

Genetic diversity and measures to reduce inbreeding in Friesian Horses

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ABSTRACT: The pedigree structure of the Friesian horse breed was analysed with the purpose to characterise inbreeding with special emphasis on the recent period in which measures to reduce inbreeding were taken. Measures taken consisted of implementing a mating quota and publishing individual kinship coefficients for breeding stallions. For many generations the average inbreeding was 0.015 per generation. Since 2000 the inbreeding rate is steadily decreasing from 0.018 to about 0.0065 during the years 2010-2012 and is preceded by a reduction in average additive genetic relationship from 0.012 in 2000 to approximately 0.006 during the years 2010-2012. This reduction coincide with the period in which the taken measures to reduce inbreeding became effective. Additionally, the method of individual kinship coefficients of the breeding stallions have been compared to the estimated genetic contributions under application of optimal contribution theory. A substantial negative relationship was found between individual kinship coefficients and genetic contributions. It was concluded that individual kinship coefficients are a reasonable approximation to genetic contributions to determine the impact of breeding animals on maintaining genetic diversity.

Keywords: horse, inbreeding, kinship, genetic contribution

Introduction

The Friesian horse is an old horse breed originating from the Netherlands with daughter studbooks in more than 30 countries. The Royal Friesian Horse Studbook has been registering horses since its foundation in 1879. The current size of the active breeding population is with about 100 stallions and 8,000 mares quite large. However, the history of the population shows several periods in which the active breeding population was much smaller (Osinga, 2000). The breed has been closed over a long period of time and this has inevitable led to accumulation of inbreeding and decrease of genetic diversity. Besides the small population size during certain time periods and the closed status of the population, selection has contributed to a substantial increase of inbreeding (Ducro et al., 2006). As a result the Friesian horse might be sensitive to inbreeding depression as well as high incidences for particular genetic defects such as dwarfism (Orr et al., 2010; Schurink et al., 2014).

To prevent the further loss of genetic diversity, emergence of new genetic disorders and to reduce the negative effects of inbreeding depression the studbook has implemented measures. From a theoretical perspective

optimal contribution selection is an effective method to conserve genetic diversity in the next generation. Practical implementation of optimal contribution selection, however, appears to be difficult. Further, optimal contribution selection requires the herdbook to be in control of imposing individual mating quota to breeding stallions as well as setting the matings. Both aspects are not applicable to horse breeding as studbooks are not the owners of the breeding animals. The role of optimal genetic contribution would therefore be restricted to attach a figure to each breeding animal by which their value for maintaining genetic diversity is expressed. An alternative strategy has been developed for the Friesian Studbook by calculating the individual kinship value of each breeding animal. For this purpose the additive genetic relation of a breeding animal to all animals of the last 3 generations has been calculated and averaged. This method has been implemented since 2003.

Now the measures have been implemented for a couple of years its effectiveness needs to be evaluated. Further, optimal contribution might outperform the implemented method and consequently there might be a need to further investigate possibilities to overcome the practical difficulties in implementing optimal contribution selection.

The aim of this study is to characterise inbreeding in the Friesian Horse breed with special emphasis on the recent period in which measures to reduce inbreeding rate were taken. Additionally, possibilities to implement optimal contribution selection will be investigated and compared to the method of individual kinship.

Materials and Methods

Data. The pedigree used in this study included the registrations from the foundation of the studbook in 1879 until the end of 2012. In total 122,644 horses were registered in the Friesian horse studbook. Each registration comprised parents, birth date and sex. Horses for which information on their parents was missing were excluded from the analysis when they had less than 3 progeny and those progeny were not parents themselves. Missing birth dates of parents were arbitrarily set to 10 years before the average birth year of their progeny. The time interval of 10 years is approximately the generation interval in horses. An arbitrary birth year was set for 18 females. After editing the pedigree data consisted of 117,322 horses, descending from 29,388 dams and 1047 sires. 18,000 dams had less than 4 progeny, and 159 dams had more than 15 progeny.

