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ORIGINAL ARTICLE

Optimal contribution selection applied to the Norwegian and the North-Swedish cold-blooded trotter – a feasibility study

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Animal model; breeding programme; horse; rate of inbreeding; selection response.

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Summary

The aim of this study was to examine how to apply optimal contribution selection (OCS) in the Norwegian and the North-Swedish cold-blooded trotter and give practical recommendations for the future. OCS was implemented using the software Gencont with overlapping generations and selected a few, but young sires, as these turn over the generations faster and thus is less related to the mare candidates. In addition, a number of Swedish sires were selected as they were less related to the selection candidates. We concluded that implementing OCS is feasible to select sires (there is no selection on mares), and we recommend the number of available sire candidates to be continuously updated because of amongst others deaths and geldings. In addition, only considering sire candidates with phenotype above average within a year class would allow selection candidates from many year classes to be included and circumvent current limitation on number of selection candidates in Gencont (approx. 3000). The results showed that mare candidates can well be those being mated the previous year. OCS will, dynamically, recruit young stallions and manage the culling or renewal of annual breeding permits for stallions that had been previously approved. For the annual mating proportion per sire, a constraint in accordance with the maximum that a sire can mate naturally is recommended.

Introduction

In the cold-blooded trotter, Norway and Sweden have a long history of exchange of genetic material (e.g. Nilsson & Stang 1990). Norwegian stallions were widely used in Sweden from right after the Second World War, but the first Swedish stallion was only approved in Norway as late as 1978 (Klemetsdal 1998). Therefore, in 1990, the trotting associations from the two countries declared the intention to regard the Norwegian and the North-Swedish cold-blooded trotter as one joint population (Klemetsdal 1998), and this was formalized in 2000 by the signing of an agreement (Norsk Hestesenter, 2008). Consequently, the Norwegian and North-Swedish trotter have the same breeding plan and joint breeding value estimation. To have a licence for breeding, the stallions need to be approved at yearly horse shows, in which their own phenotypic performance in races is considered, as well as their body conformation, movements in trotting and the temperament. In addition, there is a clinical veterinary examination to detect disqualifying conditions such as testicle rupture, sidebones or osteochondrosis. Additionally, a breeding value for trotting performance, derived multivariately from data on racing status, earnings, speed and placings, is calculated annually (Norsk

Hestesenter, 2008). The selection decisions are made by a joint selection committee, with representatives from both countries, evaluating the stallions both with respect to conformation as well as performance: own performance for young stallions (3–5 years.) and genetic evaluation for older stallions (≥6 years.). In this small population, with approximately 1200 foals born in 2011, a stallion can be approved for breeding from the age of 3 years, and whilst approved is given a yearly mating quota of 110 mares (80 in his home country and 30 in the neighbouring country). An approval is valid for 6 years, after which the owner can apply for an indefinite continuation. If granted, the stallion will be classified as elite-, A-, B- or C-stallion, depending on the performance of the offspring group. Thereafter, an approved stallion can only be culled if a disqualifying disorder is proven on the stallion himself or in many of his offspring. This means that many older stallions will be available for mating, having a negative impact on the population's inbreeding situation, because of their large number of progenies.

Árnason (2001) concluded that the rate of inbreeding in the Nordic trotter was alarmingly high and recommended consideration of inbreeding when selecting for genetic improvement of racing performance. In this respect, one method that can be applied is optimal contribution selection (OCS) (Meuwissen 1997), which maximizes the response of selection at a predefined rate of inbreeding. By adopting this method, the population will be managed at a given risk (rate of inbreeding), whilst the current practice does not put any control to risk.

However, few publications exist on experiences from implementing OCS in live populations. Studies of the method in dairy cattle, beef cattle and sheep show a substantial increase in genetic gain, but the studies also show that a coordinated breeding policy on the use of the selection candidates is needed to realize the benefits from the application (Avendaño *et al.* 2003; Colleau *et al.* 2004; Kearney *et al.* 2004). Further, Colleau & Tribout (2008) applied OCS to a pig breeding population, Niemann *et al.* (2009) to the Hanoverian breeding programme for show jumpers and Koenig & Simianer (2006) to the German Holstein dairy cattle population.

