

Implications of Connectedness in the Genetic Evaluation of Livestock

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by

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ABSTRACT

The reliability of genetic evaluations across separate management units (e.g. flocks) depends on the extent of genetic links or connections among animals in these units. Where poor connectedness exists, comparisons of estimated breeding values (EBV) across units may be biased. The objectives of this study were to identify breeding strategies to increase connectedness among units, to evaluate statistics that may reflect the reduction in bias as connectedness increases in such strategies, and to assess levels of connectedness in Suffolk and Targhee flocks participating in the National Sheep Improvement Program.

Expectations of bias when production units have different genetic means were derived for a simple sire model. These expectations were applied to data involving two flocks of animals with three different types of connections: sharing of a common reference sire or use of either a full- or half-sibling sire in each flock. Bias decreased as numbers of progeny in each flock increased for all methods. Linking through a reference sire was most effective and was the only method that eliminated bias as progeny numbers became infinite.

Pedigree and performance data on a single trait with heritability 0.25 were then simulated for 15 flocks with 40 to 140 ewes per flock. Each flock was simulated with a different founder genetic mean to introduce bias into the genetic evaluation. Flocks participated in sire referencing schemes by artificial insemination, with varying levels of participation, or by natural service. With sire referencing genetic gain was higher and inbreeding was lower than without, and bias was rapidly reduced to near-zero levels. Discontinuing the schemes led to lower genetic gain, but bias was not reintroduced. The prediction error correlation of flock genetic means was proposed as a connectedness measure because it was strongly associated with bias. Benchmarks of 0.05 and 0.10 for 'good' and 'superior' connectedness were established.

Targhee flocks have increased connectedness across the breed by actively exchanging rams over 15 yr. In the Suffolk breed, connectedness has only improved within segregated clusters of flocks. Suffolk breeders need to engage in active ram exchange to decrease risk of biased across-flock EBV comparisons.

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DEDICATION

To my beautiful wife and best friend, Brenda.

Without your support none of this would be possible.

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CHAPTER 1

Introduction

Genetic evaluation programs in domestic livestock species allow producers to make greater genetic progress in traits of economic importance than would be possible by phenotypic selection. Estimated breeding values (EBV) are calculated for traits of interest using best linear unbiased prediction (BLUP) procedures and enable producers to select parents of future generations. Through BLUP, phenotypic records are partitioned into genetic and environmental components (Henderson, 1973). Systematic environmental effects are accounted for by fitting management unit (flock or herd) and recording year as fixed effects. As a result, EBV of animals born in different flocks or herds or in different years can be equitably compared. However, in order to detect genetic differences across management units, the units must be connected (Tong et al., 1980; Kennedy, 1981).

Connectedness is generally established in genetic evaluation through use of common sires in several management units or through transfer of breeding stock among units. These animals create genetic relationships across units, establishing a basis through which non-related animals can be compared. In the absence of these genetic relationships, connectedness between units will be poor and differences between units will be attributed to environmental causes. Since EBV are predicted as random effects, with a predefined mean and variance, they can be estimated even if there is no connectedness (Fernando et al., 1983). Means of EBV are usually assumed to be equal for all animals. However, if this assumption is violated, comparisons of EBV across disconnected subunits are potentially biased if base animals from the subunits have different genetic means.

Genetic means can differ among populations due to genetic drift or selection (Falconer and Mackay, 1996). If pedigree or performance recording begin after differentiation among subpopulations and connectedness between management units is insufficient, these genetic differences will not be reflected in BLUP EBV. Differences in unit genetic means due to selection are likely if gene flow is limited among the units. In

the United States, herds of cattle and flocks of sheep are often separated by large distances. The sizes of sheep flocks, and some purebred cattle herds, are generally small, increasing potential for genetic drift. Furthermore, artificial insemination (AI) is practically non-existent in most sheep flocks, increasing their regional isolation. All of these factors increase the chance of differences in unit genetic means. Analyses of differences between herds and flocks in beef cattle and sheep, respectively, has suggested that the genetic variance between units may be as high as that within units (Cundiff et al., 1975; Lewis et al., 1999). Although beef cattle have had the potential to increase gene flow through the use of AI since the study of Cundiff et al. (1975) was conducted, sheep populations are still at risk.

Biases due to different genetic means can be accounted for by predicting breeding values using a statistical model that accounts for genetic groups (Quaas, 1988). These models can be used to estimate the mean breeding values of base animals from each unit. However, in order for genetic group effects to be estimated independently from unit environmental effects, some level of connectedness between units is required (Kennedy, 1981). These models may also be difficult to implement. Often base animals cannot be assigned to a unit of origin. Some units may be poorly represented, leading to questionable estimates of genetic group effects. As connectedness increases, bias due to differences in unit genetic means should decrease even if genetic groups are not fit in the genetic evaluation model (Kennedy, 1981).

Therefore, the establishment of connectedness among units, especially in sheep, is important in order to minimize the risk associated with comparing genetic merit of animals across management units. This objective can be achieved in two ways. First, through design of breeding programs to establish connections among different units, and second, by providing producers with a tool to monitor their level of connectedness with other units, so that they can make appropriate mating decisions to minimize risk of biased comparisons. These methods do not have to be mutually exclusive – indeed the greatest potential for increasing connectedness and reducing risk comes from adopting both approaches.

Cooperative breeding programs have long been suggested as a method to increase genetic gain in domesticated livestock species. The use of reference sires to link units

together has been shown to increase accuracy (Foulley et al., 1983; Miraei Ashtiani and James, 1991) and genetic gain (Honocq et al., 1996; Roden, 1996; Lewis and Simm, 2000) relative to within-unit selection. To that end, AI sire referencing schemes have been implemented in sheep flocks in the United Kingdom (Simm et al., 2001) to increase the rate of lean growth in their populations. However, there is some concern that the requirements for participation in these schemes may discourage their wider uptake. For instance, if producers were allowed to use natural service rather than AI matings to reference sires or to vary in their level of participation in the scheme, they might be more inclined to join a sire-referencing scheme. The effect of these alternative strategies on genetic gain and bias reduction are unknown. Since these programs are designed, in part, to improve the level of connectedness between flocks, it would be useful to monitor the changes in connectedness over time achieved in such schemes.

Several statistics (e.g. Foulley et al., 1992; Kennedy and Trus, 1993; Laloë et al., 1993) have been proposed for monitoring the risk of comparing animals across flocks, but not all of them can be easily calculated in large data sets. A review of the properties of these statistics and their ease of implementation would be beneficial. Additionally, the behavior of these statistics over time relative to bias due to different unit genetic means has not been well established. By comparing the behavior of candidate statistics to the level of bias in simulation scenarios, benchmarks for minimum levels of connectedness relative to risk could be established.

Objectives

The broad focus of this research was to characterize the importance of connectedness in relation to risk in genetic evaluation. The major objectives of this dissertation were to:

- 1) review the literature to examine the importance of connectedness in genetic evaluations and to summarize the properties of potential connectedness measures;
- 2) develop and suggest methods that producers can use to increase connectedness and, thereby, reduce bias when comparing animals across units;

- 3) compare less restrictive alternatives to continuous AI sire referencing schemes in terms of their impact on genetic gain, inbreeding, and bias;
- 4) monitor changes in connectedness statistics over time and determine how well they quantify the level of risk due to bias in EBV comparisons; and, lastly
- 5) evaluate the historic and current level of connectedness in the Suffolk and Targhee flocks participating in the National Sheep Improvement Program.

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CHAPTER 2

Managing the risk of comparing estimated breeding values across flocks or herds through connectedness: a review and application

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Introduction

The use of best linear unbiased prediction (BLUP) in genetic evaluation of livestock effectively partitions animals' phenotypic records into their genetic and environmental components (Henderson, 1973). Known environmental factors such as management unit (flock or herd) are accounted for by fitting them as fixed effects. As a result, the genetic merit of animals born in different management units can be equitably compared. However, genetic differences between management units will be undetected unless there is sufficient connectedness between the units.

Connectedness, in a strict statistical sense, relates to the estimability of contrasts involving model fixed effects (Searle, 1971). A data set is connected only if all contrasts among fixed effects are estimable. In the context of genetic evaluation, connectedness is not required in order to predict random breeding values (Fernando et al., 1983) because they are assumed to be distributed normally with a predefined mean and variance. However, when disconnected subsets of records are present in the data, resulting predictions are only unbiased under the assumption that breeding values are randomly and identically distributed across the entire population of base animals (Tosh and Wilton, 1990). This assumption is violated if either selection or genetic drift occurs before pedigree and performance recording is established and causes genetic means among units to differ. Genetic means can be added to the evaluation to correct bias, but are impossible to calculate for disconnected subsets. Establishment of connections among

units allows separation of genetic and environmental differences between units.

Connectedness is important then if units have different genetic means.

Depending on the extent of gene flow among units, differences in genetic means can be quite likely. Sheep and beef cattle populations in the United States consist of many subpopulations, partially isolated by geographical distance and by sources of purchased seedstock. Analyses of genetic differences between herds and flocks (units) have suggested that the genetic variance between units may be as high as that within units (Cundiff et al., 1975; Lewis et al., 1999). Similar results were true in dairy cattle herds (Spike and Freeman, 1978) before widespread use of artificial insemination (AI). Widespread gene flow via AI may create extensive connections, but AI is currently not widely used in either the sheep industries: less than 2% of sheep in the United States are artificially inseminated (NAHMS, 2001). At the very least, comparisons between flocks and herds in the United States are risky if connectedness is poor.

In order to manage biases when comparing animals across units, either the source of these biases must be fit in the genetic evaluation model or tools for quantifying the risk of comparing animals across units must be identified. Biases in genetic evaluations introduced from differences in unit means can be eliminated by predicting breeding values using models that include genetic groups (Quaas, 1988). These models estimate the mean breeding value for base animals from each management unit, which accounts for mean differences between units. Connectedness between units is still required, however, in order to estimate both genetic group effects and environmental unit effects accurately with little bias and with acceptable standard errors (Kennedy, 1981; Tong et al., 1980).

To quantify risks involved in comparing animals across units, several connectedness statistics have been developed to assess the quality of across-unit connections (Foulley et al., 1990; Kennedy and Trus, 1993; Laloë, 1993). An ideal statistic would provide insights into the level of risk (due to inaccurate selection decisions based on animal rankings from biased breeding value predictions) when comparing individuals from different units. Connectedness statistics could also be used to design breeding programs which effectively link units to improve the quality of an across-unit genetic evaluation in general.

The objectives of this article are to: 1) review the application of genetic groups in breeding value prediction models in order to account for genetic differences between herds and flocks and to discuss some of the problems with their implementation; 2) examine the importance of connectedness and weigh the merits of various statistics developed to quantify connectedness; and, 3) suggest methods that producers could use to increase connectedness and, thereby, reduce bias when comparing animals from poorly connected subunits. This last objective is addressed using small sire model examples.

Review

Genetic groups model

Genetic groups were initially used in sire genetic evaluation models to account for differences in mean breeding values of bulls owned by different AI bull studs when relationships among bulls owned by different AI groups were not available (Kennedy and Moxley, 1974). Pollak and Quaas (1983) added genetic groups of base animals to the mixed model equations for a sire model using modified mixed model equations (Quaas and Pollak, 1981). Sire effects were calculated as the sum of fractional contributions of genetic groups by ancestry plus the animal's genetic deviation from these groups. This method of grouping base animal was later extended to animal models by Robinson (1986) and Westell et al. (1988). If non-random selection occurred before pedigree recording, this fixed group model can be considered the 'true' model.

Model definition. The general linear mixed model including genetic groups (Pollak and Quaas, 1983) is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{ZQg} + \mathbf{Zu} + \mathbf{e}, \quad (1)$$

where \mathbf{y} is a vector of phenotypes, \mathbf{b} is a vector of fixed effects, \mathbf{g} is a vector of fixed base animal genetic group effects (due to unit of origin), \mathbf{u} is a vector of random genetic effects expressed as a deviation from the expectation of each animal's genetic group, and \mathbf{e} is a vector of residuals. Incidence matrices \mathbf{X} and \mathbf{Z} relate phenotypes to specific combinations of fixed and random genetic effects, respectively, and \mathbf{Q} specifies the expected proportion of genes in each animal arising from the various genetic groups. In \mathbf{Q} , base animals have a 1 in the column corresponding to the group in which they

originated and 0 otherwise, and descendants of base animals have coefficients which sum to 1.0 and describe the fractional contribution of each genetic group to their ancestry.

The assumed distribution of random effects in this model is:

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} \sim N \left[\begin{bmatrix} \mathbf{Xb} + \mathbf{ZQg} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{ZAZ}'\sigma_a^2 + \mathbf{I}\sigma_e^2 & \mathbf{ZA}\sigma_a^2 & \mathbf{I}\sigma_e^2 \\ \mathbf{AZ}'\sigma_a^2 & \mathbf{A}\sigma_a^2 & \mathbf{0} \\ \mathbf{I}\sigma_e^2 & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix} \right], \quad (2)$$

where \mathbf{A} is the numerator relationship matrix, σ_a^2 is the additive genetic variance, and σ_e^2 is the residual variance. Estimates of \mathbf{g} and predictions of \mathbf{u} are obtained as solutions to the resulting mixed model equations:

$$\begin{bmatrix} \mathbf{Q}'\mathbf{Z}'\mathbf{M}\mathbf{Z}\mathbf{Q} & \mathbf{Q}'\mathbf{Z}'\mathbf{M}\mathbf{Z} \\ \mathbf{Z}'\mathbf{M}\mathbf{Z}\mathbf{Q} & \mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{g} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{Q}'\mathbf{Z}'\mathbf{M}\mathbf{y} \\ \mathbf{Z}'\mathbf{M}\mathbf{y} \end{bmatrix}, \quad (3)$$

with:

$$\mathbf{M} = \mathbf{I} - \mathbf{X}(\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'$$

to adjust for (or absorb) fixed effects included in \mathbf{b} and where λ is the variance ratio σ_e^2 / σ_a^2 . Predicted breeding values ($\hat{\mathbf{u}}_G$) from this model are a function of estimated genetic group effects and random predictions of breeding value deviations so $\hat{\mathbf{u}}_G = \mathbf{Q}\hat{\mathbf{g}} + \hat{\mathbf{u}}$.

Design matrices involving fixed effects (including group) are less than full rank, so only differences between groups are estimable in connected data sets. Breeding value predictions from a genetic groups model must therefore be interpreted relative to each other rather than as absolute values. Estimability of these differences depends on whether groups are connected across levels of other fixed factors in the models such as management unit, year, or season.

In contrast to fitting genetic groups to unit of origin, most genetic evaluation in the United States is conducted using the linear mixed model:

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

where \mathbf{y} , \mathbf{b} , \mathbf{e} , \mathbf{X} , and \mathbf{Z} are as previously defined in the genetic groups model (\mathbf{b} may also contain fixed genetic group effects for factors other than unit of origin such as breed). In this reduced model, \mathbf{u}_r is a vector of random breeding values. These breeding

values are no longer expressed as deviations from genetic group means. The random effects distribution for this model is:

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{u}_r \\ \mathbf{e} \end{bmatrix} \sim N \left[\begin{bmatrix} \mathbf{Xb} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{ZAZ}'\sigma_a^2 + \mathbf{I}\sigma_e^2 & \mathbf{ZA}\sigma_a^2 & \mathbf{I}\sigma_e^2 \\ \mathbf{AZ}'\sigma_a^2 & \mathbf{A}\sigma_a^2 & \mathbf{0} \\ \mathbf{I}\sigma_e^2 & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix} \right],$$

where \mathbf{A} , σ_a^2 and σ_e^2 are defined as before. This model assumes that all base animals are randomly sampled from a common population (i.e., all base animals have the same mean breeding value). The mixed model equations used to predict breeding values in this reduced model are:

$$(\mathbf{Z}'\mathbf{MZ} + \lambda\mathbf{A}^{-1})\mathbf{u}_r = \mathbf{Z}'\mathbf{M}\mathbf{y},$$

where \mathbf{M} is as previously defined. This reduced model does not account for fixed genetic differences in unit means. The impact of ignoring these differences is discussed later.

Prediction error variance (PEV). The change in the error variance of genetic predictions between models including *versus* excluding genetic groups is of particular importance. In a model without groups, the PEV matrix of the vector of predicted breeding values is a function of the inverse of the coefficient matrix:

$$\mathbf{C}_{uu} = (\mathbf{Z}'\mathbf{MZ} + \lambda\mathbf{A}^{-1})^{-1} \sigma_e^2. \quad (4)$$

However, in the model with groups, breeding values are a function of fixed genetic groups and random genetic deviations. Hence, the PEV of the breeding values becomes:

$$\text{Var}(\hat{\mathbf{u}}_G - \mathbf{u}_G) = \text{Var}(\mathbf{Q}\hat{\mathbf{g}} + \hat{\mathbf{u}} - \mathbf{Q}\mathbf{g} - \mathbf{u}). \quad (5)$$

If

$$\begin{bmatrix} \mathbf{C}_{11} & \mathbf{C}_{12} \\ \mathbf{C}'_{12} & \mathbf{C}_{22} \end{bmatrix} \quad (6)$$

is the generalized inverse of the partitioned coefficient matrix in (3), then from Henderson (1975) the PEV in (5) is:

$$(\mathbf{Q}\mathbf{C}_{11}\mathbf{Q}' + \mathbf{C}'_{12}\mathbf{Q}' + \mathbf{Q}\mathbf{C}_{12} + \mathbf{C}_{22})\sigma_e^2. \quad (7)$$

The accuracy of estimation of fixed group effects can have a large impact on the accuracy of genetic evaluation when fitting genetic groups. If the $\mathbf{C}_{22}\sigma_e^2$ term in (7) is of similar magnitude to the PEV of breeding values in the model excluding genetic groups (4), the

PEV of the breeding values in the groups model is increased by $(\mathbf{QC}_{11}\mathbf{Q}' + \mathbf{C}'_{12}\mathbf{Q}' + \mathbf{QC}_{12})\sigma_e^2$, where $\mathbf{C}_{11}\sigma_e^2$ is the error variance of the fixed group effects. Unlike the situation for random genetic deviations in which PEV must be less than the additive variance, the error variance of the fixed genetic group effects has no upper bound. Accuracy of evaluation under this model is thus strongly dependent on the number of animals in each group and the connectedness among the groups.

Comparison of models with and without genetic groups

When all animals in the data can be traced to a common base population via a complete relationship matrix and when all measurements used for selection are included in the data, past selection and genetic drift are accounted for in derivation of BLUP breeding value predictions (EBV) (Henderson, 1973; Sorensen and Kennedy, 1983). However, when selection or genetic drift occurs before data recording, genetic differences among groups of animals separated by time or space are not accounted for by the relationship matrix alone. Herds or flocks which have undergone prior undocumented selection violate the assumption that all base animals are randomly chosen from a common base population (Henderson, 1975). The importance of including genetic groups in the genetic evaluation model depends on the perceived size of genetic differences between these heterogeneous subclasses.

In order to identify which model was better when base animals differ genetically, Kennedy (1981) derived the expectation of the bias in sire evaluation when a model without genetic groups was used but group differences exist. From this expectation one could derive the mean square error (MSE) of prediction for the model without groups as the sum of the squared bias and the PEV of the breeding values. The MSE from the model without genetic groups could then be compared to the MSE from a groups model (which is equal to the PEV since there is no bias) to determine which model is preferred for a given data set. When there are only two genetic groups, the non-groups model had lower MSE as long as the true genetic difference between groups was less than the standard error of the difference in group solutions from the groups model. These results cannot be extrapolated to data sets with more than two genetic groups but can be used as a criterion for whether or not to include groups in the genetic evaluation model.

The bias from fitting a model without genetic groups when fixed genetic group effects do exist was derived by Foulley et al. (1990) for an animal model (Westell et al., 1988). Using expectations in (2) and the vector of breeding values ($\hat{\mathbf{u}}_r$) from the reduced, non-groups model:

$$\begin{aligned} E(\hat{\mathbf{u}}_r) &= E[(\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1})^{-1}\mathbf{Z}'\mathbf{M}\mathbf{y}] \\ &= (\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1})^{-1}\mathbf{Z}'\mathbf{M}[E(\mathbf{y})] \\ &= (\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1})^{-1}\mathbf{Z}'\mathbf{M}(\mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{Q}\mathbf{g}) \\ &= (\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1})^{-1}\mathbf{Z}'\mathbf{M}\mathbf{Z}\mathbf{Q}\mathbf{g}. \end{aligned}$$

The bias in $\hat{\mathbf{u}}_r$ is then:

$$E(\hat{\mathbf{u}}_r) - E(\mathbf{u}_G) = [(\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1})^{-1}\mathbf{Z}'\mathbf{M}\mathbf{Z} - \mathbf{I}]\mathbf{Q}\mathbf{g}. \quad (8)$$

The magnitude of this bias is a primary consideration when deciding whether to fit a groups model. The bias in EBV differences between animals in separate units will always be less than or equal (when units are disconnected) to the true difference in unit genetic means. Fitting genetic groups eliminates any bias but increases the prediction error of the breeding values (equation 7). Therefore, if this bias is expected to be small, fitting a model without genetic groups may be preferable. Specifically, if the squared bias from fitting model without groups is lower than the increased prediction error from fitting a model with groups, the reduced, non-groups model should be used.

If minimization of MSE is the goal, both Tong et al. (1980) and Kennedy (1981) imply that connections between subunits or regions are critical to lower the standard error of group solutions (groups model) or to lower bias from not including genetic groups in the model. Both studies recommend that genetic groups not be fit until connections due to germplasm exchange have been established to permit direct comparison of sires from the different groups. They suggest reciprocal semen exchange involving 25 to 50% of the matings in two management units for best results in a single generation. Regardless of the model, connectedness reduced the MSE of predicted breeding value differences between units. As stated by Foulley et al. (1990) relative to genetic evaluation without groups, “the bias removal ability of a model cannot be discussed irrespective of the degree of connection.”

Genetic grouping may also affect estimates of variance components if selection has occurred prior to pedigree and performance recording. Genetic grouping by fitting base animals as fixed rather than random has been suggested as a method to account for bias in additive variance estimates when selection has occurred in ancestors of the base population (van der Werf, 1992). Assigning base animals to genetic groups according to their year of entry into the data set is one strategy to attempt to account for unrecorded effects of selection in these animals. However, using simulated data, Piermatì and Van Vleck (1993) showed that fitting genetic groups to account for prior selection can lead to artificially low estimates of additive genetic variance. Genetic grouping of base animals has also been found to reduce estimates of additive variance in real data sets (Díaz et al., 2002) relative to models without genetic groups, but issues of bias cannot be resolved in such studies since the true value of the additive variance in the base population is not known. None of these studies addressed the effect of genetic grouping according to unit (flocks or herds) of origin, but, presumably, additive variance estimates would also be decreased in these cases.

