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Integrated genetic evaluation of breeding field test traits, competition traits and test status in Icelandic horses

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Agricultural University of Iceland

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To Rakel Eir

Clarification of contribution

I hereby declare that the writing of the following thesis and the five accompanying papers is my work, done under the supervision and with assistance of my advisors Dr. Þorvaldur Árnason, Dr. Susanne Eriksson, Dr. Anna Näsholm, Dr. Erling Strandberg, Dr. Ágúst Sigurðsson and Dr. Freddy Fikse. Dr. Þorvaldur Árnason is the ideological father of the research that was further developed in cooperation with Albertsdóttir, Eriksson, Näsholm, Strandberg, Sigurðsson and Fikse, in the course of the work.

The contribution of Elsa Albertsdóttir to the papers included in this thesis was as follows:

Paper I: All co-authors participated in planning of the work. Albertsdóttir collected and merged the data from the Icelandic National Horse Association and the Swedish Icelandic Horse Association. Albertsdóttir edited and analysed the data, with assistance from Eriksson, Näsholm and Árnason. All co-authors contributed to the interpretation of the results. Albertsdóttir and Eriksson drafted the paper, further revised by the other co-authors. Albertsdóttir was responsible for correspondence with the scientific journal.

Paper II: All co-authors participated in planning of the work. Albertsdóttir collected and merged the data. Albertsdóttir was responsible for carrying out the genetic analyses, with advice from the co-authors. Albertsdóttir interpreted results together with Árnason, with assistance from the other co-authors. Albertsdóttir wrote the manuscript and corresponded with the scientific journal in collaboration with Árnason, Eriksson, Näsholm and Strandberg.

Paper III: Albertsdóttir planned the work in collaboration with the co-authors. Albertsdóttir collected and edited the data. Albertsdóttir and Árnason chose the definition of the test status trait. Albertsdóttir carried out the analyses with assistance from Árnason and Eriksson on selecting appropriate methods. Fikse contributed with technical advice. Albertsdóttir wrote the paper and corresponded with the scientific journal in collaboration with Árnason, Eriksson and Sigurðsson.

Paper IV: Árnason was the main responsible for the simulation study. Planning of the work was done by Árnason and the simulation was designed in collaboration with the co-authors. Árnason programmed the simulation and performance of analyses. He interpreted the results in collaboration with Sigurðsson, Albertsdóttir, Eriksson and Fikse. Árnason drafted the paper, with revision by Fikse and final approval by all authors.

Paper V: Albertsdóttir planned the work in collaboration with the co-authors. Albertsdóttir was responsible for gathering, merging and editing the data. Methods for analyses were chosen by Albertsdóttir, Árnason, Fikse and Eriksson. Albertsdóttir performed the analyses. Albertsdóttir interpreted the results with assistance from the co-authors. Albertsdóttir drafted the manuscript, further revised by Fikse and Eriksson and approved by all authors.

Elsa Albertsdóttir

Abstract

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The main goal in breeding the Icelandic horse is to produce aesthetically appealing and capable riding horses with five gaits and good spirit, suited both for leisure and competition. Selection of Icelandic breeding horses is based on breeding values calculated from the breeding field test records. It has been speculated that assessed horses are not a random sample of the population, a situation that would lead to bias in estimated breeding values and retards genetic improvement. The main aim of this thesis was to study integrated genetic evaluation of competition traits and breeding field test traits for Icelandic horses where the effects of preselection in the data were accounted for.

Genetic parameters of the competition traits, and of genetic relationships between competition traits and the breeding field test traits were analysed. The breeding field test data included individual records of Icelandic horses evaluated in 11 countries. The competition data included records of horses that had competed in Iceland and Sweden. The competition traits and breeding field test traits were analysed using linear animal models. The competition traits analysed were both original and combined ones covering the competition aptitude of four-gait, five-gait, toelt and pace. The combined traits were formed in order to describe the competition traits in a simpler manner. The estimated heritabilities were low to moderately high for all competition traits and the genetic correlations estimated among competition traits were generally strong and favourable with few exceptions. Moderate genetic correlations were estimated between most of the competition traits and some of the conformation traits assessed at breeding field tests. High genetic correlations were generally estimated between the competition traits and most of the riding ability traits recorded in breeding field tests. Competition traits were concluded to be suitable for genetic selection.

Breeding field test traits and test status, an all-or-none trait describing attendance at breeding field tests, were genetically analysed using bivariate animal and sire linear-threshold models. The presence of preselection in breeding field test data was verified by the estimated genetic parameters for test status: this trait had a significant genetic component and related strongly to the breeding field test traits, especially those that had

high weight in the selection index. This applied to both conformation and riding ability traits, although breeders seem to pre-select horses to attend breeding field tests more strongly on good riding qualities than on aesthetic conformation. The emphasis on riding ability as the criterion for preselection was further supported by a larger increase in estimated genetic parameters for these traits when analysed simultaneously with test status.

Environmental covariances between test status and breeding field test traits are not estimable as all individuals with test status equal to zero lack phenotypic values on the tested traits. The effect of assuming zero environmental covariances between test status and the breeding field test traits was studied in a simulation. It did not lead to serious bias in the estimated genetic parameters unless the non-estimable true environmental correlation deviated largely from zero. Moderately biased genetic parameters had only relatively small effects on the genetic evaluation. Estimation of breeding values where test status was included in the model always led to improvement in genetic progress and in higher correlations between true and estimated breeding values.

The benefits from integrating test status, competition traits or both into current genetic evaluation based on breeding field test traits were estimated. In general there were trivial differences between models. Estimated breeding values were largely unbiased for all traits, although models including test status showed minor deviances from this. The current breeding evaluation system seems therefore to be well established. However, breeding values were more accurately estimated with the inclusion of the new traits, especially the test status. The ranking of sires, based on combined indexes, changed (between 10% and 20%) with inclusion of the competition traits and test status. This indicates how large the effect of adding new traits to the genetic evaluation will have on the selection of sires. Integration of test status and competition traits increases the accuracy of the genetic evaluation and influences the ranking of sires, and therefore selection of sires for future breeding. Genetic parameters for the test status trait should be re-estimated where the trait is re-defined for all horses and all traits including both competition and breeding field test data. Competition traits can be included directly in the genetic evaluation and will give breeders an effective tool on which to base their selection.

Keywords: Horse; Genetic evaluation; Breeding field tests; Competitions; Test status; Genetic analyses; Model evaluation.

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Ágrip

Ræktunartakmark fyrir íslenska hestinn miðar almennt að því að rækta vel skapaðan, léttbyggðan, fjölhæfan, viljugan og geðprúðan hest sem fer glæsilega í reið. Við úrval hrossa er notast við kynbótamat sem byggir á kynbótadómum. Því hefur verið haldið fram að hross sem koma til dóms séu ekki slembiúrtak stofnsins. Slíkt veldur skekktu kynbótamati og dregur úr erfðaframskrif. Meginmarkmið þessarar rannsóknar var kanna samþætt kynbótamat keppniseiginleika og eiginleika sem dæmdir eru á kynbótasýningum (kynbótaeiginleika), að teknu tilliti til forvals í gögnum.

Erfðastuðlar keppniseiginleika og erfðafylgni milli kynbóta- og keppniseiginleika voru greindir. Kynbótagögnin innihéldu einstaklingsdóma frá ellefu löndum. Keppnisgögnin innihéldu endurtekna dóma á hrossum sem tóku þátt í alþjóðlega viðurkenndum mótum á Íslandi og í Svíþjóð. Línuleg einstaklinglíkön voru notuð við úreikninga. Rannsakaðir voru keppniseiginleikarnir tölt, fjórgangur, fimmgangur og gæðingaskeið. Unnið var með undirflokka framangreindra eiginleika en til einföldunar var einnig unnið með samsetta eiginleika fyrir hvern flokk. Metin arfgengi voru meðalhá fyrir alla keppniseiginleikana. Tvímælingagildi þeirra var um 60%. Sterk erfðatengsl voru jafnan metin milli keppnis- og kynbótaeiginleika. Sú ályktun var dregin að keppniseiginleikar séu hæfir til þess að byggja kynbótamat á.

Til að greina hvort forval ætti sér stað í gögnum var skilgreindur sérstakur eiginleiki sem lýsir því hvort hross mætir til kynbótadóms eða ekki. Þessi mætingareiginleiki var síðan metinn saman með kynbótaeiginleikum með tvíbreytu einstaklings- og fedra línulegum-þröskulds líkönum. Gögnin voru kynbótadómar hryssna sem fæddar voru á Íslandi. Sönnur voru færðar á tilvist forvals í kynbótagögnum með metnum erfðastuðlum: forval hefur marktækan erfðabátt og sterk erfðatengsl við kynbótaeiginleika, sér í lagi þá eiginleika dómstigans sem hafa háa vægstuðla. Þetta átti bæði við um sköpulagseiginleika og hæfileika, þó svo sýnt sé að ræktendur beiti sterkara forvali við hross sem búa yfir miklum reiðhæfileikum en þau sem eru einungis vel sköpuð. Sterkt for-úrvalsmark reiðhæfileika var enn frekar staðfest með hækkun erfðastuðla á eiginleikum með hátt vægi þegar þeir voru greindir ásamt mætingu.

Ekki er unnt að meta umhverfisfylgni milli mætingar og kynbótaeiginleika þar sem að einstaklingar sem mæta ekki til dóms, hafa ekki sviparsgildi fyrir kynbótaeiginleikana.

Áhrif þess að áætla að umhverfisfylgnin jafngilti núlli voru metin með líkindarannsókn. Slík einföldun olli ekki verulegri skekkju í metnum erfðastuðlum nema ef sönn umhverfisfylgni vék verulega frá núlli. Meðalskekktir erfðastuðlar höfðu aðeins smávægileg áhrif á kynbótamatið. Kynbótamat þar sem tekið var tillit til forvals í gögnum jók erfðaframfarir og sterkari fylgni kom fram milli sannra og metinna kynbótagilda.

