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Optimal Contribution Selection Applied to the Norwegian Cheviot Sheep Population

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Acknowledgements

This thesis marks the end of five years of studies at The Norwegian University of Life Sciences (NMBU). I have grown a lot both academically and personally over the last five years.

I have lived and worked on a sheep farm the last year, and combining sheep farming with writing a thesis about sheep breeding have therefore been very interesting for me. I have welcomed over 70 lambs into this world along with the writing of this thesis. Combining the writing process and taking care of lambs have been challenging and there have been many sleepless nights, but in the end, I have learned a lot from this experience.

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Sammendrag

Kontroll på innavlsutviklingen er viktig for alt avlsarbeid, og spesielt i små populasjoner. Seleksjon for å optimalisere genetiske bidrag (OCS) er en metode som setter en restriksjon på innavlsraten, samtidig som den maksimerer den genetiske fremgangen.

Målet for denne oppgaven er å anvende OCS for den Norske sjeviotpopulasjonen i 2014 og sammenlikne med den virkelige seleksjonen gjort samme år. Fire scenarioer for seleksjon er testet, og ønsket er å møte så mange av de biologiske og økonomiske restriksjonene som mulig.

Utrekningen for OCS er gjort med programmet Gencont 2. Nye algoritmer som reduserer utrekningstiden og tillater at man bruker OCS i større populasjoner er implementert i programmet. I tillegg er Gencont 2 tilpasset å kunne brukes ved seleksjonsmetoder med flere seleksjonssteg og overlappende generasjoner.

Datasettet er basert på dagens avlsstruktur for Sjevioten med fire væreringer og bruk av avkomstgransking innen væreringene og semin på tvers av væreringene. Alle søyer og søyelam var preselektert basert på kjennskap til lamming i 2015. Gencont 2 ble anvendt til seleksjon av værer. Ønsket var å maksimere fremgangen på O-indeks ved en innavlsrate på maksimalt 1% per generasjon.

Resultatene viser at når test- og eliteværene blir selektert med OCS, er avlsverdiene til de selekterte værene signifikant høyere enn med den virkelige seleksjonen ($P<0.001$). Dersom det kun er seminværene som blir selektert med OCS er det ingen forskjell. Restriksjonen for innavlsraten er holdt for alle seleksjonsscenarioene. Dette indikerer at om OCS implementeres i den norske Sjeviotavlen vil man kunne få høyer avlsverdier i avkom av de selekterte dyrene og dermed en større genetisk framgang sammenliknet med dagens seleksjonsmetode, samtidig som innavlsraten holdes på et akseptabelt nivå.

Abstract

Managing inbreeding is essential for all breeding work, especially in small populations. Optimal Genetic Contribution (OCS) is a selection method that restricts inbreeding while maximizing genetic gain.

The aim of this study was to apply OCS in the ram selection for Norwegian Cheviot Sheep in the mating season in 2014 and compare with the actual selection done the same year. Four different scenarios were tested, with the aim to meet as many of the biological and economical restrictions as possible.

The OCS calculations were done with the software Gencont 2. New algorithms that reduce computing time and allows for larger datasets have been implemented in the software. In addition, Gencont 2 can handle multi-stage selection schemes and overlapping generations.

The datasets were based on the current breeding structure of the Norwegian Cheviot with four ram circles, progeny testing within the ram circles and use of AI across ram circles. All females were pre-selected based on knowledge about lambing in 2015. Gencont 2 was used for ram selection. The aim was to optimize genetic progress on total merit index at an inbreeding rate of maximum 1% per generation.

When test- and elite rams are selected with OCS, the average breeding values of the selected rams are significantly higher than with today's selection ($p<0.001$). However, if only the AI rams are selected with OCS, there is no difference in the average breeding values of the selected rams. All four scenarios hold the restriction on rate of inbreeding. This indicates that if OCS is implemented in the Norwegian Cheviot population, one could achieve a greater genetic progress compared to the selection scheme used today, and still keep and acceptable rate of inbreeding.

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1 Introduction

Breeding production animals is a fine balance between high selection intensity to improve genetic progress in production traits, and controlling the inbreeding not to lose genetic variance.

Improvement of the selection methods by utilizing new technology like artificial insemination (AI) and genomic selection, have resulted in a high genetic progress in animal breeding schemes (Woolliams et al. 2015). With increased selection response, the management of inbreeding is even more important as inbreeding depression will lead to a lower performance in the long term (Woolliams et al. 2015).

A method to control the inbreeding while maximizing the genetic gain was developed by Meuwissen (1997), called Optimum Contribution Selection (OCS). Meuwissen (1997) found that the OCS could yield substantially higher selection response than truncation selection with best linear unbiased selection (BLUP) at the same rate of inbreeding (ΔF). However, computing time has been an issue for larger breeding populations as the original algorithm required inversion of the relationship matrix (Woolliams et al. 2015).

Dagnachew and Meuwissen (2014) has developed a new OCS algorithm that reduces computation time by avoiding inversion of the relationship matrix and consequently handles larger populations. A software called Gencont2 implements the new iterative algorithm (Dagnachew & Meuwissen 2014).

A feasibility study with Gencont have been done for the Norwegian and North-Swedish cold-blooded trotter (Olsen et al. 2013) with promising results. The Norwegian Association of Sheep and Goat Breeders (NSG) is considering implementing OCS in the breeding scheme for Norwegian Cheviot Sheep, and other Norwegian sheep breeds (*T. Blichfeldt, pers. comm.* 2016).

The Norwegian Cheviot breeding scheme is based on ram selection in three stages. Test and elite rams are selected for natural service within ram circles. AI rams are selected across ram circles among elite rams from previous years.

The aim of the current study is to apply OCS in the breeding program for Norwegian Cheviot Sheep by using the Gencont2 software to select the males for breeding, and to discuss whether the Norwegian Cheviot sheep breed would benefit from implementing OCS in the selection process.

2 Theory

2.1 Inbreeding

Controlling inbreeding in a population is important as rapid increase in inbreeding can cause inbreeding depression and an increase in heritable genetic diseases (Woolliams et al. 2015).

Inbreeding occurs when animals with a common ancestor are mated. It is unavoidable in a closed population. An animal having alleles that are Identical By Descent (IBD), need to have two copies of the same allele from the same ancestor. Inbreeding coefficients (F) are the probability of having alleles that are IBD in reference to a base population where no inbreeding is assumed (Falconer & Mackay 1996).

When estimating the level of inbreeding, the best approach is to find the "new" inbreeding, or the rate of inbreeding (ΔF).

(Falconer & Mackay 1996) defines rate of inbreeding at year t (ΔFt) as following:

$$\frac{(F_t - F_{t-1})}{(1 - F_{t-1})} \quad [1]$$

Where F_t is the inbreeding coefficient in year t and F_{t-1} is the inbreeding coefficient of the previous year (Falconer & Mackay 1996).

Another way to illustrate the inbreeding in a population is the effective population size. The effective population size (N_e) is defined as $\frac{1}{(2\Delta F)}$ and gives an expression of the inbreeding situation in terms of effective number of breeding animals (Falconer & Mackay 1996).

Managing inbreeding in a population is the same as managing the genetic variation, and there is a linear relationship between loss of genetic variation and increase of inbreeding (Woolliams et al. 2015).

Meuwissen (2009) states that the average relationship in generation t is the same as the average relationship of the parents in generation t-1, including an animals relationships with self, weighed by amount of offspring attained by the parents. This leads to a conclusion that by controlling the increase of the average relationships of the parents (including self-relationships), the increase of inbreeding is also controlled (Meuwissen 2009).

2.2 Optimum Contribution Selection

Increase in genetic gain (ΔG) is key for a production animal breeding program. Optimum Contribution Selection (OCS) is a selection procedure that maximizes ΔG, while setting a restriction on the rate of inbreeding (ΔF) (Meuwissen 1997). OCS restrict inbreeding by restricting the average relationship of the parents, weighed by their potential contribution to the next generation (Meuwissen 2009).

According to Wooliams et al. (2015) and illustrated in equation 2, the genetic progress in a population (ΔG) is the cross product of the long term contribution of individual *i* (r_i) and the Mendelian sampling term of individual *i* (a_i).

$$\Delta G = \sum r_i \ a_i \qquad [2]$$

Woolliams et al. (2015) describes the algorithms for Optimum Contribution Selection as follows:

G is Genetic gain and G_{t+1} is Genetic gain for the next generations, OCS maximizes G_{t+1} while constraing C_{t+1} (the group coancestry for the next generation). The mathematical statement of the problem is: Optimize over contributions $\boldsymbol{c}_t$ to maximize G_{t+1} = $\boldsymbol{c}_t^T \hat{\boldsymbol{u}}_t$.

Where $\boldsymbol{c}_t$ is a (*n* x 1) vector of contributions of selection candidates of generation t.

$\hat{\boldsymbol{u}}_t$ is a (*n* x 1) vector of estimates of breeding values of the candidates in generation t.

In addition, some constraints are needed to secure that the individual contributions are ≥0 and the contributions of all females sum to ½ and the same for all the males. The constraints are given by Woolliams et al. (2015) as:

$$\boldsymbol{c}_t^T \boldsymbol{A}_t \boldsymbol{c}_t / 2 = C_{t+1} \qquad [3]$$

$$\boldsymbol{Q}_t^T \boldsymbol{c}_t = 1/2\boldsymbol{l}. \qquad [4]$$

$C_{t,i}$ ≥0 for I = 1, … , *n* selection candidates

$\boldsymbol{A}_t$ is the (n x n) relationship matrix of the candidates in generation t

$\boldsymbol{Q}_t$ is a (n x 2) incidence matrix indicationg the sex of the candidates with 0's and 1's.

$\boldsymbol{l}$ is a (2 x 1) vector of 1's to restrict the summed contributions of males and females to ½.

