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MULTI-TRAIT SELECTION WITH DESIRED GAINS AND NON-LINEAR INDEXES

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SUMMARY

A linear selection index for multiple traits is not satisfactory in many practical cases, such as when selecting for traits that have an optimum phenotypic value with a nonlinear profit function. This paper will discuss various ways to select for a breeding objective that includes a trait with an optimum phenotype. The study shows that, contrary to general belief, a linear updated index does not always achieve a desirable result due to correlated responses in multiple trait selection. A simple derivation of weights for a restricted index is proposed to deal with the problem.

INTRODUCTION

Multiple trait selection based on a linear index can be problematic when there is uncertainty about economic weights or when some traits have economically optimal values for their phenotype. With optimal traits there may be a tendency to use a non-linear index to avoid selecting animals that deviate much from the optimal value. How to select for traits with a non-linear profit function has been addressed many times, and it is commonly accepted that a linear index is still a satisfactory approach, provided that index weights are regularly updated depending on how far the current population mean is away from the trait optimum (Goddard 1983; Dekkers *et al*. 1995; Martin-Collado *et al*. 2016). Martin-Collado *et al*. (2016) considered a case study where they compared linear indexes with non-linear indexes and linear updated indexes. They also looked at a linear index where there is no longer a weight for the phenotypic values above the optimum, which they referred to as Non-Linear-Flat (NFL Index). Valuing phenotypic values of individual selection candidates differently is a departure from the common view on index selection, where the selection weights depend on the population average rather than individual phenotypes. However, with optimum traits it is tempting to use a selection method where individuals that deviate from the optimum are penalized. Real world breeding objectives involve multiple traits and whatever weights are used for traits with an optimal value will also affect responses in other traits that may be linked to profit linearly. Equally, the correlation with other objective traits and their index weights will be important to ensure that an optimum trait is not pulled away from its optimum. This could be the case if the optimum trait has a strong correlation with other objective traits and has relatively less value. To ensure that trait responses are optimal, a restricted index, which applies a linear weight, could be used when the optimum trait mean is near its optimum. The aim of this paper is to explore trait responses for various selection strategies in a two-trait breeding objective when one trait has an economic optimum. Four selection strategies are compared, being the linear index, the linear updated index, the penalized phenotype index and the restricted linear updated index.

MATERIALS AND METHODS

A simulation study was used for a population of 2,000 progeny born in each generation. Results were averaged over 200 replicates. Males (20%) and females (80%) were selected based on an index using individual phenotypes for two traits. Two traits were considered; one with a linear profit function and a trait with a nonlinear profit function. Phenotypic standard deviations (PSD) are 1, hence trait responses are expressed in units of PSD. We assumed equal heritabilities of 0.25 and genetic and residual correlations were either 0 or 0.5 and 0.3, respectively. Random normal deviates were used in R to simulate breeding values and phenotypes for the individuals in each of 30 generations. We did not account for relationships between individuals, inbreeding or the Bulmer effect. The profit function was equal to $v_1.x_1+v_2.x_2 + c.x_2^2$, where x_i is a phenotypic value for trait i. Following Martin-Collado *et al.* (2016), we derived that $c = -v_2/(2.x_{2Opt})$, were x_{2Opt} is the optimum phenotypic value for trait 2 relative to the value in generation 0 ($x_{2(0)}$) and v_2 is the derivative of the profit equation for trait 2 at $x_{2(0)}$. We assume equal economic values of 1 for v_1, v_2 and the value for x_{2Opt} was also 1. These values could be varied to explore the relative importance of each trait and the distance of x_2 from its optimum. We used four selection strategies.

1. The linear index was derived from selection index theory, with the index weights derived as $b = \mathbf{P}^{-1}\mathbf{G}v$, where **P** is the 2x2 variance-covariance matrix among an individual's phenotypes and **G** = is the covariance matrix between phenotypes and breeding values. The vector v contains economic values derived in generation 0 as $v = [v_1, v_2]$. Individuals are selected based on b'x, where x is a vector of phenotypes $[x_1, x_2]$.
2. The linear updated index was updated every generation using the economic values as derivatives of the profit function, i.e. $v = [v_1, v_2 + 2c\bar{x}_2]$, where $\bar{x}_2$ is the population mean of x_2 at the current generation.
3. The penalized phenotype index was constructed the same way as the linear updated index, but with x_2 replaced by x_{2d}, the deviation of x_2 from the optimum value: $x_{2d} = -abs(x_{2Opt} - x_2)$.
4. The restricted linear updated index follows the updated index but once at the optimum uses a restricted index to keep the response for trait 2 equal to zero. At that point, the economic value for trait 2 in the updated index would be zero, which is the slope of the profit function at the optimum value. However, the restricted index weight for trait 2 requires a non-zero values to counterbalance a correlated response. The restricted index weight is derived below.

