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Philosophiae Doctor (PhD) Thesis 2011:05

Norwegian University of Life Sciences • Universitetet for miljø- og biovitenskap
Department of Animal and Aquacultural Sciences
Philosophiae Doctor (PhD) Thesis 2011:05

Genetic variation and management of the Norwegian horse breeds

Genetisk variasjon og forvaltning av de særnorske hesterasene

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Summary

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The Norwegian horse breeds suffer from strong competition in the market from imported, specialized breeds. Decreasing population sizes, especially for the Fjord, the Døle and the Nordland/Lyngen, and risk of rapid accumulation of inbreeding is a challenge. This challenge address the need for maintaining these breeds through knowledge of the build-up of relationships in the populations and long-term breeding plans, including breeding goals ensuring the future demand for the breed and proper selection tools which maintain the genetic variation.

The first study examined the genetic variation in the Døle and in the Nordland/Lyngen, through investigation of the pedigree structures, revealing a quite different retrospective picture in these two breeds, due to amongst others periods of imports (trotters and North-Swedish) in the Døle and indications of maximum avoidance of inbreeding in the Nordland/Lyngen. Both populations are considered to have challenges in handling the build-up of relationship, and are recommended to base future management on optimal contribution selection.

The second study was a simulation of the small, Norwegian horse populations to examine the effect of various actions on the effective population size. The main results showed that each of the breeds should be managed with at least 200 foals born and registered per year with a large fraction of the offspring from young sires, to ensure that more sires are being used. In these populations omission of selection was of minor importance for the effective population size.

In the third study different alternatives for genetic evaluation of racing performance in the North-Swedish and the Norwegian trotter was validated based on cross-validation of standardized earnings. The current bivariate linear approach, including racing status and earnings as traits, was compared with a threshold-linear model and the univariate alternative with earnings only. Racing status appeared to be highly influenced by ancestry, which resulted in a high heritability, a high genetic correlation with earnings and likely, an inflated genetic trend of earnings. However, due to earnings being predicted more accurately and the inability to discriminate between models for genetic trend, the current approach is still recommended for practise.

The fourth study describes the application of optimal contribution selection (OCS), by use of Gencont with overlapping generations, in the Norwegian and the North-Swedish cold-blooded trotter. The study showed that OCS can be used as a dynamic tool for selection in the Norwegian breeds to ensure recruitment of young stallions as well as culling of older stallions with already large genetic contributions to the population.

Sammendrag

De norske hesterasene møter sterk markedskonkurranse fra importerte og spesialiserte raser. Samtidig utfordres de på nedgang i populasjonsstørrelsen (spesielt fjordhest, dølehest og nordlandshest/lyngshest), med risiko for rask innavlsøkning. Dette gir behov for oppbygging av kunnskap rundt akkumulering av slektskap i populasjonene og langsiktige avlsplaner, med avlsmål som tar hensyn til fremtidens bruk av hesterasene, samt seleksjonsverktøy som ivaretar genetisk variasjon.

Den første studien kartla genetisk variasjon hos dølehest og nordlandshest/lynghest, ved bruk av slektskapsdata. Studien avdekket et svært ulikt historisk bilde av innavlsutviklingen i disse to rasene, blant annet på grunn av import av travere og nordsvensk hest på dølehest. Det fantes indikasjoner på 'maximum avoidance of inbreeding' hos nordlandshest/lyngshest. Begge populasjonene ansees for å ha utfordringer knyttet til innavlsøkning og det anbefales å benytte seleksjon med optimale bidrag i fremtiden.

Den andre studien var en simulering av de små, norske hestepopulasjonene med hensyn på effekten av ulike tiltak, på effektiv populasjonsstørrelse. Hovedresultatene viste at en i hver av rasene bør sikre minst 200 fødte og registrerte føll per år, med en stor andel avkom etter unge fedre. Å utelate seleksjon i disse populasjonene hadde bare liten betydning på effektiv populasjonsstørrelse.

I den tredje studien validerte en ulike modeller for bruk i avlsverdibestemmelse for travprestasjon hos nord-svensk og norsk kaldblodstraver. Den eksisterende bivariate lineære tilnærmingen, med startstatus og inntjening som egenskaper, ble sammenliknet med en terskel-lineær modell og en univariat modell for inntjening. Startstatus fremsto som sterkt påvirket av slektskap, hvilket resulterte i en høy arvegrad, høy genetisk korrelasjon med inntjening og sannsynlig en oppskalert genetisk trend for inntjening. Den eksisterende bivariate tilnærmingen anbefales fortsatt på grunn av mest nøyaktig prediksjon av inntjening, samt at det ikke var mulig å diskriminere mellom modellene med hensyn på genetisk trend.

Den fjerde studien beskriver hvordan en kan benytte seleksjon med optimale bidrag og programvaren Gencont i avlsarbeidet hos nordsvensk og norsk kaldblodstraver. Studien

anbefaler at seleksjon med optimale bidrag benyttes som et dynamisk seleksjonsverktøy, for å sikre rekruttering av unge hingster, men også for å utrangere eldre hingster som allerede har fått et høyt genetisk bidrag i populasjonen.

Preface

The studies in this thesis are funded by the Norwegian Research Council, the Norwegian Trotting Association (Det Norske Travselskap, DNT), the Swedish Trotting Association (Svenska Travsportens Centralförbund, STC), the Norwegian Equine Center (Norsk Hestesenter, NHS) and the Nordic Genetic Resource Centre (NordGen). The research was carried out at the Department of Animal and Aquacultural Sciences, University of Life Sciences, Ås, Norway.

The process in writing this thesis has been both inspiring and exciting. Special thanks to all horse breeders and horse owners I have met, being passionately interested in the Norwegian horse breeds. All of you have contributed to the joy of working with something that is both interesting and important, and contributed to my understanding of horse breeding.

I will also give my special thanks to supervisor Gunnar Klemetsdal, for all your knowledge and for bringing discussions to high levels. You have encouraged me through the process and taught me to become independent. Great thanks also to my three co-supervisors: Jørgen Ødegård, Theo Meuwissen and Thorvaldur Árnason. Your great knowledge and support have been of great value! I will also thank all other contributing colleagues in the department.

Finally, my sincerest thoughts go to my dear family for being who you are and teaching me what life is all about.

Ås, 12th April 2011
Hanne Fjerdingby Olsen

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General introduction

In Norway systematic breeding of horses started early in the first half of the 19th century, and the first official horse show was in Gudbrandsdalen in 1859 (Dahle, 2010). The governmental agronomist Johan Lindeqvist (1823-1898) defined breeds and initiated the genetic improvement programs for horses. At that time horses was widely used in agriculture, forestry, mine work, conveyance and in public services such as postal administration and the military. Originally, the Fjord and the Døle were from the western and eastern part of Norway, respectively, both used for draught purposes. From the end of the 19th century, the cold-blooded trotter evolved as a light trotting horse from the Døle, due to a growing interest for trotting and racing. The Nordland/Lyngen pony is probably the elder of the Norwegian breeds (Dahle, 2010); build up from those individuals that remained in the northern part of Norway, as late as the first half of the 20th century. After the Second World War a large number of horses were sold abroad for rebuilding purposes, which actually became the origin to the current foreign populations of the Fjord in several countries. No corresponding populations exist for the Døle or Nordland/Lyngen abroad, while for the cold-blooded trotter, there is one joint population in Norway and Sweden today.

During the 1950's agriculture and forestry was mechanized, and quite rapidly the number of horses decreased, as the horse no longer was needed for draught purposes. At the end of the 1960's the number of horses in Norway reached its lowest level, just below 20.000 animals (Dahle, 2010). However, sports- and leisure activities with horses became steadily more popular over time, with a considerable import of horses and breeds for this purpose. Thus, to survive, the Norwegian breeds had to compete with specialized breeds, a competition which has grown even stronger over time.

According to Dahle (2010), the government was responsible for Norwegian horse breeding through the governmental advisers (chief inspectors) of horse breeding, until Norwegian Equine Centre (NHS) was established in 1986, and the responsibility transferred there. The foundation NHS has employed an administrative leader of horse breeding, and in addition the board of the foundation has an advisory council for breeding matters, consisting of both scientific representatives and representatives of the member organizations. NHS consists of 16 breeding organizations, amongst them one for each of the Norwegian breeds. With the transfer of responsibility of horse breeding from the state to NHS, there was a need for a steering instrument, i.e. breeding plans. Actually, in 1995 breeding plans for all the horse breeds were finished and decided on. All breeding plans are approved by the board of NHS, according to recommendation by the advisory council of breeding. Breeding plans are the steering documents for long-term management in horse breeding, and states the breeding goal for each breed, which traits to be selected for and how to carry out selection. Today, the horse breeding is financed by funds from Norsk Rikstoto, regulated by the Ministry of Agriculture and Food. The foundation Norsk Rikstoto has the responsibility for all totalisator activities in Norway.

During the 1960's and 1970's the society became steadily more conscious regarding loss of genetic variation, and at UN's global conference on the human environment in 1972 the importance of conserving genetic material was emphasized (UNEP, 2010). In 1979 the Nordic Gene Bank was established, with responsibility for a common Nordic gene bank for plants, administered by the Nordic Council of Ministers. Later, in 1984, the Nordic Genebank Farm Animals was established (today: Nordic Genetic Resources Centre, NordGen), with responsibility for conservation of farm animal genetic resources (Adalsteinsson, 1993). In 1992, the UN's convention for biological diversity stated a national responsibility for all domestic biological diversity and its sustainable development (UN, 1992). Today, the Norwegian Ministry of Agriculture and Food has an advisory and executive organ, the Norwegian Genetic Resources Centre, for activities regarding the conservation and utilization of national genetic resources. The centre has an independent scientific advisory council, which is nominated by the Norwegian Ministry of Agriculture and Food, with responsibility for the national program concerning sustainable management and conservation of genetic resources. According to the strategic plan for the Advisory Council of Genetic Resources for the period 2000-2005 (Skjevdal and Koren, 2000), the Døle, the Nordland/Lyngen and the cold-blooded trotter were all considered to have a problem with increasing inbreeding, in addition to small population sizes of the first two. The suggested initiatives were; cooperation with the breeding organizations, publishing a yearly status report of the horse genetic resources, establish a plan for long-term storage of sperm, calculations of inbreeding and breeding advisory service towards breeders and breeding organizations. In the action programme for 2008-2010 of the Norwegian Genetic Resources Centre (Sæther, 2009), the horse is the only national species where the degree of threat against genetic diversity is not yet considered by the centre. However, in the World Watch List for domestic animal diversity (FAO, 2000) both the Døle horse and the Nordland/Lyngen pony is classified as endangered, but maintained. This classification was based on population data from 1994 and 1993, respectively, and therefore it can be stated that the current situation is quite insufficiently described.

Over the last decade there has been a downwards trend in number of matings for the Norwegian horse breeds, of great concern to the breeding organizations. Although the numbers fluctuate somewhat with the general economy, the numbers are still alarmingly low, especially for the Nordland/Lyngen (Figure 1). For the Nordland/Lyngen only 65% of the matings was done in 2009 relative to 2000, with a remarkable large drop in 2009 (Figure 1). In Fjord the corresponding number was 72%, while for Døle the number of matings was approximately stable over the last decade (Figure 1). This gradual decline in Fjord and Nordland/Lyngen is probably closely correlated to a failing demand in the market, and the competition from other horse breeds, as the breeders have problems with selling their foals and therefore are reluctant to mate their mares (Norwegian Equine Centre, 2008). The price offered for the Norwegian horse breeds is not high enough to cover the costs, and so the supply of trained horses is failing. For the cold-blooded trotters, number of matings in Norway is at a much higher level than for the other Norwegian breeds (Figure 1), between 1200 and 1800 mares. This is much higher than the corresponding numbers for this breed in the beginning of the 1970's, when only approximately 900 mares were mated annually (from 536 foals born in 1972 (Klemetsdal, 1993) and a fertility rate of 0.60 (Klemetsdal, 1999)).

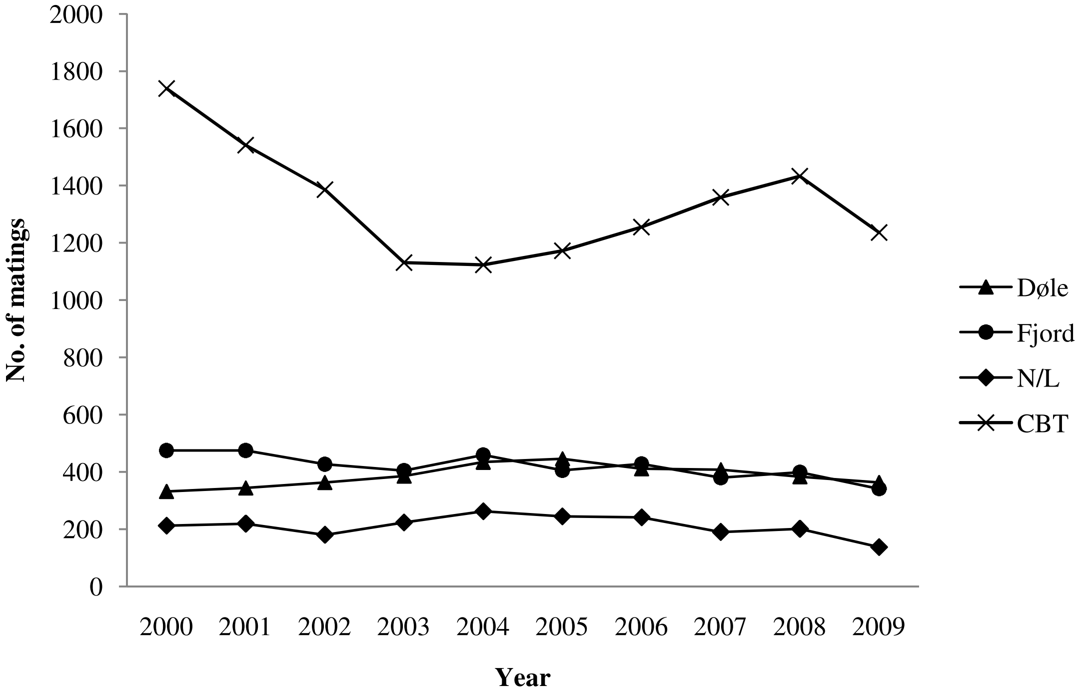

Figure 1: Number of matings in the Døle, the Fjord, the Nordland/Lyngen (N/L) and in the cold-blooded trotter (CBT), based on numbers received from the Norwegian Equine Centre in October 2010.

In Figure 2 the mean foaling rate (ratio between number of born (registered) foals relative to the number of matings) over the last decade is plotted. For the period 2000-2007 this rate was 0.58 for the Fjord, 0.60 for the Døle, 0.68 for the cold-blooded trotter and 0.70 for the Nordland/Lyngen. Actually, both the Nordland/Lyngen and the cold-blooded trotter have established proper routines for registration, which might explain the enlarged foaling rate in these breeds. For the cold-blooded trotter these numbers are higher than the result of Klemetsdal and Johnson (1989) of 0.62 from the 1980's. Corresponding historical measures are not available for the other breeds. Foaling rate, as a measure of fertility, is known to be affected by inbreeding (Klemetsdal and Johnson, 1989), but the rate is likely also market-sensitive, as the rate of registration of foals can be affected when the economy is down, which was the situation from 2008 onwards (Figure 2).