The optimal contributions is the fraction of the offspring gene pool that each candidate should be allocated (Woolliams et al. 2015). The problem of constraints was solved by Meuwissen (1997) using an unconstrained maximization of the Lagrangian function (found in Woolliams et al. (2015)) by the following equation:

$$H = \boldsymbol{c}_t^T \widehat{\boldsymbol{u}}_t - (\boldsymbol{c}_t^T \boldsymbol{A}_t \boldsymbol{c}_t - 2C_{t+1})\lambda_0 - (\boldsymbol{Q}^T \boldsymbol{c}_t - 1/2l)^T \boldsymbol{\lambda} \qquad [5]$$

Where λ_0 and $\boldsymbol{\lambda}$ are Lagrangian multipliers. The formula for optimal selection then becomes:

$$c_t = A_t^{-1}(\widehat{\boldsymbol{u}}_t - \boldsymbol{Q}_t \boldsymbol{\lambda})/(2\lambda_0) \qquad [6]$$

The Lagrangian multipliers scale the solution to attain the constraints (Woolliams et al. 2015). This solution have some problems, among them, it can give a negative value for $C_{t,i}$ for individual *i* (Woolliams et al. 2015). According to Woolliams et al. (2015) this can be solved by using an iterative algorithm that removes the candidates with negative contribution from the optimization process and sets their contribution to zero, and repeating the process until none of the candidates have a negative contribution. The final solution may not be optimal because the individuals removed could have received a contribution in the true optimal solution (Woolliams et al. 2015). Using the Lagrangian multipliers also requires an inversion of the relationship matrix, for each iteration, which requires a lot of computing time if the relationship matrix is large (Woolliams et al. 2015).

Gencont solves this by using partitioned matrix theory (Meuwissen 2002). This can save computing time if the number of animals removed is smaller than the animals retained for each iteration (Woolliams et al. 2015). Gencont still have problems in large populations with large relationship matrices. To make OCS more applicable for large scale breeding programs, Dagnachew and Meuwissen (2014) developed Gencont 2 which uses an iterative algorithm that avoids the direct inversion of the relationship matrix and instead obtains solutions iteratively. The only limitation here is the computer capacity to store the relationship matrix (Woolliams et al. 2015). Gencont 2 also uses the Gauss-Seidel method to constraint that solutions are valid (i.e. solutions are either zero or positive). However, for computational reasons, animals with their contribution fixed to zero are removed after 500 iterations for the first time and every 100 iterations until it converges (Dagnachew & Meuwissen 2014).

Woolliams et al. (2015) explains that Gencont 2 obtains c_t by solving the equations:

$$\boldsymbol{A}_t\boldsymbol{c}_t = (\widehat{\boldsymbol{u}}_t - \boldsymbol{Q}_t\,\boldsymbol{\lambda})/(2\lambda_0) \qquad [7]$$

Updating the Lagrangian Multipliers λ_0 and $\boldsymbol{\lambda}$ while running the iterations. Gencont 2 have a 90-95% faster computing time than Gencont, making it more usable for large scale breeding programs (Dagnachew & Meuwissen 2014).

2.3 Norwegian Cheviot breed description and history

Figure 1. Norwegian Cheviot Sheep. Photo: Henrik Steinsund (Regelverk for kåring av Sjeviot 2015).

The Norwegian Cheviot sheep breed is a breed mostly used by farmers on the west coast of Norway. According to the farmers keeping Cheviot, the breed is tough and adapted to the harsh coastal climate in Norway with low quality pastures (Regelverk for kåring av Sjeviot 2015). The Norwegian Cheviot sheep breed originates from the Cheviot Hills in The United Kingdom. They are characterized by their standing ears and convex nose (Regelverk for kåring av Sjeviot 2015). Figure 1 show a characteristic Norwegian Cheviot Sheep. It is a dual-purpose breed used for both meat and wool production, with a crossbreed type wool. The first documented Cheviot Sheep in Norway was imported from the United Kingdom in 1854. Systematic breeding on Norwegian Cheviot was not in place until the 1860's (Regelverk for kåring av Sjeviot 2015).

2.4 Breeding goals and EBV calculations

The breeding goal of the Norwegian Cheviot breed is to have a dual-purpose breed that gives the owner a good production economy. It should be a sheep especially adapted to rough pastures (Regelverk for kåring av Sjeviot 2015). The phenotypic traits in the breeding goal is litter size, spring weight, weaning weight, carcass weight, carcass quality and carcass fat grading. NSG use the software package DMU (Madsen & Jensen 2007) to calculate BLUP breeding values as a total merit index (O-index) with mean 100 and standard deviation 10. Breeding values are computed based on information registered by the farmers in the "Norwegian Sheep Recording System", which is a national database where farmers voluntarily register information about their sheep (The Norwegian Sheep Recording System 2014).

NSG calculates breeding value predictions 13 times a year from June – December. Schedule of index runs in 2015 are listed in Table 1. The calculations in 2014 would be on different dates, but in the same week of the year as in 2015 (*T. Blichfeldt, pers. comm.* 2016)

Table 1. Overview of index runs in 2015 (Indekskjøringene for sau 2015).

Index run	Date published
Summer - 1f* (S1f)	June 24th
S1	July 24th
S2	September 11th
S3	September 18th
Fall – 1f* (H1f)	September 25th
H1	October 2nd
H2f*	October 9th
H2	October 16th
H3f*	October 23rd
H3	October 30th
H4f*	November 6th
H4	November 20th
H5	December 11th

* The index-runs marked with f is preliminary calculations and will be overridden at the next calculations.

2.5 Breeding Structure

Sheep production in Norway is very seasonal. The lambs are born in the spring (April-May), put on pasture during the summer and slaughtered between August and November. The main mating season is November and December (*T. Blichfeldt, pers. comm.* 2016). The breeding structure for Norwegian Cheviot is adapted to the seasonal production system in Norway and the biological limits of sheep production.

In 2007, 1,6% of the Norwegian sheep were Cheviot (Årsmelding Sauekontrollen 2007). In 2014, the breed had decreased to 1,1% of the total sheep population in Norway (Årsmelding Sauekontrollen 2014). The total population size of Norwegian Cheviot Sheep counted 3379 ewes in 2014 (Årsmelding Sauekontrollen 2014), while the breeding population consists of approximately 1800 ewes in four ram circles as seen in Figure 2.

Flocks that are geographically close to each other and flocks in the same county can form a ram circle (Eikje & Lewis 2015). A flock needs to have a good health status and be approved by the Norwegian Food Safety Authority to be a member of a ram circle (Regler for væreringer og værholdslag 2011). The ram circles elect a board each year. The ram circle board selects both the elite rams and test rams for progeny testing, in addition to making sure the member flocks follow the rules for ram circle operations. (Regler for væreringer og værholdslag 2011). In order to limit spreading of contagious diseases it is not allowed to exchange animals between ram circles (Landbruksdepartementet 2002). The genetic connectedness is high both within the breeding population and between the breeding population and also with some of the flocks outside the ram circles. This is probably because it was common to move rams between ram circles before the restriction came in 2002 (Eikje & Lewis 2015). Now the genetic links between ram circles are formed by use of AI.

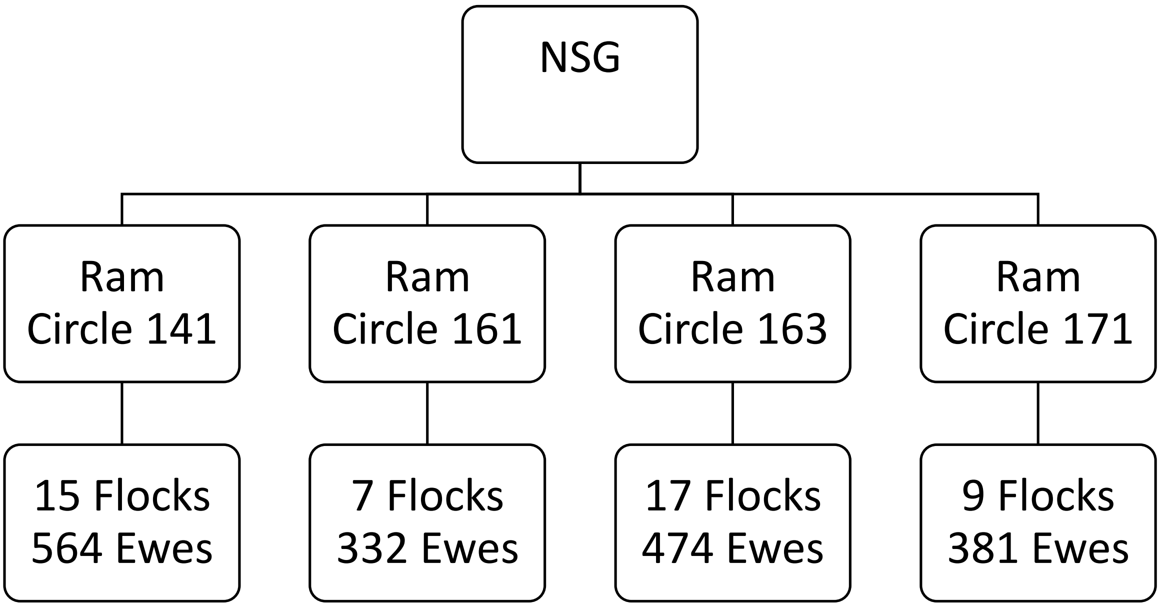

Figure 2. Breeding structure for Cheviot sheep in Norway, 2014.

2.6 Selecting AI rams

AI rams can produce many offspring, and an important aspect of selecting AI rams is to acquire enough information about the ram himself and his potential offspring by testing his progeny. The process of progeny testing and selecting AI rams takes 3-4 years, depending on whether the ram is 2.5 or 3.5 years old when selected. Most of the rams are selected in year 3. Test rams are selected based on parent average and performance test. They may also have an own spring weight and an own weaning weight. Elite and AI rams are selected based on the information above + information from progeny testing. Figure 3 illustrates the multi-stage ram selection.

