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Evaluation of breeding strategies to reduce the inbreeding rate in the Friesian horse population: Looking back and moving forward

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Abstract

In the past, small population sizes and unequal ancestor contributions have resulted in high inbreeding rates (ΔF) in the Friesian horse. Two decades ago, the studbook implemented a mating quota and started publishing individual kinships and reduced ΔF below 1% per generation. However, since then, the breeding population size has decreased and this raises the question whether current breeding strategies are sufficient to keep ΔF below desired rates. The aim of this study was to (1) reflect on past inbreeding trends and their main determinants, using pedigree analysis and (2) evaluate the effectiveness of the current and additional breeding strategies using stochastic simulations. We estimated the current ΔF (2013–2022) at 0.72% per generation. While the total contribution of the top 10 sires to the number of offspring per year has decreased from 75% in 1980 to 35% in 2022, this was mainly due to an increased number of approved studbook sires, and not due to more equalized contributions among sires. Of the simulated breeding strategies, selecting only breeding stallions with a below average mean kinship (i.e., “mean kinship selection”) was most effective to decrease ΔF (from 0.66% to 0.33%). Increasing the number of breeding sires only had an effect when also a mating quota was applied. However, its effect remained limited. For example, a ~1.5 fold increase, combined with a mating quota of 80 offspring per sire per year, reduced ΔF from 0.55% to 0.51%. When increasing the number of breeding mares, a practically unfeasible large increase was needed for a meaningful reduction in ΔF (e.g. twice as many mares were needed to reduce ΔF from 0.66% to 0.56%). Stratified mating quotas, a novel approach in which we assigned each sire a mating quota (of 60, 80, 100 or 120 offspring per year) based on its mean kinship to recently born foals, resulted in a lower ΔF (0.43%) than a general mating quota of 90 offspring per sire per year (0.55%). Overall, while the current ΔF is below 1%, we recommend to implement additional strategies to further reduce ΔF below 0.5% in the Friesian horse population. For this breed and similar populations, we recommend to focus on breeding strategies based on kinship levels to effectively reduce ΔF.

KEYWORDS
breeding strategies, horses, inbreeding, small populations

1 | INTRODUCTION

In modern horses, genetic diversity is predominantly observed between breeds, with little variation within breeds (McCue et al., 2012). In the late 19th century, studbooks emerged and breed standards were defined. As a result, the exchange of genetic material between breeds decreased. Some breeds became closed, completely prohibiting the introduction of genetic material from other breeds (Bowling & Ruvinsky, 2000). Within several horse breeds, small population sizes and narrow breeding goals, with extensive use of only a few popular sires that complied with the breeding goal, have led to high inbreeding rates (ΔF) (Głażewska & Jezierski, 2004; Gómez et al., 2009; Schurink et al., 2012; Sevinga et al., 2004; Verrier et al., 2010). To keep a genetically healthy population, it is recommended to keep ΔF below 1% (and preferably below 0.5%) per generation, corresponding to keeping the "effective population size" above 50 (preferably 100) individuals (FAO, 1998; Oldenbroek, 2017). Inbreeding, with the accompanying increase in homozygosity, increases the risk of recessive genetic disorders and reduces overall performance, a phenomenon called inbreeding depression (Doekes et al., 2021). In turn, genetic disorders and inbreeding depression form an additional threat to the survival of a breed. Thus, to keep horse populations genetically healthy, it is essential to maintain genetic diversity and limit ΔF.

The Friesian horse is the oldest native horse breed in the Netherlands and has grown to a worldwide popular breed with high social, cultural-historical and economic value. The Royal Friesian Horse Studbook (KFPS) was founded in 1879 and nowadays registers horses in 76 different countries and has members in 58 different countries (KFPS, personal communication). The current size of the active breeding population is relatively large, with about 100 breeding stallions and 4000 breeding mares each year. Approval of breeding stallions is centralized by one organization and more than 99% of the breeding stallions used internationally are approved in the Netherlands. Approximately half of the breeding stallions are stationed abroad. These stallions have first bred in the Netherlands for a few years before they were exported. Stallions are available via artificial insemination and some stallions have frozen semen available which can be used to breed mares in other countries. Preliminary research showed that the Friesian horse population can be considered as one large population without sub-populations in different countries.

Despite the substantial current size of the population and the continuous gene flow across countries, the Friesian horse population has had limited genetic diversity and high ΔF for several generations (Schurink et al., 2019). This is due to the small population sizes during certain periods in the past (population bottlenecks) combined with disproportionally large contributions of some ancestors (popular sire effect, breeders tend to breed with the champions of the annual stallion shows) and the closed status of the studbook (Schurink et al., 2019). Several breed-specific disorders have emerged, some of which are severely obstructing the animals' welfare, like dwarfism, and others even have fatal outcomes, like hydrocephalus (Ducro et al., 2015; Hisey et al., 2020; Leegwater et al., 2016). Since 2014, all breeding dams and sires are tested on carrier status for the monogenic recessive disorders dwarfism and hydrocephalus. While breeding with carriers of these disorders is allowed in the KFPS policy, carrier-by-carrier matings are fined. Over the past two decades, dwarfism and hydrocephalus have shown the same decreasing trend in carrier frequency. In 2000, carrier frequency of both disorders was ~15% and this has decreased to ~12.5% in 2021 (KFPS, personal communication). Furthermore, there have been indications of fertility problems related to inbreeding (Sevinga et al., 2004).

The KFPS studbook has implemented measures to prevent further loss of genetic diversity, the emergence of new genetic disorders and to reduce the negative effects of inbreeding depression. Theoretically, optimal contribution selection (OCS) is known to be the best strategy to conserve genetic diversity. However, OCS is practically unfeasible in the large Friesian horse population as it requires full control over all matings. Therefore, the KFPS studbook introduced two alternative strategies to reduce ΔF, which were implemented in 2003. First, a mating quota with a maximum of 180 matings per sire per year for its first three breeding years was implemented and stallion keepers are fined when their sire exceeds this limit. Second, the individual mean kinship of each breeding animal with a reference population (consisting of all foals born in the latest 3 years) is calculated and published each year (Ducro et al., 2014). No recommendations were made for these published kinships, but they can be used by individual breeders when choosing the breeding stallion for their mare. Moreover, the KFPS already provided an advice for several decades to limit the individual inbreeding of a foal below 5% within the first five generations (KFPS, 2024b). In the first years after the implementation of the alternative strategies in 2003, ΔF dropped from 1.8% in 2000 to about 0.65% during the years 2010–2012 (Ducro et al., 2014). However, 10 years since the last comprehensive pedigree analysis, there are still concerns about inbreeding and its negative consequences. Also, the studbook aims for an ΔF below 0.5%. Therefore, an updated analysis of past inbreeding trends and the effect of the previously implemented strategies, as well as an evaluation of the effectiveness of potential future strategies, is needed. Such an analysis could also benefit other species with similar characteristics.

In this study, we reflect on inbreeding trends and their main determinants in the past, using pedigree analysis, and evaluate the effectiveness of the current and additional breeding strategies using stochastic simulations based on parameters derived from the true population. The effect of increasing the number of breeding animals, stricter mating quotas, mean kinship selection and stratified mating quotas on ΔF are evaluated.

2 | MATERIALS AND METHODS

2.1 | Pedigree information

The pedigree included the registrations from the foundation of the studbook in 1879 until the end of 2022. In total, 163,014 horses were registered in the Friesian horse studbook. Each registration comprised the individual's name, registration number, birth date, sex and its parents. One individual with identifier 0 (i.e. unknown registry) was removed. Duplicate entries of individuals ($n = 3$) were also removed. Individuals that occurred as parent but were not registered as individual were added to the pedigree with parent information included, if known by the KFPS ($n = 23$), or otherwise added as founders ($n = 2$). After editing, the pedigree consisted of 163,035 horses. Pedigree completeness was evaluated per year by the percentage of animals with more than five generations in the pedigree completely known, and by the mean equivalent complete generations. The latter was computed for an individual as the sum of $(1/2)^n$ across all known ancestors, where n was the number of generations separating the individual from an ancestor (Boichard et al., 1997).

2.2 | Population parameters

Population parameters from the pedigree were derived to evaluate the main determinants of inbreeding. These parameters were derived using the Retriever software (Windig & Hulsegge, 2021). For each year, the number of newly registered foals and the number of stallions and mares that became sire or dam was retrieved. In addition, the numbers of approved and unapproved studbook sires and the number of their offspring were retrieved. Moreover, the contributions of the top 10 sires per year to the total number of foals born per year were calculated. In this paper, contribution was defined as the number of offspring per sire divided by the total number of offspring born per year.

2.3 | Inbreeding and kinship coefficients

Retriever software (Windig & Hulsegge, 2021) was used to calculate inbreeding coefficients (F_i) for each individual i, as well as kinship coefficients (f_{ij}) between individuals i and j using all available generations in the pedigree. Then, the mean inbreeding level per birth year (F) and the population mean kinship per birth year (f) were calculated. For each year, we calculated the rates of inbreeding (ΔF) and kinship (Δf) based on the previous 10 years and corresponding effective population sizes ($N_e = 1/(2 \times \Delta F)$). To account for the expected non-linear increase in inbreeding and kinship, a regression of $\text{Ln}(1 - F)$ for ΔF and $\text{Ln}(1 - f)$ for Δf on birth year was used (Pérez-Enciso, 1995). The resulting regression coefficients were multiplied with the corresponding generation interval (L) in that 10-year period to obtain ΔF and Δf per generation. L was calculated as the average age of the parents when their offspring were born per year for each 10-year period and weighted by the number of offspring born each year within that 10-year period.

