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Internal estimation and controlled selection with applications to sheep

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Summary. This paper examines the relationship of economic weights, a_i, with a general economic value surface. It is inferred that the a_i may vary across the population, as they can depend on the mean vector for the characters of interest. It is shown how these ideas extend to provide simple mechanisms for controlled selection. The problem of estimation is raised, and it is suggested that the procedures can be efficiently implemented, even in small populations, by a system of 'internal' parameter estimation. This makes the entire selection programme independent of externally generated estimates of genetic parameters.

Key words: Selection index – Economic weights – Value-function – Prior economic weights – Internal estimation

Introduction

In farm animals, mass selection for a single character poses no technical difficulty. If positive selection is practiced, the population is simply ranked with respect to the character and the best animals are kept for breeding. Moreover, if facilities permit, some assortative mating can also be used to achieve a marginal improvement in efficiency.

Provided genetic predictions are not needed, this sort of selection can proceed without the estimation of any parameters at all. But in the case of selection for multiple characters, things are different. Inefficient methods, such as tandem selection and independent culling level selection (Falconer 1983), can still be used without any parameter estimates and the same restrictions apply as for a single character. However, such techniques pay no attention to the relative economic weights of the characters concerned, and it is in part for this reason that the selection index is introduced.

Index selection has an efficiency advantage over other methods of combined selection (Cochran 1950); it is also easy to apply once the index value for each individual has been calculated, when selection proceeds as for single character selection. Nowadays, the computation of index values is mostly done by computer, so that this part of implementing index selection poses no real obstacle. Thus, the main penalty incurred in achieving the increased efficiency rests with the necessary estimations of economic weights and genetic parameters which accompany the method.

Such estimates usually come from large scale-field trials undertaken at the state or national level. The figures obtained are subject to the usual vagaries of sampling error; but more importantly, they may also suffer in terms of relevance. The requisite trials are expensive to run and they only embrace particular breeds at particular locations, in certain years. In fact, estimates used to construct a modern selection index may rely on old data on a different breed and collected in an entirely different part of the country. To say that this is unsatisfactory is an understatement.

What is required is a structure which allows breeders to estimate their own set of parameters for their own particular population, year by year. The objections of relevance, then, no longer apply; but they are replaced by questions of feasibility. In this paper we intend to show that the above ideal is not just possible, but desirable and natural in the modern computer era.

We address three main problems, each with wide ramifications which cannot be fully explored here. Nevertheless, using these ideas, enough detail is developed to allow an in-depth analysis of a simplified sheep breeding model. Expected genetic advances under a variety of selection procedures are calculated to demonstrate their short- and long-term relative behaviours, and Monte Carlo simulations are used to examine the feasibility of frequent within-flock estimation of parameters. A more extensive preliminary report of this work, which also supplies the full technical background to a standard approach to constrained selection, can be found in Tallis and Leppard (1988).

Specifically, we first set up a structure which assigns economic values to members of a particular population. This formulation depends on the economically important characters of the breed, and it shows how the relative economic weighting of these characters may depend on their expectations, μ. We let $R(\mu)$ represent this economic value function, and breeders with different mean structures in their populations may require different economic weights for the most efficient progress.

Second, a method of constrained selection is introduced which only uses $R(\mu)$ and the simple theory of unconstrained selection. Some of the arbitrariness of classical constrained selection is avoided or, at any rate, clarified by this method. Moreover, it allows complete control of the rates of progress of the constrained characters in relation to those of the unconstrained, economically important characters. This treatment introduces great simplification and we call it the method of prior economic weights.

Finally, we show how an efficient index selection method can be developed and implemented, even for small populations of 200 or less. The required parameters are estimated 'internally' and annually within the population by obtaining the necessary regressions of offspring on mid-parent values. Then, using the economic weighting appropriate to the population, the required index can be computed.

Although applications are discussed in terms of sheep breeding, the principles have a much wider relevance. The main thrust of this work is to provide a general setting for selection which, when combined with local estimation procedures, allow the highly parameterised methods of classical constrained and unconstrained selection to be by-passed.

Notation

We assume that there are m characters, $\mathscr{C}_i$, of interest. The mean of $\mathscr{C}_i$ is μ_i and for $i = 1, 2, \ldots, r < m$, it is required to move μ_i to $\mu_i + k_i$. Thus, the aim of selection is to make the maximum economic progress in a way to be specified, while controlling the direction of selection for the first r. This is a standard specification of constrained selection.

We use the following notation:

p_i; phenotype of $\mathscr{C}_i$, $E[p_i] = 0$, $i = 1, \ldots, m$
g_i; additive genotype of $\mathscr{C}_i$, $E[g_i] = 0$, $i = 1, \ldots, m$
a_i; economic weight of $\mathscr{C}_i$, $i = 1, \ldots, m$
$P = V[p]$; phenotypic covariance matrix
$G = V[g]$; additive genetic covariance matrix
x; selection vector for males
y; selection vector for females
$g'_{(1)} = (g_1, \ldots, g_r)$; $g'_{(2)} = (g_{r+1}, \ldots, g_m)$
$a'_{(1)} = (a_1, \ldots, a_r)$; $a'_{(2)} = (a_{r+1}, \ldots, a_m)$
$C_{x_j} = C[g_{(j)}, x]$; $C_{y_j} = C[g_{(j)}, y]$, $j = 1, 2$
μ_i = mean of $\mathscr{C}_i$; $i = 1, \ldots, m$
k_i = amount by which μ_i is to be altered, $i = 1, \ldots, r$
$X = V[x]$, $Y = V[y]$, $E[x] = 0$, $E[y] = 0$

Note that the fate of the μ_i, $i = r + 1, \ldots, m$ is of no consequence within the ambit of the problem. Moreover, a standard situation arises where x and y both represent p. Then, $C_{x_1} = C_{y_1} = G_1$, the $r \times m$ sub-matrix of G consisting of the first r rows and $C_{x_2} = C_{y_2} = G_2$, an $(m - r) \times m$ matrix consisting of the rest of G.

There are some well known solutions to the constrained selection problem; see Tallis and Leppard (1988) for a comprehensive account of one of these, and for a recent review, see Brascamp (1984). However, we will not pursue this line further here as the results are highly parametric and somewhat involved. Instead, we will suggest an alternative approach which is essentially much simpler.

