Methods and consequences of including feed intake and efficiency in genetic selection for multiple-trait merit

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ABSTRACT: Methods are presented for including feed intake and efficiency in genetic selection for multiple-trait merit when commercial production is from any combination of pasture or concentrates. Consequences for the production system and for individual animals are illustrated with a beef cattle example. Residual feed intake at pasture (**RFI-p**), residual feed intake in the feedlot (**RFI-f**), and cow condition score are additional traits of the breeding objective. Feed requirement change is costed in the economic values of other objective traits. Selection responses are examined when feed costs are ignored, partially or fully included in the breeding objective, and when net feed intake (**NFI**) EBVs are added to the index. When all feed cost was included and **NFI** EBVs were in the index, selection (with selection intensity, $i = 1$) increased production system \$ net return by 6.0%, \$ per unit of product by 5.2%, \$ per unit of feed by 6.6%, total product by 0.7% and product per unit of feed by 1.3%. There was little change in production system total feed. When feed cost was ignored, selection decreased production system \$ net return, \$ per unit of product, and \$ per unit of feed. At the individual trait level, when feed was fully included there were

increases in weaning weight-direct (0.8 kg), feedlot entry weight (1.4 kg), dressing % (0.04%), carcass meat % (0.36%), carcass fat depth (0.12 mm), carcass marbling score (0.02 score), cow condition score (0.01 score), calving ease-direct (0.97%), calving ease-maternal (0.22%) and cow weaning rate (1.3%), and decreases in weaning weight-maternal (-0.9 kg), **RFI-p** (-0.09 kg DM/d), **RFI-f** (-0.11 kg DM/d), sale weight (-1.6 kg) and cow weight (-8.7 kg). Gains were evident over a range of feed price. Selection for \$ net return also increased \$ net return per unit of feed, suggesting that \$ net return per unit area would increase in grazing industries. Feed cost for trait change was the source of a major genotype $\times$ environment interaction affecting animal rankings. Where industry production environments vary, and feed cost for trait change varies with the environment, we recommend that industry indexes be derived for more than one level of feed cost. Cow condition score did not decline while biological and economic efficiency of the production system and individual animal were improving, suggesting that efficiency can be improved under multiple-trait selection without compromising breeding cow welfare.

Key words: beef cattle, genetic selection, efficiency, feed cost, genotype $\times$ environment interaction, animal welfare

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INTRODUCTION

Feed intake and feed conversion efficiency have major impacts on profitability, but it is not well resolved how these should be included in selection when the aim is to improve multiple-trait

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merit. Breeding objectives have to account for feed cost (e.g., [Ponzoni and Newman, 1989](#); [Brascamp et al., 1998](#); [Barwick et al., 2011a](#)). Methods are also available for estimating the feed needed for performance (referred to as “feed requirement”) (e.g., [Freer et al., 2007](#)). Early research considered whether breeding should be for economic or biological efficiency ([Dickerson, 1970](#); [Notter et al., 1979](#)) and whether traits should be combined as linear functions or as ratios. Subsequent research concentrated on identifying indirect criteria for efficiency ([Archer et al., 2004](#); [Arthur et al., 2004](#); [Herd et al., 2004](#)), stimulated by the difficulty of measuring feed intake in grazing animals. Residual feed intake measures (e.g., [Koch et al., 1963](#)) have been widely researched, and they remain a focus in several species ([Barwick et al., 2009](#); [Basarab et al., 2011](#); [Gilbert et al., 2014](#)).

We describe methods of including feed intake and efficiency in multiple-trait selection, and illustrate these with a beef cattle example. Differences in feed intake are fully accounted for and consequences for the production system are derived in addition to those for individual animal performance. The methods were developed for the Australian beef industry, but may be applicable more widely.

MATERIALS AND METHODS

Definitions

Animal breeding aims to improve breeding value for net merit, where this is usually expressed in economic terms and is known as the breeding objective. The selection criterion for the breeding objective is commonly an index of estimated breeding values (EBVs) $\hat{\mathbf{u}}$, derived for an industry ([Barwick and Henzell, 2005](#); [Graser et al., 2005](#)), supplanting the traditional view of the selection index as an index of phenotypes. [Schneeberger et al. \(1992\)](#) showed the mixed model equations can be extended to encompass predictions of breeding values for the breeding objective traits. For a breeding objective $\mathbf{v}'\mathbf{g}$ with $\mathbf{v}$ a vector of economic values for the objective traits, the genetic variance-covariance matrix has components

$$\text{Var} \begin{bmatrix} \mathbf{u} \\ \mathbf{g} \end{bmatrix} = \mathbf{A} \otimes \mathbf{G} = \mathbf{A} \otimes \begin{bmatrix} \mathbf{G}_{11} & \mathbf{G}_{12} \\ \mathbf{G}_{21} & \mathbf{G}_{22} \end{bmatrix}$$

where $\mathbf{A}$ is the numerator relationship matrix, $\otimes$ is the Kronecker product, $\mathbf{G}_{22}$ is the genetic variance-covariance matrix among traits in the objective, $\mathbf{G}_{11}$ is the genetic variance-covariance matrix

among the EBV selection criteria in the index, and $\mathbf{G}_{12}(=\mathbf{G}'_{21})$ the genetic covariance matrix between the criteria and objective traits. Estimates of the breeding values for the objective traits for animal i are derived as $\hat{\mathbf{g}}_i = \mathbf{G}_{21}\mathbf{G}_{11}^{-1}\hat{\mathbf{u}}_i$. For a linear selection index $\mathbf{b}'\hat{\mathbf{u}}_i$ of EBVs, the weights $\mathbf{b}$ for the EBVs are derived as $\mathbf{b} = \mathbf{G}_{11}^{-1}\mathbf{G}_{12}\mathbf{v}$. The most common form of the index is $\mathbf{b}'\hat{\mathbf{u}}_i$, but it can equally be calculated as $\mathbf{v}'\hat{\mathbf{g}}_i$.