2.4 | Simulation of the base scenario using MoBPS

As a baseline scenario for our analysis, we mimicked the current Friesian horse population using stochastic simulation, meaning that all breeding actions were explicitly simulated. Simulations were done using the R-package MoBPS v.1.11.10 (Pook et al., 2020). To build up a realistic population structure, matings according to the real pedigree until 2022 were simulated and subsequently a 75-year period (2022–2097) following the current breeding strategy with input parameters derived from the actual population was used. Each scenario was run with 25 repeats, as a previous study suggested that ΔF hardly changed after 25 repeats for various simulated populations (Windig et al., 2019). Simulation of the base scenario consisted of the following steps: (1) setting input parameters, (2) adding breeding values and selection, (3) generating a starting population and (4) selecting breeding animals for the next generation. Details of the steps are described below.

2.4.1 | Setting input parameters

Input parameters were derived from the true pedigree information of year 2022 (Table 1). The base scenario consisted of 90 breeding sires and 3500 mares. These numbers were based on the true population of 2022, when only considering approved breeding sires and foals from approved breeding sires (see Section 3). The actual pedigree registration also comprises foals from unapproved sires, as it is not feasible to set up stallion selection programs in remote countries. Only offspring from approved breeding sires made up the breeding population for the next generation. Similar to the current breeding restrictions, each approved breeding sire was allowed to have a maximum of 180 offspring per year for its first three breeding years. After those first three breeding years, the sires had no restriction on the number of offspring per year. The contributions of the sires (number of offspring per sire divided by the total number of offspring born per year) were specified based on the contributions in 2022. The most popular sire was simulated to have an expected contribution of 5.4%, the next sire 4.5%, the next two sires 4.2%, up to sire 36–90 contributing 0.29% each (Table 1). This means that after the breeding restriction for the first 3 years of each breeding sire, only one sire would produce more than 180 offspring (5.4% of 3500 foals is 189 offspring) and all other sires produced less than 180 offspring. We furthermore assumed that each mare produced one offspring per year, resulting in 3500 foals each year. At the start of simulation, F was 0.170. Replacement rates were included to account for breeding animals that die but also for animals not used for breeding anymore. Replacement rates for breeding animals were age dependent and were estimated from the distribution of age of breeding animals in the real population that was generated from the Retriever software (Windig & Hulsegge, 2021). Maximum age of breeding animals was set to 22 years (Table 1).

2.4.2 | Breeding values and selection

The process of selection is of fundamental importance when analysing inbreeding as it leads to more related animals being selected. Hence, absence of selection would cause underestimation of the actual ΔF (Leroy & Rognon, 2012; Windig & Oldenbroek, 2015). In this study, the complex process of selection in horse breeding with various selection and phenotyping steps was simplified by simulating a single quantitative trait with 1.000 purely additive QTLs and assuming a prediction accuracy of 0.5, corresponding to phenotypic selection with a heritability 0.25.

2.4.3 | Generating a starting population

The whole pedigree of 163,035 horses was incorporated in the simulation to generate the starting population and

TABLE 1 Input parameters for the simulated base scenario, which reflects the current real breeding program without any additional breeding strategies. Parameters are based on actual pedigree information from year 2022.

Input parameter	Value
Number of breeding sires	90
Number of foals (= number of mares)	3500
Inbreeding level (F) at start	0.170
Max. number of offspring per year	180 per sire for its first three breeding years
Max. number of offspring per year per dam	1
Replacement rates breeding sires	0.5% until 8 years of age, 1% between 8 and 10 years of age, 5% between 10 and 12 years of age, 20% between 12 and 22 years of age
Replacement rates breeding dams	5% until 10 years of age, 10% between 10 and 15 years of age, 30% between 15 and 22 years of age
Max. age of breeding animals	22 years
Contribution of popular sire (number of sires and contribution (%))	1 (5.4%), 1 (4.5%), 2 (4.2%), 3 (4%), 1 (3.6%), 1 (3.2%), 4 (3%), 8 (2%), 1 (1.8%), 2 (1.7%), 2 (1.5%), 2 (1.4%), 1 (1.3%), 3 (1.2%), 3 (1%), 55 (16%/55)
EBV accuracy of selection trait	0.50

mimic the real-world population structure. The breeding stallions that sired foals in the actual population in 2022 were selected as breeding sires at the start of the simulation. Since about 3500 foals from approved sires were born per year in recent years, 3500 dams were selected each year in the simulation. Generating the breeding dams at start was similarly done as selection of breeding dams for the next year, which is described in the next section.

2.4.4 | Selecting breeding animals for the next generation

For each simulated breeding year, the pool of mare selection candidates was built up as followed: all alive mares that were above 4 years of age, 50% of the mares of 4 years of age and 10% of the mares of 3 years of age, both chosen at random. Then, out of this pool, the required number of dams according to the specified breeding strategy (3500 dams in the base generation) for the next year were selected as follows: two-third of the required dams (2333 dams in the base scenario) were selected based on truncation selection on the EBV. The other one-third required dams (1167 dams in the base scenario) was randomly selected from the top 25% of the remaining selection candidates. This approach was used to exclude the very low EBV animals, but also include some sub-optimal breeding dams that are used by hobby keepers. To model that not all covered mares will be pregnant, randomly 20% of the breeding dams of the previous year were not considered for in the following year. Each simulated year, breeding dams were removed from the breeding populations according to specified replacement rates (Table 1), and the removed animals were replaced by new selection candidates.

For each simulated breeding year, the active breeding sires in 2022 were removed according to the specified replacement rates (Table 1), and the removed animals were replaced by a group of sire selection candidates. This group of selection candidates consisted of stallions that were four years old. Stallions were selected through truncation selection on the EBVs (with EBVs staying constant over time). To mimic the practical breeding program, once a stallion was selected as a breeding stallion, it would be a breeding stallion for its entire lifespan and could not be deselected again.

Finally, mating was at random, except that full-sib and half-sib mating was not allowed.

2.5 | Breeding strategies

Subsequently, a variety of breeding strategies were considered by modifying the breeding scheme in one key aspect and comparing the outcomes to the baseline scenario. Each breeding strategy was separately evaluated by calculating the ΔF per generation over the 75-year simulated period.

2.5.1 | Adding breeding strategies

First, to determine the effectiveness of the current mating quota, a simulation without mating quotas for sires and with the mean contributions of sires between 1993 and 2002 (10 years before the implementation of the mating quota of 180 in 2003; Table S1) was run (strategy 1). Subsequently, different additional breeding strategies were simulated: (2) increasing the number of breeding animals, (3) stricter mating quotas, (4) a combination of increasing number of breeding animals and stricter mating quotas, (5) mean kinship selection and (6) stratified mating quotas (Table 2). To implement specific strategies, the associated input parameters (from Table 1) were changed, while all other parameters were kept the same.

In strategy 2, the number of breeding animals was increased. The number of sires was increased from 90 to 150 (in increments of 10) and combined with the current number of mares ($n = 3500$) or with twice the number of mares ($n = 7000$) (Table 2). Contributions of the popular sires were kept the same while increasing the number of sires, but the remaining contributions (of “non-popular sires”) were spread across more sires. For example, in the base scenario with 90 breeding sires each year, 16% contribution was equally divided over 55 “non-popular sires” (Table 1). When increasing the number of breeding sires to 100, then this 16% contribution was divided over 65 “non-popular” sires.

In strategy 3, stricter mating quotas for sires were simulated, where the maximum number of offspring a stallion can sire each year during its entire lifespan was decreased from 180 to 40 (in increments of 20) (Table 2). With 3500 foals born each year, this corresponds to a maximum of 5.1%, 4.7%, 4.1%, 3.4%, 2.9%, 2.3, 1.7% and 1.1% offspring per sire per year, respectively. To test whether a mating quota per sire per year for its entire lifespan was more effective than a mating quota for only its first three breeding years, we compared this with the base scenario and tested the effect of 80 offspring per sire per year for only its first three breeding years (Table 2). A mating quota of 80 offspring per sire per year, results in the 13 most popular sires had a higher contribution than the mating quota allowed (>3%, while the maximum contribution should then be 80/3500 foals × 100% = 2.3%) (Table 1). The excess of the contributions of the popular sires were added to the contributions of the “non-popular” sires proportional to their probability of being used as a sire (e.g., sire 14 with

TABLE 2 Simulated breeding strategies and their alternative input parameters. All other parameters were the same as in the base scenario (Table 1).

Breeding strategy	Parameter	Current	Alternative
1. No mating quota	Max_offspring/year	180 per sire for its first three breeding years	Inf.
2. Increase the number of breeding animals	*N*_stallions	90	100, 110, 120, 130, 140, 150
	*N*_foals	3500	7000
3. Mating quota	Max_offspring/year	180 per sire per year for its first three breeding years (equivalent to 5.1% of all offspring)	180 (5.1%), 160 (4.7%), 140 (4.1%), 120 (3.4%), 100 (2.9%), 80 (2.3%), 60 (1.7%), 40 (1.1%) per sire per year for its entire lifespan 80 (2.3%) per sire per year for its first three breeding years
4. Increasing the number of breeding sires and a mating quota	*N*_stallions	90	100, 110, 120, 130, 140, 150
	Max_offspring/year	180 per sire for its first three breeding years	100 (2.9%), 80 (2.3%) per sire for its entire lifespan
5. Mean kinship selection	MKS	None, only published	Exclude selection candidates which have above average mean kinship
6. Stratified mating quotas	Stratified_mq	None	Assign mating quota to each breeding sire based on its mean kinship: 25% lowest mean kinship = 120 25%–50% lowest mean kinship = 100 50%–75% highest mean kinship = 80 75%–100% highest mean kinship = 60

a contribution of 2% was more likely to get additional offspring than sire 36 with a contribution of 0.29%) (Table 1).