The value function $R(\mu)$

We now introduce a scalar function of $\mu + p$, $R(\mu + p)$, which reflects the economic value of phenotype p. The function R is assumed to have continuous first derivatives, so that, for

$$\mathscr{R}'(\mu) = \left(\frac{\partial R(\mu)}{\partial \mu_1}, \ldots, \frac{\partial R(\mu)}{\partial \mu_m}\right)$$

$$\Delta R(\mu) = R(\mu + \Delta) - R(\mu) \approx \mathscr{R}'(\mu)\Delta. \tag{1}$$

Now, let $g(1)$ be the vector of additive genotypes for an individual in generation one. Then we assume that $g(1)$ is related to the x and y vectors of its parents by the linear model

$$g(1) = B_x x + B_y y + \varepsilon \tag{2}$$

where $\varepsilon \perp x$, $\varepsilon \perp y$, $E(\varepsilon) = 0$, and under panmixia

$$V[g(1)] = B_x X B'_x + B_y Y B'_y + V[\varepsilon] = G$$

so that

$$V[\varepsilon] = G - B_x X B'_x - B_y Y B'_y.$$

We examine the special case mentioned above, where $x = p_x$, $y = p_y$ and

$$g(1) = B(p_x + p_y) + \varepsilon \tag{3}$$

and, assuming $p = g + e$, $e \perp g$, $E(e) = 0$, $V[e] = E$, $V[p] = G + E$ and

$$E[g(1)(p_x + p_y)'] = 2BP;$$

$$B = \tfrac{1}{2}C[g(1), p_x + p_y]\,P^{-1} = C[g(1), p_x]\,P^{-1}$$

by symmetry. Under usual assumptions, $g(1) = \frac{1}{2} g_x + \delta$ and $C[g(1), p_x] = \frac{1}{2} G$, so that

$$B = \tfrac{1}{2} G P^{-1}. \tag{4}$$

Now, under selection on x and y, the expectation of $g(1)$ changes from 0 to

$$E_s[g(1)] = B_x E_s[x] + B_y E_s[y] \tag{5}$$

where $E_s[x]$, $E_s[y]$ are the expected values of x and y after selection. In general, vector selection is cumbersome and leads to difficult formulae. For convenience, therefore, and also for defensible reasons of optimality (Cochran 1950), we introduce the linear functions $I_x = b'_x x$ and $I_y = b'_y y$. Selection is now carried out with respect to I_x and I_y.

We need two additional models

$$\begin{aligned} x | I_x &= \frac{C[x, I_x] I_x}{V[I_x]} + \varepsilon_x = \frac{X b_x I_x}{b'_x X b_x} + \varepsilon_x \\ y | I_y &= \frac{C[y, I_y] I_y}{V[I_y]} + \varepsilon_y = \frac{Y b_y I_y}{b'_y Y b_y} + \varepsilon_y . \end{aligned} \tag{6}$$

Hence, under selection,

$$E_s[x] = \frac{X b_x}{b'_x X b_x} E_s[I_x]; \qquad E_s[y] = \frac{Y b_y}{b'_y Y b_y} E_s[I_y].$$

Define $i_x = E_s[I_x/\sqrt{V[I_x]}]$, $i_y = E_s[I_y/\sqrt{V[I_y]}]$. Then if I is approximately normally distributed, $i \simeq \phi(a)/\alpha$ where $\alpha = 1 - \Phi(a)$ is the proportion saved. $\phi(x) = e^{-x^2/2}/\sqrt{2\pi}$, $\Phi' = \phi$. Thus finally,

$$E_s[x] = \frac{X b_x i_x}{\sqrt{b'_x X b_x}}; \qquad E_s[y] = \frac{Y b_y i_y}{\sqrt{b'_y Y b_y}}$$

and

$$E_s[g(1)] = \frac{B_x X b_x i_x}{\sqrt{b'_x X b_x}} + \frac{B_y Y b_y i_y}{\sqrt{b'_y Y b_y}}. \tag{7}$$

Therefore, in the first generation, μ is changed to $\mu + E_s[g(1)]$ and

$$\Delta R(\mu) = R\left(\mu + \frac{B_x X b_x i_x}{\sqrt{b'_x X b_x}} + \frac{B_y Y b_y i_y}{\sqrt{b'_y Y b_y}}\right) - R(\mu). \tag{8}$$

When the curvature of $R(\mu)$ at μ is substantial, Eq. (8) can be numerically maximised with respect to b_x and b_y, under the set of constraints if necessary, so that the greatest gain in R is achieved. On the other hand, if a linear approximation to $\Delta(\mu)$ is valid,

$$\Delta R(\mu) \approx \mathscr{R}'(\mu)\left(\frac{B_x X b_x i_x}{\sqrt{b'_x X b_x}} + \frac{B_y Y b_y i_y}{\sqrt{b'_y Y b_y}}\right) \tag{9}$$

which can be maximised directly when there are no constraints to the selection program (Rao 1973),

$$b_x = 2 B'_x \mathscr{R}(\mu); \qquad b_y = 2 B'_y \mathscr{R}(\mu). \tag{10}$$

In the special case examined earlier, $B_x = B_y = \frac{1}{2} G P^{-1}$ and $b_x = b_y = P^{-1} G \mathscr{R}(\mu)$. In the latter equation, $\mathscr{R}(\mu)$ plays the role of the vector of economic weights, a.

Thus, the classical selection index formula is retrieved as the optimal index for this general setting. The point that the expression emphasises, though, is that $a = \mathscr{R}(\mu)$, and the economic weights may depend on the mean vector, μ, for the population. Of course, if $R(\mu)$ is a plane, a will be independent of μ.

