and standard deviation (std.) of semen quality traits.

Variable	Code	Mean	Std.
TNM	TNM	1815.94	1716.50
TNM – transformed[1)]	TNMtrf	38.36	18.33
Ejaculate volume (ml)	Vol	53.49	24.59
Ejaculate volume – transformed[1)]	Vol.trf	3.88	0.45
Sperm cell concentration (x10^6/ml)	Conc	109.33	115.99
Sperm cell concentration – transformed[1)]	Conc.trf	1.85	0.42
Progressively motile sperm(%)	Motil	66.83	12.60
Morphologically normal sperm (%)	Morph	52.93	15.62
Abnormal acrosomes (%)	Acrosome	32.99	19.67

[1)] Volume and Concentration were log transformed and TNM was square-root transformed

The remaining partial inbreeding (Frmn, i.e. inbreeding due to the remaining founders which were not separately included in the analyis) was defined as, Frmn = F- Σ ($Ffnd_f$), where Σ ($Ffnd_f$) represents summation over partial inbreeding coefficients of the selected founders.

Additionally, an analysis was performed in which the set of remaining and partial inbreeding coefficients were replaced by the overall inbreeding coefficient. Testing whether partitioning of the overall inbreeding into founder inbreeding significantly improve the fitting of the model was performed using an F-test on the residuals.

There is a risk of high colinearity between partial inbreeding coefficients due to historical breeding structures in the population. Consequently, regression estimates might become unstable as a result of high colinearity. To identify potential colinearity between Ffndf , correlation coefficients between founder inbreeding coefficients were computed.

Table 7.2 Genetic standard deviation (σ_a), heritability2) (diagonal), residual (above diagonal) and genetic (below diagonal) correlations between semen quality traits

	σ_a	TNMtrf	Vol.trf	Conc.trf	Motil	Morph	Acrosome
TNMtrf1)	10.18	0.29	-0.12	0.72	0.34	0.42	-0.08
Vol.trf	0.15	-0.01	0.16	-0.40	0.07	0.05	-0.00
Conc.trf	0.21	0.78	-0.57	0.21	0.06	0.16	-0.07
Motil	6.58	0.61	0.38	0.27	0.27	0.59	-0.03
Morph	11.30	0.64	-0.01	0.14	0.34	0.52	-0.18
Acrosome	15.41	-0.52	0.20	-0.15	0.01	-0.91	0.62

1)For explanation on trait names, see Table 7.1.
2)Standard error on heritabilities < 0.07, on genetic correlations < 0.1

7.3 RESULTS

Semen quality parameters

Two of the six traits under study showed relatively large standard deviations, exceeding or almost exceeding the averages of the traits in case of TNM and concentration (Table 7.1). After data transformation the standard deviations were considerably reduced relative to the mean and the traits were approximately normally distributed. The percentages of progressively motile sperm and morphologically normal sperm were at intermediate levels (66.83% and 52.93% resp.) of the scale, whereas percentage of abnormal acrosomes was on average 33% (Table 7.1).

Heritability and genetic correlation

Heritability estimates were moderate to high, ranging from 0.16 for volume to 0.62 for abnormal acrosomes (Table 7.2). Genetic and residual correlations between the six traits were estimated simultaneously in a multivariate analysis (Table 7.2). Highly negative genetic correlation was found between percentage of morphological normal cells and percentage of abnormal acrosomes. Motility was genetically positively correlated to volume and concentration, indicating that selection on motility will increase both volume and concentration. TNM showed substantial positive genetic correlations to the underlying traits ranging from 0.61 for motility to 0.78 for concentration.

Table 7.3. Mean, standard deviation (std) and maximum (max) of partial inbreeding coefficients (%) due to founders, and number of observations with partial inbreeding over 0 (=#-nonzeros).

Founder code	Birth year	Mean	std	Max	#-nonzeros
f5	1915	0.31	0.24	2.42	1030
f6	1916	0.78	0.97	9.75	897
f12	1913	1.77	1.11	6.42	122
f15	1910	0.30	0.27	2.28	585
f26	1924	0.94	0.83	6.23	115
f28	1922	1.59	1.00	6.39	201

Overall and partial inbreeding percentages

Overall inbreeding coefficients of the stallions ranged between 11% and 22% . Mean inbreeding was 15.58% with a standard deviation of 1.6%.

The stallions descended from 1000 founders, which corresponded to 300 effective founders. Out of the 20 most influential founders, 6 founders were selected that met the criteria of at least 100 descendants in the analysis and at least 10 descendants with partial inbreeding of more than 1% on this founder (Table 7.3). All selected founders appeared to be females and were born between 1910 and 1924. Mean partial inbreeding coefficients varied between 0.30% for founder f15 and 1.77% for founder f12. Out of the 895 records analysed, 781 were partially inbred on founder 5 and 115 were partially inbred on founder 15. Two animals had a partial inbreeding coefficient of more than 9% on founder 6.

Overall and partial inbreeding depression

Overall inbreeding coefficients were negative for all traits, except for volume. Standard errors showed however that none of the estimates were significantly deviating from zero (Table 7.4).

The partitioning of overall inbreeding into partial inbreeding did not significantly improve the fitting of the model for any of the traits, as was pointed out by the F-test results. The regression coefficients for the partial inbreeding coefficients show that there are differences in inbreeding depression between founders (Table 7.4). For the trait volume the regression coefficients for the partial inbreeding coefficients varied from -0.052 for founder f6 to 0.026 for founder f8. Inbreeding on founder f12 tended to reduce percentage morphological cells and to increase of percentage of abnormal acrosomes. However, none of these regression coefficients differed significantly from zero.

Table 7.4. Estimate (est.) and standard error (s.e.) of overall inbreeding (F), partial inbreeding depression of founders f5 … f28) and remaining inbreeding (Frmn) on semen quality traits

		TNMtrf	Vol.trf	Conc.trf	Motil	Morph	Acrosome
F	est	-0.569	0.013	-0.014	-0.258	-0.389	-0.330
	s.e.	0.408	0.009	0.009	0.271	0.356	0.432
Partial							
f5	est	0.799	0.042	0.003	-1.870	-0.368	-1.177
	s.e.	3.215	0.068	0.072	2.170	2.930	3.621
f6	est	0.101	-0.052	0.019	-0.210	-0.325	-0.360
	s.e.	0.898	0.015	0.020	0.605	0.818	1.010
f12	est	-1.197	-0.004	-0.016	-0.548	-1.789	2.097
	s.e.	0.930	0.021	0.021	0.628	0.799	0.963
f15	est	-5.373	-0.041	-0.070	-0.785	-3.501	2.956
	s.e.	2.768	0.059	0.061	1.808	2.378	2.902
f26	est	1.583	0.028	0.048	-0.137	0.532	-0.658
	s.e.	1.560	0.034	0.036	1.054	1.345	1.623
f28	est	-0.664	0.026	-0.030	-0.203	0.187	-1.310
	s.e.	0.857	0.010	0.020	0.578	0.741	0.896
Frmn	est	-0.683	0.031	-0.023	-0.184	-0.186	-0.766
	s.e.	0.520	0.011	0.012	0.351	0.460	0.561

7.4 DISCUSSION

The aim of this study was to identify genetic factors (additive genetic, overall inbreeding, founder inbreeding) affected semen quality of Friesian stallions. By identifying these factors proper action can be taken to improve semen quality with the ultimate goal of improving reproduction in the Friesian horse breed.

For semen quality only second ejaculates were considered because for most of the stallions the first ejaculate was the first one ever produced. These stallions have often a better second than first ejaculate with a higher total number of spermatozoa. The majority of the stallions have a higher percentage of progressive motile spermatozoa and a higher percentage of morphologically normal live spermatozoa in the second ejaculate. Moreover, the first ejaculate might contain more aged spermatozoa.

Average values for TNM was only a third of the values seen in Dutch Warmblood (5 billion ; Parlevliet et al., 1994) and were more comparable to Shetland ponies (1.8 billion; Van Eldik et al., 2006). Ejaculate volume was 65 ml in warmblood and 23 ml in Shetland ponies and volume in this study was close to values observed in warmblood horses (Parlevliet et al., 1994). Concentration in Friesian was only half of what is commonly observed in warmblood and Shetlands. The morphology of spermatozoa plays an important role in fertility in stallions (Dowsett and Pattie, 1982; Jasko et al., 1990) and Friesian stallions from this study had lower values for morphology as compared to Shetland ponies (58%) and Dutch warmblood horses (65%). Motility, reflecting competitive fertilization performance (e.g. Oettle, 1993), was higher both in Shetland ponies (68%) and Dutch warmblood (70%) as compared to Friesians. The acrosome is particularly important in the fertilizing process, which means that a stallion with a high percentage of acrosomal abnormalities might be considered subfertile. The most striking difference as compared to other breeds was seen in the percentage of abnormal acrosomes,: values in the Friesian horse were more than twice as high as compared to Shetland ponies and more than three times as high as compared to warmblood.

Heritability and genetic correlations

Heritability estimates were moderate and varied between 0.16 (volume) and 0.27 (motility), except for percentages normal cells and abnormal acrosomes with estimates of 0.52 and 0.60. Most were different from values reported by Eldik et al. (2006), however standard errors of estimates by Eldik et al. (2006) were large due to the small sample size. The genetic correlations show that selection for TNM improves concentration, motility and morphology.

Minimum values for semen quality of the young stallions in order to get registered in the studbook is a mean total number of progressively motile morphologically normal spermatozoa of $1000*10^6$ and a mean of 50% for motility and morphology. Every year approximately 50% of the Friesian stallions submitted do not pass this semen test. Young stallions that acquire the minimal values of parameters of the semen cause problems during the breeding season when they have to serve many mares or when semen has to be stored and transported. Predicting the breeding potency of stallions can therefore be of great benefit for the stud farm and the mare owner.