In strategy 4, combinations of an increased number of breeding sires with stricter mating quotas were simulated. For this purpose, the base scenario (with 90 sires) was compared to scenarios with number of sires increased from 90 to 150 (with increments of 10), and combined with a mating quota of 180, 100, or 80 offspring per year per sire for its entire lifespan (Table 2).

Finally, two breeding strategies based on kinship level were applied. In strategy 5, mean kinship selection was used, in which only stallions with a lower than average mean kinship were selected for breeding. The mean kinship of a stallion was calculated as its average kinship to the foals born in the latest 3 years. Only the 4-year old stallions with a mean kinship below average were considered selection candidates. From these candidates, new breeding stallions were selected based on EBV (truncation selection) and replacement was depending on the replacement rates of the breeding stallions (Table 1). The mean kinship selection was only applied to stallions, so mares with a high kinship were still able to breed.

In strategy 6, a novel approach named stratified mating quota was simulated. In this approach, a mating quota was assigned to each breeding sire separately based on its individual mean kinship. First, breeding stallions were selected in the same way as in the base scenario. Then, the individual mean kinship of each selected breeding stallion to all the foals born in the latest three years of the simulation was calculated. A distribution of four kinship groups was determined based on the quantile deviation of the mean kinship (as 25% lowest mean kinship, 25%–50% lowest mean kinship, 50%–75% highest mean kinship, and 75%–100% highest mean kinship). Then, a mating quota (of 60, 80, 100 or 120 offspring per year) was assigned to each breeding stallion based on its individual mean kinship. With 3500 foals born each year, these mating quota correspond to a maximum of 1.7%, 2.3%, 2.9% and 3.4% offspring per sire per year. For example, when the individual mean kinship of a breeding stallion was below the threshold of the lowest quartile (25% lowest) of the mean kinship, then the breeding stallion got a mating quota of maximum 120 (3.4%) offspring per sire per year for its entire lifespan (Table 2).

2.5.2 | Evaluating additional breeding strategies

To evaluate the effect of the simulated breeding strategies, for each scenario the ΔF per generation (%) including a 95% confidence interval was calculated. L per year for the years 2022–2097 was calculated for the base scenario and (given that this L hardly changed over time and between different scenarios) the mean L over this period was used to calculate ΔF for all scenarios.

3 | RESULTS

3.1 | Population size and pedigree completeness

After foundation of the breed in 1879, the number of registered foals each year was small for many decades, reaching 100 foals for the first time in 1937 and 1000 foals for the first time in 1986 (Figure 1). From the 1980s to the 2000s, population size increased rapidly and the number of yearly registered foals increased to a maximum of 6713 in 2004. Between 2002 and 2009, on average more than 6000 foals were registered per year. After 2009, population size declined to 3384 registered foals in 2014 and since 2017 the numbers of yearly registered foals has stabilized at around 3900 (Figure 1). Based on the pedigree from 1879 until the end of 2018, 47.9% of all the female foals born became dam later in life and 3.5% of all male foals born became sire later in life. The mean proportion of registered male foals per year was 48.2% and was significantly ($p < 0.05$) lower than the registered female foals per year (Figure S1). This is likely due to the strict stallion selection. Breeders that do not expect to compete in the stallion inspection, might decide to not register their male foals in the studbook and thereby save registration costs. The pedigree was rather complete with over 90% of animals having more than five generations in the pedigree completely known for the last 26 years and the mean equivalent complete generations increasing from 10.6 in 1996 to 13.5 in 2022 (Figure S2).

3.2 | Number of (approved and unapproved) sires and sire contributions

Of the 3.5% male foals in the pedigree that became sire, only 17% were approved studbook sires and the other 83% sires were unapproved sires. Since 1981, coinciding with the population growth (Figure 1), the number of sires (both approved sires and unapproved sires) that sired offspring in a year has greatly increased (Figure 2a). From 2004 to 2016, the number of unique approved studbook sires that sired offspring in a year was around 100 and stabilized at around 90 since 2017 (Figure 2a). In 2022, there were 322 sires that sired an offspring that year and only 89 of these sires were approved studbook sires.

Within any given year, the contributions of sires (in number of offspring) were considerably skewed. In general, the unapproved sires had very low contributions. For example, in 2022, the majority of unapproved sires sired only one offspring and the maximum number of offspring sired by an unapproved sire was 12 (Table S2). Within the group of approved studbook sires there were unequal contributions, ranging from one to 192 offspring per sire in 2022 (Table S2). Only one of the approved studbook sires sired more than 180 offspring in 2022, and only three of the approved studbook sires were close to reaching the mating quota of 180 offspring per sire in 2022 (Table S2). In total, from the 3985 foals born in 2022, 3547 (89%) foals were sired by approved studbook sires and the remainder of 438 foals were sired by unapproved sires. The percentage of offspring per year from unapproved sires follows the same trend as the use

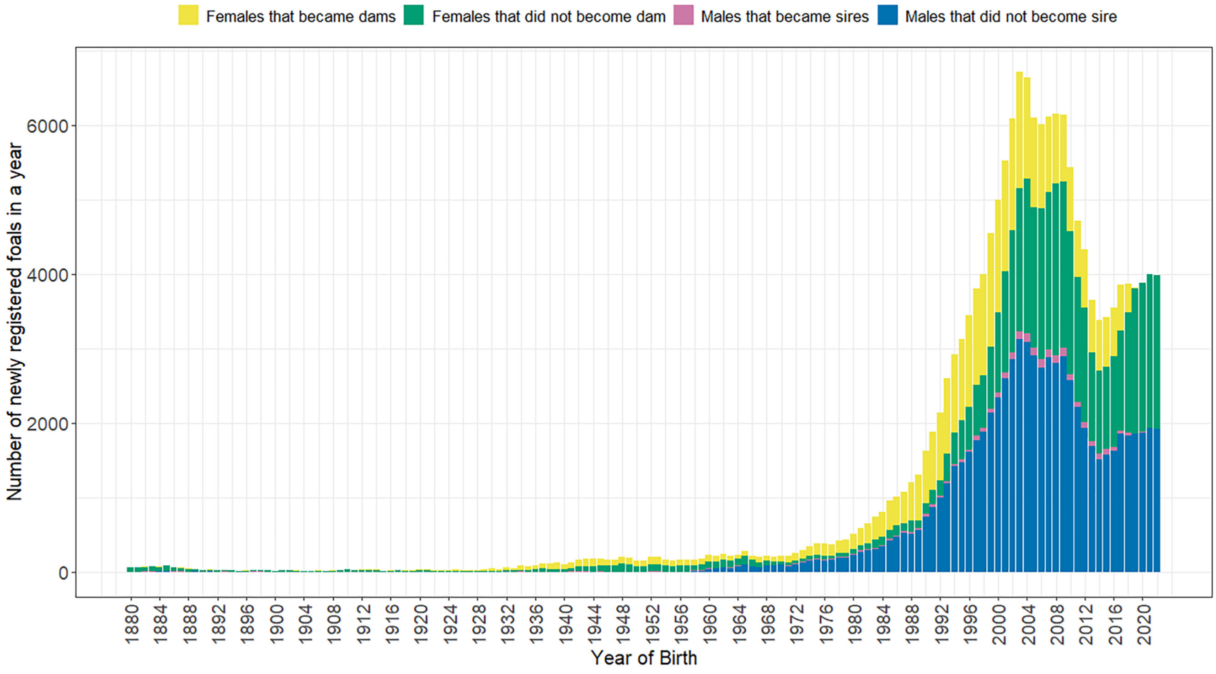


FIGURE 1 Number of newly registered foals per year. Numbers until 2018 give reliable information, because the foals born from 2019 onwards did not yet have a fair chance to become a parent.

