The effects of BLUP evaluations, population size and restrictions on selection of close relatives on response and inbreeding in egg-laying poultry.

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Introduction

While many factors play a part in optimising a commercial breeding nucleus, the three most important are 1/ rate of response, 2/ rate of inbreeding and 3/ size of the nucleus. The first two determine the technical success of the nucleus, while the latter is a principal determinant of cost. Obtaining the value (cost) of response and nucleus size is relatively straightforward. The cost of inbreeding is more difficult to find. This because inbreeding results in the separate effects of reduced genetic variation and inbreeding depression. Reduced genetic variation decreases selection response, the effect becoming more important over time, so that associated costs depend on the time horizon. Estimates of the effects of inbreeding depression have a high degree of uncertainty. The importance of inbreeding depression will also depend on other factors such as length of time the line will remain closed to immigration and whether the multiplier and/or commercial product is pure or cross-bred. As a consequence, inbreeding rates are often treated as an uncertain risk factor to be minimised while maintaining a rapid response rate.

Animal model best linear unbiased prediction (BLUP) of breeding values is becoming the method of choice for genetic evaluation in most livestock species (see ADSA, 1989). Animal model BLUP uses information from all relatives and simultaneously estimates (and thus accounts for with maximum accuracy) fixed effects. Thus BLUP evaluations are the most accurate estimates of breeding values available. In the short term, maximum accuracy should lead to maximum response. But, by maximising use of information from relatives, BLUP also leads to high correlations of estimated breeding values of close relatives, giving high co-selection probabilities and increased rates of inbreeding. This causes reduced genetic variation which can reduce
long-term responses to selection to below those of less accurate methods of selection (Quinton et al., 1992).

Sorensen (1988) simulated a pig breeding structure and found that BLUP selection gave 4% to 30% increases in response over selection indexes, depending on the heritability and the exact model used for index selection. Much of the benefit of BLUP was due to more accurate estimation of the large number of fixed effects and better estimation of breeding values across multiple overlapping cohorts of animals. However, these benefits may not be important in an egg-laying poultry population where there is often little movement of breeding stock across generations and few fixed effects to be estimated. Although, Sorensen (1988) did not examine this, it is likely that the increase in inbreeding with BLUP has little to do with its handling of fixed effects. Thus in a poultry population, BLUP may have little effect on accuracy of selection but substantial effect on inbreeding.

The two most widely used methods of controlling long-term inbreeding rates in practice are to increase breeding population sizes and to place restrictions on the number of relatives chosen for breeding. (Restrictions on mating of close relatives reduces inbreeding in the progeny but have no effect on long-term inbreeding rates.) Increased population size will increase costs and may increase selection response slightly by reducing finite sampling effects. Imposing restrictions on selection reduces response by reducing the effective selection intensity. Increasing the mating ratio (number of females mated to each male) at a given female population size increases the selection intensity on the male side but also increases inbreeding rates due to smaller effective population size.

In this paper we present results on, 1/ simulation of the effects of BLUP evaluation in an egg-laying poultry breeding structure, and 2/ an examination of multi-trait selection in populations of varying size, mating ratio and restrictions on selection of relatives. Much of this work has been published by Jeyaruban (1992) and will appear in refereed journals in the near future (Jeyaruban and Gibson, in preparation).

Methods

Stochastic computer simulations were constructed of a typical egg-laying poultry population under selection. Quantitative additive genetic inheritance of exclusively sex-limited traits was assumed, with non-overlapping generations and progeny evenly divided between two hatches per generation. The effect of inbreeding on genetic variance was included, but the effects on phenotypic performance (ie inbreeding depression) were ignored. There were an average of 8 female (recorded) and 2 male progeny per breeding female with variation in family size corresponding to what was assumed to be a random loss of birds between birth and recording of about 10%, as observed in a commercial selection line. There were 10 generations of selection from an unselected base population, with 100 replicates per parameter combination for the single trait simulations and 50
replicates for multitrait simulations. Matings of full and half-sibs were avoided wherever possible.

BLUP evaluation was compared with selection indexes including information from full-sibs (FS) only or from both full and half-sibs (HS). Males had no information on their own performance, but a female's individual performance was included in her index. BLUP evaluation included all relationships to the unselected base generation (an animal model) with fixed effects estimated simultaneously. With selection indexes, fixed effects were estimated by raw means, and data adjusted for fixed effects prior to construction of the indexes. A single trait was simulated with heritabilities of 0.1, 0.2 or 0.5. The heritability was assumed known without error in the base generation, but no allowance was made with selection indexes for altered variances in later generations arising from gametic phase disequilibrium. There were 300 females and 30 males selected for breeding each generation, with restrictions on selection as at REST.A described below.

