BALANCING SELECTION RESPONSE AND RATE OF INBREEDING BY INCLUDING GENETIC RELATIONSHIPS IN SELECTION DECISIONS

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SUMMARY

An iterative selection strategy, based on estimated breeding values (EBV) and average relationship among selected individuals, is proposed to reduce inbreeding with minimal effect on genetic progress. Stochastic simulation is used to compare rates of inbreeding and genetic gain with those of other strategies. For a range of population sizes and mating ratios, and for sex-limited and non-sex-limited traits, the new strategy gives the greatest genetic gain at a given rate of inbreeding and gives the least inbreeding at a given genetic gain. Where inbreeding is of concern, the new selection strategy always outperforms strategies currently in use. Where selection is currently by truncation on EBV with a restriction on the number of full sibs selected, the new strategy maintains similar levels of genetic gain and inbreeding with a reduction in population size of 10-30%.

INTRODUCTION

In most breeding schemes a balance between genetic gain and inbreeding is sought. Increased genetic gain in the short term is usually associated with increased inbreeding. However, this leads to decreased genetic gain in the long term, because inbreeding causes a decline in fitness and a loss of genetic variance. Three important developments in modern breeding schemes which increase short term genetic gain and inbreeding are; (1) evaluation using the records of relatives (e.g. best linear unbiased prediction using an animal model), (2)increased female reproductive rates (e.g. use of multiple ovulation and embryo transfer, or in-vitro embryo production), (3)selection of animals at a younger age, using pedigree rather than progeny information. This objective of this study is to describe a selection method designed to find an optimum balance between response and inbreeding, for a given population structure.

METHODOLOGY

Stochastic simulation of simple breeding schemes is carried out, using an additive infinitesimal genetic model, discrete generations of selection and random mating in a hierarchical paternal half-sib design. In each generation EBV are calculated using a family selection index of the individual, full-sib, and half-sib records. Four alternative selection strategies are simulated, each allowing a range of possible inbreeding and response rates. In the first strategy (OMIT) full-sib records are omitted from the index, and optimal weights are used for the remaining records. These weights are optimised in each generation to account for the effect of selection. Response and inbreeding are varied between breeding schemes by varying the number of full-sib records omitted. In the second strategy (SUBOPT), the individual and all sib records are used, but the weight on full-sib records is reduced, while the weight on the individual record is increased, so that the EBV remain unbiased (i.e. the regression of breeding value on EBV remains equal to unity). Within a breeding scheme, the index weights are constant across generations of selection. Response and inbreeding are varied between breeding schemes by varying the weight on full-sib records. Selection is by truncation on EBV for both OMIT and SUBOPT. In the third strategy (REST), the individual and all sib records are used, with constant weights across generations (optimum in generation 0), and

selection is by truncation on EBV with various restrictions on the maximum number of males and females selected from a full-sib family. REST is a commonly used strategy in animal breeding research and practice. In the fourth strategy (ADJEBV), EBV are calculated as for REST, but an iterative selection strategy is used which attempts to maximise an objective function

$$M = \frac{1}{2}\overline{EBV}_s + \frac{1}{2}\overline{EBV}_d - k\left[\frac{1}{8}\overline{a}_s + \frac{1}{4}\overline{a}_{sd} + \frac{1}{8}\overline{a}_d\right] \tag{1}$$

where EBV_s and EBV_d are the mean EBV of selected sires and dams, a_s, a_d and a_{sd} are the mean additive relationships among selected sires, dams, and between selected sires and dams, and k is a constant defining the weight on inbreeding relative to genetic gain in the breeding goal. Animals are selected initially by truncation on EBV. An adjusted EBV is calculated as

$$EBV_{s,i,adj} = \frac{1}{2}EBV_{s,i} - k\left(\frac{1}{8}\overline{a}_{s,i} + \frac{1}{4}\overline{a}_{sd,i}\right) \tag{2}$$

