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Selection index updating *

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Summary. When traits become evident at different ages or there are large differences in the costs of measuring various traits, selection by independent culling levels may give a higher aggregate economic return than index selection because not all traits need to be measured on all individuals. The problems with optimum independent culling selection is that general solutions are not possible and numerical integration is needed for specific cases. Recently, Xu and Muir (1991) developed a new independent culling level procedure by use of orthogonal transformation of the original characters. With their procedure, explicit solutions for optimum truncation points are possible without numerical integration. As such, the procedure is proficient for any number of stages, and generalized theoretical comparisons of alternative breeding strategies are possible. However, their procedure was limited to the case where selection is for one character at each stage. In this paper, our previous results are extended to the general case of multi-stage index selection, called selection index updating. This procedure is called selection index updating because as traits become available in latter stages, each subsequent index contains all of the traits available up to that stage.

The procedure is to develop sequential indices for each stage such that correlations among indices at different stages are zero. Optimum culling points are obtained for the updating procedure by using Xu and Muir's (1991) iterative equations. Due to the property of orthogonality of the updated indices, aggregate gain can be partitioned into gains due to various stages of selection. Partitioning of aggregate economic gain is useful to breeders who desire to adjust individual trait selection intensity based on facilities available at that stage. Methods are discussed to modify the procedure to obtain maximum aggregate economic return per unit of cost associated with obtaining measures on each trait. An application of multi-stage selection is demonstrated using a set of data for Rhode Island Red layer type chickens. A second example demonstrates the use of multi-stage selection optimized with respect to aggregate economic gain and costs associated with obtaining measurements.

Key words: Independent culling – Cost function – Selection index – Multi-stage selection – Optimum – Transformed culling

Introduction

Excluding costs associated with obtaining measures for all traits on all individuals, index selection is the most efficient procedure for multi-trait improvement in animal (or plant) breeding (Hazel and Lush 1942). However, when traits become evident at different ages or there are large difference in the costs of measuring various traits, selection by independent culling levels may give a higher aggregate economic return because not all traits need to be measured on all individuals (Young 1964; Xu and Muir 1991).

Most developments for independent culling level selection are limited to the case of selecting for a single character at each stage (Young and Weiler 1961; NamKoong 1970; Saxton 1989; Smith and Quaas 1982; Ducrocq and Colleau 1989; Xu and Muir 1991). In practice, it is possible that one or more traits may become available at each of several stages. Young (1964) and Cun-

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ningham (1975) presented more efficient schemes than the conventional independent culling levels by selecting for multiple traits at each stage. These schemes are called multi-stage (index) selections.

A common problem in both independent culling level and multi-stage index selection is that the selection criteria (single trait or an index) are correlated between stages. As such, selection at an earlier stage will cause the distribution of the correlated trait or index to change at a latter stage. Therefore, general solutions for optimum truncation points are not possible, and numerical integration must be used to calculate proper truncation points. Although computer programs are available to determine optimum culling points (Smith and Quaas 1982; Saxton 1989; Ducrocq and Colleau 1989), computer time requirements make these solutions impractical for more than five stages. Also, such approaches do not allow generalized theoretical comparisons of alternative breeding strategies.

Recently, Xu and Muir (1991) developed an independent culling level procedure by use of orthogonal transformation of the original characters. With this procedure, explicit solutions for optimum truncation points are possible without numerical integration. As such, the procedure can be used for any number of stages, and generalized theoretical comparisons of alternative breeding strategies are possible. However, their procedure is limited to the case where selection is for one character at each stage.

In this paper, previous results will be extendend to the general case of multi-stage index selection, called selection index updating. The term "updating" was originally used in the context of multiple regression to indicate a sequentially updated model (Seber 1977, p 336). The term was adopted for present use because of similarities to the index presented in this paper.

Notations and theory

Notation and definitions

- $\boldsymbol{y}$ nx1 vector of phenotypic values of n traits with elements y_i.
- $\boldsymbol{g}$ kx1 vector of genetic values of k traits of genetic importance with elements g_i.
- $\boldsymbol{w}$ kx1 vector of economic weights with elements w_j.
- $\mathbf{P}$ Var($\boldsymbol{y}$) an nxn phenotypic variance-covariance matrix.
- $\mathbf{G}$ Cov($\boldsymbol{y}, \boldsymbol{g}$) an nxk genetic covariance matrix.

Theory

For single-stage index selection, computation of weights for each trait was given by Hazel and Lush (1942) as:

$$\boldsymbol{b} = \mathbf{P}^{-1}\,\mathbf{G}\,\boldsymbol{w} \tag{1}$$

In the general case, where n traits are measured in m stages, $n \geq m$, $\boldsymbol{y}$ can be partitioned into m subvectors according to the number of stages, i.e.

$$\boldsymbol{y} = [\boldsymbol{x}_1\ \boldsymbol{x}_2 \ldots \boldsymbol{x}_m]'$$

where

$$\boldsymbol{x}_1 = [y_1, y_2 \ldots y_{n1}]',\ \boldsymbol{x}_2 = [y_{(n1+1)}, y_{(n1+2)} \cdots y_{(n1+n2)}]',$$
etc.

where n_i is the number of traits selected at the i^{th} stage and $\sum n_i = n$ for $i = 1, 2, \ldots m$.

