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USE OF COVARIANCE FUNCTIONS TO SELECT FOR CHANGES IN GROWTH CURVES

J.H.J. van der Werf

School of Rural Science and Natural Resources, University of New England, Armidale, NSW 2351

SUMMARY
A method is presented to optimally change growth curves by selection, or more generally to change traits that are repeatedly expressed over a trajectory. A covariance function can be estimated for such traits and the eigenfunctions of the covariance function give insight as to the scope for changing the curvature by selection. Selection can be based on the eigenvalues of the covariance function, but it is shown that this is equivalent to selection on some arbitrary ages along the curve. To maximize profit, a method is presented to find optimal index weights for selection based on different ages along the trajectory. Methods are illustrated using beef cattle growth as an example.
Keywords: Selection, growth, covariance functions.

INTRODUCTION

Some traits in animal production such as growth or lactation can be measured repeatedly on a trajectory. There is often an interest in selection of animals such that the average production curve in the population is changed to achieve higher efficiency of the production system, e.g. flatter lactation curves or growth curves with increased weight gain close to slaughter. The scope for change depends on the variance-covariance (VCV) structure among traits along the trajectory. Kirkpatrick *et al.* (1990) proposed the use of a covariance function (CF) to describe the VCV structure of "infinite dimensional" traits, i.e., for traits that could possibly be measured at any point on a given trajectory.

A growth curve is a function of weight over time and the possible changes in the growth curve made by selection depend on whether correlations between weights at different ages differ from unity. The CF contains the information about degree of similarity of traits at different ages and whether the shape of the growth curve can be altered by selection. Kirkpatrick *et al*. (1990) proposed a canonical decomposition of the CF and plotted eigenfunctions, which are basically eigenvectors as a function of time. Each eigenfunction shows selection response for each age along the trajectory when selection is for the associated canonical variable. Any selection response along the curve can be written in terms of a weighted sum of eigenfunctions (Kirkpatrick *et al*. 1990). Hence, the shape of the eigenfunctions and the magnitude of the associated eigenvalues give insight in the extent to which the growth curve can be changed. Selection on canonical variables, however, is not very appealing to the industry, but it will be shown in this paper that an equivalent index exists based on observable traits.

An optimal selection strategy requires finding optimal index weights for selection on different ages along the trajectory. The economic value of change at each age needs to be determined and index weights need to be found that maximize the response of selection when aggregated over the whole trajectory. A second objective of this paper is to present a method to find such optimal weights. The methods will be illustrated using beef cattle growth data as an example.

THEORY

Estimating covariance functions. Consider a previously estimated variance covariance matrix G of rank *t* for breeding values for body weight (BW) at *t* given ages. A CF of order *k* ($k \le t$) can be estimated from G such that $\hat{G}$ = $\mathbf{\Phi K \Phi}'$, where $\hat{G}$ is an approximation of G. The CF gives the co-variance between breeding values u_l and u_m on an animal's BW measured at ages x_l and x_m. The matrix **K** of rank *k* contains the coefficients of the CF, the matrix $\mathbf{\Phi}$ is an *t* x *k* matrix with orthogonal polynomials and can also be written as $\mathbf{M\Lambda}$, with **M** being a *t* x *k* matrix with elements $m_{ij}= a_i^{(j-1)}$ (i=1,..t; j=1,..k), and Λ being a matrix of order *k* with polynomial (e.g. Legendre) coefficients. The matrix K can be estimated from G (Kirkpatrick *et al.* 1990), based on the best goodness of fit, but K can also be estimated directly from data using random regression (Meyer 1998).

Selection response based on trait values at different ages. Selection response from index selection can be calculated as regression of additive genetic values for breeding objective traits (**a)** on index: $\mathbf{R}_a$ = **b'G**/sqrt(**b'Pb**) where selection is on Index I = **b'x**, **x** are observed index variables (phenotypes or EBV's), **b** are selection index weights calculated as $\mathbf{P}^{-1}\mathbf{Gv}$, where **P** = var(**x**) and **G** = cov(**x**,**a**) and **v** is a vector with economic values for the breeding objective traits. The index approach in conjunction with CF-derived covariances can be used to predict response to selection for any trait along the trajectory when selection is based on EBV's at an arbitrary set of ages.

