Optimal allocation of resources considering two sexes and selection in two stages

Cm Wade, Jw James

Original article

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CM Wade [1], JW James [2]

[1] *Department of Farm Animal Medicine and Producion,*
The University of Queensland, Brisbane, QLD 4072;
[2] *Department of Wool and Animal Sciences, The University of New South Wales,*
Kensington, NSW 2052, Australia

Summary – The distribution of limited testing resources between sexes and stages of selection was optimised for breeding structures employing one- or two-stage selection. The use of incomplete sampling was considered. Measurement expenditure generally favoured the sex subject to the highest selection intensity. Within a sex, the optimal intensity of measurement was dependent upon the proportion of available candidates required for breeding and on the level of available funding. It was optimal to test all of the available candidates when more than 40% was required for breeding. Single-stage selection was favoured when selection intensity was low and when the funding limit was high. The allocation of resources between stages of selection was complex. Results are expressed graphically for different relationships between measurement cost and selection accuracy, for a range of selection intensities in each sex, and for a range of funding limitations. The methods are applicable to any livestock industry where multi-stage selection is utilised and where a relationship between measurement cost and accuracy can be ascertained. A numerical illustration pertinent to a wool sheep breeding scheme is examined.

mass selection / selection response / multi-stage selection / two-stage selection

Résumé – Répartition optimale des ressources financières entre deux sexes et deux étapes de sélection. *La distribution de ressources financières limitées de contrôle entre sexes et étapes de sélection est optimisée pour des structures de sélection en une ou deux étapes. La possibilité d'utiliser un échantillonnage incomplet est envisagée. Les dépenses liées aux mesures doivent en général se porter de préférence sur le sexe soumis à la plus forte intensité de sélection. Intrasexe, la proportion optimale des candidats à mesurer dépend de la proportion des candidats disponibles qui est requise pour la reproduction et du niveau du financement disponible. Il est optimal de contrôler tous les candidats disponibles quand plus de 40 % sont requis pour la reproduction. Une seule étape de sélection doit être recommandée quand l'intensité de sélection est faible et la limite de financement élevée. L'allocation optimale des ressources entre les deux étapes de sélection est complexe. Les résultats sont exprimés graphiquement pour différentes relations entre le coût des mesures*

et la précision de la sélection, pour des valeurs variables d'intensité de sélection dans chaque sexe, et pour des limites de financement variables. Les méthodes sont applicables à n'importe quelle filière de production animale où une sélection en plusieurs étapes est utilisée et où une relation peut être établie entre le coût des mesures et la précision de la sélection. Un exemple numérique est traité, relatif à un schéma de sélection ovin lainier.

sélection massale / réponse à la sélection / sélection par étapes / sélection en deux étapes

INTRODUCTION

In breeding programs utilising mass selection it has been well documented that the greatest genetic response in a breeder's defined breeding objective is achieved when all of the available measurements are combined into a single index value, and truncation of the population takes place on this index value. While genetic response is maximised by this strategy, it is not always practical, or economically efficient, to conduct selection in a single stage. This is particularly true when the resources available to a selection scheme are limited. The limitation imposed may be a restriction on the number of testing spaces available, or otherwise, on the level of funding available for taking measurements on the selection candidates.

Two-stage selection has been considered in a range of animal species including cattle (Jain and Amble, 1962; Alenda et al, 1982; Van Raden et al, 1984; Ronningen, 1969), sheep (Brown, 1967; Mueller, 1984; Ponzoni, 1987; Atkins, 1987; Morley, 1988; Atkins, 1990; Lewer and MacLeod, 1990), horses (Hugason et al, 1987), swine and poultry (Ronningen, 1969). Some work has also considered the use of two-stage selection in plant breeding (Cochran, 1951; Finney, 1958; Namkoong, 1970; Cotterill and James, 1981; Robinson, 1984). These studies have concentrated on the optimisation of truncation levels for the maximisation of genetic gain. The selection of more than one sex has rarely been considered.

One way in which resources may be 'saved' in a breeding program is through incomplete sampling (James, 1966; Smith, 1969; Ollivier, 1990). Rather than measuring all of the available selection candidates, only a proportion of the candidates is measured. The selected individuals are chosen first from the measured candidates, and then from the unmeasured candidates if more than 50% of the measured candidates are required for breeding. It is preferable to choose an unmeasured candidate, with an expected breeding value of zero relative to the mean of the measured candidates, over a candidate known to have a negative breeding value (Ollivier, 1990).

Studies by James (1966), Smith (1969) and Ollivier (1990) have considered the use of incomplete sampling in single-stage selection programs. No study has looked at the application of incomplete sampling to save costs or to finance increased measurement accuracy in multi-stage selection programs. Smith (1969) and Ollivier (1990) also considered the allocation of testing places between sexes. The allocation of testing funds between sexes with complete testing was examined by Jackson et al (1986).

James (1966) optimised the proportion of candidates to be measured in a single stage of selection. The results were dependent on the proportion of candidates to be culled and on the assumed cost/benefit ratio for the trait selected. An example was reported relating to greasy fleece weight selection in sheep. The work focused on phenotypic response in the current generation, rather than on genetic response, and so cannot be directly compared with the results presented in this study.

While Smith (1969) considered the distribution of testing places between males and females, the measurement regime was fixed. There was no way of using a cheaper measurement on females, for example.

Mueller (1984) considered selection in two sexes and two stages. Truncation levels were optimised to achieve near maximum genetic response for an open nucleus breeding scheme. Genetic gain from the two stages was approximated using a method similar to that described by Cunningham (1975). It was assumed that different indices were used for each sex, and in each stage of selection. The index used at the second stage of selection was assumed to include measurements taken for the first-stage index. When the index at each stage was constructed with the same breeding objective, the correlation between the indices was predicted from the ratio of their respective correlations with the breeding objective. This was, in any case, the optimal method for constructing the indices. The results were presented for a range of final selection intensities and the ratio of efficiency between stage one and stage two. Neither the overall selection efficiency nor the application of incomplete sampling, was considered.

Wade and James (1990) examined the optimal proportions of available selection candidates to be tested and optimal individual measurement costs for some selection programs. The measurement strategies tested allowed for the selection of both sexes in a single stage and for the utilisation of incomplete sampling. The strategy was optimised for genetic response with limited testing expenditure.

For this study, a similar optimisation was carried out with selection allowed to take place in two-stages. The level of funding available for measuring selection candidates was limited. To optimise under these conditions, it was necessary to draw upon bivariate theory developed by Cochran (1951).

