CHAPTER 1 General Introduction

The aim of breeding programs is to improve production and biological efficiency. Large differences exist between breeds for most bioeconomic traits as a result of different selection goals in different breeds (Gregory *et al.* 1982; Cundiff *et al.* 1986). Hence selection of the most suitable breed should be done before selection within that breed (Van Vleck *et al.* 1992). However, production potential cannot be fully expressed unless animals are highly adapted to their production environment (Frisch 1997). The greatest gains are achieved when genotypes are matched to management systems, environments in which they will produce, and to markets for which they are destined (Frisch 1997).

Beef production contributed $7.8 billion to the Australian economy in 2005-06 (ABS 2007). The domestic market is Australia's largest beef market, while Japan and Korea are Australia's largest premium export beef markets. Australia is the world's largest beef exporter, contributing 25% of total beef traded at a value of $3.9 billion to the economy (ABS 2005). The most important pre-purchase considerations for beef consumers are the amount and distribution of fat, lean meat colour, fat colour and appearance, and freshness. Post-purchase, tenderness is the most important factor, followed closely by flavour and juiciness (Egan *et al.* 2001). In response to domestic and Japanese market demands for consistency of beef eating quality, the Beef Cooperative Research Centre (Beef CRC) was formed in 1993 to examine genetic and non-genetic factors influencing beef quality from breeding through to consumption. One of the key issues was the large proportion of beef coming from tropical, subtropical and semi-arid regions of northern Australia. In 2004, Queensland held 42% of Australia's 27.5 million cattle, while New South Wales and the Northern Territory held 21% and 16% respectively (ABS 2006). Queensland contributed 42% of total cattle slaughtered in 2003-04 (ABS 2005). Of the total

666,000 head of cattle in Australian feedlots in March 2004, Queensland held nearly half of these (ABS 2005). Though the percentage of cattle finished in feedlots and slaughtered in northern Australia can vary significantly from year to year due to drought conditions.

Brahman is the predominant breed in northern Australia. The tropical and subtropical climates, poor nutrition and extensive management systems under which *Bos indicus* breeds have evolved has increased their tolerance to those environments through selection pressure (Nogueira 2004). Hence, *Bos indicus* can thrive where *Bos taurus* cannot. The superior adaptation of Brahmans has meant their role in northern Australian beef production systems has continued to grow, particularly since the 1970s. More than 50% of the national herd is now estimated to have some Brahman genes (Bindon 2002). A consequence of selection pressure for adaptation has been reduced productivity and precocity (Nogueira 2004). Brahmans have a reputation for poor carcass and meat quality, poor performance in feedlots, and poor fertility relative to *Bos taurus* breeds and *Bos indicus* × *Bos taurus* crossbreds.

Crossbreeding allows the complementary blending of breed characteristics – adaptation with productive and reproductive traits. Commercial cattle producers have been using tropically adapted straightbreds, crossbreds and composites in an effort to overcome some of the shortcomings of straightbred Brahmans for beef quality, feed efficiency and fertility, while maintaining adaptation characteristics in their breeding herds. There are many studies that examine Brahman × *Bos taurus* crosses relative to *Bos taurus* performance in temperate environments, one of the most well known and comprehensive research projects being the ongoing Germplasm Evaluation Program conducted at the USDA Meat Animal Research Center at Clay Center, Nebraska (Cundiff *et al.* 1998; Cundiff *et al.* 2001). However, there are few studies examining economically important traits of Brahmans relative to *Bos taurus* × Brahman in tropical and subtropical environments. Where studies on Brahmans and Brahman crossbreds have been conducted in tropical and subtropical regions of other parts of the world, temperature extremes and rainfall patterns differ significantly to northern Australian environments. Furthermore, cattle production systems, finishing regimes, processing practices and markets differ significantly between other countries and Australia.

Therefore, the purpose of this thesis was to compare the performance of tropically adapted crossbred and composite cattle with straightbred Brahmans for economically important production and reproduction traits under tropical and subtropical conditions in northern Australian using typical commercial beef production practices. This research used data generated from the Beef CRC's Northern Crossbreeding Program and Project 2.3. This research was limited to northern Australian beef production systems, excluding the live export cattle trade, but has application in parts of the world that use Brahman and tropically adapted crossbreds and composites in their beef herds.

Chapter 2 examines the literature on beef cattle production including genetic and environmental influences on carcass and meat quality, feed efficiency and fertility of Brahmans, Brahman crossbreds and tropically adapted composites. To achieve the overall research aim, Chapters 3 and 4 examined carcass quality and meat quality (objective and sensory palatability) characteristics of straightbred Brahmans relative to Brahman crossbreds when finished on pasture and in feedlots, to domestic and export market weights. Chapter 5 examined differences in feed efficiency and feeding behaviour of straightbred Brahmans relative to Brahman crossbreds when finished in a feedlot to export market weights. Economic pressures focus animal selection on carcass and meat quality, and feed efficiency characteristics. Genetic antagonisms exist between yield and feed efficiency traits and fatness traits. As fatness is believed to be positively associated with fertility in females, selection for higher retail beef yield or feed efficiency may have detrimental effects on replacement female fertility. This may be exacerbated under the stressors of northern Australian beef production environments. To determine if there was a relationship between fatness and fertility, Chapter 6 examined the phenotypic relationships between scanned subcutaneous fat measurements and weight at the start of mating and reproductive success in straightbred Brahmans and tropically adapted composites. Finally, Chapter 7 provides a general discussion on the use of Brahman crossbreds and tropically adapted composites relative to straightbred Brahmans in northern Australia. Recommendations are made with specific relevance to beef industry application in Australia.

CHAPTER 2 Literature Review

2.1 Introduction

This literature review examines traits of economic importance to beef production in Australia. It reviews genetic and non-genetic influences on carcass quality, meat quality (including objective and sensory palatability), feed efficiency, feeding behaviour and female fertility, with specific reference to Brahmans, Brahman crossbreds and tropically adapted composites relevant to this study. Because of the limited Australian research on several traits of interest, many studies from other beef producing countries have been sourced. Some dairy cattle references have been used when there was insufficient beef research on particular fertility traits.

2.2 Beef quality

2.2.1 Importance to beef industry

The beef cattle industry is one of Australia's major agricultural industries. A total of 8.9 million cattle and calves were slaughtered during 2004-05, producing 2.16 million tonnes of pasture- and grain-finished beef, and raising more than $6.7 billion (ABS 2006). Of these, 42% were slaughtered in Queensland. Despite declining consumption of beef, the domestic market remains the largest single market for Australian beef, commanding 37% of total grain fed beef production (ABS 2005). Australia is the world's largest beef exporter contributing 25% of the total beef traded in 2003-04, worth $3.9 billion to the economy (ABS 2005). Japan is Australia's most important premium export beef market, consuming 438,500 tonnes (20.3%) of the total beef produced in Australia in 2004-05. The USA is Australia's largest importer of manufacturing beef, consuming 17.1% in the same period, while Korea is the third largest export market, consuming 5.2% (ABS 2006). In the mid-1980s, the USA realised the potential of the Japanese and Korean beef markets and became a major competitor with Australia. Since then Australian beef producers have been under increasing pressure to become consumer-driven, focussing on the consistent supply of quality beef to maintain market share.

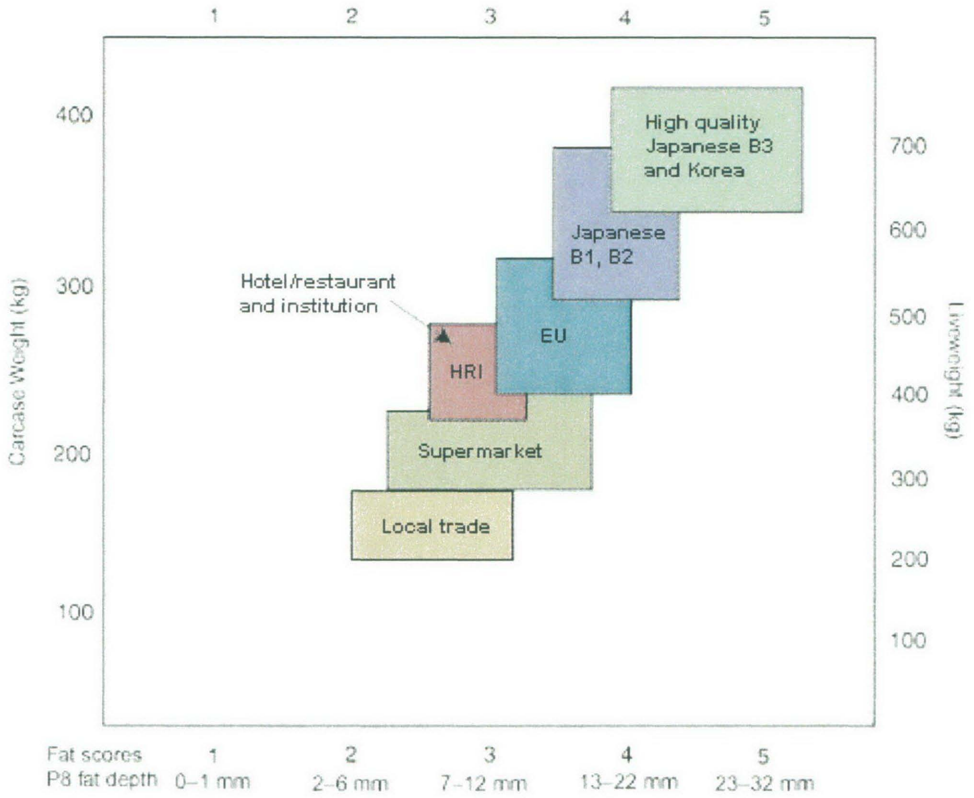
Consumers base purchase decisions on two main factors. These are visual appearance including amount and distribution of fat (marbling fat and subcutaneous fat), lean meat colour, fat colour and appearance, and eating quality including tenderness, flavour and juiciness (Egan *et al.* 2001). A review by Egan *et al.* (2001) concluded leanness was the most important factor influencing purchase decisions of domestic consumers, with a preference for lean steaks and minimal marbling. While domestic consumers select lean beef in the supermarket, they prefer the eating quality of marbled steaks in restaurants (AUS-MEAT score 2-3) where the visual bias to marbling is largely removed due to cooking (Egan *et al.* 2001). Freshness (date of packaging) was the most important raw-meat purchasing factor for the Japanese 'middle market segment', with a preference for moderate marbling and moderate fat cover. Post-purchase, household consumers and food service operators rated tenderness as the most important eating quality attribute, followed by flavour and juiciness. A study by SMART (1994) found that 77% of consumers would purchase more beef if they knew it was going to be tender. Similarly, tenderness was the single most important eating quality attribute for Japanese consumers.

2.2.2 Carcass and meat quality traits

A range of carcass and meat quality measurements have been developed in an effort to meet individual market specifications for appearance and eating quality of beef. Carcass quality traits include carcass weight, subcutaneous fat thickness at the P8 rump site and rib site (commonly between the 12th and 13th ribs), intramuscular fat score (AUS-MEAT marbling score 1-9), intramuscular chemical fat percent, dressing percentage, retail beef yield percent, kilograms of retail primals and ossification score. Meat quality traits are those that predict the tenderness, juiciness and flavour (palatability) of beef. Tenderness is commonly predicted through use of mechanical means including Warner-Bratzler shear force and instron compression, while juiciness is predicted through percent moisture loss based on a standardised cooking method. Ultimate pH is associated with cold and heat shortening of muscle fibres, so gives an indication of the tenderness and juiciness of beef. Intramuscular fat colour and percent indicate flavour. The most accurate predictor of palatability is through use of consumer taste panels.

The value of beef carcasses is determined by sex, age at slaughter, carcass weight and composition (Williams and Bennett 1995). AUS-MEAT accredited abattoirs pay beef producers on the basis of cents per kilogram of hot standard carcass weight (CWT), and provide feedback on CWT, hot P8 fat measurement (mm), dentition (age at slaughter) and bruise score (AUS-MEAT 2001). Chiller assessment includes measurements for subcutaneous rib fat, intramuscular fat score, meat colour, fat colour and eye muscle area (AUS-MEAT 1998). Market specifications are based on a combination of carcass and chiller measurements, however currently beef producers are not paid for intramuscular fat (marbling) or tenderness of their beef unless they have private contracts or slaughter cattle through Meat Standards Australia accredited abattoirs. Figure 2.1 shows the basic weight and fat specifications for Australia's main markets. Domestic market includes local trade, supermarket and hotel/restaurant and institution. The European Union (EU) market is not discussed in this thesis, though this market is consistent with specifications of the Korean market at the commencement of the Beef CRC Northern Crossbreeding Program. Minimum subcutaneous fat depths apply to each market segment. Steers are fed for 100 days (short fed) for the Japanese B1 market. The requirements for the B1 market are good meat colour, fat colour and cooking odour, attained through grain feeding to a minimum AUS-MEAT marble score of 1 (NSW Department of Agriculture 2004).

Figure 2.1 Basic weight and fat specifications for Australia's major market segments (NSW Department of Agriculture 2004).



2.2.3 *Meat Standards Australia beef grading scheme*

The Meat Standards Australia (MSA) beef grading scheme was launched in 1997 with the primary aim of providing a guarantee of eating quality to the consumer (Polkinghorne *et al.* 1999). The MSA grading scheme took on a total systems approach that aimed to identify and control important production and processing factors that have the largest effect on palatability, so that it was possible to accurately predict the quality of the final product. The scheme differentiated beef products based on eating quality rather than description. Consumer taste panels were recruited from the community to assess beef samples based on a clipped meat quality score of four attributes (CMQ4) on a scale of 0-100 which comprised tenderness 40%, juiciness 10%, flavour 20% and overall liking 30%. Higher CMQ4 scores indicate more tender beef. CMQ4 scores were then associated with relevant production and processing pathways. A pilot program to collect consumer feedback on the MSA beef grading scheme was conducted in 1998 and demonstrated a high repurchase rate by consumers if they were presented with a consistent graded product (Thompson *et al.* 1999b). Initially, MSA based their grading schemes on a maximum of 25% *Bos indicus* content. Through collaborative research with the Beef CRC, MSA identified *Bos indicus* content and growth path as critical control points in their grading scheme (Thompson *et al.* 1999a). Carcasses are now graded using indicators including carcass weight, sex, tropical breed content, carcass hanging method, ossification, marbling, rib fat, pH and temperature, and ageing (Polkinghorne *et al.* 1999; Bindon *et al.* 2001; MLA 2003). Butcher labels are generated by the grading information identifying the MSA grades, ageing periods and cooking method for each individual cut, and accompany the product from the abattoir to the retail outlet (MLA 2003).

2.2.4 Genetic selection for beef quality: heritabilities, correlations

Reviews by Koots *et al.* (1994), Marshall (1994, 1999) and Burrow *et al.* (2001) reported weight-adjusted heritability estimates in the moderate range for subcutaneous fat thickness (mean 0.46), marbling score (mean 0.36), retail beef yield (mean 0.48), and variable heritability estimates for carcass weight of 0.10-0.20 (unadjusted) and 0.15-0.59 (age-adjusted). Marshall (1999) reported mean heritability estimates for shear force (0.25; 10 studies), ultimate pH (0.15; 3 studies) and sensory tenderness (0.22; 12 studies). Similarly, Burrow *et al.* (2001) and Johnston *et al.* (2003) reported low to moderate heritability estimates for objective meat quality and palatability traits, with *Bos indicus* genotypes having slightly higher heritabilities for these traits than *Bos taurus* breeds. Therefore, while carcass quality traits will respond to selection within a breed, selection for meat quality attributes between breeds may yield more response than selection within breeds. Breed differences are discussed later in section 2.2.6.

Moderate genetic correlations exist between subcutaneous fat thickness and marbling (Marshall 1999; Reverter *et al.* 2003), however moderate to strong genetic and phenotypic antagonisms exist between carcass fatness traits and retail beef yield in *Bos taurus* and *Bos indicus* breeds (Koots *et al.* 1994b; Marshall 1999; Burrow *et al.* 2001; Reverter *et al.* 2003). Genetic correlations between retail beef yield and intramuscular fat percent (-0.43 and -0.38) and subcutaneous P8 fat (-0.28 and -0.48) in tropically adapted and temperate breeds respectively indicate selection for higher yields will result in decreased carcass fatness (Reverter *et al.* 2003). As penalties are applied to carcasses that fail to meet minimum fatness specifications, multiple trait selection indices are recommended for avoiding genetic antagonisms between carcass traits. Tenderness (Warner-Bratzler shear force) has been desirably genetically correlated with carcass weight (-0.32), retail beef yield (-0.16) and marbling (-0.31) (Koots *et al.* 1994b), though phenotypic correlations were low and estimates only included two studies. A review by Marshall (1999) reported genetic correlations between sensory tenderness and carcass weight (0.24), lean yield (-0.19), fat thickness (0.10), marbling score (0.38), intramuscular fat percent (0.30) and shear force (-0.86). Similarly, Reverter *et al.* (2003) reported generally favourable genetic correlations between sensory tenderness and carcass weight in tropically adapted and temperate breeds respectively of (0.00 and 0.06), retail beef yield (0.05 and -0.26), subcutaneous fat depth (0.21 and 0.57), intramuscular fat percent (0.31 and 0.61) and shear force (-0.79 and -0.49). However phenotypic correlations between sensory tenderness and carcass traits were low.

2.2.5 Major genes and QTL

More recently, genetic markers have been identified for beef quality traits including growth, carcass weight (Watanabe and Sugimoto 2006), marbling (Barendse *et al.* 2004; Thaller *et al.* 2003), marbling score (Casas *et al.* 2004), meat tenderness (Page *et al.* 2002; Cullen *et al.* 2003; Drinkwater *et al.* 2006), fat depth, dressing percentage, retail beef yield and eye muscle area (Hetzel *et al.* 1997; Morsci *et al.* 2006; reviews by Marshall 1999 and Burrow *et al.* 2001). Two of the most well known QTL are the myostatin double muscling mutation (Grobet *et al.* 1997) and the thyroglobulin (TG5) gene that accounted for 6.5% ($P<0.01$) of the residual variation in observed marbling in feedlot cattle (Barendse *et al.* 2004). Though there are a large number of studies that report QTL for various carcass and meat quality traits of economic importance, there are few QTL that have been successfully developed and commercialised.

The direct evaluation of breeding animals through marker assisted selection can significantly reduce the time needed for evaluation (Marshall 1999). However, genes affecting quantitative traits (QTL) are difficult to identify because their effects are small to moderate, many genes affect the trait, and the genomes of birds and mammals where most of the QTL mapping occurs are very large (Barendse 2005). The magnitude of QTL effects can often be overestimated because of the statistical effects of fitting many genetic markers (Burrow *et al.* 2001). Large samples are required to demonstrate a statistically significant result, and separate resources are required to confirm the association and to determine how widely distributed the QTL is among various breeds and populations (Barendse 2005). The choice of trait is critical to development and commercialisation of QTL, not only from an economic importance point of view, but also as to whether there are easy, alternative methods to improve the trait that are cheaper than a DNA test (Barendse 2005). Hence, the greatest application of marker assisted selection is when it is used in large populations in early generations of selection prior to measurement of the trait, for difficult to measure traits or traits that require slaughter of the animal before measurement can occur, when heritability is low, for sex-limited traits, and when the magnitude of the QTL effect is large (Burrow *et al.* 2001).

2.2.6 Beef quality of tropically adapted breeds

Most of the carcass and meat quality research has been done in temperate environments, the most well known and comprehensive project being the Germplasm Evaluation Program conducted at the USDA Meat Animal Research Center at Clay Center, Nebraska (Cundiff *et al.* 1998; Cundiff *et al.* 2001). There is limited research on carcass and meat quality of British breeds × Brahman and Continental breeds × Brahman relative to straightbred Brahmans in tropical and subtropical environments. Studies conducted in Africa, India and South America mainly involve Brahman or other *Bos indicus* breeds, tropically adapted composites and native breeds of cattle which are often used as multi-purpose animals (Abeygunawardena and Dematawewa 2004). Studies on beef quality of straightbred Brahman and Brahman × *Bos taurus* crossbreds relevant to this study have been conducted in the USA in Florida, Louisiana and Texas (Peacock *et al.* 1977, 1982; Wythes *et al.* 1989; Johnson *et al.* 1990; DeRouen *et al.* 1992a; Pringle *et al.* 1997; Bidner *et al.* 2002). However environmental conditions and nutrition differ vastly to Australia. Florida and Louisiana have a warm temperate rainy climate with no dry season, whereas cattle produced in northern Australia are grown in dry steppe and desert climates, and tropical and subtropical savanna climates with distinct wet and dry seasons (Fullard and Darby 1976). Given poor adaptation is believed to be responsible for changes in breed rankings for meat tenderness in extreme environments (Pratchett *et al.* 1988), research in temperate USA regions may not be applicable to northern Australian conditions where most of Australia's beef is produced. Further, different production and processing systems and market endpoints make it difficult to draw comparisons between USA and Australian studies.

Reviews of sire breed effects on carcass quality generally agree that *Bos indicus* breeds have moderate lean-to-fat ratios and below average marbling, British breeds have low lean-to-fat ratios and relatively high marbling scores, and Continental breeds have above average lean-to-fat ratios and average marbling (Cundiff and Gregory 1999; Marshall 1994, 1999). It is well documented that as the proportion of *Bos indicus* inheritance increases, shear force increases and marbling and sensory tenderness values decrease (Koch *et al.* 1982, 1988; Crouse *et al.* 1989; Johnson *et al.* 1990; Whipple *et al.* 1990; Marshall 1994; Shackelford *et al.* 1995; Cundiff *et al.* 1998; Thompson *et al.* 2002; Wheeler *et al.* 2001). Thompson *et al.* (1999a) reported consistent findings, stating that commercial carcasses with greater than 75% *Bos indicus* content had a palatability failure rate of 63% (based on the original MSA CMQ4 cut-off point of 48/100), and those with 25-75% *Bos indicus* content had a failure rate of 31%. Hearnshaw *et al.* (1999) reported higher cooking loss ($P<0.05$) and lower sensory palatability ($P<0.05$) of Brahmans relative to Angus sired steers from Hereford, Brahman and crossbred dams finished on pasture. On the other hand, Pringle *et al.* (1997) found no significant difference between 50% and 75% Brahman for shear force and sensory panel evaluation. Similarly, Whipple *et al.* (1990) found no difference between differing levels of *Bos indicus* inheritance for juiciness and flavour intensity.

Muscle factors associated with breed differences in meat tenderness have been identified including proteolytic potential, glycolytic rate and connective tissue properties (Harper 1999; Ferguson *et al.* 2001, Ferguson 2002). Calpastatin activity has been largely held responsible for the decreased tenderness in *Bos indicus* cattle (Wheeler *et al.* 1990; Whipple *et al.* 1990; Shackelford *et al.* 1991, 1994; Pringle *et al.* 1997; Ferguson *et al.* 2000). A study by Shackelford *et al.* (1994) found calpastatin activity was highly heritable (0.65±0.19) and responsible for a significant portion of genetic variation in Warner-Bratzler shear force (r_g 0.50±0.22). Electrical stimulation can be used to accelerate proteolysis and reduce breed differences in shear force of the *M. longissimus* (Ferguson *et al.* 2000). Method of stimulation has been shown to produce large effects on the mean and variance of shear force in carcasses from Belmont Red, Brahman and Santa Gertrudis cattle (Johnston *et al.* 2001).

Studies generally concur that cold shortening has little to do with variation in tenderness between breeds, leading to the conclusion that retarded rates of glycolysis must be associated with a change in the metabolic capacity of the muscle (Ferguson 2002). Post-mortem rates of glycolysis have been shown to be slower in *Bos indicus* muscle relative to *Bos taurus*, leading to increased shortening of the myofibrillar proteins (Shackelford *et al.* 1991). However, other research has found no difference between breeds for pH decline (Whipple *et al.* 1990), which is believed to influence catheptic and calcium-dependent protease systems. Muscle fibre type and size have also been implicated in breed differences for tenderness (Ferguson 2002) however reports vary as to its contribution to meat tenderness (Harper 1999).

Studies by Whipple *et al.* (1990) and Johnson *et al.* (1990) failed to find breed differences in collagen content and solubility. However, a study by McKay *et al.* (2001) found an increased number of thicker perimysial seams in *Bos indicus* cattle relative to *Bos taurus*, which may cause increased connective tissue toughness.

The *M. longissimus* is the most commonly assessed muscle for tenderness measurements. However studies have shown that *Bos indicus* inheritance increases shear force of the *M. longissimus* to a greater extent than other muscles on the carcass indicating the *longissimus* is not a good indicator of tenderness of all muscles on the carcass (Whipple *et al.* 1990; Shackelford *et al.* 1995).

Effects of breed are among a range of other factors that can have a significant impact on variation in eating quality (Ferguson *et al.* 2001). Nutrition, growth path, parasite stress, animal age, use of hormonal growth promotants, transportation, mixing cattle, method of electrical stimulation, ageing, hanging method, and the degree and duration of heat applied during cooking all impact on eating quality (Gazzola 1997; Harper 1999; Thompson 1999; Ferguson *et al.* 2001). Given the largest influence on beef palatability occurs immediately pre- and post-slaughter (Ferguson *et al.* 2001) the magnitude of the *Bos indicus* effect on tenderness can be substantially reduced with the application of best practice procedures (Ferguson 2002).

2.2.7 Heterosis effects on beef quality

Researchers are generally in agreement that heterosis primarily affects growth, weight and fat depth, with small positive effects on marbling and negligible effects on yield (Marshall 1994; Hearnshaw *et al.* 1999; Burrow *et al.* 2001). Heterosis effects tend to be relatively unimportant for most palatability traits (Marshall 1999). A review by Marshall (1999) concluded that *Bos taurus* × *Bos indicus* crosses may result in higher levels of favourable heterosis on beef quality relative to *Bos taurus* crosses or *Bos indicus* crosses. Combined results from the Beef CRC Northern Crossbreeding and linked Straightbreeding Programs estimated positive heterosis effects in the crossbred animals of 1% to 19% for hot carcass weight, -18% to –1% for intra-muscular fat percent and shear force, and negligible heterosis for retail beef yield (Reverter and Newman 2000). Cundiff and Gregory (1999) reported effects of heterosis on carcass traits are relatively small (3% or less) particularly when adjusted on a weight-constant basis. Peacock *et al.* (1982) reported individual heterosis effects for shear force of -0.69 ($P<0.05$) and -0.08 (n.s.) for Angus × Brahman and Charolais × Brahman crosses respectively, while Brahmans had additive genetic effects of 0.84 ($P<0.01$). Similarly, DeRouen *et al.* (1992b) reported significant direct heterosis effects on shear force for Brahman × Angus, Brahman × Charolais and Brahman × Hereford crosses which ranged from -1.05 to -2.16 kg, while Brahmans in their study had large direct additive effects of 2.46 kg ($P<0.01$). The main benefits of crossbreeding are realised through increased growth rates relative to straightbreeds, complementary blending of production, reproduction and adaptation traits, and evasion of genetic antagonisms between traits (Marshall 1994).

2.3 Feed efficiency

2.3.1 Importance to beef industry

Traditionally beef cattle research focussed on improving production including growth, fertility and carcass traits. Over the past decade the focus has shifted to reducing inputs in order to improve production efficiency and economic profitability (Archer 2000). This has been driven by demand from overseas customers for a specifically tailored, consistently high quality, year round supply of beef product which has led to the growth of the feedlot industry in Australia. Currently, there are 575 accredited feedlots with a total carrying capacity of 926,000 head (ABS 2005). Hence, the cost of providing feed for beef production is a major expense. As the level of feed intake relative to maintenance increases, the digestion of feed decreases (Oddy and Herd 2000), subsequently leading to inefficient utilisation of feed. A review by Arthur (2000) concluded that differences in efficiency of maintenance exist between breeds, and these differences are correlated to differences in the productive potential of breeds. Not surprisingly, genetic improvement of feed efficiency has been identified as the second most important research topic to the Australian beef industry after genetic improvement of meat quality (Parnell *et al.* 1992).

2.3.2 Quantifying feed efficiency

Measures of feed efficiency are indices which combine feed intake (input) with production (output). There are several feed efficiency indices and different indices are appropriate for different purposes. Efficiency of beef production systems depends on the summation of many traits expressed in the breeding herd and the slaughter generation, and not just in the slaughter generation measured over a relatively short period of time during the production period. Hence it is not possible to make uniform recommendations on a single index as being representative of a genotype's efficiency in the context of the entire beef production system (Archer *et al.* 1999). However, genetic improvement in feed efficiency has greatest potential for application in growing cattle under northern Australian production systems where markets demand grain-finished beef, and therefore this review deals primarily with feed efficiency in the slaughter generation.

Measures of feed efficiency can be categorised into growth and feed efficiency. Growth traits include liveweight, average daily gain, Kleiber ratio and relative growth rate. Average daily gain (ADG) is weight gain over time. Kleiber Ratio (KR) is weight gain per unit metabolic body weight. Relative Growth Rate (RGR) is growth relative to instantaneous size, usually expressed as percentage change in weight per day (Arthur 2000). KR and RGR require the measure of growth but not feed intake and hence are indirect measures of feed efficiency (Fitzhugh and Taylor 1971; Bergh *et al.* 1992). Selection for KR will improve some feed efficiency traits through its correlated improvement in ADG, but has little effect on feed intake and liveweight (Arthur *et al.* 2001b).

The most commonly used measures of feed efficiency are feed intake, gross efficiency (the inverse of feed conversion ratio), maintenance efficiency, partial efficiency of growth, residual feed intake and cow/calf efficiency (Archer *et al.* 1999; Arthur 2000). Of these, feed intake, feed conversion ratio and residual feed intake are the most widely used feed efficiency indicators of growing cattle. Daily feed intake (FI) is now relatively easy to measure on large numbers of animals since the development of individual feed recorders in feedlot environments, though measurement of individual FI remains expensive.

Feed conversion ratio (FCR) is defined as feed intake to weight gain over a specified period. It is well documented that gross efficiency is both phenotypically and genetically correlated with aspects of production (Archer *et al.* 1999). Selection for improved FCR may improve efficiency during growth and finishing phases, however genotypes with high growth rates (high FCR) also tend to have high mature cow weights and consequent higher feed requirements of the cow herd (Archer *et al.* 1999). Gains in economic efficiency may occur under these circumstances if the cost of feed inputs of the slaughter generation is greater than the cost of feed inputs of the breeder herd (Archer *et al.* 1999).

Residual feed intake (RFI) is regarded as the trait most useful for genetic improvement in feed efficiency in beef cattle in Australia (Archer *et al.* 1999). Koch *et al.* (1963) initially proposed the use of residual (net) feed intake as a measure of feed efficiency. Apparent genetic variation in residual feed intake in growing cattle suggests it may be possible to reduce feed intake of growing cattle without affecting growth performance, hence improving feed efficiency (Archer *et al.* 1999). RFI is defined as actual feed intake net of the expected feed requirements for maintenance of body weight and growth rate. The usual method for estimation of RFI is:

$$\text{Feed intake} = \mu + \beta_w \times \text{mean metabolic weight} + \beta_g \times \text{mean weight gain} + \text{error}$$

where μ is a constant; mean metabolic weight is $[(\text{start weight} + \text{end weight}) \div 2]^{0.75}$ of the animal during the test period; weight gain is average daily gain over the test period; and RFI is the error term. The residual portion indicates efficiency, with more efficient animals having a lower (negative) RFI.

RFI has the advantage that variation in feed intake is adjusted for differences in growth and liveweight by use of multiple regression procedures (Luiting *et al.* 1994). RFI is independent of the production traits (liveweight and ADG) used to calculate expected feed intake, allowing comparison between animals differing in level of production during the measurement period, therefore both breeding and finishing sectors benefit (Arthur and Lymbery 1999; Archer *et al.* 1999; Arthur *et al.* 2001a). Linear indices such as RFI by regression yield more response to selection than traditional ratios such as FCR (Arthur *et al.* 2001b), mainly because ratios are difficult to work with.

2.3.3 Genetic selection for feed efficiency: heritabilities, correlations

A review by Archer *et al.* (1999) reported heritability estimates within the moderate range for FCR (0.16 to 0.46) and RFI (0.08 to 0.44). Similarly, heritabilities in the moderate range have been reported for FI, ADG, RFI, FCR, KR and RGR in other studies (Fan *et al.* 1995; Herd and Bishop 2000; Arthur *et al.* 2001a, 2001b; Robinson and Oddy 2004; Schenkel *et al.* 2004). Therefore, response to single trait selection would be relatively fast. However, a study by van der Werf (2004) found that selection for RFI will not obtain a better selection response than selection on constituent traits alone. Further, van der Werf (2004) concluded that multiple trait genetic evaluation of constituent traits is likely to be more accurate than selection for RFI because the constituent traits accommodate their different models and missing data.

Genetic and phenotypic correlations between FI and RFI are high and positive. Hence selection for lower FI will have a corresponding desirable effect of lowering RFI and FCR (Herd and Bishop 2000; Arthur *et al.* 2001a, 2001b; Schenkel *et al.* 2004). Correlations between RFI and ADG are low to negligible, which is expected given RFI by definition is phenotypically independent of its component traits (Arthur *et al.* 2001a). However, correlations between feed efficiency and growth traits are variable, with most of these studies reporting moderate to high undesirable effects of selection for lower FI on ADG and liveweight.

Antagonistic correlations between selection for low RFI (high efficiency) animals and meat quality traits may also reduce the economic benefit achieved from reduced feeding costs. Luiting *et al.* (1994) reported selection for low RFI resulted in higher susceptibility to stress in hens and reduced meat quality in pigs. Similarly, Herd *et al.* (2000) reported a lower index of myofibril fragmentation and higher levels of calpastatin (a powerful inhibitor of calpain activity) in *M. longissimus dorsi* muscle samples from a single generation of divergent selection for postweaning RFI on Angus crossbred steers, indicating ongoing selection for low RFI may be accompanied by less tender meat. Richardson *et al.* (2001) and Robinson and Oddy (2004) reported undesirable (positive) genetic correlations between RFI and fatness traits (rump fat, rib fat and IMF%). Further, selection for low RFI may result in a reduced capacity to cope with nutritional stress associated with pregnancy and lactation (Cowen *et al.* 1980; cited by Pitchford 2004). A review by Pitchford (2004) of three feed intake mouse projects concluded that selection for high (-RFI) lines was associated with decreased reproductive rate, measured as litter size. Other studies have shown small positive correlations between RFI and fatness, and with variation in body composition contributing only 5% of the variation in RFI (Arthur *et al.* 2001a; Richardson *et al.* 2001), the effect of selection for RFI on fatness may be small. Further investigation of antagonistic correlations between RFI, fatness and fertility traits are warranted, hence use of multiple trait selection and economic selection indices are recommended over the use of single trait selection for improved feed efficiency.

A study of postweaning growth (ADG), net feed intake (-RFI) and cow performance on British breed cattle found postweaning NFI was significantly ($P<0.05$) correlated with mature cow NFI ($r=0.36$) and FI ($r=0.30$), indicating that females which were efficient as weaners required less feed as 4-year old cows for the same level of performance as less efficient contemporaries (Arthur *et al.* 1999). The same study reported significant ($P<0.05$) correlations between postweaning ADG and mature cow ADG ($r=0.39$), FI ($r=0.28$), liveweight ($r=0.36$) and rib fat depth ($r=-0.19$), but not for NFI. Females with high postweaning ADG were bigger and consumed more feed as mature cows, resulting in higher feed costs of the breeding herd.

2.3.4 Mechanisms for variation in feed efficiency

Systematic variation in feed efficiency is a function of the amount and type of feed eaten, the sex and breed of the animal, and the environment in which the animal is managed (Herd *et al.* 2004). The study of mechanisms causing variation in feed efficiency is a relatively new field with most research occurring within breed. Consequently, there are few studies comparing breeds for variation in feed efficiency. Further, a review by Archer *et al.* (1999) identified the knowledge gap regarding within breed variation in feed efficiency of *Bos indicus* and tropically adapted cattle. Hence, this section will discuss mechanisms thought to be responsible for variation in feed efficiency within breed, and which may be relevant to between breed differences in feed efficiency.

Variation in feed intake is associated with variation in maintenance requirements of ruminants (Oddy and Herd 2000). Within breed, selection of animals that eat less for the same liveweight and weight gain has led to the conclusion there is genetic variation in the utilisation of feed (Herd *et al.* 1997; Oddy and Herd 2000). This biological difference in efficiency of feed utilisation has been credited to variation in feed intake, digestion of feed, metabolism (anabolism and catabolism associated with and including variation in body composition), activity and thermoregulation (Oddy and Herd 2000; Herd *et al.* 2004). Feeding patterns and flight speed have also been implicated (Richardson *et al.* 2000). Richardson and Herd (2004) summarised results from a single generation of divergent selection for RFI in Angus cattle and reported contributions of biological mechanisms to variation in residual feed intake were: 9% for differences in heat increment of feeding, 10% for differences in digestion (conservative estimate; high feed intake is negatively associated with digestibility), 10% for differences in activity, 5% for differences in body composition (there is more variation in the efficiency of depositing lean gain than fat gain because of greater variation in protein turnover in lean gain), 2% for differences in feeding patterns, 37% for differences in protein turnover, tissue metabolism and stress (Richardson *et al.* 2004), and 27% for differences in other processes such as ion transport. Hence, no single mechanism is likely to be primarily responsible for the associated change in phenotype (Oddy and Herd 2000; Richardson and Herd 2004). Furthermore, in experiments where cattle differ by 6-7% in feed intake following divergent selection for RFI, the actual magnitude of difference in each mechanism will be small and difficult to measure with certainty (Herd *et al.* 2004).

2.3.5 Breed differences for feed efficiency

There are consistent known differences in rumen metabolism between *Bos taurus* and *Bos indicus* cattle pointing to potential sources of genetic variation within and between cattle breeds (Vercoe 1967; Vercoe *et al.* 1972; Hegarty 2000). Rate of eating is negatively related to mean retention time in the digestive tract and positively related to feed intake (Forbes 1972). Rate of passage is an important mechanism by which differences in fermentation occur (Hegarty 2000). Digesta kinetics, nutrient cycling in the rumen and rumen fatty acid synthesis have all been implicated in differences between breed types, with *Bos indicus* cattle having a faster fermentation rate, shorter digesta retention time (though diet is known to moderate breed differences), and higher population of rumen protozoa (expected to support greater methane emissions) (Hegarty 2000). However Brahmans have lower feed intake and a greater efficiency of energy capture relative to *Bos taurus* (Frisch and Vercoe 1977; Hegarty 2000). This supports the theory that *Bos indicus* genotypes require lower feed intake to meet maintenance requirements relative to *Bos taurus* contemporaries (Frisch and Vercoe 1969, 1977; Vercoe 1970). As *Bos indicus* breeds evolved under poor nutrition they have automatically been selected for low maintenance requirement (good survival ability), lower voluntary feed intake because of lower appetite, and consequently have lower growth rates relative to *Bos taurus* breeds even under good conditions (Frisch and Vercoe 1977).

Other studies have found no difference between *Bos indicus* and *Bos taurus* for feed efficiency. Cundiff *et al.* (1984) reported ADG of Brahman sired crossbreds tended to be lower than crossbreds from Angus and Hereford sires, though breed crosses did not differ significantly for feed efficiency (FCR). Similarly, Huffman *et al.* (1990) found no difference between straightbred Angus, ¾ Angus × ¼ Brahman, ½ Angus × ½ Brahman and ¼ Angus × ¾ Brahman breed groups for ADG, FI and FCR. Boyles (1986) reported no difference in overall feed efficiency between Angus and Brahman × Angus crossbred steers, however it was concluded that the maintenance requirement for Brahman crosses could be reduced by 6% relative to Angus under thermoneutral conditions.

2.3.6 Heterosis effects on feed efficiency

Few estimates of heterosis effects on feed efficiency exist because most studies have been done within breed and on purebreds. Given the general consensus that heterosis affects growth, weight and fat depth (reviews by Marshall 1994; Burrow *et al.* 2001), it may explain differences in liveweight, ADG, KR, RGR and possibly FI (indirect effect of increased liveweight on increased appetite) between straightbred and crossbred animals. Studies on egg production, mice and from simulation were briefly reviewed by Pitchford (2004) and conclude small positive improvements from heterosis could be expected on feed efficiency because of simple scale effects (increased size of animals). Gregory *et al.* (1999) reported mean retained heterosis from MARC I, MARC II and MARC III composite populations of -1.08 g on liveweight gain per Mcal of ME (time constant; $P<0.01$), though retained heterosis was not consistent between these populations, and these herds only contained *Bos taurus* breeds.

2.4 Female fertility

2.4.1 Quantifying fertility

Failure of a cow to conceive is the major component affecting the overall production efficiency of the cow herd (Roberts *et al.* 1993). Inherent fertility is the genetic potential for reproductive performance and is not directly measurable (Brinks 1996). Expressed fertility can be measured, but is dependent on the external environment and the additional stress created by the animal's potential for growth, size or milk production (Brinks 1996). Many studies have been conducted to find reliable indicators of fertility. These include age at puberty, days to conception, postpartum interval to conception, gestation length, days to calving, age at first calving, heifer pregnancy, pregnancy rate, calving rate, calf survival, calving interval, weaning rate, rebreeding rate, stayability and longevity. Scrotal circumference in males has successfully been used in direct selection for age at puberty in female offspring (Martin *et al.* 1992).

Improvement of female fertility in beef cattle involves selection of heifers with higher genetic potential to breed early in their first season and then continue to rebreed and calve early every year as mature females (Doyle *et al.* 2000). In a herd of Angus, Hereford, Shorthorn and first cross cows, Nunez-Dominquez *et al.* (1991) reported heifers that calved first as 2-year-olds had 10% greater economic efficiency at 6 years of age and 5% greater economic efficiency at 12 years of age relative to heifers calved first as 3-year-olds. Puberty may be defined as the process of change whereby animals are able to reproduce themselves (Kinder *et al.* 1994). Age at puberty may be the best measure of inherent fertility as it is expressed before a cow is in production and hence is less influenced by interactions with other traits (Martin *et al.* 1992). A review by Brinks (1996) concluded that heifers with an inherent ability to reach puberty early may breed at less cost than heifers with later inherent age at puberty because early puberty lines generally conceive early in the breeding season each year, conceive more calves and wean heavier calves than late puberty lines. Olson (1994) concluded early maturing heifers show greater fertility as young cows and can be maintained under less than optimal nutritional conditions when compared with later maturing heifers. On the other hand, a study by Evans *et al.* (1999) found that for every 20 day increase in age there was a corresponding 10% increase in the probability a heifer will conceive and remain pregnant. Further, decreasing age at first oestrus and subsequent calving first at 2 years of age has been linked to longer postpartum intervals to resumption of oestrus (Patterson *et al.* 1992a). Target mating weights (Short *et al.* 1994b) and rectal palpation for reproductive tract score (Brinks 1996) have traditionally been used for estimating age at puberty in heifers. More recently, transrectal ultrasonography has been used to accurately determine follicular activity and age at puberty in heifers.

Pregnancy rate is the proportion of females confirmed pregnant at 120 days post-mating out of the total number of females exposed to mating. Heifer pregnancy is defined as the probability of a heifer conceiving and remaining pregnant at 120 days, given that she was exposed at mating (Evans *et al.* 1999; Doyle *et al.* 2000). Pregnancy rate is a binary or threshold trait. Environmental influences play a strong role in determining on which side of the pregnant/non-pregnant threshold an individual record may fall (Martin *et al.* 1992). Breed, nutrition, lactation status, growth, body condition, season of birth, season of mating, length of mating season and mating method influence pregnancy rate.

Days to calving is defined as the number of days elapsing between the date of first exposure to mating and the date of calving (Davis *et al.* 1993). Days to calving is comprised of two traits that are difficult to measure directly; days to conception and gestation length. Everett *et al.* (1966) reported that days from first breeding to conception was one of the best indicators of breeding efficiency in dairy cows. A study by Davis *et al.* (1993) found that earlier conception and subsequent earlier calving in a Droughtmaster herd meant females had longer to resume cycling before the next mating season, resulting in 25% higher pregnancy rates and 25 days shorter days to calving in the high fertility line relative to the low fertility line by the third mating season. Gestation length varies within and between breeds, between years and sex of calf (Reynolds *et al.* 1990). Cows with shorter gestations have a reproductive advantage over cows with longer gestations because of shorter calving intervals and higher realised weaning weights as a result of calving earlier in the season (Brinks 1996).

