Genetic analysis of foal and studbook traits in selection for racing performance in trotters

DOCTORAL THESIS IN ANIMAL SCIENCE

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CONTENTS

LIST OF ORIGINAL ARTICLES

This thesis is based on the following original papers, which are referred to in the text by their Roman numerals:

I Suontama, M., Saastamoinen, M.T., Ojala, M. 2009. Estimates of non-genetic effects and genetic parameters for body measures and subjectively scored traits in Finnhorse trotters. Livestock Science, 124: 205-209.

II Suontama, M., van der Werf, J.H.J., Juga, J., Ojala, M. 2011. The use of foal and studbook traits in the breeding programmes of Finnhorse and Standardbred trotters. J. Anim. Breed. Genet. 128, 114-123.

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IV Suontama, M., van der Werf, J.H.J., Juga, J., Ojala, M. 2012. Genetic correlations for foal and studbook traits with racing traits and implications for selection strategies in the Finnhorse and Standardbred trotter. In press. J. Anim. Breed. Genet.

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Contribution of the author to the papers I-IV:

The author participated in planning the study, prepared the data for statistical analyses, conducted the statistical analyses, interpreted the results, and was the main author of the papers.

ABSTRACT

The objective of this thesis was to evaluate the usefulness of body measurements and functional and conformation traits of foals and studbook horses in the breeding programmes of Finnhorse and Standardbred. Thus, non-genetic effects, heritability and repeatability, and genetic correlations for foal and studbook traits were estimated. In addition, genetic parameters for trotting race performance and genetic correlations for foal and studbook traits with racing traits were assessed. Genetic response and accuracy were estimated using records of animal, half-sibs, and parents in selection scenarios for racing traits, for foal and racing traits, and for studbook and racing traits, and using records of animal, half-sibs, and parents for foal traits and racing traits of parents. Single racing time and annual earnings were the breeding objectives in the selection scenarios.

High heritability estimates (0.50 to 0.80) indicated that most part of the variation for body measurements of foals and studbook horses is additive genetic. High genetic correlations (0.74 to 0.99) between body measurements of foals and studbook horses indicated that the traits are determined by the same additive genes at all ages. Low to moderate genetic correlations between body measurements and racing traits suggested that selection favours a larger body size at all ages.

Heritability of conformation and functional traits in foals were low to moderate (0.08 to 0.46), being generally higher than studbook traits (0.06 to 0.21). Leg stances of Finnhorse foals, type, body conformation, and overall grade of foals, and leg quality of studbook Finnhorses were of moderate heritability. Genetic correlations among the traits were from low to moderate. Partially based on the previous study, there were less unfavourable genetic correlations among foal than studbook traits. Genetic correlations between the same traits in foals and studbook horses were relatively high (over 0.60), indicating that scant new information would be received through studbook traits in genetic evaluation. In addition, the foal traits of type, trot, and overall grade were moderately to highly genetically correlated (0.50 to 0.70) with several studbook traits.

Being mainly favourable for the breeding objective, genetic correlations for conformation and functional traits with racing traits were highest for the foal traits of type, trot, and overall grade and for the studbook traits of character and movements (0.37 to 0.90). Conformation traits in Finnhorse mainly had low genetic correlations with racing traits, whereas in Standardbred leg quality of studbook horses, body conformation, leg stances, and hooves of foals and studbook horses had moderate to high genetic correlations with several racing traits. The foal trait of walk is of little value in genetic evaluation of trotters due to a low heritability and low or unfavourable genetic correlations with racing traits.

The most effective way to make genetic progress for the breeding objective is direct selection for racing time and earnings. No more than the individual records of one racing year are necessary for reasonable accuracy if the average number of racing records from different information sources is available for selection. The conformation and functional traits in foals are useful in genetic evaluation because they are less pre-selected than the traits in studbook horses, which are mostly determined by selection based on racing records. The most beneficial for the breeding objective is to use the foal traits of moderate heritability and genetic correlations with racing traits (type, trot, overall grade) in selection before a racing career in the index with racing records of relatives. The greatest gain in this scenario is due to a shorter generation interval. It is possible to implement for AI stallions. Functional and conformation traits in foals would also benefit from multi-trait selection in terms of prediction accuracy in the combined index with racing traits.

The use of multivariate models for whole trait sets in estimation of covariance components would further correct for selection, resulting in more accurate estimates of genetic correlations than in this study. Investigating the economic value of foal traits and their relationship with veterinary records would elucidate the relevance of sound conformation and movements in breeding programmes. To have more effective conformation traits in selection for breeding programmes, judging based on biological variation for a specific trait using linear scores or all-or-none variables is recommended.

1 INTRODUCTION

1.1 TROTTING HORSE RACING IN FINLAND

Trotting races are organized in Finland year-round despite the cold climate, with 630 meetings and 6100 starts annually on 43 race tracks country-wide. Separate starts are arranged for the two breeds, Finnhorses and Standardbred trotters. The annual number of racing horses is around 8000 with 2200 registered drivers, and 150 professional and 7000 hobby trainers. The annual betting turnover is over 200 million euros (http://www.hippos.fi).

The population size of trotting horses in Finland is about 19 800 Finnhorses and 25 700 Standardbred trotters (http://www.hippos.fi). Finnhorse is a native horse breed. The extent of crossbreeding used in the development of the breed in the past is unknown; it is, however, assumed to be small. The Finnhorse studbook was closed for other breeds upon its establishment in 1907. Breeding for Standardbred trotters in Finland started in the 1960s. The background of Finnish-born Standardbred trotters is mainly North-American, but the impact of French trotters cannot be ignored.

Trotters in Finland are mainly domestically bred, and annually around 1400 Finnhorse and 1900 Standardbred foals are born. The number of annually imported Standardbred horses is around 450. The breeding population has about 2400 active mares and 200 stallions in Finnhorse, and about 2700 mares and 200 stallions in Standardbred. Artificial insemination is performed on 75 % of the mare population in both breeds, enabling a wide use of genetic material nationally.

1.2 BREEDING PROGRAMMES

1.2.1 Studbook inspection

Trotting sports and horse breeding are centrally co-ordinated by the Finnish Trotting and Horse Breeding Association (http://www.hippos.fi). Trotting horse breeding is standardized by the breeding regulations of the Ministry of Agriculture and Forestry (Suomen Hippos 2004). Functions in the breeding programmes are partially funded by the government subsidies.

Individual selection of stallions takes place yearly at three stallion inspections, while mares are evaluated at 70 mare inspection shows around the country. The number of annually approved stallions is 25-50 and mares 80 for each breed. A trotter can be approved for breeding after it has been judged for type, conformation, and gaits at an inspection show. Additionally, a veterinary check, including a radiographic control, is undertaken for stallions. Overall breeding class is determined by trotting race performance using phenotypic records for best racing time and earnings, and predicted breeding values (BLUP) if available.

Estimates of breeding values (BLUP) are used at progeny evaluation, where a breeding class for stallions and mares can be upgraded on the basis of trotting race records. In the case of stallions, a breeding license can be withdrawn if progeny records are not satisfactory or if evidence emerges of a hereditary defect in offspring (http://www.hippos.fi).

1.2.2 Foal inspection

Another form of breeding shows is foal inspections, which have an advisory role in breeding programmes. Approximately 850 Finnhorse foals aged one to three years, and 350 Standardbred foals aged one to two years are judged annually in conjunction with mare inspection shows.

1.3 SOUNDNESS AND RACING PERFORMANCE

1.3.1 Soundness traits

Breeding standards for many horse breeds define an optimal body size based on the horse's use. Body size is described with objective conformation traits, i.e. body measurements, of which height at withers, circumference of girth, and circumference of cannon bone are the most common in horse populations. Variation in body measurements is largely due to additive genetic effects, which account for 34-89 % of the total variation in height measurements. Heritability estimates of circumference measurements are generally lower than those of height measurements, being from 0.27 to 0.55 (Arnason 1984, van Bergen and van Arendonk 1993, Dolvik and Klemetsdal 1999, Saastamoinen and Barrey 2000, Ricard 2004, Schroderus and Ojala 2010).

Conformation and functional traits evaluated at breeding shows can be used as indirect predictions of racing performance and as expected predictions of soundness and longevity. Conformation traits, e.g. body conformation, leg stances, leg quality, and hooves, and functional traits, such as character and movements, can be evaluated based on subjective scores, linear scores, all-or-none variables, or computer technologies. Subjective scoring is commonly used in the breeding programmes for horses, where a team of judging panel scores traits on the basis of visual assessment (Arnason 1984, Saastamoinen and Barrey 2000, Schroderus and Ojala 2010). In addition, a few breeding programmes for riding horses have applied linear scoring, where the standards of judging are based on the biological variation of a trait (van Bergen and van Arendonk 1993, Koenen et al. 1995, Saastamoinen and Barrey 2000). An alternative to scoring is to qualify a trait as an all-or-none variable which was applied by Dolvik and Klemetsdal (1999). Computerized 3D technologies have been developed to assess conformation and movements in close proximity to unbiasedness (Weller et al. 2006).

