1 INTRODUCTION

Australia's northern beef production regions are characterised by extremes of heat and humidity, seasonal nutritional deficiencies and the presence of endo- and ecto-parasites (Prayaga *et al*. 2009). To cope with these challenges, *Bos indicus*, *Bos indicus* derived and tropically adapted *Bos taurus* breeds have become the dominant genotypes in this region, representing approximately 40% of Australia's national beef herd (Bindon and Jones 2001). Low reproductive performance in tropically adapted females is recognised as a limitation to productivity in Australia's tropically adapted beef genotypes (Schatz and Hearnden 2008, Johnston *et al*. 2013*a*). Management intervention, typically nutritional supplementation, which increased heifer weight at first annual mating and body condition at first and subsequent annual matings was shown in the reviews of Holroyd and Fordyce (2001) and Savage (2005) to have the capacity to significantly improve female reproductive performance at the phenotypic level. Savage (2005), however, pointed out that Australia's northern beef production regions were characterised by large paddock size and low stocking rates, remoteness to markets for both inputs and sale stock, seasonal inaccessibility, and (in many areas) year round mating, which made targeting cost effective management intervention to improve female reproductive performance difficult.

To increase uniformity and returns from slaughter stock, there is a growing trend for the steer progeny of females managed in these environments to be finished on high energy feedlot rations (Burrow *et al*. 2003). As feedlot finishing becomes a feature of Australia's northern beef industry, feed efficiency of animals on high energy rations will also impact productivity (Archer and Barwick 1999). Additionally, despite the growth in feedlot finishing, estimated *Bos indicus* content is currently applied as a discounting factor in the Meat Standards Australia quality grading system, which limits access to markets for *Bos indicus* and *Bos indicus* derived cattle (Thompson 2002, Watson *et al*.

2008). Finally, pregnancy and lactation is known to impact cow growth and body composition, and this effect has been well documented in dairy breeds (Kadarmideen 2004, Pryce *et al*. 2001, Berry *et al*. 2002 Wall *et al*. 2003, Veerkamp *et al*.2001). For tropically adapted beef genotypes, however, the degree to which tissue mobilisation occurs during lactation is unknown, and the impact of this on reproductive performance has yet to be established.

The limitations to management intervention in northern Australia make selection an appealing means of improving economically important traits. Australia's national beef genetic evaluation (BREEDPLAN) currently estimates breeding values for traits describing growth, carcass composition, male fertility and female reproductive performance in tropically adapted breeds, with residual feed intake (a measure of feed efficiency) and objective meat quality currently being examined as potential additional traits. Via this system, breeders also have access to selection indices which rank animals for genetic merit based on breeding objectives which reflect breed, market and production system specific analyses of costs and returns. A lack of estimates for genetic relationships between steer carcass and meat quality traits and female reproductive performance was cited by Barwick and Henzell (2005) as a limiting factor to genetic evaluation in beef cattle and to the estimation of selection indices. This is particularly the case for tropically adapted genotypes, and was a key motivation for the research undertaken for this thesis.

This introduction presents a brief overview of the analytical methods which underlie modern, multi-trait genetic evaluation, and how these are applied in the estimation of breeding values and selection indices. With this background, the breeding objectives, defined in the formulation of selection indices for Australia's tropically adapted breeds are examined to describe current breeding priorities in the industry. This is followed by a brief review of additional traits which research has proposed as of potential economic value to producers of tropically adapted beef cattle. The results presented in this thesis were generated using data from a large progeny test experiment, the Co-operative Research Centre for Beef Genetic Technologies' Northern Breeding Project (Beef CRC), which examined economically important traits in two genotypes of tropically adapted beef cattle (Brahman and Tropical Composite). The closing section of this introduction presents a brief summary of the design of this experiment and the breeding program which underlay it. The experimental chapters of this thesis are presented as a series of four papers which have been published, or are accepted for publication. The aims of research reported in each paper and a description of the relationships between experimental chapters are presented in the final section of this introduction.

1.2 BEST LINEAR UNBIASED PREDICTION AND THE MIXED MODEL EQUATION

Multiple trait best linear unbiased prediction (BLUP) has become the standard methodology applied to the estimation of breeding values for livestock species. The underlying generalised linear mixed model (GLMM) techniques were initially proposed by Henderson (1949) and allow fixed and random effects to be estimated simultaneously. GLMM also departs from linear regression modelling by allowing the dependant variable(s) to be non-normally distributed (Mrode 2005). The model takes the form:

$$y = Xb + Za + e$$

Where **y** is the dependant variable, **a** and **b** are solutions for fixed (**X**) and random (**Z**) effects and **e** represents a normally distributed error term. Predictors are linear functions of the measurements for a trait, and estimates of random terms ($\hat{\mathbf{a}}$) and the solutions for fixed effects ($\hat{\mathbf{b}}$) are unbiased. In the animal breeding case where, for a single trait, multiple records (measurements from a number of animals) comprise the dependent variable and its descriptors, the calculations involve matrices and vectors and take the form:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z+G^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

Where **X** is a design matrix which relates records (**y**) to fixed effects and **Z** is the design matrix which relates records (**y**) to random effects. **R** represents the variance of the error terms [R = COV(e)] and **G** is the variance of the solutions for random effects [G = VAR(a)]. It is assumed that there is no correlation between solutions for random terms and error terms [i.e. COV(a,e) = COV(e,a) = 0]. Solving this equation for $\hat{\mathbf{a}}$ produces a vector of estimated breeding values (EBV) of dimensions equal to the number of animals with measurements in **y**. This model, termed a best linear unbiased prediction (BLUP), is solved by maximising the correlation between the true breeding value (**a**) and the estimated breeding value ($\hat{\mathbf{a}}$) while minimising prediction error variance.

1.2.1 The relationship matrix

Where pedigree information is available, an animal's performance for a trait can be exploited to provide information about the expected performance (EBVs) of its relatives (assuming the trait is under a degree of genetic control), and to improve the accuracy of EBV estimation. In the GLMM this is accomplished by making the relationship matrix (**A**) a component of the **G** matrix described in the previous model. The relationship matrix, as the name implies, describes the degree to which animals are related. It is a symmetrical matrix (elements below the diagonal are a mirror of those above the diagonal) with dimensions equal to the number of animals in the pedigree (Mrode 2005). The diagonal element of **A** is equal to ($1 + F_i$), where F_i is the inbreeding coefficient of animal i, and describes the probability that two gametes taken at random from animal i will carry identical alleles by descent. The off-diagonal element, $\mathbf{a_{ij}}$, equals the numerator of the coefficient of relationship between animals **i** and **j** (Wright 1922). Henderson (1976) described a recursive method to estimate the components of **A**. A description of how the relationship matrix is included in the generalised linear mixed model equation is provided in the examination of models which contain multiple random terms (below).