Ávinningur þess að samþætta núverandi kynbótamat, sem byggir á kynbótadómum, með keppniseiginleikum og/eða taka tillit til forvals í gögnum var metinn með samanburði mismunandi líkana. Að jafnaði voru áhrif á kynbótamat kynbótaeiginleikana takmarkaður. Núverandi kynbótamatskerfi virðist því vera vel ígrundað. Metin kynbóttagildi allra líkana voru jafnan óskekkt, þó svo að nokkur frávik kæmu fram í líkönum þar sem tekið var tillit til forvals í gögnum. Öryggi kynbótamatsins jókst með því að samþætta kynbótamatið nýju eiginleikunum, sér í lagi að teknu tilliti til forvals. Uppröðun stóðhesta miðað við aðaleinkunnir breyttist (um 10-20%) með því að bæta nýjum eiginleikum við sem vísar til þess hve mikil áhrif viðbótareiginleikarnir hafa á val á framtíðarstóðhestum. Erfðastuðlar fyrir mætingu þyrfi að endurmeta þar sem eiginleikinn væri endurskilgreindur með sama hætti og notkun hans í framtíðar kynbótamati verður: mæting ætti þá við um alla hesta og næði til bæði kynbóta- og keppniseiginleika. Það er unnt að bæta keppniseiginleikum beint inn í kynbótamatskerfið. Af því mun hljótast mikill ávinningur þar sem að það mun gefa ræktendum færi á því að byggja úrval keppnishrossa á traustari grunni.

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Papers included in the thesis

The present thesis is based on the following publications, which will be referred to by their Roman numerals.

- I. Albertsdottir, E., Eriksson, S., Näsholm, A., Strandberg, E., Árnason, Th. 2006. Genetic analysis of competition data on Icelandic horses. *Livest. Sci.*, 110, 242-250.
- II. Albertsdottir, E., Eriksson, S., Näsholm, A., Strandberg, E., Árnason, Th. 2007. Genetic correlations between competition traits and traits scored at breeding field tests in Icelandic horses. *Livest. Sci.*, 114, 181-187.
- III. Albertsdóttir, E., Eriksson, S., Sigurdsson, Á., Árnason, T., 2010 Genetic analyses of 'breeding field test status' in Icelandic horses. *J. Anim. Breed. Genet.* ISSN 0931-2668. *In press.*
- IV. Árnason, T., Albertsdóttir E., Eriksson, S., Fikse, F., Sigurdsson, Á., 2010. Estimation of genetic parameters and response to selection for continuous trait subject to culling before testing. *Submitted* for publication in *J. Anim. Breed. Genet.*
- V. Albertsdóttir, E., Árnason, T., Eriksson, S., Sigurdsson, Á., Fikse, F., 2010. Effects of integrated genetic evaluations of breeding field test traits, competition traits and test status for Icelandic horses on predictive ability, accuracy and selection bias. *Submitted* for publication in *J. Anim. Breed. Genet.*

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List of abbreviations

AM: animal model

BV: Breeding value

BLUE: Best linear unbiased estimate

BLUP: Best linear unbiased prediction

DMU: Faculty Agricultural Science (**DJF**) **M**ultivariate analysis by REML

EBV: Estimated breeding value

FEIF: The International Federation of Horse Associations (Föderation Europäischer Islandpferde Freunde)

FIPO: Rule for Icelandic Horse Sport Events (FEIF Islandpferde Prüfungsordnung)

GLM: Generalised linear models

MSEP: Minimum standard error prediction

REML: Restricted maximum likelihood

SAS: Statistical analyses software

SE: Standard error

SM: Sire model

1 Introduction

Successful breeding of livestock involves a well structured breeding scheme where all traits of interest are thoroughly defined and improved by directional selection on estimated breeding values (Koenen et al., 2004). In order to be unbiased the genetic evaluation has to be based on a large amount of unselected records of the goal traits or take into account the criterion of selection (Henderson, 1975).

The main goal in breeding the Icelandic horse is to produce aesthetically appealing and capable riding horses with five gaits and good spirit, suited both for leisure and competition (FEIF, 2010a). Currently fifteen breeding field test traits meet the detailed definition of the breeding objectives but no competition traits are defined as goal traits. Numerous horses compete at international levels and a large amount of information is available on competing horses. Furthermore, competition horses are very valuable individuals which many breeders, therefore, aim to produce. There has thus been a need to evaluate suitability of the competition data for genetic evaluation and to consider subsequent integration of competition traits into the current breeding scheme.

Selection of Icelandic breeding horses is based on breeding values calculated from the breeding field test records. It has been speculated that assessed horses are not a random sample of the population, a situation that would lead to bias in estimated breeding values and retard the development of genetic improvement (Henderson, 1975; Klemetsdal, 1992). The alleged preselection was therefore studied by genetically analysing an all-or-none test status trait, and the effect of including it into the genetic evaluation of Icelandic horses was examined.

The effects of integrating either or both competition traits and test status into the breeding evaluation of Icelandic horses was tested regarding bias, predictive ability and accuracy of the estimation, correlations between breeding values estimated with different models, and ranking of sires.

1.1 Background

The Icelandic horse breed developed in Iceland, where it is the only horse breed. The first references on horses in Iceland are found in *The Book of Settlement*, which narrates the settlement of the country by the Norse in the 9th and 10th centuries. The horses that were brought by the Vikings in their ocean-going ships (called *knerrir*) over the Atlantic Ocean had to be carefully selected as the space on the ships was very restricted. The importance of the horse to the Icelanders is demonstrated throughout various Sagas of Icelanders, the skin manuscripts which contain the record of events that took place in Iceland in the 10th and early 11th centuries. In these stories descriptions of horses, their qualities and how their owners selected horses for breeding and riding are given due space, while other livestock is hardly ever referenced. Although the horse's task has changed throughout history it has always been used for riding as no roads were built in Iceland until the turn of the 19th century. In the beginning and continuing into the twentieth century the horse's primary role was as a means of transportation and for agriculture; only since mechanisation and development in the 1950's has the horse been raised primarily for leisure and competition (Björnsson & Sveinsson, 2004)

The Icelandic horse population consists of 214,002 live individuals that are registered with unique ID numbers in the stud book, Worldfengur. Approximately 55% of them are located outside Iceland, overall in 31 countries (www.worldfengur.com). Since almost no horses have been imported into Iceland for more than a thousand years, the Icelandic horse is a purebred horse breed (Adalsteinsson, 1981). Only one case of importation was reported in the 12th century (Pálsson, 1996). In 1882 all importation was forbidden by law because of health regulations (Stephensen & Jensson, 1887). Approximately 200,000 Icelandic horses have been exported to various countries since the 1850's: for the first half century as working horses in British coalmines and later as riding horses. Most went to European countries, some to North America and a few to Asia (Statistics Iceland, 1997).

The Icelandic horse is small, long-lived and hardy. The attractiveness of the breed is mainly through the horse's pleasant temperament and unique gaiting ability, including the smooth four-beat toelt and the flying pace. Almost all Icelandic horses have the toelt besides the three ground gaits of walk, trot and gallop, and some horses have also the pacing ability. Those that show pace are called five-gaited horses; others are called four-gaited horses. Toelt has the

same foot ranking as walk, where one or two feet are simultaneously on the ground and is therefore without a suspension phase. Toelt varies as it is ridden in a very slow and up to a fast tempo. Pace is a lateral two-beat gait with a suspension phase and is commonly ridden at a fast speed. Pace is considered to be a threshold trait in the sense that a horse must have a combination of genetic ability and environmental circumstances to surpass the phenotypic threshold for expressing the trait. Pacing ability is closely correlated to abilities in other gaits, especially the toelt. Horses with limited pacing ability are often not trained as five-gaiters as the pace training may impair the quality of the toelt (Árnason & Sigurdsson, 2004).

1.1.1 Breeding goal

Breeding of horses was initially legislated in 1891 in Iceland and was guided through the first years by advisory services and horse breeding associations offering horse exhibitions (Björnsson & Sveinsson, 2004). In 1950 a unique breeding assessment system was established with a scoring index for registration of individual traits on a linear scale that are assessed at breeding field tests (Árnason et al., 1994; Hugason, 1994). In 1990 a thoroughly defined breeding field assessment scale was reproduced by The Icelandic Farmers Association where all the assessed traits were detailed. Furthermore, practical use of the scale in order to make clear differences between the good and bad qualities of the traits was underlined, resulting in scoring that was less centred on the average and higher heritabilities of the traits (BÍ, 1992).

The official breeding goal that is described in *Icelandic Horse Breeding* (FEIF, 2010a), was set to breed healthy, fertile and durable horses, preferably 135-145 cm high at the withers, and to preserve all varieties of coat colours present within the breed. The breeding goal described the ideal horse to be light-bodied with emphasis on strength, flexibility and a muscular body. The conformation should facilitate exceptional gaits regarding quality and movements, a naturally good head carriage and be in all aspects aesthetically pleasing. As for riding abilities the general aim was to breed a versatile, reliable horse with five clear gaits and an excellent temperament. Although, the verbal description of the general breeding goal has remained unchanged since its establishment, the breeding system has been in continuous development and evaluation where new traits have been incorporated and the weighting of the different traits has been altered (Table 1) (Björnsson & Sveinsson, 2004). Until 1994 breeding organisation was directed exclusively from Iceland. Then a joint declaration on the breeding of Icelandic horses was signed by The International Federation of Icelandic Horse

Associations (FEIF) and the State of Iceland, recognising Iceland as the country of origin of the Icelandic horse. This declaration ensured that the eighteen FEIF member nations outside Iceland would do their best to follow the lead of Iceland in all matters of breeding and the use of the horse (FEIF, 2010c). FEIF was established in 1969 and focuses besides breeding on different aspects as the horses' welfare, competitions, education and youth work.

Table 1. Weighting of traits measured at breeding field tests, 2000-2009.

