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Selection Indices for Non-linear Profit Functions

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Summary. Conventional selection index theory assumes that the total merit or profitability of animals is a linear function of measurable traits. However, in many cases merit may be a non-linear function of these traits. A linear selection index can still be used in this situation but the optimum index depends on the selection intensity to be used and on the number of generation over which the selection response is to be maximized. Non-linear selection indices have been suggested but these result in a lower selection response than the best linear index. Linear selection indices suggested in the past are shown to correspond to the optimum linear index for either a very small selection response or, in the case of restricted indices, a very large selection response. The economic value of a trait may depend on management decisions taken by the farmer. In this situation the economic values should be calculated assuming that the management decisions taken maximize profit given the present genetic value of the animals.

Key words: Selection index – Profit function

Introduction

Selection index theory was originally formulated on the assumption that it was desired to maximize a quantity (which I shall call profit) which was a linear function of measurable traits such as growth rate and milk yield. However, in some cases profit may be better characterized by a non-linear function of these traits. For instance Moav and Hill (1966) expressed profit (y) as

$$y = c - g x_1 - \frac{n}{x_2}$$

where x_1 is productive efficiency, x_2 is reproductive efficiency and c, g and n are constants.

Many methods of constructing selection indices to improve non-linear profit functions have been proposed. This paper examines the relationships between these proposed methods and shows that one of them leads to the optimum index.

Non-linear profit functions cause difficulty because the economic value of a trait is not constant but changes as the population mean changes. A similar problem arises when the economic value of a trait depends on management decisions taken by the farmer. The best method for deriving a selection index under these conditions will also be discussed.

The interpretation on non-linear profit functions $y = f(\mathbf{x})$[1] must be clearly defined. $f(\mathbf{a})$ could represent the profit from identical animals in which $\mathbf{x} = \mathbf{a}$; or $f(\mathbf{a})$ could represent the profit from a population of animals in which $\bar{\mathbf{x}} = \mathbf{a}$, but with the same variance, skewness, etc., as the present population. Given one type of function it is possible to find the corresponding function for the alternative definition. For linear profit functions the two functions are identical and for quadratic functions they differ only by a constant. The theory of selection responses relates $\bar{\mathbf{x}}$ in one generation to $\bar{\mathbf{x}}$ in the next so it is convenient to define profit as a function of $\bar{\mathbf{x}}$. All profit functions used in the remainder of the paper are of this type.

Linear Indices

Conventional selection index theory can still be used for non-linear profit functions by approximating y by a linear function. Moav and Hill (1966) used

$$y = \frac{\partial y}{\partial x_1} x_1 + \frac{\partial y}{\partial x_2} x_2 \qquad (1)$$

where $\frac{\partial y}{\partial x_1}$ and $\frac{\partial y}{\partial x_2}$ are evaluated at $(\bar{x}_1, \bar{x}_2)$. Then $\frac{\partial y}{\partial \mathbf{x}}$

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[1] Small letters in bold type represent vectors and capital letters represent matrices

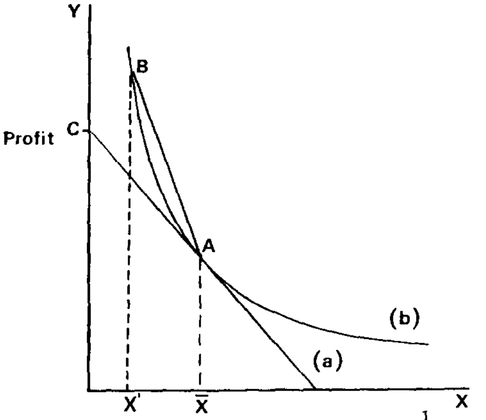

Fig. 1. Curve (*b*) is the profit function $y=\frac{1}{x}$, and line (*a*) is the linear approximation $y=\frac{dy}{dx}x+c=\frac{-1}{\bar{x}^2}x+c$. The chord *AB* shows the value of decreasing $\bar{x}$ from its present value to x′

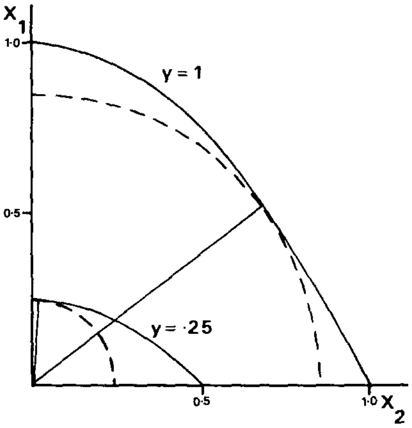

Fig. 2. Graphical method of finding the optimum index. Contours of the profit function $y=x_1+x_2^2$ are shown (solid lines). The broken lines are response circles corresponding to two intensities of selection. The present mean $\bar{x}$ is at the origin. The optimum index depends upon which intensity of selection is used

can be used as economic weights in the normal method of constructing an index.