1.2.2 Models for traits with multiple random effects

Solving the GLMM equation for traits which have more than one defined source of random variation (a maternal genetic component for example) is relevant to the analyses performed in subsequent experimental chapters, specifically those involving dam permanent environmental effects and the maternal genetic component of weaning weight. Where maternal genetic and dam permanent environmental sources of random variation are included, the model becomes:

$$y = Xb + Za + Wm + Spe + e$$

The maternal genetic component (**m**) is the vector of random (and indirect) maternal genetic effects and **W** is the incidence matrix linking these to **y**. The vector **pe** describes permanent environmental effects associated with each dam, and are related to **y** via the incidence matrix **S**. The mixed model equation to estimate $\hat{\mathbf{b}}$, $\hat{\mathbf{a}}$, $\hat{\mathbf{m}}$ and $\widehat{\mathbf{pe}}$ takes the form:

$$\begin{bmatrix} \hat{b} \\ \hat{a} \\ \hat{m} \\ \widehat{pe} \end{bmatrix} \begin{bmatrix} X'X & X'Z & X'W & X'S \\ Z'X & Z'Z + A^{-1}\alpha_1 & Z'W + A^{-1}\alpha_2 & Z'S \\ W'X & W'Z + A^{-1}\alpha_2 & W'W + A^{-1}\alpha_3 & W'S \\ S'X & S'Z & S'W & S'S + I\alpha_4 \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ W'y \\ S'y \end{bmatrix}$$

with:

$$G=\begin{bmatrix} g_{11} & g_{12} \\ g_{21} & g_{22} \end{bmatrix} \quad G^{-1}=\begin{bmatrix} g^{11} & g^{12} \\ g^{21} & g^{22} \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} \alpha_1 & \alpha_2 \\ \alpha_2 & \alpha_3 \end{bmatrix} = \sigma^2_E \begin{bmatrix} g^{11} & g^{12} \\ g^{21} & g^{22} \end{bmatrix}$$

and: $\alpha_4 = \sigma^2_E / \sigma^2_{PE}$.

1.2.3 Multivariate mixed model equations

Henderson and Quaas (1976) proposed a method by which EBVs for multiple traits could be estimated simultaneously. Where this equation contains multiple dependant variables, it is required that the covariances between traits for each of the fixed and random terms in the model be known and included in the model. The example below is for a bivariate (two trait) analysis for traits $\mathbf{y_1}$ and $\mathbf{y_2}$ (Mrode 2005), with models taking the form:

$$y_1 = X_1b_1 + Z_1a_1 + e_1 \text{ and } y_2 = X_2b_2 + Z_2a_2 + e_2$$

It is assumed that:

$$\mathrm{Var}\begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 \\ g_{21}A & g_{22}A & 0 & 0 \\ 0 & 0 & r_{11} & r_{12} \\ 0 & 0 & r_{21} & r_{22} \end{bmatrix}$$

Where **A** is the relationship matrix, $\mathbf{g_{11}}$, $\mathbf{g_{12}}$, $\mathbf{g_{21}}$ and $\mathbf{g_{22}}$ are the genetic variance and covariance components of a matrix **G** and $\mathbf{r_{11}}$, $\mathbf{r_{12}}$, $\mathbf{r_{21}}$ and $\mathbf{r_{22}}$ are the residual variance and covariance components of a matrix **R**. The mixed model equation then becomes:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z' \\ Z'R^{-1}X & Z'R^{-1}Z+[A \otimes G]^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

$[A \otimes G_{11}]^{-1}$ is the Kornecker product of A^{-1} and G^{-1}, which contains elements for $[A \otimes G_{11}]_{ij}^{-1}$ which equal $[(A)_{ij}\ G]^{-1}$. If A^{-1} is an *m* x *n* matrix and G^{-1} is a *p* x *q*, then matrix $[A \otimes G_{11}]^{-1}$ is a *mp* * *nq* matrix. The complete MME for a bivariate analysis is then:

$$\begin{bmatrix} \hat{b}_1 \\ \hat{b}_2 \\ \hat{a}_1 \\ \hat{a}_2 \end{bmatrix} = \begin{bmatrix} X'_1R^{11}X_1 & X'_1R^{12}X_2 & X'_1R^{11}Z_1 & X'_1R^{12}Z_2 \\ X'_2R^{12}X_1 & X'_2R^{22}X_2 & X'_2R^{12}Z_1 & X'_2R^{22}Z_2 \\ Z'_1R^{11}X_1 & Z'_1R^{12}X_2 & Z'_1R^{11}Z_1+A^{-1}g^{11} & Z'_1R^{12}Z_2+A^{-1}g^{12} \\ Z'_2R^{21}X_1 & Z'_2R^{22}X_2 & Z'_2R^{21}Z_1+A^{-1}g^{21} & Z'_2R^{22}Z_2+A^{-1}g^{22} \end{bmatrix}^{-1} \begin{bmatrix} X'_1R^{11}y_1 & X'_2R^{12}y_2 \\ X'_2R^{21}y_1 & X'_2R^{22}y_2 \\ Z'_1R^{11}y_1 & Z'_1R^{12}y_2 \\ Z'_2R^{21}y_1 & Z'_2R^{22}y_2 \end{bmatrix}$$

As for analyses of single traits, $\hat{\mathbf{a}}_1$ and $\hat{\mathbf{a}}_2$ are vectors of individual estimated breeding values for trait 1 and 2 of dimensions equal to the number of animals in the pedigree, multiplied by the number of independent variables, estimated with the information provided by the relationship matrix, and that from the genetic variances for and covariances between the two traits. The terms $\hat{\mathbf{b}}_1$ and $\hat{\mathbf{b}}_2$ are solutions for fixed effects. Note that the above example assumes that all terms in the model significantly affect all traits (i.e. the design matrices **X** and **Z** are the same for each trait), and that there are no missing values (**y**) for any trait. Current analytical methods can accommodate situations where one or both of these assumptions are not the case (Mrode 2005).

Multivariate BLUP, where covariances are included in the model, allow EBVs to be estimated with greater accuracy. The magnitude of this increase is a function of the absolute difference between the genetic and residual correlations between traits (Mrode 2005). Where heritability, and genetic and environmental variation between two traits are equal, EBVs from a multivariate analysis will be estimated with similar accuracy to those from a univariate model. EBVs for lowly heritable traits, however, are estimated more accurately in a multivariate analysis with more highly heritable traits, assuming there is a genetic covariance between the two. Thompson and Meyer (1986) also showed that the increased accuracy of EBV estimation from a multivariate analysis is contributed to by the residual covariance between traits. Importantly, multivariate analyses help to remove the estimation biases arising when a subset of animals is evaluated for a trait based on their performance for a second trait, if both traits are included in the analysis. The reduction of estimation bias and the opportunity to increase breeding value estimation accuracy by including estimated covariances in a multi-trait genetic evaluation was a key motivation for the research undertaken for this thesis.

1.2.4 Genetic correlations

The genetic covariances ($\mathbf{g_{12}}$ and $\mathbf{g_{22}}$ above) exploited in the BLUP estimation of EBVs provide the basis for the calculation of genetic correlations, which was a central component of the research undertaken for this thesis. Covariances are estimated as a function of the sum of the deviances of individual records from group means for two traits (**x** and **y**) and the number of observations, such that for **N** individuals:

$$COV_{xy} = (x_1 - \bar{x})(y_1 - \bar{y}) + (x_2 - \bar{x})(y_2 - \bar{y}) \ldots\ldots + (x_N - \bar{x})(y_N - \bar{y}) \;/\; N$$

Genetic correlations are the ratio of the covariance between the two traits (**x** and **y**) and the product of the genetic standard deviation (or square root of the genetic variance) for the traits (Falconer and Mackay 1996):

$$r_g = COV_{xy} / \sqrt{(\sigma^2_{A(x)})(\sigma^2_{A(y)})}$$

Using the same theory, phenotypic and environmental variances, covariances and correlations (collectively termed variance components) can also be estimated.