Two-stage selection and single-stage selection both allowing for the incomplete sampling of candidates were evaluated iteratively. The testing levels and test costs at each stage in two-stage schemes were optimised with the aim of achieving the greatest possible genetic gain for a given funding level. Two-stage selection was expected to out-perform single stage selection when funds were limited. An inexpensive first stage test would allow a test of higher accuracy to be used in the second stage. The use of incomplete sampling was also expected to have this effect when used in a single stage of selection. However, employing an objective test to nominate individuals for further testing was expected to improve the genetic response. The optimality of the two-stage procedures relied upon their costs relative to procedures where candidates were chosen at random for testing.

THEORY

Let us suppose that the aim of a selection program is to improve an aggregate genotype (H) with regard to a predefined breeding objective through selection on an index in each of two stages. Measurements included in each index are weighted to maximise the correlation between the index value and breeding value. Weightings are calculated from the partial regressions of breeding value on the traits included in the index. If the index used in the second stage of selection includes measurements for all traits that have been incorporated into the first stage index and is the population regression, then the partial regression of breeding value on index one, when index two is held constant, is zero. If this is true then the correlation between the indices will be equivalent to the ratio of their respective correlations with breeding value, ie,

$$r_{12} = \frac{r_{1H}}{r_{2H}} \tag{1}$$

where r_{12} is the correlation between the criteria used at stages one and two, r_{1H} is the correlation between the criterion of selection used at stage one and the breeding value, and r_{2H} is the correlation between the criterion of selection used at stage two and the breeding value (Cochran, 1951).

When improvement is generated solely through selection on males the genetic response to selection can be predicted for index selection in two stages by the method shown (Cochran, 1951).

$$\Delta G_m = i_1 \cdot \sigma_1 \cdot b_{1H} + i_2 \cdot \sigma_2 \cdot b_{2H} = i_2 \cdot r_{2H} \cdot \sigma_H \tag{2}$$

σ_H is the standard deviation of the breeding values, σ_1 and σ_2 are the standard deviations of measurements for indices 1 and 2, the b_1 and b_2 are the regressions of breeding value on the indices used in each stage, and i_1 and i_2 are the final selection intensities in the indices used at stages 1 and 2 of the selection process. These selection intensities result from the double truncation of the bivariate normal distribution at points x_1 and x_2 to retain a proportion (pm). If i_{x1} is the selection intensity resulting from the truncation of the univariate normal distribution of index 1 at point x_1, and i_{x2} is a similar selection intensity resulting from the truncation of the univariate distribution of index 2 then $i_1 = i_{x1} + r_{12}\,i_{x2}$, and $i_2 = i_{x2} + r_{12}\,i_{x1}$. The calculation of i_2 depends on the proportion used in each stage and the correlation between the index used at each stage. Thus, the selection intensity i_2, is never lower than that for i_1 if the index used at stage 2 incorporates measurements taken in stage 1. The gain from selection in females will be similar.

The genetic gains predicted from selection in both sexes can be combined into an equation predicting annual genetic gain such that,

$$\Delta_G = \frac{\Delta G_{\mathrm{m}} + \Delta G_{\mathrm{f}}}{L_{\mathrm{m}} + L_{\mathrm{f}}} \tag{3}$$

where L_{m} and L_{f} are the male and female generation intervals.

One may link measurement cost with selection accuracy by making use of the marginal effectiveness ratio (Jackson et al, 1986) in the following manner:

$$F(C) = 1 - k^c = \frac{r_{IH}}{r_{\max}} \qquad [4]$$

$F(c)$ describes the efficiency of selection, c the individual test cost, r_{IH} the correlation between the index on which selection is based and breeding value, and $r_{\max}$ is the maximum correlation that is possible between the criterion of selection and breeding value.

It is assumed that the correlation between the measurement made at each stage of selection and the true breeding value is affected by the expense of the measurement such that higher measurement costs relate to measurements that have a higher correlation with true breeding value. This relationship is assumed to be one of diminishing returns. When the level of expenditure is low, large increases in selection efficiency are realised with each extra unit of currency spent on measurement. When the level of expenditure is high only small increases in efficiency are realised with each extra unit of currency spent on measurement.

The marginal effectiveness ratio (k) is a general parameter relating measurement cost and selection efficiency. k is assumed to relate all possible selection measurements with efficiency and so is equal for males and for females. When k is high, high selection efficiency is achieved only at great expense and diminishing returns set in showly. At low values of k, near maximum levels of efficiency are achieved at relatively low expense so that inexpensive selection methods are nearly as efficient as more expensive selection methods, ie, diminishing returns set in rapidly.

If the index used at the second stage of selection incorporates all of the measurements taken at the first stage then the efficiency of the method used at stage 2 is related to the total cost of measurements taken in both stages, and not only those for the second,

$$r_{2H} = r_{\max}(1 - k^{Cm1 + Cm2}) \qquad [5]$$

and therefore,

$$\begin{aligned} \Delta G &= \frac{i_{2m} \cdot \sigma_H \cdot r_{2mH} + i_{2f} \cdot \sigma_H \cdot r_{2fH}}{L_m + L_f} \\ &= \frac{\sigma_H \cdot r_{\max}}{L_m + L_f} \left[i_{2m} \times (1 - k^{Cm}) + i_{2f} \times (1 - k^{Cf}) \right] \end{aligned} \qquad [6]$$

where $Cm1$ and $Cf1$ are the costs of measuring males and females in the first stage of selection, $Cm2$ and $Cf2$ are the costs of measurements made in the second stage of selection, and where $Cm = Cm1 + Cm2$ and $Cf = Cf1 + Cf2$.

If we let:

$$A = \frac{Lm + Lf}{\sigma_H \cdot r_{\max}} \qquad [7]$$

then,

$$A\Delta G = i_{2m} \times (1 - k^{Cm}) + i_{2f} \times (1 - k^{Cf}). \qquad [8]$$

The genetic gain $A\Delta G$ is a function of the final selection intensities and measurement costs in stages one and two for males and females, respectively. The selection intensity is affected by the proportion of individuals tested in stage one, the proportions of candidates selected from the tested individuals at each stage and the correlation between measurements made at stages one and two. The correlation between the measurements made at stages one and two is also influenced by the relative values of $C1$ and $C1 + C2$, $C1$ and $C2$ being the measurement cost for animals of unspecified sex.