Since the above simulations showed that BLUP evaluations had relatively little effect compared to FS + HS selection indexes, to save computing time, multi-trait simulations were based on use of multi-trait FS + HS selection indexes. The three traits, rate of lay, egg-weight and deformation were assumed to have mean values of 90.2%, 57.5g and 25.3 μm, standard deviations of 6.6%, 3.7g and 3.05μm, heritabilities of .18, .74 and .38, and economic weights, obtained from a modification to the profit function of Fairfull et al. (1991), of .176 $/bird/1%, .22 $/bird/g and .536 $/bird/μm. Genetic correlations between rate of lay and egg weight and deformation and between egg weight and deformation were, -.29, .44 and .13, with corresponding environmental correlations of -.12, -.11 and -.06. All combinations of three population sizes, 1536, 2784 or 4608 recorded females, and three mating ratios, 6, 8 and 12 females per male, were examined in all possible combinations with four sets of restrictions on the maximum number of close relatives selected for breeding, these being;

- REST.A 2 FS and 6 HS males, and 5 FS and 30 HS females,
- REST.B 2 FS and 6 HS males, and 3 FS and 15 HS females,
- REST.C 1 FS and 6 HS males, and 5 FS and 30 HS females,
- REST.D 1 FS and 3 HS males, and 5 FS and 30 HS females.

Results and Discussion

Results for BLUP vs index selection are illustrated in Figure 1 for response and Figure 2 for inbreeding, for a traits with heritability of 0.2. By generation 10, BLUP had given 3.1% and 8.3% more response than a FS+HS index and a FS only index. Corresponding relative increases in inbreeding coefficient were 14.8% and 33.7%. At a heritability of 0.1, increases in response were 5.8% and 17.9%, and in inbreeding were, 18.2% and 52.1%. While at a heritability of 0.5, increases in response were, 2.2% and 4.6% , and in inbreeding were, 10.3% and 17.2%.
With egg-laying traits, heritabilities generally lie in the range 0.3 to 0.7. In this range, BLUP gives little advantage in selection response over a family selection index including FS and HS information and incurs about a 10% increase in inbreeding rate. On this basis, there is little advantage and perhaps a disadvantage to using BLUP. A decision to move to BLUP selection will therefore be based on other considerations, such as cost of implementation, ease of computing, access to information on past and present status of the population and on marketing advantage of using the latest statistical technology.

For the multi-trait simulations, typical sets of economic responses and inbreeding coefficients are illustrated in Figures 3 and 4, for a population size of 2752, a mating ratio of 8 and four levels of restriction. Of the four levels of restriction, for all population sizes and mating ratio combinations, REST.A gave the greatest and REST.D the least response. However, the responses with REST.B and REST.C relative to each other and the other restrictions varied for different combinations of population size and mating ratio. In contrast, the relative inbreeding rates were always similar to those seen in Figure 4, with ranking from highest to lowest inbreeding rates being, REST.A, REST.B, REST.C and REST.D. The balance between response and inbreeding was always considered unacceptable with a population size of 1536; due to high inbreeding with non-stringent restrictions (REST.A) and poor response with other restrictions. Population sizes of 2784 and 4608 both gave acceptable combinations of response and inbreeding, but 2784 was preferred because of the lower costs associated with a smaller population size.

Figure 5 shows the responses at generation 10 for the twelve combinations of mating ratio and level of restriction for a population of 2784 (or 2752), and Figure 6 shows the corresponding average inbreeding coefficients. The optimum combination of
mating ratio and restriction will depend on the value given to response versus inbreeding. As a guideline, it is often desired to keep inbreeding rates below 1% per generation. Mating ratios between 6 and 8 with REST.A would meet this criterion and simultaneously maximise response. More stringent restrictions on selection of close relatives would give a proportionate reduction of inbreeding of at least 20%. But the associated loss of at least 10% in selection response is unlikely to be acceptable.

General Discussion

The simulations presented here attempted to mimic the basic structure of an egg-laying poultry population, being selected for additive genetic merit. The results clearly indicate that, in contrast to swine selection (Sorensen, 1988), there is little or no advantage in terms of response versus inbreeding to using BLUP genetic evaluations as opposed to more traditional family selection indexes. This arises because of the few fixed effects and non-overlapping generations in these poultry examples. In practice, there may well be a few males used across generations, based on their progeny test performance. With the egg-laying poultry population structure, and in contrast to a swine population with many cohorts, it would be relatively easy to correct for genetic trend with a selection index approach, and thereby avoid overestimating the genetic value of older sires. However, it must be admitted that animal model BLUP would do this automatically.