In order to understand why genetic groups cause decreased estimates of additive variance, it is useful to consider additive variance as being partitioned into two sources: variation within units and variation between units. Because units are generally fit as fixed environmental effects, additive variance between units is undetectable in genetic evaluation unless connections between units have been established. Clément et al. (2001) showed through simulation that as connections between units increased (from no to all matings from a common set of sires), the additive variance was more accurately estimated. When genetic groups are fit, variation between units is described by the genetic group solutions and additive variance estimates only describe variance within units. Therefore, additive variance estimates will be artificially low when genetic group effects are fit even though the variance explained by groups is available for selection. When genetic groups are not fit, connectedness between units is desirable for accurate variance component estimation that accounts for the additive variance between units.

These studies also raise questions about the heritability estimate to be used in predicting breeding values. If a genetic groups model is considered to be the true model, what effect does use of a heritability estimate from a non-groups model have on the bias

and PEV of the breeding values in the non-groups model? Use of a higher heritability to predict breeding values in a non-groups model may reduce both bias from ignoring groups and MSE relative to groups models.

Bias and MSE under alternative models are all sensible criteria in choosing whether or not to fit genetic group effects, as long as base animals can sensibly be assigned to groups. Unfortunately, specifying the origin of base animals can be difficult. Complex grouping strategies may lead to unsuspected confounding with other fixed effects (Quaas, 1988). If the purpose of genetic grouping is to identify and take advantage of differences between flocks or herds, base animals must be directly assigned to a flock or herd of origin. In the case of sheep evaluation in the United States, animals born in flocks that do not participate in the evaluation program appear as purchased animals in member flocks. These animals appear in insufficient numbers to accurately estimate genetic groups for their flocks of origin (unpublished results). In addition, base animals that were purchased from other member flocks may be mistakenly attributed to the flock in which they first appeared. Given this issue and the fact that connectedness is relatively low in most sheep flocks, genetic grouping is probably not a currently viable option in sheep evaluation in the United States.

Similar complications in defining genetic groups occur in beef cattle evaluations, although the extent of problem varies from breed to breed depending on the history of record keeping. However, as programs in the beef cattle industry for genetic evaluation in commercial herds (Weaber, 2004) and across breeds (Garrick and Enns, 2003) using data from crossbred animals come to fruition, grouping problems will become more prevalent. Use of genetic groups in beef cattle evaluation generally consists of grouping base animals by time of entry into the data set (Simmental evaluation; R. L. Quaas, *personal communication*) or grouping base animals according to their breed. Considering the status of genetic evaluation in sheep and beef cattle in the United States, neither industry can effectively classify base animals into genetic groups by unit of origin. Classifying newly introduced base animals into genetic groups by year of birth and breed, however, may still be beneficial.

Connectedness plays an important role if genetic groups based on flock or herd of origin are ever to be fit in sheep and beef cattle genetic evaluations. This role is best

summarized from the results of Kennedy (1981). Standard errors of prediction of the fixed genetic group solutions can only decrease if progeny from genetic groups are compared to one another. If genetic evaluation programs remain as they are now and genetic groups are not fit, connectedness will reduce the bias in EBV differences between animals born in different flocks or herds, if indeed these units have different genetic means. Measures of connectedness would give producers tools to assess the risk in comparing the EBV of their animals to animals from other units. Therefore, methods to evaluate levels of connectedness among management units (herds, flocks) and schemes to increase connectedness would benefit both industries.

Connectedness

Comparing and using animals across subpopulations. Regardless of whether or not genetic groups are included in the genetic evaluation model, accurate comparisons of animals from different management units is critical if selection decisions involve animals from different units. Consequently, many studies have focused on designing system-wide breeding programs to optimize the accuracy of such comparisons. In general, these schemes fall into one of two main categories: 1) direct comparison of animals using central test stations; and, 2) comparison of animals across separate management units through the use of common reference animals with statistical elimination of flock or herd effects (Bichard, 1987). The number of test stations in the United States has been declining, and those that do exist do not have the capacity or opportunity to compare all possible subunits. Due to cost, differing environmental factors between stations (with the possibility of genotype by environment interactions), and non-random selection of candidates, test stations are not a viable long-term solution to accurately comparing animals with different origins (Bichard, 1987). Programs that promote germplasm exchange are necessary, however, if across-unit schemes are to be effective in eliminating confounding between estimates of unit genetic and environmental means.

A balance must be achieved when utilizing breeding schemes where some type of linking sires provides connections among flocks or herds. Reference sires must have enough progeny to accurately compare animals across units while sires born within the units must have sufficient progeny to allow them to be progeny tested. Large units often

have an advantage in that both of these goals can be achieved (Hudson et al., 1980). If lowering the individual PEV of young sires born within units is the main objective (Hudson et al., 1980; Schaeffer et al., 1980), it is easy to overlook the importance of connecting the units. Fitting the reference sires as fixed rather than random in the model may only have minimal impact on the PEV of these young sires (Schaeffer et al., 1980).

Individual animal PEV is not a sufficient measure of breeding program efficiency when genetic differences exist between units. The individual PEV does not reflect this potential source of bias (in a non-groups model) or increased error (in a genetic groups model). A better criterion for optimizing the number of progeny per reference sire relative to unproven sires is the PEV of comparisons between animals (or groups of animals) from different units. If the PEV of differences between units is used as the indicator of connectedness, large numbers of reference sire progeny (20 to 45% of the total number of progeny produced) were required to accurately compare animals across units in the models used by Foulley et al. (1983) and Miraei Ashtiani and James (1991), who both considered reference sires as fixed effects and grouped unproven sires by herd or flock of origin. However, as discussed previously, PEV of differences in EBV is an insufficient measure when no genetic groups are fit due to potential biases from differing genetic means.

Ultimately, the main incentive for producers to establish connectedness among units is to take advantage of genetic resources that are potentially better than their own. They will not know if the genetic merit of their animals is inferior or superior without adequately testing their animals relative to others. Unfortunately, producers often automatically assume their animals are superior and are hesitant to purchase seedstock from other sources. To overcome this apprehension, several studies have examined the benefits of increasing connectedness, primarily through group breeding schemes such as sire referencing schemes. These schemes involve an agreement by breeders to mate a predetermined portion of their females to a common set of selected males. Simulation studies have shown that cooperative sire referencing schemes can improve genetic gain by 30 to 35% compared to within-unit selection programs while also improving accuracy of comparisons between units and slowing inbreeding (Hanocq et al., 1996; Lewis and Simm, 2000; Roden, 1996). Genetic variation between units is not required for increased

gain if the number of breeding females is low in some of the member units (Lewis and Simm, 2000) because the likelihood of producing extreme individuals is smaller with small (< 100 females) unit size. Also, the intensity of selection can be dramatically increased by selecting animals across all members of a scheme.

Maraei Ashtiani and James (1993) and Hanocq et al. (1996) both showed that if management units differ in average genetic merit, the rate of genetic change increased more rapidly on average when the units first became connected. This results from units with lower mean breeding values increasing use of genetic resources from units with higher mean breeding values. As a result, the overall genetic trend in the system improved with higher average gains in units with low initial genetic merit. Both studies suggest that the average genetic gain across all units will slow over time as the units become homogenized. If differences between units or strains were minor, and the size of the units large (>300 progeny), rates of gain were relatively unchanged by establishment of connectedness (Maraei Ashtiani and James, 1993).

Smith and Banos (1991) analytically predicted genetic responses from combined selection across and within units. Their results were in agreement with the conclusions of simulation studies. If units are small, combined selection increases potential for genetic gain. If units differ in initial genetic mean, poorer units will catch up with better units after a few generations due to homogenization. These results assume that producers adopt a common breeding objective and continue to participate in the scheme once it becomes clear which flocks or herds are superior. In making decisions on whether to continue to participate in a scheme, producers must be confident that they have reduced the risk of comparing their animals to those of other units. Measures of connectedness, therefore, can help producers to quantify the risk involved in genetic comparisons across flocks or herds.

Measuring connectedness. For fixed effects, determination of connectedness involves ascertaining if linear functions of fixed effects are estimable in N-way cross-classifications (Fernando et al., 1983; Peterson, 1978; Weeks and Williams, 1964). For a 2-factor model, this may be achieved by ‘tracing’ a perpendicular path between nonzero cells in a table counting the number of data points for each cross-classification (e.g., $\mathbf{X}'\mathbf{Z}$ matrix). A simple demonstration of this method is shown in Table 2.1. Boxes in Table

2.1 represent the path that can be taken to identify connected levels of each effect. In the connected set of Table 2.1, sire 3 is connected to sire 1 because each is directly compared to sire 2. Connectedness is not required to predict random effects, but disconnected subsets are not permitted when variance components (Schaeffer, 1975) are estimated using ANOVA methods such as Henderson's Method III (1953). Other variance component methods such as MINQUE and REML, however, do not require connectedness of random effects and allow more accurate variance component estimation by using larger data sets which include all disconnected data (Eccleston, 1978).

Foulley et al. (1990) were the first to develop a continuous measure of connectedness. The authors' goal was to develop a measure ranging from 0 to 1 in which the two extremes represent either a completely balanced data set or one with at least two disconnected subsets. To measure connectedness in a vector of contrast coefficients, \mathbf{x} , they proposed the following measure:

$$IC(\mathbf{x}) = \mathbf{x}'\mathbf{C}_R\mathbf{x} / \mathbf{x}'\mathbf{C}_F\mathbf{x},$$

where \mathbf{C}_R is a portion of the inverse coefficient matrix in some 'reduced model' (e.g., \mathbf{C}_{uu} in (4)) and \mathbf{C}_F is a portion of the inverse coefficient matrix for the same data from some 'full model' (e.g., \mathbf{C}_{22} in (6)). The reduced model would be formed by removing some set of factors (e.g., groups) from the full model. The term 'IC' stands for connectedness index from the notation of Laloë et al. (1996). Foulley et al. (1990) hypothesized that more connected data sets are more nearly orthogonal (perfectly balanced). If two factors are orthogonal to each other, there is no bias in one factor if the other is removed from the model. If a random factor is completely orthogonal to a fixed factor removed in the reduced model, PEV is the same for the random effects in both the full and the reduced models. Therefore, quadratic forms based on the full and reduced inverse coefficient matrices will be equivalent and $IC(\mathbf{x})$ will equal one. This statistic does not account for the amount of information (i.e., progeny records) in the analysis. When few progeny records are available, it is possible for $IC(\mathbf{x})$ to be near 1 while accuracy of EBV comparisons is very low.

In addition to $IC(\mathbf{x})$, Foulley et al. (1990, 1992) also developed a statistic to measure connectedness on the level of the whole design:

$$\gamma = \left[\frac{|\mathbf{C}_R|}{|\mathbf{C}_F|} \right]^{\frac{1}{n}},$$

where n is the column rank of the incidence matrix (matrices) of the parameters to which the subunits \mathbf{C}_R and \mathbf{C}_F relate. This ratio of determinants of inverse coefficient matrixes of reduced and full models was developed using the Kullback-Leibler (Kullback, 1983) distance between the joint density of the maximum likelihood estimators of all the parameters in the full model and the product of the marginal densities of the parameters removed from, and remaining in, the reduced model. If the marginal densities were orthonormal to one another, their product would be equal to the joint density of both sets of parameters, and the Kullback-Leibler distance would be zero. Like $IC(\mathbf{x})$, γ equals 1 if parameters removed from the full model are completely orthogonal to the parameters remaining in the reduced model.

For both of these orthogonality statistics the choice of full and reduced models depends on the factors between which connectedness is being measured. For instance, given the model outlined in (1), \mathbf{C}_F could be the random-effects (\mathbf{C}_{22}) portion of the inverse coefficient matrix for this full model including genetic groups (as in 6) and \mathbf{C}_R could be the random-effects portion (\mathbf{C}_{uu}) of the inverse coefficient matrix for a reduced model excluding genetic group effects (as in 4), other fixed effects, or both. The authors (Foulley et al., 1990; 1992) suggest evaluating γ using the inverse coefficient matrix of genetic group effects in models with and without the environmental fixed effects (e.g., herd, year, season). This measure would be undefined if at least some genetic group differences are not estimable since \mathbf{C}_F could not be calculated. Its value would increase as cross-classification between groups and environmental effects improve. In practice, connectedness has also been evaluated in models that do not involve genetic groups by calculating γ using a reduced model including only random genetic effects and a full model that also includes fixed effects (Laloë et al., 1996).

While orthogonality of the data is desirable, Laloë (1993) argued that a measure of precision was more appropriate in determining whether animals could be compared

across different environments, and proposed the coefficient of determination (CD) for a contrast vector of breeding values (\mathbf{x}) as a measure of precision:

$$\begin{aligned} \text{CD}(\mathbf{x}) &= 1 - \frac{\lambda(\mathbf{x}'\mathbf{C}_{uu}\mathbf{x})}{\mathbf{x}'\mathbf{A}\mathbf{x}} \\ &= \frac{\mathbf{x}'(\mathbf{A} - \lambda\mathbf{C}_{uu})\mathbf{x}}{\mathbf{x}'\mathbf{A}\mathbf{x}} \end{aligned} \quad (9)$$

where \mathbf{C}_{uu} is the random effects portion of the inverse coefficient matrix for a model without genetic groups as in (4). Using the CD to measure the precision of a contrast between animals or sets of animals in different management units would then provide a measure of their connectedness. Laloë (1993) also developed two overall measures of connectedness using the ratio of quadratic forms in (9) and relating them to the eigenvalues (μ_i) and eigenvectors (\mathbf{c}_i) resulting from the solutions:

$$[(\mathbf{A} - \lambda\mathbf{C}_{uu}) - \mu_i\mathbf{A}]\mathbf{c}_i = 0.$$

The number of eigenvalues is equal to the number of breeding values being predicted. The smallest eigenvalue will always be zero; the other eigenvalues correspond to all possible independent contrasts. The two statistics proposed by Laloë (1993) (Laloë et al., 1996) are functions of these eigenvalues:

$$\rho_1 = \sum_{i=1}^n \frac{\mu_i}{n-1}$$

and

$$\rho_2 = \left[\prod_{i=2}^n \mu_i \right].$$

Like IC and γ , these statistics range from 0 to 1 with low values indicating low precision in comparing animals across fixed-effect classes. They each give a sense of the average level of precision across all unique contrasts. If more than one eigenvalue is zero, indicating that at least one contrast is uninformative, ρ_2 will be zero. All of these statistics have generally been applied to models without genetic groups (Hanocq and Boichard, 1999; Laloë et al., 1996). The authors argue that as contrasts between animals in different units become more precise, the genetic mean difference between the units is better estimated. The vector of contrasts used in $\text{CD}(\mathbf{x})$ could be the average of the

breeding values in one unit minus the average of the breeding values in another unit. This CD will be zero if the mean difference is not estimable.

A third connectedness statistic based on the coefficient matrix was proposed by Kennedy and Trus (1993). They contend that the MSE of prediction of differences between candidates for selection is the most logical measure of connectedness. This MSE could be calculated from both a genetic groups model (PEV) and a model without groups if the differences between genetic groups (PEV + bias²) are known, as discussed earlier in this article. The authors describe application of this measure using a model without genetic groups and assuming that group effects are negligible. The PEV of a contrast under this model is then:

$$\text{PEV}(\mathbf{x}) = \mathbf{x}'\mathbf{C}_{uu}\mathbf{x} \sigma_e^2.$$

Unlike the other measures discussed, PEV(\mathbf{x}) is not restricted in range. However, the resulting measure of connectedness is closely related to CD (Laloë, 1993). The only differences are that CD may be easier to interpret because it is restricted to a range of 0 to 1 and accounts for the change in the additive variance of the true breeding values in the contrast due to relationships among animals involved in the contrast.

These three sets of measures (IC or γ , CD or ρ_1 and ρ_2 , and PEV(\mathbf{x})) are the primary theoretical connectedness statistics presented in the literature. Laloë et al. (1996) evaluated the merits of all three approaches using analytical criteria to determine which had the most favorable properties when evaluating connectedness in genetic evaluation. Their analytical comparisons were based on a model without genetic groups. Properties of IC and γ were evaluated when the reduced model included random genetic effects only and the full model also included fixed effects of management unit. Therefore, these statistics would measure orthogonality between fixed environmental and random genetic effects. The authors defined connectedness between random effects by stating that a random factor is disconnected when at least one contrast between its levels (i.e., animal breeding values) has a null CD. Using a small example, they show that neither PEV(\mathbf{x}) nor IC can exhibit this kind of disconnectedness. The PEV(\mathbf{x}) approach gives different results than the CD method because the reduced variability in true breeding values due to relationships is not accounted for in the contrast. The authors state that PEV(\mathbf{x}) can be thought of as a measure to test the null hypothesis of the contrast (\mathbf{x}) being zero, while the

CD measures the power in testing whether the contrast is different than zero. The γ statistic is never null when calculated as in this study. Both C_R and C_F are always positive definite because the random effects are always estimable. The authors show that under certain data structures, γ is highest when there is a minimal amount of data and decreases as the number of progeny per sire increases. Values of γ and IC equal one when data are perfectly balanced. This situation may be desirable in early stages of genetic evaluation, but it is impossible to make genetic progress and maintain this balanced condition. Every sire would have to be equally represented in every contemporary group, meaning no selection is taking place over time. The CD measures, on the other hand, accounts for both the amount of information in the data and its structure. The authors caution that designing programs to increase connectedness by increasing CD or lowering $PEV(\mathbf{x})$ can decrease genetic progress due to lower selection intensity.

The conclusions of Laloë et al. (1996) are helpful in evaluating connectedness statistics. The IC and γ statistics would indicate decreasing connectedness as selection occurs within the system since only a sample of individuals will be chosen as parents. Both favor balanced data, and may be useful in early stages of genetic evaluation programs when the objective is to sufficiently compare genetic means of different management units through semen exchange or test stations. The $PEV(\mathbf{x})$ and CD methods can give different results when comparing animals between units if there are related animals in both units, but in general they will probably lead to the same conclusions in terms of connectedness. In fact, all of these connectedness measures have been shown to be highly correlated in field data (Hofer, 1994). The overall connectedness measures (γ , ρ_1 , and ρ_2) may be useful for group leaders or scientists overseeing genetic evaluation programs, but are of little use to individual producers who may be trying to increase their connectedness to other units in the system. The calculation of these statistics uses all elements of the inverse coefficient matrices thereby requiring extensive computing time for large-scale genetic evaluation, which may limit their use.

Several corollary statistics have been developed in order to decrease the computing time required to calculate these statistics. Most have been developed in order to give similar results to the average PEV of differences between animals in different management units (Kennedy and Trus, 1993). Kennedy and Trus (1993) suggested using the variance in the difference between estimates of the environmental effects of management units (e.g. herds), which was highly correlated to the average PEV between herds in a small example data set. Bunter and Macbeth (1997) developed this idea further by evaluating the variance of estimated differences in genetic group effects when fitting a model that included genetic groups. Their extension to genetic groups is sensible given the relationship of the variance in group differences to the MSE as mentioned by Kennedy (1981). However, it relies on fitting a model with genetic groups, which may be problematic given the difficulties of assigning base animals to genetic groups as discussed earlier.

Recognizing that the prediction error covariance (PEC) between two animals' predicted breeding values would be zero if they were not connected, Lewis et al. (1999) proposed the correlation of breeding value prediction errors as a pairwise connectedness statistic:

$$r_{ij} = \frac{\text{PEC}(\hat{u}_i, \hat{u}_j)}{\sqrt{\text{PEV}(\hat{u}_i)\text{PEV}(\hat{u}_j)}}, \quad (10)$$

where \hat{u}_i is the estimated breeding value of the i th animal. They suggested averaging this statistic for all pairs of animals in different management units to evaluate connectedness between units. Mathur et al. (2002) introduced a similar correlation statistic, the connectedness rating (CR), to measure connectedness but replaced the prediction error (co)variances of breeding values of (10) with the error (co)variances of fixed management unit estimates (\hat{h}_i):

$$\text{CR}_{ij} = \frac{\text{COV}(\hat{h}_i, \hat{h}_j)}{\sqrt{\text{VAR}(\hat{h}_i)\text{VAR}(\hat{h}_j)}}. \quad (11)$$

They found that this measure was less dependent on herd size than the variance of the difference in herd effects of Kennedy and Trus (1993). Other connectedness measures such as functions of counts of direct links between test station groups (Roso et al., 2004)

or management units (Tosh and Wilton, 1990) have also been suggested, but the statistical properties of these measures are strongly dependent on data structure.

With all of these available connectedness measures, it is difficult to determine which is most advantageous to provide to individual producers in order to lower their potential risk in making breeding decisions. In general, no level of sufficiency has been determined for these connectedness statistics. The MSE (Kennedy, 1981) quantifies risk, but it cannot be calculated in practice under a non-groups model because the bias due to potential differences in genetic means among units is unknown. Additionally, much of the risk due to the PEV portion of MSE is already accounted for in the predicted breeding values since they are fit as random effects; animal breeding values are regressed to their midparent predicted breeding value average until they have enough information (progeny data) to deviate further from this average. Therefore, it is the risk of bias due to different genetic means that producers need to account for when making across-unit breeding decisions. An optimal connectedness measure would track the proportion of potential bias remaining when comparing predicted breeding values between sets of animals. The following section discusses strategies that small producers can use to decrease bias in predicted breeding value differences for selected animals in different flocks or herds and quantifies the relationship of some of these connectedness measures with potential bias.

Methods

In order to identify strategies to establish connectedness and reduce potential biases in breeding value predictions between animals from different flocks or herds, several small scenarios were developed. Each scenario consisted of two fixed management units (flocks) in which the goal was to determine the best strategy to adequately compare breeding values of sires originating within each group (“homebred” sires) and to eliminate bias in prediction of differences in their breeding values. Obviously, the most accurate comparison would be to progeny test homebred sires from each flock in the same contemporary group. However, producers may be more hesitant to exchange rams of unknown relative merit than to use some agreed-upon linking sire(s) in both units. Therefore, in order to compare the homebred sires, either a common

reference sire, or one of a pair of related sires, were used to link the flocks in a single generation. Each scenario was examined with three heritabilities (0.125, 0.25, 0.5) and three different proportions of progeny produced from the linking sires (50, 33, or 20%). The four linking scenarios were:

- 1) Reference sire model with three sires (RS3) such that both flocks contain progeny from one of their own homebred sires and a common reference sire;
- 2) Reference sire model with five sires (RS5) such that both flocks contain progeny from two of their own homebred sires and one common reference sire.
- 3) Full sib model (FULL) where the two flocks each contain progeny from one homebred sire and from one of a pair of full-sibling sires. Progeny of four sires in total are considered in this scenario;
- 4) Half sib model (HALF), which is the same as FULL except that the linking sires are now half siblings.