Calving interval is defined as the interval elapsing between calving dates. Subsequent rebreeding is the observation of a 2-year-old cow conceiving and remaining pregnant to palpation at 105 days, given pregnancy as a yearling and exposure during the breeding season (Doyle *et al.* 2000). To ensure reproductive efficiency within a beef herd, females should calve every 365 days (Doyle *et al.* 2000). However calving interval is a poor measure of reproductive efficiency when a short breeding season is used (Brinks 1996). Calving interval is dependent on the resumption of oestrus cycles postpartum, the occurrence and detection of oestrous and the timeliness and duration of the joining period (Peters and Ball 1995). A study by Davis *et al.* (1993) found that cows calving earlier in the calving season had longer to resume cycling and returned from lactational anoestrus earlier than late calvers, which over time yielded higher pregnancy rates. Time from calving to first oestrus averages 40-60 days in *Bos indicus* (Abeygunawardena and Dematawewa 2004). Postpartum interval to oestrus is influenced by breed, body condition, parity, lactation, suckling, month of calving, environment (exercise, parasite burdens, ambient temperature and humidity) and endocrine status (Bellows and Short 1994; Abeygunawardena and Dematawewa 2004).

In mammals, animals with long life expectancy tend to be late maturing even after adjustment for different body size (Finch 1990; cited by Essl 1998). A review of dairy cattle by Essl (1998) reported that selection for high production (milk yield, body weight, growth rate) may result in negative correlated responses for fitness or longevity traits. A review of longevity in beef cattle found lifetime calf production from females first joined as yearlings was either significantly higher or not significantly different to females first joined as 2-year olds (Morris 1980a). Longevity is often affected by culling policy, with higher net reproduction per year leading to greater longevity (Morris 1980a). The unweighted average of studies showed lifetime calf crop weaned was expected to be equivalent to an extra 0.7 calves from heifers first joined as yearlings versus 2-years old (Morris 1980a). Short *et al.* (1994b) concurred, stating heifers need to become pregnant early in the breeding season to achieve a higher lifetime production potential. Stayability is the probability of a cow being in the breeding herd at or after the age of six years, given she had a calf as a replacement heifer. Stayability is directly associated with costs and returns in a beef cow calf operation (Golden *et al.* 2000).

2.4.2 Selection for female fertility: heritabilities, correlations

Heritability estimates for fertility traits range from low to high. Most genetic parameter estimates from the literature are based on *Bos taurus* breeds and crosses. Selection for age at puberty has been shown to respond quickly and significantly in beef cattle (Morris and Wilson 1996) with selection for precocious heifers posing an effective means of improving fertility in *Bos indicus* breeds (Nogueira 2004). Mackinnon *et al.* (1990) reported 12% higher pregnancy rates in high versus low pregnancy rate lines in a Droughtmaster herd despite similar liveweights at the beginning and end of mating, indicating good response to selection for pregnancy rate. Heritability estimates for age at puberty range from 0.24-0.61 (Macneil *et al.* 1984; Koots *et al.* 1994a; Gregory *et al.* 1995; Doyle *et al.* 1996; Splan *et al.* 1996; Tosh *et al.* 1996). Heritability estimates for gestation length are also high (0.36-0.51; Bourdon and Brinks 1982; Gregory *et al.* 1995; Morris and Cullen 1996). Selection for most other fertility traits, though permanent, is very slow because the underlying genetic merit for fertility is often not expressed due to environmental influences. While Eler *et al.* (2002) reported a heritability estimate for the probability of pregnancy at 14 months for Nellore heifers of 0.57, estimates for heifer pregnancy are much lower (0.14-0.21; Evans *et al.* 1999; Doyle *et al.* 2000). Low heritability estimates have been reported for pregnancy rate (0.04-0.17), days to calving (0.05-0.11), calving success (0.08-0.14), calving rate (0.08-0.17), calving interval (0.01-0.06), stayability (0.15-0.16) and rebreeding rate (0.16-0.19) (Meyer *et al.* 1990; Koots *et al.* 1994a; Davis 1993 (review); Doyle *et al.* 1996, 2000; Hyde *et al.* 1996; Johnston and Bunter 1996; Morris and Cullen 1996; Splan *et al.* 1996).

Selection for reduced days to calving should yield desirable responses in gestation length and pregnancy rate, while selection for early maturity may adversely affect calving ease and longevity. Morris and Cullen (1996) reported genetic correlations between days to calving and gestation length of 0.65±0.34 (first parity), days to calving and pregnancy rate of -0.93±0.21 (first parity) and pregnancy rate and gestation length of -0.35±0.22 and 0.20±0.26 for first and second parities respectively. In a study by Davis *et al.* (1993), divergent selection for pregnancy rate resulted in significantly ($P<0.05$) shorter days to calving of the high pregnancy rate line relative to the low pregnancy rate line for heifers and mature cows. A single round of selection for sires based on pregnancy rate EBVs was estimated to give genetic gain equivalent to or larger than that of 20 years of culling females for pregnancy failure (0.145% change per year; Davis *et al.* 1993). However, while selection for higher pregnancy rate lines may result in superior lifetime reproductive performance with no difference in mortality rate relative to low pregnancy rate lines, it has been shown to result in permanent stunting of cows (Seifert and Rudder 1975; Hetzel *et al.* 1989). A review by Koots *et al.* (1994b) reported a negligible genetic correlation between age at first calving and calving interval of 0.06. A study by Splan *et al.* (1996) reported that selection for decreased age at puberty will result in slightly increased calving rate but also increased difficulty with calving, while a review of longevity in dairy cattle by Essl (1998) reported a significant antagonism between early maturity and longevity.

Few studies have reported genetic and phenotypic correlations between fertility traits and production traits. Differences in inherent fertility are more pronounced in poor environments than good environments (Martin *et al.* 1992). In beef cattle under nutritional stress, the relationship of productivity with expressed fertility may be antagonistic even though the relationship between inherent fertility and productivity may be favourable (Brinks 1996). Davis *et al.* (1993) reported selection of sires based on EBVs for pregnancy rate in a herd of Droughtmaster cross cattle led to improved fertility in heifers and 4-year-old lactating cows without adverse effects on progeny growth. However, as nutrition and body condition are known to affect ovarian function, selection for some carcass traits (reduced subcutaneous fatness, increased retail beef yield) may be detrimental to fertility in replacement females (Macneil *et al.* 1984). Koots *et al.* (1994b) reported a desirable genetic correlation between conception rate and retail beef yield of 0.28, however this was from only one study. Genetic associations between fertility and adaptive traits are incomplete, hence care should be taken to prevent selection for fertility at the expense of important adaptation traits within a population.

Aside from the direct approach to selection for fertility, breeders may select for an array of traits that have phenotypic and genetic correlations with fertility, such as milk production, growth rate, calving ease and body condition (Martin *et al.* 1992). Hence, multiple-trait selection would combine a number of economically important traits in a selection index to optimise expressed fertility.

2.4.3 Crossbreeding and heterosis effects on fertility

An alternative to selection within breeds for fertility is crossbreeding, which yields desirable blending of fertility traits with other economically important traits including growth rate, beef quality, feed efficiency and adaptation. Crossbred heifers reach puberty at younger ages and heavier weights than their straightbred contemporaries, however heterosis effects on age at puberty decrease with increasing age (Martin *et al.* 1992). Further, hybrids of *Bos indicus* and *Bos taurus* exhibit heterosis in respect to age at puberty, with earlier onset than expected in crossbred animals (Nogueira 2004). A study by Dow *et al.* (1982) reported that compared to straightbred contemporaries, 18% more crossbred heifers were cycling at 11.5 months, 30% more at 15 months and 12% more at 19.5 months. While heterosis has negligible effects on pregnancy rate (Dow *et al.* 1982; Martin *et al.* 1992), crossbreeding can result in desirable heterosis effects with reduced days to calving and increased calving success (Prayaga 2004). Prayaga (2004) reported significant direct dominance effects on calving success (binomial trait) for lactating *Bos taurus* × *Bos indicus* crosses of 0.09 ± 0.03 ($P<0.01$), and on days to calving for *Bos indicus* × *Bos indicus* crosses of -13.4 ± 4.7 ($P<0.01$) and *Bos taurus* × *Bos indicus* crosses of -5.3 ± 2.7 ($P<0.05$). However, postpartum interval to oestrus has been shown to be extended in dams nursing crossbred calves relative to Brahman dams nursing Brahman calves (Browning *et al.* 1995).

2.4.4 Major genes for fertility

There are few documented studies of fertility genes for beef cattle. Matjuda *et al.* (1998) reported major genes were involved in the determination of age at first calving in an Afrikaner female population. There have been many studies in dairy cattle reporting QTL for economically important traits including production, conformation, health and fertility, though most studies are formative with further investigation and validation required (Boichard *et al.* 2003; Schrooten *et al.* 2000, 2004; Munice *et al.* 2006). Liefers *et al.* (2002) investigated the association between three markers at the leptin gene locus (RFLP1, RFLP2 and BM1500) and luteal activity in dairy cattle. Though results were not significant, Liefers *et al.* (2002) could not exclude an association between RFLP2 and commencement of luteal activity.

2.4.5 Environmental effects on fertility

2.4.5.1 Nutrition

The low heritabilities of most fertility traits indicate environment plays a large role in reproductive success. The two major factors affecting reproductive performance in beef cattle are nutrition and suckling (Wettemann 1994). It is well documented that diet affects follicular dynamics in cattle (Patterson *et al.* 1991; Robinson 1996; Armstrong *et al.* 2002; Gong 2002; Ciccioli *et al.* 2003). There is close relationship between fertility, body condition and nutritional status in pre-pubertal, lactating and non-lactating female cattle (Rhodes *et al.* 1996; Robinson 1996; Gong 2002). The interaction between nutrition and reproduction in cattle is very complex as nutrition can influence multiple sites of the reproductive axis (Gong 2002). Early studies focused on the hypothesis that nutrition and related metabolic signals acted on the hypothalamus-pituitary axis to modulate secretion of gonadotropins to influence ovarian function (Gong 2002). More recently, it has been suggested that nutrition may act directly at the ovarian level to influence ovarian follicle growth, oocyte maturation, early embryo development and metabolic hormones including growth hormone, insulin, insulin-like growth factors and leptin (Gong 2002).

Age at puberty is influenced primarily by the genetic makeup of the heifer and the nutrition or rate of gain during the weaning to pre-breeding period (Patterson *et al.* 1992b; Short *et al.* 1994b; Nogueira 2004). Poor nutrition in heifers suppresses luteinising hormone pulse frequency, size and growth rate of the dominant follicle, and oestrogen secretion, delaying first ovulation (Schillo *et al.* 1992; Gong 2002; Rawlings *et al.* 2003). Post and Reich (1980) reported that drought not only delayed the onset of puberty in tropical breeds, but also suppressed ovarian activity in half of the heifers that had already reached puberty. Further, Doogan *et al.* (1991) reported that liveweight gain in *Bos indicus* heifers during the post-weaning dry season resulted in 38% higher conception rates relative to contemporaries that lost weight during that period. Improving the plane of nutrition prior to mating can enhance the development of ovarian follicles and decrease the percentage of atretic follicles in the ovaries (Maurasse *et al.* 1985).

Following parturition, females exhibit anoestrus for a period of time to allow uterine involution to occur (Senger 1999). Low energy intake in pre- and postpartum heifers and cows significantly increases the length of the anoestrus period, and in heifers results in fewer ovarian follicles, lower progesterone levels and lower conception rates (Morris 1980b; Entwistle 1983; Hill *et al.* 1990; cited by Peters and Ball 1995; Roberts *et al.* 1993; Gong 2002; Abeygunawardena and Dematawewa 2004). Reduced diameter, growth and persistence of dominant follicles, and delays in development of large ovarian follicles are also typical of postpartum anoestrus (Rhodes *et al.* 1996; Diskin *et al.* 2003). Onset of nutritional anoestrus in cattle occurs after a weight loss of approximately 20-24% of their initial body weight (Rhodes *et al.* 1996; Diskin *et al.* 2003). Nutritional anoestrus is characterised by an absence of gonadotropin releasing hormone (GnRH) pulses from the hypothalamus, inadequate secretion of gonadotropins and inactive ovaries (Senger 1999). It is particularly prominent in first-calf cows where energy requirements of lactation and growth often out strip the female's ability to consume enough dietary energy to meet her metabolic needs, resulting in negative energy balance and consequent delayed postpartum return to oestrus (Senger 1999). Postpartum females subjected to nutritional anoestrus are likely to resume cyclicity after they have regained their pre-calving weight (Abeygunawardena and Dematawewa 2004). Further, feeding cows to gain weight postpartum has been shown to advance the first ovulation postpartum and increase conception rates (Gong 2002; Ciccioli *et al.* 2003).

2.4.5.2 Lactation

Lactational anoestrus is characterised by suppression of cyclicity following parturition as a consequence of females nursing their young (Senger 1999). Davis *et al.* (1993) reported pregnancy rates of 80% in Droughtmaster heifers as opposed to only 51% in lactating primiparous cows. A review by Abeygunawardena and Dematawewa (2004) concluded suckling causes suppression of GnRH secretion, pituitary sensitivity to exogenous GnRH, gonadotropin secretion, growth of follicles and ovulation in *Bos indicus* and *Bos taurus* breeds, resulting in extended postpartum intervals to oestrus. Peters and Riley (1982) reported a mean time to resumption of ovarian cycles of 59.9±2.5 days after calving in suckling beef cows. Further, McSweeney *et al.* (1990) reported a strong negative linear relationship between days to ovulation and preweaning calf growth rates in a Droughtmaster herd ($P<0.001$).

Research from Texas A&M University suggests mammary stimulation alone is not totally responsible for lactational anoestrus (Senger 1999). Evidence suggests sensory inputs from the presence of the cow's own calf including sight, sound and smell results in GnRH suppression and consequent lactational anoestrus (Senger 1999). Another study by McSweeney *et al.* (1989) supports this theory, showing that early weaning had a greater effect on the resumption of postpartum ovarian activity in Droughtmaster females than postpartum nutritional treatments. While partial and restricted suckling and early weaning may reduce the postpartum anoestrus period and increase pregnancy rates (Abeygunawardena and Dematawewa 2004), this has to be balanced with the higher management costs associated with handling and/or rearing calves artificially.

2.4.5.3 Liveweight, body condition score and fatness

It is widely accepted that age at puberty occurs at a certain body weight or body size rather than at a certain age (Gong 2002). Hence, target liveweights have been used as an indication of puberty and readiness to breed (Short *et al.* 1994b). Within breed, higher liveweights are associated with increased calf crop (Frisch *et al.* 1987; Evans *et al.* 1999). However, a study by Davis *et al.* (1993) reported that despite pre-mating liveweights being more than 30 kg above the target liveweight in divergent Droughtmaster lines selected for pregnancy rate EBV, significant differences between lines were found for pregnancy rate, weaning rate and days to calving in favour of the high line, suggesting that liveweight itself is not sufficient to predict pregnancy success.

Body condition score is a subjective measure of cow condition given cow size and milk level in a given nutritional environment (Brinks 1996). Body condition scoring has an advantage over measuring liveweight because it accounts for different sized cows, and is therefore a more accurate method of assessing nutritional status of cows (Kunkle *et al.* 1994). However, because it is a subjective measure there may be differences in operator assessment, particularly when cows are pregnant or have differing levels of gut fill. Body condition score of cows at calving has a vital role in regulating reproductive performance (Wettemann 1994; Brinks 1996). When there is inadequate nutrition to meet maintenance requirements of the cow, body stores which regulate the secretion of hypothalamic and pituitary hormones are mobilised, affecting normal function of the ovary (Wettemann 1994). The accumulation of body lipid reserves in pregnancy is an important strategy for safeguarding reproductive investment (Friggens 2003). Research on dairy cows by Garnsworthy and Topps (1982) showed there may be a target level of body fatness. Under the same nutritional conditions postpartum, cows with three different levels of body condition at calving (high, normal and low) mobilised lipid at different rates to end up with similar body condition scores 16 weeks postpartum. Greater body condition score of cows at calving has been shown to result in more cows in oestrus ($P<0.05$) and more cows pregnant within 40 and 60 days of the subsequent mating season ($P<0.05$; Spitzer *et al.* 1995). Conversely, thin cows that are slow to regain body lipid postpartum have extended anoestrus periods. Body condition score is favourably correlated with pregnancy rate, calving interval, calf age at weaning and calf daily gain, while there does not appear to be any negative effect on calving difficulty (Wettemann 1994). However, genetic and phenotypic correlations between body condition score in 2-year old beef females and age at puberty are low and negative (-0.09 and -0.02 respectively; Gregory *et al.* 1995) indicating body condition score is not terribly useful in selection for heifer fertility.

Siebert and Field (1975) demonstrated that the onset of puberty in cattle appeared closely related to body fat content. Weight gain or loss of 10-15% (mainly fat) in humans results in amenorrhoea, suggesting there may be a minimum level of stored easily mobilised energy necessary for ovulation and menstrual cycles (Frisch 1984). The same may be true for fertility in cattle. A feature of lactation is the accompanying mobilisation of body reserves, particularly lipid reserves. Further, there appears to be an innate drive to decrease body fatness in early lactation, regardless of level of nutrition (Friggens 2003). As the reproductive priority on the current calf decreases towards weaning, the reproductive priority of the future calf increases, as does the likelihood of oestrus returning postpartum (Friggens 2003). More recently, studies have examined the link between circulating levels of hormones linked to fatness and their effect on reproduction. Leptin is a product of the adipose obese (*ob*) gene and is secreted as a hormone from adipocytes. It has been associated with energy metabolism, feeding behaviour and reproduction in several monogastric species including humans (Spicer 2001; Smith *et al.* 2002; Williams *et al.* 2002). A review by Lackey *et al.* (1999) concluded the insulin growth factor (IGF) system exerts direct and regulatory action in the establishment and maintenance of reproductive maturity and function. Circulating concentrations of IGF-I and leptin have been shown to increase during puberty in heifers (Lackey *et al.* 1999; Garcia *et al.* 2002; Williams *et al.* 2002), while others have found variable results for these hormones (Luna-Pinto and Cronje 2000). Whether nutrition acts on circulating concentrations of leptin and IGF-I to advance ovulation postpartum is also inconclusive (Gong 2002; Ciccioli *et al.* 2003).

2.4.5.4 Season of birth, season of mating, herd health, female-female and dam effects

Season of birth is important, as photoperiodic cues induce earlier age at puberty in autumn-born heifers relative to spring-born heifers (Kinder *et al.* 1994). Under subtropical conditions, *Bos indicus* heifers show a direct effect of photoperiod upon the regulation of ovulatory activity (Mezzadra *et al.* 1993). *Bos indicus* and *Bos indicus* based cattle illustrate decreased reproductive function as day length decreases (Randel 1994). Neuendorff *et al.* (1984) reported higher first service conception rates in Brahman heifers in summer (61.4%) relative to winter (36.2%). This effect may also be attributed to seasonal conditions affecting pasture quality and growth. Seasonal anoestrus most likely evolved as a method of preventing females from conceiving during periods of the year when survival for the developing embryo and neonate would be low (Senger 1999). A review by Abeygunawardena and Dematawewa (2004) concluded that cows calving towards the end of the dry season have the opportunity to take advantage of improved nutritional conditions during the subsequent rainy season to meet their requirements for maintenance, growth and lactation. This resulted in shorter postpartum intervals to oestrus relative to cows calving in the dry season.

Herd health is vital in attaining high conception rates, including controlling reproductive and other diseases (Peters and Ball 1995). Presence of internal and external parasites can have a marked effect on condition score of cows (Kunkle *et al.* 1994) and cause increased age at puberty and reduced calving rates in Brahman, Africander and Hereford×Shorthorn females bred in tropical environments (O'Kelly *et al.* 1988). While a study by Mackinnon *et al.* (1990) of a tropical beef herd found no difference in tick resistance between high and low selection lines for pregnancy rate, they reported a significant genetic antagonism between cow fertility and resistance to intestinal worms ($P<0.05$). Further, O'Kelly *et al.* (1988) reported that parasite loads reduced calving rates when pasture quality was low, however calving rates were unaffected by parasites when pasture quality was higher, resulting in higher growth rates. Ambient temperature and humidity have variable affects on fertility. Mackinnon *et al.* (1990) found no evidence of differences in heat tolerance between high and low fertility Droughtmaster lines, however Turner (1982) estimated a genetic correlation of -0.76 between rectal temperature and pregnancy rate in Zebu cross cows in a subtropical environment.

A female-female effect on inducing oestrus has also been observed. The presence of cows in oestrus can bring on oestrus in heifers and shorten postpartum anoestrus in beef cows with extended anoestrus periods (Wright *et al.* 1994). Further, Evans *et al.* (1999) reported that heifers born from mature dams were 10% more likely to conceive and remain pregnant to palpation at 120 days than heifers born from heifers as a result of a better environment to grow and attain sexual maturity. Maternal undernutrition and, under certain circumstances overnutrition, before or during pregnancy or during early postnatal life can alter reproductive function of the offspring (Rhind 2004).

2.4.6 Fertility of tropically adapted breeds

It is estimated that more than half the world's cattle population has some proportion of *Bos indicus* germ plasm (Abeygunawardena and Dematawewa 2004). Most *Bos indicus* breeds grow slowly, take longer to reach puberty, are older at first calving, and have extended pre-pubertal and postpartum anoestrous periods relative to *Bos taurus* breeds under the same environment and management conditions, implicating genetics as a major contributor to reduced fertility in *Bos indicus* (Randel 1994; Abeygunawardena and Dematawewa 2004; Nogueira 2004). A review by Friggens (2003) reported that under harsh environmental conditions, most mammals produce fewer young or depress fertility and thereby avoid futile maternal investment. The fact that fertility is diminished in undernourished animals and humans suggests an ecological adaptation to reduced food supplies which is an advantage to the survival of the population (Frisch 1984). Therefore, while *Bos indicus* breeds are known to be less fertile and have lower levels of milk production relative to *Bos taurus* breeds, their superior adaptation make them more likely to reproduce successfully long-term in tropical environments (Nogueira 2004).

A review by Abeygunawardena and Dematawewa (2004) reported that on average, *Bos indicus* cattle reach puberty 6-12 months later than *Bos taurus* cattle. Frisch *et al.* (1987) concluded that despite similar mature weights, Brahman females need to attain higher liveweights than Hereford × Shorthorn crosses before they will successfully produce a calf. *Bos indicus* cattle do not appear to achieve puberty until they reach 60% of their adult body weight, while *Bos taurus* breeds achieve puberty within 30-55% of their adult body weight

(Abeygunawardena and Dematawewa 2004). A high incidence of anovulatory oestrus has been found in *Bos indicus* heifers, along with observation of more than one nonpuberal oestrus (Kinder *et al.* 1994). Warnick (1994) reported frequency of nonpuberal oestrus ranging from 17-63% of heifers studied. Studies generally agree that *Bos indicus* and *Bos indicus* crosses achieve puberty at about 270-280 kg liveweight (Rudder *et al.* 1985; Doogan *et al.* 1991). Nutrition, disease, temperature, humidity and season of birth have all been implicated in onset of puberty in *Bos indicus* (Nogueira 2004).

In tropical climates, both *Bos taurus* and *Bos indicus* breeds may be susceptible to seasonal anoestrus, short oestrus cycles, poor conception rates and increased embryo mortality (Peters and Ball 1995). *Bos indicus* breeds have been shown to have a shorter standing oestrus than *Bos taurus* breeds (Randel 1994). Cundiff *et al.* (1993) reported *Bos indicus* × *Bos taurus* crosses had 6% higher pregnancy rates than *Bos taurus* × *Bos taurus* crosses in Florida. However, a review by Franke (1980) reported that straightbred Brahmans generally had lower calving percentage, lower calf survival rate and lower weaning rate than British straightbred contemporaries in the Gulf Coast region of the USA. Davis *et al.* (1993) observed 12% wastage between pregnancy diagnosis and tagging in *Bos indicus* in the dry tropics of coastal northern Queensland, suggesting disease, neonatal losses due to adverse environmental conditions or predation may have been responsible. On the other hand, Bellows and Short (1994) suggest early embryonic death may result from maternal heat stress adversely affecting oocyte meiotic maturation prior to fertilisation.

Bos indicus breeds tend to have longer gestation lengths than other genotypes. A review by Randel (1994) reported average gestation lengths in *Bos indicus*, *Bos indicus* crosses and *Bos taurus* of 293, 286 and 282 days respectively. Corbet *et al.* (1997) reported slightly longer gestation lengths (3 days) in Brahmans relative to Belmont Red × Brahman crosses (n.s.). In the same study, calves by British breed sires had significantly shorter gestation lengths (5.0±0.7 days; $P<0.01$) than calves by Continental and Brahman sires to Brahman dams. Mean gestation length was 284±1.5 days (range 271-296). A cow must conceive within 80 days postpartum to maintain a 365-day calving interval. Postpartum infertility can result from general infertility, lack of uterine involution following parturition, short oestrous cycles and anoestrus (Short *et al.* 1994a; Randel 1994; Bellows and Short 1994). The inherently longer gestation lengths of *Bos indicus* breeds relative to *Bos taurus*, together with adverse environmental conditions, means achieving a 365-day calving interval is difficult for *Bos indicus* breeds.

2.5 Summary

Brahman is the predominant breed in northern Australian beef herds because of its ability to survive and reproduce successfully in tropical, subtropical and semi-arid environments. The majority of Australian beef cattle are produced in northern Australia. Australia's major markets demand a year round supply of beef of consistent high eating quality. However, Brahmans are reputed to have poorer carcass and meat quality, poor performance in feedlots and poorer fertility relative to other tropically adapted breeds, *Bos taurus* breeds and crossbreds. There has been limited research on traits of economic importance conducted in northern Australia, and none that examine differences between several genotypes within a study using large numbers of animals. Studies conducted overseas lack direct relevance to Australia's northern cattle production systems, finishing regimes, processing practices and markets. Therefore, this thesis aimed to determine if tropically adapted crossbreds and composites can perform as well as straightbred Brahmans for economically important production and reproduction traits under tropical and subtropical conditions in northern Australian using commercial beef production practices.

CHAPTER 3 Carcass quality of Brahman and first-cross cattle grown on pasture and grain in subtropical and temperate Australia

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Abstract. Brahmans are known to have poorer carcass quality relative to *Bos taurus* breeds and crossbreds under temperate environments, however little is known of their performance in subtropical environments. The Beef CRC initiated a crossbred progeny test experiment to compare straightbred Brahmans with Brahman crossbreds finished on pasture and grain, in subtropical and temperate environments, to carcass quality specifications of Australian domestic and export markets. Brahman, Belmont Red, Santa Gertrudis, Angus, Hereford, Shorthorn, Charolais and Limousin sires were mated to Brahman females in subtropical Queensland over three years to produce 1750 progeny. At a common age at slaughter, Charolais crossbreds had the highest hot carcass weight (CWT) but were not significantly heavier than Limousin or British crossbred progeny. At common carcass weights, breeds within breed type (British, Continental, tropically adapted) performed similarly. British and Santa Gertrudis crossbreds had the fattest carcasses and lowest yields. British and Belmont Red crossbreds had the highest intramuscular fat percent (IMF). Continental crossbreds had the highest retail beef yield (RBY), kilograms of retail primals (RTPM) and percent retail primals (pcRTPM) and leanest carcasses. Brahmans had the lowest CWT, intermediate subcutaneous fat cover and yields and low IMF. Animals finished on subtropical pasture were significantly older, leaner and had higher RBY, RTPM and pcRTPM than subtropical feedlot-finished contemporaries. Temperate feedlot animals had significantly more IMF, less subcutaneous fat at the P8 site (HOTP8) and slightly lower yields than subtropical feedlot contemporaries, indicating possible effects of post-weaning growth path on fat distribution. Belmont Red crossbreds demonstrated the advantages of adaptation with the highest IMF in both subtropical finishing regimes, while Angus progeny had the highest IMF in the temperate feedlot environment and highest IMF overall. Significant interactions were mainly the result of scale effects rather than breed re-ranking for carcass traits across markets and finishing regimes. Therefore, breeds that performed well for certain carcass traits in subtropical environments performed consistently for those traits in temperate environments relative to other sire breeds, regardless of market endpoint or finishing nutrition. Lack of important interactions suggests that changing breeds to target different finishing regimes or different markets is not warranted.

3.1 Introduction

By the early 1990s, beef eating quality and consistency of its supply had become the key issue for Australian domestic and export markets (Bindon 2001; Egan *et al.* 2001). Despite declining consumption of beef, the domestic market remains the largest single market for Australian beef, commanding 37% of total beef production (Bindon and Jones 2001). Australia is the worlds largest beef exporter contributing 25% of the total beef traded in 2003-04, worth $3.9 billion to the economy (ABS 2005). Between 1988 and 1995, beef exports increased by 30% primarily in Japan and Korea, and in the live-export trade to south-east Asia (Bindon and Jones 2001; Bindon

2001). Japan remains Australia's most important premium export beef market consuming 20.3% of total beef production in 2004-05 (ABS 2006). The USA is Australia's largest importer of manufacturing beef, while Korea is the third largest export market. By the mid-1980s, the USA realised the potential of the Japanese and South Korean beef markets and became a major competitor with Australia. Since then Australian beef producers have been under increasing pressure to become consumer-driven, focussing on consistency and reliability of supply to maintain market share.

The majority of Australia's 27.5 million beef cattle are produced in northern states (Queensland 42%, Northern Territory 16%; ABS 2006). Production potential cannot be fully expressed unless animals are highly adapted to their production environment (Frisch 1997). Brahmans and Brahman crossbreds predominate in the tropical, subtropical and semi-arid regions of northern Australia because of their superior adaptation in harsh environments. Consequently, more than 50% of the national herd is estimated to have some Brahman genes (Bindon 2002). By the late 1980s and early 1990s, *Bos indicus* × *Bos taurus* types were supplying most of the export trade from Queensland (Ball and Johnson 1989). However, growth rates were significantly affected by seasonal fluctuations in pasture quality and supply, causing periods of fast weight gain during the wet season and weight stasis or loss during the dry season. This resulted in up to 30% of animals failing to meet target liveweights for Japanese and Korean markets by winter in many finishing areas of Queensland (Jeffery *et al.* 1993). As a consequence, the feedlot sector expanded in northern Australia to improve growth rates, reduce age at turnoff and improve carcass compliance with market specifications. However new problems were arising for the northern Australian beef industry, with Brahmans developing a reputation for poor carcass and meat quality and poor performance in feedlots relative to *Bos taurus* breeds and crossbreds, threatening their premium markets.

Considerable research has been reported on British, Continental and Brahman crossbreds grown in temperate environments, one of the most well known and comprehensive research projects being the ongoing Germplasm Evaluation Program conducted at the USDA Meat Animal Research Center (MARC) at Clay Center, Nebraska (Cundiff *et al.* 1998; Cundiff *et al.* 2001). However, there is limited research comparing carcass quality of straightbred Brahmans with Brahman × British and Brahman × Continental crossbreds finished in tropical and subtropical environments. Where carcass quality of Brahman × British and Brahman × Continental breeds have been reported in such environments (Peacock *et al.* 1977; DeRouen *et al.* 1992a) the temperature extremes and rainfall patterns differ significantly relative to Australian subtropical and semi-arid environments. Further, cattle production systems, finishing regimes, processing practices and markets differ significantly between other countries and Australia.

Consequently, the Beef Cooperative Research Centre (Beef CRC) initiated the Northern Crossbreeding Program in 1994 to examine genetic and non-genetic factors influencing beef quality from breeding through to consumption. The crossbreeding progeny test experiment aimed to compare the carcass quality characteristics of straightbred Brahmans relative to different Brahman crossbred genotypes when finished on pasture and grain, in subtropical and temperate environments, that were best suited to beef quality specifications of Australian domestic and export markets. Preliminary results were reported by Newman *et al.* (1998, 1999, 2002). The purpose of this paper is to report the final results and their implications for the Australian beef industry.

3.2 Materials and methods

3.2.1 Experimental design and animals

The Beef CRC Northern Crossbreeding Program was designed to determine genetic and non-genetic factors influencing carcass and meat quality of Brahman and first-cross animals bred in a subtropical environment, and finished on pasture and grain in subtropical and temperate environments. The finishing environments were based on the typical northern Australia beef industry practice of finishing animals at pasture or in feedlots in Queensland or northern New South Wales. Animals were grown to Australia's three main market endpoints, being domestic, Korean and Japanese. Full details of the experimental design, measurements and data storage were described by Upton *et al.* (2001).

Briefly, northern Australian pastoral companies, individual beef producers and the Queensland Department of Primary Industries donated 1,000 Brahman females for the Crossbreeding Program. Seven hundred cows were joined at 'Duckponds' and 300 cows were joined at Brigalow Research Station, both in subtropical central Queensland, to produce 1,750 Brahman and first-cross progeny over three years. The eight sire breeds selected for the experiment were based on common breeds used in industry. They represented *Bos indicus* (Brahman – purebred control), *Bos indicus* × British-derived (Santa Gertrudis), *Bos taurus* × Sanga-derived (Belmont Red; Sanga cattle originated from Africa), *Bos taurus* – British (Angus, Hereford, Shorthorn) and *Bos taurus* – Continental (Charolais, Limousin). Brahman, Santa Gertrudis and Belmont Red are tropically adapted breeds.

Selection of sires was primarily by the collaborating seedstock breeders in the Beef CRC Straightbreeding Program, as described by Upton *et al.* (2001). To compare sire performance relative to industry herds, all sires used in the program were performance-recorded through their breed society's GROUP BREEDPLAN. At the time of selection, carcass and meat quality estimated breeding values (EBVs) were not available and hence selection of sires is assumed to have been made without regard for these traits. Common sires were used across the Beef CRC Straightbreeding and Crossbreeding Programs to generate genetic linkages between the programs. Table 3.1 (derived from Table 5, Upton *et al.* 2001) shows EBVs for growth, fertility and carcass attributes for all sires used in the Crossbreeding Program. It also includes the breed average EBVs for animals born in 1997 for each trait, listed in brackets, showing that sires used in the Crossbreeding Program were close to their breed averages for most traits.

Table 3.1 Average estimated breeding values for growth, fertility and carcass attributes for all sires used in the CRC crossbreeding program. Breed average EBVs for animals born in 1997 for each of the traits are shown in brackets. (EMA = eye muscle area, IMF = intramuscular fat percentage, RBY = retail beef yield percentage; table derived from Upton *et al.* 2001).

Breed	Birth weight (kg)	200-day milk (kg)	200-day weight (kg)	400-day weight (kg)	600-day weight (kg)	Mature weight (kg)	P8 fat depth (mm)	Rib fat depth (mm)	EMA (cm^2)	IMF (%)	RBY (%)	Scrotal size (cm)	Days to calving (days)	Calving ease (d) (units)	Calving ease (m) (units)
Brahman		0.0	12	16	23		-0.4	-0.4	1.5	0.1	0.3	1.4			
		(-1.0)	(10)	(14)	(18)		(0.1)	(0.1)	(1.6)	(0.1)	(0.2)	(0.4)			
Belmont Red	2.9	0.1	10	13	19		0.2	0.0	0.8	0.1	0.0	0.6			
	(1.6)	(1.0)	(7)	(9)	(14)		(0.0)	(0.0)	(1.5)	(0.1)	(0.1)	(0.2)			
Santa Gertrudis		-1.8	6	9	8	7	-0.1	0.1	0.5	0.1	0.1	0.3			
		(0.0)	(2)	(2)	(2)	(2)	(0.0)	(0.0)	(0.6)	(0.0)	(0.2)	(0.0)			
Angus	3.4	7.2	28	57	74	78	0.0	0.0	1.8	0.3	0.2	0.9	-1.6	1.1	1.9
	(3.8)	(7.0)	(25)	(46)	(61)	(61)	(-0.1)	(-0.1)	(0.6)	(0.0)	(0.1)	(0.7)	(-0.6)	(-0.3)	(0.1)
Hereford	6.1	8.9	27	46	68	73	-0.2	-0.3	1.0	-0.3	0.4	1.4	-1.1	-4.7	0.1
	(3.6)	(5.8)	(18)	(28)	(42)	(43)	(0.0)	(0.0)	(0.3)	(-0.1)	(0.1)	(0.7)	(-0.7)	(-0.8)	(-0.1)
Shorthorn	1.8	3.9	12	14	19		-0.5	-0.4	0.2	0.0	0.1	0.5			
	(1.9)	(3.0)	(12)	(17)	(24)		(-0.5)	(-0.5)	(1.6)	(0.0)	(0.2)	(0.5)			
Charolais	0.8	2.7	10	17	28		-0.1	-0.1	0.1		-0.3	0.6		-0.2	
	(0.7)	(2.0)	(6)	(11)	(14)		(0.0)	(0.0)	(0.9)		(0.0)	(0.2)		(-0.3)	
Limousin	1.7	0.9	9	16	24	25	-0.1	-0.1	0.9	0.0	0.2	0.3	0.3	-2.3	-0.5
	(1.2)	(1.0)	(10)	(16)	(22)	(21)	(0.0)	(0.0)	(0.5)	(0.0)	(0.0)	(0.2)	(0.0)	(-1.1)	(0.0)

Artificial insemination (AI) was used to generate the majority of the crossbred progeny, followed by natural mating with back-up bulls of a different breed. Natural mating also occurred at the same time as the AI programs to prevent confounding of calves by AI and natural mating. British breeds were not used as back-up sires due to their inability to cope with northern environmental stressors. A full description of AI programs and parentage determination is given by Corbet *et al.* (1997, 1999). The aim was to produce about 10 steers and 10 heifers per sire. The optimal number of sires, offspring per sire and number of link sires between herds and allocation of animals to treatment combinations are discussed by Robinson (1995). Newman *et al.* (2002) estimated mean sire EBVs (expressed as deviations from contemporary group) to assess the randomness of sire allocations across contemporary groups, and found that sires were effectively randomly allocated. All male calves were castrated at about four months of age. Table 3.2 shows the number of sires per breed and the number and sex of progeny generated per breed.

Table 3.2 Number of sires and progeny per sire breed.

Sire breed	Number of sires	Heifer progeny	Steer progeny	Total
Brahman	14	166	154	320
Belmont Red	14	160	217	377
Santa Gertrudis	8	75	66	141
Angus	10	65	84	149
Hereford	8	68	66	134
Shorthorn	8	58	57	115
Charolais	15	114	109	223
Limousin	14	139	152	291
Total	91	845	905	1750

A designed approach using all target carcass weights and finishing regimes each year was preferable to evaluating each target carcass weight or finishing regime in turn, in order to prevent confounding of effects with years and sires (Robinson 1995). It also allowed investigation of variability over years and provided a more realistic estimate of sire and treatment effects over the range of years (Upton *et al.* 2001). Robinson (1995) developed a suite of computer programs to generate designs that were as balanced as possible with respect to (i) main effects of treatments, (ii) 2-way interactions between treatment factors, and (iii) higher order interactions for offspring of each sire, as well as for all animals in each herd and for all animals in the management group. Once the best design was identified, another program allocated the offspring of the designated sires to treatment combinations. In addition, because sires and all other factors were as balanced as possible, adjustment of treatment means for sire, age and other factors was minimised (Upton *et al.* 2001).

3.2.2 Treatments

Calves were weaned in 1996, 1997 and 1998 at about six months of age. At weaning, calves born at Brigalow Research Station were transferred to 'Duckponds'. Equal numbers of calves of each sire were assigned by sex, age and weight to one of three market endpoints; domestic, Korean, Japanese; and one of three finishing regimes; northern (subtropical) pasture, northern (subtropical) feedlot, southern (temperate) feedlot (Robinson 1995). Only steers were finished to Japanese weights. Both subtropical finishing regimes included grow out on buffel grass pasture (*Cenchrus ciliaris*) at 'Duckponds' following weaning. Mean daily temperatures ranged from 20.7 to 34.8°C in summer and 6.9 to 24.8°C in winter, with mean relative humidity ranging from 33% and 69% and an average annual rainfall of 640 mm (latitude -23.5694 S, longitude 148.1756 E, elevation 190 m; Bureau of Meteorology 2006). Following weaning, one third of the calves were transferred to temperate pasture at Glen Innes Research Station (native and introduced pastures, refer to Ayres *et al.* 2001) or 'Tullimba' (native wallaby grass, *Austrodanthonia spp.*) in north-eastern New South Wales to grow out to feedlot entry weights. In the temperate environment at Glen Innes Research Station, mean daily temperatures ranged from 12.1 to 25.2°C in summer and 0.7 to 13.9°C in winter, with mean relative humidity ranging from 65% and 81% and an average annual rainfall of 848 mm (latitude -29.6952 S, longitude 151.6936 E, elevation 1060 m; Bureau of Meteorology 2006). In the temperate environment at 'Tullimba', mean daily temperatures ranged from 13.4 to 30.3°C in summer and 0.1 to 16.5°C in winter, with an average annual rainfall of 766 mm (latitude -30.1711 S, longitude 151.0757 E, elevation 654 m; Bureau of Meteorology 2006).

Animals assigned to feedlot-finishing were transferred to their respective feedlots when they reached liveweights of 300 kg for domestic and 400 kg for export markets. Finishing treatments included subtropical buffel grass pasture at 'Duckponds', subtropical feedlot at 'Goonoo' in central Queensland, and temperate feedlot at 'Tullimba'. Domestic animals were fed for an average of 60 days, while export animals were grain fed for a minimum of 90 days (Upton *et al.* 2001). Diets between feedlots were kept as similar as possible, though commercial constraints resulted in minor differences in diets over the experimental period.

A cohort was defined by a combination of sex, year of birth, market endpoint and finishing regime. All animals within a cohort were managed as a single group during grow out, finish, pre-slaughter and slaughter, with the exception of a few cohorts that were slaughtered over two consecutive days to facilitate measurement of retail beef yield. All animals within a cohort were slaughtered when the average weight of their group reached target carcass weights of 220, 280 and 340 kg for domestic, Korean and Japanese markets respectively. One half of all steers finished in the subtropics received repeated implants of the hormonal growth promotant (HGP), Compudose 100®, every 100 days from about 15 months of age to slaughter. Experimental details and results for the HGP experiment were reported by Hunter *et al.* (2001).

3.2.3 Slaughter protocols and carcass measurements

Details of chiller measurements, sample removal and yield measurements were reported by Perry *et al.* (2001). Best practice pre- and post-slaughter procedures were used. The left side of each carcass was used for sample collection and yield measurements. Abattoir assessors measured CWT and HOTP8 prior to chilling. Carcasses were placed in chillers within one hour of slaughter and hung by the Achilles tendon. Carcasses were quartered 20-24 hours after slaughter. Abattoir personnel broke the carcass down to 17 boneless primal cuts and recorded untrimmed weights (AUS-MEAT 1998). Primals were then prepared to commercial specifications as described by Perry *et al.* (2001). RBY was calculated as described in Table 3.3. Due to disruption of commercial processing procedures, not all animals were measured for every carcass trait, resulting in different numbers of animals having records for the various traits. After July 1997, abattoir conditions precluded full yield determination on all animals, with crossbred animals measured for yield at 3 mm fat cover only (Perry *et al.* 2001). From early 1998 a modified yield measurement protocol was used because of disruptions to the commercial chain. Hence, RBY and RTPM were only recorded for the 1996 calf crop. IMF chemical fat percentage was calculated for the *M. longissimus thoracis et lumborum* using solvent extraction with Soxhlet apparatus or near infrared spectrophotometry (NIR) (Perry *et al.* 2001). Traits reported in this paper are described in Table 3.3.

Table 3.3 Abbreviations and definitions of carcass traits reported in this study (refer to Perry et al. (2001) for full description of traits).

Abbreviation	Definition of traits
AGE (days)	Age at slaughter.
CWT (kg)	Hot carcass weight. Carcasses were dressed according to AUS-MEAT standard specifications (AUS-MEAT 1998).
HOTP8 (mm)	Subcutaneous rump fat depth recorded at the P8 site on the hot carcass.
IMF (%)	Intramuscular chemical fat percentage was calculated for the *M. longissimus thoracis et lumborum*. Two procedures based on solvent extraction using Soxhlet apparatus, and a third using near infrared spectrophotometry (NIR) with a Technicon Infralyser 450, were applied to ground samples to estimate chemical fat content (refer to Perry *et al.* 2001).
RBY (%)	Adjusted retail beef yield percentage. The total weight of 17 trimmed boneless retail primal cuts (RTPM) plus the weight of adjusted manufacturing trim (all other lean tissue), expressed as a percentage of the left-side CWT.
RTPM (kg)	Weight of 17 boneless retail primals. The ribset, chuck, chuck tender, point end brisket, navel end brisket, intercostals, shin, tenderloin, thin flank and shank were trimmed to 10 mm fat thickness. The topside, outside flat, thick flank, rump, striploin, eye round and blade were trimmed to 3 mm (Perry *et al.* 2001).
pcRTPM (%)	Retail primals as a percentage of hot carcass weight.