METHODS

Evaluating an appropriate marginal effectiveness ratio (k)

In order to evaluate the marginal effectiveness ratio (k) for a specific industry, a breeding objective must first be specified. The breeding objective used to assess the suitability of the different marginal effectiveness ratios for a wool sheep breeding program might include three traits: clean fleece weight (\$49.63), average fibre diameter (−\$9.12) and hogget body weight (\$0.72). Economic values are those assumed by Woolplan (Ponzoni, 1988).

Selection criteria must be assessed for their correlations with true breeding value. For sheep, such criteria might include hogget body weight (\$1.00, $r_{IH} = 0.15$), greasy fleece weight (\$2.00, $r_{IH} = 0.35$), clean fleece weight (\$4.00, $r_{IH} = 0.49$), average fibre diameter (\$4.00, $r_{IH} = 0.29$), and various subjective sheep classing criteria as described by Lewer and MacLeod (1990) at \$1.00 per measurement or \$4.00 for all subjective measurements ($r_{IH} = 0.34$). Linear index combinations of the criteria may be tested and their selection efficiencies in predicting aggregate breeding value assessed for the assumed breeding objective. An index of all of the described measurements made on the selection candidates (with no progeny testing) has an expected accuracy of $r_{IH} = 0.69$ at a cost of \$12.50 per animal tested. In the example presented, $r_{\max}$ is assumed to be the accuracy of progeny testing all candidates for all traits with 40 progeny per candidate. Such an index demonstrates an expected correlation between index score and breeding value (r_{IH}) of 0.73.

In figure 1, the selection efficiency ($Fc = r_{IH}/r_{\max}$) of each measurement in a wool sheep breeding programme was plotted (+) against the relevant measurement cost (c). Lines corresponding to the different marginal effectiveness ratios ($k = 0.3$, 0.5, 0.8) were plotted on the same figure assuming that $Fc = r_{IH}/r_{\max} \approx (1 - k^c)$. The parameters used in the assessment were those of Lewer and MacLeod (1990). The x axis of figure 1 was the measurement cost for each index combination. While c was arbitrary, it was possible to change the value of c to reflect measurement cost in local currency. In figure 1, setting one unit of c at one Australian dollar allowed an acceptable fit with the chosen marginal effectiveness approximation. It can be observed from figure 1 that the fit of the actual measurement costs was approximate. A better fit may have been achieved by adjusting the assumed number of local currency units assigned per unit of c, and/or by choosing an intermediate value for the marginal effectiveness ratio.
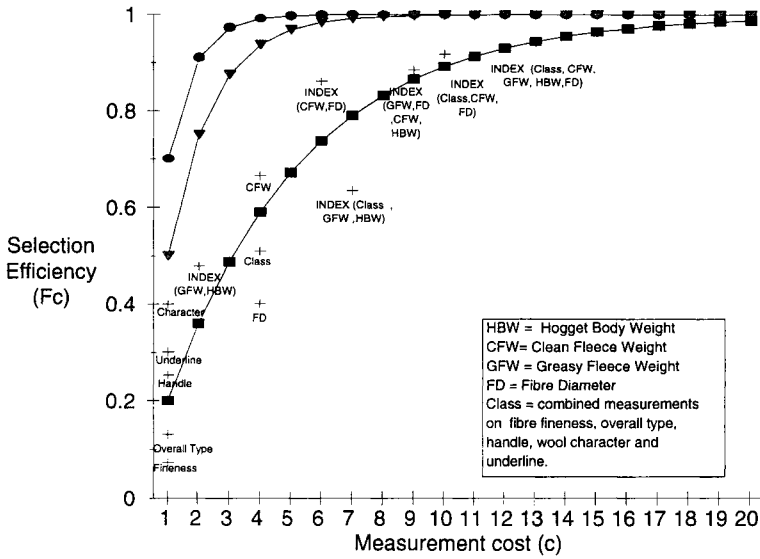
Fig 1. Selection efficiency (Fc) of measurements used as selection criteria for a wool sheep breeding objective plotted against estimated efficiencies for a range of marginal effectiveness ratios (k) and different test costs (c) (one cost unit = one Australian dollar). •: $k = 0.3$; ▼: $k = 0.5$; ■: $k = 0.8$.

Breeding programme optimisation

Throughout this study it was assumed that for any given enterprise we were able to identify an appropriate marginal effectiveness ratio, and we knew the proportions of male and female candidates that were required for breeding (pm and pf, or p for animals of unspecified sex). There was a restriction on the level of funding available to the selection scheme (T, the mean expenditure limit for one selection candidate of either sex), and so the aim of the breeding scheme was to maximise the relative genetic gain within the restriction on funding. A range of values of the above parameters was tested to provide general solutions.

Table I–III describe the parameters considered during the optimisation. These include: i) the proportions of candidates tested in the first stage of selection (Qm and Qf in males and females or q for animals of unspecified sex); ii) the individual test costs applied to those candidates measured in the first and second stages ($Cm1$, $Cm2$, $Cf1$ and $Cf2$ in males and females for stages one and two; iii) the proportions of initially available individuals that needed to be retained after the first selection to be tested in the second stage ($pm1$ and $pf1$ for males and females respectively, or $p1$ for animals of unspecified sex); and iv) the distribution of funds between the sexes (Tm and Tf for males and females or Ts for animals of unspecified sex). The distribution of funds was such that $Tm = Tm1 + Tm2$, $Tm1 = Qm \times Cm1$, $Tm2 = pm1 \times Cm2$, $Tf = Tf1 + Tf2$, $Tf1 = Qf \times Cf1$, $Tf2 = pf1 \times Cf2$, and $T = (Tm + Tf)/2$.

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Table I. Description of parameters used during stage 1 of the selection process[*].

Sex	Proportion of available candidates tested	Proportion of available candidates selected	Measurement cost at stage 1	Total stage 1 cost per available candidate	Parameters affecting genetic gain from stage 1
Male ($\circlearrowleft$)	$0 \leqslant Qm \leqslant 1$	$0 \leqslant \mathbf{pm1} \leqslant Qm$	$Cm1$	$Tm1 = QmCm1$	$Cm1, (pm1/Qf)$
Female ($\circlearrowleft$)	$0 \leqslant \mathbf{Qf} \leqslant 1$	$0 \leqslant \mathbf{pf1} \leqslant Qf$	$Cf1$	$Tf1 = QfCf1$	$Cf1, (pf1/Qf)$
Unspecified ($\circlearrowleft$ or $\circlearrowleft$)	$0 \leqslant q \leqslant 1$	$0 \leqslant p1 \leqslant q$	$C1$	$T1 = qC1$	$C1, (p1/q)$

Optimised parameters are printed in bold type.

