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Assessing genetic gain, inbreeding, and bias attributable to different flock genetic means in alternative sheep sire referencing schemes[1]

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ABSTRACT: Flocks participating in sire referencing schemes can achieve greater genetic gains than those achievable by within-flock selection. However, requirements for joining these schemes can be prohibitive to some producers. The objectives of this study were to determine whether less restrictive schemes or schemes of shorter duration could achieve rates of gain and reduce inbreeding as efficiently as continuous sire referencing schemes (SRS) and to investigate whether bias from different genetic means could be reduced by these alternative schemes. Pedigree and performance data for a single trait with a within-flock heritability of 0.25 were simulated (50 replications) for 15 flocks with 40 to 140 ewes per flock. Founder genetic means for each flock were sampled from a normal distribution with mean 0 and SD equal to the trait's genetic SD. After 10 yr of random mating, flocks had the opportunity to join an SRS and begin selection for the simulated trait. Yearling rams were chosen as reference sires randomly from the top one-sixth of the population ranked on BLUP EBV. Every year, in each flock, 3 reference sires were mated to 10 ewes. Six sire referencing scenarios were considered, in which all flocks participated in a SRS for 1) 15 yr; 2) 5 yr before discontinuing the scheme; 3) 10 yr before discontinuing the scheme; 4) 2 out of every 3 yr; 5) 15 yr with reference sire mating by natural service; and 6) no years (no use of SRS). Ewes not mated to reference sires were mated either to their own homebred sires exclusively or to a mixture of homebred and unrelated purchased rams of unknown merit. Genetic gain was equivalent whether the SRS used AI or natural service matings, although inbreeding was lower with natural service. Across all scenarios, genetic gain and inbreeding were greater when excess ewes were mated exclusively to homebred sires. Genetic gains without SRS were 80 to 82% lower than when the scheme operated for 15 yr, whereas inbreeding was considerably greater. Other scenarios were intermediate in both gain and inbreeding levels. In all SRS scenarios, bias in EBV attributable to differing flock genetic means rapidly decreased in the first 5 yr of sire referencing. Levels of bias did not substantially increase when flocks discontinued SRS after 5 or 10 yr, suggesting that further participation in an SRS may not be necessary to manage risk. Natural service and noncontinuous SRS are viable options to continuous AI SRS in terms of genetic gain, inbreeding, and bias reduction.

Key words: simulation, genetic evaluation, bias, sheep

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INTRODUCTION

Sire referencing schemes are cooperative breeding programs in which producers collaborate to increase the effective sizes of their flocks by sharing common sires. As practiced in the United Kingdom (Simm et al., 2001; Lewis and Simm, 2002), members of the scheme choose a team of reference sires and mate a fixed number of ewes (30) to these sires. Use of common reference sires increases the accuracy of comparisons among animals from the different flocks (Foulley et al., 1983; Miraei Ashtiani and James, 1991). In simulation studies, these schemes have been shown to have the potential to increase genetic progress by 30 to 35% over within-flock selection (Hanocq et al., 1996; Lewis and Simm, 2000). Gain is greatest when flocks are small (fewer than 100 breeding females) or when flocks have different genetic means, which may potentially bias comparisons of EBV among animals from different flocks.

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Table 1. Reproductive and survival parameters used across all simulation scenarios

Parameter(s)	Value(s)
Mating age of rams and ewes, mo	15, 15
Percentage of 2-yr-old ewes producing single or twin litters[1]	39.2, 59.1
Percentage of 3-yr-old ewes producing single or twin litters[1]	25.4, 69.3
Percentage of ewes >3 yr old ewes producing single or twin litters[1]	31.6, 61.8
Conception rate to AI, %	63
Conception rate to natural service, % in the first, second, or third cycle[2]	63, 63, 20
Lamb mortality, % for singles, twins, or triplets	13.0, 13.6, 15.6
Postweaning ram and ewe mortality, %	3.0
Active ram and ewe mortality, %	2.5
Cull age, yr for rams or ewes	4, 6

[1]The remaining ewes produced triplet litters.
[2]For the second and third cycles, the conception rate was among the remaining open ewes.

Requirements for joining schemes are unappealing to some producers. Small flocks may be required to mate up to 75% of their ewes to reference sires each year. Reference sire use is typically via AI, which can be costly and difficult in sheep because laparoscopic procedures are required (Wulster-Radcliffe and Lewis, 2002). To interest more producers in forming cooperative schemes, less restrictive rules may be needed, such as periodic rather than continuous flock participation in the scheme or use of natural service matings to reference sires. The effectiveness of these more flexible schemes in reducing potential bias in across-flock EBV must be examined.

The objectives of this paper were 1) to determine whether less restrictive breeding schemes or shorter periods of sire referencing could achieve rates of genetic gain and reduce rates of inbreeding as effectively as continuous sire referencing via AI, and 2) to investigate whether bias attributable to different genetic means among participating flocks could be reduced efficiently by using alternative sire referencing scheme designs.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were simulated data as described in the next section.