3.2.4 Statistical analyses

Least squares means for fixed effects were estimated using the GLM Procedure of SAS (SAS 2000). Initially a mixed model procedure was used fitting fixed effects of breed, market, finish, sex, year of birth, herd of origin and HGP treatment. Partial confounding of fixed effects and slaughter groups and missing subclasses prevented the model from converging. A second model was developed where each independent variable was fitted separately, and a second independent variable accounting for all remaining fixed effects was included. Sire nested within breed was fitted as a random effect in the breed analysis and was also used as the error term to test breed differences. The multiple-range test devised by Duncan (1955) and extended by Kramer (1957) was used to test for significant differences between means.

Beef markets dictate that animals are sent to slaughter based on liveweight and subsequent carcass weight. Therefore hot carcass weight was used as the covariate to adjust all other carcass traits to a common basis for comparison. Data were analysed across sex. AGE, HOTP8, IMF, RBY, RTPM and pcRTPM were adjusted to a common hot carcass weight for breed and finish effects and a common hot carcass weight within market endpoint for market and sex within market effects. As British crossbreds were older than other genotypes because they were all bred by AI, CWT was adjusted for age at slaughter for breed effects only. CWT was unadjusted for finish, market and sex within market effects. Steers implanted with HGP were excluded from analyses for finish and sex effects due to confounding with location and sex. Subsequently, only 1473 animals were analysed for finish and sex effects. The final models were:

Breed effects on CWT:

$$y_{ijkl} = \mu + \boldsymbol{breed}_j + \boldsymbol{otherFE}_k + \boldsymbol{sire}_{l(j)} + b_1\boldsymbol{AGE}_{ijkl} + b_2\boldsymbol{AGE}_{ijkl}^2 + \varepsilon_{ijkl} \tag{1}$$

where y_{ijkl} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{breed}_j$ is the effect of the jth sire breed, $\boldsymbol{otherFE}_k$ is the effect of the kth group that accounts for all other fixed effects concatenated into one variable (sex || market || finish || year of birth || herd of origin || HGP treatment), $\boldsymbol{sire}_{l(j)}$ is the random effect of the lth sire nested within the jth breed, $\boldsymbol{AGE}_{ijkl}$ is effect of age at slaughter fitted as a quadratic covariate, and ε_{ijkl} is the residual error term.

Breed effects on AGE, HOTP8, IMF, RBY, RTPM and pcRTPM:

$$y_{ijkl} = \mu + \boldsymbol{breed_j} + \boldsymbol{otherFE_k} + \boldsymbol{sire_{l(j)}} + \boldsymbol{b_l CWT_{ijkl}} + \varepsilon_{ijkl} \quad (2)$$

where y_{ijkl} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{breed_j}$ is the effect of the jth sire breed, $\boldsymbol{otherFE_k}$ is the effect of the kth group that accounts for all other fixed effects concatenated into one variable (sex || market || finish || year of birth || herd of origin || HGP treatment), $\boldsymbol{sire_{l(j)}}$ is the random effect of the lth sire nested within the jth breed, $\boldsymbol{CWT_{ijkl}}$ is the linear effect of carcass weight of the animal fitted as a covariate, and ε_{ijkl} is the residual error term.

Finishing regime effects on CWT:

$$y_{ijk} = \mu + \boldsymbol{finish_j} + \boldsymbol{otherFE_k} + \varepsilon_{ijk} \quad (3)$$

where y_{ijk} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{finish_j}$ is the effect of the jth finishing regime, $\boldsymbol{otherFE_k}$ is the effect of the kth group that accounts for all other fixed effects concatenated into one variable (breed || sex || market || year of birth || herd of origin; HGP treatment was excluded), and ε_{ijk} is the random residual error.

Finishing regime effects on AGE, HOTP8, IMF, RBY, RTPM and pcRTPM:

$$y_{ijk} = \mu + \boldsymbol{finish_j} + \boldsymbol{otherFE_k} + \boldsymbol{b_l CWT_{ijk}} + \varepsilon_{ijk} \quad (4)$$

where y_{ijk} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{finish_j}$ is the effect of the jth finishing regime, $\boldsymbol{otherFE_k}$ is the effect of the kth group that accounts for all other fixed effects concatenated into one variable (breed || sex || market || year of birth || herd of origin; HGP treatment was excluded), $\boldsymbol{CWT_{ijk}}$ is the linear effect of carcass weight of the animal fitted as a covariate, and ε_{ijk} is the random residual error.

Market endpoint effects on CWT:

$$y_{ijk} = \mu + \boldsymbol{market_j} + \boldsymbol{otherFE_k} + \varepsilon_{ijk} \qquad (5)$$

where y_{ijk} is the observation for a dependent variable for animal i, μ is the overall mean, $\boldsymbol{market_j}$ is the effect of the jth market endpoint, $\boldsymbol{otherFE_k}$ is the effect of the kth group that accounts for all other fixed effects concatenated into one variable (breed || sex || finish || year of birth || herd of origin || HGP treatment), and ε_{ijk} is the random residual error.

Market endpoint effects on AGE, HOTP8, IMF, RBY, RTPM and pcRTPM:

$$y_{ijk} = \mu + \boldsymbol{market_j} + \boldsymbol{otherFE_k} + \boldsymbol{CWT_{ik(j)}} + \varepsilon_{ijk} \qquad (6)$$

where y_{ijk} is the observation for a dependent variable for animal i, μ is the overall mean, $\boldsymbol{market_j}$ is the effect of the jth market endpoint, $\boldsymbol{otherFE_k}$ is the effect of the kth group that accounts for all other fixed effects concatenated into one variable (breed || sex || finish || year of birth || herd of origin || HGP treatment), $\boldsymbol{CWT_{ik(j)}}$ is the linear effect of carcass weight of the animal fitted as a covariate and nested within market endpoint, and ε_{ijk} is the random residual error. Models 5 and 6 were also used to analyse year and property of origin effects on respective carcass traits.

Sex effects on CWT:

$$y_{ijkl} = \mu + \boldsymbol{market_j} + \boldsymbol{sex_{k(j)}} + \boldsymbol{otherFE_l} + \varepsilon_{ijkl} \qquad (7)$$

where y_{ijkl} is the observation for a dependent variable for animal i, μ is the overall mean, $\boldsymbol{market_j}$ is the effect of the jth market endpoint, $\boldsymbol{sex_{k(j)}}$ is the effect of the kth sex nested within the jth market endpoint, $\boldsymbol{otherFE_l}$ is the effect of the lth group that accounts for all other fixed effects concatenated into one variable (breed || finish || year of birth || herd of origin; HGP treatment was excluded), and ε_{ijkl} is the random residual error.

Sex effects on AGE, HOTP8, IMF, RBY, RTPM and pcRTPM:

$$y_{ijkl} = \mu + \boldsymbol{market}_j + \boldsymbol{sex}_{k(j)} + \boldsymbol{otherFE}_l + b_1\boldsymbol{CWT}_{ikl(j)} + \varepsilon_{ijkl} \qquad (8)$$

where y_{ijkl} is the observation for a dependent variable for animal i, μ is the overall mean, $\boldsymbol{market}_j$ is the effect of the *j*th market endpoint, $\boldsymbol{sex}_{k(j)}$ is the effect of the *k*th sex nested within the *j*th market endpoint, $\boldsymbol{otherFE}_l$ is the effect of the *l*th group that accounts for all other fixed effects concatenated into one variable (breed || finish || year of birth || herd of origin; HGP treatment was excluded), $\boldsymbol{CWT}_{ikl(j)}$ is the linear effect of carcass weight of the animal fitted as a covariate and nested within market endpoint, and ε_{ijkl} is the random residual error.

Least squares means were estimated for two-way interactions between all fixed effects. Of particular interest were breed × finish, breed × market and market × finish interactions. Interactions were calculated with concatenated fixed effects models using the GLM Procedure of SAS (SAS 2000). The two main effects being evaluated were fitted separately and a concatenated variable comprising all remaining fixed effects was included. Interactions for CWT were adjusted for AGE, while all other carcass traits were adjusted for CWT. For example, the model used to test breed × finish interaction effects on CWT was:

$$y_{ijkl} = \mu + \boldsymbol{breed}_j + \boldsymbol{finish}_k + \boldsymbol{otherFE}_l + \boldsymbol{(breed*finish)}_{jk} + b_1\boldsymbol{AGE}_{ijkl} + b_2\boldsymbol{AGE}_{ijkl}^2 + \varepsilon_{ijkl} \qquad (9)$$

where y_{ijkl} is the observation for a dependent variable for animal i, μ is the overall mean, $\boldsymbol{breed}_j$ is the effect of the *j*th sire breed, $\boldsymbol{finish}_k$ is the effect of the *k*th finishing regime, $\boldsymbol{otherFE}_l$ is the effect of the *l*th group that accounts for all other fixed effects concatenated into one variable (sex || market || year of birth || herd of origin), $\boldsymbol{(breed*finish)}_{jk}$ is the interaction for the *j*th sire breed and *k*th finishing regime, $\boldsymbol{AGE}_{ijkl}$ is effect of age at slaughter fitted as a quadratic covariate, and ε_{ijkl} is the random residual error.

The model used to test breed × finish interaction effects on AGE, HOTP8, IMF, RBY, RTPM and pcRTPM was:

$$y_{ijkl} = \mu + \mathbf{breed}_j + \mathbf{finish}_k + \mathbf{otherFE}_l + (\mathbf{breed*finish})_{jk} + b_l\mathbf{CWT}_{ijkl} + \varepsilon_{ijkl} \qquad (10)$$

where y_{ijkl} is the observation for a dependent variable for animal ***i***, μ is the overall mean, $\mathbf{breed}_j$ is the effect of the ***j***th sire breed, $\mathbf{finish}_k$ is the effect of the ***k***th finishing regime, $\mathbf{otherFE}_l$ is the effect of the ***l***th group that accounts for all other fixed effects concatenated into one variable (sex || market || year of birth || herd of origin), $\mathbf{CWT}_{ijkl}$ is the linear effect of carcass weight of the animal fitted as a covariate, and ε_{ijkl} is the random residual error.

3.3 Results

Unadjusted carcass weights of heifers were 219±2 kg and 275±1 kg for domestic and Korean markets respectively. Unadjusted carcass weights of steers were 224±2 kg, 290±2 kg and 324±2 kg for domestic, Korean and Japanese markets respectively.

3.3.1 Sire breed effects

Least squares means for effect of sire breed are shown in Tables 3.4 and 3.5. There were significant differences between sire breeds for all traits. Differences between breeds in CWT of more than 10 kg were significant ($P<0.05$). Progeny of tropically adapted sire breeds had the lowest CWT, with Brahman carcasses weighing up to 16% less ($P<0.001$) than Continental and British crossbreds. There was no difference between British and Continental crossbreds for CWT.

At common hot carcass weights, Brahman, Belmont Red and Continental sired crossbreds were younger at slaughter than Santa Gertrudis and British crossbreds ($P<0.05$). This was probably due to the fact that the Santa Gertrudis and British sires were unable to be used for natural mating following the AI programs, and hence their progeny were older at slaughter than the other crosses.

Continental crossbreds had the leanest carcasses ($P<0.001$), while British and Santa Gertrudis sired progeny had the highest HOTP8 across markets and finishing regimes (Figure 3.1; least squares means ± standard errors are in Appendix A). Most of the fatness effect for British crosses was due to higher subcutaneous fat cover in heifers. Progeny by Belmont Red and Brahman sires had intermediate HOTP8 levels. British and Belmont Red crossbreds had more IMF than other genotypes ($P<0.001$) across markets and finishing regimes. Brahman and Santa

Gertrudis crosses had the lowest IMF but were not significantly different from the Continental crosses. Belmont Red crossbreds ranked highest for IMF in both subtropical finishing regimes (Figure 3.2; least squares means ± standard errors are in Appendix A). Angus crossbreds had the highest IMF overall and had 27% more marbling than the average of Santa Gertrudis crosses and straightbred Brahman progeny ($P<0.001$) at common carcass weights.

Table 3.4 Least squares means (± s.e.) for effect of sire breed on age at slaughter, hot carcass weight and fatness traits in steers and heifers. All traits except carcass weight are adjusted to a common hot carcass weight. Carcass weight was adjusted to a common age at slaughter.

Sire Breed	Number of animals	Age at slaughter (days)	Hot carcass weight (kg)	Hot P8 fat depth (mm)	Number of animals	Intra-muscular fat (marbling) (%)
Brahman	320	714 ± 2	244 ± 2	10.5 ± 0.3	245	2.40 ± 0.07
Belmont Red	377	716 ± 2	253 ± 2	11.1 ± 0.3	297	3.09 ± 0.06
Santa Gertrudis	141	724 ± 3	271 ± 3	11.5 ± 0.4	115	2.38 ± 0.11
Angus	149	730 ± 2	283 ± 2	12.5 ± 0.4	125	3.27 ± 0.09
Hereford	134	728 ± 2	284 ± 2	12.0 ± 0.4	109	2.92 ± 0.09
Shorthorn	115	732 ± 3	279 ± 3	12.1 ± 0.4	95	3.11 ± 0.10
Charolais	223	714 ± 3	289 ± 2	9.1 ± 0.4	191	2.72 ± 0.10
Limousin	291	716 ± 2	281 ± 2	8.9 ± 0.3	241	2.62 ± 0.07
l.s.d.		10	10	1.3		0.36
	1750	P<0.05	P<0.001	P<0.001	1418	P<0.001

l.s.d. = least significant difference for observations to be significantly different from each other.

Figure 3.1 Subcutaneous fat depth across sire breeds and finishing regimes (n = 1473). The breed × finish interaction for HOTP8 was not significant.

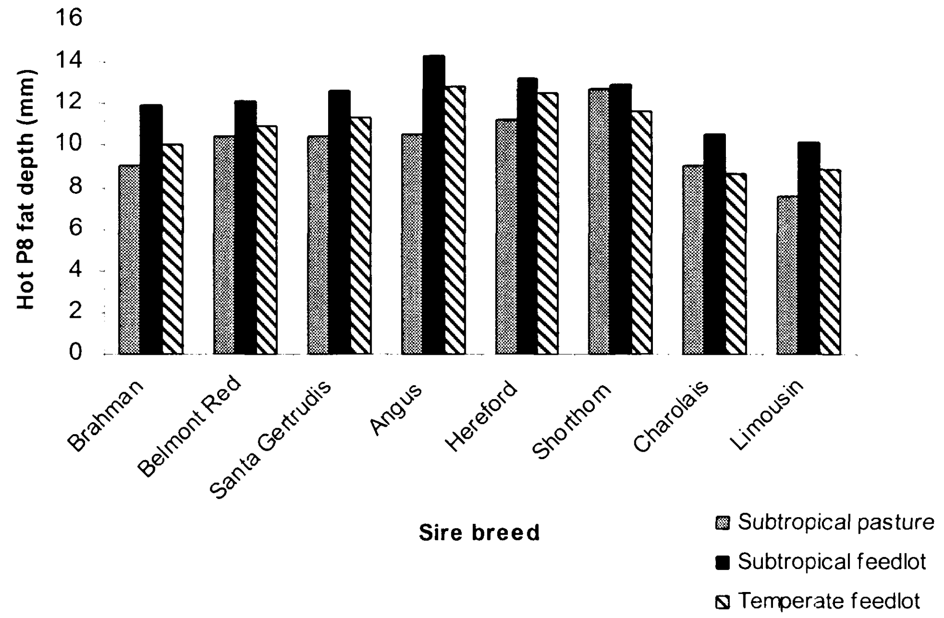
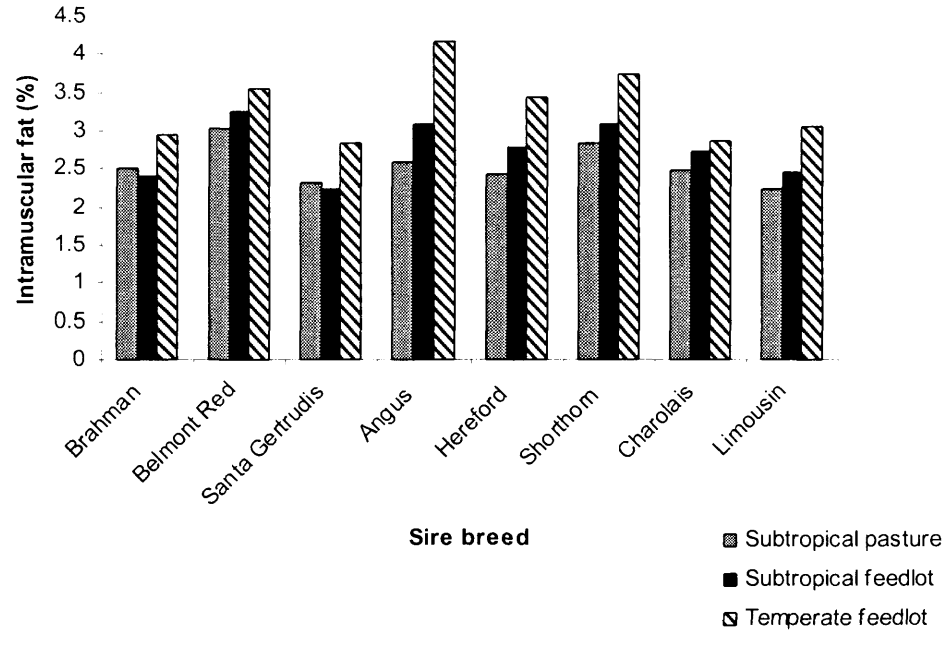


Figure 3.2 Intramuscular fat percent across sire breeds and finishing regimes (n = 1188). The breed × finish interaction for IMF was significant (P<0.05).



Continental crossbreds ranked highest for the three yield traits across all three finishing regimes and markets (Table 3.5). Limousin crosses had higher RBY, RTPM and pcRTPM than British and tropically adapted crosses ($P<0.05$). There was no significant difference in yields between Charolais crosses and all other crosses. Brahman and Belmont Red-sired progeny had intermediate yields, while Santa Gertrudis crosses were similar to the British crosses. Shorthorn sired calves yielded 2.8% lower RBY and 2.7 kg less RTPM than Limousin-sired progeny.

Table 3.5. Least squares means (± s.e.) for effect of sire breed on yield traits for steers and heifers in the 1996 calf crop. All traits are adjusted to a common hot carcass weight.

Sire Breed	Number of animals	Retail beef yield (%)	Retail primals (kg)	Percent retail primals (%)
		1996 calf crop only		
Brahman	62	66.3 ± 0.2	63.0 ± 0.2	25.1 ± 0.1
Belmont Red	46	66.3 ± 0.2	62.9 ± 0.2	25.0 ± 0.1
Santa Gertrudis	31	65.9 ± 0.3	62.5 ± 0.3	24.9 ± 0.1
Angus	16	66.1 ± 0.4	62.4 ± 0.3	24.9 ± 0.1
Hereford	18	65.9 ± 0.3	62.6 ± 0.3	24.9 ± 0.1
Shorthorn	10	65.7 ± 0.6	62.2 ± 0.6	24.7 ± 0.2
Charolais	13	67.2 ± 0.4	64.3 ± 0.4	25.5 ± 0.2
Limousin	24	68.5 ± 0.3	64.9 ± 0.3	25.7 ± 0.1
l.s.d.		1.9	1.9	0.6
	480	$P<0.05$	$P<0.05$	$P<0.05$

l.s.d. = least significant difference for observations to be significantly different from each other.

A separate analysis compared a subset of animals that had complete records for HOTP8, IMF, RBY and RTPM (n=376) adjusted to a common CWT. Breed rankings for HOTP8 and IMF changed marginally in this analysis, while there was no change in breed rankings for RBY and RTPM. Limousin crossbreds had the leanest, highest yielding carcasses with the least marbling

(P<0.05). British and Belmont Red crosses had the highest IMF, while Santa Gertrudis and British crosses had the highest HOTP8 and lowest RBY and RTPM (P<0.05).

3.3.2 Pasture versus feedlot finishing

Pasture-finished animals were 210 and 229 days older at slaughter (P<0.001) than their half-sibs finished in subtropical and temperate feedlots (Tables 3.6 and 3.7). Pasture-finished animals differed significantly from subtropical feedlot animals for most carcass traits with 2.1 mm less HOTP8, 0.9% more RBY, 1.0 kg more RTPM and 0.6% more pcRTPM. While pasture-finished animals had 0.7% less IMF than subtropical feedlot contemporaries, differences were not significant. However, when an atypical Korean heifer slaughter group finished on subtropical pasture (n=50) was excluded from the analysis, pasture finished animals had significantly less IMF than feedlot animals (P<0.001). Similar trends were apparent for the contrast between subtropical pasture versus temperate feedlot animals, however they did not differ for HOTP8.

3.3.3 Subtropical versus temperate finishing environments

Subtropical feedlot animals had higher RTPM and pcRTPM (P<0.001) but did not differ for RBY relative to temperate contemporaries (Table 3.7). Subtropical feedlot animals averaged 1.4 mm more HOTP8 (P<0.001) than temperate feedlot contemporaries, while temperate feedlot animals produced 0.54% more IMF (P<0.001) than subtropical feedlot animals (Table 3.6). Differences between northern (subtropical) and southern (temperate) feedlots for HOTP8 and IMF are shown in Figures 3.1 and 3.2.

Table 3.6 Least squares means (± s.e.) for effect of finishing regime, market endpoint and sex within market on age at slaughter, hot carcass weight and fatness traits in steers and heifers. All traits except carcass weight are adjusted to a common CWT. Carcass weight is unadjusted. Finishing regime and sex within market effects exclude steers treated with HGP.

Fixed Effects	Number of animals	Age at slaughter (days)	Hot carcass weight (kg)	Hot P8 fat depth (mm)	Number of animals	Intra-muscular fat (%)
Finishing regime						
Subtropical pasture	405	852 ± 3	266 ± 2	10.2 ± 0.3	299	2.62 ± 0.08
Subtropical feedlot	408	642 ± 3	271 ± 2	12.3 ± 0.2	391	2.74 ± 0.06
Temperate feedlot	660	623 ± 2	262 ± 1	10.9 ± 0.2	498	3.28 ± 0.07
l.s.d.		9	6	0.9		0.23
	1473	P<0.001	P<0.001	P<0.001	1188	P<0.001
Market endpoint						
Domestic	637	643 ± 4	227 ± 1	8.9 ± 0.4	474	2.78 ± 0.10
Korean	803	761 ± 2	288 ± 1	12.7 ± 0.2	685	2.87 ± 0.05
Japanese*	310	817 ± 6	327 ± 2	12.4 ± 0.5	259	3.16 ± 0.14
l.s.d.		18	9	1.5		0.41
	1750	P<0.001	P<0.001	P<0.05	1418	n.s.
Sex(market)						
Domestic heifers	351	647 ± 4	219 ± 2	10.9 ± 0.4	261	3.38 ± 0.12
Domestic steers	180	621 ± 5	224 ± 2	6.9 ± 0.4	125	2.63 ± 0.13
Korean heifers	494	775 ± 2	275 ± 1	15.4 ± 0.2	458	3.37 ± 0.06
Korean steers	228	729 ± 4	290 ± 2	10.6 ± 0.3	168	2.56 ± 0.09
Japanese steers	220	785 ± 5	324 ± 2	11.5 ± 0.5	176	3.10 ± 0.15
l.s.d.		15	6	1.5		0.46
	1473	P<0.001	P<0.001	P<0.001	1188	P<0.001

* Japanese market – steers only.

l.s.d. = least significant difference for observations to be significantly different from each other.

Table 3.7 Least squares means (± s.e.) for effect of finishing regime, market endpoint and sex within market on carcass yield traits in steers and heifers. All traits adjusted to a common hot carcass weight. Finishing regime and sex within market effects exclude steers treated with HGP.

Fixed effects	Number of animals	Retail beef yield (%)	Retail primals (kg)	Percent retail primals (%)
Finishing regime				
Subtropical pasture	74	66.8 ± 0.3	63.0 ± 0.3	25.7 ± 0.1
Subtropical feedlot	170	65.9 ± 0.2	62.0 ± 0.2	25.1 ± 0.1
Temperate feedlot	165	65.6 ± 0.2	61.0 ± 0.2	24.7 ± 0.1
l.s.d.		0.9	0.9	0.3
	409	P<0.05	P<0.001	P<0.001
Market endpoint				
Domestic	217	68.3 ± 0.3	63.7 ± 0.3	25.3 ± 0.1
Korean	189	65.5 ± 0.2	63.7 ± 0.2	25.3 ± 0.1
Japanese*	74	63.8 ± 0.5	63.3 ± 0.5	25.2 ± 0.2
l.s.d.		1.5	1.5	0.6
	480	P<0.05	n.s.	n.s.
Sex(market)				
Domestic heifers	108	67.5 ± 0.3	62.4 ± 0.3	25.3 ± 0.1
Domestic steers	74	68.8 ± 0.3	62.2 ± 0.3	25.2 ± 0.1
Korean heifers	112	63.8 ± 0.3	62.0 ± 0.3	25.1 ± 0.1
Korean steers	59	66.4 ± 0.3	63.1 ± 0.3	25.5 ± 0.1
Japanese steers	56	64.2 ± 0.5	62.2 ± 0.5	25.2 ± 0.2
l.s.d.		1.5	1.5	0.6
	409	P<0.001	n.s.	n.s.

* Japanese market – steers only.

l.s.d. = least significant difference for observations to be significantly different from each other.

An atypical domestic heifer slaughter group finished in the temperate feedlot (n=53) was responsible for the significant difference in IMF between subtropical and temperate feedlots (2.74 and 3.28% respectively; $P<0.001$). This slaughter group was the only domestic heifer slaughter group finished in the temperate feedlot, and therefore it was not possible to compare these females with contemporaries finished under the same conditions. While this slaughter group had a higher mean for IMF than other heifer groups (domestic market heifers finished in the subtropical feedlot and Korean market heifers finished in the temperate feedlot), the measurements were normally distributed and considered genuine. It is possible the process of chemical extraction of IMF for this particular group was atypical causing the higher means. However a definitive explanation is not possible given the constraints of the dataset.

In an analysis excluding the two atypical heifer slaughter groups, there was no significant difference between subtropical and temperate feedlots for IMF (n=1085). IMF for subtropical pasture, subtropical feedlot and temperate feedlot were 2.39 ± 0.05, 2.91 ± 0.05 and 3.03 ± 0.06 respectively. Therefore, while results are genuine, the apparent environmental effect on marbling should be treated with caution given the limitations of the data. Subtropical feedlot animals had 1.3 mm more HOTP8 ($P<0.001$) than temperate feedlot animals. Exclusion of the atypical slaughter groups from analyses for the other fixed effects caused little change to rankings or significance, with the exception of sex within market effects where the sexes no longer differed for IMF at domestic weights, and Korean heifers had more IMF than domestic heifers ($P<0.001$).

3.3.4 Market endpoint effects

Animals slaughtered for the domestic market had less HOTP8 and higher RBY than animals slaughtered for Korean and Japanese markets ($P<0.05$), but differences in IMF, RTPM or pcRTPM between markets were not significant (Tables 3.6 and 3.7). When the two atypical slaughter groups (n=103) were excluded from the analysis, domestic animals had less IMF than Korean and Japanese market animals ($P<0.05$). Korean market animals were fatter (HOTP8) than Japanese market animals due to the absence of heifers in the Japanese market.

Higher IMF and lower RBY were the two main differences between the two heavier market weights. Sex within market results show HOTP8 increased to Korean weights and then plateaued for steers, while IMF deposition was not significant between domestic and Korean weights, but increased significantly between Korean and Japanese weights (Tables 3.6 and 3.7). As steers aged from Korean to Japanese market weights, IMF increased by 0.54% ($P<0.001$) and RBY decreased by 2.2% ($P<0.001$), but HOTP8, RTPM and pcRTPM did not change significantly.

3.3.5 Sex effects

Heifers and steers were managed separately following weaning, so direct comparisons are not possible. However, the results show interesting trends (Tables 3.6 and 3.7). Heifers took 26 and 46 days ($P<0.001$) longer than steers to finish to domestic and Korean market weights respectively. Trends for fat deposition were consistent across sexes, however heifers had more subcutaneous and intramuscular fat ($P<0.001$) than steers at common market weights. Conversely, Korean steers had higher RBY ($P<0.001$) than heifers, while there was no difference for RTPM or pcRTPM between the sexes.

3.3.6 Herd of origin effects

Herd of origin had a significant effect on unadjusted CWT ($P<0.001$), with animals born on Duckponds being heavier at slaughter (281±1 versus 274±1) than those born on Brigalow Research Station. When CWT was adjusted to a common age at slaughter, herd of origin effects remained significant with 7 days difference in AGE ($P<0.001$).

3.3.7 Year effects

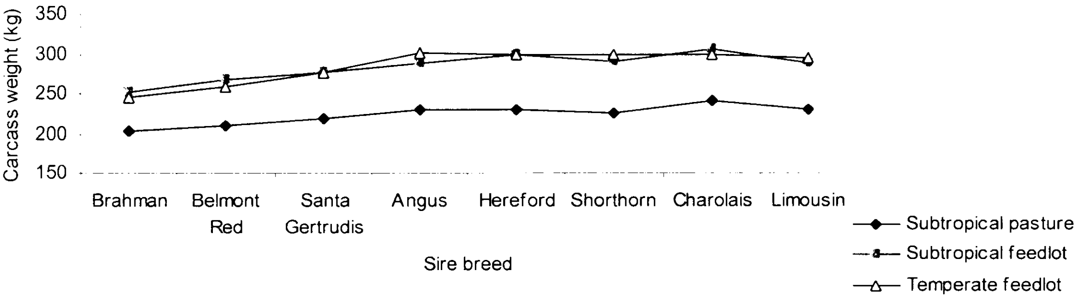
There were significant differences between years of birth for carcass traits measured over more than one year including AGE, HOTP8 and IMF ($P<0.001$). Calves born in 1998 were older at slaughter and leaner than the 1996 and 1997 calf crops, while IMF was lowest in 1996. There was no significant effect of year of birth on adjusted or unadjusted CWT.

3.3.8 Interactions

Most significant interactions were caused by scale effects rather than breed re-ranking for carcass traits. Breed × finish interactions were significant for AGE ($P<0.05$), CWT (adjusted for AGE; $P<0.001$) and IMF ($P<0.05$). Figure 3.3 shows interaction plots for CWT and AGE interactions. Figure 3.2 shows the breed × finish interaction for IMF. Least squares means ± standard errors for CWT, AGE and IMF are presented in Appendix B. The breed × finish interaction for IMF remained significant after removing the two atypical heifer slaughter groups ($n=103$) that distorted IMF results for finish effects. Figure 3.2 shows IMF differences between finishing regimes were greatest for British crossbreds, particularly when finished in the temperate feedlot. Brahman and Santa Gertrudis sired progeny marbled slightly better on subtropical pasture relative to subtropical feedlot. Breed × finish interactions were not significant for HOTP8, RBY, RTPM and pcRTPM.

Figure 3.3 Interaction plots showing significant breed × finish interactions.

(a) CWT (adjusted for AGE)

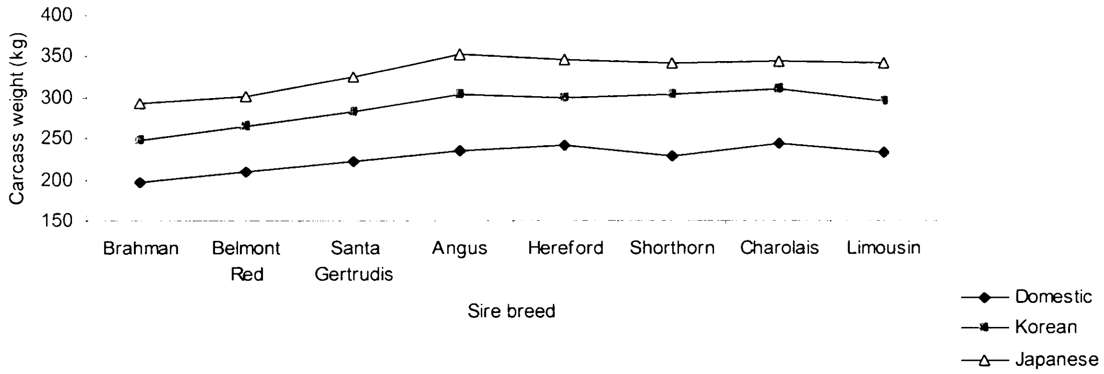


(b) AGE

Breed × market interactions were significant for AGE ($P<0.05$), CWT (unadjusted; $P<0.001$) and IMF ($P<0.001$). Least squares means ± standard errors are presented in Appendix B. Figure 3.4 shows interaction plots for significant breed× market interactions. Angus crosses were superior for IMF when finished to Japanese market weight relative to the other markets and crossbreds. There was little difference in IMF between markets for Continental crosses. Limited breed re-ranking within traits occurred between markets, and where it did occur, it was within breed type. Breed × market interactions were not significant for HOTP8, RBY, RTPM and pcRTPM.

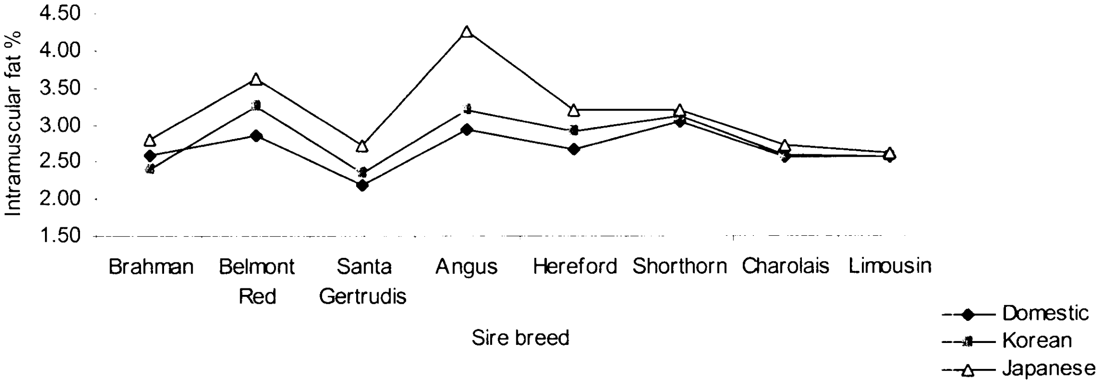
Figure 3.4 Interaction plots showing significant breed × market interactions.

(a) CWT (unadjusted)



(b) AGE

(c) IMF



Market × finish interactions were significant for AGE, CWT, HOTP8, IMF, RTPM and pcRTPM ($P<0.001$). There was no market × finish interaction for RBY. Animals slaughtered for the domestic market had significantly less HOTP8 and significantly more IMF when finished in the temperate feedlot relative to the subtropical feedlot, while animals slaughtered for Korean and Japanese markets performed similarly for both traits in both feedlot environments.

Breed × sex interactions were significant for CWT ($P<0.05$) and HOTP8 ($P<0.001$). Breed × property of origin interactions were significant for AGE ($P<0.001$), CWT ($P<0.001$), RBY ($P<0.05$), RTPM ($P<0.05$) and pcRTPM ($P<0.05$). Finish × year interactions were significant for AGE, CWT and HOTP8 and IMF ($P<0.05$). Finish × sex interactions were significant for all carcass traits ($P<0.05$) except CWT.

3.4 Discussion

3.4.1 Sire breed effects

Straightbred Brahmans performed intermediately for most traits relative to Brahman crossbreds, with the exceptions that they were lightest at slaughter age and had lower marbling relative to crossbreds. Brahman crossbreds performed to expectations, that is, in agreement with sire breed effects on carcass quality reported in reviews by Cundiff and Gregory (1999), Marshall (1994) and Marshall (1999). Despite these reviews being mainly based on animals finished in temperate environments, their findings with regard to sire breed trends were applicable to the current experiment. These reviews generally agree that *Bos indicus* breeds have moderate lean-to-fat ratios and below average marbling, British breeds have low lean-to-fat ratios and relatively high marbling scores, and Continental breeds have above average lean-to-fat ratios and average marbling. In this experiment, breeds within breed type (British-type, Continental-type) performed similarly. Therefore, cattle breeders should be able to select any breed within breed type examined in this study and achieve predictable outcomes for carcass quality traits.

Carcass attributes of *Bos taurus* and *Bos taurus* × *Bos indicus* cattle grown in temperate environments are well documented. Despite the inability to directly compare production systems and crosses, and inconsistent selection and definitions of traits examined, crossbred carcass traits from this experiment are generally consistent in direction, significance and sire breed ranking for traits with trends from Cycle V (including Brahman sires × *Bos taurus* dams) and Cycle VII (including Continental and British sires × *Bos taurus* dams) of the USDA Meat Animal Research Centre (MARC) Germplasm Evaluation Program Cundiff *et al.* 1998; Cundiff *et al.* 2001). In contrast however, no difference between Angus and Hereford sires for IMF were observed in our experiment. Our animals had relatively low IMF over all markets, so differences between sire breeds may not have been evident. The MARC animals were lotfed from weaning through to slaughter and were consequently heavier and fatter at slaughter than our animals, so breed differences in their studies may have been more apparent relative to our study. Our results also differed from those of Comerford *et al.* (1988) who reported significant differences in marbling score between Limousin × Brahman and straightbred Brahmans (12.6±0.7 and 9.4±0.6; 30 point scale), and non-significant differences in fat thickness between Limousin × Brahman and Hereford × Brahman crosses relative to straightbred Brahmans. In an experiment reported by Huffman *et al.* (1990) where Angus × Brahman steers (50% Brahman versus 75% Brahman content) were finished on grain to hot carcass weights of 310 and 318 kg, dressing percentage (62.61 versus 63.4%), adjusted fat over the ribeye (1.20 versus 1.24cm) and USDA yield grade (3.1 versus 3.1) were not different. However, the 75% Brahman content steers had lower marbling scores than 50% Brahman content steers ($P<0.05$). These results support our findings for Santa Gertrudis crosses relative to British × Brahman crosses for HOTP8, IMF and RBY.

Breed effects were generally consistent in direction and ranking with other Brahman crossbred studies conducted in subtropical environments in the USA. Peacock *et al.* (1977) reported intermediate fat depths and carcass yields of Brahman steers (6.3 mm and 50.79%) relative to Angus × Brahman (9.9 mm and 49.99%) and Brahman × Charolais (5.8 mm and 51.34%) steers grown in South Central Florida. DeRouen *et al.* (1992a) reported that relative to straightbred Brahmans, Angus × Brahman, Hereford × Brahman and Charolais × Brahman crosses slaughtered at average carcass weights of 271, 265 and 290 kg across four generations averaged 41, 35 and 60 kg higher hot carcass weights, 18, 16 and 31 kg higher retail yields, 4, 4 and 2 mm greater fat thickness, and 0.8, 0.6 and 0.5 units higher marbling scores when finished on ryegrass pasture and feedlot in subtropical Louisiana. Our results were in agreement in direction and ranking with DeRouen *et al.* (1992), with the exception of straightbred Brahmans having 1.4 mm greater P8 fat thickness than Charolais × Brahman, and more RBY and RTPM than Angus × Brahman (0.2% and 0.6 kg) and Hereford × Brahman (0.4% and 0.3 kg) crosses.

3.4.2 Pasture versus feedlot finishing

Under subtropical conditions, our experiment showed feedlot-finishing has advantages for turning cattle off several months earlier with higher fat cover and marbling, and little sacrifice in RBY, RTPM and pcRTPM, relative to pasture-finished animals. This is consistent with findings by Robinson *et al.* (2001) who reported *Bos taurus* steers finished on pasture in temperate NSW had less HOTP8 and IMF than grain-finished contemporaries. This has important implications in northern Australia where seasonal pasture availability and quality often results in animals being held over for another dry season in order to reach target market weights. Similarly, DeRouen *et al.* (1992a) recommended grain feeding for a minimum of 90 days after ryegrass grazing in subtropical Louisiana to ensure satisfactory carcass quality (hot carcass weight, retail yield, fat thickness, marbling score and quality grade) in Brahman and *Bos taurus* crosses.

Results were similar in direction and significance to results from the linked Straightbreeding Program for HOTP8 (10.46 and 12.98 mm), IMF (2.06 and 2.64%), and RBY (68.10 and 66.47%) for animals finished on subtropical pasture and subtropical feedlot respectively (Reverter *et al.* 2003). In the Straightbreeding Program, animals differed for all traits except HOTP8 when finished on pasture and feedlot in temperate environments which is consistent with results from this study for animals finished on subtropical pasture and temperate feedlot.

Bennett *et al.* (1995) reported steers with ≤50% Brahman content finished on rhizome peanut tropical grass pasture in Florida took longer to finish (197 versus 155 days, $P<0.001$), had less fat over the ribeye (8.3 versus 11.4 mm, $P<0.01$), lower USDA quality grade ($P<0.01$) and lower dressing percentage ($P<0.001$) than grain-finished steers in Texas. However, in contrast to our results, they found significantly lower marbling scores for forage-finished steers ($P<0.001$) and no difference in yield grade between finishing regimes. The higher retail yields of the pasture-finished Brahman crosses from our experiment align with the results from a two-, three- and four-breed rotational crossbreeding experiment including Angus, Brahman, Charolais and Hereford breeds (DeRouen *et al.* 1992a). However their Brahman crosses had similar fat thickness and significantly lower marbling scores than contemporaries finished on grain.

As ranking of breeds within breed type remained consistent for each carcass trait across pasture and feedlot finishing in our experiment, changing breeds to target different finishing regimes is not necessary for north Australian cattle production systems. Reverter *et al.* (2003) reported little evidence of genotype × environment interactions from the Straightbreeding Program, lending further weight to our conclusion. Furthermore, Hearnshaw *et al.* (1988) reported Brahman × Hereford animals were consistently superior in growth and carcass traits to straightbreds and backcrosses across three different temperate environments including unimproved and improved pastures and feedlot. The authors concluded that breed rankings were the same irrespective of postweaning environment. In contrast, in a New Zealand study comparing eight carcass quality traits (including hot carcass weight, subcutaneous fat depth and marbling score) of 54 pasture-finished and 148 feedlot-finished Angus steers, Charteris *et al.* (1997) reported significant ($P=0.05$) sire × finishing environment interactions for most carcass traits studied.

3.4.3 Subtropical versus temperate finishing environments

The main differences between finishing environments were significantly higher subcutaneous fat depth of subtropical feedlot animals relative to significantly higher marbling of temperate feedlot animals. Significant differences between subtropical and temperate finishing environments were also reported in the Straightbreeding Program between Brahman, Belmont Red and Santa Gertrudis breeds for HOTP8 (Oddy *et al.* 1997b; Kelly *et al.* 2001; Reverter *et al.* 2003) and scanned P8 fat depth (Johnston *et al.* 2003). Temperate feedlot-finished crossbreds had 0.54% higher IMF ($P<0.001$) and 1.4mm less HOTP8 than subtropical feedlot-finished crossbreds in our experiment. Tropically adapted straightbreds from the Straightbreeding Program had consistent results, with temperate feedlot-finished animals having 0.87% more IMF and 3.6 mm less HOTP8 than tropical feedlot straightbreds (Reverter *et al.* 2003).

Significant differences in HOTP8 and IMF between finishing environments suggest environmental effects on fat distribution in the carcass. However this hypothesis cannot be tested within the scope of this experiment. Growth path differences could be responsible for differences in fat deposition between environments, including differences in grow-out pasture quality and compensatory gain effects resulting from seasonal pasture quantity and quality fluctuations in the subtropical environment during the grow-out phase. Age at time of nutritional restriction, severity and length of restriction, diet quality following realimentation, and length of realimentation before finishing are all likely to influence body composition, fat partitioning and feed efficiency (Keele *et al.* 1992; Ball *et al.* 1997; Oddy *et al.* 1997a, b). Reverter *et al.* (2003) suggested higher fat deposition in animals eating high energy diets may have been the cause of the differences in HOTP8 and IMF between environments in the Straightbreeding Program, with fat distribution being favoured in the lumbo-sacral region against the thorax in subtropical environments as part of the thermoregulatory process. Growth path differences between north (subtropical) and south (temperate) were also suggested. Kelly *et al.* (2001) concluded that grow-out nutrition and geographic location significantly affected fatty acid composition of subcutaneous beef fat, where cattle grown in a tropical environment were older, fatter and had higher percentages of saturated fats relative to animals grown out in a temperate environment. Differences between temperate and tropical locations in ambient temperature, nutrition during the grow-out phase, and growth path were implicated in these results. Robinson *et al.* (2001) observed that steers that had better grow-out nutrition tended to have more intramuscular fat at Japanese weights, which is consistent with our crossbred results. Whether results from other studies can be extrapolated to explain why animals finished in the subtropical feedlot environment had more subcutaneous fat and less marbling than contemporaries finished in the temperate feedlot environment remains conjecture.