Here, the objective was to apply OCS to the Norwegian and the North-Swedish cold-blooded trotter, and to give practical recommendations for future breeding.

Material and methods

Data as used for the BLUP evaluations in the autumn of 2006 were utilized, consisting of 22 825 individual observations of summarized race results for horses born 1971–2003. Data were summarized over age classes 3–6 years (3–5, 3–4 and 3 years of age for the three last year classes, respectively). Further, a total of 29 004 horses were unraced, with missing information for earnings. Average earnings per race were transformed by fourth root and standardized by birth year and country. Estimated breeding values (EBVs) were calculated with a univariate animal model, as considered by Olsen *et al.* (2010). This approach provided EBVs that had a correlation with the EBVs from the current multivariate model > 0.95 (H.F. Olsen, T. Meuwissen, G. Klemetsdal, unpublished results). A pedigree file of 98 861 animals was constructed, comprising 97 411 animals registered in the period from 1846 to 2003 and 1450 parents that had no individual registration.

Individual inbreeding coefficients were calculated using the Quaas–Henderson algorithm (Henderson 1976; Quaas 1976). The effective population size (N_e) in generation *t*, unconditional of becoming selected as a parent or not in generation *t*, was calculated for two reference populations representing the last non-random changes in inbreeding fluctuations in the population; either for animals born from 1982 to 1985 or animals born from 2000 to 2003 (at time *t*), by use of the formula:

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

where the rate of inbreeding per generation, ΔF_t, is:

$$\Delta F_t = \frac{F_t - F_{t-1}}{1 - F_{t-1}} \text{ (Falconer \& Mackay 1996)},$$

which among the animals (n) in the reference populations was calculated as:

$$\Delta F_t = \frac{1}{n}\sum_{i=1}^{n} \frac{F_i - \frac{1}{2}(F_{\text{sire}_i} + F_{\text{dam}_i})}{1 - \frac{1}{2}(F_{\text{sire}_i} + F_{\text{dam}_i})}$$

with F_i being the individual coefficient of inbreeding for animal *i* in generation *t*, and F_{sire_i} and F_{dam_i} are the individual inbreeding coefficients of their parents, which will account for the selection decision of the parents in generation *t*–1, and be independent of an assumed, average generation interval.

Our perspective was to apply OCS to the population in 2006, utilizing our BLUP evaluation, for selection of sires (there is no approval of mares, and hence OCS was not used to select mares). OCS was implemented using the software Gencont (Meuwissen 2002), for overlapping generations. The genetic level of the individuals in the next generation is $G_{t+1} = \boldsymbol{c_t}'\boldsymbol{EBV_t}$, where $\boldsymbol{c_t}$ is a vector of genetic contributions to next generation for the selection candidates, as described in Meuwissen (1997), and $\boldsymbol{EBV_t}$ is the vector of EBVs. Gencont finds the value of $\boldsymbol{c_t}$, which maximizes G_{t+1}, whilst restricting the rate of inbreeding at the desired level.

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

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

where ΔF_g is the constraint on rate of inbreeding per generation, and L is a predefined generation interval, assumed to be equal to 11.1 years, according to Klemetsdal (1993).

In Gencont, it is advised, for computational reasons, to restrict number of selection candidates to approximately 3000 animals (both sexes). Data supplied by the trotting associations in Norway and Sweden, respectively, showed that 1816 mares were actually mated in 2006 in the two countries, which made them selection candidates. Among stallions, a vast majority was approved for breeding before the age of 7 years (Figure 1), which made us to limit age at first approval to 6 years of age. Thus, all young stallions (also including non-approved stallions, but geldings excluded) of the age 3–6 years, which had raced (n_3 = 319, n_4 = 317, n_5 = 295, n_6 = 254), were included as selection candidates as well as stallions older than 6 years that kept a breeding licence in 2006 (n = 122; mean age = 13.6 ± 4.8 years).