Methods. Individual inbreeding coefficients were calculated using the method of Meuwissen and Luo (1992) and averaged by year of birth. Average additive genetic

relationship among horses within a birth year were calculated based on the Pedig software and implemented in the website application Poprep (Groeneveld et al., 2009). Rate of inbreeding in a birth year was calculated as the difference of the average inbreeding of that birth year and the average of the birth year of parents (in which the parents birth year is the current birth year minus the generation interval). The difference is then scaled by $1 - F$ with F being the inbreeding in the birth year of the parents. Rate of additive genetic relationship was calculated along the same line of reasoning.

Influential ancestors of the current generation were identified based on their marginal genetic contribution to the current generation, using the software package Pedig (Boichard et al., 2002).

Active breeding population was considered to comprise of the sires with more than 10 progeny in 2012 and the dams they were mated to. Individual kinship values of these sires were calculated based on their relationship to the reference population, in which the reference population consist of the foals born in 2010-2012. Calculations were performed using the software package Pedig (Boichard et al., 2002).

Optimal genetic contribution was calculated for the sires and dams of the active breeding population using the software Gencont (Meuwissen, 2002) for overlapping generations. The software finds the optimal contribution, in terms of % of progeny, of each selection candidate which maximizes genetic gain while restricting the rate of inbreeding to the desired level. In this study maximising genetic gain was not considered and thus the rate of inbreeding was minimalized. The contribution of dams was restricted to $1/\text{\#dams}$, which implies that each dam should be covered and should produce one foal in the next round.

Results and Discussion

Pedigree Size and Completeness. During the first years after foundation of the breed the number of foals registered each year remained small and came above 50 foals for the first time in 1930. Until 1986 the number of foals yearly registered did not exceed 1,000 (Fig. 1). Since then there has been a considerable increase in population size and the number of yearly registered foals increased to a maximum of 6,719 in 2004 and remained approximately at 6,000 thereafter. The increase in population size was accompanied by an increase in the number of breeding stallions and by an increase in the average number of progeny per sire. In 1986, 47 stallions were listed for breeding while in 2004 more than 140 stallions were listed for breeding. The average number of progeny per sire was 22 in 1986 and 45 in 2004. The completeness of the pedigree, in terms of percent of ancestors known per parental generation, was over 90% for the first 7 generations, which can be considered as relative complete.

Inbreeding and kinship More than 90% of the horses in the population showed some degree of inbreeding and 20 horses had inbreeding coefficients between 0.35 and 0.38. These horses were all born in the last 30 years of the study. Mean inbreeding coefficient per birth year increased from 0.02 in 1908 to 0.162 in 2010 with considerable

fluctuations in the early years (Fig. 1). The value of 0.162 is higher than the level of inbreeding resulting from half-sib mating of unrelated parents (0.125). The rate of inbreeding increased up to 0.015 per generation but was even higher than 0.20 in the years 1997-1999. The average additive genetic relationship has been correspondingly higher during these years. Since 2000 the inbreeding rate is steadily decreasing from 0.018 to about 0.0065 during the years 2010-2012. This reduction has been preceded by a reduction in average additive genetic relationship from 0.0118 in 2000 to approximately 0.006 during the years 2010-2012. The reduction in inbreeding rate already begun a few years before the measures were introduced. Introduction of the measures started after a public discussion with the members of the herdbook. It is likely that these discussions resulted in an increasing awareness among the members of the herdbook on the problem of inbreeding. Therefore it is not surprising that the decrease in the rate of inbreeding started before the formal implementation of the measures.

Influential ancestors. The 4 ancestors with highest marginal contribution are responsible for more than 50% of the genetic diversity in the current generation. Largest marginal contribution was 23.04% and came from a male born in 1924, that had 297 progeny. Three of those top 4 ancestors were born in the 1920's indicating that the population went through a genetic bottleneck in that period. The youngest influential ancestors was born in 1956 and ranked 9. There were three females among the 10 most influential ancestors.