Heritability estimates for conformation and functional traits reported in the literature for riding horses have ranged from 0.07 to 0.41, indicating that differences in the estimates of heritability between subjective and linear scores are rather small (Arnason 1984, Preisinger et al. 1991, van Bergen and van Arendonk 1993, Koenen et al. 1995). Dolvik and Klemetsdal (1999) reported that 36 - 65 % of the total variation for all-or-none variables of leg conformation was due to additive genetic effects in Norwegian cold-blooded trotters.

1.3.2 Racing performance traits

The most important breeding objective in trotters is racing performance, which can be measured with a number of traits. The most common racing traits in genetic evaluation of trotters are annual best racing time or single racing time and annual earnings. Direct selection for racing records is evidently the most efficient method of genetic improvement because around 20 - 40 % of the total variation for racing time and earnings is due to additive genetic effects (Arnason et al. 1982, Ojala 1982, Ojala 1987, Klemetsdal 1994, Pösö and Ojala 1997, Arnason 1999, Thuneberg-Selonen et al. 1999, Bugislaus et al. 2005a, Langlois and Blouin 2007). Additionally, racing traits, such as age at first start, placings, disqualifications, and number of races, are included in genetic evaluation. The variation due to additive genetic differences is around 10 - 20 % for these traits (Arnason et al. 1982, Ojala 1987, Saastamoinen and Nylander 1996, Pösö and Ojala 1997, Arnason 1999).

1.3.3 Relationship between soundness and racing performance

In addition to genetic and non-genetic effects on racing performance, other considerable causes for lack of success and non-starting are injuries and poor health in trotters in Finland (Saastamoinen 1991). Racing success in trotters partly depends on good health, which enables optimal training (Vigre et al. 2002).

Vigre et al. (2002) reported that lameness was the most frequent health problem causing interruptions in the training of trotters in Denmark. Magnusson and Thafvelin (1990) and Dolvik and Klemetsdal (1996) indicated that only a small proportion of trotters was free of signs of lameness. According to Vigre et al. (2002), orthopaedic problems in race horses are usually caused by multiple factors. Conformational defects are among risk factors for unsoundness (Magnusson and Thafvelin 1990, Dolvik and Klemetsdal 1999), and a genetic predisposition for lameness exists (Gaustad et al. 1995, Gaustad et al. 1996). Heritability for lameness was estimated to be 0.25 for a continuous variable and 0.33 for a binary variable (Dolvik and Gaustad 1996).

Common agreement exists that unsoundness has an indirect effect on racing success through an impaired possibility for regular training, resulting in poorer records. Consequently, breaks in racing cause a deficit in annual income of trotters. One measurement for soundness is conformation, the relevance of which in breeding programmes is shown by radiographic findings having a variable relationship with racing performance in trotters (Laws et al. 1993, Storgaard Jorgensen et al. 1997, Couroucé-Malblanc et al. 2006, Robert et al. 2006). However, while evidence of a direct relationship between conformation and racing performance according to earlier studies is somewhat weak, it is statistically significant (Magnusson and Thafvelin 1990, Dolvik and Klemetsdal 1999).

1.4 SELECTION FOR BREEDING OBJECTIVES

The general breeding objective of the Finnhorse and Standardbred trotter is to produce horses that show good performance, character, movements, strength, and health (http://www.hippos.fi). Phenotypic selection of trotters at studbook inspection is predominantly based on best racing time and earnings. Accordingly, racing time and earnings can be considered the main breeding objective at individual selection. At the stage of progeny evaluation, the aggregate breeding value in the BLUP index defines the breeding objective of single racing time and annual earnings with equal weights of 40%, and age at first start and annual best racing time with weights of 10% each (http://www.hippos.fi).

Direct selection for racing time and annual earnings is inevitably an effective method for genetic improvement of trotters on the basis of heritability estimates. Additionally, high and favourable genetic correlations among racing traits support selection for overall racing performance, based on a large number of genetic correlations studied among annual racing traits in the Finnhorse and Standardbred trotter (Pösö and Ojala 1997). Moderate to high repeatability estimates for racing time traits and annual earnings in the trotter populations of Finland (Pösö and Ojala 1997, Thuneberg-Selonen et al. 1999) suggest that only a few repeated records are sufficient for reasonable accuracy of selection. Multiple measurements for highly repeatable traits yield only a slight gain in accuracy, and it is seldom worthwhile to obtain more than two or three measurements (Falconer and Mackay 1996).

A generally known dilemma in horse breeding is a long generation interval, which is mainly due to a prolonged use of horses in races. Revold et al. (2010) reported that a large amount of prize money is paid for young trotters in Norway to encourage early starting contributing to a shorter generation interval. In practice, trotters in Finland race in excess of two seasons. The number of repeated phenotypic records can be around 15-50 at studbook inspection. On the basis of genetic parameters, the amount of repeated records is unnecessary in terms of prediction accuracy. A more effective method of selection would be to use BLUP estimates of breeding values at individual selection instead of phenotypic selection, enhancing selection response and accuracy.

The purpose of foal and studbook traits in the Finnish trotter breeding programmes is to breed for sound conformation and functionality. According to earlier studies, heritability of conformation and functionality, e.g. leg stances and movements, is low (Arnason 1984, Preisinger et al. 1991, van Bergen and van Arendonk 1993, Koenen et al. 1995), and the traits are largely affected by non-genetic factors such as judging year, age, gender, and location (Arnason 1984).

The most effective way to genetically improve functionality and conformation is to use foal and studbook traits in estimation of breeding values. The value of single foal and studbook traits in genetic evaluation depends on heritability of the traits and genetic correlations among them. Foal traits are available at earlier ages than studbook traits, making foal traits more attractive because of a shorter generation interval and thereby for a larger genetic gain in the population. The efficiency of these traits in selection depends not only on genetic variation of the traits but also their genetic correlations with racing performance. Foal and studbook traits can benefit from multi-trait selection for the breeding objective if genetic correlations with trotting race traits are moderately to highly favourable. Thus, compared with phenotypic selection, genetic response and accuracy would be expected to increase for conformation and functional traits when applying multi-trait BLUP index for conformation, functional, and trotting race traits.

Selection for well-performing trotters raises many questions on breeding programme design. To meet the demand for fast, productive trotters, it can be questioned whether racing records alone are adequate in selection. Genetic parameters for foal and studbook traits and their relationship with racing traits need to be known for efficient breeding programme design.

2. OBJECTIVES OF THE STUDY

The first objective was to study non-genetic effects and estimates of heritability, repeatability, and genetic correlations for foal and studbook traits in Finnhorse and Standardbred trotters (I, II). Second, genetic parameters for trotting racing traits were estimated (III). Third, genetic correlations between foal and studbook traits and racing traits were investigated, and the efficiency of conformation and functional traits in selection scenarios examined (IV).

Studies I-IV contributed to the objectives of the study by determining the following:

I Estimates of non-genetic effects and genetic parameters for body measures and subjectively scored traits in Finnhorse trotters

II Use of foal and studbook traits in the breeding programmes of Finnhorse and Standardbred trotters

III Genetic parameters for racing records in trotters using linear and generalized linear models

IV Genetic correlations for foal and studbook traits with racing traits and implications for selection strategies in the Finnhorse and Standardbred trotter

3. MATERIALS AND METHODS

3.1 MATERIALS

3.1.1 Data sets

Three different types of data foal inspection, studbook inspection, and trotting race data, were available for the two breeds, Finnhorses and Standardbred trotters from the Finnish Trotting and Breeding Association (http://www.hippos.fi.). Data sets used in each study (Studies I-IV) are described in Table 1, where the study number, breed, number of horses, number of records, year of records, objective of study, and data type are given.

Foal inspection

Data sets for Finnhorse and Standardbred trotters from foal inspection shows included height measurements and scores for conformation and functional traits. Data were pre-processed by deleting clearly false recordings of inspection information.

Studbook inspection

Data sets for Finnhorse and Standardbred trotters from studbook inspection shows included body measurements and scores for conformation and functional traits. Data were pre-processed by adding information that was missing and deleting clearly false recordings of studbook information.

Trotting race

Trotting race data for Finnhorses and Standardbred trotters were pre-processed by removing clearly false information on records. Data sets were modified to cover records from seventeen main race tracks in country-wide. To estimate the fixed effect of a single race, data sets were further modified to contain starts with a minimum of 10 horses.