Wilton et al. (1968) devised a linear index which minimized the sum of squared differences between the index and a quadratic profit function. Let profit (y) be defined by

$$y=\bar{\mathbf{x}}'A\mathbf{x}+\mathbf{a}'\mathbf{x}$$

where $\mathbf{x}$ is a vector of genetic values and A is a matrix of constants. Then the index of Wilton et al. (1968) is

$$I=\mathbf{p}'\,(P^{-1}C(\mathbf{a}+2A\bar{\mathbf{x}}))$$

where $\mathbf{p}$ is a vector of phenotypic values

P is a matrix of phenotypic variances and covariances
C is a matrix of covariances between $\mathbf{p}$ and $\mathbf{x}$.

This is the conventional index with economic weights assumed to be $\mathbf{a}+2A\bar{\mathbf{x}}$. This is the same value as given by $\frac{\partial y}{\partial \mathbf{x}}$ evaluated at $\bar{\mathbf{x}}$ so this index is identical to that based on the use of (1).

The approximation (1) correctly predicts the increased profit obtained from a small change in $\bar{x}$ but as selection changes $\bar{x}$ the approximation becomes less accurate. For instance, Fig. 1 illustrates the profit function $y=\frac{1}{x}$. Clearly $\frac{dy}{dx}$ underestimates the value of reducing x. The slope of the chord AB gives the value of reducing $\bar{x}$ to x′.

Moav and Hill (1966) extended this graphical method to the case where profit is a function of 2 or more traits. Assume that x_1 and x_2 are of equal variance and heritability and uncorrelated. If selection is based on the index $I=x_1+bx_2$ then for a given intensity of selection the direction in which $\bar{x}$ is moved depends on b. As b is varied the points to which $\bar{x}$ is moved form a circle. If the profit contours are plotted on the same graph then the point on the response circle with the maximum profit can be found and the optimum value of b deduced (Moav and Hill 1966). This method is illustrated in Fig. 2 for a profit function

$$y=x_1+x_2^2$$

It can be seen that the optimum direction of selection and hence the optimum index depends on the intensity of selection to be used. At the point on the response circle with maximum profit the slope of the circle is the same as the slope of the profit contour. The linear approximation (1) has the same slope as the profit contour at the present mean $\bar{x}$. Therefore the selection index calculated using $\mathbf{a}=\frac{\partial y}{\partial \mathbf{x}}$ corresponds to a very small response circle (= very low intensity of selection). The difference between this solution and that of the graphical method reflects the increasing inaccuracy of $\mathbf{a}=\frac{\partial y}{\partial \mathbf{x}}$ as the selection response increases.

If it is the long term value of the selection response that we wish to maximize then x′ in Fig. 1 and the response circle in Fig. 2 should represent more than one generation improvement. However discounting gains made in the future will lead to more emphasis being placed on the short term than on the long term response.

If x_1 and x_2 are not of equal variance, equal heritability and uncorrelated the response curve will be an ellipse not a circle. However Moav and Hill (1966) present a method of transforming x_1 and x_2 so that the response curve is circular on the transformed axes.

Non-linear Selection Indices

In order to maximize a non-linear profit function it seems reasonable to consider non-linear selection indices. Wilton et al. (1968) derived a quadratic index which minimized the sum of squared differences between the index and genetic merit for a quadratic profit function and Ronningen (1971) derived a cubic index for cubic profit functions. However, maximizing the genetic merit of the parents is not identical to maximizing the genetic merit of their offspring. The following simple example illustrates this problem.