Simulation

Simulation Models. All breeding schemes were evaluated by using a modified version of the stochastic simulation of Lewis and Simm (2000). A single trait with a moderate within-flock heritability of 0.25 was simulated under an additive infinitesimal model. Fifteen flocks ranging in size from 40 to 140 breeding ewes were simulated, for a total of 1,030 breeding ewes per year in the whole scheme. Unrelated base animals were simulated for each flock; breeding values (**BV**) of base animals were obtained from a normal distribution with mean μ_j, the genetic mean for flock j, and variance (σ_a^2) 0.25. Values of μ_j for each flock were sampled from a normal distribution with mean zero and variance σ_μ^2. Previous research (Lewis et al., 1999) suggested that the variance of flock means in these terminal sire breeds was approximately equal to the within-flock additive variance. Similar values for the additive variance among production units were reported in other species before the widespread use of AI (Cundiff et al., 1975; Spike and Freeman, 1978). Therefore, σ_μ^2 was set to 0.25 for all scenarios.

Breeding values for descendants of base animals were simulated as

$$BV_i = (1/2)(BV_s + BV_d) + \phi_i,$$

where BV_s and BV_d are BV of the sire and dam, respectively, of animal i. The Mendelian sampling effect (ϕ_i) was assumed to be normally distributed with mean zero and variance $(1/2)[1 - (F_s + F_d)/2]\sigma_a^2$, where F_s and F_d are inbreeding coefficients of the sire and dam, respectively, and were obtained from the algorithm of Meuwissen and Luo (1992).

Phenotypic records (P) for the trait of interest were obtained for the ith animal as the sum of genetic, environmental, and residual variables:

$$P_{ijklmn} = BV_i + FL_j + YR_k + S_l + D_m + R_n + e_{ijklmn},$$

where FL_j, YR_k, S_l, D_m, and R_n were environmental effects of the flock in which animal i was born, the animal's birth year, the sex of the animal, the age of the animal's dam, and the animal's birth type (single vs. multiple), respectively, and e_{ijklmn} was a random residual effect for animal i. Environmental effects of flock and year were sampled from normal distributions with means of zero and variances of 0.20 and 0.05, respectively. Females were 0.85 phenotypic SD units lower in phenotype than males, animals born to ewes 3 yr of age or older were 0.20 units greater than those born to younger ewes, and animals born as twins or triplets were 0.35 units lower than those born as singles. These values correspond to standardized differences between classes for these effects in UK terminal sire breeds, as reviewed by Lewis and Simm (2000).

Random residual effects were sampled independently for each animal from a normal distribution with mean zero and variance 0.75.

Reproductive and survival parameters assumed in the simulation are summarized in Table 1. Rams and ewes were first eligible for mating at 15 mo of age. A mating season encompassing 3 estrous cycles (51 d) was assumed each year. On average, 89% of reproductively eligible ewes conceived. A minimum of 2 rams were used in each flock per year. The ram-to-ewe ratio was never lower than 1:25 nor greater than 1:20.

Before selection, each flock underwent 10 yr of random selection to create a history of performance and pedigree records for each flock. After this initial period, flocks began selection on the simulated performance trait for 15 yr and had the opportunity to join a cooperative breeding scheme. Rams used across flocks by AI or natural service, as well as rams used within flocks, were selected at random from the top one-sixth of their respective pools ranked by BLUP EBV. Enough ewes were selected to maintain a constant flock size, resulting in an annual replacement rate of approximately 26%. The mating of animals with a half-sibling relationship or greater was avoided; otherwise, mates were assigned at random.

Simulation Scenarios. Sire referencing via AI for all 15 yr of selection was used as the baseline scenario. Six rams were chosen as a team from the 15 participating flocks and were made available as reference sires. The older half of the team was replaced each year. Each flock randomly selected 3 reference sires from the team, and each sire was mated to 10 ewes within a flock; therefore, 30 ewes in each flock were mated to reference sires. Flocks were allowed to reuse 1 reference sire in consecutive years while participating in the reference scheme.

Five other breeding schemes were simulated, including 1) no exchange of rams between flocks; 2) termination of sire referencing after either 5 or 10 yr, with flocks remaining independent thereafter; 3) sporadic participation in sire referencing; and 4) natural service (as opposed to AI) sire referencing. Each alternative was chosen to quantify the effects of relaxing various restrictions placed on producers participating in sire referencing via AI.

In the scenario involving only sporadic participation in sire referencing, one-third of the 15 flocks temporarily discontinued participation in the scheme each year. Each flock participated in the scheme for 2 yr followed by a year in which reference sires were not used (although the same breeding objective was maintained). This system was systematic in that the same 5 flocks disengaged every third year, and at any one time, only 10 flocks were using reference sires. For example, flocks 1, 4, 7, 10, and 13 did not participate in sire referencing in the first year and returned the second year, and flocks 2, 5, 8, 11, and 14 did not participate in the second year. Even when flocks were not using reference sires, they were still allowed to contribute sires to the reference sire pool.