Table II. Description of parameters used during stage 2 of the selection process (only candidates selected from stage 1 are included as candidates)[*].

Sex	Proportion of stage 2 candidates measured at stage 2	Proportion of stage 2 candidates selected	Measurement cost at stage 2	Total stage 2 cost per available candidate	Parameters affecting genetic gain from stage 2
Male ($\circlearrowleft$)	1	$0 \leqslant pm2 \leqslant 1$	$\mathbf{Cm2}$	$Tm2 = pm1Cm2$	$(Cm1 + Cm2), (pm2)$
Female ($\circlearrowleft$)	1	$0 \leqslant pf2 \leqslant 1$	$\mathbf{Cf2}$	$Tf2 = pf1Cf2$	$(Cf1 + Cf2), (pf2)$
Unspecified ($\circlearrowleft$ or $\circlearrowleft$)	1	$0 \leqslant p2 \leqslant 1$	$C2$	$T2 = p1C2$	$(C1 + C2), (p2)$

[*] Optimised parameters are written in bold type.

Table III. Parameters combining stages of selection[*].

Sex	Proportion of available candidates selected	Total cost per available candidate	Parameters affecting total genetic gain
Male ($\circlearrowleft$)	$pm = pm1pm2$	$Tm = Tm1 + Tm2$	$(Cm1 + Cm2), (pm1/Qm), (pm2)$
Female ($\circlearrowleft$)	$pf = pf1pf2$	$Tf = Tf1 + Tf2$	$(Cf1 + Cf2), (pf1/Qf), (pf2)$
Unspecified ($\circlearrowleft$ or $\circlearrowleft$)	$p = p1p2$	$Ts = T1 + T2$	$(C1 + C2), (p1/q), (p2)$

[*] Optimised parameters are written in bold type.

Finney (1958) suggested that when two stages of selection were considered, the initial random discard of candidates before measurement was redundant since the first stage of selection performed this function. Incomplete sampling was not considered for the second stage of selection here, since it was always optimal to

choose candidates for further testing on their stage one performance, rather than at random. It was assumed that there were no costs involved with the retention of candidates before stage two measurement results were obtained. Alternatively, it could have been assumed that retention costs were absorbed into the measurement cost allocated.

A computer algorithm was designed to locate parameter values that maximised genetic gain for predetermined funding limits, marginal effectiveness ratios and for final selection intensities in males and females. The algorithm was programmed in Pascal. The program employed a stepping procedure to locate the optima.

Initially the available funds (average funding per selection candidate regardless of sex – T) were divided equally between the sexes ($Tm = T$, $Tf = T$) and then a within-sex optimisation was carried out. Within each sex, the funds were first allocated to testing all candidates in a single stage of selection ($T1 = Ts$, $C1 = T1$, $C2 = 0$). The program then systematically varied the proportion of selection candidates tested (q), the proportion of candidates selected during the first stage of selection ($p1$) and the measurement cost at stage one ($C1$). The measurement cost at stage two fluctuated in response to changes in the other parameters.

If the program found that two-stage selection was superior to single-stage selection, then it tested values of q, $p1$ and $C1$ on either side of the current values. The program then proceeded to alter the parameters in any direction that increased the genetic gain. This process continued until no further increase was registered for any parameter.

When the optimal allocation of resources was determined for the funding allocation already provided to each sex, the resources were redistributed between sexes to test values of Tm on either side of the current value. The within-sex process was repeated for males and then for females. The program then altered the proportion of funds allocated to males from the previous value to whatever tested value was found to be genetically favourable and repeated the entire process until no further genetic improvement was registered by changing this parameter.

The most difficult procedure in the algorithm was assessing the volume of the twice-truncated bivariate normal distribution. This procedure was written following the method of Gupta (1968), and adapting the Fortran algorithms of Thomas (1986) and Hill (1973) to Pascal for the purpose. The exact computation of the algorithm allowed the use of highly correlated stage one and two indices not suitable for the program Selind (Cunningham and Mahon, 1977) which uses an approximate method to obtain the truncated volume. Saxton (1989) made available the program INDCULL 3.0, which performs a function similar to the program used in this simulation.

RESULTS

The allocation of resources between sexes in a breeding program considering multistage selection was analysed for four different cost/benefit structures defined by a range of marginal effectiveness ratios (k). The distribution of funds between sexes (Tm and Tf) was affected by the selection intensities in males and females, the marginal effectiveness ratio and the funding allocation to the selection program (T). Figure 2 describes the optimal division of funds between sexes for different marginal

effectiveness ratios and for various combinations of pf and pm. In the figure the proportion of funds allocated to testing males ($Tm/(Tm + Tf)$) was averaged over values of T between 0.50 and 10 cost units. This enabled the representation of the data in three, rather than four, dimensions. The impact of T on the distribution of available funds between sexes was to decrease the proportion of funds allocated to males as T increased for cases when $pm < pf$ and the reverse when $pm > pf$.
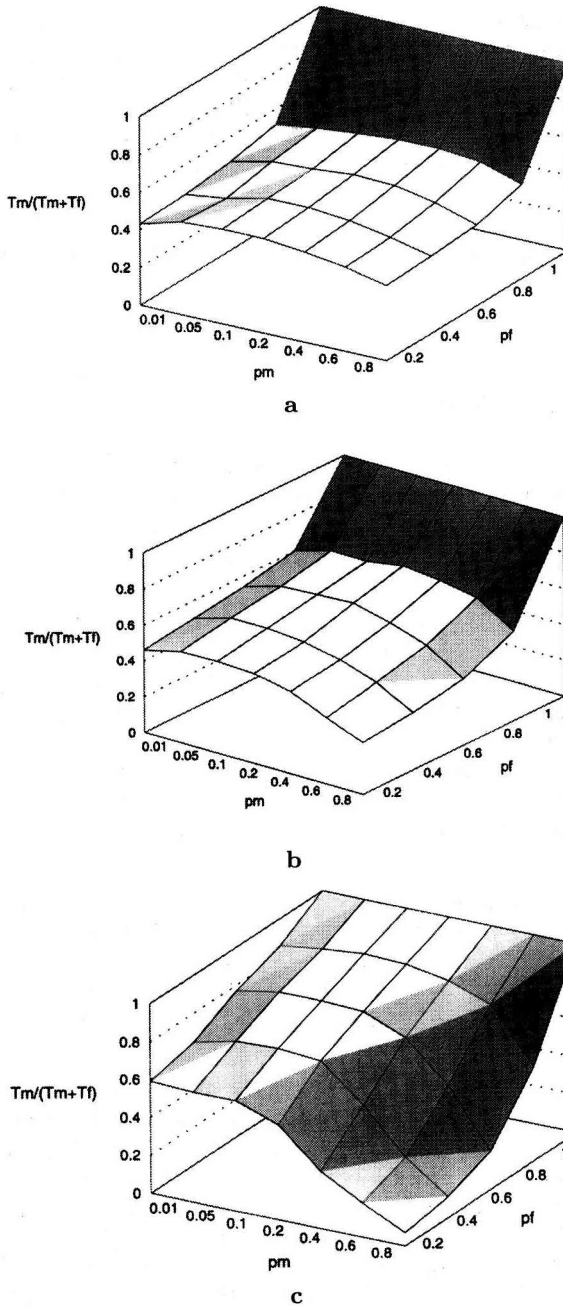
Marginal effectiveness ratio appropriate for a breeding scheme for fleece production