Breed rankings within breed type did not change across finishing environments, with the exception of a breed × finish interacation for IMF. This supports the earlier conclusion that cattle producers in subtropical and semi-arid environments in northern Australia do not need to change existing breeding programs to target different finishing environments. In the Straightbreeding Program including 320 Brahmans from the Crossbreeding Program, Johnston *et al.* (2003) found no evidence of genotype × environment interactions for weight and body composition traits from Angus, Hereford, Shorthorn, Murray Grey, Brahman, Belmont Red and Santa Gertrudis purebreds (n=7655). Johnston *et al.* (2003) concluded that changing the production system had significant effects on phenotypic expression of growth and body composition traits, but had little effect on the underlying genetic expression and subsequent ranking of sires. Newman *et al.* (2002) also concluded that crossbreeding could result in some re-ranking of sire's performance for weight-related traits, but there was little expected change in carcass traits.

3.4.4 Market endpoint effects

The effect of increasing age on carcass quality attributes is well known. As body weight increases towards an animal's mature weight the proportion of fat increases, the proportion of muscle decreases slightly or remains constant, and the proportion of bone decreases (Ball *et al.* 1997). Ball and Johnson (1989) reported that as 12th rib fat thickness increased, the percentage yield of saleable beef decreased in an experiment involving male and female Brahman crossbreds and Herefords. Our crossbred results agreed in direction and significance to those reported by Reverter *et al.* (2003) for the Straightbreeding Program for reduced RBY and increased fatness (IMF, HOTP8 and 12/13th rib fat thickness) of Brahman. Belmont Red and Santa Gertrudis straightbreds finished to heavier market endpoints. These straightbreds and crossbred animals from our experiment had similar HOTP8 across markets.

Similarly to our results, Comerford *et al.* (1988) reported consistent differences between sexes for 12th rib fat thickness, marbling score and yield grade ($P<0.01$) in a diallel breeding experiment including Limousin, Polled Hereford and Brahman beef cattle finished on grain and slaughtered at 445 days of age. Heifers and steers were slaughtered at carcass weights of 268 and 284 kg respectively. Domestic heifers in our experiment did not differ from Korean steers for HOTP8, IMF, RBY, RTPM or pcRTPM in an analysis excluding two atypical heifer slaughter groups (results not shown). Therefore, in markets where a premium is paid for marbling, our results suggest heifers could be slaughtered at a younger age and lighter weight than steers to achieve similar carcass quality and a slight advantage for RBY. Though the commercial reality of putting this into practice may be prohibitive at present due to the primary market focus being on carcass weight rather than carcass quality attributes, this could hold advantages for industry in being able to turn heifers off earlier.

3.5 Implications for industry breeding programs

The important outcome from this experiment is that once commercial cattle breeders have settled on a genotype suited to their subtropical or semi-arid production environment, they do not need to change breeds to target different markets, different nutritional regimes (pasture versus grain) or different finishing environments (subtropical versus temperate). Generally, a sire breed that performs well for a particular trait in one market or finishing environment, will perform consistently for that trait relative to other sire breeds in a different market or finishing environment. Furthermore, all genotypes tested in this experiment complied with basic weight and fat specifications for the markets to which they were targeted.

Use of tropically adapted breeds including Belmont Red and Santa Gertrudis is advantageous where terminal crossbreeding programs prevent use of straightbred British or Continental sires because of severe environmental stressors. In adverse environments, establishing a Brahman × *Bos taurus* crossbreed would allow the retention of adaptation and survival traits, coupled with the advantages of improved carcass quality relative to straightbred Brahmans. Breeders could expect similar carcass quality from established crossbreeds or multibreed composites relative to this terminal crossbreeding experiment, with the exception of a possible increase in age at slaughter because of reduced heterosis effects on carcass weight. Apart from faster growth rates, a major benefit of crossbreeding is the complementary blending of breed characteristics which can overcome genetic antagonisms between some production traits that can be encountered from within-breed selection.

Feedlot-finishing hastens growth allowing animals to reach market specifications for carcass weight, fatness and yield traits significantly earlier than pasture-finishing. This can be particularly useful in northern Australia where marked and variable wet and dry seasons cause large fluctuations in pasture availability and quality, resulting in lengthy pasture-finishing regimes often spanning more than one wet season before animals reach target carcass weights. Temperate finishing environments may have benefits for increased marbling and reduced subcutaneous fat depth over tropical finishing environments.

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CHAPTER 4 Meat quality and palatability of Brahman and first-cross cattle grown on pasture and grain in subtropical and temperate Australia

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Abstract. Market demand for a reliable supply of beef of consistently high eating quality led the Beef CRC to initiate a crossbreeding progeny test program to quantify objective and sensory meat quality differences between straightbred and first-cross Brahman genotypes bred in subtropical northern Australia and finished on subtropical pasture, subtropical feedlot and temperate feedlot. Brahman, Belmont Red, Santa Gertrudis, Angus, Hereford, Shorthorn, Charolais and Limousin sires were mated to Brahman females over three years to produce 1346 progeny that were finished to domestic, Korean and Japanese market weights (220, 280 and 330 kg respectively). The effects of sire breed, finishing regime, market endpoint and sex on sensory meat quality of four attributes score (CMQ4), ossification score (OSSIF) and Warner Bratzler shear force (SF), instron compression (IC), ultimate pH (PH) and percent cooking loss (CL) on the *M. longissimus thoracis et lumborum* (LT) and *M. semitendinosus* (ST) were determined. Straightbred Brahmans had the highest SFLT (5.39±0.07; $P<0.001$), ICLT (1.89±0.02; $P<0.05$)

and CL in both muscles ($P<0.05$). Straightbred Brahmans were the only genotype that failed to meet minimum CMQ4 grading standards (38.3; $P<0.001$). Progeny with up to 75% Brahman content successfully met minimum objective and sensory meat quality standards for tenderness. There was little difference between crossbred progeny for most meat quality traits. All crosses had IC measures below 2.2 kg indicating connective tissue toughness was not important in these animals slaughtered by an average of 24 months of age. Pasture-finishing adversely affected all meat quality traits ($P<0.001$) except CLST, with Korean and Japanese market animals having unacceptably tough SF, IC and CMQ4 measures. This was attributed to their older age at slaughter (31 and 36 months respectively) and seasonally interrupted growth path. While domestic animals slaughtered at 24 months of age off pasture had unacceptably high SF and IC, CMQ4 was acceptable. Feedlot-finishing ensured all animals were slaughtered by 24 months of age, with differences in objective meat quality between markets being minimal and all crosses, except straightbred Brahman, meeting minimum CMQ4 standards. Despite slightly more desirable SF and IC of meat from subtropical feedlot animals, animals from the temperate feedlot had higher CMQ4 scores ($P<0.001$). This anomaly may have been due to differences in growth path between subtropical and temperate pasture environments during the grow-out phase prior to feedlot entry. The lack of important genotype × environment interactions confirmed that changing breeds to target different finishing regimes is not necessary.

4.1 Introduction

Beef eating quality is particularly important to Australia's main markets. Domestic and Japanese consumers rate tenderness as the single most important eating quality attribute (Egan *et al.* 2001). A study by SMART (1994) found that 77% of consumers would purchase more beef if they knew it was going to be tender. Domestic consumers command 37% of total beef production, while Japan remains Australia's most important premium beef market. Korea is Australia's third largest export market (Bindon and Jones 2001). Australian beef producers are under mounting market pressure for a year round supply of beef of consistently high eating quality.

Brahman is the predominant cattle breed in northern Australia due to its superior adaptation to the production environment. Over 50% of the national herd is estimated to have some Brahman genes (Bindon 2002). However, it is well documented that as the proportion of *Bos indicus* inheritance increases, shear force increases and marbling and sensory tenderness values decrease (Koch *et al.* 1982; Crouse *et al.* 1989; Whipple *et al.* 1990; Marshall 1994; Shackelford *et al.* 1995; Cundiff *et al.* 1998; Thompson *et al.* 1999a, Wheeler *et al.* 2001; Thompson 2002). While there have been many studies comparing cattle with varying proportions of *Bos indicus* genes to *Bos taurus* animals in temperate environments, there are few studies comparing *Bos indicus* with *Bos indicus* × *Bos taurus* crosses in tropical and subtropical environments. The majority of experiments conducted in subtropical environments have been in the USA and vary in the breadth of the breed combinations used and findings of the effect of *Bos indicus* content on meat quality (Peacock *et al.* 1982; Wythes *et al.* 1989; Johnson *et al.* 1990; DeRouen *et al.* 1992a; Pringle *et al.* 1997; Bidner *et al.* 2002). The debate on genotype × environment interactions on meat quality remains controversial. In extreme environments, poor adaptation is believed to be responsible for changes in breed rankings for meat tenderness. A study by Pratchett *et al.* (1988) in the arid tropics of northern Australia found Shorthorns had higher shear force than Brahmans, and Africander × Shorthorn had more tender beef.

In 1994 the Beef CRC initiated its Northern Crossbreeding Program. The primary objective of this experiment was to identify differences between straightbred Brahmans and Brahman crossbreds for beef eating quality when finished on pasture and grain in subtropical and temperate environments to the specifications of Australia's three main markets. Of particular interest was whether existing national cattle breeding programs were suitable to deliver the most efficient animals for pasture- and feedlot-finishing systems, or whether there was a need to develop a separate breeding strategy for the feedlot sector (Bindon 2001). Meat Standards Australia (MSA) used all animals generated for the Crossbreeding Program to underpin and further develop their beef-grading scheme. The MSA beef-grading scheme was launched in 1997 with the primary aim of providing a guarantee of eating quality to the consumer (Polkinghorne *et al.* 1999). While genetic correlations between objective measures of tenderness and sensory tenderness are high and negative, phenotypic correlations are low (Reverter *et al.* 2003). Therefore untrained consumer taste panels were used in setting the MSA palatability grades. A pilot program conducted in 1998 demonstrated a high repurchase rate by consumers if they were presented with a consistent graded product (Thompson *et al.* 1999b). Preliminary analysis of objective meat quality traits were reported by Newman *et al.* (1999). This paper presents the full report on the effects of breed, finishing regime, market endpoint and sex on sensory and objective meat quality characteristics of crossbred Brahman progeny from the Northern Crossbreeding Program.

4.2 Materials and methods

4.2.1 Experimental design and animals

Full details of experimental design, measurements and data storage were described by Upton *et al.* (2001). Briefly, calves by 1000 Brahman dams and eight terminal sire breeds were bred over three years in subtropical central Queensland on 'Duckponds' and Brigalow Research Station. Sire breeds represented *Bos indicus* (Brahman – purebred control), *Bos indicus* × British-derived (Santa Gertrudis), *Bos taurus* × Sanga-derived (Belmont Red; Sanga cattle originated from Africa), *Bos taurus* – British (Angus, Hereford, Shorthorn), and *Bos taurus* – Continental (Charolais, Limousin). Brahman, Santa Gertrudis and Belmont Red are tropically adapted breeds. Calves were generated by natural mating and artificial insemination (AI). Most British sires were used by AI because the bulls were located in southern Australia. A full description of AI programs and parentage determination is given by Corbet *et al.* (1997, 1999). The aim was to produce about 10 steers and 10 heifers per sire. The optimal number of sires, offspring per sire and number of link sires between herds, and allocation of animals to treatment combinations are discussed by Robinson (1995). All male calves were castrated at about four months of age. Meat quality measurements were recorded for 1346 calves. Table 4.1 shows the number of sires and progeny measured per breed.

Table 4.1 Number of sires and progeny per breed.

Sire breed	Number of sires	Heifer progeny	Steer progeny	Total
Brahman	14	125	107	232
Belmont Red	14	125	154	279
Santa Gertrudis	8	65	44	109
Angus	10	55	63	118
Hereford	8	59	46	105
Shorthorn	8	48	41	89
Charolais	15	95	91	186
Limousin	14	118	110	228
Total	91	690	656	1346

4.2.2 Treatments

Calves were weaned in 1996, 1997 and 1998 at about six months of age. Calves were assigned within sire by age and weight to one of three market endpoints (domestic, Korean, Japanese) and one of three finishing regimes (subtropical pasture, subtropical feedlot, temperate feedlot). Following weaning two-thirds of calves were grown out on subtropical buffel grass (*Cenchrus ciliaris*) pasture at 'Duckponds' and the remainder were grown out on temperate pasture in New South Wales at Glen Innes Research Station (refer to Ayres *et al.* 2001 for native and improved pasture descriptions) or 'Tullimba' (native wallaby grass, *Austrodanthonia spp.*) until they reached feedlot entry weights. Calves allocated to the domestic market entered feedlots when they reached 300 kg liveweight, while Korean and Japanese market calves entered feedlots at 400 kg liveweight. Calves were finished on subtropical buffel grass at 'Duckponds', subtropical feedlot at 'Goonoo' or temperate feedlot at 'Tullimba' to 220, 280 and 330 kg carcass weights for the domestic, Korean and Japanese markets respectively. Only steers were finished to Japanese weights. Domestic animals were grain fed for an average of 60 days and export animals were grain fed for a minimum of 90 days (Upton *et al.* 2001).

A cohort was defined by the variables sex, year of birth, market endpoint and finishing regime. All animals within a cohort were managed as a single group during grow out, finish, pre-slaughter and slaughter, with the exception of a few cohorts that were slaughtered over two consecutive days. All animals within a cohort were slaughtered when the average weight of their group reached target carcass weights. One half of all steers finished in the subtropics were repeatedly implanted with the hormonal growth promotant (HGP), Compudose 100®, from about 15 months of age to slaughter. Experimental details and results for the HGP experiment are reported by Hunter *et al.* (2001).

4.2.3 Slaughter protocols and meat quality measurements

Full details of slaughter, electrical stimulation, chiller measurements, sample removal and yield measurements are reported by Perry *et al.* (2001). Best practice pre- and post-slaughter procedures were used. The aims of best practice carcass processing are to minimise myofibrillar shortening by optimising the rate of glycolysis and temperature decline, and to maximise the extent of proteolysis, while ensuring microbiological standards are met (Ferguson *et al.* 2001). Animals were stunned using a captive bolt pistol and bled immediately. Electrical stimulation was applied to all carcasses to prevent cold shortening. Depending on the abattoir, either low voltage stimulation was applied for 40 s within 5 min of stunning, or high voltage stimulation was applied to dressed sides 40-60 min post-stunning (Perry *et al.* 2001).

Carcasses were dressed to comply with AUS-MEAT standard specifications (AUS-MEAT 1998). Carcasses were placed in chillers within one hour of slaughter and hung by the Achilles tendon. Meat Standards Australia (MSA) assessors measured USDA ossification score (OSSIF). The left side of each carcass was quartered 20-24 hours after slaughter, and the entire *M. semitendinosus* (ST) and about 15 cm of the *M. longissimus thoracis et lumborum* (LT) were removed for objective measurements of meat quality. These samples were trimmed, weighed and packed in plastic for freezing at -20°C within 36 hours of slaughter (Perry *et al.* 2001). The LT muscle has low connective tissue content, is not stretched in the Achilles-hung carcass, and is susceptible to cold shortening (Harper 1999). The LT is commonly used for meat quality evaluation. The ST has high connective tissue content and is restrained from shortening post-mortem, hence it better reflects the connective tissue contribution to tenderness (Shorthose 1996; Perry *et al.* 2001). Furthermore, the ST is believed to be closer to the median value for all muscles in the carcass (Shorthose and Harris 1991). Studies have shown that *Bos indicus* inheritance increases shear force of the LT to a greater extent than other muscles tested, indicating shear force of the LT is not a good predictor of shear force of other muscles on the carcass (Whipple *et al.* 1990; Shackelford *et al.* 1995). Both muscles were measured using Warner-Bratzler shear force and instron compression. Warner-Bratzler shear force is believed to reflect both myofibrillar and connective tissue components of toughness (Harris and Shorthose 1988; Harper 1999). Instron compression mainly reflects the connective tissue toughness of muscle (Harper 1999).

Not every animal was measured for every trait. Slaughter operations moved to six different abattoirs in two states during the Crossbreeding Program due to abattoir closure or the inability of the abattoir to accommodate the demands and disruptions of experimental requirements in commercial meat-processing plants. Consequently, some precision and considerable revenue was lost (Bindon 2001). This ultimately impacted on the completeness of the Crossbreeding Program dataset. OSSIF and Clipped Meat Quality Four Score (CMQ4; refer to Table 4.2) were only measured on the 1996 and 1997 calf crops. Consequently, there were no domestic steers or domestic heifers analysed for temperate feedlot, affecting results for effects of market endpoint, finishing regime and sex within market for CMQ4 and OSSIF. The effect of these missing cells is discussed in the relevant results.

4.2.4 Statistical analyses

Least squares means for fixed effects were estimated using the GLM Procedure of SAS (SAS 2000). Partial confounding of fixed effects and slaughter groups and missing subclasses prevented convergence in the initial fixed effects model. Subsequently, each independent variable (breed, finish, market, sex, year of birth, herd of origin, HGP treatment) was fitted separately in a fixed effects model, and a second independent variable accounting for all remaining fixed effects (concatenated into one variable) was included. Sire within breed was fitted as a random effect in the breed analysis and was also used as the error term to test breed differences. Due to confounding within abattoir, electrical stimulation method was excluded from the model. Carcasses believed not to have been effectively stimulated or to have undergone cold or heat shortening were removed from the dataset (Johnston *et al.* 2001). The models used to analyse the meat quality traits are described fully in Chapter 3 (models 2, 4, 6 and 8 for breed, finish, market and sex within market effects respectively). For example, the model used to analyse the effect of breed on all meat quality traits was:

$$y_{ijkl} = \mu + \boldsymbol{breed}_j + \boldsymbol{otherFE}_k + \boldsymbol{sire}_{l(j)} + b_1\boldsymbol{CWT}_{ijkl} + \varepsilon_{ijkl} \qquad (1)$$

where y_{ijkl} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{breed}_j$ is the effect of the $\boldsymbol{j}$th sire breed, $\boldsymbol{otherFE}_k$ is the effect of the $\boldsymbol{k}$th group that accounts for all other fixed effects concatenated into one variable (sex || market || finish || year of birth || herd of origin || HGP treatment), $\boldsymbol{sire}_{l(j)}$ is the random effect of the $\boldsymbol{l}$th sire nested within the $\boldsymbol{j}$th breed, $\boldsymbol{CWT}_{ijkl}$ is the linear effect of carcass weight of the animal fitted as a covariate, and ε_{ijklm} is the residual error term.

Least squares means were estimated for two-way interactions between all fixed effects. Of particular interest were breed × finish, breed × market and market × finish interactions. Interactions were calculated using a concatenated fixed effects model similar to model 10 in Chapter 3 using the GLM Procedure of SAS (SAS 2000). For example, breed × market interaction was tested using:

$$y_{ijkl} = \mu + \boldsymbol{breed}_j + \boldsymbol{market}_k + \boldsymbol{otherFE}_l + \boldsymbol{(breed*market)}_{jk} + b_l\boldsymbol{CWT}_{ikl(k)} + \varepsilon_{ijkl} \quad (2)$$

where y_{ijkl} is the observation for a dependent variable for animal i, μ is the overall mean, $\boldsymbol{breed}_j$ is the effect of the jth sire breed, $\boldsymbol{market}_k$ is the effect of the kth market endpoint, $\boldsymbol{otherFE}_l$ is the effect of the lth group that accounts for all other fixed effects concatenated into one variable (sex || finish || year of birth || herd of origin || HGP treatment), $\boldsymbol{CWT}_{ikl(k)}$ is the linear effect of carcass weight of the animal fitted as a covariate within market, and ε_{ijkl} is the random residual error.

The multiple-range test devised by Duncan (1955) and extended by Kramer (1957) was used to test for significant differences between means.

All meat quality traits were adjusted to a common hot carcass weight for breed and finish effects, and a common hot carcass weight within market endpoint for market and sex within market effects. Steers implanted with HGP were excluded from analyses for finish and sex effects due to confounding with location and sex. Subsequently, only 1136 animals were analysed for finish and sex effects for IMF (intramuscular fat percent), SFLT (shear force of the LT muscle), ICLT (instron compression of the LT), PHLT (ultimate pH of the LT), CLLT (percent cooking loss of the LT), SFST (shear force of the ST muscle), ICST (instron compression of the ST), PHST (ultimate pH of the ST) and CLST (percent cooking loss of the

ST), and 460 animals for CMQ4 and OSSIF. Traits reported in this paper are described in Table 4.2.

Table 4.2 Abbreviations and definitions of meat quality traits.

Abbreviation	Definition of traits
SFLT (kg)	Warner-Bratzler shear force of the *M. longissimus thoracis et lumborum*. Meat below 5.0 kg is considered tender.
SFST (kg)	Warner-Bratzler shear force of the *M. semitendinosus*. Meat below 5.0 kg is considered tender.
ICLT (kg)	Instron compression of the *M. longissimus thoracis et lumborum*. Meat below 2.2 kg is considered tender.
ICST (kg)	Instron compression of the *M. semitendinosus*. Meat below 2.2 kg is considered tender.
CLLT (%)	Cooking loss percent of the *M. longissimus thoracis et lumborum*. Samples were weighed (pre-cook weight) and placed in individual bags in a preheated water bath at 70°C for 60 min, then cooled in cold running tap water for 30 min. Cooked samples were removed from bags, dried and weighed to determine a post-cook weight. Cooking loss was determined as the percentage difference between pre- and post-cooked weights (refer to Perry *et al.* 2001 for full details).
CLST (%)	Cooking loss percent of the *M. semitendinosus*. Samples were prepared as per CLLT.
PHLT (pH)	Ultimate pH of the *M. longissimus thoracis et lumborum*. Four measures of pH were taken per sample using a digital pH meter with a combination electrode, and averaged to provide a measure of ultimate pH. The acceptable range for pH is 5.3 to 5.7. A slight improvement in eating quality occurs as pH declines from 5.7 to 5.4.
PHST (pH)	Ultimate pH of the *M. semitendinosus*. Samples were measured as per PHLT.
CMQ4	Meat Standards Australia clipped meat quality score of 4 attributes. *M. longissimus thoracis et lumborum* samples were aged at 1°C for 14 days, the epimysium removed, steaks cut at 25 mm thickness and served grilled to a medium degree of doneness. Consumers were recruited from the community to represent diverse backgrounds and areas, were 20 to 50 years of age and ate beef at least once per week. Ten consumers tasted each individual cut. Each component of the score was calculated on a 0 to 100 scale comprising: tenderness 40%, juiciness 10%, flavour

	20% and overall liking 30%. The lowest and highest two scores were 'clipped', and the middle six scores averaged to produce the CMQ4 score for analysis (Perry *et al.* 2001; Polkinghorne *et al.* 1999).
OSSIF	USDA ossification score. Ossification measures the physiological maturity of the carcass and gives an indication of collagen fibre development. Ossification increases as an animal ages but can also increase with nutritional or health stress. It is measured on a scale of 0 to 500, with higher scores indicating greater maturity and poorer eating quality. Animals fed under optimal conditions could be expected to have ossification scores of 170 and 200 at 24 and 30 months of age respectively (MLA 2003).

4.3 Results

Means of age at slaughter and unadjusted hot carcass weight for sire breed, finishing regime, market endpoint and sex within market effects are reported in Chapter 3, Tables 3.4 and 3.6.

4.3.1 Sire breed effects

Tables 4.3 and 4.4 show least squares means for the effect of sire breed on objective and sensory meat quality traits. Higher shear force and instron compression values indicate less tender meat. Australian consumers would rate meat with shear force of less than 5 kg as tender (Egan 1997) and instron compression measures of less than 2.2 kg as tender (Gazzola 1997). Given all breeds had instron compression measures of the LT and ST below 2.2 kg, and breeds did not differ for ICST, connective tissue toughness did not appear to be important in these animals slaughtered at an average of 24 months of age. Overall, there was little difference between genotypes for objective measures of meat quality. Straightbred Brahmans had the toughest LT meat quality, but did not differ from Shorthorn sired crosses for SFLT ($P>0.001$) or Santa Gertrudis and Hereford sired crosses for CLLT ($P>0.05$). Angus sired progeny had the most desirable LT meat quality, but were not different to all other crossbreds except Shorthorn crosses and straightbred Brahmans for SFLT, and Santa Gertrudis crosses and straightbred Brahmans for CLLT. Conversely, Angus crossbreds along with Shorthorn crossbreds had the toughest SFST and differed from Charolais and Limousin crosses ($P<0.001$), while Hereford and Shorthorn sired progeny had the lowest CLST but only differed to straightbred Brahmans ($P<0.05$). All breeds fell within the acceptable range of 5.3 to 5.7 for ultimate pH (Ferguson *et al.* 2001). There was no difference in OSSIF between breeds, and OSSIF for all breeds was acceptable given that animals under optimal growing conditions could be expected to have an OSSIF of 170 at 24 months of age (MLA 2003).

Table 4.3 Least squares means (± s.e.) for effect of sire breed on objective measures of meat quality on the *M. longissimus thoracis et lumborum* and *M. semitendinosus* in steers and heifers. All traits are adjusted to a common hot carcass weight.

Sire breed	Number of animals	Shear force LT (kg)	Compression LT (kg)	Ultimate pH LT (pH)	Cooking loss LT (%)	Shear force ST (kg)	Compression ST (kg)	Ultimate pH ST (pH)	Cooking loss ST (%)
Brahman	232	5.39 ± 0.07	1.89 ± 0.02	5.53 ± 0.01	23.4 ± 0.1	5.01± 0.04	2.11 ± 0.02	5.57 ± 0.01	24.3 ± 0.1
Belmont Red	279	5.00 ± 0.06	1.85 ± 0.02	5.52 ± 0.01	22.8 ± 0.1	4.95 ± 0.04	2.14 ± 0.02	5.55 ± 0.01	23.6 ± 0.1
Santa Gertrudis	109	4.95 ± 0.11	1.87 ± 0.03	5.53 ± 0.01	23.2 ± 0.2	4.89 ± 0.07	2.07 ± 0.04	5.55 ± 0.01	23.9 ± 0.2
Angus	118	4.68 ± 0.09	1.78 ± 0.02	5.54 ± 0.01	22.6 ± 0.2	5.07 ± 0.05	2.10 ± 0.03	5.55 ± 0.01	23.8 ± 0.2
Hereford	105	4.80 ± 0.09	1.78 ± 0.02	5.53 ± 0.01	22.9 ± 0.2	4.97 ± 0.05	2.10 ± 0.03	5.56 ± 0.01	23.4 ± 0.2
Shorthorn	89	5.05 ± 0.10	1.87 ± 0.03	5.54 ± 0.01	22.7 ± 0.2	5.08 ± 0.06	2.15 ± 0.03	5.56 ± 0.01	23.4 ± 0.2
Charolais	186	4.90 ± 0.09	1.83 ± 0.02	5.53 ± 0.01	22.7 ± 0.2	4.81± 0.06	2.17 ± 0.03	5.56 ± 0.01	23.9 ± 0.2
Limousin	228	4.80 ± 0.07	1.79 ± 0.02	5.54 ± 0.01	22.6 ± 0.1	4.65 ± 0.04	2.07 ± 0.02	5.57 ± 0.01	23.8 ± 0.1
l.s.d.		0.36	0.10	0.03	0.6	0.23	0.13	0.03	0.6
	1346	P<0.001	P<0.05	n.s.	P<0.05	P<0.001	n.s.	n.s.	P<0.05

l.s.d. = least significant difference for observations to be significantly different from each other.

Straightbred Brahmans did not differ from Belmont Red or Santa Gertrudis sired progeny for most LT and ST meat quality traits. The exceptions were Brahmans differed to Belmont Red and Santa Gertrudis crosses for SFLT ($P<0.001$), and Brahmans differed to Belmont Red crosses for CLLT and CLST ($P<0.05$).

Table 4.4 Least squares means (± s.e.) for effect of sire breed on MSA Clipped Meat Quality 4 Score and ossification score for steers and heifers. Traits adjusted to a common hot carcass weight.

Sire breed	Number of animals	CMQ4 Score (out of 100)	Ossification score
		1996 / 1997 calf crops only	
Brahman	103	38.3 ± 1.4	175 ± 4
Belmont Red	139	50.4 ± 1.1	176 ± 3
Santa Gertrudis	56	48.8 ± 2.1	167 ± 5
Angus	46	53.8 ± 2.0	184 ± 5
Hereford	47	49.9 ± 1.9	177 ± 5
Shorthorn	37	48.4 ± 2.3	176± 6
Charolais	50	51.8 ± 2.1	182 ± 6
Limousin	99	49.9 ± 1.4	173 ± 4
l.s.d.		7.4	19
	577	$P<0.001$	n.s.

l.s.d. = least significant difference for observations to be significantly different from each other.

Straightbred Brahmans differed significantly to all crossbred genotypes for CMQ4 score (Table 4.4). Angus sired progeny had the most desirable CMQ4 scores but were not different to all other crossbreds. Straightbred Brahmans failed to meet the MSA 3-star grading cut-off point of 46.5, shown in Figure 4.1 (least squares means ± standard errors can be found in Appendix C). Despite a CMQ4 least squares mean of 38.3, 29% of the Brahmans graded 3-star or better, while 6% graded 4-star. Analyses of sex within breed showed 42% of Brahman steers and 27% of

Brahman heifers graded 3-star or better. Table 4.5 shows the percentage of progeny by each sire breed that failed to achieve MSA grading standards based on CMQ4 scores. Belmont Red and Santa Gertrudis sired crosses were the only genotypes to achieve MSA 5-star grading (CMQ4 score greater than 79 out of 100).

Figure 4.1 Sire breed effect on CMQ4 scores across finishing regimes (n=460). The line at CMQ4 score 46.5 indicates the minimum score for MSA 3-star grading.

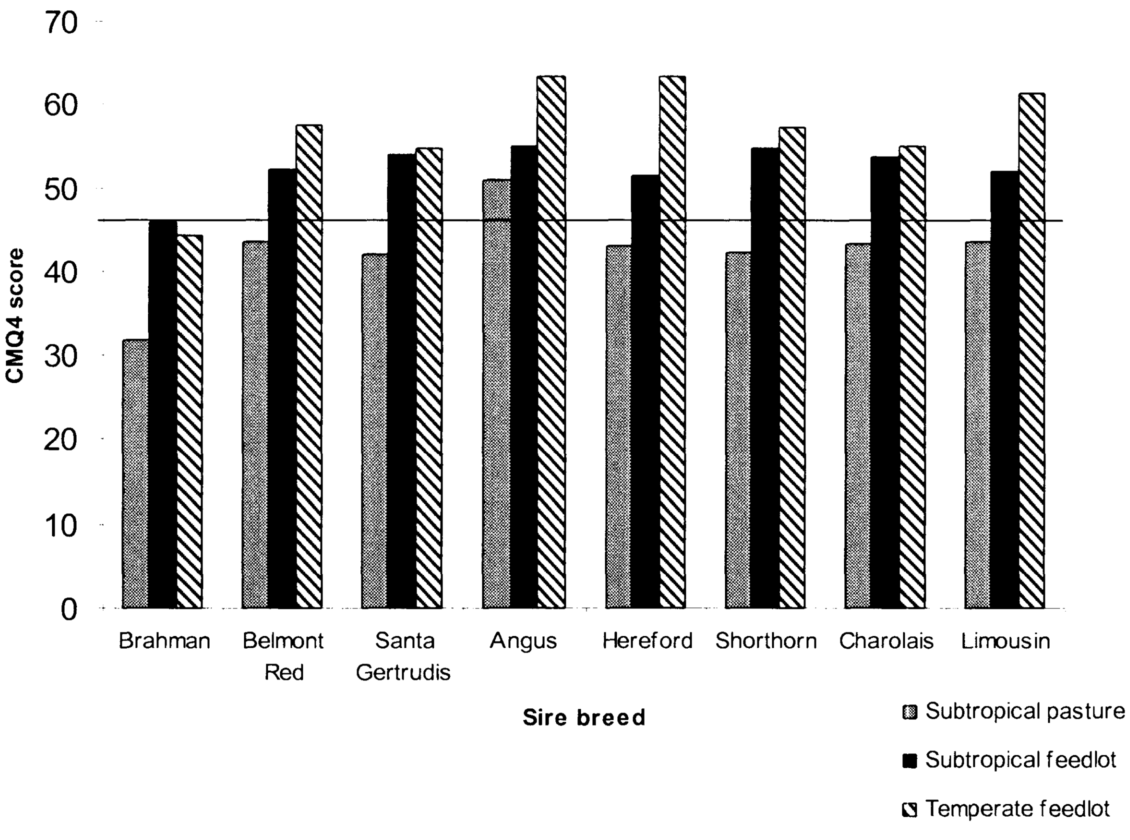


Table 4.5 Percentage of sire breeds to grade MSA 3-star, 4-star and 5-star based on CMQ4 score.

Sire breed	Number of animals	Fail (CMQ4 <46.5) (%)	3-star (CMQ4 46.5-64) (%)	4-star (CMQ4 64-79) (%)	5-star (CMQ4 79+) (%)
Brahman	103	65.1	29.1	5.8	
Belmont Red	139	40.3	44.6	13.7	1.4
Santa Gertrudis	56	48.2	39.3	10.7	1.8
Angus	46	32.6	50.0	17.4	
Hereford	47	44.7	38.3	17.0	
Shorthorn	37	46.0	37.8	16.2	
Charolais	50	50.0	44.0	6.0	
Limousin	99	50.5	36.4	13.1	
Total	577	48.2	39.3	12.1	0.4

4.3.2 Pasture versus feedlot finishing

Significant differences between pasture- and feedlot-finishing were found for all meat quality traits (P<0.001). Tables 4.6 and 4.7 show the effect of finishing regime on objective and sensory meat quality traits. Animals finished on subtropical pasture were 7 months older (28 versus 21 months; Chapter 3, Table 3.6) and had significantly higher OSSIF than subtropical feedlot-finished animals. Meat from pasture-finished animals was above acceptable consumer tenderness thresholds for SFLT, SFST and ICST (SF greater than 5.0 kg and IC greater than 2.2 kg; Egan 1997; Gazzola 1997). Ultimate pH was higher for the LT and ST muscles of pasture-finished animals, though all measures of pH were within the acceptable range of 5.3 to 5.7 (Ferguson *et al.* 2001). While CLLT was significantly higher for pasture-finished animals relative to feedlot-finished contemporaries, the opposite trend occurred for CLST.

CMQ4 scores were consistent with objective meat quality measures. Except for Angus crossbreds, pasture-finished animals were unable to achieve minimum MSA grading standards (CMQ4 scores greater than 46.5). However, there was a sex effect on sensory meat quality scores. With the exception of Angus sired crosses, no pasture-finished heifers graded MSA. Brahman, Charolais, Santa Gertrudis and Shorthorn sired steers also failed to grade MSA when finished on pasture (results not shown). The adverse effect of pasture-finishing on sensory meat quality (CMQ4) is shown in Figure 4.1 for sire breeds and in Figure 4.2 for market endpoints.

4.3.3 Subtropical versus temperate finishing environments

While there were no significant differences between feedlots for SFLT, ICLT and SFST, animals finished in the subtropical (Queensland) feedlot had slightly more favourable objective measures of LT meat quality and significantly lower ICST than contemporaries finished in the temperate (NSW) feedlot. Ultimate pH was lower in LT and ST muscles from temperate feedlot animals relative to subtropical feedlot animals ($P<0.001$), though all pH values were within the acceptable range. Shear force and instron compression measures of both muscles were within the limits associated with acceptable tenderness (5.0 kg and 2.2 kg respectively; Egan 1997; Gazzola 1997). We expected temperate feedlot animals to have higher means for OSSIF and similar means for CMQ4 relative to animals finished in the subtropical feedlot given that OSSIF increased with market age, there was no difference between markets for CMQ4, and no domestic animals were recorded for OSSIF or CMQ4 in the temperate feedlot. On the contrary, temperate feedlot animals had lower OSSIF ($P<0.001$) and higher CMQ4 scores ($P<0.001$) (see Figure 4.2; least squares means ± standard errors can be found in Appendix C) than subtropical feedlot animals. Despite these unexpected trends for OSSIF and CMQ4, animals from both feedlot environments achieved minimum MSA grading standards.

Table 4.6 Least squares means (± s.e.) for effect of finishing regime, market endpoint and sex within market on objective measures of meat quality in steers and heifers. Traits adjusted to a common hot carcass weight for finishing regime, and a common hot carcass weight within market endpoint for market and sex effects. Finishing regime and sex within market effects exclude steers treated with HGP.

Fixed Effects:	Number of animals	Shear force LT (kg)	Compression LT (kg)	Ultimate pH LT (pH)	Cooking loss LT (%)	Shear force ST (kg)	Compression ST (kg)	Ultimate pH ST (pH)	Cooking loss ST (%)
Finishing regime									
Subtropical pasture	294	5.45 ± 0.06	1.96 ± 0.02	5.57 ± 0.01	23.6 ± 0.1	5.12 ± 0.04	2.30 ± 0.02	5.60 ± 0.01	23.2 ± 0.1
Subtropical feedlot	355	4.63± 0.05	1.70 ± 0.01	5.53 ± 0.01	21.9 ± 0.1	4.90 ± 0.03	1.94 ± 0.02	5.55 ± 0.01	23.8 ± 0.1
Temperate feedlot**	487	4.69 ± 0.05	1.75 ± 0.01	5.46 ± 0.01	22.9 ± 0.1	4.81 ± 0.03	2.01 ± 0.02	5.51 ± 0.01	23.4 ± 0.1
l.s.d.		0.18	0.06	0.03	0.3	0.12	0.06	0.03	0.3
	1136	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001
Market endpoint									
Domestic**	445	5.03 ± 0.09	1.73 ± 0.02	5.48 ± 0.01	22.4 ± 0.2	4.76 ± 0.06	2.02 ± 0.03	5.50 ± 0.01	22.8 ± 0.2
Korean	668	5.01 ± 0.05	1.87 ± 0.01	5.55 ± 0.01	22.8 ± 0.1	5.03 ± 0.03	2.18 ± 0.02	5.57 ± 0.01	24.1 ± 0.1
Japanese*	233	5.17 ± 0.13	1.86 ± 0.04	5.50 ± 0.01	23.1 ± 0.3	5.24 ± 0.09	2.13 ± 0.05	5.57 ± 0.01	23.4 ± 0.3
l.s.d.		0.38	0.12	0.03	0.9	0.26	0.15	0.03	0.9
	1346	n.s.	P<0.05	P<0.05	n.s.	P<0.05	P<0.05	P<0.05	P<0.05

Table 4.6 continued

Fixed Effects:	Number of animals	Shear force LT (kg)	Compression LT (kg)	Ultimate pH LT (pH)	Cooking loss LT (%)	Shear force ST (kg)	Compression ST (kg)	Ultimate pH ST (pH)	Cooking loss ST (%)
Sex(market)									
Domestic heifers**	240	4.94 ± 0.10	1.71 ± 0.03	5.50 ± 0.01	22.1 ± 0.2	4.90 ± 0.06	2.11 ± 0.04	5.51 ± 0.01	22.6 ± 0.2
Domestic steers **	120	5.04 ± 0.11	1.68 ± 0.03	5.45 ± 0.01	22.9 ± 0.2	4.72± 0.07	1.94 ± 0.04	5.48 ± 0.01	22.6 ± 0.2
Korean heifers	450	5.01 ± 0.05	1.80 ± 0.01	5.54 ± 0.01	22.6 ± 0.1	5.11 ± 0.03	2.20 ± 0.02	5.56 ± 0.01	23.6 ± 0.1
Korean steers	162	4.72 ± 0.08	1.88 ± 0.02	5.56 ± 0.01	23.0 ± 0.1	4.92 ± 0.05	2.14 ± 0.03	5.60 ± 0.01	24.3 ± 0.2
Japanese steers	164	4.89 ± 0.12	1.83 ± 0.03	5.47 ± 0.01	23.3 ± 0.2	4.97 ± 0.08	2.02 ± 0.04	5.58 ± 0.01	23.2 ± 0.2
l.s.d.		0.37	0.09	0.03	0.6	0.25	0.12	0.03	0.6
	1136	n.s.	P<0.05	P<0.001	P<0.001	n.s.	P<0.001	P<0.001	P<0.001

* Japanese market – steers only.

** No domestic animals were finished in the temperate feedlot.

l.s.d. = least significant difference for observations to be significantly different from each other.

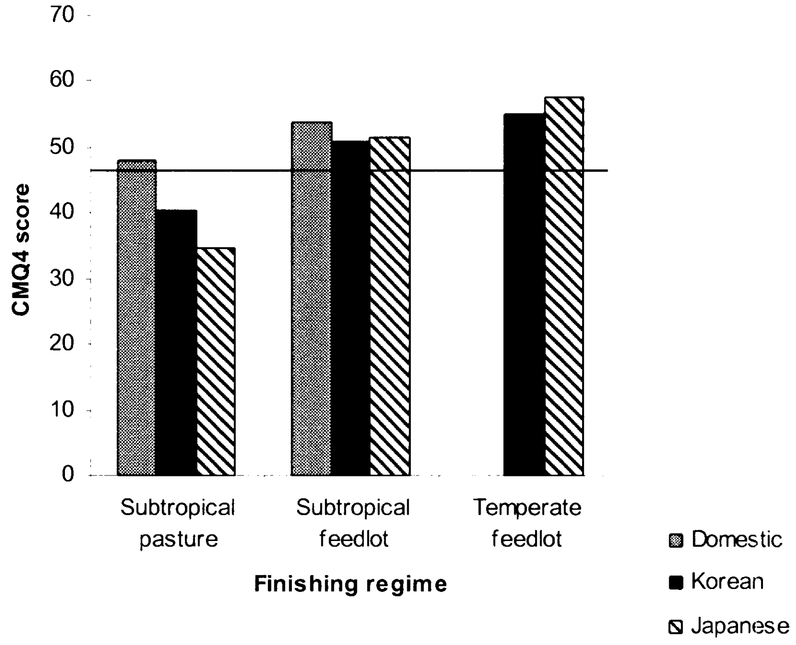
Table 4.7 Least squares means (± s.e.) for effect of finishing regime, market endpoint and sex within market on MSA CMQ4 Score and ossification score for steers and heifers. Traits adjusted to a common hot carcass weight for finishing regime, and a common hot carcass weight within market endpoint for market and sex effects. Finishing regime and sex within market effects exclude steers treated with HGP.

Fixed Effects:	Number of animals	CMQ4 Score (out of 100)	Ossification score
		1996 / 1997 calf crops only	
Finishing regime			
Subtropical pasture	172	42.7 ± 1.1	224 ± 4
Subtropical feedlot	156	52.4 ± 1.0	147 ± 3
Temperate feedlot**	132	57.4 ± 1.3	126 ± 4
l.s.d.		3.8	12
	460	P<0.001	P<0.001
Market endpoint			
Domestic**	153	46.0 ± 2.4	159 ± 8
Korean	315	47.5 ± 0.9	196 ± 3
Japanese*	109	48.4 ± 2.9	192 ± 10
l.s.d.		8.5	29
	577	n.s.	P<0.001
Sex (market)			
Domestic heifers **	84	43.0 ± 2.6	176 ± 9
Domestic steers **	35	52.4 ± 2.7	141 ± 9
Korean heifers	185	46.8 ± 1.0	217 ± 3
Korean steers	85	51.1 ± 1.5	171 ± 5
Japanese steers	71	54.8 ± 2.4	155 ± 8
l.s.d.		8.3	28
	460	P<0.001	P<0.001

* Japanese market – steers only. ** No domestic animals were finished in the temperate feedlot.

l.s.d. = least significant difference for observations to be significantly different from each other.

Figure 4.2 Effect of finishing regime on CMQ4 scores across markets (n=460). The line at CMQ4 score 46.5 indicates the minimum score for MSA 3-star grading.



4.3.4 Market endpoint effects

Market endpoint demonstrated the effect of age on meat quality. Tables 4.6 and 4.7 show meat quality results for domestic, Korean and Japanese market animals. Age at slaughter was 643±4, 761±2 and 817±6 days for respective markets. As animals aged from domestic to Korean weights, significant increases were found for ICLT, PHLT, SFST, ICST, PHST, CLST and OSSIF. Connective tissue toughness was not important for these animals, but ICST was nearing the point of unacceptable limits for export market animals, suggesting connective tissue toughness was becoming an issue for animals greater than 25 months of age. Shear force measures showed myofibrillar toughness was also becoming an issue for Japanese animals by 27 months of age. Yet they had more desirable CMQ4 scores (n.s.) relative to younger market animals. Korean and Japanese market animals only differed significantly for PHLT, but all markets were within the acceptable ultimate pH range. Despite 56 days difference in age at slaughter, Korean animals had slightly higher OSSIF (n.s.) than Japanese animals. This was a result of females taking 46 days longer than steers to finish to Korean weights, and their faster rate of physiological maturity relative to steers.