Overall and partial inbreeding

Almost all founders of the Friesian horse population are represented in the present study. Average inbreeding in the sample used in this study is in agreement with the average inbreeding found in the total Friesian horse population (Ducro et al., submitted). Moreover, inbreeding level of the stallions included in this study in time and the rate of increase corresponded to the inbreeding rate seen in the entire population.

Overall and partial inbreeding depression

Except for volume, all regression coefficients for overall inbreeding were negative. However, none of the semen traits was significantly affected by overall inbreeding. A positive effect of overall inbreeding on ejaculate volume was also found in Shetland ponies (Eldik et al., 2006).

The existence of heterogeneity in inbreeding depression can explain the controversial effect of inbreeding on sperm quality as found in several studies (Fitzpatrick et al., 2008). Results are depending on the genetic load a population is carrying and may therefore vary between populations. This is in particular true when alleles with large effects are playing a role.

The present study showed that there is variation in partial inbreeding coefficients. However, the effects were not significant. Differences in effects on inbreeding depression of alleles descending from specific founders could therefore not be demonstrated.

The results could have been affected by correlation coefficients among partial inbreeding coefficients. Correlations between partial inbreeding coefficients of these 6 founders included in this study were moderate and varied between 0.15 and 0.57. Therefore colinearity was considered not to cause any serious problems in the analysis.

From this study it can be concluded that semen quality traits of Friesian stallions were lower compared to other horse breeds, in particular

percentage of abnormal acrosomes. The semen quality traits showed moderate to high heritability estimates. Morphology and acrosome showed both high heritability estimates and relative high genetic variance. Improving these traits by selection should therefore be possible.
Inbreeding, either overall inbreeding or partial inbreeding from a set of founders, did not have a significant effect on semen quality traits in Friesian stallions.

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8

General Discussion

8.1 Introduction

Most warmblood horse studbooks aim to breed horses that can perform at high level in dressage or show-jumping competition. Performance in competition depends on the interplay of the ability of the horse and its rider. The ability of the horse does not only concern its physical ability, but also its character which comprises elements of willingness to learn, persistency and cooperative behaviour. Performing at a high level in competition requires many years of training and thus the horses' full ability for sports is in general first shown around an age of 10 years. Consequently, if breeding decisions are based on own performance, those have to be postponed until that age. Similarly the owner of a horse has to wait a long time before finding out whether or not training for a sport career was worth the investment. Therefore, both from a genetic and a training perspective, there is a need for traits measured early in life which can be used to predict the potential of a horse for sports.

In this thesis it was shown that traits on movement and jumping measured at young age appeared to have a strong genetic relation to performance in competition at later ages. Traits measured on young horses during two different inspections have been genetically analysed. The first (Chapter 3) concerned a genetic analysis of data collected on young stallions that participate in the First Stallion Inspection. The analyses indicated that measurements on free jumping and free movement have moderate to high heritabilities and moderately to highly favourable genetic correlations to the corresponding disciplines in competition. In particular, high correlations where found (0.85) between free jumping recorded during the First Stallion Inspection and show-jumping in competition. The second analysis (Chapter 2) concerned a genetic analysis of data collected on young horses during Studbook Entry. The analysis revealed that these traits were also favourably correlated to the corresponding sport traits, but correlations were less strong than traits measured during First Stallion Inspection.

The aim of this General Discussion is to determine the contribution of various traits collected during various stages of the breeding program to the accuracy of selection and to the selection response. First, an overview will be given of the information collected at different stages of the breeding program. This includes information specifically collected on stallions but also information collected during field and performance tests which are mainly meant for mares and geldings. Secondly, the role and relevance of each of the information sources will be discussed and thirdly, ways to improve the current breeding scheme will be discussed.

8.2 Studbook testing procedures

Studbooks organize several tests for young horses, starting at an age of 2.5 years (Figure 8.1), with the purpose to get an early indication of the sports ability of the horses. The owner can use the results of these tests for own use, (i.e. to decide whether or not it is worthwhile to invest in training the horse). Furthermore, the studbook can use the results for estimation of breeding values of selection candidates for the breeding program. The studbooks focus on the selection of stallions, their influence on the selection of mares is limited. The selection decisions on mares are mostly taken by their owners. Yet, several tests for mares and geldings are offered by studbooks with the aim to gain insight in sport performance of those horses that do not yet participate in competition. The studbook encourages participation of mares in these tests by offering certificates for mares when meeting minimum requirements.

The stallion breeding program consists of a series of tests. A young stallion needs to pass all subsequent stages in order to get approved as a breeding stallion.

A general outline of the KWPN testing scheme is given in Figure 8.1. The different tests in the testing scheme are discussed in more detail in the following sections.

First Stallion Inspection

On a voluntary basis breeders can decide to submit their young stallion to the First Stallion Inspection which takes place at an age of 2.5 to 3 years. The inspection is held at one location in the Netherlands. During this one day field test, the young stallions are scored by a jury for conformation and, depending on the selection discipline (dressage or jumping), on traits regarding free movement or free jumping.

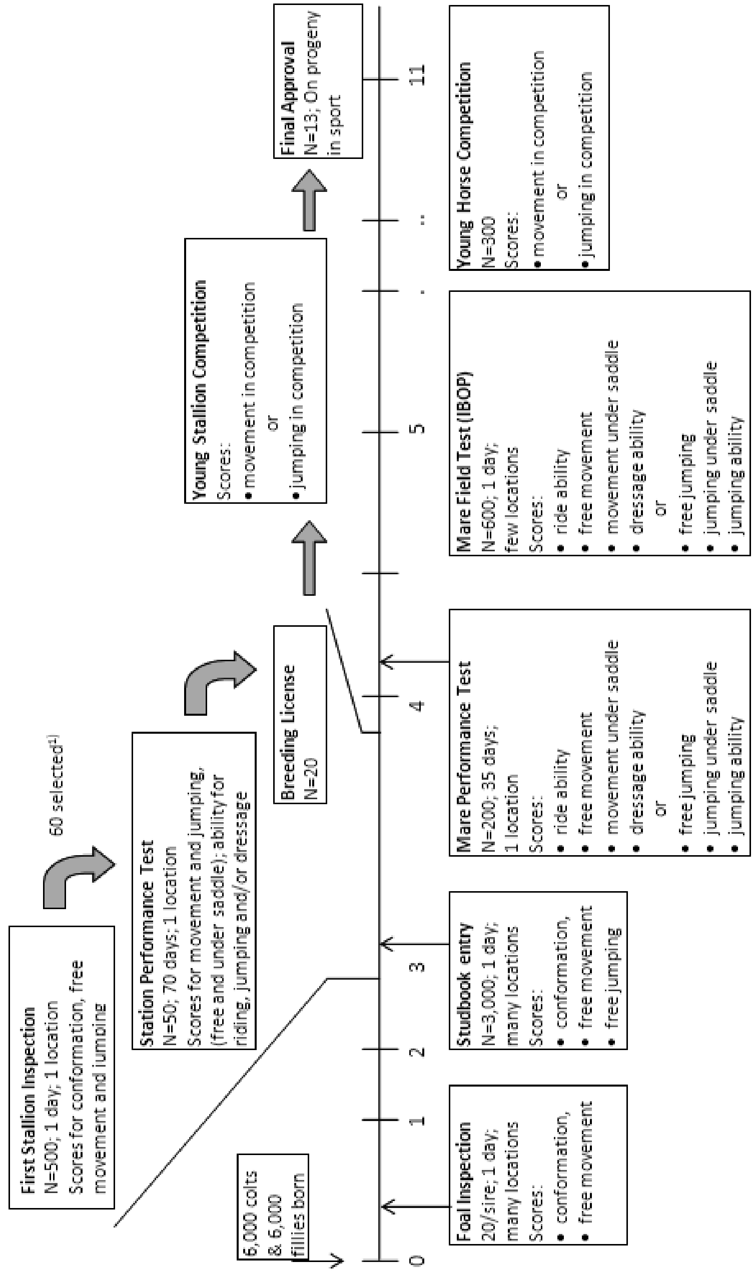

Figure 8.1. Testing scheme of Dutch Warmblood Studbook (KWPN) related to age of testing for stallion selection (above age axis) and mare tests (below age axis) with approximate number of horses, number of locations and traits measured. 1) out of 60 selected, on average 10 stallions are excluded on secondary traits (health reproduction)

Based on the results during First Stallion Inspection, stallions are selected for the Station Performance Test. Data collected at First Stallion Inspection formed the basis of the genetic analyses described in Chapter 3.

Station Performance Test

The Station Performance Test lasts 70 days during which the young stallions are tested for their potential ability in competition. The stallions are trained and tested under uniform circumstances for a sport career. The training program is carried out by a central trainer together with a team of training-riders. At regular intervals the stallions are judged by the selection committee in performance tests, either ridden by the training rider or by experienced test riders. The horse receive a final score from the committee for a set of either movement or jumping traits depending on the selection discipline. To arrive at the final score, the committee includes information from the riders and trainers of the horse. Stable and training behaviour are also scored during the Station Performance Test.

Young Stallion Competition

Stallions that pass the station performance test are allowed to breed with a limited number of mares. In addition, the selected stallions have to participate in the Young Stallion Competition. During the Young Stallion Competition information on sport ability of the horses during competition is collected. In addition to the regular judgment of horses according to rules that apply to regular competitions, a jury of experts evaluates the stallions on their jumping style or on their movement, correctness and willingness under dressage.

Studbook Entry

Registration in the studbook requires an inspection of the horse. Initially this inspection only concerned conformation, but from 1998 onwards free movement and free jumping have also been included in the inspection. Data collected at Studbook Entry formed the basis of the analyses in Chapter 2.

Mare Field test

A Mare Field Test (in Dutch abbreviated as: “IBOP”) is a one-day field test, during which the horse is ridden by its own rider. Traits scored are details of movement under saddle, or of free jumping under saddle.

Mare Performance Test

The Mare Performance Test (in Dutch abbreviated as: “EPTM”) is an ability test for jumpers and dressage horses, with a setup comparable to the Station Performance Test for stallions. Depending on the training level of the horse, the horse is tested either for a two-week or a five-week period. During the testing period the horse is evaluated by judges at regular intervals. The final scoring of the committee for a set of movement or jumping traits also includes the judgement of riders and trainers.

