The benefits of across-flock analysis

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ABSTRACT

Recent and current developments by Sheep Improvement Ltd (SIL) to provide animal evaluations for a wide variety of flocks using Best Linear Unbiased Prediction (BLUP) methods have encouraged breeders to compare animals bred in different breeding flocks. The data requirements and analytical models needed for BLUP to handle this task are discussed with major emphasis on sire-referencing as a method for achieving adequate genetic linkages among flocks by which animals bred in different flocks may be compared. Despite the high ability of BLUP to accommodate this task and the benefits perceived by many breeders, few specific studies of potential benefits for particular breeding schemes have been reported. In general terms, the impact of across-flock evaluations on annual rates of genetic gain varies for different traits, mating strategies, flock and industry structures. They may not always be cost effective in comparison to within-flock performance selection, especially for larger flocks and when the costs of implementing the flock structures needed to make them accurate and effective in evaluating and disseminating genetic merit are taken into account.

Keywords: across-flock; sire referencing; BLUP evaluation; breeding schemes.

INTRODUCTION

Benefits of across-flock analysis are discussed in relation to the data processing procedures available and under development for Sheep Improvement Ltd (SIL). SIL is a web-based animal recording scheme drawing together a number of disparate animal recording and genetic evaluation ventures previously servicing New Zealand's sheep industry. It provides access to a single database of pedigree and performance information and a common suite of animal evaluation software (Cruickshank, 2003). These developments have encouraged breeders to compare animals born in different flocks. This has been for various reasons: to introduce superior animals from outside flocks; to improve the accuracy of evaluations, especially early evaluations of sires introduced from outside flocks; to select replacement animals more intensively from a bigger pool of candidates; and to benchmark their animals against those in other flocks.

SIL's animal evaluations are based on Best Linear Unbiased Prediction (BLUP) which has a number of advantages for animals born and raised in different management groups over the selection index methods used previously. It is useful to review some of the technical and operational features of BLUP. Indeed, if the requirements of the BLUP method are not met by the data, some of the potential benefits of across-flock animal evaluations may be incomplete or not be realised at all.

FEATURES OF BLUP

Contemporary Groups

BLUP seeks to estimate the relative genetic merit of animals by assuming that each performance record (P) is made up of an additive genetic (G) and an environmental (E) component: $P=G+E$. Genetic improvement operates on the G component, the E component being a source of confusion to selection decisions through bias or reduced accuracy of the breeding value estimates (BV) of the G effects. The impact of the E effects can be reduced by ensuring that animals are allocated to contemporary groups (CG, e.g., birth rank, rearing mob) within which each has equal environmental opportunity, so that BLUP can estimate and adjust for CG effects at the same time as it estimates the BVs for each animal. How well BLUP does this depends on how well a particular set of BV effects can be untangled from a particular set of E effects using the statistical approach that is embodied in the evaluation model set-up by the SIL system. The effectiveness of BLUP in achieving this critical step depends on the size of the CGs and the magnitude of their effects, on how well genetic effects (e.g., sires and dams) are linked across CGs through genetic relationships among the animals being evaluated. Many of these features of the data are determined by the way breeders design their breeding programmes and record animal evaluation details as part of the data they provide for analysis.

The same principles hold for across-year and across-flock analyses (Garrick, 1991). Years and flocks become criteria used to define the CGs, each of them having, in addition, their own particular set of sex, mob, treatment group, *etc.* codes of the sort needed for within-year, within-flock analyses. For mixed-aged breeding flocks of reasonable size in which ewes are used repeatedly as dams over several years, the question of adequate genetic linkages over years is seldom an issue, especially when sires also are used more than once. Flock linkages however, need to be checked - many flocks may have no sires or dams in common over a finite time period (discussed below).

Information on relatives

SIL's animal-model BLUP procedures utilise all genetic relationships coming from the pedigree information exported from the database for inclusion in the analysis. They improve the accuracy of separating G from E effects and, thus, the accuracy of BV estimates because of the association among G effects for animals with common ancestors. Close relatives (parents, progeny and sibs) are of greatest value. Sire progeny records are

particularly valuable because each sire can have many progeny as contemporaries (especially under AI) spread across different management groups.