The method of prior economic weights

Suppose that it is required to move the means of $\mathscr{C}_1, \ldots, \mathscr{C}_r$ from initial values $\mu_1, \ldots, \mu_r$ to near $\mu_1 + k_1, \ldots, \mu_r + k_r$ while continuing to make gains in some economic composite of the remaining characters. Then, if $v' = (v'_{(1)}, v'_{(2)})$ is the mean vector of the population after some generations of selection, it is possible to form a composite $R(v) = f(R_1(v_{(1)}), R_2(v_{(2)}))$, where f is a suitable function, $R_1(v_{(1)})$ is a special function having zero derivatives when $v_{(1)} = \mu_{(1)} + k_{(1)}$ and $R_2(v_{(2)})$ is dictated by the actual economics of the last $m - r$ characters. For instance, we can take $f(R_1(v_{(1)}), R_2(v_{(2)}))$ as $R_1(v_{(1)}) + R_2(v_{(2)})$ or $R_1(v_{(1)}) \times R_2(v_{(2)})$ and

$$R_1(v_{(1)}) = c \exp\left\{-\sum_1^r (v_i - \mu_i - k_i)^2/c_i\right\}, \tag{11}$$

where c, c_i are chosen to adjust the relative speeds of selection, both in the direction $\mu_{(1)} + k_{(1)}$ and with respect to the unconstrained characters $\mathscr{C}_{r+1}, \ldots, \mathscr{C}_m$.

Now, standard unconstrained selection theory can be applied using, in obvious notation, $\mathscr{R}'(v) = (\mathscr{R}'_1(v_{(1)}), \mathscr{R}'_2(v_{(2)}))$ as the economic weights. The components of $\mathscr{R}(v)$ emphasise the direction of selection and as $\mathscr{R}_1(v_{(1)})$ tends to the null vector, pressure is removed from the characters requiring constraint and maximum advance is made with respect to $R_2(v_{(2)})$.

The choice of $R_1(v_{(1)})$ is open. This is because these characters are not tied into the economics of selection directly and it is simply a matter of preference in what direction, if any ($k_{(1)} = 0$), selection takes place and at what relative speeds. This is less restrictive than constrained selection, which simply controls the direction of $v_{(1)}$ but not the rates of progress to the optimum.

We refer to $R_1(v_{(1)})$ as a 'prior' value function and to $\mathscr{R}_1(v_{(1)})$ as 'prior' economic weights at $v_{(1)}$. By making R_1 sufficiently flat in a region surrounding $\mu_{(1)} + k_{(1)}$, it is possible to restrain the means of $\mathscr{C}_1, \ldots, \mathscr{C}_r$ to remain in a region, rather than require that they achieve specific values. It is this latter requirement that leads to some difficulties in the application of standard constrained selection, since when $v_{(1)}$ is near the target, subsequent generations of selection may produce significant 'overshoot' and the process can oscillate in an unattractive fashion.

In summary, then, by suitably defining $R(v)$ beyond $R_2(v_{(2)})$, it is possible to completely control the selection process without recourse to constrained selection. Moreover, the difficulty of interpreting $a_{(1)}$ (see Sect. 2) is avoided; it seems incongruous that $a_{(1)} \neq 0$ at $\mu_{(1)} + k_{(1)}$, since this appears to be a conflict of definition. When economic weights are defined in terms of a sensible prior value surface, they will automatically vanish at the optimum. Thus, $R(v)$ is the key to understanding and manipulating selection for economic progress.

The expected rate of progress can only be calculated recursively by means of the formula

$$v_{n+1} = v_n + \frac{B_{nx} X_n b_{nx} i_x}{\sqrt{b'_{nx} X_n b_{nx}}} + \frac{B_{ny} Y_n b_{ny} i_y}{\sqrt{b'_{ny} Y_n b_{ny}}} \tag{12}$$

when v_n is the mean vector for the m characters after n rounds of selection, $b_{nx} = 2B'_{nx}\mathscr{R}(v_n)$, $b_{ny} = 2B'_{ny}\mathscr{R}(v_n)$, and X_n and Y_n are the appropriate variance matrices for x and y in the nth year, and B_{nx}, B_{ny} the appropriate regression matrices. To set things in motion, put $v_0 = \mu$; also as a first approximation, assume X and Y do not depend on n.

The change in R_2 is $R_2(v_{(2)n+1}) - R_2(v_{(2)n})$ and this too can be assessed step by step, while the rate of approach of $v_{(1)}$ to $v_{(1)} + k_{(1)}$ can be examined by isolating the first r components of v_n to give $v_{(1)n}$. Various values of c and c_i in $R_1(v_{(1)})$ can be tried until selection controls the characters in an acceptable way. There is no substitute for this sort of numerical tuning of the procedure, before it is put into practice, since the effect of the relationship between R_1 and R_2 on the rates of progress under selection cannot be otherwise predicted, due to the involvement of the derivatives of R.

Internal estimation

In order to carry out selection, all that is needed are the vectors b_{nx} and b_{ny}. These, in turn, are specified in terms of $\mathscr{R}(v_n)$ and the regression matrices B_{nx} and B_{ny}. If $R(\mu)$ is given, then $\mathscr{R}(v_n)$ is specified, while the regression matrices can be estimated directly from parent-offspring data to give $\hat{B}_{nx}$, $\hat{B}_{ny}$.

If predictions of genetic progress are also required from Eq. (12), the matrices X_n and Y_n must be also estimated. This is achieved by calculating the covariance matrices for x and y prior to selection.

When $x = p$, $y = p$, $X = Y = P$, and P can be estimated by combining the estimates in the male and female populations. However, the regression matrix B can be estimated using mid-parent vectors.

When a surface $R(\mu)$ is not available, so that $\mathscr{R}(\mu)$ is not known, the latter may be estimated by regression. Since the phenotypic p vectors for each individual are known, it may be possible to assign a value $R(\mu + p_i) = \mathscr{R}_i$ to the ith animal. Then on the grounds that

$$R_i = R(\mu + p_i) \approx R(\mu) + \mathscr{R}'(\mu)\, p_i \tag{13}$$

a model of the form $R_i = \beta_0 + \beta' p_i + \varepsilon_i$ is appropriate to use for the estimation of $\mathscr{R}(\mu) = \beta = a$, the vector of economic weights at μ.

In this section we have outlined the notion of internal estimation. Its practical implementation would depend on circumstances. For instance, in any general selection program involving many sheep breeders, it may be feasible to estimate the required parameters in certain representative flocks. At least, in this way, breed, district, year and management-specific estimates could be obtained to apply to the entire industry.