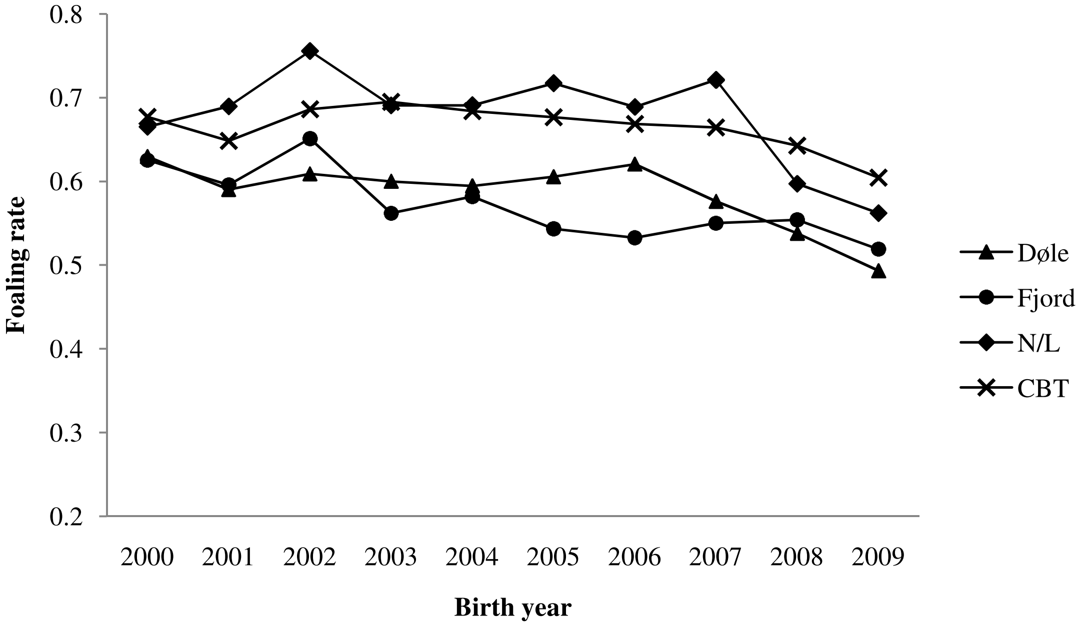

Figure 2: Foaling rate in the Døle, the Fjord, the Nordland/Lyngen (N/L) and, based on yearly number of matings and number of born foals, received from the Norwegian Equine Centre in October 2010.

Due to the fact that fertility can be affected by inbreeding (inbreeding depression), it is important to monitor this trait, with suitable measures over time in populations where inbreeding is increasing, and especially if the effective population size in addition is small. Fertility can be measured through for instance foaling rate or otherwise in semen samples. In the Norwegian horse breeds monitoring of the fertility is not an established practise, neither is there a continuous control of the build-up of relationships within the populations, although the breeds the last decades have had an increased focus on inbreeding, also with quite radical initiatives towards reduction of rate of inbreeding, such as the imports of the North-Swedish draught horse in the Døle at the beginning of the 21st century (Norwegian Equine Centre, 2006).

Therefore, one aim of this thesis was to examine the genetic variation that exists in the Norwegian horse breeds (Paper I and IV). Another aim was to examine the effect on effective population size (in Døle, Fjord and Nordland/Lyngen) of varying the population size, the fraction of offspring from young sires and whether performing phenotypic selection or not (Paper II). A third goal was to evaluate the genetic model used for calculation of breeding values for the cold-blooded trotter (Paper III) and the final goal was to explore the use of a new selection tool, optimal contribution selection, to handle the rate of inbreeding while maintaining genetic progress when selecting on breeding values in the cold-blooded trotter (Paper IV). The breeds chosen for this work was indicated to have the largest challenges linked to genetic variation; the Døle horse and the Nordland/Lyngen pony, because they are listed on FAO's list of threatened species, and the cold-blooded trotter due to a high, known inbreeding rate (Klemetsdal and Johnson, 1989). As several populations exist abroad for the Fjord horse, this breed was assumed to be less under threat than the other breeds, but the conclusions in this thesis are highly relevant also for this breed, especially due to the steadily decreasing trend of mated mares within Norway.

Paper I

Pedigree structure and genetic variation in the two endangered Norwegian horse breeds: Døle and Nordland/Lyngen

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ORIGINAL ARTICLE

Pedigree structure and genetic variation in the two endangered Norwegian horse breeds: Døle and Nordland/Lyngen

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Abstract

To examine the genetic variation in two endangered Norwegian horse breeds, the pedigree structures were investigated, and key parameters such as inbreeding coefficients, effective population size, effective number of founders, effective number of ancestors and effective number of founder genomes were calculated. The data consisted of 31,142 individuals of the Døle horse and 1973 individuals of the Nordland/Lyngen horse, for which the complete generation equivalent was 10.5 and 7.2, respectively. In both breeds, the pedigree data were more than 98.5% complete in the fourth generation, allowing the rate of inbreeding and the effective population size to be precisely estimated, actually measuring the fractional loss of heterozygosity, comparable across generations (not so for the other measures). The level of inbreeding was about 12% in both breeds, with a rather wavy pattern during the past 50 years in the Døle. Considering the last generations only, the effective population size was found to be 152 in the Døle and 42 in the Nordland/Lyngen. For both populations selection in the future should be based on optimal contribution.

Keywords: *Breed conservation, effective population size, pedigree analysis, probability of gene origin.*

Introduction

Norway is a country that is relatively rich in domestic animal genetic resources (Ruane, 2000). However, for a variety of reasons, such as changes in farming practices, many of its breeds are in danger of extinction in the near future. Conservation of these resources is a challenge, requiring a multi-faceted approach, covering a range of aspects such as increasing public awareness about their importance or ensuring that the breeds are managed in a sustainable way so that problems of inbreeding and loss of genetic variation are minimised. Here, we focus on this latter aspect and report on the pedigree structure and genetic variation in two endangered Norwegian horse breeds.

The populations of the Norwegian Nordland/Lyngen and the Døle (www.ansi.okstate.edu/breeds/horses) are small, and breeders also exercise artificial selection. Selection reduces the effective population size (N_e), because the number of breeding animals is reduced, and in an already small population it accelerates genetic drift. In such small populations genetic drift, in which allele frequencies at a locus change at random from one generation to the next, increases the probability of fixation of alleles and reduction of additive genetic variation.

Changes in allele frequencies also result in changes of genotype frequencies, and a locus will contribute to a change of the population mean due to inbreeding if a dominance effect is present (Falconer & Mackay, 1996) (in addition, mean change from allele frequency changes on non-neutral loci). The frequencies of homozygotes increase and recessives accumulate in the population, leading to the phenomenon known as inbreeding depression. The smaller the population is, the more it genetically drifts, and the larger the probability is that the alleles become identical by descent, defining the coefficient of inbreeding (*F*). In a case with a neutral locus, no mutation and no migration, the inbreeding

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coefficient thus reflects how far the process of genetic drift has progressed, relative to the base population, whereas the inbreeding rate describes the speed of the process. This study examined the pedigree structure of two endangered breeds and calculated various parameters describing genetic variation, such as the effective population size, from the rate of inbreeding and the coefficient of kinship, and those based on probabilities of gene origin, with the aim of drawing inference as to future genetic management of the breeds.

Materials and methods

Data were received from the Norwegian Equine Centre in autumn 1999. Recent birth years are not included in this work due to loss of data in the process of changing data registration system at the Norsk Rikstoto in 2006 (zeroing parents not recorded in the studbook as an individual by itself, see below, meaning that the most remote generation of ancestors could not be included in the analyses). The original material used for this study contained all the animals ever registered in these two breeds: 30,712 registered animals of the Døle and 1969 registered animals of the Nordland/Lyngen. The first registered Døle was a stallion born in 1846. In the Nordland/Lyngen, the first registered animal was a mare born in 1906. In both breeds, the last birth year of registered animals was 1998. All the ID-numbers were renumbered, and the files were edited to remove obvious errors such as ID-numbers in incorrect format or logical errors where the parent is born after its progeny, or errors where parents were not recorded in the studbook as an individual by itself. These parents were added as individuals with no pedigree information. In the Døle, the number of added animals was 430, whereas the respective number in the Nordland/Lyngen was four animals. In Døle, these were mainly Norwegian cold-blooded trotters (the light version of Døle; see www.ansi.okstate.edu/breeds/horse), but also some individuals of North-Swedish horse, with a Døle origin. Of these, 108 were added with unknown birth year (90 Norwegian cold-blooded trotters and 18 North-Swedish horses). In Nordland/Lyngen, three of the four animals were of other origin (Fjord horse). The last of the four is a fictitious animal. At the end of this procedure, the total number of records generated for the two breeds were 31,142 and 1973, respectively (Table I).

The reference populations were defined as horses born between 1990 and 1998, with a total of 1535 horses in Døle, while the corresponding number for the Nordland/Lyngen was 1050 horses (Table II).

All ancestors of the animals in the reference populations were then traced back to the founders, in an accumulation procedure (individual by individual), also to reveal the completeness of the data. The founders of these populations were defined as horses with unknown parents. When an animal had only one parent known, the unknown parent was considered as a founder (Boichard et al., 1997). In Nordland/Lyngen one Finn horse import existed, Viri (Rian, 2003), and was made a founder by deleting its pedigree information. This pedigree information was originally included only because five generations of pedigree information is required in the Norwegian studbook. In Døle, the pedigree of the imports was not deleted in the same manner as described for Nordland/Lyngen, because the number of founders originating from Norwegian cold-blooded trotters was too high, and the relationship between the two breeds is significant. However, proper identification of trotters would require access to both studbooks.

From the accumulated files, the maximum number of generations in the pedigree ($g_{\max}$) was derived as was the percentage of known ancestors per generation, as well as the complete generation equivalent (CGE):

$$CGE = \frac{1}{\mathrm{N}} \sum_{j=1}^{\mathrm{N}} \sum_{i=1}^{\mathrm{n}_j} \frac{1}{2^{g_{ij}}},$$

where N is the number of individuals in the reference population, n_j is the number of ancestors generated for animal j and g_{ij} is the number of generations between individual j and its ancestor i (Boichard et al., 1997). CGE can be interpreted as the number of generations in a comparable complete pedigree, illustrating the depth of the pedigree data.

To describe the genetic variation in a population, several measures can be used. To quantify the rate of genetic drift the rate of inbreeding is most frequently used (Boichard et al., 1997). Unfortunately, the coefficients of inbreeding are very sensitive to incomplete data. A complementary approach, which is more robust, is to analyse the probabilities of gene origin. Parameters from probabilities of gene origin, i.e. the effective number of founders (f_e), effective number of ancestors (f_a) and effective number of founder genomes (f_g), are also affected by incomplete pedigree information, but to a smaller extent than parameters derived from inbreeding coefficients (Boichard et al., 1997).

Effective population size

Individual inbreeding coefficients were calculated using the Quaas–Henderson algorithm (Henderson, 1976; Quaas, 1976). The effective population size is defined as the number of individuals in an idealised

Table I. The number of animals in the total pedigree in the Døle and in the Nordland/Lyngen, respectively.

	Døle			Nordland/Lyngen		
	Stallions	Mares	Total	Stallions	Mares	Total
Number of animals	3739	27,403	31,142	720	1253	1973

population, which would give rise to the same inbreeding rate (ΔF) as observed in the real population (Falconer & Mackay, 1996). The effective population size (N_e) in generation t, unconditional of becoming selected as parents or not in generation t, was computed according to the formula:

$$N_{e_t} = \frac{1}{2\Delta F_t},$$

where the rate of inbreeding, ΔF_t, is:

$$\Delta F_t = \frac{1}{N}\sum_{i=1}^{N} \frac{F_i - \frac{1}{2}\left(F_{sire_i} - F_{dam_i}\right)}{1 - \frac{1}{2}\left(F_{sire_i} - F_{dam_i}\right)}$$

with F_i being the individual coefficient of inbreeding for animal i in generation t (defined reference population), and F_{sire_i} and F_{dam_i} are the individual inbreeding coefficient of the parents in generation t–1.

Effective number of founders

Effective number of founders was defined as the number of equally contributing founders that would produce the same genetic diversity as in the reference population under study (Lacy, 1989):

$$f_e = \frac{1}{\sum_{k=1}^{f} q_k^2},$$

where q_k is the genetic contribution of founder k to the population's gene pool. The balance of the founder contributions measures the preservation of the genetic diversity from the founders to the present population. If each founder contributes the same, the effective number of founders equals the actual number of founders. In any other situation, the effective number is smaller than the actual number of founders. An important limitation with this approach is that it ignores potential bottlenecks in the pedigree (Boichard et al., 1997). Computation is detailed in Olsen et al., (2005).

Effective number of ancestors

The effective number of ancestors describes the minimum number of ancestors (they may or may not be founders) required to explain the complete genetic diversity of the population under study (Boichard et al., 1997):

$$f_a = \frac{1}{\sum_{k=1}^{f} p_k^2},$$

where

$$p_k = q_k\left(1 - \sum_{i=1}^{n-1} a_i\right)$$

and p_k is the marginal contribution of ancestor k to the population's gene pool, which is q_k adjusted for the genetic contribution a_i from the n–1 already

Table II. The number of registered stallions and mares in the reference population in the Døle and in the Nordland/Lyngen, respectively.

	Døle			Nordland/Lyngen		
Birth year	Stallions	Mares	Total	Stallions	Mares	Total
1990	67	91	158	42	60	102
1991	64	95	159	56	53	109
1992	58	74	132	42	64	106
1993	64	87	151	58	51	109
1994	78	89	167	39	51	90
1995	99	100	199	65	58	123
1996	96	88	184	63	68	131
1997	115	100	215	83	65	148
1998	93	77	170	64	68	132
Total	734	801	1535	512	538	1050

selected ancestors. Initially, the largest contributing ancestor was determined as the one having the largest q-value. When determined, the contribution taken out by that ancestor should not be assigned to more remote ancestors. This is taken account of by eliminating its pedigree information, leaving the animal as a "pseudo founder". The animal's descendants also need to get their contribution adjusted for the contributions from this "pseudo founder", leading to marginal contributions, i.e. contributions not explained by other ancestors. In this approach, p_k is q_k adjusted for the genetic contribution a_i from the n–1 already selected ancestors to individual k, and for each major ancestor found, its pedigree information is deleted, i.e. the sire and dam information is set to zero, eliminating redundancies. For calculations, see Olsen et al. (2005). In the Nordland/Lyngen, all ancestors with a non-zero contribution to the reference population (horses born 1990–1998) were determined. In the Døle, we stopped the procedure with the 100 highest contributing ancestors, as these individuals covered more than 97% of the contribution to the reference population. The effective number of ancestor accounts for potential bottlenecks, but still the probability of gene loss by drift needs to be considered.

Effective number of founder genomes

To account for loss of genetic variability by genetic drift, Lacy (1989, 1995) and Ballou and Lacy (1995) introduced the concept of effective number of founder genomes, or founder genome equivalent. This measures how many founder genes are maintained in the population for a given locus, and how balanced their frequency is in the offspring of the reference population. Originally, this parameter was calculated by probability calculations (Lacy, 1989) or by gene dropping analysis (MacCluer et al., 1986). Instead, Lacy (1995) proposed to stay with a definition of the founder genome equivalent as half the inverse of average kinship in generation t (the reference population):

$$f_g = \frac{1}{2\bar{f}_t}.$$

This is supported, especially from a practical point of view, by Caballero and Toro (2000) and Zechner et al. (2002). For details in computation, see Olsen et al. (2005).

Effective population size from kinship

As the inbreeding coefficient describes the similarity between two alleles in each animal and hence describes effects of past decisions, it is in addition interesting to look at the average pair wise similarity between the animals in the reference population, i.e. the coefficient of kinship (Falconer & Mackay, 1996). This gives us an indication of current bottlenecks. The coefficient of kinship between two animals equals the inbreeding coefficient of their progeny (Falconer & Mackay, 1996). Therefore, we used the average pair wise kinship to predict an approximate rate of F in the next generation (ΔF_{t+1}), given no selection:

$$\Delta F_{t+1} = \frac{f_t - F_t}{1 - F_t}$$

where f_t is the average pair wise kinship in the reference population, independent of sex and including selfing, and F_t is the corresponding average inbreeding coefficient. The calculation was done repeatedly, each year including the last three-year classes of the reference population.

Mating strategies

Kinship calculation (excluding selfing and intrasex mating) was also used to test whether systematic favour of inbreeding is practised as a mating strategy. This was done by calculating the difference between the average inbreeding coefficients in generation $t(F_t)$ and the average pair wise kinship of their parents in generation t–1(f_{t-1}), compared with a two-sample t-test.