Young Horse Competition

Most studbooks organize international competitions specifically meant for young horses. The procedure of data collection during these competitions is similar to the Young Stallion competition, though it is a competition separate from the Young Stallion competition. Besides judgment according to competition rules, a jury of experts evaluates the stallions jumping style or their movement, correctness and willingness under dressage

8.2 Selection potential of different test records in stallion selection

Data collected on individual horses in the different tests can be used in the selection of stallions. Prediction of cumulative genetic response resulting from all selection stages would require calculations accounting for correlations among information sources and reduction in variance due to selection at each stage. Instead, some basic calculations have been performed to gain insight in the relative importance of each selection stage. The relative importance of each selection stage has been expressed in the so-called selection potential. The selection potential is calculated as the product of accuracy of the estimated breeding value and the selection intensity. This corresponds to the genetic gain per unit of genetic standard deviation of the breeding goal trait (Falconer and Mackay, 1996). The calculations have been performed for both disciplines: jumping and dressage. For each discipline, the same single breeding goal trait was used for all the tests. The breeding goal was either show-jumping or dressage, both in competition. Furthermore, it is assumed that breeding values after First Stallion Inspection and at Station Performance Test are only based on own performance data collected during that particular test. Consequently, the accuracy of the breeding value (r_{IH}) at a selection stage is a function of the heritability (h^2) and the genetic correlation (r_g) of the trait recorded during the test and the breeding goal trait: $r_{IH} = \sqrt{h^2} * r_g$. Breeding values at Final Approval is based on information of progeny from either Studbook Entry data, Mare Performance Test data, or competition data. The accuracy at Final Approval is: is: $r_{IH}=\sqrt{\frac{0.25nh^2}{1+(n-1)0.25nh^2}} * r_g$,

where n refers to the number of progeny records and r_g is the genetic correlation of the trait recorded on progeny and the breeding goal trait.

The selection intensities are based on the proportions of selected stallions in each stage, which is 60 out of 500 for the First Stallion Inspection, 20 out 50 for the Station Performance Test and 13 out of 20 for the Final Approval (Figure 8.1).

The genetic parameters used were based on Chapter 2 and 3 for the breeding goal traits and traits recorded at First Stallion Inspection and Studbook Entry. Parameters of Station Performance test and the Mare Performance Test were taken from van Veldhuizen et al., (1997).

Table 8.1 Estimated heritability (h^2), the genetic correlation (r_g) of the selection trait with show-jumping in competition[1)], number of progeny ($n_{prog)}$), accuracy of selection (r_{IH}), selection intensity (i) and Selection Potential at stages of the stallion selection scheme[3)]

Information Source	selection trait	h^2	r_g	n_{prog}	r_{IH}	i	Selection Potential
FSI_{op}	Free-jumping	0.55	0.85		0.63	1.67	1.01
SPT_{op}	Jumpability	0.39	0.90		0.56	0.97	0.54
$Comp_{pt}$	Jump grade	0.15	1	16	0.62	0.57	0.35
STB_{pt}	Free jumping	0.40	0.87	70	0.82	0.57	0.47
MPT_{pt}	Jumpability	0.50	0.60	12	0.48	0.57	0.27

[1)] Heritability for show-jumping competition: h^2=0.15; [2)] FSI_{op} = First Stallion Inspection own performance, SPT_{op} =Station Performance Test, own performance and Final Approval with selection on completion data $Comp_{pt}$ =Competition of progeny, STB_{pt} =Studbook Entry of progeny, MPT_{pt} =Mare Performance Test of progeny; [3)] Selection potential expressed in genetic standard deviations of the breeding goal trait show-jumping in competition

Table 8.2 Estimated heritability (h^2), the genetic correlation (r_g) of the selection trait with dressage in competition[1)], number of progeny (n_{prog}), accuracy of selection (r_{IH}), selection intensity (i) and Selection Potential at stages of the stallion selection scheme[3)]

Information Source	selection trait	h^2	r_g	n_{prog}	r_{IH}	i	Selection Potential
$FSI^{2)}_{op}$	Free movement	0.37	0.55		0.38	1.67	0.63
SPT_{op}	Dressage ability	0.36	0.68		0.40	0.97	0.39
$Comp_{pt}$	Dressage grade	0.15	1	16	0.62	0.57	0.35
STB_{pt}	Free movement	0.34	0.69	70	0.64	0.57	0.36
MPT_{pt}	Dressage ability	0.50	0.60	12	0.48	0.57	0.27

[1)] Heritability for dressage competition: h2=0.15; [2)] FSI_{op} = First Stallion Inspection own performance, SPT_{op} =Station Performance Test, own performance and Final Approval with selection on completion data $Comp_{pt}$ =Competition of progeny, STB_{pt} =Studbook Entry of progeny, MPT_{pt} =Mare Performance Test of progeny
Selection potential expressed in genetic standard deviations of the breeding goal trait dressage in competition

The calculated selection potentials for the stallions selection scheme for the discipline show-jumping are presented in Table 8.1 and for dressage in Table 8.2. For show-jumping, the selection potential of the First Stallion Inspection is 1.01 genetic standard deviation. The selection intensity (1.67) corresponds to selecting 60 stallions out of 500 candidates. Both for show-jumping as well as for dressage the largest selection potential can be obtained based on information collected during the First Stallion Inspection. This is mainly due to the high selection intensity at this selection stage, which is nearly 3 times higher than the selection intensity achieved at the stages of Final Approval (i.e. selection stages based on progeny information). The selection potential for jumping based on information collected during First stallion Inspection is higher than the selection potential for dressage. The difference between the selection potentials for both disciplines results from the considerably higher genetic correlation between free-jumping and show-jumping during competition. Some autocorrelation is expected on this estimate. The higher correlation is the main reason for the difference between the accuracies of estimated breeding values for show-jumping and dressage.

Selection potential of the Station Performance Test is second in rank, mainly because of a lower selection intensity as compared to the First Stallion Inspection. The traits riding and jumping ability during Station Performance Test have a somewhat higher correlation to breeding goal traits, but have lower heritabilities. Consequently, the accuracies of estimated breeding values based on Station Performance Test and First Stallion Inspection are very similar.

After successfully passing the Stallion Performance Test, progeny can be produced which (partly) will be enrolled in the Studbook Entry test, Mare Performance Test or in competition. Number of progeny might vary considerably between selection candidates. Calculations in Table 8.1 and 8.2 are based on the average number of progeny, which have been derived from the annual KWPN statistics . The Final Approval of stallions is at 11 years of age, i.e. when the oldest progeny in competition is 7 years. By that time 4 batches of progeny have participated in Studbook Entry and 3 batches in Mare Performance tests. The difference in size of progeny groups is thus partly due to number of progeny batches that are old enough to participate in tests or competition.

Accuracies of estimated breeding values based on data from progeny at Studbook Entry or in competition are relatively high. For information obtained at Studbook Entry this is due to the large number of progeny with records. The high accuracies that can be obtained when selection is based on data from progeny in competition is due to the fact that selection is based on the breeding goal traits directly (genetic correlation is 1). Despite the high accuracy when data on progeny of Studbook Entry is used, the selection potential is not higher than at earlier stages, because of the low selection intensity in this selection step. However, there is an advantage when progeny data from Studbook Entry rather than progeny data from competition is used to estimate breeding values. Data from Studbook Entry is available at a younger age which could result in a Final Approval at a younger age of the stallion. Selection at an earlier age could lead to a reduction in generation interval and consequently an increase in the annual genetic gain. Consequences of differences in generation intervals have not been included in the evaluation of the selection potential for the different alternatives.

In general it can be concluded that selection based on correlated traits measured at a young age results in the highest selection potential. This is due to the high selection intensity and the substantial genetic correlations of selection traits to performance in competition. When omitting subsequent stages and selecting directly the 13 sires needed out of 500 submitted to the First Stallion Inspection a selection intensity of 2.32 can be achieved. The corresponding selection potential would become 1.46 in case of show-jumping and 0.88 in case of dressage. The subsequent stages are only justified when they contribute to additional genetic gain. This requires a more detailed analysis which is beyond the scope of the current analysis.

8.3 Using information from competition data

Direct observations on the breeding goal trait can be collected during competion. Annually approximately 3,000 studbook registered horses participate in show-jumping competition and a same number participate in dressage competition. This provides a large amount of data each year which can be used in genetic evaluations of selection candidates. In most countries equestrian sport associations are responsible for organizing competitions and they function independently from the studbooks. There might be a difference between countries in how competition results are stored and of which horses information is stored. In some countries results are stored for all horses that participated in a competition event and in others results are only stored for the placed horses. In the Netherlands the results of all horses in sport competition are recorded and it represents the accumulation of winning points gained at each event. In dressage, between 1 and 3 winning points can be gained when the jury score is above a minimum score for that event. In show-jumping, 2 winning points will be gained in case of a faultless performance and 1 winning point when not more than 1 fault has been made in the jumping track. When a certain number of winning points has been gained, promotion of the horse to the next level of competition follows, where gaining winning points will start from zero (for further details, see chapter 3).

Basically competition consist of regional, national and international level and each of these levels is further subdivided in approximately 4 to 5 levels. The equestrian sport association subsequently stores the accumulated result in a classification score representing the level of performance and the number of winning points gained.

For genetic evaluation, the classification scores are transformed to linear scores using square-root transformation to achieve a more normally distributed error term (Huizinga and Van der Meij, 1989).

In using competition results for genetic evaluation three issues need to be addressed in the procedure of breeding evaluation. These are (1) how to deal with different levels of completion; (2) how to adjust for the influence of the rider, and (3) how to avoid selection bias. These issues will be discussed in the next sections.