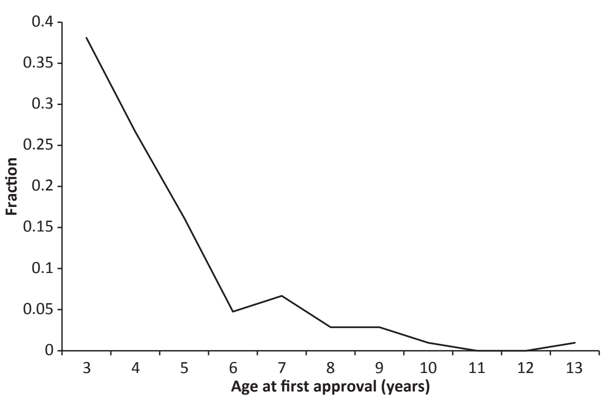

Figure 1 Distribution of ages at first approval for stallions licensed in Norway and Sweden in 2006.

The contribution of mares were assumed to be 1/1816, whilst the contribution of sires ($\boldsymbol{c}$) were calculated, for rates of inbreeding of 1% or 0.5% per generation (ΔF_g = 0.01 or 0.005), assuming either no limit on the number of mares that a sire can mate (cmax_nolim) or a situation restricting the number of mated mares to 100 mares (cmax_100) (using the 'cmax' option in Gencont). Results were compared with those from 'real life' using the 117 stallions that were mated to at least one mare in 2006 (real_life).

In practice, because of no selection among mares, the contributions of the sires have to be calculated without the knowledge of which mares that are available for mating in the relevant year. One option is to utilize as mares those being mated in the previous year (MARE_2005, n = 1711). The results were compared with those obtained with the mares actually mated in 2006 (MARE_2006). For the two mare alternatives, the number of mated mares per sire was restricted to 100, and the constraint on rate of inbreeding was 1%.

To indicate a possible sublining in the population, the pairwise kinship between all animals born within year classes was calculated for the last 4 year classes (2000–03), using the algorithm of Luo & Meuwissen (1992), and inference was drawn from histograms.

Results

The Norwegian and North-Swedish cold-blooded trotter showed a steep increase in the level of inbreeding from the mid-1950s, after a short period with a drop of inbreeding in the 1950s because of crossing. This increase lasted for a period of approximately 30 years (Figure 2), and the effective population size was low, only 31 for the period 1982–85 (ΔF = 0.0161 ± 0.0005). Later, the inbreeding increased less steep (Figure 2), resulting in a somewhat higher effective population size for the period 2000–03 (N_e = 54; ΔF = 0.0093 ± 0.0003).

Table 1 shows that remarkably few, but young sires were selected when using OCS without restriction on cmax (cmax_nolim). In addition, a considerable number of mares were assigned to some of these sires.

In 2006, the distribution of the number of mated mares per stallion in 'real life' (real_life) is shown in

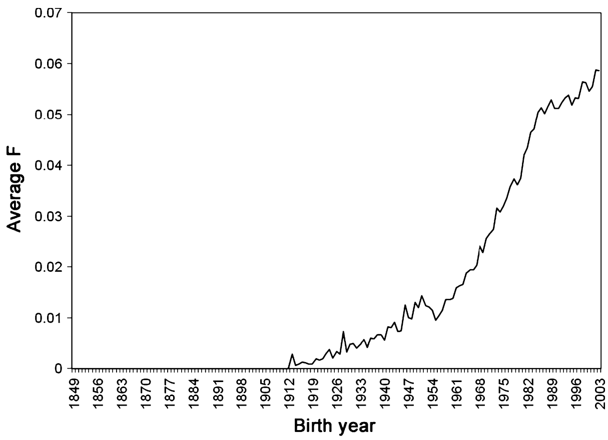

Figure 2 Average coefficient of inbreeding (*F*) per year of birth.