The use of reference sires to link flocks using a BLUP analysis is essentially progeny testing with progeny distributed across several flocks. It is usually more accurate than individual selection provided that environmental influences common to members of the same progeny group but different for members of other progeny groups are minimised or able to be well estimated from the data. The accuracy of a progeny test increases with the number of progeny per sire, in general terms about five progeny being needed to equal selection on the sire's own record (Rae, 1989).

The benefits of information coming from different relatives depend on the heritability of the trait, being higher for less-heritable traits, and are particularly useful for traits that can only be measured in one sex. Information on genetically correlated traits can also be useful for lowly heritable traits and for traits difficult to measure in live animals. These sources of information are part of the evaluation models set up by SIL, being provided as parameters describing variation and associations for both G and E effects. They are used to weight the phenotypic information coming from different relatives (and traits) according to the amount of variation and the relative accuracy of each source. Less reliable sources of information are regressed further towards zero (no emphasis) compared with more reliable sources.

The use of information on all available relatives has often been a source of confusion to breeders in early years of exposure to BLUP. This is because BV estimates will change (in either direction) as new information is incorporated into the evaluations.

Effects of selection and non-random mating

The inclusion of information on relatives is particularly useful for accounting for the effects of selection on genetic merit provided that the traits being analysed are those on which selection was based or are closely related to the selection process. This can be especially important when animals are screened in from an outside flock, provided that the CGs are linked and all contemporary animals with data are included in the across-flock evaluation. Inclusion of dams' information can also help to allow for the effects of non-random mating on the evaluation of sires; it can allow matings among elite sires and dams to be included in the analysis.

Across-year genetic trends

Across-year evaluations can be of considerable help in optimising the age structure of a breeding flock. Graphs of flock average breeding values by year of birth can also be used to show estimated genetic trends in particular traits. These provide breeders and their clients with retrospective evidence of the success of a breeding programme over a finite time period from the genetic base that a particular analysis represents.

The genetic base

BLUP breeding values are estimated relative to a base value of zero. Pedigrees are traced back to base animals whose pedigrees are unknown (not provided to the analysis). BLUP sets the average genetic merit of these animals to zero. All animals have their breeding values expressed relative to this base, taking account of the selection that has occurred, so that if genetic progress is being made subsequent crops of animals will tend to have more positive BVs than animals bred earlier. This makes the evaluation of genetic trends a simple task, even when, as in SIL, breeding values are all adjusted by the same amount so that zero values represent the average level of a more recent birth year (currently 1995).

Some flocks are made up of ancestors of quite contrasting average genetic merit, for example different breeds. This can cause bias to BV estimates if these large average genetic effects are regressed as if they were typical within-breed sources of genetic variation. SIL is currently developing a genetic groups approach in which these average G effects are estimated separately by the analysis and added to the within-group BLUP solutions. Analysis models using genetic groups are also appropriate for handling animals coming from distinct strains of the same breed.

A similar approach is being developed for handling bought-in sires but coming from flocks at a time that is quite removed from the base appropriate to the home flock. The aim is to avoid having highly selected animals from outside flocks receiving initial estimates below their potential and often tending to improve (rather than to go in either direction) as progeny information becomes available, as well as to allow different flocks to have a different genetic base.

Thus, given the adequacy of the genetic ties, an across-flock BLUP analysis can improve early evaluations of bought-in animals at several different levels. First, by including in the analysis information on the contemporaries of introduced sires and dams, but not necessarily in the BV report (for confidentiality reasons). In practice, a wider window of outside data would usually be required to capture the genetic relationships needed to link flocks. Second, information on the relatives of animals introduced from outside flock(s) could often add useful additional information if an even wider net were to be put around outside data. Third, such additional data from outside flocks could also be used to incorporate strain differences using a model embracing genetic groups.

SOME GENERAL OPERATIONAL GUIDELINES

Flock connectedness

The extent to which SIL could be developed along these lines depends not only breeder sensitivities, but also on having knowledge of the connectedness of different flocks in order to judge their suitability for inclusion in an across-flock analysis (Mathur *et al.,* 2002). The connectedness reports being developed for SIL are essentially a measure of the risk associated with the analysis of data from other flocks. Also useful, especially for breeders seeking to strengthen their genetic linkage to particular flocks through sire referencing, are two-way tables of the distribution of progeny numbers by sire and

contemporary group.