Family selection and repeated records

So far we have only considered selection based on the single vector x for males and y for females. To simplify matters, suppose that x and y are both p, the phenotypic vector of ultimate interest. For the selection of a particular individual, one may have additional information to p. In particular, these may be the measurement vector of its sire, which will be labelled x; the average of l records on its dam, $\bar{y}(l)$ and the average of k half sibs $\bar{s}(k)$.

We are required to predict $\omega = g'\mathscr{R}(v)$ for each individual, where v is the current mean of the characters and so we postulate a linear model

$$\omega = p' b_1 + \bar{s}'(k) b_2 + x' b_3 + \bar{y}'(l) b_4 + \varepsilon .$$

To calculate the b_i we need to solve

$$\begin{bmatrix} C[p,\omega] \\ C[\bar{s},\omega] \\ C[x,\omega] \\ C[\bar{y},\omega] \end{bmatrix} = \begin{bmatrix} V[p] & C[p,\bar{s}] & C[p,x] & C[p,\bar{y}] \\ \cdot & V[\bar{s}] & C[\bar{s},x] & C[\bar{s},\bar{y}] \\ \cdot & \cdot & V[x] & C[x,\bar{y}] \\ \cdot & \cdot & \cdot & V[\bar{y}] \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$$

dropping the indexes l and k.

This becomes

$$\begin{bmatrix} G\mathscr{R}(v) \\ \frac{1}{4}G\mathscr{R}(v) \\ \frac{1}{2}G\mathscr{R}(v) \\ C_{\bar{y}}(l)\mathscr{R}(v) \end{bmatrix} = \begin{bmatrix} P & \frac{1}{4}G & \frac{1}{2}G & C_{\bar{y}}(l) \\ \cdot & \frac{1}{k}(P + (k-1)G/4) & \frac{1}{2}G & 0 \\ \cdot & \cdot & P & 0 \\ \cdot & \cdot & \cdot & \bar{Y}(l) \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} \tag{14}$$

or

$$C = M\,b, \quad \text{say.}$$

We only need to estimate P, $\overline{Y}(l)$, G and $C_{\bar{y}}(l)$. Both P and $\overline{Y}(l)$ are available directly, P from the progeny group before selection, $\hat{P}$ and $\overline{Y}(l) = V[\bar{y}(l)]$ from the breeding ewes with at least l records, $\hat{\overline{Y}}(l)$. To estimate G, use the model

$$g(1) = B(x+y)/2 + \varepsilon$$

where only the first record of each ewe is used. Then, $\hat{G} = \hat{B}\,\hat{P}$ where $\hat{B}$ is the estimated matrix of regression coefficients of offspring on mid-parent. Finally, apply the model

$$g(1) = B_{\bar{y}}(l)\,\bar{y}(l) + \varepsilon$$

to show that $C_{\bar{y}}(l) = C[g(1), \bar{y}(l)] = B_{\bar{y}}(l)\,\overline{Y}(l)$ and $\hat{C}\,\bar{y}(l) = \hat{B}_{\bar{y}}(l)\,\overline{Y}(l)$, where $\hat{B}_{\bar{y}}(l)$ is estimated as for $\hat{B}$, using the first l records of those ewes with at least l.

Substitute the estimates in Eq. (14) to get

$$\hat{C} = \hat{M}\,\hat{b}, \text{ i.e. } \hat{b} = \hat{M}^{-1}\,\hat{C}. \tag{15}$$

The residual variance, $V(\varepsilon)$ is given by

$$V(\varepsilon) = \sigma^2 = \mathscr{R}'(v)\,G\,\mathscr{R}(v) - C'\,M^{-1}\,C \tag{16}$$

which is estimated by replacing G, C and M by their respective estimates.

Let ω_1 and ω_2 be the ω values for ewes 1 and 2 with index values I_1 and I_2, then we prefer 1 to 2 if and only if $P(\omega_1 > \omega_2) > \frac{1}{2}$. But, conditionally on I_1 and I_2, $\omega_i \sim N(I_i, \sigma_i^2)$ and ω_1 is independent of ω_2. Note that σ_i^2 is the conditional variance of ω_i, given I_i.

Hence

$$\begin{aligned} P(\omega_1 > \omega_2 \mid \omega_2) &= P\left(\frac{\omega_1 - I_1}{\sigma_1} > \frac{\omega_2 - I_1}{\sigma_1} \,\middle|\, \omega_2\right) \\ &= 1 - \Phi((\omega_2 - I_1)/\sigma_1) \end{aligned}$$

and

$$P(\omega_1 > \omega_2) = \int_{-\infty}^{\infty} [1 - \Phi((\sigma_2 t + I_2 - I_1)/\sigma_1)]\,\phi(t)\,dt. \tag{17}$$

The last integral shows clearly that, when $\sigma_1 = \sigma_2$, $P(\omega_1 > \omega_2) \geq \frac{1}{2}$ iff $I_1 \geq I_2$. However, in principle, a complete ordering of the ewe flock must be by means of Eq. (17).

Discrete characters

We finally consider briefly characters which can be scaled to 0 and 1. If Z is such a character, then $E[Z] = P(Z=1) = \theta$.

If it can be reasonably assumed that the expectation of Z for the offspring of parents with prediction vectors x and y is essentially linear in x and y, then analysis can proceed as for continuous characters. Thus, in Eq. (2) let $g(1)$ represent offspring phenotype, measured from the generation mean, and Eq. (7) its expectation under index selection. It is then clear that the rest of the argument does not depend in any way on the type of variables included.

This discussion emphasises an essential robustness of internal estimation. The only assumption which is used to maximise gains from one generation to the next is that the expectation of progeny means is linearly related to suitable vectors x and y in the parents. The nature of this linear relationship can change with time, for whatever reasons, but this does not interfere with the procedures, since the regression relationships are assessed year by year.

There are some obvious restrictions on θ. If $\theta \simeq 0$, no real selection for Z is possible. When $\theta \simeq 1$, selection can be restricted to those animals with $Z = 1$, and the linear models are then conditional on $Z = 1$.

Illustrations

To see how the techniques of previous sections may perform in practice, they must be applied to a reasonably credible breeding model and the expected genetic gains assessed. We choose to work with a simplified model for a breeding flock, labelled $\mathscr{E}$. Considerable detail is unavoidable here if the demonstrations are to be sufficiently coherent and convincing.