The testing of marginal effectiveness ratios for a wool sheep breeding program revealed that a marginal effectiveness ratio (k) of 0.8 most accurately described the relationship between measurement costs and selection efficiencies for fleece production traits (fig 1). The figure assumed that measurement costs were in Australian dollars. The previously suggested ratio of 0.7 (Jackson et al, 1986) was found to overestimate the effectiveness of selection for the assumed breeding objective. A ratio of $k = 0.8$ was found to underestimate selection efficiency for some measurements but not seriously so.

We can illustrate the use of the presented results (fig 2–5) with a numerical example. Assume a breeder had a population of 1 200 breeding ewes that annually produced 1 000 lambs. The breeder required 50% of ewe lamb progeny and 5% of ram lamb progeny to maintain the breeding population. The assumed marginal effectiveness ratio was 0.8 for a wool sheep breeding scheme as previously described. The breeder had \$2 000 to allocate among the 1 000 male and female selection candidates ($T = 2$). The optimal allocation of funds between the sexes was found to be $Tm/(Tm + Tf) = 0.75$ (fig 2(c)), thus, $Tm = 3$ and $Tf = 1$ (since $T = 2$ and $T = (Tm + Tf)/2$).

After allocating funds between sexes, the optimal division between stages of selection was found within-sex (fig 3–5). The distribution of funds within a sex depended upon the final proportion of selection candidates of that sex required for breeding (p), the assumed marginal effectiveness ratio (k), and the level of funding available to the measurement of that sex (Ts). This latter component was determined by the first analysis.

If the proportion of male candidates required for breeding was 0.05, the level of funding allocated to testing was ($T = 2$), and $k = 0.8$ then figures 3–5 could be consulted to determine Qm (fig 3(c)), $pm1$ (fig 4(c)) and $Tm1/Tm$ (fig 5(c)) for $p = 0.05$ and $Ts = 3$. $Cm1$ and $Cm2$ could then be derived from the relationships $Tm = QmCm1 + pm1Cm2$, and $Tm1/Tm = QmCm1/Tm$. Rearrangement reveals that $Cm1 = (Tm1/Tm) \times (Tm/Qm)$ and $Cm2 = (1 - (Tm1/Tm)) \times (Tm/pm1)$. For the case presented, the appropriate parameters were, $Qm = 0.5$, $pm1 = 0.15$, $Cm1 = 3.90$, and $Cm2 = 7$ (using $T1/Ts = 0.65$). In the case of females ($p = 0.5$, $Ts = 1$, $k = 0.8$), the appropriate distribution was $Qf = 1$, $pf1 = 0.8$, $Cf1 \approx 0.65$ and $Cf2 = 0.44$ (using $T1/Ts = 0.65$). Figures 3–5 present data points every $0.5 \times Ts$ starting at $Ts = 0.50$, and every $0.05 \times p$ starting at $p = 0.05$.
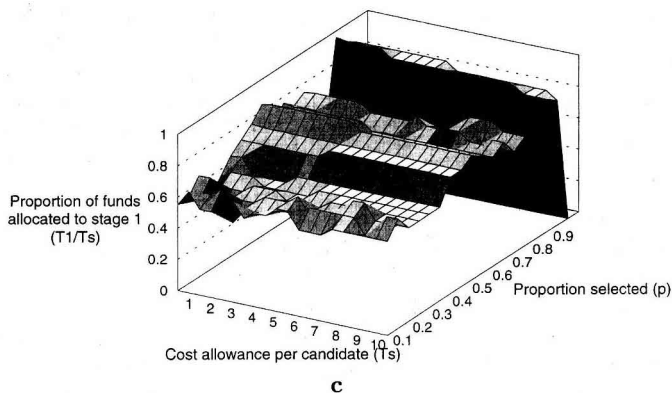
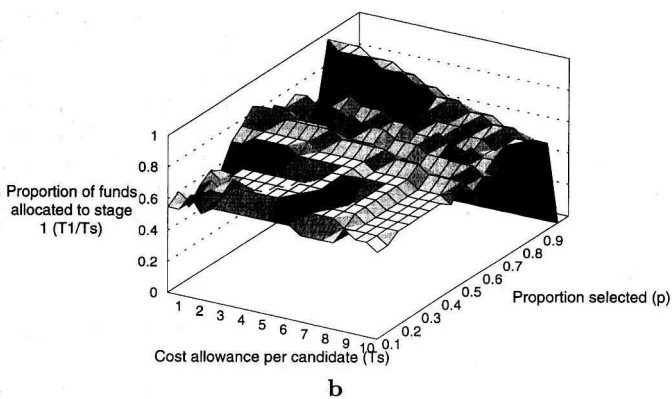**Fig 2.** Optimal proportion of funds allocated to testing males (Tm) for a range of proportions of males (pm) and females (pf) selected when the marginal effectiveness ratio (k) = 0.3 (**a**), 0.5 (**b**) and 0.8 (**c**).
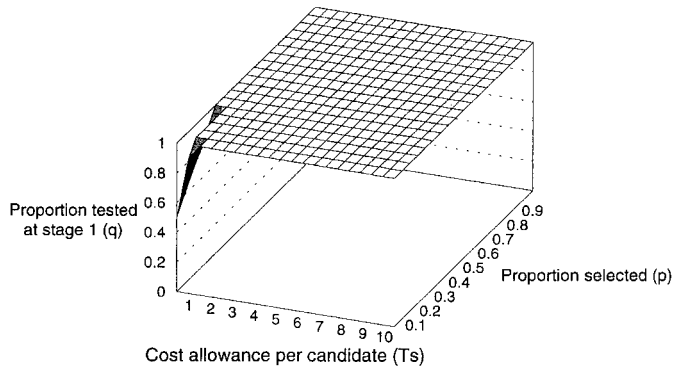
a
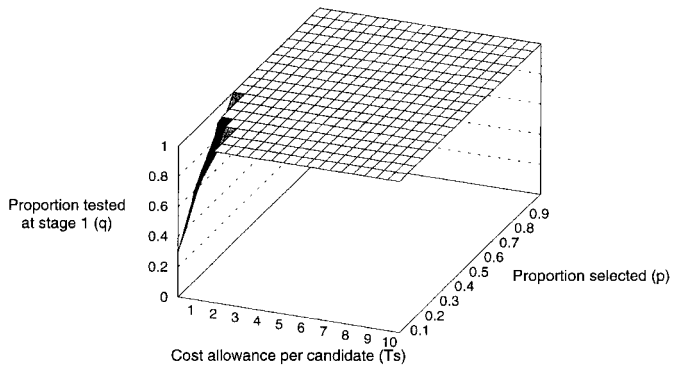
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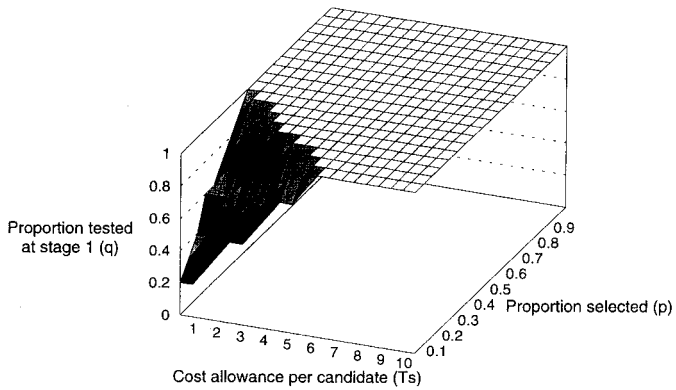
c

