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Including genetic relationships in selection decisions: alternative methodologies

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Abstract Investigations are made of variations in an iterative methodology previously introduced for reducing inbreeding by including genetic relationships in selection decisions, using adjusted estimated breeding values (EBV). An alternative computing strategy for maximising the value of the population selection criterion is shown to involve less computation, which results in function values as great or greater than the original method. Alteration of weights for different types of relationships in the adjusted EBV has no detectable effect on genetic gain at a given level of inbreeding. Selection using the adjusted EBV method in one sex and truncation on EBV in the other sex results in less genetic gain at a given level of inbreeding than using adjusted EBV in both sexes, but results in more gain at a given level of inbreeding than three selection strategies that do not include genetic relationships in selection decisions. The advantage of the adjusted EBV method over these three methods is retained when selection is for a sex-limited trait.

Key words Inbreeding · Selection · Genetic improvement

Introduction

In most breeding schemes a balance between genetic gain and inbreeding is sought. Brisbane and Gibson (1995a) proposed a selection method, termed ADJEBV, which gave greater genetic gain at a given level of cumulate inbreeding than selection on (1) a family index with reduced weight on sib information (SUBOPT), (2) an index omitting some sib information (OMIT) and (3) an index with a restriction on the number of full sibs selected (REST). AD-

JEBV involves using an iterative procedure that attempts to maximise a population selection criterion involving mean estimated breeding values (EBV) and mean relationship among selected animals. Toro and Perez-Enciso (1990) proposed a selection method using linear programming to maximise genetic merit of the progeny with a constraint on the mean inbreeding coefficient of the progeny, but this method does not account for the effect of relationships among selected parents on inbreeding in later generations. Other strategies proposed to reduce inbreeding include reducing the weight on relatives' information in mixed model evaluations (Verrier et al. 1993; Grundy et al. 1994). These methods are similar to SUBOPT (Brisbane and Gibson 1995a) and do not consider relationships among selected animals, and so it is likely that ADJEBV will outperform them. Wray and Goddard (1994) proposed several selection procedures to reduce inbreeding. One of these is similar to ADJEBV but uses a population selection criterion involving only EBV and relationships among males. A different iterative procedure was used to try to maximise the criterion with dams selected at random. Brisbane and Gibson (1995a) defined a selection objective of

$$M_1 = G_n - D \cdot F_n \quad (1)$$

where G_n is the genetic mean after n generations of selection, F_n is the mean inbreeding coefficient and D is the value of a unit of inbreeding relative to a unit of genetic gain. The mean EBV of selected sires and dams was used to predict the effect of the selection decision in generation t on G_n ($n > t$), and the mean relationship among selected sires and dams was used to predict the effect on F_n , such that a population selection criterion was defined as

$$M_2 = \frac{1}{2} \overline{EBV}_{t,s} + \frac{1}{2} \overline{EBV}_{t,d} - k \left[\frac{1}{8} \bar{a}_{t,s} + \frac{1}{4} \bar{a}_{t,sd} + \frac{1}{8} \bar{a}_{t,d} \right] \quad (2)$$

where $\overline{EBV}_{t,s}$ and $\overline{EBV}_{t,d}$ are the mean EBV of selected sires and dams, and $\bar{a}_{t,s}$, $\bar{a}_{t,d}$ and $\bar{a}_{t,sd}$ are the mean relationships among sires, among dams and between sires and dams, respectively. Mean relationships included relationships of animals with themselves. In each generation, N_m

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sires and N_f dams were selected by truncation on EBV, with $n_w/2$ progeny of each sex per dam. Adjusted EBV were calculated for selected and unselected males as

$$EBV_{s,i,adj} = \frac{1}{2} EBV_{s,i} - k \left[\frac{1}{8} \bar{a}_{s,i}^* + \frac{1}{4} \bar{a}_{sd,i} \right] \quad (3)$$

where $\bar{a}_{sd,i}$ is the mean relationship of male i with selected dams, $EBV_{s,i}$ is the EBV of sire i and $\bar{a}_{s,i}^*$ is given by

$$\bar{a}_{s,i}^* = \frac{1}{Nm} a_{s,ii} + \left(1 - \frac{1}{Nm} \right) \bar{a}_{s,i} \quad (4)$$

where $a_{s,ii}$ is the relationship of male i with itself and $\bar{a}_{s,i}$ is the mean relationship of male i with selected sires, excluding itself. Thus, if male i is a selected sire, $\bar{a}_{s,i}$ involves the averaging of $Nm-1$ relationships, but if male i is not selected, it involves the averaging of Nm relationships.