Competition at different levels

Competition results are collected as jury scores or as winning points. For both cases, the results of different horses can only be compared within a level. The system does not allow for a comparison of horses across levels, because the jury scores and the winning points do not reflect the level at which the result has been obtained. When using a scoring-percentage or a standardized score without performing a level-transformation, the same scores obtained at the lowest and at highest level of competition are treated as equal in the genetic evaluation. Given the difference in level of competition, the horses are clearly different although they obtained the same score. Recordings at higher levels therefore need to be upgraded. In the analyses of chapters 2 and 3 the original scores are transformed to a linear scale according to the standard breeding protocol (Huizinga and Van der Meij, 1989). The procedure has a rather arbitrary character as the transformation is based on the experience of practitioners. The study of Peeters et al. (2010) demonstrated that the choice of type of transformation has consequences for the genetic evaluations. They proposed a method of upgrading scores achieved at higher levels taking advantage of the situation in the Belgian competition in which a horse is allowed to participate at two adjacent levels. A correction factor for level was calculated based on the difference in the average scoring-percentage of the same horse between two levels. A more progressive upgrading of results obtained at higher levels of competition resulted in higher heritabilities. In addition, they found an optimum rather than a maximum of progressive upgrading.

As an alternative for transformation, performance at different levels of competition can be considered as different traits and analysed as such in a multivariate analysis. The study by Kearsly et al. (2008) showed that genetic correlations between levels are different from unity. This justifies to consider them as different traits. In particular, estimated genetic correlations between advanced and lower levels of competition were all lower than 0.90. The heritability estimates for show-jumping and dressage were 0.07-0.12, except for show-jumping at advanced level which had a substantially higher heritability estimate. Based on these results and similar results as found by Stewart et al. (2010), it can be concluded that performance at different levels should be considered as different traits. It would therefore be more appropriate to treat them accordingly in genetic evaluation. This implies that the genetic evaluation should be based on a multivariate model. Application of a multivariate model has two additional advantages. First, the selection bias originating from the fact that only the better horses will move to higher levels of competition is accounted for. Second, performance at different levels can be appreciated with respect to the breeding goal; e.g. when the breeding goal is about performance at the highest level, then the breeding value for performance at the highest value should receive the highest weight in the final breeding value. Application of multivariate model requiremes more from the data structure. There should be sufficient genetic links between animals that performed at different levels of competition in order to get an appropriate genetic evaluation. Given the advantages of a multivariate model. it is worthwhile to investigate the opportunities to implement this for genetic evaluation of competition results.

Rider influence

Performance in competition is the result of teamwork where the team consists of a rider and a horse. Therefore, the genetic evaluation of horses can be improved if the data is adjusted for the effect of the rider. A few studies on rider effects have been published and they show that rider effects can take up a considerable fraction of the total phenotypic variance ranging from about 10% in show-jumping (Janssens et al., 1999) to 15% for dressage (Kearsley et al., 2008). In both studies the rider variance was in the same order of magnitude as the genetic variance illustrating the importance of adjusting the data for rider effects. More importantly, ignoring rider effects will result in a heritability that is overestimated: ignoring rider effects results in a heritability estimate of 0.18 but when rider effects are accounted for the heritability estimate is 0.10 in show-jumping (Janssens et al., 1999) and dressage (Peeters et al., 2010). At present rider effects are not accounted for and therefore these results suggest that heritability estimates used in current breeding value estimations are too high.

Correction for rider effects is seldomly possible as unique rider identifications are lacking. In case rider identification is not available and genetic evaluations are based on repeated measures (e.g. results of single events), rider effects will end up in the permanent environmental effect.

Due to the confounding of rider and horse it is questionable whether rider effects can be accounted for in all cases. Furthermore, rider effects change with competition level as was shown by e.g. Kearsly et al. (2008). Further, only a fraction of the riders ride more than one horse, and those are in general more experienced riders.

In conclusion, not adjusting for rider effect will result in an upward bias of the heritability and consequently in the breeding value estimation too much weight will be put on the individual performance. Due to confounding of rider and horse it is difficult to disentangle both effects and therefore true heritabilities are at present unknown.

In order to disentangle horse and rider effects studbooks should consider setting up competitions were riders are riding multiple horses. In practice this might be complicated and an intermediate solution can be by modeling the level of the rider.

Selection bias

Not all horses participate in competition for reasons varying from injuries, character, or lack of interest of the owner, to lack of talent of the horse. When horses are not participating for reasons that are related to the breeding goal, then selection bias is expected. Of the mares that participated in the studbook inspection, about 23% also participated in dressage competition (Ducro, 2010). Selection bias cannot be completely eliminated unless the information used for selection is included in the genetic evaluation.

8.4 Opportunities for improving the breeding program

The KWPN breeding scheme described (figure 8.1) has been very successful in delivering world class horses, both for competition as for dressage. However, with such a large and complex breeding program there are always steps that can be improved, e.g by making use of new insights or new techniques. Important factors influencing genetic response are the selection intensity and the accuracy of selection.

Increasing selection intensity for selection steps where accuracy of selection is high is most efficient. This relates to the selection step involving progeny testing (Table 8.1 and 8.2). The selection intensity is based on selecting 13 out of 20 horses that pass the Station Performance Test. The selection can be increased either by selecting fewer stallions for progeny testing, or by allowing more stallions to pass the Station Performance Test. When selecting fewer stallions for progeny testing, say only 6 stallions instead of 13, the selection potential is roughly twice the values in the current situation (Table 8.1 and 8.2). However, only selecting 6 stallions is not a feasible alternative, as it will lead to too high rates of inbreeding. Furthermore, the extra response might be reduced, because the percentage of matings by older stallions likely will increase. The alternative of increasing the selection intensity by e.g. doubling the number of stallions passing the Station Performance Test would require doubling the testing capacity at the Station Performance Test (provided the selection intensity for the Station Performance Test remains unchanged). However, the Station Performance Test is rather expensive and therefore an extension of the capacity is not likely to take place in practice. With the same number of stallions tested, changing selection intensity at one stage will have consequences for the selection intensity at another stage. In contrast, higher selection intensity at the First Stallion Inspection by increasing the number of young stallions admitted would be feasible. This is a relative cheap selection stage and is not compromising the selection intensity in subsequent selection stages. E.g. doubling the number of stallions participating at First Stallion Inspection would increase selection potential by ca. 25%.

The selection potential of the breeding program can also be improved by increasing accuracy of selection. Increasing accuracy is only relevant to the steps involving progeny testing. In other steps the accuracy is based only on heritability and genetic correlation, which cannot be changed unless the selection trait is redefined. Accuracy of selection has an upper limit corresponding to the genetic correlation (Tables 8.1 and 8.2), which is e.g. 1 for selection on progeny with competition data. From Tables 8.1 and 8.2, it appears that the selection on progeny with Studbook Inspection data does not contain much opportunity for improvement, because the accuracy of selection is close to the genetic correlation. In contrast, selection on progeny with competition data or Mare Performance data shows more room for improvement. Increasing the size of the progeny group would thus increase accuracy and thus the selection potential at this stage. As with Stallion Performance Tests, extending testing capacity might be the limiting factor for performance testing in practice.

In conclusion, selection response can be increased by increasing selection intensity in the first stages of stallion selection program. In practice only increasing selection intensity at the First Stallion Inspection is feasible. The First Stallion Inspection is a relatively cheap selection stage and more stallions are available to participate. For steps at which progeny information is used in the selection step, improvement of selection potential should come from increase of the number of progeny. This is not relevant for Studbook Entry, as accuracy is already close at the genetic correlation. For progeny with performance data, this requires expansion of (expensive) testing capacity.

Selection preceding First Stallion Inspection

An initial selection step in the breeding program is created by the owners' decision to send their colt to the First Stallion Inspection. A high selection intensity can be achieved due to the large number of animals involved (Figure 8.1). It is however not a selection step controlled by the studbook, but the decision is in the hands of the owner. The exact arguments of the owners for sending in their horse are not known and might vary between owners. Koerhuis and van der Werf (1994) presumed that this selection is mainly on conformation which they assumed to be unrelated to the breeding goal traits. Conformation however has a relation to dressage and therefore indirectly selection on the breeding goal takes place. Therefore there is a clear risk of selection bias. Selection response due to owners' decisions might become evident when comparing pedigree based breeding values of stallions admitted to the First Stallion Inspection with those of all registered matings. Additionally, it would be informative to check whether all progeny with high pedigree breeding values are attending the First Stallion Inspection.

Heritability estimates for conformation and movement in warmblood foals were low to moderate, ranging from 0.15 to 0.30 (Preisinger et al. 1991; Kühl et al., 1994). Bösch et al., (2000) found higher heritabilities in Holstein foals and reported in addition moderate to high genetic correlations with mare performance. Therefore, there are indications that inclusion of foal scores in the breeding value estimation procedures could improve genetic response, although more accurate estimates of genetic parameters are necessary. Taking full benefit from the potential selection intensity at this stage requires that all foals are inspected. Alternatively, scores for young foals could be used to estimate the breeding values of their sires, i.e. the progeny tested stallions. As this information is available right after the first crop of foals is born, this adds to obtaining unbiased breeding values at a relatively young age of the stallions.

Subjectivity of scoring

Virtually all measures taken on horses are subjective observations which can be scored using a descriptive or an appreciating scale. A descriptive scale has the advantage that scoring is independent from the breeding goal, because scoring is relative to the population mean, which is placed at the center of the scale. In particular under changing breeding goals (e.g. specialization) data collection, as well as the genetic evaluation do not have to be adjusted.

