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The use of constrained selection indexes in breeding for economic merit

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Summary. Various methods exist for the derivation of restricted and/or desired gains selection indexes, and their use in applied breeding has been advocated. It is shown that there exists a set of implied linear economic weights for all constrained indexes and their derivation is given. Where economic weights are linear and known, a standard selection index is, by definition, optimal and thus a constrained index will usually be suboptimal. It is argued that economic weights can always be estimated and that the effects of uncertain weights can be examined by sensitivity analysis. If economic weights are nonlinear, use of the first order (linear) economic weights or a derived linear index, using previously described methods, will give very close to optimum economic selection responses. Examples from the literature indicate that severe losses of potential economic gain can possibly occur through use of a constrained index. It is concluded that constrained indexes should be avoided for economic genetic selection.

Key words: Economic weights – Restricted indexes – Desired gains

Introduction

In animal and plant production it is usual that several or many traits contribute to overall economic merit. For genetic selection, information on several traits can be combined by a special use of Fisher's (1936) discriminant function, as proposed by Smith (1936) and Hazel (1943). The resulting selection index can have any desired objective. But when the objective is maximum improvement in economic merit, the index can appropriately be called an economic selection index. When genetic variation is entirely additive and the economic weights of traits contributing to economic merit are linear functions of their genetic value, the economic selection index is, by definition, optimal.

Several authors have demonstrated that it is possible to construct restricted selection indexes and desired gains selection indexes (Kempthorne and Nordskog 1959; Cunningham et al. 1970; Yamada et al. 1975; Harville 1975; Brascamp 1984). In restricted selection indexes, genetic gain in one or more of the traits of interest is restricted to zero. In desired gains indexes, the relative genetic change in two or more traits is predetermined. The equivalence of various methodologies to achieve these ends has recently been demonstrated by Itoh and Yamada (1987).

There is a fundamental difference in philosophy between economic selection indexes and restricted or desired gains indexes. With economic selection indexes, the response to selection is entirely determined by the economic weights of the traits contributing to economic merit, the phenotypic covariances among the traits in the index, and the genetic covariances among the traits in the index and the traits of economic interest. With restricted and desired gains indexes, there are predetermined constraints on genetic response of some traits that partially or completely override the response determined by their economic weights. In the case of restricted indexes, economic weights of restricted traits are not defined.

Justification for the use of restricted or desired gains indexes has been either that some traits are considered already to be at an economic optimum or that economic weights are difficult or impossible to determine. However, in the former case economic weights at the optimum are by definition zero. It would then be appropriate to use an economic weight of zero or, if there is marked nonlinearity in the economic weights, to use a nonlinear selection index (e.g., Wilton et al. 1968; Goddard 1983). In the latter case, it is difficult to imagine situations in which economic weights would be entirely unknown. Implicit in any breeder's definition of desired response is an underlying assumption about the economic values of the traits. However, those economic values are often not explicitly stated.

This paper shows that there is a unique implicit set of economic weights underlying most restricted and desired gains selection indexes. By taking an example of a restricted and desired gains index from the literature, it is demonstrated that the failure to explicitly derive economic weights can potentially lead to severe losses in response to selection for overall economic merit.

Materials and methods

Derivation of implied economic weights

A standard selection index notation is used. **P** is an $n \times n$ phenotypic covariance matrix among the n variables in the selection index. **G** is an $n \times m$ genotypic covariance matrix among the n variables in the selection index and the m traits in the aggregate genotype, in this case economic merit. **g** is an $m \times 1$ vector of additive genotypic values for the traits in the aggregate genotype and **v** is the vector of economic weights for those traits. **x** is an $n \times 1$ vector of variables in the selection index and **b**, the vector of selection index coefficients. The optimum set of selection index coefficients is that which maximizes the correlation (r_{HI}) between the selection index ($I = \mathbf{b}'\mathbf{x}$) and the aggregate genotype ($H = \mathbf{v}'\mathbf{g}$). And it can be shown (Hazel 1943) that maximum r_{HI} is achieved when

$$\mathbf{P}\mathbf{b} = \mathbf{G}\mathbf{v}. \tag{1}$$

Thus, given **P**, **G**, and **v**, **b** can be derived as

$$\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}\mathbf{v}.$$

More complex derivations of **b** can be found for various forms of restricted and desired gains indexes (Brascamp 1984; Itoh and Yamada 1987).