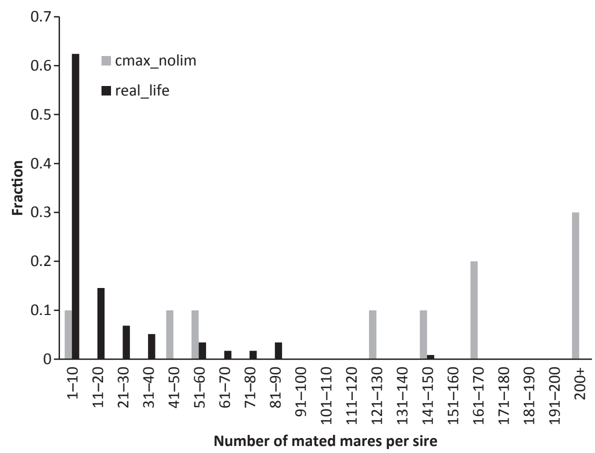

Figure 3 Distribution of number of mated mares per sire for those used in 2006 (real_life), as well as for those selected by optimal contribution selection (OCS), by assuming no limit on number of mares that a sire can mate (cmax_nolim). With OCS, the mare candidates were those that actually mated in 2006, and the constraint on rate of inbreeding was 1% per generation.

Figure 3, as well as the corresponding distribution that OCS advise, with no limit on the number of mares that a sire can mate (cmax_nolim) for a rate of inbreeding of 1% per generation. In this situation, the number of mares per stallion was high for almost all selected stallions, as only 10 sires were advised to be selected; three of the stallions were given a mating quota <60 mares and the remaining seven were supposed to mate more than 120 mares each (Figure 3). The largest mating quota assigned was as high as 454 mares (not shown), demonstrating the need to apply the cmax-option in Gencont. In contrast, in 'real life', 117 sires were selected, and almost 90% of the stallions mated <40 mares, covering almost 50% of the mares in 2006, whereas the remaining 10% of the stallions mated the last half of the mares (Figure 3) (allowed to mate a maximum of 110 mares each).

When using OCS with no limit on the number of mares per stallion (cmax_nolim), 60% of the selected stallions were 6 years or younger, whilst

Table 1 Descriptive statistics for sires used in 2006 (real life) as well as for those selected by optimal contribution selection (OCS), by assuming two different constraints on number of mares that a sire can mate (cmax_nolim and cmax_100). With OCS, the mare candidates were those that actually mated in 2006, and the constraint on rate of inbreeding (ΔF_g) was 1% or 0.5% per generation

		cmax_nolim		cmax_100	
	real_life	ΔF_g = 0.01	ΔF_g = 0.005	ΔF_g = 0.01	ΔF_g = 0.005
# sires	117	10	10	19	20
Mean # matings ± SE	17 ± 2.3	182 ± 45.2	182 ± 33.2	96 ± 7.4	91 ± 8.5
Mean age ± SE	11.37 ± 0.43	8.00 ± 1.45	8.00 ± 1.45	6.63 ± 0.91	6.75 ± 0.84
Fraction ≤6 years[a]	0.19	0.60	0.60	0.68	0.70
Fraction ≥10 years[a]	0.60	0.30	0.30	0.21	0.20
Maximum age at mating	23	16	16	16	16
Fraction used in 'real life'[a]	1.00	0.70	0.60	0.58	0.50
Fraction approved, not used in 'real life'[a]	0	0.20	0.20	0.16	0.15
Fraction non-approved[a]	0	0.10	0.20	0.26	0.35
Fraction non-approved ≤6 years	0	1.00	1.00	1.00	1.00
Mean EBV[b]	1.60	2.33	2.17	2.19	2.09
Fraction N[c]	0.79	0.60	0.50	0.68	0.65

EBV, estimated breeding value.
[a]Fraction of # sires.
[b]Weighted mean according to mating proportion.
[c]Fraction of # sires registered in Norway (N).