3.1.2 Traits

Foal traits

Height at withers and height at croup were the traits measured at foal inspection shows to describe body size.

Scores contained the conformation traits of type, body conformation, leg stances, and hooves, and the functional traits of walk and trot. In addition, overall grade was included. The traits were judged on a scale of 3 to 10, and overall grade was assessed from 0 to 9. Scoring of foal traits is done by judging panels of sixteen horse breeding associations around the country. The chairperson at judging panels is the same for different breeding associations during an election term, whereas other members differ between the breeding associations.

A number of characteristics are combined in one score for conformation and functional traits in foals. Type is a description of overall appearance, quality of horse, and gender type, i.e. masculine or feminine. Body conformation is the description of shape, muscularity, and balance of body. Regularity of leg angles from front, side, and back is judged in the scores for leg stances. Quality, shape, and size of hooves are judged in the score for hooves. Regularity and stride of gaits are evaluated in the scores of walk and trot. Overall grade is an overall qualification class based on all foal scores. However, the scores for leg stances and trot have the largest weight in overall grade.

Studbook traits

Height at withers, height at croup, body length, circumference of girth, and circumference of cannon bone were body measurements in studbook horses.

Scores were the conformation traits of body conformation, leg stances, leg quality, and hooves, and the functional traits of character and movements. The judging panel for mares is the same as at foal shows. The judging panel of stallions has a small variability between locations, and the chairperson is the same during an election term. The traits were scored on a scale from 4 to 10.

A score is a joint description of several conformational or functional characteristics in studbook horses. Body conformation, leg stances, and hooves are judged accordingly to foals. Character is a description of temperament and behaviour judged mainly during a driving test. A veterinarian scores leg quality to describe the health of legs. Walk and trot are jointly scored in movements where stride, impulsion, and regularity of gaits are evaluated.

Racing traits

There were six single trotting race traits of racing time per km (s), earnings (€), winnings (0/1), placings (0/1), breaking stride (0/1), and disqualifications (0/1), and one annual trait of earnings (€) in the analyses. Racing time (s/km) describes a trotter's speed. Earnings traits are related directly to a horse's income, and were analysed as a single purse and as annual total earnings (both in €). General racing success using single records was described by the binary (0/1) racing success traits of winnings, placings, breaking stride, and disqualifications. In these binary traits, the code of 1 was denoted as follows: for winnings indicating the horse won the race, for placings the horse finished as one of the three best horses, for breaking stride the horse broke down to gallop, and for disqualifications the horse was disqualified from the race. Placings describe a horse's level relative to the mates in the same race, whereas winnings reflect a horse's temperament and competitiveness (Ojala 1987). Breaking stride describes a horse's ability for consistent trotting movements containing the strides of gallop, whilst disqualifications include long gallops and various other incidents causing a disqualified race, e.g. a driver's error.

Table 1. Description for data sets used in Studies I-IV.

Paper	Breed	No.of horses	No. of observations	Year	Objective	Type of data
I	Finnhorse[2]	6381	6381	1971-2004	Non-genetic factors, heritability, correlations for studbook traits	Studbook inspection
II	Finnhorse[1]	6529	8548	1995-2006	Genetic correlations between foal and studbook traits	Foal inspection
	Finnhorse[2]	6596	6596	1971-2006		Studbook inspection
	Standardbred[1]	3069	3428	1995-2006		Foal inspection
	Standardbred[2]	2112	2112	1981-2006		Studbook inspection
III	Finnhorse	17792	510519	1984-2005	Heritability, repeatability, correlations for trotting race records	Racing records
	Standardbred	25536	513161	1984-2005		Racing records
IV	Finnhorse[1]	Papers II and III			Correlations for foal and studbook traits with racing records, genetic response	Foal inspection, studbook inspection, racing records
	Finnhorse[2]	Papers II and III				
	Standardbred[1]	Papers II and III				
	Standardbred[2]	Papers II and III				

[1] Foals

[2] Studbook horses

3.2 METHODS

3.2.1 Statistical analyses

The impact of fixed effects (I-III), variance components of random effects (I-III), and estimates of heritability and repeatability (I-III) was assessed with univariate linear mixed models (I-III) and univariate generalized linear mixed models (III). Covariance components (I-IV) and genetic (I-IV) and phenotypic correlations (I, III, IV) were analysed with bivariate linear mixed (I-IV) or bivariate generalized linear mixed models (III), and multivariate linear mixed models (I). Variance and covariance components were estimated using animal models (I-IV).

The fixed effect of interaction of judging year and gender and the fixed effect of age were taken into account for studbook traits (I,II, IV), whereas the fixed effect of judging year and the interaction of gender and age were fitted in models for foal traits (II, IV). The fixed effect of judging location was included in models for foal and studbook traits in Studies II and IV. Foal traits were corrected for the fixed effect of judging season in analyses (II, IV). Single racing records were corrected for the fixed effects of gender and age (III, IV), the fixed effect of interactions of starting method, starting lane, and volting group (III, IV), and either the fixed effects of racing length, race track, season, and racing year (III, IV) or the fixed effect of single race (III).

The random effect of additive genetic variance of an animal was taken into account for foal traits, studbook traits, and racing traits in all studies. The random effect of permanent environmental variance of an animal was included in models for repeated foal records (II, IV) and repeated racing records (III, IV).

Pedigree information for animals with records was at minimum three generations in Finnhorse and two generations in Standardbred (I-IV). Genetic groups based on country of birth were fitted in the base population for Standardbred trotters (III, IV).

In Study I, the estimates of fixed effects and their statistical significance were estimated with F-test for studbook traits using PEST software (Groeneveld 1990). (Co)variance components were analysed with VCE5.1.2 software in Study I (Kovac and Groeneveld 2003). The software ASReml 2.0 (Gilmour et al. 2003) was used to estimate the fixed effects and their statistical significance with F-incremental test in Study II, and (co)variance components in Studies II and IV. ASReml 3.0 (Gilmour et al. 2009) was used to estimate the fixed effects and their statistical significance with F-incremental test in Study III and (co)variance components in Studies III and IV.

3.2.2 Multi-trait selection

To evaluate the usefulness of foal and studbook traits in the selection process, four different selection scenarios, each with a specific index, were compared using the multi-trait index program (van der Werf 1999). The breeding objective was single racing time and annual earnings, and the traits were weighted equally in the aggregate breeding value in the four selection scenarios. The additional racing traits of placings and disqualifications were included in the indices in order to gauge the genetic change for these traits.

Index 1 in scenario 1 included the trotting race traits of racing time, annual earnings, placings, and disqualifications using the information sources of an animal, parents, and half-sibs. Index 2 in scenario 2 included the trotting race traits of racing time, annual earnings, placings, and disqualifications and the foal traits of type, body conformation, leg stances, hooves, walk, trot, and overall grade using the information sources of an animal, parents, and half-sibs. Index 3 in scenario 3 included the trotting race traits of racing time, annual earnings, placings, and disqualifications and the studbook traits of character, body conformation, leg stances, hooves, leg quality, and movements using the information sources of an animal, parents, and half-sibs. Index 4 in scenario 4 included the foal traits of an animal, parents, and half-sibs and the trotting race traits of parents for racing time, annual earnings, placings, and disqualifications.

Genetic response (R) was calculated per generation for the traits. In addition, the correlated response (cR) for foal and studbook traits was estimated in the index of scenario 1. The number of observations in the information sources was the same for each selection scenario (IV, Table 1). Selection intensity (i) was assumed to be 1.0 in all scenarios corresponding to a proportion of selected animals of 38 % (Falconer and Mackay 1996). (Co)variance matrices were modified to positive definitive by bending in the index program. Genetic parameters used in the selection index are presented in Tables 2-6.

Table 2. Heritability and repeatability with standard errors as subscripts used in multi-trait selection index for Finnhorse and Standardbred.