1.2.5 Breeding values estimated by BLUP

This section has provided an overview of the methods employed to exploit measurements of multiple traits from an individual and its relatives to estimate breeding values. It was shown that by comparing the performance of related individuals in different environments, herds or contemporary groups over different years and seasons, these effects could be quantified, allowing the partitioning of genetic variation. Where multiple traits are assessed, the degree to which variation in these is related can be established, and these correlations exploited to improve the accuracy of breeding value estimation. By comparing animals based on their deviation from contemporary group means, and with an understanding of relationships via a pedigree, breeding values estimated by BLUP can account for non-random matings and selection which would otherwise lead to biased breeding value estimates. As related animals are evaluated across different years, systematic variation over time can be accounted for. This allows breeding values to be compared directly, and rates of genetic gain to be estimated and used to assess the progress generated in breeding programs. A key assumption in estimating breeding values by BLUP is that genetic parameters for the trait or combination of traits under evaluation are known.

1.3 ESTIMATING VARIANCE COMPONENTS BY RESTRICTED MAXIMUM LIKELIHOOD (REML)

In the multivariate BLUP analysis described above to estimate breeding values, the assumption is that variances and covariances of traits are known. In modern genetic evaluation, the estimation of these terms can also be undertaken within the framework of the mixed model equation. The restricted maximum likelihood (REML) method was initially proposed in animal breeding by Paterson and Thompson (1971). The method makes use of a matrix of prediction error variance (PEV) for random terms ($a - \hat{a}$). In simple terms, REML estimates variance components based on residuals calculated after fitting, by ordinary least squares methods, just the fixed effects components of the mixed model equation (Searle *et al*. 1992). As described by Meyer (1989), “REML operates on the likelihood of linear functions of the vector of observations with expectations zero, so-called error contrasts, or equivalently, on the part of the likelihood (of the vector of observations) which is independent of fixed effects”. This method takes into account the loss of degrees of freedom associated with the initial fitting of fixed effects. The log likelihood (**logL**) equation takes the form:

$$\log L = -\tfrac{1}{2}\,[K + \log|V| + \log|X^{*\prime}V^{-1}X^{*}| + (y - X\hat{b})\, V^{-1}\,(y - X\hat{b})]$$

With the assumptions that **y** has a multivariate normal distribution with mean **Xb** and variance **V** (i.e. Y ~ N(Xb, V)), and where **X*** is a sub-matrix of **X**. The asterisk superscript here denotes the ‘complex conjugate transpose’ of elements of the matrix **X**. **X*** is estimated from **X** by taking the complex conjugate of each element of the transpose of **X**. This is a complex process, the details of which are beyond the scope of this introduction. By multiplying both sides of the equation by -2:

$$-2 \text{ Log } L = K + \log|R| + \log|G| + \log|C| + y'Py$$

With the assumptions that **K** is a constant, **C** is a matrix of coefficients from the MME, and where **P** is a matrix such that:

$$P = V^{-1} - V^{-1}X(X'V^{-1}X) - X'V^{-1}$$

$$= V^{-1} - V^{-1}X^{*}(X^{*\prime}V^{-1}X^{*})^{-1}\, X^{*\prime}V^{-1}$$

Note that in the initial equation logL was positive, but by multiplying both sides of the equation by -2 the term becomes negative, making the objective in fitting this model to maximise this negative value (hence the 'maximum" in REML).

There are a number of iterative techniques to solve these equations to maximise -2LogL. Meyer (1989) concluded that the Simplex procedure of Nedler and Mead (1965) provided a simple and robust means of minimising the LogL, and applied this algorithm in developing the "DFReml" and "WOMBAT" software packages. Of relevance to the analyses which are described in the experimental chapters of this thesis, Gilmore *et al*. (1995) proposed the application of an Average Information (AI) algorithm due to its ability to simultaneously estimate large numbers of variance components, which was subsequently applied in the "ASReml" software package.

1.4 BREEDING OBJECTIVES, SELECTION CRITERIA AND SELECTION INDICES

Practical animal breeders will define breeding objectives targeting more than one aspect of productivity, demanding change in multiple traits to meet those objectives (Hazel 1943). For beef cattle breeders it is generally accepted that the breeding objective is based on economic considerations, with maximising profit the most obvious aim (Harris 1970). Gibson (2005) observed that the goal of maximising profit was complicated by the question of whether profit was defined at the level of the producer, processor or retailer, or across all of these components of the modern beef industry. Profitability is a function of the inputs and outputs associated with a breeding enterprise and both of these need to be considered in the breeding objective (Barwick 1992). The process of defining breeding objectives then, becomes one of identifying traits for which a unit change will have a desirable impact on the selected definition of profitability, and prioritising these to maximise returns. The marginal change in profit for a unit change in a trait, assuming other traits are held constant, is termed its economic value (**V**). Assuming:

$$P = (1/D_i)\ (R_i - C_i)\ X_i - K.$$

Where $\mathbf{R_i}$ and $\mathbf{C_i}$ are the returns and costs associated with a unit change in trait $\mathbf{X_i}$, $\mathbf{D_i}$ is the rate at which a unit change is achieved (over a defined time period), and **K** is fixed costs. **P** is evaluated at estimated mean values for all traits and again ($\widehat{\mathbf{P}}$) with the trait in question increased by one unit. The economic value for a trait is then estimated as:

$$V = P - \widehat{P}.$$

A traits economic value will inform the development of breeding objectives and plays a central role in the formulation of profit based selection indices.

1.4.1 Selection indices using multi-trait derived EBVs

The information available from a modern multi-trait genetic evaluation can be exploited to estimate selection indices. Lin (1990) demonstrated that predicting breeding values using BLUP, based on variance components estimated in a multi-trait genetic evaluation was computationally equivalent to the calculation of selection indices for multiple traits. Schneeberger *et al*. (1992) observed that the method applied by Lin (1990) did not allow for the effect of variation in EBV accuracy when animal models are fitted to large and unbalanced data sets, and proposed an improved technique. From the previous discussion of estimating variance components and breeding values from multiple traits using generalised mixed model equations, the coefficient matrices can be estimated:

$$\begin{bmatrix} X'R^{-1}X & XR^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z+[A \otimes G]^{-1} \end{bmatrix}^{-} = \begin{bmatrix} C_{11} & C_{12} \\ C_{21} & C_{22} \end{bmatrix}$$

Henderson (1984) showed that:

$$\mathrm{Var}\,(\hat{a}) \;=\; [A \otimes G_{11}] - C_{22} \text{ and}$$

$$\mathrm{Cov}\,(\hat{a}, a') = [A \otimes G_{11}] - C_{22} = \mathrm{Var}\,(\hat{a})$$

The term $\mathbf{v'g_i}$ is the breeding objective or the aggregate measure of genetic merit (the aggregate genotype) for animal **i**, where **v** is the vector of economic values for traits in the objective and $\mathbf{g_i}$ is the vector of breeding values for animal **i** for these traits, and $\hat{\mathbf{g}}_{\mathbf{i}}$ is the vector of predicted breeding values (EBVs) for the same traits. The vector of breeding values for all animals (**g**) can be predicted (Schneeberger *et al*. 1992) by the expanded mixed model equation:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z & 0 \\ Z'R^{-1}X & Z'R^{-1}Z + [A \otimes G_{11}]^{-1} & [A \otimes G_{12}]^{-1} \\ 0 & [A \otimes G_{21}]^{-1} & [A \otimes G_{22}]^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \\ \hat{g} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \\ 0 \end{bmatrix}$$

Schneeberger *et al*. (1992) showed that, assuming the vector of index weights (**b**) is the same for all animals:

$$b = G_{11}^{-1}\, G_{12}\, v.$$

This assumes that EBVs are available for traits identified as selection criteria, and that economic values (**v**) for traits in the objective have been estimated. Also required are estimates of relevant genetic variances and covariances for the selected criteria and traits in the breeding objective

It is the need to understand, and estimate the genetic variances and, in particular, covariances associated with traits in the breeding objective, traits identified as selection criteria to represent these, and between traits in these categories, which represented a primary motivation for the research reported in this thesis.