Subjective scoring may introduce judging bias. To reduce judging bias, inspection is mostly conducted in teams. In practice, a team of inspectors is only allowed to give one single score and scores of individual inspectors are not shown. However, instead of having a “team score”, individual scores of team members are preferred. Inspectors not only differ in their mean score, but also in the range of the scale they use. The scoring behavior of individual inspectors can be accounted for in the genetic analysis, as long as inspectors are known. More important than differences in scale between inspectors is that inspectors score consistently. Consistency of scores reflects that the definition of traits is constant, both over time and between inspectors. In dairy cattle, consistency of scoring type traits by inspectors has been validated by estimating ‘within-inspector’ heritability and genetic correlations between the same traits, scored by different inspectors (Veerkamp et al., 2001). Inspectors deviating in scoring consistency, or do not score consistently for one particular trait, could easily be identified. On the other hand, traits showing large inconsistencies, indicated by low ‘within inspector’ heritabilities, might need to be redefined. These analyses will help to improve the quality of scoring at relatively low cost. Similarly, such analyses can be used to evaluate the quality of the jury in competition. However, this only can be accomplished if inspectors score independently and if scores of individual inspectors are recorded.

Objective measurements

Kinematic studies have shown that there is a difference in jumping technique between good and bad jumpers. From a small study on young Dutch warmblood horses it appeared that good jumpers were better capable of shortening their forelimbs at forelimb clearance (by bending the elbows to a greater extent), and retroflexed their hind limbs further at hind limb clearance (Bobbert et al., 2005). Consequently, good jumpers did not necessarily jump higher but they jumped more efficiently. Of particular interest was the finding that “jumping technique” remained consistent from foal to adult and was not the result of training (Santamaria, 2004). The results of this research suggest that jumping technique of foals might be predictive for jumping ability at later ages. Observations as described by Bobbert et al. (2005) concern jumping of submaximal fences. According to Lewczuk et al. (2006) jumping technique of adult horses can be scored more consistently when data are collected on higher obstacles. Lewczuk et al. (2006) found an average repeatability, for 10 aspects of jumping technique, of 0.40, whereas average repeatability was 0.35 for the same aspects without a rider. Kinetic analysis of gaits on a treadmill also showed a highly consistent pattern between measurement of foals and observations at later age: data recorded at 4 months of age could be used to predict the locomotion at 26 months of age (Back et al., 1994).

In particular consistency for most of the measures taken on foals and young horses, suggests that measures on foals have good predictive ability. Heritability-estimates are moderate to high for jumping technique (Barrey et al., 2003; Crevier-Denoix, 2008) and for gaits (Valera et., 2007), but genetic correlations with sports performance are still lacking.

Present technological possibilities of image analysis make it no longer necessary to prepare the horse by fixing over 20 skin markers at anatomical locations on the body before recording can take place. New methods are available where skin markers are fixed afterwards on the image on the computer screen (Crevier-Denoix, 2008) which reduces time of recording to a few minutes. This facilitates the use of these techniques under circumstances that closely resemble field conditions and it makes it possible to scan a large number of horses on a routine bases.

Different studies on kinematic analysis of movement and jumping show that riders make their horses move more regular. In all of these studies experienced riders were involved. Unfortunately, none of the studies report the variation due to riders, but it would be of interest to study whether differences in rider level could be detected. Quantifying rider level in an objective way would give the possibility to correct for rider in analyses of performance data.

Measuring character

The character of a horse is considered to be of essential importance in order to become successful in sport. The character is related to different aspects of working with a horse, e.g. willingness to learn, and cooperative behaviour. It is commonly assumed that character is at least partly genetically determined and improving character by selection is possible, although the relation with sport performance is not fully understood. Little is known on the contribution of behavioural assessments to the performance of horses in competition (Thorén-Hellsten et al., 2006). In a Dutch study the results of behavioural tests on young horses were related to jumping performance after the first basic training (Visser et al., 2003). The individual performance traits did not show a significant relation to any variable measured in the behavioural tests earlier in life. However, performance traits combined in a first principal component explained 65% of the traits recorded in the behavioural tests. The results showed little consistency, as different traits contributed to explaining variation in the second year of the experiment. More consistent models could be developed using cross-validation to test the models. The results point to the complexity of recording character and although behavioural tests are adequate in describing certain aspects of character, the relation to performance is complicated.

Górecka-Bruzda et al. (2011) investigated the contribution of character to performance by using statistical methods to extract information on character directly from various observations collected during performance tests. As opposed to Visser et al. (2003), who related information from separate behaviour tests to performance, no additional tests were needed. Górecka-Bruzda et al. (2011) based their approach on several German studies (e.g. Uphaus et al., 1993) which showed that inspectors, trainers and (test)riders score traits differently, as they value different aspects of a trait . E.g. ease of handling (i.e. a character trait) is likely to affect the riders' score for rideability, but not the inspectors' score. A factor analysis was applied on scorings of various traits on Polish horses under ridden work by trainers, riders and jury members (Górecka-Bruzda et al., 2011). Based on the results, the researchers concluded that it was possible to disentangle behavioural aspects of performance from physical aspects. Furthermore it was shown that jury members were especially judging the physical aptitude of the horse in jumping or dressage, whereas the test rider and the trainer focused more on the willingness to perform, which was more related with the cooperative behaviour of the horse in training and performance. Interestingly, the original traits character and temperament contributed only little to the factor that was mostly related with cooperative behavior. In practice the definitions are very close to each other and used interchangeable. Thrainers found it difficult to differentiate and tended to improvise with their own definitions (Górecka-Bruzda et al., 2011). So, clear definitions are needed.

The current selection is for performance which is a combination of physical ability and character. Therefore, it is expected that current selection will improve character for sports as well. It is however not clear to what extent character is improved or to what extent character contributes to improved performance. Disentangling aspects of physical ability and character would give insight in the relative importance of each aspect to sports performance. Further, this would allow changing selection pressure on each aspect and separate breeding values for physical ability and character would allow users to choose a horse that better fits individual preferences. This is relevant as the character of a horse competing at the highest level might differ from a horse used for recreational purposes.

Young horse competition

Most studbooks have competitions specifically meant for young horses, e.g. selected stallions have to participate. In e.g. Germany participating horses are also scored for several movement and jumping traits, which are not directly related to the ranking in competition. These competitions provide an excellent opportunity to collect data similar to what has been recorded at FSI and studbook entry. Additionally, when it is possible to set up a rider by horse competition (i.e. each rider is riding all or multiple participating horses), there are opportunities to disentangle horse and rider effects, and potentially horse by rider interaction effects.

Mare selection

Studbooks do not control the selection of mares, because the owners of the mares are responsible for selection and mating decisions. However, it would be of interest to consider the genetic response that can be achieved in this selection path. For a studbook that produces about 12,000 foals a year, the number of broodmares will be about 15,000. The replacement in broodmares is about 1,500 per year when the generation interval is 10 years. To account for rearing losses and reproduction failures, the aim is to select 2,000 mares out of the foals born. These 2,000 mares could be selected based on information collected at Studbook Entry. Assuming that 2,500 of the 3,000 attendants are female (Figure 1), the selection potential at Studbook Entry is 0.30 for show-jumping and 0.19 for dressage (selection intensity is 0.35 when proportion selected is 80%). These selection potentials are generally lower than those reported for the stallion selection path (Table 8.1 and Table 8.2). However, by encouraging participation in Studbook Entry the selection intensity can be increased considerably. When 5,000 mares are attending Studbook Entry then a selection intensity of 0.97 is possible and the selection potential can increase by a factor 2.8.

The selection potential in mares can further be enhanced by inviting the best mares to participate in Mare Performance Tests and to stimulate or even allow only the use of performance tested mares to produce stallions that enter the Station Performance Test.

In this way the selection potential in the mares' selection path can be structured which can make a significant contribution to the genetic progress of the breeding program. This actually may give studbooks a competitive edge. Due to the fast exchange of male breeding material among studbooks, the genetic level, on the male side becomes similar and therefore the available female breeding material will make the difference.

8.4.1 Genomic Selection

Introduction

With the recent publication of the horse genome (Wade et al., 2009) horse breeding has entered a new era. Sequencing of the genome has generated a massive amount of Single Nucleotide Polymorphisms (SNPs). These SNPs can be used in genome-wide association studies with the aim to identify mutations underlying genetic variation in relevant traits. Additionally, SNPs can be used in the procedures for breeding value estimation, also known marker assisted selection or genomic selection. Marker assisted selection exploits the knowledge on individual genes contributing to genetic variation to estimate breeding values for the trait of interest. In genomic selection fairly accurate estimates of breeding values can be obtained without knowledge of an individual. Genomic selection requires dense marker maps. With a dense marker map some markers will be very close to genes affecting the traits and probably in linkage disequilibrium with it (Meuwissen et al., 2001). With genomic selection important selection decisions can already be made before own performance or progeny information is available.

Prerequisites for implementing genomic selection in horse breeding

Two important aspects are relevant before genomic selection can be applied in a breeding program for sport horses. The first aspect relates to what is known as the reference or training population. The reference population is a large population of animals with both phenotypes and genotypes and is needed to establish the relation between SNP genotypes and phenotypes The reference population is used to derive the equation to predict a breeding value from SNP genotypes, the so-called prediction equation. It has been shown that the size of the reference population is a crucial factor for the accuracy of the breeding values resulting from the prediction equation (Goddard and Hayes, 2009). In dairy cattle breeding, a common reference population of about 18,000 progeny tested bulls has recently been created, by combining progeny tested bulls from several breeding organizations in Europe (Lund et al., 2010). The dairy cattle breeding organizations realized that combining reference populations could lead to a considerable improvement of the accuracy of the genomically estimated breeding values. It is not feasible to create such a large reference population in horses. For example the KWPN breeding program produces 20 progeny tested stallions per year (Figure 8.1). However, the situation in horses is different from that in dairy cattle. In dairy cattle high accuracies of genomic selection for bulls at a young age are required to outperform traditional selection of older bulls based on progeny testing. In dairy cattle progeny tested bulls have high accuracies due to the large number of daughters and the availability of routinely collected milk recordings. Breeding stallions have accuracies of 90% on their breeding values when they are 12 years old, i.e. much older than breeding bulls in dairy cattle. In addition, the number of progeny tested stallions is small, which results in a low intensity of selection. In that respect the perspectives for genomic selection in horse breeding are better, once the reference population has been established.