Corresponding partitions of $\mathbf{P}$ and $\mathbf{G}$ are:

$$\mathbf{P} = \begin{bmatrix} \mathrm{var}(\boldsymbol{x}_1) & \mathrm{cov}(\boldsymbol{x}_1, \boldsymbol{x}_2) \ldots \mathrm{cov}(\boldsymbol{x}_1, \boldsymbol{x}_m) \\ \mathrm{cov}(\boldsymbol{x}_2, \boldsymbol{x}_1) & \mathrm{var}(\boldsymbol{x}_2) \quad \ldots \mathrm{cov}(\boldsymbol{x}_2, \boldsymbol{x}_m) \\ & \vdots \\ \mathrm{cov}(\boldsymbol{x}_m, \boldsymbol{x}_1) & \mathrm{cov}(\boldsymbol{x}_m, \boldsymbol{x}_2) \ldots \quad \mathrm{var}(\boldsymbol{x}_m) \end{bmatrix}$$

$$= \begin{bmatrix} \mathbf{P}_{11} & \mathbf{P}_{12} \ldots \mathbf{P}_{1m} \\ \mathbf{P}_{21} & \mathbf{P}_{22} \ldots \mathbf{P}_{2m} \\ & \vdots \\ \mathbf{P}_{m1} & \mathbf{P}_{m2} \ldots \mathbf{P}_{mm} \end{bmatrix}$$

$$\mathbf{G} = \begin{bmatrix} \mathrm{cov}(\boldsymbol{x}_1, \boldsymbol{g}) \\ \mathrm{cov}(\boldsymbol{x}_2, \boldsymbol{g}) \\ \vdots \\ \mathrm{cov}(\boldsymbol{x}_m, \boldsymbol{g}) \end{bmatrix} = \begin{bmatrix} \mathbf{G}_1 \\ \mathbf{G}_2 \\ \vdots \\ \mathbf{G}_m \end{bmatrix}$$

where $\mathbf{P}_{ij} = \mathrm{cov}(\boldsymbol{x}_i, \boldsymbol{x}_j)$ is a $n_i \times n_j$ submatrix of $\mathbf{P}$ and $\mathbf{G}_i = \mathrm{cov}(\boldsymbol{x}_i, \boldsymbol{g})$ is $n_i \times k$ submatrix of $\mathbf{G}$.

For convenience, let:

$$\boldsymbol{Q}_{ij} = \begin{bmatrix} \mathbf{P}_{11} & \mathbf{P}_{12} \ldots \mathbf{P}_{1j} \\ \mathbf{P}_{21} & \mathbf{P}_{22} \ldots \mathbf{P}_{2j} \\ & \vdots \\ \mathbf{P}_{i1} & \mathbf{P}_{i2} \ldots \mathbf{P}_{ij} \end{bmatrix} \text{ and } \boldsymbol{A}_i = \begin{bmatrix} \mathbf{G}_1 \\ \mathbf{G}_2 \\ \vdots \\ \mathbf{G}_i \end{bmatrix}$$

for $i, j = 1, 2, \ldots m$.

The selection index at the first stage is

$$U_1 = \boldsymbol{b}'_{11} \times \boldsymbol{x}_1\,.$$

At the second stage, the updated index is constructed to include both $\boldsymbol{x}_1$ and $\boldsymbol{x}_2$ as:

$$U_2 = \boldsymbol{b}'_{12} \times \boldsymbol{x}_1 + \boldsymbol{b}'_{22} \times \boldsymbol{x}_2\,.$$

Similarly the updated index at the i^{th} stage has the form of

$$U_i = \boldsymbol{b}'_{1i} \times \boldsymbol{x}_1 + \boldsymbol{b}'_{2i}\,\boldsymbol{x}_2 + \ldots + \boldsymbol{b}'_{ii}\,\boldsymbol{x}_i\,.$$

Let $\mathbf{U}=[\mathrm{U}_1\ \mathrm{U}_2 \ldots \mathrm{U}_\mathrm{m}]'$, then

$$\mathbf{U}=\begin{bmatrix} \mathrm{U}_1 \\ \mathrm{U}_2 \\ \vdots \\ \mathrm{U}_\mathrm{m} \end{bmatrix}=\begin{bmatrix} b'_{11} & 0 & 0 \ldots & 0 \\ b'_{12} & b'_{22} & 0 \ldots & 0 \\ \vdots & \vdots & & \vdots \\ b'_{1\mathrm{m}} & b'_{2\mathrm{m}} & \ldots & b'_{\mathrm{mm}} \end{bmatrix}\begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ \mathrm{x}_\mathrm{m} \end{bmatrix}=\mathbf{B}'\,\boldsymbol{y} \qquad (2)$$

where

$$\mathbf{B}=\begin{bmatrix} b_{11} & b_{11} & \ldots & b_{1\mathrm{m}} \\ 0 & b_{22} & \ldots & b_{2\mathrm{m}} \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \ldots & b_{\mathrm{mm}} \end{bmatrix}$$

is the transformation matrix from $\boldsymbol{y}$ to $\mathbf{U}$. With this transformation, multi-stage index selection on $\mathbf{Y}$ is converted to multi-stage selection on $\mathbf{U}$, as defined by Xu and Muir (1991). The transformation matrix $\mathbf{B}$ is constructed as follows:

$$\begin{aligned} \boldsymbol{b}_1 &=[\boldsymbol{b}_{11}]'=\mathbf{Q}_{11}^{-1}\,\mathbf{A}_1\,\boldsymbol{w} \qquad (3)\\ \boldsymbol{b}_2 &=[\boldsymbol{b}_{12}\,\boldsymbol{b}_{22}]'=\mathbf{Q}_{22}^{-1}\,\mathbf{A}_2\,\boldsymbol{w} \text{ and}\\ \mathbf{b}_\mathrm{m} &=[\boldsymbol{b}_{1\mathrm{m}}\,\boldsymbol{b}_{2\mathrm{m}} \ldots \boldsymbol{b}_{\mathrm{mm}}]'=\mathbf{Q}_{\mathrm{mm}}^{-1}\,\mathbf{A}_\mathrm{m}\,\boldsymbol{w}\,. \end{aligned}$$

However, U_i's constructed in this manner are correlated. As such, selection at an earlier stage will cause the distribution of a correlated trait or index to change at a latter stage so that numeric multiple integration must be used to calculate optimal truncation points.