If the selection index coefficients, **b**, are known, the economic weights, **v**, which would have led to these coefficients in a standard selection index derivation, can be derived from Eq. (1) as

$$\mathbf{G}'\mathbf{G}\mathbf{v} = \mathbf{G}'\mathbf{P}\mathbf{b},$$

hence,

$$\mathbf{v} = (\mathbf{G}'\mathbf{G})^{-1}\mathbf{G}'\mathbf{P}\mathbf{b}$$

when $n \geq m$. When $m > n$, unique solutions can be found only if $m - n$ or more values of **v** are predetermined. Solutions can then be achieved by adding a matrix of Lagrange multipliers (**L**) to **G** and a vector of predetermined economic weights (**a**) to **Pb**, so that,

$$\mathbf{v} = \begin{bmatrix} \mathbf{G} \\ \mathbf{L} \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{P}\mathbf{b} \\ \mathbf{a} \end{bmatrix} \tag{3}$$

To illustrate, consider an example where there are only two variables in the index and four in the aggregate genotype, but the economic values of the first and third traits in the aggregate genotype are known to be a_1 and a_3. Then the order of **G** is 2×4,

$$\mathbf{L} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix} \quad \text{and } \mathbf{a} = \begin{bmatrix} a_1 \\ a_3 \end{bmatrix}$$

The solutions are then $v_1 = a_1$, $v_3 = a_3$, with the solutions for v_2 and v_4 being the implied economic weights given the predetermined weights v_1 and v_3.

Examples from the literature

Examples of constrained indexes found in the literature are usually presented as plausible working examples and may not have been intended as definitive indexes to be applied in practice. Nevertheless, it is instructive to examine an example in detail, not to criticize the specific index presented but to examine the potential for economic losses when applying a constrained index. The index chosen was that presented by Yamada et al. (1975) for improvement of an egg laying stock of chickens. The traits chosen for improvement were egg production rate over 500 days (EP) in percent eggs per day, feed conversion efficiency (FC) measured in 0.1 units of feed weight divided by yield of egg weight, and individual egg weight (EW) in grams. The constraints were to increase EP from 65% to 73% and reduce FC from 2.8 to 2.5 while holding egg weight constant at 58 g. The variables in the selection index were EW, adult body weight (BW) and the rate of egg production based on the individual plus seven full sisters' average production over 275 days (EF). Phenotypic and genetic parameters were

$$\begin{array}{cc} & \begin{array}{ccc} \mathrm{EW} & \mathrm{EF} & \mathrm{BW} \end{array} \\ \mathbf{P} = \begin{array}{c} \mathrm{EW} \\ \mathrm{EF} \\ \mathrm{BW} \end{array} & \begin{bmatrix} 16 & -1.533 & 28.8 \\ 1.533 & 25.625 & -1.125 \\ 28.8 & -1.125 & 324 \end{bmatrix} \end{array}$$

and

$$\begin{array}{cc} & \begin{array}{ccc} \mathrm{EP} & \mathrm{FC} & \mathrm{EW} \end{array} \\ \mathbf{G} = \begin{array}{c} \mathrm{EW} \\ \mathrm{EF} \\ \mathrm{BW} \end{array} & \begin{bmatrix} -7.5895 & -1.0119 & 8 \\ 11.7116 & -1.3778 & 2.6143 \\ 0 & -3.0547 & 12.8798 \end{bmatrix} \end{array}$$

Note that **G** in the present notation is the genetic covariance matrix among the actual records used in the selection index and the traits in the aggregate genotype. Yamada et al. (1975) used **G** to denote genetic covariances if selection index variables were recorded only on the candidate for selection. Thus, **G** here is equivalent to **G'R** in Yamada et al.'s notation, where **R** is an $n \times n$ diagonal matrix of Wright's coefficients of genetic relationship between the actual records used in the index and the candidate for selection. **G** presented here does not correspond exactly to **G'R** of Yamada et al. (1975) because the coefficient of relationship they used for EF did not take into account the inclusion of the candidate for selection in the full-sib mean.It is assumed that the candidate was intended to be included because this was certainly assumed in their derivation of **P**. The constraints in terms of relative desired gains of EP, FC, and EW were 8 : −3 : 0.