Fig 3. Optimal measurement intensity at stage 1 (q) for a range of final selection intensities (p) and per head measurement costs (Ts) when the marginal effectiveness ratio (k) = 0.3 (**a**), 0.5 (**b**) and 0.8 (**c**).
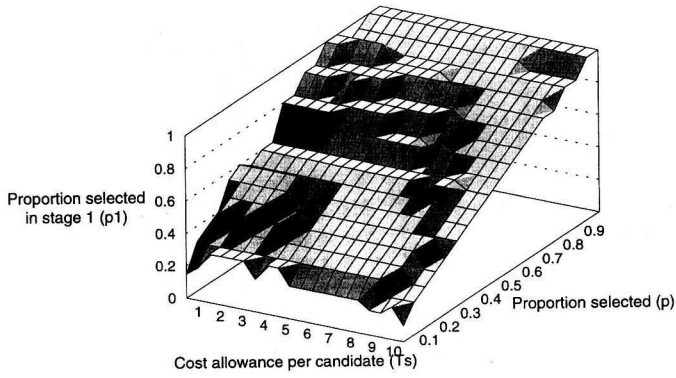
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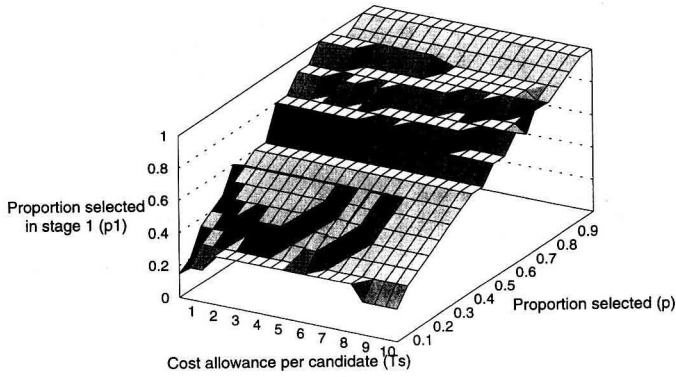
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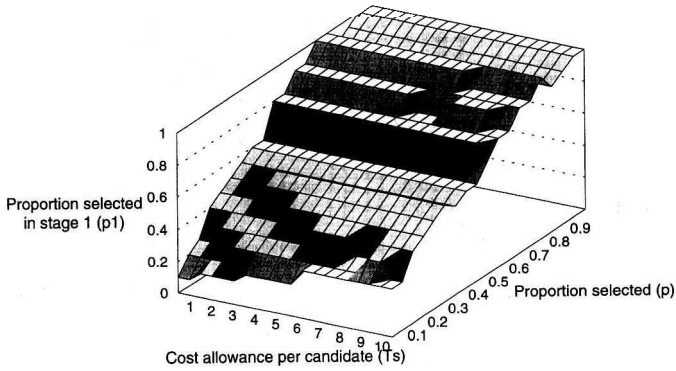
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Fig 4. Optimal proportion selected at stage 1 ($p1$) for a range of final selection intensities (p) and per head measurement costs (Ts) when the marginal effectiveness ratio (k) = 0.3 (**a**), 0.5 (**b**) and 0.8 (**c**).

a

b

c
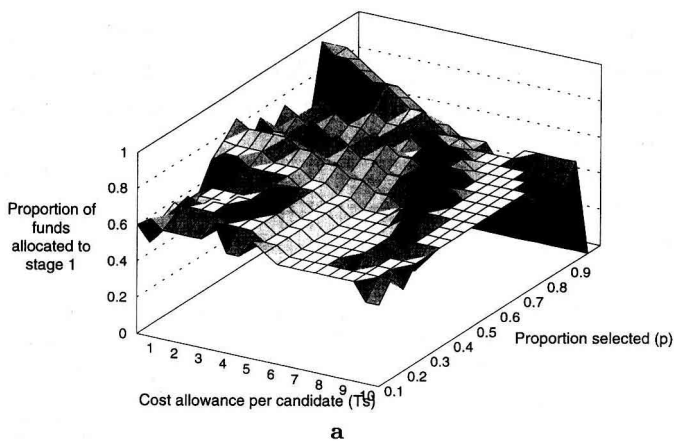
Fig 5. Optimal proportion of funds allocated to testing in the first stage of selection $(T1/Ts)$ for a range of final selection intensities (p) and per head measurement costs (Ts) when the marginal effectiveness ratio $(k) = 0.3$ (**a**), 0.5 (**b**) and 0.8 (**c**).