Adjusted EBV were calculated analogously for females. Mean relationships were calculated so that the relationship of an animal with itself carried the same weight for a selected animal as for an unselected animal. To find the maximum M_2 , an iterative procedure was used, where the unselected male with the highest adjusted EBV was switched for the selected male with the lowest adjusted EBV. If the population selection criterion (M_2 given by Eq. 2) was increased, the switch was accepted and adjusted EBV for all animals recalculated to account for the change in the selected group. Switching and updating of adjusted EBV continued, alternating between the sexes, until M_2 could not be increased (see Brisbane and Gibson 1995a for further details). This method was effective, though it was not demonstrated that M_2 was maximised at every round of selection nor that more efficient computing methods could not be found. Alternative computing strategies are examined here. The method is also extended to situations where relationships are available only in one sex, and for sex-limited traits.

With a selection objective given by Eq. 1, a series of iso-objective lines can be drawn on graphs of genetic response, G_n , versus inbreeding, F_n , where each line connects points of equal objective value, M_1 . The selection strategy maximising M_1 is found at the point on the plot that touches the iso-objective line with the highest value of M_1 . The k value used in the selection procedure must be greater than D , the slope of the iso-objective line, because of increased genetic response through increased genetic variance. Wray and Goddard (1994) took this into account with their prediction of k as $k = \delta G_L(t-1)/2 + D$, where t is the time horizon and δG_L is the rate of genetic gain assuming truncation selection with no loss in variance due to inbreeding, but accounting for the reduction in variance due to selection. Mean EBV and mean relationship among sires were used as measures of the effect of selection decisions on genetic gain and inbreeding while dams were selected randomly. Greater genetic gain may have been obtained at a given level of inbreeding if relationships of sires with dams had been included in the measure of the effect of the selection decision on F_n . This possibility and the effect of selecting dams randomly are investigated here.

Methodology

An additive infinitesimal genetic model, discrete generations of selection and random mating in a hierarchical design are assumed. Stochastic simulation was used with methodology as given by Brisbane and Gibson (1995a). Nm , N_f , n_w and h^2 denote the number of sires and dams per generation, the number of progeny per dam (exactly 1/2 of which are of each sex) and the heritability. In each generation, $Nm=8$, $N_f=64$, $n_w=6$ and $h^2=0.3$. In each study 800 replicates were used, except for the sex-limited trait, where the number was 600.

Altering the iteration scheme

In each generation, selection was carried out as for ADJEBV, except that instead of making a single animal change to the initial selected group based on adjusted EBV, all animals within each sex were re-ranked on adjusted EBV and selection was by truncation on adjusted EBV. Adjusted EBV were then recalculated based on the new selected group, and the process repeated for three cycles. The iteration scheme then reverted to single animal switches as for ADJEBV until no further increase in M_2 was observed. This procedure is denoted ADJEBV(2). Adjusted EBV were calculated according to Eq. 3. ADJEBV and ADJEBV(2) for a range of k were compared for the total number of updates required for the adjusted EBV, the maximum value of the population selection criterion achieved, and the balance of genetic gain and inbreeding.