Natural service sire referencing was similar to AI sire referencing in that each flock was required to mate 3 sires from other member flocks to 10 ewes each year. These natural service reference sires could only be used in 1 flock each year. Therefore, 45 rams were selected each year to form the reference sire pool. In common with AI sire referencing, sires could be used in consecutive years (maximum of 2 yr) if they were still alive. Half of the natural service reference sire pool was replaced each year. Unlike AI sire referencing, previously used sires were randomly reallocated to the 15 flocks (excluding their flock of origin) in their second year. By chance (1 in 14), a given sire could be used in the same flock for 2 consecutive years but normally would be moved to a different flock.

All 6 breeding schemes were simulated with 2 strategies for the acquisition and use of rams other than the reference sires. In the first case, half of the flocks mated their excess ewes exclusively to unrelated purchased rams with no pedigree or performance data. The rest of the flocks mated an average one-half of their ewes to purchased rams and one-half to their own homebred rams. Breeding values for purchased rams were sampled from a normal distribution with mean $0.8\theta_i$ and variance 0.25, where θ_i is the mean true BV of the overall scheme in year i. The value of 0.8 was chosen to reflect the genetic distance between flocks practicing within-flock vs. across-flock selection on BLUP EBV (Lewis and Simm, 2000). This sire use strategy reflects the level of purchased animal use in flocks that participate in sire referencing in the United Kingdom (Lewis and Simm, 2000) and will be referred to as the outside sire strategy.

In the second nonreference sire use strategy, all flocks used only homebred sires in addition to the required reference sires. Although not likely in practice, a strategy in which all sires were produced within the system and with a high level of use of sires born within their flock of origin provided a contrast to the purchased ram strategy. This sire use strategy is referred to as the homebred sire strategy. With these 2 sire use strategies and 6 breeding schemes, there were 12 different breeding scenarios. Each scenario was replicated 50 times.

EBV Prediction Model

The EBV were derived by using an animal model with complete relationships:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{ZQg} + \mathbf{Zu} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of phenotypes for the simulated trait; $\mathbf{b}$ is a vector of fixed effects, including contemporary group (flock and year), sex, and number of lambs born in a litter; $\mathbf{g}$ is a vector of genetic group effects assigned according to year of entry into the system; **u** is a vector of BV (as a deviation from **Qg**); and **e** is a vector of residuals. Incidence matrices **X** and **Z** relate phenotypes to fixed and random genetic effects, respectively, and **Q** is a matrix that specifies the proportion of genes in each animal originating from each genetic group.

Genetic groups, defined by the birth year of purchased sires introduced from outside the scheme, were fitted only for the outside sire strategy and were used to account for unpedigreed animals entering the system. Grouping was not used to account for the initial genetic mean differences between participating flocks. It would not have been possible to fit genetic groups to flocks of origin in the initial years of selection because these group effects would have been completely confounded with contemporary groups effects. Breeding values were estimated, assuming a heritability of 0.25, which does not account for genetic variation between flocks. An analysis of data from disconnected flocks would be expected to yield this within-flock heritability, because all differences among flocks would be assumed to be due to environmental factors (i.e., contemporary group differences).

Summary Statistics

True BV and inbreeding coefficients (F) were averaged for animals born in each year after selection began. For all scenarios, BLUP EBV were calculated under the assumption that there were no genetic differences between flocks; thus, base animals were assumed to have been drawn from a random sample with the same genetic mean. This model is common in the genetic evaluation of livestock but leads to biased predictions of EBV if flock genetic means actually differ. To quantify the adequacy of each breeding scheme at removing bias associated with differences among flock genetic means, a contrast (L_{ij}) was calculated for all pairs of ram lambs produced in each year:

$$L_{ij} = (u_i - u_j) - (\hat{u}_i - \hat{u}_j),$$

where u_i and u_j are BV of animals i and j, respectively, and $\hat{u}_i$ and $\hat{u}_j$ are the BLUP EBV of animals i and j, respectively. Ram lambs were chosen for these contrasts because they were the candidates for future reference and homebred sire selection. The statistic was squared and averaged for pairs of ram lambs across flocks, resulting in a measure of the mean squared error (**MSE**) of prediction of differences in BV of ram lambs born in different flocks. The MSE is the sum of the prediction error variance (**PEV**) of the EBV difference and the squared bias in this predicted difference. The across-flock MSE, averaged over all flocks, was compared with the average squared L_{ij} of pairs of animals born in the same flock, which should be unbiased and consist of only the PEV of EBV differences. The difference between the across- and within-flock average squared L_{ij} would therefore estimate the squared bias attributable to different flock genetic means.