for male i, where $a_{s,i}$ is the mean additive relationship with selected males and $a_{sd,i}$ is the mean additive relationship with selected females. If the male is selected, the relationship with itself is included in the mean, but if the male is not selected $a_{s,i}$ is adjusted to account for its relationship with itself. The procedure for females is analogous. The objective function, M, is calculated. The unselected male with the highest adjusted EBV is then switched for the selected male with the lowest adjusted EBV, and M is recalculated. If M is increased the switch is accepted, otherwise it is reversed. The procedure is repeated in females. If switches are accepted, and d is the mating ratio, then d switches in females are made after each switch in males, and in each case the animal moved out of the selected group remains available for reselection. The final selected parents are obtained when M cannot be increased by switching males or females. Response and inbreeding are varied between breeding schemes by varying k. In studies a to c below, for each selection strategy, mean breeding value is plotted against mean inbreeding coefficient in generation 9.

a) Effect of Population Size and Mating Ratio.
    A number of breeding schemes are simulated for each of the four selection strategies, in order to obtain the range of possible inbreeding levels and responses for each. Heritability is 0.3, there are 3 progeny of each sex per dam, 800 replicates are used and 4 population structures are considered:(1)Nm=8, Nf=64;(2)Nm=16, Nf=128;(3)Nm=8, Nf=128;(4)Nm=16, Nf=64, where Nm and Nf are the numbers of selected males and females.

b) Effect of a Sex-Limited Trait
    ADJEBV and REST are simulated assuming the trait is measured only in females. The population has Nm=8, Nf=64, there are 3 progeny of each sex per dam, heritability is 0.3 and 600 replicates are used.

c) Variations on ADJEBV
    Three variations on the ADJEBV strategy are studied: (1)MALES- switching is carried out in males only, and females are selected by truncation on EBV, (2)FEMALES- switching is carried out in females only, and males are selected by truncation on EBV, (3)MALES(0)- same as MALES except that the adjusted EBV of male i does not include relationships with selected females (i.e. the 1/4 $a_{sd,i}$ term is not included in equation (2). All simulations have Nm=8, Nf=64, 3 progeny of each sex per dam, a heritability of 0.3 and 800 replicates.

RESULTS

a) Effect of Population Size and Mating Ratio.
    In each of the four population structures simulated, the selection strategies ranked

ADJEBV>SUBOPT>REST>OMIT, in terms of genetic gain at any level of inbreeding. Figure 1 illustrates this for the first population where Nm=8, Nf=64. The lines converge on the same point
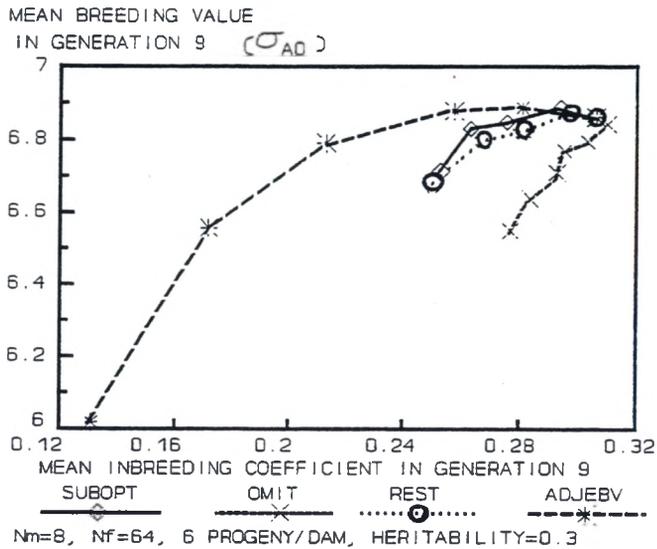
MEAN BREEDING VALUE
IN GENERATION 9   (σ_{A0})