Our purpose is to show: (a) how the method of prior economic weights previously described compares with the standard method of constrained selection for directing genetic progress; (b) how a value function, R, can be used for unconstrained selection and to examine the expected genetic progress under this system; (c) how a combined system of constrained selection, using the method of prior economic weights for some characters, and unconstrained selection, using a value function for the rest of the characters, performs. (d) Simulations: The assessments in (a), (b) and (c) assume that the value surface, R, and matrices P, G are known. We use a large simulation study to verify that selection can proceed using 'internal estimation' techniques when R and the parameter matrices are not known. Results achieved in this Monte Carlo work are compared with known expectations calculated from the actual input parameters.

The following assumptions are made.

Initial structure

(I) There is an initial flock of N ewes at time zero, $t = 0$ and N remains invariant during later years, i.e. there are not deaths or losses of ewes which remain in $\mathscr{E}$.

(II) There are two groups of lambs of ages $\frac{1}{2}$ and $1\frac{1}{2}$ years in the system, labelled $\mathscr{L}_{\frac{1}{2}}$ and $\mathscr{L}_{1\frac{1}{2}}$. Each group is of size θN, where 100θ is the lambing percentage of the flock $\mathscr{E}$.
(III) In $\mathscr{L}_{1\frac{1}{2}}$ there are equal numbers of males and females.

Continuation

(IV) Mating takes place at $t = 0$. A certain number of the females in $\mathscr{L}_{1\frac{1}{2}}$, N_e, ($N = k N_e$, $k = 1, 2 \ldots$) are selected to replace N_e ewes of $\mathscr{E}$, and N_r males are selected for breeding. When mating has occurred, all the males of $\mathscr{L}_{1\frac{1}{2}}$ and all unselected females of $\mathscr{L}_{1\frac{1}{2}}$ are discarded.
(V) At $t = \frac{1}{2}$, the N ewes of $\mathscr{E}$ give birth to θN lambs of age 0: group $\mathscr{L}_0$. The original group $\mathscr{L}_{\frac{1}{2}}$ has aged to become $\mathscr{L}_1$.
(VI) At $t = 1$, the previous groups $\mathscr{L}_0$ and $\mathscr{L}_1$ have aged to become $\mathscr{L}_{\frac{1}{2}}$ and $\mathscr{L}_{1\frac{1}{2}}$. At this time, selection from $\mathscr{L}_{1\frac{1}{2}}$ and mating with $\mathscr{E}$ occurs. The procedure cycles, with steps (IV) to (VI) repeated.
(VII) Genetic progress is assessed with respect to the group $\mathscr{E}$ just prior to mating, i.e. at times $t = 0, 1, 2$, etc.

A suitable flow description which provides the essence of the above features is given in Table 1.

It should be noted that the discarding of ewes from $\mathscr{E}$ is on the basis of age only and no account is taken of fertility. In practice, fertility is extremely important and the culling of unproductive ewes from $\mathscr{E}$ would be expected to increase θ.

As stated in (VII), selection occurs at $t = 0, 1, 2, \ldots$ and the selection index is calculated in the following manner:

Let the mean vector of $\mathscr{L}_{1\frac{1}{2}}$ be $\boldsymbol{\mu}(\mathscr{L})$ and using N_e replacement ewes for $\mathscr{E}$ gives a selection proportion of $\alpha_e = \dfrac{2N_e}{\theta N}$, since the number of available ewes in $\mathscr{L}_{1\frac{1}{2}}$ is $\frac{1}{2}\theta N$. The mean of the selected group of ewes is then

$$\boldsymbol{\mu}_e = \boldsymbol{\mu}(\mathscr{L}) + \frac{G\mathbf{b}}{\sqrt{\mathbf{b}' P \mathbf{b}}}\, i_e$$

where $i_e = \dfrac{\phi(a_e)}{\alpha_e}$, $\phi(t) = \dfrac{e^{-t^2/2}}{\sqrt{2\pi}}$. The scalar a_e is defined by

$$\alpha_e = \int_{-\infty}^{a_e} \phi(t)\, dt = \Phi(a_e).$$

If N_r selected rams are required for breeding, then α_r and $\boldsymbol{\mu}_r$ are obtained in the same way as α_e and $\boldsymbol{\mu}_e$.

From the structure of $\mathscr{E}$ indicated in (IV), there are k natural age layers in $\mathscr{E}$. The oldest layer is discarded and leaves a group with mean vector $\boldsymbol{\mu}^*(\mathscr{E})$. When the selected group of ewes from $\mathscr{L}_{1\frac{1}{2}}$ is added to those ewes retained, the resultant mean vector is

$$\boldsymbol{\mu}(\mathscr{E}) = \left(1 - \frac{1}{k}\right) \boldsymbol{\mu}^*(\mathscr{E}) + \frac{1}{k}\boldsymbol{\mu}_e. \tag{18}$$

The mean vector of the progeny of the new matings of $\mathscr{E}$ with the selected rams is then

$$\tfrac{1}{2}(\boldsymbol{\mu}(\mathscr{E}) + \boldsymbol{\mu}_r) = \mathbf{v} + \frac{G\mathbf{b}}{\sqrt{\mathbf{b}' P \mathbf{b}}}\, \tau, \tag{19}$$

where

$$\mathbf{v} = \tfrac{1}{2}\left(1 - \frac{1}{k}\right)\boldsymbol{\mu}^*(\mathscr{E}) + \tfrac{1}{2}\left(1 + \frac{1}{k}\right)\boldsymbol{\mu}(\mathscr{L})$$

$$\tau = \tfrac{1}{2}\left(\frac{i_e}{k} + i_r\right).$$

Since Eq. (19) can be put in the form of Eq. (9) by introducing economic weights, the coefficients of the selection index are given by

$$\mathbf{b} = P^{-1} G \mathscr{R}(\mathbf{v}). \tag{20}$$

With $\mathbf{b}$ determined, the updated mean of $\mathscr{E}$ and the mean of the progeny (the new group $\mathscr{L}_0$) can be calculated.