Conformation traits		Riding abilities	
Head	3%	Toelt	15%
Neck, withers and shoulders	10%	Trot	7.5%
Back and hindquarters	3%	Pace	9%
Proportions	7.5%	Canter/gallop	4.5%
Leg quality	6%	Spirit	12.5%
Leg stance	3%	General impression	10%
Hooves	6%	Walk	1.5%
Mane and tail	1.5%		

1.1.2 Breeding field tests

At breeding field tests stallions, geldings and mares are assessed in separate age-classes (4, 5, 6 and >6 years old) and 31 international judges have been certified to operate. At each assessment three judges work together evaluating horses and they give a joint score in the range of 5.0 to 10.0 with 0.5 intervals for each trait. The assessment starts with evaluation of the conformation, preferably executed indoors. Then the horses are ridden on a straight track for a maximum of five times in each direction where the riders can choose in which order they show the gaits and which gaits are performed. A score of 5.0 is given for a gait if a horse has not been shown in it. There are five gaits assessed in addition to the general impression of the horse and its spirit. When all registered horses in a given assessment have been shown once, a second ridden assessment is arranged. There, two to four horses are ridden on the track at any one time for a maximum of three times in each direction. Here judges are allowed to raise the scores if the horse shows better qualities. In Figure 1 distribution of assessments from 1990 to 2008 of neck, withers and shoulders; proportions; toelt, pace and general impression are shown.

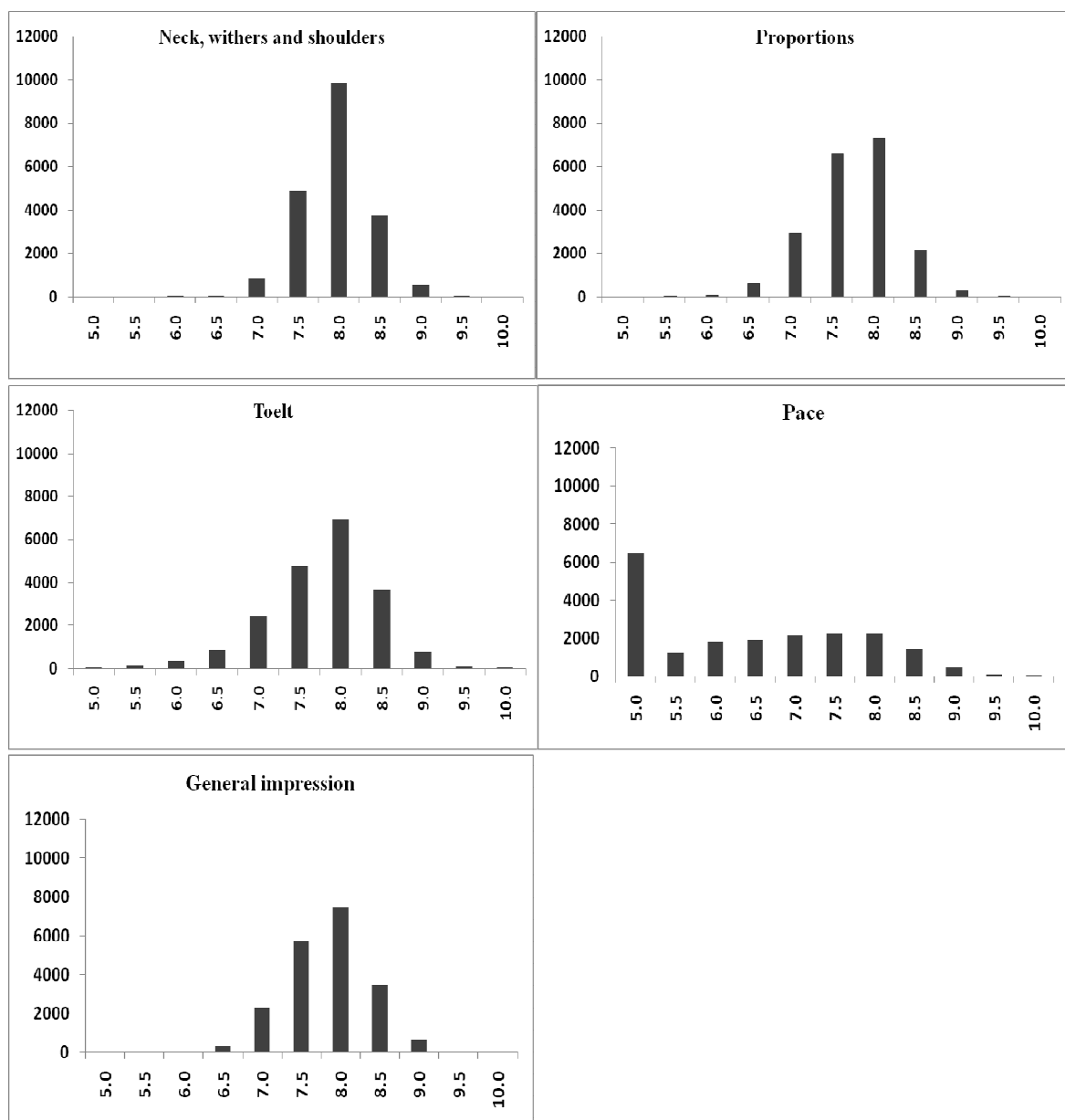


Figure 1. Distribution of assessments on five breeding field test traits, 1990-2008.

All registered and individually marked Icelandic horses with a verified pedigree aged four years or older that are healthy and without any injuries can participate at breeding field tests for as many times as the owner wishes. All stallions that come to a breeding show are parentally proven through DNA analyses, blood samples are collected and their testicles are measured in size and density as this relates to the horse's fertility. Moreover, in order to reduce the frequency of bone spavin in the Icelandic horse population x-rays of their hocks must be handed in for all stallions aged five years or older (FEIF, 2010a). All information on

health, fertility, quality of traits and verification of pedigree is registered and published on Worldfengur, the International Icelandic Horse database accessible on the web through www.worldfengur.com (Árnason et al., 2006).

1.2 Competitions

There are special equestrian competitions for Icelandic horses that have become very popular in Europe. The competitions are either open for anyone to compete in or include different levels where a minimum score for each equipment is required. There are three different types of competition: pace racing, sport competitions and *gaedinga* competitions (a riding horse quality competition), that each includes several disciplines. These special competitions follow standardised international rules (FIPO) that are reproduced and reviewed annually by FEIF (FEIF, 2006; FEIF, 2010b). In general, the disciplines involve four kinds of gaiting tests: toelt, four-gait, five-gait and pace. Toelt, four-gait and five-gait are ridden on an oval track (200-300m) while pace is ridden on a straight track (100-250m). The toelt involves two sport disciplines, T1 and T2 where the toelt gait is demonstrated in various tempos. The former is adapted for four-gaiters and the latter, the loose-rain toelt (T2), is tailored for five-gaiters. The four-gait involves one sport discipline, V1 and one *gaedinga* discipline, B-Class where four gaits: toelt, trot, gallop and walk are exhibited. The five-gait involves one sport discipline, F1 and one *gaedinga* discipline, A-Class where pace is exhibited in addition to the other four gaits. The pace involves four disciplines where one, the pace test (PP1) is a sport competition and three are pace racing disciplines where the pace is raced over different lengths (P1, P2, and P3). In the pace test not only the speed of the pace is measured in seconds, as is done in pace racing, but the quality of the pace is also assessed. Since 2009 competition records from internationally standardised events have been registered on the Worldfengur database, thereby improving the availability of competition data immensely. At competitions three or five qualified judges give separate scores that are averaged into one score for each element performed. In sport competition the quality of the rider, how he handles and sits the horse, influences greatly the score given for each gait. As such, the sport competitions acquire not only high performance ability of the horse but also great precision in the performance of the rider as in changes of gaits, etc. In the *gaedinga* competitions, first and foremost the

performance ability of the horse is evaluated. There, in addition to the gaits, the general impression and spirit of the horse are assessed (FEIF, 2006).

1.2.1 Comparisons of assessments in competition and at breeding field tests

It can take several years before a sport horse reaches its maximum performance level (Thorén-Hellsten, 2008). Imperfect competitive performances are harshly penalised in scoring, even when accompanied by a high quality of gaing ability, general impression and spirit. At breeding field tests, however the situation is different as the goal is to assess the quality of the horse independently of the level of training, riding etc., and even when demonstrated with trivial defects. Whereas young horses often lack strength and training to perform without flaws, competition horses are often older and more thoroughly trained than horses presented at breeding field tests. Furthermore, it can be expected that competitive scoring for young or inexperienced horses is frequently skewed regarding evaluation of the horses' actual merit where the effect of the rider has a great influence. It can also be safely assumed that competition horses are more carefully selected individuals than are breeding horses because competition horses are expected to be potential winners while breeding assessments aim at evaluating the genetic potential of the horse. These assumptions about age and selection make competition records less suitable as a basis of genetic evaluation compared to breeding field test records: longer generation intervals and biased estimation of genetic ability is often associated with competition data (Tavernier, 1991; Thorén-Hellsten, 2008). Nevertheless, the suitability of competition data as a basis to genetic evaluation may be studied as competitive ability is declared in the breeding goal and many breeders strive to produce capable competition horses because of their value. Inclusion of the competition traits into the genetic evaluation should thereby improve the selection criterion for breeding competition horses and add information on many new individuals as geldings often compete but few are assessed at breeding field tests.

1.2.2 Previous studies on competition traits

Besides a pilot study on pace racing traits (Ragnarsson, 2001) competition traits in Icelandic horses had not previously been genetically analysed. Competition data in the Warmblood riding horse population have however been studied a great deal where the aim has been to breed high quality competition horses, mainly in dressage and jumping (Koenen et al., 2004; Langlois & Blouin, 2004; Thorén et al., 2006). In Belgium, France and Ireland the genetic

evaluation for Warmblood riding horses is solely based on competition data, whereas in Denmark, Germany and The Netherlands competition and young horse test results are combined (Bruns et al., 2004). In Sweden competition results have been included since 2005 but prior to that time the genetic evaluation was only based on performance test results (Olsson, 2006). The BLUP animal model is generally used for the genetic evaluations of these horse breeds. Research on characteristics important to achieve international genetic evaluation of sport horses was initiated by The Interstallion Committee, with two pilot studies in 2001 where the use of international sport horse data along with young horse tests in genetic evaluations was recognised as being increasingly important since sport horse breeding has become global (Bruns et al., 2004; Thorén-Hellsten, 2008).