Results

In the Døle, animals in the reference population had an average number of 22,464 ancestors (Table III). The corresponding number in the Nordland/Lyngen was 495. Still, both breeds had a pedigree completeness of more than 98.5% in Generation 4 (Table III). Including more generations in calculations, a more complete pedigree was demonstrated in the Døle than in the Nordland/Lyngen. In Table III, the quality of the pedigree information is also indicated by the CGE. In the Døle the pedigree can be traced back a maximum of 25 generations, where CGE is 10.5. In the Nordland/Lyngen, CGE was 7.2, with tracing of pedigree for a maximum of 13 generations.

Figure 1 shows that inbreeding levels in the two breeds evolved somewhat differently throughout the past 100 years. The average inbreeding coefficient for the Døle increased to about 7% in the 1940s, after which it fell significantly before rising again towards the end of the 1970s. During the past few years, the inbreeding coefficient has been around 12%. For the Nordland/Lyngen, the average

Table III. Calculated parameters describing pedigree completeness of the reference population; in the Døle and in the Nordland/Lyngen, respectively.

		Døle	Nordland/Lyngen
Number of animals in reference population		1535	1050
Average number of ancestors per animal		22,464	495
Percentage (%) of known ancestors in generation	1	99.97	99.95
	2	99.89	99.95
	4	98.64	99.83
	6	90.51	91.09
	8	78.66	44.41
	10	66.76	6.00
Maximum number of generations generated ($g_{\max}$)		25	13
Complete generation equivalent (CGE)		10.5	7.2

inbreeding coefficient has been high throughout most of the period. At present, the average lies at the same level of inbreeding one gets with half-sib mating (12.5%).

In the reference population of the Døle, the average inbreeding coefficient was 11.75% (Table IV), while it was 12.77% in Nordland/Lyngen. The corresponding effective population sizes calculated by use of the classical formula were 152 in the Døle and 42 in the Nordland/Lyngen (Table IV).

The number of founders in Døle and Nordland/Lyngen was 770 and 42, respectively (Table IV). In both breeds, there was a larger number of female than male founders (Table V). In Døle, the founders spread out over a long-time span, while in Nordland/Lyngen the majority of the founders were born in the first half of the twentieth century (Table V).

The effective number of founders, f_e, was 48 for the Døle and 14 for the Nordland/Lyngen (Table IV). The corresponding values for effective number of ancestors, f_a, were 12 for the Døle and seven for Nordland/Lyngen, while the effective number of founder genomes, f_g, was calculated as 5.4 for the Døle and 3.7 for Nordland/Lyngen (Table IV).

Table VI shows the rate of inbreeding in generation $t+1$ over a period of 7 years (1992–1998), that results from mating of the last three-year classes, continuously. The resulting trends were in opposite in the two breeds; with an increasing trend of the rate of inbreeding in generation $t+1$ in the Døle, while it was decreasing in Nordland/Lyngen.

Table VII demonstrates a significantly higher inbreeding coefficient of offspring in the Døle, than the average, pair wise kinship of parents, indicating a mating strategy favouring inbreeding. The tendency of the opposite; a mating strategy avoiding inbreeding, was seen in the Nordland/Lyngen, although not statistically significant (Table VII).

Table VIII shows, as a curiosity, the five most important ancestors in the pedigrees of the reference populations, as represented by their marginal contributions. Together, these five contributed more than 50 and 70% to the gene pools of the reference population in the Døle and in the Nordland/Lyngen, respectively (Table VIII).

Discussion

In Norway, the Norwegian Equine Centre has been responsible for registration of the Døle and the Nordland/Lyngen, since 1988 (Norsk Hestesenter, 1988). From 1990, the rules for registration were changed, so that all horses being born could be registered (Norsk Hestesenter, 2003). Still, there is a lack of registration, probably because it is voluntary and there are some expenses with the registration

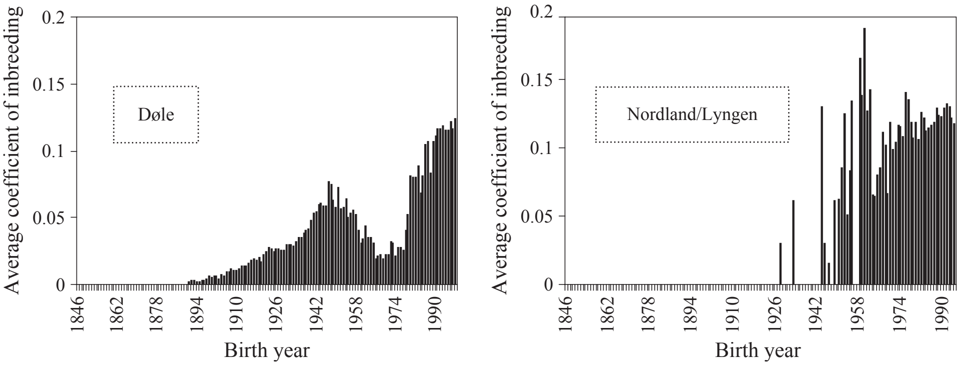

Figure 1. Average coefficient of inbreeding per year of birth; in the Døle and in the Nordland/Lyngen, respectively.

Table IV. Calculated parameters describing genetic diversity of the reference population in the Døle and in the Nordland/Lyngen, respectively.

	Døle	Nordland/ Lyngen
Average coefficient of inbreeding (F_t)	0.1175	0.1277
Rate of inbreeding ($\Delta F_t \pm$SE)	0.0033 ± 0.0455	0.0119 ± 0.0014
Effective population size (N_{e_t})	152	42
Number of founders (f)	770	42
Effective number of founders (f_e)	48	14
Effective number of ancestors (f_a)	12	7
Effective number of founder genomes (f_g)	5.4	3.7

papers, and if a horse is not to be used in breeding it may not be registered. Both breeds have developed breeding plans since 1995 (Vangen, 1996). The breeding goals include weighting of conformation, performance, temperament and durability, and selection is on phenotype. The stallions must be licensed for use in the breeding (e.g. Klemetsdal, 1998).

In the Nordland/Lyngen, the reference population accounted for almost 53% of the total pedigree. By comparison, the corresponding number in the Døle was only 5%. The reason for this can be found in a retrospective set up of the first studbook in Nordland/Lyngen in 1969 (Statens Stambokkontor, 1969), after years of struggle to keep the breed alive, while the first studbook in Døle was published back in 1902 (Det kgl. selskab for Norges Vel 1902). With a more retrospective set up, the number of animals in the pedigree became restricted, explaining most of the differences in the percentages that the reference population made up of all animals in the pedigree. Additionally, Nordland/Lyngen was nearly extinct in the 1950s, and so went through a narrow bottleneck (Roaldsøy, 1969). Many individuals of the Nordland/Lyngen were lost during the Second World War and the mechanisation in agriculture made the working horses redundant (Roaldsøy, 1969), and so the systematising of the breeding was a last attempt to save the breed. They started with very few animals in the studbook, and these became the important founders of today's current population (Statens Stambokkontor, 1969).

The proportion of founders in the pedigree of the Døle was quite high. As mentioned, the breeding of the Døle was systematised at the end of the nineteenth century, and the first studbook for the Døle included stallions approved from 1859 onwards, with unknown missing values assigned to parents that themselves were not registered in the studbook. For mares, the same registration practise was followed from 1878 onwards (Borchgrevink, 1906). With basically an open studbook as in Døle, it is obvious that the number of founders will be high, spreading out over a long-time span. Furthermore, with more female than male founders, the likelihood of missing parental information will be smallest among males, resulting in more male founders born far back in time. This result was most likely

Table V. Number of founders by sex and decade in the Døle and in the Nordland/Lyngen, respectively.

	Døle			Nordland/Lyngen		
Decade of birth	Stallions	Mares	Total	Stallions	Mares	Total
0	26	82	108	1	3	4
1840	3	0	3	–	–	–
1850	5	0	5	–	–	–
1860	6	0	6	–	–	–
1870	25	5	30	–	–	–
1880	42	61	103	–	–	–
1890	20	91	111	–	–	–
1900	12	47	59	2	4	6
1910	9	32	41	3	4	7
1920	21	31	52	2	3	5
1930	25	57	82	5	8	13
1940	29	41	70	0	1	1
1950	22	32	54	0	1	1
1960	11	19	30	1	1	2
1970	4	7	11	0	2	2
1980	3	1	4	0	0	0
1990	0	1	1	1	0	1
Total	263	507	770	15	27	42

Table VI. Rate of inbreeding in generation $t+1$, calculated each year from average, pair wise kinship (allowing selfing and intrasex mating) and inbreeding coefficients, including the last three-year classes of the reference population in the Døle and in the Nordland/Lyngen, respectively.

Year class	Døle	Nordland/Lyngen
1990–1992	0.0079	0.0157
1991–1993	0.0082	0.0148
1992–1994	0.0101	0.0149
1993–1995	0.0122	0.0129
1994–1996	0.0133	0.0091
1995–1997	0.0137	0.0101
1996–1998	0.0133	0.0121

strengthened from studbook recording being initiated later in females than in males.

From 1990 onwards, registration of horses born in Norway required, if possible, a five-generation pedigree for all horses (Seterlund et al., 1989). This is also reflected in the results for Døle and Nordland/Lyngen, as the reference populations had 98.6 and 99.8% of the ancestors in the fourth generation, respectively. Digitalisation was based on the data used by Vangen (1983), but animals only known as parents in the studbook were deleted together with their pedigrees. This led to a considerable loss of data, which could have been avoided by splitting the studbook in two. In Nordland/Lyngen, the data were very complete in the first six to eight generations of the reference population, despite data only going back to 1906. As mentioned, recording for this studbook was originally done retrospectively, restricting the number of animals in the pedigree, as well as the number of founders. A consequence of the current registration practise was that one rather recent founder was found, e.g. the one mare founder born during the 1990s (Table V), likely with an incomplete pedigree.

Two different approaches were used to quantify the amount of genetic variation; the probability of gene origin measures and the effective population size, from the rate of inbreeding. In essence, the former calculates the probability of gene loss, which by definition will change over generations (Boichard et al., 1997). In contrast, the rate of inbreeding relates to the fractional loss of heterozygosity from generation t to $t+1$, being the same in all generations, for the same breeding structure (Boichard et al., 1997). In consequence, the probability of gene loss measures is not directly comparable between breeds with different pedigree depth, as was the situation with Døle and Nordland/Lyngen. Furthermore, with the shift in registration practice in 1990, the base generation will not be precisely defined, further reducing the value of these measures. In contrast, with an almost complete pedigree for five generations in both breeds, the asymptotic rate of inbreeding will be estimated without much error (for the asymptotic rate, see e.g. Klemetsdal, 1999). With our data, this gives a preference to the rate of inbreeding and the effective population size over the probability measures. Besides, the rate of inbreeding is only slightly affected by the base definition. An improved calculation of the level of inbreeding and kinship coefficients could have been done by adopting the method of VanRaden (1992), assuming founding trotters as unrelated (although these also have a Døle origin, see e.g. Klemetsdal, 1998), and the remaining founders being related to the contemporary animals, as determined by the level of inbreeding.

The effective number of founders, f_e, only corrects for unbalanced founder contributions in the base generation. At later stages of a breeding programme, the contributions of the founders cannot be affected. Only contributions from animals in the current to the next generation can be influenced. This is possible by the use of the theory of inbreeding. The effective number of ancestors (f_a) giving the marginally most contributing ancestors (the bottlenecks) suffers from the same deficiency as the effective number of founders. The contributions of remote ancestors (Table VII) are not possible to affect at present, and thus they are only contributing through drift. Actually, the speed of drift (the rate of inbreeding) relates to the squared contributions of all ancestors (Woolliams & Thompson, 1994), not only the ones with largest marginal contributions. The value of knowing the most important marginal ancestors in our data is thus more of a cultural–historical one. The effective number of founder genomes (f_g) was calculated from the kinship in the reference population, which is sensitive to pedigree depth, while the rate of inbreeding from kinship was not. Assuming that F increases linearly with time, an

Table VII. Testing the existence of avoidance of inbreeding as a mating strategy from the difference between the average inbreeding coefficients of animals in the reference population and the average pair wise kinship between parents (f_{t-1}) (excluding selfing and intrasex mating) with a two-sample t-test.

	F_t	f_{t-1}	$\lvert t\rvert$	p
Døle	0.1175 ± 0.0013	0.1115 ± 0.0003	4.46	0.01
Nordland/Lyngen	0.1277 ± 0.0011	0.1289 ± 0.0003	1.11	n.s.

Table VIII. The five ancestors with the largest marginal contribution to the reference population; in the Døle and in the Nordland/Lyngen, respectively.

Registration number	Name	Sex	Birth year	Marginal contribution
Døle				
1185DH	Gjestar	M	1919	0.21673
0825DH	Brimin	M	1908	0.15894
1752DH	Tuftar	M	1946	0.06595
0613DH	Draupner	M	1898	0.04514
0130DH	Dovre	M	1914	0.03684
Sum				0.52360
Nordland/Lyngen				
0002NH	Rimfakse	M	1935	0.26125
0010NH	Torgrim	M	1946	0.14834
00009N	Mona	F	1935	0.13819
00003N	Bruna	F	1930	0.12669
0009NH	Bamse	M	1945	0.06071
Sum				0.73518

interrelation exists between the two measures; $f_g \approx \frac{N_e}{t}$ (Meuwissen & Woolliams, 2000). The rate of inbreeding from kinship measures the genetic variation among the mated individuals, when ignoring the generation interval and assuming that all animals in the reference population contribute equally to the next generation. If the measure is calculated standardised, e.g. on basis of the last year classes that is not yet reproductive (here: the last three), consistent changes in size of annual values may indicate a loss of genetic variance, as observed in the Døle. Actually, the rate of inbreeding from kinship allows current rather than retrospective rates of inbreeding and effective population sizes to be calculated. Hence, the two inbreeding rates may complement each other when drawing inference with respect to loss of heterozygosity.

The level of inbreeding was high in both breeds, with an average that is equivalent to half-sib matings. However, the level of inbreeding was relatively higher in the Nordland/Lyngen where the base was only 7.3 generations away, compared with 10.5 generations in the Døle. To reduce inbreeding in Døle, crossing with trotters was as mentioned practised from the 1950s onwards. Actually, stallions of the Norwegian cold-blooded trotter were allowed to breed in the Døle, for the first time in 1953 (Gaustad, 1953), to cope with possible inbreeding depression, especially with respect to reduced fertility (Gaustad, 1951). During the 1970s the breeding policies changed, showed by the steep increase in inbreeding, probably because the use of trotters in the Døle produced lighter horses. As a consequence, the cold-blooded trotter was no longer preferred, and within 5–10 years the level of inbreeding was higher than ever. During the past decade the inbreeding coefficient has been around 12%. From 2000, a North-Swedish breed (Nordsvensk brukshäst) was temporarily used in the Døle to cope with this problem (Kvam, 2003), but this is not a good long-term solution. Instead, it will be more important to gain control over the selection with optimal contribution. This will minimise the average coancestry of parents and thus also the level of inbreeding of future generations (Sonesson & Meuwissen, 2001).

The Nordland/Lyngen has, as mentioned, had difficult periods during the past, where ensuring survival of the breed has been the priority. Back in the late 1930s three men initiated conservation of the Nordland/Lyngen (Roaldsøy, 1969). They looked for purebred individuals, and found one stallion in 1939; *Rimfakse*. He was used as the starting point for further breeding, contributing 26% to the reference population (Table VIII). The Nordland/Lyngen has had a relatively high level of inbreeding for many years, with no sudden changes during the past 40–50 years. According to Ehiobu et al. (1989) slower rates of inbreeding cause less inbreeding depression than more rapid rates of inbreeding. There are no recent reports of serious health damages in the two breeds, but such data are still not systematically recorded in these breeds. It would be important to record fertility data to survey possible reductions in fitness over time. This requires that the Norwegian Equine Centre has as a first priority to utilise their newly established database, and to begin to monitor these breeds by recording health traits.