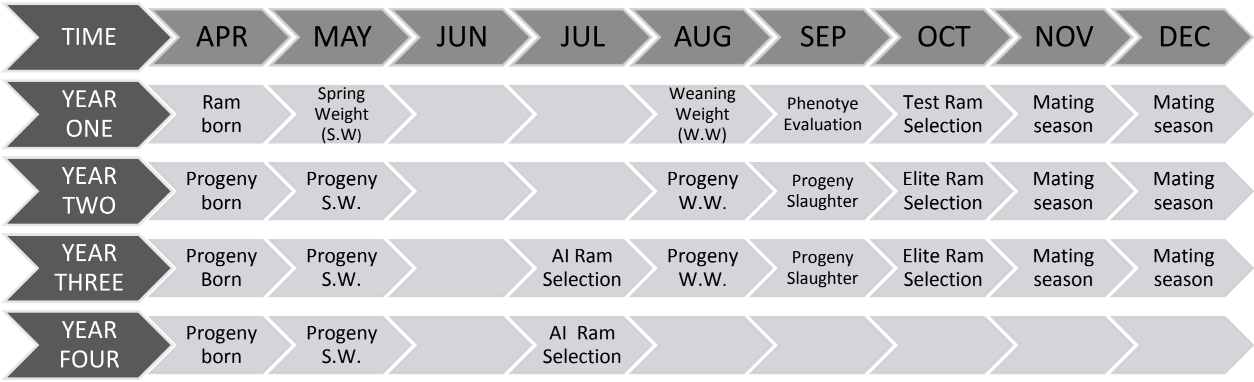

Figure 3. Timeline for the multi-stage selection of rams in Norwegian Cheviot sheep.

When the rams are about 4-5 months old the farmer selects which rams to slaughter, and which rams to bring for the phenotype evaluation (“Kåring”) during the fall (August-September). The phenotype evaluation consists of a judge scoring the ram on several traits on a scale from 5-10. The traits considered are body, legs, wool-quality, wool-length and breed characteristics. To be approved for breeding, no trait can be rated below 6/10 and the ram also need a minimum index-value of 110 (Regelverk for kåring av Sjeviot 2015). The index of a newborn ram lamb is based on pedigree information. In addition, lambs are weighed at around 6 weeks of age (spring weight) and around 20 weeks of age (weaning weight). Spring weight is voluntary and around 50% of the lambs have a recorded spring weight (*J. Jakobsen, Pers. Comm.* 2016). Weaning weight on the other hand is compulsory in order to get the ram approved (Regelverk for kåring av Sjeviot 2015).

The Ram Circle Boards select test rams among the phenotypically approved rams. The Ram Circles have different priorities for choosing test rams. Some ram circles choose the rams with the highest index regardless of phenotype scoring. Other ram circles are more concerned about the phenotype evaluation scoring and does not consider index as much as long as it is above 110 (*T. Blichfeldt, pers. comm.* 2016). Test rams are used in the following mating season with natural service on approximately 70-75% of the ewes.

In year two, the first progeny from the test rams are born (see Figure 3). To get an official O-index, test rams need a minimum of 15 slaughtered offspring (*T. Blichfeldt, pers. comm.* 2016). The best test rams are selected as elite rams for natural mating for another season. Elite rams are mated to about 20% of the ewes (*T. Blichfeldt, pers. comm.* 2016).

When the ram is 2.5 years old, they are available for AI selection. AI rams are selected by NSG among the elite rams. The AI ram selection takes place in July, as rams need to be moved to an AI station to produce semen in time for the mating season. The test- and elite rams on the other hand are not selected until middle of October (*T. Blichfeldt, pers. comm.* 2016).

The process of finding Norwegian Cheviot AI rams for the next breeding season is as follows:

- NSG breeding department selects the best 10-15 candidates among the 2.5-year-old progeny tested rams in the four ram circles purely based on their breeding value.
- Each ram circle checks if the ram candidate is available and suitable for AI service (alive and well functioning, still owned by the ram circle etc.)
- The board of the Cheviot ram circle society prioritize rams based on their correctness with respect to the breed standard (nose, ears, etc.)

NSG makes the final decision and selects 3 rams (2-4) based on breeding value, pedigree, (controlling inbreeding) and breed standard. (*T. Blichfeldt, pers. comm.* 2016).

About 10% of the Cheviot ewes with the highest breeding values are inseminated with an AI ram. Conception rate of the inseminated ewes is 70% to 80%. The ewes that do not conceive are mated with an elite ram (*T. Blichfeldt, pers. comm.* 2016).

2.7 Import and Artificial Insemination

From 2005, NSG started to import rams from UK on a regular basis. Before 2005, there were only sporadic imports (*T. Blichfeldt, pers. comm.* 2016). The Norwegian Cheviot population is small and the main reason for importation is to limit increase in inbreeding in the population. At the time of importation the ram does not have a breeding value on a Norwegian scale, and it is not until he gets progeny information in Norway that he also gets a Norwegian breeding value. It is therefore very variable how the imported rams perform in Norway (*J. Jakobsen, Pers. Comm.* 2016).

The rams with semen sale in 2014 are shown in Table 2. However, none of these rams were included as candidates for AI selection except the import ram; Glen the Prince. The two Norwegian Cheviot rams selected for AI in 2014 both died before start of semen collection. Their names were Birkelid Pilten and Valentin Børsen. Instead of selecting new AI rams, NSG decided to sell semen doses from older AI rams (*J. Jakobsen, Pers. Comm.* 2016). Valentin Børsen and Birkelid Pilten are included in the dataset as selection candidates for AI and will be considered as the real selected AI rams for this year regardless of their untimely death.

Table 2. Doses of Semen sold from Cheviot rams in 2014 (T. Blichfeldt, pers. comm. 2016).

Name	Year taken in to AI	Doses sold (frozen)
Glen the Prince	Import 2014	80
Alex	2011	3
Bosse	2012	20
Pelè	2013	83
Vladimir	2013	166
Total doses sold in 2014		361

3 Material and Method

3.1 Description of Dataset

The aim of the study was to compare which rams were selected for breeding in 2014 to the rams that are suggested by Optimal Contribution Selection using the Gencont 2 software. The mating season 2014 was chosen in order to avoid uncertainty in female selection. Females for mating in 2014 were based on actual ewes lambing in any of the ram circle flocks in 2015.

Males for mating can be separated in three ram type categories: test rams, elite rams and AI rams. Test rams are selected within ram circle. These ram lambs are born the same year as the selection takes place. In order to qualify as test ram they need to pass the phenotypic evaluation test and have an index above 110 at the time of the evaluation. Elite rams are selected within ram circle among the rams that were test rams in the ram circle in the previous mating season (2013). AI rams are selected across ram circles among the rams that were elite rams in any of the ram circles in 2013 and are still alive.

The breeding values considered for Gencont 2 is the O-index values at the time of selection. AI rams are selected in July and O-index values from the index run S1 (July) was used for AI ram candidates whereas O-index values from the index run H3 (October) was used for test ram candidates, elite ram candidates and for all females.

The schedule for index runs is shown in Table 1. One of the AI ram candidates was an import ram. At the time of import, the ram does not have index value on Norwegian scale and he was allocated an average index value of the other AI ram candidates. The average index value of all selection candidates in the data set was 111.6 and with a standard deviation of 10.64.

Figure 4 illustrates the number of ewes lambing in 2015 in each of the four ram circles as well as number of test- and elite ram candidates available for selection in 2014. The figure also show the number of AI ram candidates available for selection. The pedigree was traced as far back as possible for all selection candidates and counted a total of 6080 animals (*J. Jakobsen, Pers. Comm.* 2016).

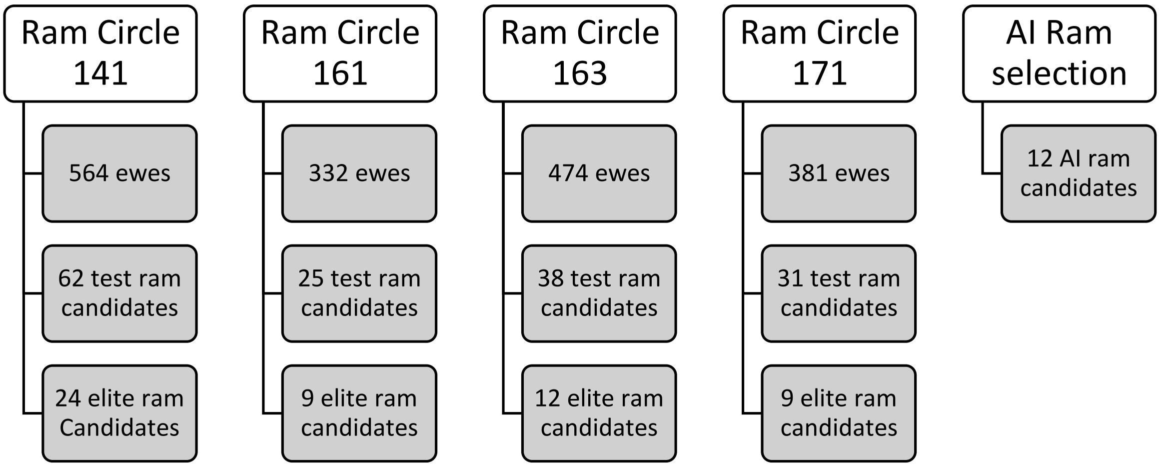

Figure 4. Number of selection candidates in each ram circle included in the dataset for the Norwegian Cheviot Sheep population in 2014.

In the Norwegian Cheviot population, AI sires 7-8% of the lambs born. This is approximately 150 pregnancies per year.

3.2 Optimal Contribution Selection using Gencont 2

Optimal Contribution Selection (OCS) was conducted on the Cheviot data described above using the Gencont 2 software (Dagnachew & Meuwissen 2014).

Gencont 2 needs input and information according to the biological, economical and structural restrictions in the population. Minimum and maximum number of matings can be set for each animal and for a group of animals. The selection was restricted according to the biological restrictions of natural service mating by setting a maximum % contribution for each ram (cmax). Another goal was to have the same amount of rams selected as the real selection in 2014. In order to have Gencont 2 select number of rams closest to the real number of rams selected in 2014, different percentage of cmax was tried out and the one that gave number of selected rams closest to the real selection in each ram circle, or across the population were used in the calculation. For ram circles 141, 161, 163 and 171, the cmax used was 3%, 8%, 4% and 4% respectively. When the whole population was considered, the cmax value was set to 1,1%. With lower cmax, more rams were selected, and with higher cmax, fewer rams were selected, while still holding the inbreeding restriction.

The restriction on inbreeding rate (ΔF) was set to a maximum of 0.01 per generation, or 0.0039 per year with a mean generation interval of 2.55 years to parent/offspring.

3.3 Selection Methods

Four selection scenarios are tested in order to find the best ways to utilize OCS in the Norwegian Cheviot population. The four scenarios are within ram circle selection, within ram circle selection with pre-selected AI rams, across ram circle selection and across ram circle selection with pre-selected test- and elite rams. The goal is to implement OCS in the breeding scheme but still make the process as close as possible to the selection process used today.

