Cumulative Discounted Expressions of Dairy and Beef Traits in Integrated Cattle Populations

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Abstract

Gene-flow methodology was used to calculate the cumulative discounted expressions (CDE) for annual/lactation, replacement heifer, cull cow, birth, yearling, and slaughter traits in both purebred and integrated cattle populations. We define an integrated cattle population as a production system where dairy germplasm enters a beef herd and/or vice versa. Generic equations were presented and parameters representing dairy-beef production systems in Ireland and Brazil were inputted. Cumulative discounted expressions for a third hypothetical case study based on a purebred dairy production system with poor cow longevity were also calculated. Absolute and relative differences in CDE existed among trait categories across alternative production systems. For example, the CDE of genes from a purebred dairy mating for beef-related traits ranged from 0.42 to 0.75 CDE of an annual/lactation trait across the three contrasting systems investigated. Such variation may alter the relative emphasis of traits on overall profitability thereby contributing to genotype by environment interactions. The results of this study highlight the necessity to consider auxiliary traits in sire selection over and above those representing the principle intended use of the sire. This was particularly so for integrated dairy and beef cattle populations

(Keywords: gene-flow, cumulative discounted expression, dairy, beef)

Abbreviation key: CDE = cumulative discounted expressions.

1. Introduction

Index selection is based on the theory of simultaneous selection for traits weighted on perceived relative importance (Hazel, 1943). However, differentials in frequency and timing of expression imply that simply weighting traits based on the marginal return per incremental change in the trait may not be optimal (McClintock and Cunningham, 1974). Instead, the weighting factors on traits within a selection objective should reflect the economic benefit of genetic change in the trait simultaneous with the frequency and timing of expressions of the trait over multiple generations. McClintock and Cunningham (1974) suggested the use of cumulative (total standard) discounted expressions (**CDE**) as a means of discounting to a pre-defined time. Cumulative discounted expressions may be calculated as the sum of all timing and frequency of expressions of a trait over multiple generations originating from one initial mating.

Gene transfer between dairy and beef production systems is not uncommon in most countries, but occurs at different frequencies and through alternative pathways. For example, in Ireland, a substantial proportion of dairy females are mated to beef males, with a portion of the subsequent crossbred females being sold or retained for use as dams in beef production systems (Irish Cattle Breeding Statistics, 2003). Similarly, a considerable proportion of animals slaughtered for beef production are generated from beef replacement cows with up to one half of their ancestry contributed by dairy breeds. In the tropics, adapted breed females are commonly mated to temperate dairy breed males to generate adapted, yet productive F_1 females for the dairy herd and the males are reared for beef (Madalena, 1998). The F_1 females generally become either terminal females or are

backcrossed to dairy breed males to generate terminal females; throughout the text terminal females refer to females whose immediate progeny are slaughtered. In some cases, the F_1 females may be mated with F_1 males to create dairy composites. This raises the question as to how much emphasis should be placed on beef traits in breeding objectives for dairy cattle and vice versa.

The objective of the present study was to calculate the CDE for categories of traits accruing from a mating between animals of the same or alternative breeds. The procedures utilized in the present study were based on the approach of Everett (1975) and van Vleck and Everett (1976), which have subsequently been modified for sheep (Amer, 1999) and beef (Amer et al., 2001) production systems. The formulae derived were applied to two contrasting dairy/beef production systems in Ireland and Brazil. Consideration was also given to the relative expressions of both lactation and non-lactation oriented traits in dairy systems where no beef breed crossing was practiced.

2. Materials and Methods

This study extends the discounted genetic expressions approach outlined by Amer et al. (2001) to a situation where descendants of specific animals are mated to more than one breed. The different breed crosses of descendants have different population structures, and are used in either dairy or beef production systems. Equations derived for predicting CDEs are then applied in three contrasting case studies.

2. 1. Lifetime Survivability and Transition Matrices

Age is defined in single year groups from birth to year *n* of life where *n* is the highest age considered possible; *n* was fixed to twelve years. Let $\mathbf{s}^{\alpha}$ be an *n* by 1 vector of the probability of a female, of breed or breed-cross α, surviving and calving from age *i*-1 to age *i* across ages *i*=1 to *n*. First calving is assumed to take place at either two or three years of age in which case $\mathbf{s}_1^{\alpha}$ or both $\mathbf{s}_1^{\alpha}$ and $\mathbf{s}_2^{\alpha}$ have values of zero, respectively. The first non-zero element of $\mathbf{s}^{\alpha}$ is the probability of a selected replacement heifer calving, given that she is born.

A variable *c* was set (whereby $c \leq n$) to represent an age culling threshold (i.e., all animals above age *c* were culled irrespective of their potential future survival); in the present study *c* was set to ten years of age as the number of cows surviving beyond this age usually make up a trivial proportion of the herd. A vector $\mathbf{a}^{\alpha}$ was calculated for each breed type (α) to represent the probability of a cow surviving to and calving at age *i*, given it was alive at age *i*=1, as follows:

$$\mathbf{a}_{\mathbf{i}}^{\alpha} = \begin{cases} \prod_{j=afc^{\alpha}}^{i} \mathbf{s}_{\mathbf{j}}^{\alpha}, & i = afc^{\alpha} \text{ to } c \\ 0, & \text{otherwise} \end{cases}$$

for *i*=1 to n and where afc^{α} denotes age at first calving for breed type α.

A vector ($\mathbf{d}^{\alpha}$) describing the probability of a cow not surviving to *i* years of age, was calculated for each breed type (α) as:

$$\mathbf{d}_{\mathbf{i}}^{\boldsymbol{\alpha}} = \begin{cases} 1 - \mathbf{a}_{\mathbf{i}}^{\boldsymbol{\alpha}} & \text{for } i = afc^{\alpha} \\ \mathbf{a}_{\mathbf{i-1}}^{\boldsymbol{\alpha}} - \mathbf{a}_{\mathbf{i}}^{\boldsymbol{\alpha}} & \text{for } i = afc^{\alpha} + 1 \text{ to } c - 1 \\ \mathbf{a}_{\mathbf{i-1}}^{\boldsymbol{\alpha}} & \text{for } i = c \\ 0 & \text{otherwise} \end{cases}$$

A vector $\mathbf{f}^{\boldsymbol{\alpha}}$ was also defined as the number of calves born (including stillbirths) per cow at *i* years of age. This vector allowed for the probability of multiple births but also for the possibility of barren cows remaining in the herd without producing a calf.

Let $\mathbf{D}^{\boldsymbol{\alpha}}$ be an *h* by *h* transition matrix with columns of survival probabilities times the probability of producing a calf, lagged by one row for each new birth year for each breed α. The variable *h* represents the planning horizon, in years, from birth of the self-replacing female. In the present study *h* was set to twenty years. Thus, the $(i,j)^{th}$ element of each $\mathbf{D}^{\boldsymbol{\alpha}}$ matrix was specified as follows:

$$\mathbf{D}_{\mathbf{i,j}}^{\boldsymbol{\alpha}} = \begin{cases} \mathbf{a}_{\mathbf{i-j}}^{\boldsymbol{\alpha}} \otimes \mathbf{f}_{\mathbf{i-j}}^{\boldsymbol{\alpha}} & \text{for } j < i - 1 \text{ and } i - j \leq c \\ 0 & \text{otherwise} \end{cases}$$

where $\otimes$ represents the Hadamard product of the respective vectors.

Matrices for cull cow expressions ($\mathbf{G}^{\boldsymbol{\alpha}}$) and replacement heifer expressions ($\mathbf{H}^{\boldsymbol{\alpha}}$) were calculated as:

$$\mathbf{G}_{\mathbf{i,j}}^{\boldsymbol{\alpha}} = \begin{cases} \mathbf{d}_{\mathbf{i-j}}^{\boldsymbol{\alpha}} & \text{for } j < i - 1 \text{ and } i - j \leq c + 1 \\ 0 & \text{otherwise} \end{cases}$$

$$\mathbf{H}_{\mathbf{i,j}}^{\boldsymbol{\alpha}} = \begin{cases} 1 & \text{for } i = j + afc^{\alpha} - 1 \\ 0 & \text{otherwise} \end{cases}$$

Thus, breed types with the same age at first calving have identical $\mathbf{H}^{\boldsymbol{\alpha}}$ matrices.