In 2004 the breeding objectives for Warmblood sport horses in a number of countries were studied. There it was observed that the breeding organisations sometimes assigned high weightings to traits that were not defined in the breeding objective, and the traits often lacked detailed definitions (Koenen et al., 2004). Additionally, the breeding objectives were often deficient in specifying what kind of performance they included, both as to the sport discipline and the level of competition. This approach was concluded to be inadequate if the aim was to gain maximum genetic response, because optimising selection strategies requires clear and well accepted breeding objectives that include thoroughly defined traits of interest with detailed descriptions and relative weightings.

1.3 The breeding organisation for Icelandic horses

1.3.1 Genetic evaluation

Selection of Icelandic breeding horses has been mainly based on estimated breeding values for more than three decades. In that time different aspects of the breeding programme have been thoroughly examined where many studies have been executed. In 1975 the first multiple trait selection indices for individual selection and progeny tests were constructed based on estimated genetic parameters on ten breeding field test traits (Árnason, 1979). The genetic parameters used in the breeding evaluation have been estimated with genetic analyses a number of times, with the most recent ones presented in 2004 from a study that was based on breeding field test records from 1990-2003 (Árnason & Sigurdsson, 2004). In 1979 a BLUP

sire model was applied in a single trait genetic evaluation of total score of breeding field test traits, but since 1983 a BLUP multivariate animal model has been used (Árnason, 1982, 1984). The first practical application of a multivariate animal model was in Icelandic horses (Carabans & Alenda, 1990; Langlois & Vrijenhoek, 2004). The current model considers the environmental factors of the interaction of year and country of assessment, and the interaction of sex and age of the horse.

Today estimated breeding values for 31 individual traits are calculated from international breeding field test scores (Árnason et al., 2006). From 1961 till 1995 only Icelandic breeding field test records were used in the genetic evaluation, then records from shows held in Denmark, Norway and Sweden were included and since 2005 records have been used from assessments in 11 countries, also including Austria, Finland, Germany, Great Britain, Switzerland, The Netherlands, and The United States. Such international genetic evaluation requires unique identification numbers, good genetic connectedness among countries and a properly synchronised cross-border assessment system carried out by qualified judges who have been authorised to operate (Árnason & Ricard, 2001; Bruns et al., 2004). In 2006 the global genetic evaluations of the Icelandic horse and the genetic connectedness between countries were evaluated. It was concluded that estimated breeding values of individual horses can be compared across countries with similar accuracy as within the country, and that good genetic connection exists between the countries (Árnason et al., 2006).

1.3.2 Selection programme

In 1987 optimal selection strategies for the Icelandic horse population were studied, and it was concluded that approximately one fourth of the breeding mares should be covered by young stallions with an outstanding pedigree index, half of the mares by performance-tested stallions selected on an index combining parental and own records, and the remaining one fourth by the very best progeny-tested stallions selected on an index combining parental and own records along with progeny average (Hugason et al., 1987). This research was continued by studying the effects of using the BLUP method across stallion age classes on genetic gain with the conclusion that it would give results close to the maximum (Hugason, 1994). Subsequently, breeders were urged to make use of the estimated breeding values in their selection decisions and to have a large number of horses assessed as early as possible at breeding field tests. Annually, ranking of horses according to the estimated breeding value of

a total score is reproduced on the Worldfengur database. The total score is calculated from all the breeding field test traits with given weightings where the conformation accounts for 40% of the total score and riding ability traits account for 60% (Table 1). Breeding values are also presented for each of the fifteen traits, along with height at withers, which gives breeders an opportunity to emphasise traits of their own choice. In practice, the distribution of covering across the three stages in the population has been found to be very satisfactory (Hugason, 1994), and calculated genetic response in the total score over the last fifteen years is equal to one additive genetic standard deviation (Árnason et al., 2006).

1.3.3 Attendance at breeding field tests

Roughly 30,000 Icelandic horses worldwide have been assessed at breeding field tests since the 1950's, accounting for approximately 12.5% of the population (www.worldfengur.com). Participation in the field tests is open for all Icelandic horses, but the tests are primarily aimed for mares and stallions. Geldings are sometimes assessed, however, especially the progeny of elite breeding horses. The number of male horses attending field tests is smaller than the number of female horses as it is common to castrate a large proportion of stallions at a young age (Hugason et. al, 1985). Young colts with a great pedigree that are aesthetically appealing and show promising gaits and movements are kept as stallions, while others are castrated, usually in their first year. Stallions that attend breeding field tests can therefore be safely assumed to be preselected to a certain degree. It is also common knowledge that breeding field assessments influence greatly the market value of horses, which in turn further restricts how many and which horses are presented at breeding field tests. Highly valued breeding horses are both those that have a high estimated breeding value and those that receive a high total score (over 8.0), or perform well in specifically valuable traits where the weighting factors are associated with market values (Table 1). An interaction can also be presumed between owner and horse as dedicated owners are more likely to own well prepared and trained quality horses that are more likely to attend breeding field tests than horses whose owners are less interested in breeding. If attending horses at field tests are assumed to be preselected, (co)variance components used in the genetic evaluation could be biased, and the ranking of sires affected. Therefore the effect of preselection should be studied (Robertson, 1966; Henderson, 1975; Meyer & Thompson, 1984; Klemetsdal, 1992).

1.3.4 *Studies on preselection*

Several studies have been made on preselection or culling of data in other horse breeds where an all-or-none trait, racing/test status is assigned for the attendance of horses: Horses are assigned a value of 0 if they have no record and a value of 1 if they have at least one performance record. This has been researched for horses competing in races like the Swedish and Norwegian trotters (Árnason, 1996, 1999), the Dutch trotter (Koerhuis and Schepers, 1998), the Finnish trotter (Thuneberg-Selonon et al., 2001), the Thoroughbred in France (Langlois and Hernu, 2003, Langlois & Vrijenhoek, 2004, Rose et al., 2007, Langlois & Blouin, 2008) and the German trotter (Bugislaus et al., 2005) as well as for the Belgian sport horse performing in sport events (Janssens et al., 2007). The attendance of horses at these events were between 35% and 62% where estimated heritabilities showed that the racing/test status had a significant genetic component and that it is correlated genetically with the breeding goal traits. Furthermore, it was shown that inclusion of the racing/test status in the genetic evaluation of these horse breeds resulted in higher correlations between true and estimated breeding values, and thus reduced the selection bias considerably and led to a different ranking of sires (Langlois & Vrijenhoek, 2004; Bugislaus et al., 2005; Janssens et al. 2007). However, the effects of including racing/test status in the genetic evaluation have been shown to be dependent on the difference between estimated genetic parameters of the traits in consideration (Bugislaus et al., 2005).

Estimation of genetic parameters for racing/test status can be problematic as all individuals with test status equal to zero lack phenotypic values on the tested traits. This leads to unestimable environmental covariances between the test status and the recorded traits (Meyer & Thompson, 1984). Given that the pedigree is deep and complete where all individuals without records have both tested and untested relatives, genetic covariances can however be estimated by use of an animal model and a complete genetic relationship matrix by restricting the environmental covariances to some predefined value. Árnason (1996; 1999) showed in a simulation study that by restricting the residual covariance to zero, selection on estimated breeding values where racing/test status was included in the genetic evaluation reduced the selection bias, increased the correlation between true and estimated breeding values and increased true genetic progress, given that the true genetic parameters were used in the genetic evaluation. It is however important to determine the consequences of using zero environmental covariance when the true values deviate from zero on estimated genetic

parameters and breeding values, and to evaluate how this affects genetic gain from selection based on BLUP and Gibbs sampler estimates of breeding values.

In order to optimise selection strategies integration of competition traits and test status in the genetic evaluation is expected to be a more adequate approach, given that competition traits are suitable for inclusion and test status is genetically significant in this context (Henderson, 1975; Koenen et al., 2004). The effect of such integration could be tested by estimating the reduction of selection bias, predictive ability of the genetic evaluation, accuracy of the genetic evaluation, correlations between estimated breeding values, and effects on ranking of sires using different models.

2 Objectives of the thesis

The main aim of the thesis was to accomplish integrated genetic evaluation of competition traits and breeding field test traits for Icelandic horses where the effects of preselection in the data were accounted for. Firstly, this involved a genetic analysis of the competition traits to find out whether they were suitable for genetic evaluation. Secondly, correlations between the competition traits and traits currently included in the breeding evaluation were estimated. Thirdly, the all-or-none trait test status was genetically analysed to find out whether it exhibited genetic variation, whether it correlated with the traits assessed in the breeding field tests, and what the effects of simultaneous genetic analysis of the test status trait and the breeding field test traits were on the estimated variance components for the latter group of traits. Fourthly, the effect of assuming zero environmental covariance between the test status trait and a breeding goal trait on the estimates of genetic parameters and evaluation of the corresponding consequences in genetic selection based on BLUP and Gibbs sampler was studied by use of stochastic simulation. Fifthly, the benefits from integrating either test status, competition traits or both into current genetic evaluation was evaluated in terms of reduction of selection bias, predictive ability and accuracy of the estimation, correlations between estimated breeding values, and ranking of sires using different models.

3 Summary of investigations

The thesis summarizes five papers where the first one included genetic analyses on competition traits; in the second paper relationships between competition traits and breeding field test traits were studied and the third paper included genetic analyses on test status and how test status related to the breeding field test traits. The fourth paper included a simulation study on what the effects were of estimating genetic parameters assuming zero environmental covariances between test status and a breeding goal trait. In addition, the responses of BLUP selection where the test status was included, based on certain premises, were evaluated. The fifth and final paper regarded the effect of integrating either or both competition traits and test status into a genetic evaluation of breeding field test records.

3.1 Material

In Paper I competition data were included where a total of ten traits, seven original and three combined competition traits, were analysed. In Paper II breeding field test data and competition data were analysed, including seventeen breeding field test traits and four competition traits: one original and the three combined ones. In Paper III breeding field test data were studied including fifteen breeding field test traits and a newly defined test status trait. In Paper V the breeding field test data and competition data were analysed where fifteen breeding field test traits, four competition traits (as in Paper II) and the test status trait were studied. In Paper IV simulated data, including test status and one continuous Gaussian trait resembling the breeding field test trait, were analysed.