ADJEBV in one sex as compared to both sexes

Various ADJEBV selection methods were examined. In strategy MALES, males were selected using the ADJEBV iterative procedure with adjusted EBV for males given by Eq. 3 and females selected by truncation on unadjusted EBV. An analogous procedure with iterative ADJEBV selection for females but truncation selection on unadjusted EBV for males was denoted FEMALES. In strategy BOTH, iterative ADJEBV selection was carried out in both sexes. The population selection criterion is given by Eq. 2 for strategies MALES, FEMALES and BOTH. For strategy MALES(0) the adjusted EBV of male i ignores relationships with selected females and is calculated as

$$EBV_{s,i,adj} = \frac{1}{2} EBV_{s,i} - k \frac{1}{8} \bar{a}_{s,i}^* \quad (5)$$

Females were selected by truncation on EBV. The population selection criterion is given by

$$\frac{1}{2} \overline{EBV}_{t,s} + \frac{1}{2} \overline{EBV}_{t,d} - k \frac{1}{8} \bar{a}_{t,s}$$

which is similar to that given by Eq. 2 but does not include relationships among dams and between sires and dams because they are assumed to be unknown. For all four strategies, single animal changes are made between each update of the adjusted EBV. When iterative selection is carried out in both sexes, d switches are attempted in females followed by 1 in males, where d is the number of females mated per male. The strategies MALES and MALES(0) were also simulated where dams were selected randomly. MALES(0) was also simulated with random selection of dams but using an alternative iterative strategy proposed by Wray and Goddard (1994) to maximise the population selection criterion through sire selection. This approach is referred to as MALES(00) and is carried out as follows. The male selection candidate with the highest EBV is selected. The value of the population selection criterion is calculated for each of the remaining male selection candidates as the second sire, assuming that only two sires are selected. The male which gives the highest value of the population selection criterion is then selected. The value of the population selection criterion is then calculated for each of the remaining male selection candidates as the third sire assuming that three sires are selected. The sire giving the highest value of the population selection criterion is again selected, and the process continues until Nm sires have been selected.

Different k for different sexes

Although average relationships are used as predictors of long-term inbreeding, actual contributions depend on subsequent selection decisions and may vary between the sexes. Thus, the effect of using different k values for the two sexes was examined with adjusted EBV calculated as

$$EBV_{s,i,adj} = \frac{1}{2}EBV_{s,i} - k_m \left(\frac{1}{8}\bar{a}_{s,i}^* + \frac{1}{4}\bar{a}_{sd,i} \right) \quad (6)$$

for male i and

$$EBV_{d,l,adj} = \frac{1}{2}EBV_{d,l} - k_f \left(\frac{1}{8}\bar{a}_{d,l}^* + \frac{1}{4}\bar{a}_{ds,l} \right) \quad (7)$$

for female l , where $EBV_{d,l}$ is the EBV of female l , and $\bar{a}_{d,l}^*$ and $\bar{a}_{ds,l}$ are the mean relationships of female l with selected dams and with selected sires, respectively, with $\bar{a}_{d,l}^*$ calculated in an analogous manner to $\bar{a}_{s,i}^*$ in Eq. 4. The ratio k_m/k_f was equal to 2/3, 1 or 3/2. The population selection criterion is given by Eq. 2 with $k=(k_m+k_f)/2$. When $k_m/k_f=1$, the strategy is the same as BOTH. Single animal switches are made between each update of the adjusted EBV.

Effect of a sex-limited trait

ADJEBV and REST were simulated, assuming the trait was measured only in females. Both ADJEBV and ADJEBV(2) iteration methods were used. The adjusted EBV was calculated according to equation 3 for male i , and analogously for females. For REST and ADJEBV, EBV of females were calculated from an index of the individual record, the mean of $n_w/2$ full-sib records (including the individual record) and the mean of $d.n_w/2$ half-sib records (including the individual and full-sib records). Conventional selection index equations were used, with matrix elements as given in Appendix 1 of Brisbane and Gibson (1995b), except that records were used from female animals only. EBV of males were calculated from an index of the mean of $n_w/2$ full-sib records and the mean of $d.n_w/2$ half-sib records (including the full-sib records).

Results

Results are presented in terms of plots of genetic gain versus cumulate inbreeding after nine generations of selection. Standard errors ranged from 0.016 to 0.020 for genetic gain, and from 0.0004 to 0.0010 for cumulate inbreeding. Curves were fitted through the points by inspection for all plots except that for REST in Fig. 5.