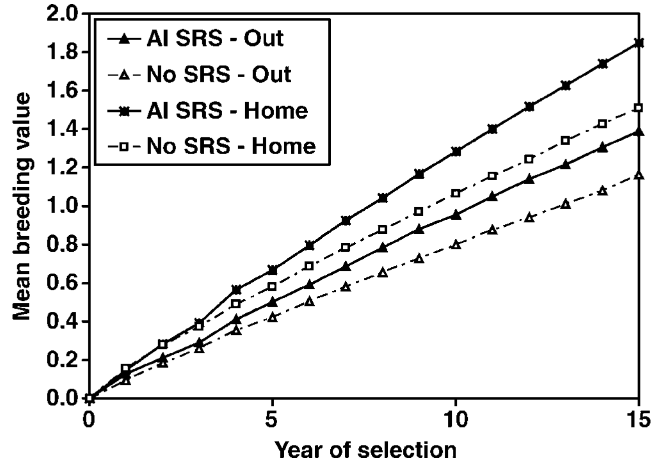

Figure 1. Average mean breeding value for 15 flocks after selection on BLUP EBV for 15 yr. Flocks either joined an AI sire referencing scheme (AI SRS) or remained autonomous (No SRS). Nonreference sires came exclusively from within participating flocks (Home) or both from within the flocks and from unknown outside sources (Out).

RESULTS

Genetic Gain and Inbreeding

Genetic merit was adjusted to zero for all scenarios at the start of selection by subtracting the average BV at year zero, because all selection decisions had been at random during the 10 yr of flock establishment. Genetic trends (BV) are illustrated for cases in which flocks either participated in a continuous sire referencing scheme via AI or remained autonomous (Figure 1). For each approach, the 2 strategies for use of nonreference sires (homebred vs. both homebred and outside sires) are shown. These 4 simulation models are used as standards for comparing results from other breeding systems. Gains were similar for the first 3 yr of selection regardless of whether the flocks participated in sire referencing. After this time, flocks become more clearly differentiated based on genetic merit (mean true BV); reference sires were increasingly chosen from the better flocks. Genetic gains in scenarios in which flocks participated continuously in sire referencing were approximately 25% greater after 15 yr than those in which flocks remained autonomous. Within breeding scenarios, use of outside sires with a mean genetic merit of 80% that of scheme member flocks reduced the rate of genetic gain.

The reduced gain with use of sires from outside the sire referencing scheme resulted from both the lower mean assumed for these sires and from a reduction in the total amount of genetic variation available in the

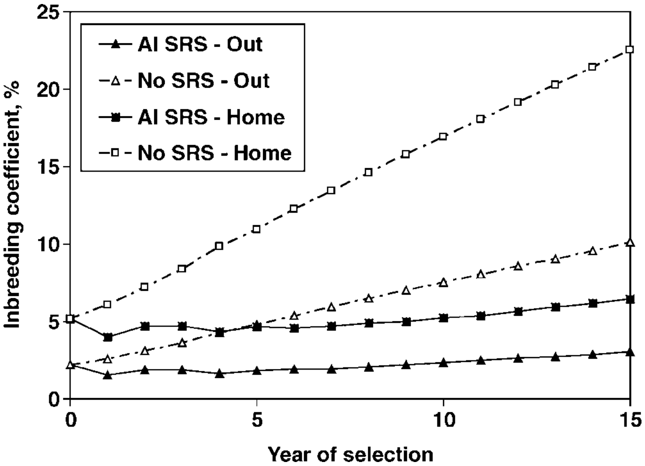

Figure 2. Average inbreeding coefficient for 15 flocks after selection on BLUP EBV for 15 yr. Flocks either joined an AI sire referencing scheme (AI SRS) or remained autonomous (No SRS). Nonreference sires came exclusively from participating flocks (Home) or came both from within the flocks and from unknown outside sources (Out).

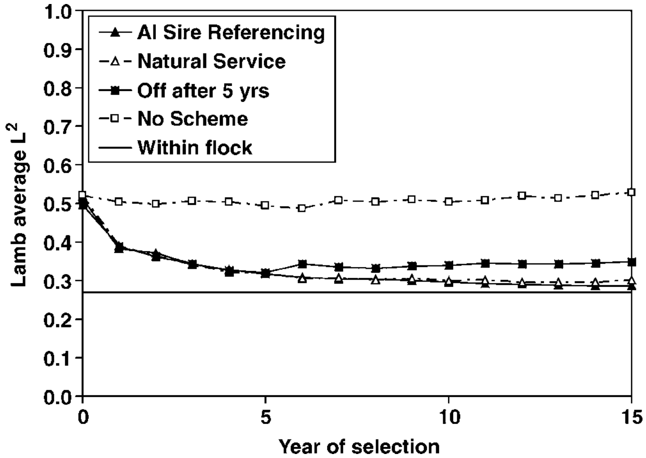

Figure 3. Average mean squared error of all possible contrasts (L^2) between pairs of ram lambs across flocks relative to all possible contrasts between pairs of ram lambs within flocks for 4 breeding schemes: AI sire referencing, AI sire referencing for 5 yr followed by flocks becoming autonomous, natural service sire referencing, and completely autonomous flocks (no scheme). Flocks were allowed to mate their ewes to nonpedigreed outside sires as well as to a mix of homebred rams and reference sires.

system. During the initial 10-yr period of random selection, the total genetic variance decreased when using outside sires because they were simulated from a distribution with a common mean. This sampling strategy may be possible in real sire referencing schemes because a group of flocks working toward a common breeding objective may sample outside rams of a similar type or from a common source. The average genetic variance, as measured by the variance in true BV for animals born the year before selection began, was reduced to approximately 0.35 when outside sires were used, whereas the variance remained at an average of approximately 0.50 (between- plus within-flock variance) when only homebred sires were used.