We demonstrate the method of prior economic weights first, using $\mathscr{C}_1$ = fibre diameter and $\mathscr{C}_2$ = stable length and $R_1(v_{(1)})$ as defined by Eq. (11), $v_{(1)}$ being the current population mean. Ultimately, however, we will use the two additional characters $\mathscr{C}_3$ = wool weight and $\mathscr{C}_4$ = body weight. The necessary parameters which are required for demonstration have been obtained from Turner and Young (1969) and are shown in Table 2. The imperial units are retained for consistency with previously published work.

Table 1. Flock size over time

Time		Numbers in Group				
		$\mathscr{E}$	$\mathscr{L}_0$	$\mathscr{L}_{1/2}$	$\mathscr{L}_1$	$\mathscr{L}_{1\,1/2}$
0	Assessment and selection	N	0	θN	0	θN
1/2	Birth	N	θN	0	θN	0
1	Assessment and selection	N	0	θN	0	θN

Table 2. Genetic parameters

$\boldsymbol{\mu}' = (23, 12, 9, 90)$

$$P = \begin{bmatrix} 2.8 & 0.16 & 0.21 & 1.68 \\ & 0.9 & 0.32 & 0.32 \\ & & 0.7 & 1.4 \\ & & & 45 \end{bmatrix} \qquad G = \begin{bmatrix} 1.3 & 0.03 & 0.09 & 0.93 \\ & 0.35 & 0.12 & -0.16 \\ & & 0.20 & 0.83 \\ & & & 29.6 \end{bmatrix}$$

Table 3. Comparison of methods for constrained selection

A						B					
Mating	R	$\mu(\mathscr{E})$				Mating	R	$\mu(\mathscr{E})$			
1	0.14	23.00	12.00	9.00	90.00	1	0.14	23.00	12.00	9.00	90.00
2	0.17	23.06	12.02	9.01	90.03	2	0.17	23.05	12.03	9.01	90.02
3	0.21	23.41	12.16	9.08	90.21	3	0.21	23.34	12.19	9.09	90.15
4	0.31	23.55	12.22	9.11	90.28	4	0.31	23.46	12.26	9.12	90.20
5	0.44	23.86	12.36	9.17	90.43	5	0.43	23.73	12.42	9.18	90.31
6	0.63	24.07	12.46	9.22	90.54	6	0.62	23.93	12.53	9.23	90.40
7	0.77	24.33	12.60	9.28	90.65	7	0.77	24.18	12.67	9.30	90.51
8	0.91	24.53	12.73	9.34	90.73	8	0.92	24.39	12.79	9.35	90.60
9	0.98	24.69	12.89	9.40	90.77	9	0.98	24.63	12.93	9.41	90.70
10	1.00	24.70	13.01	9.44	90.70	10	0.99	24.75	12.99	9.44	90.75

For demonstration purposes; $N = 1{,}000$, $N_e = 200$ and $N_r = 50$. Hence $\alpha_e = 0.4$ and $\alpha_r = 0.1$. $\theta = 1$ is also assumed.

(a) Firstly, we consider $\mathscr{C}_1$ and $\mathscr{C}_2$ only and it is required to move the respective means from (23, 12) to (24.67, 12.95), i.e. $k_1 = 1.67$ and $k_2 = 0.95$, which is approximately one standard deviation in each direction.

Table 3 A shows the generation-by-generation change in $R(\mu(\mathscr{E}))$, using R defined with $c_1 = 1.67$ and $c_2 = 0.95$, see Eq. 11 and $\boldsymbol{b}$ as in Eq. (20). Table 3 B gives the corresponding values using the traditional constrained selection method determined by $\mathbf{b} = \mathbf{P}^{-1}\,\mathbf{G}_1'\,(\mathbf{G}_1'\,\mathbf{P}^{-1}\,\mathbf{G}_1)^{-1}\,\mathbf{k}$, Tallis and Leppard (1988). These tables suggest that there is no appreciable difference between the two procedures.

(b) Secondly, we consider $\mathscr{C}_3$ and $\mathscr{C}_4$ only, and a response surface R, defined in Table 4. The entries in the body of this table are ficticious relative values for the corresponding row-column values of $\mathscr{C}_3$ and $\mathscr{C}_4$, although some semblance to reality is obtained at the maximum by multiplying the table entries by 10. Values of R for non-tabulated $\mathscr{C}_3$, $\mathscr{C}_4$ pairs are found by bivariate interpolation. This surface has a maximum in the region of (10.5, 100.5).

The generation-by-generation change in $R(\boldsymbol{\mu}(\mathscr{E}))$ and $\boldsymbol{\mu}(\mathscr{E})$ is shown in Table 5. The value of R reaches a maximum in 12 generations: $\boldsymbol{\mu}(\mathscr{E})$ fluctuates slightly for a few more generations due to the nature of the surface R and flock structure.

(c) Thirdly, a composite R is constructed from the R used in Table 3 A (now denoted R_1) and the R used in Table 5 (now denoted R_2), i.e. $R = f_1 R_1 + f_2 R_2$. The multipliers f_1 and f_2 are arbitrary constants which can be used to adjust the relative effects of R_1 and R_2, and hence the rates of change of the character pairs. We take $f_1 = f_2 = 1$. With this definition, we are in a position to examine the procedure in which $\mathscr{C}_3$ and $\mathscr{C}_4$ move to their economic maximum, while controlling the movement of $\mathscr{C}_1$ and $\mathscr{C}_2$ from (23, 12) to (24.67, 12.95) The results are shown in Table 6. R_2 reaches its maximum after 12 generations, while R_1 takes 17 generations. Thereafter, these maxima are maintained by containing the fluctuations in $\boldsymbol{\mu}(\mathscr{E})$.