There are some limits to the breeding scheme that the selection methods have different approaches to, but none of the suggested selection methods can hold all of the restriction in terms of how the selection is done today. Rams for natural mating have a maximum number of how many ewes they are capable to mate within a mating season of around 30 ewes. The test rams need a minimum of 15 slaughtered offspring for the progeny testing. It is expensive to have rams on the AI station, and this leads to an maximum number of 4 AI rams, but only 2 were selected in 2014 for the Norwegian AI rams (the imported ram is never in Norway) (*J. Jakobsen, Pers. Comm.* 2016).

Due to health restrictions, it is not allowed to circulate rams between the ram circles. As an example, a ram from ram circle 141 cannot be mated with ewes from ram circle 163. Thus rams for natural mating cannot be selected on a population scale.

The different options suggested for the selection processes using OCS is as follows:

Scenario 1. Test, elite and AI rams are selected within ram circle

In scenario 1, test and elite rams were selected by OCS among test and elite ram candidates within each of the four ram circles. As there are no exchange of rams between the four ram circles they were treated as separate populations. All AI candidates were set to available for selection for each ram circle. Number of selection candidates available for each ram circle is illustrated in Figure 5. All test ram candidates were in age group one, elite ram candidates in age group two and AI ram candidates in age group three. The maximum contribution restriction (cmax) for each ram is 3%, 8%, 4% and 4% in ram circles 141, 161, 163 and 171 respectively. As an example, any ram selected from ram circle 163 cannot have a contribution higher than 4%, but the contribution can be lower.

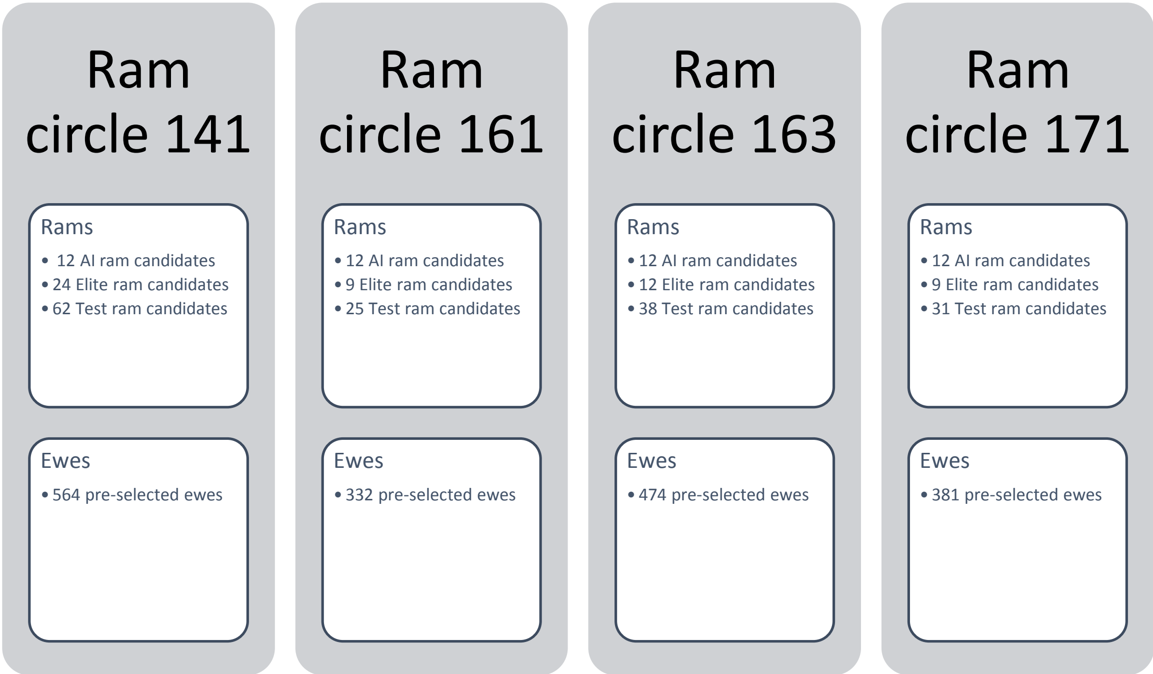

Figure 5. Set-up of datasets for calculating OCS within the ram circles.

Scenario 2. Test and elite rams are selected within ram circle. AI rams are pre-selected.

In scenario 2, test and elite rams were selected by OSC among test and elite ram candidates within each of the four ram circles. The only AI rams available for selection is the rams that were selected by NSG in 2014; 2 Norwegian rams and one imported ram. The AI rams are only pre-selected as candidates, and the contribution is still given by Gencont 2 according to their breeding value and population average relationship. As in scenario one, all test rams were in age group one, elite ram candidates in age group two and pre-selected AI rams in age group three. The maximum contribution restriction (cmax) is the same for the four ram circles as in scenario 1. Gencont 2 selected rams simultaneously from each group of selection candidates.

Scenario 3. Test, elite and AI rams are selected across ram circles

In scenario 3, all ram type categories (AI, elite- and test rams) were selected by OCS among the ram candidates across the four ram circles. This was done for the complete population in one computation. The maximum contribution of any ram selected was 1,1%. The number of candidates in each of the ram type categories is illustrated in Figure 6. In terms of selecting with OCS, this method is expected to give the largest genetic progress at a given inbreeding constraint as it will optimize for one population only and not for four sub-populations.

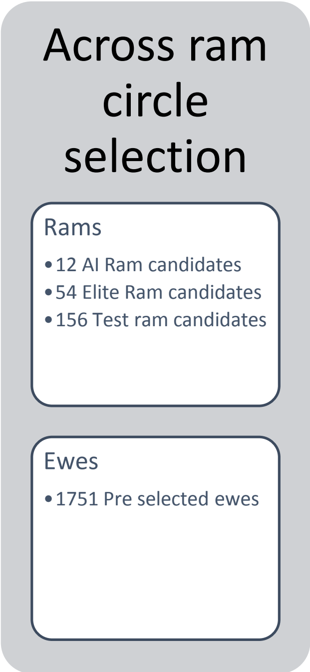

Figure 6. Distribution of ram type categories for OCS computations for the Norwegian Cheviot breed across ram circles.

Scenario 4. AI rams are selected across ram circles, test and elite rams are pre-selected by the ram circles.

In scenario 4, AI rams were selected with OCS across ram circles, and test- and elite rams were pre-selected by the four ram circle boards. The pre-selected rams are the rams that had offspring in 2015 and fills the criteria to be in the dataset. There are some rams with offspring in 2015 that is not included as selection candidates in the dataset. The rams not included in the dataset did not hold the selection criteria given, mostly because they were too old or in other ways did not fulfill the criteria given for the dataset. The way this selection method is calculated is with pre-defined contributions for the test- and elite rams and a pre-defined percentage contribution that can be allocated to the 12 AI ram candidates. The Elite- and test rams are assumed to have equal contributions of 1.33%, and the AI rams are assumed to have 8.23% contribution across the population, or equal to approximately 150 ewes inseminated with AI. This is the only selection method that allows the ram circle boards to select the test- and elite rams. However, the test- and elite rams are selected before the AI rams. This is the opposite order of, what is currently done in the actual selection where AI rams are selected in July and test- and elite rams in October.

3.4 Calculations of Inbreeding

Estimated effective population size was calculated by using RelaX2 (Stranden 2006), based on the method from Gutiérrez et al. (2009):

Estimated effective population size N_e = 117.63

Standard error of N_e = 18.766

Number of animals in the Ne calculations = 5344

Based on the estimated effective populations size, the estimated rate of inbreeding (ΔF) in the Norwegian Cheviot population = 1/(2N_e) (Falconer 1960) = 0.00425 per year

The mean generation interval for Ram-offspring (Lm) in Norwegian Cheviot is 1.7 years and for ewe-offspring (Lf) the mean is 3.4 years (*J. Jakobsen, Pers. Comm.* 2016). The mean generation interval for parent-offspring in Cheviot is estimated to be ((Lm + Lf)/ 2) which gives ((1.7 + 3.4) / 2) = 2.55 years.

Which makes estimated average ΔF per generation = 0.00425*2.55 = 0.0108

3.5 Statistical Analysis to compare selection scenarios

In order to compare the four selection scenarios and the actual selection, statistical analysis was done with the statistical software "R". The aim was to compare the breeding values of the selected rams in the different selection scenarios. The reason ram breeding values (O-index) are compared, is because there is no difference in the ewe selection, and the ram O-index is the only equal measure for genetic level available for all selection scenarios.

The model used is an ANOVA type II model

$$y_i = \mu_i + \varepsilon_i \quad [8]$$

Where the response variable (y) is the O-index for selected rams in selection scenario i (i = 1, 2, 3, 4 ,5) and the explanatory factor (μ) is selection scenario.

The data was unbalanced as there were different number of rams in the different selection scenarios. The groups, mean, standard deviation and number of rams in each group is listed in Table 3.

Post-Hoc comparison of means for different selection scenarios is done with the Tukey method with significance levels 0.001, 0.01 and 0.05.

Table 3. Mean, standard deviation (SD) and number of selected rams (n) in the different selection scenarios.

Selection scenario	Mean	SD	n
0 – Actual selection («control»)	122.7	6.85	90
1 – Within ram circle selection	125.9	3.79	81
2 – Within ram circle selection with pre-selection	125.2	4.15	90
3 – Across ram circle selection	125.7	3.47	92
4 – Across ram circle selection with pre-selection	122.6	6.64	70

4 Results

4.1 Within Ram Circle Selection of all ram type categories (scenario 1)

In scenario 1, all the ram type categories were selected with OCS within each of the four ram circles separately. Number of rams selected from each ram type category and their contribution (%) are shown in Table 4 for each of the four ram circles and in total.

Table 4 shows that there is a big variation in the amount of contribution for each ram-type across the ram circles. For example, there is seven selected rams for AI in ram circle 161, but no elite rams. In general, the contribution of the AI rams is larger (12-40%) than what is practiced today (7-8%) and the contribution of test rams is a bit lower (50-60%) than what is practiced today (70-75%). All rams are assumed to have equal contributions in their ram circle. The selected rams for this selection scenario, their corresponding O-index and contribution can be seen in Appendix 1.