Altering the iteration scheme

In Fig. 1 mean genetic gain is plotted against mean inbreeding after nine generations of selection for ADJEBV and ADJEBV(2) with ADJEBV(2) simulated only at $k=5$ and $k=10$. These two points lie slightly above the curve drawn through the ADJEBV points. For ADJEBV with $k=10$, the initial values of the population selection criterion, the increase achieved and the number of changes to the selected group in each generation of selection are given in Table 1. Table 2 presents for ADJEBV(2), with all parameters the same as for ADJEBV, the values of the population selection criterion for the initial selected group, the increases achieved by each cycle of reranking, and the overall difference between the initial selected group and the final se-

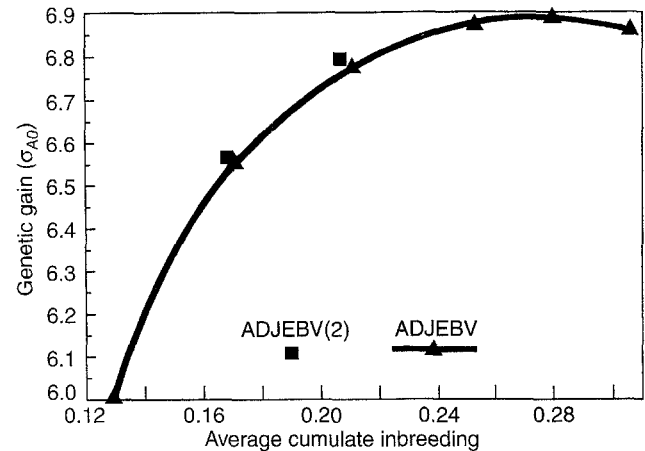


Fig. 1 Comparison of ADJEBV and ADJEBV(2): genetic gain versus inbreeding after nine generations of selection

Table 1 Increases in the population selection criterion and number of single animal changes made for ADJEBV by generation for $k=10$, and averaged over generations 2–10 for $k=10^a$ and $k=5$

Generation	Initial value	Increase	Number of changes
1	0.433	0.109	16.87±0.14
2	1.040	0.155	19.13±0.17
3	1.592	0.159	19.43±0.18
4	2.137	0.154	19.15±0.17
5	2.663	0.151	19.23±0.17
6	3.184	0.151	19.21±0.17
7	3.700	0.146	18.91±0.17
8	4.207	0.140	18.60±0.17
9	4.714	0.134	18.54±0.17
10	5.210	0.134	18.46±0.17
Average (2–10)		0.147	18.96±0.06
Average (2–10) with $k=5$		0.051	12.95±0.04

^a For $k=10$, standard errors of increases in the population selection criterion are about 0.003

lected group after all single animal changes. The number of single animal changes made after initial cycles with group changes is also given. Increases in the population selection criterion were smallest for the first generation, probably because the variance of unadjusted EBV is highest in the first generation. The other generations gave similar results, and the average of these is given for $k=10$ and $k=5$.

Average increases in the population selection criterion for ADJEBV were only 95.4% ($k=10$) and 98.1% ($k=5$) of that for ADJEBV(2) (Tables 1 and 2) and were reflected in the slightly lower genetic gain achieved at a given level of cumulate inbreeding for ADJEBV (Fig. 1). The difference in the increases in the population selection criterion between ADJEBV and ADJEBV(2) was statistically significant ($P<0.01$) when $k=10$ and approached the 5% significance level when $k=5$. When k was reduced from 10 to 5, average increases in the population selection criterion

Table 2 Increases in the population selection criterion after each cycle of reranking and number of single animal changes made for ADJEBV(2) by generation for $k=10$, and averaged over generations 2–10 for $k=10^a$ and $k=5$

Generation	Initial value	Increase due to 1st reranking	Increase due to 2nd reranking	Increase due to 3rd reranking	Overall increase	Number of changes
1	0.446	0.056	0.029	0.011	0.114	10.57±0.11
2	1.066	0.075	0.040	0.017	0.155	11.27±0.13
3	1.606	0.077	0.042	0.019	0.163	11.50±0.13
4	2.139	0.079	0.042	0.019	0.167	11.53±0.13
5	2.674	0.075	0.040	0.018	0.158	11.50±0.13
6	3.206	0.075	0.039	0.018	0.158	11.61±0.13
7	3.732	0.074	0.040	0.018	0.156	11.21±0.12
8	4.247	0.072	0.037	0.017	0.150	11.12±0.12
9	4.762	0.068	0.036	0.016	0.142	11.04±0.13
10	5.259	0.068	0.036	0.016	0.142	10.86±0.13
Average (2–10)		0.074	0.039	0.018	0.154	11.29±0.04
Average (2–10) for $k=5$		0.030	0.011	0.004	0.052	7.53±0.03