The Modeled Production System

The commercial production system can be either pasture-based or concentrate-based post-weaning, or it may include periods on each type of feed. Breeding herd females and young animals in grazing systems are exposed to potentially two types of feed period annually—a period when any increase in the animal's feed requirement would require additional feed, and a period when an increase in requirement would not require additional feed because the feed available in that period is greater than required (referred to in this article as a period of surplus feed). The price of providing extra feed when there is surplus feed available is taken as zero in this article, but can be non-zero if required.

The Breeding Objective

A generalized breeding objective is described which values increase in feed requirement in the economic value of other breeding objective traits. Residual feed intake traits are included in the objective to account for differences in feed intake that occur at the same weight and weight gain of animal. Breeding objectives formed this way are equivalent to those where feed intake is specified separately. This is illustrated in the following example from [van der Werf \(2004\)](#). For a simple breeding objective that includes only a production trait (g_1) and a feed intake trait (g_2), with economic values v_1 and v_2 respectively, the breeding objective is $v_1g_1 + v_2g_2$. Where the feed requirement for improving the production trait is included in its economic value (i.e., $v_1^* = v_1 + z v_2$, where z is the phenotypic regression of feed intake on the production trait), adding the residual trait $g_2 - zg_1$, with value v_2 , yields a breeding objective that is equivalent. This is because

$$\begin{aligned} v_1^* g_1 + v_2(g_2 - zg_1) &= (v_1 + zv_2) g_1 \\ &\quad + v_2(g_2 - zg_1) \\ &= v_1g_1 + v_2g_2 \end{aligned}$$

The breeding objective of this article targets net return per cow over the period to sale of the

finished animal. Traits in the objective are weaning liveweight-direct (kg), weaning liveweight-maternal (kg), feedlot entry liveweight (kg), finished sale liveweight (kg), residual feed intake of young animals at pasture (kg DM/d), residual feed intake of young animals in the feedlot (kg DM/d), carcass dressing %, carcass saleable meat %, carcass rump fat depth (mm), carcass marbling score, cow liveweight (kg), cow condition score, calving ease-direct (%), calving ease-maternal (%), and cow weaning rate (%). Including weaning liveweight, entry liveweight (when there is a feedlot phase) and finished sale liveweight in the same objective allows growth curve differences to be valued. Economic values of the traits are determined while other objective traits are held constant. The change in feed requirement that is associated with change in a trait is estimated and costed as part of determining the trait's economic value. Breeding objective trait economic values are thus the marginal increases in net return (i.e., Δ return – Δ feed cost – Δ management cost) from changing each trait. Because residual feed traits are included separately in the objective, feed requirement change is the component of feed cost change that is included in the other trait economic values. Economic values for the post-slaughter traits carcass dressing %, carcass saleable meat %, carcass rump fat depth and carcass marbling score are determined from the marginal increases in net return assessed for finished animals.

Including Feed Requirement in the Breeding Objective

The change in feed requirement associated with increase in each breeding objective trait is estimated from equations described by Freer et al. (2007). These are utilized together with the production system description. The equations allow for differences in the genotype, age and stage of growth of animals, and for differences in the feed provided. They thus recognize that feed requirement is not the same for all classes of animals and production systems. When considered together with separately specifying cow and young animal traits in the breeding objective, and with separately specifying residual feed traits of young animals at pasture and in the feedlot, the equations comprehensively describe feed requirement. Changes in feed requirement occur when the liveweight or growth rate of animals change, and when the trait change affects herd structure, as there are then differing proportions of the various classes of animals in the herd. If a trait change does not change liveweight, growth rate or herd structure, the estimated feed requirement does not change.

Feed requirement for maintenance and growth of the young animal. In the breeding objective described, feed requirement changes when there is a change in finished sale liveweight, feedlot entry liveweight, weaning liveweight-direct or weaning

Figure 1. Schematic illustration of growth curve differences associated with changing weaning liveweight-direct, weaning liveweight-maternal, feedlot entry liveweight and finished sale liveweight, while other breeding objective traits are constant.

liveweight-maternal. The changed growth associated with these changes is illustrated schematically in Figure 1. Average liveweights at each production stage are taken from the production system description, and growth between the weights at each stage is assumed to be linear.

Figure 1a shows the changed growth of the young animal when weaning liveweight as a trait of the individual increases and other breeding objective traits are unchanged. After weaning, feed requirement for maintenance increases and the requirement for gain decreases. The change shown in Figure 1a is between weaning and feedlot entry. When there is no feedlot phase, the changed requirement is from weaning to finished sale.

Since pasture intake by the young animal commences pre-weaning (Warner and Flatt, 1965), part of the changed growth that occurs pre-weaning is attributable to the individual. The time taken for the young animal to commence grazing can be varied, but in this article grazing is assumed to commence 1-mo pre-weaning. After that time, the individual has an increased requirement for both maintenance and gain (Figure 1a).

Figure 1b shows the changed growth of the young animal when weaning weight maternal increases and other breeding objective traits are unchanged. The changed requirement before the calf begins grazing is attributable to the dam's increased requirement to meet the calf's demand for milk. In that period, there is an increased requirement for both maintenance and gain. After the young animal begins grazing, the increased requirement is partly from the dam's increased requirement and partly from the calf's increased requirement for maintenance and gain (Figure 1b).