The principal disadvantages of BLUP evaluations are linked to the increased statistical complexity and concomitant increases in computing requirements. But with widespread in-house expertise and modern computer work stations, these problems are rapidly diminishing, even for very large data sets. The advantage of implementing BLUP is the flexibility it allows in examining past and present trends in the population. This
includes automatic estimation of inbreeding coefficients, since these are obtainable directly from the relationship matrix which is constructed as part of the BLUP evaluation procedure. The results presented here do not, therefore, indicate that BLUP should not be implemented, but merely that increased response rates should not be expected and that some increase in inbreeding will likely result.

The multi-trait simulations clearly indicate that there is little advantage to a population size of much over about 3000 recorded females, but reducing size much below this level would lead to unacceptable combinations of response versus inbreeding. Fairly relaxed restrictions on selection of close relatives, such as with REST.A, give rapid responses with acceptable levels of inbreeding at the recommended population size. But if smaller population sizes had to be maintained, more stringent restrictions would keep inbreeding within acceptable levels, albeit at a sacrifice of some selection response.

In general, while the imposition of restrictions on selection does reduce inbreeding rate, it pays a substantial cost in lost response and is therefore of limited effectiveness. A new recursive method of selecting individuals on a combination of estimated breeding value and average relationship to other selected individuals (Brisbane and Gibson, in preparation) may, however, make the imposition of restrictions obsolete. Preliminary results indicate that with traits that are not sex-limited, this new method can achieve about half the rate of inbreeding of the most stringent restrictions for about the same level of response. Performance of the method with sex-limited traits may not be quite as impressive, but should still yield substantial reductions of inbreeding and this is currently being investigated. Since this method automatically adjusts for achieved co-selection probability, the method of evaluation is irrelevant, and the disadvantage of BLUP in terms of inbreeding is removed. Also, since this method requires knowledge of the
additive genetic relationship matrix, and hence the computerised record keeping to enable this to be calculated, use of the new selection method will make implementation of BLUP evaluations that much easier.

References


Quinton, M.C., C. Smith and M.E. Goddard, 1992 Comparison of selection methods at the same level of inbreeding. J. animal Science, 70: 1060-1067

Questions to Drs. Gowe and Gibson

1993 POULTRY BREEDERS
ROUNDTABLE

Question Sheet

Speaker's name: John Gibson

Question by: Gerald Herbert

Question: Might selection for polymorphism for DNA markers (RFLPs) be helpful in avoiding increased homozygosity and, hence, some of the deleterious effects of increased levels of inbreeding?

Answer: John Gibson

I'm not sure that this question has ever been addressed. My feeling is that variation in actual heterozygosity among individuals with a given inbreeding coefficient will be relatively small in comparison to the variation in inbreeding coefficients among individuals in the population at a given time and, hence, that selection for heterozygosity of DNA markers would not be very effective at slowing inbreeding. But, this area is certainly worth investigating.
**Question Sheet**

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<tr>
<th>Speaker's name:</th>
<th>Dr. Gowen</th>
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<tr>
<td>Question by:</td>
<td>Ed Buss</td>
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<tr>
<td>Question:</td>
<td>How many hatches, one or two weeks for collection, are necessary for a valid estimate of fertility and of hatchability of fertile eggs?</td>
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<td>Answer:</td>
<td>In the study reported, we collected hatching eggs for 4 two-week save periods or 8 weeks totally up to 1993, when we had several test branch stations besides Ottawa. From 1964 to 1980, we only tested stock at Ottawa and hatched these populations from one hatch where we saved eggs for 21 days. Eggs for the oldest two weeks were bagged in Cryovac bags and gassed with Nitrogen to reduce hatchability loss from the long save period. Since we selected for fertility and hatchability on the pedigree record (i.e. the dam and sire family record), this was a quite adequate save period to give a good estimate of these traits.</td>
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Comment: In some populations of chickens, chromosome aberrations contribute considerably to early abortions. In highly selected populations of egg layers, the early abortion % is extremely low, apparently due to severe culling of low hatching individuals and families.