The **P**, **G**, and $\mathbf{G}'\mathbf{P}^{-1}\mathbf{G}$ matrixes all had only positive eigenvalues. Selection index coefficients, **b**, were obtained for the constrained index, using a special case of the generalized method of Itoh and Yamada (1987), as

$$\mathbf{b} = \phi\,\mathbf{P}^{-1}\mathbf{G}(\mathbf{G}'\mathbf{P}^{-1}\mathbf{G})^{-1}\mathbf{k}, \tag{4}$$

where ϕ is a scaling factor,

$$\phi = \mathbf{v}'\mathbf{k}/\mathbf{k}'(\mathbf{G}'\mathbf{P}^{-1}\mathbf{G})^{-1}\mathbf{k},$$

and **v** is a vector of prior, in this case arbitrary, economic weights,

$$\mathbf{v} = \begin{bmatrix} 1 \\ 1 \\ 0 \end{bmatrix} \text{ and, } \mathbf{k} = \begin{bmatrix} 8 \\ -3 \\ 0 \end{bmatrix}.$$

Table 1. Genetic change resulting from one s.d. selection on each of three indexes and economic gain if one of two explicitly derived sets of economic weights are correct

Index[a]	Economic weights			Predicted genetic change[b]			Proportion of maximum economic gain if	
	V_{EP}	V_{FC}	V_{EW}	EP	FC	EW	*a* true	*b* true
a	0.6029	−1.6733	−0.8111	3.007	0.080	−1.441	1.0	0.82
b	0.6029	−1.6733	0.000	3.016	−0.135	−0.366	0.82	1.0
c	−0.0025[c]	−1.6733[c]	−0.2525[c]	0.909	−0.341	0.0	0.39	0.55
d	0.0892[c]	−1.4287[c]	0.0	1.108	−0.415	0.893	0.22	0.67
e	0.6029	−1.6733	0.1809[c]	2.799	−0.193	0.0	0.71	0.98

[a] *a* and *b* are standard indexes using explicit economic weights and *c*, *d*, and *e* are constrained indexes. *c* has constraints on EP, EC, and EW as given in the text; *d* has constraints on EP and FC but no restriction on EW but with the economic value of EW set to zero; *e* has no constraints on EP and FC, but EW is restricted to zero genetic change

[b] Genetic change resulting from a selection intensity of one standard deviation on the index. Units are %, 0.1 units of feed weight over egg weight, and *g* for EP, FC, and EW

[c] Indicates implicit economic weight derived as given in the text; other economic weights are explicitly used in the construction of the index

This gave $\mathbf{b}' = [0.0251 \quad 0.0603 \quad -0.0278]$. The relative values of **b** differ slightly from those of Yamada et al. (1975) due to the errors in their **G′ R**. Note that in the present case, **v** could have been found directly from Eqs. (4) and (2) as

$$\mathbf{v} = \phi\,\mathbf{G}(\mathbf{G}'\mathbf{P}^{-1}\mathbf{G})^{-1}\mathbf{k}. \tag{5}$$

However, if Eq. (2) is used, there is no requirement to know the method of deriving **b**. The implied economic weights for this example, derived using either Eq. (2) or (5), are

$$\mathbf{v}' = [-0.0025 \quad -1.6734 \quad -0.2525].$$

As a result of the imposed constraints, the implied economic weights gave essentially no value to EP, a high negative value to FC, and a modest negative value to EW.

These implicit economic weights can be compared to estimates of economic weights derived explicitly for a simple egg production enterprise. The derivation is summarized in Appendix 1. The principal assumptions are that: (1) 60% of total costs are feed costs, the remainder being management costs allocated per bird; (2) discounting and costs of rearing can be ignored because all three traits in the aggregate genotype are expressed at the same time; and (3) returns equal 1.1 times costs before genetic change. A standard period of 365 days of production is considered. Economic values are the marginal change in profit per unit genetic change in the trait, all other traits in the aggregate genotype remaining constant. By setting the economic value of FC (V_{FC}) to −1.6734, as found above, V_{EP} and V_{EW} can be found after deriving the implied cost per kg feed (given V_{FC}). If it is assumed that the price of eggs is not affected by their weight, the explicitly derived economic weights, V_{EP}, V_{EC}, and V_{EW}, are 0.6029, −1,6733, and −0.8111. In the present case, V_{EP} is positive because although FC remains constant, more revenue is generated at a fixed management cost. V_{EW} has a large negative value because extra feed is required to produce more egg weight. An alternative hypothesis might be that changes in egg price would match the marginal change in feed costs, in which case V_{EW} would be 0.0. V_{EW} would also be zero if egg weight were at an economic optimum. On either assumption about V_{EW}, the explicit economic weights differ considerably from the implied economic weights.

Table 1 presents the economic genetic change resulting from each of the two alternative explicit sets of economic weights (*a* denotes egg weight independent of price per egg and *b* denotes $V_{EW} = 0$) and that from the constrained index (*c*), assuming that the explicit weights are correct. If economic weights *a* or *b* are correct, then use of the constrained index provides only 39% or 55% of the potential economic gain. In both cases the constrained index is severely suboptimal.

