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Impact of reproduction technologies on horse breeding programmes

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Abstract

In this study, the effect of artificial insemination (AI) and embryo transfer (ET) on the genetic response in show-jumping performance and inbreeding rate has been simulated. The effect of the number of sires has been evaluated in one-stage selection schemes that differed in population size and testing capacity. Compared to a situation with natural service, AI increased genetic response much more than ET. It is suggested that with large testing capacities, the systematic use of AI can minimise the use of progeny testing. This study also illustrated the complexity of predicting inbreeding rates in actual horse breeding populations under BLUP selection. Predicted inbreeding rates were in almost all situations below critical levels in closed populations with equal progeny group sizes. However, these predictions are likely to be biased as progeny group sizes are skewed in practice and breeding populations are less closed than assumed.

1. Introduction

The aim of horse breeding programmes is to improve performance, conformation and health traits by genetic selection. Advanced reproduction techniques such as artificial insemination (AI) and, more recently, embryo transfer (ET) have increasingly been used to increase selection efficiency. The use of AI (chilled or frozen semen) has now become standard technology (>80%) in the majority of the warmblood riding horse populations. The number of inseminated mares per stallion and season varies substantially within and across organisations: some stallions produce a few thousands inseminations in their entire breeding career. With ET (fresh or frozen embryos) mares can produce about six foals within three years compared with two without ET (Squires *et al.*, 2003; Strojek-Baunack, 2005). The current frequency of ET in horse breeding is high in Brazil and USA, but very low in Europe with a few hundreds of transferred embryos (Thibier, 2004).

The annual genetic response (R) of a breeding programme is a function of the selection intensity, accuracy of selection and generation interval (e.g. Rendel and Robertson, 1950). With AI and ET, breeders can increase the selection intensity as fewer breeding animals (especially stallions) are needed to produce the next generation. As a consequence of the larger offspring groups, the accuracy of estimated breeding values increases as more offspring and/or sib information can be used. With ET, mares can reproduce while continuing sport competition performance which can increase the information on selection candidates (higher accuracy) and/or the total number of selection candidates (increased selection intensity).

An important task of a breeding organisation is to design efficient testing, evaluation and selection procedures. While many studies on the optimisation of livestock breeding programmes have focussed on maximising genetic response, more recent studies also considered inbreeding rates (ΔF) (e.g. Van Arendonk and Bijma, 2003). More information on the simultaneous effects of AI and ET on R and ΔF is helpful to optimise sustainable horse breeding programmes, especially for small closed breeding populations. Hence, the aim of this study was to quantify the effects of AI and ET on R and ΔF .

2. Methods

2.1. Breeding programmes

A series of breeding programmes for jumping horses using natural service (NS), AI and ET were modelled. These programmes mainly differed in the number of parents, size of offspring groups and number of tested and selected horses (Table 1). The NS breeding programme included a population of 500 stallions and 10,000 mares. Stallions and mares had a breeding life of 6 years. With a foaling rate of 66% every sire and dam produced in total 80 and 4 offspring in this period, respectively. In the three AI programmes, the number of sires was decreased from 200 to 80, i.e. serving 50 to 125 mares per year, respectively.

In the ET programmes, a proportion of the dams (ET donor mares) produced 12 ET foals in their breeding career, i.e. three times more foals than naturally reproducing mares. The ET-1 and ET-2 alternatives included 500 and 1000 donor mares, respectively. Although the number of foal-producing mares in the population remained 10,000, the number of effective dams was lower than without ET (9000 and 8000, respectively). It was assumed that the ET programmes routinely applied AI with 140 sires.

Discrete generations were assumed: i.e. breeding animals produced in total 40,000 foals in 6 years before parents of the next generation were selected. Only tested horses could be selected; 5% of all stallions born and 90% of all mares born were tested in competition at the age of 4 years. This means that in every 6-year period 1000 stallions and 18,000 mares were available for selection. The number of tested halfsibs per selection candidates increased per year. The model calculations were based on the average number of tested halfsibs. For example, in the NS programme the number of tested male and female offspring per sire increased from 0.33 and 6 (after year 1) to 2 and 36 (after year 6), respectively. This implies that a selection candidate had on average approximately 21 tested halfsibs $((6.33+38)/2-1)$.