1.5 BREEDING OBJECTIVES AND SELECTION CRITERIA FOR TROPICALLY ADAPTED BEEF CATTLE IN NORTHERN AUSTRALIA

Australia's national, breed specific genetic evaluation for beef cattle (BREEDPLAN: Graser *et al*. 1987, Graser *et al*. 2005) uses multiple trait BLUP methods to estimate breeding values for economically important traits. Using the methods described above, EBVs are calculated based on variance components estimated by REML analyses. Traits currently included in the genetic evaluation for tropically adapted breeds are descriptors of growth, carcass composition, male fertility, and female reproductive performance, with tenderness and temperament and feed efficiency reported as "trial" EBVs for some breeds.

Variance components and estimated breeding values from BREEDPLAN are exploited in the formulation of selection indices, using economic values assigned to BREEDPLAN traits based on breed, market and production system specific modelling of costs and returns. The BREEDOBJECT software package (Barwick and Yeates 1997, Barwick *et al*. 2001, Barwick and Henzell 2005) estimates selection indices which describe genetic merit, on a dollar return per cow joined basis, for common production system and market combinations for tropically adapted breed. The following discussion of breeding objectives is presented in 2 sections. The first examines breeding objectives and the associated selection criteria identified in formulating selection indices for tropical beef breeds (termed industry breeding objectives). The second section examines traits which are not analysed in the standard BREEDPLAN evaluation, or which are currently included on a trial basis, but which have been identified as of economic importance to the tropical beef breeding, finishing, processing or retailing sectors (presented as future breeding objectives). These traits were all measured in the Beef CRCs Northern Breeding Project (described in section 1.6) and genetic evaluation of these data represent an important part of the research reported in this thesis.

1.5.1 Current industry breeding objectives

Representatives of the Brahman, Santa Gertrudis and Belmont Red breeds in Australia (Anonymous 2011, Anonymous 2010*b* and Anonymous 2010*a* respectively), in co-operation with beef geneticists and economic modellers, have developed selection indices which reflect breeding objectives agreed to at the breed level. The associated selection criteria were identified based on their relationship with these breeding objectives and economic values estimated based on breed, production system and market specific analysis of costs and returns (as described in section 1.4). Each of these breeds has developed 2 indexes which describe production, in a self replacing herd, with steers finished on pasture to meet heavy (325 to 370kg: the “Jap Ox” index for Brahmans and “Export” indices for Santa Gertrudis and Belmont Reds) or lighter (240 to 280kg: the “Domestic” indices for Santa Gertrudis and Belmont Reds) carcass weight specifications.

Figure 1 (Anonymous 2011) presents a graphical example of breeding objectives, and weightings applied to these, for the Brahman “Jap Ox” index. It is clear that female reproductive performance, defined here as cow weaning rate, is seen as the single most important driver of profitability among the listed breeding objectives, with a 47% weighting. This is consistent with the results of Johnston *et al*. (2013*a*) which reported weaning rate in Brahman cows, managed under conditions representative of those in northern Australia’s beef production environments, to be only 65% in females evaluated through up to 6 matings.

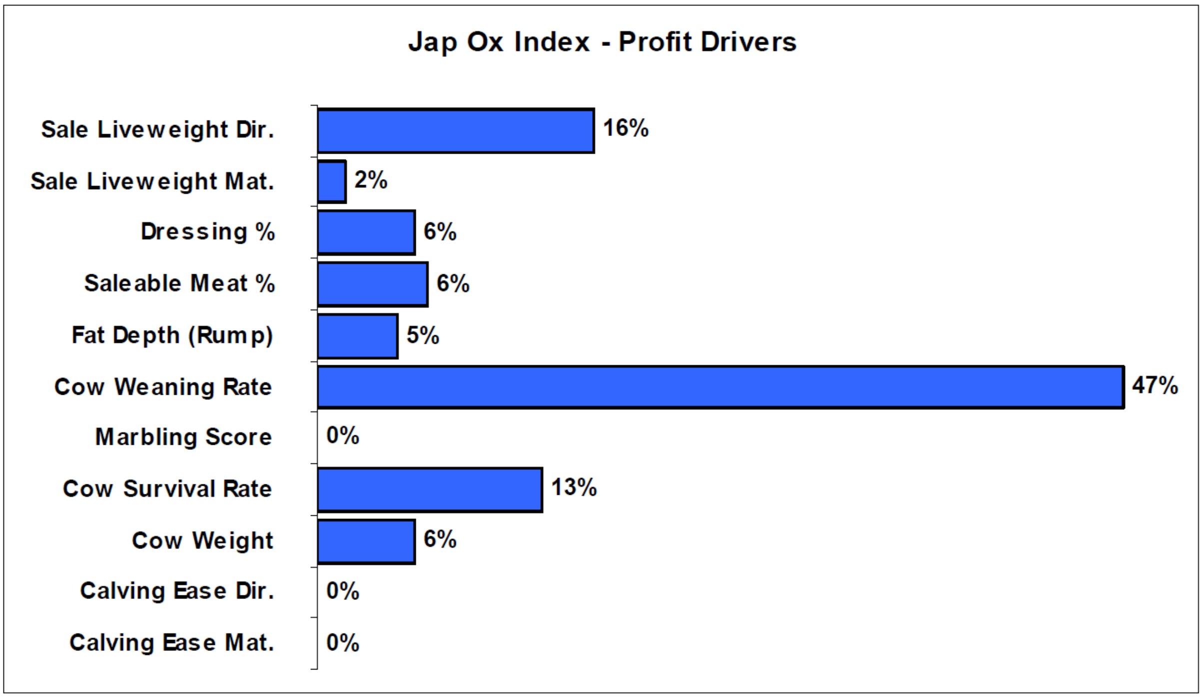

Figure 1.1. Breeding objectives for the Brahman "Jap Ox" selection index (Anonymous 2011)

These trends are maintained in the breeding objectives specified for other breed and market specific indices for tropical breeds, with cow weaning rate receiving weighting of 23 to 47% (Anonymous 2010*a*, Anonymous 2010*b* Anonymous 2011).

For the Brahman "Jap Ox" index, breeding objectives relating to the weight and carcass composition of sale stock make up the second most heavily weighted category, comprising direct and maternal sale weight, dressing percentage, saleable meat yield and P8 fat depth, with a combined total weighting of 35%. Similarly, for the remaining Brahman, Santa Gertrudis and Belmont Red indices, combined sale weight and carcass composition traits received a weighting of 31 to 60% (Anonymous 2010*a*, Anonymous 2010*b* Anonymous 2011).

Figure 2 provides an example, again for the Brahmans "Jap Ox" index, of the BREEDPLAN estimated breeding values identified as best representing the breeding objectives described above. Weightings were estimated based on economic values derived using the methods described in section 1.4.5. The emphasis placed on female reproduction in the breeding objective is reflected in the high negative weighting placed on the days to calving EBV (-0.40%), and low positive weighting on scrotal circumference (+3%). The remaining indices for tropical breeds also placed moderate to high emphasis on days to calving, with weightings of 15% to 38% (Anonymous 2010*a*, Anonymous 2010*b* Anonymous 2011).