Over the last generation there has not been any significant change in the level of inbreeding in either of the two populations, resulting in a larger effective population size in the Døle (152) than in the Nordland/Lyngen (42). During the 1990s, the rate of inbreeding from kinship indicates a likely reduction of genetic variance in the Døle (Table VI), but with somewhat improved situation in the Nordland/Lyngen. These changes are a consequence of the lack of control of the general build-up of relationships in the population.

In Døle, the build-up of relationships in the population is due to selection (also not preferring cold-blooded trotters) as well as a mating strategy favouring inbreeding. In Nordland/Lyngen, the mating strategy is somewhat in favour of less inbreeding in the offspring, reflecting the breed's problems with inbreeding in the past.

Conclusion

In Nordland/Lyngen, the loss of heterozygosity has been considerable. The population is managed with a tendency towards avoidance of inbreeding in the offspring. In the study period heterozygosity has improved, most likely from improved selection and sire usage. In the Døle, the genetic variance has been higher, due to cross-breeding with cold-blooded trotters in the past. However, heterozygosity has become reduced due to active elimination of the cold-blooded impact, resulting in a mating strategy that actually favours inbreeding. In both populations we recommend that future management is carried out with optimal contribution selection (Sonesson & Meuwissen, 2001), with no need for additional cross-breeding.

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Paper II

Management to ensure effective population size in a breeding programme for the small Norwegian horse breeds – a simulation study

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SHORT COMMUNICATION

Management to ensure effective population size in a breeding programme for the small Norwegian horse breeds – a simulation study

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Abstract
A simulation study relevant for the Norwegian horse populations (Døle, Fjord and Nordland/Lyngen), compared with how the effective population size per generation is affected by: the population size, the proportion of offspring from three-year-old sires, performing phenotypic selection of sires at three years of age and random selection amongst these at four years of age (mating for 4 years). The distribution of family size (number of mated mares per sire) was as observed in the Døle. The population size had the largest effect on the effective population size per generation, and therefore at least 200 foals should be born and registered per year. The second most limiting factor was the proportion of young sires, where higher effective population size could be obtained by having more offspring from three-year-old sires (allowing more sires selected). Omitting selection only had a minor effect on the effective size.

Keywords: *Effective population size, selection strategies, breed conservation.*

Introduction

The Norwegian horse populations, such as the Fjord, the Døle and the Nordland/Lyngen were traditionally working horses, but have during the last decades been used more frequently for sports and leisure, with strong competition in the market due to imported and specialised breeds (Olsen, et al., 2005). To stay competitive, the breeding organisations for the Fjord, the Døle and the Nordland/Lyngen and the Norwegian Equine Centre should modernise the breeding goals, and the current selection process should be modified according to new knowledge. Currently, the selection of sires in these breeds is based on the phenotype, from horse shows at 3 years of age (conformation and performance testing on the test day) for 1 year. A second selection decision is based on the extended test of functional traits at 4 years of age (conformation as well as performance, over a three-week period).

Both the Døle and the Nordland/Lyngen have been classified as "threatened – maintained" at the FAO's world watch list for domestic animal diversity, because of their small population size (FAO, 2000). Especially, the Fjord has experienced a large reduction in number of registered animals over the last decades, and is today of the same size as the two other populations, with somewhat more than 200 foals registered (all foals born can be registered) per year (Norsk Hestesenter, 2009). Due to mating with cold-blooded trotters in the Døle in the past, the genetic variation, as measured by the effective population size per generation (N_e), in the Døle has been larger than in the Nordland/Lyngen (Olsen et al., 2010).

Here, our goal was to calculate the effective population size per generation that would result from a simulation of a closed horse population with a variable number of born offspring per year (i.e. with variable census size, known to affect N_e; Falconer & Mackay, 1996), where mass selection is carried out or not and where a variable fraction of offspring is from sires selected in two stages: either as three-year-olds for the usage of 1 year and as four-year-olds for the usage of 4 years (with more

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offspring from three-year-old sires, more sires are selected, enhancing N_e (Falconer & Mackay, 1996).

Material and methods

A closed population with overlapping generations was simulated, with 100, 200 or 300 foals born per year (*N*). An overlapping female population was simulated as in Klemetsdal (1999), without selection. For males, selection was on phenotype, where a trait (the selection decision) was assumed to have a heritability of either 0.3 or 0 (no selection). Phenotypic values were simulated for all progenies, which for the *i*th progeny was:

$$y_i = u_i + \sigma_e z,$$

where u is the true (additive) breeding value, σ_e is the residual standard deviation and z represents a standard normal deviate. The true breeding value of the *i*th progeny was calculated as:

$$u_i = 0.5(u_s + u_d) + \sqrt{(0.5(1 - 0.5(F_s + F_d)))}\sigma_u z,$$

where u_s and u_d are the true additive breeding values of the sire and dam. The second term accounts for the Mendelian sampling effect, which is affected by the parents' inbreeding coefficients (*F*). Above, σ_u denotes the additive genetic standard deviation and z represents a standard normal deviate. The phenotypic standard deviation was unity.

The sires were selected in two stages: first on phenotype as three-year-olds and secondly as four-year-olds. Selection in the second stage was random amongst the sires selected at 3 years of age. By, respectively, assigning a mating quota of 1 year for three-year-olds and of 4 years for four-year-olds (Table I), and also by varying the fraction of three- to four-year-old sires, either 30 or 60% of the offspring was sired by the three-year-olds. The selected sires were mated at random to mares, although full–sib, sire–daughter or mother–son matings were not allowed. The base population spanned out for a total of 26 years (largest combination of age at first mating and reproductive life; see Klemetsdal, 1999), while offspring was generated for a total of 76 years (as in Klemetsdal, 1999) in 200 replicates, producing sufficiently small standard errors. In each replicate, the annual rates of inbreeding and genetic gain, as well as the generation intervals, were calculated on basis of individual inbreeding coefficients and true breeding values over the last 20 years of the simulation. Averages for the proportion of selected sires, size of progeny groups and number of selected sons per sire were calculated from 46 to 65 years (as in Klemetsdal, 1999; to ensure that sires had ended their reproductive life and also ensure that sons had reached their maximum age for first mating).

Table I. Cumulative distributions for number of mares mated by three-year-old sires and by older sires (≥4 years), in the Døle[a] (data spanning 1998–2008).

	Number of mares mated	Cumulative probability
Sires 3 years of age	8	0.61
	25	0.90
	43	0.98
	65	1.00
Sires ≥4 years of age	28	0.78
	92	0.95
	168	0.99
	208	1.00

Note: [a]Three-year-olds in the Døle mate 20.5% of the mares in real life.

Results and discussion

In general, the results are relevant for a programme where selection is carried out only amongst stallions, as in Norway, and in which all sires have their phenotype recorded. If recording is not complete, results for rates of genetic gain and inbreeding per generation would be smaller than what is generated.

Table II shows that 100 foals born per year result in an effective population size per generation considerably less than 100. However, effective sizes below 100 cannot be recommended for long-term conservation purposes, in which natural selection is assumed to counterbalance inbreeding depression of fitness traits (Klemetsdal, 1999). Increasing the number of foals born per year to 200 enlarged the effective population size to at least the recommended size in all situations (Table II). A considerable positive effect on effective size was also seen from increasing the fraction of offspring of three-year-old sires from 30 to 60%, while the effect of omitting selection was only minor. Selection produced genetic gain, reaching a maximum of 0.48 additive standard deviations per generation (in the situation where $N = 300$ and with 30% of the offspring from three-year-old sires).

The results show that at least 200 foals should be born and registered per year. This can, amongst others, be ensured by various political decision-making, as well as the breed adapting its selection practise to future market demand.

With enlargement of the fraction of offspring from three-year-old sires (from 30 to 60%), a larger number of sires are mating, each with smaller progeny group sizes (Table II). Actually, increasing the number of sires is a well-known approach to enlarge the effective population size (Falconer &

Table II. Simulation results (rate of genetic gain (ΔG), rate of inbreeding (ΔF), generation interval (L) between sires (s) or dams (d) and their sons (s) or daughters (d) and effective population size per generation (N_e)) obtained in breeding programmes[a] practising phenotypic selection on one trait (the selection decision) in three-year-old sires[b], assuming heritability (h^2) of either 0.3 or 0, in populations having either 100, 200 or 300 offspring born per year (N) and with either 30 or 60% of the offspring from three-year-old sires (70 or 40% from the 4 years and older sires, respectively).

	30% of offspring from three-year-olds			60% of offspring from three-year-olds		
	$N=100$	$N=200$	$N=300$	$N=100$	$N=200$	$N=300$
$h^2=0.3$						
ΔG/year[c]	0.02715	0.03099	0.03129	0.02550	0.02795	0.02765
ΔF/year[c]	0.00109	0.00062	0.00045	0.00088	0.00046	0.00032
L_{ss}	5.70	5.70	5.70	4.98	4.97	4.96
L_{sd}	5.79	5.81	5.82	5.02	5.03	5.01
L_{ds}	10.75	10.62	10.62	10.74	10.76	10.73
L_{dd}	11.15	11.10	11.10	11.12	11.09	11.11
N_e[d]	54	96	132	71	135	195
Percentage of selected sires	6.2	5.7	5.5	12.7	12.2	12.0
Number of progeny/sire	32	35	36	16	17	17
Number of selected sons/sire	1.8	1.8	1.8	2	2	2
$h^2=0.0$ (no selection)						
ΔG/year	0	0	0	0	0	0
ΔF/year	0.00095	0.00050	0.00034	0.00075	0.00041	0.00027
L_{ss}	5.76	5.76	5.79	5.02	5.02	5.02
L_{sd}	5.81	5.81	5.82	5.02	5.02	5.02
L_{ds}	11.05	11.13	11.13	11.09	11.07	11.10
L_{dd}	11.10	11.11	11.10	11.12	11.08	11.11
N_e	62	118	174	83	152	230
Percentage of selected sires	6.2	5.7	5.6	13.0	12.2	12.1
Number of progeny/sire	32	35	36	15	17	17
Number of selected sons/sire	1.8	1.7	1.7	1.9	2	2

Note: [a]Number of mated mares were as observed in the Døle.
[b]With random selection amongst these sires at 4 years of age (mating for 4 years).
[c]ΔG and ΔF: standard error $=(3.20\times10^{-4}$ to $5.24\times10^{-4})$ and $(6.23\times10^{-6}$ to $2.43\times10^{-5})$, respectively.
[d]$N_e=1/(2\times\Delta F/\text{year}\times L)$, where $L=\frac{1}{4}(L_{ss}+L_{sd}+L_{ds}+L_{dd})$.

Mackay, 1996), but it somewhat reduces genetic gain (Table II).

If sires were allowed to breed for a longer time span than the assumed 5 years, the breeding programme would change from one relying on phenotypic selection alone, to one that also allowed progeny testing. This would likely challenge the rate of inbreeding per generation (prolonged use of sires allows less sires selected per generation), and was thus not simulated.

Additionally to the factors examined, the effective population size per generation can be enlarged from restricting the number of selected sons per sire (e.g. Klemetsdal, 1999). Actually, the distribution for number of selected sons per sire was skewed (results not shown), meaning that mild restrictions would have the potential of increasing the effective population size beyond those obtained in Table II.

Conclusion

The native Norwegian horse breeds (Døle, Fjord and Nordland/Lyngen), practising phenotypic selection of sires at 3 years of age (for 1 year) and selection amongst these at 4 years of age (for 4 years), should be managed with 200 foals registered per year, ensuring an effective population size per generation of at least 100. For the observed distribution of number of mated mares per sire, the second most important factor in enlarging the effective population size is to keep a large fraction of offspring from three-year-old sires, as this ensures more sires being used. Omission of selection only enhanced effective population size to a minor degree.

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Paper III

Validation of alternative models in genetic evaluation of racing performance in North-Swedish and Norwegian cold-blooded trotters

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Validation of alternative models in genetic evaluation of racing performance in North-Swedish and Norwegian cold-blooded trotters

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Short title: Validation of alternative models in the cold-blooded trotter

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Key words: racing status, earnings, animal model, (co)variance components, cross-validation, horse, selected data

Summary

There have been several approaches to the estimation of breeding values of performance in trotters, and the objective of this study was to validate different alternatives for genetic evaluation of racing performance in the North-Swedish and Norwegian cold-blooded trotters. The current bivariate approach with the traits racing status (RACE) and earnings (EARN) was compared with a threshold-linear animal model and the univariate alternative with the performance trait only. The models were compared based on cross-validation of standardised earnings, using mean-squared errors of prediction (MSEP) and the correlation between the phenotype (Y) and the estimated breeding value (EBV). Despite possible effects of selection, a rather high estimate of heritability of EARN was found in our univariate analysis. The genetic trend estimate for EARN was clearly higher in the bivariate specification than in the univariate model, as a consequence of the considerable size of estimated heritability of RACE and its high correlation with EARN (~0.8). RACE is highly influenced by ancestry rather than the on-farm performance of the horse itself. Consequently, the use of RACE in the genetic analysis may inflate the genetic trend of EARN due to a double counting of pedigree information. Although, due to the higher predictive ability of the bivariate specification, the improved ranking of animals within a year-class and the inability to discriminate between models for genetic trend, we propose to base prediction of breeding values on the current bivariate model.

Introduction

Currently, the Norwegian and North-Swedish cold-blooded trotter populations can be considered as one single breeding population with common breeding value evaluation. Stallions have been used across the country border since the 1960's. The first joint breeding evaluation was published in 1994 (Svenska Travsportens Centralförbund & Det Norske Travselskap, 1994). Here, breeding values were calculated using a multi-trait animal model with four genetically correlated traits: racing status (raced = 1/not raced = 0), standardised earnings (within country and birth year), best racing time and percentage of races ranked as first or second (the last three performance traits were power transformed 0.25, 0.5 and 0.5, respectively. For power transformation, see e.g. Johnson and Wichern, 1982). For all traits, the model had fixed effects of birth year-country and sex. Normally, racing status is defined as raced if a horse has competed in at least one totalisator race before a certain age (Klemetsdal, 1989).

The racing status is not necessarily a biological trait of the individual, but rather a decision made by the owner, which may or may not have a biological basis. A horse may be started based on its on-farm performance, i.e. owners may avoid starting young horses showing poor trotting capacity. On the other hand, there is a risk that this decision is made based on expected racing performance (pedigree) rather than phenotypic performance on the horse itself, e.g. offspring of non-started parents may have a reduced probability of being taken to a race due to low expectations.

There have been several approaches to the estimation of breeding values of performance in trotters. Klemetsdal (1992) suggested that unraced horses should be viewed as having zero (rather than missing) earnings. The intention was to reduce the bias resulting from inclusion of raced horses only, which had been the practise when estimating breeding values for trotters (Klemetsdal, 1990). Árnason (1999) showed by simulation that the use of a multi-trait animal model, including racing status in the model and with missing performance for unraced horses, led to a substantially reduction of bias. Subsequently, this motivated a change of the genetic model used to genetically evaluate performance in several European trotter populations. In French trotters, Langlois & Vrijenhoek (2004) rejected the existing single trait animal model, in favour of a model based on career performance, including qualification status as an all-or-non trait. Bugislaus et al. (2005) also concluded that racing status should be included in a multi-trait animal model for racing performance in the German trotter, due to the contribution to reduction of bias. Langlois & Blouin (2007) stated that there was a need for a methodology to combine all-or-non traits with continuous traits, when the observations of the last are conditioned by the value of the first trait, to include unraced horses in the analysis.

Due to the sequential data structure of racing status and racing performance, i.e. that performance traits are only measurable for individuals that are started (racing status = 1), residual correlations between racing status and the performance traits are not identifiable. As a consequence, residual correlations are treated as neutral (Árnason, 1999). However, assuming a residual correlation of zero between two traits implies that there is a neutral coherence between the environments affecting the two traits.