3.1.1 Competition data

Internationally standardised competition data on horses registered on the Worldfengur database were collected from the Icelandic National Association of Riding Clubs and from the Swedish Icelandic Horse Association. In Papers I and II competition results from the period 1998 to 2004 were analysed, counting 18,981 records of 3,790 horses. In Paper V competition results from 1998 to 2008 were studied, covering 44,160 records from 7,687 horses.

In Paper I the following traits were included: seven original traits counting four-gait (B-Class) and five-gait (A-Class) from *gaedinga* competitions, and toelt (T1 and T2), four-gait (V1),

five-gait (F1) and the pace test (PP1) from sport competitions. In addition, three combined competition traits were created: Toelt (comp) (a combination of T1 and T2), 4-gait (a combination of B-Class and V1) and 5-gait (a combination of A-Class and F1). Each of the combined traits was constructed from similar traits that correlated very strongly (>90%). As different scales are used in the assessment of *gaedinga* (5.0-10.0) and sport competitions (0.0-10.0) the combined traits were rescaled to an average of zero and a standard deviation of 1.0. In Papers II and V only the combined traits were used along with one original trait, the pace test (PP1), thereby covering all the Icelandic horse disciplines: toelt, four-gait, five-gait and pace.

3.1.2 Breeding field test data

Breeding field test data were collected from the Worldfengur database where one record was included for each individual, representing the highest age-corrected total score if an individual had been assessed more than once. In Paper II 16,401 individual records from horses tested in eleven countries between 1990 and 2005 were included. Paper III studied 7,431 breeding field test records from mares born in Iceland between 1990 and 2001 and tested for the period 1994-2007, and in Paper V records from 1990-2008 covered 19,954 individual records from eleven countries.

The seventeen traits studied in Paper II were: height of withers; mane and tail; head; neck, withers and shoulders; back and hindquarters; proportions; leg quality; leg stance; hooves; walk; slow toelt; toelt; trot; pace; gallop; general impression and spirit. Pace was analysed both regarding all records and by excluding records equal to 5.0 (pace \geq 5.5) in order to examine possible differences in genetic parameters. Records equal to 5.0 reflect a lack of pacing ability and are considered to be a combination of actual deficiency of pacing aptitude and the decision of riders or owners not to show pace even though horses are capable of it. The decision is based on the assumption that pace training impairs the quality of other traits, especially the toelt. In Paper V fifteen traits were studied, including all previously mentioned traits except the height of withers and slow toelt.

3.1.3 Test status

In Papers III and V breeding field test traits and test status describing whether or not a horse was assessed in a breeding field test were studied. The data included a total of 39,443 mares born in Iceland 1990 to 2001, of which 7,431 were assessed at breeding field tests in 1994-

2007, where the average assessment age was approximately 6 years. The reason for only including data on mares was that 82% of attending horses at breeding field tests are females and attending male horses are a partially highly selected group (Hugason, 1987). Furthermore, data including only mares born in Iceland were included to avoid possible inter-country differences in attendance and differences in making decisions about attendance. Mares were assigned values according to whether or not they participated at breeding field tests, i.e. if a mare had at least one record it was assigned a value of 1, otherwise it was assigned a value of 0. It was also tested as to whether stud origin was significant, reflecting a possible interaction between a breeder and a horse by assigning missing values for test status for mares from studs where not a single horse had a breeding assessment record in the studied period.

In Figure 2 it is clear that the number of mares receiving a total score above 8.0 had increased at the same time that the number of mares receiving a total score below 7.5 had decreased. This could have been because the qualities of the mares had improved over the period and/or because attending mares were more preselected. The degree of attendance (number of mares born versus number of assessed mares six years later) became higher over the studied period from 15% in 1996 to 25% in 2007.

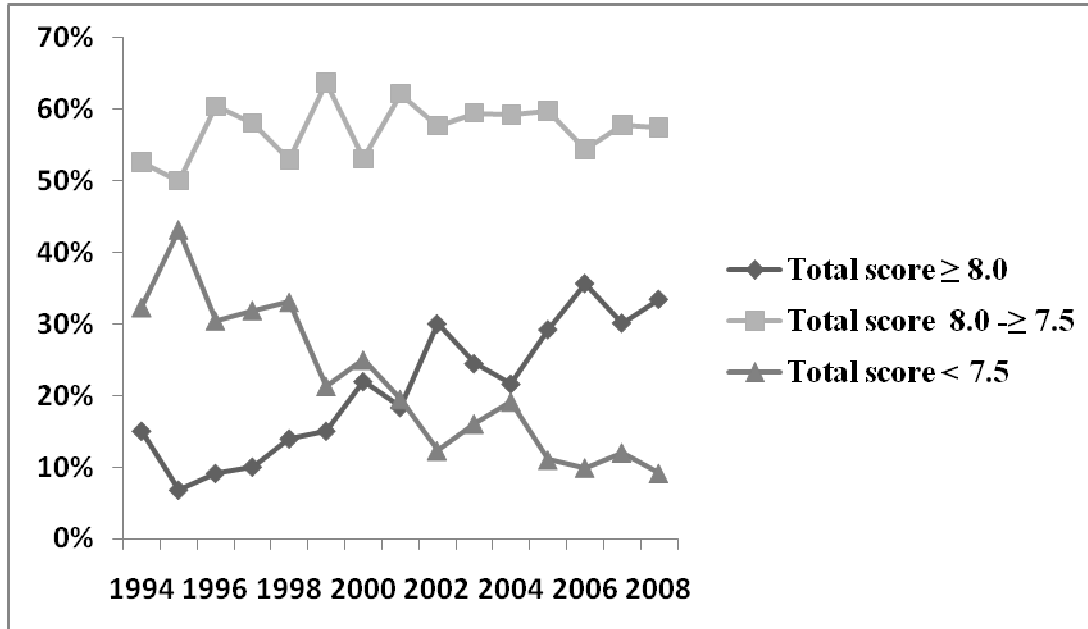


Figure 2. Division of the total score of attending mares at breeding field tests: ≥ 8.0 , $8.0 \geq 7.5$, and below 7.5.

3.1.4 Pedigree

Pedigree data including ten generations were collected from the Worldfengur database. The numbers of individuals that were included in the pedigree was 12,324 (Paper I); 30,198 (Paper II); 103,172 (Paper III) including 641 sires (of which 285 had records), each of whom had more than 20 offspring, in order to eliminate the probability that all progeny of a stallion could fall in the same category for the binary variable; and 213,591 (Paper V). Pedigrees for all horses registered in the database can be traced back to Icelandic founders (Árnason et al., 2006)

3.2 Methods

3.2.1 Statistical models

In Paper I statistical models for the competition traits were analysed to test which fixed effects were significant using the GLM procedure in the SAS package (SAS Institute Inc., 2008). In Papers II and III the same model was used for the breeding field test traits, as was used in the current genetic evaluation. The model included two fixed effects: age by sex interaction and year by country interaction, and two random effects: the additive genetic effect of the horse and the residual effect. In Paper V the same two fixed effects for breeding field test traits were used as in Papers II and III. In Paper III a statistical model for the test status trait was analysed to test which fixed effects were significant, using the GLM procedure in the SAS package (SAS Institute Inc., 2008).

3.2.2 Estimation of genetic parameters

The DMU package (Jensen & Madsen, 2009) was used in Papers I-V to estimate genetic parameters.

In Papers I and II variance and covariance components were estimated with univariate and bivariate models using an average information (AI) algorithm for restricted maximum likelihood, and the asymptotic standard errors of (co)variance components were computed from the inverse of the AI matrix. Standard errors of the heritabilities and repeatabilities were computed with a Taylor series expansion. The residual correlations between breeding field test traits and competition traits in Paper II were constrained to zero as very few horses participated both in breeding field tests and competitions.

In Paper III genetic analyses were carried out in three multivariate analyses including all breeding field test traits; all conformation traits and test status; and all riding ability traits and test status, using the Markov Chain Monte Carlo method via Gibbs sampling. An underlying non-observable continuous random variable (liability λ) was assumed for the threshold trait test status. If the liability exceeded a fixed threshold the observation for test status equalled 1; otherwise it equalled 0. Both sire and animal models were used to estimate the genetic parameters where uninformative priors were used. The residual variance of the threshold trait was assumed to be 1.0 and the threshold value was set to zero. The residual correlations between breeding field test traits and test status were constrained to zero, because those are not estimable (Meyer & Thompson, 1984). The Gibanal 2.8 program by van Kaam (1998) was used to ascertain effective numbers of samples, burn-in's and skip-parameters, and the mode of the marginal posterior distributions was defined as the point estimates of parameters.

In Paper V estimation of (co)variances between breeding field test traits and competition traits and between breeding field test traits and test status were repeated with bivariate runs using the Gibbs sampler because an additional random effect of permanent environment was added to the model for the breeding field test traits and test status for technical reasons: As some horses had both a breeding field assessment and a competition record, a permanent environmental effect was included to account for the environmental covariance between records. However, since only one breeding field assessment was used for each individual the variances of the residual effects were constrained to the small value of 0.001. Correlations between test status and the competition traits were not estimable due to insufficient data. Therefore, the correlations were calculated by assuming zero partial correlations between test status and competition traits, using a multivariate form of $\rho_{XY} = \rho_{XZ} \times \rho_{ZY}$, where X denotes test-status, Y denotes competition traits and Z denotes breeding field test traits.

3.2.3 *Simulation study*

Paper IV evaluated the effect of assuming non-estimable environmental covariances between test status and a breeding goal trait as zero when the true value deviated from zero. Corresponding consequences on a simulated genetic selection on EBVs obtained by BLUP and Gibbs sampling with these premises were also evaluated. In the simulations, a base population of 525 animals, including 25 males and 500 females, was constructed. The first three generations were randomly selected and then a mass selection was applied on subsequent five generations. The data included a total of 7,500 records on test status and the

pedigree file included 9,600 individuals. The frequency of tested animals corresponding to culling rates of 0.5 and 0.8 were studied where the heritabilities of the threshold trait test status and of the breeding goal trait were set to 0.4 and the genetic correlation was set to 0.5. Three different environmental correlations were tested: -0.5, 0.0 and 0.5.