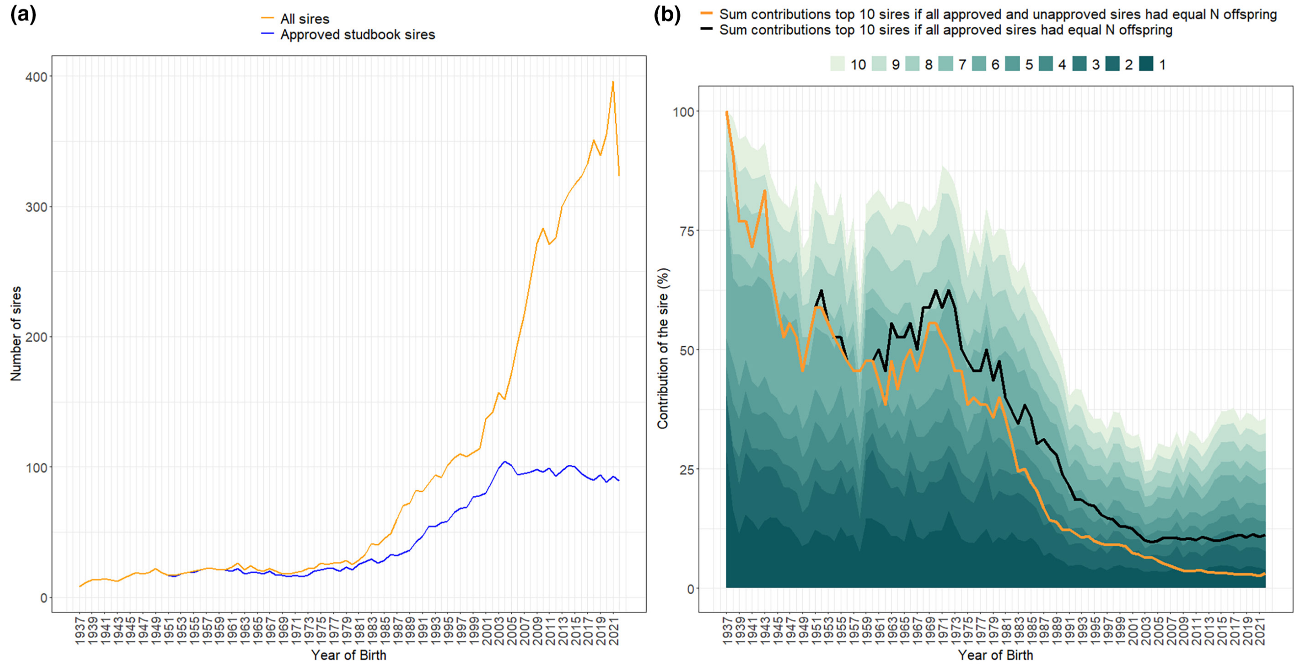


FIGURE 2 Number of sires per year and sire contributions. (a) Number of approved studbook sires and unapproved sires producing offspring each year. (b) Sire contributions (%) of the 10 most influential sires per year indicated with the 10 different colours. The black line indicates the sum of the contributions of the 10 most influential sires if all approved studbook sires had equally contributed to the number of offspring in a specific year. The orange line indicates the sum of the contributions of the 10 most influential sires if all sires (both approved and unapproved) had equally contributed to the number of offspring in a specific year.

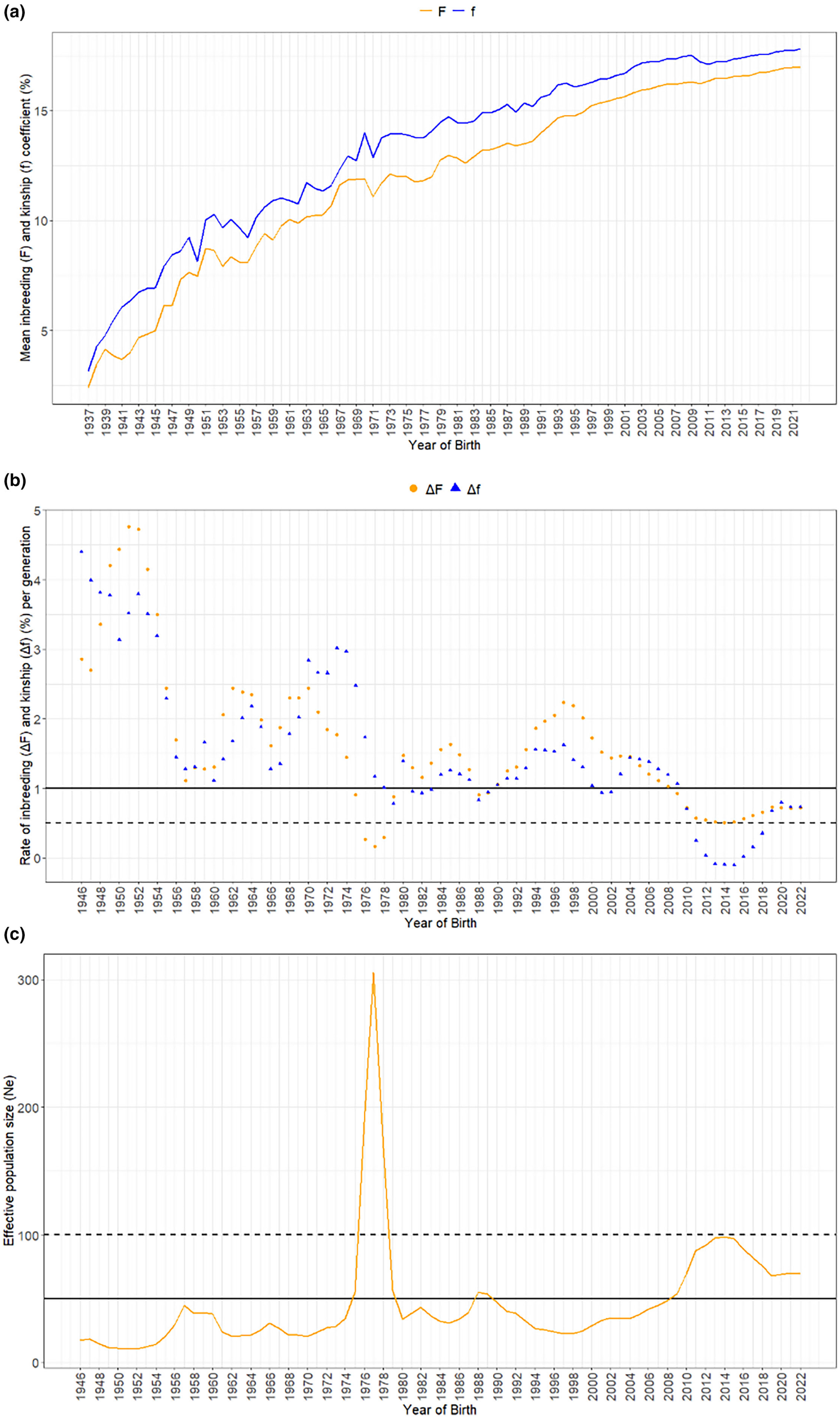
of unapproved sires (Figure 2), but is still a relative small amount of the total number of offspring (<15%, Figure S3).

The contribution of the 10 most popular sires has changed over time (Figure 2b). In 1937, only eight sires were used in total. From 1945 to 1974, the top 10 sires sired around 80% of the offspring each year with some yearly fluctuations. From 1974 to 2003 during the steep population growth (Figure 1), the contributions of the top 10 sires decreased almost every year to 27% in 2003. From 2000 to 2013, it was around 30% and, since 2014, it has been around 35% (Figure 2b). In 2022, the top 10 approved sires got 3 times more offspring (35% of all offspring born in 2022) than what they would have had if all approved studbook sires contributed equally (11%, black line in Figure 2b). In comparison, in 1980, the top 10 sires got 1.5 times more offspring (75% of all offspring born in 1980) than what they would have had if all approved sires contributed equally (48%, black line in Figure 2b). Thus, while the contribution of the top 10 sires has decreased over time (Figure 2b), this decrease is mainly due to the increased number of approved studbook sires (Figure 2a), but not due to more evenly spread contributions among the approved studbook sires.

3.3 | Inbreeding and kinship

For every year, the mean kinship per year (*f*) was a bit higher than the mean inbreeding per year (*F*) (Figure 3a). The *F* tends to follow *f* by ~1 generation (Figure 3a), suggesting no obvious deviation from random mating. *F* and *f* fluctuated substantially in the first six decades of the pedigree (1880–1937), mainly due to the low number of registered foals until 1937 ($N < 100$). *F* increased from 2.4% in 1937 to 17.0% in 2022 (Figure 3a) and *f* increased from 3.2% in 1937 to 17.8% in 2022 (Figure 3a). Until the last decade, the *F* of foals from unapproved sires highly fluctuated per year due to the small number of foals from unapproved sires ($N > 100$ for the first time

FIGURE 3 Inbreeding and kinship coefficients and rate per year. (a) Mean inbreeding (*F*) and kinship (*f*) coefficients per year of birth based on all available generations in the pedigree. (b) Rate of inbreeding (ΔF) and kinship (Δf) (%) per generation for each year with a 10-year interval. The figure can be read like as followed: the circle and triangle at year 2022 represent ΔF and Δf for the interval 2013–2022, the circle and triangle at year 2021 represent ΔF and Δf for the interval 2012–2021 and so on. The solid line represents an ΔF and/or Δf of 1% per generation. The dashed line represents an ΔF and/or Δf of 0.5% per generation. (c) Effective population size per generation for each year with a 10-year interval. The figure can be read the same as b. The solid line represents $N_e = 50$ (corresponding to an ΔF of 1%). The dashed line represents $N_e = 100$ (corresponding to an ΔF of 0.5%).