2.2 First Appearance of a Cow's Genes over Successive Generations

An *h* by 1 vector ($\mathbf{g}_{\mathbf{k}}^{\boldsymbol{\alpha}}$) describing first appearances of genes in generation *k*=1 to *m* of a cow that calves at least once for breed α were calculated as:

$$\mathbf{g}_{\mathbf{k}}^{\boldsymbol{\alpha}} = \frac{1}{2} \cdot \omega^{\alpha R} \cdot \mathbf{D}^{\boldsymbol{\alpha}} \cdot \mathbf{g}_{\mathbf{k-1}}^{\boldsymbol{\alpha}}$$

where $\mathbf{g}_{\mathbf{1}}^{\boldsymbol{\alpha}'}$=[1,0,…,0] and *m* is the number of generations for which the flow of genes were tracked; in the present study *m* was set to twelve. The factor of ½ represents the genetic contribution from one generation to the next and $\omega^{\alpha R}$ is the proportion of calves of breed α that are selected to be self-replacing females. Under the assumption of a constant herd age structure and no bought in replacements, $\omega^{\alpha R}$ can be calculated separately for each breed as

$$\omega^{\alpha R} = \frac{1}{\sum_{i=1}^{c} \mathbf{a}_{\mathbf{i}}^{\boldsymbol{\alpha}}}$$

as explained by Amer (1999); in the study of Amer (1999) $\omega^{\alpha R}$ was denoted as *f*. However, because many cattle production systems utilize replacements purchased from outside herds, we define $\omega^{\alpha R}$ explicitly based on knowledge of industry practices.

Each row of each $\mathbf{g}_{\mathbf{k}}^{\boldsymbol{\alpha}}$ vector corresponds to the year of first appearances of the genes. Aggregate yearly first appearances of genes accumulated over the *m* generations were calculated as:

$$\mathbf{gsum}^{\boldsymbol{\alpha}} = \sum_{k=1}^{m} \mathbf{g}_{\mathbf{k}}^{\boldsymbol{\alpha}}$$

In other words, the $\mathbf{gsum}^{\alpha}$ vector conveys the number of first time appearances of genes in a cow of breed α, calving at least once, plus all her self-replacing daughter descendants in each year (row) following the birth of the cow.

2.3 Multiple Expression of a Cow's Genes

The **D**, **H**, and **X** matrices are used to multiply first appearances of a cow's genes to the actual expressions throughout her life and the lives of her self-replacing female descendants. A discounting vector (**q**) was created which is used throughout the calculations to discount the expressions back to a given time period. The vector **q** accounts for a lag of one year (i.e., row) in the **D**, **H**, and **G** matrices and discounts back to the time of birth of the animal accruing from the original mating. Additional discounting was applied depending on the trait in question in subsequent formulae. The discounting vector was:

$$\mathbf{q_i} = \left(\frac{1}{1+r}\right)^{i-1}$$

where *r* is a discounting factor.

2.4 Parameter Variations for Integrated Cattle Populations

Cumulative discounted expressions in integrated cattle populations need to account for the probabilities of cow and calf trait expressions occurring through alternative pathways. A combination of possible gene pathways between two breeds, A and B, is summarized in Figure 1. The initial mating is between either an A male and an A female or between a B male and an A female; both types of matings are expected to occur within a herd of A females. Depending on the

prevailing circumstances animal breeders may be interested in the CDE following the initial mating of either a breed A male or a breed B male with a breed A female. Thus, calculations adopted herein will be conditional on either one of the two initial matings occurring, not both. Sires of breed T represent terminal sires and sires of breed M represent maternal sires to breed replacement daughters (Figure 1).

Separate $\mathbf{s}^{\alpha}$ vectors were specified for A ($\mathbf{s}^{\mathbf{A}}$) and B ($\mathbf{s}^{\mathbf{B}}$) females. For simplicity and clarity of reporting no account was taken of heterosis in the definition of the survival parameters; it was assumed that the survival rate of AB females is identical to that of either A or B females. Variations in these assumptions can be integrated into the calculations with the inclusion of additional vectors and a slight modification of the calculations reported herein. It was assumed in the present study that all elements of the $\mathbf{f}^{\alpha}$ vector were one (i.e., females surviving and calving at age *i* each produced one calf at age *i*).

A separate $\mathbf{D}^{\alpha}$ matrix was also derived for breed A ($\mathbf{D}^{\mathbf{A}}$) and breed B ($\mathbf{D}^{\mathbf{B}}$) self-replacing females. However, a self-replacing A female may be mated to an A male or a B male (Figure 1). So as to be able to account for different probabilities of mating a female of breed A with a male of breed A versus B through her life, we defined $\mathbf{p}^{\mathbf{A}}$ as an *h* by 1 vector representing the proportion of births accruing from the mating between A females and A males for each age/parity. A contrasting vector ($\mathbf{p}^{\mathbf{B}}$) was generated as the remainder of $\mathbf{p}^{\mathbf{A}}$ from one but with elements representing nulliparous animals remaining as zero. These pathways

were included in the calculations by separating the $\mathbf{D}^{\mathbf{A}}$ matrix into the two components denoted $\mathbf{D}^{\mathbf{AA}}$ and $\mathbf{D}^{\mathbf{AB}}$ where

$$\mathbf{D}_{\mathbf{i,j}}^{\mathbf{A\alpha}} = \begin{cases} \mathbf{a}_{\mathbf{i-j}}^{\mathbf{A}} \otimes \mathbf{f}_{\mathbf{i-j}}^{\mathbf{A}} \otimes \mathbf{p}_{\mathbf{i-j}}^{\boldsymbol{\alpha}} & \text{for } j < i-1 \text{ and } i-j \le c \\ 0 & \text{otherwise} \end{cases}$$

Because the expressions of replacement heifer and cull cow traits are independent of the mating sire, only one replacement heifer and cull cow expression matrix was created for breed A self-replacing females.

A separate $\mathbf{gsum}^{\boldsymbol{\alpha}}$ vector was calculated for breed A ($\mathbf{gsum}^{\mathbf{A}}$) and B ($\mathbf{gsum}^{\mathbf{B}}$) self-replacing females. Only the $\mathbf{D}^{\mathbf{AA}}$ matrix was used in the calculations of $\mathbf{gsum}^{\mathbf{A}}$. Because the proportion of females destined to become self-replacing females may differ between F_1 AB females (ω^{BR}) and crosses originating from M*AB matings (ω^{MR}), a $\mathbf{gsum}^{\mathbf{M}}$ vector was also created for F_1 AB dams.

2.5 Trait Categories

We define six main categories of traits for consideration in the present study: annual traits (e.g., reproductive efficiency, lactation), replacement heifer traits (e.g., live weight at first calving), cull cow traits (e.g., carcass weight at culling), birth traits (e.g., birth live weight), yearling traits (e.g., yearling live weight) and slaughter traits (e.g., carcass conformation). These trait groups are denoted a, h, c, b, y, s, respectively.

The vectors and matrices previously defined were used to build equations for predicting CDEs for the six trait categories identified as they are expressed along the separate pathways denoted in Figure 1.

2.5.1 Annual, replacement heifer and cull cow trait expressions.

The discounted number of annual expressions in the terminal daughters of a female of breed type α (α =A, B or AB, a cross between breeds A and B) mated to a terminal sire T can be calculated as

$$\mathrm{Xa}^{\alpha|T} = \frac{1}{2} \cdot \mathbf{q'} \cdot \mathbf{a}^{\boldsymbol{\alpha}} \cdot \left(\frac{1}{1+\mathrm{r}} \right).$$

Similarly, the replacement heifer ($\mathrm{Xh}^{\alpha|T}$) and cull cow ($\mathrm{Xc}^{\alpha|T}$) expressions in the terminal daughters of a female of breed α mated to a terminal sire T are given as:

$$\mathrm{Xh}^{\alpha|T} = \frac{1}{2} \cdot \left(\frac{1}{1+\mathrm{r}} \right)^{\mathrm{afc}}$$

$$\mathrm{Xc}^{\alpha|T} = \frac{1}{2} \cdot \mathbf{q'} \cdot \mathbf{d}^{\boldsymbol{\alpha}} \cdot \left(\frac{1}{1+\mathrm{r}} \right) \cdot (1-\mathrm{die}).$$

where ***die*** denotes the proportion of cows culled that die on farm or prior to arrival at the slaughter house (i.e., cull cow traits are not expressed by these animals). Subsequently, the number of annual trait expressions by a self-replacing AB female and her daughter descendants, when the female is mated at least once to an M sire and discounted back to the time of birth of the female herself may be calculated as:

$$\mathrm{Xa}^{\mathrm{AB|M}} = \mathbf{q'} \cdot \mathbf{D}^{\mathbf{B}} \cdot \mathbf{gsum}^{\mathbf{M}} \cdot (1 + \omega^{\mathrm{MT}} \cdot \mathrm{Xa}^{\mathrm{AB|T}}).$$

The term outside the parenthesis accounts for the repeated pathways of discounted expressions in self-replacing and terminal females across generations.