The computer program used to construct Table 6 is a powerful investigative tool. Potential breeding and selection schemes can be examined and compared, and the

Table 4. Values of $R(\mu)$ for $\mathscr{C}_3$, $\mathscr{C}_4$

		$\mathscr{C}_4$ (body weights, lbs)					
		76	83	90	97	104	111
$\mathscr{C}_3$ (fleece weight, lbs)	7	6	12	18	24	24	18
	8	7	14	21	28	28	21
	9	8	16	24	32	32	24
	10	9	18	27	40	40	27
	11	10	20	30	40	40	30
	12	9	18	27	36	36	27
	13	8	16	24	32	32	24

Table 5. Convergence to maximum $R(\mu)$

Mating	R	$\boldsymbol{\mu}(\mathscr{E})$			
1	24.00	23.00	12.00	9.00	90.00
2	25.32	23.01	12.00	9.02	90.42
3	26.51	23.10	12.00	9.11	92.97
4	28.49	23.13	12.00	9.15	94.02
5	30.77	23.22	12.00	9.25	96.33
6	34.46	23.27	12.02	9.33	97.79
7	35.35	23.33	12.10	9.50	98.41
8	36.54	23.39	12.13	9.61	99.59
9	37.55	23.45	12.20	9.77	100.21
10	38.84	23.50	12.26	9.90	100.97
11	39.88	23.56	12.32	10.06	101.67
12	40.00	23.60	12.37	10.16	102.25

Table 6. Convergence to maximum of composite $R(\mu)$

Mating	R_1	R_2	$\boldsymbol{\mu}(\mathscr{E})$			
1	0.14	24.00	23.00	12.00	9.00	90.00
2	0.14	25.33	23.01	12.00	9.02	90.42
3	0.14	26.52	23.10	11.98	9.11	92.98
4	0.15	28.50	23.14	11.98	9.15	94.03
5	0.16	30.79	23.22	11.98	9.25	96.34
6	0.18	34.48	23.28	11.99	9.34	97.79
7	0.21	35.38	23.37	12.08	9.51	98.39
8	0.25	36.57	23.43	12.12	9.62	99.54
9	0.30	37.57	23.51	12.21	9.78	100.13
10	0.37	38.85	23.59	12.27	9.91	100.86
11	0.43	39.88	23.67	12.35	10.06	101.52
12	0.55	40.00	23.79	12.43	10.17	102.08
17	1.00	40.00	24.67	13.06	10.43	101.72

consequences of choices of f_1, f_2 and R_1 can be determined.

Moreover, the program has an option in which $\boldsymbol{b}$ is specified and remains fixed, thus corresponding to the situation in which an external estimate is applied to a particular flock.

It was found that in this particular illustrative case, fixed and unchanging choices of $\boldsymbol{b}$ proved very unsatisfactory. It was only when R_2 was specified as a plane, that some choices of fixed $\boldsymbol{b}$ produced reasonable results. In all cases, however, none were as good as the optimum solution

(d) Simulation. The selection procedure described in the previous section can also be examined through a simulation model. Let the four characters $\mathscr{C}_1, \mathscr{C}_2, \mathscr{C}_3, \mathscr{C}_4$ have genotype $\mathbf{g}$

$$\mathbf{g} \sim MVN(\boldsymbol{\mu}, G) \tag{21}$$

where $\boldsymbol{\mu}$ and G are given in Table 2 and define an independent environment vector $\mathbf{e}$

$$\mathbf{e} \sim MVN(0, P - G). \tag{22}$$

Then the phenotypic vector $\mathbf{P}$, $\mathbf{p} = \mathbf{g} + \mathbf{e}$, will have the required properties $E(\mathbf{p}) = E(\mathbf{g})$ and $V(\mathbf{p}) = P$, also Table 2.

The N ewes in the initial flock $\mathscr{E}$ are formed by generating random vectors $\mathbf{g}$ and $\mathbf{e}$ from distributions (21) and (22) to form vector pairs (g, p). A "breeding group" of rams of size N_r is also generated in this way, corresponding to a randomly selected subgroup from the $N/2$ males in $\mathscr{L}_{1\frac{1}{2}}$.

Progeny from these two groups are derived by mating each ram with a group of size N/N_r selected randomly from $\mathscr{E}$, to produce a lamb group of size N. An individual in this group has genotype constructed as $\mathbf{g} = \frac{1}{2}[\mathbf{g}_E + \mathbf{g}_R] + \mathbf{g}_1$, where $\mathbf{g}_E$ and $\mathbf{g}_R$ are the genotypes of its mother and father, and $\mathbf{g}_1$ is an independent random component

$$\mathbf{g}_1 \sim MVN(\mathbf{O}, \tfrac{1}{2}G). \tag{23}$$

The phenotypic value $\mathbf{p}$ is then obtained by adding an independent environment component $\mathbf{e}$ from distribution (22).

For the purpose of this exercise, we are using known values of G and P to generate the random vectors $\mathbf{g}$ and $\mathbf{p}$. However, in a practical application, both G and P must be estimated from sample data in order to obtain $\boldsymbol{b}$. Similarly, $R(\boldsymbol{\mu})$ also has to be estimated.

An estimate of P, $\hat{P}$, can be obtained directly from the observable phenotypic vectors $\mathbf{p}$ in $\mathscr{L}_{1\frac{1}{2}}$. This is the usual sample variance matrix. An estimate of G, $\hat{G}$, can be obtained by multivariate regression of progeny phenotype on parent phenotype.

In this demonstration, we take R as was used to construct Table 5, with again $f_1 = f_2 = 1$. Since R_1 is of the form of Eq. (11), then $\mathscr{R}_1$ is available analytically at any point. In any practical application, R_2 may not be known and would have to be approximated by a tangent plane – Eq. (13).We use Table 4 to assign actual economic values to each individual sheep. Then assuming no knowledge of the R_2 surface, we approximate it by a regression plane $\hat{R}_2 \doteq \hat{b}_0 + \hat{b}_1(P_3 - \bar{P}_3) + \hat{b}_2(P_4 - \bar{P}_4)$ from which $\hat{\mathscr{R}}_2 = \binom{\hat{\mathfrak{b}}_1}{\hat{\mathfrak{b}}_2}$.

With the estimates $\hat{G}$, $\hat{P}$ and $\hat{\mathscr{R}}$, the selection vector $\hat{\mathbf{b}}$ [Eq. (20)] is constructed and selection indices for each of the N lambs are calculated. Half of the lambs are designated female at random, and on the basis of their indexes N_e of these $N/2$ ewes are selected as replacements for N_e ewes in $\mathscr{E}$. Since the data for $\mathscr{E}$ is computationally arranged in a rectangular matrix, this amounts to deleting the last N_e rows moving all remaining rows down N_e places and adding the saved ewes in the first N_e rows. In this way, an age structure is introduced into $\mathscr{E}$, with the "oldest" ewes being replaced at each selection stage. Similarly, for the $N/2$ lambs designated as rams, N_r are selected for the next breeding stage. The process is repeated for any number of generations, when R reaches a maximum, $\hat{\mathbf{b}}$ is essentially zero, so that random mating occurs and continues to occur on subsequent cycles unless random drift occurs. The selection index then becomes operative again to restore the process to its maximum.