(a)
F
f
Mean inbreeding (F) and kinship (f) coefficient (%)
5
10
15
1937 1939 1941 1943 1945 1947 1949 1951 1953 1955 1957 1959 1961 1963 1965 1967 1969 1971 1973 1975 1977 1979 1981 1983 1985 1987 1989 1991 1993 1995 1997 1999 2001 2003 2005 2007 2009 2011 2013 2015 2017 2019 2021
Year of Birth
(b)
ΔF
Δf
Rate of inbreeding (ΔF) and kinship (Δf) (%) per generation
0
1
2
3
4
5
1946 1948 1950 1952 1954 1956 1958 1960 1962 1964 1966 1968 1970 1972 1974 1976 1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012 2014 2016 2018 2020 2022
Year of Birth
(c)
Effective population size (Ne)
0
100
200
300
1946 1948 1950 1952 1954 1956 1958 1960 1962 1964 1966 1968 1970 1972 1974 1976 1978 1980 1982 1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012 2014 2016 2018 2020 2022
Year of Birth

in 1990, Figure S4). However, this had almost no effect on the total inbreeding trends (Figure S4) and, therefore, the calculation of the inbreeding (ΔF) and kinship (Δf) rates per generation were based on all registered foals per year. ΔF and Δf per generation were calculated for the first time for year 1946, which represents ΔF and Δf for the 10-year period of 1937–1946 (Figure 3b). ΔF and Δf were 2.8 to 4.8% in the period of 1946–1952 (Figure 3b), which corresponds to the steep increase in F and f from 1937 to 1952 (Figure 3a). Subsequently, from the 1950s to the early 1970s, ΔF and Δf varied between 1% and 3% per generation. In 1975–1979, ΔF and Δf temporarily dropped below 1%. From 1980 to 2003, ΔF and Δf increased again, with some fluctuations in 1988 and 2001. From 2003 to 2014, ΔF and Δf continuously decreased with the lowest ΔF of 0.51% and lowest Δf of −0.10% in 2014. Since 2009, ΔF and Δf have been below 1%. Since 2014, ΔF and Δf are increasing again, but seems to be levelling off the last few years. The most recent rates are a ΔF of 0.72% and a Δf of 0.73% in the 10-year interval of 2013–2022 (Figure 3b).

The effective population size (N_e), varied from 11 to 305 in the period 1946–2022 (Figure 3c). Prior to 2008, N_e generally was below 55, with the exception of a high peak in 1976–1978 that could be explained by relatively large fluctuations in mean inbreeding in those years (Figure 3a). Since 2009, N_e is above the FAO threshold of 50, corresponding to an ΔF below 1%.

3.4 | Generation interval

The generation interval (L) for dams fluctuated slightly, but remained considerably constant between 1937 and 2002 and increased with 1.5 year from 2002 ($L = 8.5$) to 2022 ($L = 10.0$) (Figure S5). L for sires fluctuated a bit more with a sharp decrease from 1959 ($L = 9.9$) to 1969 ($L = 7.4$), followed by a sharp increase to an L of 9.5 years in 1977 (Figure S5). Since 1988, L for sires was considerably constant and increased slightly with 0.5 years from 2005 ($L = 9.5$) to 2022 ($L = 10.0$). The mean L over the entire period was 9.1 years, with 8.8 years for dams and 9.3 years for sires (Figure S5).

3.5 | Simulation of the base scenario

Simulation of the base scenario resulted in an ΔF of 0.66% (95% CI: 0.63–0.70) per generation, which is close to the observed ΔF of 0.72% based on pedigree data (Figure 3b). Other population parameters were also similar between the simulation and actual population. Mean L of the simulated base scenario between 2022 and 2097 was 9.6 years for dams and 8.9 years for sires (Figure S6), resulting in a mean L of 9.2 years which was close to the mean L of 9.1 years based on pedigree information (Figure S5). Since pedigree data were incorporated to generate the base population in the simulation, the distribution of mean kinships of the simulated breeding sires was almost identical to that of the actual breeding sires (Figure S6), with only small differences due to the way Retriever and MoBPS dealt with semi-founders. In addition, the age structure of the breeding sires and mares, as well as the numbers of offspring for sires and mares, were comparable between the simulation and practice (Table S3; Figures S8 and S9).

3.5.1 | Effect of increasing the number of breeding animals

Increasing the number of breeding sires per year up to 150 sires had no significant effect on ΔF ($p = 0.232$) (Figure 4). However, a twofold increase in the number of breeding mares (by increasing the number of foals born per year) significantly decreased ΔF to 0.56% ($p < 0.05$) per generation (Figure 4).

3.5.2 | Effect of a sire mating quota

The scenario without any mating quota gave a similar ΔF (0.64%, $p = 0.791$) as the base scenario. This was expected, since the contributions used for this simulation were based on the 10 years before 2003 and were all below 5% offspring per sire per year (5% of 3500 foals = 175 offspring). A mating quota of maximum 180 offspring for each year a sire is allowed to breed, instead of only for the first three breeding years of a sire, also resulted in a similar ΔF of 0.66% ($p = 0.619$). In contrast, a mating quota of maximum 80 offspring per sire per year for its entire lifespan significantly reduced ΔF to 0.55% ($p < 0.05$) per generation, compared to applying this mating quota only for the first three breeding years of a sire ($\Delta F = 0.62\%$). Hence, we further focused on the effect of a stricter mating quota for each year a sire is allowed to breed and not only for its first three years. A maximum of 60 offspring per sire per year significantly reduced ΔF to 0.45% ($p < 0.05$) (Figure 5). A maximum of 40 offspring per sire per year, corresponding to approximately equal contributions across sires (since 3500 foals divided by 90 sires is approximately 40 offspring per sire), further significantly reduced ΔF to 0.40% ($p < 0.05$).

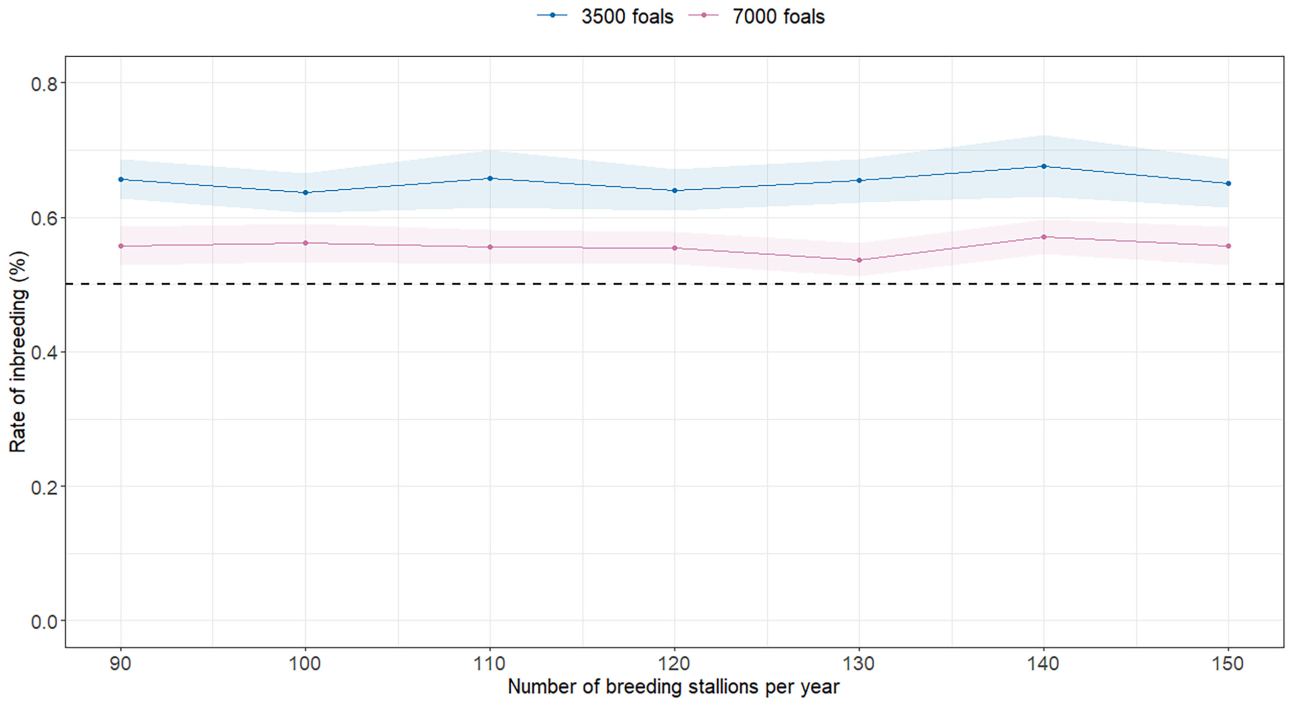


FIGURE 4 Simulated effect of increasing the number of breeding animals on the inbreeding rate (ΔF) per generation. The effect of the number of breeding sires (from 90 to 150 sires) and the number of breeding mares (based on yearly 3500 foals born or yearly 7000 foals born) on ΔF. The shaded areas represent the 95% confidence intervals. The dashed line indicates an ΔF of 0.5% per generation.