Although each scenario was compared with the same proportion of progeny born to linking sires, it is important to note that the linking sires in the FULL and HALF strategy both have half as many progeny (in a single flock) as the linking reference sires in RS3 and RS5. However, all of these strategies have the same proportion of progeny born to homebred sires. Scenario RS5 addressed the effect of the number of homebred sires on bias reduction.

In each scenario, the total number of progeny per flock was varied on a scale starting at 0 (all statistics calculated as though there were no information) and ending at 100. To analytically derive the expected bias and connectedness statistics, the relevant matrices for each scenario were calculated using mixed model equations under a sire model. Within each flock, all progeny were assumed to be evaluated in a single contemporary group. The bias associated with predictions of the difference in the average breeding values of homebred sires was calculated as a percentage using equation (8), adjusted for a sire model. Each of the two flocks was assumed to represent a different genetic group; the true breeding values of homebred sires included their respective flock's genetic group effect. All linking sires were considered to be from a third genetic group; empirically, the magnitude of the difference between this third group

and the genetic groups of the homebred sires did not matter in terms of the bias in comparing homebred sires.

Connectedness statistics for each scenario included the CD (9) of the mean difference in predicted breeding values of homebred sires, the connectedness correlation (r_{ij}) (10) of these mean differences, and the connectedness rating (CR_{ij}) (11) of the flock solution. Because the homebred sires were unrelated, $PEV(\mathbf{x})$ was directly proportional to CD and was therefore not examined as a potential statistic. The connectedness measures were plotted against the percentage of remaining bias, as measured by equation (8), to determine whether any of them were reliably associated with the bias remaining in the system as numbers of progeny per flock increased. All of these measures have the same possible range (0 to 1) and could therefore be compared using the same scale.

Results

As expected, for all scenarios the percentage of bias remaining between the breeding value predictions for homebred sires decreased at a decreasing rate as the number of progeny per group increased (Figure 2.1). Across the scenarios, higher heritability was associated with less bias at a fixed number of progeny.

Allocation of more progeny to reference sires (50 vs. 20 %) also reduced the bias of comparison between homebred sires. The remaining bias in the estimates of the differences in EBV between homebred sires with varying proportions of reference sire progeny are shown at fixed flock sizes in Table 2.2 ($h^2 = 0.25$). Although bias reductions were markedly lower with 20% linking sire progeny, differences between bias reductions when 50 vs. 33 % of progeny were from linking sires were minor.

For comparisons involving a single homebred sire from each flock, use of a common reference sire to link the flocks was more advantageous than use of related sires (Figure 2.1). With infinite numbers of progeny, linkages arising from the use of a single full-sibling (FULL) or half-sibling (HALF) pair of sires will reduce the bias to 33.3% and 42.9%, respectively. In contrast, use of a common reference sire will result in eventual removal of bias in comparison to homebred sires, but this occurs only with large numbers of progeny. When 50% of the flock progeny are from reference sires (RS3), 540 and 252

progeny per flock are required to reduce bias to 10% at heritabilities of 0.25 and 0.5, respectively. Scenario RS5 required exactly twice as many progeny to reach the same level of bias as RS3 in all cases.

Figure 2.2 shows the relationship of each of the connectedness measures (CD, r_{ij} , CR_{ij}) to the proportion of bias explained for scenarios RS3, FULL, and HALF. The number of progeny per flock was increased in units of 10, with 50% of the progeny from linking sires for a trait with heritability 0.25. Within a scenario, all three of the connectedness measures were highly correlated (greater than 95%) to the proportional reduction in the bias in the comparison of homebred sires. However, only CD maintained the same one-to-one relationship with bias across scenarios. This relationship was true regardless of the heritability or the proportion of progeny from linking sires in each contemporary group. The same relationship also held for scenario RS5 as long as the CD was based on the mean difference between homebred sires in each flock (rather than on the differences between individual homebred sires). The CD was a direct measure of the proportional reduction in bias; one minus the CD is the proportional amount of the difference in genetic groups that still remains as bias in the EBV differences. The values of the r_{ij} and CR_{ij} statistics varied depending on the type of connection. In scenario HALF, the values of r_{ij} and CR_{ij} were approximately 25 and 40% of their values in the RS3 scenario at an equivalent level of bias.

Discussion

Establishing connectedness between flocks or herds helps reduce the risks in making genetic comparisons across these units. If genetic groups are fit in the evaluation model, connections will lower risk by decreasing the standard error of the group estimates. In a model without genetic groups, connections will lower the amount of bias in EBV. By developing statistics to monitor changes in connectedness, we are able to provide producers with a tool to manage this risk. However, there are a variety of statistics available, and some are quite difficult to calculate during routine genetic evaluation. It is most desirable to use a connectedness statistic that has a strong correlation with bias reduction.

In terms of advising producers on how best to link their units in order to minimize risk associated with potentially different genetic means among flocks or herds, the results presented clearly show that the use of a common reference sire is a viable option. For flocks of limited size, mating at least one-third of the breeding females to linking sires is useful to achieve nearly optimum levels of bias reduction; allocating one-half of the flock to linking sires is probably not necessary. Results are somewhat sobering, however, in that even with 100 progeny per unit, bias remains at 37.5% or higher for a moderately heritable trait (0.25) with relatively heavy use of a common reference sire (sires 50% of the progeny within the flock or herd). This result suggests that most producers would have to continue this linking process across several years in order to make further advancements. Linking units through sires that are siblings is an option for very small flocks or herds but should not be used if the total number of progeny is greater than about 20 or 30 when the use of reference sires begin to show a distinct advantage. When flock size is this small, reduction of bias between the flocks is difficult regardless of the linking strategy. Although the results were not shown, the use of multiple sets of siblings as linking sires helped to improve the quality of the connection between units. Conversely, multiple reference sires offer no advantage in bias reduction over a single reference sire. The eventual possibility of homogenization of the units by retaining progeny from the linking sires may reduce if not preclude the necessity of repeating this linking process for several years. Although not delineated with a sire model, dam relationships and retained female progeny may expedite this process.

If producers wish to compare more than one homebred sire (RS3 vs. RS5), the quality of the connection established by linking sires will suffer, and less bias in the difference between homebred sires across units will be explained. This somewhat unexpected result is probably caused by two factors. First, only half the number of progeny per homebred sire was produced in the RS5 scenarios relative to the RS3 scenarios. Predicted breeding values of individual homebred sires were less accurate as a result. Second, in RS5, there are more sires to be evaluated in the whole system with the same total amount of information (progeny). Higher numbers of sires with the same amount of information comes at a price, which is a lower reduction in bias between the two groups of homebred sires. Allocating higher proportions of females to linking sires

thus becomes more important when multiple homebred sires are to be compared. If possible, increasing flock size would also help.

In terms of the quantification of bias reduction when group effects are not in the model but fixed genetic differences are present, only the CD showed a consistent relationship with bias reduction across all scenarios tested. These results agree with the theoretical derivation of Laloë and Phocas (2003). The one-to-one relationship of the CD with bias reduction is a very desirable property and relatively easy to explain to producers. Both of the other statistics calculated (r_{ij} , CR_{ij}) were, like CD, highly correlated with the level of bias and increased monotonically in value as bias was reduced. However, the explicit values of these statistics associated with a given level of bias differed depending on the linking strategy employed. The CD is difficult to calculate for routine genetic evaluation due to storage and processing time involved in calculating both the inverse of the coefficient matrix and the (non-inverted) relationship matrix. Therefore, further development in measuring connectedness should focus on measures that are highly correlated to CD. The $PEV(\mathbf{x})$ is obtainable using matrix absorption if one is interested in obtaining the $PEV(\mathbf{x})$ of a contrast of mean differences (Lewis et al., 1999). Because of its strong relationship with CD, this measure is a potential alternative connectedness measure. The connectedness correlation r_{ij} changed less proportionally with the scenarios than CR_{ij} and may also warrant further investigation for within-system changes in connectedness (over a period of years for example) since its relationship to bias is monotonic.

Application of these results relies on producers willingness to connect their flocks or herds in order to take advantage of their combined genetic resources (or to provide all their customers with this opportunity). If producers establish links with other units but do not take advantage of the results, there is no value to establishing connections. Establishing connections takes effort, lowers accuracy of homebred sires, and potentially reduces selection intensity within individual units. However, the resulting benefits of cooperation, a common breeding objective, and potential for higher overall gains can overcome these obstacles if producers are willing to commit to a common goal.

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Table 2.1. Examples of establishing whether 2-factor (management unit by sire) data designs are connected using a pathway method (boxes). Each cell contains a count of the number of progeny of a sire i in unit j .

Connected Data				
	Sire 1	Sire 2	Sire 3	Sire 4
Unit 1	n_{11}	n_{21}		
Unit 2		n_{22}		
Unit 3		n_{23}	n_{33}	n_{43}
Unit 4			n_{34}	

Disconnected Data				
	Sire 1	Sire 2	Sire 3	Sire 4
Unit 1	n_{11}	n_{21}		
Unit 2	n_{12}	n_{22}		
Unit 3			n_{33}	n_{43}
Unit 4			n_{34}	n_{44}

Table 2.2. Proportion of initial bias in the comparison of EBV of homebred sires across flocks at fixed flock sizes remaining when the proportion of progeny from linking sires is varied ($h^2 = 0.25$).

Linking strategy	Flock progeny (N)	Percentage of progeny from linking sire		
		50	33	20
RS3	30	0.67	0.69	0.76
	60	0.50	0.53	0.61
	90	0.40	0.43	0.51
RS5	30	0.80	0.82	0.86
	60	0.67	0.69	0.76
	90	0.57	0.60	0.68
FULL	30	0.71	0.73	0.78
	60	0.60	0.62	0.67
	90	0.54	0.56	0.61
HALF	30	0.73	0.75	0.79
	60	0.64	0.65	0.70
	90	0.59	0.60	0.64

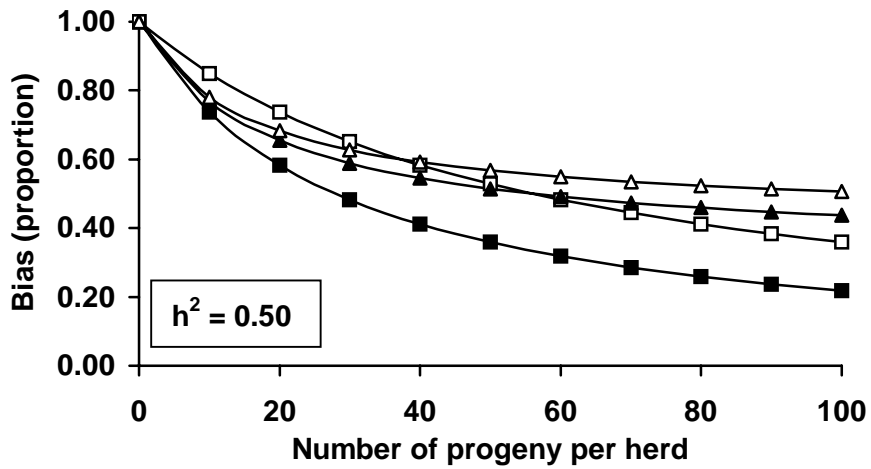
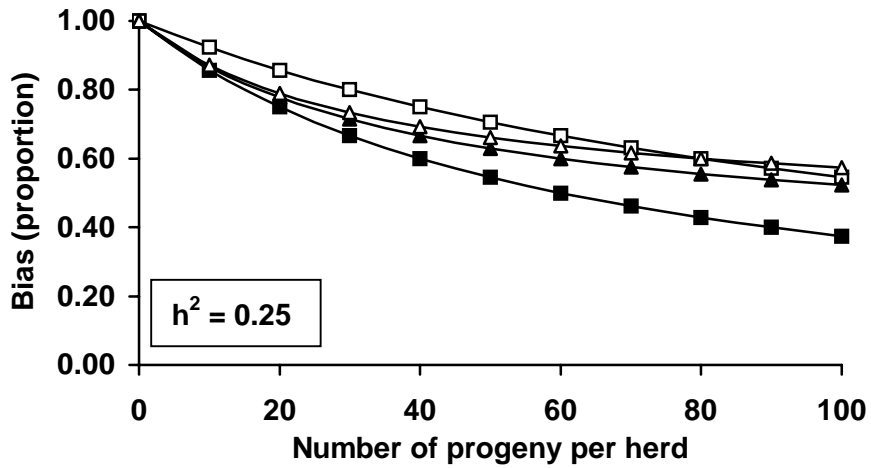


Figure 2.1. Proportionate change in the bias of the difference between average predicted breeding values of homebred sires in different management units with changing numbers of progeny. Fifty percent of the progeny are from linking sires. Scenarios are RS3 (closed square), RS5 (open square), FULL (closed triangle) and HALF (open triangle).

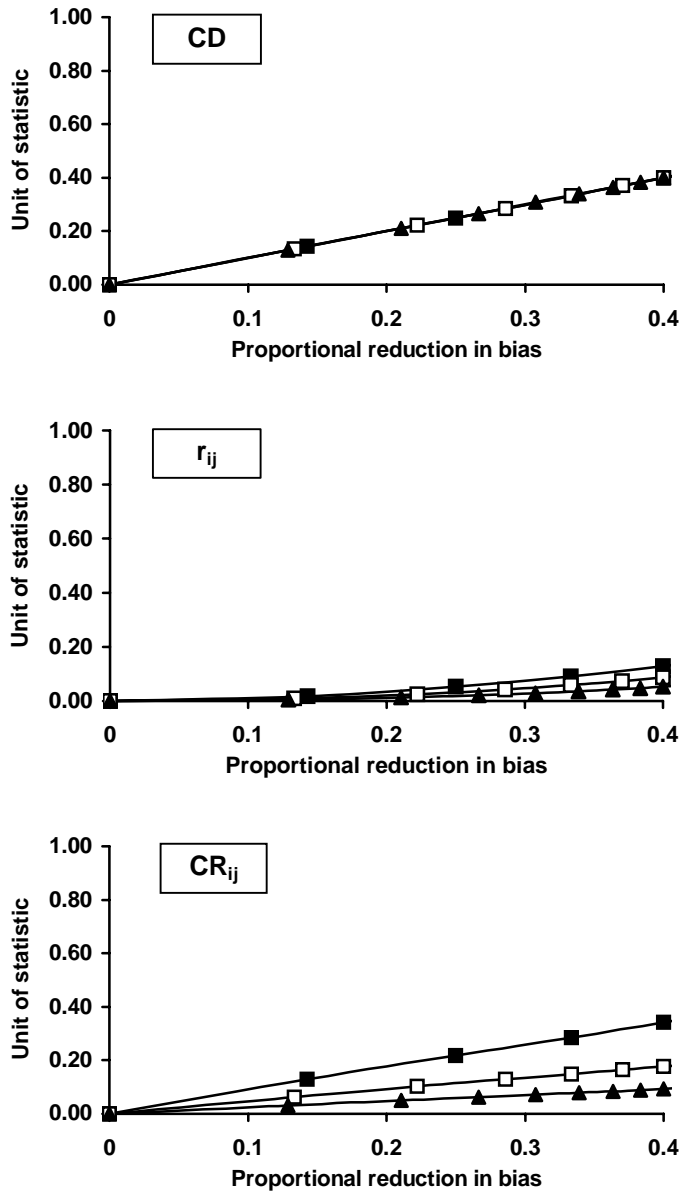


Figure 2.2. Value of connectedness statistics plotted against bias for each linking strategy (50% progeny from linking sire, $h^2 = 0.25$). Linking strategies are 3RS (closed squares), FULL (open squares), and HALF (closed triangles).

CHAPTER 3

Assessing genetic gain, inbreeding, and bias due to different flock genetic means in alternative sheep sire referencing schemes

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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 use of common sires among production units. As practiced in the U.K. (Simm et al., 2001; Lewis and Simm, 2002), members of the scheme choose a team of reference sires and mate a set number of their ewes 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 highest when flocks are small (less than 100 breeding females) or when flocks have different genetic means, which may potentially bias comparisons of EBV among animals from different flocks.

The requirements for joining these 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 usage is typically via AI, which can be costly and difficult in sheep since laparoscopic procedures are required (Wulster-Radcliffe and Lewis, 2002). In order to interest more producers in the U.K. and the U.S. in forming cooperative schemes, less restrictive regulations such as periodic rather than continuous flock participation or natural service matings may be required. The effectiveness of these schemes in reducing potential bias in across-flock EBV must also be examined.

The objectives of this paper are: 1) to determine whether less restrictive breeding schemes or shorter periods of sire referencing can achieve rates of gain and reduce rates of inbreeding as effectively as continuous sire referencing via AI, and 2) to investigate whether bias due to different genetic means among participating flocks can be efficiently reduced using variations of sire referencing schemes.

Materials and Methods

Simulation models

All breeding schemes were evaluated using a modified version of the stochastic simulation of Lewis and Simm (2000). This simulation was parameterized to reflect typical terminal sire sheep populations in the U.K. A single trait with a moderate within-flock heritability of 0.25 typical of a variety of body or component growth rates was simulated under an additive infinitesimal model.

Fifteen flocks ranging in size from 40 to 140 breeding ewes were simulated, for a total of 1030 breeding ewes per year in the whole scheme. Unrelated base animals were simulated for each flock in numbers appropriate to the target flock size. 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 between production units have been reported in other species prior to the widespread use of AI (Cundiff et al., 1975; Spike and Freeman, 1978). Therefore, σ_μ^2 was set to 0.25 for all simulated scenarios.

Breeding values for descendants of base animals were simulated as:

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

where BV_s and BV_d are breeding values 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 sire and dam, respectively, and were obtained from the algorithm of Meuwissen and Luo (1992).

Phenotypic records (P_i) for the trait of interest were obtained for each 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 animals rearing 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 standard deviations of 0.20 and 0.05, respectively. Female animals were 0.85 phenotypic standard deviation units lower in phenotype than males, animals born to ewes 3 yr of age or older were 0.20 units higher than those born to younger ewes, and animals born in multiple litters were 0.35 units lower than those born as singles. These values correspond to standardized differences between classes for these effects in U.K. 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 3.1. Rams and ewes were first eligible for mating at 15 mo. A mating season encompassing three estrous cycles (51 d) was assumed each year. On average 89% of the reproductively eligible ewes conceived. A minimum of two rams was used in each flock per year. The ram to ewe ratio was never lower than 1:25 nor higher than 1:20.

Prior to selection, each flock underwent 10 yr of random selection to create a history of performance and pedigree records for each flock. Following 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 a replacement rate of about 26% annually. The

mating of animals with a half-sibling relationship or higher was avoided; otherwise, matings 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 made available as reference sires. Half of the team was replaced each year. Each flock randomly selected three 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 one reference sire in consecutive years while participating in the reference scheme.

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

In sire referencing schemes with alternating participation of individual flocks, one third of the 15 flocks discontinued their participation in the scheme each year. In effect, 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 five 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 the first year and returned the second year, and flocks 2, 5, 8, 11, and 14 did not participate 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 three outside sires from other member flocks to 10 ewes each year. These natural service reference sires could only be used in one 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 as long as they were not deceased. 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 their

second year, excluding their flock of origin. By chance (one in 14), a given sire could be used in the same flock for two consecutive years but normally would be moved to a different flock.

All six breeding schemes were simulated with two different strategies for acquisition and use of rams other than the reference sires, as surplus ewes were available for mating. 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 adopted a policy of mating on average one half of their ewes to purchased rams and 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 breeding value of the overall scheme in year i . The value of 0.8 was chosen to reflect the genetic distance between flocks practicing within-flock versus across-flock selection on BLUP EBV (Lewis and Simm, 2000). This first sire usage strategy reflects the level of purchased animal use in flocks that participate in sire referencing in the U.K. (Lewis and Simm, 2000). Henceforth, this first strategy is referred to as the outside sire strategy.

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

EBV prediction model

All EBV used for selection in the simulation were derived assuming the following phenotypic animal model:

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

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; \mathbf{u} is a vector of breeding values (as a deviation from \mathbf{Qg}), and \mathbf{e} is a vector of residuals.

Incidence matrices \mathbf{X} and \mathbf{Z} relate phenotypes to fixed and random genetic effects, respectively, and \mathbf{Q} is a matrix which specifies the proportion of genes in each animal originating from each of the yearly genetic groups. Genetic groups, defined by the birth year of sires introduced from outside the scheme, were fitted only for the outside sire strategy and were used to account for unpedigreed outside animals entering the system over time. 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; that is, the base animals were assumed to have been drawn from a random sample with the same genetic mean. This model is common in genetic evaluation of livestock, but leads to biased predictions of EBV if flock genetic means are truly different. 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 breeding values 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 was compared to the average squared L_{ij} of pairs of animals born in the same flock, which should be unbiased and only consist of the PEV of EBV differences. The difference between the across- and within-flock average squared L_{ij} would therefore estimate the squared bias due to different flock genetic means.

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 since all selection decisions had been at random during the 10 yr of flock establishment. The average inbreeding coefficient at the start of selection was 2.2% when outside sires were allowed but increased to 5.2% when matings were restricted to only homebred rams.

Genetic trends (BV) are illustrated for cases where flocks either participated in a sire referencing scheme via AI or remained autonomous (Figure 3.1). For each approach, the two strategies for use of non-reference sires (homebred vs. a combination of homebred and outside sires) are shown. These four 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 or not the flocks were participating in sire referencing. After this time, flocks began to become more clearly differentiated based on genetic merit (mean BLUP EBV); reference sires were increasingly chosen from the better flocks. Genetic gains in scenarios where flocks remained autonomous were 80 to 82% of the gains achieved in AI sire referencing scenarios. After 3 yr of selection, the rate of genetic gain was approximately equivalent between AI sire referencing accompanied by use of a combination of outside and homebred sires (0.089 units/yr) and autonomous flocks accompanied by use of only homebred sires (0.090 units/yr). Within breeding scenarios, use of outside sires with a mean genetic merit of 80% that of scheme member flocks clearly reduced the rate of genetic gain.