A comparison of inbreeding rates from the same set of scenarios is shown in Figure 2. Inbreeding levels at the start of selection were 2.2 and 5.2% for outside and homebred sire strategies, respectively. The use of unrelated outside sires thus reduced inbreeding before and during selection. When flocks remained independent, inbreeding increased much more rapidly when only homebred sires were used (1.16%/yr) as compared with when outside sires were allowed (0.53%/yr). Inbreeding immediately fell in the first year of selection within the AI reference schemes because the reference sires used within individual flocks generally originated from other members' flocks. Regardless of whether outside or homebred sire strategies were used, inbreeding increased at a very low rate when flocks participated in the AI sire referencing scheme (from 0.13 to 0.18%/yr).

Trends in genetic gain and inbreeding were similar for other breeding schemes in that they were always greater when the homebred sire strategy was adopted (Table 2). When flocks discontinued AI sire referencing after 5 or 10 yr, rates of genetic gain and inbreeding declined to levels that were similar to those observed when no reference sires were used. For the outside sire strategy, genetic gains at yr 15 were 92.8 and 88.5% of that for AI sire referencing when flocks disengaged after 10 or 5 yr, respectively. For the homebred sire strategy, genetic gains at yr 15 were greater (97.3 and 91.9%, respectively), possibly because flocks remained more homogeneous after sire referencing and previous genetic gains were not diluted by the introduction of outside sires with a lower mean for the selected trait.

Inbreeding and genetic gain results for sporadic AI sire referencing and natural service sire referencing are also shown in Table 2. Sporadic participation in AI sire referencing resulted in slightly reduced genetic gain and a slightly greater rate of inbreeding relative to the continuous AI sire referencing scenarios. However, rates of gain were still considerably greater than without sire referencing. Natural service sire referencing was similar to AI sire referencing in terms of genetic gain. For continuous AI sire referencing, flocks achieved a 0.092 annual increase (G_{15}/15 yr) in mean BV, whereas natural service achieved a 0.097 annual increase under the outside sire strategy. Under the homebred sire strategy, both scenarios achieved approximately the same rate of genetic gain (0.123/yr). Inbreeding was lower with natural service sire referencing because flocks did not use reference sires that originated in their own flock. Under the assumed selection

Table 2. Genetic gain (G, phenotypic SD units) and inbreeding (F, %) after 5, 10, and 15 yr of selection on BLUP EBV at an intensity of one-sixth for a 0.25 heritable trait under different types of sire referencing schemes and different levels of outside sire use

Source of nonreference sires	Breeding scheme	Genetic gain			Inbreeding		
		G_5	G_{10}	G_{15}	F_5	F_{10}	F_{15}
Outside	AI continuous	0.50	0.95	1.39	1.83	2.36	3.08
	AI 5 yr	0.50	0.87	1.23	1.90	4.17	6.93
	AI 10 yr	0.49	0.94	1.29	1.85	2.26	4.31
	AI sporadic	0.53	0.88	1.29	2.40	3.03	3.73
	NS[1] continuous	0.47	1.01	1.46	1.07	1.34	1.82
	No scheme	0.42	0.80	1.16	4.80	7.54	10.13
Min SE		0.02	0.02	0.02	0.03	0.07	0.09
Max SE		0.03	0.03	0.03	0.08	0.10	0.12
Homebred	AI continuous	0.67	1.28	1.85	4.65	5.22	6.47
	AI 5 yr	0.69	1.22	1.70	4.41	9.09	15.20
	AI 10 yr	0.68	1.29	1.80	4.56	5.22	10.03
	AI sporadic	0.64	1.22	1.79	6.33	6.93	8.00
	NS continuous	0.71	1.31	1.84	2.92	3.22	4.06
	No scheme	0.58	1.06	1.51	10.94	16.94	22.53
Min SE		0.02	0.02	0.02	0.07	0.05	0.06
Max SE		0.03	0.03	0.03	0.19	0.29	0.38

[1]NS = natural service.

intensity (i.e., rams are chosen as reference sires from the top one-sixth by BLUP), natural service sire referencing was as efficient as, and perhaps preferable to, AI sire referencing.

Bias Attributable to Flock Genetic Mean Differences

The MSE associated with predicted differences in BV between pairs of ram lambs (average squared L_{ij}) across flocks are presented in Figures 3 and 4 for 4 breeding scenarios with and without the use of outside sires. In each figure, the average MSE of within-flock differences between ram lambs is presented as a proxy for the expected PEV of this difference without bias. This baseline level averaged 0.27 across all scenarios throughout the 15 yr of selection.