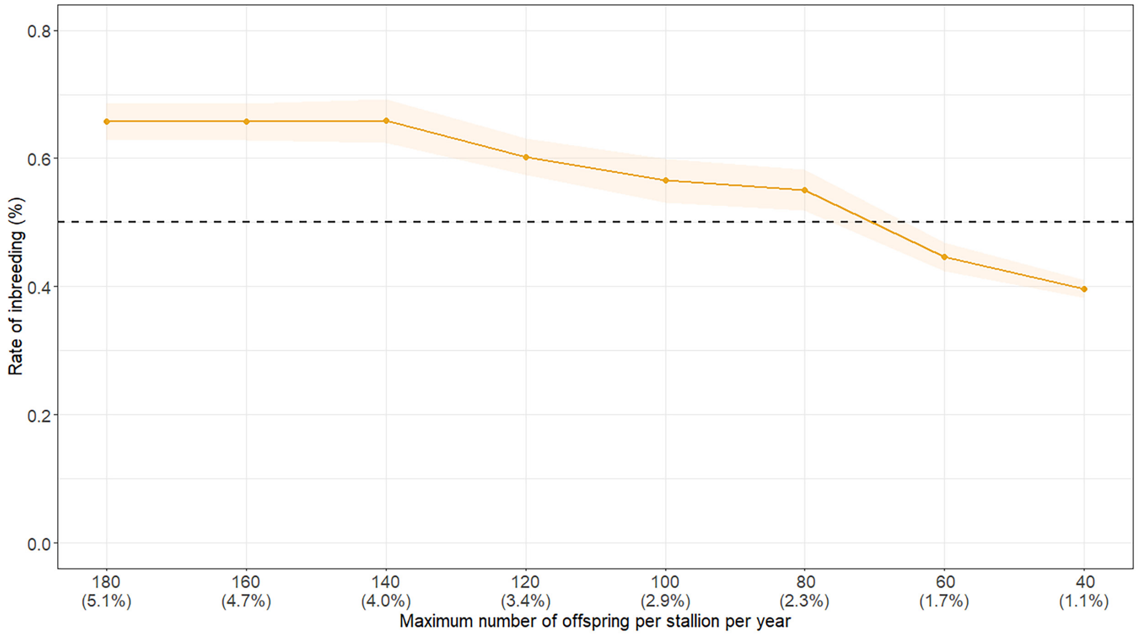


FIGURE 5 Simulated effect of a sire mating quota (defined as a maximum number of offspring per sire per year) on the inbreeding rate (ΔF) per generation. The numbers in brackets on the x-axis represent the maximum percentage of foals per sire per year. The shaded area represents the 95% confidence interval. The dashed line indicates an ΔF of 0.5% per generation.

3.5.3 | Effect of increasing the number of breeding sires and a sire mating quota

An increase in the number of sires did not tend to have an effect with a mating quota of 180 ($p = 0.323$) or 100 ($p = 0.393$) (Figure 6). However, with a mating quota of 80, increasing the number of sires tended to have a small effect on reducing ΔF. An increase in the number of breeding sires to at least 130 per year combined with a mating quota of maximum 80 offspring per year

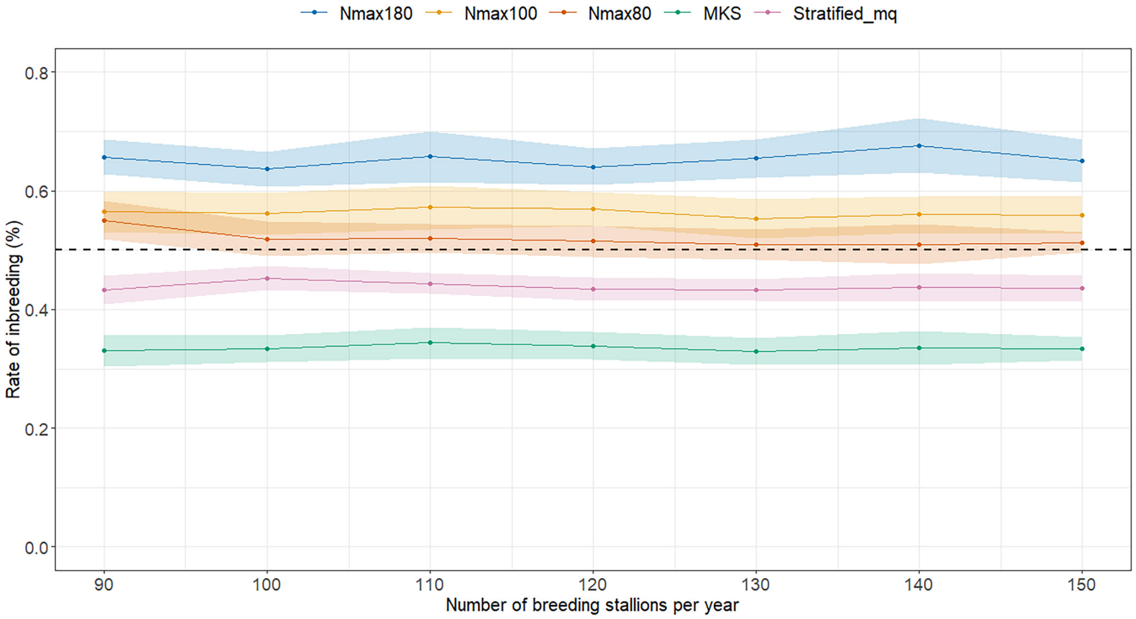


FIGURE 6 Simulation results of different breeding strategies on the inbreeding rate (ΔF) per generation. Simulation results show the combined effect of increasing the number of breeding sires per year and restricting the number of offspring per sire per year (Nmax), perform mean kinship selection (MKS), or stratified mating quotas (stratified_mq). The numbers in brackets (5.1%, 2.9% and 2.3%) represent the maximum percentage of foals per sire per year. The 95% confidence intervals are included as the shadow of the line. The dashed line indicates an ΔF of 0.5% per generation.

significantly reduced ΔF to 0.51% ($p < 0.05$) per generation, compared to an ΔF of 0.55% with 90 breeding sires and a similar mating quota of 80 offspring per year (Figure 6).

3.5.4 | Effect of breeding strategies based on kinship levels

Mean kinship selection (implemented on the selection of sires for breeding) resulted in an ΔF of 0.33% per generation without increasing the number of breeding sires per year (Figure 6). It was thereby significantly more effective to reduce ΔF than a combined strategy of both increasing the number of sires and a mating quota ($\Delta F = 0.51\%$, $p < 0.05$) (Figure 6). Mean kinship selection was also significantly more effective than a mating quota of 40 with approximately equal contributions across sires ($\Delta F = 0.40\%$, $p < 0.05$) (Figure 5). The stratified mating quotas resulted in a simulated ΔF of 0.43% per generation (Figure 6). Thereby, it was significantly less effective than mean kinship selection ($p < 0.05$), but significantly more effective than a combined strategy of both increasing the number of sires up to 130 and mating quota up to maximum 80 offspring per sire per year ($\Delta F = 0.51\%$, $p < 0.05$).

4 | DISCUSSION

Since 2009, the inbreeding rate (ΔF) in the Friesian horse population has been below the FAO limit of 1% and the most recent ΔF (2013–2022) is 0.72% per generation. With this study, we consolidate the results from Ducro et al. (2014), which showed that the implementation of a mating quota and publishment of individual kinship values in 2003 has resulted in a reduction in ΔF and kinship rate (Δf) until 2014. The last decade, however, number of foals born decreased and a larger popular sire effect was observed. Namely, the total contribution of the top 10 sires to the number of offspring per year has increased from 30% between 2000 and 2013, to 35% since 2014. This could explain the increase in ΔF and Δf per generation since 2014, which raises the question if the current mating quota is too liberal for the current active breeding population. Furthermore, the past two decades, the generation interval (L) has increased with 0.5 years for sires and 1.5 years for dams (Figure S5), which could be due to the implemented breeding strategies in 2003, resulting in breeding animals being used over a longer time period. Preferably, ΔF should be kept below 0.5% (Oldenbroek, 2017), and based on the estimated ΔF, additional breeding strategies should be implemented to reach an ΔF below 0.5%. Here, we used stochastic simulations to mimic the realistic population structure of the Friesian horse and simulated possible breeding strategies to reduce ΔF, which are discussed below.

In our simulations, we included the process of selection, leading to more related animals being selected and thereby prevent underestimation of the actual ΔF. Namely, when no selection index was added (random selection), the ΔF of the base scenario would be 0.23%, which is much lower than the actual ΔF of 0.72% based on pedigree. This suggests that selection is one of the main drivers of ΔF in Friesian horse breeding. Therefore, we included selection by adding a single quantitative trait, which resulted in a similar ΔF in the simulated base scenario compared to the ΔF based on the pedigree. However, we simplified the process of selection in the Friesian horse population by only adding a single quantitative trait, while selection goals likely differ across different breeders. The breeding goal of the KFPS is "a functionally built utility horse with the Friesian breed characteristics, and is healthy and vital, has a talent for performing in sports, has a reliable character and is workable" (KFPS, 2024a). Breeders mostly rely on phenotypic selection and some use the estimated breeding values for conformation traits and sports performance that are obtained through best linear unbiased prediction (BLUP) and published by the KFPS once a year. Each breeder prioritizes different traits. For example, some breeders prioritize a reliable character while others prioritize sport performance. In addition, the annual stallion show influences which traits are found to be most important (KFPS, personal communication). Different selection processes could influence the effect on ΔF. For example, a higher selection intensity increases ΔF and also heritability may influence ΔF (Bijma et al., 2000). Still, by keeping selection the same in all simulations, all breeding strategies should be affected by selection in a similar way, which makes relative ranking between breeding strategies valid.

Moreover, our simulations did not include selection against carriers of genetic disorders. Namely, with the current KFPS policy, only carrier-by-carrier matings are excluded, but stallions which are carrier of a genetic disorder can still be approved and become a breeding sire. In the future, it is likely that the genetic background of more genetic disorders that are segregating in the Friesian horse (Ploeg, 2015) are discovered. Then, the KFPS may weigh (some of) these genetic disorders in a selection index or excluding carriers can become part of the KFPS breeding program. Hence, there might be a risk that the effective population size decreases and then mating quotas should be reevaluated. For example, it could be possible to weigh the carrier status of a stallion into the stratified mating quotas. Hence, the assigned mating quota of a sire could not only depend on its mean kinship but also on its carrier status.