The simulation process generates $\mathbf{g}$ vectors for each sheep and these are kept until the "animal" is removed from the system. Hence in the $\mathscr{E}$ group, it is possible to calculate the average of the actual $\mathbf{g}$ values, generation by generation. These are recorded in columns 4–7, inclusive, in Table 7. For this particular run, genetic progress does not seem to have been significantly hampered by the process of internal estimation (Table 6).

As a further check of the adequacy of the estimates of the regression matrix B, $\hat{\mathbf{B}}$, estimates of $\mathbf{g}$ for each sheep were calculated using $\hat{\mathbf{g}} = \hat{\mathbf{B}}\,\bar{\mathbf{p}}$, where $\bar{\mathbf{p}}$ is the midparent

Table 7. Simulation results

Mating	R_1	R_2	Average actual **g**				Average predicted **g**			
1	0.13	23.92	22.98	12.00	8.97	90.01	22.99	11.99	8.99	89.96
2	0.15	25.07	23.06	12.01	9.01	90.71	23.01	12.00	9.01	90.72
3	0.15	26.32	23.11	12.00	9.04	91.58	23.07	12.00	9.05	91.52
4	0.16	28.18	23.12	12.01	9.12	93.09	23.10	12.02	9.13	93.07
5	0.17	30.17	23.18	12.00	9.19	94.70	23.19	11.98	9.21	94.76
6	0.18	34.24	23.26	11.99	9.31	96.85	23.25	12.00	9.34	96.92
7	0.17	34.92	23.28	11.95	9.37	98.28	23.33	11.98	9.43	98.43
8	0.20	35.97	23.38	12.00	9.50	99.81	23.40	12.05	9.58	100.02
9	0.21	36.72	23.43	12.00	9.59	100.71	23.46	12.03	9.65	100.88
10	0.27	37.71	23.55	12.07	9.71	101.65	23.55	12.12	9.80	101.86
15	0.61	40.00	23.82	12.49	10.23	100.98	23.81	12.53	10.27	101.10
20	0.85	40.00	24.07	12.78	10.56	101.47	24.04	12.80	10.56	101.39

phenotpye. The average predicted **g** is given in columns 8–11. These predictions are extremely close to the actual group averages, reinforcing confidence in the precision of the method.

Discussion

The older approaches to constrained selection are not particularly subtle. The mathematics tends to be involved and the resulting formulae complicated, unattractive and somewhat inflexible. We have included one such approach in this paper for completeness and as a basis for examining the newer methodology.

The introduction of the value function, $R(\mu)$, simultaneously establishes the relationship between economic weights and the population mean, μ. In the case of unconstrained selection, it is shown that the vector of derivatives of R at μ, $\mathscr{R}(\mu)$, act as economic weights, and the most efficient selection procedure is to use the ordinary selection index coefficients, that is $P^{-1}G\mathscr{R}(\mu)$. This is provided that the population has mean vector μ and the curvature of $R(\mu)$ is not too great. If, in fact, $R(\mu)$ cannot be approximated by a tangent plane at μ, the optimum index coefficients may have to be found by search techniques.

To introduce an index which will move a set of characters to an assigned target area, using a value function $R(\mu)$, is the essence of simplicity. In this instance, R does not have a direct economic interpretation, since in constrained (a better word is controlled) selection, economics is not of the essence. Control of the phenotype is all-important and it is not required that progress towards a particular goal, or even the goal itself, be measured directly in economic terms. Thus, we construct a suitable, simple function $R(\mu)$, which has a single horizontal tangent plane in the target area. It is usually convenient to specify the middle of this area by a mean vector $\mu + k$, where μ is the mean vector at the start of selection, and to make vanish first derivatives of R with respect to μ at $\mu + k$. As discussed in earlier sections, the relative speeds of approach of the mean vector to $\mu + k$ can also be controlled for a suitably chosen R. Once μ is near the target, selection automatically ceases and can be reduced to random mating, as the first derivatives of R tend to zero.

The more involved situation, where some characters are to be controlled while the rest advance under the control of real economic as well as selection pressures, is also easily dealt with. The value function, R, is simply partitioned into two separate functions, R_1 and R_2; R_1 produces the desired control on the first set of characters, while R_2 is the true economic value surface for the remaining ones.

Selection now proceeds as for unconstrained selection using the synthesised R function. As the derivatives related to R_1 vanish, selection ceases for the first set of characters and full selection is concentrated on those with specified economic value, or conversely. Details can be found in earlier sections.

The second main thrust of this work is internal estimation. We show that, in order to implement the selection formulae, sufficiently stable estimates of the required parameters can be obtained from the available population. This requires than the breeder keep the appropriate records and that he avail himself of computer facilities. Given these last two conditions, in general, multivariate regressions of offspring on parent provide estimates of $GP^{-1} = B$. Since P can be estimated directly from the offsping before selection, an estimate of G can be found.

The vector of economic weights at μ, $\mathscr{R}(\mu)$, can be obtained from $R(\mu)$ if R is specified, or it can be estimated by regression techniques for the particular population concerned from appropriate economic data; for details, see the simulation example.

One way or another, the entire selection program can be run independently of outside data. This is appropriate, since data from other populations collected at different times and locations may not be particularly relevant to the population of interest. Moreover, it introduces an essential robustness to change.

These ideas have been discussed in terms of sheep breeding. To test them in vitro, a common, simple flock structure was simulated on a computer, and constrained selection for three wool characters and body weight was carried out. Generations of "computer sheep" were formed according to quantitative genetic principles, and selection was practised using internal estimation in conjunction with suitable R_1 and R_2 function.

It was found that the simulated genetic progress agreed with expectation, and that the two characters whose selection direction was controlled, performed as required. Moreover, internal estimation worked well, even for moderate flock sizes of 200 or less. Thus, the conclusion was drawn that suggested procedures should work in practice, and for more complicated management systems.

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