The second aspect which is important for the introduction of genomic selection is the availability of accurate phenotypes for setting up the prediction equation. That means that traits measured on animals of the reference population should be as unbiased as possible and it should be possible to correct phenotypes for the influences of systematic factors influencing the trait. Deriving prediction equations from genotyping horses in competition and using their own competition record as input requires that the phenotypes can be corrected for the influence of the rider and level of completion. These aspect have been discussed before.

Implementing genomic selection in horse breeding

Many horses annually attend the Studbook Entry test. A reference population of sufficient size can, therefore, be created within a relatively short time span based on these data. By stimulating the owners it might even be possible to increase the number of horses that attend in a year because traits are relatively cheap to measure. Genomic breeding values based on Studbook Entry data should have higher accuracies than traditional breeding values based on Studbook Entry. Because own performance information is available, a larger reference population is required than for traits where own performance information is lacking. It seems most useful to create a reference population from horses that attended performance tests, where horses are tested and trained under uniform circumstances. Various traits concerning physical development, character and trainability can be monitored over the length of the testing period and a combination of these traits has been shown to be an accurate predictor of future sport ability.

From the simulation study of Grevenhof et al. (in prep.), it follows that a reference population should contain at minimum 10,000 phenotypes to achieve the same accuracy as mass selection for a trait with a heritability of 0.1 (which is slightly lower than 0.15 for sport performance). With ca. 60 young stallions tested at station performance tests annually, it will take many years to build a reference population of this size, even when Mare Performance Test data (Fig.1) are added to the stallion phenotypes. However, the required size of the reference population decreases substantially when the generation interval is reduced. This reduction can be realized as a result of genomic selection. When the generation interval can be reduced by 20% as a consequence of applying genomic selection, selection response will be the same for a heritability of 0.1 using a reference population of 6,000 phenotypes (van Grevenhof et al., in prep.). Even when the reference population is based on performance tests of both stallions and mares, it still takes several years to achieve a reference population of sufficient size when using information from Performance Tests only. Opportunities to combine information from Studbook Entry and Performance tests seems a more realistic option.

In conclusion, setting up a reference population of sufficient size for prediction of genomic breeding values will take a number of years in horse breeding. The best option is to build a reference population by genotyping both males and females on which information is collected which is related to the breeding goal traits.

Other applications of genomics

In the previous section, I concentrated on the use of SNPs in predicting breeding values. However, SNPs can also be used to to predict future phenotypic performance of horses. Before rearing a foal and submitting it to a training program, the owner would like to know how high the chance is for a successful career. Genotypic information can be of help in better predicting the chance for a successful career. Such a prediction would enable a better selection of promising horses. Consequently, fewer foals need to enter training to get the desired number of successful sport horses. The economic advantage of the reduced training activity should be taken into consideration when deciding on the implementation of genomic selection in horses.

8.5 Breeding in practice

Breeding values of stallions can be predicted at an early age. However, mare owners seem to hesitate to use young stallions for their mares. One problem with the use of young stallions might be that accuracies of the breeding values are low when they are first published. Breeding values are published when at least 5 progeny have information on sport performance. Increasing the accuracy of breeding values of young horses can be realised by including additional information from other tests in the genetic evaluation. Furthermore, as most of the owners only have one or a few mares, they tend to avoid risk and use stallions with more accurate breeding values. The owners put a lot of emphasis on the accuracy of the breeding value. This strategy is known to reduce the selection response in the population. A higher selection response will favour the use of younger horses. To increase the selection response, it is important to consider the first 3 stages of selection. This was also shown in the earlier section on selection potential. The importance of the first three selection stages of the stallions' breeding program was already pointed out by others (e.g. Huizinga et al. 1990, Hugason et al., 1987; Dubois et al. 2008). Hugason et al. (1987) and Huizinga et al. (1990) both concluded that more than 75% of the mares should be mated by young stallions after the station performance test; as a balance between accuracy of breeding value and generation interval. As demonstrated in this study, Studbook Entry and First Stallion Inspection provide additional information by which accuracy of breeding values of young stallions can further be increased. As a consequence, the percentage of matings by older stallions might be reduced in order to achieve a higher selection response. The use of competition performance in selection decisions needs to be critically considered,. Competition performance should remain the breeding goal but as information source it has some serious shortcomings.

8.6 Conclusions

The main conclusions of this chapter are:

- traits evaluated at the Studbook Entry inspection will favourably contribute to estimation of breeding values for sport performance.
- First Stallion Inspection comprises an important component of the stallion selection program, due to high genetic correlations to sport traits, and due to relatively high selection intensities.
- Selection potential based on competition data is relatively small, because the data become available at a late stage in the stallion selection program when selection intensity is little.
- Genomic selection offers prospects for horse breeding. Establishing a reference population of sufficient size requires the combination of information from several tests.

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Summary

Horse breeding is characterized by long generation intervals. This due to the fact that stallions are progeny tested and because information on selection traits becomes available late in life. This concerns both sport traits as well as sport related health traits. Moreover, these traits are lowly heritable due to highly variable circumstances under which these traits are measured. Therefore, there is a need for traits that can be measured early in life, with high heritabilities and which preferably can be collected on a large number of animals at low costs.

The aims of this study were to determine the role of test results of young horses in selection for sport performance, to assess the genetic diversity of a closed horse breed and the consequences of inbreeding for male reproduction.

In chapter 2 genetic parameters for traits evaluated at the Studbook Entry inspection and genetic correlations with dressage and show-jumping performance in competition were estimated. Heritabilities of the studbook entry traits were estimated in the range 0.15-0.40. The movement traits showed moderate to strong mutual genetic correlations, whereas the genetic correlations of movement traits with free-jumping traits were weak to moderate. The free-jumping traits showed strong to very strong mutual genetic correlations. Genetic correlations of the movement traits with dressage were moderate to strong, and with show-jumping weak to moderate. Genetic correlations of the free jumping traits with dressage were weak to moderate and unfavourable. The free jumping traits were genetically strongly to very strongly correlated to show-jumping. It was concluded that a selection of the traits evaluated at the studbook entry inspection will favourably contribute to estimation of breeding values for sport performance.

In chapter 3 genetic parameters for traits evaluated at the First Stallion Inspection (FSI) and genetic correlations with dressage and show-jumping performance in competition were estimated. Heritability estimates of the FSI-traits ranged from 0.25 to 0.61. FSI-traits related to gaits showed strong genetic correlations (above 0.70) and FSI-traits related to free jumping had correlations close to unity. Genetic correlation between FSI-gaits and dressage in competition were positive, ranging from 0.37 to 0.72. Genetic correlation between FSI-jumping traits and show-jumping were all above 0.80. FSI-jumping traits showed negative correlations with dressage (about -0.48). FSI-gait traits showed negative correlations with show jumping, except for canter. It is concluded that selection at First Stallion Inspection

comprises an important component of the stallion selection program, because FSI-traits have good genetic relationships with performance in competition and, due to the number of animals involved, relatively high selection intensities can be achieved.

The negative conformational trait asymmetrical or ‘uneven’ feet might be responsible for reduced sport performance. Therefore prevalence and heritability of uneven feet was assessed in chapter 4 as well as its genetic relationship to other conformation traits and to sporting performance later in life in warmblood riding horses. The prevalence of uneven feet was 5.3% on average, and the prevalence showed an increase from under 4.5% during the first 3 years of recording to over 8% in the years from 2000 onwards. Heritability estimates of foot conformation traits were moderate and ranged from 0.16 for heel height to 0.27 for hoof shape. The genetic correlation between the trait of uneven feet and performance in competition was negative but weak: -0.09 with dressage and -0.12 with show jumping.

It was concluded that predisposition to uneven feet can be reduced by selection. Because of weak genetic correlations, the increased prevalence of uneven feet is not directly associated with selection for better sports performance (dressage or jumping) or higher conformation grade.

If the trait ‘uneven feet’ arises from a disproportionate relation between height at the withers and neck length, then selection on conformation grade might result in a situation prone to development of uneven feet. In general, limb conformation has a moderate genetic relationship to conformation grade and foot conformation traits have a genetic relation to sporting performance. This study provides evidence that selection for better sport performance is not causing the increased prevalence of uneven feet. The other way round, reducing occurrence of uneven feet by selection is possible, without limiting progress in sport performance. Selection for conformation grade might induce a disproportional relation between height at withers and neck length, which indirectly would induce horses to be more sensitive to uneven feet.

The aim of Chapter 5 was to study the relation between foot conformation at young age and the length of the career of sport horses. Survival analysis was used to determine which of the conformation traits had a significant effect on duration of sport career in dressage and show jumping at basic and elite level. Length of competitive life was shorter for jumping than for dressage. A different set of risk factors was found for each level and discipline: e.g. height at withers was a risk factor at basic level in dressage and jumping, while pastern angle was a risk factor at the elite level of jumping and dressage. The trait 'uneven feet' tended to shorten the competitive life in dressage, but was a significant risk factor at the elite level of jumping. It was concluded that limb conformation, and in particular, the conformation of the distal limb, are important for length of competitive life. From the prevalence of uneven feet in sports disciplines, it may be concluded that this is an undesirable trait, particularly at the elite level of jumping, since uneven feet have a detrimental effect on the length of competitive life in a sport horse population. This study provided evidence that the conformation trait uneven feet has a negative effect on warmblood jumping performance, and therefore breeders should be instructed to possibly prevent this phenomenon already at foal age.

The aim of Chapter 6 was to describe the impact of the breeding history on the genetic diversity in the Friesian Horse breed. To investigate whether inbreeding rate was affected by population subdivision a cluster analysis was performed on simulated gene probabilities, obtained from gene dropping, of individuals from the last year of the study. Analysis of the pedigree back to foundation of the studbook showed that the Friesian Horse breed has a high inbreeding level primarily due to drift from small effective population size during several generations since the foundation of the breed. Although 4 clusters could be identified, pairwise kinships showed that they were not very distinct from each other. From the decrease in kinship and the increased variance effective number it is expected that the rate of inbreeding will decrease in the future.