We found that increasing the number of breeding sires did not reduce ΔF. This is in contrast to expectation based on Wright's formula $\Delta F = (1/8N_m) + (1/8N_f)$, where N_m is the number of breeding sires and N_f is the number of breeding dams in the population (Wright, 1931). When increasing the number of breeding sires from 90 to 150 (and keeping the number of dams the same, with 3500 dams in the base scenario), the expected ΔF would decrease from 0.14% to 0.11% based on Wright's formula. Note that these values are a lot lower than the ΔF observed we found in our simulations. Wright's equation assumes populations of constant size with discrete generations, a Poisson distribution of family size without selection and random mating. In the Friesian horse population, and accordingly in our simulations, there is variation in the contribution of sires to the next generation, with few popular sires that contribute a lot to the next generation, and many less popular or unapproved sires that contribute little (Table S2, Figure 2b). This explains both the generally higher ΔF than in Wright's equation, and the fact that we did not see a decrease in ΔF with increase in number of sires. Namely, as long as some popular sires had a high contribution, increasing the number of breeding sires had little effect on ΔF. The additional number of sires would only sire few offspring and the top contributing sires would still sire the majority of offspring. This finding is in line with simulations of Windig and Oldenbroek (2015), who observed that equalizing the number of offspring over the available sires was more effective in reducing ΔF than just increasing the number of sires. Moreover, we saw that a twofold increase in the number of foals born per year with a mating quota of maximum 180 offspring per sire per year reduced ΔF (Figure 4), as it forces breeders to use more "non-popular" sires.

The number of unapproved sires used per year has highly increased since 2003. This is mainly due to the growth in number of breeders abroad, to facilitate breeding there, and the possibility to inspect foals from unapproved sires since 2006 (KFPS, personal communication). Breeders have the possibility to use semen from approved sires, but might choose for unapproved sires for practical reasons. The number of foals from unapproved sires has increased the last two decades, but still makes up a relative small part of the total number of foals (<15%). Currently, approval of unapproved sires would likely not have any effect on ΔF, as they will not become part of the popular sires. Simulation has shown that increasing the number of sires only has effect if sire contributions are equalized. Therefore, we recommend that if the number of approved sires increases, also sire contributions should be more equalized.

One strategy to equalize contributions of breeding sires is a sire mating quota (Klemetsdal, 1999; Mäki, 2010). A common way to implement a sire mating quota is to restrict the number of matings per sire per year. The current mating quota in the Friesian horse of 180 matings per sire per year for the first three breeding years, which in our simulations was translated to a maximum of 180 offspring per sire per year, showed no effect on reducing current ΔF. This is because the limit was hardly ever met. Namely, the contributions we used as input for the simulation without a mating quota were based on the 10 years before 2003, which were all below 5% of offspring per sire per year. With the current number of foals ($n = 3500$), 5% implies in expectation 175 offspring and, thus, the limit of 180 offspring per sire will only have limited impact. However, this mating quota may have been effective to reduce the ΔF between 2003 and 2014 due to the many foals born per year between 2002 and 2009 ($n > 6000$, such that 5% corresponds to 300 foals). Hence, with the currently lower number of foals born per year, a stricter mating quota is needed to reduce ΔF. In addition, we saw that since 2003, when implementing the mating quota, the compliance level of stallion keepers was high, because per year zero to two stallions exceeded 180 offspring per year. In addition to that, from the few stallions that exceeded this limit, most of them were popular older stallions for which the mating quota was not valid. Thus, a stricter mating quota valid for every breeding year of a sire would be more effective than only for the first three breeding years of a sire.

We observed that a threefold decrease of the current mating quota (from 180 offspring per sire per year for its first three breeding years to 60 offspring per sire per year for its entire lifespan) would be needed to obtain an ΔF lower than 0.5%. Though, by combining the strategies of a mating quota and increasing the number of breeding sires, a mating quota of 80 offspring per sire per year with 130 breeding sires would be sufficient to obtain an ΔF around 0.5%. Increasing the number of sires would be only effective with a strict mating quota (<80). With a strict quota, the popular sires would have less offspring and contributions of non-popular sires would increase and would become higher than the 16% contribution that was divided over the remaining non-popular sires. Instead of a mating quota per year, a mating quota per life is also possible. However, this is less effective, as Windig and Oldenbroek (2015) showed that popular sires would then be earlier replaced by relatives. Whichever mating quota is used, an important limitation is that, once popular sires meet their limits, they tend to be replaced by a highly related stallion (son, half-brother, etc.) (Oldenbroek, 2017). To overcome this issue, it is necessary to consider the relatedness/kinships of the sire selection candidates before selecting them as new breeding stallions.

Mean kinship selection, by only selecting breeding stallions with a lower than average kinship of the population, was the most effective strategy to reduce ΔF (Figure 6). To even further reduce ΔF, breeding mares could also be selected based on their kinship value, but this is harder to implement as the studbook cannot control which mare will be used in breeding. In our study, we first selected stallions as selection candidates that had lower than population mean kinship. Then, selection candidates were selected as breeding stallions based on their EBV. This way, there is some selection for genetic gain, but not as optimal as through OCS, which maximizes genetic gain while restricting F. While OCS is theoretically the best strategy, it is practically unfeasible in the large Friesian horse population as it requires full control over all matings. However, Windig and Oldenbroek (2015) found that results for restricting breeding animals with a high kinship to the rest of the population, as we did with mean kinship selection, were rather close to the results of OCS. With mean kinship selection, we excluded high kinship stallions with high EBVs and hence, there will be some loss in genetic progress in the population. Therefore, we suggest to not only select for low kinship stallions (both with high and average qualities) but also select high kinship stallions only if they have exceptional qualities. It is also possible to select for both mean kinship and genetic gain by combining breeding values and kinships into one single index (Cole, 2015; Pryce et al., 2012). Then, it is necessary to assign weights to kinship and genetic gain. However, these weights may change over time, especially nowadays, when due to the genetic disorders present in the population, the focus on genetic health should receive much more attention than the possible loss in genetic gain in order to conserve the breed. Thus, a breeding strategy related to kinship which does not automatically exclude high kinship breeding stallions might be preferred.

A novel strategy we explored in our study is stratified mating quotas. In this approach, a breeding sire was assigned a mating quota based on its individual mean kinship compared to the population mean kinship. In this way, breeding stallions with high individual mean kinship values were still selected but were assigned a stricter mating quota compared to breeding stallions with a lower individual mean kinship to the population. While breeding sires with a high kinship have a stricter mating quota compared to the general mating quota, this could also stimulate stallion keepers to select breeding stallions with lower individual mean kinship values and hence indirectly reduce ΔF. In addition to that stratified mating quotas (with 60, 80, 100 or 120 offspring per year) resulted in a lower ΔF (0.43%) than a general mating quota of 90 offspring per sire per year (0.55%), it has some other advantages over a general mating quota. Namely, with this novel approach, breeding sires might be used over a longer time period and less soon replaced (by their close relatives), which indirectly strengthens the effect on reducing ΔF. Furthermore, with a general mating quota, a risk is that two full-brothers can be maximally used as breeding sires. However, with stratified mating quotas, the use of two full brothers will be restricted more quickly, as once one of the relatives produces many offspring, the other relative will automatically receive a higher kinship and both full brothers will get a stricter mating quota. While this issue is also covered by OCS and stratified mating quotas are not as optimal as OCS, implementing stratified mating quotas to the practice breeding program is relatively simple and only requests yearly computing individual and population mean kinship of the breeding population and assigning breeding stallions a mating quota. Thus, stratified mating quotas offers a good balance between restricting ΔF, genetic gain and ease of implementation.

Population management strategies may be applied to both selection and mating. First, in the selection process, one may decide which animals should be used for breeding and how much they should be used. Such decisions include, amongst others, whether to increase the number of selected animals and/or restrict the number of offspring per selected animal (Toro et al., 1988; Villanueva et al., 1994). Second, in the mating process, one may decide which combinations of selected animals should be mated. An example is minimum co-ancestry mating, i.e. minimizing F_i in the offspring (Caballero et al., 1996). Both selection and mating strategies have been used to reduce the ΔF in endangered horse populations (Dell et al., 2021; Nielsen & Kargo, 2020). For example, in the Jutland horse, OCS has been successfully applied as selection strategy. This was practically feasible due to the small breeding population and willingness of horse breeders to participate (Nielsen & Kargo, 2020). In such small populations, it is important to note that when using OCS, most individuals will be selected for breeding (since self-kinships are also accounted for), but how much they should contribute differs. In the Friesian horse, OCS is practically not feasible due to the large population with many individual breeders ($N > 3000$). An example of a mating strategy that has been applied in the Cleveland Bay horse population, is that matings between parents with similar mean kinship, in combination with minimizing co-ancestry between the parents, has been advocated (Dell et al., 2021). In this population, the reduction in ΔF was mainly due to the reduction in the number of highly inbred matings per year ($F_i > 0.24$) and was only evaluated on the short term (<2 generations), while it is known that such mating strategies are mostly effective on the short term (Windig & Oldenbroek, 2015). However, for small populations like the Cleveland Bay horse, with only ~50 registered foals per year (Dell et al., 2021), there is little room for selection strategies, making them more dependent on mating strategies. In the Friesian horse, we showed that one of the main determinants of ΔF is the unequal sire contribution (as part of the selection step) rather than highly inbred matings, and we focused on long-term ΔF. Therefore, using solemnly a mating strategy is expected to be not very effective, and in such larger populations, selection strategies are necessary to reduce ΔF on the long term.