The CDE for replacement heifer ($\mathrm{Xh}^{\mathrm{AB|M}}$) and cull cow ($\mathrm{Xc}^{\mathrm{AB|M}}$) traits of an AB female, mated at least once to an M sire, in both herself and her daughter

descendants discounted back to the time of birth of the female herself are calculated as:

$$\mathrm{Xh}^{\mathrm{AB|M}} = \mathbf{q'} \cdot \mathbf{H^B} \cdot \mathbf{gsum^M} + \mathbf{q'} \cdot \mathbf{D^B} \cdot \mathbf{gsum^M} \cdot \omega^{\mathrm{MT}} \cdot \mathrm{Xh}^{\mathrm{AB|T}}$$

$$\mathrm{Xc}^{\mathrm{AB|M}} = \mathbf{q'} \cdot \mathbf{G^B} \cdot \mathbf{gsum^M} \cdot (1 - \mathrm{die}) + \mathbf{q'} \cdot \mathbf{D^B} \cdot \mathbf{gsum^M} \cdot \omega^{\mathrm{MT}} \cdot \mathrm{Xc}^{\mathrm{AB|T}}.$$

In the calculation of $\mathrm{Xh}^{\mathrm{AB|M}}$, the first term represents the expression of once off replacement traits by the self-replacing females while the second term represents the once off expression of replacement traits in the terminal females which are generated in successive generations by the self-replacing female (Figure 1). Similar reasoning exists for the calculation of $\mathrm{Xc}^{\mathrm{AB|M}}$.

The CDE of annual ($\mathrm{Xa}^{\mathrm{A|A}}$), replacement heifer ($\mathrm{Xh}^{\mathrm{A|A}}$), and cull cow ($\mathrm{Xc}^{\mathrm{A|A}}$) traits of a self-replacing A female and her daughter descendants when mated, at least once, to an A male are calculated as:

$$\mathrm{Xa}^{\mathrm{A|A}} = \mathbf{q'} \cdot \mathbf{D^A} \cdot \mathbf{gsum^A} + \mathbf{q'} \cdot \mathbf{D^{AA}} \cdot \mathbf{gsum^A} \cdot \omega^{\mathrm{AT}} \cdot \mathrm{Xa}^{\mathrm{A|T}}$$

$$\mathrm{Xh}^{\mathrm{A|A}} = \mathbf{q'} \cdot \mathbf{H^A} \cdot \mathbf{gsum^A} + \mathbf{q'} \cdot \mathbf{D^{AA}} \cdot \mathbf{gsum^A} \cdot \omega^{\mathrm{AT}} \cdot \mathrm{Xh}^{\mathrm{A|T}}$$

$$\mathrm{Xc}^{\mathrm{A|A}} = \mathbf{q'} \cdot \mathbf{G^A} \cdot \mathbf{gsum^A} \cdot (1 - \mathrm{die}) + \mathbf{q'} \cdot \mathbf{D^{AA}} \cdot \mathbf{gsum^A} \cdot \omega^{\mathrm{AT}} \cdot \mathrm{Xc}^{\mathrm{A|T}}.$$

In the calculation of $\mathrm{Xa}^{\mathrm{A|A}}$, the initial term represents the annual expressions of an A female irrespective of her mate. The second term represents the annual trait

expressions of a terminal female throughout *m* generations. Similar reasoning exists for the calculation of $\mathrm{Xh}^{\mathrm{A|A}}$ and $\mathrm{Xc}^{\mathrm{A|A}}$.

The CDE of annual ($\mathrm{Xa}^{\mathrm{A|B}}$), replacement heifer ($\mathrm{Xh}^{\mathrm{A|B}}$), and cull cow ($\mathrm{Xc}^{\mathrm{A|B}}$) traits in a self-replacing female of breed A and her daughter descendants when mated, at least once, to a B male are calculated as:

$$\mathrm{Xa}^{\mathrm{A|B}} = \mathbf{q'} \cdot \mathbf{D}^{\mathbf{AB}} \cdot \mathbf{gsum}^{\mathbf{A}} \cdot \mathrm{mbs} \cdot \left(\omega^{\mathrm{BT}} \cdot \mathrm{Xa}^{\mathrm{B|T}} + \frac{1}{2} \cdot \omega^{\mathrm{BR}} \cdot \mathrm{Xa}^{\mathrm{AB|M}} \right)$$

$$\mathrm{Xh}^{\mathrm{A|B}} = \mathbf{q'} \cdot \mathbf{D}^{\mathbf{AB}} \cdot \mathbf{gsum}^{\mathbf{A}} \cdot \mathrm{mbs} \cdot \left(\omega^{\mathrm{BT}} \cdot \mathrm{Xh}^{\mathrm{B|T}} + \frac{1}{2} \cdot \omega^{\mathrm{BR}} \cdot \mathrm{Xh}^{\mathrm{AB|M}} \right)$$

$$\mathrm{Xc}^{\mathrm{A|B}} = \mathbf{q'} \cdot \mathbf{D}^{\mathbf{AB}} \cdot \mathbf{gsum}^{\mathbf{A}} \cdot \mathrm{mbs} \cdot \left(\omega^{\mathrm{BT}} \cdot \mathrm{Xc}^{\mathrm{B|T}} + \frac{1}{2} \cdot \omega^{\mathrm{BR}} \cdot \mathrm{Xc}^{\mathrm{AB|M}} \right).$$

where *mbs* is the discounted average number of matings between a breed A female and a breed B male over the lifetime of the female and is calculated as

$$\mathrm{mbs} = \left(\mathbf{a}_{\mathbf{i}}^{\mathbf{A}} \otimes \mathbf{f}_{\mathbf{i}}^{\mathbf{B}} \otimes \mathbf{p}_{\mathbf{i}}^{\mathbf{B}} \right)' \cdot \mathbf{q}_{\mathbf{i}} \cdot \left(\frac{1}{1+\mathrm{r}} \right).$$

2.5.2 Birth, yearling and slaughter trait expressions

In the present study replacement females were not included in the calculation of yearling and slaughter traits expressions. The discounted expressions of a terminal calf's birth genes given the calf is born ($\mathrm{Xb}_{\mathrm{Ter\,min\,al\,calf}}$) is one, by definition. The discounted expression of a terminal calf's yearling ($\mathrm{Xy}_{\mathrm{Ter\,min\,al\,calf}}$) and slaughter ($\mathrm{Xs}_{\mathrm{Ter\,min\,al\,calf}}$) traits given the animal is born, accounting for mortality and time delays of expressions is

$$Xy_{Terminal\ calf} = pre \cdot \left(\frac{1}{1+r}\right)^{ya}$$

$$Xs_{Terminal\ calf} = pre \cdot post \cdot \left(\frac{1}{1+r}\right)^{sa}.$$

where *pre* is survival to yearling age; *ya* is yearling age (or any other appropriate age); *post* is survival from yearling age to slaughter age; and *sa* = slaughter age.