4.3.5 Sex effects

Heifers and steers were managed separately following weaning, so direct comparisons are not possible. Nevertheless, results in Tables 4.6 and 4.7 show some interesting trends. There was little difference between the sexes for LT and ST shear force and compression measures, though domestic heifers had higher ICST relative to domestic steers ($P<0.001$), and heifers had higher OSSIF than steers at domestic and Korean weights ($P<0.001$). Differences in OSSIF ($P<0.001$) between the sexes may be explained by differences in age at slaughter ($P<0.001$; see Chapter 3, Table 3.6) and the faster rate of physiological maturity of heifers relative to steers at common weights. This was reflected in poorer CMQ4 scores for domestic heifers relative to domestic steers ($P<0.001$).

4.3.6 Herd of origin effects

Herd of origin had little effect on meat quality. The exceptions were SFLT being 5.05±0.03 and 4.83±0.05 for animals bred at 'Duckponds' and Brigalow Research Station respectively ($P<0.001$), and CLLT was 0.26% higher for Brigalow Research Station animals ($P<0.05$).

4.3.7 Year effects

Year of birth was significant for most meat quality traits. ICST, CLST, PHLT, PHST and CMQ4 were highest in 1996. In 1998, SFST was highest and ICLT was lowest ($P<0.001$).

4.3.8 HGP effects

Intensive use of HGPs adversely affected both objective and sensory meat quality traits. HGP results were reported by Hunter *et al.* (2001) on a subset of the data. An analysis on the complete dataset (n=242) showed HGP had significant negative effects on SFLT, ICLT, ICST, CLST, CMQ4 and OSSIF ($P<0.05$; results not shown), though objective meat quality measures did not exceed tenderness limits associated with consumer perceptions of toughness. The exception was SFLT that was 4.87±0.07 and 5.08±0.07 for control and implanted steers respectively. CMQ4 scores were 50.0±1.0 and 44.6±1.0 for control and implanted steers respectively ($P<0.001$). HGP use increased MSA failure rates from 10% of the control steers to 51% of the implanted steers. The negative HGP effect was evident across all markets. No Korean steers reached MSA grading standards (CMQ4 scores greater than 46.5).

4.3.9 Interactions

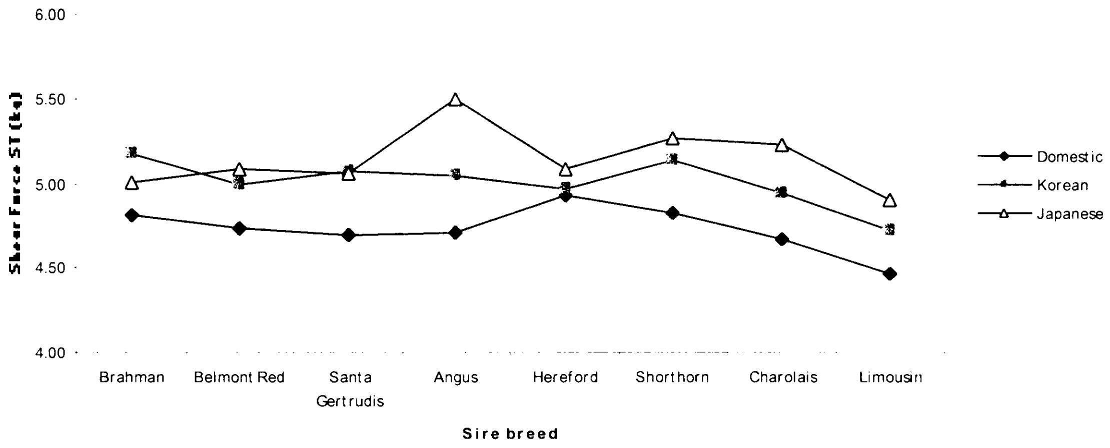
Most significant interactions were a result of scale effects rather than re-ranking of animals for meat quality traits. Figure 4.3 shows significant breed × finish interactions for ICST and ICLT. The breed × finish interaction for ICST ($P<0.05$) showed all sire breeds had slightly higher ICST in the temperate feedlot relative to the subtropical feedlot, except Limousin sired crosses. However all sire breeds finished in feedlots had ICST less than 2.2 kg, so this interaction was of little concern. The breed × finish interaction for ICLT ($P<0.05$) showed a change in ranking of Angus and Shorthorn sire breeds between feedlot finishing regimes, however all sire breeds had ICLT less than 2.2 kg for all finishing regimes indicating this interaction had little impact on changing sire breed acceptability for eating quality. Figure 4.4 shows a significant breed × market interaction for SFST ($P<0.05$) indicating a change in ranking of British type breeds for this trait. Least squares means ± standard errors for breed × finish and breed × market interactions can be found in Appendix D.

Figure 4.3 Interaction plots showing significant breed × finish interactions.

(a) ICST

(b) ICLT

Figure 4.4 Interaction plot showing a significant breed × market interaction for SFST.



Market × finish interactions were significant for all meat quality traits examined ($P<0.05$). The market × finish interaction for CMQ4 ($P<0.05$; Figure 4.2) showed Japanese animals had poorer eating quality than Korean animals when finished on pasture, while the opposite was true for both feedlot finishing regimes. This was likely due to the older age at slaughter of Japanese animals finished on pasture relative to feedlot-finishing (36 months versus 23 months for pasture and feedlot respectively). Even at 24 months of age, domestic animals finished on pasture failed to produce shear force and instron compression measures within acceptably tender limits (SF less than 5.0 kg and IC less than 2.2 kg), though CMQ4 was acceptable.

Finish × year of birth interactions were significant for all meat quality traits ($P<0.001$).

4.4 *Discussion*

4.4.1 Sire breed effects

Despite large differences between Brahman and first-cross genotypes for carcass quality traits (Chapter 3), there was little difference between sire breeds for most objective and sensory meat quality traits with the exception of straightbred Brahmans for sensory and LT meat quality. There was little evidence of important breed × finish and breed × market interactions on meat quality. Our results agreed with other meat quality studies conducted in subtropical environments. Two feedlot-finishing studies in the USA (Peacock *et al.* 1982; DeRouen *et al.* 1992a) and a pasture-based study in the Australian arid tropics (Pratchett *et al.* 1988) reported Brahman breed effects were significantly unfavourable for shear force relative to Brahman × *Bos taurus* crosses. However, all three studies reported shear force measures that would be considered unacceptably tough (greater than 5.0 kg) for all respective genotypes, which is different from our findings. This may be due to abattoir slaughter protocols in these other studies being inconsistent with best practice pre-and post-slaughter protocols implemented in Australian abattoirs in more recent times, reducing the negative effects of processing on meat toughness. The magnitude of the results for PHLT, SFST, ICST, PHST, CLST and CMQ4 were generally consistent with objective and sensory meat quality findings for tropically adapted straightbreds (Brahman, Santa Gertrudis and Belmont Red) reported in the Beef CRC Straightbreeding Program (Johnston *et al.* 2003). The main difference between CRC studies was the tropically adapted straightbreds had more desirable measurements for SFLT, ICLT and CLLT relative to the Brahman crossbreds in this experiment. In an unrelated study, Hearnshaw *et al.* (1999) reported higher cooking loss ($P<0.05$) and lower sensory palatability ($P<0.05$) of Brahmans relative to Angus sired steers from Hereford, Brahman and crossbred dams finished on pasture, consistent with our results for straightbred Brahmans relative to crossbreds.

An important outcome from this experiment is that carcasses with up to 75% *Bos indicus* content can successfully meet minimum standards for objective and sensory meat quality. Crossbreds with 50% and 75% *Bos indicus* content did not differ significantly for objective and sensory meat quality traits, except for Continental crosses for SFST. Consistent findings were reported by Johnson *et al.* (1990) and Pringle *et al.* (1997) who found no significant difference in shear force and sensory panel evaluation between Brahman × Angus steers with 50% and 75% Brahman content, feedlot-finished in Florida in separate experiments. Wythes *et al.* (1989) reported no effect of genotype on SFLT, cooking loss or ultimate pH in 25-70% *Bos indicus* content steers. On the other hand, Crouse *et al.* (1989) observed significant differences in shear force and sensory panel scores for 50% versus 75% Brahman groups, concluding that as percentage of Brahman content increased, sensory tenderness and juiciness decreased. In their study, processing practices were not controlled to the same extent as occurred in our study.

Muscle factors associated with breed differences in meat tenderness have been identified including the post-mortem rates of glycolysis and proteolysis, and connective tissue properties (Harper 1999; Ferguson *et al.* 2001; Ferguson 2002). Given instron compression measures for the LT and ST were less than 2.2 kg and not significant for ICST, it would appear connective tissue toughness was not important in these Brahman crossbreds slaughtered by an average of 24 months of age. Other studies have also failed to find significant breed differences in collagen content and solubility (Johnson *et al.* 1990; Whipple *et al.* 1990), though McKay *et al.* (2001) found an increased number of thicker perimysial seams in *Bos indicus* cattle which was believed to cause increased connective tissue toughness in that study. The myofibrillar component of muscle is believed to be the major contributor to tenderness variation (Johnson *et al.* 1990;

Whipple *et al.* 1990; Shackelford *et al.* 1995; Harper 1999). Post-mortem rates of glycolysis and subsequent pH decline have been shown to be slower in *Bos indicus* muscle relative to *Bos taurus*, leading to increased shortening of the myofibrillar proteins (Wheeler *et al.* 1990; Shackelford *et al.* 1991). However, use of electrical stimulation on all carcasses in this experiment should have eliminated problems with cold shortening, though it may inadvertently have caused problems with heat shortening (Thompson 2002). Other research has found no difference between breeds for pH decline (Wythes *et al.* 1989; Whipple *et al.* 1990) which is consistent with our findings. Muscle fibre type and size have also been implicated in breed differences for tenderness (Harper 1999). Further, palatability of muscles surrounding the spinal column appear to be more affected by increasing *Bos indicus* content than muscles elsewhere on the carcass (Thompson *et al.* 1999a). Hopkins and Thompson (2002) concluded the calpain protease system was the major candidate to explain *post-rigor* tenderisation. As *Bos indicus* content increases, an increase in calpastatin activity, and in some cases a decrease in calpain activity, leads to reduced myofibrillar degradation (Wheeler *et al.* 1990; Whipple *et al.* 1990; Shackelford *et al.* 1991, 1994; Pringle *et al.* 1997; Ferguson *et al.* 2000). Whipple *et al.* (1990) and Shackelford *et al.* (1991) also reported lower myofibrillar fragmentation indices in *Bos indicus* crossbreds, which have been shown to follow closely with breed group effects on shear force and sensory panel tenderness (Johnson *et al.* 1990). This would support our finding that straightbred Brahmans had tougher SFLT and lower sensory palatability than crossbreds, but it does not explain our SFST results.

Genetic variation can be masked by variation due to environmental sources unless environment is closely controlled (Thompson 1999). Environmental sources of variation include growth path, immediate pre- and post-slaughter environments, the extent of proteolysis and the degree and duration of heat applied during cooking. Stress, physical activity prior to slaughter, animal age, use of hormonal growth promotants and intramuscular fat have all been implicated in meat toughness (Harper 1999). Relatively low genetic variation in comparison to environmental variation and inconsistent genetic correlations between tropical and temperate breeds suggest genetic improvement in tenderness may be less important than effective pre- and post-slaughter management protocols (Robinson *et al.* 2001). The management of an animal immediately before slaughter and the carcass processing conditions applied within the first 24 hours post-slaughter have the largest influence on beef palatability, and can negate any genetic advantage in meat quality (Ferguson *et al.* 2001). Furthermore, research has shown consumers can be satisfied with beef from 100% *Bos indicus* cattle, providing they are relatively young at slaughter and appropriate pre-and post-slaughter best practice (electrical stimulation, tenderstretch, ageing) has been applied (Ferguson 2002).

There was no one sire breed or breed-type (British-, Continental-, or tropically adapted-type) that excelled for meat quality across traits. Lack of evidence of breed interactions indicates cattle breeders can use a range of crossbred combinations and do not need to change sire breeds to target different markets, different finishing regimes or different finishing environments.

4.4.2 Pasture versus feedlot finishing

Feedlot-finishing of Brahman crossbreds is an important management component if tenderness is included in market specifications, regardless of market endpoint. Relative to pasture, feedlot-finishing significantly improved all objective and sensory meat quality traits except CLST. Bennett *et al.* (1995) similarly reported that steers with no more than 50% Brahman content finished on rhizome peanut pasture in subtropical Florida had higher shear force (6.8 versus 4.0 kg; $P<0.001$), lower sensory juiciness ($P<0.01$) and lower sensory tenderness ($P<0.001$) relative to their feedlot-finished contemporaries. Ferguson *et al.* (2000)

reported significant differences in shear force ($P<0.05$) and ultimate pH ($P<0.001$) between pasture and feedlot-finished carcasses in an experiment including Hereford, Brahman × Hereford and Brahman steers and heifers, with approximately 1 kg lower shear force of feedlot-finished animals, and ultimate pH of 5.72 and 5.57 for pasture and feedlot-finishing respectively. This is consistent with our results for SFLT and ultimate pH, though differences in PHLT and PHST between pasture and grain finishing in our experiment were much smaller. Johnston *et al.* (2003) reported consistent findings in magnitude and direction for SFLT, ICLT, SFST, ICST and CLLT in the Straightbreeding Program for Brahman, Belmont Red and Santa Gertrudis animals finished on pasture and grain in the subtropics. Though CMQ4 results were lower for straightbred animals (40.9 and 47.8 for pasture and feedlot-finishing respectively) relative to our results. In contrast, Allingham *et al.* (1998) reported no significant difference in SFST or ultimate pH between Brahman cross steers finished on three regimes including improved tropical pasture (uninterrupted growth) or low quality grass hay for 100 days followed by feedlot or pasture-finishing for 157 days when slaughtered at hot carcass weights of 171 to 218 kg. Nonetheless, feedlot-finished animals had lower shear force of pressure heated ST samples ($P<0.05$), higher ST cooking loss ($P<0.05$) and lower ST compression (n.s.) than pasture-finished contemporaries, which is consistent with our findings.

Differences in meat quality between pasture and feedlot-finishing have been attributed to older age at slaughter, interrupted growth path of pasture-finished animals and growth rate. Pasture-finished animals were on average, 7 months older at slaughter than feedlot-finished contemporaries and experienced an additional dry season, possibly undergoing growth stasis or loss before reaching target market weights during the following wet season. Even at domestic market weights (24 months), objective measures of myofibrillar and connective tissue toughness of pasture-finished animals were outside acceptable tenderness limits, suggesting a growth path effect on meat quality. Tougher meat from pasture-finished animals may have been the result of older more mature intramuscular collagen and slower rates of collagen turnover relative to animals finished in the feedlot on a higher plane of nutrition (Harper *et al.* 1997).

4.4.3 Subtropical versus temperate finishing environments

Geographic region had significant effects on objective and sensory meat quality. The higher ICST and OSSIF of temperate feedlot animals is inconsistent with their more desirable sensory palatability. Results for LT and ST instron compression and SFST from the Straightbreeding Program (Johnston *et al.* 2003) were similar in magnitude but the reverse trend of these findings. Tropically adapted straightbreds (Brahman, Belmont Red, Santa Gertrudis) tended to have lower (more favourable) SFLT than our results. Similar to our findings though, Johnston *et al.* (2003) reported higher CMQ4 results for animals finished in the temperate feedlot. However there was only a difference of 1.2 units for the tropically adapted straightbreds, while crossbreds in our experiment differed by 5.0 units. A study by Johnson *et al.* (1990) reported higher sensory panel ratings for loin steaks from calves finished in the cool season relative to their contemporaries finished in the warm season. This effect was attributed to a higher percentage of heat-soluble collagen in animals finished in the cool season resulting in more connective tissue break down during cooking. Our findings of no difference in shear force between feedlots and higher sensory palatability of temperate feedlot-finished animals were consistent with those of Johnson *et al.* (1990).

Nutritional differences in seasonal pasture quality and quantity and interrupted growth of animals during grow-out prior to feedlot entry (subtropical pasture versus temperate pasture) may have influenced meat quality characteristics between finishing environments. Growth path has an important influence on meat quality (Allingham *et al.* 1998; Harper 1999, Oddy *et al.*

2001). Harper *et al.* (1997) reported that a period of severe nutritional restriction in an animal's growth path can influence the connective tissue toughness of its meat for at least 150 days following restriction. Allingham *et al.* (1998) concluded that nutrition and growth path, including a regime combining periods of weight loss and compensatory growth, decreased connective tissue toughness of ST muscles, possibly through increased intramuscular collagen turnover. Therefore, animals that had lost weight on low quality pasture and then regained weight on a grain diet had significantly lower connective tissue toughness than animals grown on an uninterrupted growth path of improved tropical pasture. Findings from Allingham *et al.* (1998) are consistent with our results and may explain why subtropical feedlot animals, exposed to greater seasonal fluctuations of pasture quality and quantity during grow-out, had lower ICST ($P<0.001$) than temperate feedlot contemporaries. Nevertheless, we did not examine growth rates in this experiment and therefore cannot confidently say differences in growth path were causative of this effect.

4.4.4 Market effects

As animals age, increased collagen concentration is believed to be the primary contributor to increased meat toughness (Berge *et al.* 1997). Results indicate that connective tissue toughness and SFST increased as animals aged. Yet, except for shear force in Japanese market animals, LT and ST shear force and instron compression were within acceptable tenderness levels, which may explain why consumer taste panels did not find a significant difference in sensory palatability between markets. In fact, there was only a difference of 2.4 units in CMQ4 between markets, lending further weight to the conclusion that connective tissue toughness was not a major issue for the meat of these animals. This finding is supported by Johnston *et al.* (2003), who concluded that age-related changes in connective tissue toughness were not large in the Straightbreeding Program in animals up to 42 months of age. In contrast, market × finish interactions showed 12 months difference in age at slaughter for Japanese animals (36 versus 24 months of age) finished on pasture and feedlot respectively did result in significant detrimental effects on LT and ST shear force and instron compression ($P<0.05$) and sensory palatability ($P<0.05$). Therefore, myofibrillar and connective tissue toughness appear to contribute more to meat quality of Brahman crossbred animals after 24 months of age, particularly in animals finished on pasture.

4.4.5 Sex effects

Despite no difference in SFLT, ICLT and SFST between the sexes, heifers had significantly lower sensory meat quality scores than steers at domestic weights, which was consistent with results from the Straightbreeding Program (Johnston *et al.* 2003). In contrast to our findings, Johnston *et al.* (2003) reported heifers had higher shear force and compression measures relative to steers. A study by Lawrence *et al.* (2001) found heifers advanced in skeletal and overall maturity at a much faster rate than steers, despite a lack of difference in shear force, sensory tenderness or cooking loss between the sexes, supporting our OSSIF results. The significant sex effect on meat quality suggests heifers need to be finished differently to steers to attain similar eating quality. For example, palatability of heifers may be improved by increased time in feedlots. The lack of difference in shear force, instron compression and sensory quality between sexes when finished to Korean market weights supports the improved meat quality of heifers when grain-fed for 100 days relative to domestic heifers fed for 70 days in this experiment.

4.5 Implications for industry breeding programs

Animals with up to 75% Brahman content can successfully meet minimum objective and sensory meat quality standards for tenderness. There was little evidence of important breed × finish and breed × market interactions on meat quality. Therefore existing cattle breeding programs are suitable for pasture- and feedlot-finishing systems regardless of market endpoint, finishing regime or finishing environment. Connective tissue toughness was not important in Brahman crossbred animals before 24 months of age. Significant market × finish interactions for all meat quality traits show pasture-finishing in subtropical environments is not desirable for Korean and Japanese market animals if meat tenderness is an important market consideration. Negative meat quality outcomes from subtropical pasture-finishing appear to be due to a combination of seasonal nutritional availability and animal growth path. This may be negated by use of improved pastures, forage crops or supplementation to reduce weight stasis or loss during dry seasons. Negative effects of growth path on meat quality during grow-out can be overcome by feedlot-finishing for a minimum of 70 days in subtropical or temperate feedlots to achieve acceptable levels of objective and sensory meat quality, with the added benefit of reduced age at slaughter. Heifers tend to have poorer sensory palatability than steers at common market weights which may be overcome by grain feeding for a longer period or grain feeding from an earlier age. The negative effects of inadequate pre- and post-slaughter management on meat quality should not be ignored, particularly as carcasses from straightbred Brahman cattle can meet minimum consumer palatability standards if best practice pre- and post- slaughter protocols are implemented. The MSA system is now rewarding beef producers with premium prices for every cut in every carcass that meets minimum eating quality standards for the domestic market.

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CHAPTER 5 Sire breed differences for feed efficiency and feeding behaviour of feedlot finished Brahman crossbreds

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Abstract. The objective of this experiment was to quantify differences in feed efficiency and feeding behaviour of 470 heifers and steers by Brahman, Belmont Red, Santa Gertrudis, Angus, Hereford, Shorthorn, Charolais and Limousin sires to Brahman dams. Animals averaged 598 days of age and 425.8 kg at the start of the feed intake test period. Sire breeds did not differ for eating rate (TIMEkg), feed conversion ratio (FCR) or relative growth rate (RGR). Generally, higher feed intakes (FI) corresponded with higher average daily gains (ADG). Straightbred Brahmans fed the most frequently (16.6±0.8 sessions per day; $P<0.05$) but spent the least time eating of all breeds (67.4±2.7 mins per day; $P<0.001$). Least squares means for Brahman, Belmont Red, Santa Gertrudis, Angus, Hereford, Shorthorn, Charolais and Limousin sired progeny respectively were 0.02±0.16, 0.14±0.13, -0.10±0.23, 0.54±0.17, -0.27±0.18, 0.29±0.18, -0.46±0.16 and -0.21±0.13 for residual feed intake (RFI; $P<0.05$), and 1.06±0.05, 1.17±0.04, 1.52±0.08, 1.47±0.06, 1.46±0.06, 1.46±0.06, 1.35±0.06 and 1.38±0.05 for ADG ($P<0.001$).

While they did not differ from all other sire breeds for RFI, the lower appetite of straightbred Brahmans relative to crossbred contemporaries resulted in the lowest FI ($P<0.001$) and lowest ADG ($P<0.001$) overall. Angus sired crosses were the least efficient feeders and spent the most time eating, consumed the most feed and had the highest RFI, but were not different to Santa Gertrudis and Shorthorn crosses for these traits. Angus sired crosses spent 24.1 and 15.4 min/day (36% and 20%; $P<0.001$) more time eating than straightbred Brahmans and Charolais crosses, and consumed 35% and 13% ($P<0.001$) more feed respectively. Charolais sired crosses were the most feed efficient with the lowest RFI and intermediate FI, and did not differ significantly to the highest ranking sire breeds for ADG or Kleiber ratio (KR). While Belmont Red crosses did not differ from all breeds for RFI, they had significantly lower FI than British and Santa Gertrudis crosses resulting in lower ADG ($P<0.001$) relative to these sire breeds. Therefore, selection of Charolais, Hereford, Limousin and Santa Gertrudis sire breeds would result in the most feed efficient (low RFI) crosses with Brahman without any sacrifice in ADG.

5.1 Introduction

A percentage of Brahman content in northern Australian breeding herds is essential for adaptation and survival in subtropical and semi-arid extensive grazing environments. More than 50% of the national herd is estimated to have some Brahman genes (Bindon 2002). Of the total 666,000 head of cattle in Australian feedlots in March 2004, Queensland held nearly half of these (ABS 2005). Feedlot-finishing of Brahman crossbreds in subtropical environments has been shown to improve carcass and meat quality attributes, including objective and sensory tenderness, and decrease age at slaughter by 7-months relative to pasture-finishing (Chapters 3 and 4). With markets demanding a reliable supply of beef of consistently high eating quality, feedlot-finishing is becoming standard practice in northern beef production systems targeting domestic and premium export markets. However, straightbred Brahmans have a reputation for poorer growth in feedlots relative to other breeds and crossbreds and this has been attributed to breed differences in feed intake and feed utilisation.

The literature generally agrees that genetic variation in feed efficiency exists (reviewed by Archer *et al.* 1999). These variations in feed efficiency potentially represent an opportunity for beef producers to significantly reduce production costs by reducing feed intake whilst maintaining growth rate. A study by Richardson *et al.* (1998) found high efficiency steers (low RFI) grew as fast as or faster than low efficiency steers but ate less feed per unit gain. However, RFI has been reported to have relatively high genetic correlations with rump and rib fat and intramuscular fat percent (0.72, 0.48 and 0.22 adjusted for age; Robinson and Oddy 2004). Therefore, selection of breeds or sires within breed for lower RFI may lead to a consequent decrease in carcass fatness which may also have implications for female fertility (review by Pitchford 2004). Further, selection for RFI may produce changes in the calpain system which may consequently affect meat tenderness (McDonagh *et al.* 2001). Other studies report only small positive correlations between RFI or FCR and fatness (Arthur *et al.* 2001; Richardson *et al.* 2001). Though antagonistic correlations between slaughter and breeding herds may be overcome through use of economic selection indices, development of feed efficiency EBVs is still in its early stages and measurement of individual feed intakes remains expensive. Hence, selection of breeds that have high feed efficiency (low RFI) for the same level of gain as low efficiency breeds, coupled with crossbreeding, may overcome some of the problems associated with within-breed selection.

Evidence from the literature indicates that both genetic and environmental factors affect the way in which nutrients are used by beef cattle. A review by Arthur (2000) concluded that differences in efficiency of maintenance exist between breeds, and these differences are correlated to differences in productive potential of breeds. Efficiency of feed utilisation has a number of variable components including feed intake, digestion of feed, metabolism (including variation in body composition), activity and thermoregulation (reviews by Archer *et al.* 1999; Herd *et al.* 2004). Early research on tropically adapted genotypes (Frisch and Vercoe 1969, 1977; Vercoe 1967, 1970; Vercoe *et al.* 1972) shows there are differences in feed intake, eating rate, weight gain, metabolic rate and efficiency of feed utilisation between breeds and across different environments. However, those early studies were based on low numbers of animals and did not include representatives of the large Continental breeds that have since been imported to Australia. Studies by Cundiff *et al.* (1984) and Huffman *et al.* (1990) examined *Bos taurus* × *Bos indicus* cattle relative to *Bos taurus* contemporaries, and Robinson and Oddy (2004) reported feed efficiency of tropically adapted breeds relative to temperate breeds. However there is a deficiency in research examining feed efficiency of *Bos indicus* breeds and their crossbreeds. Quantifying the efficiency of feed utilisation of *Bos indicus* relative to *Bos taurus* × *Bos indicus* is the next step in improving production efficiency and economic profitability for northern Australian beef producers and the feedlot sector. The objective of this experiment was to quantify differences in feed efficiency and feeding behaviour of straightbred Brahmans versus Brahman crossbreds finished to Australia's two main export markets.

5.2 Materials and methods

5.2.1 Experimental design and animals

Full details of the experimental design, measurements and data storage for the Beef CRC Northern Crossbreeding Program were described by Upton *et al.* (2001). Briefly, eight sire breeds including Brahman (purebred control), Santa Gertrudis, Belmont Red, Angus, Hereford, Shorthorn, Charolais and Limousin were mated naturally and by artificial insemination to 1,000 Brahman females over three years to produce 1,750 Brahman and first-cross progeny at two properties in subtropical central Queensland. The optimal number of sires, offspring per sire and number of link sires between herds and allocation of animals to treatment combinations were described by Robinson (1995). Calves were weaned in 1996, 1997 and 1998 at about six months of age.

'Tullimba' is a purpose-built research facility designed to allow individual feed intake recording for large numbers of animals in a commercial feedlot environment. No such facility existed in Queensland to replicate the feed efficiency experiment, so two thirds of the calves that were finished in two subtropical finishing regimes were excluded from the feed efficiency study. Because of the minimum feed intake recording protocols (discussed in section 5.2.2) , the large number of animals in 'Tullimba' at the one time and limited feed intake recorders, domestic market animals were also excluded from the study. Four hundred and seventy calves were grown out on temperate pastures at Glen Innes Research Station (native and introduced pastures, described by Ayres *et al.* 2001) or 'Tullimba' Beef Research Facility (native wallaby grass, *Austrodanthonia spp.*) in north-eastern New South Wales to feedlot entry weight of 400 kg. Table 5.1 shows the number of sires per breed and the number and sex of progeny per breed analysed for feed efficiency. Because the number of animals measured for individual feed intake was limited by the experimental design, the number of progeny per sire were low. A cohort was defined by a combination of sex, market endpoint and year of birth. All animals within a cohort were managed as a single group during grow out and finish. Calves were fed in 'Tullimba' feedlot for an average of 112 and 164 days to Korean (280 kg) and Japanese (320 kg) carcass weights.

Table 5.1 Number of sires and progeny per sire breed.

Sire breed	Number of sires	Heifer progeny	Steer progeny	Total
Brahman	14	34	43	77
Belmont Red	14	36	60	96
Santa Gertrudis	8	15	17	32
Angus	10	18	25	43
Hereford	8	19	17	36
Shorthorn	7	16	18	34
Charolais	15	40	34	74
Limousin	14	33	45	78
Total	90	211	259	470

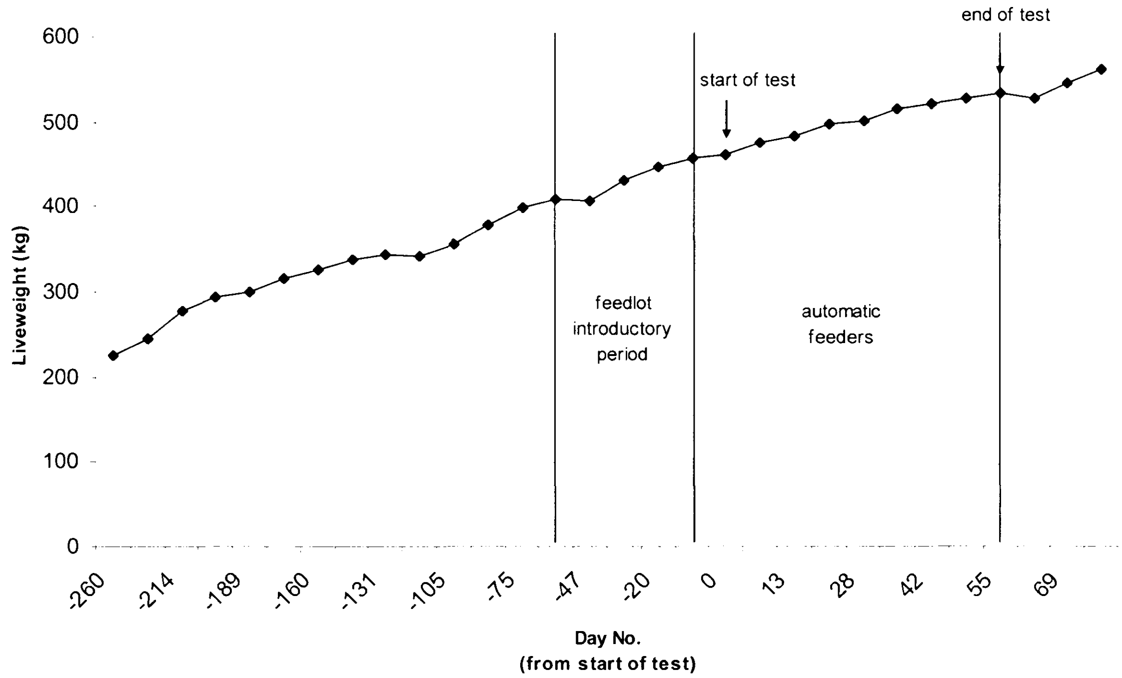
5.2.2 Data edits

During the period in the feedlot, individual feed intakes of a standard finisher ration (minimum 11.8 MJ ME/kg with a minimum of 150g crude protein per kg dry matter) offered *ad-libitum* were recorded using automatic individual feed intake recorders. Because metabolisable energy (ME) of the feed ranged between 11.8 and 12.4 MJ ME/kg DM in finishing rations for the different cohorts, all feed intake records were adjusted to 12 MJ ME/kg DM. All animals were given a minimum 21-day introductory period to the feedlot ration, followed by a 7-day adjustment period during which time they learned to use the automatic feeders. Only those animals that adapted well to the grain-based diets and learned to use the automatic feeders efficiently were used in the analyses. Animals fed for less than 48 days in the automatic feeders, due to sickness or shy feeding, were excluded from the analysis.

In order to accurately measure feed efficiency, an optimum test length of no less than 35 days is required for collection of feed intake data, and 70 days (including fortnightly weighing) is required for accurate measurement of growth rate, feed conversion and residual feed intake (Archer *et al.* 1997). The recommended period for adjustment to automatic feeders is 21 days, meaning animals would need to have individual feed intakes recorded for a minimum of 91 days to accurately measure all traits. However, due to the 21-day introductory period on feedlot rations, the adjustment period in the automatic feeder pens, limited capacity in the automatic feeder pens, and market constraints on final liveweight and total days on grain, it was not possible to measure feed intake on all animals for the recommended 70 days plus the adjustment period (Robinson 2000). A study of 1165 straightbred temperate and tropical breed animals at 'Tullimba' reported correlations between feed intakes of the same animal (excluding the first week in the automatic feeders) averaged 0.66 in different weeks and 0.71 for successive weeks, indicating feed intake measurements were reasonably repeatable (Robinson 2000). Hence a compromise was made to measure as many animals as possible, and consequently individual feed intakes were recorded for an average of 60 and 61 days for Korean and Japanese market animals from the Crossbreeding Program, including the adjustment period in the automatic feeders. Growth curves including liveweights prior to feedlot entry through to slaughter were plotted for each cohort (Figure 5.1 shows a typical growth curve). The growth curves indicated linear growth with most cohorts showing growth checks on entering the feedlot for the introductory grain period and minor growth checks following entry to the automatic feeder pens.

Weights were measured at 7-day intervals from entry to the automatic feeder pens. Given diet remained constant and growth checks were limited to 7 days upon entering the automatic feeder pens, daily feed intakes were excluded for the first 7 days in the automatic feeders rather than the standard 21-day protocol. An analysis was also run based on exclusion of a 14-day adjustment period to the automatic feeder pens and yielded consistent sire breed rankings and significance to results for the 7-day adjustment period. It was concluded that a longer period on test would present more accurate results (53 days versus 46 days for 7- versus 14-day adjustment periods respectively). Hence results from the 7-day adjustment period are presented in this paper.

Figure 5.1 Typical growth curve showing mean liveweights for one Japanese steer cohort.



Each trait was examined for outliers falling more than three standard deviations from the mean, but individual feed intake sessions (n_1=365295), feed intake for an animal for one day of the test period (n_2=24894), or all feed intake records for an animal over the duration of the study (n_3=470) were only excluded from the analysis if there appeared to be measurement error.

Individual feed intake sessions were excluded from the analysis when they satisfied both criteria of being less than 0.876 kg consumed at one feeding session and time taken to eat 1kg exceeded 16.197 min (n_1=43). This mainly included records where animals spent a long time standing inside the feeders without the primary purpose of feeding. Feed intake records from individual visits to the feed bunks were also excluded if there were problems with the feed recorders on particular days and the quality of the feed intake records were compromised (n_2). Animals that had average daily gain less than 0.3 kg/day were checked individually for daily feed intake and feeding behaviour over the duration of the test for evidence of illness or feeding problems. In all cases, low average daily gain was due to low feed intake throughout the test period, likely due to lower appetite relative to contemporaries. These animals remained in the analysis. Six outliers (n_3) for feed conversion ratio were excluded because they fell more than three standard deviations from the mean (FCR less than -24.4 or greater than 45.8) causing distortion of results. The FCR outliers excluded from the analyses were 6 of the 19 animals with ADG less than 0.3 kg/day. Consequently, a total of 470 animals were analysed for feed efficiency.

5.2.3 Statistical analyses

The feed efficiency traits analysed in this study and their definitions are described in Table 5.2. Liveweights and daily feed intake (FI) were used to calculate average daily gain by regression (ADG), feed conversion ratio (FCR), residual feed intake by regression (RFI), Kleiber ratio (KR) and relative growth rate (RGR). ADG was calculated as the regression of liveweight on time (days) for start, interim and end weights using the REG Procedure of SAS (SAS 2000). RFI was calculated as FI less expected FI (expFI), where expFI was obtained by the regression of FI on average test period liveweight (MWT) to the 0.75 power and ADG. RFI was calculated within sex using the GLM Procedure of SAS (SAS 2000). Year of birth was fitted as a class variable. RGR expressed as the percentage of weight change per day was also calculated

(Fitzhugh and Taylor 1971). A standard of 70 days on test was used to calculate end of test weight and RGR. Feeding behaviour traits including time spent eating per day (TIME), time to eat 1 kg of feed (TIMEkg) and number of feeding sessions per day (SESS) were also assessed. Descriptive statistics for feed efficiency and feeding behaviour traits are presented in Table 5.3.

Table 5.2 Abbreviations and definitions of feed efficiency traits reported in this study (from Arthur *et al.* 2001).

Abbreviation	Definition of traits
STAGE (days)	Age at the beginning of test period.
STWT (kg)	Liveweight at beginning of test period.
ENDWT (kg)	Liveweight at end of test period.
MWT (kg)	Average test period liveweight. $MWT = (STWT + ENDWT) \div 2$
MMWT (kg)	Metabolic mid-weight. $MMWT = MWT^{0.75}$
FI (kg)	Daily feed intake adjusted to 12MJ ME/kg DM.
ADG (kg)	Average daily gain. Regression coefficient from the regression of weight on time (day).
FCR	Feed conversion ratio. Feed intake per unit weight gain. $FCR = FI \div ADG$
expFI	Expected feed intake. Regression of FI on $MWT^{0.75}$ and ADG.
RFI	Residual feed intake. Feed intake net of expected feed requirements for maintenance and growth. $RFI = FI - expFI$
RGR (%)	Relative growth rate. Growth relative to instantaneous size. $RGR = 100 \times (\log \text{end weight} - \log \text{start weight}) \div \text{days on test}$ (Fitzhugh and Taylor, 1971).
KR	Kleiber ratio. Weight gain per unit metabolic body weight. $KR = 100 \times (ADG \div MWT^{0.75})$
TIME (mins)	Time spent eating per day.
TIMEkg (mins)	Time to eat 1kg feed.
SESS	Number of feeding sessions per day.

Least squares means for breed effects were estimated using the GLM Procedure of SAS (SAS 2000). Fixed effects in the model included sire breed and a concatenated variable including sex, market, year of birth and herd of origin. Sire nested within breed was fitted as a random effect and was also used as the error term. Age at the start of the test period (STAGE) and weight at the start of the test period (STWT) were fitted as covariates for all traits in separate analyses, with the exception of RFI with STWT. An unadjusted analysis was run for all feed efficiency traits as well as STAGE, STWT and metabolic mid-weight (MMWT). There was little change in the magnitude of least squares means, significance or breed rankings between the two covariates and unadjusted analyses. However, R-square values were higher for all traits when STWT was fitted as the covariate. The multiple-range test devised by Duncan (1955) and extended by Kramer (1957) was used to test for significant differences between means.

The model used to analyse STAGE, STWT, MMWT, FI, expFI, RFI, ADG, FCR, KR, RGR, TIMEkg, TIME and SESS (unadjusted) was:

$$y_{ijkl} = \mu + \boldsymbol{breed}_j + \boldsymbol{otherFE}_k + \boldsymbol{sire}_{l(j)} + \varepsilon_{ijkl} \qquad (1)$$

where y_{ijkl} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{breed}_j$ is the effect of the $\boldsymbol{j}$th sire breed, $\boldsymbol{otherFE}_k$ is the effect of the $\boldsymbol{k}$th group that accounts for all other fixed effects concatenated into one variable (sex || market || year of birth || herd of origin), $\boldsymbol{sire}_{l(j)}$ is the random effect of the $\boldsymbol{l}$th sire nested within the $\boldsymbol{j}$th breed, and ε_{ijkl} is the residual error term.

The model used to analyse FI, expFI, ADG, FCR, KR, RGR, TIMEkg, TIME and SESS adjusted to a common starting weight was:

$$y_{ijkl} = \mu + \boldsymbol{breed_j} + \boldsymbol{otherFE_k} + \boldsymbol{sire_{l(j)}} + b_I\boldsymbol{STWT_{ijkl}} + \varepsilon_{ijkl} \qquad (2)$$

where y_{ijkl} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{breed_j}$ is the effect of the $\boldsymbol{j}$th sire breed, $\boldsymbol{otherFE_k}$ is the effect of the $\boldsymbol{k}$th group that accounts for all other fixed effects concatenated into one variable (sex || market || year of birth || herd of origin), $\boldsymbol{sire_{l(j)}}$ is the random effect of the $\boldsymbol{l}$th sire nested within the $\boldsymbol{j}$th breed, $\boldsymbol{STWT_{ijkl}}$ is the linear effect of the weight of the animal at the start of the feed intake test fitted as a covariate, and ε_{ijkl} is the residual error term.

The model used to analyse FI, expFI, RFI, ADG, FCR, KR, RGR, TIMEkg, TIME and SESS adjusted to a common starting age was:

$$y_{ijkl} = \mu + \boldsymbol{breed_j} + \boldsymbol{otherFE_k} + \boldsymbol{sire_{l(j)}} + b_I\boldsymbol{STAGE_{ijkl}} + \varepsilon_{ijkl} \qquad (3)$$

where y_{ijkl} is the observation for a dependent variable for animal $\boldsymbol{i}$, μ is the overall mean, $\boldsymbol{breed_j}$ is the effect of the $\boldsymbol{j}$th sire breed, $\boldsymbol{otherFE_k}$ is the effect of the $\boldsymbol{k}$th group that accounts for all other fixed effects concatenated into one variable (sex || market || year of birth || herd of origin), $\boldsymbol{sire_{l(j)}}$ is the random effect of the $\boldsymbol{l}$th sire nested within the $\boldsymbol{j}$th breed, $\boldsymbol{STAGE_{ijkl}}$ is the linear effect of age of the animal at the start of the feed intake test fitted as a covariate, and ε_{ijkl} is the residual error term.

Table 5.3 Descriptive statistics.

Trait	Mean	SD
STAGE (days)	597.5	49.8
STWT (on-test) (kg)	425.8	66.9
STWT (by regression) (kg)	425.5	67.4
ENDWT (kg)	493.8	73.9
ENDWT by reg (kg) (70-day test)	520.0	78.1
MWT (kg)	472.7	71.4
MMWT (kg)	101.2	11.5
Actual FI (kg)	12.177	2.399
FI (kg) (adjusted to 12MJ ME/kg DM)	12.093	2.430
ADG (kg)	1.350	0.427
FCR	9.7	3.5
expFI (kg)	12.093	2.169
RFI (kg)	-0.000	1.095
RGR (%)	0.288	0.085
KR	1.33	0.39
TIMEkg (min)	6.76	1.71
TIME (min/day)	80.3	21.8
SESS (number/day)	14.7	6.3
TEST DAYS	53.0	11.3

5.3 Results

Animals averaged 598 days of age and 425.8 kg at the start of the feed intake test period. Sire breed effects on STAGE, STWT and MMWT are presented in Table 5.4. Straightbred Brahmans were youngest but did not differ in age to Belmont Red or Limousin sired-crosses, which did not differ in age to Santa Gertrudis or Charolais crosses. British crosses were the oldest at the start of test as a result of all being conceived by AI. Straightbred Brahman and Belmont Red crosses were significantly lighter than all other crosses at the start of the test.

Table 5.4 Least-squares means (± s.e.) for effect of sire breed on starting age, starting weight and metabolic mid-weight (unadjusted).

Sire Breed	Start Age (days)	Start Weight (kg)	Metabolic Mid-Weight (kg)
Brahman	571 ± 3	369.8 ± 5.5	90.2 ± 1.0
Belmont Red	577 ± 3	394.0 ± 4.6	94.9 ± 0.8
Santa Gertrudis	593 ± 5	437.9 ± 9.1	104.2 ± 1.6
Angus	601 ± 4	471.8 ± 6.8	109.3 ± 1.2
Hereford	607 ± 4	463.3 ± 7.1	107.9 ± 1.3
Shorthorn	606 ± 4	465.8 ± 7.1	108.4 ± 1.3
Charolais	593 ± 4	456.1 ± 6.4	106.1 ± 1.1
Limousin	587 ± 3	438.8 ± 5.1	103.5 ± 0.9
l.s.d.	16	29	5.2
	P<0.001	P<0.001	P<0.001

l.s.d. = least significant difference for observations to be significantly different from each other.