An alternative method for constructing $\mathbf{U}$ is to find $\mathbf{B}$ such that the correlation between U_i and $\mathrm{H}=\boldsymbol{w}'\,\boldsymbol{g}$ is maximum at each stage with constraints $\mathrm{cov}(\mathrm{U}_\mathrm{i}, \mathrm{U}_\mathrm{j})=0$, for $\mathrm{i}\neq\mathrm{j}$. An index constructed in that manner will have explicitly determined exact solutions for truncation points. However, the genetic gain will be somewhat less than that of the previous procedure because the restriction of orthogonality among the U_i's produces an effect similar to that of a restricted selection index (Kempthorne and Nordskog 1959). But without the transformation, computations to find culling points are exceedingly difficult and may not be achievable with a large number of stage. Reduction in efficiency due to this restriction was examined for the special case of $\mathrm{n}=\mathrm{m}$ by Xu and Muir (1991). But Xu and Muir (1991) also showed that under certain conditions the efficiency of transformed culling may greatly exceed that of conventional multi-stage selection because the latter does not incorporate information from previous stages of selection into the current stage.

The procedure is to develop sequential indices for each stage such that correlations among indices at each stage are zero. The orthogonal transformation matrix is derived as follows: Let

$$\mathbf{B}_\mathrm{i}=\begin{bmatrix} b_{11} & b_{12} & \ldots & b_{1\mathrm{i}} \\ 0 & b_{22} & \ldots & b_{2\mathrm{i}} \\ \vdots & \vdots & & \vdots \\ 0 & 0 & & b_{\mathrm{ii}} \end{bmatrix} \text{ and } \mathbf{J}_\mathrm{i}=\begin{bmatrix} \mathrm{U}_1 \\ \mathrm{U}_2 \\ \vdots \\ \mathrm{U}_\mathrm{i} \end{bmatrix}=\mathbf{B}'_\mathrm{i}\begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_\mathrm{i} \end{bmatrix}$$

be submatrices of $\mathbf{B}$ and $\mathbf{U}$, respectively, at the i^{th} stage. Assume the first i-1 uncorrelated indices were already developed, i.e.,

$$\mathbf{J}_{(\mathrm{i}-1)}=\mathbf{B}'_{(\mathrm{i}-1)}\begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ \mathrm{x}_{\mathrm{i}-1} \end{bmatrix}$$

Obviously, this procedure is started with $\mathrm{i}=2$, but for generality, the development was started at stage i. Optimum $\boldsymbol{b}_\mathrm{i}$'s for the i^{th} stage are found such that

$$\mathrm{cov}(\mathrm{H}, \mathrm{U}_\mathrm{i})=\boldsymbol{w}'\,\mathbf{A}'_\mathrm{i}\,\mathbf{b}_\mathrm{i} \qquad (4)$$

is maximum with constraints of

$$\mathrm{cov}(\mathrm{U}_\mathrm{i}, \mathbf{J}_{(\mathrm{i}-1)})=\boldsymbol{b}'_\mathrm{i}\,\mathbf{Q}_{\mathrm{i}(\mathrm{i}-1)}\,\mathbf{B}_{(\mathrm{i}-1)}=\mathbf{0} \text{ and} \qquad (5)$$

$$\sigma^2_{\mathrm{Ui}}=\boldsymbol{b}'_\mathrm{i}\,\mathbf{Q}_{\mathrm{ii}}\,\boldsymbol{b}_\mathrm{i}=1\,. \qquad (6)$$

The first constraint is for orthogonality while the second is to insure that solutions exist.

After introducing Lagrange multipliers of $\boldsymbol{\Phi}$ and τ, where $\boldsymbol{\Phi}$ is an $\mathrm{i}-1$ vector and τ is a scalar, the optimum $\boldsymbol{b}_\mathrm{i}$ is found by maximizing the following quantity with respect to $\boldsymbol{b}_\mathrm{i}$:

$$\mathrm{T}=(\boldsymbol{w}'\,\mathbf{A}'_\mathrm{i}\,\boldsymbol{b}_\mathrm{i})^2-2\boldsymbol{\Phi}'(\mathbf{B}'_{(\mathrm{i}-1)}\,\mathbf{Q}_{(\mathrm{i}-1)\mathrm{i}}\,\boldsymbol{b}_\mathrm{i})-\tau(\boldsymbol{b}'_\mathrm{i}\,\mathbf{Q}_{\mathrm{ii}}\,\boldsymbol{b}_\mathrm{i}-1)\,. \qquad (7)$$

Setting the derivative of T with respect to $\boldsymbol{b}_\mathrm{i}$ equal to zero, the following is obtained:

$$\delta\mathrm{T}/\delta\boldsymbol{b}_\mathrm{i}=2(\boldsymbol{w}'\,\mathbf{A}'_\mathrm{i}\,\boldsymbol{b}_\mathrm{i})\,\boldsymbol{w}'\,\mathbf{A}'_\mathrm{i}-2\boldsymbol{\Phi}'\,\mathbf{B}'_{(\mathrm{i}-1)}\,\mathbf{Q}_{(\mathrm{i}-1)\mathrm{i}} -2\tau\,\boldsymbol{b}'_\mathrm{i}\,\mathbf{Q}_{\mathrm{ii}}=\mathbf{0}$$

or

$$\boldsymbol{b}_\mathrm{i}=\mathbf{Q}_{\mathrm{ii}}^{-1}\,\mathbf{A}_\mathrm{i}\,\boldsymbol{w}\,\boldsymbol{b}'_\mathrm{i}\,\mathbf{A}_\mathrm{i}\,\boldsymbol{w}\,\tau^{-1}-\mathbf{Q}_{\mathrm{ii}}^{-1}\,\mathbf{Q}_{\mathrm{i}(\mathrm{i}-1)}\,\mathbf{B}_{(\mathrm{i}-1)}\,\boldsymbol{\Phi}\,\tau^{-1}\,.$$