Table 4. Scenario 1. Number of rams selected from each ram type category and their contribution (%) for each of the four ram circles and in total. At the bottom of the table the average O-index of the selected rams, average number of ewes mated per ram and average contribution (%) per ram.

	Ram Circle				Total
	141	161	163	171	
Number of AI rams	4	7	7	8	8*
Total contribution (%) for AI rams	12.0	40.1	28.0	32.0	30.0
Number of Elite rams	10	0	5	3	18
Total contribution (%) for Elite rams	29.2	0	19.9	12.0	15.8
Number of Test rams	20	7	13	15	55
Total contribution (%) for Test rams	59.2	56.0	52.0	56.0	55.9
Total Number of rams	34	14	25	26	81
Average Ram O-index	125.7	124.4	126.5	123.8	125.9
Average ewes mated/ ram	16.6	22.7	18.9	14.6	18.2
Average contribution (%) /ram	2.94	6.86	3.99	3.84	1.04

*Same AI rams are used across the ram circles.

The “genetic merit of the parents” is shown in Table 5. This value is very similar to the average O-index in Table 4. The difference in values is caused by the fact that the genetic merit of the parents calculated by Gencont 2 takes into account the contribution of the parents, while the average EBV's in Table 4 assume equal contribution of selected animals.

Table 5 also shows the average relationship in the population for each ram circle before (current) and after selection (solution). The constraint is the maximum value Population Average Relationship in the population can have and still keep the rate of inbreeding to a maximum of 1% per generation. The solution value for population average relationship in ram circle 161 is larger than the constraints, and this indicates that the inbreeding restriction is not fulfilled for this ram circle. The constraint of population average relationship is met by the other ram circles.

Table 5. The Population Average Relationship given by Gencont 2 for the within-ram circle calculations.

Ram Circle	141	161	163	171	Average
Population Average Relationship (current)	0.0170	0.0362	0.0226	0.0189	0.0237
Constraint	0.0248	0.0439	0.0303	0.0388	0.0344
Population Average Relationship (solution)	0.0208	0.0442	0.0290	0.0220	0.0290
Genetic merit of the parents	120.1	113.4	118.2	116.2	117.0

4.2 Test and elite rams are selected within ram circle. AI rams are pre-selected (scenario 2).

Number of rams selected from each ram type category and their contributions (%) are shown in Table 6 for each of the four ram circles and in total. In this selection scenario, there were only three AI rams available for selection, which is the three rams that NSG originally selected for AI in 2014. Apart from that, the selection candidates and selection criteria is the same as the within ram circle selection method.

In this scenario, all the available AI rams are selected, with the exception of the import ram that is not selected in ram circle 141. The percentage contributed by AI rams has decreased compared to scenario 1. The ranges of contribution from AI ram is now 6-24%, and the contribution of the test rams has increased to 60-70%. The contribution of the different ram groups is more equal to the actual selection using scenario 2 with pre-selection of AI rams instead of scenario 1 without pre-selection. The list of rams and their corresponding O-index and contribution are shown in Appendix II

Appendix II.

Table 6. Scenario 2. Number of rams selected from each ram type category and their contribution (%) for each of the four ram circles and in total. At the bottom of the table the average O-index of the selected rams, average number of ewes mated per ram and average contribution (%) per ram.

	Ram Circle				Total
	141	161	163	171	
Number of AI rams	2	3	3	3	3*
Total contribution (%) for AI rams	6.0	24.0	12.0	12.0	12.4
Number of Elite rams	10	0	5	4	19
Total contribution (%) for Elite rams	30.0	0	20.0	16.0	18.6
Number of Test rams	22	10	17	19	68
Total contribution (%) for Test rams	64.0	76.0	68.0	72.0	69.0
Total Number of rams	34	13	25	26	90
Average O-index for selected rams	126.6	125.3	126.1	122.8	125.2
Average ewes mated/ ram	16.58	25.5	18.9	13.2	18.5
Average contribution (%) /ram	2.94	7.69	3.99	3.85	1.06

*Same AI rams used across ram circles

In this scenario, as shown in Table 7, all the constraints on population average relationship is kept for all the ram circles. There is a difference in the genetic level and population average relationship in the four ram circles. Ram circle 161 has the highest population average relationship and a low genetic merit of the parents. Ram circle 141 on the other hand, has a high genetic merit, but the lowest population average relationship.

Table 7. The Population Average Relationship given by Gencont 2 for the within-ram circle selection with preselected AI rams.

	141	**161**	**163**	**171**	**Average**
Population Average Relationship (current)	0.0172	0.0400	0.0248	0.0203	0.0256
Constraint	0.0250	0.0476	0.0325	0.0280	0.0333
Population Average Relationship (solution)	0.0209	0.0463	0.0300	0.0225	0.0299
Genetic merit of the parents	120.2	116.0	118.0	115.7	117.5

4.3 Across Ram Circle Selection of all ram type categories (scenario 3).

Rams in all ram type categories were available for selection with OCS across the population. This scenario assumes allowance of movement of rams for natural service across ram circles, or with other words, all flocks are assumed to belong to one population without a ram circle structure.

Table 8. Scenario 3. Number of rams selected from each ram type category and their contribution (%) for each of the four ram circles and in total. At the bottom of the table the average O-index of the selected rams and for all the selected animals, average number of matings per ram within ram circle and for the population, and average contribution (%) per ram within ram circle and for the population

	Ram Circle				Total
	141	161	163	171	
Number of AI rams	6	6	6	6	6*
Total contribution (%) for AI rams	11.04	42.84	25.08	33.36	6.6
Number of Elite rams	15	0	5	3	23
Total contribution (%) for Elite rams	27.6	0	20.9	16.68	25.3
Number of Test rams	33	8	13	9	63
Total contribution (%) for Test rams	60.72	57.12	54.34	50.04	68.1
Total Number of rams	54	14	24	18	92
Average Ram O-index	125.1	125.6	126.6	125.4	125.7
Average ewes mated/ ram	10.4	23.7	19.8	21.2	19.1
Average contribution (%) /ram	1.84	7.14	4.18	5.56	1.09

*Same AI rams used across the ram circles.

Table 8 show the number of rams selected for each ram circle and the total number of selected rams for each ram group. When calculating across ram circles, Gencont 2 assumes all the animals is available to mate with each other.

There are 15 selected Elite rams from ram circle 141 and 3 from ram circle 171. There is also a very high amount of test rams selected from ram circle 141 compared with the other ram circles. This scenario would make it necessary to move animals between ram circles in order to have enough rams for mating in each ram circle. The number of rams selected in total for the population is 92 and this is not too far from the number of rams with registered offspring in 2015, which was 90 rams, but the rams are not distributed optimally among the ram circles.

The contribution of each ram group is close to the contributions for each group used today, just a little low contribution for the test rams and high for the elite rams. If there had been no restrictions on moving rams, this selection method would probably be the most suitable. Table 9 shows that the restriction on Average relationship for parents is held with selection scenario 3, meaning that the rate of inbreeding will not exceed 1% if the animals are mated according to selection scenario 3. The selected rams for this selection scenario, their corresponding O-index and contribution can be seen in Appendix III.

Table 9. Population Average Relationship for selection in the complete population simultaneously.

Population Average Relationship (current)	0.0106
Constraint	0.0184
Population Average Relationship (solution)	0.0144
Genetic merit of the parents	118.0

4.4 AI rams are selected across the population. Test- and elite rams are pre-selected (scenario 4).

In this selection method selects the AI ram based on the pre-selected test- and elite rams that are selected by the ram circles in 2014.

Table 10. Scenario 4. Number of rams selected from each ram type category and their contribution (%) for each of the four ram circles and in total. At the bottom of the table the average O-Index of the selected rams and for all the selected animals, average number of matings per ram and average contribution (%) per ram.

	Ram Circle				**Total**
	141	161	163	171	
Number of AI rams	1	1	1	1	1*
Total contribution (%) for AI rams					8.23
Number of Elite rams	6	2	3	4	15
Total contribution (%) for Elite rams					19.95
Number of Test rams	22	7	14	11	54
Total contribution (%) for Test rams					71.82
Total Number of rams	29	10	18	16	70
Average Ram O-index	123.7	121.2	123.4	121.9	122.6
Average ewes mated/ ram	19.4	33.2	26.3	23.8	25.0
Average contribution (%) /ram	3.44	10.0	5.5	6.2	1.4

*Same AI ram selected across ram circles.

Using this selection scenario, only one ram was selected for AI, while three were selected by NSG in the actual selection in 2014. The selection scenario where only rams for AI are selected with OCS and rams for natural mating are selected by the ram circle boards, is one of the most realistic selection scenarios to implement in the Norwegian Cheviot breeding scheme. However, the test- and elite rams are selected before the AI rams with this method. In the real selection the AI rams are selected in July, and the other rams are selected in October. The selected rams for this selection scenario, their corresponding O-index and contribution can be seen in Appendix IV.

As seen in Table 11, the restriction on average relationship for the population was held.

Table 11. The Population Average Relationship given by Gencont 2 for the across ram circle selections with pre-selected Test- and Elite rams.

Population Average Relationship (current)	0.012
Constraint	0.020
Population Average Relationship (solution)	0.012
Genetic merit of the parents	116.6

4.5 Statistical Results

Results for the pairwise comparison of actual selection in 2014 (selection scenario 0) and selection using scenario one to four are shown in Table 12. The tested hypothesis was that the five selection procedures were different.

No significant difference is found between actual selection (selection scenario 0) and selection scenario 4 with pre-selected elite and test rams. There is however a difference between the actual selection and the other three selection scenarios (1, 2 and 3), and the biggest difference from the actual selection is for the scenarios without any pre-selection($p<0.001$). There is also a significant difference between selection scenario 4 and selection scenarios 1,2 and 3. However, no significant difference is found between these three selection scenarios.

Table 12. Multi comparison of means with Tukey Contrasts for the different selection methods.