I agree that our evidence supports the reduction in the percentage of zero hatchability and very low hatchability families compared to the unselected controls as shown in the figures presented. However, this was achieved with low selection differentials and a low culling rate, not "severe culling". I suppose in some populations it may be necessary for a few generations to cull at a heavier rate if the abnormal chromosome aberrations had been allowed to accumulate or there had been no selection for these traits. However, the point was that a simple culling program is adequate to maintain these traits and it was not necessary, or the best way, to handle these traits by including them in an index.
Question Sheet

Speaker’s name: John Gibson

Question by: G. Herbert

Question:
While BLUP does not give much improvement in selection response over index procedures, is it not the case that it offers a large improvement over individual (mass selection)? Might the increased accuracy in prediction of breeding value decrease the variance of response between replicates?

Answer: John Gibson
Yes, BLUP should give better response on phenotypic selection. But, we assumed with sex-limited traits some form of family information must be used for male selection and, therefore, that most breeding programs would already be using some form of index selection.
Question by: Fred T. Shultz
Question: Would it be possible to include inbreeding depression in his model in order to assess what the effects would be on the selection of individuals? How much would inbreeding increases be slowed down and what would be the effect on superiority of BLUP over other systems?
Answer: John Gibson

Yes. Inbreeding depression could easily be incorporated in the model. Moreover, mixed model equations for BLUP can be written to account for this inbreeding depression which would give an additional advantage to BLUP. But, I would expect this advantage to be small since the variation in inbreeding coefficients within generations will be small provided mating of close relatives is avoided.
Speaker’s name: _______ Dr. Gibson

Question by: _______ Werner Hartmann

Question: _______ How might the conclusions from the model studies be influenced if selection on crossbred performance would be necessary (r<sub>maternal x pure</sub> &lt; 1.0 ≈ .5)?

Answer: John Gibson _______ Since crossbred performance would be recorded as a progeny test (to unrelated dams) with relatively high accuracy, BLUP evaluation would likely have even less advantage over a family index than in our simulations.
Question by: Ilan Levin

Question:
What is the extent of familial information used to compute the BLUP values, and is it a major component of the differences between the different methods of estimating breeding values?

Answer:
In conjunction with an animal model, BLUP uses information from all relatives included in the data. This may include several generations of ancestors. In practice, however, most of the information comes from the individual, its full- and half-sibs, its progeny (if available) and its parents. If a selection index already includes the important relatives, the advantage of BLUP is principally due to its ability to account for fixed effects, non-random mating and genetic trend.
Speaker's name:    Panel - Gibson & Gowe

Question by:       Jim Arthur

Question:      Some studies have failed to show an advantage for
selection indices vs. selection on individual records.

Could this be due in part to possible effects of recessive
deleterious genes with large effects? Can simulation

studies be run to account for these genes?

Answer: R. Gowe

There is more than one reason for the failure of some of
the studies in the literature to show an advantage for
selection indices over individual records for egg
production. As Harris et al. (1994, TAG 68:397) have
shown in a simulation study, the lymphoid leucosis virus
is responsible for the individual selection being more
effective than family selection for the trait egg
production that is influenced by this virus. These
authors thought this explained the literature results that
showed individual selection to be more effective than
family selection. There is another reason why family
selection, particularly full sib family selection, is less
effective than would be expected under the assumption
that the gene action is additive. For the trait egg
67:663) have shown that dominance and epistasis are an
important part of the genetic variance and these make
full-sib family means less useful than sire family means.
It is unlikely that major genes with large deleterious
effects would remain in a selected population, if index
selected, or if a simpler selection program is used
involving mostly individual selection.
1993 POULTRY BREEDERS

ROUNDTABLE

Question Sheet

Speaker's name: Drs. Gowe and Gibson

Question by: Bob McKay

Question: Should commercial breeding companies be using BLUP in their selection programs? Would culling on very poor livability families (post-hatch) maintain livability in your populations?

Answer: John Gibson Our results suggest choice of BLUP as method of evaluation should be based on reasons other than changes in response and inbreeding. Implementing BLUP has advantages in terms of ability to monitor selection and inbreeding in the flock and automatically will focus attention on breeding decisions. Provided expertise exists to understand BLUP and its limitations, were I running a breeding program, I would wish to have BLUP evaluations as routine.
Answer: Bob Gow

It is my opinion that culling for livability during the growing and laying periods, much like I have described for the traits fertility and hatchability, will maintain livability. There are more specific, direct approaches that should be used when selecting for major resistance genes associated with specific diseases. Nevertheless, for general non-specific mortality, the approach described for fertility and hatchability can be quite successful.