Let

$$\begin{aligned} \boldsymbol{w}'\,\mathbf{A}'_\mathrm{i}\,\boldsymbol{b}_\mathrm{i} &=\boldsymbol{b}'_\mathrm{i}\,\mathbf{A}_\mathrm{i}\,\boldsymbol{w}=\mathrm{e}\\ \mathbf{R}_{(\mathrm{i}-1)\mathrm{i}} &=\mathbf{B}'_{(\mathrm{i}-1)}\,\mathbf{Q}_{(\mathrm{i}-1)\mathrm{i}}\\ \mathbf{R}_{\mathrm{i}(\mathrm{i}-1)} &=\mathbf{Q}_{\mathrm{i}(\mathrm{i}-1)}\,\mathbf{B}_{(\mathrm{i}-1)} \end{aligned}$$

then,

$$\boldsymbol{b}_\mathrm{i}=\mathbf{Q}_{\mathrm{ii}}^{-1}\,[\mathrm{e}\,\mathbf{A}_\mathrm{i}\,\boldsymbol{w}-\mathbf{R}_{\mathrm{i}(\mathrm{i}-1)}\,\boldsymbol{\Phi}]/\tau \qquad (8)$$

and from constraint (5),

$$\boldsymbol{\Phi}=\mathrm{e}[\mathbf{R}_{(\mathrm{i}-1)\mathrm{i}}\,\mathbf{Q}_{\mathrm{ii}}^{-1}\,\mathbf{R}_{\mathrm{i}(\mathrm{i}-1)}]^{-1}\,\mathbf{R}_{(\mathrm{i}-1)\mathrm{i}}\,\mathbf{Q}_{\mathrm{ii}}^{-1}\,\mathbf{A}_\mathrm{i}\,\boldsymbol{w} \qquad (9)$$

After substituting Φ into (8)

$$b_i = (e/\tau)\{\mathbf{I} - \mathbf{Q}_{ii}^{-1}\mathbf{R}_{i(i-1)}[\mathbf{R}_{(i-1)i}\mathbf{Q}_{ii}^{-1}\mathbf{R}_{i(i-1)}]^{-1}\mathbf{R}_{(i-1)i}\} \cdot \mathbf{Q}_{ii}^{-1}\mathbf{A}_i w$$

Since (e/τ) is a constant to all elements of b_i, the term may be set to 1, thus

$$b_i = \{\mathbf{I} - \mathbf{Q}_{ii}^{-1}\mathbf{R}_{i(i-1)}[\mathbf{R}_{(i-1)i}\mathbf{Q}_{ii}^{-1}\mathbf{R}_{i(i-1)}]^{-1}\mathbf{R}_{(i-1)i}\} \cdot \mathbf{Q}_{ii}^{-1}\mathbf{A}_i w \tag{10}$$

where $\mathbf{I}$ is an identity matrix with the same dimension as $\mathbf{Q}_{ii}$. The effect of these restriction is to multiply the unrestricted b_i given in (3) by the matrix in brackets.

The resulting index, U_i, is converted to standard normal Z_i by standardizing the b_i's,

$$^*b_i = b_i(b_i' \mathbf{Q}_{ii} b_i)^{-1/2} \tag{11}$$

so that $(^*b_i' \mathbf{Q}_{ii} {}^*b_i) = 1$. Let $\mathbf{\Delta Z} = [\Delta Z_1 \, \Delta Z_2 \ldots \Delta Z_m]$ be the vector of standardized selection differentials of indices, i.e., selection intensities. The vector of genetic gains, ΔG, is predicted by

$$\Delta G = G' B \Delta Z \tag{12}$$

The corresponding gain in aggregated breeding value is

$$\Delta H = w' \Delta G = w' G' B \Delta Z \tag{13}$$

Multi-stage selection for desired genetic gains

This procedure is particularly applicable to situations in which genetic gains to accomplish a breeder's objective are known. For the special case of one trait selected at each stage, the vector of selection differentials ($\mathbf{\Delta Z}$) necessary to accomplish a set of desired genetic gains (ΔG) was given by Xu and Muir (1991) as:

$$\Delta Z = (\mathbf{T}')^{-1} G (G' \mathbf{P}^{-1} G)^{-1} \Delta G$$

where $(\mathbf{T}')^{-1}$ is the transformation matrix from Y to Z, i.e., $Z = (\mathbf{T}')^{-1} Y$. But, for the general case the transformation matrix is $\mathbf{B}'$; therefore replacing $(\mathbf{T}')^{-1}$ with $\mathbf{B}'$ gives:

$$\Delta Z = \mathbf{B}' G (G' \mathbf{P}^{-1} G)^{-1} \Delta G. \tag{14}$$

From ΔZ, truncation points, or proportions selected at each stage, can be obtained from tables relating selection intensity with proportion selected such as Falconer's (1981) Table A.