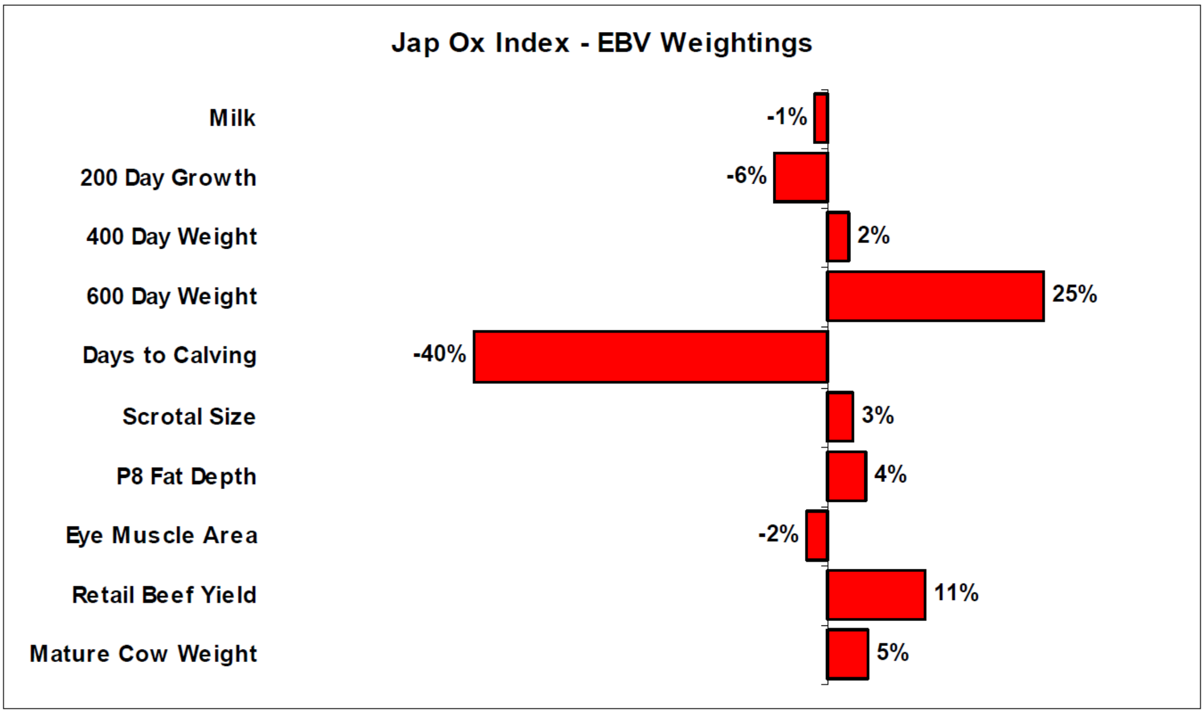

Figure 1.2. Weightings applied to BREEDPLAN EBVs for the Brahman “Jap Ox” selection index (Anonymous 2011)

While the current goals of northern Australia’s beef producers are made clear from these breeding objectives and the associated selection criteria, Barwick and Henzell (2005) observed that “An adequate knowledge of the required genetic parameters, and particularly of genetic correlations, is often a limitation in the derivation of appropriate selection indices. This applies especially to certain classes of genetic parameters, for example genetic correlations between fitness or fertility and carcass traits". The potential for estimates of genetic relationships between economically important traits to improve the accuracy of selection index estimation represents a primary motivation for the research reported in this thesis

1.5.2 Potential new breeding objectives and selection criteria

Research conducted as part of the Beef CRC Northern Breeding Project measured a number of traits not currently analysed in the national genetic evaluation for tropical breeds. These were included in the experiment because they described traits of economic importance (e.g. residual feed intake, tenderness and female reproductive performance) or were evaluated as potential genetic indicator traits for these (e.g. flight time, age at puberty and cow growth and body composition). These are described briefly below, with the estimation of genetic parameters for carcass and meat quality and cow growth and body composition traits, and the genetic relationships of these with other traits of economic importance, representing an important component of the work presented in the experimental chapters of this thesis.

1.5.2.1 Residual feed intake

Residual feed intake (RFI), as initially proposed by Koch *et al*. (1963), is a measure of feed efficiency, calculated as the difference between actual feed intake and expected feed requirement for maintenance and growth. In beef cattle (Arthur *et al*. 2001, Barwick *et al*. 2009*b*) the trait has received attention as a descriptor of feed efficiency, which is free of the association seen between feed conversion ratio (feed intake divided by weight gain) and growth. Economic analysis (Archer and Barwick 1999) demonstrated that measurement, genetic evaluation of, and selection to improve the trait could be cost effective dependant primarily on the proportion of animals which were fed a high energy, high cost ration, and the duration of this feeding.

1.5.2.2 Tenderness and meat quality traits

Tenderness, juiciness and flavor are the most important traits effecting consumer satisfaction with beef products, with tenderness contributing 71% of consumer taste panel evaluation of meat quality (Egan *et al*. 2001). Thompson (2002), in discussing critical control points associated with the management of beef eating quality, identified *Bos indicus* content as a significant contributor to lower consumer evaluation of tenderness, and *Bos indicus* content was subsequently included as a discounting factor in the Meat Standards Australia (MSA) cuts based meat quality grading system (Watson *et al*. 2008). Objectively measured shear force, the force (in kilograms) required to draw a standard blade through a standard cooked meat sample (Perry *et al*. 2001*b*), explained 55% of the variation in taste panel tenderness score (Perry *et al*. 2001*a*).

1.5.2.3 Flight time

Temperament of beef cattle is important to all sectors of the industry which involve interaction with live cattle, and poor temperament has been linked to higher incidence of dark cutting (a condition associated with low post-slaughter glycogen levels, high ultimate pH and dark coloured meat), which reduces the value of beef carcasses (Voisinet *et al*. 1997). Flight time was initially proposed by Burrow *et al*. (1988) as an objective measure of temperament in beef cattle, and Burrow and Corbet (2000), Kadel *et al*. (2006) and Barwick *et al*. (2009b) demonstrated that variation for the trait had a genetic basis in tropically adapted beef cattle. Kadel *et al*. (2006) also reported that flight time was significantly genetically related to tenderness (measured as shear force) in tropically adapted cattle.

1.5.2.4 Age at puberty and lactation anoestrus interval

As discussed above, female reproduction is among the highest priority breeding objective for breeders of tropically adapted beef cattle in northern Australia. In Australia's national genetic evaluation program, female reproductive performance is currently evaluated based on repeated records of days to calving (days from the start of the mating period to birth of the resulting calf). Estimates of heritability for days to calving are consistently low ($h^2 < 0.2$) for tropically adapted breeds (Meyer *et al*. 1990, Forni and Albuquerque 2005, Johnston *et al*. 2013*a*). In dairy (Petersson *et al.* 2007; Bamber *et al.* 2009; Wall *et al.* 2003) and beef (MacNeil *et al*. 1984, MacNeil and Newman 1994, Mialon *et al.* 2000, Morris *et al*. 2000, Johnston *et al*. 2009, Johnston *et al*. 2013*a*) breeds, traits describing underlying biological mechanisms which contribute to variation in days to calving (age at puberty and lactation anoestrus interval) have been shown to be more heritable and may offer a means to increase the potential rate of genetic gain for female reproduction traits. Additionally, Warnick (1965) and Wiltbank *et al*. (1969) observed genotype differences for age at puberty in beef cattle, reporting that *Bos indicus* breeds tended to reach puberty 6 – 12 months later than was the case for *Bos taurus*.

