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A Variable Selection Index for the Compensation of Correlated Genetic Change

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Summary. A selection index for two traits has been constructed which allows partial restriction for one of the traits. The index is used in a situation where correlated response to selection in one sex is compensated for by selection for other traits in the opposite sex. A numerical example is given.

Key words: Restricted Selection Index - Poultry - Male Selection - Correlated Response - Compensating Selection

Introduction

The theory of selection indexes for optimum genetic change in several traits is well developed. Based on linear regression it includes restriction indexes where genetic change for one or more traits is held to zero while gains in others are maximized (Kempthorne and Nordskog 1959). More recently Tallis (1962) has given an explicit solution for indexes which allow partial restriction in genetic change in some traits, proportional to their expected gains under unrestricted index selection. Tallis' formulation of the problem, while amenable to solution by linear algebra, permits an assessment of expected gains only after the index coefficients have been derived thus making it necessary to use trial and error if fixed absolute values for the restricted gains are to be attained. Thus, if fixed non-zero restrictions on gain are to be used for some traits, linear solutions to the problem cannot be found and numerical methods as outlined by Cunningham et al. (1970) must be employed.

In the present paper we consider a case of a predetermined partial restriction with an index based on two traits for which an explicit solution can be found. The problem area is in a breeding project involving a White Leghorn flock selected for large egg size over 10 generations (Hilfiker 1970). It was then intended to begin selection for reduced body weight while holding egg size at its high level of improvement. For economy of space and feed it was decided to apply mass selection for low body weight in males at high intensity and at an early age, followed by selection of females on egg weight and age at first egg. Because selection of small males would result in a predictable loss of egg weight, compensatory selection for high egg weight was to be applied in females so as to keep the total response in that trait near zero while at the same time reducing age at first egg and without direct selection on body weight of hens. Formally this approach can be considered a case of tandem selection applied to the separate sexes with adjustment in selection intensities and index procedures to maximize genetic gains at low breeding costs.

Theory

We shall consider an index applied to females, which results in fixed genetic change in egg weight (X_2) so as to exactly compensate for genetic change in that trait due to selection on body weight (X_4) of males. At the same time genetic change in age at first egg (X_1) is to be effected. The index itself is based only on two traits: age at first egg (X_1) and egg weight (X_2), with selection intensities for males ($\bar{i}_m$) as well as females ($\bar{i}_f$) fixed in advance by the breeding structure of the flocks.

We thus have the index:

$$I = b_1X_1 + b_2X_2,$$

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with the condition that the expected

$\Delta G_2 = 0$

and minimum ΔG_1, that is, maximum decrease.

Designating the genetic and phenotypic variances of trait X_i as G_{ii} and P_{ii}, respectively, and covariances between traits as G_{ij} and P_{ij}, then using the familiar predictions of genetic change from selection based on linear regression we have expected genetic changes in females due to selection of males:

$$\Delta G_{im} = \frac{\bar{i}_m}{2} \frac{G_{4i}}{\sqrt{P_{44}}} . \qquad (1)$$

Furthermore the expected genetic changes for females on the above index are after setting $b_1 = -1$ arbitrarily (thus assuming an intended reductiong in X_1)

for age at first egg: $$\Delta G_{1f} = \frac{\bar{i}_f}{2} \frac{(-G_{11}+b_2G_{12})}{\sqrt{P_I}} \qquad (2)$$

for egg weight: $$\Delta G_{2f} = \frac{\bar{i}_f}{2} \frac{(-G_{12}+b_2G_{22})}{\sqrt{P_I}}$$

where the index variance $P_I = P_{11} - 2b_2P_{12} + b_2^2P_{22}$.

We now impose the restriction for egg weight compensation:

$$\Delta G_{2f} + \Delta G_{2m} = 0$$

giving $$\frac{\bar{i}_f(-G_{12}+b_2G_{22})}{2\sqrt{P_I}} + \frac{\bar{i}_m G_{24}}{2\sqrt{P_{44}}} = 0. \qquad (3)$$

Squaring equation (3) and rearranging we have

$$\frac{\bar{i}_m^2 G_{24}^2}{P_{44}} (P_{11}-2b_2P_{12}+b_2^2P_{22}) - \bar{i}_f^2(G_{12}^2-2b_2G_{12}G_{22}+b_2^2G_{22}^2) = 0.$$

This is a quadratic equation of the form:

$$(MP_{11}-FG_{12}^2) - 2b_2(MP_{12}-FG_{12}G_{22}) + b_2^2(MP_{22}-FG_{22}^2) = 0, \qquad (4)$$

where $M = \frac{\bar{i}_m^2 G_{24}^2}{P_{44}}$ and $F = \bar{i}_f^2$.

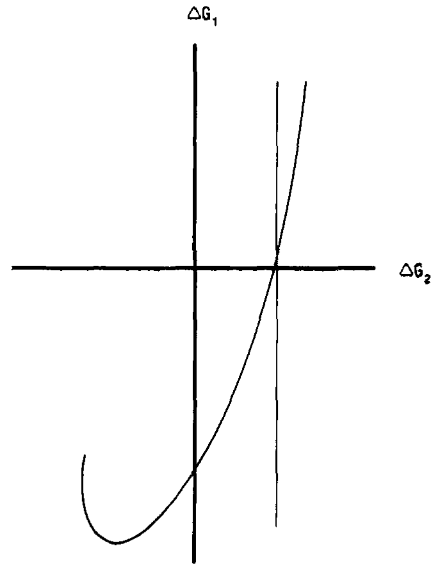

Fig. 1. Genetic gain in age at first egg (ΔG_1) and egg weight (ΔG_2) from selection in females for variable index coefficient b_2. Correlated response in egg weight (with reversed sign) to selection for body weight in males is represented by vertical line