Figure 1c shows the changed growth of the young animal when feedlot entry liveweight increases and other breeding objective traits are unchanged. Feed requirement increases for both maintenance and gain between weaning and feedlot entry. Between feedlot entry and finished sale, the requirement for maintenance increases, while the requirement for gain decreases because gain is at a lesser rate. For production systems where there is no feedlot phase, feedlot entry liveweight is not included in the breeding objective.

Figure 1d shows the changed growth of the young animal when finished sale liveweight increases and other breeding objective traits are unchanged. Feed requirement increases for both maintenance and gain between feedlot entry and finished sale. When there is no feedlot phase, the increased requirement occurs from weaning.

Feed requirement for maintenance and weight change of the cow. Cow feed requirement is assessed for the average cow of the herd. The cow's requirement for maintenance and weight change reflect differences in cow liveweight that occur at joining and also associated differences in cow liveweight that occur over an average year. The differences occur for the number of years the cow remains in the herd. The curve describing cow weight change over the year is constructed from the production system description. Key variables used are the average weight of cows at joining, the increase in joining weight occurring between years, and the loss of weight that usually occurs between calving and joining. Also used are the length of any period of cow weight stasis or loss that occurs immediately before calving, and the rates of cow weight gain that usually occur prior to weaning the calf, post-weaning when feed is unlimited, and in any period when feed is limited.

Figure 2 shows typical cow weight curves for temperate and tropical beef production systems,

a) Temperate production

b) Tropical production

Figure 2. Distributions of cow liveweight from the start of the joining period (J) through weaning (W) and calving (C), before (—) and after (---) cow liveweight change at joining, for temperate and tropical pasture-based beef cattle production.

and the changed curves when cow weight at joining increases. Cow weight loss between calving and joining is proportional to the cow's weight at calving (Walmsley et al., 2015). Cow weight differences that occur pre-calving are consequently greater than those that occur at the start of joining.

The cow weight curve is also used to assess changed feed requirement when the structure of the herd changes. This occurs, for example, when there is an increase in the herd's weaning rate. The cow weight curve is further used for assessing feed requirement change as part of calculating the economic value for cow condition score, as described below.

Feed requirement for gestation and lactation. The feed requirement for gestation and lactation increases when cow weaning rate increases, as a greater proportion of the herd is then gestating and lactating. Estimation of the requirement follows Freer et al. (2007), and is assessed over the period when feed availability is limited.

Including Residual Feed Traits in the Breeding Objective

Residual feed intake traits are included in the breeding objective to account for intake differences at the same weight and weight gain of animals. Residual feed traits are consequently defined at the same weight and weight gain of animals.

Residual feed intake of young animals at pasture. An increase of 1 kg DM/d in the residual feed intake of the young animal at pasture implies intake increases by this amount over the period the animal is at pasture. If there is no feed cost when there is surplus feed, the increased feed is over all times of the year except when there is surplus feed.

Residual feed intake of young animals in the feedlot. An increase of 1 kg DM/d in the residual feed intake of the young animal in the feedlot implies intake increases by this amount over the period the animal is in the feedlot. If the production system has no feedlot phase, the residual feed intake of young animals in the feedlot is not a part of the breeding objective.

Welfare of the Breeding Female

Cow condition score. In animal production, there is usually a range of body condition scores for breeding females at joining that it is acceptable. Scoring body condition is a practical means of monitoring the energy status of animals (Lowman et al., 1976). Figure 3 illustrates the distribution of cow condition score at the start of joining for the example beef production system of Table 3. Increasing the average condition score of breeding females decreases the proportion of animals that need additional feed to meet the minimum acceptable score and increases the proportion that exceed

Figure 3. Distribution of cow body condition score at joining for an example beef cattle production system. Increasing the mean reduces the chance of cows being too low in condition (and of dying or being culled for low condition) and increases the chance of cows being in excess condition.

the maximum acceptable score. These changed proportions are utilized in assessing the trait economic value. Also considered are the changed costs of death and of culling for low body condition, as the chances of these occurring decrease as condition score increases.

The herd cow condition score distribution is derived from the production system description. Variables used are the herd average condition score, the acceptable range for scores, and the condition score phenotypic standard deviation. The feed requirement for increasing condition score is then assessed from the requirement for changing cow liveweight by the amount needed to move the condition score of all cows to within the acceptable range (Freer et al., 2007). Feed prices are needed for lifting condition score and for exceeding the maximum score. Feed for lifting condition score is assumed to be derived in the limited feed period, so its price is that given for cow feed in the production system description (Table 3). The price of feed for exceeding the maximum score is taken as the average feed price over the whole year, since it is not known when in the year this feed was encountered.

The Price of Feed

Prices of feed are needed for valuing feed change in trait economic values. Within an animal class, the same price is used for valuing change in feed requirement and change in residual feed. The price can be different for pasture and feedlot feeds, and for young animals and cows. Where the production system provides the additional feed needed for trait change, the price is a nominated \$ per tonne for each class of feed. Where the production system does not provide the additional feed (e.g., through lack of resources, or by choice), the price is an implied price that reflects how management would change to meet the increased requirement. If cow numbers would be reduced, for example, the implied feed price (\$/MJ) is the existing production system net return per cow (\$) divided by the existing feed intake per cow (MJ).

In addition to other responses, selection responses were examined for feed priced at levels 10, 20, and 30 percent below and 10 percent above the levels described in Table 3 for young animals and cows.