Contrast of selection scenario	Estimate	Std. Error	z value	Pr(>|z|)	Significant Codes
1 - 0	3.2	0.79	4.09	< 0.001	***
2 - 0	2.5	0.77	3.27	0.00937	**
3 - 0	2.9	0.76	3.94	< 0.001	***
4 - 0	-0.1	0.81	-0.12	0.99995	
2 - 1	-0.7	0.79	-0.91	0.89361	
3 - 1	-0.2	0.78	-0.28	0.99868	
4 - 1	-3.3	0.84	-3.96	< 0.001	***
3 - 2	0.5	0.76	0.65	0.96629	
4 - 2	-2.6	0.82	-3.18	0.01273	*
4 - 3	-3.1	0.81	-3.81	0.00131	**

Significant codes: p<0.001 = ***, p<0.01 = **, p<0.05 = *

5 Discussion

5.1 Rams with tagged offspring in 2015 (Actual selection).

Rams of the three ram type categories (test, elite and AI) were used for mating and AI in the Cheviot ram circle flocks in 2014. Table 13 shows the proportion of tagged offspring born 2015 for each ram type, for each ram circle and for the complete population (% offspring). The contribution is calculated by dividing number of offspring for each ram by the total number of offspring. The table also shows numbers of rams selected.

Table 13. Number of test, elite and AI rams used in ram circles 141, 161, 163 and 171 and percentage of offspring sired by each ram type category.

	Ram Circle				Total
	141	161	163	171	
Number of test rams	23	7	16	13	59
% offspring sired by a test ram	78.9	68.0	76.5	56.0	70.8
Number of elite rams	8	3	6	9	26
% offspring sired by an elite ram	17.6	26.9	20.8	36.4	24.6
Number of AI rams	4	4	2	4	5*
% offspring sired by an AI ram	3.5	5.1	2.7	7.6	4.6
Average Ram O-Index	124.3	123.8	123.9	121.9	122.7
Average ewes mated/ ram	16.1	23.7	19.8	14.7	19.5
Average contribution (%) /ram	2.86	7.14	4.17	3.85	1.2

*The same AI rams are used across ram circles

5.2 Pre-selected Ewes

The pre-selected females for mating in 2014 were based on actual ewes lambing in any of the ram circle flocks in 2015. Because of the pre-selection, there is no difference in the ewes in the four selection scenarios or the actual selection. The number of ewes, average contribution per ewe and average O-Index is shown in Table 14.

Table 14 Pre-selected ewes. Number of ewes, average contribution (%) per ewe and the average O-Index for ewes in the different ram circles and in the total population.

	Ram Circle				Total
	141	161	163	171	
Number of ewes	564	332	474	381	1751
Average contribution (%) per ewe	0.18	0.30	0.21	0.36	0.06
Average Ewe O-Index	113.7	106.5	110.0	108.4	110.2

5.3 Comparing selection methods

Four different methods of implementing OCS in the Norwegian Cheviot population has been tested. They all have advantages and disadvantages, and some are more realistic to implement than others.

As seen in Table 15, the four different selection methods have some small differences between number of rams selected and percentage contributions.

The total number of rams selected varies from 70-92. One of the reasons why there is only 70 rams selected in scenario 4 with pre-selected elite and test rams and 90 in the actual selection, is because there are 19 rams with registered offspring in 2015 that did not meet the criteria to be included in the dataset. Four of them are the older AI rams, 10 are older elite rams and five are young rams born in 2014. The older AI rams are excluded from the dataset because the two rams that NSG selected for AI in 2014 died, and the older AI rams had frozen doses left over from previous season that were made available for sale in the 2014 mating season instead. The older elite rams had already been used at least one season as elite rams, and the dataset only included elite ram candidates born in 2013. One of the young rams not included in the dataset as selection candidate, but still had registered offspring in 2015 is a ram that were born in a flock that previously belonged to ram circle 141, but not in 2014. However, the ram was promising and the ram circle board included the ram as a test ram in the ram circle. Why the other four young rams were not included in the dataset as test ram candidates is unknown.

Table 15. Number of rams, percent contribution, average O-index, Average contribution per ram and average ewes mated per ram for each of the four scenarios and for the actual selection.

	Selection Scenario				
	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Actual Selection (scenario 0)
Number of AI rams	8	3	6	1	5(3)*
% contribution by AI rams	30.0	12.4	6.6	8.23	4.6
Number of Elite rams	18	19	23	15	26
% contribution by Elite rams	15.8	18.6	25.3	19.95	24.6
Number of Test rams	55	68	63	54	59
% contribution by Test rams	55.9	69.0	68.1	71.82	70.8
Total number of rams	81	90	92	70	90
Average O-Index for selected rams	125.9	125.2	125.7	122.6	122.7
Average contribution per ram	1.04	1.06	1.09	1.4	1.2
Average ewes mated per ram	18.2	18.5	19.1	25.0	19.5

*There were three selected rams for AI, but because two of them died, frozen semen from four older rams were made available and these are the AI rams with tagged offspring in 2015.

The within ram circle selection approach (scenario 1) would optimize the selection for one ram circle at a time and thus make each ram circle a separate population. This would make it possible to use OCS on all ram type selections and at the same time ensure an appropriate number of rams is selected for each ram circle. The average O-index for this selection scenario is marginally higher than the across ram circle selection (scenario 3). Eight different AI rams were selected for the within-ram circle selection method, but not all of them were selected for all ram circles. Ram circle 141 had only four AI rams selected, and ram circle 171 had eight AI rams selected. If this method were to be applied, maybe one option could be to only put the four rams jointly selected by the four ram circles on AI station and let the rest of the rams suggested for AI be used as elite ram for another season in their respective ram circle.

The biggest issue with the within ram circle selection method (scenario 1) is the unproportioned selection of AI rams. This is solved in selection scenario 2, where the AI rams are pre-selected. Within ram circle selection with pre-selected AI rams (scenario 2) is the only one of the suggested selection scenarios that would allow NSG to select the 2-4 AI rams needed for AI. Gencont 2 still optimizes their respective contribution. The optimization process will be done within ram circles for the test- and elite rams. The average O-index for the rams selected with selection scenario 2 is not significantly different from the average O-index for the rams selected without pre-selection (scenario 1). However, there is a significant difference between this selection scenario and the actual ram selection (scenario 0) ($p<0.01$).

The results for the across ram circle selection scenario (scenario 3) show that Gencont 2 selects the same total number of rams as the actual selection (scenario 0), but more rams from ram circle 141 compared to the other ram circles. The reason there is a difference between how many rams are selected from each ram circle is probably that there is a big difference in the genetic level of the four ram circles. In addition, the relatedness to the rest of the ram circles can influence the selection. Ram circle 141 has a low population average relationship and a high average breeding value compared to the other ram circles. Ram circle 141 is also the largest ram circle with more candidates to choose from than the other ram circles.

If there were no restrictions on moving rams between ram circles, selection scenario 3 would be a good option as it is the only scenario optimizing the Norwegian Cheviot population as a whole. However, because of the restriction of moving animals between ram circles, selection scenario 3 is not applicable today.

Across ram circle selection of AI rams with pre-selected test- and elite rams (scenario 4) is the selection method that is closest to the selection process as it is practiced today. However, the contributions of AI-rams are small compared to the other rams and thus the effect of the OCS is small. This method has no significant difference in merit of rams compared to actual selection. Only one AI ram was selected with this method. This might indicate that on a total population scale, the rate of inbreeding is low when test and elite rams are selected by the ram circles, and thus one AI ram can be selected with a contribution of 8.2% without increasing the rate of inbreeding above 1% per generation. Scenario has a high amount of ewes mated per ram compared to the other scenarios as seen in Table 15. The reason for this is probably that there are only 70 selected rams in total when the other scenarios had between 80 and 92 selected rams.

Scenario 4 requires that the test- and elite rams are selected before the AI rams. In the actual selection scheme, the AI rams are selected in July and the test- and elite rams are selected in October. Selecting elite and test rams before AI rams makes this scenario difficult to implement because elite rams are awaiting information about slaughtered offspring that is included in the fall index-runs, and the test rams are awaiting the phenotypical evaluation. Genomic selection could be a solution for this particular issue. However, the Norwegian Cheviot is a small breed and genomic selection is not likely to be applied anytime soon.

Surprisingly, the highest average O-index was obtained using the within ram circle selection method (scenario 1), and not in the across ram circle selection method (scenario 3). All animals were selected with OCS in both selection methods, but the expectation was that optimization on the larger population (across ram circle selection) would give the highest average O-index. However, there is no significant difference in the average merit between the animals selected in the two scenarios.

As shown in Table 12, there is a significant difference in the ram EBV between actual selection (scenario 0) and the within- and across ram circle selection scenarios (scenario 1 and 3)($p<0.001$). There is also a significant difference at 1% level between actual selection and the within ram circle with preselected AI rams selection method (scenario 2). There is no significant difference in average ram O-index between the actual selection and the across ram circle selection of AI rams with pre-selected test- and elite rams (scenario 4).

The results show that the highest increase in genetic gain would come from selecting all the rams with OCS. However, the cost of having AI rams is so high that having more AI rams than what is used today is not realistic. When the AI rams are pre-selected, it will still be an advantage of using OCS for selection of test and elite rams. The only restriction with this method is that the ram circles boards would lose the privilege to select rams.

In this study, the ewes were pre-selected based on information of lambing in 2015. When applying OCS in a real selection process, the information about ewes are not available with certainty. However, in a similar study by Olsen et al. (2013) on Nordic cold-blooded trotter horses, it was suggested to base the selection on the ewes used the previous year. The study showed only minor differences between stallions selected with the mares from the previous year, compared with the stallions selected with the actual mated mares the same year (Olsen et al. 2013).This approach could be used when applying OCS in the Norwegian Cheviot

Population. However, the turnover of mares are probably lower than the turnover of ewes, which is around 25% per year.

Another issue with the results from these selection methods is that the same cmax is used for all rams and age-classes. Another suggestion is to use different cmax on the different age-classes in order to select a suitable amount of rams in each age-class. However, it seems as though putting many restrictions on the OC selection with Gencont 2 gives a lower outcome in the genetic progress or average EBV. This is probably because it have less room to select the best candidates and give them a higher contribution than the lower candidates. The best way to approach applying OCS would be to restrict the selection as little as possible in order to get the best optimization of the selection.

For this study, a measure of amount of increase in genetic gain for the different selection scenarios is not calculated. The reported amount of increase in genetic gain using OCS vs. truncation selection with BLUP is very variable, and finding out the specific increase of genetic gain for the Norwegian Cheviot population can be difficult as it depends on different factors. Meuwissen (1997) reports of between 21 to 27% compared to BLUP selection with same level of inbreeding using simulated data and even as much as 60% higher when the inbreeding restriction was lower. Meuwissen and Sonesson (1998) reports that using a dynamic selection rule to allow for overlapping generations in the optimal selection calculations yielded as much as 44% higher selection response than BLUP selection.