At least part of the reduced gain with use of sires from outside the sire referencing scheme results from a reduction in the total amount of genetic variation available in the

system for making genetic progress. 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 can be anticipated in real sire referencing schemes because a group of flocks working toward a common breeding objective would likely 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, was reduced to about 0.35 when outside sires were used while 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 this set of scenarios is shown in Figure 3.2. Inbreeding levels at the start of selection were 2.2% and 5.2% for outside and homebred sire strategies, respectively. An influx of unrelated outside sires effectively reduced inbreeding prior to and during selection. Inbreeding when flocks remained independent increased much more rapidly when only homebred sires were used (1.16%/yr) as compared to 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 (0.13 to 0.18%/yr).

Genetic gain and inbreeding results were similar for other breeding schemes in that genetic gain and inbreeding were always higher when the homebred sire strategy was used (Table 3.2). The rate of genetic gain dropped and inbreeding increased when flocks discontinued AI sire referencing after 5 or 10 yr. For both measures, the rates after sire referencing discontinued were similar to scenarios where no reference sires were used. 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, with the outside sire strategy. These same relative levels were higher under the homebred sire strategy (97.3% and 91.9%), possibly because flocks remained more homogenous after sire referencing when no outside sires provided additional genetic variation (with a lower mean). When rams came from outside sources with a lower genetic mean, the reduction in gain was necessarily lower.

Inbreeding and genetic gain results for alternating AI sire referencing and natural service sire referencing are also shown in Table 3.2. Alternating participation in AI sire referencing resulted in slightly reduced genetic gain and a slightly higher rate of inbreeding relative to the base AI sire referencing scenarios. However, rates of gain were still considerably higher than with no sire referencing. Natural service sire referencing was comparable to AI sire referencing in terms of genetic gain. For both AI and natural service sire referencing, flocks achieved a 0.09 and 0.12 annual increase in mean BV (in phenotypic standard deviation units) for outside and homebred sire strategies, respectively. Inbreeding was lower with natural service sire referencing because flocks were not allowed to use a reference sire that originated in their own flock. Under this selection intensity, natural service sire referencing was as efficient as, and perhaps preferable to, AI sire referencing. When rams are chosen as reference sires from the top one-sixth by BLUP, the reference sires in AI and natural service sire referencing would be of similar merit. At higher levels of selection intensity this would no longer be true.

Bias due to flock genetic mean differences

The MSE of predicting differences in breeding values between pairs of ram lambs (average squared L_{ij}) across flocks are presented in Figures 3.3 and 3.4 for four breeding scenarios with and without outside sires, respectively. In each figure, the average MSE of differences between ram lambs within common flocks 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.

In Figure 3.3, the average squared L_{ij} for scenarios where outside sire usage was allowed are shown. Before selection began (yr 0), L_{ij} was quite variable across replicates for all scenarios with a standard error 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. After selection began, the scenarios behaved similarly with a rapid decrease in 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 L_{ij} can be directly attributed to the bias from differences in flock genetic means being better explained by the genetic evaluation model fitted as the flocks

became more connected. The same trends were observed with the strategies involving the use of homebred sires (Figure 3.4), although initial levels of bias were higher when outside sires were not used.

Both AI and natural service sire referencing performed equally well in terms of the reduction of bias of comparisons between lambs. If flocks discontinued sire referencing after 5 or 10 yr (not shown), the average squared L_{ij} increased slightly in their first year apart from the scheme. In later years, the value of the statistic remained constant. Although not shown in the figures, the alternating scenarios showed a similar, but slightly slower decrease in the average squared L_{ij} as the scheme proceeded. Approximately 10 yr were required to reach the same level of squared L_{ij} that other scenarios reached in 5 yr. If flocks remained independent during selection, the average squared L_{ij} never substantially decreased below its level before selection began.

Both sire usage strategies resulted in similar proportional reductions in bias due to implementation of sire referencing schemes. However, the initial level of average squared L_{ij} was higher in the homebred sire strategies (Figure 3.4) than in the outside sire strategies (Figure 3.3). The main reason for this discrepancy was that the full additive variation due 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 prediction error variance 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 due to between-flock variation (twice the additive flock variance). In scenarios using the outside sire strategy, this difference was only about 0.20 because flock genetic means had become homogenized by use of outside rams with a common mean, resulting in a drop in the between-flock additive variance.

Discussion

As shown by Lewis and Simm (2000), AI sire referencing with an optimum level of reference sires mated to the same number of ewes in each flock increased genetic gain and decreased inbreeding relative to flocks that remained autonomous. In their study, the optimum level of reference sire usage 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% (Roden, 1996; Hanocq et al., 1996). In the current study, gains from AI sire referencing were slightly higher than those reported by Lewis and Simm (2000) at the same relative selection intensity (top one-sixth). The primary difference between these studies was that flocks were simulated with different genetic means, providing a source of between-flock genetic variance after sire referencing began. Use of reference sire matings when flocks differ genetically has been shown to increase genetic progress relative to situations where units have the same genetic mean (Miraei Ashtiani and James, 1993; Hanocq et al., 1996). Management units with the lowest mean BV benefit through utilization of germplasm from units with high mean BV (Hanocq et al., 1996). However, connections must be sufficient to reliably estimate genetic differences between units.

Genetic gain was also higher in this study, and in Lewis and Simm (2000), under sire referencing relative to no scheme because flocks were able to take advantage of a greater amount of genetic variation through cooperative schemes. Smith and Banos (1991) analytically showed that connections were of the most benefit to subpopulations with either low genetic means or small size (less than 100 males born per year). In essence, cooperating flocks become a 'superflock' or a common population rather than distinct subpopulations. If their breeding objectives are complementary, the overall selection intensity across the 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 associated with selection from the whole population. The flock structures simulated in this study were representative of flocks of terminal sire breeds in the U.K. In general, these flocks are small with only 50 to 150 breeding females. Seedstock flocks in the U.S. 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 superior in terms of inbreeding. However, natural service sire referencing would likely be unable to achieve the same level of genetic gain as AI sire referencing if only the best animals were chosen as reference sires based on their BLUP EBV. The level of selection intensity in the current study (top one-sixth) allowed natural-service reference sires to be chosen with approximately the same genetic merit as that achieved for AI sires. Still, realistically, the level of selection intensity is likely no higher than this for actual sheep flocks in both the U.S. and the U.K. due to other selection decisions made by producers. 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 usage is as high as in this study (30 ewes per flock).

The alternating reference sire strategy lagged behind sire referencing in genetic gain and resulted in higher 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.

Achievement of predicted genetic gains from these breeding scenarios presumed the flocks were working toward a common breeding objective – in this case for a single moderately heritable trait. However, flocks may differ in breeding goals or in the intensity with which they pursue genetic increases in individual traits. Even in those cases, sire referencing schemes still can provide a way to compare animals from different flocks if genetic means differ. By increasing connectedness between flocks, these schemes would allow breeders to accurately choose animals from other member flocks based on EBV for traits prioritized within their own breeding goal once the genetic rankings between flocks were fairly clear. Their genetic means may actually become more different as selection progresses, depending on the consistency of the breeding goals and the genetic correlations between the traits in the objectives (Smith and Banos, 1991), but relative rankings of the flocks on traits of interest should still be clearer.

All breeding schemes were effective in reducing bias, which was unaccounted for in the model fitted that assumed the flock genetic means were equal. Each of the continuous sire referencing strategies (AI, natural service, alternating) reduced bias to an asymptotic level near 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 disengaging 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 unclear, but may relate to decreased accuracy from increased non-reference sire matings in this first year after leaving the scheme rather than from an increase in bias. After a flock leaves a scheme, subsequent genetic changes due 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 virtually eliminate the risk associated with making genetic comparisons across flocks in a relatively short time (5 yr). Less intense schemes, such as the alternating scenario, also achieve this same result, but may take longer (10 yr).

Base animals originating in different flocks were not genetically grouped to account for bias in EBV from differing flock genetic means. As stated earlier, it would be impossible to fit genetic groups when selection first began because group effects would be completely confounded with environmental flock effects (contemporary group). After sire referencing began, genetic groups could have been added to the model, but MSE may have been higher with groups than without groups because of the standard error associated with group solutions (Kennedy, 1981). The effectiveness of fitting genetic groups depends upon magnitude of genetic differences among flocks; if differences are large, then MSE will be high in a model without genetic groups because of bias. Fitting genetic groups according to flock of origin in real data sets may be problematic. The actual flock of origin of base animals may be unknown or the flock of origin may be severely underrepresented, which also leads to high standard error 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 as long as sufficient connectedness between flocks is established.

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

The importance of connecting flocks in order to reduce bias due to differences in genetic means depends on the extent of the differences. Differences can arise between flocks due to isolation of the flocks in combination with genetic drift or differing selection policies. The sheep industry in the U.S. and terminal sire breeds in the U.K. 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. An expectation that EBV derived across disconnected flocks will be directly comparable is unlikely to be fulfilled in many cases. If flocks do not expect to exchange germplasm with one another, or 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.

Implications

Alternative breeding systems such as natural service sire exchange and noncontinuous participation in sire referencing can provide viable options to continuous

AI sire referencing. Natural service strategies reduce inbreeding more effectively than AI strategies and can produce the same level of genetic gain and reduction in bias from genetic differences among flocks as AI sire referencing at comparable selection intensities. However, if only the best animals are selected, genetic gains using AI should still be superior. When flock genetic means differ, participation in cooperative breeding schemes results in effectively 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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Table 3.1. 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/twin litters ^a	39.2, 59.1
Percentage of 3-yr-old ewes producing single/twin litters ^a	25.4, 69.3
Percentage of ewes > 3 yr old ewes producing single/twin litters ^a	31.6, 61.8
Conception rate to AI (%)	63
Conception rate to natural service (%; 1 st , 2 nd , 3 rd cycle) ^b	63, 63, 20
Lamb mortality (%; singles, twins, triplets)	13.0, 13.6, 15.6
Pre-mating ram and ewe mortality (%)	3.0
Active ram and ewe mortality (%)	2.5
Cull age (yr; rams, ewes)	4, 6

^a Remaining ewes produced triplet litters.

^b For 2nd and 3rd cycle, conception rate among remaining open ewes.

Table 3.2. Genetic gain (phenotypic standard deviation units) and inbreeding (%) after 5, 10, and 15 yr of selection on BLUP EBV at an intensity of 1/6 for a 0.25 heritable trait under different types of sire referencing schemes and different levels of outside sire use.

Source of non-reference 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 alternating	0.53	0.88	1.29	2.40	3.03	3.73
	NS 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
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 alternating	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
Max SE		0.03	0.03	0.03	0.19	0.29	0.38

* Natural service.

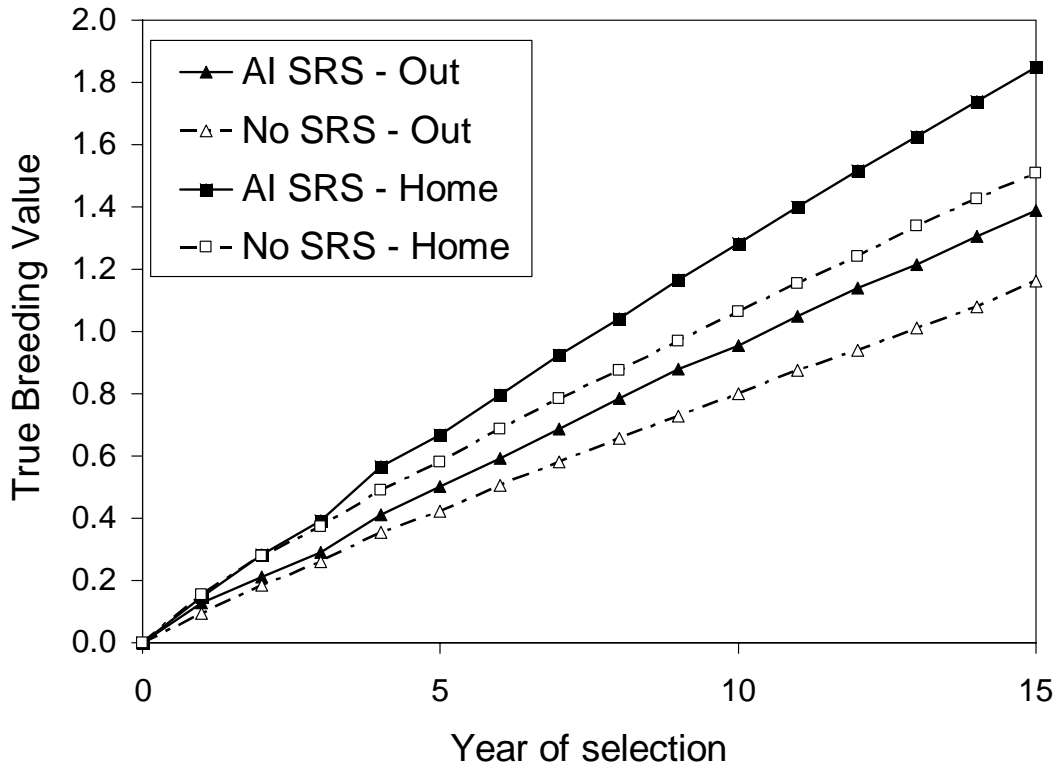


Figure 3.1. Average mean BV for 15 flocks after selection on BLUP EBV for 15 yr. Flocks either joined an AI sire referencing scheme (AI SRS) or remained autonomous (No SRS). Non-reference sires came exclusively from within participating flocks (Home) or from both within the flocks and from unknown outside sources (Out).

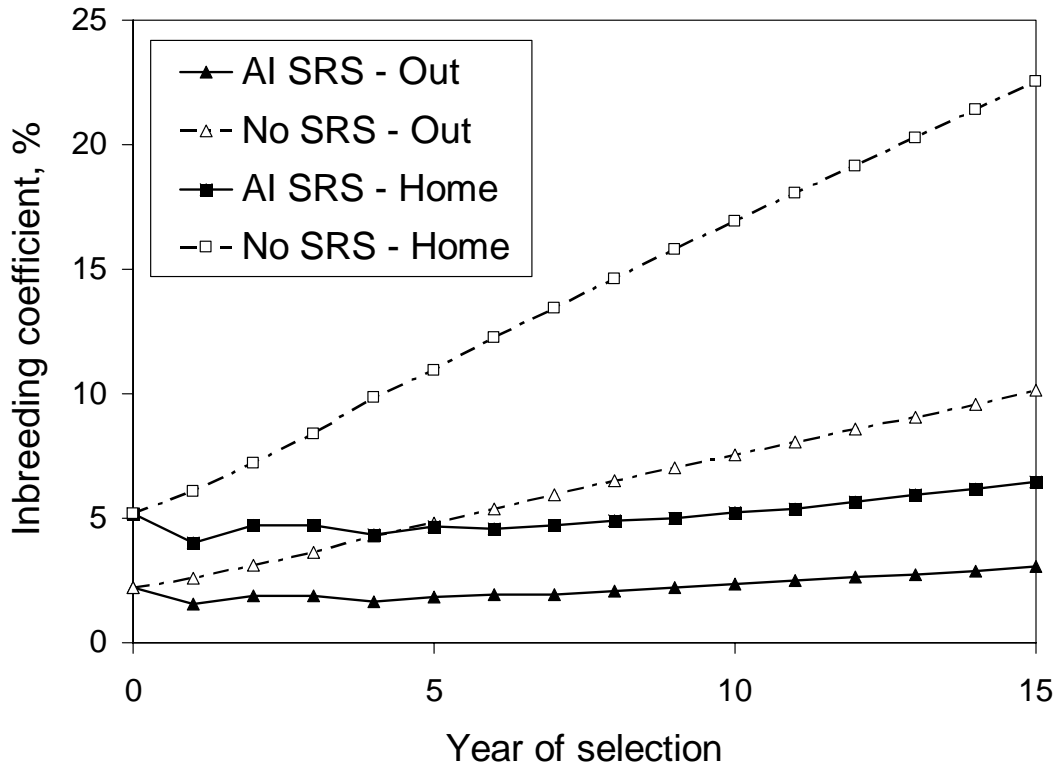


Figure 3.2. Average inbreeding coefficient for 15 flocks after selection on BLUP EBV for 15 yr. Flocks either joined an AI sire referencing scheme (AI SRS) or remained autonomous (No SRS). Non-reference sires came exclusively from participating flocks (Home) or came from both within the flocks and from unknown outside sources (Out).

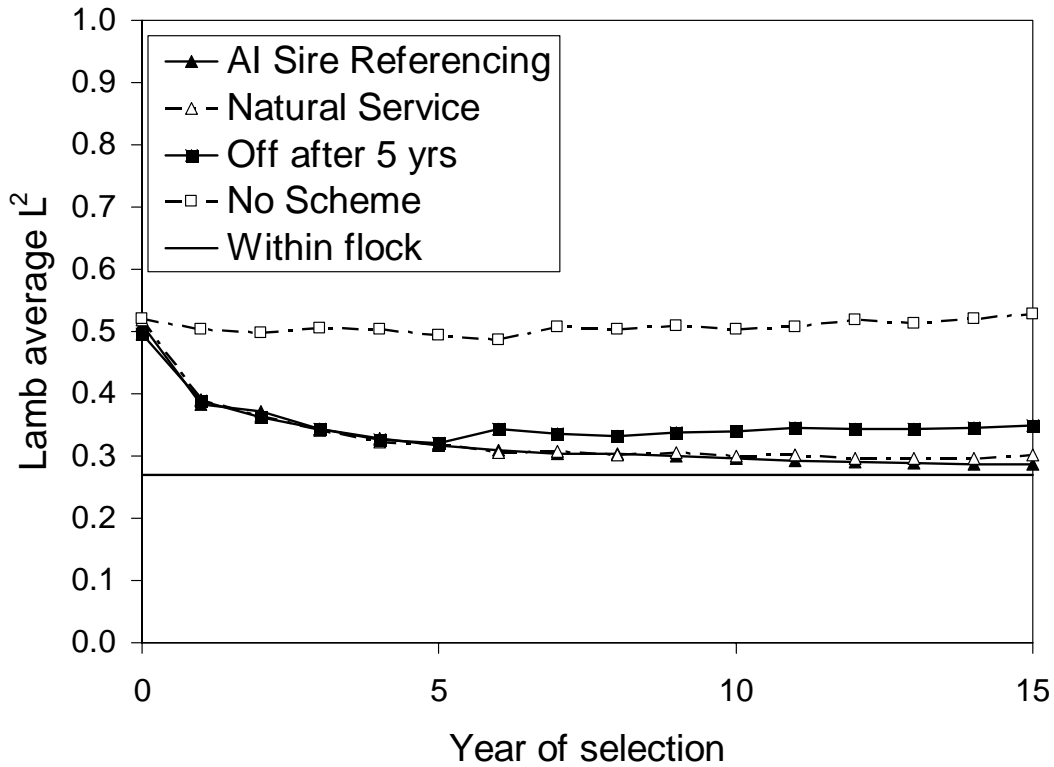


Figure 3.3. Average mean squared error of all possible contrasts between pairs of ram lambs across flocks relative to all possible contrasts between pairs of ram lambs within flocks for four different breeding schemes: AI sire referencing, AI sire referencing for 5 yr followed by flocks becoming autonomous, natural service sire referencing, and completely autonomous flocks (no scheme). Flocks were allowed to mate their ewes to non-pedigreed outside sires, as well as a mix of homebred rams and reference sires.

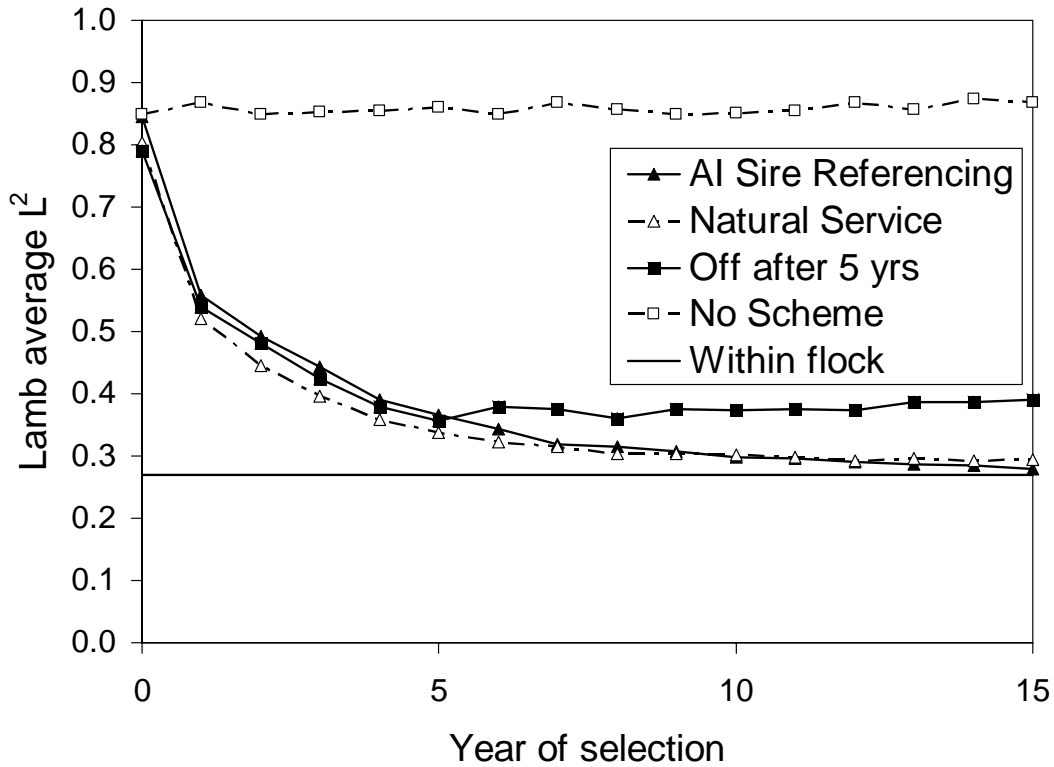


Figure 3.4. Average mean squared error of all possible contrasts between pairs of ram lambs across flocks relative to all possible contrasts between pairs of ram lambs within flocks for four different breeding schemes: AI sire referencing, AI sire referencing for five years followed by flocks becoming autonomous, natural service sire referencing, and completely autonomous flocks (no scheme). Flocks were allowed to mate their ewes only to homebred and reference sires.