Table 1. Model parameters used in the breeding programme models for natural service (NS), artificial insemination (AI) and embryo transfer (ET)

Parameter	NS	AI-1	AI-2	AI-3	ET-1	ET-2
<i>Parents</i>						
No. dams	10,000	10,000	10,000	10,000	9000	8000
No. sires	500	200	140	80	140	140
Yearly no. mares served per sire	20	50	71	125	64	57
<i>Offspring</i>						
Total no. per sire	80	200	285	500	285	285
Total no. per dam (average)	4	4	4	4	4.4	5
<i>Selection candidates</i>						
Percentage selected (males / females)	50 / 56	20 / 56	14 / 56	8 / 56	14 / 50	14 / 44
Average no. tested halfsibs	21	54	78	138	78	78

2.2. Prediction of genetic response and inbreeding rate

The breeding goal only included performance in show-jumping competition (heritability = 0.15). The selection index combined BLUP breeding values of the parents and competition results of the selection candidate and its half sibs. All foals by the same sire were assumed to be half sibs. Selection responses and ΔF were predicted by a deterministic simulation of a one-stage selection scheme using the SelAction software (Rutten *et al.*, 2002).

In a sensitivity analysis, two parameters of the AI/ET based breeding programmes were varied to study the effect on R and ΔF . First, the number of mares was varied simulating either small horse populations or larger, opening up populations which import genetic material. Secondly, the percentage of horses tested was varied to study the effect of higher selection intensities.

3. Results

3.1. Effects on genetic response and inbreeding rate

Table 2 shows predicted R in the various breeding programme alternatives.

With NS, R is 0.330 genetic standard deviations per generation of which just over 50% originates from the male selection path. With fewer sires, the (slightly) more accurate breeding values and higher selection intensities in the male selection path increased R substantially. In the alternative with only 80 sires (AI-3), R is 83% higher compared to the NS situation. Table 2 also shows that with fewer sires (increased number of offspring per sire) ΔF increases from 0.038% per generation with 500 stallions (NS) to 0.419% with 80 stallions (AI-3).

As the ET programmes already used 140 AI-sires, predicted results of ET-1 and ET-2 should be compared to the AI-2 results. The effects of ET on R and ΔF are much smaller than the effects of AI. In ET-2 (8000 mares), R increased slightly from 0.531 to 0.570 (+7%) and ΔF increased from 0.202% to 0.224% (+11%).

Table 2. Selection accuracy, response (R) and inbreeding rate (ΔF) per generation for the NS, AI and ET alternatives.

	accuracy	R (genetic standard deviations)			ΔF (%)
		sires	dams	total	
NS (500 ♂)	0.469	0.176	0.155	0.330 (= 100%)	0.038
AI-1 (200 ♂)	0.494	0.319	0.161	0.480 (= 145%)	0.127
AI-2 (140 ♂)	0.504	0.368	0.163	0.531 (= 161%)	0.202
AI-3 (80 ♂)	0.517	0.438	0.166	0.604 (= 183%)	0.419
ET-1 (9000 ♀)	0.502	0.366	0.184	0.550 (= 166%)	0.212
ET-2 (8000 ♀)	0.501	0.365	0.206	0.570 (= 173%)	0.224

3.2. Sensitivity analysis: effects of population size and testing capacity

With a population size of 10,000 dams, R can be more than doubled when reducing the number of sires from 500 (NS) to 50 or less (Figure 1). The relative increase in R is larger in smaller breeding programmes: e.g. R could be increased from 0.167 (500 sires) to 0.575 (50 sires) in a population of 5000 mares (+344%). In smaller populations, a decrease of the number of sires (with as a result more tested offspring per sire) has a relative larger effect on the selection intensity and the accuracy.

At the same time, ΔF increases dramatically when less than 100 sires are used. When 50 or less sires are used (i.e. the number of matings per sire ranged from 100 to 500), ΔF exceeds 1%.

Figure 1. Effect of number of sires on genetic response R (left) and inbreeding rate ΔF (right) with a breeding population of 5000 (.....), 10,000 (—) and 25,000 (- - -) mares.