^a For $k=10$, standard errors of increases in the population selection criterion at each reranking range from 0.0005 to 0.0015 and standard errors of overall increases range from 0.002 to 0.003

were reduced substantially (Tables 1 and 2) because there is less to gain by changing the selection from truncation on unadjusted EBV. The proportions of the total increase in the population selection criterion achieved after each cycle of reranking were similar across $k=5$ and $k=10$ and showed diminishing returns as the number of cycles was increased. At $k=10$, the number of single animal changes required after reranking (Table 2) was about 40% less than for ADJEBV (Table 1), although the total number of substitutions (including group reranking substitutions) was only about 24% less.

ADJEBV(2) resulted in a slightly greater value of the population selection criterion and required slightly less computation, with fewer cycles of calculating relationships and reranking.

Efficiency of ADJEBV in one sex as compared to both sexes

Mean genetic gain for strategies BOTH, MALES, MALES(0) and FEMALES is plotted against average cumulative inbreeding after nine generations of selection in Fig. 2. Overall, in terms of ability to reduce inbreeding at a given level of genetic gain, BOTH gave the best performance, followed by MALES, MALES(0) and FEMALES. Although results are not shown here, all strategies performed better than strategies SUBOPT, OMIT and REST described by Brisbane and Gibson (1995a).

Computational requirements were greatly reduced when ADJEBV was applied only in males, with an average of 4.24 ± 0.01 , 16.91 ± 0.05 and 19.0 ± 0.06 changes to the selected group for strategies MALES, FEMALES and BOTH, respectively, when $k=10$. The difference would be likely to increase as the mating ratio is increased. To aid

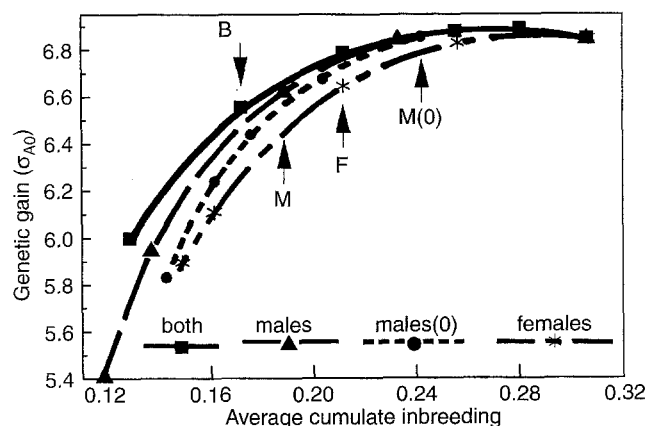


Fig. 2 Efficiency of ADJEBV when used in one sex as compared to both sexes: genetic gain versus inbreeding after 9 generations of selection, using BOTH, MALES, MALES(0) and FEMALES. The arrows labelled B, M, F and M(0) indicate the points on the plots for BOTH, MALES, FEMALES and MALES(0), respectively, when $k=10$ was used in the population selection criterion

comparison, the four points marked with an arrow in Fig. 2 are the points for BOTH, MALES, MALES(0) and FEMALES when $k=10$ was used in the population selection criterion. At this constant value of k , the reduction in inbreeding was greatest for BOTH, lower for MALES, lower still for FEMALES, and least for MALES(0). On the BOTH plot in Fig. 2, $k=5$ is the point to the right of $k=10$. BOTH at $k=5$ achieved less reduction in inbreeding than MALES at $k=10$, but required two to three times as much computation. The amount of computation was, however, small in comparison to that required for the mixed model genetic evaluation procedures used in animal breeding