The objective was to validate the current model used for genetic evaluation of racing performance in the North-Swedish and Norwegian cold-blooded trotters, based on summarized race records. An approach with racing status and one of the three racing performance traits; standardised earnings, was chosen. The current bivariate approach was compared with a threshold-linear animal model and the univariate alternative, which had been proposed in each country (utilising information on raced horses only (Árnason et al., 1989; Klemetsdal, 1989)). The models were compared based on cross-validation of standardised earnings, using mean-squared errors of prediction (MSEP) and the correlation between the phenotype (Y) and the estimated breeding value (EBV).

Material and methods

Data

Data were available on Norwegian and North-Swedish cold-blooded trotters born in the period 1971 to 2003, i.e. that the last year included with performance data was 2006. The data set included a total of 51,829 observations of racing status (raced or not) (RACE) and 22,825 observations of accumulated earnings, at 3-6 years of age (3-5, 3-4 and 3 years of age, for the three last year classes, respectively). Earnings were defined as EARN: Earnings of unraced individuals (with racing status of zero) considered as missing. Average earnings per race was transformed by fourth root and standardised by birth year and country.

A pedigree file with 98,861 animals was constructed. This file was made from all registered cold-blooded trotters in Norway and Sweden, with birth year ranging from 1849 to 2003. Table 1 shows summary statistics of the data.

Univariate animal model

The following univariate animal model was used to analyze RACE and EARN:

$$\mathbf{Y_1} = \mathbf{X_1 b_1} + \mathbf{Z_1 u_1} + \mathbf{e_1}$$

where $\mathbf{Y_1}$ is a vector of all observations on either RACE or EARN, $\mathbf{b_1}$ is a vector of fixed effects of birth year-country (66 classes) and sex (3 classes), $\mathbf{u_1}$ is a vector of additive genetic effects of all individuals in the pedigree, $\mathbf{e_1}$ is a vector of random residuals, and $\mathbf{X_1}$ and $\mathbf{Z_1}$ are the appropriate incidence matrices. Furthermore, $\mathbf{u_1} \sim N(\mathbf{0}, \mathbf{A}\sigma^2_{a1})$ and $\mathbf{e_1} \sim N(\mathbf{0}, \mathbf{I}\sigma^2_{e1})$, where **A** is the additive relationship matrix, **I** is an identity matrix of appropriate size and σ^2_{a1} and σ^2_{e1} are the additive genetic and residual variance, respectively.

Bivariate animal model

A bivariate animal model was used for analyzing RACE and EARN. The sub-model for EARN was identical to the univariate model, while the model for RACE (raced = 1, non-raced = 0) was either a linear or a logit model. The linear model was:

$$\mathbf{Y_2} = \mathbf{X_2 b_2} + \mathbf{Z_2 u_2} + \mathbf{e_2}$$

while the logit model for RACE was:

$$Pr(\mathbf{Y}_2) = \prod_{\mathrm{i}=1}^{\mathrm{N}} Bernoulli(\pi_{\mathrm{i}})$$

$$\pi_{\mathrm{i}} = \frac{exp(\eta_{\mathrm{i}})}{1 + exp(\eta_{\mathrm{i}})}$$

$$\boldsymbol{\eta} = [\eta_1 \quad \dots \quad \eta_{\mathrm{N}}]'$$

$$\boldsymbol{\eta} = \mathbf{X_2 b_2} + \mathbf{Z_2 u_2} \quad ,$$

where $\mathbf{Y_2}$ is a vector of all binary RACE observations, $\mathbf{b_2}$ is a vector of fixed effects (same effects as above), $\mathbf{u_2}$ is a vector of additive genetic effects of all individuals in the pedigree, $\mathbf{e_2}$ is a vector of random residuals, and $\mathbf{X_2}$ and $\mathbf{Z_2}$ are the appropriate incidence matrices, $\mathbf{u} = \begin{bmatrix} \mathbf{u_1}' & \mathbf{u_2}' \end{bmatrix}' \sim N(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$, where $\mathbf{G}$ is the (2 × 2) additive genetic (co)variance matrix, and $\mathbf{e}_2 \sim \mathrm{N}(\mathbf{0}, \mathbf{I}\sigma^2_{\mathrm{e2}})$.

Due to the sequential structure of data (earnings can only be observed for started horses), residual covariance between the two traits is not estimable. Hence, the two traits were assumed conditionally independent (given fixed and random effects).

Variance component estimation in cross-sectional binary data (one observation per animal) using animal-threshold models has been shown to cause bias (Hoeschele and Tier, 1995). Hence, variance components of the logit-linear model were based on transformed estimates from the univariate linear model for RACE. The linear model estimate was transformed to fit the underlying scale, using the following formula (Dempster and Lerner, 1950):

$$h^2_\lambda = h^2_y \left(\frac{p(1-p)}{z^2} \right)$$

where p is the proportion of individuals that race (0.44; see Table 1), and z is the ordinate in the truncation point for the proportion p in a standard normal distribution. Assuming a logit link function, the residual variance is $\pi^2/3$ and so the corresponding additive genetic variance, on the underlying scale, was approximated as $\pi^2 h_\lambda^2 / 3(1 - h_\lambda^2)$. In the bivariate analysis with a logit-linear model, the genetic variance component for RACE was fixed at this value. The genetic trend was transformed back to observable scale.

The ASReml software (Gilmour et al., 2006) was used in all genetic analyses.

Cross-validation

For EARN, a total of 25% of the observations over the period 1991-2000 (leaving out the three last year classes as these did not have racing information over 3-6 years of age), were randomly sampled into a validation data set. For the remaining data for EARN and RACE (the last only in the bivariate models), utilising pedigree information for all animals and the estimated variance components, effects of birth year, country and sex as well as animal solutions were computed for EARN, with the three models. The predictive ability of the models was examined by calculation of the mean-squared error of prediction (MSEP):

$$\mathrm{MSEP} = \frac{1}{n}\sum_{i=1}^{n}\left(Y_i - \hat{Y}\right)^2$$

where Y_i is the ith excluded observation and $\hat{Y}$ is the predicted value of that observation based on the remaining data set. Low MSEP values indicate high predictive ability of the model.

Additionally, the correlation between the deviation of the estimated breeding value within birth year and country and the observed Y_i of EARN (transformed and standardised) was calculated ($r_{Y,\,EBV*}$). Thus, this measure takes account of differences in genetic trend for EARN for the three alternative models. High correlation between the observed trait and the deviation of estimated breeding value indicate high predictive ability of breeding values.

Results

Estimates of genetic parameters, as well as validation parameters in the three different models, are shown in Table 2. Both validation parameters, MSEP values and $r_{Y,\,EBV*}$, somewhat favoured the linear-linear model over the linear-logit model, while the univariate model did worse for both parameters.

Analysing EARN with a univariate linear model resulted in a fairly high estimate of heritability of 0.31 (Table 2). Similar estimates were also obtained for EARN using the bivariate models (0.34 and 0.36, for linear-linear and linear-logit, respectively). Using the bivariate models, the heritability estimates for RACE were high both on the observed (0.31) and on the underlying scales (0.53). Furthermore, the estimated genetic correlations between RACE and EARN were also high, 0.84 and 0.77, for linear-linear and linear-logit, respectively.

Genetic trends for RACE using the different models are shown in Figure 1. For all models, genetic trends were favourable, but somewhat more expressed for the bivariate models. Genetic trends of EARN in the multitrait analyses were similar, while the trend for EARN from the univariate model was clearly different and generally lower, although still favourable (Figure 2).

Discussion

Genetic evaluation of horses has for a long time been carried out for ranks, through the use of earnings, normal scores or raw ranks (Ricard and Legarra, 2010). For trotters, earnings and raw ranks have been considered the most appropriate measures, with earnings being most commonly used (Tavernier, 1990), with the highest heritability for average earnings per start (Langlois, 1989). For ranks, the most sophisticated method is that of Tavernier (1990, 1991), utilizing ranks in single races, recently given a Bayesian implementation (Ricard and Legarra, 2010).

The bivariate specification of RACE and EARN was introduced to genetic evaluation of trotters by Árnason (1999) to account for possible selection in data, i.e. that raced horses may be viewed as a selected group (Klemetsdal, 1990). If not accounted for, selection in data is expected to lead to an underestimate of additive genetic variance. Despite possible effects of selection, a rather high estimate of heritability of EARN was found in our univariate analysis.

As expected a bivariate specification of RACE and EARN did slightly better in prediction of EARN than a univariate modeling. However, with the bivariate specification, the genetic trend estimate was clearly higher than in the univariate model.

This is a consequence of the considerable size of estimated heritability of RACE (of size 0.5 on the underlying scale) and its high correlation with EARN (~0.8), also showing favourable genetic trend (Figure 2). The considerable genetic correlation to EARN suggest that RACE should be a highly relevant trait in selection for improved racing performance (EARN). However, one may view RACE not as a biological trait *per se*, but rather a choice made by the owner, as indicated in the introduction. RACE may thus not only be determined by the true potential of the horse, but may also be highly influenced by the expected racing performance (based on performance of parents and other relatives) and/or a possible subdivision of the population (e.g. into horses used for trotting and recreational purposes). Therefore, RACE may actually act partially as a subpopulation indicator. Furthermore, both factors may explain the apparently high heritability of the trait as well as the high apparent genetic correlation between RACE and EARN (i.e. owners interested in trotting tend to choose horses that are offspring of raced parents with high earnings). Consequently, the use of RACE in the genetic analysis may inflate the genetic trend of EARN due to a double counting of pedigree information (as the racing status is likely influenced by ancestry). Actually, attempts were made to test for bias of genetic trend, by calculating the regression of the residuals of EARN from the different models, with sire as a fixed effect and the effect of year as independent variable, expressed as a deviate between progeny’s birth year and birth year of sire’s first progeny. However, no significant bias estimates were obtained, likely due to low power of these tests, as data for EARN are available on raced horses only (results not shown). One should also be aware that the heritabilities found for RACE in this study correspond well with values from other studies of this trait (Bugislaus et al., 2005; Langlois & Vrijenhoek, 2004), which is by far larger than those found in initial analysis of these traits (e.g. Árnason et al., 1989; Klemetsdal, 1989).

Attempts were made to reveal the true level of residual correlation between the two traits, by fixing the residual correlation at different values (positive). No differences in MSEP were found (results not shown), probably due to the bivariate model’s nature, which is adjusting all parameters accordingly. Thus, the residual correlation was set equal to zero in the analysis. Árnason et al. (2010) also analysed data with an equivalent model, when simulating with residual correlations from -0.5 – 0.5, and found underestimates of variances as well as genetic correlation for a positive residual correlation, and correspondingly overestimates for a negative residual correlation. From a practical point of view one could expect the residual correlation to be positive, i.e. an environment that is positive for the racing status of a horse will also be positive for the horse's earnings in the racing career. We have argued that the high estimates obtained in our study for the genetic correlation is due to preferential treatment.

Due to the higher predictive ability of the bivariate specification, the improved ranking of animals within a year-class and the inability to discriminate between models for genetic trend, we propose to base prediction of breeding values on the current bivariate model. In the animal model, the estimation of genetic (co)variance components relies, amongst others, on parent-offspring regression. Typically, environmental effects on parents and offspring are assumed to be uncorrelated. However, mares and their progeny are often kept in the same herd, and environmental similarities may thus exist over generations, which may inflate heritability estimates unless properly accounted for through a herd x maternal effect, as traditionally done in genetic evaluation of trotters in France (Tavernier, 1988). Additionally, racing performance is affected by environmental effects that have not been included in genetic evaluation so far, e.g. the owner effect. Another problem is the possible covariances between environment and expected breeding value. These are not easily accounted for, although Gómez et al. (2009) have proposed an interesting alternative. This illustrate that an improved modeling of environmental effects is needed to improve the knowledge on inheritance of racing performance in trotters. Furthermore, we assumed in our analysis that racing performance was the same trait over age classes, which may be in conflict with reality. The use of random regression models is a single trait approach to a multi-trait problem, that can preferably be used to model performance over age classes in competing horses (Posta et al., 2010; Posta et al., 2009; Buxadera and da Mota, 2008; Bugislaus et al., 2006). However, one could also consider to base future development on repeated records of ranks, by the proposal of Ricard and Legarra (2010).

Conclusion

Although RACE seemingly has high heritability and a highly favourable genetic correlation with EARN, there is a risk that inclusion of RACE in a joint genetic analysis inflates genetic trend estimates of EARN. This may be explained by RACE being highly influenced by ancestry rather than the on-farm performance of the horse itself. Despite these arguments, the results of this study for predictive ability points towards basing future genetic evaluations of the cold-blooded trotters in Norway and Sweden on the current bivariate approach, including both EARN and RACE.

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Table 1. Descriptive statistics of analysed data.

	Total	**Norway**	**Sweden**
# animals in pedigree	98861	-	-
# animals, raced or not	51829	32610	19219
- stallions	13128	9890	3238
- mares	24258	14506	9752
- geldings	14443	8214	6229
Fraction of raced horses	0.44	0.46	0.40
# animals with earnings	21178	14010	7168
- stallions	4189	3528	661
- mares	8822	5742	3080
- geldings	8167	4740	3427
Earnings per race (3-6 years)			
- min	0	0	0
- average	960	1051	804
- max	139167	139167	58641
Frequency of started non-earners	0.07	0.07	0.07

Table 2: Estimates of genetic parameters from univariate analysis of earnings (EARN = average earnings per start with unraced horses (racing status = 0) assigned a missing value , transformed by fourth root and standardised by birth year and country)) and bivariate analysis (linear-linear and linear-logit models) of EARN and racing status (RACE = binary trait, raced (1) or not (0)), as well as cross-validation parameters for the different models with respect to earnings; the mean squared error of prediction (MSEP) and the correlation between the deviation of the estimated breeding value within birth year-country and observed Y ($r_{Y,\ EBV*}$).

	Univariate EARN1	**Linear-linear EARN/RACE**	**Linear-logit EARN/RACE**
Genetic correlation	0	0.84	0.77
EARNINGS			
Genetic variance	0.32	0.37	0.41
Residual variance	0.72	0.72	0.72
Heritability	0.31	0.34	0.36
RACE			
Genetic variance	0.08	0.07	3.71$^{1)}$
Residual variance	0.16	0.17	3.29$^{1)}$
Heritability	0.33	0.31	0.53$^{1)}$
MSEP	0.931	0.925	0.926
$r_{Y,\ EBV*}$	0.2674	0.2776	0.2773

$^{1)}$ Estimates transformed to the underlying scale, from those obtained on the observable scale.

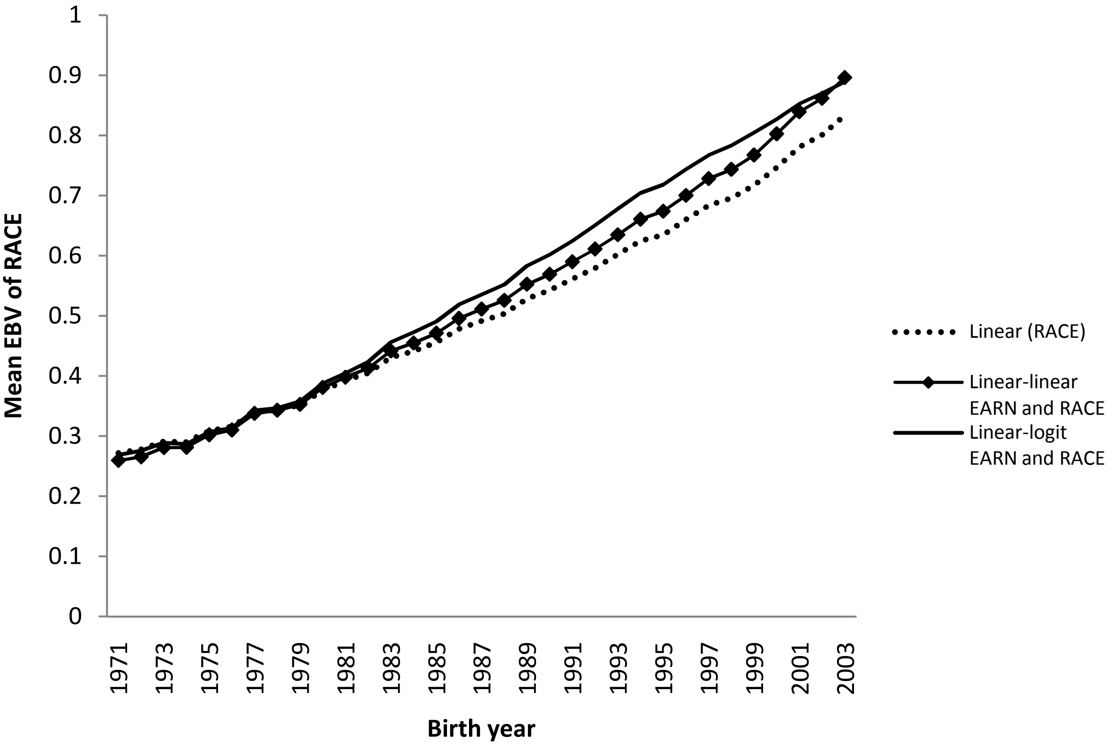

Figure 1: Genetic trend of racing status, RACE (binary trait, raced (1) or not (0)), given as the average of estimated breeding values (EBVs) per birth year in three models; univariate linear model for RACE and bivariate linear-linear and linear-logit models for EARN (average earnings per start, with unraced horses (racing status = 0) assigned a missing value, transformed by fourth root and standardised by birth year and country) and RACE.