The aim of Chapter 7 was to determine whether the degree of inbreeding affects semen quality in Friesian stallions, and whether semen quality is heritable and therefore amenable to improvement by selection. Heritability estimates were moderate to high, ranging from 0.16 for volume to 0.62 for abnormal acrosomes. Overall inbreeding coefficients ranged between 11% and 22% with a mean of 15.6%. Although some inbreeding depression was shown on most of the traits, the effects were not significant. It was therefore concluded that low semen quality in Friesian Stallions could not be attributed to inbreeding. Heritability estimates for semen quality traits were moderate to high and had substantial variation. Selection can be used to improve semen quality.

In Chapter 8 opportunities for improvement of the breeding program have been discussed. An overview is given of young horse tests commonly provided by studbooks , including those belonging to the stallion breeding program. Selection potentials are calculated to gain insight in the relative importance of each of the young horse tests to the breeding program. Additional opportunities to increase selection response have been discussed.

Main conclusions are:

- Traits evaluated at the studbook entry inspection will favorably contribute to estimation of breeding values for sport performance.
- First Stallion Inspection comprises an important component of the stallion selection program, due to good genetic correlations to sport traits, and due to relatively high selection intensities.
- Limb conformation as assessed at Studbook Entry Inspection is related to length of competitive life in dressage and show-jumping
- The Friesian Horse breed has a high level of inbreeding primarily due to drift from small effective population size during several generations since the foundation
- Low semen quality of the Friesian Horse breed is not significantly influenced by inbreeding.
- Selection potential based on competition data is relatively small because selection intensity is low.
- Genomic selection offers prospects for horse breeding. Establishing a reference population of sufficient size requires the combination of information from several tests.

Samenvatting

Een karakteristiek van de paardenfokkerij is het lange generatie interval. Fokhengsten en –merries worden lang gebruikt voor productie van nakomelingen, omdat ze zich eerst moeten bewijzen via de prestaties van hun nakomelingen, is de algemene gedachte. Dit wordt ondersteund vanuit de fokkerijtheorie omdat de meeste fokdoelkenmerken (sportprestatie en gezondheid) een relatief lage erfelijkheidsgraad hebben. Nakomelingentoetsen leveren daarom een essentiële bijdrage aan betrouwbare fokwaarden. De resultaten van nakomelingen laten lang op zich wachten, omdat een paard pas op latere leeftijd zijn sportaanleg kan laten zien, veelal vooraf gegaan door jaren van training. Voor een snellere genetische vooruitgang is daarom behoefte aan kenmerken die al op jonge leeftijd gemeten kunnen worden en die voorspellend zijn voor latere sportprestaties. Essentieel voor gebruik in de fokkerij is daarbij dat de kenmerken een voldoende hoge erfelijkheidsgraad hebben en dat ze bij voorkeur tegen lage kosten aan een groot aantal dieren gemeten kunnen worden.

Het doel van het in dit proefschrift beschreven onderzoek was drieledig: 1. om de rol van de prestatietestresultaten van jonge paarden in de selectie voor de sportprestaties te bepalen, 2. om de genetische diversiteit binnen een gesloten paardenras te beschrijven en 3. om de gevolgen van inteelt voor mannelijke reproductiecapaciteit te bestuderen.

Het eerste doel werd behaald met behulp van keurings- en afstammingsgegevens van het KWPN en sportuitslagen van het KNHS. Er zijn verschillende momenten in het leven van het jonge paard waarop het kan worden beoordeeld op zijn potentiële waarde als ouderpaard voor gebruik in de fokkerij. De relevantie voor de fokkerij is bestudeerd aan data van twee van dergelijke beoordelingen: de stamboekopname (met name merries) en de eerste bezichtiging voor de centrale hengstenkeuring.

In hoofdstuk 2 zijn genetische parameters geschat voor de bewegings- en springkenmerken waarop paarden tijdens de Stamboekopname zijn beoordeeld. Vervolgens zijn de genetische correlaties van deze kenmerken met dressuur- en springprestaties van de paarden in de landelijke competitie geschat. De erfelijkheidsgraadschattingen voor deze kenmerken varieerden van 0,15 tot 0,40. Met uitzondering van correctheid van de stap vertoonden de bewegingskenmerken onderling redelijke tot sterke genetische correlaties (0.40 tot 0.96), en dat geldt ook voor de verschillende onderdelen van het vrijspringen (0.45 tot 0.93). De genetische correlaties

tussen bewegingskenmerken en vrijspringen waren zwak tot matig (-0.10 tot 0.40).
De genetische correlaties van de bewegingskenmerken met dressuur in wedstrijdverband waren matig tot sterk (0.40 tot 0.67) en met vrijspringen zwak tot matig (0.04 tot 0.43). Genetische correlaties van het vrijspringen met sportdressuur waren zwak tot matig (-0.09 tot -0.34) en ongunstig. Vrijspringen had sterke tot zeer sterke genetische correlatie met springen in competitie (0.52 tot 0.88). Deze resultaten leidden tot de conclusie dat een deel van de kenmerken die tijdens de Stamboekopname worden geregistreerd positief kunnen bijdragen aan de schatting van fokwaarden voor sportprestaties.

In hoofdstuk 3 zijn genetische parameters geschat voor de kenmerken beoordeeld tijdens de Eerste Bezichtiging van hengsten. De Eerste Bezichtiging is de eerste fase in het selectieprogramma van hengsten. De schattingen voor de erfelijkheidsgraad voor de gemeten kenmerken varieerden tussen 0,25 tot 0,61. De gangen waren genetisch onderling sterk gecorreleerd (genetische correlaties groter dan 0,70) en de onderdelen van het vrijspringen hadden onderling zelfs genetische correlaties van bijna 1. De genetische correlatie tussen de gangen beoordeeld tijdens de Eerste Bezichtiging en dressuurprestatie in wedstrijdverband waren positief, variërend van 0,37 tot 0,72. De genetische correlaties tussen de onderdelen van het vrijspringen tijdens de Eerste Bezichtiging en springen in wedstrijdverband waren allen groter dan 0,80. De beoordelingen van springen tijdens de Eerste Bezichtiging hadden negatieve correlaties met sportdressuur en de beoordeling van beweging tijdens de Eerste Bezichtiging was negatief gecorreleerd met sportspringen. Uit deze resultaten werd geconcludeerd dat de selectie tijdens de Eerste Bezichtiging een belangrijk onderdeel van het selectieprogramma voor hengsten omvat, omdat de beoordeelde kenmerken goede genetische relaties met de sportprestaties hebben. Bovendien kan in deze selectiestap scherp geselecteerd worden vanwege het relatief grote aantal deelnemende jonge hengsten.

De keuringsresultaten van jonge paarden kunnen dus informatie opleveren die bijdragen aan een efficiënter fokprogramma voor sportprestatie. Op deze keuringen kunnen ook kenmerken worden beoordeeld die mogelijk ongunstig zijn voor een succesvolle sportcarrière en die een risico op een

voortijdige uitval uit de sport kunnen inhouden. Het exterieurkenmerk asymmetrische of 'ongelijke' voeten kan zo’n kenmerk zijn dat verantwoordelijk is voor verminderde sportprestaties. In hoofdstuk 4 is onderzocht of het verschijnsel ongelijke voeten bij KWPN paarden toeneemt, of het kenmerk erfelijk is en hoe het kenmerk genetisch is gerelateerd met andere exterieurkenmerken en met sportprestaties op latere leeftijd. In dit onderzoek is gebruik gemaakt van de registratie van ongelijke voeten tijdens de keuringen bij stamboekopname. De prevalentie van ongelijke voeten was gemiddeld 5,3% en liet een stijging zien van onder 4,5% tijdens de eerste 3 jaren tot ruim 8% in de laatste jaren van het onderzoek. De geschatte erfelijkheidsgraad voor ongelijke voeten was 0,12 op de onderliggende schaal en was daarmee lager dan de erfelijkheid van de overige beenkenmerken (0,16 voor verzenen tot 0,27 voor hoefvorm). Het kenmerk ongelijke voeten was slechts zwak negatief gecorreleerd met de fokdoelkenmerken dressuur en springen in wedstrijdverband; nl -0.09 met sportdressuur en -0.12 met sportspringen.
Geconcludeerd kan worden dat de prevalentie van ongelijke voeten verminderd kan worden door selectie. Vanwege de lage genetische correlaties, is de toegenomen prevalentie van ongelijke voeten niet rechtstreeks in verband te brengen met selectie voor sportprestaties (dressuur of springen) of exterieur. Omgekeerd zal selectie tegen ongelijke voeten geen grote gevolgen hebben voor de overige fokdoelkenmerken. Ongelijke voeten worden veelal in verband gebracht met de verhouding tussen schofthoogte en halslengte. Als ongelijke voeten voortvloeien uit een onevenredige verhouding tussen schofthoogte en de halslengte, dan zou selectie op grote paarden met een korte hals indirect resulteren in paarden die gevoeliger zijn voor ongelijke voeten. In het algemeen zijn exterieur van benen en hoeven matig gecorreleerd met exterieur en sportprestaties.

Het exterieur van benen en hoeven kan, naast een effect op het succes van de sportcarrière, van invloed zijn op de duur van de sportcarrière. In hoofdstuk 5 is de relatie tussen het exterieurscore voor benen en hoeven op jonge leeftijd en de duur van de latere sportcarrière bestudeerd. Survival analyse werd toegepast om te bepalen welke van de exterieurkenmerken een risico op verkorten van de sportcarrière in dressuur en springen vormden. In het algemeen was de sportcarrière voor springen korter dan voor dressuur. Een verschillende set van risicofactoren werd gevonden voor de niveaus van springen en dressuur; schofthoogte was een risicofactor bij het basisniveau in dressuur en springen, terwijl de kootstand een risicofactor was op eliteniveau van springen en dressuur. Dressuurpaarden met ongelijke voeten hadden een licht verhoogd risico om eerder de sportcarrière te beëindigen. Springpaarden met ongelijke voeten, daarentegen, hadden op eliteniveau een duidelijk verhoogd risico op vroegtijdig einde van hun sportcarrière. Geconcludeerd werd dat exterieur van benen en hoeven, en in het bijzonder het exterieur van de distale ledematen, belangrijk zijn voor de lengte van de sportcarrière. Uit de lagere prevalentie van ongelijke voeten in sportdisciplines kan worden geconcludeerd dat dit een ongewenste eigenschap is, met name voor springen op eliteniveau, aangezien ongelijke voeten een nadelig effect hebben op de lengte van de sportcarrière.