The Genetic Variance-Covariance Matrix

The genetic variance-covariance matrix for deriving the selection index needs to relate to the

genotype and production system that is targeted. In the Australian beef industry, the matrix is usually breed-specific. The matrix includes partitions G_{11} , G_{12} and G_{22} , described above, which may overlap. The G_{12} partition is obtained from G_{11} , G_{22} and estimates of genetic correlations that typically apply between expressions of traits in seedstock and production environments. Breeding objective trait genetic variances are varied according to the level of performance of the targeted production system, so that a constant genetic coefficient of variation (or equivalently, its heritability and phenotypic coefficient of variation) is maintained for each trait. Genetic parameters for the example of this article apply to *Bos taurus* breeds and are based on estimates used in Australian genetic evaluation (Graser et al., 2005). Details of these parameters are available from the authors on request.

Production System Changes From Selection

Methods for deriving the production system changes that occur from selection are shown in Tables 1 and 2. The changes are expressed per cow of the breeding herd, and include those in total product, total feed intake, \$ net return, product per unit of feed intake, \$ per unit of product and \$ per unit of feed intake.

a) Total product, total feed intake and \$ net return

Changes in production system total product are derived from changes in the numbers of sale steers, surplus heifers (i.e., those not required for herd replacement) and surplus cows (i.e., those not required for joining), and from any change to the amount of product per animal sold. For summing, all are expressed in kg of steer beef of equivalent value. The total product after selection is the total product before selection plus the sum of the changes occurring through change in each of the breeding objective traits. Comparing the quantities before and after selection allows the percentage change to be derived (Tables 1 and 2).

Changes in total feed requirement are derived from the sum of the feed requirement changes for maintenance and gain occurring for each of the breeding objective traits. The sum can be for young animals at pasture, in the feedlot, or overall. Adding the changes in residual feed traits gives the total change in young animal feed intake. Summing over the cow traits gives similar totals for cows. Adding the feed required for cows to be in acceptable condition at joining

Table 1. Methods of accumulating trait changes from selection for assessing effects on production system performance

Breeding objective traits (T_i)	Trait change (ΔT_i)	Value of trait change (VTC) ^a \$	Associated product change (ΔKG_i) ^b kg	Associated feed intake change, MJ		
				Young animal, pasture (ΔPF_i) ^c	Young animal, feedlot (ΔFF_i) ^d	Cow, pasture (ΔCF_i) ^e
T_1	ΔT_1	VTC_1	ΔKG_1	ΔPF_1	ΔFF_1	ΔCF_1
T_2	ΔT_2	VTC_2	ΔKG_2	ΔPF_2	ΔFF_2	ΔCF_2
.	.	.	.	.	.	.
.	.	.	.	.	.	.
.	.	.	.	.	.	.
T_n	ΔT_n	VTC_n	ΔKG_n	ΔPF_n	ΔFF_n	ΔCF_n
Total		$\Sigma(VTC_i)$	$\Sigma(\Delta KG_i)$	$\Sigma(\Delta PF_i)$	$\Sigma(\Delta FF_i)$	$\Sigma(\Delta CF_i)$

^a $VTC_i = (\Delta T_i \text{ from selection}) \times (\text{economic value of } T_i)$. ΔT_i assumes selection intensity, $i = 1$.

^bExpressed as equivalent kg of steer beef.

^cFeed requirement and RFI-p change.

^dFeed requirement and RFI-f change.

^eFeed requirement change, including for cows to be in acceptable joining condition.

gives the total change in cow feed intake. Feed requirement is assessed over only the period when feed availability is limited (i.e., when there is not a feed surplus). All quantities are calculated before and after selection, and comparing the quantities allows the percentage change to be derived (Tables 1 and 2).

The \$ net return after selection is the \$ net return before selection plus the value of the changes made to the breeding objective traits. Comparing

the quantities before and after selection allows the percentage change to be derived (Tables 1 and 2).

b) *Product per unit of feed*

This ratio broadly measures production system biological efficiency, despite encompassing product from different classes of animals. It is derived before and after selection, and comparing the quantities allows the percentage change to be derived (Tables 1 and 2).

Table 2. Methods of assessing selection effects on production system performance

Performance measure	Performance level ^a		
After selection			
Total product ^b (KG _A), kg:	KG _B + Σ(ΔKG _i)		
Young animal pasture feed ^c (PF _A), MJ:	PF _B + Σ(ΔPF _i)		
Young animal feedlot feed ^d (FF _A), MJ:	FF _B + Σ(ΔFF _i)		
Young animal total feed, MJ:	PF _A + FF _A		
Cow pasture feed ^e (CF _A), MJ:	CF _B + Σ(ΔCF _i)		
Total feed (TF _A), MJ:	PF _A + FF _A + CF _A		
\$ net return:	DNR _B + Σ(VTC _i)		
Effects of selection			
	Before selection (X _B)	After selection (X _A)	% Change
Total product, kg:	KG _B	KG _B + Σ(ΔKG _i)	(X _A /X _B × 100)
Total feed, MJ:	PF _B + FF _B + CF _B	PF _A + FF _A + CF _A	– 100
\$ net return ^f :	DNR _B	DNR _B + Σ(VTC _i)	
Product per unit of feed, kg/MJ:	KG _B /(PF _B + FF _B + CF _B)	KG _A /TF _A	
\$ per unit of product, \$/kg:	DNR _B /KG _B	{DNR _B + Σ (VTC _i)} /KG _A	
\$ per unit of feed, \$/MJ:	DNR _B /(PF _B + FF _B + CF _B)	{DNR _B + Σ(VTC _i)} /TF _A	

^aProduction system performance before selection (per cow): \$ net return (DNR_B); total product (KG_B), kg; young animal pasture feed intake (PF_B), MJ; young animal feedlot feed intake (FF_B), MJ; cow feed intake (CF_B), MJ.

^bExpressed as equivalent kg of steer beef.