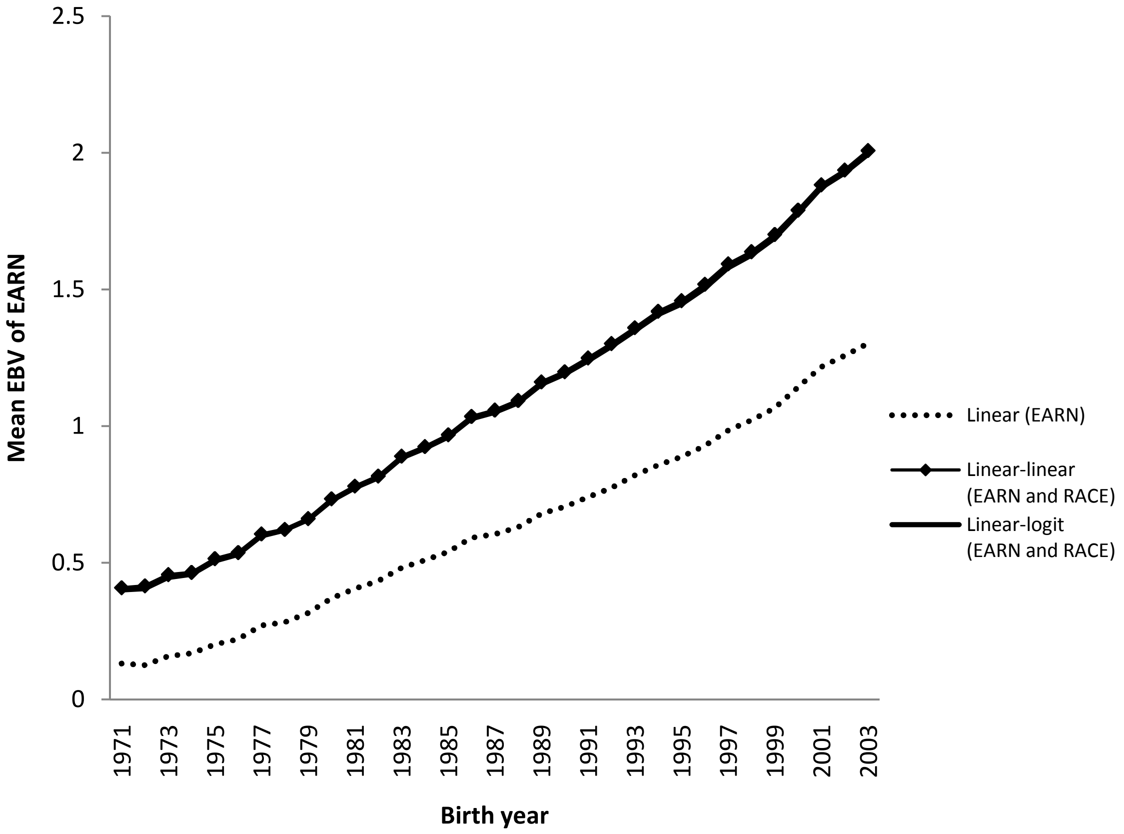

Figure 2: Genetic trend of earnings, EARN (average earnings per start with unraced horses (racing status = 0), assigned a missing value, transformed by fourth root and standardised by birth year and country), given as the average of estimated breeding values (EBVs) in three models; univariate linear for EARN and bivariate linear-linear and linear-logit models for EARN and RACE (binary trait, raced (1) or not (0)).

Paper IV

Recommendations for implementation of optimal contribution selection of the Norwegian and the North-Swedish cold-blooded trotter

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Recommendations for implementation of optimal contribution selection of the Norwegian and the North-Swedish cold-blooded trotter

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Key words: animal model, breeding program, horse, rate of inbreeding, selection response

Summary

The aim of this study was to apply optimal contribution selection (OCS), and from the results obtained, to recommend how OCS could be best used in future breeding of the Norwegian and the North-Swedish cold-blooded trotter. OCS was implemented using the software Gencont with overlapping generations, with assumptions for number of mated mares per sire, rate of inbreeding per generation and on the selection candidates. We concluded that OCS can be implemented in the Norwegian and the North-Swedish cold-blooded trotter, as a dynamic tool to both recruit young stallions as well as to assign annual breeding permit for earlier approved stallions. For number of mares per sire, a constraint in accordance with the maximum that a sire can mate naturally is recommended. Mare candidates can well be those that were mated the previous year, while the number of sire candidates need to be restricted from continuous recording of reliable information on death and gelding, as well as only considering as first-time candidates those between 3 and 10 years of age, with phenotype above average within a year class. The restriction on rate of inbreeding only had a minor effect on the selected animals.

Introduction

In year 2000, the trotting associations in Norway and Sweden signed an agreement to collaborate (Norsk Hestesenter, 2008), and consequently the Norwegian and North-Swedish trotter have the same breeding plan and joint breeding value estimation. To have a license for breeding, the stallions need to be approved at yearly horse shows; in which mostly their own phenotypic performance in races is considered, but also their body conformation, movements in trotting and temperament. In addition, there is a clinical veterinary examination of amongst others; testicles, teeth and legs, to detect disqualifying conditions as testicle rupture, sidebones or osteochondrosis. Additionally, a breeding value for trotting performance, multivariately for racing status, earnings, speed and placings, is calculated annually (Norsk Hestesenter, 2008). The selection decision is made by a joint selecting committee, with representatives from both countries. A stallion can be approved for breeding from the age of three years. The stallion is given a yearly mating quota of 110 mares (80 in his home country and 30 in the neighbouring country). An approval is valid for six years, after which the owner can apply for an indefinitely continuation. The stallion will in case be classified as elite-, A-, B- or C-stallion, depending on the performance of the offspring group. Thereafter, an approved stallion can only be culled if a disqualifying disorder is proven on the stallion himself or in many of his offspring. This means that many old stallions will be available for mating, having a negative impact on the population's inbreeding situation, due to their large number of progenies.

In the Norwegian cold-blooded trotter, Klemetsdal and Johnson (1989) estimated the effective population size to be only 32. The same authors also found that foaling rate and early abortion were affected by inbreeding depression. Some years later Klemetsdal (1993) described that the Norwegian trotter had a suboptimal breeding structure, causing the small effective population size, due to extreme length of reproductive life and large variation in the size of progeny groups of the sires. The following years, several reports were made on the effects of inbreeding; Dolvik and Klemetsdal (1994) reported an increased risk of arthritis in the carpal joints of the Norwegian trotter with increasing level of inbreeding, while Klemetsdal (1998) estimated that racing performance was depressed by inbreeding. To control the build-up of inbreeding, a change in the breeding structure was recommended, such as repeated selection for two year periods, with maximum 5 or 7 reselection rounds, a mating quota of 120 mares over two years and maximum of 6 or 10 selected sons (Klemetsdal, 1999). However, these suggestions of static selection rules have never been implemented. Later, Árnason (2001) concluded that the rate of inbreeding in the Nordic trotter was alarmingly high, and recommended to consider inbreeding when selecting for genetic improvement of racing performance.

Dynamic selection rules were invented by Wray and Goddard (1994), where a variable number of sires and matings per sire were calculated, increasing the response to selection, at a reduced level of inbreeding. The approach by Wray and Goddard (1994) was examined by simulation in trotters by Árnason (1996), as he compared selection on the object function with selection on breeding values estimated with an animal model. Klemetsdal (1999) pointed out that the method of Wray and Goddard (1994) did not guarantee a sufficient effective population size to prevent a decline in fitness, and that methods directly restricting the rate of inbreeding should be preferred, such as optimal contribution selection (OCS) (Meuwissen, 1997), which maximizes the response of selection at a predefined rate of inbreeding. However, few publications exist on experiences from implementing this method in live populations. Avendaño et al. (2003), implementing OCS in beef cattle and sheep, found that the largest increase in genetic gain was obtained when allowing selection to be carried out in both sexes. However, this lead to unrealistic reproductive rates for females, so that the most reasonable approximation was to allow for OCS only in males. Still, a substantial increase in genetic gain was obtained, but the authors pointed out the need for a coordinated breeding policy on the use of the selection candidates, to realize the benefits from the application. This conclusion was also supported by Kearney et al. (2004) and Colleau et al. (2004), in dairy cattle. Further, Colleau and Tribout (2008) found from use of OCS in pig breeding that 60% of the males selected by the procedure had already been culled by the breeders. In horses, Niemann et al. (2009) implemented OCS in the Hanoverian breeding program for show jumpers, and found, as expected, that the number of selected males decreased compared to the current breeding program, giving increased genetic gain, meanwhile the rate of inbreeding was stable. Koenig and Simianer (2006) also found 13% higher genetic gain when comparing OCS to the practical conventional selection scheme in the German Holstein dairy cattle population.

Given that breeding values is calculated with an animal model as for this population, the objective was to apply the optimal contribution selection, and from the results obtained, to recommend how OCS could be best utilised in future breeding of the Norwegian and the North-Swedish cold-blooded trotter.

Material and methods

Data used for the BLUP evaluations in the autumn of 2006 were used, consisting of 51,829 observations of individual, summarized race results for horses born 1971-2003. The later year classes were not included in this work, due to a considerable loss of data in the process of transferring data to a new data base, in Norsk Rikstoto in 2006. Estimated breeding values were calculated with a univariate animal model of annually, summarized, transformed and standardized earnings, with non-starters having missing information for earnings, as considered by Olsen et al. (2010b). A pedigree file of 98,861 animals was utilised, from the 97,411 animals registered in the period from 1846 to 2003.

Individual inbreeding coefficients were calculated using the Quaas-Henderson algorithm (Quaas, 1976; Henderson, 1976). The effective population size was calculated, as in Olsen et al. (2010a), either for animals born from 1982 to 1985 or animals born from 2000 to 2003 (at time t), by use of the formula:

$$N_{e_t} = \frac{1}{2\Delta F_t} \quad ,$$

where ΔF_t is:

$$\Delta F_t = \frac{1}{n}\sum_{i=1}^{n} \frac{F_i - \frac{1}{2}\left(F_{sire_i} + F_{dam_i}\right)}{1 - \frac{1}{2}\left(F_{sire_i} + F_{dam_i}\right)}$$

in which F_i is the individual coefficient of inbreeding of an animal i out of n animals born at time t, and F_{sire_i} and F_{dam_i} are the individual inbreeding coefficients of their parents.

OCS was implemented using the software Gencont (Meuwissen, 2002), for overlapping generations. In Gencont it is advised, for computational reasons, to restrict number of selection candidates to approximately 3000 animals (both sexes). As the majority of stallions of the cold-blooded trotter are approved for breeding before the age of 6 years (Figure 1), all young stallions (geldings excluded) of the age 3 to 6 years ($n_3 = 319$, $n_4 = 317$, $n_5 = 295$, $n_6 = 254$), that had raced, were included as selection candidates as well as all stallions approved for mating in real life in 2006 (n = 122). In total, 1307 stallions were considered as selection candidates. In addition, all mares actually mating in 2006 were included (n = 1816). The information about stallions which were approved and mares which were mated in 2006 was supplied by the trotting associations in Norway and Sweden, respectively.

In Gencont, with overlapping generations, there is a need to assign the animals to defined age classes, and more than 10 age classes is not recommended. Thus three-year classes were grouped together in age-classes as follows: 1-3 years, 4-6 years, 7-9 years, 10-12 years, 13-15 years, 16-18 years and 19 years or older, giving a total of 7 age classes. Consequently, the desired rate of inbreeding (ΔF_d) had to be calculated on an age class basis (= 3 years) as follows:

$$\Delta F_d = 3\Delta F_g / L$$

where ΔF_g is the rate of inbreeding that is accepted per generation (1%) and L is a predefined generation interval, assumed to be 11.1 years, according to Klemetsdal (1993).

One joint population in Norway and Sweden (NS) was considered. OCS of sires were calculated assuming; no limit on the number that a sire can mate (NS_nolim) and situations restricting the number of mated mares to 100 mares (NS_100), 60 mares (NS_60) and 30 mares (NS_30) (using the 'cmax' option in Gencont). Results were compared with that of the real life, stallions mating at least one mare in 2006 (NS_RL).

With a restricted number of mated mares per sire (NS_100 and NS_60), the effects of only accepting a rate of inbreeding per generation of 0.67% or 0.50% were examined. Results were compared with the corresponding results obtained for a rate of inbreeding per generation of 1%.

Finally, in practice OCS of the sires have to be calculated without knowledge as to which mares that will be mated in the relevant year. One option is to utilise as mares those being mated in the previous year (MARE_PREV, n=1711). The results were compared to those obtained with the mares actually mating in 2006 (MARE_2006). For the two mare alternatives, the number of mated mares per sire was restricted to 60 or 100, respectively.

Results

The Norwegian and North-Swedish cold-blooded trotter showed a steep increase in the level of inbreeding from the mid 1950's, for a period of approximately 30 years (Figure 2). In this period the effective population size was low, only 31 for the period 1982-85 (Table 1). Later, the inbreeding increased less steep (Figure 2), resulting in a somewhat higher effective population size for the period 2000-03 (54 individuals; Table 1).

Figure 3 shows the distribution of number of mated mares per stallion selected in 2006, when no limits were imposed on the number of mares that a sire can mate (NS_nolim), as well as the corresponding distribution obtained in real life (NS_RL). With NS_nolim, the number of mares per stallion was high for almost all selected stallions, as only 10 sires were selected; 3 of the stallions were given a mating quota less than 60 mares and the remaining 7 were supposed to mate more than 120 mares each (Figure 3). The highest mating quota assigned was 454 mares (not shown). In contrast, in real life 117 sires were selected and almost 90% of the stallions were mating less than 40 mares, covering almost 50% of the mated mares in 2006, whereas the remaining 10% of the stallions mated the last half of the mares (Figure 3).

Figure 4 shows the distribution of the age of the sires at mating for those selected in 2006, when imposing various restrictions on the number of mares that a sire can mate per year. With no limit on number of mares per stallion (NS_nolim), as much as 60% of the selected stallions were 6 years or younger. As expected, with genetic gain, this share increased somewhat from restricting the number of mares per stallions to 30 or 100 (66% and 68%, respectively). The maximum age of a selected stallion with the OCS procedure was 16 years, obtained in all three situations. However, in real life almost 60% of the stallions were 10 years or older (the oldest was 23 years old), while only 20% of the stallions were 6 years or younger (Figure 4).

