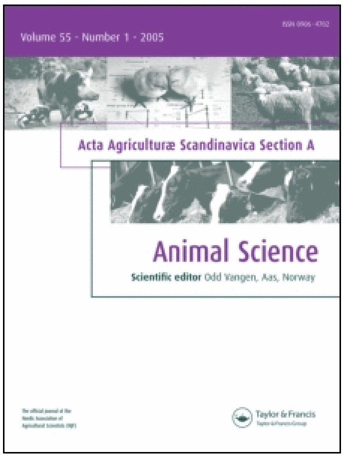

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Management to ensure effective population size in a breeding programme for the small Norwegian horse breeds - a simulation study

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SHORT COMMUNICATION

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

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

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

Introduction

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

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

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

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

Material and methods

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

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

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

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

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

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

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

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

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

Results and discussion

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

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

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

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

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

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

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

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

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

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

Conclusion

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

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