There were few differences in breed rankings and significance between unadjusted, age-constant and weight-constant results. Age-constant results are presented in Tables 5.5 and 5.6. There was no difference between sire breeds for FCR, RGR and TIMEkg. Angus sired crosses were the least efficient feeders and spent the most time eating, consumed the most feed and had the highest RFI. Angus sired crosses spent 24.1 and 15.4 min/day (36% and 20%; $P<0.001$) more time eating than straightbred Brahmans and Charolais crosses, and consumed 35% and 13% ($P<0.001$) more feed respectively. Straightbred Brahmans did not differ from all breed crosses for RFI ($P>0.05$), but had the lowest appetite which resulted in the lowest FI, TIME and ADG ($P<0.001$). Straightbred Brahmans were the most frequent feeders but only differed to Belmont Red and Shorthorn sired crosses for SESS ($P<0.05$). Aside from SESS, straightbred Brahmans did not differ significantly from Belmont Red crosses for any trait. Belmont Red crosses performed similarly to Continental crosses for FI and ADG ($P>0.05$), and did not differ from all other crosses for TIME, RFI and KR (except Santa Gertrudis crosses). Santa Gertrudis crosses performed similarly to British crossbreds for all traits. British and Santa Gertrudis crosses had the highest FI but did not differ to Continental crosses for SESS, ADG and KR. Charolais crosses differed from Angus and Shorthorn crosses for RFI ($P<0.05$). Charolais crosses were the most feed efficient with the lowest RFI and intermediate FI, and did not differ significantly from the highest ranking sire breeds for ADG, FCR, KR and RGR.

Table 5.5 Least-squares means (± s.e.) for effect of sire breed on feed efficiency traits adjusted to a constant starting age[1].

Sire Breed	Daily Feed Intake (kg/day)	Residual Feed Intake (regression) (kg/day)	Average Daily Gain (regression) (kg/day)	Feed Conversion Ratio	Kleiber Ratio	Relative Growth Rate (%)
Brahman	10.1 ± 0.3	0.015 ± 0.155	1.064 ± 0.054	10.6 ± 0.5	1.15 ± 0.05	0.256 ± 0.010
Belmont Red	11.1 ± 0.2	0.140 ± 0.128	1.166 ± 0.045	10.2 ± 0.4	1.20 ± 0.04	0.264 ± 0.009
Santa Gertrudis	12.7 ± 0.4	-0.099 ± 0.234	1.518 ± 0.081	8.7 ± 0.8	1.45 ± 0.07	0.310 ± 0.016
Angus	13.6 ± 0.3	0.542 ± 0.174	1.465 ± 0.061	10.1 ± 0.6	1.36 ± 0.05	0.287 ± 0.012
Hereford	12.5 ± 0.3	-0.267 ± 0.185	1.456 ± 0.064	9.3 ± 0.6	1.37 ± 0.06	0.290 ± 0.012
Shorthorn	13.2 ± 0.3	0.291 ± 0.184	1.463 ± 0.064	9.6 ± 0.6	1.36 ± 0.06	0.288 ± 0.012
Charolais	12.0 ± 0.3	-0.457 ± 0.165	1.345 ± 0.057	9.9 ± 0.5	1.26 ± 0.05	0.268 ± 0.011
Limousin	12.1 ± 0.2	-0.210 ± 0.134	1.376 ± 0.047	9.3 ± 0.4	1.32 ± 0.04	0.282 ± 0.009
l.s.d.	1.3	0.743	0.258	2.6	0.226	0.052
	$P<0.001$	$P<0.05$	$P<0.001$	n.s.	$P<0.05$	n.s.

[1] Average starting age = 598 days

l.s.d. = least significant difference for observations to be significantly different from each other.

Table 5.6 Least-squares means (± s.e.) for effect of sire breed on feeding patterns adjusted to a constant starting age.

Sire Breed	Time taken to eat 1kg (min)	Time spent eating (min/day)	Number of eating sessions per day
Brahman	6.63 ± 0.23	67.4 ± 2.7	16.6 ± 0.8
Belmont Red	7.25 ± 0.19	79.2 ± 2.3	11.9 ± 0.7
Santa Gertrudis	7.05 ± 0.35	88.1 ± 4.1	13.9 ± 1.3
Angus	6.77 ± 0.26	91.5 ± 3.1	14.7 ± 0.9
Hereford	7.14 ± 0.28	87.5 ± 3.3	14.8 ± 1.0
Shorthorn	6.87 ± 0.28	88.4 ± 3.3	12.0 ± 1.0
Charolais	6.40 ± 0.25	76.1 ± 2.9	13.9 ± 0.9
Limousin	6.76 ± 0.20	81.3 ± 2.4	13.1 ± 0.7
l.s.d.	1.13	13.2	4.2
	n.s.	$P<0.001$	$P<0.05$

l.s.d. = least significant difference for observations to be significantly different from each other.

5.4 Discussion

5.4.1 Sire breed differences for feed efficiency

Studies examining breed differences for feed efficiency are few, particularly for *Bos indicus* versus *Bos indicus* × *Bos taurus* crosses. Historically, the high cost and logistics of reliably measuring individual feed intakes in commercial feedlot-type environments has been prohibitive. Hence there are limited studies that include RFI with which to make comparisons. Moore *et al.* (2005) reported ADG, FI, FCR and RFI on this crossbred dataset but had differing results based on alternative methods of trait calculation and data editing. Their study excluded animals with ADG less than 0.5 kg/day and FI less than 300 g/day, did not allow for an adjustment period in the automatic feeders, and did not adjust for differences in MJ ME/kg DM between cohorts. Preliminary analyses from our study that excluded an adjustment period for the automatic feeders showed respective traits held relatively stable for sire breed ranking between unadjusted and adjusted analyses, but not for magnitude and significant differences between sire breeds. The importance of an adjustment period in the automatic feeders prior to the on-test period is discussed by Robinson (2000). In contrast to the results of Moore *et al.* (2005), this study found no difference between Belmont Red and Continental crosses for ADG and FI. Furthermore, Moore *et al.* (2005) ranked straightbred Brahmans lowest for RFI (-0.61) and significantly different to Angus, Shorthorn and Belmont Red crosses, while our results ranked straightbred Brahmans intermediately for RFI (0.02) and not significantly different to all other breed crosses. The different results for straightbred Brahmans were likely due to the fact that Brahmans had relatively low FI and ADG due to low appetite (apparent by examination of their feed intake records over the test period) rather than feeding problems, and hence were excluded from the Moore *et al.* (2005) study unnecessarily.

Studies between *Bos taurus* and *Bos taurus* × *Bos indicus* crosses, though not strictly comparable, show breed trends for feed efficiency that generally support our findings. Huffman *et al.* (1990) found no significant difference between 25%, 50% and 75% Brahman × Angus crossbred steers for ADG, feed:gain or empty rumen feed:gain when finished for 107 days on feed to similar end weights as our crossbreds, while the 50% and 75% Brahman content steers did not differ for daily dry matter intake and empty rumen ADG ($P>0.05$). This is consistent with our results for Brahman × British breed crosses (including Santa Gertrudis crosses) for FI, ADG and FCR. Frisch and Vercoe (1977) reported that feed intake per kg liveweight was consistently and significantly highest for Hereford × Shorthorn (HS) relative to Africander × HS and Brahman × HS when fed *ad libitum* lucerne which is consistent with our FI findings for British crosses relative to Belmont Red crosses and straightbred Brahmans. Cundiff *et al.* (1984) reported the average daily gain of Brahman sired crosses from Angus and Hereford cows tended to be lower during the postweaning period while being fed a high concentrate diet relative to Angus or Hereford sired calves, which is consistent with our ADG results for Brahmans relative to British and Santa Gertrudis sired calves, though our crosses were older and heavier on test. Similarly to Moore *et al.* (2005) and a study by Fan *et al.* (1995), we found progeny of Hereford sires had lower RFI than Angus sired calves. However our study did not find higher RFI was associated with higher ADG of the Angus sires relative to the Hereford sires, as reported by Fan *et al.* (1995). Similarly to our results for FCR, Cundiff *et al.* (1984) and Fan *et al.* (1995) reported no difference between breed groups for gross feed efficiency.

A study including feed efficiency and feeding behaviour of tropically adapted (Brahman, Belmont Red, Santa Gertrudis) and temperate (Angus, Hereford, Murray Grey, Shorthorn) straightbreds finished to three market weights under the same experimental protocols as this experiment was reported by Robinson and Oddy (2004). Relative to our means for respective markets and traits, Robinson and Oddy (2004) reported similar mean FI (11.9±2.0) and FCR

(9.8±2.1) and lower mean MMWT (93.9±8.8) and ADG (1.27±0.32) for tropically adapted straightbreds, which were older than our crossbreds at the start of test (mean 717±80). Hence, despite little difference in FI, tropically adapted straightbreds had similar FCR and lower ADG relative to Brahman crossbreds in this experiment. Relative to temperate straightbreds, tropically adapted straightbreds had lower FI (1.0 kg; 7.8%), lower MMWT (4.1 kg; 4.2%), lower ADG (0.06 kg/day; 4.5%), higher RFI (0.11; 3.9%) and lower FCR (0.4; 3.9%) for Korean and Japanese markets. Our results were consistent in direction for FI, MMWT and ADG for British crossbreds versus tropically adapted crossbreds, however the trend was the reverse for RFI and FCR whereby our tropically adapted sire breeds had lower RFI (more desirable) and higher FCR (less desirable; n.s.) than British sire breeds. Similarly to Robinson and Oddy (2004), we found mean daily weight gain and feed intake decreased with age while FCR increased, with respective crossbred means being ADG (1.38±0.40 and 1.15±0.37), FI (12.33±2.20 and 11.49±2.15) and FCR (9.7±3.4 and 10.8±3.4) for Korean and Japanese market steers respectively.

A study by Robinson *et al.* (1997) of Angus, Shorthorn, Hereford, Murray Grey, Santa Gertrudis and Brahman steers finished to Korean and Japanese weights reported that *Bos indicus* animals with higher feed intake gained weight faster in the feedlot. This was consistent with our results for Brahman, Belmont Red and Santa Gertrudis sired crosses for FI and ADG. However, this trend did not follow for Angus sired crosses (highest FI) relative to significantly lower FI breeds (Charolais and Limousin crosses) in our experiment where these sire breeds did not differ for ADG. Schenkel *et al.* (2004) reported similar breed rankings for young Charolais, Limousin, Hereford and Angus beef bulls for RFI (by regression) relative to our results, though Charolais crosses had lower RFI than Limousin crosses in our study. Similarly to Schenkel *et al.* (2004), we found Charolais and Limousin crosses had lower FI than Angus crosses. In contrast, we found no difference between the four respective sire breeds for ADG or FCR.

5.4.2 Sire breed differences for feeding behaviour

Relative to our means for respective markets and traits, Robinson and Oddy (2004) reported slightly higher TIME (84±23) and SESS (15.6±7.9) for the tropically adapted straightbreds. Hence, despite no difference in feed intake, tropically adapted straightbreds spent more time eating and had more eating sessions per day than straightbred Brahmans and Brahman crossbreds in this experiment. More frequent but shorter feeding sessions for straightbred Brahmans in this study were consistent with studies by Robinson *et al.* (1997) and Robinson and Oddy (2004), but we found no difference in number of feeding sessions between Brahmans and British, Continental and Santa Gertrudis sired crossbreds except Shorthorn crosses. Further, in contrast to results reported by Robinson and Oddy (2004), we found no difference in eating rate (TIMEkg) between sire breeds, possibly a result of the 50% or greater Brahman content of our crosses resulting in smaller differences between sire breeds relative to tropically adapted straightbreeds. A study of Hereford × Shorthorn (HS), Brahman × HS and Africander × HS found eating rate was highly correlated with liveweight (Frisch and Vercoe 1977), though differences between breeds were not significant. Similarly, we found no difference between sire breeds for TIMEkg.

5.4.3 Mechanisms affecting variation in feed efficiency

Within-breed selection of animals that eat less for the same liveweight and weight gain has led to the conclusion there is genetic variation in the utilisation of feed. This biological difference in efficiency of feed utilisation has been credited to variation in feed intake, digestion of feed, tissue turnover, metabolism (anabolism and catabolism associated with and including variation in body composition), activity, feeding patterns and thermoregulation (Richardson *et al.* 1999; Oddy and Herd 2000; Herd *et al.* 2004; Richardson and Herd 2004). Given that selection for weight gain or for RFI is associated with variation in intake, animals that eat less for the same performance could be expected to have lower heat production based on the heat increment of feeding (HIF) (Oddy and Herd 2000). What is clear is that no single mechanism is likely to be primarily responsible for differences in feed efficiency (Oddy and Herd 2000; Richardson and Herd 2004), and for breeds where the differences are small, the actual magnitude of difference in each mechanism affecting feed efficiency will be small and difficult to measure with certainty (Herd *et al.* 2004).

Bos indicus have a faster fermentation rate, shorter digesta retention time and higher population of rumen protozoa (expected to support greater methane emissions), but have greater efficiency of energy capture relative to *Bos taurus* (Hegarty 2000). Studies by Vercoe (1967) and Vercoe *et al.* (1972) reported dry matter and nitrogen digestibilities were consistently higher in Brahman × Hereford and Brahman × HS steers relative to Hereford and HS steers, however breed differences were not significant on low quality diets. Conversely, Boyles (1986) found Brahman × Angus crosses had higher faecal dry matter content than Angus steers, though digestibility coefficients were similar for two breed groups and there were no significant breed effects on heat production and respiratory rate. Frisch and Vercoe (1969) reported that lower feed intakes in Brahmans relative to Africanders and Shorthorn × Herefords (weight adjusted) fed ad libitum lucerne was likely due to lower maintenance requirements in the Brahmans. Another study by Vercoe (1970) suggested the lower fasting metabolism of Brahmans relative to Africander and HS bulls aged 13-22 months ($P<0.05$) may have been due to a lower requirement for energy to carry out functions of basal metabolism, or if they had similar requirements, Brahmans may have been able to use the energy released by biochemical processes occurring at basal conditions more efficiently. Therefore, it appears that *Bos indicus* cattle require lower feed intakes relative to *Bos taurus* genotypes in order to meet maintenance requirements. Frisch and Vercoe (1977) concluded that as *Bos indicus* evolved under poor nutrition they will have automatically been selected for low fasting metabolism (good survival ability) and low voluntary feed intake, resulting in low growth rates under good conditions relative to *Bos taurus* breeds. This would apply to our study. Despite no differences between straightbred Brahmans and all crossbreds for RFI and FCR, straightbred Brahmans had lower ADG as a result of lower FI due to lower appetite.

5.4.4 Limitations of study

The duration of the test was shorter than the 70-day recommended test duration for growth rate, feed conversion and residual feed intake (Archer *et al.* 1997) due to experimental design constraints. While measurement of feed intake is repeatable and requires only 35 days on test for accurate measurement following an adjustment period, estimates of gain are not highly repeatable (Robinson *et al.* 1997). An approach to improve the reliability of feed efficiency measurements where feed intake is recorded over short periods was reported by Robinson *et al.* (1999) where gain was modelled using random regression curves for 1165 animals over all weights recorded in the feedlot, not just the weights recorded during the feed intake test period.

It is also worth noting that the number of sires used per breed was small, progeny numbers per sire were small, and the sires were selected during the period of 1994-1996, hence they may not be representative of modern day sires of their breed.

5.5 Implications to breed selection for feed efficiency

Sire breed differences exist for feed efficiency and feeding behaviour. Generally, increased FI corresponds with increased ADG, however Continental crosses tend to utilise feed more efficiently than British crosses. While use of straightbred Brahmans in northern Australia holds no disadvantage for RFI or FCR relative to Brahman crossbreds, the inherently lower appetite of straightbred Brahmans results in significantly lower ADG relative to other sire breeds. Similarly, low FI in Belmont Red crossbreds results in low ADG relative to British and Santa Gertrudis crossbreds. Selection of Charolais, Hereford, Limousin or Santa Gertrudis sire breeds would yield the most feed efficient (low RFI) crosses with Brahman without any sacrifice in ADG.

Efficiency of beef production depends on feed and other inputs of all classes of animals in the production system including the breeding herd and slaughter generation. Single trait selection for feed efficiency may in fact be detrimental to carcass quality or meat tenderness in the slaughter generation, or reproduction or maintenance requirements of the breeding herd. Therefore, both within and between breed selection needs to take into consideration economically important production and reproductive traits. The advantage of between breed selection for crossbreeding is that many of the antagonistic genetic correlations between RFI and other production or reproduction traits that exist within breeds may be avoided. Furthermore, it allows complementary blending of production, reproduction and adaptation traits essential for economic efficiency and profitability of beef production in northern Australia.

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CHAPTER 6 Subcutaneous fat depth and liveweight can be used to predict female reproductive performance in tropically adapted beef breeds

Abstract. The purpose of this study was to determine if scanned subcutaneous fat depth at the 12/13th rib site (RIBFAT), P8 site (P8FAT) and into mating weight (IMWT) could be used to predict pregnancy rate and days to calving in tropically adapted beef breeds. 2158 Brahman and tropically adapted (mainly Belmont Red) females were mated by AI and natural mating over three years in tropical central Queensland. Pregnancy rate was determined using logistic regression analysis with a binomial generalised linear model. Predicted probabilities for pregnancy success were calculated for breed, previous lactation status and mating method based on significant independent variables (RIBFAT, P8FAT, IMWT). Days to calving (DTC) was determined using survival analysis so that all records, including females that failed to calve, were included in the analysis. A Cox proportional hazards analysis was used to determine DTC by regression and predict DTC based on significant independent variables. Mean pregnancy rate was 76.1%. Calving rates were 70.1% and 72.7% at 365 and 430 days (the end of the calving period) after first exposure to mating. Pregnancy rates were higher for AI than natural mating ($P<0.001$). Pregnancy rates by AI were 76.9% for Brahmans and 83.4% for composites ($P=0.05$) but there was no difference between breeds when mated naturally. IMWT was a significant predictor for DTC in 2 year old maiden heifers (explaining 15.9% of total deviance; $P<0.001$), with each 10 kg increase in IMWT associated with a 2.4 day decrease in DTC (or days to conception). Heifers with 390 kg IMWT and 7 mm RIBFAT could be expected to conceive within 1-2 oestrus cycles of first mating date. Three year old lactating (second calf) females with a minimum of 410 kg IMWT and 2.5 mm RIBFAT could be expected to conceive within 4

oestrus cycles, though year, mating period, mating method and property of origin also significantly affected DTC ($P<0.05$). Each 10 kg increase in IMWT for females mated naturally could decrease DTC by 1.5 days (IMWT explained 17.3% of total deviance; $P<0.001$). While other predictions for pregnancy rate and DTC using IMWT, RIBFAT and to a lesser degree P8FAT were significant, they explained less than 5.0% of total deviance. Consequently, pregnancy rate and days to calving would be susceptible to large environmental (previous lactation status, year, property of origin, others) and management (mating method, mating period) influences.

6.1 Introduction

Failure of a cow to conceive is the major component affecting the overall production efficiency of the cow herd (Roberts *et al.* 1993). Improvement of female fertility in beef cattle involves selection of heifers with higher genetic potential to breed early in their first season and then continue to rebreed and calve early every year as mature dams (Doyle *et al.* 2000). Selection for age at puberty has been shown to respond quickly and significantly in beef cattle (Morris and Wilson 1996) with selection for precocious heifers posing an effective means of decreasing age at puberty in *Bos indicus* breeds (Mackinnon *et al.* 1990; Nogueira 2004). While heritability estimates for age at puberty and gestation length range from 0.24-0.61 and 0.36-0.51 respectively, heritabilities for most other fertility traits are low ranging from 0.04-0.17 for pregnancy rate, days to calving, calving success, calving rate, calving interval and rebreeding rate (Bourdon and Brinks 1982; Macneil *et al.* 1984; Meyer *et al.* 1990; Koots *et al.* 1994a; Gregory *et al.* 1995; Davis 1993; Doyle *et al.* 1996, 2000; Hyde *et al.* 1996; Johnston and Bunter 1996; Morris and Cullen 1996; Splan *et al.* 1996; Tosh *et al.* 1996). Hence, environmental effects have the largest impact on expressed fertility.

There is a close relationship between fertility, body condition and nutritional status in pre-pubertal, lactating and non-lactating female cattle, though the underlying mechanisms remain poorly understood (Rhodes *et al.* 1996; Robinson 1996; Gong 2002). It is well documented that age at puberty in cattle is associated with body weight rather than age (Gong 2002). Siebert and Field (1975) demonstrated that the onset of puberty in cattle also appeared closely related to body fat content. Condition score is a subjective trait that accounts for size, liveweight and fat cover, and is commonly used to indicate the nutritional status of cows (Kunkle *et al.* 1994). The accumulation of body lipid reserves in pregnancy is an important strategy for safeguarding reproductive investment (Friggens 2003). Postpartum, lactation is accompanied by mobilisation of body reserves, particularly lipid reserves. Evidence suggests there is an innate drive to decrease body fatness in early lactation, even under conditions of nutritional abundance (Friggens 2003). As lactation progresses towards weaning the negative consequences of lactational failure and thus the need for large body reserves diminish. Furthermore, excessive body fatness has been associated with depressed reproduction (Friggens 2003). Garnsworthy and Topps (1982) found that under the same nutritional conditions postpartum, dairy cows of differing body condition (fat, average and thin) mobilised lipid at different rates, so by 16 weeks postpartum all cows had similar body condition scores. This suggests there may be a target level of body fatness for fertility. When there is inadequate nutrition to meet maintenance requirements of the cow, body stores which regulate the secretion of hypothalamic and pituitary hormones are mobilised, affecting normal function of the ovary (Wettemann 1994). Thin cows that fail to regain sufficient body lipid postpartum have longer postpartum anoestrus intervals and poorer conception rates to first insemination (Friggens 2003). More recently, studies have examined the link between circulating levels of hormones linked to fatness including leptin and IGF-I, and their effect on reproduction, though findings vary as to the effect of these hormones on fertility (Lackey *et al.* 1999; Luna-Pinto and Cronje 2000; Spicer 2001; Garcia *et al.* 2002; Gong 2002; Smith *et al.* 2002; Williams *et al.* 2002; Ciccioli *et al.* 2003).

Market demands for carcass and meat quality characteristics focus selection on liveweight, retail beef yield, subcutaneous fat cover and intramuscular fat percent. With tightening profit margins, commercial cattle producers are focusing more attention on feed efficiency of their beef herds. Recent research has shown moderate to strong genetic and phenotypic antagonisms between carcass fatness traits and retail beef yield in *Bos taurus* and *Bos indicus* breeds (Koots *et al.* 1994b; Marshall 1999; Burrow *et al.* 2001; Reverter *et al.* 2003), and undesirable genetic correlations between residual feed intake and fatness traits including rump fat, rib fat and intramuscular fat percent (Richardson *et al.* 2001; Robinson and Oddy 2004). There is growing concern that ongoing selection for improved retail beef yield or feed efficiency may reduce carcass fatness to a point where reproductive function of replacement females is compromised. This may be exacerbated under northern Australian beef production environments where seasonal fluctuations in nutrition quality, parasite loads, high ambient temperatures and humidity, along with high *Bos indicus* content in breeding herds, provide real challenges for reproductive success. We hypothesised that scanned measures of subcutaneous fat depth can be used to predict pregnancy rates and days to conception after first mating date (a component of days to calving) in Brahman and tropically adapted composite females of varying age and lactation status, and bred by AI and natural mating in a tropical environment. The aim was to set fat depth benchmarks that could allow beef producers to make informed decisions about the economic viability of changing management practices to achieve predetermined pregnancy rates and days to calving.

6.2 Materials and methods

6.2.1 Experimental design and animals

This study involved Generation 0 dams from the Beef CRC Project 2.3 (Burrow *et al.* 2003). Brahman and tropically adapted composite females aged 2-14 years were sourced from 11 properties of origin throughout Queensland and bred to sires of the same breeds at Belmont Research Station in tropical central Queensland. A total of 2158 matings occurred by artificial insemination (AI) and natural mating (NM) over three years (2000, 2001, 2002). Matings included 1115 Brahman dams and 1043 composite dams. Table 6.1 shows the number of females mated by AI and NM for each breed (BREED) and previous lactation status (PLS). All females were weighed (IMWT) and scanned for subcutaneous fat depth at the 12/13th rib site (RIBFAT) and P8 site (P8FAT) using an ALOKA 500 (ALOKA) ultrasound scanning machine at the commencement of mating each year.

Matings included AI and NM in single- and multiple-sire groups over joining periods of up to 4 months beginning in early January in 2000 and late November in 2001 and 2002. 30% of all breeding females were allocated at random to NM to generate genetic linkages between AI and NM groups and to ensure calves of sires used for AI and NM were born at the same time. The exceptions were cows that calved late in the previous calving season which were all subsequently mated by NM. Females mated by NM entered the mating paddocks at the same time as AI programs began each year. AI programs had to be staggered over the mating season to accommodate the large number of females mated by AI. Consequently, some AI groups had shorter mating periods than other AI groups and NM contemporaries. Mating periods ranged from 21-128 days for AI groups and 53-128 days for NM groups. Mating periods were 32-128 days (AI) and 82-128 days (NM) for 2 year old maiden heifers, 3 year old lactating females and

3+ year old non-lactating females, and 21-114 days (AI) and 53-114 days (NM) for 4 and 5+ year old lactating females. In the AI programs, heifers and non-lactating females were generally mated earlier in the mating season than lactating females, though cows that calved early during the calving season had mating periods similar to non-lactating cows and heifers. Cows that calved late in the calving season were mated by NM due to the expectation that they would not respond to AI. There were a total of 184 late calving cows that were mated by NM for 53-63 days.

The AI programs for 2 year old maiden heifers and non-lactating females involved 5 days of observation for natural oestrus and insemination of those females which demonstrated oestrus. After 5 days, those females that had not been inseminated were injected with synthetic prostaglandin and inseminated as they demonstrated oestrus over the next 5 days. Initially Prosolvin by Intervet was used to synchronise females. When this drug became difficult to procure, Estrumate by Schering-Plough Animal Health was used. Two AI cycles were completed for each AI group, followed by natural mating to back-up sires.

The AI programs for lactating females involved the use of Eazi-Breed CIDR progesterone intravaginal devices by Pfizer Animal Health. The CIDRs were removed after 7 days and females subjected to the same synthetic prostaglandin treatments as non-lactating females followed by AI over 7 days. A second AI cycle was completed for each AI group, followed by natural mating to back-up sires.

During mating AI females were grazed on irrigated Rhodes grass pasture. Following completion of the AI programs, AI females were moved to NM paddocks for mating with back-up sires. NM females were grazed on a mixture of non-irrigated native spear grass, Rhodes grass, green panic, urachloa and seca stylo pasture. At the end of the mating season all females were run together on non-irrigated improved pasture. For the purpose of analysis, AI followed by natural mating to back-up sires was considered standard practice for beef AI programs. Hence, calves generated by back-up sires were still considered to be from dams joined by AI. Calves were weaned at an average age of 6 months.

Pregnancy rate (PR) was determined as the number of females confirmed pregnant by rectal palpation at 120-days post-mating as a proportion of the total number of females exposed to mating. Days to calving (DTC) comprised days to conception and gestation length, and was defined as the time elapsing between the date of first exposure to mating and calving date. A study by Corbet *et al.* (1997) of Brahman heifers mated to Belmont Red, Santa Gertrudis and Brahman sire breeds reported a mean gestation length of 284±1.5 days (range 271-296 days). Brahman sired calves had a mean gestation length of 287 days, while Belmont Red and Santa Gertrudis sired calves had mean gestation lengths of 284 days (n.s. to Brahman) and 282 days ($P<0.05$ to Brahman) respectively. Therefore, as the majority of tropically adapted composites in this study were Belmont Reds, we would expect differences in DTC to be a result of differences in days to conception. Calving rate (CR) was determined as the number of calves born as a proportion of the total number of dams exposed to mating each year.

6.2.2 Data edits

Frequency histograms were plotted for IMWT, RIBFAT and P8FAT to assess normality of the data. Measurements that fell more than three standard deviations from the mean were checked individually. Consequently, 12 RIBFAT records and 10 P8FAT records were excluded from the analyses as they appeared to be the result of measurement error.

6.2.3 Statistical analyses

Pregnancy rate was analysed by logistic regression analysis with a binomial generalised linear model and link function logit $p=\log[p/(1-p)]$ using the statistical software package R (R 2006; Dalgaard 2002). Main effects including year of mating (YEAR; 2000, 2001, 2002), mating method (MM; AI, NM), mating period (MP; range 21-128 days), previous lactation status (lactating, non-lactating, heifer), dam age (2-14 years), property of origin (ORIGIN; 11 properties), breed (BREED; Brahman, composite), into mating weight (IMWT), into mating scanned rib fat (RIBFAT) and into mating scanned p8 fat (P8FAT) were fitted initially. Previous lactation status and dam age were confounded, so a concatenated variable (PLS) was fitted that included five levels; 2 year old maiden heifers, 3 year old lactating first-calf females, 4 year old lactating second-calf females, 5+ year old lactating multiparous females and 3+ year old non-lactating females (3-14 years). The final model included YEAR, MM, MP, PLS, ORIGIN, RIBFAT, IMWT, P8FAT, BREED and significant interactions. All first and second order interactions were tested and non-significant interactions excluded from the final model. There was no error term as logistic regression models the probability of an event directly, which in itself determines the variability of the binary outcome (Dalgaard 2000). The Chi-square test in analysis of deviance was used to test for significant differences between effects. Predicted probabilities for pregnancy success were calculated for the main effects of interest (BREED, PLS, MM) based on significant independent variables (IMWT, RIBFAT and P8FAT) using generalised linear models for each independent variable in the predict function in the statistical software package R (R 2006; Dalgaard 2002).

Survival analysis was used to assess DTC so all records, including females that failed to calve, were included in the analysis. The hazard function *h(t)* in survival analysis measures the chance of calving given time *t*, and is a more fundamental quantity than the mean or median for traits like DTC where females may fail to calve at all (Dalgaard 2002). $h(t) = f(t) / S(t)$, where f is the density of the time distribution, and $S(t)$ (the survival function) measures the probability of calving at a given time. Females that calved were assigned '1' for success and females that failed to calve were assigned '0' for success. Maximum DTC was estimated given the longest mating period plus the longest expected gestation length (Corbet *et al.* 1997), being 424 days. Hence, DTC was truncated at 430 days for all females that failed to calve. DTC was analysed using Kaplan-Meier estimates for main effects using the survival analysis model in the statistical software package R (R 2006; Dalgaard 2002). The Cox proportional hazards model in R (R 2006; Dalgaard 2002) was used to analyse DTC by regression. Chi-square tests in analysis of deviance were used to determine significant differences. The final model included YEAR, MM, MP, PLS, ORIGIN, RIBFAT, IMWT, P8FAT, BREED and significant interactions. This output was used to predict DTC for the main effects of interest (BREED, PLS, MM) based on independent variables (IMWT, RIBFAT and P8FAT) using generalised linear models for each independent variable in the predict function in R (R 2006; Dalgaard 2002).

6.3 Results

6.3.1 Pregnancy rate: main effects and interactions

Of the total 2158 females mated over three years, mean pregnancy rate was 76.1%. Table 6.1 shows mean unweighted pregnancy rates, calving rates, into mating weights and scanned subcutaneous fat measurements for females of each breed, previous lactation status and mating method. Large standard deviations were associated with all measurements. YEAR, PLS, MM, MP, ORIGIN, RIBFAT, IMWT ($P<0.001$) and BREED ($P=0.05$) significantly affected pregnancy rates. P8FAT was not significant. Residual deviance accounted for 71.16% (1634.06 / 2296.27) of total deviance, while YEAR × MM, YEAR × MP, YEAR × PLS, YEAR × ORIGIN and YEAR × IMWT interactions and YEAR effects ($P<0.05$) collectively explained 16.55% of total deviance. Mating period, previous lactation status and a MP × PLS interaction ($P<0.001$) explained 5.36% of total deviance. BREED × RIBFAT, BREED × P8FAT and BREED × IMWT interactions were not significant.

IMWT, RIBFAT and P8FAT averaged 444.7±73.6 kg (range 278-678 kg), 4.15±2.68 mm (range 1.0-15.0 mm) and 6.77±4.81 mm (range 1.0-27.0 mm) respectively for females that were confirmed pregnant. While the range of IMWT, RIBFAT and P8FAT were similar in females that failed to conceive, mean weight and fatness measures were lower (IMWT mean 434.6±71.7 kg, range 240-690 kg; RIBFAT mean 3.18±2.53 mm, range 1.0-15.0 mm; and P8FAT mean 4.97±4.22 mm, range 1.0-25.0 mm). RIBFAT × IMWT ($P<0.001$) and RIBFAT × P8FAT ($P<0.01$) interactions and main effects of RIBFAT, IMWT and P8FAT explained 3.69% of total deviance.

Table 6.1 Mean unweighted pregnancy rates, into mating weights and scanned subcutaneous fat measurements (± standard deviation) for females of each breed, previous lactation status and mating method.

	Number of females mated		Pregnancy rate (%)	Calving rate (%)	Into mating weight (kg)	Scanned rib fat (mm)	Scanned P8 fat (mm)
	AI	NM					
Breed							
Brahman	797	320	73.9±43.9	71.0±45.4	429.5±68.9	4.27±2.56	7.39±4.66
Composite	718	325	78.3±41.2	74.5±43.6	454.6±75.2	3.53±2.74	5.22±4.55
Previous lactation status							
2 year old maiden heifers	445	150	83.7±37.0	78.4±41.2	357.7±38.2	4.34±2.49	7.55±4.45
3 year old lactating females	208	128	60.4±49.0	58.5±49.4	427.1±47.4	2.80±1.80	4.04±3.02
4 year old lactating females	165	105	68.1±46.7	66.2±47.4	444.0±45.9	2.56±2.03	3.82±3.82
5+ year old lactating females	486	226	77.0±42.1	74.1±43.8	498.3±54.7	4.12±2.79	6.32±4.65
3+ year old non-lactating females	211	36	85.0±35.8	81.0±39.3	474.6±51.8	5.36±3.17	9.47±5.54
Mating method							
Artificial insemination	1515		80.0±40.0	76.8±42.2	437.0±73.6	3.88±2.55	6.47±4.72
Natural mating		645	66.8±47.1	63.1±48.3	455.3±70.4	4.00±2.93	6.05±4.75

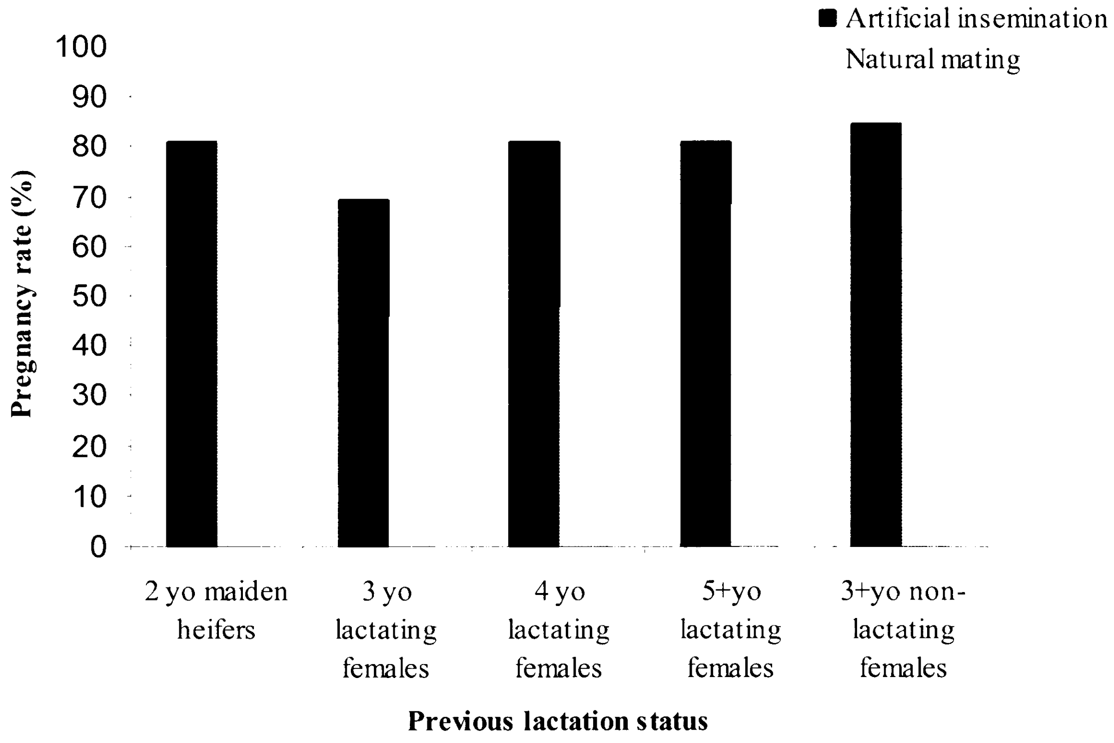
AI=artificial insemination, NM=natural mating.

Brahmans and composites differed by 4.4% for pregnancy rate ($P=0.05$). Of females mated by AI, 83.4% of composites conceived and 76.9% of Brahmans conceived. There was no difference between breeds for pregnancy rates by natural mating. Pre-natal losses between pregnancy testing and calving were 3.9% and 2.8% for composites and Brahmans respectively. Composite dams conceived at higher mean IMWT than Brahman dams across all PLS groups (IMWT range 290-690 kg for composites and 240-678 kg for Brahmans). RIBFAT ($P<0.001$) and P8FAT ($P<0.05$), and RIBFAT ($P<0.001$) and IMWT ($P<0.05$) had significant effects on pregnancy rates in Brahmans and composites respectively, with RIBFAT × IMWT interactions significant for both breeds ($P<0.05$). IMWT, RIBFAT and P8FAT for 2 year old maiden heifers were 370.5±35.8 kg, 3.70±2.73 mm and 6.05±4.73 mm for composites, and 343.0±35.8 kg, 4.91±2.12 mm and 8.87±3.71 mm for Brahmans. Composite females had consistently higher pregnancy rates than Brahman females in all PLS groups with the exception of 3+ year old non-lactating females, where Brahmans had 9.3% higher pregnancy rates than composites (87.6% versus 78.3%; n=178 and n=69 respectively). Pregnancy rates for composites and Brahmans respectively were 87.7% and 80.2% for 2 year old maiden heifers, 67.3% and 53.5% for 3 year old lactating females, 68.8% and 67.5% for 4 year old lactating females, and 80.1% and 73.3% for 5+ year old lactating females.

Females mated by AI had significantly higher pregnancy rates than females mated by natural mating ($P<0.001$). IMWT ranged from 240-648 kg for females mated by AI and 290-690 kg for females mated by natural mating. Two year old maiden heifers averaged IMWTs of 357.0±38.8 kg for AI (range 240-488 kg) and 361.6±34.2 kg for natural mating (range 290-442 kg). Mean IMWT and RIBFAT were slightly lower for females mated by AI relative to females mated naturally (refer to Table 6.1).

Figure 6.1 shows the effect of mating method on pregnancy rate for each previous lactation status group. Lactating females had significantly lower pregnancy rates relative to 2 year old maiden heifers and 3+ year old non-lactating females ($P<0.001$), as would be expected. Figure 6.1 also shows that lactating females mated naturally had significantly lower pregnancy rates than lactating females mated by AI ($P<0.001$). There may be a few reasons for this. Firstly, the proportion of non-lactating females mated by AI and NM were 43.3% and 28.5% respectively. As non-lactating females had significantly higher pregnancy rates than lactating females, this disproportion in allocation of females to mating method may have contributed to higher pregnancy rates for AI. Another reason may be the management practices associated with AI programs. A group of females that calved towards the end of the calving season were mated by AI (n=264) and NM (n=166) and had subsequent pregnancy rates of 73.1±44.4% and 41.0±49.4% respectively. This suggests that synthetic synchronisation treatments may have been advantageous in returning lactating females to oestrus earlier than would occur naturally under natural mating conditions. Further, close monitoring and timely insemination of females under AI programs may have also contributed to higher pregnancy rates of lactating females mated by AI versus natural mating.

Figure 6.1 Effect of mating method on pregnancy rate.



6.3.2 Predicting the probability of pregnancy success

Initially, the probability of pregnancy success was predicted based on the original logistic regression model and analysis of deviance using the significant independent variables measured prior to mating (RIBFAT, IMWT). P8FAT was not included as a predictor due to its non-significant effect on pregnancy rate in that model. RIBFAT and IMWT explained 1.45% and 0.63% of null deviance respectively ($P<0.001$). However, the RIBFAT and IMWT predictions for probability of pregnancy success would not be useful in practice because of the significant differences in pregnancy rates between PLS groups (lactating versus non-lactating females) and mating method (AI versus NM).

An analysis was run to compare AI with NM because of their significantly different effects on pregnancy rate. RIBFAT and IMWT significantly affected pregnancy rates of females mated by NM ($P<0.001$), with both traits and their interactions ($P<0.05$) explaining 6.19% of total deviance. RIBFAT was significant for pregnancy rates by AI ($P<0.001$), with RIBFAT and its significant interaction with IMWT explaining 1.91% of total deviance.

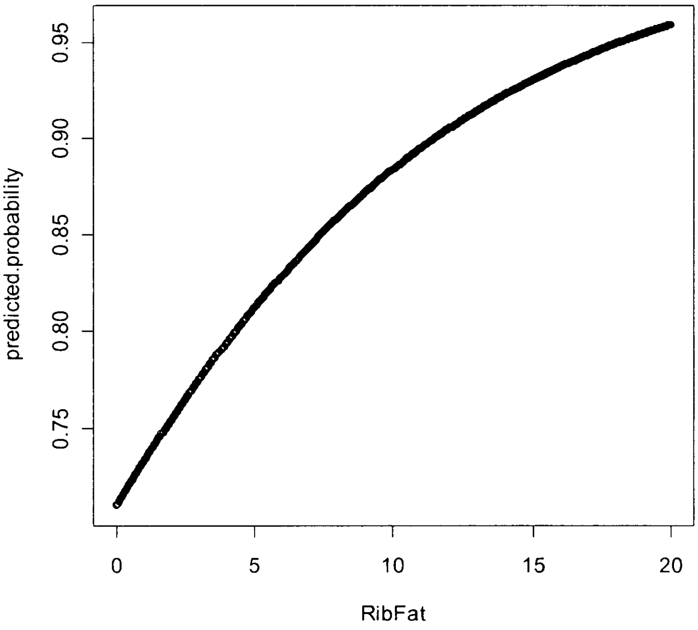
Separate analyses were run for non-lactating females and lactating females and predictions made for significant IMWT, RIBFAT and P8FAT effects. Analysis of deviance for 2 year old maiden heifers showed significant effects of YEAR, MM, MP, RIBFAT, P8FAT and ORIGIN ($P<0.05$) on pregnancy rate, with RIBFAT and P8FAT explaining 4.58% and 2.05% of total deviance respectively. IMWT and BREED were not significant. Predictions on RIBFAT for 2 year old heifers indicated 80% probability of pregnancy success with 0 mm RIBFAT and 90% probability of pregnancy success with 15 mm RIBFAT. Similarly, the probability of pregnancy success between 80 and 90% could be expected with P8FAT between 0 and 30 mm. Of more importance to pregnancy success in 2 year old maiden heifers were mating period and property of origin, explaining 18.08% and 13.15% of total deviance respectively ($P<0.001$). Residual deviance accounted for 51.63% of total deviance. Analysis of deviance in 3+ year old non-lactating females showed significant effects of mating period ($P<0.001$), property of origin

($P<0.05$) and a YEAR × MM interaction ($P<0.05$) on pregnancy rate. RIBFAT, P8FAT and IMWT were not significant for pregnancy success in 3+ year old non-lactating females.

In an analysis of 3, 4 and 5+ year old lactating females, RIBFAT and IMWT accounted for 1.99% and 0.80% of total deviance respectively ($P<0.001$), with significant RIBFAT × IMWT and RIBFAT × P8FAT interactions explaining another 1.84% of total deviance ($P<0.05$). Mating method, year and their interaction ($P<0.001$) explained 8.74% of total deviance. Predictions for probability of pregnancy success of 60, 70, 80 and 90% in lactating females were associated with RIBFAT of 1.0, 2.5, 5.5 and 9.0 mm respectively. Predictions for probability of pregnancy success of 50, 60, 70, 80 and 90% were associated with IMWT of 350, 400, 460, 525 and 620 kg respectively.

