SELECTION IN SMALL POPULATIONS WHERE 
EX SITU CONSERVATION IS USED TO REDUCE INBREEDING

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INTRODUCTION

In situ conservation schemes are preferred over ex situ schemes (Convention on Biological Diversity, 1992), because the population can evolve in its original environment with in situ schemes. Thus, the population can continue to improve genetically and genetic improvement is possible. Genetic improvement helps to conserve the population either by selecting against genetic defects or improving the breed such that its demand increases (e.g. by selection for a niche market).

The aim of this study is to present a scheme that takes advantage of ex situ frozen semen in an in situ conservation scheme in order to reduce the risk of inbreeding and still achieve genetic improvement in very small populations. We will study the resulting breeding scheme and genetic gain (ΔG) for very small populations with a stringent restriction on rate of inbreeding (ΔF = 0.01 per generation). We assume that semen from all sires is frozen and kept in gene banks and that dams are only used for one generation.

MATERIAL AND METHODS

Algorithm. The selection algorithm of Meuwissen and Sonesson (1998) that maximises ΔG under a restriction on ΔF in populations with overlapping generations is used. Here follows a brief description of the selection algorithm.

We want to optimise $c_t$ every generation such that the expected genetic merit of the progeny is as high as possible, i.e. we maximise $G = c_t'EBV_t$, where $EBV_t$ is a (n x 1) vector of BLUP breeding value estimates of animals in generation t. The maximisation of $G$ is under two restrictions. The first restriction is on the average relationship of the population, $C_t = r^1_r^t c_t' A_t c_t + 2r^t c_t' J_t r^2 + r^2_t A_t r^2$, where $A_t$ is an (n x n) relationship matrix of the selection candidates in generation t, $r$ is a vector of long-term contributions of age-classes 1 through $q$, whereby subscript 1 points to the age-class of new-born animals and 2 to the age-classes of older already born animals, $J_t$ is a (n x q) matrix of average relationships of selection candidates with every age-class, $A_t$ is a (q x q) matrix with average relationships of age-classes. The value of the constraint, $C_t$, increases by approximately $\Delta F(2-C_{t-1})$ every generation, where $\Delta F$ is the desired rate of inbreeding. The factor (2-$C_{t-1}$) arises because average relationship increases by approximately twice the rate of inbreeding, and its increase levels off when current levels of relationship, $C_{t-1}$, increase. The second restriction is on the maximum contribution of the males/females of $\frac{1}{2}$, $Q'c = \frac{1}{2} I_{2t}$, where $Q$ is a (n x 2) known incidence matrix of the sex of all
selection candidates. The algorithm of Meuwissen (1997) uses Lagrangian multipliers to solve for optimum $c_t$, which maximises $G$ under the two constraints.

The solution vector $c_t$ times $2N$, rounded to integers, equals a vector of optimal number of progeny that each candidate should obtain, where $N$ is the total number of new-born progeny per generation. This is not guaranteed to give the optimum integer solution, but it probably yields a reasonable approximation.

**Simulated schemes.** The general structure of the simulated scheme was that of a closed nucleus breeding scheme with discrete generations. The trait is recorded on sires and dams before selection. Thereafter, all females are culled and replaced by their daughters, but the sires can still be used unlimited, because semen of all sires is frozen. Mating was at random. Each mating pair produces two offspring, one male and one female. Genotypes, $g_i$, for base animals were sampled from a distribution $N(0, \sigma^2_a)$, where $\sigma^2_a$ is base generation genetic variance of 0.30. Later generations were obtained by simulating progeny genotypes from $g_i = \frac{1}{2}g_s + \frac{1}{2}g_d + m_i$, where $s$ and $d$ denote sire and dam of progeny and $m_i$ equals the Mendelian sampling component, which is sampled from $N(0, \frac{1}{2}(1-F)\sigma^2_a)$, where $F$ is the average inbreeding coefficient of parents $s$ and $d$. Phenotypes are simulated by adding an environmental effect to the genotypes, which was sampled from $N(0,(1-\sigma^2_e))$. Estimates of breeding values (EBVs) are obtained by using the BLUP breeding value estimation procedure (Henderson, 1984). The restriction on $\Delta F$ is set as $1/2N$, where $N$ is the number of new-born animals per generation for the first five generations. This rather high inbreeding is used, because at the beginning of the program, there is no semen from old males yet. After generation five, the inbreeding rate was reduced to 0.01 per generation. Results are based on 100 replicated schemes of 50 selection rounds. Inbreeding, genetic response, generation interval and number of selected sires and dams were monitored.