1.5.2.5 Tropical adaptation traits

The adaptations which allow animals to survive, grow and reproduce in harsh tropical, sub-tropical and semi-arid environments are fundamental to beef production in northern Australia. It is, therefore, critical that any selection to improve productivity is carried out with an understanding of possible consequences for tropical adaptation traits. However, studies defining quantitative traits which describe tropical adaptation are not common in the literature. An exception to this is coat traits, which have received some evaluation as descriptors of adaptation to thermal stressors. Turner and Schleger (1960), Turner (1964) and the later review of Hansen (2004) all discussed the importance of coat traits to thermoregulation and recognised coat sleekness as a key adaptation to tropical environments. Schleger (1962) examined coat colour (on a lightness to darkness scale within red-coated animals) and reported that the trait was heritable (h^2 = 0.36 to 0.62) in animals of different ages and under varying environmental conditions, and that, significant relationships existed with descriptors of performance. Finch *et al*. (1984) showed that lighter (and sleeker) coats reflected a greater proportion of solar radiation, and played a role in thermoregulation in beef cattle. Prayaga *et al*. (2009) defined tropical adaptation traits which described faecal worm egg count, coat length score, coat colour score, navel score, rectal temperature and buffalo fly lesion score, and reported consistently moderate heritabilities for these (h^2= 0.15 to 0.62) in the Brahman and Tropical Composite females involved in the Beef CRC Northern Breeding Project. This study also reported moderate genetic correlations of buffalo fly lesion score and coat length score with age at puberty in Brahman females (r_g = 0.48 and 0.73 respectively).

1.5.2.6 Growth and body composition in lactating first calf cows

Barwick *et al*. (2009a) examined the genetic parameters for tropically adapted female growth and body composition traits prior to first mating, at 18 and 24 months of age, and established that these were heritable, at levels consistent with corresponding measurements collected in steers prior to slaughter. Pregnancy and lactation have been shown to impact female growth and body composition traits in dairy breeds (Kadarmideen 2004, Pryce *et al*. 2001, Berry *et al*. 2002 Wall *et al*. 2003, Veerkamp *et al*.2001). The degree to which body reserves are mobilized in tropically adapted beef females during pregnancy and lactation is not well understood, however, and the impact of these changes in weight and body composition on female reproductive performance have yet to be documented.

1.6 THE CO-OPERATIVE RESEARCH CENTRE FOR BEEF GENETIC TECHNOLOGIES NORTHERN BREEDING PROJECT

The data analysed for the experimental chapters of this thesis were the product of a large progeny test experiment designed to estimate genetics parameters for economically important traits in

Australia's tropically adapted genotypes of beef cattle. Among the range of traits evaluated for this study were the steer growth, feed intake, carcass composition and meat quality, and female tropical adaptation and reproductive performance traits described above as current and future breeding objectives. The genotypes represented were Brahman and Tropical Composites. Tropical Composites were bred to comprise 50% tropically adapted genetics from tropically adapted *Bos taurus* genotypes (predominantly African N'Dama genetics via the Afrikaner component of the Belmont Red breed) or *Bos indicus* genotypes.

The experiment was designed to produce 40 – 60 progeny for 100 (50 Brahman and 50 Tropical Composite) sires (Burrow *et al*. 2003). Sires were selected to maximize genetic linkage to other experiments and, in the case of Brahmans, to data in the breed's national genetic evaluation. Animals were bred on 8 co-operating properties, selected to be representative of the environmental conditions which prevail in Australia's northern beef production regions. Matings to produce experimental animals took place annually from 1999/2000 to 2002/2003 by a combination of natural mating and artificial insemination (AI). Allocation of natural mating and AI sires was made for each year and breeding location to insure genetic linkage across these. Barwick *et al*. (2009*b*) provided a summary of sire progeny numbers by year and location for steers, and Barwick *et al*. (2009*a*) provided similar information for heifer progeny.

Details of the experimental design and breeding program employed to generate animals for this study were presented by Burrow *et al*. (2003). Steer management and live animal trait definitions and measurement protocols were detailed by Barwick *et al*. (2009*b*). Heifer management, trait definitions and measurement protocols up to their first annual mating were detailed by Barwick *et al*. (2009*a*). Heifer puberty trait definitions and measurement protocols were described by Johnston *et al*. (2009), and traits evaluated as descriptors of female reproductive performance through 6 matings were described by Johnston *et al*. (2013*a*). Prayaga *et al*. (2009) defined the traits evaluated as descriptors of tropical adaptation in the females initially described by Barwick *et al*. (2009*b*), and Corbet *et al*. (2013) provided details of growth and body composition traits measured in the bull progeny of the females described above. Traits evaluated as descriptors of steer carcass and meat quality and female growth and body composition at calving, following their first mating and at Mating 2, are defined, and modeling and analysis procedures described in Chapter 2 and 3 of this thesis respectively.

1.7 CONCLUSIONS

Modern beef cattle genetic evaluation uses a multi-trait BLUP model to estimate breeding values, which relies on genetic parameters determined in REML analyses. These are calculated based on phenotypes collected from animals of documented management history, and an understanding of the relationship between individuals. As a component of Australia's national beef genetic evaluation, selection indices are calculated which rank animals for genetic merit based on economically based breed, market and production system specific breeding objectives. Accurate estimates of genetic relationships between traits will improve the accuracy of breeding value and selection index estimation.

In formulating selection indices for tropically adapted breeds, steer carcass weight and composition and female reproductive performance have been given the highest priority in the breeding objective. The current lack of estimates for the genetic relationships between these aspects of herd productivity is a limiting factor in the estimation of selection indices and was a key motivation for the research undertaken for this thesis. Additionally, traits describing steer residual feed intake, meat quality, temperament, female growth and body composition and direct measures of the biological mechanisms underlying female reproductive performance have been identified as of potential economic importance. These traits were measured as part of a large progeny test experiment involving cattle of two tropically adapted beef genotypes (Brahman and Tropical Composite). The experimental chapters of this thesis are presented as a series of four published (or accepted for publication) papers which, by analysing data from the Beef CRC Northern Breeding Project, had the broad aim to identify opportunities for breeders of tropically adapted beef cattle to improve whole herd productivity by selection. The aims of research reported in each paper and a description of the relationships between experimental chapters are presented below.

1.8 RELATIONSHIP BETWEEN EXPERIMENTAL CHAPTERS AND AIMS OF THESIS

The broad aim of this thesis was to identify opportunities for breeders of tropically adapted beef cattle to improve whole herd productivity by selection. This required that economically important male and female traits be defined and measured in animals of known management history and pedigree. Models were developed to account for fixed and random sources of variation for the steer carcass and meat quality, and lactating female body composition traits evaluated, and additive variances estimated for these. To address the key aims of this thesis, genetic correlations between heritable, economically important male and female traits were estimated. Genetic relationships of difficult to measure steer carcass and meat quality and cow body composition traits with more easily assessed and earlier measures in males and females were also estimated to identify possible genetic indicators traits. The results of genetic analysis reported in the papers described below will provide breeders of tropically adapted beef cattle in northern Australia with new opportunities to apply selection to economically important traits. The genetic relationships estimated will provide a new basis for the determination of multi-trait breeding objectives and can increase the accuracy of breeding value and selection index estimation.

The first experimental chapter (Chapter 2) examines the genetics of steer carcass and meat quality traits to establish whether, in tropically adapted beef genotypes, variation in these has a genetic basis. This chapter also examines how carcass and meat quality traits are genetically associated with live animal measurements of growth and body composition in the steers evaluated for this study and their half-sib sisters, and with steer feed intake and efficiency. The aims of Chapter 2 were, in Brahman and Tropical Composite steers and heifers, to:

- Define steer carcass and meat quality traits and determine the degree to which variation in these was genetic.
- Identify early in life steer and heifer measurements which could act as genetic indicators for steer carcass and meat quality traits.
- Determine whether selection to improve steer carcass and meat quality traits will have significant genetic consequences for residual feed intake and steer and heifer growth and body composition.