^cFeed requirement and RFI-p.

^dFeed requirement and RFI-f.

^eFeed requirement, including for cows to be in acceptable joining condition.

^fFeed price for \$ net return before selection is based on a land value of \$400/DSE^g, leased at 7% p.a. (Davies and Mortensen, 2007).

^gDSE is defined as the feed required by a 50kg dry sheep (9.7 MJ/head/d) (Turner and Alcock, 2000).

Table 3. Key characteristics for an example self-replacing beef cattle production system producing 100-d feedlot finished steers

Characteristic	Value
Calendar	
Month of joining	Oct.
Month of start of period of limited feed ^a	Jan.
Month of end of period of limited feed ^a	Sept.
Young animals	
Age at weaning, m	7
Growth rate at pasture in limited feed period (relative to surplus feed period), -1.0 to 1.0	0.7
Cost of extra feed at pasture, \$/tonne	130
Quality of extra feed at pasture, MJ/kgDM	8
Period of feedlot finishing, d	100
Steer liveweight at feedlot entry, kg	450
Cost of extra feedlot feed, \$/tonne	270
Quality of extra feedlot feed, MJ/kgDM	10
Age at finished sale, m	22
Steer liveweight at finished sale, kg	640
Finished steer sale price, c/kg carcass	456
Cows	
Weaning %	85
Weight loss from calving to joining, kg	50
Liveweight at joining, kg	650
Mean condition score at joining ^b	3-
Min. acceptable condition score at joining ^b	2+
Max. acceptable condition score at joining ^b	4+
Cost of extra cow feed, \$/tonne	130
Quality of extra cow feed, MJ/kgDM	8
Liveweight of surplus cows, kg	550
Sale price for surplus cows, \$	990

^aAll periods of the year except when there is surplus feed.

^bCow condition scored on a 15 point scale from 1- (emaciated) to 5+ (obese).

c) \$ per unit of product and \$ per unit of feed

These ratios measure production system economic efficiency. They are derived before and after selection, and comparing the quantities allows the percentage change to be derived (Tables 1 and 2).

Individual Trait Changes From Selection

Individual trait changes from selection are assessed with standard index software (e.g., the MTIndex software of J. van der Werf), which assume a similar amount of information is available for all animals. If assessments are made as part of industry genetic evaluation, where animals commonly differ in the amount of information available, the method described by Barwick et al. (2013) is used. In that case the prediction error variance-covariance matrix for each individual ($\mathbf{C}^i$) (that used in

the original genetic evaluation analysis) first needs to be estimated. The variance of the index potentially differs between animals, i.e.,

$$Var(\mathbf{b}'\hat{\mathbf{u}}_i) = \mathbf{b}'Var(\hat{\mathbf{u}}_i)\mathbf{b} = \mathbf{b}'(\mathbf{a}_i\mathbf{G}_{11} - \mathbf{C}^i)\mathbf{b}$$

where $\mathbf{a}_i$ is $(1 + F_i)$, and F_i is the animal's inbreeding coefficient (Schneeberger et al., 1992).

To approximate $\mathbf{C}^i$, prediction error variances of

the EBVs (i.e., PEV_{ij} for EBV j of animal i) are used to form the diagonal elements of the inverse coefficient matrix ($\mathbf{C}^{-1}$) of the mixed model equations.

A matrix $\hat{\mathbf{T}}_i$ is used to estimate $\mathbf{C}^i$ by iterating until its diagonal elements approximate the diagonal elements of $\mathbf{C}^{-1}$. The PEV_i of the index is $\mathbf{k}'\hat{\mathbf{T}}_i\mathbf{k}$, where $\mathbf{k}$ is the vector of index coefficients applied to the EBVs (usually $\mathbf{b}$). If inbreeding is accommodated in the accuracies of the individual EBVs, the standard deviation of the index, $\sigma_{\hat{I}_i}$ is $\sigma_{\hat{I}_i} = \{\mathbf{k}'\mathbf{G}_{11}\mathbf{k} - \mathbf{k}'\hat{\mathbf{T}}_i\mathbf{k}\}^{0.5}$. The changes in the selection criteria, δ_i , per unit of increase in the index, are then given by $\delta_i = (\mathbf{G}_{11} - \hat{\mathbf{T}}_i)\mathbf{b} / \sigma_{\hat{I}_i}^2$, and the changes in the breeding objective traits, η_i , per unit of increase in the index, by $\eta_i = \mathbf{G}_{21}\mathbf{G}_{11}^{-1}\hat{\delta}_i$. The per generation change in the breeding objective, ΔH ,

from selection on the index $\hat{I}_i$ is $\Delta H = \Delta \hat{I}_i = i\sigma_{\hat{I}_i}$ where i refers to selection intensity. The respective changes in the individual selection criteria, $\Delta\Omega$, and breeding objective traits, $\Delta\Psi$, per generation are $\Delta\Omega_i = \delta_i i\sigma_{\hat{I}_i}$ and $\Delta\Psi = \eta_i i\sigma_{\hat{I}_i}$.

RESULTS AND DISCUSSION

Numerical Example

A beef cattle example for a commonly encountered production system is used to illustrate the methods. Key aspects of the production system are shown in Table 3. The breeding objective for the example is illustrated in Figure 4. Variations of the same system, with feed priced 20% higher and where a terminal sire role is assumed, are also examined.