CHAPTER 4

Changes in connectedness over time in alternative sheep sire referencing schemes

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Introduction

Sire referencing schemes are cooperative breeding programs where genetic links between flocks are formed by sharing rams among flocks. Participation in these schemes has been clearly shown to accelerate the rate of genetic gain (Hanocq et al., 1996; Roden, 1996; Lewis and Simm, 2000). These schemes improve the accuracy of across-flock comparisons (Foulley et al., 1983) and reduce rates of inbreeding (Lewis and Simm, 2000; Kuehn and Lewis, 2006). Biases due to differences in genetic means among flocks decrease through connections among management units in the schemes (Hanocq et al., 1996; Kuehn and Lewis, 2006).

Despite these benefits, restrictions such as AI mating and commitment to use selected rams, may limit producer participation in sire referencing schemes, at least for extended periods. Still, it is useful for producers to know the relative rank of their animals in the population for effective genetic improvement using outside sources of germplasm. If producers are not sufficiently connected to other management units (e.g., flocks or herds) there is risk of bias in across-unit genetic comparisons. Therefore, it would be useful to have a measure of the risk of biased comparisons across units.

Various connectedness measures have been proposed including the average prediction error of EBV differences across units (Kennedy and Trus, 1993) and the

correlation of prediction errors across units (Lewis et al., 1999; Lewis et al., 2005). These measures are currently used in Canada and the U.K. to measure connectedness. However, the behavior of these measures over time and relative to biases due to different unit genetic means has not been well established.

The objectives of this study were to use simulation to evaluate the pattern of change over time in selected connectedness measures in sire referencing schemes, and to determine how effectively these measures quantify the level of risk due to bias in EBV comparisons across production units.

Materials and Methods

Simulation models

Data sets were simulated using a modified version of the stochastic simulation of Lewis and Simm (2000). This simulation was designed to be characteristic of the seedstock sector of terminal sire breeds in the U.K. Specific parameters defining mating, reproductive, and survival characteristics were described by Kuehn and Lewis (2006).

Fifteen flocks ranging in size from 40 to 140 breeding ewes were simulated, for a total of 1030 breeding ewes per year. A single trait with a moderate within-flock heritability of 0.25, typical of growth and yield traits, was simulated for each animal. In order to create genetic differences among flocks, breeding values for base animals were obtained from normal distributions with genetic means μ_j for flock j and common within-flock additive variance (σ_a^2) 0.25. Values of μ_j for each flock were sampled from a normal distribution with mean zero and variance 0.25. Breeding values and phenotypes for all animals were derived using the same procedures as Kuehn and Lewis (2006).

Each flock underwent 10 yr of random selection followed by 15 yr of selection on the simulated performance trait. Rams selected from across the scheme as well as rams selected for use within their respective flocks were selected at random from the top one-sixth of their respective pools as ranked by BLUP EBV. Ewes were selected by EBV to maintain a constant flocks size resulting in a 26% replacement rate on average.

Simulation scenarios. Connectedness was measured across flocks participating in several types of cooperative breeding schemes. Each scheme was replicated 50 times. Two schemes were used as baseline for comparison: (i) all flocks participating in an AI sire referencing scheme for all 15 yr of selection; or, (ii) flocks that remained autonomous for all 15 yr of selection (no connections), with selection strictly within flock. For the AI sire referencing scheme, six rams were chosen as a team from the 15 flocks and made available as reference sires. Half of the team was replaced each year. Each flock randomly selected three reference sires from the team and mated each sire to 10 ewes. Flocks were allowed to reuse one reference sire in consecutive years while participating in the scheme.

In addition to the baseline schemes, four other breeding schemes were simulated: termination of sire referencing after 5 or 10 yr with the flocks remaining autonomous thereafter; flocks with alternating participation in sire referencing; and natural service (as opposed to AI) sire referencing which involves exchange of rams among flocks. Changes in connectedness and bias in estimation of breeding values across flocks were compared for these scenarios.

In sire referencing schemes with alternating participation of individual flocks, one third of the 15 flocks discontinued their participation in the scheme each year. Each flock therefore participated in the scheme for 2 yr followed by a year in which reference sires were not used (although these flocks were allowed to contribute reference sires to the pool). This process was systematic in that the same five flocks disengaged every third year and then returned the following year; 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 the first year and returned the second year, and flocks 2, 5, 8, 11, and 14 did not participate the second year.

Natural service sire referencing was similar to AI sire referencing in that each flock was required to mate three outside sires from other member flocks to 10 ewes each year. These natural service reference sires could only be used in one flock each year. Therefore, 45 rams were selected each year to form the reference sire pool. As with AI sire referencing, surviving sires could be used in consecutive years. 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 their second year, excluding their flock of origin. By chance (one in 14), a given sire could be used in the same flock for two consecutive years but normally would be moved to a different flock.

All six breeding scheme scenarios were simulated with two different 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 to unrelated purchased rams with no pedigree or performance data, and the rest of the flocks mated on average one half of their excess ewes to purchased rams and half to their own homebred rams. Breeding values for the 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 breeding value of the overall scheme in year i . The value of 0.8 was chosen to reflect the genetic distance between flocks practicing within-flock versus across-flock selection on BLUP EBV (Lewis and Simm, 2000). This first sire usage strategy reflects the level of purchased animal use in flocks that participate in sire referencing in the U.K. (Lewis and Simm, 2000) and henceforth will be referred to as the ‘outside’ sire strategy.

In the second sire usage strategy, all flocks used only their own homebred sires in addition to the required reference sires. While not likely in practice, this strategy provided a contrast to the purchased ram strategy. This sire usage strategy will henceforth be referred to as the ‘homebred only’ sire strategy. With these two sire use strategies (outside versus homebred), and the six breeding schemes, 12 scenarios were explored.

The scenarios considered were the same as those used in Kuehn and Lewis (2006) to evaluate the effectiveness of natural service and discontinuous sire referencing schemes compared to AI sire referencing at removing bias due to differing flock genetic means. Their results suggested that bias decreases at a decreasing rate as sire referencing schemes progressed. Bias was dramatically reduced after 5 yr with natural service and AI sire referencing, and after 10 yr in with alternating participation in the AI scheme. For this study, several connectedness measures were compared to determine whether the loss of bias could be detected using these statistics. In practice, true breeding values are unknown so a measure to detect the decreases in potential for biased EBV comparisons among flocks would be useful.

EBV prediction model

All EBV used for selection in the simulation were derived assuming the following phenotypic animal model:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{Q}\mathbf{g} + \mathbf{Z}\mathbf{u} + \mathbf{e},$$

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, \mathbf{u} is a vector of breeding values (as a deviation from \mathbf{g}), and \mathbf{e} is a vector of residuals. Incidence matrices \mathbf{X} and \mathbf{Z} relate phenotypes to fixed and random genetic effects, respectively, and \mathbf{Q} is a matrix which specifies the proportion of genes in each animal originating from various genetic groups. Genetic groups, defined by the birth year of sires introduced from outside the scheme, were fitted only for the outside sire strategy and were used to account for unpedigreed outside animals entering the system over time. 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 be completely confounded with contemporary group effects. Breeding values were estimated assuming a heritability of 0.25 which does not take into account the 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

Connectedness between groups of animals has traditionally been measured using functions of the inverse of the coefficient matrix (\mathbf{C}) (Foulley et al., 1992; Kennedy and Trus, 1993; Laloë, 1993):

$$\mathbf{C} = [\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1}],$$

where \mathbf{M} is the fixed effect absorption matrix, λ is the ratio of residual and additive variances (σ_e^2/σ_a^2), and \mathbf{A} is the numerator relationship matrix. The inverse elements of \mathbf{C} , multiplied by σ_e^2 , are the prediction error (co)variances of estimated breeding values.

For this study, two different connectedness measures based on functions of prediction error were calculated for each year of selection in each simulated data set. The first measure was the connectedness correlation (Lewis et al., 1999; Lewis et al., 2005):

$$r_{ij} = \frac{\text{PEC}(\hat{u}_i, \hat{u}_j)}{\sqrt{\text{PEV}(\hat{u}_i)\text{PEV}(\hat{u}_j)}},$$

where PEC and PEV stand for prediction error covariance and prediction error variance, respectively, and \hat{u}_i and \hat{u}_j are EBV of animals i and j , respectively. The connectedness correlation was calculated and averaged each year for all pairs of ram lambs born in different flocks across all 15 flocks (lamb r_{ij}). This statistic was also calculated yearly on a flock mean basis:

$$r_{ij} = \frac{\text{PEC}(\hat{\bar{u}}_i, \hat{\bar{u}}_j)}{\sqrt{\text{PEV}(\hat{\bar{u}}_i)\text{PEV}(\hat{\bar{u}}_j)}},$$

where $\hat{\bar{u}}_{i(j)}$ is the mean breeding value of all animals recorded in flock $i(j)$ since recording began. This flock connectedness correlation (flock r_{ij}) was shown by Lewis et al. (1999, 2005) to have a strong relationship with bias arising from different flock genetic means. Flock r_{ij} then is a measure of connectedness for all animals in the pedigree while lamb r_{ij} is descriptive of the current generation.

The second connectedness statistic calculated was the scaled prediction error variance of the difference in EBV between animals in different flocks:

$$\text{scaled PEV}(\hat{u}_i - \hat{u}_j) = [\text{PEV}(\hat{u}_i) + \text{PEV}(\hat{u}_j) - 2\text{PEC}(\hat{u}_i, \hat{u}_j)] / \sigma_a^2.$$

Like the connectedness correlation, this statistic was calculated each year both for all pairs of ram lambs from different flocks (lamb PEVD) and for the mean EBV of all animals since recording began in each flock (flock PEVD). Scaling the PEV difference by the additive variance (σ_a^2) allowed it to be expressed on a unitless basis. The average PEV of EBV differences across management units was first suggested by Kennedy and Trus (1993) as the most appropriate measure of connectedness because it measures the

inherent risk in comparing these animals. They hypothesized that a lower average PEV corresponds to a reduced risk of comparisons across units.

The ideal connectedness statistic would measure the risk of biased EBV comparisons across flocks due to different initial flock genetic means. Therefore, after the behavior of these statistics over time was assessed, candidate connectedness measures were plotted relative to the bias remaining in the system due to simulation of different initial flock genetic means. As in Lewis et al. (1999), to quantify the bias associated with comparisons of animals between flocks, a contrast (L_{ij}) was calculated for all current 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 the true breeding values 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 breeding values of ram lambs born in different flocks. The MSE is the sum of the prediction error variance (PEV) and the squared bias in this predicted difference. In addition to the between-flock MSE (MSE_B), the average squared L_{ij} of pairs of lambs born within the same flock was also computed. The within-flock MSE (MSE_W) was assumed free of bias since the lambs were born in the same flocks and, hence, would only consist of the PEV of EBV differences. Therefore the difference between MSE_B and MSE_W would be an estimate of the squared bias due to different flock genetic means.

In their previous study, Kuehn and Lewis (2006) found that the amount of bias in year zero of selection was dependent on whether outside sires were allowed or excluded. When both homebred and outside sires were used, MSE_B averaged 0.50 at year zero; when no outside sires were allowed, MSE_B averaged 0.83. Across all years, MSE_W remained at an average level of 0.27. Since the starting level of bias in across-flock breeding value differences was strategy dependant, a percentage decrease from the original level of bias was calculated for this study to compare to the connectedness measures:

$$\% \text{ Bias} = \frac{MSE_{B_i} - MSE_W}{MSE_{B_0} - MSE_W} \times 100 = \frac{MSE_{B_i} - 0.27}{MSE_{B_0} - 0.27} \times 100,$$

where MSE_{B0} is the mean squared across-flock L_{ij} in selection year 0 of the current simulation replicate and MSE_{Bi} is the mean squared L_{ij} in selection year i .

Results

Connectedness statistics

Connectedness correlations. As selection and sire exchange across flocks began, the value of both of the correlation connectedness statistics (lamb r_{ij} and flock r_{ij}) increased in the sire referencing scheme scenarios (Figure 4.1, Table 4.1). When no sire referencing was undertaken, both lamb and flock r_{ij} necessarily remained at zero. Lamb and flock r_{ij} in continuous AI sire referencing and AI sire referencing for 5 or 10 yr scenarios were expected to be the same after 5 yr of selection; observed differences were within the standard error. The magnitudes of lamb and flock r_{ij} differed by a factor of approximately 10, indicating a greater level of confidence in estimates of difference in mean EBV between flocks than in estimates of difference in individual lamb EBV. This was to be expected since means are less variable than individual predictions.

Lamb r_{ij} increased rapidly the first year after breeding schemes began and thereafter increased at a slow but constant rate as long as the schemes remained in effect. Lamb r_{ij} increased most rapidly in AI sire referencing schemes, while in alternating and natural service schemes lamb r_{ij} increased at a slower rate. When sire referencing discontinued after 5 or 10 yr (Figure 4.1), lamb r_{ij} then rapidly decreased and stabilized or slowly declined thereafter.

Like lamb r_{ij} , flock r_{ij} began to increase as soon as sire referencing was initiated. However, the rate of increase in flock r_{ij} was generally constant from year to year as long as flocks continued to participate in the scheme. As in the case of lamb r_{ij} , flock r_{ij} increased more slowly in alternating scenarios relative to their AI and natural service sire referencing counterparts. However, unlike lamb r_{ij} , flock r_{ij} increased more rapidly under natural service sire referencing than AI sire referencing. When flocks discontinued reference sire matings after 5 or 10 yr, flock r_{ij} did not decrease as was the case with lamb r_{ij} . Instead, the level of flock r_{ij} increased at a decreasing rate, eventually reached a peak, and then slowly declined.

Both of the connectedness correlation measures increased more rapidly when only homebred sires were used for non-reference sire matings. Rates of gain in connectedness using these measures were nearly double across all breeding scheme scenarios. The introduction of non-pedigreed sires dilutes the average relationship between animals in different flocks, resulting in a lower level of prediction error covariance between them and, therefore, a lower connectedness correlation.

Prediction error differences. As expected, both lamb and flock PEVD decreased as soon as group breeding schemes began (Figure 4.2, Table 4.2). When no scheme was implemented, lamb and flock PEVD slowly increased over all 15 yr, probably due to increased levels of inbreeding and average relationship within the independent flocks. Differences in lamb and flock PEVD in continuous AI sire referencing and AI sire referencing for 5 or 10 yr scenarios were expected to be the same after 5 yr of selection; differences were within the standard error.

Patterns of lamb PEVD mirrored those in lamb r_{ij} in that lamb PEVD dropped quickly the first year after the breeding scheme began followed by a gradual decline thereafter. When flocks discontinued their participation in a scheme after 5 or 10 yr, lamb PEVD rapidly increased the following year. When flocks systematically alternated their participation in the scheme, the rate of decrease in lamb PEVD was slower than when flocks participated continually. Similar to lamb r_{ij} , gains in connectedness as measured by lamb PEVD were slower for natural service sire referencing than when sire referencing was by AI. Higher lamb PEVD in natural service as compared to AI schemes indicate that the accuracy of comparisons of lambs across flocks were lower with use of natural service than AI reference sires. The average level of lamb PEVD after 15 yr ranged from 1.108 with AI sire referencing and no outside sires allowed to 1.460 with no reference sire use and no outside sires allowed.

For both lamb and flock PEVD levels were higher at yr 0 if outside sire use was not allowed relative to scenarios where outside sires were used. Likely, this discrepancy is due to the higher inbreeding in these scenarios (5.2% and 2.2%, respectively) after 10 yr of random mating prior to selection as reported by Kuehn and Lewis (2006). Inbreeding and within-flock relationships increase the additive variance between flocks, which is the upper limit of PEVD. Once breeding schemes were initiated, flock PEVD

dropped more rapidly in the scenarios with no outside sires, eventually converging with the flock PEVD from the other scenarios. As found when comparing flock to lamb r_{ij} , natural service sire referencing was no longer disadvantageous relative to AI sire referencing based on flock PEVD. As expected, declines in flock PEVD were slower with alternating participation in the scheme and flock PEVD increased slightly if flocks discontinued participation in the scheme altogether.

Connectedness measures relative to bias

Kuehn and Lewis (2006) illustrated that for all of these simulated breeding schemes, bias decreased at a decreasing rate as the schemes progressed. Their results show that the MSE of across-flock comparisons of lamb EBV asymptotically approach the MSE of the within-flock comparisons over time, indicating a reduction in bias in the across-flock genetic evaluations. Bias continued to decline over time, and did not increase in cases where flocks discontinued sire referencing after 5 or 10 yr. Therefore, in choosing a candidate connectedness measure, it was important that the statistic was monotonic as year of selection increased. From the four measures described, flock r_{ij} and flock PEVD fit this criterion and were plotted against the percentage reduction in bias due to differing flock means in Figure 4.3 and Figure 4.4, respectively.

In Figure 4.3, the percentage decrease in bias relative to flock r_{ij} is shown. Points on the lines represent selection year averages for both statistics. Since bias reduces as connectedness accumulates, points on the figure associated with higher r_{ij} values correspond with more years of sire referencing. Regardless of whether outside sires were allowed, the percentage of bias decreased as flock r_{ij} increased. Both the percentage of bias explained ($1 - \% \text{ Bias}$) and flock r_{ij} were higher when outside sires were not used. Although the pattern was more variable among scenarios when outside sires were used, the relationship between bias and flock r_{ij} was reasonably consistent. When flock r_{ij} was 0.05, the bias remaining was around 20%, and when flock r_{ij} was 0.10, the bias decreased to less than 10%. It is difficult to extrapolate the relationship further since bias asymptotes at about 3%.

As shown in Figure 4.1 and Table 4.1, when flocks disengaged from sire referencing after 5 or 10 yr, flock r_{ij} continued to increase even though new physical

connections between the flocks were no longer established. This same pattern can be observed in Figure 4.3, particularly when outside sires were not allowed. Bias no longer decreased after sire referencing stopped (Kuehn and Lewis, 2006) even though flock r_{ij} continued to increase, resulting in a disparity with the customary relationship between bias and flock r_{ij} .

The relationship between flock PEVD and bias is shown for all scenarios in Figure 4.4. Points on the figure associated with lower values of flock PEVD coincided with more years of sire referencing. In general, as flock PEVD decreased, bias also decreased. However, unlike flock r_{ij} , the relationship between PEVD and bias is not consistent, especially between strategies where outside rams were either allowed or barred. Bias was lower while flock PEVD remained higher when only homebred non-reference sires were used. For the same flock PEVD, the bias was somewhat higher when outside sires were allowed. The inconsistency of this pattern raises into question the use of flock PEVD as a diagnostic measure to manage risk in across-flock genetic evaluations where differences among the genetic means of flocks may introduce biases into the evaluation.

Discussion

All of the connectedness measures followed expected patterns over 15 yr of selection within each scenario evaluated. The correlation measures increased as flocks participated in any form of sire referencing scheme and prediction error variance of EBV differences decreased. There were two possible reasons why these connectedness measures may have changed: a decrease in prediction error variance of animals or flock means, or a positive prediction error covariance between animals or their means. Prediction error variance decreases as more information becomes available to predict EBV. Based on Figure 4.2, connecting flocks together through sire referencing schemes does reduce individual lamb prediction error, especially in small flocks with limited information within a single year (Smith and Banos, 1991). However, much of the gain observed in these connectedness measures came from prediction error covariance.

Prediction error covariance between animals is zero when no connections (due to reference sires in this case) exist. Adding connections through related animals or through direct comparisons causes the prediction error covariance between animals in separate flocks to increase. This positive covariance reflects a correlation between errors of breeding value prediction for two separate animals: errors are more likely to be in the same direction. With correlated errors, sources of bias between flocks should decrease as prediction error covariance increases.

Evaluating connectedness from the perspective of the current generation (i.e. lamb measures) had advantages and disadvantages. Lamb measures of connectedness (lamb r_{ij} and lamb PEVD) were more sensitive to changes in the design of breeding schemes than their counterpart flock-based measures. Immediately after flocks disengaged from sire referencing, the connectedness, as measured by lamb statistics, decreased. This sudden response can be attributed to lamb connectedness being measured only on the current generation rather than historic data captured by the flock r_{ij} and PEVD. Individual lambs are not, on average, highly related to one another across flocks and do not have enough information to produce highly accurate EBV in the year their performance was first recorded. These lamb measures therefore assess the precision of comparing lamb EBV across flocks in the current year of evaluation and could be used to rapidly detect changes in between-flock mating systems. However, they do not effectively address the rate of removal of bias in the evaluation over time due to flocks initially having different genetic means.

Lamb measures are highly dependent on pedigree relationships among lambs in different flocks. When large numbers of half-sibs were born each year in different flocks through AI sire referencing, lamb r_{ij} was high relative to natural service sire referencing for which lambs in different flocks were at most cousins. However, flock r_{ij} increased as rapidly (if not faster) in natural service referencing scenarios as compared to AI sire referencing scenarios, suggesting that mean flock EBV are effectively compared with natural service schemes even though lambs are not as highly related. With natural service, individual flocks both contributed and used more rams from other member flocks in the scheme thereby establishing strong relationships among lambs across years. As a caveat, this result may not be general. In this study, the rams selected as reference sires

were chosen from the top 1/6 on EBV. Reference sire use was also heavy in these small flocks with a majority of ewes mated to reference sires; heterogeneity in flock genetic means quickly reduced once sire referencing began. As a consequence, most flocks not only used but contributed rams to the reference sire pool. This mutual exchange of rams leads to strong connectedness.

Measures of connectedness involving flock means are based on the mean EBV of all animals within each flock. Therefore, they are functions of the accuracy of prediction of flock genetic means, which are the source of bias we are concerned about in this study. Both flock r_{ij} and PEVD therefore assess how well the model predicts differences in flock genetic means. Flock r_{ij} measures correlations in errors of predicted genetic means and flock PEVD measures the precision with which differences in genetic means are estimated. Since these measures are based on information on whole flocks, they are less sensitive to changes in mating strategies between flocks and better reflect the monotonic decrease in bias observed by Kuehn and Lewis (2006) and in other simulation studies (e.g. Hanocq et al., 1996). Therefore, these two measures were chosen as candidate statistics to diagnose the reduction in the percentage of bias remaining as selection proceeded for the different scenarios simulated.