**RESULTS**

It is possible to select from a population with very few ($N = 6, 10$ or 20) animals, whereby frozen semen from gene-banks is used in addition to live sires (Table 1). The desired $\Delta F$ was achieved for all three schemes (Table 1) and $F$ was stable over generations (Figure 1).

For schemes with 10 new-born animals (five males and five females) per generation, $\Delta G$ was 0.043 $\sigma_p$ units per generation (Table 1). The generation interval was 4.5 for sires and 1.0 for dams, because dams could only be selected once. There were 4.5 sires and 3.6 dams selected. For larger schemes with 20 new-born animals per generation, there were more selection candidates, such that younger sires with higher EBVs could be selected. More sires (8.5) and dams (6.4) were however selected for the larger scheme to keep the average coancestry sufficiently low.
Table 1. Rate of inbreeding ($\Delta F$), genetic gain per generation ($\Delta G$), generation interval of sires (L) and the number of selected sires/dams (Sel) for schemes with $\Delta F$ restricted to 0.01 and 6, 10 or 20 new-born animals per generation.

<table>
<thead>
<tr>
<th>Number of animals</th>
<th>$\Delta F$ (se) $^a$</th>
<th>$\Delta G$ (σp-units)</th>
<th>L (generations)</th>
<th>Sel. sire/dam</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>0.014 (0.004)</td>
<td>0.028</td>
<td>7.2</td>
<td>3.0/2.3</td>
</tr>
<tr>
<td>10</td>
<td>0.011 (0.002)</td>
<td>0.043</td>
<td>6.1</td>
<td>4.5/3.6</td>
</tr>
<tr>
<td>20</td>
<td>0.010 (0.001)</td>
<td>0.074</td>
<td>4.2</td>
<td>8.5/6.4</td>
</tr>
</tbody>
</table>

$^a$ se = standard error

Figure 1. Inbreeding levels (F) of schemes with 6, 10 or 20 new-born animals per generation.

DISCUSSION

In combined *in situ* and *ex situ* conservation schemes, it is possible to achieve a substantial genetic gain in very small populations when taking advantage of frozen semen of a gene-bank, thus allowing the use of older less related sires. For schemes with 5 sires and 5 dams born per generation, $\Delta G$ was 0.043 $\sigma_p$ when $\Delta F$ was restricted to 0.01 per generation. For example, for dairy cattle, $\sigma_p \approx 1000$ kg, $\Delta G$ would be 40-45 kg. Without the use of frozen semen, presented schemes could not achieve $\Delta F = 0.01$, but a larger scheme of 50 males and 50 females per...
generation, would achieve $\Delta G = 0.195 \sigma_p$. Thus, $\Delta G$ was only five times lower than in a ten times larger scheme, although generation interval was six times longer and there was low selection intensity in the dam path. With a less stringent restriction on $\Delta F$, younger sires with higher EBVs would have been selected, thus increasing $\Delta G$.

For such small schemes as the ones simulated here, the main interest may not be to increase $\Delta G$, but instead to reduce $\Delta F$. In such combined in situ and ex situ conservation scheme, it is possible to reduce $\Delta F$ to zero, by repeatedly using the semen of old sires (Sonesson et al., 2002).

The constraint on $\Delta F$ was $1/2N$ for the first 5 generations and thereafter it was 0.01, which would imply an effective population size of 50 animals per generation, the minimum viable effective population size (FAO, 1998). However, the generation structure of sires became overlapping, because the use of older sires, resulting in an effective population size $< 50$.

Dams had discrete generation structure in these schemes, but results are expected to be similar for populations with overlapping generations. Results based on a population with overlapping generation structure are, however, more specific to the chosen age-structure, measurement of trait (age, which sex) and whether progeny testing is possible or not.

CONCLUSIONS
A combined in situ and ex situ conservation scheme was presented, where genetic improvement was achieved by selecting males and females with a restriction on $\Delta F$. Due to the use of frozen semen, the restriction on $\Delta F$ of 0.01 could be kept, which is lower than the lowest $\Delta F$ possible in a live population of the same size. Furthermore, substantial $\Delta G$ was achieved: $\Delta G$ was only five times lower than in a ten times larger scheme, although generation interval was six times longer and there was low selection intensity in the dam path.

REFERENCES