Foal Trait	Finnhorse	Standardbred
Type	$0.28_{0.03}$ $0.37_{0.02}$	$0.38_{0.06}$ $0.42_{0.04}$
Body conformation	$0.31_{0.03}$ $0.38_{0.02}$	$0.46_{0.04}$ $0.46_{0.04}$
Leg stances	$0.23_{0.03}$ $0.39_{0.02}$	$0.14_{0.03}$ $0.31_{0.05}$
Hooves	$0.15_{0.03}$ $0.22_{0.02}$	$0.10_{0.03}$ $0.23_{0.05}$
Walk	$0.14_{0.02}$ $0.30_{0.02}$	$0.08_{0.03}$ $0.24_{0.05}$
Trot	$0.19_{0.03}$ $0.40_{0.02}$	$0.17_{0.04}$ $0.31_{0.05}$
Overall grade	$0.31_{0.03}$ $0.52_{0.02}$	$0.36_{0.05}$ $0.51_{0.04}$
Studbook Trait		
Character	$0.12_{0.02}$	$0.17_{0.06}$
Body conformation	$0.10_{0.03}$	$0.13_{0.05}$
Leg stances	$0.12_{0.02}$	$0.13_{0.05}$
Hooves	$0.16_{0.03}$	$0.09_{0.04}$
Leg quality	$0.21_{0.04}$	$0.06_{0.04}$
Movements	$0.18_{0.02}$	$0.11_{0.04}$
Racing Trait		
Racing time	$0.34_{0.02}$ $0.77_{.003}$	$0.33_{0.01}$ $0.59_{.003}$
Fourth root annual earnings	$0.19_{0.01}0.39_{0.01}$	$0.27_{0.01}$ $0.46_{0.01}$
Placings	$0.10_{0.01}$ $0.16_{.003}$	$0.09_{.004}$ $0.14_{.002}$
Disqualifications	$0.06_{0.01}$ $0.16_{.003}$	$0.07_{0.01}$ $0.17_{.003}$

Table 3. Genetic (below the diagonal) and phenotypic correlations used in multi-trait selection index for Finnhorse foals.

TY	BO	LG	HOF	WLK	TRT	OVG	SQVS	KM	PL	DISQ
	0.39	0.13	0.06	0.07	0.19	0.53	-0.1	-0.44	0.05	-0.04
0.64		0.16	0.14	0.09	0.14	0.51	-0.3	-0.1	0.03	-0.03
0.3	0.43		0.07	0.2	0.11	0.55	0.01	-0.33	0.01	-0.01
0.04	0.48	0.23		0.07	0.07	0.22	-0.04	-0.36	0.04	-0.02
0.04	0.2	0.21	0.26		0.2	-0.02	-0.02	-0.07	0	0.01
0.41	0.46	0.29	0.39	0.38		0.06	0.04	-0.42	0.05	-0.04
0.79	0.84	0.67	0.49	0.35	0.67		0	-0.21	0.06	-0.04
0.37	0.18	0.16	0.25	0.02	0.52	0.43		-0.74	0.35	-0.24
-0.41	-0.15	-0.13	-0.33	-0.02	-0.54	-0.44	-1		-0.43	0.23
0.3	0.15	0.09	0.33	-0.02	0.37	0.32	0.99	-0.98		-0.28
-0.34	-0.23	-0.1	-0.19	0.07	-0.35	-0.33	-0.91	0.88	-0.48	

TY=type, BO=body conformation, LG=leg stances, HOF=hooves, WLK=walk, TRT=trot, OVG=overall grade, SQVS=fourth root annual earnings, KM=single racing time, PL= placings, DISQ= disqualifications

Table 4. Genetic (below the diagonal) and phenotypic correlations used in multi-trait selection index for Standardbred foals.

TY	BO	LG	HOF	WLK	TRT	OVG	SQVS	KM	PL	DISQ
	0.52	0.13	0.06	0.02	0.17	0.52	0.11	-0.29	0.09	-0.05
0.83		0.11	0.07	0.07	0.14	0.51	0.11	-0.2	0.09	-0.05
0.3	0.39		0.15	0.21	0	0.54	0.07	-0.22	0.02	-0.02
0.1	0.4	0.83		0.06	0.11	0.1	0.02	-0.21	0.04	-0.03
0.02	0.19	0.19	0.1		0.21	0.32	-0.02	-0.08	-0.01	-0.01
0.36	0.26	0.2	-0.09	0.56		0.34	0.07	-0.18	0.04	-0.04
0.88	0.85	0.61	0.49	0.31	0.58		0.12	-0.24	0.09	-0.07
0.43	0.38	0.38	0.48	-0.03	0.44	0.54		-0.72	0.37	-0.26
-0.45	-0.38	-0.37	-0.45	-0.1	-0.43	-0.54	-0.99		-0.43	0.29
0.47	0.44	0.2	0.41	-0.07	0.34	0.47	0.98	-0.98		-0.29
-0.31	-0.26	-0.18	-0.36	-0.14	-0.37	-0.39	-0.87	0.86	-0.62	

TY=type, BO=body conformation, LG=leg stances, HOF=hooves, WLK=walk, TRT=trot, OVG=overall grade, SQVS=fourth root annual earnings, KM=single racing time, PL= placings, DISQ= disqualifications

Table 5. Genetic (below the diagonal) and phenotypic correlations used in multi-trait selection index for studbook Finnhorses.

CH	BOD	LG	HOF	LQ	MOV	SQVS	KM	PL	DISQ
	0.1	0.12	0.1	0.03	0.26	0.09	-0.35	0.06	-0.06
0.43		0.18	0.11	-0.01	0.15	-0.03	-0.09	0	0
0.25	0.42		0.15	0.24	0.27	-0.14	-0.05	0.01	-0.02
0.24	0.26	0.31		0.15	0.14	0.02	-0.07	0.03	-0.02
-0.16	-0.2	0.19	0.29		0.1	-0.04	-0.04	0.03	-0.02
0.51	0.2	0.28	0.39	-0.14		0	-0.3	0.09	-0.07
0.61	-0.1	0.3	0.24	0.3	0.69		-0.74	0.35	-0.24
-0.68	0.14	-0.18	-0.27	-0.08	-0.7	-1		-0.43	0.23
0.55	-0.03	0.1	0.25	0.21	0.63	0.99	-0.98		-0.28
-0.66	0.01	-0.21	-0.21	-0.2	-0.64	-0.91	0.88	-0.48	

CH=character, BOD=body conformation, LG=leg stances, HOF=hooves, LQ=leg quality, MOV=movements, SQVS=fourth root annual earnings, KM=single racing time, PL=placings, DISQ=disqualifications

Table 6. Genetic (below the diagonal) and phenotypic correlations used in multi-trait selection index for studbook Standardbreds.

CH	BOD	LG	HOF	LQ	MOV	SQVS	KM	PL	DISQ
	0.04	0.12	-0.02	0.06	0.28	0.13	-0.24	0.1	-0.04
0.16		0.04	0.08	0.01	0.03	-0.1	-0.31	0.08	-0.03
-0.32	0.57		0.18	0.25	0.35	0.07	-0.16	0.03	-0.01
0.61	-0.05	0.05		0.15	0.13	0.02	-0.12	0.03	-0.03
0.12	-0.16	0.55	0.64		0.23	-0.44	-0.44	0.03	-0.03
-0.12	0.72	0.48	0.03	-0.02		-0.48	-0.38	0.09	-0.09
0.7	0.6	0.37	0.29	0.45	0.88		-0.72	0.37	-0.26
-0.63	-0.69	-0.4	-0.51	-0.44	-0.9	-0.99		-0.43	0.29
0.67	0.71	0.3	0.38	0.3	0.73	0.98	-0.98		-0.29
-0.35	-0.27	-0.11	-0.33	-0.31	-0.74	-0.87	0.86	-0.62	

CH=character, BOD=body conformation, LG=leg stances, HOF=hooves, LQ=leg quality, MOV=movements, SQVS=fourth root annual earnings, KM=single racing time, PL=placings, DISQ=disqualifications

4. RESULTS AND DISCUSSION

4.1 NON-GENETIC EFFECTS

4.1.1 Foal traits

Effect of age and gender

The interaction of age and gender had a significant effect ($p < 0.001$) on all foal traits in Finnhorse, whereas in Standarbred it had no effect on leg stances and walk (II). In both breeds, colts were larger than fillies at all ages for both height at withers and height at croup. Finnhorse colts at all ages had higher scores than fillies for conformation and functional traits, except for walk. In Finnhorse, colts in older age classes had better scores than their younger peers, whereas two-year-old fillies obtained the lowest scores for type, leg stances, and trot across all classes. In Standardbred, the effect of age and gender for conformation and functional traits was not as clear, possibly due to a smaller number of classes for the effect; however, two-year-old foals had higher scores than one-year-old foals.

The effect of age and gender in Finnhorse can be explained by fillies and colts having different development and growth spans at early ages. Saastamoinen (1993) reported similar results for height measurements in Finnhorse foals, but contrary to this study colts had lower scores for subjective traits than fillies. The current results are in agreement with those of Schroderus (2006), which are based on partly the same data, but where age and gender were fitted as separate effects in the model. Preisinger et al. (1991) reported that the age of foals should be included in the estimation of breeding values for mares in the Trakehner population. Riding horse fillies had better scores than colts, except for movements (Bhatnagar et al. 2011).