The birth trait expressions in the progeny of a terminal female of breed α, mated at least once to sire T, discounted back to the birth of the female are calculated as:

$$Xb^{\alpha|T} = \frac{1}{2} \cdot \mathbf{q}' \cdot \left(\mathbf{a}^{\alpha} \otimes \mathbf{f}^{\alpha}\right) \cdot \left(\frac{1}{1+r}\right) \cdot Xb_{Terminal\ \ calf}.$$

The $\frac{1}{2}$ in the equation accounts for half the genes of the terminal female being passed on to its progeny. As before, only slight modifications are required for yearling ($Xy^{\alpha|T}$) and slaughter ($Xs^{\alpha|T}$) trait expressions in the terminal female's progeny by accounting for mortality and discounting back to the birth of the female herself.

$$Xy^{\alpha|T} = Xb^{\alpha|T} \cdot Xy_{Terminal\ calf}$$

$$Xs^{\alpha|T} = Xb^{\alpha|T} \cdot Xs_{Terminal\ calf}.$$

The number of birth traits expressed over the lifetime of a self-replacing AB female and her descendants, when mated at least once to an M male, and discounted back to the time of birth of the female herself ($Xb^{AB|M}$) first requires the calculation of $Xtb^{AB|M}$, the expressions of birth traits in the progeny of the terminal daughters of an AB female when mated at least once to a terminal male.

$$\mathrm{Xtb}^{\mathrm{AB|M}} = \omega^{\mathrm{MT}} \cdot \mathrm{Xs}^{\mathrm{AB|M}} \cdot \mathrm{Xb}^{\mathrm{AB|T}}.$$

Thus,

$$\mathrm{Xb}^{\mathrm{AB|M}} = \mathbf{q'} \cdot \mathbf{D^B} \cdot \mathbf{gsum^M} \cdot \left(\frac{1}{2} + \mathrm{Xtb}^{\mathrm{AB|M}} \right) + 1.$$

Note that $\mathrm{Xs}^{\mathrm{AB|M}} = \mathrm{Xs}^{a|\mathrm{T}}$ since the discounted expressions of slaughter traits in the progeny of terminal daughters is assumed to be equivalent to the discounted first expression of heifer traits in terminal daughters. The $\mathrm{Xtb}^{\mathrm{AB|M}}$ accounts for the proportion of progeny that enter the terminal female pathway (ω^{MT}), the discounted number of those daughters that calve ($\mathrm{Xs}^{\mathrm{AB|M}}$), and whose progeny in turn express $\mathrm{Xb}^{\mathrm{AB|T}}$ discounted number of birth traits. The inclusion of $\mathbf{q'} \cdot \mathbf{D^B} \cdot \mathbf{gsum^M}$ outside the parenthesis accounts for the repeated pathway expressions in self-replacing females, terminal females and surplus progeny described inside the parenthesis. The number one at the end of the equation accounts for the expression of the birth trait in the AB female herself.

The CDE of yearling ($\mathrm{Xy}^{\mathrm{AB|M}}$) and slaughter ($\mathrm{Xs}^{\mathrm{AB|M}}$) traits in the progeny of a self-replacing female of breed AB when mated, at least once, to an M male require a simple alteration of the formula for $\mathrm{Xb}^{\mathrm{AB|M}}$ to account for the lack of expression of yearling and slaughter traits in self-replacing and terminal females (including the original female of breed AB), mortality and further discounting as follows:

$$\mathrm{Xy}^{\mathrm{AB|M}} = \mathbf{q'} \cdot \mathbf{D^B} \cdot \mathbf{gsum^M} \cdot \left(\mathrm{Xty}^{\mathrm{AB|M}} + \mathrm{Xpy}^{\mathrm{AB|M}} \right)$$

$$\mathrm{Xs}^{\mathrm{AB|M}} = \mathbf{q'} \cdot \mathbf{D^B} \cdot \mathbf{gsum^M} \cdot \left(\mathrm{Xts}^{\mathrm{AB|M}} + \mathrm{Xps}^{\mathrm{AB|M}} \right)$$

where

$$Xt\lambda^{AB|M} = \omega^{MT} \cdot Xs^{AB|M} \cdot X\lambda^{AB|T}$$

$$Xpy^{AB|M} = \frac{1}{2} \cdot (1 - \omega^{MR} - \omega^{MT}) \cdot Xy_{\text{Terminal calf}}$$

$$Xps^{AB|M} = \frac{1}{2} \cdot (1 - \omega^{MR} - \omega^{MT}) \cdot Xs_{\text{Terminal calf}}$$

and λ= *y* or *s* for yearling and slaughter traits, respectively.

The probability of a mating between a breed A female and a breed B male is determined by the vector $\mathbf{p^B}$; likewise, the probability of a breed A female being mated to a breed A male is described by the vector $\mathbf{p^A}$. Thus, the expression of a terminal female's genes of breed A, mated at least once, to a male of breed α for birth ($Xxb^{A|\alpha}$) traits in her daughters over her lifetime discounted back to the time of birth of the female herself may be computed as follows:

$$Xxb^{A|\alpha} = \frac{1}{2} \cdot \left(\mathbf{a^A} \otimes \mathbf{f^A} \otimes \mathbf{p^\alpha}\right)' \cdot \mathbf{q} \cdot \left(\frac{1}{1+r}\right).$$

The CDE of a self-replacing female's genes of breed A mated, at least once, to a B male for birth ($Xb^{A|B}$), yearling ($Xy^{A|B}$), or slaughter ($Xs^{A|B}$) traits in herself (only for $Xb^{A|B}$) and her descendants may be described as:

$$Xb^{A|B} = \omega^{BT} \cdot Xxb^{A|B} + Xtb^{A|B} + Xpb^{A|B} + \omega^{BR} \cdot Xxb^{A|B} \cdot Xb^{AB|M}$$

$$Xy^{A|B} = Xty^{A|B} + Xpy^{A|B} + \omega^{BR} \cdot Xxb^{A|B} \cdot Xy^{AB|M}$$

$$Xs^{A|B} = Xts^{A|B} + Xps^{A|B} + \omega^{BR} \cdot Xxb^{A|B} \cdot Xs^{AB|M}$$

where

$$Xt\lambda^{A|B} = \omega^{BT} \cdot Xs^{A|B} \cdot X\lambda^{B|T}$$

$$Xp\lambda^{A|B} = X\lambda^{B|T} \cdot \left(1 - \omega^{BR} - \omega^{BT}\right)$$

and λ=*b*, *y* or *s* denoting birth, yearling and slaughter traits, respectively.

The term $\omega^{BT} \cdot Xxb^{A|B}$ describes the discounted birth trait expression of the terminal daughters of the A female mated to a B male over the lifetime of the A female. The term $Xtb^{A|B}$ describes the birth trait expressions of the progeny of the terminal females, while $Xpb^{A|B}$ calculates the discounted birth trait expressions of the immediate surplus progeny following the mating of an A female and a B male over the lifetime of the A female. The term $\omega^{BR} \cdot Xxb^{A|B} \cdot Xb^{AB|M}$ describes the discounted birth trait expressions of the immediate self-replacing daughters and their subsequent progeny already previously described through the mating of the AB female with the M male.

The CDE of a self-replacing female's genes of breed A mated to an A male for birth ($Xb^{A|A}$), yearling ($Xs^{A|A}$), or slaughter ($Xs^{A|A}$) traits in herself (only for $Xb^{A|A}$) and her progeny where the A female is mated at least once are calculated as:

$$Xb^{A|A} = \mathbf{q'} \cdot \mathbf{D^A} \cdot \mathbf{gsum^{AA}} \cdot \left(\frac{1}{2} + Xtb^{A|A} + \frac{1}{2} \cdot Xb^{A|B} \right) + 1$$

$$Xy^{A|A} = \mathbf{q'} \cdot \mathbf{D^A} \cdot \mathbf{gsum^{AA}} \cdot \left(Xpy^{A|A} + Xty^{A|A} + \frac{1}{2} \cdot Xy^{A|B} \right)$$

$$Xs^{A|A} = \mathbf{q'} \cdot \mathbf{D^A} \cdot \mathbf{gsum^{AA}} \cdot \left(Xps^{A|A} + Xts^{A|A} + \frac{1}{2} \cdot Xs^{A|B} \right)$$

where

$$Xt\lambda^{A|A} = \omega^{AT} \cdot Xs^{A|A} \cdot X\lambda^{A|A}$$

$$Xpy^{A|A} = \frac{1}{2} \cdot \left(1 - \omega^{AR} - \omega^{AT}\right) \cdot Xy_{\text{Ter min al calf}}$$

$$\mathrm{Xps}^{\mathrm{A|A}} = \frac{1}{2} \cdot \left(1 - \omega^{\mathrm{AR}} - \omega^{\mathrm{AT}}\right) \cdot \mathrm{Xs}_{\mathrm{Ter\,min\,al\ calf}}$$

and λ=*b*, *y* or *s* representing birth, yearling and slaughter traits, respectively. Relatively simple algebra may subsequently be used to calculate the cumulative discounted expressions for any trait category for any animal of interest. The cumulative number of expressions for each trait category when a breed A female is mated to a breed A male, or when a breed A female is mated to a breed B male discounted back to the time of birth of the initial progeny are summarized in Table 1 and 2, respectively.