Before selection began (yr 0), the average squared L_{ij} was quite variable across replicates for all scenarios, with an SE of 0.02. Hence, not all scenarios had the same initial average squared L_{ij} before selection, even though they had undergone the same set of conditions until that point. However, differences between scenarios within sire use strategies were not significant. Figure 3 shows the average squared L_{ij} for scenarios in which outside sire use was allowed. After selection began, the scenarios behaved similarly, with a rapid decrease in average squared L_{ij} in the first few years of sire referencing, followed by a continued asymptotic decline as the between-flock MSE approached the value of the within-flock error. This reduction in average squared L_{ij} occurred because bias associated with initial differences in genetic means among flocks was better explained by the genetic evaluation model as flocks became more connected and more homogeneous. The same trends were observed for strategies involving the use of homebred sires (Figure 4), although initial levels of bias were greater when outside sires had not been used.

Both sire use strategies resulted in similar proportional reductions in bias attributable to implementation of sire referencing schemes. However, the initial level of average squared L_{ij} was greater in the homebred sire strategies (Figure 4) than in the outside sire strategies (Figure 3). The main reason for this discrepancy was that the full additive variation attributable to between- and within-flock differences remained after the initial 10 yr of random selection for the homebred strategy (before selection and sire referencing). The expected level of the squared L_{ij} for these pairwise comparisons of ram lambs should equal the PEV of the contrast L_{ij} plus twice the variance in flock means (which is unaccounted for when no connections between flocks are present). Therefore, in the homebred sire strategy, the difference between the within-flock average squared L_{ij} and the between-flock average squared L_{ij} was close to the expected difference of 0.50 (i.e., the sum of the additive variance within and among flocks). In scenarios using the outside sire strategy, this difference was only approximately 0.20 because flock genetic means had become somewhat homogenized by use of outside rams with a common mean, resulting in a drop in the between-flock additive variance.

During the initial 10-yr period of random mating, the variance among flock means decreased from the starting value of 0.25 units^2 to 0.14 units^2 with the outside sire strategy. That reduction was due to these outside rams being drawn from a distribution with a common mean. For the homebred sire strategy, the variance among flock means changed less, and actually

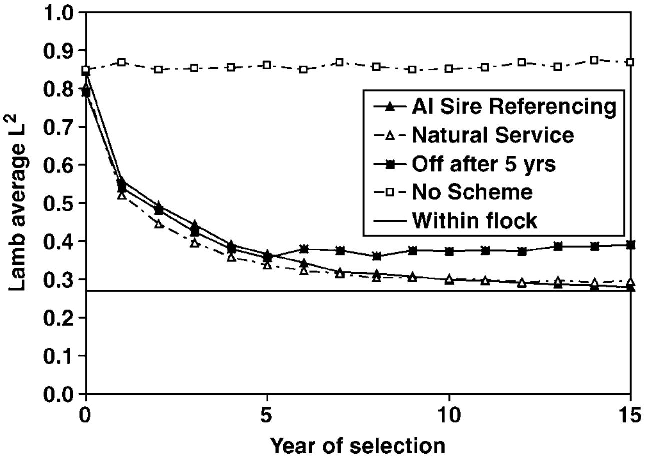

Figure 4. Average mean squared error of all possible contrasts (L^2) between pairs of ram lambs across flocks relative to all possible contrasts between pairs of ram lambs within flocks for 4 breeding schemes: AI sire referencing, AI sire referencing for 5 yr followed by flocks becoming autonomous, natural service sire referencing, and completely autonomous flocks (no scheme). Flocks were allowed to mate their ewes only to homebred and reference sires.

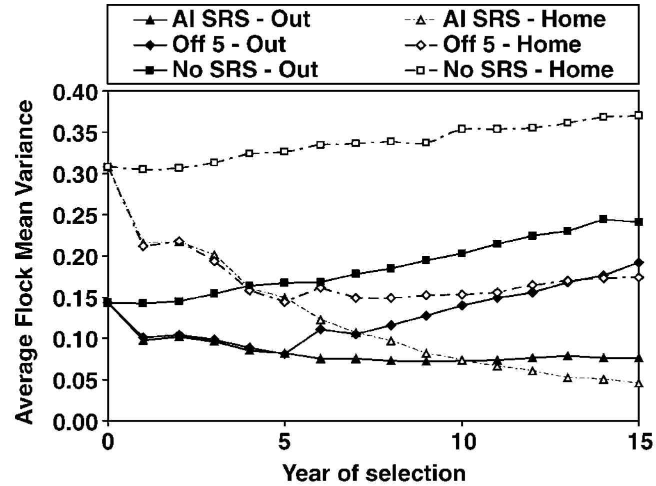

Figure 5. Average variance among flock means for 15 flocks after selection on BLUP EBV for 15 yr. Flocks either joined an AI sire referencing scheme (AI SRS), joined an AI sire referencing scheme for 5 yr followed by flocks becoming autonomous (Off 5), or remained autonomous (No SRS). Nonreference sires came exclusively from participating flocks (Home) or came both from within the flocks and from unknown outside sources (Out).

increased slightly, over the random mating period, averaging 0.31units^2. Selection affected the variance among flock means. Sire referencing of any form decreased this variance, coinciding with an increasing genetic homogeneity of the flocks within a scheme. In both sire use strategies, and where sire referencing was continuous (i.e., AI, natural service, sporadic), the variance among flock means decreased to levels below 0.10 units^2 after 15 yr of selection. Natural service scenarios were the most homogeneous, with an average variance of 0.04 units^2 among flock means at yr 15; sporadic scenarios had the greatest value, 0.09 units^2. These lower values for the variance among flock means were obtained more rapidly under the outside sire strategies, likely because they were already lower at the start of selection. When sire referencing stopped (or never began), the variance among flock means increased. Under the outside sire strategy, the rate of increase was 0.007 units^2/yr with no sire referencing, and 0.011 and 0.013 units^2/yr, respectively, when sire referencing ceased after 5 and 10 yr. For these same scenarios, the variance increased by 0.003 to 0.004 unit^2/yr under the homebred sire strategy. Representative examples of these variance trends are shown in Figure 5.