Effect of judging year

A strong fluctuation between judging years was observed in body measurements and conformation and functional traits of foals ($p < 0.001$) (II). Differences for body measurements between years may reflect an annual variation in environmental conditions such as quality of nutrition and amount of grazing. The annual variation for conformation and functional traits can indicate sporadic changes in the standards of judging; however, the traits of body conformation, leg stances, walk, and trot can also be affected by environmental factors such as climatic conditions, amount of exercise, and grazing.

Judging of foals usually fluctuates between years (Preisinger et al. 1991, Schroderus 2006, Bhatnagar et al. 2011). According to Preisinger et al. (1991), the effect of judging year reflects not only the effect of judges, but also changes in pre-selection criteria and differences in environmental conditions.

Effect of season

Judging season had a large effect ($p < 0.01$) on body measurements and conformation and functional traits in Finnhorse (II). In Standardbred, season had an influence ($p < 0.05$) on all traits, except leg stances and trot (II). In both breeds, foals measured in autumn were larger than those measured in early spring. There was an indication of seasonal trend on foal traits. In both breeds, the foal traits of body conformation, walk, and trot consistently improved from the first season of judging (March to April), being at their highest in the fourth season (July to September). This was also the case for overall grade in Finnhorse and for type, leg stances, and overall grade in Standardbred. Unsurprisingly, foal traits are affected by season reflecting the influence of age and grazing on development and growth. This can be interpreted as foals being at better condition and as having better gaits after grazing season in late summer and early autumn.

Similar results for the effect of season on foal traits were reported by Saastamoinen (1993), and scoring of young Shetland ponies by their coat condition was found to be influenced by season (van Bergen and van Arendonk 1993).

Effect of location

In Finnhorse foals, body measurements and conformation traits had large differences between locations ($p < 0.01$), whereas the functional traits of walk and trot did not differ between locations (II). In Standardbred, locations had a large effect ($p < 0.001$) on foal traits other than leg stances, walk, and overall grade (II). The effect of location on body measurements may due to different environmental conditions for growth between breeding associations. The effect of location on foal traits can be explained by judging teams.

Saastamoinen (1993) and Schroderus (2006) reported similar results in Finnhorse and Standardbred foals. Preisinger et al. (1991) reported that judging teams had the largest effect on scoring when compared with other non-genetic effects.

4.1.2 Studbook traits

Effect of year and gender

The interaction of judging year and gender had a large effect ($p < 0.001$) on studbook traits in both breeds (I, II). A declining environmental trend was noted for cannon bone measurement in Finnhorse mares, whereas only annual fluctuations were evident for other body measurements in Finnhorse and Standardbred. An unwritten change for stricter judging commenced in 1987, reflected as a clear declining trend for character, leg stances, hooves, and movements in the Finnhorse. Annual fluctuations were characteristic for studbook traits in Standardbred trotters. Finnhorse stallions were smaller than mares in traits other than cannon bone circumference. In Finnhorse, stallions had lower scores than mares for traits other than character, and no differences emerged between genders in movements. In Standardbred, stallions were larger for height at withers and clearly had lower scores for leg stances, leg quality, and hooves than mares.

The interaction of judging year and gender reflects the effects of selection. In earlier studies, stallions have had larger body measurements than mares, except for girth circumference (Arnason 1984, Magnusson and Thafvelin 1990, Dolvik and Klemetsdal 1999). According to Arnason (1984), differences between judging years in scored traits arise from changes in judging criteria and differences in quality of horses and shows.

Effect of age

Age at judging had an effect ($p < 0.001$) on traits other than height at withers and body conformation in Finnhorses, whereas in Standardbred trotters all traits were affected by age ($p < 0.001$) (I, II). In Finnhorse, body length, circumference of girth, and cannon bone consistently increased from the age of six onwards, and in Standardbred an increasing trend with age was evident for body length and girth circumference. Finnhorses aged 8 years and above had lower scores than younger horses, particularly for the traits of character, leg quality, and movements. In Standardbred, no trend with age was seen. The development of body structure as a result of growth and training can explain increased body measurements with age. A stricter judging of elderly horses and a postponed studbook inspection of inferior horses may explain lower scores at older ages in Finnhorse.

Similarly to this study, Arnason (1984) reported growing measurements for circumference of girth and cannon bone with age in Icelandic horses, but contrary to this study, older horses had higher scores for leg stances and movements. The effect of age on scored traits may also reflect the attitude of the judging towards aged individuals. Many studies for conformation and functional traits have dealt with horses of the same age (Magnusson and

Thafvelin 1990, van Bergen and van Arendonk 1993, Samore 1997, Dolvik and Klemetsdal 1999).

Effect of location

Height at withers, circumference of girth, and cannon bone, and all studbook traits differed between locations in Finnhorse ($p < 0.01$), whereas the effect of location was less significant ($p < 0.02$) for body measurements and studbook traits in Standardbred (I, II). The effect of location on body size can be explained by environmental conditions in different parts of the country. However, differences in horse material may contribute to some extent. Scoring of conformation and functional traits is likely to be influenced by judging teams' personal preferences. Differences between judging teams could be reduced by creating written standards for the traits in the judging scheme.

The effect of judging panels on subjective traits has been highly significant in many riding horse populations (Preisinger et al. 1991, van Bergen and van Arendonk 1993, Koenen et al. 1995). According to Arnason (1984), the same chairperson in panels had a diminishing influence on fluctuations in judging.

4.2 ESTIMATES OF HERITABILITY AND REPEATABILITY

Body measurements

Body measurements of foals and studbook horses are highly heritable traits. In Studies I and II, estimates of heritability ranged from 0.41 to 0.84. The highest heritability estimates were obtained for height at withers and height at croup in both foals and studbook horses, heritabilities being lower for these traits in studbook horses than in foals. Circumference of girth had the lowest heritability in both breeds. Repeatability estimates for foal height measurements were of a similar magnitude as heritabilities, indicating that permanent environmental variation is small for the traits.

Generally lower estimates of heritability were obtained for studbook body measurements in the Standardbred trotter than in Finnhorse. On the basis of variance components, this can be a consequence of the diminishing effect of selection on additive genetic variance. In addition, a larger environmental variation was apparent for the traits in Standardbred than in Finnhorse, except body length. Nevertheless, high heritability estimates indicated that body size is mainly determined by additive genetic effects. On the other hand, a relatively small residual variance suggests that random environmental effects on the growth of foals and the body size of adult horses are quite uniform.

Due to the distinction of horse breeds, heritability estimates reported in the literature have a wide range of values. However, heritability estimates in this study were in accordance with earlier studies, where height measurements generally had higher estimates of heritability than circumference measurements (Arnason 1984, van Bergen and van Arendonk 1993, Dolvik and Klemetsdal 1999, Ricard 2004, Schroderus and Ojala 2010).

Conformation and functional traits

The foal traits were low to moderately heritable (0.08 to 0.46) (II). Type, body conformation, and overall grade in both breeds and leg stances in Finnhorse foals showed moderate estimates of heritability. Other traits in foals had low estimates of heritability. The foal traits of leg stances, walk, and trot indicated moderately high estimates of repeatability. The studbook traits in both breeds had low estimates of heritability (0.06 to 0.21) (I, II), except that leg quality of Finnhorse was moderately heritable.

Heritability of foal traits was generally higher than that of studbook traits, considering that the set of foal traits is only partly the same as studbook traits. Nevertheless, the same traits of body conformation, leg stances, and trot (foals) or movements (studbook horses) resulted in a noticeably higher estimate of heritability in foals than studbook horses. In Finnhorse, hooves had slightly lower heritability in foals, but in Standardbred only a marginally higher estimate of heritability was obtained in foals than in studbook horses. Conformation at later ages is more likely to be influenced by environmental factors such as training and overall management, and the foal traits may reflect a wider and more unbiased representation of the genetic resources in predicting a horse’s genetic potential more accurately. A large permanent environmental variation for leg stances, walk, and trot of foals is likely due to hoof care, training, and handling at shows.

Low estimates of heritability for conformation traits can be a consequence of scoring, as combining a number of characteristics in one score may conceal some part of the additive genetic variation. Heritability estimates in the population are dependent on all components contributing to variation, and genetic components are affected by gene frequencies, which are sensitive to the effects of selection. In small populations, gene frequencies tend to fix after ongoing selection, and heritability estimates are expected to be lower than in large populations (Falconer and Mackay 1996).

Heritability estimates for functional and conformation traits in trotters (Dolvik and Klemetsdal 1999, Schroderus and Ojala 2010) and in foals are few (Preisinger et al. 1991, Schroderus and Ojala 2010, Bhatnagar in 2011), whereas a larger number of studies on adult riding horses have been reported (Arnason 1984, Preisinger et al. 1991, van Bergen and van Arendonk 1993, Koenen et al. 1995, Samore et al. 1997). Heritability estimates in this study are within the range of values presented in the literature.