Optimization with respect to economic gain

In order to form an optimum index, a ΔZ vector must be chosen such that ΔH is maximum for a fixed total proportion selected. For each Z_i let u_i and q_i be the corresponding truncation point and proportion selected. The relationship between ΔH and ΔZ, given previously by (13), is:

$$\begin{aligned}\Delta H &= \mathbf{w}' \Delta G \\ &= \mathbf{w}' G' B \Delta Z \\ &= \sum_{i=1}^{m} \mathbf{w}' A_i' \mathbf{b}_i' \Delta Z_i \qquad (15) \\ &= \sum_{i=1}^{m} \mathbf{w}' A_i' \mathbf{b}_i \left[\frac{\exp(-1/2\, u_i^2)}{q_i (2\pi)^{1/2}}\right]. \qquad (16)\end{aligned}$$

Because (16) gives an explicit expression relating ΔH to the truncation point of each transformed variable, the optimum ΔH can be found by maximizing ΔH with respect to all u_i given the constraint $\prod_{i=1}^{m} q_i = p$, i.e., the product of proportions selected at each stage must equal a predetermined total proportion selected, p. To maximize ΔH with this restriction, the constraint must be incorporated into the computations for ΔZ. This result may be accomplished by expressing the last selection differential, ΔZ_m, as a dependent function of the others. Set the proportion selected for the last variable as:

$$q_m = \frac{p}{\left[\prod_{i=1}^{m-1} q_i\right]} \quad \text{therefore} \quad \Delta Z_m = \frac{\exp(-1/2\, u_m^2)}{q_m (2\pi)^{1/2}}$$

where $u_m = \text{PROBIT}(1 - q_m)$. Optimum truncation points can now be found by taking partial derivatives of ΔH with respect to u_i and setting those equal to zero.

$$\frac{\delta \Delta H}{\delta u_i} = \mathbf{w}' A_i' \mathbf{b}_i \left[\frac{\delta \Delta Z_i}{\delta u_i}\right] + \mathbf{w}' A_m' \mathbf{b}_m \left[\frac{\delta \Delta Z_m}{\delta u_m}\right]\left[\frac{\delta u_m}{\delta u_i}\right] = 0$$

where

$$\frac{\delta \Delta Z_i}{\delta u_i} = \Delta Z_i (\Delta Z_i - u_i)$$

and

$$\frac{\delta u_m}{\delta u_i} = -\frac{\Delta Z_i}{\Delta Z_m} \qquad \text{(see Xu and Muir, 1991).}$$

Therefore,

$$\begin{aligned}\frac{\delta \Delta H}{\delta u_i} &= \mathbf{w}' \mathbf{A}_i' \mathbf{b}_i \Delta Z_i (\Delta Z_i - u_i) \\ &\quad - \mathbf{w}' \mathbf{A}_m' \mathbf{b}_m \Delta Z_m (\Delta Z_m - u_m)\left[\frac{\Delta Z_i}{\Delta Z_m}\right] = 0 \\ &= \mathbf{w}' \mathbf{A}_i' \mathbf{b}_i (\Delta Z_i - u_i) - \mathbf{w}' \mathbf{A}_m' \mathbf{b}_m (\Delta Z_m - u_m) = 0\end{aligned}$$

or

$$\mathbf{w}' \mathbf{A}_i' \mathbf{b}_i (\Delta Z_i - u_i) = \mathbf{w}' \mathbf{A}_m' \mathbf{b}_m (\Delta Z_m - u_m) = \tau \tag{17}$$

where τ is a constant chosen such that

$$\prod_{i=1}^{m} q_i = p. \tag{18}$$

Since ΔZ_i, q_i, and u_i are interrelated by:

$$q_i = 1 - \Phi(u_i), \text{ where}$$

$$\Phi(u_i) = \frac{1}{(2\pi)^{1/2}} \int_{-\infty}^{u_i} \exp(-1/2\, Z^2)\, dZ$$

$$\Delta Z_i = \left[\frac{\exp\{-\frac{1}{2} u_i^2\}}{q_i (2\pi)^{1/2}}\right]$$

values of τ and u_i that satisfy (17) may be found by trial and error. Alternatively, a system of m + 1 nonlinear eqations may be constructed based on relationships given by (17) and (18): (19)

$$\begin{bmatrix} \mathbf{f} \\ \\ r \end{bmatrix} = \begin{bmatrix} f_1 \\ f_2 \\ \vdots \\ f_m \\ r \end{bmatrix} = \begin{bmatrix} \mathbf{w}' \mathbf{A}_1' \mathbf{b}_1 (\Delta Z_1 - u_1) - \tau \\ \mathbf{w}' \mathbf{A}_2' \mathbf{b}_2 (\Delta Z_2 - u_2) - \tau \\ \vdots \\ \mathbf{w}' \mathbf{A}_m' \mathbf{b}_m (\Delta Z_m - u_m) - \tau \\ \prod_{i=1}^{m} q_i - p \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ 0 \end{bmatrix}$$

This set of nonlinear equation may be solved iteratively for τ and u_i's using a multidimensional Newton's method (see Xu and Muir, 1991).

Optimization with respect to economic gain and costs.

The previous procedure was developed to maximize ΔH regardless of the relative costs associated with obtaining measures on the various traits. The procedure may be modified to obtain a maximum ΔH per unit of cost (NamKoong 1970; Cunningham 1975) for any given cost function. NamKoong (1970) proposed a linear cost function for two-stage selection. The general linear cost function per individual for m stages of selection may be expressed as

$$\text{cost} = a_1 + \sum_{i=2}^{m} a_i \left[\prod_{j=1}^{i-1} q_j\right] \qquad (20)$$

where a_i is the cost of obtaining measures on all traits in the i^{th} stage and q_i is the proportion selected at the i^{th} stage. Given the linear cost function, the quantity to be maximized is

$$Q = \Delta H/\text{cost} \qquad (21)$$

subject to constraint (18). Since numeric integration is not necessary, a set of q_i's which maximizes Q with the given constraint can be found by trial and error. But, a general computer program for any number of traits or stages of selection, written in SAS/IML (SAS 1985), is available from the authors.