3.2.4 Model evaluation

In Paper V the effects of including the competition traits and the test status trait in the genetic evaluation were evaluated by comparing the performance of four sets of multivariate models: Model 15 – including 15 breeding field test traits; Model 16 – including the 15 breeding field test traits and test status; Model 19 – including the 15 breeding field test traits and 4 competition traits; and Model 20 – including the 15 breeding field test traits, 4 competition traits and test status. The models were compared on the basis of (i) (Method R) the regression coefficient of EBVs based on the whole data set on EBVs obtained from five subsamples of the data, each with 50% of the observations left; (ii) the phenotypic predictive ability (MSEP) using the five subsamples; (iii) the standard errors of EBVs; (iv) the Pearson's correlation between EBVs for sires with five or more tested offspring; and (v) comparing number of sires ranking among the top 10% in common.

If the linear regression coefficient (R) deviated from 1.0 it indicated incorrectly estimated breeding values, where values below 1.0 imply overestimation of EBVs and values of R above 1.0 imply too low estimates (Reverter et al., 1994). The predictive ability was evaluated by calculating the mean square error of prediction (MSEP) of phenotypic values, i.e. the phenotypic values that were discarded in each of the five subsamples were predicted and compared to the real phenotypic values in the whole data set. Therefore low values are preferred for the MSEP. A total of 668 sires had five or more tested offspring. Sires were grouped into four categories according to number of tested offspring: (i) 474 sires had 5-19 tested offspring; (ii) 116 sires had 20-49 tested offspring; (iii) 45 sires had 50-99 tested offspring; and (iv) 33 sires had 100 or more tested offspring. The average standard errors were estimated for the sires, considering all traits. Low values are preferred. Pearson correlations were estimated for EBVs for the sires considering three combined indexes: total conformation score, total riding ability score, and total score where the high values are preferred. The common ranking, with different models, of sires with more than five tested offspring was also tested for these combined indexes.

The (co)variance matrices used in the genetic evaluation were made positive definite using a bending method (Hayes & Hill, 1981): a bending factor of 0.1 was needed for the permanent environmental (co)variance matrix and a bending factor of 0.6 was needed for the genetic (co)variance matrix. Linear models were used for the test status trait in the genetic evaluation and heritabilities from the underlying scale were transformed to the observed scale using Robertson's formula (Dempster & Lerner, 1950) where an intermediate value from analyses using sire and animal models was used.

The DMU5 module was used to estimate breeding values for the R-method and MSEP while the Gibbs sampling procedure was used to estimate the standard errors of the EBVs. In estimation of the SE, for each model the average from five different chains of 30,000 iterations was used where burn-in's and interleave was set to zero, applying EBVs from the DMU5 runs as starting values.

4 Main findings

4.1 Statistical models

For all traits, both original and combined ones, the fixed effects of age, sex and event were significant ($P < 0.01$). Additionally, the fixed effect of competition level was statistically significant for the four original sport traits (T1, V1, F1 and PP1). To examine the influence of the fixed effect of competition level, i.e. whether it was only a measurement of the rider's skills, it was also tested to exclude competition level as a fixed effect from the model for the traits T1, T2, V1 and F1. The fixed effect of rider was statistically significant for all traits; however, due to the fact that approximately 80% of all riders competed only on one or two horses, the rider effect was excluded from the model in order to avoid confounding. For relevant competition traits the same models were used in Paper I, Paper II and Paper V. In addition to the fixed effects, three random effects were included in the models that were used in estimation of variance and covariance components, i.e. the additive genetic effect of the horse, the permanent environmental and the residual effect.

The fixed effect of birth year was statistically significant ($P < 0.01$) for test status and was included in the model. In Paper III the random additive genetic effect of the horse and the random residual effect were included in the model for test status. In Paper V the fixed effect of sex was added to the model for test status as well as the random permanent environmental effect, as previously described for the breeding field test traits.

4.2 Genetic analyses

4.2.1 Competition traits

In Papers I and II estimated heritabilities for the original competition traits ranged between 0.33 and 0.35 for the *gaedinga* competition traits and between 0.18 and 0.23 for the sport competition traits (Table 2). Heritabilities did not generally change with regard to whether or not competition level was included as a fixed effect in the model. For the combined traits estimated heritabilities ranged between 0.19 and 0.22. Standard errors for the estimated heritabilities ranged between 0.05 and 0.23 where the values were the lowest for the combined traits. Repeatabilities were around 60% (0.42-0.68). In Paper II higher estimated heritabilities were observed for the competition traits when analysed in bivariate runs together with highly correlated breeding field test traits.

Table 2. Summary of estimated heritabilities on competition traits with standard errors within parentheses in Papers I and II

Competition traits	Heritability	
	Paper I	Paper II
T1	0.18 (0.05)	
T2	0.23 (0.14)	
V1	0.19 (0.05)	
F1	0.19 (0.07)	
PP1	0.21 (0.11)	0.17-0.24
B-Class	0.33 (0.21)	
A-Class	0.35 (0.23)	
Toelt(comp)	0.19 (0.05)	0.18-0.37
4-gait	0.22 (0.05)	0.21-0.44
5-gait	0.22 (0.07)	0.20-0.42

Toelt(comp) combination of T1 and T2, 4-gait combination of B-Class and V1, 5-gait combination of A-Class and F1

The *gaedinga* competition traits (A- and B-Class) correlated moderately (0.43) (Table 3). The sport competition traits related moderately or strongly with each other: genetic correlations ranged between 0.63 and 0.96 where toelt (T1) and four-gait (V1); loose-rain toelt (T2) and five-gait (F1); and five-gait (F1) and pace (PP1) all correlated very strongly (>0.85). Comparable *gaedinga* and sport competition traits associated very strongly, i.e. B-Class to T1, T2 and V1 (0.93-1.00) and A-Class to F1 and PP1 (0.94-0.97). Estimated genetic correlations amongst the combined competition traits were very similar to those observed amongst the original ones and ranged between 0.62 and 0.90. Again genetic correlations between the combined traits were estimated with lower standard errors compared with genetic correlations amongst the original competition traits.

Table 3. Genetic correlations with S.E. as subscripts between competition traits in Paper I.

	T1	T2	V1	F1	PP1	A-Cl.	Toelt(comp)	4-gait	5-gait
T2	0.71 _{0.19}								
V1	0.85 _{0.07}	0.74 _{0.22}							
F1	0.63 _{0.18}	0.96 _{0.14}	0.71 _{0.19}						
PP1	0.43 _{0.24}	0.10 _{0.41}	-0.03 _{0.30}	0.93 _{0.17}					
B-Cl.	0.93 _{0.17}	1.00 _{0.34}	0.93 _{0.26}	0.18 _{0.43}	-0.42 _{0.42}				
A-Cl.	0.84 _{0.33}	0.50 _{0.54}	0.50 _{0.35}	0.94 _{0.25}	0.97 _{0.49}	0.43 _{0.51}			
4-gait							0.90 _{0.05}		
5-gait							0.74 _{0.14}	0.62 _{0.16}	
PP1							0.38 _{0.24}	-0.12 _{0.25}	1.00 _{0.13}

Toelt(comp) combination of T1 and T2, 4-gait combination of B-Class and V1, 5-gait combination of A-Class and F1

4.2.2 Associations between breeding field test traits and competition traits

In Paper II estimated genetic correlations between fifteen breeding field test traits and four competition traits, including the three combined ones (toelt, 4-gait and 5-gait) and one original sport trait (PP1) ranged between -0.24 and 0.96 (Table 4). The conformation traits: neck, withers and shoulders; back and hindquarters; proportions; and hooves associated moderately strong with the competition traits. Other conformation traits related only weakly with the competition traits. The riding ability traits: slow toelt, toelt, gallop, spirit and general impression related very strongly with the combined traits. Walk showed moderately high genetic correlations with the combined traits 4-gait and 5-gait and furthermore pace was highly genetically correlated with 5-gait. The riding ability traits: toelt, pace, spirit and general impression associated moderately strongly with the pace test (PP1).

Table 4. Genetic correlations with S.E. in parentheses between competition traits and breeding field test traits in Paper II.

Trait	Toelt(comp)	4-gait	5-gait	PP1
Height on withers	0.15 (0.09)	0.15 (0.09)	0.14 (0.10)	0.38 (0.15)
Mane and tail	0.08 (0.10)	0.09 (0.09)	0.22 (0.11)	0.07 (0.15)
Head	0.28 (0.09)	0.23 (0.10)	0.24 (0.11)	-0.05 (0.15)
Neck, withers & shoulders	0.52 (0.08)	0.41 (0.08)	-0.05 (0.18)	0.29 (0.14)
Back and hindquarters	0.41 (0.10)	0.29 (0.10)	0.54 (0.12)	0.26 (0.15)
Proportions	0.39 (0.09)	0.32 (0.09)	0.45 (0.11)	0.17 (0.14)
Leg quality	0.06 (0.09)	0.15 (0.09)	0.03 (0.10)	0.01 (0.14)
Leg stance	-0.03 (0.11)	-0.07 (0.11)	-0.24 (0.12)	0.13 (0.17)
Hooves	0.52 (0.09)	0.45 (0.09)	0.39 (0.11)	0.41 (0.16)
Slow toelt	0.93 (0.06)	0.89 (0.55)	0.73 (0.10)	0.34 (0.18)
Walk	0.23 (0.12)	0.71 (0.08)	0.51 (0.14)	-0.10 (0.18)
Toelt	0.96 (0.03)	0.87 (0.04)	0.84 (0.08)	0.55 (0.15)
Trot	0.91 (0.05)	0.95 (0.04)	0.79 (0.08)	0.16 (0.16)
Pace (records ≥ 5.5)	0.38 (0.11)	0.12 (0.11)	0.86 (0.08)	0.83 (0.15)
Gallop	0.93 (0.06)	0.90 (0.05)	0.65 (0.11)	0.36 (0.17)
Spirit	0.94 (0.04)	0.87 (0.04)	0.79 (0.09)	0.43 (0.15)
General impression	0.88 (0.05)	0.75 (0.06)	0.83 (0.08)	0.68 (0.20)

Toelt(comp) combination of T1 and T2, 4-gait combination of B-Class and V1, 5-gait combination of A-Class and F1

4.2.3 Breeding field test traits

Estimated heritabilities, both from univariate and bivariate analyses including two breeding field test traits, ranged between 0.15 and 0.60 (Table 5), and were very similar to those of previous research (Árnason & Sigurðsson, 2004). Standard errors for the estimated heritabilities ranged between 0.02 and 0.08. In Paper II slight increases were observed in

estimated heritabilities when the analyses included highly correlated breeding field test traits and competition traits. This was also the case in Paper III when bivariate models included highly correlated breeding field test traits and test status.