Sire-referencing guidelines

Breeding Matters (1994) recommended at least two reference sires to reduce the risks of infertility on progeny numbers and suggested aiming for at least 20 but preferably 30-50 progeny from each sire in each flock. It also gave guidance on which rams might be used and on when and how they might be mated, and which sort of scheme a breeder might seek to join. For small flocks in the UK, inseminating each of two reference sires to 15 ewes was the aim in early years of many schemes (Simm, 1998). These are very general guidelines and are not as useful as those coming from specific connectedness investigations and more-focused studies of optimal scheme design.

Other important operational guidelines include reminders that estimated breeding values are only comparable when derived from the same across-flock analysis and that these can change as new data and new relatives become available. Since breeding values are estimated for every animal included in the pedigree file, this applies to ancestors as well as to current animals, even those without new information if they are linked to the animals with new data, or even if they are not and the base changes from one analysis to another.

IMPACT ON GENETIC PROGRESS

Without specific details on the goals and structure of a particular breeding programme, potential benefits of across-flock genetic analysis can only be discussed in relation to the above background considerations on how BLUP works and some of the key issues arising from the structural relationships of participating flocks. Very few studies have been reported.

Introduction of animals from outside flocks

Breeders often seek to benchmark their flock against outside flocks in attempts to remain competitive by assessing how well their animals are performing in relation to those from other flocks. Ignoring important sire x flock interactions (Wickham, 1998), across-flock sire-referencing can be one way of increasing the effective number of progeny per sire, while at the same time evaluating a reasonable number of sires. Miraei Ashtiani & James (1992) demonstrated that prediction error variances for estimated breeding values for non-reference sires tended to be minimal when about one third of all progeny were allocated to reference sires. The optimal proportion tended to be higher for lowly heritable traits (0.40 for $h^2 = 0.1$), than for highly heritable traits (0.28 for $h^2 = 0.5$). For mating ratios giving 50 progeny from each sire, the proportion was also higher for small evaluation schemes (150 total progeny), compared with larger schemes (450 progeny): 0.39 versus 0.28, respectively.

Introductions of sires from outside flocks are likely to be of greater value in small compared with larger flocks because of additional concerns over the breadth of the genetic base (inbreeding).

Increased selection intensity, selection accuracy and annual rates of genetic progress

Increased selection intensity among sires arises from the greater number of candidate sires in an across-flock analysis. But more progeny per reference sire means fewer progeny per homebred sire or fewer homebred sires. Furthermore, it takes time for the progeny to reach the age when the trait of interest can be measured. Blair's (1989) example calculations for dual-purpose ram breeding flocks of moderate size demonstrated some of these principles. He compared estimates of annual genetic gain from across-flock sire referencing (10 flocks of 500 ewes each), for either fleece weight (FW) or number of lambs born (NLB), relative to those to be expected from selection within a single flock of 500 ewes mated to five new sires each year. Within-flock selection gave annual genetic gain estimates of 0.068 kg for FW and 0.030 lambs/ewe for NLB. For either trait, annual genetic gain was lower than this base for flocks linked by two sires mated to 20 ewes in each flock, the additional 460 ewes being mated to each of 20 homebred sires (i.e., 8% of ewes mated to reference sires). When the two reference sires were each mated to 50 ewes and 10 homebred rams to 40 ewes each (10% of all ewes mated to reference sires), annual rates of gain were improved by 4% for FW and 20% for NLB. The percentage increases when the two reference sires were each mated to 150 ewes and 10 homebred sires each to 20 ewes (60% of ewes mated to reference sires) were 19% and 37%, respectively. These examples were very broad and did not consider all of the issues. For example, they neglected the impact of different degrees of reference linkages over flocks and years, of flock and age group differences in average genetic merit, and of the very deliberate use of elite matings of the sort undertaken in central nucleus flocks of group breeding schemes. Nevertheless, they do indicate the importance of making good use of high-performing animals as reference sires if a widespread dissemination of their superior genes is to be achieved. As emphasised by Garrick (1989), if the increase in selection intensity or selection accuracy obtained by sire referencing is not greater than the increase in generation interval resulting from using progeny tested sires, overall rate of genetic gain may be reduced relative to within-flock selection on individual merit. Artificial insemination, by allowing more progeny and greater selection differentials for identified elite sires than can be obtained in each flock under natural mating, will assist towards this goal. However, this brings extra costs to the breeding programme.