Assume that profit $y = x^2$ and that $h_x^2 = 1.0$ and $\bar{x} = 0$. The animals with the highest genetic merit are those with highly positive and those with highly negative values of x, and these are the animals selected by the index of Wilton et al. (1968). But when these animals are mated together the mean of the offspring will still be $\bar{x} = 0$. We normally assume that offspring inherit the mean of the additive genetic value of their parents not the complete distribution of their additive genetic values. If the offspring have the same distribution as the previous generation before selection then they will have the same mean profit. Although the variation in x is additive genetic, the variation in y is epistatic (additive x additive) which explains why the superiority of the parents in y is not passed on to their offspring. In this extreme situation using $a = \frac{dy}{dx}$ leads to the prediction that no improvement in y is possible, whereas the graphical method shows that one should select either for $+x$ or $-x$ but not both. In general if $y = f(\mathbf{x})$, it is not $\bar{y}$ which the index should maximize but $f(\bar{\mathbf{x}})$. I will now discuss a method of finding the index which does this.

Consider two traits x_1 and x_2 having a bivariate normal distribution, equal variances, equal heritabilities and uncorrelated. What is the index that will move the mean $(\bar{x}_1, \bar{x}_2)$ the greatest possible distance from its present position? Because the problem is radially symmetrical the maximum distance that $(\bar{x}_1, \bar{x}_2)$ can be moved is the same in all directions. Therefore let us find the index that maximizes the distance that the mean can be moved in the x_2 direction. The best possible index is simply $I = x_2$ because any index that involved x_1 would result in some selected animals having a lower x_2 value than some non-selected animals and hence lowering the selection differential.

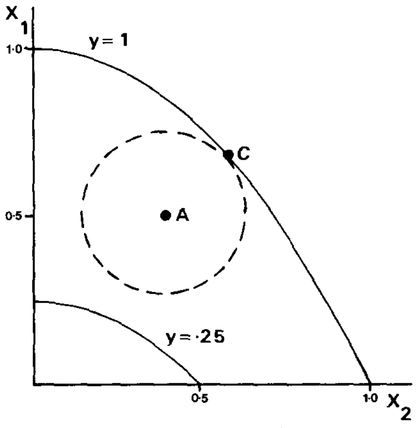

Fig. 3. Contours of the profit function $y = x_1 + x_2^2$ are illustrated (solid lines). The broken line is the response circle, *A* is the present mean $(\bar{x}_1, \bar{x}_2)$ and *C* is the point of highest profit on the response circle

Thus the index that maximizes the distance moved by the mean in the x_2-direction has index contours which are straight lines perpendicular to the x_2-direction. But because of the radially symmetrical nature of the problem the index that maximizes the response in any direction is therefore one with straight index contours perpendicular to the desired direction i.e. a linear index.

Now consider some profit function $y = f(\bar{x}_1, \bar{x}_2)$. Figure 3 illustrates the countours for $y = \bar{x}_1 + \bar{x}_2^2$ as an example. Point A is the present position of $(\bar{x}_1, \bar{x}_2)$. The circle is the response circle for linear indices with a fixed intensity of selection. There are two situations which must be considered:

(1) y has no maximum within the response circle. In Fig. 2 the point C represents the linear index which maximizes profit (y). All nonlinear indices move $(\bar{x}_1, \bar{x}_2)$ by a smaller distance than the linear index and hence the new value of $(\bar{x}_1, \bar{x}_2)$ will lie within the response circle. But no position within the circle has a y-value as high as C, so all non-linear indices are inferior to the linear index represented by C.

(2) y has a maximum within the response circle. In this case we can decrease the intensity of selection so that the radius of the circle decreases until the point with maximum y lies on the circle. Then the argument in situation (1) applies. It is always desirable to reduce the intensity of selection if this can be done without decreasing the response because selection is costly in terms of animals which are culled and/or missed opportunities for selection on other criteria.

If x_1 and x_2 are not of equal variance, equal heritability and uncorrelated then a linear transformation of x_1 and x_2 can be found in which the response curve is circular (Moav and Hill 1966) and so the argument presented above can be applied. Generalization to more than two dimensions follows similar lines.

Thus for any profit function the linear index derived by the graphical method of Moav and Hill (1966) either achieves the maximum increase in profit possible for a given intensity of selection, or reaches the maximum of the profit surface with the minimum intensity of selection.