this share increased somewhat (68% and 70%) when restricting the number of mares per stallions to 100, for the two rates of inbreeding, ΔF_g, equal to 1% and 0.5%, respectively (Table 1). In addition, a number of these were currently non-approved. The maximum age of a selected stallion with the OCS procedure was 16 years, obtained in all four situations (combination of cmax and ΔF_g values) (Table 1). However, in 'real life', only 19% of the stallions were 6 years or younger, and as much as 60% of the stallions were 10 years or older (the oldest was 23 years old) (Table 1). Generally, with OCS, the average EBV of sires was approximately 30–45% higher than in 'real life', and the least increase was obtained for the most constrained alternative (Table 1).

Relative to 'real life', OCS favoured Swedish sires, as the fraction of Norwegian sires decreased to 50%, with no restriction on the number of mares that a sire was allowed to mate (cmax_nolim) and a rate of inbreeding of 0.005 (Table 1). As with cmax_nolim and $\Delta F_g = 0.01$, only 10 sires were selected, as four of the five Swedish stallions showed a low genetic relationship with the selection candidates (Table 2). Furthermore, the mating proportions varied somewhat between the two cmax_nolim situations (ΔF_g of 0.01 and 0.005, respectively). In both these latter situations, at least nine of the 10 selected sires were represented in all the other situations, and more sires were first added when restricting the number of matings per sire to 100 (Table 2). For ΔF_g of 0.005, the algorithm replaced the least contributing sire(s) with mediocre stallion(s), which had a low relationship with the selection candidates.

Table 3 shows results for the number of sires selected and their average EBV, when selected using the relationships to mares mated the previous year (MARE_2005), relative to those that were actually mated (MARE_2006). There were only minor differences between the sires selected in the two situations, supported by their mean EBV. In addition, 16 of the 17 sires selected with MARE_2005 were also selected with MARE_2006 (results not shown).

Table 2 Stallions selected by the use of optimal contribution selection and their nationality [Norway (N) or Sweden (S)], birth year (BYR), estimated breeding value (EBV), assigned mating proportions (MP) (in %) and average relationship with the selection candidates (Av.rel.), assuming two different constraints on number of mares that a sire can mate (cmax_nolim and cmax_100) and constraint on rate of inbreeding (ΔF_g) of either 1% or 0.5% per generation

			cmax_nolim				cmax_100			
			$\Delta F_g = 0.01$		$\Delta F_g = 0.005$		$\Delta F_g = 0.01$		$\Delta F_g = 0.005$	
Stallion	BYR	EBV	MP	Av.rel.	MP	Av.rel.	MP	Av.rel.	MP	Av.rel.
H.G. Balder (N)	2001	2.78	25.0	0.169	20.4	0.159	6.0	0.149	6.0	0.144
Sundbo Kravall (S)	2001	2.27	19.1	0.134	15.9	0.131	6.0	0.121	6.0	0.121
Moe Brage (N)	2002	2.70	16.0	0.163	11.3	0.154	6.0	0.151	6.0	0.148
Lome Kongen (N)	2000	2.49	9.3	0.149	6.9	0.143	6.0	0.145	6.0	0.142
Fakse (S)	2000	1.83	9.0	0.104	11.6	0.107	6.0	0.101	6.0	0.102
Jærvsøfuxen (S)	1990	1.46	8.7	0.08	13.7	0.086	6.0	0.075	6.0	0.076
Ulfrigg (N)	1991	1.96	7.1	0.113	8.0	0.114	6.0	0.119	6.0	0.118
Frigg Mollyn (N)	1999	2.04	2.8	0.119	2.7	0.118	6.0	0.124	6.0	0.124
Pelle Babs (S)	1994	1.53	2.7	0.084	7.8	0.090	6.0	0.084	6.0	0.084
Slått Eld (N)	2002	2.52	0.2	0.151	–	–	6.0	0.158	6.0	0.153
Grym (S)	2002	1.22	–	–	1.8	0.073	2.4	0.073	6.0	0.079
Faksen J:r (S)	2002	2.50	–	–	–	–	6.0	0.164	6.0	0.162
Lome Elden (N)	1995	2.54	–	–	–	–	6.0	0.182	–	–
Lundfrigg (N)	1998	2.01	–	–	–	–	6.0	0.129	6.0	0.128
Stjerne Faks (N)	2003	2.23	–	–	–	–	6.0	0.142	6.0	0.141
Wikvinn (N)	2001	2.19	–	–	–	–	6.0	0.148	6.0	0.143
Åsajerven (N)	2002	2.40	–	–	–	–	6.0	0.153	6.0	0.153
Tonar (N)	2003	2.26	–	–	–	–	1.3	0.148	–	–
Keik Jo (N)	2002	2.22	–	–	–	–	0.4	0.145	–	–
Edolles Ivar (S)	2001	1.01	–	–	–	–	–	–	2.6	0.066
Karamba (N)	2001	0.71	–	–	–	–	–	–	0.7	0.047
Lauvin (N)	1995	1.56	–	–	–	–	–	–	0.6	0.099
Bles Høvding (N)	2000	1.57	–	–	–	–	–	–	0.1	0.100