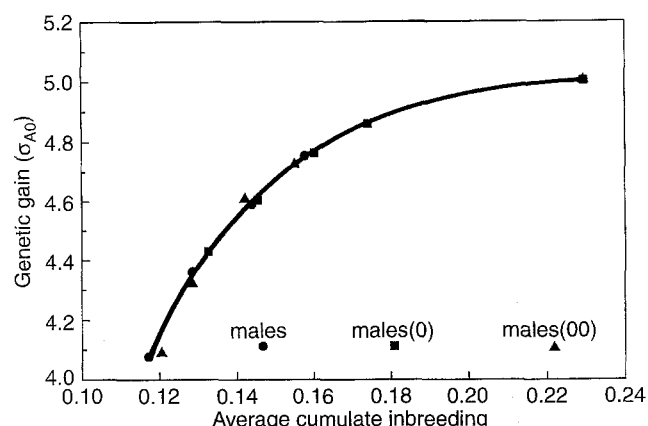


Fig. 3 Genetic gain versus inbreeding after nine generations of selection for MALES, MALES(0) and MALES(00) when dams were selected randomly

practice, and so computation time is not likely to be an important consideration in choosing a strategy to implement.

Although results are not shown, at a given value of k fewer of the sires selected initially by truncation on EBV remained in the final selected group under MALES than under BOTH (e.g. at $k=10$, average proportions across generations 2–10 are 0.616 and 0.724 with standard errors of about 0.001). Similarly, fewer of the initially selected dams remained in the final selected group under FEMALES than under BOTH. Thus, when the procedure was done in only one sex, more changes were made to the initially selected group in that sex to reduce relationships because parents of the other sex were not being changed.

Mean genetic gain for strategies MALES, MALES(0) and MALES(00) when dams are selected randomly is plotted against average cumulate inbreeding after nine generations of selection in Fig. 3: the slope of the plots is steeper and genetic gain and inbreeding are smaller than when dams were selected by truncation on EBV (Fig. 2). There were no detectable differences in performance among MALES, MALES(0) and MALES(00). Thus, genetic gain at a given level of inbreeding was increased by including relationships with dams only when dams were genetically selected. The k values used in MALES were 5, 10, 25 and 40 when dams were genetically selected (Fig. 2) and 10, 15, 25 and 40 when dams were randomly selected (Fig. 3). Slopes of the tangents (iso-objective lines) to the achieved curves at these k values were about 3, 8, 22 and 34 in the first case, and 7, 12, 17 and 31 in the second. Thus, when relationships with dams were included in the adjusted EBV, the k value required to maximise a given objective was not noticeably affected by whether or not the dams were genetically selected. The k value required was similar to that required using BOTH (in Fig. 2, k values of 5, 10 and 25 for BOTH give points with tangents with slopes of about 4, 9 and 16, respectively).

The k values used in MALES(0) were 10, 25, 50, 75 and 150 when dams were genetically selected (Fig. 2) and 10, 15, 25 and 40 when they were randomly selected (Fig. 3).

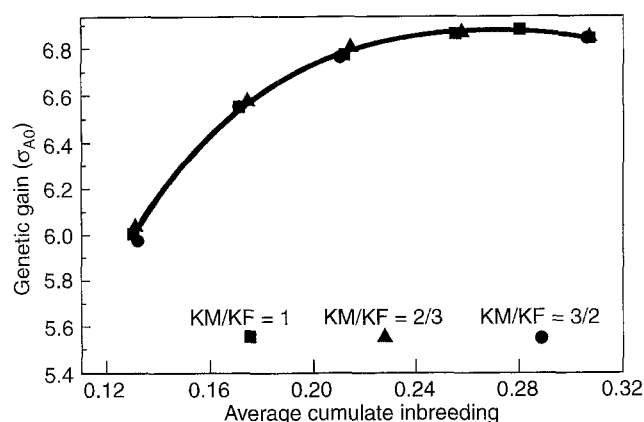


Fig. 4 Genetic gain versus inbreeding after nine generations of selection, using ADJEBV with different k for males and females