2.6 Case Studies

In order to explore the application of the derived equations, input parameters for three case studies were substituted into the equations. Pathways described are illustrated in Figure 1 and abbreviations used are defined in Table 4.

2.6.1 Case study I

This case study represents the Irish system of cattle farming where a strong relationship exists between dairy (Breed A) and beef (Breed B) enterprises (Irish Cattle Breeding Statistics, 2003) with a large proportion of dairy farms either supplying animals to or operating a beef enterprise. Initial parameters required for the calculations were obtained from national data (Irish Cattle Breeding Statistics, 2003; Department of Agriculture and Food, Ireland 2004). The survival vector for dairy females ($\mathbf{s}^{\mathbf{A}}$) was derived from the proportion of each parity in milk recorded herds in Ireland (Irish Cattle Breeding Statistics, 2003). The survival vector for

beef females ($\mathbf{s}^{\mathbf{B}}$) was that previously used by Amer et al. (2001). The vector summarizing the proportion of self-replacing dairy females of different ages mated to beef males was based on national data (John Carroll, Department of Agriculture and Food, personal communication). The $\mathbf{s}^{\mathbf{A}}$, $\mathbf{s}^{\mathbf{B}}$, and $\mathbf{p}^{\mathbf{B}}$ vectors are summarized in Table 3. Other input parameters are outlined in Table 4.

In a situation of complete market failure the benefits to the dairy farmer of generating superior crossbred replacement females for the beef herd are not realized through premium prices. The opposite occurs when beef farmers actively seek specific replacement females from dairy herds and pay premiums for these females (e.g., replacement females from dairy cows with favorable beef attributes). In reality the intensity of market failure will vary from complete to none. The effects of degree of market failure were investigated using sensitivity analyses within this case study. Market failure was accounted for in the model calculations by not summing the expressions throughout the self-replacing and terminal pathways of crossbred AB females, although animals still entered those pathways so that the value of their gene expressions are not included in the cumulative expressions. Sensitivity analyses were performed by altering ω^{BR} and ω^{BT} simultaneously with the intensity of market failure.

2.6.2 Case study II

The second case study is based on a contrasting system of farming in Brazil. In Brazil Zebu females (Breed A) are commonly mated to either Zebu males or Holstein (Breed B) males (Madalena, 1998; Guimarães et al., 2004). The purebred Zebu females maintain the original herd age structure while the F_1 females are

sold as dairy herd replacements and generally become terminal females; surplus progeny are slaughtered for beef production. The survival vector of purebred and crossbred Zebu females were both assumed to be equivalent to the survival vector for the crossbred females reported by Lemos et al. (1996) in low management herds. Low management herds, as described by Madalena et al. (1990), fed less concentrates, utilized more family labor, had a lower frequency of machine milking, used lower levels of artificial insemination and had an inferior health program that high management herds. The probability of crossbreeding occurring ($\mathbf{p}^{\mathbf{B}}$) was assumed to be constant by parity. The crossbreeding vector was designed such that the probability of a mating between a Zebu male and a Zebu female was sufficient to maintain the herd age structure assuming a sex ratio of 1:1 and that 90% of the surviving Zebu heifers were suitable to become replacements. The surplus matings were to Holstein males to generate F_1 crossbreds. The survival and probability vectors under low management levels are summarized in Table 3. The proportion of progeny (both male and females) from a mating between a Holstein male and a Zebu female that become terminal females (ω^{BT}) was set to 0.45 to account for a 1:1 sex ratio as well as 90% of candidate females becoming terminal. Remaining input parameters are summarized in Table 4. Heifers were assumed to calve at three years of age (Lemos et al., 1996; Guimarães et al., 2004). Pre-yearling mortality was set at 6% (Guimarães et al., 2004); post-yearling mortality was set at 1% (Guimarães et al., 2004). The proportion of cows that die on farm thereby not exhibiting a cull trait was the sum of the “accident” and “other reasons” outlined by Lemos et al. (1996).

Sensitivity analysis was performed by substituting the survival probabilities of the low management group with those of the high management group (Lemos et al., 1996); all other input parameters were identical to the low management group with the exception that no cows died on farm (Lemos et al., 1996). The survival vector for females on the high management systems is outlined in Table 3.

A second sensitivity analysis represented an alternative scenario in Brazil whereby the F_1 Zebu*Holstein females are sometimes back crossed to a Holstein sire (Breed M in Figure 1); the selected females become terminal (i.e., the immediate progeny of these females are slaughtered). Thus, in Figure 1 $\omega^{BT}=0$, $\omega^{BR}=0.45$, $\omega^{MT}=0.45$ and $\omega^{MR}=0$; all other parameters were assumed the same as defined in Tables 3 and 4.

2.6.3 Case study III

The third case study represents a purebred dairy (Breed A) production system with no crossbreeding (i.e, the elements of the $\mathbf{p}^{\mathbf{B}}$ vector are all zeros) and no terminal females (i.e., $\omega^{AT}=0$). Thus, in this case study interest is only on matings between dairy males and dairy females. This system is typical in many countries with poor dairy longevity, such that all dairy females must be mated to dairy males to generate sufficient herd replacements. The survival vector ($\mathbf{s}^{\mathbf{A}}$) and other input parameters for case study III are summarized in Tables 3 and 4 and are typical of many dairy production systems in North America (Collard et al., 1999; USDA, 2002).

3. Results

3.1 Case Study I

The CDE for each of the six trait categories following an initial mating between either a dairy male (Breed A) or a beef male (Breed B) with a dairy female are summarized in Table 5. The difference in CDE between annual and birth traits is largely a function of the number of dairy progeny destined to become replacement females (i.e., pathways ω^{AR} and ω^{AT} in Figure 1). As the proportion of progeny becoming replacements increases the relative difference between CDE for annual and birth traits diminishes.

Assuming that shortly after birth crossbred (AB) females destined to become replacement females enter a beef herd, then less than 13% of the total CDE for all trait categories (using current input parameters) are expressed in the beef herd when the initial mating is between a dairy male and a dairy female.

The effect on the CDE of birth traits from simultaneously altering both the number of crossbred progeny that become beef female replacements, and the proportion of beef farmer satisfaction that is relayed back to the dairy farmer (i.e., the intensity of market failure) is illustrated in Figure 2; ω^{BR} and ω^{BT} were assumed to be equivalent throughout. When no crossbred progeny enter beef herds the intensity of market failure is irrelevant. Under complete market failure the CDE of a dairy sire's genes for birth traits when mated to a dairy female decreased as the proportion of crossbred females entering the beef herd increased. The opposite was true when no market failure existed. If complete market failure prevails (i.e., the superiority of replacement crossbred females is not recognized by the purchaser) then the CDE for annual, replacement, cull cow, birth, yearling

and slaughter traits decreased by 0.10, 0.03, 0.01, 0.10, 0.06, and 0.05, respectively.

The CDE of a beef sire for all traits when mated to a dairy female were lower than for a dairy sire mated to a dairy female because of the low proportion of resulting progeny that enter the beef herd as beef replacements ($\omega^{BR}+ \omega^{BT}$). Based on the parameters used in the present study, the CDE of yearling/slaughter trait genes of a beef sire are greater than the discounted expressions of annual cow trait genes of the sire. The difference between birth and yearling/slaughter traits was low because very few self-replacing female replacements were sourced from this breed type.

3.2 Case Study II

Under low management environments the number of purebred Zebu female calves required, per breeding female, to supply sufficient replacement females to perpetuate the purebred Zebu herd was 0.18. Thus, the proportion of purebred Zebu females mated to Zebu males was 0.42 to account for a 1:1 sex ratio, selection among candidate females and mortality. The CDE for annual, replacement heifer, cull cow, birth, yearling and slaughter traits accruing from an initial mating between a Zebu male and a Zebu female (i.e., an AxA mating) or between a Holstein male and a Zebu female (i.e., a BxA mating) are summarized in Table 5.