This equation has two real solutions for b_2 of which the positive one is desired in this case provided that female selection ($\bar{i}_f$) is strong enough to allow compensation for selection in males. This obviously imposes a limiting relation between $\bar{i}_f$ and $\bar{i}_m$, which is obtained by letting the argument of the root in the solution of equation (4) equal zero. This occurs when

$$\frac{\bar{i}_m^2}{\bar{i}_f^2} = \frac{(G_{12}^2P_{22}+G_{22}^2P_{11}-2P_{12}G_{12}G_{22})P_{44}}{(P_{11}P_{22}-P_{12}^2)G_{24}^2} . \qquad (5)$$

It should be noted that the above index solution of equation (4) requires the determination of only the b_2 value and is completely determined by the imposed restriction. This point as well as the nonlinear nature of the solution can be demonstrated graphically by plotting expected genetic gain for age at first egg (ΔG_{1f}) against that for egg weight (ΔG_{2f}) from the selection of females with variable index coefficient b_2. The resulting curve is a section of an ellipse for a bivariate normal distribution of X_1 and X_2 (Moav and Hill 1966). The dimension and orientation depend on the genetic and phenotypic parameters of the two traits as well as the selection intensity ($\bar{i}_f$). The genetic gains for the desired index are then located at the intersection of the straight line $\Delta G_{2f} = -\Delta G_{2m}$ with the curve, as shown in Fig. 1. With strong selection in males and

Table 1. Genetic and phenotypic parameters for age at first egg, egg weight and body weight in a flock of chickens. Genetic variances and covariances are in the upper right half of the table and phenotypic variances and covariances in the lower left

	X_1 Age at first egg (days)	X_2 Egg weight (grams)	X_3 Body weight ast 20 weeks (kg) females	X_4 Body weight males (kg
X_1	76.8 256.0	16.6	0.102	0.122
X_2	40.0	10.0 25.0	0.184	0.196
X_3	0.240	0.375	0.0135 0.0225	0.0216
X_4	-	-	-	0.024 0.040

required compensation, the two lines may not intersect thus necessitating either an adjustment of either male or female selection intensity. The limiting ratio of selection intensities given in equation (5) is then represented by the point where the straight line is tangent on the response curve.

The computation of genetic gains for combined selection of males and females follows from linear regression and selection differentials applied in both sexes as follows.

Genetic gain in egg weight (X_2):

$$\Delta G_2 = \Delta G_{2m} + \Delta G_{2f} = 0,$$

genetic gain in age at first egg (X_1):

$$\Delta G_1 = \Delta G_{1m} + \Delta G_{1f} = \frac{\bar{i}_m}{2} \frac{G_{14}}{\sqrt{P_{44}}} + \frac{\bar{i}_f}{2} \frac{(-G_{11}+b_2G_{12})}{\sqrt{P_I}},$$

genetic gain in body weight of females (X_3):

$$\Delta G_3 = \Delta G_{3m} + \Delta G_{3f} = \frac{\bar{i}_m}{2} \frac{G_{34}}{\sqrt{P_{44}}} + \frac{\bar{i}_f}{2} \frac{(-G_{13}+b_2G_{23})}{\sqrt{P_I}}.$$

The inclusion of a third or more variables such as body weight of female (X_3) in the female index can be handled by trial and error using the technique suggested by Cunningham et al. (1970) with the fixed restriction of $\Delta G_{2f} + \Delta G_{2m} = 0$.

A Numerical Example

Genetic and phenotypic parameters for the population in question have been given by Hilfiker (1970) and representative values are given in Table 1. Notice that phenotypic covariance of male body weight (X_4) with the traits of females do not exist, whereas genetic correlations can be estimated from means of related males and females such as full sibs.

Using the above values, solutions to equation (4) can be computed for various combinations of male and female selection intensities. Thus for the case of $\bar{i}_m = 0.9$ and $\bar{i}_f = 0.6$ we obtained a b_2 value of 4.74 giving a female index:

$$I = -X_1 + 4.74X_2.$$

With expected gains of 0.25 days in sexual maturity (ΔG_1), zero change in egg weight (ΔG_2) and a decrease of 0.038 kg in body weight of females (ΔG_3).

According to equation (5) the critical ratio of male to female selection intensity for this case turns out to be:

$$\bar{i}_m/\bar{i}_f = 2.04.$$

Conclusions

A selection index designed to effect fixed genetic change in egg weight on the basis of traits measured on females was used to compensate for expected genetic change due to preceding selection on body weight of males. Adequate numerical techniques for handling such a problem have already been given by Cunningham et al. (1970). It seemed of interest, nevertheless, to explore a possible application of such an index for the simplest possible case of two variables with restriction on one of them. In the present case, moreover, the amount of restriction required each generation depends on the selection intensities employed in selecting males and females, respectively, thus necessitating new index solutions in adaptation to changes in these parameters, even when all phenotypic and genetic variances and covariances remain the same.

In practice the need for compensation by index selection for unwanted expected genetic changes, may arise whenever selection is applied at different stages of the life cycle or in both sexes independently. The potential for strong early selection of males on growth rate arises in many circumstances and may seriously prejudice what can be achieved by subsequent selection in females. Thus selection in broilers or turkeys for rapid growth rate is usually very intensive in males and applied at an early marketing age, while genetic improvement of reproductive performance is practiced in females. Under these conditions an elevation of correlated responses to strong male selection and necessary compensatory selection of hens becomes of interest. If critical selection intensity ratios are exceeded a change in the breeding structure of flocks may be advisable towards reduced early selection of males.

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