The EBVs included in indexes were those for calving ease (direct) (75), calving ease maternal (62), birth weight (94), 200 d weight (direct) (91), 200 d weight (maternal) (79), 400 d weight (90), 600 d weight (90), mature cow weight (85), carcass

fat depth (79), carcass eye muscle area (78), carcass retail beef % (74), carcass intra-muscular fat % (75), days to calving (58), scrotal size (86), net feed intake (post-weaning) (62), and net feed intake (feedlot) (63). In Australia, these are BREEDPLAN EBVs derived from multi-trait analyses (Graser et al., 2005). Net feed intake EBVs are the primary criteria for the residual feed intake traits. The EBVs listed here are shown together with average accuracies (in parentheses) that apply for active Angus sires in the Australian industry. The EBVs of these sires are used in the example.

Indexes and responses to selection were derived with the MTIndex software of J. van der Werf, using levels of information for the EBVs that reflected the above accuracies. Intermediate results of selection for the objective of Figure 4 are shown in Tables 4 and 5. The percentage changes achieved, at production system and individual breeding objective trait level, are shown in Figures 5 to 9.

Responses for differing levels of accounting for feed. Responses to selection were examined for differing levels of accounting for feed. Selection for each objective was examined 1) ignoring feed cost in the breeding objective, with no measure of feed intake in the index, 2) costing feed requirement in the objective, with no measure of feed intake in the index, 3) costing feed requirement and residual feed in the objective, with no measure of feed intake in the index, and 4) costing feed requirement and residual feed in the objective, with NFI EBVs included in the index. Production system responses to selection are shown in Figures 5 and 6. Responses involving feed intake and \$ net return are illustrated

with all feed included and priced at the levels shown for young animals and cows in Table 3, irrespective of how feed was treated in the selection strategies.

Results for the objective of Figure 4 show that when feed was fully included and NFI EBVs were in the index, a single generation of selection increased production system \$ net return by 6.0% (Figure 5c, variation 4), \$ per unit of product by 5.2% (Figure 6b) and \$ per unit of feed by 6.6% (Figure 6c) compared to when no selection was practiced. Total product and product per unit of feed from the production system increased by 0.7% (Figure 5a) and 1.3% (Figure 6a), respectively. By contrast, when feed cost was ignored, selection decreased \$ net return by 1.3% (Figure 5c, variation 1), \$ per unit of product by 8.7% (Figure 6b) and \$ per unit of feed by 5.8% (Figure 6c). Total product increased by 8.0% and feed intake by 4.7%. There was a 3.2% increase in product per unit of feed. Production system \$ per unit of product and \$ per unit of feed both increased in association with \$ net return (Figures 5 and 6).

Results for the objective with higher feed costs, and that for the terminal variation, followed a similar pattern (Figures 5 and 6). Differences for the terminal objective were smaller, and those for the objective with higher feed costs were the same or larger than those for the objective of Figure 4.

Responses when feed price differs. Selection responses were examined for feed priced at levels 10, 20, and 30 percent below and 10 percent above the levels described in Table 3, for both young animals and cows. Production system responses are shown in Figure 7 and individual trait responses are

Figure 4. Illustration of the breeding objective, encompassing trait economic values and genetic variances, showing the relative economic importance of traits for the example production system producing 100-d feedlot finished steers.

Table 4. Accumulated trait changes for assessing selection effects for the example production system producing 100-d feedlot finished steers^a

Breeding objective traits	Trait change	Value of trait change, \$	Associated product change, kg	Associated feed intake change, MJ		
				Young animal, pasture	Young animal, feedlot	Cow, pasture
Weaning liveweight - direct, kg	0.77	0.08	0	-5.6	0	-0.2
Weaning liveweight - maternal, kg	-0.95	0.78	0	0	0	-77.3
Residual feed intake - pasture, kg/d	-0.09	1.60	0	-107.2	0	0
Entry liveweight, kg	1.41	0.14	0	52.3	-44.6	11.9
Residual feed intake - feedlot, kg/d	-0.11	1.66	0	0	-112.0	0
Sale liveweight, kg	-1.62	-0.99	-0.59	0	-68.5	0
Dressing %	0.04	0.70	0.19	0	0	0
Carcass meat %	0.36	4.54	1.23	0	0	0
Carcass fat depth, mm	0.12	0.10	0	0	0	0
Carcass marbling score ^b	0.02	1.14	0	0	0	0
Cow liveweight, kg	-8.66	5.65	-2.31	0	0	-629.8
Cow condition score ^c	0.01	0.06	0	0	0	-5.5
Calving ease - direct, %	0.97	4.44	0	0	0	0
Calving ease - maternal, %	0.22	0.40	0	0	0	0
Cow weaning %	1.29	3.61	2.78	302.1	262.4	99.0
Total:		23.91	1.30	241.6	37.5	-601.9

^aMethods used for accumulating changes are shown in Table 1.

^bScored on a 12 point scale from 1 (least) to 12 (most) (AusMeat, 2006).

^cScored on 15 point scale from 1- (emaciated) to 5+ (obese).

shown in Figure 8. Responses involving \$ net return are illustrated with all feed priced at the levels of Table 3 irrespective of how feed was treated in the selection strategies.

When feed price was lower than that of Table 3, selection increased total product, total feed and product per unit of feed for the production system, and decreased \$ net return, \$ net return per unit of product and \$ net return per unit of feed (Figure 7). When feed price was higher than that of Table 3, selection decreased total product, total feed and product per unit of feed, and increased \$ net return per unit of product and \$ net return per unit of feed. Production system \$ net return also decreased when feed price was higher, as this was maximized at the feed price levels of Table 3.