Desired gain index. A response to selection can be predicted for each of the breeding objective traits as a vector $d_g = \mathbf{V}v/\sqrt{(v'\mathbf{V}v)}$, where **V** is the variance-covariance matrix of the estimated breeding values (EBVs) for the objective traits for an individual, and v is vector with economic values of the objective traits. The matrix **V** can be derived from selection index theory as $\mathbf{G.P}^{-1}\mathbf{G}$ and $v'\mathbf{V}v$ is the variance of the index, which can also be written as $b'\mathbf{P}b$. However, it is important to note that the selection response only depends on the covariance matrix among EBVs (**V**) and the weights used for these EBVs in the index (v). Now let d_{desg} be a vector of desired responses. Then the vector with weights to achieve these responses would be derived as $v_{desg} = \mathbf{V}^{-1}d_{desg}.\sqrt{(v'_{desg}.\mathbf{V}.v_{desg})}$. The last term is a scalar (variance of the index) and can be ignored as it is only important to know relative weights. In our case, with two traits, the response for the second trait needs to be zero, i.e. $d_{desg} = [z, 0]$. Therefore, taking the ijth elements of the inverse of **V** (v^{ij}) gives desired gain weights $v_{desg} = [v^{11}.z, v^{22}.z]$, or relative weights are $[1, v^{21}/v^{11}]$.

RESULTS

The response to selection based on the four index strategies is shown in Fig.1 for the case where there are no genetic correlations between the traits. The response for the linear index is linear for both traits. When the optimum trait is not correlated with the other traits, the updated index strategy is an adequate method to keep the phenotypic mean of the non-linear trait at its optimal value. The response of the restricted linear updated index is identical to the response of the linear updated index. When the response for the non-linear trait is slowing down near the optimum value, the response for the other objective trait can increase and shows a higher response compared to the linear index. The penalised phenotype strategy also converges toward the optimum phenotype value but at a slower rate than the updated indexes.

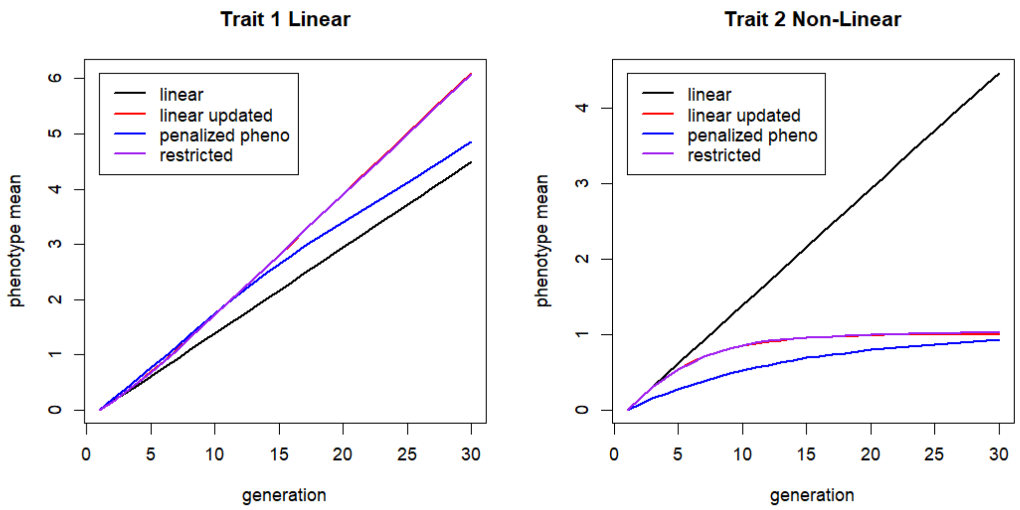

Figure 1. Response to selection for two traits that are related to profit in a linear and non-linear way. The non-linear trait has an optimal value at 1 phenotypic standard deviation above the current mean. The traits have equal economic value in generation 0. Responses are compared for four different index selection strategies (see main text for detail) for the case where both genetic and environmental correlations are 0