Furthermore, Table 2 shows that OCS favoured Swedish stallions, relative to Norwegian ones, and the ratio Swedish/Norwegian increased with a less stringent restriction on the number of mares that a sire was allowed to mate. Further, OCS advised to select a number of stallions that were not approved in real life, and the fraction of non-approved stallions selected by OCS became larger for a smaller number of mares per sire. Generally, with OCS, genetic gain increased 30-40% relative to that in real life, with only a limited reduction in genetic gain for the smallest number of mares per sire. Likewise, change of the restriction on the rate of inbreeding from 1% per generation to 0.67% or 0.5%, corresponding to effective population sizes of 75 and 100, respectively, only had a minor impact on genetic gain, more so for the largest number of mares per sire (Tables 2 and 3). Actually, with the smallest number of mares per sire, the same sires were selected for different constraints on ΔF, meaning that the constraint was met by alteration of the contribution from each sire.

Table 4 shows similar results for number of sires selected and their average EBV when using as mares those mated the previous year (MARE_PREV) relative to those actually being mated. Table 5 supports this result, as MARE_2006 shows a rank correlation to MARE_PREV of 0.97.

Discussion

The rate of inbreeding in this population was larger up till 1990 than later. In the period 1982-85, the effective population size was calculated as 32, corresponding well with the estimate of 31 of Klemetsdal and Johnson (1989) in Norwegian trotter. Later (2000-03), the effective population size increased to 54, only marginally above the least recommended value of 50 individuals (Bijma, 2000). This increase of N_e is likely due to a change of the marginally most important ancestor; from Steggbest to Elding (Olsen and Klemetsdal, 2009), which has the potential to reduce ΔF temporarily. However, with large variation in progeny groups, as before, and no culling of sires on their contributions, the rate of inbreeding will eventually increase again. Thus, it is recommended to gain control over the general build-up of relationships in the population from minimising the average coancestry of parents and thus also the level of inbreeding of future generations by OCS (as for the Døle horse and Nordland/Lyngen pony, discussed by Olsen et al. (2010a)).

The estimated breeding values in this study were calculated using a univariate animal model of earnings, considered adequate with the goal of this study: to advice on how OCS should be utilised in breeding of the Norwegian and North-Swedish cold-blooded trotter, according to the discussion of the results of Olsen et al. (2010b). However, practical future implementation should obviously be based on the running breeding value estimation.

The OCS algorithm allowed for not more than approximately 3000 selection candidates. The results demonstrate that, for the selection of males by Gencont, mare candidates can well be chosen as those being mated the previous year (there is no selection on mares), although also some other mares will be used in practise. With as much as 1800 mares mated and the need for inclusion of already selected stallions, only 4 age classes of the youngest male candidates could be added. With this distribution of male candidates on age-classes and with a considerable genetic trend for the trait selected (Olsen et al., 2010b), obviously a majority of the selected stallions were 6 years or younger. With limitation on the number of male candidates, a continuous update of whether a male is gelded or dead will be important. Furthermore, for computational reasons, only inclusion of males with phenotype above average within a year-class would double the number of year-classes to be included with OCS. Yet, another alternative would be to implement an alternative algorithm allowing for a larger number of selection candidates (Hinrichs et al., 2006).

It is demonstrated that OCS increased genetic gain. Actually, with no restriction on number of mares per stallion, OCS selects quite few stallions, some with extremely large mating quotas. These mating quotas are far larger than can be covered by sires by natural mating, which is predominantly used in this population. However, as mean breeding values of selected sires were only marginally reduced by restricting the number of mares per sire, we recommend OCS calculated with a constraint on number of mares per sire in this population. One should also be aware of that this study only consider one year of selection, starting from a population with quite unbalanced coancestries. The assignment of mating quotas is thus expected to change over time, i.e. that smaller quotas may be assigned when the system becomes more balanced with respect to coancestry.

For all restrictions on number of mares per sire (but more so for the most stringent restriction), OCS advises to use a considerable fraction of non-approved sires. This fact illustrates that the OCS procedure includes stallions for breeding, which normally would not have been considered in real life. Thus, preferably the results from OCS could be used to propose which sires that are candidates for approval, i.e. that a practise with active recruitment of stallions for approval should be established.

Generally, OCS reduced the mean age of selected stallions, and did not in any situation assign a quota to a sire that was more than 16 years of age. Thus, OCS actively culls sires from breeding based on their previous genetic contributions. Therefore, it is recommended to establish a practise with an annual breeding permit for earlier approved stallions, if they are selected by OCS. Such a practise will be self-adjusting, as sires that are widely used one year will have a reduced probability of becoming reselected. The practise will complement the weakness of the current selection strategy: all approved sires are only classified in one out of five classes based on their progeny, i.e. that they can all be used for their entire lifetime, being harmful both for the average coancestry, rate of inbreeding and genetic gain in the population.

Conclusion

It is recommended to implement optimal contribution selection in future breeding of the Norwegian and North-Swedish cold-blooded trotter. Mare candidates used in Gencont for selecting sires can well be those that were mated the previous year, while the number of sire candidates need to be restricted from continuous recording of reliable information on death and gelding, as well as only considering as first-time candidates those between 3 and 10 years of age, with phenotype above average within a year class. The results from OCS are recommended to actively recruit first-time candidates for approval, as well as assignment of an annual breeding permit for earlier approved stallions. For number of mares per sire, a constraint in accordance with the maximum that a sire can mate in natural mating is recommended.

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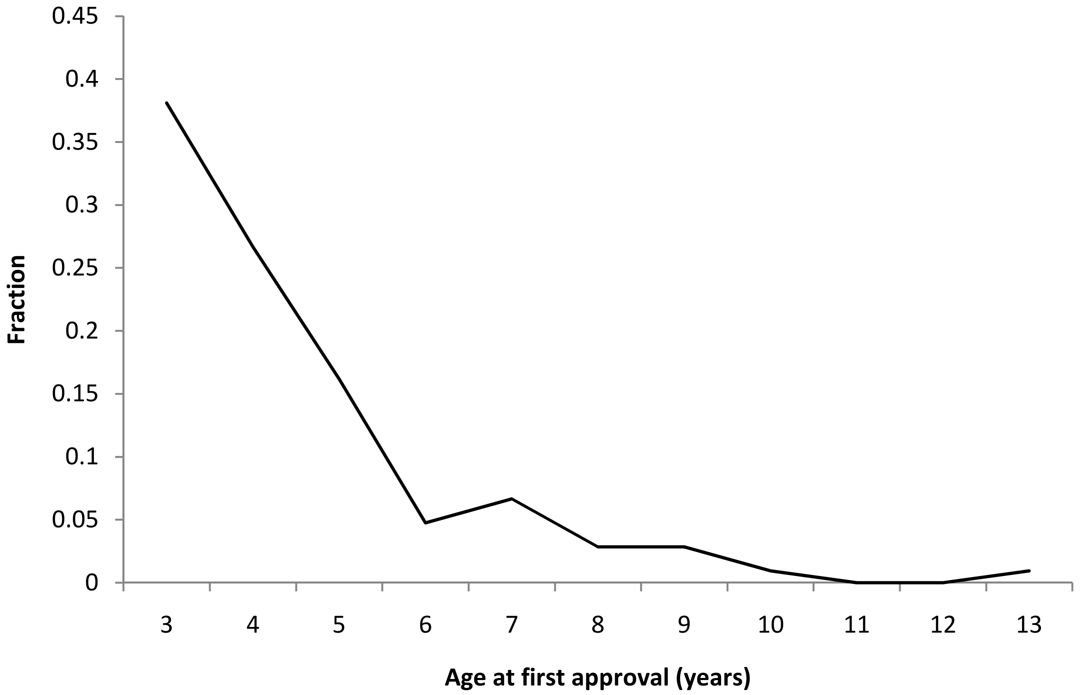

Fig. 1: Distribution of ages at first approval of stallions

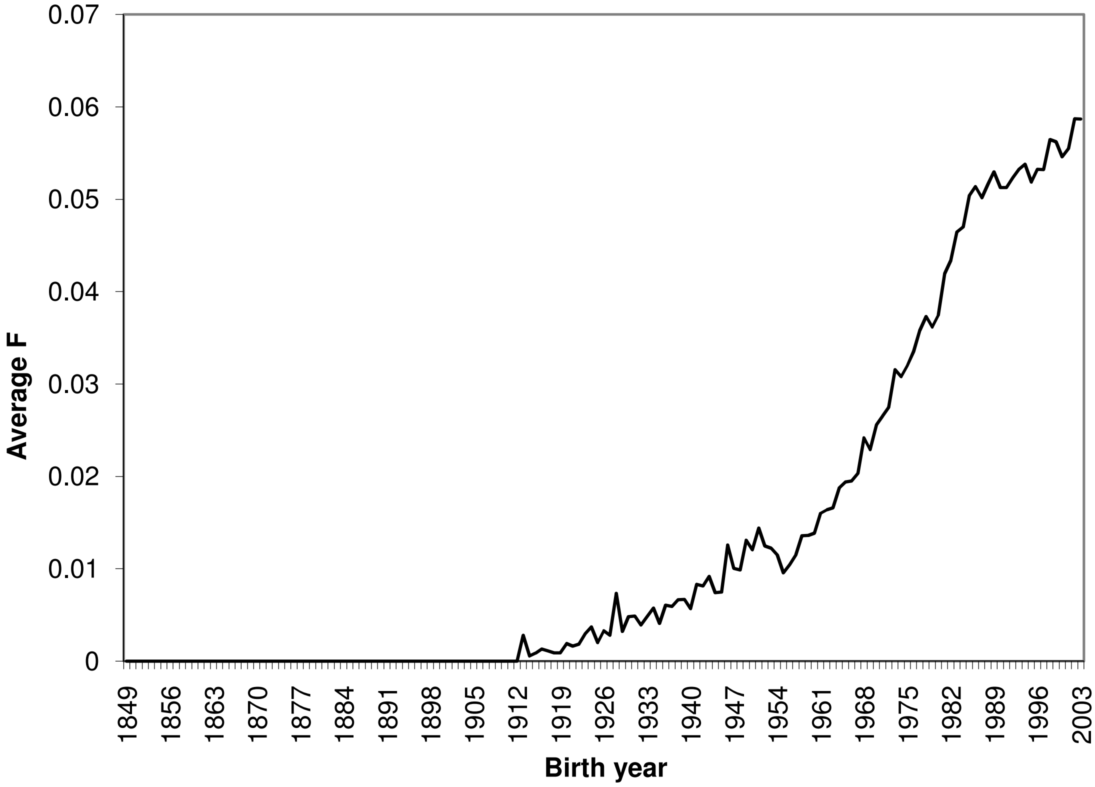

Fig. 2: Average coefficient of inbreeding (F) per year of birth.

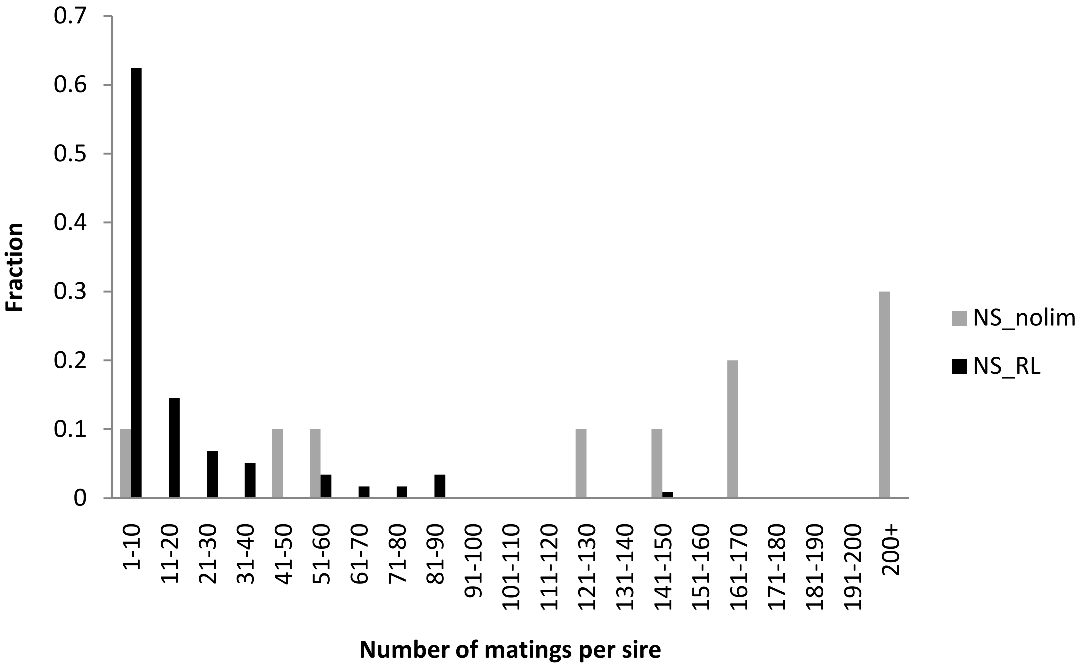

Fig. 3: Distribution of number of mated mares per sire for those selected/used in 2006, considering one population in Norway and Sweden (NS), by assuming no limit on number of mares that a sire can mate (nolim), as well as the corresponding distribution in real life (RL). With NS_nolim, the mares assumed were those that actually mated in 2006, and the constraint on rate of inbreeding was equivalent to 1% per generation.

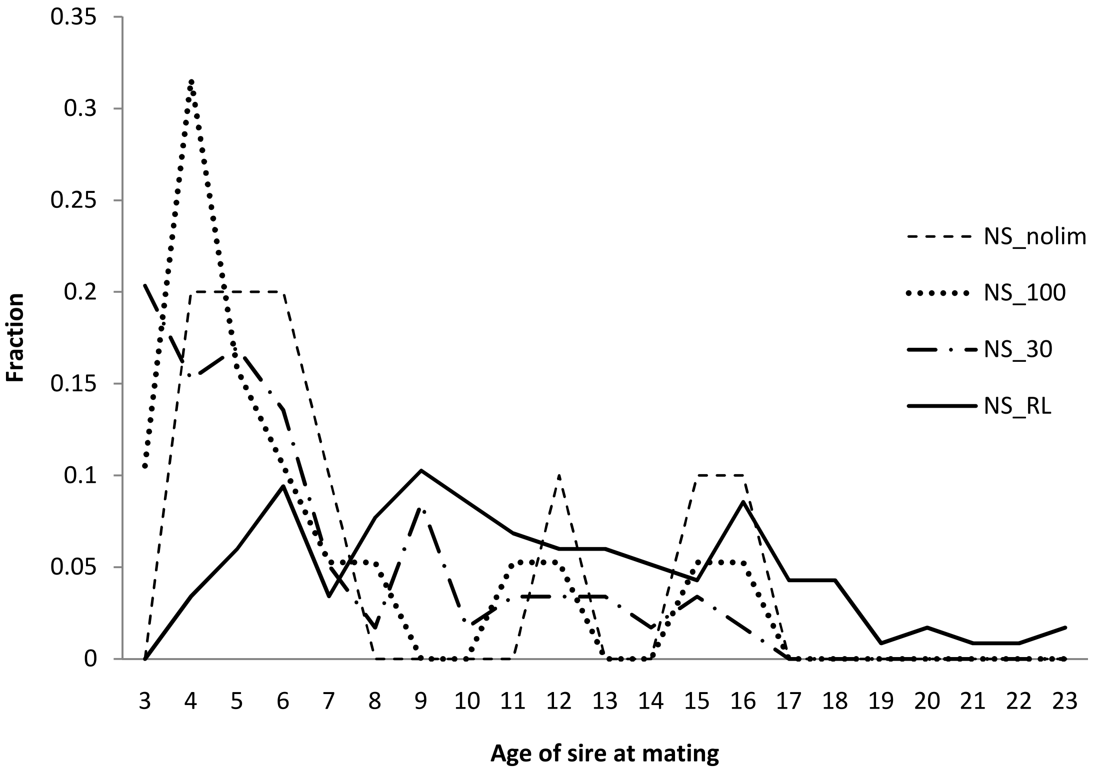

Fig. 4: Distribution of age of sire at mating for those selected/used in 2006, considering one population in Norway and Sweden (NS), by assuming various constraints on number of mares that a sire can mate (nolim, 100 and 30), as well as the corresponding distribution in real life (RL). With NS_nolim, NS_100 and NS_30, the mares assumed were those that actually mated in 2006, and the constraint on rate of inbreeding was equivalent to 1% per generation.