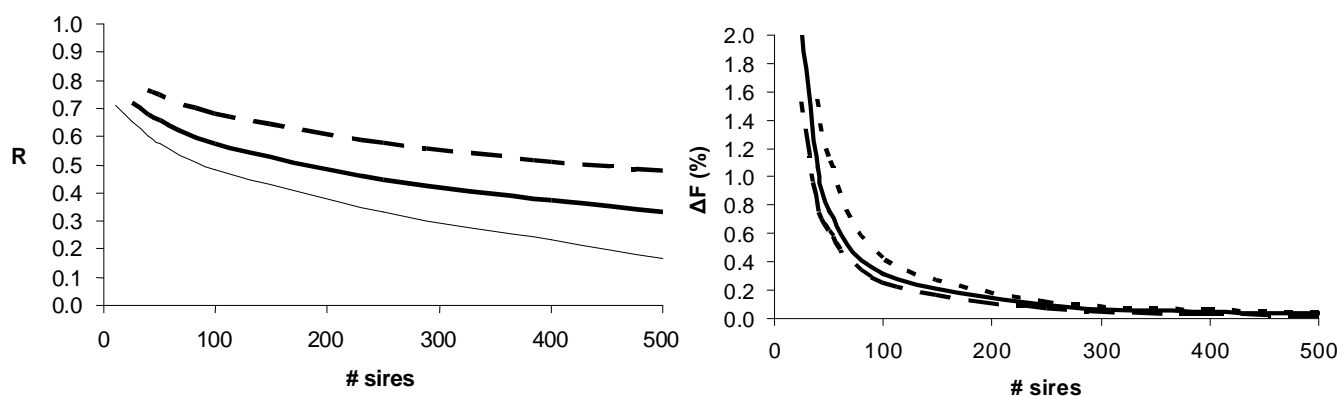
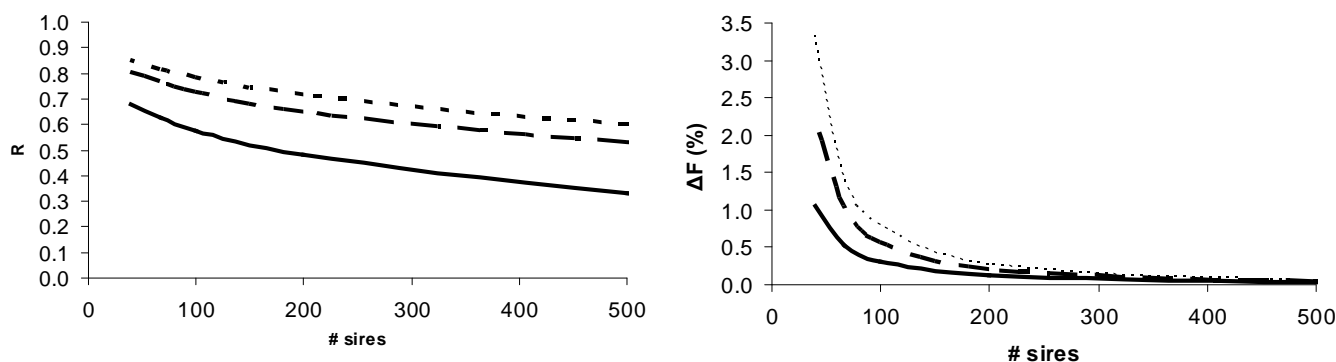


Figure 2 illustrates the effect of testing capacity of young stallions on R and ΔF . An increase of the male testing capacity from 5% to 25% has a much larger effect on R than an increase from 25% to 50%, especially with many sires (small progeny groups).

With a larger testing capacity (allowing a more intense selection), the favourable effect of fewer sires is relatively smaller than with a smaller testing capacity. A larger male testing capacity also increases ΔF , where ΔF at low sire numbers is more sensitive than the size of the breeding population (Figure 1).

Figure 2. Effect of number of sires on genetic response R (left) and inbreeding rate ΔF (right) with 5% (—), 25% (---) and 50% (.....) of all stallions tested.



4. Discussion

4.1. Genetic response and inbreeding in closed populations

This study predicted R and ΔF in closed breeding populations. Although there has already been an exchange of live horses for many decades, recent developments of AI and ET techniques have dramatically increased the opportunities to exchange genetic material across organisations. Many breeders increasingly use genetic material across populations (Ruhlmann *et al.*, 2006; Thorén-Hellsten *et al.*, 2006a). By enlarging the group of selection candidates, a higher R may be expected, although problems in retrieving and interpreting breeding information are likely to be a serious handicap in making correct selection decisions (Koenen and Aldridge, 1998).

In breeding populations that are not closed, realised ΔF is expected to be lower than predicted in this study as the effective population size is larger than with closed populations.