Both AI and natural service sire referencing performed equally well in terms of the reduction of bias in comparisons between lambs. If flocks discontinued sire referencing after 5 or 10 yr (not shown), the average squared L_{ij} increased slightly in the first year they left the scheme. However, in later years, the average squared L_{ij} remained constant. Sporadic participation in sire referencing (also not shown) resulted in a slightly slower decrease in the average squared L_{ij} compared with continuous sire referencing; approximately 10 yr were required to reach the same level of average squared L_{ij} that other scenarios reached in 5 yr.

DISCUSSION

As shown by Lewis and Simm (2000), optimally designed AI sire referencing schemes increased genetic gain and decreased inbreeding relative to flocks that remained autonomous. In their study, the optimal level of reference sire use was 3 reference sires each mated to 10 ewes. Similar studies have also shown that sire referencing can increase genetic gain by 30 to 35% (Hanocq et al., 1996; Roden, 1996). In the current study, gains from AI sire referencing were slightly greater than those reported by Lewis and Simm (2000) at the same relative selection intensity (top one-sixth) because flocks were simulated with different genetic means, providing a source of between-flock genetic variance after sire referencing began. The use of reference sire matings when flocks differ genetically has been shown to increase genetic progress relative to situations in which units have the same genetic mean (Miraei Ashtiani and James, 1993; Hanocq et al., 1996). Management units with the lowest mean BV benefit by using germplasm from units with high mean BV (Hanocq et al., 1996). However, connections must be sufficient to allow reliable estimation of genetic differences between units.

Genetic gains were also increased with sire referencing as compared with no scheme because individual flocks were able to take advantage of greater genetic variation across cooperating flocks. Smith and Banos (1991) showed analytically that connections were of the most benefit to flocks with either low genetic means or small sizes (less than 100 males born per year). In essence, cooperating flocks become a "superflock" or common population rather than distinct subpopulations. If their breeding objectives are complementary, the overall selection intensity across flocks is increased in this larger population. Therefore, even if the flocks do not differ in genetic mean, there can be benefits from cooperative breeding systems. As shown in this study, leaving the cooperative scheme reduced genetic gain, primarily because of decreased selection intensity within flock. The flock structures simulated in this study were representative of terminal sire breeds in the United Kingdom. In general, these flocks are small, with only 50 to 150 breeding females. Seedstock flocks in the United States are of similar size and would likely observe similar benefits from participation in sire referencing schemes.

Natural service sire referencing was comparable to AI sire referencing in terms of genetic gain and was superior in terms of inbreeding. However, if only the best animals were chosen as reference sires based on their BLUP EBV, natural service sire referencing would likely be unable to achieve the same level of genetic gain as AI sire referencing. Approximately 700 rams were weaned each year within the 15 flocks. If only the best rams were kept for the reference sire pool each year (3 rams for AI; approximately 23 for natural service), the corresponding intensity values (i) would be approximately 2.23 and 2.94 for natural service and AI sire referencing, respectively. The level of selection intensity in the current study (top one-sixth; $i = 1.50$) allowed natural-service reference sires to be chosen with approximately the same genetic merit as that achieved for AI sires. Nevertheless, realistically, the level of selection intensity is likely no greater than this for sheep flocks in both the United States and the United Kingdom. If done persistently, natural service sire referencing (ram exchange) provides producers with a strategy to connect their flocks without the expense and difficulty of AI matings, at least when the level of reference sire use is as high as that in this study (30 ewes per flock).

Sporadic participation in sire referencing reduced genetic gain and resulted in greater inbreeding. However, if producers would like more freedom in choosing rams, this strategy would allow them to ignore the restrictions of the scheme in every third year. This compromise may be useful if it is difficult to convince producers to join cooperative schemes. Interestingly, the gains at yr 15 were very similar to those in the comparable strategies in which sire referencing ceased after 10 yr. With sporadic participation, individual flocks would also be part of the scheme for 10 of the 15 yr.

Achievement of the predicted genetic gains presumed that the flocks had a common breeding objective—in this case, improvement in a single moderately heritable trait. In reality, flocks often differ in breeding goals, but even in those cases, sire referencing schemes still provide for more accurate comparisons of animals from different flocks. Increasing connections among flocks thus allow breeders to assess animals more accurately from other member flocks regardless of their breeding goal. With different breeding goals, and depending on the genetic correlations among traits in these goals (Smith and Banos, 1991), genetic means may actually diverge among flocks as selection progresses. Nevertheless, the rankings of the flocks for individual traits of interest would become more reliable with sound connections among flocks. Evaluation of measures of the level of connection among flocks is the subject of a subsequent manuscript (Kuehn et al., 2008).