Estimates of the genetic basis for variation in female growth and body composition traits in lactating first calf cows have not previously been reported in the literature for tropically adapted genotypes. Chapter 3 examines the genetics of these traits in lactating first calf cows and the impact on these of maternal weaning weight, an estimate of the genetic potential for milk production. The aims of Chapter 3 were, in Brahman and Tropical Composite cows, to:

- Define growth and body composition traits in lactating first calf cows and determine the degree to which variation for these was genetic.
- Quantify the change in growth and body composition traits during first lactation and determine the degree to which variation for these was genetic.

- Estimate the maternal genetic component of weaning weight and its genetic association with female growth and body composition traits described above.

Chapter 4 examines the genetic relationship of female growth and body composition as heifers at 18 months of age (examined in Chapter 2) and during first lactation (Chapter 3), with female reproductive performance to determine whether selection which impacts lactating first calf cow growth and body composition may have genetic consequences for female reproduction. In Chapter 3, maternal weaning weight was shown to significantly impact growth and body composition traits in lactating first calf cows. Chapter 4 also examines the genetic relationships of maternal weaning weight with female reproductive performance in lactating first calf Brahman and Tropical Composite cows. Chapter 4 aimed, in Brahman and Tropical Composite females, to:

- Determine whether selection which impacts growth and body composition in lactating first calf cows may have genetic implications for female reproductive performance
- Determine the genetic association of maternal weaning weight with female reproductive performance.
- Identify possible genetic indicator traits for female reproductive performance from the cow growth and body composition traits (defined in chapter 3) and corresponding measures evaluated in these animals earlier in life.

Estimates of the genetic relationships of steer growth, residual feed intake, carcass composition and meat quality traits with female reproductive performance can be exploited in the determination of multi-trait breeding objectives for tropically adapted breeds and in their estimation of breeding values and selection indices. To date, estimates of these relationships have not been available for the tropically adapted genotypes examined for this study. Chapter 5 examines the genetic relationships of steer growth, residual feed intake, carcass composition and meat quality traits (introduced in chapter 2), with female reproductive performance. This chapter addresses the key question of whether selection can be undertaken to improve these simultaneously, or whether genetic antagonisms exist which may preclude this. As measurements in young bulls represent the dominant source of growth and body composition records submitted to Australia's national genetic evaluation for tropically adapted breeds, traits consistent with these, measured in the bull progeny of the females evaluated for reproductive performance (at 15 months of age), are included in the analyses performed for this study. The aims of Chapter 5 were, in Brahmans and Tropical Composites, to:

- Determine whether selection could be undertaken to simultaneously improve steer growth, body composition, residual feed intake, carcass and meat quality traits and female reproduction in tropically adapted genotypes of beef cattle.
- Identify any significant genetic antagonisms between economically important steer traits and female reproduction.

6 CONCLUSIONS

The beef production regions of northern Australia are characterised by harsh environments and extensive production systems, and by the tropically adapted beef cattle genotypes which have been introduced to cope with these conditions. Steer growth and carcass composition directly influence productivity in these systems and research has shown that traits describing feed efficiency and meat quality can also impact returns to sectors of north Australia's beef industry. Studies have also shown that low female reproductive performance in tropically adapted genotypes is a limitation to the productivity of beef breeding enterprises in these environments and, via its impact on selection intensity, to potential genetic gains. The opportunities for management intervention to effect change in these traits, under northern Australian conditions, are limited, making the prospect of improving economically important traits by selection appealing. For genetic improvement of these traits to be successful, however, it requires that the genetic basis for variation in these traits be understood and that genetic relationships between them be estimated.

The research reported in this thesis analysed data from a large progeny test experiment which evaluated male and female aspects of productivity for Australia's northern beef industry. This study aimed to improve understanding of the genetic basis, and consequences of selection, for growth, body composition, meat quality and female reproduction traits in tropically adapted beef cattle. Genetic parameters estimated in this study can be incorporated into the BREEDPLAN evaluation for tropically adapted breeds to improve the accuracy of breeding value and selection index estimation. This will provide breeders of tropically adapted beef cattle with a means of increasing rates of genetic gain for economically important traits.

6.1 Opportunities for selection to improve steer carcass and meat quality traits in tropically adapted beef cattle and implications of this for steer and heifer body composition, and steer residual feed intake

The results presented in Chapter 2 confirmed that if Brahman and Tropical Composite breeders included tenderness in their genetic evaluation, and gave the trait priority as a breeding objective, it could be improved by selection. If genetic progress is to be achieved for the trait, however, it will need to be measured directly, as there are limited opportunities to exploit earlier in life measures as genetic indicators for both genotypes. The difficulty and expense associated with direct measurement of meat quality traits, however, mean that this may be unlikely. For this reason, studies examining the potential of genomic technologies to provide information to beef breeders have placed a high priority on meat quality traits (Hocquette *et al*. 2007, Fortes *et al*. 2009). BREEDPLAN is equipped to include genomic data in the multi-trait evaluation for tropical breeds and this may present an opportunity for breeders to apply selection pressure to tenderness. Temperament is an important trait in tropical beef production systems, and previous studies (Kadel *et al*. 2006) have estimated favourable genetic relationships with tenderness in tropically adapted breeds. From the results of this thesis, it can only be concluded that if breeders select to improve temperament there would be no unfavourable impact on economically important carcass or meat quality traits.

Results presented in Chapter 2 confirmed that selection can be undertaken to improve the economically important steer carcass weight and composition traits currently included in the BREEDPLAN analysis for tropical breeds. Additionally, genetic relationships between live and carcass measures of growth and body composition supported the current BREEDPLAN strategy to exploit live measures as genetic indicators of carcass traits. For Brahmans the weaker genetic relationships of live measures collected in heifers and bulls with steer carcass traits, compared to those observed in

Tropical Composites, suggested the possibility of significant genotype by environment, or genotype by sex, interactions. For both genotypes, including direct measures of carcass traits in their genetic evaluation would allow breeding values to be estimated more accurately and provide a means of increasing the rate of genetic gain for these traits, though this improvement would be greater for Brahmans than for Tropical Composites.

Feed efficiency has been shown to impact beef production profitability, particularly for systems which include feedlot finishing (Archer and Barwick 1999). While the trait is not currently a component of the BREEDPLAN evaluation for tropically adapted breeds, the results of an associated study (Barwick *et al*. 2009*b*) showed that it could be improved by selection in these genotypes. Genetic relationships reported in Chapter 2 suggest that selection to reduce carcass fatness and increase eye muscle area and retail beef yield may produce favourable correlated responses in residual feed intake. Conversely, if residual feed intake were measured, included in the genetic evaluation for tropical breeds and added to the breeding objective, there would be correlated responses in carcass fatness, eye muscle and retail beef yield.

6.2 Genetic relationships of steer growth, residual feed intake, carcass composition and meat quality with female reproduction

Steer carcass weight and composition and female reproduction are key drivers of productivity for beef producers in northern Australia. While BREEDPLAN currently estimates breeding values for traits which describe both of these components of herd productivity for tropical breeds, estimates of the genetic relationships between them have not previously been documented. Genetic correlations estimated in this thesis suggest that if selection pressure is applied to increasing steer carcass weight and eye muscle area, and decreasing carcass fat depth, there will not be significant correlated responses in female lifetime reproductive performance for either of the tropically adapted genotypes evaluated. This also means that if breeders measure steer carcass and female reproduction traits, submitted these for genetic evaluation and prioritise them in the breeding objective, genetic progress can be achieved simultaneously for both.