Table 3 Number of sires selected by use of optimal contribution selection and their mean estimated breeding value (EBV), assuming that sires are allowed to mate a maximum of 100 mares per year (cmax_100) and that the mares mated were either those actually mated (MARE_2006) or those mated the previous year (MARE_2005). The constraint on rate of inbreeding was 1% per generation

	MARE_2006	MARE_2005
# sires	19	17
Mean EBV[a]	2.19	2.17

[a]Weighted mean according to mating proportion.

Figure 4 shows the distribution of the pairwise kinship values calculated between the 1610 animals born in 2002. The distribution is somewhat multi-modal, as expected from a frequency of half-sib matings, but the somewhat increased frequency of low kinship values may indicate some sublining of the population.

Discussion

In this population, the rate of inbreeding was larger up till 1990 than later. In the first period considered, 1982–85, the effective population size was calculated as 32, corresponding well with the estimate of 31 of Klemetsdal & Johnson (1989) in Norwegian trotter. Later (2000–03), the effective population size increased to 54, only marginally above the recommended minimum value of 50 (Meuwissen & Woolliams 1994). This increase in the effective population size is expected to be minor affected by changes in mating policy between the two periods (considered by, e.g. Gutierrez *et al.* (2008)), as the reference periods were well within the periods studied (before or after 1990). Rather, the increase of N_e is likely due to a change of the most important ancestor; from Stegg-best to Elding (Olsen & Klemetsdal 2009), born 36 years apart, which has the potential to reduce ΔF at least temporarily. However, with large variation in progeny groups, as before, and no balancing of sires on their contributions, the rate of inbreeding will eventually increase again.

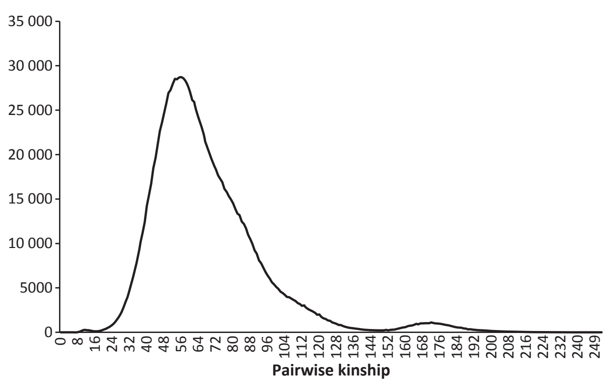

Figure 4 The distribution of the pairwise kinship (×1000) among horses born in year 2002.

The EBVs in this study were calculated using a univariate animal model of earnings and were considered adequate with the goal of this study, which was to advise on how OCS should be utilized. However, practical future implementation should obviously be based on the most current breeding value estimates.