Het fokken van paarden gebeurt voornamelijk binnen rassen, zoals bij Lipizzaner, IJslandse paard en het Friese ras. Het inkruisen van andere rassen gebeurt op beperkte schaal of helemaal niet. Fokkerij binnen een gesloten ras biedt de mogelijkheid om een unieke populatie te creëren, maar verlies van genetische diversiteit en toename van inteelt is onvermijdelijk. Een te snelle inteeltstijging kan een bedreiging vormen voor het voortbestaan van de populatie. Fokkerij richt zich, naast verbetering van fokdoelkenmerken, tevens op het behoud van genetische diversiteit. In dat verband is in hoofdstuk 6 het verlies aan genetische diversiteit onderzocht in het Friese paardenras. Het ras heeft een lange fokkerijhistorie met sterk variërende gebruiksdoelen en een sterk variërende populatieomvang. Het doel van hoofdstuk 6 was om de impact van de fokkerijhistorie op de genetische diversiteit in het Friese paardenras te beschrijven. Daartoe werd de gehele stamboom van het ras vanaf de oprichting van het stamboek geanalyseerd. Gekeken is of er perioden te onderscheiden zijn waarin de genetische diversiteit versneld is afgenomen en welke factoren daarvoor verantwoordelijk zijn. Via een cluster-analyse op gesimuleerde frequentieverdeling van de genenstructuur in de laatste jaargang is onderzocht of er sprake is van een opdeling van het ras in een aantal subpopulaties, wat versterkend kan werken op de afname van genetische diversiteit.

Analyse van de stamboom laat zien dat sinds de oprichting van het stamboek de genetische diversiteit fors is gedaald. Voor een belangrijk deel is de afname te wijten aan toeval, wat is toe te schrijven aan de kleine effectieve populatiegrootte gedurende meerdere generaties. De grootste daling van genetische diversiteit vond plaats in de eerste generatie na de oprichting van het stamboek. In de populatiestructuur konden 4 clusters worden geïdentificeerd, maar de paarsgewijze verwantschappen tussen de clusters lieten zien dat de genetische verschillen niet groot waren. De huidige generatie heeft een gemiddelde inteelt niveau van 16%. De bijdragen van 4 invloedrijke voorouders verklaren wel 50% van de huidige genetische diversiteit . De verwachting is dat de inteelt minder sterk zal stijgen in de volgende generatie, omdat de gemiddelde verwantschap in de huidige generatie minder snel is gestegen.

Het is bekend dat een sterke inteelttoename kan leiden tot inteeltdepressie. In hoofdstuk 7 is onderzocht of de matige spermakwaliteit van Friese hengsten het resultaat is van inteeltdepressie , of dat mogelijk andere genetische factoren verantwoordelijk zijn. Een genetische analyse werd uitgevoerd op resultaten van het standaard kwaliteitsonderzoek van sperma afkomstig van 1146 jonge Friese hengsten. Inteelt coëfficiënten van deze hengsten varieerden tussen 11% en 22% met een gemiddelde van 15,6%. De erfelijkheidsgraden voor de spermakwaliteitskenmerken waren redelijk tot hoog, variërend van 0,16 voor volume tot 0,62 voor percentage abnormale acrosomen. Hoewel de meeste spermakwaliteitskenmerken enige relatie met de inteeltcoëfficiënt van de hengst vertoonden, waren de effecten niet significant. Daarom werd geconcludeerd dat de matige spermakwaliteit in de Friese hengsten niet kan worden toegeschreven aan inteeltdepressie. De hoge erfelijkheidsgraden voor spermakwaliteit en de aanzienlijke variatie, suggereren dat spermakwaliteit in de Friese hengsten via selectie verbeterd kan worden.

In de algemene discussie (hoofdstuk 8) is een deel van de resultaten uit dit proefschrift ingepast in het KWPN-fokprogramma. De rol van de verschillende keuringen als aanvullende informatiebron voor fokwaardeschatting of als selectiestap is besproken. Om het relatieve belang van de verschillende keuringen aan te geven is het selectiepotentieel van een keuring berekend uit het aantal deelnemende paarden en de genetische parameters. Uit de resultaten werd geconcludeerd dat deze keuringen van grote waarde zijn voor het behalen van genetische vooruitgang. Bovendien is het verzamelen van deze gegevens relatief eenvoudig en goedkoop en daarmee een zeer aantrekkelijke manier om de genetische vooruitgang te vergroten. Een tweede mogelijkheid tot verbetering van het fokprogramma is selectie in de merries via bestaande keuringsgegevens, zoals stamboekopname en verrichtingstesten. Een derde mogelijkheid is het toepassen van genomische selectie, omdat op zeer jonge leeftijd een betere inschatting van de genetische aanleg van een paard verkregen kan worden. Een belangrijke beperking hierbij is de omvang van de referentiepopulatie die voor succesvolle toepassing groot moet zijn.

Belangrijkste conclusies van dit proefschrift zijn:

- Kenmerken geëvalueerd tijdens de stamboekopname kunnen een positieve bijdrage leveren aan de schatting van de fokwaarden voor sportprestaties op latere leeftijd.
- De Eerste Bezichtiging van jonge hengsten is een belangrijk onderdeel van het selectieprogramma van hengsten, vanwege de goede genetische correlaties tussen de gemeten kenmerken en de latere sportprestaties.
- Beenkenmerken zoals beoordeeld bij stamboekopname zijn gerelateerd aan de lengte van de sportcarrière.
- Het Friese paard heeft een hoge inteelt. Dit is in de eerste plaats toe te schrijven aan de kleine effectieve populatiegrootte gedurende verschillende generaties sinds de oprichting van het stamboek.
- De lage spermakwaliteit van het Friese paard ras wordt niet veroorzaakt door het hoge inteeltniveau.
- Genomische selectie biedt perspectieven voor het fokken van paarden. Om te komen tot een referentiepopulatie van voldoende omvang moet informatie uit verschillende tests worden gecombineerd.

Curriculum Vitae

Bernardus Johannes (Bart) Ducro was born on 2 June 1962 in Amsterdam and grew up in Castricum. After graduation from secondary school he studied at the Agricultural University of Wageningen with specialisation in Animal Breeding. From 1989 until 1995 he has worked at the Poultry Department of the National Institute of Animal Science in Foulum, Denmark. Most of the work concerned selection-experiments in broilers, and running breeding programs at the experimental farm. In 1995 he returned to the Netherlands and got employed as a researcher in poultry breeding at the Institute of Animal Health in Zeist/Lelystad. He was involved in a research project on ascites in broilers and on egg quality in laying hens. In 1997 he worked for a year as a software developer at PW-Consulting in Culemborg. In this job he developed software applications in SAS. From the end of 1997 he is employed at the Animal Breeding and Genetics Group of the Wageningen University, starting as a scientific assistant and later on as assistant professor. The research in thesis has been carried out in this job. He is member of the board of Interstallion and of the board of the 'Stichting Zeldzame Huisdierrassen' (Rare Breed Survival Trust). Furthermore he is member of the Advisory Committee for Recognition and Supervision of breeding animals of the ovine and caprine species.

Bart is married to Dorothé Ducro-Steverink and they have 2 children, Luciel en Pietjan.

Curriculum vitae

Bernardus Johannes (Bart) Ducro werd geboren op 2 juni 1962 te Amsterdam en groeide op in Castricum. Na het behalen van het OVWO-diploma aan het Berlingh College in Beverwijk is hij begonnen aan de studie Zoötechniek aan de Landbouwuniversititeit te Wageningen met als specialisatie Veefokkerij. Met het ingenieursdiploma op zak is hij in 1989 als wetenschappelijk medewerker begonnen op de Pluimveeafdeling van het National Institute of Animal Science te Foulum in Denemarken. Hij was voornamelijk betrokken bij de selectie-experimenten met vleeskuikens en de uitvoer van fokprogramma's op het proefbedrijf. In 1995 begon hij als onderzoeker pluimveefokkerij bij ID-DLO te Zeist/Lelystad. Daar was hij voornamelijk betrokken bij onderzoek naar ascites bij vleeskuikens en eikwaliteit bij leghennen. In 1997 heeft hij een jaar gewerkt als programmeur bij het softwarebedrijf PW-Consulting te Culemborg, van waaruit hij in detachering SAS-database applicaties ontwikkelde. Vanaf eind 1997 is hij werkzaam bij de leerstoelgroep Fokkerij en Genetica eerst als wetenschappelijk medewerker en later als universitair docent. Hij is bestuurslid van Interstallion en van de Stichting voor Zeldzame Huisdierrassen. Hij is tevens lid van de Commissie Erkenning en Toetsing van Stamboeken voor schapen en geiten.

Bart is getrouwd met Dorothé Ducro-Steverink en ze hebben 2 kinderen, Luciel en Pietjan.

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Het gezegde 'achter iedere succesvolle man staat een sterke vrouw', is misschien niet algemeen geldend. Maar achter mij staat zeker een sterke vrouw. Hoewel… meestal loop je vóór me uit en is alles al geregeld. Lieve Dorothé, steun en toeverlaat, dankzij jou is het toch nog wat geworden en is de boel thuis niet in het honderd gelopen. Je positieve instelling gaf me vaak weer energie om verder te gaan. Daar ben ik je zeer dankbaar voor. Misschien ben je nog blijer met de voltooiing van het proefschrift dan ik.

Lieve Luciel en Pietjan, dan heeft papa eindelijk zijn werkje af.

Colophon

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