For the specified conditions the optimum allocation of testing funds was:

Males. Test 250 (0.5×500) ram hoggets at \$3.90 per head in stage one: \$975

Select the best 75 (0.15×500) rams from stage one and retest in stage two at \$7.00 per head: \$525

Females. Test 500 (1×500) ewe hoggets at \$0.65 per head in stage one: \$325

Select the best 400 (0.8×500) ewes from stage one and retest in stage two at \$0.44 per head: \$176

Total outlay: \$2001

In a practical breeding program it is difficult to match the optimal allocation plan precisely. The relationship between selection accuracy and measurement cost is not a smooth one and measurements chosen will only approximate the optima. An appropriate stage one selection criterion for male sheep in the example presented might have been to measure clean fleece weight ($r_{IH} = 0.49$). This would cost approximately \$4.00 per head. In the second stage of selection candidates may then have been measured for average fibre diameter and fibre diameter deviation (\$6.00 per head). A visual classing criterion might also be included in the stage two index such as wool character (\$1.00 per head). The new measurements would then be included with the first stage measurement to produce a comprehensive index score. For females, a selection scheme based on the recommended optima would be difficult to achieve given the measurement types available. In such cases, an appropriate strategy might be to measure all ewes on a characteristic such as wool character or hogget body weight (up to \$1 per head) in a single stage of selection.

General trends in the results

The allocation of resources between sexes (fig 2) usually favoured the sex subject to the highest selection intensity.

An erratic representation of the division of resources between stages of the selection program within-sex ($T1/Ts$) (fig 5) was observed. Similar genetic gains could have been achieved from quite different allocation strategies. In figure 5(c), for example, the optimal selection strategy when $k = 0.8$, $p = 0.85$, $Ts = 5$ ($q = 1.0$, $p1 = 0.95$, $T1/Ts = 0.9$) and a strategy of single stage selection ($q = 1$, $p1 = 1$, $T1/Ts = 0$) demonstrated a difference in genetic gain of $4e^{-4}$. When the proportion of individuals required for breeding was high (> 0.7), the manner in which funds were divided between stages of the selection program was of low importance. Fine adjustments of the selection strategy at high values of p resulted in only minor changes in genetic gain. The recorded optimal allocation of resources may be different depending upon the direction from which the optimum is approached. The program does not recognise improvements in genetic gain of less than 0.000 01.

The optimal proportion of individuals to test in the initial stage of selection was clearly affected by k. As the value of k decreased, the optimal proportion of tested candidates increased. It was always optimal to test all candidates when $p > 0.4$.

Generally, it was optimal to undertake single-stage selection when $p > 0.8$. For regions where $q = 1$, $p1 < 1$, and $T1 = 0$, the application of single-stage selection with incomplete sampling was optimal. For values of $p \leqslant 0.8$, the appropriate level of stage-two testing was dependent upon the final proportion of candidates required.

DISCUSSION

The distribution of funds between sexes almost always favoured the sex subject to the highest selection intensity, usually the male. The distribution of funds favoured females when k was low, the proportion of males ultimately required was very small and resources were not greatly limited. Once there were sufficient funds to achieve near the maximum gain in males there was greater benefit in allocating funds to females than in spending more on males. For $pm = 0.01$ and $pf = 0.2 - 0.5$ the allocation of resources began to favour females for values of T greater than $T = 2.5$. For higher values of pf, the critical value of T was larger. When k was high, it was always preferable to spend resources on the sex subjected to the greatest selection pressure.

Within a sex, the interaction of factors leading to the optimal distribution of funds between stages in the selection program was complex (fig 5). The genetic gain resulting from selection appeared to be fairly robust to small changes in the distribution ratio. Choosing a ratio within the specified bounds should be sufficient to realise a genetic gain close to the optimum.

For the range of input parameters examined the optimum selection strategy varied considerably, particularly for individual measurement cost. Within sex, the alteration in genetic gain with the change in p and T was smooth (fig 6). This phenomenon was also observed by Smith (1969). The genetic gain was greatest when T was high and p was low, and was lowest when T was low and p was high, as is to be expected.
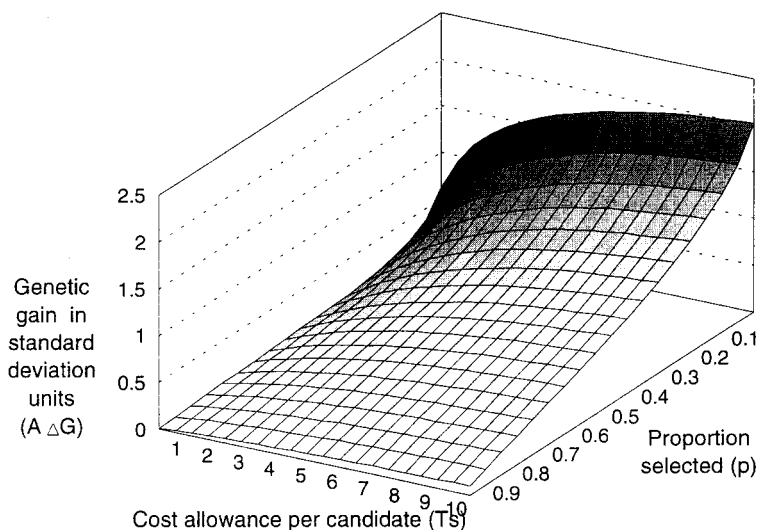
Fig 6. Genetic gain in standard deviation units using the optimal allocation of resources for a range of final selection intensities (p) and measurement cost allocations (Ts) when the marginal effectiveness ratio (k) = 0.8.

Often the differences between gains from different selection strategies were slight, so that there may have been more than one method of obtaining a similar level of gain. The program provides only one such method as output. The different patterns shown reflect that the breeder has options in choosing an efficient selection strategy.

The assumed marginal effectiveness ratio had a substantial impact on the appropriate division of resources between sexes and stages of selection. The results were comparable with those of Wade and James (1990) for similar combinations of k, pm, pf and T. The differences in reported strategy at $pm = 0.01$ and $pf = 0.5$ reflected the difference in the assumed marginal effectiveness ratio. When k was 0.7, measuring females was beneficial and even an inexpensive measurement created some increase in genetic gain. For a higher value of k ($k = 0.8$), there was greater benefit in devoting resources to the more intensely selected sex. Distributing funds to females was found to create less genetic gain than that lost by reducing the efficiency of selection in males.