Individual kinship values. Kinship to the reference population was calculated for 74 stallions, which were identified as active breeding stallions in 2012. The average individual kinship was 0.175, which can be considered as an estimate of the inbreeding level in the next generation, when these stallions would contribute equally to the next generation. The kinship of individual stallions ranged between 0.156 and 0.193.

Genetic contributions. Optimal genetic contributions were calculated for the breeding stallions available for the year 2012. Under the restriction that all females available should be covered optimal contribution to the next round of selection was calculated using Gencont. There were 27 out of 74 stallions that should not be used any longer for mating. The contributions of the remaining breeding sires varied between 0.06% and 8.43%. As a reference, if all 74 breeding stallions would equally contribute then each stallion would produce 2.1% of the progeny crop and if all 27 selected breeding stallions would contribute equally, then each sire would produce 7.7% of the progeny crop. Selection according the Gencont analysis would reduce the average inbreeding from 17.2% in the parental generation to 4.2% in the progeny generation. This value can be considered a lower bound of what can be achieved when all selection capacity is devoted to inbreeding reduction.

The relation between optimal contributions and the individual kinship is negative indicating that stallions with high kinship estimate should contribute less to the next crop of foals (Figure 2). Deviations from a straight line are due to the zero-boundary of %progeny in case of optimal

contribution. A few stallions with low individual kinship have a genetic contribution of (close to) zero, probably because they have a close relative among the sires. Individual kinships do not account for relationships among the stallions, whereas optimal contribution does not account for progeny of the stallions already included in the population. The latter is an option for further fine-tuning in applying the Gencont program.

Conclusion

Breeding history of the Friesian horse shows an inbreeding rate over many years which is much higher than the limit set by FAO (1998). The studbook has implemented measures to reduce the inbreeding rate, namely mating quota and publishing future kinship estimates of the selected stallions. Future kinships are a reasonable proxy for the optimal contribution values, and might give the same source of information to the studbook members. Measures taken by the studbook coincide with a reduction in inbreeding rate down to 0.006 which is accompanied by a reduction of the additive genetic relationship down to 0.056. From the latter it is expected that the reduction in inbreeding rate will be continuing in the coming years.

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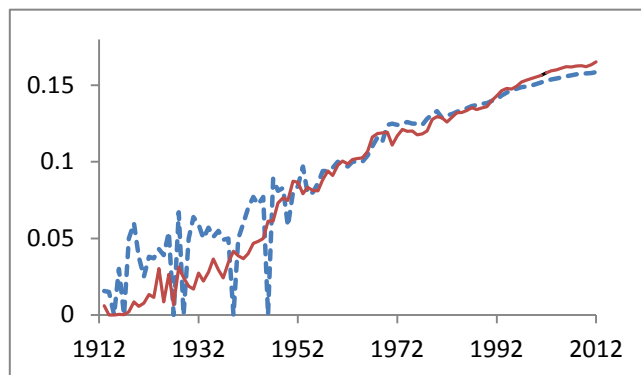


Figure 1. Average additive genetic relationship (broken line) and inbreeding coefficient (solid line) by year of birth.

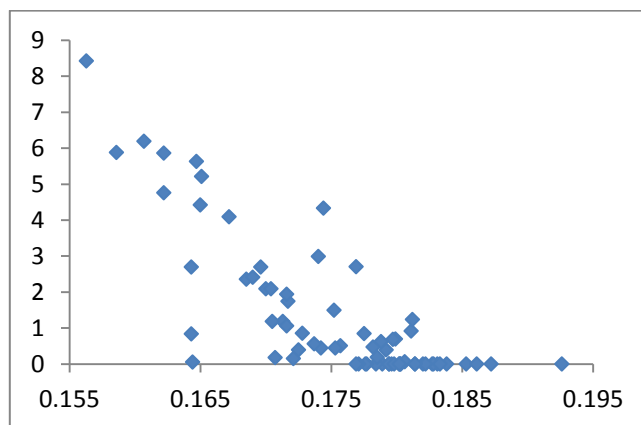


Figure 2. Relation between individual kinship coefficients (x-axis) and genetic contribution (y-axis; as %_progeny) of breeding stallions.