Slopes of the tangents to the achieved curves at these points were about 3, 6, 11, 17 and 31 in the first case, and 6, 7, 12 and 17 in the second. When this strategy is used, when relationships with dams were not included in the adjusted EBV, the k value required to maximise a given objective when dams were genetically selected was at least twice as high as that when dams were randomly selected. When dams were randomly selected, the k value required to maximise a given objective was slightly greater than that required using MALES or using BOTH. The k values used in MALES(00) were the same as those used in MALES(0), so that the points shown in Fig. 3 show that a given k value has a greater effect on response and inbreeding when the iterative method of MALES(00) is used. MALES(00) corresponds to the selection method of Wray and Goddard (1994) for which they could predict k to within a relative error of about $\pm 10\%$. The results obtained here suggest that for random selection of dams predictions should be of similar accuracy for MALES but may underpredict k for MALES(0). If dams were to be genetically selected, Wray and Goddard (1994) would use a larger value of δG_L , giving a larger predicted value of k , as required for MALES(0), but not for MALES. Given the large difference between the k values required for MALES and MALES(0) when dams are genetically selected, a different predictor seems necessary in each situation. All slopes were estimated from the graphs by eye, but this is sufficient given the size of the differences involved.

Different k for different sexes

In Fig. 4 mean genetic gain is plotted against mean inbreeding after nine generations of selection when adjusted EBV are given by Eqs. 6 and 7 and $k_m/k_f=2/3$, 1 or $3/2$. No distinguishable differences in performance were found between the three ratios for k_m/k_f , and so the same curve is drawn through all points. The most extreme k_m/k_f ratios of ∞ and 0, correspond to MALES for $k_m/k_f=\infty$ and to FEMALES for $k_m/k_f=0$ (Figure 2). The results in Fig. 4

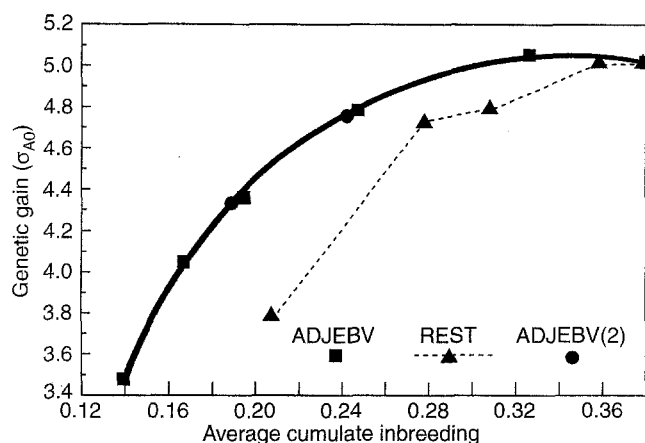


Fig. 5 Genetic gain versus inbreeding after nine generations of selection for three selection strategies with a sex-limited trait

show that ADJEBV is not very sensitive to k_m/k_f . There is no evidence that any ratio of k_m/k_f other than unity gives better results.

Effect of a sex-limited trait

In Fig. 5 mean genetic gain for a sex-limited trait is plotted against mean inbreeding after nine generations of selection for ADJEBV, ADJEBV(2) and REST, which corresponds to the same situation as that for a non-sex-limited trait shown in Fig. 1. Genetic gain was smaller and inbreeding was greater when the trait is sex-limited (Fig. 5 vs. Fig. 1), as is to be expected from the reduced accuracy and increased correlation among EBV. For a given k , ADJEBV achieved a greater reduction in inbreeding when the trait was sex-limited. For example, after nine generations of selection with $k=5$, inbreeding was reduced by 0.094, from 0.306 to 0.212, when the trait was not sex-limited, and by 0.132, from 0.379 to 0.247, when the trait was sex-limited. Corresponding reductions in genetic gain were 0.074 and 0.223, respectively. In proportional terms, response was reduced by 1.1% for a 31% reduction in inbreeding when the trait was not sex-limited and by 4.5% for a 35% reduction in inbreeding when the trait was sex-limited. In terms of maintaining genetic gain while reducing inbreeding, performance of ADJEBV was similar for sex-limited and non-sex limited traits. In both cases (Figs. 1 and 5), inbreeding could be reduced proportionately by about 20% and 30% for proportionate reductions in response of 0% and 2% relative to truncation selection on EBV. Performance of REST when the trait was sex-limited was similar to that when it was not, except that when the trait was sex-limited a given restriction had a larger effect on response and inbreeding. ADJEBV retained advantages over REST for both non-sex-limited and sex-limited traits.