All cooperative breeding schemes were effective in reducing bias in BV predictions. Each of the continuous sire referencing strategies (AI, natural service, sporadic) reduced bias asymptotically to nearly zero after 15 yr. When flocks ceased participation in sire referencing, the MSE of predicted pairwise ram lamb differences rose slightly in the first year after disengagement and then remained relatively constant for the remaining years of selection. Once bias was removed from the system, it did not again increase, even when flocks were no longer actively connecting to one another. The reason for the initial increase in the MSE after disengagement is not obvious, but may reflect decreased accuracy of BV prediction when reference sires were no longer used rather than from an increase in bias. Even if a flock leaves a scheme, subsequent genetic changes attributable to selection or random drift can be explained by the relationship matrix, as postulated by Sorensen and Kennedy (1983), as long as pedigree and performance recording continues. Therefore, participation in one of the sire referencing schemes described here can nearly eliminate the risk associated with making genetic comparisons across flocks in a relatively short time (5 yr). Less intense schemes involving sporadic participation in the scheme can achieve similar reductions in bias but require longer periods of time (10 yr).

Base animals originating in different flocks were not genetically grouped to attempt to account for bias in EBV from differing initial flock genetic means. As stated earlier, genetic group effects could not be estimated when selection first began because group effects would be completely confounded with nongenetic flock differences. After sire referencing began, genetic groups could have been added to the model, but MSE may be greater when group effects are included because of the error associated with estimating the group solutions (Kennedy, 1981). The effectiveness of fitting genetic groups thus depends on the magnitude of genetic differences among flocks and on the amount of information available for estimation of group effects: if differences are large, then MSE will be high in models without genetic groups because of bias, but if genetic differences are modest or group sizes are small, genetic grouping may actually increase MSE by incorporating relatively imprecise estimates of genetic group effects. Additional problems may arise in fitting genetic group effects in real data sets. The actual flock of origin of base animals may not be reported or the flock of origin may be poorly represented (e.g., by only 1 or 2 sires), potentially leading to very high SE of group estimates. In this study, bias from not fitting genetic groups rapidly decreased through participation in sire referencing schemes, implying that fitting genetic groups may not be important if sufficient connections among flocks are established.

The use of outside sires was detrimental to genetic gain in this study, primarily because these sires were assumed to be sampled from a distribution with a lower genetic mean than the flocks participating in sire referencing. If flocks outside the sire referencing scheme are participating in improvement programs, this assumption may not be valid. However, for these outside flocks to have greater genetic merit than the sire referencing flocks, they must be either participating in a cooperative scheme or selecting their animals with greater selection intensity. Participants in sire referencing schemes often aspire to find superior sires from outside the scheme to achieve greater levels of genetic progress, but the likelihood of identifying a superior outside sire is probably low, given the potential rates of gain within sire referencing schemes.

Assuming that outside sires arose from a common distribution with the same mean may not wholly mimic sire referencing schemes in practice. In this study, flocks became more homogeneous prior to selection because of this assumption. If outside sources of rams were flock dependent, and as a result had different means, flocks would not homogenize as quickly (as seen in the reduction of variance among flock means). However, variance among flock means would still decrease with sire referencing as long as flocks worked toward a common breeding objective. Although the population of outside rams was less variable in this study, this assumption made the 2 sire use strategies more distinct and broadened the inference of the results.

The importance of connecting flocks to reduce bias caused by differences in genetic means depends on the extent of the differences. Differences can arise between flocks because of their physical isolation combined with genetic drift and because of differing selection policies. The sheep industry in the United States and terminal sire breeds in the United Kingdom both are characterized by seedstock flocks that are small (averaging less than 100 females), and therefore may be susceptible to genetic drift. Differences in geographic regions and target markets have potentially led to different breeding objectives. Therefore, the prospect that EBV derived across disconnected flocks are directly comparable is unlikely. If flocks do not expect to exchange germplasm with one another or do not compete with each other for the same commercial markets, the ranking of animals across these flocks is of little importance. However, if seedstock producers (or their clients) wish to make accurate comparisons across flocks, sire referencing by AI or natural service provides an excellent means to decrease bias in these comparisons in a relatively short period of time.

Breeding systems such as natural service sire exchange and irregular participation in sire referencing can still capture many of the benefits of continuous use of reference sires by AI. Natural service strategies reduce inbreeding more effectively than AI strategies and, at comparable selection intensities, produce the same level of genetic gain. Furthermore, presuming that flocks differ in their genetic means, natural service strategies reduce bias in the genetic evaluation as effectively as schemes based on the use of AI reference sires. However, if only the best animals are selected, genetic gains using AI would likely be superior. When flock genetic means differ, participation in cooperative breeding schemes results in unbiased estimation of genetic differences among animals from different flocks after only a few years, and can help participants take advantage of genetic variation among flocks.

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