The effect of dropping the restriction of zero change in EW or of dropping the constraint of defined proportional gains in EQ and FC is examined in examples *d* and *e* in Table 1. In case *d*, the economic weight of EW (V_{EW}) is set to zero, which is its marginal economic value if EW is at an economic optimum. If V_{EW} is actually zero, a single restriction on EW causes only 2% loss in economic gain (column "*b* true", row *e* versus row *b* of Table 1), while the constraint of proportional gain in EP and FC of 8 : −3 causes a 33% loss in economic gain (column "*b* true", row *d* versus row *b* of Table 1). Although the restriction on EW has almost no effect on its own, it further reduces economic gain by 12% if imposed on top of the joint constraint on EP and FC (column "*b* true", row *d* versus row *c*, Table 1). Thus, constraints are not necessarily additive but, as in this case, may interact.

Constrained indexes *c*, *d*, or *e* cause greater losses in economic gain if *a* is true than if *b* is true. This result may not seem surprising since *b* sets V_{EW} to zero, consistent with the concept that EW is at an economic optimum, which belief presumably would prompt the imposition of a restriction of no change in EW. However, this situation will not always be true. In the present case, if the true value of V_{EW} was small but positive and V_{EP} and V_{FC} remained as presently defined, then index *c* would be more efficient when judged against *a* than against *b*.

Other examples in the literature were examined, but few provided sufficient information to allow a realistic set of explicit economic weights to be derived. One exception is another poultry example provided by Itoh and Yamada (1987). However, in that example both the **P** and **C** (matrix of genetic covariances among traits in the aggregate genotype; equivalent to **G** in the example given) matrixes had negative eigenvalues, so that little meaning could be attached to the answers obtained.

Discussion

It is not the intention of this paper to call into question the various methods proposed for deriving constrained selection indexes. Optimal procedures and the relationships between different methods have been well described by Brascamp (1984) Itoh and Yamada (1987). The question is whether constrained indexes should have a role in applied breeding. Where economic merit is not a consideration, the answer may well be yes. In animal species kept solely for human pleasure or companionship, one may wish to maintain or enhance certain characteristics of a perticular breed to conform to the breed standards. For example, with pit bull terriers it might be deemed that the breed should maintain a specific ratio of ugliness to vicious temperament, and a constrained index could incorporate this requirement along with any other breeding objectives deemed appropriate. Constrained indexes are also appropriate in experiments where a predetermined biological change is desired in order to examine the consequences of such change. An example of such usage was Eisen's (1977) selection of mice for increased postweaning gain while holding feed intake constant, in order to examine the effects on efficiency of growth and other related traits.

Where the objective of breeding is the improvement of economic merit of the species, breed, or variety concerned, it is difficult to find convincing arguments for the use of a constrained index. As shown here, most constrained indexes have an implied and unique set of linear economic weights. Where the assumptions of linearity are correct, a linear selection index will, by definition, promote maximum improvement of economic merit. The potential loss of economic gain through use of a constrained index is clearly demonstrated in the example given for egg-laying poultry, where the constrained index made only 39% and 55% of the economic gain of two alternative unconstrained indexes based on explicit economic weights. It needs to be reiterated that in this case it is not intended to state categorically that the explicit economic weights are correct for this situation; they are merely reasonable estimates for the situation described. Neither is it intended to imply that Yamada et al. (1975) advocated use of their example of a constrained index in practice. Nevertheless, there is considerable discordance between the implied economic weights from what might seem a reasonable constrained index and reasonable estimates of actual economic weights. And there is clearly the potential for large losses in economic gain through use of a constrained index.

In the literature on constrained indexes, justification for the use of such indexes is singularly lacking. Brascamp (1984) reviewed five instances where the justification given was a desire to see no change in a particular trait because such change was perceived as detrimental. In a sixth example the desire was to promote genetic changes "more in harmony with" increase in another trait that was not included in the aggregate genotype. Pesek and Baker (1969) justified their use of such indexes with the statement that "few breeders are prepared to assign relative economic weights to traits but most would be willing to specify the amount of gain they would like to see in each trait ...". It seems reasonable to suppose that the justification for constrained indexes is that economic values of some traits are difficult to estimate, uncertain or variable over time, or that the trait is at an economic optimum.

It is difficult to imagine a situation where economic weights cannot be estimated at all. Perhaps the most difficult position is that of a breeding company that must assess both the economic production potential of a stock and its marketability in relation to the stock of competing companies. But even here methods exist to quantify economic values, as recently discussed by de Vries (1989). And, while it is accepted that economic values may vary over time, it is usually possible to identify likely long-term values and potential ranges to those values. Such values should then be used in a selection index, and the effects of varying the economic weights of different traits can be examined. Often, selection indexes are insensitive to rather large changes in economic weights. The problem with a constrained index is that it can easily imply an economic weight well outside any reasonable range. The implied essentially zero economic weight for egg production in the example of Yamada et al. (1975) is a case in point. While there may be some uncertainty as to the true economic value, it is very difficult to imagine a situation where increased egg production per bird per year has no value.