Jackson et al (1986) presented optima for a range of k and T values, but only one breeding situation was illustrated. The situation is the equivalent to $pm = 0.01$, $pf = 0.45$, and $k = 0.7$. At $T = 4$, it was found to be optimal to distribute 39% of the available funds to testing females. This agrees approximately with the results of this analysis which suggest that between 30 and 40% of funds should be allocated to the measurement of females in the same circumstance.

The results reported in the figures are approximate for any predefined breeding program and are not species-specific. To utilise the data for specific breeding scenarios it is necessary to define a marginal effectiveness ratio appropriate to the species and to the assumed breeding objective.

A progression from this study would be to test the theory using simulated populations of selection candidates. In reality, there are often measurements available at around the same cost that have different selection efficiencies. The measurement costs do not always rise in an even manner. For any defined breeding objective, some low cost measurements may have greater selection accuracy than more expensive measurements.

Factors other than those examined in this study affected the aptitude of the strategies chosen. For example, the use of progeny testing increases the generation interval, and so the genetic gain may not increase as much as would be expected given the high accuracy of selection. The appropriate selection strategy will depend on the types of measurements available and on the assumed breeding objective. Ollivier (1990) considered the optimisation of generation length in a single stage of selection with incomplete sampling. An extension to a scheme involving multi-stage selection would be a logical progression.

The treatment of the problem was based on an Australian Merino breeding industry where few pedigrees are available. If best linear unbiased predictors were used then it is expected that the relationship between expenditure on measurements and measurement accuracy would be altered. There is no reason why the approach taken could not be altered to such a situation.

REFERENCES

Alenda R, Martin TG, Harris DL (1982) Effectiveness of one- and two-stage selection of sires based on own and progeny test for a single trait: Selection of beef sires for 365 day weight. *J Anim Sci* 55, 48-59

Atkins KD (1987) Potential responses to selection in Merino sheep given current industry structure and selection practices. *Merino Improvement Programs in Australia* (BJ McGuirk, ed), Australian Wool Corporation, Melbourne, 299-312

Atkins KD (1990) The scope for early selection to improve wool production. In: *Proceedings of the Eighth Conference, Australian Association of Animal Breeding and Genetics, Hamilton and Palmerston North, New Zealand 5–9 February 1990*, Massey University, Palmerston North, New Zealand, 277-281

Brown GH (1967) The use of correlated variables for preliminary culling. *Biometrics* 23, 551-562

Cochran WG (1951) Improvement by means of selection. *Proc 2nd Berkely Symp on Math, Stat and Probability* (J Neyman, ed), University of California Press, CA, USA 449-470

Cotterill PP, James JW (1981) Optimising two-stage independent culling selection in tree and animal breeding. *Theor Appl Genet* 59, 67-72

Cunningham EP, Mahon GAT (1977) SELIND. A Fortran computer program for genetic selection indexes. User's Guide, Mimeograph

Cunningham EP (1975) Multi-stage index selection. *Theor Appl Genet* 46, 55-61

Finney DJ (1958) Plant selection for yield improvement. *Euphytica* 7, 83-106

Gupta SS (1968) Probability integrals of multivariate normal and multivariate *t*. *Ann Math Stat* 34, 792-838

Hill ID (1973) Algorithm AS66. The Normal integral. *Appl Stat* 22, 424-427

Hugason K, Arnason TH, Norell L (1987) Efficiency of three-stage selection of stallions. *J Anim Breed Genet* 104, 350-363

Jackson N, Lax J, Wilson RL (1986) Sex and selection for fleece weight in Merino sheep. *J Anim Breed Genet* 103, 97-115

Jain JP, Amble, VN (1962) Improvement through selection at successive stages. *J Ind Soc Agric Stat* 14, 88-109

James JW (1966) Incomplete sampling for a fixed proportion. *Aust J Stat* 8, 127-137

Lewer RP, MacLeod IM (1990) One- and two- stage selection indexes for Australian Merino sheep incorporating visual selection criteria. In: *The Fourth World Congress on Genetics Applied to Livestock Production, Edinburgh*, International Committee for World Congress on Genetics Applied to Livestock Production, Edinburgh, UK, 15, 61-64

Morley FHW (1988) Two-stage selection of Merino sheep. *Proc Aust Soc Anim Prod* 17, 258-261

Mueller JP (1984) Single and two-stage selection on different indices in open nucleus breeding systems. *Ann Génét Sél Anim* 16, 103-120

Namkoong G (1970) Optimum allocation of selection intensity in two stages of truncation selection. *Biometrics* 26, 465-476

Ollivier L (1990) Mass selection in livestock using limited testing facilities. *Genet Sel Evol* 22, 109-117

Ponzoni RW (1987) Woolplan – design and implications for the Merino industry. In: *Merino Improvement Programs in Australia* (BJ McGuirk, ed), Australian Wool Corporation, Melbourne, 25-40

Ponzoni RW (1988) Accounting for both income and expense in the development of breeding objectives. In: *Proceedings of the Seventh Conference, Australian Association*

of Animal Breeding and Genetics, Armidale, 26–29 September 1988, University of New England, Armidale, NSW, Australia, 55-56

Robinson DL (1984) A study of sequential variety selection systems. *J Agric Sci Camb* 102, 119-126

Ronningen K (1969) Studies on selection in animal breeding. 1. The efficiency of two-stage selection compared with single-stage selection with respect to progeny testing in animal breeding. *Acta Agric Scan* 19, 149-174

Saxton AM (1989) INDCULL Version 3.0. Independent culling for two or more traits. *J Hered* 80, 166-167

Smith C (1969) Optimum selection procedures in animal breeding. *Anim Prod* 11, 433-442

Thomas GE (1986) Remark ASR65, A remark on algorithm AS76: An integral useful in calculating non-central t and bivariate normal probabilities. *Appl Stat* 35, 310-312

Van Raden PM, Freeman AE, Rothschild MF (1984) Maximising genetic gain under multiple-stage selection. *J Dairy Sci* 67, 1761-1766

Wade CM, Jame JW (1990) Optimal allocation of test funds in selection for genetic gain. In: *Proceedings of the Eighth Conference, Australian Association of Animal Breeding and Genetics, Hamilton and Palmerston North, 5–9 February 1990*, Massey University, Palmerston North, New Zealand, 5-56