Racing traits

Single racing time differed from the normal distribution, but of all racing traits was closest to normal (III, Table 2). The distribution of racing time is skewed, having a long tail to the right, but with most of the values concentrated around the mean, giving a peaked distribution. Linear models on the logarithmic scale and gamma distribution on the underlying logarithmic scale did not show a difference between variance components (III, Table 4). However, the variance between observations diminished using linear models on the logarithmic scale or alternatively using gamma distribution on the underlying logarithmic scale compared with variance components using linear models on the normal scale (III, Table 4). Estimates of heritability for single racing time were from 0.32 to 0.34 with a race track model in both breeds (III, Table 4). Repeatability for racing time was high, 0.77 to 0.78, in Finnhorse, and moderate, 0.58 to 0.59, in Standardbred. Corrected for the fixed effect of race, heritability for racing time was 0.23 to 0.29, and repeatability ranged from 0.48 to 0.62 (III, Table 5).

Racing time is a moderately heritable and highly repeatable trait. Selection of animals for racing time is effective, and because of high repeatability, only a few repeated measurements are needed for a reasonably accurate selection. A notably higher estimate of repeatability was obtained in Finnhorse, indicating that permanent environmental factors affecting racing time are more substantial than in Standardbred. A wide range of heritability estimates (0.19 to 0.35) has been reported for racing time using many different types of data sources (single, annual, career) and methods of estimation (Arnason et al. 1982, Ojala 1987, Saastamoinen and Nylander 1996, Pösö and Ojala 1997, Arnason 1999, Thuneberg-Selonen et al. 1999, Bugislaus et al. 2005a). Heritability estimates of single racing time corrected for race track were higher here than in Bugislaus et al. (2005a). Estimates of heritability and repeatability of single racing time corrected for the race effect are in accordance with the literature (Thuneberg-Selonen et al. 1999, Bugislaus et al. 2005a, Bugislaus et al. 2005b).

Non-normal distributions of single and annual earnings improved considerably with fourth root transformation (III, Table 2). Single earnings resulted in more greatly reduced variance components using GLMM models compared with fourth root transformation, especially in Standardbred, whereas in Finnhorse differences between variance components using fourth root transformation and multinomial distribution on the underlying logistic scale were smaller (III, Table 4). Single earnings is a lowly heritable and repeatable trait, with heritability ranging from 0.07 to 0.09 and repeatability from 0.11 to 0.17 (III, Tables 4 and 5). Fourth root of annual earnings showed moderate estimates of heritability and repeatability, 0.19 and 0.39 in Finnhorse and 0.27 and 0.46 in Standardbred (III, Table 4).

The low estimates of heritability and repeatability for single earnings in this study are in agreement with earlier research (Thuneberg-Selonen et al.

1999, Bugislaus et al. 2005a). Moderate estimates of heritability and repeatability for annual earnings have been reported in previous studies as well (Arnason et al. 1982, Ojala 1987, Klemetsdal 1994, Saastamoinen and Nylander 1996, Pösö and Ojala 1997, Arnason 1999), although annual earnings is a lower heritable trait in young trotters at the age of 3-4 years (Ojala 1987, Klemetsdal 1994, Saastamoinen and Nylander 1996). Selection of trotters is usually based on annual earnings; in terms of accuracy, 10 single records would result in higher accuracy than one annual record based on the current genetic parameters.

Binary racing success traits of winnings, placings, breaking stride, and disqualifications on the underlying logistic scale were of low heritability (0.04 to 0.13) and repeatability (0.11 to 0.20) (III, Table 6). In both breeds, winnings had the highest and breaking stride the lowest estimates of heritability.

Heritability for single racing success was lower in this study than for annual racing success variables reported in previous studies (Ojala 1987, Pösö and Ojala 1997, Arnason 1999). In accord with this thesis, a low heritability for rankings from single races has previously been reported (Thuneberg-Selonen et al. 1999, Bugislaus et al. 2005a).

4.3 GENETIC CORRELATIONS

4.3.1 Foal and studbook traits

Body measurements

Body measurements of trotters are determined by the same additive genes at all ages. Genetic correlations were highly positive between studbook measurements (0.75 to 0.98), and between foal and studbook measurements (0.74 to 0.99), and phenotypic correlations between body measurements ranged from moderately to highly positive (0.58 to 0.95) (I, II). Highly positive genetic and phenotypic correlations between body measurements of foals for the same population were described by Schroderus and Ojala (2010).

Highly positive genetic correlations among body measurements indicated that genetic background for the measurements is similar. Genetic correlations between foals and studbook horses suggested that body size in foals and adult horses is mainly determined by the same additive genes. Saastamoinen and Barrey (2000) reported highly positive genetic correlations for these traits in a large number of studies on a large variety of breeds.

Conformation and functional traits

Genetic correlations among studbook traits and between foal and studbook traits ranged from low to high (I, II). The traits at all ages were mainly favourably genetically associated, but a number of unfavourable genetic correlations also exist. Phenotypic correlations among studbook traits were close to zero or low in both breeds. Due to a small number of the same animals having a foal and a studbook trait, phenotypic correlations between foal and studbook traits could not be estimated.

Genetic and phenotypic correlations among foal conformation and functional traits for the same population were estimated in the recent study by Schroderus and Ojala (2010).

Studbook conformation and functional traits

Genetic correlations among studbook scores were from lowly negative to moderately positive in Finnhorse (-0.20 to 0.51). Moderately negative to highly positive genetic correlations were obtained in Standardbred (-0.32 to 0.72); however, estimates can only be considered indicative because of large standard errors.

In Finnhorse, the highest favourable genetic correlation was between character and movements. In addition, character and body conformation (0.43), body conformation and leg stances (0.42), leg stances and hooves (0.31), and hooves and movements (0.39) were moderately genetically correlated. Quality of legs in Finnhorse was unfavourably genetically correlated with character, body conformation, and movements (-0.14 to -0.20).

In Standardbred, the highest genetic correlation was obtained between body conformation and movements. Moreover, in this breed, leg conformation traits were moderately genetically correlated: leg stances and leg quality 0.55, and hooves and leg quality 0.64. The scores for leg stances also had a moderate genetic correlation with the scores of body conformation and movements. Unfavourable genetic correlations were obtained for a small number of studbook scores in Standardbred. A moderate negative genetic correlation was obtained between character and leg stances, yet the majority of unfavourable genetic correlations in the Standardbred were close to zero.

Foal and studbook conformation and functional traits

The respective traits in foals and studbook horses were highly genetically associated (0.62 to 1.00) in both breeds, but also the foal trait of overall grade had moderately to highly favourable genetic correlations (0.30 to 0.72) with all studbook traits. The foal trait of type and the studbook trait of body conformation were highly genetically correlated (0.61, 0.64) in both breeds. Leg stances of foals showed moderate to high positive genetic correlations with studbook traits for leg quality (0.94), hooves (0.68), and movements (0.53) in Standardbred. In Finnhorse, a moderate genetic correlation was estimated between the foal trait of leg stances and the studbook trait of leg quality (0.55). The foal trait of trot had a high genetic correlation with the studbook trait of movements, being higher in Standardbred than in Finnhorse (0.64, 0.89). Genetic correlation between the foal trait of walk and the studbook trait of movements was moderate (0.58) in Finnhorse, but low (0.09) in Standardbred.

All foal and studbook traits were favourably genetically associated in Finnhorse, whereas a highly negative genetic correlation was obtained for the foal trait of walk and the studbook trait of character (-0.69) in Standardbred.

Genetic correlations among all conformation and functional traits

In the study by Schroderus and Ojala (2010), genetic correlations among foal traits ranged from 0.04 to 0.64 in Finnhorse and from -0.09 to 0.83 in Standardbred. Overall grade had the highest genetic correlations with other foal traits in both breeds, but the correlations with hooves and walk were only moderate. Type and body conformation were also highly genetically correlated in both breeds. Walk was weakly genetically associated with other foal traits; however, the association with trot was moderate in Finnhorse and high in Standardbred. Phenotypic correlations among foal traits were mainly low (Schroderus and Ojala 2010).

Generally higher and mostly favourable genetic correlations among foal traits (Schroderus and Ojala 2010) are anticipated to be more effective in selection than studbook traits. In studbook horses, rather low negative genetic correlations between quality of legs and body conformation, and between quality of legs and movements in Finnhorse suggested that breeding for soundness of legs is not expected to prevent progress in other traits. Low genetic correlations among many studbook traits may be due to the effect of selection on gene frequencies. Studbook traits represent a narrower range of genetic resources, being pre-selected based on racing records, whereas foal traits are less pre-selected.