If some traits are already at an optimum, economic weights for such traits are nonlinear. However, unless the nonlinearity is extreme, nonlinearity will cause second-order effects of minor importance in relation to the rates of genetic gain expected. In such cases a linear selection index will be very close to optimum. The appropriate economic weight for a trait at an optimum is zero, and if the population moves away from the optimum following selection, the economic weight should be continuously adjusted to equal the tangent to the profit curve at the population mean for that trait. If nonlinearity is marked, then construction of a nonlinear index (e.g., Wilton et al. 1968) or the appropriate linear index taking into account nonlinear weights (Goddard 1983) is an optimum or very close to optimum procedure. These close-to-optimum procedures allow for genetic change in the mean of a trait currently at its own economic optimum to occur. Such change occurs if dictated by its economic value in relation to other traits and the genetic and phenotypic covariances among those traits. Arbitrarily constraining that trait to zero genetic change will therefore be suboptimal. In Yamada et al.'s (1975) example, the constraint of zero change in egg weight caused less than 1% loss in economic gain when no other constraints were applied, but caused a 15% loss in the presence of constraints on EP and FC. Thus, even if a single constraint causes little loss in economic genetic gain, it may be severely detrimental in the presence of other constraints.

It is concluded that constrained indexes are always suboptimum economically and can cause severe losses in potential economic gain. Economic values, if not known exactly, can be estimated and given reasonable ranges. These estimates can be used to obtain optimum or close-to-optimum selection indexes for economic genetic gain. If economic weights are uncertain, the effect of setting economic weights to extreme values can be examined, and the index modified if necessary.

Appendix 1

Derivation of economic weights for poultry breeding example from Yamada et al. (1975)

Basis. Consider a time period of 365 days and evaluate values per bird. Interest is in marginal economic value of genetic change; therefore, costs of rearing and discounting can be ignored. This will not affect relative values, since all traits are expressed during the same period.

Assume 60% of costs are feed costs (increasing linearly with weight of eggs produced) and the remainder are management costs allocated on a per bird basis.

Population currently has an average egg production rate of 0.65 and average egg weight of 0.058 kg.

Derive a standard cost of feed. As a standard, use $V_{FC} = 1.6734$ per 0.1 unit, the implied economic weight for Yamada et al.'s (1975) index.

Total weight of eggs per year $= 365 \times 0.65 \times 0.058 = 13.7605$ kg

At FC of 2.8, expected feed intake $= 13.7605 \times 2.8 = 38.5294$ kg

A 0.1 reduction in FC would reduce feed intake by

$$38.5294 \times \frac{2.7}{2.8} = 1.37605 \text{ kg}$$

Since $V_{FC} = 1.6733$ per 0.1 unit, implied feed cost is

$$\frac{1.6734}{1.3705} = \underline{1.2209/\text{kg}}$$

Derive returns per egg. Total feed requirements cost

$$= 365 \times 0.65 \times 0.058 \times 2.8 \times 1.2209$$
$$= 47.042 \text{ per bird per year}$$

Total costs, if 60% costs are due to feed, $= 47.042 \times \frac{(0.6+0.4)}{0.6}$

$= 78.403$ per bird

Total cost per egg $= \frac{78.403}{365 \times 0.65}$ per year

$= 0.3305$

If returns $= 1.1 \times$ costs, returns per egg $= 1.1 \times 0.3305$

$= 0.3636$

Derive the marginal value of increased EP, V_{EP}. One percent increase in EP causes increased feed costs of

$365 \times 0.01 \times 0.058 \times 2.8 \times 1.2209 = 0.7237$ per bird per year and increased returns of $365 \times 0.01 \times 0.3636 = 1.3266$ per year.

Therefore, increased profit $= V_{EP} = 1.3266 - 0.7237$

$= \underline{0.6029 \text{ per } \%}$

Derive the marginal value of increased egg weight, V_{EW}. Marginal costs of increased egg weight are all feed costs.

$365 \times 0.65 \times 0.001 \times 2.8 \times 1.2209 = 0.8111$ per g per bird per year

Therefore, if the price of eggs is unaffected by weight

$V_{EW} = -0.8111$ per g.

But, if price differential is equal to the costs of producing larger eggs, $V_{EW} = 0.0$ per g.

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