Consequences for rankings and welfare. Varying the extent to which feed was taken into account markedly changed the breeding objective. The correlation between breeding objectives where feed was fully costed and where feed cost was ignored was 0.60 for the objective of Figure 4, 0.36 for the objective with higher feed costs, and 0.84 for the terminal objective (Figure 9a). The corresponding correlations among resulting indexes, computed for active Angus sires of the Australian industry,

ranged from 0.11 to 0.41 (Figure 9b). Where feed requirement was the only feed that was costed in the objective (i.e., variation 2 of Figure 9b), the correlation between the resulting index and that where feed was fully costed was high (0.96) if the price of feed was high, and low (0.33) if the price of feed was low.

Cow condition score did not decline when multiple-trait selection increased efficiency at both production system (Figure 7e and f) and individual animal levels (Figure 8c and e). Cow condition score increased by 0.01 of a score when cow condition score was included in the breeding objective (Figure 8l). It also increased by 0.01 of a score when it was not included in the breeding objective (not presented). Using a lower feed price in the objective resulted in a further small increase in cow condition score (Figure 8l).

Utility of the Methods

The methods described fully account for feed intake and efficiency in selection and can be used when the production system is pasture or concentrate-based, or when both are involved. Substantial gains of between 3.6% and 6.6% in \$ net return

Example objective producing 100-d feedlot finished steers^a

Example objective with 20% higher feed costs

Terminal sire variation of the example objective

Figure 5. Production system responses from a single generation of selection (with selection intensity $i = 1$) for three breeding objectives, as affected by the extent to which feed cost is taken into account (Key: 1 = feed cost ignored in the breeding objective; 2 = feed requirement costed in the breeding objective; 3 = feed requirement, RFI-p and RFI-f costed in the breeding objective; 4 = as for 3, plus NFI-p and NFI-f EBVs included in the index). ^aAs shown in Figure 4. ^bIllustrated with all feed included, including any not costed in the breeding objective.

(Figure 5), and between 4.4% and 9.0% in \$ net return per unit of feed (Figure 6) occurred across three breeding objectives from a single generation of selection (with selection intensity, $i = 1$) when selection fully accounted for feed. There were favorable responses to selection in all breeding objective traits except sale weight, which slightly decreased through its correlation with the reduction achieved in cow weight. The favorable response seen in cow weaning rate decreased as the price of feed increased (Figure 8). Specifying feed intake traits separately, rather than as associated and residual effects as here, would yield similar results because the resulting breeding objectives are equivalent.

The methods described have been implemented in the BreedObject system for beef cattle breeders

(Barwick and Henzell, 2005). Similar principles are expected to apply in other grazed species. In intensive production systems, feed may never be surplus to requirement and in this circumstance would be costed over all of the year. The cost of feed may still differ, however, if differing qualities of feed are supplied for different periods.

Effect of Feed Cost Level on Animal Rankings

Figure 9 shows rankings of animals are sensitive to the extent to which feed is taken into account in selection. Individual trait responses from selection are also sensitive to the price of feed (Figure 8). Traits are differentially affected by feed cost and the feed cost of trait change may differ between production environments.

Example objective producing 100-d feedlot finished steers^a *Example objective with 20% higher feed costs* *Terminal sire variation of the example objective*

Figure 6. Production system feed and economic efficiency responses from a single generation of selection (with selection intensity $i = 1$) for three breeding objectives, as affected by the extent to which feed cost is taken into account (Key: 1 = feed cost ignored in the breeding objective; 2 = feed requirement costed in the breeding objective; 3 = feed requirement, RFI-p and RFI-f costed in the breeding objective; 4 = as for 3, plus NFI-p and NFI-f EBVs included in the index). ^aAs shown in Figure 4. ^bIllustrated with all feed included, including any not costed in the breeding objective.

This results in feed cost for trait change being the source of major genotype $\times$ environment interaction. Where the production environment or its management is such that the feed cost for trait change is inexpensive, increasing growth is desirable. If the feed cost for trait change is expensive, increasing growth is less desirable or undesirable (Figures 8 and 9).

The feed cost for trait change may be lower in grazed animals in production environments where pasture growth is greater and stocking rates are lower. It may be higher where pasture growth is less, where stocking rates are higher, and where production is more profitable, the opportunity cost of reducing stocking rate then being higher. In more intensive production systems, the feed cost for trait change may be higher as a result of feed prices being generally higher.

The desirability of increasing growth in beef cattle has previously been examined from the viewpoint of single trait selection. Parnell et al. (1994) found greater yearling growth increased returns in an Angus growth selection experiment commenced in 1974, but noted that the size of any benefit would depend on feed cost. Walmsley et al. (2017) showed that both the growth and feed intake of Angus cattle have increased since that time.

In grazing industries, profitability usually increases when more use is made of pasture, at least while pasture sustainability is unaffected (Barnett, 2007). If higher stocking rates align with a higher feed price, the feed price that should be used in animal selection might be high. This follows if the feed price to use is that when management is optimal. Where pasture is poorly utilized, greater

Figure 7. Production system, feed and economic efficiency responses from a single generation of selection (with selection intensity $i = 1$) for the example objective producing 100-d feedlot finished steers, as affected by the price of feed (Key: 1 = feed prices 30% lower than the example; 2 = feed prices 20% lower than the example; 3 = feed prices 10% lower than the example; 4 = feed prices as in the example; 5 = feed prices 10% higher than the example). ^aIncludes all feed intake, including any not costed in the breeding objective. ^bAs shown in Figure 4.

animal growth can assist both pasture utilization and genetic improvement (Barwick et al., 2011b). Where an industry has variable production environments, and a feed cost for trait change that varies with the environment, it is recommended that rankings for the industry be derived for more than one level of feed cost.

