

BEST LINEAR UNBIASED PREDICTION (BLUP) AND THE DESIGN OF BREEDING PROGRAMS

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SUMMARY

The adoption of Best Linear Unbiased Prediction (BLUP) procedures for the evaluation of the genetic merit of individuals has important ramifications for the design of breeding programs. Several developments in short-term quantitative genetic theory have provided the basis for a more precise examination of the outcome of alternate breeding strategies utilising BLUP. A large study is currently underway to combine these various developments with stochastic simulation procedures for use in defining the likely impact of the combined adoption of BLUP and artificial breeding technology on optimum designs for breeding programs.

INTRODUCTION

One of the major advances in animal genetics in recent years has been the development and application of BLUP procedures for the evaluation of the genetic merit of breeding animals from field performance records. Much of the potential power of BLUP has not yet been widely applied to practical breeding programs, largely because of the computational costs involved. Nevertheless, as Quaas and Pollak (1980) point out, the history of BLUP application has been that more of the theory becomes relevant with the continuing development of computing strategies and increases in computer power. Three beef cattle breeds in Australia are now utilising various BLUP procedures, those employed by the Australian Simmental being the most advanced (see Graser et al. 1982). BLUP procedures are also being developed for regular use in the Dairy Industry under the Australian Dairy Herd Improvement Scheme (Anon. 1983). The adoption of BLUP technology has important ramifications for the design of breeding programs and work is currently underway to define these more precisely.

BEST LINEAR UNBIASED PREDICTION

Of all possible linear procedures for the estimation of breeding values BLUP will be the best (being unbiased and having minimum variance) provided the analytical model used makes correct allowance for all important environmental and genetic biases (Henderson 1973). The general flexibility of BLUP allows the formulation of a mathematical model to represent each particular situation, making optimum use of all information on each individual and its relatives and simultaneously adjusting for systematic biases such as dam age, season of calving, sex, and herd management group differences. If adequate connectedness exists among performance data valid comparisons of breeding values for individuals in different herd-year-season (HYS) groups can be made, even though the overall data structure may be very unbalanced. Connectedness can either be direct, where within-HYS comparisons exist, or indirect, where individuals in different HYS's are directly 'linked' to common ('reference') individuals. The accuracy of breeding value estimates obtained from the simultaneous consideration of within-HYS comparisons and between-HYS comparisons using BLUP will be lower than that predicted by classical selection index theory because of the error involved in the estimation of group differences, which is largely dependent on the degree of connectedness among the groups (Foulley et al. 1983).

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Genetic relationships between animals may contribute considerable information to the prediction of breeding values and can be incorporated into BLUP using the Numerator Relationship Matrix (NRM) (Henderson 1975). Taylor (1981) showed that genetic trend resulting from selection can be adequately accounted for in BLUP by the inclusion of the NRM and/or use of genetic grouping to represent sub-population differences over time. In addition, the inclusion of sires and maternal grandsires in a BLUP analysis, along with the use of the NRM substantially eliminates any biases due to non-random mating (Fimland 1983). A useful extension from the application of BLUP procedures is the possibility to compute 'estimates of annual genetic trend from predicted age group differences, providing a direct monitor of what is happening in practice.

Schaeffer (1979) has drawn together many of the theoretical and statistical concepts of the linear mixed model techniques used in BLUP. McClintock and Taylor (1982) outlined some of the problems associated with its application to practical situations and highlighted areas where future developments could take place.

DESIGN OF BREEDING PROGRAMS

The majority of earlier studies on the optimization of the design of breeding programs were based on the classical model of Dickerson and Hazel (1944) and Rendel and Robertson (1950) for the prediction of long term rates of selection response over each of the four pathways of gene transmission (male and female parents to male and female progeny). Subsequently, Hill (1974) presented a more precise approach based on matrix algebra to describe the flow of genetic improvement between age groups and sexes in the early years of newly initiated selection programs for populations with overlapping generations. This procedure is particularly useful when predicted returns are discounted over time, as the fluctuating responses obtained in the early years become relatively more important. Johnson (1977a and b) showed how Hill's procedure could be applied to the prediction of fluctuating rates of inbreeding and of genetic drift in the early years of a selection program.

Using the logic introduced by Bichard et al. (1973) to account for the effects of genetic trend resulting from selection in age-structured populations, Hopkins and James (1977) extended Hill's (1974) methodology to predict genetic gains and optimum selection procedures in situations where correct allowance is made for the effects of genetic differences between progeny from parents of different ages, and between individuals of different ages. In a further contribution, Hopkins and James (1978) provided formulae for the prediction of selection response and optimum structures for open nucleus breeding schemes. This theory can also be readily applied to determine optimum designs for less formally structured hierarchical mating systems (James 1980).

When BLUP procedures are used for the estimation of breeding values, the problems associated with the effects of genetic trend on comparisons of individuals themselves of different ages or having parents of different ages, can be largely accounted for (Hill 1977). Consequently, selection decisions can be made solely on predicted breeding value and the number of years for which individuals should remain in a population need not be specified in advance (Hill 1981). In this situation the need to emphasise generation interval when implementing breeding programs is no longer applicable as outstanding individuals can be validly retained for many years regardless of their age. Hammond (1982) pointed out that the combined use of BLUP and artificial breeding techniques, which allow higher reproductive rates, provide the potential for greatly enhanced selection intensities and small effective population size such that the impact of inbreeding and reduction in additive genetic variance becomes more important in deter-

mining optimum designs. Hammond emphasised the need for further detailed analyses to clarify the ramifications for the design of breeding programs of the adoption of these technologies.

CURRENT WORK

A large study is currently underway combining the various developments in short-term prediction theory to define optimum designs for breeding programs incorporating BLUP procedures and artificial breeding techniques (eg., artificial insemination (AI), embryo transfer). For the purposes of this study, three categories of breeding program have been defined:

1. Small, closed populations (eg., within-herd breeding schemes).
2. Multi-herd schemes with minimum use of AI (eg., progeny testing schemes using reference sires).
3. Industry-wide schemes with widespread use of AI (eg., large-scale progeny testing schemes).

In order to evaluate alternative designs for each of these situations, rates of genetic response, of inbreeding and genetic drift and of reduction in additive genetic variance are obtained for a range of important variables in population structure and breeding policy. Where progressive culling strategies are considered the sequential multi-stage index selection theory developed by Cunningham (1975) is used to approximate the accuracy of selection at each successive stage. Prediction of genetic differences among age groups and of the appropriate proportions selected from each group is obtained using the theory of Hopkins and James (1977). A generalisation of the open nucleus breeding scheme framework of Hopkins and James (1978) is applied in the analysis of hierarchical breeding structures involving assortative mating and progeny testing.

A comprehensive stochastic simulation model has been developed for the generation of individuals in populations exposed to selection programs in which BLUP procedures are used. Replicated simulations of various designs for a particular population and breeding objective will complement and validate the deterministic studies and provide the opportunity for further investigation of the influence of chance, selection and connectedness of performance data on the mean and variance of predictions in successive years of a breeding program.

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