The OCS algorithm allowed for not more than approximately 3000 selection candidates. The results demonstrate that, for the selection of males by Gencont, assuming the mare candidates to be the same as the previous year was adequate. This is because there is no selection on mares and generations are only turning over slowly, but the need for this is that there is no other information on what mares might be available for mating.

With as many as 1800 mares mated, and the need for inclusion of already selected stallions, only four age classes of the youngest male candidates could be added. With this distribution of male candidates on age classes and with a considerable genetic trend for the trait selected (Olsen *et al.* 2010), obviously a majority of the selected stallions were 6 years or younger. With a limitation on the number of male candidates that can be included, as here, a continuous update of whether a male is gelded or dead will be important. Furthermore, only inclusion of males with phenotype above average within a year class would double the number of year classes to be included with OCS. Yet, another alternative would be to implement an alternative algorithm, allowing for a larger number of selection candidates (e.g. Hinrichs *et al.* 2006). Another approach, like semidefinite programming, would not necessarily solve the problem with large number of selection candidates, but would rather guarantee finding the optimum solution (Pong-Wong and Woolliams, 2007).

OCS selected a remarkably low number of sires, by turning over the generations faster through selection of younger sires, being less related, on average, to the mares. In addition, OCS selected a number of Swedish sires, with a low average relationship with the other selection candidates. Selection of younger sires implies that OCS will impact the assumed generation interval, making it shorter, increasing ΔF_d again. Further, the finding of some less related Swedish sires and also a fraction of very low kinship values indicate that the population might be somewhat sublined and that future clustering are needed to give further insight.

One should be aware that this study only considers 1 year of selection, starting from a population with quite unbalanced coancestries. When the system becomes more balanced with respect to coancestry, the assignment of mating proportions will probably change, that is that more sires will be selected, and smaller proportions will be assigned to each sire. This fact, and also that the mating quotas are far larger than can be covered by sires in natural mating (of predominant use in this population) and also that mean breeding values of selected sires were only marginally reduced by restricting the number of mares per sire, lead us to recommend OCS calculated with a constraint on number of mares per sire.

With a restriction on number of mares per sire, OCS advises a considerable fraction of non-approved sires. This fact illustrates that the OCS procedure includes stallions for breeding, which normally would not have been considered in 'real life'. These stallions are not registered for approval, majorly because the owner is unaware of the animals' genetic potential. Thus, the results from OCS could be used to propose which sires that are candidates for approval, that is that a practice with active recruitment of stallions for approval could be established.

With a vast majority of young selection candidates [that actually resembles practice (Figure 1)], OCS generally reduced the mean age of selected stallions and did not in any situation assign a proportion to a sire that was more than 16 years of age. In addition, of the 10 most popular stallions in 'real life' in 2006 (covering almost 43% of the mares) (results not shown), only one was selected by OCS. Thus, OCS actively culls sires from breeding based on their total genetic contributions and replaces them with younger stallions with less impact on the overall coancestry. Therefore, it is recommended to establish a practice with an annual breeding permit for earlier approved sires, if they are selected by OCS. Such a practice will be self-adjusting, as sires that are widely used will have a reduced probability of becoming reselected.

Conclusion

The current breeding practice in the Norwegian and North-Swedish trotter does not control the risk from generating a too large rate of inbreeding, which, however, can be solved by adopting OCS. Such an implementation is feasible by using mares that were mated the previous year to select the sires, to overcome the lack of an inventory of current available mares. The list of sire candidates needs to be continuously updated because of deaths and geldings, and first-time male candidates should be restricted to those with phenotype above average within a year class. This will allow selection candidates from many year classes to be included. We propose the results from OCS used to actively recruit first-time candidates for approval, as well as assignment of an annual breeding permit for earlier approved stallions. For the annual mating quota, a constraint in accordance with the maximum that a sire can mate in natural mating is recommended.

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