The results support an earlier suggestion (Barwick et al., 2011a) that beef cattle selection would be improved if feed costs were fully included in breeding objectives even when no industry feed

intake measure is available. Figure 9b shows having NFI EBVs in the index had a much smaller effect on \$ net return than ignoring feed cost, if feed price was high. When feed price was lower, however, the need for a feed measure to be included in the index was greater (Figure 9b).

The Need to Account for All Feed

The breeding objective literature includes coverage of ways of combining returns and costs

Table 5. Selection effects for the example production system producing 100-d feedlot finished steers

Performance measure		Performance level ^a	
After selection			
Total product (KG _A), kg:	174.28		
Young animal pasture feed (PF _A), 1000 MJ:	12.85		
Young animal feedlot feed (FF _A), 1000 MJ:	11.08		
Young animal total feed, 1000 MJ:	23.93		
Cow pasture feed (CF _A), 1000 MJ:	31.60		
Total feed (TF _A), 1000 MJ:	55.53		
\$ net return:	421.91		
Effects of selection			
	Before selection (X _B)	After selection (X _A)	% Change
Total product, kg:	172.98	174.28	0.7
Total feed, 1000 MJ:	55.85	55.53	−0.6
\$ net return ^b :	398.00	421.91	6.0
Product per 1000 MJ feed, kg:	3.10	3.14	1.3
\$ per kg product:	2.30	2.42	5.2
\$ per 1000 MJ feed:	7.13	7.60	6.6

^aMethods for assessing effects are shown in Table 2.

^bFeed price for \$ net return before selection is based on a land value of \$400/DSE^c, leased at 7% p.a. (Davies and Mortensen, 2007).

^cDSE is defined as the feed required by a 50-kg dry sheep (9.7 MJ/head/d) (Turner and Alcock, 2000).

Figure 8. Individual trait responses from a single generation of selection (with selection intensity, $i = 1$) for the example objective producing 100-d feedlot finished steers, as affected by the price of feed (Key: 1 = feed cost 30% lower than the example; 2 = feed cost 20% lower than the example; 3 = feed cost 10% lower than the example; 4 = feed cost as in the example; 5 = feed cost 10% higher than the example). *As shown in Figure 4.

in the breeding objective (e.g., Dickerson, 1970; Brascamp et al., 1985; Smith et al., 1986; Amer and Fox, 1992; James, 1993). In this article, the indexes examined maximize \$ net return to the production system (i.e., returns net of feed and management costs), and consistent with this, \$ net return had its highest value when feed was priced at the levels of Table 3 (Figure 7c). Production system \$ net return per unit of product and per unit of feed both increased in association with \$ net

return (Figures 6 and 7). If \$ net return per unit of feed aligns with \$ net return per unit area in grazing situations, these results show increasing \$ net return for the production system also increases \$ net return per unit area when feed is fully costed (Figures 6c, 6f, 6i, and 7f).

Favorable selection responses were observed over a range of feed price (Figures 7 and 8) provided at least feed requirement was costed (Figures 5 and 6). Feed requirement change is the element of feed intake

a) Correlation between breeding objectives

b) Correlation between indexes^a

Figure 9. Correlation of breeding objectives and indexes with that fully accounting for feed (i.e., strategy 4) for three breeding objectives, according to the extent to which feed is taken into account (Key: — objective shown in Figure 4; - - - objective with 20% higher feed costs; - - - terminal sire variation of the objective; 1 = feed cost ignored in the breeding objective; 2 = feed requirement costed in the breeding objective; 3 = feed requirement, RFI-p and RFI-f costed in the breeding objective; 4 = as for 3, plus NFI-p and NFI-f EBVs included in the index). ^aComputed for active Angus sires of the Australian industry.

change most commonly considered in breeding objectives. It is costed, for example, in all earlier versions of BreedObject (Barwick and Henzell, 2005). Where feed requirement is the only element of feed that is costed, animals may still re-rank for their differences in residual intakes. To avoid this, and to maintain full equivalence with the separate specification of feed intake traits in the breeding objective, we suggest that costing of residual feed intake in breeding objectives should be considered in all species.

Integrating Genetic and Management Improvement

Greater integration is needed of efforts to improve animal performance genetically

and through management. While the effect of enhanced animal growth on pastures is unclear, it might be assumed to have increased pasture utilization. In that situation, stocking rates would either have to be reduced or feed efficiency improved to prevent the animal's environment from declining. In a declining environment, genetic gains may not be realized and animal welfare may be compromised (Walmsley et al., 2017). If stocking rate reductions have occurred to offset the pasture effects of increasing animal growth, the feed cost effects on animal rankings would remain as described here, and the stocking rate reductions will have prevented the animal's environment from declining.

Efficiency and Breeding Female Welfare

Rauw et al. (1988) and Veerkamp (2002) warn of the potential for genetic improvement to jeopardize animal welfare. Kanis and de Vries (1992) also suggest feed intake in swine needs to increase to meet the demands of high performing animals. The concern for animal welfare stems from efficiency increases being associated with probable reductions in feed intake. In the present results, cow body condition score did not decline while efficiency improvements were being made at both the production system and individual animal level. Under the selection considered, residual feed intake was indeed reduced (Figure 8), although the total feed intake of the production system was little affected (Figure 5b). Feed intake increased in association with the responses achieved in other production traits. We conclude from this that production system and individual animal efficiency improvements are likely to be able to be achieved under multiple-trait selection without compromising breeding female welfare.

CONCLUSIONS

1. For industries that include production environments that are variable, and where the feed cost for trait change varies with the environment, rankings should be derived for more than one level of feed cost.
2. Selection that increases \$ net return per cow also increases production system \$ net return per unit of feed when feed is fully costed.
3. Efficiency of the production system and of individual animals can be improved with multiple-trait selection without compromising breeding female welfare measured by condition score.

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