Based on the percentage of F_1 terminal females entering a dairy herd in Brazil, assumed to be ω^{BT}=0.45, the CDE for annual, replacement heifer and cull cow traits expressed in the dairy herd was 0.44, 0.09 and 0.02 respectively when the

initial mating was between a Zebu male and a Zebu female. Hence, the expression of annual traits in dairy herds represents 50% of the total annual CDE.

The CDE for birth, yearling and slaughter traits exhibited in a dairy herd ranged from 0.10 to 0.13 when the initial mating was between a Zebu male and a Zebu female. When the initial mating was between a Holstein male and a Zebu female the CDE for birth, yearling and slaughter traits exhibited in a dairy herd was 0.16, 0.14 and 0.13, respectively.

The CDE of all trait categories increased linearly as the proportion of F_1 females mated to a maternal sire (in Brazil this is usually a Holstein sire) increased. When 90% of F_1 females in dairy herds were mated to a maternal sire the CDE for annual, replacement heifer and cull cow traits expressed in the dairy herds increased by 0.34, 0.08 and 0.02, respectively when the initial mating was between a Zebu male and Zebu female; the corresponding increase in CDE for birth, yearling and slaughter traits was 0.41, 0.31 and 0.21, respectively. Note that this is a non equilibrium situation, the herd size is either growing, or females are being sold off to herds that do not breed their own replacements

Under high management levels, as described by Madalena et al. (1990), the number of calves required per breeding female to perpetuate the purebred Zebu herd was 0.15; this is attributable to the superior survival of cows under this management system. Thus, under high management levels the proportion of Zebu females mated to Holstein males may be as high as 0.65. The CDE of all trait categories in the high production environments were consistently larger than the corresponding CDE in the low production environments (Table 5). The proportion of total CDE for all trait categories expressed in dairy herds increased under high

management levels, attributable mainly to the larger proportion of Zebu female matings to Holstein sires.

3.3 Case Study III

The input parameters assumed in case study III, resulted in 0.40 female calves per breeding female being required to supply sufficient replacements to maintain the herd structure. In this case study, no dairy (Breed A) females were mated to beef (Breed B) males. Assuming on average half the progeny are male and after accounting for mortality, the replacement policy described in this system can accommodate a "wastage" (e.g., failure to conceive, morphological defects, selection of females) of 20% among dairy heifers that might otherwise reach age at first calving. The CDE for annual, replacement heifer, cull cow, birth, yearling and slaughter traits are summarized in Table 5. Despite no crossbreeding occurring in this case study, the CDE of yearling/slaughter traits represented over 40% of the CDE of annual traits (e.g., lactation).

4. Discussion

Equations derived in the present study to calculate CDE for alternative trait categories have been demonstrated to be robust and applicable to contrasting production environments. The calculated CDE are sensitive to the prevailing population parameters, especially the probability of a cow surviving from one age to the next. The relative differences between CDE of trait categories across farming systems highlights the necessity to investigate the economic consequences of diverse breeding goals incorporating traits that reflect both dairy

and beef characteristics. These investigations should consider the cost of recording and evaluating the auxiliary traits and their predictor traits, as well as the economic values and CDEs of these traits. The same applies in purebred dairy production systems where non-lactation related traits have been shown here to represent over 40% of the CDE of a dairy sire for lactation related traits.

Although based on the same principles, the approach used in the present study to track the flow of genes throughout a population is somewhat different to that employed by others (Hill, 1974; Brascamp, 1975; Elsen, 1990; Groen, 1999; Jiang et al., 1999; Wolfová and Nitter, 2004). The aforementioned authors used procedures that tracked the flow of genes, through aging and reproduction, across alternative pathways of males to males, males to females, females to males and females to females simultaneously. These pathways are synonymous with the sire to sire, sire to dam, dam to sire and dam to dam pathways, respectively, as described by Rendel and Robertson (1950). Hill (1974) used the gene flow principles to evaluate optimal breeding scheme designs so that the expected financial returns from future generations could be compared with returns from current generations. Expressions within each pathway may also be calculated separately using current procedures and re-defined input parameters.

The approach used in this study has focused on the gene-flow of a specific sire conditional on the breed of cow mated. It is primarily intended to assist with the establishment of appropriate breeding objectives but can also be used to derive the differences in values of specific animals or matings using information on estimated breeding values and the economic values per unit change in traits of interest. We believe that our approach has benefits over the alternative approaches

of the aforementioned studies in that it involves aggregation of a number of intermediate parameters, each with its own interest in its own right. For example, when computing the value of a purchased in calf replacement heifer based on expected expressions of her genetic merit in her own lifetime, and the lifetime of her descendents. In contrast, the alternative approaches to calculating CDEs rely on the definition of transition matrices that become very large and unwieldy under complicated scenarios with integrated populations. However, given identical parameters and assumptions, our expectation is that each method should yield identical results.

4.1 Trait Categories

The calculation of the CDE in the present study accounts for the rate and number of years over which the trait is expressed, genetic contribution across generations, a discounting factor, the survival rate of females across time, the survival rate of progeny, the proportion of females becoming self-replacing or terminal, fecundity, and the probability of cross-breeding occurring.

A large contributing factor to the difference in CDE between annual and replacement heifer traits is that heifer replacement traits are only expressed once per animal. Cumulative discounted expressions of cull cow traits are in turn lower than the CDE for replacement heifer traits because a cow can only be culled once, yet only a proportion (i.e., 1-*die*) actually exhibit the trait, but also culling occurs after a substantial time delay and so culled cow expressions are discounted accordingly. The relative difference between the CDE for replacement heifer traits

and cull cow traits is reduced when cow longevity is poorer, as in case study III, and/or when cow mortality on farm is lower.

The difference between the CDE for birth traits and yearling/slaughter traits arises because females destined to become replacements were not counted as expressing yearling or slaughter traits. Other contributing factors to the difference between expressions are mortality from birth to yearling/slaughter and higher discounting to older ages. Differences in the CDE for yearling and slaughter traits reflect mortality from yearling to slaughter and higher discounting to age at slaughter.

It is important to bear in mind that some annual traits may be economically relevant in dairy enterprises but not in beef enterprises, and vice versa. For example, the genetic merit of a dairy sire in Ireland for lactation milk yield (annual trait) will be irrelevant to a beef farmer; hence the expressions of these traits in beef herds should not be included in the CDE of a dairy sire for lactation milk yield. Also, the CDE of slaughter traits reported in the present study are not applicable to calves slaughtered shortly after birth for veal production or otherwise.

4.2 Cow Survival

The impact of improved cow survival on CDE is illustrated in case study II. With higher cow survival (i.e., high management level) the CDE of all trait categories increases. The CDE for annual traits increase relatively more than the other traits; this is because females live longer thereby producing more daughters that in turn live longer. Benefits of improved cow survival in the Zebu herd were also observed by the ability to mate more Zebu females to Holstein sires thereby

maximizing farm profit through the sale of F_1 females to dairy enterprises for price premiums. Farm profit of Zebu herds is expected to be further augmented as the proportion of crossbreeding increases since the growth rate and feed conversion efficiency of the F_1 males is expected to be superior to that of the purebred Zebu males (Paiva et al., 1992).

As cow survival deteriorates (e.g., case study III) the number of heifer replacements required to maintain the herd structure increases, thereby diminishing the opportunity to select among candidate replacement females and/or to mate females to beef sires. Also the relative difference in CDE between yearling/slaughter traits and birth traits increases as cow survival deteriorates, since fewer surplus females are slaughtered and fewer females are mated to beef sires; an analogous trend exists when the herd is expanding.

4.3 Integrated Cattle Populations

Results from the first two case studies illustrate the contribution of enterprises, different to those where the initial mating took place, on the CDE of a sire. In Ireland, a small proportion (<13%) of the CDE of a dairy sire's genes for all trait categories, when mated to a dairy female, are expressed in beef herds through the sire's crossbred female descendants. However, a number of the purebred dairy expressions for yearling and slaughter traits may occur in the beef herds since a large proportion of surplus purebred and crossbred dairy progeny in Ireland will be finished in beef herds.