Flock r_{ij} outperformed flock PEVD when comparing associations with the pattern of change in percentage of bias explained over time. The general pattern in flock r_{ij} shown in Figure 4.3 was consistent regardless of the type of breeding scheme and whether or not homebred rams alone were mated to ewes not bred to reference sires. The pattern was noisier when outside sires were allowed for non-reference sire matings, but the relationship between flock r_{ij} and bias remained relatively consistent. Some of the noise observed when outside sires were allowed was due to the decreased bias in the system after the 10 yr of random mating that occurred before group breeding schemes were initiated. Since the outside sires were drawn from a population with a common mean, flock genetic means regressed during the 10 yr of random mating and part of the bias simulated between flocks decreased (Kuehn and Lewis, 2006). The amount of regression depended on the policy individual flocks adopted for the use of outside rams, which varied between replicates of the simulation. This extra level of stochasticity, in

addition to the sampling of flock genetic means, most likely accounts for the extra variance observed in Figure 4.3 for scenarios where outside sires usage was allowed.

The relationship of flock PEVD to bias, on the other hand, was highly dependent on the scenario used, especially in terms of whether outside rams were allowed for non-reference sire matings. Although within a scenario, bias decreased as flock PEVD decreased, it is difficult to clearly define threshold values for PEVD to quantify the risk of comparing animals across flocks. The inconsistent pattern in PEVD relative to bias may partially be due to differences in inbreeding and average relationships within flocks in the two strategies used for mating surplus ewes. Since the relationship between animals within flocks must be higher when no unpedigreed outside animals are brought into the system, the additive variance of mean comparisons across flocks should be higher, at least until connections are made between flocks which would reduce this variance. The variance of the differences among flock genetic means is an upper bound for flock PEVD. Although the values of the numerator relationship matrix were not available and could not be easily calculated with this level of replication, it may be useful to standardize flock PEVD using the average genetic relationship of animals between and within flocks as described by Laloë (1993).

The pattern for flock r_{ij} lends itself to possible benchmarks for the management of risk due to different flock means in genetic evaluations. If two flocks reach a connectedness level of 0.05 for their flock r_{ij} , about 80% of bias due to differences in initial genetic means should be explained (20% remaining). Increasing the flock r_{ij} to 0.10 should equate to a remaining level of bias equivalent to 10% of the initial level. These benchmarks can help producers decide whether further matings between flocks are desirable to further improve connectedness.

Implications

Establishing connections among flocks is important when the genetic means of flocks differ since biases in the genetic evaluation may otherwise result. Connectedness measures can be increased with designed mating programs. The connectedness correlation of flock genetic means is the most consistent measure of the risk of bias in

across-flock comparisons. Producers seeking to lower their risk when comparing the genetic merit of their animals to those in other flocks should enter into ram exchange programs and monitor their connectedness using the flock connectedness correlation. Benchmark flock connectedness correlation values of 0.05 for ‘good’ connectedness and 0.10 for ‘superior’ connectedness will assist producers in deciding what level of connectedness is sufficient to safeguard selection decisions made across flocks.

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Table 4.1. Levels of lamb and flock connectedness correlations (r_{ij}) after 5, 10 and 15 yr of selection under different types of sire referencing schemes and different levels of outside sire use.

Source of non-reference sires	Breeding scheme	Lamb r_{ij}^*			Flock r_{ij}^*		
		5	10	15	5	10	15
Outside allowed	AI continuous	0.009	0.010	0.011	0.033	0.064	0.092
	AI 5 yr	0.009	0.004	0.002	0.033	0.045	0.045
	AI 10 yr	0.009	0.011	0.004	0.034	0.065	0.079
	AI alternating	0.006	0.007	0.008	0.025	0.048	0.069
	NS continuous**	0.006	0.007	0.008	0.047	0.087	0.123
Homebred only	AI continuous	0.016	0.025	0.033	0.067	0.144	0.233
	AI 5 yr	0.016	0.015	0.015	0.067	0.100	0.109
	AI 10 yr	0.016	0.025	0.023	0.067	0.144	0.194
	AI alternating	0.012	0.021	0.028	0.050	0.110	0.178
	NS continuous**	0.013	0.019	0.025	0.088	0.178	0.271

*SE for lamb r_{ij} and flock r_{ij} were less than 0.0003 and less than 0.003, respectively.

** Natural service.

Table 4.2. Levels of average prediction error differences (scaled by the additive variance^{*}) of lamb EBV and flock mean EBV (PEVD) after 5, 10 and 15 yr of selection under different types of sire referencing schemes and different levels of outside sire use.

Source of non-reference sires	Breeding Scheme	Lamb PEVD ^{**}			Flock PEVD ^{**}		
		5	10	15	5	10	15
Outside allowed	AI continuous	1.168	1.152	1.144	0.056	0.040	0.032
	AI 5 yr	1.168	1.248	1.276	0.060	0.052	0.056
	AI 10 yr	1.172	1.152	1.240	0.060	0.040	0.036
	AI alternating	1.204	1.188	1.172	0.064	0.048	0.036
	NS continuous ^{***}	1.196	1.188	1.184	0.048	0.032	0.024
	AI continuous	1.316	1.332	1.348	0.104	0.116	0.128
Homebred only	AI continuous	1.152	1.124	1.108	0.072	0.052	0.040
	AI 5 yr	1.152	1.236	1.288	0.072	0.072	0.080
	AI 10 yr	1.152	1.121	1.208	0.072	0.052	0.048
	AI alternating	1.188	1.156	1.132	0.088	0.064	0.052
	NS continuous ^{***}	1.180	1.168	1.156	0.060	0.044	0.032
	No scheme	1.372	1.416	1.460	0.156	0.192	0.228

^{*}PEVD are unitless measures since they have been divided by the additive variance.

^{**}SE for lamb PEVD and flock PEVD were each less than 0.003.

^{***}Natural service.

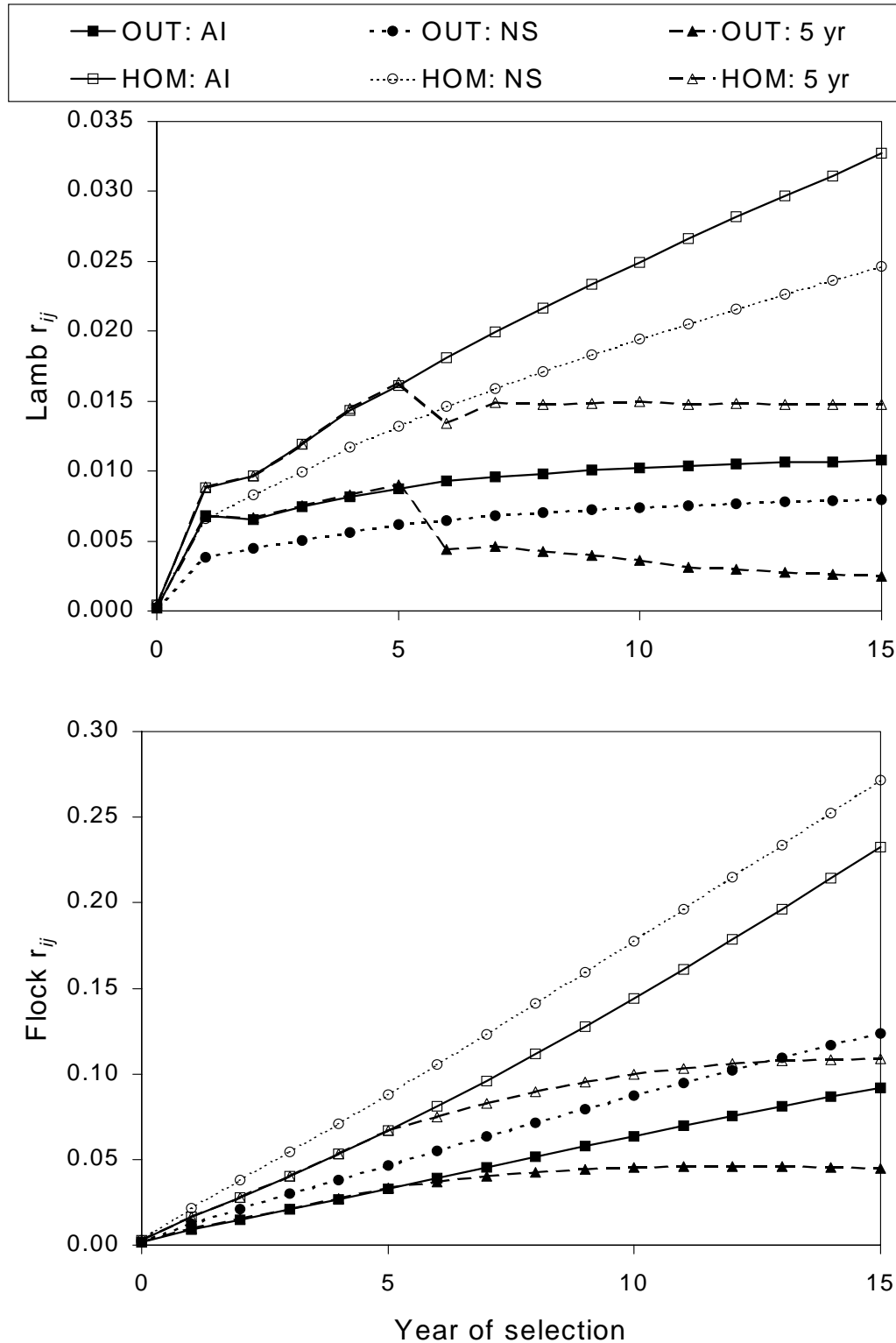


Figure 4.1. Average lamb and flock connectedness correlation (r_{ij}) between 15 flocks over 15 yr of selection for three different breeding schemes: AI sire referencing (AI), natural service sire referencing (NS), and sire referencing for 5 yr followed by 10 yr

where flocks are independent (5 yr). Flocks were either allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

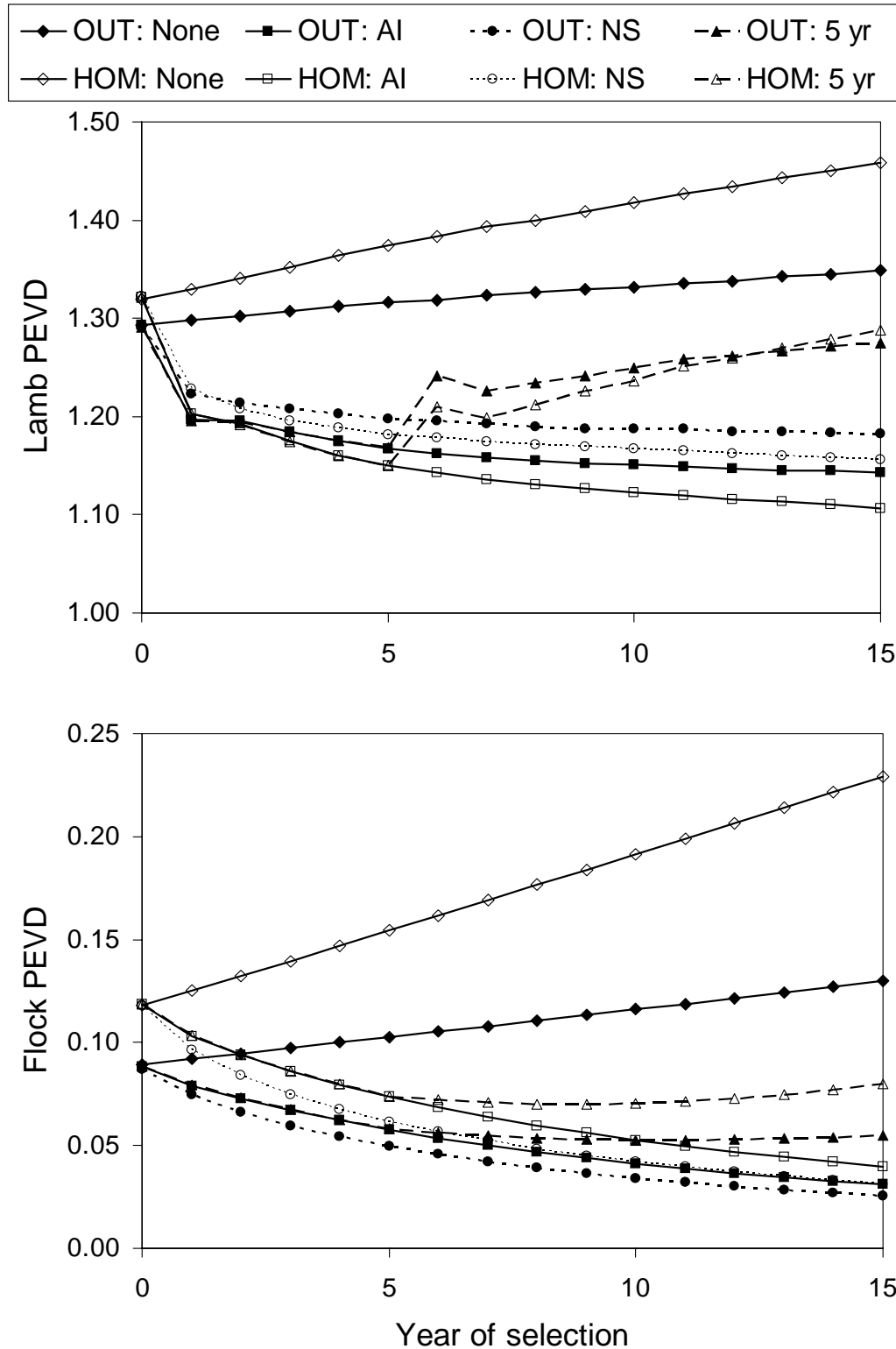


Figure 4.2. Average prediction error of differences (PEVD) in lamb EBV and flock mean EBV between 15 flocks after over 15 yr of selection for four different breeding schemes: no reference sire use (None), AI sire referencing (AI), natural service sire referencing

(NS), and sire referencing for 5 yr followed by 10 yr where flocks are independent (5 yr). Flocks were either allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

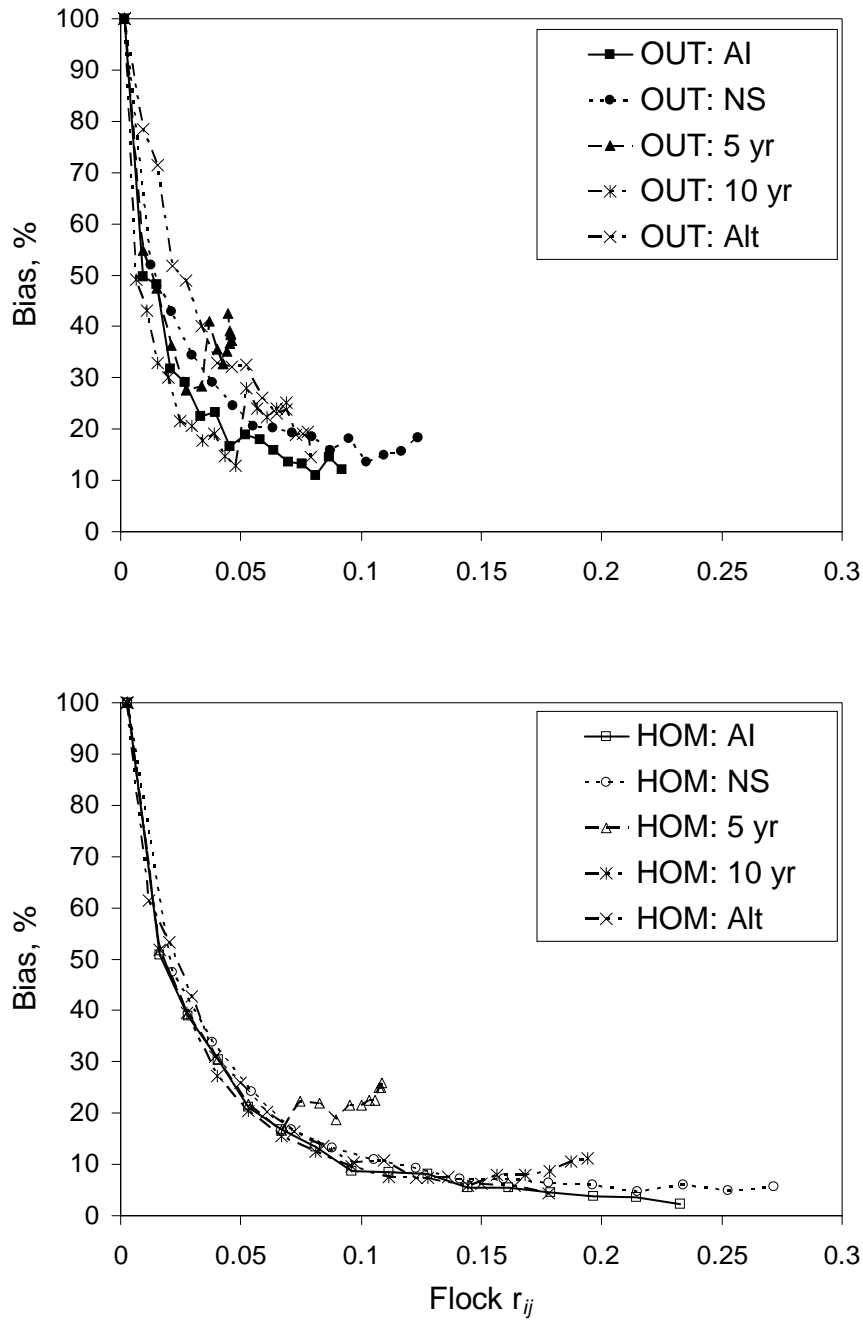


Figure 4.3. Average percentage of bias relative to flock connectedness correlation (r_{ij}) between 15 flocks over 15 yr of selection for different breeding schemes. Schemes are AI sire referencing (AI), natural service sire referencing (NS), sire referencing for 5 yr (5 yr), sire referencing for 10 yr (10 yr) and alternating participation in sire referencing (Alt). Flocks were either allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

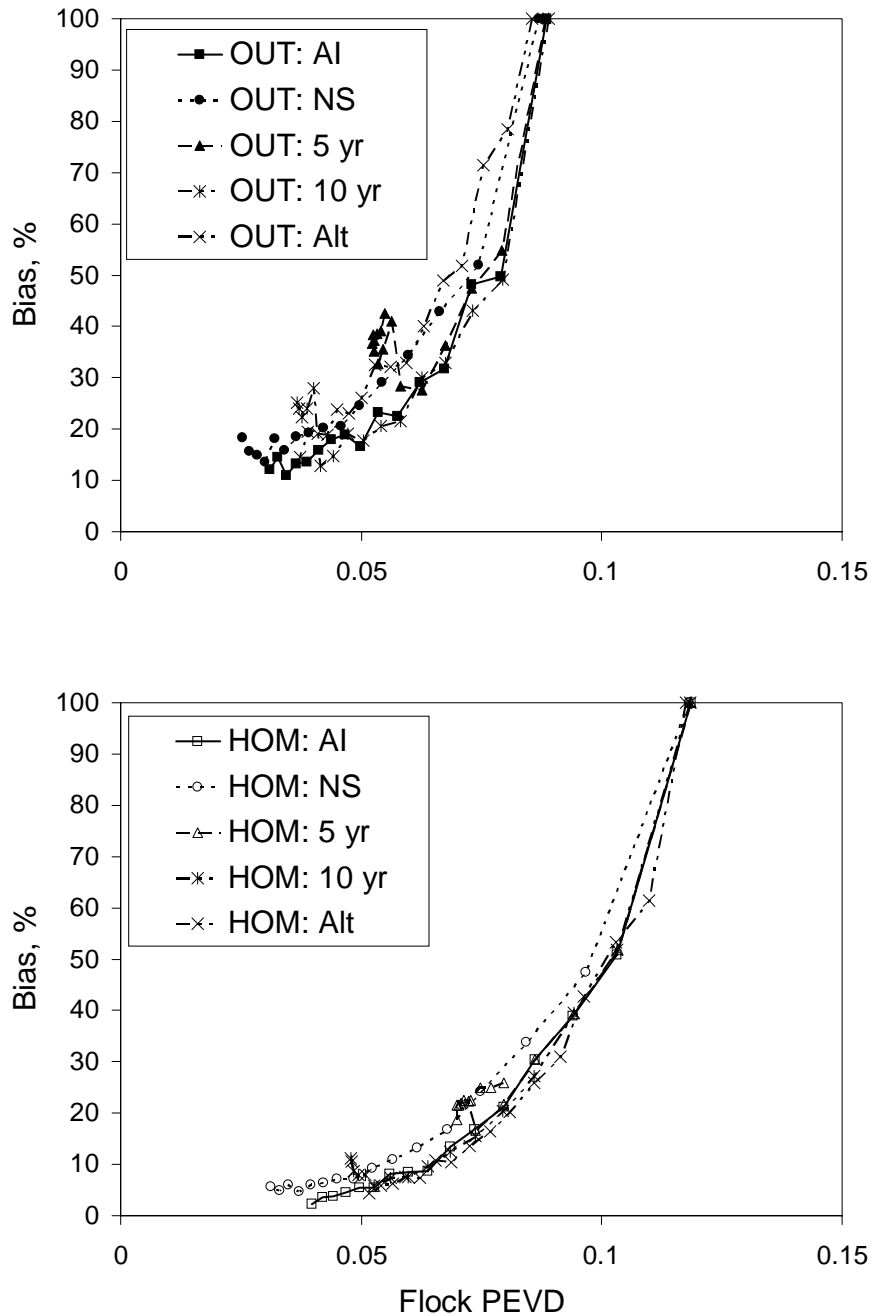


Figure 4.4. Average percentage of bias relative to the prediction error difference of mean flock EBV (PEVD) between 15 flocks over 15 yr of selection for different breeding schemes. Schemes are AI sire referencing (AI), natural service sire referencing (NS), sire referencing for 5 yr (5 yr), sire referencing for 10 yr (10 yr) and alternating participation in sire referencing (Alt). Flocks were either allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

CHAPTER 5

Connectedness in Targhee and Suffolk flocks participating in the U.S. National Sheep Improvement Program

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Introduction

Genetic evaluation in the U.S. sheep industry is available to individual producers through the National Sheep Improvement Program (NSIP; Notter, 1998). Through NSIP, BLUP EPD are predicted for animals within participating flocks for a variety of traits. Producers can use these EPD to make selection decisions within and across flocks in order to improve the performance of their flock as a whole. However, comparisons of animals across flocks may be biased if base animals within different flocks have different genetic means (Lewis et al., 1999) and if connectedness among flocks is insufficient (Kuehn and Lewis, 2006).

Genetic means can differ among populations due to genetic drift or selection (Falconer and Mackay, 1996). If either drift or selection occurs prior to collection of pedigree and performance recording, differences in flock genetic means may not be properly accounted for in the genetic evaluation model until sufficient connectedness has been achieved (Hanocq et al., 1996; Kuehn and Lewis; 2006).