Examples

Optimization with respect to economic gain

An application of multi-stage selection will be demonstrated with poultry breeding using a set of data for Rhode Island Red layer type chickens reported by Akbar et al. (1986).

Traits to be selected are:

y_1 = age of sexual maturity, defined as the age in days at which the first trap-nested egg was laid;
y_2 = rate of lay, defined as 100 x (total eggs in the laying period)/(total days in the laying period);
y_3 = body weight, in pounds, measured at 32 weeks of age;
y_4 = average egg weight, in ounces per dozen, of all the eggs laid to 32 weeks of age.

The traits of genetic concern are the same as those selected. The corresponding economic weights for the four traits are

$$\mathbf{w} = [-3.555 \quad 19.536 \quad -113.746 \quad 48.307]'$$

The phenotypic and genetic variance-covariance matrices are

$$\mathbf{P} = \begin{bmatrix} 137.178 & -90.957 & 0.136 & 0.564 \\ -90.957 & 201.558 & 1.103 & -1.231 \\ 0.136 & 1.103 & 0.202 & 0.104 \\ 0.564 & -1.231 & 0.104 & 2.874 \end{bmatrix}$$

and

$$\mathbf{G} = \begin{bmatrix} 14.634 & -18.356 & -0.109 & 1.233 \\ -18.356 & 32.029 & 0.103 & -2.574 \\ -0.109 & 0.103 & 0.089 & 0.023 \\ 1.233 & -2.574 & 0.023 & 1.225 \end{bmatrix}$$

The overall proportion selected is set to $p = 20\%$, leading to $i = 1.39981$.

Single-stage index selection

Selection decisions must be made after all traits are measured on all birds. The index weights are:

$$\mathbf{b} = \mathbf{p}^{-1} \mathbf{G} \mathbf{w} = [-0.5924 \quad 2.7793 \quad -49.4459 \quad 3.7539]'.$$

Gains predicted from use of this index are:

$$\Delta \mathbf{G} = \mathbf{G} \mathbf{b} (\mathbf{b}' \mathbf{P} \mathbf{b})^{-1/2} i = [-1.5267 \quad 2.6150 \quad -0.1217 \quad -0.1359]'$$

and $\Delta \mathbf{H} = \mathbf{w}' \Delta \mathbf{G} = 63.7947$.

Two-stage index selection

Since age at sexual maturity (y_1) is measured earlier than the other three traits, selection can be completed in two stages with

$\mathbf{x}_1 = y_1$ and $\mathbf{x}_2 = [y_2\ y_3\ y_4]'$

$n_1 = 1,\ n_2 = 3$ and $n = n_1 + n_2 = 4.$

(i) Index for the first stage:

$U_1 = \mathbf{b}'_{11}\mathbf{x}_1 = \mathbf{b}'_1\mathbf{x}_1$ with

$\mathbf{b}_1 = \mathbf{Q}_{11}^{-1}\mathbf{A}_1\mathbf{w} = -2.4688$ and $\sigma_{U1} = (\mathbf{b}'_1\mathbf{P}\mathbf{b}_1)^{1/2}$
$= 28.9154$

the rescaled $\mathbf{b}_1$ is obtained by

$^*\mathbf{b}_1 = \mathbf{b}_1/\sigma_{U1} = -0.0854$

now $\mathbf{B}_1 = {}^*\mathbf{b}_1$,

(ii) Index for the second stage:

$$U_2 = \mathbf{b}'_{12}\mathbf{x}_1 + \mathbf{b}'_{22}\mathbf{x}_2 = \mathbf{b}'_{22}\begin{bmatrix}\mathbf{x}_1\\ \mathbf{x}_2\end{bmatrix}$$

where

$$\mathbf{b}_2 = \{\mathbf{I} - \mathbf{Q}_{22}^{-1}\mathbf{R}_{21}[\mathbf{R}_{12}\mathbf{Q}_{22}^{-1}\mathbf{R}_{21}]^{-1}\mathbf{R}_{12}\}\mathbf{Q}_{22}^{-1}\mathbf{A}_2\mathbf{w}$$
$$= [1.8764\quad 2.7793\quad -49.4459\quad 3.7539]'$$

$\sigma_{U2} = (\mathbf{b}'_2\mathbf{Q}_{22}\mathbf{b}_2)^{1/2} = 35.2260.$

The rescaled $\mathbf{b}_2$ is

$^*\mathbf{b}_2 = \mathbf{b}_2/\sigma_{U2} = [0.0533\quad 0.0789\quad -1.4037\quad 0.1066]'.$

Now, by combining $^*\mathbf{b}_1$ and $^*\mathbf{b}_2$, the $\mathbf{B}$ matrix is obtained:

$$\mathbf{B} = \begin{bmatrix} -0.0854 & 0.0533\\ 0 & 0.0789\\ 0 & -1.4037\\ 0 & 0.1066 \end{bmatrix}$$

and

$\Delta H = 28.9154\,\Delta Z_1 + 35.2260\,\Delta Z_2.$

Using a multidimensional Newton's method (Xu and Muir 1991) the optimal sets of ΔZ_i's, u_i's and q_i's were:

$\mathbf{\Delta Z} = [0.7315\quad 1.0227]'$

$\mathbf{u} = [-0.1062\quad 0.3350]'$

$\mathbf{q} = [0.5423\quad 0.3688]'$

giving a maximum economic gain of:

$\Delta H = 57.177$

Four-stage independent culling level selection

For comparison, Xu and Muir's (1991) transformed culling procedure was used. Their procedure is limited to a single trait selected at each stage and is thus a special case of the procedure described in this paper. The notation is that of Xu and Muir (1991).