In Brazil, a considerable proportion of a Zebu sire's genes, when mated to a Zebu female, are expressed in dairy herds; the expression of the Zebu sire's genes are

augmented when dairy herds also produce F_2/backcross terminal females. In case study III (i.e., no transfer of genes between dairy and beef enterprises), the CDE of yearling and slaughter traits represented over 40% of the CDE of annual traits (e.g., lactation traits). However, in some production environments surplus progeny are slaughtered immediately or shortly after birth; the economic impact of sire genetic merit for beef production will subsequently be small. Nevertheless, all case studies exemplify the need to investigate further the economic consequences of diverse breeding objectives in both purebred and integrated cattle populations.

4.4 Market Failure

Results from case study I reveal an important interaction between the effects of market failure and the proportion of crossbred females from the dairy herd that become beef replacement females. Market failure does not exist if a farmer operates both a dairy and beef enterprise or a dairy farmer has a reputation for producing superior crossbred replacement females. For example, an Irish beef farmer may actively seek crossbred females from dams with favorable beef characteristics. Similarly, in Brazil a dairy farmer may prefer crossbred replacement females from Zebu cows exhibiting dairy characteristics (e.g. Gir cows). However, in the majority of countries the full economic benefits of crossbred animals and their descendants are rarely realized by the generating farmer; this questions the (full) inclusion of such expressions in the CDE of the original sire.

Nevertheless, the fundamental aim of all national breeding organizations should be to maximize genetic gain in profitability across all cattle. Thus, a national

breeding organization may choose to ignore market failure thereby servicing the entire cattle industry as a whole. In such situations a single across-breed selection objective in dairy or beef cattle, where animals of alternative breeds are ranked concurrently, may be optimal. Liinamo and van Arendonk (1999) using a series of alternative selection objectives/indexes reported that selection on carcass traits simultaneous with selection on milk production did not affect genetic gain in fat and protein yield to any large degree. The lack of antagonistic effects on genetic gain for fat and protein yield was attributable to the dominating selection emphasis on protein yield within the breeding objective and the favorable genetic correlations between most beef traits and milk production; genetic correlations between carcass fatness and milk production were positive. Similarly, van Veldhuizen et al. (1991) reported that genetic selection on milk and beef production increased net profit by 15% over selection on milk production alone; overall profit increased despite a reduction in genetic gain for milk production. Nonetheless, the marginal cost of incorporating some beef-related traits (e.g. carcass conformation and yield) into breeding objectives is minimal since slaughter houses already routinely record carcass information for internal use.

Alternatively if a national breeding organization is funded through farmer levies, it may be decided to bias towards the product and/or farmers paying the levy. Similar situations might exist among commercial breeding organizations or in countries where alternative enterprises are relatively unprofitable. The degree of inclusion of expressions in the CDE of an animal will also be dictated by prevailing circumstances and the degree of interdependence among enterprises. For example, in Brazil, the sole purpose of certain purebred Zebu herds is to

supply quality F_1 females to dairy producers (Madalena, 1993). Half the CDE of annual traits (e.g. lactation) in case study II, for a Zebu sire when mated to a Zebu female, were expressed in dairy herds. This signifies the importance of superior genes for dairy characteristics in Zebu males (used to generate purebred Zebu females for mating to Holstein males), the magnitude of which increases as the required number of matings between Zebu females and Zebu males is reduced.

4.5 Genotype by Environment Interactions

Differences in relative CDEs across the case studies investigated may also contribute to possible genotype by environment interactions for profitability across production environments. For example, the CDE of slaughter traits, from a purebred mating, ranged from 0.42 to 0.66 CDE of an annual/lactation trait across the three contrasting case studies. Liinamo and van Arendonk (1999) reported that the CDE of carcass traits in bulls (expressed at 550 days of age) relative to the CDE of milk traits was 0.53. Changes in the relative CDE among trait categories will translate to changes in the relative emphasis among traits in a breeding objective; this may result in re-ranking of sires across environments for the overall breeding objective.

5. Conclusions

Results from the present study highlight the necessity to investigate the economic value of beef merit in dairy breeding objectives and vice versa especially, although not exclusively, within integrated cattle production systems. Calculated CDE using the procedures outlined in the present study may be integrated into a

breeding objective as described by McClintock and Cunningham (1974). The product of the marginal economic value of a trait and its appropriate CDE will provide a superior definition of breeding goals by accounting for differential rates and timing of expression. Although the case studies outlined in the present study referred to cattle, the reported techniques may be simply adapted to other species (e.g., sheep, pigs and poultry) where the timing and frequency of expression of alternative traits also differ.

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Table 1. *Summary of expressions for annual, replacement heifer, cull cow, birth, yearling and slaughter traits following the conditional mating between an A female and an A male discounted back to the time of birth of the immediate progeny*

Annual	$\frac{1}{2}\left\{\omega^{AT}\cdot\cdot\mathbf{q}'\cdot\mathbf{a}^{\mathbf{A}}\otimes\mathbf{f}^{\mathbf{A}}\cdot\frac{1}{1+r}+\omega^{AR}\cdot\left(Xa^{A\|A}+Xa^{A\|B}\right)\right\}$
Replacement heifer	$\frac{1}{2}\left\{\omega^{AT}\cdot\left(\frac{1}{1+r}\right)^{afc}+\omega^{AR}\cdot\left(Xh^{A\|A}+Xh^{A\|B}\right)\right\}$
Cull cow	$\frac{1}{2}\left\{\omega^{AT}\cdot\mathbf{q}'\cdot\mathbf{d}^{\mathbf{A}}\cdot(1-die)\cdot\frac{1}{1+r}+\omega^{AR}\cdot\left(Xc^{A\|A}+Xc^{A\|B}\right)\right\}$
Birth	$\frac{1}{2}\left\{\left(1-\omega^{AR}-\omega^{AT}\right)+\omega^{AT}\cdot\left(\mathbf{q}'\cdot\mathbf{a}^{\mathbf{A}}\otimes\mathbf{f}^{\mathbf{A}}\cdot\frac{1}{1+r}+Xtb^{A\|A}\right)+\omega^{AR}\cdot\left(Xb^{A\|A}+Xb^{A\|B}\right)\right\}$
Yearling	$\frac{1}{2}\left\{Xy_{Ter\,min\,al\,calf}\cdot\left(1-\omega^{AR}-\omega^{AT}\right)+\omega^{AT}\cdot Xty^{A\|A}+\omega^{AR}\cdot\left(Xy^{A\|A}+Xy^{A\|B}\right)\right\}$
Slaughter	$\frac{1}{2}\left\{Xs_{Ter\,min\,al\,calf}\cdot\left(1-\omega^{AR}-\omega^{AT}\right)+\omega^{AT}\cdot Xts^{A\|A}+\omega^{AR}\cdot\left(Xs^{A\|A}+Xs^{A\|B}\right)\right\}$

Table 2. *Summary of expressions for annual, replacement heifer, cull cow, birth, yearling and slaughter traits following the conditional mating between an A female and a B male discounted back to the time of birth of the immediate progeny*

Annual	$\frac{1}{2}\left\{\omega^{BT}\cdot\mathbf{q}'\cdot\mathbf{a}^{\mathbf{B}}\otimes\mathbf{f}^{\mathbf{B}}\cdot\frac{1}{1+r}+\omega^{BR}\cdot Xa^{AB\|M}\right\}$
Replacement heifer	$\frac{1}{2}\left\{\omega^{BT}\cdot\left(\frac{1}{1+r}\right)^{afc}+\omega^{BR}\cdot Xh^{AB\|M}\right\}$
Cull cow	$\frac{1}{2}\left\{\omega^{BT}\cdot\mathbf{q}'\cdot\mathbf{d}^{\mathbf{B}}\cdot(1-die)\cdot\frac{1}{1+r}+\omega^{BR}\cdot Xc^{AB\|M}\right\}$
Birth	$\frac{1}{2}\left\{\left(1-\omega^{BR}-\omega^{BT}\right)+\omega^{BT}\cdot\left(\mathbf{q}'\cdot\mathbf{a}^{\mathbf{B}}\otimes\mathbf{f}^{\mathbf{B}}\cdot\frac{1}{1+r}+Xtb^{A\|B}\right)+\omega^{BR}\cdot Xb^{AB\|M}\right\}$
Yearling	$\frac{1}{2}\left\{Xy_{terminal\ calf}\cdot\left(1-\omega^{BR}-\omega^{BT}\right)+\omega^{BT}\cdot Xty^{A\|B}+\omega^{BR}\cdot Xy^{AB\|M}\right\}$
Slaughter	$\frac{1}{2}\left\{Xs_{terminal\ calf}\cdot\left(1-\omega^{BR}-\omega^{BT}\right)+\omega^{BT}\cdot Xts^{A\|B}+\omega^{BR}\cdot Xs^{AB\|M}\right\}$

Table 3. *Survival vectors for breed A (S_A) and breed B (S_B) females, and the proportion of matings between A females and B males by year group (P_B) implemented for the three case studies*[a].