Figure 1:   **Mean genetic gain and mean inbreeding after 9 generations of selection using OMIT, SUBOPT, REST and ADJEBV.**

at the right of the graph, where selection is by truncation on EBV calculated using the optimum index weights using all full and half-sib records in generation 0. The range of points to the left for ADJEBV is obtained by increasing k from 0 to 25. Similarly, the range of points for SUBOPT is obtained by decreasing the weight on full-sib records by 0% to 79%, for OMIT by decreasing the number of full-sib records included from 5 to 0, and for REST by increasing restrictions on the selection of full sibs from no restrictions up to no more than 1 male and 2 females selected from a full-sib family. From Figure 1, it is possible to reduce inbreeding in generation 10 from 0.31 to 0.23 with no loss of genetic response, using ADJEBV. Similar results are obtained with the larger population size (Nm=16, Nf=128) and different mating ratios (Nm=8, Nf=128 and Nm=16, Nf=64).
b)Effect of a Sex-Limited Trait
   Results for a sex-limited trait are similar to those in Figure 1 and are not shown here. Inbreeding is reduced from 0.38 to 0.25 with no loss of genetic response using ADJEBV, and ADJEBV gives higher genetic gain at a given level of inbreeding than REST.
c)Variations on ADJEBV
   Figure 2 shows results for selection methods ADJEBV, MALES, FEMALES and MALES(0). In terms of genetic gain at constant inbreeding, the strategies rank ADJEBV>MALES>MALES(0)>FEMALES. Because there are more dams than sires, use of the strategy MALES involves much less computation than ADJEBV, while FEMALES involves only slightly less computation. MALES gives slightly more inbreeding at a given level of genetic gain, than ADJEBV. For MALES(0), the adjusted EBV of a male considers only relationships with selected males, and not with selected females, but inbreeding at a given level of genetic gain is still lower than for FEMALES, even though the adjusted EBV of a female considers relationships with

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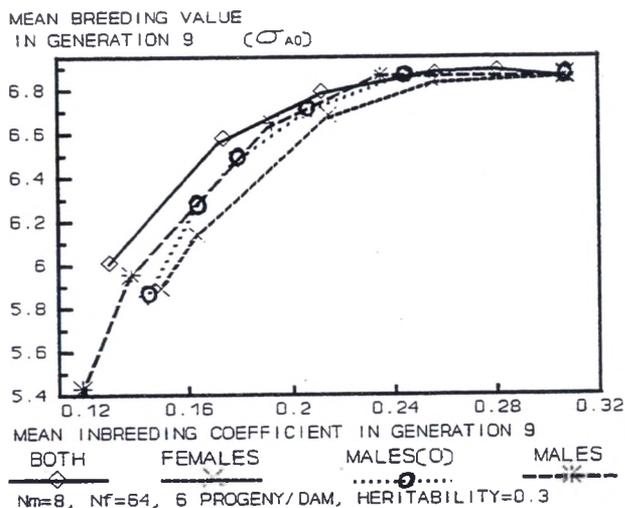
Figure 2:   Mean genetic gain and mean inbreeding after 9 generations of selection using
ADJEBV, MALES, MALES(0) and FEMALES.

currently selected animals of both sexes. Choice of males has a greater impact on inbreeding
because fewer of them are selected.

DISCUSSION AND CONCLUSIONS

The ADJEBV method uses unbiased maximum accuracy EBV and information on relationships
in an objective manner, and could be expected to outperform other methods with arbitrary
restrictions or suboptimum EBV, as was clearly demonstrated here.   Simulations at varying
population sizes (results not shown here), indicate that ADJEBV can obtain the same rate of
inbreeding and genetic gain as REST with a 10-30% reduction in population size.   The advantage
over REST in practical schemes will, however, need to be obtained in situations with overlapping
generations. Reducing the variance of response is of concern in breeding schemes, but these
simulations indicated little reduction in variance associated with reductions in inbreeding (results not
shown). Other strategies have been proposed to reduce inbreeding (Verrier et al, 1992;Grundy and
Hill, 1993) which involve reducing the weight on relatives' information in mixed model evaluations.
These methods are similar to SUBOPT and do not consider relationships among selected animals,
and so it is likely that ADJEBV will outperform these methods. The ADJEBV method here is similar
to that developed by Wray and Goddard for use in one sex only.

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