The vector of $\mathbf{Z}$ scores was constructed as

$\mathbf{Z} = (\mathbf{T}')^{-1}\mathbf{y}$ where $\mathbf{T}'\mathbf{T} = \mathbf{P}.$

From the set of parameters previously given,

$$(\mathbf{T})^{-1} = \begin{bmatrix} -0.0854 & 0.0558 & 0.0151 & 0.0022\\ 0 & 0.0841 & 0.0193 & 0.0065\\ 0 & 0 & -2.2835 & -0.3447\\ 0 & 0 & 0 & 0.5973 \end{bmatrix}$$

and

$$\Delta H = 28.9154\,\Delta Z_1 + 27.7960\,\Delta Z_2 + 20.7053\,\Delta Z_3 + 6.2844\,\Delta Z_4.$$

Using the multidimensional Newton's method, the optimal sets of ΔZ_i's, u_i's, and q_i's were:

$\mathbf{\Delta Z} = [0.8026\quad 0.7484\quad 0.4131\quad 0.0005]'$

$\mathbf{u} = [0.0073\quad -0.0788\quad -0.6974\quad -3.6584]'$

$\mathbf{q} = [0.4971\quad 0.5314\quad 0.7572\quad 0.9999]'$

giving a maximum economic gain of:

$\Delta H = 52.5657.$

Table 1 provides a summary of results of various selection schemes. Although the relative efficiency of two-stage to single-stage selection is approximately 90%, the two-stage procedure allows approximately 46% of chickens to be discarded at the first stage. If the time period between the first and second stages is large enough, cost savings due to earlier culling may compensate loss of gains.

Results from four-stage independent culling show a relative efficiency of only 82% as compared to single-stage selection. Since y_2, y_3, and y_4 were measured at the same time, with little difference in cost, separation of those traits would not be advantageous.

Table 1. Predicted gains with differing stages of selection

Gain	Selection scheme		
	One-stage	Two-stage	Four-stage
ΔG_1	−1.5256	−1.3071	−1.4997
ΔG_2	2.6150	2.3025	2.5515
ΔG_3	−0.1217	−0.1161	−0.0744
ΔG_4	−0.1359	−0.1170	−0.2293
ΔH	63.7947	57.1773	52.5657
Relative efficiency	1.0000	0.8963	0.8240

Optimization with respect to economic gain and costs (Q)

For White Leghorn poultry, Wing and Nordskog (1982) gave the phenotypic and genetic correlation, heritabilities, and economic weights for the traits body weight (W), egg mass (M), and feed consumption (F), all measured in grams. Measurement of these traits might occur as follows. Since birds are handled at time of housing, or at approximately 20 weeks of age, body weight should be measured at this time. Egg mass is determined by multiplying the average egg weight, sampled for short duration, by the total number of eggs produced. Assume that egg production will be measured fom 20 through to 36 weeks while egg weights will be samples at 36 weeks of age for 1 week. Similarly, due to cost considerations, feed consumption is estimated from data collected over a short duration. Assume that feed consumption will be determined from that ingested during a 4-week period starting at 37 weeks of age. With this schedule, a generation interval of 1 year can be maintained.

Costs associated with obtaining these measures per bird were estimated from the Poultry Research Facility of Purdue University. Assuming an hourly wage of $ 10.00, these were 16.7 ¢, 179 ¢, and 250 ¢ respectively for W, M, and F. Although genetic parameters given by Wing and Nordskog (1982) were for slightly different time periods, they will serve for this example, which were:

$$\mathbf{w} = \begin{bmatrix} 0.022 \\ 23.0 \\ -4.32 \end{bmatrix} \quad \mathbf{P} = \begin{bmatrix} 32829 & 281.5 & 1231.4 \\ 281.5 & 48.1 & 40.59 \\ 1231.4 & 40.59 & 135.9 \end{bmatrix}$$

$$\mathbf{G} = \begin{bmatrix} 20682 & 123.73 & 746.35 \\ 123.73 & 8.802 & 12.79 \\ 746.35 & 12.79 & 50.96 \end{bmatrix}$$

Single-stage and certain multi-stage indices, optimized with respect to the economic objective but ignoring costs associated with obtaining the measures, are given in Table 2. Comparison of Cases 1 and 4 shows that the relative efficiency of three-stage selection was 99.8% of that for single-stage index. However, costs associated with the single-stage index were 81.4% higher than those for the three-stage. As a result, relative return (Q) was 81.0% higher for three-stage selection than for single-stage.

Alternative multi-stage indices, optimized with respect to economic objectives and costs associated with obtaining the measures, are given in Table 3. Comparison of three-stage selection, with and without optimization with respect to costs (Cases 4 and 8), shows that optimizing reduced ΔH by 2.67 ¢ per bird but also reduced costs by 34.6 ¢ per bird. Comparison of all alternative optimized selection programs shows that two-stage selection, based only on traits W and M (Case 9), was the most efficient.