Kempthorne and Nordskog (1959) suggested two other methods of deriving selection indices for non-linear profit functions. Firstly, we could treat terms such as x^2 as additional traits to be included in the calculation of the index by $b = P^{-1} Ca$. As an example, assume that $y = x_1 - x_2^2$ so that $\bar{x}_2 = 0$ maximizes profit. If all the additive genetic variance in x_2^2 ($A_{x_2^2}$) is due to additive genetic variance in x_2, then $A_{x_2^2}$ can be found by considering the effect on x_2^2 of a gene substitution which has a small effect (Δx) on x_2 from

$$E(x_2 + \Delta x)^2 - E(x_2^2) \simeq 2\bar{x}_2 \Delta x$$

Thus $A_{x_2^2} \simeq k^2 A_{x_2}$, where $k = 2\bar{x}_2$ and A_{x_2} is the additive genetic variance of x_2.

The phenotypic covariance between x_1 and x_2^2 (Cov $(x_1 x_2^2)$) equals

$$\mathrm{Cov}\,(x_1, kx_2 + (x_2^2 - kx_2))$$

$$= k\,\mathrm{Cov}\,(x_1, x_2)$$

Cov $(x_1, x_2^2 - kx_2) = 0$ if x has a multivariate normal distribution because of symmetry about $x_2 = \frac{k}{2} = \bar{x}_2$. Similar results apply for the additive genetic covariance. Thus the rows and columns in P and C which correspond to x_2^2 are simply k times the rows and columns corresponding to x_2 except that the phenotypic variance of x_2^2 is larger than this rule would predict because the heritability of x_2^2 is less than that of x_2. Consideration of the equations $Pb = Ca$ shows that due to these linear dependencies the b coefficient corresponding to x_2^2 must be zero and the solutions are those that would have been obtained by deleting all elements referring to x_2^2 and giving x_2 the economic weight k. This is in fact the normal index obtained by $\mathbf{a} = \frac{\partial y}{\partial \mathbf{x}}$ since $\frac{\partial y}{\partial x_2} = 2\bar{x}_2 = k$.

Provided x has a multivariate normal distribution, the quadratic index calculated in this way reduces to the normal linear index for all quadratic profit functions. As usual this index is also that derived by the graphical method using a very small response ellipse as shown in Fig. 4a.

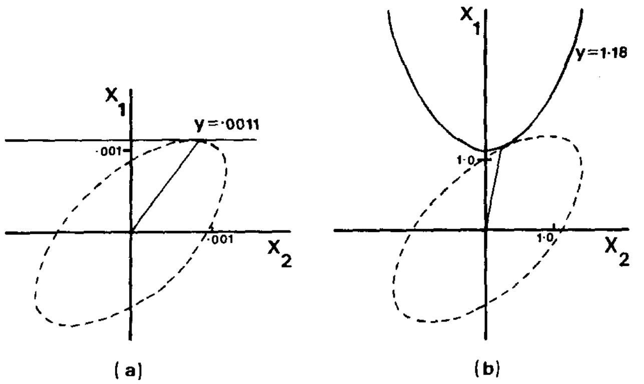

Fig. 4a and b. The optimum selection indices for the profit function $y = x_1 - x_2^2$ are illustrated for both a very small response ellipse (**a**) and a larger response ellipse (**b**). For convenience the two graphs are drawn to different scales. As the response increases the optimum direction of selection moves toward no change in x_2. (The correlation between x_1 and x_2 is 0.64)

The second suggestion of Kempthorne and Nordskog (1959) is to maximize profit subject to a restriction that certain traits do not change. Intuitively this seems a reasonable approach when the population mean is already at an optimum value for these traits. For instance assume that $y = x_1 - x_2^2$ and that $\bar{x}_2 = 0$. Maximizing y subject to the restriction that x_2 remains zero is equivalent to the graphical method assuming a very large response ellipse (Fig. 4b).

Bulmer (1980) presents a different method of finding the best selection index for non-linear profit functions. His method involves maximizing a function of the mean of the selected group. This emphasizes the point that the value of any one animal depends on which other animals are selected along with it. However, this method would be impractical to use because it would require the index to be evaluated for all possible groups of animals that might be selected, in order to chose the best group.

For non-linear profit functions, Allaire (1977) pointed out that non-random mating can increase the average phenotypic merit of the progeny. He derived non-linear indices to select the best mate for a given preselected parent. The optimum index depends on the phenotype of the parent already chosen. The non-random mating caused by the use of these indices does not increase the long term rate of genetic gain but it utilizes the epistatic variation to maximize the phenotypic merit of the next generation. Further generations do not build on top of this advance – it must be recreated in each new generation. Thus the best policy is to use a linear index to select the parents of the next generation and then use assortative matings amongst these pre-selected parents.