Table 1: Rate of inbreeding (ΔF) as well as the corresponding effective size in two time periods.

	1982-85	**2000-03**
ΔF ± s.e.	0.0161±0.0005	0.0093±0.0003
N_e	31±1	54±2

Table 2: Simple statistics for sires selected/used in 2006, considering one population in Norway and Sweden (NS), by assuming various constraints on number of mares that a sire can mate (nolim, 100, 60 and 30), as well as the corresponding statistics in real life (RL). With NS_nolim, NS_100, NS_60 and NS_30, the mares were those that actually mated in 2006, and the constraint on rate of inbreeding was 1% per generation.

	NS_RL	**NS_nolim**	**NS_100**	**NS_60**	**NS_30**
# sires	117	10	19	31	59
Mean # matings ± s.e.	17±2.3	182±45.2	96±7.4	59±1.4	31±0.1
Mean age ± s.e.	11.37±0.43	8.00±1.45	6.63±0.91	6.65±0.65	6.54±0.47
Fraction ≤6 yrs	0.19	0.60	0.68	0.65	0.66
Fraction ≥10 yrs	0.60	0.30	0.21	0.23	0.19
Fraction N/S[a]	0.79/0.21	0.60/0.40	0.68/0.32	0.68/0.32	0.71/0.29
Fraction used in RL	1.00	0.70	0.58	0.55	0.41
Fraction approved, not used in RL	0	0.20	0.16	0.13	0.19
Fraction non-approved	0	0.10	0.26	0.32	0.40
Mean EBV ± s.e.	1.55±0.04	2.16±0.15	2.17±0.10	2.10±0.08	2.01±0.05

[a] = ratio of selected stallions registered in Norway (N) or Sweden (S), respectively.

Table 3: Simple statistics for sires selected/used in 2006, considering one population in Norway and Sweden (NS), by assuming that the sire can mate either 100 or 60 mares, the mares were those that actually mated in 2006, and the constraint on rate of inbreeding (ΔF) was either 0.067 or 0.005 per generation, respectively.

	ΔF_{gen} = 0.067		**ΔF_{gen} = 0.005**	
	NS_100	*NS_60*	*NS_100*	*NS_60*
# sires	21	31	20	31
Mean # matings ± s.e.	87±9.0	59±1.4	91±8.5	59±1.4
Mean age ± s.e.	6.57±0.83	6.68±0.64	6.75±0.84	6.68±0.64
Fraction ≤6 yrs	0.67	0.65	0.70	0.65
Fraction ≥10 yrs	0.19	0.23	0.20	0.23
Fraction N/S[a]	0.71/0.29	0.71/0.29	0.65/0.35	0.71/0.29
Fraction used in RL	0.53	0.55	0.50	0.55
Fraction approved, not used in RL	0.14	0.10	0.15	0.10
Fraction non-approved	0.33	0.35	0.35	0.35
Mean EBV ± s.e.	2.10±0.09	2.08±0.08	1.95±0.13	2.08±0.08

[a] = ratio of selected stallions registered in Norway (N) or Sweden (S), respectively.

Table 4: Number and mean EBV of sires selected in 2006, considering one population in Norway and Sweden (NS), by assuming that sires can mate either 100 or 60 mares per year and that the mares mated were either those actually mated (MARE_2006) or those mated the previous year (MARE_PREV). The constraint on rate of inbreeding was 1% per generation.

	MARE_2006	**MARE_PREV**
NS_100		
# sires	19	17
Mean EBV ± s.e.	2.17±0.10	2.15±0.12
NS_60		
# sires	31	29
Mean EBV ± s.e.	2.10±0.08	2.10±0.08

Table 5:Pearson (above the diagonal) and rank correlation for number of matings per sire, for those sires being selected in 2006, considering one population in Norway and Sweden, by assuming that sires can mate 100 mares per year and that the mares were either those mated (MARE_2006) or those mated the previous year (MARE_PREV). The constraint on rate of inbreeding was 1% per generation.

	MARE_2006	**MARE_PREV**
MARE_2006	1	0.9955
MARE_PREV	0.9755	1

General discussion

The Norwegian horse breeds, here represented by the Døle, the Nordland/Lyngen pony and the cold-blooded trotter, have challenges with genetic variation, as discussed in Paper I and Paper IV. In the Døle horse, attempts have been made to reduce the rate of inbreeding, as discussed in Paper I, by crossing with both cold-blooded trotters (from the 1950's) and North-Swedish draught horse (from year 2000), but despite these initiatives, the build-up of relationship in the population still increases (Farestveit, 2009). In the Nordland/Lyngen pony the recent focus has been to increase the use of younger, approved stallions, which ensures low variation in progeny group size and so reduces the build-up of relationship, as advised in Paper II. From 2011, the Nordland/Lyngen has proposed a lifetime quota of 40 mares per stallion, in which they can only mate a maximum of 25% of the mares in their first breeding season (Norwegian Equine Centre, 2010). The genetic variation of the cold-blooded trotter is also threatened, as discussed in Paper IV. As the long-term use of the stallions is not controlled, a future rapid build-up of relationship in the population is expected, due to too heavy use of some stallions (e.g. Elding). In the cold-blooded trotter individual inbreeding coefficients are published as well as breeding values, otherwise there is no monitoring in any of the populations as regards the general build-up of relationship, neither are there systematically registrations of fertility, which would be important to inspect in these populations, especially if one take into consideration the last years with downwards trends both in number of mated mares per breed and year and the generally low foaling rate, as exposed in Figure 1 and 2 in the general introduction.

To maintain genetic variation in the Norwegian horse breeds a proper selection tool like optimal contribution selection (OCS) needs to be implemented. Such a selection procedure allows for genetic progress with a predefined constraint on the rate of inbreeding (Meuwissen, 1997). The application of the method in the joint Norwegian and Swedish cold-blooded trotter population, in Paper IV, shows that this selection method will both recruit young and cull older stallions from breeding, as also recommended in Paper II. The work also shows that individual or maximum mating quotas for stallions are not crucial, as OCS anyway cull stallions that have had too many offspring, just earlier in life.

In Paper IV, OCS was applied with a univariate model for earnings, while Paper III shows an enlarged genetic trend for the same trait, when also utilising information on start status in the BLUP evaluation. Thus, if information on start status is utilised in genetic evaluation together with other performance traits, it is expected that young sires will have an even larger contribution, as a group, than in our univariate approach. Further, when Paper IV shows that implementation of OCS is feasible with a large population as the Norwegian and the North-Swedish trotters it can also easily be applied in the three smaller Norwegian breeds. The Nordland/Lyngen has proposed to introduce mating quotas from 2011, and should, hence, adapt OCS rather than relying on static selection rules, as proposed. In the cold-blooded trotter one may anticipate reluctance towards culling of sires by OCS. However, these sires have contributed enough given their genetic potential, for the given rate of inbreeding. Actually, they are replaced by a group of younger sires that, as a group, is genetically superior, even though their individual breeding values are less accurate, resulting in larger genetic gain. An enlarged genetic gain for a controlled rate of inbreeding, will also ensure that the Norwegian and North-Swedish trotter will be superior to the Finnish trotter, which will give no scientific argument for crossing with the Finnhorse trotter, as earlier has been an issue of discussion (Klemetsdal, 1998). So implementation of OCS will also as such contribute to conservation of the genetic resource represented by the Norwegian and the North-Swedish trotter.

In a not too far future historical effective population size might be more correctly estimated from utilizing marker data than from pedigree information (Hayes et al., 2003). The DNA from hair roots, sampled for the current paternity control, can be used for this purpose, although these samples give lower quality of the prepared DNA (Mikko et al., 2010). The release of the Illumina Equine SNP50 BeadChip® has increased the potential for genomic analysis of the equine genome (Corbin et al., 2010). In Norwegian Standardbred trotters, several SNPs associated with OCD have been identified applying the Illumina Equine SNP50 BeadChip® for genome-wide association study of osteochondritis dissecans (OCD) in horses (Lykkjen et al., 2010).. Similarly, a genome scan study in Thoroughbred horses has discovered candidate athletic-performance genes within regions targeted by selection, principally responsible for fatty acid oxidation, increased insulin sensitivity and muscle strength (Gu et al., 2009). Genomic selection is also gradually implemented in several breeding programs, mainly dairy, but for the time being it is not widely explored in horse breeding, but there is a potential in combining genomic selection with selection on phenotypes or corresponding breeding values. For instance, Sitzenstock et al. (2010) showed the potential for combining genomic selection in a functional trait together with a conventional breeding program selecting for performance traits.

Future management of the Norwegian horse breeds has to be long-termed and structured, to fulfil the terms of responsibility, as stated in the UN's convention for biological diversity. The responsibility is undoubtedly placed on the Ministry of Agriculture and Food, and the belonging operating organs: the Norwegian Genetic Resources Centre and the Norwegian Equine Centre. Until now, monitoring of the inbreeding situation has only been done through the work presented in Paper I and Paper IV, the earlier work of Vangen (1983) and two master theses at UMB in 2009 (Seilen and Johnsen, 2009; Farestveit, 2009). In addition, Norwegian horse breeds have to cope with serious competition from other international breeds like for instance the Icelandic horse and different pony breeds, in which many are specialized in their sports activities, which contributes to a relatively rapid decline of the population sizes. The situation calls for an overall strategic plan of action for future management of the Norwegian horse breeds, to ensure proper initiatives and financial funds. Such a plan should include initiatives that ensure the three corner stones in future Norwegian horse production; product development, product quality and marketing, which is needed to increase the profitability of these horse breeds and to ensure the population sizes and thereby being the best long-term strategy for conservation and survival of these breeds (Meuwissen, 2009). Such a strategy needs to be supported by other long-term management strategies like cryo-conservation for back-up, and possible cryo-aided breeding programs.

According to the results shown in Paper II, it was recommended that at least 200 foals were born per breed annually. The numbers received from the Norwegian Equine Centre in October 2010 show that the Døle (179), the Fjord (177) and the Nordland/Lyngen (77) had less than 200 born foals (registered) in 2009. The number for Nordland/Lyngen is alarmingly low.

To increase the population sizes, these breeds have to enhance their demand in the market. Future demand is characterised by being in the market for leisure and sport, of that of young people. In Iceland, they realised this development several decades ago, and has met this by inventing a sport event in which the equipage can compete towards others, taking advantage of the natural preference of the breed (the gaits; pace and especially toelt). The product has been refined and developed through selective breeding, making the Icelandic Toelter one important export product in Iceland. To learn from the Icelandic experience, each Norwegian breed needs to develop its own sport or activity that take preference of the natural advantages of each specific breed, acting as a signature for the breed. The Døle is expected to have advantages for instance as a heavy draught horse, the Fjord as well-suited for riding in rough terrain and the Nordland/Lyngen as a small, but strong, riding horse, due to their origin and history. With the strength of each breed agreed, the breeding goal can be refined and breeding can be used as a mean to strengthen this advantage (product development) and thus strengthen the competitive edge for these breeds. Thus, sport has to be integrated with selective breeding and through the sport the aim is also to collect data on relevant performance traits. The sport or activity for each breed needs to be organised such that it has a natural progression in difficulty with age.

Currently, for Døle, Fjord and Nordland/Lyngen, selection of stallions is based on the results from the horse shows (at 3-years of age) and also from the extended test of usage traits (at 4-years of age). However, pre-selection of young stallions is strong, resulting in low participation at horse shows (< 10% of born stallions) as 3-years olds (Olsen et al., 2005b). Thus, to increase selection intensity there is a need for methods that ideally record the relevant information for all young horses. By integrating a sport activity in the horse shows, it should be possible to combine competition with recording of important traits in the breeding goal, amongst others traits in the temperament complex, ideally for all horses in an age class, one to three years olds, in contrast with now only from 3-years olds. This will also allow for progeny testing at a low age of sires. The temperament complex contains traits that are common for the horse breeds and regarded as very important for the over-all use of the horses. Other traits important to horse breeding are; defects, that can preferably be recorded by veterinarians at identification of foals; health traits, that should at least be recorded only once in a lifetime (as a prevalence), preferably integrated in the horse shows as now, and also fertility, as earlier mentioned.

For each foal born, there is a need to ensure the highest possible quality of the final product, by optimal training, nutrition and health care. In this respect, an initiative has been taken by the breeding organizations of the Døle, the Fjord and the

Nordland/Lyngen, as well as the Norwegian Equine Centre to educate owners to raise young horses, as an attempt to serve the market with educated horses, as well as the fact that trained horses also are good ambassadors for the breeds. This initiative is at current financed by the breeding organizations, with breeding stimulating funds from the Norwegian Equine Centre. The initiative needs further development regarding product and quality development, and should be part of an overall strategic plan of action.

A similar training programme have been initiated by the Norwegian Trotting Association, with the aim to stimulate early training and investment in young horses, and by this contribute to an increased starting frequency. The starting frequency was earlier likely influenced positively by introduction of qualifying races, as shown for 3-years olds in Klemetsdal (1994). The starting frequency up till 4-years of age in cold-blooded trotters in Norway has been somewhat fluctuating, but was just below 35% in 2009 (DNT, 2009), compared to approximately 50% in 1975 (Klemetsdal, 1994). The higher number of foals born recently than in the 1970's, as mentioned in the general introduction, and the fact that today, only 40% of the races are prioritised for the cold-blooded trotter (Tron Gravdal, pers. comm.), probably explains how the frequency of raced horses within a year class has been pushed downwards. So, there is likely bred a surplus of cold-blooded trotters within Norway today.

Marketing needs to be directed towards both existing and new segments in the market, as many people have little knowledge about these breeds, their qualities and range of use. In a marketing strategy it is important to focus on each breed's qualities. Examples of such qualities is as mentioned before; the Døle as a heavy draught horse within work, sport and tourism, the Fjord as a riding horse in rough terrain for instance as an extreme sport or within leisure and tourism, and the Nordland/Lyngen as a small, but strong and bright, riding horse for various activities within sports, leisure and tourism. The goal is to create and market the Norwegian horse breeds as "branded goods", which is associated with quality, competence, safety and Norwegian nature. The tools should be professional image building in combination with targeted use of internet and social media, news paper articles and productions for television and radio. In addition, there should be targeted use of Norwegian horse breeds in educational establishments, such as the Norwegian Equine Centre. These initiatives would also have some relevance for the cold-blooded trotter, even though this breed is somewhat different from the other three breeds as it is already bound up towards trotting. As mentioned, there is already an overcapacity in number of born cold-blooded trotters, so there is no need to increase the population size further. Many of the non-raced trotters are sold out as low-priced "left-overs". This is not positive for an over-all marketing of the Norwegian breeds, and should be handled through proper initiatives in the Norwegian Trotting Association.

Conclusion

The horse is becoming more and more important in our society, both as a sports and leisure companion and as a health worker. The demand for horses is growing, but unfortunately the Norwegian horse breeds suffer from the strong competition in the market from imported, specialized breeds. The study points out that future management of the Norwegian horse breeds should focus to increase the population sizes through ensuring the three corner stones; product development, product quality and marketing, which is needed to ensure the profitability of these horse breeds. The future breeding goals of the breeds must reflect the area of use, defined according to the demand in the market, to face the increasing competition from imported breeds. At least 200 foals needs to be born (and registered) per year in each breed, which is equivalent to more than 300 mated mares per year. This is a considerable challenge for the Døle, the Fjord and the Nordland/Lyngen, which calls for a strategic plan of action. For the cold-blooded trotter similar initiatives are not needed, as this breed is maintained trough the races, by assigning a sufficient share of races for the breed. For all breeds, future management should include a long-term breeding programme which properly balances between genetic gain and rate of inbreeding. All the breeds are recommended to implement optimal contribution selection (OCS) as a tool for maintaining genetic variation, ensuring active recruitment of young stallions and culling of older stallions with already large, genetic contributions to the population.

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