Genetic correlations between foal and studbook traits indicated that scores are largely determined by similar pleiotropic gene effects at different ages. The respective conformation traits in foals and in studbook horses can be considered genetically similar. An overall grade of moderate heritability would be one alternative in simultaneous selection for conformation and functionality based on high genetic correlations with other foal traits and a number of studbook traits. High genetic correlations between foal and studbook traits indicated that selection could be based on foal traits of higher heritability and earlier availability, as only a limited amount of new information is received through studbook traits.

Scored traits have mainly been highly and favourably genetically correlated in earlier studies (Preisinger 1991, Bhatnagar et al. 2011). However, a wide range of genetic correlations, varying from low to high, and a small number of unfavourable genetic correlations among scored traits have been reported in the literature (Arnason 1984, van Bergen and van Arendonk 1993, Koenen et al. 1995, Samore et al. 1997).

4.3.2 Racing traits

Racing traits were highly and favourably genetically correlated (0.70 to 1.00) (III, Table 7). A high genetic correlation of 0.97 to 1.00 was obtained for racing time with earnings, winnings, and placings as well as for earnings with winnings and placings in both breeds. Racing time and earnings had generally lower, yet high genetic correlations with disqualifications (0.84 to 0.91) and with breaking stride (0.70 to 0.84). Phenotypic correlations were low to moderate, except for the correlation between racing time and annual earnings, which were high.

Selection for racing time and earnings would be effective and a correlated response for other racing traits would be substantial based on high genetic correlations. Racing time, earnings, winnings, and placings can be considered genetically similar traits. Estimates of genetic correlations have ranged from moderate to high for career, annual, or single racing records in the literature (Arnason et al. 1982, Saastamoinen and Nylander 1996, Pösö and Ojala 1997, Arnason 1999, Bugislaus et al. 2005a, Gomez et al. 2010). The current results were similar to those of a study in German trotters, where a high genetic correlation between ranking and earnings was obtained, but other genetic correlations in this thesis were higher (Bugislaus et al. 2005a, 2005b). Genetic correlations were higher in the current study between single racing time and annual earnings than in the Spanish trotter (Gomez et al. 2010). The current genetic correlations were of similar magnitude as those between annual repeated records of best racing time and earnings in a study in Finnhorse and Standardbred (Pösö and Ojala 1997). However, genetic correlations for racing time and earnings traits with racing success in the present study were higher than for annual traits in Pösö and Ojala (1997). High genetic correlations between best racing time and earnings for career and annual records were estimated in the Swedish Standardbred (Arnason et al. 1982, Arnason 1999), but in the present study higher genetic correlations were estimated for racing time and placings and for earnings and placings than in previous reports.

It would be expected that phenotypic correlations between racing time and placings as well as between single earnings and placings were higher and closer to the estimates of genetic correlations. Lower phenotypic correlations are probably due to non-homogeneous distributions for racing times and earnings among races. These distributions are likely to be explained by different racing times per kilometre between races and dissimilar purses between races. Similarly to this study, lower phenotypic correlations between these traits have been reported with a race track and a single race model in the German trotter by Bugislaus et al. (2005a).

4.3.3 Foal or studbook traits and racing traits

Body measurements and racing traits

Low to moderate genetic correlations between body measurements and racing traits indicated that selection should favour bigger horses at all ages (IV, Tables 2-5). The highest genetic correlations among these traits in foals were for height at withers and height at croup with breaking stride (-0.30, -0.33) in Finnhorse and with winnings (0.33, 0.34), placings (0.31, 0.31), and racing time (-0.30, -0.30) in Standardbred. In studbook Standardbred horses, moderate genetic correlations emerged for circumference of girth with racing time (-0.37), winnings (0.33), and placings (0.30), whereas in Finnhorse these correlations were low.

Genetic correlations were higher for foals than for studbook horses, suggesting that the influence of body measurements on selection diminishes with age. Foal body measurements describe not only body size but also development, as growth is completed no earlier than at the age of 4-5 years. The foal height measurements would assist in selection against breaking stride in Finnhorse and in selection for racing time and rankings in Standardbred. Genetic correlations between body measurements and trotting race performance are in accordance with breeding aim, where early maturing horses and a young age at starting a racing career are anticipated and favourably correlated with later racing success (Saastamoinen 1991).

The relationship between body measurements and racing performance was different in this thesis than in the Swedish Standardbred (Magnusson and Thafvelin 1990) and partially similar to in that Norwegian cold-blooded trotters (Dolvik and Klemetsdal 1999). Based on phenotypic regression coefficients for body measurements, smaller body size was favourably associated with racing performance in the Swedish Standardbred (Magnusson and Thafvelin 1990). Height at withers in the Norwegian cold-blooded trotter had a positive regression on earnings, whereas negative regression coefficients were estimated for circumference of girth and earnings (Dolvik and Klemetsdal 1999).

Conformation and functional traits and racing traits

Genetic correlations with racing traits were highest for the foal traits of type, trot, and overall grade and for the studbook traits of character and movements, being mainly favourable for the breeding objective (IV, Tables 2-5). Genetic correlations for foal and studbook conformation traits with racing traits were mainly low in Finnhorse and moderate to high in Standardbred. A number of unfavourable but low genetic correlations were found in Finnhorse and Standardbred foals. The foal trait of walk had low genetic correlations with all racing traits.

In foals, the highest genetic correlations were for trot with racing time (-0.54), and earnings (0.52) in Finnhorse and for overall grade with racing time (-0.54) and earnings (0.54) in Standardbred. In studbook horses, high genetic correlations emerged for character with racing time and earnings in Finnhorse (-0.68, 0.61) and Standardbred (-0.63, 0.70), and also for movements with racing time and earnings in Finnhorse (-0.70, 0.69) and Standardbred (-0.90, 0.88).

In Finnhorse, the foal traits of body conformation and leg stances had low genetic correlations with racing traits, whereas in Standardbred moderate genetic correlations were found for body conformation with racing time (-0.38), earnings (0.38), winnings (0.42), and placings (0.44) and for leg stances with racing time and earnings (-0.37, 0.38). In addition, the foal trait of hooves had moderate genetic correlations (±0.30 to 0.48) with all racing traits in Standardbred, and in Finnhorse with racing time and placings (-0.33, 0.33). Studbook conformation traits had low genetic correlations with racing traits in Finnhorse, but in Standardbred body conformation, leg stances, leg quality, and hooves showed moderate to high genetic correlations with several racing traits.

Genetic correlations suggested that selection for racing performance also results in a favourable genetic change of type, trot, and overall grade of foals and character and movements of studbook horses. These results are expected because the traits in question describe the qualities in horses that presumably contribute to racing success. In foals and studbook horses of Finnhorse, conformation traits such as body conformation and leg stances are weakly genetically associated with racing traits, whereas in Standardbred these traits are more closely genetically associated. One reason for low genetic correlations may indeed be the biological nature of the traits. Low genetic correlations for many conformation traits with racing traits may not necessarily mean that these traits are useless in breeding programmes. However, more efficient ways of measuring traits should be taken into consideration in the judging schemes and only the most relevant traits included in selection.

Studbook horses are strongly pre-selected based on racing records because a horse must fulfil a minimum criterion for racing time and earnings for studbook inspection. Foal traits may not represent similarly selected genetic resources as studbook traits because entering a foal show is not based on any criterion defined by the breeding programmes. A larger variation for foal than studbook traits was evident in Study II. The amount of pre-selection for foal shows done by owners is unknown, although it can be assumed to take place to some extent.

Low and unfavourable genetic correlations can be explained by the effect of long-term selection on (co)variances, which have a tendency to be reduced under selection. In the study, selection was partially taken into account for bivariate analyses. However, the use of multivariate analyses of whole trait sets would be expected to result in more accurate estimates of genetic correlations.

Genetic and residual covariances for the traits may have been influenced by the data structure of this study, where the number of animals having both a foal or studbook trait and a racing record was relatively small compared with the total number of horses. The number of sires that had offspring both in the foal or studbook data and in the racing data was reasonable (20-40%). However, genetic covariances would certainly be more accurate, as the number of animals having a record in both data sets and the number of common sires in the data sets would be increased. Estimates are likely to be subject to large sampling errors when more information on covariance components comes via relatives, unless animals are highly related or data sets are large (Meyer 1991).

The relationship between conformation and trotting race performance has not been strong in earlier studies. Magnusson and Thafvelin (1990) reported phenotypic regression coefficients, indicating that racing performance was positively associated with good orthopaedic health and conformation in Swedish Standardbred trotters. Dolvik and Klemetsdal (1999) emphasized the value of direct selection for racing performance and the use of estimates of breeding values for racing performance, having reported significant but not very strong relationships for the traits describing leg stances and leg conformation with racing records of starting status and earnings in Norwegian cold-blooded trotters.