The difference in selection response is higher in small populations and with lower constraints on the rate of inbreeding (Meuwissen & Sonesson 1998). Gandini et al. (2014) used simulations of young bull schemes to compare OCS with truncation selection. They report a difference in genetic gain between 2% and 6.3%. They also agreed with the results from Meuwissen and Sonesson (1998) that OCS is more favorable with lower rates of inbreeding (Gandini et al. 2014). Gourdine et al. (2012) simulated OCS in local pig breeds to select for meat quality. The results showed that the genetic gain using OCS was lower than that of truncation selection with BLUP. However, the study was not comparing the genetic gain on the same level of inbreeding, as the cumulative level of inbreeding for the BLUP selection increased substantially, the OC selection stayed low, but still allowed for an increase in genetic gain of between 69% and 98% of the BLUP selection (Gourdine et al. 2012). Based on these studies, one can assume that applying OCS in the Norwegian Cheviot population would restrict in the very least, the rate of inbreeding to the desired rate while maintaining the same genetic progress as is today. However, the increased O-index in the selected rams with selection method 1, 2 and 3, indicate that there might be room to increase the genetic progress in the Norwegian Cheviot Sheep by applying OCS in the selection scheme.

Four selection scenarios were applied to the Norwegian Cheviot population with promising results. However, the scenarios tested have some limits that could be solved with further testing of different selection scenarios. In these selection scenarios, all ram type categories were given the same cmax, but i.e. AI rams have a higher capacity in terms of matings per ram than rams used with natural service. One suggested selection scenario could be to apply different cmax for different ram type categories. Other suggested scenarios are i.e. with only natural service rams, without elite rams and higher amount of AI, or scenarios involving OC selection of ewes

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6 Conclusion

Using OCS to select rams for the Norwegian Cheviot population will give a higher average O-index among the selected rams compared to the selection currently done, leading to genetic gain and keeping the rate of inbreeding below one percent.

None of the four selection scenarios is however able to fulfill all the current biological, economical or structural restrictions. The large AI-usage and post-selection of rams for AI across the ram circles are disadvantages for scenario 1. The manual pre-selection of rams for AI is a limit for scenario 2, as well as the selection of rams for natural mating by OCS instead of ram circle boards that is a limitation to scenario 1, 2 and 3. The prohibition by the Norwegian Food Safety Authority to move ram circles between ram circles limits Scenario 3. In scenario 4, pre-selecting test- and elite rams before selecting AI rams with OCS is limited by insecure breeding values.

Solutions to overcome these limits can be to use more AI in the Norwegian Cheviot population to accommodate scenario 1. If adaptions to the software makes it possible change the manual pre-selection of AI ram candidates into selecting 2-4 AI rams with OCS, scenario 2 is more applicable. Educating the ram circle boards and flock owners to understand the benefits of OCS selection is also a solution to the issue of changing the selection structure in scenario 1, 2 and 3. As long as there is limitations against moving animals between ram circles by Norwegian law, scenario 3 does not have a realistic application. If genomic selection is implemented, a higher security for the O-index could be achieved and this could solve the limits of selection method 4. However, using genomic selection in such a small population is not realistic as of today.

A modification of selection scenario 2, where the AI selection with OCS is limited to 2-4 rams, and the ram circle board agrees to use OCS for test- and elite ram selection is recommended.

Even so, implementing OCS in the selection scheme requires change. NSG, the ram circles and the flock owners need to discuss and decide possible changes in the current selection procedure to find out how to implement OCS in order to benefit the Norwegian Cheviot population in the best manner possible.

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Appendices

Appendix 1

Within ram circle selection of all ram type categories (scenario 1).

Ram Circle 141

Ram animal ID	% contribution	O-index	Ram type category
38713483	3	126	AI
40805034	3	130	AI
40805036	3	126	AI
38711481	2.99	123	AI
38711305	3	129	Elite
38712317	3	129	Elite
38712645	3	129	Elite
38823266	3	124	Elite
38824443	3	127	Elite
38887456	3	125	Elite
38887571	3	138	Elite
39583202	3	125	Elite
39700653	3	130	Elite
39606488	2.691	123	Elite
70062489	3	128	Test
70062501	3	132	Test
70089382	3	124	Test
70089769	3	124	Test
70090960	3	132	Test
70192810	3	125	Test
70192891	3	124	Test
70474185	3	124	Test
70474257	3	128	Test
70483776	3	124	Test
70567301	3	128	Test
70688130	3	124	Test
70688327	3	129	Test
70861754	3	125	Test
70861758	3	127	Test
70862889	3	124	Test
70864980	3	125	Test
71235711	3	126	Test
71235916	3	129	Test
71236066	1.14	123	Test

Ram Circle 161

Ram animal ID	% contribution	O-index	Ram type category
38711481	8	123	AI
38713483	8	126	AI
45938656	8	123	AI
68045172	6.124	122	AI (Import)
43977821	5.948	122	AI
43960255	2.129	118	AI
38711665	1.878	121	AI
69935852	8	128	Test
70093459	8	126	Test
70093521	8	129	Test
70968168	8	123	Test
71144049	8	125	Test
71239479	8	123	Test
71274871	8	133	Test

Ram Circle 163

Ram animal ID	% contribution	O-index	Ram type category
38711481	4	123	AI
38713483	4	126	AI
40805034	4	130	AI
40805036	4	126	AI
43977821	4	122	AI
45938656	4	123	AI
68045172	4	122	AI (Import)
43445416	3.979	122	Elite
43445656	4	126	Elite
43797050	4	135	Elite
43800402	4	132	Elite
44686926	4	123	Elite
69717456	4	130	Test
69717556	4	124	Test
69766832	4	130	Test
69878077	4	124	Test
70157251	4	124	Test
70855500	4	127	Test
71461380	4	126	Test

71461628	4	123	Test
72108481	4	134	Test
72112848	4	127	Test
72146630	4	127	Test
72600408	4	126	Test
72600747	4	130	Test

Ram Circle 171

Ram animal ID	% contribution	O-index	Ram type category
38711481	4	123	AI
38711665	4	121	AI
38713483	4	126	AI
40805034	4	130	AI
40805036	4	126	AI
43977821	4	122	AI
45938656	4	123	AI
68045172	4	122	AI (Import)
43976634	4	126	Elite
43977349	4	123	Elite
43978804	4	127	Elite
69715178	4	123	Test
69788506	4	120	Test
69827969	4	124	Test
70800801	4	125	Test
70971479	4	124	Test
70989634	4	126	Test
70989701	4	119	Test
70991498	4	130	Test
70992585	4	132	Test
70998114	4	120	Test
73196351	4	125	Test
73199416	4	119	Test
73795484	4	124	Test
70972009	3.641	119	Test
69788510	0.356	119	Test

Appendix II

Within ram circle selection with pre-selected AI rams (scenario 2).

Ram Circle 141

Ram animal ID	% contribution	O-index	Ram type category
40805034	3	130	AI
38713483	3	126	AI
38887571	3	138	Elite
39700653	3	130	Elite
38711305	3	129	Elite
38712317	3	129	Elite
38712645	3	129	Elite
38824443	3	127	Elite
38887456	3	125	Elite
39583202	3	125	Elite
38823266	3	124	Elite
39606488	3	123	Elite
70062501	3	132	Test
70090960	3	132	Test
70688327	3	129	Test
71235916	3	129	Test
70062489	3	128	Test
70474257	3	128	Test
70567301	3	128	Test
70861758	3	127	Test
71235711	3	126	Test
70192810	3	125	Test
70861754	3	125	Test
70864980	3	125	Test
70089382	3	124	Test
70089769	3	124	Test
70192891	3	124	Test
70474185	3	124	Test
70483776	3	124	Test
70688130	3	124	Test
70862889	3	124	Test
71236066	3	123	Test
70688181	2.463	123	Test
70482113	1.534	123	Test

Ram Circle 161

Ram animal ID	% contribution	O-index	Ram type category
38713483	8	126	AI
40805034	8	130	AI
68045172	8	122	AI
69867216	8	122	Test
69935852	8	128	Test
70093459	8	126	Test
70093521	8	129	Test
70968168	8	123	Test
71144049	8	125	Test
71239479	8	123	Test
71274871	8	133	Test
70093348	7.291	121	Test
70977193	4.708	121	Test

Ram Circle 163

Ram animal ID	% contribution	O-index	Ram type category
38713483	4	126	AI
40805034	4	130	AI
68045172	4	122	AI (Import)
43445416	4	122	Elite
43445656	4	126	Elite
43797050	4	135	Elite
43800402	4	132	Elite
44686926	4	123	Elite
69717456	4	130	Test
69717556	4	124	Test
69766832	4	130	Test
69878077	4	124	Test
70157251	4	124	Test
70360291	4	121	Test
70855500	4	127	Test
71461380	4	126	Test
71461628	4	123	Test
72108481	4	134	Test
72112848	4	127	Test
72142290	4	121	Test
72146630	4	127	Test
72600408	4	126	Test
72600542	4	121	Test
72600747	4	130	Test
72137661	3.983	121	Test

Ram Circle 171

Ram animal ID	% contribution	O-index	Ram type category
40805034	4	130	AI
38713483	4	126	AI
68045172	4	122	AI (Import)
43978804	4	127	Elite
43976634	4	126	Elite
43977349	4	123	Elite
43976813	4	118	Elite
70992585	4	132	Test
70991498	4	130	Test
70989634	4	126	Test
70800801	4	125	Test
73196351	4	125	Test
69827969	4	124	Test
70971479	4	124	Test
73795484	4	124	Test
69715178	4	123	Test
69788506	4	120	Test
70998114	4	120	Test
69788510	4	119	Test
70972009	4	119	Test
70989701	4	119	Test
73199416	4	119	Test
70969818	4	118	Test
73348242	4	118	Test
71854928	2.745	118	Test
73199987	1.255	118	Test

Appendix III

Selected rams for the Across ram circle selection (scecnario 3).