In many situations the linear approximation (1) will be adequate. However if the population mean is already near optimum in some traits this approximation may not be satisfactory. As an example, assume again that $y = x_1 - x_2^2$ and $\bar{x}_2 = 0$. The index based on $\mathbf{a} = \frac{\partial y}{\partial \mathbf{x}}$ implies selection for x_1 only, but if x_1 and x_2 are correlated this will eventually lead to a decline in $-x_2^2$. An analogous situation occurs in many selection experiments. Selection for a quantitative character often leads to a decline in traits closely related to natural fitness despite the fact that fitness was uncorrelated with the character under selection in the base population (Merritt 1974). Fitness is often maximized at an intermediate value of a quantitative trait and so correlated changes in this trait as a result of selection could explain the decline in fitness. The preceding analysis shows that including fitness traits in the profit function is not sufficient to prevent this decline unless the curvilinear nature of the relationship between traits is recognized.

The argument presented above in favour of linear indices assumes that all additive genetic variation in y is due to additive genetic variation in $\mathbf{x}$. It is possible that additive variation in y could be represented by epistatic variation in $\mathbf{x}$. In this case one could follow the suggestion of Kempthorne and Nordskog (1959) and include terms such as x^2 in the index as if they were additional traits. In this case the genetic variances and covariances involving terms such as x^2 must be estimated directly from data and not derived from those of x.

This situation might arise if some trait of overall productivity had more biological unity than the components into which we divide it. Because of the difficulty in defining better components, selection based directly on overall productivity as suggested by Beilharz (1972), might be the safest procedure. Alternatively if a transformation of x on which the genetic variance was additive could be found, the transformed variables could be used in a linear index.

Even when the genetic variation in $\mathbf{x}$ is additive, non-linear indices would have one advantage over linear indices in that they would be more stable. Again assume that $y=x_1-x_2^2$ and that x_1 and x_2 have the same heritability and are uncorrelated. The selection index $I=x_1-x_2^2$ could be used regardless of the value of $\bar{\mathbf{x}}$, but this is not true for any linear index.

Producer-supplied Variables

The profit that a farmer makes depends not only on the genetic value of his animals but also on the level of other variables which he sets by management decisions. For instance, profit from beef production in an area in which ticks are endemic depends on the tick resistance of the animals and on the number of times they are dipped in acaricide. If there is no interaction between the animal variables and the management variables then the latter do not need to be taken into account when constructing selection indices. But if there is an interaction, then the economic values of the animal variables depend on the levels of the management variables chosen. Melton et al. (1979) present a method of determining the economic weights to be used in this situation. Their method is equivalent to the following:

Let profit (y) be a function of animal variables $(\mathbf{x})$ and management variables $(\mathbf{z})$

$$y=f(\mathbf{x},\mathbf{z})$$

The optimum level of $\mathbf{z}(\mathbf{z}_m)$ can be found from

$$\frac{\partial y}{\partial \mathbf{z}}=0$$

evaluated at the present mean $(\bar{\mathbf{x}})$. The economic weights appropriate for x can then be found as before by

$$\mathbf{a}=\frac{\partial y}{\partial \mathbf{x}} \text{ evaluated at } (\bar{\mathbf{x}}, \mathbf{z}_m)$$

However I found the description of the method by Melton et al. (1979) confusing. The reason for this confusion is explained in the Appendix.

One feature of the method of Melton et al. may appear unreasonable. Surely the value of improving $\mathbf{x}$ should be calculated while simultaneously changing $\mathbf{z}$ so that it remains at the optimum value. In our beef cattle example the principal advantage to be gained by increasing tick resistance may be due to decreasing the number of times the cattle must be dipped. Is it correct to calculate the economic value of increasing tick resistance when the number of dippings remains constant at the level required for the less resistant cattle?