4.4 IMPLICATIONS FOR SELECTION STRATEGIES

4.4.1 Genetic response and accuracy

Racing traits in the breeding objective had a high genetic response in the units of genetic standard deviation per generation (0.79 to 0.82) in indices 1-3 due to moderate heritability and moderate to high repeatability and high genetic correlations for the traits (IV, Tables 6 and 7). Indirect selection would also be effective for additional racing traits of low heritability, because of high genetic correlations with the breeding objective. Only a slight increase in the genetic response and the accuracy of the total index was obtained by the inclusion of scored foal or scored studbook traits in the indices in scenarios 2 and 3. In scenario 4, where selection was done on the basis of foal traits of an animal and its parents and half-sibs and racing records of the parents, genetic response for racing traits was obviously much lower than in the other scenarios, being from 0.50 to 0.61 in Finnhorse and 0.51 to 0.63 in Standardbred (IV, Tables 6 and 7). The greatest benefit of this scenario would be obtained through a shorter generation interval, as animals could be selected well before their own racing career.

The correlated response of foal traits was somewhat lower (0.00 to 0.39 in Finnhorse, 0.05 to 0.42 in Standardbred) than including them in the index (0.03 to 0.47 in Finnhorse, 0.05 to 0.51 in Standardbred). Similarly, the correlated response of studbook traits was only a little lower -0.09 to 0.54 in Finnhorse, 0.29 to 0.73 in Standardbred than inclusion in the index (-0.09 to 0.56 in Finnhorse, 0.32 to 0.73 in Standardbred). However, selection accuracy for conformation and functional traits in foals and studbook horses would benefit from the combined use with racing traits in the indices of scenarios 2 and 3. Type, trot, and overall grade in foals and character and movements in studbook horses, which had the highest genetic correlations with racing traits, resulted in the largest genetic response. In Standardbred, the traits of low heritability, such as body conformation of studbook horses and leg quality, clearly benefited from multi-trait selection due to high genetic correlations with racing traits.

4.4.2 Implications for selection

The most effective way to make genetic progress is direct selection for racing time and earnings. Inclusion of the records of one racing year for an animal in the total index is sufficient for reasonable accuracy if the average number of racing records from different information sources is available in selection. The foal or studbook traits are of limited value in genetic evaluation of trotters if the racing records of the animal itself are available. Selection for racing time and annual earnings would improve conformation and functional traits without including them in the index based on correlated responses in scenario 1. However, selection accuracy of conformation and functional traits would benefit from the combined selection with racing records in the total index.

The usefulness of multi-trait evaluation for conformation and functional traits and racing traits depends on the reliability of genetic correlations between them. For this reason, it is essential to estimate all relevant correlations for genetic evaluation using multivariate models for whole trait sets as well as including every piece of information on which selection is based. Foal traits are likely to be less pre-selected than studbook traits because a larger proportion of foals than studbook horses in the population is evaluated. Selection criteria are also likely to be less systematic for foal than studbook shows, which demand certain racing records. In addition, evaluation of studbook horses is probably influenced by their racing records, whereas foals would have more independent evaluations in the absence of their own racing records. Based on these arguments, it can be assumed that foal traits would be a better alternative in genetic analyses.

Evaluating conformation and functional traits at an early age is also recommended because studbook traits are more largely influenced by non-genetic factors. On the other hand, there is a larger additive genetic variation for foal than for studbook traits. In addition, many foal and studbook traits can be considered genetically similar based on high genetic correlations between them. Consequently, a very limited amount of new information is received through studbook traits. Multi-trait selection would be useful for prediction accuracy, in particular, for foal traits of low heritability. Foal traits other than walk would benefit from multi-trait selection because genetic correlations with the breeding objective are higher than heritabilities for these traits. The foal trait of walk is not useful for inclusion in selection of trotters, as it is mainly affected by environmental factors and is not associated with racing traits.

Two important aspects that make more use of conformation and functional traits are scaling and standardization of evaluation both of which may have an effect on estimates of genetic parameters for these traits. Linear scores or all-or-none variables for specific traits could improve the effectiveness of conformation and functional traits in breeding programmes by describing differences between animals more clearly. Relevant differences emerged in scoring between judging teams that could be assumed to contribute to low genetic parameters if the traits were evaluated on an inconsistent basis. Specific trait descriptions would be expected to result in higher estimates of heritability and genetic correlations with the breeding objective as a result of more harmonized evaluation than is the case currently.

The greatest advantage of conformation and functional traits in genetic evaluation is to use of the foal traits in prediction of racing performance before a racing career. In this case, the accuracy of selection would obviously be lower, but the greatest gain in genetic response is achieved through a considerably shorter generation interval. However, using horses alternatively in sports or breeding would raise financial concerns because owners are likely to want to race their horses long enough to achieve maximum profits. This scenario is only theoretical for mares because all mares showing trotting ability would probably be used for racing before breeding. Embryo transfer would enable an earlier use of mares, but it is not used in practical breeding, probably due to high costs. In addition, in Standardbred only one embryo per mare per year is allowed according to an international agreement, so accelerating genetic improvement with good individuals in this way is banned. Earlier breeding use could be implemented in young stallions, as the main breeding method in current breeding programmes is artificial insemination.

This study elucidates the relationship of conformation and functional traits with racing performance. Good racing performance itself is an indirect indication of soundness. However, a more straightforward evaluation of these traits with soundness could be accomplished based on analysis of foal traits and veterinary data, where variables such as injuries of joints and tendons are relevant. One problem in this approach is the limited availability and the complex structure of veterinary data. Genetic relationships and economic values of conformation and functional traits with related injuries could provide some further information on the relevance of these traits in breeding programmes.

5. CONCLUSIONS

Body measurements in foals and studbook horses are highly heritable traits, being determined by similar genetic effects at all ages based on the high genetic correlations among them. Genetic correlations between body measurements and racing traits ranged from low to moderate, indicating that selection should favour a bigger body size at all ages.

Being largely affected by environmental factors, conformation and functional traits in foals showed low to moderate estimates of heritability. They were generally higher than the studbook traits, which proved to have low heritability. Conformation and functional traits were mainly highly genetically associated in foals and studbook horses. Type, trot, and overall grade are the most effective foal traits in selection, having moderate estimates of heritability as well as moderate genetic correlations with racing traits. Character and movements would benefit from high genetic correlations with racing traits in selection of studbook horses. Conformation traits showed moderate to high genetic correlations with several racing traits in Standardbred, whereas in Finnhorse, conformation traits mainly had low genetic correlations with racing traits.

Selection for single racing time and annual earnings is effective based on moderate estimates of heritability and moderate to high repeatability, having a reasonable accuracy using one-year racing records for an animal in multi-trait selection. Selection for additional racing traits of low heritability, such as placings and disqualifications, would be effective because of high genetic correlations among racing traits. Foal and studbook traits are of limited value in genetic evaluation of trotters if the racing records of the animal itself are available. Correlated responses for foal and studbook traits were of similar magnitude, as including them in the index suggested that genetic change for these traits occurs even if including only racing traits in selection. However, to increase selection accuracy of conformation and functional traits, it would be useful to include them in the total index. Foal traits would be more beneficial in selection because they are less pre-selected than studbook traits. Evaluating foals rather than studbook horses is useful because of a larger additive genetic variation and a smaller environmental variation. Selection was partially taken into account in estimation of covariance components using bivariate models in the study; however, to have more accurate estimates of covariances, multivariate models should be used for the whole set of traits in genetic evaluation. Low or unfavourable genetic parameters can be explained by long-term selection having a diminishing effect on genetic variation of correlated traits.

The greatest advantage of conformation and functional traits in genetic evaluation for the prediction of racing performance would be to use the foal traits before a racing career. In this case, the greatest gain in genetic response would be achieved through a considerably shorter generation interval. An earlier use for breeding would be feasible to implement for young stallions, as the main breeding method in current breeding programmes is artificial insemination.

There were differences between judging teams that may contribute to low (co)variation for conformation and functional traits. Higher genetic parameters could be expected if the traits were evaluated according to a standardized judging scheme. To improve the usefulness of conformation and functional traits in breeding programmes, judging based on biological variation for a specific trait using linear scores or all-or-none variables is recommended.

This study attempted to elucidate the relationship between conformation and functional traits and racing performance. Genetic relationships and economic values of conformation and functional traits with related injuries could provide further information on the relevance of the traits in breeding programmes for sound conformation and movements.

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