Estimated genetic correlations among breeding field test traits ranged between -0.07 and 0.69 and were similar to previous estimations (Árnason & Sigurðsson, 2004). Standard errors on genetic correlations ranged between 0.02 and 0.09. Height of withers; head; neck, withers and shoulders; back and hindquarters; and proportions, related genetically moderately strongly with other conformation and riding ability traits. Other conformation traits showed generally only weak genetic correlations with other traits. Genetic correlations among riding ability traits were in general moderate or strong but ranged overall between -0.22 and 0.92, where the traits walk and pace associated weakly with other traits.

4.2.4 Test status

In Paper III the degree of preselection was indicated by comparing BLUP, BLUE and average total scoring of assessed mares in a given period. As the average age of assessed mares was 6 years the BLUPs of total score and BLUEs of the fixed effects (interaction of year and country) from the birth years 1990-2001 were compared with yearly assessments in the period 1997-2007. In the period 1997-2007 the average total scoring of attending mares increased steadily from 7.58 to 7.81. The genetic gain for mares born in 1990 to 2001 was 0.15 points in the total score. Therefore, the difference of approximately 0.11 points between genetic trend (0.15) and total scoring (0.26), given that the BLUE was steady over the studied period, may in part be attributed to stricter pre selection of horses which attended the field tests.

Genetic parameters for test status were estimated with animal and sire models using univariate and bivariate analyses where test status and breeding field test traits were included. The estimated heritabilities for test status ranged between 0.51 and 0.67, where the animal model gave the higher results.

Estimated genetic correlations between test status and breeding field test traits ranged between 0.00 and 0.87 for the animal model and between 0.08 and 0.73 for the sire model. Test status related moderately strongly with all conformation traits except leg quality, leg stance, and mane and tail, and strongly with all riding ability traits except walk. Thus, test status related strongly with most breeding field test traits with high weighting proportions in the index (Table 1).

Table 5. Heritabilities (h^2) for test status and breeding field test traits, whether or not including test status in the runs, and genetic correlations (r_g) between test status and breeding field test traits estimated with animal and sire models using Gibbs sampler, with standard errors as subscripts (Paper III).

Traits	Animal model			Sire model	
	test status not included	test status included	r_g	test status included	
	h^2	h^2		h^2	r_g
Test status (con)*		0.67 _{0.02}		0.53 _{0.06}	
Test status (rid) [†]		0.63 _{0.02}		0.51 _{0.09}	
Head	0.27 _{0.04}	0.29 _{0.04}	0.41 _{0.08}	0.33 _{0.05}	0.28 _{0.10}
Neck, withers & shoulders	0.49 _{0.04}	0.54 _{0.03}	0.67 _{0.04}	0.39 _{0.06}	0.49 _{0.08}
Back and hindquarters	0.31 _{0.03}	0.31 _{0.03}	0.49 _{0.07}	0.31 _{0.05}	0.46 _{0.09}
Proportions	0.39 _{0.03}	0.48 _{0.04}	0.69 _{0.05}	0.33 _{0.05}	0.43 _{0.09}
Leg quality	0.43 _{0.04}	0.42 _{0.03}	0.12 _{0.08}	0.31 _{0.05}	0.08 _{0.10}
Leg stance	0.15 _{0.03}	0.17 _{0.03}	0.00 _{0.11}	0.17 _{0.04}	0.12 _{0.12}
Hooves	0.45 _{0.04}	0.47 _{0.04}	0.46 _{0.06}	0.31 _{0.05}	0.33 _{0.10}
Mane and tail	0.56 _{0.04}	0.57 _{0.04}	0.25 _{0.07}	0.59 _{0.07}	0.14 _{0.09}
Toelt	0.53 _{0.05}	0.56 _{0.03}	0.82 _{0.03}	0.36 _{0.06}	0.68 _{0.08}
Trot	0.44 _{0.04}	0.49 _{0.04}	0.63 _{0.05}	0.33 _{0.05}	0.35 _{0.10}
Pace (records ≥ 5.5)	0.60 _{0.03}	0.62 _{0.03}	0.68 _{0.06}	0.73 _{0.05}	0.47 _{0.10}
Gallop	0.42 _{0.03}	0.47 _{0.04}	0.77 _{0.05}	0.29 _{0.05}	0.58 _{0.08}
Spirit	0.54 _{0.03}	0.63 _{0.02}	0.85 _{0.04}	0.29 _{0.05}	0.73 _{0.07}
General impression	0.56 _{0.03}	0.63 _{0.03}	0.87 _{0.03}	0.39 _{0.06}	0.71 _{0.06}
Walk	0.18 _{0.04}	0.20 _{0.03}	0.12 _{0.11}	0.26 _{0.05}	0.01 _{0.12}

*Test status analysed together with all conformation traits

[†]Test status analysed together with all riding ability traits

4.2.5 Simulation study

In Paper IV the effects of assuming zero environmental covariances between test status and a breeding goal trait on estimated heritability and genetic correlations were studied. The results showed that unbiased estimates of all genetic parameters were obtained when the true environmental correlation was zero. When the true environmental correlation was 0.5, the assumption of zero environmental correlation led to a clear underestimation of the genetic correlation and slight underestimation of the variance components, even though the heritability estimates remained practically unbiased. On the other hand, for a true negative environmental correlation of -0.5, upward bias was observed in the genetic correlation, in the genetic variance and in heritability of the breeding goal trait, while the heritability estimate of test status remained unbiased. Heritability estimates seemed therefore to be relatively unbiased unless the environmental correlation was strongly negative, but the estimated

genetic correlations were much more affected if the true environmental correlation deviated heavily from zero.

The study showed that genetic progress through selection was reduced when preselection existed in the data. However, the reduction in genetic progress was considerably less when index selection (AM-BLUP) was applied compared to mass selection. This shows how robust animal models account for selection in data. The reduction in the genetic response was even greater when test status was included in the model: compared to mass selection the genetic progress increased between 20-40% depending on the degree of preselection. Furthermore, the estimated response from index selection was generally robust to moderate errors in the used parameters.

4.2.6 Model evaluation

In Paper V estimated breeding values for all models appeared to be largely unbiased according to estimated regression coefficients ($R = 1.019$). The predictive abilities of the different models were very similar. The estimated standard errors were reduced with inclusion of new traits, especially in the case of test status (Table 6). High correlations were estimated between EBVs on total conformation, total riding ability and total score from different models (Table 7). Ranking of sires changed between models (Table 8). Differences between models for ranking and standard errors were largest for sires with 5-19 offspring. Common ranking and estimated standard errors for other groups of sires followed the same trend, though the differences became smaller as the number of tested offspring increased.

Table 6. Average estimated standard errors on EBVs for sires (#474) with 5-19 tested offspring

Trait	Model 15	Model 16	Model 19	Model 20
Test status		0.110		0.109
<i>Breeding field test traits</i>				
Head	0.162	0.162	0.163	0.162
Neck, withers, shoulders	0.142	0.139	0.142	0.139
Back and hindquarters	0.168	0.166	0.168	0.166
Proportions	0.153	0.150	0.154	0.150
Leg quality	0.180	0.179	0.179	0.178
Leg stance	0.164	0.164	0.164	0.164
Hooves	0.174	0.172	0.174	0.172
Mane and tail	0.282	0.282	0.282	0.280
Toelt	0.193	0.187	0.191	0.186
Trot	0.219	0.215	0.216	0.214
Pace	0.295	0.290	0.294	0.289
Gallop	0.186	0.182	0.185	0.180
General impression	0.154	0.149	0.153	0.147
Spirit	0.169	0.164	0.168	0.163
Walk	0.235	0.235	0.235	0.233
<i>Competition traits</i>				
Toelt(comp)			0.258	0.254
4-gait			0.254	0.251
5-gait			0.256	0.251
PP1			0.244	0.243

Toelt(comp) combination of T1 and T2, 4-gait combination of B-Class and V1, 5-gait combination of A-Class and F1

Table 7. Pearson correlation between EBVs from different models for sires (#668) with 5 or more tested offspring

Trait	Total conformation score			Total riding ability score			Total score		
	M-15	M-16	M-19	M-15	M-16	M-19	M-15	M-16	M-19
Model 16	97.9			96.6			96.6		
Model 19	99.2	97.8		98.0	95.9		98.2	96.0	
Model 20	97.2	99.2	97.4	98.0	98.5	96.2	95.7	98.7	96.1

Table 8. Number of sires (#47) with 5-19 tested offspring ranking commonly in the top 10%

Trait	Total conformation score			Total riding ability score			Total score		
	M-15	M-16	M-19	M-15	M-16	M-19	M-15	M-16	M-19
Model 16	40			40			40		
Model 19	43	38		39	40		30	29	
Model 20	38	44	39	38	42	38	38	43	38

4.2.7 Current breeding evaluation model (Model 15)

The estimated regression coefficients ($R = 1.011$) for all traits in Model 15 were on average close to 1.0 and ranked second best after Model 19 in the comparison of models. The predictive ability (MSEP) for model 15 was on average 0.258 when pace (MSEP = 1.382) was not included, accounting for the second worst ranking of all models, just before Model 16. Model 15 gave in general higher estimated standard errors than other models.