Solving $\frac{\partial y}{\partial \mathbf{z}}=0$ leads to simultaneous equations whose solution can be expressed as $\mathbf{z}=z(\mathbf{x})$. Then the profit resulting from changing $\mathbf{x}$ and changing $\mathbf{z}$ according to $\mathbf{z}=z(\mathbf{x})$ is

$$y=f(\mathbf{x}, z(\mathbf{x}))=g(\mathbf{x})$$

The economic weights of $\mathbf{x}$ are then $\frac{\partial g}{\partial \mathbf{x}}$. However $\frac{\partial g}{\partial \mathbf{x}}=\frac{\partial y}{\partial \mathbf{x}}+\frac{\partial z}{\partial \mathbf{x}}\frac{\partial y}{\partial \mathbf{z}}$. But since $\frac{\partial y}{\partial \mathbf{z}}=0, \frac{\partial g}{\partial \mathbf{x}}=\frac{\partial y}{\partial \mathbf{x}}$

That is, the increased profit obtained by a small change in x is the same whether it is calculated by simultaneously optimizing z or by maintaining z constant at the value which maximized profit prior to selection. However, if larger changes in x are to be considered by the graphical method then the contours of $g(\mathbf{x})$ not $f(\mathbf{x},\mathbf{z})$ at $\mathbf{z}_m$ should be plotted.

Conclusion

Even for non-linear profit functions a linear selection index achieves the greatest increase in profit. This conclusion is in keeping with the basic assumption of quantitative genetics that it is the additive value of genes which determines the response to selection. If the curvature of the profit contours in small relative to that of the response circle (as will usually be the case if $\bar{x}$ is not already near optimum in some traits) then estimating the economic weights by $\mathbf{a}=\frac{\partial y}{\partial \mathbf{x}}$ should be satisfactory. However a response circle of more than one generation should be considered. If this is not the case then the graphical method or equivalent algebraic or numerical methods could be used. $\mathbf{a}=\frac{\partial y}{\partial \mathbf{x}}$ will be especially inadequate in the vicinity of a minimum, a saddlepoint or an inflection but I suspect that these will be rare phenomena in real life. However, maxima or intermediate optima for some traits may be quite common especially in situations where natural fitness is an important part of profitability. In these cases continued use of the index based on $\mathbf{a} = \frac{\partial y}{\partial \mathbf{x}}$ will also be unsatisfactory. I believe it is important that we recognize the existence of intermediate optima so that the best long term selection procedure can be adopted and so that we can realistically estimate the amount of genetic improvement which is possible.

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Appendix

In their method of deriving economic values Melton et al. (1979) define a variable (π)

$$\pi = p_w w - \mathbf{p}'_x \mathbf{x} - \mathbf{p}'_z \mathbf{z}$$

where p_w is the price of the product
w is the amount of product produced and is a function of $\mathbf{x}$ and $\mathbf{z}$
$\mathbf{p}'_x$ are the economic weights of the traits $\mathbf{x}$
$\mathbf{p}'_z$ are the costs of the inputs $\mathbf{z}$

They call this variable π a profit function but this is illogical since the animal variables do not cost money. It could represent the profit of a farmer who buys animals from a breeder at a price dependent on their genetic merit but it would not be sensible to maximize this 'profit' since $\mathbf{p}'_x \mathbf{x}$ is loss to one farmer but profit to another. Although Melton et al. (1979) state they maximize π by solving

$$\frac{\partial \pi}{\partial \mathbf{x}} = \frac{\partial \pi}{\partial \mathbf{z}} = 0$$

they do not maximize π since they do not solve these equations for $\mathbf{x}$ and $\mathbf{z}$ but for $\mathbf{p}_x$ and $\mathbf{z}$. What in fact their method does is to find the value of $\mathbf{z}$ which maximizes

$$y = p_w w - \mathbf{p}'_z \mathbf{z}$$

and to use this value of $\mathbf{z}$ in the normal method of calculating economic weights.

The method of Melton et al. (1979) is interpreted in a different way by Thompson (1980). He argues that π is maximized with respect to x by

$$\frac{\partial \pi}{\partial x} = p_w \frac{\partial w}{\partial x} - p_x = 0$$

and if the present population mean $\bar{x}$ is already optimum then this implies

$$p_x = p_w \frac{\partial w}{\partial x} (\bar{x}, z_m)$$

But if the present population mean is optimum then no genetic progress is possible and seeking economic weights does not seem worthwhile. This interpretation depends on the illogical definition of π as profit with the result that, as Thompson (1980) points out, π can easily be minimized rather than maximized. (This happens if

$$\frac{\partial w^2}{\partial^2 x} (\bar{x}) > 0)$$

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