Table 2. Comparison of alternative single- and multi-stage selection schemes without optimization with respect to costs assoiated with obtaining measurements

Case	Stage	Traits selected[a]	Percentage selected	Cost (¢)	ΔH (¢)[b]	Q%[c]
1	1	W M F	0.20	445.7	30.97	6.95
2	1	W M	0.20	195.7	30.92	15.80
3	1	W F	0.20	266.7	12.96	4.86
4	1	W	1.00			
	2	W M	0.20			
	3	W M F	1.00	245.7	30.91	12.58
5	1	W	1.00			
	2	W M	0.20	195.7	30.91	15.79

[a] W, Pullet weight; M, egg mass; F, feed consumption
[b] ΔH = Aggregate change in economic value based on W, M, and F
[c] Q% = (100 × ΔH)/costs

Table 3. Comparison of alternative multi-stage selection schemes optimized with respect to **Q** (ΔH/cost), where costs were those associated with obtaining measurements

Case	Stage	Traits selected[a]	Percentage selected (q_i)	Cost (¢)	ΔH (¢)[b]	Q%
6	1	W	0.415			
	2	W M F	0.482	194.7	18.69	9.69
7	1	W M	0.205			
	2	W M F	0.976	246.9	30.69	12.43
8	1	W	0.805			
	2	W M	0.250			
	3	W M F	0.994	211.1	29.24	13.38
9	1	W	0.445			
	2	W M	0.449	96.4	19.82	20.57
10	1	W	0.415			
	2	W F	0.482	120.5	8.04	6.67
11	1	M	0.205			
	2	M F	0.975	230.2	30.17	13.10

[a] W, Pullet weight; M, egg mass; F, feed consumption
[b] ΔH = Aggregate change in economic value based on W, M, and F

While genetic improvement was greatly reduced with that program, costs associated with obtaining those improvements were also greatly reduced as compared to other programs. Note that the cost associated with measuring feed consumption would have to be close to zero before that trait would be included in an optimized index because the efficiency of single-stage index selection without measuring F (Case 2) was 99.8% as efficient as an index in which the trait was included (Case 1).

Comparison of Cases 5 and 9 dramatically illustrates the effect of optimizing with respect to costs. In both cases birds were culled first based on weight, but in Case 5 less than 1% were culled based on that trait, while in the other, 55% were culled. Since the cost of measuring M was over 10 times that of W, the optimum program was to cull severely based on W.

Discussion

This particular multi-stage index selection is called selection index updating because as traits become available in latter stages, each subsequent index contains all of the traits available up to that stage. These indices are similar to Young's (1964) part and whole indices. But, Young's (1964) indices were correlated, which creates difficulties in determining optimum culling points.

Due to the property of orthogonality of our updated indices, the aggregate gain can be partitioned into gains due to various stages of selection. The partitioning is:

$$\Delta H = \mathbf{w}' \mathbf{G}' \mathbf{B} \Delta \mathbf{Z} = \Delta H_1 + \Delta H_2 + \ldots + \Delta H m$$

where $\Delta H_i = \mathbf{w}' \mathbf{A}_i' \mathbf{b}_i \Delta Z_i$ is the gain due to the i^{th} stage of selection. Partitioning of ΔH is useful to breeders who desire to adjust ΔZ_i on the basis of facilities available at that stage.

Xu and Muir's (1991) transformed culling procedure is a special case of multi-stage index selection where the number of traits equals the number of stages. In that paper $(\mathbf{T}')^{-1}$ was used as the transformation matrix to obtain $\mathbf{Z} = (\mathbf{T}')^{-1} \mathbf{y}$, where $\mathbf{T}' \mathbf{T} = \mathbf{P}$, whereas in this paper, $\mathbf{B}'$ was used to transform $\mathbf{y}$ into $\mathbf{Z}$, i.e., $\mathbf{Z} = \mathbf{B}' \mathbf{y}$. The equivalence between $\mathbf{B}$ and $\mathbf{T}^{-1}$ will be shown as follows: since, only one trait is selected at each stage, $\mathbf{B}$ is an $n \times n$ upper triangular matrix of full rank and $\mathbf{y} = (\mathbf{B}')^{-1} \mathbf{Z}$. The phenotypic variance matrix $\mathbf{P}$ can be expressed as $\mathrm{Var}(\mathbf{y}) = \mathbf{P} = (\mathbf{B}')^{-1} \mathbf{B}^{-1} = \mathbf{T}' \mathbf{T}$. Because both $\mathbf{T}$ and $\mathbf{B}$ are upper triangular, the decomposition of $\mathbf{P}$ is unique (Martin et al. 1965), therefore $\mathbf{B} = \mathbf{T}^{-1}$.

Use of the linear cost function given in the example assumes that profit is generated from the sale of produced by the animals rather than the sale of the animal itself. Such a cost function is reasonable for vertical and self-contained enterprises, such as some swine and beef cattle operations. However, the poultry industry is structured horizontally. Primary breeders earn profits from sale of their animals to others who rear the animal and sell the product. Demand for a particular breeder's birds is based on the perceived genetic superiority of that breed. As such, rather than maximizing the ratio of aggregate economic gain to measurement costs, an optimum index should maximize profits to the primary breeder from sales of genetic stock. A simplistic profit function is:

$$\text{Profit} = N(b\,kp\,\Delta H - \text{vcost}) - \text{fcost}$$

where: ΔH is a measure of the genetic superiority of the breed, k is the number of times the breed is multiplied before distribution, b is the slope of the supply-demand curve, N is the number of birds in the breeding nucleus, vcost are variable costs, such as those in the previous linear cost function plus feed, and fcost are fixed costs. Such a function will place more emphasis on genetic superiority and will give results intermediate to those presented in Tables 2 and 3. If k is large, as in the poultry industry, and b is close to 1 – i.e., a buyer will pay 1 ¢ more for a bird if the bird is expected to produce 1 ¢ more worth of product – the optimum index will be close to that which maximizes ΔH ignoring costs associated with measuring traits.

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