4.2.8 Inclusion of test status (Model 16)

The average estimated regression coefficients ($R = 1.026$) for all traits deviated more from 1.0 with integration of test status (Model 16) compared to Models 15 and 19, but were similar to Model 20 where test status was also included. Model 16 gave on average the worst predictive ability (MSEP = 0.259) of all models. Model 16 gave in general the second lowest estimated standard errors after Model 20.

4.2.9 Inclusion of competition traits (Model 19)

With integration of the competition traits into the genetic evaluation, the average estimated regression coefficient ($R = 1.009$) for all traits deviated the least from 1.0 compared to other models. Model 19 had on average the best predictive ability (MSEP = 0.256) along with Model 20. Model 19 gave lower estimated standard errors on most traits compared to Model 15 but higher than Model 16 and Model 20.

4.2.10 Inclusion of test status and competition traits (Model 20)

On average the estimated linear regression coefficient was 1.030 for all traits in Model 20. The average predictive ability (MSEP = 0.256) was the best for Model 20 along with Model 19. The lowest estimated standard errors were obtained in Model 20 for all competition traits and for all breeding field test traits.

5 General discussion

5.1 Genetic analyses

5.1.1 *Competition traits*

Competition traits are suitable for genetic evaluation; they are normally distributed with moderately estimated heritabilities, correlate strongly with the breeding field test traits and the genetic parameters were estimated with low standard errors. Higher estimates of heritabilities for the competition traits when analysed together with breeding field test traits indicate that the effects of preselection in competition data were reduced when analysed simultaneously with less selected breeding field test data. With integration of the competition data into the genetic evaluation, which is currently based on breeding field test data, the breeding goal is better reflected. In addition, a large amount of information on new horses will become utilised as many competing horses are geldings, and breeding of competition horses based on selection indices is expected to increase the genetic gain.

The combined competition traits should preferably be included in the genetic evaluation as they were the most stable in the sense that their estimated parameters were very similar, irrespective of which other traits they were analysed with. Furthermore, their genetic parameters were estimated with greater precision compared to the original competition traits. Combined competition traits express competing ability in toelt, four-gait and five-gait in a simpler manner than the original traits and may therefore be more readily accepted by breeders. In order to cover pacing ability in competition, the pace test could be used in the genetic evaluation in addition to the combined competition traits.

5.1.2 *Associations between breeding field test traits and competition traits*

Estimated genetic correlations between breeding field test traits and competition traits show that comparable traits are assessed similarly in both events. Conformation traits assessed at breeding field tests genetically relate in a comparable way to performance abilities in both breeding assessments and competitions. Having quality hooves seems to be even more important in competition performance than in breeding field tests, and this could be expected as competition horses are often older and therefore need strong and durable hooves to be able to perform. Performance ability in competition and in breeding field tests seems to be controlled to a great deal by the same genes.

5.1.3 Breeding field test traits

There was consistency between previous results (Árnason & Sigurdsson, 2004) and current results on estimated genetic parameters for the breeding field test traits. Árnason and Sigurdsson based their estimation of genetic parameters on a data set which was similar to, and overlapped with, that used in the present study. Estimation of genetic parameters for the pace changed considerably, whether the data included all records or pace scores equal to 5.0 were excluded: in the latter case heritability estimates were lower and genetic correlations were moderately to highly positive instead of being negative for the most part. This is coherent with earlier results and indicates that genetic parameters analysed on data where pace scores equal to 5.0 are excluded are less biased and should therefore be used in genetic evaluation.

Higher estimated genetic parameters on the breeding field test traits, when analysed together with strongly associated competition traits and test status, show that these traits are controlled to great deal by the same genetic components that support integrated genetic evaluation.

5.1.4 Test status

Breeding field tests became more popular and better accepted by breeders over the studied period as shown by the increase in the number of attending mares. These events have proven to be a good venue for promotion by the breeders, and in general have led to increased market values for highly assessed horses. Breeders have therefore been indirectly led to preselecting which horses attend the field tests.

The signs of preselection of horses during the studied period were verified by the estimated genetic parameters for the test status: this trait had a significant genetic component and related strongly to breeding field test traits, especially those with a high weight in the selection index. This applied to both conformation and riding ability traits, although breeders seem to preselect horses to attend breeding field tests more strongly on good riding qualities than on aesthetic conformation. The emphasis on riding ability as the criterion for preselection was further supported by the larger increase in estimated genetic parameters for these traits (compared to conformation traits) when they were analysed simultaneously with test status.

It is probable, however, that estimated genetic parameters for test status were inflated to some degree due to the positive interactions between the genetic value of a horse and the environmental effect associated with its breeder. Enthusiastic breeders are more likely to own

horses with good potential and pedigree which they prepare and train thoroughly prior to assessments. Differences in estimates of genetic variance from sire and animal models, where the former gave lower results, supports this, as the environmental effects of the breeders related to maternal/stud effects are largely eliminated in sire models as sires are cross-classified across studs (Rose et al., 2007).

5.1.5 Simulation study

Assuming zero environmental covariances between test status and the breeding field test traits did not lead to a serious bias on the estimated genetic parameters unless the non-estimable true environmental correlation deviated largely from zero. Moderately biased genetic parameters had relatively small effects on the genetic evaluation. Estimation of breeding values where test status was included in the model always led to improvement in genetic progress and in higher correlations between true and estimated breeding values.

5.1.6 Model evaluation

In general there were trivial differences between models regarding Method R and predictive ability. Estimated breeding values were largely unbiased for all traits, although models including test status showed minor deviances from this. The current breeding evaluation system seems therefore to be very thoroughly and well established. However, breeding values were more accurately estimated with the inclusion of the new traits, specially the test status (Model 16 and 20). Ranking of sires, based on total EBVs, changed with inclusion of the competition traits and test status. This indicates how large an effect adding new traits to the genetic evaluation will have on the selection of sires.

Test status was differently defined in the genetic analyses (Paper III) and genetic evaluation (Paper V). The genetic parameters for the test status trait should therefore be re-estimated with linear models where test status would be re-defined as attendance of horses both in competition and/or at breeding field tests, a method that was used in the genetic evaluation. In this way a larger data set covering both competition data and breeding field test data, would be utilised and the trait would apply to all horses – stallions, mares and geldings, instead of only mares attending breeding field tests, as was done in the genetic analyses.

Competition traits strengthened the genetic evaluation, especially when looking at the results on Method R, predictive ability, and strong correlations between EBVs from the current

model and the model including the competition traits. These traits can therefore be included in the genetic evaluation directly. Inclusion of the competition traits will provide additional information on many new individuals and will give breeders an effective tool on which to base their selection. Many breeders aim to produce good competition horses. Selection of sires will therefore be affected as ranking of the best sires changed with inclusion of the competition traits into the genetic evaluation.

Árnason, Sigurdsson and Lorange (2006) calculated genetic response in the total score over the last fifteen years to be equal to one additive genetic standard deviation. This genetic response is strong but probably biased as assessed horses at breeding field tests are not a random sample of the population (Henderson 1975; Klemetsdal 1992). The current study showed that competition traits can and should be included in the genetic evaluation. Addition of competition traits as goal traits would better reflect the breeding goal and would therefore lead to increased genetic improvement and less biased estimates of genetic progress, according to selection theories (Koenen et al., 2004).

Addition of re-defined test status should reduce the bias even further when correct genetic parameters have been obtained. With inclusion of the test status into the genetic evaluation breeders and owners of sires and their offspring are subsequently urged to have as many offspring as possible tested to avoid reduction of the sires' EBVs.

In future genetic evaluations of the Icelandic horse, the large genetic gain should also be balanced against the rate of inbreeding. A pilot study (Kristjánsson, 2003) showed that inbreeding depression was present in almost all valuable traits of the Icelandic horse. Furthermore, the rate of inbreeding per generation has increased from 0.14% in the period 1978-1989 to 0.52% in the period 1991-2001. During the same time effective population size was reduced from 365.5 individuals to 97 according to the same study. Application of optimal contribution methodology showed a good possibility of better utilizing the genetic variation in the Icelandic horse without significant reduction of genetic progress.

Other general breeding goal traits such as fertility, health and temperament may also be of importance to consider more in the future genetic evaluation when a sufficient amount of information is available for the appropriate studies to be made.

6 Conclusions

- Competition traits are suitable for genetic selection.
- Performance abilities in competition and at breeding field tests are closely correlated genetically.
- Selection bias in the estimation of genetic parameters of competition data reduces when highly correlated competition traits and breeding field test traits are analysed simultaneously.
- International competition data should be genetically analysed and pace racing traits should also be included.
- The presence of preselection in breeding field test data was verified based on estimated genetic parameters.
- Small differences from model comparisons showed that current genetic evaluation is thoroughly studied and well established.
- Integration of test status and competition traits gives some advantages over the current system.
- Integration of test status and competition traits increases accuracy of the genetic evaluation, affects ranking of sires and therefore selection of sires for future breeding.
- Genetic parameters for the test status trait should be re-estimated where the trait is re-defined for all horses and all traits, including both competition and breeding field test data.
- Competition traits can be included directly in the genetic evaluation and will give breeders an effective tool on which to base their selection.

Future research

The possible economic benefits of integrated genetic evaluation and consequent genetic gain in both breeding field test traits and competition traits should be studied. Records from pace racing competitions should be genetically analysed to find out whether they are suitable to include in the genetic evaluation along with other competition traits when a sufficient amount of standardised pace racing data is available. International competition data should be studied including all available internationally standardised competition results. Genetic parameters should be re-estimated for a re-defined test status trait where it accounts for both genders irrespective of whether the horses are competing and/or being assessed at breeding shows. Possible interaction between breeders and horses should be further analysed where the stud effects are more thoroughly defined. Preselection in international competition data and in international breeding field test data should be studied as future integrated genetic evaluation should involve this factor. Then the effect of integrating test status into the genetic evaluation should be done after re-analysed genetic parameters have been obtained.

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