Ram animal ID	% contribution	Ram Circle	O-index	Ram type category
38711481	1.1		123	AI
38713483	1.1		126	AI
40805034	1.1		130	AI
40805036	1.1		126	AI
43977821	1.1		122	AI
68045172	1.1		122	AI (Import)
38711305	1.1	141	129	Elite
38711802	1.1	141	122	Elite
38712048	1.1	141	122	Elite
38712317	1.1	141	129	Elite
38712645	1.1	141	129	Elite
38823266	1.1	141	124	Elite
38823801	1.1	141	123	Elite
38824443	1.1	141	127	Elite
38887456	1.1	141	125	Elite
38887571	1.1	141	138	Elite
39583202	1.1	141	125	Elite
39583799	1.1	141	122	Elite
39606488	1.1	141	123	Elite
39700653	1.1	141	130	Elite
39767048	1.1	141	122	Elite
43445416	1.1	163	122	Elite
43445656	1.1	163	126	Elite
43797050	1.1	163	135	Elite
43800402	1.1	163	132	Elite
44686926	1.1	163	123	Elite
43976634	1.1	171	126	Elite
43977349	1.1	171	123	Elite
43978804	1.1	171	127	Elite
45938656	1.1	141	123	Test
69726730	1.1	141	122	Test
69974279	1.1	141	122	Test
70062489	1.1	141	128	Test
70062501	1.1	141	132	Test
70089382	1.1	141	124	Test
70089769	1.1	141	124	Test
70090960	1.1	141	132	Test
70192810	1.1	141	125	Test
70192891	1.1	141	124	Test
70474185	1.1	141	124	Test
70474257	1.1	141	128	Test
70482113	1.1	141	123	Test
70483572	1.1	141	123	Test
70483776	1.1	141	124	Test
70567301	1.1	141	128	Test
70687351	1.1	141	122	Test
70688130	1.1	141	124	Test
70688181	1.1	141	123	Test
70688327	1.1	141	129	Test
70861754	1.1	141	125	Test
70861758	1.1	141	127	Test
70862828	1.1	141	123	Test
70862889	1.1	141	124	Test
70864980	1.1	141	125	Test
70865641	1.1	141	122	Test
71235024	1.1	141	122	Test
71235711	1.1	141	126	Test
71235916	1.1	141	129	Test
71236066	1.1	141	123	Test
71236068	1.1	141	122	Test
71361691	1.1	141	123	Test
71235599	0.873	141	122	Test
69935852	1.1	161	128	Test
70093459	1.1	161	126	Test
70093521	1.1	161	129	Test
70968168	1.1	161	123	Test
71144049	1.1	161	125	Test
71239479	1.1	161	123	Test
71274871	1.1	161	133	Test
69867216	0.125	161	122	Test
69717456	1.1	163	130	Test
69717556	1.1	163	124	Test
69766832	1.1	163	130	Test
69878077	1.1	163	124	Test
70157251	1.1	163	124	Test
70855500	1.1	163	127	Test
71461380	1.1	163	126	Test
71461628	1.1	163	123	Test
72108481	1.1	163	134	Test
72112848	1.1	163	127	Test
72146630	1.1	163	127	Test
72600408	1.1	163	126	Test

72600747	1.1	163	130	Test
69715178	1.1	171	123	Test
69827969	1.1	171	124	Test
70800801	1.1	171	125	Test
70971479	1.1	171	124	Test
70989634	1.1	171	126	Test
70991498	1.1	171	130	Test
70992585	1.1	171	132	Test
73196351	1.1	171	125	Test
73795484	1.1	171	124	Test

Appendix IV

Selection of AI rams based on pre-selected test- and elite rams (scenario 4).

Ram animal ID	% contribution	Ram Circle	O-index	Ram type category
40805034	8.23		130	AI
38711305	1.33	141	129	Elite
38712645	1.33	141	129	Elite
38823801	1.33	141	123	Elite
38887456	1.33	141	125	Elite
38887571	1.33	141	138	Elite
39583202	1.33	141	125	Elite
43445416	1.33	163	122	Elite
43445656	1.33	163	126	Elite
43976634	1.33	171	126	Elite
43976813	1.33	171	118	Elite
43977349	1.33	171	123	Elite
43978804	1.33	171	127	Elite
44686926	1.33	163	123	Elite
45959971	1.33	161	117	Elite
46126337	1.33	161	117	Elite
69717456	1.33	163	130	Test
69717556	1.33	163	124	Test
69726730	1.33	141	122	Test
69726970	1.33	141	115	Test
69766404	1.33	141	111	Test
69788506	1.33	171	120	Test
69827969	1.33	171	124	Test
69878077	1.33	163	124	Test
69935852	1.33	161	128	Test
69964336	1.33	163	109	Test
69964338	1.33	163	109	Test
70062489	1.33	141	128	Test
70062501	1.33	141	132	Test
70062597	1.33	141	109	Test
70089382	1.33	141	124	Test
70093315	1.33	161	120	Test
70093459	1.33	161	126	Test
70157070	1.33	163	119	Test
70192891	1.33	141	124	Test
70360291	1.33	163	121	Test
70482266	1.33	141	114	Test
70483177	1.33	141	114	Test
70483572	1.33	141	123	Test
70483776	1.33	141	124	Test
70567301	1.33	141	128	Test
70687351	1.33	141	122	Test
70688130	1.33	141	124	Test
70688181	1.33	141	123	Test
70800801	1.33	171	125	Test
70855500	1.33	163	127	Test
70861758	1.33	141	127	Test
70862828	1.33	141	123	Test
70862889	1.33	141	124	Test
70864980	1.33	141	125	Test
70963489	1.33	161	105	Test
70972009	1.33	171	119	Test
70977193	1.33	161	121	Test
70989634	1.33	171	126	Test
70990111	1.33	171	107	Test
70991498	1.33	171	130	Test
70992585	1.33	171	132	Test
70993508	1.33	171	109	Test
71144049	1.33	161	125	Test
71235916	1.33	141	129	Test
71236066	1.33	141	123	Test
71239479	1.33	161	123	Test
71461380	1.33	163	126	Test
71854780	1.33	171	117	Test
72108481	1.33	163	134	Test
72110280	1.33	163	115	Test
72146630	1.33	163	127	Test
72600408	1.33	163	126	Test
72600747	1.33	163	130	Test
73348242	1.33	171	118	Test

Appendix V

Rams with tagged offspring in 2015.

Ram Circle 141

Ram animal ID	O-index	Ram type category	% contribution
68045172	122	AI (Import)	3.19
***200852396**	117	AI	0.09
***201050458**	132	AI	0.09
***201151789**	144	AI	0.09
38712574	125	Elite	3.28
38711305	129	Elite	4.88
38887571	138	Elite	2.44
38712645	129	Elite	0.94
38887456	125	Elite	2.06
***201350943**	122	Elite	0.09
39583202	125	Elite	3.19
38823801	123	Elite	0.75
70688130	124	Test	4.22
70687351	122	Test	0.84
70062597	109	Test	3.47
70062489	128	Test	0.09
70062501	132	Test	3.28
70688181	123	Test	0.66
69726970	115	Test	4.22
70482266	114	Test	4.32
70483177	114	Test	4.41
70068923	129	Test	3.66
69766404	111	Test	4.22
69726730	122	Test	4.78
70483572	123	Test	4.03
70862828	123	Test	3.10
70864980	125	Test	3.85
70861758	127	Test	4.22
70862889	124	Test	4.60
70089382	124	Test	3.75
71235916	129	Test	3.66
71236066	123	Test	3.10
70192891	124	Test	3.85
70567301	128	Test	3.38
70483776	124	Test	3.19

*Animal ID was not found for some animals that were not included in the dataset. Their Pheontypic Evaluation ID was used instead.

Ram Circle 161

Ram animal ID	O-index	Ram type category	% contribution
68045172	-	AI (Import)	1.58
***201050205**	117	AI	0.70
***201050458**	132	AI	1.41
***201151789**	144	AI	1.41
45938656	135	Elite	11.4
45959971	117	Elite	7.6
46126337	117	Elite	7.9
71144049	125	Test	8.10
71239479	123	Test	15.3
69935852	128	Test	9.51
70977193	121	Test	9.33
70963489	105	Test	10.2
70093315	120	Test	7.04
70093459	126	Test	8.45

*Animal ID was not found for some animals that were not included in the dataset. Their Pheontypic Evaluation ID was used instead.

Ram Circle 163

Ram animal ID	O-index	Ram type category	% contribution
68045172	122	AI (Import)	1.290
***201151789**	144	AI	1.407
***201258234**	114	Elite	0.234
43763558	123	Elite	3.048
44686926	123	Elite	5.275
43445416	122	Elite	2.345
43445656	126	Elite	4.807
***201355551**	135	Elite	5.041
72146630	127	Test	4.924
69717456	130	Test	7.386
69717556	124	Test	6.096

***201456355**	123	Test	0.586
70855500	127	Test	4.572
72110280	115	Test	5.744
72108481	134	Test	7.268
***201456374**	119	Test	0.117
70360291	121	Test	1.524
72600408	126	Test	7.620
72600747	130	Test	2.931
69878077	124	Test	3.986
70157070	119	Test	4.220
71461380	126	Test	8.324
69964336	109	Test	6.565
69964338	109	Test	4.689

*Animal ID was not found for some animals that were not included in the dataset. Their Pheontypic Evaluation ID was used instead.

Ram Circle 171

Ram animal ID	O-index	Ram type category	% contribution
68045172	-	AI (Import)	1.356
***201050205**	117	AI	0.493
***201050458**	132	AI	2.713
***201151789**	144	AI	3.083
43988728	119	Elite	6.289
43959060	123	Elite	7.768
43960255	120	Elite	4.686
***201258267**	115	Elite	0.617
43977821	123	Elite	2.343
43978804	127	Elite	4.439
43976634	126	Elite	2.219
43976813	118	Elite	5.795
43977349	123	Elite	2.219
***201456116**	118	Test	0.617
71854780	117	Test	3.576
70989634	126	Test	5.302
***201456131**	116	Test	1.603
69788506	120	Test	6.042
69827969	124	Test	5.179
70800801	125	Test	3.453
70990111	107	Test	5.055
70991498	130	Test	4.809
70993508	109	Test	4.069
70972009	119	Test	4.809
70992585	132	Test	6.165
73348242	118	Test	5.302

*Animal ID was not found for some animals that were not included in the dataset. Their Pheontypic Evaluation ID was used instead.

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