Because of the significant difference between lactating females mated by AI and natural mating, another analysis was run. For lactating females mated by AI, YEAR × MP, YEAR × PLS, ORIGIN, PLS ($P<0.001$) and RIBFAT ($P<0.05$) were significant. Residual deviance accounted for 85.96% of total deviation. RIBFAT and its interaction with P8FAT explained 1.89% of total deviance. Figure 6.2 shows predicted probabilities of pregnancy success given 0-20 mm RIBFAT. For example, an 80% probability of pregnancy success is predicted for lactating females with 4 mm RIBFAT when mated by AI. Females with 2.8 mm RIBFAT (ie. 3 year old lactating females, refer to Table 6.1) would have a 78% probability of pregnancy success when mated by AI.

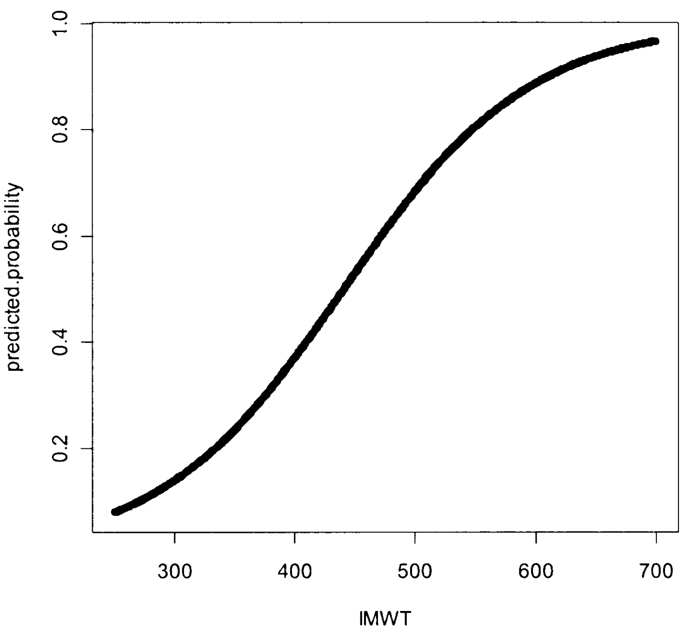
Figure 6.2 Probability of pregnancy success in lactating females mated by AI based on subcutaneous fat depth at the 12/13th rib site (mm). The x-axis shows scanned subcutaneous rib fat depth (mm). The y-axis shows the predicted probability of pregnancy success (×100 %).



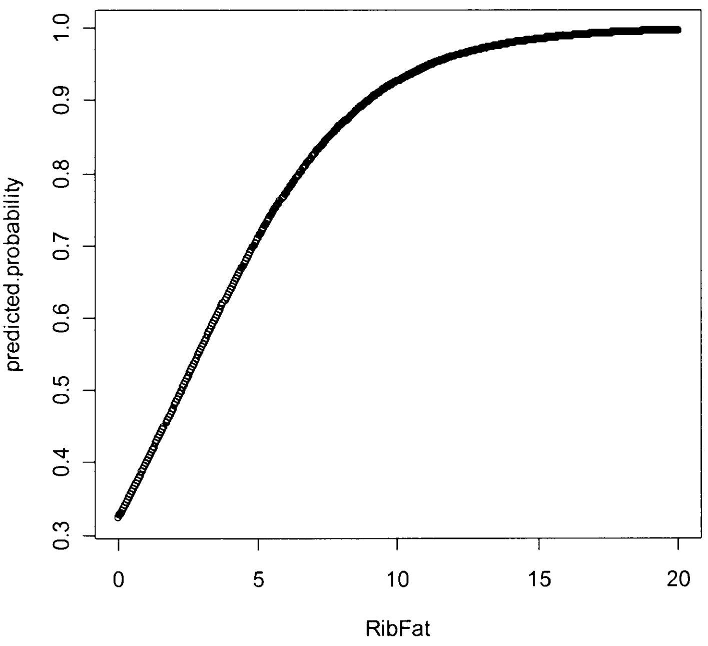
For lactating females mated naturally (NM), main effects of YEAR, IMWT, RIBFAT and a RIBFAT × IMWT interaction were significant ($P<0.001$). RIBFAT, IMWT and their significant interactions explained 11.29% of total deviance, suggesting these traits would be more useful for predicting pregnancy rate for females mated naturally relative to females mated by AI. Figure 6.3 shows predicted probabilities of pregnancy success for lactating females when mated naturally based on measures of IMWT (a) and RIBFAT (b). Prediction figures show that an 80% probability of pregnancy success can be expected in lactating females mated by NM with IMWT of 550 kg and RIBFAT of 6.5 mm. Figures 6.2 and 6.3(b) show that lactating females mated naturally require more RIBFAT to achieve the same probability of pregnancy success relative to lactating females mated by AI.

Figure 6.3 Probability of pregnancy success in lactating females mated by natural mating. The y-axis shows the predicted probability of pregnancy success (×100 %).

(a) Into mating weight (kg)



(b) Scanned subcutaneous fat depth at the 12/13th rib site (mm).



6.3.3 Days to calving: main effects and interactions

Figure 6.4 shows a survival curve with confidence bands for days to calving, right-censored at 430 days. Shorter DTC are desirable, with lower DTC indicating fewer days to conception after first mating date and/or shorter gestation length. By 365 days after first mating date, 70.1±1.0% of cows had calved. Table 6.2 contains several of the Kaplan-Meier estimates for survival (± standard errors) used to generate the survival curve in Figure 6.4. Survival is the proportion of females remaining to calve at specified days to calving based on calving events. Estimates in Table 6.2 are reported at 21-day intervals from 284 days (the first expected date of calving being mean gestation length). 265 and 419 DTC mark the first and last calving events.

Figure 6.4 Survival curve with confidence bands showing the proportion of females to calve after first mating date (bands show approximate confidence intervals). At 250 days to calving, 100% of females mated had not calved (survival = 1.0). At 365 days to calving, 28.9% of females mated had not calved (survival = 0.289). At the truncation point of 430 days to calving, 27.3% of females mated had not calved (survival = 0.273).

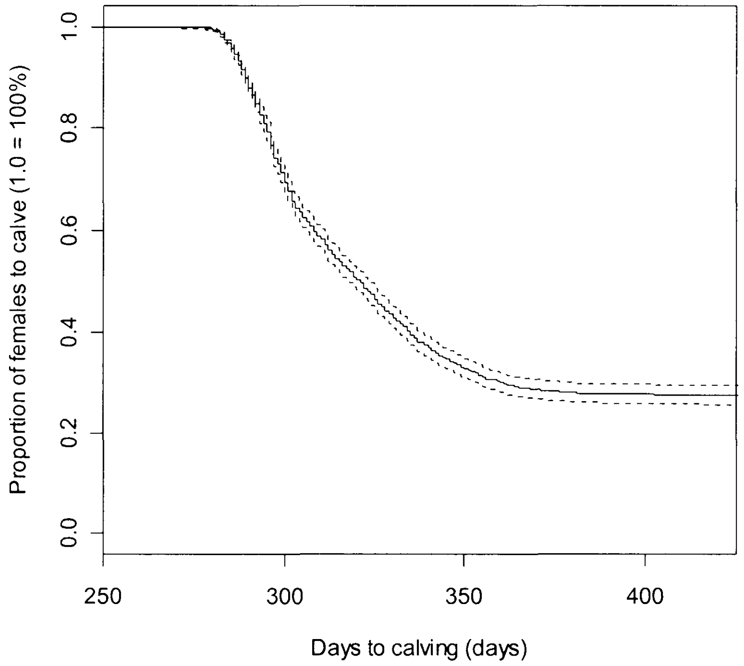


Table 6.2 Percentage of females to calve (± standard error) from 265 days (first calving) after first mating date to 419 days (last calving). DTC are reported at 21-day intervals from 284 days (mean gestation length).

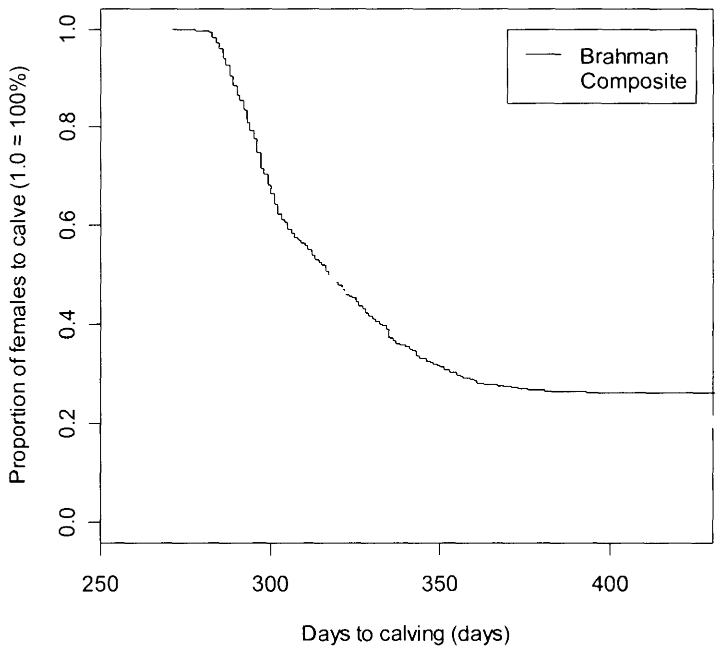
Days to calving (DTC) after first exposure to mating	Percentage of females to calve (± s.e.) (%)
265	100.0±0.05
284	96.7±0.4
305	62.5±1.0
326	45.6±1.1
347	33.8±1.0
368	28.6±1.0
389	27.7±1.0
410	27.4±1.0
419	27.3±1.0

The Cox's proportional hazards regression analysis showed main effects including YEAR, MM, PLS, ORIGIN, BREED, IMWT, RIBFAT and P8FAT were significant for DTC ($P<0.05$). Significant interactions were YEAR × MP, YEAR × MM, YEAR × PLS, IMWT × RIBFAT ($P<0.001$) and MP × PLS ($P<0.05$) (R square = 0.228). IMWT, RIBFAT, P8FAT and the IMWT × RIBFAT interaction explained 6.07% of total deviance. Residual deviance accounted for 92.1% of total deviance. BREED × RIBFAT, BREED × P8FAT and BREED × IMWT interactions were not significant.

Because of the significant differences in DTC between BREED, PLS (lactating versus non-lactating females) and mating method (AI versus NM) separate regression analyses were run for levels of interest in each effect (for example, lactating females mated by AI, lactating females mated by NM, non-lactating females mated by AI, and so on). These results were the basis for predicting DTC using significant independent variables (IMWT, RIBFAT and P8FAT).

BREED differences for DTC (P<0.001) explained less than 0.2% of total deviance in separate regression models for 2 year old maiden heifers, 3+ year old non-lactating females and 5+ year old lactating females. BREED differences for DTC were not significant for 3 and 4 year old lactating females.

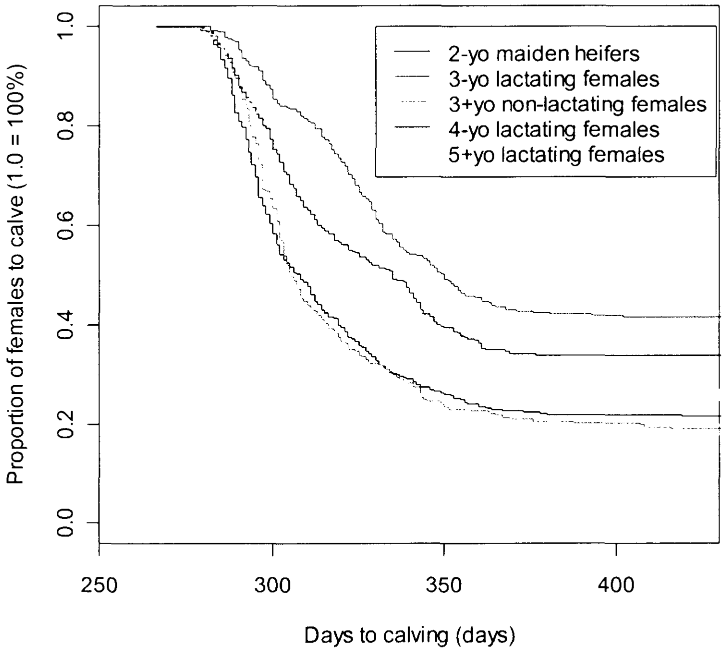
Figure 6.5 Survival curve showing breed differences for days to calving when mated by AI (P<0.05). The y-axis shows the proportion of females to calve after first exposure to mating (x100%).



Composite and Brahman females differed significantly for DTC when mated by AI (P<0.05) but not when mated naturally. Differences were mainly the result of higher calving rates of composites relative to Brahman females, consistent with BREED results for pregnancy rates by AI. Figure 6.5 shows BREED differences for DTC when females were mated by AI. Calving rates by AI were 79.8±1.5% and 74.1±1.6% for composites and Brahmans respectively ($P<0.05$). Respective calving rates by natural mating were 62.8±2.7% and 63.4±2.7% (n.s.).

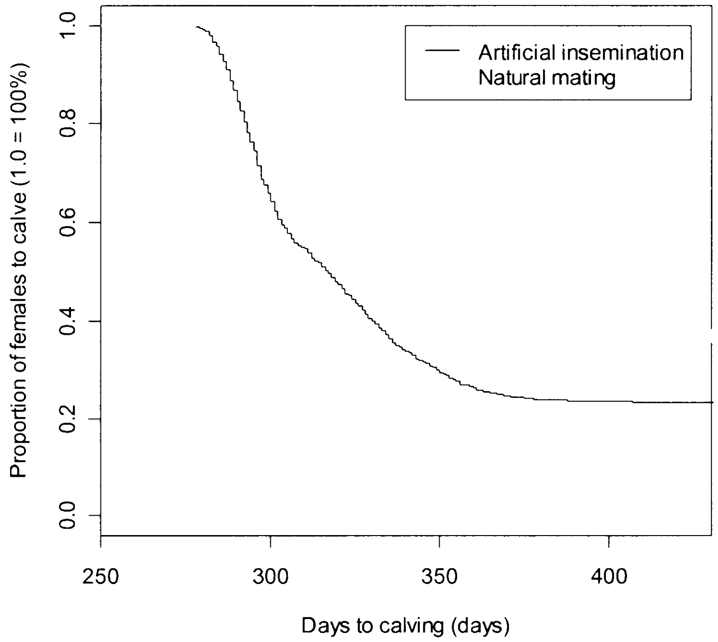
Figure 6.6 shows there was little difference between 2 year old maiden heifers and 3+ year old non-lactating females for DTC. However, DTC were longer at equivalent calving rates for lactating females relative to non-lactating females, and final calving rates were lower for lactating females relative to non-lactating females. For example, at 350 DTC, 73.9±1.8% of 2 year old maiden heifers and 76.6±2.7% of 3+ year old non-lactating females had calved, while only 50.7±2.7% of 3 year old lactating females, 60.7±3.4% of 4 year old lactating females and 69.3±1.7% of 5+ year old lactating females had calved. Three year old primiparous females conceived later after the start of the mating season relative to all other PLS groups (evidenced by later DTC) and had the lowest calving rates overall.

Figure 6.6 Survival curve showing effect of previous lactation status on days to calving ($P<0.001$). The y-axis shows the proportion of females to calve after first exposure to mating (x100%).



Females mated naturally took significantly longer to conceive and subsequently calve than females mated by AI, and had lower calving rates by truncation at 430 days (63.1±1.9% versus 76.8±1.1% for NM and AI respectively). Effect of mating method on DTC is shown in Figure 6.7. Separate regression analyses for each PLS group showed no significant difference in DTC between mating methods for 2 year old maiden heifers, 3+ year old non-lactating females and 5+ year old lactating females. Reasons for the difference in DTC and calving rates between AI and NM were the disproportion of non-lactating females allocated to AI versus NM and the advantageous synchronisation and management practices associated with AI programs, as described in section 6.3.1.

Figure 6.7 Survival curve showing effect of mating method on days to calving ($P<0.001$). The y-axis shows the proportion of females to calve after first exposure to mating (x100%).



6.3.4 Predicting days to calving

Conception within 4 oestrus cycles (84 days) of first mating date would achieve calving intervals of approximately 12 months. Therefore, the aim was to determine measures of IMWT, RIBFAT and P8FAT significantly associated with conception within 4 oestrus cycles of first mating date. Initial predictions were based on significant IMWT, RIBFAT and P8FAT effects in the main regression analysis. Each effect was run separately in a linear model to predict DTC. Initial predictions using the main model spanned the fatness range for both RIBFAT and P8FAT between 284 and 365 DTC, with higher fatness associated with lower DTC. Minimum IMWT for calving within 365 days was 380 kg. However, because of the significant differences for DTC between previous lactation status groups and mating methods, separate regression analyses and predictions were done.

Initially prediction analyses were done for lactating (3, 4 and 5+ year old lactating females) and non-lactating (2 year old maiden heifers and 3+ year old non-lactating females) groups (R square = 0.208 and 0.194 respectively), but inconsistencies between PLS groups for significant traits and predictions led to separate analyses for each PLS group.

Regression analysis on 3+ year old non-lactating females found RIBFAT, P8FAT and mating period were significant for pregnancy rate ($P<0.001$; R square = 0.123). However, residual deviance accounted for 93.54% of total deviance. Separate linear models for RIBFAT and P8FAT failed to produce significant predictions for either of these traits.

Regression analysis on 2 year old maiden heifers found IMWT, RIBFAT, MP, BREED ($P<0.001$) and ORIGIN ($P<0.05$) effects were significant for DTC (R square = 0.249). IMWT explained 15.87% of total deviance, while RIBFAT and its interaction with IMWT ($P<0.05$) explained 0.97% of total deviance. Figure 6.8 shows significant predictions for DTC based on (a)

IMWT levels in 2 year old maiden heifers (intercept 420.49±22.66, slope -0.24±0.06) and (b) RIBFAT levels in 2 year old maiden heifers (intercept 344.24±4.45, slope -2.59±0.89). For example, heifers with more than 390 kg IMWT and 7 mm RIBFAT could be expected to conceive within 1-2 oestrus cycles (284-326 DTC) of first mating date. Predictions show that each 10 kg increase in IMWT would be associated with a 2.4 day decrease in DTC (or days to conception from first mating date).

Figure 6.8 (a) Prediction for days to calving based on into mating weights in 2 year old maiden heifers.

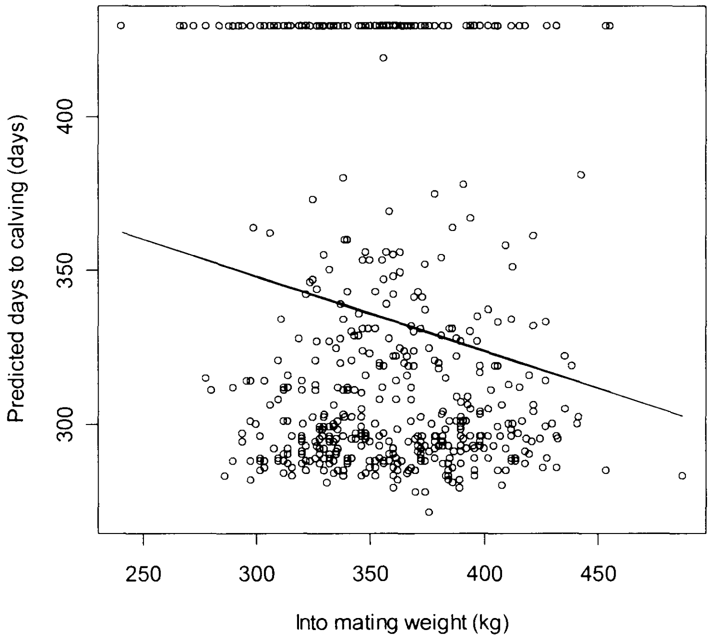
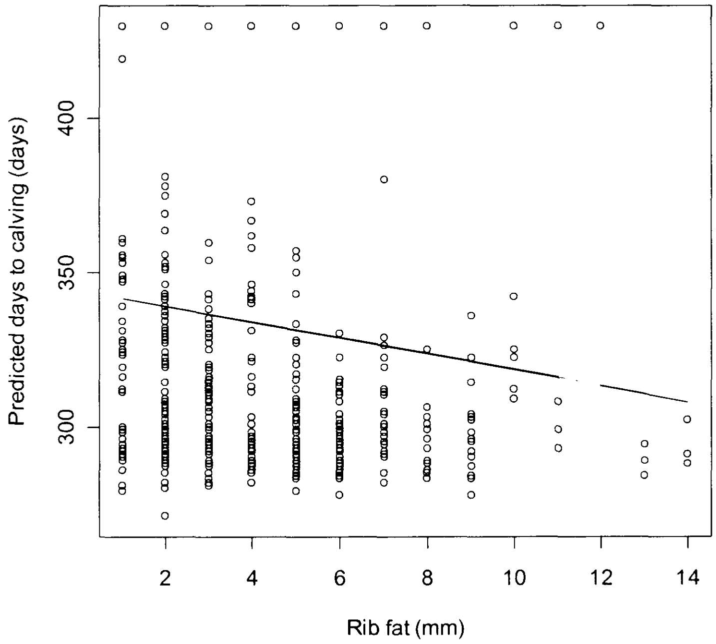
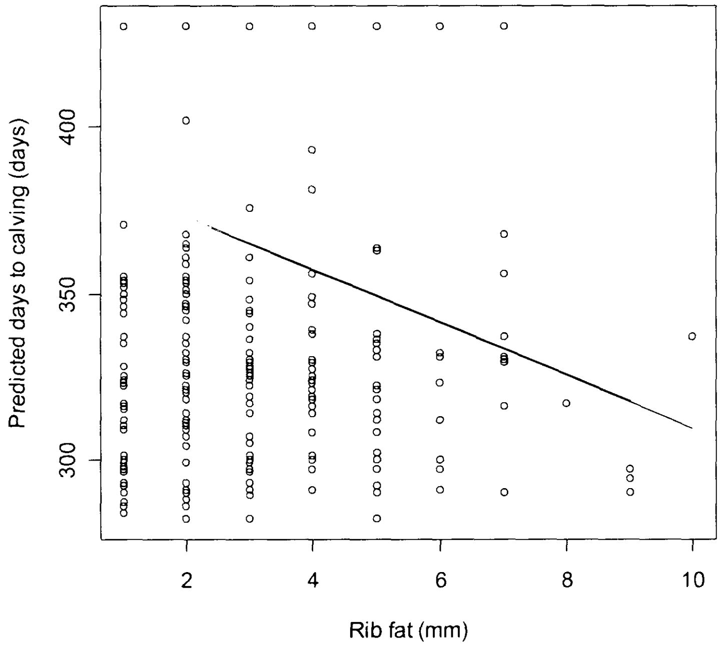


Figure 6.8 (b) Prediction for days to calving based on scanned subcutaneous rib fat measures in 2 year old maiden heifers.



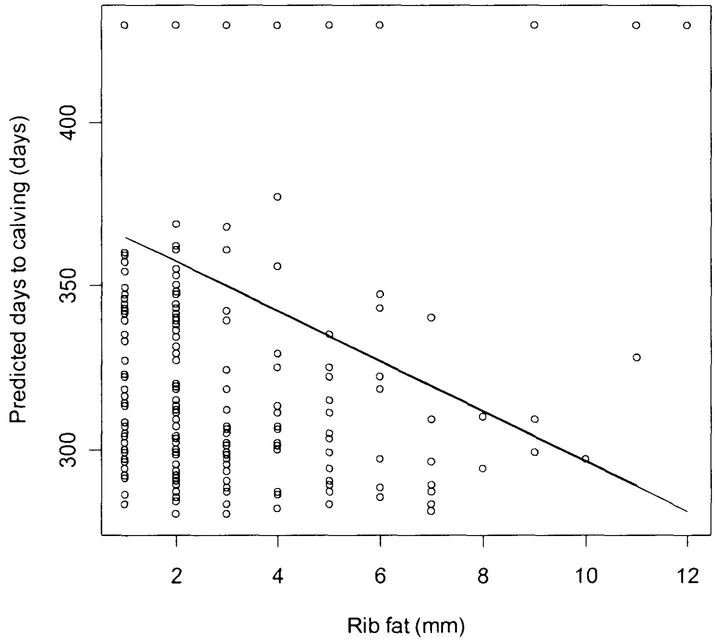
Regression analysis on 3 year old lactating females showed RIBFAT, YEAR ($P<0.001$), IMWT, MP, MM and ORIGIN ($P<0.05$) significantly affected DTC (R square = 0.306). RIBFAT and IMWT explained 1.78% and 0.38% of total deviance respectively. Residual deviance explained 94.28% of total deviance. Prediction models were completed for RIBFAT (intercept 389.25±5.48, slope -7.968±1.65; Figure 6.9) and IMWT (intercept 462.58±27.30, slope -0.22±0.06). Of note was that 3 year old primiparous females require a minimum of approximately 2.5 mm RIBFAT and 410 kg IMWT to conceive within 4 oestrus cycles of the first mating date.

Figure 6.9 Prediction for days to calving based on scanned subcutaneous rib fat measures in 3 year old primiparous females.



RIBFAT, MM ($P<0.001$), YEAR and MP ($P<0.05$) were significant for DTC in 4 year old lactating females (R square = 0.352). RIBFAT and its interactions with IMWT and P8FAT explained 2.01% of total deviance. The prediction model for RIBFAT (intercept 372.61±5.53, slope -7.62±1.69) is shown in Figure 6.10. Predictions show 4 year old lactating females require 6.5-11.5 mm RIBFAT to achieve conception within 1-2 oestrus cycles of first mating date. Each 1 mm increase in RIBFAT should be associated with a 5.5 day decrease in DTC.

Figure 6.10 Prediction for days to calving based on scanned subcutaneous rib fat measures in 4 year old lactating females.



P8FAT, IMWT, RIBFAT, YEAR, MP (P<0.001) and BREED (P<0.05) significantly affected DTC in 5+ year old lactating females (R square = 0.119). Residual deviance accounted for 97.65% of total deviance. Predictions for P8FAT (intercept 352.76±3.44, slope -1.56±0.44) and RIBFAT (intercept 352.57±3.64, slope -2.30) showed a minimum of 17 mm P8FAT and 13 mm RIBFAT would be required for conception within 1-2 oestrus cycles of first mating date. Minimum P8FAT and RIBFAT for conception within 4 oestrus cycles of first mating date were 0 mm for both traits. The IMWT prediction was not significant.

RIBFAT, P8FAT, IMWT ($P<0.001$) and a RIBFAT × IMWT interaction ($P<0.05$) were significant for DTC for females mated by AI, explaining 1.47% of total deviance (R square = 0.175). Residual deviance explained 97.07% of total deviance. RIBFAT (intercept 346.74±2.54, slope -2.10±0.55) and P8FAT (intercept 346.24±2.37, slope -1.20±0.30) predictions were significant. Figure 6.11 shows a minimum of 11 mm RIBFAT (a) and 18mm P8FAT (b) are required for conception within 1-2 cycles (284-326 DTC) of first mating date for females mated by AI.

Figure 6.11 (a) Prediction for days to calving based on scanned subcutaneous rib fat measures in females mated by AI.

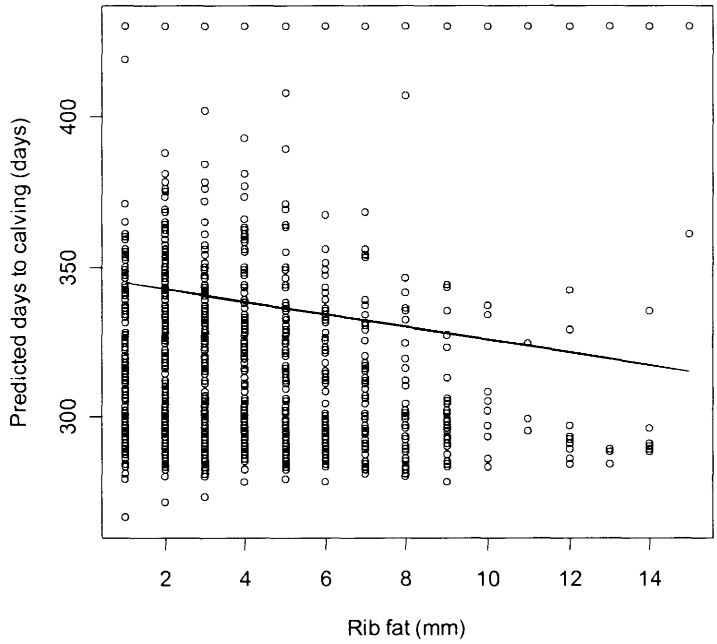
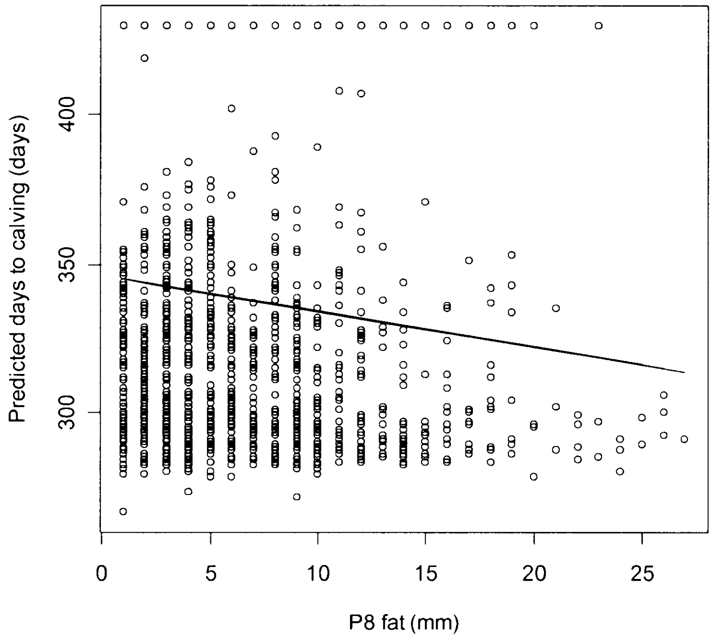


Figure 6.11 (b) Prediction for days to calving based on scanned subcutaneous P8 fat measures in females mated by AI.



IMWT was the most important variable for females mated naturally, explaining 17.26% of total deviance (P<0.001). IMWT, RIBFAT and P8FAT and a RIBFAT × IMWT interaction (P<0.05) collectively explained 19.59% of total deviance (R square = 0.297). Mating period and previous lactation status were also significant (P<0.05). IMWT (intercept 427.60±15.76, slope -0.15±0.03), RIBFAT (intercept 383.93±3.64, slope -6.79±0.73) and P8FAT (intercept 383.13±3.46, slope -4.39±0.45) predictions for DTC for females mated naturally were significant (P<0.001). The IMWT prediction showed a minimum of 375 kg is required for conception within 4 oestrus cycles of first mating date (based across all PLS). Predictions for RIBFAT and P8FAT are shown in Figure 6.12 (a) and (b) respectively. Of note was females mated by natural mating require less RIBFAT and P8FAT (minimum 9 mm and 14 mm respectively) to achieve conception within 1-2 oestrus cycles of first mating date relative to females mated by AI (minimum 11 mm and 19 mm respectively for the same period).

Figure 6.12 (a) Prediction for days to calving based on scanned rib fat in females mated by natural mating.

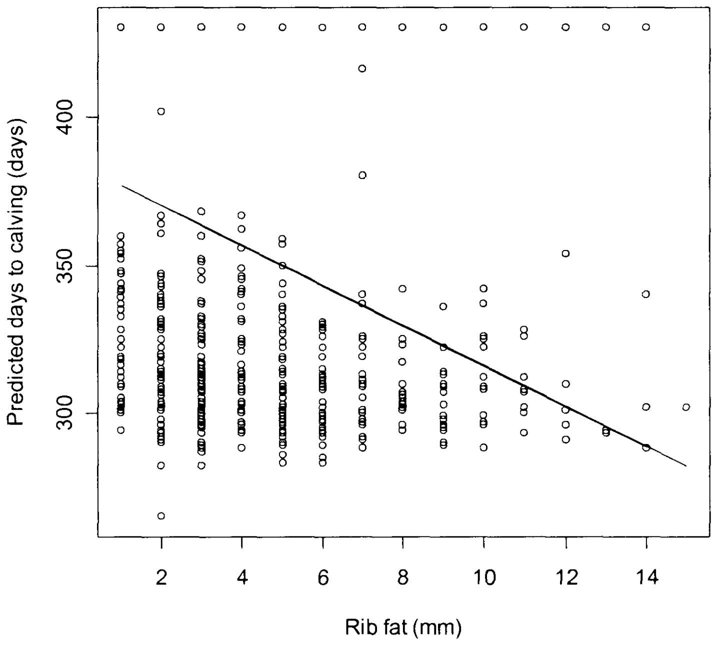
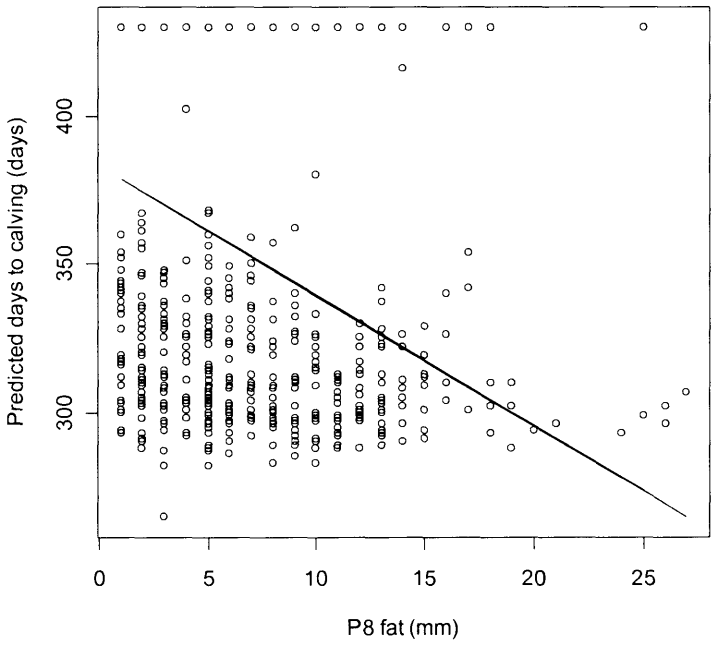


Figure 6.12 (b) Prediction for days to calving based on scanned P8 fat in females mated by natural mating.



6.4 Discussion

6.4.1 Breed differences for fertility

While *Bos indicus* breeds are known to grow slowly, take longer to reach puberty, are older at first calving, have lower calving rates and extended pre-pubertal and postpartum anoestrus periods relative to *Bos taurus* breeds and crossbreeds under the same management conditions, their superior adaptation make them more likely to reproduce successfully in tropical environments (Franke 1980; Randel 1994; Abeygunawardena and Dematawewa 2004; Nogueira 2004). A study by Mackinnon *et al.* (1989) reported mean calving rates of 54.9% in Brahman females relative to 58.3% in F_n BX (50% Brahman, 25% Hereford, 25% Shorthorn), 68.3% in F_n AX (50% Africander, 25% Hereford, 25% Shorthorn; otherwise known as Belmont Red), and 68.1% in F_n AX×BX / BX×AX from mating periods of between 3 and 10 weeks duration beginning in December each year. However, our study found only small differences between Brahmans and composites for pregnancy rate (4.4%; P=0.05) and calving rate (3.3%) and no difference between breeds for days to calving.

The difference between breeds for pregnancy rate and subsequent calving rate was due to higher pregnancy rates of composites relative to Brahmans when mated by AI (83.4% versus 76.9%). A review by Nogueira (2004) concluded that low fertility rates of *Bos indicus* cows following AI may be attributed to the management, nutrition and genetic characteristics of the animal. Property of origin significantly affected pregnancy rates in Brahman females mated by AI (P<0.05), and DTC in Brahman and composite females mated by AI (P<0.05), however BREED differences were not observed for pregnancy rate or DTC for females mated by NM. Another explanation for BREED differences for pregnancy rate and calving rate is the use of oestrus synchronisation treatments in AI programs. The use of hormonal treatments to induce ovulation postpartum and increase pregnancy rates has been shown to have varying effects in *Bos indicus* breeds, with most studies reporting little or no effect in Brahmans (Frisch *et al.* 1987; Abeygunawardena and Dematawewa 2004; Baruselli *et al.* 2004).

6.4.2 Previous lactation status effects on fertility

Lactational anoestrus is characterised by suppression of cyclicity following parturition as a consequence of females nursing their young, resulting in extended postpartum intervals to oestrus in *Bos indicus* and *Bos taurus* breeds (Senger 1999; Abeygunawardena and Dematawewa 2004). As expected, lactating females had lower pregnancy rates, lower calving rates and longer DTC than non-lactating females. There was little difference between 2 year old maiden heifers and 3+ year old non-lactating females for pregnancy rate, calving rate and DTC. Davis *et al.* (1993) reported similar results in a study on Droughtmaster females, with pregnancy rates of 80% in 2 year old heifers relative to 51% in 3 year old lactating females, 65% in 4 year old lactating females, and significantly longer DTC in lactating second and third parity females. The difference in DTC between 3+ year old non-lactating females and lactating females at 70% calving rate in this study was 19 days, which agrees with findings of Hetzel *et al.* (1989) where lactating dams in a tropical beef herd calved 19 days later than non-lactating dams.

Nutritional anoestrus occurs in cattle after a weight loss of approximately 20-24% of their initial body weight (Rhodes *et al.* 1996; Diskin *et al.* 2003). It is endemic in first-calf cows where energy requirements for lactation and growth often out strip the female's ability to consume enough dietary energy to meet her metabolic needs, resulting in negative energy balance and consequent delayed postpartum return to oestrus (Senger 1999). Nutritional anoestrus would explain the lower pregnancy rates, delayed days to conception and subsequent longer DTC, and lower calving rates of lactating 3 year old primiparous females relative to lactating multiparous females and non-lactating females.

It may also be suggested at this point that the trait DTC does not adequately penalise non-lactating females sufficiently for their failure to calve during the previous season, and therefore present results may be biased in favour of non-lactating females. Days open is a trait used in the dairy industry to encompass the number of days from calving date to subsequent conception date, and may include more than one mating season. Lopez de Maturana *et al* (2007) applied a data augmentation technique to censored days open data in order to overcome problems with bias. This approach could possibly be used to overcome bias for the truncated DTC data.

6.4.3 Mating method effects on fertility

Placing females on a rising plane of nutrition prior to and during the mating season enhances the development of ovarian follicles and decreases the percentage of atretic follicles in the ovaries (Maurasse *et al.* 1985). Improved nutrition, daily observation for oestrus, timely insemination and oestrus synchronization are typical of AI programs. Females mated by AI in this study were not placed on irrigated pasture until commencement of the mating season, so it is unlikely that nutrition improved pregnancy rates by AI. However, the other management practices associated with AI including close observation for oestrus, timely insemination and oestrus synchronisation, together with the higher proportion of non-lactating females mated by AI relative to natural mating, are the likely reason for higher pregnancy rates by AI. Further, it is likely that hormone treatments (CIDRs) hastened postpartum return to oestrus in lactating females relative to what would occur naturally under natural mating systems in tropical environments, resulting in higher pregnancy rates and reduced days to conception (observed as lower DTC) in females mated by AI. A timed AI study by Baruselli *et al.* (2002) on lactating

Brangus beef cows in Brazil reported conception rates of 65.0% for females treated with CIDRs relative to 19.1% for females in the control group after 45 days of the breeding season. At the end of the breeding season of 90 days, pregnancy rates were similar (79.0% versus 80.9% respectively). Therefore, it is likely that lactating females (all of which were treated with CIDRs and had variable mating periods of 21-128 days) contributed to the higher pregnancy rates by AI relative to natural mating, particularly as AI practices did not significantly improve pregnancy rates or DTC in 2 year old maiden heifers or 3+ year old non-lactating females relative to natural mating.

6.4.4 Liveweight effects on fertility

Many studies attribute poor pregnancy rates of tropically adapted breeds to insufficient liveweight to successfully conceive, particularly in heifers (Rudder *et al.* 1985; Mackinnon *et al.* 1989; Patterson *et al.* 1991). Target liveweights have long been associated with age at puberty in dairy and beef cattle (Gong 2002). A study by Frisch *et al.* (1987) concluded that despite similar mature weights, Brahman females need to attain higher liveweights than tropically adapted Hereford×Shorthorn crosses before they will successfully produce a calf. A review by Abeygunawardena and Dematawewa (2004) agreed, stating *Bos indicus* breeds do not appear to achieve puberty until they reach 60% of their adult body weight and are consequently 6-12 months older than *Bos taurus* heifers that tend to reach puberty at 30-55% of their adult body weight. Doogan *et al.* (1991) reported that a target liveweight of 270 kg for *Bos indicus* cross heifers was recommended to achieve a conception rate of 80% in the dry tropics of north Queensland. Another study by Rudder *et al.* (1985) on tropically adapted *Bos indicus* × *Bos taurus* crosses suggested target joining liveweights of 275 kg and 375 kg for yearling heifers and cows, though heifers were mated up to 12 months younger than those in our study. Average IMWT for 2 year old maiden heifers in this study were more than 65 kg heavier than the minimum recommended by Rudder *et al.* (1985) and Doogan *et al.* (1991). The majority of 2 year old maiden heifers in this study would have already reached puberty, which is likely the reason that IMWT was not significant for pregnancy rates in this age group. The minimum IMWT at which pregnancy occurred in 2 year old maiden heifers was 278 kg (IMWT mean 358 kg, range 240-488 kg). IMWT was important for DTC in 2 year old maiden heifers, with each 10 kg increase in IMWT associated with a 2.4 day decrease in DTC (or days to conception) ($P<0.001$). Mean IMWTs of composite females were higher than Brahman females, resulting in correspondingly higher pregnancy rates. The exception was for 3+ year old non-lactating females where the lighter Brahmans (461 kg versus 510 kg) had the higher pregnancy rate (87.6% versus 78.3%) relative to composites.

6.4.5 Fatness effects on fertility

A study of Droughtmaster females by Davis *et al.* (1993) reported significant differences between divergent pregnancy rate lines for pregnancy rate, weaning rate and days to calving in favour of the high line despite all females being more than 30 kg above the recommended target mating weight of 270-280 kg, suggesting that liveweight itself was not sufficient to predict pregnancy success. Our study confirmed that scanned subcutaneous rib fat depth, and to a lesser extent P8 fat depth, are significantly related to pregnancy rate and DTC, though these fatness measures tended to explain less than 5.0% of total deviance. Many studies have examined relationships between fatness and fertility (reviews by Gong 2002; Friggens 2003), but these mainly discussed fatness in terms of metabolic markers or body condition score. Siebert and Field (1975) concluded that the onset of oestrus appeared to be more closely related to body fat content, being 8.4% of weight in *Bos indicus* × *Bos taurus* heifers, than to liveweight. An experiment examining postpartum body condition score of dairy cows and subsequent return to oestrus suggested there may be a target level of fatness for fertility in cattle (Garnsworthy and

Topps 1982). They concluded that despite being under the same nutritional conditions, patterns of fat mobilisation occurred at different rates between three groups of cows so that fat cows lost lipid and thin cows gained lipid during the 16 weeks postpartum. Friggens *et al.* (2003) observed that under the same feeding and management conditions, Holstein cows with body condition scores (BCS) between 3.5 and 4.0 (good condition) returned to oestrus within 50 days of calving, while those with BCS of 3.0 or 4.5 returned to oestrus within 55 days of calving, and those with BCS of 2.5 (poor) took up to 73 days to return to oestrus.

6.4.6 Year and nutritional effects on fertility

Environmental conditions have the largest influence on fertility as seen with large year effects and year interactions for the traits studied. Hence, results from this experiment are confined to the breeds and environmental conditions under which these females were joined. Similarly, another study of tropically adapted crossbreds found year effects had the largest and most consistent influence on joining liveweight, pregnancy rate and days to calving (Rudder *et al.* 1985). Nutrition and its subsequent effects on follicular dynamics, liveweight and fatness play a significant role in fertility, particularly in northern Australian where seasonal fluctuations and frequent droughts wreak havoc on feed availability and quality. Other studies on reproduction in cattle have drawn similar conclusions, stating that weight gain in the season prior to first mating and adequate nutrition pre- and postpartum for lactation and growth are vital in ensuring early age at puberty, early conceptions and subsequent early days to calving, high pregnancy and calving rates, and reduced postpartum anoestrus interval (Morris 1980b; Entwistle *et al.* 1983; Doogan *et al.* 1991; Roberts *et al.* 1993; Wettemann 1994; Gong 2002; Ciccioli *et al.* 2003; Friggens 2003).