In the U.S., genetic differences among sheep flocks are likely. Many sheep breeds have flocks spread over a wide geographical region. Flocks sizes are generally small relative to other livestock species, and AI use, an effective tool for connecting herds of beef and dairy cattle, is practically non-existent (NAHMS, 2001). Unlike in other countries (e.g., U.K.; Lewis and Simm, 2000), cooperative breeding schemes, which are designed to create such genetic links, have rarely been used. By assessing

connectedness within U.S. sheep breeds that participate in NSIP, it may be possible to determine the risk in comparing EPD among animals from flocks in an industry where genetic links may be weak (Kuehn et al., 2006).

The objectives of this study were to assess the current level of risk in comparing EPD across Targhee or Suffolk flocks participating in NSIP and to recommend future breeding strategies for these producers to use in order to manage this risk.

Materials and Methods

Data

The U.S. NSIP was initiated in 1987 to provide genetic evaluations for the U.S. sheep industry (Wilson and Morrical, 1991). Producers (rather than breed associations) submitted pedigree and performance data yearly to a central processing center and received EPD for their active animals. Initially, traits were analyzed using within-flock single-trait models (Notter, 1998). In 1994, multiple-trait across-flock analyses began for the Targhee breed. Similar approaches were implemented for the Suffolk and Polypay in 1995 and 1996, respectively. In 2005, across-flock BLUP EPD were produced for nine different sheep breeds. Of these breeds, several Targhee and Suffolk flocks had participated in NSIP since its inception, and the extent of connectedness and quantity of data were highest for the Targhee and Suffolk. Hence, these breeds were selected to evaluate changes in connectedness over time and current levels of connectedness.

Currently EPD are derived for 120-d weaning weight, yearling gain, fleece weight, fiber diameter, staple length, and percent lamb crop (number of lambs born per 100 ewes lambing) in Targhee, while Suffolk breeders receive EPD for 60-d weaning weight, 60 to 120 d postweaning gain, and percent lamb crop. Weaning weight and percent lamb crop are the only traits evaluated in both breeds. For this study, connectedness in genetic evaluation of weaning weight was evaluated for both breeds as a basis of comparison between the two data sets.

Valid weaning weights were defined as those recorded within 60-d windows (30 to 90 d for 60-d weaning weight in the Suffolk; 90 to 150 d for 120-d weaning weight in the Targhee). Weaning weights were excluded for animals without a reported ewe age or

type of birth and rearing, or if the lamb was fostered or artificially reared. Contemporary groups for weaning weight were formed based on flock, producer supplied management code, and weigh period (Notter, 1998). In order to be classified within the same weigh period, lambs had to be weighed in the same 7-d window. Management codes defined whether animals were or were not creep-fed and whether dams were fed alike or according to the number of lambs nursed. Producers also had the opportunity to augment management codes if lambs were treated differently for other reasons. Suffolk contemporary groups were further augmented by the animals' age at weaning; animals less than 40 d of age, 40 to 80 d of age and greater than 80 d of age were placed in separate contemporary groups.

A summary of pedigree and performance data is presented in Table 5.1. Targhee flock sizes ranged from approximately 20 to 230 breeding ewes with a median flock size of about 65 ewes. Targhee flocks were more localized within a single region, with only 8 states represented in the data. The currently active Targhee flocks were from only 4 states; 13 of the 16 active flocks were from Montana. Weaning weight records were reported from 1984 through 2004. Targhee flocks began an active exchange of rams in 1994, about the time across-flock analysis began. Because of this policy and the relatively close proximity of the flocks to one another, connectedness in Targhee was not expected to be a problem.

In the Suffolk database, flocks ranged in size from approximately 20 to 140 breeding ewes per year with a median flock size of about 40 ewes. Suffolk flocks were spread widely across the U.S., with 27 states represented. The currently active Suffolk flocks were located in 14 states. Weaning weight performance data were reported from 1983 through 2005. The NSIP Suffolk flocks have never attempted a formal exchange of rams among flocks. A fair amount of exchange is believed to have taken place through purchases of rams from prominent breeders and at national shows. However, many of the purchased rams did not come from NSIP flocks and therefore would not provide connections for genetic evaluation. Due to the wide distribution of flocks across the U.S. and lack of an active exchange program, connectedness was expected to be more limited among Suffolk flocks.

Measuring connectedness

In its 18 yr history, participation in NSIP has been variable. Several flocks joined NSIP at some point but no longer participate. Since connectedness is of much greater relevance to the flocks that are currently active in the program, connectedness measures and counts were summarized only for active flocks.

Connectedness across flocks is established primarily through the use of common sires in different flocks and through the purchase of rams born in other NSIP member flocks. One way to map the establishment of connectedness is to count the number of progeny of such linking sires with recorded weaning weights. Sires were thus classified into one of four different categories: 1) sires used in multiple flocks; 2) sires used in a single flock but born in a different NSIP flock; 3) sires used in the NSIP flock in which they were born; and, 4) non-NSIP sires used in a single flock. Sires used in multiple flocks included both NSIP and non-NSIP sires. Sires used in the same NSIP flocks in which they were born do not contribute to connectedness among flocks. However, they are an important source of connectedness between contemporary groups within their flock and therefore allow linking sires to have a greater impact across different years. The number of progeny from each sire type was calculated for each of the 18 yr of pedigree and performance data recording. The origins of sires of lambs born before the start of NSIP could not be definitively established.

Connectedness between flocks was measured through the use of prediction error correlations (Lewis et al., 1999; Lewis et al., 2005; Kuehn et al., 2006), also known as connectedness correlations. Prediction errors were derived under the following linear animal model:

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

where \mathbf{y} is a vector of weaning weights; \mathbf{b} is a vector of fixed effects; \mathbf{u} is a vector of breeding values, and \mathbf{e} is a vector of residuals. Incidence matrices \mathbf{X} and \mathbf{Z} relate phenotypes to fixed and random genetic effects, respectively. Only contemporary group was fit as a fixed effect; adjustments for effects of age of dam, type of birth and rearing, and lamb age were applied before analysis of the data (Bradford, 2003). Prediction error (co)variances of EBV from this model are derived from the inverse of the coefficient matrix (\mathbf{C}) used to derive EBV:

$$\mathbf{C} = [\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1}],$$

where \mathbf{M} is the fixed effect absorption matrix ($\mathbf{M} = \mathbf{I} - \mathbf{X}(\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'$), λ is the ratio of residual and additive variances (σ_e^2/σ_a^2), and \mathbf{A} is the numerator relationship matrix. Inverse elements of \mathbf{C} , multiplied by σ_e^2 , are prediction error (co)variances of estimated breeding values. The connectedness correlation (flock r_{ij}) proposed by Lewis et al. (1999; 2005) was derived for flocks i and j as:

$$r_{ij} = \frac{\text{PEC}(\hat{u}_i, \hat{u}_j)}{\sqrt{\text{PEV}(\hat{u}_i)\text{PEV}(\hat{u}_j)}},$$

where $\hat{u}_{i(j)}$ is the mean EBV of all animals in flock $i(j)$, $\text{PEC}(\hat{u}_i, \hat{u}_j)$ is the prediction error covariance between these means, and $\text{PEV}(\hat{u}_i)$ and $\text{PEV}(\hat{u}_j)$ are the prediction error variances of the means EBV of flocks i and j . Heritability estimates of 0.10 for Targhee and 0.15 for Suffolk (Notter, 1998) were used in the model to derive prediction error variances and covariances.

Using simulation, Kuehn et al. (2006) established that flock r_{ij} can be used as a measure of the risk in comparing EBV of animals across flocks. In that study, flocks were simulated with different genetic means in order to introduce partial bias in comparing animals across flocks. Connecting flocks through the use of different sire referencing schemes decreased the bias in comparisons of EBV of animals from different flocks. The decrease in bias had a strong relationship with flock r_{ij} ; a flock r_{ij} of 0.05 approximately corresponded to an 80% reduction in bias and a flock r_{ij} of 0.10 approximately corresponded to a 90% reduction. These benchmarks of 0.05 and 0.10 were proposed for use in monitoring risks associated with comparing animals across flocks.

These benchmarks were based on scenarios using a heritability of 0.25 (Kuehn et al., 2006). In order to validate that the same benchmark levels of flock r_{ij} were applicable to data with lower heritability, 25 replicates of a continuous A.I. sire referencing scheme with selection on a trait with heritability of 0.125 were simulated over 15 yr using methods described in Kuehn and Lewis (2006) and Kuehn et al. (2006). Flock r_{ij} in each year of the program were plotted against the percentage reduction in bias (Figure 5.1).

The relationship between bias and flock r_{ij} over time was essentially the same as that reported by Kuehn et al. (2006). Therefore, benchmarks of 0.05 for ‘good’ connectedness and 0.10 for ‘superior’ connectedness were used to evaluate results obtained for Targhee and Suffolk flocks.

In order to examine how connectedness has changed, flock r_{ij} were calculated between pairs of currently active flocks at three different times: 1990, 1995, and the most recent year in which data were available (2004 for Targhee and 2005 for Suffolk). These years were chosen to reflect the state of connectedness shortly after NSIP began (1990), during the year that across-flock evaluations began (1995), and currently. Data sets for 1990 and 1995 were created by removing pedigree and performance records of animals born after these years from the current databases. Pedigree and performance data from flocks that are not currently active in NSIP were retained to allow for potential indirect connections. Of the 16 currently active Targhee flocks, four were participating in NSIP in 1990 and 10 were participating in 1995. In Suffolk, six of the currently active 24 flocks were members of NSIP in 1990 and nine were members in 1995. Flock r_{ij} was summarized for these active flocks relative to each of the three time points.

Using flock r_{ij} calculated from the most recent data, hierarchical clustering of active flocks in each breed was performed. Flock r_{ij} was used to measure the distance between flocks. Clustering was based on the group-average criterion. The similarity between two flocks or clusters of flocks was defined as the average distance between all pairs of units involving a member of each group. Groups merged with whichever groups were closest in average distance, and the average similarity of the resulting cluster with other groups was recalculated. The resulting links between flocks and clusters were plotted as dendrograms. The clustering results and dendrogram plots were obtained using CLUSTER and TREE procedures in SAS (SAS Institute; Cary, NC). It was hypothesized that by examining the connected clusters formed within each of these breeds, matings that would enhance connectedness across all flocks could be identified.

Results

Numbers of progeny from linking sires

Figures 5.2 and 5.3 show numbers of progeny produced by each type of sire in the Targhee and Suffolk breeds, respectively. In the last 5 yr, 1,911 progeny weaning weights were recorded per year on average in 16 Targhee flocks while an average of 1,202 was recorded in 24 Suffolk flocks. In both breeds, the proportion of animals with weaning weight records that were progeny of sires from non-NSIP flocks was relatively constant across years but the average proportion was much lower in Targhees (16%) than in Suffolks (39%).

When across-flock analysis began in Targhee in 1995, there was an increase in the number of weaning weights recorded due to new (currently active) flocks joining the evaluation. As expected, the number of progeny from multiple-use and the number of progeny born to sires that were transferred to other member flocks also began to increase at about this time. From 1995 through 2004, 44% of the Targhee lambs with weaning weight records were born from sires which were either transferred to a different flock or used in multiple flocks.

The number of Suffolk weaning weight records increased relatively little in the years immediately following introduction of the across-flock analyses in 1995. The number of weaning weights recorded in the Suffolk breed in the intermediate years is higher than that shown in Figure 5.2; however a large number of flocks discontinued their membership in NSIP (Table 5.1) and thus their data are not included. However, numbers of weaning records have steadily increased in the last 5 yr, primarily because new flocks began to enroll after 1999. As mentioned previously, only 9 of the currently active flocks participated in NSIP in 1995. Since then, 13 new flocks have enrolled, bringing the total number of active flocks to 24. In the last 10 yr, 23% of the animals with weaning weight records were from sires used in multiple flocks or sires transferred to other member NSIP flocks, and the use of transferred sires has grown over the past 5 yr.

Connectedness correlations

The mean, median, and standard deviation of flock r_{ij} for groups of active Targhee and Suffolk flocks are summarized in Tables 5.2 and 5.3. Across all years and groups of flocks, connectedness was much higher in the Targhee breed than in the Suffolk breed. Targhee flocks which have been active since at least 1990 achieved average flock r_{ij} levels of 0.28 in 2004. Across all active Targhee flocks, mean flock r_{ij} in 2004 was well above the higher benchmark level of 0.10. The mean and median flock r_{ij} were generally similar in Targhee, suggesting that the values of flock r_{ij} were not heavily skewed in either direction.

Suffolk connectedness did not increase between 1990 and 1994 for the six currently active flocks that were also active in this period. Even by 2005, the mean level of flock r_{ij} in these six flocks was only 0.04. In all cases, the median value of flock r_{ij} was lower than the mean value, indicating a right-skewed distribution caused by a large number of pairs of flocks with near-zero flock r_{ij} values. In 2005, over 25% of all pairwise flock r_{ij} values were less than 0.002. However, an additional 25% of these values were over 0.036, causing the mean to increase relative to the median. The presence of several r_{ij} values that were close to zero as well as several moderate flock r_{ij} values suggest that Suffolk flocks may be connecting primarily within smaller clusters rather than across the whole breed.

A dendrogram based on the group-average criterion for currently active Targhee flocks is presented in Figure 5.4. Flocks 1 through 4 in the figure represent the flocks that joined NSIP before 1990, and flocks 5 through 10 represent flocks that joined between 1990 and 1995. Two pairs of flock were very highly connected: flocks 9 and 13 had a flock r_{ij} of 0.69, and flocks 2 and 15 had a flock r_{ij} of 0.53. In both cases, the rams used in one of the flocks came almost exclusively from the other flock (flock 13 from flock 9 and flock 15 from flock 2). All Targhee flocks merged into clusters at or above the level of 0.05, the 'good' connectedness benchmark. Flocks 1, 2, 3, 4, 9, 13, and 15 all merged into one cluster with an average flock r_{ij} above 0.20. Only two flocks (10 and 14) did not merge with the main cluster at a flock r_{ij} level of 0.10 or above.

Clusters formed and merged at lower levels of flock r_{ij} in the Suffolk breed (Figure 5.5). Flocks 1 through 6 represent the active flocks that began NSIP before 1990.

Flock 7, 8 and 9 joined NSIP by 1995, and the remaining flocks (10 through 24) joined between 1995 and 2005. As seen in the dendrogram, five pairs of flocks/clusters had a pairwise flock r_{ij} of 0.20 or higher. Four clusters of flocks were formed at a threshold flock r_{ij} of 0.05 or higher. Cluster A consisted of flocks 1 and 9; cluster B contained flocks 2, 3, 11, 12, 13, 14, 15, 18, and 22; cluster C contained flocks 4, 5, 7, 20, 23, and 24; and cluster D consisted of flocks 16 and 17. Several other flocks were isolated from these larger clusters (e.g., flock 19). Cluster D, containing flocks 16 and 17, and flock 19 were basically unconnected from all of the other flocks. The two large clusters (B and C) both contained several flocks which have participated in NSIP for over 10 yr. From these results, and those shown in Table 5.3, it appears there has been little incentive for some flocks that are long term participants in NSIP to connect with one another.

Discussion

Connectedness in genetic evaluation is important if management units (e.g., flocks or herds) differ in their genetic mean. By increasing connectedness, the risk of biased EBV comparisons among units is reduced (Kennedy, 1981). Therefore, a measure of the level of connectedness would allow producers to monitor the risk of comparing their animals to those in other management units. Most measures developed to measure connectedness have been functions prediction error (co)variances (e.g., Kennedy and Trus, 1993; Laloë 1993; Mathur et al., 2002), as was flock r_{ij} in this study. These statistics have been used to measure connectedness in dairy cattle (Hanocq and Boichard, 1999), swine (Hofer, 1994; Bunter and Macbeth, 1997; Mathur et al., 2002), and beef cattle (Roso et al., 2004). In general, these studies have either shown that connectedness was sufficient in the population of interest (e.g., dairy cattle; Hanocq and Boichard, 1999) or revealed outlying flocks or herds that need to improve connections to increase the accuracy of comparisons with animals in other management units (e.g. swine; Hofer et al., 1994). Currently, connectedness evaluations are routinely conducted in Canada for swine using the correlation between the standard errors of estimated herd effects (Mathur et al., 2002) and in sheep flocks in the U.K. using flock r_{ij} (Simm et al., 2001). Producers are able to make future mating decisions based on their existing and(or) desired level of

connectedness to other herds or flocks. Using the results of this study, Targhee and Suffolk sheep breeders will have a similar opportunity.

Based on both numbers of progeny of linking sires and connectedness levels summarized by flock r_{ij} , the Targhee breed has clearly emphasized the establishment and maintenance of connections to a larger extent than the Suffolk breed. Continuing use of the same sires in multiple flocks and the purchase of rams from other NSIP member flocks has clearly been a priority for Targhee breeders. As a result, connectedness among NSIP Targhee flocks has consistently grown over time, especially since across-flock genetic evaluations began in 1995. By 2004, some of the newer Targhee flocks in NSIP were effectively satellite units of other flocks that had participated over many years. By using sires from well-connected NSIP flocks, these new flocks became strongly connected with other Targhee flocks in NSIP. New flocks entering NSIP can therefore rapidly become connected to the entire breed by purchasing sires from flocks that are already well-connected. None of the Targhee flocks had poor overall connectedness. However, from Figure 5.3, flocks 10 and 14 could lower their risk when comparing the EPD of their animals to those in other NSIP flocks by increasing their use of sires originating from these flocks; this could be achieved most efficiently by choosing rams from the four Targhee flocks that had participated longest in NSIP.

Overall use of linking sires in the Suffolk breed has been much lower than in the Targhee breed, but did occur consistently, especially after 1995. The clusters formed using flock r_{ij} imply that many of the linkages that occurred were within distinct subsets of flocks. Connectedness was reasonable between flocks within these clusters but generally much poorer between the clusters. Even some of the flocks that have participated in NSIP since before 1990 still were not very well connected. Comparisons of EPD across these clusters may therefore be risky.

The difference in connectedness levels between the two breeds mainly seems to be due to different patterns of ram exchange: between all flocks in the Targhee *versus* within clusters or subsets of flocks in the Suffolk. This situation likely reflects, at least in part, their structural features. The Targhee is a western range breed with flocks primarily located within the same region; all but three of the flocks in this analysis were located in Montana. Since almost all of the matings in the U.S. sheep industry are by natural

service, the close proximity of these flocks has made ram exchange more feasible. Despite being a dual-purpose breed raised for both wool and meat production, Targhee breeders participating in NSIP appear to have consistently had similar breeding objectives, creating a potential for many flocks to purchase and use related individuals.

Suffolk connections may have been more challenging to establish. Unlike Targhee, Suffolk flocks in this analysis were scattered across the U.S. Suffolk breeders have not formed cooperative ram exchange programs, in part because of the physical distances between flocks. In addition, although the Suffolk had the highest number of annual registrations of any U.S. sheep breed (*The Banner*; March 2005), numbers of animals recorded in NSIP have been considerably lower than in Targhee. As seen in Table 5.1, several Suffolk flocks that participated in NSIP and contributed a large portion of the weaning weight data later quit. Although there has been resurgence in both flock and animal numbers in the last 5 yr, most Suffolk flocks are not currently enrolled in NSIP. A large proportion of the rams used in NSIP Suffolk flocks came from non-recording flocks, especially before 2000 (Figure 5.3). Since the pedigrees of these animals are not reported and they are used in single flocks, they do not contribute to connectedness.

An additional characteristic of the Suffolk breed that likely affects connectedness is divergent selection toward two different biological types (S. P. Greiner, *personal communication*): one selected primarily for traditional terminal sire characteristics such as large mature size and another with greater emphasis on moderate mature size and evidence of muscling. Breeders with these separate priorities are unlikely to purchase rams from one another, and this situation may be part of the reason for the separation of flocks into the clusters seen in Figure 5.5. Both of the larger clusters contain flocks from similar geographical regions that have never formed connections to one another.

Further improvement of connectedness in Targhee need not be a priority. As long as current practices continue, risks of comparing animals across flocks in this breed should be of no concern. In addition, while not quantified by the measures considered in this study, the absolute risk of comparing animals across Targhee flocks is probably also lower than in Suffolk due to the more recent establishment of the Targhee breed

(Bromley et al., 2000). Genetic means between Targhee flocks have thus had less time to diverge.

If Suffolk breeders or their commercial customers wish to compare animals across clusters of flocks, greater exchange of rams between the clusters is critical. However, if the producers in these clusters truly are selecting toward different types of Suffolk sheep, connectedness between clusters may be of little importance; animals will only be selected from the cluster that matches the buyers' breeding goals. New flocks joining NSIP and current members that are poorly connected generally should purchase animals from the cluster that fits their breeding objective. Additional recruitment of flocks into NSIP that are influential to the breed as a whole could also improve connectedness by creating additional pedigree linkages between flocks. If groups of breeders wish to work toward a common goal, a cooperative ram exchange program would improve rates of genetic gain and connectedness between flocks (Kuehn and Lewis, 2006).

Connectedness relative to traits such as fleece weight in Targhee and litter size in both breeds should be evaluated to determine whether connections are sufficient between flocks for these economically important traits.

Implications

Both Targhee and Suffolk breeds have established genetic connections between flocks through participation in the National Sheep Improvement Program (NSIP). Connections in Targhee are effective across the entire breed while Suffolk connectedness is confined to subsets or clusters of flocks. Exchange of rams and purchase of rams from other flocks can effectively increase connectedness and reduce the risk of bias when EPD of animals from different flocks are compared. Flocks joining genetic evaluation programs such as NSIP should purchase rams from members with established genetic links to other flocks within the breed.

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Table 5.1. Summary of pedigree and weaning performance data for the Targhee and Suffolk breeds participating in the National Sheep Improvement Program.

	Targhee		Suffolk	
	All flocks	Active flocks*	All flocks	Active flocks*
Number of inventoried animals	41,894	35,794	36,239	18,311
Number of sires	934	661	2,525	1,233
Number of dams	11,933	9,627	11,370	5,185
Number of sires with progeny weaning weights	429	350	1,235	640
Number of flocks	41	16	83	24
Number of weaning weight records	27,464	25,404	26,165	14,017
Number of contemporary groups	405	320	2,451	1,322
Average contemporary group size	67.8	79.4	10.7	10.6
Median contemporary group size	27.0	40.5	5.0	5.0
Average number of sires per contemporary group	3.0	3.3	2.0	2.1

* Active flocks were those who reported data for lambs born in 2004 in Targhee and 2005 for Suffolk.