Across-flock sire referencing has developed considerably in the UK in recent years, especially for meat breeds where pedigree flocks are small and within-flock selection intensities low (Simm, 1998). The same is true in Australia (Banks, 1997). Across-flock sire referencing can be useful under these circumstances, especially where common selection goals serve to encourage a widespread use of proven sires. Similar developments are occurring in this country (Johnson *et al.,* 2001), some schemes embracing linkages to central progeny test flocks for a more direct evaluation of carcass traits for sires

representing different breeds (Campbell & Jopson, 2003).

There is little published guidance on optimal design of across-flock breeding schemes, both in general terms and for specific goals. The development of integrated mate allocation and selection procedures should provide the tools needed to improve this situation for specific goal-focused outcomes (Hayes *et al.* 1997, Piper, 2003). These methods may be useful in accommodating DNA and other new-technology evaluations of genetic merit as well.

Additional benefits

In the early years of a sire referencing scheme, the breeders who benefit most are those whose flocks are of the lowest genetic merit. As well as broadening their genetic base for improved long-term advantage, they come to invest in the genetic merit provided by sires coming from flocks of superior merit. Once these flocks have caught up, benefits arising from the size of the scheme as a whole apply to all flocks in the scheme (Garrick *et al.*, 2000).

Across-flock evaluations are often perceived to offer breeders marketing advantages. While this can certainly be real, at least in the short term, for flocks of high average genetic merit, it is unlikely to be true for the scheme as a whole, other than through growing buyer confidence in collective rather than individual breeder enterprise. Both can, nevertheless, be of overall benefit to the industry as a whole.

Similar 'catch-up' arguments also apply to ram buyers. Hopefully, such initial incentives will serve to improve the focus of ram buyers on the long-term goals of their breeders, rather than just on the historical trends or good fortune built into their breeders' current evaluations.

CONCLUSIONS

- BLUP technology is capable of comparing genetic merit across different management groups and flocks, provided that breeders record these details for their inclusion in the evaluation model and that the level of genetic linkages across them is adequate. In general terms, balanced sire reference designs achieving 33% of progeny from reference sires provide the most accurate comparison of new rams in different flocks.
- Annual long-term rates of genetic improvement for an across-flock scheme as a whole, depend on interactions among selection accuracy, selection intensity, and generation interval.
- Little published guidance is available for the New Zealand sheep industry.
- For dual-purpose sheep in flocks of moderate size an even more widespread use of high-performing reference rams than is needed for effecting adequate flock linkages, is likely to be needed to ensure effective dissemination of superior genetic merit to participating flocks. AI can assist this, but may not be cost effective. Breeders will need to be in reasonable agreement on breeding goals if this sire-dissemination process is to be effective for traits of interest to the scheme as a whole.
- BLUP methodology is also capable of handling genetic differences among breeds and strains, including flocks of different average genetic merit. It can, thus, provide a better focus on flocks that have been most effective in targeting particular selection goals.
- Inbreeding considerations provide additional motivation for development of across-flock breeding schemes, especially for small flocks. New integrated selection and mate allocation evaluation methods should also help in planning effective elite mating designs that transcend participating flocks of different average genetic merit. Their inclusion of cost outcomes will be of particular value.
- Across-flock analyses also offer ram-marketing advantages, mainly of short-term benefit to particular flocks. They also provide 'catch-up' opportunities to ram buyers. Both will impact on the general level of industry awareness of animal and flock variations in genetic merit.

Thus, across-flock analysis has the potential to improve the accuracy of breeding value rankings and can do so for a wide range of industry circumstances involving genetically linked flocks. By extending selection decisions across a larger pool of candidates it can greatly improve selection intensities as well. But how well these potential benefits can be realised as improved rates of genetic improvement depends on the design and implementation of the breeding scheme that the across-flock analyses serve.

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