6.5 Implications for the beef industry

This study confirmed that scanned measures of subcutaneous rib fat depth, P8 fat depth and into mating liveweight had significant effects on pregnancy rate and days to calving in Brahman and tropically adapted composite females of different age and lactation status, and bred by AI and natural mating in a tropical environment. Practices associated with AI resulted in significant differences between breeds for pregnancy rate and subsequent calving rate. IMWT was a significant predictor for DTC in 2 year old maiden heifers, with each 10 kg increase in IMWT associated with a 2.4 day decrease in DTC (or days to conception) ($P<0.001$), while each 10 kg increase in IMWT for females mated by natural mating could decrease DTC by 1.5 days ($P<0.001$). These IMWT predictions explained 15.9% and 17.3% of total deviance respectively. While other predictions for pregnancy rate and DTC using IMWT, RIBFAT and to a lesser degree P8FAT were significant, they explained less than 5.0% of total deviance. Consequently, pregnancy rate and days to calving would be susceptible to large environmental (year, property of origin, others) and management (mating method, mating period) influences. Further refinement of prediction models (residual deviance accounted for the majority of total deviance in most models) including development of other predictors leading to implementation of such simple prediction methods could be of immense benefit to the commercial breeding sector, as fat scanning and weighing are relatively inexpensive and easy to measure in practice. Particularly when compared with bleeding or collection of tissue samples for genetic screening for presence of metabolic markers or QTL, which at present remain to be discovered or conclusively linked to fertility.

Acknowledgements

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CHAPTER 7 General Discussion

The purpose of this thesis was to compare the performance of tropically adapted crossbred and composite cattle with straightbred Brahmans for economically important production and reproduction traits under tropical and subtropical conditions in northern Australian using typical commercial beef production practices. The studies conducted in this thesis confirmed that straightbred Brahmans differ significantly from Brahman crossbreds and tropically adapted composites for carcass quality, objective and sensory measures of meat quality, feed efficiency, feeding behaviour and to some extent reproductive success. Environmental effects on traits of economic importance were also discussed.

7.1 Breed selection for carcass and meat quality

There were significant differences between straightbred Brahmans and Brahman crossbreds for carcass quality. At common carcass weights, breeds within breed type (British – Angus, Hereford, Shorthorn; Continental – Charolais, Limousin) had similar carcass quality. Table 7.1 shows sire breed rankings for carcass quality, meat quality and feed efficiency traits where sire breeds were significantly different. Straightbred Brahmans had carcasses up to 16% lighter than Continental and British sired crossbreds (age-adjusted; $P<0.001$), intermediate subcutaneous fat cover (HOTP8), retail beef yields (RBY) and kilograms of retail primals (RTPM), and low marbling (IMF) (Tables 3.4, 3.5 and 7.1). British and Belmont Red sired crossbreds had the highest IMF, while British and Santa Gertrudis sired crossbreds had the fattest carcasses. Angus crossbreds averaged 27% more IMF than Santa Gertrudis crosses and straightbred Brahmans at common carcass weights. Continental crossbreds had the highest RBY, RTPM and pcRTPM, leanest carcasses and intermediate IMF. Breed differences for carcass quality were generally consistent with Brahman crossbred studies conducted in Louisiana and Florida in the USA (Peacock *et al.* 1977; Huffman *et al.* 1990; DeRouen *et al.* 1992a). Similar sire breed rankings were reported from Cycle V and Cycle VII of the USDA Meat Animal Research Center Germplasm Evaluation Program conducted in Nebraska (Cundiff *et al.* 1998; Cundiff *et al.* 2001) and in reviews of carcass quality mainly based on animals finished in temperate environments (Cundiff and Gregory 1999; Marshall 1994, 1999). In contrast to our results, Comerford *et al.* (1988) reported significant differences between Limousin × Brahman and straightbred Brahmans for marbling and no difference in fat thickness between Limousin × Brahman and Hereford × Brahman crosses relative to straightbred Brahmans. Huffman *et al.* (1990) found Angus × Brahman steers (50% Brahman versus 75% Brahman content) did not differ for dressing percentage, adjusted fat over the ribeye or USDA yield grade, and DeRouen *et al.* (1992a) found straightbred Brahmans had higher P8 fat thickness than Charolais × Brahman, and more RBY and RTPM than Angus × Brahman and Hereford × Brahman crosses. Importantly, straightbred Brahmans and Brahman crossbreds complied with basic weight and fat specifications for the markets for which they were destined. However, if targeting premium marbling markets like the Japanese market, British breed or Belmont Red crosses with Brahman is recommended over straightbred Brahman or Continental crossbreds, as shown in Table 3.4.

Despite large differences between Brahman and first-cross genotypes for carcass quality traits, there was little difference between sire breeds for most objective and sensory meat quality traits. The exception was straightbred Brahmans that differed from Brahman crossbreds for sensory and LT meat quality. Straightbred Brahmans had the highest LT shear force (5.39±0.07; $P<0.001$), LT instron compression (1.89±0.02; $P<0.05$) and cooking loss in the LT and ST muscles ($P<0.05$; Tables 4.3 and 7.1), and were the only breed that failed to meet minimum MSA CMQ4 grading standards (38.3±1.4; $P<0.001$; Table 4.4; Figure 4.1). Other studies have also found significant differences between Brahmans and Brahman × *Bos taurus* crossbreds finished on pasture and in feedlots (Peacock *et al.* 1982; Pratchett *et al.* 1988; DeRouen *et al.* 1992a). All Brahman crossbreds successfully met minimum objective and sensory meat quality standards for tenderness (shear force less than 5.0 kg, Egan 1997; instron compression less than 2.2 kg, Gazzola 1997; CMQ4 score greater than 46.5; Tables 4.3 and 4.4). Straightbred Brahmans and Brahman crossbreds had instron compression measures below 2.2 kg indicating connective tissue toughness was not important in these animals slaughtered by an average of 24 months of age. There was little difference between crossbred progeny for most meat quality traits, including 75% Brahmans (Santa Gertrudis crossbreds), which is consistent with separate studies by Johnson *et al.* (1990) and Pringle *et al.* (1997) of Brahman × Angus steers feedlot-finished in Florida. On the other hand, Crouse *et al.* (1989) observed significant differences in shear force and sensory panel scores for 50% versus 75% Brahman groups, concluding that as percentage of Brahman content increased, sensory tenderness and juiciness decreased. However their study was conducted in temperate Nebraska. Abattoir slaughter protocols in other non-Australian studies may be different from best practice pre-and post-slaughter protocols implemented in Australian abattoirs. These practices reduce the negative effects of processing on meat toughness. Management of an animal immediately before slaughter and the carcass processing conditions applied within the first 24 hours post-slaughter have the largest influence on beef palatability, and can negate any genetic advantage in meat quality (Ferguson *et al.* 2001). Therefore, breeds with up to 75% Brahman content can successfully meet minimum objective and sensory meat quality standards for tenderness when slaughtered by 24 months of age (discussed in section 7.2) and best practice pre- and post-slaughter protocols are used (Tables 4.3 and 4.4). Furthermore, 34.9% of straightbred Brahman carcasses achieved MSA 3-star grading or better (Table 4.5), indicating there is genetic variation within the breed that may be exploited to improve sensory palatability in straightbred Brahman herds.

Genetic variation within breeds can be exploited to speed genetic progress through selection of sires with desirable traits of moderate to high heritability such as subcutaneous fat thickness (mean 0.46), marbling score (mean 0.36), retail beef yield (mean 0.48), shear force (mean 0.25) and sensory tenderness (mean 0.22) (mean heritabilities from reviews by Koots *et al.* 1994; Marshall 1994, 1999; Burrow *et al.* 2001). Furthermore, the sire breeds used in the Northern Crossbreeding Program were selected over 10 years ago. Hence, it is likely that genetic progress for carcass and meat quality traits has been made in the Brahman breed since then. With ongoing development and use of gene marker tests for beef quality traits including growth, carcass weight (Watanabe and Sugimoto 2006), marbling (Barendse *et al.* 2004; Thaller *et al.* 2003), marbling score (Casas *et al.* 2004), meat tenderness (Page *et al.* 2002; Cullen *et al.* 2003; Drinkwater *et al.* 2006), fat depth, dressing percentage, retail beef yield and eye muscle area (Hetzel *et al.* 1997; Morsci *et al.* 2006; reviews by Marshall 1999 and Burrow *et al.* 2001), carcass and meat quality of straightbred Brahmans and tropically adapted crossbreds will improve as seedstock breeders adopt genetic technologies as part of their selection strategy.

Table 7.1 Sire breed rankings for carcass quality, meat quality and feed efficiency traits where sire breeds differed significantly[1]. Sire breeds[2] are ranked from most desirable at the top of the columns to least desirable at the bottom for most traits[3] based on least squares means from Tables 3.4, 3.5, 4.3, 4.4, 5.5 and 5.6.

AGE* (days) (low to high)	CWT** (kg) (high to low)	HOTP8** (mm) (high to low	IMF** (%) (high to low)	RBY* (%) (high to low)	RTPM* (kg) (high to low)	pcRTPM* (%) (high to low)	SFLT** (kg) (low to high)	ICLT* (kg) (low to high)	CLLT* (%) (low to high)	SFST** (kg) (low to high)	CLST* (%) (low to high)	CMQ4** (/100) (high to low)	FI** (kg/day (low to high)	RFI* (kg/day (low to high)	ADG** (kg/day) (high to low)	KR* (low to high)	TIME** (min/day) (low to high)	SESS* (low to high)
BB,CC	CC	AA	AA	LL	LL	LL	AA	AA,HH	AA,LL	LL	HH,SS	AA	**BB**	CC	SG	**BB**	**BB**	BR
BR,LL	HH	SS	SS	CC	CC	CC	HH,LL	LL	CC,SS	CC	BR	CC	BR	HH	SS	BR	CC	SS
SG	AA	HH	BR	**BB**,BR	**BB**	**BB**	CC	CC	BR	SG	AA,LL	BR	CC	LL	AA	CC	BR	LL
HH	LL	SG	HH	AA	BR	BR	SG	BR	HH	BR	CC	HH,LL	LL	SG	HH	LL	LL	CC,SG
AA	SS	BR	CC	HH	HH	AA,HH,SG	BR	SG, SS	SG	HH	SG	SG	HH	**BB**	LL	AA,SS	HH	AA
SS	SG	**BB**	LL	SG	SG	SS	SS	**BB**	**BB**	**BB**	**BB**	SS	SG	BR	CC	HH	SG	HH
	BR	CC	**BB**	SS	AA		**BB**			AA		**BB**	SS	SS	BR	SG	SS	**BB**
	BB	LL	SG		SS					SS			AA	AA	**BB**		AA	

[1] Significance: * (P<0.05), ** (P<0.001).

[2] Sire breeds: Angus = AA, **Brahman = BB**, Belmont Red = BR, Charolais = CC, Hereford = HH, Limousin = LL, Santa Gertrudis = SG, Shorthorn = SS.

[3] Traits: AGE = age at slaughter, CWT = hot carcass weight, HOTP8 = hot subcutaneous fat depth, IMF = intramuscular fat percent, RBY = retail beef yield, RTPM = kilograms of retail primals, SFLT = shear force of the LT muscle, ICLT = instron compression of the LT muscle, CLLT = cooking loss percent of the LT muscle, SFST = shear force of the ST muscle, CLST = cooking loss percent of the ST muscle, CMQ4 = clipped meat quality of 4 attributes score, FI = daily feed intake, RFI = residual feed intake, ADG = average daily gain, KR = Kleiber ratio, TIME = time spent eating per day, SESS = number of eating sessions per day. Carcass quality and meat quality traits were adjusted to a common hot carcass weight with the exception of CWT that was adjusted to a common age at slaughter. Feed efficiency and feeding behaviour traits were adjusted to a constant starting age.

7.2 Environmental factors affecting carcass and meat quality

Finishing nutrition and finishing environment were found to have significant effects on carcass and meat quality in straightbred Brahmans and Brahman crossbreds. Feedlot-finishing has advantages for turning cattle off several months earlier with more HOTP8 ($P<0.001$), slightly higher IMF (n.s.), lower RBY ($P<0.05$) and lower RTPM and pcRTPM ($P<0.001$) relative to pasture-finishing (Tables 3.6 and 3.7). Robinson *et al.* (2001) reported a similar finding for *Bos taurus* steers finished on pasture and grain in temperate NSW. DeRouen *et al.* (1992a) recommended grain feeding for a minimum of 90 days after ryegrass grazing in subtropical Louisiana to ensure satisfactory carcass quality (hot carcass weight, retail yield, fat thickness, marbling score and quality grade) in Brahman and *Bos taurus* crosses. Relative to pasture, feedlot-finishing significantly improved all objective and sensory meat quality traits except CLST (Tables 4.6 and 4.7). Similar findings for Brahman crossbreds were reported by Bennett *et al.* (1995) and Ferguson *et al.* (2000), and Johnston *et al.* (2003) reported consistent meat quality findings in magnitude and direction for straightbred Brahman, Belmont Red and Santa Gertrudis.

Even at domestic market weights (24 months of age), objective measures of myofibrillar and connective tissue toughness of pasture-finished animals were outside acceptable tenderness limits (shear force less than 5.0 kg, Egan 1997; instron compression less than 2.2 kg, Gazzola 1997), though sensory palatability was acceptable (Figure 4.2). Tougher meat from pasture-finished animals (Tables 4.6 and 4.7) may be the result of older more mature intramuscular collagen and slower rates of collagen turnover relative to animals finished in feedlots (Harper *et al.* 1997) as a consequence of poorer feed quality and growth path interruptions. Feedlot finishing ensures carcasses from Brahmans and Brahman crossbreds have the best opportunity to meet market specifications for subcutaneous fat depth and marbling (Table 3.6), improves objective and sensory meat quality, and reduces age at turnoff by several months relative to pasture finishing. Feedlot-finishing for a minimum of 70 days is recommended for straightbred Brahmans and Brahman crossbreds. Pasture-finishing is not recommended for export market animals if meat quality is an important market consideration.

Finishing tropically adapted cattle in temperate feedlots appears to have advantages for carcass fat distribution (Table 3.6, Figure 3.2) and objective and sensory meat quality (Tables 4.6 and 4.7, Figure 4.2). Animals finished in the temperate feedlot had more IMF ($P<0.001$) and less HOTP8 ($P<0.001$) than contemporaries finished in the subtropical feedlot, suggesting possible post-weaning growth path effects on fat distribution. Consistent trends were observed in the linked Beef CRC Straightbreeding Program (Reverter *et al.* 2003) and in a study by Robinson *et al.* (2001). Johnston *et al.* (2003) also reported higher CMQ4 results for straightbred Brahman, Belmont Red and Santa Gertrudis animals finished in the temperate feedlot relative to subtropical feedlot. Limitations of the Beef CRC Crossbreeding Program experimental design prevent conclusive recommendations being made about climatic effects (subtropical versus temperate) on carcass fat distribution and eating quality. Other studies have suggested growth path differences (Allingham *et al.* 1998; Harper 1999, Oddy *et al.* 2001), including nutritional restrictions and compensatory growth (Oddy *et al.* 1997a, b; Ball *et al.* 1997; Keele *et al.* 1992), thermoregulation (Reverter *et al.* 2003), fatty acid composition of subcutaneous fat, ambient temperature and pasture quality (Kelly *et al.* 2001) may be responsible for environmental differences in fat distribution. Therefore, it is probably safe to conclude that maintaining an uninterrupted growth path during the grow-out phase prior to feedlot entry in subtropical environments may reduce variation in fat distribution, while also providing significant advantages such as reduced age at slaughter and improved meat quality. Maintaining an uninterrupted growth path may be achieved though use of improved pastures or forage crops, or supplementation to improve feed utilisation during the dry season to prevent weight stasis or weight loss. Further research on post-weaning growth path effects (grow-out pasture quality and quantity, nutritional restriction, compensatory gain, etc.) and climatic effects (subtropical versus temperate) on carcass fat distribution (subcutaneous versus intramuscular fat) and eating quality (objective and sensory measures of meat quality) would provide northern Australian beef producers with invaluable knowledge to further improve their compliance with target market specifications.

The lack of important breed × finish and breed × market interactions confirmed that cattle breeders can select any breed within breed type and achieve predictable outcomes for carcass quality and meat quality, regardless of finishing nutrition (pasture versus grain), finishing environment (subtropical versus temperate) or market. Other studies have also reported lack of breed × finishing environment interactions for Brahman, Belmont Red and Santa Gertrudis straightbreds between tropical and temperate finishing environments (Reverter *et al.* 2003; Johnston *et al.* 2003), and for Brahman crossbreds finished on pasture and grain in temperate environments (Hearnshaw *et al.* 1988).

7.3 Breed selection for feed efficiency

Feedlot-finishing is becoming standard practice in northern beef production systems as domestic and export markets demand a consistent product with minimum quality standards. Sire breed differences exist for feed efficiency and feeding behaviour. Biological differences in feed utilisation have been linked to variation in feed intake, digestion of feed, metabolism, body composition, activity, thermoregulation, feeding patterns and temperament (Oddy and Herd 2000; Richardson *et al.* 2000; Herd *et al.* 2004; Richardson and Herd 2004). *Bos indicus* breeds have a faster fermentation rate, shorter digesta retention time and higher population of rumen protozoa (expected to support greater methane emissions), but have greater efficiency of energy capture relative to *Bos taurus* (Hegarty 2000). Therefore, *Bos indicus* cattle should require lower feed intakes relative to *Bos taurus* genotypes in order to meet maintenance requirements (Frisch and Vercoe 1969; Vercoe 1970). However RFI results did not reflect this. Our study showed straightbred Brahmans did not differ from Brahman crossbreds for residual feed intake (RFI). However, straightbred Brahmans spent the least time eating and consequently had the lowest feed intake (FI; $P<0.001$) and lowest average daily gains (ADG; $P<0.001$) overall (Tables 5.5 and 5.6). Hence, while straightbred Brahmans may be efficient feeders, their low feed intake inhibits fast growth rates. As *Bos indicus* evolved under poor nutrition they will have automatically been selected for low fasting metabolism and low appetite, so that even under good conditions they will have low FI and low growth rates relative to *Bos taurus* that evolved in less stressful environments (Frisch and Vercoe 1977). Similarly, Belmont Red crossbreds did not differ from all other crossbreds and straightbred Brahmans for RFI, but had low FI ($P<0.001$) and low ADG ($P<0.001$) relative to British and Santa Gertrudis crosses. The Belmont Red is a tropically adapted *Bos taurus* breed that was derived from Africander × Hereford/Shorthorn crosses. The Africander is from Africa where its evolution would have been under similar environmental stressors to that of *Bos indicus* breeds, and therefore has low FI and low ADG relative to *Bos taurus* breeds from Britain and the Continent. The advantage of using Belmont Red in tropical environments is their superior carcass and meat quality relative to straightbred Brahman.

Angus × Brahman crosses were the least efficient feeders (highest RFI), consuming 35% and 13% ($P<0.001$) more feed than straightbred Brahmans and Charolais × Brahman crosses respectively (Tables 5.5 and 5.6). Findings from other studies between *Bos taurus* and *Bos taurus* × *Bos indicus* crosses (Frisch and Vercoe 1977; Cundiff *et al.* 1984; Huffman *et al.* 1990) generally support breed trends for feed efficiency and feeding behaviour in our study. Robinson and Oddy (2004) reported similar mean FI and FCR and lower mean ADG for straightbred Brahman, Belmont Red and Santa Gertrudis animals at lower mean metabolic mid-weights, while Schenkel *et al.* (2004) reported consistent breed rankings for young Charolais, Limousin, Hereford and Angus beef bulls for RFI (by regression) relative to our results, though Charolais crosses had lower RFI than Limousin crosses in our study. Similarly to Schenkel *et al.* (2004), we found Charolais and Limousin crosses had lower FI than Angus crosses. In contrast, we found no difference between the four relevant sire breeds for ADG or FCR. Therefore, use of Charolais, Hereford, Limousin and Santa Gertrudis sire breed crosses with Brahman would result in the most feed efficient (low RFI) animals without any sacrifice in ADG.

The most feed efficient sire breeds tend to align with those with the leanest, highest yielding carcasses (Table 7.1). Conversely, the least feed efficient sire breeds align with those with the highest marbling. Therefore, breeders would need to select breeds based on their individual environment (climate, nutrition, parasite burdens), breeding objectives, target markets and finishing regimes. For example, British breed and Belmont Red would provide the most suitable crosses with Brahman for the Japanese market. However premiums from the superior marbling of the British crosses would have exceed the additional costs of feedlot feeding these breeds relative to using a more feed efficient and lower marbling sire breed.

7.4 Breed selection for reproductive success

Brahman females had significantly lower pregnancy rates than composite females when mated by AI (83.4% versus 76.9%; P=0.05), but breed differences were not observed for pregnancy rates of females joined by natural mating. Breed differences for days to calving (DTC) were mainly the result of higher calving rates of composites relative to Brahman females as a consequence of pregnancy rates by AI. Differences in pregnancy rates by AI were likely due to management practices associated with AI including use of CIDRs for lactating females (Baruselli *et al.* 2002) and the likelihood that Brahman females did not respond to hormone treatments as well as composite females. The use of hormonal treatments to induce ovulation postpartum and increase pregnancy rates has been shown to have varying effects in *Bos indicus* breeds, with most studies reporting little or no effect in Brahmans (Frisch *et al.* 1987; Abeygunawardena and Dematawewa 2004; Baruselli *et al.* 2004). Therefore, if breeders intend to join their females by natural mating, there should be little difference between straightbred Brahmans and tropically adapted composites (including Belmont Red) for pregnancy rates or DTC. However, considering sire breed performance across the range of carcass quality, meat quality and feed efficiency traits (Table 7.1), tropically adapted crossbreds and composites would yield greater economic benefits to the northern Australian beef producer.

7.5 Fatness and weight effects on reproductive success

Composite dams conceived at higher mean into mating weights (IMWT) and had higher pregnancy rates than Brahman dams across all previous lactation status groups (IMWT range 290-690 kg for composites and 240-678 kg for Brahmans), with the exception of 3+ year old non-lactating females where Brahman dams had higher pregnancy rates than composites. Subcutaneous rib fat depth (RIBFAT) significantly affected pregnancy rates in both breeds ($P<0.001$), while IMWT ($P<0.05$) significantly affected pregnancy rates in composites, subcutaneous P8 fat depth (P8FAT; $P<0.05$) significantly affected pregnancy rates in Brahmans, and RIBFAT × IMWT interactions ($P<0.05$) affected pregnancy rates in both breeds. Though effects of these traits on reproductive success were significant, they explained less than 2.81% of total deviation in pregnancy rate in both breeds.

Many studies attribute poor pregnancy rates of tropically adapted breeds to insufficient liveweight to successfully conceive, particularly in heifers (Rudder *et al.* 1985; Mackinnon *et al.* 1989; Patterson *et al.* 1991). Target liveweights for *Bos indicus* cross heifers have been recommended at above 270 kg (Rudder *et al.* 1985; Doogan *et al.* 1991). Average IMWT for 2 year old maiden heifers in this study were more than 70 kg heavier than these recommendations. Therefore the majority of 2 year old maiden heifers in this study would have already reached puberty, which may explain why IMWT was not significant for pregnancy rates in this age group. IMWT significantly affected DTC in 2 year old maiden heifers, with predictions showing that each 10 kg increase in IMWT was associated with a 2.4 day decrease in DTC (or days to conception) ($P<0.001$). IMWT predictions for lactating females joined by natural mating showed that for each 10 kg increase in IMWT, DTC would decrease by 1.5 days ($P<0.001$). These IMWT predictions explained 15.9% and 17.3% of total deviance respectively, suggesting they would be useful as prediction tools in the northern Australian beef industry.

This study confirmed that scanned subcutaneous rib fat depth, and to a lesser extent P8 fat depth, are significantly related to pregnancy rate and DTC, though these fatness measures tended to explain less than 5.0% of total deviance. Many studies have examined relationships between fatness and fertility (reviews by Gong 2002; Friggens 2003), but these mainly discussed fatness in terms of metabolic markers and body condition score, and were relevant to dairy females where there may be other priorities in allocation of resources. Siebert and Field (1975) concluded that the onset of oestrus appeared to be more closely related to body fat content, being 8.4% of weight in *Bos indicus* × *Bos taurus* heifers, than to liveweight. An experiment examining postpartum body condition score of dairy cows and subsequent return to oestrus suggested there may be a target level of fatness for fertility in cattle (Garnsworthy and Topps 1982). However neither of these studies has direct relevance to predicting reproductive success based on objective subcutaneous fat depth measures. Ultrasound scanning has been used to measure ovarian activity in tropically adapted females, however this requires a skilled operator with expensive equipment (Burrow *et al.* 2003). Therefore, further refinement of prediction models for subcutaneous fat depth or development of other predictors would be beneficial in establishing benchmarks for reproductive success for the northern Australian breeding herds, particularly if they can be developed for traits that are relatively inexpensive and easy to measure in practice as are scanned subcutaneous fat depth and liveweight.

Despite significant effects of IMWT, RIBFAT and P8FAT in this study, in most cases they explained less than 5% of total deviation for pregnancy rate and DTC, and these traits would apparently be susceptible to large environmental influences. Two of the most important factors affecting female fertility are lactation and nutrition (Wettemann 1994). There is close relationship between fertility, body condition and nutritional status in pre-pubertal, lactating and non-lactating female cattle (Rhodes *et al.* 1996; Robinson 1996; Gong 2002). Lactational anoestrus is characterised by suppression of cyclicity following parturition as a result of lactation and can result in extended postpartum intervals to oestrus in *Bos indicus* and *Bos taurus* (Senger 1999; Abeygunawardena and Dematawewa 2004). It is well documented that diet affects follicular dynamics in cattle (Patterson *et al.* 1991; Robinson 1996; Armstrong *et al.* 2002; Gong 2002; Ciccioli *et al.* 2003). Nutritional anoestrus mainly occurs in first-calf cows where the female cannot consume enough dietary energy to meet her metabolic needs plus the needs for lactation and growth (Rhodes *et al.* 1996; Senger 1999; Diskin *et al.* 2003). Lactational anoestrus was evident amongst lactating females in our study (Table 6.1). Similarly, the lower pregnancy rates of 3 year old lactating (second-calf) females indicate nutritional anoestrus affected their fertility (Table 6.1). To improve fertility in lactating females (increase pregnancy rates and reduce days to conception), breeders can provide supplementation, or graze females on improved pastures or forage crops prior to joining.

7.6 Implications for breed selection in northern Australia

Efficiency of beef production depends on feed and other inputs of all classes of animals in the production system including the breeding herd and slaughter generation. Therefore, within and between breed selection needs to take into consideration economically important production and reproduction traits. Moderate to strong genetic and phenotypic antagonisms have been reported between carcass fatness traits and retail beef yield in *Bos taurus* and *Bos indicus* breeds (Koots *et al.* 1994b; Marshall 1999; Burrow *et al.* 2001; Reverter *et al.* 2003), and undesirable genetic correlations between RFI and fatness traits including rump fat, rib fat and intramuscular fat percent (Richardson *et al.* 2001; Robinson and Oddy 2004). As fatness is known to significantly affect fertility, there is growing concern that ongoing selection for improved retail beef yield or feed efficiency may reduce carcass fatness to a point where reproductive function of replacement females is compromised. Within breed variation can be exploited through selection of individuals with desirable combinations of traits of economic importance.

Apart from faster growth rates, a major benefit of crossbreeding is the complementary blending of breed characteristics which can overcome genetic antagonisms between some production and reproduction traits that can be encountered from within-breed selection. Use of tropically adapted crossbreds and composites including Belmont Red and Santa Gertrudis may be advantageous where terminal crossbreeding programs prevent use of straightbred British or Continental sires because of their reduced ability to survive and breed when subjected to severe environmental stressors. AI programs have been used extensively during the Beef CRC breeding programs in northern Australia. Hence, their implementation in commercial beef herds is one method by which genetics of British and Continental sire breeds may be disseminated under adverse conditions. Using an existing tropically adapted composite or establishing a tropically adapted crossbreed from among the sire breeds discussed in this thesis would allow the retention of adaptation and survival traits synonymous with the Brahman breed, coupled with improved carcass and meat quality, feed efficiency and reproductive success, to ensure economic efficiency and profitability of beef production in northern Australia.

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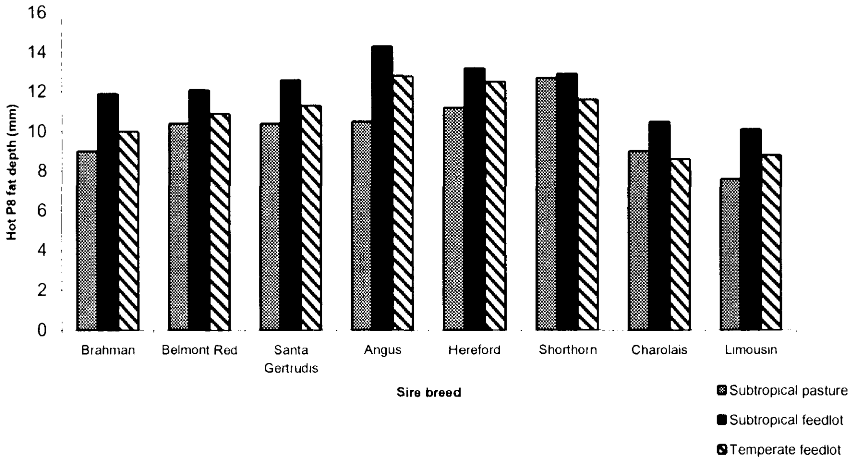
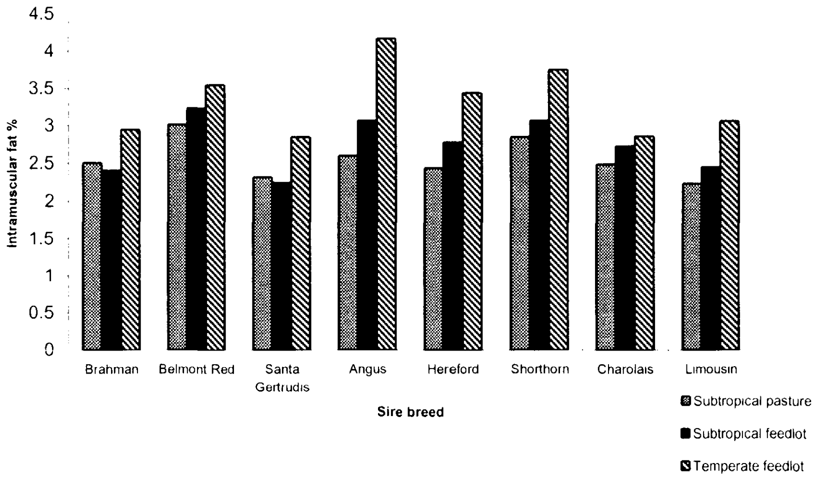
APPENDICES

APPENDIX A. Least squares means (±se) for breed*finish interactions for Figure 3.1 (HOTP8) and Figure 3.2 (IMF).

HOTP8 breed*finish	**(n.s.)**		n=1473
	Subtropical pasture	Subtropical feedlot	Temperate feedlot
Brahman	9.0±0.5	11.9±0.5	10.0±0.4
Belmont Red	10.4±0.5	12.1±0.5	10.9±0.4
Santa Gertrudis	10.4±0.7	12.6±0.7	11.3±0.6
Angus	10.5±0.8	14.3±0.7	12.8±0.6
Hereford	11.2±0.8	13.2±0.7	12.5±0.6
Shorthorn	12.7±0.8	12.9±0.8	11.6±0.7
Charolais	9.0±0.6	10.5±0.6	8.6±0.5
Limousin	7.6±0.5	10.1±0.5	8.8±0.4

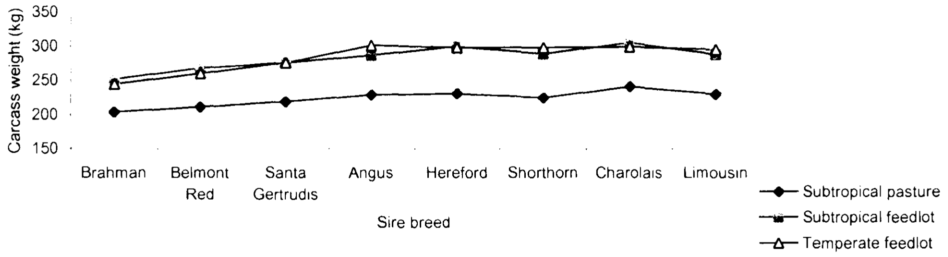


IMF breed*finish	**(P=0.0412)**		n=1188
	Subtropical pasture	Subtropical feedlot	Temperate feedlot
Brahman	2.51±0.16	2.41±0.13	2.95±0.12
Belmont Red	3.02±0.14	3.24±0.12	3.55±0.12
Santa Gertrudis	2.32±0.21	2.25±0.18	2.85±0.17
Angus	2.60±0.23	3.07±0.18	4.17±0.16
Hereford	2.44±0.22	2.78±0.19	3.44±0.18
Shorthorn	2.85±0.23	3.07±0.19	3.75±0.19
Charolais	2.49±0.18	2.73±0.17	2.86±0.13
Limousin	2.23±0.14	2.45±0.13	3.06±0.13



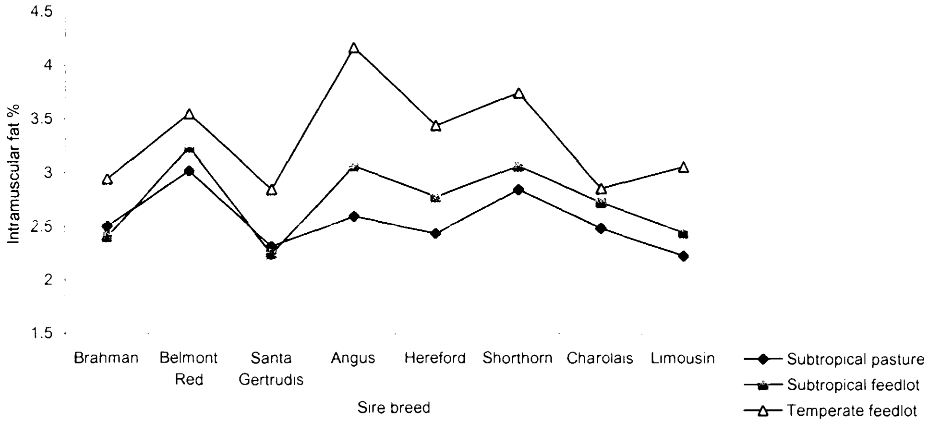
APPENDIX B. Least squares means (+se) for significant breed*finish and breed*market interactions for carcass quality traits.

CWT breed*finish	(AGE adjusted) Subtropical pasture	(P<0.0001) Subtropical feedlot	n=1473 Temperate feedlot
Brahman	204±3	252±3	245±3
Belmont Red	211±3	268±3	260±2
Santa Gertrudis	219±5	276±4	276±4
Angus	229±5	287±4	301±3
Hereford	231±5	300±4	298±4
Shorthorn	225±5	289±5	298±4
Charolais	241±4	305±4	299±3
Limousin	230±4	288±3	295±3



AGE breed*finish	(P=0.0253) Subtropical pasture	Subtropical feedlot	n=1473 Temperate feedlot
Brahman	846±6	647±6	642±5
Belmont Red	864±5	648±5	628±4
Santa Gertrudis	857±8	647±8	630±7
Angus	862±9	640±8	616±6
Hereford	845±9	635±9	614±7
Shorthorn	860±9	645±9	613±8
Charolais	832±7	622±7	611±5
Limousin	845±6	640±6	606±5

IMF breed*finish	(P=0.0412) Subtropical pasture	Subtropical feedlot	n=1188 Temperate feedlot
Brahman	2.51±0.16	2.41±0.13	2.95±0.12
Belmont Red	3.02±0.14	3.24±0.12	3.55±0.12
Santa Gertrudis	2.32±0.21	2.25±0.18	2.85±0.17
Angus	2.60±0.23	3.07±0.18	4.17±0.16
Hereford	2.44±0.22	2.78±0.19	3.44±0.18
Shorthorn	2.85±0.23	3.07±0.19	3.75±0.19
Charolais	2.49±0.18	2.73±0.17	2.86±0.13
Limousin	2.23±0.14	2.45±0.13	3.06±0.13



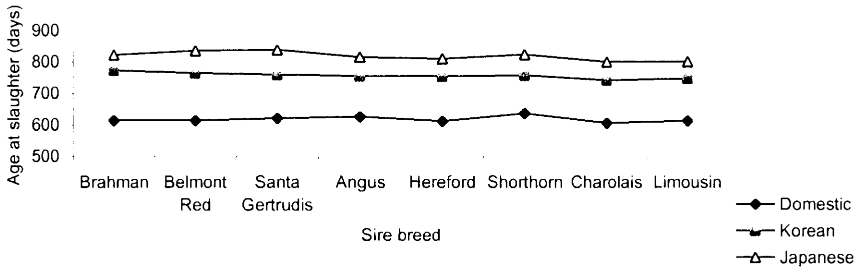
APPENDIX B. continued

CWT breed*market **(unadjusted)** **(P=0.0151)** n=1750

	Domestic	Korean	Japanese
Brahman	196±3	249±2	293±4
Belmont Red	209±2	265±2	302±3
Santa Gertrudis	222±4	283±4	325±6
Angus	235±4	303±3	352±5
Hereford	242±4	300±4	346±6
Shorthorn	230±5	304±4	343±7
Charolais	243±3	310±3	345±5
Limousin	233±3	295±3	343±4

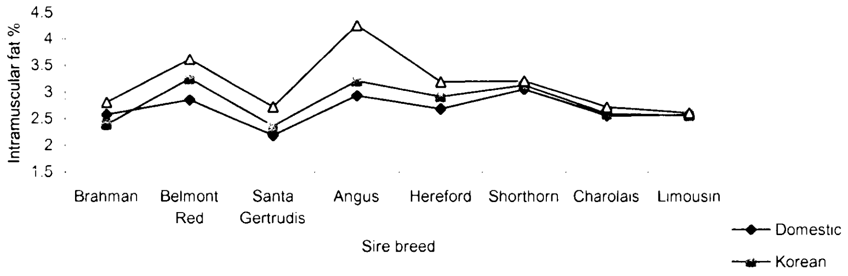
AGE breed*market **(P=0.0120)** n=1750

	Domestic	Korean	Japanese
Brahman	615±6	774±4	824±7
Belmont Red	615±5	766±4	837±6
Santa Gertrudis	623±7	761±7	840±10
Angus	628±7	757±6	817±10
Hereford	613±7	756±7	811±11
Shorthorn	638±8	759±7	825±12
Charolais	607±6	743±5	801±9
Limousin	614±5	748±5	802±8



IMF breed*market **(P=0.0009)** n=1418

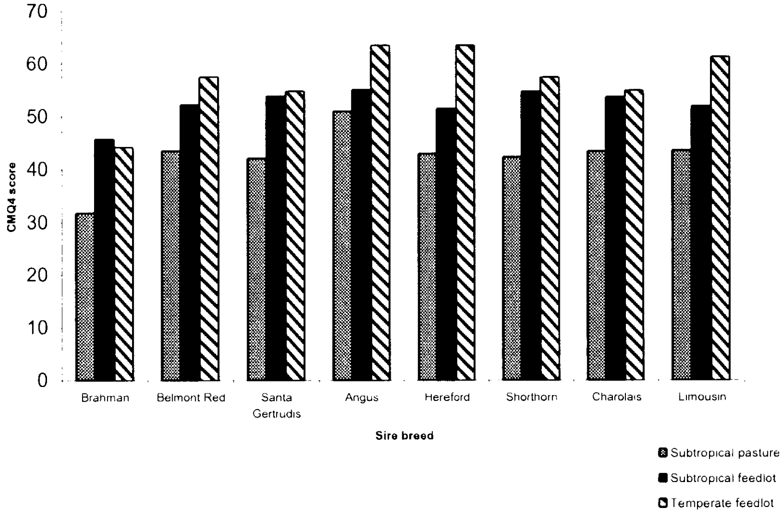
	Domestic	Korean	Japanese
Brahman	2.58±0.13	2.39±0.09	2.81±0.16
Belmont Red	2.85±0.11	3.25±0.09	3.62±0.13
Santa Gertrudis	2.18±0.16	2.36±0.13	2.72±0.23
Angus	2.93±0.15	3.21±0.13	4.26±0.20
Hereford	2.68±0.16	2.91±0.13	3.19±0.24
Shorthorn	3.05±0.18	3.13±0.14	3.21±0.25
Charolais	2.55±0.14	2.59±0.11	2.72±0.19
Limousin	2.57±0.11	2.56±0.10	2.61±0.16



APPENDIX C. Least squares means (±se) for Figure 4.1 (breed*finish interaction for CMQ4 score) and Figure 4.2 (market*finish interaction for CMQ4 score).

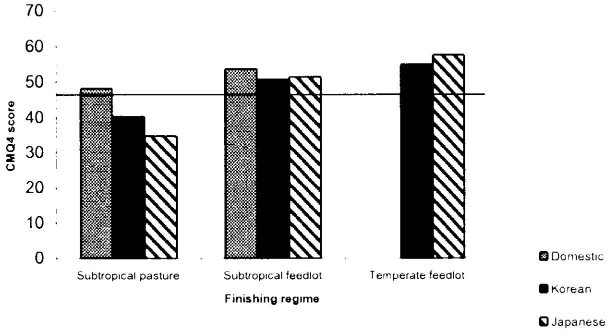
CMQ4 breed*finish (n.s.) n=460

	Subtropical pasture	Subtropical feedlot	Temperate feedlot
Brahman	31.9±2.1	45.7±2.1	44.2±2.5
Belmont Red	43.5±1.8	52.2±2.0	57.5±2.1
Santa Gertrudis	42.1±2.7	53.9±2.7	54.8±3.1
Angus	51.0±3.4	55.1±3.3	63.5±3.4
Hereford	43.0±3.0	51.5±2.9	63.5±3.7
Shorthorn	42.3±3.2	54.7±3.0	57.4±4.2
Charolais	43.4±2.8	53.7±3.1	54.9±3.7
Limousin	43.6±2.1	51.9±2.1	61.3±2.5



CMQ4 market*finish (P=0.0305) n=460

	Subtropical pasture	Subtropical feedlot	Temperate feedlot
Domestic	48.2±1.6	53.7±2.1	.
Korean	40.4±1.6	50.8±1.2	55.0±1.2
Japanese	34.8±3.2	51.4±2.8	57.6±2.4



APPENDIX D. Least squares means (+se) for significant breed*finish and breed*market interactions for meat quality traits.

ICST breed*finish **(P=0.0346)** n=1346

	Subtropical pasture	Subtropical feedlot	Temperate feedlot
Brahman	2.22±0.04	1.98±0.04	1.99±0.03
Belmont Red	2.34±0.04	1.97±0.04	2.04±0.03
Santa Gertrudis	2.22±0.06	1.85±0.05	2.04±0.05
Angus	2.41±0.06	1.95±0.05	1.99±0.04
Hereford	2.31±0.06	1.91±0.05	2.00±0.05
Shorthorn	2.28±0.06	1.96±0.06	1.98±0.05
Charolais	2.31±0.04	1.89±0.05	2.06±0.04
Limousin	2.29±0.04	1.94±0.04	1.87±0.04

ICLT breed*finish **(P=0.0295)** n=1346

	Subtropical pasture	Subtropical feedlot	Temperate feedlot
Brahman	1.99±0.03	1.72±0.03	1.85±0.03
Belmont Red	1.95±0.03	1.68±0.03	1.78±0.02
Santa Gertrudis	2.01±0.04	1.73±0.04	1.79±0.04
Angus	1.99±0.05	1.72±0.04	1.65±0.03
Hereford	1.93±0.05	1.71±0.04	1.68±0.04
Shorthorn	2.01±0.05	1.69±0.04	1.74±0.04
Charolais	1.99±0.04	1.65±0.04	1.75±0.03
Limousin	1.93±0.03	1.70±0.03	1.68±0.03

SFST breed*market **(P=0.0342)** n=1346

	Domestic	Korean	Japanese
Brahman	4.81±0.07	5.17±0.05	5.01±0.09
Belmont Red	4.74±0.07	5.00±0.05	5.09±0.08
Santa Gertrudis	4.70±0.09	5.07±0.08	5.06±0.13
Angus	4.71±0.09	5.05±0.07	5.50±0.12
Hereford	4.93±0.09	4.97±0.08	5.09±0.14
Shorthorn	4.82±0.10	5.14±0.08	5.26±0.16
Charolais	4.67±0.08	4.94±0.06	5.22±0.11
Limousin	4.47±0.07	4.72±0.06	4.90±0.10