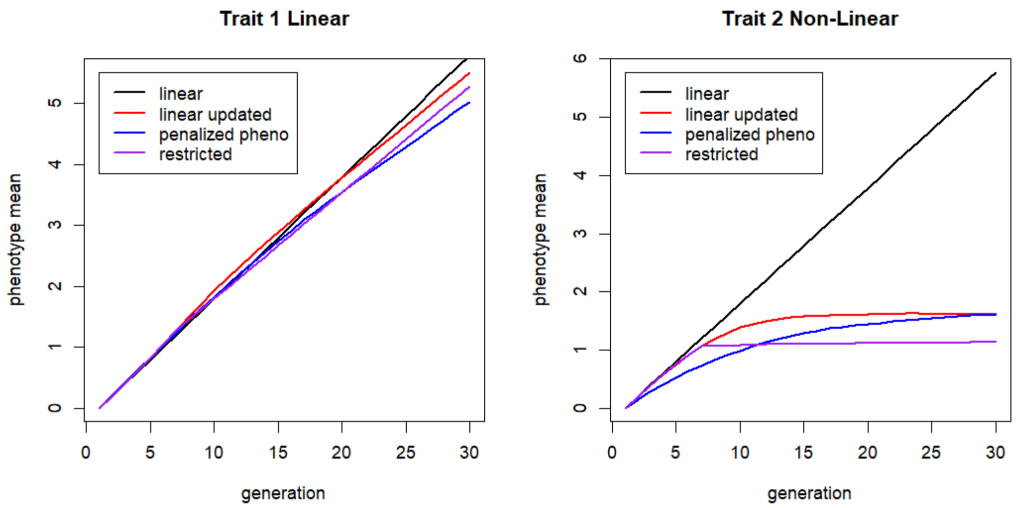

Figure 2. Response to selection for two correlated traits related to profit in a linear and a non-linear way. The non-linear trait has an optimal value at 1 phenotypic standard deviation above the current mean. The traits have equal economic value in generation 0. Responses are compared for four different index selection strategies (see main text for detail) for the case where genetic and environmental correlations are 0.5 and 0.3, respectively

When the two traits are correlated the updated index method does not keep the nonlinear trait at its optimum value while with the restricted index approach the trait 2 response does converge to its optimum (Figure 2). However, the overall profit of these two indices is very similar as for the updated index the cost of overshoot in trait 2 is compensated by more genetic gain for trait 1.The penalized phenotype index also converges to the same value as the linear updated index strategy, but at a slower rate. A stronger genetic correlation increases the value at which the updated linear index approach converges to. Similarly, if the economic value of trait 1 is relatively higher, then the convergence value for the optimum trait is also higher, i.e. further above the optimum value.

DISCUSSION

Several papers have suggested that the updated linear index is an adequate method to select for optimum traits. This is true for single trait selection or if the optimum trait is not correlated with the other objective traits. However, in multiple trait selection, updated economic values do not always guarantee traits to converge to an optimum value. A restricted index was used to keep the nonlinear traits at its optimal value, and restricted index weights were derived from the variance covariance matrix of EBVs for the objective traits. Although this was illustrated in a two-trait example, the method can easily be extended to more traits (e.g. see Van der Werf and Clark 2022).

Martin-Collado *et al*. (2016) illustrated updated linear indexes for a sheep scenario and found the method to be suitable. However, in their case the genetic correlation was close to zero and the non-linear trait had relatively a higher economic value. In most cases, the other objective traits combined will have more value and if these traits combined have a significant correlation with the nonlinear trait, we cannot expect the updated linear index to converge to the optimum for traits with an optimal value. The higher phenotypic value that the response converges to depends on the correlation and the economic value of the other traits, i.e. it is a function of the pull from the residual objective traits. The derivative of the profit function for the nonlinear trait at its optimum is zero, but in most cases this economic weight is not sufficient to counterbalance a correlated response. The restricted index used values that were designed for that purpose, i.e. they are effectively the implicit economic values used in desired gains indexes. Constrained selection indexes for optimal traits were also proposed by Goddard (1983) and Dekkers *et al* (1995) but less straightforward compared to the method proposed in this paper.

The penalized phenotype index method showed a slower response than the linear index method but ultimately converges to the same phenotypic mean. The time to convergence could be increased could be increased by penalising the deviations more strongly (i.e. $P_{2d} = -abs(P_{2Opt} - P_2).\lambda$, where a higher λ-value (>1) is a penalty). However, this is at the expense of the response for trait 1. The penalized phenotype selection method is overall less effective than a linear index, and a mate allocation strategy might be a more efficient way to avoid extreme phenotypes.

CONCLUSION

In multiple trait selection a linear updated selection index method is not adequate for traits with an optimum value as it does not sufficiently control the correlated response with other objective traits. We derived restricted index weights that ensure phenotypic optimal values in multiple trait selection.

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