In this study, we simulated breeding strategies at the level of selection, which is important for limiting population ΔF. Additionally, individual breeders can make appropriate mating decisions by, e.g. minimizing the co-ancestry between parents (Windig & Oldenbroek, 2015), which limits the inbreeding of individual foals and could further help in reducing ΔF in the short term. However, breeding strategies at the selection step are of paramount importance for reducing the population ΔF in the long term.

5 | CONCLUSION

The current study focused on reflecting on inbreeding trends and evaluating the effectiveness of the breeding strategies using simulations in the Friesian horse population. We found that the main determinants of ΔF and Δf are selection and the unequal contribution of breeding sires to the number of offspring. Although the current ΔF in the Friesian horse population is not excessive, additional breeding strategies are advised. Our simulations show that breeding strategies related to kinship levels are the most effective in reducing ΔF. We recommend to imply a novel approach named stratified mating quotas, where breeding sires are assigned a mating quota based on their individual mean kinship compared to the population mean kinship. The outcomes of this study are not only applicable to the Friesian horse population but also to other horse breeds and species with high ΔF and small effective population sizes.

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CONFLICT OF INTEREST STATEMENT

The “Koninklijke Vereniging het Friesch Paarden-Stamboek” was involved in the study as funder for data collection and preparation of the manuscript. All authors declare that the results are presented in full and as such present no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author. Restrictions apply to the availability of these data, which were used under licence for this study. Data are available from the corresponding author with the permission of the "Koninklijke Vereniging het Friesch Paarden-Stamboek".

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REFERENCES

Bijma, P., Van Arendonk, J. A. M., & Woolliams, J. A. (2000). A general procedure for predicting rates of inbreeding in populations undergoing mass selection. *Genetics*, *154*(4), 1865–1877.

Boichard, D., Maignel, L., & Verrier, E. (1997). The value of using probabilities of gene origin to measure genetic variability in a population. *Genetics Selection Evolution*, *29*(1), 5–23.

Bowling, A. T., & Ruvinsky, A. (2000). *The genetics of the horse*. CAB International.

Caballero, A., Santiago, E., & Toro, M. A. (1996). Systems of mating to reduce inbreeding in selected populations. *Animal Science*, *62*(3), 431–442.

Cole, J. B. (2015). A simple strategy for managing many recessive disorders in a dairy cattle breeding program. *Genetics Selection Evolution*, *47*(1), 1–13.

Dell, A., Curry, M., Hunter, E., Dalton, R., Yarnell, K., Starbuck, G., & Wilson, P. B. (2021). 16 Years of breed management brings substantial improvement in population genetics of the endangered Cleveland Bay Horse. *Ecology and Evolution*, *11*(21), 14555–14572.

Doekes, H. P., Bijma, P., & Windig, J. J. (2021). How depressing is inbreeding? A meta-analysis of 30 years of research on the effects of inbreeding in livestock. *Genes*, *12*(6), 926.

Ducro, B. J., Schurink, A., Bastiaansen, J. W. M., Boegheim, I. J. M., van Steenbeek, F. G., Vos-Loohuis, M., Nijman, I. J., Monroe, G. R., Hellinga, I., Dibbits, B. W., Back, W., & Leegwater, P. A. J. (2015). A nonsense mutation in B3GALNT2 is concordant with hydrocephalus in Friesian horses. *BMC Genomics*, *16*(1), 1–9.

Ducro, B. J., Windig, J. J., Hellinga, I., & Bovenhuis, H. (2014). Genetic diversity and measures to reduce inbreeding in Friesian horses. In *Proceedings, 10th World congress of genetics applied to livestock production*.

FAO. (1998). *Secondary guidelines for development of national farm animal genetic resources management plans – Management of small populations at risk*. FAO.

Głażewska, I., & Jezierski, T. (2004). Pedigree analysis of Polish Arabian horses based on founder contributions. *Livestock Production Science*, *90*(2–3), 293–298.

Gómez, M. D., Valera, M., Molina, A., Gutiérrez, J. P., & Goyache, F. (2009). Assessment of inbreeding depression for body measurements in Spanish Purebred (Andalusian) horses. *Livestock Science*, *122*(2–3), 149–155.

Hisey, E. A., Hermans, H., Lounsberry, Z. T., Avila, F., Grahn, R. A., Knickelbein, K. E., Duward-Akhurst, S. A., McCue, M. E., Kalbfleisch, T. S., & Lassaline, M. E. (2020). Whole genome sequencing identified a 16 kilobase deletion on ECA13 associated with distichiasis in Friesian horses. *BMC Genomics*, *21*(1), 1–13.

KFPS. (2024a). *KFPS fokdoel*. https://kfps.nl/fokdoel/

KFPS. (2024b). *KFPS fokprogramma*. https://kfps.nl/fokprogramma/

Klemetsdal, G. (1999). Stochastic simulation of sire selection strategies in North-Swedish and Norwegian cold-blooded trotters. *Livestock Production Science*, *57*(3), 219–229.

Leegwater, P. A., Vos-Loohuis, M., Ducro, B. J., Boegheim, I. J., van Steenbeek, F. G., Nijman, I. J., Monroe, G. R., Bastiaansen, J. W. M., Dibbits, B. W., van de Goor, L. H., Helllinga, I., Back, W., & Schurink, A. (2016). Dwarfism with joint laxity in Friesian horses is associated with a splice site mutation in B4GALT7. *BMC Genomics*, *17*(1), 1–9.

Leroy, G., & Rognon, X. (2012). Assessing the impact of breeding strategies on inherited disorders and genetic diversity in dogs. *The Veterinary Journal*, *194*(3), 343–348.

Mäki, K. (2010). Population structure and genetic diversity of worldwide Nova Scotia duck tolling retriever and Lancashire heeler dog populations. *Journal of Animal Breeding and Genetics*, *127*(4), 318–326.

McCue, M. E., Bannasch, D. L., Petersen, J. L., Gurr, J., Bailey, E., Binns, M. M., Distl, O., Guérin, G., Hasegawa, T., & Hill, E. W. (2012). A high density SNP array for the domestic horse and extant Perissodactyla: Utility for association mapping, genetic diversity, and phylogeny studies. *PLoS Genetics*, *8*(1), e1002451.

Nielsen, H. M., & Kargo, M. (2020). An endangered horse breed can be conserved by using optimum contribution selection and preselection of stallions. *Acta Agriculturae Scandinavica, Section A—Animal Science*, *69*(1–2), 127–130.

Oldenbroek, J. K. (2017). *Genomic management of animal genetic diversity*. Wageningen Academic Publishers.

Pérez-Enciso, M. (1995). Use of the uncertain relationship matrix to compute effective population size. *Journal of Animal Breeding and Genetics*, *112*(1–6), 327–332.

Ploeg, M. (2015). *Challenging Friesian horse diseases: Aortic rupture and megaesophagus*. [Thesis, Utrecht University].

Pook, T., Schlather, M., & Simianer, H. (2020). MoBPS – Modular breeding program simulator. *G3: Genes, Genomes, Genetics*, *10*(6), 1915–1918. https://doi.org/10.1534/g3.120.401193

Pryce, J. E., Hayes, B. J., & Goddard, M. E. (2012). Novel strategies to minimize progeny inbreeding while maximizing genetic gain using genomic information. *Journal of Dairy Science*, *95*(1), 377–388.

Schurink, A., Arts, D. J. G., & Ducro, B. J. (2012). Genetic diversity in the Dutch harness horse population using pedigree analysis. *Livestock Science*, *143*(2–3), 270–277.

Schurink, A., Shrestha, M., Eriksson, S., Bosse, M., Bovenhuis, H., Back, W., Johansson, A. M., & Ducro, B. J. (2019). The genomic makeup of nine horse populations sampled in the Netherlands. *Genes*, *10*(6), 480.

Sevinga, M., Vrijenhoek, T., Hesselink, J. W., Barkema, H. W., & Groen, A. F. (2004). Effect of inbreeding on the incidence of retained placenta in Friesian horses. *Journal of Animal Science*, *82*(4), 982–986.

Toro, M. A., Nieto, B., & Salgado, C. (1988). A note on minimization of inbreeding in small-scale selection programmes. *Livestock Production Science*, *20*(4), 317–323.

Verrier, E., Leroy, G., Blouin, C., Mériaux, J. C., & Rognon, X. (2010). Estimating the effective size of farm animals populations from pedigree or molecular data: A case study on two French draught horse breeds. In *Proceedings of the 9th World congress on genetics applied to livestock production: 1–6 August 2010; Leipzig*.

Villanueva, B., Woolliams, J. A., & Simm, G. (1994). Strategies for controlling rates of inbreeding in MOET nucleus schemes for beef cattle. *Genetics Selection Evolution*, *26*(6), 517–535.

Windig, J. J., & Hulsegge, I. (2021). Retriever and pointer: Software to evaluate inbreeding and genetic management in captive populations. *Animals*, *11*(5), 1332.

Windig, J. J., & Oldenbroek, K. (2015). Genetic management of Dutch golden retriever dogs with a simulation tool. *Journal of Animal Breeding and Genetics*, *132*(6), 428–440.

Windig, J. J., Verweij, M. J. W., & Oldenbroek, J. K. (2019). Reducing inbreeding rates with a breeding circle: Theory and practice in Veluws Heideschaap. *Journal of Animal Breeding and Genetics*, *136*(1), 51–62.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, *16*(2), 97–159.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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