CASE STUDY I			CASE STUDY II[b]			CASE STUDY III	
S_A	S_B	P_B	S_A-Low	S_A-High	P_B	S_A	P_B
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.98	0.95	0.51	0.00	0.00	0.00	0.87	0.00
0.86	0.94	0.41	0.96	0.96	0.63	0.76	0.00
0.77	0.93	0.42	0.98	1.00	0.63	0.64	0.00
0.85	0.88	0.44	0.92	0.96	0.63	0.65	0.00
0.79	0.83	0.46	0.90	0.95	0.63	0.58	0.00
0.63	0.70	0.53	0.92	0.95	0.63	0.50	0.00
0.60	0.60	0.48	0.83	0.95	0.63	0.47	0.00
0.50	0.50	0.48	0.82	0.95	0.63	0.44	0.00
0.30	0.50	0.48	0.59	1.00	0.63	0.42	0.00
0.30	0.50	0.48	0.37	0.78	0.63	0.34	0.00
0.30	0.50	0.48	0.14	0.57	0.63	0.44	0.00

[a] Case study I=Ireland; Case study II=Brazil; Case study III=North America.

[b] S_A – Low refers to the survival vector for the low management level; S_A – High refers to the survival vector for the high management level

Table 4. *Input parameters (text abbreviations in parenthesis) applied in the three case studies*[a].

	CASE STUDY I	CASE STUDY II	CASE STUDY III
Discount rate (r) %	0.07	0.07	0.07
Pre-yearling survival (Pre) %	0.95	0.94	0.90
Post-Yearling survival (Post) %	0.99	0.99	0.97
Slaughter age (sa) years	2.5	3	2
Yearling age (ya) years	1	1	1
Age at first calving (afc) years	2	3	2
Proportion of cows culled that die on farm (die) %	0.03	0.17	0.05
Proportion of A progeny that become self-replacing females (ω^{AR}) %	0.38	0.18	0.40
Proportion of A progeny that become terminal females (ω^{AT}) %	0.00	0.00	0.00
Proportion of F_1 AB progeny that become self-replacing females (ω^{BR}) %	0.06	0.00	NA
Proportion of F_1 AB progeny that become terminal females (ω^{BT}) %	0.06	0.45	NA
Proportion of MAB progeny that become self-replacing females (ω^{MR}) %	0.05	0.00	NA
Proportion of MAB progeny that become self-replacing females (ω^{MT}) %	0.05	0.00	NA

[a] Case study I=Ireland; Case study II=Brazil; Case study III=North America.

Table 5. *Cumulative discounted expressions for annual, replacement heifer, cull cow, birth, yearling and slaughter traits for each of the three case studies*[a]

	CASE STUDY I		CASE STUDY II				CASE STUDY III
			Low management		High management		
	A x A	B x A	A x A	B x A	A x A	B x A	A x A
Annual	0.89	0.24	0.84	0.86	1.10	1.02	0.91
Replacement heifer	0.28	0.06	0.18	0.18	0.20	0.18	0.43
Cull cow	0.19	0.04	0.07	0.11	0.07	0.12	0.32
Birth	1.05	0.66	0.90	1.30	0.92	1.55	0.95
Yearling	0.66	0.45	0.62	0.39	0.66	0.47	0.42
Slaughter	0.59	0.41	0.54	0.33	0.57	0.40	0.38

[a] Case study I=Ireland; Case study II=Brazil; Case study III=North America.

Figure 1. *Illustration of the possible pathways of gene-flow from an original mating between an A female and an A male or between an A female and a B male.*

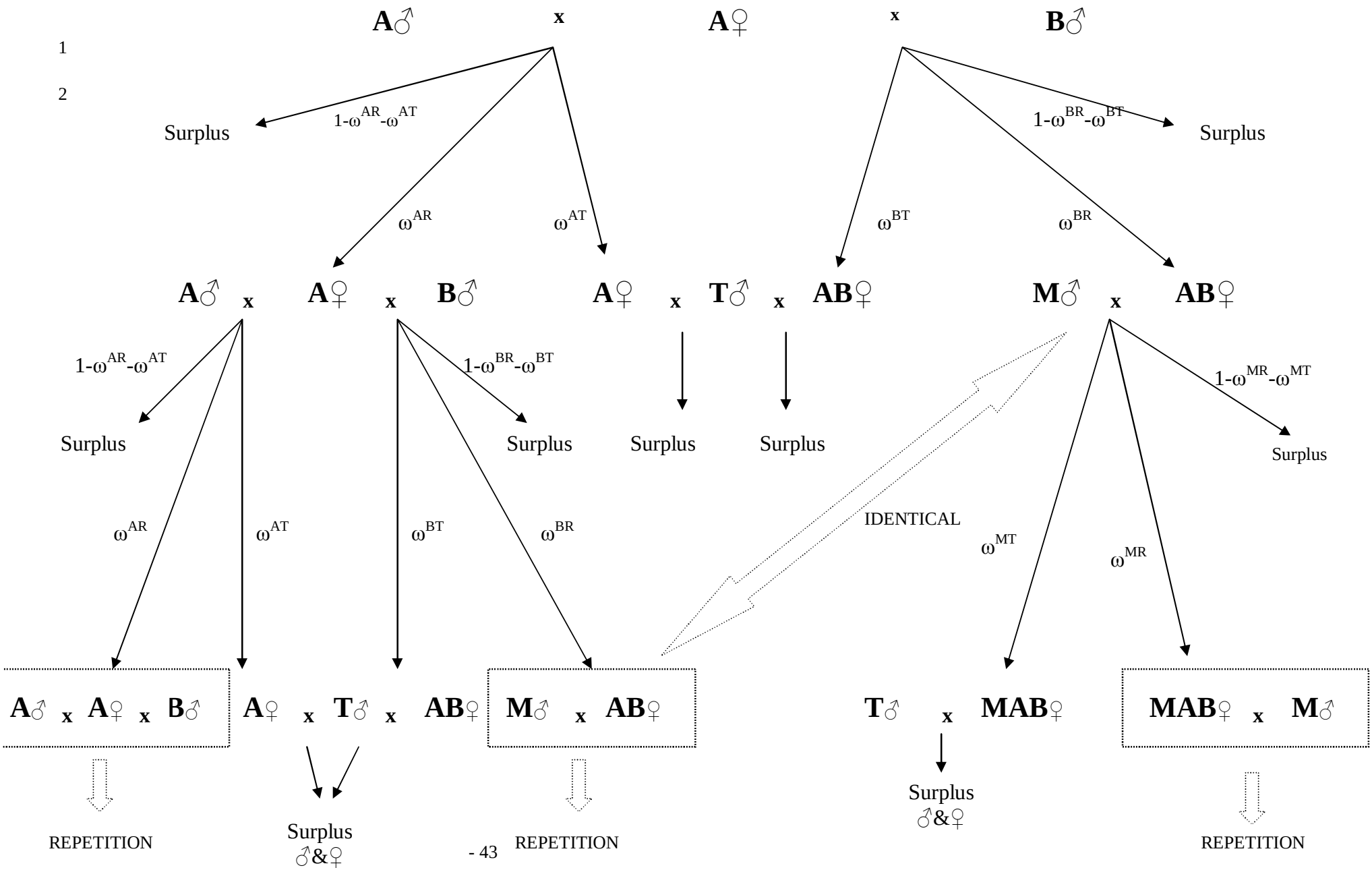

Figure 2. *Effect on cumulative discounted expressions in Case study I of both the proportion of AB progeny becoming female replacements and the intensity of market failure.*