Selection response based on eigenfunctions. The matrix **K** can be decomposed into eigenvalues **D** and eigenvectors **E** as **K** =**EDE**', and we can evaluate eigenfunctions **Q** for a given set of ages as $\mathbf{\Phi E}$ **= Q**. The *k* columns of **Q** represent the eigenfunctions, with each of them having an eigenvalue attached to it, and the rows refer to the *t* ages. Associated with each eigenfunction is a canonical variable z_i with variance equal to the i^{th} diagonal of D and single trait selection on each z_i gives a response along the trajectory proportional to its eigenfunction. Consider an index based on the vector **z** with *k* canonical variates: is **I** = $\mathbf{b}_z$'**z**. Note that var(**z**)= **D**. If **z** were equal to true additive genetic values, the response would be $\mathbf{R}_z$ = $\mathbf{b}_z$'**D**/sqrt($\mathbf{b}_z$'$\mathbf{Db}_z$). For the response at a given set of ages we can derive $\mathbf{\Phi}$ and **Q** and the response in canonical variates **z** can be transformed into response for observable traits, as shown below.

For comparison, consider selection on true breeding values for BW, making **x** = **a**, **P** = **G** and index weights being equal to economic values: **b** = **v**. As the true breeding values for BW can be written as a linear combination of the canonical variates (**a** = **Qz**), an index based on canonical variates I = $\mathbf{b}_z$'**z** is equivalent to an index based on variables on the observed scale I = **b'a** when the latter index weights are $\mathbf{b} = (\mathbf{Q}^{-1})'\mathbf{b}_z$. Using **G = QDQ'** it also can be shown that the response for BW ($\mathbf{R}_a$) is a linear function of the response vector for canonical variates: $\mathbf{R}_a = \mathbf{R}_z\mathbf{Q}$. Note that **Q** can only be inverted when it is a square matrix, i.e. the number of ages to consider should be equal to the number of eigenvalues, which is equal to the order of **K**. This implies that the maximum number of ages to consider for selection does not need to exceed the number of significant eigenvalues in the covariance function. Selection on true breeding values is considered here, giving index weights equal to economic weights for breeding objective traits. Actual selection is based on EBV's, with optimal weights and response also affected by prediction errors, but this will not be presented in this paper.

Economic optimisation of selection on growth. Any selection on BW will give a change in the growth curve that affects profit at all ages. The change in profit due to selection therefore needs to be accumulated over all ages. For a given selection index the response R_a can be determined for a large number of ages over the entire trajectory and the change of profit at each age can be determined. A genetic algorithm can be used to determine index weights that optimize change in profit for a given set of economic and technical parameters.

EXAMPLE

A VCV matrix for additive genetic effects of BW was derived based on an analysis by Albuquerque and Meyer (2001). Data for their analysis was supplied by the Brazilian Zebu Breeders Association and consisted of 74,591 weight records on 10,751 Nelore animals, weighed, on average, every 90 days from birth to 730 days of age. Albuquerque and Meyer (2001) used random regression to estimate CF coefficients for direct additive, maternal and permanent environmental effects with order 6, 4 and 6, respectively. Based on the 6th order CF for the additive genetic variance a VCV matrix was reconstructed for 6 equidistant ages. In turn, this VCV matrix was fitted with a CF of order 3, following Kirkpatrick *et al.* (1990), as in isolation the fit of this matrix could not be significantly improved with a higher order fit. Plots of eigenfunctions computed from this CF are in Figure 1, showing that selection on the second canonical variate (z_2) would decrease BW at early ages and increase final weight. However, z_2 accounts for only 4% of total variance and single trait selection on