Table 5.2. Descriptive statistics for flock r_{ij} for currently active Targhee flocks recording in the National Sheep Improvement Program since 1990, 1995 and 2004.

Year of evaluation	Currently active flocks recording in: ^a					
	1990 (4)		1995 (10)		2004 (16)	
	mean (SD)	med ^b	mean (SD)	med ^b	mean (SD)	med ^b
1990	0.10 (0.075)	0.09				
1995	0.19 (0.055)	0.18	0.08 (0.072)	0.04		
2004	0.28 (0.049)	0.28	0.18 (0.092)	0.19	0.13 (0.110)	0.11

^aNumbers of flocks are shown in parentheses.

^bmed=median.

Table 5.3. In Suffolk, descriptive statistics for flock r_{ij} as evaluated among currently active flocks recording in the National Sheep Improvement Program since 1990, 1995 and 2004.

Year of evaluation	Currently active flocks also recording in: ^a					
	1990 (6)		1995 (9)		2005 (24)	
	mean (SD)	med ^b	mean (SD)	med ^b	mean (SD)	med ^b
1990	0.02 (0.041)	0.001				
1995	0.02 (0.025)	0.005	0.01 (0.024)	0.004		
2005	0.04 (0.040)	0.022	0.04 (0.049)	0.020	0.03 (0.051)	0.010

^aNumbers of flocks are shown in parentheses.

^bmed=median.

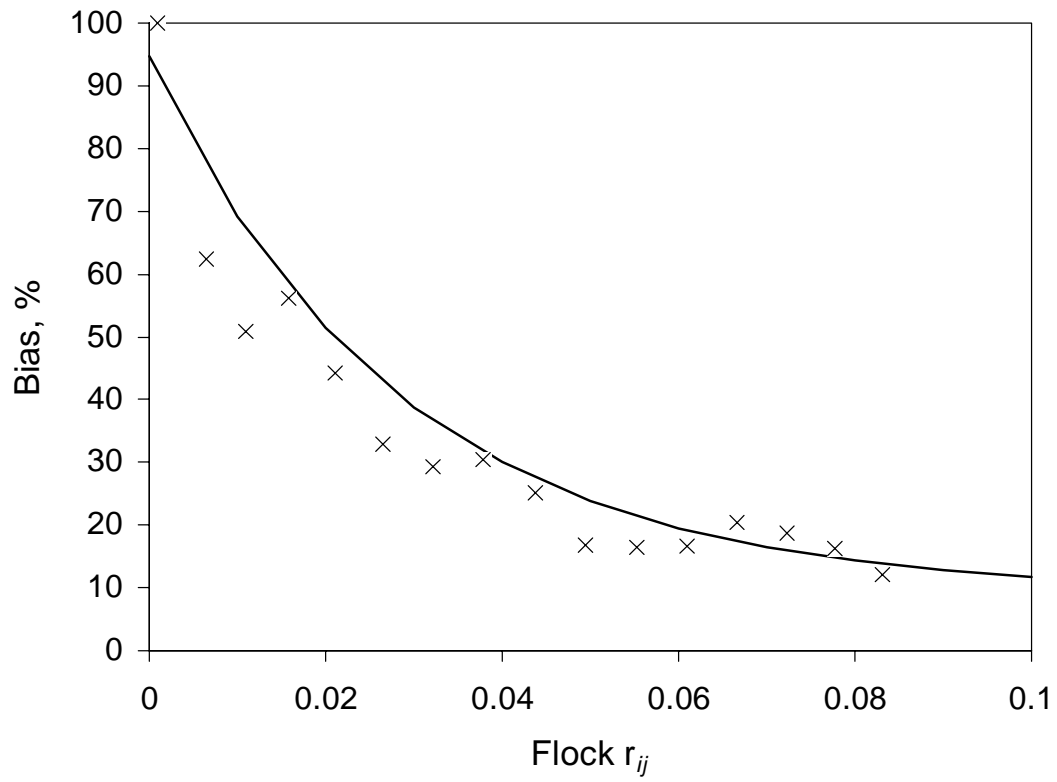


Figure 5.1. Relationships between average percentage of bias remaining and flock connectedness correlation (flock r_{ij}) for 15 flocks participating in a sire referencing scheme over 15 yr of selection on trait with a heritability of 0.125.

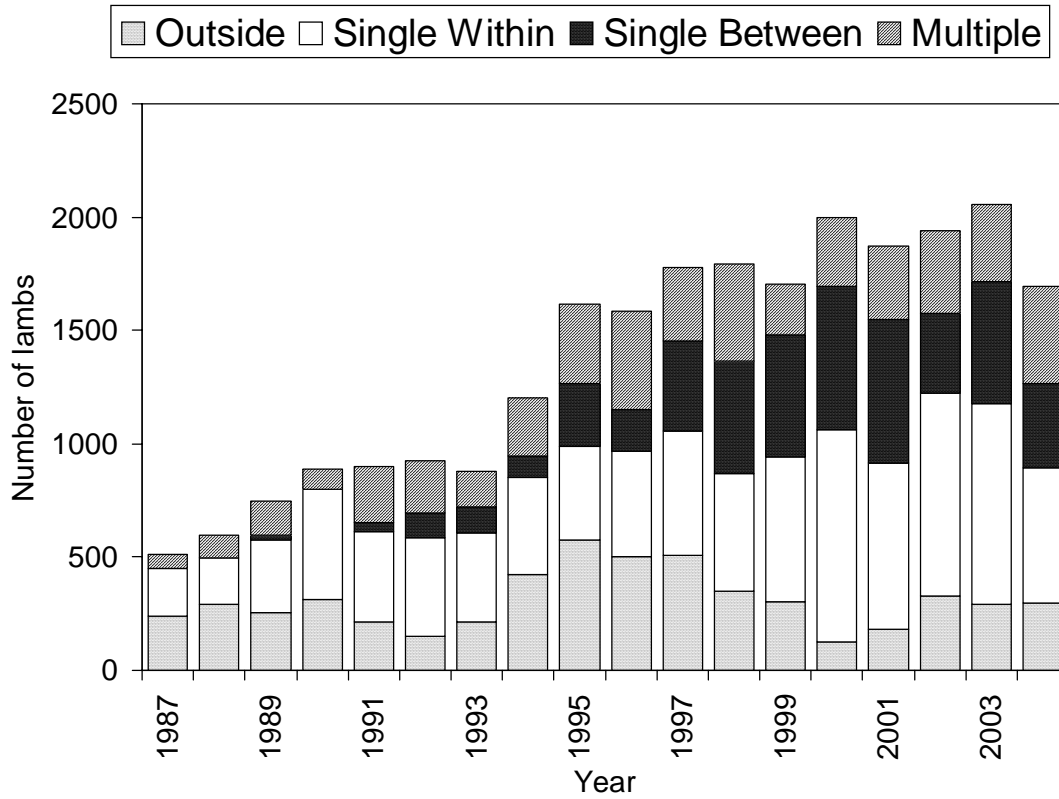


Figure 5.2. Numbers of Targhee lambs with weaning weight records born from 1987 through 2004 from sires originating outside the National Sheep Improvement Program (NSIP) (Outside), sires used only in their flock of origin (Single Within), sires born in an NSIP flock but used only in a different NSIP flock (Single Between), and sires used in multiple NSIP flocks (Multiple).

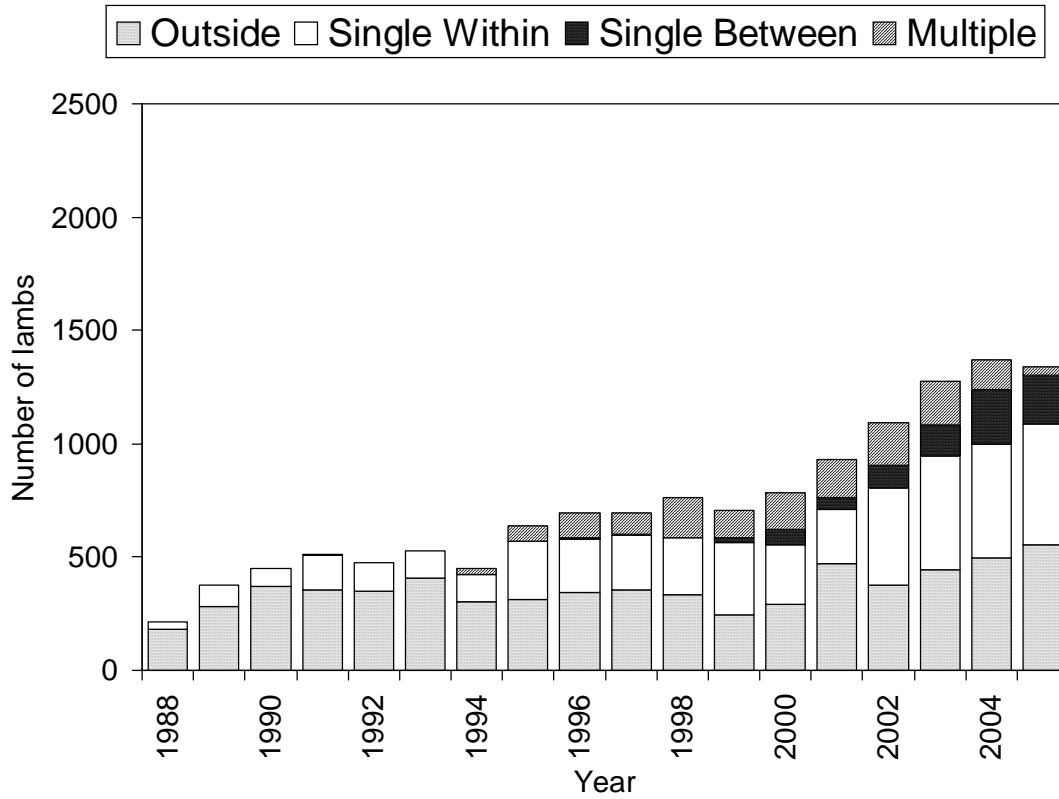


Figure 5.3. Numbers of Suffolk lambs with weaning weight records born from 1987 through 2004 from sires originating outside the National Sheep Improvement Program (NSIP) (Outside), sires used only in their flock of origin (Single Within), sires born in an NSIP flock but used only in a different NSIP flock (Single Between), and sires used in multiple NSIP flocks (Multiple).

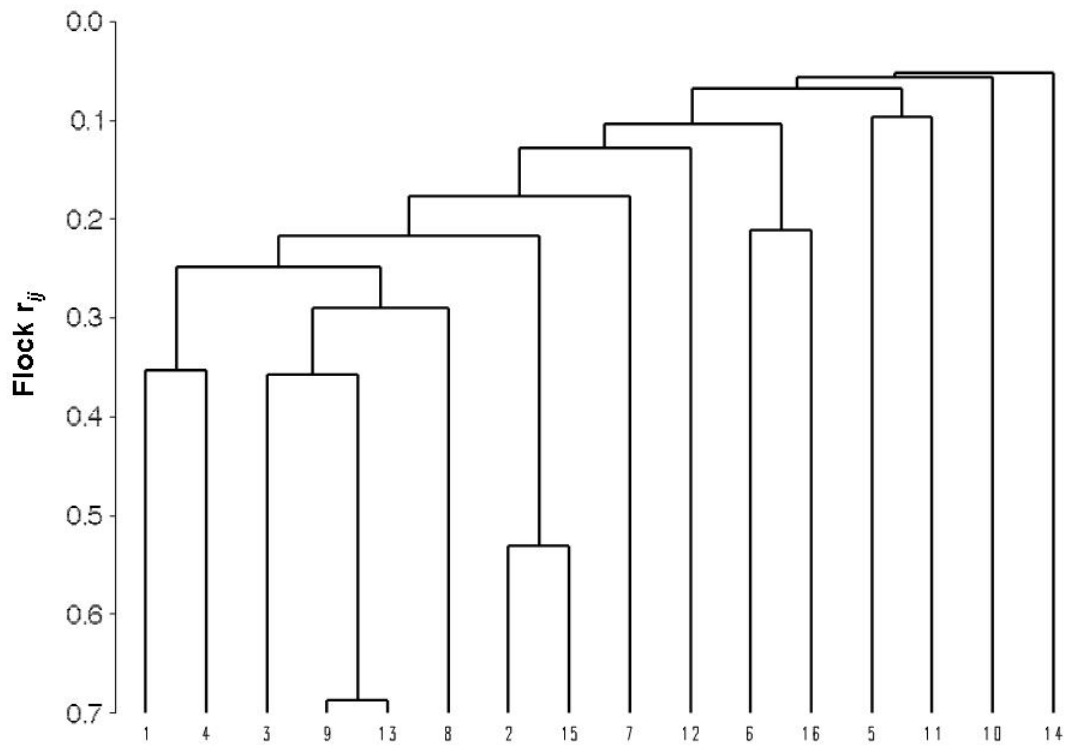


Figure 5.4. Cluster analysis of active National Sheep Improvement Program Targhee flocks where groups are merged at their average distance (flock r_{ij}).

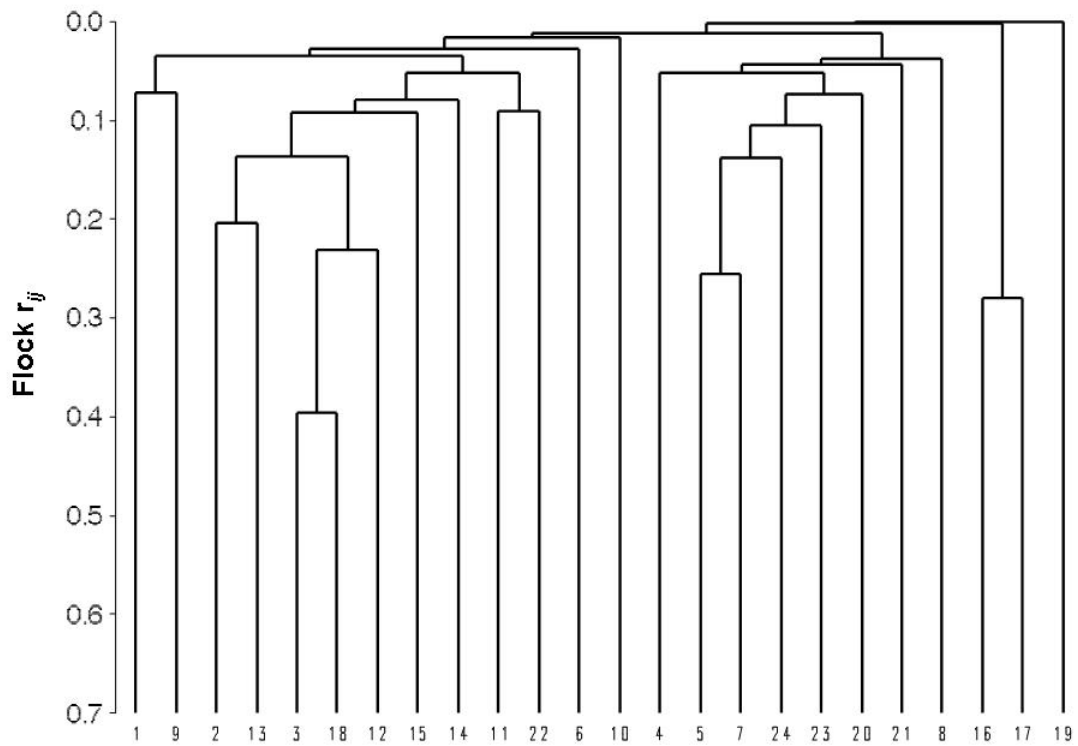


Figure 5.5. Cluster analysis of active National Sheep Improvement Program Suffolk flocks where groups are merged at their average distance (flock r_{ij}).

CHAPTER 6

General Discussion

Establishing connectedness is potentially important in all domesticated livestock species undergoing genetic evaluation. At the same time, connectedness generally is not a problem in several of these species due to the high level of AI use (dairy cattle) or because proprietary lines are selected in isolation with no intention of comparing EBV across production units (swine and poultry). It is likely the AI use in beef cattle has increased enough over the last 10 yr to alleviate most of the risk in comparing EBV across herds, though further research in some breeds may be warranted. However, as genetic evaluations across breeds and in commercial cattle come to fruition, connectedness among beef cattle herds may become more important. Small ruminant livestock species have the most risk of insufficient connectedness. Genetic evaluation is still relatively young in sheep and almost non-existent in most other small ruminants. Prior to the initiation of the National Sheep Improvement Program (NSIP) in 1987, performance recording within U.S. sheep flocks was largely nonexistent or exclusive to individual flocks. The remainder of this discussion relates to establishing connectedness in sheep flocks.

As found in the previous literature and the studies conducted in this dissertation, connectedness was necessary in order to remove bias between flocks simulated to have different genetic means. Whether or not genetic group effects are fit, other investigators show connectedness improves the accuracy of prediction of breeding values by reducing the mean squared error of comparisons of animals across flocks. If genetic group models are used, the mean squared error decreases due to a lower standard error of the estimated genetic group solutions. If genetic groups are not fit, then connectedness will reduce the bias in EBV (and thereby, the mean squared error) because the genetic means of founder animals are more accurately estimated.

The analytical and simulation results of this research provided further evidence of the reductions in bias due to improved connectedness. The bias between homebred sires in two different flocks was analytically derived under scenarios in which different linkage

strategies were used to tie the flocks together in a single generation. The flocks were linked by using either a common reference sire or full- or half-sibling rams in each flock. With 90 progeny per flock, the bias decreased by as much as 60% when the flocks were linked by reference sires. However, bias only decreased by 41% when linking using half-sibs. Asymptotically, with infinite flock sizes, it was possible to remove all bias using reference sires. However, even in this extreme case, bias could only be decreased to about 33 and 44% of the mean difference between the flocks when linkage was through single pairs of full- and half-sib rams, respectively. Based on these results, it seems difficult to remove bias completely regardless of the type of link between flocks in only one generation when flock sizes are small (<100 progeny per year).

However, through simulation of different forms of sire referencing schemes, it was shown that bias could be virtually eliminated after 5 yr of participation in an AI or natural service sire referencing scheme, even when flock sizes were small. If restrictions were relaxed and flocks only were required to participate in the scheme in two of every three years, it took 10 yr to achieve the same level of bias reduction. When flocks completely discontinued participation in the cooperative breeding scheme, the reduction in bias which had been achieved was maintained; that is, bias was not re-introduced into the system as long as pedigree and performance recording continued after the flocks disengaged. These results are encouraging since they show that risk of comparing animals across flocks can be avoided by actively exchanging germplasm across flocks over a relatively small number of years. Producers who wish to discontinue an active sire exchange program can do so with only minor risk that future comparisons of their animals' EBV with other flocks will be biased. Of course, this result assumes that the producer continues to actively collect pedigree and performance information for incorporation in the genetic evaluation system, and that animals they purchase do not alter their flock genetic mean dramatically.

If flocks use animals from outside the system with unknown pedigree relationships and performance, there is a chance that connections will have to be continually updated because these new base animals may change the flock genetic mean. In the simulation studies, this was not the case because the outside animals were assumed to come from a population with a common genetic means, thereby causing flocks that

used them to regress toward this common mean. This situation is not unlikely if flocks have similar breeding objectives. If the flocks are working toward a common goal, producers are likely to select animals that are of a similar biological type. If flocks have different breeding objectives, this will not be the case and connectedness will have to be continually re-established as flocks drift away from each other. However, if the flocks are truly working toward different goals, and especially if those goals are antagonistic, comparison of their EBV may be of minimal importance anyway.

With ‘real’ data, true breeding values are unknown and thus bias in their estimation impossible to calculate. In order to assess risk of comparing animals across management flocks, connectedness measures are required. Based on the results of the analytical portion of this research, Laloë’s (1993) coefficient of determination had the strongest relationship to bias in the genetic evaluation. However, this statistic is difficult to obtain in practice with large data sets because it requires the calculation and storage of the numerator relationship matrix for the whole pedigree. Therefore, two alternative measures were proposed: 1) the prediction error variance (Kennedy and Trus, 1992) of the difference between mean flock EBV; and 2) the flock prediction error correlation (flock r_{ij} ; Lewis et al., 1999). From the analytical results, the relationship of flock r_{ij} to bias depended on the type of connections used to link flocks (reference sire vs. sibling links). However, when using the simulated data to evaluate the efficiency of different types of sire referencing schemes, only the flock r_{ij} had a consistent relationship to bias across all types of scenarios. When reference sire links are the most prevalent form of connection, as in sire referencing schemes and as would be suggested to increase connectedness in NSIP, flock r_{ij} can be calculated between pairs of flocks to provide a level of confidence in comparisons of EBV across flocks. From this study, benchmarks of 0.05 and 0.10 were chosen to establish levels of ‘good’ and ‘superior’ connectedness. These levels corresponded to 20 and 10% of the bias remaining in comparisons of EBV across flocks, respectively.

Using these benchmark levels, connectedness was evaluated in the Targhee and Suffolk flocks participating in NSIP using their weaning weight records. Connectedness in the Targhee breed was very good overall, achieving an average level of flock r_{ij} that was well above the 0.10 benchmark. Flocks which had participated in NSIP since at least

1990 had increased in connectedness over time due to frequent use of rams in common and the transfer of rams born in one flock to other participating member flocks. In the Suffolk breed, connectedness was much lower and the flocks were seen to be segregating into two predominant clusters with moderate within cluster levels of flock r_{ij} ; the ram exchange within the Suffolk breed was thus predominantly confined to within these clusters. The exact reason why these clusters formed is unknown, since both contain flocks from a large geographic region, but it is likely that the breeding objectives and desired biological types of Suffolk differed between the two clusters. The fact that connectedness had not increased between members of the separate clusters despite their participation in NSIP since at least 1990 is further support of this argument; these breeders apparently have little interest in the sheep being produced in the other cluster.

If producers wish to increase their connectedness with other flocks because of concerns about the quality of their EBV comparisons, flock r_{ij} provides a tool to achieve this goal. By buying rams from flocks with high levels of flock r_{ij} , they can quickly connect their flock to the rest of the breed. Flock r_{ij} can also be used to identify clusters of flocks, as in the Suffolk breed. If separate clusters of these flocks were not intentionally avoiding the exchange of animals, their connectedness can be improved relatively quickly through the systematic trade of rams; the efficacy of that approach is demonstrated by the Targhee breed and by the simulation results presented.