For any k , when the trait was sex-limited, population selection criterion values were lower (results not shown) because there was more inbreeding and less genetic gain.

Increases in the population selection criterion were greater. At $k=10$, the increase in the population selection criterion, averaged over generations 2–10, between the initially and finally selected animals, was 0.197 ± 0.001 for the sex-limited trait and 0.147 ± 0.001 for the non-sex-limited trait. There were more single animal changes (e.g. 22.3 ± 0.07 vs. 19.0 ± 0.06 , averaged over generations 2–10 when $k=10$), and the proportion of the initially selected animals in the finally selected group was lower. The difference in the number of changes made was much greater for males than for females. At $k=10$, 0.647 and 0.724 of initially selected sires were in the finally selected group for sex-limited and non-sex-limited traits, respectively. For dams the proportions were more similar at 0.778 and 0.808, as expected because the difference between traits in the correlation of EBV among males is much greater than the difference in the correlation of EBV among females.

Increases in the population selection criterion for ADJEBV(2) were significantly larger than for ADJEBV [e.g. at $k=10$ the difference between the population selection criterion averaged across generations 2–10 for the initially and finally selected groups is 0.220 ± 0.001 for ADJEBV(2) and 0.197 ± 0.001 for ADJEBV(1)], as was observed for the non sex-limited trait (Table 1 vs. Table 2). However, there was no distinguishable difference between the performance of ADJEBV and that of ADJEBV(2) in terms of genetic gain at a given rate of inbreeding (Fig. 5), in contrast to the non sex-limited trait, where ADJEBV(2) was found to have a slightly better performance (Fig. 1).

Discussion and conclusions

Much of the advantage of ADJEBV in terms of genetic gain at a given level of inbreeding was retained when the procedure was only used for males. Thus, if the selection of females is not under the control of the breeding organisation (but selected females and their pedigrees are known), then the ADJEBV method could be applied to the selection of sires only (i.e. strategy MALES) with only a small loss in performance. If selected females are not identified when males are selected, then ADJEBV could be applied to the selection of sires only, considering only the relationships among sires (strategy MALES(0)), with only a slight loss in performance. If dams are not genetically selected there is no loss in performance when switching from MALES to MALES(0). Fewer sires than dams are selected, and so the choice of sires has a greater impact on inbreeding. As the mating ratio is increased, the benefit of including females in the ADJEBV procedure is likely to become smaller because computational requirements will increase and the contribution of dams to inbreeding will decrease. The results show no evidence that greater genetic gain at a given level of inbreeding can be achieved by having different weights against relationships for the two sexes. The iterative procedure used by Wray and Goddard (1994) gave the same performance as MALES(0) when dams were selected randomly, although for a given k value their proce-

cedure gave a much larger reduction in inbreeding and response. Wray and Goddard (1994) also presented other selection methods to reduce inbreeding, which involved allowing variation in the number of sires selected and the number of matings per sire.

The ability of ADJEBV selection to maintain genetic gain while reducing inbreeding was retained when selection was for a sex-limited trait. For both sex-limited and non-sex-limited traits, the alternative iteration procedure, ADJEBV(2), based on reranking and truncation selection on adjusted EBV, achieved larger increases in the population selection criterion than ADJEBV, although the increase in genetic gain at a given level of inbreeding was small. All of the iterative ADJEBV methods used obtained greater genetic gain at a given level of inbreeding than methods that reduced the weight on information from relatives or restricted the selection of sibs, but did not incorporate genetic relationships in selection decisions.

For most of the situations considered here, the k value maximising the objective was about 1.2 to 2 times the slope (D) of the iso-objective line within the range of the curve where $0 < D < 40$, in agreement with Brisbane and Gibson (1995a). MALES(0) with the genetic selection of dams was an exception, where the k value maximising the objective

was about 4 to 4.5 times the slope of the iso-objective line. A substantial difference in the k value was required to maximise the objective between MALES and MALES(0) with the genetic selection of dams.

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