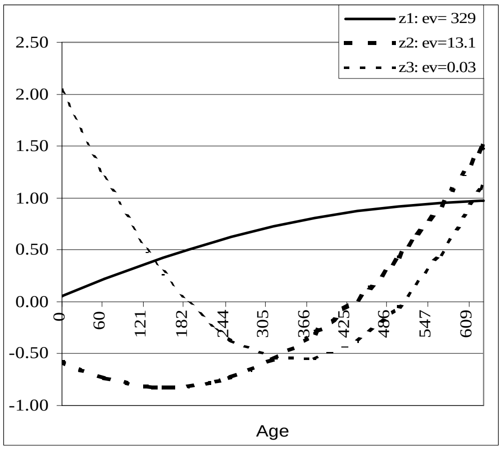

Figure 1. Eigenfunctions for the example based on a covariance function of order 3. The lines represent single trait selection response for canonical variates (z_i), each of them with an associated variance (ev = eigenvalue)

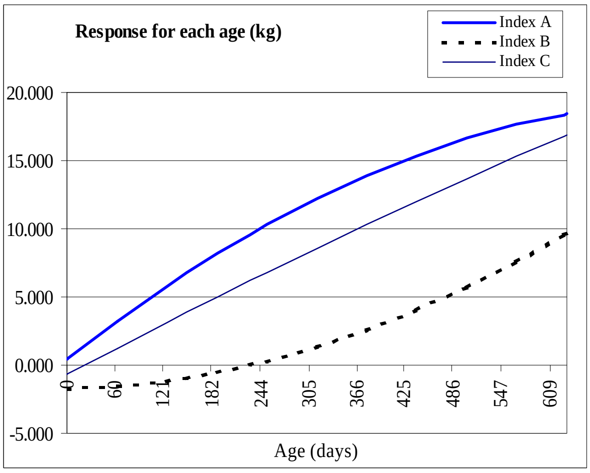

Figure 2. Response to selection on weight at each age when selection is on final weight (index A), or optimized selection accounting for either low (B) or high (C) feed costs.

Table 1. Index weights for specific ages and for canonical variates for three indices compared

Index	Index weights for BW at specific ages			Index weights for canonical variates		
	5 days	300 days	600 days	1	2	3
A	0	0	1	1	1.56	1.17
B	1	-1.54	1.59	1	4.38	7.73
C	1	-1.50	1.11	1	19.7	43.1

Table 2. Body weight (BW) at 3 ages, revenue, feed cost and profit per head for no selection, or after one round of selection on index A, B or C, for two feed cost scenarios

	BW at day				scenario 1[a]		scenario 2[a]	
index	5	300	630	$revenue[a]	$feed cost	$profit	$feed cost	$profit
none	40	235	412	618	521	97	608	10
A	40	246	430	646	544	102	634	11.6
B	39	243	429	643	540	103	631	12.5
C	39	236	421	633	531	101	619	13.3

[a] Assumed beef price is $1.5/kg; feed cost in scenario 1 and 2 is $0.12/kg and $0.14 /kg, respectively

z_2 would increase final weight to 30% of the response to single trait selection for final weight. Figure 2 compares selection response (per unit of selection intensity per selection round) for three selection strategies: selection on final weight (index A), and optimal selection when feed costs are $0.12/kg (index B) and $0.14/kg (index C), respectively. To determine optimal weights, a simple profit model was applied; accounting for feed cost (maintenance and growth) at all ages, and only final weight determining revenue ($1.50/kg). The index weights for the three indices and BW change at different ages, as well as the change in revenue, feed cost and profit is given in Tables 1 and 2.

DISCUSSION

CF can demonstrate a lack of robustness if measurements to estimate their coefficients are not well scattered over the whole trajectory. A similar caution is necessary when choosing selection criteria, as prediction of selection response based on CF is not very accurate when extrapolated. However, a CF is a necessary tool to predict response for all ages across the trajectory. The method presented in this paper forms a useful basis to optimize selection on growth curves. The method can be extended to account for prediction error in selection, for more sophisticated profit models (including the role of mature weight) as well as for multiple trait changes of growth, with a joint optimization of selection for weight, fat and muscle.

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