4.2. Number of selection stages

The evaluated programmes essentially combined mass selection with parental and sib information and selected all breeding animals at 4 years of age. The programmes did not include a (later) selection step based on the results of tested progeny.

In practice, however, many breeding organisations select older stallions (from 8 years of age) when the performances of their first offspring have become available. At that stage the accuracy of the sires has increased considerably: whilst the accuracy was approximately 0.50 after completing their own performance test (Table 2) it could increase to a range from 0.62 (10 tested offspring) to 0.87 (100 tested offspring). The effect of this additional selection step on the annual genetic response depends on the selection intensity in the second step and changes in the generation interval. Earlier studies on the relative importance of own performance and progeny tests (Germany: Bruns and Schade, 1998; The Netherlands: Huizinga, 1991; Sweden: Ström and Philipsson, 1978; Philipsson *et al.*, 1990) generally emphasised the importance of an intensive selection on own performance and large progeny groups of young sires. One of the main bottlenecks in maximising R has often been the limited testing capacity of young horses. In more recent years, more young-horse tests have been implemented and analysed (e.g. Ducro *et al.*, 2006; Thorén-Hellsten *et al.*, 2006b) increasing the opportunities for breeding organisations to select young horses more efficiently. Furthermore,

the improvement of the quality and availability of national genetic evaluations has facilitated efficient pre-selection of the selection candidates on basis of their parent averages. This implies that the systematic use of AI in combination with efficient testing and selection procedures of young horses (efficient pre-selection of tested horses and large testing capacities) may change the design of current horse breeding programmes by making progeny selection obsolete.

4.3. Predicted versus realised inbreeding rates

In this study ΔF was predicted under the assumption of BLUP selection (Rutten *et al.*, 2002). With BLUP selection ΔF is often substantially higher than under random selection (Bijma and Woolliams, 2000). Also in our study the more commonly used prediction formula as a function of the number of sires and dams (Falconer and Mackay, 1996) clearly underestimated ΔF , especially with intense BLUP selection. For example, without BLUP selection ΔF in the AI-3 alternative (80 sires) was 0.158% whereas it was 0.419% with BLUP selection.

Earlier studies (e.g. FAO, 1998; Bijma, 2000) recommended that ΔF should not exceed 0.5-1% which makes ΔF an important evaluation criteria when optimising the breeding scheme. Except for some extreme breeding programmes (<50-80 sires), most alternatives in this study resulted in lower ΔF (Table 2, Figure 1). This would imply that ΔF does not reach unacceptable levels when a breeding programme uses at least 100 sires. All simulations, however, assumed that all sires had the same number of offspring. In reality, the number of covered mares per sire shows a very skewed distribution. For example, in 2005 in the Dutch KWPN breeding programme for riding horses 234 breeding stallions covered 11,061 matings (average 47), with 30 stallions covering approximately 50% of all mares (KWPN, 1996). This means that in a practical breeding programme realised ΔF is (significantly) higher than ΔF predicted on the number of sires only. As no deterministic formulas are available to predict ΔF for unequal progeny group sizes under BLUP selection, predicted ΔF can only be approximated. If 40 stallions all covered 250 mares, ΔF was 1.056%. This implies that in a population of 10,000 mares realised ΔF is expected to be between 0.127% (Table 2) and 1.056%. The unfavourable effect of a limited number of sires with very many offspring may increase when breeders more frequently select the same sires across organisations, although the total number of selection candidates increases.

These few examples with unequal progeny group sizes and international selections illustrate the complexity of an *a priori* estimate of ΔF in practical horse breeding programmes. Breeding organisations are therefore recommended to routinely monitor realised ΔF in their population, even when many sires are used in breeding.

5. Conclusions

- The use of AI can increase R by 50% or more compared to natural service. The increase in R mainly results from enabling a more intensive selection at young age, whereas the effect of increased accuracy of estimated breeding values on R is small.
- The use of ET can increase R by about 10%, which is much smaller than the effects of AI.
- The combination of AI and a large testing capacity of young horses is expected to reduce the relevance of progeny testing schemes in horse breeding.
- Intensive use of AI and ET have an unfavourable effect on ΔF . This can be critical in small populations and/or situations with very skewed numbers of progeny per stallion. As ΔF is hard to predict, breeding organisations are advised to monitor realised ΔF .

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