While the strategy of exploiting live measurements of growth and body composition traits in young bulls as genetic indicators of their steer carcass equivalents had been confirmed in this study, it is also shown that this may have unfavourable consequences for female reproduction in Brahmans. Current genetic trends for weight and eye muscle area in that breed are positive, and measures in young bulls represent the majority of growth and body composition information submitted to BREEDPLAN for genetic evaluation. The unfavourable genetic associations of bull liveweight and eye muscle area with reduced female lifetime reproductive performance suggest that current genetic trends may be having unfavourable consequences for female reproduction. Genetic relationships estimated for residual feed intake also suggest that selection to improve the trait may produce unfavourable correlated responses in early female reproductive performance for Brahmans. Importantly, these correlations are not unity, suggesting that if both traits are included in the breed's multi-trait genetic evaluation and selection indices, animals could be identified which were genetically superior for both steer residual feed intake and female reproductive performance.

The results presented in Chapter 5 also suggest that selection to improve objectively measured meat tenderness in Tropical Composites will have unfavourable genetic consequences for female reproduction. This means that if Tropical Composite breeders prioritise tenderness in the breeding objective, it will be important that records describing female reproduction are also included in the analysis to allow this genetic antagonism to be managed. Again, these correlations are not unity, suggesting that animals can be identified which are genetically superior for both.

6.3 Genetics of female growth and body composition and relationships with reproductive performance

Results of this study show that lactating first calf Brahman and Tropical Composite cows lost significant weight and body condition in late pregnancy and early lactation. The large differences observed in growth and body composition traits, and the degree to which fat and muscle tissues were mobilised over this period have not been reported previously for the tropically adapted genotypes examined in this thesis. Results show that variation in these traits has a significant genetic basis and hence, performance could be altered by selection. It was also demonstrated that selection pressure applied to change corresponding growth and body composition traits evaluated in heifers at 18 months of age, would produce moderate to strong and positive correlated responses in lactating first calf cows. This result provides breeders of tropically adapted beef cattle with a means of changing growth and body composition in lactating first calf cows by selection based on earlier measurements. An additional advantage of this strategy will be that, as most of the removal of females from the breeding herd occurs after 18 months of age, contemporary groups will be more complete and the data more useful for genetic evaluation. Finally, it was shown that if breeders sought to reduce weight and body condition loss in lactating first calf cows, this could be also achieved by applying negative selection pressure to maternal weaning weight.

For Brahmans, selection for higher heifer growth and body composition would also produce favourable correlated responses in first mating reproductive outcomes, and that this would have no unfavourable consequences for subsequent reproductive performance. For Tropical Composites these relationships tended to be weaker, and it can only be concluded that selection which impacted female growth and body composition, whether measured in heifers or in lactating first calf cows, would produce no significant correlated responses in female reproductive performance.

For tropically adapted breeds in Australia, there are more records submitted to BREEDPLAN for weaning weight than for any other trait. Results presented in this thesis suggest that selection to increase maternal weaning weight will produce unfavourable correlated responses in female reproductive performance, if reproduction is not also recorded and included in the breeding objective. In the current selection indices for tropical breeds, maternal weaning weight is given very low emphasis or weighting (-3% to +3%) compared to days to calving (-40% to -15%) (Anonymous 2011, Anonymous 2010*b* and Anonymous 2010*a*). The correlations estimated here are, therefore, unlikely to produce a decline in female reproductive performance if breeders practice selection based on current selection indices.

6.4 Genetic relationships of tropical adaptation with female reproduction

For the genotypes examined in this study, adaptation to the harsh tropical, sub-tropical and semi-arid environments in which these animals are managed are fundamental to beef production in northern Australia. It is, therefore, critical that any selection to improve productivity be carried out with an understanding of possible consequences for tropical adaptation traits. Results from the research presented in this thesis and associated studies (Prayaga *et al*. 2009) have showed that selection to improve key aspects of steer and female productivity will have no unfavourable consequences for tropical adaptation. In Australia, the genetic evaluations for tropically adapted genotypes do not currently include descriptors of tropical adaptation. Given the ease and timeliness with which traits like coat length, coat colour and navel score can be measured, there may be merit in including these in the evaluation to allow monitoring of genetic trends for tropical adaptation traits, particularly as new traits are added to the evaluation and breeding objectives change. Additionally, tropical adaptation traits were among the few early in life measures evaluated in this study which showed promise as genetic indicators of female reproductive performance. In Brahmans, coat score and fly lesion score both displayed significant genetic relationships with female reproduction. These traits could, therefore, also be included in the Brahman BREEDPLAN evaluation to provide an early source of information about female reproductive performance, and a means of increasing the rate of genetic gain for the trait.

6.5 Opportunities for further research

Measurements of cow weight and body composition were recorded regularly in the females examined for the current study, through up to 6 matings. Genetic analysis of mature cow weight and body composition and their relationship with female reproduction traits would provide important insight into the consequences of selection for growth and carcass composition. Tropical adaptation traits were also recorded in these females throughout their time in the project. Traits describing coat and hide characteristics, internal and external parasite resistance and body temperature may display variation throughout a cow's life. Quantifying the genetic basis for this variation, if it existed, and its relationships with female reproductive performance, may also provide insight into the cow performance traits already analysed for this experiment. Also of interest in analysing these data would be an examination, at both the phenotypic and genetic level, of cow longevity and the role of weight and body composition, tropical adaptation, reproductive performance, and their interactions, in traits describing the retention of females in the breeding herd.

It was demonstrated in Chapter 2 that there are moderate to strong genetic relationship between steer carcass weight and composition, and corresponding traits evaluated in heifers, though there were differences observed in the magnitude of these in Brahmans and Tropical Composites. The genetic relationships of steer carcass traits with corresponding measures in reproductively active cows are still unknown, however, and this represents a clear area for future research. This could provide further insight into the genetic differences observed between Brahmans and Tropical

Composites, in the relationships of growth and body composition traits in feedlot finished steers and females managed under extensive pasture conditions.

Finally, polled status has received significant attention in tropical breeds as a factor influencing carcass value and animal welfare issues. DNA marker discovery research has identified genes which describe variation in polledness for tropically adapted beef breeds, and these are now being marketed to beef producers as a means of managing polledness in their herds. DNA samples and horned/polled phenotypes are available for a proportion of the animals involved in the current study, and for related animals from industry. To date, no examination of the relationships of polled genotypes with either steer or cow productivity traits has been undertaken. This research is required to determine whether genetic antagonisms exist between polled genotypes and productivity traits and, if identified, to allow these to be managed.

6.6 Final Conclusions

Results presented in this thesis show that, for breeders of tropically adapted beef cattle in northern Australia, selection can be successfully undertaken to improve economically important steer and female traits simultaneously. It is also shown that first calf tropically adapted cows mobilise significant fat and muscle during their first lactation, that there is a genetic basis for variation in these tissue mobilisation traits, and that this is genetically associated with variation in maternal weaning weight (a descriptor of genetic milk production potential). If breeders of tropically adapted beef cattle select to reduce maternal weaning weight, tissue mobilisation during first lactation will be reduced as a consequence. Results also suggested that such a strategy will produce favourable correlated responses in female reproductive performance.

Incorporating these results into the genetic evaluation for tropically adapted breeds will provide opportunities for breeding objectives to be defined in terms of previously unavailable traits of economic importance, and the genetic relationships reported from this study will allow breeding values and selection indices to be estimated with greater accuracy. This will provide opportunities for breeders of tropically adapted beef cattle to more accurately identify animals of superior genetic merit, thereby increasing rates of genetic gain for economically important traits and improving productivity in Australia's northern beef industry.

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